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Quantifying muskox plant biomass removal and spatial relocation of nitrogen in a high arctic tundra ecosystem

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ABSTRACT

The muskox (*Ovibos moschatus*), a key species in the arctic tundra, is the only large-bodied herbivore in Northeast Greenland. Here, we quantify the biomass removal and fecal deposition by muskoxen during the snow-free period in the years 1996 to 2013 in the high arctic tundra ecosystem at Zackenberg, Northeast Greenland. We show that despite high densities, muskoxen removed only 0.17% and 0.04% of the available forage in graminoid-dominated areas and in *Salix* snowbeds (including *Salix* dominated heaths), respectively, during the main plant growing season (from mid-June to end of August). Into the autumn, the biomass removal increased to ~4.6% and 0.19% in the graminoid-dominated areas and *Salix* snowbeds, respectively. Muskoxen forage mainly in the graminoid-dominated areas, but defecate primarily in *Salix* snowbeds, resulting in net nutrient transfers from the nitrogen-rich wet habitats to the nitrogen-poor, drier habitats, corresponding to an addition of 0.016 g m⁻² of nitrogen in the *Salix* snowbeds per year. This nitrogen addition is of same magnitude as the dissolved inorganic nitrogen pool in similar arctic soils. Hence, while the quantitative impact of muskox biomass removal seems negligible, the nitrogen relocation may be important for the arctic vegetation and associated biota in the tundra ecosystem.

INTRODUCTION

Arctic herbivores face difficult living conditions with low temperature, short plant growing season, and nitrogen limitation of primary production, resulting in some of the least productive ecosystems in the world (Billings and Mooney, 1968; Nadelhoffer et al., 1991). The short summer growing season encompasses typically mid-June to late August or early September (Muc, 1977; Arndal et al., 2009). During the arctic winter, most of the plant forage is unavailable to the herbivores due to leaf senescence or because of a thick snow cover (Klein and Bay, 1994). Across all ecosystems worldwide, herbivores

generally consume 1%–10% of the aboveground plant production (Chapin et al., 2002), with the least consumption in unproductive habitats, such as tundra ecosystems (McNaughton et al., 1989). However, the impact on the nutrient budgets of plants may be larger, as herbivores tend to feed on plant parts that are rich in nutrients (Chapin et al., 2002). Herbivores therefore also play a key role in turnover of elements as nitrogen, which often limit arctic plant growth (Nadelhoffer et al., 1991). Not only do herbivores remove nitrogen when feeding on plants, they may also redistribute nitrogen and other nutrients through defecation and urination across the landscape (McKendrick et al., 1980;

Hobbs, 1996; Van der Wal et al., 2004). Nitrogen deposition does not necessarily take place in the areas used for foraging (Williams and Haynes, 1995), which may lead to a relocation of nutrients between different areas.

As one of the few large herbivores in the tundra ecosystem, the muskox, *Ovibos moschatus*, is regarded as a key species. Being a large grazer, with its large body size, rumen, and gut (Hofmann, 1989), the muskox is capable of processing large amounts of forage (Jefferies et al., 1994) and has been associated with changes in the vegetation cover, biodiversity, shrubification, and ultimately the carbon balance of the ecosystem (Post and Pedersen, 2008; Falk et al., 2014, 2015). Despite their size, muskoxen are selective in their diet and habitat use (Raillard and Svoboda, 2000; Kazmin and Abaturov, 2011; Kristensen et al., 2011). During summer, muskoxen forage mainly in wet and low-lying fen- and grassland areas, where their diet is dominated by leaves and stems of graminoids and willows (*Salix* spp.), while dominated by senescent graminoids and willow twigs during the winter (e.g., Thing et al., 1987; Klein and Bay, 1990, 1991, 1994; Larter and Nagy, 2004). In the Arctic, muskoxen are found at generally low densities (~ 1 animal km^{-2}) and are widely distributed across the landscape (Parker and Ross, 1976; Wilkinson et al., 1976; Hubert, 1977; Thing et al., 1987; Raillard and Svoboda, 2000). However, during certain periods, such as late summer, animals may aggregate in specific habitat types (often low-lying graminoid-dominated fens), where densities may be more than 6 muskoxen per km^2 (Raillard and Svoboda, 2000; Tolvanen and Henry, 2000; Schmidt et al., 2015). At Zackenberg Research Station in Northeast Greenland, muskoxen have been monitored as part of the long-term monitoring program BioBasis since its implementation in 1996 (Schmidt et al., 2015). Muskoxen are the only large herbivores there and can be found there in some of the highest densities in the High Arctic (Schmidt et al., 2015), which is why we expect muskoxen to exert a high grazing pressure in the low-lying graminoid-dominated areas there. Recently we reported the long-term patterns in inter- and intra-annual variation in the muskox demographics at Zackenberg, including the intra- and interannual variation in muskox abundance and group composition (Schmidt et al., 2015). In this study, we aim

at quantifying the grazing pressure of muskoxen at Zackenberg. Quantifying herbivory is, however, challenging due to difficulties in estimating the true primary productivity (McNaughton et al., 1996). As suggested by McNaughton et al. (1996) we therefore utilize the long-term data on muskox abundance to quantify the amount of the available forage that the muskoxen at Zackenberg remove during the snow-free season. Also, we quantify the spatial relocation of nitrogen by muskoxen between different vegetation types within our study area. By doing this, we aim at not only quantifying the muskox as a key herbivore, but also its role as redistributor of nutrients.

MATERIALS AND METHODS

Study Area

The study was carried out inside the designated muskox census area covering ~ 47 km^2 (Schmidt et al., 2015) in the Zackenberg valley, Northeast Greenland ($74^{\circ}28'N$; $21^{\circ}33'W$). The valley has a high arctic climate with an annual mean air temperature of -9 $^{\circ}C$ and a total precipitation of about 260 mm, mainly falling as snow (Hansen et al., 2008). The valley is covered by a mosaic of different vegetation types (Elberling et al., 2008). During summer, muskoxen forage mainly in graminoid-dominated areas (grasslands and fens), but also in *Salix* snowbeds and *Salix*-dominated heaths (hereafter termed *Salix* snowbeds) (Kristensen et al., 2011). The graminoid-dominated areas cover 42% of the study area and are widely scattered and found in the wetter parts of the valley (Bay, 1998). Here, the vegetation is dominated by several species of Cyperaceae, Juncaceae, and Poaceae. *Salix* snowbeds cover 15% of the study area and are mainly found on sloping sites with a prolonged snow cover. Here, the vegetation is characterized by the deciduous dwarf-shrub *Salix arctica*, but various forbs and graminoids are also present (Bay, 1998). The remaining part of the study area is primarily covered by different dwarf-shrub heaths and open fell fields (Elberling et al., 2008). These vegetation types are in this study lumped together as “Other vegetation types” (43% of the study area). These three vegetation types are all visited by muskoxen in summer (Berg et al., 2008), but foraging takes

place in the graminoid-dominated areas and *Salix* snowbeds (Kristensen et al., 2011) (see below).

