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Ryan T. Choi
Utah State University

Karen H. Beard
Utah State University

A. Joshua Leffler
South Dakota State University

Katharine C. Kelsey
University of Alaska-Anchorage

Joel A. Schmutz
Alaska Science Center

Jeffrey M. Welker
University of Alaska-Anchorage

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KAREN H BEARD (Orcid ID : 0000-0003-4997-2495)

DR JOEL SCHMUTZ (Orcid ID : 0000-0002-6516-0836)

Title: Phenological mismatch between season advancement and migration timing alters Arctic plant traits

Running head: Plant response to phenological mismatch

Authors: Ryan T. Choi[1], Karen H. Beard[1], A. Joshua Leffler[2], Katharine C. Kelsey[3], Joel A. Schmutz[4], Jeffrey M. Welker[3,5]

[1]Department of Wildland Resources, Utah State University and the Ecology Center, Logan, UT 84322-5230 USA

[2]Department of Natural Resource Management, South Dakota State University, Brookings, SD 57006 USA

[3]Department of Biological Sciences, University of Alaska-Anchorage, Anchorage, AK 99508 USA

[4]U.S. Geological Survey, Alaska Science Center, Anchorage, AK 99508 USA

[5]UArctic, Ecology and Genetics Research Unit, University of Oulu, Oulu, Finland

Corresponding Author: Karen H. Beard, karen.beard@usu.edu, 1-435-797-8220

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ABSTRACT

1.   Climate change is creating phenological mismatches between herbivores and their plant resources throughout the Arctic. While advancing growing seasons and changing arrival times of migratory herbivores can have consequences for herbivores and forage quality, developing mismatches could also influence other traits of plants, such as above- and belowground biomass and the type of reproduction, that are often not investigated.

2.   In coastal western Alaska, we conducted a three-year factorial experiment that simulated scenarios of phenological mismatch by manipulating the start of the growing season (ca. 3-weeks early and ambient) and grazing times (3-weeks early, typical, 3-weeks late, or no-grazing) of Pacific black brant (*Branta bernicla nigricans*), to examine how the timing of these events influence a primary goose forage species, *Carex subspathacea*.

3.   After three years, an advanced growing season compared to a typical growing season increased stem heights, standing dead biomass, and the number of inflorescences. Early season grazing compared to typical season grazing reduced above- and belowground biomass, stem height, and the number of tillers; while late season grazing increased the number of inflorescences and standing dead biomass. Therefore, an advanced growing season and late grazing had similar directional effects on most plant traits, but a 3-week delay in grazing had an impact on traits 3 to 5 times greater than a similarly timed shift in the advancement of spring. In addition, changes in response to treatments for some variables, such as the number of inflorescences, were not measurable until the second year

of the experiment, while other variables, such as root productivity and number of tillers, changed the direction of their responses to treatments over time.

4. *Synthesis*: Factors affecting the timing of migration have a larger influence than earlier springs on an important forage species in the breeding and rearing habitats of Pacific black brant. The phenological mismatch prediction for this site of earlier springs and later goose arrival will likely increase above- and belowground biomass and sexual reproduction of the often-clonally reproducing *C. subspathacea*. Finally, the implications of mismatch may be difficult to predict because some variables required successive years of mismatch to respond.

INTRODUCTION

The Arctic is experiencing rapid warming and this has led to earlier growing seasons and alterations in the timing of migration by herbivores (Forchhammer, Post, & Stenseth, 1998; Inouye, Barr, Armitage, & Inouye, 2000; Ward et al., 2016). Many migratory species have evolved to synchronize periods of peak nutrient demand, especially during breeding, with periods of high resource availability (Lepage, Gauthier, & Reed, 1998; Sedinger & Raveling, 1986). While some species have started to migrate earlier in response to climate-induced seasonal advancement (Boelman et al., 2017; Kölzsch et al., 2015), the potential for 'phenological mismatch' still exists, especially for long-distance migrants, due to the differing rates of green-up in their winter and summer ranges (Clausen & Clausen, 2013; Lameris, Scholten, et al., 2017; Mayor et al., 2017). Under the phenological mismatch (i.e., match-mismatch) hypothesis, there are two requirements: first, both species, the producer and consumer, must have a degree of seasonality; and second, the producer must exert bottom-up control on the recruitment or survival of the consumer (Durant, Hjermann, Ottersen, & Stenseth, 2007). Because of the rapidly advancing conditions in the Arctic and potentially incorrect cues regarding migration in the winter range, this mismatch often takes the

form of migratory species arriving phenologically 'late' to their breeding grounds compared to the start of the growing season (Both, Bouwhuis, Lessells, & Visser, 2006; Both et al., 2010).

Much of the research on phenological mismatch has focused on the population-level consequences at the higher trophic level, often herbivores (e.g., Post and Forchhammer 2008; Doiron et al. 2015; Rickbeil et al. 2018). However, because herbivores play a critical role in structuring Arctic plant communities, and climate change is influencing the timing of their migration (Jefferies, Klein, & Shaver, 1994; Post, Pedersen, Wilmers, & Forchhammer, 2008), it is also important to understand how these developing mismatches affect species at lower trophic levels (i.e., plant resources; Fig. 1) (Nakazawa & Doi, 2012). Thus far, empirical studies in terrestrial systems investigating phenological mismatch at the lower trophic level have focused on reductions in forage quality for herbivores (Beard et al., 2019; Doiron, Gauthier, & Lévesque, 2014; Lameris, Jochems, et al., 2017; Zamin, Côté, Tremblay, & Grogan, 2017), and how mismatches between plants and pollinators influence seed production (Forrest, 2015; Kudo & Ida, 2013). An often-overlooked component is how phenological mismatches influence the producer itself (i.e., biomass, growth form, and population growth) (Nakazawa & Doi, 2012). These studies are needed to understand not only the consequences of mismatch for the producer and its potential feedbacks to consumers, but also to understand changes to ecosystems as a whole via changes to C and N cycling (Kelsey et al., 2018; Leffler et al., 2019). However, to our knowledge, there have not been any empirical studies investigating how phenological mismatch between plants and herbivores influence plant traits unrelated to forage quality and plant reproduction.

Studies on how the timing of herbivory influences plant traits could inform hypotheses on how mismatch may influence these traits. However, there are only a handful of studies focusing on the timing of herbivory in Arctic systems (Archer & Tieszen, 1983; Beaulieu, Gauthier, & Rochefort, 1996; Hik, Sadul, & Jefferies, 1991; Person, Babcock, & Ruess, 1998), with more studies from temperate regions (e.g., Sullivan and Howe 2009, Davis et al. 2014). There are northern latitude studies focused on the frequency (Little, Cutting, Alatalo, & Cooper, 2017; Sjögersten, van der Wal, &

Woodin, 2012) and intensity of grazing (e.g., Mulder and Ruess 2001), but it is unclear how these studies inform how the timing of grazing influences vegetation traits. The relevant manipulative experiments investigating the effects of timing of grazing on Arctic graminoids generally suggest that earlier grazing reduces above- and belowground biomass (Archer and Tieszen 1983; Beaulieu et al. 1996), and that late grazing has the opposite effect (Hik et al. 1991). However, this response is not always observed because other studies investigating timing of grazing on Arctic graminoids have found no effect of grazing timing on biomass (Beaulieu et al. 1996; Raillard and Svoboda 1999; Person et al. 1998) or tiller production (Archer & Tieszen, 1983; Beaulieu et al., 1996). Further, studies in other systems have found that the timing of grazing can reduce sexual reproduction in flowering plants, with plant species responding to both early and late grazing (Knight 2003; Sullivan and Howe 2009; Akiyama and Ågren 2012; *but see* Wallace et al. 2008); however, these responses may be different with graminoids, especially if they reproduce clonally. These results highlight the complex nature of grazing timing on plant traits, and the need to investigate how these changes may interact with other climate-induced effects in Arctic ecosystems.

