

**MUSKOXEN/SEDGE MEADOW INTERACTIONS, NORTH-CENTRAL
BANKS ISLAND, NORTHWEST TERRITORIES, CANADA**

A Thesis

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in Partial Fulfillment of the Requirements
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Doctor of Philosophy
in the
Department of Crop Science and Plant Ecology
University of Saskatchewan
Saskatoon

by

David L. Smith

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SUMMARY OF DISSERTATION

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of the requirements for the

DEGREE OF DOCTOR OF PHILOSOPHY

by

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Department of Crop Science and Plant Ecology
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Spring 1996

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Muskoxen/sedge meadow interactions, north-central Banks Island, Northwest Territories, Canada

The interactions between muskoxen (Ovibos moschatus) and graminoid meadows, their primary summer range, were examined in an area of high muskoxen density on north-central Banks Island, N.W.T., Canada (73°50'N, 119°53'W). The objective was to test the herbivore optimization hypothesis, i.e., moderate grazing intensities boost rates of net above-ground primary productivity (NAPP) above ungrazed, lightly grazed and heavily grazed levels.

Microplots (1 X 1m) were clipped once (1X) or twice (2X) per growing season, exposed to muskoxen, temporarily protected from muskoxen for one growing season, or permanently protected. These treatments removed from 0 to 40% of shoot tissue each growing season. Contrary to the predictions of the herbivore optimization hypothesis, over-compensation did not occur anywhere across this gradient of tissue removal. Four methods of calculating net above-ground primary productivity (NAPP) consistently demonstrated that the more intense treatments (1X and 2X clipping) showed more under-compensation (64% of the time) while less intense treatments (grazing by muskoxen) show more exact-compensation (75% of the time). Clipping and grazing also decreased below-ground standing crop with less severe treatments showing exact-compensation.

Mortality and fecundity of Eriophorum triste ((T. Fries) Hadac & A. Löve) populations were unaffected by grazing and clipping. Clipping (2X) or intense grazing treatments initially decreased rates of leaf extension, rates of increase in height and rates of increase in number of leaves per tiller, however within a year these parameters were boosted above or equaled control levels. Less intense treatments decreased population-level growth rates during the entire study suggesting that severe shoot tissue removal and a time lag of at least one year after the initial treatment are required to initiate compensatory growth in Eriophorum triste populations.

The study site with the highest density of muskoxen fecal pats had the largest green standing crops, the most nutritious forage, the warmest microclimate, the highest soil NH_4 levels and the most favorable soil moisture regime. High standing crops were the result of large quantities of overwintering green tissue rather than increased rates of NAPP.

Although compensatory growth occurred in intensely clipped and grazed populations of Eriophorum triste, community-level data demonstrate that graminoid meadows in the study area are limited in their ability to tolerate high grazing and clipping intensities. Increased

forage quality and large green standing crops after grazing serve to ameliorate the potentially negative effects of reduced NAPP on muskoxen.

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ABSTRACT

The interactions between muskoxen (Ovibos moschatus) and graminoid meadows, their primary summer range, were examined in an area of high muskoxen density on north-central Banks Island, N.W.T., Canada (73°50'N, 119°53'W). The objective was to test the herbivore optimization hypothesis, i.e., moderate grazing intensities boost rates of net above-ground primary productivity (NAPP) above that of ungrazed, lightly grazed and heavily grazed levels.)

Microplots (1 X 1m) were clipped once (1X) or twice (2X) per growing season, exposed to muskoxen, temporarily protected from muskoxen for one growing season, or permanently protected. These treatments removed from zero to 40% of shoot tissue each growing season. Contrary to the predictions of the herbivore optimization hypothesis, over-compensation did not occur anywhere across this gradient of tissue removal. Four methods of calculating net above-ground primary productivity (NAPP) consistently demonstrated that the more intense treatments (1X and 2X clipping) showed more under-compensation (64% of the time) while less intense treatments (grazing by muskoxen) show more exact-compensation (75% of the time). Clipping

and grazing also decreased below-ground standing crop with less severe treatments showing exact-compensation.

Mortality and fecundity of Eriophorum triste (Th. Fries) Hadac & Löve populations were unaffected by grazing and clipping. Clipping (2X) or intense grazing treatments initially decreased rates of leaf extension, rates of increase in height and rates of increase in number of leaves per tiller, however within a year these parameters were boosted above or equaled control levels. Less intense treatments decreased population-level growth rates during the entire study suggesting that severe shoot tissue removal and a time lag of at least one year after the initial treatment are required to initiate compensatory growth in Eriophorum triste populations.

The study site with the highest density of muskox fecal pats had the largest green standing crops, the most nutritious forage, the warmest microclimate, the highest soil NH₄ levels and the most favorable soil moisture regime for plant growth. High standing crops were the result of large quantities of overwintering green tissue rather than increased rates of NAPP.

Although compensatory growth occurred in intensely clipped and grazed populations of Eriophorum triste, community-level data demonstrate that graminoid meadows in the study area are limited in their ability to

tolerate high grazing and clipping intensities. Increased tiller growth in Eriophorum triste populations was not great enough to offset the community-level response. Increased forage quality and large green standing crops after grazing serve to ameliorate the potentially negative effects of reduced NAPP on muskoxen.

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DEDICATION

To the memory of my grandparents; Charlie and Susan Smith, and Grace and Stephen Takacs.

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1.0 GENERAL INTRODUCTION

1.1. The Herbivore Optimization Hypothesis

The herbivore optimization hypothesis predicts that moderate grazing intensities boost rates of net above-ground primary productivity (NAPP) above ungrazed and lightly grazed levels (Figure 1-1, McNaughton 1979a; Hilbert et al. 1981). Not until heavy grazing levels are imposed does NAPP drop below ungrazed controls. There has been considerable debate surrounding this hypothesis (Belsky 1986a; Painter and Belsky 1993; DeAngelis and Huston 1993; McNaughton 1993) in part because of: 1) a confounding of scales used in evaluating herbivore impacts (Belsky 1987; Brown and Allen 1989); 2) methodological problems in studies addressing this hypothesis (see review in Belsky 1986a); 3) spatial and temporal variability among studies, and; 4) generalizations about the outcome of herbivory in vastly different ecosystems. There are inconsistencies in the literature because many variables influence the outcome of grazing or clipping on NAPP (see section 2.6 for review).

Numerous researchers have reported that herbivores are a significant ecological force in arctic and sub-

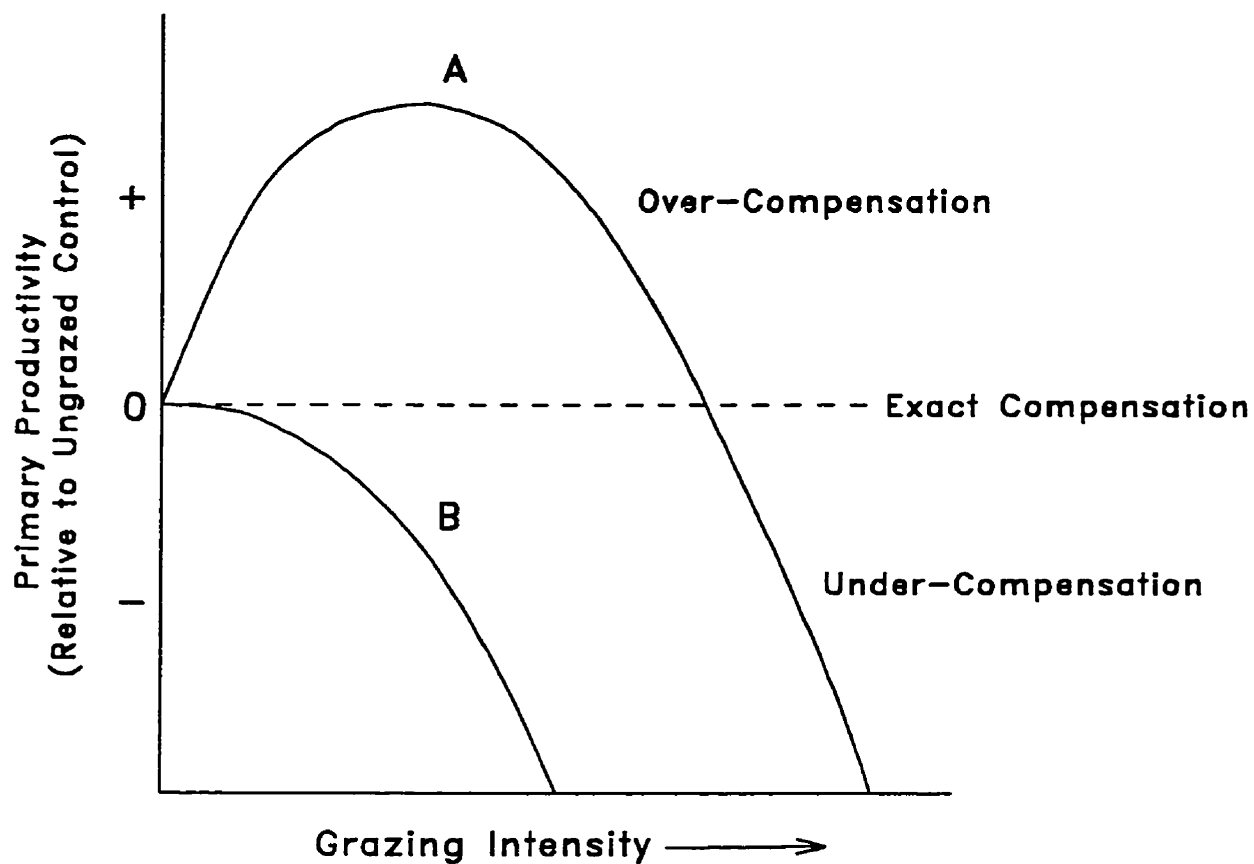


Figure 1-1. Relationship between net primary productivity and grazing intensity for grazing-tolerant (A) and grazing-sensitive (B) plant species. Modified from Holechek et al. (1989).

arctic meadow plant communities. Lemmings (Lemmus spp., Dicrostonyx spp.) have been reported to remove 90% of shoot tissue (Schultz 1969), snow geese (Anser caerulescens caerulescens) to remove 80% (Cargill and Jefferies 1984b), and muskoxen (Ovibos moschatus) to remove up to 40% (Chapter 3). Conversely, Pimentel (1988) and Bliss (1986) predict that herbivores play a relatively minor role in the arctic due to the severity of the climate and low herbivore densities. On a regional scale Pimentel (1988) and Bliss (1986) are probably correct, however within localized areas of high primary productivity (e.g., graminoid meadows) herbivores are a significant ecological force on vegetation (Raillard 1992; Chapter 3).

Snow geese take advantage of summer forage production by migrating from lower latitudes. Unlike muskoxen their populations are not limited by winter-time food availability and quality in the Arctic. Lemmings cycle from low to high densities, and have significant effects on vegetation during periods of high density (Batzli 1975). Muskox and caribou (Rangifer arcticus) populations are susceptible to high mortality rates during the winter (Vibe 1967; Parker et al. 1975; Miller et al. 1977; Gray 1987; Gunn et al. 1989) particularly if a layer of ice forms over their forage in the autumn. Muskoxen also have

lower fecundity rates than either lemmings or snow geese. The result is that snow geese and lemmings remove greater proportions of shoot tissue through their grazing activities than muskoxen. Within the study area on Banks Island (Figure 1-2) snow geese were rare. Lemmings were very abundant in 1991, abundant in 1992 and rare in 1993. Other herbivores are assumed to have a negligible effect within the graminoid meadow plant community (pers. obs. 1991-1993).

Despite the environmental constraints on their populations, over 42,000 muskoxen live on Banks Island, Northwest Territories, Canada (Gunn pers. comm. 1991). Muskox densities are particularly high ($1.52/\text{km}^2$) in the Thomsen River Valley of north-central Banks Island (McLean et al. 1989). Selective grazing by muskoxen on graminoid meadow plant communities during the summer months in Canada (Parker and Ross 1976; Raillard 1992) contributes to the high grazing intensities in these communities (Chapter 3).

Although overgrazing by snow geese has occurred in the sub-arctic (Hik et al. 1992), plant community responses to grazing in the arctic and sub-arctic are generally neutral or positive (Cargill and Jefferies 1984a; Henry and Svoboda 1989; Smith 1990; Raillard 1992) because of the rapid recycling of nutrients associated

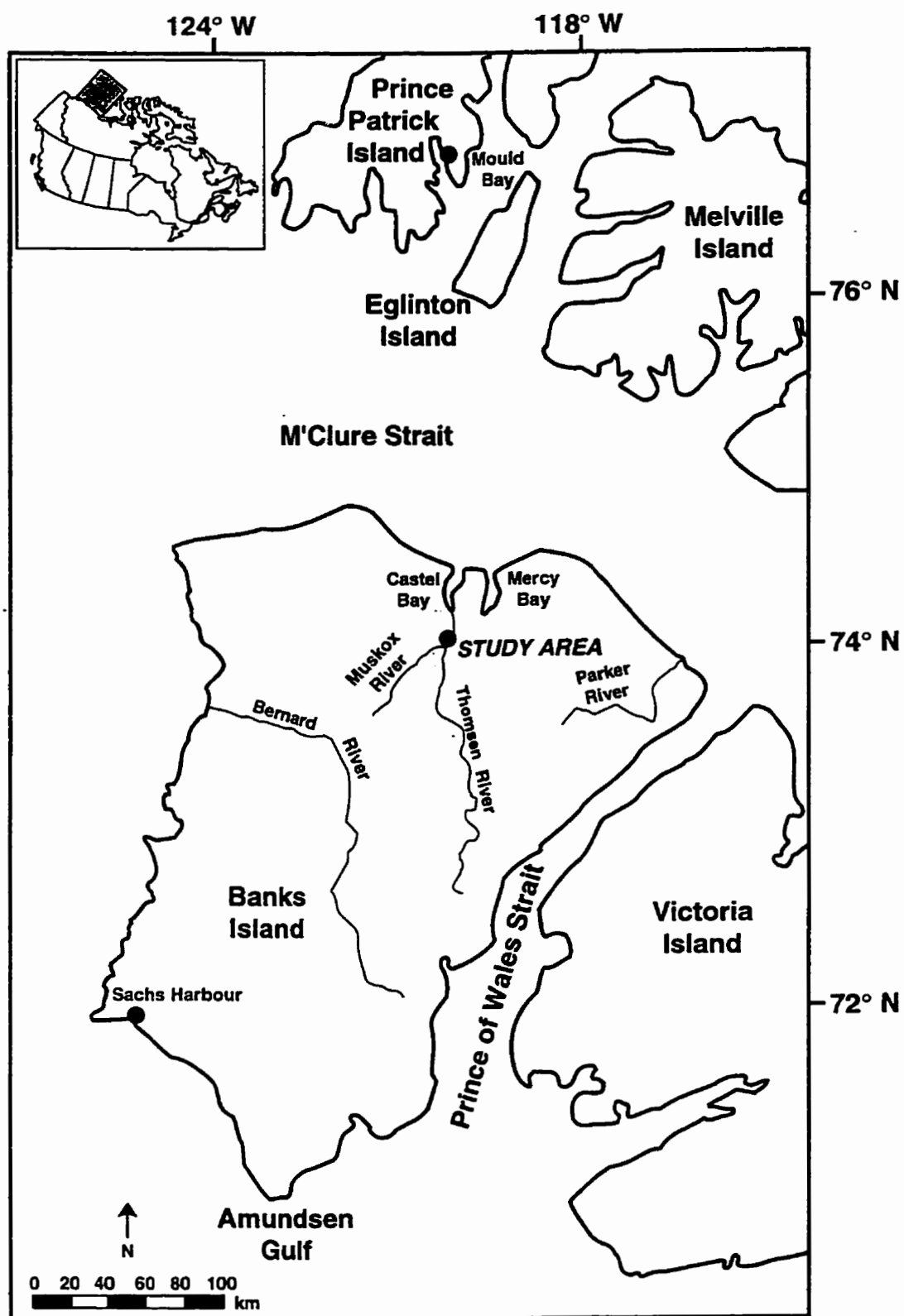


Figure 1-2. Location of study area on north-central Banks Island, Northwest Territories, Canada.

with the deposition of feces and urine (Hik and Jefferies 1990). Since sedge meadow vegetation is nutrient- rather than carbon-limited (Tamm 1954; Goodman and Perkins 1968; Chapin et al. 1975; Babb and Whitfield 1977; Chapin and Slack 1979; Bliss 1986; Chapin et al. 1986a; Hilbert et al. 1987; Henry et al. 1994b) higher soil nutrient levels after grazing can increase NAPP significantly (Hik and Jefferies 1990). Given the increase in nutrient cycling that occurs in these meadows after grazing it is hypothesized that moderate grazing by muskoxen will increase community-level NAPP in graminoid meadows.

Clipping differs from grazing in the following ways:

- 1) Clipped plots lack input of saliva or products from saliva (e.g., thiamine) that may promote plant growth (Reardon et al. 1974; Hori 1975; Dyer and Bokhari 1976; Howe et al. 1982; McNaughton 1985b);
- 2) Clipped plots lack selective removal of preferred plant tissue, input of feces and urine and trampling by grazers; and
- 3) Clipped plots lack natural litter accumulation patterns.

Because the permanent exclosures in this study were three years old in 1991 (beginning of study) and five years old in 1993 (end of study) and because water and dissolved nutrients move laterally across the study sites (pers. obs. 1991-1993) the lack of nutrient addition in permanent exclosures is expected to be of minor

consequence. Numerous studies have refuted the hypothesis that saliva increases growth rates (Belsky 1986a; Johnston and Bailey 1972; Detling et al. 1980; Paige and Whitham 1987). Therefore, if any differences are observed among clipped and grazed treatments they will likely reflect the higher proportions of shoot tissue removed in clipped than in grazed plots.

Moderate grazing by muskoxen should have little influence on live root biomass. Other arctic and sub-arctic studies that have examined root biomass in response to shoot tissue removal have reported increases or no change after grazing (Cargill and Jefferies 1984b; Henry and Svoboda 1989). By maintaining active uptake of nutrients from the soil, NAPP is independent of root nutrient reserves except during early summer (Chapin and Shaver 1989). Chapin et al. (1986a) found that carbon reserves were not depleted after clipping Eriophorum vaginatum L., suggesting that carbon will not be drained from root reserves after clipping or grazing in the present study. In contrast, in carbon-limited plant communities, grazing and clipping significantly reduce root biomass (Stoddart et al. 1975).

1.2 Interaction of Plant Community Structure, Reproductive Output, and Environmental Attributes with Natural and Artificial Herbivory

Herbivores affect structural and environmental properties of plant communities and structural and reproductive properties of plant populations within communities. Likewise, environmental factors play key roles in determining plant community structure (e.g., sward height and species abundances), reproductive output and NAPP. Herbivore populations are ultimately affected by the abiotic factors (e.g., temperature, light intensity, precipitation amounts) that influence forage quality and quantity. If the herbivore-optimization hypothesis is tested within the context of a grazing system, realistic predictions about grazing-induced vegetation changes on herbivores become attainable. In the arctic, for example, wind speed and duration, light quality and quantity, ambient air and soil temperatures, precipitation, patterns of water drainage, soil nutrient content, soil texture, depth to permafrost, organic matter content of soil and thickness of litter layer all influence the outcome of field studies that test the herbivore optimization hypothesis. Although laboratory experiments are valuable in separating the relative

influences of different factors on NAPP in a controlled environment they are limited in scope in predicting the role that these factors play in a grazing system (O'Neill et al. 1986).

Numerous studies show that herbivores create a more prostrate plant community through their grazing and trampling activities (Jameson 1963; Harper 1977; McNaughton 1983a; Belsky 1986b; Smith 1990). Shifts in species composition usually accompany these changes in physiognomy. Light-competitive, erect growth forms are excluded after grazing with more prostrate, laterally spreading plants that increase in abundance (Paine 1966; Belsky 1986a; Hay 1986). In arctic meadows, however, species diversity (e.g., species richness and evenness in distribution) is low and dominant species are capable of growing in disturbed and undisturbed sites (Fetcher and Shaver 1983). Therefore it is predicted in this study that grazing and clipping will produce in a more prostrate community. This change in gross structure should not, however, be accompanied by a change in species composition.

Absolute fitness can be defined as the contribution that a genotype makes to the next generation (Belsky 1986a). Seed head density is easily measured but it ignores variability in seed number per inflorescence,

seed mortality, and germination, emergence and establishment success rates. Despite these limitations the parameter provides a rough index of reproductive output. An abundant literature shows that grazing or clipping reduces sexual reproductive output (Roberts 1958; Dawson 1970; Hendrix 1979; Solomon 1983; Belsky 1986a; Smith 1990) although other studies show increases in seed production (Dyer 1975; Inouye 1982; Richards 1983; Paige and Whitham 1987; Henry and Svoboda 1989). Given the nutrient limitations that arctic plants are under (Henry and Svoboda 1994b), the costs associated with producing seeds (Stoddart *et al.* 1975) and the physical removal of seeds by grazers, it is predicted that grazing and clipping will reduce seed head densities.

Grazers increase rates of nutrient cycling in arctic meadows (Cargill and Jefferies 1984a; Henry and Svoboda 1989; Hik and Jefferies 1990). Instead of being locked up in dead and senescent tissue, nutrients are made more available to plants in the form of feces and urine. The hypothesis that herbivores influence nutrient availability at sites is supported by the observations of Batzli (1978) who reported that grazers spatially redistribute nutrients. Several other studies have also found that herbivores increase the availability of

nutrients (Carran et al. 1982; Cargill and Jefferies 1984a, 1984b; Bazely and Jefferies 1989; Henry and Svoboda 1989; Hik and Jefferies 1990). It is predicted therefore in this study that heavily grazed sites with abundant fecal pats will show higher soil nutrient content than less used sites.

Grazing by muskoxen and clipping should increase soil temperatures through the removal of dead and senescent tissue and the reduction of standing crop. Increased temperatures are significant, particularly because arctic graminoid meadows are temperature-limited (Webber, 1978).

1.3 Changes in Forage Quality after Grazing and Clipping

Herbivores not only affect plant community NAPP, structure, reproductive output and environmental properties, but they also have a pronounced effect on forage quality. Grazers decrease the proportion of dead plant tissue in samples, thereby increasing forage quality. Arctic plants compensate for herbage removal by replacing tissue lost to herbivores with highly digestible, new growth. New plant tissue characteristically is better quality forage than older plant tissue (Anderson and Talbot 1965; Dyer and Bokhari

1970-1971.

Highly complex

regional survey

Their observations

optical forage

will be used

the results of

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1.4. Response

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1976; Klein 1977; Milton 1979; Bryant et al. 1983).

Highly digestible regrowth can attract herbivores that regrazed previously grazed swards (McNaughton 1984, 1986). These observations are consistent with the predictions of optimal foraging theory which suggests that herbivores will select forage that is of higher quality when given the choice (Pyke et al. 1977). It is predicted therefore that both grazing and clipping will increase the proportion of both live tissue and crude protein in plant samples. Grazing and clipping should also decrease the acid detergent fiber (i.e., cellulose, lignin and hemicellulose) content of samples. Muskoxen should feed more often at graminoid meadows with abundant, nutritious forage.

1.4 Response of Eriophorum triste Populations to Grazing and Clipping

Confounding of scale in herbivore impact studies contributes to the lack of agreement among studies that test the herbivore-optimization hypothesis (Belsky 1987; Brown and Allen 1989). It is important therefore to identify the scale(s) at which the hypothesis is being tested at the beginning of the experiment and to investigate herbivore-effects at a number of levels of

biological organization if time and resources permit. In addition to investigating community-level responses (Chapter 3) this study also addresses plant responses of Eriophorum triste populations to grazing and clipping (Chapter 4). Physiological-, population- and community-level responses to grazing will be elucidated by expanding the study to include plant populations. Eriophorum triste is the most abundant species in each of the 3 study sites (Chapter 4).

Numerous studies have shown that Eriophorum vaginatum in Alaska is tolerant of disturbance (Wein and Bliss 1974; Chapin and Shaver 1981; Fetcher and Shaver 1982, 1983). Both mortality and tillering rates increased in Eriophorum vaginatum with disturbance. With high mortality and tillering rates, Eriophorum vaginatum was able to persist at disturbed sites. Low mortality rates and low tillering rates allowed Eriophorum vaginatum to persist at undisturbed sites. The wide range of tolerance to disturbance in Eriophorum vaginatum enabled it to survive in a variety of disturbance regimes (Fetcher and Shaver 1983). The tolerance of Eriophorum vaginatum to disturbance likely contributed to community- and ecosystem- level stability (e.g, resistance and resilience to disturbance) within Fetcher and Shaver's (1983) study area.

Based on the results of studies on Eriophorum vaginatum, it is predicted that mortality rates and daughter tiller production will increase with grazing and clipping. Similarly, rates of change in total number of leaves per tiller, leaf extension rates, and vertical (height) extension rates for tillers of Eriophorum triste are expected to increase with grazing and clipping. Both community-level seed head density and population-level seed head density are expected to decrease after grazing and clipping.

1.5 Study Objectives

The main goal of this thesis is to test the herbivore optimization hypothesis using muskoxen and a graminoid meadow plant community on north-central Banks Island, Northwest Territories. The remaining sections of this Chapter describe the study area and study sites. Chapter 2 provides a more extensive literature review that stresses the complexity of plant-animal interactions and provides an aid for interpretation. Chapter 3 gives the results of tests of the herbivore optimization hypothesis using grazing by muskoxen and clipping in the context of an arctic environment. Changes in below-ground standing crop are also examined after grazing and clipping.

Chapter 4 describes the effects of grazing and clipping on plant community structure, reproductive output and environmental properties. The effects of environment on plant community attributes are also considered. Chapter 5 examines how clipping influences crude protein and acid detergent fiber. Selection of sites with the most nutritious forage by muskoxen is addressed. Chapter 6 focuses on how populations of Eriophorum triste responded to grazing and clipping. Chapter 6 expands the study by considering more than one level of biological organization at the plant-animal interface. Chapter 7 provides a synopsis that integrates all chapters.

It is predicted that muskoxen exert a significant impact on graminoid meadows on Banks Island (Figure 1-2). These effects are predicted to occur from the level of individual plant growth to the level of plant community productivity.

1.6 Study Area

The study area is located near the confluence of the Thomsen and Muskox Rivers on north central Banks Island, Northwest Territories (74° N, 120° W) (Figure 1-2). Three study sites were located in heavily grazed sub-hygric graminoid meadows that were within walking distance of

base camp. Sites were chosen based on their logistical and biological suitability. Banks Island has a higher proportion of meadow plant communities than the other islands within the Canadian Arctic Archipelago (G. Henry pers. comm. 1991), which explains why muskoxen are so abundant on Banks Island. Interaction of muskoxen and predators (i.e., wolves (Canis lupus) and polar bears (Ursus maritimus)) is intermittent. Wolves are actively hunted in the study area and remain at low densities (pers. obs. 1991-1993). During the seven summers that the study area was used by researchers, only one polar bear was observed.

The climate is Arctic Desert with long cold winters (mean January temperature is -30 °C) and short cold summers (mean July temperature is 4 °C) (Zoltai et al. 1980). Occasionally winds blew steadily for two days at 40 km/hr (pers. obs. 1991-1993). Very little precipitation falls over the study area (9 cm annual mean) (Zoltai et al. 1980). No permanent weather station exists at the study area. Zoltai et al. (1980) extrapolated the above data from data collected at Sachs Harbour, Holman Island, and Mould Bay.

All three study sites and the entire study area lie within the Arctic Lowland Physiographic Province (Bostock 1964, 1970) and the Mid-Arctic Ecoclimatic Region

(Ecoregions Working Group 1989). The area is underlain by Cretaceous sandstone and shale bedrock, but has been altered by proglacial lakes and glacial action (Zoltai et al. 1980). Soils at the three study sites belong to the Gleysolic Static Cryosol Subgroup (Table 1-1, Agriculture Canada 1987). At each of the three study sites two soil profiles were dug at random locations in August 1993 to obtain a greater understanding of site characteristics. The two profiles at each site were similar; therefore it is assumed that the data presented are representative of the site. The results of one selected profile at each site are presented. Classification is based on The Canadian System of Soil Classification (Agriculture Canada 1987).

Wilkinson et al. (1976) delimited the area into five different habitat types: 1) Barren uplands; 2) Sedge meadows; 3) Sand dunes; 4) Tundra tussocks, and; 5) Lakes/peripheries. Ferguson (1991) further divided the sedge meadow category into 1) wet sedge meadows and 2) graminoid tundra which reflects the drier conditions in graminoid tundra (i.e., sub-hygric) compared to wet sedge meadows (i.e., hygric). This study focuses on heavily grazed sub-hygric graminoid tundra meadows and on populations of Eriophorum triste within these meadows. Previous studies suggest that these monocot-dominated

Table 1-1. Descriptions of soil profiles* at the three study sites in 1993.

| <u>Horizon</u> | <u>Depth (cm)</u> | <u>Color (Matrix) (dry)</u> | <u>(Mottles) (dry)</u> | <u>Texture</u> |
|----------------------|-----------------------|---------------------------------|----------------------------|----------------|
| <u>Muskox River</u> | | | | |
| Om | 10 - 0 | 10YR 4/3 | 10 YR 4/4 | NA |
| Cg | 0 - 20 | 10YR 5/2 | 10 YR 5/4 | heavy clay |
| Cz | 20+ | 10YR 5/2 | NA | clay |
| <u>Thomsen River</u> | | | | |
| Om | 10 - 0 | 10YR 3/3 | 10 YR 3/4 | NA |
| Cg | 0 - 23 | 10YR 5/2 | 10 YR 5/4 | heavy clay |
| Cz | 23+ | 10YR 5/2 | NA | clay |
| <u>Umingmuk Hill</u> | | | | |
| Omg | 10 - 0 | 10YR 3/6 | 7.5 YR 4/6 | NA |
| Cg | 0 - 32 | 10YR 5/4 | 10 YR 5/8 | heavy clay |
| Cz | 32+ | 10YR 5/2 | NA | clay |

* All soil profiles belong to the Gleysolic Static Cryosol Subgroup.

plant communities are a crucial source of forage for muskoxen throughout northern North America (Parker and Ross 1976; Wilkinson et al. 1976; Muc 1977; Thing 1984; Henry 1987; Oakes 1989; Klein and Bay 1990; Raillard 1992; Henry et al. 1994a).

The study area is gently rolling with the hilltops rarely exceeding 250 m in elevation (Wilkinson et al. 1976). The three study sites within the study area are located between 10 and 40 m a.s.l. The Thomsen River (TR) study site is located within the Thomsen River valley. The Muskox River (MR) study site is located between two hills approximately 7 km west of the Thomsen River valley and 3 km north of the Muskox River valley. The Umingmuk Hill (UH) site is located on a slope at the edge of the Thomsen River valley, 2 km north of the TR site. Snow accumulates at the crest of the hill near Umingmuk Hill during the winter. Meltwater from the snowbank feeds into the UH study site during the summer. Because they are in low areas, the MR and TR sites receive most of their moisture from the surrounding hills. Permafrost prevents the meltwater from leaching through the soil profile. Even though the region receives very little precipitation all three study sites were moist during all three summers of the study.

Sedges (e.g., Eriophorum triste and Carex aquatilis Wahlenb.) are abundant at all three study sites. Grasses (e.g., Arctagrostis latifolia (R. Br.) Griseb., Dupontia fischeri R. Br.) are abundant but they are less common than sedges. Dicots (e.g., Salix arctica Pall.) are not common, occupying less than 5% of the meadow surface. Eriophorum triste is the most abundant species at all three sites (Chapter 4).

1.6.1 Fecal pat density

Fecal pat surveys were conducted in grazed areas at the end of each growing season along each transect (Figure 3-1). All new (i.e., less than three months old) fecal pats underneath a 3 m swath along belt transects were counted. New fecal pats were dark brown and soft in consistency. Old fecal pats were hard and light brown or white. Data were analyzed with one-way analysis of variance and means were compared with the LSD test (Sokal and Rohlf 1981). Umingmuk Hill had the highest fecal pat density among the three study sites in 1992 and 1993. Muskox River had a higher density than TR in 1992 however in 1993 TR and MR had similar densities. Fecal pat densities were higher in 1992 than in 1993 (Table 1-2).

Table 1-2. Comparison of fecal pat densities (# 100 m⁻²) (mean) in transects (n=10) at three study sites during the 1992 and 1993 growing seasons.*

| <u>Date</u> | <u>Study Sites</u> | | | <u>MS Error</u> |
|--------------|--------------------|-------------------|--------------------|-----------------|
| | <u>Muskox R.</u> | <u>Thomsen R.</u> | <u>Umingmuk H.</u> | |
| Aug. 15 1992 | 5.7 _b | 3.1 _c | 9.6 _a | 7.8 |
| Aug. 20 1993 | 1.4 _b | 1.1 _b | 3.7 _a | 1.5 |

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

1.6.2 Habitat selection by muskoxen

The degree to which muskoxen utilize the graminoid meadow plant community was determined by observing in which plant communities muskoxen grazed during the 1992 and 1993 growing seasons (Tables 1-3 and 1-4). Numbers of muskoxen grazing in each plant community were counted and recorded on a daily basis. Sightings took place from base camp, from study sites and during travel between base camp and study sites. Every effort was made not to disturb the animals. The study area has a higher percentage of graminoid meadow vegetation (20% estimate) than is present on a regional scale (i.e, 5%) (Ferguson 1991, pers. obs. 1991-1993). If the same group of muskoxen was encountered during the same day, they were not counted after the first sighting. The same animals were likely counted on different days because these observations took place in a relatively small area. Muskoxen also showed fidelity towards favorable feeding areas that made counting the same animals unavoidable. This study followed the vegetation classification system used by Ferguson (1991). Habitat selection data were analyzed with the Two tailed test for differences between proportions (Levin 1981). Graminoid meadows were

preferred over the other communities for grazing during the summers of 1992 and 1993.

Table 1-3. Number and (percentage*) of muskoxen observed grazing in habitats within the study area in 1992.

| <u>Dates</u> | <u>Habitat</u> | <u># and % of Muskoxen</u> | |
|-----------------|-----------------------|----------------------------|--------------------|
| June 25-July 4 | Dwarf Shrub/Gram.Tun. | 74 | (57 _a) |
| | Graminoid Tundra | 55 | (43 _b) |
| | Wet Sedge Meadow | 0 | (0 _c) |
| | Dwarf Shrub | 0 | (0 _c) |
| | Polar Desert | 0 | (0 _c) |
| | All Habitats Combined | 129 | (100) |
| July 5-July 19 | Graminoid Tundra | 131 | (78 _a) |
| | Dwarf Shrub/Gram.Tun. | 30 | (18 _b) |
| | Polar Desert | 7 | (4 _c) |
| | Wet Sedge Meadow | 0 | (0 _c) |
| | Dwarf Shrub | 0 | (0 _c) |
| | All Habitats Combined | 168 | (100) |
| July 20-Aug. 15 | Wet Sedge Meadow | 55 | (48 _a) |
| | Graminoid Tundra | 39 | (34 _b) |
| | Dwarf Shrub | 20 | (18 _c) |
| | Dwarf Shrub/Gram.Tun. | 0 | (0 _d) |
| | Polar Desert | 0 | (0 _d) |
| | All Habitats Combined | 114 | (100) |
| June 25-Aug. 15 | Graminoid Tundra | 225 | (55 _a) |
| | Dwarf Shrub/Gram.Tun. | 104 | (25 _b) |
| | Wet Sedge Meadow | 55 | (13 _c) |
| | Dwarf Shrub | 20 | (5 _{cd}) |
| | Polar Desert | 7 | (2 _d) |
| | All Habitats Combined | 411 | (100) |

* Percentages are in parentheses.
Percentages with the same subscript are not significantly different at $P \leq 0.10$.

Table 1-4. Number and (percentage*) of muskoxen observed grazing in habitats within the study area in 1993.

| <u>Dates</u> | <u>Habitat</u> | <u># and % of Muskoxen</u> | |
|----------------|-----------------------|----------------------------|--------------------|
| June 22-Jul. 4 | Graminoid Tundra | 104 | (80 _a) |
| | Dwarf Shrub/Gram.Tun. | 20 | (15 _b) |
| | Dwarf Shrub | 6 | (5 _{bc}) |
| | Wet Sedge Meadow | 0 | (0 _c) |
| | All Habitats Combined | 130 | (100) |
| Jul. 5-Jul.19 | Graminoid Tundra | 27 | (52 _a) |
| | Dwarf Shrub | 24 | (46 _a) |
| | Dwarf Shrub/Gram.Tun. | 1 | (2 _b) |
| | Wet Sedge Meadow | 0 | (0 _b) |
| | All Habitats Combined | 52 | (100) |
| Jul.20-Aug.25 | Graminoid Tundra | 104 | (84 _a) |
| | Wet Sedge Meadow | 13 | (11 _b) |
| | Dwarf Shrub/Gram.Tun. | 4 | (3 _b) |
| | Dwarf Shrub | 2 | (2 _b) |
| | All Habitats Combined | 123 | (100) |
| June 22-Aug.25 | Graminoid Tundra | 235 | (77 _a) |
| | Dwarf Shrub | 32 | (11 _b) |
| | Dwarf Shrub/Gram.Tun. | 25 | (8 _b) |
| | Wet Sedge Meadow | 13 | (4 _b) |
| | All Habitats Combined | 305 | (100) |

* Percentages are in parentheses.
Percentages with the same subscript are not significantly different at $P \leq 0.10$.

