Peatland warming strongly increases fine-root growth

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Belowground climate change responses remain a key unknown in the Earth system. Plant fine-root response is especially important to understand because fine roots respond quickly to environmental change, are responsible for nutrient and water uptake, and influence carbon cycling. However, fine-root responses to climate change are poorly constrained, especially in northern peatlands, which contain up to two-thirds of the world’s soil carbon. We present fine-root responses to warming between +2 °C and 9 °C above ambient conditions in a whole-ecosystem peatland experiment. Warming strongly increased fine-root growth by over an order of magnitude in the warmest treatment, with stronger responses in shrubs than in trees or graminoids. In the first year of treatment, the control (+0 °C) shrub fine-root growth of 0.9 km m−2 yr−1 increased linearly by 1.2 km m−2 yr−1 (130%) for every degree increase in soil temperature. An extended belowground growing season accounted for 20% of this dramatic increase. In the second growing season of treatment, the shrub warming response rate increased to 2.54 km m−2 °C−1. Soil moisture was negatively correlated with fine-root growth, highlighting that drying of these typically water-saturated ecosystems can fuel a surprising burst in shrub belowground productivity, one possible mechanism explaining the “shrubification” of northern peatlands in response to global change. This previously unrecognized mechanism sheds light on how peatland fine-root response to warming and drying could be strong and rapid, with consequences for the belowground growing season duration, microtopography, vegetation composition, and ultimately, carbon function of these globally relevant carbon sinks.

Significance

Peatlands store up to two-thirds of the world’s soil carbon, but this carbon may be released under warmer conditions, creating an important climate feedback. The belowground warming response of peatlands is particularly uncertain even though factors such as plant root growth regulate ecosystem water, carbon, and nutrient cycles. We studied how peatland fine roots respond to warming in a whole-ecosystem experiment. Fine-root growth increased dramatically, +130% for a degree of warming, primarily driven by soil drying. This warming response is 20 times stronger than in other ecosystem experiments, highlighting peatland vulnerability to warming. Our study elucidates large and rapid belowground changes that will affect peatlands of a warmer world and their ability to store carbon into the future.

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Northern peatlands contain some of the most carbon-rich soils globally (1, 2), and their warming response could feed back to further climate warming, given that carbon (C) losses from warming soils depend on the initial ecosystem C stocks (3–4). Our understanding of peatland responses to environmental change is based primarily on aboveground plant dynamics (5–7). Investigations of plant belowground responses to altered environmental conditions are relatively few (8–9). In uplands, environmental changes can alter fine-root production and mortality, thereby affecting ecosystem functions such as nutrient and water uptake, ecosystem respiration, and ultimately, soil C storage (10–13). These adaptive fine-root responses are poorly understood and thus, not well represented in peatland C cycling models (14).

Ecosystem-scale experiments help define the response of ecological processes to climate change and improve the predictive power of terrestrial biosphere models spanning spatial scales from individual ecosystem processes to the entire land surface (15). We investigated fine-root response to experimental whole-ecosystem warming and elevated [CO2] at the SPRUCE (Spruce and Peatland Responses Under Changing Environments) experiment, in an ombrotrophic peatland in northern Minnesota, the United States. This whole-ecosystem warming experiment in a trenched peatland includes both above- and belowground warming and provides a wide range of warming treatments. In 10 large open-top enclosures (7-m tall and 12.8 m in diameter), belowground warming (to 2-m depth) and air warming were initiated in 2014 and 2015, respectively. There were five temperature treatments (+0 °C, +2.25 °C, +4.5 °C, +6.75 °C, and +9 °C above ambient) and two CO2 treatments (ambient and elevated). Elevated [CO2] was initiated in June 2016 and had a target of +500 ppm above ambient (~900 ppm) (16). In each of the 10 experimental enclosures, we used root-ingrowth cores to measure in situ new root growth and tissue chemistry between 2014 and 2017.