In addition to the timing of herbivory, climate change is also advancing the start of the growing season in northern latitudes (Walther, 2010). Studies investigating the effects of an advanced growing season on plants show that many species produce greater early season above- and belowground growth (e.g., Sullivan and Welker 2005), but some species with fixed growth strategies do not respond to early season conditions (Livensperger et al., 2016; Radville, Post, & Eissenstat, 2016). In general, with early season warming, we expect to see taller plants (Hollister, Webber, & Tweedie, 2005; Hudson, Henry, & Cornwell, 2011), and earlier flowering and senescence (Arft et al., 1999; Semenchuk et al., 2016; Sherwood, Debinski, Caragea, & Germino, 2017), with some species even able to alter their reproductive output based on size or resource availability (Schmid, Bazzaz, & Weiner, 1995). While season advancement may extend the duration of the growing season, earlier initiation of growth may also negatively affect plants due to colder ambient temperatures and shorter days (Kudo & Hirao, 2006). In summary, while we expect both the timing

of the growing season and timing of grazing to influence plant traits, and hypothesize that both earlier growing seasons and later arrival by migratory species may have similar effects on some traits, the relative importance of these variables for plants and their potential interactive effects are not well studied.

More than a million migratory birds arrive in the Yukon-Kuskokwim (Y-K) Delta in coastal western Alaska each spring for breeding and brood-rearing (Gill & Handel, 1990). Several migratory goose species, including Pacific black brant (*Branta bernicla nigricans*), are highly dependent on monospecific stands of the sedge, *Carex subspathacea*, which when heavily grazed takes on a short growth form with extensive clonal tillering, lack of inflorescences, and consistent regrowth (Person et al., 1998; Ruess, Uliassi, Mulder, & Person, 1997). The arrival time of migratory geese is thought to have evolved to coincide with the seasonal availability of high quality forage (Sedinger & Raveling, 1986), which can have bottom-up control on gosling growth and subsequent survival (Lindholm & Gauthier, 1994; Sedinger & Flint, 1991). However, because the timing of goose arrival is often not advancing as quickly as vegetation phenology in many northern ecosystems (Dickey, Gauthier, & Cadieux, 2008; Tombre et al., 2008), the potential for phenological mismatch exists at this site, and is likely to become more common in the future (Both et al., 2010; Clausen & Clausen, 2013; Forchhammer et al., 1998). While others have studied how phenological mismatch may influence goose populations in similar systems (Brook, Leaflor, Abraham, & Douglas, 2015; Doiron et al., 2015; Ross, Alisauskas, Douglas, & Kellett, 2017), our study focuses on understanding how a potential developing mismatch may influence plant traits of a critical forage species. To address our objective, we conducted a three-year field experiment that manipulated the start of the growing season (advanced and ambient) and the timing of migratory goose grazing (early, typical, and late) to examine how the timing of these events and their interaction influence the growth responses of *C. subspathacea*, including above- and belowground biomass, standing dead biomass, growth form, and vegetative and sexual reproduction.

METHODS

Study site

We conducted research near the mouth of the Tutakoke River in the central coast region of the Y-K Delta in western Alaska (61°15'N, 165°37'W; elevation 2 m) (see Fig. S1 in the supplement). The Y-K Delta encompasses over 75,000 km^2 of sub-Arctic tundra and coastal wetlands along the Bering Sea between the Yukon and Kuskokwim Rivers. We conducted our experiment in a brackish wet sedge meadow on the active floodplain within 1 km of the coast. Climate is moderated by the Bering Sea with mean monthly temperatures ranging from 10 °C in the summer (May through July) to -14 °C midwinter (Jorgenson & Ely, 2001).

The coastal Y-K Delta is one of the primary nesting and brood-rearing areas for ca. 50% of the world's Pacific black brant (*Branta bernicla nigricans*), with densities of ca. 500 nests km^2 around the Tutakoke River (Fischer, Williams, & Stehn, 2017). Recent data suggest, however, that Pacific black brant have declined by 2-4% annually in the Y-K Delta over the past decade (Fischer et al., 2017; Leach et al., 2017; Sedinger, Riecke, Leach, & Ward, 2019). Brant typically arrive 6 to 12 days before nesting (Lindberg, Sedinger, & Flint, 1997), with historic mean hatch on 21-June and mean annual dates from 11-June to 30-June over the past 34 years, 1983-2016 (Fischer, Stehn, & Walters, 2008; Fischer et al., 2017). Goose grazing intensity increases in the period following hatch when goslings begin to forage and females recover from nutrient deficits following incubation (Sedinger & Raveling, 1990).

In addition to the variation in timing of peak grazing, the timing of green-up varied by over 30 days in the Y-K Delta over the last 30 years, although the general trend is towards an advancing spring (Ross et al., 2017). We used the day of year when the 50% maximum NDVI (normalized difference vegetation index) is achieved as a vegetation phenology metric, and found that green-up varied between 23-May and 25-June from 1982-2014 (NDVI methods follow Brook et al., 2015). While green-up and hatch dates across years are highly correlated in the Y-K Delta, for every day

that green-up has advanced, hatch date only advanced 0.5 days, which suggests there will be greater mismatch between brant and their forage in the future (Beard et al., 2019; Leffler et al., 2019).

Carex species dominate the Tutakoke landscape with specific species dependent on modest changes in elevation. The most tidally proximal *C. subspathacea* occurs in nearly monotypic stands and is so heavily grazed (i.e., brant do not grub) and modified by brant that it is often referred to as 'grazing lawn' (Person et al., 2003). *C. subspathacea* is an important circumpolar forage species for geese, and when grazed, sexual reproduction is suppressed in favor of extensive clonal reproduction (Perillo, Wolanski, Cahoon, & Brinson, 2009). It is only after herbivory is removed that *C. subspathacea* grows taller and initiates inflorescence production (Schmid et al., 1995).

Experimental design

We conducted a three-year experiment using a fully factorial design with two timings of season treatments (advanced and ambient) crossed with four timings of grazing treatments (early, typical, late, and no-grazing) for a total of eight treatments, plus a background grazing control. Our factorial crossings of growing seasons and grazing times simulated different phenological mismatch scenarios, where we advanced the growing season by three weeks (see below), and altered the timing of goose grazing by minus-three, zero, and plus-three weeks (early, typical, and late grazing). These eight treatments represent different degrees of mismatch between the start of the season and goose arrival ranging from -3 weeks (e.g., typical green-up and early goose arrival) to +6 weeks (i.e., early green-up and late goose arrival), and are described in Table 1. The 'no-grazing' treatment represents conditions where goose populations substantially decline or fail to arrive at the breeding ground.

We had six replicate blocks located within a 400-m radius for a total of 54 plots, each 1.7 m x 0.85 m in size. We installed plots in April 2014 and applied treatments over the growing season from 1 May through 15 August for three years. To exclude wild goose grazing, we installed fencing around all experimental plots, except the background grazing control plots.

To advance the growing season, we used two adjacent conical open-top chambers (OTCs; 30 cm height x 85 cm base dia. x 50 cm top dia.) (Marion et al. 1997). OTCs are often used to increase temperature through passive warming, but can also accelerate growth at the start of the season (Post et al., 2008; Sullivan & Welker, 2005). OTCs were placed on plots 1-May until 1-July, long enough to advance the growing season by three weeks when comparing stem height of warmed shoots to ambient. We removed OTCs during this period only for goose grazing treatments. We monitored air and soil temperature (10 cm above- and belowground) using ibutton microloggers (models DS1921G/Z, Maxim Integrated, San Jose, CA) in every plot.

