

1           **Intra-specific variation in phenology offers resilience to climate**  
2                           **change for *Eriophorum vaginatum***  
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24 Abstract:

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

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41

42 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

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

70  
71 Climate change in the Arctic is multifaceted and will affect aspects of plant performance in  
72 different ways (Post et al. 2009; Box et al. 2019). For example, summer growing seasons are  
73 extending in the Arctic due to reductions in snow cover duration (SCD) (Box et al. 2019). Model  
74 projections indicate that SCD over much of the Arctic will decline by about 10-30% by the end  
75 of this century as a consequence of delayed onset of snow cover as well as earlier snowmelt  
76 (Brown et al. 2017). The projected decrease in SCD implies that the potential growing season  
77 should lengthen, as found by Park et al. (2016), who used the normalized difference vegetation  
78 index (NDVI) to analyze changes in growing season length in boreal and arctic vegetation.

79 Broadly speaking, plant phenology in the Arctic has been shown to be sensitive to abiotic  
80 conditions (Assmann et al. 2019; Prevéy et al. 2017). At the beginning of the growing season,  
81 earlier snowmelt should result in earlier green-up, as abundant sunshine and the disappearance of  
82 snow produces good growing conditions. Many studies have documented the importance of  
83 snowmelt timing for controlling the phenology of arctic plants with earlier snowmelt, which  
84 usually results in earlier onset of growth (Høye et al. 2007; Bjorkman et al. 2015; Khorsand Rosa  
85 et al. 2015; Semenchuk et al. 2016; May et al. 2020). Once the growing season is underway, it is  
86 less clear whether higher average temperatures will affect plant phenology in part because of  
87 interactions with snowmelt timing (Oberbauer et al. 2013). Geographical patterns in phenology  
88 further complicate the response of arctic plants to climate change. Across the Arctic, phenology  
89 of plants from more northern sites exhibited greater sensitivity to warming temperatures than  
90 plants from sites at more southern latitudes (Prevéy et al. 2017).

91

92           Increasing temperatures in autumn (Box et al. 2019) may offer an opportunity to plant  
93 communities to grow for longer, but it is difficult to forecast the effect of mid- and late-season  
94 growing conditions on phenology in the autumn. If autumn temperatures increase, it is not clear  
95 that arctic plants will respond by extending their growing season (Parker et al. 2017). Many  
96 species start to turn yellow in August when temperatures are still warm (Shaver and Laundre  
97 1997). This may be because, in the Arctic, harsh winter conditions may appear suddenly, which  
98 could result in the loss of valuable resources through frost damage to live aboveground biomass  
99 that hasn't fully senesced. Some functional groups, notably some graminoids, may be able to  
100 delay senescence in response to warming conditions, while other functional groups may have  
101 fixed leaf life spans which are correlated with average growing season lengths (Oberbauer et al.  
102 2013). Manipulation of the timing of green-up by removing snow or adding it with snow fences  
103 has shown that the length of phenological stages such as growth, flowering, or seed setting  
104 remained invariant even though the dates of start-up varied greatly (Khorsand Rosa et al. 2015;  
105 Semenchuk et al. 2016). Semenchuk et al. (2016) concluded that a range of herbaceous and shrub  
106 species in their study are periodic, meaning that the duration of phenological periods is  
107 genetically fixed. By extension, therefore, even if the end of season environment is suitable for  
108 continued growth, tundra plants may senesce early if their green-up was early.

109  
110           While many studies have focused on variation at the species and community level of  
111 organization, few studies have looked at intraspecific variation in phenology of tundra plants.  
112 Since most arctic plants have widespread distributions, local adaptations are likely to be  
113 important for many species (Linhart and Grant 1996). Local adaptation is widespread in plant  
114 populations, especially those with many individuals covering a wide geographic range (Leimu  
115 and Fischer 2008; Hereford et al. 2009). Wagner and Simons (2009) reported differences  
116 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 radicum* 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

