

Intra-specific variation in phenology offers resilience to climate change for *Eriophorum vaginatum*

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Abstract:

Phenology of arctic plants is an important determinant of the pattern of carbon uptake and may be highly sensitive to continued rapid climate change. *Eriophorum vaginatum* has a disproportionate influence over ecosystem processes in moist acidic tundra, but it is unclear whether its growth and phenology will remain competitive in the future. We asked whether northern tundra ecotypes of *E. vaginatum* could extend their growing season in response to direct warming and transplanting into southern ecosystems. At the same time, we asked whether southern ecotypes could adjust their growth patterns in order to thrive further north, should they disperse quickly enough. Detailed phenology measurements across three reciprocal transplant gardens and two years showed that some northern ecotypes were capable of growing for longer when conditions were favourable, but their biomass and growing season length was still shorter than the southern ecotype. Southern ecotypes retained large leaf length when transplanted north and mirrored the growing season length better than the others, mainly due to immediate green-up after snowmelt. All ecotypes retained the same senescence timing, regardless of environment, indicating a strong genetic control. *E. vaginatum* may remain competitive in a warming world if southern ecotypes can migrate north.

Key Words: Phenology, Tundra, *Eriophorum vaginatum*, Ecotype, Climate Change

43 Introduction

44 The Arctic is warming at twice the global average, resulting in profound changes in not only
45 temperature but also precipitation and growing season lengths (Mudryk et al. 2019). Biological
46 processes in the Arctic are closely tuned to environmental cues and as such are showing signals
47 of change in response to a changing climate (Post et al. 2009). This is important because living
48 organisms hold critical control over biogeochemical, energy, and hydrological fluxes with huge
49 potential to further exacerbate climate change (Wookey et al. 2009). Plant communities across
50 the Arctic have shown particularly striking changes in response to warming as they grow taller
51 (Bjorkman et al. 2018), increase cover, and undergo shifts in dominance with mosses often in
52 decline and deciduous shrubs in ascendance (Elmendorf et al. 2012b). Natural observations of
53 change are supported by experimental evidence that shows that there are clear winners and losers
54 in the plant community as the climate continues to change (Elmendorf et al. 2012a).

55
56 The direct effects of warming on arctic plant community composition and growth have been
57 well studied through a circumpolar network of open-top chamber (OTC) experiments
58 (Elmendorf et al. 2012a). These generally show that plant growth increases with warming and
59 that deciduous shrubs increase in dominance but also that responses are mediated by site
60 conditions such as local climate and soil moisture (Elmendorf et al. 2012a). Wider observation
61 networks are detecting 'greening' signals with increases in height and cover at the plot level
62 (Bjorkman et al. 2018) and increases in Normalised Difference Vegetation Index (NDVI) at
63 satellite levels (Epstein et al. 2012). Observations of the expansion of deciduous shrub cover are
64 consistent with these trends (Myers-Smith et al. 2011). One of the key findings is that certain
65 groups in the community such as mosses decrease in cover as the community responds to
66 warming, while the response of other groups such as sedges is mixed (Elmendorf et al. 2012a). It
67 is important to understand how all constituents of the plant community will change in the future

because they all contribute significantly to ecosystem processes such as primary productivity, reflectance, and phenology, among others (Myers-Smith et al. 2019).

Climate change in the Arctic is multifaceted and will affect aspects of plant performance in different ways (Post et al. 2009; Box et al. 2019). For example, summer growing seasons are extending in the Arctic due to reductions in snow cover duration (SCD) (Box et al. 2019). Model projections indicate that SCD over much of the Arctic will decline by about 10-30% by the end of this century as a consequence of delayed onset of snow cover as well as earlier snowmelt (Brown et al. 2017). The projected decrease in SCD implies that the potential growing season should lengthen, as found by Park et al. (2016), who used the normalized difference vegetation index (NDVI) to analyze changes in growing season length in boreal and arctic vegetation. Broadly speaking, plant phenology in the Arctic has been shown to be sensitive to abiotic conditions (Assmann et al. 2019; Prevéy et al. 2017). At the beginning of the growing season, earlier snowmelt should result in earlier green-up, as abundant sunshine and the disappearance of snow produces good growing conditions. Many studies have documented the importance of snowmelt timing for controlling the phenology of arctic plants with earlier snowmelt, which usually results in earlier onset of growth (Høye et al. 2007; Bjorkman et al. 2015; Khorsand Rosa et al. 2015; Semenchuk et al. 2016; May et al. 2020). Once the growing season is underway, it is less clear whether higher average temperatures will affect plant phenology in part because of interactions with snowmelt timing (Oberbauer et al. 2013). Geographical patterns in phenology further complicate the response of arctic plants to climate change. Across the Arctic, phenology of plants from more northern sites exhibited greater sensitivity to warming temperatures than plants from sites at more southern latitudes (Prevéy et al. 2017).

Increasing temperatures in autumn (Box et al. 2019) may offer an opportunity to plant communities to grow for longer, but it is difficult to forecast the effect of mid- and late-season growing conditions on phenology in the autumn. If autumn temperatures increase, it is not clear that arctic plants will respond by extending their growing season (Parker et al. 2017). Many species start to turn yellow in August when temperatures are still warm (Shaver and Laundre 1997). This may be because, in the Arctic, harsh winter conditions may appear suddenly, which could result in the loss of valuable resources through frost damage to live aboveground biomass that hasn't fully senesced. Some functional groups, notably some graminoids, may be able to delay senescence in response to warming conditions, while other functional groups may have fixed leaf life spans which are correlated with average growing season lengths (Oberbauer et al. 2013). Manipulation of the timing of green-up by removing snow or adding it with snow fences has shown that the length of phenological stages such as growth, flowering, or seed setting remained invariant even though the dates of start-up varied greatly (Khorsand Rosa et al. 2015; Semenchuk et al. 2016). Semenchuk et al. (2016) concluded that a range of herbaceous and shrub species in their study are periodic, meaning that the duration of phenological periods is genetically fixed. By extension, therefore, even if the end of season environment is suitable for continued growth, tundra plants may senesce early if their green-up was early.

While many studies have focused on variation at the species and community level of organization, few studies have looked at intraspecific variation in phenology of tundra plants. Since most arctic plants have widespread distributions, local adaptations are likely to be important for many species (Linhart and Grant 1996). Local adaptation is widespread in plant populations, especially those with many individuals covering a wide geographic range (Leimu and Fischer 2008; Hereford et al. 2009). Wagner and Simons (2009) reported differences between arctic and alpine populations in phenology of the annual *Koenigia islandica*, where the

117 arctic population flowered earlier than the alpine population. Bjorkman et al. (2017) reported that
118 southern populations of the arctic plants *Oxyria digyna* and *Papaver radicatum* were slower to
119 leaf out and to initiate senescence than northern (local) populations. Likewise, Parker et al.
120 (2017) showed that senescence of *Eriophorum vaginatum* grown in a common garden occurs
121 later for populations from the southern portions of a latitudinal gradient in the Alaskan Arctic.
122 Although growth rates were the same, the southern populations were able to accumulate more
123 biomass because of the longer growing season (Parker et al. 2017). Thus, it is important to base
124 models of phenology on not only a generalized phenotype but also to consider the variation
125 within species across their range where local dynamics may vary, although the assemblage
126 remains the same.

