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## **Above and belowground responses of four tundra plant functional types to deep soil heating and surface soil fertilization**

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**Abstract:** 1.Climate warming is faster in the Arctic than the global average. Nutrient availability in the tundra soil is expected to increase by climate warming through 1) accelerated nutrient mobilization in the surface soil layers, and 2) increased thawing depths during the growing season which increases accessibility of nutrients in the deeper soil layers. Both processes may initiate shifts in tundra vegetation composition. It is important to understand the effects of these two processes on tundra plant functional types. 2.We manipulated soil thawing depth and nutrient availability at a Northeast-Siberian tundra site to investigate their effects on above and belowground responses of four plant functional types (grasses, sedges, deciduous shrubs and evergreen shrubs). Seasonal thawing was accelerated with heating cables at 15 cm depth without warming the surface soil, whereas nutrient availability was increased in the surface soil by adding slow-release NPK fertilizer at 5 cm depth. A combination of these two treatments was also included. This is the first field experiment specifically investigating the effects of accelerated thawing in tundra ecosystems. 3.Deep soil heating increased the aboveground biomass of sedges, the deepest-rooted plant functional type in our study, but did not affect biomass of the other plant functional types. In contrast, fertilization increased aboveground biomass of the two dwarf shrub functional types, which both had very shallow root systems. Grasses showed the strongest response to fertilization, both above and belowground. Grasses were deep-rooted, and they showed the highest plasticity in terms of vertical root distribution, as grass root distribution shifted to deep and surface soil in response to deep soil heating and surface soil fertilization, respectively. 4.Synthesis - Our results indicate that increased thawing depth can only benefit deep-rooted sedges, while the shallow-rooted dwarf shrubs as well as flexible-rooted grasses take advantage of increased nutrient availability in the upper soil layers. Our results suggest that grasses have the highest root plasticity, which enables them to be more competitive in rapidly changing environments. We conclude that root vertical distribution strategies are important for vegetation responses to climate-induced increases in soil nutrient availability in Arctic tundra, and that future shifts in vegetation composition will depend on the balance between changes in thawing depth and nutrient availability in the surface soil.

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**Above and belowground responses of four tundra plant functional types to  
deep soil heating and surface soil fertilization**

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## Summary

**1.** Climate warming is faster in the Arctic than the global average. Nutrient availability in the tundra soil is expected to increase by climate warming through 1) accelerated nutrient mobilization in the surface soil layers, and 2) increased thawing depths during the growing season which increases accessibility of nutrients in the deeper soil layers. Both processes may initiate shifts in tundra vegetation composition. It is important to understand the effects of these two processes on tundra plant functional types.

**2.** We manipulated soil thawing depth and nutrient availability at a Northeast-Siberian tundra site to investigate their effects on above and belowground responses of four plant functional types (grasses, sedges, deciduous shrubs and evergreen shrubs). Seasonal thawing was accelerated with heating cables at ~15 cm depth without warming the surface soil, whereas nutrient availability was increased in the surface soil by adding slow-release NPK fertilizer at ~5 cm depth. A combination of these two treatments was also included. This is the first field experiment specifically investigating the effects of accelerated thawing in tundra ecosystems.

**3.** Deep soil heating increased the aboveground biomass of sedges, the deepest-rooted plant functional type in our study, but did not affect biomass of the other plant functional types. In contrast, fertilization increased aboveground biomass of the two dwarf shrub functional types, which both had very shallow root systems. Grasses showed the strongest response to fertilization, both above and belowground. Grasses were deep-rooted, and they showed the highest plasticity in terms of vertical root distribution, as grass root distribution shifted to deep and surface soil in response to deep soil heating and surface soil fertilization, respectively.

4. *Synthesis* - Our results indicate that increased thawing depth can only benefit deep-rooted sedges, while the shallow-rooted dwarf shrubs as well as flexible-rooted grasses take advantage of increased nutrient availability in the upper soil layers. Our results suggest that grasses have the highest root plasticity, which enables them to be more competitive in rapidly changing environments. We conclude that root vertical distribution strategies are important for vegetation responses to climate-induced increases in soil nutrient availability in Arctic tundra, and that future shifts in vegetation composition will depend on the balance between changes in thawing depth and nutrient availability in the surface soil.

**Key-words:** accelerated thawing, active layer thickness, Arctic tundra, climate warming, competition, nutrient availability, plant functional types, root biomass, vertical root distribution, vegetation composition

## Introduction

Global temperatures have increased by 0.7 °C since the 1900s (IPCC 2013). This trend will continue this century with 1.5 degrees or more, particularly in the Arctic (IPCC 2013). Arctic warming has already resulted in large scale thawing of permafrost (Romanovsky, Smith & Christiansen 2010), thereby accelerating decomposition of earlier-frozen soil organic matter (Aerts 2006), which releases carbon and nutrients (Schuur *et al.* 2009; Belshe, Schuur & Bolker 2013). Tundra vegetation is responding to climate warming by increasing aboveground productivity (Verbyla 2008; Hill & Henry 2011; Epstein *et al.* 2012) and shifting species composition (Tape, Sturm & Racine 2006; Wookey *et al.* 2009; Callaghan *et al.* 2011; Myers-Smith *et al.* 2011). Since vegetation characteristics can have decisive impacts on greenhouse gas emissions (Cahoon *et al.* 2012; Nauta *et al.* 2015) and the energy balance of the earth surface (Chapin *et al.* 2005; Blok *et al.* 2010; Pearson *et al.* 2013), the crucial question is how plant species composition in Arctic ecosystems will respond to climate warming. One of the key factors influencing the competitive balance between plant species is their capacity to monopolize the newly available resources.

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Due to the low temperatures and short growing season, microbial decomposition and nutrient mineralization are very slow, making the tundra ecosystem highly nutrient-limited (Chapin 1987; Chapin *et al.* 1995). Climate warming can influence nutrient availability in tundra soils along different pathways. With climate warming, the depth of active layer which is frozen during the winter and thaws in the growing season is prone to increase (Hinkel & Nelson 2003; Burn & Kokelj 2009; Park, Kim & Kimball 2016). Increased thawing depth can release nutrients that were previously locked up in the frozen soil, thus increasing nutrient availability in the deep soil (Frey & McClelland 2009; Keuper *et al.* 2012). On the other hand, microbial activity can be stimulated by climate warming (Mikan, Schimel & Doyle 2002). As a result, nutrient availability in the surface soil is expected to increase due to accelerated microbial decomposition and mineralization of organic matter in the surface soil (Aerts 2006; Craine, Fierer & McLauchlan 2010). Fertilization experiments in tundra ecosystems have hitherto focused on the effects of increased nutrient availability in the surface soil showing that both shrubs and graminoids, particularly grasses, can benefit from the increased nutrient availability (Dormann & Woodin 2002; Gough & Hobbie 2003; Gough *et al.* 2012; Zamin, Bret-Harte & Grogan 2014). However, to our knowledge no study explored the effects of increased nutrient availability in deeper soil layers as a result of increased thawing depth.

Since fine roots are the plant parts that absorb soil nutrients, the responses of fine root mass will likely determine which species can take advantage of the expected increase in nutrient availability. Shallow-rooted dwarf shrubs such as *Betula nana* L. and *Vaccinium vitis-idaea* L. are likely to monopolize nutrients released in the surface soil whereas deep-rooted species such as the grass *Calamagrostis holmii* Lange and the sedge *Eriophorum vaginatum* L. are likely to forage on nutrients at the deeper thawfront (Keuper *et al.* 2014; Oulehle *et al.* 2016). In addition, plants that have short-lived roots can better adapt the placement of their roots to changes in nutrient availability than plants that have long-lived roots (Eissenstat *et al.* 2000), which probably gives them a competitive advantage in changing environments . Until now, it remains unresolved however to what extent aboveground vegetation responses can be traced back to belowground root foraging strategies.

To improve our understanding of climate warming effects on tundra plants and vegetation composition, we investigated the effects of accelerated thawing and surface soil nutrient availability on above and belowground responses of tundra plant functional types. Specifically, our hypotheses were:

- 1) Deep-rooted plants such as grasses and sedges will have an advantage over shallow-rooted plants when thawing is accelerated, as they can actively forage at the deeper thaw front;
- 2) Shallow-rooted plants such as dwarf shrubs will have an advantage over deeper-rooted species when nutrient availability in the surface soil increases, as they already have a well-established root system in the surface soil;
- 3) Aboveground responses of plant species to accelerated thawing or nutrient availability are linked to belowground shifts in vertical rooting patterns.

