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RESEARCH ARTICLE

Herbivory in a low Arctic wetland alters intraspecific plant root traits with consequences for carbon and nitrogen cycling

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Abstract

1. High latitude wetlands are ecologically important ecosystems due to their large carbon (C) storage capacity and because they serve as breeding and nesting habitat for large populations of migratory birds. Goose herbivory in wetland meadows affects leaf chemical and morphological traits and also influences soil properties by increasing soil temperature and depositing faeces. Grazing-induced changes to above-ground traits and soil properties impact C cycling, but the influence of grazing on root-mediated C and nitrogen (N) cycling has not been explored.
2. We investigated how goose herbivory in a low-Arctic coastal wetland in western Alaska affected root morphological, physiological and chemical traits of a dominant graminoid by assessing plant traits in ungrazed versus heavily grazed sedge meadows. We also performed a 11-week lab-based root incubation experiment to determine how grazing affects CO_2-C efflux, the size and decay rate of the fast-cycling C pool (i.e. C with a mean residence time of days to weeks, determined via CO_2-C efflux), and patterns of N mineralization during root decomposition.
3. Goose grazing altered root chemical traits by increasing root N by 7%, cellulose by 12%, and ash content by 17%, indicating that grazing shifted root chemical traits towards a resource-acquisition strategy. Grazing did not alter root biomass, morphology or bulk C exudation. In our root incubation, soils that included the roots of grazed plants tended to exhibit greater CO_2-C efflux than those containing ungrazed plant roots due to a larger fast-cycling C pool. Additionally, grazing-induced increases in soil temperature led to greater CO_2-C efflux due to a faster decay rate of the fast-cycling C pool. Finally, compared with ungrazed roots, we found that the decomposition of grazed roots resulted in more N being transferred to root necromass from the surrounding soil, suggesting that microbial communities decomposing grazed roots immobilized N.
4. *Synthesis*. Overall, our results indicate that goose grazing increased C-cycling rates by influencing soil environmental conditions and by altering the ecological strategy of grazed plants. In contrast, grazing decreased net N mineralization by

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promoting N immobilization. These results suggest that changing patterns and abundances of herbivores can have substantial effects on elemental cycles.

KEYWORDS
plant ecological strategy, plant economics spectrum, plant–herbivore interactions, root chemistry, root economics spectrum, soil carbon pools, soil nitrogen pools

1 | INTRODUCTION

As herbivores continue to decline globally (Atwood et al., 2020), understanding their roles in modifying ecosystem structure and function is becoming increasingly urgent (Schmitz et al., 2018). It has been suggested that grazing influences ecosystems by altering plant morphological and chemical traits, and studies have shown that grazer-mediated shifts in these traits can influence litter decomposition, nutrient cycling and ecosystem carbon (C) storage (Bai et al., 2012; Bardgett & Wardle, 2003; Deyn et al., 2008; Tuo et al., 2024). However, most of the research on the impacts of grazing on plant traits has focused on above-ground structures like leaves, with less attention given to how grazing influences root traits (Cai et al., 2024). Yet, roots play an integral and disproportionate role in controlling essential functions like C storage and nutrient cycling (Bardgett et al., 2014; Rasse et al., 2005). Therefore, understanding the links between grazing, root traits and ecosystem functioning is necessary for managing herbivore populations for sustained ecosystem services.

Intraspecific variation in plant traits is believed to occur because plants modify their traits to adapt to a wide range of environmental conditions. This idea is based on the hypothesis that plants in different environmental conditions will invest in their traits differently, depending on trade-offs between maximizing resource acquisition to enhance productivity or maximizing resource conservation to support longevity (Reich et al., 2003). When applied to roots, this theoretical framework, called the root economics spectrum, classifies suites of correlated root traits into plant ecological strategies associated with resource acquisition or resource conservation (Reich, 2014). Root systems associated with a resource acquisition strategy are characterized by traits that promote rapid nutrient uptake. These resource acquisition traits include higher specific root length, root exudation rates and root nitrogen (N) concentrations and lower root tissue density, root lignin and shorter lifespans compared with root systems associated with a resource conservation strategy (McCormack et al., 2012; Prieto et al., 2015; Roumet et al., 2016).

Although there is limited research on the topic, above-ground herbivory has been shown to shift root traits in a way that suggests they are expressing a resource acquisition strategy (Cai et al., 2024; Zhou et al., 2024). For example, grazing generally increases specific root length and decreases root diameter and root tissue density (Cai et al., 2024; Heinze, 2020; Zhou et al., 2024). These changes likely occur because above-ground herbivory reduces photosynthetic rates, thereby decreasing C available for root production (Detling et al., 1979; Klumpp et al., 2009). With reduced C availability, plants invest in fine, low-density roots rather than C-intensive coarse roots, allowing the plant to exploit a similar volume of soil at a lower C cost (de la Riva et al., 2021; Eissenstat, 1992). In addition to morphological shifts, grazing shifts physiological root traits towards a resource acquisition strategy, including increasing root exudation and respiration rates (Hamilton et al., 2008; Holland et al., 1996), traits that are associated with N uptake (Hamilton et al., 2008; Reich et al., 2008; Wen et al., 2022). Consequently, grazing typically results in higher root N concentrations and lower C:N ratios (Bai et al., 2012; Heyburn et al., 2017).

A shift in morphological and chemical root traits towards a resource acquisition strategy could influence the decomposition rates of root necromass. For example, root decomposition rates are positively related to specific root length, N concentrations and hemicellulose concentrations, and are negatively related to root diameter and lignin concentrations (Prieto et al., 2016; Roumet et al., 2016). However, linking above-ground grazing to below-ground ecosystem functions is complex due to the interplay between grazing effects on both root traits and soil environmental conditions. Specifically, in addition to potentially altering root decomposition rates through changes in root traits, grazers can influence soil conditions that underlie decomposition through various processes. For example, the removal of above-ground vegetation by grazers can influence soil temperatures (Kelsey et al., 2016; Stark et al., 2015) and grazer faeces can alter nutrient availability (Beard et al., 2023; Frost & Hunter, 2007; McKendrigk et al., 1980). Understanding how grazing-induced shifts in root traits and soil environments concurrently influence C and nutrient cycling will help us address critical gaps in our knowledge about the role of different grazing mechanisms in shaping ecosystem functioning. Integrating controlled laboratory experiments that reveal the mechanistic drivers of ecosystem functions with field studies that capture real-world variations in plant trait expressions between grazed and ungrazed areas is crucial for advancing our understanding of grazing impacts. Such approaches provide valuable insights into how grazing-induced shifts in root traits and soil environments interact to influence carbon and nutrient cycling, addressing key knowledge gaps about the role of grazing mechanisms in shaping ecosystem functioning.

