LETTER • OPEN ACCESS

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

To cite this article: A Joshua Leffler et al 2019 Environ. Res. Lett. 14 084030

View the article online for updates and enhancements.
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

A Joshua Lef
er1, Karen H Beard1, Katharine C Kelsey1, Ryan T Choi1, Joel A Schmutz2 and Jeffrey M Welker3,5

1 Department of Natural Resource Management, South Dakota State, University, Brookings, SD 57006, United States of America
2 Department of Wildland Resources, Utah State University and the Ecology Center, Logan, UT 84322-5230, United States of America
3 Department of Biological Sciences, University of Alaska-Anchorage, Anchorage, AK 99508, United States of America
4 US Geological Survey Alaska Science Center, Anchorage, AK 99508, United States of America
5 UArctic, Ecology and Genetics Research Unit, University of Oulu, Finland

E-mail: joshua.lef
er@sdstate.edu

Keywords: phenological mismatch, net ecosystem exchange, migratory geese, grazing, herbivory, Arctic ecosystem, cloud cover

Abstract

Rapid warming in northern ecosystems over the past four decades has resulted in earlier spring, increased precipitation, and altered timing of plant–animal interactions, such as herbivory. Advanced spring phenology can lead to longer growing seasons and increased carbon (C) uptake. Greater precipitation coincides with greater cloud cover possibly suppressing photosynthesis. Timing of herbivory relative to spring phenology influences plant biomass. None of these changes are mutually exclusive and their interactions could lead to unexpected consequences for Arctic ecosystem function. We examined the influence of advanced spring phenology, cloud cover, and timing of grazing on C exchange in the Yukon–Kuskokwim Delta of western Alaska for three years. We combined advancement of the growing season using passive-warming open-top chambers (OTC) with controlled timing of goose grazing (early, typical, and late season) and removal of grazing. We also monitored natural variation in incident sunlight to examine the C exchange consequences of these interacting forcings. We monitored net ecosystem exchange of C (NEE) hourly using an autochamber system. Data were used to construct daily light curves for each experimental plot and sunlight data coupled with a clear-sky model was used to quantify daily and seasonal NEE over a range of incident sunlight conditions. Cloudy days resulted in the largest suppression of NEE, reducing C uptake by approximately 2 g C m−2 d−1 regardless of the timing of the season or timing of grazing. Delaying grazing enhanced C uptake by approximately 3 g C m−2 d−1. Advancing spring phenology reduced C uptake by approximately 1.5 g C m−2 d−1, but only when plots were directly warmed by the OTCs; spring advancement did not have a long-term influence on NEE. Consequently, the two strongest drivers of NEE, cloud cover and grazing, can have opposing effects and thus future growing season NEE will depend on the magnitude of change in timing of grazing and incident sunlight.

Introduction

Arctic warming over the past several decades has been nearly twice as rapid as at lower latitudes (Elmendorf et al. 2012) leading to new environmental conditions in northern ecosystems (Hinzman et al. 2013). These new states include changes to precipitation regimes and cloud cover (Schweiger 2004, Zhang et al. 2013, Klein et al. 2015), a greening of the landscape with earlier spring (Hoye et al. 2007, Tape et al. 2012, Ju and Masek 2016), and altered phenology of plant–animal interactions (Brook et al. 2015, Doiron et al. 2015). Each of these changes independently affect ecosystem functions such as carbon (C) uptake (Chapin and Shaver 1985, Post and
Pedersen 2008, Kelsey et al. 2018, Leffler et al. 2019) but they act in concert with potentially synergistic consequences.

Springtime in Arctic and sub-Arctic systems is occurring earlier (Cleland et al. 2007, Wang et al. 2018), advancing as rapidly as 3.5 days decade$^{-3}$ in North America (Ross et al. 2017). These changes are leading to longer growing seasons and earlier peak C uptake and maximum NDVI (Xu et al. 2016, Gonsamo et al. 2018), and in some cases greater total C uptake (Lafluer and Humphreys 2007) although warmer soils may mitigate enhanced ecosystem level photosynthesis through greater respiration (Parmentier et al. 2011, Leffler et al. 2019).

Advancing spring leads to phenological mismatch between plants and animals in Arctic systems (Brook et al. 2015, Doiron et al. 2015, Ross et al. 2017). Phenological mismatch occurs when organisms in different trophic positions respond to advancing spring at different rates (Inouye 2000, Nakazawa and Doi 2012) and can negatively affect animal populations (Post and Forchhammer 2008, Ross et al. 2017) and has consequences for ecosystem function. For example, delayed herbivory with respect to plant phenological stage can enhance C uptake in a coastal Alaskan wetland by allowing plants to accumulate greater aboveground biomass (Choi et al. 2019) before herbivores consume leaves (Kelsey et al. 2018, Leffler et al. 2019), and timing of herbivory influences forage quality and fecal N which are important drivers of N cycling (Beard et al. 2019).

