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CLIMATE-DRIVEN IMPACTS OF WARMING AND GRAZING ON SUB-ARCTIC COASTAL WETLANDS IN ALASKA

by

Ryan T. Choi

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

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Logan, Utah

2021

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ABSTRACT

Climate-Driven Impacts of Warming and Grazing on Sub-Arctic Coastal Wetlands in Alaska

by

Ryan T. Choi, Doctor of Philosophy

Utah State University, 2021

Major Professor: Dr. Karen H. Beard
Department: Wildland Resources

Anthropogenic climate change is altering migratory herbivore patterns and affecting Arctic plant communities and forage resources. Warmer temperatures can increase plant productivity and affect biogeochemical cycling, which can alter resource availability for herbivores. Changes in the timing of biotic interactions have the potential to create phenological mismatch between plants and herbivores. While investigations of mismatch often focus on the effect on herbivores, shifts in trophic interactions can also have important ecological consequences for forage availability, nutrient cycling, and plant community diversity and composition.

In chapter 2, I use a manipulative field experiment to investigate how season advancement and shifts in goose grazing affects plant physical traits in *Carex* grazing lawns. I show that earlier grazing by geese reduces plant biomass, while season advancement and late goose grazing initiate a shift from clonal to sexual reproduction. Earlier growing seasons and late grazing have similar effects, but delayed grazing has a greater impact than an equivalent shift in season. Further, some measurements are not detectable for several years, while others alter their directional response to treatments over time.

In chapter 3, I examine how phenological mismatch between migratory geese and their forage influences soil N availability. I demonstrate that early grazing increases inorganic and organic soil N availability, while late grazing decreases inorganic soil N. Season advancement increases inorganic soil N, however, this effect is less than that of grazing. Although both early grazing and advanced springs are likely to increase N availability in the future, earlier goose arrival is likely to be more significant than earlier springs in influencing soil N.

In chapter 4, I investigate how warming and grazing interact to affect community diversity and composition in three different coastal plant communities. I show that both grazing and warming generally increase community diversity. Grazing changes functional group composition by increasing forbs and decreasing grasses in the two more coastal communities and decreasing sedges in the most inland community, while warming does not affect functional group composition. I also show that treatment effects vary at different spatial scales, which suggests the importance of investigating climate-driven disturbance at both ecosystem- and site-levels.

(195 pages)

PUBLIC ABSTRACT

Climate-Driven Impacts of Warming and Grazing on Sub-Arctic Coastal Wetlands in Alaska

by

Ryan Choi

Climate change is rapidly warming the Arctic, especially at lower latitudes. Warmer temperatures and earlier springs are altering the timing of plants and animals, especially for long-distance migratory herbivores. Changes in the timing of both plants and herbivores have the potential to impact plant productivity and nutrient cycling, while also altering plant community diversity and composition.

In chapter 2, I conducted a field experiment to investigate how earlier growing seasons and differences in arrival times of migratory geese influence physical traits of sedge forage species. I found that both an earlier growing season and late grazing by geese had similar effects on plant traits but delays in grazing had a greater effect than a change in spring.

In chapter 3, I examined how earlier springs and differences in timing of goose herbivores affect soil nitrogen availability in sedge grazing lawns. I found that both earlier growing season and early grazing by geese increased soil nitrogen, while late grazing decreased soil nitrogen. However, early grazing resulted in a greater increase in soil nitrogen than an earlier growing season.

In chapter 4, I investigated how warming and grazing interact to affect plant community diversity and composition in three different coastal wetland plant communities. I found that both warming and grazing increase community diversity but can also interact to mediate or synergistically increase community effects. Grazing decreased dominant grasses but increased low-lying forbs, while warming had little effect on functional groups across different communities.

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Ryan Choi

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CHAPTER 1

INTRODUCTION

Introduction

Anthropogenic climate change is rapidly warming high-latitude regions (IPCC 2014). The Arctic has warmed on average nearly 2°C at rates twice as fast as lower latitudes (Thoman et al. 2020). Season advancement and warmer temperatures are altering the timing of biotic interactions, specifically between plants and herbivores (Cohen et al. 2018, Kharouba et al. 2018, Renner and Zohner 2018). One of the significant consequences of climate change is the temporal decoupling of consumers from their forage resources (Visser and Both 2005). Further, climate-driven shifts in the timing and intensity of these trophic interactions have the potential to restructure communities, affect biogeochemical processes, and alter ecosystem function (Tylianakis et al. 2008, Grimm et al. 2013, Bjorkman et al. 2018, Kelsey et al. 2018).

In this introductory chapter, I review the potential for phenological mismatch to affect plant-herbivore interactions. I then review the effects of warming and herbivory on Arctic ecosystems and highlight the predicted impacts in high-latitude coastal wetlands. I conclude this chapter by outlining how my dissertation chapters attempt to improve our understanding of climate-driven trophic mismatch using novel field-based approaches.

Phenological Mismatch

Climate change is altering species phenology and range distributions around the globe, with advanced growing conditions resulting in warmer, earlier springs (Parmesan and Yohe 2003, Post et al. 2009). Shifts in the timing of ecological events can drive ‘phenological mismatch’ between species that are adapted to rely on one another, which can result in asynchronous timing of life history events that can negatively affect the survival of one or both species. Migratory species are particularly vulnerable due to their dependence on long-distance teleconnections and sensitivity to changes across different latitudes (Tombre et al. 2008). Some migratory species are shifting their timing earlier in response to climate-induced season advancement (Kölzsch et al. 2015, Boelman et al. 2017), however, there is still potential for phenological mismatch between consumers and their resources due to differing rates of change in their winter and summer ranges (Mayor et al. 2017, Lameris et al. 2017).

Phenological mismatch is caused by climate-driven shifts in the timing of trophic interactions, often between producers and consumers (Miller-Rushing et al. 2010). However, in order for mismatch to occur, both a producer and a consumer must express some degree of seasonality and the producer must directly affect the survival of the consumer (Durant et al. 2007). Further, when investigating consequences of phenological mismatch, there is a need to focus on species sensitive to changes in climate-induced warming (Beard et al. 2019b). Because mismatch can occur between a wide array of different taxa across global terrestrial ecosystems (e.g. plant-goose (Dickey et al. 2008); plant-caribou (Post and Forchhammer 2008); salmon-grizzly (Deacy et al. 2017); insect-bird (Reed et al. 2013); plant-pollinator (Korösi et al. 2018)), it is difficult to define a standardized yardstick of climate-driven change (Visser and Both 2005).

The timing of migratory behaviors are often synchronized to maximize resource availability and to optimize growth and reproductive success. For example, with Arctic migratory geese, the timing of nesting has evolved to coincide with peak plant N available for goslings at time of hatch (Sedinger and Raveling 1986). However, warmer springs can alter the foliar N availability and rate of seasonal decline (Doiron et al. 2014). Because geese are highly sensitive to forage quality (Sedinger and Flint 1991, Lindholm and Gauthier 1994), shifts in timing and availability of forage can exert strong bottom-up controls and negatively impact gosling growth and survival (Doiron et al. 2015, Ross et al. 2017, Lohman et al. 2019). Thus, asynchronous shifts in the availability of primary resources can have demographic consequences for herbivores and potentially result in population declines.

Figure 1.1 illustrates potential shifts in timing between producers and migratory consumers. Ideally, consumers time their behaviors to arrive during peak resource quantity and quality (Figure 1.1B), However, due to mismatched cues (for example, warming spring conditions compared to fixed photoperiod initiating migration (Bauer et al. 2008)), consumers can arrive early or late relative to producers (Figure 1.1A&C), which may negatively impact populations. Similarly, advanced growing conditions can result in an earlier shift in primary productivity, with consumers arriving on time relative to historical patterns but still relatively late to optimize available resources (Figure 1.1D). However, if consumers are able to track changes, they may be able to keep up with resource availability and avoid asynchronous mismatch (Figure 1.1E). In addition to altering the timing of herbivore migration, climate-driven changes can also alter the abundance and duration of these relationships which can further drive phenological mismatch (Miller-Rushing et al. 2010).

Climate Warming

Warmer temperatures can change Arctic plant communities by altering primary productivity (Walker et al. 2006, Elmendorf et al. 2012). Warming can promote growth and increase abundance of certain functional groups, like shrubs and graminoids (Arft et al. 1999, Tape et al. 2016, Liu et al. 2018). For example, warmer temperatures are driving the shrubification of Arctic regions, which can in turn restructure plant communities (Myers-Smith et al. 2011). In Arctic and alpine regions, climate-driven warming can reduce species diversity and evenness (Hollister et al. 2005, Kaarlejärvi et al. 2017), and alter plant community structure and composition (Post and Pedersen 2008, Myers-Smith et al. 2011, Yu et al. 2011). Changes in Arctic plant community composition and productivity can influence herbivore diversity and abundance (Barrio et al. 2016); affect biotic processes including ecosystem productivity, biogeochemical cycling, and decomposition (Cornwell et al. 2008, Sjögersten et al. 2008, Myers-Smith et al. 2011); and abiotic conditions like temperature, albedo, and snow deposition (Sturm et al. 2001, 2005, Blok et al. 2010).

Climate-driven warming can also directly affect biogeochemical processes, such as nutrient cycling. Arctic ecosystems are often nitrogen (N) limited due to cold temperatures and relatively short growing seasons (Schimel et al. 1996). Earlier springs and warmer soils can stimulate microbial enzymatic activity and increase rates of N-mineralization (Buckeridge and Grogan 2010, Bardgett et al. 2013, Sistla and Schimel 2013). Season advancement can also increase the labile organic N pool and amino acids (Darrouzet-Nardi et al. 2019), which are utilized by Arctic coastal graminoids (Henry and Jefferies 2003). However, while warmer temperatures can increase soil N availability, earlier growing seasons also increase plant growth and lead to greater uptake and reduction of soil N (Lin et al. 2010, Natali et al. 2012). Thus, overall soil nutrient availability is highly dependent on the strength of drivers influencing N demand and availability.

Migratory Herbivores

The distribution and abundances of migratory herbivores are changing across Arctic landscapes (Fox and Madsen 2017, Amundson et al. 2019, Joly et al. 2019). Generally, herbivores track green waves of resources along their spring migration routes to fuel their intensive energy demands (van der Graaf et al. 2006, Merkle et al. 2016). However, some migratory species are shifting northward following retreating thermal gradients and optimal temperature envelopes (La Sorte and Thompson 2007, Gornish and Tylianakis 2013, Tombre et al. 2019). Some species are shortening migration distance travelled, accelerating rates of seasonal migration, or skipping migration stopovers to keep up with advancing spring (Ward et al. 2009, La Sorte and Fink 2017, Lameris et al. 2018).

Herbivores play a critical role in structuring Arctic plant communities (Jefferies et al. 1994, Post et al. 2008), primarily through vegetation removal, trampling, and feces deposition (Mulder 1999, Zacheis et al. 2002). These effects of herbivory can directly alter plant species composition and community structure (Olofsson et al. 2001, Christie et al. 2015, Falk et al. 2015). Because herbivory can stimulate productivity through compensatory growth, herbivores can also mediate effects of warming and provide community stability and ecological resilience to climate-driven change (Olofsson et al. 2009, Eskelinen et al. 2017, Kaarlejärvi et al. 2017).

Geese are the primary herbivores in Arctic coastal wetlands (Gauthier et al. 2004, Madsen et al. 2011). Due to their high-densities, geese can play primary roles in controlling biogeochemical processes in Arctic systems (Ruess et al. 1989, Speed et al. 2010). Geese have positive dynamic feedbacks in regulating their forage resources. Specifically, their ability to through grazing which can increase forage availability on the landscape (Person et al. 2003, Uher-Koch et al. 2019). Because geese play a critical role in structuring vegetation habitat, altering forage resource quality, and affecting biogeochemical cycling (Kelsey et al. 2018, Leffler et al. 2019, Beard et al. 2019a), changes in the abundance or timing of migratory goose herbivores could have consequences for nutrient availability in an N-limited system.

Predicted Impacts in Arctic Coastal Wetlands

Low-elevation Arctic coastal ecosystems are particularly vulnerable to climate-driven increases in global sea level and tidal inundation (Jones et al. 2009, Tape et al. 2013). Warmer temperatures are reducing the winter extent of shorefast sea ice that would normally buffer coastlines from storm surge events (Vermaire et al. 2013). Coastal flooding is increasing in both frequency and intensity and leading to greater rates of erosion with losses of up to 15 m year^{-1} in some regions (Terenzi et al. 2014, Jorgenson et al. 2018).

The Yukon-Kuskokwim (Y-K) Delta is one of the largest river deltas in the world encompassing over 75,000 km^2 of coastal wetlands (Thorsteinson et al. 1989). It is a critical breeding ground for millions of migratory waterfowl and shorebirds that travel thousands of miles annually to rear their young (Gill and Handel 1990). The Y-K Delta supports the breeding populations of four North American goose species that nest in the active coastal floodplain (Saalfeld et al. 2017): Pacific black brant (*Branta bernicla nigricans*), cackling geese (*B. hutchinsii minima*), emperor geese (*Chen canagica*), and greater white-fronted geese (*Anser albifrons frontalis*). While most Y-K Delta goose species are relatively stable (Fischer et al. 2017), populations of Pacific black brant are declining possibly due to reductions in *Carex* grazing lawns in the coastal floodplain over the past few decades (Sedinger et al. 2019, Lohman et al. 2019, Uher-Koch et al. 2019).

The Y-K Delta is predicted to undergo dramatic changes in the coming decades. Coastal regions adjacent to the Bering Sea are expected to be submerged by rising sea levels forcing low-elevation plant communities and goose herbivores to shift inland (Jorgenson et al. 2018). Novel community assemblages will be subjected to wetter and warmer conditions and extended growing seasons (Post et al. 2019, SNAP 2020), which will exert significant pressure on plant-herbivore interactions and result in complex ecological processes on the landscape. Ecological disturbances that hinder plant community productivity may compromise the ability of these coastal wetlands to support historic goose abundances (Fondell et al. 2011), especially because the inland terraces are lower in forage resource density compared to the coastal margin (Person et al. 2003). Further, coastal processes threaten the loss of critical breeding habitat for migratory birds typically within 15 km of the coast where preferred plant communities are most common (Sedinger and Raveling 1984, Babcock and Ely 1994, Schmutz et al. 2002). Goose herbivores may potentially respond to plant community shifts by relocating to areas where resources are more abundant or altering their migratory behaviors altogether (Ward et al. 2009, Flint et al. 2014).

A Novel Experimental Approach

Investigating how climate-driven changes in magnitudes and patterns of trophic interactions impact communities are important for predicting and understanding the future of functional ecosystems (Walther 2010). Further, the timing of biotic interactions is a critical and often missing piece to understanding the ecological consequences of phenological mismatch; others have highlighted the need for multi-year experiments that investigate shifts between the timing of two species at different trophic levels and measure ecosystem responses under current and future scenarios (Beard et al. 2019b). In the following chapters, I use a series of novel field experiments to investigate the effects of trophic mismatch and shifting spatial patterns on coastal plant communities and biogeochemical processes to better understand the potential interacting effects of warming and grazing in a rapidly changing Arctic.

Dissertation Outline

Chapter 2 – Phenological Mismatch Between Season Advancement and Migration Timing Alters Arctic Plant Traits

Climate changes is causing season advancement in Arctic regions, which is likely to create phenological mismatch between long-distance migratory geese and their forage resources. Most studies investigating mismatch have focused on the direct effect on herbivores (e.g., Post and Forchhammer 2008; Doiron et al. 2015; Rickbeil et al. 2018), however, few studies have investigated the effects of developing mismatches at the lower trophic level. Further, the majority of studies that investigated grazing impacts have utilized the presence or absence of herbivores or changes in grazing intensity or frequency, and not the timing of grazing (e.g. Pastor and others 1993; Frank and Evans

1997; Tracy and Frank 1998). We used a novel approach to investigate climate-driven phenological mismatch in the Y-K Delta by manipulating the timing of the growing season and the timing of herbivory by migratory geese to determine effects on physical characteristics and reproductive traits of *Carex* forage in grazing lawns.

Chapter 3 – Early Goose Arrival Increases Nitrogen Availability More Than an Advancing Spring in Coastal Western Alaska

Soil N availability is often limiting in Arctic systems and shifts in the timing of spring and goose arrival have consequences for nutrient cycling in coastal ecosystems. Even subtle shifts in temporal N availability are important due to the ephemeral nature of labile soil N pools (Darrouzet-Nardi and Weintraub 2014). We used a similar experimental approach as chapter 2 to investigate how phenological mismatch between goose herbivores and their forage can influence soil N availability in *Carex* grazing lawns. We also present a novel approach to better measure soil N availability using ion-exchange resins during intertidal periods to avoid ionic loss during coastal flooding events.

Chapter 4 – Climate-Induced Changes Alter Coastal Wetland Plant Communities

Coastal processes are expected to shift plant communities and herbivores inland (Jorgenson et al. 2018). While *Carex* grazing lawns are critical forage habitat for migratory geese, they comprise less than 1% of the active coastal floodplain in the Y-K Delta (Macander et al. 2012). The adjacent coastal terrace communities are also important foraging habitat and brood-rearing areas for migratory goose populations (Sedinger and Raveling 1986, Lindberg and Sedinger 1998). If coastal erosion and flooding result in loss of primary *Carex* grazing lawn habitat, the adjacent coastal communities will likely experience a new suite of trophic interactions between plants and herbivores further inland. We investigated how shifts in spatial patterns in warming and herbivory affect plant communities by using a similar field-based approach to chapters 2 and 3. In this experiment, we substituted season-long warming for season advancement to investigate how greater temperature and spatial shifts in herbivore grazing affect plant diversity and composition in three adjacent coastal vegetation communities.

Chapter 5 – Conclusions

In chapter 5, I summarize the major findings from each chapter and suggest other areas of potential research on trophic mismatch.

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Figures

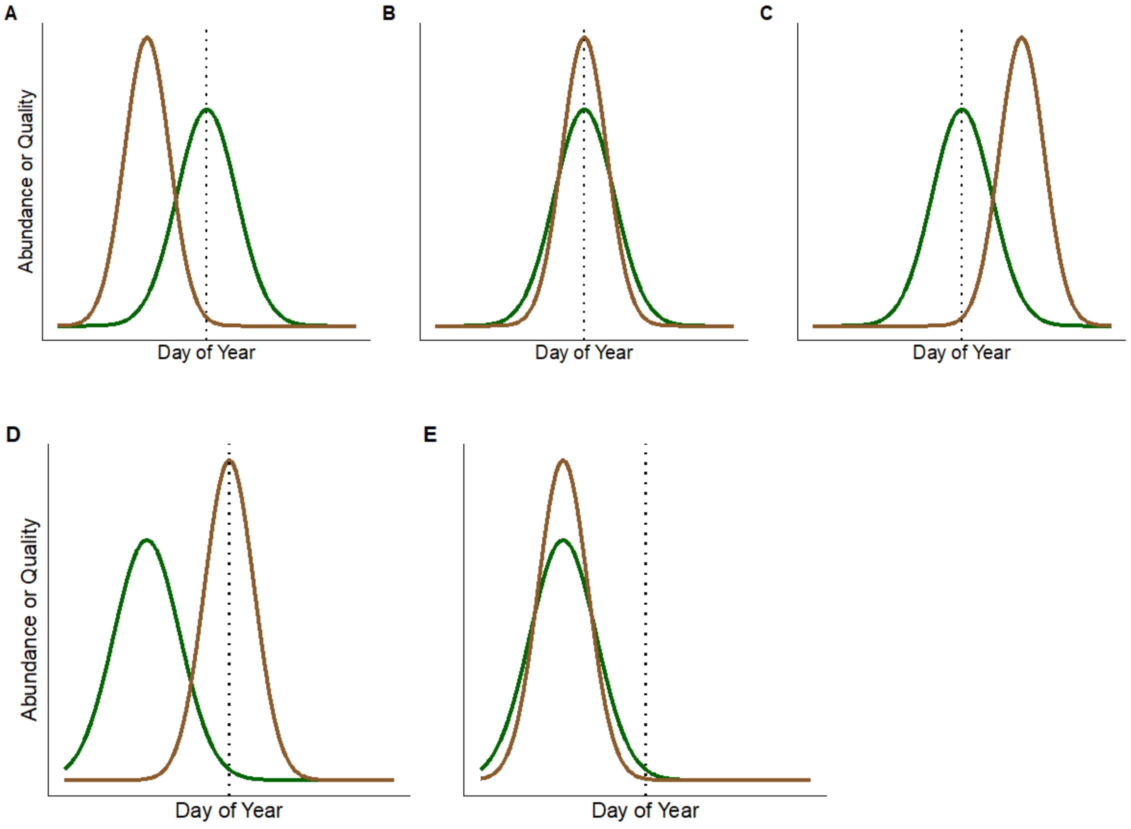

Figure 1.1. Examples illustrating potential shifts in timing between producers and migratory consumers that may result in phenological mismatch. Consumers can arrive (A) early, (B) on time, or (C) late relative to resource availability. Alternatively, warmer temperatures can (D) advance spring conditions and result in mismatch; however, (E) if consumers are able to track shifting phenology, they can avoid asynchronous mismatch with their resources. Producers = green line; consumers = brown line; historical mean timing = dotted line.

CHAPTER 2

PHENOLOGICAL MISMATCH BETWEEN SEASON ADVANCEMENT AND MIGRATION TIMING ALTERS ARCTIC PLANT TRAITS[1]

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

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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.

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. 2.1) (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, Leafloor, 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. A1 in the appendices). 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 2.1. 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 $\Delta\text{AIC} < 2$, 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 2.1). 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. A2 in the appendices). 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 A1 in the appendices). 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 A1 in the appendices). By year 3, background controls were not different from early goose grazing treatments (Table A1 in the appendices). 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 2.2). 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 2.2). 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. 2.2A-C).

For stem height, the top model included year, season advancement, and an interaction between timing of goose grazing and DOY (Table 2.2). 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. 2.2D-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 2.2). 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. 2.2G-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 A2 in the appendices).

The best-fitting model for seasonal root productivity included an interaction between year and timing of goose grazing (Table 2.2). 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. 2.3; Table A2 in the appendices).

The best-fitting model for tiller number included DOY and an interaction between timing of goose grazing and year (Table 2.2). In general, tiller number decreased over the season (Fig. 2.2J-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 A2 in the appendices).

For inflorescence counts, the top model included year, season advancement and an interaction between timing of grazing and DOY (Table 2.2). 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. 2.2M-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 2.3). 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. 2.4). 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 A3 in the appendices).

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. 2.4). 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. 2.4; Table A3 in the appendices). 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. 2.5). 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.

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. 2.5). 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 12829% 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. 2.2M). 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. 2.6). 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. 2.6). 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. 2.4). 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 2.4 & 2.6). 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. 2.2A-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 2.2 & 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 2.2J & 2.3). 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.

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Tables

Table 2.1. 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 2.2. 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 2.3. 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

Figures

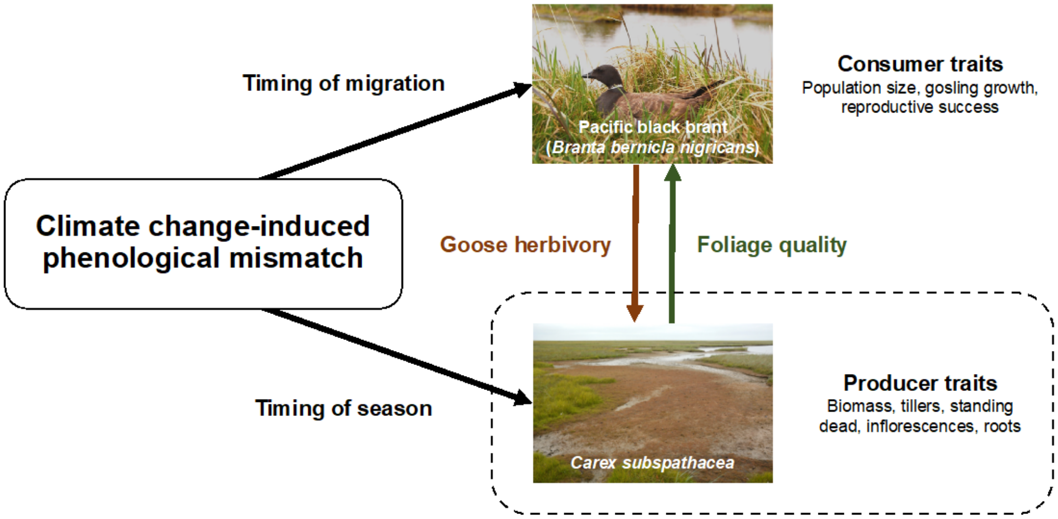

Figure 2.1. Conceptual diagram of the understudied aspect of phenological mismatch using the Yukon-Kuskokwim Delta as an example. Most studies on phenological mismatch focus on the effects on consumer traits. Few studies focus on the effects on producer traits (dotted box), which is also important and the focus of this study.

