Utah State University

DigitalCommons@USU

Ecology Center Publications

Ecology Center

1-2-2020

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

Ryan T. Choi
Utah State University

Karen H. Beard
Utah State University

Katharine C. Kelsey
University of Colorado Denver

A. Joshua Leffler
South Dakota State University

Joel A. Schmutz
U.S. Geological Survey Alaska Science Center

Jeffrey M. Welker
University of Alaska-Anchorage

Follow this and additional works at: https://digitalcommons.usu.edu/eco_pubs

Part of the Ecology and Evolutionary Biology Commons

Recommended Citation

UtahStateUniversity
MERRILL-CAZIER LIBRARY

Title: Early goose arrival increases soil nitrogen availability more than an advancing spring in coastal western Alaska

Running head: Soil nitrogen response to phenological mismatch

Authors: Ryan T. Choi[1], Karen H. Beard[1], Katharine C. Kelsey[2,3], A. Joshua Leffler[4], Joel A. Schmutz[5], Jeffrey M. Welker[2,6]

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

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

[3]Geography and Environmental Science Department, University of Colorado Denver, Denver, CO 80217

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

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

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

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

Paper Type: Research Article

1 ABSTRACT

2 An understudied aspect of climate change-induced phenological mismatch is its effect on

3 ecosystem functioning, such as nitrogen (N) cycling. Migratory herbivore arrival time may alter

4 N inputs and plant-herbivore feedbacks, while earlier springs are predicted to increase N cycling

5 rates through warmer temperatures. However, the relative importance of these shifts in timing

6 and how they interact to affect N cycling are largely unknown. We conducted a three-year

7 factorial experiment in coastal western Alaska that simulated different timings of Pacific black

8 brant (*Branta bernicla nigricans*) arrival (3-weeks early, typical, 3-weeks late, or no-grazing)

9 and the growing season (ca. 3-weeks advanced and ambient) on adsorbed and mobile inorganic

10 (NH_4^+-N, NO_3^--N), and mobile organic N (amino acid) pools. Early grazing increased NH_4^+-N,

11 NO_3^--N, and amino acids by 103%, 119%, and 7%, respectively, while late grazing reduced

12 adsorbed NH_4^+-N and NO_3^--N by 16% and 17%, respectively. In comparison, the advanced

13 growing season increased mobile NH_4^+-N by 26%. The arrival time by geese and the start of the

14 season did not interact to influence soil N availability. While the onset of spring in our system is

15 advancing at twice the rate of migratory goose arrival, earlier goose migration is likely to be

16 more significant than the advances in springs in influencing soil N, although both early goose

17 arrival and advanced springs are likely to increase N availability in the future. This increase in

18 soil N resources can have a lasting impact on plant community composition and productivity in

19 this N-limited ecosystem.

20

21 Key words: *Carex subspathacea*; global change ecology; migration timing; nitrogen; Pacific

22 black brant; phenological mismatch; plant-herbivore interactions; trophic mismatch.

23

24 HIGHLIGHTS:

25 1.   Soil N increased with early goose grazing and decreased with late grazing.

26 2.   Combined early goose arrival and season advancement lead to greater soil N.

27 3.   Early grazing had a greater influence on soil N than an advanced growing season.

28

29 INTRODUCTION

30   Northern latitudes are experiencing rapid warming and spring advancement, which is

31 altering the timing of biological interactions, especially for long-distance migratory species

32 (Cohen and others 2018; Renner and Zohner 2018). While some species, such as migratory

33 geese, have started to shift the timing of their migration earlier in response to climate-induced

34 season advancement (Kölzsch and others 2015; Boelman and others 2017), there is still potential

35 for resource-consumer 'phenological mismatch' due to the different rates of climatic change in

36 their winter and summer ranges (Lameris and others 2017; Mayor and others 2017).

37 Phenological mismatch between long-distance migratory birds and their resources is already

38 negatively affecting higher trophic herbivores through reductions in resource availability and

39 forage quality (Doiron and others 2015; Ross and others 2017). While it is unclear if the

40 mismatch will persist, it is likely that these mismatches will have long-term consequences for

41 some northern systems due to the rapid occurrence of change in the Arctic (Miller-Rushing and

42 others 2010). An understudied aspect of phenological mismatch is how ecosystem-level

43 processes, such as nutrient cycling, may be impacted (Kelsey and others 2018; Heberling and

44 others 2019; Leffler and others 2019), and until recently this has been largely overlooked (Beard

45 and others 2019b).

46   Investigating how developing phenological mismatch influences soil nitrogen (N)

47   availability is fundamental for understanding how northern latitudes are changing because N is

48   often a limiting resource for plant growth in these systems (Schimel and others 1996). Shifts in

49   the timing of trophic interactions (i.e., changes in herbivory) and subsequent N inputs (i.e., litter,

50   feces) may alter soil N available for plant uptake and microbial immobilization over the brief

51   summer growing season (Ruess and others 1997); however, the direction or magnitude of these

52   responses is uncertain. Because plant growth is highly coupled to N availability (Grogan and

53   Zamin 2018), climate-induced changes to inorganic (NH_4^+-N, NO_3^--N) and organic N (amino

54   acid) pools can directly alter ecosystem functioning, including changes in plant productivity and

55   microbial respiration (Belay-Tedla and others 2009; Sistla and others 2012; Schaeffer and others

56   2013), or even lead to ecosystem loss of N through leaching or denitrification (Buckeridge and

57   others 2010; Martinsen and others 2012) (Figure 1). Determining the effects of resource-

58   consumer phenological mismatch on N cycling requires investigating shifts in the timing of the

59   consumer (i.e., herbivory) and shifts in the timing of the resource (i.e., plant growing season) as

60   separate temporal controls.

61   The first critical temporal controls are changes in the seasonal timing of herbivory

62   (Clausen and Clausen 2013; Lameris and others 2017). Migratory geese, for example, are

63   arriving earlier to their Arctic breeding grounds, but some species are not arriving early enough

64   to match the advanced rate of plant green-up (Doiron and others 2015; Ross and others 2017).

65   The timing of migratory goose arrival is expected to be particularly important to N cycling,

66   especially in the coastal Arctic where geese occur at high densities and function as ecosystem

67   engineers (e.g. Uher-Koch and others 2019). Goose herbivory has the ability to affect N cycling

68   in three ways: the direct removal of aboveground tissue through grazing, the addition of soluble

69 N through fecal deposition, and the trampling of standing dead litter into the soil promoting the

70 turnover of organic material and rapid decomposition (Bazely and Jefferies 1989; Ruess and

71 others 1997; Zacheis and others 2002). Previous work found that early goose grazing reduced

72 above- and belowground plant biomass while later arrival and grazing had the opposite effect

73 (Choi and others 2019). The changing arrival time of geese also alters the timing of goose fecal

74 inputs, which can be an important source of soluble organic N (Henry and Jefferies 2002). Based

75 on our understanding of how the timing of goose herbivory influences vegetation, and the ability

76 of coastal graminoids to utilize amino acids and inorganic N forms (Henry and Jefferies 2003;

77 Welker and others 2003), we predict that shifts in the timing of goose arrival have the potential

78 to alter both organic and inorganic N availability (Figure 1).

