The Impacts of Wood Bison Grazing on a Sub-Hygric Shrub Meadow Plant Community Type

Mackenzie Bison Sanctuary, Northwest Territories

By David L. Smith

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THE IMPACTS OF WOOD BISON (BISON BISON ATHABASCAE) GRAZING ON A SUB-HYGRIC SHRUB MEADOW PLANT COMMUNITY TYPE, MACKENZIE BISON SANCTUARY, NORTHWEST TERRITORIES

by

DAVID L. SMITH

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ABSTRACT

Non-woody, vascular plants within the Shrub Meadow plant community type, the primary summer range of Wood Bison (Bison bison athabascae), showed exact- and over-compensation in response to natural and simulated herbivory during the 1986 and 1987 growing seasons. Vegetation that over-compensated in response to herbivory had higher above-ground primary productivity (g $m^{-2}d^{-1}$) than ungrazed controls. Vegetation that compensated exactly for herbivory had similar productivity relative to ungrazed controls. Absolute quantities of standing dead tissue were much higher in ungrazed plots. It is proposed that extrinsic mechanisms (e.g., changes in microclimate and the physical obstruction of plant growth associated with the accumulation of dead tissue) were in part responsible for lower productivity in ungrazed plots compared with grazed areas. Naturally grazed and artificially grazed vegetation had similar productivity, indicating that Wood Bison had no additional effect on productivity over simple clipping in the short-term. However, in the long-term Wood Bison may have boosted the productivity of the Lake 650 study site by importing nutrients in the form of feces and urine. Grazing intensities, consumption rates, and the number of fecal pats were higher at Lake 650 than at any other study site. Productivity rates were considerably higher in 1986 than in 1987, probably due to higher rainfall in 1986.

Wood Bison selected Carex atherodes (CXAT) over all other species within the Shrub Meadow c.t. Grasses were consumed at intermediate levels and forbs remained ungrazed. It is hypothesized that Wood

Bison were able to consume more high quality forage by feeding on dense stands of high quality CXAT than by feeding on lower quality grass stands or on sparsely vegetated, prostrate forb stands.

Moderate grazing intensities shifted the species composition of meadows from graminoid-dominated, species-poor assemblages with low species diversity to species-rich, diverse associations of graminoids and forbs. Wood Bison grazing reduced the height of plants, removed competitively superior, graminoids, and created patches of bare ground, thus reducing interspecific competition in plots. Reproductive output was lower in grazed genets. Heavy accumulation of dead tissue in ungrazed plots at Lake 650 and lower summer precipitation were also responsible for decreased reproductive output from 1986 to 1987.

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TABLE OF CONTENTS

LIST OF TABLES

List of Tables (cont.)

LIST OF FIGURES

List of Figures (cont.)

LIST OF APPENDICES

Table of Appendices (continued)

Table of Appendices (continued)

Table of Appendices (continued)

1. INTRODUCTION

Large grazing animals can impact vegetation in a variety of ways. Changes in the productivity, species composition, species richness, species diversity, physiognomy, nutritional quality and reproductive ability of vegetation can occur. The degree to which these changes take place to a large extent reflects grazing intensity.

The accumulation of dead and live tissue at ungrazed sites reduces productivity rates (Ellison 1960; McNaughton 1983; Cargill and Jefferies 1984). The microclimate of ungrazed sites may become cooler and accumulating plant tissue may lower light intensities and create a physical barrier slowing new growth. Since dead and senescent tissue is lower in food quality (Stoner et al. 1982; McNaughton 1985) ungrazed plants may be less valuable forage than grazed plants. Interspecific competition is characteristically more intense in ungrazed areas (Menge and Sutherland 1976; Whittaker and Levin 1977). This leads to species-poor, homogeneous stands where erect competitively-superior species are common and grazing-tolerant, laterally-oriented, competitively-inferior forbs are rare. The reproductive output and absolute fitness (e.g., the contribution that a genotype makes to the next generation) of ungrazed genets can be relatively high (Harper 1977).

Overgrazed plants have depleted carbohydrate and nutrient reserves (Kennedy 1950; Albertson 1953; Cook et al. 1958) which lead to low productivity rates. Overgrazed areas commonly have larger proportions of bare ground and may be eroded in places. By selecting competitively superior, palatable dominants, grazers free resources for competitively inferior grazing-tolerant forbs, thus decreasing interspecific competition for resources. The species richness and diversity of overgrazed areas may be low because only a few species can tolerate such high grazing intensities (Grime 1973). Although overgrazed sites have plants with little or no dead tissue and structural carbohydrates, they are also sparsely vegetated, and thus provide little food value and support fewer grazers.

In contrast, moderately grazed areas tend to be more productive than ungrazed and overgrazed areas (Prins et al. 1980; Cargill and Jefferies 1984), although there has been considerable debate over this in the literature (Belsky 1986). Rapidly growing grazed plants tend to have less structural carbohydrates, lower quantities of dead tissue, and higher nutrient levels than ungrazed plants (Jameson 1963; McNaughton 1985; Seastedt 1985). Because moderate grazing intensities free resources for grazing-tolerant forbs, interspecific competition decreases and species richness and diversity increase, resulting in a mix of erect, light-seeking graminoids and prostrate, grazing-tolerant forbs. The high species richness and diversity at moderately grazed sites may increase the resistance (the ability to maintain a steady state) of vegetation to disturbance (Odum 1953; Ellison 1960; Clarke 1962; Connell and Orias 1964; Holling 1973; Whittaker and Levin 1977; McNaughton 1985). However, the reproductive output and absolute fitness of meadow vegetation is commonly decreased by moderate grazing (Belsky 1986).

In 1963, 18 Wood Bison (Bison bison athabascae) were introduced into the Mackenzie Bison Sanctuary (MBS) adjoining the west shore of Great Slave Lake in the Northwest Territories. Since then the population has grown exponentially and now numbers over 2,000 (Gates and Larter 1990). Because of this very rapid increase and because some areas of the primary summer range of Wood Bison, the Shrub Meadow community type (c.t.) (Larter 1988) appeared to be overgrazed, it was important to quantify and qualify some of the impacts Wood Bison are having on this c.t. Chapter 2 examines how Wood Bison grazing influences the productivity of the Shrub Meadow c.t. relative to artificial grazing or no grazing. The effect of these grazing treatments at different intensities and frequencies on productivity rates is examined. This chapter offers hypotheses on how increased quantities of standing dead tissue and slower plant growth in ungrazed plots affects plant quality. Spatial and temporal trends in productivity within this c.t. are examined and conclusions are made on why these trends occurred and how grazing intensities and consumption rates were affected. Chapter 3 examines the food habits of Wood Bison in this c.t. Predictions are made about the relative value of sedge, grass and forb stands to Wood Bison. Chapter 4 examines how the feeding patterns of Wood Bison influence the species structure, physiognomy and reproductive output of Shrub Meadow vegetation and proposes hypotheses on how grazing might influence the resistance of vegetation to disturbance. Based on the observed shift in species composition in grazed plots, Chapter 4 provides conclusions on how grazing affects interspecific competition in plants within this c.t. In Chapter 5, the General Discussion, I relate each of the chapters and arrive at conclusions about the condition of the MBS Shrub Meadow c.t. in the late 1980's.

1.1 Study Area

All of the study sites lie within the 5829 km^2 area designated as the Mackenzie Bison Sanctuary (MBS) (Figure 1-1). The MBS is in the Upper Mackenzie Section of the Boreal Forest Region (Rowe 1972) and is part of the Great Slave Lake Plain, which forms part of the Interior Plains physiographic province (Bostock 1964). The sanctuary thus occurs on part of a glacial lake which receded in post-glacial time. Lake Athabasca and Great Slave Lake are both remnants of this glacial lake. Soils in the area were derived from glacial till deposited by the Laurentide ice sheet (Douglas 1959) and from lacustrine sediments deposited by Glacial Lake McConnell (Mychaisw 1986). Day (1968) found that 24% of the Upper Mackenzie Area (which includes the MBS) is covered by organic soils.

The topography is level with some undulations. Slopes range from .5% to 2.5%. Elevation ranges from 180m to 240m (Mychaisw 1986). Because the slope gradient is low, drainage is characteristically sluggish. Accumulation of water in lower areas has resulted in the formation of a wide range of organic terrain types (Mychaisw 1986). Most streams in the area are intermittent, including the Bluefish River, the major water course in the west-central part of the sanctuary (Mychaisw 1986). The most important topographical feature to bison is the large area of lacustrine depressions. Falaise Lake, the largest in the sanctuary (Figure 1-1) covers an area of 7,500 ha (Mychaisw 1986). These wet depressions are relict lakes with relatively small portions of persistent water. Stands of *Carex* spp. and grasses are abundant in these depressions and appear to supply

Wood Bison with most of their food. Vegetation is characteristically more shrubby (Salix spp.) around the peripheries of these lake beds than in more central areas.

Burns (1973) described the thermal regime of the area. Primarily cold arctic air masses are present over the Sanctuary during the winter (October - March). During the summer (June - August) and the transition periods (May and September), the arctic air recedes and the area is covered with warmer air. On average the MBS has 275 days per year with frost. The 30 year normal annual precipitation amount for Fort Providence (80 km SW of the MBS) is 279.5 mm with 34% of this falling during the growing season (Table 1-1, Atmospheric Environment Service 1985). The mean monthly temperature during the growing season is 14.6°C. Mean monthly temperatures can range 43.8°C from the coldest month (January) to the warmest month (July) (Mychaisw 1986). The absolute minimum and absolute maximum temperatures recorded between 1951 and 1980 in Fort Providence were -50°C in February and 36°C in August, respectively (exact dates were not available, Atmospheric Environment Service 1985).

Mychaisw (1986) has described and calculated the areas of the community types in the MBS (Tables 1-2 and 1-3). The Sedge and Shrub Meadow components are the most important to bison as a food resource. In this study, meadow vegetation was divided into two community types (c.t.) Shrub and Sedge Meadow.

All data were collected from the Shrub Meadow c.t., a sub-hygric, i.e., moist meadow type found in peripheral areas of relict lake beds. Soils are lacustrine and gleyed with a thick humus layer present. I classified the soils within this c.t. to be in the Cryosolic order, the Static Cryosol Great Group and the Brunisolic Static Cryosol Subgroup (see Chapter 2). Raup (1933), Larter (1988) and I observed that bison prefer the Shrub Meadow c.t. during the summer months (June, July, August).

The Sedge Meadow c.t. is found in sub-hydric, i.e., in wetter areas. Soils are lacustrine and gleyed with a thin humus layer. They are almost continuously saturated with water. Bison utilize these meadows during the winter months when soil is frozen (Raup 1933; Larter 1988). Bison take advantage of the cooler conditions in these meadows during exceptionally warm summer days (Larter pers. comm. 1986).

Five sites were selected for intensive study: Calais Lake East, Calais Lake West, Lake 690, Lake 650, and Dieppe Lake (Figure 1-1). Bison exclosures were located at all sites.

Table 1-1. Mean Monthly Precipitation (mm) and Mean Daily Temperature (Celsius) Data with Ranges Collected at Fort Providence, N.W.T. Meteorological Station from 1951-1980.

Month	Precipitation			Temperature		
	Min.	Normal	Max.	Min.	Normal	Max.
January	7.2	21.9	39.4	-32.4	-27.5	-18.5
February	3.3	15.0	39.6	-26.5	-22.9	-15.0
March	4.1	18.3	43.4	-21.3	-16.0	-11.8
April	1.5	16.3	49.0	-14.0	-3.3	-0.1
May	0.5	19.4	62.7	4.3	7.1	11.7
June	3.6	25.9	62.2	10.6	13.1	16.3
July	7.9	37.5	79.0	13.3	16.3	18.0
August	4.6	30.4	101.1	10.9	14.5	17.0
September	7.9	28.6	44.5	6.0	7.8	10.5
October	1.8	19.3	49.3	-4.7	-0.2	2.5
November	3.8	24.7	53.3	-20.8	-12.2	-5.4
December	8.1	22.2	48.5	-26.5	-23.0	-16.3
ANNUAL	174.4	279.5	359.1	-5.4	-3.9	-2.8

Table 1-2. Physiognomic Classification* of Plant Community Types at the Mackenzie Bison Sanctuary

Plant Communities	Differentiating Characteristics
Sedge Meadow (SEM)	Less than 15% shrub cover, mesic to hygric fens, sedges generally more abundant than grasses.
Shrub Meadow (SHM)	Shrub cover 15-35% , drier than SEM, mesic to sub-hygric moisture, usually occurs between sedge meadow and forest cover types, grasses and sedges present in varying amounts.
Shrubland (SHL)	Shrub cover more than 35% , lower stratum includes grasses, sedges, and forbs.
Mixed Forest (MIX)	Deciduous (*Populus* spp.) and coniferous (*Pinus banksiana*) tree species occurring together in varying proportions with deciduous species dominant.
Pine Forest (PNE)	Continuous occurrence of *Pinus banksiana*. Deciduous species and *Picea* spp. may represent up to 25% of cover in tree stratum.

(Continued)

Table 1-2. concluded

Plant Communities	Differentiating Characteristics
Spruce Forest (SPF)	Continuous occurrence of *Picea* spp., other species may represent up to 25% of the tree stratum.
Mixed Pine and Spruce (MCF)	*Picea* spp. and *Pinus banksiana* occur in varying proportions in the tree stratum.
Organic Terrain (ORG)	Wet areas characterized by organic soil. *Betula* spp. and ericaceous shrubs present beneath open *Picea mariana*, *Larix laricina* canopy.
Sparsely Vegetated (SPV)	Calcareous marl, boulders present, stunted *Populus balsamifera* and *P. tremuloides* are patchy in distribution.
Burns (BUR)	Early successional, post-fire stands of *Populus* spp. A matrix of standing or fallen dead trees, saplings, and veteran trees.
Water (WAT)	Permanent water bodies (e.g. the centres of some of the larger lacustrine depressions.

*From: Mychaisw (1986)

Table 1-3. Areas of Plant Communities at the Mackenzie Bison Sanctuary*

Plant Communities P.C's	Hectares	Relative Abundance (%)
Coniferous Forest	266,949.0	45.8
Mixed Forest	95,005.8	16.3
Organic Terrain	62,948.7	10.8
Sparsely Vegetated	55,371.5	9.5
Shrubland	33,222.9	5.7
Sedge Meadow	16,320.1	2.8
Burns	15,737.1	2.7
Shrub Meadow**	13,405.7	2.3
Water	8,160.0	1.4
Unclassified	15,737.2	2.7
Total	582,850.0	100.0

*From: Mychaisw, 1986

** Focus of this study

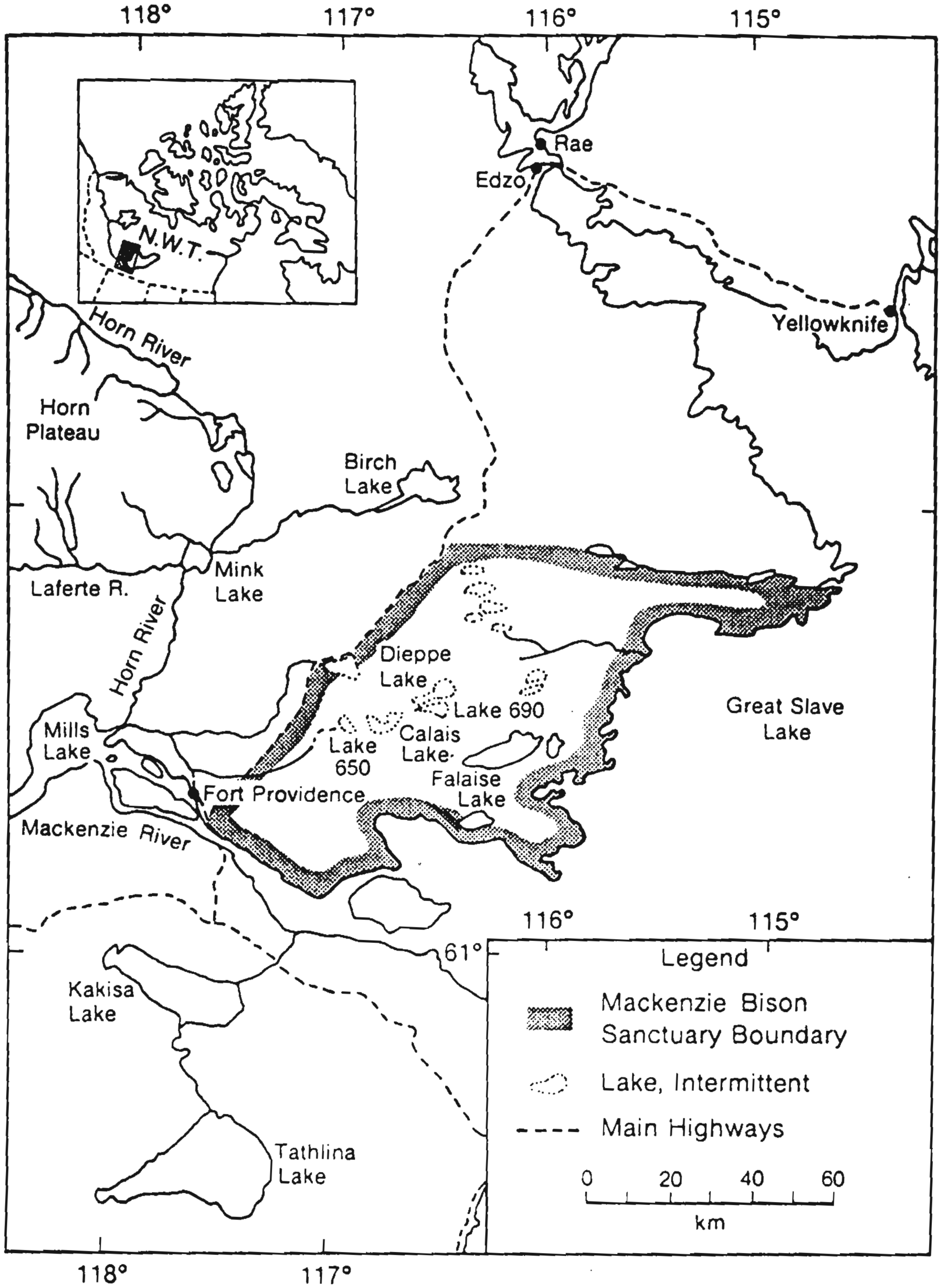

Fig. 1-1 The Mackenzie Bison Sanctuary and the five study sites.
From: GNWT (1987)

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2. INFLUENCE OF WOOD BISON GRAZING ON PRODUCTIVITY OF SHRUB MEADOW VEGETATION, MACKENZIE BISON SANCTUARY, N.W.T.

2.1 Introduction

Herbivores can increase (Vickery 1972, McNaughton 1976, 1979b, 1985a, Prins et al. 1980, Cargill and Jefferies 1984a), decrease (Pearson 1965, Sims and Singh 1978, Lacey and Van Poollen 1981) or have no affect on (Solomon 1983, Sterner 1986) net above-ground primary productivity (NAPP). Because vegetation responds in such different ways to grazing it is clear that many factors influence the NAPP of meadows during and after grazing.

Environmental factors such as temperature (Dyer and Bokhari 1976), precipitation (Pearson 1965), and soil properties (McKendrick et al. 1980, McNaughton and Chapin 1985) can influence NAPP. The species composition of swards and the physiological responses of these species to grazing can vary substantially among areas (Archer and Tieszen 1980). The frequency (Prins et al. 1980), intensity (McNaughton 1979b) and the season of grazing (Bedard et al. 1986) all influence NAPP. 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 NAPP subsequent to grazing. Different herbivore species alter NAPP in different ways (McNaughton 1976) and their feces and urine can substantially change NAPP (Cargill and Jefferies 1984b). Because NAPP is influenced by so many factors it is important to examine the effects of grazers on vegetation productivity for the specific grazing system in question.

Eighteen Wood Bison were introduced into the Mackenzie Bison Sanctuary (MBS) in 1963. The population has been growing exponentially since then and numbers now exceed 2000 animals (Gates and Larter 1990). The herd expanded its range as population size increased, in a pattern suggesting density-threshold dispersal. Some areas appear to be overgrazed (Gates pers. comm. 1987).

The influence of Wood Bison (*Bison bison athabascae*) on the productivity of shrub meadow vegetation was investigated during the summers of 1986 and 1987 at the MBS. The objectives of this study were:

1) To determine the influence of Wood Bison grazing of different intensities on the productivity of Shrub Meadow vegetation.

2) To determine the influence of precipitation on the productivity of shrub meadow vegetation.

3) To determine the influence of Wood Bison grazing on the absolute biomass and proportion of standing dead plant tissue in a sward.

4) To determine if varying the frequency and/or season of artificial grazing (clipping with scissors) influences the productivity of shrub meadow vegetation.

5) To determine if some study sites within the Shrub Meadow plant community type were more heavily grazed than others.

6) To determine if study sites within the Shrub Meadow plant community type vary in their rates of productivity.

7) To determine if artificial grazing alters the productivity of shrub meadow vegetation similarly to natural grazing.

