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Root phenology in an Arctic shrub-graminoid community: the effects of long-term warming and herbivore exclusion

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Abstract

Background: Shifts in phenology have been widely reported in response to global warming and have strong effects on ecosystem processes and greenhouse gas emissions. It is well documented that warming generally advances many phenophases of aboveground plant phenology, but its influence on root phenology is unclear. Most terrestrial biosphere models assume that root and shoot growth occur at the same time and are influenced by warming in the same manner, but recent studies suggest that this may not be the case. Testing this assumption is particularly important in the Arctic where over 70 % of plant biomass can be belowground and warming is happening faster than in other ecosystems. Herbivory may mediate the impacts of warming, and carbon removal from grazing may alter carbon available for root growth. In 2013 and 2014 we examined the timing of root growth in Arctic shrub-graminoid communities in a fully factorial design of plots that were warmed or ambient and excluded or permitted access by large herbivores.

Results: Peak root growth occurred two and one half weeks before leaf growth, suggesting that spring root phenology is not controlled by carbon produced during spring photosynthesis. This may uncouple spring root phenology from spring shoot phenology. Consistent with such uncoupling, spring leaf cover was advanced by warming and delayed by herbivory, but neither treatment significantly affected root phenology. Root growth was not driven by soil temperature, and occurred in near-freezing temperatures above the permafrost. Additionally, summer root production appeared to be linked to soil moisture at this relatively dry site, and autumn phenology was not driven by photoperiod as previous studies have suggested.

Conclusions: Root phenology was not directly driven by temperature in this system, promoting differential above- and belowground phenological responses to warming and herbivore exclusion. Aboveground phenology, one of the most widely measured aspects of climate change, may not represent whole-plant phenology or indicate the timing of whole-plant carbon fluxes as commonly assumed.

Keywords: Root phenology, Arctic, Climate change, Herbivory

Background

The timing of plant phenology is important to ecosystem function, species interactions, and patterns of carbon exchange [1–4]. Shifts in plant phenology are one of the more sensitive indicators of climate change and have been widely reported in response to climate change. For example, spring phenology has advanced by about

2.5 days per decade in Europe with recent warming [5]. While temperature may be the most important environmental factor controlling the timing of aboveground growth [6], the effects of warming on belowground phenology are not well understood.

These impacts are particularly important in the Arctic, where over 70 % of biomass can be belowground and warming is occurring at twice the global rate [7, 8]. In the Arctic, impacts of climate change may be more pronounced than in other regions [9, 10]. The Arctic is important both as a sink for carbon dioxide and as a source of methane, but the total effect of warming on

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future carbon cycling in the Arctic is unclear [11]. Currently, several studies have documented aboveground advances in phenology in the Arctic [12–17], but they do not account for belowground growth.

We currently do not have clear understanding of how factors such as temperature, moisture, and day length impact root phenology, and this limits understanding of how warming will impact whole-plant phenology. Because root phenology and soil temperature are correlated [18–20], increased temperatures should promote higher rates of root production [21], reduced root lifespan [22], and an extended root growing season [23]. However, studies that failed to find a correlation between root phenology and soil temperature suggest that endogenous factors, such as photosynthate availability, may be more important to root phenology [24–26]. Soil moisture may also be important, because, according to at least one study, fine root growth increases exponentially with increasing soil water content [27]. Although the influence of endogenous and exogenous factors on root phenology is unclear, it is likely that both control root production to some extent [20, 25]. Accurate predictions of whole-plant responses to global warming require a better understanding of the biotic and abiotic factors that control root phenology. Current climate models assume root and shoot growth are synchronous and controlled by the same factors, but this may not be the case [28, 29].

We also have a poor understanding of the relationship between above- and belowground growth and how the relationship is affected by warming. Most climate models include root carbon allocation as a fixed, synchronous fraction of aboveground carbon, but, in many ecosystems, root growth is asynchronous with shoot growth. With decreasing annual temperatures, some studies show a greater asynchrony between root and shoot growth, with root growth occurring much later than shoot growth [28]. For example, in woody plants in the sub-Arctic, root growth peaked about a month later than leaf growth [30]. Above- and belowground phenology may be linked, however, as root and leaf turnover are positively correlated in a variety of arctic communities [31]. The link between above- and belowground growth is important to understand in regions that experience seasonal herbivory, such as arctic regions exposed to migratory caribou (*Rangifer tarandus*) populations. Through removal of aboveground biomass, herbivores may reduce carbon available for root growth and may mediate root responses to climate change. The influence of herbivory on root growth varies across ecosystems, and herbivory may mitigate the effects of warming on plant community composition [32]. By examining the influence of herbivory, we can examine how natural removal of aboveground biomass, or of herbivore

mediation of interspecific interactions among plants, affects the timing of root growth.

