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The Effects of Aboveground Herbivory on Root Traits and Root Decomposition

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THE EFFECTS OF ABOVEGROUND HERBIVORY ON ROOT TRAITS AND ROOT DECOMPOSITION

by

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ABSTRACT

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and Root Decomposition

by

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Utah State University, 2024

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Soil represents the largest pool of terrestrial carbon (C) on earth, and C storage is largely determined by the interaction of biotic and abiotic factors that influence the rate of soil respiration. In Alaska's Yukon-Kuskokwim (YK) Delta, it is well documented that goose herbivory in *Carex subspathacea* meadows modify soil and vegetative characteristics, resulting in the alteration of soil respiration rates. Although we know that goose herbivory leads to the alteration of C outputs via soil respiration, we know little about how goose herbivory alters C inputs, especially concerning root C, which is a primary contributor to soil C. These knowledge gaps limit our ability to understand C cycling processes, such as root litter decomposition, which influences soil respiration in the YK Delta.

To understand how aboveground herbivory affects root C and soil respiration, we collected *C. subspathacea* root samples from either grazed or ungrazed habitats within the YK Delta to examine if aboveground herbivory creates intraspecific differences in their morphological (specific root length, root volume, and root surface area), chemical

(carbon: nitrogen ratio, %C, %N, acid detergent fiber, and phosphorus), and physiological traits (root exudates). Additionally, we designed a laboratory experiment to assess how aboveground herbivory affects root decomposition rates and C loss using weekly CO_2 efflux as a proxy for the decomposition rate. Within this experiment, we manipulated root treatment, feces deposition, and temperature to simulate the effects of aboveground herbivory on root litter and soil.

In this study, we demonstrated that aboveground herbivory did not alter root morphological traits but did affect root chemical and physiological traits. Specifically, grazing led to lower root C:N, higher %N content, higher %C, and lower %ADF (a measurement of cellulose and lignin). Although we did not see differences in root morphology, differences in root chemistry and exudation point to more labile and easily decomposable root C in roots collected from the grazing lawns. Furthermore, our experiment confirmed that aboveground herbivory alters the rate of root decomposition and leads to increased C loss. Our study demonstrates that aboveground herbivory alters root chemical expression, leading to effects on soil respiration and C loss.

(91 pages)

PUBLIC ABSTRACT

The Effects of Aboveground Herbivory on Root Traits and Root Decomposition

Emily Ann Chavez

Soil holds more carbon (C) than the Earth's atmosphere and vegetation combined. Soil loses carbon through soil respiration and releases CO_2 from the soil. The soil respiration rate can vary based on the chemistry of the plant litter inputs and physical factors, such as soil temperature and nutrient content. In Alaska's Yukon-Kuskokwim (YK) Delta, grazing by geese affects the chemistry of plants and the soil's physical qualities, thus altering the rate of soil respiration. Although we know that goose herbivory leads to changes in the rate of soil respiration, we know very little about how goose herbivory affects the inputs of plant roots. Roots are an important factor in soil respiration because roots contribute a substantial amount of C to the soil. This knowledge gap limits our ability to truly understand C cycling processes like root decomposition, which may influence soil respiration in the YK Delta.

To better understand how goose herbivory affects root C and soil respiration, we collected *C. subspathacea* root samples, a common sedge in the YK Delta, from either grazed or ungrazed habitats to understand if goose herbivory creates intraspecific differences in their morphological (specific root length, root volume and root surface area), chemical (carbon: nitrogen ratio, %C, %nitrogen, %phosphorus and ADF), and physiological traits (root exudates). Additionally, we created a laboratory experiment to assess how goose herbivory affects root decomposition and C loss using weekly CO_2

efflux as a proxy for the decomposition rate. Within this experiment, we manipulated root treatment by using roots that were either exposed to aboveground grazing or not, feces deposition (present/absent), and temperature to simulate the range of effects aboveground herbivory has on plant litter and soil physicochemical properties.

In this study, we demonstrated that aboveground herbivory did not alter root morphology but affected root chemistry and exudation. Specifically, aboveground grazing led to lower C:N, higher %N, lower %C, %ADF (a measurement of cellulose and lignin), and a greater rate of root exudation. Although we did not see differences in root morphology, the differences in root chemistry and exudation are often associated with faster plant decomposition. Our root decomposition experiment confirmed that aboveground herbivory alters the rate of root decomposition and leads to increased C loss directly by altering indirectly by increasing soil temperatures and directly by altering root inputs. Our study demonstrates that aboveground herbivory can significantly alter root trait expression, which may increase the loss of C from the soil.

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Emily Ann Chavez

CONTENTS

Page

LIST OF TABLES

Page

LIST OF FIGURES

Page

INTRODUCTION

Grazing impacts greenhouse gas dynamics of ecosystems by influencing vegetation and soil characteristics (He et al., 2020; Schmitz et al., 2018; Sjögersten et al., 2012). In most cases, studies have focused on the effects of grazers on aboveground vegetation traits and how shifts in those traits impact carbon (C) cycling (Liu et al., 2016). For example, several studies have suggested that grazers impact carbon dioxide (CO_2) plant uptake through changes in leaf area and aboveground biomass (Cahoon et al., 2012; Leffler et al., 2019; Metcalfe & Olofsson, 2015). However, roots disproportionately impact soil C cycling, especially in systems where most C is stored belowground (Bardgett et al., 2014; Rasse et al., 2005). Furthermore, studies on the effects of environmental variables on root traits suggest that grazing could influence roots via impacts on plant nutrient allocation (Bardgett et al., 1998; Bardgett & Wardle, 2003), soil physicochemical characteristics (Lai & Kumar, 2020), and plant community composition (Li et al., 2017). Though many studies have explored how aboveground grazing affects root biomass (Bardgett et al., 1998; Sjögersten et al., 2012; Wilson et al., 2018), few studies have investigated how grazing affects other root traits and their subsequent impacts on soil processes (Heinze, 2020; Paterson et al., 2005; Thorne & Frank, 2009). To address these knowledge gaps, this study aims to (1) examine the effect of aboveground herbivory on intraspecific root traits and (2) assess how aboveground herbivory affects the rate of root decomposition and C loss.

Root Traits

The primary functions of roots are to provide structural support for plants and to take up growth-limiting resources such as nutrients and water. However, plants must deal with a diversity of conditions across space and time that constrain the availability of resources and alter the surrounding environment. Thus, root traits can be highly plastic within and across plant species to deal with this variation (Hodge, 2004; Kumar et al., 2019).

Root traits can be broken into five categories: architectural, morphological, physiological, chemical, and biological (Bardgett et al., 2014; McCormack et al., 2017). Architectural traits refer to the spatial configuration and describe the shape and structure of the root system of an individual plant (Freschet et al., 2021; Hodge et al., 2009), while morphological traits provide information on the biomass invested into the root shape (Freschet et al., 2021). Morphological traits, such as root diameter and specific root length (SRL), can influence chemical traits because finer roots tend to have a different chemistry than coarse roots (Zhang & Wang, 2015). Chemical traits of roots include carbon: nitrogen ratios (C:N), nitrogen (N) concentrations, and lignin content, all of which are important factors that influence the rate of root decomposition. Physiological traits include root exudation, nutrient uptake, and root respiration and are closely associated with biotic traits (Bais et al., 2006). Finally, biotic traits involve direct interactions with soil biota, such as mycorrhizae associations (Bardgett et al., 2014; McCormack et al., 2017), and are highly influenced by the quality and quantity of root exudates (McCormack et al., 2017).

Root traits can vary among individuals of the same species. Intraspecific differences in root traits result from spatial heterogeneity in the physicochemical properties of the soil and are affected by above- and below-ground pressures (Ettema, 2002). Variations in soil properties (e.g., temperature, soil moisture, soil bulk density, and nutrient availability) can occur on scales from millimeters to entire landscapes, leading to unique micro-and macro environments that can result in intraspecific variations in architectural, morphological, chemical, physiological, and biotic root traits (Ettema, 2002; Hodge, 2004; Weemstra et al., 2021). High levels of intraspecific diversity can occur because root characteristics are generally highly plastic, allowing them to adapt to variations in local conditions (Hodge, 2004). Table 1 summarizes the general responses of various root traits to individual soil physicochemical properties. While there is variation in the directionality of some responses, the research demonstrates that root traits respond to their surrounding environment.

Root Trait Influences on Soil Processes and Biogeochemical Cycling

Many root traits influence critical soil processes and ecosystem functions (Bardgett et al., 2014; Rasse et al., 2005; Schmidt et al., 2011). For example, all root trait categories have individual traits that can influence soil C inputs and affect decomposition rates (Bardgett et al., 2014; Funk et al., 2017; Gill et al., 1999; Hodge et al., 2009). Furthermore, biotic traits, specifically mycorrhizae associations, strongly increase soil organic matter (SOM) stabilization in the short, mid, and long term (Frey, 2019; Poirier et al., 2018), while morphological, architectural, physiological, and chemical traits vary in their impact on SOM stability and persistence (Poirier et al., 2018).

Architectural traits, such as branching density and rooting depth, can influence the location, magnitude, and rate of C inputs into the soil (Figure 1), (Bardgett et al., 2014). For example, Gill et al. (1999) found that root decomposition rates decline with soil depth, suggesting that roots deposited deeper within the soil profile will likely have slower root decomposition rates. Furthermore, the root tip is typically the site of root exudation (Badri & Vivanco, 2009), which is a significant source of C inputs to the soil (de Kroon & Visser, 2003; Hinsinger et al., 2009). Thus, variations in rooting depth can affect the location of root exudation and the amount of soil volume exposed to exudation. In turn, rooting depth can change the extent of the rhizosphere in the soil profile, where the microbial community is most active, and influence how much organic matter is available for decomposition.

Morphological traits, such as SRL and root diameter, affect C cycle processes by influencing C inputs and decomposition rates. Plants with a higher SRL tend to have a higher fine: coarse root ratio and a low average root diameter (Zhang & Wang, 2015). Fine roots have a shorter lifespan compared to coarse roots (Gill & Jackson, 2000; King et al., 2002) and, therefore, have a higher root turnover rate than coarse roots, which is the creation, dieback, and decay of a root (Lukac, 2012; Pregitzer et al., 2007). Thus, plants with higher SRL will have a higher rate of C input into the soil profile than plants with a lower SRL (King et al., 2002; Lukac, 2012). Additionally, because high SRL is tightly correlated with fine roots, plants with high SRL generally have more chemically labile roots and decompose faster than coarse roots, which tend to be more recalcitrant (Graaff et al., 2013; Silver & Miya, 2001).

Plant chemistry is a major driver of soil organic matter decomposition rates, and as a result, root chemical traits can significantly affect nutrient cycling. Regarding C cycling, root chemical traits of significance are C:N, and lignin and cellulose content (a.k.a., acid detergent fiber) (Alexander, 1977; Silver & Miya, 2001; Yue et al., 2016; Zhang & Wang, 2015). For example, Silver and Miya (2001) found that fine roots typically have low C:N and are correlated with faster decomposition when compared to coarse roots. Plants with a lower C:N ratio are often considered more labile, and an influx of labile plant matter can create hotspots of enhanced microbial activity (Kuzyakov & Blagodatskaya, 2015). These microbial hotspots can prime soil in a way that helps microbes break down previously unavailable soil organic matter (Kuzyakov and Blagodatskaya, 2015), thereby increasing CO_2 efflux (Poirier et al., 2018).

Physiological traits, specifically root exudates, are a significant source of C inputs to the soil profile and represent a high C cost to plants (Badri & Vivanco, 2009; Bardgett et al., 2014). Plants invest a significant portion of their fixed C to root exudation. For example, some seedlings can lose 30-40% of their fixed C to exudates (Whipps, 1990). Despite the substantial input of C to the soil via root exudation, increases in net C storage because of increased root exudation are context dependent (Liang et al., 2018). Root exudates are composed primarily of low-molecular-weight compounds, such as sugars and amino acids (Badri and Vivanco, 2009), that are rapidly consumed by the soil microbial community (Bais et al., 2006; Bardgett et al., 2014). The increase in labile C from root exudates can also create a priming effect that can increase the decomposition of previously stable soil organic matter (Bengtson et al., 2012; Kuzyakov & Blagodatskaya, 2015).

Biotic traits such as mycorrhizae associations increase soil C inputs and are also known to affect decomposition rates (Bardgett et al., 2014). For example, mycorrhizae colonization of roots increases soil C inputs by assimilating fixed plant C into fungal biomass (Clemmensen et al., 2013) and distributing that C throughout the soil profile. Additionally, mycorrhizae exudates and fungal necromass are considered significant inputs of soil C (Frey, 2019; Toljander et al., 2007). Moreover, mycorrhizae can entangle themselves with soil particles to physically protect the C from decomposition, thus increasing stable SOM (Frey, 2019). Although living mycorrhizal biomass, mycorrhizae exudates, and fungal necromass initially increase soil C, each factor can lead to SOM destabilization by providing labile C to the external microbial community and by enhancing the breakdown of organic matter through mycorrhizae exudates (Bardgett et al., 2014; Frey, 2019; Talbot et al., 2008).

Herbivore Impacts on Root Traits and Soil Physicochemical Properties

Aboveground herbivores can directly affect root traits, and thus the ecosystem processes they support, by altering nutrient allocation and trait expression within plants via grazing, trampling, and defecation (Bardgett et al., 1998; Bardgett & Wardle, 2003). Studies have shown that aboveground herbivory can affect morphological root traits, with grazing typically increasing SRL and decreasing root diameter (Heinze, 2020; Thorne & Frank, 2009). These changes likely occur because aboveground herbivory reduces photosynthetic rates (Liu et al., 2016), decreasing C flow to roots (Bardgett et al., 1998). In this scenario, based on the C limitation hypothesis, plants are more likely to invest in building fine roots than building coarse roots because fine roots require less C to develop (Whipps, 1990; Zhang & Wang, 2015). Though not as well studied, the changes to root

morphological traits suggest that aboveground herbivory could also alter chemical traits. Bai et al. (2012), demonstrated that aboveground herbivory generally decreases C:N and C:P ratios, though the effects varied by ecosystem. Furthermore, when aboveground herbivory changes C allocation within a plant, root exudation and the quality of root exudates may increase as a mechanism to stimulate the microbial community to increase nutrient access to adjust to the loss of biomass (Bardgett et al., 1998; Bokhari & Singh, 1974; Hamilton et al., 2008). Because root exudation is tightly connected to biotic traits, alterations to root exudation can affect mycorrhizae associations. In a meta-analysis, Barto & Rillig (2010) found that aboveground herbivory decreased rates of mycorrhizae root colonization.

Herbivory can also indirectly affect root traits through changes in soil physicochemical properties. For example, herbivores affect soil physicochemical properties by grazing vegetation, trampling, defecation, and urination (Braden et al., 2021; Lai & Kumar, 2020). Across many systems and herbivore taxa, these behaviors by herbivores have been shown to influence important soil characteristics (e.g., soil temperature, soil moisture, soil bulk density, and soil nutrient content) that affect many root traits (Table 1).