To manipulate timing of grazing, we constructed fenced goose exclosures (ca. 7.6 m^2) around paired advanced and ambient growing season plots, and introduced wild-caught geese into the exclosures at certain times during the season. The early, typical and late grazing treatments began 30-May, 20-June, and 9-July, respectively, to approximate the 30-day variation in the range of hatch dates (3-June to 9-July) observed over the past three decades in the Tutakoke River brant population (Fischer et al., 2008, 2017). Further, these dates accounted for the logistical challenges of using actual goose grazing (as opposed to simulated), and thus began after we captured nesting female geese in late May.

Grazing treatments (early, typical, and late) consisted of two geese that grazed, trampled, and defecated inside exclosures for four 24-h bouts, each separated by 12 days over a total of 37 days to simulate approximately 40 days of intense post-hatch grazing (Mickelson, 1975). The experimental treatments lasted 3.5 months; thus, we created the same grazing intensity in each goose grazing treatment of 7.2 goose-hours m^{-2} $month^{-1}$, which was based on a previous controlled-grazing study in the same population of geese (Herzog & Sedinger, 2004). Total grazing time did not vary between grazing treatments, and thus the experimental treatments only differed in the timing of grazing initiation. Prior to each treatment, we held geese without food for two hours to allow feces from supplemented feed to pass through their digestive system (Prop & Vulink, 1992). After completion of the 24-h treatments, we held birds for an additional two hours and returned any

treatment-derived feces to appropriate experimental plots. When not used in grazing treatments, we held geese in a fenced enclosure, allowed them to graze freely on natural vegetation, and supplemented goose feed *ad libitum*. We released all captured geese to the wild at the end of each season.

Vegetation and soil measurements

In all 54 plots, we established 10 cm x 10 cm demarcated quadrats where we made measurements every three weeks in 2014, and weekly in 2015 and 2016 (~13-May to 20-August). In these quadrats, we measured stem height of 10 randomly selected stems and counted all observed inflorescences. In each plot, we also destructively harvested aboveground biomass every three weeks from different randomly selected 5 cm x 5 cm areas all three years. The 5 cm x 5 cm areas were at least 10 cm from the established 10 cm x 10 cm quadrant. From these samples, we counted tillers and separated live and dead aboveground biomass. We measured seasonal root productivity in each plot using two in-growth root cores (4 cm dia. x 15 cm length) made of 2 mm plastic mesh (Nadelhoffer, Johnson, Laundre, Giblin, & Shaver, 2002). We filled in-growth cores with root-free substrate, placed them in plots on 25-May, and removed them on 25-August each year. We washed aboveground live biomass, dead leaves, and roots free of soil, dried them at 60 °C to constant weight, and weighed samples in the laboratory.

Statistical analyses

All analyses employed a linear mixed model framework with model selection using Akaike Information Criteria (AIC). We used the nlme package within the R statistical computing environment (Pinheiro et al. 2017; R Core Development Team) to fit our models. To compare models with ΔAIC < 2, we used the ANOVA function and selected the most parsimonious model. We log-transformed all predictor variables prior to analysis to meet assumptions of normality and homogeneity of variance.

First, we analyzed the effectiveness of OTCs to advance the growing season as the response variable. We used stem heights because we had the most frequent measurements prior to OTC removal, and restricted data to plots that did not experience grazing before 1-July to remove the effect of grazing. The model included categorical predictors of year and treatment (either ambient or advanced growing season), a continuous predictor of day of year (DOY), all interactions, and a random plot-within-block effect. We used regression coefficients to calculate the amount of time needed for ambient plots to reach the same height as advanced plots. We presented this analysis in Leffler et al. (2019), but present the findings here for completeness.

Next, we examined the effectiveness of our grazing treatments to simulate background grazing levels using aboveground biomass as the response variable. We used aboveground biomass because we could use complete season data from each year for this analysis. We limited analyses to the background control and experimental plots that did not receive season advancement. The model included the categorical goose grazing treatments and a continuous predictor of DOY, and treated plot nested within block as a random effect. We ran each year separately.

Then, we tested the effects of timing of the growing season (advanced, ambient) and timing of goose grazing (early, typical, late, no-grazing) on plant traits. We used plant variables (aboveground live biomass, stem height, standing dead biomass, root biomass, tillers, inflorescences) as continuous response variables, experimental treatments (start of the growing season, goose grazing) and year as categorical and DOY as a continuous fixed effect predictor variables, and treated plot nested within block as a random effect. We coded ambient season and typical grazing plots as the reference category for the growing season and grazing timing treatment as appropriate, and included a first-order autocorrelation structure to account for repeated measures within subjects over time. We limited model combinations to include interactions with no more than two predictor variables and determined the most important variables as those present in the top performing model. We tested the importance of experimental treatment effects on changes in number of inflorescence from years 2 and 3 because we did not detect any inflorescences in year

1. We fitted this model using the Automatic Differentiation Model Builder with a Poisson response distribution using the glmmADMB package in R (Bolker, Skaug, Magnusson, & Nielsen, 2012). This framework corrected for non-normal distributions and fitted over-dispersed data and zero-inflated values.

We conducted a separate analysis to isolate the effects of each of the eight experimental mismatch treatments compared to the ambient season–typical grazing treatment (0 mismatch, no shifting in timing; Table 1). We ran models for vegetation variables (aboveground live biomass, stem height, standing dead biomass, root biomass, tillers, inflorescences) as continuous response variables, where treatment, year, DOY, and their interactions were all treated as fixed effects, and treated plot nested within block as a random effect. Inflorescences were fitted using the Poisson response distribution as described above.

RESULTS

Treatment effectiveness

OTCs warmed plots on average between 0.6 and 1.7 °C (10 cm aboveground) and 0.6 and 1.0 °C (10 cm belowground) from 1-June to 1-July. Following OTC removal on 1-July and for the remainder of the season, temperature differences were < 0.3 °C between advanced and ambient treatments. As summarized in Leffler et al. (2019), OTCs were effective at advancing the growing season over each of the three years for both stem height and growth rates (see Fig. S2 in the supplement). Modeled height was 37, 78, and 163 mm in the advanced growing treatment and 18, 42, and 99 mm in the ambient treatment in late June of 2014, 2015, and 2016, respectively. Plant growth rate differed between season advancement treatments; in 2016, season advancement had a higher rate of growth (3.1 mm d^{-1}) than the ambient treatment (1.9 mm d^{-1}). Modeled rates of growth indicated that the treatment advanced the season by 22, 18, and 21 days by the end of June 2014, 2015, and 2016, respectively, but the differences between treatment growth rates did not extend beyond the dates OTCs were installed on plots.

In year 1 of the experiment, aboveground biomass in background control plots was not different from early, typical, or late grazing treatments, but was lower than no-grazing plots (Table S1 in the supplement). By year 2, background control aboveground biomass was not different from early or typical plots, but was lower than late and no-grazing plots (Table S1 in the supplement). By year 3, background controls were not different from early goose grazing treatments (Table S1 in the supplement). This result was expected because experimental plots were subjected to three years of manipulations based on the historic 30-year average grazing time by geese in the Y-K Delta. The last year of the experiment (2016) had the earliest observed mean hatch date on record (11-June), while all three years of the experiment (2014-2016) had three of the earliest six mean hatch dates over the last 34 years in the Y-K Delta (Fischer et al., 2017). Thus, it was expected that background control plots would have aboveground biomass more similar to early grazing plots by year 3.

Vegetation response to treatments

In this section, vegetation trait responses are compared to ambient season for the advanced growing season treatment and to typical grazing for the timing of grazing treatments. Vegetation trait percent change is presented as the mean across the last year of the experiment unless otherwise indicated. There was no significant interaction between grazing timing and season advancement for any of these variables (Table 2). Timing of grazing did interact with DOY in most top models; however, we do not describe the nature of this relationship here because it typically reflected the starting and stopping of grazing treatments at different times of year.

