

Changes in fine root biomass of *Picea abies* forests: predicting the potential impacts of climate change

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Abstract

Aims

The impact of global warming on belowground processes, especially on fine root production, is poorly understood in comparison with its aboveground counterpart.

Methods

Here, we compiled 227 measurements to assess the influence of temperature and precipitation on fine root biomass of Norway spruce (*Picea abies* [L.] Karst) forest ecosystems in the Eurasia boreal region.

Important Findings

We found that fine root biomass decreased significantly with latitudes. There was a biomass increase of 0.63 Mg ha⁻¹ and 0.32 Mg ha⁻¹ for fine roots <2 and <1 mm in diameter, respectively, with 1°C increase of mean annual temperature. There was an increase of 0.5 and 0.1 Mg ha⁻¹ per 100 mm year⁻¹ precipitation for the two size classes of fine roots. If the adaption of root production

can match the pace of global warming and water is not a limiting factor for plant growth, fine root biomass would be expected to increase by 40–140% in response to the predicted increase in temperature (3–10°C) over the next century. Our analyses highlighted the strongly positive influences of temperature and precipitation on belowground function, suggesting that predicted future climate change could substantially enhance belowground biomass in the boreal region where the greatest warming is anticipated. This potential increase of belowground biomass, coupled with aboveground biomass, may provide a better understanding of climate–ecosystem feedbacks.

Keywords: boreal forest, carbon, climate change, fine roots, latitudinal gradient, mean annual temperature and precipitation, Norway spruce, *Picea abies*, production and biomass

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INTRODUCTION

Over the past century, global warming, primarily driven by greenhouse gas emissions, has abnormally increased the Earth's average surface temperature by 0.85°C, and the future temperature will continue to increase 2–4°C by 2100 (IPCC 2014). The warming due to greenhouse gas enrichment is expected to be greatest at northern latitudes and high elevations, especially during the winter time (Kaufman *et al.* 2009). The boreal region in Canada, for instance, is projected to warm by 3–10°C (IPCC 2014). Boreal forests comprise 8%

of all terrestrial biomes and 22% of global forest area and contain ~60% of the global forest soil carbon (C) (470 Pg) and 25% of the forest tree C (88 Pg) (Dixon *et al.* 1994; Marty *et al.* 2015). It has been found that the role of boreal forests at high latitudes is unique in regulating the Earth's temperature by storing large quantities of C (Bartsev *et al.* 2012; Goodale *et al.* 2002). Because fine roots are an important contributor to C flow and biogeochemical cycles in terrestrial ecosystems (Jackson *et al.* 1997; Persson and Stadenberg 2009) and sensitive to global climate change (Pregitzer *et al.* 2000; Sloan *et al.* 2013; Yuan and Chen 2010), a better understanding of

temperature controls on fine root functions in boreal forest ecosystems could help us better forecast how terrestrial ecosystems may respond to future climate change.

It is labor intensive and costly to quantify fine root biomass, and the overall response of fine roots to climatic warming is still not well understood (Clark *et al.* 2001; Di Iorio *et al.* 2016; Nadelhoffer and Raich 1992; Vogt *et al.* 1996; Yuan and Chen 2010). To date, there are three approaches, each with advantages and disadvantages, for the assessment of temperature effects on fine root systems:

- 1) Controlled laboratory experiments, such as seedlings in greenhouse or garden experiments (Kandeler *et al.* 1998; Mucha *et al.* 2015; Uselman *et al.* 1999), can directly study how root systems respond to environmental changes. However, these experiments cannot duplicate conditions in natural habitats where plant adaptation takes place over a long time. Furthermore, the response of adult trees in the field does not necessarily resemble that of seedlings because of their different stages of individual tree life and stand development (Brassard *et al.* 2009).
- 2) Field manipulation appears to produce more realistic results (Leppalammi-Kujansuu *et al.* 2014; Rustad 2008; Volder *et al.* 2007; Weltzin *et al.* 2000). However, this approach often lacks sufficient site replications due to the expense, and precludes responses of long-term adaption due to relatively short durations.
- 3) Comparative studies along an environmental gradient in natural habitats may provide us valuable information about the long-term adaptive response of fine roots to increasing temperature (Jiao *et al.* 2016). Using this approach, plant adaptation to local temperature regime may be studied by selecting only mature stands, and relatively rich literature can allow for statistical analysis. This method is often used in studies of the biodiversity of many taxa including bats, fish, mammals, termites, plants and fossil foraminifera (Davies *et al.* 2010; Hawkins and Agrawal 2005; Yasuhara *et al.* 2009; Yuan *et al.* 2016), of body size in animals (Cardillo 2002), of seed size (Moles *et al.* 2007) and of plant foliar traits (Doi and Takahashi 2008; Yuan and Chen 2009a; Yuan and Chen 2009b, 2015), but this method has rarely been applied to plant root systems.