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

147

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

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

158

159

## 160 Materials and methods.

### 161 *Site description and experimental design.*

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

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

168  
169 Three common gardens of reciprocally transplanted tussocks of *E. vaginatum* were  
170 established at Sagwon (SG; 69.42°N, 148.72°W, elev. 300 m), Toolik Lake (TL; 68.63°N,  
171 149.36°W, elev. 760 m) and Coldfoot (CF; 67.26°N, 150.17°W, elev. 331 m) along the Dalton  
172 Highway in Alaska, USA. CF is approximately 4 °C warmer than the other sites during the  
173 summer months of June and July and average temperature stays above freezing for 2 more  
174 months during Spring and Autumn, resulting in more thawing degree days (Fig S1,  
175 Supplementary Figure S2). Although SG is further north, it is at a lower elevation than TL,  
176 resulting in similar overall temperature regimes (Fig S1, Supplementary Figure S2). Tussocks of  
177 *E. vaginatum* dominate all three sites with deciduous (*Betula nana* L., *Salix* spp., and *Vaccinium*  
178 *uliginosum* L.) and evergreen shrubs (*Vaccinium vitis-idaea* L, *Rhododendron tomentosum*  
179 Harmaja), mosses, and lichens growing in between the tussocks. The northern ecotypes of *E.*  
180 *vaginatum* are found at Sagwon, which is on the northern edge of moist acidic tundra and may  
181 not have been glaciated during the Pleistocene, and at Toolik Lake, which is in moist acidic  
182 tundra near the Brooks Range and was most recently glaciated in the Late Wisconsinian  
183 (~20,000 yr BP) (Hamilton 2003, Kaufman and Manley 2004, Kaufman et al. 2011, Walker et al.  
184 2005). One of the southern ecotypes is found at Coldfoot, which is in muskeg with encroaching  
185 trees (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) that were not present in 1982 when  
186 previous common gardens were established (Shaver et al. 1986). Coldfoot was glaciated during  
187 the Early Wisconsinian (~70,000 - ~40,000 yr BP), but probably not during the Late  
188 Wisconsinian (Kaufman and Manley 2004, Kaufman et al. 2011). The three sites were likely  
189 colonised by *E. vaginatum* at different times and therefore were differentiating as ecotypes for



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

192  
193 In August 2014 mature tussocks were transplanted between the three sites with tussocks  
194 from each home site transplanted into their home site to act as controls according to methods  
195 specified in Bennington *et al.* (2012) and Schedlbauer *et al.* (2018). Briefly, a serrated knife was  
196 used to sever the rhizomes from roots and soil at a tussock's base and remove it from the tundra.  
197 Tussocks were then placed in the vacant positions at the common garden where local tussocks  
198 had been removed. This method has a high success rate because of *E. vaginatum*'s deciduous  
199 rooting habit; although roots are severed during transplanting, new roots grow in each  
200 subsequent year, restoring full root function (Bennington *et al.* 2012). Tussocks were planted in  
201 clusters of three, approximately 0.5 m apart from each other. Clusters were paired at SG and TL  
202 where one cluster of each pair was passively warmed using open-top chambers (OTC)  
203 (Schedlbauer *et al.* 2018). Ten pairs of clusters of the three populations were arranged in an  
204 approximately 25 m x 30 m grid. Open-top chambers were placed on the selected clusters from  
205 11 July until 28 August in 2015, from 2 June until 28 August in 2016, and from 30 May until  
206 26 August in 2017 causing a mean hourly air temperature increase of 1.16°C and 1.04°C at  
207 Sagwon in 2016 and 2017, respectively. At Toolik Lake, the respective temperature increases  
208 were 0.60°C and 1.01°C. At CF, where there was no warming treatment, clusters were arranged  
209 as singletons in a smaller grid (25 m x 15 m). At each site, 10 non-transplanted tussocks were  
210 identified next to the transplant garden in order to assess the effect of transplanting on measured  
211 response variables.

### 212 *Leaf Measurements*

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

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

### 222 *Tiller Phenology Data Processing*

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

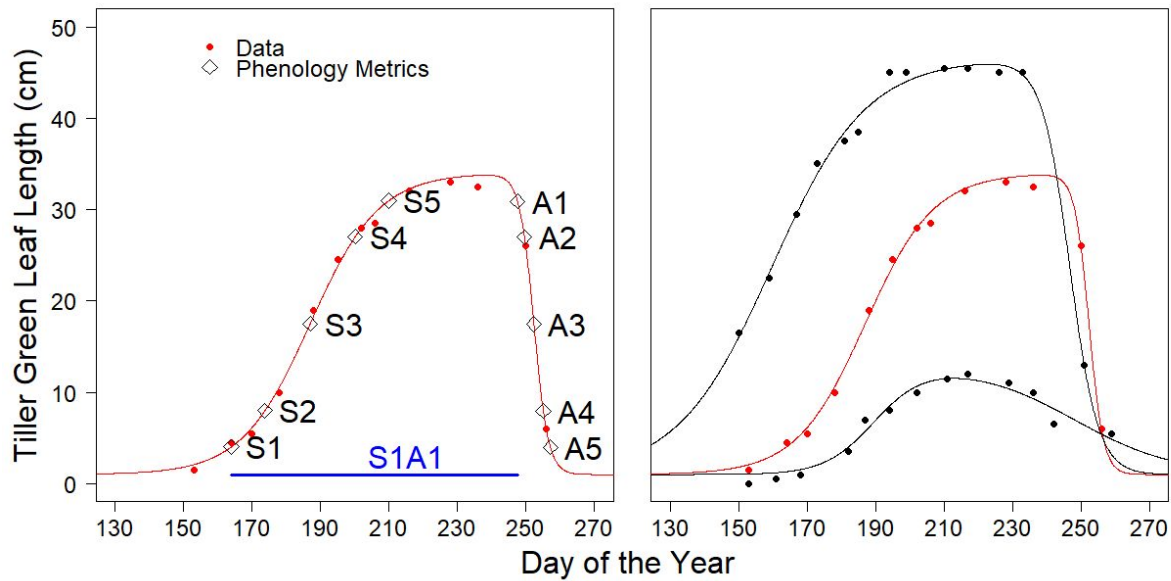
$$232 \quad G(d) = (G_{Min} + (G_{Max} - G_{Min})) \left( \frac{1}{1 + e^{-mS(d-S)}} + \frac{1}{1 + e^{-mA(d-A)}} - 1 \right) \quad \text{Equation 1.}$$