2.2 Methods

2.2.1 Comparison of Control, Apparent and Actual Productivity in 1986 and 1987

All voucher specimens collected during 1986 and 1987 were deposited in the University of Alberta herbarium. Plant nomenclature follows Porsild and Cody (1980). During the 1986 field season, non-woody vegetation inside and outside a 10 x 10m exclosure was sampled at each of five study sites in the shrub meadow community type (Fig. 1-1). These exclosures were erected in September 1985. Totals of 10 and 20 ($0.25m^2$) microplots were sampled inside and outside the exclosures, respectively, every 3 to 4 weeks between 1 June (before new growth occurs) and 31 August (after all growth is complete).

Two of the 5 existing exclosures were expanded to 25m x 25 in May 1987. These two study sites (Calais Lake East and Lake 650) were studied intensively during the 1987 field season, while the remaining three study sites (Lake 690, Calais Lake West, and Dieppe Lake) were sampled only at the end of the 1987 growing season (late August). Prior to analyses, a distinction was made between vegetation exclosed in September 1985 and vegetation exclosed in May 1987. Ten microplots were sampled from each of the exclosures established in 1985, 15 from the exclosures established in 1987, and 25 from the grazed areas, every 3 to 4 weeks from 1 June to 31 August, 1987. Again, only non-woody tissue was clipped in 1987.

Each of the five study sites (Calais Lake East, Calais Lake West, Lake 690, Lake 650, and Dieppe Lake (Fig. 2-1) consisted of one 10m x 10 exclosure with the expanded 25m^2 x 25 exclosures at Calais Lake East and Lake 650. The study sites surrounding the exclosures were approximately 1 ha in size. The length of each study site was measured, then a random number was chosen between 0 and the total length, and a permanent stake was installed at this random spot. The total length was divided by ten, and this number was the interval at which the remaining stakes were laid out (e.g., if total length was 300 paces, first stake installed at pace number 108, remaining stakes placed 30 paces apart). Ten transects were run perpendicular to this base line from the 10 stakes. Transect length varied, depending upon obstructions (willows). Because willows in the MBS are dispersed linearly (Jacobson 1974), the resulting study site was roughly rectangular in shape. Two random numbers between zero and the total length of a particular transect were selected for each transect to determine the locations of the sample plots. Surveys were conducted along these transects to determine the density of Wood Bison feces. Fecal pats were counted within 1 metre of the centre line of each transect (2 metres in width) in 1986. In 1987, pats were counted within 1.5 metres of the centre line (3 metres in width). Microplots were located outside of this belt. The pats were removed every month so only new pats were counted. This survey provided an index of use of the study site by bison. In addition, two soils pits were dug at each study site. Dry samples of each horizon were taken to the lab where color (using Munsell chart), texture, and carbonate content (using hydrochloric acid) were determined. Horizon depth, consistance, and structure were determined in the field. Only one soil profile was described per study site.

Microplots inside exclosures were located with a grid system. The west and south sides of each exclosure were divided into 20 intervals, each .5m long. At the larger exclosures, there were 25 intervals, each 1m long. Random pairs of numbers were selected to determine plot locations. New plots were selected for each exclosure in June, July, and August. The north half of each plot was clipped to 3 cm above ground inside and outside exclosures. Each species was clipped and bagged separately. In the lab only completely dead material was removed. Early in the growing season this tissue was most often "old dead". "Old dead" was defined as standing tissue from the previous year's growing season. Later in the growing season as the effects of weathering became more pronounced, a larger amount of completely senesced current years growth was removed. Samples were dried at 60°C for 8 hours and weighed to the nearest 0.01 g. The biomass data from this study were used to calculate control, apparent, and actual productivities. All productivities are expressed as $g\ m^{-2}\ d^{-1}$.

"Control productivity" was calculated by measuring the change in both green and total biomass inside permanent exclosures over a period of time. Control '85 refers to vegetation that had been exclosed since September 1985. Control '87 refers to vegetation that had been exclosed since May 1987. At the end of the 1987 growing season Control'85 plots were ungrazed for 2 summers and Control'87 plots were ungrazed for 1 summer. "Apparent productivity" was calculated by measuring the change in green and total biomass in grazed areas over a period of time. Estimates of apparent productivity ignored the fact that bison consumed vegetation during the sampling periods.

In 1987, 20 movable exclosures (2 m in diameter) were placed randomly along the established transects at Calais Lake East and Lake 650. The exclosures were moved every 3 to 4 weeks throughout the growing season. A 0.25 m^2 plot was placed in the centre of each movable exclosure. The vegetation was subsequently harvested as described above. This allowed vegetation, which had been previously grazed, to grow undisturbed for three to four weeks. These positive biomass increments were added to calculate the "actual productivity" of grazed vegetation during a particular period of time. This method assumes that vegetation exclosed for ca. 30 days has the same productivity as grazed vegetation. This method also assumes that site differences between the moveable exclosures and the permanent exclosure are minimal.

All estimates of primary productivity are expressed in g m^{-2} d^{-1}. Productivity can be positive or negative. "Green productivity" refers to production of above-ground green biomass only; "total productivity" includes both live (green) and dead above-ground tissue. Productivity estimates are given for specific time periods at each study site (e.g., June 9-August 21 at Calais Lake East). The Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf 1981) was used to test each data-set for normality (e.g., Calais Lake East biomass data for June 9 was tested for normality as was data for August 21). If a data-set was not normal, (i.e., $P<0.05$) both $Y = \log (X + 1)$ and $Y = (X + 1/2)^{0.5}$ transformations were applied. One or 1/2 was added to biomass data (X) before log or square root transformations were performed, respectively. The transformation that resulted in the most normally distributed data-sets was used. The same transformation was used on data-sets that were tested for significance. Bartlett's test of homogeneity of variances (Sokal and Rohlf 1981) was used to determine if variances were homogeneous prior to significance testing (e.g., if Control 0.5yr data were tested against Apparent data (Table 1), a total of four variances (from Control and Apparent data-sets June 9 and August 21) were tested for homogeneity). If $P \geq 0.05$ then variances were considered sufficiently homogeneous and a derivation of a t-test of the differences between two means was used (Sokal and Rolhf 1981):

$$t = \frac{(y_2-y_1)/d_1 - (y_4-y_3)/d_2}{\sqrt{\dfrac{(n_2-1)s_2^2/d_1^2 + (n_1-1)s_1^2/d_1^2 + (n_4-1)s_4^2/d_2^2 + (n_3-1)s_3^2/d_2^2}{n_1 + n_2 + n_3 + n_4 - 4}\left(\dfrac{1}{n_1}+\dfrac{1}{n_2}+\dfrac{1}{n_3}+\dfrac{1}{n_4}\right)}} \qquad [1]$$

where, with the exception of variable d, variables with subscripts 1 and 2 were from ungrazed plots, variables with subscripts 3 and 4 were from grazed plots (subscript 2 and 4 at later date), y = mean standing crop, d_1 = number of days between sampling dates in ungrazed plots, d_2 = number of days between sampling dates in grazed plots, s = standard deviation, n = sample size.

If $P<0.05$ the variances were considered heterogeneous, and a derivation of the test of "Equality of the Means of Two Samples Whose Variances are Assumed to be Unequal" was used. In this test, critical values of t were calculated as described by Sokal and Rohlf, 1981. All t-tests performed were two-tailed. Because transformed data were analyzed, productivity estimates are expressed as means and their 95% confidence intervals. Note that some of the means for the same treatments were not identical. This is because different transformations were used, e.g. for a given mean, backtransforming a square root transformed mean gave a slightly different value than backtransforming a log transformed mean.

2.2.2 Productivity of Artificially Grazed, Control and Actual Treatments

The Green Productivity (g m^{-2} d^{-1}) of Artificially Grazed vegetation was compared with Actual and Control Productivity estimates. Non-normal data sets were transformed. A derivation of the t-test of the differences between two means (Sokal and Rohlf 1981) was used. The F_{max} test (Sokal and Rohlf 1981) was used to test the variances for homogeneity.

2.2.3 Cumulative Green Biomass Estimates from Artificially Grazed Plots

An artificial grazing study was conducted to determine how the frequency of grazing influences the above-ground green primary productivity of exclosed vegetation. Plots clipped in permanent exclosures were reclipped at later dates as described below. All plots were clipped to 3 cm above-ground. A negligible amount of completely dead tissue was removed as described above (many plots had no dead tissue at all). In 1986 the following 3-part schedule was followed at all five 10 x 10 m exclosures: (1) clippings in June, July, and August (i.e. plots originally clipped in June were reclipped in July and August), (2) clippings in July and August, and (3) clippings in August only. In 1987, clippings were made in permanent exclosures established in 1985 and in 1987 at Calais Lake East and at Lake 650 in 1) June and August, 2) July and August, and 3) in August only.

The total amount of green biomass produced by an individual plot during the growing season was calculated by adding green biomass estimates from each clipping. Cumulative biomass estimates were tested for normality and transformed if necessary. Means were tested for significance using the t-test of the difference between two means (Sokal and Rohlf, 1981). Variances were tested for homogeneity using the F variance ratio (Sokal and Rohlf 1981).

2.2.4 Grazing Intensity at Study Sites

Grazing Intensity (G) was calculated for each sampling period at each study site as:

$$G = 1 - \frac{S_g}{S_u} \qquad [2]$$

Where, S_u is the Mean Standing Crop of Ungrazed Vegetation and S_g is the Mean Standing Crop of Grazed Vegetation. Standing Crop is the dry weight of above-ground plant tissue (live and dead tissue) clipped to a 3 cm height at a particular point in time, and G is calculated using "Control '85" or "Control '87" Standing Crop data. This is made clear in the Results. Grazing Intensity differences among study sites were tested for significance using the two-tailed test for difference between proportions (Levin 1981).

2.2.5 Comparison of Consumption Estimates Among Study Sites

Consumption Estimates (C) (g $m^{-2}d^{-1}$) were calculated for study sites during a particular period of growth as:

C_g= Green Actual Productivity - Green Apparent Productivity

and,

C_t= Total Actual Productivity - Total Apparent Productivity.

Since the movable exclosure experiment used to calculate Actual Productivity was conducted in 1987, C's are for study sites in 1987 only. Non-normal data sets were transformed. Consumption Estimates among study sites were tested for significance using a derivation of the t-test of the difference between two means. Variances were tested for homogeneity using the F_{max} test (Sokal and Rohlf 1981).

2.2.6 Comparison of 1986 and 1987 Standing Crop Biomass

Green and Total Standing Crop Biomass estimates for 1986 and 1987 were compared. Green Standing Crop refers to the standing crop of green biomass and Total Standing Crop refers to the standing crop of green and dead biomass. Comparisons were made only if 1987 harvests were within one week of the 1986 harvest date. This restriction did not cause a loss of many comparisons. Non-normal data-sets were transformed. Biomass means are surrounded by their 95% confidence intervals and are expressed in g/m^2. Variances were tested for homogeneity using the F variance ratio (Sokal and Rohlf 1981). Means were tested for significance using the t-test of the differences between two means (Sokal and Rohlf 1981).

2.2.7 Abundance of Standing Dead Tissue in Grazed and Ungrazed Areas

Standing dead plant tissue was removed from clipped samples in the lab. "Old dead" or dead tissue from previous years growth was removed. "New dead" or dead tissue from the current years growth was not removed. Only completely dead plant tissue was removed (this may have included some current years growth). All samples were dried for 8 hours at 60°C and weighed to the nearest 0.01g. Non-normal data-sets were transformed so means (g/m^2) are surrounded by their 95% confidence intervals. Variances were tested for homogeneity using the F variance ratio (Sokal and Rohlf 1981). Means were tested for significance using the t-test of the difference between two means (Sokal and Rohlf 1981).

Percent of Standing Dead Tissue in Control and Grazed plots was computed as: SDT% = 100(Standing Crop of St. Dead / Total St. Crop)%. Comparisons of grazed and ungrazed sites and between 1986 and 1987 estimates were made using the Two-tailed test for differences between proportions (Levin 1981).

2.2.8 Cumulative Heat Sums and Precipitation Data

Dry bulb temperature and precipitation data were recorded at noon each day in Fort Providence, which is 60 km SW of the MBS. Mean daily temperatures (°C) were added together from May 17 to August 14 in 1986 and to August 22 in 1987 to obtain summer heat sum values for 1986 and 1987. Cumulative precipitation data were added from June 1 to mid-August in 1986 and 1987.

2.2.9 Glossary

Control Productivity: The change in biomass in a permanent exclosure over a period of time. This is the productivity of ungrazed vegetation. Expressed as green or total biomass.

Apparent Productivity: The change in biomass in grazed areas over a period of time.

Actual Productivity: The change in biomass within a temporary exclosure over a period of time. This is the productivity of grazed vegetation.

Green Productivity: The change in green biomass over a period of time.

Total Productivity: The change in green and dead biomass over a period of time.

Control'85: Refers to vegetation exclosed starting in September 1985.

Control'87: Refers to vegetation exclosed starting May 1987.

Ungrazed'85: Same as Control'85.

Ungrazed'87: Same as Control'87.

Standing Crop: The dry weight of vegetation clipped 3 cm above-ground from a quadrat.

Grazing Intensity: 1 - (standing crop grazed vegetation/standing crop ungrazed vegetation). Ungrazed vegetation is located in the Control'85 or Control'87 exclosures.

Green Consumption Estimate: Net Actual Productivity - Net Apparent Productivity.

Total Consumption Estimate: Total Actual Productivity - Total Apparent Productivity.

Green Standing Crop: Standing crop of green biomass.

Total Standing Crop: Standing crop of dead and green biomass.

2.3 Results

2.3.1 The Effects of Natural and Artificial Grazing on Plant Growth

Artificially grazed plots in exclosures clipped at the beginning and end of the growing season and naturally grazed plots grazed by Wood Bison throughout the growing season produced similar quantities of above-ground biomass in 1987 (Table 2-1). Exact- and over-compensation were observed in both artificially grazed and naturally grazed plots during the 1986 and 1987 growing seasons. (Note that exact-compensation refers to grazed vegetation that has the same productivity as ungrazed vegetation and overcompensation refers to grazed vegetation that has a higher productivity than ungrazed vegetation). In this study, no clipping or grazing regime resulted in depressed productivity relative to ungrazed controls. In 1987 exact compensation was observed in naturally grazed plots relative to 1985 control (ungrazed) plots at Calais Lake East in July and at Lake 650 from mid-June to mid-July. Plots overcompensated in response to herbivory in June at Calais Lake East and from mid-July to mid-August at Lake 650 (Table 2-2). Similar results were observed in naturally grazed plots relative to 1987 Control plots (Appendix 2a-8) and in plots ungrazed since 1987 relative to plots ungrazed since 1985 (Table 2-3).

In 1986, artificially grazed plots didn't respond positively or negatively to clipping. At all 5 study sites exact compensation was observed from June to August (Table 2-4). However in 1987, plots clipped once prior to the end of season clip in August overcompensated relative to 1985 Control plots at Lake 650 and at Calais Lake East (Table 2-5). (Note that Table 2-4 refers to "clip 1" and "clip 2". The date beneath each column refers to the date these plots were clipped. Note that Control plots were unclipped throughout the growing season.) Similar trends were noted at Calais Lake East in artificially grazed plots relative to 1987 Control plots (Appendix 2a-16).

2.3.2 Accumulation of Standing Dead Tissue in Grazed and Ungrazed Areas

Grazing reduced absolute and to a lesser degree proportions of standing dead tissue. The most notable reductions were at the most productive site, Lake 650. In 1986, absolute quantities of standing dead were higher in ungrazed plots at Calais Lake East and Lake 650 in August, at Lake 690 and Calais Lake West in July, and at Dieppe Lake in June and July (Table 2-6). Similar trends were observed in 1987 at Calais Lake East in June and August and at Lake 650 throughout the growing season. There was more standing dead tissue in grazed plots at lightly grazed Lake 690 and Dieppe Lake in August (Table 2-7). Ungrazed stands of <u>Calamagrostis</u> spp. contributed to the abundant standing dead at these two sites (see Chapter 3). Absolute quantities of standing dead also were higher in Control'85 plots than in Control'87 plots at Calais Lake East and Lake 650 in July and August 1987 (Table 2-8).

Overall, proportions of standing dead were slightly higher in ungrazed than in grazed sites. Lake 650 had a higher percentage of standing dead in July in ungrazed plots relative to grazed plots, however (Table 2-9). Percentages of standing dead also increased in the exclosure established in 1985 from 1986 to 1987 at Lake 650 in June. Calais Lake East showed similar increases but they were not significant (Table 2-10).

2.3.3 Temporal and Spatial Patterns in Plant Growth During the 1986 and 1987 Growing Seasons

Green Standing Crop Biomass was much higher in 1986 than in 1987 for all dates at all study sites. Higher standing crops and an extended growing season in 1986 corresponded to higher precipitation amounts (Table 2-11). Temperatures during both growing seasons, however, were similar (Appendix 2c-10). In addition to temporal variation in standing crop, there were pronounced differences in productivity among the study sites in 1986.

Lake 650 is by far the most productive site followed by Calais Lake East, Calais Lake West, Dieppe Lake and Lake 690 (Table 2-12a). Because the periods of growth examined differed among study sites, results may not be completely accurate for Calais Lake West and Dieppe Lakes. The periods for the remaining study sites are very similar, however. This spatial trend is consistent with the results observed in a more intensive examination of similar data (Appendix 2c-16).

Variation among the soils at the five study sites was also examined. Soil profiles at the 5 study sites were very similar (Table 2-13). All profiles belonged to the Cryosolic Order, the Static Cryosol Great Group, and the Brunisolic Static Cryosol Subgroup (Agriculture Canada 1987). All these profiles had permafrost within 1 meter of the surface, little cryoturbation, and Bm horizons more than 10 cm thick. Lake 650's profile didn't seem to have any unique characteristics.

It appears that the most productive study site was also the most heavily grazed in 1986 and 1987 (Table 2-12b). For the entire 1986 growing season, the sward at Lake 690 was the least grazed, followed by Calais Lake West, Dieppe Lake, Calais Lake East, and Lake 650. Similar trends were observed during early, middle and late summer in 1986 and during late summer in August 1987. The negative G for CLW in 1987 indicates that standing crop was higher in grazed plots than in ungrazed plots.

Consumption rates were only available for Calais Lake East and Lake 650 in 1987. They are consistent with the results for grazing intensity. Wood Bison consumed much more plant tissue at Lake 650 than at Calais Lake East (Table 2-14). Fecal pat accumulation data also agreed with G data, but to a lesser extent than consumption estimates (see Appendix 2c-11).

Table 2-1. Green Productivity ($g\ m^{-2}d^{-1}$) of Artificially Grazed (n=10) and Green Actual Productivity of Grazed (n=25) Shrub Meadow Vegetation at Lake 650 in 1987.

Period of Growth	95% Confidence Intervals						Prob.
	Art. Grazed			Actual			
	L1	Mean	L2	L1	Mean	L2	
June 13-Aug.15	0.68*	1.08*	1.58*	0.98	1.49	2.11	P>.10
June 13-Aug.15	1.16**	1.62**	2.14**	0.98	1.49	2.11	P>.10
July 12-Aug.15	0.92*	1.27*	1.69*	0.94	1.41	1.97	P>.10
July 13-Aug.15	1.09**	1.35**	1.65**	0.94	1.41	1.97	P>.10

Artificially grazed plots clipped at beginning and end of period of growth.

* Exclosure established September 1985.

** Exclosure established May 1987.

Table 2-2. Green Control Productivity (g $m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established Aug. 1985, n=10) and Green Actual Productivity of Grazed (n=25) Shrub Meadow Vegetation at Two Study Sites in 1987.

Period of Growth	95% Confidence Intervals						Probability
	Control '85			Actual			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 3-July 30	0.53	0.76	1.08	0.70	1.07	1.63	P>.10
June 3-July 2	0.79	1.08	1.49	1.16	1.53	2.03	P≤.05
July 5-July 30	0.29	0.40	0.56	0.38	0.53	0.73	P>.10
			Lake 650				
June 13-Aug.13	0.14	0.48	1.02	0.98	1.49	2.11	P>.10
June 13-July 12	0.98	1.86	3.02	1.02	1.59	2.29	P>.10
July 12-Aug.13	-1.48	-0.76	-0.27	0.94	1.41	1.97	P≤.001

Table 2-3. Green Control Productivity (g $m^{-2}d^{-1}$) of Ungrazed'85 (Permanent Exclosure Established in Aug. 1985, n=10) and Ungrazed'87 (Permanent Exclosure Established in May '87, n=15) Shrub Meadow Vegetation at Two Study Sites in 1987.