79   The second temporal controls are changes in climate-driven shifts in the resource, most

80 often through advancement of the growing season and resulting higher rates of soil N cycling (N

81 mineralization [N_{min}], ammonification, denitrification) (Buckeridge and Grogan 2010; Bardgett

82 and others 2013). Warmer soil temperatures from season advancement can stimulate microbial

83 enzymatic activity (Sistla and Schimel 2013), which can increase soil NH_4^+-N and NO_3^--N pools,

84 and gaseous N efflux (Blankinship and Hart 2012; Bai and others 2013). Earlier springs can also

85 increase the labile organic N pool and amino acids (Darrouzet-Nardi and others 2019), which are

86 an important source of N for coastal graminoids in Arctic systems (Henry and Jefferies 2003).

87 However, advanced growing seasons also increase plant growth and demand (Lin and others

88 2010), thereby reducing N pools through greater plant uptake (Natali and others 2012) and

89 microbial immobilization (Jonasson and others 1999). Because of the microbial response to

90 earlier warmer temperatures and extension of the growing season, we predict that season

91 advancement will mobilize more soil N than can be assimilated by plant growth.

92   There is a growing climate-driven phenological mismatch between the timing of

93   herbivory by wild geese and the timing of the growing season, and a gap in our knowledge of

94   how changes in the relative importance of these processes influence N cycling and soil N pools.

95   To address this, we conducted a three-year field experiment that manipulated the timing of

96   migratory goose arrival (early, typical, late, and no arrival) and the growing season (advanced

97   and ambient). We then measured how the timing of these events and their interactions influence

98   inorganic (NH_4^+-N, NO_3^--N) and organic (amino acid) soil N pools and N_{min} rates. We

99   hypothesized that: H1) early goose arrival results in larger inorganic and organic N pools earlier

100   in the season because early goose grazing reduces above- and belowground plant biomass (Choi

101   and others 2019) and initiates earlier fecal inputs and trampling, while late migration has the

102   opposite effect (Figure 1); H2) season advancement and associated early season soil warming

103   stimulate microbial net N mobilization (i.e. the production and release of organic N and

104   inorganic N_{min}), which outweighs any reduction from early season plant growth (Leffler and

105   others 2019), and results in larger inorganic N pools compared to an ambient season; and H3) the

106   interaction between earlier goose arrival and season advancement synergistically increase pools

107   of inorganic and organic N because of the combined effect from warmer soil temperatures and

108   earlier grazing, feces, and trampling.

109

110   METHODS

111   *Study site*

112   We conducted this study near the Tutakoke River in the central coastal region of the

113   Yukon-Kuskokwim (Y-K) Delta in western Alaska (61°15'N, 165°37'W; elevation 2 m). The Y-

114   K Delta is over 125,000 km^2 of coastal tundra between the Yukon and Kuskokwim Rivers along

115   the Bering Sea. We established experimental plots within 1 km of the coast in a wet sedge

116   meadow on the active floodplain. Climate in the area is moderated by the Bering Sea with mean

117   temperatures ranging from -14 to 10 °C in midwinter and summer, respectively (Jorgenson and

118   Ely 2001).

119   Soils at our site are saturated and brackish, often mesohaline (8,000-30,000 μS cm^{-1}; 0.5-

120   18 ppt), frequently inundated by monthly tides, and characterized by interbedded layers of silt

121   and sandy loams (Jorgenson 2000). Permafrost, while found further inland, is not present in the

122   active coastal floodplain. Soils are classified as histosols and have a bulk density of 0.69 g cm^{-3},

123   and 9.5% organic content consisting of 4.7% C and 0.3% N.

124   *Carex* graminoids are the dominant vegetation in the coastal Y-K Delta. *C. subspathacea*,

125   in particular, is a critically important goose forage species, that occurs in near monotypic stands

126   along the margins of ponds and tidal flats, and is so heavily grazed and modified by geese that

127   when altered, it is referred to as 'grazing lawn' (Person and others 2003). Using the day of year

128   when NDVI (normalized difference vegetation index) reaches 50% of its maximum as a

129   vegetation phenology metric (Brook and others 2015), green-up has varied over 30 days (23-May

130   to 25-June) over the last 35 years (1982-2016), but has occurred on average 0.3 days earlier per

131   year (Leffler and others 2019).

132   Geese time their long-distance migration to optimize their nutrient demands with a

133   narrow window of peak nutrient availability in the spring (Sedinger and Raveling 1986).

134   Approximately 50% of the world's Pacific black brant (*Branta bernicla nigricans*) nest in the

135   coastal Y-K Delta, with ca. 30-day variation in the range of hatch dates (3-June to 9-July)

136   observed over 34 years (1983-2016) (Fischer and others 2008, 2017). However, the three years

137   of our experiment (2014, 2015, 2016) had three of the earliest six hatch dates for black brant in

138   the Y-K Delta, especially year 3 (2016), which was the earliest on record (Fischer and others

139   2017). At our site, there is a positive correlation between NDVI spring advancement and hatch

140   date ($R^2 = 0.78$), but geese do not appear able to keep up with the timing of spring with

141   migratory arrival occurring on average 0.14 days earlier per year (Fischer and others 2017).

142

143   *Phenology experiment*

144   We conducted a three-year fully factorial experiment simulating scenarios of

145   phenological mismatch. This experiment has been used to investigate changes in greenhouse gas

146   flux (Kelsey and others 2018; Leffler and others 2019), forage quality (Beard and others 2019a)

147   and plant traits (Choi and others 2019) and is described in those studies. Briefly, we used four

148   timings of grazing (early, typical, late, and no-grazing) crossed with two timings of the growing

149   season (advanced and ambient) for a total of eight treatments. We altered the timing of goose

150   grazing by minus-three, zero, and plus-three weeks (early, typical, and late treatments,

151   respectively), and advanced the growing season by three weeks (see below). The 'typical' goose

152   treatment represented historic mean arrival and grazing and acted as the grazing treatment

153   control, while the 'no-grazing' treatment represented potential future scenarios where goose

154   populations decline to near zero or fail to arrive. We also had a background grazing control plot

155   in each block that was used to compare the effectiveness of our experimental grazing, but not as

156   a statistical comparison for our treatments. Thus, we had a total of 54 plots in six replicate blocks

157   located within 700 m. All plots were established in April 2014 and were 1.7 m x 0.85 m in size.

158   We installed fencing around all paired advanced and ambient growing season plots, except the

159   background grazing control, to exclude wild goose grazing. Treatments were assigned randomly

160   and applied to the same plots from 1-May through 15-August each year.

161   We manipulated timing of grazing by introducing wild-caught geese into fenced goose

162   exclosures (ca. 7.6 m^2) at specific times during the season. Early, typical and late grazing

163   treatments began on 30-May, 20-June, and 9-July, respectively, to approximate the 30-day

164   variation in the range of historic mean hatch dates (3-June to 9-July) (Fischer and others 2017).

165   These dates are the biologically relevant means for our system and allowed us to use actual geese

166   (as opposed to simulated grazing) in our experiments, which required treatments to start after

167   nest initiation so they could be captured. Aboveground biomass in background control plots did

168   not differ from typical grazing plots in years 1 and 2 or early goose grazing plots for all three

169   years (Choi and others 2019). Because the experiment coincided with three of the six earliest

170   mean hatch dates in the Y-K Delta over the last 34 years and the last year of our experiment was

171   the earliest on record (Fischer and others 2017), we expected that background controls would be

172   more similar to early goose grazing treatments by year 3.