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

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

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

256



257  
 258 **Figure 1: Example of double logistic model (Equation 1) fit to the growth pattern of a tiller**  
 259 **over a growing season and metrics that can be calculated from this curve (in red, left panel)**  
 260 **and fit to two other example datasets (in black, right panel).**

261

### 262 *Environmental data processing*

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

273 average temperature because cold-snaps can happen at any time in the season and we chose 1 °C  
274 because the seven-day running average of 0 °C did not occur until long after all plant activity had  
275 ceased (October). Note that this was the authors' judgement of a 'potential growing season  
276 length' for the purpose of this paper, to our knowledge there is no recognised definition in this  
277 system. Late season temperature was defined as the average air temperature at each site between  
278 1 August and 14 August in any given year. This was deemed a period of time when plants are  
279 green but potentially receptive to phenological cues for senescence.

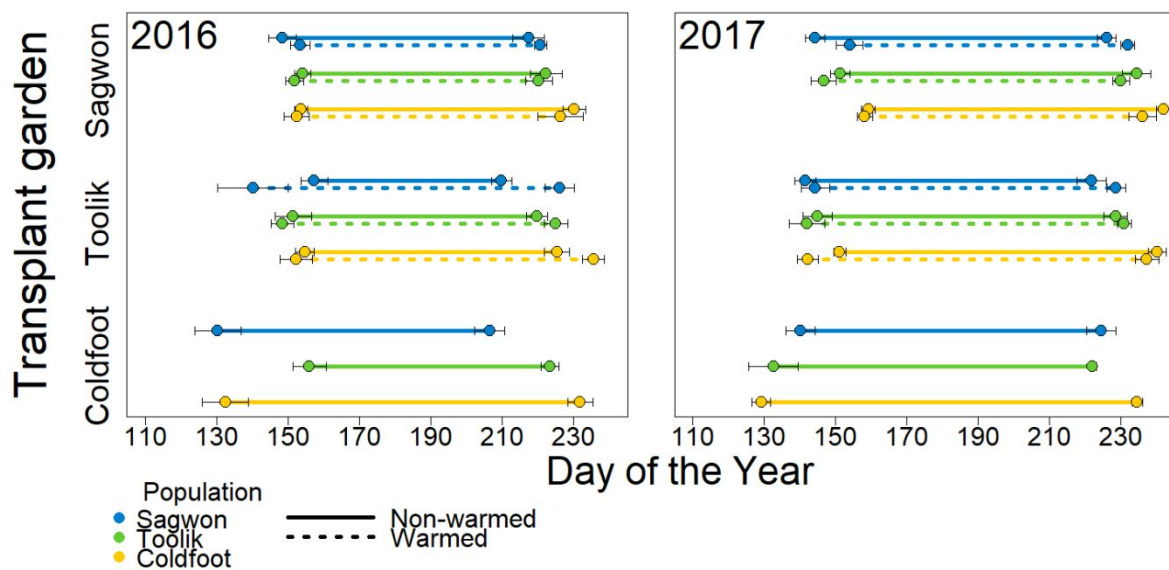
### 280 *Statistical Analysis*

281 Linear mixed effects models (Pinheiro et al. 2017) were used to test whether phenology  
282 variables (onset of growing season (S1), onset of senescence (A1), and growing season length  
283 (S1-A1)) were significantly affected by fixed effects: population source, common garden site, or  
284 sampling year using the 'nlme' package in R (R Development Core Team, 2016, Pinheiro et al.  
285 2017). The tussock ID was used as a random intercept term. Models were simplified by  
286 removing interaction terms if they did not have a significant effect in order to get best estimates  
287 of main fixed effects (Crawley 2007). The effect of each factor in the final model was assessed  
288 relative to the null model (intercept only) by ANOVA (Crawley 2007). Linear mixed effects  
289 models (tussock ID as random intercept term) were used to assess the effect of population and  
290 environmental factors: potential growing season length and the effect of snowmelt date and late  
291 season temperature on the onset of growth, and onset of senescence, respectively. The number of  
292 days between the onset of growth and onset of senescence was used to determine actual growing  
293 season length. All analyses were carried out with R v3.3.3 (R Development Core Team, 2016).