Period of Growth	95% Confidence Intervals						Probability
	Control '85			Control '87			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 3-Aug.21	0.13	0.26	0.44	0.29	0.46	0.66	P>.10
June 3-July 4	0.42	1.15	1.88	1.56	2.70	3.84	P≤.10
June 3-July 29	0.45	0.78	1.19	0.51	0.90	1.39	P>.10
July 4-July 29	-0.09	0.38	0.88	-2.11	-1.02	-0.32	P>.10
July 4-Aug.21	-0.49	-0.25	-0.09	-1.38	-0.83	-0.42	P>.10
July 29-Aug.21	-1.78	-0.97	-0.41	-1.32	-0.61	-0.17	P>.10
			Lake 650				
June 14-Aug.13	0.14	0.48	1.02	0.94	1.31	1.74	P≤.10
June 14-July 10	0.98	1.86	3.02	0.96	1.67	2.57	P>.10
July 10-Aug.13	-1.48	-0.76	-0.27	0.61	1.06	1.62	P≤.05

Table 2-4. Green Productivity (g $m^{-2}d^{-1}$) of Artificially Grazed (n=10) and Green Control Productivity* of Ungrazed (n=10) Shrub Meadow Vegetation at Five Study Sites in 1986.

Period of Growth	95% Confidence Intervals						Probability
	Art. Grazed			Control '85			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 9-Aug.21	1.70	2.17	2.71	1.63	2.44	3.41	P>.10
			Lake 690				
June 12-Aug.9	1.52	2.02	2.60	1.28	1.68	2.12	P>.10
			Calais Lake West				
June 14-July 26	1.97	3.37	5.14	1.28	2.04	2.97	P>.10
			Lake 650				
June 17-Aug.13	2.79	3.55	4.40	3.29	5.39	8.01	P>.10
			Dieppe Lake				
June 26-Aug.17	1.20	1.41	1.63	1.20	1.86	2.65	P>.10

Artificially grazed plots clipped at beginning, in the middle, and at the end of period of growth.

* Exclosure established September 1985.

Table 2-5. Cumulative Green Biomass Estimates (g m^{-2}) (n=10) of Artificially Clipped* Control Plots (Permanent Exclosure Established Aug. 1985) in 1987.

Date of Clips		95% Confidence Intervals						Prob.
		Clip1			Clip2			
Clip1	Clip2	L1	Mean	L2	L1	Mean	L2	
				Calais Lake East				
June 4 Aug. 21	July 3 Aug. 22	83.61	111.44	143.24	84.17	100.70	118.71	P>.10
June 4 Aug. 21	July 29 Aug. 22	83.61	111.44	143.24	73.86	99.70	129.39	P>.10
June 4 Aug. 21	Aug.21	83.61	111.41	143.24	56.93	74.67	94.79	P≤.05
July 3 Aug. 22	July 29 Aug. 22	82.81	99.00	118.32	73.67	96.72	126.90	P>.10
July 3 Aug. 22	Aug.21	82.81	99.00	118.32	57.73	73.13	92.58	P≤.05
July 29 Aug. 22	Aug. 21	73.67	96.72	126.90	57.73	73.13	92.58	P≤.10
				Lake 650				
June 14 Aug. 12	July 10 Aug. 12	79.21	128.55	189.72	135.23	164.11	195.77	P>.10
June 14 Aug. 12	Aug. 8	79.21	128.55	189.72	63.33	91.66	125.18	P>.10
July 10 Aug. 12	Aug. 8	135.23	164.11	195.77	63.33	91.66	125.18	P≤.01

* Note that plots were clipped on dates under "clip1" and "clip2" column headings.

Table 2-6. Above-ground Standing Crop Biomass (g m^{-2}) of Standing Dead Plant Tissue in Ungrazed (Permanent Exclosure Established in Aug. 1985, n=10) and Grazed (n=20) Shrub Meadows in 1986.

Date	95% Confidence Intervals						Prob.
	Ungrazed			Grazed			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 9	6.77	11.59	19.41	3.85	7.67	14.49	P>.10
July 1	3.14	5.97	10.73	2.76	4.74	7.76	P>.10
July 22	4.92	7.17	10.26	3.31	6.13	10.80	P>.10
Aug. 21	21.53	39.74	72.66	9.31	12.80	17.48	P≤.001
			Lake 690				
June 12	8.15	15.98	30.52	8.84	16.78	31.13	P>.10
July 10	17.01	22.06	27.75	6.98	10.79	15.38	P≤.01
Aug. 9	18.43	22.25	26.43	11.18	17.31	24.73	P>.10
			Calais Lake West				
June 14	5.87	11.75	19.53	3.91	8.44	14.56	P>.10
July 5	6.37	11.88	21.52	2.70	5.11	9.09	P≤.10
July 26	14.95	20.20	26.23	4.22	9.30	16.21	P≤.10
			Lake 650				
June 17	3.37	7.77	16.61	1.49	3.25	6.23	P≤.10
July 14	NA	NA	NA	2.09	5.07	10.90	NA
Aug. 14	27.63	40.69	59.69	7.71	11.59	17.21	P≤.001
			Dieppe Lake				
June 26	11.07	15.98	22.90	2.49	4.43	7.45	P≤.01
July 20	19.76	33.67	56.91	3.99	7.97	15.13	P≤.01
Aug. 17	22.11	29.08	36.05	17.92	23.37	28.82	P>.10

Table 2-7. Above-ground Standing Crop Biomass (g m^{-2}) of Standing Dead Plant Tissue in Ungrazed (Permanent Exclosure Established Aug. 1985, n=10) and Grazed (n=25) Meadows in 1987.

Date	95% Confidence Intervals						Prob.
	Ungrazed			Grazed			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 3	14.61	19.39	24.83	7.83	10.59	13.75	$P \leq .01$
July 5	6.14	11.02	19.24	8.02	14.14	24.39	$P > .10$
July 30	12.19	21.03	32.19	13.60	19.93	27.44	$P > .10$
Aug. 21	19.91	37.90	71.37	11.16	15.58	20.71	$P \leq .05$
			Lake 650				
June 13	20.27	54.56	105.24	15.12	22.16	30.50	$P \leq .05$
July 12	47.35	86.10	155.89	2.85	5.11	8.70	$P \leq .001$
Aug. 13	32.38	45.77	64.54	7.97	12.80	20.25	$P \leq .001$
			Lake 690				
Aug. 19	12.79	17.06	21.91	18.50	23.51	29.11	$P \leq .10$
			Calais Lake West				
Aug. 20	17.68	23.31	29.71	19.68	26.23	33.70	$P > .10$
			Dieppe Lake				
Aug. 19	15.09	19.75	25.02	21.29	28.02	35.64	$P \leq .10$

Table 2-8. Above-ground Standing Crop Biomass (g m^{-2}) of Standing Dead Plant Tissue in Ungrazed'85 (Permanent Exclosure Established Aug. 1985, n=10) and Ungrazed'87 (Permanent Exclosure Established May 1987, n=15) Plots in 1987.

Date	95% Confidence Intervals						Prob.
	Ungrazed '85			Ungrazed '87			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 4	16.04	21.03	26.67	8.88	15.26	23.28	P>.10
July 4	6.14	11.02	19.24	1.51	3.27	6.26	P≤.01
July 29	12.50	19.42	29.87	10.99	15.60	21.97	P>.10
Aug. 21	19.91	37.90	71.37	14.41	20.38	28.67	P≤.10
			Lake 650				
June 14	20.27	54.56	105.24	18.30	29.53	43.38	P>.10
July 10	47.35	86.10	155.89	4.02	10.48	25.26	P≤.001
Aug. 8	32.38	45.77	64.54	9.19	18.95	38.09	P≤.05

Table 2-9. Comparison of Percent Standing Dead Tissue in Control'85 Plots and Grazed Plots in 1987.

Date	Study Site	Control'85	Grazed	Probability
June 3	C.L.East	.27±.11	.30±.09	P>.10
July 5	C.L.East	.14±.08	.10±.06	P>.10
July 30	C.L.East	.19±.09	.25±.09	P>.10
Aug. 21	C.L.East	.47±.12	.26±.09	P>.10
June 13	Lake 650	.49±.12	.23±.08	P>.10
July 12	Lake 650	.54±.11	.14±.07	P≤.01
Aug. 13	Lake 650	.36±.11	.33±.09	P>.10
Aug. 19	Lake 690	.15±.08	.26±.09	P>.10
Aug. 20	C.L.West	.27±.09	.25±.09	P>.10
Aug. 19	Dieppe L.	.22±.05	.38±.10	P>.10

Table 2-10. Comparison of Percent Standing Dead Tissue in Control'85 Plots (Permanent Exclosure Established September 1985) in 1986 and 1987.

Date	Study Site	1986	1987	Probability
June 7	C.L.East	.17±.10	.27±.11	P>.10
July 2	C.L.East	.04±.05	.14±.08	P>.10
July 26	C.L.East	.04±.05	.19±.09	P>.10
Aug. 21	C.L.East	.17±.10	.47±.12	P>.10
June 16	Lake 650	.10±.08	.49±.12	P≤.05
July 14	Lake 650	*******	.10±.07	*****
Aug. 11	Lake 650	.10±.08	.36±.11	P>.10
Aug. 14	Lake 690	.12±.09	.15±.08	P>.10
Aug. 18	Dieppe L.	.16±.09	.22±.05	P>.10

Table 2-11. Green Standing Crop Biomass (g m^{-2}) of Control Vegetation (Permanent Exclosure Established in Aug. 1985) for 1986 (n=10) and 1987 (n=10) with Corresponding Cumulative (since June 1) Precipitation Data (mm).

Date	95% Confidence Intervals								Prob.
	1986				1987				
	L1	Mean	L2	Precip	L1	Mean	L2	Precip	
				Calais Lake East					
June 7	61.03	75.23	89.43	10.6	42.26	55.48	68.70	5.6	$P \leq .05$
July 2	125.68	165.91	211.69	43.2	68.70	86.92	107.28	31.2	$P \leq .001$
July 26	177.87	217.06	260.14	83.9	71.09	96.92	126.72	54.4	$P \leq .001$
Aug. 21	179.38	244.47	333.06	NA	57.73	73.13	92.58	94.1	$P \leq .001$
				Lake 650					
June 16	65.15	116.92	168.69	13.7	43.32	70.90	98.48	5.6	$P \leq .10$
July 10	Not Available			79.3	92.12	117.50	142.88	40.8	NA
Aug. 11	287.49	414.44	564.50	142.8	63.33	91.66	125.18	82.4	$P \leq .001$
				Dieppe Lake					
Aug. 18	118.15	161.81	212.29	156.1	58.57	72.09	87.01	90.9	$P \leq .001$
				Lake 690					
Aug. 14	136.65	163.84	191.03	114.2	81.05	97.93	114.81	90.9	$P \leq .001$

Table 2-12a. Comparison of Green Control Productivity Estimates* (g $m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established Sept. 1985, n=10) Shrub Meadow Vegetation among Five Study Sites for the 1986 Growing Season.

SITE:	L650	CLE	CLW	DL	L690
PROD.:	$5.39_{\underline{a}}$	$2.44_{\underline{b}}$	$2.04_{\underline{b}}$	$1.86_{\underline{b}}$	$1.68_{\underline{b}}$

* Sites with 1 or more common subscripts do not differ significantly at $P \leq 0.05$.

Table 2-12b. Comparison of Grazing Intensity (G)* at Five Study Sites Throughout the 1986 Growing Season and at the end of the 1987 Growing Season.

		EARLY SUMMER 1986			
SITE:	L650	DL	CLW	CLE	L690
G:	$0.69_{\underline{a}}$	$0.49_{\underline{ab}}$	$0.40_{\underline{bc}}$	$0.27_{\underline{c}}$	$0.04_{\underline{d}}$
		MIDDLE SUMMER 1986			
SITE:	CLE	L650	DL	L690	CLW
G:	$0.75_{\underline{a}}$	$0.62_{\underline{ab}}$	$0.43_{\underline{bc}}$	0.41_{bc}	$0.33_{\underline{c}}$
		LATE SUMMER 1986			
SITE:	L650	CLE	CLW	DL	L690
G:	$0.79_{\underline{a}}$	$0.59_{\underline{ab}}$	$0.45_{\underline{bc}}$	$0.35_{\underline{c}}$	$0.27_{\underline{c}}$
		LATE SUMMER 1987			
Site:	L650	CLE	DL	L690	CLW
G:	$0.58_{\underline{a}}$	$0.53_{\underline{a}}$	$0.16_{\underline{b}}$	$0.16_{\underline{b}}$	$-0.28_{\underline{c}}$

* Sites with 1 or more common subscripts do not differ significantly at $P \leq 0.10$.

Table 2-13. Descriptions of Soil Profiles at the Five Study Sites in 1987.

Horizon	Depth (cm)	Color (dry)	Texture	Structure	Consistency
			Calais Lake East		
Om	34 - 0	10YR 2/1	loam	fine(f) granular	soft
Bmk	0 - 36	10YR 2/1	clay loam	f.sub-angular blocky	slightly hard
Ckg	37+	10YR 6/1	clay	amorphous	very hard
			Lake 650		
Om	30 - 0	10YR 2/1	loam	f. granular	soft
Bmk	0 - 35	10YR 3/1	silty loam	m.sub-angular blocky	slightly hard
Ck	35+	10YR 5/1	sandy loam	amorphous	slightly hard
			Lake 690		
Om	20 - 0	10YR 3/2	loam	f. granular	soft
Bmk	0 - 40	10YR 4/1	loam	f. granular	soft
Ck	40+	10YR 5/1	loam	amorphous	slightly hard
			Calais Lake West		
Om	31 - 0	10YR 2/1	loam	f. granular	soft
Bmk	0 - 22	10YR 2/1	clay loam	m.sub-angular blocky	slightly hard
Ckg	22+	10YR 6/1	loam	amphorous	slightly hard
			Dieppe Lake		
Om	40 - 0	10YR 2/1	loam	f. granular	soft
Bmk	0 - 30	10YR 3/1	loam	m.sub-angular blocky	slightly hard
Ck	30+	10YR 4/1	loam	amorphous	slightly hard

Table 2-14. Total Consumption Estimates* (C_t) ($g\ m^{-2}d^{-1}$) at Two Study Sites in 1987.

Study Site	Period of Growth	95% Confidence Interval			Probability
		L1	Mean	L2	
C.L.East	June 3-July 31	0.11	0.17	0.24	
Lake 650	June 13-Aug.18	2.38	2.59	2.81	$P \leq .05$
C.L.East	June 3-July 4	0.46	0.54	0.61	
Lake 650	June 13-July 14	2.89	3.09	3.31	$P \leq .01$
C.L.East	July 7-July 31	-0.26	-0.17	-0.11	
Lake 650	July 15-Aug.18	1.93	2.10	2.28	$P \leq .05$

*C_t = Total Actual Productivity - Total Apparent Productivity

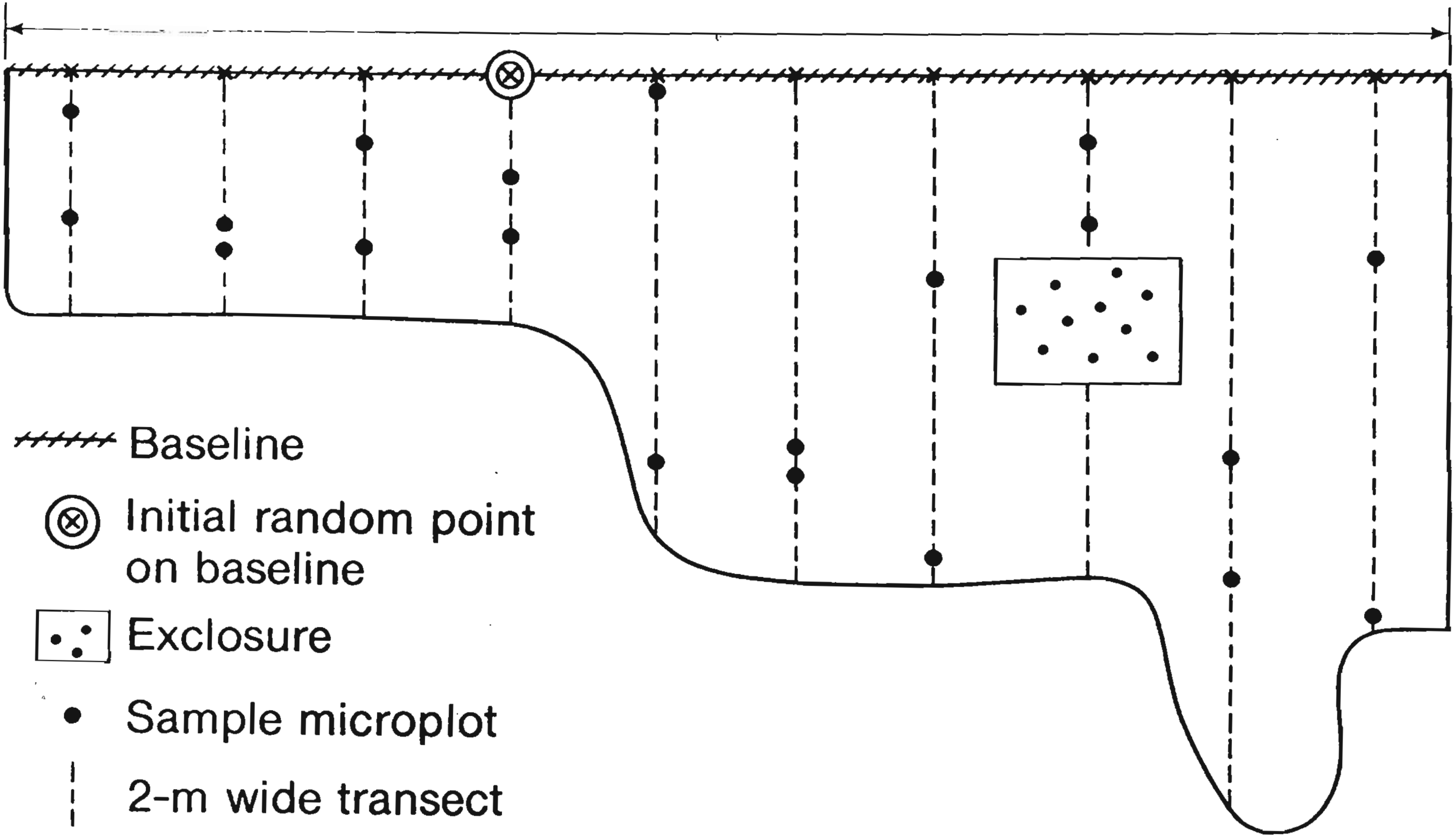

Fig. 2-1 Pictorial description of sampling method in representative study site.

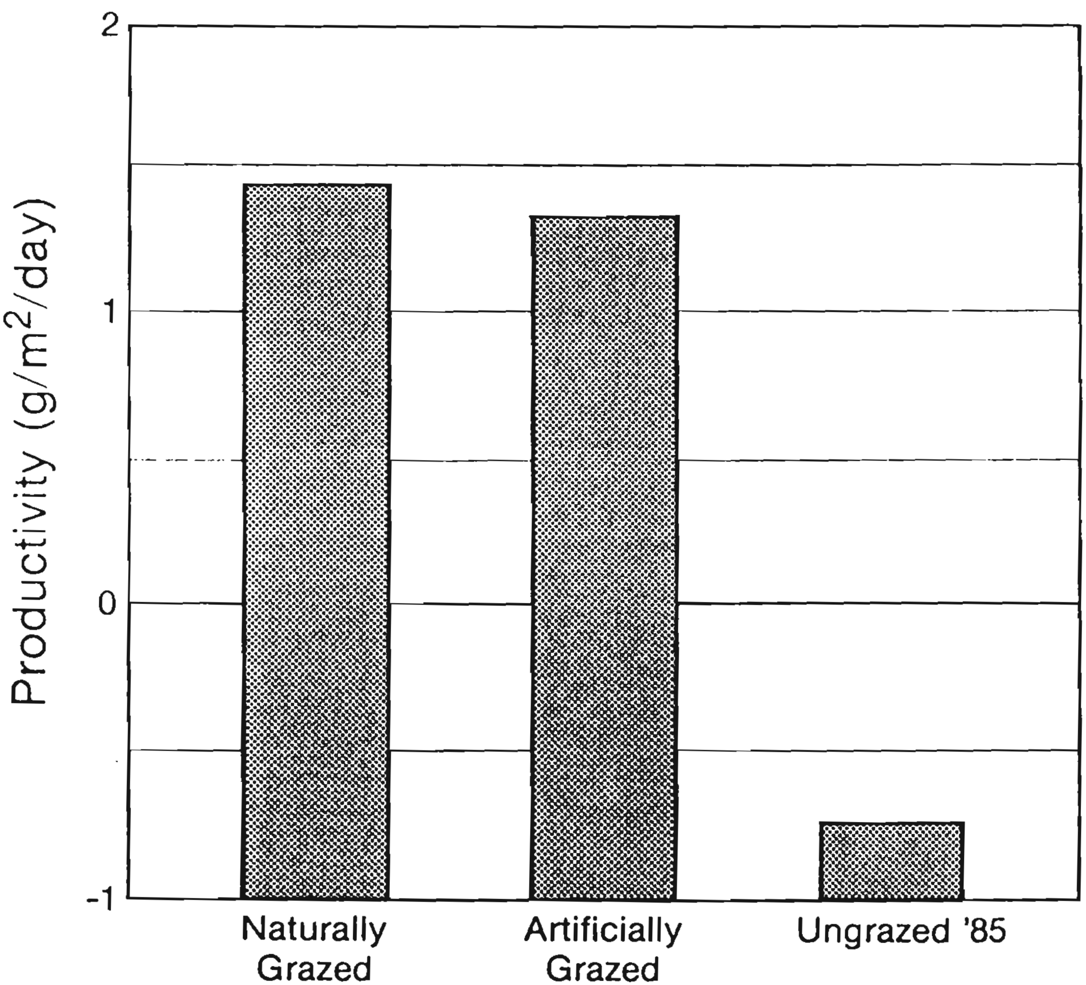

Fig. 2-2 Green productivity of naturally grazed, artificially grazed and ungrazed vegetation at Lake 650 from July 12 to August 13 in 1987.

