

Root phenology unresponsive to earlier snowmelt despite advanced above-ground phenology in two subarctic plant communities

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Summary

1. Earlier snowmelt at high latitudes advances above-ground plant phenology, thereby affecting water, nutrient and carbon cycles. Despite the key role of fine roots in these ecosystem processes, phenological responses to earlier snowmelt have never been assessed below-ground.
2. We experimentally advanced snowmelt in two contrasting plant community types (heath and meadow) in northern Sweden and measured above- and below-ground phenology (leaf-out, flowering and fine root growth). We expected earlier snowmelt to advance both above- and below-ground phenology, and shrub-dominated heath to be more responsive than meadow.
3. Snow melted on average 9 days earlier in the manipulated plots than in controls, and soil temperatures were on average 0.9 °C higher during the snowmelt period of 3 weeks. This resulted in small advances in above-ground phenology, but contrary to our expectations, root phenology was unresponsive, with root growth generally starting before leaf-out. These responses to the snowmelt treatment were similar in both plant community types, despite strong differences in dominating plant functional types and root properties, such as root length and turnover.
4. The lack of a response in root phenology, despite warmer soil temperatures and above-ground phenological advances, adds evidence that above-ground plant responses might not be directly translated to below-ground plant responses, and that our understanding of factors driving below-ground phenology is still limited, although of major importance for water, nutrient and carbon cycling.

Key-words: alpine, arctic, climate change, fine roots, phenology, root growth, root production, snowmelt

Introduction

Recent climate change has altered phenology (the timing of recurring life-history events), and has led to an earlier start of the growing season over much of the Northern Hemisphere (Pau *et al.* 2011; Wolkovich *et al.* 2012; Xu *et al.* 2013). The strongest advances have been observed in seasonally snow-covered ecosystems at high latitudes and altitudes (Høye *et al.* 2007), which experience higher than average warming (IPCC 2013), and where the timing of snowmelt is a universally important driver of the start of the growing season and thus plant development (Dunne, Harte & Taylor 2003; Wipf & Rixen 2010; Diez *et al.*

2012; Iler *et al.* 2013; Richardson *et al.* 2013; Bjorkman *et al.* 2015). Changes in plant phenology have been shown to affect plant fitness, reproduction and population dynamics (Cleland *et al.* 2012; Diez *et al.* 2012; Caradonna, Iler & Inouye 2014), and to impact ecosystem processes such as cycles of water, carbon and nutrients (Richardson *et al.* 2013). However, studies on the role of an earlier snowmelt on plant phenology have thus far solely focused on above-ground phenology, despite the widely acknowledged importance of plant roots for many ecosystem processes.

Root dynamics remain one of the least understood aspects of ecosystems (Wookey *et al.* 2009; Smithwick *et al.* 2014; Iversen *et al.* 2015), even though a large portion of plant biomass is situated below-ground (Mokany,

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Raison & Prokushkin 2006) and fine root production and turnover represent around 32% of terrestrial net primary production in boreal forests (Yuan & Chen 2010) and up to 90% in tundra (Iversen *et al.* 2015). Fine roots also play a disproportionately large role in water, carbon and nutrient cycling (Finzi *et al.* 2015; McCormack *et al.* 2015), as they are the plant–soil interface for water and nutrient uptake, and the pathway for photosynthetically fixed carbon into the soil. About 30–50% of all assimilated carbon is allocated below-ground, where it stimulates soil microbial activity both through exudation of 15–25% of the carbon as labile compounds, and via litter inputs of dead roots (Kuzyakov 2002; Schmidt *et al.* 2011). The timing of root production, i.e. root phenology, influences the seasonal uptake of water and nutrients, as well as carbon fluxes to the soil (Nord & Lynch 2009; Schmidt *et al.* 2011; McCormack *et al.* 2014a). Yet, data on root phenology from natural ecosystems remain scarce, particularly so from high latitudes, and the drivers of root phenology are poorly understood (Smithwick *et al.* 2014; Iversen *et al.* 2015; Radville *et al.* 2016).

While most terrestrial biosphere models assume synchronous plant growth above- and below-ground (Smithwick *et al.* 2014; Iversen *et al.* 2015), recent studies indicate that these processes are largely asynchronous in many ecosystems (Abramoff & Finzi 2015), and might be particularly detached in high latitude systems (Blume-Werry *et al.* 2016; Sloan, Fletcher & Phoenix 2016). Assessing changes in root phenology in response to various climate change factors is thus important to enable terrestrial biosphere models to correctly model future ecosystem processes (Smithwick *et al.* 2014; Iversen *et al.* 2015; Warren *et al.* 2015). For example, warmer temperatures early in the season can induce earlier root growth in arctic tundra (Sullivan & Welker 2005) and temperate trees (McCormack *et al.* 2014b). Whether and how root phenology responds to earlier snowmelt, a key factor in high altitude and latitude systems, remains unknown. Since the growing season is short, and the period of snowmelt represents a time of relatively high nutrient availability in these generally nutrient-poor systems (Brooks, Williams & Schmidt 1996; Edwards *et al.* 2006), it seems likely that below-ground phenology will shift in response to snowmelt timing. On the other hand, given the uncertainty concerning controls of root phenology, earlier snowmelt might impact the timing of root growth in unexpected ways.

It is known from above-ground phenology that local responses to earlier snowmelt can differ between plant communities or even single species, despite the overall trend of earlier green-up and earlier flowering (Forrest, Inouye & Thomson 2010; Wipf 2010; Diez *et al.* 2012; Semenchuk, Elberling & Cooper 2013). For example, flowering phenology has been shown to be most responsive to earlier snowmelt in evergreen dwarf shrubs, followed by deciduous dwarf shrubs and forbs, and finally grasses (Wipf & Rixen 2010). Similar differences may prevail below-ground, as plant functional types can differ

in root phenology (Abramoff & Finzi 2015; Iversen *et al.* 2015; Sloan, Fletcher & Phoenix 2016), and evergreen species might be able to supply recent photosynthates for root growth earlier in the season than deciduous ones. In addition, plant functional types might differ in amount and location of stored carbohydrates. In Fennoscandia, heath and meadow communities, differing in both species composition and soil conditions, co-occur at all elevations from subalpine birch forest to high alpine tundra (Sundqvist *et al.* 2011; Milbau *et al.* 2013). Whether and how their phenology responds in a similar way to earlier snowmelt above- and below-ground has not been investigated, although important for future ecosystem functioning.

To better understand how climate change in seasonally snow-covered ecosystems influences phenology, and root phenology in particular, we experimentally advanced snowmelt and measured commonly assessed above-ground phenological parameters (flowering and leaf-out), as well as below-ground phenology (fine root growth) in northern Sweden. We did this in both heath and meadow, which are two co-dominant but contrasting plant communities in subarctic regions.