294

295 Results

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



305  
 306 **Figure 2: Summary of growing season of Coldfoot (yellow) Toolik Lake (green) and**  
 307 **Sagwon (blue) populations across all three common gardens and over two years. Points on**  
 308 **the left signify mean (+/- 1 standard error) onset of growing season (metric S1) and points**  
 309 **on the right signify mean (+/- 1 standard error) onset of senescence (metric A1). The**  
 310 **number of days between these (colored line) signifies the length of the growing season**  
 311 **(metric A1S1). Statistics testing the effect of population, transplant garden (site) and year**  
 312 **are found in Table 1, for model details, see Supplementary Table S5.**

314 **Table 1: Test statistics from linear mixed effects models showing the effect of fixed factors**  
 315 **on growth patterns in *E. vaginatum*. Data are divided into an analysis of transplant only**  
 316 **tussocks (no warming treatment, three common gardens) and an analysis that includes the**  
 317 **effect of warming with open-top chambers (Sagwon and Toolik sites only). For model**  
 318 **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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319

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

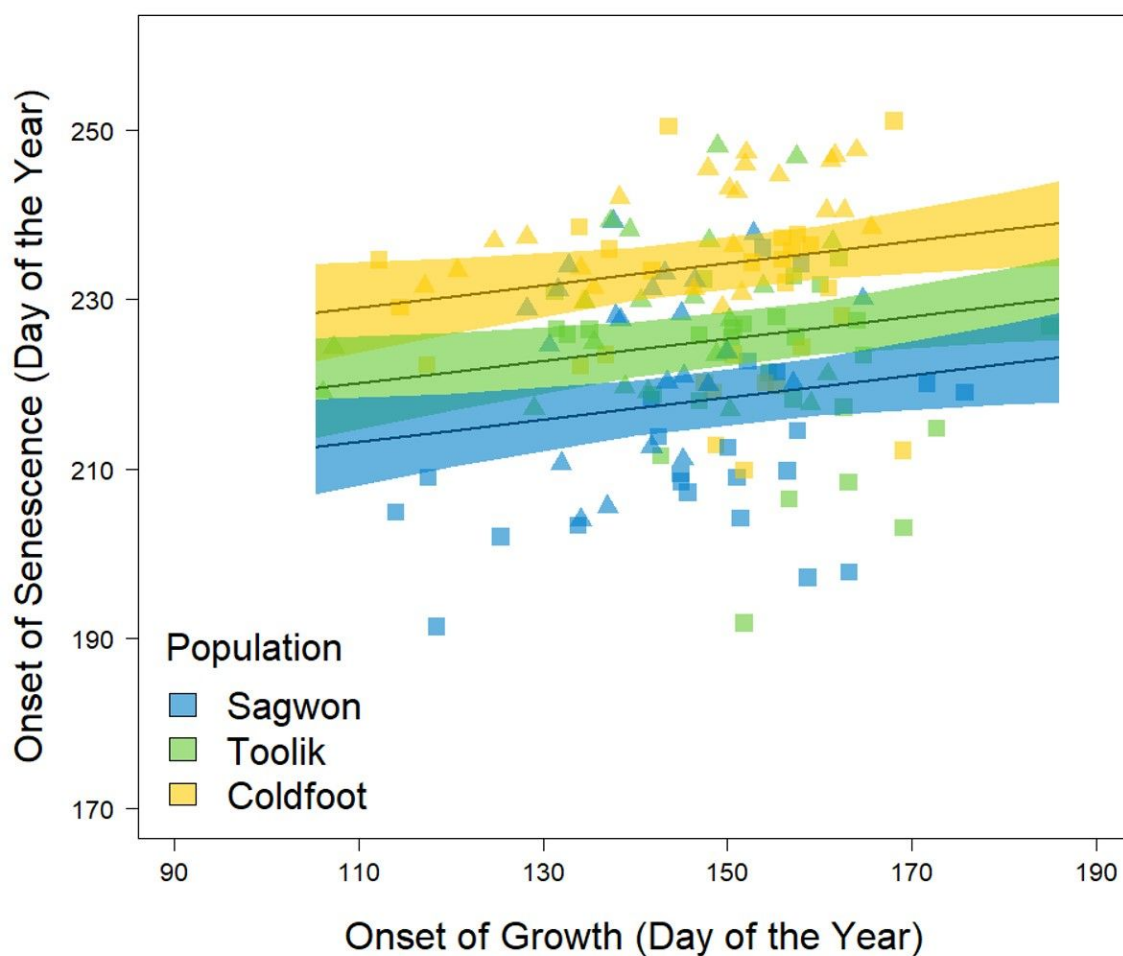
327 The effect of transplanting was analysed by comparing tussocks that were transplanted into  
 328 their 'home' site with non-transplanted 'control' tussocks. Across all sites transplanting did not  
 329 affect onset of growth (metric S1 (Supplementary Figure S4, Supplementary Figure S5,  
 330 Supplementary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