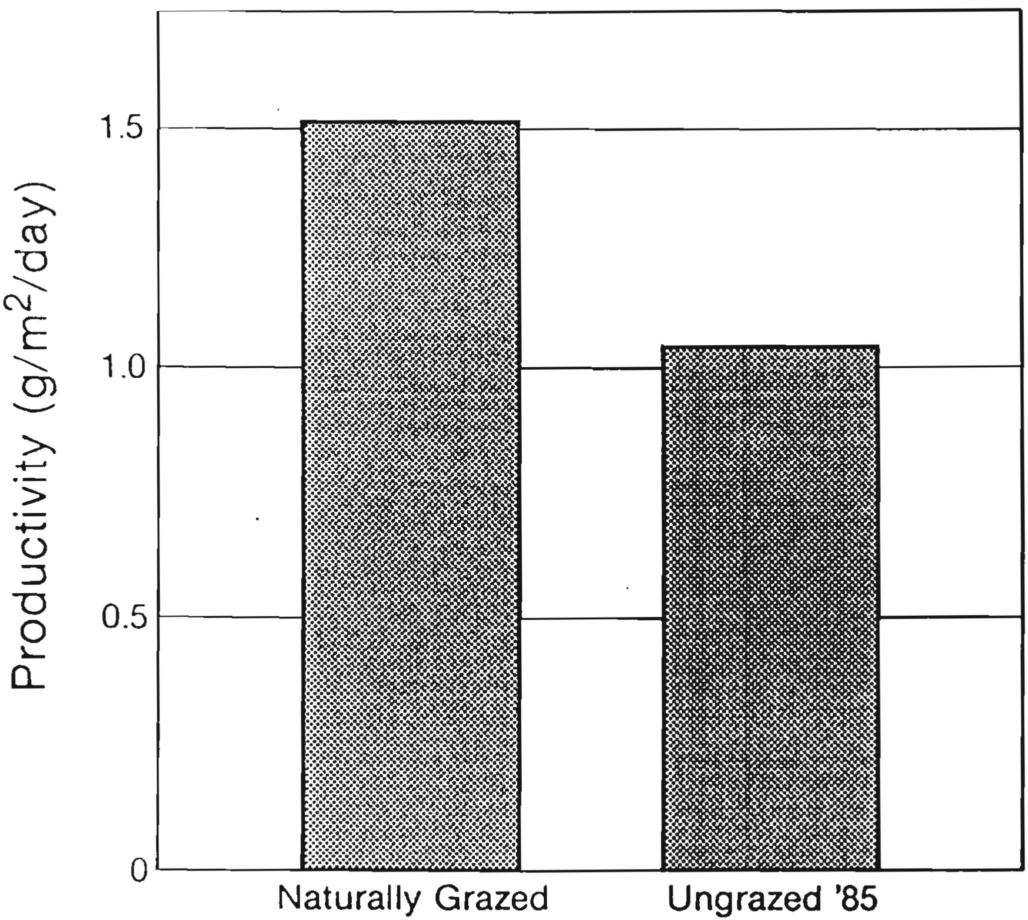

Fig. 2-3 Green productivity of naturally grazed and ungrazed '85 vegetation at Calais Lake East from June 3 to July 2, 1987.

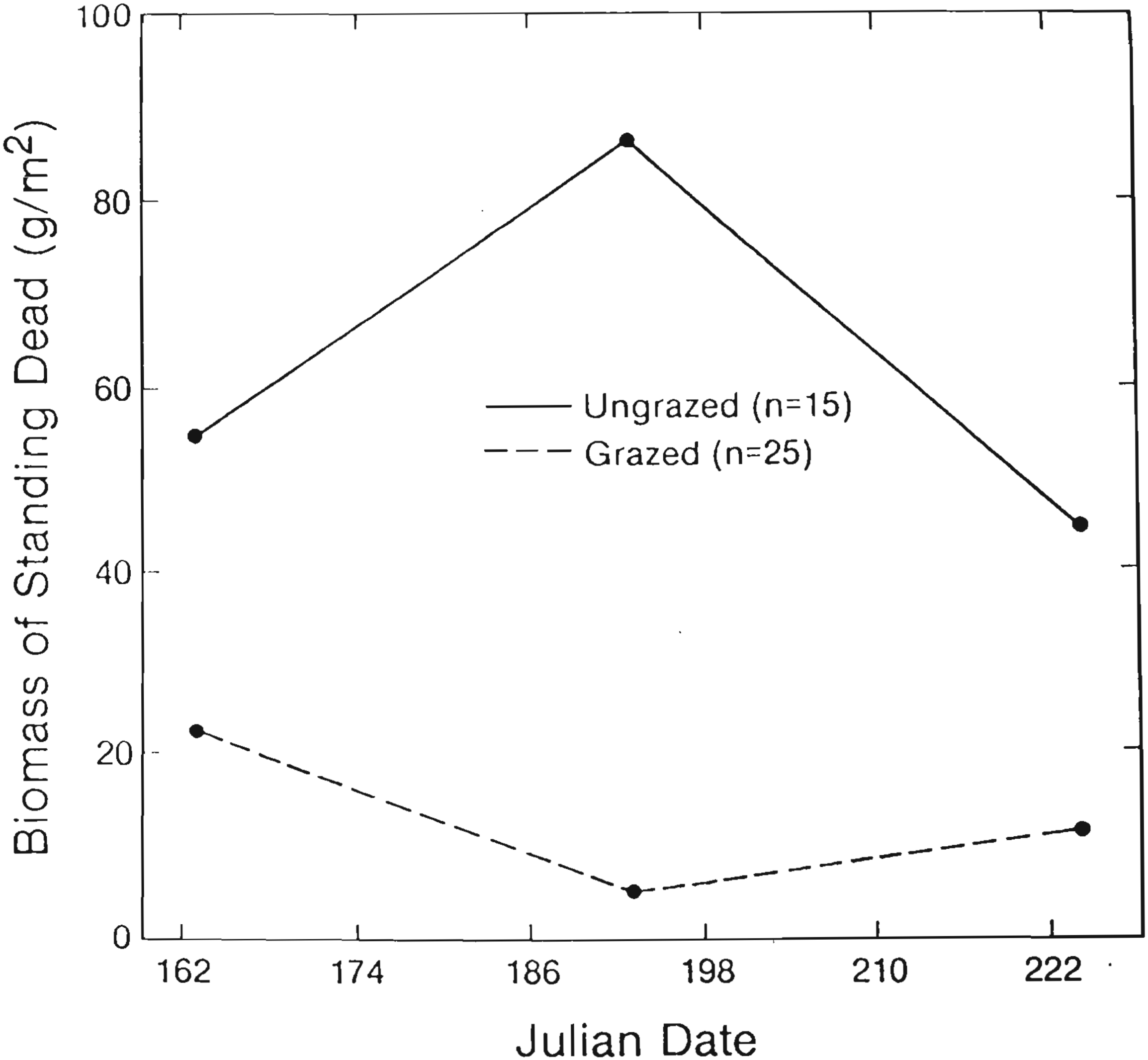

Fig. 2-4 Absolute quantities of standing dead tissue in grazed and ungrazed '85 plots at Lake 650 in 1987.

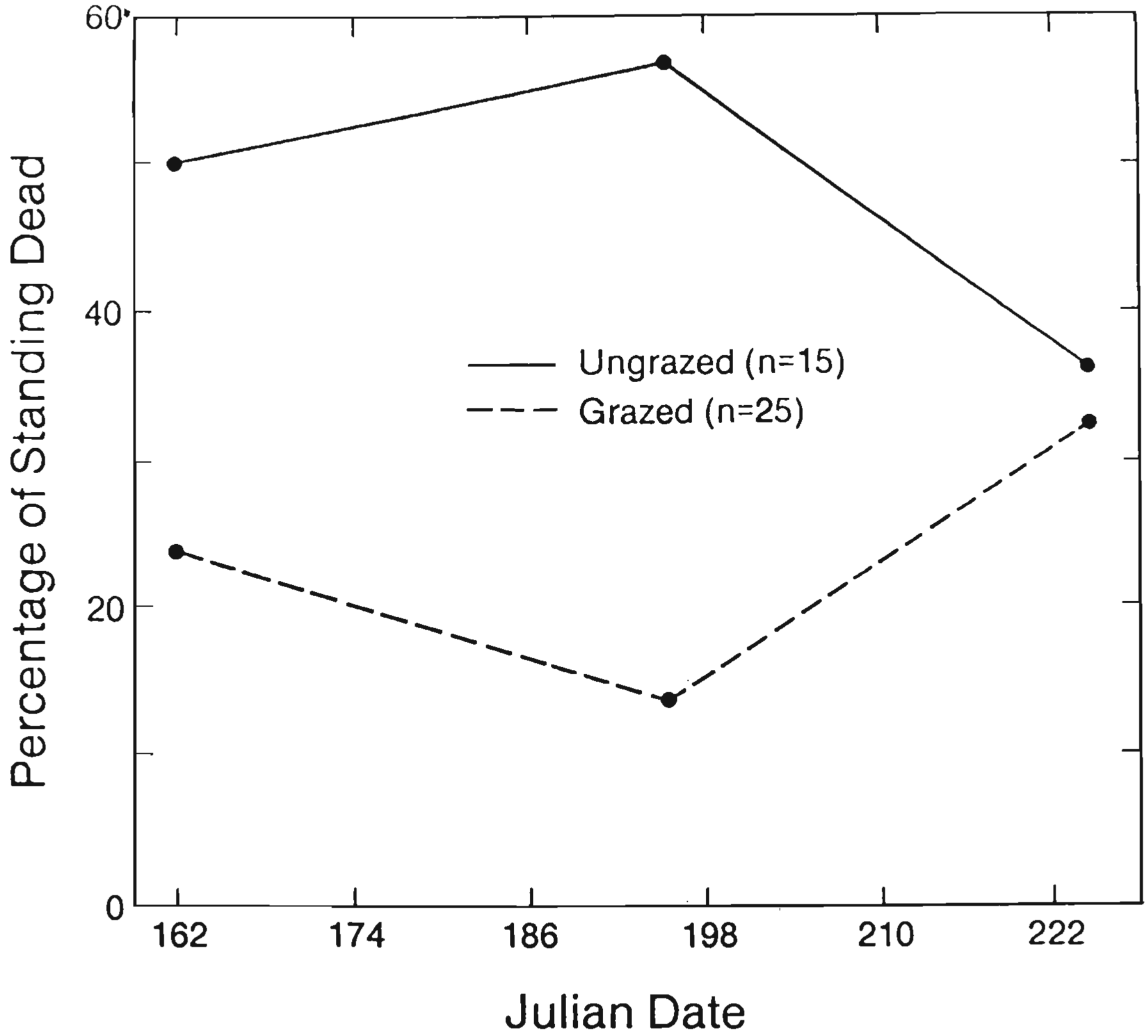

Fig. 2-5 Percentage of standing dead tissue in grazed and ungrazed '85 plots at Lake 650 in 1987.

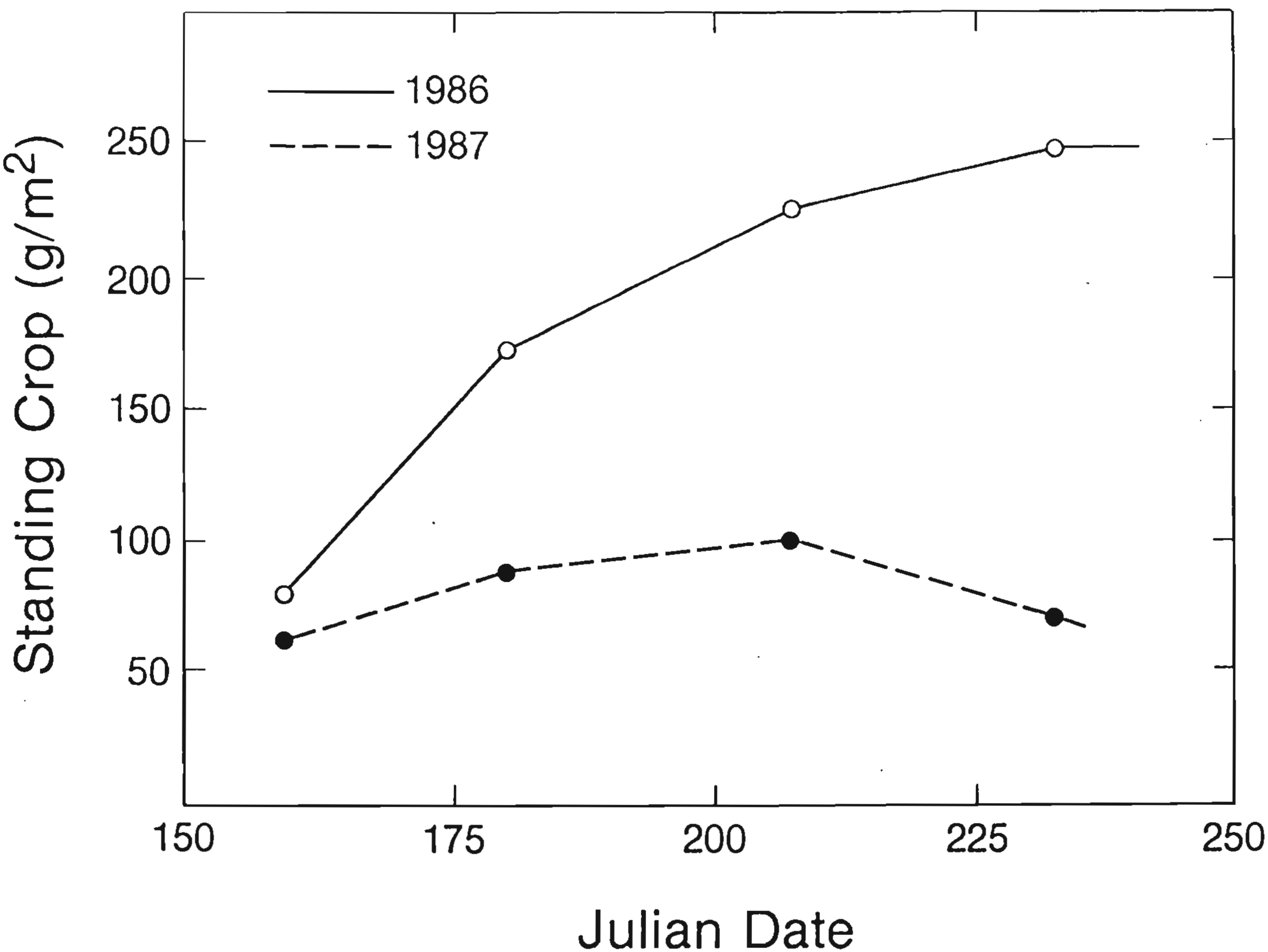

Fig. 2-6 Green standing crop (g/m^2) of ungrazed '85 vegetation at Calais Lake East in 1986 and 1987.

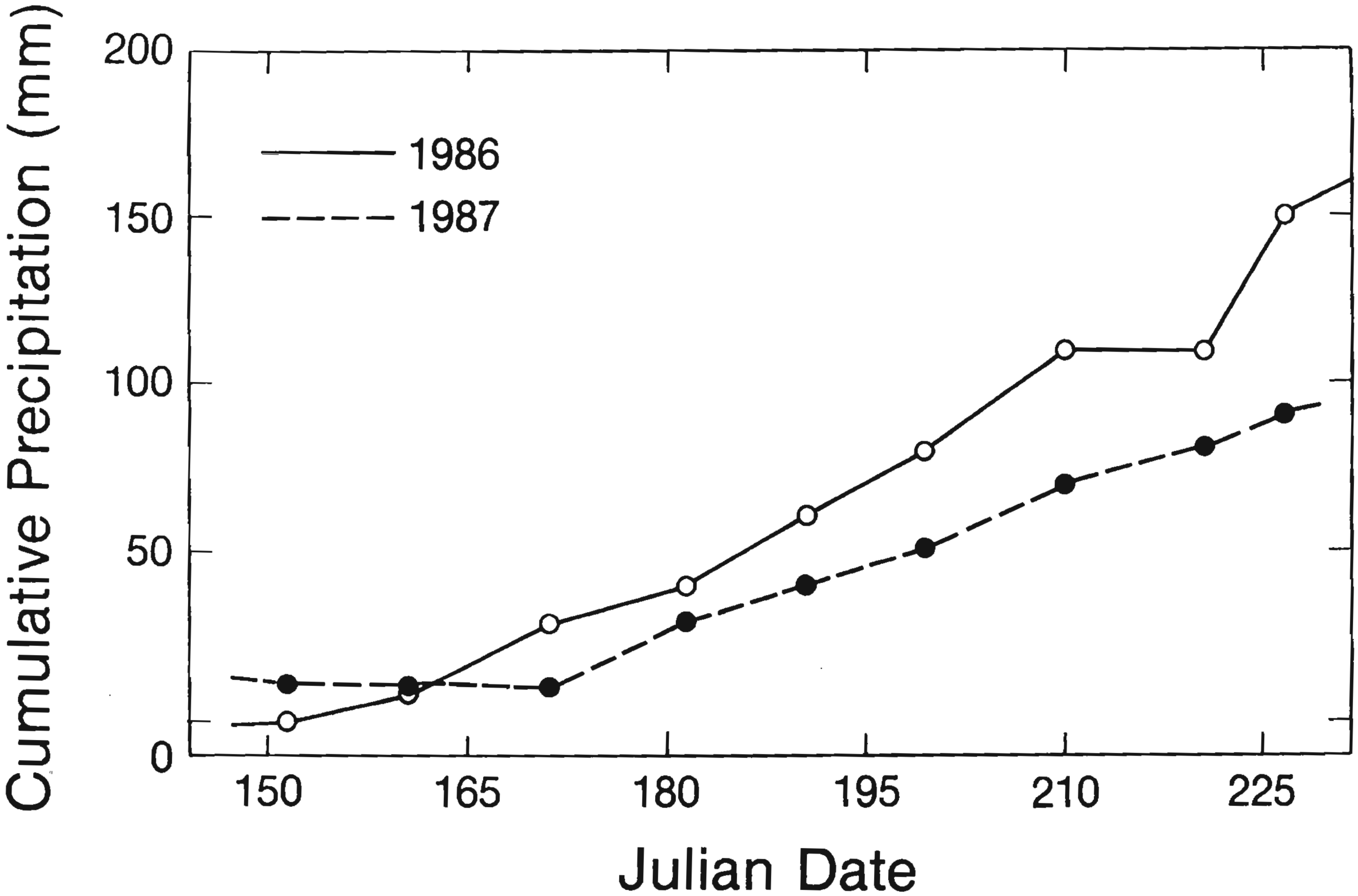

Fig. 2-7 Cumulative precipitation (mm) at Fort Providence since June 1 in 1986 and 1987.

