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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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).

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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).

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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).

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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.

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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

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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

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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?

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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

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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).

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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

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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

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

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.

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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 1st, growth rate

249   (mS) above 0.4 cm day $^{-1}$) 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).

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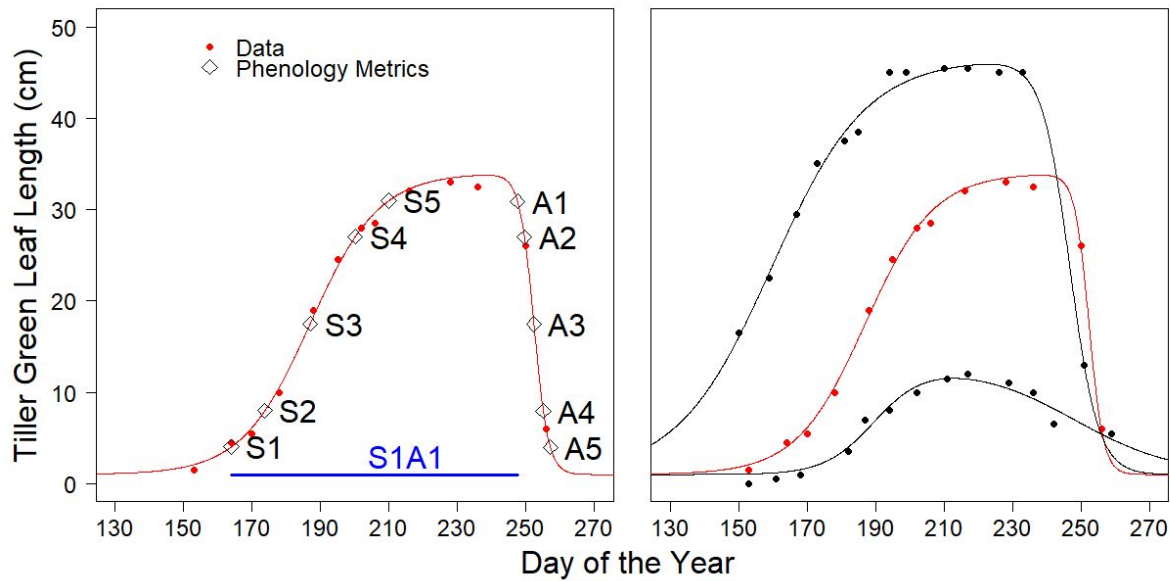
Figure 1: Example of double logistic model (Equation 1) fit to the growth pattern of a tiller over a growing season and metrics that can be calculated from this curve (in red, left panel) and fit to two other example datasets (in black, right panel).

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

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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).

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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.
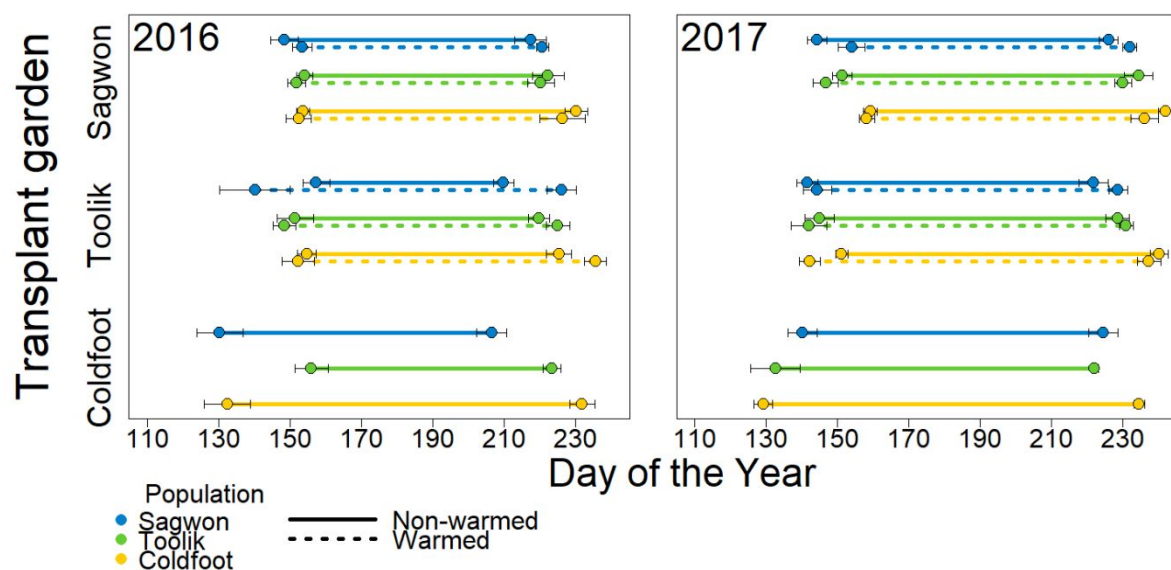
306   **Figure 2: Summary of growing season of Coldfoot (yellow) Toolik Lake (green) and**

