

INTERPRETATIONS OF CLIMATE CHANGE ON GRAZING SYSTEMS: THE  
COMPARISON OF ARCTIC AND SUBARCTIC *CAREX*

By

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## Abstract

Stresses imposed by climate change are altering arctic and subarctic ecosystem structure and function. On the Yukon-Kuskokwim River Delta (YKD) in subarctic western Alaska, Pacific Black Brant geese (*Branta bernicla nigricans*) are losing their available grazing lawns of short-statured *Carex subspathacea* due to its conversion into a taller, less nutritious growth form. However, *C. subspathacea* on Alaska's Arctic Coastal Plain (ACP) grows in extensive lawns that remain short even when ungrazed. Our goal was to compare the growth responses between arctic *C. subspathacea* and subarctic *C. subspathacea* when grown in arctic and subarctic conditions. We used reciprocal common gardens to study the variation in height, tiller density, aboveground biomass, and green leaf nitrogen percentage between these reputed taxa. We explored the growth responses that occur in *C. subspathacea* when grown in the arctic and subarctic using linear mixed effect models. We found that environmental differences between these regions influence the morphology of these taxa. Subarctic *C. subspathacea* is phenotypically plastic, and was able to grow tall in subarctic conditions, while remaining short in the Arctic. However, arctic *C. subspathacea* was short in both gardens, suggesting arctic *C. subspathacea* will not grow tall under warming conditions. Understanding the functional causes of the difference between these two grazing systems is important for predicting the effects of future climate change on both regions. This study provides insight to how changing climate will impact these different growth forms and affect future grazing dynamics along arctic and subarctic coasts.



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## Introduction

The Arctic is warming at a rate near double the global average (Cohen et al., 2014; Hwang et al., 2019), and stresses imposed by climate change are altering subarctic and arctic ecosystems (Cowden et al., 2019; Fraser et al., 2019; Galappaththi et al., 2019). As warming continues, the potential increases for widespread redistribution of arctic vegetation, spurring geographic changes among plant-herbivore interactions (Coley et al., 1998, Boelman et al., 2019). Climate change may ultimately alter animal communities and species distributions through redistribution of vegetation and changes in available food sources (Bergengren, 2011).

As climate warms in arctic and subarctic landscapes, the abundance and distribution of nesting geese are also changing. On the Yukon-Kuskokwim Delta (YKD), which encompasses over 75,000 km<sup>2</sup> of wetland habitat between the Yukon and Kuskokwim Rivers in subarctic western Alaska (Fig. 1), the numbers of Pacific Black Brant Geese (*Branta bernicla nigricans*) (hereafter “Brant”) breeding in large colonies have been declining since the early 2000s (Wilson, 2013), whereas the numbers of breeding Brant on the Arctic Coastal Plain (ACP) of Alaska are increasing (Amundson et al., 2019). Given that YKD and ACP breeding Brant are largely sympatric during the spring, fall, and winter, it’s likely that the cause of differing population trends originates on the breeding grounds. Since goslings require high forage quality throughout

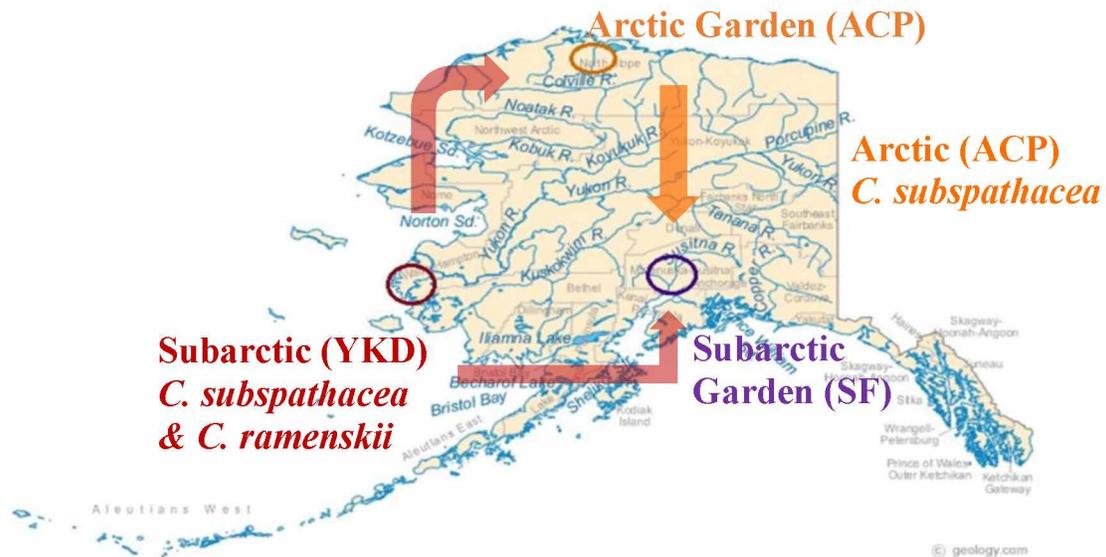


Figure 1: Sample collection locations and garden locations are shown. Short and Tall subarctic *C. subspathacea* were collected from the Yukon-Kuskokwim River Delta (YKD; red circle), and transplanted to the arctic garden (red arrow to orange circle) and to the subarctic garden located in Susitna Flats (SF) (red arrow to purple circle). Arctic *C. subspathacea* was collected from the Arctic Coastal Plain (ACP; orange circle) and transplanted into the arctic garden (orange circle) and the subarctic garden (orange arrow to purple circle).

their growing season, and multiple studies have correlated forage quality with gosling growth and subsequent survival and recruitment (Sedinger & Flint, 1991; Sedinger et al., 1995; Sedinger et al., 2004; Sedinger & Chelgren, 2007), it has been hypothesized that forage dynamics may play a large role in these disparate population trajectories (Sedinger et al., 2001, 2016, 2019; Hupp et al., 2017).

The coastal fringes of the YKD were thought to be dominated by two prevalent plant communities; grazed short (<5cm) *Carex subspathacea* (Hoppner's sedge) which rarely flowers and is maintained by geese as short "grazing lawns" along the fringes of wetlands and mudflats, and ungrazed tall (>10cm) *Carex ramenskii* that flowers irregularly (Ruess et al., 1997; Person et al., 1998; Tande & Lipkin, 2003). However, genetic research has recently shown that these short and tall sedges on the YKD, which are important for goose grazing, are not two separate species, but actually are all *C. subspathacea* exhibiting two growth forms (short and tall) (Takebayashi et al., in prep). On the YKD, Brant maintain short-statured, rapidly growing grazing lawns of *C. subspathacea*; in the absence of grazing, short *C. subspathacea* reverts to the taller, less nutritious growth form (Ruess et al., 1997; Person et al., 2003; Fondell et al., 2011). This reversion from short to tall triggers a feedback loop, where a reduction in available short grazing lawns reduces the forage quantity and quality for goslings, thereby impacting recruitment for future generations (Person et al., 2003; Sedinger et al., 2019).

The key feature of this grazing system is that in the absence of grazing, short *C. subspathacea* grows to be tall within 3 years, and with frequent intensive grazing, tall *C. subspathacea* will become short (Person et al., 2003). As such, geese are responsible for maintaining their forage base; grazing lawn boundaries increase when grazing pressure is high and decrease when grazing pressure is low for multiple seasons (Person et al., 2003; Sedinger et al., 2016). As a result of this dynamic, geese maintain grazing lawns on the YKD and the annual foraging offtake of available aboveground biomass in these *C. subspathacea* lawns typically exceeds 90% (Person et al., 1998).

Short *C. subspathacea* has a circumpolar distribution along arctic and subarctic coastlines, but curiously, there has been no tall *C. subspathacea* identified in arctic landscapes (Flora of North America, 1993). On the coastal fringes of Alaska's ACP (Fig. 1), *C. subspathacea* grows in extensive lawns that are not confined to margins of wetlands and mudflats. The sedge remains short (<5cm) even when ungrazed and appears to flower annually

(Flint & Meixell, 2021). Grazing pressure along the ACP is far lower than on the YKD and annual offtake of aboveground biomass is <50% (Sedinger et al., 2001; Hupp et al., 2017; Flint & Meixell, 2021). Moreover, *C. subspathacea* does not appear to convert to the tall growth form in the absence of grazing even when warmed a few degrees in greenhouse structures (Flint & Meixell, 2021). Thus, under current or slightly warmer conditions, grazing is not required to maintain forage on the ACP.