In addition to advancing phenology, Arctic precipitation patterns are expected to change with associated influences on cloud cover and photosynthesis. Studies have reported increased storm activity (Serrette et al. 2000), higher precipitation (Min et al. 2008), and greater river discharge (Zhang et al. 2013) in the far north. Cloud cover is observed on 65%-85% of days Arctic-wide and although temporal trends in cloud cover can be difficult to detect given the short duration of satellite records (Comiso and Hall 2014) the frequency of cloudy days appears to be increasing in spring and summer (Wang and Key 2003, 2005, Schweiger 2004, but see Comiso 2003). Furthermore, coastal Arctic wetlands are rarely dry suggesting increased precipitation would not enhance C uptake by alleviating moisture stress, but rather that a cloudier future Arctic may limit available light for photosynthesis and C uptake during the short Arctic growing season.

The influence of early spring onset, phenological mismatch, and cloud cover are integrated in coastal wetlands of Arctic and sub-Arctic systems where these drivers simultaneously have important influences on C uptake. Here, spring is occurring earlier, it is frequently cloudy, and the wetlands are grazed during summer by millions of migratory birds yet the synergistic consequences of changes in each of these important drivers of C uptake remain largely unexplored. For example, grazing removes considerable photosynthetic tissue (Ruess et al. 1997), fundamentally reducing the ability of plants to capture sunlight and drive C uptake in this system. We previously demonstrated a small increase in ecosystem respiration with earlier spring and increased C uptake with delayed grazing (Leffler et al. 2019). These previous measurements were spatially extensive, but too temporally limited to address the effects of changes in light, despite light being a critical factor in ecosystem C uptake.

Here we combine experimental manipulation of spring and grazing phenology with observed incident sunlight and measure C uptake as the response to all three variables with a continuous chamber-based C flux system. Understanding the simultaneous consequences of variation in spring phenology, timing of grazing, and cloud cover requires high temporal resolution observations of C uptake that have seldom been accomplished in remote regions of the far North. We hypothesized that season advancement would increase C uptake because of earlier and more rapid growth in the spring; that early grazing would reduce C uptake while late grazing and no grazing would enhance C uptake because of shorter and longer periods of growth prior to herbivory, respectively; and that cloud cover would reduce C uptake in all scenarios, but that uptake would be suppressed the most in treatments with high C uptake because of the greater leaf area in these treatments.

**Materials and methods**

**Study location**

All research took place in a coastal wetland in the Yukon–Kuskokwim Delta (Y–K Delta) near the mouth of the Tutakoke River (61.25°N, 165.62°W; figure S1 is available online at stacks.iop.org/ERL/14/084030/mmmedia). The Y–K Delta is a sub-Arctic wetland transitioning to tundra inland to the east. The region is covered in snow and ice from late autumn to mid-spring, although there is no permafrost at the study site. The landscape consists of tidal mudflats with brackish wet-sedge meadows at higher topographic positions. Soils are silty loams with neutral pH (Jorgenson 2000) and typically exceed 50% water content during much of the spring and summer (Leffler, unpublished data).

The region experiences short, cool growing seasons and cold winters. Temperatures vary between ca. –14 °C in winter to ca. 10 °C during summer (Jorgenson and Ely 2001). The timing of spring, defined here as the day of year when 50% maximum NDVI (normalized difference vegetation index) is achieved (Brook et al. 2015), has varied between 23 May and 25 June (figure S2) between 1982 and 2016 at the study site (Douglas, unpublished data). The Y–K Delta experiences frequent cloud cover. Twelve years of MODIS (moderate resolution imaging spectroradiometer) continuous remote sensing data...
suggest that the region within a 10 km radius of our study site is clouded 73%, 83%, and 81% of days during June, July, and August, respectively.

The coastal area near the mouth of the Tutakoke River in the Y–K Delta is a nesting and brood-rearing area for Pacific black brant (Branta bernicla) with ca. 500 nests km$^{-2}$ (Fischer et al 2017). Other species including emperor geese (Anser canagica), cackling geese (B. hutchinsi minima), and greater white-fronted geese (Anser albifrons) breed nearby. Pacific black brant primarily feed on a sedge (Carex subspathacea) near brackish ponds which form ‘grazing lawns’ (a shorter stature, more nutritious growth form) when heavily grazed by geese (Ruess et al 1997, Person et al 2003). Pacific black brant and the other most abundant species (cackling geese) at this study site do not grub for belowground tissue (Person et al 2003). Intensity of grazing lawn use is tied closely to hatching date, as females recover from nutrient deficits and goslings begin to consume vegetation (Sedinger and Raveling 1990). Mean day of hatch within a year (figure S2) has varied between 11 June and 30 June (1983–2016); median hatch date among years is 21 June but the earliest and latest observed hatch has been 3 June and 9 July, respectively (Fischer et al 2008).

Long-term trends suggest the size of this goose colony may be declining. The largest populations were observed in the mid-1990s and recent recruitment has been too low to maintain populations (Sedinger et al 2007). Moreover, survival of Pacific black brant has declined between 1990 and 2015 (Leach et al 2017) potentially leading to less extensive grazing lawn and taller sedges (Ruess et al 1997, Person et al 2003).

