

# Differential responses of ecotypes to climate in a ubiquitous Arctic sedge: implications for future ecosystem C cycling

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## Summary

- The response of vegetation to climate change has implications for the carbon cycle and global climate. It is frequently assumed that a species responds uniformly across its range to climate change. However, ecotypes – locally adapted populations within a species – display differences in traits that may affect their gross primary productivity (GPP) and response to climate change.
- To determine if ecotypes are important for understanding the response of ecosystem productivity to climate we measured and modeled growing season GPP in reciprocally transplanted and experimentally warmed ecotypes of the abundant Arctic sedge *Eriophorum vaginatum*.
- Transplanted northern ecotypes displayed home-site advantage in GPP that was associated with differences in leaf area index. Southern ecotypes exhibited a greater response in GPP when transplanted.
- The results demonstrate that ecotypic differentiation can impact the morphology and function of vegetation with implications for carbon cycling. Moreover they suggest that ecotypic control of GPP may limit the response of ecosystem productivity to climate change. This investigation shows that ecotypes play a substantial role in determining GPP and its response to climate. These results have implications for understanding annual to decadal carbon cycling where ecotypes could influence ecosystem function and vegetation feedbacks to climate change.

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## Introduction

Vegetation is responding to global climate change (IPCC 2014), thereby altering ecosystem productivity (Euskirchen *et al.*, 2006; Heimann & Reichstein, 2008; Guay *et al.*, 2014). These responses have implications for the carbon (C) cycle and global climate (Heimann & Reichstein, 2008), especially in the Arctic where rapid climate change is occurring and large amounts of C are stored in vegetation and soils (Epstein *et al.*, 2012; Hugelius *et al.*, 2014). In Arctic ecosystems, it is uncertain whether stimulation of vegetative primary productivity by increased temperatures will offset increased soil respiration (Abbott *et al.*, 2016). This balance will partially determine whether future arctic C cycling will have a positive feedback (through increased soil respiration) or a negative feedback (through increased productivity) on changes in climate (Abbott *et al.*, 2016). Therefore, understanding how vegetation responds to climate change is key to improving net C balance projections for these ecosystems (Sitch *et al.*, 2007; McGuire *et al.*, 2009).

Past investigations of shifts in primary productivity assume that individuals within a species or a group of species (that is plant functional types) have a uniform response to climate change

(Sitch *et al.*, 2007; McGuire *et al.*, 2009). However, variation within a species (intraspecific variation) may impact vegetation form and function (Seliskar *et al.*, 2002; Des Roches *et al.*, 2018). Ecotypes – locally adapted populations within a species – are a source of intraspecific variation in plants. Ecotypes exist in numerous plant species, including a number of arctic species, due to local environmental selection pressures (Mooney & Billings, 1961; Chapin & Chapin, 1981; McGraw & Antonovics, 1983; Bennington *et al.*, 2012). This raises the question: ‘Are ecotypes important for understanding the response of ecosystem productivity to climate change?’

Ecotypes can be particularly sensitive to climate (Aitken *et al.*, 2008; Souther & McGraw, 2011) and often have a competitive advantage in the climate in which they have formed, known as home-site advantage (Linhart & Grant, 1996). But local adaptation can incur a cost by limiting the performance of ecotypes when the environment changes (Aitken *et al.*, 2008; Atkins & Travis, 2010; Souther & McGraw, 2011; McGraw *et al.*, 2015). This is because, unlike physiological acclimation to site condition that occurs over the course of days or months, local adaptation occurs at much longer (decadal to centennial) time scales (Aspinwall *et al.*, 2017). The ability of an ecotype to respond to a

rapidly changing climate may be determined by its home-site environment due to trade-offs between traits that maximize and stabilize productivity (Kelley, 1985; Fetcher & Shaver, 1990). For example, ecotypes formed in colder northern environments with less interannual variation may employ a conservative strategy to maintain growth, while ecotypes formed in warmer southern environments with more interannual variation employ an opportunistic strategy that allows them to rapidly respond to annual variations in climate (Fetcher & Shaver, 1990). The implications of these complex responses to climate have been examined in population biology, but rarely in ecosystem C cycling studies, which normally use coarse groupings to represent vegetation (Atkins & Travis, 2010; McGraw *et al.*, 2015; Des Roches *et al.*, 2018; Walker *et al.*, 2019). However, the differences in structure and function between ecotypes suggest that thorough investigation of the impact of ecotypes on C cycling is warranted.

Gross primary productivity (GPP) via photosynthesis is the main input of atmospheric C into the terrestrial biosphere and ultimately influences ecosystem C sequestration (Chapin *et al.*, 2006; Bonan, 2008; Beer *et al.*, 2010). Ecotypes display differences in physiological and morphological traits, which regulate GPP. GPP is largely determined by leaf area index (LAI) and leaf-level photosynthetic rates (Campbell & Norman, 1998; Bonan, 2008), both of which have been shown to differ among ecotypes (Potvin, 1986; Oleksyn *et al.*, 1998; Weber & Schmid, 1998; Souther *et al.*, 2014; Parker *et al.*, 2017). Despite these observations, the link between ecotype trait differences and ecosystem C cycling has remained unexplored largely because ecosystem-level processes, like GPP, are assumed to be more influenced by the collective behaviour of groups of species rather than individual species (Seliskar *et al.*, 2002; Des Roches *et al.*, 2018).

*Eriophorum vaginatum* is an arctic sedge that is a foundational species of moist acidic tundra (Oberbauer *et al.*, 2007), where it can account for up to one-third of ecosystem productivity (Chapin & Shaver, 1985). This is important as moist acidic tundra is widespread in the circumpolar Arctic (Walker *et al.*, 2005), with *E. vaginatum* being prevalent throughout Northern Alaska, N. Canada and N. Russia (Wein, 1973). *E. vaginatum* develops dense tussocks that form mounds that are raised above the surrounding vegetation. Tussocks can range from new tussocks that are free from invading species to degraded tussocks that are heavily invaded by evergreen and deciduous shrubs, sedges, mosses, and lichens (Fetcher & Shaver, 1982; Fetcher, 1985). These tussocks can live for > 100 yr (Mark *et al.*, 1985) and exhibit low rates of seedling establishment (McGraw & Shaver, 1982). *E. vaginatum* exhibits ecotypes adapted to local climate (Bennington *et al.*, 2012). As a result, its poor capacity for recruitment could diminish its ability to respond to rapid climate change.

Large morphological and physiological differences among *E. vaginatum* ecotypes, combined with its role as a foundation species, make it ideal for investigating the role of ecotypes in C cycling. Shaver *et al.* (1986) found that *E. vaginatum* tiller mass declined along a transect from Fairbanks to Prudhoe Bay, while production of new tillers was more variable. The concentration

of leaf nitrogen (N) increased along the southern foothills of the Brooks Range and then declined in the northern foothills, while leaf phosphorus was low in the southern foothills and increased sharply at the northern tree limit (Shaver *et al.*, 1986). It appeared that nutrient concentrations were poorly correlated with growth and productivity and may have been more responsive to local soil conditions.

