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Early Goose Arrival Increases Soil Nitrogen Availability More Than an Advancing Spring in Coastal Western Alaska

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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, whereas 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 3-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, whereas 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. This increase in soil N resources can have a lasting impact on plant community composition and productivity in this N-limited ecosystem.

Key words: *Carex subspathacea*; Global change ecology; Migration timing; Nitrogen; Pacific black brant; Phenological mismatch; Plant–herbivore interactions; Trophic mismatch.

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HIGHLIGHTS

- Soil N increased with early goose grazing and decreased with late grazing.
- Combined early goose arrival and season advancement lead to greater soil N.
- Early grazing had a greater influence on soil N than an advanced growing season.

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 the higher trophic level (i.e., herbivores) through reductions in resource availability and forage quality (Doiron and others 2015; Ross and others 2017). While it is unclear if these mismatches will persist, it is likely that at least some 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 (that is, changes in herbivory) and subsequent N inputs (that is, 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). Determining the effects of resource–consumer phenological mismatch on N cycling requires investigating shifts in the timing of the consumer (that is, herbivory) and shifts in the timing of the resource (that is, plant growing season) as separate temporal controls.

The first critical temporal control is 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 (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 research has 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 will alter both organic and inorganic soil N availability (Figure 1).

The second temporal control is changes in climate-driven shifts in the resource, most often through advancement of the growing season which often results in higher rates of soil N cycling (N mineralization [N_{min}], ammonification, denitrification) (Buckeridge and Grogan 2010; Bardgett

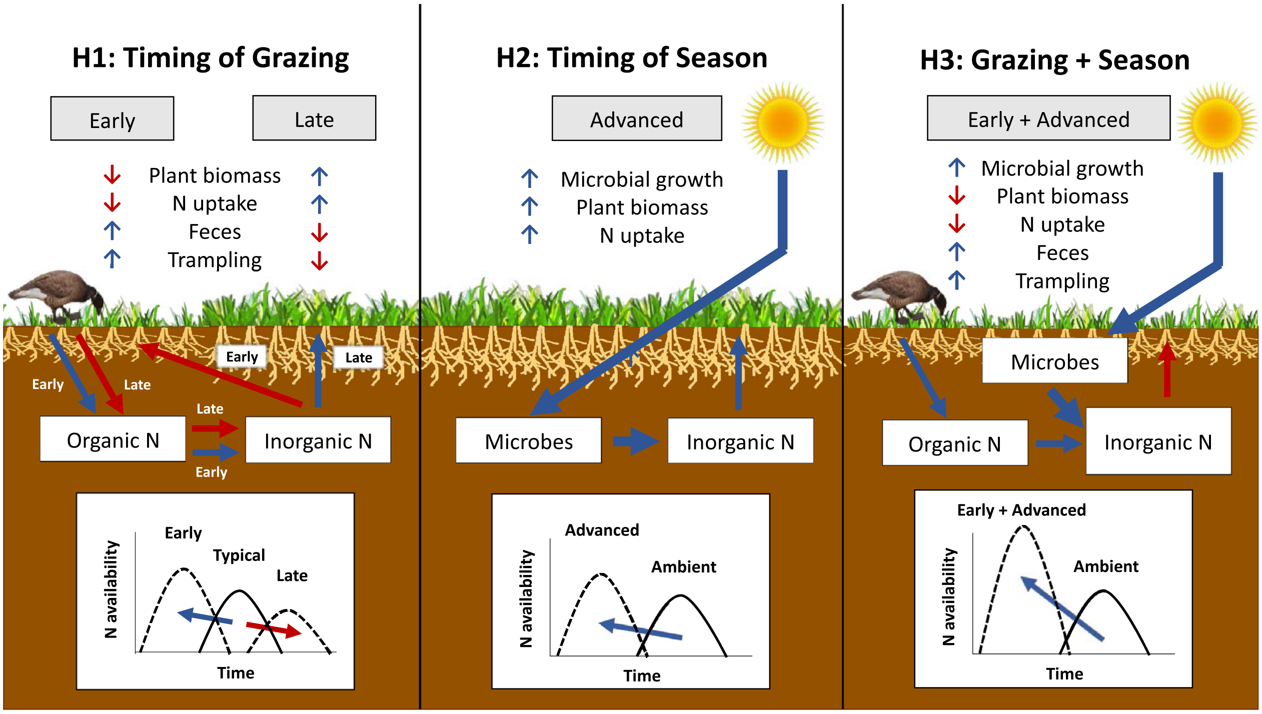

Figure 1. Conceptual figure of experimental hypotheses (H1, H2, H3) regarding the influence of the timing of goose grazing and the start of the growing season and their interaction on soil N availability. Arrows indicate hypothesized influence on N pools; blue arrows indicate positive effects and red arrows indicate negative effects. Goose herbivory removes aboveground tissues and hence decreases plant N uptake, whereas 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 (Color figure online).