Along with fine-root growth responses to soil temperature, soil moisture, and elevated [CO2], we assessed fine-root incorporation of 13C-depleted C from the elevated [CO2] treatment, which could indicate changes in root population turnover time, and δ15N shifts in roots, which could indicate changes in root N source (17–19). We captured root growth across three key northern peatland plant functional types (PFTs; ericaceous shrubs, trees, and graminoid species) and two microtopographical features (bumpmows and hollows) so that our treatment response
functions may be compared with other sites or used to parameterize Earth System Models (20).

**Fine Roots Increase with Warming but Due to Drying**

On the plot scale (summed across all PFTs), fine-root growth increased significantly with warming treatments but was better predicted by drying than by warming or elevated [CO2] (mixed effects model $R^2 = 0.68$) (Fig. 1 and Table 1). Since soil moisture and temperature were not correlated (SI Appendix, Fig. S2), our analyses isolated the stronger influence of drying over warming on root growth.

Among PFTs, the fine roots of ericaceous shrubs responded most strongly to drying (mixed effects model $R^2 = 0.59$) (Table 1). Fine roots of the deciduous conifer *Larix laricina* (larch) also increased (Table 1), while the evergreen conifer *Picea mariana* (spruce) and graminoids had no significant response.

Tree and shrub PFTs differed in their root morphology and thus, resource acquisition strategies; shrub roots had up to 20-fold higher specific root length (SRL; root length per unit root mass) than the trees (SRL mean and SE for fine roots of shrubs = 0.38 ± 0.01 km g$^{-1}$, larch = 0.02 ± 0.001 km g$^{-1}$, and spruce = 0.04 ± 0.002 km g$^{-1}$ km g$^{-1}$). Thus, thin-rooted shrubs may be more efficient in investing C per unit of root length for resource foraging compared with thicker-rooted trees (21), although shrubs and trees also differ in their association with ericoid and ectomycorrhizal fungi, respectively. While shrubs responded strongly to warming by increasing fine-root length, the more limited length response but higher biomass response of larch fine roots may be related to differing resource acquisition strategies (SI Appendix, Fig. S3). Shrubs may be taking a “do-it-yourself” approach by increasing the length production of new roots for foraging, while larch may be mainly “outsourcing” resource acquisition by investing in mycorrhizal fungal partners (22); both strategies have implications for total belowground C input, decomposition rates (23), and ultimately, peatland C storage. Lastly, the tree fine-root response may be mirroring aboveground C gain; parallel investigations have found that seedlings of the two tree species differ in their aboveground responses to warming (positive for larch, negative for spruce) (24). Investigations of PFT-specific root–fungal interactions and aboveground–belowground linkages in the bog are underway, but for the remainder of the manuscript, we focus on the shrub fine root-length response given that it was the strongest and earliest response and has implications for peatland C function through negative effects of shrubs on the growth of keystone *Sphagnum* mosses.

**Strong Increases in Shrub Fine-Root Growth**

During the growing season, shrub fine-root growth increased with warming (Fig. 2B) or drying (SI Appendix, Fig. S4A). We also quantified fine-root growth outside of the typical growing season (October to June; henceforth termed nongrowing season); it was zero in 2014 but increased in the warmed plots after whole-ecosystem warming began in 2015 (Fig. 2A). This additional growth

![Fig. 1.](image_url)
between autumn and spring suggests an extension of the belowground growing season due to warming.

