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## EDITED BY

Daniela Yaffar,  
University of Hamburg, Germany

## REVIEWED BY

Lilli Zeh,  
Technical University Dresden, Germany  
Monique Weemstra,  
Florida International University, United States

## \*CORRESPONDENCE

Avni Malhotra  
✉ avni.malhotra@geo.uzh.ch

RECEIVED 20 February 2023

ACCEPTED 03 April 2023

PUBLISHED 05 May 2023

## CITATION

Bucher M, Ofiti NOE and Malhotra A (2023)  
Plant functional types and microtopography  
mediate climate change responses of fine  
roots in forested boreal peatlands.  
*Front. For. Glob. Change* 6:1170252.  
doi: 10.3389/ffgc.2023.1170252

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# Plant functional types and microtopography mediate climate change responses of fine roots in forested boreal peatlands

Melina Bucher, Nicholas O. E. Ofiti and Avni Malhotra\*

Department of Geography, University of Zurich, Zurich, Switzerland

Peatlands store one-third of the world's soil carbon, and their climate change response is a key unknown in the global carbon cycle-climate change feedback. In particular, peatland fine root responses to varied environmental changes are poorly constrained. Here, we synthesized fine root responses to warming and water level drawdown by performing a meta-analysis of existing data from boreal forested peatlands. We found seven studies and evaluated root responses from 65 observations. Overall, both warming (from 0 to 9.0°C) and water level drawdown (from 4.0 to 62.5 cm) increased fine root growth by over an order of magnitude, with plant functional type (PFT; graminoid, shrub, and tree) better predicting fine root biomass than treatment magnitude. We observed stronger responses for trees (+374.5% for warming and +868.6% for water level drawdown) than for shrubs (+44.0% for warming and +11.5% for water level drawdown) and graminoids (+59.5% for warming and -59.8% for water level drawdown). Among PFTs, tree fine roots increased significantly and non-linearly with increasing warming treatment, while graminoid fine roots responded significantly to lowering water level, decreasing 1.7% for every 1 cm decrease in water level. Fine roots in hollows, especially of shrubs, increased more strongly than those in hummocks, suggesting a possible flattening of peatland topography with sustained hollow growth from extended warming. Our synthesis highlights the important role of PFT's in modulating fine root responses and the need for additional belowground data from these carbon-rich and globally relevant peatland soils. The altered fine root growth documented here, implies possible shifts in plant nutrient and water uptake as well as root inputs to soil carbon stocks, which in turn could strongly moderate and shape boreal peatland responses to future climate change.

## KEYWORDS

fine root, peatland, boreal, warming, water level drawdown, plant functional type (PFT), microtopography

## 1. Introduction

Peatlands cover only about 3% of the earth's land surface but store up to one-third of global terrestrial soil carbon (C) in deep peat deposits (Gorham, 1991; Bridgman et al., 2006; Yu et al., 2010). But these ecosystems are facing increasing temperatures that are likely to exceed 5°C by the end of the century (Soong et al., 2020). Warming and associated soil

drying could destabilize the large C pools, formed by the net C uptake over thousands of years, leading to an accelerated emission of greenhouse gases into the atmosphere (Gruber et al., 2004; IPCC, 2007; Limpens et al., 2008; Munir et al., 2014). Besides accelerated C loss, rising temperatures are expected to alter plant growth and functioning with implications on the C storage (Buttler et al., 2015; Zhong et al., 2020). Specifically, warming and associated hydrological changes may alter plant dynamics such as fine root production, which in turn can further influence ecosystem functions such as nutrient and water uptake, ecosystem respiration, and ultimately, soil C storage (Wan et al., 2004; Iversen et al., 2008, 2012; Jackson et al., 2017). Furthermore, fine roots are an important component of peatland carbon cycling, contributing between 25 and 75% of the annual net primary production (reviewed in Iversen et al., 2018) and providing C for peat formation (Laiho et al., 2003). Thus, changes in fine root growth could influence plant resource acquisition and primary productivity, which could influence the amount and quality of soil organic matter entering the soil (Laiho et al., 2003; Iversen et al., 2018). Fine root growth could further influence the decomposition of this soil organic matter if root exudation and rhizosphere priming also change (Jackson et al., 2017). To be able to understand these ecosystem functional responses, we first need to understand how environmental change influences fine root growth. However, mechanisms behind belowground plant responses to climate-driven changes are poorly understood in peatlands and thus, not well accounted for in our future estimates of peatland C balance.

