



# Goose Feces Effects on Subarctic Soil Nitrogen Availability and Greenhouse Gas Fluxes

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## ABSTRACT

Vertebrate herbivore excrement is thought to influence nutrient cycling, plant nutrition, and growth; however, its importance is rarely isolated from other aspects of herbivory, such as trampling and leaf removal, leaving questions about the extent to which herbivore effects are due to feces. We hypothesized that as a source of additional nutrients, feces would directly increase soil N concentrations and N<sub>2</sub>O emission, alleviate plant, and microbial nutrient limitations, resulting in increased plant growth and foliar quality, and increase CH<sub>4</sub> emissions. We tested these hypotheses using a field experiment in coastal western Alaska, USA, where we manipulated goose feces such that naturally grazed areas received three treatments: feces removal, ambient amounts of feces, or double ambient amounts of feces. Doubling feces marginally increased NH<sub>4</sub><sup>+</sup>-N in soil water, whereas both doubled feces and feces removal significantly in-

creased NO<sub>3</sub><sup>-</sup>-N; N<sub>2</sub>O flux was also higher in removal plots. Feces removal marginally reduced root biomass and significantly reduced productivity (that is, GPP) in the second year, measured as greater CO<sub>2</sub> emissions. Doubling feces marginally increased foliar chemical quality by increasing %N and decreasing C:N. Treatments did not influence CH<sub>4</sub> flux. In short, feces removal created sites poorer in nutrients, with reduced root growth, graminoid nutrient uptake, and productivity. While goose feces alone did not create dramatic changes in nutrient cycling in western Alaska, they do appear to be an important source of nutrients for grazed areas and to contribute to greenhouse gas exchange as their removal increased emissions of CO<sub>2</sub> and N<sub>2</sub>O to the atmosphere.

**Key words:** Carbon dioxide; Feces fertilization; Forage quality; Grazing; Greenhouse gas flux; Methane; Nitrous oxide; Plant–herbivore interactions; Soil nutrient availability; Wetland tundra.

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## HIGHLIGHTS

- Feces removal reduced root growth and gross primary productivity.
- Doubling feces marginally increased soil nitrogen

availability and foliar nitrogen.

- Removal of geese feces could increase greenhouse gas flux.

## INTRODUCTION

A key mechanism by which vertebrate herbivores influence ecosystem processes is through urine and feces deposition on the landscape. Urine and feces return nutrients to the soil in highly decomposable forms instead of nutrient-poor litter, and this increase in labile nutrients can increase the quality and abundance of plant material (Bazely and Jefferies 1985; Day and Detling 1990), change N mineralization rates (Ruess and McNaughton 1987; Seagle and others 1992; Pastor and others 1993), and influence vegetation communities (Wal and others 2004; Barthelemy and others 2015), especially where nutrients are limited. Greater labile nutrients can also increase microbial activity and biomass, and convert nutrients into greenhouse gases (Wang and others 2020). While we may expect urine and feces to influence vegetative growth, foliage quality, and nutrient cycling, experimental evidence of the effects separated from other forms of herbivory under typical field conditions are rare (Barthelemy and others 2015), leaving questions about the extent to which herbivore effects can be attributed to feces. Further, no studies that we know of have isolated the effects of feces or urine on carbon (C) exchange ( $\text{CO}_2$  and  $\text{CH}_4$  flux) and nitrous oxide ( $\text{N}_2\text{O}$ ) fluxes in an experimental field setting, though we might expect these fluxes to be affected (but see Winton and Richardson 2017; Wang and others 2020).

While we expect urine and feces to play an important role in ecosystem functioning, the effects are not always strong. For example, where excretory N is a minor input or patchily distributed, effects are small (Day and Detling 1990; Pastor and others 1993; Sørensen and others 2009). Effects also can take years to observe and be temporally variable (Wal and others 2004; Barthelemy and others 2015). Geese have been studied for the importance of fecal deposition because they have high densities, produce evenly distributed feces, and their feces are highly visible with clear white deposits that contain soluble N in the form of uric acid and ammonium ( $\text{NH}_4^+$ ) ions. Yet studies on goose fecal effects only (that is, not including other aspects of goose herbivory, such as offtake and trampling) can show small to no measurable effects on ecosystem parameters, particularly in aquatic systems (reviewed in Dessborn and others 2016).

Studies attribute this tendency to mechanisms ranging from nutrients in feces sinking to the bottom of freshwater systems (Unckless and Makarewicz 2007) to stronger effects of top-down control on plant productivity (Pettigrew and others 1997; Geest and others 2007) to greater influences from grazing, trampling, (Winton and Richardson 2017), and grubbing (Jefferies 1988; Esselink and others 1997; Wal and others 2007; Gornall and others 2009), which are not often isolated from fecal effects.

Goose feces may play a more important role in northern-latitude graminoid systems because these systems have limited edaphic N, cold temperatures limiting decomposition and nutrient turnover, and short growing seasons that constrain plant growth (Cargill and Jefferies 1984a,b; Bazely and Jefferies 1989; Ruess and others 1989; Beaulieu and others 1996). Studies isolating the effects of goose feces in northern systems have found that snow goose feces additions to swards of *Puccinellia phryganodes* increased standing crop and N concentrations in foliage, but effects were not significant until the second year (Bazely and Jefferies 1985; Hik and Jefferies 1990). An experiment on the effects of black brant feces on ungrazed *Triglochin palustris* found reduced bulbs and increased flowering, but no effects where plants were grazed (Mulder and Ruess 1998). While these studies suggest that goose feces can affect plant biomass and foliar chemistry in northern-latitude graminoid systems, effects were not consistent across conditions. Other studies in these systems have isolated goose fecal effects on specific fluxes within the N cycle, such as on N mineralization and volatilization, and uptake into foliage (for example, Ruess and others 1989; Zachais and others 2002; Sjogersten and others 2010). Thus, while goose feces deposition alone can influence plant biomass and structure and soil N cycling, knowledge of its importance for key ecosystem parameters, such as greenhouse gas flux, is still rudimentary because experimental evidence remains scarce.

The goal of this research was to isolate the effects of fecal deposition in a black brant colony on aspects of their dominant forage, the sedge *Carex subspathacea*, soil chemistry, and greenhouse gas flux in coastal western Alaska, USA, a system where we expected the effects of feces to be potentially important. First, we determined fecal deposition rates and chemistry because many studies investigating fecal deposition and chemistry use previously published estimates, and there have been calls for more collection of these primary data (Dessborn and others 2016). Then, we determined

how feces influenced soil N availability, biomass production, vegetation quality (C:N), and greenhouse gas fluxes, by removing feces completely and doubling the quantity, while allowing natural grazing and trampling during a two-year experiment. We had three main predictions for the experiment: (1) that as a source of additional nutrients, in particular N, feces would directly increase soil available N and N<sub>2</sub>O emission; (2) by increasing N availability in soil, feces would alleviate plant nutrient limitations and increase both above- and belowground plant productivity (measured as biomass, changing vegetation structure, and CO<sub>2</sub> uptake), as well as foliar and root chemical quality (that is, higher %N and lower C:N ratios); and (3) feces would increase CH<sub>4</sub> emissions by relieving microbial nutrient limitations. While, in nature, feces deposition will not often be spatially isolated from other herbivore effects, this study helps us to separate what effects might be due to feces from effects that might be due to grazing, trampling, or grubbing, for example.

