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A test of the herbivore optimization hypothesis using muskoxen and a graminoid meadow plant community

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Abstract: A prediction from the herbivore optimization hypothesis is that grazing by herbivores at moderate intensities will increase net above-ground primary producrivity more than at lower or higher intensities. I tested this hypothesis in an area of high muskox (*Ovibos moschatus*) density on north-central Banks Island, Northwest Territories, Canada (73°50'N, 119°53'W). Plots (1 m^2) in graminoid meadows dominated by cottongrass (*Eriophorum triste*) were either clipped, exposed to muskoxen, protected for part of one growing season, or permanently protected. This resulted in the removal of 22-44%, 10-39%, 0-39% or 0%, respectively, of shoot tissue during each growing season. Contrary to the predictions of the herbivore optimization hypothesis, productivity did not increase across this range of tissue removal. Productivity of plants clipped at 1.5 cm above ground once or twice per growing season, declined by 60±5% in 64% of the tests. The productivity of plants grazed by muskoxen declined by 56±7% in 25% of the tests. No significant change in productivity was observed in 36% and 75% of the tests in clipped and grazed treatments, respecrively. Clipping and grazing reduced below-ground standing crop except where removals were small. Grazing and clipping did not stimulate productivity of north-central Banks Island graminoid meadows.

Key words: grazing, arctic, biomass, plant community, roots.

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Introduction

The herbivore optimization hypothesis is a prediction that grazing by herbivores at moderate intensities increases net above-ground primary productivity above ungrazed, lightly grazed and heavily grazed levels (McNaughton, 1979). Its validity is equivocal (Painter & Belsky, 1993) because of the confounding problems of scale (Brown & Allen, 1989), methodology (see Belsky, 1986) and spatial and temporal variation among studies. Subarctic graminoids increased in productivity after being grazed by wood bison (*Bison bison athabascae*) at more productive sites, but not at less productive sites because plants at ungrazed sites smothered in a thick litter layer (Smith, 1990). Productivity of nutrient-limited meadows increased in response to snow goose (*Anser caerulescens caerulescens*) grazing and increased rates of nutrient cycling (Bazely & Jefferies, 1989; Hik & Jefferies, 1990). In contrast, carbon-limited plant species often decline in productivity after being grazed (Lacey & Van Poollen, 1981) because of reduced photosynthetic leaf area.

Since the 1950s, the population of muskoxen on Banks Island grew exponentially (Vincent & Gunn, 1981; McLean *et al.*, 1989). Muskox densities are particularly high (1.52/km^2) in the Thomsen River Valley of north-central Banks Island (McLean *et al.* 1989). Despite the eruption of muskox populations across North America (Smith, 1984; Thing *et al.*, 1984; Henry *et al.*, 1994), little is known about the summer range of muskoxen in northern Canada (Parker & Ross, 1976).

Muskoxen at Sverdrup Pass on Ellesmere Island feed in sparsely vegetated uplands with shallow snow cover during winter and on more productive lowland meadows during summer (Raillard, 1992). However, if snow cover is soft and shallow in meadows during winter, muskoxen will graze meadows all year (Hubert, 1977).

Consistent with the herbivore-optimization hypothesis, I predicted that: (1) Graminoid meadows would increase production in response to moderate clipping or herbivory by muskoxen; (2) Removal of shoot tissue by clipping or by muskoxen would have no effect on the standing crop of live roots.

Methods

Study Area

The study area was located near the confluence of the Thomsen and Muskox Rivers on north central Banks Island (73°50'N, 119°53'W). The climate is Arctic Desert with long cold winters, with mean January temperatures of -30°C, and short cold summers with mean July temperatures of 4°C. Average precipitation is only about 9 cm annually (Zoltai *et al.*, 1980). The topography is gently rolling with the hilltops rarely exceeding 250 m in elevation a.s.l..