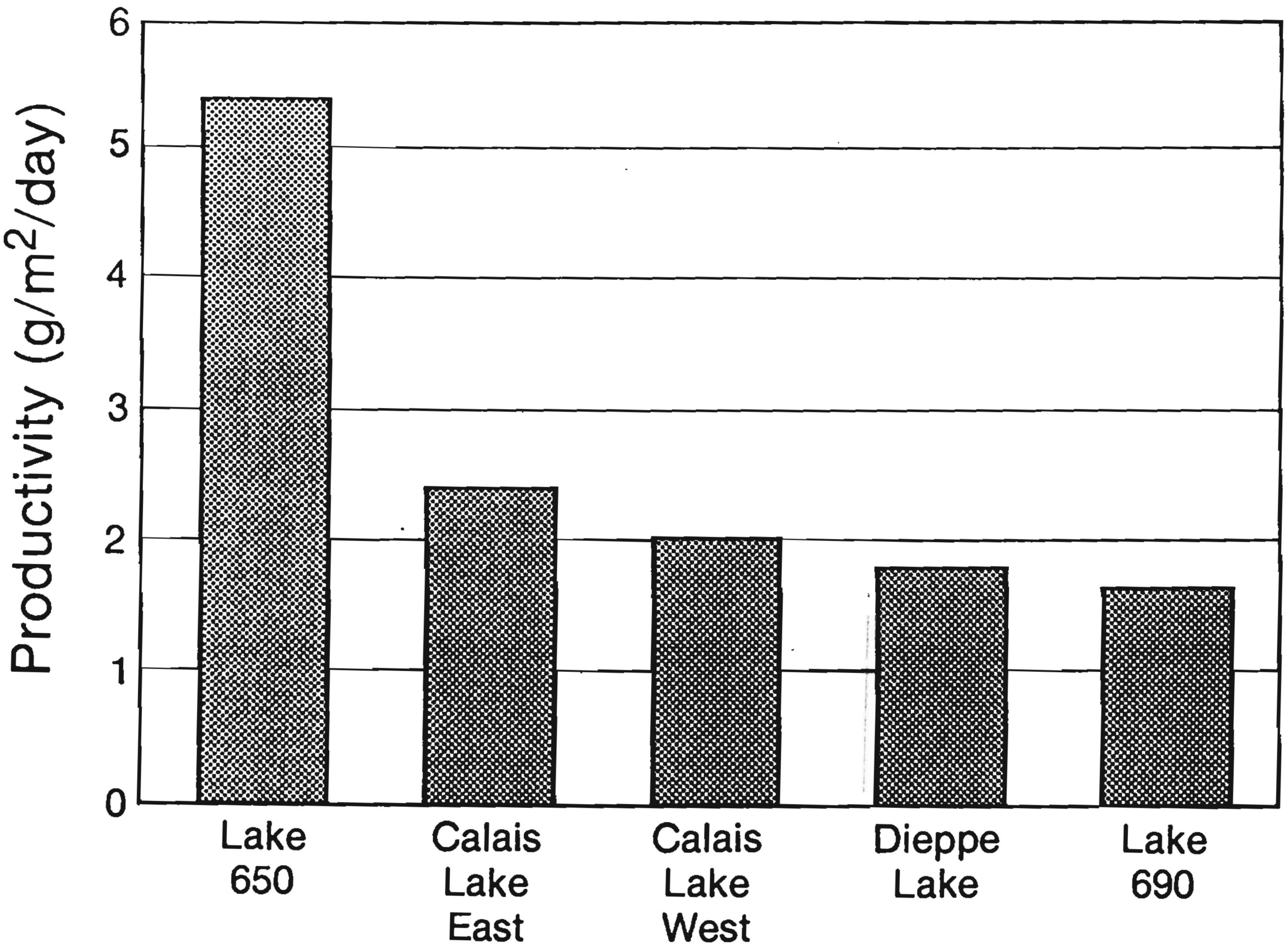

Fig. 2-8 Green productivity of ungrazed vegetation at all five study sites for the 1986 growing season.

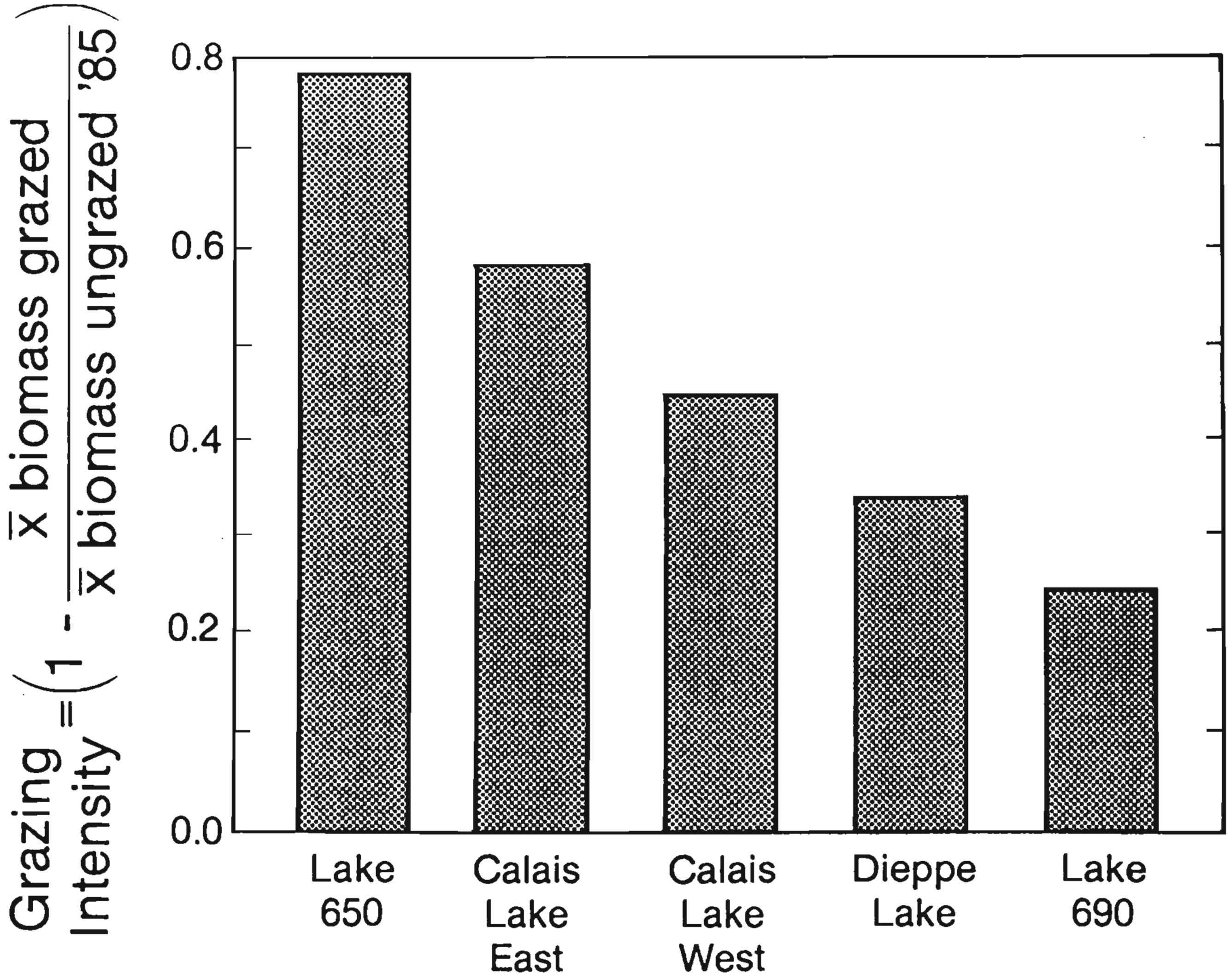

Fig. 2-9 Grazing intensity at five study sites in August 1987.

2.4 Discussion

2.4.1 The Relative Effects of Natural and Artificial Grazing on Plant Growth

The absence of differences in Green Productivity between naturally grazed and artificially grazed plots suggests that the presence of Wood Bison during the experimental period had no additional effect on plant growth over simple clipping (Fig. 2-2). This inference contrasts with abundant published evidence that artificial grazing differs substantially from natural grazing. For example, many researchers have found that saliva or products from saliva (e.g. thiamine) promote plant growth (Reardon et al. 1974; Hori 1975; Dyer and Bokhari 1976; Howe et al. 1982; McNaughton 1985b). However, Belsky (1986a) pointed out that most studies conclude that saliva does not stimulate plant growth under normal growing conditions. Johnston and Bailey (1972) observed no difference in yields of tops or roots between control and saliva-treated grasses. Detling et al. (1980) noted no significant changes in shoot and root CO_2 exchange rates; regrowth of leaves, crowns, and roots; ^{14}C allocation patterns; or tiller production following foliar application of bison saliva to *Bouteloua gracilis*. And Paige and Whitham (1987) demonstrated that there were no significant differences in fitness and plant biomass between artificially grazed and naturally grazed *Ipomopsis aggregata*.

It appears that Wood Bison saliva and other factors associated with natural grazing do not stimulate herbaceous plant growth in the MBS study area. These results (with regard to the non-stimulatory effects of saliva on plants) should be viewed with caution. In addition to saliva, artificially grazed plots lack natural litter accumulation patterns, trampling effects, input of feces and urine, and selective removal of preferred plant tissue. Because the permanent exclosures are relatively new, the lack of feces and urine in artificially grazed plots may not yet be important in influencing productivity. It is difficult to predict how the lack of trampling and selective grazing and how changes in litter accumulation patterns may have altered the Green Productivity in artificially grazed plots. Most studies show that trampling decreases standing crop or productivity (McNaughton 1976; Owaga 1980; Belsky 1986b). More research is needed to determine the effects of saliva and other effects of Wood Bison on plant growth at the MBS. Some of this research should be conducted in the lab to minimize other factors that may influence Green Productivity.

2.4.2 The Influence of Natural and Artificial Grazing on Plant Growth

It appeared that no clipping or grazing regime was heavy enough to deplete carbohydrate or nutrient reserves to a point where regrowth was adversely affected. Graminoids in the Shrub Meadow c.t. are thus capable of withstanding moderate clipping and grazing regimes for at least several growing seasons. It is possible that carbohydrate reserves and subsequent regrowth could be depleted if the intensity and frequency of grazing or clipping episodes was increased (Kennedy 1950; Albertson et al. 1953; Cook et al. 1958; Reardon et al. 1974). It is unlikely that moderate levels of herbivory or clipping would deplete carbohydrate reserves even if extended for long periods of time, however. The results of this study indicate that Shrub Meadow vegetation in the MBS was not adversely affected by artificial and natural grazing regimes during the 1986 and 1987 growing seasons (Fig. 2-2).

The "exact compensation" (i.e., balanced replacement of plant tissue consumed by herbivores) I observed in response to artificial and natural grazing in the MBS has been demonstrated in other studies. Solomon (1983) determined that the response of Solanum carolinense to host-specific herbivory by Frumenta nundinella after 13 weeks was exact compensation. Sterner (1986) observed that the fertilizing effects of zooplankton compensated for the loss of algae from zooplankton herbivory.

The "overcompensation" (i.e., stimulation of plant productivity above ungrazed control rates) I observed in naturally grazed plots during the second half of the growing season at Lake 650 and during the first half of the growing season at Calais Lake East in 1987, as well as in artificially grazed plots in 1987, could be explained by the presence of a microclimate more favorable for rapid growth in grazed or clipped plots. A cooler possibly more moist microclimate with lower light intensities in ungrazed and unclipped plots may have slowed spring growth at Calais Lake East. The accumulation of dead tissue during the growing season in ungrazed and unclipped plots at Lake 650 may have been responsible for their substantially reduced productivity relative to grazed and clipped plots (see next section). In addition, dead tissue in ungrazed and unclipped plots was physically obstructing growth of new tillers, especially at Lake 650 where the mulch layer was extremely thick (pers. obs. 1986-87). It seems reasonable to expect that ungrazed and unclipped plots will be even less productive in the future since these exclosures are relatively new.

The overcompensation observed in 1987 is consistent with that reported in a number of other studies. Canfield (1939) found that dry matter yield of Hilaria mutica was greater on plots clipped for 11 years than on unclipped plots. McNaughton (1979b) observed that the maximum productivity of Kyllinga nervosa (a grass adapted to heavy grazing in the Serengeti) was attained by clipping daily at 4cm. Prins et al. (1980) noted that moderate clipping of Plantago maritima gave an increase in total herbage accumulation compared with no clipping or with intense, frequent clipping. Paige and Whitham (1987) showed that Ipomopsis aggregata was more productive when artificially grazed than when ungrazed. In Wyoming, Lang and Barnes (1942) found that the productivity of short grasses increased with more frequent clipping. Turner and Klipple (1952) had similar findings in Colorado.

In addition to the extrinsic mechanisms there are many physiological or intrinsic mechanisms which could have increased productivity in grazed and clipped plots in 1987 (Detling et al. 1980). McNaughton (1979a), in his thorough literature review, listed the following intrinsic and extrinsic mechanisms that could be involved in overcompensation:

1. Photosynthesis is commonly inhibited by the accumulation of photosynthetic storage products. Increasing the drain on leaf substrates commonly results in increased photosynthetic rates (Neales and Incoll 1968; Thorne and Koller 1974).
2. Partial defoliation can stimulate increases in photosynthetic rate per unit of remaining leaf tissue because of increases in assimilate demand in the meristems of remaining shoots (Wareing et al. 1968; Gifford and Marshall 1973).
3. Photosynthetic rates can increase in leaves remaining after partial defoliation as a result of a decrease in mesophyll resistance to CO_2 diffusion (Gifford and Marshall 1973; Deinum 1976).
4. Defoliation may allow for more efficient light utilization by reducing mutual leaf shading (Hughes 1969; Heslehurst and Wilson 1971; Robson 1973).
5. In graminoids, older less efficient tissues are preferentially removed, leading to greater light intensities on younger previously shaded tissues (Rechenthin 1956; Jameson 1963; Langer 1972).

6. Following defoliation, a greater flow of growth promoting hormones from the roots to the shoots occurs (Weiss and Vaadia 1965; Meidner 1967; Pallas and Box 1970; Torrey 1976). This increased flow to residual meristems promotes cell division and enlargement in previously quiescent meristems (McNaughton 1979a).

7. After long-term defoliation, a reduction in the rate of photosynthesis decline associated with leaf aging occurs (Richmond and Lang 1957; Woolhouse 1967; Neales et al. 1971; Gifford and Marshall 1973).

There have been contradictions to these findings, however. Davidson and Milethorpe (1966) reported that, after defoliating Dactylis glomerata, the rate of photosynthesis per unit leaf area remained approximately constant. Several others observed that severe simulated or actual grazing by insects on single leaves often results in reduced photosynthetic rates per unit leaf area (Hall and Ferree 1975, 1976; Poston et al. 1976). However, it is possible that one or more of the intrinsic mechanisms reviewed by McNaughton (1979a) and the author could be operating but they should be tested experimentally before any conclusions are made.

Although tillering in graminoids was not examined, increased tillering is another intrinsic mechanism that could have contributed to the overcompensation observed in 1987. When shoot apices are removed (thus removing apical dominance) or a more favourable light environment is created in closed stands, enhanced tillering is often observed (Youngner 1972). In a laboratory experiment examining the effects of grasshopper grazing on Bouteloua gracilis, Dyer and Bokhari (1976) found that grazing resulted in increased tillering, probably as a result of hormonal effects (Harris 1974). McNaughton (1976) noted vigorous tillering of graminoids in grazed areas of the Serengeti Plains. And Belsky (1986b) observed that clipping Andropogon greenwayi increased the number of tillers by a factor of 2.5 or more. Although removal of stem apices may stimulate tillering, total yield of dry matter may be reduced (Jameson and Huss 1959). Decreases in tillering after defoliation have also been observed (Ellison 1960; Detling et al. 1980).

Until now, only the quantity of regrowth has been discussed. Quality of regrowth also is an important factor in grazing systems. This study did not examine the quality of regrowth, although samples from the MBS have been retained for future analysis. To illustrate the importance of plant quality to herbivores, Thaine (1954) demonstrated moderate increases in productivity of Russian Wild Ryegrass with increased clipping frequency. But he found pronounced increases in the protein content of regrowth and pounds of protein per acre available to grazers with increased clipping frequency. Similar results were reported from other studies (Albertson et al. 1953; Jameson 1963; McNaughton 1976, 1984, 1985a; Prins et al. 1980;

Cargill and Jefferies 1984a; Seastedt 1985). Therefore, it is possible that the regrowth in both naturally and artificially grazed plots in this study was of higher quality than the growth in ungrazed plots. Wood Bison may be substantially increasing their dietary intake of protein providing that they regraze the same swards. I observed Wood Bison regularly regrazing swards at Lake 650 and Calais Lake East during the 1986 and 1987 growing seasons.

In any exclosure experiment, there is the problem of site differences between the exclosed area and the area exposed to herbivores, and this study is no exception. These site differences, if any, may have contributed to some of the variation between treatments. Control estimates were from permanent exclosures that were set up in relatively homogeneous areas. Estimates of Actual and Apparent productivity were gathered from relatively heterogeneous, randomly selected plots from swards ca. 1 ha in area within the Shrub Meadow c.t.. Of 25 comparisons of standing crop biomass estimates in grazed and ungrazed areas, variances were higher in 13 grazed and in 5 ungrazed; in 7 comparisons, grazed and ungrazed were very similar. I suspect that these site differences were minimal, however. Most differences between Control and Actual productivity estimates occurred during one-half (early or late) of the growing season. If site differences were pronounced, differences between Control and Actual estimates would most likely occur throughout the growing season.

2.4.3 The Ecological Implications of Dead Tissue Accumulation in Grazed and Ungrazed Areas

The reduced productivity in plots ungrazed by Wood Bison since 1985, especially at more productive Lake 650 (Figs. 2-2 and 2-3), and the higher absolute and relative quantities of standing dead tissue in ungrazed areas and in plots ungrazed since 1985 may indicate that the changes in microclimate associated with accumulating dead tissue slowed plant growth (Fig. 2-4). Productive ungrazed plots, in particular, accumulated standing dead tissue faster than the tissue decomposed (an equilibrium may be reached in the future). In contrast, grazed areas had relatively low proportions of standing dead tissue (SDT) at the most productive sites because grazers increased decomposition rates by depositing feces and urine and because Wood Bison removed vegetation semi-continuously in grazed areas, reducing rates of dead tissue accumulation (Fig. 2-5).

In ungrazed areas a correlation existed between the productivity of the site (Table 2-12), the resulting accumulation of dead tissue (in relative and absolute terms) and the degree to which productivity was subsequently reduced. Because biomass accumulated faster than it decomposed at Lake 650 and Calais Lake East relative to the other less productive sites, and because productivity was reduced to a greater extent at the productive sites, this conclusion seems credible.

These trends are consistent with numerous other studies. Cargill and Jefferies (1984a) showed that geese grazing in northern Manitoba reduced the accumulation of litter and that litter accumulation was higher the year after a productive growing season. They demonstrated that grazing increased NAPP (Net Above-Ground Primary Productivity) mainly by prolonging the period of active growth. Curtis and Partch (1950) noted that grazing in Wisconsin stimulated early vegetative growth and increased soil temperature during the growing season.

This study is consistent with others that showed increases in the quantity of dead tissue in ungrazed sites. For example, Sims and Singh (1978) showed that grazed meadows in western North America had less biomass in "recent dead" (material produced and senesced during the current growing season) and "old dead" (material produced and senesced during previous years) compartments. And in the Serengeti, McNaughton (1979a) reported that "dry biomass" was more abundant and "green biomass" was less abundant in a 12 year old exclosure. In contrast to these findings, Belsky (1987) noted that exclosed plants at Serengeti National Park remained green 4-6 weeks longer than nearby grazed plants.

Decreases in the quantity of dead tissue at grazed sites have important implications for how grazers may increase their dietary intakes of protein by regrazing the same swards. It was discussed earlier that the regrowth after a grazing episode may be of higher quality than ungrazed vegetation. Coupled with this is the smaller quantity of poor quality senescent tissue associated with grazed areas. This lends support to the hypothesis that Wood Bison may be maintaining grazing lawns of relatively high nutritional quality at the MBS. Grazing lawns (McNaughton 1984, 1986) are characterized by high productivity, forage quality and biomass concentration (g cm^{-3}) in comparison to ungrazed lawns. It is well documented that lower quantities of dead tissue result in more nutritious forage. Stoner et al. (1982) noted lower levels of nitrogen, phosphorous, and potassium in dead subarctic tundra vegetation than in live. And in the Serengeti, McNaughton (1985a) reported that high-quality vegetation accumulated during the wet season and was subsequently converted to low-quality forage at the onset of the dry season. Because the digestive efficiency of Bison is high, particularly on low quality forage, and because Bison are capable of using limited resources rather completely (Hudson and Frank 1987) the importance of these "grazing lawns" is probably not as great to Wood Bison as it is for example, to Thomson's gazelles in the Serengeti which regrazed areas previously grazed by Wildebeest (McNaughton 1976).

2.4.4 Spatial and Temporal Differences in Plant Growth within the Shrub Meadow Community Type

The substantial variation in productivity and standing crop between the 1986 and 1987 growing seasons and the extended growing season in 1986 reported in this study can be attributed to differences in growing season rainfall amounts (Figs. 2-6 and 2-7).

Since temperature differences were slight, temperature most likely wasn't a factor that influenced productivity differences between growing seasons. The higher rainfall in 1986 resulted in greater productivity than in 1987, indicating that the productivity of subhygrophytic Shrub Meadow vegetation is limited by rainfall amounts. It is also possible that accumulation of dead tissue may have contributed to a microclimate less favorable for growth in plots ungrazed since 1985 during the 1987 season. However, even plots not expected to show such microclimate-induced decreases in productivity, (e.g., grazed plots or plots that were ungrazed for short periods of time) were substantially less productive in 1987. Even a higher grazing intensity at Calais Lake East in 1986 did not lower the apparent productivity (see Methods) at grazed sites in 1986 relative to 1987 (Appendix 2c-8).

Variation in productivity and standing crop estimates within the 1986 and 1987 growing seasons was probably controlled by fluctuating nitrogen levels (see fecal pat data, Appendix 2c-12), temperature, and/or light intensity. The high productivity estimates in ungrazed plots early in the growing season and the steady decreases later in the growing season observed in 1986 and 1987 have also been reported by others. Sims et al. (1978) noted that most growth occurred early in the growing season at sites dominated by cool season plants. Most of the water available for plant growth is from snowmelt early in the growing season (Sims and Singh 1978).

Rainfall is an important factor that limits above-ground productivity of Shrub Meadow vegetation at the Mackenzie Bison Sanctuary. In plant communities where water is not a limiting factor, such as the more hygrophytic Sedge Meadow c.t., productivity and standing crop estimates probably did not respond to fluctuations in rainfall as closely as they did in the mesophytic Shrub Meadow c.t.. The author observed that peripheral areas of the Sedge Meadow c.t. were considerably drier in 1987 than in 1986. These areas probably were less productive in 1987 than in 1986.

