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Leaf and root phenology and biomass of *Eriophorum vaginatum* in response to warming in the Arctic

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Abstract

The response of plant leaf and root phenology and biomass in the Arctic to global change remains unclear due to the lack of synchronous measurements of above- and belowground parts. Our objective was to determine the phenological dynamics of the above- and belowground parts of *Eriophorum vaginatum* in the Arctic and its response to warming. We established a common garden located at Toolik Lake Field Station; tussocks of *E. vaginatum* from three locations, Coldfoot, Toolik Lake and Sagwon, were transplanted into the common garden. Control and warming treatments for *E. vaginatum* were set up at the Toolik Lake during the growing seasons of 2016 and 2017. Digital cameras, a handheld sensor and minirhizotrons were used to simultaneously observe leaf greenness, normalized difference vegetation index and root length dynamics, respectively. Leaf and root growth rates of *E. vaginatum* were asynchronous such that the timing of maximal leaf growth (mid-July) was about 28 days earlier than that of root growth. Warming of air temperature by 1 °C delayed the timing of leaf senescence and thus prolonged the growing season, but the temperature increase had no significant effect on root phenology. The seasonal dynamics of leaf biomass were affected by air temperature, whereas root biomass was correlated with soil thaw depth. Therefore, we suggest that leaf and root components should be considered comprehensively when using carbon and nutrient cycle models, as above- and belowground productivity and functional traits may have a different response to climate warming.

Keywords *Eriophorum vaginatum*, phenology, warming, aboveground biomass, belowground biomass

北极地区气候变暖对莎草地上和地下部分物候和生物量的影响

摘要：北极地区的土壤和植被中存储了大量的碳，在气候变化的大背景下，北极升温速度几乎是地球其他地区的2倍。由于缺乏同步测量，尚不清楚北极地区植被地上部分和地下部分的物候和生物量对气候变化的反应。在2016和2017年的生长季节，我们在北极的Toolik Lake站点上建立了一个移植花园，并沿纬度变化从高到低依次从 Sagwon、Toolik Lake和Coolfoot这3个站点移植了3种不同生态类型的莎草(*Eriophorum vaginatum*)。一半莎草用作增温处理，另一半为控制处理。我们用物候相机、手持式

光谱仪和微根窗分别观测3种生态型莎草的绿色度、归一化植被指数(NDVI)和根长动态，根据NDVI和根长计算了叶片和细根的生物量。研究发现，莎草的叶和根生长是异步的，叶片开始生长的时间比根系生长的时间早约28天。气温升高1°C会延迟叶片衰老的时间，从而延长生长期，但温度升高对根系物候没有显着影响，变暖在统计学上没有增加叶片和根的生物量。此外，叶片生长的季节动态受气温的影响，但根的生长与土壤融化深度有关。因此，我们建议在使用碳和养分循环模型时，应将叶和根成分分开考虑，因为地上和地下的以及功能属性可能对气候变暖有不同的反应。

关键词：莎草，物候，气候变暖，地上生物量，地下生物量

INTRODUCTION

Global mean surface temperature has increased by 0.8–1.2 °C from 1950 to 2017 with a rate of 0.1–0.3 °C per decade (IPCC 2013). Temperature controls the rate of many biogeochemical reactions in the ecosystem, and affects many ecological processes and functions. As temperature increases, plants can adjust phenology and biomass allocation according to the amount of temperature variation (Bardgett *et al.* 2014; De Frenne *et al.* 2011; Freschet *et al.* 2013). Plants may trade off biomass allocation between aboveground (light and CO_2) and belowground resources (water and nutrients) for local adaptation (Freschet *et al.* 2015; Poorter *et al.* 2012; Steinaker and Wilson 2008; Walther *et al.* 2002).

Many warming experiments, such as open-top chambers (OTCs), have been performed to explore the effects of warming on plants. The studies on the influence of warming on the aboveground phenology of different species (such as woody, herbaceous and alpine meadow) have been well documented (Hu *et al.* 2020; Makoto *et al.* 2020; Yu *et al.* 2010). In most warming experiments, warming has advanced aboveground onset time or increased aboveground biomass in many species (Richardson *et al.* 2013; Rosa *et al.* 2015; Yu *et al.* 2010). Also, the elevated temperature may delay timing of plant senescence, which can extend the growing season (Wang *et al.* 2014). Phenological responses to warming are species-specific (including positive, neutral and negative responses), and there are also differences in the phenological responses to different growing periods (Yu *et al.* 2010). Further, the response of aboveground growth phenology to warming can be attributed to the variation in plant traits including plant height growth, the biomass ratio of root to shoot and seed mass (Hu *et al.* 2020; Liu *et al.* 2020).

However, knowledge of the effects of warming on root phenology and biomass is very limited with high uncertainty in the results (Hobbie and Chapin 1998; Iversen *et al.* 2015; Pregitzer *et al.* 2000; Sullivan and Welker 2005). For example, most existing studies suggest that warming does not have significant effects on total belowground phenology or fine root biomass (Radville *et al.* 2016b, 2018; Wang *et al.* 2016). On the other hand, some studies showed manipulated warming can significantly increase biomass and extend the growing season of roots (Björk *et al.* 2007; Sistla *et al.* 2013; Sullivan and Welker 2005). Consequently, it is poorly understood how warming will impact phenology and biomass allocation between above- and belowground tissues of Arctic plants (Hobbie and Chapin 1998; Shipley and Meziane 2002; Sloan *et al.* 2013; Wolkovich *et al.* 2012).

Above- and belowground phenology may respond differently to climate change, resulting in shifting carbon allocation and ecosystem functioning (Abramoff and Finzi 2016; Cleland *et al.* 2007; Radville *et al.* 2016a, 2016b). Some studies have demonstrated that the relationship between the phenology of above- and belowground growth varies with different species (Abramoff and Finzi 2015; Sloan *et al.* 2016; Steinaker and Wilson 2008; Steinaker *et al.* 2010). In the Arctic, phenological differences in the above- and belowground growth of different vegetation types have also been observed. For example, Sloan *et al.* (2016) demonstrated that root production of sub-Arctic plant communities occurs after the peak of leaf production and that, compared with sedges, deciduous shrubs have greater asynchrony in root and leaf production. However, Radville *et al.* (2016b) found that peak root growth of deciduous shrubs, primarily *Salix glauca* and *Betula nana*, occurred 2.5 weeks before leaf growth. In response to the changing environment, the response of different populations to climate change may be inconsistent for the above- and belowground components (Freschet *et al.* 2013; Wang *et al.* 2016). Plants may allocate more photosynthate to roots to increase water/nutrient absorption for survival in a harsh environment (Song *et al.* 2006; Sun and Wang 2016). Studies have proven that decreasing light supply and nutrient availability commonly drives an increase in total leaf area and root length for a given unit of plant biomass (Poorter and Nagel 2000).