127
128 Many arctic plant species are distributed along the latitudinal gradient from Low to High
129 Arctic, which provides ample scope for locally adapted populations or ecotypes. Strong
130 adaptation to local climates may render arctic plants vulnerable to rapid climate change in their
131 locales if they are not able to respond quickly enough (McGraw et al. 2015). The degree of
132 phenotypic plasticity of ecotypes of arctic plants may determine their potential to take advantage
133 of, or survive, warmer conditions. *Eriophorum vaginatum* is a foundational species of moist
134 acidic tundra, meaning that it strongly dictates the system's physical structure as well as its
135 process rates (Chapin and Shaver 1985). *E. vaginatum* demonstrates clear ecotypic
136 differentiation in phenotypes (Shaver et al. 1986; Fetcher and Shaver 1990) and gene expression
137 (Mohl et al. 2020) across its South-North distribution in Alaska which reflects a wide range in
138 growing season conditions. McGraw et al. (2015) showed that the optimal environment for
139 tussock survival and tiller population growth in *E. vaginatum* had shifted northwards, meaning
140 that this important species may suffer from 'adaptational lag' and not keep pace with current
141 rates of climate change. To address the lag in the performance of local populations, they may

need to be supplemented by gene flow from the south (McGraw et al. 2015). Performance of the northern ecotypes of *E. vaginatum* is less flexible than the southern ecotypes in both net ecosystem exchange (NEE) (Curasi et al. 2019) and leaf growth (Fetcher and Shaver 1990). But as previously stated, changes in growing season length offer new opportunities to grow for longer and remain competitive in their environment.

Here we investigate the role of genetic background and environmental conditions as they affect the phenology of *E. vaginatum* growing in a reciprocal transplant experiment in northern Alaska. We use this system to ask:

1. Can the phenology of *E. vaginatum* ecotypes match growing conditions when transplanted into warmer ecosystems with longer growing seasons?
2. Do southern populations retain their growth patterns when transplanted north?
3. Do local ecotypes increase growth and growing season length when experimentally warmed *in situ*?
4. Does *E. vaginatum* exhibit a fixed periodicity in its phenology, i.e. if it starts growing early will it senesce early?

Materials and methods.

Site description and experimental design.

Eriophorum vaginatum L. (Cyperaceae) is a tussock-forming sedge that has a strong influence on tundra microclimate and carbon cycling potential (Chapin et al. 1979, Curasi et al. submitted). It covers large areas of northeastern Siberia (Walker et al. 2005) and is also found in wetlands and moorlands throughout the circumpolar region (Wein 1973). In Alaska, full-sized

adult tussocks can consist of 300–600 live tillers (Fetcher and Shaver 1982). Tussocks can live for well over 100 years (Mark et al. 1985) and can vary widely in size (Shaver et al. 1986).

Three common gardens of reciprocally transplanted tussocks of *E. vaginatum* were established at Sagwon (SG; 69.42°N, 148.72°W, elev. 300 m), Toolik Lake (TL; 68.63°N, 149.36°W, elev. 760 m) and Coldfoot (CF; 67.26°N, 150.17°W, elev. 331 m) along the Dalton Highway in Alaska, USA. CF is approximately 4 °C warmer than the other sites during the summer months of June and July and average temperature stays above freezing for 2 more months during Spring and Autumn, resulting in more thawing degree days (Fig S1, Supplementary Figure S2). Although SG is further north, it is at a lower elevation than TL, resulting in similar overall temperature regimes (Fig S1, Supplementary Figure S2). Tussocks of *E. vaginatum* dominate all three sites with deciduous (*Betula nana* L., *Salix* spp., and *Vaccinium uliginosum* L.) and evergreen shrubs (*Vaccinium vitis-idaea* L, *Rhododendron tomentosum* Harmaja), mosses, and lichens growing in between the tussocks. The northern ecotypes of *E. vaginatum* are found at Sagwon, which is on the northern edge of moist acidic tundra and may not have been glaciated during the Pleistocene, and at Toolik Lake, which is in moist acidic tundra near the Brooks Range and was most recently glaciated in the Late Wisconsinian (~20,000 yr BP) (Hamilton 2003, Kaufman and Manley 2004, Kaufman et al. 2011, Walker et al. 2005). One of the southern ecotypes is found at Coldfoot, which is in muskeg with encroaching trees (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) that were not present in 1982 when previous common gardens were established (Shaver et al. 1986). Coldfoot was glaciated during the Early Wisconsinian (~70,000 - ~40,000 yr BP), but probably not during the Late Wisconsinian (Kaufman and Manley 2004, Kaufman et al. 2011). The three sites were likely colonised by *E. vaginatum* at different times and therefore were differentiating as ecotypes for

different amounts of time, nonetheless they have all had at least 20,000 years to potentially develop traits that reflect their home environments.

In August 2014 mature tussocks were transplanted between the three sites with tussocks from each home site transplanted into their home site to act as controls according to methods specified in Bennington *et al.* (2012) and Schedlbauer *et al.* (2018). Briefly, a serrated knife was used to sever the rhizomes from roots and soil at a tussock's base and remove it from the tundra. Tussocks were then placed in the vacant positions at the common garden where local tussocks had been removed. This method has a high success rate because of *E. vaginatum*'s deciduous rooting habit; although roots are severed during transplanting, new roots grow in each subsequent year, restoring full root function (Bennington et al. 2012). Tussocks were planted in clusters of three, approximately 0.5 m apart from each other. Clusters were paired at SG and TL where one cluster of each pair was passively warmed using open-top chambers (OTC) (Schedlbauer et al. 2018). Ten pairs of clusters of the three populations were arranged in an approximately 25 m x 30 m grid. Open-top chambers were placed on the selected clusters from 11 July until 28 August in 2015, from 2 June until 28 August in 2016, and from 30 May until 26 August in 2017 causing a mean hourly air temperature increase of 1.16°C and 1.04°C at Sagwon in 2016 and 2017, respectively. At Toolik Lake, the respective temperature increases were 0.60°C and 1.01°C. At CF, where there was no warming treatment, clusters were arranged as singletons in a smaller grid (25 m x 15 m). At each site, 10 non-transplanted tussocks were identified next to the transplant garden in order to assess the effect of transplanting on measured response variables.

Leaf Measurements

Through the growing seasons of 2016 and 2017 (early June - mid-September), leaf growth and senescence were monitored on transplanted tussocks. Growing season air temperatures at

each transplant garden during the measurement years were representative of typical climatic conditions of each site (Supplementary Table S1). A tiller from one tussock of each cluster was tagged and monitored according to Shaver and Laundre (1997) and Parker et al. (2017). A small zip tie was secured around the base of the tiller, so as to include all leaves with any visible green portions while excluding any previously senesced leaves from previous growth. The total leaf length and the length of the green portions were measured to the nearest 5 mm approximately once a week for each leaf in a tiller, from oldest to youngest.