These relations between productivity and environment have been reported elsewhere. In western Kansas, Albertson et al. (1953) noted that biomass closely followed the summer rainfall curve and that growth was greatest when soil moisture was plentiful. Pearson (1965) irrigated a desert community in eastern Idaho with 9cm of water and found that productivity increased 41%. Anderson and Talbot (1965) observed that the greater rainfall and lower evapotranspiration in the western portion of the Serengeti Plains produces more vigorous growth of vegetation than found elsewhere in the region. In western North America, Sims and Singh (1978) demonstrated that peak, live, above-ground biomass increased with increasing amounts of growing season precipitation and that peak biomass tends to level out when water is no longer a limiting factor to plant growth. Hoefs (1984) reported that the productivity of sheep range in Yukon Territory varied between years primarily because of fluctuating rainfall. McNaughton (1985a) showed that productivity of ungrazed control plots was linearly related to annual rainfall in Serengeti National Park.

In addition to these wide temporal variations in productivity there are intrinsic site differences causing some swards to be much more productive than others (Fig. 2-8). Soil texture and structure probably did not contribute to the spatial variation in productivity of exclosed vegetation (Table 2-13). A number of soil-related factors were not examined, however. Soil moisture, temperature, and nutrient levels may differ between sites. The productivity of ungrazed vegetation may also have been influenced by the grazing history of the site. In this study, Wood Bison sometimes increased the productivity of grazed plots relative to ungrazed plots. Similarly, Wood Bison may have increased the productivity of Lake 650 relative to other study sites by acting as nutrient conduits, moving nutrients among vegetation types, and as nutrient concentrators, harvesting nutrients over large areas and concentrating them into smaller areas (Carran et al. 1982). It is possible that Wood Bison imported nutrients into the Lake 650 area over the last 25 years. The increase in nutrient levels may have boosted productivity (Cargill and Jefferies 1984b). Therefore the differences seen in productivity estimates of ungrazed plots among study sites do not necessarily reflect the differences that would be observed in the long-term absence of grazers. Long-term exclosure studies and an intensive examination of the soils within the Shrub Meadow c.t. could answer some of the questions about a sward's intrinsic primary productivity.

Wood Bison responded to and contributed to these between-site differences in productivity by spending more time grazing, wallowing and ruminating in more productive sites (Fig. 2-9). The results in localized areas of higher productivity within the Shrub Meadow community type. A more favorable mesoclimate at Lake 650 attracted Wood Bison. The wallows at Lake 650 were located on a berm (a ridge ca. 1 metre high formed from ice pushing up against the shore) and most of the ruminating took place on a windy portion of the berm (possibly with fewer insects) adjacent to Lake 650 proper (pers. obs., 1986-1987). On particularly hot days Wood Bison ruminated in the shade of <u>Salix</u> trees located on the berm. On numerous occasions, I observed herds moving into the study area. At one point I intercepted them en route; ten minutes later they appeared at the study site. The Lake 650 study site was a common destination for Wood Bison. On other occasions after a two or three week absence from Lake 650, I would return to an unrecogizable site with extensive trampling and wallows. The amount of feces deposited during these episodes was prodigious (Appendix 2c-11).

Similar trends have been reported elsewhere. McNaughton (1985a) noted that localized areas of higher primary productivity act as grazing foci at Serengeti National Park. Havstad and Malechek (1982) showed that the energy expenditures of cattle increased with declines in forage productivity. Therefore, it is advantageous for the grazer to feed in relatively productive areas, assuming forage quality is constant. Similarly, McNaughton (1985) observed that grazers increase their net energy and nutrient gains by concentrating on localized areas of higher forage availability.

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3. SELECTIVE GRAZING BY WOOD BISON IN A SUB-HYGRIC SHRUB MEADOW PLANT COMMUNITY TYPE, MACKENZIE BISON SANCTUARY, N.W.T.

3.1 Introduction

Whether or not a herbivore is selective in its food habits (i.e., consumes plant species or plant parts in a greater or lesser proportion than they are found) depends on the availability of plants as well as a number of animal and plant-related factors. Some characteristics of the herbivore that can influence selection include its digestive capacity, daily foraging time, daily energy requirements, daily nutrient requirements, body size, and mouth size (Hanley 1982; Belovsky 1986). Other animals such as biting insects and predators may also influence selectivity in a herbivore's food habits.

Plant 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, 1985; White 1978; Milton 1979; Bryant and Kuropat 1980; Mattson 1980; Chapin et al. 1986), 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 within a plant community can also influence what a herbivore chooses, especially for large animals such as Wood Bison that need to consume large quantities of food. 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).

Since herbivores choose 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 Wood Bison should attempt to consume large quantities of forage because of their size. Because they are ruminants, Wood Bison can tolerate low quality forage (Hudson and Frank 1987). If relatively high quality forage is abundant, however, Wood Bison should choose it over low quality forage (assuming their intake rates aren't reduced). Like most herbivores, Wood Bison should avoid plants with offensive (e.g. toxic) secondary compounds. Most studies examining Bison food habits were conducted in areas other than the MBS (Peden et al. 1974, Peden 1976, Reynolds et al. 1978, Hudson and Frank 1987). It was important to learn more about the food habits of Wood Bison in their preferred summer range because this population has been growing exponentially since 1963. Food habits information is also an important component of any study that examines the impact of a grazing species on a plant community type.

The objectives of this study were:

1) To determine whether or not Wood Bison select sedges, grasses, or forbs within the Shrub Meadow plant community type.

2) To determine if Wood Bison select for or avoid any of the 10 most abundant plant species within the Shrub Meadow c.t.

3.2 Methods

To determine if Wood Bison selected certain herbaceous species within the Shrub Meadow plant community type, ocular cover estimates and grazing ratings were made for each species in a given $0.25m^2$ plot along a transect (see Chapter 2). Plant nomenclature follows Porsild and Cody (1980). These plots were located in a systematic random manner. In 1986, data were collected from 5 study sites at 3-4 week intervals throughout the growing season. During each sampling period at a given sward, cover estimates and grazing ratings were estimated for each species in 20 plots. In order to reduce standard errors, estimates were gathered from 25 plots/sward in 1987. Two study sites were sampled during the 1987 growing season at 3-4 week intervals. In late August 1987, all 5 study sites were sampled.

Grazing ratings and ocular cover estimates were compared for the 10 most abundant species in the Shrub Meadow c.t. The grazing rating was based on an estimate of the percentage of ramets of species i grazed in plot j. Ocular cover estimates were expressed as the percentage of plot j that species i occupied. Each grazing rating class and cover class was associated with a mid-point (e.g. class 7 (range 96-100%) means approximately 98% of ramets of species i were grazed in plot j or that species i covers 98% of plot j.) The midpoints for other classes were: class 6 (76-95%) 85.5%, class 5 (51-75%) 63%, class 4 (26-50%) 38%, class 3 (16-25%) 20.5%, class 2 (6-15%) 10.5%, class 1 (1-5%) 3%, class + 0.8%, class R 0.5%, class T

0.3%. Since the mid-points for the grazing ratings were not normally distributed, even after square root and log transformations, the nonparametric Mann-Whitney U-test (Sokal and Rohlf 1981) was used to determine if Wood Bison selected one herbaceous species over another, given their relative cover values. Since the number of species combinations was very large with 40 species, the most important 2 sedge, 3 grass, and 5 forb species were selected. Only ramets available to Wood Bison (i.e. greater than 3 cm in height) were considered in the grazing rating analysis, whereas cover estimates included ramets of all heights. Ramets that were grazed to heights below 3cm were not ignored.

Whether or not Wood Bison selected or avoided certain plant growth forms was also addressed. To determine if there was selection of one growth form (sedges, grasses, and forbs) over another, the standing crops (the dry weight of above-ground biomass) of species within these growth forms were lumped in grazed areas and in adjacent ungrazed areas. Plots were clipped 3 cm above-ground. Each species was bagged seperately in the field. Samples were dried in a propane oven at 60°C for 8 hours. Standing crops for sedges and grasses were compared using the t-test of the differences between two means, and standing crops for forbs were compared using the Mann-Whitney U-test (Sokal and Rohlf 1981).

The effect of species abundance on species grazing ratings was also investigated. Median grazing ratings were plotted against mean percent cover estimates to determine if the abundance of a species affects its grazing rating and to determine if differences between species grazing ratings could be attributed to their abundances. Wood Bison could be considered selective feeders if the grazing ratings of species of similar abundances were different. If changes in species grazing ratings are not proportional to species abundances in some consistant way, it could be concluded that Wood Bison showed a functional response to increases in mean cover (see Smith 1980).

3.3 Results

Median grazing ratings for the most abundant species were compared to determine if Wood Bison selected one plant species over another within the Shrub Meadow c.t. These species included 2 sedges, Carex atherodes (CXAT) and Carex aquatilis aquatilis (CXAQ); 3 grasses, Calamagrostis inexpansa and/or C. neglecta (CAIN), Hordeum jubatum (HOJU), and Agropyron trachycaulum (AGTR); and 5 forbs, Senecio pauperculus and/or S. indecorus (SESP), Stachys palustris (STPA), Potentilla pensylvanica and/or P. multifida (POSP), Geum macrophyllum (GEMA), and Potentilla norvegica (PONO). Calamagrostis neglecta and Senecio indecorus were rare relative to C. inexpansa and S. pauperculus.

Wood Bison consistently selected Carex atherodes over all other species within the Shrub Meadow c.t. (Figure 3-1; Tables 3-4 and 3-5). C. aquatilis was not as heavily grazed as the more abundant C. atherodes. Similarly, sedges as a growth form were selected for over grasses and forbs in mixed sedge/grass swards (Figure 3-2; Tables 3-1 - 3-3b). At grass-dominated Lake 650 mainly grasses were consumed in 1986 and 1987 because grasses were much more abundant than sedges; however, C. atherodes was more heavily grazed than any grass species at Lake 650 in 1987.

Of the grass species, Agropyron trachycaulum was selected over Calamagrostis inexpansa and Hordeum jubatum (Tables 3-4 and 3-5). Ungrazed stands of Calamagrostis adjacent to heavily grazed stands of

Carex atherodes and Agropyron were common. Stands of Hordeum were consumed, but if the plants were in flower Wood Bison seemed to avoid them. Grasses as a growth form were not as important to Wood Bison as sedges as indicated by their relatively similar standing crops inside and outside exclosures (Tables 3-1 and 3-2).

Forbs were the least important growth form for Wood Bison. Standing crops were similar between grazed and ungrazed areas indicating that forbs were unimportant as a food source (Table 3-3a and 3-3b). Some forb species had high grazing ratings which indicated that they were probably palatable but because their cover estimates were so low, utilization by Wood Bison was low (Tables 3-4 and 3-5). It should be pointed out that because of the small number of plots that a given forb species occupied in a sward, some of the grazing ratings for forb species may not be significantly different from ratings that appear very different. Wood Bison selected for forbs as a growth form in 1986 at Dieppe Lake and Calais Lake East (Table 3-3) but in most cases forb species were not grazed at all. Of those forb species studied, there does not appear to be selection of any species in particular.

There were pronounced differences in median grazing ratings of some species within study sites during a growing season. The median grazing rating of Carex atherodes at Calais Lake East was high in June 1987 but by August 1987 it had dropped substantially (Fig. 3-3). In 1987 at Lake 650 the median grazing rating of Agropyron trachycaulum peaked in July and was much lower in June and August

(Fig. 3-4). The median grazing ratings of species also varied among years. In 1986 at Lake 650, the median grazing rating of A. trachycaulum was very high and the median grazing rating of C. atherodes was relatively low. By 1987 the trend had reversed, the median grazing rating of A. trachycaulum had dropped and the median grazing rating of C. atherodes had risen (Tables 3-4 and 3-5). The median grazing ratings of some species varied considerably among study sites. For example, A. trachycaulum had low median grazing ratings at most study sites in 1986. However, at Lake 650 it had a very high median grazing rating (Table 3-4).

Grazing ratings did not show a classical functional response to increases in abundance, however grazing ratings were not proportional to cover. The mean percent cover of C. atherodes did not influence the changes observed in its grazing rating at Calais Lake East in 1987 (Fig. 3-3). Relatively rare C. atherodes had higher median grazing ratings than more abundant A. trachycaulum at Lake 650 in 1987 (Fig. 3-4). As well, the abundance of C. atherodes and Calamagrostis spp. at all study sites in 1987 was similar. Carex had much higher grazing ratings (Fig. 3-5). However, after an intense grazing episode at Lake 650 in July 1987, both the mean cover and median grazing rating of A. trachycaulum were reduced (Fig. 3-4).

Table 3-1. Comparison of Green Standing Crop Biomass Estimates of *Carex* and Grasses in Control'85 and Grazed Plots in 1986.

Date		95% Confidence Intervals						Prob.
		Control '85			Grazed			
		L1	Mean	L2	L1	Mean	L2	
				Calais Lake East				
June 9	*Carex*	29.39	46.29	66.95	11.86	20.57	31.59	P≤.05
	Grasses	3.58	11.54	23.71	9.57	15.18	22.02	P>.10
July 1	*Carex*	79.65	113.78	153.94	7.94	15.50	25.46	P≤.001
	Grasses	8.00	15.90	26.38	4.02	7.62	12.27	P≤.10
July 22	*Carex*	106.39	151.78	205.17	16.14	27.70	42.28	P≤.001
	Grasses	5.88	22.54	49.53	14.83	26.75	42.07	P>.10
Aug.21	*Carex*	102.63	183.10	286.62	34.08	56.05	83.40	P≤.001
	Grasses	17.84	44.12	81.89	23.04	42.27	67.20	P>.10
				Lake 690				
June 12	*Carex*	20.16	29.20	39.87	10.03	18.08	28.39	P>.10
	Grasses	17.39	29.75	45.34	9.84	15.50	22.39	P≤.05
July 10	*Carex*	36.66	60.50	90.20	12.59	24.00	38.96	P≤.05
	Grasses	27.73	43.72	63.29	17.60	28.02	40.79	P>.10
Aug.9	*Carex*	55.62	84.69	119.82	23.59	41.49	64.33	P≤.05
	Grasses	39.21	53.38	69.69	25.85	42.01	62.01	P>.10
				Calais Lake West				
June 14	*Carex*	37.42	54.85	75.58	12.50	20.66	30.80	P≤.01
	Grasses	32.50	41.36	51.27	18.12	25.51	34.13	P≤.05
July 5	*Carex*	48.89	79.07	116.40	28.72	50.19	77.55	P>.10
	Grasses	54.38	71.41	90.74	29.38	38.44	48.69	P≤.01
July 26	*Carex*	39.60	72.43	115.01	16.93	30.08	46.91	P≤.05
	Grasses	84.46	103.74	125.00	29.15	43.86	61.52	P≤.001
				Lake 650				
June 17	*Carex*	0.40	7.34	21.13	0.73	3.83	8.81	P>.10
	Grasses	46.05	89.75	147.78	8.62	16.89	27.79	P≤.001
July 14	*Carex*	1.79	12.60	32.31	3.24	8.20	15.23	P>.10
	Grasses	152.96	262.26	400.78	33.19	62.38	100.62	P≤.001
Aug.14	*Carex*	11.60	45.47	101.14	5.27	13.26	24.69	P≤.05
	Grasses	252.42	352.19	468.50	26.83	46.42	71.27	P≤.001
				Dieppe Lake				
June 26	*Carex*	17.18	33.96	56.28	9.00	15.58	23.89	P≤.05
	Grasses	11.17	19.66	30.46	8.09	13.34	19.83	P>.10
July 20	*Carex*	29.40	49.06	73.67	20.60	31.20	43.94	P>.10
	Grasses	42.94	53.96	66.24	22.02	37.94	58.10	P>.10
Aug.17	*Carex*	29.84	57.56	94.20	21.57	35.02	51.65	P>.10
	Grasses	43.57	75.54	116.17	25.60	42.14	62.72	P≤.10

Table 3-2. Comparison of Green Standing Crop Biomass Estimates of *Carex* and Grasses in Control'85 and Grazed Plots in 1987.

Date		95% Confidence Intervals						Prob.
		Control '85			Grazed			
		L1	Mean	L2	L1	Mean	L2	
				Calais Lake East				
June 3	*Carex*	26.02	40.46	58.03	9.18	12.82	17.04	P≤.001
	Grasses	3.82	7.62	12.61	4.83	7.12	9.81	P>.10
July 5	*Carex*	52.56	70.90	91.96	12.63	22.73	35.71	P≤.001
	Grasses	5.30	8.99	13.57	13.33	20.84	29.98	P≤.05
July 30	*Carex*	55.14	75.54	99.12	16.38	28.44	43.74	P≤.01
	Grasses	8.58	17.82	30.62	17.20	24.30	32.60	P>.10
Aug.21	*Carex*	29.55	47.52	69.69	18.92	29.75	42.97	P>.10
	Grasses	10.96	21.31	34.96	7.30	9.93	12.95	P≤.01
				Lake 650				
June 13	*Carex*	25.28	38.56	54.60	7.33	12.60	19.23	P≤.001
	Grasses	9.93	23.61	42.94	41.04	52.50	65.35	P≤.01
July 12	*Carex*	19.09	31.76	47.58	3.63	6.90	11.11	P≤.001
	Grasses	61.06	77.65	96.20	21.04	27.48	34.77	P≤.001
Aug.13	*Carex*	8.42	16.56	27.31	4.37	8.56	14.04	P≤.10
	Grasses	47.72	71.75	100.62	13.38	20.38	28.81	P≤.001
				Lake 690				
Aug.19	*Carex*	43.15	58.02	75.08	14.04	27.27	44.75	P≤.05
	Grasses	19.64	28.66	39.34	19.32	26.02	33.70	P>.10
				Calais Lake West				
Aug.20	*Carex*	13.89	24.40	37.78	19.35	31.20	45.81	P>.10
	Grasses	31.57	35.86	40.43	23.67	35.38	49.39	P>.10
				Dieppe Lake				
Aug.19	*Carex*	24.78	40.59	60.22	15.57	21.78	29.00	P≤.05
	Grasses	16.77	24.80	34.36	11.17	18.08	26.58	P>.10

Table 3-3a. Comparison of Median and Range of Green Standing Crop Biomass Estimates (g m^{-2}) of Forbs in Control'85 and Grazed Plots at Five Study Sites in 1986.

Date	Median Standing Crop						
	Min.	Control	Max.	Min.	Grazed	Max.	Prob.
			Calais Lake East				
June 9	0.0	7.82	25.28	0.0	5.28	44.80	P>.10
July 1	3.4	21.90	133.20	0.0	5.50	13.76	P≤.01
July 22	0.0	22.76	88.88	0.0	13.76	60.24	P>.10
Aug. 21	0.0	2.46	26.24	0.0	6.28	52.32	P>.10
			Lake 690				
June 12	0.0	1.08	6.64	0.0	2.24	38.28	P>.10
July 10	0.0	5.56	21.20	0.0	3.36	30.40	P>.10
Aug. 9	0.0	6.08	86.00	0.0	5.02	58.60	P>.10
			Calais Lake West				
June 14	0.0	0.20	2.20	0.0	1.50	19.76	P≤.05
July 5	0.0	1.06	30.60	0.0	4.34	56.24	P>.10
July 26	0.0	4.60	0.10	0.0	8.28	53.88	P≤.01
			Lake 650				
June 17	0.0	0.0	7.16	0.0	0.56	40.68	P>.10
July 14	0.0	0.0	175.50	0.0	1.28	63.44	P>.10
Aug. 14	0.0	0.0	20.96	0.0	3.92	88.36	P>.10
			Dieppe Lake				
June 26	0.0	5.50	10.88	0.0	0.00	9.44	P≤.001
July 20	0.0	23.24	55.12	0.0	0.00	20.08	P≤.001
Aug. 17	0.0	8.28	28.56	0.0	0.00	5.36	P≤.01

Table 3-3b. Comparison of Median and Range of Green Standing Crop Biomass Estimates (g m^{-2}) of Forbs in Control'85 and Grazed Plots at Five Study Sites in 1987.

Date	Median Standing Crop						
	Min.	Control	Max.	Min.	Grazed	Max.	Prob.
			Calais Lake East				
June 3	0.0	3.06	5.76	0.0	0.48	35.16	P>.10
July 5	0.0	1.74	23.20	0.0	4.56	31.40	P>.10
July 30	0.0	0.00	2.72	0.0	1.64	51.96	P≤.05
Aug. 21	0.0	0.00	0.00	0.0	0.00	26.00	P>.10
			Lake 650				
June 13	0.0	0.00	0.00	0.0	2.28	51.12	P≤.05
July 12	0.0	0.00	0.96	0.0	3.28	116.76	P≤.01
Aug. 13	0.0	0.00	1.08	0.0	2.44	75.04	P≤.01
			Lake 690				
Aug. 19	0.0	1.84	44.92	0.0	2.24	15.20	P>.10
			Dieppe Lake				
Aug. 19	0.0	0.00	2.68	0.0	0.00	9.72	P>.10
			Calais Lake West				
Aug. 20	0.0	0.00	0.24	0.0	0.00	31.64	P>.10

Table 3-4. Comparison of Median Grazing Ratings*(R) and Mean Ocular Cover Estimates* (±SE) for the Most Abundant Species** at Five Study Sites in 1986.