It is unknown what causes the apparent difference in these two grazing systems which share the same primary forage plant species (Takebayashi et al., in prep). Many studies support the pattern that as temperature increases, plant biomass and height increase, while green leaf nitrogen concentration often declines (Chapin et al., 1995; Arft et al., 1999; Doiron et al., 2014; Lameris et al., 2017). Thus, the conversion of *C. subspathacea* to the taller, less palatable growth form on the YKD in the absence of grazing may primarily be a direct effect of temperature.

The YKD has a longer and warmer growing season than the ACP, suggesting that *C. subspathacea* in the Arctic may not revert to a tall growth form because it is constrained by temperature and growing season length. Alternatively, there may be other causes which restrict the phenotypic plasticity of *C. subspathacea* in the Arctic. Understanding the functional causes of the difference between these two grazing systems is important for predicting the effects of future climate change on both regions.

Our goal was to compare the growth responses of arctic, short subarctic, and tall subarctic *C. subspathacea* when grown in arctic and subarctic conditions, to assess evidence of morphological plasticity, and determine how environment influences expression of plasticity. Understanding these relationships will improve predictions of how changing climate will impact these different growth forms and affect future grazing dynamics along arctic and subarctic coasts. To assess the effects of environmental conditions on plant growth form and plant origin (YKD and ACP), we used a reciprocal transplant design to study the variation in height, tiller density, aboveground biomass, and green leaf nitrogen concentration across 3 years. We established gardens in the arctic and subarctic and transplanted plant samples from and to both locations, allowing for direct comparison of growth patterns of both growth forms and plant origins when grown in identical conditions. We predicted that if the apparent differences in YKD and ACP grazing systems were entirely environmental, we would see little variation in how plants from these disjunct locations grow under common conditions.

## Methods

### *Sample Collection for Transplant*

Live samples of *Carex subspathacea* were collected from arctic and subarctic Brant goose foraging habitats on the Arctic Coastal Plain (ACP) and the Yukon-Kuskokwim River Delta (YKD; subarctic) (Fig. 1). For each region, samples were collected from 5 sites from each of two river systems (Table A1). The ACP samples were collected along the Smith and Colville Rivers, where short *C. subspathacea* grows but the tall growth form is not present. The YKD samples (short subarctic and tall subarctic) were collected from the lower, tidally influenced reaches of the Tutakoke and Kashunuk Rivers (Fig. 1). At each location and for each growth form, sod samples measuring 40 x 60 cm were dug to a minimum depth of 20 cm, placed in rubber tubs, and shipped to the arctic and subarctic gardens (Fig. 1). We collected 30 sod samples for each garden (a total of 60) for the reciprocal transplant experiment.

### *Terminology/Taxonomy*

We initially thought we were sampling both *C. subspathacea* (short) and *C. ramenskii* (tall) from the YKD grazing areas for our study. However, our recent genetic analysis demonstrates that only a single species exists in these grazing areas and it should be classified as *C. subspathacea* (Takebayashi et al., in prep). Previous publications had mis-identified the tall form of *C. subspathacea* on the YKD and Susitna Flats (SF) as *C. ramenskii* (Ruess et al. 1997, Person et al. 2003, Ruess et al. 2019). Throughout this manuscript we refer to the tall subarctic growth form as *C. subspathacea* but in the literature we cite, these plants were referred to as *C. ramenskii*. This may lead to confusion when comparing our results with previous literature using alternate nomenclature (Person et al., 2003), but we think it is important to incorporate what we now know about its taxonomic identity.

### *Reciprocal Transplant Gardens*

Reciprocal transplant gardens were established to assess whether variation in arctic and subarctic conditions explained the growth differences (height, tiller density, aboveground biomass, and leaf nitrogen percentage) between subarctic and arctic *C. subspathacea*. The collected sod samples of arctic, short subarctic, and tall subarctic *C. subspathacea* were transplanted in August of 2015 to the same latitudes as the collection sites. The arctic garden was located near the mouth of the Colville River Delta (Fig. 1; 70° 14.484' N, 150° 48.338' W) and was within a large *C. subspathacea* grazing lawn. We were unable to obtain a permit to import

arctic plants to the YKD; therefore, the subarctic garden was established on the Susitna Flats (SF; Fig. 1; 61°14'22.4"N 150°47'51.3"W). This site was selected because it is the same latitude as the YKD collection site, has a similar tidal flooding regime, tall *C. subspathacea* hybrids naturally occur there (Zacheis et al., 2001; Takebayashi et al., in prep), and logistics were much easier than on the YKD. The subarctic garden was placed within a healthy tall *C. subspathacea* hybrid meadow. For each sod transplanted into the gardens, we excavated a 40 cm x 60 cm x 20 cm deep plot of vegetation and inserted the imported samples into the hole. Each garden contained 30 *C. subspathacea* plots: ten from the arctic, ten plots of short subarctic plants, and ten plots of tall subarctic plants. Transplants were arranged in both gardens as shown in Figure A1 and then fenced with mesh netting to preclude grazing or trampling by geese.

Previous work has shown that grazing has a major effect on the height of *C. subspathacea* on the subarctic YKD and is essential to maintaining short grazing lawns (Ruess et al., 1997; Person et al., 2003). Conversely, sedges on the ACP are short whether they are grazed or not (Flint & Meixell, 2021). To determine whether this was due to environmental differences between arctic and subarctic conditions or to grazing, we measured differences in the effect of simulated grazing in both gardens. Each plot was split into two clipping treatments. Half of the plot was unclipped to represent ungrazed vegetation, and the other half was clipped with scissors to near soil surface once a year during late summer to simulate a low frequency of intensive grazing. The placement of treatments within each plot was randomly selected.

Gardens were allowed to root and recover from transplanting stress for a year before initiating clipping and data collection, which occurred in the summers of 2016, 2017, and 2018 (Table 1). Each summer prior to clipping, plant height and tiller density were measured in each treatment. Tiller height was measured to the nearest mm from five haphazardly chosen tillers each year, and tiller density was measured by counting all tillers within a 5 x 5 cm square.

Table 1: Data collection dates by year for the two common gardens, located on the Colville River Delta (CRD) and Susitna Flats (SF).

Year	Garden	Sampling Date
2016	Susitna Flats (subarctic)	May 25
2016	Colville River (arctic)	July 10
2017	Susitna Flats (subarctic)	June 22
2017	Colville River (arctic)	July 11
2018	Susitna Flats (subarctic)	May 24
2018	Colville River (arctic)	July 24

Aboveground biomass (dry weight) was measured by collecting the tissue from a 5 x 5 cm square placed randomly in a different spot each year. In 2016 and 2017, tissue was only collected from the clipped treatment since we could not collect tissue from the unclipped treatment without altering the treatment. Tissue was collected from all treatments in the last year of the study, 2018. Plant clippings were dried for one week at 50°C, ground, weighed, and a 2 mg sample was used to obtain total carbon and nitrogen percentage by continuous-flow isotope ratio mass spectrometry at the Alaska Stable Isotope Facility at the University of Alaska Fairbanks's Water and Environmental Research Center. All transplanted vegetation in the gardens was removed at the end of the 2018 sampling season.