Tiller Phenology Data Processing

The senesced portions of leaves were fragile and sometimes broke off; since this occurred after leaves had reached their full length, the total length was corrected to match the last measurement of the unbroken leaf. Where lengths of single leaves were missing for a time point due to human error, they were replaced with the mean of the previous and following time points. Only leaves that were growing during the season of measurement were measured, thereby excluding leaves that were grown in the previous year and were senescing as well as leaves that had been initiated for the next year but were not elongating. A double logistic phenology model (Busetto *et al.* 2010) was fit using non-linear least squares regression to green leaf growth pattern over the growing season on every tiller in each year (See Fig.1 for example fits):

$$G(d) = (G_{Min} + (G_{Max} - G_{Min})) \left(\frac{1}{1 + e^{-mS(d-S)}} + \frac{1}{1 + e^{-mA(d-A)}} - 1 \right) \quad \text{Equation 1.}$$

where $G(t)$ is the green leaf length (cm) at day of the year (d), G_{Max} is the maximum green leaf length observed, G_{Min} is the minimum green leaf length over the year (here set to 1 cm because *E. vaginatum* retains a small amount of green biomass over winter (Shaver & Laundre, 1997)), mS is the spring growth rate, and mA is the autumn senescence rate at time-points S and A , which are found halfway on the increase and decrease curves, respectively.

Phenology metrics specified by Busetto et al. (2010) as significant points on the phenology curve were extracted from each curve (Fig. 1). S1, S5, A1, and A5 are the time points at which changes in curvature are at their maximum or minimum (Busetto *et al.* 2010). S2, S4, A2, and A4 are dates at which the double logistic curve transitions from linear to non-linear (or *vice versa*), and S3 and A3 are the points of maximum increase or decrease of the curve (Busetto et al. 2010). The tiller growing season (S1A1) was calculated as the number of days between metrics S1 and A1, which represents the period between the beginning of peak growth rate and the end of peak biomass (before senescence) and therefore when the majority of primary productivity takes place.

Poorly fitting models for individual tillers were removed from the dataset if they made biologically unrealistic estimates of Spring (onset of growth (S1) before April 1st, growth rate (*mS*) above 0.4 cm day⁻¹) and peak growing season (S5A1) phenology (metric A1-S5 less than 0). Additionally, if the any phenology model had a particularly poor fit to the extent that it was an outlier compared to other fit models (RMSE higher than 95 % percentile of all model fits), it was discarded. After this process, 130 curves from the three gardens could be analyzed in 2016 and 113 in 2017 (20 total removed). The curves were split relatively evenly between populations (SG, TL, or CF), sites (SG, TL, or CF) and treatments (OTC or control), resulting in even replication across all combinations (Supplementary Figure S1).

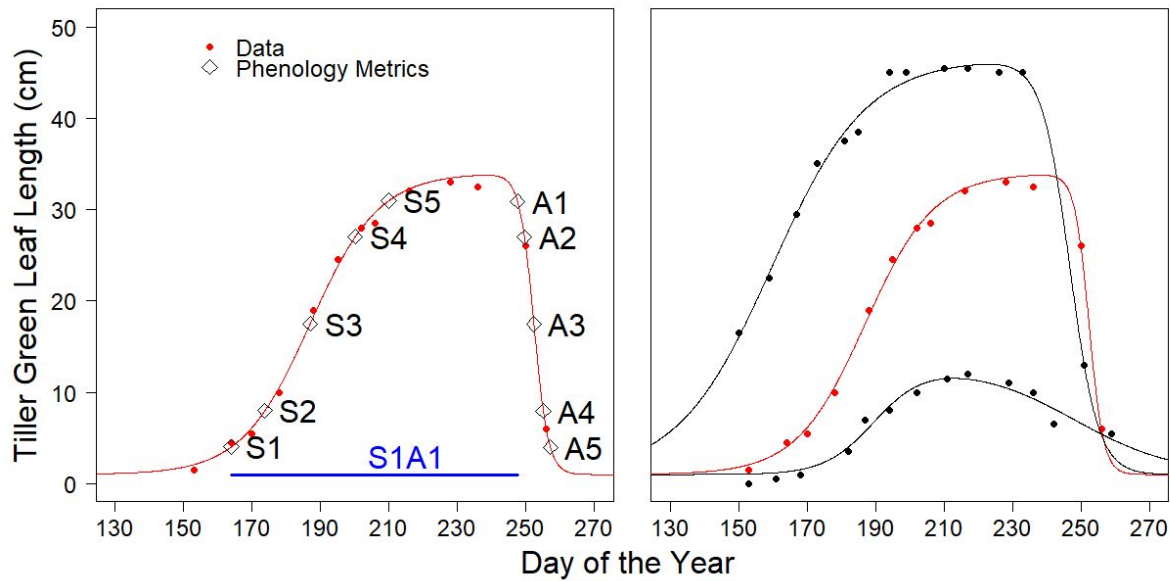


Figure 1: Example of double logistic model (Equation 1) fit to the growth pattern of a tiller over a growing season and metrics that can be calculated from this curve (in red, left panel) and fit to two other example datasets (in black, right panel).

Environmental data processing

Air temperatures for Coldfoot and Sagwon were extracted and calculated from daily average data from the SNOTEL database (<http://www.wcc.nrcs.usda.gov/snow/>) and from the Toolik Field Station Environmental Data Center (EDC) of the University of Alaska, Fairbanks (*Environmental Data Center Team*) for the Toolik Lake site. Snowmelt timing was extracted from the SNOWTEL database for Sagwon and Coldfoot and from the Environmental Data Center for the Toolik site (Environmental Data Center, University of Alaska, Fairbanks; <https://toolik.alaska.edu/edc/index.php>). The end of the growing season was defined as the first day in autumn that the prior seven-day running average minimum daily air temperature returned to 1°C; consequently, the potential growing season length was determined as the number of days between snowmelt and a return to consistently low temperatures. We used a seven-day running

average temperature because cold-snaps can happen at any time in the season and we chose 1 °C because the seven-day running average of 0 °C did not occur until long after all plant activity had ceased (October). Note that this was the authors' judgement of a 'potential growing season length' for the purpose of this paper, to our knowledge there is no recognised definition in this system. Late season temperature was defined as the average air temperature at each site between 1 August and 14 August in any given year. This was deemed a period of time when plants are green but potentially receptive to phenological cues for senescence.

Statistical Analysis

Linear mixed effects models (Pinheiro et al. 2017) were used to test whether phenology variables (onset of growing season (S1), onset of senescence (A1), and growing season length (S1-A1)) were significantly affected by fixed effects: population source, common garden site, or sampling year using the 'nlme' package in R (R Development Core Team, 2016, Pinheiro et al. 2017). The tussock ID was used as a random intercept term. Models were simplified by removing interaction terms if they did not have a significant effect in order to get best estimates of main fixed effects (Crawley 2007). The effect of each factor in the final model was assessed relative to the null model (intercept only) by ANOVA (Crawley 2007). Linear mixed effects models (tussock ID as random intercept term) were used to assess the effect of population and environmental factors: potential growing season length and the effect of snowmelt date and late season temperature on the onset of growth, and onset of senescence, respectively. The number of days between the onset of growth and onset of senescence was used to determine actual growing season length. All analyses were carried out with R v3.3.3 (R Development Core Team, 2016).