In 2013 and 2014 we examined the influence of warming and herbivory on the timing of root and shoot growth in an arctic system and evaluated environmental controls on these, including soil temperature, soil moisture, and photoperiod. We examined the influence of soil temperature on root phenology at different soil depths throughout the season. We also characterized the relationship between above- and belowground phenology, particularly in response to both warming by open-top chambers and herbivory by large mammals. Minirhizotrons were used to non-destructively evaluate the timing of root growth. This study took place near Kangerlussuaq, Greenland, where mixed-vegetation plots have experienced a warmed/unwarmed treatment (with open-top chambers) and herbivore absence/presence (with fences) for 13 years [33]. We hypothesized that warming would advance both above- and belowground growth, and herbivory would reduce aboveground growth and delay belowground growth. We also hypothesized that above- and belowground phenology would be offset, with root growth occurring after shoot growth, as observed in previous studies [19, 28].

Methods

Experimental site and design

This study took place in low shrub tundra near Kangerlussuaq, Greenland (67.11°N, 50.37°W). This site is on dry acidic tundra on noncarbonated bedrock in Arctic shrub-tundra [34]. The vegetation community is characterized by patches of deciduous shrubs, primarily *Salix glauca* and *Betula nana*, and graminoid species, such as *Poa pratensis* and *Carex* spp. This is a permafrost ecosystem, and the average active layer depth at a nearby site was 63 cm between May and August in 2014 [35], and there is a mossy organic layer in all plots. The mean annual air temperature was -4.1 C in 2013 and -4.5 C in 2014.

In 2013 and 2014, we measured root phenology and aboveground phenology in 24 long-term study plots in a fully factorial design of warming by herbivory. Warming has been achieved with open-top chambers seasonally since 2003 and large herbivores [muskoxyen (*Ovibus moschatus*) and caribou (*Rangifer tarandus*)] have been excluded with fences since 2002 ($N=6$ per warming/herbivore exclusion treatment). The 1.5-m-wide open-top chambers were constructed following ITEX protocols [36] and were placed on the plots from May–July each year. Minirhizotrons, clear, hollow tubes used to follow seasonal root growth, were installed in two of the three 800 m² experimental herbivore enclosures, so these enclosures were utilized in this study. The study site and

experimental design have been described in detail in previous publications [32].

Root phenology

One minirhizotron tube was installed in each plot in July 2005. Minirhizotron tubes were clear acrylic tubes buried at a 30-degree angle to the vertical and anchored into the soil with steel rods. Tubes were insulated with foam tubing, and each minirhizotron tube was sealed with a plumbing plug. The aboveground portion of the tube was wrapped with electrical tape, painted white, and covered with a white, aluminum cover to exclude light and prevent solar radiative heating. A minirhizotron camera (Bartz Technology Corporation, CA USA) was lowered into the tube, and images of the roots were taken at 1.3 cm depth intervals along the tube. From May to August 2013 and May to September 2014 we photographed tubes weekly in the shoulder seasons, when rapid changes in growth occurred, and less frequently in mid-season, when change was slow. Ice obscured the view of roots in several images, so these were excluded. Root production and root standing crop were tracked through the season by tracing images of roots with Rootfly software (Clemson University, Clemson SC). This program determines the length of roots growing against tubes on each date. Root length was divided by area of the tube visible in the image to get standing crop (cm roots · cm⁻² viewing surface). To calculate root production, only the length of new root initiation and elongation occurring between two consecutive dates was divided by viewing surface area, which was then divided by the number of days since the previous measurement (cm roots · cm⁻² viewing surface · day⁻¹). In order to examine the influence of depth on the timing of root growth, roots were further separated into categories according to the soil depth at which roots were produced (1–10 cm, 11–20 cm, 21–30 cm, and 31–40 cm).