Muskox Censuses

Data on muskox abundance, and the sex and age composition of groups, were obtained from the long-term biological monitoring program (BioBasis) running at Zackenberg. Since its implementation in 1996, the muskox population has been monitored by multiple annual censuses within an ~47 km² designated census area (Schmidt et al., 2015). Data presented here cover the years 1996 to 2013. At weekly intervals, during most of the snow-free season, the census area was covered on foot. All muskox groups within the census area were registered, and the sex and age composition of the group determined (calf, yearlings, 2-year-old male and females, 3-year-old males and females, and ≥4-year-old males and females; following Olesen and Thing [1989]). In a few cases, the census protocol was deviated—for instance, due to bad weather. Also, during the censuses conducted in 1997, only herd size was registered, and on the first census round in 1998, no separation between the 3-year-old and ≥4-year-old categories was made (3.7% of all observations). Unspecified adults constituted 5.0% of all observations. The temporal coverage of the censuses has varied over the years. While the arctic summer months (June–August) were covered in all years, a number of additional censuses have been conducted outside this period whenever possible. See Schmidt et al. (2015) for further details on the muskox censuses during the period.

Forage Availability

Weekly estimates of aboveground dry weight plant standing crop in the dominant vegetation types in Zackenberg throughout an entire growing season in 2004 were obtained from Arndal et al. (2009). The total standing crop was defined as both stems and leaves of graminoids and willows in the main growing period (9 weeks from mid-June to the end of August; Table 1). Based on data from their study (weekly estimates of g m⁻²) we calculated the weekly total aboveground plant standing crop, or in other words, the total forage availability inside the different vegetation types in our study area for each week. This was done by

TABLE 1

The weekly aboveground standing crop (dry weight, g m⁻²) from different vegetation types inside the study area. The aboveground standing crop includes stem and foliar biomass and was obtained from Arndal et al. (2009).

Week	Aboveground standing crop (g m ⁻²)	
	Graminoid-dominated areas	<i>Salix</i> snowbeds
1	20.41	61.66
2	35.02	123.14
3	32.21	66.87
4	56.76	134.73
5	58.35	164.03
6	73.53	112.98
7	54.11	117.48
8	65.29	212.02
9	36.58	140.62
Mean	48.03	125.95

multiplying the standing crop estimations (weekly g m⁻²) with the known area sizes of the different vegetation types within the study area: the graminoid-dominated areas (19.4 km²) and the *Salix* snowbeds (6.9 km²). Implicitly, we assumed that the availability of forage was constant throughout the week. Forage availability was estimated for all weeks and years (Table 2 shows total yearly standing crop estimations). However, as plant phenology varies with the interannual variation in snow-melt (Ellebjerg et al., 2008), we used information on the annual mean date of 50% snow cover in 22 permanent monitoring plots at Zackenberg to temporally align the onset of growing season to match the melt patterns of a given year. Hence, while the growth phenology within years was the same across years, the onset of the growing season shifted with the snow conditions compared to 2004, which was the year Arndal et al. (2009) estimated the weekly plant standing crops. A polynomial regression model was then used to extend the growing season (Tamstorf et al., 2007) until winter standing crop values were reached. Winter standing crop was set to 5.0 g m⁻² for graminoids as reported by Henry et al. (1990). For willows, the winter standing crop was set to be the twigs-biomass of 83.6 g m⁻², which was obtained from Arndal et al. (2009).

TABLE 2

Summary table showing the total muskox density (ind. km⁻²) and biomass (tons km⁻²), as well as the total available plant biomass (tons), and the associated biomass removal (tons) and fecal deposition (tons) by muskoxen in the different vegetation types within the 47 km² census area during the main growing season (mid-June to the end of August) in the years 1996 to 2013.

Year	Muskox density (ind. km ⁻²)	Muskox biomass (tonskm ⁻²)	Biomass available (tons)			Biomass removal (tons)			Fecal deposition (tons)		
			Graminoid-dominated areas	Salix snowbeds	Other vegetation	Graminoid-dominated areas	Salix snowbeds	Other vegetation	Graminoid-dominated areas	Salix snowbeds	Other vegetation
1996	9.41	1.58	7785.26	7250.26	—	4.51	1.13	—	0.22	1.48	0.69
1997	7.80	1.09	8398.92	7866.69	—	4.22	1.06	—	0.20	1.38	0.65
1998	7.30	1.29	7785.26	7250.26	—	4.10	1.03	—	0.19	1.34	0.63
1999	6.10	1.22	6613.80	5982.69	—	4.09	1.02	—	0.19	1.34	0.63
2000	6.25	1.17	8398.92	7866.69	—	4.95	1.24	—	0.24	1.62	0.76
2001	7.54	1.41	7785.26	7250.26	—	6.64	1.66	—	0.32	2.18	1.02
2002	10.17	1.80	8398.92	7866.69	—	5.91	1.48	—	0.28	1.95	0.91
2003	9.38	1.69	8398.92	7866.69	—	5.70	1.42	—	0.27	1.87	0.88
2004	9.45	1.97	8398.92	7866.69	—	6.23	1.56	—	0.30	2.05	0.96
2005	14.38	2.57	7739.00	7744.47	—	8.76	2.19	—	0.42	2.89	1.35
2006	10.68	2.18	7785.26	7250.26	—	9.84	2.46	—	0.47	3.24	1.52
2007	26.62	5.23	8511.48	8018.92	—	17.42	4.36	—	0.84	5.77	2.70
2008	14.43	2.82	8398.92	7866.69	—	10.89	2.72	—	0.52	3.59	1.68
2009	12.60	2.56	7270.54	3507.68	—	10.46	2.62	—	0.50	3.45	1.61
2010	11.38	2.32	8511.48	8018.92	—	8.19	2.05	—	0.39	2.70	1.26
2011	10.91	2.28	8511.48	8018.92	—	9.08	2.27	—	0.43	2.99	1.40
2012	9.83	2.07	7785.26	7250.26	—	7.29	1.82	—	0.35	2.40	1.12
2013	13.49	2.82	7270.54	3507.68	—	11.00	2.75	—	0.53	3.63	1.70
Mean	10.98	2.12	7986.01	7125.04	—	7.74	1.93	—	0.37	2.55	1.19