Climate-driven changes are predominant environmental stress factors expected to affect belowground plant growth in northern peatlands (Murphy et al., 2009b; Iversen et al., 2018; Malhotra et al., 2020). Notably, key factors associated with climate change in peatlands, such as soil warming and associated lower water tables can alter belowground root production directly or indirectly through altered nutrient mineralization, water availability, and plant carbon fixation and allocation (Weltzin et al., 2003; Buttler et al., 2015; Hartmann et al., 2020; Zhong et al., 2020). However, the effect of warming on belowground root production is not consistent across plant functional types (PFTs) or microtopographical features. This is because as peatlands become warmer and drier, the relative abundance and productivity of dominant PFTs and belowground plant productivity and properties can change depending on PFTs sensitivity to environmental stressors (Weltzin et al., 2000; Camill, 2011; Lohila et al., 2011; Malhotra et al., 2020). For example, fine root biomass production can increase in warmer and drier peatlands (Bhuiyan et al., 2017; Malhotra et al., 2020; Iversen et al., 2022), but primarily for PFTs that are well-adapted to dry conditions, such as woody shrubs or trees (Munir et al., 2014). Due to these PFT differences in belowground responses, warmer and drier conditions are predicted to increase peatland shrubification i.e., a shift from a *Sphagnum*-dominated toward a woody shrub and tree dominated system (Weltzin et al., 2000; Camill, 2011; Lohila et al., 2011; McPartland et al., 2019; Malhotra et al., 2020). Shrub, graminoid and tree fine root response may also vary because the PFTs have different resource acquisition strategies given that they fall on the opposite ends of the “root economic spectrum” (RES; Bergmann et al., 2020). Thinly rooted shrubs and graminoids, with high specific root length (SRL), based on the RES, are expected to increase their resource acquisition by

increasing fine root investment since roots are not as “costly” (“do-it-yourself approach”; Bergmann et al., 2020). On the other hand, thicker and lower SRL roots of trees, where investment to roots is costly, are expected to increase resource acquisition by increasing investment into mycorrhizal partners (“outsourcing approach”; Bergmann et al., 2020). Besides PFTs, microtopographical features in peatlands (such as hummocks and hollows) provide a moisture gradient to which plants respond differentially (Murphy et al., 2009b; Malhotra et al., 2016). Given that different species have different optimal growth conditions across microtopographical features (Bubier et al., 2006), changes in moisture conditions at these features will result in variable responses (Malhotra et al., 2020). For example, a lowering of the water table may make hummocks too dry for some PFTs such as graminoids but may make hollow moisture conditions optimal for shrub growth (Bubier et al., 2006). Other trajectories of root response to warming and drying are also possible, for example, a lower allocation to fine roots if nutrients are abundant and water is not limiting, for example, in a high precipitation site, or in a hollow relative to a hummock (Hartmann et al., 2020; Zhong et al., 2020). A synthetic quantification of fine-root responses to temperature and water table changes change is therefore necessary.

We focus here on boreal forested peatlands because boreal forests comprise one-third of the forested areas globally and carbon-rich peatland soils underlay 24% of the global boreal forests (Wieder and Vitt, 2006). Our knowledge of fine root dynamics in boreal peatlands has primarily been based on data from relative aboveground growth rates, sequential soil coring, root colonization of in-growth cores, or minirhizotrons (Reader and Stewart, 1972; Backeus, 1990; Laiho and Finér, 1996; Weltzin et al., 2000; Bond-Lamberty et al., 2004; Sullivan and Welker, 2005; Wieder, 2006; Murphy et al., 2009a; Murphy and Moore, 2010; Munir et al., 2014; D’Imperio et al., 2018; Iversen et al., 2018; Malhotra et al., 2020). However, fine-root responses to warming and drying, and interactions with PFTs or microtopography have not been synthesized across boreal peatland studies. Thus, our aims were to (1) quantify the observed range of fine root biomass responses to warming and water level drawdown in different peatland PFTs and micro topographic features and (2) evaluate the drivers of these fine-root changes. We conducted a meta-analysis of existing peer-reviewed literature on how fine root biomass responds to warming and water level drawdown in boreal peatlands (seven studies). We hypothesized that fine root biomass will increase linearly with both warming and water level drawdown due to a deeper aerobic layer as well as increased nutrient availability under warmer and drier conditions (Murphy et al., 2009a; Munir et al., 2017; Iversen et al., 2018, 2022). We also expected major peatland PFTs (trees, ericaceous shrubs, and graminoids) to vary in their fine-root responses. Under warmer and drier conditions, primarily driven by moisture limitation since nutrients are expected to increase with warming (Iversen et al., 2022), tree roots would increase their water acquisition by increasing “outsourcing” to mycorrhizal fungal partners (Defrenne et al., 2021), while thinly-rooted shrubs and graminoids would take a “do-it-yourself” approach instead by increasing production of new fine roots for foraging (Bergmann et al., 2020). Thus, we expected stronger fine root biomass responses in shrubs and graminoids than in trees to both warming and drying. Graminoid species are particularly sensitive to changes in moisture availability and thus should have the highest responses to

water level drawdown (Bubier et al., 2006; Malhotra et al., 2016). We also expected microtopographical features to vary in their fine root response to warming and water level drawdown wherein fine root biomass would decrease through exacerbated moisture limitation in hummocks; but fine root biomass would increase in hollows where moisture conditions would become suitable for new PFTs such as shrubs. Lastly, non-linear responses of roots may be possible due to limiting moisture or nutrients in very high warming or water table treatments. For example, while some warming may stimulate growth, resulting in increased root growth, very high warming may push the system into a moisture limitation such that the plant may no longer be able to perform basic physiological functions, thus leading to decreased root growth.