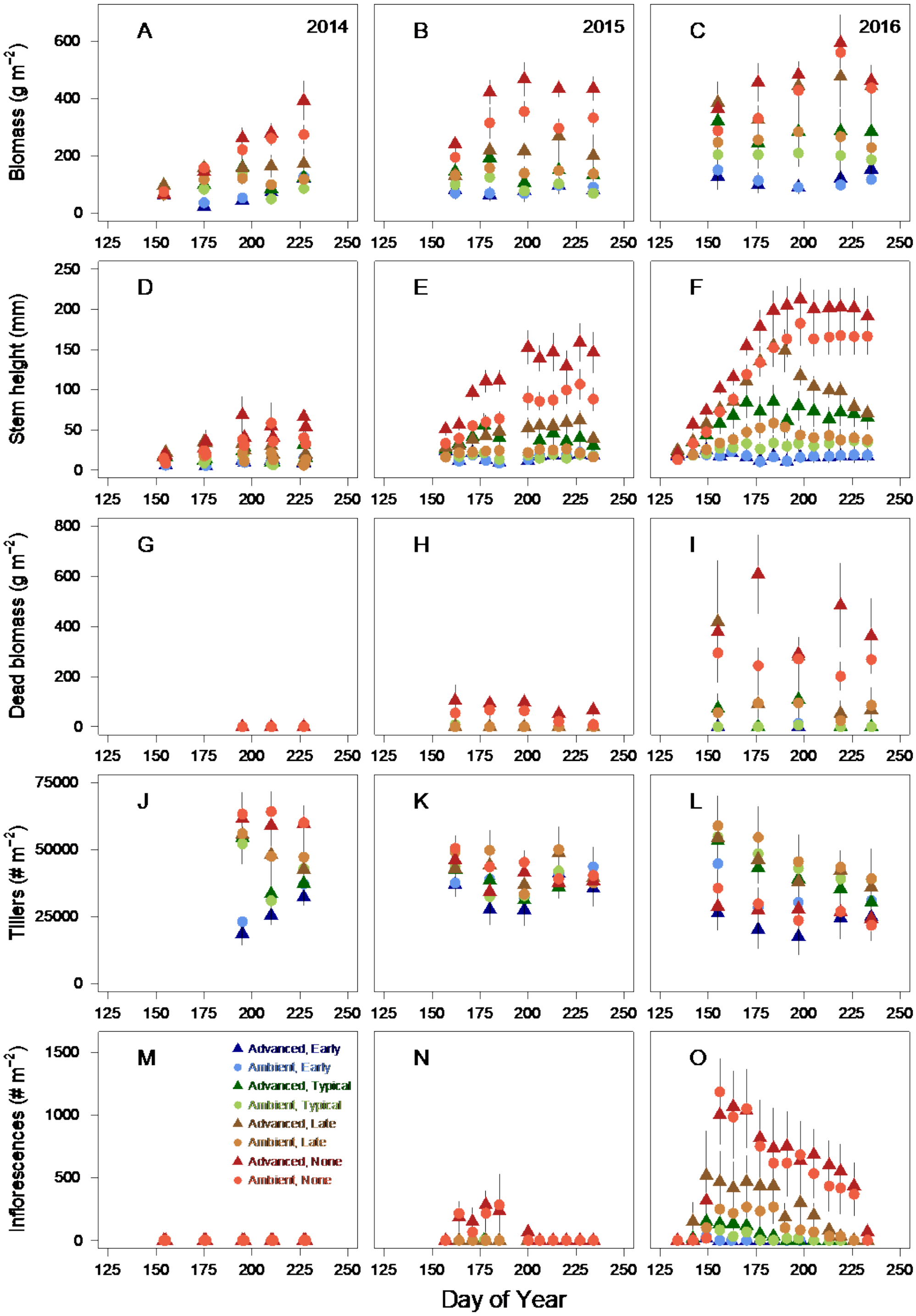

Figure 2.2. Mean plant trait responses to experimental season advancement and timing of grazing treatments from 2014-2016. (A-C) aboveground dry biomass (g m^{-2}), (D-F) stem heights (mm), (G-I) standing dead biomass (g m^{-2}), (J-L) number of tillers (# m^{-2}), (M-O) number of inflorescences (# m^{-2}). Error bars are ± 1 SE (n=6 replicates).

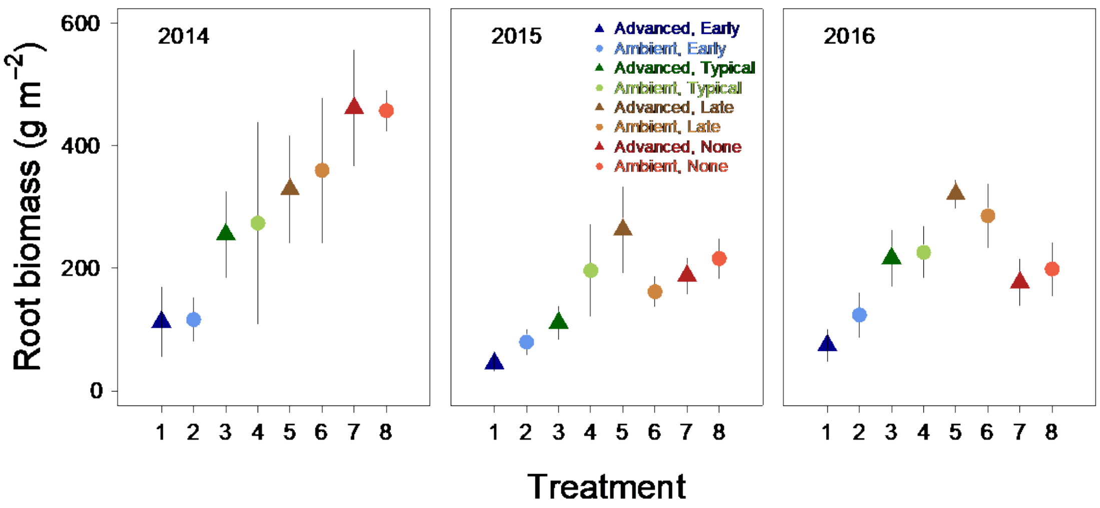

Figure 2.3. Season-long root biomass (g m^{-2}) (± 1 SE) (~25-May to 25-August) collected from 15 cm in-growth root cores for treatment plots from 2014-2016 (n=6 replicates). For Treatment key, see Table 2.1.

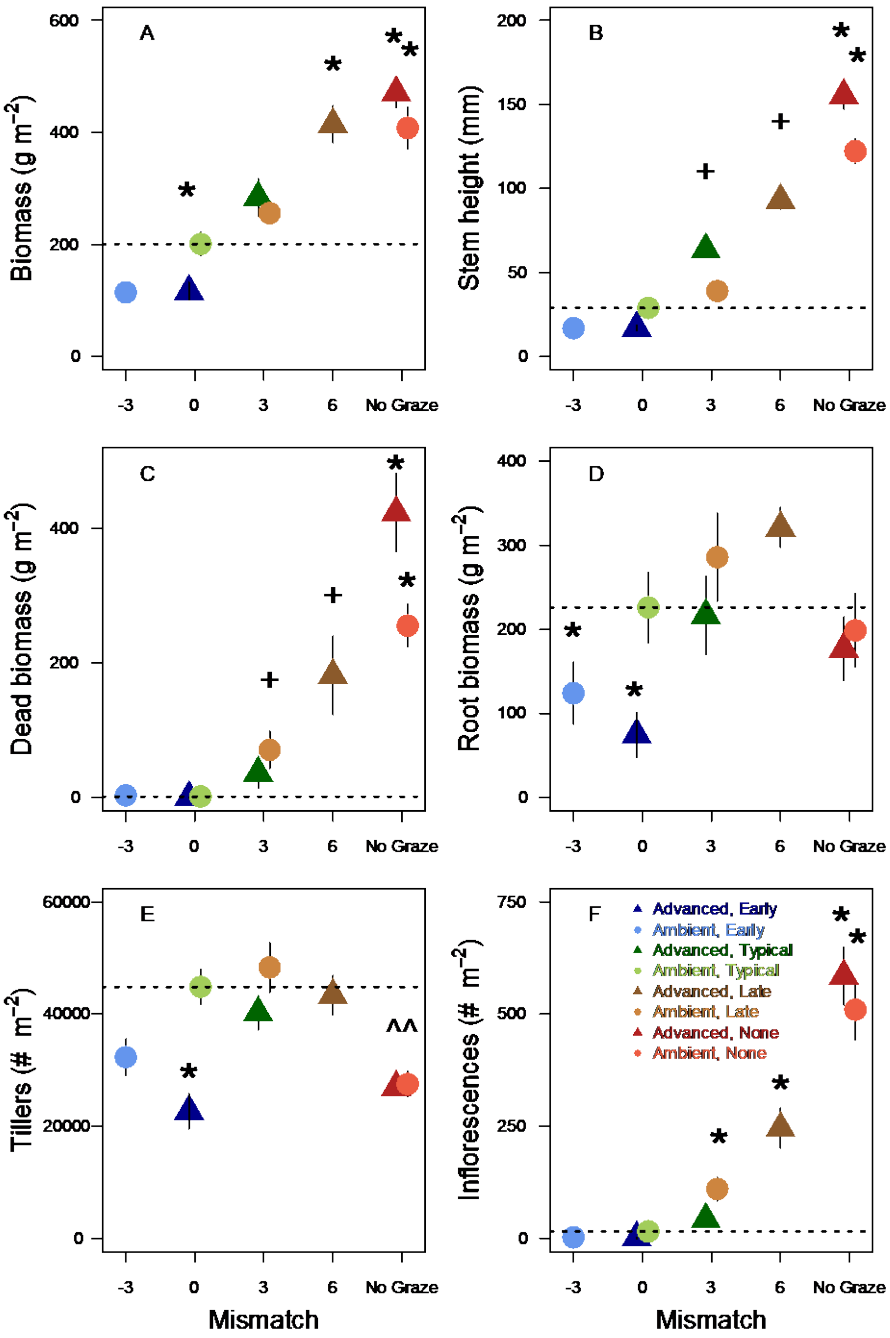

Figure 2.4. Season-long mean plant trait responses to experimental mismatch treatments from 2016. (A) aboveground dry biomass (g m^{-2}), (B) stem heights (mm), (C) standing dead biomass (g m^{-2}), (D) root biomass (g m^{-2}), (E) number of tillers (# m^{-2}), and (F) number of inflorescences (# m^{-2}). 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).

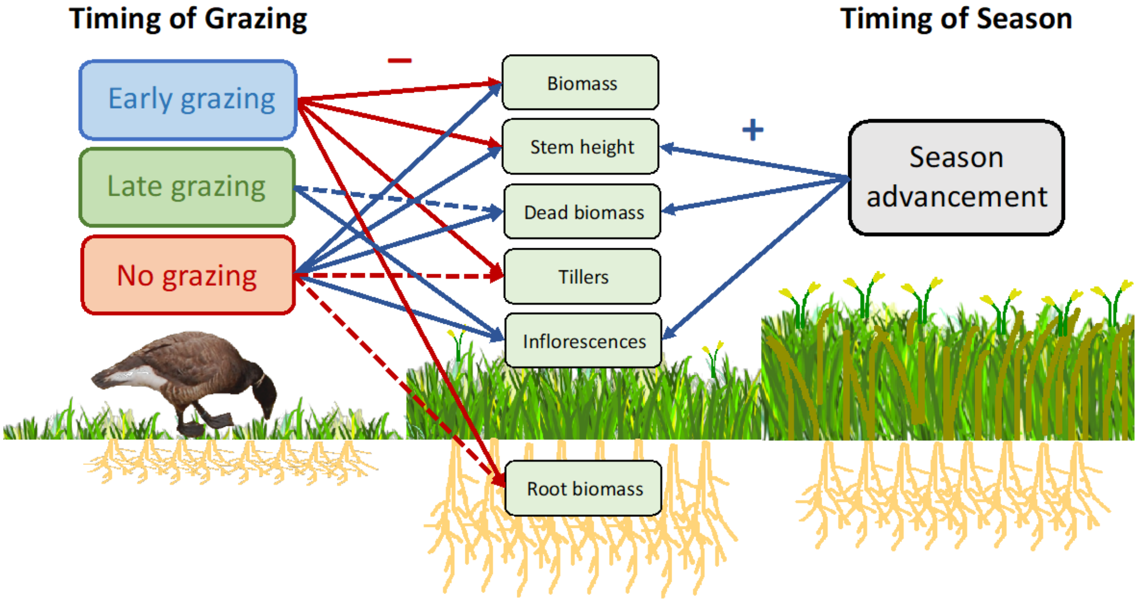

Figure 2.5. Conceptual figure of experimental treatments (timing of grazing and season advancement) on plant trait responses compared to typical grazing and ambient season after three years. Red arrows (–) indicate a negative effect; blue arrows (+) indicate a positive effect. Solid lines indicate an effect observed in all years; dashed lines indicate an effect only observed after the first season.

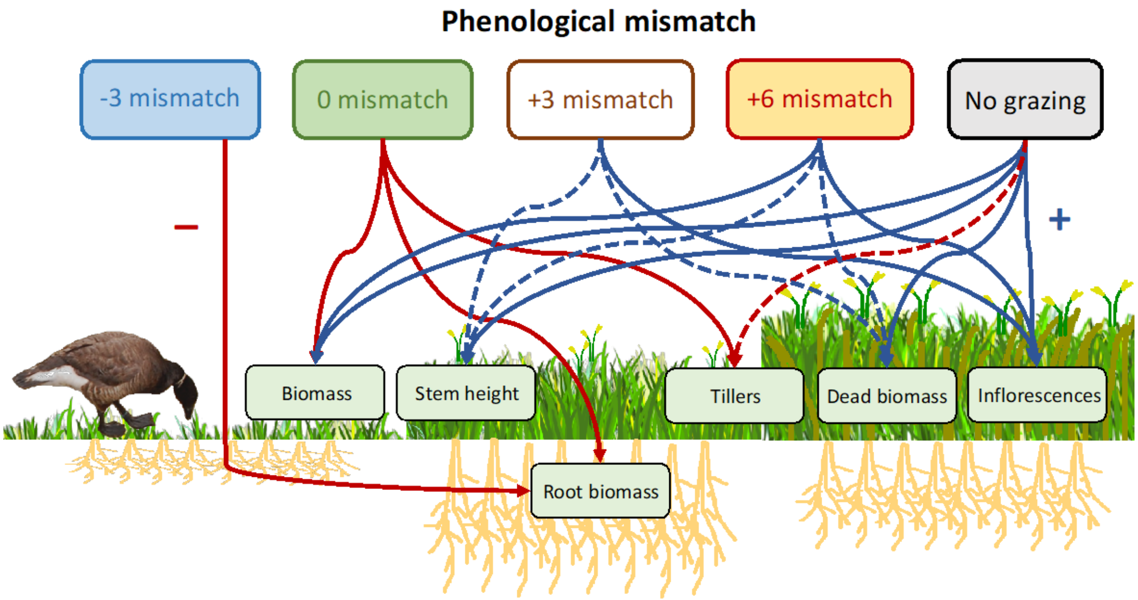

Figure 2.6. Conceptual figure of experimental mismatch on plant trait responses compared to ambient season-typical grazing (no shift in timing) after three years of treatments. Red arrows (-) indicate a significant negative effect; blue arrows (+) indicate a significant positive effect. Solid lines indicate an effect observed in all years; dashed lines indicate an effect only observed after the first season.

CHAPTER 3

EARLY GOOSE ARRIVAL INCREASES SOIL NITROGEN AVAILABILITY MORE THAN AN ADVANCING SPRING IN COASTAL WESTERN ALASKA[2]

Abstract

An understudied aspect of climate change-induced phenological mismatch is its effect on ecosystem functioning, such as nitrogen (N) cycling. Migratory herbivore arrival time may alter N inputs and plant-herbivore feedbacks, while earlier springs are predicted to increase N cycling rates through warmer temperatures. However, the relative importance of these shifts in timing and how they interact to affect N cycling are largely unknown. We conducted a three-year factorial experiment in coastal western Alaska that simulated different timings of Pacific black brant (*Branta bernicla nigricans*) arrival (3-weeks early, typical, 3-weeks late, or no-grazing) and the growing season (ca. 3-weeks advanced and ambient) on adsorbed and mobile inorganic (NH_4^+-N, NO_3^--N), and mobile organic N (amino acid) pools. Early grazing increased NH_4^+-N, NO_3^--N, and amino acids by 103%, 119%, and 7%, respectively, while late grazing reduced adsorbed NH_4^+-N and NO_3^--N by 16% and 17%, respectively. In comparison, the advanced growing season increased mobile NH_4^+-N by 26%. The arrival time by geese and the start of the season did not interact to influence soil N availability. While the onset of spring in our system is advancing at twice the rate of migratory goose arrival, earlier goose migration is likely to be more significant than the advances in springs in influencing soil N, although both early goose arrival and advanced springs are likely to increase N availability in the future.

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This increase in soil N resources can have a lasting impact on plant community composition and productivity in this N-limited ecosystem.

Introduction

Northern latitudes are experiencing rapid warming and spring advancement, which is altering the timing of biological interactions, especially for long-distance migratory species (Cohen and others 2018; Renner and Zohner 2018). While some species, such as migratory geese, have started to shift the timing of their migration earlier in response to climate-induced season advancement (Kölzsch and others 2015; Boelman and others 2017), there is still potential for resource-consumer 'phenological mismatch' due to the different rates of climatic change in their winter and summer ranges (Lameris and others 2017; Mayor and others 2017). Phenological mismatch between long-distance migratory birds and their resources is already negatively affecting higher trophic herbivores through reductions in resource availability and forage quality (Doiron and others 2015; Ross and others 2017). While it is unclear if the mismatch will persist, it is likely that these mismatches will have long-term consequences for some northern systems due to the rapid occurrence of change in the Arctic (Miller-Rushing and others 2010). An understudied aspect of phenological mismatch is how ecosystem-level processes, such as nutrient cycling, may be impacted (Kelsey and others 2018; Heberling and others 2019; Leffler and others 2019), and until recently this has been largely overlooked (Beard and others 2019b).

Investigating how developing phenological mismatch influences soil nitrogen (N) availability is fundamental for understanding how northern latitudes are changing because N is often a limiting resource for plant growth in these systems (Schimel and others 1996). Shifts in the timing of trophic interactions (i.e., changes in herbivory) and subsequent N inputs (i.e., litter, feces) may alter soil N available for plant uptake and microbial immobilization over the brief summer growing season (Ruess and others 1997); however, the direction or magnitude of these responses is uncertain. Because plant growth is highly coupled to N availability (Grogan and Zamin 2018), climate-induced changes to inorganic (NH_4^+-N, NO_3^--N) and organic N (amino acid) pools can directly alter ecosystem functioning, including changes in plant productivity and microbial respiration (Belay-Tedla and others 2009; Sistla and others 2012; Schaeffer and others 2013), or even lead to ecosystem loss of N through leaching or denitrification (Buckeridge and others 2010; Martinsen and others 2012) (Figure 3.1). Determining the effects of resource-consumer phenological mismatch on N cycling requires investigating shifts in the timing of the consumer (i.e., herbivory) and shifts in the timing of the resource (i.e., plant growing season) as separate temporal controls.

The first critical temporal controls are changes in the seasonal timing of herbivory (Clausen and Clausen 2013; Lameris and others 2017). Migratory geese, for example, are arriving earlier to their Arctic breeding grounds, but some species are not arriving early enough to match the advanced rate of plant green-up (Doiron and others 2015; Ross and others 2017). The timing of migratory goose arrival is expected to be particularly important to N cycling, especially in the coastal Arctic where geese occur at high densities and function as ecosystem engineers (e.g. Uher-Koch and others 2019). Goose herbivory has the ability to affect N cycling in three ways: the direct removal of aboveground tissue through grazing, the addition of soluble N through fecal deposition, and the trampling of standing dead litter into the soil promoting the turnover of organic material and rapid decomposition (Bazely and Jefferies 1989; Ruess and others 1997; Zacheis and others 2002). Previous work found that early goose grazing reduced above- and belowground plant biomass while later arrival and grazing had the opposite effect (Choi and others 2019). The changing arrival time of geese also alters the timing of goose fecal inputs, which can be an important source of soluble organic N (Henry and Jefferies 2002). Based on our understanding of how the timing of goose herbivory influences vegetation, and the ability of coastal graminoids to utilize amino acids and inorganic N forms (Henry and Jefferies 2003; Welker and others 2003), we predict that shifts in the timing of goose arrival have the potential to alter both organic and inorganic N availability (Figure 3.1).

The second temporal controls are changes in climate-driven shifts in the resource, most often through advancement of the growing season and resulting higher rates of soil N cycling (N mineralization [N_{min}], ammonification, denitrification) (Buckeridge and Grogan 2010; Bardgett and others 2013). Warmer soil temperatures from season advancement can stimulate microbial enzymatic activity (Sistla and Schimel 2013), which can increase soil NH_4^+-N and NO_3^--N pools, and gaseous N efflux (Blankinship and Hart 2012; Bai and others 2013). Earlier springs can also increase the labile organic N pool and amino acids (Darrouzet-Nardi and others 2019), which are an important source of N for coastal graminoids in Arctic systems (Henry and Jefferies 2003). However, advanced growing seasons also increase plant growth and demand (Lin and others 2010), thereby reducing N pools through greater plant uptake (Natali and others 2012) and microbial immobilization (Jonasson and others 1999). Because of the microbial response to earlier warmer temperatures and extension of the growing season, we predict that season advancement will mobilize more soil N than can be assimilated by plant growth.

There is a growing climate-driven phenological mismatch between the timing of herbivory by wild geese and the timing of the growing season, and a gap in our knowledge of how changes in the relative importance of these processes influence N cycling and soil N pools. To address this, we conducted a three-year field experiment that manipulated the timing of migratory goose arrival (early, typical, late, and no arrival) and the growing season (advanced and ambient). We then measured how the timing of these events and their interactions influence inorganic (NH_4^+-N, NO_3^--N) and organic (amino acid) soil N pools and N_{min} rates. We hypothesized that: H1) early goose arrival results in larger inorganic and organic N pools earlier in the season because early goose grazing reduces above- and belowground plant biomass (Choi and others 2019) and initiates earlier fecal inputs and trampling, while late migration has the opposite effect (Figure 3.1); H2) season advancement and associated early season soil warming stimulate microbial net N mobilization (i.e. the production and release of organic N and inorganic N_{min}), which outweighs any reduction from early season plant growth (Leffler and others 2019), and results in larger inorganic N pools compared to an ambient season; and H3) the interaction between earlier goose arrival and season advancement synergistically increase pools of inorganic and organic N because of the combined effect from warmer soil temperatures and earlier grazing, feces, and trampling.

Methods

Study site

We conducted this study near the Tutakoke River in the central coastal region of the Yukon-Kuskokwim (Y-K) Delta in western Alaska (61°15'N, 165°37'W; elevation 2 m). The Y-K Delta is over 125,000 km^2 of coastal tundra between the Yukon and Kuskokwim Rivers along the Bering Sea. We established experimental plots within 1 km of the coast in a wet sedge meadow on the active floodplain. Climate in the area is moderated by the Bering Sea with mean temperatures ranging from -14 to 10 °C in midwinter and summer, respectively (Jorgenson and Ely 2001).

Soils at our site are saturated and brackish, often mesohaline (8,000-30,000 µS cm^{-1}; 0.5-18 ppt), frequently inundated by monthly tides, and characterized by interbedded layers of silt and sandy loams (Jorgenson 2000). Permafrost, while found further inland, is not present in the active coastal floodplain. Soils are classified as histosols and have a bulk density of 0.69 g cm^{-3}, and 9.5% organic content consisting of 4.7% C and 0.3% N.

Carex graminoids are the dominant vegetation in the coastal Y-K Delta. *C. subspathacea*, in particular, is a critically important goose forage species, that occurs in near monotypic stands along the margins of ponds and tidal flats, and is so heavily grazed and modified by geese that when altered, it is referred to as 'grazing lawn' (Person and others 2003). Using the day of year when NDVI (normalized difference vegetation index) reaches 50% of its maximum as a vegetation phenology metric (Brook and others 2015), green-up has varied over 30 days (23-May to 25-June) over the last 35 years (1982-2016), but has occurred on average 0.3 days earlier per year (Leffler and others 2019).