Biomass Removal

The amount of biomass removed by muskoxen was calculated as suggested by McNaughton et al. (1996) using herbivore density and body size, as well as their forage intake rates. Our calculations were based on population census data from Zackenberg (Table 2) combined with data on muskox weights and forage intake rates from the literature: Data on body weights of wild muskoxen are rare, but Latour (1987) scaled a large number of muskoxen collected from Banks Island in spring. However, while Latour (1987) separated muskoxen until the age of five, our data only classified individuals to the age of four. Consequently, we used the average values of four- and five-year-olds as adult weights. Moreover, though the body weight of adult muskoxen may vary during the year (Hubert, 1977; Adamczewski et al., 1997), we assumed the spring weights of the Canadian muskoxen to correspond to the summer weights of individuals from Zackenberg. Calves were not included in the calculations, as they are observed nursing in the wild to age of 15 months (Hubert, 1977). Several authors have investigated the daily intake requirement for muskoxen (e.g., gram forage per kilogram bodyweight per day), and there are some variations in the estimates (see Table 3). Using the weekly estimates of muskox density inside our study area, and the weight estimations from Latour (1987), we estimated the biomass of muskoxen present in the study area in each week. We calculated the weekly plant biomass removal by muskoxen in the area using the different forage intake rates (Table 3), and afterward we used the mean of these estimates as our weekly estimate of biomass removal. Again, implicitly, we assumed that

the density of muskoxen, and thus their biomass removal, was constant throughout the week. Further, Kristensen et al. (2011) estimated that approximately 80% of the summer forage for muskoxen at Zackenberg was in the graminoid-dominated areas, while the remaining 20% was in the *Salix* snowbeds. Hence, the calculated weekly plant biomass removal by muskoxen inside the study area was thereafter divided between the graminoid-dominated areas (80%) and the *Salix* snowbeds (20%) (Kristensen et al., 2011). The estimates of weekly plant biomass removal by muskoxen were then compared to the weekly availability of aboveground plant biomass calculated earlier for the two vegetation types. This produced a fraction (%) of how much of the available plant standing crop had been consumed by the muskoxen in each week during the main growing season. Consumption in the “Other vegetation types” was not quantified because muskoxen rarely forage there (Kristensen et al., 2011) but use these areas for resting and ruminating. As most data included in this study stem from the main growing season (i.e., the first nine weeks), we mainly report results from this period, but include estimates of the biomass removal into the autumn as well.

Fecal Deposition

The weekly total fecal deposition by muskoxen was calculated following the same approach as for biomass removal, using the rates of fecal output provided by the same studies as the required daily intake (see Table 3). We estimated the relative spatial distribution in fecal deposition among the three vegetation types (“graminoid-dominated areas,” “*Salix* snowbeds,” and “Other vegetation types”)

TABLE 3

Muskox forage intake and fecal output (dry weight) rates from different studies used in the present study to calculate biomass removal and fecal deposition at Zackenberg, Northeast Greenland.

Forage intake	Fecal output	Study	Animal	Season	Reference
22.00*	5.50*	Wild	Bulls	July–August	Hubert (1977)
151.00**	71.70**	Wild	Mixed	July	Kazmin and Abaturov (2011)
17.14*	4.98*	Captivity	Bulls	August–September	Calculated from Barboza et al. (2006)
50.00**	—	Captivity	Cows	July–August	Adamczewski et al. (1994)
102.00**	—	Captivity	—	June–August	White et al. (1984)

*g dw kg⁻¹ day⁻¹.

**g dw kg^{-0.75} day⁻¹.

by estimating the densities of fresh muskox feces along a minimum of five 100–300 m long transects within the census area during summer. “Other vegetation types” comprise several, less dominant vegetation types inside the census area, including fell field and *Dryas* heath. Only feces from the current summer were included, as the persistence of feces differs in different vegetation types (Klein and Bay, 1994).

Nitrogen Relocation

To estimate the relocation of nitrogen by muskoxen, we calculated the nitrogen content in the plant material consumed by muskoxen, as well as the nitrogen content in the feces deposited by muskoxen during the main growing season (nine weeks). For this purpose, we used published data on local nitrogen contents of muskox summer forage (*Salix* snowbeds: 2.2%, Graminoid-dominated areas: 1.6%) and feces (2.8%) (Kristensen et al., 2011). Again, we assumed that 80% of the plant forage found in muskox summer feces derived from the graminoid-dominated areas, while 20% derived from the *Salix* snowbeds (Kristensen et al., 2011). As a conservative measure of urinary nitrogen loss, we assumed the urinary nitrogen loss to be ~50% of the total nitrogen loss (Sponheimer et al., 2003; Robinson et al., 2005), and we therefore assumed the total nitrogen deposition to be twice the amount of nitrogen deposited from feces alone.

RESULTS

Biomass Removal

Across the 18 years of study, the mean annual amount of biomass removed during the main growing season within the ~47 km² census area was estimated to 9.7 ± 0.14 tons (Table 2; mean \pm standard error; $n = 18$). Of these, 7.74 ± 0.11 tons (0.399 g m^{-2}) derived from the graminoid-dominated areas and 1.93 ± 0.03 tons (0.280 g m^{-2}) from the *Salix* snowbeds (Table 2). Compared to the weekly aboveground total standing crop in the two habitat types, the muskoxen on average only removed 0.17% and 0.04% of the available weekly standing crop during the main growing season in the graminoid-dominated areas and in *Salix* snowbeds, respectively (Fig. 1). In late summer, and into

the arctic autumn, however, the mean density of muskoxen in the Zackenberg valley increases markedly (Schmidt et al., 2015; Fig. 1). The concomitant increase in biomass removal in late summer and into the autumn resulted in muskoxen removing ~2.40% of the available forage in the graminoid-dominated areas in this period (Fig. 1), and only ~0.10% of the available forage (twigs) from the *Salix* snowbeds (Fig. 1). In the very last week, the biomass removal peaked with ~4.6% and 0.20% of the available forage being removed by muskoxen inside the graminoid-dominated areas and *Salix* snowbeds, respectively (Fig. 1).