## MATERIALS AND METHODS

### Study Site

Research was conducted along the Tutakoke River in the central portion of the Yukon-Kuskokwim (Y-K) Delta in western Alaska, near the coast of the Bering Sea (61°24'N, 165°61'W; elevation 3 m; Figure 1a). The Y-K Delta is a 75,000 km<sup>2</sup> expanse of wetland and tundra between the Yukon and Kuskokwim Rivers. Climate in the region is maritime; mean monthly temperature ranges from –14 °C in midwinter to 10 °C in midsummer (Tande and Jennings 1986). Mean annual rainfall is 270 mm, and total mean annual snow accumulation is 1600 mm (Tande and Jennings 1986). The soil at our site is a silty loam with a neutral pH (6.8), no organic horizon (2.5% total organic C, 0.17% total organic N), and no underlying permafrost (Jorgenson 2000; Foley and others 2021).

Plots were located on *C. subspathacea* ‘grazing lawns’ within 1 km of the coast, on the active floodplain (Kincheloe and Stehn 1991) near the Tutakoke River Pacific black brant (*Branta bernicla nigricans*) colony. The vegetation surrounding lawns were saline wet meadow dominated by *Carex* species, unlike inland tundra vegetation, this habitat has no bryophytes. Nest density in spring is about 500 km<sup>–2</sup> (Fischer and others 2017). Pacific black brant and the co-occurring cackling geese (*Branta hutchinsii minima*) maintain the dominant sedge (*C. subspathacea*) in a near monoculture of a

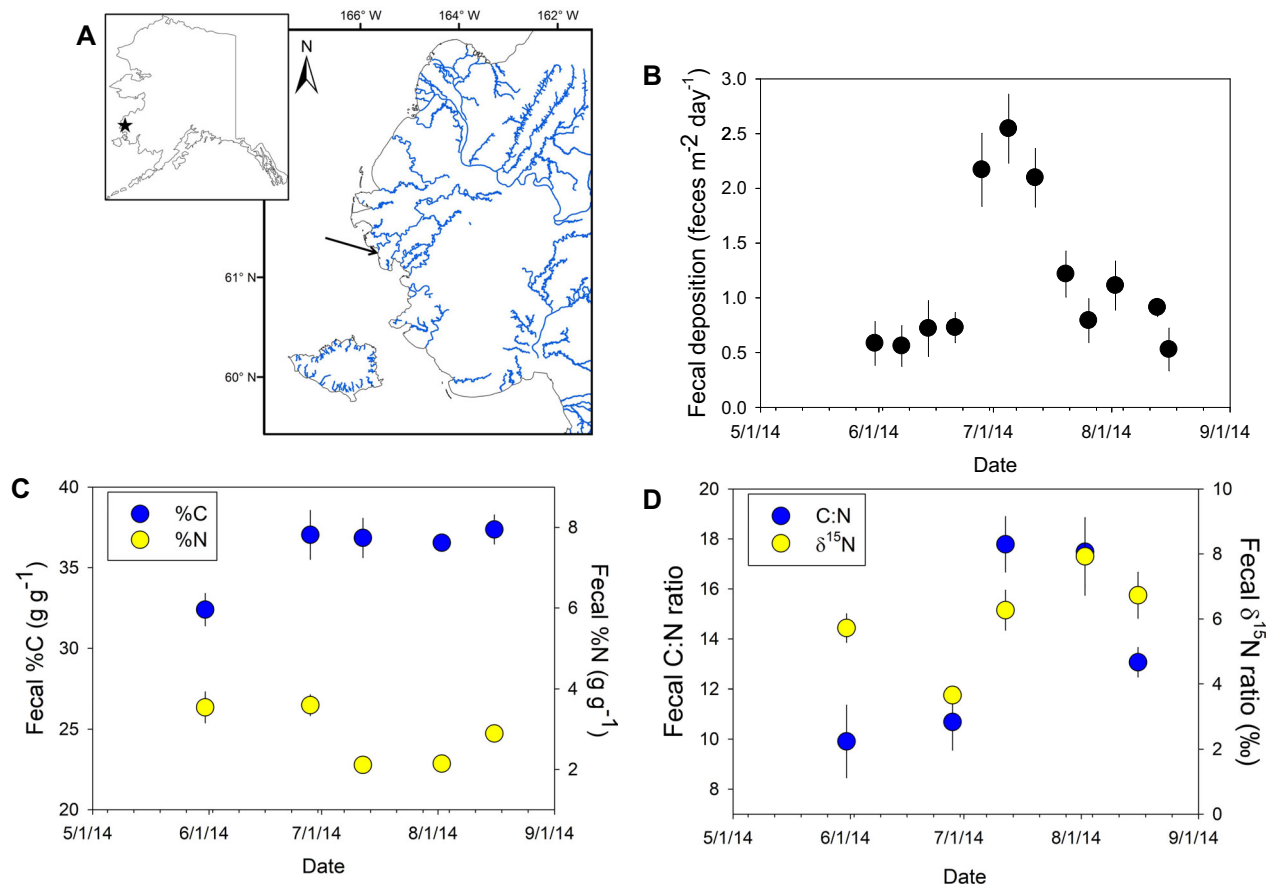
short growth form (that is, ‘grazing lawns’). Geese primarily consume high-quality sedge and grass in grazing lawns during brood rearing, and this forage is critical for gosling growth (Sedinger and others 2001). Grazing lawns are typically found on the boundaries of mudflats and saline ponds that experience greater inundation than surrounding terrestrial plant communities (Jorgenson 2000).

### Experimental Design

To determine fecal deposition rates, feces removal and control plots were established on 24 May 2014 and monitored through 16 August 2014. This study consisted of six replicate blocks within 1 km of each other; each block contained two plots [ambient fecal density (control), fecal removal]. All plots were 1.7 m × 0.85 m. Plots were not fenced so that they were exposed to wild goose grazing and trampling as well as fecal deposition. Once a week, fecal counts in each plot were recorded, and feces were removed from the removal plots. Five times during the summer, fresh feces were collected from removal plots to be analyzed for %C, %N, and δ<sup>15</sup>N. Samples were oven-dried at 60 °C to constant weight, weighed, and then ground with a Wiley mill (Thomas Scientific, Swedesboro, NJ) and homogenized before being analyzed at the UAA ENRI Stable Isotope Laboratory using a Costech ECS 4010 elemental analyzer (Costech, Valencia, CA) in line with a ThermoFinnigan DeltaPlus XP continuous-flow isotope ratio mass spectrometer (CF-IRMS; Thermo Scientific, Bremen, Germany) for δ<sup>15</sup>N. Photographs were taken once a week of single demarcated feces in each control plot to monitor visual changes in feces over time.

In late May 2015, the experiment to measure ecosystem responses to fecal deposition was started. New feces removal plots were created, and a feces addition treatment was added to each block, so that the experiment consisted of six replicate blocks with three plots (ambient fecal density, fecal removal, and double ambient fecal density). Fecal treatments were maintained late May through late August 2015 and 2016. Twice weekly, fecal abundance counts were made in each plot, and feces were moved from the removal plots to the addition (double) plot in each block. Because feces were moved every 3.5 days, on average, over two seasons, feces likely remained in removal plots for on average 1.75 days, and in some cases up to 4 days, prior to being moved to addition plots.