**Experimental design**

The effects of season advancement, timing of grazing, and cloud cover on net ecosystem exchange (NEE, gross ecosystem photosynthesis minus ecosystem respiration) in grazing lawns were tested using experimental (figure 1, S2) and observational approaches for three growing seasons (1 May–20 August) from 2014 to 2016. The effects of growing season advancement and timing of grazing were tested using an experiment while we used natural variation in sunlight to examine the influence of cloud cover. There were a total of eight 1.7 m × 0.85 m plots in the experiment that had two growing season treatments (advanced and ambient) crossed with four timing of grazing treatments (early, typical, late and no grazing). We manipulated the timing of the growing season using two side-by-side passive-warming open-top chambers (OTCs; Marion et al 1997) in each advanced-season plot that were installed in early May each year.
following snowmelt; OTCs were not placed to advance snowmelt in the system nor did they substantially alter soil water content because the system receives frequent rains. Chambers were 85 cm diameter at the base, 30 cm tall, and 50 cm at the top; they warm air and soil by 1 °C–2 °C and accelerate plant growth (Post and Pedersen 2008, Leffler et al 2016, Kelsey et al 2018). Chambers were removed prior to 1 July during grazing bouts, and on 1 July, once the growing season had been advanced. Each advanced-season plot was paired with an adjacent plot without season advancement (ambient), surrounded by fencing, and subject to the same grazing treatments. We quantified season advancement using measurements of vegetation height every 1–3 weeks on 10 shoots within 10 cm × 10 cm quadrats in each plot (Leffler et al 2019).

We altered timing of grazing using four enclosures (7.6 m², one enclosure for each grazing treatment) around paired season-advancement and ambient season plots. Grazing treatments were designed to simulate the period of peak goose grazing post-hatch and were initiated at early (30 May), typical (20 June), and late (9 July) times in the season relative to historic timing of hatch (figure S2). All grazing periods lasted 37 days. We also included a set of ambient and advanced-season plots that were not grazed during the experiment. Female Pacific black brant were captured from nests and held in a fenced area after flight feathers were clipped; grazing treatments consisted of two geese randomly selected from the captive flock for four 24 h bouts inside each enclosure; bouts were separated by 12 days. Prior to each bout geese were held without food for two hours to allow any material to pass the digestive system (Prop and Vulink 1992); all feces produced for two hours following grazing bouts were collected and returned to the experimental enclosure. Treatments resulted in a grazing intensity of 7.2 goose h m⁻² month⁻¹ regardless of treatment (i.e. only differed in grazing timing), which was similar to the grazing intensity in previous studies in this system (Herzog and Sedinger 2004).

Weather conditions were monitored during each field season (Figures S3, S4). A meteorological station (Campbell Scientific, Logan, UT) located within 50 m of our plots recorded air temperature, relative humidity, wind speed and direction, precipitation, and photosynthetically active radiation (PAR, incident sunlight 400–700 nm) at 5 min intervals. These data were used to record natural variability in PAR to model effects of cloud cover.

CO₂ exchange measurements and light response curves
We monitored CO₂ exchange hourly using an autochamber system measuring NEE between 1 June and ca. 18 Aug during the three-year experiment. One autochamber (model 8100–104 C, Licor, Inc., Lincoln, NE) with a clear dome was assigned to each of the eight experimental plots and connected via a multiplexer to an infrared gas analyzer (IRGA; model 8100 A/81 50, Licor, Inc., Lincoln, NE). Each autochamber was seated to a 20 cm diameter PVC ‘collar’ installed ca. 5 cm into the soil. The IRGA was calibrated weekly. Autochambers were removed only for grazing bouts. NEE was calculated using linear and nonlinear fits of the relationship between time and [CO₂] during chamber closure. Positive values are net C release to the atmosphere, negative values are net C uptake.

Continuous NEE data were examined using the curvilinear relationship between PAR and NEE (i.e. light curves). Data from 2014 to 2016 were combined for construction of light curves using a 7 day moving window to ensure adequate variation in PAR. All PAR data were extracted from the local weather station for the 5 min average closest in time to the NEE measurement. We related NEE to PAR using a rectangular hyperbolic function (Gilmanov et al 2003):

\[
\text{NEE} = \frac{-(a \times b \times \text{PAR})}{(a \times \text{PAR} + b)} + \text{ER},
\]

where \(a\) and \(b\) are fitted parameters describing the initial slope of the curve and the asymptote respectively, and \(ER\) is dark respiration which we calculated as the mean NEE during observations with PAR < 20 μmol m⁻² s⁻¹. NEE, PAR and ER are in units of μmol m⁻² s⁻¹. The model was fit using a nonlinear 50% quantile regression in the NRLQ function of the QUANTREG package in the R Statistical Computing Environment (R Development Core Team 2017). One light response curve and the standard error of fitted parameters was produced daily for each experimental treatment between day of year 151 (30 May) and day of year 229 (17 August).

Daily NEE was calculated for each experimental treatment from the light response curves and locally observed PAR. We combined PAR data among years and used a 7 day moving window to calculate 25th, 50th, and 75th percentile PAR at a 15 min time step. These data were used as inputs to the light curve for each day and experimental treatment combination. Standard error of fitted parameters was used to bootstrap NEE and error (5000 iterations). These values were summed to calculate a daily mean and confidence interval of NEE (g C m⁻² d⁻¹) for each experimental treatment. These means and confidence intervals were summed over the observation period to estimate growing season NEE.