173   Grazing treatments only differed in the timing of grazing initiation; we kept total grazing

174   time constant among treatments. While earlier shifts in migratory goose arrival might result in a

175   longer available season for grazing, the duration of time spent on *Carex* grazing lawns is

176   constrained by the development time of goslings, typically ca. 40 days (Sedinger and others

177   2001). Furthermore, differences in timing of grazing treatments are attributed to the timing of

178   grazing initiation, and not variation in the duration of grazing. Experimental grazing treatments

179   (early, typical, and late grazing) consisted of two brant geese grazing, trampling and defecating

180   inside exclosures during four 24 h bouts separated by 12 days over a total of 37 days to simulate

181   post-hatch grazing. Unlike other goose species in the Y-K Delta, black brant are grazers and do

182   not grub during the summer (Sedinger and Raveling 1984). Prior to each grazing treatment, we

183   held geese for two hours without food to allow feces from captive feeding to pass through their

184   digestive system. After each 24 h grazing treatment, we held birds for an additional two hours to

185   collect feces which were returned to the appropriate plots. In between grazing treatments, we

186   held geese in a fenced enclosure and allowed them to graze freely on natural vegetation,

187   supplemented *ad libitum* with commercial goose feed. Captive geese were released into the wild

188   at the end of each season.

189   We used two adjacent conical passive-warming open-top chambers (OTCs; 30 cm height

190   x 85 cm base dia. x 50 cm top dia.) to initiate an earlier growing season in the advanced season

191   plots. We placed OTCs on plots from 1-May to 1-July, and removed them only during goose

192   grazing treatments. We monitored air and soil temperature (10 cm above- and belowground)

193   inside and outside OTCs in every plot each growing season. These OTCs doubled mean

194   vegetation height and advanced the growing season by 22, 18, and 21 days by the end of June

195   2014, 2015, and 2016, respectively (Leffler and others 2019). OTCs warmed plots on average

196   between 0.6 and 1.7 °C (aboveground) and 0.6 and 1.0 °C (belowground).

197

198   *Soil N measurements*

199   We measured inorganic (NH_4^+-N, NO_3^--N) and organic N (amino acids) and N

200   mineralization in all treatments of the experiment. Inorganic N (NH_4^+-N, NO_3^--N) was measured

201   via two methods, while organic N (amino acids) was measured via one method over three years.

202   N_{min} was measured only during the third year of the experiment.

203   We used ion-exchange resin strips (2.5 cm wide x 10 cm length; CR67 & AR204SZRA,

204   General Electricals, Watertown, MA) to measure inorganic N (NH_4^+-N, NO_3^--N) available to

205   adsorb to soil particles (Qian and Schoenau 1995). We prepared cation and anion strips

206   separately using the same procedure. We immersed and shook strips in baths of 0.5 M HCl for 1

207 h and 0.5 M NaHCO₃ for 5 h, and then washed and stored them with deionized water. In the

208 center of each plot, we installed six to eight cation and anion resin pairs vertically 10 cm into the

209 ground until the top was even with the surface of the soil. We collected resins every two weeks,

210 each time yielding a cumulative measure of adsorbed inorganic N. Upon collection, we froze all

211 resins in the field. In the laboratory, we washed all resins using 50 mL of 2M KCl and froze

212 extracts until analysis.

213   Because some of our plots experienced seasonal inundation during high tide events, we

214 used an additional resin approach to measure soil inorganic N. Seawater has a high ionic

215 potential and tidal flooding can interfere with measurements by striping resin ion-exchange sites

216 of adsorbed inorganic N (McBride 1989). High spring tides flooded and inundated several

217 experimental blocks each season (Julian date 2014 (205), 2015 (186), 2016 (185, 210)), which

218 corresponded with a drop-off in resin-collected N on strips that remained *in situ* (Figure 2). To

219 address this problem in years 2 and 3, we installed intertidal resin sets for three weeks between

220 monthly peak tides, determined from regional NOAA tide predictions (Dall Point, AK;

221 tidesandcurrents.noaa.gov), and collected pairs from plots before the next peak tidal event. Both

222 cumulative and intertidal resin incubations had their own strengths and results show similar

223 trends, so we present both datasets for completeness. Resin measurements represent N adsorption

224 by soil ion-exchange sites over time, and separate resin collections are referred to as either

225 'cumulative' or 'intertidal'.

226   We used microlysimeters to measure labile inorganic (NH_4^+-N, NO_3^--N) and organic N

227 (amino acids) pools in soil pore water. At the center of each plot, we installed a single 10-cm

228 rhizon soil moisture microlysimeter (Eijkelkamp, Giesbeek, Netherlands) perpendicular into the

229 soil surface and left them in place over the season. We used plastic syringes to collect 10 mL

230   pore water samples from the top 10 cm of soil every two weeks, and used 1μm, 25-mm diameter

231   Acrodisc glass fiber syringe filters (Pall Laboratory, Port Washington, NY) to pre-filter soil pore

232   water before storing and freezing samples until analysis. Microlysimeter measurements represent

233   labile N available in soil pore water at the time of collection.

234   During the final year of the experiment, we measured net N_{min} rates in each experimental

235   plot (n = 54) using the buried bag technique (Robertson and others 1999). On 1-June, we took

236   two, 4-cm diameter cores from the top 10 cm of soil in each plot. We collected one core and

237   placed the other intact in a polyethylene bag and buried it *in situ* until 1-August. We

238   homogenized, sieved, and extracted both cores within 24 h of collection. From each core, we

239   extracted 10 g of root-free soil in 50 mL of 2M KCl, filtered, and froze samples until analysis.

240   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

241   between the initial harvest and final harvest divided by the total number of days *in situ*.

242   We analyzed filtrate from resin extracts, microlysimeter samples, and N_{min} measurements

243   using colorimetric (NH_4^+-N, NO_3^--N) or fluorometric (amino acid) microplate assays. We used

244   the Berlethot reaction for NH_4^+-N (Rhine and others 1998) and the Griess reaction for NO_3^--N

245   (Doane and Horwáth 2003). We measured organic N (amino acid) using fluorescence of samples

246   with *o*-phthaldialdehyde and β-mercaptoethanol (Jones and others 2002). Absorbance and

247   fluorescence values were measured with a Synergy^{TM} H4 Hybrid Multi-Mode Microplate Reader

248   (Bio-Tek Inc., Winooski, VT) at Utah State University.

249

250   *Statistical analysis*

251   We tested the effects of timing of goose grazing (early, typical, late, no-grazing) and

252   timing of the growing season (advanced, ambient) on soil N availability. We used NH_4^+-N, NO_3^-

253 -N and amino acids, and N_{min} measurements as continuous response variables, experimental

254 treatments (timing of goose grazing, start of the growing season), sampling date, and year as

255 fixed-effect predictor variables, and treated plot nested within block as a random effect. Separate

256 models were used for each measured N pool (cumulative and intertidal resin NH_4^+-N and NO_3^--

257 N, and microlysimeter NH_4^+-N, NO_3^--N, and amino acids). We tested distributions of continuous

258 variables for normality and homogeneity of variance, and log-transformed all predictor variables

259 prior to analysis to meet these assumptions. We coded ambient season and typical grazing plots

260 as the reference comparison for the growing season and grazing season treatment, as appropriate.