Abiotic conditions

We measured mid-day (between 11 am and 1 pm) soil moisture and temperature in all plots on each date that root images were obtained. Soil temperature was measured with a thermocouple placed at 5 cm below the organic layer in 2013, and 5- and 10 cm below it in 2014. The organic layer thickness (approximately 5 cm) and mineral soil physical and chemical properties were similar among plots. In both years, soil moisture was measured with a TDR (time domain reflectometry) waveguide placed from 0 to 10 cm below the organic layer. Continuous meteorological measurements, including air temperature (°C, 2 m above soil surface), precipitation (mm), soil temperature (°C, 0.1, 0.2, and 0.3 m below soil organic layer), and volumetric soil water content (0.1 m below soil organic layer) were collected

hourly at a weather station located within the study site using a CR-1000 datalogger, in place since 2008. Day length was calculated for each day using sunrise and sunset times for Kangerlussuaq, Greenland. Soil temperature was averaged hourly at 10, 20, and 30 cm below the organic layer using copper-constantan thermocouples. In order to estimate maximum daily soil temperature at each of these depths in the study plots, we used estimation techniques from Campbell and Norman [37]. Data from the weather station were used to determine the monthly damping depth for these soils (Damping depth = (depth 1 – depth 2)/[ln(amplitude of temperature at depth 2) – ln(amplitude of temperature at depth 1)]), where depth 1 was 10 cm and depth 2 was 20 cm). The amplitude of temperature variation in each plot was estimated as the difference between the measured soil temperature and the average seasonal air temperature. The relationship between the daily observed maximum temperature and daily soil temperature at 11 am was determined from the weather station data for all three depths. Once the temperature at each depth at 11 am was determined, these regression relationships were used to estimate the maximum daily soil temperature at each depth in each plot.

Aboveground phenology

We used NDVI (normalized difference vegetation index) to estimate the relative area in each plot covered by photosynthetically active vegetation. In this study, $NDVI = (R_{800} - R_{660}) / (R_{800} + R_{660})$, where R_{800} is the reflectance at 800 nm, and represents a near-infrared wavelength, while R_{660} is reflectance at 660 nm and represents a photosynthetically active wavelength (as in [38]). NDVI was determined from measurements of incident and reflected light obtained with a Unispec-DC (PP Systems, Haverhill, MA USA). The spectrometer records radiance from 300 to 1100 nm. The Unispec-DC was centered 2 m above each plot and had a measurement footprint of 0.39 m². Measurements were obtained on each day root images were taken, and three measurements were averaged over each plot. At the beginning of each day, the Unispec-DC was calibrated with a white standard to account for daily light conditions.

Statistical analyses

To examine the timing of root production and to remove noise associated with high variation among plots in absolute root production, data were normalized to the maximum value for that plot during that year. For example, the proportion of maximum root production on a given date is calculated by: root production on that date divided by maximum cumulative root production occurring in that plot during that year. The proportion of maximum NDVI and the proportion of maximum root standing crop for each plot were obtained in the

same way. The date of peak root production for each plot was measured as the date of maximum root production over the previous sampling date in each year. The date of peak NDVI was the date at which the maximum vegetation cover occurred in each plot and in each year. In plots where the vegetation cover reached a maximum amount and remained at this value, the date of peak NDVI was recorded as the first date that reached this maximum value.

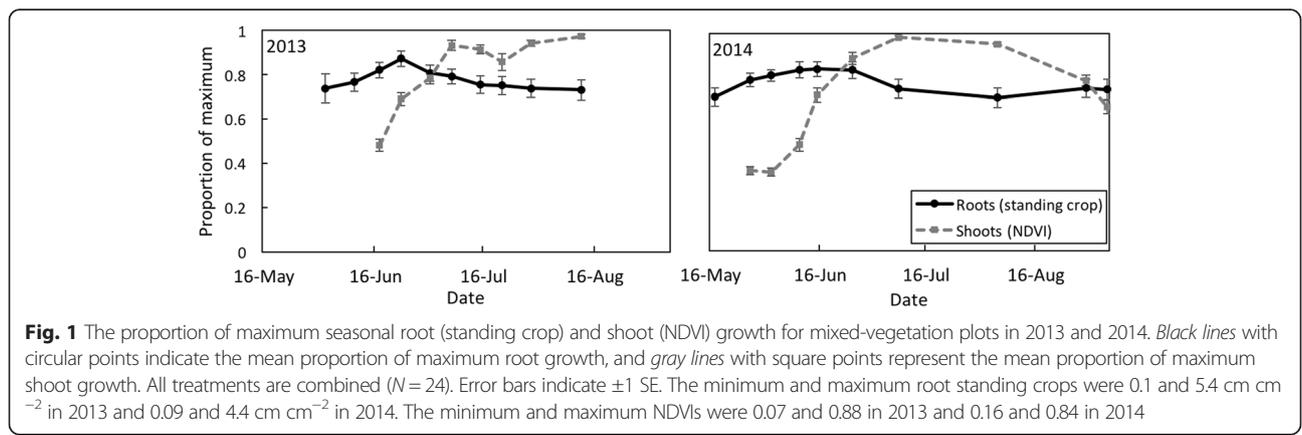
To examine seasonal differences between treatments in volumetric soil water content, soil temperature, proportion of maximum root production, proportion of maximum root standing crop, and NDVI, each of these variables was analyzed with a mixed model using time, treatment, and time*treatment as fixed effects. Plot nested within date was included as a random effect in order to account for non-independence of plots measured repeatedly through time. Non-normally distributed variables were transformed with a Box-Cox transformation [39]. To examine correlations between root growth and abiotic factors, we used Pearson product-moment correlations to compare the daily proportion of maximum root production, soil temperature, soil moisture, Julian date, day length, and NDVI. All analyses were performed in SAS JMP Pro 10.0.2 (2012, Cary, NC)