### ***Data Analysis***

We explored growth responses of *C. subspathacea* when grown in arctic and subarctic conditions using linear mixed effect models with the package *lme4* version 1.1-26 in R version 4.0.4 (Bates, 2010; R Core Team, 2017). Height, tiller density, aboveground biomass, and nitrogen percentage at the end of the common garden experiment (2018) were the dependent variables to the fixed effects of garden location (Arctic, subarctic), morphogroup (Arctic, short subarctic, and tall subarctic) and grazing treatment (clipped or not clipped). We included two random effects (random intercepts), the river effect and the individual plot/site effect, to account for the variation among sampling locations and micro-environmental gradient among plots. In order to assess changes in height and tiller density over 3 years, we used similar linear mixed effect models with an additional fixed effect, year since transplantation, as a continuous variable. For the yearly change of tiller density, clipping treatment was left out of the model since the measurements were only taken from the clipped treatment.

We used model selection procedures to assess the ability of our fixed and random effects to explain variation in our data. First, we fitted the full factorial models with all interactions among fixed effects using AICc estimated using maximum likelihood (ML) method and compared models differing in which random effects were included with the package *AICcmodavg* 2.3 (Säfken et al., 2018). To double check our results, we also calculated cAIC using restricted maximum likelihood (REML) because it tends to optimize fitting of the random effects (Greven & Kneib, 2010). We used backwards-stepwise model selection on random effects at first, and then on fixed effects with the selected random effect structure. We selected

the model with cAIC when there was a discrepancy between the two information criteria (Jacot, 2016), although they agreed in most cases.

Separately, we also directly assessed the probability that a given factor was included in a model purely by chance. We accomplished this using a log likelihood ratio statistic where the probability of the observed ratio, given the data, was compared to a distribution estimated by parametric bootstrapping (Faraway, 2016). The test statistic,  $D$ , is twice the difference in the log likelihood of two models:  $D = -2 * (\ln(\text{Likelihood for a simpler model}) - \ln(\text{likelihood for a model with more parameters}))$ . In the steps of model selection and calculation of p-values, we fitted the model using ML. This approach makes no assumption regarding the distribution of the test statistic but is dependent on the parameter estimates and associated error distribution of the parameter estimates. In the majority of analyses, models selected from this procedure were consistent with information criteria-based selection. We included the model selection results of log-likelihood test in the supplementary tables, but mainly focused on the information criteria in the main text (Table A2; Table A3; Table A4; Table A5; Table A6).

We assessed normality and homogeneity of variance with Quantile-Quantile plots (Faraway, 2016) and transformed height and tiller density data using log transformation. Biomass was transformed with 2 parameter Box-Cox transformations (Hawkins & Weisberg, 2017; Table A7; Table A8; Table; A9) using the R package *car* 3.0. Nitrogen concentration did not require transformation.

Since most of the interaction effects were included in the most parsimonious models, we conducted post-hoc comparison of cell means. Tukey's Honestly Significantly Different test was used to analyze all pair-wise comparisons of cell means and P-values were calculated with multivariate t-distribution (adjust= "mvt" option) using the R package *emmeans* 1.5.3 (Lenth, 2020). For the analysis of yearly change, we calculated the simple slopes against each year for each cell. P-values of the simple slope analysis were adjusted for multiple comparisons with Holm's correction (Holm, 1979).

## Results

### *Tiller Height*

The model selected to explain variation in tiller height in the last year of data collection (2018) included individual plot/site as the random effect and all three fixed effects and their interactions (Table A10). This indicates that fixed effects of garden location (Arctic, subarctic), morphogroup (Arctic, short subarctic, tall subarctic) and grazing treatment (clipped or not clipped), all influenced tiller height.

Examination of post-hoc comparisons revealed that in 2018 (at the end of the study), short and tall subarctic *C. subspathacea* were significantly shorter in the arctic garden than in the subarctic garden, while arctic plants remained short in both gardens (Fig. 2A). Thus, arctic plants appear to be genetically constrained to short stature, whereas subarctic plants are plastic. Clipping had no significant effect on plant height except through its effect on reducing height of subarctic tall tillers in the Arctic garden (Fig. 2A). Finally, the three morphogroups were clearly different from each other when grown in the subarctic garden; the subarctic tall plants were the tallest, the subarctic short plants were intermediate, and the arctic plants were the shortest. This pattern was observed regardless of clipping. However, in the arctic garden, the differences became less obvious; tall sub-arctic *C. subspathacea* was still significantly taller than the others when plants were not clipped, but the short subarctic plants were indistinguishable from the arctic plants. Height differences among the three morphogroups disappeared when the plants were clipped in the arctic garden (Fig. 2A).

### *Height Change Over Years*

When all 3 years of data were included in the analysis, with year as a fixed effect, the model selected to explain variation in tiller height included individual plot/site for the random effect and all four fixed effects and their four-way interactions (Table A11). As a four-way interaction is not readily interpretable, we looked at the simple slope analyses to understand the effect of year on how height changed over time in the common gardens (Table A12). In the subarctic garden, the height of the subarctic morphogroups increased over the three years while the arctic morphogroup decreased regardless of clipping (Fig. 3A & 3B). Arctic plants simply grew poorly in the subarctic garden. In the arctic garden, the height of subarctic short plants increased slightly for both clipped and unclipped plants. The height of subarctic tall plants decreased when clipped but did not vary among years in unclipped plants. We did not detect

changes in height over three years for either clipped or unclipped arctic plants in the arctic garden. The persistent differences between short and tall subarctic plants indicate that even though there are no genetic differences between these morphogroups (Takebayashi et al., in prep), they are different, perhaps due to different levels of resources stored in the perennial rhizomes, or epigenetic differences.

### ***Tiller Density***

The model selected to explain variation in tiller density in the final year (2018) included individual plot/site for the random effect, all three fixed main effects, and the two-way interaction between garden and morphogroup (Table A13). Tiller density was higher in the arctic garden than the subarctic garden for all morphogroups, though the difference was only significant for arctic and short subarctic *C. subspathacea* (Fig. 2B). Arctic plants showed the largest decrease in tiller density when grown in the subarctic garden, driving a significant 2-way interaction between garden and morphogroup. Clipping decreased tiller density for all morphogroups in the arctic garden. In the subarctic garden, clipping decreased tiller density for the two subarctic morphogroups, but increased tiller density of arctic plants (Fig. 2B).

Comparing morphogroups within gardens, tiller density was generally higher for plants in their home garden. Subarctic plants had higher tiller density than the arctic plants when grown in the subarctic garden regardless of clipping. Arctic plants had higher density than subarctic plants in the arctic garden; however, only the two extremes (the densest arctic plants vs the least dense tall subarctic plants) showed statistically significant differences.

### ***Tiller Density Change Over Years***

When tiller density across all 3 years was analyzed, the selected model included river and individual plot/site for the random effects, all 3 fixed effects, and their three-way interactions (Table A14). The fixed effects included year, garden location, and morphogroup. Grazing treatment (clipped or not clipped) was included in the analysis, as density estimation required clipping plants, and could only be estimated in clipped treatments for the first two years of the study. AICc selected a model without the river random effect; however, generally cAIC is considered to be more appropriate, especially for optimization of random effects. Therefore, we retained both random effects for the subsequent model selection of fixed effects. The main fixed effects of this model were garden, morphogroup and year. As a three-way interaction is not readily interpretable, we looked at the simple slope analyses to understand the effect of year on

how tiller density changed over time in the common gardens (Table A15). Tiller density of clipped arctic and subarctic short plants declined over time in both gardens. Density of clipped subarctic tall *C. subspathacea* did not change consistently in either garden (Fig. 3C)