We hypothesized that (i) earlier snowmelt will advance both above- and below-ground phenology, and (ii) shrub-dominated heath communities will be more responsive to an earlier snowmelt, both above- and below-ground, compared to meadows given the early start of photosynthesis in evergreen dwarf shrubs and their responsiveness to snowmelt in flowering phenology.

Materials and methods

STUDY SITE

The study was carried out at the foot of the east-facing slope of Mount Nuolja, located c. 2 km west of the Abisko Scientific Research Station in northernmost Sweden (68°21' N 18°45' E) at an elevation of c. 400 m a.s.l. The bedrock consists of metagraywacke, phyllite and mica schist (SGU, Sveriges Geologiska Undersökning, www.sgu.se). The site is characterized by a subarctic climate with a mean annual temperature of -0.1 °C, a mean July temperature of 11.6 °C and a mean annual precipitation of 335 mm (all meteorological data are from 1981 to 2010, Abisko Scientific Research Station, 380 m.a.s.l., www.polar.se). Snow cover is usually persistent from early October to late May (Andrews *et al.* 2011). The tree line is at c. 550 m a.s.l., below which there is a very open subalpine birch forest formed by *Betula pubescens* ssp. *czerepanovii* (mountain birch), which is often polycormic (multistemmed) and generally low-growing (2–3 m) (Tømmervik *et al.* 2004). This forest type is widespread in Fennoscandia (Wehberg, Thannheiser & Meier 2005). We conducted our study in two co-dominant but contrasting plant community types in the understorey, namely heath and meadow (see Table S1, Supporting Information for a species list). Heath communities are dominated by evergreen and deciduous dwarf shrubs and have lower plant species richness and diversity than meadows, which are dominated by forbs (Sundqvist *et al.* 2011; Milbau *et al.* 2013). Heath communities are also characterized by low pH and nitrogen availability, whereas meadow communities have higher soil pH and are found in relatively fertile patches

(Björk *et al.* 2007; Sundqvist *et al.* 2011; Milbau *et al.* 2013). From the end of May to mid-July, the sun never sets at the study site.

EXPERIMENTAL DESIGN

Our study design consisted of 28 paired plots, of which half were in each heath and meadow communities and one randomly selected plot per pair received the treatment of earlier snowmelt, resulting in seven replicates per treatment and community type. Sites had similar slopes, aspects, and topography to exclude confounding effects of these factors. Soil temperatures were measured hourly in each plot with iButtons (1-wire Thermochron, DS1921G, Maxim Integrated, San Jose, CA, USA), which were installed at the end of October 2013 at the same depth as root observations, i.e. 10 cm below the surface. From these, we calculated average daily soil temperature values for each plot. We also de-seasonalised the soil temperature data for analysis by subtracting the average daily value from all plots (of both treatments and both vegetation types) from the daily value of each individual plot, such that values above zero indicate a higher than average value and values below zero a lower than average value. This was done to control for the generally increasing soil temperatures over the course of the experiment.

SNOW MANIPULATIONS

We measured snow depth once a week from 7 April 2014 (DOY = 97) onwards until melting accelerated in the beginning of May, thereafter twice a week until snow had melted completely. We reduced the snow cover by accelerating the melting process with a 1.5 × 1.5 m large black fabric (designed for weed control in gardens, Clas Ohlson, Insjön, Sweden) on top of the snow surface, ensuring similar inputs of water and nutrients from the snow on the control and treatment plots. The black fabric was put on the snow surface once the snow depth had decreased to below 70 cm (22nd April, DOY = 112, for the first plots) and was removed when snow depth was below 30 cm to reduce stress by altering light conditions under the snow. The remaining snow was removed by hand, down to the top of the tallest plants and then left to melt naturally.

ABOVE-GROUND PHENOLOGY

We monitored above-ground phenology by recording the furthest phenological stage of each species in the central 1 m² of each plot. Phenology was categorized into three stages: first leaf (unfolding in the case of chamaephytes, emerging from the soil in the case of hemicryptophytes and cryptophytes), maturation of first flower (corolla is open, or stigma is receptive), and senescence of the last flower (petals falling, seeds have begun to develop). We started with these observations when most plots were emerging out of the snow (23 May 2014, DOY = 143), and monitored twice a week until the beginning of July (DOY = 188). Data are presented only for species that occur in >50% of the plots in at least one of the vegetation types. Flower senescence was not included in the data presentation or analyses because this phenological state was only reached in a small subset of species during the duration of our experiment.

BELOW-GROUND PHENOLOGY

We used minirhizotrons to monitor below-ground phenology. These consist of transparent tubes (cellulose acetate butyrate) buried in the soil, and a digital camera system (Bartz Technology Corporation, Carpinteria, CA, USA), with which we took pictures

of the soil interface, including roots. As the position of the camera is fixed with an indexing handle, it is possible to repeatedly observe the same spot. Minirhizotrons thus are a non-destructive method, allowing observations of temporal development of fine roots *in-situ* (Johnson *et al.* 2001). In each of the plots, one 93 cm long tube with 5 cm internal diameter was installed horizontally at 10 cm below the surface at natural steps in the terrain, so that the entrance of the tube was exposed. Tape and a lid on the exposed part prevented light from entering the tubes. Installation took place in August 2011, allowing the vegetation ample time to recover from the disturbance before measurements began on the 9 May 2014 (DOY = 129). On this date, five plot pairs (10 minirhizotrons) were measured, and additional ones were added successively at each measurement time as the snow cover declined, with the full set of 28 minirhizotrons being measured from 26 May onwards (DOY = 146). We measured weekly until the 2 July (DOY = 183), resulting in a total of nine root sampling events.

In each tube, we measured root growth, i.e. elongation of existing roots and the appearance of new roots, between measurement rounds. At the end of the experiment, total root length was measured along the full length of the meadow tubes, and in a randomly selected but constant subset of 10 pictures for each heath tube. The latter corresponds to 23% of observed tube area and was done due to very high root density in the heath community. All root length and growth measurements were done in ROOTFLY version 2.0.2 (Birchfield & Wells, Clemson University, Clemson, SC, USA).

We sampled below-ground phenology less frequently than above-ground phenology, because time intervals of up to 3 weeks have been shown to give robust estimates of root production in different ecosystems, two of which were subarctic and close to our study site (Balogianni, Blume-Werry & Wilson 2016), and our weekly measurements were thus much more frequent than that. Furthermore, since root growth is measured by increments in length over time, it is less sensitive to the frequency of sampling compared to date of leaf-out or flowering.

DATA ANALYSES

All statistics and visualizations were done in R (version 3.2.3) using the packages `LME4` (version 1.1-10), `lmerTest` (version 2.0-29), `sjplot` (version 1.1-0) and `nlme` (version 3.1-122). We tested for differences in snowmelt timing between the treatments, between plant community types and their interactions with a linear mixed effect model with treatment and plant community type as fixed factors and plot pair (block) as random factor (package `nlme`). Differences in de-seasonalised soil temperatures were tested in a similar way.