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.**

<u>Non-warmed transplanted tussocks</u>

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

<u>Warmed and non-warmed transplant tussocks</u>

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

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Warming	1, 115	1.8	0.184

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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),

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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
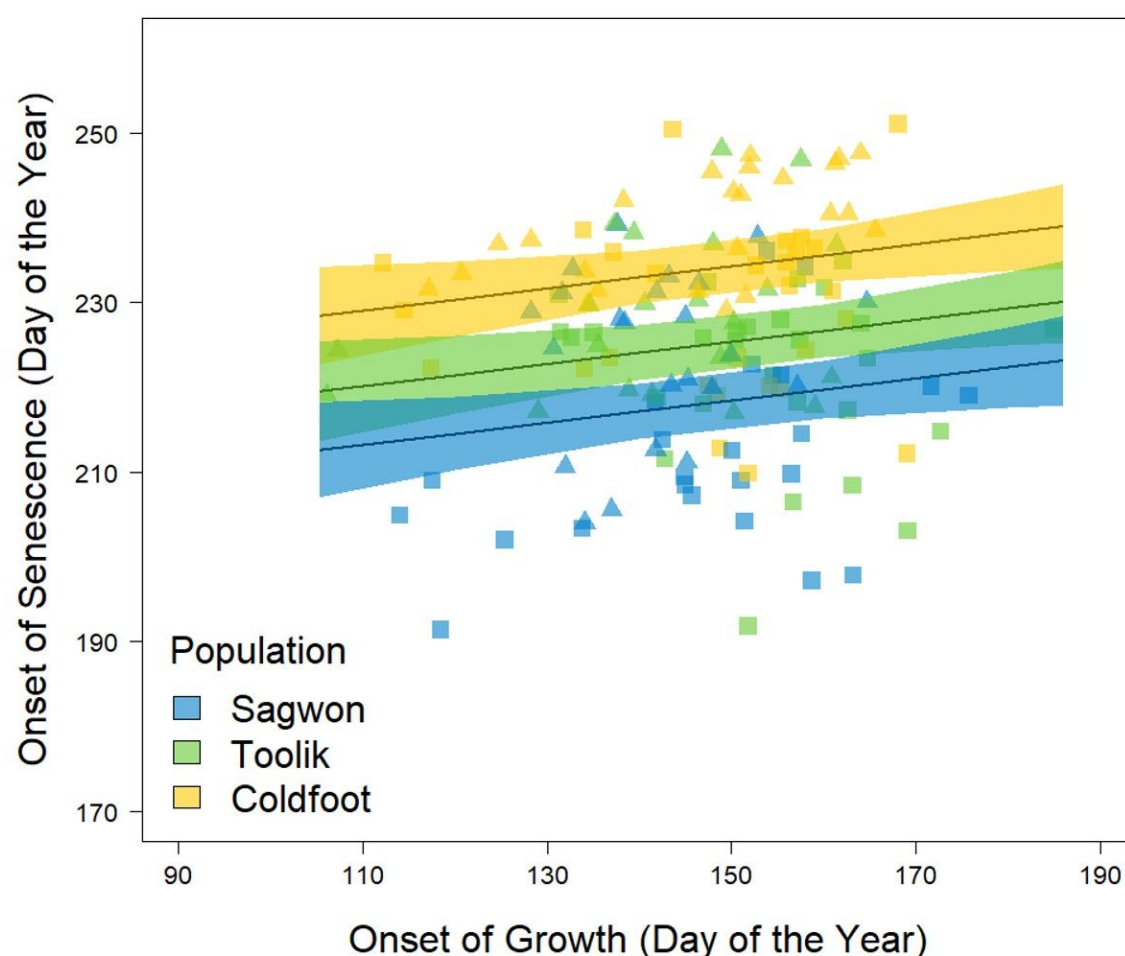
354
355   **Figure 3: The day of onset of growth and the day of onset of senescence of leaves of *E.***