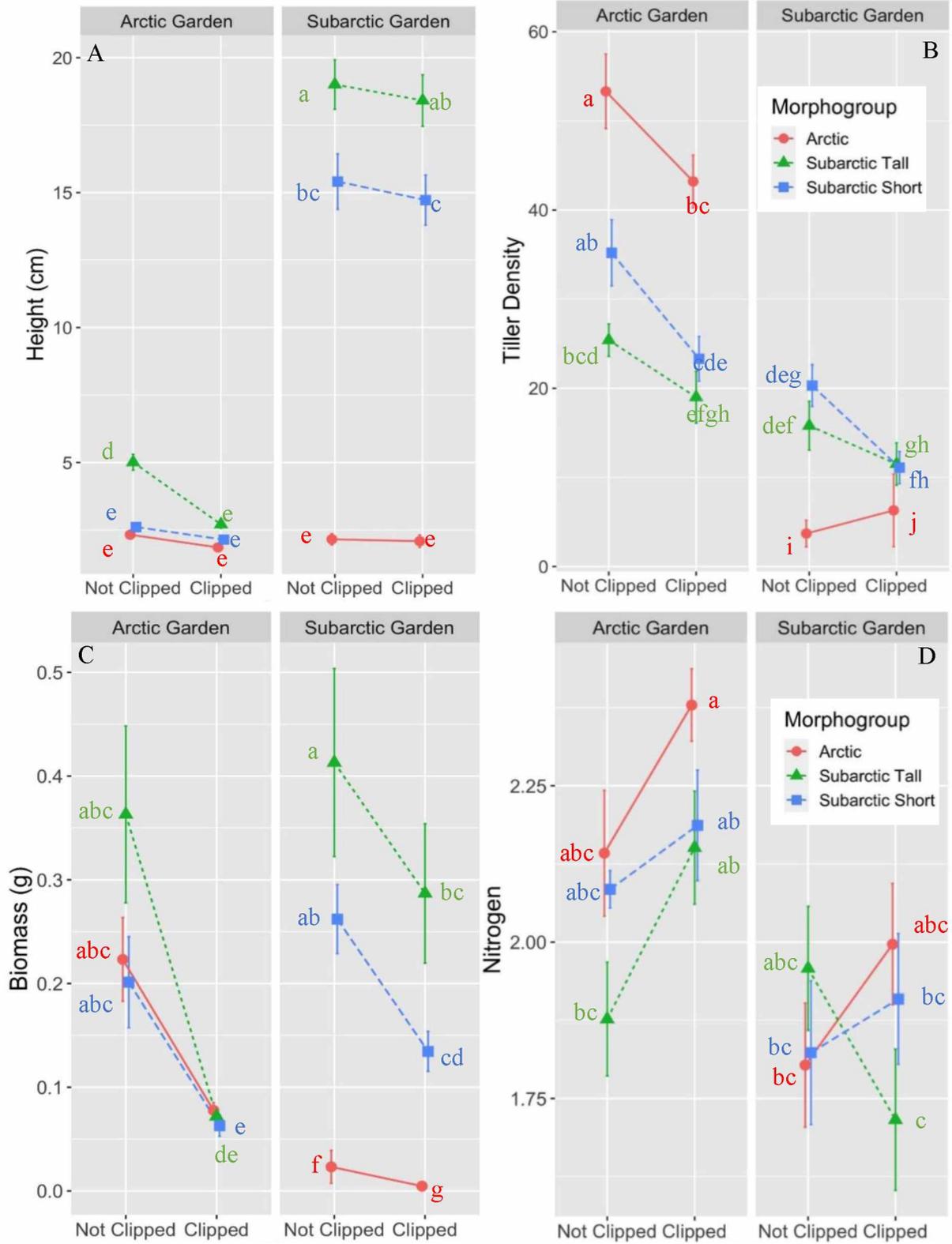


Figure 2: Average values of (A) sedge height (cm), (B) tiller density (tillers/25cm<sup>2</sup>), (C) aboveground biomass (g/25cm<sup>2</sup>), and (D) leaf nitrogen concentration (w/w % in dry weight) in Arctic and sub-Arctic gardens at the end of the common garden experiment (2018). The error bars are standard errors. Letters indicate significant differences among points. The same letters indicate grouping of estimated marginal means with adjusted  $P > 0.05$  from all pairwise comparisons (i.e., a compact letter display).

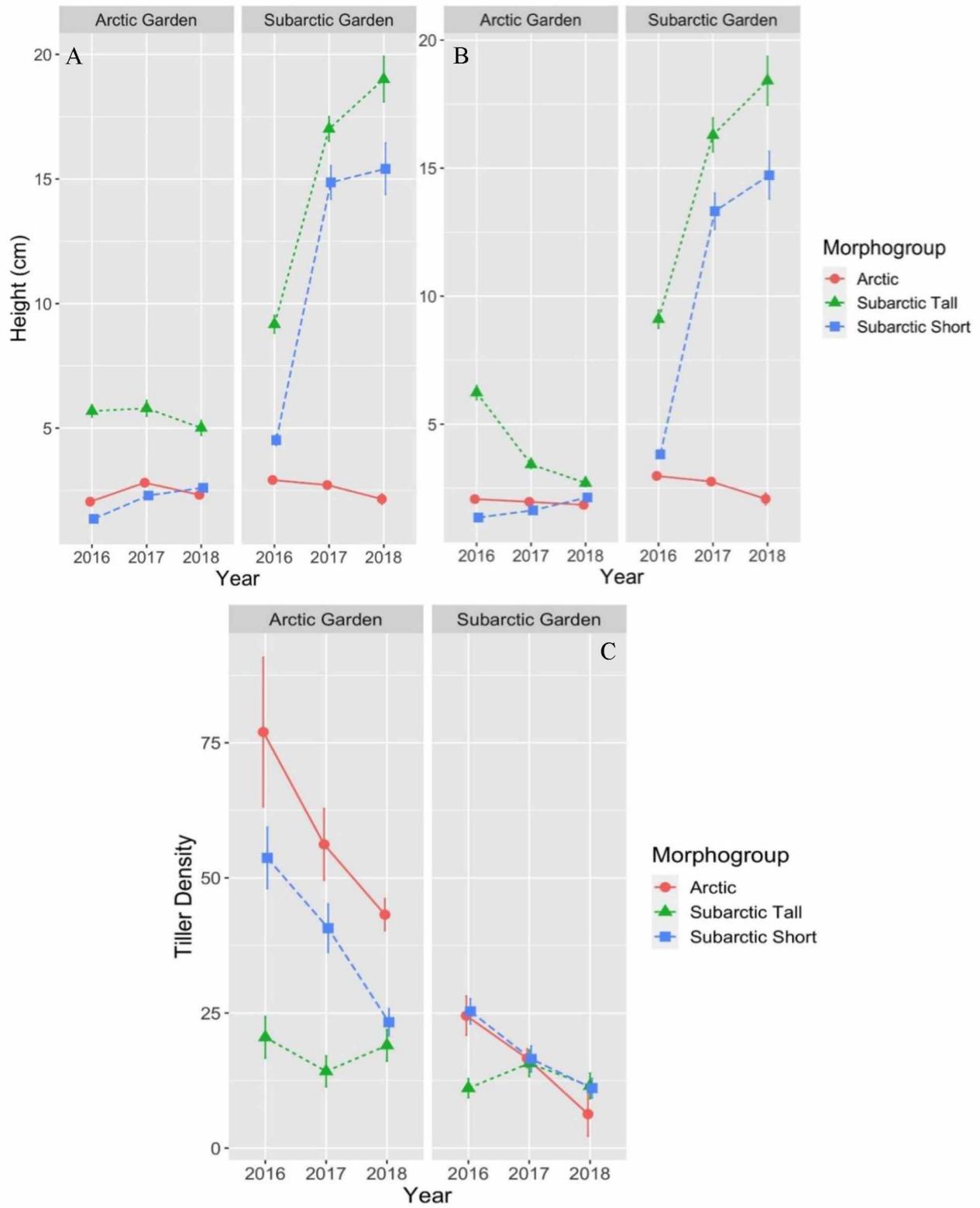


Figure 3: Changes in (A) unclipped sedge height (cm), (B) clipped sedge height (cm), and (C) tiller density of clipped treatments (tiller/5cm<sup>2</sup>) across 3 years in the Arctic and sub-Arctic garden. The error bars are standard errors.