To test these hypotheses we carried out a field experiment in which the June – July thawing depth and nutrient availability were manipulated at a Siberian tundra site. In this experiment soil thawing was accelerated by deep soil heating without increasing temperature in the surface soil, while nutrient availability in the surface soil was increased by fertilization.

## **Materials and methods**

### **Study site**

We performed our research at the long-term research facility Chokurdakh Scientific Tundra Station in the Kytalyk Nature reserve (70°49'N, 147°29'E) which is 28 km Northwest of the town of Chokurdakh (Yakutia, Russian Federation), 150 km south of the Arctic Ocean. The site is in the Low-Arctic climate zone with a mean annual air temperature of  $-13.4^{\circ}\text{C}$  (1981 – 2010), and a mean July temperature of  $10.3^{\circ}\text{C}$ . Annual precipitation at the nearest climate station (Chokurdakh, WMO station code 21946, 27 km away from the study site) is 196 mm (1981 – 2010), of which 76 mm falls in the summer (June – August).

The study area is located in the lowlands of the Indigirka River and underlain by thick continuous permafrost with a shallow active layer. The circumpolar Arctic Vegetation Map (Walker et al., 2005) classifies the vegetation of the research area as tussock-sedge tundra, dominated by *E. vaginatum* and

dwarf shrubs, with high moss cover (G4). The experiment is located on top of a 20 – 30 m elevated ridge that surrounds part of a drained thaw lake basin. This ridge is probably a remaining Pleistocene river terrace surface (Van der Molen et al., 2007). The 200 – 300 m wide ridge is covered by a relatively homogeneous moist tussock tundra vegetation with *E. vaginatum* as the dominant graminoid species and abundant dwarf shrubs such as *B. nana*, *Salix pulchra* Cham., *Rhododendron tomentosum* Harmaja and *V. vitis-idaea*. Throughout the ridge a moss layer with some lichens is present below the vascular plants. Frost boils without any vegetation cover are sparsely distributed on the ridge. Soils are classified as Gelisol according to USDA soil taxonomy and consist of an organic layer on top of silty clay parent deposits. The organic layer varies in thickness from a few cm up to 25 cm.

### **Experimental set-up**

We established 20 plots of 1.5 by 1.5 m in 2010. The plots were clustered in 5 blocks containing 4 plots each. Plot selection was based on vegetation composition: we made sure each plot contained species of four vascular plant functional types (grasses, sedges, deciduous shrubs, and evergreen shrubs). Within each block we randomly assigned 4 treatments, comprising 2 levels of fertilization: fertilized and unfertilized; and 2 levels of heating: deep soil heating treatment with heating cable, control treatment with cable but without heating (Fig. 1a).

The deep soil heating treatment was realized by heating cables buried in the soil and connected to solar panels. The heating cables were inserted into the soil at a depth of about 15 cm below the soil surface (defined as the top of the moss layer) in July 2010 (Fig. S1). The horizontal spacing in between the cable lines was 20 cm. The cables were inserted into the soil from excavated trenches at two opposing sides of the plots to minimize disturbance of roots and microbial activity within the plots. The total length of the cable for a single plot was 15 m and the total resistance was 15 Ohm. In the heating plots, the heating cables were connected to two parallel connected solar panels of 85 Watt each on July 3, 2011, which is one year after cable installation. No battery was included in the circuit, so the solar energy directly enlarged the natural ground heat flux and allowed for diurnal and seasonal variation in solar intensity, as

the main aim of this study was to increase thaw depth in the summer, which is one of the expected consequences of climate warming. The seasonal variation in ground heat flux, which drives the seasonal thawing of permafrost, is connected to the incoming solar energy. Therefore the heating treatment has enhanced the ambient ground heat fluxes. The two solar panels had an angle of 60° to each other in order to capture sunlight during 20 hours per day.

Plots were fertilized by inserting slow-release fertilizer tablets (Osmocote Exact Tablet 3-4M, Scotts International BV, Waardenburg, The Netherlands) into the soil at 5 cm below soil surface in early July 2011 and again in late June – early July 2013. Fertilizer was added within a 1.75 × 1.75 m area for each plot, making sure plants at the plot margin with roots beyond the plot border also completely experience the fertilization treatment. Within the 1.75 × 1.75 m area, 68 tablets of 5 g fertilizer were inserted into the soil in a pattern with 25 cm spacing between the tablets. We added 5.6 g N m<sup>-2</sup> yr<sup>-1</sup>, 1.4 g P m<sup>-2</sup> yr<sup>-1</sup> and 3.7 g K m<sup>-2</sup> yr<sup>-1</sup>, but as we do not know exactly how fast the nutrients were released from the slow release fertilizer tablets, the actual nutrient release rates could have been lower.

## Measurements

### *Environmental factors*

The thawing depth and soil moisture were measured 2 – 4 times from late June to late July/early August from 2010 to 2014 at five points in each plot. Thawing depth was measured by inserting a metal stick into the soil until hitting the frozen soil. Integrated soil moisture between 0 and 10cm soil depth was measured using a Thetaprobe soil moisture sensor (ML3 ThetaKit, Delta-T Devices, UK).

Soil temperature was measured continuously in each plot at depths of 0, 5, 15 and 25 cm below the soil surface from 8<sup>th</sup> August 2010 to 30<sup>th</sup> July 2014. Temperature was recorded automatically every 3 hours using miniature temperature loggers (iButton DS1922L/DS1921G, Maxim Integrated, USA).

Soil nutrient availability was assessed by measuring soil exchangeable nutrient concentrations in each plot at depths of 5 and 25 cm below the soil surface using resin bags. The resin bags at 5 cm were all in the organic layer, and the resin bags at 25 cm were all in the mineral layer. The differences between the

two depths also reflect the differences between the organic and mineral soil in nutrient availability. Each resin bag contained 5 g ion-exchange resin (TMD-8, H<sup>+</sup>/OH<sup>-</sup> Form, Type 1, Mixed Bed Resin, 16 – 50 mesh, Avantor, USA) in a 5 × 5 cm polypropylene bag with a 100 μm mesh size. The bags were first inserted in 2010 and replaced by new ones at the same spots at the beginning of August each year until 2014. Resin bags were extracted overnight in 50 ml 2 M NaCl in 0.1 M HCl. The extracts were brought to neutral pH by the addition of NaOH and analyzed spectrophotometrically for NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup>, PO<sub>4</sub><sup>-</sup> and K<sup>+</sup> using an auto-analyser (Skalar, Breda, The Netherlands).

#### *Plant abundance*

The abundance of each plant species in each plot was recorded in the 50 × 50 cm plot centre (Fig. 1b) in early July 2010 before the installation of heating cables and in late July – early August 2013, by taking point intercept measurements on a grid of 11 by 11 points spaced 5 cm apart. The 121 grid points were used to determine species abundances. To determine species presence at each point in the grid, a thin rod was lowered from above the point to the ground and each plant species it touched on its descent to the ground was recorded. A species, e.g. *B. nana*, could be hit multiple times at one point. The total number of hits for each species in a plot is taken as the indicator of the abundance of that species in that plot.

#### *Biomass*

Aboveground and belowground plant biomass was harvested on 1 – 15 August 2014. In each plot, two 25 × 25 cm sub-plots were sampled (Fig. 1b). In each sub-plot, aboveground plant parts were clipped at the moss surface and sorted into different fractions for the four PFTs: leaves for grasses (*Arctagrostis latifolia* (R. Br.) Greseb. and *C. holmii*) and sedges (*E. vaginatum* and *Carex bigelowii* Torr. ex Schwein.), leaves and stems for deciduous (*B. nana* and *S. pulchra*) and evergreen shrubs (*R. tomentosum* and *V. vitis-idaea*). Plant tissues below the moss surface were considered belowground, as many shrub roots, particularly evergreen shrub roots, grew in the moss layer. Root biomass was sampled by taking a soil core (8 cm diameter) in the centre of the sub-plot. Organic layer thickness was measured for each soil core. The

soil cores were separated into 4 layers: 0 – 5 cm as first layer, 5 – 15 cm as the second layer, 15 – 30 cm as third layer and 30 – thawing depth as the fourth layer. To take into account the differences in soil volume between layers, we used the biomass density ( $\text{g m}^{-3}$ ) when comparing the rooting patterns over layers.