356   ***vaginatum* across all gardens populations in 2016 (squares) and 2017 (triangles). A linear**

4

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.**
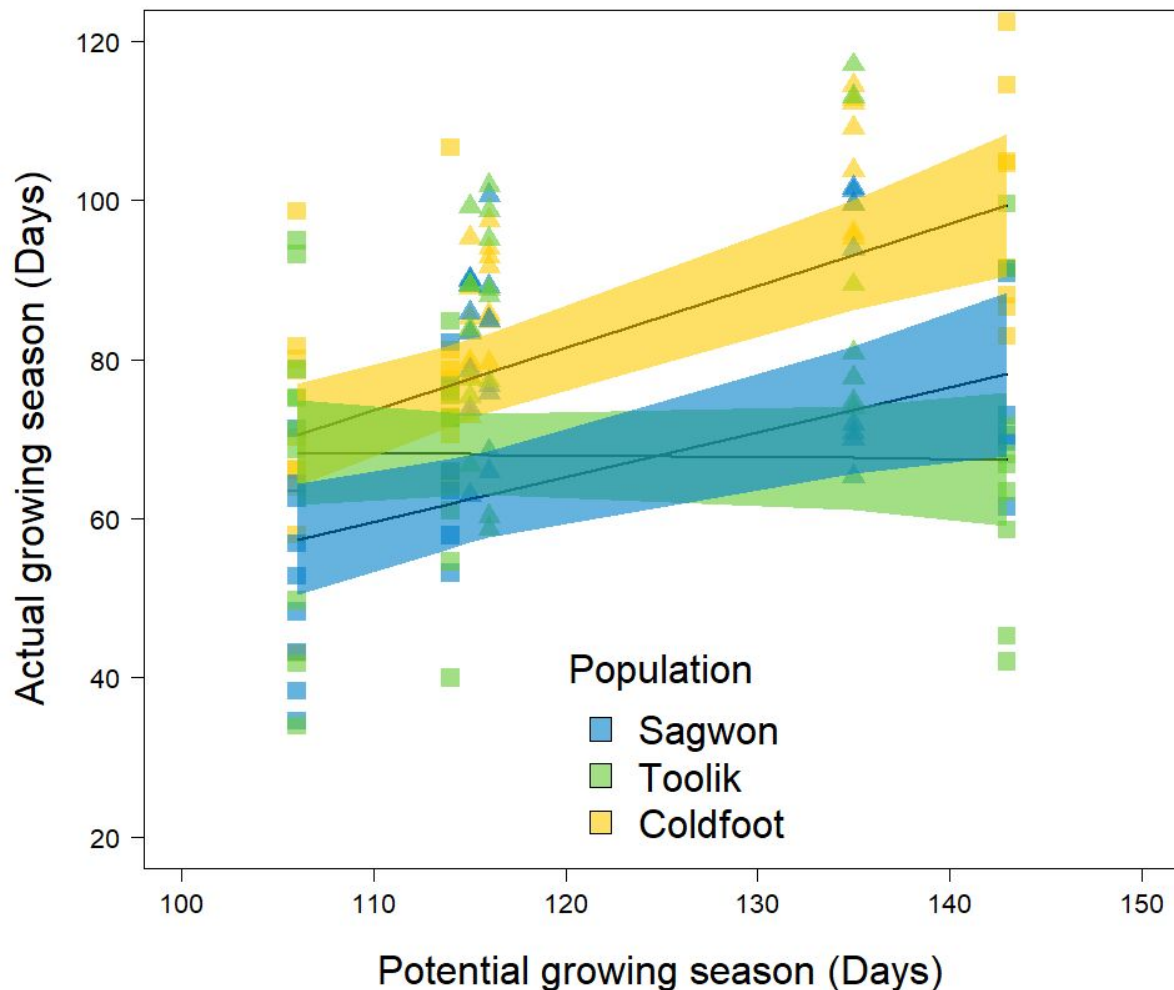
Figure 4: Relationship between the potential growing season (snowmelt - return of cold