The best-fitting model for aboveground live biomass included year and an interaction between timing of grazing and DOY (Table 2). Aboveground biomass generally increased across years. Aboveground live biomass was not different in advanced growing season plots, but aboveground biomass was 52% lower in the early grazing treatment and 81% greater with no-grazing than typical grazing (Fig. 2A-C).

For stem height, the top model included year, season advancement, and an interaction between timing of goose grazing and DOY (Table 2). Like aboveground biomass, stem heights generally increased across years. However, unlike aboveground biomass, stems were 58% taller in the advanced growing season treatment than in ambient plots (Fig. 2D-F). Stems were also 63% shorter in the early grazing, and 200% taller with no-grazing compared to typical grazing treatments.

The best-fitting model for standing dead biomass included season advancement and an interaction between timing of grazing and year (Table 2). Standing dead biomass was 101% greater in the advanced growing season treatment compared to ambient plots, but was 569% and 1697% greater in the late and no-goose grazing treatments, respectively, compared to typical grazing (Fig. 2G-I). Dead biomass increased across years, but a response to treatments was not detected in no-grazing plots until year 2 and late grazing plots until year 3 (Table S2 in the supplement).

The best-fitting model for seasonal root productivity included an interaction between year and timing of goose grazing (Table 2). Root growth was 55% lower in early season grazing plots, while root growth increased by 74% in no-grazing plots in year 1, but was 15% lower by year 3, compared to typical grazing (Fig. 3; Table S2 in the supplement).

The best-fitting model for tiller number included DOY and an interaction between timing of goose grazing and year (Table 2). In general, tiller number decreased over the season (Fig. 2J-L). Advancing the growing season did not change the total number of tillers. Conversely, tiller numbers were 35% lower with early grazing; and 46% greater with no-grazing in the first year, but declined over each successive growing season. By year 3, tiller numbers were 36% lower with no-grazing compared to typical grazing treatments (Table S2 in the supplement).

For inflorescence counts, the top model included year, season advancement and an interaction between timing of grazing and DOY (Table 2). The total number of inflorescences were 36% greater in the advanced growing season treatment compared to ambient plots; but the late and no-grazing plots produced 515% and 1795% more inflorescences, respectively, than typical grazing (Fig. 2M-O).

Comparing degrees of mismatch

Top models for vegetation responses to treatments all included treatment and either year, DOY, or an interaction between year and DOY (Table 3). Compared to the ambient season–typical grazing treatment (no shift in timing), the advanced season–early grazing treatment (0 mismatch) resulted in reductions in aboveground biomass, root biomass, and tiller numbers, while the ambient season–early grazing treatment (-3 mismatch) only had a reduction in root biomass (Fig. 4). While the advanced season–typical grazing treatment (+3 mismatch) was designed to simulate earlier plant phenology without changing timing of goose grazing, stem height was the only measurement to increase compared to the ambient–typical treatment (no shift in timing), and this was only detected in the third year of treatments (Table S3 in the supplement).

Both the ambient season–late grazing (+3 mismatch) and advanced season–late grazing (+6 mismatch) treatments resulted in increased inflorescences and standing dead by the third year compared to the ambient–typical treatment (no shift in timing); however, the advanced season–late grazing treatment (+6 mismatch) also had increased aboveground biomass and taller stem heights by year 3 (Fig. 4). Both no-grazing plots had taller stem heights and increased aboveground biomass, standing dead, inflorescences, and decreased tiller numbers by year 3 compared to the ambient-typical treatment (no shift in timing) (Fig. 4; Table S3 in the supplement). The ambient–no-grazing treatment was the only ambient season treatment that had greater stem height than the ambient–typical treatment (no shift in timing).

DISCUSSION

To the best of our knowledge, this is one of the first experimental studies designed to investigate the effects of plant-herbivore phenological mismatch on the traits of the producer instead of the consumer. Here, we highlight three primary findings. First, both treatments simulating conditions consistent with future predictions for the Y-K Delta (an earlier growing season and delayed grazing) had similar effects and generally resulted in greater aboveground biomass and increased

inflorescence production. Future climate change in the Y-K Delta is expected to advance the growing season (Hinzman et al., 2013); however, the response in timing of arrival by geese is less certain as geese have alternatives for dealing with climate change, such as migrating to different breeding sites or not migrating as far south in the winter (Ward et al., 2009, 2005). If geese in this system start to delay their migrations, as they have in other systems (Clausen & Clausen, 2013; Ross et al., 2017), our results suggest that the responses to the advanced growing season will be even greater for *C. subspathacea*.

Second, the response of geese to climate change has greater implications for *C. subspathacea* than advancing local spring conditions (Fig. 5). The advanced growing season treatment successfully advanced the timing of plant growth by about 20 days, similar to the 21-day difference in timing of our experimental grazing treatments, making the shift in timing of the two treatments comparable. Notably, for the variables where both the advanced growing season and grazing treatments both had an effect (standing dead and inflorescences), late grazing effects on plant traits were between 3 and 5 times greater than the effects of a similar advancement of the growing season. Thus, determining how *C. subspathacea* will change in the future is largely dependent on how climate change influences migratory goose arrival to this system.

Third, some plant responses were not evident until the second or third year of the experiment, suggesting that consistent directional changes in mismatch over consecutive years may be needed to produce measurable effects of vegetation on the landscape. Treatments were repeated at the same plots in subsequent years, and because natural inter-annual variability in the start of the growing season and goose arrival across years is quite large (Fischer et al., 2017; Leffler et al., 2019), it might take several years to observe these effects in real time. Further, this result also has implications for shorter-term experiments that might underestimate the long-term consequences of mismatch on lower trophic level processes.

Plant variable responses to treatments

Treatment effects on aboveground live, dead, and root biomass

Timing of grazing treatments had a greater effect on aboveground vegetation responses than did season advancement (Fig. 5). Both aboveground biomass and stem heights were reduced by early grazing and increased with no-grazing treatments. These responses are similar to findings by Archer and Tieszen (1983) and Beaulieu et al. (1996), but differ from studies that found no effect of timing of grazing on aboveground biomass in Arctic graminoids (Person et al., 1998; Raillard & Svoboda, 1999). In addition, results differ from Hik et al. (1991) who found that graminoid growth in Hudson Bay was reduced with late grazing. We speculate that we did not find this result because our late grazing treatments ended 3 weeks earlier than Hik et al. (1991) and additional seasonal growth may have allowed plants to recover. While we did not find an effect of the advanced growing season on live aboveground biomass, similar to other studies (e.g., Hudson et al. 2011, Radville et al. 2016), we found that stem heights were taller with season advancement (Hollister et al., 2005; Hudson et al., 2011). Standing dead biomass also increased 101% with an advanced growing season; although, the effect was 3 to 9 times greater with late and no-grazing, respectively.

Our aboveground treatments had effects on belowground plant responses as well. Similar to other studies (Blume-Werry, Jansson, & Milbau, 2017; Radville et al., 2016), we found that an advanced growing season had no effect on root productivity. However, seasonal root productivity was reduced by 55% with early grazing (Archer & Tieszen, 1983). These results suggest that the timing and presence of aboveground grazing in this system can influence the annual root production of C, which is an important input of C in the Arctic (Iversen et al., 2015; Tarnocai et al., 2009).

These results are important because changes of aboveground and belowground biomass have consequences for C-cycling in this system. More specifically, the condition of greatest mismatch, advanced growing season and later arrival by geese (+6 mismatch), is expected to result in vegetation with 106% more aboveground biomass, 220% taller stem heights and 12830% more standing dead biomass, as well as increased photosynthesis and C-uptake (Leffler et al., 2019).