Belowground biomass was sorted into different fractions for the four PFTs: belowground stems (diameter > 5 mm), coarse roots (1 mm < diameter < 5 mm) and fine roots (diameter < 1 mm) for deciduous and evergreen shrubs; rhizomes (diameter > 1 mm, including stem bases of *E. vaginatum*) and fine roots (diameter < 1 mm) for grasses and sedges.

Belowground stems were easily identified to species as they resemble their aboveground parts. Roots that were not attached to the belowground stems were identified according to their colour and texture (Hobbie & Chapin 1998). We used root systems still attached to shoots to identify and characterize the species (see Fig. S2). *A. latifolia* and *C. holmii* roots are white and smooth and with a light yellow colour for older roots. *E. vaginatum* roots are also white and smooth, but unbranched, which differs from grass roots. *C. bigelowii* roots are tan coloured, with a pubescent texture. Deciduous shrubs roots are reddish to brown coloured, with woody structure and usually can be recognized by the colonization of ectomycorrhizal fungi. Evergreen shrub roots are reddish to brown coloured and much finer than deciduous shrub roots, and they usually form root clusters with high density of very fine roots. The morphology of the two shrub types also differs. Deciduous shrub roots are relatively straight compared to evergreen shrub roots, with short first-order roots and visible ectomycorrhizal fungi colonization. In contrast, evergreen shrub roots are usually more curled and branched with relatively long first-order roots. If fine root density was very high, we took a sub-sample with a known proportion of the original sample for root sorting. It has to be noted that even a great effort was made to distinguish the roots of different PFTs, there still was uncertainty of the identification of some fine roots (about 5 %), particularly for root fragments of shrubs.

All samples were air-dried at the field station before they were transported to Spasskaya Pad Scientific Forest Station, Yakutsk, Russian Federation (62°14' N, 129°37' E) where they were dried in an oven at

the temperature of 70 °C for at least 24 hours. After the samples were transported to the Netherlands, they were further dried in an oven at the temperature of 65 °C for 72 hours and weighed.

## Analysis

We used linear mixed effects models (LMM) with heating treatment, fertilization treatment and their interaction as fixed factors, and block as random effect to test for treatment effects on the environmental factors, including soil temperature at different depths, thawing depth, soil moisture and soil exchangeable nutrients (nitrogen and phosphorus) at different depths.

To test for the treatment effects on the abundance changes from 2010 to 2013 (differences in hits between 2010 and 2013), aboveground biomass, belowground biomass and fine root biomass of the four PFTs, we used linear mixed models and included heating, fertilization, PFT and their interactions as fixed factors, block and plot as random effects in a nested structure (plot within block). Then we did the analyses for PFTs individually, with heating, fertilization and their interaction as fixed factors, and block as random effect, to check the treatment effects on each PFT.

To test for differences in the vertical distribution of fine roots of different PFTs and treatment effects, we calculated mean root depth of each PFT in each treatment:

where  $b_i$  is the biomass of layer  $i$ ,  $D_i$  is the depth of the middle of layer  $i$ . For the fourth layer, the depth was calculated as the middle from 30 cm to the depth beyond which no roots were found any more. Then the same procedure as the analyses of other plant variables was carried out. To further investigate changes in root distribution, we analysed the proportion of root biomass in each layer separately for each PFT, using linear mixed effects models with heating, fertilization and their interaction as fixed factors, block as random effect.

The differences in the abundance change, aboveground biomass, belowground biomass and fine root biomass of vascular plants of the whole plot community were also tested, using linear mixed effects models with heating and fertilization as fixed factors, and block as random effect. Least Significant

Difference (LSD) method was used for post hoc tests when an effect was significant in one of the above models.

Biomass variables and soil nutrient variables were ln transformed to achieve normal distribution and homoscedasticity of errors. Analyses were performed with R (version 3.2.1) in RStudio (version 0.98.1091). Linear mixed model analyses were made using package *lme4* version 1.1-7 (Bates *et al.* 2014); *P* values were calculated using package *lmerTest* version 2.0-20 (Kuznetsova, Brockhoff & Christensen 2014).

## Results

### Environmental factors

The deep soil heating treatment significantly warmed the deeper soil layers (15 and 25 cm) from April until October, irrespective of experimental year, with the largest temperature difference among treatments taking place in July (Fig. S3). In 2014 the heating treatment increased thawing depth in July 2014 by 7 cm on average (Fig. S4). The heating treatment did not affect soil exchangeable nutrient concentrations significantly (Fig. S4), although the exchangeable phosphorus concentration at 25 cm depth tended to be increased by thawing ( $F_{1,12} = 3.56$ ,  $P = 0.083$ ).

Fertilization cooled all soil layers by 0.6 – 0.9 °C, reduced thawing depth in July 2014 by 4 cm and increased soil exchangeable nutrient concentrations in the top layer (5 cm) four (nitrogen) to five (phosphorus) times (Fig. S4). Neither heating nor fertilization affected soil moisture at 0 – 10 cm depth significantly (Fig. S4, Table S1). In the control plots soil exchangeable nitrogen was higher at 5 cm depth than at 25 cm depth ( $P = 0.028$ ), but exchangeable phosphorus did not differ between the two depths ( $P = 0.732$ ; Fig. S4).

### Aboveground plant responses

Deep soil heating did not affect community aboveground biomass ( $F_{1,12} = 0.1$ ,  $P = 0.809$ ; Fig. S5) but did significantly increase sedge aboveground biomass (Fig. 2a; Table 1, 2). The other PFTs did not

respond to the heating treatment (Table 2). In contrast, fertilization increased community aboveground biomass by 60% ( $F_{1,12} = 15.9$ ,  $P = 0.002$ ; Fig. S5). For each PFT except sedges, fertilization increased the aboveground biomass and/or abundance (Fig. 2a, Fig. S6; Table 2). The aboveground biomass increase was strongest for grasses (Fig. 2a). Abundance of mosses and lichens decreased with fertilization as vascular plants increased (Fig. S6; Table S2).

### **Belowground plant responses**

Community belowground biomass was about three times as high as aboveground biomass ( $F_{1,28} = 15.7$ ,  $P < 0.001$ ; Fig. S5). The deep soil heating treatment did not affect belowground biomass and fine root biomass at the community (Fig. S5) or individual PFT level (Fig. 2b; Table 1, 2). Deep soil heating significantly increased community mean root depth ( $F_{1,12} = 5.9$ ,  $P = 0.031$ ), although it did not significantly affect mean root depth of any individual PFT (Table 2). However, grasses tended to shift their root distribution to the deeper soil layers in response to deep soil heating: heating marginally decreased the proportion of grass roots in the second layer and significantly increased that in the third layer (Fig. 3a;  $F_{1,16} = 3.1$ ,  $P = 0.098$ ;  $F_{1,16} = 5.1$ ,  $P = 0.038$  respectively). The other PFTs did not show significant responses to the heating treatment in their root distribution over the four soil layers (Fig. 3a).

Fertilization did not affect belowground biomass and mean root depth at the community level, but did affect them at the PFT level: fertilization significantly increased fine root biomass of grasses but decreased that of evergreen shrubs (Table 2). Fertilization also decreased the mean root depth of grasses and evergreen shrubs by 4 and 1.5 cm respectively (Table 2). When zooming in to specific layers, grasses increased their root biomass proportion in the first layer and decreased that in the third layer in response to the fertilization (Fig. 3b;  $F_{1,12} = 16.0$ ,  $P = 0.002$ ;  $F_{1,16} = 10.3$ ,  $P = 0.005$  respectively), while evergreen shrubs increased their root proportion in the first layer and decreased that in the second layer (Fig. 3b;  $F_{1,16} = 9.7$ ,  $P = 0.007$ ).

## Discussion

Our results show that aboveground responses of tundra vegetation to deep soil heating and fertilization depend on functional type and are related to their belowground root distribution. Increased thawing depth benefited the deep-rooted sedges in their aboveground biomass and tended to increase the root distribution of grasses to deeper soil layers without changing total root biomass. Fertilization promoted aboveground biomass of the shallow-rooted dwarf shrubs and the flexible-rooted grasses, at the cost of the moss and lichen cover. Overall, our results suggest that deep-rooted sedges may benefit in their aboveground biomass from increased thawing depth and shallow-rooted species can benefit from increased nutrient contents in the upper soil. The competitive relationship between the two rooting strategies will depend on the balance between the nutrient changes in the surface and deep soil, while the flexible-rooted grasses may benefit in rapidly changing conditions.