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 3-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 1); (H2) season advancement and associated early season soil warming stimulate microbial net N mobilization (that is, 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 (8000–30,000 $\mu S\ cm^{-1}$; 0.5–18 ppt), frequently inundated by monthly tides, and characterized by interbedded layers of silt and sandy loams (Jorgenson 2000). Permafrost, although 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. *Carex 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 an approximate 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 3 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 to be 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 3-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 timing of grazing treatments (early, typical, late, and no-grazing) crossed with two timing of the growing season treatments (advanced and ambient) for a total of eight treatments. We altered the timing of goose grazing by minus-three, zero, and plus-3 weeks (early, typical, and late treatments, respectively), and advanced the growing season by 3 weeks (see below). The 'typical' goose treatment represented historic mean arrival and grazing and acted as the grazing treatment control, whereas 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 determine 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 × 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 to 15 August each year.

We manipulated the 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 3 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 2 h without food to allow feces from captive feeding to pass through their digestive system (Prop and Vulnik 1992). After each 24-h grazing treatment, we held birds for an additional 2 h 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 × 85 cm base dia. × 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, whereas organic N (amino acids) was measured via one method over 3 years. N_{min} was measured only during the third year of the experiment.

We used ion-exchange resin strips (2.5 cm wide × 10 cm length; CR67 and 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 2 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 2 M 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 2). To address this problem in years 2 and 3, we installed intertidal resin sets for 3 weeks between monthly peak tides, determined from regional NOAA tide predictions (Dall Point, AK; tidesandcurrents.noaa.gov) and collected pairs from plots before each 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 mois-

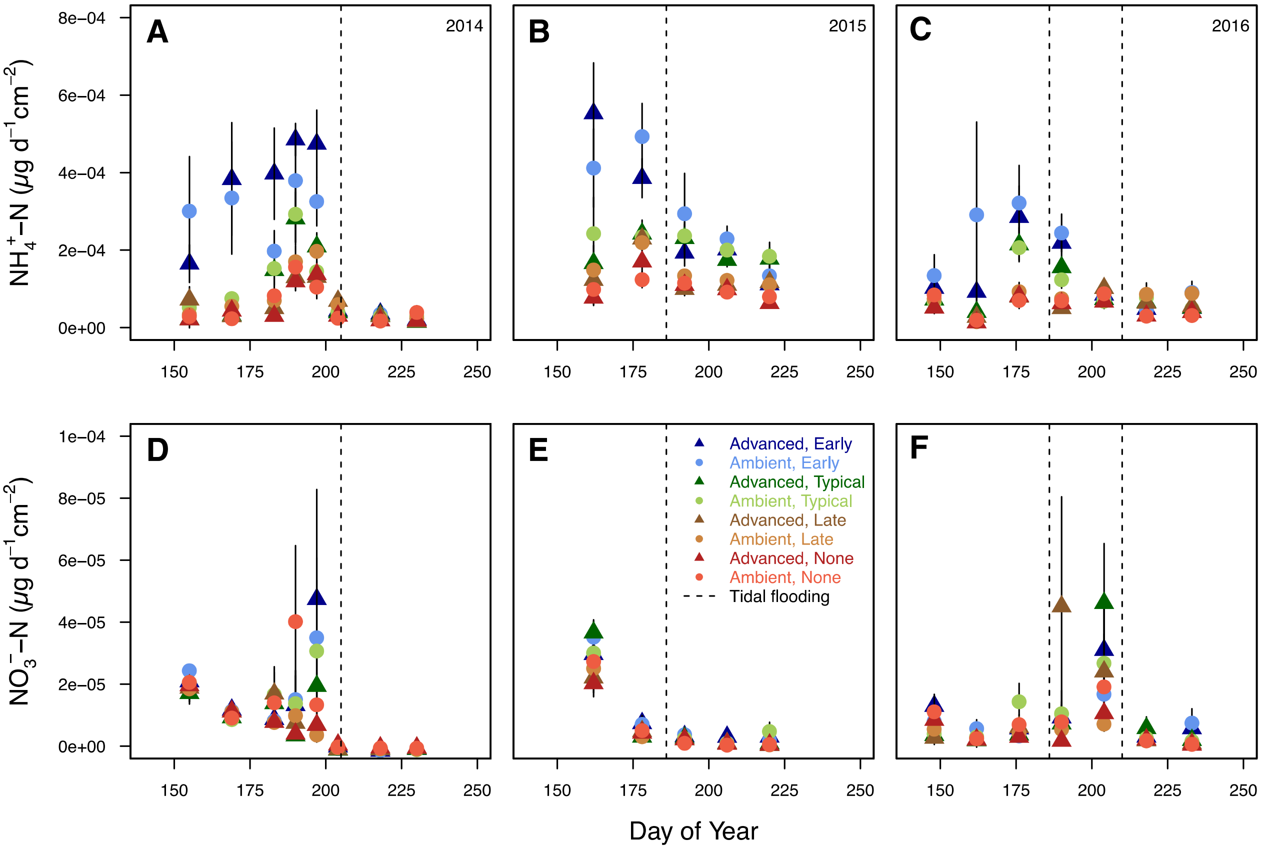

Figure 2. Mean cumulative resin $NH_4{}^{+}$–N and $NO_3{}^{-}$–N (μg d^{-1} cm^{-2}) (± 1 SE) from experimental timing of grazing and season advancement treatments. **A**–**C**, and **D**–**F** represent data collected from 2014, 2015, and 2016, respectively. Dotted lines represent high tide events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

ture 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 2 weeks and used 1 μm, 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 2 M 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 Berthelot 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™ 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 re-