Our data suggest that for every degree increase in soil temperature, shrub fine-root growth increased by 0.96 ± 0.28 km m⁻² in the 2016 growing season (\(R^2 = 0.52, P = 0.01\)) (Fig. 2B) and by 0.24 ± 0.09 km m⁻² in the nongrowing season (\(R^2 = 0.45, P = 0.03\)) (Fig. 2C). In the growing season of 2017, shrub root warming response was even stronger with a 2.54 ± 0.87-km m⁻² °C⁻¹ increase (\(R^2 = 0.32, P = 0.01\)) (Fig. 2C). Thus, relative to the shrub fine-root growth in the control plot (0.9 km m⁻² y⁻¹) (+0 °C and ambient [CO₂] plot in Fig. 2B), our data suggest a linear annual increase of 1.2 km m⁻² y⁻¹ for every degree increase in soil temperature, at least within the +0 °C to 9 °C applied experimental warming range (using the conservative estimate of 2016 rather than 2017 when the slope more than doubles). The magnitude of this response (130% increase of fine root-length production for a degree increase in temperature) is much higher than upland estimates of a 58% increase in fine-root biomass averaged across ~30 warming and elevated [CO₂] experiments (25) or a 7.1% increase in belowground productivity per 1 °C warming estimated from over a thousand manipulative studies (26).

Rapid adaptation of shrub root-length production (and thus, resource acquisition) in response to environmental change could be one mechanism by which shrubs outcompete other peatland PFTs, especially Sphagnum mosses—key peatland ecosystem engineers driving the accumulation of carbon in peatlands—under warmer and drier conditions. This “shrubification” of peatlands in response to warming or drying has been reported previously (5), but mechanisms of this phenomenon are poorly understood (27). While Sphagnum moss growth is negatively influenced by shrubs primarily via shading (28), the influence of shrubification on other PFTs such as trees could be positive. Peat drying and increases in nutrients could increase tree recruitment and growth (29), and we see some evidence of this in the increased larch fine-root biomass (SI Appendix, Fig. S3) and aboveground growth (24).

Given the potential for ericaceous shrubs to rapidly change the C balance of peatland ecosystems through cascading effects on other species, we focus next on the broad-scale implications of the shrub fine-root warming response. In the northern peatlands of North America, based on RCP 4.5 (Representative Concentration Pathway 4.5; CO₂ stabilization scenario), an average warming of 3 °C is expected by midcentury (ranges shown in Fig. 3). Given these temperature scenarios, we extrapolated a simple estimate of potential increases in shrub fine root-length production (Fig. 3). We recognize that this approach is an oversimplification because not all peatland areas contain shrubs; for example, fens typically contain few or no ericaceous shrub species (30). Furthermore, since we do not know future shrub occurrence across peatlands, we simply show the ranges of expected future temperatures and corresponding potential shrub fine-root growth across all peatlands in North America (a similar approach could be used on northern peatlands globally). While our extrapolation assumes a linear response of shrub fine roots to warming based on our data (Fig. 2), we can envision nonlinear responses as the SPRUCE warming treatment continues. The most plausible scenario would be that at a temperature threshold, moisture would...
Warming and Elevated [CO2] Influence Peatland Nutrient Cycling

Influence peatland resilience to environmental change (36, S6). Increased shrub abundance in hollows could raise them up by soil temperature and CO2 treatment. Data are shown for both hummocks and hollows and ambient and elevated [CO2] treatments in the growing season. In the 2017 growing season, shrub fine-root growth increased by 2.54 ± 0.87 km m⁻²°C⁻¹ where \( R^2 = 0.32 \) and \( P = 0.01 \) (full factorial regression of root length predicted by soil temperature and CO2 treatment).

We also assessed fine-root tissue chemistry (results from 2015 instead of 20 because the two highest-growth outliers were removed from the regression but are shown in B; these two points are not outliers when regressed against moisture as they were the driest plots as shown in SI Appendix, Fig. S4A).

Drivers of Shrub Fine-Root Responses

Shrub fine-root response was better predicted by drying than warming (Table 1). One possible reason for fine-root growth change is increased belowground allocation to fine roots relative to aboveground production of stems and leaves due to a moisture or nutrient limitation (31). We expected drying to increase the ratio of shrub fine-root length to aboveground biomass (31); instead, the ratio of fine-root growth to aboveground biomass increased with increasing nutrients (SI Appendix, Fig. S5 shows increasing nutrients with warming, inferred from ion-exchange resins), again highlighting the relative importance of drying over warming or over increases in nutrient availability (8, 31–35). Increases in root growth may also be driven by increased aerobic peat space as the water table lowers with drying. Raised hummocks were drier and had more roots than lower-elevation hollows prior to warming (Fig. 1) (11). However, root growth in hollows increased strongly after drying in these previously inundated areas (Fig. 1 and SI Appendix, Fig. S6). Increased shrub abundance in hollows could raise them up to hummocks and could flatten the existing microtopography, influencing peatland resilience to environmental change (36–38).