In this study, we combined a field survey and a controlled laboratory study to examine how goose grazing in the low Arctic coastal wetlands of Alaska's (USA) Yukon–Kuskokwim (Y-K) River Delta impacts root traits and root decomposition of *Carex subspathacea*, a dominant wetland plant and key food resource for migratory geese. Previous research in the Y-K Delta has shown that above-ground grazing by geese significantly influences above-ground plant traits, soil environmental characteristics and C and N cycling in this ecosystem (Choi et al., 2020; Foley et al., 2022; Kelsey et al., 2016; Saunders et al., 2023). However, to date, no studies have examined whether grazing impacts the root traits of *C. subspathacea* and whether these changes in root traits contribute to the effects of grazing on C and N cycling. We hypothesized that (1) grazing would shift *C. subspathacea* morphological, physiological and chemical root traits towards a resource acquisition strategy, and (2) that the shift in root traits and soil environmental conditions would increase C and N cycling rates during root decomposition. Our study addresses knowledge gaps related to the mechanisms that control grazing effects on ecosystem functioning in the Y-K Delta and also enhances our broader understanding of intraspecific variations in root traits globally and the processes that influence them.

2 | MATERIALS AND METHODS

2.1 | Study site

We collected soil and root samples from *C. subspathacea*-dominated communities in western Alaska's Y-K River Delta. All fieldwork was conducted under the United States Fish and Wildlife Service Special Use Permit Number FF07RYKD00–20-01. The mean daily summer temperature in the region is 12.5°C, and the mean annual precipitation is 499 mm (Palecki et al., 2021). The soils from our collection areas are predominantly silt and sand deposits (Tande & Jennings, 1986). In the study area, at a soil depth of 10 cm, the soil pH is approximately neutral, soil carbon (C) ranges from ~1.5% to 5%, and soil nitrogen (N) ranges from ~0.1% to 0.4% (Adkins et al., Unpublished Data; Foley et al., 2022).

In coastal regions of the Y-K Delta, herbivory by Pacific Black Brant Geese (*Branta bernicla*) and Cackling Geese (*Branta hutchinsii*) creates ‘grazing lawns’ on pond margins adjacent to ungrazed, monospecific *C. subspathacea* meadows (Person et al., 1998). The extensive grazing in these lawns converts *C. subspathacea* to a persistently short-statured form, exhibiting stem heights <2 cm, whereas *C. subspathacea* in ungrazed meadows exhibits stem heights >15 cm (Kelsey et al., 2016). Grazing alters *C. subspathacea* leaf chemistry, with the grazed form exhibiting greater %N than the ungrazed form (Person et al., 1998; Saunders et al., 2023). The decreased plant biomass in grazing lawns also results in higher soil temperatures (~13°C) compared with ungrazed meadows (~10°C) (Kelsey et al., 2016; Person et al., 1998). Owing to the positive influence of leaf N on gosling growth, geese annually return to grazing lawns to feed, thereby maintaining persistent differences in plant characteristics and soil environmental conditions year after year (Beard et al., 2019).

2.2 | Natural root trait survey

2.2.1 | Morphological and chemical traits

To assess root morphological and chemical traits of grazed and ungrazed *C. subspathacea* in the Y-K Delta, we collected 3-cm diameter soil cores to a depth of 50 cm from five sites along the Kashunuk River (61.34° N 165.45° W) and from five sites along the Tutakoke River (61.24° N 165.63° W) in July 2022. All collections were conducted within monospecific stands of *C. subspathacea* to ensure that all root traits measured were exclusively attributable to *C. subspathacea*. The Kashunuk River collection sites were located within 11 km of each other, and the Tutakoke River sites were within a 6 km range. From each of the 10 collection sites, we collected three cores from grazing lawns and three cores from adjacent ungrazed meadows for a total of 30 samples per habitat type. We separated each soil core into five depth subsections (10 cm increments) and isolated roots from soils by wet-sieving (250 μm mesh). We then oven-dried the isolated roots at ~65°C.

In the laboratory, we measured root biomass for each core increment. From the 60 samples collected, we randomly selected 12 samples for morphological analysis (three cores per habitat × river combination). We used WinRhizo software (Regent Instruments, Inc., Quebec) to determine total root length, root surface area, root volume and root diameter distribution of each 10-cm sample subsection. We calculated specific root length, specific surface area, root tissue density and mean rooting depth as described in Freschet et al. (2021).

After morphological analysis, we homogenized the root subsections from each original core, and we sent sub-samples to the University of Hawaii at Hilo Analytical Laboratory to determine C and N concentrations ($N = 60$). We determined acid detergent fibre (ADF), proximate cellulose (hereafter cellulose), proximate lignin (hereafter lignin), the detergent soluble fraction and ash content in the roots using the approach described in Gessner (2005). Due to root mass availability constraints, we performed these analyses on roots from 20 grazing lawn cores and 25 ungrazed meadow cores (out of 30).

2.2.2 | Root exudation

To assess root exudation rates, we collected 18 (nine from each habitat type) *C. subspathacea* + soil samples from grazing lawns and adjacent ungrazed meadows from five sites along the Kashunuk River in August 2022. Each sample was collected by excavating a 4 × 4 cm block of soil to a depth of 10 cm using a sterile knife while leaving the above-ground biomass intact. The below-ground portion of each sample was covered in plastic wrap and secured in a plastic bag; the above-ground biomass was left uncovered to allow for gas exchange. We stored the samples on ice and transported them to Utah State University within 96 h of collection.

We used a hydroponic method to collect root exudates (Oburger & Jones, 2018). We placed the plant + soil samples in a temperature-controlled room at 13°C under lights with photosynthetically active radiation (PAR) of ~30 mol day^{-1} to mimic natural growing-season conditions (Kelsey et al., 2016). After 48 h of acclimation, we removed soils from the roots by rinsing them with deionized water. We then transferred the soil-free root samples to 125 mL glass jars containing 50 mL of deionized water and placed them back in the temperature-controlled room for another 48 h, replacing the deionized water after 24 h. We then filtered the water through 11 μm Whatman filter paper and froze the extracts until they were analysed for total dissolved organic carbon. We measured total dissolved organic C in the extracted exudate solutions by digesting them in a potassium dichromate + sulfuric acid solution followed by colorimetric analysis (Adkins & Miesel, 2021; Cai et al., 2011).

2.3 | Root incubation experiment

2.3.1 | Sample collection and processing

We collected root and soil samples from monospecific *C. subspathacea* meadows and grazing lawns from a site near the Kashunuk River (61.33° N, 165.48° W) on 4 August 2021. We collected four 5-cm diameter soil cores to a depth of 15 cm from ungrazed meadows and grazing lawns for a total of eight cores. We collected the ungrazed meadow cores at 20-m increments along a 60-m transect. We collected the grazing lawn cores from four separate grazing lawns near the transect, and we also collected fresh goose faeces from the grazing lawns.