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



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

353

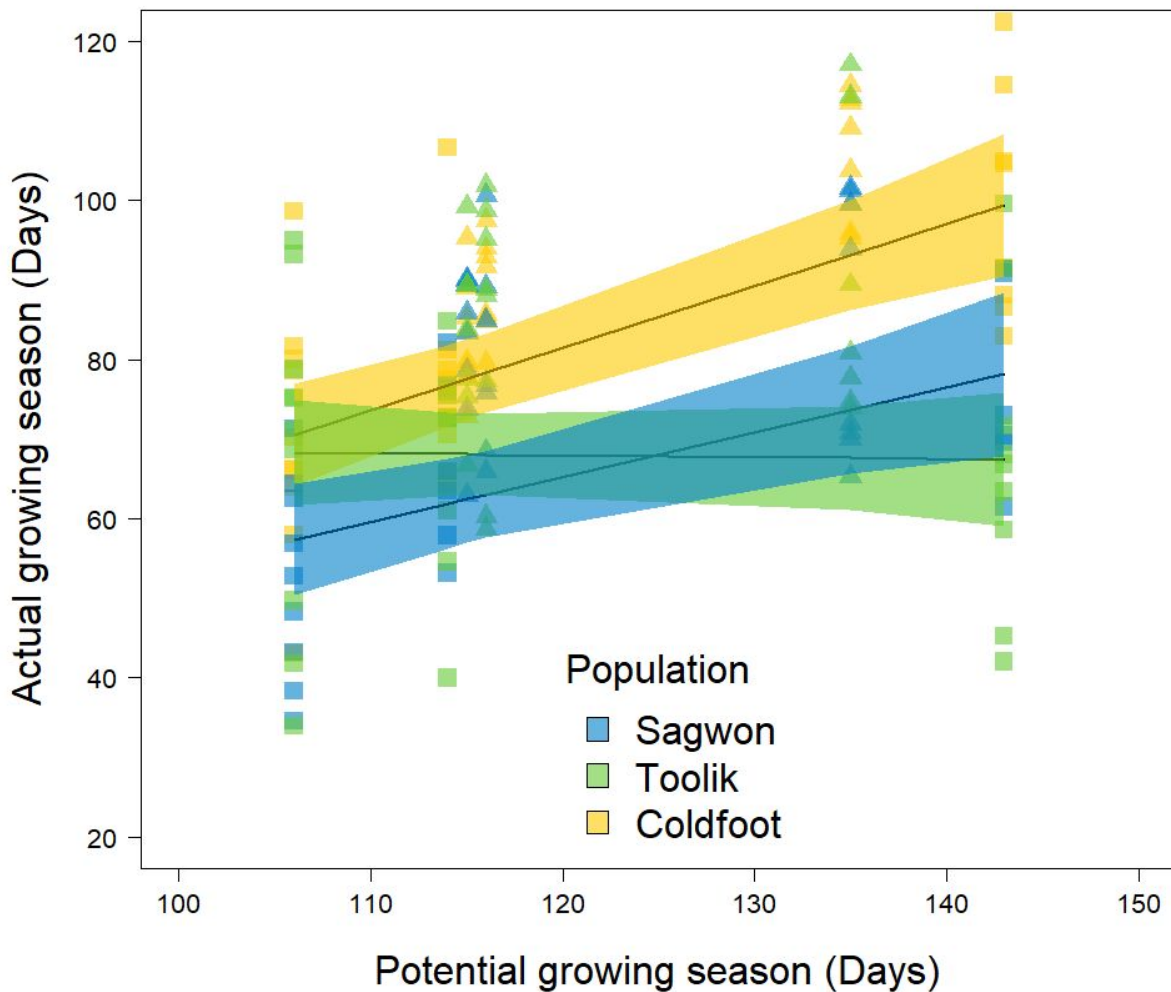


354

355 **Figure 3: The day of onset of growth and the day of onset of senescence of leaves of *E.***356 ***vaginatum* across all gardens populations in 2016 (squares) and 2017 (triangles). A linear**