## 2. Materials and methods

### 2.1. Data compilation

For the meta-analysis, we searched peer-reviewed publications using Google Scholar, Web of Science, Scopus, Northern Research Station, and swisscovery with the keywords “roots” or “root biomass” and “peatland” or “wetland” or “bog” or “mire” or “fen” or “histosol” and “boreal” with the additional specification “warming,” “elevated temperature,” “water level drawdown,” “drainage,” or “lower water table” to narrow down the search. The search was conducted in January 2022 and included all articles published from January 1996 until December 2021. The following conditions had to be met for the study to be included:

- (1) The study reported fine root biomass (< 2 mm or as reported by the study) responses to climate change factors in a boreal peatland.
- (2) Studies had to have examined at least one of the two climate change factors, namely, warming and water level drawdown (WLD).
- (3) Studies had to quantitatively provide data on the magnitude of warming or WLD to compare data points.
- (4) Only *in situ* studies were considered. However, one exception was the Ge et al. (2012) study that sampled *in situ* but then moved their samples to controlled environmental chambers.

In total, we found seven peer-reviewed papers (Supplementary Table 1). From these studies, we collected data on the experimental site, treatment magnitude, experimental duration, experimental method, plant functional type (PFT) examined, topography, soil depth to which roots were analyzed, and the difference in fine root biomass between the control and treatment groups. In addition, we considered different treatments within a study (i.e., different sites, treatment magnitudes, etc.) as different observations. As a result, this current study consists of 65 data points including, 35 observations from warming experiments and 30 from water level drawdown experiments.

If the difference between treatments in fine root biomass was not explicitly stated, it was acquired from the graphs using the trial version of Digitizelt version 2.5 (Bormann, 2015). Therefore, these data points are subject to a small, systematic error. When a treatment lasted for several years but only values for the individual

years were provided, the result for the entire treatment period was calculated as the mean of all individual values. Missing data on climatic conditions of the study sites were complemented based on information from other studies conducted on the same study site [for Malhotra et al. (2020) from Sebestyen et al. (2020) and for Laiho and Finér (1996) from Murphy et al. (2009a)]. Topography (hummock or hollow) could not be determined conclusively for all data points. Data points were aggregated into three plant functional types: graminoid, shrub, and tree using categorizations based on species names provided in the papers. However, seven data points from Laiho and Finér (1996) were not categorizable as combined data for shrub and tree (apart from pine) fine root biomass combined was reported. Therefore, a fourth group called “shrub + tree” was used for these data points.

### 2.2. Data analyses

The difference in fine root biomass between the control and treatment groups was evaluated using the following equation. To better display the values, the results were converted from decimals to percentages by multiplying by 100.

$$\text{Difference to control (\%)} = \frac{\text{Treatment fine root biomass} - \text{Control fine root biomass}}{\text{Control fine root biomass}} \times 100$$

The dataset was then analyzed and visualized primarily using JMP version 15.2 (SAS Institute Inc, 2014). Due to non-normality of data, analyses were run on log transformed differences to controls rather than on untransformed values. First, to determine whether trends are linear or non-linear, either a simple linear model ( $y = a \cdot x + b$ ) or a simple quadratic model ( $y = a \cdot x^2 + b \cdot x + c$ ) with the method of least squares was

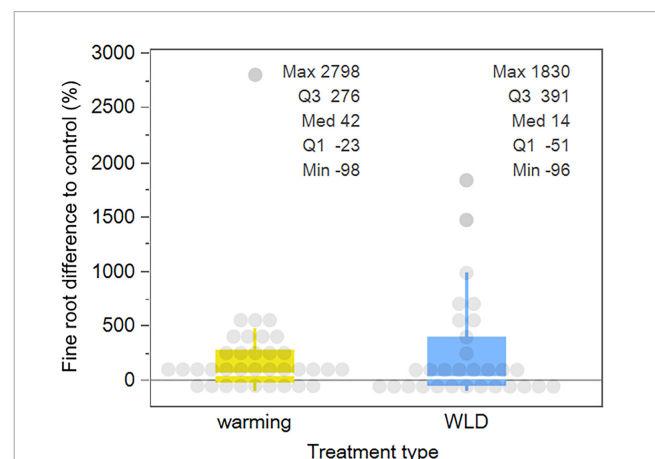
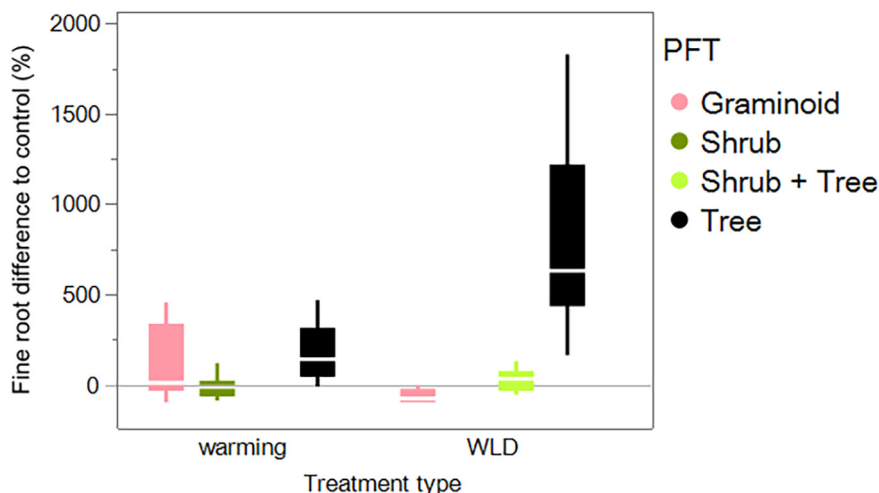


FIGURE 1

Distributions of fine root responses to warming and water level drawdown (WLD) across the synthesized seven studies. Box plots and reported values indicate minimum, maximum, and median values along with first and third quartiles (all units are % difference of treatment to control). Raw data points are also shown in gray. Positive values indicate that treatment fine root biomass increased while negative values indicate that fine root biomass decreased relative to control.