Large amounts of carbon are stored in vegetation and soils in the Arctic (Epstein *et al.* 2012; Hugelius *et al.* 2013, 2014), which has warmed nearly twice as fast as the rest of the planet over the past half century (IPCC 2013). Plant species at high latitudes or altitudes may respond differently from those in more temperate climates (Hu *et al.* 2020). In Arctic ecosystems, elevated temperature has been shown to extend the plant growing season (Bjorkman *et al.* 2015; Hoye *et al.* 2013; Sullivan and Welker 2005) and also accelerate nutrient availability and carbon release rate (Chapin *et al.* 1995; Craine *et al.* 2010; Schuur *et al.* 2009). Synchronous measurements of above- and belowground plant growth dynamics in the Arctic region are important for understanding carbon allocation dynamics within plants and whole plant response strategies to changing environments and plant competition (Cleland *et al.* 2007; Poorter *et al.* 2012; Shaver *et al.* 1986; Steinaker *et al.* 2010). *Eriophorum vaginatum* L. is a foundational species of moist acidic tundra, where it can account for up to one-third of ecosystem productivity (Chapin and Shaver 1985).

In this study, we used OTCs to determine leaf and root phenology along with biomass response of populations of *E. vaginatum* to increasing temperature. The objectives of this study were (i) to investigate the phenological pattern of leaves vs. roots over the season and explore the main environmental factors that drive dynamics of leaf and root production in the Arctic; (ii) to investigate the response of *E. vaginatum* leaf and root phenology and biomass to warming treatment. Specifically, we hypothesize that: Given the observations of greater plasticity of aboveground phenology, we hypothesize that the aboveground components will display a more variable response to warming than belowground components.

MATERIALS AND METHODS

Experimental site and design

This study took place in moist acidic tussock tundra near Toolik Lake, Alaska (68°38′ N, 149°36′ W). The vegetation community is dominated by tussocks of *E. vaginatum*, deciduous shrubs (*B. nana* L. and *Salix* spp.) and evergreen shrubs (*Vaccinium vitis-idaea* L., *Rhododendron tomentosum* Harmaja and *Cassiope tetragona* L.) (Parker *et al.* 2017). In August 2014, tussocks of *E. vaginatum* from three populations growing at three locations Coldfoot (CF, 67°15′32″ N, 150°10′12″ W), Toolik Lake (TL, 68°37′44″ N, 149°35′0″ W) and Sagwon (SG, 69°25′26″ N, 148°42′49″ W) along a latitudinal gradient (each separated by ~1° in latitude) were transplanted into the gardens located at Toolik Lake. The mean air temperature was 11.5 °C from June to August in 2016 and 2017. The ecosystem is underlain by permafrost, and the average thaw depth was 40 cm between June and August in 2016 and 2017. In 2014, 60 *E. vaginatum* tussocks were transplanted into 20 clusters (3 tussocks in a cluster) according to the protocol of Schedlbauer *et al.* (2018). Ten clusters were warmed using OTCs, and the remaining 10 clusters were controls, yielding 10 replicates per treatment. The OTCs were in an open-ended cone shape with 1.23 m diameter at the base, 0.84 m diameter at the top and 0.70 m height. The chambers were constructed of fiberglass glazing (Sun-Lite HP, Kalwall Corp., Manchester, NH) and secured with rope and tent stakes.

Microclimate measurements

The height of *E. vaginatum* in Alaska is less than 20 cm in summer. In order to observe the warming effect, air temperature at 20 cm above the ground surface (above the *E. vaginatum* canopy) was measured hourly in control and OTC treatments with shielded iButtons (DS1921G-F5#, Maxim Integrated, San Jose, CA) mounted 20 cm above the ground surface. The radiation shields were manufactured by 3D LAB (Abisko, Sweden) using a 3D-Printer (M2 from MakerGear; MakerGear™ LLC, Beachwood, OH). Soil temperature at 2, 10 and 20 cm below the ground was measured (iButton DS1922L/DS1921G, Maxim Integrated) during the growing seasons. Among the three depth layers, the soil temperature at 2 cm was most affected by environmental changes. There were six replicate measurements of temperature for both treatments at each site. Three plots of air temperature and soil temperature were averaged for two treatments (control and OTC). In the experimental design, we observed the soil moisture, but we found that the soil moisture data are not available due to damage to the probes. So, the effect of soil/air moisture on *E. vaginatum* had not been analyzed. Thaw depth measurement was performed mechanically with a graduated rod. The probe was a 1 m long stainless-steel rod with a tapered point, 1 cm in diameter and an attached handle. Thaw depths were recorded once a week during the growing seasons in 2016 and 2017 for both OTC and control plots. Thaw depth data were the average of six plots over each measurement interval. The temporal differences between leaf and root growth were estimated as the difference between the highest peaks determined by the model. The length of time between leaf startup and senescence is the duration of the growing season. Root growth was still active at the end of August when our monitoring stopped.

Leaf measurements

Digital cameras

Greenness indices from digital cameras were used to monitor timing and seasonal dynamics of canopy phenology. Two digital cameras collected images for one OTC and one control treatment for one cluster from each population that was selected from the 20 cluster plots during the growing season in 2016 and 2017, making a total of six cameras. Camera images were saved in 24-bit JPEG format, at 1-h intervals, 4 h a day (1000–1400 local time). The data preprocessing process included: (i) screening the collected images to exclude images of poor quality such as blur, excessive or weak light; (ii) using a reference image to select regions of interest polygons to extract time-series data of a vegetation index (green chromatic coordinate [GCC]); (iii) fitting the optimal growth curve by using Equation (1) (Gu *et al.* 2009) and identifying phenological phase changes (Toomey *et al.* 2015; Yang *et al.* 2014).

$$\mathrm{GCC} = y_0 + \frac{a_1}{1+\exp\left(\frac{-(t-t_{01})}{b_1}\right)^{c_1}} - \frac{a_2}{1+\exp\left(\frac{-(t-t_{02})}{b_2}\right)^{c_2}} \tag{1}$$

where GCC is a green chromatic coordinate i.e. widely used to monitor canopy development; t is the day of year. y_0, a_1, a_2, b_1, b_2, c_1, c_1, t_{01} and t_{02} are empirical parameters to be estimated. The extreme points obtained by the maximum curvature method correspond to the dates of leaf growth startup, leaf maximum and senescence, respectively. The calculation of the curve curvature is shown in Equation (2)

$$\rho(t) = \frac{g''(t)}{\left(1+g'(t)\right)^{3/2}} \tag{2}$$

where $\rho(t)$ is the curvature, $g'(t)$ is the first derivative of the function t and $g''(t)$ is the second derivative of the function t.