261 Our models included interactions of fixed-effect predictors, but we limited interactions to

262 combinations of no more than two variables. We determined variable importance by inclusion in

263 the top-performing model. We included a first-order autocorrelation structure to account for

264 repeated measures within subjects over time.

265 For all analyses, we used a linear mixed model framework with model selection and

266 Akaike Information Criteria (AIC). We fit all models using the nlme package within the R

267 statistical computing environment (Pinheiro and others 2017, R Core Development Team). We

268 selected top models based on ΔAIC and considered models to be similar if ΔAIC<2 (Burnham

269 and others 2011). Using the nlme summary function, we determined the fixed effect parameter

270 estimates for top model variables that were statistically different from the reference intercept

271 (ambient season, typical grazing) (Supplemental Table S1). For simplicity and to capture the

272 effects after three years of experimental treatments, we present soil N percent change as the

273 mean across the last year of the experiment unless otherwise indicated.

274

275 RESULTS

276   Across all N pool measurements, both timing of grazing and timing of season were

277   included in the top models highlighting the strength of timing of goose herbivory and season

278   advancement treatments on soil N availability (Table 1). There were no interactions between the

279   timing of grazing and timing of season in any of our top models.

280   Cumulative and intertidal ion-exchange resins and soil pore water in early grazing plots

281   had 62%, 21% and 103% more NH_4^+-N, respectively, compared to typical grazing treatment

282   (Figs. 2-4). Intertidal resins had 16% less NH_4^+-N available in late grazing than typical grazing

283   treatments (Figs. 3A-B). Comparatively, the advanced growing season had a 2% and 26%

284   increase in intertidal and soil pore NH_4^+-N pools, respectively, compared to the ambient

285   treatment by year 3 (Supplemental Table S1). The top-ranking models for resin-adsorbed soil

286   NH_4^+-N included year, season advancement, and an interaction between timing of grazing and

287   sampling date, whereas top-ranking models for NH_4^+-N in soil pore water included timing of

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

289   Early grazing had seasonal peaks in intertidal resin-adsorbed NH_4^+-N that coincided with

290   early grazing treatments (~30-May to 10-July), ~30 days earlier than typical grazing. Similarly,

291   late grazing delayed seasonal peak intertidal resin-adsorbed NH_4^+-N by ~20 days later in the

292   season compared to typical grazing plots (Figs. 3A-B), which coincided with the timing of late

293   grazing treatments (~9-July to 15-August). Unlike early grazing, an advanced growing season

294   did not shift the peak timing of soil NH_4^+-N available for biological assimilation.

295   Cumulative resin-adsorbed NO_3^--N declined while intertidal resin and soil pore NO_3^--N

296   increased across the three years. Top models for resin-adsorbed and soil pore NO_3^--N all

297   included timing of grazing, season advancement, and year, or an interaction between timing of

298   grazing or year, and sampling date (Table 1). Intertidal and soil pore NO_3^--N increased 139% and

299   119% in the early grazing treatment compared to typical grazing treatment, while cumulative

300   resin-adsorbed NO_3^--N decreased by 17% in late grazing treatment (Figs. 2-4, Table 2). Intertidal

301   resins also had 51% more NO_3^--N in no-grazing treatment than typical grazing plots in the last

302   year of the experiment, but had 21% less NO_3^--N in the same plots the previous year (Figs. 3C-

303   D, Table 2). While season advancement was found in all the top models, it was not significant

304   (Supplemental Table S1).

305   Experimental treatments had no measurable effect on net N_{min} rates in year 3. The top

306   models for both net N_{min} NH_4^+-N and NO_3^--N either included just season advancement or the null

307   model (Table 1). In general, the advanced growing season decreased N_{min} rates for NH_4^+-N and

308   NO_3^--N by 176% and 8%, respectively; however, these effects were not significant

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

310   dry soil^{-1} d^{-1} and 0.22 ± 0.07 µg NO_3^--N g-dry soil^{-1} d^{-1}, or a total of 0.31 ± 0.25 µg inorganic N

311   g-dry soil^{-1} d^{-1}.

312   Amino acids increased by 7% in the early grazing treatment compared to the typical

313   grazing treatment, with peaks in availability observed early in the growing season (Figs. 4G-I).

314   The top model for soil pore amino acid concentrations included timing of grazing and an

315   interaction between year and sampling date, while the second-ranked model with $\Delta AIC < 2$ also

316   included season advancement (Table 1). While season advancement was included in the second-

317   ranked model, it was not significant (Supplemental Table S1).

318

319   DISCUSSION

320   Our experimental results suggest that the timing of migratory goose grazing (i.e. goose

321   arrival date) has a greater impact on soil N availability than advancement of the growing season

322   in this N-limited coastal ecosystem. Early goose grazing had the greatest measurable effect on

323   soil N by increasing both inorganic and organic soil N pools. Season advancement also increased

324   soil NH_4^+-N availability, but compared to early grazing only had a limited effect on soil N pools,

325   despite a similar three-week shift in timing (Figure 5). Furthermore, there was no synergistic

326   interaction between timing of goose arrival and timing of spring advancement on soil N

327   availability. Our findings suggest that in coastal western Alaska, where migratory geese are

328   arriving earlier into a phenologically advanced system, soil N availability will increase. Larger

329   soil N pools are important for plant nutrient availability, and even short-term impacts on soil N

330   pools can have lasting effects on forage quality (Ruess and others 2019), or alter plant

331   community composition and productivity (Ruess and others 1997; Boyer and Zedler 1999).

332   These shifts in N may facilitate shifts from graminoid to shrub-dominant vegetation, resulting in

333   a reduction of *Carex* grazing lawns and goose forage resources (Myers-Smith and others 2011;

334   Carlson and others 2018). Finally, increased N availability can also result in the greater

335   likelihood of N leaching and potential loss (Jonasson and others 1999).

336

337   *Soil inorganic N response to timing of grazing treatments*

338   Our findings support hypothesis (H1) that timing of grazing can affect inorganic soil N

339   pools (NH_4^+-N, NO_3^--N), and early grazing had the greatest impact (Figure 5). More specifically,

340   early grazing increased resin-adsorbed and soil pore NH_4^+-N availability, which suggests the

341   long-term and short-term influence of this treatment on the different extractable pools. Late

342   grazing also influenced soil N, primarily by reducing intertidal resin-adsorbed NH_4^+-N but not

343   soil pore NH_4^+-N (Table 2), which suggests that the draw down may have taken time (up to three

344   weeks for intertidal resins) for effects to accumulate. By delaying peak NH_4^+-N availability and

345   storing N in plant tissues, late grazing retains N in the system and returns it slowly through

346   decomposition and microbial turnover, reducing the potential for N leaching and loss.