## Environmental changes caused by the treatments

The deep soil heating treatment increased June – July thawing depth without increasing soil temperatures in the upper organic soil layer, for the first time enabling us to separate the effects of increased thawing depth from the effects of surface soil environmental changes in the tundra. Earlier studies manipulated thawing depth in field experiments using either open-top chambers (OTC) to increase air and soil temperatures or snow-fences to increase snow depth in the experimental plots (e.g., Wahren, Walker & Bret-Harte 2005; Björk *et al.* 2007; Natali, Schuur & Rubin 2012; Zamin, Bret-Harte & Grogan 2014). OTC treatments usually only increased the air temperature in the chamber and did not influence thawing depth much or not at all (Sullivan & Welker 2005; Natali, Schuur & Rubin 2012). Snow fence treatments had opposing effects on thawing depth depending on the soil thermal conditions and snowmelt time (Hinkel & Hurd 2006; Leffler *et al.* 2016). In addition, the larger snow depth provided a thicker protective layer against frost damage in winters, which is to the benefit of taller plants, and increased spring water flow (Wahren, Walker & Bret-Harte 2005; Wipf 2010), making it difficult to isolate soil thawing effects on vegetation. In our study we did not measure ALT in late August, so we do not have

hard evidence to prove that the maximum thaw depth has been increased by the heating treatment.

However, there was a significant effect of the heating treatment on August temperatures at 25 cm depth (Fig. S3); therefore it is very likely that also ALT late in the growing season differs. We also observed that at the time of our sampling the soil thawing depth was as deep as 55 cm, whereas the deepest roots we found were at 45 cm depth, suggesting that the increased thawing depth in the early and middle season probably already exceeded the maximum root depth of the plants given the growing season length at the site. Therefore we think it is reasonable to extrapolate our results to the scenario of increased thaw depth.

In our study, deep soil heating did not significantly influence nutrient availability at either 5 or 25 cm depth. On average the organic layer thickness of the experimental plots was 13 cm, so the heated soil was mostly mineral soil and probably its organic matter content was rather low. Moreover, although the average soil temperature in the deeper layers was increased by 0.7 degree, the soil temperatures were still low compared to the temperatures of the surface soil, thereby limiting mineralization of soil organic matter.

In contrast to the deep soil heating treatment, fertilization decreased soil temperature and thawing depth, probably through increased shading by vascular plants (Chapin *et al.* 1995), as suggested by a significant correlation between total aboveground biomass and average June – July soil temperature of all depths ( $P = 0.037$ ,  $R^2 = 0.29$ ,  $n = 15$  plots with temperature records). This shading effect on thawing depth illustrates a negative feedback between plant productivity and soil temperature, which can mitigate changes resulting from climate warming.

### **Plant responses in biomass**

In our study each PFT only had two species, which is inherent to species-poor communities like tundra. However, all these species in our study are very common and wide-spread in tundra ecosystems, particularly in the moist tussock, dwarf shrub tundra. Therefore, we use PFT for generality and for comparison with other studies with similar species composition.

Increased thawing depth had minor effects on plant biomass in our experiment, which might be due to the fact that nutrient availability was not influenced much by soil heating, as nutrient availability is an

important limiting factor for plant growth in tundra ecosystems (Chapin *et al.* 1995; Chapin *et al.* 1996).

However, the deep-rooting sedges, which had the highest root proportion below 15 cm depth ( $F_{1,18} = 4.5$ ,  $P = 0.048$ ), did benefit a little from the deep soil heating treatment. As the phosphorus concentration in the deep soil showed a marginally significant increase, it suggests that sedges might have profited from the slightly higher nutrient availability deeper in the soil. In addition, increased soil volume can increase the total amounts of nutrients (Keuper *et al.* 2012) as well as water available to the plants, which could be absorbed by the sedges, thereby enhancing their growth. Possibly, the increased water availability close to the thaw front contributed to their aboveground biomass increase, which is in agreement with the competitive advantage of sedges in wet locations (Shaver & Chapin 1991; Shaver *et al.* 1998). This can also explain the lack of sedge response to fertilization.

To further explore the role of potential rooting depth in explaining plant responses, we related abundance change of each species in response to soil heating to the maximum root depth of plant species obtained from Iversen *et al.* (2015). We found that abundance change had a significantly positive relationship with maximum root depth (Fig. S7), which may be an important predictor of plant responses to increasing thawing depth in the tundra. Apart from vertical root distribution, horizontal root spacing can also be important in explaining the PFT responses observed in our study. Some species, such as the grasses and shrubs, can spread out roots horizontally and thus can possibly benefit more from the way we introduced fertilizer (in 68 spots spacing 25 cm apart), while the dominant sedge species *E. vaginatum* mainly grows roots vertically downward, which may have limited its ability to make use of the nutrient hotspots in the surface soil.

In our study, increased nutrient availability benefited vascular plants at the expense of mosses and lichens, which has also been found in previous studies (Chapin *et al.* 1995; Dormann & Woodin 2002; Gough *et al.* 2012; DeMarco *et al.* 2014). Among the vascular plants, the response to fertilization was strongest in grasses and deciduous shrubs. Grasses increased in both the aboveground and belowground biomass, while deciduous shrubs increased in the aboveground biomass but not in the belowground biomass. Evergreen shrubs also only increased in the aboveground biomass and took a third position in the

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responses to fertilization. Sedges did not respond to fertilization, which might be due to the intensified competition in the surface soil (0 – 15 cm) where most roots of the other PFTs were. Also in other studies grasses were very responsive to fertilization (Dormann & Woodin 2002), as well as deciduous shrubs (Shaver & Chapin 1986; Gough & Hobbie 2003). However, responses of sedges and evergreen shrubs to fertilization have been quite mixed in previous studies. Positive, negative and neutral responses have been observed in different studies/sites (Shaver & Chapin 1986; Grellmann 2002; Gough *et al.* 2012; Zamin, Bret-Harte & Grogan 2014), which suggests that the limiting factor for the growth of sedges and evergreen shrubs differs from site to site, such as nutrients, soil moisture and/or snow depth in winter (Shaver & Chapin 1986). The temporal duration of the studies is another issue to consider when interpreting effects of environmental changes on plant growth. For example, Chapin and Shaver (1996) showed that fertilization did not significantly affect the biomass of evergreen shrubs after 3 years, but after 9 years, biomass of the evergreen shrubs had declined drastically in the fertilization treatment.

It is well known that increased nutrient availability results in reduced root: shoot ratio (Brouwer 1962; Chapin 1980), which was also the case in our experiment (Table S3). In addition, we found that fertilization increased fine root biomass of grasses while shrub roots did not increase significantly. The increases in the fine root biomass of grasses can help grasses to absorb more nutrients and thus increase their aboveground biomass. However, shrubs also increased their aboveground biomass in response to fertilization without an increase in their root biomass. The reason could be that shrubs increased the nutrient absorption efficiency of their roots, and/or that they enhanced the symbiosis with mycorrhizal fungi, which can absorb nutrients in the soil and provide them to host plants (Newsham, Upson & Read 2009).

### **Vertical root distribution**

To our knowledge this study is the first to show changes in vertical root distribution in response to environmental changes in tundra. Increased thawing depth increased community root depth, suggesting that with climate warming and deeper thawing depth during root growth, tundra vegetation can exploit the

thawing soil and thus affect the carbon cycle there. In our study the mean root depth of PFTs followed the order: sedge/grass > deciduous shrub > evergreen shrub. Although the individual PFTs did not show significant responses in rooting depth to the deep soil heating, grasses did show a trend of increasing deep root proportion, indicating that when climate warming causes more rapid thawing of deep soil and more nutrients and water are available in the deeper soil due to increased soil volume, grasses have the potential to grow roots deeper, at a soil depth where dwarf shrubs have hardly any roots.