Every two weeks 10 ml samples of soil pore water were collected from every plot using rhizon soil moisture microlysimeters (Eijkelkamp, Gies-



**Figure 1.** **A** Map of the study site location and mean ( $\pm 1$  SE) for **B** deposition rates from removal plots, **C** feces percent C and N, and **D** fecal C:N ratio and isotopic  $\delta^{15}\text{N}$  ( $n = 6$  blocks).

beek, Netherlands). Inorganic and organic N were quantified using colorimetric reactions. Samples were analyzed for  $\text{NH}_4^+\text{-N}$  using the Berlethot reaction (Rhine and others 1998), nitrate ( $\text{NO}_3^-\text{-N}$ ) using the Griess reagent (Doane and Horwath 2003), and amino acids using the fluorometric OPAME procedure (Jones and others 2002) on a SynergyTM H4 Hybrid Multi-Mode Microplate Reader (BioTek, Winooski, VT) at Utah State University.

In 2015 and 2016, above- and belowground growth and tissue C and N of *C. subspathacea* were determined throughout the growing season. Each week, stem heights were measured from the same 10 cm  $\times$  10 cm demarcated quadrat in each plot on 10 randomly selected stems. Aboveground biomass was destructively harvested every three weeks from a randomly selected 5 cm  $\times$  5 cm quadrat in each unfenced plot. From these samples, tillers were counted, and vegetation was separated into dead and live biomass. Root growth was measured using two 4-cm diameter by 15-cm long in-growth root cores with 2-mm plastic mesh

(Nadelhoffer and others 2002). Cores were filled with root-free substrate, placed in each plot on 25 May, and removed on 25 August each year. Aboveground vegetation and roots were washed free of soil, and samples were dried at 60 °C to constant weight and weighed. Shoot samples each year and root samples from 2016 were ground with a Wiley mill, homogenized, and analyzed for %C, %N, and  $\delta^{15}\text{N}$  using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer at the UC Davis Stable Isotope Facility.

Net ecosystem exchange (NEE) and ecosystem respiration (ER) were measured, while gross primary productivity (GPP) was assumed to be the difference, on each plot between once and twice per week within 3 h of solar noon using a closed-chamber circulation system consisting of a transparent ca. 6-L chamber attached to an infrared gas analyzer for measuring  $[\text{CO}_2]$  (model LI820, Licor Inc., Lincoln, NE). Air was circulated through the chamber/analyzer system using ca. 150 cm of 4 mm (inside diameter) Bev-A-Line tubing by an



air pump with a flow rate of ca.  $1 \text{ L min}^{-1}$ . Chamber temperature, humidity, and incident sunlight (PAR, photosynthetically active radiation) were monitored during measurements, and air inside the chamber was circulated using a small fan. All data were recorded at 1 Hz using a datalogger (model CR800, Campbell Scientific Inc., Logan, UT). Each 120-s measurement entailed connecting the flange of the chamber to a flange on a 20-cm diameter PVC collar inserted ca. 5 cm into the soil. Two measurements were made; each time,  $\text{CO}_2$  flux was recorded. The first used the transparent chamber and allowed the calculation of NEE. For the second measurement, the chamber was covered with an opaque cloth to stop photosynthesis allowing calculation of ER. GPP was calculated as the difference between NEE and ER. The chamber was returned to ambient temperature, humidity, and  $[\text{CO}_2]$  between measurements.

$\text{CH}_4$  and  $\text{N}_2\text{O}$  trace gas fluxes were measured once or twice per week using a separate system consisting of an opaque about 6-L chamber attached to a cavity ring-down spectroscopy analyzer (Model G2308, Picarro Inc., Santa Clara, California). Due to the power requirements of this larger instrument, data were only collected from plots in three of the six blocks (1, 5, and 6). Air circulated from the chamber to the instrument at  $0.23 \text{ L min}^{-1}$  through ca. 1000 cm of 4-mm (inside diameter) Bev-A-Line tubing. An additional fan circulated air within the chamber. Gas concentrations were measured every 5 s for 5 min and recorded using a computer onboard the analyzer. Chamber temperature (type T thermocouple) and pressure (model 278, Setra, Boxborough, Massachusetts) were measured every 5 s and recorded using a datalogger (model CR800, Campbell Scientific, Logan, Utah).

Fluxes of  $\text{CO}_2$ ,  $\text{CH}_4$ , and  $\text{N}_2\text{O}$  were calculated using two methods, one specific to each measurement system. For NEE and RE, raw analyzer  $[\text{CO}_2]$  was corrected to dry  $[\text{CO}_2]$ . An exponential model was fit for the period of consistent  $[\text{CO}_2]$  change in the chamber between 30 (that is, a 'dead band') and 120 s after chamber closure. Initial chamber temperature and the exponential fit were used to calculate NEE and ER at the time of chamber closure. Fluxes of  $\text{CH}_4$  and  $\text{N}_2\text{O}$  were calculated using non-linear curve fits (Hutchinson and Mosier, 1981) between approximately 60 and 300 s after chamber closure using software developed by Picarro Inc (Soil Flux Processor). Uncertainty in the regression fit of  $\text{CH}_4$  and  $\text{N}_2\text{O}$  fluxes was characterized in the same software package using a bootstrap analysis.

## Data Analysis

Data were analyzed in a linear mixed-model framework followed by tests of fixed effects in the nlme package of the R statistical computing environment (version 4.0.0, R Development Core Team, 2020). For fecal counts and deposition rates in every year of the study and 2014 fecal chemical content variables, fixed effects were collection date and random effects were plot within block. We used Tukey HSD contrasts to detect differences among time periods.

For each response variable measured in 2015 and 2016, fixed effects included treatment (control, addition, or removal), year of experiment as a factor, and the interaction of these predictors. Random effects were plot within block and sampling date. A select set of variables were only measured in 2016 (%C, %N, and  $\delta^{15}\text{N}$  of root growth) at the end of the season, leaving treatment as the only fixed effect and plot within block as the only random effect. There were flooding events at the site in mid-July and mid-August in 2015 and in mid-August of 2016 where three blocks (3, 4, and 5) were affected (following 7 July in 2015 and 31 July in 2016), but there were no differences in the results with and without these dates for these blocks included, and treatments were maintained (that is, differences in the number of feces among treatments) despite flooding. Therefore, we present all data in the analyses.

All variables were examined for normality using Q-Q Plots and transformed as necessary with either log or arcsine square-root (fractional data). Tests of fixed effects were considered significant at  $p < 0.05$ , but marginally significant results are also discussed at  $p < 0.10$ . In cases when no significant treatment  $\times$  year interaction was detected, the mean treatment effect (that is, mean slope,  $\beta$ ) across 2015 and 2016 is reported ('emmeans' package)(Lenth 2020). Post-hoc Tukey HSD contrasts were used to explore differences among treatments.

## RESULTS

### Fecal Deposition Rates and Chemical Content

During the 2014 season, daily fecal deposition rates were higher on removal plots,  $1.20 \text{ feces m}^{-2} \text{ day}^{-1}$  ( $\pm 0.87 \text{ SD}$ ), than on control plots,  $0.38 \text{ feces m}^{-2} \text{ day}^{-1}$  ( $\pm 0.93 \text{ SD}$ ) ( $F_{1,53} = 59.39$ ,  $p < 0.001$ ). The rate of feces deposition varied over the season and was higher post-hatch from late June to mid-

July ( $F_{11,55} = 13.91$ ,  $p < 0.001$ ; Figure 1b). On average, there were  $31.36 (\pm 14.20 \text{ SD})$  feces  $\text{m}^{-2}$  on control plots and  $12.12 (\pm 7.35 \text{ SD})$  feces  $\text{m}^{-2}$  on removal plots before weekly removals.