For above-ground phenology, we analysed when the first leaf was unfolded with a linear mixed effect model with treatment and plant community type as fixed factors and species nested within plot pair as random factor (package `nlme`). We similarly analysed when the first flower was mature. In addition, we also analysed the first leaf and flower phenology for each plant species separately with a linear mixed effect model with treatment as a fixed factor and plot pair as a random factor to see which species were driving the observed pattern. Below-ground phenology (root growth) was analysed with a linear mixed effect model with treatment, plant community type and day of year as fixed factors, and plot pair nested in day of year as random factor to account for repeated measurements (package `LME4`). We did this both for the whole time period of the experiment (13 May–2 July), as well as specifically for the snowmelt period (13 May–2 June). Differences in root length at the end of the experiment were tested for with a linear mixed effect model with treatment and plant community type as fixed factors and plot pair as random factor (package `nlme`). We analysed whether assumptions of normality and

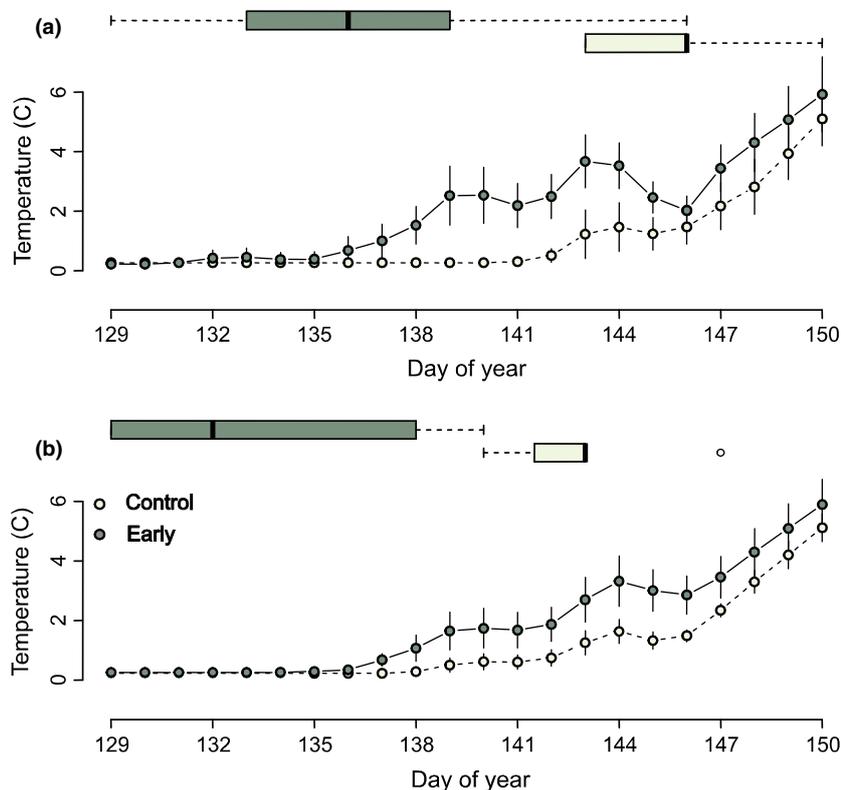


Fig. 1. Day of year of melt-out (boxplots), and soil temperatures (lines and dots) at 10 cm depth in control (light grey boxplots and dots) and early snowmelt (dark grey boxplots and dots) plots during the snowmelt period in (a) heath and (b) meadow communities, $n = 7$, dots are means \pm SE, boxplots show median and whiskers extend to data points 1.5 times the interquartile range from the box. Day of year 135 is 15 May. Weekly root measurements were taken between day of year 129–183.

homogeneity of variance of the residuals were met by examining normal qq-plots and residual vs. fitted plots of the model, respectively. Root length and root growth data were square root-transformed to improve fit.

Results

SNOWMELT TIMING AND SOIL TEMPERATURES

Snow melted around mid-May and on average 9 ± 1.2 days (mean \pm SE) earlier in the manipulated plots compared to the control of the same pair, in both heath and meadow (Fig. 1, Table 1, for snow depth see Fig. S1). Average daily air temperatures during the snowmelt period ranged from -0.6 to 11.7 °C at the Abisko Scientific Research Station, and generally increased towards the end of the snowmelt period. Minimum daily air temperatures regularly dropped below freezing, even towards the end of the snowmelt period, and went as low as -3.2 °C

Table 1. Effect of snowmelt treatment, plant community type (heath or meadow) and their interaction on snowmelt timing and soil temperatures (tested on de-seasonalised values)

Source of variation	Snowmelt		Soil temperatures	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Snowmelt treatment (T)	54.9 _{1,12}	<0.0001	87.0 _{1,556}	<0.0001
Plant community (P)	2.2 _{1,12}	0.17	0.1 _{1,12}	0.76
T \times P	0.0 _{1,12}	0.91	0.1 _{1,556}	0.77

Significant differences in bold, $n = 7$.

(Fig. S2). Soil temperatures at 10 cm depth in our experiment started out at around 0 °C and increased to around 5 °C at the end of the snowmelt period (DOY = 129–150, Fig. 1). During winter, soils either did not freeze due to the insulating snow cover, or only did so during January or February returning to around 0 °C afterwards (data not shown), which is why we did not measure thaw depth. The earlier snowmelt in the manipulated plots increased soil temperatures by 0.9 °C compared to ambient conditions during the snowmelt period of 3 weeks, but soil temperatures were similar between plant community types (all tested on de-seasonalised values, Table 1, Fig. S3).

ABOVE-GROUND PHENOLOGY

The first leaves appeared in the beginning of June (DOY = 152), and were 4 days earlier in the meadow than in the heath communities (Fig. 2a, Table 2). Earlier snowmelt led to a slightly but significantly earlier appearance of the first leaf compared to ambient conditions (1.5 days), and the two plant community types did not differ in their responsiveness to the snowmelt treatment. The maturation of the first flower in mid-June (DOY = 165) did not differ between plant community types (Fig. 2b), but was also slightly (0.5 days), but significantly, earlier with earlier snowmelt. Again, there was no difference in responsiveness to the snowmelt treatment between the plant community types.