Root biomass, the balance of root production and mortality, is determined by both biotic and abiotic factors. These factors include ecosystem types, stand ages, soil characteristics and climate factors (Clark *et al.* 2001; Nadelhoffer and Raich 1992; Vogt *et al.* 1996; Yuan and Chen 2010, 2012). In particular, it has been found that fine root biomass, production and turnover were all influenced by environmental factors, e.g. climate factors, especially air temperature and precipitation (Yuan and Chen 2010). Roots have been generally hypothesized to grow faster at higher temperatures (Pregitzer *et al.* 2000). This hypothesis has received support by some laboratory studies (Uselman *et al.* 1999) and field experiments (Volder *et al.*

2007; Zeleznik *et al.* 2016); but it has been refuted in other laboratory studies (Kandeler *et al.* 1998) or field experiments (Björk *et al.* 2007; Bronson *et al.* 2008), indicating that the responses of root biomass to temperature are dependent on environmental interactions such as water and nutrient availability in soils (Brassard *et al.* 2009). In addition to biotic and abiotic factors of temperature, soil nutrient availability and acidity, water availability is also a key factor impacting fine root growth (Hertel *et al.* 2013; Leuschner *et al.* 2004; Li *et al.* 2015; Meier and Leuschner 2008). Increasing water availability is often found to enhance fine root production in diverse ecosystems, including Norway spruce forests (Majdi 2001). Furthermore, because fine root biomass varies greatly among tree species (over an order of magnitude, from 0.5 to 10 Mg ha⁻¹) (Chen *et al.* 2016; Valverde-Barrantes *et al.* 2007; Yuan and Chen 2010, 2012), previous studies on fine roots in a worldwide perspective cover multiple vegetation types (Cairns *et al.* 1997; Gill and Jackson 2000; Vogt *et al.* 1996), in which the large variation in fine root biomass among species tends to couple with the effect of climate. No study, however, has examined the geographic variations in fine root biomass for a single type of plant community along a climatic gradient at a large regional scale. By this approach, the 'noisy' factors can be removed and simple effect can be investigated with less independent variables.

Norway spruce (*Picea abies* [L.] Karst), as an essential tree species, occupies a wide range of temperature regimes, soils and other climatic variables such as precipitation throughout Europe and Asia (Tjoelker *et al.* 2007). From a view of eco-physiological point, *P. abies* is a tree species that adapts better to climate change than other native tree species (Battipaglia *et al.* 2009). The extensive geographic range of temperature regimes and broad-scale environmental heterogeneity offer an opportunity to assess the impacts of temperature on its belowground growth at a large scale. This tree species has been found to be more sensitive to greenhouse gas-induced warming, and its root production increases with increasing temperatures in warming experiments (Leppalammi-Kujansuu *et al.* 2014; Majdi and Ohrvik 2004). Climatic warming has been found to affect aboveground production and phenology such as bud burst (Bergh *et al.* 1998; Schleip *et al.* 2008). However, the progressive nitrogen limitation associated with elevated CO₂-induced warming (Finzi *et al.* 2006) could offset the increase in temperature-driven root production. Although variations in local site conditions such as the availability of soil water and nutrients strongly influence fine root growth (Waisel *et al.* 2002; Yuan and Chen 2010, 2012), climate-related gradients in fine root biomass are expected to emerge across the broader geographic range of *P. abies*.

To evaluate the influence of climate change on fine root systems in single species-dominated stands, we collected fine root biomass data of *P. abies* stands across a large temperature and precipitation gradient. The objective of our study was to determine the pattern of fine root biomass in