Finally, we used our light response curves to predict daily NEE under completely sunny conditions. We simulated full-sun conditions to demonstrate the impact that clouds have relative to other drivers of CO₂ exchange in the ecosystem. We created a 15 min time step PAR dataset using a clear-sky model. We used the INSOL package in R to calculate direct and diffuse solar radiation and converted these values to PAR as their sum multiplied by 1.9455 (Pankaew et al 2014). This conversion resulted in alignment of the
99.9th percentile of modeled and locally measured PAR. The modeled PAR was used as input to the light curves to produce a daily full-sun estimate of NEE.

Data analysis
The effectiveness of the season advancement treatment was estimated by comparing vegetation height in the ambient and advanced season treatments using only plots that were not grazed prior to 1 July of each experimental year (Lefler et al 2019). We used a linear mixed model with year, day of year, and treatment (ambient versus advanced) as fixed effects and a random plot effect to calculate vegetation height at the end of June. Confidence intervals were produced using 5000 iterations of a bootstrap. All analyses were performed using the R Statistical Computing Environment.

CO₂ exchange data were analyzed by calculating effect sizes. We used log response ratio of treatment and controls as the effect size metric (Hedges et al 1999) and treated NEE each day as a separate measure using a random effect. We used combinations of plots to test for significant differences between treatment and controls. Effects are considered significant if the 95% confidence interval does not overlap zero or the confidence intervals of other treatments.

We tested our first hypothesis, that season advancement would increase C uptake, by using ambient season plots as controls and advanced-season plots as the treatment regardless of their grazing regime (i.e. \( n = 4 \) chambers for each season treatment). We tested this hypothesis for two time frames: when the OTCs were in place (June) and following their removal (July and August); and a one-week window immediately before removal and a one-week window starting seven days following removal (to account for the time-lag associated with using seven days to construct light curves) to examine the short-term influence of the OTCs on NEE. Finally, we examined the effect size of season advancement in each grazing treatment (one plot for each grazing treatment) on NEE. We tested our second hypothesis, that early grazing would reduce C uptake while late grazing and no grazing would enhance uptake, by comparing the early, late, and grazing exclusion treatments to the typical grazing treatment as a control regardless of season advancement (\( n = 2 \) plots for each grazing treatment). We tested our third hypothesis, that cloud cover would reduce C uptake most in treatments with greater C uptake, using NEE modeled from median daily PAR (figure S4) as the treatment and the clear-sky model of daily NEE as the control. We further analyzed the influence of clouds in each season advancement treatment (\( n = 4 \) plots) and grazing treatment (\( n = 2 \) plots). Cumulative NEE and confidence intervals were calculated by summing daily values for the period 1 June–16 August.

Results
The season advancement treatment resulted in vegetation that was approximately twice as tall as the ambient treatment by late June in all three years of the study (figure 2). Based upon differences in growth rates derived from repeated height measurements, we estimate that our treatment advanced the growing season between 20 and 27 days. Mean air temperature when the OTCs were in place was 0.7 °C, 1.0 °C, and 2.4 °C warmer in the advanced compared to the ambient season treatment in 2014, 2015, and 2016,
between 1.3 and 1.6 g C m$^{-2}$ day$^{-1}$.

The advanced growing season reduced daily C uptake had a similar effect size as the longer-term analysis. In the delayed grazing treatment reduced daily C uptake was significantly less (effect size = 0.37) while the passive warming chambers were present, but the effect disappeared following removal of the OTCs after 1 July (figure 3(a)). The ephemeral nature of this effect is apparent when examining the one week periods before and one week following removal (figure 3(b)), which had a similar effect size as the longer-term analysis. The advanced growing season reduced daily C uptake between 1.3 and 1.6 g C m$^{-2}$ day$^{-1}$ (95% CI), but only while the OTCs were in place. The effect of the advanced growing season on C exchange did not vary while the OTCs were in place. The effect of the OTCs on C exchange did not vary significantly among grazing treatments (figure 3(c)).

Altering the timing of grazing significantly affected daily NEE (figure 3(d)). Specifically, late grazing increased C uptake relative to typical grazing (effect size = 0.55), but early grazing and grazing removal did not significantly alter C uptake (effect sizes = 0.08 and −0.20, respectively). The significant effect size of delayed grazing corresponded to an increase in C uptake between 1.3 and 2.2 g C m$^{-2}$ day$^{-1}$.

Cloudy days reduced C uptake in all treatments (figure 3(e)). We observed a nearly significant difference in the impact of cloudy days on ambient (effect size = 0.81) compared to advanced season (effect size = 0.54) treatments and the effect size of cloudy days did not differ between early, typical, and grazing removal treatments (effect size = 0.39, 0.40, and 0.70, respectively). Late grazing, however, was more affected by cloud cover (effect size = 1.13) than any treatment except grazing removal. Overall, the significant effect of cloudy days in the delayed grazing treatment reduced daily C uptake between 2.4 and 4.1 g C m$^{-2}$ day$^{-1}$. Averaged among all treatments, cloud covered days reduced C uptake between 1.8 and 2.1 g C m$^{-2}$ day$^{-1}$.