Although we found an overall shift in phenology, only a few individual species (of those present in >50% of the

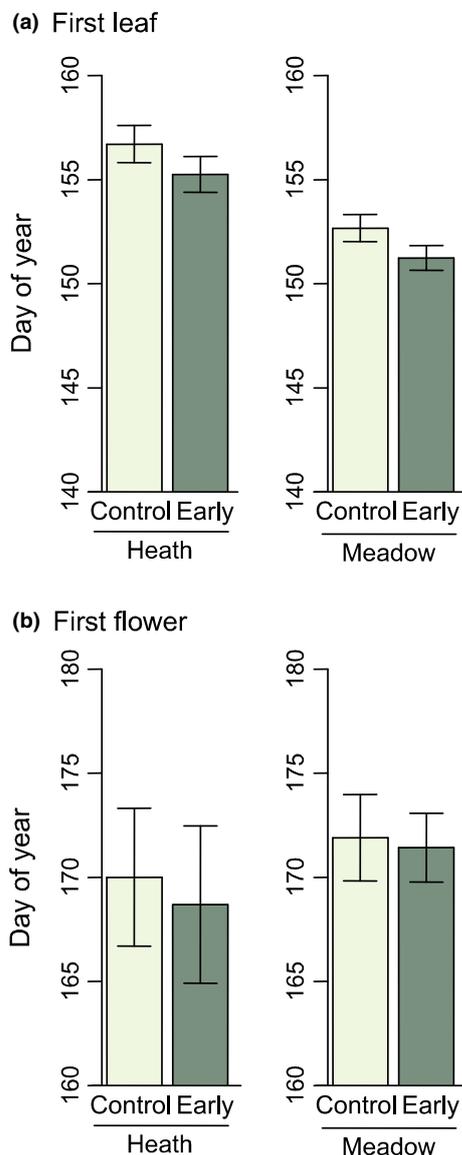


Fig. 2. Day of year at which (a) the first leaves emerged, and (b) the first flowers matured of each present species in control and early snowmelt plots in both heath and meadow communities, $n = 7$, means \pm SE. Day of year 160 is 9 June. Note that mean values and SEs in this figure are calculated across all species of one treatment category, whereas statistical models account for species-specific timing of phenology.

plots in each plant community type), responded to the snowmelt treatments (Table 2). These were four species regarding first leaf emergence (*Empetrum hermaphroditum*, 3 days earlier; *Geranium sylvaticum*, 4 days earlier; *Melampyrum pratense*, 6 days earlier; *Vaccinium vitis-idaea*, 3 days earlier) and four species regarding maturation of the first flower (*E. hermaphroditum*, 6 days earlier; *M. pratense*, 7 days earlier; *Myosotis decumbens*, 5 days earlier; *Vaccinium myrtillus*, 3 days earlier). As half of these species occur in the species-poor heath (cf. Table S1), a larger proportion of heath species advanced their phenology compared to the species-rich meadow. In all cases, above-ground phenology advanced less than snowmelt.

BELOW-GROUND PHENOLOGY

Root growth started with low values in the very beginning of the season and increased significantly over time (Table 3a, Fig. 4), earlier so in meadow than heath, albeit showing large variation. For example, at least 10% of the total observed root growth during the study period had occurred in the period before 19 May (DOY = 139, ambient) and 26 May (DOY = 146, early snowmelt) in meadow and 2 June (DOY = 153, early) and 11 June (DOY = 162, ambient) in heath sites (Fig. 4). The earlier snowmelt did not affect root growth, but total root growth was 5.4 times higher in the meadow communities than in the heath despite the higher root length in the heath communities (total root growth observed during experiment: meadow $39.41 \pm 0.54 \text{ mm cm}^{-2}$, heath $7.35 \pm 0.12 \text{ mm cm}^{-2}$). There were no interactions between day of year, treatment and plant community type (Table 3a, Fig. 4). When we only considered the period of snowmelt (shaded area in Fig. 4), where one would expect the strongest treatment effects, we again did not find any response of root growth to the snowmelt treatment. During this period, root growth did not differ with time, but was again higher in meadow than in heath (Table 3b).

At the end of the experiment, root length per observed surface area was 2.8 times higher in heath than in meadow communities (heath: $50.22 \pm 6.93 \text{ mm cm}^{-2}$, meadow: $17.94 \pm 1.81 \text{ mm cm}^{-2}$; $F = 21.5_{1,12}$, $P < 0.0001$, Fig. 3), but there were no differences between the snowmelt treatments ($F = 0.3_{1,12}$, $P = 0.56$) and no plant community type \times treatment interaction ($F = 0.4_{1,12}$, $P = 0.53$).

Discussion

Our experiment effectively simulated a future climate with earlier snowmelt and increased soil temperatures, as observed and predicted in many high latitude and altitude regions (Dye 2002; Stone *et al.* 2002; Rikiishi, Hashiya & Imai 2004). Assuming similar lapse rates of spring advance as previously observed at our study site (Andrews *et al.* 2011), and generally at high altitudes and latitudes of the Northern Hemisphere (Dye 2002; Rikiishi, Hashiya & Imai 2004), our manipulation of on average 9 days earlier snowmelt corresponds to the advance in snowmelt expected in one or two decades. We found that earlier snowmelt led to an earlier leaf-out and earlier flowering in both heath and meadow communities, but we did not observe a corresponding change in root phenology.

ADVANCED ABOVE-GROUND PHENOLOGY

Earlier snowmelt resulted in earlier leaf-out and earlier flowering in both plant communities. This is consistent with other studies (e.g. Dunne, Harte & Taylor 2003; Wipf, Stoeckli & Bebi 2009; Wipf & Rixen 2010; Iler *et al.* 2013; Khorsand Rosa *et al.* 2015; Gezon, Inouye & Irwin 2016), although the advance in phenology compared to the

Table 2. Effect of snowmelt treatment, plant community type (heath or meadow) and their interaction on emergence of first leaf and maturation of first flower, as well as effect of snowmelt treatment on emergence of first leaf and maturation of first flower on each individual species that was present in >50% of plots (species names and plant functional type are shown)