347   Similar to soil NH_4^+-N, our findings supported hypothesis (H1) that the timing of grazing

348   also affected NO_3^--N pools. Changes in pool sizes of NH_4^+-N with both early and late grazing

349   resulted in similar relative changes in NO_3^--N with the same treatment. However, overall NO_3^--N

350   concentrations observed across all treatments were 10 times lower than NH_4^+-N. We offer four

351   potential mechanisms for this pattern. First, NO_3^--N is highly mobile in the soil and easily lost

352   through leaching or uptake by plants (Miller and Cramer 2005). Second, saturated soils and low

353   O_2 conditions can limit rates of aerobic nitrification (White and Reddy 2003). Third, the

354   anaerobic microbial dissimilatory nitrate reduction to ammonium pathway, a process that

355   converts NO_3^--N back into NH_4^+-N and occurs in highly reducing environments or flooded soils,

356   may have suppressed NO_3^--N accumulation (Giblin and others 2013). Finally, it is also possible

357   that NO_3^--N produced in the soil can be denitrified (Tiedje 1988); however, concurrent

358   measurements in our experimental plots found no significant N_2O gaseous efflux from our

359   ecosystem (Kelsey and others 2018), suggesting that this is an unlikely pathway.

360

361   *Soil inorganic N response to season advancement*

362   Our results support hypothesis (H2) that, by stimulating microbial activity through

363   warmer early season conditions, season advancement increased soil NH_4^+-N pools in excess of

364   any increased plant uptake. Similar to other studies investigating season advancement (Borner

365   and others 2008; Buckeridge and others 2010; Rogers and others 2011), we found a moderate

366   effect of an advanced growing season on soil NH_4^+-N. Season advancement also increased soil

367   respiration in our experimental plots (Leffler and others 2019), which suggests that higher rates

368   of microbial N cycling contributed to N pools. Despite having a similar shift in timing of grazing

369   (+3 weeks), this increase was less than the effect of early grazing, which had a four-fold increase

370   in soil pore NH_4^+-N (Table 2), and highlights the importance of earlier migratory arrival at our

371   site. While an advanced growing season increased NH_4^+-N, it did not result in a significant

372   increase in NO_3^--N pools, likely due to the anaerobic suppression of nitrification in saturated

373   soils earlier in the season.

374

375   *N mineralization response to treatments*

376   We found that N_{min} had no measurable response to an advanced season or timing of

377   grazing treatments and was highly variable among plots, which refutes hypotheses (H1 & H2)

378   that earlier grazing and an advanced growing season stimulated net N mobilization. Others have

379   found that N_{min} rates were not affected by vegetation clipping treatments in *Carex* grazing lawns

380   at our site (Person and Ruess 2003) or by goose grazing in the Hudson Bay (Wilson and Jefferies

381   1996). Studies reporting increases in N_{min} from experimental warming had soil temperature

382   increases of 1-3 ºC (e.g. DeMarco and others 2011), suggesting that perhaps our season

383   advancement treatments (0.6 to 1.0 ˚C at 10 cm belowground only for the first half of the season)

384   were insufficient to increase season-long rates of N_{min} and production. The lack of an N_{min}

385   response suggests that the observed changes in N pools from timing of grazing and season

386   advancement were likely driven by plant uptake or microbial immobilization.

387

388   *Soil organic N pool response to treatments*

389   Our findings support our hypothesis (H1) that early grazing increases organic N (amino

390   acid) concentrations (Figs. 2G-H). Early peaks in amino acids were observed in all treatments

391   and may have resulted from the post-melt release of organic N from the lysing of root and

392   microbial cells during freeze/thaw events in the fall and early spring (Grogan and others 2004).

393   The rapid decline in amino acid concentrations early season coincided with the uptake of

394   available N by roots for plant growth, as suggested by others in high latitude systems (Weintraub

395   and Schimel 2005; Edwards and others 2006), and likely occurred to a lesser degree in the early

396   grazing treatment due to reduced plant growth (Choi and others 2019). Because microlysimeters

397   measured labile inorganic and organic N available in soil pore water (Darrouzet-Nardi and

398   Weintraub 2014), the observed season-long draw down of the organic N pool suggests that plants

399   and microbes are utilizing the most easily available limiting resources (Hobbie and Hobbie 2012)

400   (Figs. 2G-I).

401

402   *N pathways*

403   We propose that reduced plant uptake was the primary mechanism driving the increase in

404   available soil N in the early grazing treatments. Although grazing has the potential to stimulate

405   graminoid productivity through compensatory growth (Grogan and Zamin 2018), in our

406   treatments early grazing reduced above- and belowground biomass by 52% and 55%,

407   respectively, while late grazing increased inflorescences and dead biomass by 515% and 569%,

408   respectively (Choi and others 2019), compared to typical grazing plots (Figure 5). These grazing

409   effects had lasting legacy effects on plant productivity in subsequent seasons (Choi and others

410   2019), which corresponded with changes in soil N availability by the end of our three year

411   experiment.

412   It is possible that other mechanisms contributed to the observed increases in soil N

413   availability. In northern latitudes where geese are the dominant herbivores, feces are thought to

414   be important sources of soil N (Bazely and Jefferies 1985). Research conducted in another Arctic

415   coastal system detected amino acid signatures of goose feces in the soil profile (Henry and

416   Jefferies 2002), and plant foliar δ^{15}N from our early grazing treatments had enriched δ^{15}N values

417   (3.3‰) that more closely matched the values of goose feces (3.7‰), as opposed to late and no-

418   grazing treatments (2.7‰ and 2.1‰, respectively) (Beard and Choi 2017). Because of the non-

419   mycorrhizal nature of graminoids (Welker and others 2003; Craine and others 2009), changes in

420   leaf δ^{15}N of *Carex* species are often due to shifts in N sources, such as herbivore N inputs

421   (Sjögersten and others 2010), and the observed changes are likely indicative of substantial N

422   recycling between geese and plants.

423   Although it is likely that geese are important sources of N for plants, the effect of goose

424   feces on N pool sizes remains unclear. An experiment at our site that manipulated goose fecal

425   densities on *Carex* grazing lawns by creating plots with double, ambient, and no feces found no

426   changes in inorganic or organic soil N availability using the same N collection methods used in

427   the present study (Beard and Choi 2017). Further, changes in fecal density did not change *Carex*

428   biomass or forage quality (Beard and Choi 2017). Observations of goose feces at our site suggest

429   that pellets often dry up and are not incorporated into the soil through trampling, while frequent

430   flooding and high tide events redistributed or removed 85-90% of feces (Beard and Choi 2017).

431   Because soluble N rapidly declines in goose feces after deposition (Bazely and Jefferies 1985),

432   we speculate that a portion of N volatilizes into the atmosphere. While we believe that goose

433   feces play a role in soil N availability, the magnitude of its influence on soil N pools at our site

434   still warrants further investigation.

435

436   *Treatment interactions*

437   While both early grazing and an advanced growing season, in general, increase N

438   availability in soil pools, there were no observed interactions between timing of grazing and

439   timing of season treatments (H3). It is possible that the compensatory growth response of *Carex*

440   grazing lawns to early goose herbivory, in particular because of the increased soil N availability

441   (Grogan and Zamin 2018), may have dampened the increase in N availability from early grazing

442   and the advanced season (Choi and others 2019). Alternatively, while warmer temperatures and

443   reduced leaf shading seemed to increase N mobilization, these conditions also likely lowered soil

444   water content, thereby limiting rates of microbial decomposition and accumulation of inorganic

445   N pools (Skopp and others 1990). Because both earlier goose arrival and advancing green-up are

446   occurring at our site, our findings suggest that there will be additive, but not synergistic,

447   increases in soil N availability.