**FIGURE 2** Overview of fine root biomass responses among plant functional types from seven studies. Data points on warming include 21 on graminoids, eight on shrubs, and eight on trees, with a mean of 377.3, 50.3, and 400.0% and a standard deviation of 499.2, 81.6, and 148.4%, respectively. Data points on water level drawdown (WLD) include 12 on graminoids, two on shrub, seven on “shrub + tree”, and nine on trees, with a mean of -59.8, 11.5, 38.6, and 868.6% and a standard deviation of 35.6, 22.0, 47.0, and 436.5%, respectively. Warming treatments range from 0.8 to 9.0°C, while WLD treatments range from 4.0 to 62.5 cm (Supplementary Table 2). For aesthetic reasons, the range of the y-axis has been adjusted so that one outlier is not visible (warming, graminoid: 3950.0%). In the warming treatment, there are no significant differences between the PFTs. In the WLD treatment, there are significant differences among PFTs [Based on an ANOVA where  $F_{(3,26)} = 22.6, p < 0.0001$ ]. Furthermore, a Tukey’s HSD test suggests that each of the PFTs in WLD treatment are significantly different from each other.

used to visualize and qualitatively analyze potential trends in the data. Once establishing linearity or making necessary data transformations to linearity, mixed-effects models were used to evaluate predictors of warming or water table responses. Random effects included data source (seven studies) while fixed effects were magnitude of treatment, duration of treatment, PFT, topography, soil depth to which roots were analyzed, MAT, MAP, Latitude, and Longitude. Interactions among PFT, topography and treatment were also checked but were not significant. Models were checked for variance inflation factors (VIFs) and any predictor with  $VIF > 2$  was removed from the model.

### 3. Results

#### 3.1. Highly variable fine root responses to warming and water level drawdown

The synthesized studies encompassed applied warming ranging from 0 to 9.0°C and water level drawdown ranging from a lowering of 4.0 to 62.5 cm. Fine root biomass responses to warming and water level drawdown were highly variable across the synthesized studies (Figure 1), and across plant functional types (Figure 2). Responses to warming and water level drawdown were highest for trees ranging from 105.5 to 708.5% with a median of 374.5% and from 165.5 to 1830.5% with a median of 782.5%, respectively (Figure 2). Shrub fine root biomass also increased for warming and water level drawdown, ranging from -76.5 to 244.5%, with a median of 44.0%, and from -3.0 to 26.0%, with a median of 11.5%, respectively (Figure 2). Graminoid fine root biomass increased for warming, with a median of 60.5% (range: -34.5 to 3950.0%), but decreased for water level drawdown, with a median of -77.8%

**TABLE 1** Best-fit multiple linear regression model of fine root response to warming.

Term	Estimate	Std. error	t ratio	Prob. >  t
Intercept	0.95	1.07	0.88	0.3828
Magnitude warming	-0.10	0.07	-1.25	0.2217
Topography (hollow)	0.74	0.19	3.81	0.0008
PFT (graminoid)	-0.17	0.29	-0.59	0.5590
PFT (shrub)	-0.68	0.30	-2.28	0.0317
Treatment duration (years)	-0.01	0.35	-0.02	0.9812