Fecal Deposition

The total fecal deposition by the muskox population within the census area was estimated to 4.11 ± 0.06 tons per year during the main growing season (Table 2). The spatial variation in fecal deposition between the three vegetation types revealed that 62% of all feces were deposited in *Salix* snowbeds. Only 9% was found in the graminoid-dominated areas, while 29% were deposited in the remaining parts of vegetation types (other vegetation). This corresponds to $\sim 0.37 \pm 0.01$ tons (0.02 g m^{-2}) being deposited in the graminoid-dominated areas, while $2.55 \text{ tons} \pm 0.04 \text{ tons}$ (0.37 g m^{-2}) were deposited within the *Salix* snowbeds. Other vegetation types received $\sim 1.19 \pm 0.02$ tons (0.06 g m^{-2} ; Table 2 and Fig. 2).

Nitrogen Relocation

The estimated quantities of biomass removal and feces deposition were converted to nitrogen intake and loss, respectively. During the nine weeks of the main growing season in Zackenberg, the muskox population removed a total of 124 ± 1.82 kg of nitrogen within the graminoid-dominated areas (0.006 g m^{-2}), and a total of 43 ± 0.63 kg nitrogen within the *Salix* snowbeds (Fig. 2). The total nitrogen input from defecation and urination to the graminoid-dominated areas was estimated to 21 ± 0.31 kg (0.001 g m^{-2}), and 143 ± 2.12 kg (0.02 g m^{-2}) to the *Salix* snowbeds. Other vegetation types received a total nitrogen input of 67 ± 0.10 kg (0.003 g m^{-2} ; Fig. 2). This pattern resulted in a net transfer of nitrogen from the graminoid-dominated areas to the *Salix* snowbeds of 110 kg of

nitrogen within the census area, corresponding to a net addition of 0.016 g m^{-2} of nitrogen in the *Salix* snowbeds (Fig. 2).

DISCUSSION

During the short snow-free period, muskoxen have to restore their fat reserves before the onset of winter. The amount of deposited fat influences winter survival and other vital population parameters, such as pregnancy rates (Adamczewski et al., 1997, 1998). Therefore, arctic herbivores, including muskoxen, have to maximize their nitrogen uptake during the summer (Forchhammer and Boomsma, 1995; Gustine et al., 2011). Consequently, in summer, muskoxen at Zackenberg forage mainly in the productive and nitrogen-rich areas in the landscape (Kristensen et al., 2011), that is, those dominated by graminoids (Arndal et al., 2009). As the densities of muskoxen at Zackenberg are among the highest reported for the High Arctic (Schmidt et al., 2015), we expected a substantial grazing pressure in the graminoid-dominated areas. Indeed, the muskoxen did remove large quantities of plant forage from the graminoid-dominated areas within the census area. Nonetheless, compared to the availability of plant forage, the fraction of plant biomass removed by herbivores during the main growing season was negligible (Fig. 1). Less than 1% of the available forage in the most heavily grazed areas (the graminoid-dominated areas)

was consumed during the main growing season each year. However, as the density of muskoxen increased into the autumn, where the available plant biomass had declined, the fraction of plant biomass consumed within the graminoid-dominated areas increased up to $\sim 5\%$ by the end of October (Fig. 1). These fractions are similar to previously reported fractions of consumption by muskoxen (Hubert, 1977; Bliss, 1986), though fractions up to about 50% have also been reported (Raillard and Svoboda, 2000). Hubert (1977) reported that muskoxen on Devon Island consumed 4.9% of the available biomass within meadows during a 12-month period, though it was especially the winter biomass removal that contributed to this estimate. Biomass removal by muskoxen at Zackenberg is thus of the same magnitude as biomass removal by invertebrate herbivores in the Arctic with less than 1% (Roslin et al., 2013), a percentage that traditionally has led to invertebrates being overlooked as important arctic herbivores (Haukioja, 1981; MacLean, 1981). The biomass removal from the *Salix* snowbeds was even less than the graminoid-dominated areas. Even though the *Salix* snowbeds only cover about one-third of the graminoid-dominated areas, the availability of plant biomass in the two was almost similar due to the high standing crop of willows (Fig. 1). Nonetheless, at Zackenberg the muskoxen removed less than 0.05% of the available biomass inside the *Salix* snowbeds during the main growing season. This fraction only increased up to 0.10% in

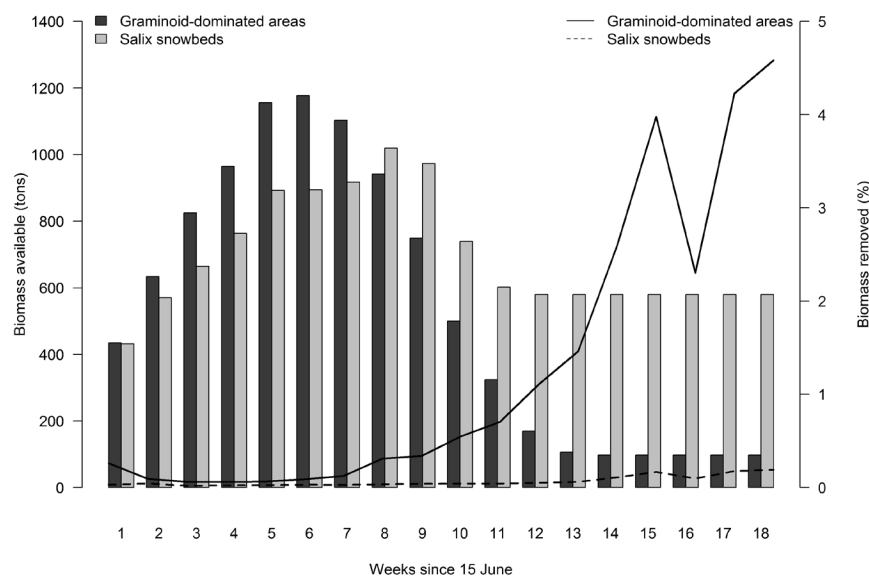


FIGURE 1. Weekly plant biomass availability (total standing crop) and plant biomass removed by muskoxen at Zackenberg, Northeast Greenland. Bars show the aboveground standing crop within the two main vegetation types (graminoid-dominated areas, and *Salix* snowbeds; data obtained from Arndal et al., 2009). Lines indicate the fraction (%) of plant standing crop removed by muskoxen. The first 9 weeks cover the main growing season at Zackenberg (i.e. mid-June to end of August).

late October due to the continuing high overwintering standing crop in the twigs (Fig. 1). Based on these low biomass removal rates by muskoxen, we therefore conclude that plant forage during summer, per se, is not a limiting factor for the muskox populations in high arctic areas, and there seems to be sufficient plant forage available each year for them to replenish their fat reserves during the summer. This is also supported by the lack of correlation between muskox abundance and plant biomass availability in summer reported by Schmidt et al. (2015). The same study concluded that the snow cover and persistence are major determinants of the muskox population at Zackenberg and most likely also across the Arctic (Schmidt et al., 2015).