The percent graminoid cover in each plot was used as a covariate in all analyses of NDVI because NDVI was significantly different among vegetation types. Forty-two percent of plots had greater than 50 % cover of *Betula nana*, and these plots had an average NDVI of 0.64 ± 0.02 (SE). Twenty-five percent of plots had greater than 50 % cover of *Salix glauca*, and these had an NDVI of 0.61 ± 0.04 (mean \pm SE). Sixteen percent of plots were dominated by graminoids, and these had an NDVI of 0.49 ± 0.04 (mean \pm SE). The percent of graminoid cover in each plot was also used as a covariate in analysis of the herbivore enclosure treatment because vegetation type was significantly different inside and outside the enclosures (Post and Pedersen 2008). Inside the

herbivore enclosures, 2.5 ± 1 % (mean \pm SE) of each plot was composed of graminoids, but 40 ± 6 % (mean \pm SE) of each plot outside the enclosure was graminoid-covered. Graminoid cover was not a significant factor for the warming treatment. Average graminoid cover in warmed plots was 24 ± 5.6 % (SE), and average graminoid cover in ambient plots was 19 ± 4.6 % (SE).

Results

The timing of root growth was asynchronous with that of shoots (Fig. 1). Contrary to some studies, such as Blume-Werry et al. in the Arctic [29], but in accordance with other studies, such as McCormack et al. in a temperature ecosystem [40], root growth preceded shoot growth. Peak root standing crop occurred 18 days earlier than peak aboveground cover. Both root production and root standing crop peaked on July 3 (Julian date 184 ± 5 ; mean \pm SE), and leaf cover peaked on July 21 (Julian date 202 ± 3). The dates of peak root standing crop, peak root production, and peak vegetation cover did not differ by warming or enclosure treatments (Fig. 2, Additional file 1: Table S1). There was high variation around the peak root production that may have masked treatment differences, as ambient plots peaked on day 180 ± 28 (SD) and warmed plots peaked on day 188 ± 35 (SD). The average total root production was 1.9 ± 0.3 cm cm⁻² (\pm SE) in 2013 and 2.1 ± 0.2 cm cm⁻² (\pm SE) in 2014. The maximum standing crop was 5.4 cm cm⁻² in 2013 and 4.4 cm cm⁻² in 2014. Neither warming nor herbivore enclosure significantly changed the timing of maximum root standing crop across the whole season (Fig. 2; Additional file 1: Table S1). Variation was high among plots and this may have masked treatment differences. All treatments followed the general trend in Fig. 1, with root production preceding the majority of shoot production. In support of the asynchrony between leaf and root phenology, daily root production was negatively correlated with leaf cover (Table 1).