Table 1. Top Four Performing Models for Soil N Response Variables Based on AIC Model Selection for Experimental Treatments Over 3 Years (2014–2016)

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

The (*) symbol indicates an interaction effect in the model.
Models with interaction terms imply inclusion of the main effect.
Grazing = timing of goose grazing treatment, season = season advancement treatment, date = sampling date.
Bolding indicate top models with ΔAIC < 2.

sponse 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

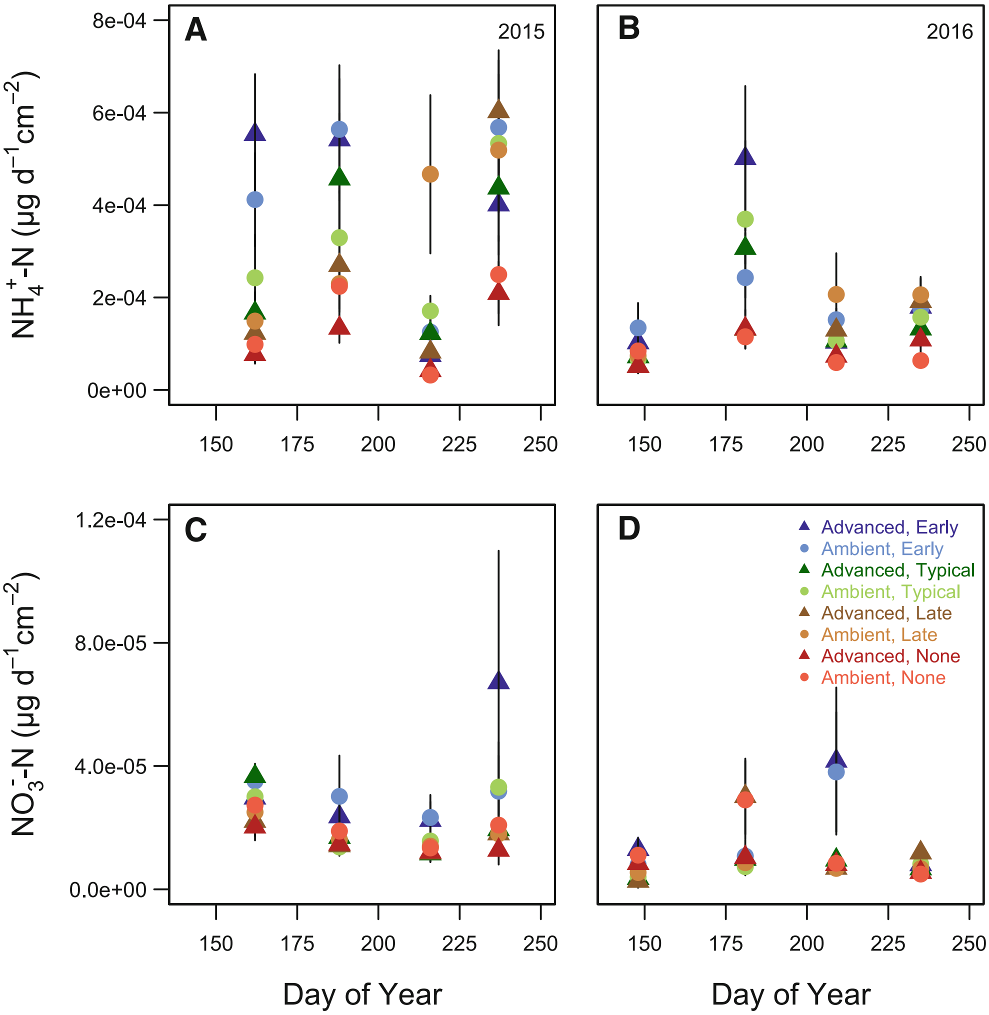

Figure 3. Mean intertidal resin NH_4^+–N and NO_3^-–N (µg d^{-1} cm^{-2}) from experimental timing of grazing and season advancement treatments. Because cumulative resins experienced coastal flooding, intertidal resins collected soil inorganic N during periods in between monthly tidal inundation to avoid ionic loss of N from resins in situ. **A**, **B** and **C**, **D** represent data collected from 2015 and 2016, respectively. Error bars are ± 1 SE (*n* = 6 replicates).

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 ΔAIC was less than 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) (Supplemental Table S1). For simplicity and to capture the effects after 3 years of experimental treatments, we present in the text soil N percent change as the mean across the last year of the experiment unless otherwise indicated.