2.0 LITERATURE REVIEW

This review provides the reader with essential background information for understanding the main body of the thesis. The review examines how arctic sedge meadow communities and plants within these communities respond to defoliation by herbivores and human disturbances within the context of the herbivore optimization hypothesis. These meadows are the most productive in the arctic (Bliss 1977) and provide muskoxen (Ovibos moschatus) with most of their forage in Canada (Parker and Ross 1976; Raillard 1992). These communities also provide habitat for caribou (Rangifer tarandus), lemmings (Lemmus spp., Dicrostonyx spp.) and snow geese (Anser caerulescens caerulescens) (White and Trudell 1980; Batzli 1983; Cargill and Jefferies 1984a). Many muskox populations have been introduced recently across North America and are growing exponentially. The effects of their grazing activities are largely unknown (Gunn et al. 1984; Thing et al. 1984; Smith 1984; Gunn et al. 1989; Gunn et al. 1991; Henry et al. 1994a). No study to date examines the effects of muskoxen on graminoid meadows on Banks Island, Northwest Territories, although Banks Island supports one-third (42,000) of the world's muskoxen (Gunn pers. comm. 1991). Research is needed to

assist in herd management by agencies such as the Department of Renewable Resources (Government of the Northwest Territories), Parks Canada and the Sachs Harbour Hunters and Trappers Committee.

In the context of the herbivore optimization hypothesis and an arctic environment this review examines: selective feeding, physiognomy and species abundances, reproduction, herbivory tolerance, productivity, forage quality, limiting factors, and competition. A synopsis is included at the end of the review which integrates all sections.

2.1 Selective Feeding: Why are Sedge Meadows Important?

Whether a herbivore is selective in its feeding (i.e., feeds in habitats or consumes plant species or parts in a greater or lesser proportion than they are found) depends on the availability of forage and many animal- and plant-related factors. Some herbivore characteristics that can influence selection include digestive capacity, daily foraging time, daily energy requirements, daily nutrient requirements, body size, and mouth size (Hanley 1982). Other animals such as biting insects and predators and abiotic conditions such as

extreme temperatures or high winds may also influence selectivity in a herbivore's food habits.

Forage quality can also influence a herbivore's food habits. These plant-related factors include age (Anderson and Talbot 1965; Dyer and Bokhari 1976; Klein 1977; Milton 1979; Bryant *et al.* 1983), nutrient content (Arnold 1964; Sinclair 1975; McNaughton 1976, 1985a; White 1978; Milton 1979; Bryant and Kuropat 1980; Mattson 1980; Chapin *et al.* 1986a), the presence of secondary compounds and other defenses against herbivory (Esau 1960; Prudhomme 1983; White 1983; MacLean and Jensen 1985; Belovsky 1986), fiber content (Van Soest 1965, 1982; Spalinger *et al.* 1986), digestibility (Dyer and Bokhari 1976; Prins *et al.* 1980; Minson 1982; Wilson 1982; Illius *et al.* 1987) and water content (Stanley-Price 1977).

The availability of plants among habitats and within habitats can also influence where herbivores feed and what is chosen at a feeding site, especially for large animals such as muskoxen that must consume large quantities of food during the short growing season. These factors include biomass availability (Hodgson 1977; White and Trudell 1980; Trudell and White 1981; Hudson and Frank 1987; Vivas and Saether 1987; Etchberger *et al.*

1988), height (Allden and Whittaker 1970), and life-form (MacLean and Jensen 1985).

Because herbivores select their foods based on all or some of these factors, it is important to consider characteristics of both the grazer and its forage. Large ruminants such as muskoxen attempt to consume large quantities of forage because of their size. It is especially important for muskoxen to maximize their rates of forage intake during the summer as forage quality decreases after the two month growing season (Thing et al. 1987; Klein and Bay 1990) and the harsh winter conditions may cause death (Vibe 1967; Parker et al. 1975; Miller et al. 1977; Gray 1987; Gunn et al. 1989) unless sufficient reserves are stored during the summer.

Because they are ruminants, muskoxen can tolerate low quality forage (Bell 1971; Hudson and Frank 1987; Mathiesen and Orpin 1989) allowing them to feed in monocot-dominated meadows. The selection of high quality, nitrogen-fixing forbs by muskox calves in sparsely vegetated habitats has been observed (Oakes 1989). This is understandable considering calves consume small quantities of forage.

Overall however, sedge meadow communities, the most productive habitats in arctic ecosystems (Bliss 1977), provide muskoxen with most of their forage in Canada

(Parker and Ross 1976; Raillard 1992). Banks Island, for example, has abundant sedge meadows but muskoxen densities are high enough so that many of these meadows are grazed to within a few centimeters of the ground or moss layer (pers. obs. 1991-1993). Muskoxen have adopted an energy efficient strategy of foraging by feeding and ruminating in large patches of low quality forage. In contrast, concentrate feeders such as Peary caribou move between small patches of high quality forage which increases their energy expenditures considerably (Miller 1990).

2.2 Physiognomy and Species Abundances

Large herbivores tend to decrease the amount of above-ground plant tissue (standing crop biomass) through their grazing and trampling activities (McNaughton 1985a). If grazing intensities are moderate to high the vegetation commonly becomes prostrate relative to ungrazed vegetation (Jameson 1963; Harper 1977; McNaughton 1983a; Belsky 1986b). Selective removal of palatable and competitively superior plant species by herbivores decreases interspecific competition within the community (Menge and Sutherland 1976; Whittaker and Levin 1977), creating openings for grazing-tolerant species to

invade. Conversely, in ungrazed meadows, prostrate, grazing-tolerant plants are rare or absent (Smith 1990). Thus, abundances of plants commonly shift after grazing, with prostrate species being favored at the expense of graminoids that are light-competitive (McNaughton 1979a).

In arctic sedge meadows, however, graminoids selected by muskoxen are tolerant of disturbance (Wein and Bliss 1973, 1974; Chapin and Chapin 1980; Chapin and Shaver 1981; Fetcher and Shaver 1983). The ability of Eriophorum vaginatum to grow well on disturbed sites in the arctic probably contributes to the stability of these meadow communities after grazing. These areas are low in species richness (Klein and Bay 1990) and grazing-tolerant forbs apparently are not present to colonize disturbed sites. The absence of prostrate forbs in grazed sedge meadow communities is probably not important in making these communities less resistant to herbivory than temperate meadows, because the plants that are present grow low to the ground to avoid blowing snow and ice (i.e., there are no erect genotypes) (Porsild 1951). Thus, plants in arctic sedge meadows have a growth form that may make them less susceptible to herbivory than their temperate counterparts that are more erect. However, in the sub-arctic Cargill and Jefferies (1984a) observed that some graminoid species are intolerant of geese grazing near

Hudson Bay. Calamagrostis neglecta (Ehrh.) Gaertn., Mey. & Scherb. colonized exclosures while Carex subspathacea Wormsk. and Puccinellia phryganodes (Trin.) Scribn. and Merr. grew in grazed areas. Isostatic uplift also contributes to the exclusion of Carex and Puccinellia from upland meadows (Hik et al. 1992). Batzli (1975) reported that lemmings in the low arctic had a significant effect on species composition through their grazing activities. These observations reflect the higher species richness in the low- and sub-arctic.

2.3 Sexual Reproduction

Grazed ramets (i.e., reproductive clones) may not have the photosynthetic and/or nutrient resources to reproduce sexually or they may have their flowers removed in either a developed or an immature state (Roberts 1958; Dawson 1970; Hendrix 1979; Solomon 1983; Belsky 1986b). However, in the arctic the harsh climate forces ramets to rely more on vegetative reproduction even if they remain ungrazed and resources are plentiful (Bliss 1971; Chapin and Shaver 1981; Lachenbruch et al. 1981; McGraw and Shaver 1982; Gartner et al. 1986).

Other studies however, show increases in the density of seed heads after grazing (Dyer 1975; Inouye 1982;

Richards 1983; Paige and Whitham 1987; Henry and Svoboda 1989). The removal of apical meristems can activate axillary buds (Youngner 1972), leading to an increase in the number of reproductive culms. Raillard (1992) reported lower seed head production in plots clipped during the middle of the growing season than in unclipped plots on Ellesmere Island, but natural herbivory by muskoxen was not intense enough to reduce flowering.

2.4 Vegetative Reproduction

Unlike most northern rhizomatous sedges, Eriophorum vaginatum produces its tillers intravaginally resulting in a tussock growth form. Fetcher and Shaver (1982) examined differences in growth characteristics of E. vaginatum tussocks at disturbed and undisturbed sites near Eagle Creek, Alaska. Patterns of tillering and flowering in E. vaginatum varied greatly from site to site and from tussock to tussock. They found that the tillering rate was higher on a vehicle track and a bladed area than on undisturbed sites. The authors concluded that E. vaginatum has a plastic response to a variety of conditions. This plasticity enables E. vaginatum to grow on disturbed and undisturbed sites.

In Alaskan tussock tundra, physical disturbance increases primary productivity and nutrient content of E. vaginatum (Chapin and Shaver 1981). The direct addition of nutrients has also been shown to increase productivity and nutrient content of E. vaginatum (Tamm 1954; Goodman and Perkins 1968). The positive effects of disturbance on plant growth prompted Fetcher and Shaver (1983) to compare the demography of Eriophorum vaginatum from several disturbed and undisturbed sites in Alaska. They wanted to determine how E. vaginatum is able to persist on such varied sites. Undisturbed tundra was compared with disturbed vegetation in a vehicle track that had been in use 15 years prior to sampling and with vegetation on a site that had been scraped clear with a bulldozer at the same study site used in their 1982 study. The authors compared age-specific rates of tiller survival and daughter tiller production in these different treatments. Ramet dynamics are particularly important for E. vaginatum because, in undisturbed tundra, seedling recruitment is rare (Lachenbruch et al. 1981).

Physical disturbance of tussock tundra was associated with a change in age-specific tiller mortality and tillering rate of E. vaginatum (Fetcher and Shaver 1983). Both tillering and tiller mortality took place at earlier

ages on disturbed sites. Survival was reduced on sites that were scraped with a bulldozer and driven over with vehicles, but increased tillering rates compensated for increased mortality rates (Fetcher and Shaver 1983).

The greater longevity of tillers in undisturbed tundra resulted in greater rates of litter accumulation which prevented the invasion of shrubs and mosses. The combination of tussock longevity and litter production may explain why E. vaginatum is not often replaced in undisturbed areas. The ability of E. vaginatum to reproduce rapidly and exploit available resources explains its persistence after disturbance. E. vaginatum adjusted to higher nutrient concentrations on disturbed sites by switching from low tillering rates and high survival to high tillering rates and low survival. Fetcher and Shaver's 1983 study reinforced the findings of their 1982 study: plastic responses allow E. vaginatum to survive in undisturbed and disturbed conditions.

2.5 Herbivory Tolerance

Tundra graminoids have extensive below-ground reserves (Muc 1977) which aid in regrowth after above-ground tissues are removed. In addition, resource sharing among tillers in high latitude sedge meadows ameliorates

the potentially negative effects of herbivory (Jonsdottir and Callaghan 1989). Thus, sedge meadow graminoids are tolerant of low and moderate grazing intensities (Henry and Svoboda 1989; Raillard 1992). However, very frequent and intense herbivory or clipping may increase mortality rates and deplete nutrient reserves and below-ground biomass.

The tolerance of these graminoids to herbivory may be attributed in part to the increased availability of nutrients from the deposition of feces and urine by herbivores (Henry and Svoboda 1989; Hik and Jefferies 1990). Chapin and Slack (1979) found that even ramets with depleted below-ground reserves in Alaska maintained above-ground growth by actively absorbing nutrients from the soil. Thus, large reserves may not be necessary to support above-ground growth if muskoxen or other herbivores provide a source of nutrients readily available to plants. Some studies found reduced uptake of nutrients following defoliation (Davidson and Milthorpe 1966; Bokhari 1977; Clement *et al.* 1978), but these were in carbon-limited graminoids.

Sedge meadow graminoids are more nutrient-limited than carbon-limited (Chapin 1978; McKendrick *et al.* 1978; Shaver *et al.* 1986; Henry *et al.* 1994b) suggesting that ramets must have sufficient nutrient reserves to regrow

immediately after defoliation. Nutrient reserves present in the rhizomes are sometimes depleted after defoliation (Shaver et al. 1986), but because uptake of nutrients from the soil increases (Chapin and Slack 1979; Shaver et al. 1986) grazed graminoids are able to maintain growth rates comparable to ungrazed plants. Henry and Svoboda (1989) found that below-ground biomass was much higher in grazed than in ungrazed meadows on Ellesmere Island.

Shaver and Billings (1975) quantified the storage and turnover of energy, using biomass as an index, in plant root systems of the wet tundra. Three species were considered: Eriophorum vaginatum, Carex aquatilis, and Dupontia fisheri. These three species contribute 57-95% of the above-ground standing crop at the study site. The site was near Barrow, Alaska, and is typical of the polygonal wet tundra of coastal north-slope Alaska. Regionally, the dominant species are grasses and sedges.

Root turnover rates varied considerably: the range was from an annual turnover in Eriophorum to 6-8 years in Carex. An estimate of root turnover on an ecosystem basis was about $100 \text{ g m}^{-2} \text{ y}^{-1}$ or 25% of the live root biomass. Eriophorum invested a considerable amount of energy and material in the production of an annual root system. This is odd in a supposedly nutrient- and energy-limited ecosystem. A possible explanation is that Eriophorum

roots follow the progress of the thaw. By season's end, many of its root tips were located deep in the active layer. During the next growing season these roots were frozen until mid-July. It may be more advantageous for these roots to die (perhaps after translocation of soluble materials upward.) New roots are produced in the thawed soil.

Trends in root weight per unit length and root longevity were apparent. Eriophorum produced large numbers of deep growing roots every year. Of all species considered Eriophorum invested the least amount of energy and materials in producing 1 mm of root. Dupontia root longevity was intermediate. Dupontia invested an intermediate amount of energy in root length. Old roots of Dupontia weighed up to four times as much as new roots. Carex spent 5-6 times as much as Eriophorum per unit length of root, but these roots provided a return which continued for at least 5-6 years longer. The authors concluded that the arctic environment is not as restrictive as is often claimed. Rather, a number of adaptive strategies are available.

2.6 Above- and Below-Ground Productivity

There are many indices of vigor for plants (Buwai and Trlica 1977; Menke and Trlica 1981), but above-ground productivity of grazed swards may be the most important. Below-ground organs in arctic graminoids are also important because they buffer the potentially negative effects of defoliation (Chapin and Slack 1979). The status of this buffer (biomass or carbon and nutrient content) can be used to estimate the long-term health of the sward. The rate of nutrient uptake, however, should not be ignored. Smaller root systems, with depleted reserves, have been reported to have higher P uptake rates than the root systems of undefoliated plants (Chapin and Slack 1979).

Vegetation response to herbivory is extremely complex. Numerous studies have focused on how herbivores affect above-ground productivity. The results are contradictory with some studies reporting increases (Vickery 1972; McNaughton 1976, 1979a, 1985a; Prins et al. 1980, Cargill and Jefferies 1984a; Oba 1994), others showing decreases (Pearson 1965, Sims and Singh 1978, Lacey and Van Poolen 1981) and others demonstrating no change (Solomon 1983, Sterner 1986) after herbivory.

Environmental factors including temperature (Dyer and Bokhari 1976), precipitation (Pearson 1965), and soil properties (McKendrick et al. 1980, McNaughton and Chapin 1985) also influence above-ground productivity. The species composition of swards and the physiological responses of plants to grazing can vary substantially from area to area (Archer and Tieszen 1980). The frequency (Prins et al. 1980), intensity (McNaughton 1979a), and the season of grazing (Bedard et al. 1986) all influence above-ground production. The developmental stage of the plant at the time of defoliation (Tanisky 1969) and the type of plant tissue removed (Dunn and Engel 1971) influence above-ground productivity subsequent to grazing. Different herbivore species alter above-ground production in different ways (McNaughton 1976) and rapid recycling of nutrients contained in their feces and urine can substantially change above-ground productivity (Cargill and Jefferies 1984a).

The accumulation of plant litter in sub-hygic meadow communities that are ungrazed can reduce above-ground productivity (Smith 1990). Herbivory reduces the accumulation of litter and standing dead tissue (Sims and Singh 1978; McNaughton 1979a), possibly producing a warmer microclimate more favorable for plant growth (Curtis and Partch 1950; Cargill and Jefferies 1984a).

Because tundra graminoids have most of their biomass below-ground (Muc 1977) and these graminoids are nutrient-limited (Tamm 1954; Goodman and Perkins 1968; Chapin et al. 1975), either moderate natural or artificial defoliation usually does not affect production rates negatively in the short-term. These grazing-tolerant graminoids retain their large below-ground reserves following moderate defoliation by increasing rates of nutrient uptake (Chapin and Slack 1979; Raillard 1992).

Cargill and Jefferies (1984a) examined the effects of continuous grazing by geese in the coastal Carex/Puccinellia marshes of the Hudson Bay Lowlands throughout the growing season. The study examined how grazing by lesser snow geese Anser caerulescens affected net primary production and the nutritional quality of forage. For geese, the major determinant of forage quality is nitrogen content (Harwood 1977). Net primary production of these salt marshes is nitrogen- not phosphorous-limited (Cargill and Jefferies 1984b).

Net above-ground primary production (NAPP) of salt marsh vegetation ungrazed by geese was estimated by using exclosures (Cargill and Jefferies 1984a). NAPP was estimated by adding all positive biomass increments

inside exclosures during the growing season. Living tissue present at snowmelt was not included in the estimate of NAPP since it represents the previous years production. Sod blocks were used to measure below-ground primary production. The roots were washed free of soil over a 1 mm sieve. Each sample was suspended in a tray of water where live and dead roots were separated visually. Live roots and rhizomes were white and firm, while dead tissues were dark brown and flaccid (Cargill and Jefferies 1984a).

Over 90% of the plant biomass was below ground (Cargill and Jefferies 1984a). Large proportions of plant biomass below-ground have been reported elsewhere in the arctic (Bliss et al. 1973; Dennis et al. 1978). There was no significant difference in below-ground biomass among grazed and ungrazed swards suggesting that intensive grazing by geese did not deplete below-ground reserves. Grazing by lesser snow geese resulted in an 80% increase in NAPP in 1980 and a 35% increase in NAPP in 1979 relative to ungrazed controls. A lower increase in NAPP in 1979 was the result of lower NAPP in exclosures. Grazing prolonged the period of active growth but did not increase growth rates which suggests that sub-arctic meadows are productive but that their annual production may be limited by a short growing season. Grazed plants

maintained a high total nitrogen content which is typical of young, fast-growing tissues. Plants inside exclosures contained more senescent tissue and lower nitrogen levels. Other studies have also shown that protein content of vegetation increased in response to grazing (McNaughton 1979a; Mattson 1980). The mechanisms that increased the NAPP and nitrogen content of Carex and Puccinellia were unknown at the time of the study. Increased rates of nutrient cycling (Hik and Jefferies 1990) and nitrogen fixation (Bazely and Jefferies 1989) played key roles.

Cargill and Jefferies (1984a) suggest that geese may have increased the amount of nitrogen available to plants. Rather than accumulating as litter, plant tissue was converted into goose droppings. These droppings are composed of small fragments that provide a large surface area for decomposing organisms. This hypothesis is supported by the fact that application of goose droppings to ungrazed vegetation increased NAPP. Because grazing reduced litter accumulation, bare areas of sediment that are colonized by nitrogen-fixing blue-green algae became more abundant after grazing (Alexander et al. 1978). Defoliation may also stimulate growth by reducing self-shading if the Leaf Area Index before grazing is above the optimum for photosynthesis (Lee and Bazzaz 1980).

Because water is often abundant in these communities, growth is lush and leaf area indices are high. By feeding in large groups, the geese maintain these meadows as Carex-Puccinellia communities, that produce large quantities of high quality forage.

As pointed out earlier the herbivore-optimization model (Hilbert et al. 1981) describes how moderate grazing intensities optimize net above-ground primary production. Although some studies support this hypothesis (Cargill and Jefferies 1984a), the general applicability of this model to grazed swards remains highly controversial (Belsky 1986a; McNaughton 1986; Painter and Belsky 1993). Hik and Jefferies (1990) tested the herbivore-optimization model using captive goslings of lesser snow geese (Chen caerulescens caerulescens L.) that grazed on vegetation in a sub-arctic salt marsh. Hik and Jefferies (1990) attempted to determine the utility of the model in describing the effects of grazing on plants at different scales of organization. The outcome of grazing may be different for individuals, populations and communities (Brown and Allen 1989) therefore the scale of organization examined should be specified at the beginning of the study. Hik and Jefferies (1990) also addressed the effects of herbivory on forage quality and the role of feces in boosting net above-ground primary

productivity (NAPP). This study was conducted in the same coastal meadows as that used by Cargill and Jefferies (1984a).

Hik and Jefferies (1990) found support for the herbivore-optimization hypothesis. Grazing by lesser snow geese led to an increase of NAPP at low to moderate grazing intensities compared to ungrazed swards. This increase in NAPP was dependent on the presence of goose feces indicating that the recycling of nutrients from feces and urine is essential for regrowth to occur (Ruess and McNaughton 1987). In addition, increased rates of nitrogen fixation boosted NAPP in grazed swards (Bazely and Jefferies 1989). The decreased ability of plants to regrow as the growing season progressed reflected the greater foraging efficiency of the goslings. Forage quality also increased after grazing in this study. The authors concluded that grazing by snow geese increased NAPP and forage quality in Puccinellia communities at the physiological, individual, population and community levels. A more recent study shows that grubbing by geese for roots and rhizomes has seriously damaged these meadows (Hik et al. 1992).

2.7 Forage Quality

Many of the papers cited in this review demonstrate an increase in forage quality after grazing. Herbivores decrease the amount of standing dead tissue in swards (Sims and Singh 1978; McNaughton 1979a; Cargill and Jefferies 1984b; Smith 1990). Because dead tissue is lower in quality than live tissue (Stoner et al. 1982; McNaughton 1985a) herbivores can increase the quality of forage.

Forage quality of regrowth after defoliation is higher because of higher levels of nutrients and/or lower levels of structural carbohydrates (Albertson et al. 1953; Jameson 1963; McNaughton 1976, 1984, 1985a; Prins et al. 1980; Cargill and Jefferies 1984a; Seastedt 1985). In another study Thaine (1954) demonstrated moderate increases in productivity of Russian Wild Ryegrass (Elymus junceus) with increased clipping frequency. Pronounced increases in the protein content of regrowth and kg/protein/ha available to grazers with increased clipping (grazing) frequency were also reported. However, root biomass and the total carbohydrate pool decreased.

In arctic graminoids, that are nutrient-limited, herbivores create a new sink for nutrients by removing photosynthetic tissue. These graminoids respond by

increasing their uptake of nutrients from the soil and allocating a higher proportion of nutrients to new above-ground tissues (Chapin et al. 1975; Chapin and Slack 1979). This phenomenon may occur, especially if herbivores are increasing the rate of nutrient cycling through the deposition of feces and urine. In the absence of feces and urine, slow rates of decomposition in the arctic (Whidden 1977; Henry 1987) might not provide the input of nutrients into the soil that are necessary for ramets to increase nutrient uptake rates. Because biotic and abiotic conditions vary from site to site, the effect of herbivory on forage quality should be examined at the site concerned before any conclusions are made.

2.8 Limiting Factors for Plant Growth

In the long-term, plant growth in the arctic is limited by low nutrient availability, low irradiance, low air temperature and the short growing season (Webber and Ives 1978; Chapin and Shaver 1985). In the short-term, seasonal peak biomass in tundra is determined by the amount of live biomass that survives the winter, environmental factors that control the short-term productivity, and the length of the growing season (Chapin and Shaver 1985). Chapin et al. (1986a) examined

the seasonal changes in carbon-, nitrogen-, and phosphorous-containing chemical fractions in Eriophorum vaginatum and how the fractions change after the experimental manipulation of air temperature, light intensity, nutrient availability, and frequency of foliage removal. The study was conducted to determine which factors limit the growth of E. vaginatum in the short-term and how E. vaginatum changes its patterns of allocation in response to immediate environmental change.

There was a 400% seasonal fluctuation in E. vaginatum rhizome nitrogen concentration which contrasts with the 10% seasonal fluctuation in total nonstructural carbohydrates. Spring growth depleted nitrogen reserves much more than carbohydrate reserves. The incorporation of N and P in new growth in early spring is derived from stored reserves. Late season nutrient uptake serves to replenish reserves and supports growth only when tissues concentrations are above some minimum threshold (Shaver et al. 1986). In E. vaginatum the most pronounced changes in carbohydrate and nutrient reserves took place when the roots were still frozen in the soil indicating that active translocation is possible at temperatures below 0 °C. New leaves became photosynthetically self-sufficient quickly (Miller et al. 1976) so that spring growth was not highly dependent on carbohydrate reserves. Grazing by

lemmings and caribou may be a major factor selecting for high carbohydrate reserves of E. vaginatum to support repeated regrowth of leaves.

A 50% reduction in irradiance and a 5 °C increase in air temperature did not strongly affect annual carbon gain. Tundra plants have low light compensation points (Chapin and Shaver 1985) allowing them to photosynthesize effectively at the low irradiances found in the arctic. Fertilization with nitrogen increased uptake and N-concentrations. Fertilization with sugar had no effect on total soluble carbohydrate content. Severe clipping at ten day intervals throughout the growing season caused large reductions in carbohydrate concentrations, however, these concentrations returned to control levels after a year of recovery. Clipping caused a disproportionate increase in leaf blade nitrogen in this study (Chapin et al. 1986).

Eriophorum vaginatum is well-adapted to low temperatures and low irradiances, however the length of time allowed for growth in the arctic severely limited its peak standing crop biomass. The stability of non-structural carbohydrate concentrations in the rhizomes between seasons suggests that photosynthesis and respiration closely balanced the carbon requirements for new biomass production. In E. vaginatum and other tundra

species, large carbohydrate reserves may be necessary to ensure survival after repeated grazing which is likely to occur during a genet's long lifespan (100+ years, Mark et al. 1985). Unlike its plastic response to increased nutrient levels, Eriophorum was unable to take advantage of higher light intensities and temperatures.

In another study, Shaver et al. (1986) assessed the relative importance of temperature, light and nutrient availability in limiting peak seasonal biomass in tundra ecosystems. The research was conducted in the northern foothills of the Brooks Range, Alaska. Temperature was manipulated with a glasshouse, nutrient availability was improved by fertilization and irradiance was altered by shading. The effects of grazing were assessed by clipping.

Annual productivity of Eriophorum vaginatum was regulated mainly by nutrient reserves early in the growing season. New growth was supplemented by nutrient uptake after mid-July of the current year. After peak biomass was reached, additional nutrients taken up were stored in the rhizomes and leaf sheaths. These reserves were mobilized to support growth the following spring. A reduction in irradiance by half and a 5 °C increase in air temperature had no effect on peak biomass. Fertilized plants grew an extra month compared to controls and

suggested that the extra time is needed to use up larger nutrient reserves.

The high N and P concentrations in clipped plants suggested that Eriophorum has a capacity for luxury uptake even when under stress. This occurred despite a reduction of root biomass to one-third of control values. Recovery of total biomass in clipped plants took one year. These results are consistent with those of Chapin and Slack (1979). The increase in Eriophorum biomass with fertilization was due to increases in tiller number. Thus, the long-term effects of fertilization are likely to be dominated by a numerical response rather than a size response. This is consistent with the results of Chapin and Shaver (1981) and Fetcher and Shaver (1982).

Nitrogen, and to a lesser extent phosphorous, limited vascular plant growth at Eagle Creek (Shaver and Chapin 1980). These species have been selected for maintenance of high physiological efficiency of nutrient use. Large storage reserves were necessary in an environment with long dormant periods and a short, frequently stormy growing season (Bliss 1971).

2.9 Competition

Roots of different arctic species occupy distinct soil horizons (Shaver and Cutler 1979) suggesting a temporal and spatial partitioning of resources among tundra species. Light intensity, air temperature and nutrient availability were altered to determine the primary factor limiting growth of each major vascular species in an Alaskan tussock tundra (Chapin and Shaver 1985). Water availability was above field capacity and was not tested as a possible limiting factor. Differences in species response within the community reflect inherent species differences in environmental requirements.

Canopy species (Betula nana, Ledum palustre) required full ambient light for normal growth. Understory species (e.g., Vaccinium vitis-idaea) were not strongly affected by a similar reduction in light intensity. Species within a single community were limited by different environmental factors. Although the productivity of individual species varied substantially among years, years that were more favorable for some species were unfavorable for others and community productivity remained relatively constant among years. Thus, there is a lack of a single common factor limiting plant growth in tussock and wet meadow tundra. Each species is

specialized to use different levels of environmental resources.

Tussock and wet meadow tundra exhibit clear examples of niche specialization (different rooting depths, canopy heights, photosynthetic rates, light responses, nutrient absorption rates, and growth rates (review in Chapin and Shaver 1985)). Competition may be a factor that produced this species assemblage where each species is limited by a set of different environmental factors. Contrary to the conclusions of Grime (1977), Chapin and Shaver (1985) suggest that competition in low resource environments is strong. It was thought that the severe environmental factors in the arctic override competitive interactions in importance. Given the niche partitioning among species in arctic meadow communities, intraspecific competition is likely to have greater effects than interspecific competition.

2.10 Synopsis

Tundra graminoids tolerate herbivory well because nitrogen, the factor most limiting to plant growth, is more available after grazing or minor human disturbance. Tundra graminoids increase rates of nutrient uptake after defoliation. Increased uptake rates are accompanied by

increased rates of nutrient cycling and nitrogen fixation. Thus, the ability of the plant to take up nitrogen and the availability of nitrogen to the plant increase after herbivory. Tundra graminoids respond plastically to increases in nitrogen availability. Their responses to increases in temperature, light intensity and available carbon (fertilization with sucrose) are rigid and under genetic control. The adaptability and plasticity of these graminoids to environmental constraints and short-term perturbations respectively, has resulted in their proliferation throughout the arctic.

The extrapolation of studies between areas, even within the arctic, can lead to erroneous conclusions. Therefore the studies in this review cannot be applied to all arctic meadows. In addition, major disturbances such as altering permafrost and climatic patterns may have a far greater impact upon these communities than simple clipping. The ability of these communities to recover from disturbance is constrained by the short growing season. More work needs to be done, especially in different regions to ensure that these generalizations are correct. By understanding how arctic meadow ecosystems and their components function we will be better able to ensure their viability in the future. This

knowledge will lead to the protection of particularly sensitive areas (e.g., Thomsen River Valley, Banks Island).

3.0 A TEST OF THE HERBIVORE OPTIMIZATION HYPOTHESIS USING MUSKOXEN AND A GRAMINOID MEADOW PLANT COMMUNITY

3.1 Introduction

The herbivore optimization hypothesis predicts that grazing by herbivores at moderate intensities increases the rate of net above-ground primary productivity (NAPP) above ungrazed, lightly grazed and heavily grazed levels (McNaughton 1979a). There is no general agreement about the validity of the hypothesis (Painter and Belsky 1993) partly because of the confounding problems of scale of biological organization (Brown and Allen 1989), methodology problems (see Belsky 1986a), and spatial and temporal variation among studies. Subarctic graminoids overcompensated after being grazed by wood bison (Bison bison athabasca) at more productive sites, but compensated exactly at less productive sites (Smith 1990). Hik and Jefferies (1990) found that nutrient-limited meadows overcompensated in response to snow goose (Anser caerulescens caerulescens) grazing. In contrast, carbon-limited plant species often undercompensate for tissue lost to grazers (Lacey and Van Poollen 1981).

Since the 1950's the population of muskoxen on Banks Island, Northwest Territories, Canada has been growing exponentially (Vincent and Gunn 1981; McLean et al. 1989). Despite the inherent susceptibility of arctic ungulates to catastrophic die-offs (Miller et al. 1977), the threat of industrial development, the contentious issue of muskox management on Banks Island (Sachs Harbour HTC pers. comm. 1992) and the eruption of muskox populations across North America (Smith 1984; Thing et al. 1984; Henry et al. 1994a) little is known about the critical summer range of muskoxen in northern Canada (Parker and Ross 1976). In the context of the herbivore-optimization hypothesis it was hypothesized that: (1) Muskoxen remove significant proportions of shoot tissue from graminoid meadows; (2) Graminoid meadows within the study area will overcompensate in response either to moderate clipping or to herbivory by muskoxen; (3) Removal of shoot tissue either by clipping or by muskoxen has no effect on the standing crop of live roots.

3.2 Methods

3.2.1 Experimental Design

All biomass data were gathered from three sites during the course of this study. Two sites, Muskox River (MR) and Thomsen River (TR) contained a 10 X 10 m permanent exclosure (Figures 3-1 and 3-2). These exclosures were erected in mid-August 1988, some three years before the beginning of this study. The third site, Umingmuk Hill (UH) is located on a hill which rises at the edge of the Thomsen River valley; there is no permanent exclosure at this site. Ten 1 m X 1 m microplots (plots) per treatment were clipped at 1.5 cm (Table 3-1).

In 1992 and 1993 randomly located 0.25 X 0.25 m sub-plots inside the permanent exclosures were clipped to the ground (n=5 per treatment) four times during each growing season. Sub-plots were located in five randomly chosen plots in 1992 and in the other five in 1993 and provided a way of monitoring growth after clipping treatments. After a sub-plot was clipped to the ground a marker was left to ensure it was not clipped again. Plots of a given treatment were located adjacent to each other within the permanent exclosure (Figure 3-1). Extensive analyses were

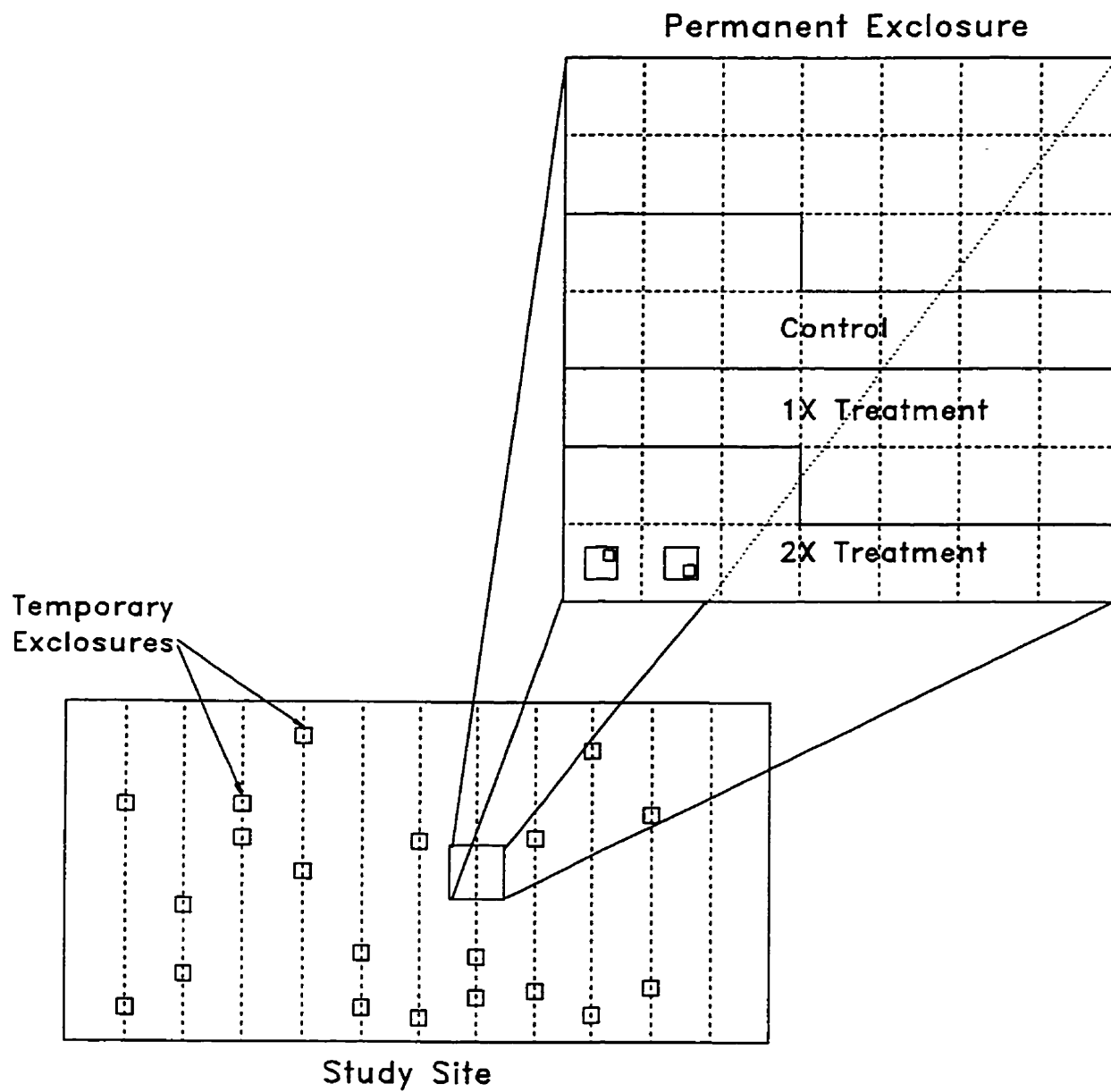
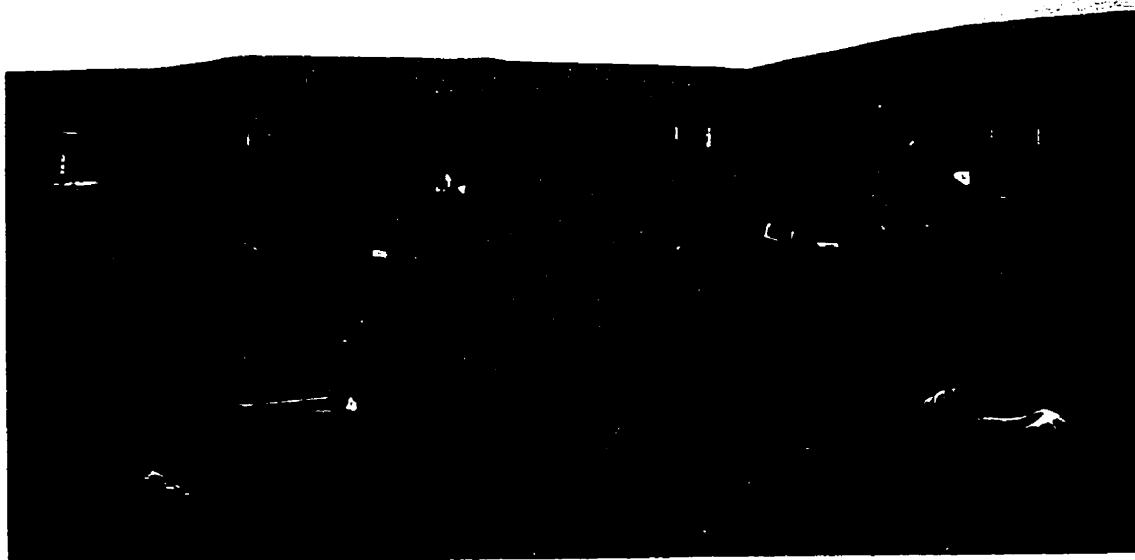


Figure 3-1. Sampling and treatment plot layout at a representative study site.