Results

Across all populations, tillers of *E. vaginatum* initiated growth earlier at Coldfoot than the other two sites (Table 1, Fig. 2) but there was no significant difference between populations across all gardens ($P = 0.195$, Table 1). However, the CF population responded to differences in site growing conditions more than the other populations, resulting in a significant interaction between populations and site (Table 1). The CF population started to senesce later than the northern ecotypes as represented by the TL and SG populations at all of the sites (Fig. 2). But the onset of growth at Toolik Lake and Sagwon was significantly delayed after snowmelt in 2016, which had low temperatures in early June (Table 1, Supplementary Figure S1). Thus, early June temperatures appeared to exert some control on the initiation of growth.

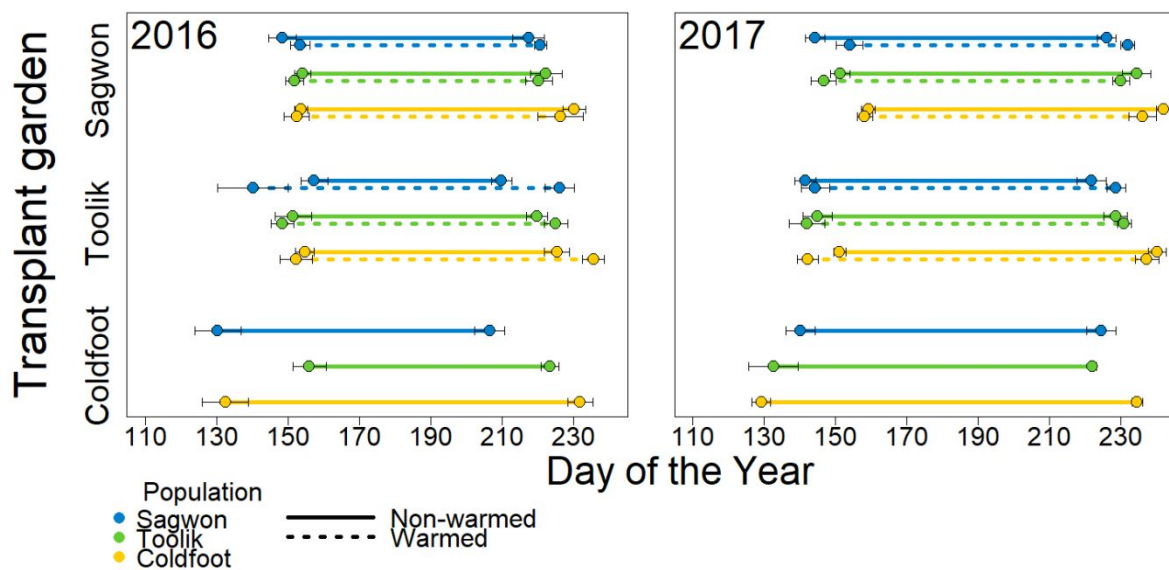


Figure 2: Summary of growing season of Coldfoot (yellow) Toolik Lake (green) and Sagwon (blue) populations across all three common gardens and over two years. Points on the left signify mean (+/- 1 standard error) onset of growing season (metric S1) and points on the right signify mean (+/- 1 standard error) onset of senescence (metric A1). The number of days between these (colored line) signifies the length of the growing season (metric A1S1). Statistics testing the effect of population, transplant garden (site) and year are found in Table 1, for model details, see Supplementary Table S5.

Table 1: Test statistics from linear mixed effects models showing the effect of fixed factors on growth patterns in *E. vaginatum*. Data are divided into an analysis of transplant only tussocks (no warming treatment, three common gardens) and an analysis that includes the effect of warming with open-top chambers (Sagwon and Toolik sites only). For model details, see Supplementary Table S5.

Non-warmed transplanted tussocks

Response variable	Fixed effect	d.f		F	P
S1 (Onset of Growth)	Population	2,	81	1.7	0.195
	Site	2,	81	21.6	< 0.001
	Year	1,	57	7.0	0.011
	Population x Site	4,	81	4.0	0.005
A1 (Onset of Senescence)	Population	2,	85	32.4	< 0.001
	Site	2,	85	3.4	0.038
	Year	1,	57	40.7	< 0.001
S1A1 (Growing Season)	Population	2,	81	12.5	< 0.001
	Site	2,	81	13.1	< 0.001
	Year	1,	57	42.3	< 0.001
	Population x Site	4,	81	3.7	0.008
Maximum Green length	Population	2,	87	19.2	< 0.001
	Site	2,	87	10.1	< 0.001
	Year	1,	68	33.9	< 0.001

Warmed and non-warmed transplant tussocks

Response variable	Fixed effect	d.f		F	P
A1 (Onset of Senescence)	Population	2,	112	18.4	< 0.001
	Site	1,	112	0.4	0.552
	Year	1,	79	58.4	< 0.001
	Warming	1,	112	2.4	0.125
S1A1 (Growing Season)	Population	2,	112	10.6	< 0.001
	Site	1,	112	3.7	0.056
	Year	1,	79	38.3	< 0.001
	Warming	1,	112	6.0	0.016
Maximum Green length	Population	2,	115	13.4	< 0.001
	Site	1,	115	10.8	0.001
	Year	1,	91	38.3	< 0.001

Warming	1,	115	1.8	0.184
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The southern ecotype had significantly longer leaves than the northern ecotypes ($P < 0.001$, Table 1), although this difference was less pronounced at Toolik Lake than at the other two sites (Table 1, Supplementary Figure S3). Warming with OTCs had no effect on leaf length (Table 1), but on average, over the two years, it did result in a significantly ($P < 0.05$) longer growing season, defined by the number of days between S1 and A1 (Table 1, Fig. 2). Warming did not affect spring phenology or autumn phenology in a statistically detectable way, but the combined effects may have increased the overall season length slightly.

The effect of transplanting was analysed by comparing tussocks that were transplanted into their 'home' site with non-transplanted 'control' tussocks. Across all sites transplanting did not affect onset of growth (metric S1 (Supplementary Figure S4, Supplementary Figure S5, Supplementary Table S3)) but on average make onset of senescence marginally earlier (metric A1 ($P = 0.066$, Supplementary Figure S4, Supplementary Figure S5, Supplementary Table S3)), although this pattern was not consistent and depended on population. Growing season length was not affected by transplanting (metric S1A1 (Supplementary Figure S4, Supplementary Figure S5, Supplementary Table S3)), but transplanting did significantly reduce maximum green length compared to non-transplanted controls ($P = 0.01$, Supplementary Figure S4, Supplementary Figure S5, Supplementary Table S3).