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

361

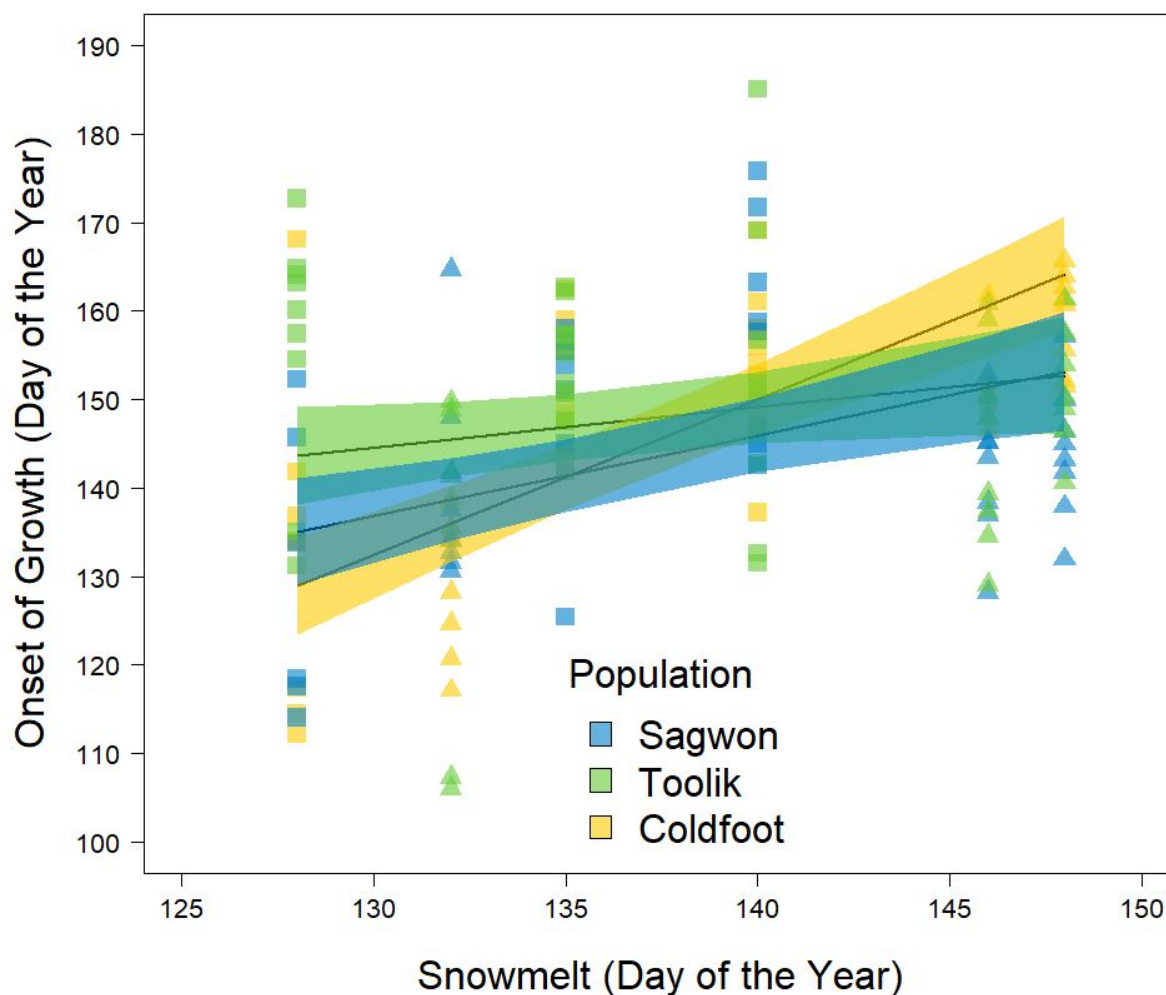


362

363 **Figure 4: Relationship between the potential growing season (snowmelt - return of cold**  
 364 **temperatures) and the actual growing season (S1A1) for three populations in 2016**  
 365 **(squares) and 2017 (triangles). See Supplementary Table S4 for linear mixed effects models**  
 366 **showing a significant effect of population ( $P < 0.001$ ), a significant positive effect of**  
 367 **potential growing season ( $P < 0.001$ ) and a significant interaction between the two ( $P =$**   
 368 **0.002). Modelled marginal effects (with 95 % confidence intervals) of potential growing**