	Plant functional type	Source of variation	Leaf			Flower		
			<i>n</i> (control, early)	<i>F</i>	<i>P</i>	<i>n</i> (control, early)	<i>F</i>	<i>P</i>
All species		Snowmelt treatment (T)	7,7	16.6 _{1,89}	<0.0001	7,7	5.3 _{1,41}	0.021
		Plant community (P)	7,7	9.8 _{1,12}	0.002	7,7	0.6 _{1,12}	0.444
		T × P	7,7	0.0 _{1,89}	0.862	7,7	0.1 _{1,41}	0.787
<i>Calamagrostis phragmitoides</i> Hartm.	Grass	Snowmelt treatment (T)	5,5	2.6 _{1,3}	0.107	0,2	n.a.	
<i>Carex vaginata</i>	Sedge	Snowmelt treatment (T)	6,6	1.8 _{1,4}	0.182	4,5	0.1 _{1,2}	0.773
<i>Chamerion angustifolium</i> L.	Forb	Snowmelt treatment (T)	5,5	§		0,1	n.a.	
<i>Empetrum hermaphroditum</i> Lange ex Hagerup	Evergreen dwarf shrub	Snowmelt treatment (T)	7,7	14.4 _{1,6}	<0.001	2,3	24.2 _{1,1}	<0.0001
<i>Geranium sylvaticum</i> L.	Forb	Snowmelt treatment (T)	7,7	7.5 _{1,6}	0.006	7,7	0.2 _{1,6}	0.689
<i>Luzula pilosa</i>	Rush	Snowmelt treatment (T)	3,3	1.0 _{1,1}	0.317	4,4	0.1 _{1,2}	0.765
<i>Melampyrum pratense</i> L.	Forb	Snowmelt treatment (T)	5,7	9.6 _{1,4}	0.002	5,7	7.8 _{1,4}	0.005
<i>Myosotis decumbens</i> Host	Forb	Snowmelt treatment (T)	3,5	0.8 _{1,2}	0.357	3,5	4.6 _{1,2}	0.032
<i>Paris quadrifolia</i> L.	Forb	Snowmelt treatment (T)	3,4	§		1,2	n.a.	
<i>Pyrola minor</i> L.	Forb	Snowmelt treatment (T)	4,4	0.2 _{1,2}	0.672	0,1	n.a.	
<i>Rubus saxatilis</i> L.	Forb	Snowmelt treatment (T)	3,5	§		1,2	n.a.	
<i>Solidago virgaurea</i> Praecox	Forb	Snowmelt treatment (T)	6,3	§		0,0	n.a.	
<i>Stellaria nemorum</i> L.	Forb	Snowmelt treatment (T)	3,4	0.7 _{1,2}	0.410	3,3	0.0 _{1,2}	0.929
<i>Trientalis europaea</i> L.	Forb	Snowmelt treatment (T)	4,7	§		4,7	0.6 _{1,3}	0.430
<i>Vaccinium myrtillus</i> L.	Deciduous dwarf shrub	Snowmelt treatment (T)	8,7	1.9 _{1,6}	0.169	4,3	4.3 _{1,1}	0.038
<i>Vaccinium vitis-idaea</i> L.	Evergreen dwarf shrub	Snowmelt treatment (T)	13,11	10.5 _{1,10}	0.001	6,6	0.1 _{1,4}	0.820
<i>Valeriana sambucifolia</i> ssp. <i>Procurrens</i> (Wallr.) Á. Löve	Forb	Snowmelt treatment (T)	5,4	0.0 _{1,3}	0.885	0,0	n.a.	

'n.a.' depicts cases with three or less observations in total and thus no ANOVA results, whereas '§' depicts cases with too little variation for ANOVA thus showing no treatment effect. Significant differences in bold.

Table 3. Effect of snowmelt treatment (early snowmelt or control), plant community type (heath or meadow), day of year as well as their interactions on root growth during a) the whole experiment and b) during the snowmelt period

a) During the whole experiment			b) During snowmelt period		
Source of variation	<i>F</i>	<i>P</i>	Source of variation	<i>F</i>	<i>P</i>
Snowmelt treatment (T)	0.0 _{1,91}	0.825	Snowmelt treatment (T)	0.2 _{1,35}	0.683
Plant community (P)	77.9 _{1,87}	<0.0001	Plant community (P)	30.4 _{1,35}	<0.0001
Day of year (DOY)	27.5 _{1,7}	0.001	Day of year (DOY)	5.3 _{1,2}	0.135
T × P	0.0 _{1,91}	0.855	T × P	0.2 _{1,35}	0.662
T × DOY	0.2 _{1,92}	0.623	T × DOY	0.1 _{1,35}	0.706
P × DOY	0.4 _{1,89}	0.537	P × DOY	1.6 _{1,35}	0.214
T × P × DOY	0.2 _{1,92}	0.627	T × P × DOY	0.1 _{1,35}	0.780

Significant differences in bold, root growth was square root-transformed, *n* = 7.

advance in snowmelt was less than in some other cases (e.g. Wipf & Rixen 2010; Iler *et al.* 2013; Gezon, Inouye & Irwin 2016). In addition to advancing snowmelt, our treatment also warmed soils, two factors that have previously been shown to explain most variation in above-ground plant phenology (Dunne, Harte & Taylor 2003). In line with previous findings (Wipf & Rixen 2010), not all species tracked the advance in snowmelt with their phenology. Furthermore, relatively more species advanced their phenology in heath than in meadow, which indicates a

stronger dependence of the former to snowmelt timing and potentially a better adaptation to variation in climate. Interspecific differences in phenological change can reduce fitness of some species and thus change species' abundance and distribution (Cleland *et al.* 2012), co-flowering patterns (CaraDonna, Iler & Inouye 2014), trophic interactions (Høye *et al.* 2013), and the ability to adapt to novel climatic conditions (Diez *et al.* 2012). In addition to these potential consequences for species interactions, changes in phenology also influence the microclimate (such as

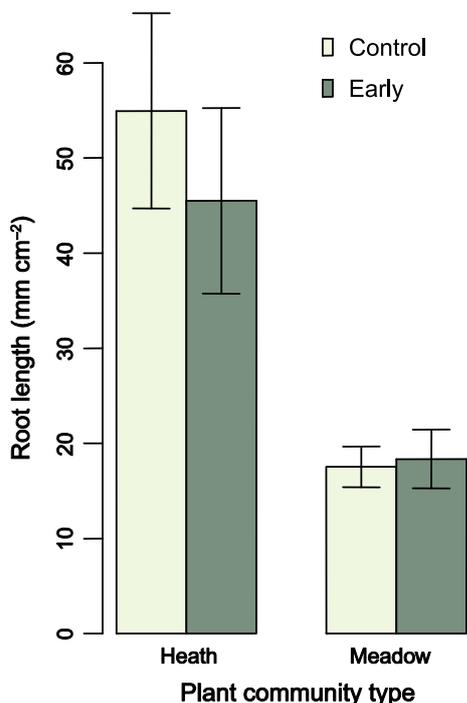


Fig. 3. Root length per observed area in control (light grey bars) and early snowmelt (dark grey bars) plots in heath and meadow communities, $n = 7$, means \pm SE.

temperature, humidity, soil moisture, radiation), and feedback to the climate system (Richardson *et al.* 2013). These feedbacks are manifested through changes in albedo, surface roughness, canopy conductance, photosynthesis and respiration, water and nutrient uptake. For example, evapotranspiration increases and atmospheric carbon dioxide decreases at leaf-out, and an earlier leaf-out increases net carbon uptake per growing season (Richardson *et al.* 2013).

UNRESPONSIVE ROOT PHENOLOGY

As expected, there was very little root growth at the onset of our study, followed by a rapid increase in root growth in the second half of May and early June, when soil temperatures slowly started to rise but were still close to zero. Root growth generally increased as spring progressed, more rapidly so in the meadow. Contrary to our expectations, however, advanced snowmelt did not change root phenology.