Fertilization shifted root distribution of both grasses and evergreen shrubs to shallower soil layers. However, fertilization increased fine root biomass of grasses but decreased that of evergreen shrubs, suggesting a competitive advantage for the grasses over the evergreen shrubs. The increase in fine root biomass in the surface soil (Fig. S8) could enable grasses to make better use of the available nutrients, which probably explains their strong increase in abundance and aboveground biomass due to fertilization, since nutrient availability in the 5 – 15 cm layer was probably the highest as the fertilizer tablets were inserted into the soil at ca. 5 cm depth. The shift of root distribution of grasses towards the depth of newly available nutrients and/or water, both in the fertilization and heating treatments, suggests a high plasticity for reacting quickly to changes in resource availability.

It has been shown that vertical niche differentiation of rooting zones is an important mechanism for plant species diversity in tundra (McKane *et al.* 2002). The lack of a significant effect of the interaction between the heating and fertilization treatments suggests a possibility for sustaining biodiversity in the future if climate warming increases both nutrient availability in the surface soil and increases soil volume in the deep soil, in which case the different vertical root distribution patterns of these PFTs can help them to make use of nutrients at different depths.

### **Implications for plant competitive relationships in the warmer future**

Our results suggest that the responses of tundra vegetation to climate warming will depend on the balance between changes in thawing depth and nutrient availability in the surface soil. The surface soil receive fresh litter input and the temperatures are more influenced by the increases of air temperature

(Jobbágy & Jackson 2000; Jobbágy & Jackson 2001; Tarnocai *et al.* 2009), which means that the decomposition in the surface soil is likely to be accelerated more than that in the deep soil. In this case, mineralization of soil organic matter increases more in the surface soil than in the deeper soil with climate warming, and thus dwarf shrubs will gain more advantage through their shallow roots. However, warming can also dry the surface soil (Hinzman *et al.* 2005; Smith *et al.* 2005), thereby limiting nutrient mineralization rates in the surface soil (Aerts 2006; Hicks Pries *et al.* 2013), decreasing the advantage of the shallow-rooted shrubs. Instead, the deeper rooted sedges and/or the plastic graminoids, can ‘escape’ the dried out surface soil and forage the thaw front instead (Keuper *et al.* 2012; Oulehle *et al.* 2016), perhaps even leading to graminoid dominance.

Another study found that *Arctagrostis latifolia*, which was the dominant grass species in our study, responded rapidly to disturbances and changing soil conditions (Jorgenson *et al.* 2015). Our results suggest that the fast response of grasses to changing conditions can be explained by having the highest root plasticity among the four PFTs in terms of vertical root distribution, as they responded to both heating and fertilization. This plasticity may enable grasses to better deal with the changes in both deep and surface nutrients as consequences of climate warming, which may give grasses an advantage over sedges if climate warming results in more erratic nutrient distributions in the future.

Elmendorf *et al.* (2012) found that in recent decades shrubs and grasses increased their maximum heights and/or abundances across tundra ecosystems based on plot observations, which can be related to climate warming in the summers. Also shrub expansion has been observed in many tundra sites (Myers-Smith *et al.* 2011). In combination with our findings that shrubs can profit from increased nutrient availability in the surface soil and grasses can respond to both changes in the surface and deep soil, their results suggest that recent climate warming may have increased nutrient availability in the surface soil. In the deep soil, however, climate warming has either not increased thaw depth significantly as a result of the insulation effect of the vegetation and organic soil layer (Walker *et al.* 2003), or climate warming only has had minor effects on nutrient availability in the deep soil in tundra ecosystems.

## **Conclusions**

In our field experiment at a Siberian tundra site, increased thawing depth had modest effects, and only affected aboveground biomass of sedges which had the deepest root distribution. Fertilization strongly increased aboveground biomass of the shallow-rooted dwarf shrubs as well as deeper-rooted grasses, whose strong response can be explained by shifts in vertical root distribution to depths where new nutrients became available. Increased thawing depth and increased nutrient availability in the upper soil have different effects on plants that differ in rooting depths and plasticity, which might have important consequences for further successional trajectories. The high root plasticity of grasses may enable them to gain advantage over dwarf shrubs and sedges in the competition for soil nutrients if climate warming leads to more erratic environmental conditions.

## **Author's Contributions**

MMPDH, ALN, GS-S, DB and FB conceived the experiment; PW, ALN, MMPDH, JL and TCM collected the data; PW, JvR, MMPDH, LM and JL analysed the data; PW, JL, MMPDH, JvR, LM and FB wrote the manuscript. All authors contributed substantially to the drafts and gave final approval for publication.

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## Data Accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.vd129>

## References

- Aerts, R. (2006) The freezer defrosting: global warming and litter decomposition rates in cold biomes. *Journal of Ecology*, **94**, 713-724.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. <http://CRAN.R-project.org/package=lme4>.
- Belshe, E.F., Schuur, E.A.G. & Bolker, B.M. (2013) Tundra ecosystems observed to be CO<sub>2</sub> sources due to differential amplification of the carbon cycle. *Ecology Letters*, **16**, 1307-1315.
- Björk, R.G., Majdi, H., Klemmedtsson, L., Lewis-Jonsson, L. & Molau, U. (2007) Long-term warming effects on root morphology, root mass distribution, and microbial activity in two dry tundra plant communities in northern Sweden. *New Phytologist*, **176**, 862-873.
- Blok, D., Heijmans, M.M.P.D., Schaepman-Strub, G., Kononov, A.V., Maximov, T.C. & Berendse, F. (2010) Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Global Change Biology*, **16**, 1296-1305.
- Brouwer, R. (1962) Nutritive influences on the distribution of dry matter in the plant. *Netherlands Journal Agricultural Science*, **10**, 399-408.
- Burn, C.R. & Kokelj, S.V. (2009) The environment and permafrost of the Mackenzie Delta area. *Permafrost and Periglacial Processes*, **20**, 83-105.
- Cahoon, S.M., Sullivan, P.F., Shaver, G.R., Welker, J.M. & Post, E. (2012) Interactions among shrub cover and the soil microclimate may determine future Arctic carbon budgets. *Ecology Letters*, **15**, 1415-1422.
- Callaghan, T., Tweedie, C., Åkerman, J., Andrews, C., Bergstedt, J., Butler, M., Christensen, T., Cooley, D., Dahlberg, U., Danby, R., Daniëls, F.A., de Molenaar, J., Dick, J., Mortensen, C., Ebert-May, D., Emanuelsson, U., Eriksson, H., Hedenås, H., Henry, G.H.R., Hik, D., Hobbie, J., Jantze, E., Jaspers, C., Johansson, C., Johansson, M., Johnson, D., Johnstone, J., Jonasson, C., Kennedy, C., Kenney, A., Keuper, F., Koh, S., Krebs, C., Lantuit, H., Lara, M., Lin, D., Lougheed, V., Madsen, J., Matveyeva, N., McEwen, D., Myers-Smith, I., Narozhniy, Y., Olsson, H., Pohjola, V., Price, L., Rigét, F., Rundqvist, S., Sandström, A., Tamstorf, M., Van Bogaert, R., Villarreal, S., Webber, P. & Zemtsov, V. (2011) Multi-decadal changes in tundra environments and ecosystems: synthesis of the International Polar Year-Back to the Future Project (IPY-BTF). *Ambio*, **40**, 705-716.
- Chapin, F.S., III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, 233-260.
- Chapin, F.S., III (1987) Environmental controls over growth of tundra plants. *Ecological Bulletins*, **38**, 69-76.
- Chapin, F.S., III, Bret-Harte, M.S., Hobbie, S.E. & Zhong, H. (1996) Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science*, **7**, 347-358.
- Chapin, F.S., III, Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694-711.
- Chapin, F.S., III, Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., McGuire, A.D., Rupp, T.S., Lynch, A.H., Schimel, J.P., Beringer, J., Chapman, W.L., Epstein, H.E., Euskirchen, E.S., Hinzman, L.D., Jia, G., Ping, C.-L., Tape, K.D., Thompson, C.D.C., Walker, D.A. & Welker, J.M. (2005) Role of land-surface changes in arctic summer warming. *Science*, **310**, 657-660.
- Chapin, F.S.I. & Shaver, G.R. (1996) Physiological and growth responses of arctic plants to a field experiment simulating climatic change. *Ecology*, **77**, 822-840.
- Craine, J.M., Fierer, N. & McLaughlan, K.K. (2010) Widespread coupling between the rate and temperature sensitivity of organic matter decay. *Nature Geoscience*, **3**, 854-857.
- DeMarco, J., Mack, M.C., Bret-Harte, M.S., Burton, M. & Shaver, G.R. (2014) Long-term experimental warming and nutrient additions increase productivity in tall deciduous shrub tundra. *Ecosphere*, **5**, art72.
- Dormann, C. & Woodin, S. (2002) Climate change in the Arctic: using plant functional types in a meta - analysis of field experiments. *Functional Ecology*, **16**, 4-17.
- Eissenstat, D.M., Wells, C.E., Yanai, R.D. & Whitbeck, J.L. (2000) Building roots in a changing environment: implications for root longevity. *New Phytologist*, **147**, 33-42.