In the laboratory, we air-dried the goose faeces and the soil cores. We separated roots from soils by first dry-sieving them (2 mm mesh) and then removing any remaining roots with forceps. We then immersed the roots in water for cleaning and to further separate roots from non-root organic matter via flotation. We then air-dried the clean roots.

2.3.2 | Root incubation experimental setup

We performed an 11-week soil incubation experiment to determine how above-ground grazing influenced *C. subspathacea* root decomposition. The duration of the incubation period emulates the average length of the growing season in the Y-K Delta (Leffler et al., 2019). We homogenized soils from all of the field-collected cores, and we separately homogenized all ungrazed roots and all grazed roots, respectively. We added 10 g of the homogenized soil to 125 mL glass containers fitted with gas-tight lids and septa, and we applied three treatments in a fully factorial design. The treatments included: (1) root type (ungrazed, grazed, or no roots), (2) faeces additions (goose faeces added or omitted) and (3) temperature (10°C or 13°C). For the root treatments, we placed 0.1 g of roots from grazed or ungrazed *C. subspathacea* in a 250 μm mesh bag and buried it in the soil; for the no-root treatments, we buried an empty bag. The ratio of roots to soil represents an addition rate commonly used in root decomposition experiments (Cotrufo & Ineson, 1995; de Graaff et al., 2010, 2013). For the goose faeces treatments, we mixed 0.01 g of dried goose faeces into the soil, corresponding to the natural faecal density found in grazing lawns (Foley et al., 2022). Chemical characteristics of the faeces have been previously described (Saunders et al., 2023). To apply the temperature treatments, we placed microcosms in either a 10°C or 13°C stable temperature chamber, which reflects the mean growing season temperatures at the soil surface in ungrazed meadows and grazing lawns, respectively (Kelsey et al., 2016). We maintained soil moisture in the microcosms at 60% water holding capacity via weekly deionized water additions based on microcosm mass loss.

We took weekly CO_2 gas measurements from the headspace of the microcosms to determine the CO_2-C efflux rate and the size and decay rate of the fast-cycling C pool. On each measurement day, we flushed the microcosms with ambient air and then sealed the jar for 24 h to allow CO_2 to accumulate in the headspace. After 24 h, we collected a 10 mL aliquot from the headspace of each microcosm. We measured the headspace CO_2 concentrations on a LI-7810 Trace Gas Analyser (LI-COR Inc., Lincoln, Nebraska). We determined the size (C_a; μg C g^{-1} soil) and decay rate (k; day^{-1}) of the fast-cycling C pool in the microcosms by fitting our weekly CO_2-C efflux measurements to the following one C pool exponential decay model (Kuzyakov, 2011):

$$CO_{2(t)} = C_a \times \left(1 - e^{-kt}\right)$$

where $CO_{2(t)}$ is cumulative CO_2-C efflux (μg C g^{-1} soil) at sampling period *t* (days). We consider C_a and *k* to represent parameters of the fast-cycling C pool (sensu Kuzyakov, 2011; often alternatively referred to as the active C pool or labile C pool) because over the short duration of our incubations, emitted C would primarily originate from this pool (Paul et al., 2006). Our approach does not distinguish between CO_2 originating from roots versus native soil organic matter, so the fast-cycling C pool is a property of both roots and soil C.

After the 11-week incubation, we removed the roots from the soil and measured ADF, %C and %N of the post-incubated roots from each microcosm using the methods described above. We performed the same analysis on three subsamples of the homogenized, pre-incubated grazed and ungrazed roots to determine changes in ADF, %C and %N over the incubation. Chemical characteristics of pre-incubated roots are provided in Table 1.

We partitioned the amount of N-mineralization that was attributable to roots versus soil + faeces by determining the total inorganic N content in three pre-incubated soil subsamples, as well as in all post-incubated samples. We extracted inorganic N using 2 M KCl and measured total nitrate (NO_3^-) and total ammonium (NH_4^+) using colorimetric methods described by Keeney & Nelson (1982) and Sims et al. (1995), respectively. The difference in inorganic N between pre- and post-incubated soils represents net N mineralized from all organic material in the microcosms (i.e. soils, roots, faeces, depending on treatment combination; hereafter referred to as whole microcosm N-mineralization).

TABLE 1 Chemical characteristics (means ± SD) of roots from grazed and ungrazed *Carex subspathacea* used for the decomposition experiment.

	Grazed	Ungrazed
Carbon (%)	38.60 ± 0.27	40.40 ± 0.32
Nitrogen (%)	1.12 ± 0.046	1.00 ± 0.045
Carbon:Nitrogen	34.51 ± 1.37	40.54 ± 1.50
ADF (%)	49.91 ± 0.96	53.23 ± 1.37

Note: Standard deviations are based on three analytical replicates. Roots collected from different sites were homogenized prior to analysis, so statistical differences are not reported.

Abbreviation: ADF, acid detergent fibre.

TABLE 2 *Carex subspathacea* root chemistry, morphological and physiological traits (means ± SE) for the natural root traits survey experiment.

	Grazed	Ungrazed
Carbon (%)	33.42 ± 0.63	34.53 ± 0.46
Nitrogen (%)	**1.07 ± 0.029**	**1.00 ± 0.020**
Carbon:Nitrogen	**31.61 ± 0.89**	**35.15 ± 0.96**
Ash (%)	**19.31 ± 1.11**	**16.50 ± 0.68**
ADF (% ash-free biomass)	60.68 ± 1.67	57.17 ± 1.29
Cellulose (% ash-free biomass)	**25.07 ± 0.91**	**22.37 ± 0.69**
Lignin (% ash-free biomass)	35.61 ± 1.40	34.79 ± 1.26
Detergent Soluble Fraction (% ash-free biomass)	39.32 ± 1.67	42.83 ± 1.29
Root biomass (g)	5.09 ± 0.43	5.44 ± 0.62
Specific root length ($\mathrm{m\,g^{-1}}$)	149.47 ± 5.80	159.86 ± 10.80
Specific surface area ($\mathrm{cm^2\,g^{-1}}$)	692.61 ± 25.24	709.89 ± 35.07
Root tissue density ($\mathrm{mg\,cm^{-3}}$)	146.42 ± 6.51	151.71 ± 4.71
Mean rooting depth (cm)	23.35 ± 0.78	22.47 ± 1.30
Exudation rate ($\mathrm{mg\,C\,g^{-1}\,root\,day^{-1}}$)	0.54 ± 0.12	0.44 ± 0.04

Note: Bold values indicate statistically significant differences between grazed and ungrazed roots. Chemical and morphological trait measurements were performed on roots collected at 0–50 cm. Root exudation rates were assessed on roots collected at 0–10 cm.