### ***Aboveground Biomass***

The model selected to explain variation in sedge aboveground biomass in 2018 included individual plot/site for the random effect, all three fixed effects and the two-way interactions between garden and morphogroup and garden and clipping (Table A16). Clipping significantly decreased aboveground biomass of all morphogroups in both gardens. When clipped, both subarctic morphogroups had higher biomass in the subarctic garden compared to the arctic garden but showed no garden effect when unclipped. The biomass of both clipped and unclipped arctic plants was significantly reduced when grown in subarctic conditions (Fig. 2C). In the subarctic garden, subarctic sedges had significantly more biomass than arctic sedges. However, in the arctic garden, the biomass of the 3 morphogroups was indistinguishable, despite differences among morphogroups in density and height. The low nutrient availability and cold soils of the arctic garden were apparently not a deterrent to growth of subarctic plants unless they were grazed, where decreases in plant height of all morphogroups were made up for by increases in density to produce an overall similar biomass.

### ***Nitrogen Concentration***

Since the optimized model explaining variation in sedge nitrogen concentration had no random effects (Table A17), we analyzed the data using analysis of variance (ANOVA; Table A18). Leaf nitrogen concentrations were significantly higher in the arctic garden compared to the subarctic garden for the clipped subarctic tall morphogroup (Fig. 2D). The effect of clipping on nitrogen concentrations was marginally significant; clipping had a tendency to increase the nitrogen concentration except for subarctic tall plants in the subarctic garden (Fig. 2D).

### **Discussion**

We aimed to test the environmental influence on the growth of short and tall subarctic *C. subspathacea*, and arctic *C. subspathacea* as it directly relates to differences in grazing systems on the subarctic Yukon-Kuskokwim Delta (YKD) and Arctic Coastal Plain (ACP), using a reciprocal transplant experiment. We measured differences in sedge height, tiller density, aboveground biomass, and leaf nitrogen concentration for plants grown within common gardens in arctic and subarctic environments. Our data demonstrate that the difference between arctic and subarctic grazing systems is primarily driven by functional differences in the plants between regions, in spite of the fact they are identified as the same species. *C. subspathacea* on the YKD is morphologically plastic whereby grazed plants take on a short form and ungrazed plants grow

much taller. This is directly related to forage quality and this plasticity is expressed more clearly in warmer conditions. Conversely, the arctic *C. subspathacea* does not have high levels of morphological plasticity regardless of environmental conditions. These data also suggest that the YKD grazing system is likely to change in response to warming conditions; whereas the ACP system would appear to be relatively resistant to increases in temperature or changes in grazing pressure.

### ***Garden Effects***

Our results generally agree with previous work showing a positive relationship between temperature and biomass production, at least for subarctic plants (Chapin et al., 1995; Arft et al., 1999; Doiron et al., 2014; Lameris et al., 2017, Flint & Meixell 2021). Similar to growth responses seen on the YKD, short subarctic *C. subspathacea* converted to a taller growth form when grown in the subarctic garden and ungrazed. As such in the subarctic garden, there was relatively little difference between short and tall subarctic *C. subspathacea* (i.e., both grew tall, and the height of short subarctic plants increased across years). Conversely, arctic plants did not show increased aboveground growth when grown in either garden (i.e., they maintained a short growth form). This demonstrates that aboveground growth (and the tradeoffs between tiller height and density) in subarctic *C. subspathacea* is plastic and that the expression of this plasticity is dependent on environmental conditions.

Flint and Meixell (2021) found that arctic *C. subspathacea* showed relatively small increases in biomass ( $\sim 10 \text{ g/m}^2/\text{year}$  dry weight) when warmed  $1 \text{ }^\circ\text{C}$  in small greenhouses near Teshekpuk Lake on the ACP. On the contrary, we found that the biomass of arctic *C. subspathacea* actually decreased when moved to the subarctic garden. Environmental differences between our arctic and subarctic gardens were much greater than the differences in Flint and Meixell (2021), with an average July temperature difference of  $13.1 \text{ }^\circ\text{C}$  between the gardens (Alaska Climate Research Center, 2021), in addition to other environmental differences between gardens, such as soil temperature and nutrient availability, day length, tidal regimes, etc. This suggests that the results of Flint and Meixell (2021) may not scale up; larger increases in temperature may not equate to larger increases in biomass. Our data support the prediction that arctic *C. subspathacea* will remain short even as arctic temperatures continue to rise.

Sedinger et al. (1991) found that arctic *C. subspathacea* had higher aboveground biomass but lower nitrogen concentration compared to the YKD subarctic short *C. subspathacea*. However, this pattern may have been heavily influenced by the inherently high grazing pressure on the short YKD grazing lawns and associated effects of goose feces on plant growth and leaf N concentrations. Flint and Meixell (2021) showed similar nitrogen concentration of short *C. subspathacea* on the ACP to that reported by Person et al. (2003) on the YKD. Biomass and nitrogen were not strongly influenced either by garden location or plant provenance in our study. Thus, our study does not strongly support the idea that forage quality in the arctic is higher than in the subarctic.

There was a trade-off in growth allocation patterns in the different climates. Subarctic plants allocated resources to height growth at the expense of tiller production when growing in the subarctic garden, but in arctic conditions, produced more tillers with lower growth per tiller but similar biomass per unit area. This response may be due to plants investing more in perennial structures (increase tiller density) instead of height when grown in cold environments. Arctic *C. subspathacea* produced more tillers than subarctic morphogroups in the arctic garden, while subarctic plants had greater height in the subarctic garden, however aboveground biomass was similar between gardens.

Other *Carex* species have been shown to produce longer leaves when transplanted into warmer temperatures (Stenström & Jónsdóttir, 2003), and other high-arctic tundra plants have been shown to increase leaf size and plant height in response to warmer conditions (Hudson et al., 2011). In our study, the highest tiller density was found in arctic *C. subspathacea* growing in the arctic garden, but these plants did not show an increase in height growth when tiller density declined in the subarctic garden. Similarly, northern ecotypes of *Eriophorum vaginatum* grown in southern sites did not produce longer leaves. Arctic *C. subspathacea* appears to be locally adapted, lacking the plasticity to respond to more favorable environmental conditions (Bennington et al., 2012).

### ***Grazing effects***

Our data showed that plants had different responses to grazing depending on their morphogroup and garden location. However, we caution that our clipping treatment may have been a poor simulation of true grazing. Clipping was conducted only once per year and removed

>90% of aboveground biomass. Clipping was conducted in July which is fairly late in the season and during a time when plants are senescing. Thus, our clipping treatments simulate a single intensive grazing event but did not include the fecal input of nutrients that is typical of natural grazing. The effects of the previous years' clipping were measured in subsequent years prior to the next clipping treatment. In subarctic conditions, this single clipping event did not prevent the reversion of short subarctic *C. subspathacea* to the tall morphogroup over 3 years. However, in both gardens, clipping reduced biomass suggesting that this level of offtake may not be sustainable over the long term, although regrowth may have been reduced without the nutrients from feces that normally accompany grazing. Nevertheless, biomass reductions from clipping were relatively greater in the arctic garden implying that arctic habitats may be more vulnerable to overgrazing. The extreme cold and arctic conditions are likely limiting the aboveground net primary productivity in the Arctic, leading to reduced response to grazing in the Arctic (Moss et al., 2011).

Flint and Meixell (2021) showed minimal offtake due to natural grazing and no net increase in nitrogen concentration of *C. subspathacea* in response to grazing on the ACP. Likewise, in our experiment, simulated grazing had no significant effects on nitrogen concentration in either garden. Thus, the key feedback where grazing and the removal of standing crop generally results in regrowth with higher nitrogen concentration (Person et al., 2003; Bazely & Jefferies, 1985; Bazely & Jefferies, 1989) does not appear to be supported in our results. However, these results may not be representative of true grazing since we did not have the added nitrogen from geese feces which has been shown to be critical for the positive responses of NPP and leaf nitrogen percentage (Cargill & Jefferies, 1984; Hik & Jefferies, 1990).

