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Environmental Research Letters

LETTER

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

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OPEN ACCESS

RECEIVED
28 December 2018

REVISED
18 April 2019

ACCEPTED FOR PUBLICATION
25 April 2019

PUBLISHED
2 August 2019

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

Supplementary material for this article is available online

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^{-1} 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 (Lafleur 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 (Serreze *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/mmedia). 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

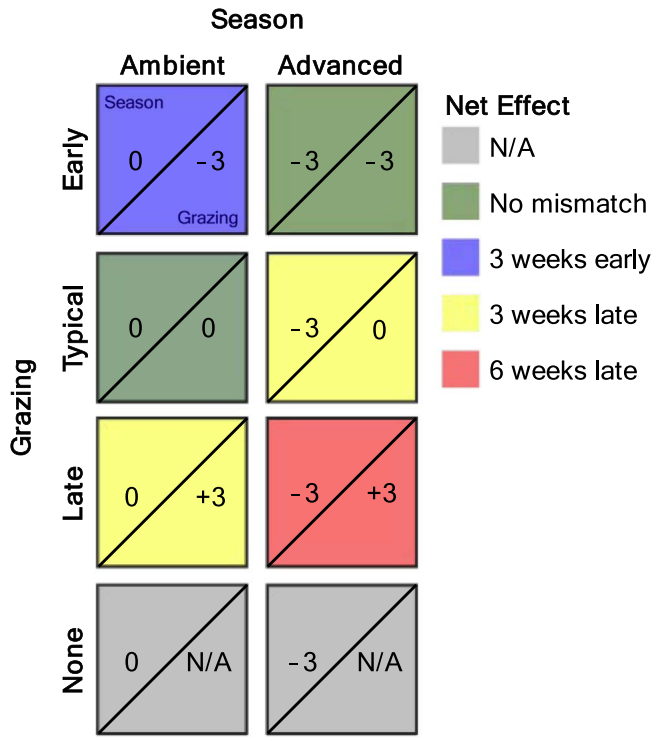

Figure 1. Design of the experimental manipulation of season and grazing phenology. The experiment consists of eight study plots: half of the plots receive the season-advancement treatment ('Advanced') between early May and 1 July while the others are not altered ('Ambient'). Those plots are then divided among grazing treatments ('Early', 'Typical', 'Late', 'None'). Values indicate the number of weeks change in season or grazing timing, negative values indicate early, positive values indicate late. Shading indicates the net effect of the treatments in weeks. Mismatch is not possible in the no grazing treatment because no plant–animal interaction exists.

(King *et al* 2013, MOD06, recent data at https://earthobservatory.nasa.gov/images/85843/cloudy-earth) 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. hutchunsii 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 exclosures (7.6 m^2, one exclosure 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 exclosure; 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.

CO_2 exchange measurements and light response curves

We monitored CO_2 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 [CO_2] 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):

$$\mathrm{NEE} = (-a * b * \mathrm{PAR})/(a * \mathrm{PAR} + b) + \mathrm{ER}, \quad (1)$$

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 CO_2 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

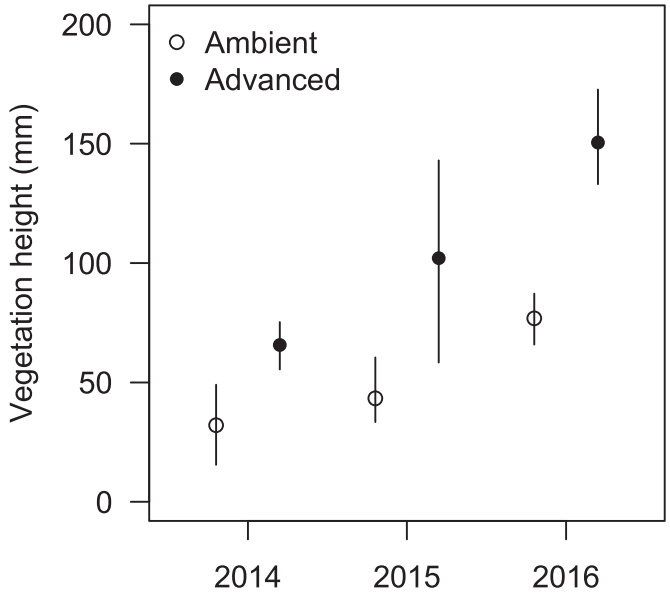

Figure 2. Vegetation height in the ambient and advanced treatments. Values are the median vegetation height and 95% confidence intervals on 30 June of each year in plots that received no grazing prior to that date. Growth rate data used to produce this figure suggests the OTCs advanced the growing season by at least three weeks.

