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RESEARCH ARTICLE

Goose herbivory effects on early-stage litter decomposition in coastal Alaskan wetlands

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Abstract

Aims Herbivores create large differences in litter decomposition rates, but identifying how they do this can be difficult because they simultaneously influence both biotic and abiotic factors. In the Yukon-Kuskokwim (Y-K) River Delta in western Alaska, geese are dominant herbivores in wet-sedge meadows, where they create 'grazing lawns' that have nutrient-rich litter and an open habitat structure. To understand how geese affect decomposition, we tested the effects of litter quality and habitat type on litter decomposition over one year.

Methods We performed a litter bag study in which we collected two litter types representing grazed and ungrazed vegetation conditions (high quality litter similar to grazed litter, and lower quality senesced, ungrazed litter), then incubated them in 'grazing lawn' and ungrazed meadows. Litter mass loss, carbon, nitrogen, cellulose and lignin content were measured after 3, 6, 9, and 52 weeks. We also monitored abiotic conditions (i.e., soil temperature, UV radiation, throughfall, and soil moisture content) in each habitat type.

Results High-quality litter (lower lignin:N ratios) lost more mass than low-quality ungrazed litter over the whole study. However, at different times during the decomposition process, lower quality litter decomposed faster in grazed habitat, whereas higher quality litter decomposed faster in ungrazed habitat. This occurred despite abiotic conditions in grazed habitat that generally promote faster decomposition.

Conclusion Results suggest that herbivore-induced increases in litter quality increase decomposition rates, and that the accumulation of the low-quality litter in ungrazed habitats is partly due to slow decomposition rates. While herbivores influence habitat conditions, the effects of habitat on decomposition differed across litter qualities, which suggests that other variables, such as differing microbial communities, play a role in decomposition processes.

Keywords *Carex* · Geese · Home-field advantage · Litter bag study · Microbial communities · Western Alaska

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Introduction

Herbivores influence a variety of ecosystem carbon (C) and nitrogen (N) pools (e.g., in aboveground biomass and litter) and fluxes that influence, or emerge from, the dynamics of litter decomposition. Especially in Arctic and sub-Arctic regions, herbivores can exert an outsized effect on C and N cycling because they shape habitats and change the distribution of nutrients on the landscape (Koltz et al. 2022). While their role in biogeochemical cycles is often overlooked at global scales, herbivores influence decomposition rates by removing biomass, which can affect litter quality (Chollet et al. 2021) and influence soil microclimates (Penner and Frank 2019), but the relative importance of these biotic vs. abiotic changes is debated. Further, whether herbivores positively or negatively affect decomposition rates in Arctic and sub-Arctic ecosystems is dependent on multiple factors (Olofsson and Oksanen 2002; Sjögersten et al. 2012; Tuomi et al. 2019). Identifying the main drivers behind herbivore-induced differences in litter decomposition rates will facilitate understanding of C and N cycling both within and across Arctic ecosystems.

One of the main mechanisms by which herbivores exert indirect effects on litter decomposition is through their effects on litter quality (Wardle et al. 2004). In non-nutrient limited ecosystems, plants may respond to grazing by regrowing plant tissue with higher N and lower lignin content (Wardle et al. 2002; Chapman et al. 2003), and subsequently, decomposition rates can increase as litter with higher N and lower lignin content often decomposes faster (Olofsson and Oksanen 2002; Sjögersten et al. 2012). Where this occurs, it can form positive feedbacks between high quality forage and herbivores because herbivores tend to select plants with higher N (Wardle et al. 2002; Barthelemy et al. 2015). These herbivore-induced increases in litter quality increase decomposition rates by alleviating nutrient limitations on decomposers.

Herbivore grazing may also influence litter decomposition by affecting soil microclimates. Grazing-induced loss of plant biomass exposes soils to increased solar radiation, which can influence decomposition through UV exposure (Lin and King 2014; Austin et al. 2016). Loss of plant cover can also increase soil temperature and throughfall (Sjögersten et al. 2012). Reduction of leaf area also decreases transpiration, which can result in higher soil moisture (Frank et al. 2018). Such changes to temperature and soil moisture could increase decomposition rates by increasing microbial respiration and activity (Chuckran and Frank 2013; Kelsey et al. 2018) and litter leaching rates (García-Palacios et al. 2016; Petraglia et al. 2019).

Finally, herbivores also directly affect litter decomposition by depositing readily available forms of nitrogen and other nutrients to soil in the form of feces and urine (Sitters et al. 2017). This may release soil microbes from nutrients limitation, particularly in ecosystems where nutrient availability strongly constrains microbial growth. These nutrient additions can also change microbial community composition (Bardgett et al. 2001; Eldridge et al. 2017; Foley et al. 2022), which can further impact decomposition (Saunders et al. 2023).

Spatial variation in the intensity of goose herbivory in coastal ecosystems in western Alaska provides a ‘natural laboratory’ to investigate the influence of herbivores on litter decomposition. Tens of thousands of herbivorous geese migrate to the coastal wetlands in the Yukon–Kuskokwim (Y-K) Delta during the summer breeding season (Sedinger et al. 1993). Geese in these ecosystems primarily feed on the abundant sedge species, *Carex subspathacea* (hereafter referred to as *Carex*), creating’grazing lawns’ of short-statured *Carex* with higher quality forage (decreased C:N ratios and lignin content) compared to immediately adjacent ungrazed *Carex* meadows (Person et al. 2003; Beard et al. 2019; Ruess et al. 2019). Compared to the ungrazed meadows, grazing lawns have very little aboveground vegetation, small amounts of standing dead vegetation, higher soil temperature, and greater soil moisture (Foley et al. 2022). Grazing lawns generally remain in the same locations year to year, but can change in space and time with goose abundance via positive feedback dynamics (Uher-Koch et al. 2019). Despite the same species of *Carex* dominating both grazing lawns and meadows, grazing-mediated differences in vegetation quality and abiotic habitat features likely impact litter decomposition rates.