Wilkinson *et al.* (1976) described 5 habitat types including sedge meadows and Ferguson (1991) further divided the sedge meadows into: (1) wet sedge meadows (hygric), and (2) graminoid tundra (subhygric).

Eriophorum triste and *Carex aquatilis* var. *stans* are rhizomatous sedge species that overwinter with a small amount of basal green tissue. During summer, plants are composed of 1-2 potentially fertile culms surrounded by 2-8 sterile, leafy shoots (Porsild and Cody, 1980). The 2 species were abundant in northern Banks Island graminoid meadows (Smith, 1996). Muskoxen on northern Banks Island grazed graminoid meadows where *Eriophorum triste* was dominant more often than less productive wet sedge meadows where *Carex aquatilis* var. *stans* was dominant (pers. obs.).

Experimental design

Biomass data were gathered from 3 study sites within the graminoid plant community. Two study sites, Muskox River (MR) and Thomsen River (TR) each contained a 10 m x 10 m permanent exclosure erected in mid-August 1988. Ten 1 m X 1 m plots per treatment were clipped 1.5 cm above the ground. At Muskox River, a group of plots was clipped once in 1991 and twice in 1992; another group served as a control in 1991 and was clipped once in 1992. At Thomsen River, a group of plots was clipped twice in both 1991 and 1992; another group was clipped once in both 1991 and 1992; Controls were not clipped. Plots were not clipped in 1993. Clipping intensity was the proportion of standing crop removed by clipping at one time. Cumulative green biomass was green shoot tissue removed by previous clipping added to the standing crop of green tissue. Standing crop was the weight of green tissue and standing dead tissue. Productivity was the change in standing crop, usually green tissue, over time.

Four 25 cm x 25 cm sub-plots were randomly located in each of 5 randomly-chosen plots per treatment in 1992 and in the other 5 plots per treatment in 1993. A different sub-plot was clipped to ground level inside each plot 4 times during each of the 1992 and 1993 growing seasons.

Study areas of about 2 ha and 4 ha, adjacent to the permanent exclosures at MR and TR, respectively, were exposed to muskox grazing. A third meadow area of about 1 ha was Umingmuk Hill (UH). Ten transects were laid out at 10-15 m intervals, with the first transect located randomly. Distance between transects was dependent on study site size. Temporary exclosures ("exclusions") were also randomly located using a random numbers table along the transects in late June 1992 and 1993 (2 per transect at MR and TR and 1 per transect at UH). These exclosures, 1.5 m in diameter, were made from aluminum fencing wire, which allowed the passage of small mammals and birds. At the end of each growing season, I counted all new fecal groups (i.e., < 3 months old) in a 3 m-wide belt along each transect.

To measure grazing intensity, a different sub-plot (25 cm x 25 cm) was clipped to ground level inside and out of each temporary exclosure 4 times during each of the 1992 and 1993 growing seasons. Grazing intensity was the proportion of standing crop consumed by muskoxen during a time period (McNaughton, 1985a): $G = 1 - S_g/S_e$, where, G, S_g

and S_e were the grazing intensity, standing crop in grazed areas and standing crop in temporary exclosures, respectively.

All herbage samples were dried at 40-60°C for 24 hours and later dried for 48 hours at 60°C. Each sample was thoroughly mixed and a sub-sample of about one-third of the total was divided into live and dead tissue and extrapolated to the whole sample. Ten samples per year were separated entirely to determine if sub-samples were representative of the whole.

In 1992, I estimated the proportion of live tissue in each sample. Estimates were corrected by a regression equation developed after comparing actual and estimated proportions of live tissue in 166 samples. The equation was: $y = 4.21 + 0.84x$ ($r^2 = 0.86$), where, y and x were the actual and estimated percentage of live tissue, respectively. In 1993 all samples were separated.