Warming and Elevated [CO2] Influence Peatland Nutrient Cycling

We also assessed fine-root tissue chemistry (results from 2015 and 2016) to further elucidate mechanisms of belowground responses to climatic change. Plant isotopes can reflect differences in nutrient availability and acquisition strategies among PFTs and in response to environmental change (19, 39–41).

Warming and elevated [CO2] influenced peatland nitrogen cycling. Shrub fine-root tissue \( \delta^{15}N \) increased strongly with warming in 2015 (\( R^2 = 0.93, P = 0.0075 \)) (SI Appendix, Fig. S7A). Increased tissue \( \delta^{15}N \) could be due to a shift in N acquisition by fine roots to deeper layers given the strong \( 15N \) gradient with depth at the SPRUCE (42), particularly given the observed drying of the aerobic layer (SI Appendix, Fig. S6). It could also be due to increased N mineralization rates and subsequent plant uptake (18) in warmed plots (inferred from both increasing fine-root growth and from measurements of plant-available N assessed with ion-exchange resins as shown in SI Appendix, Fig. S5); N availability was also a significant predictor of shrub tissue \( \delta^{15}N \) (SI Appendix, Fig. S8). Increased N availability could also potentially decrease dependence on mycorrhizal acquisition, which could also increase \( \delta^{15}N \) (19, 39). Lastly, continued increase in the growth of ericaceous shrub roots with warming could mean an increased abundance of ericoid mycorrhizal fungi (ERM). Shifts to an ERM-dominated system could result in increased peat decomposition rates via greater production of phenol-oxidizing enzymes (43) or decreased peat decomposition rates as ERM compete with saprotrophic fungal decomposers (the “Gadgil effect”) (44).

The addition of elevated [CO2] beginning in 2016 may have increased plant N limitation, as reflected by lower shrub root \( \delta^{15}N \) and higher C:N relative to the ambient CO2 plots (SI Appendix, Fig. S7 B and F, respectively). This trend also matches the trend of higher shrub fine-root growth in the elevated [CO2] plots relative to ambient (Fig. 2 B and C) and is supported by evidence that labeled new photosynthate was quickly incorporated into new shrub fine roots within the same growing season (SI Appendix, Fig. S7D). As the SPRUCE treatments continue, we expect to see more responses in the elevated [CO2] plots and interactions with warming: for example, a deepening of fine-root distribution driven by nutrient limitation and not just moisture limitation (11, 12).

Implications

Our study revealed strong and rapid belowground responses to whole-ecosystem peatland warming via drying, especially by ubiquitous understory shrubs. Peatland drying has led to shrub encroachment in previous mesocosm or open-top chamber warming experiments (45, 46) and our study elucidates belowground mechanisms of this change. Our results suggest the higher fine-root plasticity of thinly rooted shrubs over other PFTs (21) as a possible cause for rapid peatland shrubification in response to warming (via drying). Continued warming and increased aboveground shrub cover at the SPRUCE (47) may not be as limiting as shrub fine-root production would decrease after an initial increase. Future work could apply our temperature response parameters to mechanistic models and improve extrapolations.