Our goal was to assess how herbivore-driven differences in litter quality and abiotic factors in the Y-K Delta influence decomposition rates of *Carex* litter. We hypothesized that: 1) goose-driven increases in litter quality (higher N, lower lignin content) mean that grazed litter will generally decompose faster than ungrazed litter, and 2) both low- and high-quality litter types will decompose faster in grazed habitats compared to ungrazed habitats because of more favorable abiotic conditions for decomposition (i.e., increased temperatures, soil moisture and UV radiation). To address these hypotheses, we investigated rates of mass, labile C and N, cellulose, and lignin losses from two types of litter (representing both grazed and ungrazed habitats) in two habitats (grazing lawns and ungrazed meadows) over the course of one year. To gain insights into how the environmental conditions in grazing lawns and ungrazed meadows interact with litter quality to affect litter decomposition, we monitored abiotic variables in both habitats, including soil temperature, UV radiation, throughfall, and soil moisture content. We assessed how these environmental parameters related to observed differences in decomposition rates (Elliott and Henry 2011; Frank et al. 2018; Vaieretti et al. 2018).

Materials and methods

Study site

We conducted this study in the Y-K Delta National Wildlife Refuge along the bank of the Kashunuk River (61°19′59″ N, 165°37′52″ W; approximately 4 km from the coast, elevation < 1 m; Fig. 1). The climate is maritime, with mean winter (January-March) air temperatures of −12.2 °C and mean summer (June–August) air temperatures of 12.5 °C (Palecki et al. 2021). Mean annual snowfall is 1626 mm and mean annual precipitation (rain + snow-water equivalent) is 499 mm (Palecki et al. 2021). The ground is typically covered with snow from October until around May (Ely et al. 2018; Palecki et al. 2021). The growing season is usually late May until mid- to late August, with plants starting to senescence at our study sites in early to mid-August. Soils have a pH between 6.8 and 7.0 and are predominantly silt and sand deposits (Tande and Jennings 1986; Foley et al. 2022).

Within the Refuge, grazing by *Branta bernicla nigricans* (Pacific black brant) and *Branta hutchinsii* (cackling geese) converts *Carex subspathacea*,

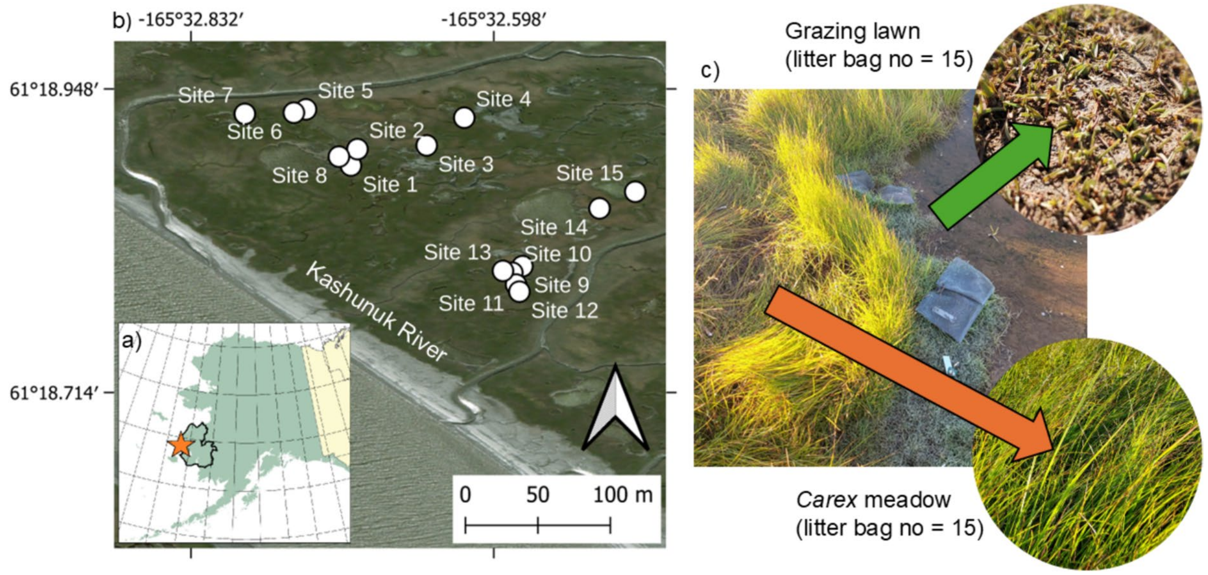

Fig. 1 Map of the Yukon-Kuskokwim Delta refuge outlined in black within Alaska with the star indicating where the study was located (**a**), the 15 study site locations with the refuge (**b**), and photos showing a representative site with both habitat types (grazing lawn and *Carex* meadow), which received four litter bags of each litter type (**c**). A total of 240 litter bags (15 sites × 2 habitat types × 2 litter types × 4 collection periods) were used in the study, so n = 15 for each litter type per habitat per collection period

the dominant vegetation in ungrazed meadows into a short-statured vegetation type called 'grazing lawns' (Person et al. 2003). Grazing lawn vegetation is typically 1–2 cm tall, while vegetation in the ungrazed *Carex* meadow is 15–16 cm tall (Kelsey et al. 2016). Grazing lawns are usually around pond margins and are patchy on the landscape but always directly adjacent to *Carex* meadows. Both habitat types are > 90% *Carex subspathacea* for both biomass and cover. Daytime soil temperatures are higher in the heavily grazed 'grazing lawn' than in nearby ungrazed *Carex* meadow, with mean daily summer temperatures around 13 °C in grazing lawn and around 10 °C in *Carex* meadow (Kelsey et al. 2016). At the end of the growing season, standing dead vegetation covers more than three times the area in *Carex* meadow than in grazing lawn (Kelsey et al. 2016). At the beginning of each growing season in the meadows, plants grow through layers of senesced material deriving from previous summers.