Treatment effects on tiller and inflorescence number

Graminoids are highly tolerant of grazing and defoliation compared to other plant species (Briske & Richards, 1995; Coughenour, 1985), and while grazing can initiate the production of new tiller growth, it can also reduce the number of tillers and their size (Jónsdóttir, 1991; Welker, Briske, & Weaver, 1987). Season advancement had no observable effect on tiller number, but tiller number was influenced by the timing of grazing. Early grazing initially reduced the number of tillers; however, in year 2, early grazing was associated with increased tiller number and then again decreased tiller number in year 3. This is dissimilar to previous research that found no tiller response to grazing timing on Arctic graminoids (Archer & Tieszen, 1983; Beaulieu et al., 1996), although both of these studies were conducted with different plant species than the one used in this study. These results suggest that if geese arrive too early, they could negatively impact the abundance of their forage species.

Goose herbivory at our site maintains short tiller height and low standing biomass in grazing lawns (Person et al., 2003; Sedinger & Raveling, 1986), and *C. subspathacea* typically does not produce inflorescences but rather reproduces clonally (Perillo et al., 2009) (Fig. 2M). However, if grazing is reduced or removed, once *C. subspathacea* reaches a minimum size and stores sufficient resources, it often initiates sexual reproduction (Schmid et al., 1995). While the biomass and height response to treatments was immediate, the reproductive response by *C. subspathacea* to changes in herbivory was delayed for one to two seasons. For example, no plots produced inflorescences in year 1 of the experiment, while some no-grazing treatment plots produced inflorescences in year 2. By year 3, the advanced growing season (compared to ambient), late, and no-grazing treatments (compared to typical grazing) increased the number of inflorescences by 36%, 515%, and 1795%, respectively. Interestingly, both season advancement and timing of grazing treatments did not change the timing of peak inflorescence production (~10 June), even though other studies show the advancement of inflorescences with an earlier growing season (Blume-Werry et al., 2017; Semenchuk et al., 2016; Sherwood et al., 2017). Under the simulated condition of greatest

mismatch, season advancement and late grazing, we observed a 1478% increase in sexual reproduction, which will likely increase genetic diversity and potentially influence long-term plant dynamics in this system.

Differences in mismatch comparisons

The treatments with the greatest changes in plant response variables were the plots with no grazing, which resulted in significant changes for all measured plant traits except root biomass (Fig. 6). The advanced season–late grazing (+6 mismatch) is the treatment with the greatest degree of experimental mismatch (six-weeks) and had the second greatest number of significant differences in response variables compared to the ambient season–typical grazing treatment (no shift in timing; Fig. 6). The advanced season–late grazing combination (+6 mismatch) received two treatments, both season advancement and delayed grazing, with similar directional effects on response variables; therefore, we would expect this treatment to have a compounding impact on vegetation traits. If geese continue to arrive late to a landscape with an advanced growing season, or not arrive at all, vegetation will become taller, older, and lower quality forage for geese (Beard et al., 2019), and possibly shift from clonal to sexual reproduction.

While the treatments were designed to examine different degrees of phenological mismatch, the timing and direction of the mismatch also influenced plant response. For example, both the advanced season–typical grazing (+3 mismatch) and ambient season–late grazing (+3 mismatch) conditions had the same size and direction of mismatch. More specifically, advanced season–typical grazing (+3 mismatch) had a three-week advance in the growing season with no advance in grazing, while ambient season–late grazing (+3 mismatch) had no advance in the growing season and a three-week delay in grazing. However, these two similar mismatch conditions had differing effects; the advanced season–typical grazing had a delayed response in stem height by the third year, while the ambient season–late grazing had an increase in inflorescences and a delayed increase in dead biomass (Fig. 4). Similarly, while the advanced season–early grazing treatment (0

mismatch) and ambient season–typical grazing treatment (no shift in timing) both simulated no mismatch between the growing season and goose arrival, the advanced season–early grazing treatment resulted in significant reductions in aboveground live biomass, tiller number, and root biomass (Figs 4 & 6). Our results suggest that phenological mismatches can have different influences on plant responses, depending on environmental conditions and when they occur seasonally.

Delays in plant response over time

In our experiment, we maintained the same treatment in each plot over three years so we could investigate the effects of multiple years of treatments. Some plant responses to treatments, such as aboveground biomass and stem heights, were measurable in the first year and did not change direction over the experiment (Fig. 2A-F). However, other variables such as tillers, inflorescences, and standing dead biomass, required multiple years of the same recurring treatments to observe the effect (Figs 2 & 4). While there is a directional expectation with phenological mismatch, such that the season starts earlier and the geese arrive functionally later (Brook et al., 2015; Forchhammer et al., 1998; Ross et al., 2017), in reality there is a high inter-annual variation in the timing of these events (Fischer et al., 2017; Leffler et al., 2019), and it might require multiple years of directional change in these timings for plants to exhibit a response.

Despite the strong directional response of some plant growth variables to our treatments, other responses shifted in direction over time. For example, both tiller number and root growth increased in response to no-grazing in the first year (Figs 2J & 3). However, tiller numbers were significantly reduced by year 2 and root growth by year 3 in the no-grazing treatment. As stem height and biomass increased, there was greater shading and higher competition for light resources between tillers (Jónsdóttir, 1991). Additionally, soil measurements made in the same experimental plots suggest that late and no-grazing treatments had reduced soil nitrogen availability due to increased plant uptake and a depletion of resources in the rooting zone (Beard & Choi, 2017). This

suggests that some plant traits can have initial responses to timing of grazing that might change once plants reach a certain size or resource availability threshold.

Additive treatment effects

For some variables, it appears that changes to both the timing of grazing and season advancement were necessary to observe a measurable response. For example, while advanced season–early grazing (0 mismatch) and ambient season–early grazing (-3 mismatch) treatments both had early season grazing, the aboveground biomass and tiller number declined with 0 but not -3 mismatch. This suggests that an advanced growing season in addition to early grazing was required for plants to demonstrate this response. This result is interesting for two reasons. First, the advanced season– early grazing treatment had no mismatch between the start of the season and grazing, while the ambient season–early grazing treatment (-3 mismatch) had three-weeks of earlier grazing prior to the start of the growing season. We found, counterintuitively in this case, that the no mismatch treatment had a larger effect on plant response than the treatment with a three-week mismatch. Second, the direction of the response observed in the advanced season–early grazing treatment (0 mismatch), with decreased aboveground biomass and tiller numbers, seems counter to the effects of an earlier growing season. It is possible that the additive stress of an advanced growing season, such as shorter day length and colder temperatures earlier in the year, and early grazing limited the ability of plants to grow, even under conditions of no mismatch. These results highlight the unexpected changes that may be observed in plants experiencing phenological mismatch.

CONCLUSION

The manipulative use of timing of the growing season and timing of herbivory in our experiment offers a novel approach to investigating climate-driven phenological mismatch. Our results indicate that climate-driven changes in the timing of goose arrival have much greater consequences for coastal sedge vegetation than a similar shift in timing of local spring conditions. Thus, determining

how climate change will influence the timing of migratory goose arrival to these systems is critical to understanding plant responses. The long-term implications for phenological mismatch on vegetation may be difficult to predict in some cases because some variables require years to observe changes or alter their directional response over time. However, it seems that important thresholds can be reached in as little as two years; for example, *C. subspathacea* shifted from being clonally to sexually reproductive. Thus, even short-term phenological mismatch may have long-term implications for the genetic diversity and population dynamics of important forage species in the Arctic.