Table 1. Proportions of the standing crop removed by muskoxen at 4 dates in summers 1992 and 1993 at 3 study sites on Banks Island, NWT.[1]

Time Period	Study Sites: Muskox R.	Thomsen R.	Umingmuk H.
Jun 25 – Jul 9 1992	0.16a	0.27a	0.13a
Jun 25 – Jul 21	0.32a	0.26a	0.00b
Jun 25 – Jul 31	0.29a	0.23a	0.29a
Jun 25 – Aug 9	0.10b	0.12b	0.39a
Jun 25 – Jul 6 1993	0.09a	0.17a	0.30a
Jun 25 – Jul 22	0.26a	0.10a	0.22a
Jun 25 – Aug 3	0.25a	0.28a	0.23a
Jun 25 – Aug 17	0.18a	0.19a	0.29a

[1] Means with the same subscript within rows are not significantly different at $P \leq 0.10$.

Below-ground biomass

Ten soil cores (10 cm x 10 cm) were removed from each treatment at each site in late August 1993. The soil cores were frozen in the field and transported to the laboratory. The cores were dried at 70°C for 72 hours, broken apart, and crushed with a rolling pin. The material was sifted through 0.5 mm and 0.25 mm sieves. A sub-sample of about one-third was removed from each coarse and fine root sample. Live roots were weighed in all 120 sub-samples of coarse material and 15 randomly chosen sub-samples of fine material.

The volume of each core was used to calculate the weight of roots for each 1 m x 1 m plot. Because few roots grew below 10 cm in 6 soil profiles, I concluded that root biomass estimates were slightly low. In another arctic meadow community, Muc (1977) found that 65% of below-ground standing crop was above 10 cm in soil profiles.

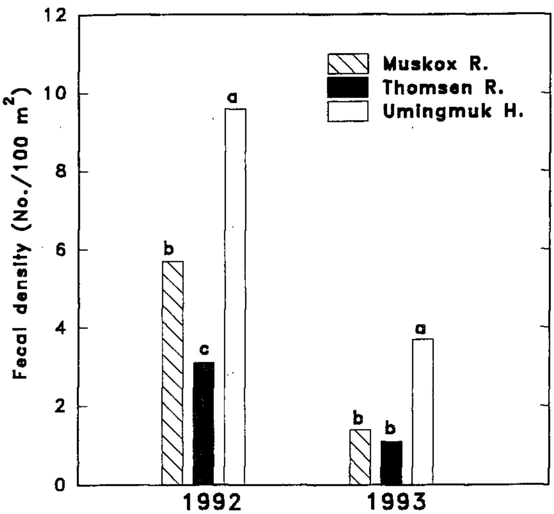

Fig.1. Fecal densities (no./100m²) (mean) in transects (n=10) at 3 study sites during the 1992 and 1993 growing seasons on northern Banks Island, Canada. Means with the same subscript within years are not significantly different at $P \leq 0.10$.

Data analysis

All data were tested for normality using the Shiparo Wilks W test (SAS, 1988) and variances were tested for homogeneity using the F_{max} test (Sokal & Rohlf, 1981). If necessary, data were transformed by log + 1 or square root + 0.5 in order to satisfy the assumptions of parametric statistics. One-way analysis of variance was conducted on the results for all treatments. Means were compared with the LSD test (Sokal & Rohlf, 1981). Statistical significance was assumed to be at $P \leq 0.10$.

Results

Grazing and clipping intensities

Umingmuk Hill had the highest fecal density among the 3 study sites in both years (Fig. 1). Proportions of the standing crop removed by muskoxen ranged from 0-39% of the available forage over 4 periods during a growing season (Table 1).

Table 2. Proportion of plant tissue removed in 1992 by clipping 1 m x 1 m plots (mean±SE) (n=5) inside permanent exclosures at 2 study sites.