GreenSeeker

The GreenSeeker (Trimble, Inc., Sunnyvale, CA) sensor employs a patented technology to measure crop reflectance and calculate normalized difference vegetation index (NDVI).

$$\mathrm{NDVI} = (\mathrm{NIR} - \mathrm{R})/(\mathrm{NIR} + \mathrm{R}) \tag{3}$$

where NIR is near-infrared radiation (760–780 nm) and R is red radiation (650–670 nm). We took four scans at 60 cm above the tussock to cover it representatively with the oval field of view. The GreenSeeker was mounted on a vertical pole with drilled holes every 5 cm to adjust the field of view based on the tussock size. Ten tussocks at the Toolik Lake site were sampled at six to seven time points over the growing season. We used NDVI to calculate aboveground biomass according to Berner *et al.* (2018).

$$\mathrm{Biomass}_{\mathrm{above}} = 0.0256 \times \exp(5.32 \times \mathrm{NDVI}) \tag{4}$$

where $\mathrm{Biomass}_{\mathrm{above}}$ is aboveground biomass and NDVI is normalized difference vegetation index.

Root phenology

Minirhizotron installation and scaling of minirhizotron measurements

In August 2015, six minirhizotron acrylic tubes with a diameter of 7 cm were installed under individual tussocks within the plots of *E. vaginatum* at a 45° angle to the surface, one with OTC warming and one without an OTC from each population for a total of six. The lengths that tubes entered the soil varied from 55 to 90 cm (see Supporting Information), depending on how deeply the soil was thawed when the minirhizotron tubes were installed. The bottoms of the tubes were sealed with a plug. The aboveground portion of the tubes was 25 cm and covered with foil to reflect light and prevent heating of the tube. The horizontal distance of the tubes from the center of the tussocks varied between 14 and 24 cm. Tube holes were cored using a core slightly smaller than the tube size to obtain close contact between the tubes and the soil. We filled tubes with rubber stoppers and painted the aboveground portions white to keep light from entering and to minimize temperature differentials in tubes.

Digital images with a grid size of 640 × 480 pixels, corresponding to an area of 18 mm × 13.5 mm, were captured with a minirhizotron digital camera system (BTC-2 Bartz Technology Co., Santa Barbara, CA). From 2016 to 2017, we photographed tubes once a week during the two growing seasons. Digital images were processed using Rootfly software (Wells and Birchfield, Clemson University) to calculate the number of roots and root length. Images at 0–50 cm vertical depth of each minirhizotron tube were used for calculation and analysis.

Equation (5) was used to simulate the root phenology of tussocks to determine the dates of transition of root growth. We used a maximum curvature method to identify the transition dates of root phenology.

$$\mathrm{RL} = a + \frac{b}{[1 + \exp(c - dt)] \times [1 + \exp(e - ft)]} \quad (5)$$

Here, RL is root length (mm), t is day of year and a, b, c, d, e and f are parameters. The dates of root startup and maximum value were determined by the extreme value of the curvature.

Root biomass

We also collected soil samples from the garden at the end of the growing season (13 September 2017). Twelve soil samples were taken from the 0–50 cm soil layer with a 5-cm diameter soil corer at two sites. We divided the soil samples into four layers (0–5, 5–15, 15–30 and 30–45 cm) and picked out the roots in each layer of soil by washing with distilled water. The root biomass was estimated by combining the data from the soil samples with the images according to studies by Johnson *et al.* (2001) and Taylor *et al.* (2014) (see Supporting Information for the specific calculations).

Statistical analyses

To test for differences in the duration of root growth, we determined the growth duration from root startup to reach its maximum. The influence of warming and years on the aboveground variables, leaf biomass, leaf startup date, leaf stabilization date and leaf growth duration, was examined with a linear model ANOVA (R 2.8.1, R Core Team 2016). The same method was used to study the response of warming and years on belowground variables, root length, root biomass, root startup date, root stabilization date and root growth duration. In order to determine the relationship between phenology and microclimate, and between biomass and microclimate, we performed regression analysis on the environmental factors (soil temperature and soil thaw) and aboveground phenology, belowground phenology, leaf biomass and root biomass.

RESULTS

Environmental conditions and warming effect

During the study period (13 June to 28 August), the daily air temperature at 20 cm aboveground (T_{air}) ranged from 0.4 °C (June) to 23.9 °C (July) (Fig. 1) with a mean value of 11.5 °C. During the same period, the daily soil temperature at 2 cm belowground (T_{soil}) varied between 0.5 °C (June) and 11.4 °C (August) with a mean value of 5.8 °C. Mean monthly T_{air} in 2017 was significantly higher than in the same period of 2016, except for August. Mean monthly T_{soil} in 2016 was slightly higher than in the same period of 2017, irrespective of the month. The OTC treatment increased the daily air temperature at 20 cm aboveground during the two growing seasons by 0.9 °C ($F = 20.7$, $P < 0.01$, Table 1; Fig. 1). At 2 cm belowground, the soil temperature in the OTC treatment was about 0.3 °C higher than in the control plot, but there was no statistically significant difference ($F = 3.4$, $P < 0.06$, Table 1; Fig. 1). Thaw depth gradually increased over the season from 5.1 to 61.9 cm, and the thaw depth in 2017 was deeper than in 2016.

Leaf and root phenology of *E. vaginatum* with and without warming

Because of low sample size, the differences between populations were not significant. We therefore focus on the response of *E. vaginatum* tussocks regardless of their site of origin. The response of individual clusters and tussocks is shown in Supporting Information.

Leaf growth of *E. vaginatum* started to increase early in early June, with rates rising sharply to a maximum in mid-July, and then entered a steady-state period until senescence in mid-August (Fig. 2). The duration of leaf growth was about 90 days. There was a significant difference in both the timing of leaf startup and the duration of leaf growth during the 2-year observation period ($F = 23.1$, $P < 0.005$; $F = 12.4$, $P < 0.02$, Supporting Information). According to the maximum curvature method, *E. vaginatum* leaves in 2016 started growing DOY 145, which was earlier than in 2017 when the leaves started growing at DOY 154 ($F = 23.1$, $P < 0.005$). The duration of leaf growth was 6 days longer in 2017 than in 2016 ($F = 12.38$, $P < 0.02$).