Abbreviation: ADF, acid detergent fibre.

We estimated net N-mineralization that was specifically attributable to roots by considering the mass of root C that was mineralized, as well as post-incubation root C:N and calculating the net N-mineralization/immobilization that must have occurred to achieve this C:N. For each microcosm that received root additions, we estimated the mass of root C that was mineralized as cumulative CO_2-C emitted from those microcosms less the mean cumulative CO_2-C emitted from the microcosms that did not receive roots, with the mean calculated for each faeces × temperature treatment combination. We then calculated net root-N mineralization with the following equation:

$$\text{Root N Mineralization} = \text{Root N}_{\text{Pre}} - \frac{\text{Root C}_{\text{Pre}} - \text{Root C}_{\text{min}}}{\text{Root C:N}}$$

where root N_{pre} is the mass of root N present prior to the incubation, root C_{pre} is the mass of root C present prior to the incubation, root C_{min} is the mass of root C emitted as CO_2-C, and root C:N is post-incubation C:N. In this approach, negative root net N-mineralization values indicate the immobilization of N by the decomposer community. We estimated non-root (i.e. soil or soil + faeces, depending on the treatment) net N-mineralization as the difference between whole microcosm net N-mineralization and root net N-mineralization. We emphasize that our calculations represent *estimates* of root net N mineralization because we did not directly trace the fate of root N (e.g. with isotopic-tracer approaches). We also acknowledge that our approach assumes that greater C mineralization in root versus no-root microcosms is entirely attributable to root decomposition and does not account for potential priming effects.

2.4 | Statistical analysis

2.4.1 | Natural root trait survey

We performed all statistical analyses in the R Statistical Computing Environment (R Core Team, 2024). We used linear mixed-effects models to analyse differences in root morphology, chemistry and root exudation between habitats using the *nlme* package (Pinheiro & Bates, 2000). For models assessing morphology, we included main and interactive effects of habitat type and root depth, with collection site as a random effect. We included a fixed effect of habitat type and a random effect of collection site in models assessing root chemistry and exudation. Models assessing %N required log transformation of response variables to meet normality assumptions. We determined the significance of main and interactive effects using Type II Analysis of Deviance in the *car* package (Fox & Weisberg, 2019). We performed Tukey-adjusted post hoc analyses using the *emmeans* package (Lenth, 2024). We determined whether root diameter distributions differed between habitat types using Kolmogorov–Smirnov tests.

2.4.2 | Root incubation experiment

We assessed all main and interactive effects of root, temperature and faeces treatments on cumulative CO_2-C efflux after the 11-week incubation using linear models fit with the lm function in the *stats* package (R Core Team, 2024). Cumulative CO_2-C efflux was log-transformed to meet normality assumptions.

We used non-linear regression to fit our one-C pool exponential decay models and to assess the main and interactive effects of treatments on C_a and *k*; we performed these analyses using the *nlme* package (Pinheiro & Bates, 2000).

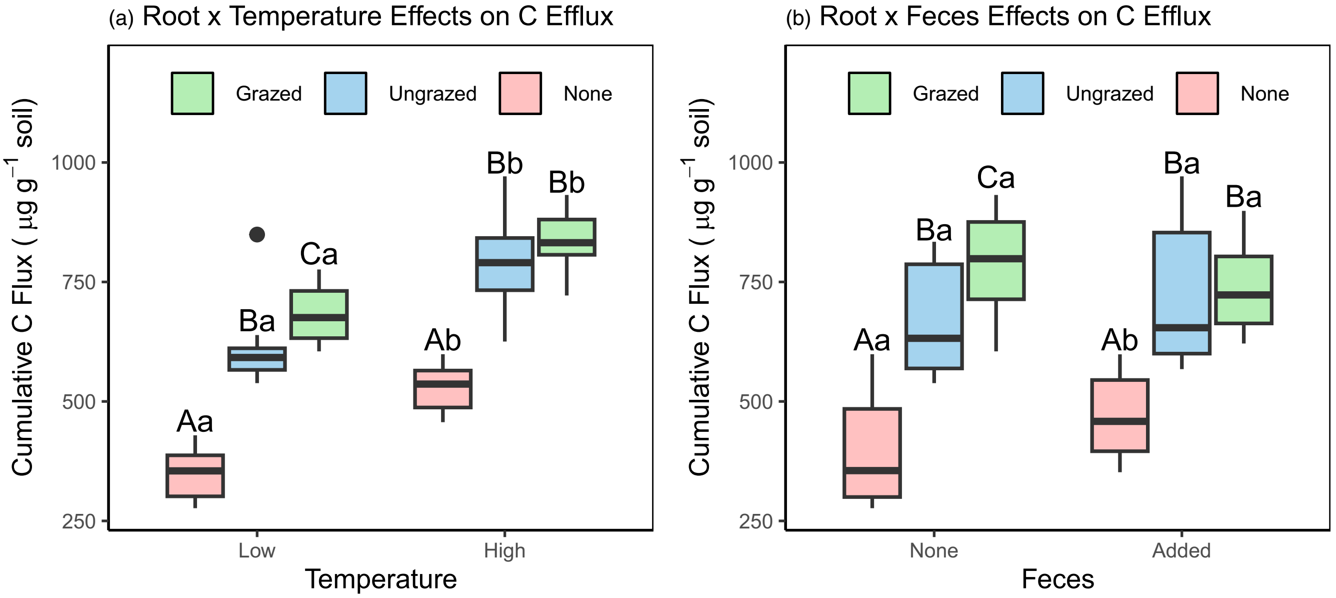


FIGURE 1 Effect of Root type, temperature and faeces additions on total carbon dioxide (CO_2-C) efflux. (a) Root × temperature effects and (b) root × faeces effects on total CO_2-C emitted over the 11-week incubation experiment. For each box and whisker plot, the heavy middle line is the median, the hinges are the first and third quartiles, and the whiskers represent the maximum and minimum values no further 1.5 times the interquartile range from the hinges. The lower temperature (10°C) represents soil temperatures in ungrazed meadows, while the higher temperature (13°C) corresponds to soil surface temperatures in grazing lawns. In panel (a), uppercase letters denote statistically significant differences among root treatments within temperature treatments, and lowercase letters denote significant differences among temperature treatments within root treatments. In panel (b), uppercase letters denote significant differences among root treatments within faeces treatments, and lowercase letters denote significant differences among faeces treatments within root treatments.

We used linear models to investigate the changes in soil inorganic N, root C, root N, root C:N and root ADF over the incubation. For all analyses, we conducted Tukey-adjusted pairwise comparisons using the *emmeans* package (Lenth, 2024).