448

449   *Soil N collections and limitations*

450   The different methods of N measurements we employed captured different aspects of the

451   available soil N pools. We used microlysimeters to measure the labile soil pore N pools at

452   biweekly intervals and this N was more sensitive to short-term differences in availability,

453   compared to the less frequently collected ion-exchange resins that accumulated changes in soil

454   adsorbed N over time. Of the resin measurements, it is not surprising that intertidal resins

455   detected a stronger response to grazing treatments given that they were designed to reduce

456   interference from tidal inundation. Because N availability in northern coastal systems has high

457   temporal and spatial variability (McLaren and others 2017; Darrouzet-Nardi and others 2019),

458   our relatively high frequency of measurements and multiple approaches helped improve our

459   understanding of soil N fluctuations and availability across the growing season.

460

CONCLUSIONS

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

483   Refuge staff; and the people of Chevak, AK. Permits obtained for this work include - ADF&G

484   permit: 16–23; USFWS NWR special use permit: FF07RYKD0-14-06; USFWS Migratory Bird

485   permit: MB28352B-0; USU IACUC: 2004. Data are published online at the NSF Arctic Data

486   Center (doi: 10.18739/A22274). Any use of trade, firm, or product names is for descriptive

487   purposes only and does not imply endorsement by the US Government.

488

489   Conflict of Interest: The authors declare that they have no conflict of interest.

490

491   LITERATURE CITED

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

494   Bardgett RD, Manning P, Morriën E, De Vries FT. 2013. Hierarchical responses of plant-soil
495   interactions to climate change: consequences for the global carbon cycle. J Ecol 101:334–
496   43.

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

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

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

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

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

509   Belay-Tedla A, Zhou X, Su B, Wan S, Luo Y. 2009. Labile, recalcitrant, and microbial carbon
510   and nitrogen pools of a tallgrass prairie soil in the US Great Plains subjected to
511   experimental warming and clipping. Soil Biol Biochem 41:110–6.

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

514   Boelman NT, Krause JS, Sweet SK, Chmura HE, Perez JH, Gough L, Wingfield JC. 2017.

515   Extreme spring conditions in the Arctic delay spring phenology of long-distance migratory
516   songbirds. Oecologia 185:1–12.

517   Borner AP, Kielland K, Walker MD. 2008. Effects of simulated climate change on plant
518   phenology and nitrogen mineralization in Alaskan Arctic tundra. Arctic, Antarct Alp Res
519   40:27–38.

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

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

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

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

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

533   Carlson LG, Beard KH, Adler PB. 2018. Direct effects of warming increase woody plant
534   abundance in a subarctic wetland. Ecol Evol:1–12.

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

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

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

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

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

550   Darrouzet-Nardi A, Weintraub MN. 2014. Evidence for spatially inaccessible labile N from a
551   comparison of soil core extractions and soil pore water lysimetry. Soil Biol Biochem 73:22–
552   32.

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

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

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

560   Edwards KA, McCulloch J, Kershaw GP, Jefferies RL. 2006. Soil microbial and nutrient
561   dynamics in a wet Arctic sedge meadow in late winter and early spring. Soil Biol Biochem
562   38:2843–51.

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

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

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

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

574   Grogan P, Zamin TJ. 2018. Growth responses of the common arctic graminoid *Eriophorum
575   vaginatum* to simulated grazing are independent of soil nitrogen availability. Oecologia
576   186:151–62.

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

579   Henry HAL, Jefferies RL. 2002. Free amino acid, ammonium and nitrate concentrations in soil
580   solutions of a grazed coastal marsh in relation to plant growth. Plant, Cell Environ 25:665–
581   75.

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

584   Hobbie JE, Hobbie EA. 2012. Amino acid cycling in plankton and soil microbes studied with
585   radioisotopes: measured amino acids in soil do not reflect bioavailability. Biogeochemistry
586   107:339–60.

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

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

591   34:1893–902.

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

594   Jorgenson T, Ely C. 2001. Topography and flooding of coastal ecosystems on the Yukon-
595   Kuskokwim Delta, Alaska: implications for sea-level rise. J Coast Res 17:124–36.

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

599   Kölzsch A, Bauer S, de Boer R, Griffin L, Cabot D, Exo KM, van der Jeugd HP, Nolet BA.
600   2015. Forecasting spring from afar? Timing of migration and predictability of phenology
601   along different migration routes of an avian herbivore. J Anim Ecol 84:272–83.

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

605   Leffler AJ, Beard KH, Kelsey KC, Choi RT, Schmutz JA, Welker JM. 2019. Delayed herbivory
606   by migratory geese increases summer-long CO2 uptake in coastal western Alaska. Glob
607   Chang Biol 25:277–89.

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

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

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

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

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

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

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

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

628   Natali SM, Schuur EAG, Rubin RL. 2012. Increased plant productivity in Alaskan tundra as a

629   result of experimental warming of soil and permafrost. J Ecol 100:488–98.

630   Person BT, Herzog MP, Ruess RW, Sedinger JS, Anthony RM, Babcock CA. 2003. Feedback
631   dynamics of grazing lawns: coupling vegetation change with animal growth. Oecologia
632   135:583–92.

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

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

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

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

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

643   Robertson GP, Wedin D, Groffman PM, Blair JM, Holland EA, Nadelhoffer KJ, Harris D. 1999.
644   Soil carbon and nitrogen availability: nitrogen mineralization, nitrification, and soil
645   respiration potentials. In: Robertson GP, Coleman DC, Bledsoe CS, Sollins P, editors.
646   Standard Soil Methods for Long-Term Ecological Research. New York, NY: Oxford
647   University Press. pp 258–71.

648   Rogers MC, Sullivan PF, Welker JM. 2011. Evidence of nonlinearity in the response of net
649   ecosystem CO2 exchange to increasing levels of winter snow depth in the High Arctic of
650   northwest Greenland. Arctic, Antarct Alp Res 43:95–106.

651   Ross M V., Alisauskas RT, Douglas DC, Kellett DK. 2017. Decadal declines in avian herbivore
652   reproduction: density-dependent nutrition and phenological mismatch in the Arctic. Ecology
653   98:1869–83.

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

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

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

662   Schimel JP, Kielland K, Chapin FS. 1996. Nutrient availability and uptake by tundra plants. In:
663   Reynolds JF, Tenhunen JD, editors. Landscape Function and Disturbance in Arctic Tundra.
664   Ecological Studies (Analysis and Synthesis), vol 120. Springer Berlin Heidelberg. pp 203–
665   21.

666   Sedinger JS, Herzog MP, Person BT, Kirk MT, Obritchkewitch T, Martin PP, Stickney AA.

667   2001. Large-scale variation in growth of Black Brant goslings related to food availability.
668   Auk 118:1088–95.

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

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

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

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

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

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

682 Tiedje JM. 1988. Ecology of denitrification and dissimilatory nitrate reduction to ammonium. In:
683   Zehnder AJB, editor. Environmental Microbiology of Anaerobes. John Wiley & Sons, N.Y.
684   pp 179–244.