The warming treatment increased the aboveground temperature by 1 °C. The warming temperature significantly affected the timing of leaf senescence

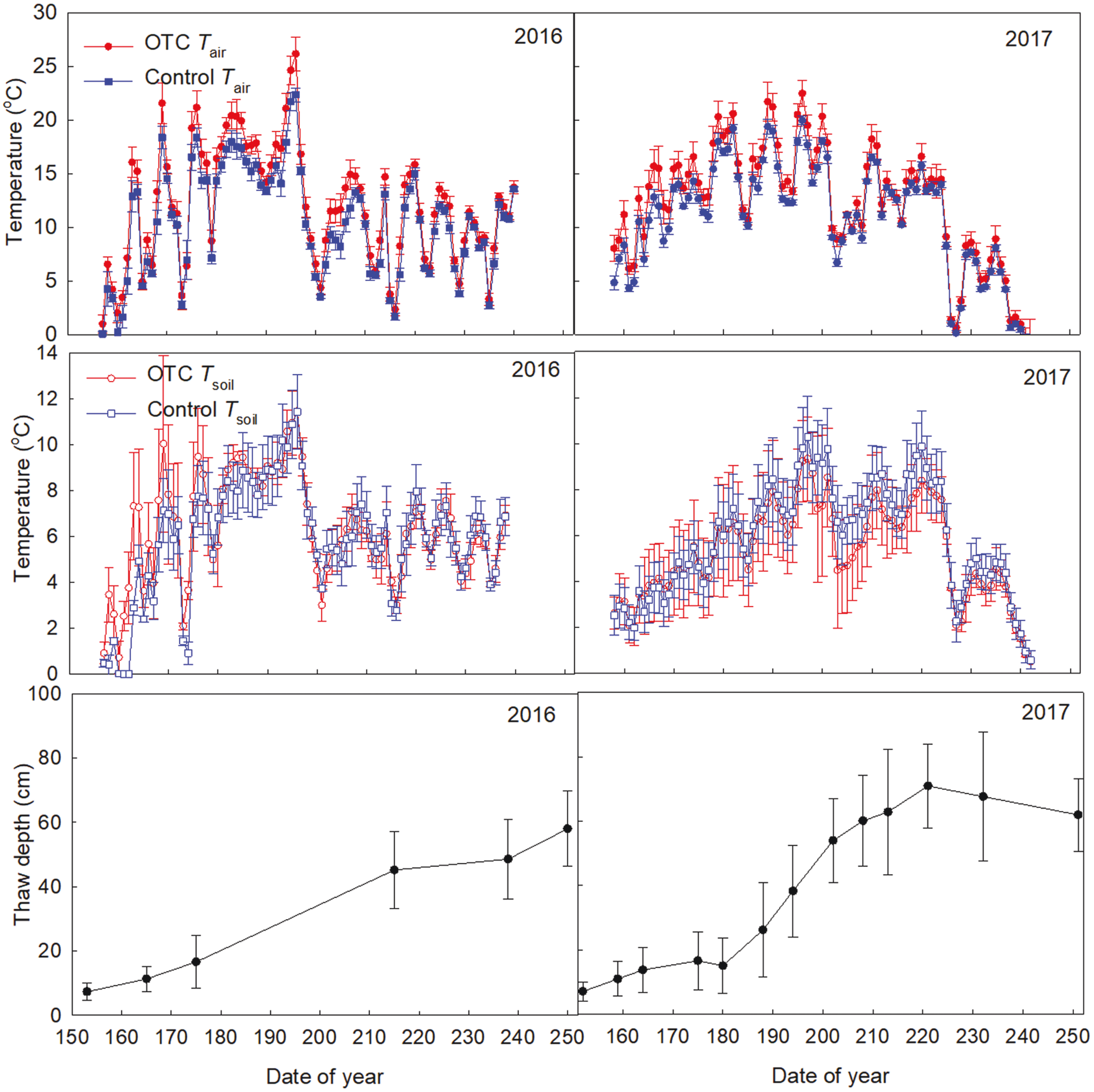

Figure 1: Daily variation of air temperature at 20 cm aboveground (T_{air}), soil temperature at 2 cm belowground (T_{soil}) under two treatments (control and OTC), and thaw depth during growing seasons in 2016 and 2017.

(F = 16.67, $P < 0.009$) and duration of leaf growth (F = 7.59, $P < 0.04$).

Fine root growth of *E. vaginatum* started at the end of June and continued to rise until it entered a steady-state period in mid-August. In 2016, the times of root startup and maximum growth were DOY 184 and 228, respectively, which was later than the times of the startup (DOY 173) and senescence (DOY 216) in 2017 (F = 14.81, $P < 0.001$; F = 12.68, $P < 0.001$). The duration of root growth from the beginning to the maximum was longer than that of leaf growth. The warming treatment had no significant effect on the phenological transition time of roots (F = 0.32, $P < 0.57$; F = 0.54, $P < 0.47$; F = 1.41, $P < 0.25$).

Root and leaf phenology of *E. vaginatum* were asynchronous. The startup date of root growth lagged the startup date for leaf growth, and the date when root growth reached its peak lagged behind the peak of leaf growth for 16–40 days (Fig. 2). In 2016, the lag between roots and leaves was longer than that of

Table 1: Mean monthly air temperature (20 cm above the soil surface) and soil temperature (−2 cm below the soil surface) with standard deviation (*n* = 3) during the growing season (June to August) and under the experimental warming treatment and the control at and Toolik Lake

	2016			2017		
Toolik Lake	**OTCs (°C)**	**Control (°C)**	**Difference**	**OTCs (°C)**	**Control (°C)**	**Difference**
T_{soil}						
June	5.7 ± 1.6	4.4 ± 0.8	1.3	4.4 ± 1.7	4.3 ± 0.9	0.1
July	7.4 ± 0.7	7.4 ± 1.1	0	6.8 ± 1.9	7.8 ± 1.1	−1.0
August	5.6 ± 0.6	5.7 ± 0.8	−0.1	4.5 ± 0.7	5.1 ± 0.8	0.6
Mean	6.3 ± 1.0	5.9 ± 0.9	0.4	5.8 ± 1.4	5.7 ± 0.9	0.1
T_{air}						
June	10.7 ± 1.0	9.3 ± 0.8	1.5	12.9 ± 1.1	10.7 ± 0.6	2.2
July	15.4 ± 0.9	13.3 ± 0.7	2.1	15.7 ± 0.8	14.2 ± 0.4	1.5
August	9.7 ± 0.6	8.7 ± 0.4	1.0	9.5 ± 0.8	8.8 ± 0.3	0.7
Mean	11.9 ± 0.8	10.3 ± 0.9	1.6	12.7 ± 0.9	11.2 ± 0.4	1.5