P. abies-dominated forest stands along the temperature and precipitation gradient throughout Europe and Asia.

MATERIALS AND METHODS

Data selection

Data on fine root biomass of stands dominated by Norway spruce (*Picea abies* [L.] Karst) were collected from publications (see supplementary material) by searching Web of Science, PubMed, JSTOR and Google Scholar. We excluded measurements that resulted from laboratory experiments, planted or fertilized systems or young stands (<50 years old) in order to avoid the potential confounding factors. A study was included if it included fine roots to at least 20 cm depth in soils (most studies went substantially deeper). According to diameter, roots were separated into two classes: very fine roots <1 mm and fine roots <2 mm in diameter. Because of the low number of studies on the root class of 1–2 mm, we did not include this size class in our analyses. The data of latitudes were taken from site descriptions in source papers. Data on mean annual temperature and precipitation were gained from the original publications. If climate data were not included in the source publications, temperature and precipitation data were gained

from the WorldClim (<http://www.worldclim.org/>) (Hijmans et al. 2005). Our data set covered most of the natural geographical distribution for Norway spruce, including 50 sources from 40 *P. abies*-dominated sites located in Europe and Asia (see supplementary material; Fig. S1), ranging from 44 to 68°N for latitude, from 0.7 to 8.4°C for mean annual temperature, and from 470 to 1700 mm for mean annual precipitation.

Data analysis

To assess the influence of latitude on fine root biomass, the mean values were used for latitudinal analysis (Middleton and McKee 2004), i.e. we averaged overall values of fine root biomass that fall within a single degree of latitude in order to remove the effects of unidentifiable factors other than climate factors. This method was more effective in meeting the assumption of normality required by regression analysis (Kirwan et al. 2009; Pitcher and Stutchbury 1998; Underwood 1997). Simple linear regression was conducted to test the impact of climate (temperature and precipitation) on fine root biomass, and multiple regression analysis was used to evaluate the collective response of fine root biomass to mean annual temperature and precipitation. The Spearman's and Kendall's correlation coefficients between fine root biomass

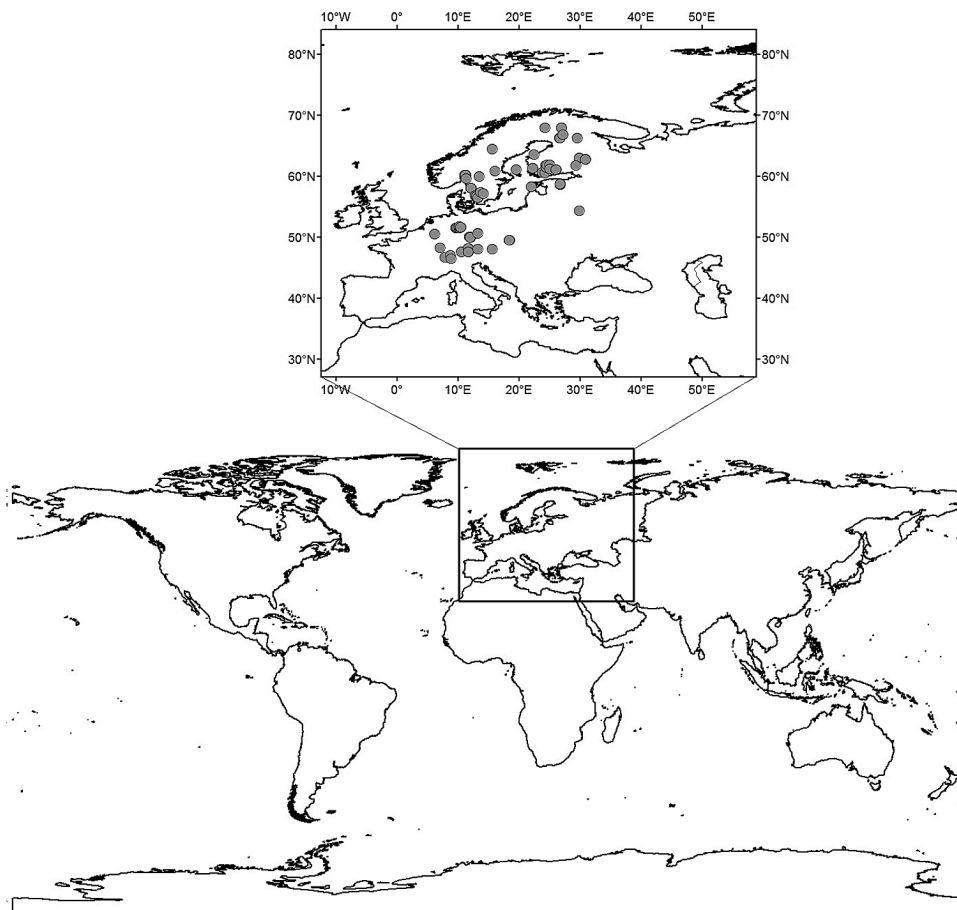


Figure 1: geographic distribution of *Picea abies*-dominated sites in boreal forests included in this study.

and climate were also calculated. All statistical analyses in our study were conducted by R version 3.3.3 statistical software (R Development Core Team 2017).