In spite of the quantitatively small biomass removal, the muskoxen may still have important qualitative impacts on the ecosystem structure and function (Mulder and Harmsen, 1995; Tolvanen and Henry, 2000; Tolvanen et al., 2001, 2002; Post and Pedersen, 2008; Elliott and Henry, 2011; Falk et al., 2014, 2015). For example, Post and Pedersen (2008) found that muskox grazing tends to decrease dwarf shrubs, increase the plant biodiversity, and even oppose the climate change effects on the vegetation. Additionally, decreased net primary production has been found in grazed areas (Elliott and Henry, 2011), which along with decreased litter accumulation and trampling in grazed area may affect the carbon balance of the system (Falk et al., 2014, 2015). Additionally, large herbivores have long been scrutinized as an important driver in the nitrogen cycle in the Arctic (Van der Wal et al., 2004; Barthelemy et al., 2015). Not only do large herbivores remove large quantities of tissues with high nitrogen levels (i.e., new shoots), they also precede resorption and release easily accessible nitrogen through defecation and urination to the soil. In severely nutrient-limited ecosystems, such as the Arctic, defecation and urination by muskoxen may increase nitrogen uptake in plants, reduce their C/N ratios, increase plant growth, but also stimulate microbial growth and decomposition, and increase herbivory (McKendrick et al., 1980; Chapin et al., 1995; Ball et al., 2000; Pennings et al., 2005; Christiansen et al., 2012). However, perhaps more important, large herbivores are capable of transferring large quantities of nutrients between areas, as defecation and urination may not occur in the

same areas utilized for foraging. Indeed, we found the majority of fecal droppings inside the *Salix* snowbeds even though most of the foraging took place in the graminoid-dominated areas. Spatial relocation of nutrients by water and windblown litter has long been recognized as a major driver in these nitrogen-limited tundra ecosystems (Kummerow et al., 1987; Chapin et al., 1988; Oberbauer et al., 1989; Murray, 1991; Fahnestock et al., 2000), and recently Olofsson (2009) suggested that the spatial decoupling of herbivore consumption and excretion is of major importance in arctic terrestrial ecosystems.

Quantifying the spatial relocation of nitrogen between the different vegetation types revealed a net export of nitrogen from the graminoid-dominated areas of about 160 kg of nitrogen each year during the main growing season (Fig. 2), which corresponds to a loss of 0.008 g m⁻² each year from the graminoid-dominated areas. Of these, about 110 kg nitrogen net is transferred to the *Salix* snowbeds. Murray (1991) reported a similar spatial relocation of nutrients from fens to *Salix* snowbeds at Sverdrup Pass, Canada. Across the main growing season, our results suggest that a net addition of 0.016 g m⁻² easily accessible nitrogen is relocated to the *Salix* snowbeds each year—a number eight times higher than those estimated from another high arctic site (Henry and Svoboda, 1986). In general, soils from graminoid-dominated fen and grassland areas hold the largest nitrogen pool in the Arctic (Giblin et al., 1991; Elberling et al., 2008), and Giblin et al. (1991) estimated the total stock of dissolved inorganic nitrogen from wetlands to be about 0.055 g m⁻² in the uppermost soil layer. Hence, the total loss of nitrogen from the graminoid-dominated areas (0.009 g m⁻²; Fig. 2) is small compared to the available, inorganic nitrogen pool in this relatively nutrient-rich plant community. However, shrub-dominated areas are among the arctic vegetation types with the lowest plant available soil nitrogen pools in the Arctic, and Giblin et al. (1991) estimated the total stock of dissolved inorganic nitrogen in such soils to be about 0.015 g m⁻² in the uppermost soil layer. Thus, the addition of nitrogen to the *Salix* snowbeds by muskoxen is likely to have a significant impact, as both the microbial community and the plants within the *Salix* snowbeds receive eas-