Litter decomposition experiment

Towards the beginning of the growing season, we collected plant samples that best represent the types of litter that would decompose in grazed and ungrazed habitats over the growing season. In this low Arctic ecosystem, *Carex* does not senesce in either habitat type until mid- to late August. We therefore collected senesced litter in *Carex* meadow from the uppermost portion of the litter layer, because this material best represents litter from the previous year of growth. It had not yet experienced growing season decay yet had experienced winter decomposition. To represent grazing lawn litter, we collected live, green *Carex* from meadows for two reasons: (1) it was not possible to collect enough vegetation from grazing lawns for the experiment without denuding large swaths of this critical goose habitat, and (2) early season green *Carex* is very similar in quality to end-of-the growing season grazing lawn litter (Table 1; Saunders et al. 2023). We recognize this was not actual grazing lawn or grazed litter and discuss the limitations of litter choices in the Discussion – however, our design did capture litters with very different chemistries (Table 1).

More specifically, in late May and early June 2022, we collected random samples of senesced litter from the uppermost portion of the litter layer, and green, live *Carex* strands from a 100 m × 100 m area to fill 240 litter bags. Half of the litter bags were filled with green, live *Carex* (hereafter referred to as green litter) and half were filled with senesced *Carex* (hereafter referred to as senesced litter). We placed approximately 5 g of dry-weight litter material in the 240, 10 cm × 10 cm litter bags with 2 mm mesh (Karberg et al. 2008). To determine the amount of litter added to each bag, we retained air-dried subsamples of pre-decomposition litter that had been weighed in the field, dried them at 65 °C to constant weight, and determined an air-dried to dry-weight conversion ($n = 10$ per litter type).

We placed half the litter bags of each litter type on the soil surface in *Carex* 'grazing lawn' and the other half of the litter bags in ungrazed *Carex* meadows. We used 15 replicate sites, with on average 21 m separating sites, where we placed four bags of each litter type (i.e., 4 in the grazing lawn and 4 in *Carex* meadow) within 5 m of each other (Fig. 1). In total, there were 16 bags per site (2 litter types x 2 habitat types × 4 collection periods). For all meadow sites, because they contained a layer of senesced litter on the soil surface, we lifted the litter, placed the litter bag so that it had direct contact with the soil,

Table 1 Chemistry of pre-decomposition litter used in litter bags collected toward the beginning of the growing season included new green (current season) leaves and senesced (previous season) litter from *Carex* meadow. For comparison, chemistry of litter collected at the end of the growing season of senescing *Carex* from grazing lawn, and green senescing (end of season) leaves and senesced (previous season) litter from *Carex* meadow from Saunders et al. (2023). n = sample size. *from Saunders et al. (2023)

Collected	Habitat	Leaf Type	*n*	C%	N%	Lignin %	Lignin:N	C:N
End of season*	Grazing Lawn	Senesced	4	45.12	3.35	17.63	5.26	13.47
Early season	Meadow	Green	5	40.53	2.39	14.58	6.10	16.96
End of season*	Meadow	Green	4	45.10	2.15	12.55	5.84	21.01
Early season	Meadow	Senesced	5	37.37	0.45	10.33	22.96	83.04
End of season*	Meadow	Senesced	4	40.91	0.61	13.68	23.38	67.56

and replaced the senesced litter layer on top of the bag. We installed all litter bags on 17 June 2022, and, after 3 weeks (7 July), 6 weeks (27 July), 9 week (14 August), and 52 week (16 June 2023), we collected one litter bag of each litter type from each habitat per site ($n = 15$).

From 17 June to 14 August 2022, we measured abiotic factors in both habitat types, at seven of the replicate fifteen sites ($n = 14$ habitats total). To measure throughfall, we installed 50 mL Falcon tubes (2.8 cm diameter, 12 cm depth) into the ground, protruding 1 cm above the soil surface. We collected water in the tubes after 3 weeks (representing throughfall from 0–3 weeks), 6 weeks (representing throughfall from 3–6 weeks), and 9 weeks (representing throughfall from 6–9 weeks). We measured soil surface temperature continuously using Thermochron iButtons (iButtonLink Technology, Whitewater, Wisconsin). We averaged daily temperature at solar noon for each habitat type during each 3-week collection period for analysis. We measured UV radiation at the soil surface in grazing lawn and *Carex* meadow habitat approximately weekly for a total of 11 sampling days throughout the growing season using an UVA/B Light Meter 850009 at the soil surface (SPER Scientific, Arizona, USA). For each measurement, we determined UV radiation for 5 min in each habitat type within 4 h of mid-day, alternating habitat types to reduce bias from cloud cover and sun angle. We only used records where the cloud cover remained the same between alternating measurements. We averaged these for each 3-week collection period for analysis. We measured soil moisture at 5 cm depth using EC-5 soil moisture probes in four nearby reference grazing lawn and *Carex* meadow plots (LI-COR, Nebraska, USA). We took soil moisture measurements from 4 June 2022 until 20 July 2022 because monthly high tides flooded the grazing lawn instruments and they were unable to record data after this point. Permit conditions restricted us from taking abiotic measurements over winter.