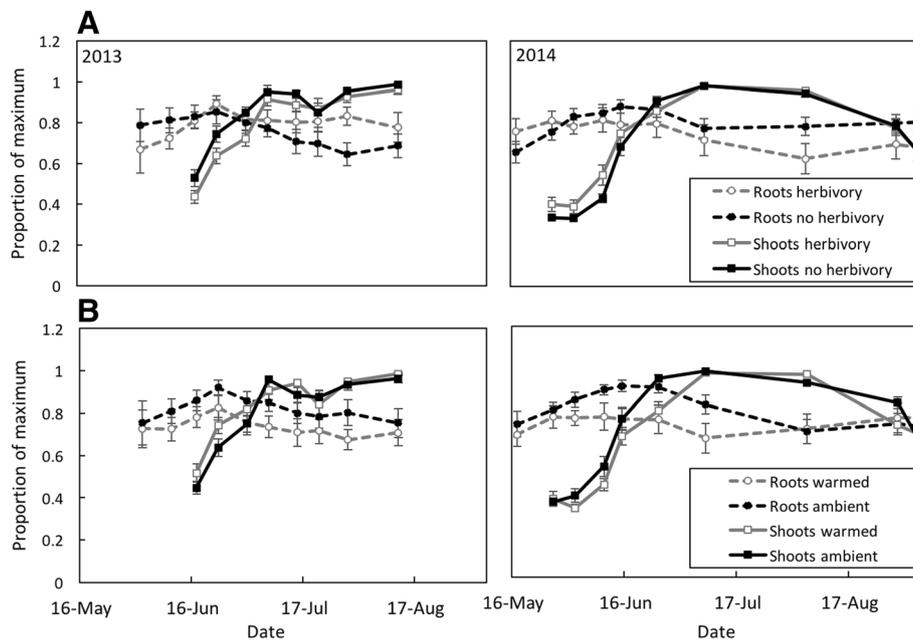


Fig. 2 The proportion of maximum seasonal root (standing crop) and shoot (NDVI; leaf cover) growth for mixed-vegetation plots in 2013 and 2014, separated by warming and exclusion treatments. **a** Proportion maximum shoot and root growth in 2013 and 2014, separated by exclusion treatment with warming treatments combined. *Black dashed lines* with closed circles indicate root standing crop with no herbivory, *gray dashed lines* with open circles are root standing crop with herbivory, *gray solid lines* with open squares are NDVI with herbivory, and *black solid lines* with closed squares are NDVI without herbivory. The timing of leaf cover was significantly different between plots with and without herbivory, but the timing of root standing crop was not. **b** Proportion maximum shoot and root growth in 2013 and 2014, separated by warming treatment with exclusion treatments combined. *Black dashed lines* with closed circles indicate ambient root standing crop, *gray dashed lines* with open circles are warmed root standing crop, *gray solid lines* with open squares are warmed NDVI, and *black solid lines* with closed squares are ambient NDVI. The timing of leaf cover was significantly different between warmed and unwarmed plots, but the timing of root standing crop was not. Sample size (N) was 12 for each of the two treatments (Error bars indicate ± 1 SE)

Both treatments altered the timing of seasonal leaf production, measured as a proportion of the maximum yearly leaf cover (Fig. 2, Additional file 1: Table S1), although the direction of change differed between years. The amounts of absolute leaf cover (the NDVI values without converting to proportions) differed between treatments in consistent ways. Warmed plots had more vegetation cover early in the season (June 17 to July 1 in 2013 and May 26 to June 15 in 2014; 2013: $F_{1,55} = 39.4$, $p < 0.001$; 2014: $F_{1,88} = 11.3$, $p = 0.001$). Herbivory reduced early-season leaf cover in both years (2013: $F_{1,55} = 3.3$, $p = 0.08$; 2014: $F_{1,70} = 4.5$, $p = 0.04$).

Contrary to a previous study of autumn phenology in *Dupontia fischeri* and *Eriophorum angustifolium*, conducted in the Arctic using phytotrons in the field and in

the laboratory [41], root growth did not appear to be constrained by day length. Root growth per day ($\text{cm cm}^{-2} \text{ day}^{-1}$) over the last three dates of the season (July 29 to August 12 in 2013 and August 5 to September 5 in 2014) did not decrease as day length decreased (Table 1). Also, root production per day increased at the end of the season in both years (Fig. 3), and root production per hour daylight ($\text{cm cm}^{-2} \text{ hr daylight}^{-1}$) did not change at the end of 2013 and increased at the end of 2014 (2013: $F_{2,68} = 1.1$, $p = 0.34$; 2014: $F_{2,69} = 12.4$, $p < 0.001$). If day length constrained root production, we would expect root production per day to decrease over this interval. We did not find evidence for a lagged effect of day length on root growth, because daily root production was uncorrelated with day length at the previous measurement (Spearman's $\rho = -0.064$, $p = 0.45$).

Table 1 Correlations (Spearman's ρ) with daily root production ($\text{cm cm}^{-2} \text{ day}^{-1}$). End of season represents July 29 to August 12 in 2013 and August 5 to September 5 in 2014

Duration	NDVI	Soil water content	Soil temperature	Day length	Julian day
Whole season	-0.37 ***	0.26 **	-0.067 (ns)	0.30 ***	-0.11 *
End of season	-0.13 (ns)	0.16 (ns)	0.0079 (ns)	-0.062 (ns)	0.062 (ns)