### ***Morphogroups in arctic and subarctic grazing systems***

The growth traits we observed for *C. subspathacea* genotypes growing in Alaskan arctic and subarctic environments have implications for the dynamics of grazing systems in these two regions. On the YKD, the rapid conversion from the short to tall growth form occurs at two important temporal/spatial scales. Early in the growing season, adult geese often graze and maintain the tall *C. subspathacea* growth form as short ephemeral grazing lawns. But as the season progresses, the inherently rapid growth of this tall growth form “gets away from the geese”, and it is only the swards of *C. subspathacea* that are grazed frequently and intensively over multiple years that constitute the short-statured phenotype characteristic of perennial

grazing lawns. Our single clipping of short and tall CSUB was not sufficient to create a short lawn on the YKD, it is only through intensive grazing that the highly palatable and manageable short growth form of *C. subspathacea* exists. At larger temporal and spatial scales, grazing lawns of *C. subspathacea* revert to a less nutritious tall growth form within 3 years without grazing, or with low intensity grazing, and can serve as a negative feedback to population growth.

Reductions in goose populations due to fox predation in the 1990s resulted in the loss of grazing lawns across a broad regional extent, and the widespread reversion to the tall growth form across the landscape slowed population recovery once geese were released from heavy predation (Person et al., 2003).

On the ACP, *C. subspathacea* is only found as a short-statured plant and never reverts to the taller, less palatable growth form despite the fact that there is minimal annual offtake by foraging geese (Sedinger et al., 1991, Hupp et al., 2017, Flint & Meixell, 2021). This inherently short growth stature of arctic *C. subspathacea* may have contributed to the recent rapid expansion of ACP goose populations because the carrying capacity of the foraging habitat is unrelated to annual fluctuations in goose abundances and associated grazing intensity across the landscape. Thus, it appears that the complex grazing-vegetation-goose population interactions found on the YKD do not occur on the ACP (Ruess et al., 1997; Sedinger et al., 2016). Growth characteristics of *C. subspathacea* on the ACP suggest the potential for further growth of arctic goose populations (Flint & Meixell 2021); however, it is uncertain whether the species can sustainably tolerate higher grazing intensities such as are currently found on the YKD. Our data show that in the arctic even very low-level grazing dramatically reduces tiller density and total biomass in subsequent years.

### ***Response to Climate Change***

Our data demonstrated functional differences between arctic and subarctic *C. subspathacea*. Subarctic *C. subspathacea* shows considerable phenotypic plasticity for growth and tiller height on the YKD, which we found was moderated when transplanted to the arctic, likely by reduced soil and air temperatures and/or season length. However, arctic *C. subspathacea* did not show this degree of tiller height plasticity under the range of conditions we used. Genetic data clearly identifies both of these populations as *C. subspathacea*, but shows some degree of geographic genetic differentiation between the subarctic and arctic populations due to geographic distance between populations (Takebayashi et al., in prep).

To thrive under the inter-annual and intra-annual variable climate, subarctic taxa have plastic traits that enable survival under a broad range of environmental conditions (Schlichting, 1986). In contrast, arctic species, and other taxa growing in extreme environments, often show strong ecotypic specialization but relatively limited phenotypic plasticity in growth traits when transferred to subarctic environments (Souther et al., 2014; McGraw et al., 2015). We found that subarctic plants grew well in both gardens displaying their phenotypic plasticity, but arctic plants remained short in the subarctic garden showing ecotypic specialization for the cold arctic climate. Our data suggest that continued warming in Alaska may interact with these regionally adapted *C. subspathacea* growth forms in potentially different ways given that phenotypic plasticity appears to have been strongly shaped by the climatic differences of these two regions.

We did not observe arctic *C. subspathacea* changing from short to tall growth form in the subarctic. Thus, we don't predict major changes in the grazing system on the ACP as a result of near-term potential increases in temperature and current grazing pressure. On the YKD, elevating air temperatures with greenhouses dramatically increased growth and reduced nitrogen concentration of *C. subspathacea* in both ungrazed meadows and grazing lawns (Ruess, personal observation). Thus, increases in air temperature and growing season length would likely increase the rate and spatial extent of conversion of short to tall *C. subspathacea* on the YKD, making it more difficult for geese to maintain grazing lawns and to initiate new grazing lawns (Ruess et al., 2019). At a landscape scale, a decline in the ratio of grazing lawns to brood density, coupled with a likely decline in forage quality will have a negative feedback on goose population growth. This process may already be occurring in response to existing climate change, which may explain the recent declines of grazing lawns and Brant populations on the YKD over recent decades (Sedinger et al., 2016).

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## Appendix

Table A1: Sample collection sites by region with GPS coordinates are listed. Subarctic samples were collected haphazardly from the Tutakoke River (TUT) and the Kashunuk River (KASH) on the Yukon-Kuskokwim River Delta (YKD). Arctic samples were haphazardly collected from the Smith and Colville River Delta (CRD) haphazardly along a transect centered around the coordinates on Alaska's Arctic Coastal Plain (ACP). If the collection site has a known name, the name is shown in parenthesis.

Site	GPS coordinates
<b>YKD</b>	
TUT 0	61.24678 N, 165.61687 W
TUT 1	61.24044 N, 165.55067 W
TUT 2	61.23870 N, 165.53737 W
TUT 3	61.24389 N, 165.52075 W
TUT 4	61.24584 N, 165.51118 W
KASH 0	61.27845 N, 165.60006 W (Mouth of Kashunuk)
KASH 1	61.32220 N, 165.66606 W (Village Slough)
KASH 2	61.33860 N, 165.58757 W (Hock Slough Camp)
KASH 3	61.33370 N, 165.47551 W (Kavink Slough)
KASH 4	61.33908 N, 165.43559 W (Emperer's Bend)
<b>ACP</b>	
SMITH 0	70.910736 N 153.186667 W
SMITH 1	70.910736 N 153.186667 W
SMITH 2	70.910736 N 153.186667 W
SMITH 3	70.910736 N 153.186667 W
SMITH 4	70.910736 N 153.186667 W
CRD 0	70.46071 N, 150.75957 W
CRD 1	70.46071 N, 150.75957 W
CRD 2	70.46071 N, 150.75957 W
CRD 3	70.46071 N, 150.75957 W
CRD 4	70.46071 N, 150.75957 W

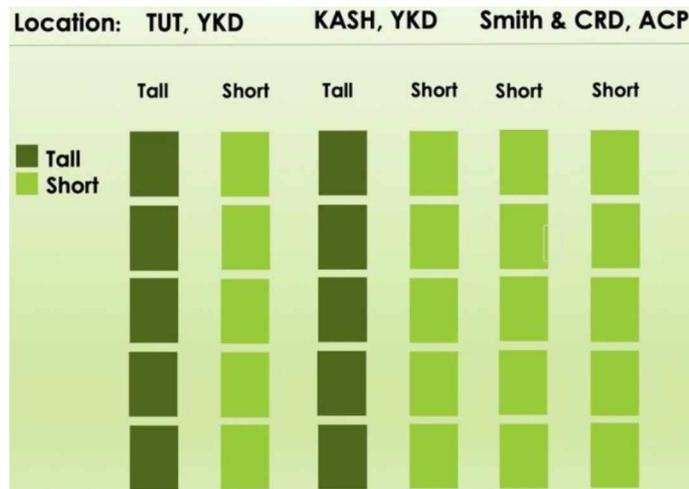


Figure A1: Transplants from Tutakoke River (TUT), the Kashunuk River (KASH), the Smith River and Colville River Delta (CRD) were arranged in each garden as displayed. Dark green represents the tall morphogroup while lime green is representing the short morphogroup from each collection site.

Table A2: Height model selection for random and fixed effects using log likelihood-ratio test. The test statistics  $D$ , is twice the difference in the log likelihood of two models:  $D = -2*(\ln(\text{Likelihood for a simpler model}) - \ln(\text{likelihood for a model with more parameters}))$ . The data shown are from the final year (2018) of measurement.

Model	Removed Factor	D	P
<i>Random Effect Selection</i>			
River + Location	Location	97.49	<0.001
River + Location	River	4.55x10 <sup>-13</sup>	0.257
River	River	97.49	<0.001
<i>Fixed Effect Selection</i>			
Full Factorial model with all interactions	3-way interaction	7.94	0.019

Table A3: Height model selection for random and fixed effects using log-likelihood ratio test. The test statistics  $D$ , is twice the difference in the log likelihood of two models:  $D = -2*(\ln(\text{Likelihood for a simpler model}) - \ln(\text{likelihood for a model with more parameters}))$ . The data shown include all three years.