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

5

369 **season and population on actual growing season are displayed, for model details, see**

370 **Supplementary Table S5.**

371

372
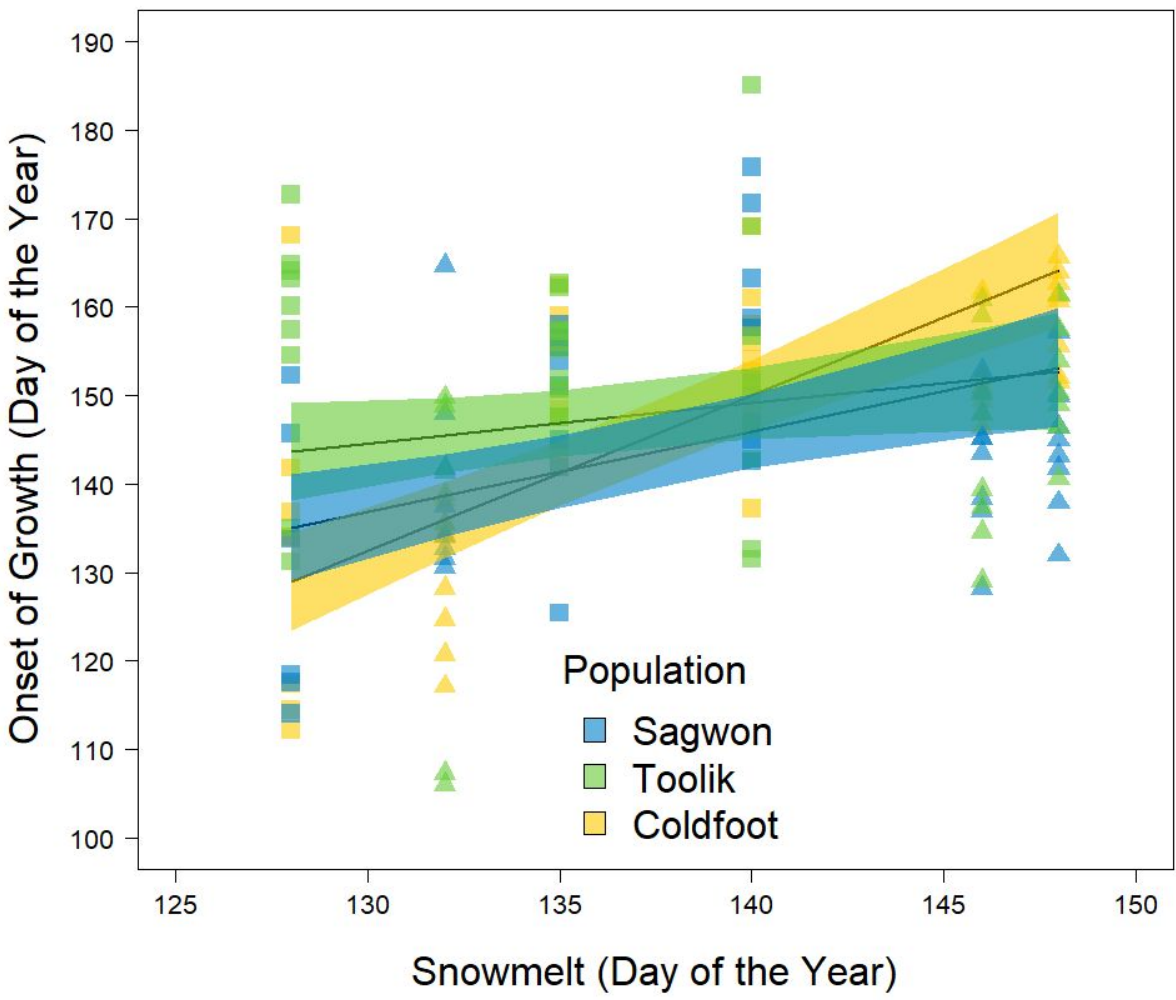
373 **Figure 5: Relationship between snowmelt timing and onset of growth (S1) for three**