RESULTS

For fine roots <2 mm in diameter, the biomass was on average 4.6 Mg ha⁻¹ with the 90% confidence interval between 1.5 and 10.5 Mg ha⁻¹ (Fig. 2). With increasing latitude, the biomass of this size class declined significantly with the fitted linear regression explaining 82% of the variation in the biomass, and the rate of decline was 0.22 Mg ha⁻¹ per one degree of latitude (Fig. 3A). For fine roots <1 mm in diameter, the biomass was on average 2.16 Mg ha⁻¹ with the 90% confidence interval between 1.0 and 4.0 Mg ha⁻¹ (Fig. 2); it also decreased with latitude with the fitted linear regression explaining 58% of the variation in biomass, and the rate of biomass decline was 0.08 Mg ha⁻¹ per one degree of latitude along the entire geographic range (Fig. 3B).

Fine root biomass strongly increased with increasing temperature ($r^2 = 0.62$ and 0.80 for fine roots <2 and <1 mm in diameter, respectively; both $P < 0.0001$), where 1°C increase of mean annual temperature corresponded to an increase of 0.63 and 0.32 Mg ha⁻¹ of biomass for the two size classes of fine roots, respectively (Fig. 4A and B). Fine root biomass also increased significantly with increasing precipitation, with an increase of 0.5 and 0.1 Mg ha⁻¹ per 100 mm year⁻¹ precipitation for the two size classes of fine roots ($P < 0.001$ and < 0.01 , respectively) (Fig. 4C and D).

The relationships between fine root biomass and latitudes, mean annual temperature and precipitation were best described by simple linear regressions with the r^2 values

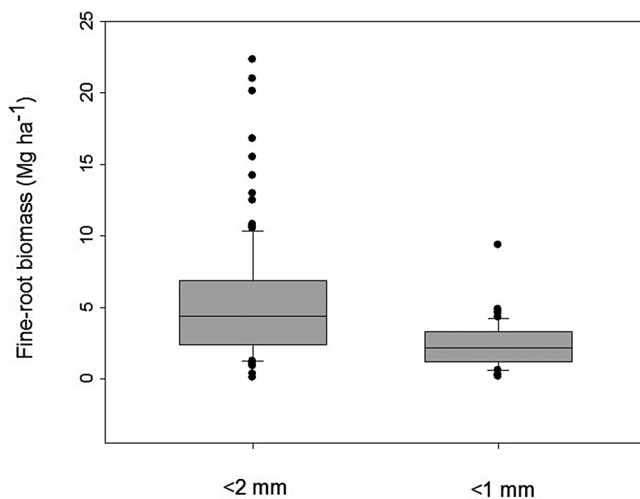


Figure 2: box plot of the fine root biomass. The plots summarize the distribution of samples for each group, indicating interquartile ranges (gray-shaded area), medians (horizontal line in the box), 25th and 75th percentiles (lower and upper box margins), 10th and 90th percentiles (lower and upper error bars) and observations outside the 10th percentiles.

varying from 0.566 to 0.820 (Table 1). The no-parametric analyses by using Spearman and Kendall correlations revealed that fine root biomass of Norway spruce was closely correlated to latitude, temperature and precipitation (Table 2). The biomass of fine roots <2 and <1 mm in diameter were both negatively correlated to latitude and positively correlated to mean annual temperature and precipitation.

Climate variables of temperature and precipitation were found to collectively explain 82% and 92% of the biomass variations of fine roots <2 and <1 mm in diameter, respectively (Table 3). The influences of mean annual temperature and mean annual precipitation were additive since their interactions were not significant.

DISCUSSION

In our analysis, we found a significant decrease in fine root biomass of *P. abies*-dominated forest stands along a latitudinal gradient. Linear regression explained 83% and 58% of variability in biomass of <2 and <1 mm fine roots, respectively, revealing a strong latitudinal trend of fine root biomass in *P. abies*-dominated ecosystems. The significant effects of both