Model	Removed Factor	D	P
<i>Random Effect Selection</i>			
River + Location	Location	64.91	<0.001
River + Location	River	0.00	0.318
River	River	69.34	<0.001
<i>Fixed Effect Selection</i>			
Full Factorial model with all interactions	4-way interaction	5.61	0.072
Full factorial model - 4-way interaction	Morphogroup:Clip:Garden	8.72	0.009
Full factorial model - 4-way interaction	Morphogroup:Clip:Year	8.73	0.018
Full factorial model - 4-way interaction	Morphogroup:Garden:Year	248.96	<0.001
Full factorial model - 4-way interaction	Clip:Garden:Year	13.64	0.001

Table A4: Tiller density model selection for random and fixed effects using log likelihood-ratio test. The test statistics  $D$ , is twice the difference in the log likelihood of two models:  $D = -2*(\ln(\text{Likelihood for a simpler model}) - \ln(\text{likelihood for a model with more parameters}))$ . The data shown are from the final year (2018) of measurement.

Model	Removed Factor	D	P
<i>Random Effect Selection</i>			
River + Location	Location	7.31	0.001
River + Location	River	0.00	0.307
Location	Location	7.31	0.003
<i>Fixed Effect Selection</i>			
Full Factorial model with all interactions	3-way interaction	1.01	0.600
Full Factorial model - 3-way interaction	Clip:Garden	0.0004	0.989
Full Factorial model - 3-way interaction	Clip:Morphogroup	3.38	0.211
Full Factorial model - 3-way interaction	Garden:Morphogroup	81.47	<0.001
Garden + Morphogroup + Clip + Garen:Morphogroup + Clip:Morphogroup	Clip:Morphogroup	3.38	0.246
Garden + Morphogroup + Clip + Garen:Morphogroup + Clip:Morphogroup	Garden:Morphogroup	81.47	<0.001
Garden + Morphogroup + Clip + Garden:Morphogroup	Garden:Morphogroup	79.55	<0.001
Garden + Morphogroup + Clip + Garden:Morphogroup	Clip	11.33	<0.001

Table A5: Tiller density model selection for random and fixed effects using log likelihood-ratio test. The test statistics  $D$ , is twice the difference in the log likelihood of two models:  $D = -2*(\ln(\text{Likelihood for a simpler model}) - \ln(\text{likelihood for a model with more parameters}))$ . The data shown are from all three years.

Model	Removed Factor	D	P
<i>Random Effect Selection</i>			
River + Location	Location	4.85	0.036
River + Location	River	1.01	0.033
<i>Fixed Effect Selection</i>			
Full Factorial model with all interactions	3-way interaction	16.96	0.001

Table A6: Aboveground biomass model selection for random and fixed effects using log likelihood-ratio test. The test statistics  $D$ , is twice the difference in the log likelihood of two models:  $D = -2 * (\ln(\text{Likelihood for a simpler model}) - \ln(\text{likelihood for a model with more parameters}))$ . The data shown are from the final year (2018) of measurement.

Model	Removed Factor	D	P
<i>Random Effect Selection</i>			
River + Location	Location	2.05	0.082
River + Location	River	0.24	0.086
Location	Location	0.31	0.182
River	River	2.12	0.015
<i>Fixed Effect Selection with River random effect</i>			
Full Factorial model with all interactions	3-way interaction	1.50	0.516
Full Factorial model - 3-way interaction	Morphogroup:Clip	1.24	0.544
Full Factorial model - 3-way interaction	Morphogroup:Garden	110.44	<0.001
Full Factorial model - 3-way interaction	Clip:Garden	8.78	0.005
Garden+Morphogroup+Clip+Morphogroup:Garden + Clip:Garden	Morphogroup:Garden	109.68	<0.001
Garden+Morphogroup+Clip+Morphogroup:Garden + Clip:Garden	Clip:Garden	8.69	<0.001

Table A7: Estimated coefficients and 95% confidence intervals (CI) of the best-fit linear mixed effect model for Height (final measurement, 2018). The dependent variable was transformed with  $\log(x+1)$ , where  $x$  was the height in cm.

	Estimated Coefficients	95% CI
<i>Fixed effects</i>		
<i>main effects</i>		
Intercept	1.162	0.993, 1.333
morphogroup = Tall SSub	0.574	0.334, 0.814
morphogroup = Short SSub	0.098	-0.142, 0.339
Clipped = Yes	-0.132	-0.271, 0.007
Garden = SF	-0.166	-0.305, -0.027
<i>two-way interactions</i>		
(morphogroup = Tall SSUB) x (Clipped = Yes)	-0.333	-0.529, -0.137
(morphogroup = Short SSub) x (Clipped = Yes)	0.005	-0.191, 0.202
(morphogroup = Tall SSub) x (Garden = SF)	1.365	1.169, 1.561
(morphogroup = Short SSub) x (Garden = SF)	1.598	1.402, 1.794
(Clip = Yes) x (Garden = SF)	0.076	-0.120, 0.272
<i>three-way interactions</i>		
(morphogroup = Tall SSUB) x (Garden = SF) x (Clip = Yes)	0.351	0.073, 0.628
(morphogroup = Short SSUB) x (Garden = SF) x (Clip = Yes)	0.096	-0.268, 0.287
<i>Random effects</i>		
	estimated Std. dev.	
Location	0.228	0.154, 0.313
Residual	0.356	0.334, 0.375

Table A8: Estimated coefficients and 95% confidence intervals (CI) of the best-fit linear mixed effect model for tiller density. The dependent variable was transformed with  $\log(x+1)$ , where  $x$  was the tiller density per 5 x 5 cm area.

	Estimated Coefficients	95% CI
<i>Fixed effects</i>		
<i>main effects</i>		
Intercept	4.026	3.730; 4.321
morphogroup = Tall SSUB	-0.800	-1.199; -0.401
morphogroup = Short SSub	-0.529	-0.928; -0.130
Clipped = Yes	-0.318	-0.500; -0.137
Garden = SF	-2.745	-3.600; -2.431
<i>two-way interactions</i>		
(morphogroup = Tall SSub) x (Garden = SF)	2.242	1.797; 2.686
(morphogroup = Short SSub) x (Garden = SF)	2.103	1.658; 2.547
Random effects	estimated std dev	
Location	0.291	0.110; 0.451
Residual	0.515	0.439; 0.583

Table A9: Estimated coefficients and 95% confidence interval (CI) of the best-fit linear mixed effect model for aboveground biomass. Dependent variable was transformed by Box-Cox transformation with non-positive values with  $\lambda = -0.090$  and  $\gamma = 0.019$  (Hawkins and Weisberg, 2017).

	estimated coefficients	95% CI
<i>Fixed effects</i>		
<i>main effects</i>		
Intercept	-1.668	-2.032; -1.304
morphogroup = Tall SSub	0.202	-0.257; 0.662
morphogroup = Short SSub	-0.222	-0.681; 0.237
Clipped = Yes	-1.369	-1.700; -1.037
Garden = SF	-3.233	-3.703; -2.763
<i>two-way interactions</i>		
(morphogroup = Tall SSub) x (Garden = SF)	3.563	2.988; 4.138
(morphogroup = Short SSub) x (Garden = SF)	3.516	2.941; 4.091
(Clip = Yes) x (Garden = SF)	0.743	0.273; 1.213
Random effects	estimated Std. dev.	
Location	0.065	0.000; 0.429
Residual	0.450	0.570; 0.751

Table A10: Height model selection for random and fixed effects using AICc and cAIC. Lowest values in bold display best fit model. The data shown are from the final year (2018) of measurement.

Model	AICc	cAIC
<i>Random Effect Selection</i>		
River + Location	533.45	-*
Location	<b>531.35</b>	<b>495.06</b>
River	628.84	628.40
none	626.74	626.12
<i>Fixed Effect Selection</i>		
Full Factorial model with all interactions	<b>531.35</b>	<b>495.06</b>
- 3-way interaction	535.10	499.17

\*: Since the variance component for River random effect was estimated to be 0, cAIC automatically refits the model with only Location random effect.