Grazing or defoliation by aboveground herbivores affects soil temperature, soil moisture, and soil nutrient content, all of which have been shown to strongly influence C processing. Aboveground grazing reduces shading on the soil surface via defoliation and litter removal. The reduction in shading generally increases soil temperatures by exposing the soil surface to increased solar radiation (Kelsey et al., 2016; Schmitz et al., 2018; van der Wal et al., 2001). Defoliation also increases soil evaporation, decreasing soil moisture

(Deutsch et al., 2010; Greenwood & McKenzie, 2001). However, in some cases, grazing decreases evapotranspiration, which can decrease water loss from the soil, thus increasing soil water content (Greenwood & McKenzie, 2001). Furthermore, removing aboveground biomass, and in some cases belowground biomass, by grazing decreases the amount of vegetative litter that enters the soil, thus decreasing the supply of C and other nutrients to the soil (Lai & Kumar, 2020; Schlesinger, 1991).

Trampling by animals affects the physical properties of the soil and vegetation. Trampling directly increases soil bulk density (Evans, 1998; Leroux et al., 2020) by creating stress on the soil surface, decreasing soil pore space, and increasing soil compaction (Greenwood & McKenzie, 2001; Tuomi et al., 2021). The loss of pore space in compacted soil results in a lower water-holding capacity (Greenwood & McKenzie, 2001) and an eventual decline in soil moisture (Lai & Kumar, 2020; Zhao et al., 2011). Additionally, the mechanical damage caused by trampling can damage aboveground biomass, decreasing plant coverage and increasing soil temperature, though effects vary by trampling intensity (Olofsson, 2009; Tuomi et al., 2021). Furthermore, Olofsson 2009, found that trampling increases N mineralization (Guntiñas et al., 2012), which likely occurs because of changes in soil temperature and moisture from trampling. Thus, soil N availability may increase when trampling occurs on a landscape.

Defecation and urination by herbivores can be a substantial source of nutrient input into the soil profile, affecting total soil nutrient content and availability (Beard et al., 2023; Frost & Hunter, 2007; McKendrick et al., 1980). Animal excrements are typically N-rich and increase N availability where deposited (Beard et al., 2023; Frost & Hunter, 2007; McKendrigk et al., 1980), which can be a limited resource in some

ecosystems (Vitousek et al., 1997). Additionally, animal excrements generally decrease total soil phosphorus while increasing available soil phosphorus (McKendrigk et al., 1980). The changes to soil nutrients from animal excrements are not always homogeneous in a landscape where herbivores are present (Liu et al., 2016; McKendrick et al., 1980). Generally, the site of waste expulsion will have higher soil nutrient content than the surrounding area (McKendrigk et al., 1980), creating spatial variation in nutrients across a landscape (Liu et al., 2016).

Study Objectives

Although interest in root traits is increasing among ecologists, soil scientists, and biogeochemists, significant knowledge gaps need to be addressed. We currently have a poor understanding of the linkage among aboveground herbivory, root traits, and C cycling (Bardgett et al., 1998, 2014; Bardgett & Wardle, 2003). Furthermore, most studies on root traits are concentrated in temperate regions, limiting our understanding of root traits in other systems (Iversen & McCormack, 2021). My study aims to address these knowledge gaps by (1) documenting root traits of *Carex subspathacea* in the sub-Artic region of Alaska's Yukon-Kuskokwim (YK) Delta, where there are currently no documented studies on root traits (Iversen & McCormack, 2021), (2) examining the effect of aboveground herbivory on intraspecific root traits, and (3) assessing how aboveground herbivory affects root decomposition and C loss.

Study Background

Soil represents the largest pool of terrestrial carbon (C) on earth (Raich & Schlesinger, 1992; Smith, 2004). Currently, it is estimated that ecosystem uptake of CO_2

via plant photosynthesis equals the amount respired by soil during processes such as decomposition (Parmesan et al., 2023), creating net zero CO_2 emission from the soil. However, climate change may impact ecosystem processes and interactions, influencing soil respiration rates. Even small changes to these processes and interactions could create significant imbalances in soil CO_2 emissions, affecting global C budgets and reinforcing the negative effects of climate change.

The Arctic and sub-Arctic are particularly vulnerable to the effects of climate change. The Arctic and sub-Arctic are warming faster than any other biome (Meredith et al., 2019), a trend likely to influence the global C cycle for two reasons. First, the Arctic and sub-Arctic hold roughly 40% of the world's available soil C (McGuire et al., 2009). Warming will likely speed up the decomposition rate of previously stable soil C, threatening to turn this former C sink into a significant C source (McGuire et al., 2009). Second, warming is leading to shifts in the abundance and distribution of herbivore populations (Koltz et al., 2022), which have been well-documented to affect C cycling processes in the Arctic and sub-Arctic regions (Beard et al., 2023; Kelsey et al., 2016; Leroux et al., 2020; Metcalfe & Olofsson, 2015; van der Wal et al., 2001).

Along the coastal wetlands of Alaska's Yukon-Kuskokwim (YK) Delta, the grazing behavior of migratory waterfowl has been observed to influence the plant community, soil physicochemical characteristics, and ecosystem C exchange. During the summer growing season in the YK Delta, extensive grazing by Pacific Black Brant Geese (*Branta bernicla*) and Cackling Geese (*Branta hutchinsii)* creates patches of “grazing lawns” within otherwise ungrazed wet sedge meadows. Both the meadow habitats and the grazing lawns are dominated by *Carex subspathacea* (Jorgenson & Ely, 2001; Kincheloe

& Stehn, 1991). However, due to grazing, *C. subspathacea* within the grazing lawn is shorter, with an average height of 1.5 cm, and expresses a floret leaf structure. Conversely, in the meadow, *C. subspathacea* reaches an average height of 15 cm, with 3-5 long leaves that are broad at the base and narrow at the tips (Kelsey et al., 2016). Additionally, grazing lawns exhibit higher soil temperatures, soil moisture, and lower gross primary production than adjacent ungrazed meadows (Kelsey et al., 2016).

However, studies have indicated that the abundance of geese in the YK Delta is changing in response to climate change and other factors (Pacific Flyway Council, 2016; Sedinger et al., 2019). These investigations have revealed a significant decline in Black Brant while Cackling Geese populations have been increasing. Despite the increase in Cackling Geese, studies have shown a decline in grazing lawns which has resulted in an overall decline in grazing lawns (Pacific Flyway Council, 2016; Sedinger et al., 2019; Uher-Koch et al., 2019).

Despite the extensive work done in the YK Delta to understand herbivore effects on C cycling, the effects of goose herbivory on root traits and root decomposition have been largely neglected. Roots are important in C cycling because roots make up the largest contribution to the soil C pool (Rasse et al., 2005). Growing evidence demonstrates that root traits affect C cycling processes (Dornbush et al., 2002; Li et al., 2022; Silver & Miya, 2001; Zhang & Wang, 2015) and that changes to the soil physicochemical properties caused by herbivores can alter root traits (Table 1; Bardgett et al., 2014).

Root traits alter C cycling processes by affecting C inputs' location, chemistry, and availability (Bardgett et al., 1998; Silver & Miya, 2001). How plants express traits

such as specific root length (SRL), root diameter, root C: N ratios (C:N), and root exudates can determine the stability of root C in the soil. For example, plants with a high SRL tend to have a low root diameter and are more labile, thus, decomposing faster than plants with low SRL and coarse roots (Zhang & Wang, 2015). Furthermore, root exudates can contain significant amounts of labile C, stimulating soil microbial communities and decomposition (Girkin et al., 2018).

To deal with small scale differences in the soil physicochemical environments, roots can quickly respond to changes in the soil's environment and are often highly plastic (Hodge, 2004; Karlova et al., 2021; Kumar et al., 2019). As a result, root traits may respond to the additional effects that aboveground herbivory can have on factors such as soil temperature, nutrient content, moisture, and bulk density (Liu et al., 2016; McKendrick et al., 1980) (Table 1). For example, temperature may decrease root diameter and increase C:N, while nutrient additions may increase root diameter and may increase root exudation (Defrenne et al., 2019; Uselman et al., 2000; Weemstra et al., 2021). In the YK Delta, goose herbivory increases soil temperature, moisture, and bulk density (Kelsey et al., 2016) and decreases total soil N (Foley et al., 2022). Consequently, herbivory may lead to intraspecific variations in root traits and, by extension, differences in below-ground carbon processes between ungrazed *C. subspathacea* meadows and grazing lawns.

Our understanding of the connection between aboveground herbivory, root traits, and their impact on below-ground processes affecting C cycling remains limited (Bardgett et al., 1998, 2014; Bardgett & Wardle, 2003). Moreover, research on root traits has predominantly focused on temperate regions, leaving gaps in our knowledge

regarding root traits in other regions (Iversen & McCormack, 2021). To address these knowledge gaps, my study aims to (1) examine the effect of aboveground herbivory on intraspecific root traits of *C. subspathacea* collected from coastal wetlands in the YK Delta, (2) assess whether the effects of aboveground herbivory on root traits and soil properties influence *C. subspathacea* root decomposition, as measured by CO_2 soil efflux, and C loss.

To address our first objective, we compared root traits of *C. subspathacea* plants collected from natural grazing lawns and ungrazed meadows in YK Delta. We hypothesized that *C. subspathacea* collected from grazing lawns would have higher SRL, volume, and surface area; lower root C:N, higher %N, and higher %C; and greater rates of root exudation than plants collected from ungrazed meadows. To address our second objective, we conducted a laboratory experiment to test whether *C. subspathacea* roots collected from grazing lawns and ungrazed meadows vary in decomposition rates and whether alteration to the soil temperature and nutrient additions from goose feces further affected decomposition. We predicted that the higher quality roots in grazing lawns, as indicated by lower C:N, higher %N, and lower percent acid detergent fiber (ADF), would decompose faster and have greater C loss than ungrazed *C. subspathacea*. Additionally, we predicted that grazing-mediated increases in soil temperatures and nutrient availability from goose feces would further increase decomposition rates and C loss.

METHODS

Study Site

For the natural root trait study, we collected root samples from *C. subspathacea* communities growing in the YK River Delta along the Kashunuk and Tutakoke Rivers in western Alaska (Permit # 21-01). For the decomposition study, roots were collected along the Kashunuk River. Both rivers are brackish tidal rivers 2016). The town of Bethel, which is 170 km east of our field location and is the site of the nearest long-term climate dataset, has a mean summer temperature of ~12.2 ℃ and a mean annual precipitation of 449 mm (from both snow and rainfall) (Pelecki et al. 2021). The soils in the grazing lawns and the ungrazed meadows are predominantly fine silts and sandy loams from annual sediment deposition (Foley et al., 2022; Jorgenson, 2000).

Throughout the YK Delta, herbivory from Pacific Black Brant Geese (*Branta bernicla*) and Cackling Geese (*Branta hutchinsii)* create grazing lawns on pond margins (Mickelson, 1975; Person et al., 1998) that are adjacent to ungrazed *C. subspathacea* meadows. The grazing lawns consist of short-statured *C. subspathacea* with a height of 1.3± 0.04 cm (± s.e.) and exhibit higher foliar %N than ungrazed meadows. Additionally, grazing lawns lack a surface litter layer and exhibit higher soil temperatures (~13^{o} C) than meadows (~10^{o} C) (Kelsey et al., 2016; Person et al., 1998). The ungrazed meadows are also dominated by *C. subspathacea* (Kincheloe & Stehn, 1991; Person & Ruess, 2003; Ruess et al., 2019), however, the meadows are characterized by dense patches of *C. subspathacea* with a live stem height of 11.7 ± 0.12 cm at peak growing season (personal observation). The meadows also have a thick layer of senesced and decomposing litter biomass and cooler soil temperatures by ~3^{o} C (Kelsey et al., 2016; Person et al., 1998).

Natural Root Trait Survey

Root Collection

To assess the natural root traits of *C. subspathacea* from grazing lawns and ungrazed meadows within the YK Delta, we collected 3 cm diameter soil cores to a depth of 50 cm from ten sites along the Kashunuk River and Tutakoke River in July 2022. The sites were chosen based on their presence and access to grazing lawns and meadows. Three paired samples from grazing lawns and ungrazed meadows were taken at each site for a total of 60 cores (30 per habitat type). Paired samples were collected within 3 m of each other, and all samples were collected within 1 m to 2 m from the habitat margin. In the field, we separated each soil sample into five depth subsections (0-10 cm, 10-20 cm, 20-30 cm, 30-40 cm, and 40-50 cm) to assess if SRL, root volume, and root surface area varied by depth. Soil was removed from the roots by placing subsamples onto a 250 µm mesh sieve, submerging the sieve in water, and gently shaking the sections until most of the soil was removed. The roots were then rinsed with a squirt bottle to remove any remaining soil. Root samples were oven-dried at ~65 °C and transported back to the lab at Utah State University for further analyses.

In the laboratory, we removed residual soil or foreign organic matter from the root sections by stacking three different sieves (1 mm, 0.5 mm, and 0.25 mm) and rinsing the roots with DI water. All samples were dried at 60 °C to a constant weight and stored at ambient temperature until processed.

To assess DOC concentrations in root exudates, we collected a total of 18 (nine for each habitat type) 4 cm x 4 cm x 10 cm soil plugs from grazing lawns and ungrazed meadows from five sites along the Kashunuk River in August 2022. The belowground

portions of the samples were wrapped and secured in a plastic bag, and the aboveground biomass was left uncovered to allow for gas exchange. Samples were stored on ice and transported back to the lab at Utah State University.

Root Morphology

From the 60 samples collected from the Kashunuk and Tutakoke Basins, we randomly selected 12 samples for morphological analysis (six per habitat type). We used WinRhizo software (RHIZO 2019a, Regent Instruments, Inc., Quebec), a typical software used for root trait analysis, to determine the total length, surface area, and root volume of each sample section. Using root length, SRL was calculated as follows:

$$SRL\ m/g = \frac{Total\ Length\ (m)}{Total\ Mass\ (g)}$$

For our root trait samples, the total sample SRL was determined by summing each subsection's total root length and total biomass. Additionally, we used the scanned images to find the diameter distribution of each sample and the total length of roots within each diameter size class using WinRhizo. Each root sample was separated into 21 diameter size classes starting at 0.05 mm and increasing in 0.05 mm intervals to 1.0 mm. WinRhizo software typically auto-sorts diameter sizes classes by 0.5 intervals to 2 mm intervals; however, this distribution did not capture the variability in root diameter of our samples since very few roots were > 1 mm in diameter. The subsection data was then combined to find each sample's total diameter size class distribution. This process was repeated for root area and volume.