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

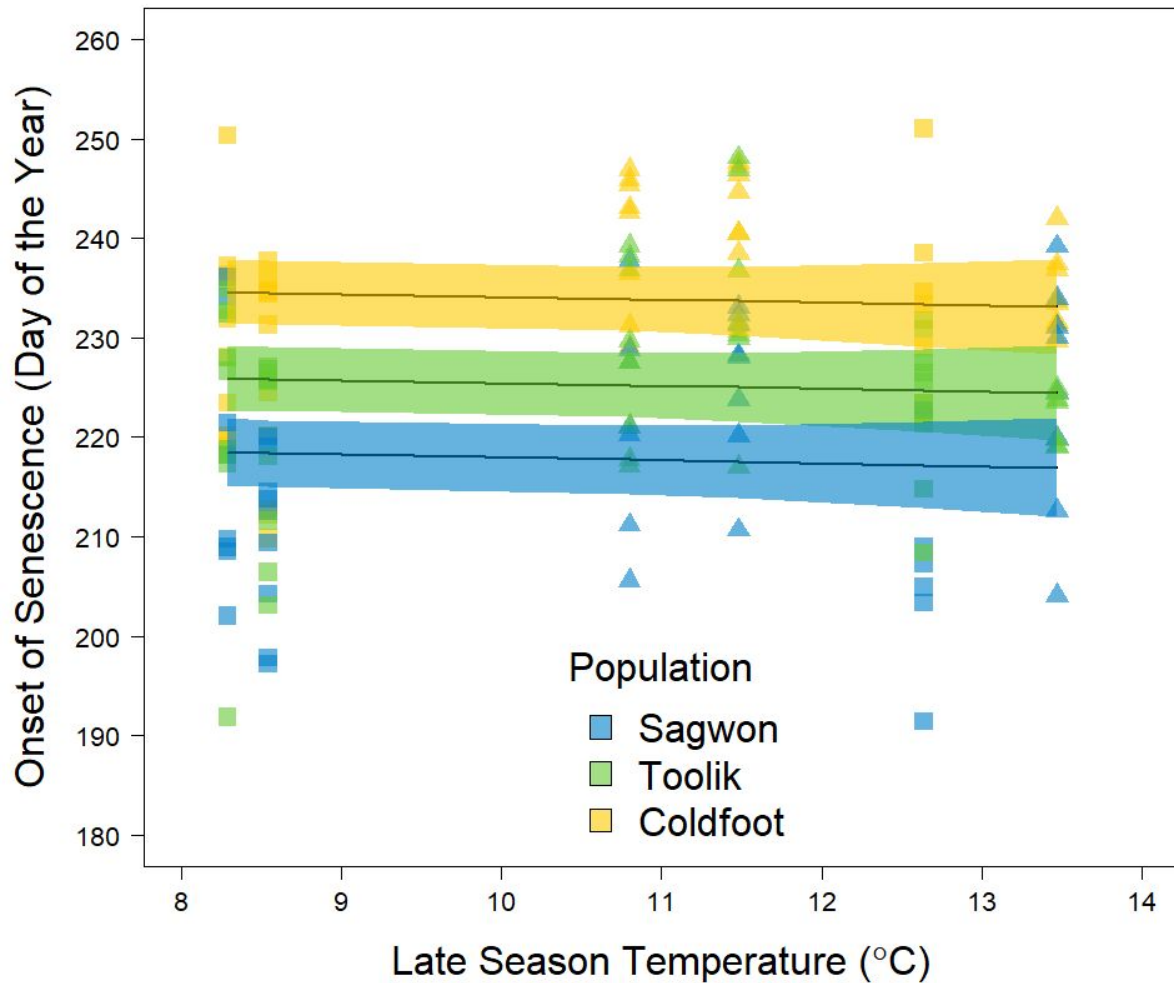
371



372

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

380



381  
 382 **Figure 6: Relationship between late season temperature and onset of senescence (A1) for**  
 383 **three populations in 2016 (squares) and 2017 (triangles). See Supplementary Table S4 for**  
 384 **linear mixed effects models showing a significant effect of population ( $P < 0.001$ ) but no**  
 385 **effect late season temperature ( $P = 0.575$ ). Modelled marginal effects (with 95 % confidence**  
 386 **intervals) of late season temperature and population on onset of senescence are displayed,**  
 387 **for model details, see Supplementary Table S5.**  
 388

389 Discussion

390 *Response of northern ecotypes to warming*

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

408  
409 *Effects of transplanting on phenology of Eriophorum vaginatum*

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

414 al. 2018) but rarely tested. One of the advantages of *E. vaginatum* for reciprocal transplants is its  
415 deciduous root system and lack of mycorrhizal symbiosis, which means that tussocks can be  
416 transplanted without disturbing the belowground environment (Shaver et al 1986, Parker et al.  
417 2017, Schedlbauer et al. 2108). To this feature, we can now add the relative lack of response of  
418 phenology to transplanting. The timing of onset of growth and the length of the growing season  
419 was not different. The timing of senescence was overall marginally earlier, and the maximum  
420 length of leaves was slightly shorter which perhaps reflects a less well established connection  
421 between rhizomes and the soil resulting in less effective nutrient uptake. These data further  
422 underline the usefulness of *E. vaginatum* as a model species to study ecotypic variation of traits  
423 in mature plants.