There was no significant relationship between the date of growth onset and the date of senescence onset across populations and no interaction between onset of growth and population (Fig. 3, Supplementary Table S4). CF populations consistently senesced later than the others, but this was unrelated to the onset of growth. Over the whole growing season, the actual growing season of leaves (Metric S1A1) of all populations was positively affected by potential growing length but the CF tussocks responded particularly strongly. This resulted in a statistically significant effect of potential growing season, population origin (CF was highest on average),

and an interaction between the two (Fig. 4, Supplementary Table S4). The onset of growth in spring was positively related to the day of snowmelt across all populations but the CF population was particularly responsive, with initiation of growth closely tracking the loss of snow at any given site (Fig. 5, Supplementary Table S4). In autumn, none of the populations in either year were responsive to differences in late season environmental conditions, in this case, temperature in the first half of August. Instead, the populations maintained a significant difference in senescence timing regardless of the garden they were present in with CF senescing particularly late (Fig. 6, Supplementary Table S4). There were significant differences between years with most tussocks senescing later in 2017 than 2016.

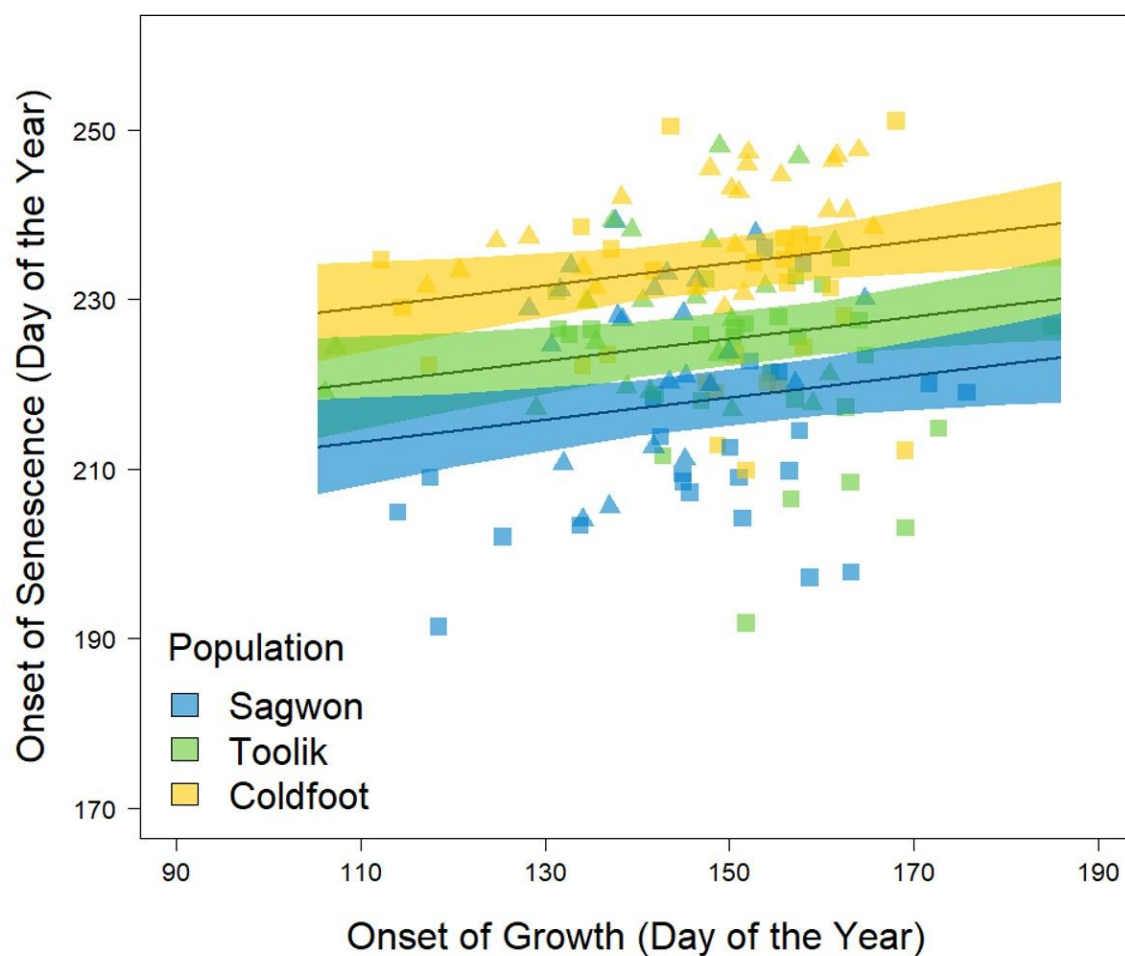


Figure 3: The day of onset of growth and the day of onset of senescence of leaves of *E. vaginatum* across all gardens populations in 2016 (squares) and 2017 (triangles). A linear

mixed effects model (Supplementary Table S4) showed no effect of onset of growth on onset of senescence ($P = 0.388$) but significant effect of population ($P < 0.001$). Modelled marginal effects (with 95 % confidence intervals) of onset of growth and population on the onset of senescence are displayed, for model details, see Supplementary Table S5.