Lake 650 - July 14

	AGTR	CXAT	PONO	CAIN	STPA
R	86.0a	38.0b	38.0abc	0.0c	0.0c
%COV	33±8	9±3	7±4	27±9	5±3

Dieppe Lake - July 21

	CXAT	AGTR	SESP	CAIN	CXAQ	HOJU
R	38.0a	38.0ab	8.0ab	1.5b	0.5b	0.0b
%COV	24±4	5±4	3±2	29±7	2±2	5±2

Calais Lake East - July 22

	CXAT	CAIN	STPA	AGTR	HOJU	SESP	POSP	PONO
R	16.0a	3.0b	0.3bc	0.0bc	0.0c	0.0c	0.0c	0.0c
%COV	23±4	25±7	14±6	15±5	8±5	21±5	3±2	3±2

Calais Lake West - July 27

	CXAT	CAIN	AGTR	SESP	HOJU	PONO	POSP
R	38.0a	1.8b	1.8b	1.5bc	0.0bc	0.0bc	0.0c
%COV	27±5	28±6	16±5	8±4	15±6	2±2	4±2

Lake 690 - August 10

	CXAT	CXAQ	CAIN	SESP	HOJU	STPA
R	38.0a	16.0b	0.5c	0.0cd	0.0d	0.0d
%COV	25±6	4±2	44±7	3±3	10±5	13±4

*Grazing Rating = Percentage of ramets grazed for species i
% Cover = % of plot j that species i occupied
Medians with the same letters are not significantly different at $P \leq 0.05$

** CXAT = *Carex atherodes* Spreng.
CXAQ = *Carex aquatilis* var. *aquatilis* Wahlenb.
CAIN = *Calamagrostis inexpansa* A. Gray
HOJU = *Hordeum jubatum* L.
AGTR = *Agropyron trachycaulum* (Link) Malte
SESP = *Senecio pauperculus* Michx. and/or *S. indecorus* Greene
STPA = *Stachys palustris* L.
POSP = *Potentilla pensylvanica* L. and/or *P. multifida* L.
GEMA = *Geum macrophyllum* Wild.
PONO = *Potentilla norvegica* L.

Table 3-5. Comparison of Median Grazing Ratings* (R) and Mean Ocular Cover Estimates (±SE) for the Most Abundant Species** at Five Study Sites in 1987.

Calais Lake East - June 3

	CXAT	AGTR	CAIN	SESP	POSP
R	63.0a	3.0b	0.0c	0.0c	0.0c
%COV	14±3	19±6	18±4	10±3	2±2

Lake 650 - June 13

	CXAT	HOJU	AGTR	CAIN	STPA	GEMA	PONO
R	63.0a	16.0ab	3.0b	0.0c	0.0c	0.0c	0.0c
%COV	13±4	6±4	41±5	18±6	9±3	3±2	3±2

Calais Lake East - July 7

	CXAT	AGTR	HOJU	CXAQ	CAIN	SESP	STPA
R	38.0a	7.0b	3.0bc	0.5bc	0.5c	0.0cd	0.0d
%COV	21±4	17±5	7±4	7±4	16±4	8±2	5±2

Lake 650 - July 15

	CXAT	AGTR	GEMA	HOJU	CAIN	PONO	STPA
R	63.0a	50.5ab	27.0bc	3.0c	1.8cd	0.0cd	0.0d
%COV	9±3	24±4	4±2	9±3	9±4	4±1	5±3

Calais Lake East - August 1

	CXAT	CXAQ	HOJU	CAIN	AGTR	POSP	STPA	SESP
R	4.0a	3.0a	3.0ab	0.5b	0.5b	0.0bc	0.0c	0.0c
%COV	24±4	3±2	9±5	21±5	15±4	3±2	3±1	6±2

Lake 650 - August 18

	CXAT	CAIN	AGTR	HOJU	GEMA	PONO
R	86.0a	3.0b	1.8b	0.5b	0.0b	0.0b
%COV	12±3	15±4	11±3	19±5	2±1	3±1

Dieppe Lake - August 19

	CXAT	CXAQ	AGTR	CAIN	SESP	HOJU
R	3.0a	0.5a	3.0ab	0.5bc	0.0bc	0.0c
%COV	17±2	3±1	5±3	28±5	2±2	3±1

Lake 690 - August 19

	CXAT	CXAQ	CAIN	HOJU	STPA
R	0.5a	0.5a	0.5a	0.0a	0.0b
%COV	10±2	6±2	31±4	4±2	7±1

Calais Lake West - August 20

	CXAT	POSP	CXAQ	CAIN	HOJU	AGTR	GEMA
R	3.0a	8.0ab	1.9ab	0.5b	0.3b	0.0b	0.0b
%COV	19±4	2±2	4±3	18±4	17±4	7±3	4±2

Calais Lake East - August 21

	CXAQ	CXAT	CAIN	AGTR	HOJU
R	20.5a	3.0a	0.5b	0.5b	0.0b
%COV	3±2	19±3	9±3	7±2	5±2

* - see footnotes Table 3-4

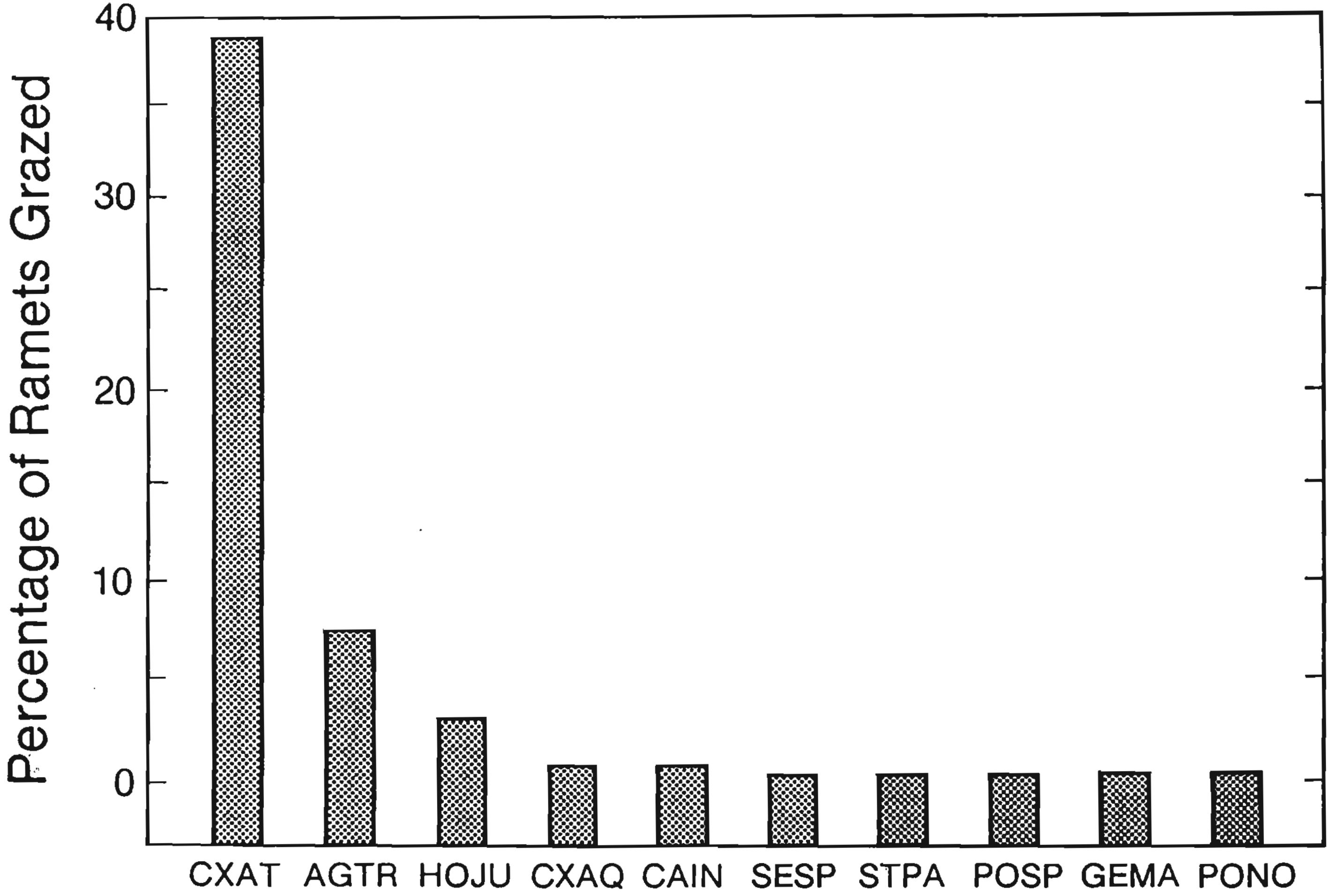

Fig. 3-1 Percentage of sedge, grass and forb ramets grazed in early July 1987 at Calais Lake East. See Table 3-4 for species names.

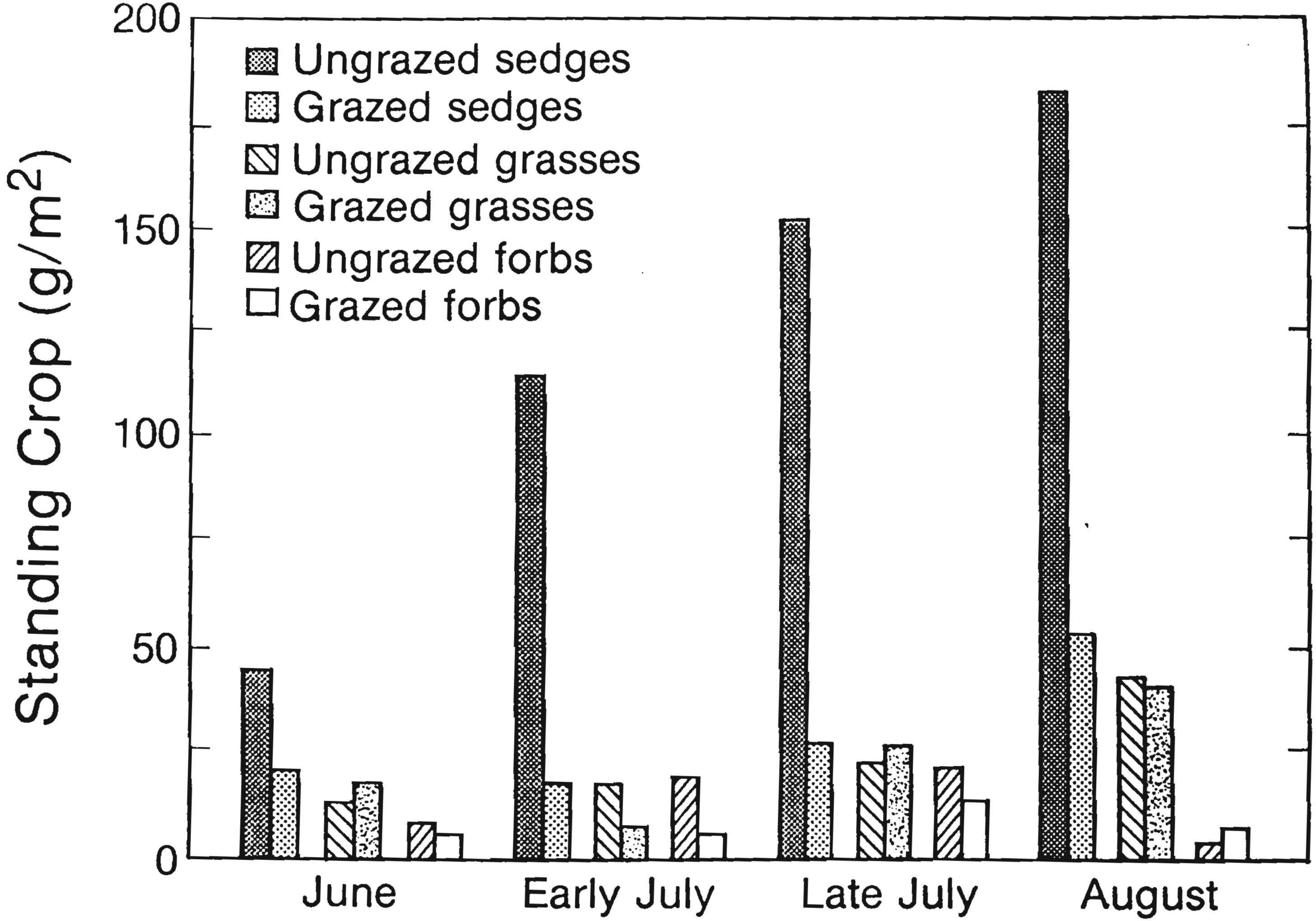

Fig. 3-2 Green standing crop (g/m^2) of sedges, grasses, and forbs in ungrazed and grazed areas at Calais Lake East in 1986.

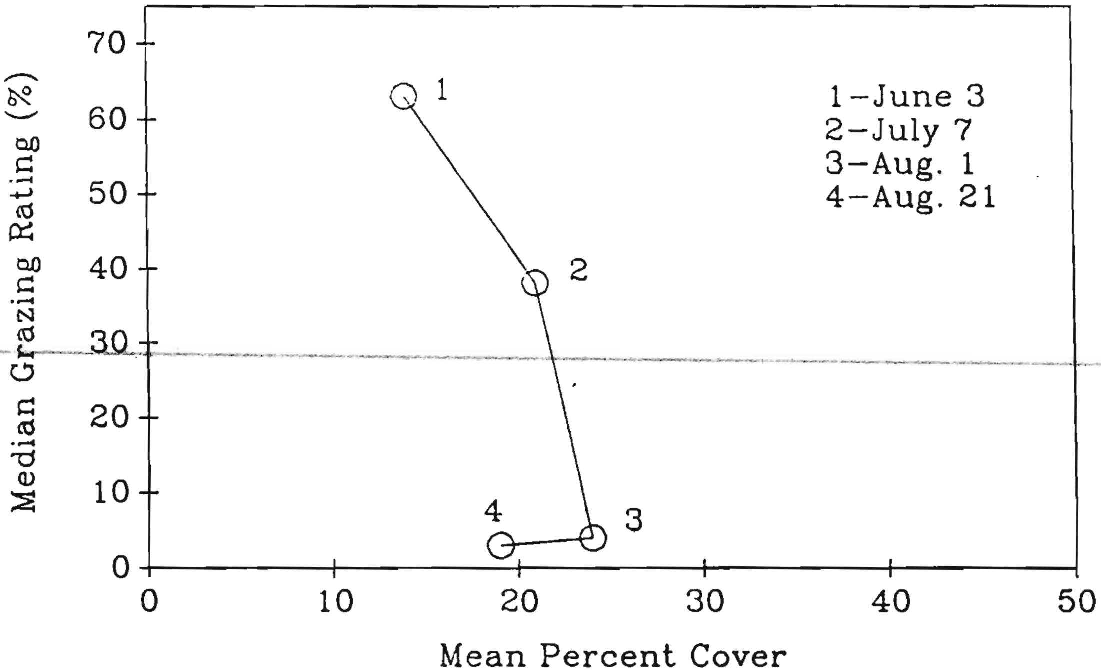

Fig. 3-3. Relationship between grazing rating and percent cover of <u>Carex</u> <u>atherodes</u> at Calais Lake East during the 1987 growing season.

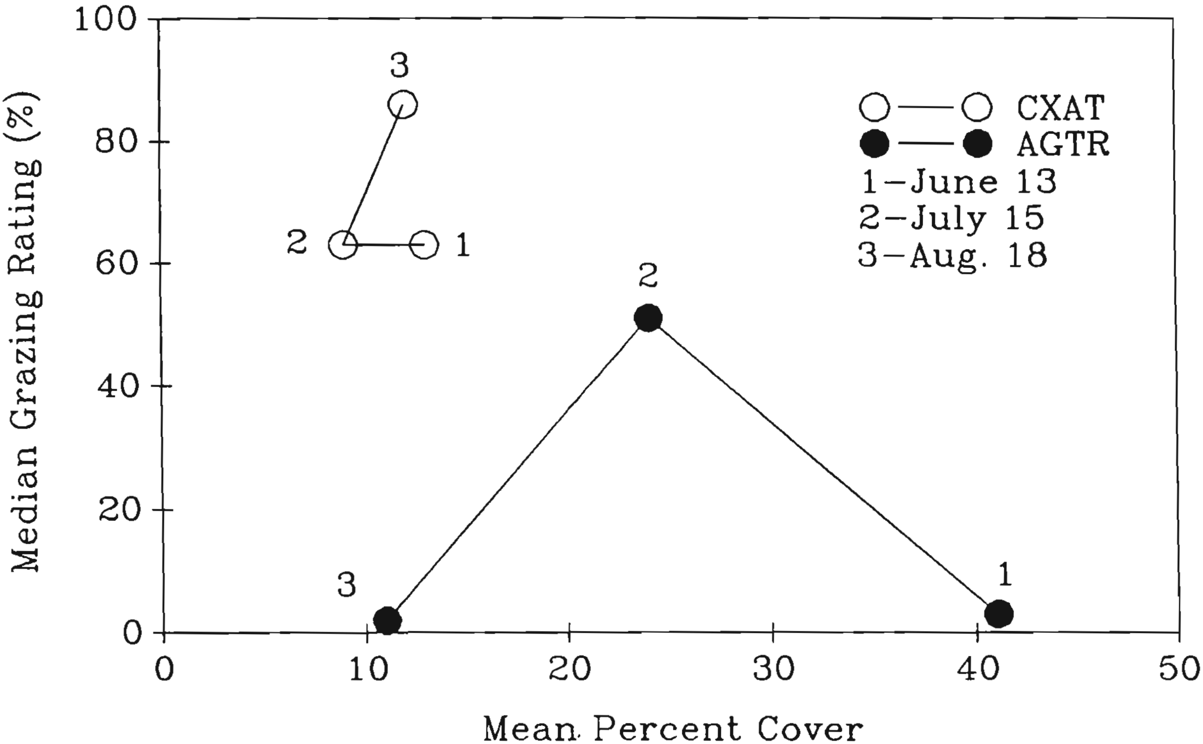

Fig. 3-4. Relationship between grazing rating and percent cover of Carex atherodes (CXAT) and Agropyron trachycaulum (AGTR) at Lake 650 in 1987.

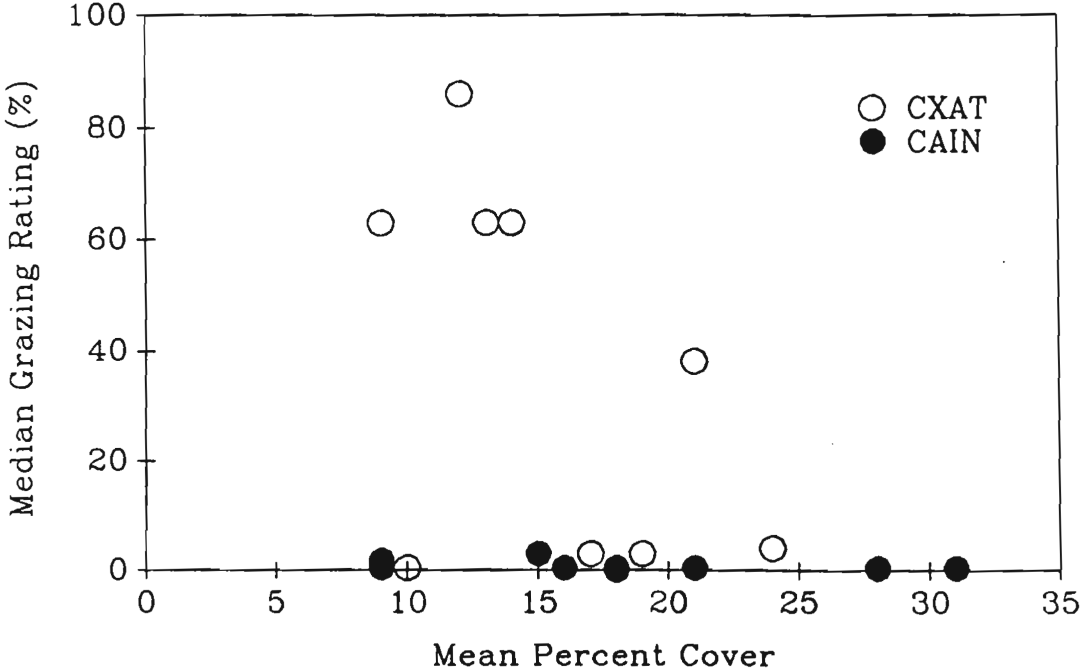

Fig. 3-5. Relationship between grazing rating and percent cover of *Carex atherodes* (CXAT) and *Calamagrostis spp.* (CAIN) at all study sites in 1987.