Our treatments simulated NEE for the period 1 June through 17 August. Typical, late, and grazing removal treatments were similar in uptake during the early season but diverged later; early grazing suppressed C uptake most of the season (figures 4(a)-(c)). The ambient growing season, typical grazing and median PAR treatment represents current conditions with a 95% CI of net C uptake between 58.6 and 109 g C m$^{-2}$ (figures 4(b),(d)). Advancing the season with no change in grazing reduced uptake of C to between 5.66 and 1.21 g C m$^{-2}$.
43.1 g C m\(^{-2}\). In contrast, advancing the season with a delay in grazing increased C uptake to between 137 and 200 g C m\(^{-2}\). Future cloud cover in the Y–K Delta that reduces incident sunlight to the 25th percentile (figure S4) of our PAR observations will fully offset any gains in C uptake achieved by delayed grazing to between 52.3 and 111 g C m\(^{-2}\), or result in a net C loss of up to 36.0 g C m\(^{-2}\) if the season is advanced but the timing of grazing by geese remains unchanged (figures 4(a), (d)).

**Discussion**

Future climate warming will lead to cascading influences on weather patterns and biological activity. Early green-up (Elmendorf et al. 2012), ensuing phenological mismatch for migratory species (Brook et al. 2015, Ross et al. 2017), and possibly cloudier skies in summer (Schweiger 2004, Wang and Key 2005) are already occurring in the Arctic. We suggest that these ongoing changes in a northern coastal wetland are exerting contradictory forcings on NEE adding to the complexity of ecosystem function responses to climate change. Early spring results in a small decrease in net C uptake, while delayed grazing by migratory geese, which may occur when geese arrive into a phenologically advanced system, enhances C uptake. Greater cloud cover will decrease C uptake and potentially offset some of the gains achieved from delayed grazing. Consequently, biotic and abiotic drivers may impose counteracting effects dampening the impact of future climate conditions on NEE in a coastal Alaskan wetland.

Counter to our hypothesis that season advancement would increase C uptake as a result of early and more rapid growth in the spring, advancing the growing season decreased C uptake when the OTCs were in place. Previous studies suggest earlier spring may increase season-long C uptake (Cahoon et al. 2016, Gonsamo et al. 2018) but others suggest no correlation or a negative relationship between the start of the growing season and ecosystem productivity (Humphreys and Lafleur 2011, Gamon et al. 2013, Choi et al. 2019). Reduced C uptake in our season advancement treatment likely resulted from increased ER. We observed greater instantaneous ER under season advancement but little effect on gross primary productivity (Lefler et al. 2019) possibly due to N limitations (Ruess et al. 1997, Sistla et al. 2012, Lefler and Welker 2013) in this and similar systems. Our high temporal resolution NEE data also indicate that the reduction in C uptake under season advancement is transitory because the effect disappeared shortly after removal of the OTCs on 1 July; consequently, the
effect is likely linked to higher soil temperature, which coincide with early growing season. Other studies in Arctic systems grazed by geese suggest that warming has little influence on NEE during the growing season but increases ER during winter (Sjögersten et al. 2008).

Consistent with our hypothesis, delaying grazing significantly increased C uptake. Previously we reported that delayed grazing enhances instantaneous C uptake for much of the spring and early summer (Leffler et al. 2019) consistent with other studies suggesting removal of tissue is an important driver of NEE in Arctic systems grazed by geese (Sjögersten et al. 2008). However, lack of grazing resulted in a smaller increase in C uptake than delayed grazing, possibly because of increased self-shading from living or standing-dead biomass (Archer and Tieszen 1983, Choi et al. in press), lower per unit leaf area photosynthetic rate (Leffler et al. 2019), slower N cycling in the absence of defecation by geese (Russ et al. 1997, Zachies et al. 2002), or compensatory growth in response to grazing (Hik and Jefferies 1990).

Median cloud cover compared to full sun reduced daily C uptake most in the late grazing treatment. This finding supports our hypotheses that cloud cover would reduce C uptake in all treatments, but suppression would be greatest in treatments that accumulated the most C because these treatments had greater leaf area for photosynthesis. Cloud cover clearly reduces photosynthesis and is an important limiting factor in CO₂ assimilation especially in ecosystems or periods of the growing season when water is sufficient (Graham et al. 2003). Diffuse light on cloudy days can increase light use efficiency and partly offset reductions in PAR (Mercado et al. 2009), although the diffuse light effect is most critical in forests where direct-beam irradiance results in considerable shadows (Roderick et al. 2001). Other long-term experiments in Arctic locations simulating increased cloud cover through shading indicate that photosynthesis can be limited by light, but responses to shade were species specific (Chapin and Shaver 1985), and not always observed in NEE (Shaver et al. 1998).

Our study highlights some outstanding areas for research on the effects of cloud cover on NEE in this region. First, clouds can contribute to surface warming (Vavrus 2004) suggesting Arctic ecosystems that respond to warming with reduced C uptake may experience further reductions in C uptake in response to cloud cover as a synergistic consequence. Second, our analysis most closely simulates changes in cloud density rather than cloud frequency because we examine NEE across a sampled distribution of PAR, and because our comparisons capture the difference between whole days without clouds versus typical conditions rather than cloud frequency within days. Future research should separate the effects of altered cloud density versus cloud frequency. Nevertheless, these data provide insights into the interactions between cloud cover and other anticipated climate-induced changes on NEE in coastal tundra ecosystems.

