Small rodent disturbance impact on Arctic graminoid forage quality.

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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 three of the most common graminoid species (*Calamagrostis sp.*, *Carex nigra* and *Deschampsia cespitosa*) in the tundra meadows of the Varanger Peninsula, Norway. We selected 32 experimental plots representing both rodent-disturbed and adjacent, undisturbed control graminoid patches. During 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 increased fiber content may be a defensive adaptation against herbivory.

Introduction

Rodents have long been 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 predominant in 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, small rodents often consume even more plant materials than larger herbivores, and they can have dramatic impacts on vegetation – especially during population peaks (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 for review). 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). In particular, reduced plant quality has been hypothesized to lead to rodent population cycles if high abundance of rodents leads to lower-quality foods, either through fallback on lower quality plant species or by decreased quality of the foods they prefer.

It has been long understood that northern latitude plants defend against herbivory by decreasing nutritional quality to herbivores (Schultz 1964; Batzli et al. 1980). 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 support for induction of phenolics in response to herbivory by rodents is not clear (Saetnan and Batzli 2009; Huitu et al. 2014).

An alternative mechanism leading to reduced plant quality due to rodent herbivory is changes in the 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). In this light, there has been surprisingly little work done to consider the impact of herbivory by rodents on plant fiber content (but see Bergeron & Jodoin 1989 and Hambäck et al 2002). Alternatively, plant quality may 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 high rodent density associated with higher plant N 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. We selected the graminoid species based on growth form: the mat grass, *Calamagrostis sp.*, the sedge, *Carex nigra*, and the tussock grass, *Deschampsia cespitosa*.

Material and Methods

Site and experimental design

This study took place in the riparian meadows along tributaries of river Bergebyelva, Varanger Peninsula, Norway (70.30^{o} N, 29.02 ^{o} 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 595 mm, and annual temperature – 1.16 ^{o} C during 1961–1990, and the bedrock is a mixture of rich slate and limestone dominated types and poor sandstone types (Ims et al. 2013). These valleys are part of 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 (https://coat.no/en/Small-rodent).

We established a total of 16 sites in two riparian valleys (Torvhaugdalen, 70.31^{o} N, 29.08^{o} E and Bergebydalen 70.29^{o} N, 28.96^{o} E) in July 2023. At each site, areas with low and high rodent disturbance of (hereafter denoted as Undisturbed and Rodent Disturbed) indicated by vegetation clipping, runways, and feces presence were located within each dominant plant type (Fig. S1). We then established a 0.5m x 0.5m plot in both disturbed and undisturbed, so that each plot-pair was dominated by one of the targeted graminoids (Table 1). The plots were at least 7m from each other.

Initial plot conditions were determined by listing all vascular plant species for a measure of species richness, estimating the percent cover per species, measuring plant height (four corners of the plot), and rodent disturbance intensity–percentage of the plot with graminoid clippings or runways and feces presence.

Table 1
Number of plots by location (Bergebydalen & Torvhaugdalen) in Varanger, Norway for each dominant graminoid and rodent disturbance treatment. Mean percent cover and range of the dominant graminoid for each treatment.

River Valley	**Dominant graminoid**	**Rodent Disturbance**	**N**	**Mean % cover (range)**
Bergebydalen	*Calamagrostis sp*.	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 sp*.	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)

Plant harvest and nutritional analyses

The plots were sampled in July 2023. Approximately 40 grams of fresh leaves were collected from the dominant graminoid in each control and rodent-disturbed plot. Plant samples were dried in the field in dehydrators at 40°C. Dried samples were sealed in paper bags with desiccant and were exported to the Nutritional and Isotopic Ecology Lab (NIEL) at the University of Colorado Boulder for nutritional analyses. Approximately ~ 10 grams of dried sample were ground with a Retsch® centrifugal mill using a ~ 2mm 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 × 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 fixed effects on CP, ADF, and CP/ADF responses, and riparian valley as a random effect. The *glmmTMB* function within the *glmmTMB* package (1.1.9) using R statistical software (4.4.0), Models were assessed using the simulation-based package *DHARMa* (0.4.6) and *ggplot2* package (v3.5.1) for figures were used. For significant treatment effects, we performed a post-hoc pairwise comparison with Tuckey adjustment using *emmeans* (*emmeans* package v1.10.1)

Results

Fiber (ADF)

Calamagrostis sp. had the highest ADF (30.8%), *Carex nigra* had the lowest ADF (24.3%), and *Deschampsia cespitosa* an intermediate ADF (27.7%, Fig. 1). We found statistically significant effects of both species and disturbance, but not interaction (Table 2). Rodent-disturbed plots had the highest ADF (28.5%) compared to undisturbed plots 26.6%.

Crude Protein

Carex nigra had the highest crude protein content, with 18.2%. In *Calamagrostis sp*. it was 15.9% and lowest in *D. cespitosa* (11.1%). We found statistically significant effect of species, but not of disturbance or 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 0.76, followed by *Calamagrostis sp.* 0.53 and *Deschampsia cespitosa* 0.40. We found statistically significant effect of species, and a significant effect of disturbance, but none for interaction (Table 2). Rodent-disturbed plots had the lowest ratio (0.533) compared to undisturbed plots 0.588.

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

	Variable	Chisq	df	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

Discussion

Rodents have a vast 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 by reducing 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.