Geese time their long-distance migration to optimize their nutrient demands with a narrow window of peak nutrient availability in the spring (Sedinger and Raveling 1986). Approximately 50% of the world's Pacific black brant (*Branta bernicla nigricans*) nest in the coastal Y-K Delta, with ca. 30-day variation in the range of hatch dates (3-June to 9-July) observed over 34 years (1983-2016) (Fischer and others 2008, 2017). However, the three years of our experiment (2014, 2015, 2016) had three of the earliest six hatch dates for black brant in the Y-K Delta, especially year 3 (2016), which was the earliest on record (Fischer and others 2017). At our site, there is a positive correlation between NDVI spring advancement and hatch date ($R^2 = 0.78$), but geese do not appear able to keep up with the timing of spring with migratory arrival occurring on average 0.14 days earlier per year (Fischer and others 2017).

Phenology experiment

We conducted a three-year fully factorial experiment simulating scenarios of phenological mismatch. This experiment has been used to investigate changes in greenhouse gas flux (Kelsey and others 2018; Leffler and others 2019), forage quality (Beard and others 2019a) and plant traits (Choi and others 2019) and is described in those studies. Briefly, we used four timings of grazing (early, typical, late, and no-grazing) crossed with two timings of the growing season (advanced and ambient) for a total of eight treatments. We altered the timing of goose grazing by minus-three, zero, and plus-three weeks (early, typical, and late treatments, respectively), and advanced the growing season by three weeks (see below). The 'typical' goose treatment represented historic mean arrival and grazing and acted as the grazing treatment control, while the 'no-grazing' treatment represented potential future scenarios where goose populations decline to near zero or fail to arrive. We also had a background grazing control plot in each block that was used to compare the effectiveness of our experimental grazing, but not as a statistical comparison for our treatments. Thus, we had a total of 54 plots in six replicate blocks located within 700 m. All plots were established in April 2014 and were 1.7 m x 0.85 m in size. We installed fencing around all paired advanced and ambient growing season plots, except the background grazing control, to exclude wild goose grazing. Treatments were assigned randomly and applied to the same plots from 1-May through 15-August each year.

We manipulated timing of grazing by introducing wild-caught geese into fenced goose exclosures (ca. 7.6 m^2) at specific times during the season. Early, typical and late grazing treatments began on 30-May, 20-June, and 9-July, respectively, to approximate the 30-day variation in the range of historic mean hatch dates (3-June to 9-July) (Fischer and others 2017). These dates are the biologically relevant means for our system and allowed us to use actual geese (as opposed to simulated grazing) in our experiments, which required treatments to start after nest initiation so they could be captured. Aboveground biomass in background control plots did not differ from typical grazing plots in years 1 and 2 or early goose grazing plots for all three years (Choi and others 2019). Because the experiment coincided with three of the six earliest mean hatch dates in the Y-K Delta over the last 34 years and the last year of our experiment was the earliest on record (Fischer and others 2017), we expected that background controls would be more similar to early goose grazing treatments by year 3.

Grazing treatments only differed in the timing of grazing initiation; we kept total grazing time constant among treatments. While earlier shifts in migratory goose arrival might result in a longer available season for grazing, the duration of time spent on *Carex* grazing lawns is constrained by the development time of goslings, typically ca. 40 days (Sedinger and others 2001). Furthermore, differences in timing of grazing treatments are attributed to the timing of grazing initiation, and not variation in the duration of grazing. Experimental grazing treatments (early, typical, and late grazing) consisted of two brant geese grazing, trampling and defecating inside exclosures during four 24 h bouts separated by 12 days over a total of 37 days to simulate post-hatch grazing. Unlike other goose species in the Y-K Delta, black brant are grazers and do not grub during the summer (Sedinger and Raveling 1984). Prior to each grazing treatment, we held geese for two hours without food to allow feces from captive feeding to pass through their digestive system. After each 24 h grazing treatment, we held birds for an additional two hours to collect feces which were returned to the appropriate plots. In between grazing treatments, we held geese in a fenced enclosure and allowed them to graze freely on natural vegetation, supplemented *ad libitum* with commercial goose feed. Captive geese were released into the wild at the end of each season.

We used two adjacent conical passive-warming open-top chambers (OTCs; 30 cm height x 85 cm base dia. x 50 cm top dia.) to initiate an earlier growing season in the advanced season plots. We placed OTCs on plots from 1-May to 1-July, and removed them only during goose grazing treatments. We monitored air and soil temperature (10 cm above- and belowground) inside and outside OTCs in every plot each growing season. These OTCs doubled mean vegetation height and advanced the growing season by 22, 18, and 21 days by the end of June 2014, 2015, and 2016, respectively (Leffler and others

2019). OTCs warmed plots on average between 0.6 and 1.7 °C (aboveground) and 0.6 and 1.0 °C (belowground).

Soil N measurements

We measured inorganic (NH_4^+-N, NO_3^--N) and organic N (amino acids) and N mineralization in all treatments of the experiment. Inorganic N (NH_4^+-N, NO_3^--N) was measured via two methods, while organic N (amino acids) was measured via one method over three years. N_{min} was measured only during the third year of the experiment.

We used ion-exchange resin strips (2.5 cm wide x 10 cm length; CR67 & AR204SZRA, General Electricals, Watertown, MA) to measure inorganic N (NH_4^+-N, NO_3^--N) available to adsorb to soil particles (Qian and Schoenau 1995). We prepared cation and anion strips separately using the same procedure. We immersed and shook strips in baths of 0.5 M HCl for 1 h and 0.5 M $NaHCO_3$ for 5 h, and then washed and stored them with deionized water. In the center of each plot, we installed six to eight cation and anion resin pairs vertically 10 cm into the ground until the top was even with the surface of the soil. We collected resins every two weeks, each time yielding a cumulative measure of adsorbed inorganic N. Upon collection, we froze all resins in the field. In the laboratory, we washed all resins using 50 mL of 2M KCl and froze extracts until analysis.

Because some of our plots experienced seasonal inundation during high tide events, we used an additional resin approach to measure soil inorganic N. Seawater has a high ionic potential and tidal flooding can interfere with measurements by striping resin ion-exchange sites of adsorbed inorganic N (McBride 1989). High spring tides flooded and inundated several experimental blocks each season (Julian date 2014 (205), 2015

(186), 2016 (185, 210)), which corresponded with a drop-off in resin-collected N on strips that remained *in situ* (Figure 3.2). To address this problem in years 2 and 3, we installed intertidal resin sets for three weeks between monthly peak tides, determined from regional NOAA tide predictions (Dall Point, AK; tidesandcurrents.noaa.gov), and collected pairs from plots before the next peak tidal event. Both cumulative and intertidal resin incubations had their own strengths and results show similar trends, so we present both datasets for completeness. Resin measurements represent N adsorption by soil ion-exchange sites over time, and separate resin collections are referred to as either 'cumulative' or 'intertidal'.

We used microlysimeters to measure labile inorganic (NH_4^+-N, NO_3^--N) and organic N (amino acids) pools in soil pore water. At the center of each plot, we installed a single 10-cm rhizon soil moisture microlysimeter (Eijkelkamp, Giesbeek, Netherlands) perpendicular into the soil surface and left them in place over the season. We used plastic syringes to collect 10 mL pore water samples from the top 10 cm of soil every two weeks, and used 1µm, 25-mm diameter Acrodisc glass fiber syringe filters (Pall Laboratory, Port Washington, NY) to pre-filter soil pore water before storing and freezing samples until analysis. Microlysimeter measurements represent labile N available in soil pore water at the time of collection.

During the final year of the experiment, we measured net N_{min} rates in each experimental plot ($n = 54$) using the buried bag technique (Robertson and others 1999). On 1-June, we took two, 4-cm diameter cores from the top 10 cm of soil in each plot. We collected one core and placed the other intact in a polyethylene bag and buried it *in situ* until 1-August. We homogenized, sieved, and extracted both cores within 24 h of collection. From each core, we extracted 10 g of root-free soil in 50 mL of 2M KCl, filtered, and froze samples until analysis. We calculated net N_{min} (μg N g-dry soil^{-1} d^{-1}) as the difference in total NH_4^+-N and NO_3^--N between the initial harvest and final harvest divided by the total number of days *in situ*.

We analyzed filtrate from resin extracts, microlysimeter samples, and N_{min} measurements using colorimetric (NH_4^+-N, NO_3^--N) or fluorometric (amino acid) microplate assays. We used the Berlethot reaction for NH_4^+-N (Rhine and others 1998) and the Griess reaction for NO_3^--N (Doane and Horwáth 2003). We measured organic N (amino acid) using fluorescence of samples with *o*-phthaldialdehyde and β-mercaptoethanol (Jones and others 2002). Absorbance and fluorescence values were measured with a Synergy^{TM} H4 Hybrid Multi-Mode Microplate Reader (Bio-Tek Inc., Winooski, VT) at Utah State University.

Statistical analysis

We tested the effects of timing of goose grazing (early, typical, late, no-grazing) and timing of the growing season (advanced, ambient) on soil N availability. We used NH_4^+-N, NO_3^--N and amino acids, and N_{min} measurements as continuous response variables, experimental treatments (timing of goose grazing, start of the growing season), sampling date, and year as fixed-effect predictor variables, and treated plot nested within block as a random effect. Separate models were used for each measured N pool (cumulative and intertidal resin NH_4^+-N and NO_3^--N, and microlysimeter NH_4^+-N, NO_3^--N, and amino acids). We tested distributions of continuous variables for normality and homogeneity of variance, and log-transformed all predictor variables prior to analysis to meet these assumptions. We coded ambient season and typical grazing plots as the reference comparison for the growing season and grazing season treatment, as appropriate. Our models included interactions of fixed-effect predictors, but we limited interactions to combinations of no more than two variables. We determined variable importance by inclusion in the top-performing model. We included a first-order autocorrelation structure to account for repeated measures within subjects over time.

For all analyses, we used a linear mixed model framework with model selection and Akaike Information Criteria (AIC). We fit all models using the nlme package within the R statistical computing environment (Pinheiro and others 2017, R Core Development Team). We selected top models based on ΔAIC and considered models to be similar if $\Delta AIC<2$ (Burnham and others 2011). Using the nlme summary function, we determined the fixed effect parameter estimates for top model variables that were statistically different from the reference intercept (ambient season, typical grazing) (Table B1 in the appendices). For simplicity and to capture the effects after three years of experimental treatments, we present soil N percent change as the mean across the last year of the experiment unless otherwise indicated.

Results

Across all N pool measurements, both timing of grazing and timing of season were included in the top models highlighting the strength of timing of goose herbivory and season advancement treatments on soil N availability (Table 3.1). There were no interactions between the timing of grazing and timing of season in any of our top models.

Cumulative and intertidal ion-exchange resins and soil pore water in early grazing plots had 62%, 21% and 103% more NH_4^+-N, respectively, compared to typical grazing treatment (Figures 3.2-3.4). Intertidal resins had 16% less NH_4^+-N available in late grazing than typical grazing treatments (Figures 3.3A-B). Comparatively, the advanced growing season had a 2% and 26% increase in intertidal and soil pore NH_4^+-N pools, respectively, compared to the ambient treatment by year 3 (Table B1 in the appendices). The top-ranking models for resin-adsorbed soil NH_4^+-N included year, season advancement, and an interaction between timing of grazing and sampling date, whereas top-ranking models for NH_4^+-N in soil pore water included timing of grazing, season advancement, and an interaction between year and sampling date (Table 3.1).

Early grazing had seasonal peaks in intertidal resin-adsorbed NH_4^+-N that coincided with early grazing treatments (~30-May to 10-July), ~30 days earlier than typical grazing. Similarly, late grazing delayed seasonal peak intertidal resin-adsorbed NH_4^+-N by ~20 days later in the season compared to typical grazing plots (Figures 3.3A-B), which coincided with the timing of late grazing treatments (~9-July to 15-August). Unlike early grazing, an advanced growing season did not shift the peak timing of soil NH_4^+-N available for biological assimilation.

Cumulative resin-adsorbed NO_3^--N declined while intertidal resin and soil pore NO_3^--N increased across the three years. Top models for resin-adsorbed and soil pore NO_3^--N all included timing of grazing, season advancement, and year, or an interaction between timing of grazing or year, and sampling date (Table 3.1). Intertidal and soil pore NO_3^--N increased 139% and 119% in the early grazing treatment compared to typical grazing treatment, while cumulative resin-adsorbed NO_3^--N decreased by 17% in late grazing treatment (Figures 3.2-3.4, Table 3.2). Intertidal resins also had 51% more NO_3^--N in no-grazing treatment than typical grazing plots in the last year of the experiment, but had 21% less NO_3^--N in the same plots the previous year (Figures. 3.3C-D, Table 3.2). While season advancement was found in all the top models, it was not significant (Table B1 in the appendices).

Experimental treatments had no measurable effect on net N_{min} rates in year 3. The top models for both net N_{min} NH_4^+-N and NO_3^--N either included just season advancement or the null model (Table 3.1). In general, the advanced growing season decreased N_{min} rates for NH_4^+-N and NO_3^--N by 176% and 8%, respectively; however, these effects were not significant (Table B1 in the appendices). Across all plots, mean net N_{min} rates were 0.10 ± 0.24 µg NH_4^+-N g-dry soil^{-1} d^{-1} and 0.22 ± 0.07 µg NO_3^--N g-dry soil^{-1} d^{-1}, or a total of 0.31 ± 0.25 µg inorganic N g-dry soil^{-1} d^{-1}.

Amino acids increased by 7% in the early grazing treatment compared to the typical grazing treatment, with peaks in availability observed early in the growing season (Figures 3.4G-I). The top model for soil pore amino acid concentrations included timing of grazing and an interaction between year and sampling date, while the second-ranked model with $\Delta AIC<2$ also included season advancement (Table 3.1). While season advancement was included in the second-ranked model, it was not significant (Table B1 in the appendices).

Discussion

Our experimental results suggest that the timing of migratory goose grazing (i.e. goose arrival date) has a greater impact on soil N availability than advancement of the growing season in this N-limited coastal ecosystem. Early goose grazing had the greatest measurable effect on soil N by increasing both inorganic and organic soil N pools. Season advancement also increased soil NH_4^+-N availability, but compared to early grazing only had a limited effect on soil N pools, despite a similar three-week shift in timing (Figure 3.5). Furthermore, there was no synergistic interaction between timing of goose arrival and timing of spring advancement on soil N availability. Our findings suggest that in coastal western Alaska, where migratory geese are arriving earlier into a phenologically advanced system, soil N availability will increase. Larger soil N pools are important for plant nutrient availability, and even short-term impacts on soil N pools can have lasting effects on forage quality (Ruess and others 2019), or alter plant community composition and productivity (Ruess and others 1997; Boyer and Zedler 1999). These shifts in N may facilitate shifts from graminoid to shrub-dominant vegetation, resulting in a reduction of *Carex* grazing lawns and goose forage resources (Myers-Smith and others 2011; Carlson and others 2018). Finally, increased N availability can also result in the greater likelihood of N leaching and potential loss (Jonasson and others 1999).

Soil inorganic N response to timing of grazing treatments

Our findings support hypothesis (H1) that timing of grazing can affect inorganic soil N pools (NH_4^+-N, NO_3^--N), and early grazing had the greatest impact (Figure 3.5). More specifically, early grazing increased resin-adsorbed and soil pore NH_4^+-N availability, which suggests the long-term and short-term influence of this treatment on the different extractable pools. Late grazing also influenced soil N, primarily by reducing intertidal resin-adsorbed NH_4^+-N but not soil pore NH_4^+-N (Table 3.2), which suggests that the draw down may have taken time (up to three weeks for intertidal resins) for effects to accumulate. By delaying peak NH_4^+-N availability and storing N in plant tissues, late grazing retains N in the system and returns it slowly through decomposition and microbial turnover, reducing the potential for N leaching and loss.

Similar to soil NH_4^+-N, our findings supported hypothesis (H1) that the timing of grazing also affected NO_3^--N pools. Changes in pool sizes of NH_4^+-N with both early and late grazing resulted in similar relative changes in NO_3^--N with the same treatment. However, overall NO_3^--N concentrations observed across all treatments were 10 times lower than NH_4^+-N. We offer four potential mechanisms for this pattern. First, NO_3^--N is highly mobile in the soil and easily lost through leaching or uptake by plants (Miller and Cramer 2005). Second, saturated soils and low O_2 conditions can limit rates of aerobic nitrification (White and Reddy 2003). Third, the anaerobic microbial dissimilatory nitrate reduction to ammonium pathway, a process that converts NO_3^--N back into NH_4^+-N and occurs in highly reducing environments or flooded soils, may have suppressed NO_3^--N accumulation (Giblin and others 2013). Finally, it is also possible that NO_3^--N produced in the soil can be denitrified (Tiedje 1988); however, concurrent measurements in our experimental plots found no significant N_2O gaseous efflux from our ecosystem (Kelsey and others 2018), suggesting that this is an unlikely pathway.

Soil inorganic N response to season advancement

Our results support hypothesis (H2) that, by stimulating microbial activity through warmer early season conditions, season advancement increased soil NH_4^+-N pools in excess of any increased plant uptake. Similar to other studies investigating season advancement (Borner and others 2008; Buckeridge and others 2010; Rogers and others 2011), we found a moderate effect of an advanced growing season on soil NH_4^+-N. Season advancement also increased soil respiration in our experimental plots (Leffler and others 2019), which suggests that higher rates of microbial N cycling contributed to N pools. Despite having a similar shift in timing of grazing (+3 weeks), this increase was less than the effect of early grazing, which had a four-fold increase in soil pore NH_4^+-N (Table 3.2), and highlights the importance of earlier migratory arrival at our site. While an advanced growing season increased NH_4^+-N, it did not result in a significant increase in NO_3^--N pools, likely due to the anaerobic suppression of nitrification in saturated soils earlier in the season.

N mineralization response to treatments

We found that N_{min} had no measurable response to an advanced season or timing of grazing treatments and was highly variable among plots, which refutes hypotheses (H1 & H2) that earlier grazing and an advanced growing season stimulated net N mobilization. Others have found that N_{min} rates were not affected by vegetation clipping treatments in *Carex* grazing lawns at our site (Person and Ruess 2003) or by goose grazing in the Hudson Bay (Wilson and Jefferies 1996). Studies reporting increases in N_{min} from experimental warming had soil temperature increases of 1-3 ºC (e.g. DeMarco and others 2011), suggesting that perhaps our season advancement treatments (0.6 to 1.0 ˚C at 10 cm belowground only for the first half of the season) were insufficient to increase season-long rates of N_{min} and production. The lack of an N_{min} response suggests that the observed changes in N pools from timing of grazing and season advancement were likely driven by plant uptake or microbial immobilization.

Soil organic N pool response to treatments

Our findings support our hypothesis (H1) that early grazing increases organic N (amino acid) concentrations (Figures 3.2G-H). Early peaks in amino acids were observed in all treatments and may have resulted from the post-melt release of organic N from the lysing of root and microbial cells during freeze/thaw events in the fall and early spring (Grogan and others 2004). The rapid decline in amino acid concentrations early season coincided with the uptake of available N by roots for plant growth, as suggested by others in high latitude systems (Weintraub and Schimel 2005; Edwards and others 2006), and likely occurred to a lesser degree in the early grazing treatment due to reduced plant growth (Choi and others 2019). Because microlysimeters measured labile inorganic and organic N available in soil pore water (Darrouzet-Nardi and Weintraub 2014), the observed season-long draw down of the organic N pool suggests that plants and microbes are utilizing the most easily available limiting resources (Hobbie and Hobbie 2012) (Figures 3.2G-I).

N pathways

We propose that reduced plant uptake was the primary mechanism driving the increase in available soil N in the early grazing treatments. Although grazing has the potential to stimulate graminoid productivity through compensatory growth (Grogan and Zamin 2018), in our treatments early grazing reduced above- and belowground biomass by 52% and 55%, respectively, while late grazing increased inflorescences and dead biomass by 515% and 569%, respectively (Choi and others 2019), compared to typical grazing plots (Figure 3.5). These grazing effects had lasting legacy effects on plant productivity in subsequent seasons (Choi and others 2019), which corresponded with changes in soil N availability by the end of our three year experiment.

It is possible that other mechanisms contributed to the observed increases in soil N availability. In northern latitudes where geese are the dominant herbivores, feces are thought to be important sources of soil N (Bazely and Jefferies 1985). Research conducted in another Arctic coastal system detected amino acid signatures of goose feces in the soil profile (Henry and Jefferies 2002), and plant foliar $\delta^{15}N$ from our early grazing treatments had enriched $\delta^{15}N$ values (3.3‰) that more closely matched the values of goose feces (3.7‰), as opposed to late and no-grazing treatments (2.7‰ and 2.1‰, respectively) (Beard and Choi 2017). Because of the non-mycorrhizal nature of graminoids (Welker and others 2003; Craine and others 2009), changes in leaf $\delta^{15}N$ of *Carex* species are often due to shifts in N sources, such as herbivore N inputs (Sjögersten and others 2010), and the observed changes are likely indicative of substantial N recycling between geese and plants.

Although it is likely that geese are important sources of N for plants, the effect of goose feces on N pool sizes remains unclear. An experiment at our site that manipulated goose fecal densities on *Carex* grazing lawns by creating plots with double, ambient, and no feces found no changes in inorganic or organic soil N availability using the same N collection methods used in the present study (Beard and Choi 2017). Further, changes in fecal density did not change *Carex* biomass or forage quality (Beard and Choi 2017). Observations of goose feces at our site suggest that pellets often dry up and are not incorporated into the soil through trampling, while frequent flooding and high tide events redistributed or removed 85-90% of feces (Beard and Choi 2017). Because soluble N rapidly declines in goose feces after deposition (Bazely and Jefferies 1985), we speculate that a portion of N volatilizes into the atmosphere. While we believe that goose feces play a role in soil N availability, the magnitude of its influence on soil N pools at our site still warrants further investigation.

Treatment interactions

While both early grazing and an advanced growing season, in general, increase N availability in soil pools, there were no observed interactions between timing of grazing and timing of season treatments (H3). It is possible that the compensatory growth response of *Carex* grazing lawns to early goose herbivory, in particular because of the increased soil N availability (Grogan and Zamin 2018), may have dampened the increase in N availability from early grazing and the advanced season (Choi and others 2019). Alternatively, while warmer temperatures and reduced leaf shading seemed to increase N mobilization, these conditions also likely lowered soil water content, thereby limiting rates of microbial decomposition and accumulation of inorganic N pools (Skopp and others 1990). Because both earlier goose arrival and advancing green-up are occurring at our site, our findings suggest that there will be additive, but not synergistic, increases in soil N availability.

Soil N collections and limitations

The different methods of N measurements we employed captured different aspects of the available soil N pools. We used microlysimeters to measure the labile soil pore N pools at biweekly intervals and this N was more sensitive to short-term differences in availability, compared to the less frequently collected ion-exchange resins that accumulated changes in soil adsorbed N over time. Of the resin measurements, it is not surprising that intertidal resins detected a stronger response to grazing treatments given that they were designed to reduce interference from tidal inundation. Because N availability in northern coastal systems has high temporal and spatial variability (McLaren and others 2017; Darrouzet-Nardi and others 2019), our relatively high frequency of measurements and multiple approaches helped improve our understanding of soil N fluctuations and availability across the growing season.

Conclusion

Climate-driven advances in spring green-up and goose arrival are occurring in the Y-K Delta. While both earlier growing seasons and earlier goose arrival result in increased soil NH_4^+-N availability, the effect of season advancement was less than that of early goose grazing, even though both treatments were earlier by about three weeks. Our findings suggest that climate-driven changes in the timing of migratory goose arrival has important top-down control on the timing and availability of N, which is a critical limiting resource in this northern coastal wetland. While larger soil N pools are important for plant nutrient availability, they can also result in a greater likelihood of leaching and potential loss. If these earlier migratory patterns persist, greater soil N availability is also likely to result in altered vegetation community composition and potential loss of goose forage resources.

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Tables

Table 3.1. Top four performing models for soil N response variables based on AIC model selection for experimental treatments over three years (2014-16). Abbreviations: Grazing = timing of goose grazing treatment, Season = season advancement treatment, Date = sampling date. Models with interaction terms imply inclusion of the main effect. Bolding indicate top models with ΔAIC<2.