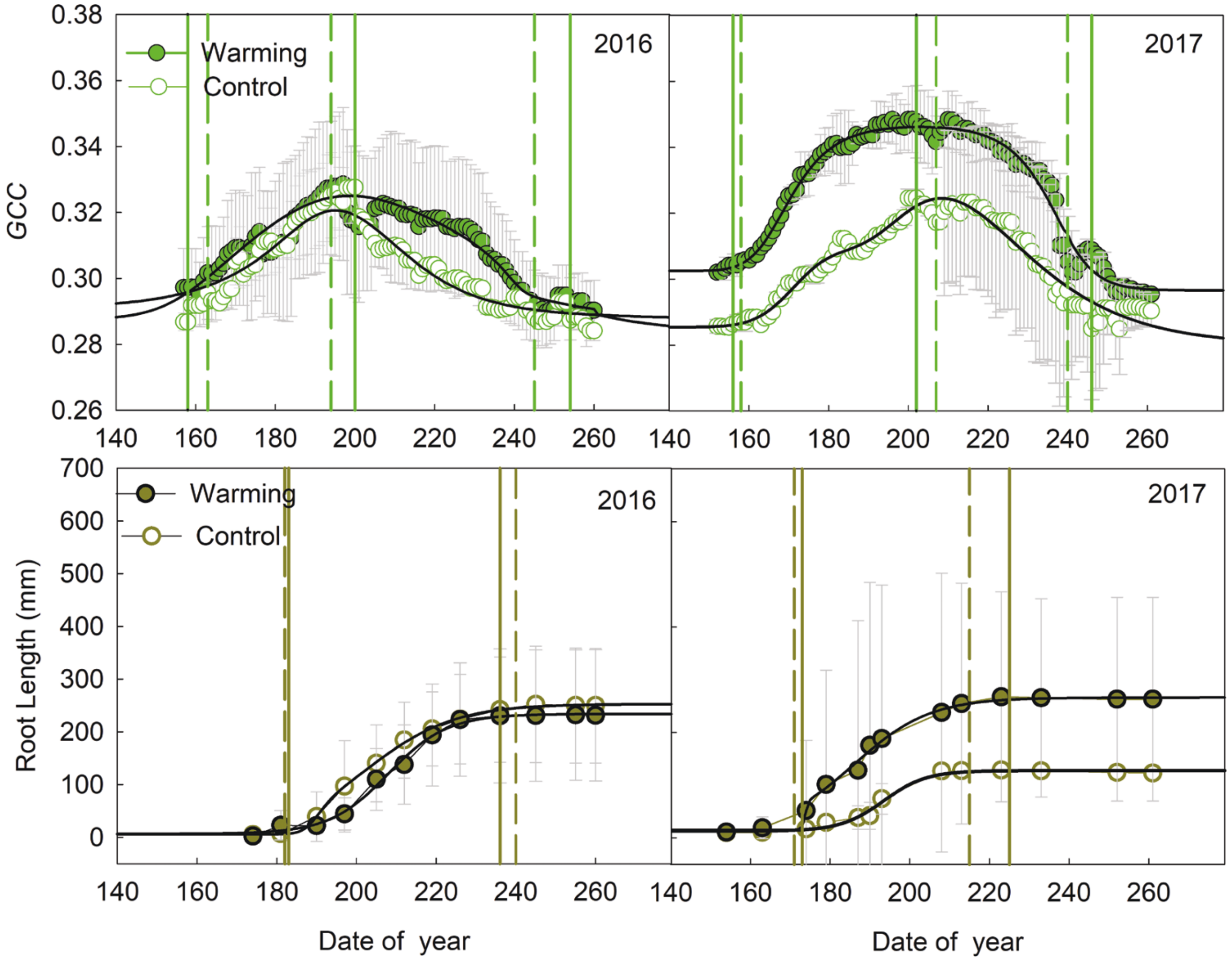

Figure 2: The growth dynamics of leaves and roots of *Eriophorum vaginatum* at Toolik Lake in 2016 and 2017 (*n* = 6).

2017. We also compared the onset, peak and offset time for leaf phenology and root phenology in Fig. 3. The offset time between leaf and root phenology was 37 days in 2016, but 19 days in 2017.

Biomass of *E. vaginatum* leaves and roots after warming

Leaf biomass of *E. vaginatum* under control and warming treatments in mid-August was 175.9 ± 41.1 and 204.3 ± 88.7 g/m^2, respectively. Although large, this difference was not statistically significant ($F = 0.82$, $P < 0.39$). Root biomass under control and warming treatments were 97.27 ± 36.53 and 159.73 ± 135.54 g/m^2, respectively, and the increase in temperature did not statistically affect root biomass ($F = 0.35$, $P < 0.57$). Leaf and root biomass was not significantly different in 2016 and 2017 ($F = 0.08$, $P < 0.78$; $F = 0.73$, $P < 0.42$).

The root–shoot ratio (R/S) of *E. vaginatum* varied between 0.01 (late June) and 1.4 (early September) in 2016 and 2017 during the growing season from June to September. R/S gradually increased over the growing season (Fig. 4). The warming treatment did not affect the R/S ($F = 3.8$, $P < 0.09$) and there was no difference in R/S between the two growing seasons ($F = 1.27$, $P < 0.27$).

Effects of temperature and thaw depth on leaf and root biomass

In the study, we tried to analyze the data with correlation to determine the relationship between phenology and microclimate. The obvious conclusion is that root phenology and microclimate were linearly related (Supporting Information). That is, the later that roots start growth, the higher the soil temperature. The later the root system stops growing, the lower the temperature. This conclusion also applies to air temperature and leaf phenology. For thaw depth, it is certain that the later the leaves and roots start to grow, the deeper the thaw depth, the later the peak time of the leaves and roots and the deeper the thaw depth.

We also analyzed the data with correlation to determine the relationship between biomass and microclimate. We found a slight lag in the logarithmic relationship between *E. vaginatum* leaf biomass and seasonal air temperature (T_{air}) in 2016–2017 (Fig. 5a). In spring and summer, leaf biomass increased with increasing air temperature, but leaf biomass was still increasing when air temperature reached a maximum. For roots, there was no significant correlation between the seasonal variation of biomass and soil temperature at 2 cm depth (T_{soil}, Fig. 5b).

As the thaw depth increased, there was a significant linear positive correlation between leaf biomass and thaw depth, and between root biomass and thaw depth that could explain 34% ($P < 0.05$) and 57% ($P < 0.01$) of the leaf and root biomass dynamics during the growing season, respectively (Fig. 6).