Table A11: Height model selection for random and fixed effects using AICc and cAIC. Lowest values in bold display best fit model. The data shown include all three years.

Model	AICc	cAIC
<i>Random Effect Selection</i>		
River + Location	1108.18	-*
Location	<b>1106.12</b>	<b>1076.79</b>
River	1171.03	1163.24
none	1173.40	1172.67
<i>Fixed Effect Selection</i>		
Full Factorial model with all interactions	<b>1106.12</b>	<b>1076.79</b>
- 4-way interaction	1107.62	1078.42

\*: Since the variance component for River random effect was estimated to be 0, cAIC automatically refits the model with only Location random effect.

Table A12: Estimated simple slopes against year since transplantation. Simple slopes were obtained from the best fit model, which contained Morphogroups, Clip, Garden, Year, and all interactions as fixed effects, and Location random effects. The dependent variable was transformed with  $\log(x+1)$ , where  $x$  was the height in cm. The  $p$ -values were adjusted with Holm's correction for multiplicity of hypothesis testing.

Garden	Clip	Morphogroup	Estimated slope	95% CI	t-ratio	adjusted P-value
NS	No	Arctic	0.040	-0.023; 0.103	1.24	0.431
	No	Subarctic Tall	-0.066	-0.129; 0.003	-2.04	0.123
	No	Subarctic Short	0.216	0.153; 0.279	6.69	<b>&lt;0.0001</b>
	Yes	Arctic	-0.036	-0.099; 0.028	-1.10	0.431
	Yes	Subarctic Tall	-0.336	-0.399; -0.273	-10.41	<b>&lt;0.0001</b>
	Yes	Subarctic Short	0.150	0.087; 0.213	4.65	<b>&lt;0.0001</b>
SF	No	Arctic	-0.176	-0.239; -0.113	-5.46	<b>&lt;0.0001</b>
	No	Subarctic Tall	0.324	0.260; 0.387	10.04	<b>&lt;0.0001</b>
	No	Subarctic Short	0.509	0.446; 0.572	15.78	<b>&lt;0.0001</b>
	Yes	Arctic	-0.206	-0.269; -0.142	-6.37	<b>&lt;0.0001</b>
	Yes	Subarctic Tall	0.309	0.246; 0.373	9.59	<b>&lt;0.0001</b>
	Yes	Subarctic Short	0.553	0.490; 0.616	17.15	<b>&lt;0.0001</b>

Table A13: Tiller density model selection for random and fixed effects using AICc and cAIC. Lowest values in bold indicate the most parsimonious model. In the Model column of fixed effect selection, '-' indicates removed factors relative to the full factorial model with all interactions, and ':' indicates the interaction effect of factors.

Model	AICc	cAIC
<i>Random Effect Selection</i>		
River + Location	225.06	- *
Location	<b>222.44</b>	<b>209.95</b>
River	229.75	222.39
No Random Effect	227.18	223.75
<i>Fixed Effect Selection</i>		
Full Factorial model with all interactions	222.44	209.95
- 3-way interaction	218.37	206.53
- 3-way, - Clip:Garden	215.90	204.23
- 3-way, - Clip:Morphogroup	216.85	206.00
- 3-way, - Garden:Morphogroup	294.94	298.12
- 3-way, - Clip:Garden, - Clip:Morphogroup	<b>214.47</b>	<b>203.73</b>
- 3-way, - Clip:Garden, - Garden:Morphogroup	292.56	287.13
Garden + Morphogroup + Clip	289.39	293.16
Garden + Morphogroup + Garden:Morphogroup	223.47	215.06

\*: Since the variance component for River random effect was estimated to be 0, cAIC automatically refits the model with only Location random effect.

Table A14: Tiller density model selection for random and fixed effects using AICc and cAIC. Lowest values in bold indicate the most parsimonious model. In the Model column of fixed effect selection, '-' indicates removed factors relative to the full factorial model with all interactions, and ':' indicates the interaction effect of factors. The data are from all three years.

Model	AICc	cAIC
<i>Random Effect Selection</i>		
River + Location	310.80	<b>297.40</b>
Location	<b>309.44</b>	297.78
River	313.28	303.69
No Random Effect	316.92	314.73
<i>Fixed Effect Selection</i>		
Full Factorial model with all interactions	<b>310.80</b>	<b>297.40</b>
- 3-way interaction	323.03	311.69

Table A15: Estimated simple slopes against year since transplantation. Simple slopes were obtained from the best fit model, which contained Morphogroups, Clip, Garden, Year, and all interactions as fixed effects, and Location random effects. The dependent variable was transformed with  $\log(x+1)$ , where  $x$  was the tiller density per 5 x 5 cm area. The  $p$ -values were adjusted with Holm's correction for multiplicity of hypothesis testing.

Garden	Clip	Morphogroup	Estimated slope	95% CI	t-ratio	adjusted P-value
NS	Yes	Arctic	-0.204	-0.431; 0.0229	-1.777	0.233
	Yes	Subarctic Tall	-0.044	-0.271; 0.1827	-0.385	1.00
	Yes	Subarctic Short	-0.394	-0.621; -0.1671	-3.432	<b>0.003</b>
SF	Yes	Arctic	-1.002	-1.229; -0.7756	-8.732	<b>&lt;0.0001</b>
	Yes	Subarctic Tall	0.010	-0.217; 0.2369	0.088	1.00
	Yes	Subarctic Short	-0.422	-0.649; -0.1954	-3.678	<b>0.002</b>

Table A16: Aboveground biomass model selection for random and fixed effects using AICc and cAIC. Lowest values in bold indicate the most parsimonious model. In the Model column of fixed effect selection, '-' indicates removed factors relative to the full factorial model with all interactions, and ':' indicates the interaction effect of factors. The data shown are from the final year (2018) of measurement.

Model	AICc	cAIC
<i>Random Effect Selection</i>		
River + Location	280.05	271.26
Location	<b>277.67</b>	<b>270.57</b>
River	279.48	271.79
No Random Effect	279.03	275.60
<i>Fixed Effect Selection</i>		
Full Factorial model with all interactions	277.67	270.57
- 3-way interaction	274.23	267.94
- c	<b>270.68</b>	<b>265.05</b>
- 3-way interaction - Morphogroup:Garden	381.45	375.71
- 3-way interaction - Clip:Garden	281.23	276.27
Garden + Morphogroup + Clip + Clip:Garden	377.21	372.07
Garden + Morphogroup + Clip + Morphogroup:Garden	277.65	273.27

Table A17: Leaf nitrogen concentration model selection for random effects using AICc and cAIC. Lowest values in bold indicate the most parsimonious model. In the Model column of fixed effect selection, '-' indicates removed factors relative to the full factorial model with all interactions, and ':' indicates the interaction effect of factors. The data shown are from the final year (2018) of measurement.

Model	AICc	cAIC
<i>Random Effect Selection</i>		
River + Location	56.03	-*
Location	53.33	-*
River	53.33	48.77
No Random Effect	<b>50.69</b>	<b>46.81</b>

\*: Since the variance component for random effects was estimated to be 0, cAIC automatically refits the model with no random effects

Table A18: Analysis of variance (ANOVA) table for nitrogen concentration model selection. We used a linear model instead of linear mixed effect model since the model selection indicated the model with no random effects was best fit. P-values lower than 0.05 are in bold.

	Sum of Squares	F Value	P
Intercept	418.99	5246.08	<b>&lt;2.2 * 10<sup>-16</sup></b>
Morphogroup	0.41	2.56	0.083
Clip	0.31	3.84	0.053
Garden	1.89	23.67	<b>4.47 * 10<sup>-06</sup></b>
Morphogroup:Clip	0.17	1.05	0.353
Morphogroup:Garden	0.14	0.90	0.409
Clip:Garden	0.24	3.02	0.086
Morphogroup:Clip:Garden	0.37	2.32	0.103
Residuals	7.67		