A



B

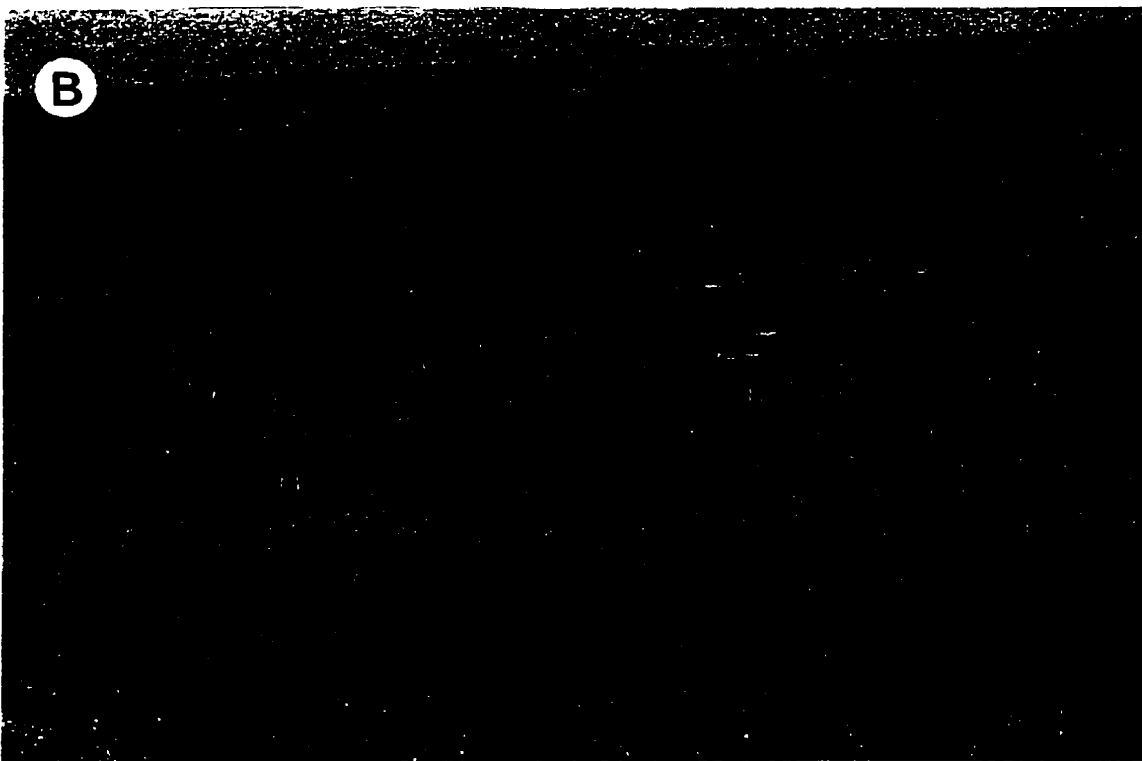


Figure 3-2. A. The permanent 10 X 10 m enclosure at the Thomsen River study site. B. Temporary Exclosures 1.5 m in diameter at Thomsen River study site.

Table 3-1. Clipping schedule at Muskox River and Thomsen River study sites in 1991 and 1992.

| <u>Clipping Schedule</u> | | |
|----------------------------------|----------------------------------|----------------------------|
| <u>1991 treatment</u> | <u>1992 treatment</u> | <u>Total times clipped</u> |
| <u>Muskox River</u> | | |
| Clipped 1X (early July) | Clipped 2X (early & mid-July) | Clipped 3X |
| Control | Clipped 1X (early July) | Clipped 1X |
| Control | Control | Not clipped |
| <u>Thomsen River</u> | | |
| Clipped 2X (early & mid-July) | Clipped 2X (early & mid-July) | Clipped 4X |
| Clipped 1X | Clipped 1X (early July) | Clipped 2X |
| <u>Control</u> | <u>Control</u> | <u>Not clipped</u> |

conducted to determine if this arrangement affected the results of the clipping experiments (Appendix A). The conclusion is that it did not. The arrangement of plots is not a concern for comparisons among temporarily protected, grazed and control treatments because all were randomly located.

Adjacent to the permanent exclosures at MR and TR were about 2- and 4-ha study areas, respectively that were exposed to muskoxen. Umingmuk Hill (UH) site was about 1 ha in size.

Ten transects were laid out at each site in a systematic manner. Restrictions by non-meadow communities caused some of the transects to differ slightly in length. Temporary exclosures were located randomly along the transects in late June 1992 and 1993 (two per transect or $n=20$ at MR and TR and one per transect or $n=10$ at UH) and were disassembled at the end of each growing season (Figure 3-2). Temporary exclosures (1.5 m in diameter) were made from standard aluminum fencing wire which allowed the passage of small mammals and birds. Muskoxen reduced the number of intact temporary exclosures in 1992 at TR and UH by rubbing against them.

Microplots (0.25 X 0.25 m) were clipped to the ground inside and outside of each temporary exclosure four times during each growing season (1992 and 1993

only) which allowed for the comparison of temporarily protected and grazed areas. As in permanent exclosures, care was taken so that the same areas were not clipped more than one time.

Samples were predried in the field at 40-60 °C for 24 hours in an oven placed over a propane stove. Samples were later dried for 48 hours at 60 °C in the laboratory. After drying, each sample was homogenized by mixing and a representative sub-sample (ca. one-third of sample) was removed. Live and dead tissues were separated in each sub-sample and the resulting proportions were extrapolated to the larger sample. All samples and sub-samples were weighed to the nearest 0.01 g. Several samples were separated entirely into three sub-samples to determine if sub-samples were representative of the whole.

In 1992 the number of samples collected made separating each one too time-consuming, so the following regression equation was used:

$$y = 4.21 + 0.84x \quad R^2 = 0.86 \quad [3.1]$$

where, y = actual percentage of live tissue

x = subjectively estimated percentage of live tissue

In 1993 all sub-samples were separated manually (i.e., no regression equation was used).

3.2.2 Below-ground standing crop

Ten soil cores were removed from each treatment at each site in late August 1993 using a small shovel. One soil core was removed from the center of each randomly chosen plot. Plants growing on each core were clipped at ground level, bagged and dried. Cores were standardized in size in the field to about 10 cm in length and 10 cm in diameter.

Soil cores were frozen in the field and remained frozen during transport by air to Saskatoon. The cores were dried at 70 °C for 72 hours. The dried cores were broken apart using a fork and a rolling pin. The material was sieved (0.50 mm opening) until only coarse material remained. The fine material which passed through was sieved once again with a finer mesh (0.25 mm). After homogenization and removing a sub-sample (about 30% of whole) all coarse and 15% (five randomly chosen per study site) of fine root sub-samples were manually separated into live and dead components. Live roots were white and

firm, dead roots were brown or black and flaccid. Fifteen samples were broken down entirely into sub-samples to determine if sub-samples were representative of the whole.

The volume of each core was determined in the laboratory. Thus, the biomass of roots could be determined for each 1 m² plot. Owing to logistical constraints, all roots below 10-cm depth in the profile were not considered in this study. Because very few roots grew below the 10-cm mark of soil profiles (n=6) dug to permafrost, root biomass estimates are similar to those occurring in the field.

3.2.3 Data Analysis

All data were tested for normality using the Shapiro Wilks W test (SAS 1988) and variances were tested for homogeneity using the F_{\max} test (Sokal and Rohlf 1981). If necessary, data were transformed with log + 1 or square root + 0.5 equations to satisfy the assumptions of parametric statistics. Analysis of variance was conducted on 2X/1X/control data and on Temporary Exclosure/Grazed/Control data. Means were compared with the LSD test (Sokal and Rohlf 1981).

3.2.4 Terminology

Absolute Productivity (AP): The positive or negative change in live biomass plus the positive change in standing dead over a period of time.

Clipping Intensity (C): $1 - (\text{TSC clipped} / \text{TSC unclipped})$

Compensation: The increase in productivity of plant communities, plant populations or individual plants after being grazed or clipped.

Cumulative Green Biomass (CGB): The absolute quantity of green tissue produced in a plot.

Grazing Intensity (G): $1 - (\text{TSC grazed} / \text{TSC temporary exclosures})$

Green Productivity (GP): The change in biomass of green tissue over a period of time.

Green Standing Crop (GSC): The mean weight of green plant tissue. Expressed as the mean at all sampling dates, or the peak value over the season.

Total Productivity (TP): The change in biomass of live and dead tissue over a period of time.

Total Standing Crop (TSC): The mean weight of live and dead plant tissue combined, but excluding litter.

Expressed as the mean at all sampling dates, or the peak value over the season.

3.3 Results

3.3.1 The effect of grazing and clipping on total standing crop

Clipping inside permanent exclosures at Muskox River (MR) and Thomsen River (TR) decreased mean total standing crop (TSC) below control (i.e., unclipped) levels in 1992 and 1993. By late July 1993 (the recovery year) at MR, however, mean total standing crop was similar in clipped and unclipped treatments (Table 3-2).

Mean total standing crop was lower in plots exposed to muskoxen than in adjacent temporarily protected microplots in 1992 and 1993 (Table 3-3). Total standing crop was similar in control and grazed plots at MR in 1992 and 1993 however at TR, control plots had the highest standing crops (Table 3-3).

3.3.2 Grazing intensity at the study sites

Grazing intensity (G) (using temporary exclosure data in calculation) was similar among the three sites (Tables 3-4). Similar grazing intensities were also measured between years. Estimates in late July/early August from all three sites in 1992 and 1993 show that

Table 3-2. Comparison of total standing crop estimates* (g m⁻²) (mean) among treatments in 1992 and 1993 1 X 1 m microplots (n=5) inside permanent exclosures. Microplots were unclipped (control), clipped twice (2X), or clipped once (1X) in 1991 and 1992 at two study sites.

| <u>Date</u> | <u>Total Standing Crop</u> | | | <u>MS Error</u> |
|---------------------------|----------------------------|------------------|------------------|-----------------|
| | <u>2X</u> | <u>1X</u> | <u>Control</u> | |
| <u>1992 Muskox River</u> | | | | |
| July 3 | 63 _a | 30 _a | 47 _a | 1257 |
| July 17 | 26 _b | 26 _b | 68 _a | 482 |
| July 27 | 45 _b | 59 _b | 111 _a | 574 |
| Aug. 5 | 54 _b | 61 _b | 78 _a | 195 |
| <u>1992 Thomsen River</u> | | | | |
| July 8 | 78 _c | 162 _b | 288 _a | 4381 |
| July 22 | 66 _c | 92 _b | 335 _a | 1629 |
| July 31 | 106 _b | 129 _b | 392 _a | 1855 |
| Aug. 10 | 57 _c | 116 _b | 342 _a | 1205 |
| <u>1993 Muskox River</u> | | | | |
| June 27 | 46 _{ab} | 50 _a | 34 _b | 137 |
| July 16 | 96 _{ab} | 111 _a | 72 _b | 696 |
| July 29 | 121 _a | 125 _a | 151 _a | 832 |
| Aug. 18 | 83 _a | 95 _a | 103 _a | 672 |
| <u>1993 Thomsen River</u> | | | | |
| July 4 | 35 _b | 91 _a | 81 _a | 1057 |
| July 21 | 67 _b | 108 _b | 255 _a | 4525 |
| Aug. 3 | 148 _b | 157 _b | 316 _a | 6814 |
| Aug. 17 | 129 _b | 161 _b | 328 _a | 5008 |

* Total Standing Crop is the biomass of live and dead plant tissue not yet classified as debris. Means with the same subscript within rows are not significantly different at $P \leq 0.10$

Table 3-3. Comparison of total standing crop (g m^{-2}) estimates* (mean) among treatments in 1992 and 1993 1 X 1m microplots. Microplots were unclipped (control) (n=5), temporarily protected (since June 25, 1992 or 1993) (n=20 at MR and TR)** or grazed (i.e., exposed to muskoxen) (n=20 at MR and TR).*

| <u>Date</u> | | <u>Total Standing Crop</u> | | | |
|------------------------|--|----------------------------|------------------|-------------------|-----------------|
| | | <u>Temp.Excl.</u> | <u>Grazed</u> | <u>Control</u> | <u>MS Error</u> |
| <u>Muskox River</u> | | | | | |
| July 4 1992 | | 55 _a | 46 _a | 47 _a | 822 |
| July 18 | | 100 _a | 68 _b | 68 _{ab} | 860 |
| July 28 | | 140 _a | 99 _b | 111 _{ab} | 2029 |
| Aug. 6 | | 135 _a | 121 _a | 78 _b | 1678 |
| June 30 1993 | | 79 _a | 72 _a | 34 _b | 685 |
| July 18 | | 129 _a | 96 _b | 73 _b | 2365 |
| July 30 | | 155 _a | 116 _b | 151 _a | 1748 |
| Aug. 18 | | 131 _a | 108 _b | 103 _{ab} | 1724 |
| <u>Thomsen River**</u> | | | | | |
| July 10 1992 | | 172 _b | 125 _c | 288 _a | 3727 |
| July 22 | | 197 _b | 146 _c | 335 _a | 5429 |
| July 31 | | 268 _b | 206 _c | 392 _a | 5785 |
| Aug. 10 | | 233 _b | 204 _b | 342 _a | 4514 |
| July 7 1993 | | 148 _a | 123 _b | 81 _c | 2161 |
| July 22 | | 205 _{ab} | 184 _b | 255 _a | 4023 |
| Aug. 3 | | 228 _b | 165 _c | 316 _a | 6232 |
| Aug. 17 | | 217 _b | 176 _c | 328 _a | 4961 |
| <u>Umingmuk Hill**</u> | | | | | |
| July 14 1992 | | 161 _a | 140 _a | NA | 2174 |
| July 25 | | 203 _a | 203 _a | NA | 4657 |
| Aug. 4 | | 305 _a | 217 _b | NA | 7849 |
| Aug. 13 | | 339 _a | 207 _b | NA | 11611 |
| July 13 1993 | | 279 _a | 194 _b | NA | 4917 |
| July 26 | | 316 _a | 248 _b | NA | 6136 |
| Aug. 7 | | 311 _a | 240 _b | NA | 7154 |
| Aug. 18 | | 299 _a | 212 _b | NA | 6295 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$

** n=18 on Aug. 1 and n=11 on Aug. 10 1992 at TR t.excl. n=10 in grazed and temporary exclosure treatment at Umingmuk Hill. n= 8 (first 2 dates) and n=7 (last 2 dates) in temporary exclosure at Umingmuk Hill in 1992.

Table 3-4. Comparison of grazing intensities (1-ratio of grazed to temporary exclosure standing crops) among study sites (first subscript) and within each study site (second subscript) during the 1992 and 1993 growing seasons.*

| <u>Date</u> | <u>Study Sites</u> | | |
|-------------|-----------------------|----------------------|-----------------------|
| | <u>Muskox R.</u> | <u>Thomsen R.</u> | <u>Umingmuk H.</u> |
| July 9 1992 | 0.2 _a (AB) | 0.3 _a (A) | 0.1 _a (AB) |
| July 21 | 0.3 _a (A) | 0.3 _a (A) | 0.0 _b (B) |
| July 31 | 0.3 _a (AB) | 0.2 _a (A) | 0.3 _a (A) |
| Aug. 9 | 0.1 _b (B) | 0.1 _b (A) | 0.4 _a (A) |
| July 6 1993 | 0.1 _a (A) | 0.2 _a (B) | 0.3 _a (A) |
| July 22 | 0.3 _a (A) | 0.1 _a (B) | 0.2 _a (A) |
| Aug. 3 | 0.3 _a (A) | 0.4 _a (A) | 0.2 _a (A) |
| Aug. 17 | 0.2 _a (A) | 0.2 _a (B) | 0.3 _a (A) |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$. Subscripts for within site comparisons are in parentheses.

muskoxen removed from 20 to 40% of the available forage during a growing season.

Plots clipped once in 1992 had similar proportions of tissue removed early in the season, but plots clipped twice had from 8 to 30% of tissue removed on two occasions in July 1992 (Table 3-5). Therefore the 2X treatment represents the most intense treatment while 1X and grazing represent equally intense treatments. Clipping treatments removed forage from the plots early in the growing season (early to mid-July) whereas grazing was more evenly spread throughout the growing season. Unlike clipped treatments, deposition of feces and urine occurred in the grazed treatment (see Section 1.6.1).

3.3.3 Effects of clipping and grazing on cumulative green biomass and productivity

The cumulative green biomass (CGB) inside clipped plots in 1992 was highest in the control treatment and lowest in the 2X (Table 3-6). The more intense removal of forage in the 2X treatment did not have an additional effect over the 1X treatment at MR however.

Estimates of Green (GP), Total (TP) and Absolute Productivity (AP) were higher in control plots than in clipped plots in 1992 and 1993, however there were

Table 3-5. Clipping intensity estimates (proportion of plant tissue removed by clipping treatments, mean (CV)) in 1992 inside 1 X 1 m microplots (n=5) in permanent exclosures at two study sites.

| <u>Date of Clip</u> | <u>Treatment</u> | <u>Clipping Intensity</u> |
|----------------------|------------------|---------------------------|
| <u>Muskox River</u> | | |
| July 2 | 1X | 0.22 (45) |
| July 1 | 2X | 0.08 (38) |
| July 16 | 2X | 0.26 (18) |
| <u>Thomsen River</u> | | |
| July 8 | 1X | 0.25 (42) |
| July 8 | 2X | 0.30 (30) |
| July 22 | 2X | 0.14 (34) |

Table 3-6. Comparison of cumulative green biomass estimates* ($\text{g m}^{-2} \text{d}^{-1}$) (mean) in 1992 1 X 1 m microplots (n=5) inside permanent exclosures. Microplots were unclipped (control), clipped twice (2X), or clipped once (1X) in 1991 and 1992 at two study sites.

| <u>Date</u> | <u>Cumulative Green Biomass</u> | | | <u>MS Error</u> |
|----------------------|---------------------------------|-------------------|--------------------|-----------------|
| | <u>2X</u> | <u>1X</u> | <u>Control</u> | |
| <u>Muskox River</u> | | | | |
| July 3 | 19.3 _a | 11.2 _a | 16.4 _a | 78 |
| July 17 | 16.3 _b | 18.9 _b | 41.4 _a | 141 |
| July 27 | 38.7 _b | 40.5 _b | 70.6 _a | 232 |
| Aug. 5 | 38.4 _a | 41.5 _a | 46.5 _a | 92 |
| <u>Thomsen River</u> | | | | |
| July 8 | 25.8 _b | 53.5 _a | 38.6 _b | 157 |
| July 22 | 46.1 _b | 60.6 _b | 102.7 _a | 316 |
| July 31 | 57.5 _c | 86.5 _b | 136.3 _a | 268 |
| Aug. 10 | 43.9 _b | 77.7 _a | 96.6 _a | 531 |

* Green Productivity includes only live (green) plant tissue. Means with the same subscript within rows are not significantly different at $P \leq 0.10$

several cases in 1993 where exact compensation (e.g., balanced replacement of tissue lost to clipping) occurred (Table 3-7). There was more exact-compensation in 1993 than in 1992 especially with green productivity estimates at TR where the 2X treatment had the same green productivity as the control or 1X treatment.

More exact-compensation occurred in comparisons among productivity estimates in temporarily protected and control treatments (Table 3-8) than inside permanent exclosures. In a few cases under-compensation was observed, mostly at TR. Productivity in grazed areas was lower than productivity in temporary exclosures in most cases. Productivity in grazed areas at UH was similar to productivity in temporary exclosures despite the high fecal pat densities and large amounts of tissue removed by muskoxen (sections 1.6.1 and 3.3.1). Overall, estimates of AP were higher than GP and TP at the three sites during 1992 and 1993. GP and TP estimates were similar during the study.

In conclusion, the different estimates of productivity (including CGB) during the 1992 and 1993 growing seasons consistently demonstrated that more intense defoliation (e.g., 2X and 1X) caused more under-compensation (64% of cases) ("case" refers to

Table 3-7. Comparison of green (GP), total (TP) and absolute productivity (AP) estimates* ($\text{g m}^{-2} \text{d}^{-1}$) (mean) among treatments in 1992 and 1993 1 X 1 m microplots (n=5) inside permanent exclosures. Microplots were unclipped (control), clipped twice (2X), or clipped once (1X) in 1991 and 1992 at two study sites.

| <u>Date</u> | | | <u>Prod</u> | <u>2X</u> | <u>1X</u> | <u>Control</u> | <u>MS Error</u> |
|----------------------|--------|-------|-------------|-------------------|-------------------|------------------|-----------------|
| <u>Muskox River</u> | | | | | | | |
| Jul | 3-Jul | 27/92 | GP | 0.8 _b | 1.2 _b | 2.3 _a | 0.4 |
| Jun | 27-Jul | 29/93 | GP | 2.6 _a | 2.7 _a | 3.4 _a | 1.0 |
| Jul | 3-Jul | 27/92 | TP | -0.3 _b | 1.4 _a | 2.7 _a | 1.9 |
| Jun | 27-Jul | 29/93 | TP | 2.5 _{ab} | 2.4 _b | 3.5 _a | 1.0 |
| Jul | 3-Jul | 27/92 | AP | 0.8 _b | 1.4 _{ab} | 2.7 _a | 0.9 |
| Jun | 27-Jul | 29/93 | AP | 2.6 _a | 2.7 _a | 3.6 _a | 1.0 |
| <u>Thomsen River</u> | | | | | | | |
| Jul | 8-Jul | 31/92 | GP | 1.4 _b | 1.4 _b | 4.4 _a | 0.5 |
| Jul | 4-Aug | 3/93 | GP | 2.5 _a | 1.6 _a | 1.6 _a | 0.7 |
| Jul | 8-Jul | 31/92 | TP | 2.5 _a | 0.2 _b | 4.5 _a | 3.6 |
| Jul | 4-Aug | 3/93 | TP | 4.2 _b | 2.5 _b | 7.8 _a | 7.3 |
| Jul | 8-Jul | 31/92 | AP | 2.5 _b | 1.4 _c | 5.2 _a | 1.5 |
| Jul | 4-Aug | 3/93 | AP | 4.2 _b | 2.6 _b | 7.8 _a | 7.2 |

* Green productivity includes only live (green) plant tissue. Total productivity includes live (green) and dead plant tissue. Absolute productivity includes live (green) plant tissue plus the transfer of live to dead tissue. Means with the same subscript within rows are not significantly different at $P \leq 0.10$

Table 3-8. Comparison of green (GP), total (TP) and absolute (AP) productivity ($\text{g m}^{-2} \text{d}^{-1}$) estimates* (mean) among treatments in 1992 and 1993 1 x 1m microplots. Microplots were unclipped (control) (n=5), temporarily protected (since June 25, 1992) (n=20) and grazed (i.e., exposed to muskoxen) (n=20).*

| <u>Dates</u> | <u>Prod</u> | <u>T.Ex</u> | <u>Grz</u> | <u>Cont</u> | <u>MS Error</u> |
|------------------------|-------------|-------------------|------------------|-------------------|-----------------|
| <u>Muskox River</u> | | | | | |
| Jul 4-Jul 28/92 | GP | 2.3 _a | 1.6 _b | 2.3 _{ab} | 1.3 |
| Jun 30-Jul 30/93 | GP | 2.1 _b | 1.6 _b | 3.4 _a | 1.6 |
| Jul 4-Jul 28/92 | TP | 3.5 _a | 2.2 _b | 2.7 _{ab} | 5.3 |
| Jun 30-Jul 30/93 | TP | 2.6 _a | 1.5 _b | 3.5 _a | 2.9 |
| Jul 4-Jul 28/92 | AP | 3.6 _a | 2.6 _a | 2.7 _a | 4.0 |
| Jun 30-Jul 30/93 | AP | 2.9 _a | 1.9 _b | 3.6 _a | 2.3 |
| <u>Thomsen River**</u> | | | | | |
| Jul 10-Aug 1/92 | GP | 3.8 _{ab} | 2.7 _b | 4.4 _a | 3.5 |
| Jul 7-Aug 3/93 | GP | 2.3 _a | 0.3 _b | 1.6 _{ab} | 3.5 |
| Jul 10-Aug 1/92 | TP | 4.1 _a | 3.7 _a | 4.5 _a | 17.5 |
| Jul 7-Aug 3/93 | TP | 3.0 _b | 1.6 _b | 7.8 _a | 8.7 |
| Jul 10-Aug 1/92 | AP | 5.4 _a | 4.4 _a | 5.2 _a | 10.3 |
| Jul 7-Aug 3/93 | AP | 3.3 _b | 2.2 _b | 7.8 _a | 6.8 |
| <u>Umingmuk Hill**</u> | | | | | |
| Jul 14-Aug 4/92 | GP | 4.4 _a | 3.7 _a | NA | 3.4 |
| Jul 13-Aug 7/93 | GP | 1.0 _a | 1.2 _a | NA | 8.0 |
| Jul 14-Aug 4/92 | TP | 6.8 _a | 3.5 _a | NA | 12.5 |
| Jul 13-Aug 7/93 | TP | 1.2 _a | 1.9 _a | NA | 14.1 |
| Jul 14-Aug 4/92 | AP | 7.5 _a | 4.4 _a | NA | 9.7 |
| Jul 13-Aug 7/93 | AP | 2.0 _a | 2.9 _a | NA | 7.2 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$

** 1992 Only: n=19 in TR temporary exclosure treatment
n= 7 in UH temporary exclosure treatment

measurements from the active growth period, i.e., from first to third sampling date or from late June/early July to late July/early August) and some exact-compensation (36% of cases). Less intense treatments (e.g., grazing by muskoxen) showed more exact-compensation (75% of cases) and some under-compensation (25% of cases). The 2X treatment resulted in the same percentage of under-compensation cases as the 1X treatments. Similarly, the clipping experiment resulted in more under-compensation in 1992 (88% of cases) than in 1993 (33% of cases). Under no conditions across this gradient of tissue removal did over-compensation occur.

3.3.4 Effects of clipping and grazing on below-ground standing crop of roots

Clipping reduced the standing crop of roots at TR, but moderately clipped plots showed an increase in below-ground standing crop at MR (Table 3-9). Exact-compensation occurred in temporarily protected plots at MR and TR as indicated by below-ground standing crops that were similar in temporarily protected and control plots; however, areas grazed by muskoxen had reduced below-ground standing crop at MR (Table 3-10). These results are consistent with the results reported for

Table 3-9. Comparison of the biomass (g m^{-2}) of live roots (mean) in 1 x 1m microplots (n=10) inside permanent exclosures in late August 1993. Microplots were unclipped (control), clipped twice (2X), or clipped once (1X) in 1992 at two study sites. Root:Shoot ratios in parentheses.

| <u>Date</u> | <u>Biomass of Live Roots</u> | | | |
|----------------------|------------------------------|-------------------------|------------------------|-----------------|
| | <u>2X</u> | <u>1X</u> | <u>Control</u> | <u>MS Error</u> |
| <u>Muskox River</u> | | | | |
| Aug. 21 | 980 _b (8) | 1,260 _a (10) | 1,070 _b (7) | 50,000 |
| <u>Thomsen River</u> | | | | |
| Aug. 23 | 420 _b (3) | 560 _a (4) | 620 _a (2) | 30,000 |

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

Table 3-10. Comparison of the biomass (g m^{-2}) of live roots (mean) in 1 X 1m microplots (n=10). Microplots were unclipped (control), temporarily protected (since June 25, 1993) and grazed (i.e., exposed to muskoxen) root:shoot ratios in parentheses.

| <u>Date</u> | <u>Biomass of Live Roots</u> | | | |
|----------------------|------------------------------|----------------------|-----------------------|-----------------|
| | <u>Temp.Excl</u> | <u>Grazed</u> | <u>Control</u> | <u>MS Error</u> |
| <u>Muskox River</u> | | | | |
| Aug. 21 | 1070 _a (7) | 650 _b (6) | 1070 _a (7) | 100,000 |
| <u>Thomsen River</u> | | | | |
| Aug. 23 | 530 _a (2) | 610 _a (4) | 620 _a (2) | 50,000 |
| <u>Umingmuk Hill</u> | | | | |
| Aug. 22 | 810 _a (3) | 960 _a (4) | NA | 110,000 |

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

above-ground plant tissues. Removal of plant tissue by clipping or by muskoxen grazing decreased below-ground standing crop and above-ground productivity. Less severe treatments showed exact-compensation.

The inconsistencies in the data are: (1) the large root standing crop in the 1X treatment inside the permanent exclosure at MR and (2) the lower than expected standing crop in the grazed area at MR. Low standing crop of roots (SCR) in areas exposed to muskoxen at MR led to the large difference with estimates from adjacent temporarily-protected areas.

Root:shoot ratios were higher at MR than at the other two sites (Table 3-10). Clipped and grazed treatments showed higher root:shoot ratios than protected treatments.

3.4 Discussion

3.4.1 Removal of plant tissue by clipping and grazing

The results of total standing crop, grazing intensity, clipping intensity show that muskoxen and clipping removed significant proportions of plant tissue. Raillard (1992) using an indirect method based on muskox density data, calculated that the grazing intensity in

Sverdrup Pass Ellesmere Island was 3.9% during the summer, much lower than the values recorded in this study. In contrast, Cargill and Jefferies (1984a) reported that snow geese removed 80% of forage available in a sub-arctic salt marsh. Lemmings removed as much as 90% of available forage (Schultz 1969). However, for a study focusing on muskoxen the present study exhibits higher than usual grazing intensities. This is consistent with the muskox density data ($1.52/\text{km}^2$) for the Thomsen River Valley provided by McLean *et al.* (1989) and the data from other areas across the arctic (Hubert 1977; Gunn 1984; Thing *et al.* 1987; Raillard 1992).

Fecal pat density data further document the use of these meadows by muskoxen. These data are consistent with the observations that 55% and 77% of muskoxen observed grazing during the summers of 1992 and 1993, respectively, were within the graminoid meadow plant community (Chapter 1). These findings are significant in light of the fact that graminoid meadows make up a small proportion of the study area. Ferguson (1991) found that graminoid meadows made up only 4.5% of his larger study area on northern Banks Island. Other studies also have documented that graminoid meadows are an important source of forage for muskoxen (Tener 1963; Parker and Ross 1976; Wilkinson *et al.* 1976; Thing 1984).

Despite the fact that clipping and grazing removed significant proportions of plant tissue there are some important differences between the two treatments: (1) Grazing was spread more evenly throughout the growing season whereas clipping was concentrated early in the season; (2) In 1992 clipping (2X treatment) removed a greater proportion of plant tissue than grazing whereas the 1X treatment and grazing removed similar proportions; (3) Deposition of feces and urine (Putman 1984) and saliva (Reardon *et al.* 1974; Hori 1975; Dyer and Bokhari 1976; Howe *et al.* 1982; McNaughton 1985b), trampling (McNaughton 1976; Owaga 1980; Belsky 1986b), and selective herbivory (Bryant *et al.* 1983; Belovsky 1986; Chapin *et al.* 1986b; Illius *et al.* 1987; Etchberger *et al.* 1988; Oakes 1989) were lacking in the clipped treatments but present in grazed areas. However, because permafrost prevents water from being leached deeply into the soil profile, the lateral transfer of water soluble nutrients (e.g, from feces and urine) may be more predominant in the Arctic, however, than in more temperate ecosystems with similar soil textures.

3.4.2 Effect of grazing and clipping on total standing crop

The observation that clipping reduced the total standing crop (TSC) in permanent exclosures more at TR than at MR may have been related to the use of the MR exclosure as a lemming nest during the winter of 1990-91. Higher soil moisture levels (% O.D.W.) inside the MR (381%) than in the TR (220%) exclosure (Chapter 4) also may have made the additional effect of clipping less apparent at MR. A thick moss layer at MR and at other hygric sites may have physically obstructed the growth of graminoids and acted as a nutrient sink which decreased NH_4 levels (Chapter 4). Vegetation inside the MR exclosure was more limited by intense lemming herbivory, a thick moss layer and super-hygric conditions than by the clipping treatments imposed.

The large difference in TSC among treatments in the TR exclosure even after a year of recovery in 1993 demonstrates that clipping at TR had significant lasting effects on the amount of available forage. The reduction in peak total standing crop in grazed areas versus temporarily protected areas at all three study sites in 1992 and 1993 (Figure 3-3) demonstrates that muskoxen also remove significant amounts of plant tissue. These

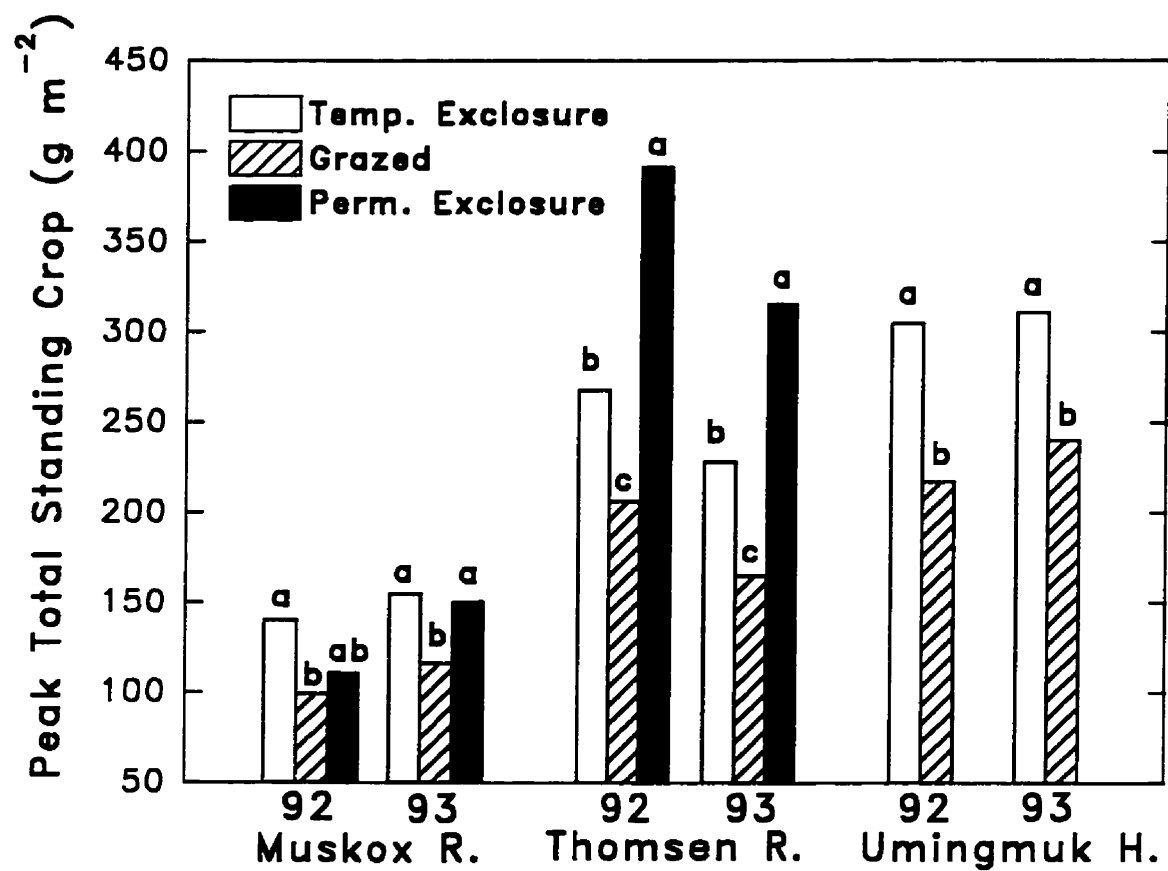


Figure 3-3. Comparison of peak total standing crop (g m⁻²) in temporarily protected, grazed and control microplots at three study sites in 1992 and 1993.

data clearly show that both grazing and clipping reduce TSC. Thus, smaller absolute quantities of tissue are available to other grazers after these treatments. Despite the lower quantities of forage available after grazing, muskoxen are clearly not limited by forage during the summer because over 2/3 of the above-ground standing crop remains ungrazed. The forage base, therefore, escapes herbivory because even high density muskox populations cannot possibly graze all the forage associated with the short but intense burst of primary production during the summer months. This ungrazed forage is likely important in sustaining muskoxen during the winter. Raillard (1992) reported similar findings on Ellesmere Island.