- Elmendorf, S.C., Henry, G.H., Hollister, R.D., Björk, R.G., Boulanger-Lapointe, N., Cooper, E.J., Cornelissen, J.H., Day, T.A., Dorrepaal, E. & Elumeeva, T.G. (2012) Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature climate change*, **2**, 453-457.
- Epstein, H.E., Raynolds, M.K., Walker, D.A., Bhatt, U.S., Tucker, C.J. & Pinzon, J.E. (2012) Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. *Environmental Research Letters*, **7**, 015506.
- Frey, K.E. & McClelland, J.W. (2009) Impacts of permafrost degradation on arctic river biogeochemistry. *Hydrological Processes*, **23**, 169-182.
- Gough, L. & Hobbie, S.E. (2003) Responses of moist non-acidic arctic tundra to altered environment: productivity, biomass, and species richness. *Oikos*, **103**, 204-216.
- Gough, L., Moore, J.C., Shaver, G.R., Simpson, R.T. & Johnson, D.R. (2012) Above- and belowground responses of arctic tundra ecosystems to altered soil nutrients and mammalian herbivory. *Ecology*, **93**, 1683-1694.
- Grellmann, D. (2002) Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. *Oikos*, **98**, 190-204.
- Hicks Pries, C.E., Schuur, E.A.G., Vogel, J.G. & Natali, S.M. (2013) Moisture drives surface decomposition in thawing tundra. *Journal of Geophysical Research: Biogeosciences*, **118**, 1133-1143.
- Hill, G.B. & Henry, G.H.R. (2011) Responses of High Arctic wet sedge tundra to climate warming since 1980. *Global Change Biology*, **17**, 276-287.
- Hinkel, K.M. & Hurd, J.K. (2006) Permafrost destabilization and thermokarst following snow fence installation, Barrow, Alaska, U.S.A. *Arctic, Antarctic, and Alpine Research*, **38**, 530-539.
- Hinkel, K.M. & Nelson, F.E. (2003) Spatial and temporal patterns of active layer thickness at Circumpolar Active Layer Monitoring (CALM) sites in northern Alaska, 1995-2000. *Journal of Geophysical Research-Atmospheres*, **108**.
- Hinzman, L.D., Bettez, N.D., Bolton, W.R., Chapin, F.S., III, Dyurgerov, M.B., Fastie, C.L., Griffith, B., Hollister, R.D., Hope, A. & Huntington, H.P. (2005) Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic change*, **72**, 251-298.
- Hobbie, S.E. & Chapin, F.S., III (1998) The response of tundra plant biomass, aboveground production, nitrogen, and CO<sub>2</sub> flux to experimental warming. *Ecology*, **79**, 1526-1544.
- IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Jobbágy, E. & Jackson, R. (2001) The distribution of soil nutrients with depth: Global patterns and the imprint of plants. *Biogeochemistry*, **53**, 51-77.
- Jobbágy, E.G. & Jackson, R.B. (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications*, **10**, 423-436.
- Jorgenson, J.C., Raynolds, M.K., Reynolds, J.H. & Benson, A.-M. (2015) Twenty-five year record of changes in plant cover on tundra of northeastern Alaska. *Arctic, Antarctic, and Alpine Research*, **47**, 785-806.
- Keuper, F., Dorrepaal, E., Bodegom, P.M.v., Logtestijn, R.S.P.v., Venhuizen, G., Hal, J.v. & Aerts, R. (2014) Foraging the thaw front: Increased nutrient uptake at the permafrost surface enhances biomass production of deep-rooting subarctic peatland species. Doctor, Vrije Universiteit.
- Keuper, F., van Bodegom, P.M., Dorrepaal, E., Weedon, J.T., van Hal, J., van Logtestijn, R.S.P. & Aerts, R. (2012) A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Global Change Biology*, **18**, 1998-2007.
- Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2014) lmerTest: Tests in Linear Mixed Effects Models. R package version 2.0-20. <http://cran.r-project.org/web/packages/lmerTest/index.html>.
- Leffler, A.J., Klein, E.S., Oberbauer, S.F. & Welker, J.M. (2016) Coupled long-term summer warming and deeper snow alters species composition and stimulates gross primary productivity in tussock tundra. *Oecologia*, 1-11.
- McKane, R.B., Johnson, L.C., Shaver, G.R., Nadelhoffer, K.J., Rastetter, E.B., Fry, B., Giblin, A.E., Kielland, K., Kwiatkowski, B.L., Laundre, J.A. & Murray, G. (2002) Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, **415**, 68-71.
- Mikan, C.J., Schimel, J.P. & Doyle, A.P. (2002) Temperature controls of microbial respiration in arctic tundra soils above and below freezing. *Soil Biology and Biochemistry*, **34**, 1785-1795.
- Myers-Smith, I.H., Forbes, B.C., Wilkening, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.A., Schmidt, N.M., Schaeppman-Strub, G., Wipf, S., Rixen, C., Ménard, C.B.,

- Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E. & Hik, D.S. (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, **6**, 045509.
- Natali, S.M., Schuur, E.A.G. & Rubin, R.L. (2012) Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. *Journal of Ecology*, **100**, 488-498.
- Nauta, A.L., Heijmans, M.M.P.D., Blok, D., Limpens, J., Elberling, B., Gallagher, A., Li, B.X., Petrov, R.E., Maximov, T.C., van Huissteden, J. & Berendse, F. (2015) Permafrost collapse after shrub removal shifts tundra ecosystem to a methane source. *Nature climate change*, **5**, 67-70.
- Newsham, K.K., Upson, R. & Read, D.J. (2009) Mycorrhizas and dark septate root endophytes in polar regions. *Fungal Ecology*, **2**, 10-20.
- Oulehle, F., Rowe, E.C., Myska, O., Chuman, T. & Evans, C.D. (2016) Plant functional type affects nitrogen use efficiency in high-Arctic tundra. *Soil Biology & Biochemistry*, **94**, 19-28.
- Park, H., Kim, Y. & Kimball, J.S. (2016) Widespread permafrost vulnerability and soil active layer increases over the high northern latitudes inferred from satellite remote sensing and process model assessments. *Remote Sensing of Environment*, **175**, 349-358.
- Pearson, R.G., Phillips, S.J., Loranty, M.M., Beck, P.S., Damoulas, T., Knight, S.J. & Goetz, S.J. (2013) Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature climate change*, **3**, 673-677.
- Romanovsky, V.E., Smith, S.L. & Christiansen, H.H. (2010) Permafrost thermal state in the polar Northern Hemisphere during the international polar year 2007–2009: a synthesis. *Permafrost and Periglacial Processes*, **21**, 106-116.
- Schuur, E.A.G., Vogel, J.G., Crummer, K.G., Lee, H., Sickman, J.O. & Osterkamp, T.E. (2009) The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature*, **459**, 556-559.
- Shaver, G. & Chapin, F.S., III (1986) Effect of fertilizer on production and biomass of tussock tundra, Alaska, USA. *Arctic and Alpine Research*, **18**, 261-268.
- Shaver, G.R. & Chapin, F.S., III (1991) Production: biomass relationships and element cycling in contrasting arctic vegetation types. *Ecological Monographs*, **61**, 1-31.
- Shaver, G.R., Johnson, L.C., Cades, D.H., Murray, G., Laundre, J.A., Rastetter, E.B., Nadelhoffer, K.J. & Giblin, A.E. (1998) Biomass and CO<sub>2</sub> flux in wet sedge tundras: responses to nutrients, temperature, and light. *Ecological Monographs*, **68**, 75-97.
- Smith, L., Sheng, Y., MacDonald, G. & Hinzman, L. (2005) Disappearing arctic lakes. *Science*, **308**, 1429-1429.
- Sullivan, P.F. & Welker, J.M. (2005) Warming chambers stimulate early season growth of an arctic sedge: results of a minirhizotron field study. *Oecologia*, **142**, 616-626.
- Tape, K., Sturm, M. & Racine, C. (2006) The evidence for shrub expansion in northern Alaska and the Pan - Arctic. *Global Change Biology*, **12**, 686-702.
- Tarnocai, C., Canadell, J.G., Schuur, E.A.G., Kuhry, P., Mazhitova, G. & Zimov, S. (2009) Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, **23**.
- Verbyla, D. (2008) The greening and browning of Alaska based on 1982–2003 satellite data. *Global Ecology and Biogeography*, **17**, 547-555.
- Wahren, C.H.A., Walker, M.D. & Bret-Harte, M.S. (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, **11**, 537-552.
- Walker, D.A., Jia, G.J., Epstein, H.E., Reynolds, M.K., Chapin, F.S., III, Copass, C., Hinzman, L.D., Knudson, J.A., Maier, H.A., Michaelson, G.J., Nelson, F., Ping, C.L., Romanovsky, V.E. & Shiklomanov, N. (2003) Vegetation-soil-thaw-depth relationships along a low-arctic bioclimate gradient, Alaska: synthesis of information from the ATLAS studies. *Permafrost and Periglacial Processes*, **14**, 103-123.
- Wang, P., Limpens, J., Mommer, L., van Ruijven, J., Nauta, A., Berendse, F., Schaepman-Strub, G., Blok, D., Maximov, T., Heijmans, M. (2016) Data from: Above and belowground responses of four tundra plant functional types to deep soil heating and surface soil fertilization. *Journal of Ecology*. doi:10.5061/dryad.vd129
- Wipf, S. (2010) Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations. *Plant Ecology*, **207**, 53-66.
- Wookey, P.A., Aerts, R., Bardgett, R.D., Baptist, F., Bråthen, K.A., Cornelissen, J.H.C., Gough, L., Hartley, I.P., Hopkins, D.W., Lavorel, S. & Shaver, G.R. (2009) Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology*, **15**, 1153-1172.