Root Chemistry

After morphological analysis, root sections for all 60 individual samples were homogenized and dried at 60° C for 48 hr and then weighed. Roughly 3 g of dried root sample was packaged and sent to the Analytical lab at the University of Hilo, Hawaii, for C:N and phosphorus analysis. C:N samples were run on a Costech 4100 Elemental Analyzer (Costech Analytical Technologies, Inc., Valencia, CA) with a detection limit of 0.01 mg for N and 0.20 mg for C. Plant phosphorus was extracted using a methodology from (Richards, 1993) and then ran on a Thermo iCAP Duo 7400 ICP-OES Spectrometer (Thermo Fisher Scientific Inc., Waltham MA) with a detection limit of 0.100 mg L^{-1}

Root Exudate Extraction

We used a hydroponic method to collect root exudates (Canarini et al., 2016; Hayes et al., 2004; Oburger et al., 2013; Ström et al., 1994). Plant plugs were placed in a temperature-controlled room at 13° C and under grow lights with photosynthetic active radiation (PAR) ranging from 339 µmols/m^2/s to 370 µmols/m^2/s to mimic natural grazing lawn conditions. The plants were left undisturbed in the temperature chamber for 48 hours to allow plants to recover from travel stress. Then, soil from the roots was rinsed with DI water until the water ran clear. We wrapped glass jars in foil to limit root light exposure and filled the glass jars with 50 mL of DI water. Once the roots were thoroughly cleaned, the soil-free plugs were put into the glass jars and placed back into the temperature chamber for 24 hr to allow the plants to acclimate to their new environment (Strom et al., 1994). After 24 hr, the DI water was discarded and replaced with 50 mL of fresh DI water. After another 24 hr, we collected the DI water, filtered it

through 11 µm Whatman filter paper into plastic bottles, and immediately froze the extracts. Before extractions, plastic bottles were soaked in a 2M NaCl solution for 48 hr to leech out any soluble C in the plastic.

Total dissolved organic C (DOC) in the exudate solution was measured using a digestion procedure and colorimetric analysis (Adkins, 2019; Cai et al., 2011). We digested the exudate extracts in a 10.9 mM potassium dichromate solution + 15.8 M nitric acid at 95 ºC for one hour. The absorbance of the digested solution was read at 350 nm using a Molecular Devices SpectraMax M2 (Molecular Devices, LLC., San Jose, CA) and compared to standard glucose solutions.

Decomposition Experiment

Sample Collection

Root samples for the decomposition experiment were collected from *C. subspathacea* meadows and grazing lawns along the Kashunuk River in YK Delta in 2021. Four, 5 cm diameter cores to a depth of 15 cm were collected from each habitat type for a total of eight cores. Additionally, we collected fresh goose feces from grazing lawns. Samples were placed on ice and transported back to Utah State University within 24 hr of collection.

In the laboratory, samples were air-dried and then repeatedly sieved through 2 mm and 1 mm sieves to remove the roots from the soil. As a final root collection step, we immersed the collected biomass in water to separate the roots from unknown organic matter via root flotation. The soil from all cores was homogenized together, and a 24 g sub-sample was set aside to measure pre-incubation inorganic N (NH_4^+ and NO_3^-). The remaining soil was set aside for use in constructing the microcosms. Finally, the collected

roots were cleaned thoroughly with DI water and air-dried. The goose feces were air-dried in the lab and then sub-sampled to determine moisture content.

Before starting the soil incubation experiment, we examined root morphology (SRL, root volume, and surface area), root C:N, and root ADF. Root C:N was measured using the same methods as those from the natural root trait survey described above, and root ADF is described below. Morphological analyses were performed on each core. Due to limited sample material, root C:N and ADF were analyzed from habitat type-specific homogenized subsamples.

Soil Incubation Experiment

We performed an 11-week soil incubation experiment to measure potential differences in root decomposition rates, as measured by CO_2 efflux, between grazed and ungrazed treatments. The length of the experiment was chosen to replicate the length of the growing season in the YK Delta. We constructed 72 gas-tight microcosms from 125 ml glass containers fitted with a gas-tight lid and septa. In each microcosm, we added 10 g of soil that was collected and homogenized from natural grazing lawns and ungrazed meadows. Microcosms were then assigned one of 12 treatments in a fully factorial design. Treatments included root type (ungrazed, grazed, or no roots), nutrients (goose feces added or omitted), and temperature (10 ºC or 13 ºC). For treatments with root additions, 0.1 g of grazed or ungrazed roots were added into a 250 µm mesh bag. For treatments with no root additions, we used an empty 250 µm mesh bag. Bags were sealed, placed into a microcosm with soil, and then covered with remaining soil. For treatments that received additional nutrients in the form of goose feces, we mixed 0.01 g of dried goose feces into the soil, corresponding to the natural goose fecal density found

in grazing lawns (Foley et al., 2022). Once the microcosms were fully constructed, they were placed in a 10º C or a 13º C stable temperature chamber. The experimental temperatures were chosen to represent surface soil conditions typical of grazing lawns (13º C) and ungrazed meadows (10º C) (Kelsey et al. 2016). Each root type received both temperature treatments.

CO_2 Flux Rate

To examine potential differences in root decomposition across treatments, we took weekly CO_2 gas measurements from the headspace of the microcosms to determine the CO_2 flux rate (μg CO_2-C g $soil^{-1}$ hr^{-1}) for a total of 11 weeks. During the measurement periods, microcosms were flushed and then sealed to allow gas to build in the air-tight microcosms for 24 hr. Following the 24 hr gas buildup, 10 ml of gas was extracted from each microcosm's headspace using a syringe. The syringe was injected into exetainers for storage until processing on a LICOR Trace Gas Analyzer 7810 (Licor Inc., Lincoln, Nebraska) with a sensitivity of 0 to 10,000 ppm.

C Loss Response Ratio

To further understand how root decomposition affects total C loss, we calculated the cumulative μg CO_2-C g $soil^{-1}$ emitted from each microcosm throughout the experiment by finding the integral of the CO_2 flux rate. We then determined the amount of C added to each microcosm using the following equation:

$$C_{input} = \frac{\left(\frac{\overline{\%C} * Mass_{input}}{100}\right)}{Soil\ Mass}$$

Where $\overline{\%C}$ is the average %C found in the pre-incubation root mass per root treatment. $Mass_{input}$ is the total mass of the roots added into an individual microcosm, and *Soil Mass* is the total soil added into a given microcosm, with C_{input} being the total root C added per g relative to the total soil mass. Finally, we found the ratio between the total C input and output by dividing the cumulative μg CO_2-C g^{-1} soil by $C_{input,}$ resulting in a response ratio.

Soil Inorganic N Determination

Eleven weeks after the start of the incubation, we destructively harvested the soil and root bags from the microcosm and analyzed them for soil inorganic N and post-incubation root chemistry. We subsampled 8 g of soil from each microcosm and took three samples from the pre-incubated homogenized soil. The inorganic N in the subsamples was extracted in 20 mL of 2 M KCl and shaken on an orbital shaker for one hr. The extracts were filtered through 11 µm Whatman filters and frozen until processed.

Using a colorimetric method, we measured total nitrate (NO_3^-) in pre- and post-incubated soils (Keeney & Nelson, 2015). To determine NO_3^- in the extracts, we reacted 85 µL of the extract with VCl_3 in microplate wells. The microplates were incubated in the dark at room temperature for ~16 hr for color development. The plate was read at 540 nm absorbance using a Molecular Devices SpectraMax M2 (Molecular Device, LLC., San Jose, CA.), and NO_3^-concentration was determined by comparison to standard curves.

Total ammonium (NH_4^+) in the pre- and post-incubation soils was also determined using a colorimetric method (Sims et al., 1995). To determine NH_4^+ concentrations in the extracted solution, the KCl extracts were reacted with citrate, salicylate-nitroprusside, and hypochlorite. The color was developed for 30 min and read

on a Molecular Devices SpectraMax M2 (Molecular Device, LLC., San Jose, CA.) at 667 nm. NH_4^+ concentrations were determined by comparison to standard curves.

Pre- and Post-Incubation Chemistry

We measured ADF, a measurement of cellulose and lignin, in the root samples following the approach from Gessner, 2005. Here, we air-dried ground root samples to a size of ≤ 0.2 mm and then subsample 0.25 g for tissue analysis. The remaining 0.25 g of roots were oven-dried at 60 ºC for 24 hr, and the oven-dried mass was recorded. Using the oven-dried subsample, moisture content (MC) was determined using the following formula:

$$MC = \frac{W - W_{dry}}{W_{dry}} * 100$$

Where W is the weight of the sample prior to drying, W_{dry} is the oven-dried sample mass. Using moisture content, the oven-dried mass equivalent of the air-dried samples was determined using the following:

$$W_{dry} = \frac{100 * W_{wet}}{100 + \%MC}$$

Where W_{wet} is the air-dried sample's weight, and MC is the moisture content.

We extracted ADF (cellulose and lignin) from roots using 20 mL of acid-detergent solution and 0.4 mL of decahydronaphthalene. The acid detergent solution was prepared from 0.5 M sulphuric acid and cetyl trimethyl ammonium bromide. Root samples were digested in the solution for 60 min at 100 °C. Samples were then filtered onto Whatman's filter paper and oven-dried. ADF was calculated as follows:

$$ADF = \frac{W_0}{W_{dry}} * 100$$

Where, W_0 mass of the dried fiber and W_{dry} is the oven-dried sample weight pre-digestion.

Additionally, pre-incubation ungrazed and grazed root samples and post-incubation ungrazed and grazed root samples were ground with a mortar and pestle and sent to the University of Hilo analytical lab for %C, %N, and C:N analyses.

STATISTICAL ANALYSIS

Natural Root Trait Survey

Root Morphology

We performed all statistical analysis in the R Statistical Computing Environment (R Core Team, 2023). To analyze differences in root morphological characteristics by depth (SRL, volume, surface area) between habitats, we conducted a linear mixed effects model in the R-package nlme (Pinheiro, 2000). In this model, habitat type and root depth were classified as fixed effects, and collection location was classified as a random effect to account for potential site variation. We determined the significance of independent and interactive effects of habitat type and root depth using Type II Sums of Squares in the "car" package (Fox & Weisberg, 2019). We ran a Tukey-adjusted post-hoc analysis using the "emmeans" package (Lenth, 2023) to identify differences in root morphological characteristics between habitat types for each depth interval pairing. To assess differences in whole core morphology (0-50 cm, e.g., depth sections combined) between habitat types, we ran a linear mixed effects model where habitat type was classified as a fixed

effect and collection location was set as a random effect, we determined significance using Type II Sum of Squares from the car package (Fox & Weisberg, 2019).

Root Chemistry and Exudates

To assess if aboveground herbivory affects root chemistry (C, N, and P) and exudates, we used a similar process as we did for the whole core morphological characteristics, where habitat type was set as a fixed effect, and location was a random effect. Additionally, we log-transformed %N and %P to meet normality assumptions.

Decomposition Experiment

Root Morphology

Because roots for the decomposition experiment were collected in a different year from the trait survey, we also compared bulk root morphologies between grazing lawns and ungrazed meadows in the decomposition experiment. We conducted statistical analyses using R-package “stats” (R Core Team, 2023). Specifically, we employed t-tests to assess the differences in average SRL, root volume, and surface area between habitat types. To investigate differences between root morphology by diameter size class, we assessed length, root volume, and surface area per diameter size class as a function of habitat type. For this, we utilized the "aov" function in the “stats" package (R Core Team, 2023) and log-transformed length, volume, and surface area per diameter size class to better meet the model assumptions. These models integrated the main and interactive effects of diameter size class and habitat type. For significant factors, we then ran a Tukey-adjusted post-hoc analysis using the “emmeans” package (Lenth, 2023) to compare the significance between factor levels.

Pre-Incubation Root Chemistry and Pre-Post Chemistry Comparisons

To assess if pre-incubation root chemistry (%ADF, C:N, %C and %N) differed between paired habitat types, we conducted a p-adjust Bonferroni Welch's t-test using function "p.adjust" from the "stats" package in R (R Core Team, 2023). The new level of significance for all tests ran with a Bonferroni correction was 0.016. We repeated this analysis to compare pre- and post-incubation root chemistry between habitat types.

The Rate of Root Decomposition from Change in CO_2 Flux

We used a generalized linear mixed model to assess how root type (grazed, ungrazed, or no roots), temperature (10°C and 13°C), feces treatment (absent/present), and incubation day (time) affected the natural CO_2 flux rate (ug CO2-C g $soil^{-1}$ hr^{-1}), which we used as a proxy for root decomposition. For the generalized linear mixed model, we used the "glmmTMB" function from the R-package "glmmTMB" (Brooks et al., 2017). We considered all main and three-way interactive effects while including microcosm identifiers as a random effect to account for repeated measurements. To address unequal variance in the temperature and root treatment, we utilized the "dispformula" function from package glmmTMB in our statistical model to assume unequal variance for root and temperature treatment groups. In this context, the model output will provide an estimate for the decline in flux rate per incubation day (the slope of CO_2 vs time). We assessed the statistical significance of parameters using the Type II Wald Chi-Square Test with the "car" package (Fox & Weisberg, 2019). For significant parameters, we conducted Tukey-adjusted pairwise comparisons using the "emmeans" package (Lenth, 2023) to test if factor level means differ from one another.

C Loss Response Ratio

To determine if aboveground herbivory alters the C loss response ratio, we used an Analysis of Variance model using the function “aov” from the R-package “stats” (R Core Team, 2023). Our fixed effects were root, temperature, and feces treatment. For significant factors, we implement a Tukey-adjusted pairwise comparison using the “emmeans” package in R to understand how factor levels affect the C loss response ratio.

Soil Inorganic N

We ran an Analysis of Variance model using the "lm" function in the R-package stats (R Core Team, 2023) to investigate the fixed effects of roots, temperature, and feces treatment on post-incubation soil inorganic N (NH_4^+ and NO_3^-). Since our model only included soil inorganic N concentrations at the end of the experiment, we did not include a random effect in this model. Additionally, we log-transformed soil NO_3^- to meet the model assumption for normality. For significant factors, we conducted Tukey-adjusted pairwise comparisons using the “emmeans” package to compare the relationship between factor levels.

Post- Incubation Root Chemistry

For post-incubation root chemistry, we primarily ran an Analysis of Variance model using the function “aov” in the stats package from R (R Core Team, 2023). This analysis was used for post-incubation root C:N, %C, and log-transformed %N. We excluded the "no root" root treatment for these analyses mentioned above because they relied on root presence for assessment. For significant interactions, we ran the Tukey-adjusted pairwise to compare the relationship between interactive effects.

To understand how the decomposition process influences post-incubation root %ADF, we employed a generalized linear mixed effects model using the "glmmTMB" function and considered the "dispformula" to account for unequal variance in the temperature treatment. Additionally, we divided %ADF by 100 and performed a logit transformation to better meet model normality. This analysis included all possible main effects and two-way interactions based on significance values.

RESULTS

Natural Root Trait Survey

Root Morphology

For root morphology by depth, we found differences in SRL (chisq = 10.954, df = 4, p = 0.027), biomass (chisq= 27.036, df = 4, p<0.001), volume (chisq= 34.497, df = 4 p<0.001), total length (chisq = 37.685, df = 4, p<0.001), and root surface area (chisq = 42.754, df = 4, p<0.001), between depth sections, but not between habitat types. Our post-hoc analysis showed that plants allocate the most biomass, volume, length, and surface area between 10-40 cm below the soil surface (Figure 2). However, the post-hoc analysis did not detect differences in SRL among depth sections.