Location	Date clipped	Total no. of clippings in 1992	No. of previous clippings 1991	No. of previous clippings 1992	Proportion removed
Muskox R.	July 2	1	0	0	0.22±0.05
Muskox R.	July 1	2	1	0	0.08±0.02
Muskox R.	July 16	2	1	1	0.26±0.02
Thomsen R.	July 8	1	1	0	0.25±0.05
Thomsen R.	July 8	2	2	0	0.30±0.04
Thomsen R.	July 22	2	2	1	0.14±0.02

Table 3. Standing crop estimates (g/m²) (mean±SE) (n=5 per treatment) obtained in 1992 and 1993 for plots with variable clipping histories inside permanent exclosures in 1992 and 1993, northern Banks Island, Canada.

		Standing crop (Mean±SE, g/m²)[1]						
		Previous clippings			Previous clippings			
Location	Date clipped	'91	'92	Standing crop	'91	'92	Standing crop	Control[2]
Muskox R.	July 27/92	1	2	45± 6b	0	1	59± 7b	111±16a
Muskox R.	July 29/93	1	2	121±13a	0	1	125±11a	151±14a
Thomsen R.	July 31/92	2	2	106±12b	1	1	129± 7b	392±30a
Thomsen R.	Aug. 3/93	2	2	148±12b	1	1	157±13b	316±57a

[1] Means with the same subscript within rows are not significantly different at $P\leq.10$.

[2] The control had a high proportion of standing dead material, whereasthe clipped plots contained mostly green material.

Table 4. Standing crop in late July-early August, 1992 and 1993 where grazed, where muskoxen were excluded after June 25 that season, and in control (permanent exclosures) plots onnorthern Banks Island, NWT. (Number of plots are in parentheses).[1]

		Mean Standing Crop (g/m²)(±SE)		
Location	Date Clipped	Grazed	Exclusion[2]	Control
Muskox R.	Jul. 28/92	99±12b (20)	140± 9a (20)	111±16ab (5)
Muskox R.	Jul. 30/93	116± 9b (20)	155±11a (20)	151±14a (5)
Thomsen R.	Jul. 31/92	206±20c (20)	268±16b (18)	392±30a (5)
Thomsen R.	Aug. 3/93	165±16c (20)	228±17b (20)	316±57a (5)
Umingmuk H.	Aug. 4/92	217±20b (10)	305±44a (7)	NA
Umingmuk H.	Aug. 7/93	240±24b (10)	311±30a (10)	NA

[1] Means with the same subscript within rows are not significantly different at $P\leq0.10$.

[2] Muskoxen excluded after June 25 for that season only.

Plots clipped once in early 1992 had 22-25% of tissue removed but plots clipped twice had 34-44% of tissue removed per growing season (Table 2).

Above ground standing crop

Clipping of plots in permanent exclosures at Muskox River (MR) and Thomsen River (TR) reduced standing crop 17 to 73% below the controls in 1992 and 1993 (Table 3). By late July 1993, however, standing crop was similar in clipped and unclipped plots at MR, averaging 132±13 g/m².

Standing crop was 23-29% lower when grazed by muskoxen than in exclusions. Standing crop was 23% and 48% lower in the grazed plots than in

Table 5. Cumulative production of green biomass at 2-5 clippings over 1 and 2 growing seasons and in controls at 2 areas of northern Banks Island, NWT.

		Green biomass (Mean±SE, g/m²)[1]						
		Previous clippings			Previous clippings			
Location	Date clipped	'91	'92	Cumulative biomass	'91	'92	Cumulative biomass	Control
Muskox R.	July 27/92	1	2	38.7±3.9b	0	1	40.5±5.6b	70.6± 9.6a
Thomsen R.	July 31/92	2	2	57.5±3.4c	1	1	86.5±6.8b	136.3±10.2a

[1] Cumulative green biomass includes green shoot tissue removed through clipping added to green standing crop on date indicated. Means with the same subscript within rows are not significantly different at $P \leq 0.10$.

Table 6. Mean (±SE) green, total and absolute productivity estimates[1] (g m^{-2} d^{-1}) among treatments in 1992 and 1993 1m x 1m plots (n=5) inside permanent exclosures.

