Polar Biology (2025) 48:81
https://doi.org/10.1007/s00300-025-03400-x

BRIEF REPORT

Small rodent disturbance impact on Arctic graminoid forage quality

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Received: 21 October 2024 / Revised: 20 May 2025 / Accepted: 21 May 2025 / Published online: 14 June 2025
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Abstract

Arctic rodents influence tundra plant communities by altering species diversity, structure, and nutrient dynamics. These dynamics are intensified during rodent population peaks. Plants are known to induce defenses in response to rodent herbivory. However, changes in plant tissue digestibility may also play a role in deterring rodents or impacting their survival. This study presents a first look at the impacts of rodent herbivory on crude protein (CP) and acid detergent fiber (ADF) of two of the most common graminoid species (*Carex nigra* and *Deschampsia cespitosa*) and graminoid genus (*Calamagrostis* spp.) in the tundra meadows of the Varanger Peninsula, Norway. We selected 32 experimental plots representing both rodent-disturbed and adjacent, undisturbed control graminoid patches. In the summer of a rodent population peak, the disturbed plots had higher ADF (28.5%) values than less disturbed ones (26.6%), controlling for plant species. We also found differences between species, with *Carex nigra* having the lowest fiber content (24.3%, ADF) and highest protein content (18.2% CP)—making it the most palatable species. These results show that rodent activity can potentially alter plant food quality, suggesting that increasing fiber content may be a defensive response to herbivory.

Keywords Acid detergent fiber · Crude protein · Herbivory · Tundra

Introduction

Rodents have been long recognized as ecosystem engineers, (e.g., Dickman 1999; Legagneux et al. 2012) important for regulating biospheric activity. They are key species affecting plant and predator abundances (Krebs 2011). They aerate and increase groundwater recharge through soil turbation, aid in decomposition and nutrient cycling, and provide habitats for other species. They control plant productivity, species richness and composition, and promote ecological succession (e.g., Zhang et al. 2003; Prugh and Brashares 2012; Tschumi et al. 2018; Ballová et al. 2019).

Rodent impact is especially importantin the Arctic, where lemmings (*Dicrostonyx* spp. and *Lemmus* spp.) and voles (*Microtus* spp. and *Myodes* spp.) modify tundra plant communities influencing plant diversity, structure, and nutrient dynamics (Tuomi et al. 2019; Lindén et al. 2021). Indeed, when small rodent population density is high, they can impact vegetation nutrient dynamics more than do large herbivores, such as reindeer (Petit Bon et al. 2020). Not only do rodents eat tundra plants, but they also alter vegetation to create structures such as winter nest-storages, runways, and latrines (Roy et al. 2022). An understanding of high-latitude terrestrial ecosystems thus demands study of impacts of rodent activity on plant communities.

There have been hundreds of studies of the effects of rodents on vegetation in northern ecosystems (see Soininen and Neby 2024). Many of these focus on rodent population cycle dynamics and the complex interactions between these herbivores and the plant communities they rely on (Andreassen et al. 2021)—notwithstanding the role of predators (e.g., Hanski et al. 2001). Both reduced plant quantity and quality following intensive grazing at high rodent abundance

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have been hypothesized to drive or contribute to the rodent cycles, in particular if the effects last long enough to induce delayed density-dependence (Soininen and Neby 2024). Reduced diet quality could result from plants being nutritionally depleted through grazing, from grazing induced plant defenses, or through fallback on lower quality plant species. This may in turn affect rodent health or population growth rate.

It has been long understood that plants defend against herbivory by decreasing nutritional quality to herbivores (Schultz 1964; Batzli et al. 1980; DeGabriel et al. 2014; Burkepile and Parker 2017; Fernández de Bobadilla et al. 2022). In some plants, this happens through induction of defenses. Graminoids, for example, often respond to herbivory by increasing their silica content (Massey and Hartley 2006; Soininen et al. 2013a). This can wear teeth (Calandra et al. 2016) and lead to decreased digestive efficiency and calorie assimilation, which might explain decreased body mass, and increased mortality (Huitu et al. 2014). Phenolics have also been suggested as plant defenses against rodent activity (Oksanen et al. 1987). These defensive compounds bind to a herbivore's digestive enzymes and inactivate them (Velickovic and Stanic-Vucinic 2018); though the degree to which phenolics are inducted in response to herbivory by rodents remains a matter of debate (Saetnan and Batzli 2009; Huitu et al. 2014).