Mean fecal C and N concentrations were  $36.04 \pm 3.09\%$  and  $2.86 \pm 0.85\%$  (SD), respectively. Yet, feces C and N contents (%C, %N, C:N ratios, and  $\delta^{15}\text{N}$ ) changed over the season ( $p < 0.01$  for all tests; Figure 1; Table 1). Tukey contrasts show that fecal %C increased over the season (Figure 1c). C:N followed a similar increase but declined toward the end of the season (Figure 1d). Fecal %N was highest early season, declined mid-season, and then increased end of season (Figure 1c), while fecal  $\delta^{15}\text{N}$  was greatest late season (Figure 1d).

We monitored single feces in control plots starting on 14 June 2014. In 4 of 6 blocks, feces moved during the season, either by being washed away during high tide flooding events or kicked away by geese, such that they could not be monitored all season. The two blocks where we could monitor all season, the feces decomposed visually within one month of deposition (Supplemental Figures 1 and 2).

During 2015 and 2016, feces were moved from the removal plots and added to “addition” plots on average every 3.5 days ( $\pm 0.60 \text{ SD}$ ) and 3.6 days ( $\pm 0.51 \text{ SD}$ ), respectively. Between June 8 and August 22, there were, on average, 3.8 feces  $\text{m}^{-2}$  on the removal plots before removal, 39.3 feces  $\text{m}^{-2}$  on the control plots, and 80.4 feces  $\text{m}^{-2}$  on the addition plots in 2015; and there were, on average, 2.5 feces  $\text{m}^{-2}$  on the removal plots before removal, 23.2 feces  $\text{m}^{-2}$  on the control plots, and 58.6 feces  $\text{m}^{-2}$  on addition plots in 2016.

Like 2014, during 2015 and 2016, fecal deposition rates were higher on removal than on control plots ( $F_{1,106} = 53.14$ ,  $p < 0.001$ ,  $F_{1,125} = 8.76$ ,  $p = 0.004$ , respectively). Deposition rates were, on average, 1.05 feces  $\text{m}^{-2} \text{ day}^{-1}$  on removal plots, 0.53 feces  $\text{m}^{-2} \text{ day}^{-1}$  on control plots, and 0.55 feces  $\text{m}^{-2} \text{ day}^{-1}$  on addition plots in 2015, and 0.65 feces  $\text{m}^{-2} \text{ day}^{-1}$  on removal plots, 0.40 feces  $\text{m}^{-2} \text{ day}^{-1}$  on control plots, and 0.42 feces  $\text{m}^{-2} \text{ day}^{-1}$  on addition plots in 2016.

Addition plots had a large increase in the number of feces over time, whereas the number of feces on control plots increased at the beginning of the season and then was more stable over time, and feces number on removal plots was the most stable, but still varied slightly (2015:  $p < 0.001$ ; 2016:  $p < 0.05$ ; Figure 2).

There were fewer feces in 2016 on all plots than in 2015 (treatment\*year:  $F_{1,631} = 30.06$ ,

$p < 0.001$ ). There were significantly more feces on the addition plots and fewer on the removal plots throughout the experiment. The only pairwise contrast among treatments and years that was not significantly different was for the control plots between years (contrast:  $t = 0.418$ ,  $p = 0.9943$ ). Other treatments between and within years were highly significantly different (contrasts:  $p < 0.001$ ). The standard deviation among treatments increased over each season, particularly for the feces addition plots, because of the flooding that occurred mid- to late season on three of the six blocks each year (Figure 2).

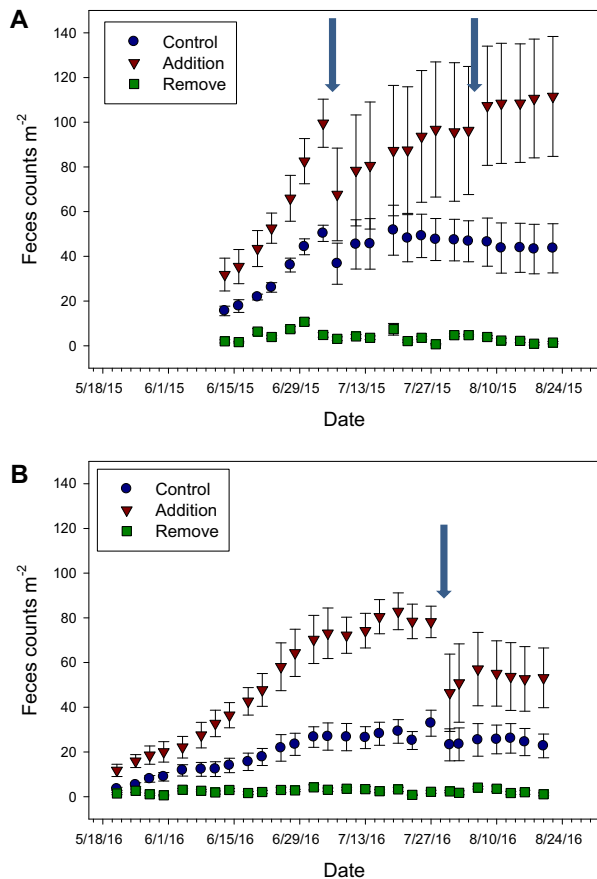
## Responses to Fecal Treatments

Bi-weekly lysimeter data suggest that there was marginally more soil water  $\text{NH}_4^+$  in the addition plots than in the control plots ( $F_{2,10} = 3.27$ ,  $p = 0.081$ ; Figure 3a). There was also significantly greater concentration of  $\text{NO}_3^-$  in soil water in the addition and removal plots compared to control plots ( $F_{2,10} = 8.28$ ,  $p = 0.008$ ; Figure 3b). There was no difference among treatments for the amount of amino acids in the soil water. We found greater  $\text{N}_2\text{O}$  flux to the atmosphere in the removal treatments than in the control plots across years ( $F_{2,6} = 6.33$ ,  $p = 0.033$ ; Figure 3c; Supplemental Figure 3).

Root biomass was marginally affected by treatments, trending toward less root biomass in the feces removal plots in both years ( $F_{2,25} = 2.84$ ,  $p = 0.078$ ; Figure 3d). Aboveground biomass metrics differed between years ( $p < 0.001$ ; Table 2), such that there was greater aboveground biomass, greater stem heights, and lower tiller counts in the second year. In contrast, aboveground biomass, stem height, and numbers of tillers were not different by treatment.

We found a significant interaction between treatment and year for NEE ( $F_{2,10} = 0.174$ ,  $p = 0.002$ ) and GPP ( $F_{2,10} = 8.16$ ,  $p < 0.001$ ), such that in the second year, all treatments had much lower  $\text{CO}_2$  uptake, and the feces removal plots had become a source of  $\text{CO}_2$  to the atmosphere (Figure 4; Supplemental Figure 4). We found no treatment effects on ER (Figure 4).

But, both foliar %N and C:N had a marginally significant interaction between treatment and year ( $P = 0.076$ , and  $P = 0.071$ , respectively; Table 2), reflecting greater foliar %N and lower C:N ratios in the fecal addition plots in the second year (Figure 5a, b).  $\delta^{15}\text{N}$  values in foliage also increased significantly in the fecal addition plots in the second year, as revealed in the Tukey post-hoc tests



**Figure 2.** Number of feces ( $\pm 1$  SE) on the control, addition (double), and removal plots as measured every 3–4 days during the **A** 2015 and **B** 2016 growing seasons. Arrows indicate when flooding occurred on three of the six blocks.