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 (Leffler *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.

CO_2 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,

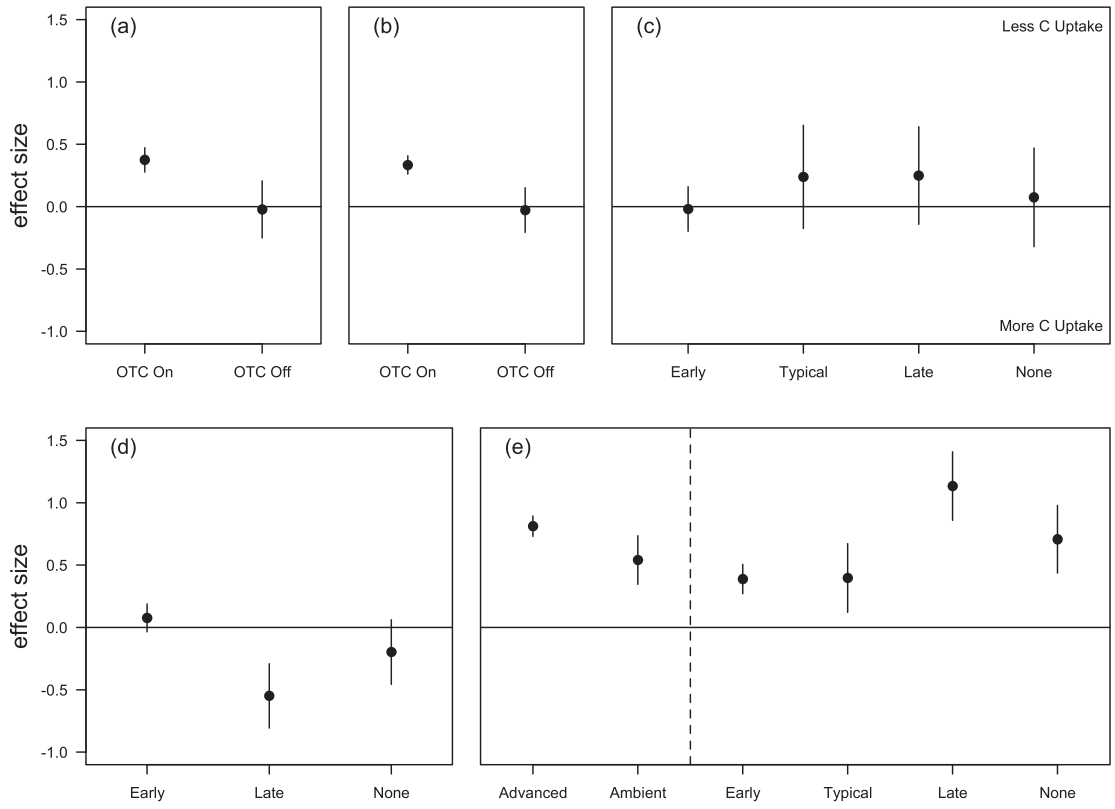

Figure 3. Effect size and 95% confidence intervals for experimental treatments and PAR. Season advancement is examined by calculating effect size as the difference between advanced (treatment) and ambient (control) plots during the entire period of study (a) and one week before and one week following removal of the OTCs (b), and in the different grazing phenology treatments (c). 'OTC on' indicates 1 May–30 June when the OTCs were in place. 'OTC off' indicates the period 1 July until mid-August after the OTCs were removed. Timing of grazing is examined by calculating effect size as the difference between early, late, or no grazing (treatments) and typical grazing (control) for the entire study period (d). The influence of clouds is examined by calculating effect size as the difference between median PAR days (treatment) and modeled clear-sky PAR days (control) for all treatment combinations (e). Positive effect size indicates less C uptake in treatment compared to control while negative effect size indicates greater C uptake in treatment compared to control.

respectively. Mean soil temperature was up to 0.9 °C warmer inside the OTCs.