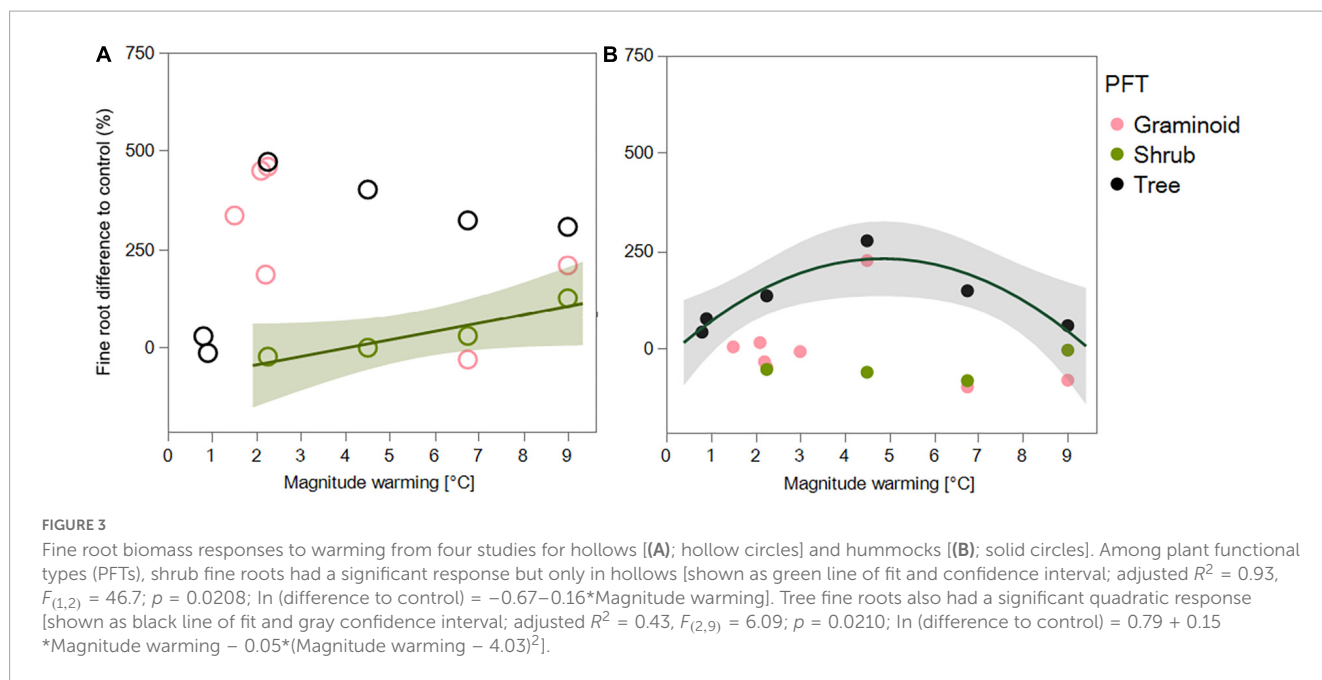
Adjusted  $R^2 = 0.40, F_{(5,24)} = 4.99, p = 0.0028$ . Study source and soil depth were removed from the model as they were non-significant and increased the variance inflation factor. Note that the analysis and thus slope values are on log transformed data.

(range: -96.0 to 1.5%). Non-assignable data points reported in the category “shrub + tree” increased with water level drawdown, with a median of 37.5% and ranging from -47.0 to 127.0%, (Figure 2). In the next two sections, we discuss the best predictors of these fine root responses to warming and water level drawdown.

#### 3.2. Plant type and topography drive fine root responses to warming

Fine root biomass responses to warming were primarily explained by topography and PFT (Table 1). The best fit model explained 40% [ $F_{(5,24)} = 4.99, p = 0.0028$ ] of the variance in fine root biomass warming responses and suggested that fine roots in hollows increased more than fine roots in hummocks (Table 1). Only trees and hollow shrubs showed significant fine root warming





**TABLE 2** Best-fit multiple linear regression model of fine root response to WLD.

Term	Estimate	Std. error	t ratio	Prob. >  t
Intercept	1.14	0.39	2.92	0.0072
PFT (graminoid)	-1.89	0.28	-6.82	0.0000
PFT (shrub)	-0.54	0.52	-1.03	0.3133
PFT (shrub + tree)	0.40	0.34	1.17	0.2527
Magnitude WLD (cm)	-0.03	0.01	-2.94	0.0069

Adjusted  $R^2 = 0.76$ ,  $F_{(4,25)} = 24.07$ ,  $p < 0.0001$ . Study source, soil depth, topography and duration of experiment were removed from the model as they were non-significant and increased the variance inflation factor. Note that the analysis and thus slope values are on log transformed data.

responses when analyzing each PFT and topography individually. In trees, 43% [ $F_{(2,9)} = 6.09$ ,  $p = 0.0210$ ; quadratic regression] of the variation in the fine root response was explained by the magnitude of warming and in hollow shrubs, the 93% [ $F_{(1,2)} = 46.7$ ,  $p = 0.0208$ ; positive linear regression] of the variation was explained albeit with a limited sample size of 4 (Figure 3).

### 3.3. Degree of drawdown and plant type regulate fine root responses to water level drawdown

Fine root biomass response to water level drawdown was significantly related to the magnitude of the drawdown and PFT (Table 2). Topography was not a significant driver of fine root response to water level drawdown. When analyzing PFTs individually, only graminoids responded significantly to water level drawdown [ $R^2 = 0.87$ ,  $F_{(1,10)} = 78.72$ ,  $p < 0.0001$ ; Figure 4]. The linear regression suggested a  $1.74 \pm 0.25\%$  decrease in graminoid fine root biomass for every 1 cm decrease in water level (Figure 4).

## 4. Discussion

This meta-analysis quantifies the effects of climate change factors on belowground plant dynamics and provides evidence that warming, and water level drawdown influence fine root biomass production in boreal peatlands. We found strong non-linear and linear fine root biomass responses to warming and water level drawdown, respectively, with PFTs and topography varying significantly. Notably, we found that fine root biomass in hollows may increase more from warming than fine root biomass in hummocks and that tree fine roots have the strongest (and non-linear) warming increases across PFTs. Under lowered water tables, only graminoid fine roots showed a significant linear decrease in biomass. Since studies on the response of boreal peatland fine roots to global change drivers are limited and available data show inconsistent responses, our findings offer insights on the climate change drivers of boreal peatland plant roots. Moreover, our synthesis highlights the importance of investigating individual PFTs and topographic responses to climate change factors such as warming and water level drawdown. Lastly, the significantly altered fine root biomass responses to climate change (ranging between -96 and +1830% across treatments and PFTs) documented here imply that altered root inputs to soil carbon stocks, may not only affect overall ecosystem C balance but also peatland structure via plant community changes and resilience to environmental change via topographic changes.