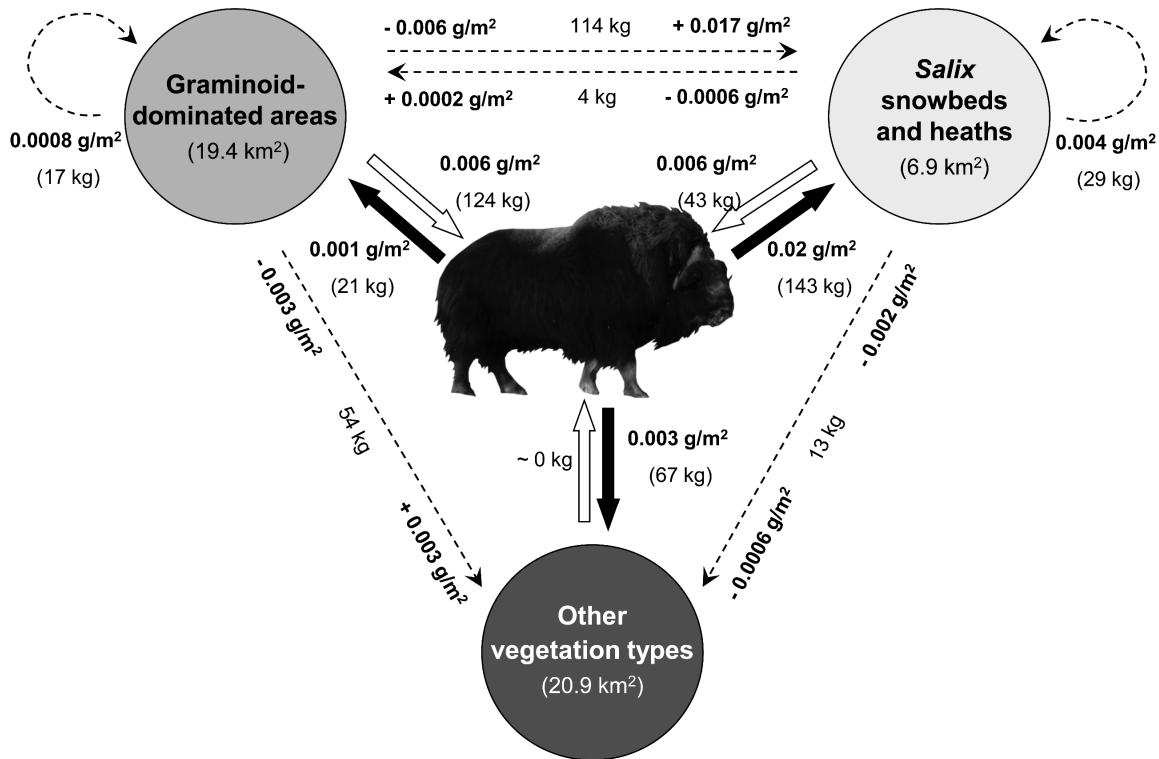


FIGURE 2. Flow diagram showing the gross removal, deposition, and relocation of nitrogen caused by muskoxen during the main growing season within the designated 47 km² census area at Zackenberg, Northeast Greenland. Broad arrows indicate the muskox removal (white) and fecal and urine deposition (black). Dashed arrows indicate the relocation of nitrogen associated with the fecal and urine deposition (see text for further explanation). Nitrogen quantities (g m⁻²) specific to the vegetation type are given in bold, whereas the raw quantities (kg) are given in brackets.

ily accessible nitrogen from muskoxen in amounts equal to the total dissolved inorganic pool. Additionally, nitrogen deposition by fecal and urine input is likely to continue outside the growing season and into the autumn, although these nutrients may be redistributed farther by meltwater streams during snowmelt (Kummerow et al., 1987; Oberbauer et al., 1989; Murray, 1991; Fahnestock et al., 2000). Nonetheless, the nitrogen relocation by muskoxen is likely to have large qualitative effects on the plant communities. Numerous studies have shown enhanced primary productivity in arctic plant communities after nitrogen addition (Chapin and Shaver, 1996; Jonasson et al., 1996; Grellmann, 2002), and recently Barthelemy et al. (2015) reported a strong plant response in a long-term reindeer feces experiment. Here reindeer feces were added to two different arctic vegetation types, graminoid-dominated meadow and shrub-dominated heath. Both vegetation types showed increased primary production, as well as an in-

creased growth of deciduous shrubs on the heath. Hence, the relocation of nitrogen through muskox grazing and defecation and urination is likely to be significant, and to have large qualitative impacts on plant (and other) communities in our study area, but also in general in the nitrogen limited ecosystems in the High Arctic.

CONCLUSION

In the present study, we have provided a, albeit coarse, quantification of muskox biomass removal and fecal deposition, thereby allowing for the estimation of the net nitrogen relocation between different vegetation types. We have shown that even though the area at Zackenberg holds large densities of muskoxen, the fraction of available plant forage consumed by muskoxen is generally low and almost negligible during summer. Nonetheless, the spatial relocation of nitrogen by muskoxen is likely to assert a significant impact on tundra communities.

Our results thus stress the central role of muskoxen in the tundra ecosystem.

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REFERENCES CITED

- Adamczewski, J. Z., Flood, P. F., and Gunn, A., 1997: Seasonal patterns in body composition and reproduction of female muskoxen (*Ovibos moschatus*). *Journal of Zoology*, 241(2): 245–269.
- Adamczewski, J. Z., Fargey, P. J., Laarveld, B., Gunn, A., and Flood, P. F., 1998: The influence of fatness on the likelihood of early-winter pregnancy in muskoxen (*Ovibos moschatus*). *Theriogenology*, 50(4): 605–614.
- Arndal, M. F., Illeris, L., Michelsen, A., Albert, K., Tamstorf, M., and Hansen, B. U., 2009: Seasonal variation in gross ecosystem production, plant biomass, and carbon and nitrogen pools in five high arctic vegetation types. *Arctic, Antarctic, and Alpine Research*, 41(2): 164–173.
- Ball, J. P., Danell, K., and Sunesson, P., 2000: Response of a herbivore community to increased food quality and quantity: an experiment with nitrogen fertilizer in a boreal forest. *Journal of Applied Ecology*, 37(2): 247–255.
- Barthelemy, H., Stark, S., and Olofsson, J., 2015: Strong responses of subarctic plant communities to long-term reindeer feces manipulation. *Ecosystems*: 1–12, doi <http://dx.doi.org/10.1007/s10021-015-9856-y>.
- Bay, C., 1998: *Vegetation Mapping of Zackenberg Valley, Northeast Greenland*. Denmark: Danish Polar Center & Botanical Museum, University of Copenhagen.
- Berg, T. B., Schmidt, N. M., Høye, T. T., Aastrup, P., Hendrichsen, D. K., Forchhammer, M. C., and Klein, D. R., 2008: High-Arctic plant-herbivore interactions under climate influence. In Meltofte, H., Christensen, T. R., Elberling, B., Forchhammer, M. C., and Rasch, M. (eds.), *Advances in Ecological Research*. London: Elsevier.
- Billings, W. D., and Mooney, H. A., 1968: The ecology of arctic and alpine plants. *Biological Reviews*, 43(4): 481–529.
- Bliss, L. C., 1986: Arctic ecosystems: their structure, function and herbivore carrying capacity. In Gudmundsson, O. (ed.), *Grazing Research at Northern Latitudes*. New York: Springer, NATO ASI Series, 5–25.
- Chapin, F. S., III, and Shaver, G. R., 1996: Physiological and growth responses of Arctic plants to a field experiment simulating climatic change. *Ecology*, 77(3): 822–840.
- Chapin, F. S., Fetcher, N., Kielland, K., Everett, K. R., and Linkins, A. E., 1988: Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing soil water. *Ecology*, 69(3): 693–702.
- Chapin, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., and Laundre, J. A., 1995: Responses of Arctic Tundra to Experimental and Observed Changes in Climate. *Ecology*, 76(3): 694–711.
- Chapin, F. S., Matson, P. A., and Mooney, H. A., 2002: Terrestrial plant nutrient use. In *Principles of Terrestrial Ecosystem Ecology*. New York: Springer-Verlag, 176–196.
- Christiansen, C. T., Svendsen, S. H., Schmidt, N. M., and Michelsen, A., 2012: High Arctic heath soil respiration and biogeochemical dynamics during summer and autumn freeze-in—effects of long term enhanced water and nutrient supply. *Global Change Biology*, 18: 3224–3236.
- Elberling, B., Tamstorf, M. P., Michelsen, A., Arndal, M. F., Sigsgaard, C., Illeris, L., Bay, C., Hansen, B. U., Christensen, T. R., Hansen, E. S., Jakobsen, B. H., and Beyens, L., 2008: Soil and plant community-characteristics and dynamics at Zackenberg. In Meltofte, H., Christensen, T. R., Elberling, B., Forchhammer, M. C., and Rasch, M. (eds.), *Advances in Ecological Research: High-Arctic Ecosystem Dynamics in a Changing Climate*. London: Elsevier, 223–248.
- Ellebjer, S. M., Tamstorf, M. P., Illeris, L., Michelsen, A., and Hansen, B. U., 2008: Inter-annual variability and controls of plant phenology and productivity at Zackenberg. In Meltofte, H., Christensen, T. R., Elberling, B., Forchhammer, M. C., and Rasch, M. (eds.), *Advances in Ecological Research: High-Arctic Ecosystem Dynamics in a Changing Climate*. London: Elsevier, 249–273.
- Elliott, T., and Henry, G., 2011: Effects of simulated grazing in ungrazed wet sedge tundra in the High Arctic. *Arctic, Antarctic, and Alpine Research*, 43(2): 198–206.
- Fahnestock, J. T., Povirk, K. L., and Welker, J. M., 2000: Ecological significance of litter redistribution by wind and snow in Arctic landscapes. *Ecography*, 23(5): 623–631.
- Falk, J., Schmidt, N., and Ström, L., 2014: Effects of simulated increased grazing on carbon allocation patterns in a high arctic mire. *Biogeochemistry*, 119(1–3): 229–244.
- Falk, J. M., Schmidt, N. M., Christensen, T. R., and Ström, L., 2015: Large herbivore grazing affects the vegetation structure and greenhouse gas balance in a High Arctic mire. *Environmental Research Letters*, 10(4): 045001, doi <http://dx.doi.org/10.1088/1748-9326/10/4/045001>.
- Forchhammer, M., and Boomsma, J., 1995: Foraging strategies and seasonal diet optimization of muskoxen in West Greenland. *Oecologia*, 104(2): 169–180.