Small differences in control and temporarily protected treatments at MR (Figure 3-3) are the result of more lemming herbivory in the control and to a lesser extent super-hygic conditions inside the MR enclosure. Soil moisture (% O.D.M.) was only slightly lower in grazed areas (293%) vs control plots (381%) at MR (Chapter 4). The higher total standing crop at UH than at MR and TR is related to the higher fertility at UH ($\text{NH}_4\text{-N}$ concentrations in soil were 43.5, 29.9 and 17.7 $\mu\text{g/g}$ at UH, TR and MR, respectively). In addition, a large snowbank fed meltwater into the UH site throughout each

growing season during the study. Unlike TR and MR, UH was on a 15% slope which resulted in better drainage than at the other sites. Muskox River in particular smelled of sulphide from anerobic soil conditions. Meltwater at MR was trapped since the site was surrounded by high ground. Likewise fecal pat density data show that muskoxen were attracted to UH which was probably a consequence of high total standing crops and large proportions of live tissue (Chapter 5).

In summary, both muskoxen grazing and clipping treatments were of a large enough magnitude to elicit a significant response from the graminoid meadow plant community. The study area has some of the highest muskoxen densities reported in the Arctic. However standing crop data do not provide answers on how this community responds to grazers over time nor do they address the herbivore-optimization hypothesis.

3.4.3 Effects of clipping and grazing on green biomass and productivity

The original hypothesis that graminoid meadows will over-compensate in response to moderate clipping and grazing by muskoxen is rejected. Despite the fact that the proportion of plant tissue removed by clipping and

grazing was variable (0-40%), no case of over-compensation was observed. The results consistently demonstrated that removal of plant tissue by clipping and to a lesser extent by grazing causes plants to under-compensate for tissue removal (Figures 3-4 and 3-5). The fact that exact-compensation was also a significant response particularly in grazed areas shows clearly that this community responds in a number of ways to tissue removal depending on the intensity and timing of herbage removal.

It was important to document the response of this community to the treatments by using different estimates of productivity. Because estimates of cumulative green biomass (CGB), green productivity (GP), total productivity (TP) and absolute productivity (AP) all show identical responses after herbage removal these measurements are not discussed separately. However, since estimates of absolute productivity were higher than estimates of green productivity and total productivity, the transfer of green tissue into the standing dead compartment was greater than the transfer of standing dead into the litter compartment during the 1992 and 1993 growing seasons. Thus, there was die-back during the growing season, however, most of the litter was formed during the winter. Snow cover likely compresses standing

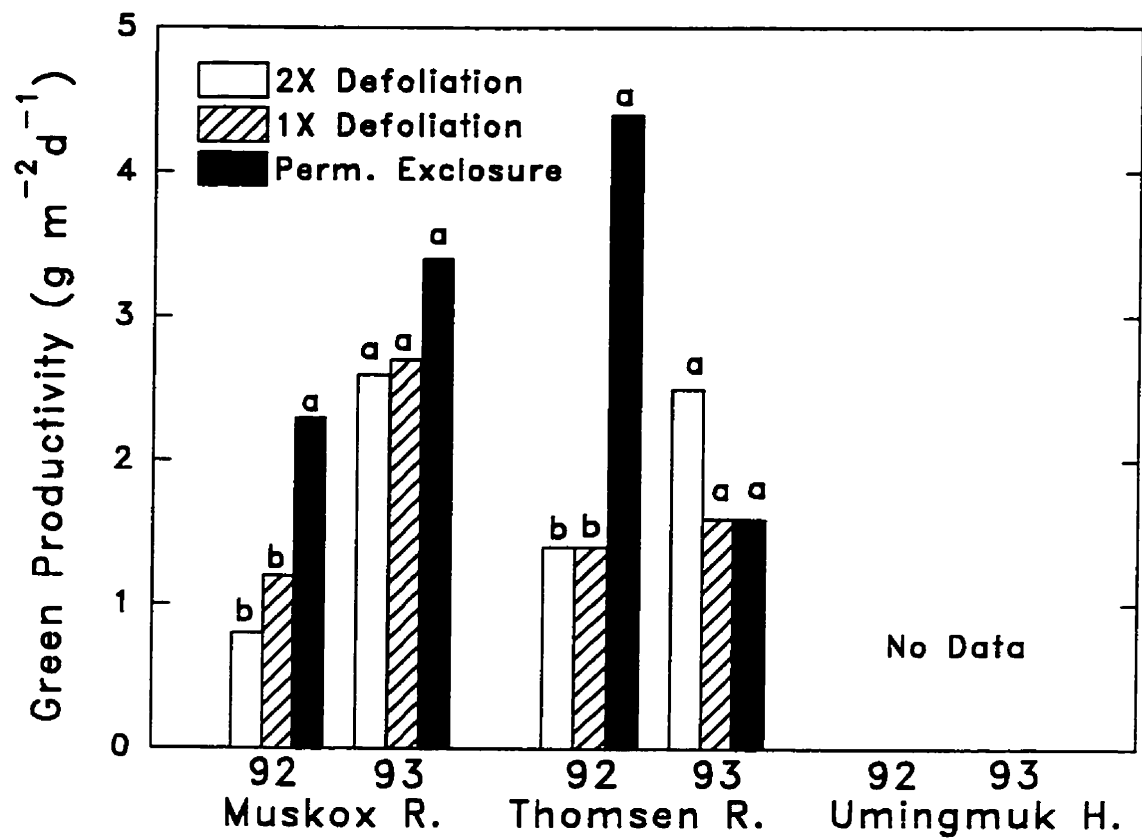


Figure 3-4. Comparison of mean green productivity estimates among treatments in 1992 and 1993 1 X 1 m microplots inside permanent enclosures. Microplots were unclipped (control), clipped twice (2X) or clipped once (1X) in 1991 and 1992 at two study sites.

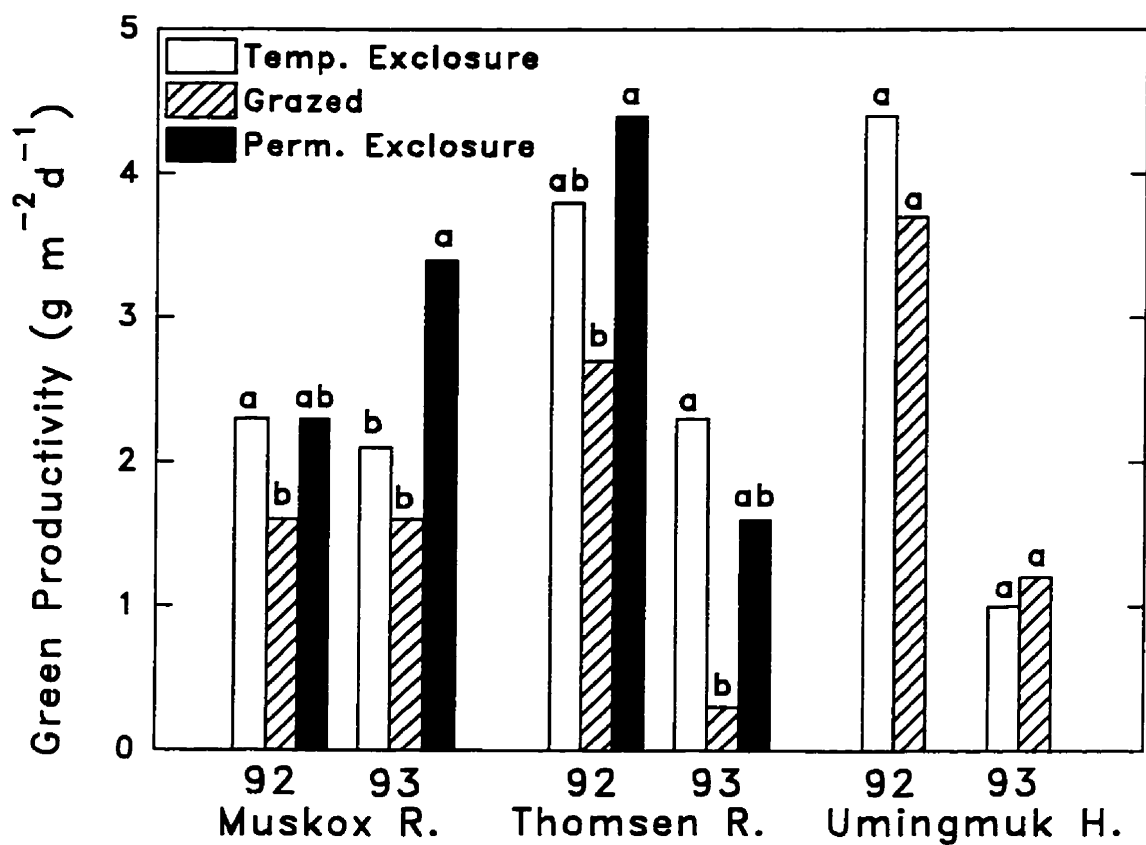


Figure 3-5. Comparison of mean green productivity estimates among treatments in 1992 and 1993 1 X 1 m microplots. Microplots were unclipped (control), temporarily protected or grazed (i.e, exposed to muskoxen). Sample sizes in text.

dead into the litter compartment. This hypothesis is consistent with the observations of other researchers. Sims and Singh (1978) found that litter dynamics responded closely to precipitation events in western North American grasslands. Snow depth also affected decay rates of litter in alpine tundra (O'Lear and Seastedt 1994).

The observation that clipping resulted in more under-compensation than grazing is consistent with the fact that clipping removed a greater proportion of tissue than grazing. Clipping was also concentrated early in the season rather than being spread through it as with grazing. Plants are often most vulnerable to grazing early in the growing season (Stoddart *et al.* 1975; Bedard *et al.* 1986). Mattheis *et al.* (1976) and Chapin (1977) also found that intensive clipping of arctic graminoids resulted in under-compensation.

Fewer cases of under-compensation in 1993 than in 1992 in permanent exclosures (Figure 3-4) suggest that clipped plants inside the exclosure were recovering in the season following severe treatments. Although growth rates decreased after clipping, the plants had the resources to recover to a large extent only one summer after the clipping treatments. A number of mechanisms could buffer the potentially negative effects of herbage

removal in this plant community (see review in McNaughton 1979a). Specifically, arctic graminoids are tolerant of herbivory by the following mechanisms: more active uptake of nutrients after defoliation (Chapin and Slack 1979; Shaver *et al.* 1986), extensive below-ground reserves (Muc 1977), resource sharing among tillers (Jonsdottir and Callaghan 1989), increased availability of nutrients from feces and urine (Henry and Svoboda 1989), and the ability of these species to grow at disturbed and undisturbed sites (Shaver and Billings 1975).

Exact-compensation was the most common response to grazing by muskoxen despite the high grazing intensities (G) reported in this study. However, because under-compensation occurred to the extent that it did, it too is a significant and perhaps a more important response. The graminoid meadow plant community showed some detrimental side-effects to grazing by muskoxen.

Although there were large differences in total standing crop among the study sites (Figure 3-3), the lack of differences in productivity among the study sites (Figures 3-4 and 3-5) suggests more green tissue overwinters at the most productive site (UH) than at less productive sites (MR and TR). This conclusion is consistent with the higher total standing crops in temporary exclosures at UH and the lower total standing

crops at MR and TR at the beginning and end of each growing season. Thus, the muskoxen benefit more from an environment that maintains large standing crops of plant tissue overwinter than from high rates of production during the growing season. This observation is consistent with the fact that the growth of these plants is largely constrained by low nutrient availability, low irradiance, low air temperature and the short growing season (Webber and Ives 1978; Chapin and Shaver 1985). Although higher NH_4 levels in the soil and favorable soil moisture conditions at UH (Chapter 4) did not boost rates of production they contributed to larger standing crops of plant tissue. Future research might be directed at describing snow conditions that insulate and maintain large forage bases over the winter.

3.4.4 Effect of clipping and grazing on below-ground standing crop of roots

Despite a few inconsistencies in the data, tissue removal by grazing and clipping had similar effects on below-ground biomass as on above-ground growth. The depression of root biomass after above-ground tissue removal suggests that these meadows have limitations in their ability to withstand grazing pressure (Figure 3-6).

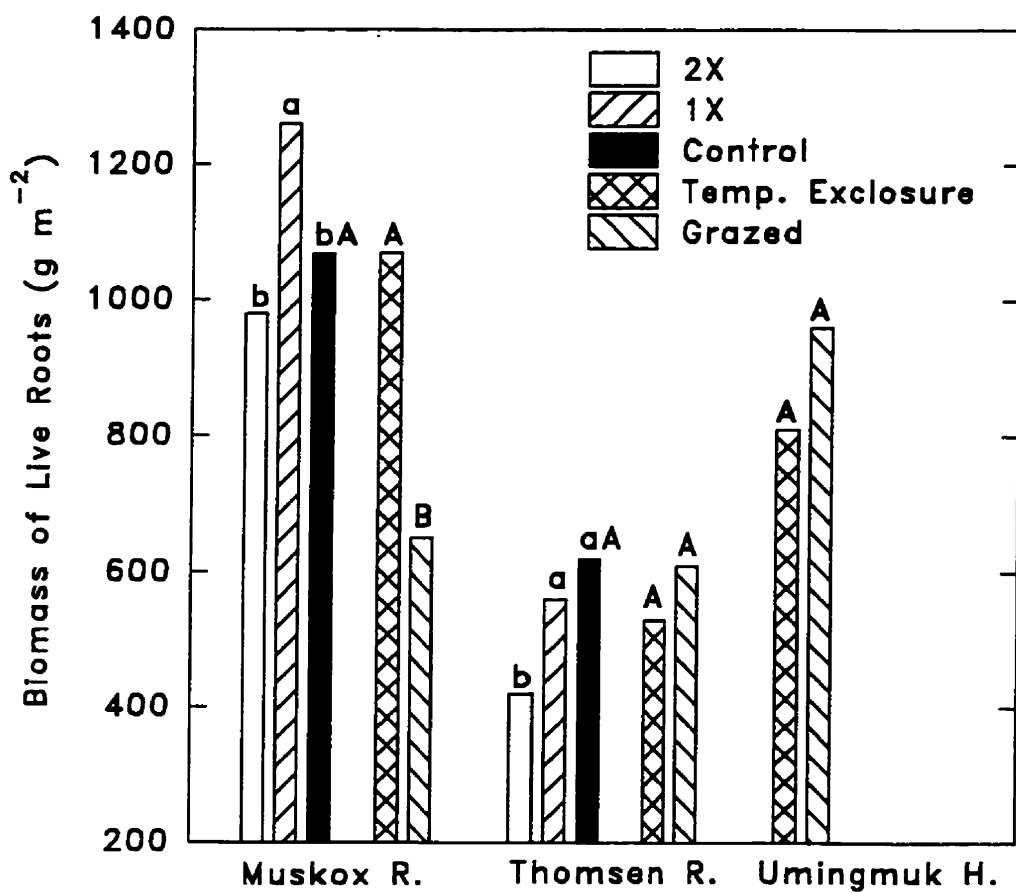


Figure 3-6. Comparison of root biomass (g m^{-2}) in clipped (2X and 1X) and unclipped (control) 1 X 1 m microplots (lower case) and in temporarily protected, grazed and control microplots (upper case) at three study sites in 1993.

The results for below-ground tissue do not support the herbivore optimization hypothesis.

There is often a time lag after tissue removal before changes in standing crop of roots (SCR) become apparent (Stoddart et al. 1975). Thus, standing crop of root data may be a more accurate reflection of long-term perturbation than total standing crop data. The higher standing crops in the 1X treatment inside the MR enclosure are not completely unexpected since clipping had little additional effect over the constraints on these plants imposed by lemming herbivory (pers. obs. 1991, 1992), a thick moss layer, poor soil nutrient conditions, and super-hygic soil (Chapter 4). It should also be pointed out that determining standing crop of roots in any study is a difficult task. There is no doubt that the inadvertent inclusion of mineral material, the subjectivity in determining which roots were live and which were dead and the problem of the time needed after perturbation before changes in standing crop of roots could be documented all contributed to the inconsistencies observed in the data. Interpretations of standing crop of root data would likely become more clear if treatment effects were imposed over many years (e.g.,

comparison of grazed and historically non-grazed meadows).

Other studies examining the effects of grazers on roots in high latitude meadows have demonstrated neutral or positive responses after perturbation. Cargill and Jefferies (1984b) showed that intensive snow goose grazing had no effect on below-ground reserves. Henry and Svoboda (1989) found that root and rhizome biomass was greater in muskox-grazed than in non-grazed meadows on Ellesmere Island, which is not entirely unexpected since nutrient-limited meadow plants should invest a large portion of their resources into organs that improve nutrient acquisition. Increases in uptake rates of nutrients have also been reported after tissue removal in arctic graminoids (Chapin and Slack 1979). Most studies from carbon-limited ranges in more temperate regions show reduced root growth after grazing (Stoddart et al. 1975). Carbon-limited plants must invest most of their resources into organs which capture light energy.

Lower root:shoot ratios in protected treatments reflect the accumulation of above-ground tissue due to the lack of herbivory or clipping. Higher root:shoot ratios at the MR enclosure than at the TR enclosure were the result of lemming herbivory and superhygric conditions at MR. Lower TSC combined with higher SCR

values at MR than the other two sites accentuated the differences observed in root:shoot ratios among the sites.

The fact that SCR values were high across the MR site suggests that these graminoids invested a large proportion of their resources into organs that take up nutrients. This site had the lowest $\text{NH}_4\text{-N}$ level of all sites (Chapter 5). Perhaps nutrient acquisition is less efficient at sites such as MR where stagnant water keeps soils above field capacity and where abundant moss acts as a nutrient sink that physically obstructs growth of graminoids. Other arctic studies have also reported high root:shoot ratios (Bliss *et al.* 1973; Muc 1977; Dennis *et al.* 1978; Cargill and Jefferies 1984a).

3.4.5 Whole-plant responses to grazing and clipping

Lower NAPP and SCR in clipped and grazed treatments in this study reflect high grazing and clipping intensities, large clipped (1 X 1 m) microplots in the clipping experiment, and a severe climate. Because the treatments cover a broad range of tissue removal, the complete absence of over-compensation in this study suggests that it is not an important ecological phenomenon on northern Banks Island. Climatic conditions

play an important role in limiting NAPP within the arctic (Edlund and Alt 1989). Northern Banks Island, in particular, is under the influence of the central arctic air mass which causes summers to be cloudy, damp and cool (Edlund and Alt 1989). The geographical features that make Truelove Lowland (Bliss 1977), Sverdrup Pass (Freedman *et al.* 1994), and Polar Bear Pass (Gray 1987) ecological oases are not present to the same degree on northern Banks Island. Instead, northern Banks Island supports a more even distribution of meadow habitat (Ferguson 1991) which reflects more subtle topographical features and fine textured soil parent material capable of supporting meadow vegetation.

In conclusion, clipping treatments, and to a lesser extent grazing by muskoxen, reduced above-ground growth and below-ground standing crop (*i.e.*, under-compensation occurs). This strongly suggests that this plant community has limits to the amount of grazing or clipping that it can withstand. Graminoid meadows on northern Banks Island were stressed due to severe environmental conditions. However, the data also show that this community showed signs of recovery one year after intense clipping treatments. Future research should be directed at determining the long-term consequences of these high grazing intensities.

4.0 HERBIVORY- AND CLIPPING-INDUCED CHANGES IN STRUCTURAL, REPRODUCTIVE AND ENVIRONMENTAL CHARACTERISTICS OF A MUSKOXEN-GRAZED GRAMINOID MEADOW PLANT COMMUNITY

4.1 Introduction

There is a clear link between changes in the physiognomy and species structure of plant communities after grazing. In tropical, temperate and sub-arctic regions grazers facilitate the creation of prostrate plant communities (Jameson 1963; Harper 1977; McNaughton 1983a; Belsky 1986b; Smith 1990) where erect growth forms are less able to withstand the effects of grazing and trampling. Grazers free resources that were formerly sequestered by competitively superior plants for use by grazing-tolerant plants (MacArthur and Wilson 1967; MacArthur 1972; Schoener 1974; Menge and Sutherland 1976; Harper 1977; Whittaker and Levin 1977; Whittaker 1979; McNaughton 1983b; Belsky 1986a; Pyke 1986). In arctic sedge meadows, however, graminoids selected by muskoxen are tolerant of disturbance and grow well on undisturbed sites (Wein and Bliss 1973, 1974; Chapin and Chapin 1980; Chapin and Shaver 1981; Fetcher and Shaver 1983). These meadows are low in species richness (Klein and Bay 1990)

and grazing tolerant forbs and graminoids simply are not present to colonize disturbed sites. In undefended (Cates and Orians 1975; Bryant and Kuropat 1980; MacLean and Jensen 1985) or grazing intolerant plants (Caldwell et al. 1981; Briske and Anderson 1990) fecundity decreases after herbivory, which in turn influences species and genotypic composition in plant communities.

There are reports of higher (Dyer 1975; Inouye 1982; Richards 1983; Paige and Whitham 1987; Henry and Svoboda 1989), lower (Roberts 1958; Dawson 1970; Hendrix 1979; Solomon 1983; Belsky 1986a; Smith 1990) and unchanged sexual reproductive outputs (Raillard 1992) after tissue removal. Physical removal of reproductive organs, reduction in litter accumulation, removal of apical meristems and depletion of plant carbon and nutrient reserves by grazers all change seed head densities (Roberts 1958; Dawson 1970; Youngner 1972; Hendrix 1979; McNaughton 1979a; Solomon 1983; Smith 1990). Vegetative reproduction (i.e., tillering) often increases after herbivory (Dyer and Bokhari 1976; McNaughton 1976; Belsky 1986b) although decreases also have been observed (Ellison 1960; Detling et al. 1980).

It is well documented that grazers affect the microclimate and soils at sites. Curtis and Partch (1950) found that grazing increased soil temperature during the

growing season and stimulated early vegetative growth. Soil water may be conserved, due to the reduction in transpiration surface after grazing (Jameson 1963). Carran et al. (1982) reported that grazers act as nutrient conduits harvesting nutrients over large areas and concentrating them into smaller areas. Other studies have reported increased soil bulk density after trampling and grazing (Stoddart et al. 1975).

This chapter specifically addresses the effects of grazing and clipping on structural, reproductive, and environmental properties of muskoxen-grazed graminoid meadows on northern Banks Island. In Chapter 3 which examined NAPP in the same muskoxen-grazed, clipped and control treatments, the herbivore-optimization hypothesis was rejected. In no case was over-compensation observed across a gradient of tissue removal that varied from 0 to 40%. Exact-compensation occurred most often, with under-compensation occurring in treatments with higher proportions of tissue removal.

Given the negative effects of tissue removal by muskoxen and clipping on NAPP it was hypothesized that muskoxen have had significant effects on other community attributes. Quantifying how these attributes respond to grazing and clipping will elucidate the interactive relationship muskoxen have with the plant community that

provides them with most of their forage (Parker and Ross 1976; Wilkinson et al. 1976; Muc 1977; Henry 1987; Oakes 1989; Raillard 1992; Henry et al. 1994a). The following were predicted: (1) Grazing by muskoxen and clipping results in a more prostrate plant community than is found under protection from grazing; (2) Species abundances do not shift after tissue removal; (3) Seed head density is lower after grazing and clipping; (4) Heavily grazed sites with abundant fecal pats show higher soil nutrient content than less-used sites; and (5) Grazed and clipped treatments have a warmer microclimate than protected treatments.

4.2 Methods

4.2.1 Experimental Design

This experiment follows the experimental design described in detail in Chapter 3. The study site, sampling methods, and schedule are the same as those described in Chapter 3. Three study sites were sampled in 1992 and 1993: Muskoxen River (MR), Thomsen River (TR) and Umingmuk Hill (UH). Umingmuk Hill was not sampled in 1991. All data were obtained using 1 X 1 m microplots at the same time biomass data were collected (four and three

times per growing season in 1992 and 1993, respectively). Species composition, soil moisture, and soil nutrient data were all collected in late August 1993 from the same microplots. Soil temperature, depth to permafrost, and litter layer thickness data were collected from the microplots in 1993. In each treatment, sample sizes for physiognomy, seed head density, soil temperature, depth to permafrost, and litter layer thickness data were as follows:

MR - 2X, 1X and control n=10

MR - Temporary protection and grazed n=20

TR - 2X, 1X and control n=10

TR - Temporary protection and grazed n=20

In 1992, temporary protection variable (n=11, Aug. 10).

UH - Temporary protection and grazed n=10

In 1992, temporary protection variable (n=7, Aug. 4&13).

4.2.2 Species abundances

The species abundances within each treatment at each study site were determined by using a point frame with five points, each 10 cm apart. Pins were lowered until

they touched a live plant or the ground (the term ground includes litter, moss or bare soil). The frame was placed at four random locations in each microplot, so 20 (4 X 5) hits were recorded per microplot resulting in a total of 200 points per treatment in permanent exclosures and 400 points per treatment outside permanent exclosures. Data from each microplot were combined and considered to be the experimental unit (i.e., microplots were replicates).

4.2.3 Plant physiognomy

Within each 1 X 1 m microplot the average height of all ramets (monocots and dicots combined) was determined. This was not a difficult task since the graminoid meadow plant community is unistratal with the exception of a few low-growing young tillers and prostrate dicots. The average ramet height (ARH) of monocots and dicots was also measured separately.

4.2.4 Seed head density

Seed head density (SHD) was also determined within each 1 X 1 m microplot by counting monocot and dicot inflorescences. If the SHD was too great to make an

accurate count the microplot was divided in half. The number of seed heads in the north half of high-density microplots was counted. In this study if a ramet was in flower it was considered to have one seed head. Thus, no more than one seed head was counted per ramet. This method avoided the subjectivity in determining what a seed head is as divisions between inflorescences can be tenuous.

4.2.5 Soil nutrients and soil moisture

Root cores were removed from microplots as described in Chapter 3. The cores were frozen immediately after extraction and kept frozen or at low temperature en route to Saskatoon, after which they were promptly dried. Root material was separated from soil as described in Chapter 3. Soil pH was measured with a Metrohm 672 Titroprocessor using standard techniques (Allen et al. 1986). Dry soil samples from grazed and control treatments (n=4) were tested for the following nutrients by the Plains Innovative Laboratory Services in Saskatoon, Saskatchewan (methods follow the nutrient):

| | |
|-----------------------------------|---|
| NH ₄ | <u>2.0 N KCl extractable</u> |
| NO ₃ , SO ₄ | <u>Extractable with 0.001 M CaCl₂</u> |
| P, K | <u>Modified kelowna method</u> |
| Fe, Mn, Cu, Zn | <u>DTPA - Extractable Fe, Mn, Cu, Zn</u> |
| Ca, Mg, Na, K | <u>Extractable cations with NH₄OAc</u> |

Soil moisture was determined by removing a soil plug from the center of each microplot (n=15 grazed, n=10 control) with a small shovel and placing it into an aluminum canister (7.5 cm diameter, 5 cm deep). Above-ground portions of plants were removed from the immediate sampling areas before extraction. Canisters were sealed with duct tape in the field and shipped to Saskatoon. Soil was weighed before and after drying for 96 h at 70 °C. Each canister was weighed separately to account for small variations in weight. Soil moisture (%SM) was calculated as:

$$\%SM = \frac{(\text{wet weight} - \text{dry weight})}{\text{dry weight}} \times 100$$

4.2.6 Microclimate and macroclimate

Soil temperature was measured at 6 and 9 cm below the surface using an Atkins thermocouple meter (Model #39658-T). A thermocouple attached to a wooden probe was

inserted at random in each microplot. Temperatures were recorded 3 min after insertion.

Depth to permafrost was measured at a random location within each microplot using an aluminum probe (ca. 5 mm diameter). The probe was inserted at a right angle to the ground surface until permafrost was reached. Thickness of the litter layer was measured using a similar probe.

Environment Canada provided temperature and precipitation data from the weather station at Mould Bay, Northwest Territories on Prince Patrick Island approximately 260 km north of the study area. Weather data from Sachs Harbour, the only other station in the area, had too many missing data points to be of any use. Heat sums were calculated by adding positive or negative noon temperatures (0 °C base) for each field season. Precipitation sums were calculated by adding rainfall amounts for each day during each field season.

4.2.7 Data analysis

All data were tested for normality using the Shiparo-Wilks W-test (SAS 1988). Variances were tested for homogeneity using the F_{\max} test (Sokal and Rohlf 1981). If the assumptions of parametric statistics were

not met, transformations (log+1 or square root+0.5) were made before testing data with one-way analysis of variance and LSD mean comparisons (Sokal and Rohlf 1981). If transformed data did not meet the assumptions of parametric statistics, the non-parametric Mann-Whitney U-test was used (Sokal and Rohlf 1981).

Seed head density in 1992 was the only parameter that did not meet the assumptions of parametric statistics after transformation. Results were very similar for the two statistical methods (i.e., parametric and non-parametric) thus for the sake of consistency only parametric test results are reported.

4.3 Results

4.3.1 Species abundances in graminoid meadows

Eriophorum triste, Carex aquatilis and Dupontia fischeri are the most common species in the graminoid meadows studied (Table 4-1). Dicots were rare at all study sites. Clipping did not affect the species composition in the exclosure at MR. However at TR Eriophorum was more abundant in 2X plots. Carex and Dupontia were less common in 2X than in 1X or control plots at TR.

Table 4-1. Comparison of 1993 species abundance estimates* (percent of total hits using a point frame) (mean) in 1 X 1m microplots (n=10) inside permanent exclosures. Microplots were unclipped (control), clipped twice (2X), or clipped once (1X) in 1992 at two study sites.

| <u>Species</u> | <u>Percent of Total Hits Using Point Frame</u> | | | |
|--------------------------|--|-----------------|-----------------|-----------------|
| | <u>2X</u> | <u>1X</u> | <u>Control</u> | <u>MS Error</u> |
| <u>Muskox River</u> | | | | |
| <u>Eriophorum triste</u> | 53 _a | 57 _a | 62 _a | 167 |
| <u>Carex aquatilis</u> | 18 _a | 11 _a | 11 _a | 81 |
| <u>Dupontia fischeri</u> | 21 _{ab} | 26 _a | 18 _b | 93 |
| Other Species | 0 _b | 1 _a | 0 _b | 1 |
| Litter | 2 _{ab} | 1 _b | 3 _a | 12 |
| Moss | 7 _a | 4 _a | 6 _a | 61 |
| Bare Ground | 0 _b | 1 _a | 0 _b | 3 |
| <u>Thomsen River</u> | | | | |
| <u>Eriophorum triste</u> | 63 _a | 54 _b | 54 _b | 138 |
| <u>Carex aquatilis</u> | 5 _b | 18 _a | 21 _a | 146 |
| <u>Dupontia fischeri</u> | 3 _b | 11 _a | 10 _a | 41 |
| Other Species | 10 _a | 6 _a | 6 _a | 46 |
| Standing Dead | 17 _a | 10 _b | 11 _b | 62 |
| Litter | 3 _a | 2 _a | 0 _b | 8 |
| Bare Ground | 0 _a | 0 _a | 0 _a | 0 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$
 200 points gathered for each treatment, 20 per microplot

Eriophorum was more abundant in control plots than in grazed plots at MR, however at TR, Eriophorum was more common in grazed plots (Table 4-2). Carex was less abundant in grazed than in control plots at TR. Eriophorum was more common at TR and UH whereas Carex and Dupontia favored MR.

4.3.2 Plant physiognomy

Clipping in 1991 and 1992 reduced the average ramet height (ARH) of plants in the exclosures at MR and TR in 1993 (Table 4-3). Similarly, grazing reduced the height of vegetation compared to temporary protection at all three study sites (Table 4-4). Plants in control plots attained greater heights than plants in adjacent grazed and temporarily protected areas. Umingmuk Hill had the highest average ramet height of all three study sites.

Dicots are rare and grow very low to the ground in these graminoid meadows (Tables 4-5 and 4-6).

4.3.3 Seed head density

Clipping reduced seed head density (SHD) inside the permanent exclosure at MR and TR in 1991 (Table 4-3).

Table 4-2. Comparison of 1993 mean species abundance estimates* (percent of total hits using a point frame) in 1 X 1m microplots in unclipped (control) (n=10) and grazed (n=20) treatments at 2 study sites (first subscript). Second subscript designates among site comparisons.

| <u>Species</u> | <u>Percent of Total Hits Using Point Frame</u> | | |
|--------------------------|--|---------------------|-----------------|
| | <u>Control</u> | <u>Grazed</u> | <u>MS Error</u> |
| <u>Muskox River</u> | | | |
| <u>Eriophorum triste</u> | 62 _a | 45 _{b[b]} | 199 |
| <u>Carex aquatilis</u> | 11 _a | 11 _{a[a]} | 108 |
| <u>Dupontia fischeri</u> | 18 _a | 23 _{a[a]} | 151 |
| Other Species | 0 _a | 4 _{a[a]} | 44 |
| Litter | 3 _b | 14 _{a[a]} | 70 |
| Moss | 6 _a | 3 _{a[a]} | 33 |
| Bare Ground | 0 _a | 0 _{a[a]} | 0 |
| <u>Thomsen River</u> | | | |
| <u>Eriophorum triste</u> | 54 _b | 72 _{a[a]} | 227 |
| <u>Carex aquatilis</u> | 21 _a | 4 _{b[b]} | 127 |
| <u>Dupontia fischeri</u> | 10 _a | 7 _{a[c]} | 73 |
| Other Species | 6 _a | 7 _{a[a]} | 41 |
| Litter | 11 _a | 8 _{a[a]} | 67 |
| Moss | 0 _a | 2 _{a[ab]} | 7 |
| Bare Ground | 0 _a | 0 _{a[a]} | 1 |
| <u>Umingmuk Hill</u> | | | |
| <u>Eriophorum triste</u> | NA | 70 _{NA[a]} | NA |
| <u>Carex aquatilis</u> | NA | 9 _{NA[a]} | NA |
| <u>Dupontia fischeri</u> | NA | 12 _{NA[b]} | NA |
| Other Species | NA | 6 _{NA[a]} | NA |
| Litter | NA | 3 _{NA[b]} | NA |
| Moss | NA | 1 _{NA[b]} | NA |
| Bare Ground | NA | 0 _{NA[a]} | NA |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$
 200 points gathered for all control plus grazed at UH,
 20 per microplot
 400 points gathered for MR and TR grazed treatments, 20
 per microplot

Table 4-3. Comparison of mean 1993 average ramet height* (cm) (ARH) and 1991, 1992 and 1993 seed head density (# m⁻²) (SHD) estimates among treatments in 1 X 1m microplots (n=10) inside permanent exclosures. Microplots were unclipped (control), clipped twice (2X), or clipped once (1X) in 1991 and 1992 at two study sites.

| <u>Date</u> | <u>Parameter</u> | <u>2X</u> | <u>1X</u> | <u>Cont</u> | <u>MS Err</u> |
|----------------------|------------------|-----------------|------------------|------------------|---------------|
| <u>Muskox River</u> | | | | | |
| June 27/93 | ARH | 7 _b | 7 _b | 8 _a | 1 |
| July 16/93 | ARH | 11 _b | 12 _{ab} | 13 _a | 5 |
| July 29/93 | ARH | 11 _b | 12 _{ab} | 13 _a | 2 |
| July 15/91 | SHD | NA | 0 _a | 0 _a | 0 |
| July 24/91 | SHD | NA | 0 _b | 101 _a | 4777 |
| 1992 season | SHD | 0 _a | 0 _a | 0 _a | 0 |
| June 27/93 | SHD | 0 _a | 0 _a | 0 _a | 0 |
| July 16/93 | SHD | 16 _a | 27 _a | 20 _a | 242 |
| July 29/93 | SHD | 13 _b | 34 _a | 20 _{ab} | 343 |
| <u>Thomsen River</u> | | | | | |
| July 4/93 | ARH | 7 _c | 9 _b | 10 _a | 1 |
| July 21/93 | ARH | 9 _c | 11 _b | 13 _a | 2 |
| Aug. 3/93 | ARH | 7 _a | 8 _a | 8 _a | 4 |
| July 4/91 | SHD | 0 _a | 0 _a | 0 _a | 0 |
| July 20/91 | SHD | 5 _b | 9 _b | 18 _a | 57 |
| July 27/91 | SHD | 2 _b | 28 _a | 34 _a | 475 |
| July 8/92 | SHD | 1 _a | 1 _a | 2 _a | 5 |
| July 22/92 | SHD | 0 _b | 3 _a | 4 _a | 7 |
| July 31/92 | SHD | 0 _b | 22 _a | 0 _b | 497 |
| Aug. 10/92 | SHD | 2 _b | 10 _a | 8 _{ab} | 150 |
| July 4/93 | SHD | 0 _b | 5 _a | 2 _{ab} | 18 |
| July 21/93 | SHD | 6 _b | 13 _a | 5 _b | 37 |
| Aug. 3/93 | SHD | 9 _{ab} | 14 _a | 6 _b | 58 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$. Estimates are average height of all live monocot and dicot ramets inside microplots.