DISCUSSION

The dynamic growth of *E. vaginatum* leaf and root are asynchronous

In our study, leaves reached their peak in mid-July, which is consistent with observations in similar sub-Arctic vegetation (Radville *et al.* 2018; Sloan *et al.* 2016). This result is also consistent with the results obtained by Parker *et al.* (2017) using the method of tagging and measuring leaf length at the Toolik Lake site. However, the maximum root length appeared

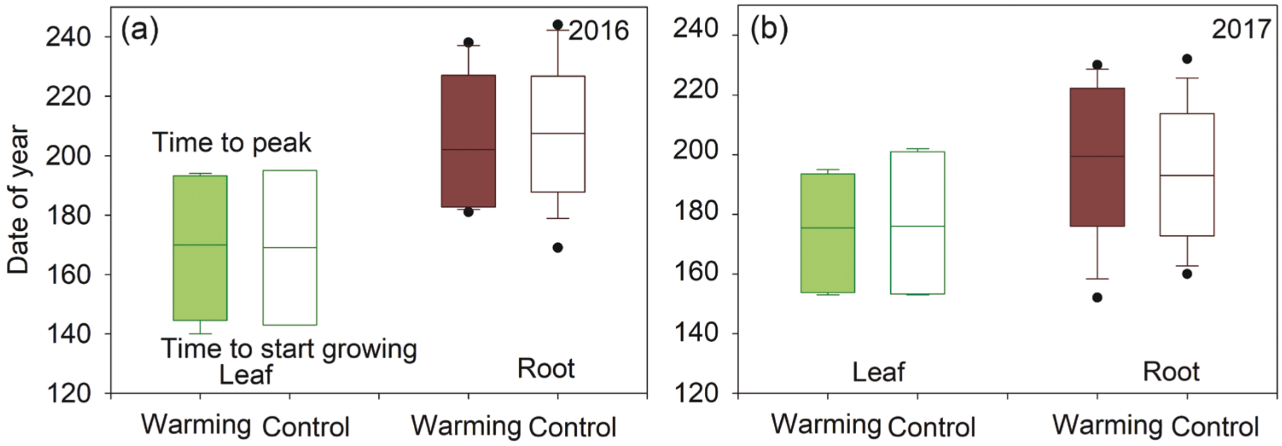

Figure 3: The onset, peak and offset time for leaf phenology and root phenology in 2016 (**a**) and 2017 (**b**).

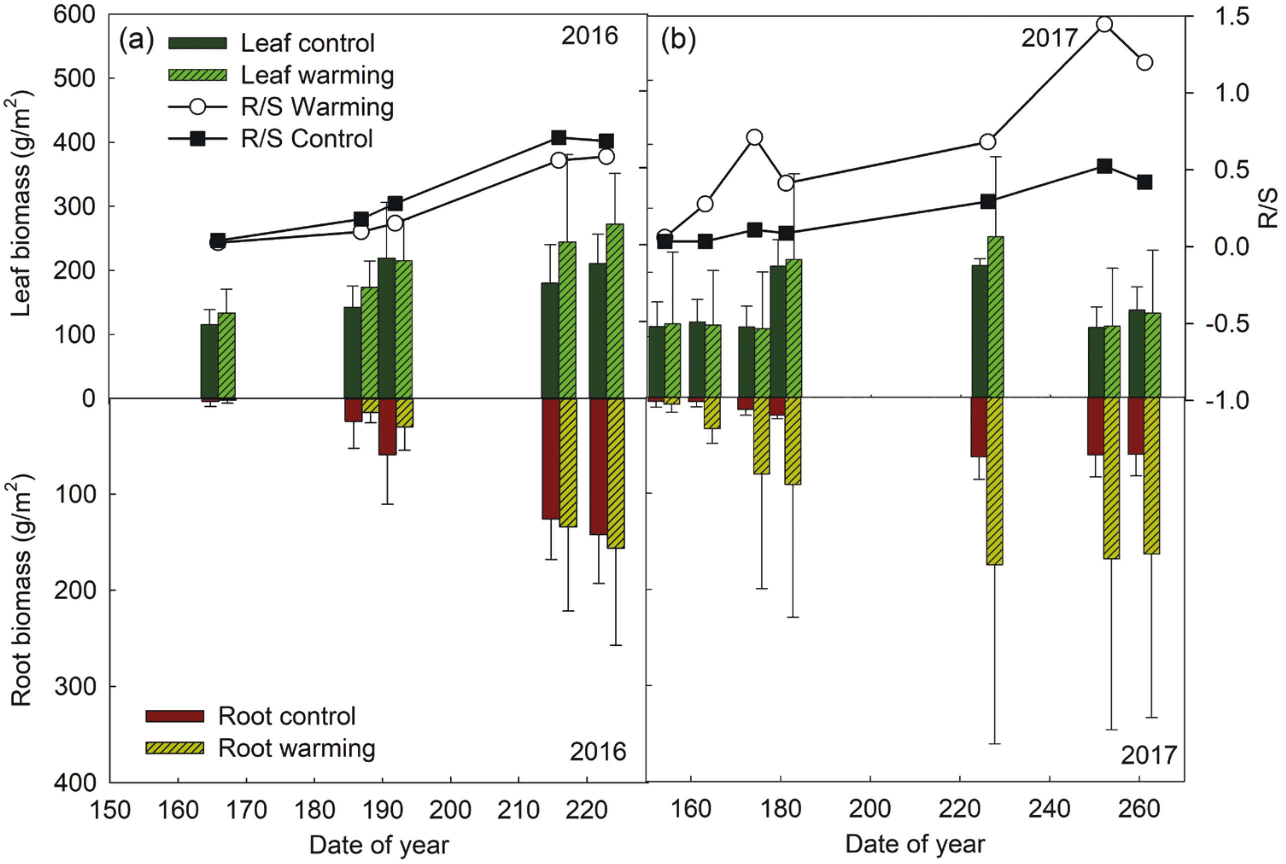

Figure 4: Leaf biomass and root biomass of *Eriophorum vaginatum* during the growing season in 2016 (**a**) and 2017 (**b**). Bars indicate mean ± SE ($n = 6$).