Model	logLik	AIC	ΔLogLik	ΔAIC	df	weight
Cumulative resin NH_4^+-N						
Year + Grazing*Date	-1155.1	2338.3	111.2	0.0	14	0.564
Year + Grazing*Date + Season	-1154.4	2338.8	112.0	0.5	15	0.434
Year*Date + Grazing	-1162.3	2350.6	104.0	12.3	13	0.001
Year*Date + Grazing + Season	-1161.6	2351.1	104.8	12.9	14	<0.001
Intertidal resin NH_4^+-N						
Year + Grazing*Date + Season	-404.7	837.5	84.6	0	14	0.923
Year + Grazing*Date	-408.2	842.5	81.1	5	13	0.077
Year*Season + Grazing + Date	-426.0	876.1	63.3	38.6	12	<0.001
Year*Grazing + Season + Date	-424.1	876.1	65.3	38.6	14	<0.001
Microlysimeter NH_4^+-N						
Year*Date + Grazing	-1360.2	2746.5	24.9	0.0	13	0.323
Year*Date + Grazing + Season	-1359.7	2747.4	25.5	0.9	14	0.206
Year*Date	-1364.0	2748.0	21.2	1.5	10	0.152
Year*Date + Season	-1363.5	2749.1	21.6	2.6	11	0.088
Cumulative resin NO_3^--N						
Year*Date + Grazing	-1239.7	2505.3	184.6	0.0	13	0.723
Year*Date + Grazing + Season	-1239.7	2507.3	184.6	2.0*	14	0.267
Year*Date	-1247.2	2514.5	177.0	9.2	10	0.007
Year*Date + Season	-1247.2	2516.5	177.0	11.2	11	0.003
Intertidal resin NO_3^--N						
Year + Grazing*Date	-390.1	806.1	56.6	0	13	0.369
Year*Date + Grazing	-392.6	807.3	54.1	1.1	11	0.211
Year + Grazing*Date + Season	-390.1	808.1	56.6	2.0*	14	0.136
Year*Date + Grazing + Season	-392.6	809.2	54.1	3.1	12	0.078

Microlysimeter NO$_3^-$-N						
Year*Date	-1498.3	3016.6	50.2	0.0	10	0.380
Year*Date + Season	-1497.6	3017.3	50.8	0.7	11	0.270
Year*Date + Grazing	-1495.9	3017.9	52.5	1.3	13	0.200
Year*Date + Grazing + Season	-1495.3	3018.6	53.2	1.9	14	0.150
N-mineralization NH$_4^+$-N						
Season	-13.6	37.3	1.6	0.0	5	0.543
Null model	-15.3	38.5	0.0	1.3	4	0.291
Grazing + Season	-12.2	40.4	3.1	3.1	8	0.114
Grazing	-14.2	42.4	1.0	5.2	7	0.041
N-mineralization NO$_3^-$-N						
Null model	8.7	-9.3	0.0	0.0	4	0.638
Season	8.7	-7.4	0.0	1.9	5	0.242
Grazing	9.6	-5.1	0.9	4.2	7	0.079
Grazing + Season	9.6	-3.2	0.9	6.2	8	0.029
Microlysimeter amino acids						
Year*Date + Grazing	-1290.6	2607.3	99.2	0.0	13	0.504
Year*Date + Grazing + Season	-1290.0	2608.0	99.8	0.7	14	0.349
Year*Date	-1295.4	2610.8	94.4	3.5	10	0.086
Year*Date + Season	-1294.8	2611.5	95.1	4.2	11	0.061

Table 3.2. Mean percent changes in soil N by treatment for each year. The reference level was the ambient growing season or typical grazing timing treatment, respectively. Abbreviations: Early = early grazing, Late = late grazing, None = no-grazing, Advanced = advanced growing season treatment. Bolding indicates treatment effect with $p<0.05$; (*) indicates sampling date interaction.

	Cumulative resin			Intertidal resin			Microlysimeter		
	NH_4^+-N			NH_4^+-N			NH_4^+-N		
Effect	2014	2015	2016	2014	2015	2016	2014	2015	2016
Early	**128%**	**44%**	**62%***	-	**32%**	**21%***	**112%**	**88%**	**110%**
Late	-28%	-32%	-26%	-	**-1%**	**-16%***	39%	11%	1%
None	-44%	-51%	-43%	-	-57%	-48%	75%	-3%	-22%
Advanced	5%	-7%	-15%	-	**-13%**	**2%**	**29%**	**19%**	**26%**

	Cumulative resin			Intertidal resin			Microlysimeter		
	NO_3^--N			NO_3^--N			NO_3^--N		
Effect	2014	2015	2016	2014	2015	2016	2014	2015	2016
Early	28%	11%	-10%	-	**49%**	**139%**	**55%**	**3%**	**119%**
Late	**-28%**	**-28%**	**-17%**	-	-21%	39%	33%	14%	39%
None	-2%	-28%	-41%	-	**-21%**	**51%***	8%	14%	34%
Advanced	-17%	-4%	32%	-	-4%	9%	22%	-3%	7%

	N-mineralization			N-mineralization			Microlysimeter		
	NH_4^+-N			NO_3^--N			amino acids		
Effect	2014	2015	2016	2014	2015	2016	2014	2015	2016
Early	-	-	-1706%	-	-	161%	**23%**	**7%**	**7%**
Late	-	-	1387%	-	-	113%	-28%	-9%	-4%
None	-	-	1279%	-	-	8%	-18%	-31%	-1%
Advanced	-	-	-176%	-	-	-8%	-17%	-15%	-6%

Figures

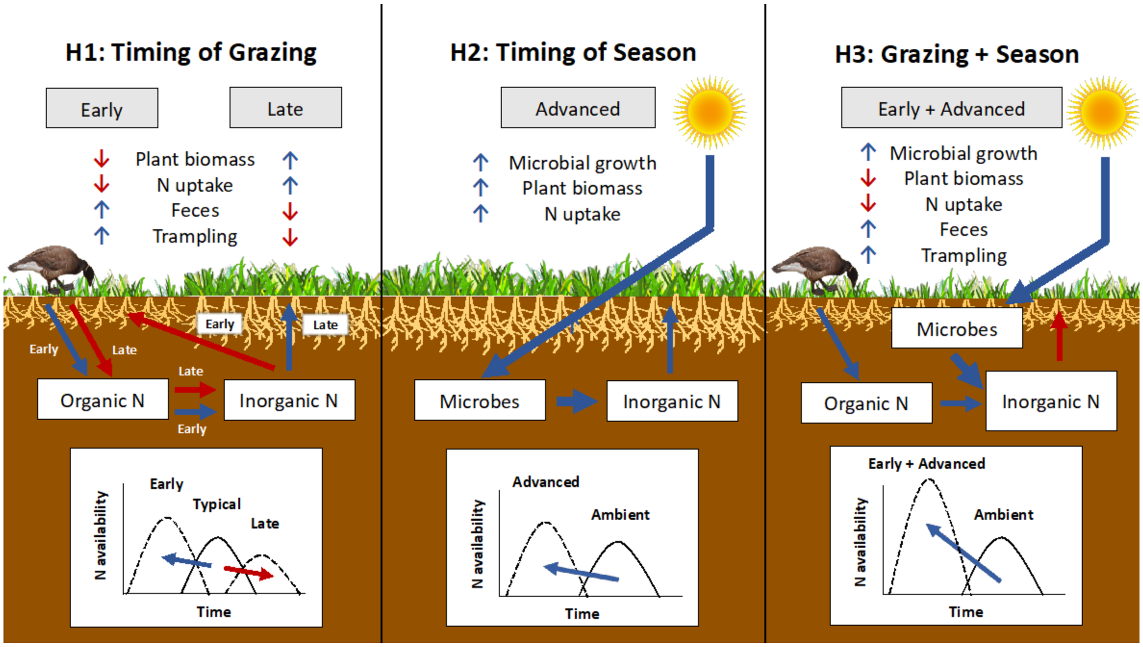

Figure 3.1. Conceptual figure of experimental hypotheses (H1, H2, H3) regarding the influence of the timing of goose grazing and the start of the growing season and their interaction on soil N availability. Arrows indicate hypothesized influence on N pools; blue arrows indicate positive effects and red arrows indicate negative effects. Goose herbivory removes aboveground tissues and hence decreases plant N uptake, while trampling and fecal deposition increase N availability; an advanced spring with warmer soil temperatures stimulates earlier plant and microbial growth; the interaction increases N availability due to increase microbial activity with less aboveground biomass to increase N uptake. Sub-figures are the hypothesized directional response of treatments on soil N availability.

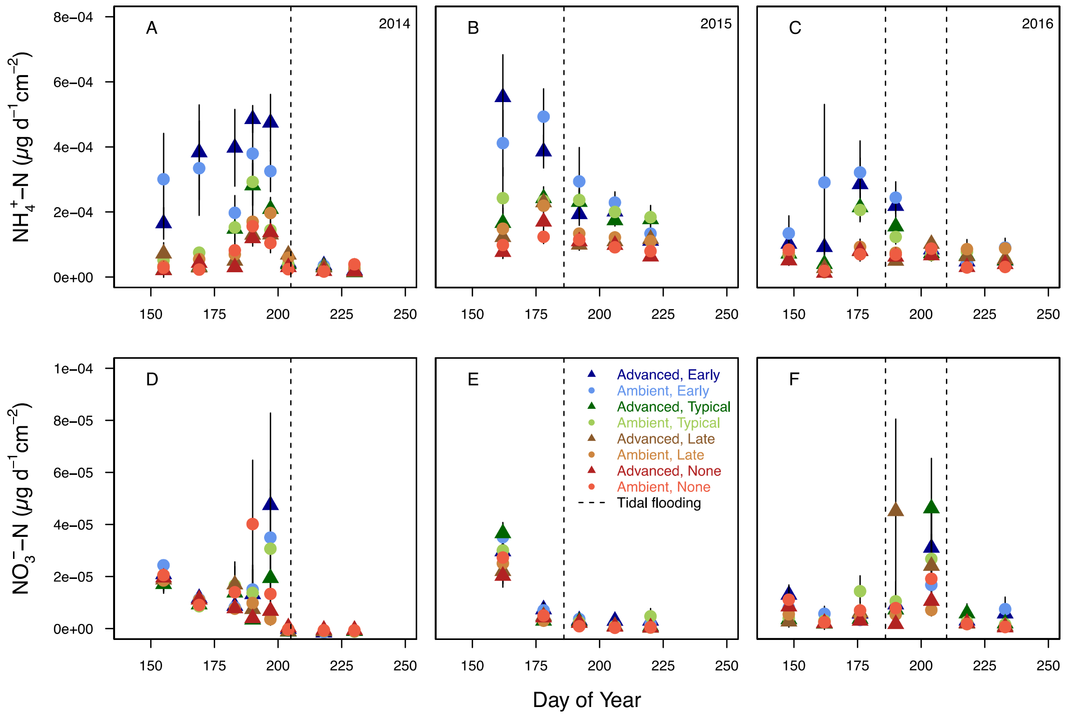

Figure 3.2. Mean cumulative resin NH_4^+-N and NO_3^-- N (µg d^{-1} cm^{-2}) (± 1 SE) from experimental timing of grazing and season advancement treatments. Panels A, B, C, and D, E, F represent data collected from 2014, 2015, and 2016, respectively. Dotted lines represent high tide events that flooded plots and *in situ* resins (Julian dates 2014 (205), 2015 (186), 2016 (186, 210)).

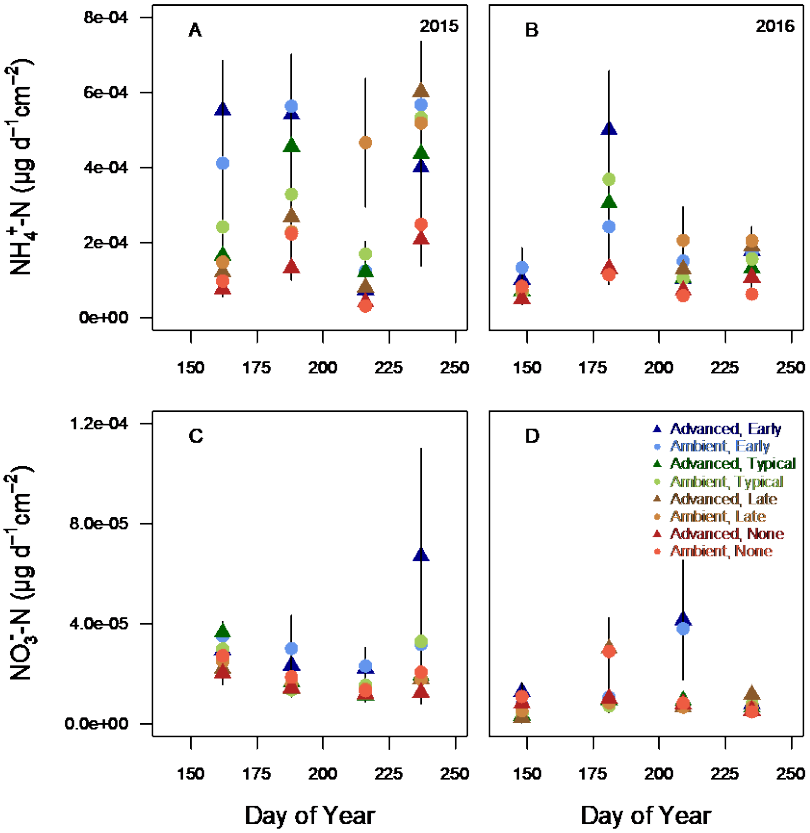

Figure 3.3. Mean intertidal resin NH_4^+-N and NO_3^-- N (μg d^{-1} cm^{-2}) from experimental timing of grazing and season advancement treatments. Because cumulative resins experienced coastal flooding, intertidal resins collected soil inorganic N during periods in between monthly tidal inundation to avoid ionic loss of N from resins *in situ*. Panels A, B and C, D represent data collected from 2015 and 2016, respectively. Error bars are ± 1 SE (n=6 replicates).

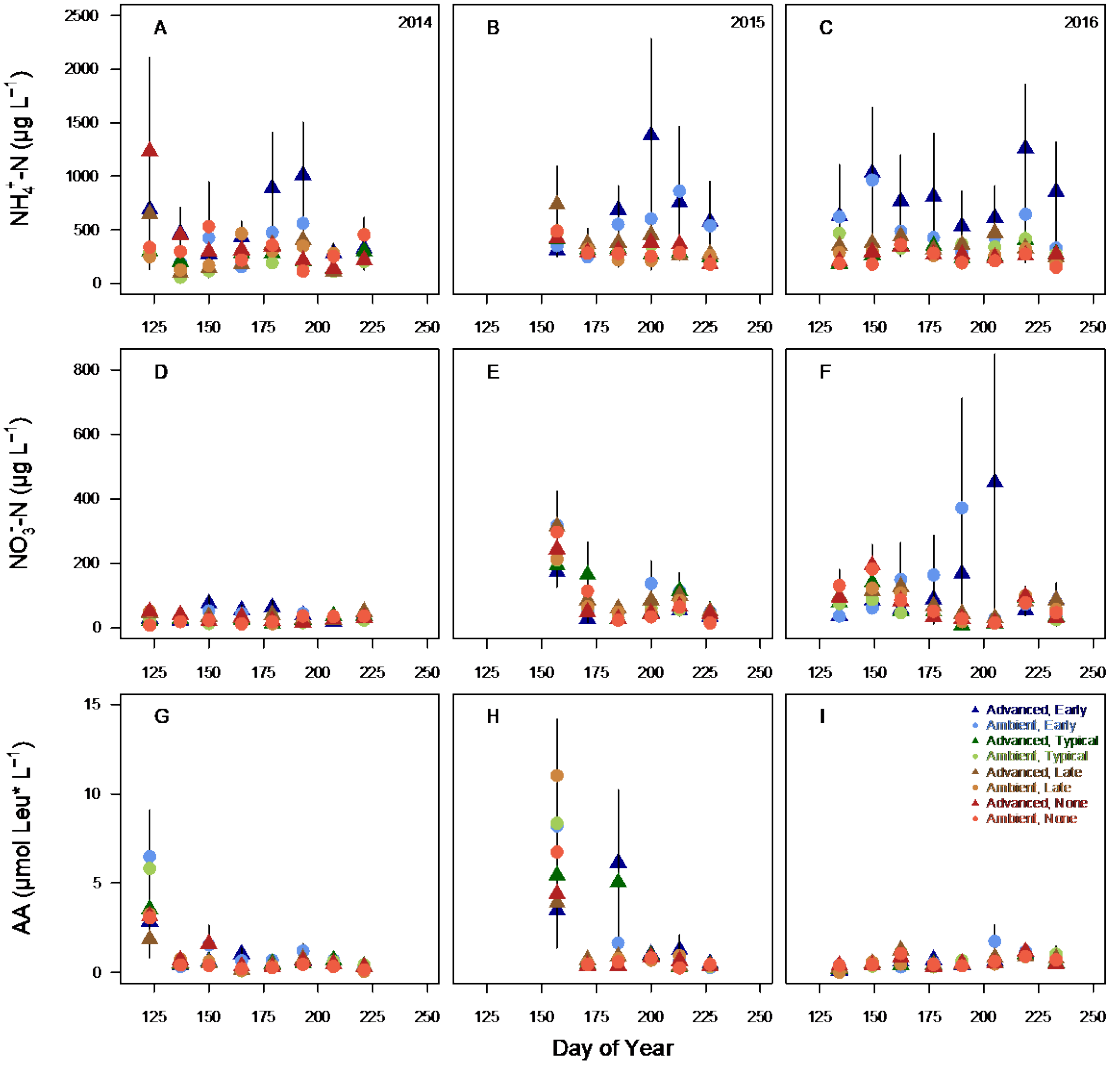

Figure 3.4. Mean microlysimeter NH_4^+-N and NO_3^--N (µg L^{-1}) and amino acids (AA) (µmol L^{-1}) (± 1 SE) from soil pore water for treatment plots. Panels A, B, C, and D, E, F, and G, H, I represent data collected from 2014, 2015, and 2016, respectively. Leu* = Leucine equivalent.

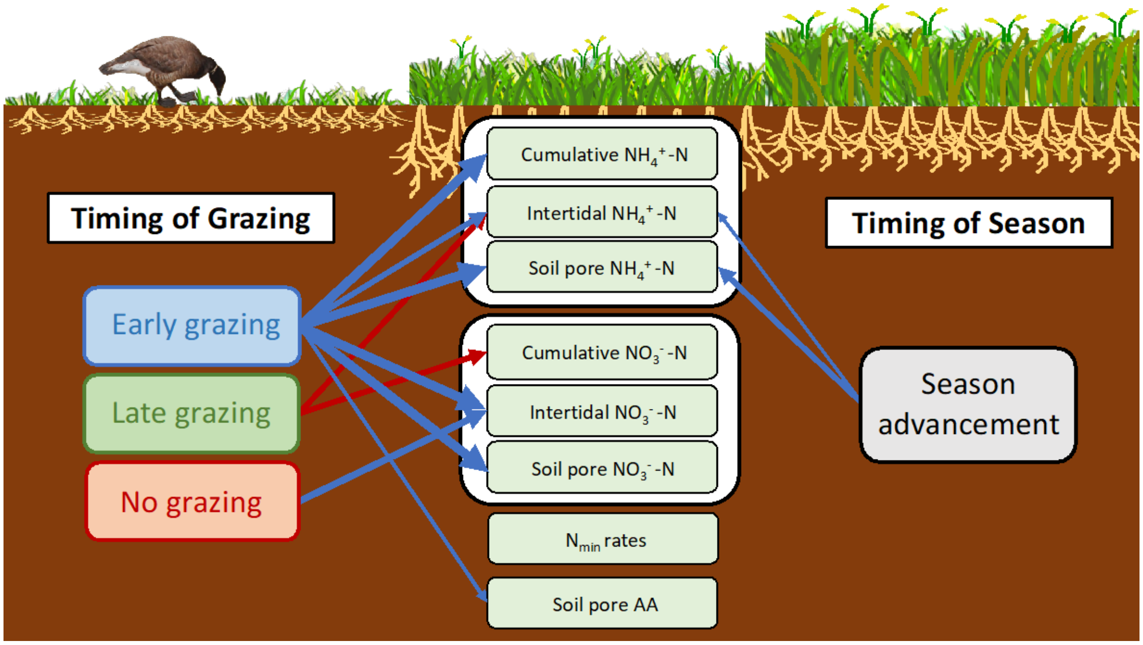

Figure 3.5. Conceptual figure of experimental treatments (timing of grazing and season advancement) on soil N measurements (cumulative and intertidal resins, and microlysimeter pore water) compared to typical grazing and ambient season treatments after three years. Arrow thickness indicates relative treatment effect size. Blue arrows indicate a positive effect; red arrows indicate a negative effect. Measurements without arrows had no significant measured treatment effect. Depicted above- and belowground vegetation represent actual measurements from early grazing and season advancement treatments, respectively (Choi and others 2019).

CHAPTER 4

CLIMATE-INDUCED CHANGES ALTER COASTAL WETLAND PLANT COMMUNITIES[3]

Abstract

Question: Warming temperatures are altering herbivore distributions and affecting plant communities throughout the Arctic. While grazing often increases species diversity and changes functional group composition, higher temperatures can have the opposite effect, and interaction between these factors complicate predictions about how communities will change in the future. How these forcings influence northern latitude wetland plant communities is particularly important because these systems are highly threatened by changes in grazing pressure and increasing temperature in the future.

Location: Yukon-Kuskokwim Delta, Alaska.

Methods: We conducted a two-year experiment where we applied goose grazing and warming treatments in three coastal wetland plant communities that were located along a 6-km transect from the coast moving inland. We measured percent cover to determine how treatments influenced measures of community diversity, functional group and species composition, and if these effects change among communities.

Results: Across all three coastal communities, both grazing and warming increased species richness, and warming caused a greater increase. Grazing also increased evenness and Shannon diversity across terraces, which when combined with warming, had non-additive effects, resulting in no overall change or a synergistic increase, respectively. We

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also found that of the three communities, the most coastal and most inland had the lowest levels of diversity and demonstrated the greatest responses to our treatments. Grazing changed functional group composition by increasing forbs and decreasing grasses in the two more coastal communities and decreasing sedges in the most inland community, while warming did not affect functional group composition.

<u>Conclusions:</u> Our findings suggest that grazing and warming generally increase cross-terrace community diversity. We also found that treatment effects varied at differing spatial scales, and suggest the importance of investigating climate-driven disturbance at both ecosystem- and site-level to better assess regional impacts.

Introduction

Climate change is rapidly altering high-latitude ecosystems. Over the past several decades, the Arctic has warmed nearly 2°C and about twice as rapidly as lower latitudes (IPCC 2014; Thoman et al. 2020). Warmer temperatures are influencing the spatial patterns and abundances of some herbivores (Post et al. 2009; Tape et al. 2016; Joly et al. 2019), with consequences for plant community diversity and composition (Grimm et al. 2013; Uher-Koch et al. 2019). Higher temperatures are also reorganizing plant communities by increasing stress and changing interspecific competition (Elmendorf et al. 2012; Bjorkman et al. 2020). Because grazing and warming often have opposing effects on vegetation (Olofsson & Post 2018; Post et al. 2021), it can be difficult to predict how changing grazing patterns and warming temperatures taken together will affect plant communities in the future.

The abundance and distributions of migratory herbivores are changing across Arctic landscapes (Ward et al. 2016; Fox & Madsen 2017; Amundson et al. 2019). This is important for plant communities because many migratory herbivores often control vegetation structure and community composition in these high-latitude ecosystems (Jefferies et al. 1994; Post & Pedersen 2008). Migratory herbivores often increase plant species diversity and change composition through selective herbivory and biomass removal (Mulder 1999; Olofsson et al. 2001). However, because grazing can stimulate compensatory growth in preferred species (Cargill & Jefferies 1984; Beaulieu et al. 1996), herbivores can also maintain or stabilize community composition (Klein et al. 2004; Zhang et al. 2017). Thus, as climate change alters migratory herbivore patterns or abundances, vegetation communities are likely to change.

Warming can also change vegetation communities and alter plant productivity in Arctic systems (Walker et al. 2006; Elmendorf et al. 2012). Unlike grazing, warming has generally been found to reduce species diversity and evenness (Arft et al. 1999; Hollister et al. 2005). Warming often shifts species dominance and restructures communities (Post et al. 2009; Sistla et al. 2013; Løkken et al. 2019), because certain functional groups, for example woody shrubs, respond favorably to increases in temperature (Myers-Smith et al. 2011; Tape et al. 2016). While warming can drive community change, community functional composition and local abiotic conditions, such as soil moisture, can result in site-specific responses (Ackerman et al. 2017; Bjorkman et al. 2020).

Although grazing and warming often have opposing responses on plant community diversity and composition (Post & Pedersen 2008; Olofsson et al. 2009), their interacting effects on plant communities can negate one another or result in non-additive responses (Klein et al. 2004; Kohli et al. 2020). For example, warming-induced expansion of Arctic shrubs can be limited by ungulate grazing (Christie et al. 2015).

Grazing can also reverse the negative effects of warming on species richness and primary productivity (Eskelinen et al. 2017; Kaarlejärvi et al. 2017). Grazing by goose herbivores can either decrease or increase graminoid abundance through compensatory growth (Jefferies & Rockwell 2002; Person et al. 2003), while warming often increases graminoid abundance at cold sites (Elmendorf et al. 2012). Depending on the specific plant communities and local conditions, interactions between grazing and warming could result in complex synergistic community effects.