Grazing lawns actively used by Pacific black brant currently accumulate between 58.6 and 109 g C m⁻² between early June and mid-August (figure 4). Future C balance may range from a net loss of C (36.0 g C m⁻²) to a nearly doubling of net C uptake (200 g C m⁻²) depending on when geese arrive and spring/summer cloud cover. Goose arrival is variable; in the last 30 years, median hatch of Pacific black brant has varied between 11 June and 30 June with early median hatch dates of 16 June in 2014 and 2015, and 11 June in 2016 (Fischer et al. 2017), indicating earlier migration and grazing, and suggesting less C uptake in the future. Local data suggest no trend in the frequency of cloudy days; however, these trends are difficult to observe because long-term satellite data are limited (Comiso and Hall 2014).

Migratory geese, however, are responding in several ways to changing climate. Some geese are not migrating as far south in the winter (Ward et al. 2016) or migrating faster by minimizing stop-overs en route reducing but not eliminating mismatch in the spring (Lameris et al. 2018). Furthermore, Pacific black brant populations on the Y–K Delta may be declining (Leach et al. 2017), possibly reducing the amount of tissue removed by geese in the summer. Any process that results in earlier grazing in the system, regardless of trends in spring green-up phenology, will likely result in less C uptake while a decline in the number of geese will result in more extensive tall-sedge communities (Person et al. 2003), greater C uptake, and altered emissions of CH₄ (Kelsey et al. 2016, 2018). In summary, future summer NEE in this region will likely be particularly sensitive to the timing of grazing, but the interactions between grazing timing, temperature, and cloud conditions could also be critical in determining C balance.

Acknowledgments

This work was funded by the National Science Foundation (ARC1304523 & ARC1304879) and RC received support from the National Science Foundation under DGE1633756. This research was supported by the South Dakota Agriculture Experiment Station. This research was supported by the Utah Agricultural Experiment Station, Utah State University, and approved as journal paper number 9150. We thank CH2MHill PolarField Services for logistical support; ‘Sedinger Camp’ for their wisdom about remote field science in the Y–K Delta; and R Hicks, M Holdrege, H Braithwaite, J Ferguson, L Carlson, K Lynöe, and T DeMasters for their assistance in the field. D Douglas (USGS) provided satellite-derived green-up dates for our study area. This work was permitted through USU IACUC (USU2004), Alaska Department of Fish & Game (16-023), US Fish & Wildlife Service (Migratory
Bird Scientific Collection permit MB28352B-0), and Yukon Delta National Wildlife Refuge (Special Use Permit FF07/RYKD00-14-06). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

**ORCID iDs**

A Joshua Leffler @ https://orcid.org/0000-0002-3389-2493
Karen H Beard @ https://orcid.org/0000-0003-4997-2495
Katharine C Kelsey @ https://orcid.org/0000-0002-4631-8538
Ryan T Choi @ https://orcid.org/0000-0003-2060-5671
Joel A Schmutz @ https://orcid.org/0000-0002-6516-0836
Jeffrey M Welker @ https://orcid.org/0000-0002-3865-4822