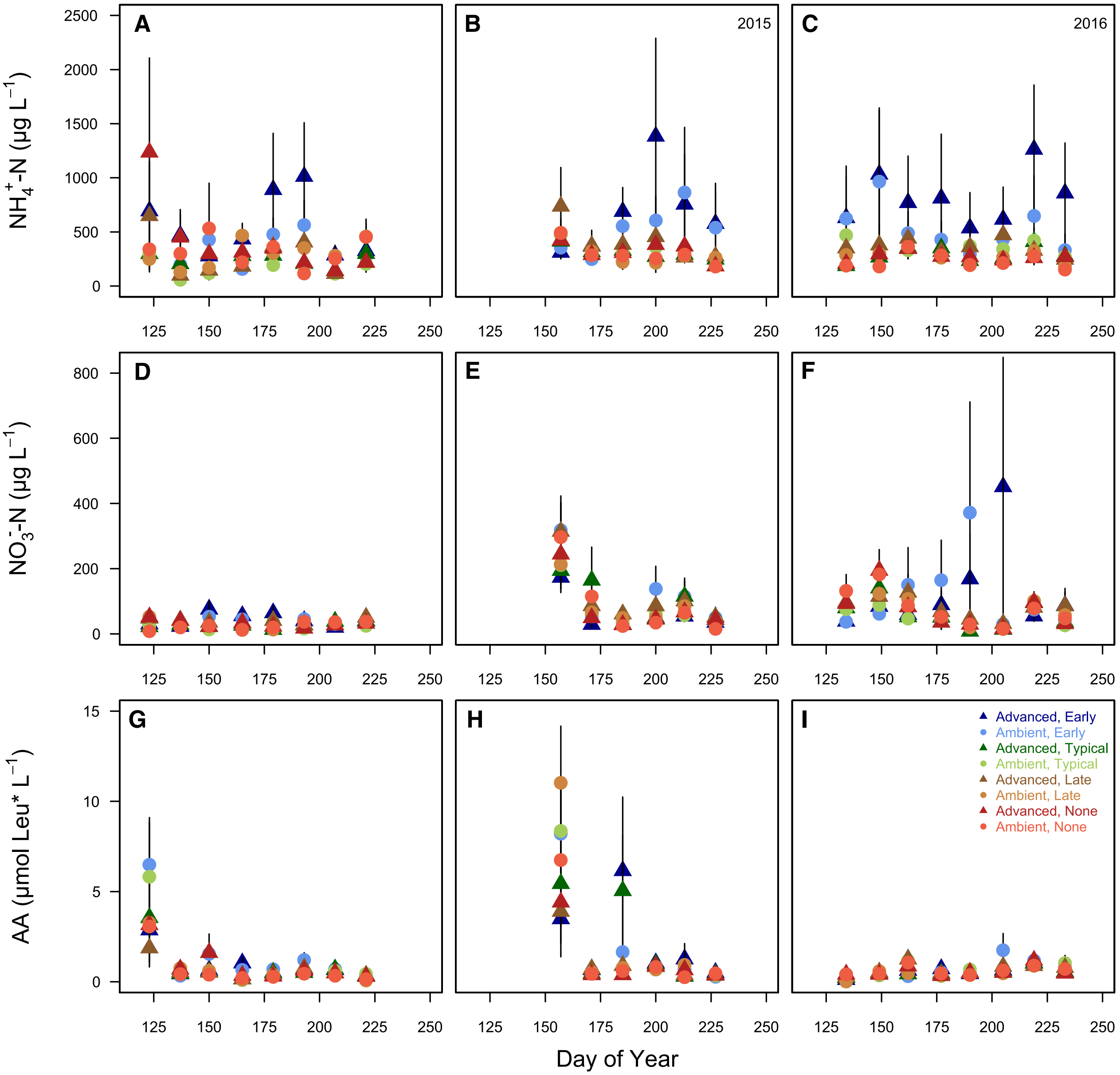

Figure 4. Mean microlysimeter NH_4^+–N and NO_3^-–N (µg L^{-1}) and amino acids (AA) (µmol L^{-1}) (± 1 SE) from soil pore water for treatment plots. **A–C**, and **D–F**, and **G–I** represent data collected from 2014, 2015, and 2016, respectively. Leu* = Leucine equivalent.

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 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 2, 3, 4). Intertidal resins had 16% less NH_4^+–N available in late grazing than typical grazing treatments (Figure 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 (Supplemental Table S1). 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

Table 2. Mean Percent Changes by Treatment for Each Year

	Cumulative resin NH_4^+–N (%)			Intertidal resin NH_4^+–N (%)			Microlysimeter 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 NO_3^-–N (%)			Intertidal resin NO_3^-–N (%)			Microlysimeter 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 NH_4^+–N (%)			N-mineralization NO_3^-–N (%)			Microlysimeter 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

The reference level was the ambient growing season or typical grazing timing treatment, respectively.
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.*

timing of grazing, season advancement, and an interaction between year and sampling date (Table 1).

Early grazing had seasonal peaks in intertidal resin-adsorbed NH_4^+–N that coincided with early grazing treatments (~ 30 May to 10 July), approximately 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 (Figure 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.

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 2, 3, 4, Table 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 (Figure 3C, D, Table 2). 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 1). Although season advancement was found in all the top models, it was not significant (Supplemental Table S1).