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = not significant

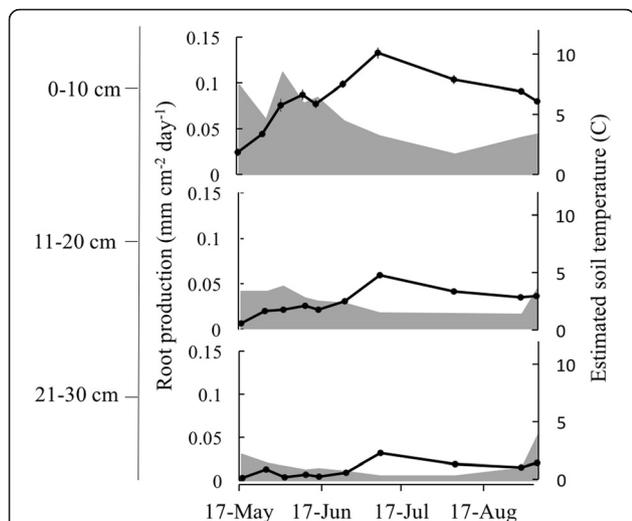


Fig. 3 Grey area on left y-axis represents mean daily new root production (cm cm⁻² day⁻¹) in mixed-vegetation plots in 2014, separated by soil depth. The date of peak root production was June 2 in 2014 and the average total root production from May 17 to September 5 2014 was 2.1 ± 0.2 cm cm⁻² (±SE). The black line on the right y-axis is the estimated soil temperature for each depth. Error bars indicate ±1 SE. All treatments are combined (N = 24). Top row represent roots 1 to 10 cm below soil organic layer, second row represents roots 11–20 cm below soil organic layer, and bottom row represents roots 21–30 cm below soil organic layer. Figure is adapted from Radville et al. [55]

Root phenology did not appear to track temperature in this cold environment. Root production was, instead, positively correlated with soil water content (Table 1). Although soil temperature and soil water content were negatively correlated (Spearman’s $\rho = -0.29$, $p < 0.001$), soil temperature alone was not correlated with root production (Table 1). The modeled maximum soil temperature was significantly colder deeper in the soil and deeper soil warmed more slowly throughout the season (Fig. 3, Additional file 1: Table S1, $p < 0.001$), but root phenology was not significantly different among soil depths (Additional file 1: Table S1, $p = 0.16$).

Neither warming nor the herbivore exclosure treatment significantly affected soil water content or soil temperature (Additional file 1: Table S1). Soil moisture was highest at the first sampling date of the season, immediately after snowmelt, and reached a low in late July. In 2014, when measurements were taken into September, we observed a slight increase in soil moisture in late August and early September (Fig. 4a). Soil temperature at 10 cm below the organic layer was close to 0 °C in late May and reached a maximum of about 8–10 °C in late July in both years (Fig. 4b). The period May - September, 2013, was cooler and wetter than the same period in 2014: on average air temperature in 2013 was 4.8 °C ± 0.1 (±SE) with 104.1 mm ± 0.003 total precipitation and air temperature in 2014 was 7.3 °C ± 0.1 with 74.2 mm ± 0.003 total precipitation.