### 4.1. Non-linear fine root responses to warming

We hypothesized a linear increase in fine-root biomass with increased warming and generally observed this. However, in trees we observed a non-linear relationship between warming and fine root biomass. Our analysis suggests a maximum tree fine root biomass growth at +5.4°C (relative to ambient), comparing well to

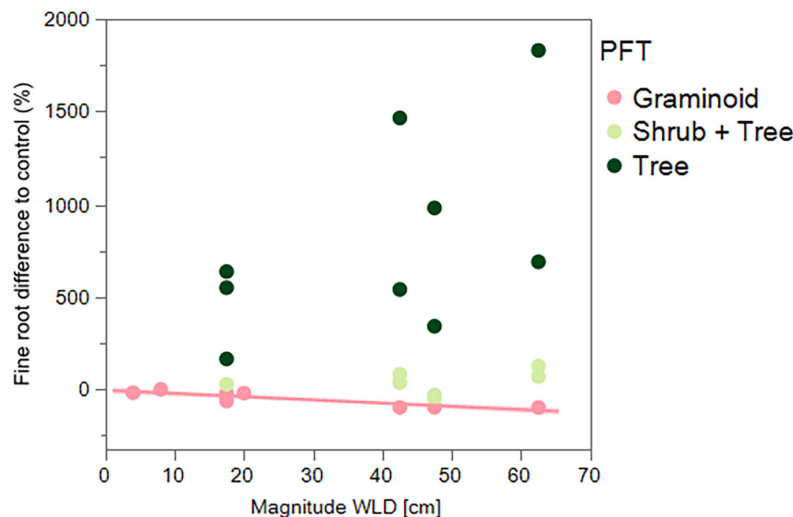


FIGURE 4

Fine root biomass responses to water level drawdown from four studies. When analyzing PFTs individually, only graminoids responded significantly to water level drawdown [shown as pink line of fit and confidence interval; adjusted  $R^2 = 0.87$ ,  $p < 0.0001$ ;  $F_{(1,10)} = 78.7$ ;  $\ln(\text{difference to control}) = 0.45 - 0.07 * \text{Magnitude WLD}$ ]. Despite a visual trend of increase, tree fine root biomass did not respond significantly to WLD [adjusted  $R^2 = 0.21$ ,  $p = 0.12$ ;  $F_{(1,7)} = 3.18$ ;  $\ln(\text{difference to control}) = 1.30 + 0.19 * \text{Magnitude WLD}$ ].

a previously suggested value of  $+4.8^\circ\text{C}$  (Lin et al., 2010; Figure 3). A possible reason for this quadratic relationship could be that, at first, warming stimulates increased plant growth both above and belowground both from direct temperature effects as well as from indirect increases in nutrients due to increased mineralization of organic matter (Munir et al., 2017; Iversen et al., 2022). However, continued warming may lead to a moisture or nutrient limitation (Poorter et al., 2012). For example, while plants are expected to allocate more belowground when nutrients are limiting, with sustained limitation and given the high nitrogen cost of fine roots, fine root growth increases may halt in the longer term (Iversen et al., 2008; Norby et al., 2010). Another reason, perhaps more likely in peatlands, could be warming-induced drying combined with increased evapotranspiration; wherein moisture becomes too limiting for physiological activity at a certain temperature threshold, and fine root increase stops (Lin et al., 2010; Malhotra et al., 2020).

Despite being highly variable, the overall warming-induced stimulation of fine root biomass in this study (on average  $+159.9\%$ , with a 95% confidence interval of  $107.1\text{--}212.8\%$ , for warming treatments ranging from  $0.8$  to  $9.0^\circ\text{C}$ ) is the first synthesized value of its kind. It is also worth noting that our reported fine-root responses are much larger than those reported in global meta-analyses for other ecosystems where fine roots increased by  $8.7$  (Wang et al., 2021) or  $13\%$  (Lin et al., 2010); highlighting that peatland fine root parameterization in models should be different than that of mineral soils. Nevertheless, our results are consistent with the few individual peatland studies using a response ratio approach, all of which were examined in this study; Sullivan and Welker (2005) on average  $+157.8\%$ , with a 95% confidence interval of  $27.9\text{--}287.7\%$ , with warming treatments ranging from  $0.8$  to  $0.9^\circ\text{C}$ ; Malhotra et al. (2020) on average  $+207.2\%$ , with a 95% confidence interval of  $131.9\text{--}282.5\%$ , with warming treatments ranging from  $2.25$  to  $9.0^\circ\text{C}$ ). Lastly, it is worth noting that our observed fine-root biomass changes could

be a result of either an increase in fine-root production, a lengthening of the belowground growing season or decreases in fine-root mortality, or a combination of these different mechanisms (Malhotra et al., 2020; Defrenne et al., 2021). The exact mechanisms of fine root biomass change are important to test in future studies.