Fig. 2. Shrub fine-root growth response (A) from October 2015 to June 2016 nongrowing season, (B) from June to October 2016 growing season, and (C) from June to October 2017 growing season. Note that both x and y axes have different scales in each panel. In the nongrowing season, shrub fine-root growth increased by 0.24 ± 0.09 km m⁻²°C⁻¹ (\( R^2 = 0.45, P = 0.03; \) bivariate linear regression of root length predicted by soil temperature, \( n = 10 \) because only hummock cores had nonzero growth in this season and elevated [CO2] was not yet initiated). In the 2016 growing season, shrub fine-root growth increased by 0.96 ± 0.28 km m⁻²°C⁻¹ where \( R^2 = 0.52 \) and \( P = 0.01 \) (full factorial regression of root length predicted by soil temperature and CO2 treatment). In the 2017 growing season, shrub fine-root growth increased by 2.54 ± 0.87 km m⁻²°C⁻¹ where \( R^2 = 0.32 \) and \( P = 0.01 \) (full factorial regression of root length predicted by soil temperature and CO2 treatment).
has details on models used. The black dot shows the location of the
but since we do not have a map of how species ranges may change in the
GCMs. Note that not all these peatland regions contain ericaceous shrubs,
based on the mean annual surface temperature projected by the MMM of 10
potential changes in peatland shrub root growth. The RCP 4.5 scenario was
year of full treatment) and strong (over 130% increase for a
initial response of the ecosystem. Nevertheless, we elucidate
loss of which has already been observed (48), and thus, decrease
long-term C storage capacity of the peatland because Sphagnum
decomposes more slowly than shrub litter (49).
Our results may reflect a short-term (first 4 y of experiment),
initial response of the ecosystem. Nevertheless, we elucidate
mechanisms that have longer-term implications: a rapid (within
a year of full treatment) and strong (over 130% increase for a
degree of warming) adaptive response of fine roots, variable
response of plant functional and microtopography types, and the
dominance of moisture feedbacks over temperature or nutrient
feedbacks. An extension of the belowground growing season is
also an important ecosystem response that is in line with
observations on extended aboveground growing season (50). Lastly,
our results provide magnitudes and ranges of fine-root responses
that are required to model peatland structure and function in a
warmer world.

Methods
Site Description. The SPRUCE experiment is located in the S1 bog (47°30.4760′
N; 93°27.1620′W; 418 m above mean sea level) at the Marcell Experimental
Forest in northern Minnesota, the United States. This site is considered es-
specially vulnerable to climate change because it is at the southern boundary
of the boreal region. The S1 bog is an ombrotrophic peatland (primarily
precipitation fed with minimal influence from groundwater) that receives
768 mm of precipitation annually and has an annual average air tempera-
ture of 3.3 °C (1961 to 2005 averages) (51).
The SPRUCE was established in a regrowth treed bog that had the tree
layer removed in 1974. All studied trees have since regenerated through
natural processes (5- to 8-m current tree height). The dominant tree species
at the site are P. mariana (Mill.) B.S.P. and L. laricina (Du Roi) Koch (re-
ferred to as spruce and larch, respectively, in the text). At nearly 45 y post-
cutting, the tree overstory is still progressing through postharvest succession
to the closed canopy forest that was present preharvest. In the understory,
there is a near-continuous ground layer of Sphagnum mosses, dominated
by Sphagnum angustifolium (C.E.O. Jensen ex Russow) C.E.O. Jensen
and

Fig. 3. Hypothetical increases in shrub fine root-length production given
expected temperature increases (based on RCP 4.5) in northern peatlands
(North America example). We used the 2016 linear model of 1.2-km⁻² m⁻²
y⁻¹ increase in shrub fine-root length per degree warming to calculate the
potential changes in peatland shrub root growth. The RCP 4.5 scenario was
based on the mean annual surface temperature projected by the MMM of 10
GCMs. Note that not all these peatland regions contain ericaceous shrubs,
but since we do not have a map of how species ranges may change in the
future, we could not mask out regions without shrubs. S1 Appendix, Table S4
details on models used. The black dot shows the location of the
SPRUCE site.