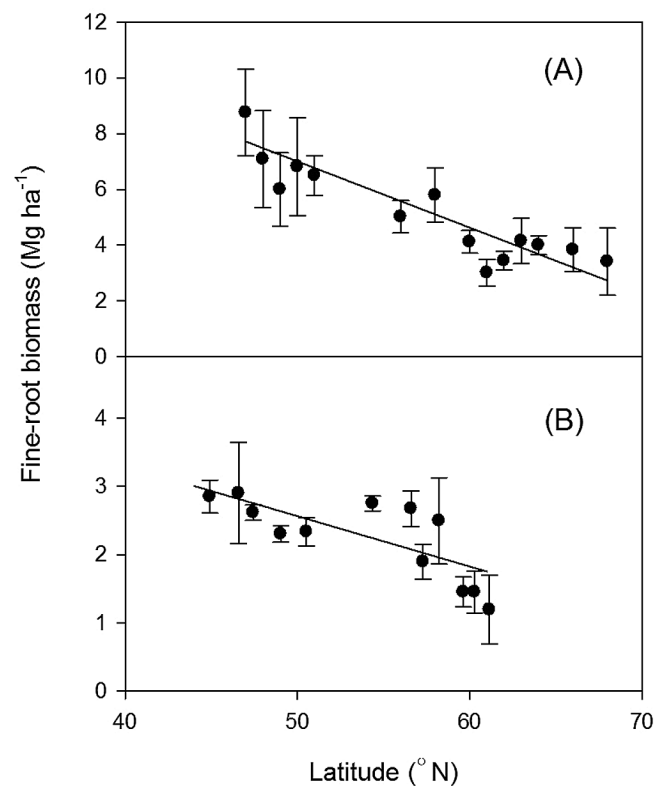


Figure 3: fine root biomass (mean \pm 1 SE) of *Picea abies*-dominated sites in boreal forests in relation to latitude: (A) fine roots <2 mm and (B) fine roots <1 mm in diameter. The relationships between fine root biomass and latitude are best described by linear regressions (for fine roots <2 mm in diameter: $y = -0.217x + 17.566$, $r^2 = 0.82$; for fine roots <1 mm in diameter: $y = -0.078x + 6.430$, $r^2 = 0.58$; $P < 0.001$ for both regressions).

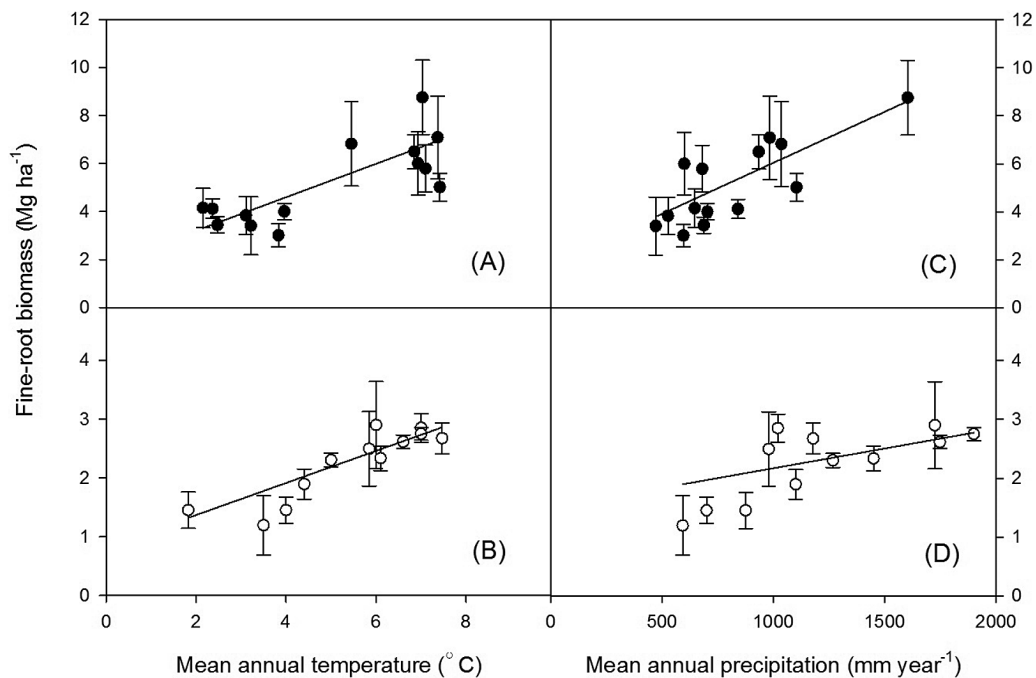


Figure 4: fine root biomass (mean \pm SE) of *Picea abies*-dominated sites in boreal forests: (A) fine roots <2 mm (filled circles) in relation to mean annual temperature ($y = 0.633x + 1.976$, $r^2 = 0.62$, $P < 0.001$), (B) fine roots <1 mm (open circles) in relation to mean annual temperature ($y = 0.317x + 0.535$, $r^2 = 0.80$, $P < 0.001$), (C) fine roots <2 mm (filled circles) in relation to mean annual precipitation ($y = 0.005x + 1.415$, $r^2 = 0.48$, $P < 0.001$) and (D) fine roots <1 mm (open circles) in relation to mean annual precipitation ($y = 0.001x + 0.949$, $r^2 = 0.52$, $P < 0.001$).