The Yukon-Kuskokwim (Y-K) Delta in western Alaska is an important coastal wetland and breeding area for millions of migratory waterfowl. The region is warming rapidly (SNAP 2020) and the abundance and distribution of the avian community are changing (Fischer et al. 2017; Sedinger et al. 2019). Geese play a critical role in structuring habitat in the Y-K Delta and shifts in their phenology and distribution can change plant traits and affect biogeochemical cycling (Choi et al. 2019; Leffler et al. 2019; Choi et al. 2020). With sea-level rise (Jones et al. 2009; Tape et al. 2013), and increasing coastal erosion and storm surge frequency and intensity (Vermaire et al. 2013; Terenzi et al. 2014; Jorgenson et al. 2018), geese and coastal vegetation are predicted to shift inland in the future. A greater understanding of how grazing and warming affect these coastal plant communities may allow for better predictions of how these changes will influence plant communities in the future.

We investigated the effects of goose grazing and increasing temperature on three wetland plant communities along a 6-km gradient from the coast inland. We addressed the following questions: 1) How do grazing, warming, and their interaction affect plant community diversity?; 2) How do grazing, warming, and their interaction affect plant community composition of functional groups and species?; and 3) Do the relative effects of grazing and warming change among different coastal plant communities? We predicted that grazing would increase diversity metrics while warming may decrease diversity and perhaps mediate this effect. We also predicted that species and functional groups and plant communities that historically experience greater grazing intensity will be more resistant to grazing, while particular functional groups, such as woody species, may increase more with warming.

Methods

Study area

The Yukon Delta National Wildlife Refuge encompasses over 75,000 km^2 of sub-arctic coastal wetlands and tundra between the Yukon and Kuskokwim Rivers in western Alaska along the coast of the Bering Sea. We conducted our experiment on the coast of the Y-K Delta near the mouth of the Kashunuk and Tutakoke Rivers (61°15'N, 165°37'W). More specifically, we conducted the experiment on three coastal 'terraces', which are part of the estuarine chenier plain and are defined by parallel sets of deposited beach ridges with surficial deposits approximately 3,000-5,000 years old (Hoare & Condon 1968) (Figure 4.1).

Each coastal terrace is 1-3 km wide and characterized by a low elevational profile rising from near sea level on the active coastal margin (terrace 1: T1) to approximately 2 m on the inactive floodplain (T3) about 6 km inland (Jorgenson & Ely 2001). The three terraces comprise 44% of the terrestrial central coastal floodplain region of the Y-K Delta with T1, T2, and T3 occupying 2.0%, 16.6%, and 25.4%, respectively, with the remaining area comprised of sloughs, ponds, and tundra uplands (Macander et al. 2012). Vegetation communities in these coastal terraces form distinct deltaic ecotypes: T1 is an active coastal floodplain dominated by brackish levee moist herb meadows (*Argentina egedei, Leymus mollis*) and tidal flat margins (*Puccinellia phryganodes*); T2 is an inactive floodplain dominated by saline wet meadows (*Carex glareosa, C. ramenskii*); and T3 is an inactive floodplain with thick organic deposits dominated by brackish wet sedge-shrub meadows (*C. rariflora, Salix fuscescens*) (Kincheloe and Stehn 1991, Jorgenson 2000) (Table C1 in the appendices).

The coastal terraces also differ in local abiotic conditions. T1 and T2 are characterized by relatively lower gravimetric soil moisture (62% and 81%, respectively), and low total organic soil C (1.7% and 3.9%, respectively), compared to T3 with more saturated soils and higher gravimetric soil moisture (255%) and higher organic soil C (12.3%) (Foley 2020). T1 has higher rates of fine sediment deposited during storm surge flooding events (6.5-8 mm year^{-1}) and is characterized by denser, more mineral soils, while T3 is colder, with thick organic layers and underlain by near-surface permafrost (Jorgenson 2000; Jorgenson & Ely 2001). During the experiment, mean summer temperature 10 cm aboveground for T1, T2, and T3 were 13.6°C, 14.4°C, and 14.3°C, respectively, while mean summer temperatures 5 cm belowground were 11.1°C, 11.1°C, and 10.1°C, respectively.

The three coastal terraces are important nesting and brood-rearing habitat for several migratory goose herbivores. The dominant geese species are both grazers and forage primarily on *Carex* sedges; Pacific black brant (*Branta bernicla nigricans*) nest in high densities on T1 and T2 (Lindberg & Sedinger 1998), while cackling geese (*B. hutchinsii minima*) nest further inland on T2 and T3 (Sedinger & Raveling 1986).

Experimental design

During the growing seasons of 2015 and 2016, we conducted a full-factorial, field experiment using two grazing treatments (grazed, ungrazed) crossed with two warming treatments (warmed, ambient). We replicated each of the four treatments in eight blocks on the three coastal terraces for a total of 96 plots. We placed blocks at 25-m intervals along a 175-m north-south oriented transect on each terrace. Transects were located a minimum of 0.5 km from the Tutakoke River channel to minimize the influence of seawater infiltration and riverbank flooding during high tide.

Treatment plots were 0.85 m in diameter to match the size of the conical open-top chambers (OTCs; 0.30 m height x 0.85 m base dia. x 0.50 m top dia.) used for experimental warming (Marion et al. 1997). OTCs were placed on plots after snowmelt (ca. 20 May) and were removed at the end of the summer (mid-August). We measured air temperature (10 cm aboveground) hourly in one set of plots on each terrace using temperature dataloggers (models DS1921G/Z, Maxim Integrated, San Jose, CA). OTCs increased mean temperatures 10 cm aboveground by 1.0°C, 2.0°C, and 1.4°C on T1, T2, and T3, respectively, and simulated predicted future increases in temperature in the Y-K Delta by mid-century (2060-69; SNAP 2020).

We based grazing treatments on rates of goose offtake in *C. subspathacea* grazing lawns from the literature (Person et al. 1998). We used the same level of grazing intensity across terraces so results would be comparable (0.6 g dwt m^{-2} day^{-1} over 42 days), the total of which was less than 25% of end-of-season aboveground biomass for all three terraces. Futher, this is likely a higher grazing intensity from heavily-use grazing areas, and demonstrates what increased grazing intensity might do in different terrace communities. We clipped leaves and stems of all species in proportion to their relative presence in plots. We removed all clipped vegetation from the plots. We applied treatments on four occasions each season to reflect the seasonal shift in peak goose grazing intensity (Sedinger & Flint 1991) (8 June: 3.7 g dwt m^{-2}, 22 June: 8.6 g dwt m^{-2}; 6 July: 8.6 g dwt m^{-2}; 20 July: 3.7 g dwt m^{-2}). To control for wild goose grazing, we fenced off each block using poultry netting starting ca. 20 May each year.

Vegetation surveys

We measured percent cover using the point-intercept method. We used a 9 x 9 point grid (0.85 m x 0.85 m; total 81 points) to determine changes in vegetation percent cover at three intervals: early-growing season (early June), mid-growing season (early July), and late-growing season (early August). We identified vegetation beneath each of the overlapping grid points to species (Hultén 1968) and sorted taxa into functional groups (dead, forb, grass, moss, sedge, low-lying shrub) based on USDA NRCS Plant Database classifications (Table C1 in the appendices). From cover measurements, we calculated species richness, evenness, and the Shannon diversity index.

Statistical analyses

To investigate how grazing, warming, and their interaction influence plant community diversity (species richness, evenness, Shannon diversity), we conducted a two-way analysis of variance (ANOVA) using the ‘lme’ function in the nlme package (Pinheiro et al. 2019) in R statistical software (R Development Core Team 2020 version

4.0.2). We analyzed diversity (richness, evenness, Shannon diversity) in a cross-terrace analysis to determine treatment effects across all three communities and on each terrace separately. We treated experimental treatments (grazing, warming), terrace (T1, T2, T3), and collection date as fixed-effect predictor variables and plot nested within block as a random effect to isolate the effects of each treatment separately and combined. We applied an arcsine square root transformation to all percent cover data and log-transformed biomass data before analysis to meet assumptions of normality. We used Tukey HSD pairwise comparisons to investigate differences in all four treatment combinations using the 'cld' function in the lsmeans package (Lenth 2016); from this, we were able to calculate the non-additive effects of treatments. Lastly, we calculated standardized effect size indices and 95% confidence intervals using the 'cohens_d' function in the effectsize package (Ben-Shachar et al. 2020). We determined significance as $p < 0.05$. We present percent change for each treatment in the text as the mean across the last year of the experiment unless otherwise specified.

To investigate how treatments and a grazing * warming interaction influence species and functional groups, we performed two separate permutational multivariate analysis of variances (PERMANOVAs) using the 'adonis' function in the vegan package (Oksanen et al. 2019). To determine how treatments differed across all three terraces, or cross-terrace, we used the Bray-Curtis dissimilarity measure and 999 permutations to calculate pairwise distances between treatments. Similar to the diversity analyses, we also ran a separate analysis for each terrace to determine treatment effects for all three communities. We conducted non-metric multidimensional scaling (NMDS) ordinations using the Bray-Curtis dissimilarity measure and 999 permutations using the 'metaMDS' function. We identified significant species and functional groups in NMDS ordination using the ‘envfit’ function and assessed treatment effects using two-way ANOVAs and Tukey post-hoc comparisons (see above). We determined the percent change in composition cover for species and functional groups as the relative change in overall cover for each taxon across the last year of the experiment. For ease of interpretation, we only present ordinations for the end-of-season percent cover measurements from the last year of the experiment. In all analyses, sampling date was significant for most models, but we primarily focus our discussion on the main treatment effects because we expected to see accumulated treatment effects over the growing season.

Results

Cross-terrace community diversity and composition

Both grazing and warming significantly increased cross-terrace species richness (+4.8% and +5.6%, respectively), with no significant interactions (Table C2 in the appendices; Figure 4.2). Grazing increased cross-terrace evenness (+4.5%), while warming alone did not affect evenness, but there was a significant three-way interaction between treatments and terrace. When combined with warming, grazing counteracted the decrease in evenness induced by warming alone, however this was primarily driven by significant responses on T1, while T2 and T3 demonstrated no interactive response. Grazing increased cross-terrace Shannon diversity (+11.2%), but there was a significant interaction with warming (Table C2 in the appendices; Figure 4.2). While warming had no effect on its own, grazing and warming together increased Shannon diversity above the effect of grazing alone (+10.9%).

Grazing, but not warming, influenced cross-terrace functional group and species composition (PERMANOVA and NMDS; Table C3 & Figure C1 in the appendices). In general, forbs increased and grasses decreased with grazing across terraces (Table C4 in the appendices; Figure 4.4), but specific functional group responses varied among terraces.

Community differences by terrace

Mean richness, evenness, and Shannon diversity varied among terraces, with the highest diversity found on T2 and the lowest on T1 (Table 4.1). Despite a significant cross-terrace effect, grazing and warming did not affect T1 or T2 richness. Grazing increased species richness on T3 (+9.8%) while warming had no effect; however, grazing and warming combined interacted synergistically to increase richness (+13.6%) (Table C5 in the appendices; Figure 4.2).

Grazing and warming had opposing interacting effects on T1 evenness, such that when combined, grazing mediated the negative warming effect and resulted in no change (Table C5 in the appendices; Figure 4.2). Similarly, grazing increased T1 Shannon diversity and interacted with warming to mediate the decrease from warming alone (Figure 4.2).

Grazing effects on community composition varied among terraces, while warming had no effect (Table C2 in the appendices; Figure 4.3). On T1, grazing changed the relative abundance of functional groups by increasing low-lying forbs (+69%) and decreasing grass cover (-23%) (Figures 4.3A-B & 4.4). Similarly, on T2, grazing increased forbs (+76%) and decreased grasses (-16%) (Figure 4.3C-D & 4.4). On T3, grazing decreased sedges (-28%) and increased standing dead litter (+34%) (Figures 4.3E-F & 4.4).

Some coastal grasses responded positively to grazing (*Deschampsia caespitosa*, *P. phryganodes*), but grazing reduced the cover of dominant grasses (*L. mollis, Poa eminens*) (Table C6 in the appendices). Dominant T2 sedges, *C. glareosa* and *C. ramenskii*, had opposing responses to grazing (+24% and -18%, respectively).

Discussion

Grazing and warming effects on plant communities

We found in a two-year field experiment across three wetland plant communities in coastal western Alaska that both grazing and warming treatments generally increased plant diversity. More specifically, both grazing and warming increased species richness across the three plant communities and warming had an even greater effect on increasing richness than grazing did. While grazing also increased evenness and Shannon diversity across terraces, warming did not. But, when grazing was combined with warming, their interactions resulted in no overall change in evenness and a synergistic increase in Shannon diversity, respectively. We also found that of the three communities, the most coastal and most inland had the lowest levels of species richness and evenness, and demonstrated the greatest responses to our treatments (Table 4.1; Figures 4.2 & 4.4).

Grazing increased plant community diversity and altered community composition, primarily through an increase in forbs and reduction in dominant grasses (Tables C5 & C6 in the appendices; Figure 4.4). Low-lying and less abundant species (i.e., on T2: *Chrysanthemum arcticum, Stellaria humifusa*) increased two-fold with grazing, likely because of increased light availablility with the reduction of tall, dominant graminoid species. These findings are similar to other studies that have found grazing increases species diversity as result of biomass removal (Olofsson et al. 2001; Lu et al. 2017). While grazing increased species diversity and changed the relative proportions of different functional groups, not all species within functional groups had the same response to treatments. In addition, although grazing reduced the cover of *Carex* species, the primary forage of the goose herbivores in our system, grazing also increased secondary forage species (*P. phryganodes, Triglochin palustris*). While these species could partially offset this reduction in goose forage, specific species responses may play out differently under selective foraging (for example, *T. palustris*; Mulder 1999) that we did not simulate in this study.

Similar to other Arctic and cold ecosystem studies, we found warming to have little to no significant effects on community diversity (Grime et al. 2000; Hudson & Henry 2010; Little et al. 2017). The only significant effect of warming on diversity that we detected was a signficiant cross-terrace increase in species richness, which surprisingly was even stronger than the grazing effect. With this exception, warming had a smaller effect on plant community diversity and structure than grazing. This smaller effect could be a result of the moderate degree of warming created by our treatments, but the change in temperature we created is expected in the coastal Y-K Delta by mid-century and therefore should represent impacts in the coming decades (2060-69; SNAP 2020). In most cases, while not significant, warming tended to decrease diversity metrics like evenness and Shannon diversity while grazing increased these metrics; warming also tended to decrease forbs and increase grasses while grazing had the opposite effects.

Further, while others often find that warming increases Arctic shrub growth (Myers-Smith et al. 2011; Carlson et al. 2018), we found no change in low-lying dwarf shrub cover with warming in this experiment, which did not support our prediction.

Though not common in our analysis, we found instances of grazing and warming interacting to mediate and synergistically influence treatment effects at differing scales. This is important because although grazing and warming both increased cross-terrace species richness, they did so through differing mechanisms. Grazing primarily increased richness through removal of taller biomass and indirectly increasing the abundance of less-conspicuous, low-lying forbs, which translated into greater cross-terrace evenness and Shannon diversity. Comparatively, warming increased cross-terrace species richness with non-significant increases in grasses which croweded out forbs (Figure 4.3A-B), and thereby decreased evenness (T1). When grazing and warming were combined, these mechanistic differences resulted in interactive effects that counteracted increases with grazing and reductions with warming and provided community-level resilience to disturbance (Klein et al. 2004; Post 2013; Zhang et al. 2017). Treatments also interacted synergistically to increase cross-terrace Shannon diversity and T3 richness. In these instances, grazing removed vegetation to expose low-lying species while warming positively influenced growth, and there by increased richness and diversity greater than either treatment alone.

Differences in terrace responses

The individual terraces had variable responses to grazing which were likely driven by differences in both abiotic and biotic conditions. The most coastal terrace, T1, had the strongest response to our grazing and warming treatments (Figures 4.2 & 4.4), and this might have been due in part to the differences in soil moisture found across the terraces. T1 had lower soil moisture than the other terraces, which can make communities less resilient to disturbance (Speed et al. 2010) and more responsive to shifts in temperature because the soils respond more quickly to thermal changes (Oberbauer et al. 2013).

Comparatively, the middle terrace, T2, had no community diversity responses to grazing and warming (Figure 4.2). T2 also had the highest diversity measurements (Table 4.1) and is the community that has historically experience greater grazing intensity. It is possible that the existing community heterogeneity of saline wet meadows and adapted response to goose herbivores may have provided ecological resilience to disturbance. For example, the dominant T2 sedge species (*C. glareosa*, *C. ramenskii*) had opposing responses to grazing and resulted in no overall change in sedges.

On T3, the most inland terrace, we found that grazing but not warming increased community diversity and changed functional group composition. Grazing reduced T3 sedge cover, and through the removal of taller, living vegetation exposed and increased cover of standing dead. T3 is also the terrace with the lowest density of geese (Fischer et al. 2017) and likely has fewer plant species adapted to grazing. In addition, we also observed significant increases in T3 evenness and Shannon diversity only at the end of the growing season (Table C5 in the appendices). Because T3 soils are the closest in proximity to permafrost, colder soil temperatures may have slowed the plant growth response to disturbance (Rustad et al. 2001).

Species did not respond to treatments uniformly between different terraces. Some forb species (*A. egedei*, *S. humifusa*) are present on both T1 and T2, but are more abundant on T1 (Table C1 in the appendices). Grazing significantly increased the abundance of these forbs on T2, greater than on T1, which suggests that increased grazing pressure may facilitate inland shifts of certain coastal plant species and increase disturbance-driven colonization.

Finally, we also found that grazing and warming had varying impacts at different spatial scales. Grazing increased all metrics of cross-terrace diversity, but only had significant increases in evenness and Shannon diversity on T1. Similarly, warming increased cross-terrace richness, but did not significantly affect local species richness or plant community composition on individual terraces. These scaled differences in treatment effects suggest the importance of both cross-site and site-level measurements to better assess regional climate-driven impacts (Post et al. 2021).

Conclusion

The Y-K Delta is predicted to undergo dramatic changes in the coming decades with changing herbivore abundances and distributions and increasing temperatures. Our findings suggest that grazing is likely to increase community diversity and the abundance of low-lying secondary species which may offset the reduction in primary goose forage availability. Warmer temperatures are also predicted to interact with grazing, potentially resulting in additive and non-additive effects on community diversity. Thus, the strength and direction of these coastal community responses to grazing and warming have consequences for migratory geese and biogeochemical processes in a critically important and rapidly changing Arctic system.

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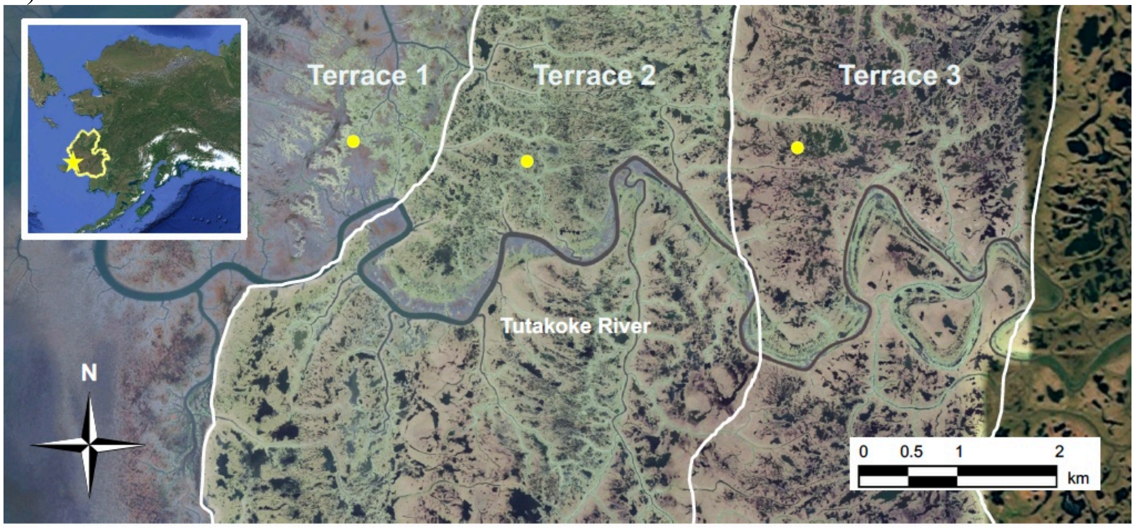
Tables

Table 4.1. Mean plant community diversity values per plot (± 1 SE) averaged across all treatments for the three coastal terraces from end-of-season cover measurements. Plots were 0.85 m x 0.85 m. Letters indicate Tukey significant differences between means.

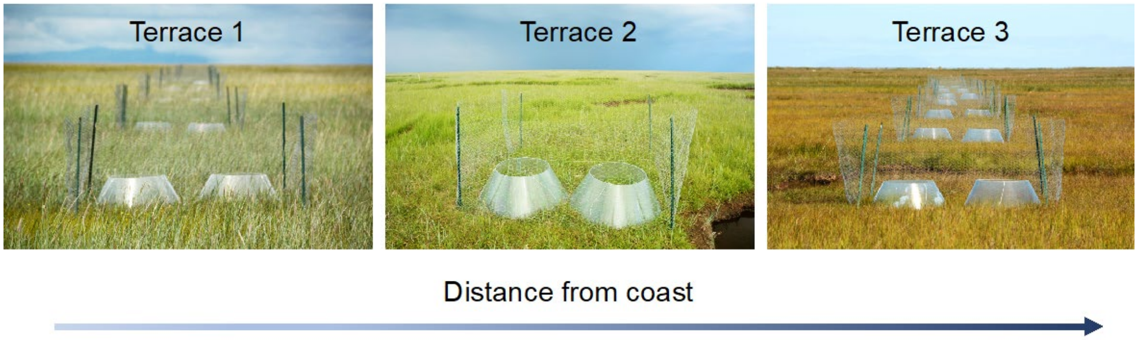
	Richness	Evenness	Shannon diversity
	Mean (SE)	Mean (SE)	Mean (SE)
Terrace 1	5.47 (0.12)^{a}	0.70 (0.01)^{a}	1.32 (0.04)^{a}
Terrace 2	5.98 (0.12)^{b}	0.80 (0.01)^{b}	1.52 (0.02)^{b}
Terrace 3	5.28 (0.11)^{a}	0.79 (0.01)^{b}	1.46 (0.02)^{b}

Figures

A) Yukon-Kuskokwim Delta coastal terraces



B) Coastal communities



C) Experimental block

D) Elevational composition

Figure 4.1 (A) Coastal terrace communities near the mouth of the Tutakoke River, Yukon-Kuskokwim Delta, AK. Yellow polygon = NWR boundary; yellow star = study site. Satellite imagery from Google Earth. (B-C) Hierarchical study design. (D) Schematic of dominant functional group composition (forbs, grasses, sedges, shrubs; Table C1 in appendices).

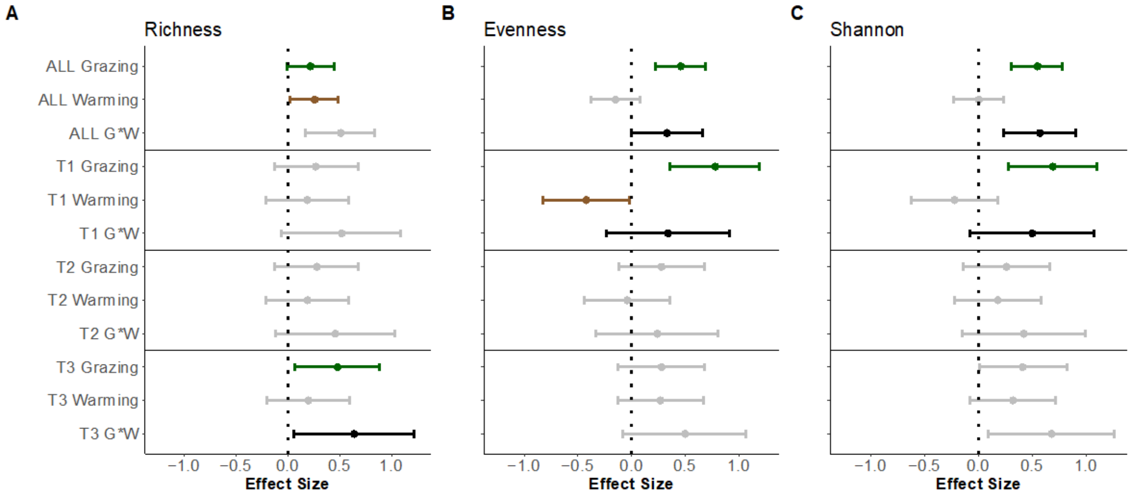


Figure 4.2. Standardized effect sizes of main treatment effects (grazing, warming) and interactions (G*W) on species percent cover community diversity measurements (richness, evenness, Shannon diversity; A-C). Solid colors indicate significant ANOVA results (Tables C2 & C5 in the appendices) across all and on individual terraces (T1, T2, T3). Error bars 95% confidence intervals. Green = grazing; brown = warming; black = interaction; gray = non-significance.