An alternative mechanism leading to reduced plant quality due to rodent herbivory is changes in nutritional content. For instance, structural compounds, such as lignin and cellulose, reduce plant digestibility and the energy that an herbivore can extract from a plant (e.g., Distel et al. 2005). Surprisingly, there has been little work done to consider the impact of herbivory by rodents on plant fiber content (but see Bergeron and Jodoin 1989 and Hambäck et al. 2002). Higher fiber content might mean that rodents need to eat more to meet their nutrient needs. Alternatively, plant quality may actually increase due to rodent herbivory, as plants may contain more protein where they have been fertilized by small rodent feces. See, for example, Tuomi et al. (2019), who found that plants in areas with high rodent density had higher nitrogen content.

Our study presents a first look at the impacts of rodent herbivory on crude protein and acid detergent fiber (ADF—cellulose and lignin) on common tundra graminoids in the tundra meadows of the Varanger Peninsula, Norway. This study will add to knowledge about the interactions between rodents and plants, a field of research where a recent review concluded that evidence was insufficient to reach a consensus allowing to reject hypotheses testing their key assumptions (Soininen and Neby 2024). We selected three graminoid species based on growth form: the mat grass, *Calamagrostis* spp., the sedge, *Carex nigra*, and the tussock grass, *Deschampsia cespitosa*.

Materials and methods

Site and experimental design

This study took place in the riparian meadows along tributaries of river Bergebyelva, Varanger Peninsula, Norway (70.30° N, 29.02° E). These riparian meadows are vegetated by a diverse composition of species which include graminoids (e.g., *Avenella flexuosa*, *Carex* spp. *Deschampsia cespitosa*, *Juncus filiformis*), forbs (e.g., *Rumex acetosa*, *Trollius europaeus*, *Viola* spp.), and cryptograms (e.g., *Equisetum* spp. and mosses). Annual precipitation was 633 mm, annual temperature − 1.24 °C, and July precipitation 73 mm and temperature 10.77 °C for climate normals during 1991–2020 based on ERA5 analysis of the study area. The bedrock is a mixture of rich slate and limestone dominated types and poor sandstone types (Ims et al. 2013). The meadows are within the study area of the Climate-ecological Observatory for Arctic Tundra (COAT, www.coat.no), which is a long-term monitoring system of food webs, including rodents and plants. The study was conducted in 2023, which was a peak year of the cyclic small rodent populations in the region (Ehrich 2025).

We established study plots in two riparian valleys (Torvhaugdalen, 70.31° N, 29.08° E and Bergebydalen 70.29° N, 28.96° E) in July 2023 (Fig. S1). In both valleys, we identified substantial populations of the three dominant graminoids: *Deschampsia cespitosa*, *Carex nigra*, *Calamagrostis* spp. (*Calamagrostis* was identified to the genus level only, as the species present cannot be distinguished in the field unless they have reproductive structures. Most clones likely belong to *C. phragmitoides*, but *C. lapponica* and *C. neglecta* may also occur). For each identified population, we recorded whether it had no visual signs of rodent disturbance or high levels of rodent disturbance, denoted as Undisturbed and Disturbed. We established a 0.5 × 0.5 m plot in each included population. These plots were on average 57.9 m (2.9–273.1 m range) from each other within a graminoid type in each valley. Rodent disturbance was identified by vegetation clipping, runways, and feces presence (Fig. S2). No barrier was used to limit rodent disturbance after the experiment was established. Across the study area, each combination of dominant graminoid and rodent disturbance has between five and seven replicates (Table 1).

Initial plot conditions were determined visually. All vascular plant species for a measure of species richness were listed and percent cover per species was estimated. All cover estimates were obtained by two observers (KAB and MH) who calibrated their results against each other.

Table 1 Number of plots (N) by location (Bergebydalen & Torvhaugdalen) in Varanger, Norway for each dominant graminoid and rodent disturbance treatment

River valley	Dominant graminoid	Rodent disturbance	*N*	Dominant graminoid cover (%)
Bergebydalen	*Calamagrostis* spp.	Undisturbed	3	67.5 (60–75)
		Disturbed	3	41.6 (25–70)
	Carex nigra	Undisturbed	2	67.5 (60–75)
		Disturbed	4	56.7 (40–70)
	Deschampsia cespitosa	Undisturbed	2	75.0 (70–80)
		Disturbed	3	66.7 (60–75)
Torvhaugdalen	*Calamagrostis* spp.	Undisturbed	3	60.0 (50–70)
		Disturbed	2	55.0 (30–95)
	Carex nigra	Undisturbed	3	90.0 (80–100)
		Disturbed	3	93.3 (80–100)
	Deschampsia cespitosa	Undisturbed	3	80.0 (75–85)
		Disturbed	3	71.7 (50–85)