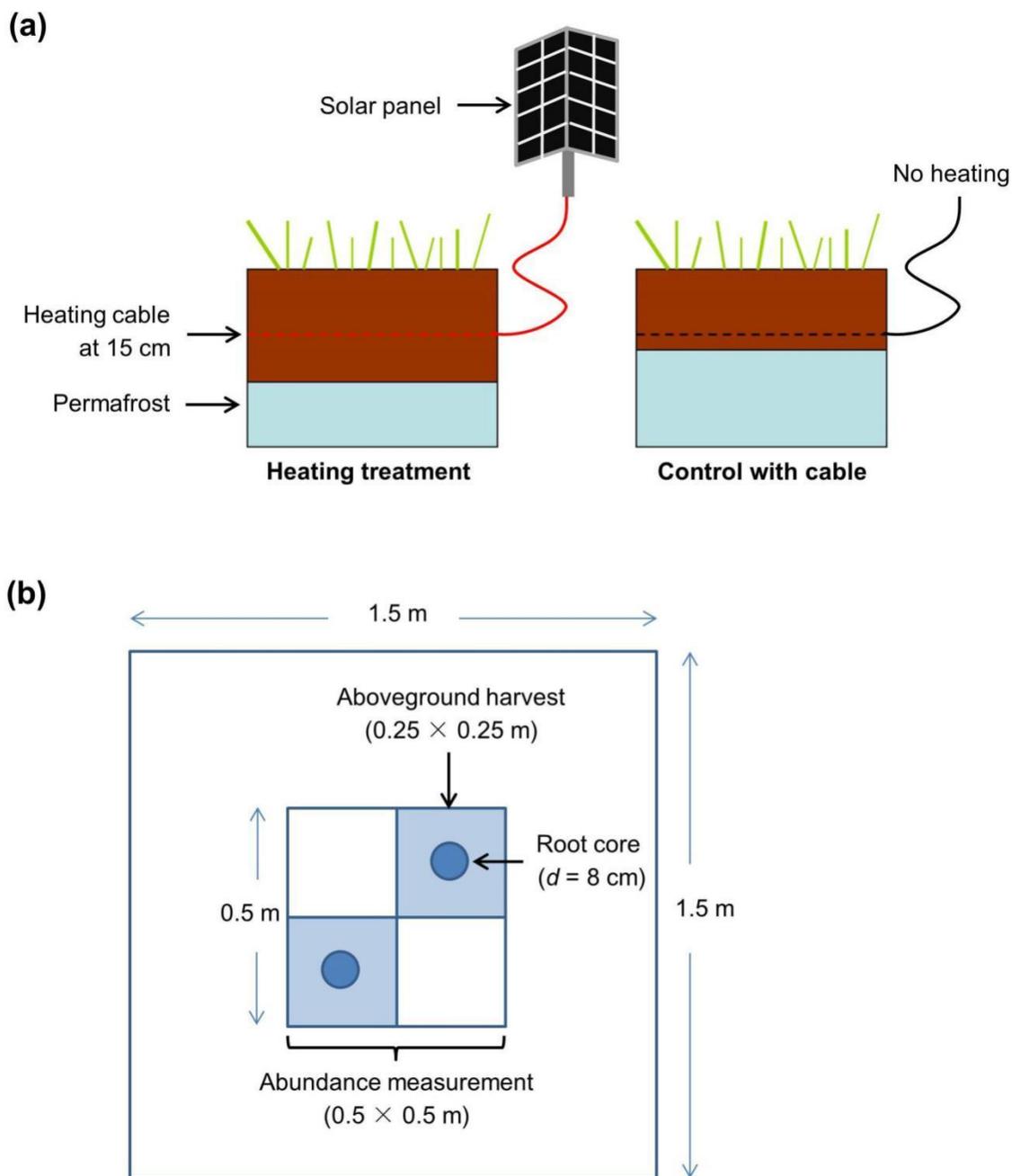


Figure 1. Diagrams showing the set-up of the heating and control treatments (a) and the location of point-quadrat measurements and harvests of above and belowground biomass (b).