Table 4-4. Comparison of mean 1993 average ramet height (cm) (ARH) and 1991, 1992 and 1993 seed head density (# m⁻²) (SHD) estimates among treatments in 1 X 1m microplots. Microplots were unclipped (control) (n=5), temporarily protected (since June 25) (n=20) or grazed (i.e., exposed to muskoxen) (n=20).*

| Date | Parameter | T.Excl | Grz | Cont | MS Error |
|----------------------|-----------|------------------|------------------|------------------|----------|
| <u>Muskox River</u> | | | | | |
| June 30/93 | ARH | 8 _a | 8 _a | 8 _a | 1 |
| July 18/93 | ARH | 9 _b | 9 _b | 13 _a | 4 |
| July 30/93 | ARH | 10 _b | 8 _c | 13 _a | 3 |
| July 4/92 | SHD | 0 _a | 0 _a | 0 _a | 0 |
| July 18/92 | SHD | 1 _{ab} | 2 _a | 0 _b | 8 |
| July 28/92 | SHD | 11 _a | 8 _a | 0 _b | 224 |
| Aug. 6/92 | SHD | 6 _a | 6 _a | 0 _b | 85 |
| June 30/93 | SHD | 38 _a | 17 _a | 0 _b | 914 |
| July 18/93 | SHD | 79 _a | 33 _b | 20 _b | 5881 |
| July 30/93 | SHD | 56 _a | 51 _a | 20 _b | 3074 |
| <u>Thomsen River</u> | | | | | |
| July 7/93 | ARH | 10 _a | 9 _b | 10 _{ab} | 3 |
| July 22/93 | ARH | 11 _b | 10 _c | 13 _a | 3 |
| Aug. 3/93 | ARH | 10 _a | 7 _b | 8 _b | 7 |
| July 10/92 | SHD | 4 _a | 2 _a | 2 _a | 41 |
| July 22/92 | SHD | 16 _a | 5 _a | 4 _a | 445 |
| July 31/92 | SHD | 12 _a | 9 _a | 0 _a | 188 |
| Aug. 10/92 | SHD | 16 _a | 6 _b | 8 _{ab} | 216 |
| July 7/93 | SHD | 70 _a | 67 _a | 2 _b | 6953 |
| July 22/93 | SHD | 109 _a | 71 _b | 5 _c | 3037 |
| Aug. 3/93 | SHD | 118 _a | 81 _a | 6 _b | 8090 |
| <u>Umingmuk Hill</u> | | | | | |
| July 13/93 | ARH | 16 _a | 12 _b | NA | 10 |
| July 26/93 | ARH | 16 _a | 13 _b | NA | 12 |
| Aug. 7/93 | ARH | 17 _a | 12 _b | NA | 12 |
| July 14/92 | SHD | 0 _a | 2 _a | NA | 5 |
| July 25/92 | SHD | 10 _a | 3 _a | NA | 248 |
| Aug. 4/92 | SHD | 10 _a | 27 _a | NA | 608 |
| Aug. 13/92 | SHD | 21 _a | 22 _a | NA | 1635 |
| July 13/93 | SHD | 146 _a | 81 _b | NA | 3205 |
| July 26/93 | SHD | 228 _a | 108 _b | NA | 15279 |
| Aug. 7/93 | SHD | 200 _a | 103 _b | NA | 13308 |

* Means with the same subscript within rows are not significantly different at P<0.10. Estimates are average height of all live monocot and dicot ramets inside microplots. In 1992: n=18 on Aug. 1, n=11 on Aug. 10 at TR T.Excl. In 1992: n=8 first two dates, n=7 last dates in T.Excl. at UH.

Table 4-5. Comparison of mean (\pm SE_x) height estimates⁺ (cm) of monocot and dicot ramets in control microplots (1 X 1m) (n=10) at two study sites in 1992.

| <u>Date</u> | <u>Average Ramet Height</u> | |
|----------------------|-----------------------------|--------------------------|
| | <u>Monocot</u> | <u>Dicot</u> |
| <u>Muskox River</u> | | |
| July 4 | 7 \pm 0.3 | NA |
| July 18 | 9 \pm 0.5 | NA |
| July 27 | 10 \pm 0.4 | NA |
| Aug. 5 | 10 \pm 0.3 | NA |
| <u>Thomsen River</u> | | |
| July 8 | 8 \pm 0.3 _a | 7 \pm 0.6 _a |
| July 22 | 13 \pm 0.5 _a | 9 \pm 0.6 _b |
| July 31 | 11 \pm 0.3 _a | 8 \pm 0.6 _b |
| Aug. 10 | 11 \pm 0.6 _a | 8 \pm 0.9 _b |

NA = denotes when no dicots were present in sample plots

⁺ Means with the same subscripts within rows were not significantly different at $P \leq 0.10$

Table 4-6. Comparison of mean (\pm SE_x) height estimates⁺ (cm) of monocot and dicot ramets in grazed microplots (1 x 1m) at three study sites in 1992.

| <u>Average Ramet Height</u> | | |
|-----------------------------|---------------------------|--------------------------|
| <u>Date</u> | <u>Monocot</u> | <u>Dicot</u> |
| <u>Muskox River</u> | | |
| July 5 | 6 \pm 0.3 _a | 3 \pm 0.0 _b |
| July 19 | 7 \pm 0.3 _a | 4 \pm 0.7 _b |
| July 28 | 8 \pm 0.3 _a | 4 \pm 1.2 _b |
| Aug. 7 | 8 \pm 0.2 _a | 1 \pm 0.0 _b |
| <u>Thomsen River</u> | | |
| July 12 | 10 \pm 0.3 _a | 5 \pm 0.4 _b |
| July 23 | 11 \pm 0.6 _a | 7 \pm 0.5 _b |
| Aug. 2 | 10 \pm 0.3 _a | 5 \pm 1.2 _b |
| Aug. 11 | 9 \pm 0.5 _a | 4 \pm 0.5 _b |
| <u>Umingmuk Hill</u> | | |
| July 15 | 11 \pm 0.4 _a | 4 \pm 0.6 _b |
| July 25 | 11 \pm 0.7 _a | 5 \pm 0.6 _b |
| Aug. 4 | 10 \pm 0.7 _a | 5 \pm 0.9 _b |
| Aug. 13 | 10 \pm 0.9 _a | 4 \pm 0.9 _b |

⁺ Means with the same subscripts within rows are not significantly different at $P \leq 0.10$
n=20 at MR, n=19 at TR, n=10 at UH

However, at TR in 1992 and 1993 densities were lowest in 2X and control plots. Clipping had no effect on SHD at MR in 1992 and 1993, however late in 1993 2X plots had reduced SHD.

At MR, controls had consistently low SHD in 1992 and 1993 compared to temporarily protected and grazed plots (Table 4-4). In 1993 at TR, controls had reduced SHD compared to adjacent grazed and temporarily protected plots. Temporarily protecting plots at MR and TR increased SHD in mid-July 1993 when grazed plots had lower densities at both sites. In August 1992 grazing also lowered SHD at TR, however, no other differences were measured in 1992. Grazing reduced SHD at UH in 1993, however in 1992 muskoxen had no effect on seed head production. The most productive year for seed head production was 1993. Umingmuk Hill had the highest SHD's of all three sites in 1993.

4.3.4 Soil nutrients and soil moisture at the study sites

Temporarily protected, grazed and permanently protected treatments had homogeneous soil NH_4 levels within study sites, however, permanent protection at MR decreased soil NH_4 concentrations (Table 4-7). Umingmuk

Table 4-7. Comparison of NH_4 soil nutrient data* (mean) (n=4) ($\mu\text{g/g}$) from temporarily protected, grazed and permanently protected 1 X 1 m microplots at three study sites in 1993.

| Study Site | NH_4 Content in Soil | | | MS Error |
|---------------|-------------------------------|--------------------|--------------------|----------|
| | T.Excl. | Grazed | Control | |
| Muskox River | 19.05 _a | 17.65 _a | 11.75 _b | 20.4 |
| Thomsen River | 22.70 _a | 29.88 _a | 33.30 _a | 106.0 |
| Uminomuk Hill | 36.70 _a | 43.50 _a | NA | 281.0 |

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

Table 4-8. Comparison of soil nutrient data* (mean) (n=4) from areas exposed to muskoxen at three study sites in 1993.

| Soil Nutrient | MR | TR | UH | MS Error |
|-----------------------------------|--------------------|--------------------|--------------------|----------|
| pH | 5.7 _a | 5.6 _a | 5.3 _a | 0 |
| NH_4 ($\mu\text{g/g}$) | 17.7 _b | 29.9 _{ab} | 43.5 _a | 164 |
| NO_3 ($\mu\text{g/g}$) | 0.3 _b | 0.3 _b | 0.5 _a | 0 |
| P ($\mu\text{g/g}$) | 1.9 _a | 2.0 _a | 0.5 _b | 1 |
| K ($\mu\text{g/g}$) | 46.1 _a | 33.6 _a | 48.6 _a | 233 |
| SO_4 ($\mu\text{g/g}$) | 59.6 _a | 25.7 _a | 57.3 _a | 1092 |
| Cu ($\mu\text{g/g}$) | 3.4 _a | 1.8 _b | 1.1 _c | 0 |
| Fe ($\mu\text{g/g}$) | 318.5 _a | 342.0 _a | 419.5 _a | 12365 |
| Zn ($\mu\text{g/g}$) | 7.5 _a | 15.6 _a | 13.1 _a | 89 |
| Mn ($\mu\text{g/g}$) | 87.3 _a | 153.5 _a | 173.7 _a | 8607 |
| Ca (meq/100g) | 17.2 _b | 22.0 _a | 13.8 _b | 8 |
| Mg (meq/100g) | 10.1 _a | 10.2 _a | 5.8 _b | 1 |
| Na (meq/100g) | 0.5 _a | 0.2 _b | 0.4 _{ab} | 0 |
| K (meq/100g) | 1.4 _a | 1.1 _a | 1.3 _a | 0 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$

Hill soils had much more NH_4 than soils at MR, however P was least abundant in UH soils (Table 4-8). Thomsen River had moderate NH_4 levels. Potassium, SO_4 (high at all sites), Fe (high at all sites), Zn, Mn, and Mg were equally common at all three sites. Soils at TR were lower in Cu and Na but soils at UH were lowest in Cu, Ca, and Mg.

Soil moisture levels were high at all three study sites with MR being the most hygric (Table 4-9). The permanent exclosure at TR was more moist than the adjacent grazed area.

4.3.5 The effect of clipping and grazing on microclimate

Soil temperature at a 6-cm depth within the graminoid meadow plant community was low throughout the growing season (Table 4-10 and 4-11). At no time did soil temperature exceed 10 °C. There was no clear pattern in the response of soil temperature to clipping and grazing.

Clipping and grazing did not affect the depth of thaw in soils during this study (Tables 4-10 and 4-11). Depth to permafrost was similar among treatments in the exclosure at MR, and varied slightly at TR. Depth to permafrost was similar among grazed and temporarily protected areas. Control plots did not thaw to depths as

Table 4-9. Comparison of mean soil moisture (% O.D.W.) in ungrazed controls (n=10) and in microplots exposed to muskoxen (n=15) (first subscript) and among study sites in grazed microplots (second subscript) (n=10 at UH) on August 20 1993.*

| Study Site | Mean Soil Moisture | | MS Error |
|---------------|--------------------|-----------------------|----------|
| | Control | Grazed | |
| Muskox River | 381 _a | 293 _a (A) | 44892 |
| Thomsen River | 220 _a | 114 _b (B) | 5459 |
| Umingmuk Hill | NA | 118 _{na} (B) | NA |

* Means with the same subscript are not significantly different at $P \leq 0.10$. Subscripts for among site comparisons are in parentheses.

Table 4-10. Comparison of mean 1993 soil temperature (6cm depth, ST6), depth to permafrost (DP) (cm) and thickness of litter layer (LL) (cm) estimates among treatments in 1 x 1m microplots (n=10) inside permanent exclosures. Microplots were unclipped (control), clipped twice (2X), or clipped once (1X) in 1991 and 1992 at two study sites.

| <u>Date</u> | <u>Parameter</u> | <u>2X</u> | <u>1X</u> | <u>Cont</u> | <u>MS Error</u> |
|----------------------|------------------|-------------------|------------------|-------------------|-----------------|
| <u>Muskox River</u> | | | | | |
| June 27/93 | ST6 | 8.2 _{ab} | 8.9 _a | 7.7 _b | 1.4 |
| July 16/93 | ST6 | 5.7 _a | 6.6 _a | 3.3 _b | 2.5 |
| July 29/93 | ST6 | 1.3 _b | 2.8 _a | 1.4 _b | 0.5 |
| June 27/93 | DP | 21 _b | 22 _{ab} | 23 _a | 2 |
| July 16/93 | DP | 31 _a | 32 _a | 31 _a | 16 |
| July 29/93 | DP | 31 _a | 32 _a | 33 _a | 26 |
| June 27/93 | LL | 1 _a | 1 _a | 1 _a | 1 |
| July 16/93 | LL | 1 _a | 0 _a | 1 _a | 0 |
| July 29/93 | LL | 1 _a | 0 _a | 0 _a | 0 |
| <u>Thomsen River</u> | | | | | |
| July 4/93 | ST6 | 4.0 _b | 5.9 _a | 5.1 _a | 1.5 |
| July 21/93 | ST6 | 2.8 _b | 4.3 _a | 3.2 _b | 0.6 |
| Aug. 3/93 | ST6 | 2.4 _a | 1.4 _b | -0.1 _c | 0.5 |
| July 4/93 | DP | 21 _b | 25 _a | 23 _{ab} | 14 |
| July 21/93 | DP | 28 _a | 31 _a | 29 _a | 21 |
| Aug. 3/93 | DP | 33 _b | 36 _a | 35 _{ab} | 15 |
| July 4/93 | LL | 4 _b | 3 _b | 8 _a | 2 |
| July 21/93 | LL | 2 _b | 2 _b | 5 _a | 2 |
| Aug. 3/93 | LL | 1 _b | 1 _b | 3 _a | 1 |

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

Table 4-11. Comparison of mean 1993 soil temperature (6cm depth, ST6), depth to permafrost (DP) (cm) and thickness of litter layer (LL) (cm) estimates among treatments in 1 X 1m microplots. Microplots were unclipped (control) (n=5), temporarily protected (since June 25, 1993) (n=20) or grazed (i.e., exposed to muskoxen) (n=20).*

| <u>Date</u> | <u>Parameter</u> | <u>T.Excl</u> | <u>Grz</u> | <u>Control</u> | <u>MS Error</u> |
|----------------------|------------------|-------------------|-------------------|-------------------|-----------------|
| <u>Muskox River</u> | | | | | |
| June 30/93 | ST6 | 9.3 _a | 7.7 _b | 7.7 _b | 2.0 |
| July 18/93 | ST6 | 3.7 _a | 4.2 _a | 3.3 _a | 2.2 |
| July 30/93 | ST6 | 2.9 _a | 3.3 _a | 1.4 _b | 0.9 |
| June 30/93 | DP | 26 _a | 24 _b | 23 _b | 8 |
| July 18/93 | DP | 33 _a | 31 _a | 31 _a | 21 |
| July 30/93 | DP | 36 _a | 35 _{ab} | 33 _b | 18 |
| June 30/93 | LL | 2 _a | 2 _a | 1 _a | 1 |
| July 18/93 | LL | 1 _a | 1 _a | 1 _a | 1 |
| July 30/93 | LL | 1 _a | 1 _a | 0 _b | 0 |
| <u>Thomsen River</u> | | | | | |
| July 7/93 | ST6 | 5.7 _{ab} | 5.7 _a | 5.1 _b | 1.0 |
| July 22/93 | ST6 | 7.2 _a | 6.9 _a | 3.2 _b | 1.3 |
| Aug. 3/93 | ST6 | 0.0 _b | 2.8 _a | -0.1 _b | 1.0 |
| July 7/93 | DP | 34 _a | 32 _a | 23 _b | 25 |
| July 22/93 | DP | 35 _a | 36 _a | 29 _b | 23 |
| Aug. 3/93 | DP | 40 _a | 37 _b | 35 _b | 32 |
| July 7/93 | LL | 2 _b | 2 _b | 8 _a | 2 |
| July 22/93 | LL | 1 _c | 1 _b | 5 _a | 1 |
| Aug. 3/93 | LL | 1 _c | 1 _b | 3 _a | 1 |
| <u>Umingmuk Hill</u> | | | | | |
| July 13/93 | ST6 | 3.9 _b | 5.1 _a | NA | 0.7 |
| July 26/93 | ST6 | 3.5 _a | 2.2 _b | NA | 0.3 |
| Aug. 7/93 | ST6 | 0.3 _a | -0.8 _b | NA | 0.2 |
| July 13/93 | DP | 46 _a | 41 _b | NA | 18 |
| July 26/93 | DP | 44 _a | 41 _a | NA | 47 |
| Aug. 7/93 | DP | 46 _a | 45 _a | NA | 19 |
| July 13/93 | LL | 1 _a | 1 _a | NA | 1 |
| July 26/93 | LL | 0 _b | 1 _a | NA | 1 |
| Aug. 7/93 | LL | 0 _a | 0 _a | NA | 0 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$.
n=10 at Umingmuk Hill

great as plots outside the permanent exclosure, however there was a lack of a similar trend after clipping inside permanent exclosures. Umingmuk Hill soils thawed to the greatest depth while TR and MR ranked second and third, respectively.

Clipping inside exclosures did not decrease the thickness of the litter layer at MR, however at TR there was a significant reduction (Tables 4-10 and 4-11). Muskoxen did not reduce the thickness of the litter layer in one growing season.

4.4 Discussion

4.4.1 Clipping and grazing effects on physiognomy

Clipping and grazing created a low-growing plant community (Figure 4-1). This is consistent with the results in Chapter 3 which reported that both clipping and grazing removed up to 40% of plant tissue. Several studies have shown similar findings (Jameson 1963; Harper 1977; McNaughton 1983a; Belsky 1986b).

The greater average ramet heights (ARH) observed at UH are the result of higher soil NH_4 levels, a favorable soil moisture regime, and a constant supply of fresh water. A 15% slope at UH results in a steady flow of

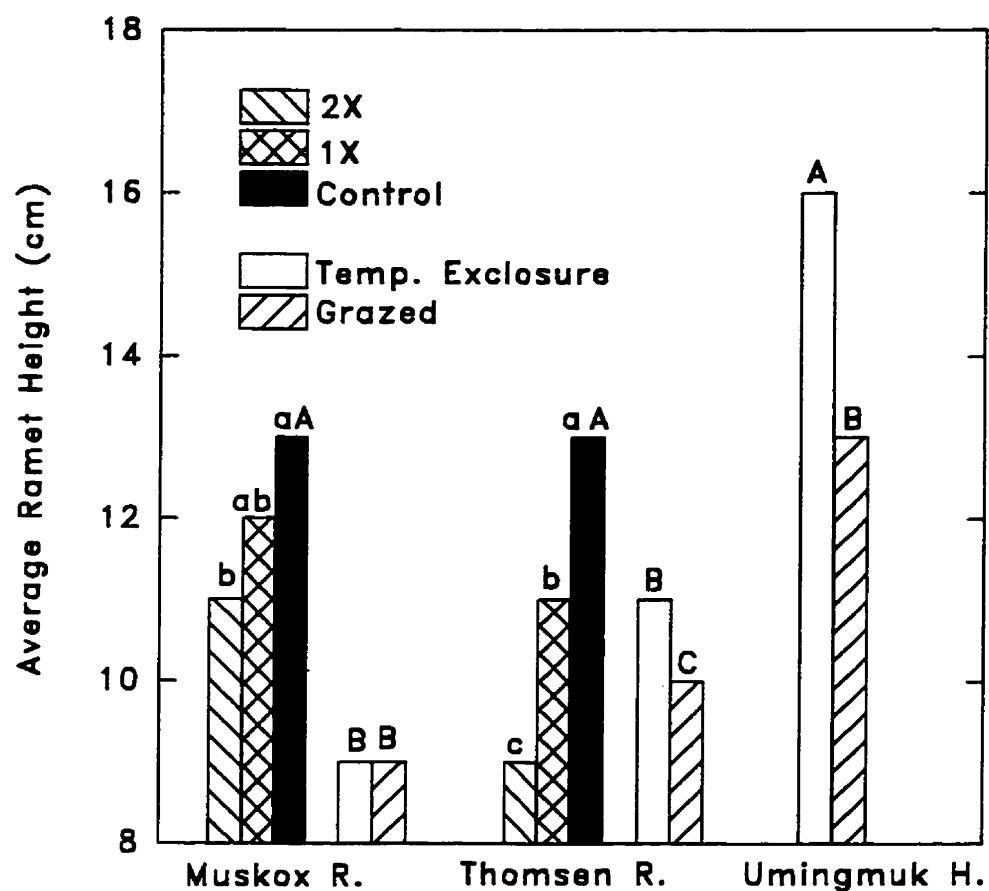


Figure 4-1. Average ramet height (cm) in clipped (2X and 1X) and unclipped (control) 1 X 1 m microplots (lower case) and in temporarily protected, grazed and control microplots (upper case) in mid-July 1993.

water from a large snowbank throughout the summer. These environmental factors affected the vertical structure (height) and the absolute quantity of vegetation available to muskoxen. Total standing crop (TSC) was also much higher at UH than the other two sites during the entire study (Chapter 3). Plant community physiognomy of graminoid meadows is a reflection both of environmental factors, and of grazing and clipping.

Grazing and clipping treatments were significant enough to elicit measurable changes in physiognomy within the graminoid meadow plant community. Thus, the original hypothesis that grazing and clipping result in a more prostrate plant community than protection is accepted. Changes in physiognomy were related to removal of plant tissue by muskoxen and clipping, not to shifts in species composition.

4.4.2 Changes in species abundances after grazing and clipping

Species already present shifted in abundance slightly after grazing or clipping. Other studies conducted in areas where a seed source of prostrate forbs and other invading plants is present report shifts in species composition after grazing or clipping (Helle and

Aspi 1983; McNaughton 1984, 1985; Facelli et al. 1989; Gibson 1989; Noy Meir et al. 1989). The limited species diversity and small number of safe sites for invading plants (i.e., no bare ground present) in graminoid meadows on Banks Island makes a shift in species composition unlikely. Muskoxen and clipping freed resources for a grazing-tolerant species, Eriophorum triste, that was already present in undisturbed meadows. Higher abundances of Eriophorum triste in clipped and grazed areas compared to less used areas (Figure 4-2) can be explained by this species' tolerance of disturbance. Other studies also demonstrate that species within the genus Eriophorum, including Eriophorum triste are tolerant of disturbance (Wein and Bliss 1973, 1974; Chapin and Shaver 1981; Fetcher and Shaver 1983). Tissue removal has been reported to alter inter-specific competitive interactions in numerous other studies (MacArthur and Wilson 1967; MacArthur 1972; Schoener 1974; Menge and Sutherland 1976; Harper 1977; Whittaker and Levin 1977; Whittaker 1979; McNaughton 1983b; Belsky 1986a; Pyke 1986). Increased abundance after grazing reflects greater resource acquisition by the most abundant, grazing-tolerant species.

As predicted, species presence and absence were similar among the different treatments. This is

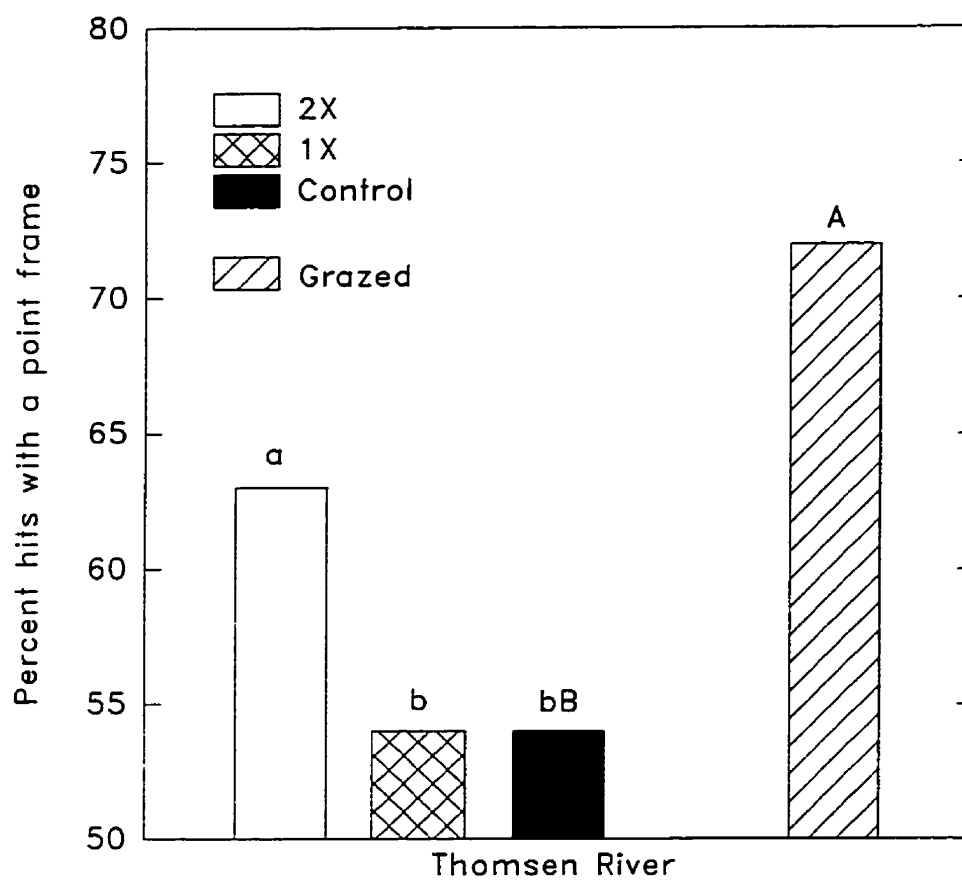


Figure 4-2. Abundance of *Eriophorum triste* in clipped (2X and 1X) and unclipped (control) 1 X 1 m microplots (lower case) and in grazed and control microplots (upper case) at Thomsen River in 1993.

consistent with the observations of Shaver and Billings (1975) and Fetcher and Shaver (1983) who found that arctic plant species have the ability to grow in disturbed and undisturbed habitats. Thus the ability of Eriophorum triste to occupy a wide niche breadth (i.e., in this case grazed/clipped and ungrazed/unclipped sites) compensates for low species richness in the meadows. The ability to adapt also provides these species with the option of specializing if interspecific competition is strong (Shaver and Cutler 1979; Chapin and Shaver 1985).

4.4.3 Changes in seed head density after grazing or clipping

The reduced seed head densities (SHD) in grazed areas compared to temporarily protected treatments (Figure 4-3) suggest that muskoxen significantly influence the sexual reproductive output of plants within the graminoid meadow plant community in the short-term. The lack of differences in the MR enclosure was predictable because of the heavy lemming herbivory that took place there during the winter of 1991-92. That is, the additional effect of clipping inside the MR enclosure was minimal compared to the effects of lemming herbivory and water-saturated soil in limiting the sexual

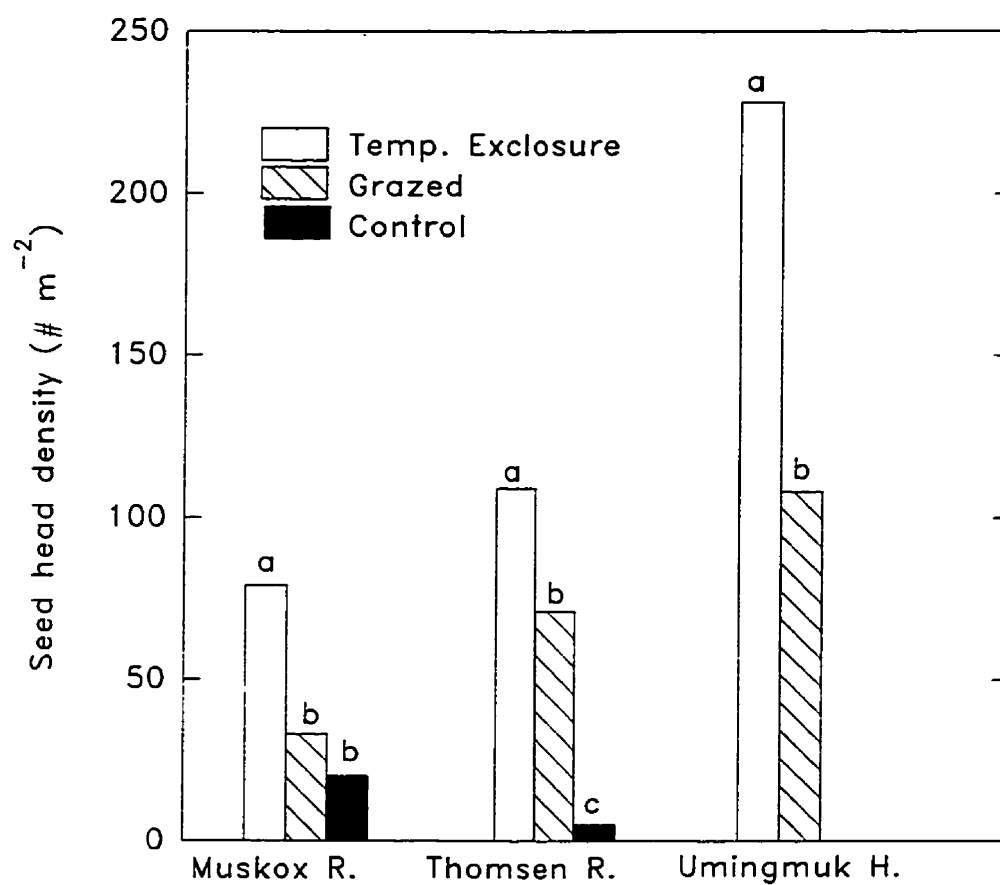


Figure 4-3. Seed head density in temporarily protected, grazed and control treatments in mid/late July 1993 at three study sites.

reproductive output of plants. Higher SHD inside the 1X treatment than in control and 2X treatments at the TR exclosure reflect the intensity of tissue removal within the 2X treatment and the inhibitory effects of litter accumulation on seed head production in the control treatment.

It was not clear why SHD was lower in intensely grazed, clipped or in undisturbed treatments where litter accumulated. Some possible explanations include physical removal of reproductive organs and/or the depletion of plant carbon and nutrient reserves (Roberts 1958; Dawson 1970; Hendrix 1979; Solomon 1983; Belsky 1986b). Accumulation of litter in undisturbed treatments has been reported to affect reproductive output in other studies (Curtis and Partch 1950; Weaver and Rowland 1952). Future research should examine the effects of lower light levels and the impediment of growing through a thick litter layer in lowering seed head density.

Higher SHD in 1993 can be explained by the fact that the 1993 growing season was the warmest of all three growing seasons during the course of this study (Figure 4-4). Although 1993 was also the driest summer (Figure 4-5), this did not result in drier soil (pers. obs. 1991-93). Melting permafrost in 1993 kept soils extremely moist throughout the summer. Other studies have reported

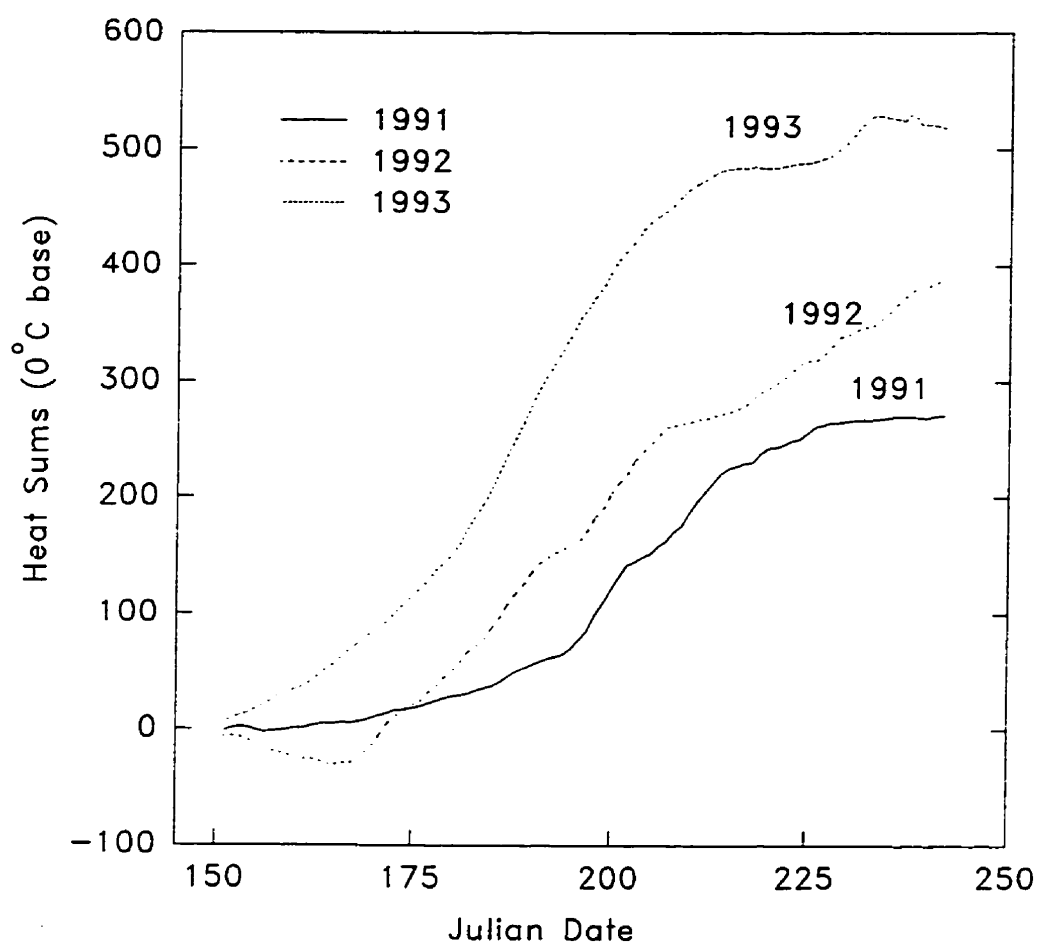


Figure 4-4. Heat sums for the 1991, 1992 and 1993 growing seasons.