Upon collection, we brushed litter bags of any visual soil and placed litter bag contents in paper bags to allow them to air dry. We shipped samples to Utah State University, where we dried them at 65 °C until constant weight. We determined mass loss to decomposition as final weight of litter subtracted from the initial weight. We corrected masses by combusting a subsample of each litter bag at 550 °C for 4 h to determine ash-free dry mass (AFDM) conversions (Harmon et al. 1999). Combustion allowed us to correct for potential residual soil contamination.

For all chemical analyses, to reduce the number of samples analyzed, we combined samples from the 15 sites into 5 groups of 3 sites each, that were close together spatially. This created 5 samples of the same litter and habitat type throughout the experiment that we analyzed chemically ($n = 5$ per litter type, habitat, and collection week combination). In addition, we conducted chemical analyses on litter samples collected at the beginning of the experiment ($n = 4$ per litter type). The Analytical Lab at University of Hawai'i at Hilo analyzed these initial and combined samples for C and N using an elemental analyzer (ECS4010, Costech Analytical Technologies, Valencia, CA, USA). We adjusted C and N concentrations on a mass basis, and present them as percent of initial mass remaining after each time point. We also analyzed these initial and combined samples for cellulose and lignin in our laboratory using the acid-detergent method (Gessner 2005).

Statistical analyses

All statistical analyses were performed in the R statistical computing environment v. 4.4.2 (R Core Team 2023). We used linear mixed effects models from the nlme package to determine the effect of litter type, habitat, and collection week on litter mass loss, modelling the site identity as a random effect (Pinheiro et al. 2024). Because samples were combined for chemical analyses, we used linear models to determine the effect of litter type, habitat, and collection week on total C, total N, C:N ratios, cellulose, and lignin remaining in litter bags and did not include random effects. Prior to analysis, C, N, cellulose and lignin were adjusted to initial proportions in litter. We also used linear models to determine the effect of habitat (grazing lawn vs. meadow) and collection weeks (0–3, 3–6, and 3–9) on environmental variables: soil surface temperature, UV radiation, throughfall, and soil moisture. Prior to analysis, we averaged all environmental variables for each time period (0–3 weeks, 3–6 weeks, and 6–9 weeks) and only included data from the seven sites for which this data was collected. For residual checks, we did visual inspections looking at Q-Q residuals, constant leverage, residuals vs.

fitted, and scale-location plots. We log-transformed N and C:N data to meet assumptions of normality. No other transformations were necessary. We used the package "emmeans" to perform post-hoc comparisons with Sidak adjustments (Lenth 2022), and determine model estimates and standard errors for each treatment.

To determine decomposition rate among litter type and habitat combinations across the entire year, we used the total AFDM (ash free dry mass), in the following decomposition function equation (Karberg et al. 2008):

$$\ln(X_t/X_0) = -kt$$

where X_t is the AFDM at the end of the experiment, X_0 is the initial AFDM, k is the decomposition rate constant, and t is time (Wieder and Lang 1982). We used k to determine mean residence time ($1/k$) and time to 95% decomposition ($3/k$).

We used the "AICcmodavg" package in R for a model selection approach to determine which combination of litter type, habitat type, and/or abiotic factors (UV radiation, throughfall, and soil surface temperatures) best explained variance in litter mass loss rates (Mazerolle 2023). Our models included litter type alone; litter type with each abiotic variable alone; and all combinations of abiotic variables. We only included data in these models from the seven sites where we collected abiotic data. We also included models representing only litter type and habitat type, comparing these with the more complex models described above. In so doing, we assumed that 'habitat type' captured our measured abiotic variables as well other differences we did not specifically quantify, e.g., cross-habitat variation in the decomposer community. Prior to analysis, environmental variables were averaged for each time period (0–3 weeks, 3–6 weeks, and 6–9 weeks) as appropriate. We did not include soil moisture in AIC models because soil moisture data was collected in nearby reference plots instead of across litter bag sites, and therefore could not be associated with decomposition of specific litter bags. We checked for collinearity among the abiotic predictor variables used for model selection by calculating the variance inflation factors, using the vif() function in the car package in R (Fox and Weisberg 2019). All of the values were within an acceptable range ($\mathrm{VIF} < 5$).

Results

Decomposition rates

Litter type affected AFDM (hereafter, mass) loss independently and in an interaction with habitat as well as collection week (Fig. 2a; Table S1). In general, green litter decomposed faster than senesced litter (Table S1). Post-hoc tests revealed that after 52 weeks, within the *Carex* meadow habitat, green litter lost 11.5% more mass than did senesced litter (Table S2). However, after 52 weeks, in the grazing lawn habitat, green and senesced litter did not significantly differ in mass loss. Green litter overall lost 9.6% more mass in meadow than in grazing lawn. Senesced litter overall lost 5.4% more mass in grazing lawn than in meadow.

Between the start of the experiment and week 3, senesced litter lost 12.2% more mass than green litter. However, after 9 weeks and after 52 weeks, green litter had lost 11.4% and 25.0% more mass than senesced litter, respectively. For green litter, 61.8% of the total mass loss occurred during the growing season (between week 0 and 9), and only 38.2% occurred during the winter (between week 9 and one-year). For senesced litter, 60.7% of the total mass loss occurred during the growing season (between week 0 and 9), and only 39.3% occurred during the winter (between week 9 and one-year).

We calculated that decomposition rates were faster for green than senesced litter and that mean residence times for green litter were slightly over one year whereas they were over two years for senesced litter (Table 2). In addition, our results suggest that in both habitat types, green litter could exist on the landscape for 3–4 years whereas senesced litter could exist for 6–7 years.