A reciprocal transplant experiment with *E. vaginatum* that used six sites ranging from Eagle Creek to Prudhoe Bay found large morphological and physiological differences between ecotypes located north and south of tree line. Northern ecotypes had smaller tillers and were less plastic than southern ecotypes (Shaver *et al.*, 1986; Fetcher & Shaver, 1990). These differences were maintained 31 yr after transplanting (Bennington *et al.*, 2012; Souther *et al.*, 2014). Furthermore, the different ecotypes showed home-site advantage in flowering (Bennington *et al.*, 2012) as well as tiller size and photosynthesis (Souther *et al.*, 2014). Conversely, McGraw *et al.* (2015) found evidence for adaptive lag in which the optimum climate for annual rate of tiller production and survival was shifted to the north of each ecotype's present location. This experiment demonstrated that *E. vaginatum* in northern Alaska consists of locally adapted ecotypes, of which the most striking is the division between ecotypes north and south of the tree line. The ecotypic differences between northern and southern ecotypes have been largely attributed to differences in leaf phenology that translate into morphological differences (Parker *et al.*, 2017). Conversely, there is some evidence for ecotypic differences in the response of photosynthetic capacity after transplanting to different latitudes (Schedlbauer *et al.*, 2018). These earlier studies focused on ecotypic effects on primary productivity at the scale of leaves (gas exchange measurements) and tillers (proxy measurements of productivity). However, as in many other species, our understanding of the impacts of *E. vaginatum* ecotypes on GPP at the canopy/tussock-level and their role in the Arctic C cycle remains limited.

To investigate the influence of ecotypes on the response of arctic ecosystems to climate change we measured the GPP of three *E. vaginatum* ecotypes that were part of the original (30+ yr) experiment (Shaver *et al.*, 1986) in a second reciprocal transplant experiment. The new experiment was designed to assay ecosystem-level characteristics and included experimental warming. The c. 4.3°C difference in mean annual temperature between the northernmost and southernmost sites of origin mirrors the 3–5°C range for warming projected for the Arctic region by the 2090s (ACIA, 2004). We specifically address three hypotheses. First, given the differences in morphology and function observed between *E. vaginatum* ecotypes, we hypothesize that when *E. vaginatum* ecotypes are transplanted to new environments their GPP will be influenced by traits specific to each ecotype (partially decoupled from climate). Second, given that home-site advantage in photosynthetic traits, leaf morphology, and tiller production have been observed in *E. vaginatum* ecotypes, we hypothesize that ecotypes will display the highest GPP at their home site. Third, given the observations of greater plasticity of ecotypes south of tree line, we hypothesize that GPP in ecotypes from warmer southern sites will display a more variable response

to climate change. Addressing these hypotheses will illustrate whether ecotypes affect the response of primary productivity to climate change.

## Materials and Methods

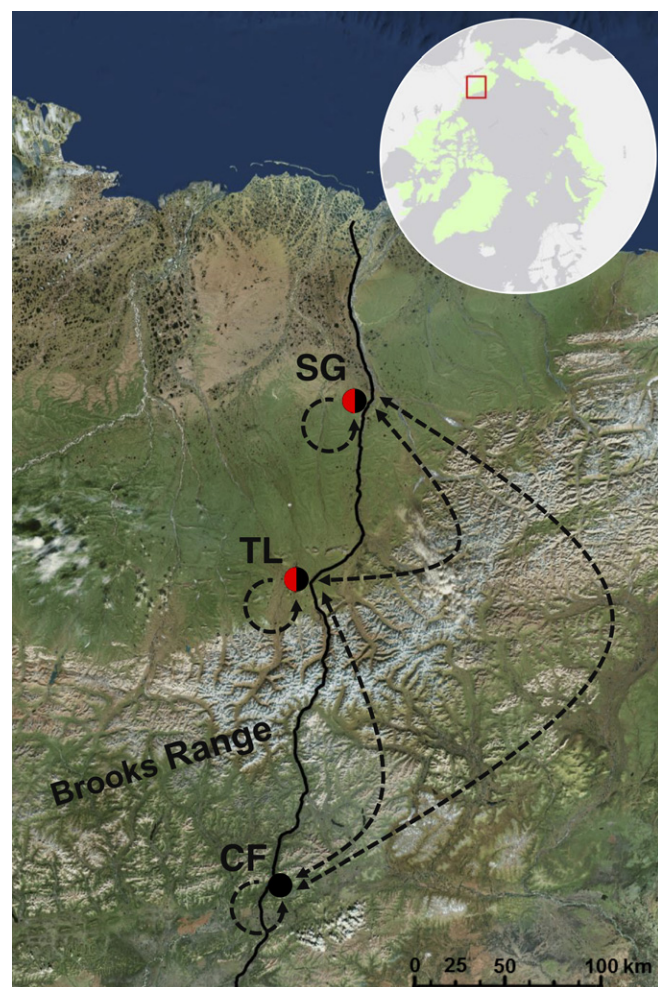
### Site description and experimental design

For the reciprocal transplant experiment, three common gardens of *Eriophorum vaginatum* L. tussocks were established at Sagwon (SG; 69.42°N, 148.72°W), Toolik Lake (TL; 68.63°N, 149.36°W) and Coldfoot (CF; 67.26°N, 150.17°W) along the Dalton Highway in Alaska, USA (Fig. 1). Each garden had representatives of all three ecotypes. Tussocks of *E. vaginatum* dominate all three sites with deciduous (*Betula nana* L., *Salix* spp. and *Vaccinium uliginosum* L.) and evergreen shrubs (*Vaccinium vitis-idea* L., *Rhododendron tomentosum* Harmaja), mosses, and lichens growing in-between the tussocks. SG and TL are

classified as moist acidic tundra (Walker *et al.*, 2005), while the CF site has *E. vaginatum* tussocks along with other common species found at SG and TL as well as seedling and young trees (*Picea glauca*) that were not present in 1982 when previous common gardens were established (Shaver *et al.*, 1986). In August 2014 mature tussocks were transplanted between the three sites according to Bennington *et al.* (2012) and Schedlbauer *et al.* (2018). A serrated knife was used to sever the rhizomes from roots and soil at a tussock's base and remove it from the tundra. Tussocks were then placed in the vacant positions at the common garden where local tussocks had been removed. Home-site tussocks were transplanted into different positions from where they originated. This method has a high success rate because of the unusual rooting habit of *E. vaginatum* in which annual roots develop each spring growing directly downward below the tussock following soil thaw (Chapin *et al.*, 1979). Although roots are severed during transplanting, new roots grow in each subsequent year, restoring full root function (Bennington *et al.*, 2012). Tussocks were planted in clusters of three, *c.* 0.5 m apart from each other. Clusters were paired at SG and TL where one cluster was passively warmed using open-top chambers (OTCs). Ten pairs of clusters of the three ecotypes were arranged in a *c.* 25 × 30 m grid. OTCs (modified from Marion *et al.*, 1997) were placed on the selected clusters from 11 July until 28 August 2015 and from 2 June until 28 August 2016. At CF there was no warming treatment, therefore clusters were arranged as singletons in a smaller grid (*c.* 25 × 15 m). All other in-grown vegetation in the transplanted tussocks was removed to prevent any confounding effects of other species.