Experimental Setup. At the SPRUCE experiment, deep peat (2-m depth) and
defined peat and air warming were initiated in 10 large-scale enclo-
closures in June 2014 and June 2015, respectively. Each treatment plot is an
octagonal enclosure with an open top to allow precipitation, measuring 7-m
tall by 12.8 m in diameter with a mean area of 114.8 m² (16). Experimental
warming was achieved for five temperature targets (+0 °C, +2.25 °C, +4.5 °C,
+6.75 °C, and +9 °C above ambient) and was homogenous within the en-
closure boundaries (16). Elevated [CO₂] treatments were initiated in June
2016. We had a target of +500 ppm above ambient (+900 ppm). The added
CO₂ had a δ¹³C value of approximately −54% (relative to atmospheric CO₂
of −8%).

A sheet pile corral spanning down to the glacial till and protruding 0.5 m
above the peat surface was installed around each enclosure with an outflow
system to allow natural lateral water flow from each enclosure (53). Thus,
water table fluctuations for each enclosure are similar to those of an
independent ombrotrophic system (i.e., the water table is a function of in-
coming precipitation and direct weather temperature changes applied
and is independent from those of the larger bog area).

Fine-Root Growth. The ingrowth core approach was used to capture newly
grown fine roots during two time periods (from June to October and from
October to June) in 2014, 2015, and 2016 and from June to October for 2017.
Paired hummock–hollow ingrowth cores constructed of rigid polypropylene
mesh and filled with moist peat were installed for each of the 10 experimental
enclosures. To ensure that the peat within the ingrowth cores represented similar
conditions to the surrounding bog peat, we con-
structed ingrowth cores with similar bulk density (0.1 g cm⁻³). We also
checked that carbon and nitrogen contents of the commercial peat were
similar to the surrounding peat. Average values for bog peat within the top
30 cm were 1.1% for N and 48.5% for C (54), while commercial peat aver-
age values were 0.97% N and 48.9% C for C.

Ingrowth cores were snugly placed into holes made using a modified hole
saw to 10-cm depth below adjacent hollow surface in the hummocks and to
30-cm depth below peat surface in the hollows. Cores were collected and
replaced with similarly constructed cores in June and October of each year.
Because the actual “growing season” length varies among temperature
treatments (50), our measurements do not represent traditional growing
and non-growing seasons. Here for simplicity, we refer to our sampling
periods as growing (June to October) and nongrowing (October to June)
seasons in the text.

Upon removal from the peat, ingrowth cores were frozen at −20 °C until
processing. Frozen cores were sectioned into 10-cm increments and thawed
in the refrigerator (1 to 3 d), and all fine roots (<2 mm in diameter) were
methodically removed using forceps with the aid of jeweler’s glasses. We
separated the living fine roots of each tree species (P. mariana and L. lar-
icina; spruce and larch, respectively) from multiple ericaceous shrub species
identified as “shrubs” (shrub roots were indistinguishable from another one)
and graminoid species. We refer to these groups as PFTs (shrub,
graminoid, spruce, or larch). Roots were defined as alive or dead based on
color and how brittle they were. All of the analyses in this paper are of the
fine roots, which include both the most distal roots, orders 1 to 3 (the
“absorptive” fine roots), as well as orders 4 and above (“transport” fine
roots) up to 2 mm in diameter (55). After fine roots were removed from the peat
and cleaned with distilled water, we scanned them at 1,400 dpi on an
EPSON V700 Photo Scanner (Model J221A; Epson America Inc.) and
quantified root length and average diameter using WinRhizo software
(Regent Instruments Inc.). Fine roots were then oven dried for at least 3 d at
70 °C and weighed to determine biomass. Fine-root growth values were
estimated using both length and biomass summed for each 10-cm-depth
increment on a length or grams of root per meter squared of soil per sam-
ping period basis by accounting for peat volume and soil bulk density.
extrapolation over North American Northern Peatlands. For Fig. 3, we used monthly mean surface temperature data rendered by 10 Global Climate Models (GCMs) (SI Appendix, Table S4) shows additional details from the Coupled Model Intercomparison Project 5 (64). Data from the GCMs were obtained from the World Climate Research Program’s Working Group for the Coupled Model Intercomparison Project—Phase 5 (see https://esgf-node.llnl.gov/projects/esgf-llnl) and regridded to a common 0.5° × 0.5° grid. We calculated the changes, from 1961 to 1990 to 2036 to 2065, in the multi-model mean (MMM) of the surface temperature according to the RCP 4.5 scenario (i.e., the RCP that stabilizes radiative forcing at 4.5 W m\(^{-2}\) in the year 2100) (65). Although several ensembles are available for some models, the MMM of the temperature was computed by using estimates rendered by the first ensemble of each model. This approach aimed to avoid assigning more weight to one model over the other.