- Giblin, A. E., Nadelhoffer, K. J., Shaver, G. R., Laundre, J. A., and McKerrow, A. J., 1991: Biogeochemical diversity along a riverside toposequence in Arctic Alaska. *Ecological Monographs*, 61(4): 415–435.
- Grellmann, D., 2002: Plant responses to fertilization and exclusion of grazers on an Arctic tundra heath. *Oikos*, 98(2): 190–204.
- Gustine, D. D., Barboza, P. S., Lawler, J. P., Arthur, S. M., Shults, B. S., Persons, K., and Adams, L. G., 2011: Characteristics of foraging sites and protein status in wintering muskoxen: insights from isotopes of nitrogen. *Oikos*, 120(10): 1546–1556.
- Hansen, B. U., Sigsgaard, C., Rasmussen, L., Cappelen, J., Hinkler, J., Mernild, S. H., Petersen, D., Tamstorf, M. P., Rasch, M., and Hasholt, B., 2008: Present-day climate at Zackenberg. In Meltotte, H., Christensen, T. R., Elberling, B., Forchhammer, M. C., and Rasch, M. (eds.), *Advances in Ecological Research: High-Arctic Ecosystem Dynamics in a Changing Climate*. London: Elsevier, 111–149.
- Haukioja, E., 1981: Invertebrate herbivory at tundra sites. In Bliss, L. C., Heal, O. W., and Moore, J. J. (eds.), *Tundra Ecosystems*. Cambridge, U.K.: Cambridge University Press, 547–556.
- Henry, G. H. R., and Svoboda, J., 1986: Dinitrogen fixation (acetylene reduction) in high arctic sedge meadow communities. *Arctic and Alpine Research*, 18(2): 181–187.
- Henry, G. H. R., Svoboda, J., and Freedman, B., 1990: Standing crop and net production of sedge meadows of an ungrazed polar desert oasis. *Canadian Journal of Botany*, 68(12): 2660–2667.
- Hobbs, N. T., 1996: Modification of ecosystems by ungulates. *The Journal of Wildlife Management*, 60(4): 695–713.
- Hofmann, R. R., 1989: Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia*, 78(4): 443–457.
- Hubert, B. A., 1977: Estimated productivity of muskox on Truelove Lowland. In Bliss, L. C. (ed.), *Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem*. Edmonton: University of Alberta Press, 467–491.
- Jefferies, R. L., Klein, C. J., and Shaver, G., 1994: Vertebrate herbivores and northern plant communities: reciprocal influences and responses. *Oikos*, 71: 193–206.
- Jonasson, S., Michelsen, A., Schmidt, I., Nielsen, E., and Callaghan, T., 1996: Microbial biomass C, N and P in two Arctic soils and responses to addition of NPK fertilizer and sugar: implications for plant nutrient uptake. *Oecologia*, 106(4): 507–515.
- Kazmin, V. D., and Abaturon, B. D., 2011: Quantitative characteristics of nutrition in free-ranging reindeer (*Rangifer tarandus*) and musk oxen (*Ovibos moschatus*) on Wrangel Island. *Biology Bulletin*, 38(9): 935–941.
- Klein, D. R., and Bay, C., 1990: Foraging dynamics of muskoxen in Peary Land, northern Greenland. *Ecography*, 13(4): 269–280.
- Klein, D. R., and Bay, C., 1991: Diet selection by vertebrate herbivores in the High Arctic of Greenland. *Holarctic Ecology*, 14: 152–155.
- Klein, D. R., and Bay, C., 1994: Resource partitioning by mammalian herbivores in the High Arctic. *Oecologia*, 97(4): 439–450.
- Kristensen, D. K., Kristensen, E., Forchhammer, M. C., Michelsen, A., and Schmidt, N. M., 2011: Arctic herbivore diet can be inferred from stable carbon and nitrogen isotopes in C₃ plants, faeces, and wool. *Canadian Journal of Zoology*, 89: 893–900.
- Kummerow, J., Mills, J. N., Ellis, B. A., Hastings, S. J., and Kummerow, A., 1987: Downslope fertilizer movement in Arctic tussock tundra. *Ecography*, 10(4): 312–319.
- Larter, N. C., and Nagy, J. A., 2004: Seasonal changes in the composition of the diets of Peary caribou and muskoxen on Banks Island. *Polar Research*, 23(2): 131–140.
- Latour, P. B., 1987: Observations on demography, reproduction, and morphology of muskoxen (*Ovibos moschatus*) on Banks Island, Northwest Territories. *Canadian Journal of Zoology*, 65(2): 265–269.
- MacLean, S. F. J., 1981: Fauna of tundra ecosystems: invertebrates. In Bliss, L. C., Heal, O. W., and Moore, J. J. (eds.), *Tundra Ecosystems*. Cambridge, U.K.: Cambridge University Press, 509–516.
- McKendrick, J. D., Batzli, G. O., Everett, K. R., and Swanson, J. C., 1980: Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. *Arctic and Alpine Research*, 12(4): 565–578.
- McNaughton, S. J., Oesterheld, M., Frank, D. A., and Williams, K. J., 1989: Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, 341(6238): 142–144.
- McNaughton, S. J., Milchunas, D. G., and Frank, D. A., 1996: How can net primary productivity be measured in grazing ecosystems? *Ecology*, 77(3): 974–977.
- Muc, M., 1977: Ecology and primary production of sedge-moss communities, Truelove Lowland. In Bliss, L. C. (ed.), *Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem*. Edmonton: University of Alberta Press, 157–184.
- Mulder, C. P. H., and Harmsen, R., 1995: The effect of muskox herbivory on growth and reproduction in an Arctic legume. *Arctic and Alpine Research*, 27(1): 44–53.
- Murray, J. L., 1991: Biomass Distribution and Nutrient Pool and Dynamics in the Major Muskox-Grazed Communities at Sverdrup Pass (79°N) Ellesmere Island, N.W.T, Canada. Master's thesis, University of Toronto, 183 pp.
- Nadelhoffer, K. J., Giblin, A. E., Shaver, G. R., and Laundre, J. A., 1991: Effects of temperature and substrate quality on element mineralization in 6 Arctic soils. *Ecology*, 72(1): 242–253.
- Oberbauer, S. F., Hastings, S. J., Beyers, J. L., and Oechel, W. C., 1989: Comparative effects of downslope water and nutrient movement on plant nutrition, photosynthesis, and growth in Alaskan tundra. *Holarctic Ecology*, 12(3): 324–334.
- Olesen, C. R., and Thing, H., 1989: Guide to field classification by sex and age of the muskox. *Canadian Journal of Zoology*, 67(5): 1116–1119.
- Olofsson, J., 2009: Effects of simulated reindeer grazing, trampling, and waste products on nitrogen mineralization