			Biomass Production (Mean±SE, g/m²/day)						
			Previous clippings			Previous clippings			
Location	Production period	Productivity component	'91	'92	Biomass production	'91	'92	Biomass production	Control
Muskox R.	Jul 3 – Jul 27/92	Green	1	2	0.8±0.2b	0	1	1.2±0.2b	2.3±0.4a
Muskox R.	Jun 27 – Jul 29/93	Green	1	2	2.6±0.4a	0	1	2.7±0.4a	3.4±0.6a
Muskox R.	Jul 3 – Jul 27/92	Total	1	2	-0.3±0.3b	0	1	1.4±0.3a	2.7±0.7a
Muskox R.	Jun 27 – Jul 29/93	Total	1	2	2.5±0.4ab	0	1	2.4±0.3b	3.5±0.6a
Muskox R.	Jul 3 – Jul 27/92	Absolute	1	2	0.8±0.2b	0	1	1.4±0.3ab	2.7±0.6a
Muskox R.	Jun 27 – Jul 29/93	Absolute	1	2	2.6±0.4a	0	1	2.7±0.4a	3.6±0.5a
Thomsen R.	Jul 8 – Jul 31/92	Green	2	2	1.4±0.1b	1	1	1.4±0.3b	4.4±0.4a
Thomsen R.	Jul 4 – Aug 3/93	Green	2	2	2.5±0.6a	1	1	1.6±0.2a	1.6±0.2a
Thomsen R.	Jul 8 – Jul 31/92	Total	2	2	2.5±0.5a	1	1	0.2±0.4b	4.5±1.3a
Thomsen R.	Jul 4 – Aug 3/93	Total	2	2	4.2±0.7b	1	1	2.5±0.7b	7.8±1.8a
Thomsen R.	Jul 8 – Jul 31/92	Absolute	2	2	2.5±0.5b	1	1	1.4±0.3c	5.2±0.7a
Thomsen R.	Jul 4 – Aug 3/93	Absolute	2	2	4.2±0.7b	1	1	2.6±0.6b	7.8±1.8a

[1] "Green productivity" is live (green) plant tissue. "Total productivity" is live (gteen) and dead plant tissue. "Absolute productivity" is live (green) plant tissue plus the transfer of live to dead tissue. Means with the same subscript within tows are not significantly different at $P \leq 0.10$.

control plots at MR in 1993 and at TR in both years, respectively (Table 4).

Herbage biomass and productivity

Productivity did not increase after removing 0% to 44%. The Cumulative Green Biomass in 1992 was greatest in the control and lowest when clipped twice. The 2 clippings had no additional effect over the single clipping at MR (Table 5). Estimates of green, total and absolute productivity were higher in the control than in clipped plots in 1992 and 1993; however by 1993 no change in production occurred in over one-half the cases (Table 6). There were fewer decreases in production in 1993 (42% of cases) than in 1992 (81% of cases).

Productivity declined in 25% of the grazed plots compared with 64% of the clipped plots. Production of clipped and grazed plants declined by 60±5% and 56±7%, respectively. Productivity in grazed areas was lower than production in temporary exclosures in 28% of the cases (Table 7).

Root biomass

Clipping reduced the weight of roots at TR by 10% to 32%, but moderately clipped plots had 18% more below-ground biomass than the control at MR

Table 7. Green, total and absolute productivity (g m^{-2} d^{-1}) estimates (Mean±SE) among treatments in 1992 and 1993 1 m x 1 m plots. (Sample sizes in parentheses).[1]