## 4.2. Water level drawdown responses strongest in graminoid fine roots

While water level drawdown generally increased fine root biomass (Figure 2), our predictive model suggests that this variability was mostly driven by PFT differences. As per our hypothesis we saw the strongest fine-root responses to water level drawdown in graminoids, wherein graminoid fine root biomass decreased significantly with water level drawdown.

While not significantly related to the degree of water level drawdown, in accordance with our hypothesis, we did see overall water level drawdown-induced stimulation of fine root biomass in this study (on average  $+246.4\%$ , with a 95% confidence interval of  $110.9\text{--}381.9\%$ , for water level drawdown treatments ranging from  $4.0$  to  $62.5$  cm). To our knowledge, these are the first synthesized values for fine root water table response in boreal peatlands, and they are much higher than individual site studies reporting, for example, an average  $12\%$  increase in fine root biomass for a  $17.5$  cm drawdown (Murphy et al., 2009a). However, our high average response of fine roots to water level drawdown could be due to the large range of treatment magnitudes across our studies (a water level lowering of  $4\text{--}62.5$  cm) that represent not just likely climate change-driven water level changes but also changes from more drastic peatland drainage for human uses such as agriculture. It is also worth noting that if averaging across PFT and topography, the results of this meta-analysis indicate a linear increase in fine root biomass production of  $7.2\%$  per cm water level drawdown

(**Supplementary Figure 1**). While the importance of PFT and microtopography are clear across our results, this value could serve as an ecosystem-scale reference for further investigations since, so far, the few individual studies discussing the nature of this relation did not report the slope of the linear regression, if any was performed at all (Laiho and Finér, 1996; Murphy et al., 2009a; Ge et al., 2012; Munir et al., 2014). This ecosystem-scale reference is particularly important for many boreal forested peatlands where graminoids may be a small component of the total ecosystem-scale fine root biomass (e.g., Iversen et al., 2018).

Water availability is an essential driver of fine root growth in boreal peatlands. Previous boreal peatland warming experiments have reported that it is not warming that determines fine root biomass responses, but drying (caused by warming), and that fine-root biomass production increases linearly with decreasing soil moisture (Malhotra et al., 2020). However, when moisture becomes too scarce, fine root production decreases after an initial increase (Lin et al., 2010; Malhotra et al., 2020). While our results suggest a linear fine root biomass response to water level drawdown (**Figure 4**), we expect non-linear responses as water level drawdown continues and moisture availability becomes a limiting factor for plant growth (Cagampan and Waddington, 2008; Macrae et al., 2013). Our compiled data only had either warming or water table drawdown as treatments and thus we could not explicitly test for interactions among the two factors. Future data collection and synthesis efforts could prioritize moisture x warming crossed designs to tease apart these interactions.

### 4.3. Warming and water table responses of fine roots are modulated by PFT and topography

Across both warming and water level drawdown treatments, our meta-analysis suggests that PFT and topography are more important predictors of fine root responses than the degree of treatment applied. Warming and water level drawdown seems to support a shift to woody PFTs (via increasing shrub and tree fine roots and decreasing graminoid fine roots). Sustained increases in woody PFT fine root growth may eventually drive peatland shrubification by outcompeting other PFTs (Malhotra et al., 2020; McPartland et al., 2019). We observed that both trees and shrubs may benefit from the warmer and drier improved growing conditions. Based on our limited data reflecting only fine roots and not mycorrhizae, we did not see strong support of our hypothesis that shrubs would increase their foraging capacity by increasing fine root biomass more than trees (that would take an approach of outsourcing to fungal symbionts; Bergmann et al., 2020). We had also expected that thinly-rooted graminoids would increase fine root biomass under warmer conditions but instead we only saw evidence for graminoid sensitivity to moisture (with decreasing graminoid fine root biomass under lower water tables). Either way, as a result of a shift toward woodier PFTs, increased shading could limit *Sphagnum* moss growth (Laine et al., 1995; Minkkinen et al., 1999; Mäkiranta et al., 2017; Norby et al., 2019; Malhotra et al., 2020). *Sphagnum* is a key ecosystem engineer in boreal peatlands and such changes in the plant community composition (and in the C source) would directly affect C cycling in peatlands by altering

nutrients (Salmon et al., 2021), the amount and quality of organic matter inputs, and decomposition parameters that dictate peatland C storage (Ofiti et al., 2022).