Additionally, when we combined the root depth sections to analyze morphological characteristics for the whole core morphology (0-50 cm), we found no differences in SRL (chisq = 0.718, df = 1, p=0.397), biomass (chisq = 0.603, df = 1, p=0.530), volume (chisq = 0.025, df =1, p=0.875), total length (chisq = 0.916, df =1, p=0.339), or surface area (chisq = 0.531, df =1, p= 0.466) between habitat types.

Root Chemistry

We did observe differences in C:N (chisq = 7.256, df=1, p=0.007) and %N (chisq = 5.716, df=1, p = 0.017) between habitat types (Figure 3), but not between habitat types in root %C (chisq = 2.63, df=1, p=0.105) or -%P (chisq = 0.371, df=1, p= 0.543). Roots from ungrazed *C. subspathacea* meadow had an 11% greater C:N of 35.14 ± 0.96 (mean ± SE) compared to a grazed *C. subspathacea* which had a root C:N of 31.61 ± 0.89. Additionally, roots from the grazed *C. subspathacea* grazing lawn had an 8% greater root %N (1.04 ±0.03% N) compared to the ungrazed meadow, which had a %N of 1.00 ± 0.02 (Table 2).

Root Exudates

We observed a marginally significant difference in root exudation between habitat types (chisq = 3.818, df = 1, p = 0.051, Table 3). We found that the grazed treatment produced more DOC per g root per day than the ungrazed root treatment (Table 3). This suggests that roots exposed to aboveground grazing pressure released ~48% more DOC from root exudates compared to ungrazed plants.

Decomposition Experiment

Root Morphology

For our root decomposition samples, we found no significant differences in SRL (df = 4.20, t = -0.992, p = 0.407), root surface area (t = -1.229, p = 0.266), root volume (t = -1.5862, p = 0.164), or root mass (t = -0.137, p = 0.896) between habitat types for whole core morphology (Figure 4).

We found statistical differences in root morphology by diameter size class for root length ($F = 36.15$, $df = 1$, $p<0.001$), surface area ($F = 35.99$, $df = 1$, $p<0.001$), and volume ($F = 35.89$, $df = 1$, $p<0.001$) throughout diameter size classes between habitat types. On average, grazed *C. subspathacea* had 10% greater length, 18% greater surface area, and 21% more volume than ungrazed *C. subspathacea* throughout diameter size classes (Figure 5). Additionally, we found differences in length ($F = 64.92$, $df = 20$, $p<0.001$), surface area ($F = 18.79$, $df = 20$, $p<0.001$), and volume ($F = 26.89$, $df = 20$, $p<0.001$) between diameter size classes. Our post-hoc analysis demonstrated both grazed and ungrazed roots have more length and surface area in the finest diameter size classes, and the most volume was in the greatest diameter size class. Our analysis did not detect an interactive effect between diameter size class and habitat type for any morphological characteristics.

Pre-Incubation Root Chemistry

We found pre-incubation root litter C:N ($df = 3.97$, $p=0.021$) and root %C ($df = 3.90$, $p=0.006$) significantly differed by root treatment, while %N did not ($df= 4.0$, $p=0.089$). Ungrazed root litter had 17% greater C:N and 4% greater root %C (Figure 6) compared to the pre-incubation grazed root treatment. Additionally, pre-incubation root %ADF did not significantly vary between root treatments (Figure 7).

The Rate of Root Decomposition from the Change in CO_2 Flux

Over an 11-week incubation period, the CO_2 flux rate exhibited significant dependencies on several interactive factors. Notably, we observed a significant three-way interaction among root type x temperature x incubation day, two-way interaction between

root type and incubation day, two-way interaction between root type and incubation day, and a two-way interaction between temperature and incubation day (Figure 8, Table 4).

Specifically, we observed that the presence or absence of root treatments influenced the CO_2 flux rate through alterations to the slope of the log-transformed response. The flux rate in microcosms without any root additions had a 67% greater decrease in flux rate per incubation day than those with ungrazed roots and a 76% greater decrease in flux rate per incubation day than those with grazed roots (Table 5, Figure 8). No significant difference in the change in CO_2 flux rate per incubation day was found between microcosms treated with ungrazed and grazed roots, demonstrating that root type does not have a significant effect on flux rate. Additionally, the flux rate in microcosms treated with the high-temperature treatment had a 17% greater decrease in CO_2 flux rate per incubation day than in microcosms treated with the low-temperature treatment (Table 6, Figure 8).

Furthermore, our post-hoc analysis revealed that the impact of the three-way interaction between root treatment, temperature treatment, and incubation day was contingent on the specific combination of levels (Figure 8). Notably, the flux rate of microcosms treated with the grazed roots/high-temperature treatment had a 42% greater decrease in the CO_2 flux rate per incubation day than grazed roots/low-temperature treatment combination as indicated by the slope of the log-transformed response ($df = 753$, $p<0.001$). The flux rate for microcosms treated with the ungrazed/high-temperature treatment had a 31% greater decrease in the CO_2 flux rate per incubation day compared to microcosms treated with the ungrazed/low-temperature treatment combination, as

indicated by the slope of the log-transformed response (df = 753, $p<0.001$ for both). Temperature had no significant effect on microcosms with no root additions.

C Loss Response Ratio

We found that the C loss response ratio was 14% greater for microcosm treated with the grazed roots compared to the ungrazed roots (Table 7). Additionally, the C loss response ratio in the high-temperature treatment was 22% greater than in the low-temperature treatment (Figure 9, Table 7). Microcosms with feces additions had a 6% lower C loss response ratio compared to those with no feces (df = 1, p=0.048). Furthermore, the interaction between root and feces treatments affected the C loss response ratio (Table 7), and our post-hoc analysis revealed that the grazed root and feces additions microcosms had a 13% lower C loss compared to the grazed root feces omitted treatment combination, (df = 40, p=0.004). Feces additions had no effect on the carbon loss response ratio for microcosms with the ungrazed root treatment (Figure 9). Additionally, when feces were omitted, the C loss response ratio between root treatments differed. The grazed root/no feces treatment was 21% greater than the ungrazed root/feces omitted treatment (df = 40, $p<0.001$). However, no differences were detected between root treatments when feces were present (Figure 9).

Soil Inorganic N

We discovered significant impacts on post-incubation soil NH_4^+ concentrations from both root treatments and temperature treatments (Table 8). Post-hoc analysis revealed that microcosms subjected to the no root treatment exhibited 15% and 42% greater $\mu g\ NH_4^+\ g\ soil^{-1}$ compared to those treated with ungrazed root and grazed root

treatments, respectively (Figure 10). Additionally, microcosms treated with ungrazed roots exhibited 23% greater μg NH_4^+ g $soil^{-1}$ than those with grazed roots. Concerning the impact of temperature on post-incubation soil NH_4^+ concentrations, microcosms subjected to low-temperature treatment had 20% greater μg NH_4^+ g $soil^{-1}$ than those exposed to high-temperature treatment. Finally, there was a marginally significant interaction (p=0.052) between feces treatment and root treatment.

There was a significant interaction between feces and temperature on soil NO^-_3 concentrations (Table 9). Our post-hoc analysis showed that within the low-temperature treatment, microcosms without feces had 40% greater soil NO^-_3 concentrations compared to microcosms with feces additions (Figure 10, Table 9). Feces had no effect on NO^-_3 concentrations within the high-temperature treatments (Figure 10).

Post-Incubation Root Chemistry and Pre-Post Chemistry Comparisons

Prior to the incubation experiment, the ungrazed root treatment had an average of 40% root C, 1% root N, 53.2% root ADF and a C:N ratio of 40.5. The grazed root treatment had an average of 38.6% C, 1.12% N, 49.9% root ADF, and a C:N ratio of 34.5. Post-incubation root C:N was affected by root treatment and temperature treatment as the main effects (Table 10). On average, ungrazed root litter had a 40% root C:N compared to grazed root litter, which had 28% root C:N at the end of the incubation experiment (Figure 6), and root litter incubated in the low-temperature treatment had 35% root C:N compared to root litter incubation at the high-temperature treatment which had 33% root C:N. Additionally, the decomposition processes significantly affected post-incubation root C:N for the grazed root treatment, which declined by 22% when compared to the start of the experiment (Figure 6, df = 3.15, p=0.015). The C:N for the

ungrazed root treatment did not change through the course of the experiment (Figure 6, df = 3.349, p=1).

Post-incubation root %N was only affected by root treatment (Table 11). Ungrazed root litter had an average of 23% less root %N than grazed roots at the end of the experiment (Figure 6); the grazed root treatment had roughly 1.3% root N compared to 1.0% in ungrazed root treatment. Moreover, the decomposition process significantly increased the root %N for the grazed root treatment by 13% (df = 4.429, p=0.011) but had no effect on the ungrazed root treatment.

We found that root treatment (df = 1, $p<0.001$), temperature treatment (df = 1, $p<0.001$), and a three-way interaction between roots, feces, and temperature drove post-incubation root %C values (Table 12). We found a lower post-incubation root C concentration in roots exposed to grazing pressure than in roots that were not (Figure 6). When we explored the interactions, we found that when there were no feces, temperature had a greater effect on the ungrazed root treatment than grazed roots. When feces were added, the temperature had a greater effect on the grazed root treatment than the ungrazed root treatment (Figure 11). Furthermore, the decomposition process significantly decreased the root %C for the grazed root treatment by 5% (Figure 6, df = 21.93, $p<0.001$) but had no effect on the ungrazed root treatment.

Temperature and root treatment interacted to affect post-incubation root %ADF (Table 13). Within this interaction, the high-temperature treatment drove differences in post-incubation root %ADF between root treatments (Figure 7), where the ungrazed treatments had 65% ADF compared to only 60% ADF in the grazed root treatment (df = 37, p=0.032). Furthermore, temperature drove differences between post-incubation

%ADF of the ungrazed root treatment (Figure 7), where the ungrazed root treatment treated with low temperatures had 58% ADF compared to 65% ADF in the high-temperature treatment (Figure 7, df= 37, $p<0.001$).

Finally, we saw significant differences between pre- and post-incubation root %ADF. We saw that concentrations of root ADF increased in both the ungrazed and grazed root treatments throughout the experiment. Root %ADF increased by 19% throughout the experiment in the grazed root treatment (df = 15.585, $p<0.001$) and by 16% in the ungrazed root treatment (df= 15.32, $p<0.001$).

DISCUSSION

While we observed no discernible differences in morphological traits among habitat types within the natural root trait samples or the root decomposition samples, our study uncovered compelling evidence that aboveground herbivory induces intraspecific variations in root chemistry for *C. subspathacea* and root exudation. Specifically, grazing was found to enhance the quality of roots as indicated by lower C:N ratios, higher %N, and greater rates of root exudation. These findings suggest that aboveground herbivory influences the quantity and quality of belowground inputs from roots. Furthermore, findings from our laboratory microcosm experiment show that roots exposed to aboveground herbivory decompose faster and lose more C through respiration, suggesting that herbivory increases the turnover time of root C in soils. This investigation enhances our understanding of the intricate relationship between aboveground herbivory and below-ground C inputs and how changes to grazers in the YK Delta can influence C cycling.

The Effects of Aboveground Herbivory on Intraspecific *Carex subspathacea* Root Traits

Morphology/Biomass

We did not see differences in SRL, root surface area, or root volume between habitat types across 10 sites sampled on the Y-K Delta. Our initial hypothesis was that the grazed *C. subspathacea* would exhibit greater SRL, surface area, length, and volume than the ungrazed *C. subspathacea* due to higher soil temperatures, C limitation, and feces additions from aboveground grazing. Although we could not reject the null hypothesis, similar work has shown that clipping aboveground foliage can increase SRL (Heinze, 2020; Thorne & Frank, 2009) and that warmer soil temperatures (as are typical of grazing lawns in the YK) can lead to root elongation (Karlova et al., 2021). However, these responses by roots to grazing and temperature are not universal (Leuschner et al., 2013). Recent work by Bergmann et al. (2020) proposed a conceptual framework that may explain the discrepancies in the response of SRL to herbivory. When C is limited for root growth, roots can outsource nutrient acquisition (the typical function of fine roots) to mycorrhizae, whose presence can vary based on climate, latitude, and environmental conditions (Kivlin et al., 2011). Thus, the discrepancies in the SRL response to aboveground herbivory may be driven by the presence of mycorrhizae, which can be highly variable (Chen et al., 2016). Additionally, variation in root morphology may only exhibit low-medium plasticity (McCormack et al., 2017), and our sample size of 12 could have been too small to detect finer resolution differences in root morphology. Despite no clear indication that root morphology differed between grazed and ungrazed *C. subspathacea*, our results show that grazed *C. subspathacea* has a greater belowground to aboveground biomass ratio. While we saw no difference in root biomass between habitat

types, the aboveground biomass of *C. subspathacea* in ungrazed meadows is five times greater than in grazing lawns, with ~14 times greater stem heights (Kelsey et al., 2016). These results suggest that resource allocation to belowground biomass is relatively consistent regardless of grazing pressure and its effects on soil microclimate. Finally, despite that we did not find differences in morphology between habitat types, we did see differences in morphological characteristics between depths. It is not surprising that depth played a role in morphological distribution as (Jackson et al., 1996) found that 80-90% of root biomass is allocated to the top 30 cm of the soil in cold regions, which suggests that the greatest concentrations of nutrients are within this section of soil.

Chemistry

For the natural root trait samples, we found no differences between root types in %C, though there was difference in the decomposition samples or %P. However, grazed *C. subspathacea* had 8% higher root %N and 11% lower root C:N than ungrazed *C. subspathacea*. Our results coincide with studies that investigated the impacts of wildlife, livestock, and simulated grazing on root chemistry (Ayres et al., 2004; Bai et al., 2012; Johnson & Matchett, 2001). For example, Ayres et al. (2004) found that clipping vegetation increased root %N between 5% - 14% and decreased root C:N by 9% - 19%. Our results suggest that aboveground herbivory in the YK Delta increases the root quality of *C. subspathacea,* and because we did not see differences in root biomass between habitat types, there is a greater availability of high-quality roots in grazing lawns compared to the meadows.

The effect of plant litter quality on decomposition is widely debated (Lehmann & Kleber, 2015; Poirier et al., 2018). In many studies, high-quality plant litter is often

associated with a faster turnover of organic matter. Recent work by Saunders et al. (2023) demonstrated that in the YK Delta, low-quality litter substantially decreases C loss via respiration. Thus, if the distribution or abundance of grazing lawns vs meadows changes due to altered migratory bird patterns, a shift in litter quality may influence soil C storage. Furthermore, because there is a strong association between temperature and decomposition rates, the combined influence of higher temperatures and greater root quality in grazing lawns could interact to influence C loss.