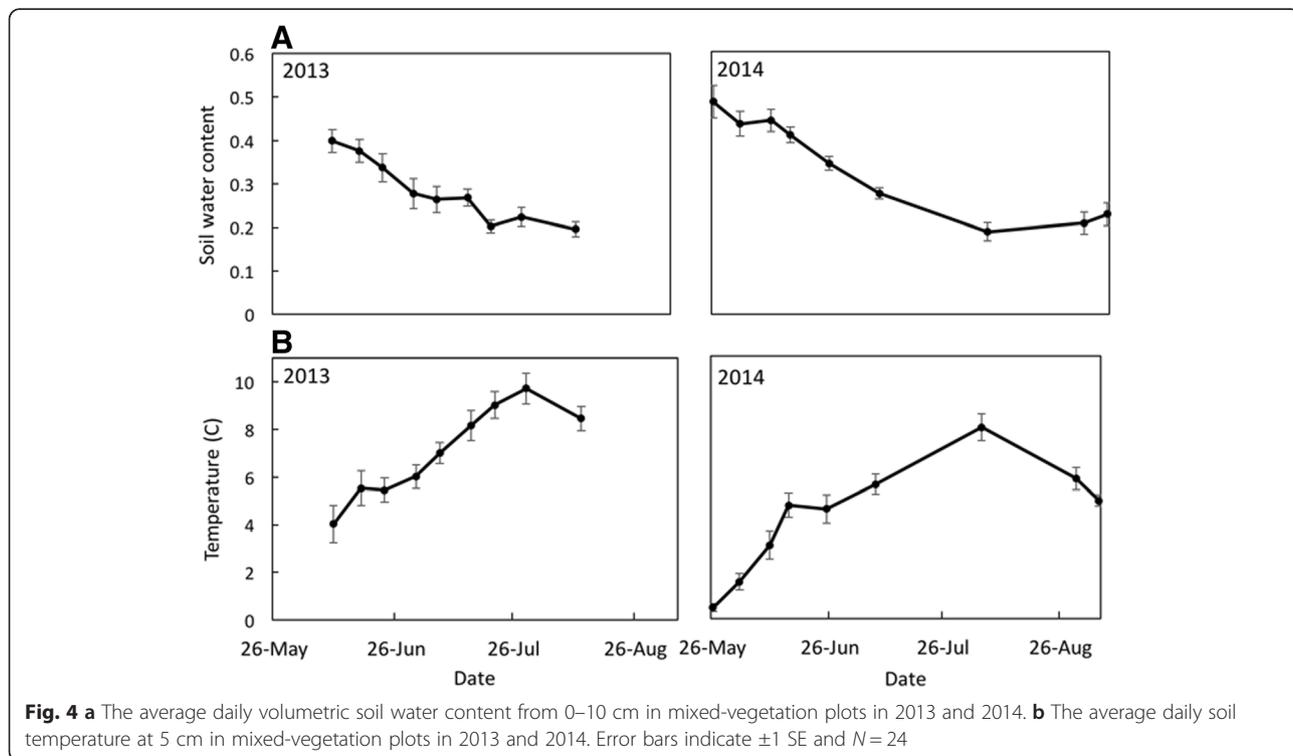


Fig. 4 a The average daily volumetric soil water content from 0–10 cm in mixed-vegetation plots in 2013 and 2014. **b** The average daily soil temperature at 5 cm in mixed-vegetation plots in 2013 and 2014. Error bars indicate ±1 SE and N=24

Discussion

In this highly seasonal environment, soil temperature was not correlated with root phenology. If root growth were solely, or even primarily, limited by temperature, we would expect shallow roots to commence growth before deep roots because soils warm more slowly in deep soil layers. We did not see this trend, and deeper roots grew very early in the season even though estimated maximum temperatures were only slightly above 0 °C (Fig. 3). Other studies in the Arctic have also documented root growth at soil temperatures of 1–2 °C [41–43]. Shaver and Billings [41] suggested that temperatures above 0 °C may not be limiting to cold-adapted species, and hypothesized that other factors, such as soil nutrients, may be more limiting. Sullivan et al. [44] suggest that soil nutrient availability may be more important than growing season temperatures in limiting growth of arctic plants [44]. We did not directly measure soil nutrients, but nutrient availability and mineralization in the Arctic are directly related to water availability and movement [45]. Although soil temperature may limit root phenology in some ecosystems [19], our results suggest that other factors, such as soil moisture, were likely of primary importance in controlling root phenology at this site. Temperature may be a secondary or weak control on root phenology in species that are adapted to cope with extreme temperatures.

Previous experimental evidence indicated that late season Arctic root growth is controlled by photoperiod in some species [41], but we found that late season root growth did not decrease with decreasing day lengths (Table 1). In wet tussock tundra, Shaver and Billings (1977) suggested that in species with annual roots, photoperiod may cue remobilization of carbohydrates aboveground before soil freezes. In dry tundra species of this study, where many roots are perennial, it may be more important to slightly increase root production in late fall to prepare roots for the spring pulse of water and nutrients. Factors that control root production in the Arctic, such as photoperiod, may differ between ecosystems and species and may depend on limiting conditions at each site.

Leaf and root phenology were asynchronous, and peak root growth occurred 18 days before peak leaf cover (Fig. 1). These results appear to be in opposition to patterns documented in a meta-analysis in which peak root growth followed that of shoot growth by 48 days in the boreal zone [28]. Some of this discrepancy could be due to the use of alternate methods of papers comprising the basis of that meta-analysis (such as sequential coring, as opposed to nondestructive minirhizotrons). Alternatively, root phenology in different ecosystems may be adapted to occur when conditions are most favorable for nutrient and water acquisition. We reported a positive correlation between root growth and soil moisture,

suggesting that soil water content was a strong constraint on root production. In this dry, nutrient-limited system, soil moisture is highest in early spring, presumably coincident with the timing of snowmelt. It may be most advantageous to proliferate roots when the soil is moist and nutrients are mobile, particularly in arctic ecosystems where nitrogen availability is highly seasonal [46]. In other ecosystems with seasonal constraints on water availability, root growth initiates quickly during periods of high rainfall [47] and slows or ceases entirely during dry periods [48, 49]. Although we did not directly examine seasonal nutrient availability, it is likely linked to water availability. These results suggest that root phenology may differ widely between ecosystems as roots proliferate during the most favorable periods of the year. These differences may be most apparent in temperature-limited ecosystems, such as the Arctic, where the short growing season requires root phenology to occur during the brief window of favorable conditions.