3 | RESULTS

3.1 | Natural root trait survey

We found that grazing significantly affected root chemistry but did not significantly influence total root biomass, morphological traits, or root exudation rates (Table 2). Specifically, roots from grazing lawns exhibited decreased C:N ($p = 0.007$) and increased percent N ($p = 0.029$), cellulose ($p = 0.017$) and ash ($p = 0.012$) compared with ungrazed *C. subspathacea* roots. Root morphological traits at different soil depth increments are provided in Figures S1–S6.

3.2 | Root incubation experiment

Cumulative CO_2-C efflux after 11 weeks of incubation was significantly impacted by root × temperature ($p = 0.003$) and root × faeces ($p = 0.002$) interactions, as well as by the main effects of roots ($p < 0.001$), temperature ($p < 0.001$) and faeces ($p = 0.030$; Figure 1). Cumulative CO_2-C efflux was always greater in high-temperature treatments than in low-temperature treatments, exhibiting 22%–51% higher emissions ($p < 0.001$). Within temperature treatments, cumulative CO_2-C efflux was significantly different among all root treatments ($p \leq 0.016$), with the exception that grazed and ungrazed root treatments did not differ within the high-temperature treatment. Compared with the no-root treatments, CO_2-C efflux was 58%–95% greater in the grazed root treatments and 49%–74% greater in the ungrazed root treatments. Compared with the no-faeces treatments, faeces additions increased cumulative CO_2-C efflux only in the no-root treatments, where it increased by ~17% ($p < 0.001$).

Our exponential decay model indicated that the size of the fast-cycling C pool was significantly affected by root × temperature ($p = 0.003$), root × faeces ($p = 0.009$) and temperature × faeces ($p = 0.043$) interactions, as well as by the main effect of root treatment ($p < 0.001$; Figure 2). Within both the high- and low-temperature treatments, the size of the fast-cycling C pool significantly differed among all three root treatments ($p \leq 0.030$). Grazed root treatments had the largest fast-cycling C pools; fast-cycling C pools in grazed root treatments were 97%–171% larger than in no-root treatments and 10%–22% larger than in ungrazed root treatments. Temperature only significantly affected the size of the fast-cycling C pool within the no-root treatments, where the higher temperature increased the pool size by 29% compared with the lower temperature ($p < 0.001$).

Compared with the no-faeces treatments, faeces additions increased the size of the fast-cycling C pool in the no-root treatment by 17% and in the ungrazed roots treatments by 11% ($p \leq 0.030$). Additionally, compared with the no-faeces treatments, faeces

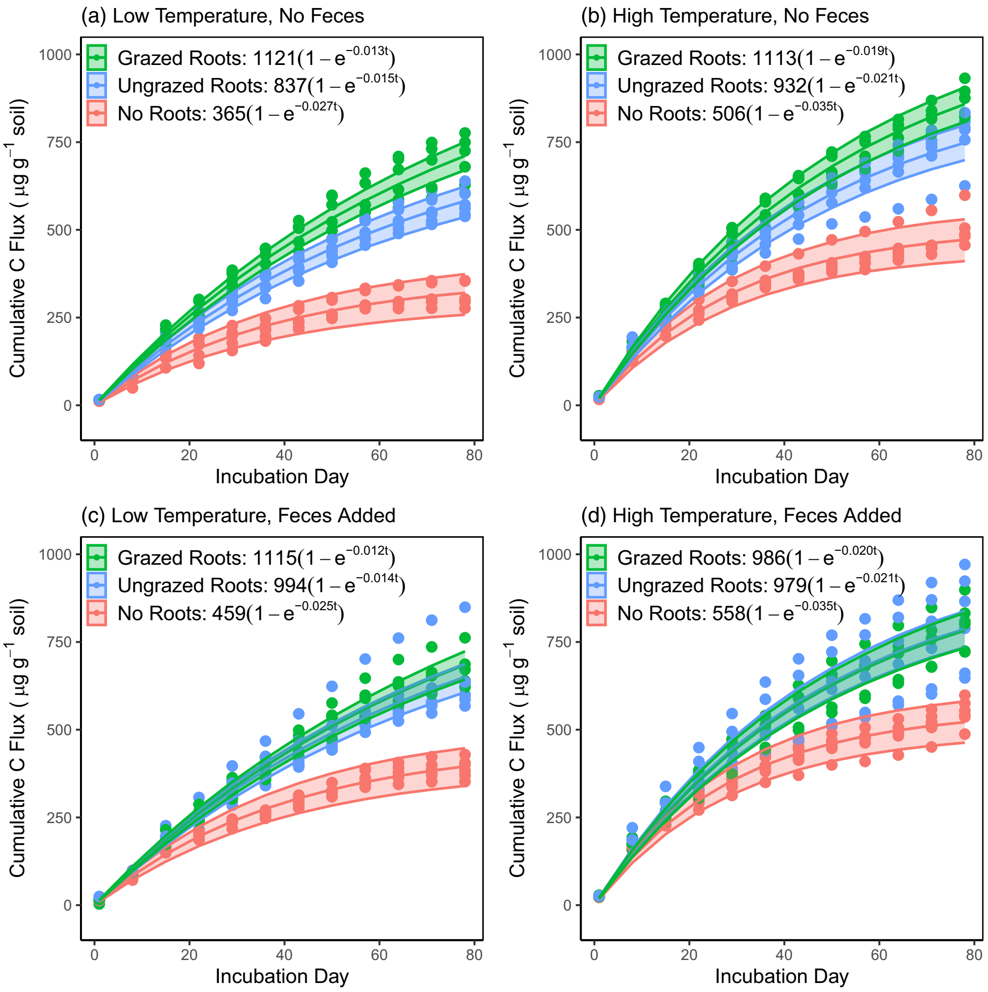


FIGURE 2 Mean cumulative carbon dioxide (CO_2-C) flux over the 11-week decomposition experiment. The different panels (a-d) represent the four distinct temperature × faeces treatment combinations. The lower temperature (10°C) represents soil temperatures in ungrazed meadows, while the higher temperature (13°C) corresponds to soil surface temperatures in grazing lawns. The lines of best fit and displayed equations are based on non-linear regression of the one carbon pool model described in the main text. Bands around lines of best fit are 95% confidence intervals.

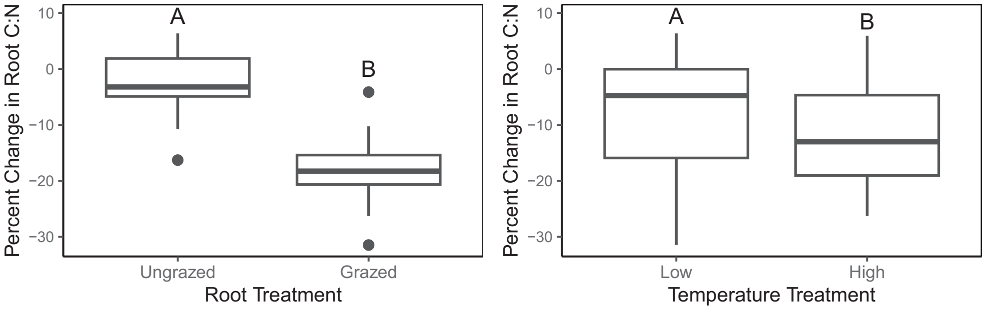
additions increased the size of the fast-cycling C pool within the low-temperature treatment by 10% ($p = 0.020$).