Exudates

Our results indicate that roots in grazing lawns produced 38% more DOC than roots from ungrazed meadows. This suggests that soils in grazing lawns receive a substantially higher input of labile carbon per gram of root via root exudation than *C. subspathacea* meadows. Previous research has found that simulated grazing increases root exudation by 1.5-fold (Hamilton et al., 2008), a magnitude similar to our results. It has been proposed that plants increase root exudate production after initial defoliation to increase nutrient uptake in response to stress (Hamilton & Frank, 2001; Paterson et al., 2005). Since *C. subspathacea* in YK Delta grazing lawns are grazed throughout the growing season, there is likely a continuous input of highly labile C within the grazing lawns. However, the extent of grazing lawn habitat is closely correlated with goose abundance (Uher-Koch et al., 2019), and in the absence of goose grazing, lawns will revert to meadows. While our findings indicate that transitioning back to meadows will decrease C inputs and turnover originating from roots, the duration of the lingering effects of past grazing remains uncertain.

Overall, our natural root trait survey demonstrated that aboveground herbivory does not affect root morphological characteristics but does influence root chemical trait expressions. Specifically, we found that grazing results in higher-quality roots as shown through lower C:N in grazed *C. subspathacea.* Furthermore, our study showed that grazing increased C input through increases in the rate of root exudations per g root compared to ungrazed roots, suggesting that grazing increases both root C input and root C quality.

The Effects of Aboveground Herbivory on CO_2 Efflux and Soil N

Carbon Efflux and Carbon Loss Response Ratio

Our field data showed that *C. subspathacea* exposed to aboveground grazing have more N-rich roots than ungrazed plants. Considering that the quality of plant material significantly influences decomposition rates, we predicted that the observed grazing-mediated changes in root %N and C:N could influence root decomposition. Grazing also increases soil temperatures through the removal of aboveground biomass, and goose feces can be an extra source of nutrients that can prime decomposition. These grazing-mediated changes in soil properties, either independently or in concert with changes to root chemistry, could result in significantly different root decomposition rates between grazing lawns and meadows.

Our data supports our hypothesis that roots from grazed *C. subspathacea* decompose faster than roots from ungrazed *C. subspathacea* due to differences in root chemistry. Initial respiration rates and C loss ratio were greater for grazed root treatments than ungrazed root treatments, but only when feces were not present. Differences in decomposition between grazed and ungrazed roots could be due to the starting chemistry

for the grazed root treatment, which was more labile and of higher quality than the ungrazed root treatment, as indicated by higher %N and lower %ADF. Previous research has shown that more labile plant material leads to faster decay rates (Silver & Miya, 2001; Wardle et al., 2002; Zhang et al., 2008). Greater lability of grazed roots vs. ungrazed roots could have increased decomposition in two ways. One explanation is a functional response: labile grazed roots are easier to utilize by the microbial community, thus increasing the individual respiration rates of microbes in grazed soils. A second, non-exclusive explanation is that the greater amount of labile roots material in the grazed soils supported more microbial biomass, increasing total respiration rates.

Interestingly, when feces were added, the C loss ratio and respiration rates did not differ between microcosms with grazed and ungrazed roots. This might be because goose feces are rich in N and P (Beard et al., 2023; Frost & Hunter, 2007; Saunders et al., 2023). Past literature has shown a positive relationship between carbon use efficiency (CUE) and available soil N content because greater N availability decreases N-mining by microbes (Manzoni et al., 2012). “N-mining” refers to the decomposition of organic matter solely to obtain N, and it decreases CUE because C is available in excess relative to N and is therefore respired (Averill & Waring, 2018; Manzoni et al., 2012). The high N in feces could alleviate N limitation of decomposers and, therefore, decrease N-mining from the added roots. Feces additions only decreased C respiration in the grazed root treatments, which suggests that decomposers in grazed root treatments were more N-limited than in ungrazed root treatments. This is an unexpected finding considering that grazed roots have lower C:N than ungrazed roots, but this result is supported by the patterns of N-mineralization we observed at the end of the incubation (discussed further

below). Furthermore, previous research by Beard et al. (2023) demonstrated that when feces were removed from natural grazing lawns in the YK Delta, CO_2 efflux increased, providing *in situ* support for our results. Overall, our results suggest that grazing increases root decomposition by altering root chemistry, but this effect is offset by feces deposition, which occurs simultaneously.

Regarding the effect of temperature on decomposition rates, the positive relationship between temperature and decay rate is not surprising considering that it is well-known that temperature heavily influences microbial activity (Devêvre & Horwáth, 2000; von Lützow & Kögel-Knabner, 2009), thus leading to faster organic matter turnover (Kirschbaum, 1995; Silver & Miya, 2001). In the YK delta, previous research has found that aboveground herbivory increases soil temperature (Kelsey et al., 2016); thus, our data suggests that herbivore-driven changes to soil temperatures will influence the decay rate. Because grazing-driven differences in root chemistry and fecal deposition exhibit offsetting effects on root decomposition, increased temperature may represent the primary pathway by which grazing influences root decomposition.

Root Chemistry

The results of our study revealed significant differences in pre-incubation root litter chemistry based on habitat type. Specifically, pre-incubation ungrazed root litter exhibited a 17% higher C:N ratio and 4% higher root %C compared to the pre-incubation grazed root treatment. These findings, alongside the results of the natural root traits, provide substantial evidence that across the YK Delta, aboveground herbivory decreases root C:N, thus enhancing root quality.

Furthermore, the decomposition processes altered the %C, %N, and C:N of the grazed root treatment but had no effect on the %C, %N, or C:N of the ungrazed root treatment. Additionally, significant differences between pre-and post-incubation root %ADF were observed. Both ungrazed and grazed root treatments experienced an increase in root %ADF throughout the experiment.

An increase in litter nutrient content, such as %N, is typical in the decomposition process as the result of the microbial community immobilizing nutrients from the surrounding environment until the available litter reaches the appropriate stoichiometry (Berg & McClaugherty, 2014; Manzoni et al., 2012). Furthermore, the degree to which C:N ratios increase during decomposition is positively related to the rate at which decomposition occurs and is often associated with starting C:N ratios (Gosz et al., 1973). Thus, the changes in litter stoichiometry for the grazed root treatment suggest that root C in microcosms treated with the grazed root treatment was more actively decomposed and was a primary source of energy for microbial respiration than the root C in microcosms treated with ungrazed root treatment. Although there is an increase in %ADF for ungrazed root litter, it suggests that the microbial community initially degraded the labile carbon present in ungrazed roots and subsequently transitioned to other C sources as the experiment progressed.

Soil N

Our investigation into soil NH_4^+ concentrations unveiled a significant influence of both root and temperature treatments on the inorganic N pool. The soil NH_4^+ concentrations per root treatment followed this order: none >ungrazed >grazed, which was the same order decomposition rate followed from slowest to fastest. This strongly

suggests a link between C loss and N-limitation in our study. The lower amounts of NH_4^+ in the grazed root treatments compared to ungrazed root treatments suggest that microbial communities immobilized more inorganic N in the grazed root treatments, potentially indicating that these microbial communities had higher N demand. A high N demand could explain why grazed root treatments with no feces exhibited the greatest C loss: high N demand led to N-mining and increased C mineralization. It is possible that feces addition alleviated the N demand in the grazed root treatments, decreasing N-mining and explaining why C loss was lower for the grazed root treatments with feces added. In fact, although the difference was only marginally significant ($p = 0.059$), feces addition resulted in ~10% more inorganic N in the grazed root treatments, suggesting less N limitation with feces additions.

A link between N-demand and C-loss is also supported by changes in root stoichiometry over the incubation. The C:N ratio of ungrazed roots did not change over the incubation, indicating that microbes were not more or less limited by either element in ungrazed root treatments. In contrast, the C:N ratio of grazed roots decreased over the incubation, indicating more mineralization of root C than root N and, therefore, excess C (and limited N) relative to microbial demand. This finding is particularly interesting given that prior to the incubation, grazed roots had lower C:N than ungrazed roots. Therefore, even though grazed roots had more N than ungrazed roots, microbial communities were still more N-limited in these treatments. This could suggest differences in microbial communities between grazed and ungrazed root treatments. This assumption is supported by previous work done by Foley et al. (2022), which found that meadow habitats support greater fungal and prokaryotic richness. Root chemistry may have also

played a role in post-incubation soil NH_4^+ concentrations (none >ungrazed >grazed) in microcosms with root additions. The lower N demand in the ungrazed root treatments suggests the presence of a slow-growing, low-energy microbial community with high C and N use efficiency (Manzoni et al., 2008). Conversely, the high N demand and high C loss response ratio in grazed root treatments suggest a fast-growing microbial community with a high energetic cost (Manzoni et al., 2008).

The impact of temperature on NH_4^+ concentrations revealed that low-temperature treatment resulted in elevated NH_4^+ concentrations compared to high-temperature treatment. This observation aligns with the known temperature sensitivity of microbial processes in soils, such as mineralization and nitrification, which influence NH_4^+ dynamics because high temperatures are often associated with low nutrient availability and greater microbial metabolism, thus resulting in a higher N demand (Manzoni et al., 2012; Miller & Geisseler, 2018). The increased NH_4^+ concentrations in the low-temperature treatment highlight the potential for temperature variations to affect soil nutrient availability, which has implications for plant growth and ecosystem productivity as goose populations fluctuate in the YK Delta.

In contrast to NH_4^+ concentrations, our study found that feces and temperature treatments interacted to influence soil NO_3^- concentrations. Specifically, the addition of feces led to a notable decrease in soil NO_3^- concentrations for microcosms treated in the low-temperature treatment but had no effect on microcosms treated at the high temperature (Figure 10). The difference in the response between temperature treatments indicates that temperature may modulate the impact of feces on NO_3^- concentrations due to an increased nutrient demand for microbial communities in soil at higher temperatures.

This may suggest that the input of feces may decrease nitrifying bacteria or increase denitrifying bacteria through alteration to soil pH, which heavily influences N cycling (Šimek & Cooper, 2002).

In summary, many of the treatments associated with aboveground herbivory decreased soil inorganic N concentrations in the soil, suggesting aboveground herbivory may influence microbial N demand in the YK Delta, with corollary effects on decomposition and soil C loss. Our results suggest that aboveground herbivory increases decomposition rates and increases the loss of C and alters inorganic N concentrations of the soil through abiotic alteration of the environment. These findings contribute to our broader understanding of nutrient availability and ecosystem functioning. Further research is needed to understand the underlying mechanisms driving these observed effects and to elucidate their ecological significance in diverse ecosystems.

CONCLUSION

Our study found that aboveground herbivory in the YK Delta created intraspecific differences in *C. subspathacea*. While root morphology did not differ significantly between habitat types, aboveground herbivory increased root quality, as shown by root C:N in grazed *C. subspathacea*. Though we have found that aboveground herbivory does influence root chemical trait expression, we cannot disentangle the main driver to the root plasticity observed in our study. However, we know that root plasticity can be affected by hotspot nutrient additions from feces (Hodge, 2004), C input limitations from reduced photosynthesis via clipping (Thorne & Frank, 2009; Wiley & Helliker, 2012), or changes to soil moisture (Thorne & Frank, 2009). It is important that future work disentangles

these effects due to their implications for climate change. For example, if the main driver of root trait plasticity in the sub-Arctic is temperature, we may see whole community shifts in root trait expression as climate change continues to warm the sub-arctic.

Furthermore, we provided evidence that aboveground herbivory alters the rate of root decomposition and C loss, and those alterations are primarily driven by changes to the soil physicochemical environment. As grazing regimes continue to shift in the YK Delta and climate change further increases soil temperatures, ecosystem processes such as decomposition and soil respiration will follow suit. Future work should focus on how long it takes *Carex subspathacea* root trait expression to change from the ungrazed chemical composition to the grazed form and the influence these traits have on both microbial carbon use efficiency. Additionally, future work should attempt to disentangle if the primary driver of intraspecific differences in root chemistry is soil temperature, nutrient additions, or clipping because the mechanism of these changes may help provide insight into how *C. subspathacea* communities will shift as climate change continues to alter both grazing and climatic patterns within the sub-Arctic.

DISCUSSION

Soil is the largest terrestrial carbon pool (1500 Pg C) on earth (Batjes, 1996) and contributes significantly more CO_2 to the atmosphere than the burning of fossil fuels (Raich & Schlesinger, 1992; Smith, 2004; Smith et al., 2015). Even small shifts in soil efflux rates could affect global carbon budgets (Raich & Schlesinger, 1992). There is increasing evidence that herbivores increase soil efflux (Leroux et al., 2020) through biotic and abiotic environmental alterations. However, few studies have explored the

effects of aboveground herbivory on root traits and belowground processes, such as root decomposition (Bardgett & Wardle, 2003). Due to the disproportionate contribution of roots to soil carbon (Rasse et al., 2005), understanding their response to aboveground pressure is important to build an accurate understanding of soil efflux.

Furthermore, sub-Arctic and Arctic wetlands have historically been carbon sinks due to low annual temperatures, leading to low decomposition rates (McGuire et al., 2009). However, climate change is causing both the sub-Arctic and the Arctic to warm faster than any other biome in the world (Meredith et al., 2019), threatening to turn this biome into a large carbon source instead of a carbon sink (Kirschbaum, 1995; Lundin et al., 2016). In addition, the increasing annual temperatures are extending the duration of the growing season in these regions (McGuire et al., 2009), thus increasing the duration that herbivores can graze in each area (Hinzman et al., 2005). These changes are leading to a phenological mismatch between the early arrival of geese and vegetative greening, which can further alter the grazing regimen and soil respiration rates (Choi et al., 2020; Leffler et al., 2019). Despite the fact that some geese populations are increasing along the YK Delta, declines in one of the primary creators of grazing lawns in the YK, Black Brant, have been met with overall declines in grazing lawns (Fondell et al., 2011; Pacific Flyway Council, 2016; Sedinger et al., 2019; Uher-Koch et al., 2019). The shifting populations could lead to changes in grazing lawn areas (Choi et al., 2020), affecting ecosystem soil respiration (Leffler et al., 2019), thus emphasizing the need to fully comprehend the current interactions between above- and belowground processes.

We believe that by exploring the intraspecific traits of a species within the family *Cyperaceae* and, more specifically, the genus *Carex,* our study can provide insight into

grazing dynamics throughout the Arctic and sub-Arctic. Currently, there are roughly 140 species of *Carex* in the Arctic and sub-Artic, which provide critical forage for birds and a plethora of grazing herbivorous mammals (Small & Cayouette, 2016). Furthermore, the value of exploring intraspecific differences of *Carex* in the context of large *Carex* meadows, where interspecific competition is limited, should not be underestimated due to the high prevalence of meadow habitats throughout the coastal Arctic (Small & Cayouette, 2016; Van Der Graaf et al., 2004; Zacheis et al., 2001). Finally, by linking the effects of aboveground herbivory to belowground root traits and, in turn, its influence on C cycling processing, we can address a large knowledge gap in Arctic plant research and Arctic soil biogeochemistry research.

TABLES & FIGURES

Table 1

The Relationship Between Root Traits and Soil Physicochemical Properties. Positive relationships are indicated with a (+) sign. Negative relationships are indicated with a (–) sign. Varied relationships are indicated with a (– +) and suggest local or species-specific responses. Relationships that remain unknown are indicated with an (x). If there was only sufficient evidence for whole plant responses, "(plant)" is added to the directional symbol.