Location	Production Period	Productivity Component	Biomass production (Mean±SE)(g/m^2/day) Grazed	Exclusion[2]	Control
Muskox R.	Jul 4 – Jul 28/92	Green	1.6±0.3b (20)	2.3±0.2a (20)	2.3±0.4ab (5)
Muskox R.	Jun 30 – Jul 30/93	Green	1.6±0.3b (20)	2.1±0.3b (20)	3.4±0.6a (5)
Muskox R.	Jul 4 – Jul 28/92	Total	2.2±0.6b (20)	3.5±0.4a (20)	2.7±0.7ab (5)
Muskox R.	Jun 30 – Jul 30/93	Total	1.5±0.4b (20)	2.6±0.4a (20)	3.5±0.6a (5)
Muskox R.	Jul 4 – Jul 28/92	Absolute	2.6±0.5a (20)	3.6±0.4a (20)	2.7±0.6a (5)
Muskox R.	Jun 30 – Jul 30/93	Absolute	1.9±0.3b (20)	2.9±0.4a (20)	3.6±0.5a (5)
Thomsen R.	Jul 10 – Aug 1/92	Green	2.7±0.4b (20)	3.8±0.5ab (19)	4.4±0.4a (5)
Thomsen R.	Jul 7 – Aug 3/93	Green	0.3±0.4b (20)	2.3±0.4a (20)	1.6±0.2ab (5)
Thomsen R.	Jul 10 – Aug 1/92	Total	3.7±1.0a (20)	4.1±0.9a (19)	4.5±1.3a (5)
Thomsen R.	Jul 7 – Aug 3/93	Total	1.6±3.1b (20)	3.0±0.6b (20)	7.8±1.8a (5)
Thomsen R.	Jul 10 – Aug 1/92	Absolute	4.4±0.9a (20)	5.4±0.6a (19)	5.2±0.7a (5)
Thomsen R.	Jul 7 – Aug 3/93	Absolute	2.2±0.5b (20)	3.3±0.5b (20)	7.8±1.8a (5)
Umingmuk	Jul 14 – Aug 4/92	Green	3.7±0.6a (10)	4.4±0.7a (7)	NA
Umingmuk	Jul 13 – Aug 7/93	Green	1.2±1.2a (10)	1.0±0.5a (10)	NA
Umingmuk	Jul 14 – Aug 4/92	Total	3.5±0.9a (10)	6.8±1.9a (7)	NA
Umingmuk	Jul 13 – Aug 7/93	Total	1.9±1.5a (10)	1.2±0.8a (10)	NA
Umingmuk	Jul 14 – Aug 4/92	Absolute	4.4±0.8a (10)	7.5±1.7a (7)	NA
Umingmuk	Jul 13 – Aug 7/93	Absolute	2.9±1.1a (10)	2.0±0.6a (10)	NA

[1] Means with the same subscript within rows are not significantly different at $P \leq 0.10$.
[2] Muskoxen excluded after June 25 for that season only.

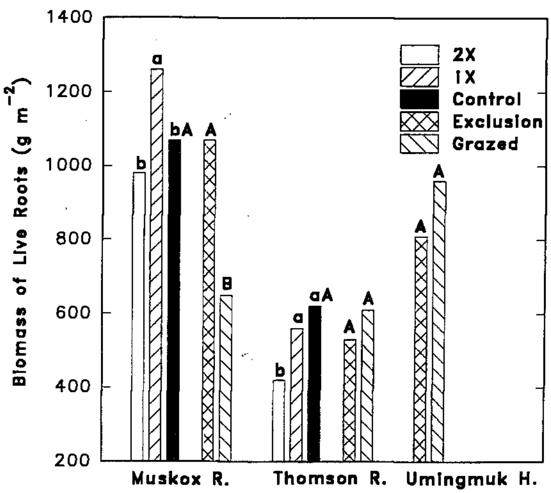

Fig. 2. Mean root biomass (g/m^2) in clipped (twice=2X and once=1X) and unclipped plots (lower case subscript) and in exclusions, grazed and unclipped plots (upper case subscript) in August 1993 on northern Banks Island, Canada. Means with the same subscripts within study sites are not significantly different at $P \leq 0.10$. Clipping schedule in text.