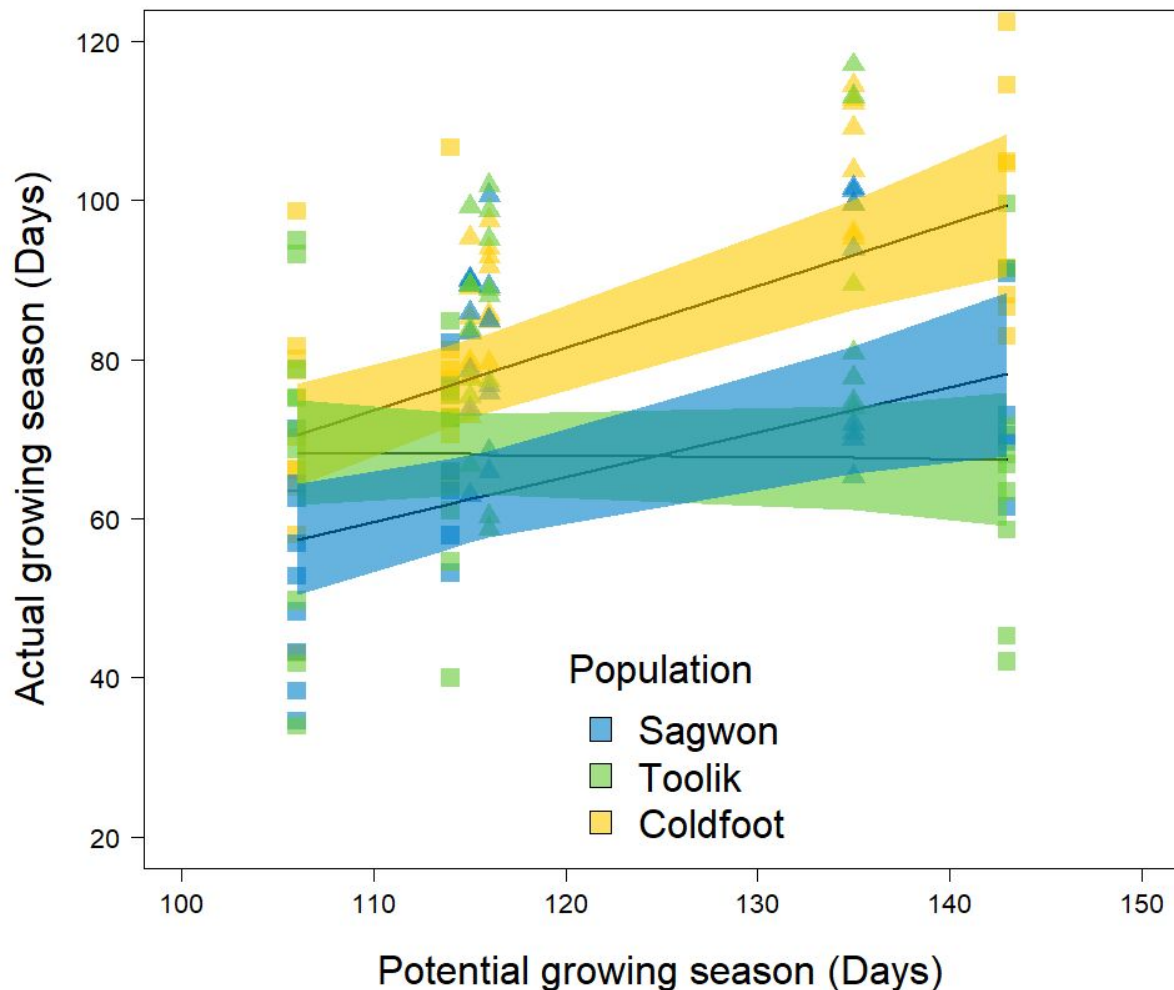


Figure 4: Relationship between the potential growing season (snowmelt - return of cold temperatures) and the actual growing season (S1A1) for three populations in 2016 (squares) and 2017 (triangles). See Supplementary Table S4 for linear mixed effects models showing a significant effect of population ($P < 0.001$), a significant positive effect of potential growing season ($P < 0.001$) and a significant interaction between the two ($P = 0.002$). Modelled marginal effects (with 95 % confidence intervals) of potential growing

season and population on actual growing season are displayed, for model details, see
Supplementary Table S5.

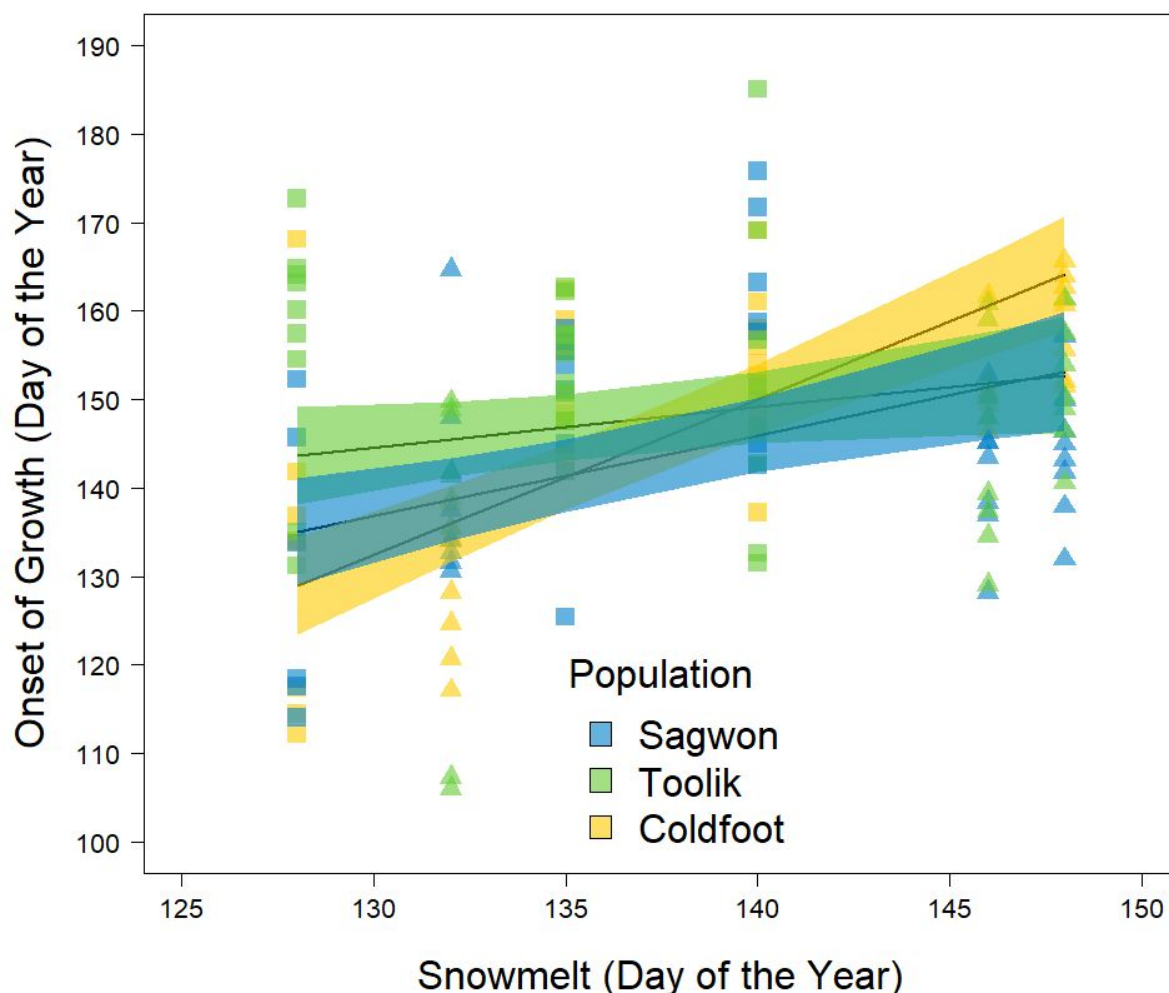


Figure 5: Relationship between snowmelt timing and onset of growth (S1) for three populations in 2016 (squares) and 2017 (triangles). See Supplementary Table S4 for linear mixed effects models showing no significant effect of population ($P = 0.188$), positive effect of snowmelt day ($P < 0.001$) and a significant interaction between the two ($P < 0.001$). Modelled marginal effects (with 95 % confidence intervals) of snowmelt day and population on onset of growth are displayed, for model details, see Supplementary Table S5.