(Figure 5c). Foliar %C was not affected by treatments (Table 2). There were no differences among treatments in the chemical composition of the roots (Table 2).

We also found no treatment effects on CH<sub>4</sub> flux (Figure 5d), even though there were many more sampling points with high CH<sub>4</sub> flux ( $> 50$  nmol m<sup>-2</sup> s<sup>-1</sup>) in removal plots (32% of the sample points) than in the control plots (16%), and much more than in addition plots (3%), in both years (Supplemental Figure 5). There was no difference among treatments because most of the explained variation was at the plot level.

## DISCUSSION

Our results support the idea that goose feces can influence ecosystem processes in coastal, sub-Arctic wetlands. Regarding our first prediction, as expected, we found that feces addition increased N in

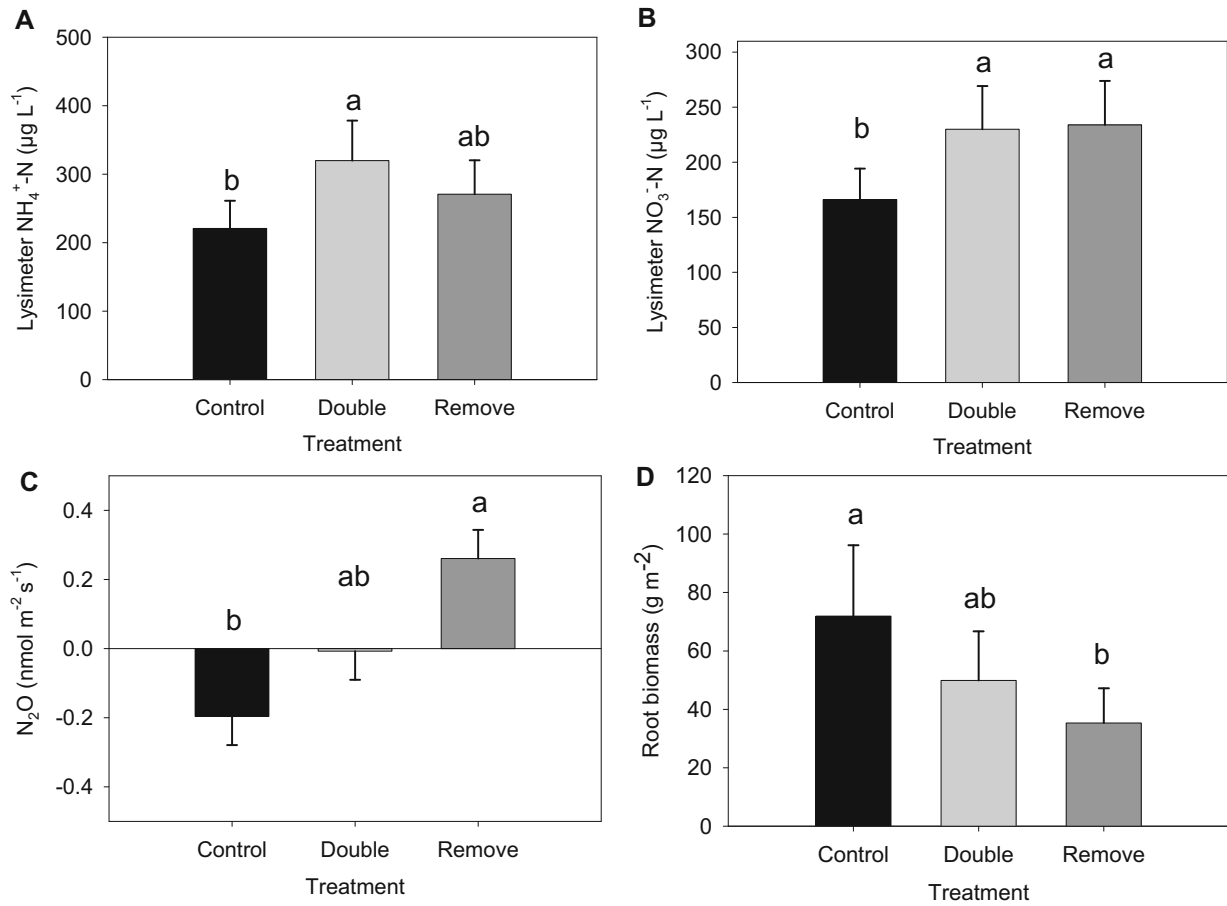
soil water, yet contrary to expectation, feces removal also increased soil water N, in particular NO<sub>3</sub><sup>-</sup>, as well as N<sub>2</sub>O flux to the atmosphere. We also found support for our second prediction in that productivity rates (that is, GPP) and root biomass were at least marginally lower in feces removal plots, resulting in greater CO<sub>2</sub> flux to the atmosphere, while feces addition marginally increased %N in foliage. Finally, while we expected feces to increase CH<sub>4</sub> emissions, we found treatments were not significantly different. In summary, although not always dramatic, the removal of feces and associated nutrients appeared to create sites with reduced root growth, C fixation, and nutrient uptake. Our results also shed light on the role of feces in greenhouse gas flux, suggesting that removing geese feces could increase both CO<sub>2</sub> and N<sub>2</sub>O flux to the atmosphere.

## Fecal Deposition and Chemistry

In response to calls for more primary data collection of feces deposition rates and chemistry (Dessborn and others 2016), an aspect of this study was the quantification of goose feces, and in particular, fecal C and N throughout a season in a brant breeding colony. We found that the background fecal deposition rates in control areas varied among years, from 2014 to 2016, in the same six grazing lawns and ranged from an average of 0.38 feces m<sup>-2</sup> day<sup>-1</sup> to 0.53 feces m<sup>-2</sup> day<sup>-1</sup>, likely as a function of the variation in goose abundance across years (Person and others 2003). If an individual feces is on average 0.74 g dw (Foley 2020), we estimate that brant at our study site produces about 0.12 g C m<sup>-2</sup> day<sup>-1</sup> and 0.01 g N m<sup>-2</sup> day<sup>-1</sup> or ca. 12 g dw m<sup>-2</sup> fecal C and 1 g dw m<sup>-2</sup> fecal N over the season.

Notably, there was also a large and consistent difference in fecal deposition rates among treatments, namely that deposition rates were much higher in the removal plots. However, we do not believe this rate difference greatly influenced our results because over two growing seasons, we created plots with, on average, 2–2.5 times the amount of feces on addition plots compared to control plots, and over 20 times the amount compared to removal plots over the growing seasons. Further, feces were always transferred from removal to addition plots within a couple days, but we take this potential effect into account in our interpretation.

We found that goose fecal density and chemistry changed over the growing season. This is illustrated well in the 2014 data, in which goose fecal density



**Figure 3.** Mean belowground biomass and soil water chemistry ( $\pm 1$  SE) in feces control, addition (double), and removal plots for **A**  $\text{NH}_4^+\text{-N}$  in soil water, **B**  $\text{NO}_3^-\text{-N}$  in soil water, **C**  $\text{N}_2\text{O}$  emission from the soil, and **D** root biomass. Letters indicated significant differences with Tukey adjusted  $\alpha = 0.1$  for (A) and (D) and  $\alpha = 0.05$  for (B) and (C).

was greatest in late June and early July, post-hatch (Fischer and others 2017). This post-hatch peak was expected because this is the time of year that goslings are on the landscape and adults are molting, and, thus, have their highest energy requirements. The change in fecal chemistry over the season aligned with foliar %N of *C. subspathacea* as would be expected as fecal N content often reflects digested plants in geese because of their rapid gut passage (Beard and others 2019).