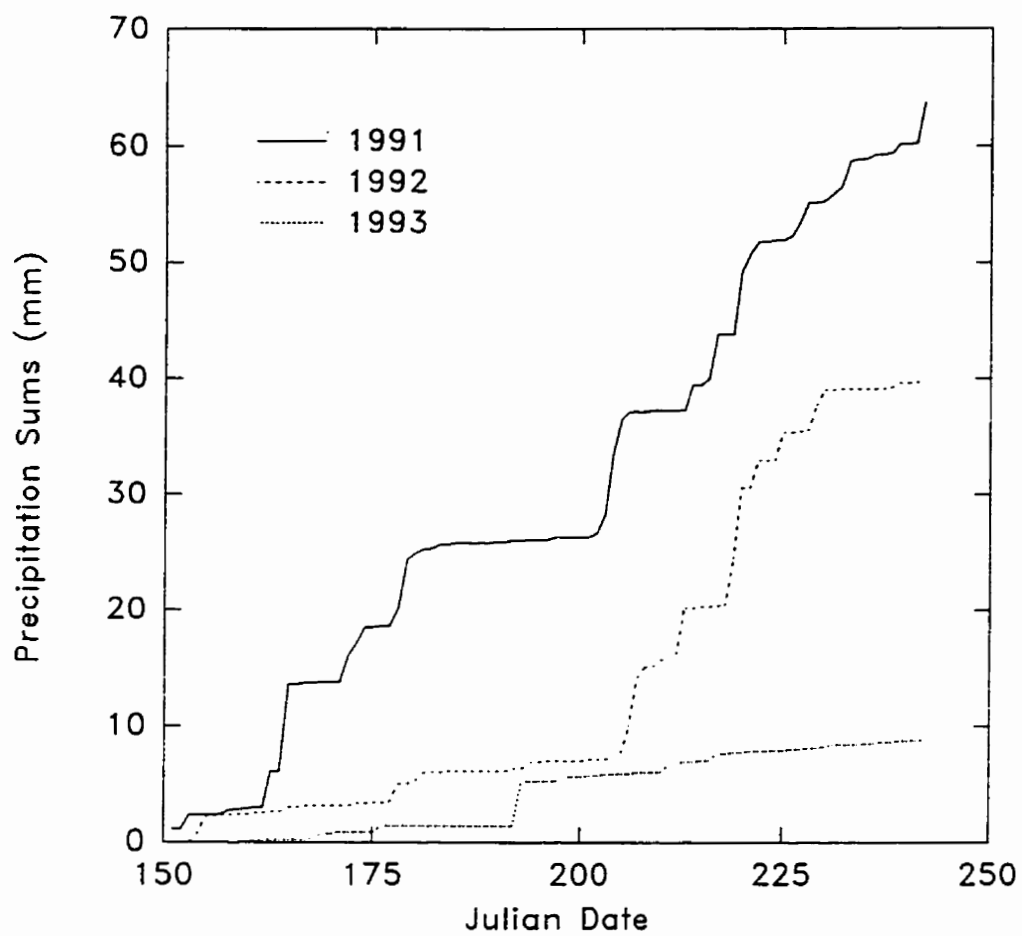


Figure 4-5. Precipitation sums for the 1991, 1992 and 1993 growing seasons.

that environmental factors such as temperature and precipitation affect reproductive output in plants (Jameson 1963; Pyke 1986).

Higher SHD at UH than at the other two sites probably were the result of higher NH_4 levels at UH. It is well documented that soil nitrogen levels affect the reproductive output of plants (Henry et al. 1994b).

The changes in SHD reported above could ultimately affect the genetic composition of the graminoid meadows. This is particularly true for the control treatment at TR where a thick litter layer likely reduces light levels and physically impedes establishing seedlings. By freeing previously sequestered resources and possibly increasing the number of safe sites for seedling establishment, grazing and clipping could increase genetic recombination in graminoid meadows despite the lower absolute number of seed heads produced at grazed and clipped sites. The abundance of wind-pollinated seed in these meadows decreases the influence of locally low SHD. This conclusion warrants further investigation. Nevertheless, the prediction that grazing and clipping reduces SHD is supported by the evidence.

4.4.4 Changes in soil nutrient status

The lack of higher NH_4 soil levels in grazed areas than in temporarily protected plots demonstrates that muskoxen do not influence soil NH_4 content in the short term. Low soil NH_4 levels at the MR permanent enclosure can be explained by the depletion of soil NH_4 pools through active uptake by lemming-grazed plants. Chapin and Slack (1979) have documented that clipped arctic graminoids have greater uptake of nutrients than unclipped plants.

The observation that UH had the highest soil NH_4 levels of the three study sites partially explains why it also has the largest standing crop (Chapter 3), the highest SHD, and the greatest average ramet height. These observations are consistent with the fact that UH also has the highest density of fecal pats (Chapter 1). Muskoxen are attracted to UH because of a large standing crop. Soil moisture status at UH is favorable for plant growth and deep snow conditions allow for the maintenance of large quantities of green tissue overwinter (Chapter 3). By grazing at UH more often than the other study sites, muskoxen increase soil NH_4 levels and possibly rates of nutrient cycling. Nutrients in muskox excreta

are more rapidly available to plants than those stored in litter.

Muskoxen may also import nutrients from other areas into the UH site. Carran et al. (1982) found that grazers acted as nutrient conduits harvesting nutrients from large areas and concentrating them into small areas. Other studies have reported that grazers are attracted to areas of higher productivity (Hodgson 1977; White and Trudell 1980; Trudell and White 1981; Hudson and Frank 1987; Vivas and Saether 1987; Etchberger et al. 1988) where they can maximize their rates of intake and forage efficiently (Havstad and Malecheck 1982; McNaughton 1985a). Grazers also have been reported to increase soil ammonium levels (Li and Redmann 1992b), rates of nutrient cycling (Carran et al. 1982; Cargill and Jefferies 1984a, 1984b; Henry and Svoboda 1989; Hik and Jefferies 1990), and/or rates of nitrogen fixation (Bazely and Jefferies 1989).

Soil moisture played a key role in determining the standing crop of plant tissue at a given site (Chapter 3). The soil moisture levels reported in this study confirm that both UH and TR are favorable sites for plant growth compared to super-hygic MR. Umingmuk Hill had the added advantage of being on a 15% slope which caused

plants at this site to be provided continuously with a fresh supply of oxygenated water.

Low levels of P at UH did not affect standing crops which suggests that NH_4 is more limiting than P within the study area. High levels of Fe in soils at all sites explain the preponderance of Yersinia pseudotuberculosis and Yersiniosis among muskoxen within the study area. Researchers have found a link between the disease and high levels of Fe (Conte et al. 1994; Ewald et al. 1994).

The prediction that soil nutrient levels would be higher at heavily grazed sites with abundant fecal pats is supported by the evidence. Favorable soil moisture and a large quantity of overwintering green tissue at UH resulted in a large summer forage base which attracted muskoxen. As muskoxen fed, rested and ruminated they deposited feces and urine that boosted NH_4 levels.

4.4.5 Microclimatic changes after grazing and clipping

The results confirm that other factors override the effects of clipping and grazing on soil temperature. It is hypothesized that ambient temperature and light intensity play a significant role in regulating soil temperature in upper levels of the soil profile. Logistical constraints limited the collection of

temperature data but after having recorded hundreds of soil temperature entries it became obvious that on warm days with bright sunshine, soil temperature was warmer, and on cold, cloudy days, soil temperature was colder. This observation is inconsistent with our prediction that grazed and clipped treatments will be warmer than protected treatments.

Grazing and clipping did not significantly warm sites to a point where depth of thaw was affected. The intersite variation in depth to permafrost suggests that UH is a warmer site than MR and TR. A southerly aspect provided UH with more radiation than the level sites, MR and TR. Greater depth to permafrost at UH is consistent with the soil moisture, standing crop, fecal pat and soil nutrient data which all demonstrate that UH is a favorable site for plant growth and for maintenance of large standing crops. Super-hygic conditions at MR likely contributed to the shallow depth of thaw there.

The degree of litter accumulation within the permanent exclosure at TR did not translate into a cooler microclimate. Litter layer thickness played no measurable role in influencing temperature within microplots in this study. These findings are consistent with the rejection of our original prediction that grazing and clipping would result in a warmer microclimate. The absolute

quantities of plant tissue within these arctic meadows are not great enough to alter microclimate significantly. More productive sites, such as those in the grassland region of North America show more changes in microclimate after grazing and clipping (Whitman and Wolters 1967).

5.0 HERBIVORY-INDUCED CHANGES IN FORAGE QUALITY WITHIN MUSKOXEN-GRAZED GRAMINOID MEADOWS

5.1 Introduction

Although the herbivore optimization hypothesis predicts that net above-ground primary productivity (NAPP) of plant tissue increases with moderate grazing intensities the hypothesis does not address concomitant changes in forage quality with varying grazing intensities. The quality of forage is just as important or even more important to herbivore populations than the absolute quantity of forage available. The abundance of studies in the literature that assess forage quality (e.g., protein, acid detergent fiber (ADF), neutral detergent fiber (NDF)) attests to the importance of this parameter to herbivores (Bell 1971; Batzli and Jung 1980; Van Soest 1982; Hudson and Frank 1987; Illius et al. 1987; Thing et al. 1987; Klein and Bay 1990; Bryant and Reichardt 1992).

Tissue removal decreases the proportion of dead plant tissue (Sims and Singh 1978; McNaughton 1979a; Cargill and Jefferies 1984b; Smith 1990) thereby increasing the quality of forage left for future grazers; however, the opposite trend also has been reported

(Belsky 1987). Other studies report increased NAPP and forage quality after grazing (McNaughton 1984, 1986) which results in more nutrients (e.g., protein) per unit area of range (Thaine 1954). Tissue removal results in higher levels of nutrients and lower levels of structural carbohydrates in residual tissue (Albertson *et al.* 1953; Jameson 1963; McNaughton 1976, 1984, 1985a; Prins *et al.* 1980; Cargill and Jefferies 1984a; Seastedt 1985) because less structural material is needed to support low-growing plants. More digestible residual tissue combined with higher rates of nutrient cycling after the grazing episode act as a positive feedback mechanism which enhances the fecundity of the herbivore populations (McNaughton 1985a; Jefferies 1988; Henry *et al.* 1994a).

It should be pointed out however that there is a vast literature that demonstrates the negative effects of herbivory on plant growth and carbohydrate reserves (Davidson and Milthorpe 1966; White 1973; Mueggler 1975; Bokhari 1977; Buwai and Trlica 1977; Trlica *et al.* 1977; Clement *et al.* 1978; Lacey and Van Poollen 1981; McLean and Wikeem 1985; Willms 1991) and subsequent declines in herbivore fecundity rates (Klein 1968; Cooch *et al.* 1991). This outcome is particularly common in western North America where carbon and water are limiting factors and at intensely-grazed, nutrient-limited sites in arctic

North America. Under these circumstances any advantage of increased forage quality after grazing will be offset by decreases in NAPP. However, in moderately grazed, nutrient-limited, wet meadows where dead tissue accumulates (Hik and Jefferies 1990; Smith 1990) and where clipped plants increase uptake rates of nutrients (Chapin and Slack 1979) a more positive outcome to grazing (e.g., increased NAPP and forage quality) can be expected.

The exponential growth of muskox populations on Banks Island prompted the examination of NAPP responses to tissue removal described in Chapter 3. At present no other study examines the quantitative and qualitative responses of meadow vegetation to herbivory on Banks Island. Although several studies examine qualitative plant responses to tissue removal in sub-arctic and arctic grazing systems (Bryant and Kuropat 1980; Bryant *et al.* 1983; Cargill and Jefferies 1984a; Chapin *et al.* 1986a; Raillard 1992) spatial extrapolation of results from system-to-system can result in erroneous conclusions. Based on the available evidence in the literature and the fact that arctic meadows are hygric/sub-hygric (Muc 1977) and nutrient-limited (Henry *et al.* 1994b) the following predictions were made:

- 1) Grazing and clipping increase the proportion of live plant tissue compared to the lack of grazing in controls.
- 2) Grazing by muskoxen increases crude protein content in live, dead and combined (live plus dead) plant samples compared to the lack of grazing in control treatments.
- 3) Grazing by muskoxen decreases acid detergent fiber content in live, dead and combined plant samples compared to the lack of grazing in control treatments.

Logistics prevented determining whether or not muskoxen feed selectively within graminoid meadows and the degree to which muskoxen assimilate ingested forage.

5.2 Methods

5.2.1 Experimental design

This experiment follows the experimental design described in detail in Chapter 3. The study site sampling method and schedule are identical to that described in Chapter 3. Three study sites were sampled in 1992 and 1993: Muskox River (MR), Thomsen River (TR) and Umingmuk Hill (UH). Umingmuk Hill was not sampled in 1991. Data in this chapter were obtained from 1 X 1 m microplots at the same time that biomass data were collected (four times per growing season in 1992 and 1993), with the exception

that forage quality data were from late July/early August 1993. Four random samples from each grazed and control treatment at each site were analyzed for forage quality. Sample sizes in each treatment for percent live tissue and green standing crop data are as follows:

MR - 2X, 1X and control (n=5)

MR - Temporary protection and grazed (n=20)

TR - 2X, 1X and control (n=5)

TR - Temporary protection and grazed (n=20)

In 1992, Temporary protection variable (n=18, Jul. 31; n=11 Aug. 10).

UH - Temporary protection and grazed (n=10)

In 1992, temporary protection variable (n=8, first 2 dates; n=7, last 2 dates).

5.2.2 Percent live tissue and green standing crop

Each plant sample used to calculate productivity and standing crop estimates was separated into dead and live components as described in Chapter 3. The ratio of live shoot biomass to total shoot biomass (i.e., live plus dead components) provided an index of forage quality. The absolute quantity of live tissue (green standing crop, GSC) provided a measure of the availability of nutritious

forage. Green standing crop is the biomass of green tissue per unit area (see terminology in Section 3.2.4). All biomass and forage samples were obtained by clipping randomly located 0.25 X 0.25 m subplots at ground level (Chapter 3, Figure 3-1).

5.2.3 Forage quality

Peak above-ground biomass samples from 1993 (i.e., late July/early August) were analyzed for crude protein, acid detergent fiber (ADF) and CP/ADF ratios using the Kjeldahl method for protein and ADF method #973.18 at the Feed Testing Laboratory, Department of Animal Science, University of Saskatchewan (A.O.A.C. 1990). Data are for specific forage components including live tissue, dead tissue and combined live and dead components. The forage quality of a combined plant sample for a given microplot was calculated by using the following formula:

$$Q_C = Q_L(\%L) + Q_D(\%D) \quad [5.1]$$

where, Q_C = the forage quality measurement from the combined live and dead components, Q_L = the forage quality measurement from the live component of a plant sample, Q_D = the forage quality measurement

from the dead component of a plant sample, %L = percent live tissue in a plant sample and %D = percent dead tissue in a plant sample.

5.2.4 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 and Rohlf 1981). If necessary, data were transformed in order to satisfy the assumptions of parametric statistics. One-way analysis of variance was conducted on 2X/1X/Control data and on Temporary Exclosure/Grazed/Control data. If more than two means were compared the LSD test was used. If two means were compared the two-sample T-test was used (Sokal and Rohlf 1981).

5.3 Results

5.3.1 Comparisons of relative and absolute quantities of green plant tissue among treatments and sites

Clipping had very little effect on the percentage of live tissue in the permanent exclosure at MR in 1992 and 1993 (Table 5-1). The only difference was observed in

Table 5-1. Comparison of mean percent live tissue estimates* in 1992 and 1993 1 X 1 m microplots (n=5) inside permanent exclosures. Microplots were unclipped (control), clipped twice (2X), or clipped once (1X) in 1991 and 1992 at two study sites.

| <u>Date</u> | <u>Percent Live Plant Tissue</u> | | | |
|----------------------|----------------------------------|-----------------|-----------------|-----------------|
| | <u>2X</u> | <u>1X</u> | <u>Control</u> | <u>MS Error</u> |
| <u>Muskox River</u> | | | | |
| Jul. 3/92 | 34 _a | 47 _a | 39 _a | 150 |
| Jul.17/92 | 57 _a | 65 _a | 62 _a | 80 |
| Jul.27/92 | 71 _a | 64 _b | 64 _b | 24 |
| Aug. 5/92 | 58 _a | 64 _a | 60 _a | 54 |
| Jun.27/93 | 75 _a | 62 _a | 71 _a | 294 |
| Jul.16/93 | 87 _a | 86 _a | 93 _a | 85 |
| Jul.29/93 | 92 _a | 93 _a | 89 _a | 69 |
| Aug.18/93 | 53 _a | NA | 62 _a | 95 |
| <u>Thomsen River</u> | | | | |
| Jul. 8/92 | 34 _a | 34 _a | 14 _b | 47 |
| Jul.22/92 | 58 _a | 54 _a | 32 _a | 91 |
| Jul.31/92 | 42 _b | 57 _a | 35 _c | 32 |
| Aug.10/92 | 50 _a | 56 _a | 29 _b | 58 |
| Jul. 4/93 | 76 _a | 69 _a | 45 _b | 70 |
| Jul.21/93 | 80 _a | 78 _a | 35 _b | 110 |
| Aug. 3/93 | 67 _a | 72 _a | 31 _b | 298 |
| Aug.17/93 | 44 _a | 37 _a | 14 _b | 235 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$

late July in 1992 when 2X plots had higher percentage of live tissue estimates. In contrast, at TR clipping consistently increased percentage of live tissue in samples in both 1992 and 1993. Between year comparisons showed that percent live tissue increased in samples from 1992 to 1993 except at the TR control where values stayed the same. Among site comparisons showed that the MR exclosure had higher percentage of live tissue values than the TR exclosure.

Grazing by muskoxen during the 1992 growing season increased percentage of live tissue at MR early in the summer, however, by late July and August, percentage of live tissue was the same in temporarily protected and grazed treatments (Table 5-2). In 1993, grazing by muskoxen at MR had no effect on percentage of live tissue in the short term. Long term protection from muskoxen, but not from lemmings, increased percentage of live tissue at MR in 1992 and 1993. At TR grazing increased percentage of live tissue early in 1992, however in 1993 grazed plots had lower percentage of live tissue than temporarily protected plots late in the season. In one-half of the cases reported, muskoxen had no effect on percentage of live tissue estimates in both 1992 and 1993 at TR. In contrast, long-term protection decreased percentage of live tissue in 1992 and 1993 at TR. Data

Table 5-2. Comparison mean percent live tissue estimates* in 1992 and 1993 1 X 1 m microplots. Microplots were unclipped (control) (n=5), temporarily protected (since June 25, 1992 or 1993) (n=20)** or grazed (i.e., exposed to muskoxen) (n=20).

| Date | Percent Live Tissue | | | MS Error |
|------------------------|---------------------|-----------------|------------------|----------|
| | Temp.Excl | Grazed | Control | |
| <u>Muskox River</u> | | | | |
| Jul. 4/92 | 34 _b | 40 _a | 39 _{ab} | 70 |
| Jul.18/92 | 48 _c | 54 _b | 62 _a | 88 |
| Jul.28/92 | 53 _b | 59 _b | 64 _a | 122 |
| Aug. 6/92 | 54 _a | 54 _a | 60 _a | 189 |
| Jun.30/93 | 53 _b | 52 _b | 71 _a | 158 |
| Jul.18/93 | 67 _b | 71 _b | 93 _a | 192 |
| Jul.30/93 | 67 _b | 74 _b | 89 _a | 204 |
| Aug.18/93 | 25 _b | 27 _b | 62 _a | 242 |
| <u>Thomsen River**</u> | | | | |
| Jul.10/92 | 33 _b | 43 _a | 14 _c | 117 |
| Jul.22/92 | 46 _b | 52 _a | 32 _c | 106 |
| Jul.31/92 | 52 _a | 56 _a | 35 _b | 113 |
| Aug.10/92 | 42 _a | 49 _a | 29 _b | 160 |
| Jul. 7/93 | 66 _a | 69 _a | 45 _b | 189 |
| Jul.22/93 | 71 _a | 67 _a | 35 _b | 215 |
| Aug. 3/93 | 69 _a | 59 _b | 31 _c | 309 |
| Aug.17/93 | 42 _a | 28 _b | 14 _b | 394 |
| <u>Umingmuk Hill**</u> | | | | |
| Jul.14/92 | 60 _a | 55 _a | NA | 214 |
| Jul.25/92 | 65 _a | 71 _a | NA | 216 |
| Aug. 4/92 | 65 _a | 74 _a | NA | 267 |
| Aug.13/92 | 57 _a | 61 _a | NA | 303 |
| Jul.13/93 | 76 _a | 84 _a | NA | 170 |
| Jul.26/93 | 76 _a | 80 _a | NA | 120 |
| Aug. 7/93 | 76 _a | 78 _a | NA | 170 |
| Aug.18/93 | 36 _a | 36 _a | NA | 185 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$

** In 1992: n=18 on July 31 and n=11 on Aug. 10 at TR t.excl.
n=10 in grazed treatment at Umingmuk Hill
n= 8 (first 2 dates) and n=7 (last 2 dates) in temp. excl. at Umingmuk Hill.
In 1993: n=10 in each treatment at Umingmuk Hill

for 1992 and 1993 showed that muskoxen had no effect on percentage of live tissue in the short term at UH. As with the clipped samples from inside the permanent exclosure, samples from outside the large exclosures showed increases in percentage of live tissue in 1993 over 1992 values. Percent live tissue was higher at UH than at MR and TR.

Muskoxen had a relatively minor affect on percentage of live tissue in the short term. Of the 24 comparisons made (Table 5-2) only four (17%) showed that muskoxen increased percentage of live tissue in the short term. Eighteen of the comparisons (75%) showed that muskoxen had no effect on percentage of live tissue estimates in the short term. The remaining two (8%) comparisons had higher percentage of live tissue estimates in temporarily protected plots.

Umingmuk Hill had greater absolute quantities of green plant tissue (i.e., more green standing crop) than MR or TR in 1992 and 1993. Muskox River had the lowest green standing crop in 1992, however in 1993 control plots at MR had higher green standing crop than control plots at TR (Table 5-3). With only a few exceptions, grazing and clipping tended to increase or not change the percentage of live tissue of samples. The site with the highest proportion of live tissue also had the largest

Table 5-3. Comparison of peak season green standing crop (g m^{-2}) among study sites in 1992 and 1993 1 X 1 m microplots. Treatments include temporarily protected (since June 25 1992 or 1993) (n=20), grazed (i.e., exposed to muskoxen) (n=20) and control (n=5).*

| <u>Ca. Date</u> | <u>Treatment</u> | <u>Green Standing Crop</u> | | | <u>MS Error</u> |
|-----------------|------------------|----------------------------|------------------|------------------|-----------------|
| | | <u>MR</u> | <u>TR</u> | <u>UH</u> | |
| Jul.31/92 | Temp.Excl. | 73 _b | 137 _a | 186 _a | 1612 |
| Jul.31/92 | Grazed | 57 _c | 111 _b | 158 _a | 1243 |
| Jul.31/92 | Control | 71 _b | 136 _a | NA | 489 |
| Aug. 3/93 | Temp.Excl. | 104 _c | 159 _b | 229 _a | 2825 |
| Aug. 3/93 | Grazed | 85 _b | 93 _b | 188 _a | 1851 |
| Aug. 3/93 | Control | 135 _a | 83 _b | NA | 844 |

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

In 1992: n=18 on Aug. 1 and n=11 on Aug. 10 in TR temporary exclosure treatment.

n=10 in grazed treatment at Umingmuk Hill

n= 8 (first 2 dates) and n=7 (last 2 dates) in temporary exclosure treatment at Umingmuk Hill.

In 1993: n=10 in each treatment at Umingmuk Hill

absolute quantity of green plant tissue.

5.3.2 Forage quality

Permanent protection from muskoxen increased crude protein, but did not affect ADF levels in live tissue at MR (Table 5-4). CP/ADF increased in live tissue at MR as a result of permanent protection from muskoxen. At TR, grazing did not change the percentage of crude protein in live tissue compared to controls, however ADF levels in live tissue were higher in grazed plots. CP/ADF was higher in permanently protected live tissue than live tissue exposed to muskoxen.

Similarly, the control plots at MR had higher crude protein levels and CP/ADF in dead tissue than the grazed treatments. At TR, however, grazing had no effect on the amount of crude protein or ADF in dead tissue. Too few replications were available to analyze ADF content of dead tissue among treatments at MR because there was very little dead tissue present.

Data from combined live and dead tissue samples revealed that there was more crude protein in MR control plots than in the adjacent muskoxen-grazed plots. No differences were observed for ADF in grazed and control plots at MR, however CP/ADF was higher in controls. These

Table 5-4. Comparison of (mean±SE) live, dead and combined sample forage quality estimates (% crude protein, % acid detergent fiber and CP/ADF) (n=4) in 1 X 1 m microplots among permanently protected (i.e., control) and grazed treatments (i.e., exposed to muskoxen) at two study sites in late July/early August 1993.*

| <u>Parameter</u> | <u>Forage Quality</u> | |
|----------------------|-----------------------|---------------------|
| | <u>Control</u> | <u>Grazed</u> |
| <u>Muskox River</u> | | |
| Protein.Live | 14.23± .36 <u>a</u> | 11.19± .52 <u>b</u> |
| ADF.Live | 22.90± .33 <u>a</u> | 23.48± .48 <u>a</u> |
| CP/ADF.Live | 0.62± .02 <u>a</u> | 0.48± .02 <u>b</u> |
| Protein.Dead | 7.80± .82 <u>a</u> | 5.30± .26 <u>b</u> |
| ADF.Dead | 37.46 | 36.69± .22 |
| CP/ADF.Dead | 0.21± .02 <u>a</u> | 0.14± .01 <u>b</u> |
| Protein.Combined | 13.23± .45 <u>a</u> | 9.34± .48 <u>b</u> |
| ADF.Combined | 24.92± .67 <u>a</u> | 27.28±1.31 <u>a</u> |
| CP/ADF.Combined | 0.53± .03 <u>a</u> | 0.35± .03 <u>b</u> |
| <u>Thomsen River</u> | | |
| Protein.Live | 12.12± .46 <u>a</u> | 11.29± .19 <u>a</u> |
| ADF.Live | 25.04± .23 <u>b</u> | 28.01± .41 <u>a</u> |
| CP/ADF.Live | 0.48± .02 <u>a</u> | 0.40± .01 <u>b</u> |
| Protein.Dead | 4.65± .03 <u>a</u> | 5.01± .19 <u>a</u> |
| ADF.Dead | 41.97± .52 <u>a</u> | 40.21± .76 <u>a</u> |
| CP/ADF.Dead | 0.11± .00 <u>a</u> | 0.13± .01 <u>a</u> |
| Protein.Combined | 7.18± .71 <u>a</u> | 7.50± .65 <u>a</u> |
| ADF.Combined | 36.34±1.93 <u>a</u> | 35.43±1.56 <u>a</u> |
| CP/ADF.Combined | 0.20± .03 <u>a</u> | 0.22± .03 <u>a</u> |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$

results are similar to those reported for live and dead components. At TR, data for combined live and dead components showed that muskoxen did not affect crude protein or ADF levels of forage.

There were no significant differences in crude protein levels of live tissue at grazed plots among the study sites (Table 5-5). In contrast, MR had the lowest live tissue ADF values and the highest live tissue CP/ADF values. Umingmuk Hill had more crude protein and higher CP/ADF values in dead tissue than MR and TR. Analysis of dead tissue ADF levels was not possible due to the small quantity of dead tissue at UH. Umingmuk Hill had the highest and TR had the lowest crude protein levels and CP/ADF values in combined plant samples. Thomsen River had the highest ADF and UH and MR had the lowest ADF in combined plant samples (Table 5-5).

The differences among control and grazed treatments were minor for the 6 parameters examined except at MR where lemmings boosted forage quality. In contrast, UH and MR showed significantly higher forage quality than TR.

Table 5-5. Comparison of mean live, dead and combined sample forage quality estimates (% crude protein, % acid detergent fiber and CP/ADF) (n=4) in 1 X 1 m grazed microplots among study sites in late July/early August 1993.*

| <u>Parameter</u> | <u>Forage Quality</u> | | | <u>MS Error</u> |
|------------------|-----------------------|--------------------|--------------------|-----------------|
| | <u>MR</u> | <u>TR</u> | <u>UH</u> | |
| Protein.Live | 11.19 _a | 11.29 _a | 12.08 _a | 0.81 |
| ADF.Live | 23.48 _b | 28.01 _a | 26.37 _a | 1.86 |
| CP/ADF.Live | 0.48 _a | 0.40 _b | 0.46 _b | 0.00 |
| Protein.Dead | 5.30 _b | 5.01 _b | 7.07 _a | 0.61 |
| ADF.Dead | 36.69 | 40.21 | 34.34 | NA |
| CP/ADF.Dead | 0.14 _b | 0.13 _b | 0.21 _a | 0.00 |
| Protein.Combined | 9.34 _a | 7.50 _b | 10.81 _a | 1.91 |
| ADF.Combined | 27.28 _b | 35.43 _a | 28.45 _b | 6.56 |
| CP/ADF.Combined | 0.35 _a | 0.22 _b | 0.38 _a | 0.00 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$

5.4 Discussion

5.4.1 The effects of clipping and grazing by muskoxen on relative and absolute quantities of green plant tissue

Similar percent live tissue estimates among treatments inside the MR permanent exclosure suggest that intense lemming herbivory in 1991 and 1992 (Chapter 3) and superhygric soil moisture status (Chapter 4) imposed a greater influence on plant growth and decomposition than the clipping treatments. Similar conclusions were made after examining the net above-ground primary productivity (NAPP) data in Chapter 3. In contrast, higher percentage of live tissue estimates in clipped than in permanently protected plots in the TR exclosure demonstrates that dead plant tissue accumulated faster than it decomposed in the long-term absence of grazing (since 1988) or clipping.

In the short term, grazing by muskoxen did not affect percentage of live tissue estimates, however in the long-term muskoxen significantly boosted percentage of live tissue in forage samples as predicted. Muskoxen should maintain a forage base that is more nutritious than would be found in the long-term absence of grazers.

These data show that by removing dead and live tissue and by depositing feces and urine, muskoxen increase the percentage of live tissue in their forage (Chapter 4). Alternatively, at ungrazed sites such as permanently protected plots at TR, poor quality standing dead tissue is abundant. Grazing boosts rates of nutrient cycling (Cargill and Jefferies 1984a; Henry and Svoboda 1989; Hik and Jefferies 1990).

Climate also played a key role in controlling the proportion of live tissue available to muskoxen. Warmer temperatures and higher soil moisture levels from melting permafrost in 1993, compared to 1992 (Chapter 4), increased green standing crop within temporarily protected plots in 1993 relative to 1992. Similarly, the warmest site (UH) (Chapter 3) showed higher green standing crop than MR and TR in temporarily protected plots (Figure 5-1). Large green standing crops boosted percentage of live tissue in 1993 over 1992 values. Similarly, larger green standing crops at UH than at MR and TR increased percentage of live tissue estimates (Figure 5-2).

Several other factors besides green standing crop could have influenced percentage of live tissue in forage samples in this study. For example, warm moist conditions also increase rates of decomposition (Whidden 1977;

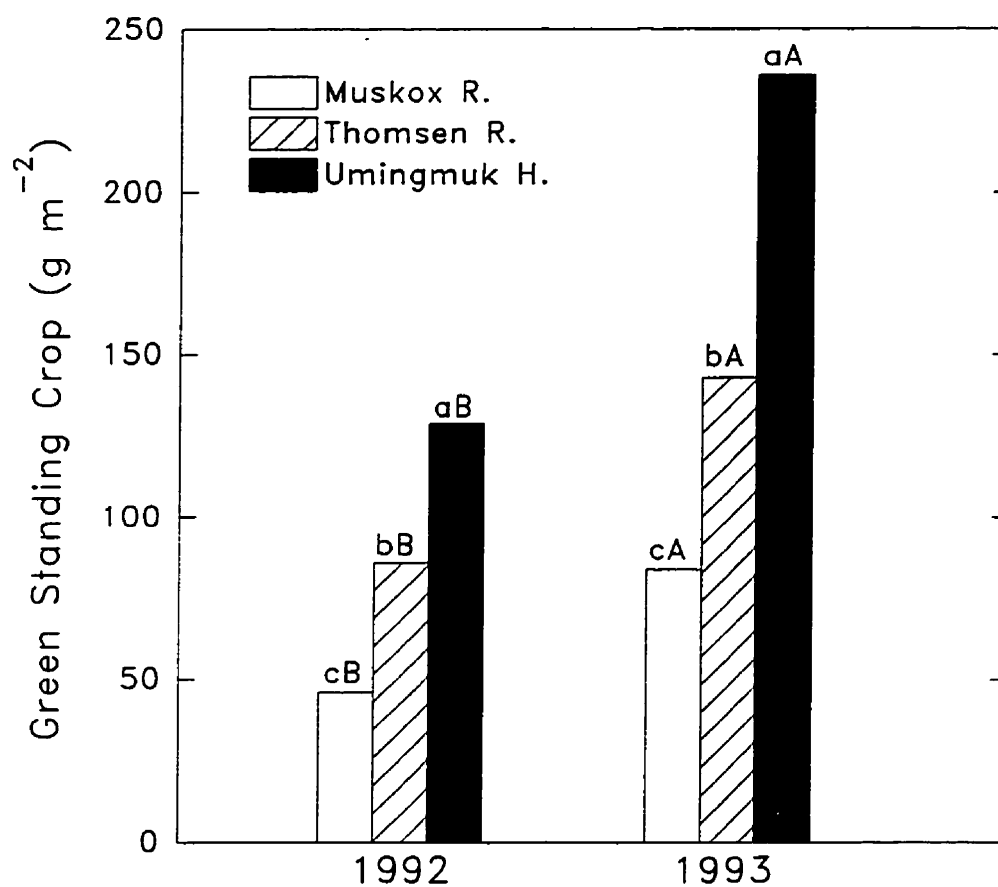


Figure 5-1. Comparisons of green standing crop estimates in temporarily protected 1 X 1 m microplots in mid/late July among study sites (lower case) and between years (upper case).

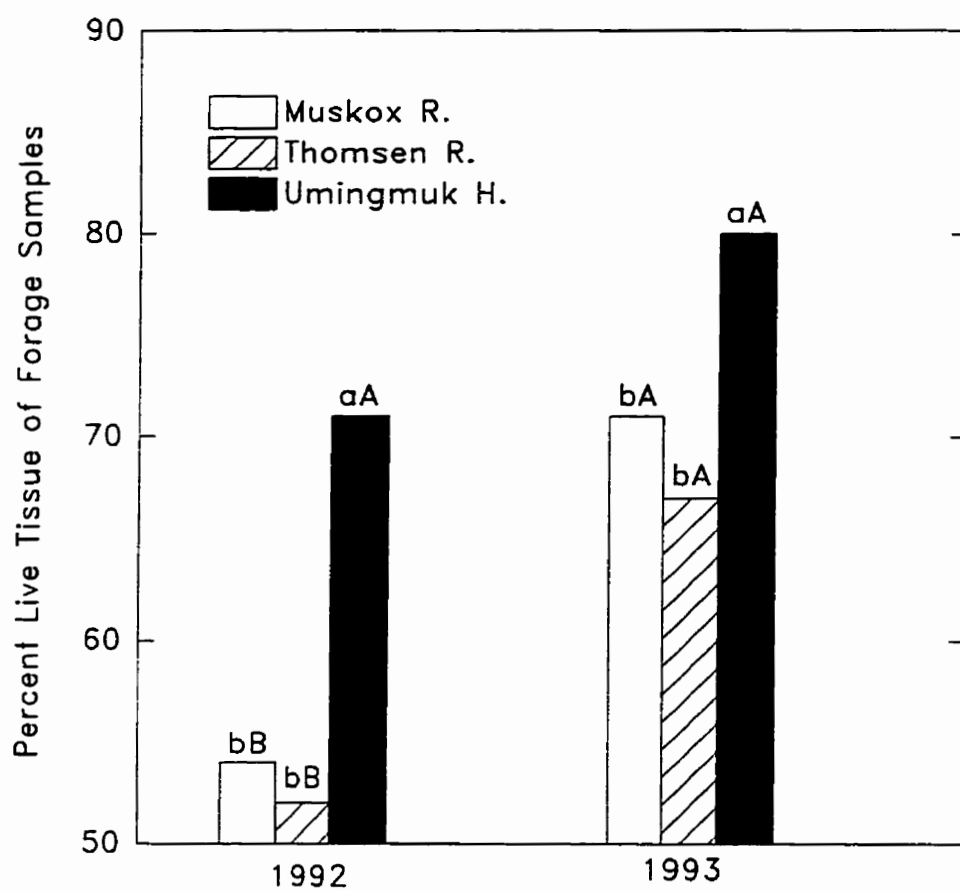


Figure 5-2. Comparisons of percent live tissue among study sites (lower case) and between years (upper case) in 1 X 1 m microplots exposed to muskoxen in mid/late July 1992 and 1993.

O'Lear and Seastedt 1994) and precipitation events facilitate the transfer of standing dead to the litter compartment (Sims and Singh 1978). Both processes increase the percentage of live tissue available to herbivores. Since precipitation levels were relatively low and since the weather was warm and moist in 1993 (Chapter 4) decomposition likely played a more important role than the transfer of standing dead to the litter compartment in contributing to high percentage of live tissue estimates in 1993.

Other studies have also reported that clipping or grazing increases forage quality by reducing the proportion of dead tissue (Sims and Singh 1978; McNaughton 1979a; Smith 1990). By regrazing previously grazed swards herbivores are exposed to higher quality forage which in turn can increase herbivore fecundity rates (Jefferies 1988; Henry *et al.* 1994a). Increases in forage quality, however, are not mutually exclusive to carbohydrate and/or nutrient reserve depletion in overgrazed plants. Numerous studies from western North America show that carbohydrate reserves are reduced after grazing (Davidson and Milthorpe 1966; White 1973; Mueggler 1975; Bokhari 1977; Buwai and Trlica 1977; Trlica *et al.* 1977; Clement *et al.* 1978; McLean and Wikeem 1985; Willms 1991). Overgrazing or intense

clipping has also been shown to decrease below-ground biomass (Stoddart *et al.* 1975, Chapter 3). Plant community responses to grazing are by no means exclusively positive.

5.4.2 Forage quality in live, dead and combined shoot tissue compartments in grazed and permanently protected treatments

Higher crude protein content and CP/ADF values of live, dead and combined (i.e., live plus dead) tissue samples from MR control plots than from adjacent muskox-grazed plots demonstrate that lemming herbivory maintains higher quality forage than grazing by muskoxen. ADF was higher in dead tissue from control plots than from grazed plots at MR, however quantities of dead tissue were too small to affect combined samples. Grazing intensity at TR was not high enough to affect crude protein levels in live and dead samples of forage. Although ADF was unexpectedly higher and CP/ADF values were unexpectedly lower in live tissue from grazed sites than in controls at TR, combined samples were unaffected.