### Tussock gas flux measurements

A custom-made chamber was used to measure net ecosystem exchange (NEE) and ecosystem respiration (ER) of tussocks under a variety of environmental conditions. The chamber was connected to an LI-6400XT Photosynthesis System (Li-Cor Biosciences, Lincoln, NE, USA) that operated in closed system mode. The chamber was a 30 cm clear acrylic cube (Optix; Plaskolite, Columbus, OH, USA) with a 6 ml polyethylene sheet secured *c.* 6 cm from the base. The sheet was secured around the base of the chamber and folded around a cord forming a 30 cm diameter circular opening. The two ends of this cord ran through holes at opposite ends of the base of the chamber. When drawn tight, the cord cinched the sheet around the base of a transplanted tussock in a sphincter-like action forming a tight seal (sealed chamber volume =  $2.17 \times 10^4$  cm<sup>3</sup>). Fans were mounted inside the chamber to ensure air mixing. A good seal between tussock and the sheet at the base of the chamber was confirmed if gas concentrations showed a steady rate of change for 20 s. Following the methods of Shaver *et al.* (2007), when a stable change in CO<sub>2</sub> concentrations was observed, CO<sub>2</sub> concentration, H<sub>2</sub>O concentration, chamber air temperature, atmospheric pressure and photosynthetic photon flux density (PPFD; inside the chamber) were logged every 2 s for 40 s. Instantaneous CO<sub>2</sub> concentrations (*C*, μmol CO<sub>2</sub> mol<sup>-1</sup>) were corrected for dilution by water



**Fig. 1** Map showing the location of the study sites. Reciprocal transplants of *Eriophorum vaginatum* tussocks are denoted with dashed lines and a red and black marker denotes a site with a warming treatment. The inset shows the extent of the study area and the circumpolar extent of arctic tundra (CF, Coldfoot; TL, Toolik Lake; SG, Sagwon). Basemap and imagery source: Esri.



vapor as a function of the instantaneous concentration of water vapor ( $\bar{W}$ ,  $\text{mmol H}_2\text{O mol}^{-1}$ ) yielding  $C_{\text{dry}}$  ( $\mu\text{mol CO}_2 \text{mol}^{-1}$ , Li-Cor Bioscience, 2011, Eqn 1).

$$C_{\text{dry}} = \frac{C}{1 - \frac{\bar{W}}{1000}} \quad \text{Eqn 1}$$

Flux ( $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ ) was then calculated as a function of the linear change in  $\text{CO}_2$  concentration in dry air observed over time ( $\text{d}C_{\text{dry}}/\text{d}t$ ,  $\mu\text{mol CO}_2 \text{mol}^{-1} \text{s}^{-1}$ ), air density calculated using the ideal gas law ( $\rho$ ,  $\text{mol m}^{-3}$ ), volume ( $V$ ,  $\text{m}^3$ ), surface area ( $S$ ,  $\text{m}^2$ ) and the average concentration of water vapor ( $\bar{W}$ ,  $\text{mmol H}_2\text{O mol}^{-1}$ ; Li-Cor Bioscience, 2011; Eqn 2). The linear fits ( $\text{d}C_{\text{dry}}/\text{d}t$ ) were checked for goodness of fit (mean  $R^2 = 0.89$ ).

$$\text{Flux} = \frac{\rho V \left(1 - \frac{\bar{W}}{1000}\right)}{S} \frac{\text{d}C_{\text{dry}}}{\text{d}t} \quad \text{Eqn 2}$$

Flux was expressed on a per area basis depending on the area of the tussock the chamber was tightened around. The  $S$  value was adjusted for every tussock depending on its surface area as determined by two diameter measurements taken with tree calipers. Tussocks were selected for flux measurements if they had a regular circular or oval shape, were tall enough ( $> 5$  cm) to ensure a tight seal around the base and were of a consistent size (12–22 cm diameter). In all, 58 individuals met these criteria; 14 at CF, 27 at TL, and 17 at SG. Ecotypes were sampled relatively evenly over the gardens with 16 from CF, 19 from TL, and 23 from SG. The OTCs were removed during measurements to accommodate the flux chamber.

After 23 months of acclimation following transplantation, flux measurements were taken between 5 July and 25 July 2016 between the hours of 10:00 a.m. and 5:00 p.m. A combination of ambient light and layers of shade cloth (40% and 80%) were used to simulate variation in light intensities. A group of light measurements were immediately followed by a dark measurement made by covering the chamber with an opaque tarp. Flux measurements were screened for quality and instrumentation errors leaving 154 measurements of NEE and 105 measurements of ER. GPP was computed as the difference between NEE and ER. We use the atmospheric convention whereby negative NEE represents net uptake of  $\text{CO}_2$  by plants.

## Normalised Difference Vegetation Index (NDVI) and Leaf Area Index

Before each flux measurement, the NDVI of the tussock was determined by averaging two replicate measurements taken using a hand-held, self-illuminated reflectance unit (GreenSeeker; Trimble Inc., Sunnyvale, CA, USA). The height at which the instrument was held was determined using the diameter of the tussock and the instruments optical characteristics in order to ensure that the field of view encompassed the whole tussock while excluding surrounding vegetation. To convert NDVI to LAI, the relationship between the two was determined by harvesting non-transplanted tussocks (transplanted tussocks could not be harvested). The NDVI of nontransplanted tussocks (with other vascular species removed) was measured, individual's green biomass was harvested, and projected leaf area was measured with a Li-Cor 3100 leaf area meter (Li-Cor Inc.). NDVI was fitted to LAI with the equation using nonlinear least-squares (NLS) regression (Eqn 3; Supporting Information Fig. S1; Table S1).

$$\text{LAI} = ae^{b\text{NDVI}} \quad \text{Eqn 3}$$

The analysis yielded the following parameterisation ( $R^2 = 0.88$ ,  $a = 0.03$ ,  $\text{SE}_a = 0.01$ ,  $b = 7.65$ ,  $\text{SE}_b = 0.62$ ) (Sweet *et al.*, 2015; Elzhov *et al.*, 2016). This equation was used to convert NDVI measurements in the field to LAI ( $\text{m}^2 \text{m}^{-2}$ ).

## Statistical analysis, modelling selection and model intercomparison

To determine the impacts of the site, warming treatment, and ecotype on GPP we calculated means and analyses of variance (ANOVAs) followed by contrasts. We used unshaded GPP measurements (flux measurements collected without the use of shade cloth; see Table 1) to test for site and ecotype-level effects. To test for warming treatment effects, we used unshaded GPP on tussocks at SG and TL and included both ambient (A) and warmed (W) tussocks. All analyses were carried out using the R base package unless otherwise noted (R Core Team, 2016).

To further disentangle the effects of the warming treatment, ecotypes, and environmental conditions on photosynthesis in *E. vaginatum* we fitted the model of GPP developed by Rastetter *et al.* (1992, 2010, Eqn 4) to observed GPP (all flux measurements collected including those collected using shade cloth; see Table 1).

**Table 1** Ranges and means for leaf area index (LAI), photosynthetic photon flux density (PPFD) and air temperature (Temp.) during the gas flux measurements and runs of the modified gross primary productivity (GPP) model.