### Changes in Belowground Responses and N

Our system is generally N-limited, so goose fecal material is thought to be an important source of organic N but also inorganic N as  $\text{NH}_4^+$  (Cargill and Jefferies 1984b). In biweekly lysimeter measurements in the feces addition plots, we found marginally more  $\text{NH}_4^+$  and significantly more  $\text{NO}_3^-$  than in the control plots but not more than in removal plots. Considering the much larger amount

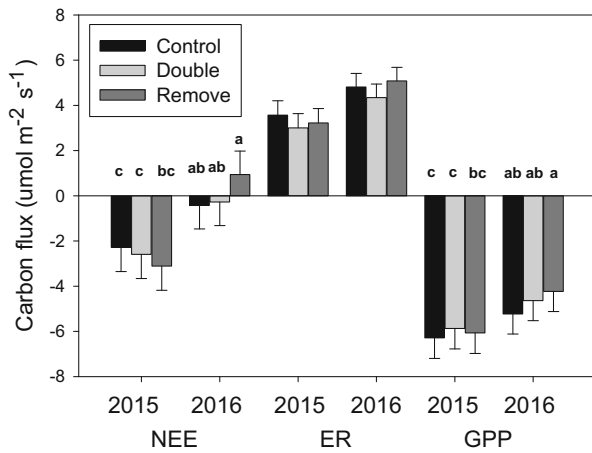
**Table 1.** ANOVA results for fecal chemistry over the season

| Response              | F     | <i>p</i>          |
|-----------------------|-------|-------------------|
| C (%)                 | 3.626 | <b>0.023*</b>     |
| N (%)                 | 9.123 | <b>&lt; 0.001</b> |
| C:N                   | 10.24 | <b>&lt; 0.001</b> |
| $\delta^{15}\text{N}$ | 4.871 | <b>0.007</b>      |

All tested effects are 'Date' with numerator degrees of freedom of 4 and denominator of 20. Feces were collected five times over the season in 2014 across six blocks. Bolding indicates significant differences  $p < 0.05$ .

of feces on addition plots, we expected more  $\text{NH}_4^+$  if it came directly from the breakdown of fecal material. Further, because some of this  $\text{NH}_4^+$  will be mineralized (Ruess and others 1989), we expected more  $\text{NO}_3^-$  in soil water in these treatments (Jefferies 1988); although other studies have found no increase of exchangeable  $\text{NH}_4^+$  in the soil in goose grazed versus ungrazed areas, which they

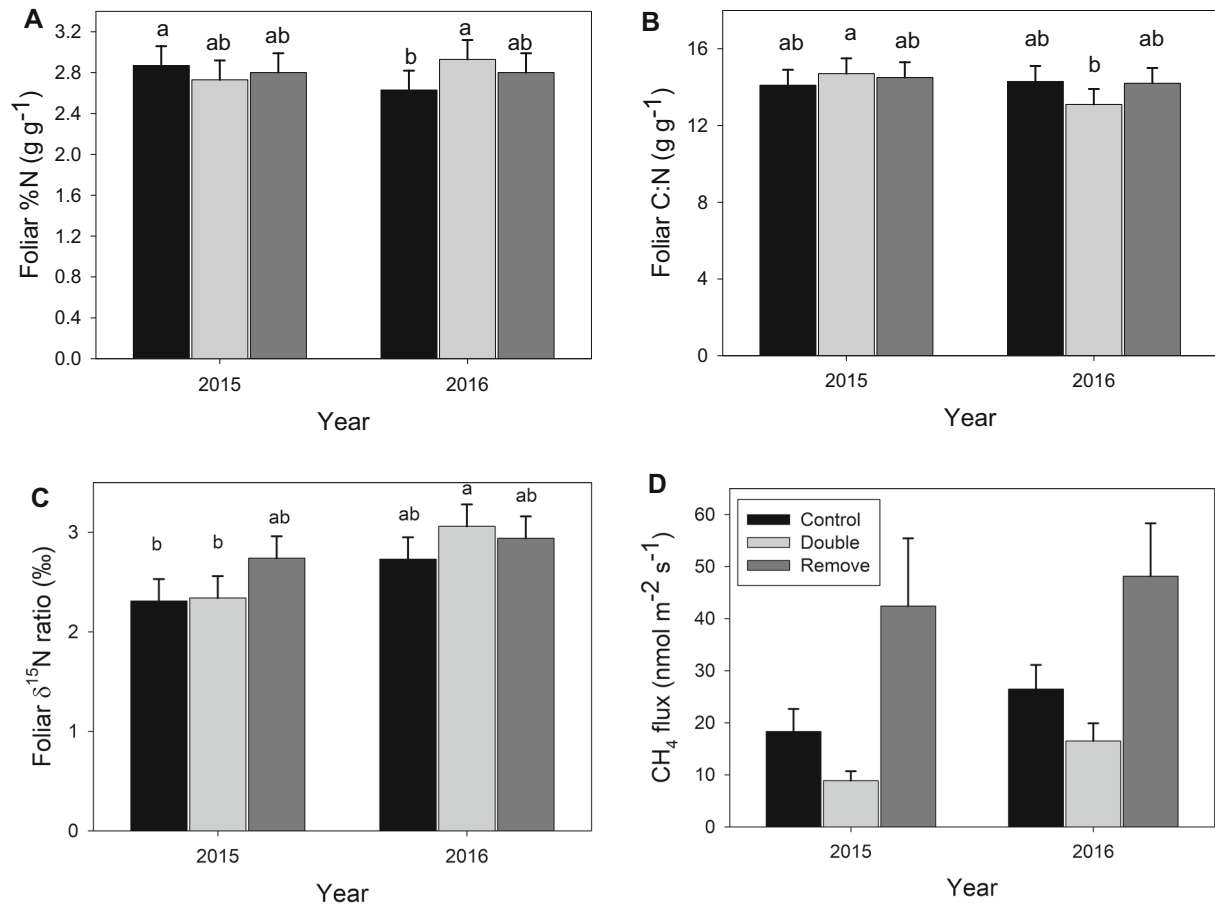




**Figure 4.** Mean carbon dioxide flux measurements ( $\pm 1$  SE) as net ecosystem exchange (NEE), ecosystem respiration (ER), and gross primary productivity (GPP) in 2015 and 2016 from feces control, addition (double), and removal plots ( $n = 6$ ). Letters indicated significant differences with Tukey adjusted  $\alpha = 0.05$ .

have attributed to N volatilization, immobilization by soil microbes, or uptake by the plants (Bazely and Jefferies 1989). We did not detect treatment differences in amino acid concentrations, even though studies have found amino acid signatures of goose feces in the soil profile (for example, Henry and Jefferies 2002).

We found a marginal reduction in root biomass in the removal plots in both years, which might most obviously be a direct response to the lower amount of nutrients and, thus, reduced need and ability to grow in these plots. There was also a greater amount of  $\text{NO}_3^-$  in soil water in removal plots compared to control plots, which could result from the smaller root area absorbing soluble N, so more in the soil solution, and if  $\text{NH}_4^+$  is not taken up, more to supply  $\text{NO}_3^-$ . This increase could also reflect the rapid release of soluble N from feces before they were removed from plots (Bazely and Jefferies 1985), especially considering the higher



**Figure 5.** Mean foliar chemistry and  $\text{CH}_4$  flux ( $\pm 1$  SE) in feces control, addition (double), and removal plots for **A** foliar percent nitrogen, **B** foliar C:N ratios, **C** foliar isotopic  $\delta^{15}\text{N}$  and **D**  $\text{CH}_4$  flux. Letters indicated significant differences with Tukey adjusted  $\alpha = 0.1$ .