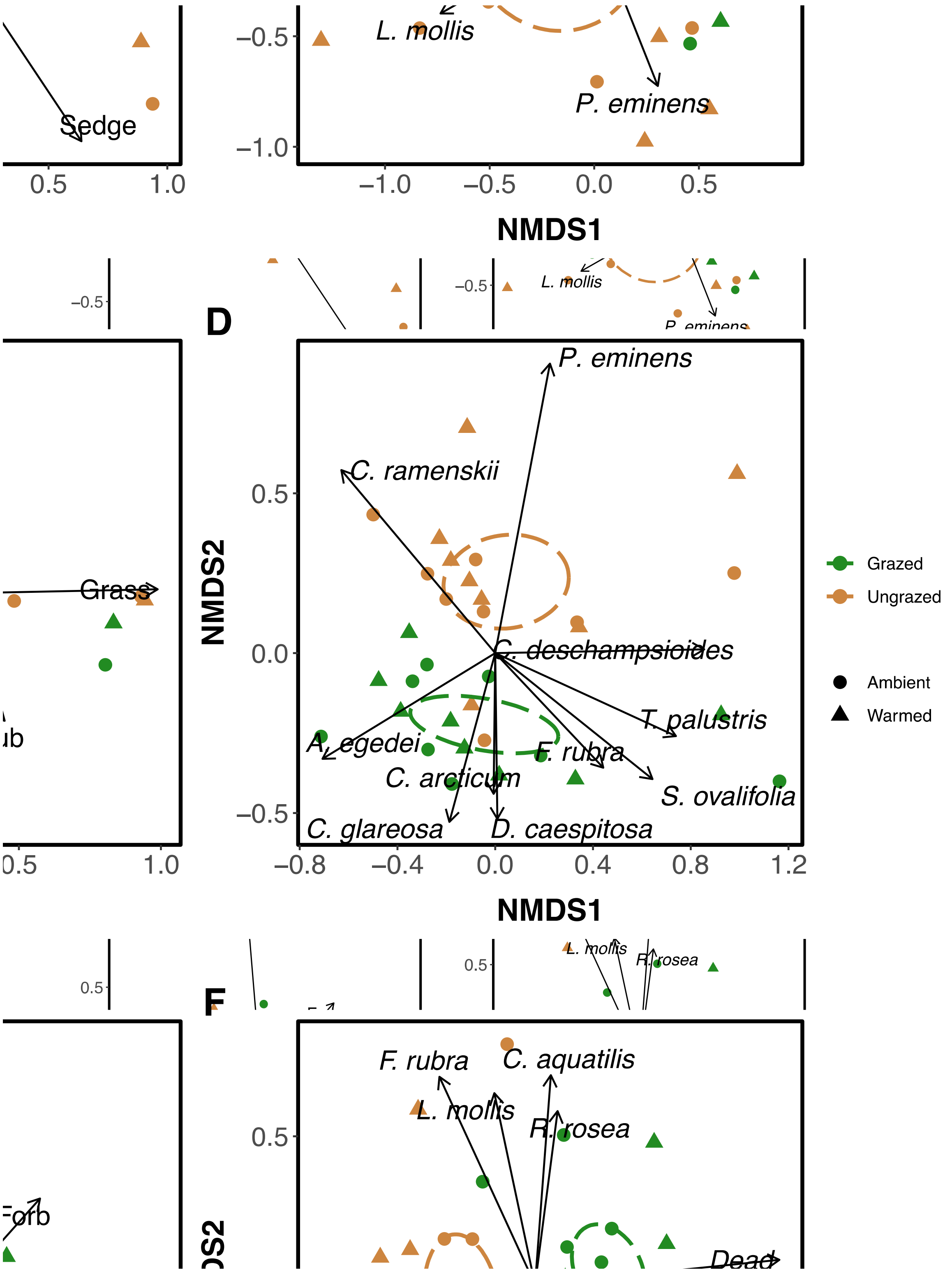


Figure 4.3. T1 percent cover composition by (A) functional group and (B) species; T2 percent cover by (C) functional group and (D) species; T3 percent cover by (E) functional group and (F) species. Ellipses indicate 95% confidence values (SE).

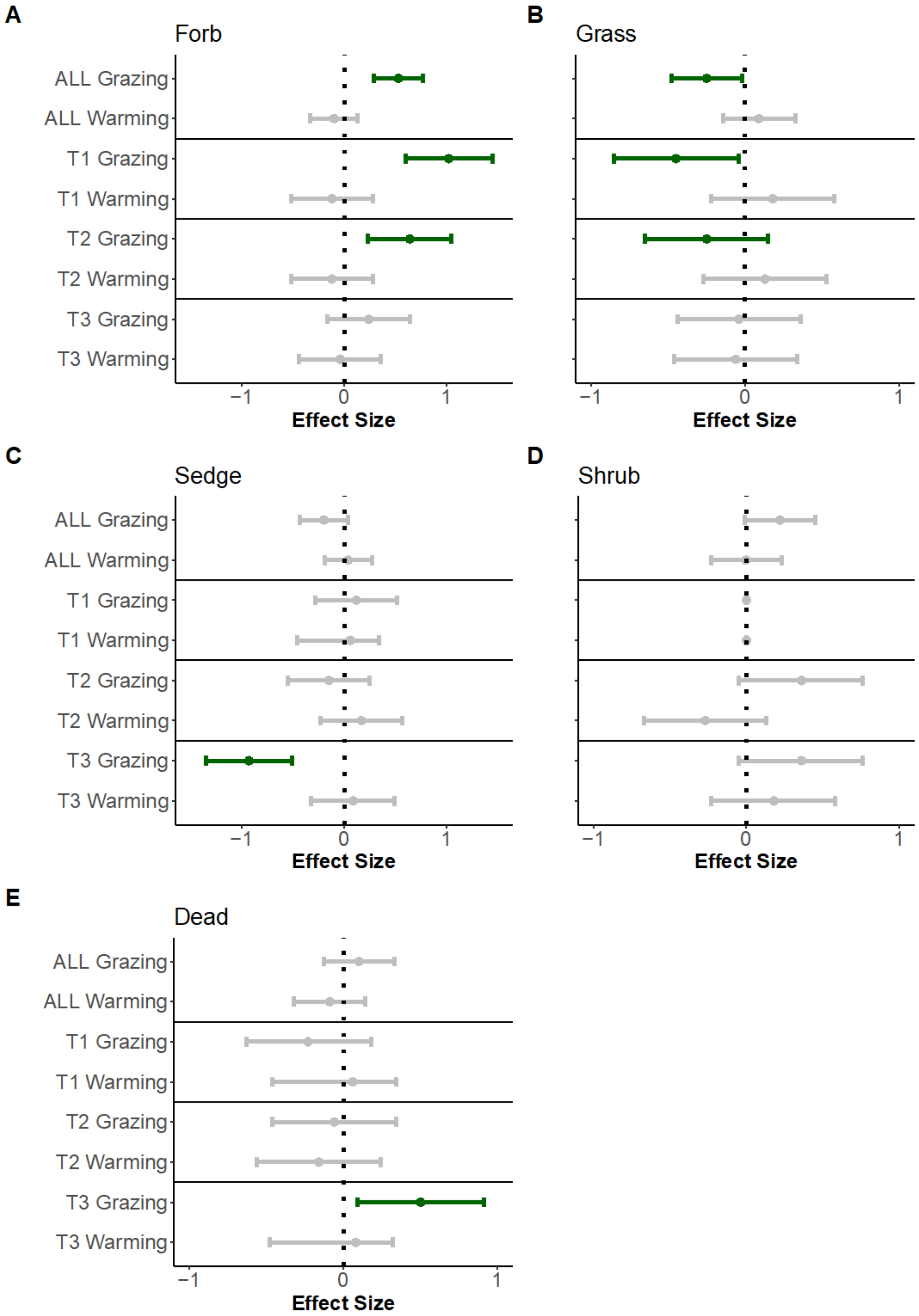


Figure 4.4. Standardized effect sizes of main treatment effects (grazing, warming) on percent cover of plant community functional groups (A-E). There were no significant treatment interactions or warming effects. Solid color indicates significant ANOVA results (Tables C4 & C6 in the appendices) across all and on individual terraces (T1, T2, T3). Error bars 95% confidence intervals. Green = grazing; gray = non-significance.

CHAPTER 5

CONCLUSIONS

Climate-induced phenological mismatch and shifts in spatial patterns between plants and migratory herbivores has the potential to alter forage availability, impact biogeochemical processes, and change plant communities (Kelsey et al. 2018, Choi et al. 2019, 2020, Leffler et al. 2019, Beard et al. 2019). Generally, shifts in the timing or presence of herbivore grazing had greater effects than similar changes in season advancement or warming. Our findings suggest that factors influencing timing of long-distance migration in the wintering grounds can have ecosystem consequences in the Arctic.

In chapter 2, we found that timing of grazing by migratory herbivores has a greater impact on forage biomass in *Carex* grazing lawns than a similar shift in the timing of the growing season. The phenological mismatch prediction for this site of earlier springs and later goose arrival will likely increase above- and belowground biomass and initiate sexual reproduction of the often-clonally reproducing *C. subspathacea*. Late goose grazing had a similar shift in timing and response as season advancement. While some impacts of phenological mismatch are immediate, other variables may be difficult to predict because some responses can take years of mismatch to respond. Although we investigated the effects of three consecutive years of mismatch, it is unknown whether alternating years of intermittent mismatch conditions could reverse or counteract the effects of asynchrony.

In chapter 3, we investigated how phenological mismatch between goose herbivores and their forage can influence biogeochemical processes and soil nitrogen (N) availability. We found that early grazing increases inorganic and organic soil N, while late grazing decreases N availability. Earlier springs increased inorganic N, but less than the effect of grazing. Because N is often limiting in Arctic systems (Sistla et al. 2012), temporal changes in soil N pools can regulate microbes and plant uptake at times of greatest demand (Bilbrough et al. 2000, Edwards and Jefferies 2010). Further, while geese can increase N pools with grazing, it is still unclear how goose feces might contribute as potential N sources. Kelsey et al. (2018) found no gaseous loss of N_2O from experimental plots, while we detected $\delta^{15}N$ foliar enrichment with early grazing, which suggests that there may be some N recycling between geese and plants (Beard and Choi 2017). While there is some evidence of direct goose influence on soil N process, the exact mechanisms are unclear and further investigation into the specific N cycling pathways is recommended in these coastal N-limited systems.

The timing of grazing had strong influence on both forage resources and nutrient availability, where early and late grazing had often opposing effects. Early grazing reduced forage availability but maintained higher forage quality, while late grazing resulted in greater forage but lower forage quality. Early grazing also increased N pools but also resulted in shifting the system from a sink to a source (Kelsey et al. 2018). Comparatively, late grazing reduced N pools, but resulted in greater carbon uptake and storage. Depending on either timing of relative arrival and grazing, geese have the potential to alter ecosystem processes with phenological mismatch, which suggests the importance of timing of migratory herbivores in this system.

In chapter 4, we examined the community-level consequences of climate change for migratory goose populations in different coastal habitats. Both grazing and warming increased diversity across communities. Maintaining or increasing community diversity could help buffer ecosystems through the portfolio effect, whereby diversification of species with varying phenology and life-history traits can provide ecological resiliency to climate-driven disturbance (Schindler et al. 2015, Anderson et al. 2015). Grazing had a stronger influence on community composition compared to warming, increasing forbs and decreasing grasses in the most coastal communities and decreasing sedges on the most inland community. Because coastal processes are predicted to shift plant communities and goose herbivores further inland, it is possible that increased grazing can reduce the extent of sedge forage on the landscape. Lastly, because these community-level responses can vary at both site- and ecosystem-levels, our findings highlight the importance of using manipulative field experiments to investigate climate-driven impacts at multiple spatial scales (Post et al. 2021).

Community responses to climate-driven warming are likely going to be site-specific and highly dependent on local species composition (Gruner et al. 2017). For example, abiotic conditions, like soil moisture and salinity, and local soil microbial communities vary between the different terraces and likely play a strong role in driving community responses to warming and grazing (Jorgenson 2000, Jorgenson and Ely 2001, Foley 2020). Further, future climate drivers may reshuffle communities resulting in new species associations and interactions (Post et al. 2009, Alexander et al. 2015). For example, grazing marginally increased low-lying dwarf shrub cover (*Salix ovalifolia*) in wet sedge meadows. Moose (*Alces alces*) are increasing in abundance in the coastal Y-K Delta (Wald and Nielson 2014). Increases in shrub abundance could potentially facilitate on-going range expansion, which could result in novel trophic interactions and herbivore pressures.

How species interact with climate to affect coastal ecosystems and process will be dependent on the strength of both biotic and abiotic factors. Recent work suggests that phenological mismatch and interactive effects between plants and herbivores are not likely to have straight-forward or predictable outcomes on ecosystem processes and community diversity. Our findings highlight the complexity of these effects and the importance of using novel experimental field approaches to improve our understanding of climate-driven influences on trophic interactions in a rapidly warming future.

With warmer winters

Geese graze their grasses early

Timing matters most

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APPENDICES

Appendix A – Supplementary Information for Chapter 2

Table A1. Linear-mixed model results comparing Ambient goose grazing treatments to Ambient control plots on log-transformed aboveground biomass. DOY = day of year. Bolding indicates p > 0.05.

Year 1 – 2014 Parameter	Value	SE	*DF*	*t*	*p*
Intercept	2.41	0.34	119	7.10	0.00
Early Grazing	-0.10	0.14	20	-0.71	**0.49**
Typical Grazing	0.10	0.14	20	0.70	**0.49**
Late Grazing	0.30	0.14	20	2.13	**0.05**
No Grazing	0.91	0.14	20	6.49	0.00
DOY	0.01	0.00	119	5.67	0.00

Year 2 – 2015 Parameter	Value	SE	*DF*	*t*	*p*
Intercept	4.02	0.38	119	10.60	0.00
Early Grazing	0.10	0.22	20	0.45	**0.66**
Typical Grazing	0.38	0.22	20	1.70	**0.11**
Late Grazing	0.78	0.22	20	3.51	0.00
No Grazing	1.58	0.22	20	7.06	0.00
DOY	0.00	0.00	119	0.04	0.97

Year 3 – 2016 Parameter	Value	SE	*DF*	*t*	*p*
Intercept	4.33	0.29	117	14.75	0.00
Early Grazing	0.28	0.20	20	1.36	**0.19**
Typical Grazing	0.80	0.20	20	3.98	0.00
Late Grazing	1.12	0.20	20	5.55	0.00
No Grazing	1.54	0.20	20	7.66	0.00
DOY	0.00	0.00	117	0.08	0.93

Table A2. Fixed effects of the top-performing model on plant traits for experimental treatments. Missing parameter estimates (-) indicate the top model did not include those effects. The reference level for the model (i.e., the intercept) was 2014, Typical goose grazing, and Ambient growing season. Abbreviations: Advanced = advanced growing season, Early = early grazing, Late = late grazing, None = no-grazing, DOY = day of year. Bolding indicates $p < 0.05$.

	Aboveground biomass			Stem height			Standing dead		
Effect	Value	SE	P	Value	SE	P	Value	SE	P
Intercept	**5.57**	**0.35**	**0.00**	**1.74**	**0.27**	**0.00**	**-0.13**	**0.22**	**0.56**
2015	0.05	0.06	0.41	**0.64**	**0.06**	**0.00**	-	-	-
2016	**0.58**	**0.06**	**0.00**	**1.07**	**0.06**	**0.00**	0.38	0.27	0.15
Early	**-2.70**	**0.48**	**0.00**	**-0.95**	**0.34**	**0.01**	-0.07	0.28	0.81
Late	-0.45	0.48	0.34	0.21	0.33	0.54	-0.07	0.28	0.81
None	**-1.21**	**0.48**	**0.02**	**-1.07**	**0.34**	**0.00**	**2.57**	**0.28**	**0.00**
DOY	**-0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.02**	-	-	-
Advanced	-	-	-	**0.42**	**0.09**	**0.00**	**0.40**	**0.15**	**0.01**
Early*DOY	**0.01**	**0.00**	**0.00**	0.00	0.00	0.20	-	-	-
Late*DOY	0.00	0.00	0.08	0.00	0.00	0.92	-	-	-
None*DOY	**0.01**	**0.00**	**0.00**	**0.01**	**0.00**	**0.00**	-	-	-
Early*2015	-	-	-	-	-	-	-	-	-
Early*2016	-	-	-	-	-	-	-0.29	0.38	0.45
Late*2015	-	-	-	-	-	-	-	-	-
Late*2016	-	-	-	-	-	-	**1.53**	**0.38**	**0.01**
None*2015	-	-	-	-	-	-	-	-	-
None*2016	-	-	-	-	-	-	**2.31**	**0.38**	**0.00**

	Root biomass			Tiller number			Inflorescence number		
Effect	Value	SE	P	Value	SE	P	Value	SE	P
Intercept	**5.13**	**0.24**	**0.00**	**5.09**	**0.17**	**0.00**	**-0.00**	**0.03**	**0.00**
2015	-0.46	0.22	**0.04**	-0.13	0.09	0.16	-	-	-
2016	0.12	0.26	0.65	-0.06	0.09	0.52	**1.81**	**0.16**	**0.00**
Early	**-0.86**	**0.29**	**0.00**	**-0.44**	**0.16**	**0.01**	-2.95	5.67	0.60
Late	0.45	0.29	0.12	0.07	0.16	0.65	**-4.18**	**1.52**	**0.01**
None	**0.95**	**0.29**	**0.00**	**0.37**	**0.16**	**0.02**	**-5.66**	**1.45**	**0.00**
DOY	-	-	-	**-0.00**	**0.00**	**0.00**	**-0.01**	**0.00**	**0.00**
Advanced	-	-	-	-	-	-	**0.12**	**0.06**	**0.03**
Early*DOY	-	-	-	-	-	-	-0.00	0.06	0.90
Late*DOY	-	-	-	-	-	-	**0.03**	**0.01**	**0.00**
None*DOY	-	-	-	-	-	-	**0.05**	**0.01**	**0.00**
Early*2015	0.03	0.31	0.92	**0.31**	**0.13**	**0.02**	-	-	-
Early*2016	0.10	0.39	0.80	-0.03	0.13	0.81	-	-	-
Late*2015	0.10	0.31	0.74	0.02	0.13	0.89	-	-	-
Late*2016	-0.04	0.37	0.90	-0.05	0.13	0.69	-	-	-
None*2015	-0.37	0.31	0.24	**-0.30**	**0.13**	**0.02**	-	-	-
None*2016	**-1.16**	**0.37**	**0.00**	**-0.81**	**0.13**	**0.00**	-	-	-

Table A3. Fixed effects of the top-performing model on vegetation traits for treatment comparisons. Missing parameter estimates (-) indicate the top model did not include those effects. The reference level for the model (i.e., the intercept) was 2014, Typical goose grazing, and Ambient growing season (treatment 4). Abbreviations: 1-3; 5-8 = treatment; DOY = day of year. Bolding indicates $p < 0.05$.

	Aboveground biomass			Stem height			Standing dead		
Effect	Value	SE	P	Value	SE	P	Value	SE	P
Intercept	**2.30**	**0.31**	**0.00**	**1.31**	**0.22**	**0.00**	0.13	0.28	0.63
1	**-0.52**	**0.20**	**0.01**	-0.35	0.24	0.15	-0.13	0.37	0.72
2	-0.32	0.20	0.11	-0.32	0.24	0.19	-0.13	0.37	0.72
3	0.32	0.20	0.11	0.27	0.24	0.26	-0.13	0.37	0.72
5	**0.67**	**0.20**	**0.00**	0.46	0.24	0.06	-0.13	0.37	0.72
6	0.30	0.20	0.13	0.01	0.24	0.95	-0.13	0.37	0.72
7	**1.09**	**0.20**	**0.00**	**0.99**	**0.24**	**0.00**	**3.16**	**0.37**	**0.00**
8	**0.91**	**0.20**	**0.00**	**0.66**	**0.24**	**0.01**	**1.85**	**0.37**	**0.00**
2015	**2.00**	**0.39**	**0.00**	0.30	0.17	0.08	-	-	-
2016	**2.57**	**0.37**	**0.00**	**0.71**	**0.16**	**0.00**	0.07	0.37	0.84
DOY	**0.01**	**0.00**	**0.00**	**0.01**	**0.00**	**0.00**	-	-	-
1*2015	-	-	-	0.18	0.24	0.44	-	-	-
2*2015	-	-	-	0.20	0.24	0.40	-	-	-
3*2015	-	-	-	0.35	0.24	0.14	-	-	-
5*2015	-	-	-	0.41	0.24	0.08	-	-	-
6*2015	-	-	-	0.11	0.24	0.63	-	-	-
7*2015	-	-	-	**0.82**	**0.24**	**0.00**	-	-	-
8*2015	-	-	-	**0.68**	**0.24**	**0.00**	-	-	-
1*2016	-	-	-	0.02	0.23	0.92	-0.08	0.52	0.89
2*2016	-	-	-	-0.03	0.23	0.91	0.08	0.52	0.88
3*2016	-	-	-	**0.44**	**0.23**	**0.05**	0.62	0.52	0.23
5*2016	-	-	-	**0.66**	**0.23**	**0.00**	**2.35**	**0.52**	**0.00**
6*2016	-	-	-	0.28	0.23	0.23	**1.33**	**0.52**	**0.01**
7*2016	-	-	-	**0.73**	**0.23**	**0.00**	**2.25**	**0.52**	**0.00**
8*2016	-	-	-	**0.77**	**0.23**	**0.00**	**2.98**	**0.52**	**0.00**
2015*DOY	**-0.01**	**0.00**	**0.00**	-	-	-	-	-	-
2016*DOY	**-0.01**	**0.00**	**0.00**	-	-	-	-	-	-

	Root biomass			Tiller number			Inflorescence number		
Effect	Value	SE	P	Value	SE	P	Value	SE	P
Intercept	**5.26**	**0.26**	**0.00**	**5.08**	**0.21**	**0.00**	**2.18**	**0.67**	**0.00**
1	**-1.06**	**0.31**	**0.00**	**-0.56**	**0.22**	**0.01**	-1.99	1.08	0.06
2	**-0.65**	**0.31**	**0.04**	-0.32	0.22	0.14	-1.98	1.08	0.07
3	-0.01	0.31	0.96	0.00	0.22	0.99	0.52	0.50	0.30
5	0.55	0.31	0.08	0.05	0.22	0.81	**2.24**	**0.47**	**0.00**
6	0.36	0.31	0.24	0.09	0.22	0.66	**1.37**	**0.46**	**0.00**
7	0.38	0.31	0.22	0.36	0.22	0.11	**3.18**	**0.41**	**0.00**
8	0.44	0.31	0.16	0.39	0.22	0.08	**3.22**	**0.41**	**0.00**
2015	**-0.52**	**0.12**	**0.00**	-0.12	0.13	0.34	-	-	-
2016	-0.18	0.14	0.21	0.00	0.13	0.97	-	-	-
DOY	-	-	-	**-0.00**	**0.00**	**0.00**	**-0.02**	**0.00**	**0.00**
1*2015	-	-	-	0.31	0.19	0.10	-	-	-
2*2015	-	-	-	0.31	0.19	0.10	-	-	-
3*2015	-	-	-	-0.01	0.19	0.97	-	-	-
5*2015	-	-	-	0.01	0.19	0.97	-	-	-
6*2015	-	-	-	0.02	0.19	0.91	-	-	-
7*2015	-	-	-	**-0.37**	**0.19**	**0.05**	-	-	-
8*2015	-	-	-	-0.24	0.19	0.19	-	-	-
1*2016	-	-	-	-0.18	0.19	0.35	-	-	-
2*2016	-	-	-	-0.03	0.19	0.89	-	-	-
3*2016	-	-	-	-0.13	0.19	0.49	-	-	-
5*2016	-	-	-	-0.13	0.19	0.52	-	-	-
6*2016	-	-	-	-0.11	0.19	0.54	-	-	-
7*2016	-	-	-	**-0.86**	**0.19**	**0.00**	-	-	-
8*2016	-	-	-	**-0.90**	**0.19**	**0.00**	-	-	-

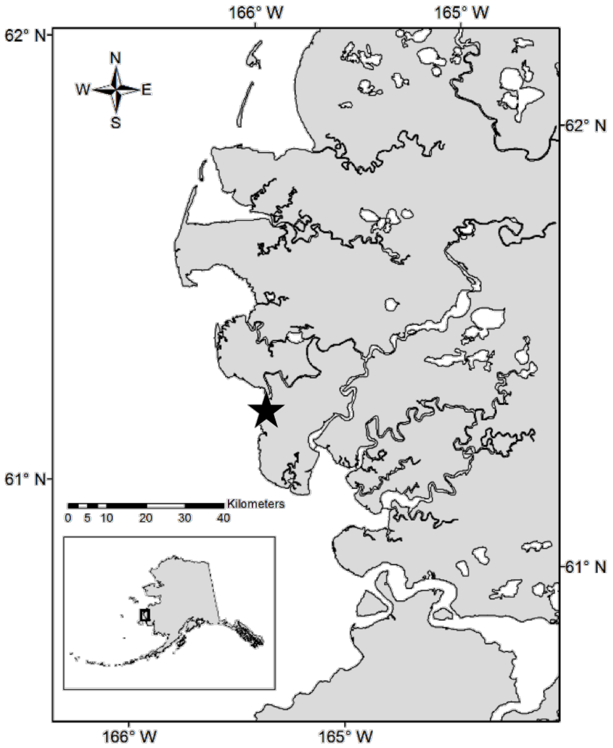

Figure A1. Map of the coastal region in the Yukon-Kuskokwim Delta, Alaska. Star indicates location of Tutakoke River field site.