The increase in root length estimated in peatlands over North America is based on the change, from 1961 to 1990 to 2036 to 2065, in MMM of the surface temperature according to the RCP 4.5 scenario. The peatland area was adopted from the PEATMAP project (66) after regridding to the same 0.5° × 0.5° grid used for the GCMs. The extrapolation used the slope derived from the regression analysis between root growth and temperature in the conservative year (2016; slope = 1.2 km fine roots m\(^{-2}\) y\(^{-1}\) C\(^{-1}\)).

Statistical Analyses. Analyses were first conducted at the plot scale (PTTs summed) to gain an ecosystem-scale understanding and then, individually for each PFT. Growth analyses presented are on fine root–length production, but biomass showed similar trends (SI Appendix, Fig. S1) shows length and biomass comparisons). The two topographical features within each plot were kept as individual data points to capture the range of temperatures and moisture in the hummocks and hollows (analyzed as random effects in predictive models). After finding the strongest fine-root growth responses in shrubs, fine-root growth and comparison with aboveground biomass analyses focused on only 2016 and 2017 shrubs, given that these years had both warming and elevated \([\text{CO}_2]\). The fine-root chemistry analyses were conducted on 2015 and 2016 for each of the plant types.

To evaluate the effect of the experimental treatment on fine-root growth (first plot scale, then for each plant type), log-transformed fine root–length production was predicted using mixed effects linear models. Fixed effects were experiment, plant type, soil temperature treatment, soil moisture treatment, and aboveground biomass. The interaction effect was always nonsignificant and thus, removed in the reported best-fit models. In addition to topography as a random effect, all mixed effects linear regression models included year of sampling as a random effect (given that 2014 and 2015 had incomplete experimental treatments) (Experimental Setup has details). A full model with nonsignificant terms as well as the fixed effect of year is also shown in SI Appendix, Table S2 as a supplement to Table 1.

To understand mechanisms behind fine-root growth responses, we investigated both above–belowground responses as well as root tissue chemistry. We analyzed fine-root growth from the most responsive plant type (shrubs) in the full treatment year (2016) as a ratio to aboveground biomass allocation. For fine-root tissue chemistry, we evaluated warming or drying response of fine-root tissue percentage C and N, \(\delta^{13}\text{C}\), and \(\delta^{15}\text{N}\) using bivariate linear regression models with either moisture or temperature as a predictor and ran a model for each sampling year, PFT, topographical feature, and the nonsignificant temperature effect was removed from the model; random effect was topography. For fine-root tissue chemistry, we evaluated warming or drying response of fine-root tissue percentage C and N, \(\delta^{13}\text{C}\), and \(\delta^{15}\text{N}\) using bivariate linear regression models with either moisture or temperature as a predictor and ran a model for each sampling year, PFT, topographical feature, and the nonsignificant temperature effect was removed from the model; random effect was topography. For fine-root tissue chemistry, we evaluated warming or drying response of fine-root tissue percentage C and N, \(\delta^{13}\text{C}\), and \(\delta^{15}\text{N}\) using bivariate linear regression models with either moisture or temperature as a predictor and ran a model for each sampling year, PFT, topographical feature, and the nonsignificant temperature effect was removed from the model; random effect was topography.

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