The effect of growing season advancement on NEE was significant. Advancing the growing season decreased daily C uptake (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 following chamber 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} d^{-1} (95% CI), but only while the OTCs were in place. The effect of the advanced growing season 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} d^{-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} d^{-1}. Averaged among all treatments, cloud covered days reduced C uptake between 1.8 and 2.1 g C m^{-2} d^{-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

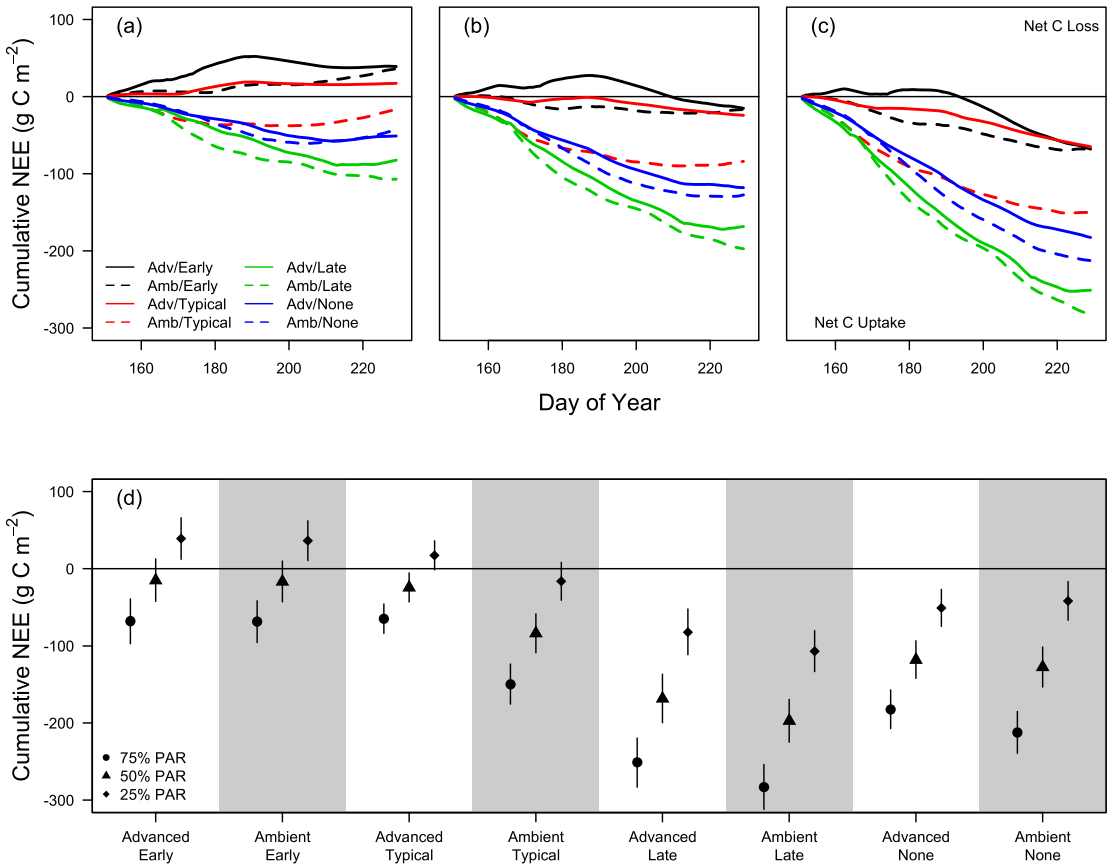

Figure 4. Cumulative net ecosystem exchange (NEE) each day under the 25th (a), 50th (b), and 75th (c) percentile of observed PAR for each experimental plot; and the final cumulative NEE and 95% confidence interval for the period of study in the same PAR regimes. Positive values indicate net C release, negative values indicate net C uptake. Abbreviations: Adv = Advanced, Amb = Ambient.

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 (Leffler *et al* 2019) possibly due to N limitations (Ruess *et al* 1997, Sistla *et al* 2012, Leffler 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 (Ruess *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 CO_2 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 enroute 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 CH_4 (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 FF07RYKD00-14-06). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

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