	Date range	LAI ( $\text{m}^2 \text{m}^{-2}$ )			PPFD ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )			Temp. ( $^{\circ}\text{C}$ )		
		min	mean	max	min	mean	max	min	mean	max
Observed GPP	5 July to 25 July	0.19	0.42	1.64	71	752	1335	14.2	22.4	33.3
Unshaded GPP	5 July to 25 July	0.19	0.46	1.64	437	939	1335	14.2	23.8	33.3
Modelled peak season GPP	20 June to 10 August	0.13	0.46	2.23	0	431	1543	−4.1	12.1	30.7

$$\text{GPP} = \frac{P_{\text{maxL}}}{k} \ln \left( \frac{P_{\text{maxL}} + E_0 I}{P_{\text{maxL}} + E_0 I e^{-k \text{LAI}}} \right), \quad \text{Eqn 4}$$

where GPP ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) is a function of the light-saturated photosynthetic rate per unit leaf area ( $P_{\text{maxL}}$ ;  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf area s}^{-1}$ ), the Beer's law extinction coefficient ( $k$ ;  $\text{m}^2 \text{ m}^{-2}$ ), the initial slope of the light response curve ( $E_0$ ;  $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$  photons absorbed), incident photosynthetically active radiation ( $I$ ;  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) and leaf area per unit ground (LAI;  $\text{m}^2 \text{ m}^{-2}$ ). This model has been utilized at a range of spatial and temporal scales across numerous tundra vegetation types (Shaver *et al.*, 2007; Rastetter *et al.*, 2010; Loranty *et al.*, 2011; Stoy *et al.*, 2013; Sweet *et al.*, 2015). A modelling approach enables a more robust assessment of vegetation level processes than would have been possible using the field observations alone. NLS regression was used to fit the model to the entire set of flux data collected in the field (Elzhov *et al.*, 2016). As suggested by Shaver *et al.* (2007, 2013)  $k$  was set to the realistic value of  $0.5 \text{ m}^2 \text{ m}^{-2}$  during the model fitting. Inspection of the residuals resulting from these fits indicated an effect of air temperature on observed GPP (Fig. S2). To account for this effect, given the potential impact of ecotype on the vegetation's response to the temperature conditions at each site (Souther *et al.*, 2014; Schedlbauer *et al.*, 2018) we modified the above model to include a temperature effect of the form developed by Xiao *et al.* (2005; Eqns 5,6):

$$T_{\text{scalar}} = \frac{(T - T_{\text{min}})(T - T_{\text{max}})}{[(T - T_{\text{min}})(T - T_{\text{max}})] - (T - T_{\text{opt}})^2}, \quad \text{Eqn 5}$$

$$\text{GPP} = T_{\text{scalar}} \frac{P_{\text{maxL}}}{k} \ln \left( \frac{P_{\text{maxL}} + E_0 I}{P_{\text{maxL}} + E_0 I e^{-k \text{LAI}}} \right). \quad \text{Eqn 6}$$

The modified GPP model (Eqns 5,6) explains observed GPP as a function of air temperature ( $T_{\text{air}}$ , °C) and the minimum, maximum, and optimum temperatures for photosynthesis ( $T_{\text{min}} = 0$ ,  $T_{\text{max}} = 35$ ,  $T_{\text{opt}} = 15$ , °C).  $T_{\text{scalar}}$  is set to zero if the temperature falls below  $T_{\text{min}}$  or above  $T_{\text{max}}$ .  $P_{\text{maxL}}$  and  $E_0$  become the light-saturated photosynthetic rate per unit leaf area at  $T_{\text{opt}}$  and the initial slope of the light response curve at  $T_{\text{opt}}$ , respectively. The modified GPP model was fitted to observed GPP via NLS regression. A residual sum of squares  $F$ -test confirmed that using the more complex model produced a statistically significant increase in explanatory power ( $P < 0.001$ ; Table S2). The modified GPP model (Eqns 5, 6) was fit to subsets of the flux dataset grouped by site, ecotype, and warming treatment and an  $F$ -test of the residual sum of squares was used to test for significant variation in the physiological parameters governing photosynthetic rates (Potvin *et al.*, 1990; Methods S1).

The sensitivity of the model parameterization to different variables was quantified by predicting the modified GPP model at points spanning the range of variables observed during the unshaded GPP measurements (PPFD = 437–1335 in  $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$  steps, air temperature = 14.2–33.3 in  $0.5^\circ\text{C}$  steps, and

LAI = 0.19–1.64 in  $0.1 \text{ m}^2 \text{ m}^{-2}$  steps; Table 1). The sensitivity metrics were calculated as the standard deviation of the mean flux rates at each step across the range of values for a particular variable of interest. We used ANOVAs to test for significant variation in preflux LAI (LAI measurements taken immediately before each flux) that had to be log transformed to stabilize variance.

### Peak season LAI assessment and GPP modelling

LAI measurements were collected for individual tussocks in the common gardens (30 at CF, and 60 at SG and TL) over the course of the growing season (7 June to 29 August 2016;  $\geq 9$  visits per site). The LAI measurements were linearly interpolated to produce a continuous daily LAI time series for individuals in the common gardens. Hourly average air temperature data (June to August, 2016) for SG, CF, and TL and hourly average PPFD data from TL were obtained from Snow Telemetry (SNOTEL) and Toolik Field Station (NRCS, 2016; EDC, 2017).

The daily LAI driver along with hourly PPFD and air temperature drivers were used to calculate hourly GPP rates for every individual in the common garden during the peak of the growing season (20 June to 10 August 2016; Eqns 5,6; Table 1). Modeled peak season GPP was then calculated by taking means of these peak season flux rates for individuals and then taking the mean flux rates by site, ecotype, warming treatment, and ecotype within site. Because photosynthetic capacity per unit leaf area does not vary seasonally in *E. vaginatum* (see Fig. S3 and Heskell *et al.*, 2014), GPP can be estimated over the peak of the growing season, outside the range of dates of the flux measurements (Sweet *et al.*, 2015). The error in modeled peak season GPP from the interpolated LAI driver was quantified via a bootstrap resampling of LAI measured in the field (1000 resamples leaving out 30% of the data). The mean deviations in modeled peak season GPP flux for each of these groups were calculated from the absolute values of the deviations between the mean modeled peak season GPP and the modeled peak season GPP of each group of individuals. Individuals' modeled peak season GPPs were regressed against the median total of thawing degree days (TDD) for the period from 2001 to 2011 (Souther *et al.*, 2014).

Summary statistics were calculated on peak season LAI (LAI measurements collected during the same period as modeled peak season GPP was calculated, 20 June to 10 August 2016). Linear mixed effects models and contrasts implemented using the 'nlme' package in R were used to analyse the effect of ecotype, site, and warming treatment (fixed effects) on peak season LAI with individuals as a random effect to account for the repeated measures (Pinheiro, 2016). LAI had to be log transformed before all statistical tests to produce normally distributed residuals.

## Results

### Reciprocal transplant and warming treatment

In 2016, mean growing season air temperature (June to August) was 13.5, 8.8, and  $9.2^\circ\text{C}$  at CF, TL and SG, respectively. Mean growing season soil temperature (at 2 cm depth) was 11.1, 6.1,

and 5.5°C at CF, TL and SG, respectively. The warming treatment resulted in a 1.6 and 0.6°C increase in mean growing season air temperature and a 0.4 and 0.3°C increase in mean growing season soil temperature at TL and SG, respectively.