Litter nutrients and chemical composition

Carbon concentrations adjusted to initial proportions in litter were affected by two-way interactions between litter type and week collected and litter type and habitat (Table S3). After 3 weeks, senesced litter lost 12.2% more of its initial C than green litter (Fig. 2b, Table S4). However, by week 9, green litter had lost 9.3% more of its initial C than senesced litter. Within grazing lawn, green litter lost 4.2% more of its initial C than did senesced

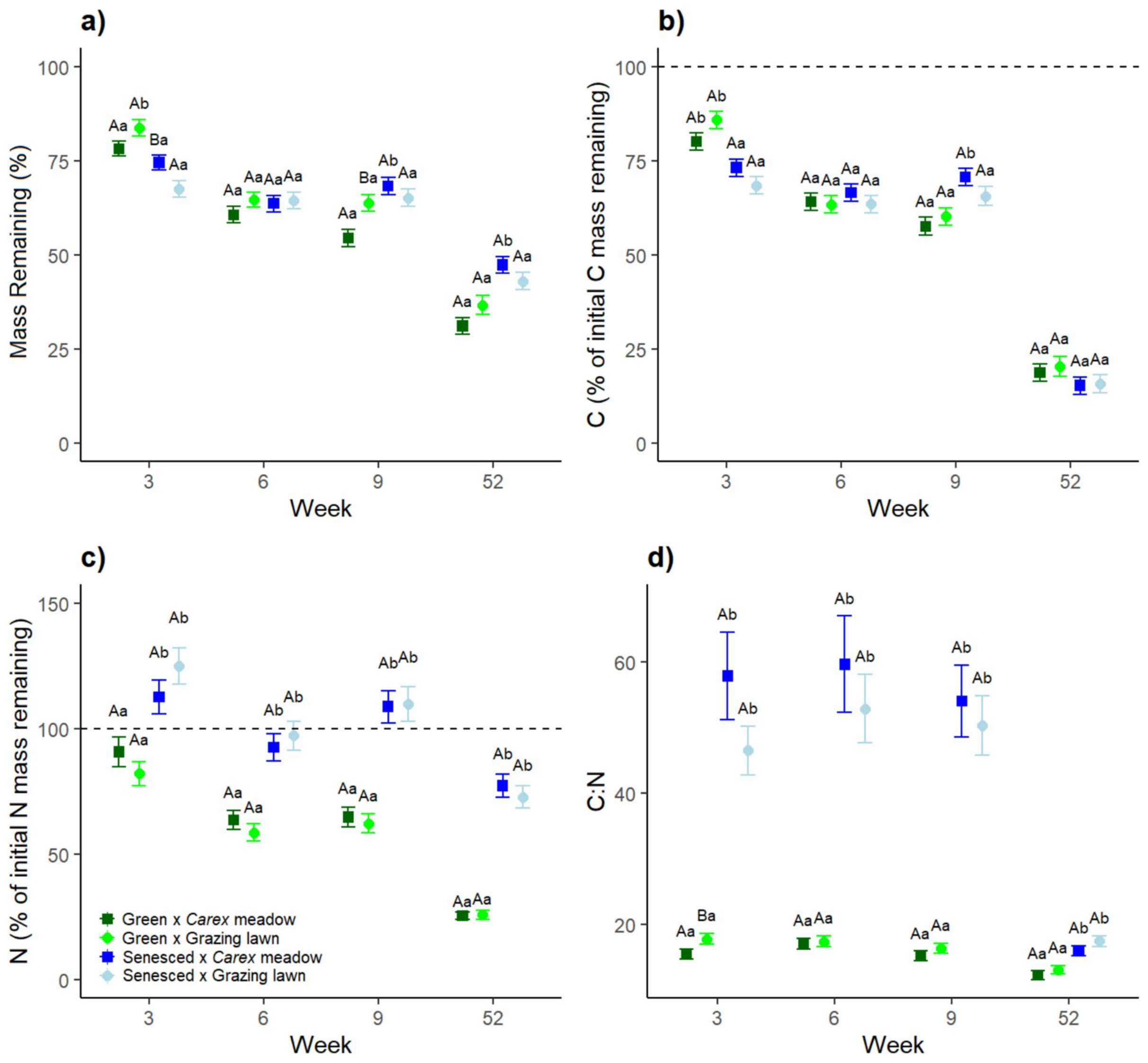

Fig. 2 For each time period by litter type and habitat combinations, modeled means (± SE) for percent of mass remaining (**a**), C remaining as a percent of initial mass (**b**), N remaining as a percent of initial mass (**c**), and C:N ratio (**d**). For each time period, capital letters denote significant differences for a litter type between habitats, while lowercase letters denote litter type differences within habitat ($P < 0.05$). We do not illustrate if there are differences between litter types in different habitats

Table 2 Decomposition constant (k), mean residence time (MRT; 1/k), and time to reach 95% decomposition (3/k) for habitat and litter type combinations. The numbers in the table are calculated based on mass loss values after one year

Habitat	Litter Type	k (days^{-1})	MRT (years)	3/k (years)
Carex Meadow	Green	0.00236 ± 0.00016	1.16 ± 0.77	3.49
	Senesced	0.00118 ± 0.00015	2.32 ± 0.29	6.97
Grazing Lawn	Green	0.00208 ± 0.00016	1.32 ± 0.10	3.95
	Senesced	0.00132 ± 0.00016	2.08 ± 0.26	6.23

litter. There were no significant differences between green litter and senesced litter in *Carex* meadow. Between week 9 and week 52, green litter experienced a 39.3% drop in proportion of initial C remaining, whereas senesced litter experienced a 49.6% drop in initial C remaining.