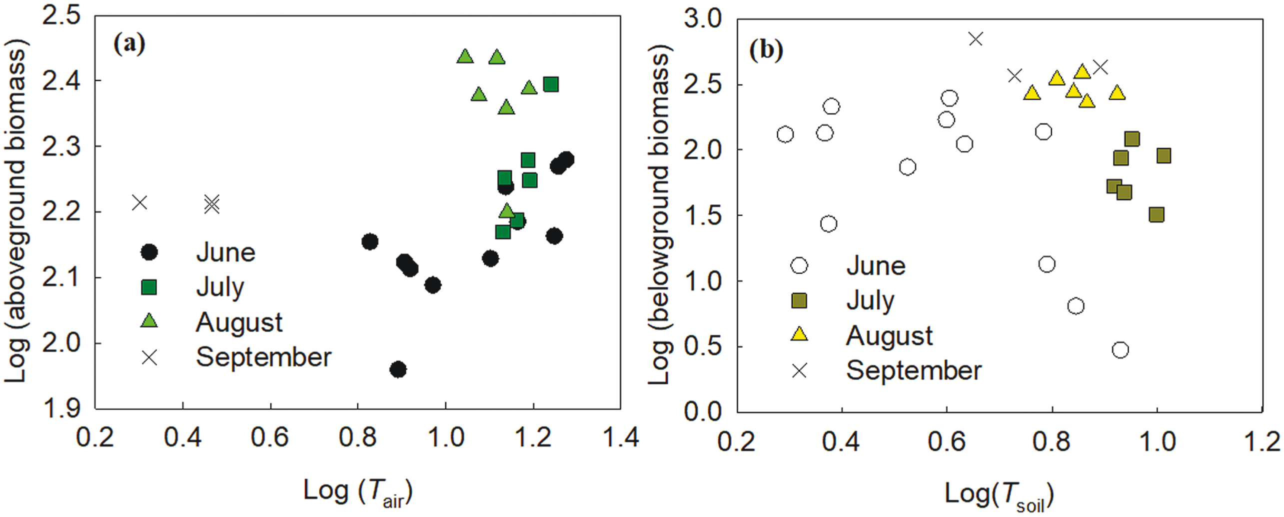

Figure 5: (**a**) Logarithmic relationship between air temperature at 20 cm aboveground (T_{air}) and *Eriophorum vaginatum* leaf biomass, and (**b**) logarithmic relationship between soil temperature at 2 cm belowground (T_{soil}) and root biomass ($n = 33$).

in mid-August (Sloan *et al.* 2016). On average, leaf growth preceded root growth, but root growth was still detected after mid-August after leaf senescence. In other words, the peaks of leaf and root growth of *E. vaginatum* did not coincide. This phenological relationship between leaves and roots has also been found in studies of other species or other sedges (Abramoff and Finzi 2015; Blume-Werry

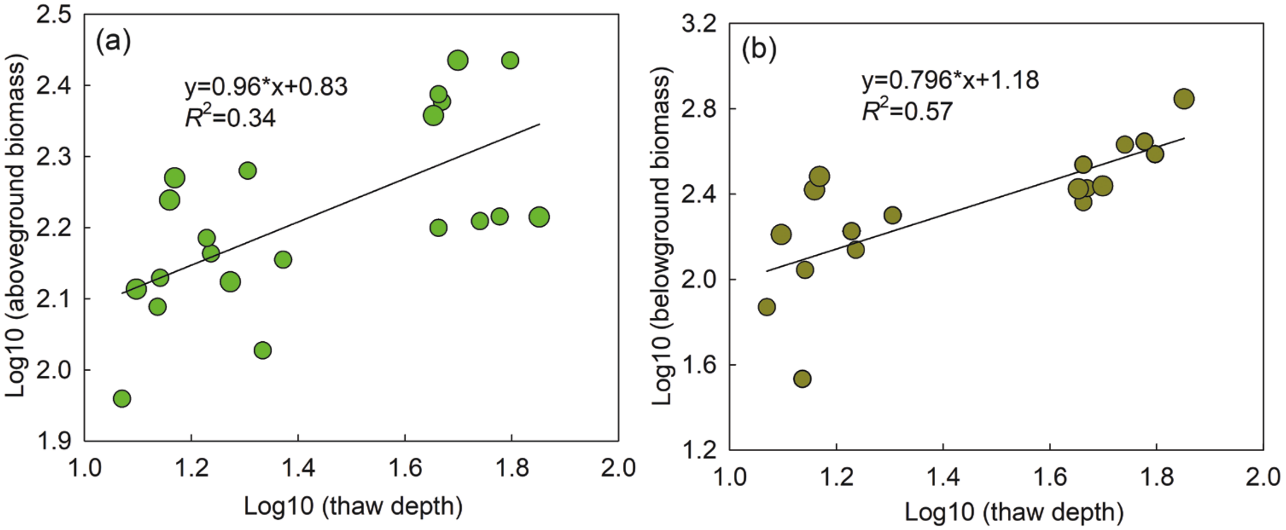

Figure 6: (**a**) Logarithmic relationship between thaw depth and *Eriophorum vaginatum* leaf biomass, and (**b**) the logarithmic relationship between thaw depth and *E. vaginatum* root biomass (*n* = 33).

et al. 2016; Sloan *et al.* 2016; Steinaker and Wilson 2008; Steinaker *et al.* 2010). Thermal buffering of soil temperature in autumn is a possible reason why roots remain active after leaf senescence (Abramoff and Finzi 2015; Steinaker *et al.* 2010). In our study, the atmosphere warmed faster than the soil in spring, while in August the soil temperature dropped more slowly than air temperature and the soil thaw depth did not decrease (Fig. 1), which allowed the roots to remain active in the soil and not encounter the risk of freezing quickly. Previous studies have observed that new root growth of *Eriophorum angustifolium* and *Carex rostrata* in late-season was a combination of new root initiation close to the soil surface and extension of existing roots deep in the soil profile (Blume-Werry *et al.* 2016; Sloan *et al.* 2016). Furthermore, the asynchrony between leaf and root phenology may be related to the fact that root growth is less affected by the photoperiod and the snow cover plays a role in heat preservation (Blume-Werry *et al.* 2016). Our result showed that at the end of September, the soil thaw depth is still around 60 cm (Fig. 1), which made it possible for the root system to continue to grow. In addition, the production, storage and transport of photoassimilate may also affect the phenological relationship between leaf and root. Olsrud and Christensen (2004) demonstrated that in mid-September most carbon was allocated to the finest roots that are most involved in nutrient uptake. The roots are still alive after the leaf senescence in our site, indicating that late-season root growth is fueled by stored carbohydrates rather than by current photosynthate production (Blume-Werry *et al.* 2016; Jonasson *et al.* 1999; Nordgren *et al.* 2003). Meanwhile, late-season carbon i.e. stored in rhizomes also provides a carbon source for roots before the leaves are fully expanded in these sedge communities (Chapin *et al.* 1980; Sloan *et al.* 2016; Sloan and Jacobs 2008). The asynchronism of leaves and roots may affect the carbon and nitrogen cycle in the Arctic. Models that use coupled leaf and root phenology to predict the effects of climate change on the Arctic may underestimate the effects of roots on soil carbon and nitrogen (Iversen *et al.* 2015). Both leaf and root growth entered a steady-state period after reaching a maximum and showed 'shoulder seasons', which are important for carbon uptake in Arctic tundra (Mbufong *et al.* 2014; Richardson *et al.* 2013). The duration of leaf growth of *E. vaginatum* in our study was about 90 days, which corresponds to previous estimates of growing season length in the Low Arctic (84–100 days) (Blume-Werry *et al.* 2016; Bokhorst *et al.* 2008; Karlsen *et al.* 2008).