Soil Physicochemical Property	**Root Traits**						
	Rooting Depth	SRL	Biomass	Root Diameter	C:N	Exudates	References
Soil Moisture	x	– +	+	–	+	+	(Defrenne et al., 2019; Dijkstra & Cheng, 2007; Freschet et al., 2017; Ostonen et al., 2007; Rovira, 1969; Valverde-Barrantes et al., 2017; Weemstra et al., 2021)
Soil Temperature	x	– +	+	+	– +	+	(Defrenne et al., 2019; Karlova et al., 2021; Freschet et al., 2017; Pramanik et al., 2000; Rovira, 1969; Sebastian et al., 2015; Steele et al., 1997; Uselman et al., 2000; Valverde-Barrantes et al., 2017; Weemstra et al., 2021; Zadworny et al., 2016)
Soil Bulk Density	+	–	+	+	x	+	(Ola et al.; Alessa and Earnhart, 1999; Tracy et al., 2013; Freschet et al., 2020)
Nitrogen	x	–	+	+	– *(plant)*	+	(Li et al., 2021; Sun et al., 2020; Uselman et al., 2000; Weemstra et al., 2021)
Phosphorus	x	–	+	+	– *(plant)*	–	(Kim & Li, 2016; Kumar et al., 2019; Ratnayake et al., 1978; Sun et al., 2022)

Table 2

Carex subspathacea root traits. Roots were collected from grazing lawns and ungrazed meadows in the coastal wetlands of the Yukon-Kuskokwim Delta, Alaska. Root traits (0-50 cm) are reported as means ± standard error for percent carbon, (%C), percent nitrogen (%N), C:N ratios, percent phosphorus (%P), root biomass, specific root length (SRL), root volume, and root surface area.

Trait	Grazed	Ungrazed
%C	33.415±0.630	34.526±0.458
%N	1.074±0.029	0.996±0.020
CN	31.609±0.891	35.141±0.962
%P	0.071±0.006	0.070±0.006
Biomass (g)	4.476 ±0.509	4.684 ±0.427
SRL (m g^{-1})	149.47±5.80	159.86 ±10.80
Volume (cm^3)	34.83± 2.65	35.49± 3.27
Surface Area (cm^2)	3485.38 ± 219.56	3813.21± 392.83

Table 3

Root exudation rates for *Carex subspathacea*. Roots were collected from grazing lawns and ungrazed meadows in the coastal wetlands of the Yukon-Kuskokwim Delta, Alaska. Results are reported as average ± standard error in the amount of dissolved organic carbon (DOC) produced per gram of root per day. N=sample size.

Treatment	ug DOC g $root^{-1}$ day^{-1}	N
Grazed	10.740 ± 2.424	9
Ungrazed	7.265 ± 1.606	9

Table 4

Carex subspathacea root decomposition as measured by CO_2 efflux. Independent and interactive effects of root type (no roots, grazed, ungrazed), temperature (10 C & 13 C), feces additions (present or absent), and time on ln (CO_2 efflux) over an 11-week microcosm study. Significant factors with an alpha < 0.05 are indicated in bold.

Term	Chi^2	df	p-value
Root Treatment	**361.419**	**2**	**<0.001**
Feces Treatment	2.070	1	0.150
Temperature Treatment	**76.079**	**1**	**<0.001**
Incubation Day	**2,707.921**	**1**	**<0.001**
Root Treatment: Feces Treatment	**9.398**	**2**	**0.009**
Root Treatment: Temperature Treatment	4.646	2	0.098
Root Treatment: Incubation Day	**118.132**	**2**	**<0.001**
Feces Treatment: Temperature Treatment	2.060	1	0.151
Feces Treatment: Incubation Day	0.850	1	0.357
Temperature Treatment: Incubation Day	**31.939**	**1**	**<0.001**
Root Treatment: Feces Treatment: Temperature Treatment	0.334	2	0.846
Root Treatment: Feces Treatment: Incubation Day	0.199	2	0.905
Root Treatment: Temperature Treatment: Incubation Day	**6.876**	**2**	**0.032**
Feces Treatment: Temperature Treatment: Incubation Day	2.619	1	0.106

Table 5

Post-hoc analysis on the interactive effects of root treatment x incubation day on root decomposition as measured by CO_2 flux [log(μg CO_2 g^{-1} soil hr^{-1})]. The estimate demonstrates that microcosms treated with no root additions have a greater incremental decrease in CO_2 flux per incubation day than microcosms treated with the grazed or ungrazed root treatment. Bolded treatments indicate significant differences.

Contrast	estimate	std error	df	T-ratio	p-value
None - Ungrazed	**-0.012**	**0.001**	**753**	**-9.902**	**<0.001**
None - Grazed	**-0.013**	**0.001**	**753**	**-10.771**	**<0.001**
Ungrazed - Grazed	-0.001	0.001	753	-1.136	0.492

Table 6

Post-hoc analysis on the interactive effects of temperature treatment x incubation day on root decomposition as measured by CO_2 flux [log(μg CO_2 g^{-1} soil hr^{-1})]. The estimate demonstrates that microcosms treated with the high-temperature treatment lost more CO_2 per incubation day. Significant factors are indicated in bold.

Contrast	Estimate	std error	df	T-ratio	p-value
Low-High	**0.004**	**0.001**	**753**	**3.839**	**<0.001**

Table 7

Carex subspathacea root decomposition as measured by carbon loss response ratio. Independent and interactive effects of root type (grazed or ungrazed), temperature (10 C or 13 C), and feces additions (present or absent). Significant factors with an alpha < 0.05 are indicated in bold.

Term	DF	Sum Sq	f-statistic	p-value
Root Treatment	**1**	**0.006**	**17.246**	**<0.001**
Feces Treatment	**1**	**0.001**	**4.167**	**0.048**
Temperature Treatment	**1**	**0.014**	**41.646**	**<0.001**
Root Treatment: Feces Treatment	**1**	**0.002**	**5.087**	**0.030**
Root Treatment: Temperature Treatment	1	0.000	0.270	0.606
Feces Treatment: Temperature Treatment	1	0.000	0.952	0.335
Root Treatment: Feces Treatment: Temperature Treatment	1	0.000	0.094	0.761
Residuals	40	0.013		

Table 8

Effect of *Carex subspathacea* root decomposition on soil NH^+_4 concentrations. Independent and interactive effects of root type (none, grazed or ungrazed), temperature (10 C or 13 C), and feces additions (present or absent) on soil NH^+_4 *concentrations*. Significant factors with an alpha < 0.05 are indicated in bold.

Variable	Sum sq	DF	F-value	p-value
Root Treatment	**3979.2**	**2**	**59.730**	**<0.001**
Temperature Treatment	**1609.7**	**1**	**48.327**	**<0.001**
Feces Treatment	0.3	1	0.010	0.919
Root Treatment: Temperature Treatment	87.8	2	1.319	0.275
Root Treatment: Feces Treatment	206.5	2	3.100	0.052
Temperature Treatment: Feces Treatment	12.3	1	0.368	0.546
Root Treatment: Temperature Treatment: Feces Treatment	105.7	2	1.586	0.213
Residuals	1998.6	60		

Table 9

Effect of *Carex subspathacea* root decomposition on logged soil nitrate (NO^-_3) concentrations. Independent and interactive effects of root type (none, grazed or ungrazed), temperature (10 C or 13 C), and feces additions (present or absent). Significant factors with an alpha < 0.05 are indicated in bold.

Variable	Sum sq	DF	F-value	p-value
Root Treatment	0.128	2	0.525	0.594
Temperature Treatment	0.001	1	0.009	0.927
Feces Treatment	0.278	1	2.277	0.137
Root Treatment: Temperature Treatment	0.182	2	0.746	0.479
Root Treatment: Feces Treatment	0.046	2	0.189	0.828
Temperature Treatment: Feces Treatment	**0.611**	**1**	**5.00**	**0.029**
Root Treatment: Temperature Treatment: Feces Treatment	0.105	2	0.430	0.652
Residuals	7.3280	60		

Table 10

Effect of *Carex subspathacea* root decomposition on post-incubation root C:N. Independent and interactive effects of root type (grazed or ungrazed), temperature (10 C or 13 C), and feces additions (present or absent). Significant factors with an alpha < 0.05 are indicated in bold.

Variable	Sum sq	DF	F-value	p-value
Root Treatment	**1,503.398**	**1**	**345.801**	**0.000**
Temperature Treatment	**20.880**	**1**	**4.803**	**0.034**
Feces Treatment	0.095	1	0.022	0.883
Root Treatment: Temperature Treatment	0.030	1	0.007	0.935
Root Treatment: Feces Treatment	4.863	1	1.119	0.297
Temperature Treatment: Feces Treatment	1.038	1	0.239	0.628
Root Treatment: Temperature Treatment: Feces Treatment	9.920	1	2.282	0.139
Residuals	169.556	39		

Table 11

Effect of *Carex subspathacea* root decomposition on post-incubation logged root %N. Independent and interactive effects of root type (grazed or ungrazed), temperature (10 C or 13 C), and feces additions (present or absent). Significant factors with an alpha < 0.05 are indicated in bold.

Variable	Sum sq	DF	F-value	p-value
Root Treatment	**0.795**	**1**	**203.298**	**<0.001**
Temperature Treatment	0.001	1	0.242	0.626
Feces Treatment	0.001	1	0.220	0.641
Root Treatment: Temperature Treatment	0.000	1	0.122	0.723
Root Treatment: Feces Treatment	0.004	1	0.900	0.349
Temperature Treatment: Feces Treatment	0.005	1	1.311	0.259
Root Treatment: Temperature Treatment: Feces Treatment	0.000	1	0.009	0.927
Residuals	0.152	39		

Table 12

Effect of *Carex subspathacea* root decomposition on post-incubation root %C. Independent and interactive effects of root type (grazed or ungrazed), temperature (10 C or 13 C), and feces additions (present or absent). Significant factors with an alpha < 0.05 are indicated in bold.

Variable	Sum sq	DF	statistic	p-value
Root Treatment	**102.403**	**1**	**52.209**	**<0.001**
Temperature Treatment	**37.965**	**1**	**19.356**	**<0.001**
Feces Treatment	3.146	1	1.604	0.213
Root Treatment: Temperature Treatment	0.181	1	0.093	0.763
Root Treatment: Feces Treatment	0.225	1	0.115	0.737
Temperature Treatment: Feces Treatment	1.223	1	0.623	0.435
Root Treatment: Temperature Treatment: Feces Treatment	**17.475**	**1**	**8.909**	**0.005**
Residuals	76.495	39		

Table 13

Effect of *Carex subspathacea* root decomposition on post-incubation root logit transformed acid fiber detergent (%ADF). Independent and interactive effects of root type (grazed or ungrazed), temperature (10 C or 13 C), and feces additions (present or absent). Significant factors with an alpha < 0.05 are indicated in bold.

Variable	Chi sq	DF	p-value
Root Treatment	0.227	1	0.634
Temperature Treatment	**8.599**	**1**	**0.003**
Feces Treatment	3.207	1	0.073
Root Treatment: Temperature Treatment	**6.224**	**1**	**0.013**
Root Treatment: Feces Treatment	0.579	1	0.447
Temperature Treatment: Feces Treatment	1.623	1	0.203

Figure 1

A conceptual diagram of root C inputs and likely decomposition rates. Root decomposition and C input rates can vary based on C:N, morphology, and architecture. If an individual plant's trait expression shifts to increasing coarse or deep roots, the total C input and C in the soil may increase. Alternatively, if root exudates increase or fine root production increases, root decomposition may increase.

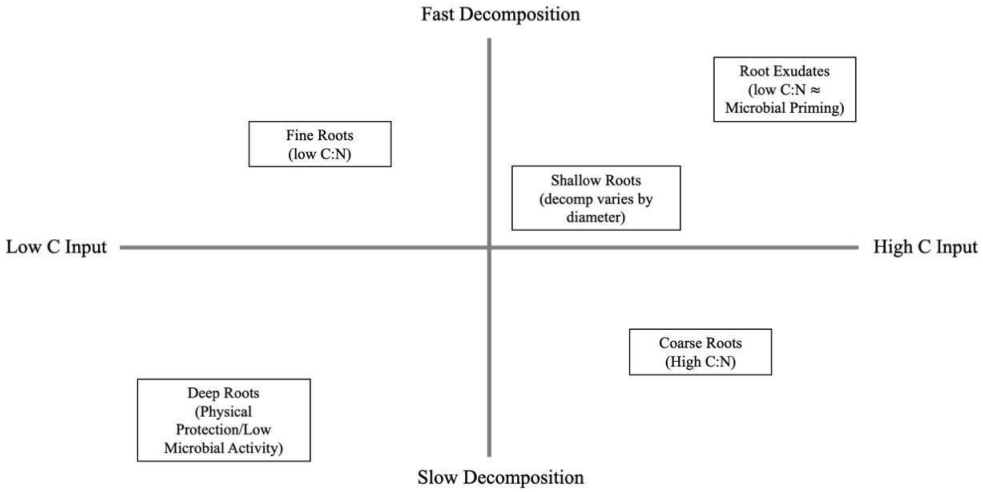


Figure 2

Carex subspathacea root morphology by depth and habitat type (grazing lawn and ungrazed meadow) for the natural root trait survey in the Yukon Kuskokwim Delta. All y-axes are soil depth. On the x-axis from the top left panel to the right are total root length, root volume, root surface area, root biomass, and specific root length. We did not observe differences in morphological traits between habitat types, but we did see differences in trait expression at different depths.

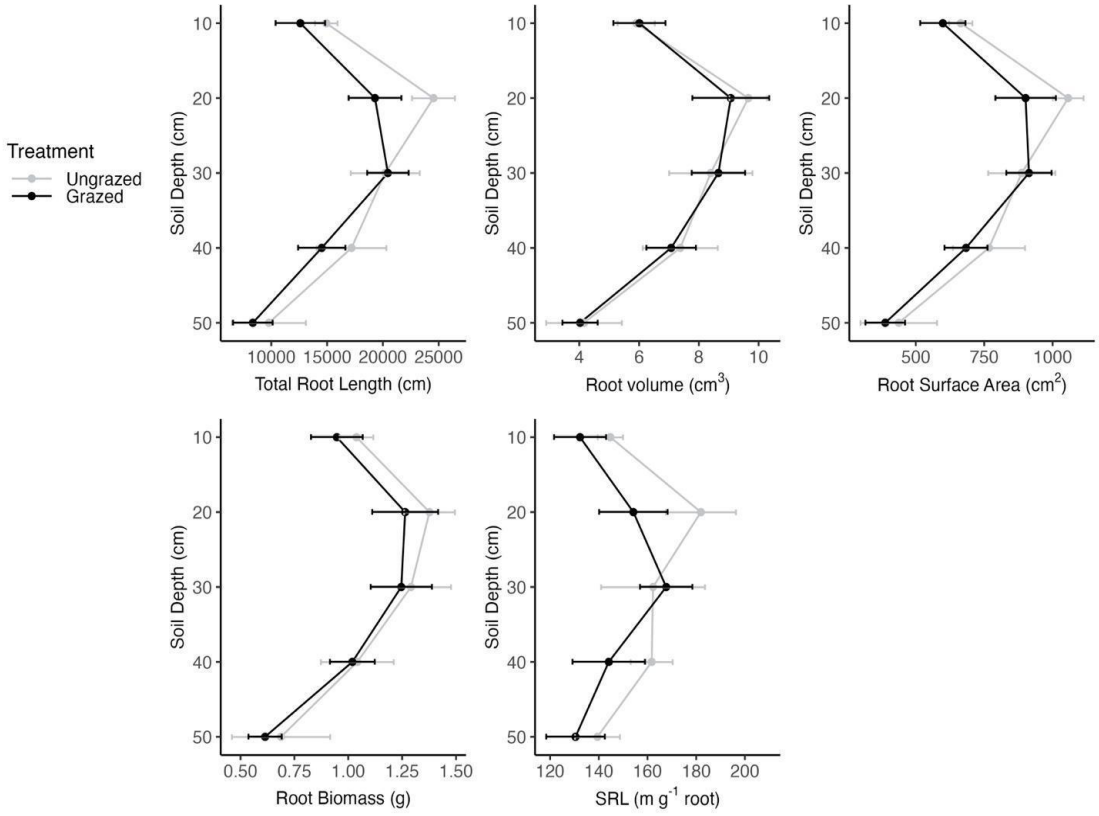


Figure 3

Carex subspathacea root chemistry by habitat type (grazing lawn and ungrazed meadow) for the natural root trait survey in the Yukon Kuskokwim Delta. Root chemical composition shown in average ± standard error per habitat type. Top left- Percent root carbon (%C). Top Right – Mean carbon to nitrogen ratios (CN). Bottom left – Mean percent root nitrogen (%N). Bottom Right- Mean percent root phosphorus (%P). The capital letters in each figure indicate if there are significant differences in the response variable between habitat types.