Mean percent cover of dominant graminoid and range for each rodent disturbance treatment

Plant harvest and nutritional analyses

The plots were sampled in July, 2023. Approximately 40 g of mature fresh leaves with no signs of herbivory were collected from the dominant graminoid within each plot (*Deschampsia cespitosa*, *Carex nigra* or *Calamagrostis* spp.) in each Undisturbed and Disturbed treatment. Plant samples were dried in the field in dehydrators at 40 °C for a minimum of 48 h. Dried samples were sealed in paper bags with desiccant and exported to the Nutritional and Isotopic Ecology Lab (NIEL) at the University of Colorado Boulder for nutritional analyses. Approximately ~ 10 g of dried sample were ground with a Retsch® centrifugal mill using a ~ 2 mm sieve. The ground sample was used to analyze crude protein (CP), and acid detergent fiber (ADF), with all values reported as a percentage of dry weight. Crude protein was measured with a LECO® FP 528 nitrogen analyzer using the standard $\%N \times 6.25$ conversion to obtain %CP. %ADF were measured with an ANKOM® 2000 fiber analyzer.

Statistical analyses

A generalized linear mixed model was used to evaluate the effects of plant species and rodent disturbance as fixed effects on CP, ADF, and CP/ADF responses, and riparian valley as a random effect. The *glmmTMB* function within the *glmmTMB* package (Brooks et al. 2025; v1.1.9) using R statistical software (R Core Team 2025; v4.4.0), Models were assessed using the simulation-based package *DHARMa* (Hartig 2024; v0.4.6) and *ggplot2* package (Wickham et al. 2025; v3.5.1) for figures were used. For significant treatment effects, we performed a post-hoc pairwise comparison with Tuckey adjustment using *emmeans* package (Lenth 2025; v1.10.1).

Results

Fiber (ADF)

All three graminoids differed in acid detergent fiber, with *Calamagrostis* spp. having the highest at 30.8% (95% confidence interval CI: 29.4–32.1%), *Carex nigra* having the lowest at 24.3% (CI: 22.9–25.6%), and *Deschampsia cespitosa* an intermediate at 27.7% (CI: 26.3–29.0%, Fig. 1). We found statistically significant effects of both species and disturbance, but no interaction between them (Table 2). Rodent-disturbed plots had higher ADF 28.5% (CI: 27.4–29.6%) compared to undisturbed plots 26.6% (CI: 25.5–27.8%).

Crude protein

All three graminoids also differed in crude protein, with *Carex nigra* having the highest crude protein content at 18.2% (CI: 17.2–19.2), followed by *Calamagrostis* spp. at 15.9% (CI: 14.9–16.9%) and *D. cespitosa* at 11.1% (CI: 10.1–12.1%). We found statistically significant effects of species, but not of disturbance nor any interaction (Table 2). Yet, all species showed a tendency of change to the same direction, i.e., lower CP in disturbed plots.

CP/ADF

Carex nigra had the highest CP/ADF ratio at 0.76 (CI: 0.71–0.81), followed by *Calamagrostis* spp. at 0.52 (CI: 0.47–0.57) and *Deschampsia cespitosa* at 0.40 (CI: 0.35–0.45). We found statistically significant effects for species and disturbance, but not for the interaction between the