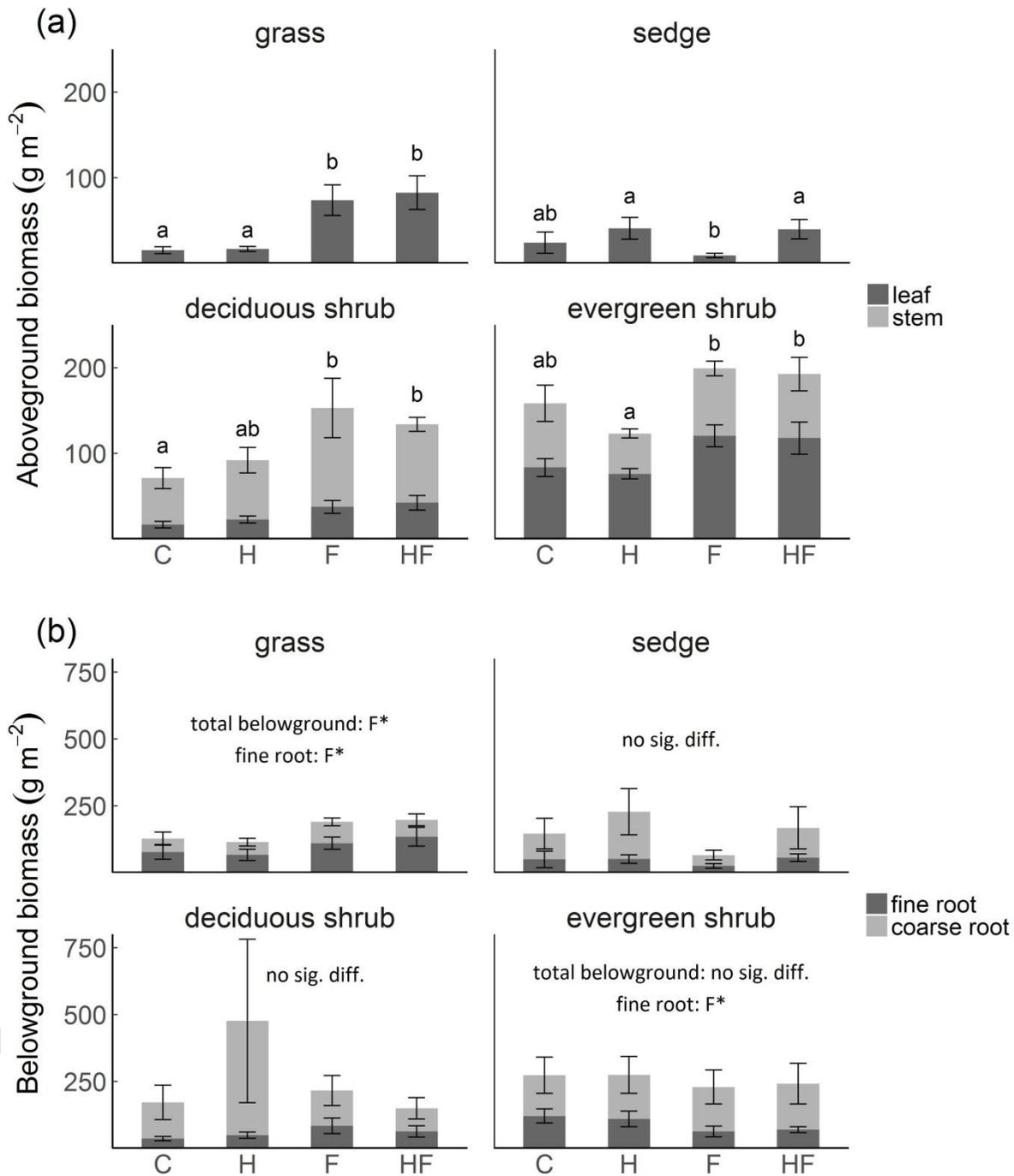
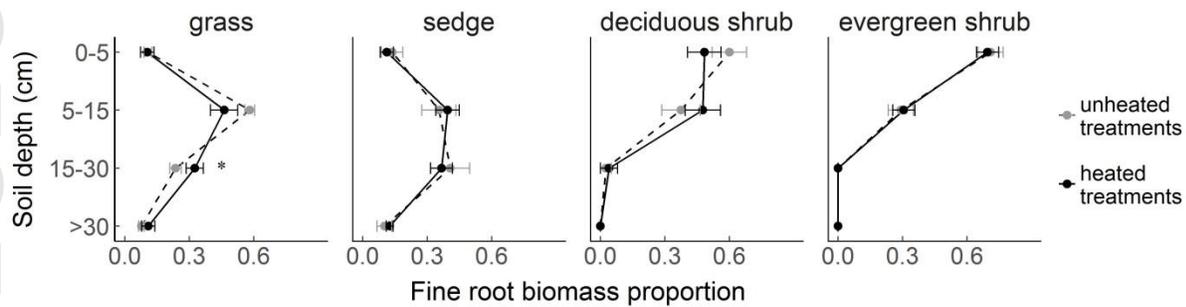


Figure 2. Aboveground (a) and belowground (b) biomass of the four PFTs separated by tissue type. C, control; H, heating treatment; F, fertilization treatment; HF, combined heating and fertilization treatment. Belowground stems (shrubs) and rhizomes (graminoids) were included in the coarse root category. Letters above the bars in Fig. 2a represent pairwise statistical differences in total aboveground biomass. Total belowground biomass did not show significant pairwise differences among treatments while there were some overall fertilization effects.

(a) heating effect



(b) fertilization effect

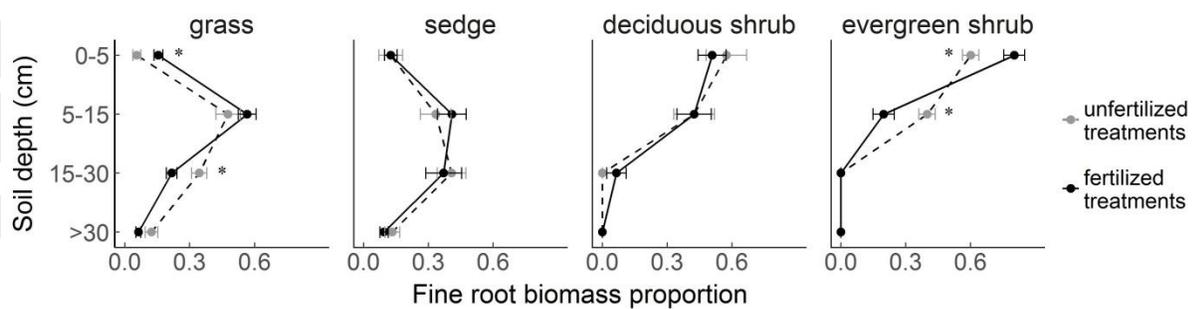


Figure 3. Proportional distribution of fine root biomass over the four soil layers for each PFT in a) the heated and unheated treatments and b) the unfertilized and fertilized treatments. Heating effects and fertilization effects are illustrated separately as there was no significant interaction between the two treatments on the proportional biomass distribution. Unheated treatments include control treatment and fertilization treatment, heated treatments include heating treatment and combined heating and fertilization treatment; unfertilized treatments include control treatment and heating treatment, fertilized treatments include fertilization and combined heating and fertilization treatment. Error bars represent  $\pm$  SE (n = 10 plots). Asterisks indicate significant differences.

Table 1. Analysis of PFT differences in and treatment effects on abundance change, aboveground biomass, belowground biomass, fine root biomass and mean root depth. Biomass data were  $\ln(x+1)$  transformed

Source	df	Abundance change 2010 – 2013		Aboveground biomass		Belowground biomass		Fine root biomass		Mean root depth	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Heating	1	6.3	0.028 *	6.6	0.012 *	0.9	0.345	0.6	0.529	2.2	0.146
Fertilization	1	11.0	0.006 *	21.5	< 0.001 *	< 0.1	0.883	3.3	0.072 .	5.3	0.025 *
PFT	3	8.5	< 0.001 *	67.5	< 0.001 *	4.0	0.012 *	11.0	< 0.001 *	98.4	< 0.001 *
Heating × fertilization	1	0.1	0.769	0.3	0.603	< 0.1	0.900	0.9	0.393	1.8	0.188
Heating × PFT	3	0.3	0.828	4.5	0.007 *	0.2	0.862	0.5	0.826	0.4	0.723
Fertilization × PFT	3	0.7	0.528	10.6	< 0.001 *	0.8	0.510	2.5	0.068 .	3.1	0.035 *
Heating × fertilization × PFT	3	3.0	0.040 *	1.0	0.389	0.4	0.722	0.4	0.881	0.4	0.782

. 0.05 < *P* < 0.10; \* *P* < 0.05

Table 2. Analysis of treatment effects on abundance change, total aboveground, total belowground biomass, fine root biomass and mean root depth of each plant functional type separately. Biomass data were  $\ln(x+1)$  transformed

PFT	Source	df	Abundance change 2010 – 2013		Aboveground biomass		Belowground biomass		Fine root biomass		Mean root depth	
			<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Grass	Heating	1	2.8	0.119	0.5	0.477	0.0	0.888	< 0.1	0.958	2.9	0.107
	Fertilization	1	13.7	0.003 *	46.1	< 0.001 *	4.9	0.046 *	5.2	0.042 *	11.4	0.004 *
	Heating × Fertilization	1	0.1	0.712	< 0.1	0.965	0.0	0.880	0.2	0.670	2.1	0.169
Sedge	Heating	1	3.8	0.074 .	16.3	0.002 *	0.6	0.456	0.7	0.429	0.07	0.799
	Fertilization	1	0.7	0.410	1.5	0.239	0.1	0.802	0.2	0.699	0.6	0.437
	Heating × Fertilization	1	4.0	0.069 .	2.3	0.152	0.1	0.712	0.9	0.359	0.4	0.550
Deciduous shrub	Heating	1	1.6	0.235	0.4	0.533	0.7	0.410	< 0.1	0.942	1.5	0.250
	Fertilization	1	8.7	0.012 *	6.8	0.019 *	0.8	0.385	1.2	0.292	2.3	0.157
	Heating × Fertilization	1	0.1	0.791	0.6	0.452	1.4	0.254	0.6	0.458	0.02	0.872
Evergreen shrub	Heating	1	1.5	0.246	0.6	0.447	0.1	0.761	< 0.1	0.914	0.04	0.837
	Fertilization	1	2.2	0.162	4.8	0.049 *	0.5	0.504	5.2	0.041 *	9.7	0.007 *
	Heating × Fertilization	1	2.3	0.152	0.1	0.767	0.2	0.680	0.6	0.471	0.3	0.578

. 0.05 < *P* < 0.10; \* *P* < 0.05