Both endogenous and exogenous factors have been suggested as drivers of root phenology and it has been pointed out that their roles might differ between ecosystems or even species, balancing competitive needs for water and nutrients with internal carbon allocation (Abramoff & Finzi 2015; Radville *et al.* 2016). The lack of an effect of earlier snowmelt on root phenology, despite advances in above-ground phenology and increases in soil temperature of 0.9 °C, further emphasizes the question of which cues drive below-ground phenology in general, and specifically

initiate root growth in spring. The general paucity of studies that track root growth over the season and simultaneously measure an array of biotic and abiotic factors makes this a difficult question to answer. Our data did not support soil temperature as a general cue for the timing or amount of root growth, given that the treatment warmed soils without affecting root phenology. The generally observed correlation of soil temperatures with root growth in seasonal environments (Abramoff & Finzi 2015; Radville *et al.* 2016) might be a result of the inclusion of the winter season with very limited root growth and low soil temperatures, and thus co-incident (see also Sloan, Fletcher & Phoenix 2016).

If the initiation of root growth depends on within-plant signalling and availability of recent photosynthates (Farrar & Jones 2000), one would expect above- and below-ground phenology to be tightly coupled in spring or root growth to lag behind leaf-out. An earlier leaf-out with earlier snowmelt would then support higher amounts of root growth early in the season. This should be especially pronounced in heath communities, where a large amount of evergreen species can photosynthesize immediately at snowmelt. However, our minirhizotron observations with unusually high temporal resolution show that earlier snowmelt and earlier leaf-out did not translate into earlier or higher amounts of root growth, in either meadow or heath communities. As in most root growth studies in natural ecosystems, the data showed high variation. While this could potentially mask responses to a treatment, there was no evidence of that in this study. Interestingly, root growth started very early: before average leaf-out in both plant communities, more pronounced so in meadow communities. It has been previously shown that root growth can start, or even peak, before leaf-out (McCormack *et al.* 2014b). The early start of root growth also rules out the possibility that the absence of a response to the snowmelt manipulation was caused by the difference in methods of recording phenological events above- and below-ground, more precisely leaf-out and flowering as distinct events per plot, and root growth as the average increment per plot. As many plots showed some small amounts of root growth in the first week that we measured, albeit insignificant amounts compared to later measurements, we did not compare the first appearance of root growth between early and ambient snowmelt. In the meadow communities, significant root growth occurred before melt-out of the control plots (Figs 1b and 4). Our results thus support mounting evidence that significant amounts of root growth can occur outside of the photosynthetically active period (see also McCormack *et al.* 2014b; Blume-Werry *et al.* 2016; Sloan, Fletcher & Phoenix 2016), urging a decoupling of those processes in terrestrial biosphere models.

Our study showed no plot-level effect of root growth at the observed depth in response to a moderate advance in snowmelt. As we observed root growth at the plot level, it is possible that some species advanced their root growth in

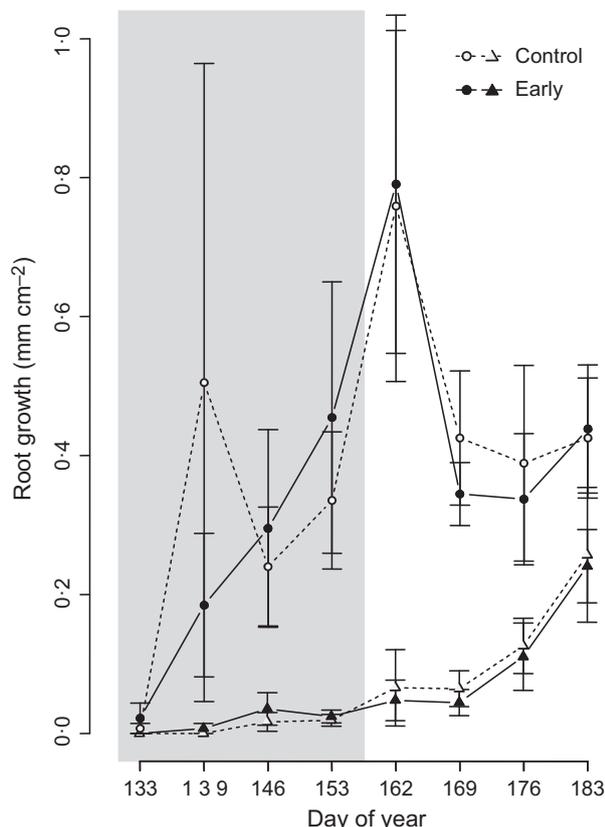


Fig. 4. Root growth per observed area in control (light grey symbols, dashed lines) and early snowmelt (dark grey symbols, solid lines) plots in heath (triangles) and meadow (dots) communities, $n = 7$, means \pm SE. Each symbol represents the amount of root growth leading up to that date between two sampling occasions. Shaded area indicates the sampling occasions that were included for analyses of root growth during snowmelt. Day of year 135 is 15 May and day of year 166 is 15 June.

response to earlier snowmelt whereas others delayed it, resulting in no net change. If indeed root phenology remains stable in the future despite advances in snowmelt and higher soil temperatures in spring, this could potentially lead to a mismatch between available resources (such as nutrients and water) and plant uptake, and maybe even restrict how much above-ground phenology can advance. If, on the other hand, single species do change their root phenology, whereas the majority of them do not, those species could benefit from this strategy, which in turn could modify competitiveness between species, similar to changes in above-ground phenology.

A more extreme snowmelt manipulation might have led to a change in root phenology, but we were interested in responses to near-term climate changes. An advantage of these rather moderate snow manipulations with passive advancement of snowmelt is that other abiotic conditions, such as temperature and soil moisture, vary in accordance. For example, shovelling away snow early in spring can lead to snow-free conditions in air temperatures that would not have been sufficient to melt snow or uncharacteristically alter soil moisture content and might thus lead

to atypical plant responses in contrast to the passive advancement used here.

In general, the very early start of root growth, before soil temperatures had risen considerably and before leaf-out, suggests that root growth starts early in spring regardless of snowmelt conditions and the system is thus still adapted to the earliest possible start of root growth. This suggests that pre-emption of soil resources may offer competitive advantages, making plants invest stored energy to roots early in the season to enhance later growth and that climate warming-induced higher soil temperatures in spring do not change this pattern.

CONSISTENTLY SIMILAR RESPONSES TO EARLIER SNOWMELT IN CONTRASTING VEGETATION TYPES

Even though a higher proportion of the species present advanced their above-ground phenology in heath than meadow, the overall above- and below-ground responses to earlier snowmelt did not differ between the plant communities, contrary to our expectations. The communities, however, differed greatly both in above-ground and below-ground properties. The dwarf shrub-dominated, species-poor heath had a several times higher root length than the species-rich, forb and graminoid-dominated meadow. In contrast, root growth was more than twice as high in the meadow, showing that fine root turnover is higher. It has been proposed that species or plant communities with high root turnover experience substantial root mortality in fall, leading to few roots in spring which is compensated by rapid growth in large amounts during spring (McCormack *et al.* 2014a). This pattern seems to be well reflected here. Similarly, Sloan, Fletcher & Phoenix (2016) observed limited root growth early in the season in shrub-dominated compared to sedge-dominated communities.