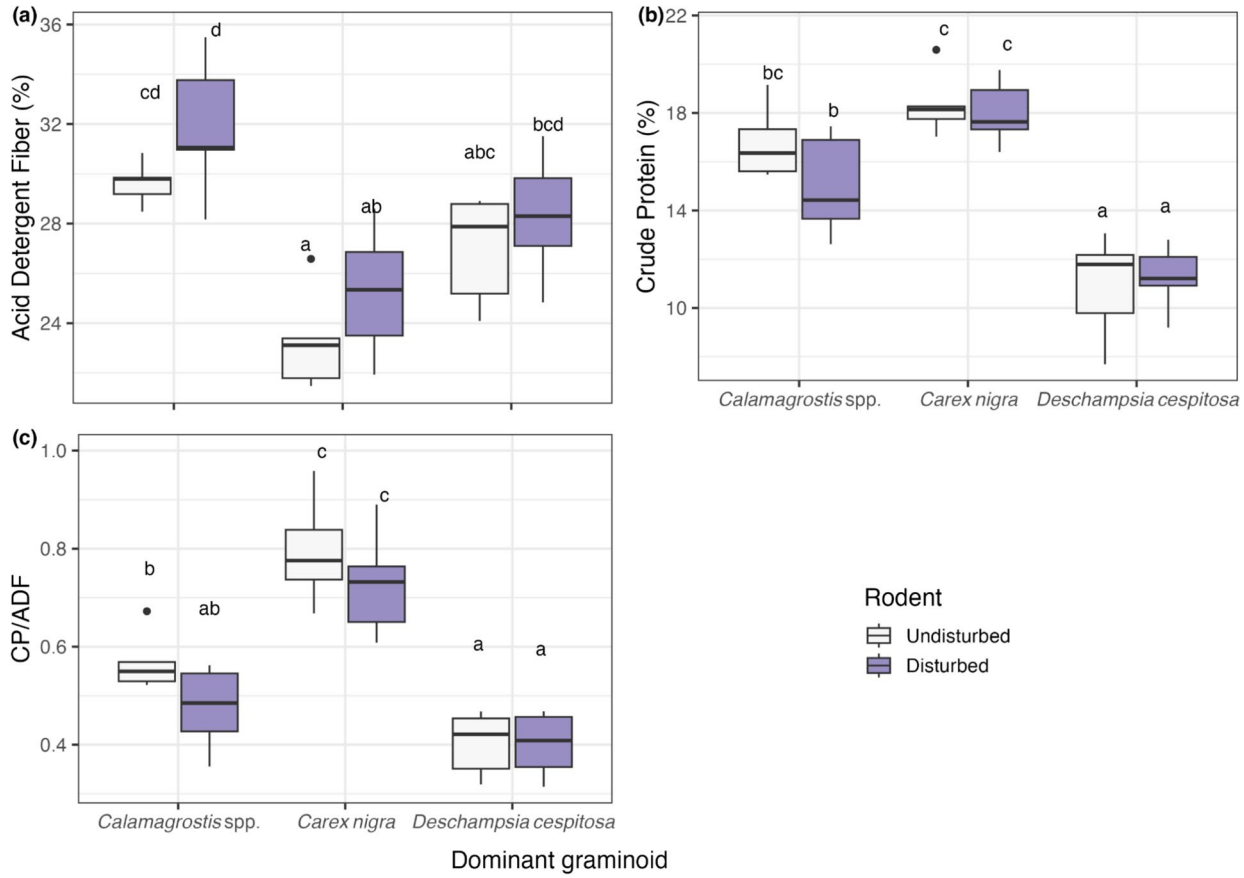


Fig. 1 Box plots (horizontal line is median, box are first and third quartiles, and black dots are outliers) of measured percentage of acid detergent fiber (**a**), crude protein (**b**) and the ratio of crude protein to acid detergent fiber (**c**) for each dominant graminiod and type of disturbance in tundra meadows, Varanger, Norway. Letters correspond to Tukey adjusted post-hoc pairwise comparisons, where treatment groups that do not differ significantly are provided with the same letter

Table 2 Generalized linear mixed model results for the relationship between species and disturbance and their interaction on crude percent protein—CP, Acid detergent fiber—ADF, and ration CP/ADF responses

	Variable	Chisq	d*f*	*p*-value
ADF				
	Dominant graminoid	58.650	2	< 0.0001
	Rodent disturbance	7.119	1	0.0076
	Dominant graminoid X Rodent disturbance	0.281	2	0.8687
CP				
	Dominant graminoid	142.640	2	< 0.0001
	Rodent disturbance	1.200	1	0.2734
	Dominant graminoid X Rodent disturbance	2.958	2	0.2279
CP/ADF				
	Dominant graminoid	134.128	2	< 0.0001
	Rodent disturbance	4.572	1	0.0325
	Dominant graminoid X Rodent disturbance	2.194	2	0.3338

Analysis of Deviance Table (Type II Wald chi-square tests).

two (Table 2). Rodent-disturbed plots had the lowest ratio 0.53 (CI: 0.49–0.57) compared to undisturbed plots 0.59 (CI: 0.55–0.63).