Nitrogen concentration remaining in litter was affected by litter type and a two-way interaction between litter type and week collected (Table S5). Across all week and habitat combinations of the experiment, green litter lost proportionately more initial N than senesced litter (Fig. 2c, Table S6). Senesced litter became enriched with N compared to its initial N mass for some time periods, with total N for senesced litter greater than its initial N mass after 3 and 9 weeks. After 52 weeks, senesced litter had lost 36.9% of the N mass remaining, while green litter had lost 70.3% of the N mass remaining.

The C:N ratio in litter was affected by litter type and an interaction between litter type and collection week (Fig. 2d, Table S7). Pre-decomposition C:N ratios were 79.5% lower in green litter compared to senesced litter, and across weeks and habitat combinations was lower for green than senesced litter during the experiment. Compared to senesced litter, green litter had 68.2% lower C:N on week 3, 69.4% lower C:N on week 6, 69.9% lower C:N on week 9, and 24.6% lower C:N on week 52 (Table S8).

The percent cellulose remaining in litter was affected by a three-way interaction between litter type, habitat, and collection week (Fig. 3a, Table S9). Initial losses of cellulose were much higher in senesced litter than in green litter, but green litter cellulose losses were higher by week 52 (Table S10). Senesced litter lost 39.2% of its initial cellulose mass in grazing lawn by week 3, more than 12 times the amount that green litter lost in grazing lawn. However, by week 52, there was no significant difference in cellulose losses between senesced and green litter in grazing lawn. In *Carex* meadow, senesced litter lost 27.5% of its initial cellulose mass by week 3, which was a nearly six-fold higher loss of cellulose than green litter experienced. However, in *Carex* meadow by week 52, green litter had lost 70.9% of its initial cellulose, while senesced litter had lost 54.9% of its initial cellulose.

The percent lignin remaining in litter was affected by a three-way interaction between litter type, habitat, and collection week (Fig. 3b, Table S11, Table S12). By week 52 in *Carex* meadow, senesced litter retained 38.8% more lignin than green litter did, but the amount of lignin remaining between

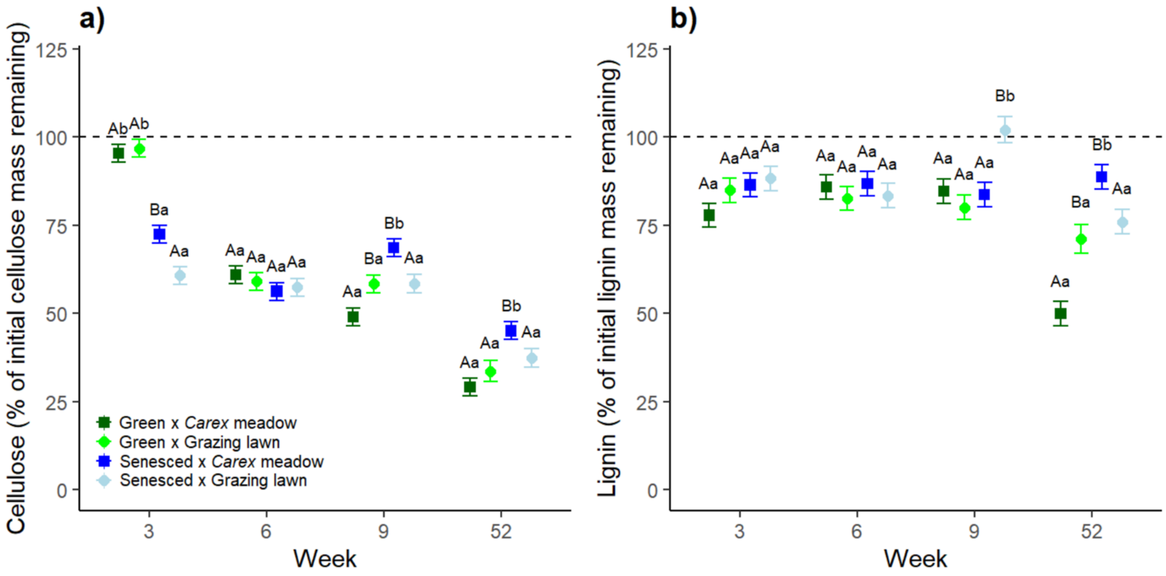

Fig. 3 For each time period by litter type and habitat combinations, modeled mean (±SE) for percent of initial cellulose remaining (**a**) and initial lignin remaining (**b**). For each time period, capital letters denote significant differences between habitats within litter type, while lowercase letters denote litter type differences within habitat ($P < 0.05$). We do not illustrate if there are differences between litter types in different habitats

litter types in grazing lawn did not differ. Green litter in grazing lawn after 52 weeks retained 21.2% more lignin than green litter in *Carex* meadow. On the other hand, senesced litter after 52 weeks had 16.7% more lignin in *Carex* meadow than in grazing lawn. Lignin remaining was significantly different between week 9 and week 52 for green litter in *Carex* meadow and senesced litter in grazing lawn. Lignin remaining in green litter in *Carex* meadow was 35.9% lower after 52 weeks than 9 weeks. Lignin remaining in senesced litter in grazing lawn was 25.6% lower after 52 weeks than 9 weeks.

Environmental factors

Daytime soil surface temperatures were 9% higher in grazing lawn than in *Carex* meadow, approximately 1.5 °C higher over the growing season ($P = 0.003$; Fig. S1). UV radiation was 32.5% higher in grazing lawn compared to *Carex* meadow ($P = 0.009$; Fig. S2). Recorded throughfall volume was 6% higher in grazing lawn compared to *Carex* meadow ($P = 0.015$; Fig. S3). Soil moisture was 27.6% higher in grazing lawn compared to *Carex* meadow ($P < 0.001$; Fig. S4). Despite these strong differences in abiotic factors, AIC model selection indicated that the interaction between litter type and habitat type was more strongly associated with differences in mass remaining than were litter type and any of the environmental factors measured (Table 3).