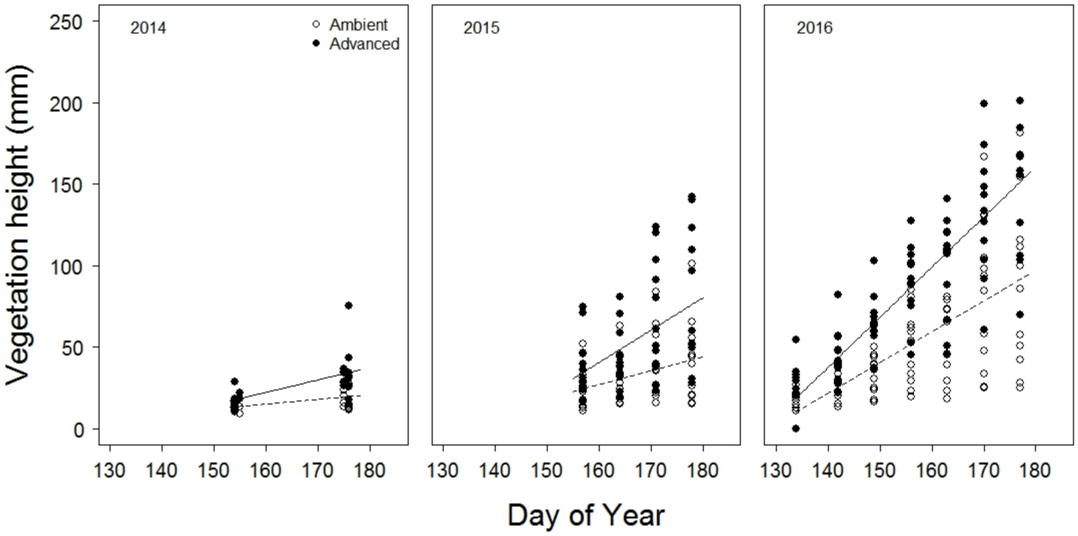

Figure A2. Modeled effect of OTC advancement of the growing season on aboveground stem height in plots not receiving early season grazing from 2014-2016. Solid regression lines are for advanced growing season plots; dashed regression lines are for ambient plots.

Appendix B – Supplementary Information for Chapter 3

Table B1. Fixed effects of the top-performing models with ΔAIC<2 on soil N for experimental treatments. Missing parameter estimates indicate the top model did not include those effects. The reference level for the model (i.e., the intercept) was 2014 (2015 for intertidal resins), Typical goose arrival, and Ambient growing season. Abbreviations: Advanced = advanced growing season, Early = early grazing, Late = late grazing, None = no-grazing, Date = sampling date. Bolding indicates $p<0.05$.

	Cumulative resin NH_4^+-N model 1			Cumulative resin NH_4^+-N model 2			Intertidal resin NH_4^+-N model 1		
	Year + Grazing*Date			Year + Grazing*Date + Season			Year + Grazing*Date + Season		
Effect	Value	SE	P	Value	SE	P	Value	SE	P
Intercept	**-9.14**	**0.49**	**0.00**	**-9.11**	**0.49**	**0.00**	**-8.73**	**0.44**	**0.00**
2015	**0.93**	**0.08**	**0.00**	**0.94**	**0.08**	**0.00**	-	-	-
2016	0.02	0.08	0.83	0.02	0.08	0.82	**-0.43**	**0.05**	**0.00**
Early	**3.24**	**0.67**	**0.00**	**3.24**	**0.67**	**0.00**	**1.59**	**0.58**	**0.01**
Late	-1.03	0.67	0.13	-1.03	0.67	0.13	**-2.52**	**0.58**	**0.00**
None	-0.36	0.67	0.59	-0.37	0.67	0.59	0.13	0.58	0.82
Date	0.00	0.00	0.26	0.00	0.00	0.26	0.00	0.00	0.40
Advanced	-	-	-	-0.08	0.06	0.23	**-0.14**	**0.05**	**0.01**
Early*Date	**-0.01**	**0.00**	**0.00**	**-0.01**	**0.00**	**0.00**	**-0.01**	**0.00**	**0.02**
Late*Date	0.00	0.00	0.24	0.00	0.00	0.24	**0.01**	**0.00**	**0.00**
None*Date	0.00	0.00	0.78	0.00	0.00	0.78	0.00	0.00	0.12
2015*Date	-	-	-	-	-	-	-	-	-
2016*Date	-	-	-	-	-	-	-	-	-

	Microlysimeter NH_4^+-N model 1			Microlysimeter NH_4^+-N model 2			Microlysimeter NH_4^+-N model 3		
	Year*Date + Grazing			Year*Date + Season + Grazing			Year*Date		
Effect	Value	SE	P	Value	SE	P	Value	SE	P
Intercept	**4.39**	**0.32**	**0.00**	**4.33**	**0.32**	**0.00**	**4.53**	**0.31**	**0.00**
2015	**2.14**	**0.55**	**0.00**	**2.13**	**0.55**	**0.00**	**2.14**	**0.55**	**0.00**
2016	**0.91**	**0.42**	**0.03**	**0.91**	**0.42**	**0.03**	**0.91**	**0.42**	**0.03**
Early	**0.39**	**0.15**	**0.01**	**0.39**	**0.15**	**0.01**	-	-	-
Late	0.11	0.15	0.46	0.11	0.15	0.46	-	-	-
None	0.07	0.15	0.64	0.07	0.15	0.64	-	-	-
Date	**0.00**	**0.00**	**0.02**	**0.00**	**0.00**	**0.02**	**0.00**	**0.00**	**0.02**
Advanced	-	-	-	**0.39**	**0.15**	**0.01**	-	-	-
Early*Date	-	-	-	-	-	-	-	-	-
Late*Date	-	-	-	-	-	-	-	-	-
None*Date	-	-	-	-	-	-	-	-	-
2015*Date	**-0.01**	**0.00**	**0.00**	**-0.01**	**0.00**	**0.00**	**-0.01**	**0.00**	**0.00**
2016*Date	0.00	0.00	0.12	0.00	0.00	0.12	0.00	0.00	0.12

	Cumulative resin NO_3^--N model 1			Cumulative resin NO_3^--N model 2			Intertidal resin NO_3^--N model 1		
	Year*Date + Grazing			Year*Date + Season + Grazing			Year + Grazing*Date		
Effect	Value	SE	P	Value	SE	P	Value	SE	P
Intercept	**-2.85**	**0.74**	**0.00**	**-2.85**	**0.74**	**0.00**	**-11.23**	**0.48**	**0.00**
2015	1.57	1.04	0.13	1.57	1.04	0.13	-	-	-
2016	**-6.78**	**0.86**	**0.00**	**-6.78**	**0.86**	**0.00**	**-0.85**	**0.07**	**0.00**
Early	0.20	0.13	0.13	0.20	0.13	0.13	0.51	0.66	0.45
Late	**-0.28**	**0.13**	**0.03**	**-0.28**	**0.13**	**0.03**	0.05	0.67	0.95
None	-0.22	0.13	0.08	-0.22	0.13	0.08	**2.01**	**0.67**	**0.00**
Date	**-0.05**	**0.00**	**0.00**	**-0.05**	**0.00**	**0.00**	0.00	0.00	0.60
Advanced	-	-	-	-0.01	0.09	0.94	-	-	-
Early*Date	-	-	-	-	-	-	0.00	0.00	0.75
Late*Date	-	-	-	-	-	-	0.00	0.00	1.00
None*Date	-	-	-	-	-	-	**-0.01**	**0.00**	**0.00**
2015*Date	**-0.01**	**0.01**	**0.05**	**-0.01**	**0.01**	**0.05**	-	-	-
2016*Date	**0.03**	**0.00**	**0.00**	**0.03**	**0.00**	**0.00**	-	-	-

	Intertidal resin NO_3^--N model 2			Intertidal resin NO_3^--N model 3			Microlysimeter NO_3^--N model 1		
	Year*Date + Grazing			Year + Grazing*Date + Season			Year*Date		
Effect	Value	SE	P	Value	SE	P	Value	SE	P
Intercept	**-9.96**	**0.37**	**0.00**	**-11.23**	**0.48**	**0.00**	**3.07**	**0.40**	**0.00**
2015	-	-	-	-	-	-	**5.17**	**0.72**	**0.00**
2016	**-2.15**	**0.48**	**0.00**	**-0.85**	**0.07**	**0.00**	**2.30**	**0.55**	**0.00**
Early	**0.30**	**0.11**	**0.01**	0.50	0.66	0.45	-	-	-
Late	0.04	0.11	0.71	0.05	0.67	0.95	-	-	-
None	0.01	0.11	0.95	**2.01**	**0.67**	**0.01**	-	-	-
Date	**-0.01**	**0.00**	**0.00**	0.00	0.00	0.61	0.00	0.00	0.67
Advanced	-	-	-	0.00	0.08	0.96	-	-	-
Early*Date	-	-	-	0.00	0.00	0.75	-	-	-
Late*Date	-	-	-	0.00	0.00	1.00	-	-	-
None*Date	-	-	-	**-0.01**	**0.00**	**0.00**	-	-	-
2015*Date	-	-	-	-	-	-	**-0.02**	**0.00**	**0.00**
2016*Date	**0.01**	**0.00**	**0.01**	-	-	-	**-0.01**	**0.00**	**0.00**

	Microlysimeter NO_3^--N model 2			Microlysimeter NO_3^--N model 3			Microlysimeter NO_3^--N model 4		
	Year*Date + Season			Year*Date + Grazing			Year*Date + Season + Grazing		
Effect	Value	SE	P	Value	SE	P	Value	SE	P
Intercept	**3.02**	**0.40**	**0.00**	**2.92**	**0.41**	**0.00**	**2.87**	**0.41**	**0.00**
2015	**5.17**	**0.72**	**0.00**	**5.15**	**0.72**	**0.00**	**5.15**	**0.72**	**0.00**
2016	**2.31**	**0.55**	**0.00**	**2.31**	**0.55**	**0.00**	**2.31**	**0.55**	**0.00**
Early	-	-	-	**0.26**	**0.13**	**0.04**	**0.26**	**0.13**	**0.04**
Late	-	-	-	0.19	0.12	0.14	0.19	0.12	0.14
None	-	-	-	0.12	0.12	0.35	0.12	0.12	0.36
Date	0.00	0.00	0.66	0.00	0.00	0.65	0.00	0.00	0.64
Advanced	0.10	0.09	0.26	-	-	-	0.10	0.09	0.26
Early*Date	-	-	-	-	-	-	-	-	-
Late*Date	-	-	-	-	-	-	-	-	-
None*Date	-	-	-	-	-	-	-	-	-
2015*Date	**-0.02**	**0.00**	**0.00**	**-0.02**	**0.00**	**0.00**	**-0.02**	**0.00**	**0.00**
2016*Date	**-0.01**	**0.00**	**0.00**	**-0.01**	**0.00**	**0.00**	**-0.01**	**0.00**	**0.00**

	N-mineralization NH_4^+-N model 1			N-mineralization NH_4^+-N model 2			N-mineralization NO_3^--N model 1		
	Season			Null model			Null model		
Effect	Value	SE	P	Value	SE	P	Value	SE	P
Intercept	**1.66**	**0.07**	**0.00**	-	-	-	-	-	-
2015	-	-	-	-	-	-	-	-	-
2016	-	-	-	-	-	-	-	-	-
Early	-	-	-	-	-	-	-	-	-
Late	-	-	-	-	-	-	-	-	-
None	-	-	-	-	-	-	-	-	-
Date	-	-	-	-	-	-	-	-	-
Advanced	-0.19	0.10	0.08	-	-	-	-	-	-
Early*Date	-	-	-	-	-	-	-	-	-
Late*Date	-	-	-	-	-	-	-	-	-
None*Date	-	-	-	-	-	-	-	-	-
2015*Date	-	-	-	-	-	-	-	-	-
2016*Date	-	-	-	-	-	-	-	-	-

	N-mineralization NO_3^--N model 2			Microlysimeter amino acid model 1			Microlysimeter amino acid model 2		
	Season			Year*Date + Grazing			Year*Date + Season + Grazing		
Effect	Value	SE	P	Value	SE	P	Value	SE	P
Intercept	**0.80**	**0.06**	**0.00**	**1.72**	**0.31**	**0.00**	**1.75**	**0.31**	**0.00**
2015	-	-	-	**3.26**	**0.58**	**0.00**	**3.26**	**0.58**	**0.00**
2016	-	-	-	**-3.62**	**0.45**	**0.00**	**-3.61**	**0.45**	**0.00**
Early	-	-	-	**0.20**	**0.09**	**0.04**	**0.20**	**0.09**	**0.04**
Late	-	-	-	-0.05	0.09	0.63	-0.04	0.09	0.64
None	-	-	-	-0.04	0.09	0.64	-0.04	0.09	0.65
Date	-	-	-	**-0.01**	**0.00**	**0.00**	**-0.01**	**0.00**	**0.00**
Advanced	-0.01	0.06	0.82	-	-	-	-0.07	0.07	0.27
Early*Date	-	-	-	-	-	-	-	-	-
Late*Date	-	-	-	-	-	-	-	-	-
None*Date	-	-	-	-	-	-	-	-	-
2015*Date	-	-	-	**-0.01**	**0.00**	**0.00**	**-0.01**	**0.00**	**0.00**
2016*Date	-	-	-	**0.02**	**0.00**	**0.00**	**0.02**	**0.00**	**0.00**

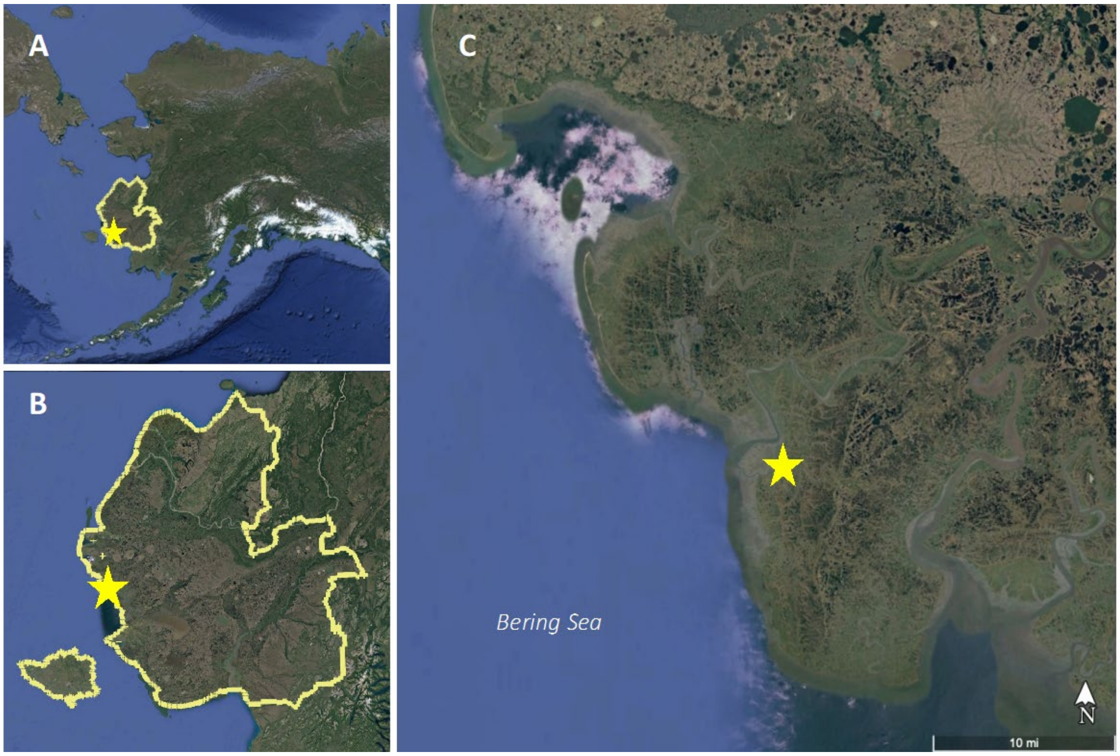

Figure B1. Map of Tutakoke River field site in the coastal Yukon-Kuskokwim Delta, Alaska. (A) Alaska; (B) Yukon Delta National Wildlife Refuge; (C) Tutakoke River field site. Yellow line = refuge boundary; yellow stars = field camp location. Imagery from Google Earth.

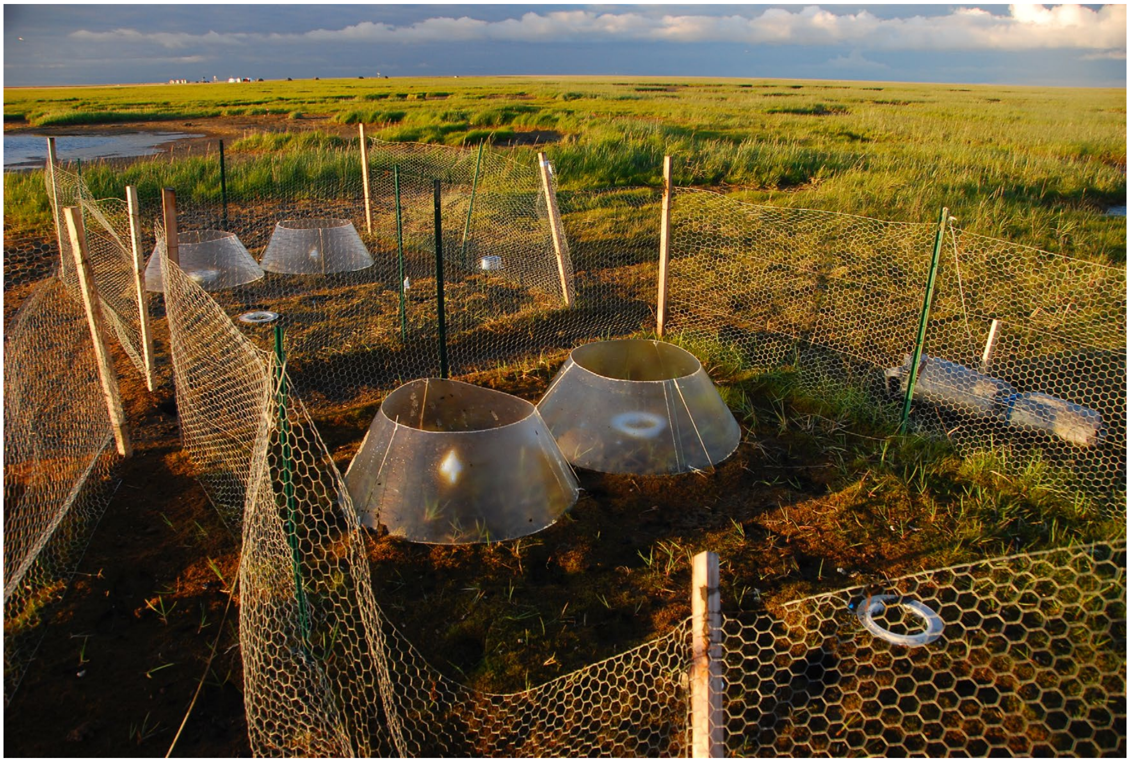

Figure B2. Experimental treatment plots. Open-top chambers were used for season advancement treatments. Fenced exclosures were used for goose grazing treatments.

Figure B3. Flooded experimental treatment plots during a high spring tide. Plots were inundated by brackish seawater for several hours at peak flood.

Appendix C – Supplementary Information for Chapter 4

Table C1. Coastal terrace vegetation percent cover averaged across all treatments. Functional group classifications from the USDA NRCS Plant Database (https://plants.sc.egov.usda.gov).

Species	Functional Group	Percent Cover		
		T1	T2	T3
Dead biomass		14.54%	16.09%	33.83%
Argentina egedei	Forb	19.20%	10.51%	
Calamagrostis deschampsioides	Grass	5.57%	0.98%	
Carex aquatilis	Sedge			1.98%
Carex glareosa	Sedge	5.83%	13.13%	0.14%
Carex lyngbyaei	Sedge			0.09%
Carex ramenskii	Sedge	14.94%	26.77%	8.82%
Carex rariflora	Sedge		0.12%	27.29%
Chrysanthemum arcticum	Forb	0.59%	0.73%	2.22%
Conioselinum chinense	Forb			0.05%
Deschampsia caespitosa	Grass	5.85%	9.21%	7.07%
Empetrum nigrum	Shrub			2.57%
Festuca rubra	Grass	0.26%	7.61%	7.36%
Leymus mollis	Grass	16.77%	1.04%	0.80%
Ligusticum scoticum	Forb	0.03%	1.18%	0.03%
Moss sp.	Moss			0.36%
Parnassia palustris	Forb		0.00%	
Poa eminens	Grass	7.15%	8.20%	0.50%
Primula borealis	Forb		0.01%	0.04%
Puccinellia phryganodes	Grass	3.64%	0.00%	
Rhodiola rosea	Forb			0.19%
Rumex arcticus	Forb			0.00%
Salix fuscescens	Shrub			4.81%
Salix ovalifolia	Shrub		1.23%	
Stellaria humifusa	Forb	1.90%	0.63%	
Triglochin palustris	Grass	3.73%	2.55%	1.84%
TOTAL		100.00%	100.00%	100.00%

Table C2. ANOVA results for species percent cover community diversity measurements (richness, evenness, Shannon diversity) across all terraces (T1, T2, T3). Bolding indicates P < 0.05; DF = degrees of freedom.

		Cross-terrace diversity		
	DF	Richness	Evenness	Shannon
Warming	1	**0.020**	0.121	0.971
Grazing	1	**0.045**	**<0.001**	**<0.001**
Terrace	2	**<0.001**	**<0.001**	**<0.001**
Date	2	**<0.001**	**0.022**	**<0.001**
Warming * Grazing	1	0.398	0.122	**0.040**
Warming * Terrace	2	0.872	**0.015**	0.175
Grazing * Terrace	2	0.646	**0.002**	0.122
Warming * Grazing * Terrace	2	0.266	**0.021**	0.138
Residuals	274			
Total	287			

Table C3. PERMANOVA results for vegetation community percent cover composition by functional group and species across on individual terraces (T1, T2, T3). Bolding indicates $p < 0.05$; DF = degrees of freedom; SS = sum of squares; MS = mean of squares.