Discussion

Rodents have a substantive impact on ecosystems and understanding the drivers of their population cycles is needed due to their cascading effects on plants, other herbivores, and predators. Plants are thought to be one of the drivers of cycling through reduction of plant quality in the presence of high rodent densities. A key assumption of this hypothesis is that rodent herbivory modifies the plant quality. Our study evaluated the impacts of rodent herbivory on two plant quality metrics, crude protein and acid detergent fiber (ADF) for three of the common graminoid species in tundra meadows as a snapshot in the middle of a rodent peak summer.

Graminoid species generally have higher fiber content (ADF) compared to forbs (Lee 2018) and show high variability between species, particularly in temperate and tundra regions (1–55% ADF, Lee 2018). Differences between species we observed were as expected, with *Carex nigra* exhibiting the lowest fiber content (24.3% ADF) and highest protein content (18.2% CP), making it the most palatable species we analyzed. Crude protein and fiber change with plant phenology, with the highest crude protein and lowest fiber concentrations during early plant development (Klein and Bay 1990; Barboza et al. 2018). The marked difference between species in crude protein and fiber may be related to differences in phenology between sedge and grass synchrony of leaf and root production (Sloan et al. 2016; Li et al. 2021). Although the tundra voles' diet in the focal tundra grasslands is species rich (~ 26 species) and on average dominated by forbs (~ 80%), graminoids are second in preference (~ 13% of diet) (Soininen et al. 2013b). Further, the graminoid contribution to tundra voles' diet varies depending on their abundance and seasonal availability, and can reach over 50% (Soininen et al. 2013b; Soininen and Neby 2024). Changes to the palatability of graminoid species could, therefore, affect rodent diets either by reducing the quality of ingested food or by reducing selection for graminoids. One caveat to this interpretation is that, in this study we did not address rodent diets directly but focused on plant responses to herbivory.

We found that graminoids in rodent-disturbed plots decreased in nutrient quality, as they increased in fiber (ADF) and decreased in crude protein:ADF ratio. This differs from the findings of an earlier study on rodent impacts on graminoid ADF, which found an opposite pattern (Bergeron and Jodoin 1989). While Bergeron and Jodoin (1989) addressed different plant and rodent species than the current study, making direct comparisons difficult, they found no clear difference in ADF-levels between preferred and avoided plants. Rather, annual variation within groups was up to 6%, indicating that the 2% increase we found in this study is relatively small. Still, other studies of graminoids in northern Norwegian tundra have shown them to respond to rodent disturbance with increased nitrogen and phosphorus content (Tuomi et al. 2019; Petit Bon et al. 2020), thus increasing their nutritional quality. One possible explanation for the seemingly contradictory results could be methodological differences, as we measured different compounds than Petit-Bon et al. (2020), and contrasted individual plants in the same study site and year rather than different locations and years like Tuomi et al. (2019). Furthermore, the strength of rodent-plant interactions can differ between population peaks even in the same location (Soininen et al. 2018) and differences between studies may be related to such phenomena. While the impact of a 2% increase in ADF on rodent fitness remains unclear, the difference between disturbed and undisturbed plots was statistically significant, still supporting rt the idea that rodent herbivory can alter plant palatability.

Our results indicate that rodent herbivory may decrease graminoid nutritional quality through increased fiber content and consequent decreased digestibility. As strictly speaking our results are correlative, a further study should confirm the findings using exclosures and assigning treatments randomly. Whether the decreased nutritional quality can have feedback effects to rodent population dynamics requires study of the extent to which rodents ingest these nutritionally lower quality plants, whether such diets have negative consequences to their health to the extent that it affects population growth rate, and whether the low nutritional quality prevails long enough to affect rodent population densities with a time-lag. In any case, our results suggest that increased fiber content may be a defensive adaptation against herbivory.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00300-025-03400-x.

Acknowledgements We thank Berit Tønsberg Gaski for help with field assistance. This study is a contribution from the Navigating the New Arctic Fennoscandia project and the Climate-Ecological Observatory for Arctic Tundra (COAT).

Author contributions G.C., K.B., D.E., O.P., M.S., M.H., E.S., and P.U. conceived the ideas and designed methodology; G.C., K.B., D.E., O.P., M.S., M.H., and P.U. collected the data; GC was involved in formal analysis; PU project administration and funding acquisition; G.C. led the writing of the manuscript and visualization. All authors contributed critically to the drafts and gave final approval for publication.

Funding This research was made possible by funding from Navigating the New Arctic—National Science Foundation (award—2126796).

Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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