Phenology and biomass of leaves and roots of *E. vaginatum* respond differently to warming air temperature

In our study, warming air 1 °C with OTCs significantly delayed the timing of *E. vaginatum* leaf senescence and extended the duration of leaf growth during the growing season. Previous warming experiments in the Arctic have demonstrated that warming generally can change aboveground phenology of deciduous shrubs and sedges (Bjorkman *et al.* 2015; Blume-Werry *et al.* 2017; Collins *et al.* 2021; Starr *et al.* 2000; Sullivan and Welker 2005). Previous studies showed that *E. vaginatum* within the warming chambers grew for a longer period than in control plots during the period of highest photosynthetically active radiation (Schedlbauer *et al.* 2018; Sullivan and Welker 2005). However, the warming treatment at our site had had no significant effect on root phenology (Bjorkman *et al.* 2015; Blume-Werry *et al.* 2017; Kummerow and Ellis 1984; Radville *et al.* 2018; Schwieger *et al.* 2018). In our study, 1 °C warming of air had little effect on soil temperature at 2 cm belowground and therefore would not have been sufficient to stimulate earlier startup or later senescence of roots.

Plant species differ in many functional traits that drive differences in biomass allocation (Falster *et al.* 2018). The root-to-shoot ratio shown in Fig. 4 showed that the distribution among *E. vaginatum* organs are more in line with the allometric distribution theory. The biomass ratio between organs of *E. vaginatum* does not respond to changes in climate or soil environmental gradients (Liu *et al.* 2020). The Arctic region is an area with low nitrogen content (Liu *et al.* 2018). *Eriophorum vaginatum* needs to allocate more biomass to the underground part to effectively increase the uptake of nutrients and water by *E. vaginatum*. Therefore, when the leaf growth period is extended, most of the biomass of the products of photosynthesis may contribute to the belowground part.

There are many reasons for the response of plant phenology to the environment; variables such as soil moisture, photoperiod, functional traits and the availability of nitrogen can play important roles in controlling the phenology of root growth in the Arctic (Barichivich *et al.* 2013; Liu, *et al.* 2017; Radville *et al.* 2016a). In our research, we did not observe the photoperiod, functional traits and the nitrogen availability of *E. vaginatum*, but we observed that atmospheric temperature is closely related to leaf phenology. The soil thaw depth is synchronized with the trend of root phenology (Figs 1 and 2), indicating that the soil thaw depth affects root phenology.

Although there was a trend toward higher production within the chambers, statistical analysis showed that warming did not significantly increase the biomass of leaves and roots. The results of Parker *et al.* (2017) at the Toolik Lake site also showed that warming did not affect the growth rate of *E. vaginatum*. Many previous studies have also shown that warming does not significantly increase root biomass or photosynthetic rate (Hobbie and Chapin 1998; Hollister and Flaherty 2010; Starr *et al.* 2000). Cold growing season temperatures *per se* do not directly affect sedge productivity in the tundra. Other factors controlled by low temperatures, such as low nutrient availability or short growth duration, may indirectly affect tundra biomass (Hollister and Flaherty 2010; Post *et al.* 2009; Rosa *et al.* 2015; Shaver and Billings 1977). Laboratory experiments also detected low total C and N contents in the roots (8.4 g/kg) and soils (1.1 g/kg) of *E. vaginatum* tussocks in Toolik Lake site; hence *E. vaginatum* root growth may be limited by N content in the soil (Liu *et al.* 2018).

Interannual variation and environmental factors impacting biomass

Our study showed the date at which the *E. vaginatum* leaves and roots start to grow in 2017 was later than in 2016 and there was more biomass of leaves and roots in 2017 than in 2016. These differences in phenology and biomass coincided with differences in abiotic conditions between 2016 and 2017. Higher temperatures at the beginning of the growing season in 2017 may have been a cue for growth initiation. Furthermore, mean daily air temperature in the 2017 growing season was slightly higher than in 2016, and thaw depth in 2017 was deeper than in 2016 (Fig. 1). These conditions would facilitate the nutrient uptake of deep roots and increase the biomass of leaves and roots (Chapin and Shaver 1985).

Our results also showed there was slight hysteresis between air temperature and leaf biomass in that leaf biomass remained high in September even when air temperature had dropped (Fig. 5). Given the adaptation of tundra plants to low temperatures, factors other than temperature, such as light, nutrient availability and snow cover, may exert equally important controls over *E. vaginatum* growth (Chapin and Shaver 1985; Rosa *et al.* 2015; Sullivan *et al.* 2015). In growing season, the ratio of root to shoot (R/S) of *E. vaginatum* gradually increases with time, but most of it is less than 1, indicating that more biomass may be allocated to leaves relative to roots (Kummerow and Ellis 1984; Wang *et al.* 2016). Wang *et al.* (2016) also showed that aboveground biomass of tundra increased significantly with local mean annual temperature, but belowground biomass did not increase over a mean annual temperature gradient of more than 20 °C. Such a shift in allocation to leaf biomass can impact carbon cycling in tundra ecosystems through altered litter input in the soil (Day *et al.* 2008; Pendall *et al.* 2004; Wang *et al.* 2016). The depth of thaw in our study was positively correlated with root biomass, consistent with other studies (Shaver and Billings 1977; Wipf and Rixen 2010). This indicates that the root growth late in the growing season is not a result of limiting soil temperatures in the year. The depth of thaw may increase the potential for nutrient uptake and water uptake from existing deep roots (Farrar and Jones 2000; Myers-Smith and Hik 2013). *Eriophorum* root growth vertical distribution deepens as the active layer is increased artificially (Blume-Warry *et al.* 2019). *Eriophorum* species can consistently take up N at greater depth in thaw profile, even after aboveground senescence (Blume-Warry *et al.* 2019; Keuper *et al.* 2017; Wang *et al.* 2018; Zhu *et al.* 2016), which directly affects the dynamics of root biomass. Our findings, therefore, suggest that there are differences in the environmental factors that drive the temporal variation of leaf and root growth, which may help to simulate or predict carbon and nitrogen losses as well as biomass changes under rapid climate change (Freschet *et al.* 2013; Wardle 2004).

CONCLUSIONS

This study examined the responses of phenology and biomass of *E. vaginatum* leaves and roots to experimental warming of Arctic tundra using OTCs. We observed the dynamics of leaves and roots of *E. vaginatum* synchronously and used a model to describe the phenology of leaves and roots of *E. vaginatum*. The phenology of the leaves in the growing season responded quickly to changes in temperature, but the phenology of the root system was not affected by the increase in temperature, implying that leaves and roots may be decoupled in response to environmental changes. The phenology and biomass of leaves and roots have interannual variation. Air temperature and soil thaw depth are important factors affecting leaf and root phenology, respectively. However, temperature is not the main factor that affects leaf and root biomass.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Distribution of carbon and nitrogen in the above- and belowground organs and soils of three ecotypes.

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