**Table 2.** ANOVA results for response variables from fecal manipulation experiment

| Response                                            | Effect   | DF     | F      | p                |
|-----------------------------------------------------|----------|--------|--------|------------------|
| Lys. $\text{NH}_4^+$ ( $\mu\text{g N/L}$ )          | Trt      | 2, 10  | 2.891  | <b>0.081*</b>    |
|                                                     | Year     | 1, 186 | 0.1021 | < 0.001          |
|                                                     | Trt*Year | 2, 189 | 0.0586 | 0.818            |
| Lys. $\text{NO}_3^-$ ( $\mu\text{g N/L}$ )          | Trt      | 2, 10  | 8.284  | <b>0.017*</b>    |
|                                                     | Year     | 1, 157 | 20.30  | 0.009            |
|                                                     | Trt*Year | 2, 157 | 0.0004 | 0.872            |
| Lys. AA ( $\mu\text{mol/L}$ )                       | Trt      | 2, 10  | 0.9055 | 0.435            |
|                                                     | Year     | 1, 231 | 25.98  | < 0.001          |
|                                                     | Trt*Year | 2, 231 | 0.0180 | 0.982            |
| Root Biomass ( $\text{g/m}^2$ )                     | Trt      | 2, 25  | 2.837  | <b>0.078*</b>    |
|                                                     | Year     | 1, 25  | 1.960  | 0.174            |
|                                                     | Trt*Year | 2, 25  | 0.4822 | 0.623            |
| Biomass ( $\text{g/m}^2$ )                          | Trt      | 2, 10  | 0.3584 | 0.707            |
|                                                     | Year     | 1, 159 | 37.24  | < 0.001          |
|                                                     | Trt*Year | 2, 159 | 0.3049 | 0.738            |
| Stem height ( $\text{num/m}^2$ )                    | Trt      | 2, 10  | 1.012  | 0.398            |
|                                                     | Year     | 1, 159 | 22.28  | < 0.001          |
|                                                     | Trt*Year | 2, 159 | 0.3272 | 0.711            |
| Tillers ( $\text{num/m}^2$ )                        | Trt      | 2, 10  | 0.0964 | 0.909            |
|                                                     | Year     | 1, 159 | 13.26  | < 0.001          |
|                                                     | Trt*Year | 2, 159 | 0.0142 | 0.986            |
| Foliar C (% g/g)                                    | Trt      | 2, 10  | 0.0456 | 0.956            |
|                                                     | Year     | 1, 159 | 17.46  | < 0.001          |
|                                                     | Trt*Year | 2, 159 | 0.2938 | 0.746            |
| Foliar N (% g/g)                                    | Trt      | 2, 10  | 0.2095 | 0.815            |
|                                                     | Year     | 1, 159 | 0.0396 | 0.842            |
|                                                     | Trt*Year | 2, 159 | 2.618  | <b>0.076*</b>    |
| Foliar C:N                                          | Trt      | 2, 10  | 0.2643 | 0.773            |
|                                                     | Year     | 1, 159 | 2.407  | 0.123            |
|                                                     | Trt*Year | 2, 159 | 2.688  | <b>0.071*</b>    |
| Foliar $\delta^{15}\text{N}$ (‰)                    | Trt      | 2, 10  | 1.206  | 0.340            |
|                                                     | Year     | 1, 159 | 19.14  | < 0.001          |
|                                                     | Trt*Year | 2, 159 | 2.172  | 0.117            |
| Root C (% g/g)                                      | Trt      | 2, 10  | 0.3696 | 0.700            |
| Root N (% g/g)                                      | Trt      | 2, 10  | 0.9353 | 0.424            |
| Root $\delta^{15}\text{N}$ (‰)                      | Trt      | 2, 10  | 2.291  | 0.152            |
| NEE ( $\mu\text{mol/m}^2/\text{s}$ )                | Trt      | 2, 10  | 0.1735 | 0.843            |
|                                                     | Year     | 1, 644 | 108.3  | < 0.001          |
|                                                     | Trt*Year | 2, 644 | 6.513  | <b>0.002**</b>   |
| ER ( $\mu\text{mol/m}^2/\text{s}$ )                 | Trt      | 2, 10  | 0.2976 | 0.794            |
|                                                     | Year     | 1, 645 | 42.07  | < 0.001          |
|                                                     | Trt*Year | 2, 645 | 0.6968 | 0.499            |
| GPP ( $\mu\text{mol/m}^2/\text{s}$ )                | Trt      | 2, 10  | 0.5772 | 0.579            |
|                                                     | Year     | 1, 618 | 41.58  | < 0.001          |
|                                                     | Trt*Year | 2, 618 | 8.162  | < <b>0.001**</b> |
| $\text{CH}_4$ ( $\text{nmol/m}^2/\text{s}$ )        | Trt      | 2, 4   | 0.8816 | 0.482            |
|                                                     | Year     | 1, 200 | 2.882  | 0.091            |
|                                                     | Trt*Year | 2, 200 | 0.0004 | 0.999            |
| $\text{N}_2\text{O}$ ( $\text{nmol/m}^2/\text{s}$ ) | Trt      | 2, 4   | 6.341  | <b>0.058*</b>    |
|                                                     | Year     | 1, 200 | 0.0046 | 0.946            |
|                                                     | Trt*Year | 2, 200 | 1.535  | 0.218            |

Data were collected from six blocks over the 2015 and 2016 season. DF degrees of freedom of numerator and denominator. Bolding indicates significant treatment or treatment\*year differences. Significance codes: \*\*  $p < 0.01$  \*  $p < 0.05$ ,  $p < 0.10$ .

fecal deposition rate in these plots, and less root biomass to take advantage of these nutrients.

Removal plots released more  $\text{N}_2\text{O}$  to the atmosphere than other treatments. This may have occurred as a direct response of the greater deposition rates of fresh feces in removal plots or through denitrification of  $\text{NO}_3^-$  (Kelsey and others 2018). There was more  $\text{NO}_3^-$  in the removal plots and less root biomass to take up available N and water, perhaps creating anaerobic conditions conducive to denitrification. However,  $\text{N}_2\text{O}$  can also be produced through nitrification, in which case greater  $\text{NO}_3^-$  concentration and  $\text{N}_2\text{O}$  production in the removal plots could be evidence of increased nitrification (Grosso and others 2000). The addition plots also trended toward a greater  $\text{N}_2\text{O}$  flux than control plots, again suggesting that feces may be a direct source of the  $\text{N}_2\text{O}$  emission. Overall, our observations of treatment effects on  $\text{N}_2\text{O}$  emission are noteworthy considering the very small background  $\text{N}_2\text{O}$  emissions from our study system (Kelsey and others 2018), and that waterfowl feces have not been found to influence  $\text{N}_2\text{O}$  emission in other studies (Winton and Richardson 2017).