The asynchrony between root and shoot phenology suggests that above- and belowground organs are either controlled by different biotic and abiotic factors, or that they compete for carbon-use. A carbon trade-off between roots and shoots has been found in other systems, in which carbon is allocated to leaf and root growth at different times of the year due to constraints on carbon availability (e.g. [50]). In support of a carbon trade-off between root and shoot growth, the two were negatively correlated throughout the season (Table 1). This correlation could not be uncoupled from other factors that also varied throughout the season, however, and may be confounded with periods of high soil moisture. Because roots and shoots differ in the timing of carbon use, they are likely influenced differently by the environment. Warmer spring temperatures, for example, may not influence root phenology if spring root phenology is not driven by temperature or leaf carbon production.

Because root production occurs before leaf photosynthate production, root growth was probably fueled by stored carbohydrates rather than by current photosynthate production, as has been noted in other species [51]. In accordance with this assumption, warming and herbivore exclusion altered the timing of spring leaf cover but not the timing of root standing crop or production (Fig. 2, Additional file 1: Table S1). Although both treatments altered aboveground phenology, belowground phenology may have been timed to coincide with early-season water availability and was not driven by photosynthate availability. The second flush of root growth in late fall may be a means of acquiring nutrients that become available in newly fallen leaf litter as well as an adaptation to prepare roots for the pulse of nutrients in early spring. Although these plants seem capable of

root growth at least at near-freezing temperatures, they may be mechanically unable to grow in completely frozen soil.

These results may be ecosystem-specific, because other studies in the Arctic found that experimental warming increased root production [52] and advanced root growth [53]. This study was conducted in a much drier environment than prior studies, so our results suggest that water availability and potentially nutrient availability may be stronger drivers of root growth in dry Arctic tundra. Another explanation for these results is that high spatial and interannual variability in root growth masked the effect of treatment on root phenology in this study. For example, the average date of peak root growth differed by 8.6 days between warming treatments, which could be biologically significant, but there were large standard deviations around each mean and the difference was not statistically significant ($p = 0.36$). These responses were measured across the entire plant community, but individual species may have responded differentially to herbivore exclusion and warming. Despite these caveats, these findings provide evidence that current climate model treatment of roots as a fixed, synchronous fraction of aboveground growth are not accurate [28]. Roots may be under different constraints than canopy tissues, and use of carbon stores for spring root growth may mediate the impacts of climate change on root phenology.

Belowground biomass can be up to five times greater than aboveground biomass in the Arctic [54], and the uncoupling of root phenology from leaf phenology makes it very difficult to estimate whole-plant phenology without intensive root monitoring. Controls on root phenology may differ by ecosystem, and root phenology may not be driven by temperature or spring carbon production in some species. This would uncouple root and shoot phenology further, as production of aboveground tissues is strongly constrained by air temperature.

Conclusions

Root phenology was not directly driven by temperature or day length in this ecosystem, and above- and belowground phenology did not respond in the same way to warming and herbivore exclusion. These results suggest that aboveground phenology, one of the most widely measured aspects of climate change, may not represent whole-plant phenology and may be a less accurate predictor of the timing of whole-plant carbon fluxes than commonly assumed.

Plant material

The authors declare that because they did not remove any plant material or move plants across borders, they were not required to obtain licenses or permissions for this study.

Additional file

Additional file 1: Table S1. Peak date of root production is the date on which new root growth over the previous week was highest. Peak date of root standing crop is date with largest total length of roots. Peak date of vegetation cover is date with largest NDVI. The percent of maximum root production is a metric of seasonality, calculated as the new root growth on each date divided by the maximum root production in that plot and year. Percent of maximum standing crop and NDVI are calculated in the same way. "Warming" denotes warming/ambient treatments, "Exclosure" denotes herbivores present/absent, and "Depth" is a comparison of 0-10 cm, 10-20 cm, and 20-30 cm. (DOC 51 kb)

Abbreviations

ITEX: International tundra experiment; NDVI: normalized difference vegetation index.

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Availability of data and supporting materials

Data are publicly available at the NSF Arctic Data Center (David Eissenstat. 2016. Greenland root phenology: warming and herbivory. NSF Arctic Data Center. arctic-data.6185.2.)

Authors' contributions

EP conceived of experimental design and implemented long-term warming and herbivore exclusion. DME conceived of minirhizotron installation at this site. LR collected and analyzed data. LR drafted first version of the manuscript and all authors contributed to final version of manuscript. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

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