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 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 (Supplemental Table S1). Across all plots, mean net N_{min} rates were 0.10 ± 0.24 µg NH_4^+–N g-dry soil^{-1} d^{-1} and

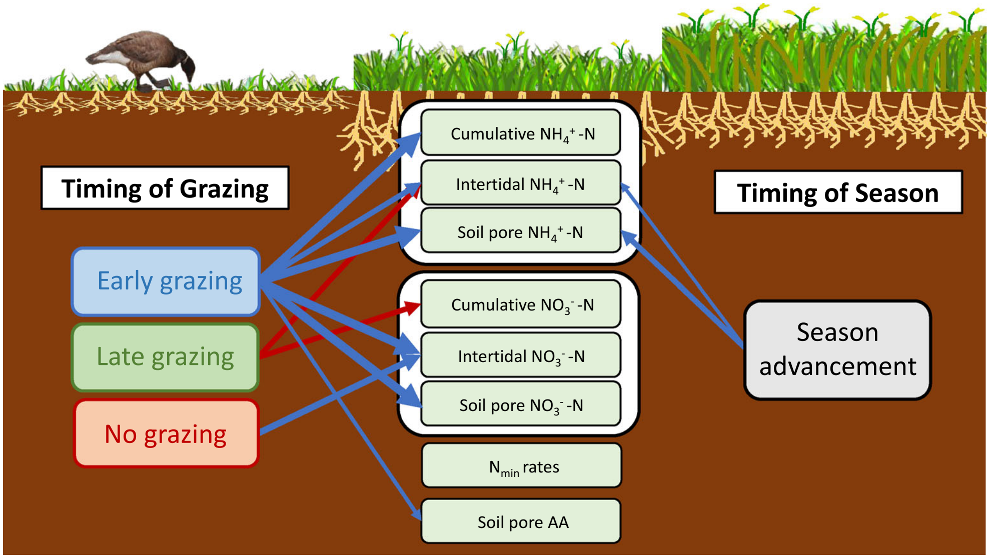

Figure 5. Conceptual figure of experimental treatments (timing of grazing and season advancement) on soil N measurements (cumulative and intertidal resins, and microlysimeter pore water) compared to typical grazing and ambient season treatments after 3 years. Arrow thickness indicates relative treatment 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) (Color figure online).

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 (Figure 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 ΔAIC below 2 also included season advancement (Table 1). Although season advancement was included in the second-ranked model, it was not significant (Supplemental Table S1).

Discussion

Our experimental results suggest that the timing of migratory goose grazing (that is, 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 3-week shift in timing (Figure 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) and alter plant community composition and productivity (Ruess and others 1997; Boyer and Zedler 1999). Earlier springs and increases 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 the timing of grazing can affect inorganic soil N pools (NH_4^+–N, NO_3^-–N), and early grazing had the greatest impact (Figure 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 2), which suggests that the draw down may have taken time (up to 3 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 fourfold increase in soil pore NH_4^+–N (Table 2) and highlights the importance of earlier migratory arrival at our site. Although 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 and 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 °C (e.g., DeMarco and others 2011), suggesting that perhaps our season advancement treatments (0.6–1.0 °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 (Figure 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) (Figure 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, whereas late grazing increased inflorescences and dead biomass by 515% and 569%, respectively (Choi and others 2019), compared to typical grazing plots by the end of year 3 (Figure 5). Grazing had legacy effects on plant productivity in subsequent seasons (Choi and others 2019), and corresponded with changes in soil N availability.

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 δ^{15}N from our early grazing treatments had enriched δ^{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 δ^{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. A two-season 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. Although 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

Although 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, although 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.

CONCLUSIONS

Climate-driven advances in spring green-up and goose arrival are occurring in the Y–K Delta. Although 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 3 weeks. Our findings suggest that climate-driven changes in the timing of migratory goose arrival have important top-down control on the timing and availability of N, which is a critical limiting resource in this northern coastal wetland. Although 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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DATA AVAILABILITY

The dataset from this manuscript has been uploaded to https://doi.org/10.18739/a22274.

Compliance with Ethical Standards

Conflict of interest

The authors declare that they have no conflict of interest.

REFERENCES

Bai E, Li S, Xu W, Li W, Dai W, Jiang P. 2013. A meta-analysis of experimental warming effects on terrestrial nitrogen pools and dynamics. New Phytol 199:441–51.

Bardgett RD, Manning P, Morriën E, De Vries FT. 2013. Hierarchical responses of plant-soil interactions to climate change: consequences for the global carbon cycle. J Ecol 101:334–43.

Bazely DR, Jefferies RL. 1985. Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. J Appl Ecol 22:693–703.

Bazely DR, Jefferies RL. 1989. Lesser snow geese and the nitrogen economy of a grazed salt marsh. J Ecol 77:24–34.

Beard KH, Choi RT. 2017. Data from: Asynchrony in the timing of goose-vegetation interactions: implications for biogeochemical cycling in wet sedge tundra Tutakoke River, Yukon Delta NWR, Alaska, 2014-2016.

Beard KH, Choi RT, Leffler AJ, Carlson LG, Kelsey KC, Schmutz JA, Welker JM. 2019a. Migratory goose arrival time plays a larger role in influencing forage quality than advancing springs in an Arctic coastal wetland. PLoS One 14:e0213037.

Beard KH, Kelsey KC, Leffler AJ, Welker JM. 2019b. The missing angle: ecosystem consequences of phenological mismatch. Trends Ecol Evol 34:885–8.