## Changes in Aboveground Biomass and Foliar Chemistry

The overall effects of fecal deposition on NEE are dependent on the balance between productivity and respiration, both of which could increase in response to increased nutrient availability with feces (Mack and others 2004). Our fecal manipulations affected NEE. Grazed *C. subspathacea* plots where feces were removed transitioned from a summer-season C sink in the first year to a summer-season C source in the second year (Figure 5). This is somewhat remarkable because previous research in our systems showed that grazing lawns are typically sinks for C, and only in rare situations, such as under very early season grazing, are they C sources (Leffler and others 2019a, 2019b). A point to note is that while feces removal increased  $\text{CO}_2$  emissions, grazing removal as a whole often decreases  $\text{CO}_2$  emissions through increased biomass accumulation (Sjogersten and others 2008; Sjogersten and others 2011), so the relative importance of these effects needs to be compared in future studies.

Higher NEE values in the removal plots indicate that less C was taken up by plants during the second year and is supported by the significant reduction in GPP in the removal plots the second year. We know that plant growth in this system is N-limited (Ruess and others 1997), and that plants

acquire available N quickly (Choi and others 2020). Thus, because feces removals took away forms of readily available N, this likely reduced photosynthetic capacity. The shift in removal plots from sink to source between years was accompanied by an increase in ER in all treatments, potentially due to warmer soils in 2016 than 2015 (mean air temperature from June 1 to Aug 15 was  $10.0^\circ\text{C}$  in 2015 and  $12.4^\circ\text{C}$  in 2016; Leffler and others 2019a). But because there were no ER treatment differences, these changes alone do not explain the sink to source transition in removal plots.

We found that doubling feces did not affect measures of aboveground plant biomass. Changes in plant biomass can be hard to detect without a mechanism to account for removal through grazing (Bazely and Jefferies 1985; Mulder and Ruess 1998); thus, GPP is probably a better measure of production. For example, if geese were grazing more heavily in some treatment plots, such as those receiving additional nutrient inputs (Day and Detling 1990; Drent and Van der Wal 1999), compensatory growth could result in greater productivity despite measurements of biomass and plant height appearing the same (Hik and Jefferies 1990; Person and others 1998). Further, geese may avoid plots that have reduced plant growth as a result of treatments. Similar to other studies (Van der Wal and others 2000), we found counterevidence of these mechanisms in that removal plots had significantly higher fecal deposition rates than control plots, suggesting that geese select areas with fewer feces to graze in (Hutchings and others 1999), despite these areas having lower GPP by the second year.

In the feces addition plots, we found a 10% increase in foliar %N, a 30% increase in  $\delta^{15}\text{N}$  values, and an 8% decrease in foliar C:N of *C. subspathacea* in the second year. The 10% increase in leaf N content is within the range of tundra plant responses to other environmental perturbations, such as deeper winter snow and long-term warming (Welker and others 2005; Pattison and Welker 2014). A goose feces study in La Perouse Bay, Canada with lesser snow geese found that %N in *P. phryganodes* foliage increased in medium and high feces plots compared to low and no feces plots (Bazely and Jefferies 1985), yet in that system *C. subspathacea* was less responsive to fecal treatments (Hik and Jefferies 1990; Zellmer and others 1993). The increase in foliar  $\delta^{15}\text{N}$  with feces addition suggests that at least some of the increase in %N comes from feces because feces are enriched in  $\delta^{15}\text{N}$  compared to litter (Sjogersten and others 2010). Foliar chemistry values for removal plots

were largely in-between control and addition plots values, which may reflect the more frequent fresher feces deposited on these plots.

## Changes in CH<sub>4</sub> Flux

There are at least two ways that feces could influence CH<sub>4</sub> flux. First, fecal addition can enhance CH<sub>4</sub> flux by relieving microbial nutrient limitations, which has been shown to happen in plant-free soils from our system (Foley and others 2021). In contrast, Winton and Richardson (2017) hypothesized that waterfowl feces could increase N cycling in which case the greater availability of soil NO<sub>3</sub><sup>-</sup> would be an efficient alternate electron acceptor, inhibiting CH<sub>4</sub> production and reducing CH<sub>4</sub> emission. However, their data found no support for the effect of waterfowl feces as a driver of CH<sub>4</sub> production, and rather grazing-reduced oxygen transport to the rhizosphere was the primary driver of CH<sub>4</sub> flux. We did not observe treatment effects on CH<sub>4</sub> flux. Although not significant, CH<sub>4</sub> emissions were greatest where feces were removed and lowest where they were added (Figure 3d; Supplemental Figure 5). This could have resulted from greater trampling effects in the more intensely used removal plots, impacting pore space and oxygen transport, or the greater root biomass in the feces addition plots may support increased oxygen-transport belowground causing C to be oxidized rather than released as CH<sub>4</sub> where waterfowl feces are present.

## What happens to the feces?

The small measurable effects that we found, and some surprising results from the feces removal plots, bring up the question of what exactly happens to fecal nutrients after deposition. We moved feces that were on average 1.75 days old over each season. Previous studies, although in a site warmer than ours, have estimated that 53% of the N in goose feces is soluble and that after only 2 h, there is a large drop in soluble fecal N with continuing declines of 62% after 30 h and no further decline after 48 h (Bazely and Jefferies 1985). From this, we might expect that some soluble N in feces was lost before we moved them from removal plots.

The question is what happens to this N? Bazely and Jefferies (1985) attributed this loss to volatilization and leaching of NH<sub>4</sub><sup>+</sup> into sediments. However, Ruess and others (1989) estimated that under typical field conditions at our site, only about 8% will be volatilized, thus, being a relatively minor pathway for soluble N loss, with the remainder either being released as soluble inor-

ganic N into the sediments or immobilized by microbes. Ruess and others (1989) suggest that a significant portion of the soluble fecal N unaccounted for by Bazely and Jefferies (1985) after 48 h was immobilized by microbes within the fecal dropping. Once the feces are deposited, further microbial activity may result in the net mineralization of organic N, and release of soluble inorganic N into the sediments, but the time frame might not be measurable in our experiment.

More specifically, because we moved feces that were, on average, 1.75 days old, our treatments could have transported only about 35% of the soluble N because 65% could have been lost, 8% of which to volatilization (although volatilization would have occurred on all plots). However, if this N was largely immobilized in the feces as suggested by Ruess and others (1989), then it would have moved with the feces. The amount moved could have been influenced by weather conditions as well, for example, with wet or rainy conditions moving more N into the soil quickly. We still expected our treatments to have effects but appreciate that they did not have the full effect from soluble N expected based on fecal counts. For feces removal and addition to have full effects in these types of experiments, they should be collected very shortly after deposition (Bazely and Jefferies 1985).

We conducted this research in a terrestrial system where the location of grazing lawns are along pond and tidal margins, and thus, subject to frequent coastal flooding events (Jorgenson 2000). We observed that in half of our study blocks, feces were washed away from our plots about halfway through the season each year, while they accumulated over the season in the other half (Figure 2). When we tested for the effects of this loss due to flooding in our experiment, we did not detect any changes to our overall findings, but flooding undoubtedly plays a role in reducing fecal effects in this system. Feces that we were able to monitor throughout the season dissolved into the soil about one month after deposition (Supplemental Figures 1 and 2), likely due to the wet nature of these soils but also suggesting that goose treading may play a large role. Our study isolated the effects of feces while treading and grazing were still occurring. To completely isolate the effects of feces, treading, and grazing or grubbing (Zacheis and others 2002; Egelkraut and others 2020), future studies should focus on these effects in isolation and conjunction to gain a greater understanding of the effects of goose herbivores on these systems (Olofsson 2009).



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## DATA AVAILABILITY

Data are published online at the NSF Arctic Data Center: <https://doi.org/10.18739/A22274>

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