There were significant main effects of root and temperature treatments on the decay rate constant, k, but no interactive effects. The three root treatments were all significantly different from one another ($p \leq 0.001$), with the no-root treatments exhibiting the fastest decay rates, followed by ungrazed roots and then grazed roots (Figure 2). The high-temperature treatment resulted in faster decay rates than the low-temperature treatment.

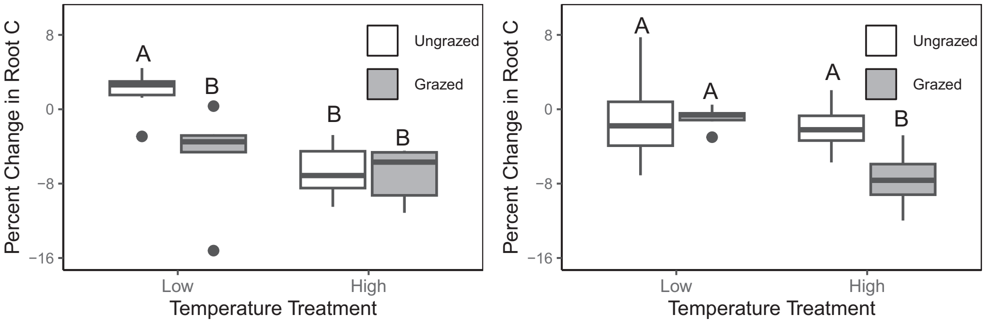
Root and temperature treatments both affected the change in root C:N over the decomposition period (Figure 3a,b). Grazed roots exhibited an eightfold greater decline in root C:N than ungrazed roots ($p < 0.001$). The high temperature treatment resulted in a 41% greater decline in root C:N than the low temperature treatment ($p = 0.036$). Change in root %C was affected by a root × temperature × faeces interaction ($p = 0.005$) and by the main effects of root treatment ($p = 0.010$) and temperature treatment ($p < 0.001$). When differences were statistically significant, grazed roots exhibited a greater decline in %C than ungrazed roots (Figure 3c,d). High temperature treatments tended to exhibit a greater decline in root %C than low temperature treatments. Change in root %N was impacted by root treatment ($p < 0.001$), with grazed roots exhibiting a 16% increase in %N and ungrazed roots exhibiting no change (Figure 3e). Changes in root %ADF were affected by temperature ($p = 0.017$) and by a temperature × root interaction ($p = 0.038$; Figure 3f).

There were significant main effects of root ($p < 0.001$) and temperature ($p < 0.001$) treatments on whole microcosm net N-mineralization over the decomposition period (Figure 4a). All root treatments differed in whole microcosm net N-mineralization, with grazed root treatments exhibiting net N-mineralization that was 26% lower than ungrazed root treatments and 39% lower than no-root treatments. High temperature treatments exhibited 22% lower net N mineralization than low temperature treatments (data not shown).

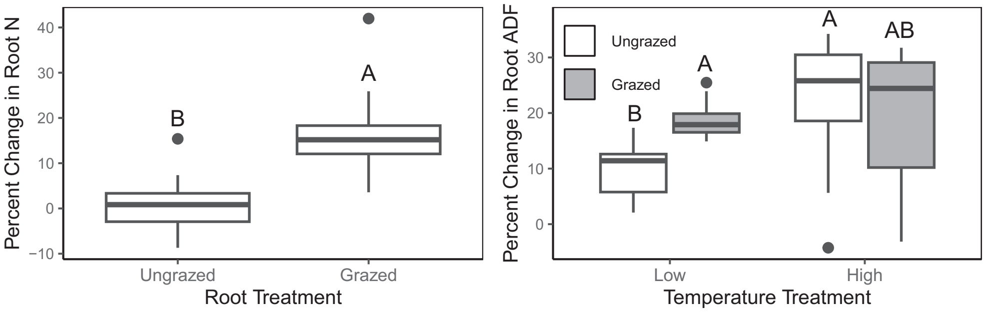
Estimated root N mineralization was significantly affected by root treatments ($p < 0.001$), with ungrazed roots exhibiting positive


(a) Root Treatment Effects on Root C:N

(b) Temperature Treatment Effects on Root C:N


(c) Root x Temperature Effects on Root C (No Feces)

(d) Root x Temperature Effects on Root C (Feces Added)


(e) Root Treatment Effects on Root N

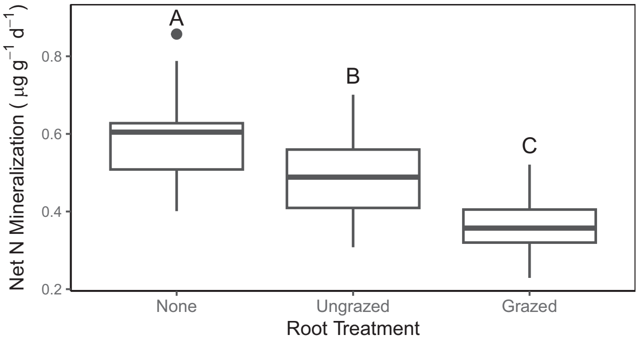
(f) Root x Temperature Effects on Root ADF

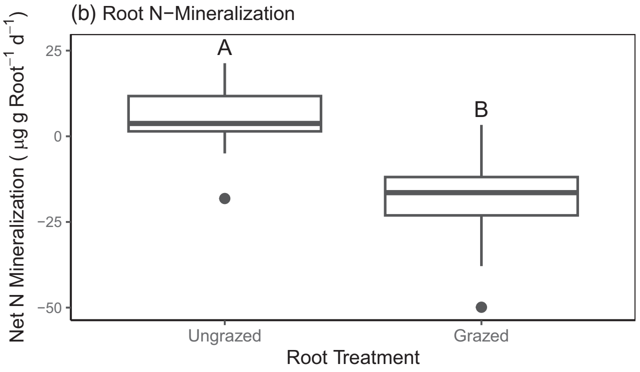
FIGURE 3 Relative percent changes in (a-b) root carbon-to-nitrogen ratio, (c-d) root carbon, (e) root nitrogen, and (f) root acid detergent fibre over the 11-week decomposition experiment. For each root chemistry parameter, only experimental factors that had significant effects on that parameter are shown. For each box and whisker plot, the heavy middle line is the median, the hinges are the first and third quartiles, and the whiskers represent the maximum and minimum values no further than 1.5 times the interquartile range from the hinges.

net N mineralization and grazed roots exhibiting negative net N mineralization (i.e. N immobilization; Figure 4b). Root treatments also affected the amount of non-root net N mineralization ($p < 0.001$), with grazed and no-root treatments exhibiting positive non-root net N mineralization and ungrazed treatments exhibiting non-root net N mineralization that was not significantly different from zero (Figure 4c).