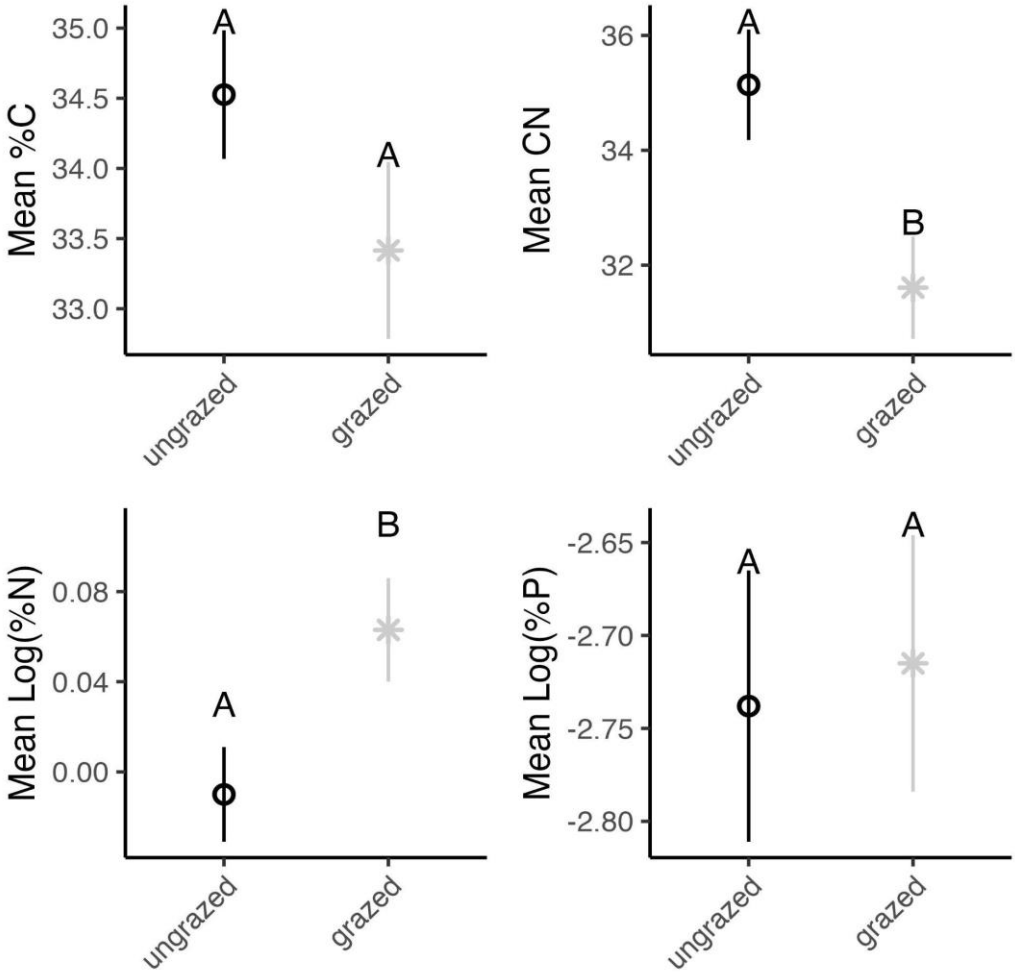


Figure 4

Carex subspathacea root morphological traits by habitat type (grazing lawn and ungrazed meadow) for root samples used in the decomposition experiment. Left- shows specific root length (SRL) by habitat type, Middle - is root volume by habitat type, and Right - is root surface area by habitat type. There were no significant differences between the morphological characteristics of habitat types.

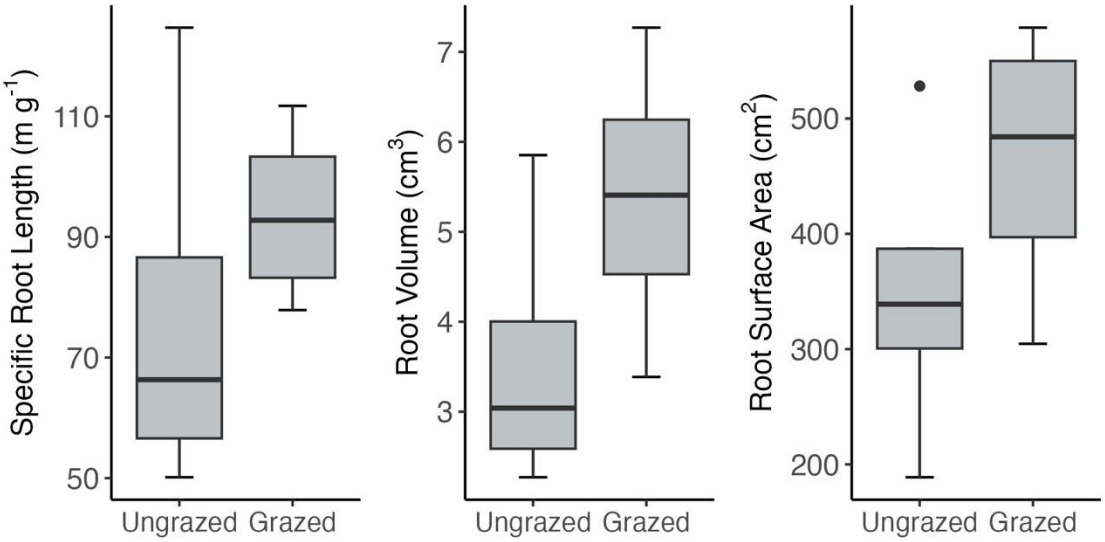


Figure 5

Carex subspathacea root morphological traits by habitat type (grazing lawn and ungrazed meadow) and diameter size class for root samples used in the YK Delta decomposition experiment. Values are depicted in means ± standard error. The y-axis shows the diameter size class by millimeter, and from the top panel down is root length, root surface area, and root volume. Roots from the grazing lawn have a greater length in the finest diameter size class than roots from the ungrazed meadows. There are also differences between morphological root trait expression in the largest diameter size class for root volume and root surface area.

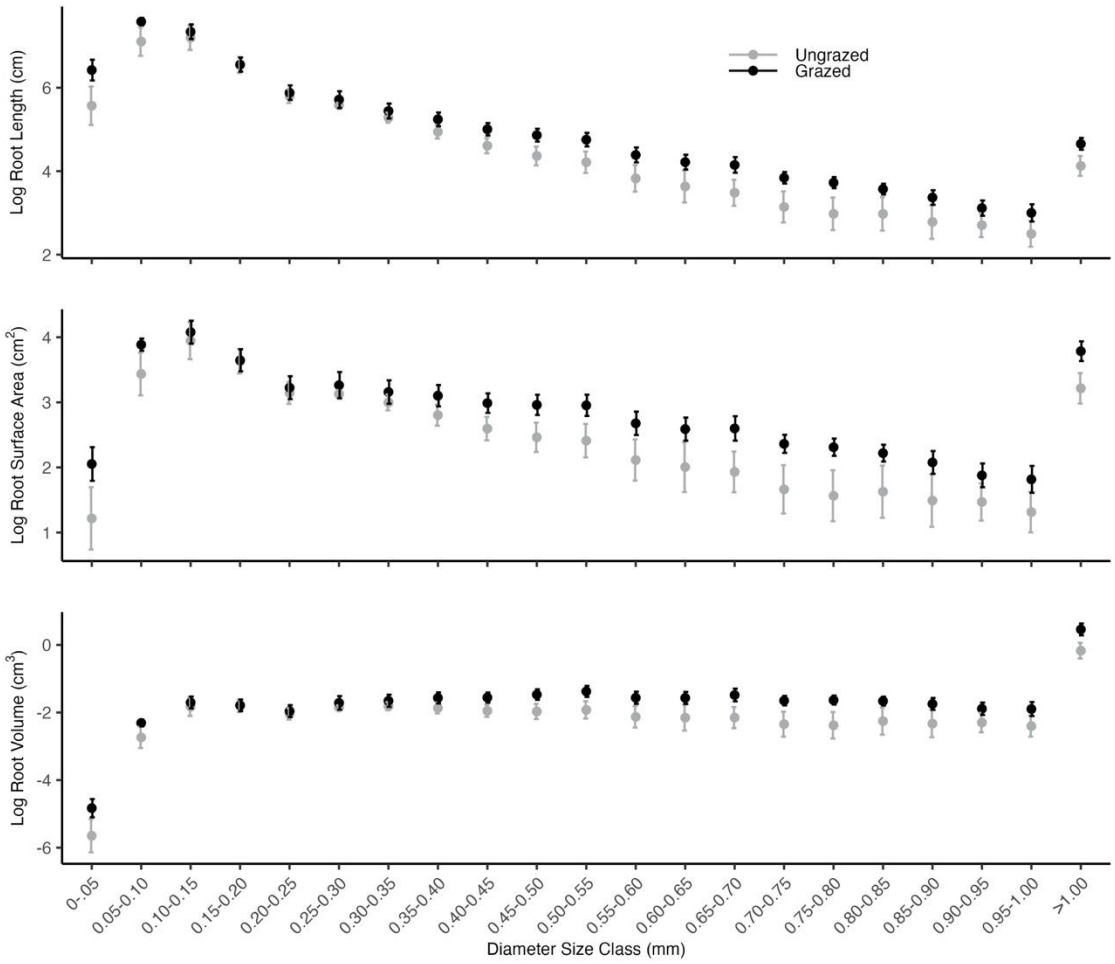


Figure 6

Carex subspathacea root chemical composition by habitat type (grazing lawn and ungrazed meadow) for root samples used in the decomposition experiment. The figure includes percent nitrogen (N), percent carbon (C), and C:N of root litter pre- and post-microcosm incubation. “Pre” indicates the root treatment prior to the incubation process. Post-incubation values are labeled grazed or ungrazed, depending on root treatment. The grazed litter treatment shows significantly different pre- and post-incubation values in root %N, root %C, and C:N. The ungrazed root litter treatment did not differ from pre-incubation values in root %N or C:N but was marginal for root %C. The grazed root litter treatment and the ungrazed root litter treatment were significantly different in pre- and post-incubation values for root %N, root %C, and C:N.

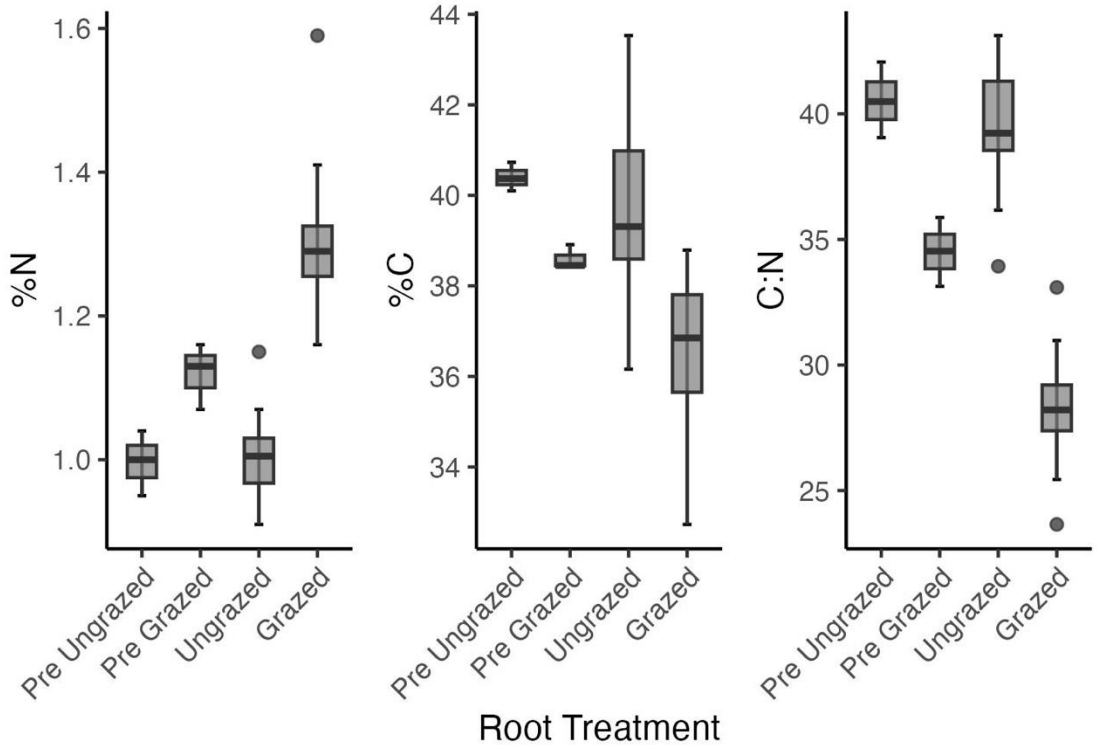


Figure 7

Carex subspathacea root % Acid Fiber Detergent (ADF) by habitat type per (grazing lawn and ungrazed meadow) for the root decomposition experiment. Effects of decomposition and temperature treatment (ungrazed/low = 10 °C and grazed/high = 13 °C) on root %ADF. Root %ADF differed between habitat types for the pre-incubation root treatment, as indicated with different lettering. Pre-incubation grazed ungrazed root (Pre-Ungrazed) Further, we see that temperature treatment significantly affected root %ADF for the ungrazed root treatment but had no effect on the grazed root treatment.