temperature and precipitation on fine root biomass indicate that the changing temperature and precipitation are likely the major mechanisms responsible for the latitudinal changes in fine root biomass. Therefore, our results provide an insight into the potential effects of predicted climate changes on root growth of *P. abies*-dominated ecosystems.

In this study, we selected only stands dominated by one single species, and thus the changes in fine root biomass of *P. abies* across the latitudinal gradient did not include large variations caused by different species as reported in previous studies (Caldwell et al. 1996; Sullivan et al. 2007). Roots grow slowly when the soil is cold but they grow fast when the soil is warmed to some optimal temperature (Pregitzer et al. 2000). The close relationships between fine root biomass and latitudes and mean annual temperature (Figs. 3 and 4) support the hypothesis that temperature is an important driver to regulate fine root growth of *P. abies* in the northern climate.

We also found that fine root biomass was positively correlated to mean annual precipitation (Fig. 4). Experimental drought strongly reduces root growth rates of *P. abies* (Peskova et al. 2015; Pregitzer et al. 2000), whereas experimental water addition increases root biomass of *Leymus chinensis* (Huang et al. 2009) and those of *P. abies* (Majdi and Andersson 2005). In our analysis, temperature positively changed with precipitation ($r^2 = 0.32$, $P < 0.001$, $n = 227$), suggesting that the positive influence of precipitation on the growth of fine roots is coupled with that of temperature, but their influences appear to be additive in the natural habits of *P. abies* because the

interaction effect of temperature and precipitation was not statistically significant on fine root biomass (Table 3). The strong responses of fine root biomass to both temperature and precipitation (Fig. 4; Table 1) imply that the fine root growth of this species is driven by climatic variables of temperature and precipitation. The observed patterns of fine root biomass associated with temperature and precipitation may reflect the positive effect of rising soil temperature on nutrient availability in boreal forests due to the fact that nutrient mineralization is often closely correlated to the metabolic activity of soil microbes that are driven by temperature (Bonan and van Cleve 1992; Pregitzer and King 2005). Previous studies have found that an increase in soil nutrient availability can also lead to an increase in fine root growth in northern sites where N availability is limited (Huang et al. 2008; Nadelhoffer 2000; Yuan et al. 2006).

In our analyses, fine root biomass of *P. abies* was positively correlated to both climate variables, especially to mean annual temperature (Table 1; Fig. 4), likely reflecting the occurrence of low N mineralization in *P. abies* ecosystems in cold environments (Bonan and van Cleve 1992; Pregitzer and King 2005). Previous studies indicate that water limitations control the southern forests and temperature limitations control the northern forests (Brooks et al. 1998; Hogg 1994). Based on our analyses, the fine root growth for *P. abies* is very likely limited more by temperature than by water availability in much of its natural habitats. Changes in temperature could interact with changes in other important

Table 1: equations and R^2 values that describe the explanatory power of each model for the biomass of fine roots in relation to latitude (Lat, °N), mean annual temperature (MAT, °C) and precipitation (MAP, mm year⁻¹)