The decrease of graminoid fine roots with lower water table was expected as graminoids are better suited to wetter conditions than shrubs and trees. Unlike woody plants, graminoids have aerenchyma that transports O<sub>2</sub> from the surface to the roots, allowing them to function under anaerobic conditions below the water table (Iversen et al., 2018). Therefore, graminoids are more likely to be negatively affected by warming-induced drying and, as a result, less able to compete with trees and shrubs under warming (Murphy et al., 2009a). However, one important caveat is that the data in our meta-analysis do not allow us to fully evaluate plant adaptation. In addition to missing diameter and specific root length data that could be more reflective of belowground adaptation strategies, rooting depth changes would also be needed to fully assess if graminoids are indeed not adapting to dry conditions as well as trees and shrubs. Nevertheless, we know from peatland survey studies (e.g., Bubier et al., 2006; Malhotra et al., 2016) that the aboveground biomass of graminoids and woody PFT abundances decreases and increase with a lower water table, respectively. Until we have better belowground niche tolerances of these PFTs, we can only make inferences about plant adaptation from aboveground surveys. We also expected that water level drawdown should increase the surface aerobic soil layer and improve conditions for growth of woody plants that do not form aerenchymatous roots (Murphy et al., 2009a; Iversen et al., 2018). However, while we did not see statistical evidence of shrub and tree fine roots increasing with lower water levels, we do see trends pointing toward increased fine roots although with a lot of variability (**Figure 4**). Furthermore, we observed a statistically significant increase in PFT-averaged water table response that is likely driven by the large tree fine root biomass responses (**Figure 4** and **Supplementary Figure 1**). With continued drying, graminoids likely cannot compete with trees and shrubs under drier conditions (Laine et al., 1995) and these responses should have implications for various ecosystem processes, notably a potential reduction in methane emissions due to a decrease in plant-mediated methane transport through graminoids (Lai, 2009).

Topography was also an important predictor with higher fine root biomass responses to warming for sunken hollows than for raised hummocks, consistent with previous studies (Strack et al., 2006; Malhotra et al., 2020). Our results indicate that peatland microtopography predicts fine root growth more significantly than warming magnitude (**Table 1**). Continued higher fine root biomass in hollows with warming could raise them to hummocks and flatten the existing microtopography, influencing peatland resilience to environmental change and its C balance (Belyea and Malmer, 2004; Rietkerk and van de Koppel, 2008; Malhotra et al., 2016, 2020).

### 4.4. Limitations

This study is subject to several potential limitations that could be addressed in future research. First, there has been little research on boreal peatland fine root biomass responses to warming or water level drawdown (only seven studies synthesized here). Because of this limitation, our study had small sample sizes for some

plant functional types and no observations for PFTs such as forbs. Despite great efforts developing manipulation experiments to assess climate change responses, there are still only very few *in situ* experiments in boreal peatlands, highlighting the need for further experimental development in this ecosystem. Our dataset only has one study site each from Canada, USA, and Greenland, as well as three sites from Finland; leaving large swaths of the boreal forest unrepresented in our study. For example, we did not have representative data from Scandinavia, Eastern Europe, Asia, Eastern Canada, USA, and Alaska. Thus, we require a lot more sites to be able to draw conclusive trends regarding fine root response to climate change in boreal forested peatlands. It is also important to note that even though, during our analyses, we always confirmed that our results were robust with and without study sources that were the most data rich, our data were dominated by two study sources and this bias should be noted while interpreting our results (**Supplementary Figures 2, 3** and **Supplementary Table 1**). Another important limitation is that while we base our hypotheses on the root economic spectrum framework (Bergmann et al., 2020), we acknowledge that a more direct test of these hypotheses would require data on fine root diameter, specific root length and mycorrhizal colonization intensity. Since these data are rarely reported, we had to use fine root biomass response as a simple indicator of whether plants are increasing investment into roots (as opposed to into mycorrhizae). Thus, we recommend future peatland climate change experiments to quantify additional belowground traits. Lastly, the duration of most warming treatment studies examined was very short (max. 3.3 years). Therefore, ecosystem studies with longer durations should be assessed to verify that the trends in our study reflect long-term responses of peatland ecosystems.

## 5. Conclusion

Peatland plants are known to shape peat properties through their above and belowground functional traits, given the tight ecohydrological feedbacks in these ecosystems (Waddington et al., 2014; Malhotra et al., 2016). Our study showed that warming and water level drawdown can increase the environmental sensitivity of belowground plant components in boreal forested peatlands and the effects of lowered water level can be further modulated by plant functional type and peatland topography. Although we show that climate warming and associated water level drawdown will benefit fine root growth in shrub and tree PFTs, warming could still cause lasting impacts on species composition, which in turn could alter belowground C cycling. Indeed, we observed a decline in fine root biomass in the graminoid PFT and given that peatland plant communities are already projected to shift from bryophytes to vascular plants in response to future climate change (Dieleman et al., 2015; McPartland et al., 2019; Norby et al., 2019; Malhotra et al., 2020), shifts toward shrub/tree-dominated peatlands could decrease peat C storage (Hanson et al., 2020; Ofiti et al., 2022). Our study reports highly variable fine root biomass responses to warming and water table drawdown in boreal forested peatlands;

and our synthesized PFT- and microtopography-dependent response functions could help improve predictions of peatland ecosystem structure and C sink function responses to climate change.

## Data availability statement

All data presented in the manuscript are included in the **Supplementary material (Supplementary Table 2)**, further inquiries can be directed to the corresponding author.

## Author contributions

AM and MB conceived and designed the study and conducted the analyses, with input from NO. MB collected and combined the data and wrote the first manuscript draft. AM and NO wrote the different sections and refined the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

## Funding

We acknowledge funding support from the University of Zurich Stiftung für Wissenschaftliche Forschung (STWF-22-028) to AM and the Swiss National Science Foundation (Post-doc mobility grant P500PN\_206708) to NO.

## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2023.1170252/full#supplementary-material>



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