	DF	SS	MS	F-model	R^2	*p*
Cross-terrace functional cover						
Warming	1	0.052	0.052	0.926	0.002	0.403
Grazing	1	0.598	0.598	10.623	0.018	**0.001**
Terrace	2	8.974	4.487	79.661	0.276	**0.001**
Date	2	6.671	3.336	59.219	0.205	**0.001**
Warming * Grazing	1	0.061	0.061	1.083	0.002	0.334
Warming * Terrace	2	0.063	0.031	0.555	0.002	0.731
Grazing * Terrace	2	0.633	0.317	5.622	0.019	**0.001**
Warming * Grazing * Terrace	2	0.078	0.039	0.693	0.002	0.617
Residuals	274	15.433	0.056		0.474	
Total	287	32.563			1	
Cross-terrace species cover						
Warming	1	0.078	0.078	0.706	0.001	0.618
Grazing	1	1.045	1.045	9.411	0.016	**0.001**
Terrace	2	25.792	12.896	116.119	0.389	**0.001**
Date	2	7.226	3.613	32.532	0.109	**0.001**
Warming * Grazing	1	0.113	0.113	1.014	0.002	0.374
Warming * Terrace	2	0.128	0.064	0.578	0.002	0.848
Grazing * Terrace	2	1.341	0.670	6.037	0.020	**0.001**
Warming * Grazing * Terrace	2	0.144	0.072	0.648	0.002	0.788
Residuals	274	30.430	0.111		0.459	
Total	287	66.297			1	
T1 functional cover						
Warming	1	0.049	0.049	0.550	0.005	0.590
Grazing	1	0.517	0.517	5.803	0.052	**0.009**
Date	2	1.546	0.773	8.674	0.156	**0.001**
Warming * Grazing	1	0.070	0.070	0.785	0.007	0.455
Warming * Date	2	0.031	0.015	0.171	0.003	0.949
Grazing * Date	2	0.231	0.116	1.298	0.023	0.256
Warming * Grazing * Date	2	0.012	0.006	0.068	0.001	0.981
Residuals	84	7.485	0.089		0.753	
Total	95	9.940			1	
T1 species cover						

Warming	1	0.093	0.093	0.523	0.005	0.779
Grazing	1	1.166	1.166	6.556	0.062	**0.001**
Date	2	2.067	1.033	5.810	0.109	**0.001**
Warming * Grazing	1	0.165	0.165	0.925	0.009	0.445
Warming * Date	2	0.111	0.055	0.311	0.006	0.994
Grazing * Date	2	0.353	0.177	0.993	0.019	0.458
Warming * Grazing * Date	2	0.042	0.021	0.117	0.002	0.999
Residuals	84	14.940	0.178		0.789	
Total	95	18.936			1	
T2 functional cover						
Warming	1	0.044	0.044	0.762	0.006	0.486
Grazing	1	0.204	0.204	3.519	0.026	**0.027**
Date	2	2.529	1.264	21.853	0.318	**0.001**
Warming * Grazing	1	0.003	0.003	0.059	0.000	0.955
Warming * Date	2	0.052	0.026	0.451	0.007	0.819
Grazing * Date	2	0.254	0.127	2.195	0.032	0.073
Warming * Grazing * Date	2	0.006	0.003	0.052	0.001	0.998
Residuals	84	4.860	0.058		0.611	
Total	95	7.953			1	
T2 species cover						
Warming	1	0.051	0.051	0.540	0.004	0.694
Grazing	1	0.666	0.666	7.044	0.053	**0.001**
Date	2	3.341	1.671	17.680	0.266	**0.001**
Warming * Grazing	1	0.014	0.014	0.148	0.001	0.966
Warming * Date	2	0.074	0.037	0.391	0.006	0.943
Grazing * Date	2	0.441	0.221	2.336	0.035	**0.028**
Warming * Grazing * Date	2	0.023	0.012	0.123	0.002	0.993
Residuals	84	7.937	0.094		0.633	
Total	95	12.547			1	
T3 functional cover						
Warming	1	0.010	0.010	0.522	0.002	0.586
Grazing	1	0.479	0.478	24.159	0.083	**0.002**
Date	2	2.869	1.435	72.435	0.496	**0.002**
Warming * Grazing	1	0.072	0.072	3.635	0.012	**0.046**
Warming * Date	2	0.029	0.015	0.742	0.005	0.584
Grazing * Date	2	0.628	0.314	15.848	0.109	**0.002**
Warming * Grazing * Date	2	0.034	0.017	0.868	0.006	0.480
Residuals	84	1.664	0.020		0.288	
Total	95	5.785			1	

T3 species cover						
Warming	1	0.063	0.063	1.113	0.007	0.358
Grazing	1	0.554	0.554	9.824	0.061	**0.001**
Date	2	2.796	1.398	24.773	0.310	**0.001**
Warming * Grazing	1	0.078	0.078	1.383	0.009	0.234
Warming * Date	2	0.040	0.020	0.356	0.004	0.954
Grazing * Date	2	0.712	0.356	6.306	0.079	**0.001**
Warming * Grazing * Date	2	0.038	0.019	0.338	0.004	0.958
Residuals	84	4.741	0.056		0.525	
Total	95	9.022			1	

Table C4. ANOVA p-values for vegetation percent cover by functional groups (FG) across all terraces. Bolding indicates *p* < 0.05

	Warming	Grazing	Terrace	Warm*Graz	Warm*Terr	Graz*Terr	W*G*T
Cross-terrace FG	*p*	*p*	*p*	*p*	*p*	*p*	*p*
Dead	0.304	0.092	**<0.001**	0.289	0.996	**0.011**	0.672
Forb	0.255	**<0.001**	**<0.001**	0.355	0.523	**0.001**	0.357
Grass	0.366	**0.020**	**<0.001**	0.408	0.383	**0.060**	0.705
Sedge	0.873	0.343	**<0.001**	0.356	0.494	**0.003**	0.489
Shrub	0.465	0.089	**<0.001**	0.235	0.742	0.129	0.052

Table C5. ANOVA results for species percent cover community diversity measurements (richness, evenness, Shannon diversity) on terraces (T1, T2, T3). Bolding indicates $p < 0.05$; DF = degrees of freedom.

		T1			T2			T3		
	DF	Richness	Evenness	Shannon	Richness	Evenness	Shannon	Richness	Evenness	Shannon
Warming	1	0.272	**0.028**	0.231	0.244	0.833	0.354	0.185	0.197	0.142
Grazing	1	0.108	**<0.001**	**<0.001**	0.096	0.158	0.189	**0.002**	0.189	0.061
Date	2	0.271	0.863	0.288	**<0.001**	**0.003**	**<0.001**	**0.043**	**<0.001**	**<0.001**
Warming * Grazing	2	0.151	**0.045**	**0.030**	0.617	0.401	0.992	**0.004**	0.240	0.924
Warming * Date	1	0.479	0.505	0.567	0.460	0.768	0.687	0.896	0.523	0.801
Grazing * Date	2	0.421	**0.029**	0.251	0.641	0.687	0.611	0.637	**0.003**	**0.038**
Warm*Grazing*Date	2	0.911	0.491	0.864	0.920	0.368	0.491	0.213	0.964	0.885
Residuals	84									
Total	96									

Table C6. ANOVA p-values for vegetation percent cover by species and functional group selected as significant by NMDS ordination on individual terraces (T1, T2, T3). Bold indicates $p < 0.05$. Warm = warming treatment; Gr

	Warm	Graz	Date	Warm* Graz	Warm* Date	Graz* Date	W*G*D
T1 functional cover	p	p	p	p	p	p	p
Dead	0.520	0.298	**<0.001**	0.110	0.737	**<0.001**	0.738
Forb	0.205	**0.000**	**0.049**	0.118	0.085	**0.035**	0.447
Grass	0.203	**0.001**	**<0.001**	0.559	**0.018**	**<0.001**	0.287
Sedge	0.443	0.080	**0.005**	0.132	0.327	0.762	0.099
T1 species cover							
A. egedei	0.530	**<0.001**	**0.024**	0.103	0.065	**0.023**	0.382
C. deschampsioides	0.185	0.742	**<0.001**	0.417	0.142	0.531	0.363
C. glareosa	0.457	0.070	0.052	0.485	0.269	0.281	0.793
C. ramenskii	0.113	0.684	**0.009**	0.064	**0.049**	0.816	0.071
D. caespitosa	0.218	**<0.001**	**<0.001**	0.112	0.960	0.962	0.635
L. mollis	0.687	**<0.001**	0.316	0.169	0.881	**0.057**	0.291
P. eminens	0.434	**0.019**	**<0.001**	0.941	0.575	**0.016**	0.373
P. phryganodes	0.880	**0.014**	**<0.001**	0.382	0.821	**0.008**	0.631
T. palustris	0.873	0.052	**<0.001**	0.291	0.518	0.397	0.633
T2 functional cover							
Dead	0.111	0.108	**<0.001**	0.841	0.102	**<0.001**	0.470
Forb	0.743	**<0.001**	**<0.001**	0.759	0.957	**0.026**	0.555
Grass	0.126	**0.004**	**<0.001**	0.914	0.158	**0.024**	0.597
Sedge	0.099	0.258	**0.008**	0.890	0.263	**<0.001**	0.906
Shrub	0.236	0.100	0.303	0.868	0.221	0.480	0.325
T2 species cover							
A. egedei	0.381	**0.002**	0.323	0.862	0.429	0.063	0.854
C. deschampsioides	0.725	0.819	**0.002**	0.666	0.913	0.856	0.967
C. glareosa	0.250	**0.004**	0.421	0.530	0.592	0.531	0.967
C. ramenskii	0.176	**0.001**	**0.003**	0.908	0.134	**<0.001**	0.971
C. arcticum	0.137	**0.002**	**<0.001**	0.346	**0.026**	**0.011**	0.460
D. caespitosa	0.760	**0.004**	**<0.001**	0.719	**0.045**	0.871	0.502
F. rubra	0.597	0.181	0.976	0.394	0.421	0.665	0.553
L. mollis	0.996	**0.006**	**<0.001**	0.666	0.829	0.567	0.759
L. scoticum	0.332	0.759	**0.002**	0.833	0.801	0.872	0.493
P. eminens	0.053	**<0.001**	**<0.001**	0.972	0.185	**<0.001**	0.699
S. ovalifolia	0.236	0.100	0.303	0.868	0.221	0.480	0.325
S. humifusa	0.478	**0.009**	0.302	0.954	0.056	0.649	0.183
T. palustris	0.710	0.120	**<0.001**	0.714	0.759	0.782	0.463

T3 functional cover							
Dead	0.197	**<0.001**	**<0.001**	0.124	0.240	**<0.001**	**0.016**
Forb	0.520	0.101	**<0.001**	0.591	0.816	0.139	0.868
Grass	0.712	0.995	**<0.001**	0.060	0.126	0.074	**0.038**
Sedge	0.472	**<0.001**	**<0.001**	0.414	0.411	**<0.001**	0.683
Shrub	0.799	0.241	**<0.001**	0.134	0.340	**0.005**	0.464
T3 species cover							
C. aquatilis	0.413	0.674	0.074	0.303	0.815	0.946	**0.037**
C. ramenskii	0.778	0.325	**<0.001**	0.092	0.359	**0.001**	0.189
C. rariflora	0.360	**<0.001**	**<0.001**	0.671	0.110	**<0.001**	0.530
C. arcticum	0.563	0.075	**<0.001**	0.537	0.615	0.229	0.790
D. caespitosa	0.976	0.604	**<0.001**	0.851	0.806	0.893	0.496
F. rubra	0.462	0.886	**<0.001**	0.338	**0.033**	0.188	0.603
L. mollis	0.620	0.316	0.226	0.364	0.942	0.488	0.732
R. rosea	-	-	-	-	-	-	-
S. fuscescens	0.110	0.338	**<0.001**	0.138	0.589	**0.013**	0.551

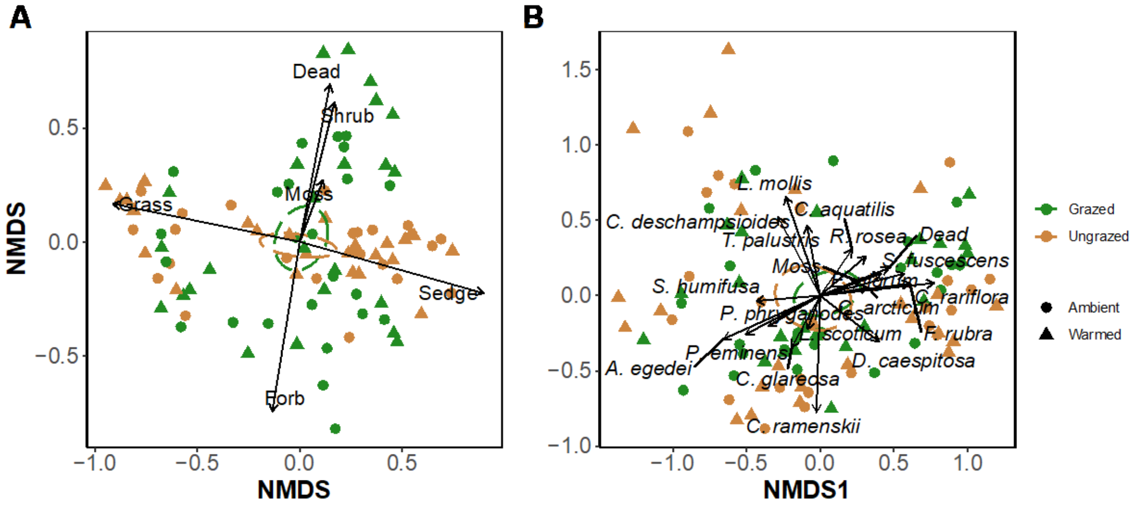

Figure C1. Percent cover composition across all coastal terraces by (A) functional group and (B) species. Ellipses indicate 95% confidence values (SE).

CURRICULUM VITAE

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Education

2021	Ph.D. in Ecology Utah State University	Studied climate-driven impacts of warming and grazing in coastal sub-arctic wetlands. Graduated with Emphasis in Climate Adaptation Science.
2011	M.S. in Ecology Utah State University	Studied impacts of invasive frogs on arthropod communities in the sub-tropics.
2005	B.A. in Biology Whitman College	Studied phylogeographic distribution of lizards in the desert southwest. Graduated with Distinction.

Peer-reviewed Publications

Choi, R.T., K.H. Beard, A.J. Leffler, K.C. Kelsey, J.A. Schmutz, J.M. Welker. 2020. Early goose arrival increases soil nitrogen availability more than an advancing spring in coastal western Alaska. *Ecosystems*. 23(6): 1309-1324. DOI: 10.1007/s10021-019-00472-9

Leffler, A.J., K.H. Beard, K.C. Kelsey, R.T. Choi, J.A. Schmutz, J.M. Welker. 2019. Cloud cover and delayed herbivory relative to timing of spring onset interact to dampen climate change impacts on net ecosystem exchange in a coastal Alaskan wetland. *Environmental Research Letters,* 14(8):084030. DOI: 10.1088/1748-9326/ab1c91

Choi, R.T., K.H. Beard, A.J. Leffler, K.C. Kelsey, J.A. Schmutz, J.M. Welker. 2019. Phenological mismatch between season advancement and migration timing alters Arctic plant traits. *Journal of Ecology*, 107(5): 2503-2518. DOI:10.1111/1365-2745.13191

Beard, K.H., R.T. Choi, A.J. Leffler, L.G. Carlson, K.C. Kelsey, J.A. Schmutz, J.M. Welker.

2019. Migratory goose arrival time plays a larger role in influencing forage quality than advancing springs in an Arctic coastal wetland. *PLoS ONE* 14(3): e0213037. DOI: 10.1371/journal.pone.0213037

Leffler, A.J., K.H. Beard, K.C. Kelsey, R.T. Choi, J.A. Schmutz, J.M. Welker. 2019. Delayed herbivory by migratory geese increases summer-long CO2 uptake in coastal western Alaska. *Global Change Biology* 25(1): 277-289. DOI: 10.1111/gcb.14473

Prudencio, L., R.T. Choi, E. Esplin, M. Ge, N. Gillard, J. Haight, P. Belmont, C. Flint. 2018. The impacts of wildfire characteristics and employment on the adaptive management strategies in the Intermountain West. *Fire* 1(3): 46. DOI: 10.3390/fire1030046

Adler, P.B., D. Smull, K.H. Beard, R.T. Choi, T. Furniss, A. Kulmatiski, J.M. Meiners, A.T. Tredennick, K.E. Veblen. 2018. Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology Letters* 21(9): 1319-1329. DOI: 10.1111/ele.13098

Kelsey, K.C., A. J. Leffler, K.H. Beard, R.T. Choi, J.A. Schmutz, J.M. Welker. 2018. Phenological mismatch in coastal western Alaska may increase summer season greenhouse gas uptake. *Environmental Research Letters.* 13(4): 044032. DOI: 10.1088/1748-9326/aab698

Kelsey, K.C., A.J. Leffler, K.H. Beard, J.A. Schmutz, R.T. Choi, and J.M. Welker. 2016. Interactions among climate, topography and herbivory control greenhouse gas (CO_2, CH_4, and N_2O) fluxes in a subarctic coastal wetland. *Journal of Geophysical Research – Biogeosciences* 121(12): 2960-2975. DOI:10.1002/2016JG003546

Ferreira, R.B., K.H. Beard, R.T. Choi, and W.C. Pitt. 2015. Diet of the introduced Greenhouse frog (Eleutherodactylidae*: Eleutherodactylus planirostris*) in Maui, Hawaii. *Journal of Herpetology* 49(4): 586-593. DOI: 10.1670/14-103

Choi, R.T., and K.H. Beard. 2012. Coqui frog invasions change invertebrate communities in Hawaii. *Biological Invasions* 14(5): 939-948. DOI: 10.1007/s10530-011-0127-3

In Review

Choi, R.T., S.C. Reed, C.L. Tucker. *In review.* Multiple resource (co-) limitation of dryland soil carbon cycling. *Ecology.*

Choi, R.T., K.H. Beard, A.J. Leffler, K.C. Kelsey, J.M. Welker. *In review* Climate-induced changes alter coastal wetland plant communities. *Journal of Vegetation Science.*

Teaching

BIOL 1625 - Introductory Biology II. 2021. Graduate Teaching Assistant. 48 students.
BIOL 1615 - Introductory Biology I. 2020. Graduate Teaching Assistant. 48 students.

WILD 2400 - Wildland Resource Techniques. 2020. Graduate Teaching Assistant. 54 students.

BIOL 2420 - Human Physiology. 2020. Graduate Teaching Assistant. 48 students.

WILD 2200 - Ecology of Our Changing World 2020. Graduate Teaching Assistant. 90 students.

BIOL 4400 - Plant Physiology. 2020. Graduate Teaching Assistant. 48 students.

WILD 4600 - Conservation Biology. 2011. Graduate Teaching Assistant. 24 students.

Conference Presentations and Abstracts (*Selected*)

Choi, R.T., Beard, K.H., A.J. Leffler, K.C. Kelsey, J.M. Welker. Climate-induced vegetation changes differ with distance from the coast in sub-arctic Alaska. Ecological Society of America Annual Meeting, 3-6 August 2020. Online presentation.

Reed, S.C., M. Phillips, R. Reibold, R.T. Choi, C. Tucker. More than just water: Multiple resource control over dryland ecosystem function. Ecological Society of America Annual Meeting, 3-6 August 2020. Online presentation.

Leffler, A.J., K.H. Beard, K.C. Kelsey, R.T. Choi, J.M. Welker. Phenological mismatch in a coastal Alaskan wetland: Impacts on N-cycling and C uptake. Ecological Society of America Annual Meeting, 3-6 August 2020. Online presentation.

Beard, K.H., A.J. Leffler, K.C. Kelsey, R.T. Choi, J.M. Welker. What are phenological mismatch studies missing? Perspectives on adding in ecosystem responses. Ecological Society of America Annual Meeting, 3-6 August 2020. Online presentation.

Leffler, A.J., K.H. Beard, K.C. Kelsey, R.T. Choi, J.M. Welker. Net effects of early phenology, increased cloud cover, and altered timing of plant interactions dampen climate change impacts on net ecosystem exchange of C in a coastal Alaska wetland. American Geophysical Union Fall Meeting, Washington D.C., 12 December 2018. Poster presentation.

Choi, R.T., E. Esplin, M. Ge, N. Gillard, J. Haight, L. Prudencio, P. Belmont, C. Flint. Assessing fire trends, economic effects and adaptive management strategies in the Intermountain West. American Geophysical Union Fall Meeting, Washington D.C., 10 December 2018. Poster presentation.

Choi, R.T., K.H. Beard, A.J. Leffler, L.G. Carlson, K.C. Kelsey, J.A. Schmutz, J.M. Welker. Asynchrony in the timing of goose-vegetation interactions: Implications for biogeochemical cycling in wet sedge tundra. Ecological Society of America Annual Meeting, Portland, Oregon, 10 August 2017. Oral presentation.

Kelsey, K.C., A.J. Leffler, K.H. Beard, R.T. Choi, J.M. Welker. Climate driven changes in the timing of grazing alters greenhouse gas emissions (CO_2, CH_4, and N_2O) from Alaskan coastal tundra. Ecological Society of America Annual Meeting, Portland, Oregon, 8 August 2017. Oral presentation.

Beard, K.H., L.G. Carlson, R.T. Choi, T. DeMasters, A.J. Leffler, K.C. Kelsey, J.M. Welker. Mechanisms of herbivory interact to maintain high quality forage and reduce greenhouse gas emissions. Ecological Society of America Annual Meeting, Portland, Oregon, 7 August 2017. Poster presentation.

Choi, R.T., K.H. Beard, A.J. Leffler, L.G. Carlson, K.C. Kelsey, J.A. Schmutz, J.M. Welker. Interactions between the start of the growing season and migratory goose arrival influence C and N cycling in wet sedge tundra. Ecological Society of America Annual Meeting, Fort Lauderdale, Florida, 12 August 2016. Poster presentation.

Leffler, A.J., K.H. Beard, K.C. Kelsey, R.T. Choi, and J.M. Welker. Earlier growing seasons and changes in timing of grazing by Black Brant alter net ecosystem exchange in an Arctic coastal wetland. Ecological Society of America Annual Meeting, Fort Lauderdale, Florida, 11 August 2016. Oral presentation.

Leffler, A.J., K.H. Beard, K.C. Kelsey, R.T. Choi, and J.M. Welker. Earlier growing seasons and changes in migration timing influence carbon uptake and plant production in Arctic coastal wetlands. American Geophysical Union Fall Meeting, San Francisco, California, 16 December 2015. Oral presentation.

Kelsey, K.C., A.J. Leffler, K.H. Beard, R.T. Choi, and J.M. Welker. Sub-arctic wetland greenhouse gases (CO_2, CH_4, & N_2O) emissions are driven by interactions of environmental controls and herbivore grazers. American Geophysical Union Fall Meeting, San Francisco, California, 16 December 2015. Oral presentation.

Choi, R.T., K.H. Beard, A.J. Leffler, J.A. Schmutz, and J.M. Welker. Leaf tissue C:N and soil N are modified by growing season and goose grazing phenology in a sub-arctic coastal wetland of Western Alaska. American Geophysical Union Fall Meeting, San Francisco, California. 12 December 2014. Poster presentation.

Grants, Scholarships, and Awards

2019

School of Graduate Studies Dissertation Fellowship, Utah State University - $5,000

2018

Research and Graduate Studies Graduate Student Travel Grant (AGU), Utah State University – $300
College of Natural Resources Travel Grant (AGU), Utah State University - $300
Department of Wildland Resources Travel Grant (AGU), Utah State University - $300
Ecology Center Travel Grant (AGU), Utah State University - $750
Climate Adaptation Science Program Travel Grant (AGU), Utah State University - $900

2017

Research and Graduate Studies Dissertation Enhancement Award, Utah State - $10,000
Ecology Center Travel Grant (ESA), Utah State University - $400
Department of Wildland Resources Travel Grant (ESA), Utah State University - $300

2016

NSF Climate Adaptation Science Fellowship, Utah State University - $34,000
Ecology Center Research Award, Utah State University - $4,000

2015
J.W. Marr Ecology Fund Research Grant, University of Colorado Boulder - $1000
Ecology Center Research Award, Utah State University - $3,000

2014
Ecology Center Travel Grant (AGU), Utah State University - $383
Department of Wildland Resources Travel Grant (AGU), Utah State University - $300
Presidential Doctoral Research Fellowship, Utah State University - $80,000

2010
Terry Lynn Steel Award, Utah State University - $400

2009
Xi Sigma Pi, Natural Resource Honor Society, Utah State University
Ecology Center Research Award, Utah State University- $3,000

2008
S.J. & Jessie E. Quinney Masters Fellowship, Utah State University - $30,000

Popular Media

Journal of Ecology video abstract: Phenological mismatch between season advancement and migration timing alters Arctic plant traits (2019) https://www.youtube.com/watch?v=G6K3CYqmuPQ&t=3s

KZMU Science Moab radio interview: Keeping Pace with Climate Change (2018) https://soundcloud.com/user-495802209/keeping-pace-with-climate-change

Frontier Scientists online video: Birds, Plants, and Climate Transform the Y-K Delta (2017) https://frontierscientists.com/videos/migratory-birds-vegetation-climate-transform-yukon-delta-ecosystem/

Frontier Scientists online video: Charlotte – A Gas Analyzer System in the Y-K Delta (2017) https://frontierscientists.com/videos/charlotte-greenhouse-gas-analyzer-science-equipment-climate-flux-data/

Frontier Scientists online video: Grazing, Trampling, & Fecal Deposition (2017) https://frontierscientists.com/videos/grazing-trampling-fecal-deposition-geese-vegetation-carbon-nitrogen-ratio/

Frontier Scientists online video: Setting Up Camp on the Tutakoke River (2017) https://frontierscientists.com/videos/research-camp-tutakoke-river-yukon-refuge-alaska-fieldwork-scientists/

Indie Alaska online video: Life at a Remote Research Camp (2016) https://www.youtube.com/watch?v=krPCzXTnqNc&feature=emb_title