### Field observations of GPP

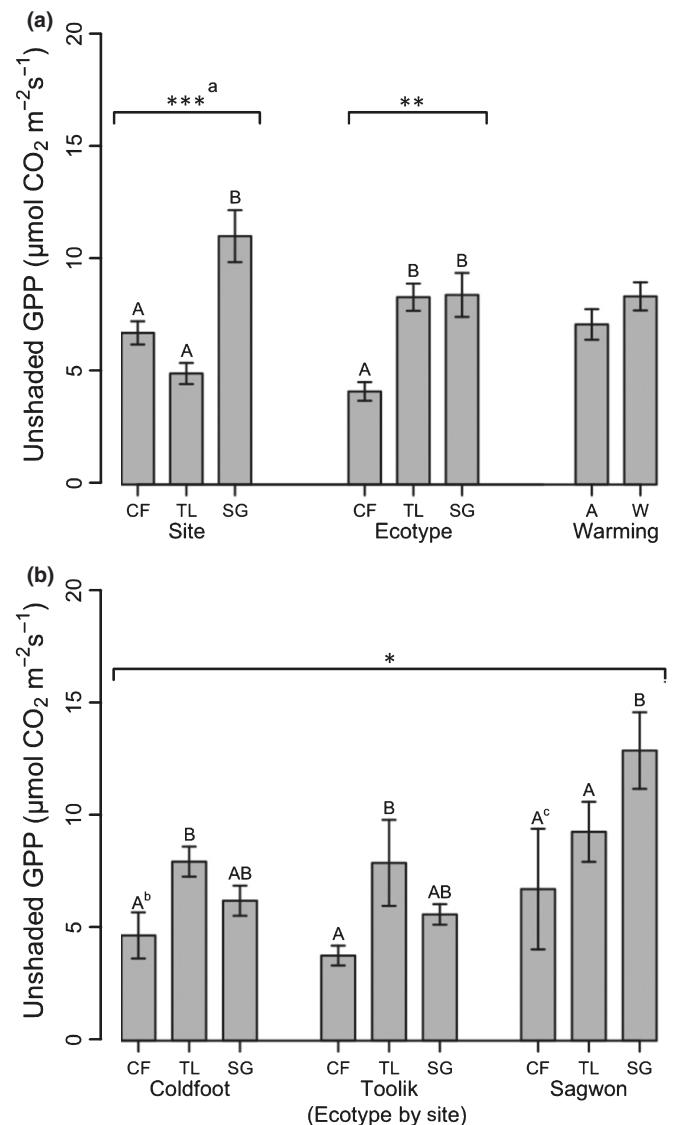
We observed significant variation in unshaded GPP due to site ( $F_{2,55} = 13.66$ ,  $P < 0.001$ ), ecotype ( $F_{2,55} = 6.18$ ,  $P < 0.01$ ), and the interaction between site and ecotype ( $F_{4,55} = 2.57$ ,  $P < 0.05$ , Fig. 2). Unshaded GPP was generally lower overall for the CF ecotype (Fig. 2a). At TL and SG the home-site ecotypes had the highest unshaded GPP (Fig. 2b). Conversely, warming treatment or interactions with warming treatment were not significant. Significant differences in chamber air temperature during the unshaded GPP measurements were observed across sites ( $F_{2,55} = 17.48$ ,  $P < 0.001$ ) with the southernmost site, CF (mean = 28.4°C) and the northern most site, SG (mean = 19.2°C) being the warmest and coldest sites, respectively, when compared to TL (mean = 25.2°C). There were also significant variations in chamber PPFD during the unshaded GPP measurements with site ( $F_{2,55} = 6.56$ ,  $P < 0.01$ ); these were relatively small, however, and chamber PPFD was generally above saturation (means = 1041, 952, and 833  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at CF, TL, and SG, respectively).

### GPP model selection

The modified GPP model fit well to the entire observed GPP dataset ( $R^2 = 0.55$ ; Table 2; Figs S4, S5; Eqns 5, 6). This generalized fit yielded a temperature optimum of photosynthesis ( $T_{\text{opt}}$ ) of 25.3°C, a maximum light-saturated photosynthetic rate per unit leaf area at  $T_{\text{opt}}$  ( $P_{\text{maxLT}}$ ) of 23.6  $\mu\text{mol CO}_2 \text{m}^{-2} \text{leaf area s}^{-1}$  and an initial slope of the light response curve at  $T_{\text{opt}}$  ( $E_{0T}$ ) of 0.1  $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ . Parameterizing multiple models of observed GPP by ecotype or warming treatment resulted in a small but insignificant improvement in fit relative to the generalized parameterization as shown by extra sum of squares  $F$ -tests ( $P > 0.1$ ; Table 2; Methods S1). For the ecotype and warming treatment specific parameterizations  $T_{\text{opt}}$  ranged from 23.5 to 25.9°C.  $P_{\text{maxLT}}$  fell between 21.9 and 29.5  $\mu\text{mol CO}_2 \text{m}^{-2} \text{leaf area s}^{-1}$  and  $E_{0T}$  was between 0.06 and 0.14  $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ . Overall leaf-level photosynthetic capacity did not appear to differ with experimental factors (Table 2; Fig. S3a,b; Methods S2). Because the generalized parameterizations of the modified GPP best explained observed GPP, it was used in subsequent modeling operations.

### Preflux LAI

We observed significant variation in preflux LAI due to site ( $F_{2,55} = 12.38$ ,  $P < 0.001$ ), ecotype ( $F_{2,55} = 3.42$ ,  $P < 0.05$ ) and the interaction between ecotype and site ( $F_{4,55} = 2.8$ ,  $P < 0.05$ ). These differences tracked variation in average unshaded GPP. The flux model's sensitivities to LAI, air temperature and PPFD



**Fig. 2** Means, standard errors and ANOVA results for unshaded gross primary productivity (GPP) in *Eriophorum vaginatum* by (a) site, ecotype and warming treatment and (b) ecotypes by site (CF, Coldfoot; TL, Toolik Lake; SG, Sagwon; A, ambient; W, warmed). <sup>a</sup>Significance codes: \*\*\*, 0.001; \*\*, 0.01; \*, 0.05. <sup>b</sup>Capital letters denote significant differences between ecotypes within a given site. <sup>c</sup>Only a single measurement was available for this combination, therefore this error bar was derived from the ANOVA.

across their ranges from the unshaded GPP measurements (Table 1) were 6.3, 1.9 and 1.2  $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ , respectively, with LAI accounting for 3.3 times more variation in GPP than air temperature and 5.3 times more than PPFD.

### Peak season LAI

Significant differences in peak season LAI were observed due to ecotype ( $F_{2,81} = 15.79$ ,  $P < 0.001$ ) and site ( $F_{2,81} = 4.93$ ,  $P < 0.01$ , Fig. 3a). There were also significant differences due to ecotype at the TL ( $F_{2,27} = 12.19$ ,  $P < 0.001$ ) and SG ( $F_{2,27} = 6.98$ ,  $P < 0.01$ ) sites, but not at CF (Fig. 3b). The overall

**Table 2** Fitted means, standard errors, fit statistics and extra sum of squares  $F$ -test results comparing the generalized and ecotype and warming treatment specific parameterizations of the modified gross primary productivity model for *Eriophorum vaginatum* ( $T_{\text{opt}}$ , temperature optimum of photosynthesis;  $P_{\text{maxLT}}$ , light-saturated photosynthetic rate per unit leaf area at  $T_{\text{opt}}$ ;  $E_{\text{OT}}$ , initial slope of the light response curve at  $T_{\text{opt}}$ ).

Ecotype	Warming	$P_{\text{maxLT}}$ ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1}$ )		$E_{\text{OT}}$ ( $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ )		$T_{\text{opt}}$ ( $^{\circ}\text{C}$ )		$R^2$	RSS	df	$F$ -test	
		Estimate	SE	Estimate	SE	Estimate	SE				$F$	$P$
All	All	23.56	2.90	0.10	0.03	25.25	0.86	0.55	1254.89	151	0.28	0.97
Coldfoot	All	27.87	9.01	0.06	0.03	23.48	1.52	0.55	156.03	44		
Toolik	All	23.56	5.34	0.10	0.06	25.70	1.51	0.35	393.95	41		
Sagwon	All	22.21	3.76	0.14	0.09	25.88	1.62	0.54	685.28	60		
									1235.27	142	1.11	0.35
All	Ambient	29.49	8.21	0.06	0.02	25.71	1.08	0.58	579.35	84		
All	Warmed	21.87	3.09	0.14	0.07	24.41	1.46	0.53	638.41	64		
									1217.76	146		

interaction between site and ecotype was not significant ( $F_{4,81} = 2.17$ ,  $P < 0.1$ , Fig. 3b). Peak season LAI was generally lower in the CF ecotype, and at TL and SG the home-site ecotype had the highest peak season LAI. No consistent effects of warming treatment on peak season LAI were observed. Instead peak season LAI varied significantly with the interaction between ecotype, site, and warming treatment ( $F_{2,108} = 4.39$ ,  $P < 0.05$ ; Fig. S6).