Model	Lat		MAT		MAP	
	Equation	r^2	Equation	r^2	Equation	r^2
<2 mm						
Linear	$y = -0.217x + 17.566$	0.820***	$y = 0.633x + 1.976$	0.619**	$y = 0.005x + 1.415$	0.637**
Logarithmic	$y = -12.322\ln x + 54.943$	0.835***	$y = 2.765\ln x + 0.958$	0.582**	$y = 4.406\ln x - 21.762$	0.616**
Inverse	$y = 692.566/x - 7.119$	0.847***	$y = -10.337/x + 7.671$	0.506**	$y = -3074.6/x + 9.316$	0.558**
Quadratic	$y = 0.009x^2 - 1.28x + 47.438$	0.862***	$y = 0.044x^2 + 0.195x + 2.875$	0.623**	$y = -1.55 \times 10^{-7}x^2 + 0.005x + 1.278$	0.637**
Cubic	$y = 0 \times x^3 + 0.009x^2 - 1.28x + 47$	0.862***	$y = -0.21x^3 + 2.99x^2 - 12.52x + 19$	0.768**	$y = 8 \times 10^{-10}x^3 - 3 \times 10^{-6}x^2 + 0.01x + 0.6$	0.637*
Compound	$y = 51.863 \times 0.960^x$	0.816***	$y = 2.632 \times 1.132^x$	0.653***	$y = 2.496 \times 1.001^x$	0.571**
Power	$y = 61229x^{-2.335}$	0.826***	$y = 2.168x^{0.538}$	0.605**	$y = 0.034x^{0.747}$	0.579**
S-curve	$y = e^{-0.728 + 130.779/x}$	0.832***	$y = e^{-1.993 + 2.075/x}$	0.519**	$y = e^{2.374 - 579.73/x}$	0.546**
Growth	$y = e^{3.949 - 0.041x}$	0.816***	$y = e^{0.968 + 0.124x}$	0.653***	$y = e^{0.915 + 0.001x}$	0.571**
Exponential	$y = 51.863 \times e^{-0.041x}$	0.816***	$y = 2.632e^{0.124x}$	0.653***	$y = 2.496e^{0.001x}$	0.571**
<1 mm						
Linear	$y = -0.078x + 6.430$	0.577**	$y = 0.317x + 0.534$	0.802***	$y = 0.001x + 0.949$	0.566**
Logarithmic	$y = -4.045\ln x + 18.344$	0.559**	$y = 1.255\ln x + 0.204$	0.71**	$y = 1.317\ln x - 7.031$	0.644**
Inverse	$y = 208.897/x - 1.680$	0.541**	$y = -3.828/x + 3.067$	0.543**	$y = -1401.1/x + 3.548$	0.688**
Quadratic	$y = -0.009x^2 + 0.914x - 19.66$	0.695**	$y = 0.016x^2 + 0.162x + 0.859$	0.808**	$y = -1.28 \times 10^{-6}x^2 + 0.004x - 0.884$	0.681**
Cubic	$y = -0.0001x^3 + 0.009x^2 - 4.17$	0.709**	$y = -0.05x^3 + 0.68x^2 - 2.62x + 4.24$	0.925***	$y = 2 \times 10^{-9}x^3 - 8 \times 10^{-6}x^2 + 0.01x - 3.3$	0.702**
Compound	$y = 17.81 \times 0.962^x$	0.565**	$y = 0.913 \times 1.173^x$	0.783***	$y = 1.112 \times 1.001^x$	0.573*
Power	$y = 7046x^{-2.033}$	0.544**	$y = 0.77x^{0.634}$	0.699**	$y = 0.017x^{0.684}$	0.670**
S-curve	$y = e^{-0.728 + 130.779/x}$	0.832***	$y = e^{-1.993 + 2.075/x}$	0.519**	$y = e^{2.374 - 579.73/x}$	0.546**
Growth	$y = e^{3.949 - 0.041x}$	0.816***	$y = e^{0.968 + 0.124x}$	0.653***	$y = e^{0.915 + 0.001x}$	0.571**
Exponential	$y = 51.863e^{-0.041x}$	0.816***	$y = 2.632e^{0.124x}$	0.653***	$y = 2.496e^{0.001x}$	0.571**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 2: the relationships between fine root biomass (<2 and <1 mm in diameter, respectively) and latitude (Lat, °N), mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm year⁻¹) in *Picea abies*-dominated stands

Source	Lat	MAT	MAP
<2 mm			
Pearson	-0.906**	0.787**	0.798**
Kendall	-0.736**	0.341	0.560**
Spearman	-0.877**	0.640*	0.732**
<1 mm			
Pearson	-0.759**	0.895**	0.752**
Kendall	-0.657**	0.708**	0.565*
Spearman	-0.809**	0.846**	0.690*

Values are Pearson's r , Kendall's Tau and Spearman's Rho , respectively. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

resources, thus influencing root growth. For example, the availability of both soil water and nutrients often covary with changing temperature. Higher temperatures generally lead to enhanced N mineralization, particularly at high latitudes where ecosystems are limited by low temperature (Pregitzer

Table 3: effects of mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm year⁻¹) on biomass of fine roots (<2 and <1 mm in diameter, respectively) in *Picea abies*-dominated stands

Source	r^2	MS	F	P
<2 mm				
	0.814			
MAT		23.646	33.250	0.0002***
MAP		7.154	10.059	0.0099**
MAT × MAP		0.275	0.389	0.5479 NS
<1 mm				
	0.914			
MAT		3.149	74.398	0.00003***
MAP		0.231	5.441	0.0479*
MAT × MAP		0.210	4.964	0.0565 NS

The F ratios and their significance are shown for each of the dependent variables. Values in bold indicate significant effects ($P < 0.05$). NS, not significant; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

et al. 2000). The positive relationship between fine root biomass and temperature for *P. abies* in our analyses, therefore, likely reflects the low temperature-induced covarying eco-physiological changes.