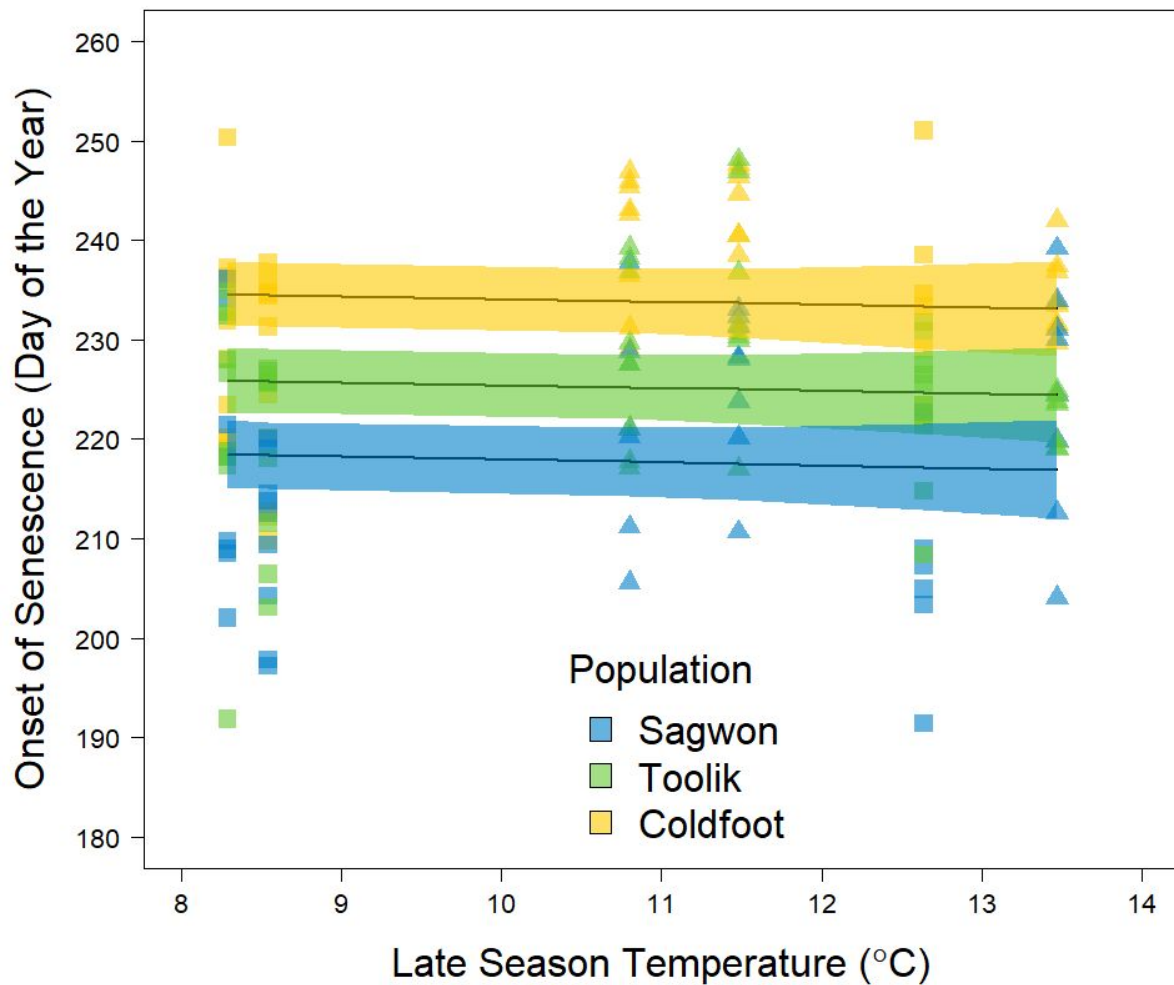


Figure 6: Relationship between late season temperature and onset of senescence (A1) for three populations in 2016 (squares) and 2017 (triangles). See Supplementary Table S4 for linear mixed effects models showing a significant effect of population ($P < 0.001$) but no effect late season temperature ($P = 0.575$). Modelled marginal effects (with 95 % confidence intervals) of late season temperature and population on onset of senescence are displayed, for model details, see Supplementary Table S5.

Discussion

Response of northern ecotypes to warming

Climate change is progressing rapidly in arctic ecosystems so it is essential for tundra plants, which are adapted to cold environments, to respond in kind. For the foundational species of moist acidic tundra, *Eriophorum vaginatum*, there is evidence that these long-lived species are already growing outside of their optimal climates (McGraw et al. 2015). To better understand how this species will respond to climate change, we measured phenology and growth in reciprocal transplant experiment combined with warming using OTCs. Firstly, we asked whether the phenology of the northern ecotypes can match longer growing seasons when transplanted south. The Sagwon population did grow for longer when transplanted south to Coldfoot, managing to take advantage of earlier snowmelt, followed by warm temperatures. Although the length of the growing season of the Toolik population did not change when moved southward, the initiation of growth following snowmelt was earlier in 2017 compared to its home site. When experimentally warmed with OTCs, there was a general pattern across all populations to slightly increase their growing season length, but they did not grow any larger. Taken together, phenology of the northern ecotypes showed some responsiveness to climate change simulation, but the effects were mixed and relatively small. This is consistent with the lack of change in tiller size when northern populations from Sagwon, Toolik Lake, and Prudhoe Bay were moved south in an earlier experiment (Fetcher and Shaver 1990, Souther et al. 2014).

Effects of transplanting on phenology of Eriophorum vaginatum

By comparing phenology leaf growth of tussocks transplanted into their 'home' site with non-transplanted tussocks, we show that there is a minimal effect of the physical disturbance on measured phenology traits (Supplementary Figure S4, Supplementary Figure S5). This is an effect that often assumed in such experiments (Parker et al. 2017, Curasi et al. 2018, Walker et

al. 2018) but rarely tested. One of the advantages of *E. vaginatum* for reciprocal transplants is its deciduous root system and lack of mycorrhizal symbiosis, which means that tussocks can be transplanted without disturbing the belowground environment (Shaver et al 1986, Parker et al. 2017, Schedlbauer et al. 2108). To this feature, we can now add the relative lack of response of phenology to transplanting. The timing of onset of growth and the length of the growing season was not different. The timing of senescence was overall marginally earlier, and the maximum length of leaves was slightly shorter which perhaps reflects a less well established connection between rhizomes and the soil resulting in less effective nutrient uptake. These data further underline the usefulness of *E. vaginatum* as a model species to study ecotypic variation of traits in mature plants.

Tussock competitiveness in a warming tundra

Eriophorum vaginatum will need to contend with changing temperature regimes as well as increasing competition from plant functional types that respond well under warming. The Arctic is warming rapidly (Mudryk et al. 2019) and there is only limited evidence as to how well *E. vaginatum* will fare in these warmer conditions. Parker et al. (2017) were not able to detect a response to simulated warming but Sullivan and Welker (2005) showed that warming to similar levels as in our experiments initiated early season growth of *E. vaginatum* in the tundra. Our study showed that tussocks across all populations stayed green for 3.76 days longer in response to direct warming but little else was responsive, therefore it is not clear whether the response of *E. vaginatum* to a gradual temperature increase will have tangible ecosystem effects. OTC experiments have recently shown that tundra plant communities (including moist acidic tundra, dominated by *E. vaginatum*) extend their growing season when warmed (May et al. 2020). This suggests that contemporary plant communities can take advantage of milder growing conditions, at least in the short term. In the long term, however, the future success of *E. vaginatum* may

depend more on the performance of its fellow community members than on its own. Many areas of tundra are becoming more productive and taller in response to climate change (Bjorkman et al. 2018) and deciduous shrubs are often the plants that increase growth the most as climate warms (Elmendorf et al. 2012a). If deciduous shrubs overgrow tussocks, which are more limited in their ability to grow taller, then the foundation species of moist acidic tundra may suffer declines. However, if tussocks remain green for longer in extended growing seasons (Park et al. 2016), and extend beyond that of shrubs, they may retain an important place in northern ecosystems. *E. vaginatum* remains photosynthetically active as long as it holds green leaves into August (Curasi et al. 2019), hence tussocks that can delay senescence may continue to accumulate carbon later into the season, after other species have dropped their leaves.