#### 425 *Tussock competitiveness in a warming tundra*

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

439 depend more on the performance of its fellow community members than on its own. Many areas  
440 of tundra are becoming more productive and taller in response to climate change (Bjorkman et al.  
441 2018) and deciduous shrubs are often the plants that increase growth the most as climate warms  
442 (Elmendorf et al. 2012a). If deciduous shrubs overgrow tussocks, which are more limited in their  
443 ability to grow taller, then the foundation species of moist acidic tundra may suffer declines.  
444 However, if tussocks remain green for longer in extended growing seasons (Park et al. 2016),  
445 and extend beyond that of shrubs, they may retain an important place in northern ecosystems. *E.*  
446 *vaginatum* remains photosynthetically active as long as it holds green leaves into August (Curasi  
447 et al. 2019), hence tussocks that can delay senescence may continue to accumulate carbon later  
448 into the season, after other species have dropped their leaves.

#### 449 450 *Plasticity and competitiveness of southern ecotypes*

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

464 ecotypes can migrate north in sync with climate warming they may increase the fitness of a  
465 species which is currently suffering *in situ* (McGraw et al. 2015). Southern ecotypes grow taller  
466 leaves (Fetcher and Shaver 1990) and maintain green tissue later in the season than northern  
467 ecotypes, therefore they may have a greater capacity for C fixation (Shaver et al. 2007).  
468 Dependent on dispersal by wind and suitable ecosystem disturbance for establishment (McGraw  
469 et al. 2015), northward migration of southern ecotypes could potentially have ecosystem-level  
470 impacts by influencing net ecosystem exchange. This needs to be tested by explicitly considering  
471 tussocks (transplanted and non-transplanted) in ecosystem analyses. Further, studies that measure  
472 ecosystem processes are currently limited by peak season-only measurements (Souther et al.  
473 2014, Walker et al. 2018, Curasi et al. 2019), to integrate ecotypes into ecosystem gas exchange,  
474 the whole growing season needs to be considered.

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

486

487 *Environmental vs genetic controls on phenology*



488 Because snowmelt in the tundra is getting earlier and causing earlier plant green-up (Park  
489 et al. 2016; Assmann et al. 2019), one of the next questions is how does this affect biological  
490 processes later in the growing season and how does this compare with other important controls  
491 on late season phenology? Our Question 4 arose from the hypothesis that some arctic plant  
492 species are periodic (Semenchuk et al. 2016). Under this hypothesis, early green-up would result  
493 in early senescence due to genetic control over the length of *E. vaginatum*'s growing season. We  
494 found no evidence to support this hypothesis. In contrast to other authors (Khorsand Rosa et al.  
495 2015; Semenchuk et al. 2016) we found no relationship between timing of early season and late  
496 season phenology. Instead, we find that timing of senescence is best predicted by the population  
497 origin of the tussock. This is postulated as the result of genetic adaptations to past environmental  
498 conditions, which genotype-environment association studies support as a driver in forming  
499 population structure conditions and patterns of *E. vaginatum* in north central Alaska (glaciation  
500 (Elizabeth Stunz, pers. comm.)). Senescing at the right time is particularly important in the Arctic  
501 where the abrupt start of winter can be harsh and damaging to exposed tissues (McGraw and et  
502 al. 1983). Therefore, it is plausible that genetic control over average timing of the return of cold  
503 temperatures at each of the home sites has a role in shaping the observed phenology patterns in  
504 the three populations studied.

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

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

521

## 522 *Conclusions*

523 In the tundra ecosystem dominated by *E. vaginatum*, the growing season of the northern  
524 ecotypes had a limited response to longer, more favorable growing conditions when transplanted  
525 south and therefore limited the potential to sequester C during warm shoulder seasons. The  
526 Arctic is warming faster than any other biome on Earth (Park et al. 2018) and warming is  
527 particularly pronounced at the shoulder seasons, resulting in longer growing seasons (Park et al.  
528 2016). Our results support a hypothesis that the southern ecotype of *E. vaginatum* is better  
529 adapted to take advantage of this warming through having more plasticity in phenological  
530 response, but the northern ecotypes are more constrained, therefore would be unable to take  
531 advantage of a lengthened growing season (Fetcher and Shaver 1990). If the Arctic continues to  
532 become more productive (Epstein et al. 2012) and grow taller (Bjorkman et al. 2019), locally  
533 adapted ecotypes lacking the ability extend growth in height or phenology in the northern part of  
534 their range, as found for *E. vaginatum*, may need to rely on gene flow from southern populations  
535 to maintain a competitive balance in the ecosystem. At the present rate of climate change, the  
536 northern ecotypes already appear to be poorly adapted if the climate warms to the temperatures  
537 currently encountered by the southern ecotype (McGraw et al. 2015). Given the slow growth and

538 longevity of tussock forming plants in the arctic, the chances for establishment of southern  
539 ecotypes in the north seem unlikely, outside of assisted gene flow or migration (Borrell et al.  
540 2020).

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546  
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548 The authors declare there are no competing interests

549  
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558  
559 Data availability statement

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

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