4 | DISCUSSION

Our study uncovered compelling evidence that above-ground herbivory induces changes in the root chemistry of *C. subspathacea*. In support of our first hypothesis, grazing shifted chemical root traits further towards a resource acquisition strategy, as evidenced by lower C:N ratios and higher %N and mineral content (measured as ash; de la Riva et al., 2021; Prieto et al., 2015; Roumet et al., 2016). Additionally, grazed *C. subspathacea* exhibited greater root cellulose content. Only a few quantitative studies have included cellulose in root economic frameworks (Prieto et al., 2015; Wang et al., 2024) but evidence is emerging that higher root cellulose contributes to the tensile strength necessary for soil exploration, thereby supporting a resource acquisition strategy (Genet et al., 2005; Wang et al., 2024). While root chemical traits consistently shifted towards a resource acquisition strategy in response to grazing, the magnitude of trait changes was relatively minor compared with the variation typically observed in studies comparing root trait values across different species. This, however, is to be expected as intraspecific trait variation is far more constrained than interspecific trait variation (Siefert et al., 2015; Weemstra et al., 2021). We also found support for our second hypothesis; grazing influenced soil elemental cycling by altering the patterns


(a) Whole Microcosm N−Mineralizaton


(b) Root N−Mineralization

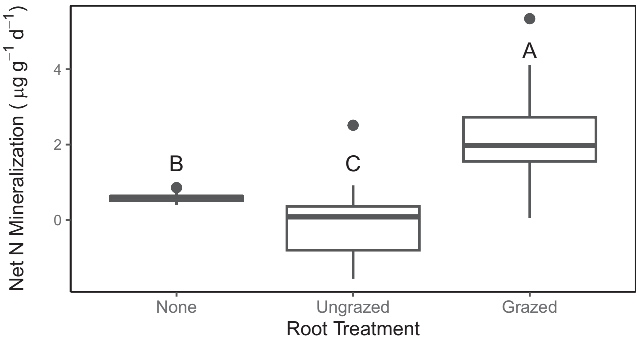

(c) Non−Root N−Mineralization

FIGURE 4 Net nitrogen (N) mineralization over the 11-week decomposition experiment. Nitrogen mineralization is partitioned into (a) nitrogen mineralized from all sources (i.e. roots + faeces + soil), (b) nitrogen mineralized from non-root sources (i.e., soil or soil + faeces depending on treatment combination), and (c) nitrogen mineralized from roots. For each box and whisker plot, the heavy middle line is the median, the hinges are the first and third quartiles, and the whiskers represent the maximum and minimum values no further 1.5 times the interquartile range from the hinges.

of root C and N loss during decomposition and the size and decay rate of the fast-cycling C pool. Overall, we found that grazing increased CO_2-C efflux due to changes in soil environmental conditions and root chemical traits, with grazing-induced increases in root N playing a central role.

Despite chemical traits in grazed roots reflecting a shift towards a resource acquisition strategy, we did not observe any differences in root morphology or root exudation rates that are typical of resource acquisition strategies (e.g. high specific root length, high exudation rates; Wen et al., 2022; Williams et al., 2022). This suggests that grazed *C. subspathacea* increases soil resource acquisition without altering root morphology or exudation rates. There are several potential explanations for a change in chemical traits without a concomitant shift in morphology. First, root morphological traits are more phylogenetically conserved than chemical traits (Wang et al., 2024), so morphological traits may be less plastic than chemical traits in response to grazing. Another potential explanation is that higher goose faeces deposition in grazed areas increases nutrient availability to roots without requiring changes to root morphology or exudation. Indeed, previous research in the Y-K Delta has shown soil N availability and root growth are positively related to goose faeces deposition (Beard et al., 2023). Another possibility is that grazed *C. subspathacea* increases resource acquisition by increasing investment in mycorrhizal associations, which is an alternative mechanism to morphological shifts (Spitzer et al., 2021; Van Der Heijden et al., 2015).

There were no differences in root biomass between grazed and ungrazed *C. subspathacea*. A previous study conducted in the Y-K Delta showed that there were not strong differences in root production between grazed and ungrazed *C. subspathacea* under typical grazing conditions (Choi et al., 2019). However, that study found that an atypical early onset of seasonal grazing can strongly decrease root production, and the exclusion of grazers from previously grazed swards led to strong—but short-term—increases in root production. These conflicting results suggest that under consistent grazing, *C. subspathacea* can maintain its root biomass (this study, Choi et al., 2019), but that the timing and past history of grazing can influence root production dynamics (Choi et al., 2019). The fact that both Choi et al. (2019) and our study found little difference between root biomass in grazed and ungrazed *C. subspathacea* under normal grazing conditions is somewhat surprising because, compared with grazing lawns, the above-ground biomass of *C. subspathacea* in ungrazed meadows is ~five times greater and CO_2 uptake is ~two times greater (Kelsey et al., 2016). Thus, grazed *C. subspathacea* appears to maintain investment in belowground biomass despite greater C limitation resulting from lower photosynthesis. One apparent mechanism by which *C. subspathacea* could achieve this is by decreasing the C cost of root biomass, as has been found for other plant species that exhibit a resource acquisition strategy (de la Riva et al., 2021). Our data show some support for this mechanism as roots from grazing lawns have greater concentrations of cellulose and ash, which cost less C to synthesize or obtain compared with other tissue components (Martínez et al., 2002).

The grazing-induced shift in root traits towards a resource acquisition strategy likely increases C-cycling rates in multiple ways. Plant roots associated with a resource acquisition strategy typically exhibit faster turnover times and greater specific respiration compared with resource conservation strategists, an effect that is driven by lower root C:N (McCormack et al., 2012; Roumet et al., 2016). Our results corroborate this prediction as we found that grazing leads to increased C fluxes during root decomposition. Over the decomposition period, cumulative CO_2-C efflux, the size of the fast-cycling C pool, and root C loss tended to be higher in grazed root treatments than in ungrazed root treatments.