AUTHORS' CONTRIBUTIONS

KB, JS, JW, and JL conceived the ideas and designed methodology; RC and KK collected the data; RC analyzed the data; RC and KB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

LITERATURE CITED

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Figure Legends

Figure 1. Conceptual diagram of the understudied aspect of phenological mismatch using the Yukon-Kuskokwim Delta as an example. Most studies on phenological mismatch focus on the effects on consumer traits. Few studies focus on the effects on producer traits (dotted box), which is also important and the focus of this study.

Figure 2. Mean plant trait responses to experimental season advancement and timing of grazing treatments from 2014-2016. (A-C) aboveground dry biomass (g m^{-2}), (D-F) stem heights (mm), (G-I) standing dead biomass (g m^{-2}), (J-L) number of tillers (# m^{-2}), (M-O) number of inflorescences (# m^{-2}). Error bars are ± 1 SE (n=6 replicates).

Figure 3. Season-long root biomass (g m^{-2}) (± 1 SE) (~25-May to 25-August) collected from 15 cm in-growth root cores for treatment plots from 2014-2016 (n=6 replicates). For Treatment key, see Table 1.

Figure 4. Season-long mean plant trait responses to experimental mismatch treatments from 2016. (A) aboveground dry biomass (g m^{-2}), (B) stem heights (mm), (C) standing dead biomass (g m^{-2}), (D) root biomass (g m^{-2}), (E) number of tillers (# m^{-2}), and (F) number of inflorescences (# m^{-2}). Dashed lines indicate the ambient–typical treatment (no shift in timing). (*) indicates effect of mismatch compared to the ambient season–typical grazing treatment (+) indicates effect not detected until year 2 or 3; (^) indicates change in direction of response to treatments over time ($p<0.05$). Error bars are ± 1 SE (n=6 replicates).

Figure 5. Conceptual figure of experimental treatments (timing of grazing and season advancement) on plant trait responses compared to typical grazing and ambient season after three years. Red arrows (–) indicate a negative effect; blue arrows (+) indicate a positive effect. Solid lines indicate an effect observed in all years; dashed lines indicate an effect only observed after the first season.

Figure 6. Conceptual figure of experimental mismatch on plant trait responses compared to ambient season-typical grazing (no shift in timing) after three years of treatments. Red arrows (-) indicate a significant negative effect; blue arrows (+) indicate a significant positive effect. Solid lines indicate an effect observed in all years; dashed lines indicate an effect only observed after the first season.

Table 1. Treatments used in the experiment described using degree of phenological mismatch. Season indicates if the season started either 3 weeks early (-3) or ambient timing (0). Grazing indicates if the grazing started 3 weeks early (-3), typical timing (0), or 3 weeks late (+3). Mismatch indicates the relative difference in weeks between the timing of season and goose grazing. N/A=non-applicable.
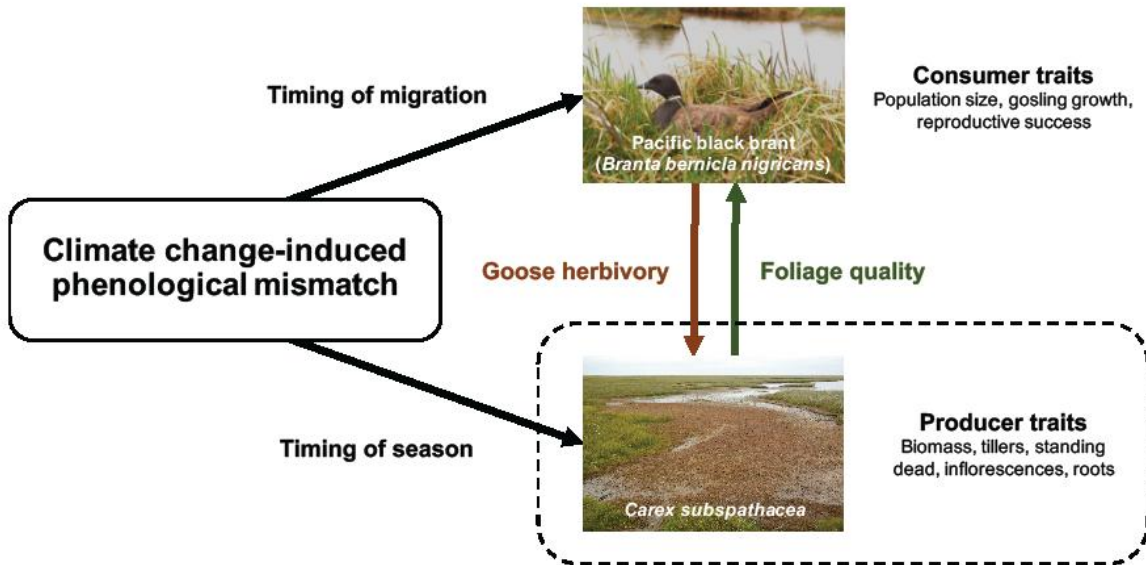
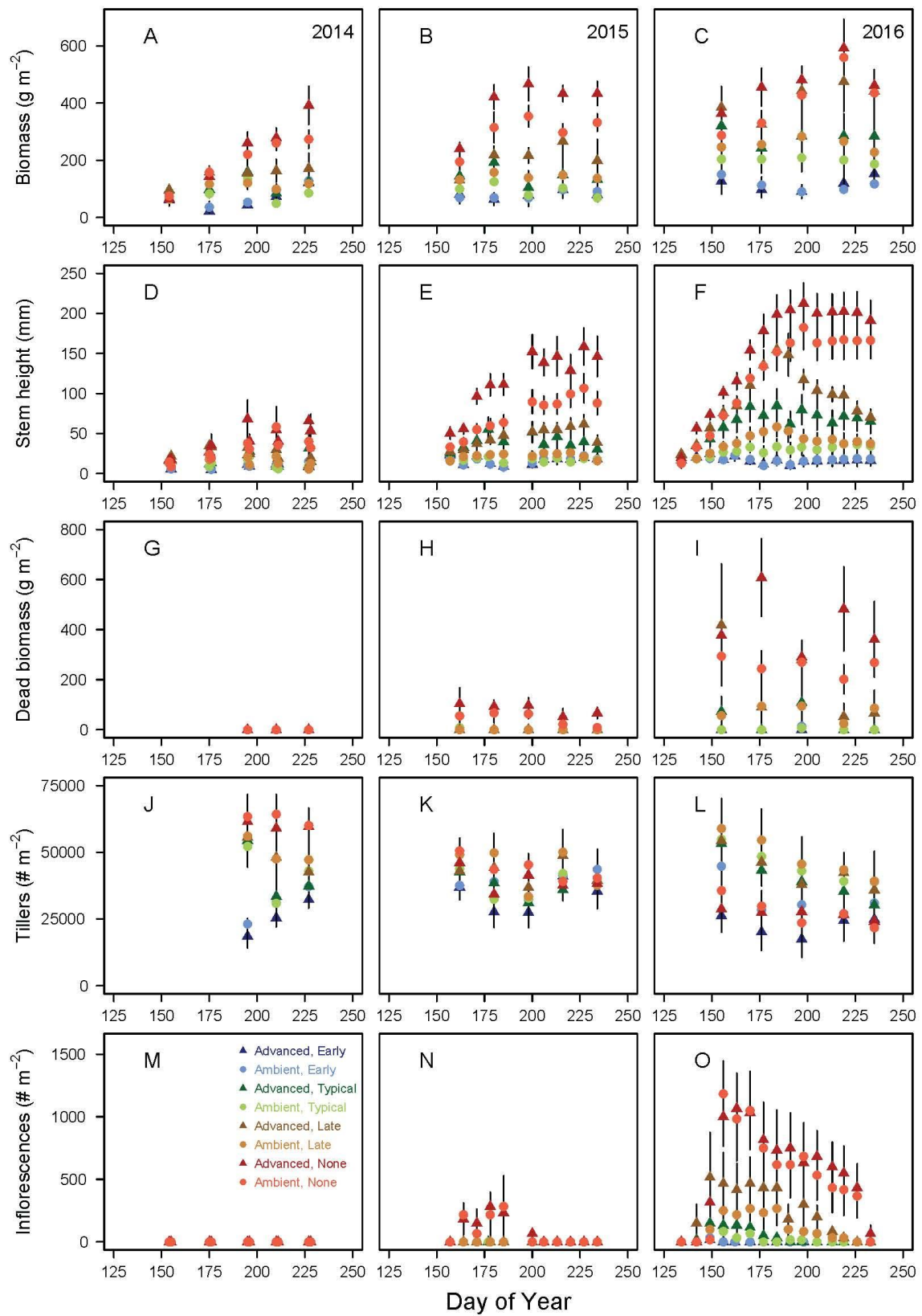| Treatment	Season	Grazing	Season	Grazing	Mismatch	Result
1	Advanced	Early	-3	-3	0	Geese match early green-up with early grazing
2	Ambient	Early	0	-3	-3	Geese arrive early in a season with current green-up time
3	Advanced	Typical	-3	0	+3	Early green-up with no change in goose grazing
4	Ambient	Typical	0	0	No shift in timing	Represent long-term, typical conditions of the system
5	Advanced	Late	-3	+3	+6	Early green-up with geese arriving late
6	Ambient	Late	0	+3	+3	Normal green-up with late goose grazing
7	Advanced	None	-3	N/A	N/A	No mismatch; early green-up and no grazing
8	Ambient	None	0	N/A	N/A	No mismatch; normal green-up and no grazing