### Peak season GPP modeling

Modeled peak season GPP in the three common gardens (20 June to 10 August 2016; using the generalized parameterization of the modified GPP model; Table 2) was  $2.15 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . Variation in modeled peak season GPP was affected by the various experimental factors (Fig. 4a–c). The greatest mean percent deviation in modeled peak season GPP (13.5%) was observed as a function of ecotype within site, which exceeded the deviation due to site (5.6%) and ecotype (12.9%) alone (Fig. 4c). Warming treatment accounted for only a small mean percentage of deviation in modeled peak season GPP (3.6%).

### Ecotypes response to environmental change

There was a positive correlation between site-level TDD at each site (median 2001–2011) and modeled peak season GPP for individuals transplanted from the southernmost site, CF ( $F_{1,28} = 19.54$ ,  $P < 0.001$ ,  $R^2 = 0.41$ ), but not for individuals from the TL and SG site (Fig. 5).

## Discussion

This investigation demonstrates that ecotypes play an important role in determining primary productivity and its response to climate change through canopy-level gas exchange measurements and builds upon past work done at the leaf and tiller level. GPP of *E. vaginatum* ecotypes in the reciprocal transplant experiment was partially decoupled from climate and displayed some evidence of home-site advantage at two out of the three sites. These differences in GPP between ecotypes were linked to LAI

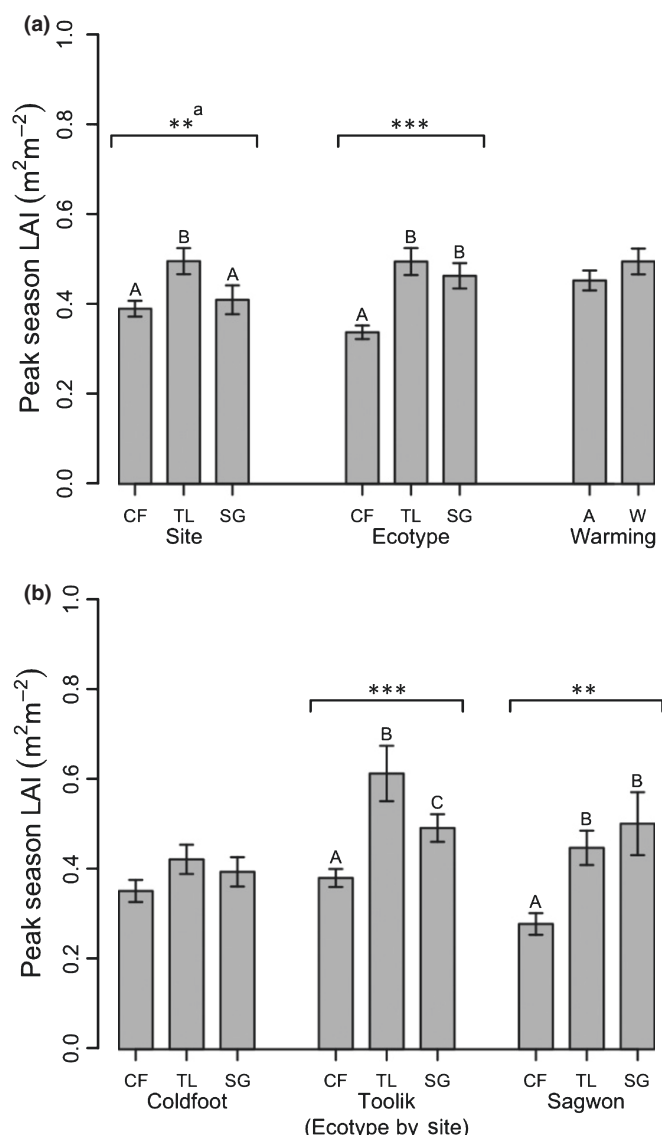
(Figs 2, 3), which exerts strong control over GPP, especially in arctic ecosystems (Shaver *et al.*, 2007, 2013). Ecotype home site contributed to the response of GPP to climate. Our results indicate that an understanding of ecotypic variation is important for investigations of the response of ecosystems to climate, which challenges the notion that vegetation can be represented at a coarse scale in C cycling and species distribution models (that is environmental niche models).

Ecotypes are the result of natural selection and gene flow as influenced by environmental variation across landscapes and have been observed in numerous ecosystems (Linhart & Grant, 1996). Moreover, population biology has recognized that ecotypes can be very sensitive to climate change with implications for species distributions and abundance (Atkins & Travis, 2010; McGraw *et al.*, 2015; Des Roches *et al.*, 2018). Ecotypes are known to display differences in traits linked to primary productivity (Linhart & Grant, 1996). These differences are usually not recognized in studies of C cycles, which largely assume that coarse scale groupings of vegetation have a uniform response to climate change (Sitch *et al.*, 2007; McGuire *et al.*, 2009). Our observations link differences in LAI between ecotypes to differences in GPP and the response of GPP to climate. We suggest how intraspecific variation can influence broader vegetation responses to climate and begin to explore the mechanisms that need to be understood to simulate the impact of these differences.

### Ecotypes partially decouple GPP from climate

Our results supported the hypothesis that GPP was influenced by ecotype-specific traits (Fetcher & Shaver, 1990). Across the range of environmental conditions simulated in our experiment ecotypic differences were more important in determining GPP than the environment because ecotypic differences in GPP persisted even under the same climatic conditions. Furthermore, GPP and LAI did not respond consistently to experimental warming, likely because of variation in the response to climate among ecotypes. Ecotypes demonstrated different sensitivities to the environment (Fig. 5), meaning that the responses of individual ecotypes to warming are likely to have obscured the overall warming effect.





**Fig. 3** Means, standard errors and mixed effects model results for peak season leaf area index (LAI) measurements in *Eriophorum vaginatum* by (a) site, ecotype and warming treatment and (b) ecotypes by site (CF, Coldfoot; TL, Toolik Lake; SG, Sagwon; A, ambient; W, warmed).

<sup>a</sup>Significance codes: \*\*\*, 0.001; \*\*, 0.01.

These results, which challenge the notion that short term (annual to decadal) GPP is solely controlled by the environment, are supported by recent work demonstrating that biologic factors explain as much variation in C fluxes as the environment (Richardson *et al.*, 2007; Yuan *et al.*, 2009; Reichstein *et al.*, 2014; Walker *et al.*, 2019). The results supported the role of biological factors in influencing GPP, a conclusion that is strengthened by our use of a reciprocal transplant design that allowed us to manipulate both ecotypic and environmental factors (Kawecki & Ebert, 2004). These types of experiments are widely used in population and evolutionary biology, but less so in ecosystem ecology and biogeochemistry (Linhart & Grant, 1996; Kawecki & Ebert, 2004). Our results indicate that reciprocal transplants may be

useful for further understanding the response of vegetation to climate change.