The lack of differences in combined samples from control and grazed plots at TR is an unfortunate side-effect of small sample size. Given the high proportion of

dead tissue in TR control plots and the low forage quality of dead tissue it might be expected that grazers would facilitate the creation of a high quality forage base as discussed above. The four random samples selected from the grazed site at TR had much higher proportions of dead tissue than the average for that treatment (i.e., 41 percentage of live tissue for the four samples, 59 percentage of live tissue for treatment mean). Once this problem is recognized, however, it becomes obvious that the forage quality of combined live and dead components inside TR control plots is lower than the combined samples from adjacent grazed plots (Figure 5-3).

In this study the most intensely grazed vegetation (i.e., MR controls and UH grazed) is also the most nutritious. The ability of forage to cure well (i.e., to retain its crude protein content after death) is in part responsible for the high protein content and CP/ADF values of UH combined samples. The large difference in crude protein content and CP/ADF ratios of live tissue among control and grazed treatments at MR suggests that lemmings maintain live tissue that is on average younger than live tissue in muskoxen-grazed areas. It is well established that younger plant tissue has higher N concentrations than older tissue (Anderson and Talbot 1965; Dyer and Bokhari 1976; Klein 1977; Milton 1979;

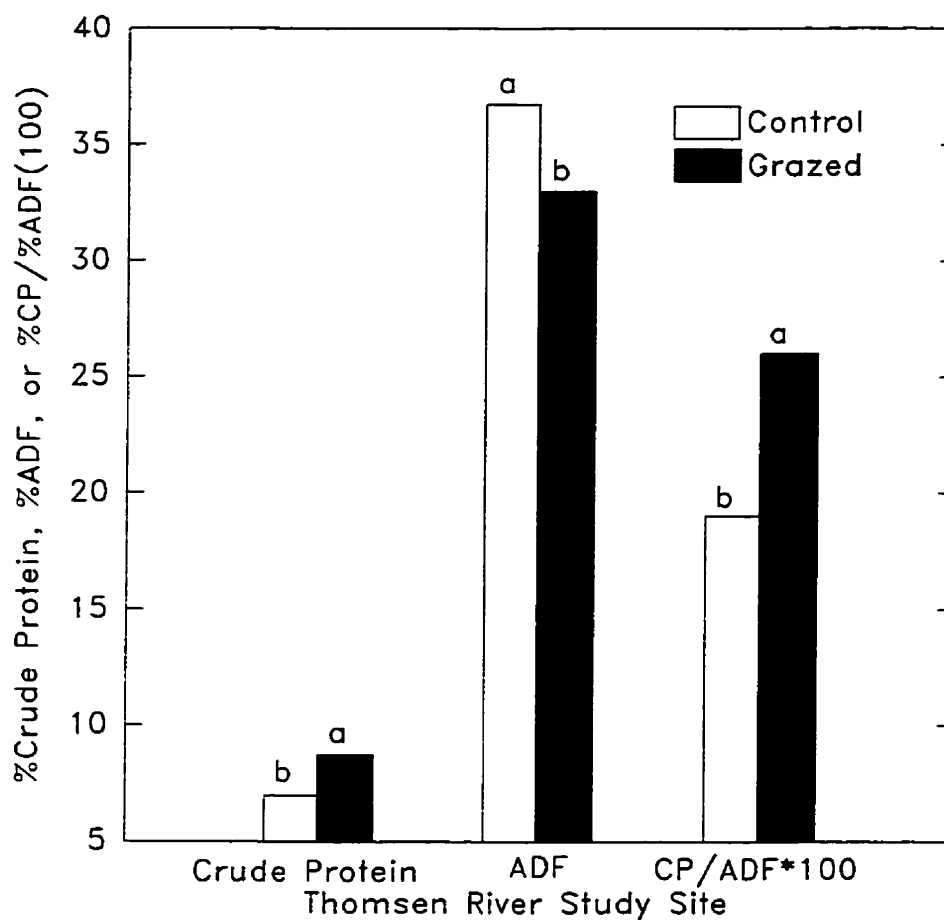


Figure 5-3. Comparisons of mean crude protein, ADF, and CP/ADF(100) of combined samples among permanently protected and grazed treatments at Thomsen River in late July/early August 1993 using treatment mean percent live tissue estimates in calculations.

Bryant et al. 1983; Li and Redmann 1992a). Muskoxen had a similar effect in maintaining more nutritious forage at TR (Figure 5-3).

High soil NH_4 levels at UH in combination with high fecal pat densities, warm soil conditions, a steady supply of oxygenated water and moderate grazing intensities (Chapters 3 and 4) contributed to the more nutritious forage base at UH (Figure 5-4). Muskoxen are attracted to the site that has the most favorable growing conditions. By grazing at UH more often, muskoxen import feces into the site and increase nutrient recycling rates *in situ*, which increase soil NH_4 levels. High NH_4 levels in turn boost the standing crop of forage (Li and Redmann 1992b) which again attracts more muskoxen (Chapter 3). More muskoxen means a reduction in average age of plant tissue, a reduction in the proportion of dead tissue and an increase in forage quality. The UH site also provided muskoxen with a good view of the surrounding land which could be an advantage in avoiding predation by wolves. These positive feedback mechanisms to grazing have been reported elsewhere (McNaughton 1984; 1985a).

In conclusion, in the long-term muskoxen maintain a more nutritious forage base with a higher percentage of live tissue and crude protein and lower percentages of ADF than would be found in the absence of grazers.

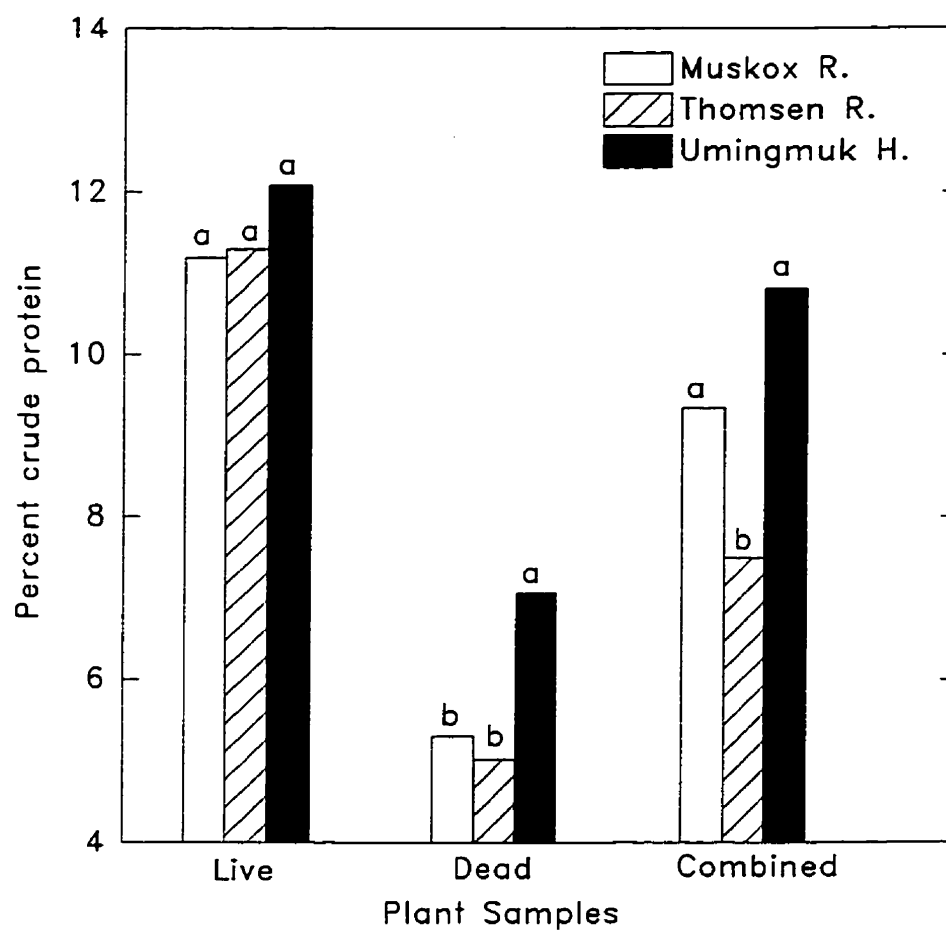


Figure 5-4. Comparisons of percent crude protein in live, dead and combined plant samples from 1 X 1 m microplots exposed to muskoxen among three study sites in late July/early August 1993.

Lemmings probably contribute to maintaining more nutritious forage in the study area by reducing the average age of plant tissue in their feeding areas. Muskoxen are able to recognize productive sites with nutritious forage by feeding in them more often.

The forage quality levels in this study are comparable to those of Larter (1988) for graminoids in the Mackenzie Bison Sanctuary, Northwest Territories and those of Raillard (1992) for graminoids in Ellesmere Island sedge meadows. Studies from Greenland report more nutritious graminoid forage samples (Thing et al. 1987; Klein and Bay 1990).

6.0 THE RESPONSE OF ERIOPHORUM TRISTE POPULATIONS TO MUSKOXEN GRAZING AND CLIPPING WITHIN A GRAMINOID MEADOW PLANT COMMUNITY.

6.1 Introduction

Since the herbivore optimization hypothesis was first postulated by McNaughton (1979a) and Hilbert *et al.* (1981) it has remained the controversial focus of studies that address the effects of grazers on net above-ground primary productivity (NAPP). The hypothesis predicts that moderate grazing intensities will lead to greater rates of NAPP than lower or higher grazing intensities. Researchers have expanded the hypothesis to include plant fitness (Paige and Whitham 1987), however most studies that test the hypothesis address community-level NAPP (Pearson 1965; Vickery 1972; McNaughton 1979a, 1983a, 1985a; Sims and Singh 1978; Lacey and Van Poollen 1981; Cargill and Jefferies 1984a; Hik and Jefferies 1990). In contrast to the abundance of community-level studies, relatively few studies address concomitant plant population responses to grazing within the context of the herbivore optimization hypothesis (McNaughton 1979b; Solomon 1983; Dyer *et al.* 1991; Oba 1994).

Populations of the tussock forming cotton grass Eriophorum vaginatum were intensively examined in northern Alaska (Fetcher and Shaver 1983). Disturbances such as vehicle tracks and bulldozed areas increased tillering and mortality rates compared to undisturbed controls. Greater tillering rates balanced higher mortality rates at disturbed sites. Other population-level studies also report increased rates of tillering after clipping or grazing (Dyer and Bokhari 1976; McNaughton 1976; Belsky 1986b).

Henry and Svoboda (1989) found that densities of flowering shoots of Eriophorum triste and Carex aquatilis were greater in grazed meadows than in non-grazed meadows on Ellesmere Island. This is surprising considering the climatic stress with which these plants are faced. A number of studies from arctic locations stress the importance of vegetative reproduction in a harsh climate (Bliss 1971; Chapin and Shaver 1981; Lachenbruch et al. 1981; McGraw and Shaver 1982; Gartner et al. 1986). However, at more moderate latitudes, Paige and Whitham (1987) documented that Ipomopsis aggregata (scarlet gilia) in Arizona had greater plant fitness after mechanical clipping. Other non-arctic studies have shown similar population-level increases in seed production after grazing or clipping (Binnie and Clifford 1980;

Richards 1983; Solomon 1983; Ambasht et al. 1984) although decreases have also been reported (Crawley 1983).

Although NAPP is of primary importance to herbivores, studies of responses of plant populations or plant parts (e.g. rate of leaf extension) to grazing, elucidate the relationship herbivores have with the basic constituents of plant communities (Harper 1977). This added insight into the response of important forage species to grazing is particularly relevant to land managers in heavily grazed areas. This study examines the effects of grazing by a high-density muskox population and clipping on populations of Eriophorum triste within graminoid meadows of north-central Banks Island.

Eriophorum triste is the most abundant plant species on disturbed and undisturbed sites within these meadows and is abundant even in intensively clipped treatments (Chapter 4). Graminoid meadows provide the bulk of forage for muskoxen in northern Canada (Parker and Ross 1976; Wilkinson et al. 1976; Muc 1977; Henry 1987; Oakes 1989; Raillard 1992; Henry et al. 1994a).

Based on the available background information it was predicted that Eriophorum triste would respond to grazing and clipping in the following ways: Compared to ungrazed/unclipped controls (1) mortality rates and

daughter tiller production would increase; (2) seed head density would decrease; (3) rates of change in total number of leaves per tiller, leaf extension of the oldest non-senescing leaf, and vertical (height) extension would increase.

6.2 Methods

6.2.1 Experimental design

This experiment follows the design, study site sampling method and sampling schedule described in detail in Chapter 3. All data in this chapter were obtained from 1 X 1 m microplots at the same time that non-biomass, community level data were collected (Chapter 4). Muskox River (MR), Thomsen River (TR) and Umingmuk Hill (UH) were sampled 4 and 3 times per growing season in 1992 and 1993, respectively. In 1991 MR and TR were sampled two and three times, respectively. At the beginning of the experiments in 1991 and 1992 randomly selected tillers of Eriophorum triste were marked around their bases with plastic chicken leg bands that were approximately 15 mm in diameter. During the winter of 1992 and 1993 some tiller markers inside the permanent exclosures were displaced by high water levels. If displacement did

occur, new randomly selected tillers, were marked in order to maintain a constant sample size.

Sample sizes are included in the data tables. Sample sizes of mortality, vegetative reproduction and seed head data are as follows (n is the number of replicate microplots; the number of tillers per microplot is given in parentheses):

MR - 2X, 1X and Control n=10 (10)

MR - Temporary Protection n=20 (5)

MR - Grazed n=10 (10)

TR - 2X, 1X and Control n=10 (10)

TR - Temporary Protection n=20 (5)

In 1992, n varied (n=14, Aug. 10 only)

TR - Grazed n=10 (10)

UH - Temporary Protection n=10 (15)

In 1992, n=8 on first two dates, n=7 on last two dates

UH - Grazed n=10 (15)

6.2.2 Mortality rates, vegetative and sexual reproduction

Percent mortality was calculated by dividing the number of dead tillers at time two by the number of

tillers marked at time one. If a tiller died, a new, randomly selected, tiller was marked so that the number of tillers per microplot was held constant. The vegetative fecundity of tillers was calculated in a similar manner. The number of tillers that gave rise to daughter tillers was divided by the total number of marked tillers in each microplot. A daughter tiller was defined as any young Eriophorum triste tiller growing inside the area confined by the tiller markers. Tiller markers were moved slightly after sampling so that no daughter tillers grew inside the confines of the marked space. This method was implemented to ensure that daughter tillers were not recounted and to avoid the confusion associated with marking two or more tillers with one marker.

The percent of Eriophorum triste tillers that produced seed heads was determined for each treatment at each study site. This measurement avoided the subjectivity associated with counting the number of seed heads per tiller, and provided an accurate measure of reproductive potential. After three summers of observation I concluded that the number of seed heads per tiller was not highly variable.

6.2.3 Rate of change in total number of leaves per tiller, leaf length and height

During each sampling period the number of leaves per tiller was counted and recorded. The rate of change in total number of leaves per tiller was calculated by subtracting the total number of leaves per tiller at time one from the number at time two. The difference was divided by the number of days that separate time one from time two. The quotient was multiplied by ten which resulted in data that document the rate of change in total number of leaves per tiller over a ten day period.

The mean rate of extension of the oldest non-senescing leaves on marked tillers in each microplot was also calculated. Each tiller was normally flanked by two leaves that were dying. These leaves contained large proportions of dead tissue and very little live tissue. In contrast, vigorously growing leaves were located at more central locations. These leaves were characterized by having no or very little dead tissue and by growing vertically as opposed to the horizontally oriented old leaves. The oldest non-senescing leaf (i.e., the "first leaf") was defined as the largest leaf that was still

growing vigorously early in the growing season. These leaves were located at less central locations than the youngest leaves (e.g., second and third leaves). In 1992 and 1993 the length of each first leaf was measured to the nearest centimeter at time one and time two as described above for total number of leaves per tiller. In 1991 calculations were made using the same procedure, however the length of leaves was expressed and measured as a decimal fraction of the maximum leaf length of that leaf cohort at a particular site. Leaf length data for all three years were expressed as growth rates over ten day intervals.

Rate of change in height was measured in a similar manner. Height of each tiller was measured to the nearest centimeter at time one and time two and the difference was divided by the number of days separating the two times. Data were then multiplied by ten. The resulting data show how tillers increase or decrease in height over 10-day periods among the different treatments.

If microplots were clipped, all population-level data were collected both before and after clipping. Rate data were calculated by subtracting the quantity immediately after clipping at time one from the quantity before clipping at time two. These data were also expressed as rates of change over ten-day intervals. As

pointed out earlier, the unit of replication for all data in this chapter is the combined data of tillers in a given microplot. All rate data were calculated by using differences between mean values for parameters in a microplot over a period of time.

6.2.4 Biomass of tillers

At the end of the population-level experiments in August 1993 all marked tillers were clipped to ground level. Tillers of a given microplot were combined and placed in small paper bags in the field. Dead tissue was removed from each tiller before the samples were predried at 40-60 °C for 24 hours. The samples were transported to Saskatoon and dried further at 60 °C for 48 hours, and weighed. Data are expressed as grams per ten tillers.

6.2.5 Data analysis

All data were tested for normality using the Shiparo-Wilks W test (SAS 1988). Variances were tested for homogeneity using the F_{\max} test (Sokal and Rohlf 1981). If the assumptions of parametric statistics were not met, transformations (log+1) or (square root+0.5)

were made before one-way analysis of variance and LSD mean comparisons (Sokal and Rohlf 1981).

If transformed data did not meet the assumptions of parametric statistics, the non-parametric Mann-Whitney U-test was used (Sokal and Rohlf 1981). Percent mortality and the percent of tillers with seed heads were the only parameters that did not meet the assumptions of parametric statistics even after transformation. Results were very similar for the two statistical methods (i.e., parametric and non-parametric) thus, for the sake of consistency only parametric test results are reported.

6.3 Results

6.3.1 The effect of clipping and grazing on the mortality of Eriophorum tillers

Clipping and grazing had very little effect on tiller mortality during the summers of 1991, 1992 and 1993, however a slight increase in mortality occurred in 2X plots at MR compared to controls and 1X plots. Mortality was low in all treatments at all three sites (Tables 6-1 and 6-2). There was no mortality of marked tillers during the summer of 1991, but high overwinter mortality in the exclosure at MR was recorded early in

Table 6-1. Comparison of mean percent mortality estimates of marked Eriophorum triste tillers in 1 X 1m microplots. Microplots were unclipped (control), clipped twice (2X), or clipped once (1X) in 1992 at two study sites.*

| <u>Time Period</u> | <u>Percent Mortality</u> | | | <u>MS Error</u> |
|----------------------|--------------------------|-----------------|-----------------|-----------------|
| | <u>2X</u> | <u>1X</u> | <u>Control</u> | |
| <u>Muskox River</u> | | | | |
| Jul.24/91-Jul. 2/92 | NA | 22 _a | 16 _a | 411 |
| Jul. 2/92-Aug. 5/92 | 1 _a | 0 _b | 0 _b | 3 |
| Jun.27/93-Jul.29/93 | 3 _a | 0 _b | 0 _b | 8 |
| <u>Thomsen River</u> | | | | |
| Jul.27/91-Jul. 8/92 | 6 _a | 8 _a | 4 _a | 150 |
| Jul. 8/92-Aug.10/92 | 0 _a | 0 _a | 2 _a | 6 |
| Jul. 4/93-Aug. 3/93 | 1 _a | 0 _a | 0 _a | 3 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$
 Overwinter (1992/93) mortality could not be estimated because of disturbed tiller markers.

Table 6-2. Comparison of mean percent mortality estimates of marked Eriophorum triste tillers in 1 X 1m microplots. Microplots were unclipped (control) (n=10), temporarily protected (n=20, n=10 at UH), grazed (i.e., exposed to muskoxen) (n=10) and protected in 1992 but exposed to muskoxen in 1993 (n=20).*

| <u>Time Period</u> | <u>Percent Mortality</u> | | | | <u>MS Error</u> |
|----------------------|--------------------------|-----------------|-----------------|-----------------|-----------------|
| | <u>T.Excl</u> | <u>Grz</u> | <u>Prt'92</u> | <u>Cont</u> | |
| <u>Muskox River</u> | | | | | |
| Jul.24/91-Jul. 4/92 | NA | 2 _b | NA | 16 _a | 144 |
| Jul. 4/92-Aug. 6/92 | 0 _a | 0 _a | NA | 0 _a | 0 |
| Aug. 6/92-Jun.30/93 | NA | 8 _a | 11 _a | NA | 169 |
| Jun.30/93-Jul.30/93 | 0 _b | 0 _b | 3 _a | 0 _b | 18 |
| <u>Thomsen River</u> | | | | | |
| Jul.27/91-Jul.10/92 | NA | 14 _a | NA | 4 _a | 216 |
| Jul.10/92-Aug.10/92 | 0 _a | 1 _a | NA | 2 _a | 7 |
| Aug.10/92-Jul. 7/93 | NA | 9 _a | 5 _a | NA | 84 |
| Jul. 7/93-Aug. 3/93 | 0 _a | 0 _a | 1 _a | 0 _a | 2 |
| <u>Umingmuk Hill</u> | | | | | |
| Jul.14/92-Aug.13/92 | 0 _a | 1 _a | NA | NA | 6 |
| Aug.13/92-Jul.13/93 | NA | 4 _a | 3 _a | NA | 41 |
| Jul.13/93-Aug. 7/93 | 1 _a | 2 _a | 0 _a | NA | 11 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$
1992 only: n=20 T.Excl at MR and TR, n=14 last date TR
n=8 T.Excl. first 2 dates, n=7 last 2 dates at UH
T.Excl.- temporary protection; Grz - grazed; Prt'92 - temporary protection in 1992, grazed in 1993; Cont - control

1992. Overwinter mortality data were not available early in the 1993 growing season inside the permanent exclosures because some tiller markers were disrupted by flooding.

6.3.2 The effect of clipping and grazing on daughter tiller and seed head production in populations of Eriophorum

Clipped tillers produced the same number of daughter tillers as unclipped tillers in 1992 and 1993 at MR and TR (Table 6-3). The only exception was at TR where 1X tillers produced fewer daughter tillers than unclipped and 2X tillers in 1992. No other differences were observed in the permanent exclosures.

Grazed and control tillers produced more daughter tillers than temporarily protected tillers in 1992 at TR (Table 6-4). In contrast, control tillers at MR produced fewer tillers than grazed tillers in 1992. No other differences were observed in 1992. Temporary and longer term protection from muskoxen did not affect daughter tiller production in 1993. In 1993, TR tillers protected in 1992 but exposed to muskoxen in 1993 produced more daughter tillers than tillers in other treatments.

Table 6-3. Comparison of number of daughter tillers per 100 adult tillers of Eriophorum triste in 1992 and 1993 1 x 1 m microplots (n=10) inside permanent exclosures. Microplots were unclipped control (cont.), clipped twice (2X), or clipped once (1X) in 1992 at two study sites.

| <u>Dates</u> | <u>Number of Daughter Tillers per 100 Adult Tillers</u> | | | |
|----------------------|---|----------------|-----------------|-----------------|
| | <u>2X</u> | <u>1X</u> | <u>Cont.</u> | <u>MS Error</u> |
| <u>Muskox River</u> | | | | |
| Jul. 2-Jul.27/92 | 5 _a | 3 _a | 0 _a | 39 |
| Jun.27-Jul.29/93 | 8 _a | 6 _a | 6 _a | 90 |
| <u>Thomsen River</u> | | | | |
| Jul. 8-Jul.31/92 | 6 _a | 1 _b | 10 _a | 42 |
| Jul. 4-Aug. 3/93 | 9 _a | 8 _a | 3 _a | 128 |

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

** Ten tillers were marked in each of the 10 microplots per treatment.

Table 6-4. Comparison of number of daughter tillers per 100 adult tillers of Eriophorum triste in 1992 and 1993 1 X 1m microplots. Microplots were unclipped (control) (n=10), temporarily protected (since June 25, 1992 or 1993) (n=20) or grazed (i.e., exposed to muskoxen) (n=10).*

| <u>Date</u> | <u>Number of Daughter Tillers per 100 Adult Tillers</u> | | | | |
|----------------------|---|-----------------|-----------------|-----------------|-----------------|
| | <u>T.Excl</u> | <u>Grz</u> | <u>Prt.'92</u> | <u>Cont</u> | <u>MS Error</u> |
| <u>Muskox River</u> | | | | | |
| Jul. 4-Jul.28/92 | 3 _{ab} | 8 _a | NA | 0 _b | 59 |
| Jun.30-Jul.30/93 | 6 _a | 7 _a | 12 _a | 6 _a | 293 |
| <u>Thomsen River</u> | | | | | |
| Jul.10-Jul.31/92 | 0 _b | 8 _a | NA | 10 _a | 27 |
| Jul. 7-Aug. 3/93 | 1 _b | 5 _b | 16 _a | 3 _b | 84 |
| <u>Umingmuk Hill</u> | | | | | |
| Jul.14-Aug. 4/92 | 1 _a | 1 _a | NA | NA | 10 |
| Jul.13-Aug. 7/93 | 7 _a | 10 _a | 3 _a | NA | 111 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$
In 1992: n=19 at Thomsen River, n=20 at Muskox River
n=10 in grazed treatment at Umingmuk Hill
n= 8 (first 2 dates) and n=7 (last 2 dates) in temp. excl. at Umingmuk Hill.
In 1993: n=14 in Prot.'92 at TR, n=10 in each treatment at UH

Table 6-5. Comparison of percent of marked Eriophorum triste tillers (mean) in 1993 1 X 1 m microplots that produce seed heads. Microplots were unclipped (control) (n=10), temporarily protected (since June 25, 1993) (n=20), grazed (i.e., exposed to muskoxen) (n=10) and protected in 1992 but exposed to muskoxen in 1993 (n=20).*

| <u>Date</u> | <u>Percent Eriophorum Tillers with Seed Heads</u> | | | | |
|----------------------|---|-----------------|----------------|----------------|-----------------|
| | <u>T.Excl</u> | <u>Grz</u> | <u>Prt.'92</u> | <u>Cont</u> | <u>MS Error</u> |
| <u>Muskox River</u> | | | | | |
| July 30/93 | 4 _a | 1 _a | 1 _a | 0 _a | 46 |
| <u>Thomsen River</u> | | | | | |
| Aug. 3/93 | 5 _a | 1 _{ab} | 0 _b | 0 _b | 36 |
| <u>Umingmuk Hill</u> | | | | | |
| Aug. 7/93 | 2 _a | 2 _a | 2 _a | NA | 26 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$
n=14 in Prot.'92 at TR, n=10 in each treatment at UH except Prot.'92 n=7
Only 1993 peak season data are included, see text

Seed head production was near zero in 1991 and 1992 and no differences among treatments were observed (Table 6-5). There were similar results in the permanent exclosures at MR and TR in 1993 (all zeros) and in adjacent grazed and temporarily protected areas. Tillers in control plots at TR had lower seed head production than temporarily protected tillers in 1993. To save space, only peak-season data are included. Data throughout the 1993 growing season show very similar results. In considering the entire 1991-1993 data set (daughter tiller and seed head production) it can be concluded that clipping and grazing had little affect on vegetative and sexual reproduction in Eriophorum populations. Very few differences occurred among treatments over the three years this study was conducted.

6.3.3 The effect of clipping and grazing on rate of change in number of leaves per tiller in Eriophorum populations

Clipping did not affect the rate of change in total number of leaves per tiller (TLR) in exclosures in 1992 and 1993 at MR and TR (Table 6-6). However, in 1991 clipping reduced TLR at MR and TR.

Table 6-6. Comparison of the mean rate of change in total number of leaves (TLR), length of oldest non-senescent (first) leaves (FLR) (cm), and height (HR) (cm) of *Eriophorum triste* tillers ($10 \text{ days}^{-1} \text{ tiller}^{-1}$) among treatments in 1 x 1 m microplots (n=10). Treatments inside permanent exclosures include unclipped (control), clipped twice (2X), or clipped once (1X) per growing season at two Study Sites*.

| <u>Dates</u> | <u>Parameter</u> | <u>2X</u> | <u>1X</u> | <u>Cont</u> | <u>MS Error</u> |
|----------------------|------------------|------------------|-------------------|------------------|-----------------|
| <u>Muskox River</u> | | | | | |
| Jul.15-Jul.24/91 | TLR | NA | 0.3 _b | 0.6 _a | 0.1 |
| Jul. 2-Jul.27/92 | TLR | 0.4 _a | 0.4 _a | 0.4 _a | 0.0 |
| Jun.27-Jul.29/93 | TLR | 0.5 _a | 0.5 _a | 0.5 _a | 0.0 |
| Jul.15-Jul.24/91 | FLR ⁺ | NA | 0.3 _a | 0.3 _a | 0.0 |
| Jul. 2-Jul.27/92 | FLR | 2.6 _a | 2.7 _a | 2.7 _a | 0.1 |
| Jun.27-Jul.29/93 | FLR | 3.0 _a | 2.9 _a | 2.3 _b | 0.3 |
| Jul.15-Jul.24/91 | HR | NA | 4.6 _b | 5.7 _a | 1.6 |
| Jul. 2-Jul.27/92 | HR | 2.8 _a | 2.4 _b | 1.2 _c | 0.2 |
| Jun.27-Jul.29/93 | HR | 2.2 _a | 2.0 _a | 1.6 _b | 0.2 |
| <u>Thomsen River</u> | | | | | |
| Jul. 2-Jul.27/91 | TLR | 0.1 _b | 0.2 _b | 0.4 _a | 0.0 |
| Jul. 8-Jul.31/92 | TLR | 0.3 _a | 0.3 _a | 0.3 _a | 0.0 |
| Jul. 4-Aug. 3/93 | TLR | 0.2 _a | 0.1 _a | 0.1 _a | 0.0 |
| Jul. 2-Jul.27/91 | FLR ⁺ | 0.1 _b | 0.1 _{ab} | 0.2 _a | 0.0 |
| Jul. 8-Jul.31/92 | FLR | 1.6 _b | 1.9 _b | 2.4 _a | 0.2 |
| Jul. 4-Aug. 3/93 | FLR | 2.5 _a | 1.6 _b | 2.2 _a | 0.2 |
| Jul. 2-Jul.27/91 | HR | 1.4 _b | 1.8 _a | 2.2 _a | 0.3 |
| Jul. 8-Jul.31/92 | HR | 1.6 _a | 1.6 _a | 1.1 _b | 0.1 |
| Jul. 4-Aug. 3/93 | HR | 1.7 _a | 1.4 _b | 1.3 _b | 0.2 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$.
Ten tillers were marked in each of the ten microplots per treatment.

+ 1991 FLR units are: proportion of maximum leaf length grown in ten days, see methods

Table 6-7. Comparison of the mean rate of change in total number of leaves (TLR), length of oldest non-senescent (first) leaves (FLR) (cm), and height (HR) (cm) of *Eriophorum triste* tillers (10 days⁻¹ tiller⁻¹) among treatments in 1 x 1 m microplots. Treatments include unclipped (control) (n=10), temporarily protected (since June 25, 1992 or 1993) (n=20), grazed (i.e., exposed to muskoxen) (n=10) and protected in 1992 but exposed to muskoxen in 1993 (n=20).*

| <u>Dates</u> | <u>Param</u> | <u>T.Excl</u> | <u>Grz</u> | <u>Prt.'92</u> | <u>Cont</u> | <u>MS</u> | <u>Err</u> |
|----------------------|------------------|-------------------|------------------|------------------|------------------|-----------|------------|
| <u>Muskox River</u> | | | | | | | |
| Jul.15-Jul.24/91 | TLR | NA | 0.6 _a | NA | 0.6 _a | 0.2 | |
| Jul. 4-Jul.28/92 | TLR | 0.2 _b | 0.2 _b | NA | 0.4 _a | 0.0 | |
| Jun.30-Jul.30/93 | TLR | 0.2 _b | 0.1 _b | 0.2 _b | 0.5 _a | 0.0 | |
| Jul.15-Jul.24/91 | FLR ⁺ | NA | 0.2 _b | NA | 0.3 _a | 0.0 | |
| Jul. 4-Jul.28/92 | FLR | 2.2 _b | 1.9 _b | NA | 2.7 _a | 0.4 | |
| Jun.30-Jul.30/93 | FLR | 1.6 _b | 1.6 _b | 1.3 _b | 2.3 _a | 0.5 | |
| Jul.15-Jul.24/91 | HR | NA | 2.5 _b | NA | 5.7 _a | 1.3 | |
| Jul. 4-Jul.28/92 | HR | 1.1 _a | 1.0 _a | NA | 1.2 _a | 0.3 | |
| Jun.30-Jul.30/93 | HR | 0.9 _b | 0.7 _c | 0.7 _c | 1.6 _a | 0.3 | |
| <u>Thomsen River</u> | | | | | | | |
| Jul. 2-Jul.27/91 | TLR | NA | 0.3 _a | NA | 0.4 _a | 0.0 | |
| Jul.10-Aug. 1/92 | TLR | 0.2 _a | 0.1 _a | NA | 0.2 _a | 0.1 | |
| Jul. 7-Aug. 3/93 | TLR | 0.1 _a | 0.0 _b | 0.1 _a | 0.1 _a | 0.0 | |
| Jul. 2-Jul.27/91 | FLR ⁺ | NA | 0.2 _a | NA | 0.2 _a | 0.0 | |
| Jul.10-Aug. 1/92 | FLR | 2.4 _a | 2.1 _a | NA | 2.4 _a | 0.5 | |
| Jul. 7-Aug. 3/93 | FLR | 1.1 _b | 1.2 _b | 1.2 _b | 2.2 _a | 0.3 | |
| Jul. 2-Jul.27/91 | HR | NA | 2.3 _a | NA | 2.2 _a | 0.4 | |
| Jul.10-Aug. 1/92 | HR | 1.0 _a | 1.1 _a | NA | 1.1 _a | 0.4 | |
| Jul. 7-Aug. 3/93 | HR | 0.7 _b | 0.7 _b | 0.6 _b | 1.3 _a | 0.2 | |
| <u>Umingmuk Hill</u> | | | | | | | |
| Jul.14-Aug. 4/92 | TLR | 0.2 _b | 0.3 _a | NA | NA | 0.0 | |
| Jul.13-Aug. 7/93 | TLR | -0.1 _a | 0.0 _a | 0.1 _a | NA | 0.0 | |
| Jul.14-Aug. 4/92 | FLR | 2.4 _b | 3.2 _a | NA | NA | 0.6 | |
| Jul.13-Aug. 7/93 | FLR | 0.8 _b | 1.1 _a | 0.8 _b | NA | 0.1 | |
| Jul.14-Aug. 4/92 | HR | 1.1 _a | 1.6 _a | NA | NA | 0.3 | |
| Jul.13-Aug. 7/93 | HR | 0.5 _b | 0.9 _a | 0.5 _b | NA | 0.1 | |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$. Ten tillers were marked in each of the microplots per treatment. 1992: n=19 at TR T.Excl.; n=7 T.Excl., n=10 Grz at UH. 1993: n=14 Prot.'92 at TR; n=10 Grz and T.Excl, n=7 Prot.'92 at UH

+ 1991 FLR units are: proportion of maximum leaf length grown in 10 days, see methods

Temporary protection of tillers increased TLR at TR in 1993 (Tables 6-7). Control tillers had higher TLR than tillers exposed to muskoxen at MR in 1992 and 1993 and at TR in 1993. Protecting tillers in 1992 but exposing them to muskoxen in 1993 increased TLR above grazed levels at TR.

6.3.4 The effect of clipping and grazing on the rate of extension of the oldest non-senescing leaf on tillers of Eriophorum

Clipping depressed the rate of extension of the oldest non-senescing leaf (FLR) on tillers of Eriophorum at TR in 1991 and 1992 (Table 6-6). Clipping had no effect at MR in 1991 and 1992, however in 1993 (one year after clipping) FLR at MR and TR was higher on tillers that had been intensely clipped compared to controls (MR) or less intensely clipped tillers (TR). Clipping depressed FLR at first but FLR returned to control or higher than control levels during the recovery year.

Temporarily protecting tillers at MR and TR did not increase FLR (Table 6-7). In 1991, 1992 and 1993 at MR and in 1993 at TR, FLR in control tillers was higher than in grazed or temporarily protected tillers. In contrast, UH tillers exposed to muskoxen had higher FLR than

temporarily protected tillers. In considering the entire three years of data the results show that long-term protection resulted in increased FLR however muskoxen did not depress FLR in the short-term.

6.3.5 The effect of clipping and grazing on height growth of Eriophorum tillers.

In 1991 clipping decreased the rate of increase in height (HR) of Eriophorum tillers at MR and TR (Table 6-6). In 1992 and 1993 however, the trend was reversed with increases in HR in clipped plots.