(Fig. 2). Root weights were stable in temporarily protected plots (exclusions) at MR and TR, however grazed plots had reduced root weights by 39% compared to controls and exclusions at MR.

Discussion

The absence of increased productivity above- and below-ground, across a broad range of shoot tissue removal suggests that increased productivity after grazing is not an important ecological phenomenon on northern Banks Island. Lower aerial productivity and root biomass in clipped and grazed than in controls in this study reflect high grazing and clipping intensities, large clipped plots in the clipping experiment and severe climate. The hypothesis that graminoid meadows become more productive in response to moderate clipping and grazing by muskoxen is rejected.

Given the ability of these plants to recover after removal of shoot tissue and the predominance of stable productivity after grazing, current grazing intensities are not likely to cause prolonged damage to the graminoid meadows. Muskox densities would have to be much higher to inflict damage to graminoid meadows. The decreased productivity in grazed areas is presently of little consequence to Banks Island muskoxen because the current population cannot graze all the forage produced during the summer. Meadows were intensively grazed compared with the values reported from other terrestrial ecosystems (Crawley, 1983; Pimentel, 1988; Raillard, 1992). However, muskoxen clearly were not food-restricted during the summer because over two-thirds of the forage remained ungrazed.

Productivity declined more after clipping than after grazing. Clipping was concentrated early in the season, while grazing was spread more evenly throughout the growing season. In 1992, 2 clippings removed more shoot tissue than grazing and a single clipping. Deposition of feces and urine (Putman, 1984), saliva (McNaughton, 1985b), trampling (Belsky, 1986), and selective herbivory (Bryant *et al.*, 1983) were present only in grazed areas. Plants are most vulnerable to damage from grazing early in the growing season (Bedard *et al.*, 1986). Mattheis et al. (1976) also found that intensive clipping of arctic graminoids resulted in reduced productivity. However, on Ellesmere Island, Canada, intensively clipped and unclipped plots had similar above-ground productivity (Raillard, 1992).

The plants had adequate reserves to largely recover from clipping in only 1 summer. Factors that could have played a role in the recovery in 1993 were more active uptake of nutrients after defoliation (Chapin & Slack, 1979; Shaver *et al.*, 1986), reliance on extensive below-ground reserves (Muc, 1977), resource sharing among tillers (Jonsdottir & Callaghan, 1989), increased availability of nutrients from feces and urine (Henry & Svoboda, 1989), and the ability of tundra graminoids to occupy disturbed and undisturbed sites (Shaver & Billings, 1975).

The apparent depression of root biomass after grazing or clipping is consistent with decreased above-ground productivity. Such decreases can occur after short-term clipping (Richards, 1984), however, root weights more accurately reflect long-term perturbation than above-ground production. There is a time lag after herbivory before changes in root biomass become apparent (Stoddart *et al.*, 1975). Higher root weights when clipped once at MR were unrelated to clipping *per se*, given the constraints on these plants imposed by lemming herbivory (pers. obs.). The MR exclosure was used as a lemming (*Lemmus* spp., *Dicrostonyx* spp.) nest during the winter of 1990-91 (pers. obs.). Lemmings can remove 90% of available forage (Schultz, 1969).

The inadvertent inclusion of mineral material on roots and subjectivity in determining live roots from dead ones both contributed to inconsistencies observed in the MR exclosure data. Root standing crop dynamics would become clearer if treatment effects were imposed over many years. Other studies examining the effects of grazers on root biomass in high latitude meadows have demonstrated neutral or positive responses (Cargill & Jefferies, 1984; Henry & Svoboda, 1989).

Graminoid meadows showed decreased above-ground productivity after clipping and grazing treatments, large standing crops in grazed areas and the ability to largely recover from severe clipping treatments in only 1 growing season. This decreased productivity is unlikely to adversely affect muskoxen in the short-term. Future research should be directed at determining the long-term consequences of high grazing intensities and at protecting this critical muskox habitat.

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