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

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

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

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

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

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

699

TABLES

Table 1.

Model	logLik	AIC	ΔLogLik	ΔAIC	df	weight
Cumulative resin NH$_4^+$-N						
Year + Grazing*Date	-1155.1	2338.3	111.2	0.0	14	0.564
Year + Grazing*Date + Season	-1154.4	2338.8	112.0	0.5	15	0.434
Year*Date + Grazing	-1162.3	2350.6	104.0	12.3	13	0.001
Year*Date + Grazing + Season	-1161.6	2351.1	104.8	12.9	14	<0.001
Intertidal resin NH$_4^+$-N						
Year + Grazing*Date + Season	-404.7	837.5	84.6	0	14	0.923
Year + Grazing*Date	-408.2	842.5	81.1	5	13	0.077
Year*Season + Grazing + Date	-426.0	876.1	63.3	38.6	12	<0.001
Year*Grazing + Season + Date	-424.1	876.1	65.3	38.6	14	<0.001
Microlysimeter NH$_4^+$-N						
Year*Date + Grazing	-1360.2	2746.5	24.9	0.0	13	0.323
Year*Date + Grazing + Season	-1359.7	2747.4	25.5	0.9	14	0.206
Year*Date	-1364.0	2748.0	21.2	1.5	10	0.152
Year*Date + Season	-1363.5	2749.1	21.6	2.6	11	0.088
Cumulative resin NO$_3^-$-N						
Year*Date + Grazing	-1239.7	2505.3	184.6	0.0	13	0.723
Year*Date + Grazing + Season	-1239.7	2507.3	184.6	2.0*	14	0.267
Year*Date	-1247.2	2514.5	177.0	9.2	10	0.007
Year*Date + Season	-1247.2	2516.5	177.0	11.2	11	0.003
Intertidal resin NO$_3^-$-N						
Year + Grazing*Date	-390.1	806.1	56.6	0	13	0.369
Year*Date + Grazing	-392.6	807.3	54.1	1.1	11	0.211
Year + Grazing*Date + Season	-390.1	808.1	56.6	2.0*	14	0.136
Year*Date + Grazing + Season	-392.6	809.2	54.1	3.1	12	0.078
Microlysimeter NO$_3^-$-N						
Year*Date	-1498.3	3016.6	50.2	0.0	10	0.380
Year*Date + Season	-1497.6	3017.3	50.8	0.7	11	0.270
Year*Date + Grazing	-1495.9	3017.9	52.5	1.3	13	0.200
Year*Date + Grazing + Season	-1495.3	3018.6	53.2	1.9	14	0.150
N-mineralization NH$_4^+$-N						
Season	-13.6	37.3	1.6	0.0	5	0.543
Null model	-15.3	38.5	0.0	1.3	4	0.291

Grazing + Season	-12.2	40.4	3.1	3.1	8	0.114
Grazing	-14.2	42.4	1.0	5.2	7	0.041
N-mineralization NO$_3^-$-N						
Null model	8.7	-9.3	0.0	0.0	4	0.638
Season	8.7	-7.4	0.0	1.9	5	0.242
Grazing	9.6	-5.1	0.9	4.2	7	0.079
Grazing + Season	9.6	-3.2	0.9	6.2	8	0.029
Microlysimeter amino acids						
Year*Date + Grazing	-1290.6	2607.3	99.2	0.0	13	0.504
Year*Date + Grazing + Season	-1290.0	2608.0	99.8	0.7	14	0.349
Year*Date	-1295.4	2610.8	94.4	3.5	10	0.086
Year*Date + Season	-1294.8	2611.5	95.1	4.2	11	0.061

Table 2.

Effect	Cumulative resin NH$_4^+$-N			Intertidal resin NH$_4^+$-N			Microlysimeter NH$_4^+$-N		
	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%**

Effect	Cumulative resin NO$_3^-$-N			Intertidal resin NO$_3^-$-N			Microlysimeter NO$_3^-$-N		
	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%

Effect	N-mineralization NH$_4^+$-N			N-mineralization NO$_3^-$-N			Microlysimeter amino acids		
	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%

TABLE LEGENDS

Table 1. Top four performing models for soil N response variables based on AIC model selection for experimental treatments over three years (2014-16). Abbreviations: Grazing = timing of goose grazing treatment, Season = season advancement treatment, Date = sampling date. Models with interaction terms imply inclusion of the main effect. Bolding indicate top models with ΔAIC<2.

Table 2. Mean percent changes by treatment for each year. The reference level was the ambient growing season or typical grazing timing treatment, respectively. Abbreviations: Early = early grazing, Late = late grazing, None = no-grazing, Advanced = advanced growing season treatment. Bolding indicates treatment effect with p<0.05; (*) indicates sampling date interaction.

FIGURE LEGENDS

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, while trampling and fecal deposition increase N availability; an advanced spring with warmer soil temperatures stimulates earlier plant and microbial growth; the interaction increases N availability due to increase microbial activity with less aboveground biomass to increase N uptake. Sub-figures are the hypothesized directional response of treatments on soil N availability.