**References**

Archer S and Tieszen L L 1983 Effects of simulated grazing on foliage and root production and biomass allocation in an arctic tundra sedge (Eriophorum vaginatum) Oecologia 58:92–102
Beard K H, Choi R T, Leffler A J, Carlson L G, Kelsey K C, Schmutz J A and Welker J M 2019 Migratory goose arrival time plays a larger role in influencing forage quality than advancing springs in an Arctic coastal wetland PLoS One 14 e0213037
Brook R W, Leathem J O, Abraham K F and Douglas D C 2015 Density dependence and phenological mismatch: consequences for growth and survival of sub-arctic nesting Canada Geese Avian Conservation Ecology 10 1
Cahoon S M P, Sullivan P F and Post E 2016 Greater abundance of Betula nana and early onset of the growing season increase ecosystem CO2 uptake in west Greenland Ecosystems 19 1149–63
Chapin F S III and Shaver G R 1985 Individualistic growth responses of tundra plants species to environmental manipulations Ecology 66 564–76
Choi R T, Beard K H, Leffler A J, Kelsey K C, Schmutz J A and Welker J M 2019 Phenological mismatch between season advancement and migration timing alters Arctic plant traits J. Ecology (https://doi.org/10.1111/1365-2745.13191)
Cleland E E, Chuiine I, Menzel A, Mooney H A and Schwartz M D 2007 Shifting plant phenology in response to global change Trends Ecology Evol. 22 357–65
Comiso J C 2003 Warming trends in the Arctic from clear sky satellite observations J. Clim. 16 3498–510
Comiso J C and Hall D K 2014 Climate trends in the Arctic as observed from space WIREs Clim. Change 5 389–409
Doiron M, Gauthier G and Levesque E 2015 Trophic mismatch and its effects on the growth of young in an Arctic herbivore Glob. Change Biol. 21 4364–76
Elmgren R C and S C C 2012 Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time Ecology Lett. 15 164–75
Fischer J B, Stehn R A and Walters G 2008 Nest Population Size and Potential Production of Geese and Spectacled Eiders on the Yukon–Kuskokwim Delta, Alaska, 2007 Unpublished Report Anchorage, AK, Department of Interior, US Fish and Wildlife Service
Fischer J B, Williams A R and Stehn R A 2017 Nest Population Size and Potential Production of Geese and Spectacled Eiders on the Yukon–Kuskokwim Delta, Alaska, 1985–2016 Unpublished Report Anchorage, AK, Department of Interior, US Fish and Wildlife Service
Gamon J A, Huemmrich K F, Stone R S and Tweedie C E 2013 Spatial and temporal variation in primary productivity (NDVI) of coastal Alaskan tundra: decreased vegetation growth following earlier snowmelt Remote Sens. Environ. 129 144–53
Gilmanov T G, Verma S B, Sims P L, Meyers T P, Bradford J A, Burba G G and Suyker A E 2003 Gross primary production and light response parameters of four Southern Plains ecosystems estimated using long-term CO2-flux tower measurements Global Biogeochem. Cycles 17 40-1-40-16
Gonsamo A, Chen J M and Ooi Y W 2018 Peak season plant activity shift towards spring is reflected by increased carbon uptake by extratropical ecosystems Global Change Biol. 24 2117–28
Graham E A, Mulkey S S, Kitajima K, Phillips N G and Wright S J 2003 Cloud cover limits net CO2 uptake and growth of a rainforest tree during tropical rainy seasons Proc. Natl Acad. Sci. 100 572–6
Hedges L V, Gurevitch J and Curtis P S 1999 The meta-analysis of response ratios in experimental ecology Ecology 70 1150–6
Herzog M P and Sedinger J S 2004 Dynamics of foraging behavior associated with variation in habitat and forage availability in captive Black Brant (Branta bernicla nigricans) goslings in Alaska Auk 121 210–23
Hik D S and Jefferies R L 1990 Increases in the net aboveground primary production of a salt-marsh forage grass—a test of the predictions of the herbivore–optimization model J. Ecology 78 180–95
Hinzman L D, Deal C J, Mcguire A D, Mankin S H, Polyakov I V and Walde J E 2013 Trajectory of the Arctic as an integrated system Ecological Appl. 23 1837–68
Hoye T T, Post E, Meltofte H, Schmidt N M and Forchhammer M S 2007 Rapid advancement of spring in the high Arctic Curr. Biol. 17 449–51
Humphreys E R and Lafleur P M 2011 Does earlier snowmelt lead to greater CO2 sequestration in two low Arctic tundra ecosystems? Geophys. Res. Lett. 38 L09703
Inouye D W 2000 The ecological and evolutionary significance of frost in the context of climate change Ecology Lett. 3 457–63
Jorgenson M T 2000 Hierarchical organization of ecosystems at multiple spatial scales on the Yukon–Kuskokwim Delta, Alaska, USA Arctic, Antarctic, Alpine Res. 32 221–39
Jorgenson T and Ely C 2001 Topography and flooding of coastal ecosystems on the Yukon–Kuskokwim Delta, Alaska: implications for sea-level rise J. Coast. Res. 17 124–36
Ju J and Masek J G 2016 The vegetation greenness trend in Canada and US Alaska from 1984–2012 landsat data Remote Sens. Environ. 176 1–16
Kelsey K C, Leffler A J, Beard K H, Choi R T, Schmutz J A and Welker J M 2018 Phenological mismatch in coastal western Alaska may increase summer season greenhouse gas uptake Environ. Res. Lett. 13 044032
Kelsey K C, Leffler A J, Beard K H, Schmutz J A, Choi R T and Welker J M 2016 Interactions among vegetation, climate, and herbivory control greenhouse gas fluxes in a subarctic coastal wetland J. Geophys. Res. Biogeosci. 121 2960–75
King M D, Platnick S, Menzel W P, Ackerman S A and Hubanks P A 2013 Spatial and temporal distribution of clouds observed by MODIS onboard the Terra and Aqua satellites IEEE Trans. Geosci. Remote Sens. 51 3626–52
Klein E S, Cherry J E, Young J, Noone D, Leffler A J and Welker J M 2015 Arctic cyclone water vapor isotopes support past sea ice retreat recorded in Greenland ice core Proc. Natl Acad. Sci. Rep. 5 02929
Lafleur P M and Humphreys E R 2007 Spring warming and carbon dioxide exchange over low Arctic tundra in central Canada Global Change Biol. 14 740–56
Lameris T K, Van Der Jeugd H P, Eichhorn G, Dokter A M, Bouten W, Boom M P, Lintin K E, Ens B J and Nolet B A 2018 Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch Curr. Biol. 28 2467–73
Leach A G, Ward D H, Sedinger J S, Lindberg M S, Boyd W S, Hupp J W and Ritchie R J 2017 Declining survival of black brant from subarctic and arctic breeding areas J. Wildlife Manage. 81 1210–8

Leffler A J, Beard K H, Kelsey K C, Choi R T, Schmutz J A and Welker J M 2019 Delayed herbivory by migratory geese increases summer-long CO₂ uptake in coastal western Alaska Global Change Biol. 25 277–89

Leffler A J, Klein E S, Oberbauer S F and Welker J M 2016 Coupled long-term summer warming and deeper snow alters species composition and stimulates gross primary productivity in tussock tundra Oecologia 181 287–97

Leffler A J and Welker J M 2013 Long-term increases in snow pack elevate leaf N and photosynthesis in Salix arctica: responses to a snow fence experiment in the high Arctic of NW Greenland Environ. Res. Lett. 8 025023