Plasticity and competitiveness of southern ecotypes

If the northern populations of *E. vaginatum* have only limited potential to respond to climate warming, can tussock tundra be maintained if southern populations or their genes move northward? In our study, the Coldfoot ecotype from the warmer site, south of the treeline (CF) did show plasticity in spring because the timing of green-up varied with the time of snowmelt. At the same time, senescence of the southern ecotype occurred later than that of the northern ecotypes across all environments, resulting in an apparent plasticity of growing season length in the CF ecotype. Parker et al. (2017) showed, using a single common garden in moist acidic tundra, that the southern ecotype grows later into the season and suggested that this trait is driven by adaptation to their warmer home site in the south. We show here that the southern ecotype maintains green leaves on average longer than the northern ecotypes (16 days longer than SG and 9 days longer than TL), regardless of which common garden they are growing in (700 thawing degree days difference between CF and SG gardens). Green leaves in *E. vaginatum* retain active photosynthetic tissue late into August (Curasi et al. 2019), therefore if southern

ecotypes can migrate north in sync with climate warming they may increase the fitness of a species which is currently suffering *in situ* (McGraw et al. 2015). Southern ecotypes grow taller leaves (Fetcher and Shaver 1990) and maintain green tissue later in the season than northern ecotypes, therefore they may have a greater capacity for C fixation (Shaver et al. 2007). Dependent on dispersal by wind and suitable ecosystem disturbance for establishment (McGraw et al. 2015), northward migration of southern ecotypes could potentially have ecosystem-level impacts by influencing net ecosystem exchange. This needs to be tested by explicitly considering tussocks (transplanted and non-transplanted) in ecosystem analyses. Further, studies that measure ecosystem processes are currently limited by peak season-only measurements (Souther et al. 2014, Walker et al. 2018, Curasi et al. 2019), to integrate ecotypes into ecosystem gas exchange, the whole growing season needs to be considered.

The pattern of greater spring phenological plasticity in the southernmost *E. vaginatum* population stands in contrast to results from that of the community-wide large-scale synthesis of phenology (Prevéy et al. 2017). The results from this synthesis extended over 21 degrees of latitude and over 10 degrees further north than our most northern site (SG). At very high latitudes, in the harsh growing conditions of High Arctic desert, the benefit of earlier spring green-up may outweigh the risk of damage by variation in early season weather (cold-snaps) (Prevéy et al. 2017), thus more northern sites had higher plasticity. In the present experiment, the southern ecotypes showed more plasticity in the timing of green-up. At Coldfoot, there may be less environmental risk to greening-up as soon as the snow melts, whereas in the tundra there is a high risk that harsh growing conditions will return post snowmelt (Supplementary Table S2, Parker et al. 2017).

Environmental vs genetic controls on phenology

Because snowmelt in the tundra is getting earlier and causing earlier plant green-up (Park et al. 2016; Assmann et al. 2019), one of the next questions is how does this affect biological processes later in the growing season and how does this compare with other important controls on late season phenology? Our Question 4 arose from the hypothesis that some arctic plant species are periodic (Semenchuk et al. 2016). Under this hypothesis, early green-up would result in early senescence due to genetic control over the length of *E. vaginatum*'s growing season. We found no evidence to support this hypothesis. In contrast to other authors (Khorsand Rosa et al. 2015; Semenchuk et al. 2016) we found no relationship between timing of early season and late season phenology. Instead, we find that timing of senescence is best predicted by the population origin of the tussock. This is postulated as the result of genetic adaptations to past environmental conditions, which genotype-environment association studies support as a driver in forming population structure conditions and patterns of *E. vaginatum* in north central Alaska (glaciation (Elizabeth Stunz, pers. comm.)). Senescing at the right time is particularly important in the Arctic where the abrupt start of winter can be harsh and damaging to exposed tissues (McGraw and et al. 1983). Therefore, it is plausible that genetic control over average timing of the return of cold temperatures at each of the home sites has a role in shaping the observed phenology patterns in the three populations studied.

While previous selection pressure clearly has a part to play in shaping contemporary late season phenology, it is important to consider the plastic response of phenology to environmental factors. Cold-snaps and frost can cause senescence in multiple species (McGraw et al. 1983) and a warm late season can delay senescence (May et al. 2017). We observed later senescence at the northern sites in 2017 compared with 2016 when late season temperatures were significantly warmer (Fig. 6) but more years of measurements at the same sites would be needed to start to determine the driving factors behind this variation. Temperatures towards the end of the growing season are quite variable, but photoperiod or the quality of light could be a more reliable cue for

triggering senescence. The length of photoperiod was shown to be critical for growth cessation in *Salix pentandra*, with northern populations requiring a shorter dark period to stop growth (Juntilla and Kaurin 1985). This is consistent with the need to cease growing before an early frost occurs, which is more likely at higher latitudes. Another potentially important but equally understudied light cue for senescence in arctic plants is the ratio of red:far red light as monitored by the phytochrome photoreceptors (Buchanan et al. 2015). As discussed by Parker et al. (2017) research into the sensitivity of tundra plants to light quality should remain a priority for research in the future.

Conclusions

In the tundra ecosystem dominated by *E. vaginatum*, the growing season of the northern ecotypes had a limited response to longer, more favorable growing conditions when transplanted south and therefore limited the potential to sequester C during warm shoulder seasons. The Arctic is warming faster than any other biome on Earth (Park et al. 2018) and warming is particularly pronounced at the shoulder seasons, resulting in longer growing seasons (Park et al. 2016). Our results support a hypothesis that the southern ecotype of *E. vaginatum* is better adapted to take advantage of this warming through having more plasticity in phenological response, but the northern ecotypes are more constrained, therefore would be unable to take advantage of a lengthened growing season (Fetcher and Shaver 1990). If the Arctic continues to become more productive (Epstein et al. 2012) and grow taller (Bjorkman et al. 2019), locally adapted ecotypes lacking the ability extend growth in height or phenology in the northern part of their range, as found for *E. vaginatum*, may need to rely on gene flow from southern populations to maintain a competitive balance in the ecosystem. At the present rate of climate change, the northern ecotypes already appear to be poorly adapted if the climate warms to the temperatures currently encountered by the southern ecotype (McGraw et al. 2015). Given the slow growth and

longevity of tussock forming plants in the arctic, the chances for establishment of southern ecotypes in the north seem unlikely, outside of assisted gene flow or migration (Borrell et al. 2020).

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Competing interests

The authors declare there are no competing interests

Contributors statement

NF, MLM and JT and TCP designed the experiment and measurement routine, TCP, NF and SU took the measurements. All Authors contributed to writing the manuscript.

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Data availability statement

Raw leaf length data that underpin the paper are supplied in Supplemental file 2

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