Discussion

Overall, we found support for the hypothesis that litter quality influences decomposition rates, with the higher quality litter, representing herbivore-induced litter quality changes, experiencing greater mass loss over a year. However, habitat type played a more complicated role. During particular stages of the decomposition process, higher quality (representing grazed) litter tended to decompose faster in the ungrazed habitat whereas lower quality (ungrazed) litter tended to decompose faster in the grazed habitat. This is different from our hypothesis, where we expected that the environmental conditions in grazed habitat would increase decomposition rates of both litter types. Our results suggest that interactive effects of litter quality and habitat affect litter decomposition in unexpected ways, and suggest that other variables, such as microbial communities, may interact with litter quality or environmental factors to influence decomposition.

Litter decomposition and chemical composition

Although litter type impacted decomposition as expected, with high-quality green litter losing more mass over the year than low-quality litter (Hoeber et al. 2020; Prieto et al. 2019; Chollet et al. 2021), we observed that litter type affected the temporal pattern of decomposition in unexpected ways. For example, in the initial 3-week decomposition period, senesced litter decomposed faster than green litter. The lower initial lignin in senesced litter may have driven this

Table 3 Candidate linear model results for mass remaining at 3, 6 and 9 weeks as a response variable. Included in models are combinations of litter types, habitats, and environmental variables averaged by collection period. K = the number of estimated parameters, AICc = corrected for small sample size Akaike Information Criterion, and ΔAICc = the difference in AIC

Candidate models	K	AICc	ΔAICc
Litter * Habitat	5	−268.41	0
Habitat	3	−261.84	6.57
Litter	3	−261.44	6.97
Litter * Soil Surface Temperature	5	−175.89	92.52
Litter * UV	5	−153.94	114.47
Litter * Throughfall	5	−126.85	141.56
Litter * (Throughfall + UV)	7	−100.62	167.79
Litter * (Throughfall + Soil Surface Temperature)	7	−86.07	182.34
Litter * (Soil Surface Temperature + UV)	7	−66.75	201.66
Litter * (Throughfall + Soil Surface Temperature + UV)	9	−60.53	207.88

early mass loss, given that low-lignin material is palatable to decomposers (Austin and Ballaré 2010). This is supported by the 6 to 12 times greater loss of cellulose and carbon, respectively, in the senesced litter compared to the green litter in the first three weeks in both habitat types. This finding suggests that senesced litter had more readily decomposable forms of carbon and that, for this species and location, litter quality (lignin:N ratios) alone did not predict patterns of decomposition.

Other unexpected patterns emerged between the litter types when investigating the loss of C and N, and changes in C:N ratios during the stages of decomposition. Throughout the experiment, senesced litter had much lower (about five times) N concentrations than green litter whereas C concentrations were more similar between the litter types throughout the study. However, during the experiment, senesced litter became enriched in N, likely contributing to its eventual faster later stages of decomposition. More specifically, the enriched N senesced litter is likely due to microbial colonization that contributed to the faster loss of carbon from senesced than green litter between weeks 9 and 52 (Saunders et al. 2023). The relative N enrichment of senesced litter and loss of N in green litter resulted in a convergence of C:N ratios between the litter types, with slightly higher ratios for senesced litter, at the end of the experiment. These results illustrate how the process of microbial breakdown differed between the litter types.

Abiotic and other habitat effects on decomposition

While litter type appeared to play a much stronger role in governing rates of mass loss, there was an interaction with habitat type. As expected, based on the abiotic conditions in grazed habitat, early in the experiment, low-quality senesced litter decomposed faster in grazing lawn. On the other hand, by the end of the growing season, green litter (representing grazed, higher quality litter) decomposed faster in *Carex* meadow. This result was surprising as we expected both litter types to decompose faster in the habitat with abiotic conditions favorable to decomposition, namely grazing lawn. As expected, we found higher temperatures, UV radiation, throughfall, and soil moisture in grazing lawns, all factors that other studies suggest tend to promote decomposition (Lin and King 2014; García-Palacios et al. 2016; Petraglia et al. 2019). It could be that senesced litter decomposition was more susceptible to these abiotic factors than green litter. For example, it has been found previously that decomposing senesced litter requires higher activation energy, and therefore are more sensitive to temperature than green litter (Li et al. 2021). Alternatively, factors other than the abiotic conditions we measured, such as differences in the microbial communities, could be more important in influencing litter decomposition in these habitats.

Because we did not see independent habitat effects on mass loss, decomposition rate differences between habitat types in this region are likely primarily due to biological interactions between litter and soil (Kelsey et al. 2016; Foley et al. 2022). We suspect that the faster decomposition of green litter in meadows may be driven by the large microbial community differences between grazing lawns and meadows (Foley et al. 2022). Different microbial communities affect the loss of recalcitrant C versus labile C (Osono 2020). We know that fungal species richness is substantially greater in meadows than in grazing lawns (Foley et al. 2022). Fungal groups are typically the first microbes to decompose materials, and the initial colonizing community dictates decomposition rates (Cline and Zak 2015). Thus, the highly diverse fungal community found in *Carex* meadow (Foley et al. 2022), which is already accustomed to breaking down the large quantities of litter typically found in the ungrazed areas, may be more ready to break down high quality litter when it is present.