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

6
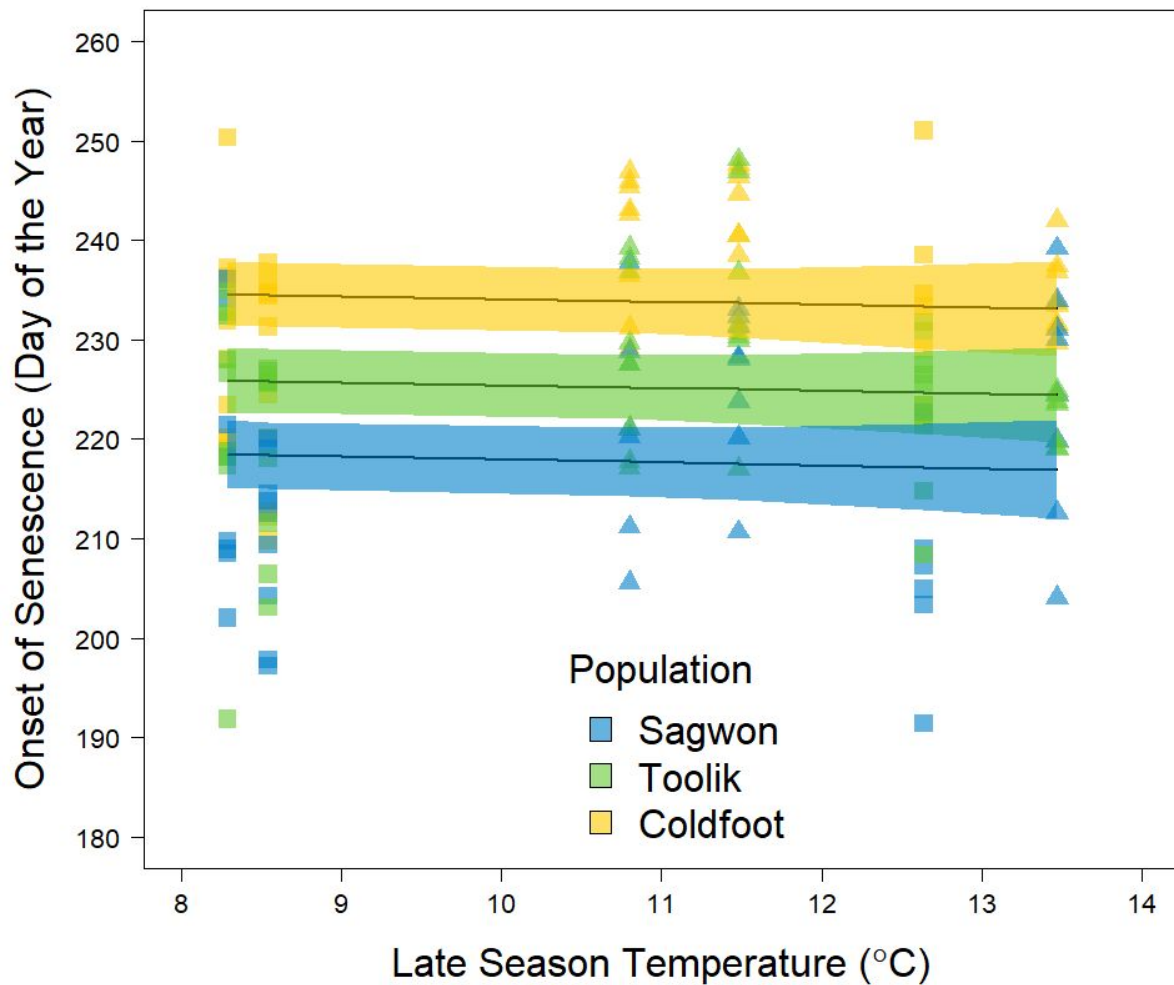
Figure 6: Relationship between late season temperature and onset of senescence (A1) for three populations in 2016 (squares) and 2017 (triangles). See Supplementary Table S4 for linear mixed effects models showing a significant effect of population (*P* < 0.001) but no effect late season temperature (P = 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.

7

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

8

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.

424

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

9

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

10

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*

11

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

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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

13

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).

541

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546

547 Competing interests

548 The authors declare there are no competing interests

549

550 Contributors statement

551 NF, MLM and JT and TCP designed the experiment and measurement routine, TCP, NF and SU

552 took the measurements. All Authors contributed to writing the manuscript.

553

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558

559 Data availability statement

14

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

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