Belay-Tedla A, Zhou X, Su B, Wan S, Luo Y. 2009. Labile, recalcitrant, and microbial carbon and nitrogen pools of a tallgrass prairie soil in the US Great Plains subjected to experimental warming and clipping. Soil Biol Biochem 41:110–16.

Blankinship JC, Hart SC. 2012. Consequences of manipulated snow cover on soil gaseous emission and N retention in the growing season: a meta-analysis. Ecosphere 3:1–20.

Boelman NT, Krause JS, Sweet SK, Chmura HE, Perez JH, Gough L, Wingfield JC. 2017. Extreme spring conditions in the Arctic delay spring phenology of long-distance migratory songbirds. Oecologia 185:1–12.

Borner AP, Kielland K, Walker MD. 2008. Effects of simulated climate change on plant phenology and nitrogen mineralization in Alaskan Arctic tundra. Arct Antarct Alp Res 40:27–38.

Boyer KE, Zedler JB. 1999. Nitrogen addition could shift plant community composition in a restored California salt marsh. Restor Ecol 7:74–85.

Brook RW, Leafloor JO, Abraham KF, Douglas DC. 2015. Density dependence and phenological mismatch: consequences for growth and survival of sub-arctic nesting Canada Geese. Avian Conserv Ecol 10:1.

Buckeridge KM, Cen Y-P, Layzell DB, Grogan P. 2010. Soil biogeochemistry during the early spring in low arctic mesic tundra and the impacts of deepened snow and enhanced nitrogen availability. Biogeochemistry 99:127–41.

Buckeridge KM, Grogan P. 2010. Deepened snow increases late thaw biogeochemical pulses in mesic low arctic tundra. Biogeochemistry 101:105–21.

Burnham KP, Anderson DR, Huyvaert KP. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav Ecol Sociobiol 65:23–35.

Carlson LG, Beard KH, Adler PB. 2018. Direct effects of warming increase woody plant abundance in a subarctic wetland. Ecol Evol 8:2868–79.

Choi RT, Beard KH, Leffler AJ, Kelsey KC, Schmutz JA, Welker JM. 2019. Phenological mismatch between season advancement and migration timing alters Arctic plant traits. J Ecol 107:2503–18.

Clausen KK, Clausen P. 2013. Earlier Arctic springs cause phenological mismatch in long-distance migrants. Oecologia 173:1101–12.

Cohen JM, Lajeunesse MJ, Rohr JR. 2018. A global synthesis of animal phenological responses to climate change. Nat Clim Change 8:224–8.

Craine JM, Elmore AJ, Aidar MPM, Bustamante M, Dawson TE, Hobbie EA, Kahmen A, MacK MC, McLauchlan KK, Michelsen A, Nardoto GB, Pardo LH, Peñuelas J, Reich PB, Schuur EAG, Stock WD, Templer PH, Virginia RA, Welker JM, Wright IJ. 2009. Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. New Phytol 183:980–92.

Darrouzet-Nardi A, Steltzer H, Sullivan PF, Segal A, Koltz AM, Livensperger C, Schimel JP, Weintraub MN. 2019. Limited effects of early snowmelt on plants, decomposers, and soil nutrients in Arctic tundra soils. Ecol Evol 9:1820–44.

Darrouzet-Nardi A, Weintraub MN. 2014. Evidence for spatially inaccessible labile N from a comparison of soil core extractions and soil pore water lysimetry. Soil Biol Biochem 73:22–32.

DeMarco J, Mack MC, Bret-Harte MS. 2011. The effects of snow, soil microenvironment, and soil organic matter quality on N availability in three Alaskan Arctic plant communities. Ecosystems 14:804–17.

Doane TA, Horwáth WR. 2003. Spectrophotometric determination of nitrate with a single reagent. Anal Lett 36:2713–22.

Doiron M, Gauthier G, Levesque E. 2015. Trophic mismatch and its effects on the growth of young in an Arctic herbivore. Glob Change Biol 21:4364–76.

Edwards KA, McCulloch J, Kershaw GP, Jefferies RL. 2006. Soil microbial and nutrient dynamics in a wet Arctic sedge meadow in late winter and early spring. Soil Biol Biochem 38:2843–51.

Fischer JB, Stehn RA, Walters G. 2008. Nest population size and potential production of geese and spectacled eiders on the Yukon-Kuskokwim Delta, Alaska, 2008. Anchorage (AK): U.S. Fish and Wildlife Service, Migratory Bird Management.

Fischer JB, Williams AR, Stehn RA. 2017. Nest population size and potential production of geese and spectacled eiders on the Yukon-Kuskokwim Delta, Alaska, 1985-2016. Anchorage (AK): U.S. Fish and Wildlife Service, Migratory Bird Management.

Giblin AE, Tobias CR, Song B, Weston N, Banta GT, Rivera-Monroy VH. 2013. The importance of dissimilatory nitrate reduction to ammonium (DNRA) in the nitrogen cycle of coastal ecosystems. Oceanography 26:124–31.

Grogan P, Michelsen A, Ambus P, Jonasson S. 2004. Freeze–thaw regime effects on carbon and nitrogen dynamics in sub-arctic heath tundra mesocosms. Soil Biol Biochem 36:641–54.