Table 2. Results from the experimental treatments analysis showing the top four performing models for plant trait response variables based on AIC model selection over three years (2014-16). Abbreviations: Grazing = goose grazing treatment, Season = season advancement treatment, DOY = day of year. Models with interaction terms imply inclusion of the main effect. (†) indicates parsimonious model selection for top models with ΔAIC < 2.
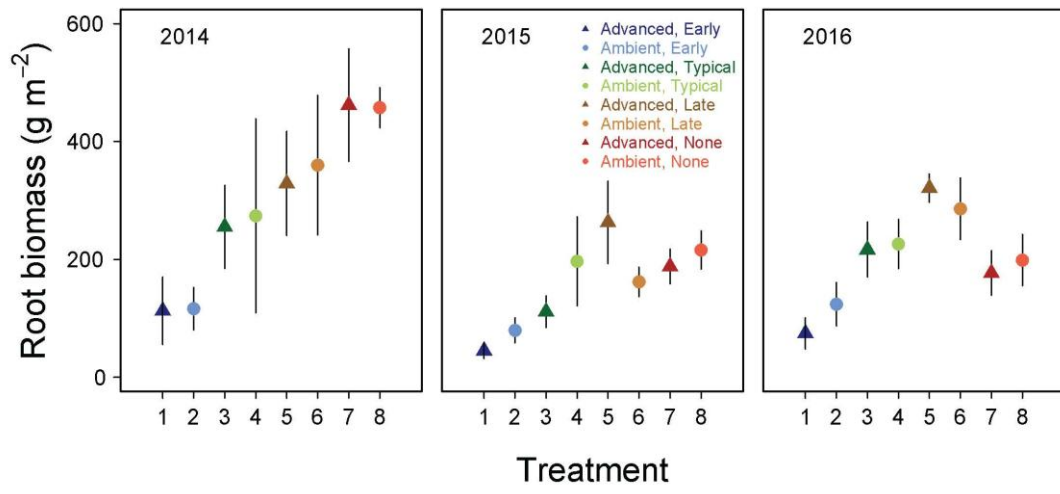
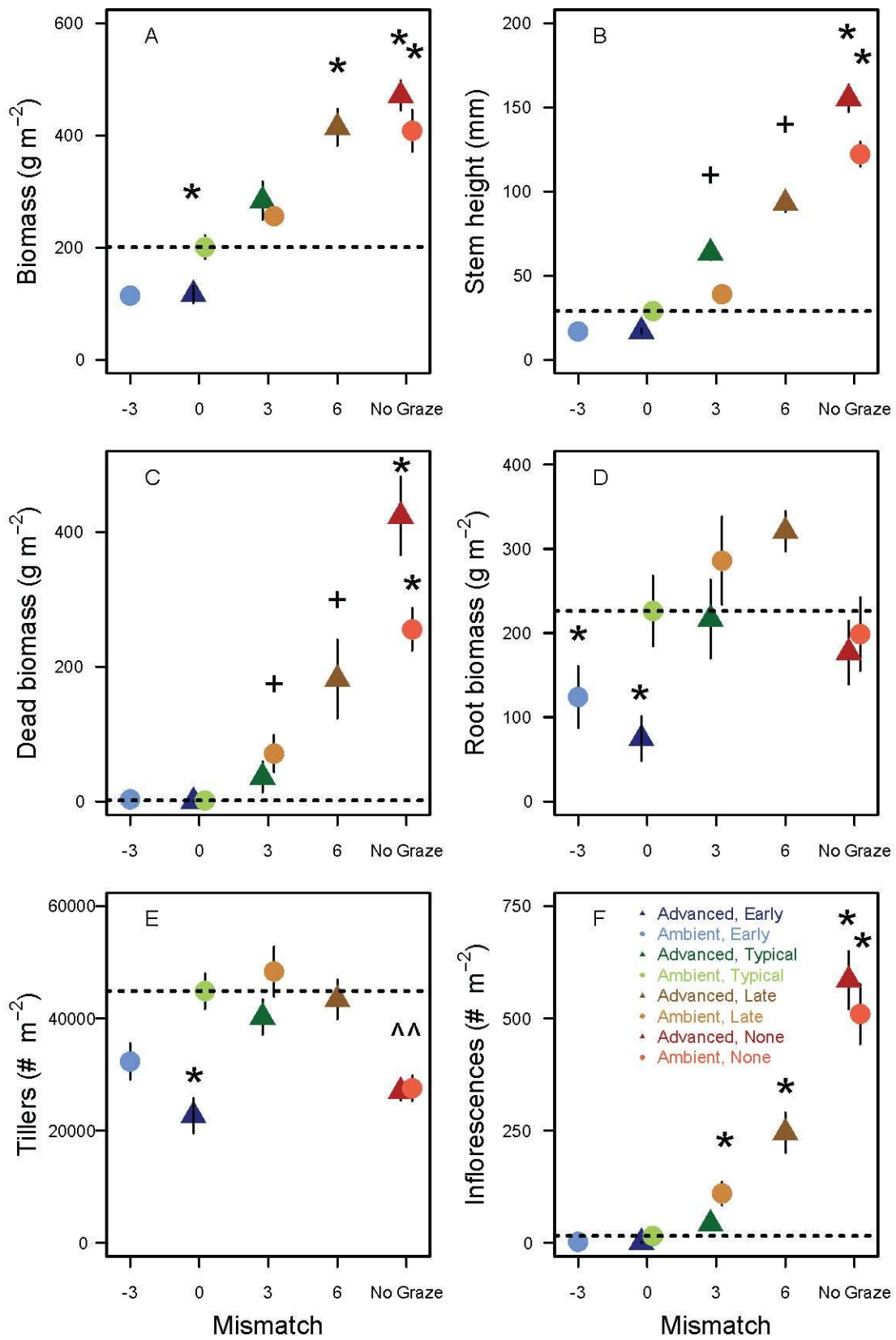| Model	logLik	AIC	ΔLogLik	ΔAIC	Df	Weight
Aboveground biomass						
Year + Grazing*DOY + Season	-530.7	1091.5	107.2	0.0	15	0.560
Year + Grazing*DOY	-532.0	1092.0	106.0	0.5	14	0.440 †
Year*Grazing + Season + DOY	-536.3	1108.6	101.6	17.1	18	<0.001
Year*Grazing + DOY	-537.5	1109.0	100.5	17.5	17	<0.001
Stem height						
Year + Grazing*DOY + Season	-572.5	1175.0	169.3	0.0	15	1
Year + Grazing*DOY	-580.7	1189.4	161.2	14.4	14	<0.001
Year*Grazing + Season + DOY	-590.1	1216.2	151.8	41.2	18	<0.001
Year + Grazing*Season + DOY	-599.8	1229.6	142.1	54.6	15	<0.001
Standing dead						
Year*Grazing + Season	-853.3	1732.5	106.9	0.0	13	0.573 †
Year*Grazing + Season + DOY	-852.8	1733.5	107.4	1.0	14	0.348
Year*Grazing	-856.7	1737.5	103.4	4.9	12	0.049
Year*Grazing + DOY	-856.2	1738.5	103.9	5.9	13	0.030
Root biomass						
Year*Grazing	-140.2	312.3	35.5	0.0	16	0.637 †
Year*Grazing + Season	-140.1	314.2	35.6	1.8	17	0.257
Year + Grazing	-148.4	316.8	27.3	4.4	10	0.070
Year + Grazing + Season	-148.3	318.6	27.4	6.2	11	0.028
Tiller number						
Year*Grazing + DOY	-276.9	579.8	42.2	0.0	13	0.542 †
Year*Grazing + Season + DOY	-276.1	580.2	43.0	0.4	14	0.449
Year*Grazing	-282.7	589.3	36.4	9.5	12	0.005
Year*Grazing + Season	-281.9	589.7	37.2	9.9	13	0.004
Inflorescence number						
Year + Grazing*DOY + Season	-1132.3	2286.6	274.8	0.0	11	0.78
Year + Grazing*DOY	-1134.6	2289.1	272.5	2.5	10	0.22
Year + Grazing*Season + DOY	-1144.4	2310.8	262.7	24.2	11	<0.001
Year + Grazing + Season +DOY	-1154.0	2324.1	253.1	37.4	8	<0.001