Our results differed from those of [Vogt *et al.* \(1996\)](#) who did not find an effect of temperature, but did find a weak effect of precipitation on root biomass in evergreen boreal forests. There were a number of reasons for this discrepancy: (i) we had larger sample size (227 versus 25); (ii) we focused on one species-dominated stands, whereas [Vogt *et al.* \(1996\)](#) had included various vegetation types which typically varied in fine root biomass and therefore resulted in a larger error for testing the effect of temperature; (iii) to minimize data heterogeneity, our data set only considered fine roots <2 and <1 mm in diameter, whereas [Vogt *et al.* \(1996\)](#) included large roots with 2–5 mm in diameter; (iv) we selected only studies that sampled roots in at least the uppermost 20 cm soils because fine root biomass was greatest at the surface, with more 85% of total fine root biomass distributed in the top 20 cm soil ([Persson *et al.* 1995](#)). By contrast, [Vogt *et al.* \(1996\)](#) did not differentiate soil layers; and (v) our data set included only mature stands with >50-year-old *P. abies*, whereas the data set of [Vogt *et al.* \(1996\)](#) selected stands of all ages including very young stands of 1-year old. Previous studies found that fine root biomass increased rapidly in young stands, and it peaked in ~50-year-old stands in boreal forests, and then gradually leveled off ([Børja *et al.* 2008](#); [Claus and George 2005](#); [Leuschner and Hertel 2003](#); [Makkonen and Helmisaari 2001](#)). Our data also showed that fine root biomass of *P. abies* was highest in 60-year-old stands for <1 mm fine roots and in 55-year-old stands for <2 mm fine roots (data not shown). The discrepancy suggested the importance of removing ‘noisy’ variables when investigating the true response of fine roots to climate change in a real world.

Our results revealed that fine root growth was sensitive to climatic variations. Based on the differences between slopes, however, the biomass of <2 mm fine roots seemed to respond more sensitively to temperature/precipitation than <1 mm very fine roots ([Fig. 4](#)). Because root biomass is the integration balance of root production and mortality ([Yuan and Chen 2013](#)), we could not conclude which ecological process, either root production or mortality, was more important in controlling their final balance, i.e. root biomass. Although the underlying mechanisms existing between the two diameter classes remained unclear, our analyses could not exclude that fine roots <1 mm in diameter might represent the most sensitive root parts to climate change. If this is true, fine roots with larger diameter might be speculated to play a bigger role in the function of root growth than death in response to environmental changes.

The latitudinal gradient that we observed may provide a basis for predicting the response of fine root biomass of *P. abies* ecosystems to climate change. Assuming the adaption of root biomass can match the pace of global warming, our results indicate that the predicted temperature increase of 2–4°C in boreal forests over the next century ([IPCC 2014](#)) may result in an increase by 1.9–6.3 and 1.0–3.2 Mg ha⁻¹ for <2 and <1 mm fine roots, respectively ([Fig. 4](#)). Such increases represent approximately a 37–122% and 44–148% increase for

the two size classes of fine roots, respectively. These patterns suggested that both temperature and precipitation exerted positive influences on fine root biomass, although we did not know how they affected the processes of fine root production or mortality.

In summary, our results show a large-scale pattern in fine root biomass of *P. abies* across a latitudinal gradient. This large-scale pattern indicates that both temperature and precipitation are important environmental variables that affect fine root biomass and that climatic warming will lead to increasing fine root biomass, possibly by enhancing root production more than mortality in *P. abies* forest ecosystems, providing that water is limiting. Since fine root production could account for up to 75% of the total net primary production ([Nadelhoffer and Raich 1992](#)) and root turnover contributes to long-term storage of C in soils ([Maeght *et al.* 2015](#); [Wang *et al.* 2014](#)), our analyses suggest that the potential increase of fine root biomass, which is often positively correlated to fine root production, in the northern forest region associated with climate warming may provide improved quantitative predictions regarding the roles of fine roots in terrestrial ecosystem and root-climate feedback under future climate regimes.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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