- and primary production. *Arctic, Antarctic, and Alpine Research*, 41(3): 330–338.
- Parker, G. R., and Ross, R. K., 1976: Summer habitat use by muskoxen (*Ovibos moschatus*) and Peary caribou (*Ranifer tarandus pearyi*) in the Canadian High Arctic. *Polarforschung*, 46(1): 12–25.
- Pennings, S. C., Clark, C. M., Cleland, E. E., Collins, S. L., Gough, L., Gross, K. L., Milchunas, D. G., and Suding, K. N., 2005: Do individual plant species show predictable responses to nitrogen addition across multiple experiments? *Oikos*, 110(3): 547–555.
- Post, E., and Pedersen, C., 2008: Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences*, 105(34): 12353–12358.
- Raillard, M., and Svoboda, J., 2000: High grazing impact, selectivity, and local density of muskoxen in Central Ellesmere Island, Canadian High Arctic. *Arctic, Antarctic, and Alpine Research*, 32(3): 278–285.
- Robinson, T. F., Roeder, B. L., Schaalje, G. B., Hammer, J. D., Burton, S., and Christensen, M., 2005: Nitrogen balance and blood metabolites of alpaca (*Lama pacos*) fed three forages of different protein content. *Small Ruminant Research*, 58(2): 123–133.
- Roslin, T., Wirta, H., Hopkins, T., Hardwick, B., and Várkonyi, G., 2013: Indirect interactions in the High Arctic. *PLoS ONE*, 8(6): e67367, doi <http://dx.doi.org/10.1371/journal.pone.0067367>.
- Schmidt, N., Pedersen, S., Mosbacher, J., and Hansen, L., 2015: Long-term patterns of muskox (*Ovibos moschatus*) demographics in high arctic Greenland. *Polar Biology*, 38(10): 1667–1675.
- Sponheimer, M., Robinson, T., Ayliffe, L., Roeder, B., Hammer, J., Passey, B., West, A., Cerling, T., Dearing, D., and Ehleringer, J., 2003: Nitrogen isotopes in mammalian herbivores: hair $\delta^{15}\text{N}$ values from a controlled feeding study. *International Journal of Osteoarchaeology*, 13(1–2): 80–87.
- Tamstorf, M., Illeris, L., Hansen, B., and Wisz, M., 2007: Spectral measures and mixed models as valuable tools for investigating controls on land surface phenology in High Arctic Greenland. *BMC Ecology*, 7(1): 9.
- Thing, H., Klein, D. R., Jingfors, K., and Holt, S., 1987: Ecology of muskoxen in Jameson Land, northeast Greenland. *Ecography*, 10(2): 95–103.
- Tolvanen, A., and Henry, G. H. R., 2000: Population structure of three dominant sedges under muskox herbivory in the High Arctic. *Arctic, Antarctic, and Alpine Research*, 32(4): 449–455.
- Tolvanen, A., Schroderus, J., and Henry, G. H. R., 2001: Demography of three dominant sedges under contrasting grazing regimes in the High Arctic. *Journal of Vegetation Science*, 12(5): 659–670.
- Tolvanen, A., Schroderus, J., and Henry, G. H. R., 2002: Age- and stage-based bud demography of *Salix arctica* under contrasting muskox grazing pressure in the High Arctic. In Stuefer, J. F., Erschbamer, B., Huber, H., and Suzuki, J. I. (eds.), *Ecology and Evolutionary Biology of Clonal Plants*. Dordrecht: Springer Netherlands, 221–240.
- Van der Wal, R., Bardgett, R. D., Harrison, K. A., and Stien, A., 2004: Vertebrate herbivores and ecosystem control: cascading effects of faeces on tundra ecosystems. *Ecography*, 27: 242–252.
- Wilkinson, P. F., Shank, C. C., and Penner, D. F., 1976: Muskox-caribou summer range relations on Banks Island, N.W.T. *The Journal of Wildlife Management*, 40(1): 151–162.
- Williams, P. H., and Haynes, R. J., 1995: Effect of sheep, deer and cattle dung on herbage production and soil nutrient content. *Grass and Forage Science*, 50(3): 263–271.

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