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, and *Carex nigra* exhibited 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, having the highest crude protein and lowest fiber concentration during early plant development (Klein 1990; Barboza et al. 2018). The marked difference between species in crude protein and fiber may be related to differences in phenology between sedges and grasses synchrony of leaf and root production (Sloan et al. 2016; Li et al. 2021).

Although tundra voles' diet is species rich in the tundra grasslands (~ 26 species), graminoids are among the preferred plants (~ 13% of diet) after forbs, with minimal variation in seasonal or spatial preference (Soininen et al. 2013b). Any changes to the palatability or quality of graminoid species could, therefore, have dramatic impacts on rodent diets.

We found that graminoids in rodent disturbed plots decreased on nutrient quality, as they increased in fiber (ADF) and decrease 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). However, as this study addressed different plant and rodent species than our study, it is difficult to make direct comparisons. 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 explanation to the seemingly contradictory results could be in methodology, 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. Yet, our results support the idea that rodent herbivory can alter plant palatability and thus affect rodents' food selectivity or quality.

Our results indicate that rodent herbivory may decrease graminoid nutritional quality through increased fiber content and consequent decreased digestibility. Whether such mechanism can have feedback effects to rodent population dynamics requires further knowledge on the extent rodents ingest these nutritionally lower quality plants, whether such diet has 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.

Declarations

Competing interests

The authors declare that they have no conflict of interest.

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Author Contribution

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.

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Figures

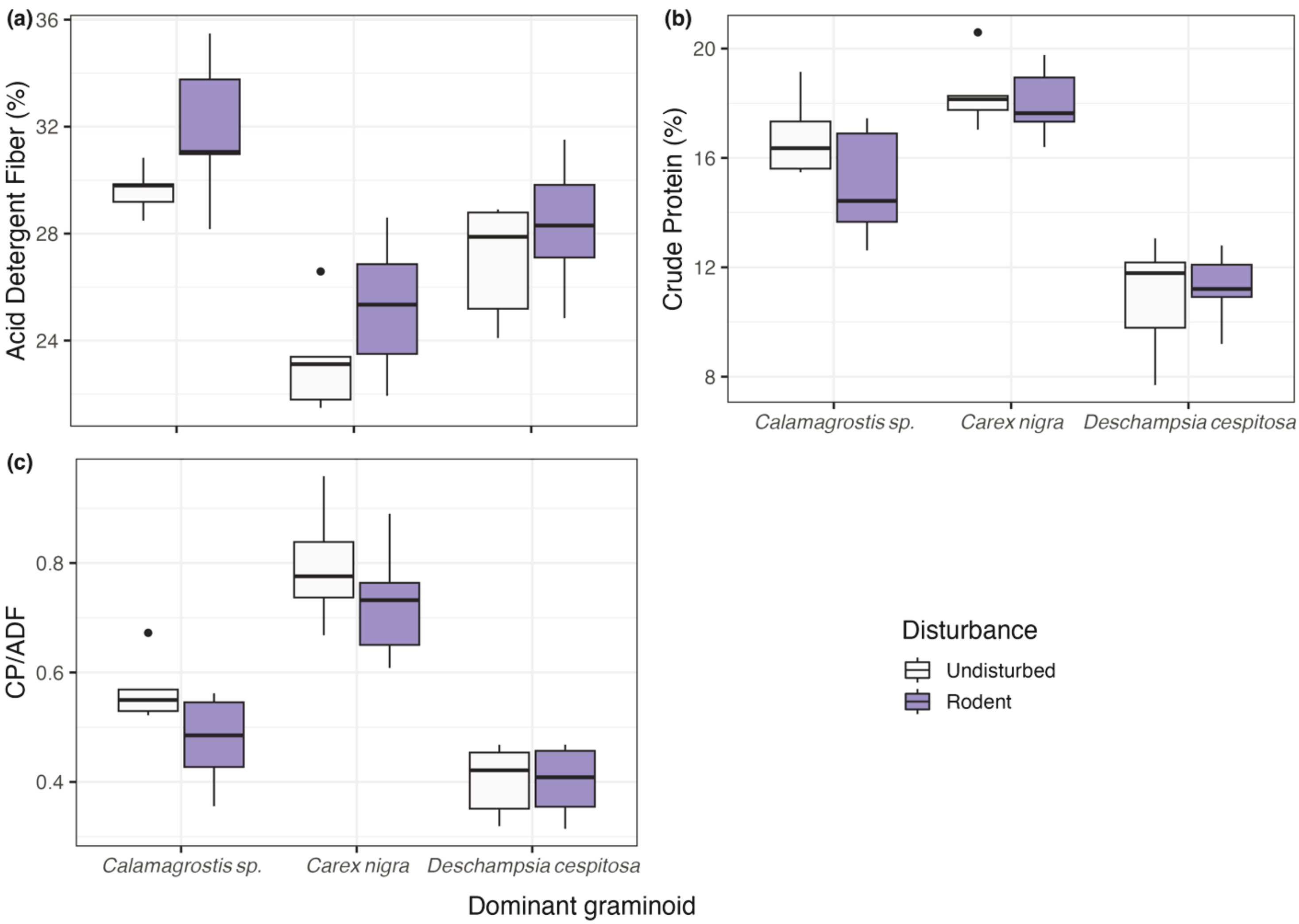

Figure 1

Boxplots (horizontal line is median and box are first and third quartiles) of measured percentage of acid 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.

Supplementary Files

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- SupplementCelis2024.pdf