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

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

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

Figure 5. Conceptual figure of experimental treatments (timing of grazing and season advancement) on soil N measurements (cumulative and intertidal resins, and microlysimeter pore water) compared to typical grazing and ambient season treatments after three years. Arrow thickness indicates relative treatment effect size. Blue arrows indicate a positive effect; red arrows indicate a negative effect. Measurements without arrows had no significant measured treatment effect. Depicted above- and belowground vegetation represent actual measurements from early grazing and season advancement treatments, respectively (Choi and others 2019).
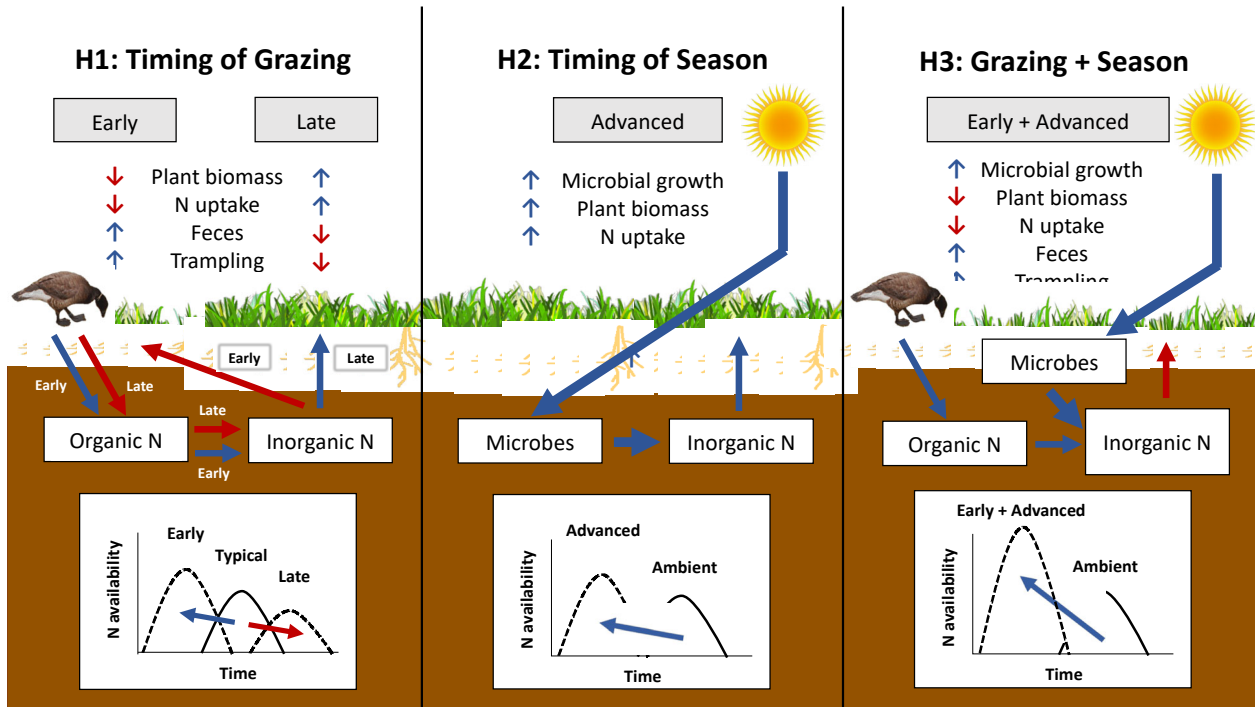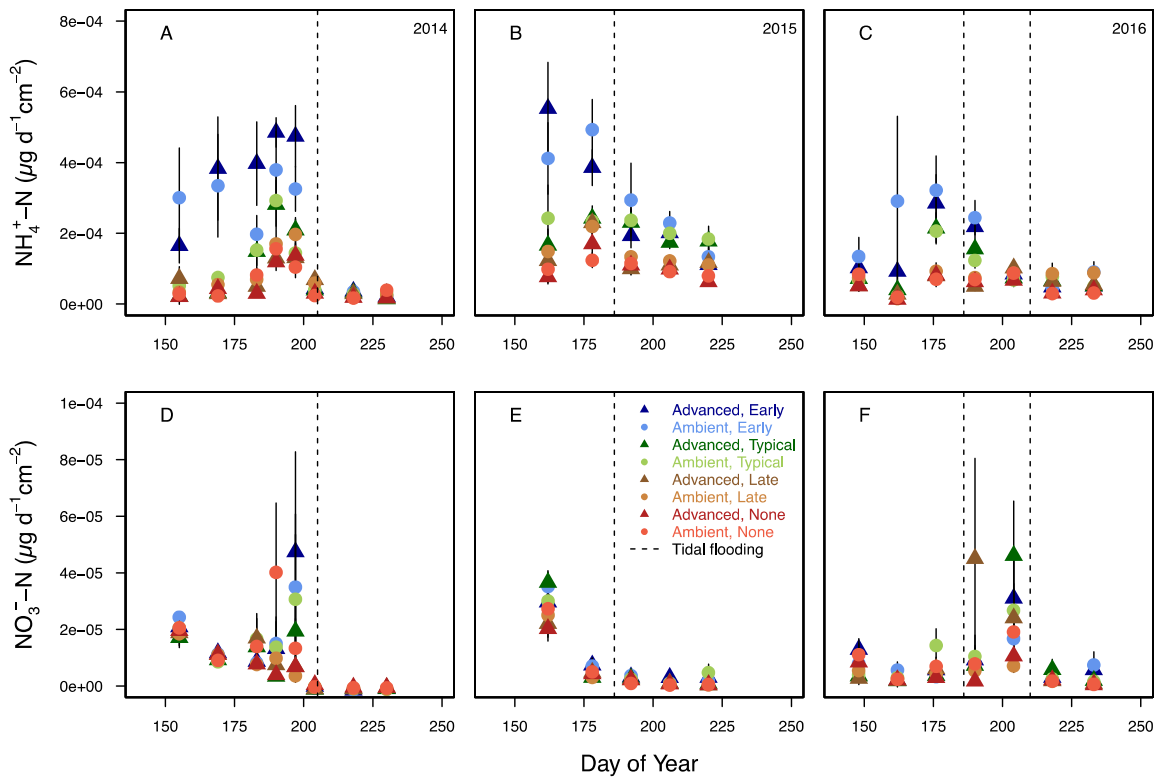
FIGURES

H1: Timing of Grazing

Early   Late

↓ Plant biomass ↑
↓ N uptake ↑
↑ Feces ↓
↑ Trampling ↓

Early   Late

Early   Late
Organic N ──Late──► Inorganic N
        ──Early──►

Early
Typical
Late

N availability

Time

H2: Timing of Season

Advanced

↑ Microbial growth
↑ Plant biomass
↑ N uptake

Microbes ──► Inorganic N

Advanced
Ambient

N availability

Time

H3: Grazing + Season

Early + Advanced

↑ Microbial growth
↓ Plant biomass
↓ N uptake
↑ Feces
  Trampling

Microbes
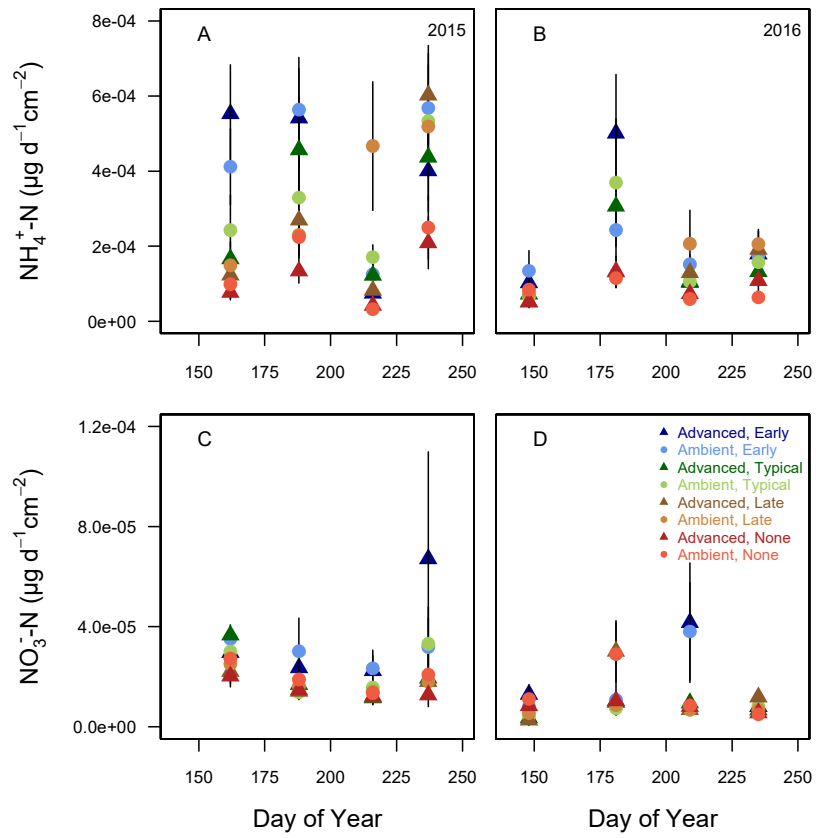
Organic N ──► Inorganic N

Early + Advanced
Ambient

N availability

Time

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.