Our study was not explicitly designed to test microbial community differences between habitats; however, our results may be viewed in light of home-field advantage effects. The home-field advantage describes how litter tends to decompose more quickly in soil that are typically associated with their respective vegetation type (Allison et al. 2013; Creamer et al. 2015), and these effects are thought to be mediated by differences in microbial communities among habitats (Palozzi and Lindo 2018; Pugnaire et al. 2023). Based on home-field advantage effects, we might expect senesced litter to decompose faster in *Carex* meadow and green litter to decompose faster in grazing lawn, where similar litter quality types are found, but we did not find evidence for this. While the home-field advantage does typically cause vegetation to decompose faster in its home environment (Ayres et al. 2009; Veen et al. 2015), this does not hold true for every system (Palozzi and Lindo 2018; Lyu et al. 2019; Chollet et al. 2021). Given that the species in grazing lawn and *Carex* meadow is the same (predominantly *Carex subspathacea*), our results support the idea that the home-field advantage is weaker in systems that have highly similar plant community composition (Veen et al. 2015). In addition, the low amount of litter reaching the ground in grazing lawn could make this hypothesis less likely in that it may contribute to a lack of specialization of decomposers in grazing lawns. Finally, this experiment measured decomposition over one year, and studies suggest that the home-field advantage may play a larger role in longer decomposition periods (Palozzi and Lindo 2018).

In addition, we did not use litter from grazing lawns (due to collection challenges), but rather a surrogate of similar litter quality. This could have influenced our ability to detect the home-field advantage. This high-quality litter, while generally similar in chemistry to senesced grazing lawn litter, may have decomposed at a different rate than grazing lawn litter would have decomposed in either habitat. While enough grazing lawn material can be collected for very small-scale microcosm experiments (Saunders et al. 2023), we needed an amount for this study that was beyond what could be collected without denuding critical habitat. If we tried to exclude geese, we would have been able to collect more, but it would have changed the chemistry and therefore not reflected natural grazing lawns (Beard et al. 2019). Further, we collected early season senesced litter from the uppermost portion of the litter layer to ensure they had not experienced growing season decomposition. This litter did appropriately experience overwintering decomposition and we believe represented well litter that would have decomposed during the next growing season. However, considering how long it takes for senesced litter to decompose in this system, it is possible that senesced litter from mid-sections of senesced litter, for example, would more appropriately represent decomposition during the study growing season, and could have different decomposition rates.

Seasonal effects on decomposition

Effects of Arctic winter on litter decomposition are often site-specific (Rixen et al. 2022), but winter snow cover can interact with litter quality and soil microbial communities as an important component of biomass and nutrient integration into the soil (Ibanez et al. 2021). Previous research in this system found that graminoids lose only around 20% of their mass during the summer season, suggesting that winter decomposition accounts for an important component of decomposition (Petit Bon et al. 2024). While mass losses were greatest between the end of the season and start of spring, decomposition rates were slowest for all litter and habitat combinations from week 9 (which represents the end of the growing season in this system) to the one-year period. The effect of extremely low temperature (<0 °C) and snow cover on litter decomposition, in addition to diminished labile C and N, likely accounts for the decreased decomposition during this period (Prescott 2010). Persistent mass loss patterns for litter and habitat types between 9 and 52 weeks were likely due to chemical differences, but could be due to differences in habitat features, like snowpack, that were not directly observed (Saccone et al. 2013). Shifts in winter abiotic conditions and seasonality due to climate change could alter these seasonal decomposition dynamics in the future (Bokhorst et al. 2010; Blok et al. 2016), making our report on decomposition rates relevant for future studies on breakdown and assimilation of litter materials in this area.

Additionally, flooding potentially affected litter decomposition after the growing season. On 17 September 2022, Typhoon Merbok hit western Alaska, and resulted in widespread flooding in the Y-K Delta before the ground was frozen. Our study site and litterbags were underwater during this storm event. Grazing lawns are often found along pond margins, and because of their proximity to water, they can flood at monthly high tides and certainly flood more often than meadow habitats. However, these high tide events only last generally for a few hours, whereas storm surges can flood areas for nearly 14 h (Terenzi et al. 2014). The effects of leaching or physical breakdown of litter may be relevant to these longer storm surge situations, more so than other decomposition mechanisms. As flooding events in this lowland northern wetland are expected to increase in the future (Petit Bon et al. 2024), the effect of cold, saline storm surge flood waters on litter decomposition could be investigated in future studies.

Conclusions

Goose herbivory in the Y-K Delta results in less aboveground biomass, increased forage and litter quality, and influences environmental conditions. Our results suggest that in general goose herbivory increases decomposition rates by creating litter that decomposes more quickly. However, while grazed habitat should increase decomposition rates due to changed environmental conditions favoring decomposition, that was not the case for high quality litter, which decomposed faster in ungrazed areas. As a result, the role of herbivores in influencing early stages of decomposition was not straightforward. While not directed tested in this study, decomposition rates could be influenced by the different microbial communities known to exist between grazing lawn and *Carex* meadow (Foley et al. 2022). We suggest that further understanding of herbivore-microbial-soil interactions could be critical to understanding nutrient dynamics within this ecosystem.

While goose herbivores consume most of the vegetation in grazed areas, and hence there is little litter in these areas, our results help explain the build-up of the senesced layers in ungrazed habitats in this ecosystem, because that litter type in that habitat type took the longest to decompose. This is the first report that we know of investigating mean residence time of litter in a large Alaskan river delta. Our study found that while much of the material is lost over a year, around 25 to 50% of mass remains. More specifically, senesced litter could potentially remain aboveground for an additional 5–6 years or longer.

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Data availability Dataset generated during this study are available at the NSF Arctic Data Center. https://doi.org/10.18739/A2H41JP43.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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