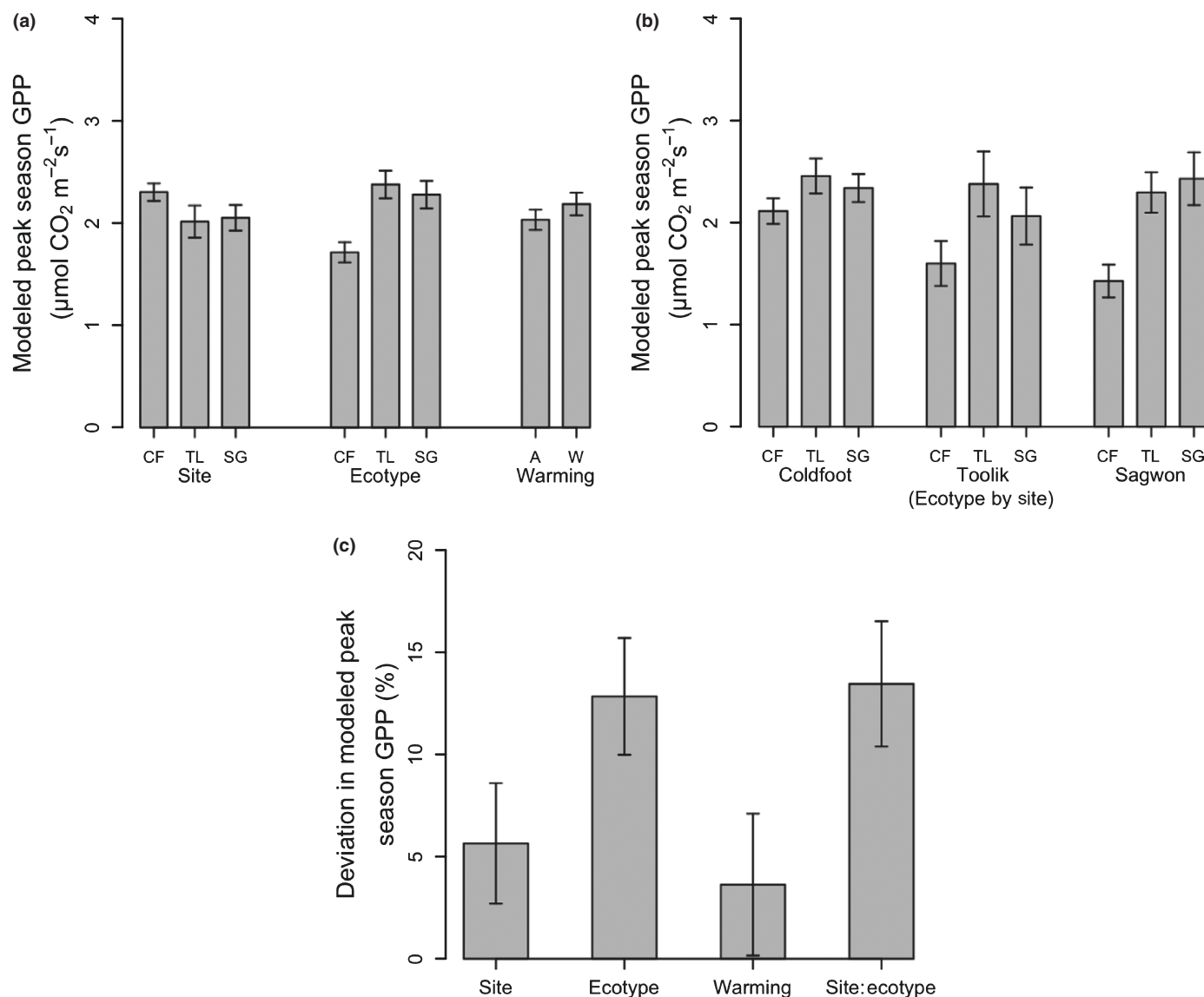
### Home-site advantage in GPP

Our results partially supported the hypothesis that ecotypes will display the highest GPP at their home site. Home-site ecotypes had the highest GPP at a given site with the exception of the southernmost CF site. The CF ecotype had the lowest GPP at all sites in our study and the second lowest rate of home-site tiller production (*c.* 1.5%, the more southern No Name Creek site, which had the lowest rate was not sampled here) in the study of McGraw *et al.* (2015). This suggests that optimal climate conditions may have shifted northward since the formation of the *E. vaginatum* ecotypes, impacting the CF home-site ecotype (McGraw *et al.*, 2015). Another possibility is that the CF ecotype is primarily adapted to a longer, more variable, growing season (Fetcher & Shaver, 1990). In this example, the peak season GPP model would not fully capture its home-site advantage. Home-site advantage in GPP is consistent with the morphological differences observed among ecotypes of *E. vaginatum* and other species (Linhart & Grant, 1996; Souther *et al.*, 2014). Ecotype-specific morphologies have been observed for decades and linked to ecotypic formation and success (Clausen *et al.*, 1948; Núñez-Farfán & Schlichting, 2001). However, ecotype-specific morphologies have rarely been put in the context of C cycling. Given that GPP is fundamentally linked to growth, survivorship, and reproduction, it is likely that traits related to primary productivity are important for the formation and success of ecotypes. Depending upon the pace of processes such as migration and gene flow, home-site advantage may not persist in the face of a rapidly changing climate (McGraw *et al.*, 2015). This has implications for understanding the future distribution and productivity of *E. vaginatum*.

### Differences in LAI, not photosynthetic capacity, determine GPP differences

At the canopy level, differences in GPP among ecotypes were not a result of differences in photosynthetic parameters. Canopy-level photosynthetic rates were best explained by a single generalized parameterization of the modified GPP model rather than ecotype-specific parameterization. Also, leaf-level photosynthetic capacity did not appear to differ with experimental factors. These results differ from reports of differences in leaf-level photosynthetic rates in reciprocally transplanted ecotypes of *E. vaginatum* from the previous 30+ yr experiment (Souther *et al.*, 2014) and individuals in the TL and SG transplant gardens (Schedlbauer *et al.*, 2018), but are consistent with work highlighting functional convergence in arctic tundra vegetation (Shaver *et al.*, 2007, 2013). Previously reported differences in leaf-level photosynthetic parameters might not translate into effects at higher scales (canopy level) under less controlled conditions, as GPP is determined by a combination of factors including matter and energy exchange as well as canopy structure (Farquhar *et al.*, 1980; Colatz *et al.*, 1991; Campbell & Norman, 1998). Across a spectrum



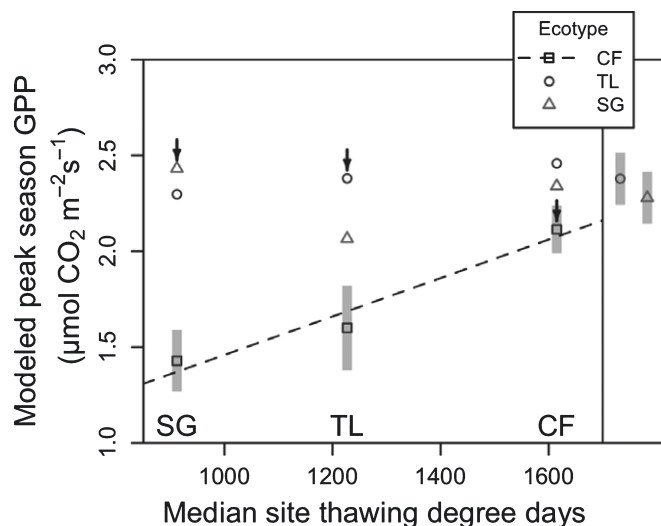


**Fig. 4** (a) Mean modeled peak season gross primary productivity (GPP) in *Eriophorum vaginatum* (20 June 2016 to 10 August 2016) and 95% CI derived via bootstrap resampling, by site, ecotype and warming treatment and (b) ecotypes by site (CF, Coldfoot; TL, Toolik Lake; SG, Sagwon; A, ambient; W, warmed). (c) The mean percent deviation in modeled peak season GPP as a function of the various experimental factors.

of vegetation types with remarkably different leaf-level photosynthetic rates, the majority of variation in GPP was explained by a single set of photosynthetic parameters (Shaver *et al.*, 2007). This was likely to be the result of tight coupling between leaf area, N availability and photosynthetic capacity (Van Wijk *et al.*, 2005; Shaver *et al.*, 2007). More recent work has also found no difference in specific leaf N or specific leaf area – functional traits strongly linked to photosynthetic capacity – among ecotypes or warming treatments in *E. vaginatum* (Schedlbauer *et al.*, 2018). Given that ecotypic differences in GPP are not controlled by photosynthetic parameters, such differences must be driven by vegetation morphology.