Grogan P, Zamin TJ. 2018. Growth responses of the common arctic graminoid *Eriophorum vaginatum* to simulated grazing are independent of soil nitrogen availability. Oecologia 186:151–62.

Heberling JM, McDonough MacKenzie C, Fridley JD, Kalisz S, Primack RB. 2019. Phenological mismatch with trees reduces wildflower carbon budgets. Ecol Lett 22:616–23.

Henry HAL, Jefferies RL. 2002. Free amino acid, ammonium and nitrate concentrations in soil solutions of a grazed coastal marsh in relation to plant growth. Plant Cell Environ 25:665–75.

Henry HAL, Jefferies RL. 2003. Plant amino acid uptake, soluble N turnover and microbial N capture in soils of a grazed Arctic salt marsh. J Ecol 91:627–36.

Hobbie JE, Hobbie EA. 2012. Amino acid cycling in plankton and soil microbes studied with radioisotopes: measured amino acids in soil do not reflect bioavailability. Biogeochemistry 107:339–60.

Jonasson S, Michelsen A, Schmidt IK. 1999. Coupling of nutrient cycling and carbon dynamics in the Arctic, integration of soil microbial and plant processes. Appl Soil Ecol 11:135–46.

Jones DL, Owen AG, Farrar JF. 2002. Simple method to enable the high resolution determination of total free amino acids in soil solutions and soil extracts. Soil Biol Biochem 34:1893–902.

Jorgenson MT. 2000. Hierarchical organization of ecosystems at multiple spatial scales on the Yukon-Kuskokwim Delta, Alaska, U.S.A. Arct Antarct Alp Res 32:221–39.

Jorgenson T, 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.

Kelsey KC, Leffler AJ, Beard KH, Choi RT, Schmutz JA, Welker JM. 2018. Phenological mismatch in coastal western Alaska may increase summer season greenhouse gas uptake. Environ Res Lett 13:044032.

Kölzsch A, Bauer S, de Boer R, Griffin L, Cabot D, Exo KM, van der Jeugd HP, Nolet BA. 2015. Forecasting spring from afar? Timing of migration and predictability of phenology along different migration routes of an avian herbivore. J Anim Ecol 84:272–83.

Lameris TK, Scholten I, Bauer S, Cobben MMP, Ens BJ, Nolet BA. 2017. Potential for an Arctic-breeding migratory bird to adjust spring migration phenology to Arctic amplification. Glob Change Biol 23:4058–67.

Leffler AJ, Beard KH, Kelsey KC, Choi RT, Schmutz JA, Welker JM. 2019. Delayed herbivory by migratory geese increases summer-long CO_2 uptake in coastal western Alaska. Glob Change Biol 25:277–89.

Lin D, Xia J, Wan S. 2010. Climate warming and biomass accumulation of terrestrial plants: a meta-analysis. New Phytol 188:187–98.

Martinsen V, Mulder J, Austrheim G, Hessen DO, Mysterud A. 2012. Effects of sheep grazing on availability and leaching of soil nitrogen in low-alpine grasslands. Arct Antarct Alp Res 44:67–82.

Mayor SJ, Guralnick RP, Tingley MW, Otegui J, Withey JC, Elmendorf SC, Andrew ME, Leyk S, Pearse IS, Schneider DC. 2017. Increasing phenological asynchrony between spring green-up and arrival of migratory birds. Sci Rep 7:1902.

McBride MB. 1989. Surface chemistry of soil minerals. Miner Soil Environ 2:35–87.

McLaren JR, Darrouzet-Nardi A, Weintraub MN, Gough L. 2017. Seasonal patterns of soil nitrogen availability in moist acidic tundra. Arct Sci 4:AS-2017-0014.

Miller-Rushing AJ, Høye TT, Inouye DW, Post E. 2010. The effects of phenological mismatches on demography. Philos Trans R Soc Lond B Biol Sci 365:3177–86.

Miller AJ, Cramer MD. 2005. Root nitrogen acquisition and assimilation. Plant Soil 274:1–36.

Myers-Smith IH, Forbes BC, Wilmking M, Hallinger M, Lantz T, Blok D, Tape KD, Macias-Fauria M, Sass-Klaassen U, Lévesque E, Boudreau S, Ropars P, Hermanutz L, Trant A, Collier LS, Weijers S, Rozema J, Rayback SA, Schmidt NM, Schaepman-Strub G, Wipf S, Rixen C, Ménard CB, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen V, Welker J, Grogan P, Epstein HE, Hik DS. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environ Res Lett 6:045509.

Natali SM, Schuur EAG, Rubin RL. 2012. Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. J Ecol 100:488–98.

Person BT, Herzog MP, Ruess RW, Sedinger JS, Anthony RM, Babcock CA. 2003. Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. Oecologia 135:583–92.

Person BT, Ruess RW. 2003. Stability of a subarctic saltmarsh: plant community resistance to tidal inundation. Ecoscience 10:351–60.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2017. nmle: linear and nonlinear mixed effects models. R Packag version 31-131. https://CRANR-project.org/package=nlme. Accessed 27 July 2017.