Marion G M et al 1997 Open-top designs for manipulating field temperature in high-latitude systems Global Change Biol. 3 20–32

Mercado L M, Bellouin N, Sitch S, Boucher O, Huntingford C, Wild M and Cox P M 2009 Impact of changes in diffuse radiation on the global land carbon sink Nature 458 1014–7

Min S-K, Zhang X and Zwieter F 2008 Human-induced arctic moistening Science 320 518–20

Nakazona T and Doi H 2012 A perspective on match/mismatch of phenology in community contexts Oekos 121 489–95

Pankaw P, Milton E J and Dash J 2014 Estimating hourly variation in photosynthetically active radiation across the UK using MSG SEVIRI data Earth Environ. Sci. 17 012069

Parmentier F J W, van der Molen M K, van Huistjenden J, Karssanoev S A, Kononov A V, Suzzalov D A, Maximov T C and Dolman A J 2011 Longer growing seasons do not increase net carbon uptake in the northeastern Siberia tundra J. Geophys. Res. 116 C04013

Person B T, Herzog M P, Rues R W, Sedinger J S, Anthony R M and Babcock C A 2003 Feedback dynamics of grazing lawns: coupling vegetation change with animal growth Oecologia 135 583–92

Post E and Forchhammer M C 2008 Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch Phil. Trans. R. Soc. B 363 2369–75

Post E and Pedersen C 2008 Opposing plant community responses to warming with and without herbivores Proc. Natl Acad. Sci. 105 12353–8

Prop J and Vulink T 1992 Digestion by Barnacle Geese in the annual Lef

R Development Core Team 2017 R: A Language and Environment for Statistical Computing. Reference Index Version 3.3.3 (Vienna: R Foundation for Statistical Computing)

Roderick M L, Farquhar G D, Berry S L and Noble I R 2001 On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation Oecologia 129 21–30

Ross M V, Alisauskas R T, Douglas D C and Kellett D K 2017 Decadal declines in avian herbivore reproduction: density-dependent nutrition and phenological mismatch in the Arctic Ecology 98 1669–83

Rues R W, Uliassi D D, Mulder C P H and Person B T 1997 Growth responses of Carex tenuis to defoliation, salinity, and nitrogen availability: implications for geese-ecosystem dynamics in western Alaska Ecoscience 4 170–8

Schweiger A J 2004 Changes in seasonal cloud cover over the Arctic seas from satellite and surface observations Geophys. Res. Lett. 31 L12207

Sedinger J S, Nicolai C A, Lensink C J, Wentworth C and Conant B 2007 Black Brant harvest, density dependence, and survival: a record of population dynamics J. Wildlife Manage. 71 496–506

Sedinger J S and Raveling D G 1990 Parental behavior of cackling Canada geese during brood rearing: division of labor within pairs Condor 92 174–81

Serreze M C et al 2001 Observational evidence of recent change in the northern high-latitude environment Climate Change 46 159–207

Shaver G R, Johnson L C, Cades D H, Murry G, Laundre J A, Rastetter E B, Nadelhoffer K J and Gilbin A E 1998 Biomass and CO₂ fluxes in wet sedge tundras: responses to nutrients, temperature, and light Ecological Monographs 68 75–97

Stisla S A, Asao S and Schmel J P 2012 Detecting microbial N-limitation in tussock tundra soil: implications for Arctic soil organic carbon cycling Soil Biol. Biochem. 55 78–84

Stige at the S, Van Der Wal R and Woodin S J 2008 Habitat type determines herbivory controls over CO₂ fluxes in a warmer Arctic Ecology 89 2103–16

Tape K D, Hallinger M, Welker J M and Rues R W 2012 Landscape heterogeneity of shrub expansion in Arctic Alaska Ecosystems 15 711–24

Vavrus S 2004 The impact of cloud feedbacks on Arctic climate under greenhouse forcing J. Clim. 17 603–13

Wang L, Tian F, Yu W, Zhi W, Schurgers G and Fengshui R 2018 Acceleration of global vegetation greenup from combined effects of climate change and human land management Global Change Biol. 24 5484–99

Wang X and Key J R 2003 Recent trends in arctic surface, cloud, and radiation properties from space Science 299 1725–8

Wang X and Key J R 2005 Arctic surface, cloud, and radiation properties based in the AVHRR polar pathfinder dataset II. recent trends J. Clim. 18 2575–83

Ward D H, Helmericks J, Hupp J W, Mcmanus L, Budde M, Douglas D C and Tape K D 2016 Multi-decadal trends in spring arrival of avian migrants to the central Arctic coast of Alaska: effects of environmental and ecological factors J. Avian Biol. 47 197–207

Xu C, Liu H, Williams A P, Yin Y and Wu X 2016 Trends toward an earlier peak of the growing season in Northern Hemisphere mid-latitudes Global Change Biol. 22 2852–60

Zacheis A, Ruess R W and Hupp J W 2002 Nitrogen dynamics in an Alaskan salt Marsh following spring use by geese Oecologia 130 600–8

Zhang X, He J, Zhang I, Polyakov I, Gcred R, Inoue J and Wu P 2013 Enhanced poleward moisture transport and amplified northern high-latitude wetting trend Nat. Clim. Change 3 47–51