Our results indicated that differences in LAI determined differences in GPP among ecotypes. LAI differed significantly with the interaction between ecotype and site. LAI was the most significant variable in our flux model, reflecting its importance in

determining canopy-level photosynthetic rates (Rastetter *et al.*, 1992). Differences in LAI among ecotypes were likely to have been driven by ecotype-specific responses of tillering rates, phenology, and/or leaf biomass production, to environmental conditions (Bennington *et al.*, 2012; Souther *et al.*, 2014; McGraw *et al.*, 2015). Given that photosynthetic parameters are similar among ecotypes, differences in LAI may arise through differences in C allocation to above-/below-ground tissues and storage, a hypothesis that has yet to be tested. Allocation to roots and belowground tissues used for nutrient storage is associated with species living in nutrient-limited environments such as tundra (Iversen *et al.*, 2015). Patterns of allocation could determine the long-term response of ecotypes to increased nutrient availability in a warmer Arctic (Wright & Rocha, 2018; Chapin and Shaver, 1996; Chapin *et al.*, 1995). Regardless of the physiological mechanism, the response of LAI to environmental conditions is the



**Fig. 5** Mean modeled peak season gross primary productivity (GPP) in *Eriophorum vaginatum* by ecotypes within sites plotted against median site thawing degree days from 2001 to 2011. For the Coldfoot (CF) ecotype the significant ( $P < 0.001$ ) regression is shown as a dashed line and 95% CI by site are shown as shaded boxes. For Toolik Lake (TL) and Sagwon (SG) ecotypes pooled means and 95% CI are shown to the right. Arrows indicate the home-site ecotype.

key determinant of productivity in *E. vaginatum* ecotypes (Shaver *et al.*, 2007) and further understanding of its growth and phenology will no doubt improve long-term C cycling predictions in arctic tundra (Shaver *et al.*, 2013).

### Ecotypes differ in their response to climate

GPP of ecotypes from the warmer southern site displayed the sharpest response to a change in ambient climate. GPP increased in the southernmost ecotype (CF) as TDD increased, whereas northern ecotypes (TL and SG) exhibited no significant change in GPP with TDD. This result is consistent with the observation that tiller size of ecotypes from colder northern sites responded less to transplantation (Fetcher & Shaver, 1990), as well as the suggestion that ecotypes adapted to northern environments with a shorter active period may have a limited ability to increase their productivity in response to climate change. Moreover, our results present further evidence that the most striking division within northern Alaska's *E. vaginatum* ecotypes exists close to the tree line where the habitat changes from muskeg to moist acidic tundra.

If we take tree line just south of the Brooks Range as a rough boundary between northern and southern ecotypes and calculate the area of the Alaskan tundra region (Walker *et al.*, 2005) on either side of this boundary, we estimated that the response observed in the TL and SG ecotypes may characterize *E. vaginatum* across up to 59% of the Alaskan tundra region. If we do the same calculation using the potential range of *E. vaginatum* in Alaska (Wein, 1973) we estimated that the response observed in the TL and SG ecotypes may characterize *E. vaginatum* across up to 22% of its potential Alaskan range (Fig. S7). Because *E. vaginatum* can account for up to one-third of ecosystem productivity in tundra sites, where it is dominant

(Chapin & Shaver, 1985), these less responsive ecotypes could limit the response of tundra vegetation productivity to climate change. The responses observed across the  $c. 4.3^{\circ}\text{C}$  or 703 TDD gradient in the transplant may foreshadow the response of *E. vaginatum* ecotypes to the  $3\text{--}5^{\circ}\text{C}$  of warming projected for the Arctic region by the 2090s (ACIA 2004). Moreover, it may reflect how *E. vaginatum* ecotypes have responded to an estimated 140 km or 362 TDD northward shift of optimum climate conditions since the 1980s (McGraw *et al.*, 2015).

Differences in the sensitivity of ecotype productivity to climate has probably arisen from conservative strategies aimed at maintaining growth in northern ecotypes (Fetcher & Shaver, 1990) and trade-offs between traits that maximize productivity and those that ensure stable productivity (Kelley, 1985; Fletcher & Shaver, 1990; Hereford, 2009). Ecotypes adapted to low resource environments may be similar to plants adapted to increase productivity when nutrient limitation is loosened (Fletcher & Shaver, 1990; Chapin *et al.*, 1993). Given the prevalence of ecotypes (Linhart & Grant, 1996) and the importance of GPP in controlling plant growth, ecotypic control of GPP has the potential to limit the response of ecosystem productivity to climate.

### Implications for ecosystem responses to climate

It is clear that vegetation morphology and function can differ among ecotypes; differences which have implications for C cycling. There remain large uncertainties in projections of the Arctic C cycle over both the short term and long term. Intraspecific variation has largely been ignored in investigations of C cycling in the Arctic because vegetation is represented coarsely and is thought to be in equilibrium with climate over the long term. However, our results highlight implications for understanding shorter-term (annual to decadal) C cycling processes under climate change in which ecotypes could alter ecosystem function and population structure.

Further investigation is necessary to develop a comprehensive understanding of the role of ecotypic differentiation and other forms of intraspecific variation in the C cycle. Investigations of ecotypic impacts on productivity in other ecosystems, with different environmental stresses, could further our mechanistic understanding of the role of ecotypes in the responses of vegetation to climate. Investigations of the ecotypes' role in C cycling at larger scales could further demonstrate the importance of intraspecific variation and biological factors in the C cycle. Finally, fundamental research is necessary to develop frameworks for representing intraspecific variation in global carbon cycling models.



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## Author contributions

SRC, TCP, AVR, MLM, JT and NF collectively conceived the research, and interpreted the results. TCP collected the field data, SRC and AVR designed and conducted the modeling analysis, and all authors wrote and edited the manuscript.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Plot of NDVI vs LAI for harvested tussocks.

**Fig. S2** Plot of temperature vs residual GPP.

**Fig. S3** Plots of the quantum yield of photosystem II (PSII) by experimental factors and throughout the growing season.

**Fig. S4** Plot of predicted vs observed GPP.

**Fig. S5** Plot of PPFD vs observed GPP.

**Fig. S6** Plots of peak season LAI and modeled peak season GPP by ecotype, site and warming treatment.

**Fig. S7** Map showing the reciprocal transplant experiment in relation to the Alaskan tundra region and *E. vaginatum*'s range in Alaska.

**Methods S1** *F*-test methods.

**Methods S2** Chlorophyll fluorescence methods.

**Table S1** Model fit statistics for harvested tussock.

**Table S2** *F*-test results for candidate GPP models.

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