Prop J, Vulink T. 1992. Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. Funct Ecol 6(2):180–9.

Qian P, Schoenau JJ. 1995. Assessing nitrogen mineralization from soil organic matter using anion exchange membranes. Fertil Res 40:143–8.

Renner SS, Zohner CM. 2018. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. Annu Rev Ecol Evol Syst 49:165–82.

Rhine ED, Mulvaney RL, Pratt EJ, Sims GK. 1998. Improving the Berthelot reaction for determining ammonium in soil extracts and water. Soil Sci Soc Am J 62:473–80.

Robertson GP, Wedin D, Groffman PM, Blair JM, Holland EA, Nadelhoffer KJ, Harris D. 1999. Soil carbon and nitrogen availability: nitrogen mineralization, nitrification, and soil respiration potentials. In: Robertson GP, Coleman DC, Bledsoe CS, Sollins P, Eds. Standard soil methods for long-term ecological research. New York (NY): Oxford University Press. p 258–71.

Rogers MC, Sullivan PF, Welker JM. 2011. Evidence of nonlinearity in the response of net ecosystem CO_2 exchange to increasing levels of winter snow depth in the High Arctic of northwest Greenland. Arct Antarct Alp Res 43:95–106.

Ross MV, Alisauskas RT, Douglas DC, Kellett DK. 2017. Decadal declines in avian herbivore reproduction: density-dependent nutrition and phenological mismatch in the Arctic. Ecology 98:1869–83.

Ruess RW, McFarland JW, Person B, Sedinger JS. 2019. Geese mediate vegetation state changes with parallel effects on N cycling that leave nutritional legacies for offspring. Ecosphere 10:e02850.

Ruess RW, Uliassi DD, Mulder CPH, Person BT. 1997. Growth responses of *Carex ramenskii* to defoliation, salinity, and nitrogen availability: implications for geese-ecosystem dynamics in western Alaska. Ecoscience 4:170–8.

Schaeffer SM, Sharp E, Schimel JP, Welker JM. 2013. Soil-plant N processes in a High Arctic ecosystem, NW Greenland are altered by long-term experimental warming and higher rainfall. Glob Change Biol 19:3529–39.

Schimel JP, Kielland K, Chapin FS. 1996. Nutrient availability and uptake by tundra plants. In: Reynolds JF, Tenhunen JD, Eds. Landscape function and disturbance in Arctic Tundra. Ecological Studies (Analysis and Synthesis), vol 120. Berlin: Springer. pp 203–21.

Sedinger JS, Herzog MP, Person BT, Kirk MT, Obritchkewitch T, Martin PP, Stickney AA. 2001. Large-scale variation in growth of Black Brant goslings related to food availability. Auk 118:1088–95.

Sedinger JS, Raveling DG. 1984. Dietary selectivity in relation to availability and quality of food for goslings of Cackling Geese. Auk 101:295–306.

Sedinger JS, Raveling DG. 1986. Timing of nesting by Canada geese in relation to the phenology and availability of their food plants. J Anim Ecol 55:1083–102.

Sistla SA, Asao S, Schimel JP. 2012. Detecting microbial N-limitation in tussock tundra soil: Implications for Arctic soil organic carbon cycling. Soil Biol Biochem 55:78–84.

Sistla SA, Schimel JP. 2013. Seasonal patterns of microbial extracellular enzyme activities in an arctic tundra soil: Identifying direct and indirect effects of long-term summer warming. Soil Biol Biochem 66:119–29.

Sjögersten S, Kuijper DPJ, van der Wal R, Loonen MJJE, Huiskes AHL, Woodin SJ. 2010. Nitrogen transfer between herbivores and their forage species. Polar Biol 33:1195–203.

Skopp J, Jawson MD, Doran JW. 1990. Steady-state aerobic microbial activity as a function of soil water content. Soil Sci Soc Am J 54:1619.

Tiedje JM. 1988. Ecology of denitrification and dissimilatory nitrate reduction to ammonium. In: Zehnder AJB, Ed. Environmental microbiology of anaerobes. New York (NY): Wiley. p 179–244.

Uher-Koch BD, Schmutz JA, Wilson HM, Anthony RM, Day TL, Fondell TF, Person BT, Sedinger JS. 2019. Ecosystem-scale loss of grazing habitat impacted by abundance of dominant herbivores. Ecosphere 10:e02767.

Weintraub MN, Schimel JP. 2005. The seasonal dynamics of amino acids and other nutrients in Alaskan Arctic tundra soils. Biogeochemistry 73:359–80.

Welker JM, Jonsdottir IS, Fahnestock JT. 2003. Leaf isotopic (d13C and d15N) and nitrogen contents of *Carex* plants along the Eurasian Coastal Arctic: Results from the Northeast Passage expedition. Polar Biol 27:29–37.

White JR, Reddy KR. 2003. Nitrification and denitrification rates of Everglades wetland soils along a phosphorus-impacted gradient. J Environ Qual 32:2436.

Wilson DJ, Jefferies RL. 1996. Nitrogen mineralization, plant growth and goose herbivory in an Arctic coastal ecosystem. J Ecol 84:841–51.

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