Grazers reduced HR compared to control in 1991 and 1993, however in 1992 no differences were observed (Table 6-7). Temporary protection had little influence on HR except at MR in 1993 when an increase above grazed levels was measured. In contrast, at UH grazing increased HR above temporarily protected levels.

6.3.6 The effect of clipping and grazing on the green biomass of Eriophorum triste tillers

Tillers inside the exclosure at MR in 1993 (after a summer of recovery) were the same weight regardless of the clipping treatment imposed in 1991 and 1992 (Table 6-

8). At TR however, tillers weighed less in 2X plots and more in control plots.

At all three sites temporary protection had no effect on tiller weights (Table 6-9). However at TR, tillers protected in 1992 and exposed to muskoxen in 1993 weighed more than tillers exposed to muskoxen during both years. Control tillers weighed more than those outside the permanent exclosure at MR, however, at TR long-term protection resulted in low green tiller biomass. UH tillers weighed more than tillers at MR and TR.

Table 6-8. Comparison of mean Eriophorum triste tiller biomass (g 10 tillers⁻¹) in 1 X 1 m microplots (n=10) inside permanent exclosures in 1993. Microplots were unclipped (control), clipped twice (2X), or clipped once (1X) in 1992 at two study sites.

| <u>Date</u> | <u>Biomass of Tillers</u> | | | |
|----------------------|---------------------------|-------------------|-------------------|------------------|
| | <u>2X</u> | <u>1X</u> | <u>Control</u> | <u>MS Error.</u> |
| <u>Muskox River</u> | | | | |
| July 29 | 0.88 _a | 0.88 _a | 0.89 _a | 0.1 |
| <u>Thomsen River</u> | | | | |
| Aug. 3 | 0.32 _b | 0.38 _a | 0.40 _a | 0.0 |

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

** Ten tillers were marked in each of the 10 microplots per treatment.

Table 6-9. Comparison of mean 1993 Eriophorum triste tiller biomass (g 10 Tillers⁻¹) in 1 x 1 m microplots. Microplots were unclipped (control), temporarily protected (since June 25, 1993) (n=20), grazed (i.e., exposed to muskoxen) (n=10) and protected in 1992 but exposed to muskoxen in 1993 (n=20).*

| <u>Date</u> | <u>Biomass of Tillers</u> | | | | |
|-------------------------|---------------------------|--------------------|-------------------|-------------------|-----------------|
| | <u>Temp.Ex.</u> | <u>Grz.</u> | <u>Prot.'92</u> | <u>Cont.</u> | <u>MS Error</u> |
| <u>Muskox River</u> | | | | | |
| July 30 | 0.53 _b | 0.43 _b | 0.50 _b | 0.89 _a | 0.1 |
| <u>Thomsen River</u> ** | | | | | |
| Aug. 3 | 0.61 _{ab} | 0.49 _{bc} | 0.63 _a | 0.40 _c | 0.0 |
| <u>Umingmuk Hill</u> ** | | | | | |
| Aug. 7 | 0.98 _a | 0.98 _a | 1.02 _a | NA | 0.1 |

* Means with the same subscript within rows are not significantly different at $P \leq 0.10$

** n=10 in each treatment at Umingmuk Hill
n=14 in Prot.'92 at Thomsen River only.

6.4 Discussion

6.4.1 The effects of grazing and clipping on mortality rates of Eriophorum triste

Three years of data demonstrated that grazing and clipping treatments were not severe enough to cause increased tiller mortality rates above control levels during winter and summer. Although summer mortality occurred, it was not the result of grazing by muskoxen or clipping because differences among treatments were slight or non-existent. Tillers in the 2X treatment at MR showed a slight increase in summer-time mortality above control levels because of the combined stress of water saturated soils, clipping and intense lemming herbivory (Chapter 4). Grazing by lemmings had a far greater effect on winter mortality of Eriophorum triste than did clipping inside the permanent exclosure at MR. Winter-time mortality of tillers was far greater than summer-time mortality in this study and it reflects the length of the winter season and the extreme conditions these tillers are faced with for nine months or more.

6.4.2 The effects of grazing and clipping on the fecundity of Eriophorum triste populations.

The lack of consistent and significant differences in tillering and seed head production among the different treatments suggests that both clipping and grazing do little to increase or decrease fecundity in populations of Eriophorum triste. Although significant differences were measured among treatments, rates of tillering and seed head production remained low during the three years this study was conducted. Low levels of tillering and very low seed head production were balanced by low levels of tiller mortality during the summer and small decreases in tiller survivorship overwinter.

Moderate rates of tillering after intense clipping (Figure 6-1) or moderate grazing show that this species persists well in grazed areas. Maintenance of moderate tillering rates in permanently protected plots is consistent with the wide range of tolerance (e.g., to disturbed and undisturbed treatments) shown by Eriophorum vaginatum in Alaska (Fetcher and Shaver 1983). Eriophorum triste also tolerates a wide variety of disturbance regimes.

The low seed head production by Eriophorum triste in this study is consistent with the work of other

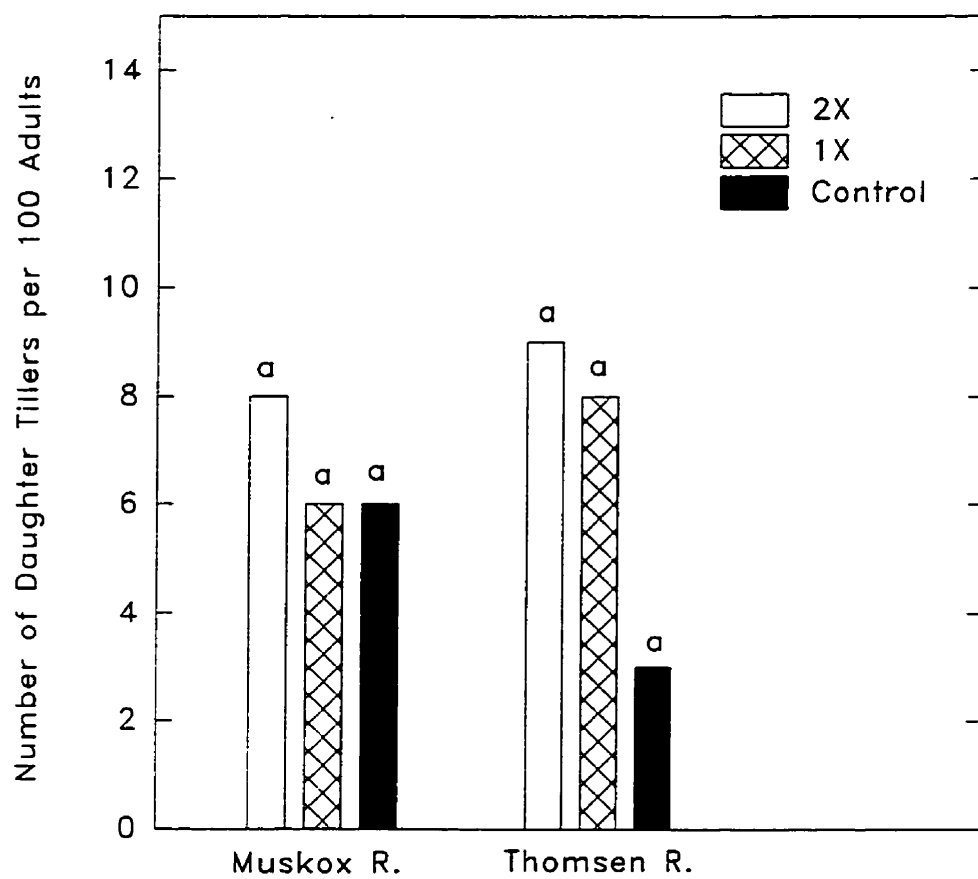


Figure 6-1. Number of daughter tillers produced per 100 adult tillers in 2X, 1X and control microplots at two study sites in 1993.

researchers who found that flowering in the arctic is limited by severe environmental conditions and a short growing season (Bliss 1971; Chapin and Shaver 1981; Lachenbruch *et al.* 1981; McGraw and Shaver 1982; Gartner *et al.* 1986).

The lack of any large differences in tillering or seed head production among sites suggests that the high NH_4 levels in Uminguk Hill soils (Chapter 3) did little to increase fecundity of Eriophorum triste. Fertilization with N or NPK has been reported to increase tillering and seed production in other arctic studies (Babb and Whitfield 1977; McCown 1978; McKendrick *et al.* 1980; Kummerow and Krause 1982; Henry *et al.* 1994b).

These results contradict Fetcher and Shaver (1982), who found that human disturbances such as vehicle tracks and a bladed area, resulted in greater mortality and fecundity rates in Alaskan Eriophorum vaginatum populations, largely as a response to increased nutrient availability, lower quantities of litter and a lower density of competitors. Although mortality rates went up after disturbance, they were balanced by higher rates of tillering. Other researchers (Henry and Svoboda 1989) found that Eriophorum triste had a higher density of flowering shoots in grazed meadows than in non-grazed meadows on Ellesmere Island. In the same study the

density of Eriophorum triste tillers was the same in grazed and non-grazed meadows.

6.4.3 The effects of clipping and grazing on rates of change in leaf number of Eriophorum triste tillers

Distinct short and long term responses to tissue removal exist in this population. Lower rates of change in total leaf number (TLR) on clipped tillers in 1991 compared to controls demonstrates that clipping initially depressed TLR. No differences in 1992 and 1993 shows that the longer-term consequences of the clipping treatments on TLR were neutral. Clipped tillers had the capacity to recover from initial decreases in TLR even after an additional year of clipping in 1992. Long-term responses to tissue removal include the high TLR of lemming-grazed tillers inside the exclosure at MR and of muskoxen-grazed tillers at UH. The increased rates of TLR in control tillers compared to tillers outside the permanent exclosure at MR are in contrast to the under-compensation observed for the plant community at the same site (Chapter 3). Eriophorum triste is thus more tolerant of intense tissue removal than the community as a whole. At least one year after intense clipping or moderate grazing

compensatory mechanisms allow TLR to return to or above control levels. These observations are consistent with the results reported for rates of change in lengths of the oldest non-senescing (first) leaves (FLR).

6.4.4 The effects of clipping and grazing on rates of change in leaf lengths on Eriophorum triste tillers

The additional effect of clipping over and above the effects of lemming herbivory and superhygric (i.e., saturated) soil in the MR exclosure was minimal on FLR in 1991 and 1992. By 1993 however, compensatory growth increased FLR in clipped tillers at MR. Similarly, at TR initial decreases in FLR were balanced by later increases in FLR in intensely clipped tillers during the recovery year. Although a year of recovery was necessary to initiate compensatory growth, the results demonstrate once again that these tillers were tolerant of clipping. Henry and Svoboda (1989) documented that leaf growth was the same in clipped and unclipped tillers of Eriophorum triste. In this study grazing intensities in the short term were not high enough to decrease FLR at MR and TR however grazing intensities in the long-term were high enough to decrease FLR at TR in 1993.

It is possible that the compensatory mechanisms for FLR are dependent on increased soil nutrient uptake rates in plants. This hypothesis is supported by the fact that grazed tillers at UH and control tillers at MR had high crude protein content (Chapter 5) and high FLR values (Figure 6-2). High protein levels in MR control forage samples suggest that soil nitrogen uptake rates were high despite the low soil NH_4 levels (Chapter 4). UH had the most nutritious forage and the highest soil NH_4 levels of the three study sites (Chapters 3 and 4). The observations at UH are consistent with those of Hik and Jefferies (1990) who found that compensatory growth after goose grazing was present if goose feces were applied and with those of Chapin et al. (1986a) who found that Eriophorum vaginatum in Alaska was largely limited by nitrogen. Thomsen River had the lowest quality forage of all 3 sites in 1993 combined with relatively dry soil conditions throughout the growing season (Chapters 4 and 5, pers. obs. 1991-93) which explains why FLR was higher in controls. The environmental conditions in the area exposed to muskoxen at TR were not conducive to rapid uptake of nutrients by plants and to compensatory growth in Eriophorum triste populations.

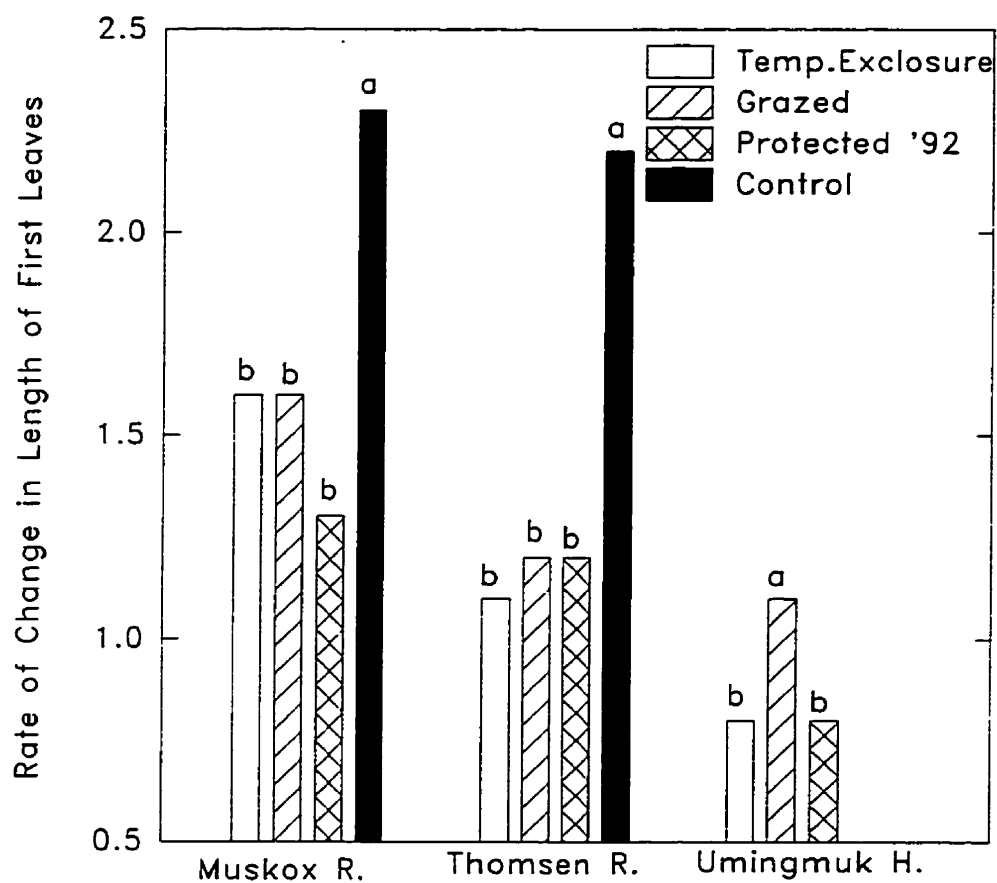


Figure 6-2. Comparison of the mean rate of change in length of the oldest non-senescent (first) leaves of *Eriophorum triste* tillers (cm (10 days)⁻¹ tiller⁻¹) among treatments in 1 X 1 m microplots. Treatments include unclipped (control), temporarily protected, grazed and protected in 1992 but exposed to muskoxen in 1993. Sample sizes in text.

6.4.5 The effects of clipping and grazing on rates of change in height of Eriophorum triste tillers

Rate of increase in height (HR) of clipped tillers showed an initial decrease and eventually an increase above control levels (Figure 6-3) as did the other parameters (TLR and FLR) in this experiment. This confirms that compensatory mechanisms to tissue removal exist in populations of Eriophorum triste. These data are consistent with the fact that the abundance of Eriophorum triste is higher in grazed and clipped treatments than in controls (Chapter 4). The decreases in HR observed in tillers exposed to muskoxen at TR are consistent with the community level results (i.e., exact- and under-compensation) from Chapter 3. More intense grazing by lemmings of MR control tillers and by muskoxen of UH tillers resulted in increased HR.

The results consistently show that a threshold exists, and that grazing/clipping intensities above the threshold initially decrease but eventually increase tiller growth. Grazing intensities below the threshold decrease or do not change tiller growth. The relationship between tiller growth and tissue removal is confounded by time and by nutrient availability/uptake rates. Given time, intensely clipped or grazed tillers will compensate

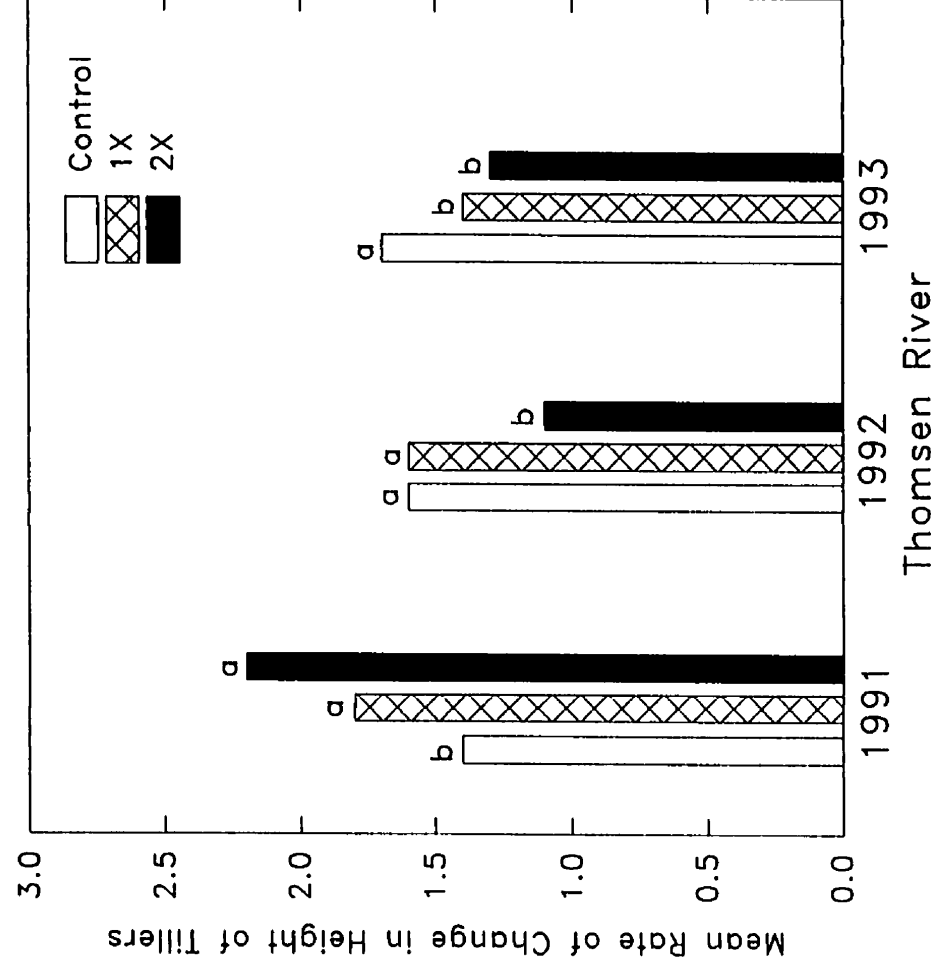


Figure 6-3. Comparison of the mean rate of change in height of *Eriophorum triste* tillers (cm 10 days⁻¹) among treatments inside 1 x 1 m microplots. Treatments inside permanent enclosure included unclipped (control), clipped twice (2X) or clipped once (1X) per growing season at Thomsen River.

for tissue removal. The high crude protein levels in MR control forage samples (Chapter 5) and the low NH_4 levels in MR control soil samples suggests that there is rapid uptake of N as it mineralized. The ability to acquire mineralized nitrogen from the soil and/or root reserves is more important than soil NH_4 levels *per se*. The biphasic response of intensely clipped tillers suggests that the mechanisms that boost tiller growth require at least one year to begin operating. In some cases as in FLR, compensatory growth only occurred during the recovery year which suggests that replenishment of carbohydrate reserves was necessary in order for FLR to exceed control levels.

Intensely clipped or grazed Eriophorum tillers compensate for tissue losses by allocating most of their resources into increased leaf length and vertical growth. The cost of compensatory growth is reduced root biomass (Chapter 3) and/or depleted soil NH_4 pools (Chapter 4). Chapin and Slack (1979) documented that clipped Eriophorum vaginatum plants with depleted root systems had higher uptake rates of P than controls. This mechanism may have contributed to the compensatory growth observed in this study as it is well documented that tundra graminoids are more nutrient- than carbon-limited (Chapin et al. 1986b). There is no guarantee, however,

that these tillers could continuously withstand such high clipping intensities year after year because carbohydrate reserves would likely become depleted.

6.4.6 Grazing- and clipping-induced changes in tiller biomass

Despite the population-level compensatory growth observed in 1993 at TR, clipped tillers were not able to attain the same size as unclipped tillers by the end of the experiment. At the MR permanent exclosure, compensatory growth balanced the negative effects of intense lemming herbivory and superhygric conditions. Grazed tillers at UH compensated for tissue losses through increased growth rates. The demonstrated ability of Eriophorum triste tillers to compensate for short-term losses to grazers contrasts with community-level productivity data that shows exact- and some under-compensation to muskoxen herbivory (Chapter 3).

In addition to having greater standing crops (Chapter 3), UH also had greater tiller weights than the other two sites. These results are consistent with the observations in Chapter 3 which document that the UH site is more favorable for plant growth than MR or TR sites. The aggregate response of tiller growth rates to grazing

and clipping is the persistence of Eriophorum triste in undisturbed treatments and its increased abundance in clipped and grazed treatments (Chapter 4).

7.0 GENERAL DISCUSSION AND SYNOPSIS

7.1 The Herbivore-Optimization Hypothesis

The lack of any community-level, over-compensation and the degree of under-compensation observed after grazing and clipping suggests that graminoid meadows in the study area are limited in their ability to withstand herbivory. Lower root standing crops observed after grazing and clipping at MR and TR respectively, strengthen the conclusion that plant growth at the community-level is negatively affected by both types of defoliation. High grazing intensities over a number of years probably contributed to the under-compensation observed in this study. This conclusion is based on the fact that the study area supports some of the highest muskox densities reported in the arctic (Hubert 1977; Gunn 1984; Thing et al. 1987; McLean et al. 1989; Raillard 1992). Clipping removed even more shoot tissue than grazing which no doubt contributed to the greater occurrence of under-compensation in clipped than in grazed plots.

The lack of any community-level over-compensation across a gradient of shoot tissue removal that varied from 0-40% refutes the herbivore optimization hypothesis

in the tundra graminoid meadow system. Contrary to the predictions of the hypothesis, moderate grazing intensities (e.g., 10%) did not stimulate plant growth.

The community-level responses are influenced by the ages of the permanent exclosures (6-8 years). If the exclosures were significantly older, decreases in NAPP of control plots compared to moderately grazed plots would be more likely. It takes many years for a mulch layer to form in the arctic (Henry and Svoboda 1989), thus there is a time lag required for substantial decreases in NAPP in ungrazed plots. Aside from the complicating factor of litter accumulation, the results clearly show that grazing and clipping *per se* do not stimulate plant growth at the plant community level.

Initial decreases in tiller growth in intensely clipped/grazed tillers and throughout the study in moderately or lightly clipped tillers is consistent with community-level data. Clipping and grazing *per se* decrease tiller growth, however intrinsic mechanisms exist to help tillers withstand intense shoot tissue removal. Genets are long-lived in the arctic (e.g., 100+ years (Mark et al. 1985)) thus, the chance of being grazed is high during a genets' life span. Intrinsic mechanisms of compensation as well as growth form characteristics aid Eriophorum triste and other species

in arctic graminoid meadows to tolerate herbivory and other disturbances. A well-established literature shows that rhizomatous graminoids possess characteristics such as ground-level meristems, compensatory photosynthesis and resource allocation patterns (Chapin *et al.* 1980; McNaughton 1983a, 1985a; Briske 1986) that enable them to tolerate herbivory. Physical and physiological attributes enable Eriophorum triste to increase in abundance at disturbed sites (Chapter 4). The balanced mortality and fecundity in all grazing/clipping regimes reported in this study (Chapter 6) also contributes to the presence of Eriophorum triste in clipped, grazed and control treatments in this study (Chapter 4).

Populations of Eriophorum triste showed a variety of responses to clipping and grazing compared to the graminoid meadow plant community. Tolerance of grazing and clipping in Eriophorum triste can be attributed in part to the delayed increase in tiller growth rates after intense shoot tissue removal (Chapter 6). The physiological mechanisms that allow Eriophorum triste to increase in abundance in disturbed environments are activated only in intensely clipped and grazed tillers. Soil nutrient levels in the study area are sufficient to allow this mechanism to operate. Other researchers have reported that uptake rates of soil nutrients increase if

intense clipping or grazing occurs (Chapin and Slack 1979). Because carbon is rarely a limiting factor in the arctic (Chapin 1978; McKendrick et al. 1978; Shaver et al. 1986; Henry et al. 1994b) increased nutrient uptake rates are assumed to play an important role in compensatory growth of arctic graminoids. In this study, the increase in nitrogen content of live shoot tissue after lemming grazing suggests that increased uptake of nitrogen is involved in the compensatory growth observed in Eriophorum triste tillers.

7.2 Forage Quality

Both muskoxen and lemmings contribute to a more nutritious forage base in the study area by decreasing the percentage of dead tissue in forage samples in the long-term. Although NAPP was reduced by lemming herbivory and to a lesser extent by muskoxen, increases in forage quality may have offset any disadvantages of decreased forage availability in sustaining muskoxen in the study area. Forage availability in graminoid meadows is not a limiting factor for muskoxen during the summer months. Heavily grazed patches were uncommon and characteristically small ($>15 \text{ m}^2$) and irregularly shaped (pers. obs. 1991-1993). Green standing crop (GSC) data in

grazed areas confirm that muskoxen left significant amounts of green plant tissue.

The hypothesis that muskoxen and lemmings benefit from the effects of their grazing is supported by the fact that the most nutritious forage in this experiment is also the most heavily grazed. Large standing crops of nutritious forage at UH allow muskoxen to feed in large groups (e.g., 60 or more animals (pers. obs. 1991-1993)). This explains why the site has higher fecal pat densities than MR even though forage quality was similar at the two sites. Smaller groups of muskoxen or single animals took advantage of high forage quality at MR. The site with the lowest forage quality (i.e., TR) had the lowest fecal pat densities.

Site characteristics no doubt affected forage quality in this study. The close proximity of permanent exclosures to adjacent grazed areas and the consistency with which heavily grazed vegetation showed high forage quality suggests that herbivores contribute to maintaining and to creating a nutritious forage base in the study area. Muskoxen play an important role in maintaining nutritious forage and in increasing forage quality in the long-term.

7.3 Plant Community Changes in Structure, Reproductive Output and Environment after Clipping and Grazing

Changes in plant community physiognomy after grazing and clipping reinforce grazing intensity and fecal pat density data and confirm that muskoxen are indeed a significant ecological force within the study area. The observation that community-level species composition remains constant after grazing and clipping supports the observation that Eriophorum triste populations persist in clipped, grazed and control treatments (Chapter 6). Prostrate forbs (e.g., Antennaria spp.) simply are not present to invade disturbed sites in arctic meadows. The low-growing physiognomy of arctic meadow vegetation likely contributes to the stability of species structure in these communities. However, the wide range of tolerance to disturbance of arctic sedges (Fetcher and Shaver 1982, 1983; Cargill and Jefferies 1984a; Hik and Jefferies 1990; Chapter 6) does not preclude niche specialization. Chapin and Shaver (1985) found little niche overlap in an Alaskan tussock tundra meadow. It is hypothesized that the tolerance of graminoid meadow plant species to disturbance increases the meadow's resistance to perturbation.

The mechanisms that increase growth rates of Eriophorum triste tillers in intensively clipped and grazed treatments enable the species to persist after disturbance. Soil moisture also affects species abundances in graminoid meadows. Eriophorum triste is less abundant in hygric than in sub-hygric meadows. Conversely, Carex aquatilis and Dupontia fischeri are more common in hygric than in sub-hygric meadows (Chapter 4). Although soil moisture influences the abundance of Eriophorum triste, the consistency with which the species increases in abundance in grazed and clipped plots suggests that these treatments play a role in altering the species abundance.

Seed head density was reduced in graminoid meadows as a consequence of grazing and clipping. The low seed head density in graminoid meadows and in populations of Eriophorum triste in this study support other studies (Bliss 1971; Chapin and Shaver 1981; Lachenbruch et al. 1981; McGraw and Shaver 1982; Gartner et al. 1986) documenting the low rate of sexual reproduction in the arctic. Although populations of Eriophorum triste showed few differences in seed head densities among treatments the community-level data demonstrate that grazing and clipping have the potential to alter the genetic composition of meadows.

Fecal pat density data confirm that UH is a favored site for grazing muskoxen. The site characteristics at UH that maintain a large quantity of overwintering green plant tissue, large green standing crops (Chapter 3), a warm microclimate, a steady supply of meltwater (Chapter 4) and a nutritious forage base (Chapter 5) attract muskoxen. By depositing more feces at UH, muskoxen increase soil nutrient content (Chapter 4). Higher levels of soil nutrients at UH contribute to the maintenance of the site as a favorable grazing area.

Both site characteristics, and clipping and grazing influence NAPP data. The consistent response of NAPP to grazing and clipping suggests that these treatments were indeed important factors in regulating NAPP. The results accurately portray the response of vegetation to grazing and clipping in an arctic environment. How vegetation responds to grazing under these environmental conditions will ultimately affect muskoxen populations.

7.4 Synopsis

This study confirms that muskoxen removed up to 40% of shoot tissue during a single growing season and thus are a significant ecological force in the study area. By concentrating their feeding, resting and ruminating

activities into small areas (i.e., graminoid meadows) muskoxen have significant effects upon a number of ecological parameters including: net above-ground primary productivity, tiller growth rates, above- and below-ground standing crops, forage quality, community physiognomy, litter layer thickness, seed head densities, species abundances and soil nutrient levels. These results contrast with previous work (Bliss, 1986 and Pimentel, 1988) which concluded that herbivores play a minor role in arctic ecosystems due to low herbivore densities and severe climatic conditions. This study suggests that the role of herbivory in arctic ecosystems might have to be redefined.

High grazing and clipping intensities had negative effects on NAPP. None of the community-level data gathered provide evidence to support the herbivore optimization hypothesis. This study is the first to document that under-compensation is a significant ecological response to muskox-grazing and mechanical clipping treatments in arctic meadows. In contrast, Cargill and Jefferies (1984a) and Hik and Jefferies (1990) found that snow geese increase rates of NAPP in sub-arctic meadows. Generalizations about plant-animal interactions are inappropriate since the plant-animal

interface is influenced by a vast number of variables that differ spatially and temporally.

Increases in forage quality in heavily grazed areas and compensatory growth in the most abundant meadow species ameliorates the potentially negative effects of under-compensation observed in this study. Specific mechanisms that allow muskoxen to benefit from regrazing previously grazed areas include: 1) Increased forage quality at heavily grazed sites; 2) Increased rates of growth in intensely clipped or grazed tillers of Eriophorum triste and 3) Higher soil nutrient levels at heavily grazed sites. The long-term association of Banks Island graminoid meadows and muskoxen, as suggested by fossil evidence (Nelson, 1989), may have played a role in the development of these mechanisms.

Large standing crops and good forage quality in grazed areas confirms that summer forage did not limit muskox populations in the early 1990's within the study area. Disease (Blake et al. 1989) and winter forage availability (Miller et al. 1977) play a more important role in limiting muskox populations than availability and quality of summer forage in graminoid meadows. Muskoxen are not limited by predators in the study area. If muskox densities continue to increase, the degree of under-compensation observed will increase. However, severe

winter conditions are much more likely to reduce muskox densities before the vegetation becomes seriously damaged.

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APPENDIX A. HOMOGENEITY OF VEGETATION INSIDE PERMANENT EXCLOSURES.

The homogeneity of vegetation inside permanent exclosures was assessed because microplots were distributed nonrandomly (Figure 3-1). Data in Tables A1 and A2 address this problem by comparing parameters among spatially separate treatment blocks at points in time and by comparing parameters among years (before (1991) and after clipping (1992)), respectively.

Methods are identical to those presented in the main body of the thesis. Data were analyzed using one-way analysis of variance and LSD mean comparisons tests (Sokal and Rohlf 1981). Total standing crop (TSC), average ramet height, and total number of leaves per tiller (TL#) data were compared among treatments before any clipping took place at MR and TR study sites in 1992 and 1991 respectively. These data document the homogeneity of vegetation within permanent exclosures during the early stages of the experiment. In 1993 strips of undisturbed vegetation were located between treatment microplots. Total standing crop, height, and depth to permafrost data were collected from these undisturbed areas in an attempt to document the homogeneity of vegetation within the permanent exclosures at the end of

the experiment. Green standing crop (GSC), dead standing crop (DSC) and total standing crop (TSC) data were compared among years (1991 and 1992) in a given treatment in order to determine if clipping had a significant ecological effect. Data from 1991 were collected prior to any clipping. Data from 1992 were collected one year after the initiation of clipping treatments.

Total standing crop, height and total leaf number data were similar among treatments before any clipping took place inside the two permanent exclosures (Table A1). Of the six mean comparisons made prior to clipping, only one showed a significant difference. Comparisons from undisturbed treatments adjacent to treatment microplots at the end of the experiment showed similar results. Of the 18 mean comparisons made, only two were significantly different.

Green standing crop, dead standing crop and total standing crop data compared among years at MR predictably showed only one significant difference out of three comparisons (Table A2). Clipping had a minimal effect at MR due to the intense lemming herbivory and superhygric soil moisture status at the site. In contrast, at TR clipping had a significant effect on green standing crop, dead standing crop and total standing crop data. All six mean comparisons showed significant differences. Control

1992 data were similar to early-season 1991 data (before clipping took place) from 2X and 1X treatments.

These data confirm the homogeneity of vegetation within each permanent exclosure at the beginning and end of this thesis research. Any small environmental differences that exist within an exclosure were overridden by the severity of the clipping treatments.

Table A1. Comparison of mean (MS error) total standing crop (TSC) (g m^{-2}) (n=5), total number of leaves per tiller of *Eriophorum triste* (TL#) (n=10), height (cm) and depth to permafrost (cm) (n=10) estimates in undisturbed microplots prior to clipping (1991 and 1992) or adjacent to treatments microplots (1993) inside permanent Exclosures in 1993.*

| <u>Date</u> | <u>Parameter</u> | <u>2X</u> | <u>1X</u> | <u>Cont</u> | <u>MS Error</u> |
|----------------------|------------------|------------------|------------------|------------------|-----------------|
| <u>Muskox River</u> | | | | | |
| Jul. 4/92 | TSC | NA | 5 _a | 5 _a | 5 |
| July 4/92 | Height | NA | 7 _a | 7 _a | 1 |
| Jul. 4/92 | TL# | NA | 3 _a | 3 _a | 0 |
| Aug. 1/93 | TSC | 167 _a | 135 _a | 151 _a | 1063 |
| Aug. 4/93 | Height | 13 _a | 13 _a | 14 _a | 3 |
| Aug. 4/93 | D.Permafrost | 39 _a | 35 _b | 34 _b | 3 |
| <u>Thomsen River</u> | | | | | |
| Jul. 2/91 | TSC | 104 _a | 90 _a | NA | 937 |
| July 2/91 | Height | 7 _a | 5 _b | NA | 1 |
| Jul. 2/91 | TL# | 3 _a | 3 _a | NA | 0 |
| Aug. 4/93 | TSC | 261 _a | 270 _a | 316 _a | 7636 |
| Aug. 1/93 | Height | 6 _a | 6 _a | 8 _a | 6 |
| Aug. 4/93 | D.Permafrost | 36 _a | 38 _a | 38 _a | 10 |

* 1991 and 1992 microplots clipped at 1.5 cm
1993 microplots clipped at ground level
2X and 1X microplots adjacent to clipped microplots
All data from undisturbed microplots
Means with the same subscripts within rows are not significantly different at $P \leq 0.10$

Appendix A2. Comparison of mean (\pm SE_x) green (TSC), dead (DSC) and total standing crop* (TSC) estimates (g m^{-2}) among years (n=5) inside permanent exclosures.

| Date | Parameter | Treatment | Mean Standing Crop | |
|----------------------|-----------|-----------|---------------------|--------------------|
| | | | 1991 | 1992 |
| <u>Muskox River</u> | | | | |
| Jul. 8 | GSC | 1X | 1± 0 _b | 2± 0 _a |
| | DSC | 1X | 3± 1 _a | 3± 1 _a |
| | TSC | 1X | 4± 1 _a | 4± 1 _a |
| <u>Thomsen River</u> | | | | |
| Jul. 3 | GSC | 2X | 3± 1 _b | 7± 1 _a |
| | DSC | 2X | 101± 8 _a | 15± 1 _b |
| | TSC | 2X | 104± 9 _a | 23± 2 _b |
| Jul. 6 | GSC | 1X | 4± 1 _b | 13± 1 _a |
| | DSC | 1X | 86±10 _a | 25± 2 _b |
| | TSC | 1X | 90±11 _a | 39± 4 _b |
| Jul. 8 | GSC | Cont. | NA | 4± 1 |
| | DSC | Cont. | NA | 101± 8 |
| | TSC | Cont. | NA | 106± 8 |

* 1991 and 1992 microplots clipped at 1.5 cm
Means with the same subscript within rows are not significantly different at $P \leq 0.10$