Table 3. Results from the experimental treatment analysis showing the top four performing models for plant trait response variables based on AIC model selection for treatment comparisons over three years (2014-16). Abbreviations: Treatment = difference between ambient-typical conditions and other treatments, DOY = day of year. Models with interaction terms imply inclusion of the main effect. (†) indicates parsimonious model selection for top models with ΔAIC < 2.
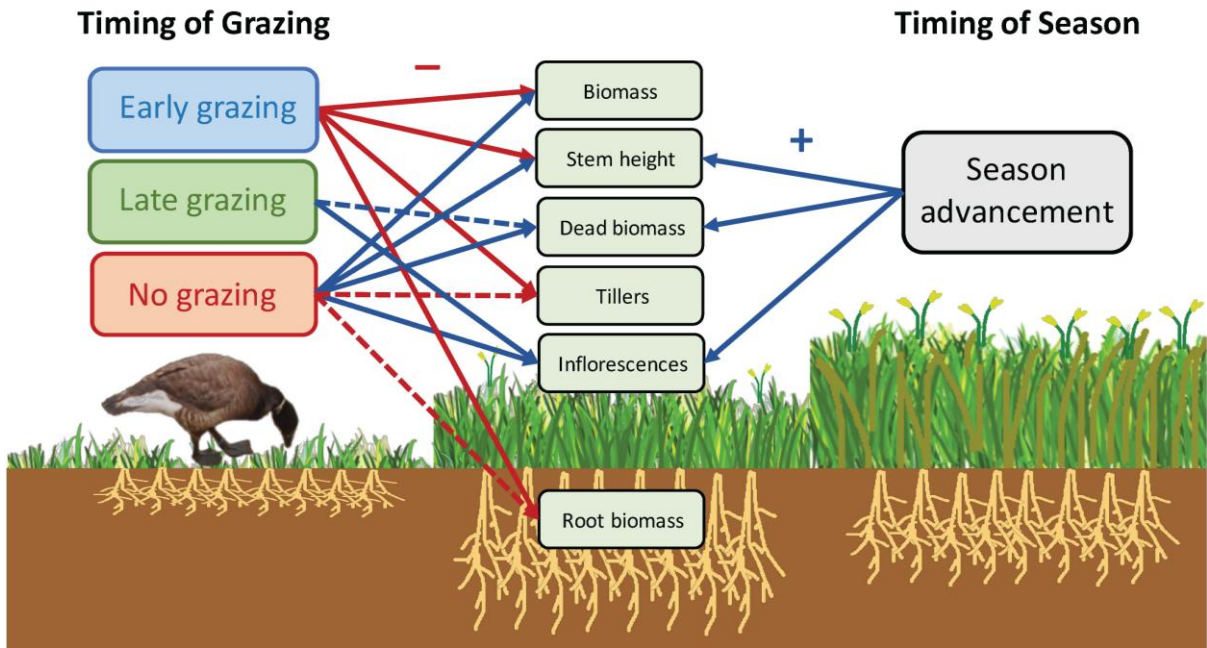
Model	logLik	AIC	ΔLogLik	ΔAIC	Df	Weight
Aboveground biomass						
Treatment + Year*DOY	-533.2	1100.4	104.7	0.0	17	1
Treatment*Year + DOY	-532.7	1123.3	105.3	22.9	29	<0.001
Treatment + Year + DOY	-548.0	1126.0	89.9	25.6	15	<0.001
Treatment*Year	-561.8	1143.5	76.2	43.1	10	<0.001
Stem height						
Treatment*Year + DOY	-561.1	1180.2	156.3	0.0	29	0.55 †
Treatment + Year*DOY	-573.3	1180.6	144.1	0.4	17	0.44
Treatment + Year + DOY	-578.6	1187.3	138.8	7.1	15	0.02
Year + DOY	-614.3	1248.5	103.1	68.4	10	<0.001
Standing dead						
Treatment*Year	-845.6	1731.1	114.6	0.0	20	0.62 †
Treatment*Year + DOY	-845.0	1732.1	115.1	0.9	21	0.38
Treatment + Year	-878.4	1782.8	81.7	51.7	13	<0.001
Treatment + Year + DOY	-878.1	1784.1	82.1	53.0	14	<0.001
Root biomass						
Treatment + Year	-147.3	322.6	28.4	0.0	14	0.97
Treatment*Year	-136.8	329.6	38.9	7.0	28	0.03
Treatment	-157.6	339.2	18.1	16.6	12	<0.001
Year	-164.2	342.4	11.5	19.8	7	<0.001
Tiller number						
Treatment*Year + DOY	-268.4	594.9	50.7	0.0	29	0.99
Treatment*Year	-274.4	604.9	44.7	10.0	28	0.01
Year + DOY	-304.1	624.2	15.0	29.3	8	<0.001
Treatment + Year + DOY	-297.2	624.3	22.0	29.4	15	<0.001
Inflorescence number						
Treatment + DOY	-1036.8	2095.6	279.7	0.0	11	0.87
Treatment*DOY	-1031.7	2099.3	284.8	3.7	18	0.13
Treatment	-1053.6	2127.2	262.9	31.6	10	<0.001
Treatment*Year + DOY	-1127.1	2264.2	189.4	168.5	5	<0.001

Timing of migration

Pacific black brant
(*Branta bernicla nigricans*)

Consumer traits
Population size, gosling growth,
reproductive success

**Climate change-induced
phenological mismatch**

Goose herbivory

Foliage quality

Timing of season

Carex subspathacea

Producer traits
Biomass, tillers, standing
dead, inflorescences, roots

Phenological mismatch