The larger C fluxes in the grazed root treatments were accompanied by negative net root N-mineralization, indicating a flux of N to decomposing roots. This flow of N to grazed roots likely derives from the low initial C:N ratios of grazed roots (relative to ungrazed roots) promoting decomposer communities that have high N requirements and must 'mine' N from the surrounding soil to satisfy demand (Chen et al., 2014; Hicks et al., 2020). This is further supported by the patterns in non-root net N-mineralization. Here, the grazed root microcosms exhibited positive non-root net N-mineralization, which indicates that the microbial communities colonizing grazed root necromass imported N from the surrounding soil. This 'N-mining' effect—which refers to the decomposition of organic matter solely to obtain N—could explain higher CO_2-C efflux in the grazed root treatments because N-mining leads to excess C being respired to maintain stoichiometric balance (Averill & Waring, 2018; Manzoni et al., 2012). Ultimately, grazed root decomposition increased the amount of N mineralized from the surrounding soil matrix, but because most of this N was then immobilized by the root decomposers, there was actually an overall decrease in the net N-mineralization rate in the system.

In addition to root chemistry effects, we found that grazing-induced shifts to the soil environment influenced C-cycling. The high-temperature treatment—which is characteristic of soil temperatures in grazing lawns during the growing season—substantially increased the cumulative CO_2-C efflux and the decay rate constant, indicating faster C-cycling rates in grazing lawns. The high-temperature treatment also increased the size of the fast-cycling C pool, but only when no roots were added. The positive impact of temperature on the decay rate constant is likely due to a positive relationship between temperature and enzyme activity rates (Conant et al., 2011; German et al., 2012). The positive effect of temperature on the size of the fast-cycling C pool could be due to a number of mechanisms, including shifts in microbial community composition, negative impacts on microbial C use efficiency, or increased desorption of C from soil minerals (Conant et al., 2011; Hale et al., 2019; Li et al., 2019; Li, Yang, et al., 2021).

The effect of goose faeces additions on C-cycling parameters was more complex. Although faeces had temperature-dependent effects on CO_2-C efflux and the size of the fast-cycling C pool in the no-root and ungrazed root treatments, faeces did not influence C parameters in grazed root treatments. These results indicate that while faeces and grazed roots both had positive effects on the same C-cycling parameters, these effects were not additive. The fact that the positive effects of faeces on C-cycling rates were limited to soils with ungrazed roots lends further support to the notion that N availability plays a central role in dictating elemental cycling in the system. Goose faeces is rich in N (Saunders et al., 2023), so faeces additions could have alleviated N limitations imposed by the high C:N ratios of the ungrazed roots. In contrast, faeces additions may have had limited effects in the grazed root treatments because grazed roots already have low C:N (relative to ungrazed roots), and those soils therefore may have been less N limited. Previous field research supports our findings, demonstrating that adding or removing faeces from natural grazing lawns had no effect on ecosystem respiration (Beard et al., 2023). However, that study did show that faeces removal can increase net ecosystem exchange by decreasing gross primary production.

Overall, our study shows that grazing impacts both C- and N-cycling in low Arctic wetlands by shifting root chemical traits towards a resource acquisition strategy and by affecting soil conditions. Previous studies have found that C-efflux from grazing lawn soils can equal or exceed that of ungrazed meadow soils (Foley et al., 2022; Kelsey et al., 2016), despite grazing lawns exhibiting substantially lower above-ground biomass and CO_2 uptake compared with ungrazed meadows (Kelsey et al., 2016). While these unexpectedly high C emissions can be partially explained by differences in soil temperatures, goose faeces and leaf litter chemistry between the two habitats (Beard et al., 2023; Foley et al., 2022; Saunders et al., 2023), our study is the first to show that root traits also contribute to these patterns. Specifically, grazed roots lead to faster C-cycling rates during decomposition, likely due to shifts in root chemical traits increasing root quality and promoting N-mining. This accelerated decomposition may be exacerbated by the large below-ground source of root-derived organic matter available for decomposition, as evidenced by our finding that root biomass and root exudation do not decrease under grazing. Soil C-cycling rates could be even further enhanced if the shift towards a resource acquisition strategy is accompanied by higher respiration from living roots, as others have found (McCormack et al., 2012; Roumet et al., 2016).

In contrast to the clear and consistent positive effect of grazed roots on soil C-cycling rates, grazed roots differentially impacted various aspects of the soil N-cycle, with likely consequences for ecosystem function. Although the decomposition of grazed roots led to an increase in the rate of N mineralized from the soil matrix, most of this N was immobilized by the microbes decomposing the root tissue, leading to a net decrease in the amount of free inorganic N available in soil compared with ungrazed roots. Over the short term, the lower inorganic N in soils with grazed roots compared with ungrazed roots could limit the amount of N that is readily available for plant re-uptake following root turnover. However, over the long term, the greater N immobilization by decomposers could contribute to larger N stocks because immobilized N is less susceptible to leaching losses and can be remineralized for plant uptake later (Li, Zeng, et al., 2021). Overall, our results show that grazing impacts elemental cycling in ecosystems not only through direct effects like biomass removal and faeces deposition, but also indirectly by altering the root ecological strategies of the plants being grazed. Understanding the feedbacks between grazing activity, plant leaf and root ecological strategies and elemental cycling is therefore an important component of understanding how ecosystem functions will respond to global changes in herbivore populations.

AUTHOR CONTRIBUTIONS

Jaron Adkins, Emily A. Chavez and Trisha B. Atwood conceived and designed the experiments. Emily A. Chavez, Ryan T. Choi, Lindsay Miller and Taylor Saunders collected data. Emily A. Chavez and Jaron Adkins analysed the data and wrote initial manuscript drafts. All authors contributed to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to disclose.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70028.

DATA AVAILABILITY STATEMENT

Data is available from the NSF Arctic Data Center: https://doi.org/10.18739/A2P55DJ5J (Chavez et al., 2024).

STATEMENT ON INCLUSION

Our study was conducted by scientists based in the country where the research was performed. Our study was conducted on the historical territory of the Cup'ik and Yup'ik peoples. Our research sites were selected under advisement from the Chevak Traditional Council and the residents of Chevak, AK.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Root mass by 10 cm depth increments for grazed and ungrazed *Carex subspathacea* in 3 cm diameter soil cores collected to 50 cm depth.

Figure S2. Root length within each diameter size class for grazed and ungrazed *Carex subspathacea* in 3 cm diameter soil cores collected to 50 cm depth.

Figure S3. Root length within each diameter size class for grazed and ungrazed *Carex subspathacea* at 10 cm depth increments.

Figure S4. Specific root length by 10 cm depth increments for grazed and ungrazed *Carex subspathacea* in 3 cm diameter soil cores collected to 50 cm depth.

Figure S5. Root tissue density by 10 cm depth increments for grazed and ungrazed *Carex subspathacea* in 3 cm diameter soil cores collected to 50 cm depth.

Figure S6. Root specific surface area by 10 cm depth increments for grazed and ungrazed *Carex subspathacea* in 3 cm diameter soil cores collected to 50 cm depth.

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