The differences in below-ground properties of the two plant communities correspond to differences in above-ground properties, pointing towards differences in whole-plant strategies for growth and turnover (Freschet *et al.* 2013; Sloan *et al.* 2013). Plants of meadow communities have little overwintering tissue, thus high turnover, and rapid growth in spring, whereas plants of heath communities have many woody structures that overwinter, and turnover only a small fraction of their biomass.

Conclusions and future outlook

Earlier snowmelt and concomitant higher soil temperatures advanced leaf-out and flowering phenology in two contrasting plant communities of the subarctic, further underlining the importance of snowmelt in influencing above-ground phenology. However, no similar response was seen in root growth phenology in either of the plant communities, even though both higher soil temperatures and availability of recent photosynthates have previously been suggested as important drivers of root phenology.

This raises important new research questions: What, if not the steep rise in soil temperatures and earlier availability of recent photosynthates, initiates root growth in spring? Is early root growth an inherent feature of communities growing in places with a short growing season, or present in a variety of ecosystems? Can these patterns be generalized to other seasonally snow-covered ecosystems, as suggested by the similar response of heath and meadow in our study? We are only at the beginning of uncovering root phenological responses to a changing climate, and more studies are needed to shed light on these important but notoriously difficult responses. Importantly, our findings show that above-ground responses might not be directly translated to below-ground responses, and we thus need to consider other factors to expand our understanding of what drives below-ground phenology, which is paramount given its importance in ecosystem cycles of water, nutrients and carbon.

Authors' contributions

G.B.W. and A.M. designed the study, G.B.W. performed field work and analysed the data with input from R.J. and A.M. G.B.W. wrote the manuscript with contributions from A.M. and R.J.

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Data accessibility

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.21bg6> (Blume-Werry, Jansson & Milbau 2017).

References

- Abramoff, R.Z. & Finzi, A.C. (2015) Are above- and below-ground phenology in sync? *New Phytologist*, **205**, 1054–1061.
- Andrews, C., Dick, J., Jonasson, C. & Callaghan, T. (2011) Assessment of biological and environmental phenology at a landscape level from 30 years of fixed-date repeat photography in northern Sweden. *Ambio*, **40**, 600–609.
- Balogianni, V.G., Blume-Werry, G. & Wilson, S.D. (2016) Root production in contrasting ecosystems: the impact of rhizotron sampling frequency. *Plant Ecology*, **11**, 1359–1367.
- Björk, R.G., Klemedtsson, L., Molau, U., Harndorf, J., Ödman, A. & Giesler, R. (2007) Linkages between N turnover and plant community structure in a tundra landscape. *Plant and Soil*, **294**, 247–261.
- Bjorkman, A.D., Elmendorf, S.C., Beamish, A.L., Vellend, M. & Henry, G.H.R. (2015) Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. *Global Change Biology*, **21**, 4651–4661.
- Blume-Werry, G., Jansson, R. & Milbau, A. (2017) Data from: Root phenology unresponsive to earlier snowmelt despite advanced aboveground phenology in two subarctic plant communities. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.21bg6>.
- Blume-Werry, G., Wilson, S.D., Kreyling, J. & Milbau, A. (2016) The hidden season: growing season is 50% longer below than above ground along an arctic elevation gradient. *New Phytologist*, **209**, 978–986.
- Brooks, P.D., Williams, M.W. & Schmidt, S.K. (1996) Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. *Biogeochemistry*, **32**, 93–113.
- CaraDonna, P.J., Iler, A.M. & Inouye, D.W. (2014) Shifts in flowering phenology reshape a subalpine plant community. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 4916–4921.
- Cleland, E., Allen, J., Crimmins, T., Dunne, J., Pau, S., Travers, S.E., Zavaleta, E.S. & Wolkovich, E.M. (2012) Phenological tracking enables positive species responses to climate change. *Ecology*, **93**, 1765–1771.
- Diez, J.M., Ibáñez, I., Miller-Rushing, A.J., Mazer, S.J., Crimmins, T.M., Crimmins, M.A., Bertelsen, C.D. & Inouye, D.W. (2012) Forecasting phenology: from species variability to community patterns. *Ecology Letters*, **15**, 545–553.
- Dunne, J.A., Harte, J. & Taylor, K.J. (2003) Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. *Ecological Monographs*, **73**, 69–86.
- Dye, D.G. (2002) Variability and trends in the annual snow-cover cycle in Northern Hemisphere land areas, 1972–2000. *Hydrological Processes*, **16**, 3065–3077.
- Edwards, K.A., McCulloch, J., Kershaw, G.P. & Jefferies, R.L. (2006) Soil microbial and nutrient dynamics in a wet Arctic sedge meadow in late winter and early spring. *Soil Biology and Biochemistry*, **38**, 2843–2851.
- Farrar, J.F. & Jones, D.L. (2000) The control of carbon acquisition by roots. *New Phytologist*, **147**, 43–53.
- Finzi, A.C., Abramoff, R.Z., Spiller, K.S., Brzostek, E.R., Darby, B.A., Kramer, M.A. & Phillips, R.P. (2015) Rhizosphere processes are quantitatively important components of terrestrial carbon and nutrient cycles. *Global Change Biology*, **21**, 2082–2094.
- Forrest, J., Inouye, D.W. & Thomson, J.D. (2010) Flowering phenology in subalpine meadows: does climate variation influence community co-flowering patterns? *Ecology*, **91**, 431–440.
- Freschet, G.T., Cornwell, W.K., Wardle, D.A. *et al.* (2013) Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide. *Journal of Ecology*, **101**, 943–952.
- Gezon, Z.J., Inouye, D.W. & Irwin, R.E. (2016) Phenological change in a spring ephemeral: implications for pollination and plant reproduction. *Global Change Biology*, **22**, 1779–1793.
- Høye, T.T., Post, E., Meltøfte, H., Schmidt, N.M. & Forchhammer, M.C. (2007) Rapid advancement of spring in the High Arctic. *Current Biology*, **17**, 449–451.
- Høye, T.T., Post, E., Schmidt, N.M., Trøjelsgaard, K. & Forchhammer, M.C. (2013) Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nature Climate Change*, **3**, 759–763.
- Iler, A.M., Høye, T.T., Inouye, D.W. & Schmidt, N.M. (2013) Nonlinear flowering responses to climate: are species approaching their limits of phenological change? *Philosophical Transactions of the Royal Society B*, **368**, 20120489.
- IPCC. (2013) Chapter 11. Near-term climate change: projections and predictability. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds T.F. Stocker, D. Qin, G.-K. Plattner *et al.*), pp. 953–1028. Cambridge University Press, Cambridge, UK and New York, NY, USA.
- Iversen, C., Sloan, V., Sullivan, P.F., Euskirchen, E.S., McGuire, A.D., Norby, R.J., Walker, A.P., Warren, J. & Wullschlegel, S.D. (2015) The unseen iceberg: plant roots in arctic tundra. *New Phytologist*, **205**, 34–58.
- Johnson, M.G., Tingey, D.T., Phillips, D.L. & Storm, M.J. (2001) Advancing fine root research with minirhizotrons. *Environmental Botany*, **45**, 263–289.
- Khorsand Rosa, R., Oberbauer, S.F., Starr, G., Parker La Puma, I., Pop, E., Ahlquist, L. & Baldwin, T. (2015) Plant phenological responses to a long-term experimental extension of growing season and soil warming in the tussock tundra of Alaska. *Global Change Biology*, **21**, 4520–4532.
- Kuzakov, Y. (2002) Review: factors affecting rhizosphere priming effects. *Journal of Plant Nutrition and Soil Science*, **165**, 382–396.
- McCormack, M.L., Adams, T.S., Smithwick, E.A.H. & Eissenstat, D.M. (2014a) Variability in root production, phenology, and turnover rate among 12 temperate tree species. *Ecology*, **95**, 2224–2235.
- McCormack, M.L., Gaines, K.P., Pastore, M. & Eissenstat, D.M. (2014b) Early season root production in relation to leaf production among six diverse temperate tree species. *Plant and Soil*, **389**, 121–129.