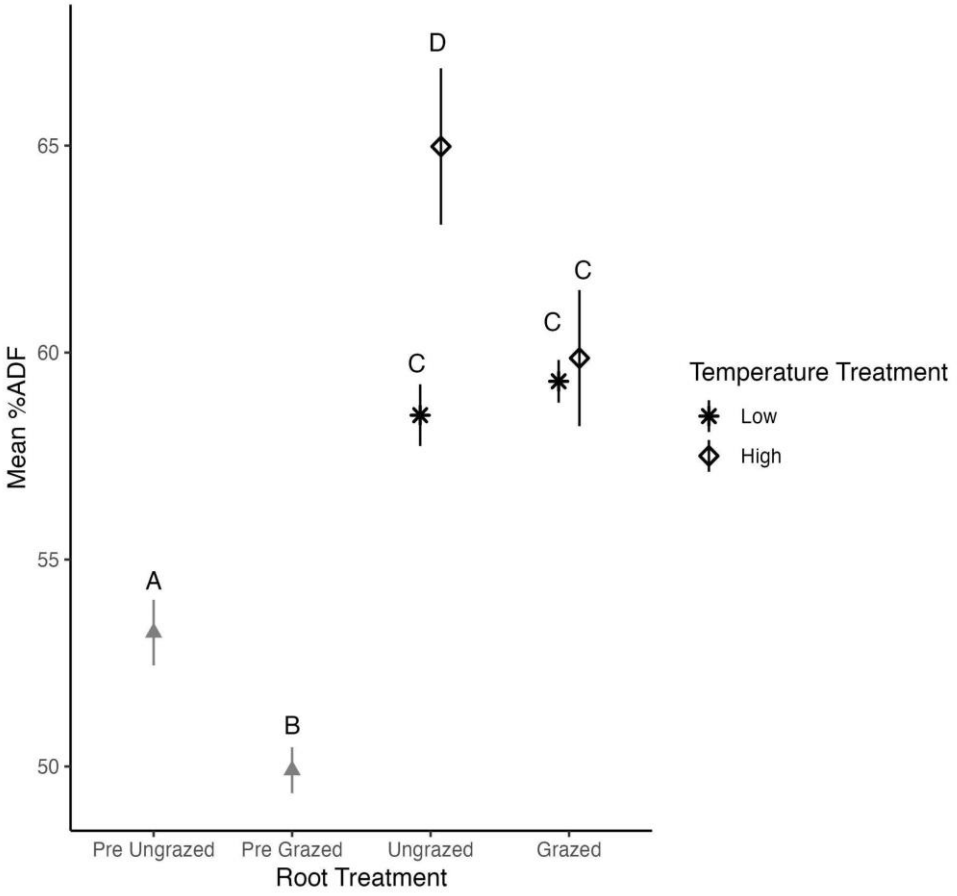


Figure 8

Carex subspathacea root decomposition CO_2 flux rate for the YK Delta root decomposition experiment. Experiment treatments included root treatment (none, ungrazed, grazed), temperature treatment (low = 10 °C and high = 13 °C), and feces additions (none or added). Left- The linear predicted change in flux modeled from the generalized linear mixed mode shown on the response scale (μg CO_2 -C g^{-1} soil hr^{-1}) for the interaction between root treatments and temperature treatments. Top- The effect of temperature on mean (± standard error) CO_2 flux rate is shown as a data summary. Bottom – The effect of root treatment on the mean (± standard error) on CO_2 flux rate is shown as a data summary.

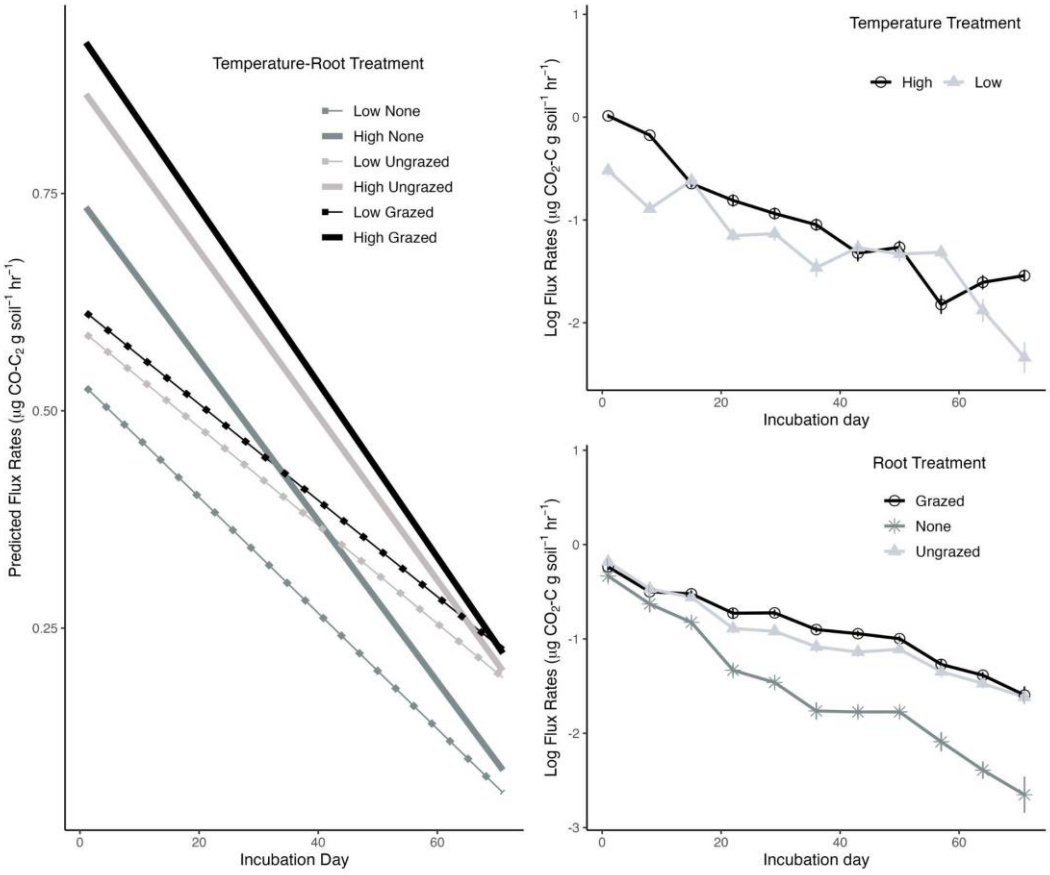


Figure 9

Carex subspathacea root decomposition carbon (C)loss response ratio for the Yukon Kuskokwim Delta root decomposition experiment. Left: Effects of root and feces treatment interaction on the C loss response ratio (C loss via CO_2 efflux per C input) shown as the mean ± standard error. A variable denoted with the letter "A" indicates there were no significant differences between treatment combinations. Statistical differences are denoted with the letter B (grazed, feces omitted) and the letter "C" (grazed, feces added). Right: Effects of the temperature treatment (low =10° C, high = 13° C) on C loss shown as the mean ± standard error. Different letters above the variables (A and B) indicate that the microcosm treated in the high-temperature treatment had a significantly higher C loss response ratio.

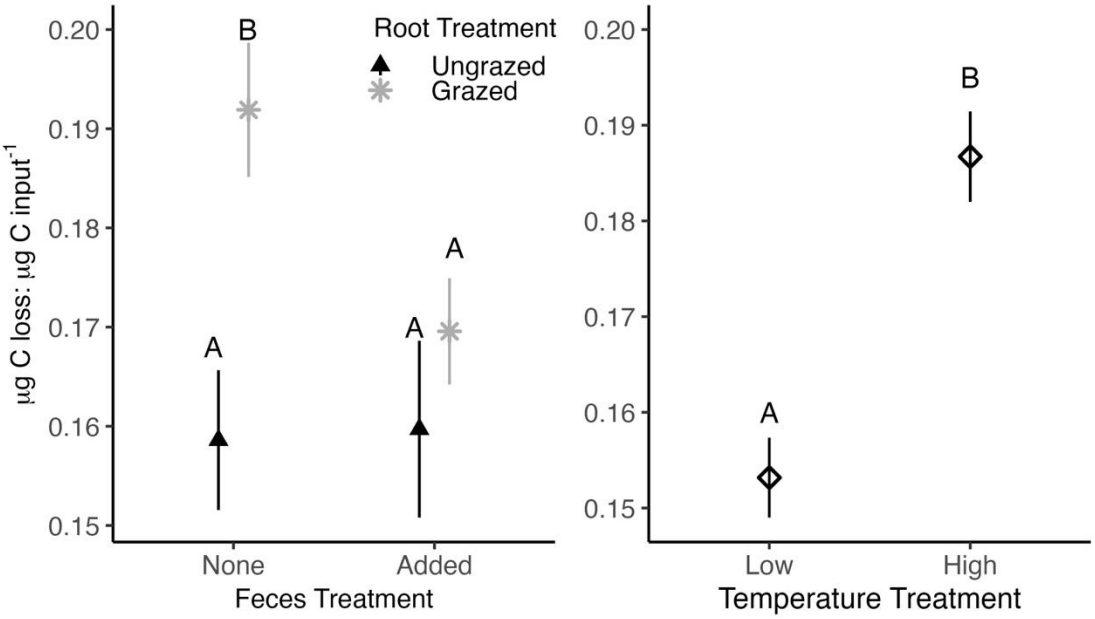


Figure 10

Carex subspathacea root decomposition effects on soil inorganic nitrogen concentrations for the YK Delta root decomposition experiment. Treatment effects include root treatment (none, ungrazed, grazed), feces treatment (none, added), and temperature treatment (low at 10 °C and high at 13°C). Left: This graph illustrates the interactions between feces treatment and temperature treatment on post-incubation soil inorganic nitrate (NO_3^-) concentrations, represented as the means ± standard error (SE). Capital letters indicate significant differences resulting from feces treatment across temperature variations. Middle: The impact of root treatment on post-incubation soil NH_4^+ concentrations, depicted as average values ± standard error. Capital letters indicate significant differences compared to the other treatments. Right: This section portrays the influence of temperature treatment on post-incubation soil ammonium (NH_4^+) concentrations, presented as means ± standard error.

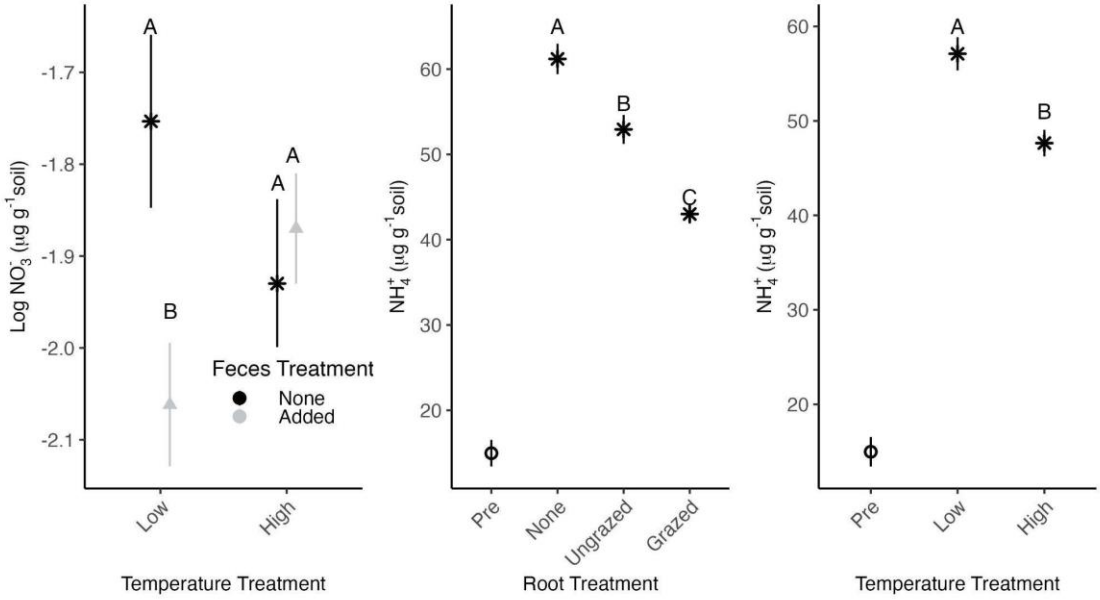
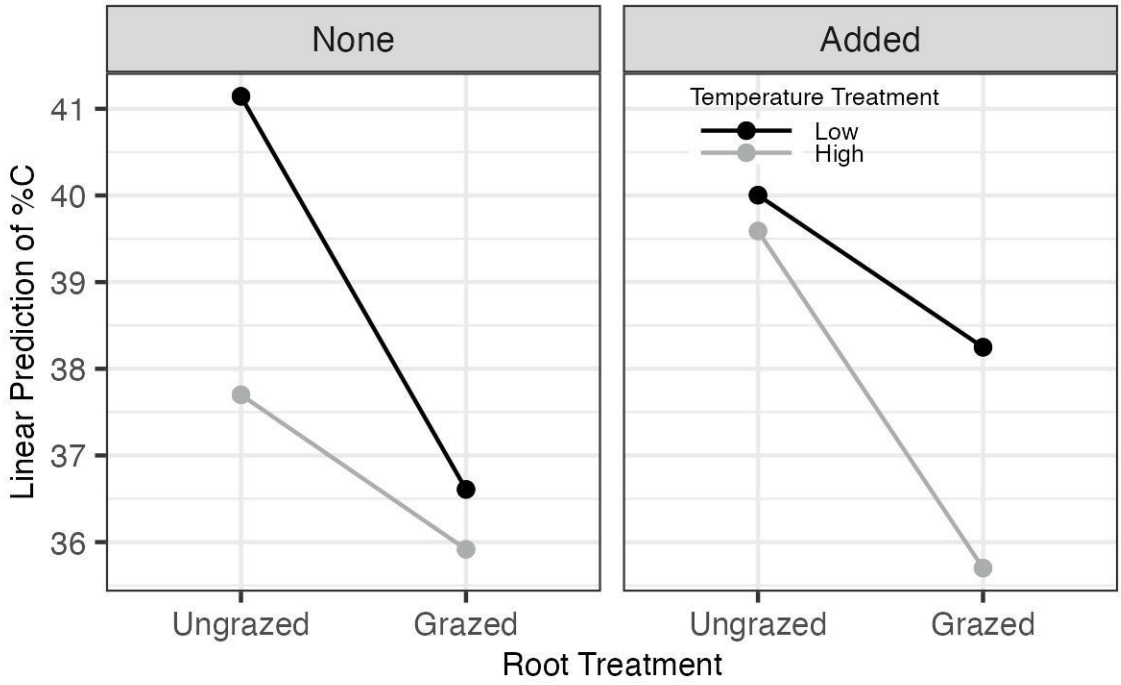


Figure 11

Decomposition effects on *Carex subspathacea* root % carbon (C). The predicted three-way interaction of root, feces, and temperature on root %C post-incubation. The column on the right represents how root and temperature treatment affect root litter root %C when feces is omitted, and the left column depicts the same interaction when feces is added. In all cases, there is a lower root C concentration in root litter exposed to grazing compared to ungrazed, suggesting that root treatment has a strong influence on root %C.



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