- McCormack, M.L., Dickie, I.A., Eissenstat, D.M. *et al.* (2015) Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist*, **207**, 505–518.
- Milbau, A., Shevtsova, A., Osler, N., Mooshammer, M. & Graae, B.J. (2013) Plant community type and small-scale disturbances, but not altitude, influence the invasibility in subarctic ecosystems. *New Phytologist*, **197**, 1002–1011.
- Mokany, K., Raison, R.J. & Prokushkin, A.S. (2006) Critical analysis of root : shoot ratios in terrestrial biomes. *Global Change Biology*, **12**, 84–96.
- Nord, E.A. & Lynch, J.P. (2009) Plant phenology: a critical controller of soil resource acquisition. *Journal of Experimental Botany*, **60**, 1927–1937.
- Pau, S., Wolkovich, E.M., Cook, B.I., Davies, T.J., Kraft, N.J.B., Bolmgren, K., Betancourt, J.L. & Cleland, E.E. (2011) Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology*, **17**, 3633–3643.
- Radville, L., McCormack, M.L., Post, E. & Eissenstat, D.M. (2016) Root phenology in a changing climate. *Journal of Experimental Botany*, **67**, 3617–3628.
- Richardson, A.D., Keenan, T.F., Migliavacca, M., Ryu, Y., Sonnentag, O. & Toomey, M. (2013) Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, **169**, 156–173.
- Rikiishi, K., Hashiya, E. & Imai, M. (2004) Linear trends of the length of snow-cover season in the Northern Hemisphere as observed by the satellites in the period 1972–2000. *Annals of Glaciology*, **38**, 229–237.
- Schmidt, M.W.I., Torn, M.S., Abiven, S. *et al.* (2011) Persistence of soil organic matter as an ecosystem property. *Nature*, **478**, 49–56.
- Semenchuk, P.R., Elberling, B. & Cooper, E.J. (2013) Snow cover and extreme winter warming events control flower abundance of some, but not all species in high arctic Svalbard. *Ecology and Evolution*, **3**, 2586–2599.
- Sloan, V.L., Fletcher, B.J. & Phoenix, G.K. (2016) Contrasting synchrony in root and leaf phenology across multiple sub-Arctic plant communities. *Journal of Ecology*, **104**, 239–248.
- Sloan, V.L., Fletcher, B.J., Press, M.C., Williams, M. & Phoenix, G.K. (2013) Leaf and fine root carbon stocks and turnover are coupled across Arctic ecosystems. *Global Change Biology*, **19**, 3668–3676.
- Smithwick, E.A.H., Lucash, M.S., McCormack, M.L. & Sivandran, G. (2014) Improving the representation of roots in terrestrial models. *Ecological Modelling*, **291**, 193–204.
- Stone, R.S., Dutton, E.G., Harris, J.M. & Longenecker, D. (2002) Earlier spring snowmelt in northern Alaska as an indicator of climate change. *Journal of Geophysical Research*, **107**, 1–13.
- 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.
- Sundqvist, M.K., Giesler, R., Graae, B.J., Wallander, H., Fogelberg, E. & Wardle, D.A. (2011) Interactive effects of vegetation type and elevation on aboveground and belowground properties in a subarctic tundra. *Oikos*, **120**, 128–142.
- Tømmervik, H., Johansen, B., Tombre, I., Thannheiser, D., Høgda, K.A., Gaare, E. & Wielgolaski, F.E. (2004) Vegetation changes in the Nordic mountain birch forest: the influence of grazing and climate change. *Arctic, Antarctic and Alpine Research*, **36**, 323–332.
- Warren, J., Hanson, P., Iversen, C.M., Kumar, J., Walker, A.P. & Wulschleger, S.D. (2015) Root structural and functional dynamics in terrestrial biosphere models—evaluation and recommendations. *New Phytologist*, **205**, 59–78.
- Wehberg, J., Thannheiser, D. & Meier, K.-D. (2005) Vegetation of the Mountain Birch Forest in Northern Fennoscandia. *Plant Ecology, Herbivory, and Human Impact in Nordic Mountain Birch Forests* (ed F.E. Wielgolaski), pp. 35–52. Springer-Verlag, Berlin, Germany.
- Wipf, S. (2010) Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations. *Plant Ecology*, **207**, 53–66.
- Wipf, S. & Rixen, C. (2010) A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Research*, **29**, 95–109.
- Wipf, S., Stoeckli, V. & Bebi, P. (2009) Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climatic Change*, **94**, 105–121.
- Wolkovich, E.M., Cook, B.I., Allen, J.M. *et al.* (2012) Warming experiments underpredict plant phenological responses to climate change. *Nature*, **485**, 494–497.
- Wookey, P.A., Aerts, R., Bardgett, R.D. *et al.* (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.
- Xu, L., Myneni, R.B., Chapin, F.S. III *et al.* (2013) Temperature and vegetation seasonality diminishment over northern lands. *Nature Climate Change*, **3**, 581–586.
- Yuan, Z.Y. & Chen, H. (2010) Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and meta-analyses. *Critical Reviews in Plant Sciences*, **29**, 204–221.

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Snow depth in control and early snowmelt treatments during snowmelt period.

Fig. S2. Average, minimum and maximum daily air temperatures at the Abisko Scientific Research Station.

Fig. S3. De-seasonalised soil temperatures (temperature deviations) at 10 cm depth during the snowmelt period.

Table S1. List of all species present in heath and meadow plots, and the day of year of leaf-out and flowering under ambient conditions.