3.4 Discussion

3.4.1 Availability of Forage

The food choices of Wood Bison are a reflection of their physiological requirements. Because of their large size and high absolute demands for energy it is important for Wood Bison to consume large quantities of food. Thus, the availability of forage in the various c.t.'s of the Mackenzie Bison Santuary (MBS) and the spatial arrangement of plants within these c.t.'s played a major role in influencing Wood Bison food habits. Wood Bison chose the Shrub Meadow c.t. over others during the summer because high-quality forage is abundant there relative to other c.t.'s (Larter 1988). Within the Shrub Meadow c.t., Wood Bison chose to feed on pure stands of sedge, because these stands contained little standing dead relative to grasses (see next section), and because more forage was available relative to forb-dominated areas.

Forbs were not an important part of Bison diets at the MBS (Larter 1988) or at the Peace-Athabasca Delta (McCourt 1970). Within the Shrub Meadow c.t., forbs were infrequently grazed because of the need for Wood Bison to consume large quantities of forage. Because forbs of the MBS Shrub Meadow c.t. are prostrate, only the flowering stalk of a forb plant was available to Wood Bison. Forbs were associated with bare ground in heavily disturbed areas which reduced further the forage available for grazing at these sites.

3.4.2 Spatial and Temporal Variation in Grazing Ratings

The results suggest that plant species abundance plays a some role in whether certain species are selected or avoided. It is possible, that some forb species may have escaped herbivory because of their relative rarity. As well, an intense grazing episode in July 1987 at Lake 650 decreased the abundance of Agropyron trachycaulum which subsequently reduced the grazing rating of A. trachycaulum in August (Fig. 3-4). There are other factors that influence spatial and temporal variations in species grazing ratings as well. The decrease in median grazing ratings observed for Carex atherodes at Calais Lake East from June to August 1987 can be attributed to low grazing intensities at Calais Lake East during the middle of the 1987 growing season (Fig. 3-3; see Chapter 2). Wood Bison numbers were below the carrying capacity of their range in 1986 and 1987 (C. Gates pers. comm 1987; see Chapter 5). Low grazing intensities, and low median grazing ratings were the result. Similarly, the median grazing ratings for A. trachycaulum were lower in June and August than in July 1987 because Lake 650 was less intensely grazed in June and August (Fig. 3-4; see Chapter 2). Therefore species at study sites where grazing ratings are low are not necessarily avoided if grazing intensities are low. If a species is avoided, it consistently has low median grazing ratings, even at intensely grazed study sites (Fig. 3-5, see Chapter 2).

Wood Bison at Lake 650 selected C. atherodes more in 1987 than in 1986 because grazing intensities were lower in 1987. This perhaps gave them the opportunity to be more selective. In addition, Wood Bison may have selected C. atherodes more in August 1987 because of the relatively low abundance of A. trachycaulum. The high grazing rating of A. trachycaulum at Lake 650 in 1986 relative to other study sites was most likely the result of Wood Bison being attracted to Lake 650 because of its favorable mesoclimate and its high productivity (see Chapter 2). Wood Bison consumed what was available at Lake 650, mainly A. trachycaulum, but it is clear that they selected rarer C. atherodes in 1987 (Fig. 3-4).

3.4.3 Plant Quality

Unlike some smaller mammals, Bison cannot afford to carefully select their food items (Hudson and Frank 1987). Because Wood Bison are ruminants, they are capable of processing low-quality food efficiently (Bell 1971; Hudson and Frank 1987), but pure stands of relatively high-quality Carex atherodes (awned sedge) were available especially in 1986 (see Chapter 2), so this was unnecessary. Pure stands of grass were avoided relative to sedges because of the intrinsically lower food quality of MBS grasses (Larter 1988) and the lower quantity of standing dead associated with sedge stands. Other studies have also shown selection against low-quality senescent tissue in favor of rapidly growing high-quality new growth (Owen-Smith 1982; McNaughton 1985).

The heavy grazing that took place at the grass-dominated Lake 650 study site is contradictory to the observation that grasses were avoided relative to sedges because of their lower quality (Fig. 3-1). This may be explained by the rapid growth and high rate of use of plants associated with grazing lawns (McNaughton 1984, 1986) such as Lake 650. The high grazing intensity at Lake 650 resulted in low rates of dead tissue accumulation (see Chapter 2). The high nutrient content of rapidly growing graminoids (Olubajo et al. 1974; Sinclair 1977, McNaughton 1979; Coppock et al. 1983; Detling and Painter 1983) at Lake 650 may have compensated for the intrinsically lower quality of grasses.

Similarly, grasses may have been lower in quality than sedges because grasses were lightly grazed relative to sedges. Lower grazing intensities may have caused dead tissue to accumulate faster in grass stands. The author has not reviewed any studies other than Larter's (1988) that suggest sedges are more nutritious than grasses. Renecker and Hudson (1988) reported that grasses in central Alberta had less fiber in the spring than sedges and that the proportions of cell solubles and crude protein in grasses and sedges were similar during the summer. In northern and central Alberta, _Carex_ _atherodes_ and _Calamagrostis_ _canadensis_ had similar nitrogen concentrations (T. Hogg, unpubl. data; Corns and Schraa 1962; Corns 1974). Therefore it is possible that Wood Bison grazing may have maintained relatively high quality sedges by decreasing quantities of dead tissue and by promoting rapid growth (see Chapter 2). Growth form probably also influenced the quantity of dead tissue that accumulated and thus the quality of forage in grass and sedge stands. Visual observations in 1986 and 1987 indicated that there was less dead tissue in ungrazed sedge stands than in ungrazed grass stands. This may have occurred because Carex atherodes decomposed faster than grasses. T. Hogg (unpubl. data) found that Carex atherodes decomposed more quickly than Calamagrostis canadensis in northern Alberta. Therefore both intrinsic plant quality (which was probably influenced by growth form) and grazing intensity may have affected the quality of grasses relative to sedges.

Plant quality may have also played a role in influencing Wood Bison to select C. atherodes over C. aquatilis. This preference has been reported in other studies (McCourt 1970; Allison 1973; Reynolds et al. 1978; Larter 1988). C. aquatilis contains calcium oxalates (Abaza et al. 1967; Batzli and Jung 1980) and has a lower nitrogen/acid detergent fiber ratio than C. atherodes (Larter 1988). Selection for C. atherodes over other sedge and grass species by Wood Bison in northern mesophytic meadows has been noted in other studies (McCourt 1970; Allison 1973: Reynolds et al. 1978; Larter 1988).

Nutritionally, forbs could be a valuable food source (Mattson 1980; Belovsky 1986; Renecker and Hudson 1988), but because of the prostrate growth form of species present in the study site, they were of little value to Wood Bison. Forbs were consumed if they reached a sufficient size. For example, after a temporary exclosure was removed from a wallow, Chenopodium album was grazed within a few days. If forbs were undisturbed by Wood Bison they [illegible] ungrazed sites probably could provide a valuable food source for Wood Bison if standing crops were sufficiently high. Visual inspection in 1986 and 1987 indicated that there was very little dead tissue in areas with abundant forbs.

3.4.4 Secondary Compounds

Although chemical defenses against herbivory were not examined in this study, they should not be overlooked. *Phalaris arundinacea* (PHAR), which grows in more hygric areas of the Shrub Meadow c.t. has high silica (Van Soest 1967) and alkaloid contents (Audette et al. 1970; Hagman et al. 1975). The presence of these compounds clearly protected *Phalaris* from being grazed in 1986 and 1987; it was not consumed by Wood Bison or any other herbivores.

Chemical defenses against herbivory probably play a minor role in the early successional Shrub Meadow c.t. as a whole, however. Mychaisw (1986) reported that *Salix* spp. has been steadily increasing in abundance within this c.t. since observations began in the 1940's. Plants in seral c.t's generally have low levels of anti-herbivore defenses because they place a premium on rapid growth and because they are unpredictable in time and space (Cates and Orians 1975). Unlike the other species in the Shrub Meadow c.t., *Phalaris*'s grew in narrow bands around the wetter portions of the Shrub Meadow c.t. It is possible that the intolerance of other species to *Phalaris's* niche, and/or the ability of Phalaris to outcompete other species in these areas, made Phalaris more prominent in time and space than the other species in this c.t.

As well, Phalaris's high nutrient and low fiber content (Larter 1988) may have contributed to selection processes that resulted in the formation of these anti-herbivore defenses. It is well documented that plants evolve feedback mechanisms that serve to limit herbivore feeding pressure (Pimentel 1988). Herbivores also evolve to moderate exploitation of their food resource (Pimentel 1961; Levin and Pimentel 1981). The other species within the Shrub Meadow c.t. may not have required such defenses because of their relatively low quality. Low food quality alone acts as a defense against herbivory (White 1976).

In addition, the Shrub Meadow c.t. is relatively nutrient-rich, underlain by black soils that are high in organic matter content (see Chapter 2). Plants from nutrient-rich c.t.'s have the necessary carbon and nutrient reserves to replace tissue lost to herbivores (Bryant et al. 1983; MacLean and Jensen 1985). Thus, most plants within the Shrub Meadow c.t. probably do not use their resources to protect photosynthetic tissue because if tissue is lost to herbivores, it would have little effect on the plant's fitness relative to slower growing plants at more nutrient-poor sites.

3.5 References

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4. THE IMPACTS OF WOOD BISON GRAZING ON THE STRUCTURAL PROPERTIES AND REPRODUCTIVE OUTPUT OF A SHRUB MEADOW PLANT COMMUNITY TYPE, MACKENZIE BISON SANCTUARY, N.W.T.

4.1 Introduction

Ungulates have a significant impact upon species composition, species richness, species diversity, reproductive output, and physiognomy of plant communities (Larson 1940; Helle and Aspi 1983; McNaughton 1984, 1985; Facelli et al. 1989; Gibson 1989; Noy-Meir et al. 1989). Grazing intensity, grazing frequency, season of grazing and the availability of propagules for colonization at a site influence the degree to which these changes occur (Denslow 1980; Miller 1982; Malanson 1984). Ungrazed vegetation is commonly composed of erect genotypes. These competitively superior plants have higher proportions of stem tissue and thus tend to be of lower food quality than grazed plants (McNaughton 1979a; Prins et al. 1980; Cargill and Jefferies 1984; Seasted 1985). Ungrazed areas tend to have lower species richness and diversity (Grime 1973; Whittaker and Levin 1977; Glasser 1979; Collins 1987; Gibson 1988) and, hence, may be less resistant (ability to maintain a steady state) to disturbance than moderately grazed areas.

In heavily grazed areas, only species adapted to high grazing intensities survive. Overgrazed areas are commonly species-poor (Grime 1973) because only a few prostrate and/or mechanically or chemically defended species can tolerate such high grazing intensities. Overgrazed ranges provide little forage value for herbivores and erosion can cause their degradation or even destruction (Ellison 1960; Stoddart et al. 1975). In contrast, moderate grazing intensities can result in diverse, species-rich, high quality vegetation with a variety of growth forms.

While the resistance of moderately grazed sites may be higher (because of higher species richness and diversity) than in overgrazed or ungrazed sites, moderate grazing may decrease the reproductive output and fitness of genets. There is conflicting evidence regarding the reproductive output of grazed or clipped genets relative to ungrazed genets. Some studies report that genets partially consumed by herbivores show increases in reproductive output (Dyer 1975; Inouye 1982; Richards 1983; Paige and Whitham 1987) while others report decreases (Roberts 1958; Dawson 1970; Hendrix 1979; Solomon 1983; Belsky 1986a). The large number of variables and their interactions controlling seed production, germination, and seedling survival in plants is doubtless responsible for the conflicting results of these studies.

This study examined the reproductive output of genets in grazed and clipped areas relative to ungrazed areas. The species richness, species diversity and physiognomy of grazed and ungrazed areas were compared. Absolute fitness was not measured. The objectives of this study were:

1) To determine how Wood Bison influence the species richness, species diversity, and physiognomy of sites with different grazing intensities within the Shrub Meadow plant community type.

2) To determine how Wood Bison influence the reproductive output of Shrub Meadow vegetation.

4.2 Methods

4.2.1 Structural Properties

Plant nomenclature follows Porsild and Cody (1980). To quantify and qualify some of the structural changes that took place in grazed plots relative to ungrazed plots, the height, the percent cover of bare ground, graminoids and forbs and the species richness and diversity of grazed and ungrazed Shrub Meadow communities were compared. Species richness is the number of species per unit area and species diversity is species richness weighted by species eveness (see table 4-7 for formula, Barbour et al. 1987). Plots were located in grazed and ungrazed areas in a systematic random manner during the 1986 and 1987 growing seasons (see Chapter 2). In 1986 at each of 5 study sites, 20 plots were sampled in the grazed area and 10 plots were sampled inside the permanent exclosure. Sample sizes were increased to 15 plots inside exclosures and to 25 plots in grazed areas in 1987.

The height of each species that occupied 0.25m^2 microplots was measured. Only the 10 most abundant graminoid and forb species were considered in the results, however. Since some of the data sets did not meet the assumptions made by parametric statistics, median heights were tested for significance using the Mann-Whitney U-test (Sokal and Rohlf 1981).

The abundance of graminoid and forb species and the percentage of bare ground were visually estimated in 25 grazed and 15 ungrazed plots using the cover-classes described in Chapter 3. Because this study did not focus on the effects of wallows on Shrub Meadow vegetation (which were obvious), wallows were not sampled (i.e., microplots were randomly located on transect space not occupied by wallows). Median bare ground percent cover estimates were tested for significance using the Mann-Whitney U-test (Sokal and Rohlf 1981).

Vascular plant species richness in grazed and ungrazed plots was compared. The number of species within each microplot was counted using percent cover data. All species regardless of their relative abundances were counted. Since these data sets were normally distributed the t-test of the differences between two means was used to determine if there were any differences between grazed and ungrazed treatments. Variances were tested for homogeneity using the F_{max} test (Sokal and Rohlf 1981).

The vascular plant species diversity of 25 grazed and 15 ungrazed microplots was compared using percent cover data. Simpson's diversity index (Krebs 1989) was calculated for each microplot in grazed and ungrazed areas. (See Table 4-6 for formula). The indices for each plot were subtracted from 1. Medians for grazed and ungrazed treatments were then tested for significance using the Mann-Whitney U-test (Sokal and Rohlf 1981).

4.2.2 Reproductive Output

To determine if natural and artificial grazing had an effect on the reproductive output of Shrub Meadow vegetation, inflorescences were counted in each microplot for naturally grazed, artificially grazed and ungrazed treatments. Seed-heads were counted in artificially grazed plots so that the cumulative number of seed heads formed in a given plot under a given clipping regime (e.g., clipped from one to four times during growing season) was recorded. For example, in a clipping regime where plots were clipped in June and reclipped in July and August, the cumulative number of inflorescences formed in each plot from June to August was calculated by adding the number of inflorescences observed in June, July and August. This method was identical to the method used to determine the productivity of artificially grazed plots (see Chapter 2). In ungrazed and naturally grazed treatments, inflorescences were counted at each sampling date. Ungrazed and naturally grazed plots were sampled without replacement. This method assumes that each infloresence produces an equal quantity of seeds. Only seed heads on live ramets were counted. The median number of seed heads in grazed and ungrazed areas was compared using the Mann-Whitney U-test (Sokal and Rohlf 1981).

4.3 Results

4.3.1 Structural Properties

Associated with the decreased height and % cover of graminoids (Fig. 4-1; Table 4-1) and the increased cover of bare ground and forbs (Fig. 4-2; Table 4-1) in grazed microplots were increases in species richness and diversity. Grazed microplots were consistently more species rich at all five study sites in 1986 (Table 4-2). Differences between grazed and ungrazed microplots were even more pronounced in 1987 (Table 4-3). The larger differences observed in 1987 can be attributed to the decline in species richness observed in ungrazed microplots from 1986 to 1987 (Table 4-4). It appears that the lack of grazing inside permanent exclosures caused the number of forb species to decrease while the number of graminoid species remained constant (Table 4-1). This was particularly noticeable at Lake 650. The species richness in grazed microplots, however, was relatively unchanged from 1986 to 1987 (Table 4-5). Similarly, microplots inside the exclosures established in 1985 were species poor relative to plots inside the the exclosures established in 1987, especially at Lake 650 (Table 4-6). It appears that heavily and lightly grazed sites (see Chapter 2) were not species-poor relative to moderately grazed sites. Heavily grazed Lake 650 was moderately species-rich while lightly grazed Calais Lake West was the most species-rich site. Moderately grazed Calais Lake East was moderately species-rich (Tables 4-2 and 4-3).

Simpson vascular plant species (VPS) diversity indices changed similarly to richness estimates by increasing in response to grazing. In 1986, however, diversity indices were relatively similar in grazed and ungrazed microplots. Only grazed microplots at Lake 650 showed highly significant differences in species diversity relative to ungrazed microplots (Table 4-7). By 1987, however, differences between grazed and ungrazed microplots became more pronounced. The most productive study site, Lake 650, again had the largest differences (Table 4-8). The diversity of ungrazed microplots at Calais Lake East decreased from 1986 to 1987 (Table 4-9). Overall, the diversity of grazed microplots at all 5 study sites remained constant from 1986 to 1987 (Table 4-10).

The hypotheses that grazing increases diversity and that the lack of grazing decreases diversity were again supported by the fact that the plant communities inside the exclosures established in 1985 were considerably less diverse than the ones inside the exclosures established in 1987 (Table 4-11). This trend was particularly apparent at Lake 650. As for species richness estimates, species diversity estimates were not higher at moderately grazed sites (e.g., heavily grazed Lake 650 and lightly grazed Lake 690 did not have lower species diversity than moderately grazed Calais Lake East). That is, there was no evident tendency for species diversity to peak at moderate grazing intensities (Tables 4-7 and 4-8).

4.3.2 Reproductive Output

In 1986 there were more seed heads in ungrazed than in grazed microplots (Table 4-12). This trend was especially strong at productive, heavily grazed Lake 650. Less productive and relatively lightly grazed Lake 690 and Dieppe Lake had similar quantities of seed heads inside and outside exclosures, however.

In 1987, there were again more seed heads in ungrazed plots than in grazed plots at Calais Lake East. At Lake 650, however, the trend was reversed (Table 4-13); there were considerably more seed heads in grazed plots relative to ungrazed plots. The other study sites had similar quantities of seed heads inside and outside exclosures. In 1987, plots inside the exclosure established in 1985 at productive Lake 650 had very few seed heads relative to plots exclosed since 1987 (Table 4-14). Similarly, at Lake 650 and Calais Lake East plots ungrazed for 30 days produced more seed heads than the plots ungrazed since 1985 (Appendix 4-6). Similar trends were observed for artificially grazed plots (Appendix 4-7 - 4-9).

Another interesting trend was the substantial decrease in the reproductive output of plants from 1986 to 1987. The decrease was particularly large at Lake 650. The fecundity of grazed plots, however, remained relatively stable between the two years (Tables 4-12 and 4-13).

Table 4-1. Mean Percent Cover Estimates of 20 Plant Species* in Ungrazed (n=15) and Grazed (n=25) Areas at Calais Lake East on ca. July 30 1987 and at Lake 650 on ca. August 13 1987.

	Calais Lake East		Lake 650	
Species	Ungrazed	Grazed	Ungrazed	Grazed
		Graminoids		
CXAT	44.40±6.43	23.78±3.98	13.37±3.35	12.12±2.69
CXAQ	0.00±0.00	2.63±1.70	0.45±0.27	0.00±0.00
CAIN	4.30±2.35	20.72±5.45	2.53±2.53	15.04±4.07
HOJU	0.16±0.11	9.04±4.73	0.40±0.27	18.56±5.07
AGTR	32.50±9.02	15.16±4.41	66.20±4.82	11.08±3.16
		Forbs		
SESP	2.35±1.06	5.82±1.88	0.00±0.00	0.27±0.17
STPA	0.00±0.00	3.20±1.42	0.00±0.00	0.92±0.48
POSP	0.38±0.30	3.00±1.69	0.00±0.00	1.79±0.93
GEMA	0.35±0.30	0.44±0.20	0.20±0.20	2.18±1.15
RUCH	0.05±0.05	0.24±0.17	0.00±0.00	0.00±0.00
ACMI	0.00±0.00	0.37±0.20	0.05±0.05	4.03±3.44
CHAL	0.00±0.00	0.00±0.00	0.00±0.00	2.03±1.52
ANSP	0.00±0.00	1.54±1.52	0.00±0.00	0.00±0.00
ASPA	0.00±0.00	0.33±0.17	0.00±0.00	0.00±0.00
STSP	0.00±0.00	0.00±0.00	0.00±0.00	1.53±1.52
TXDU	0.00±0.00	0.00±0.00	0.00±0.00	0.47±0.44
PESA	0.00±0.00	0.00±0.00	0.00±0.00	0.92±0.48
FRVI	0.30±0.30	0.00±0.00	0.00±0.00	0.00±0.00
SOCA	0.00±0.00	0.24±0.17	0.00±0.00	0.00±0.00
PONO	0.00±0.00	0.66±0.45	0.60±0.32	2.77±0.89

* CXAT - *Carex atherodes*
CXAQ - *Carex aquatilis*
CAIN - *Calamagrostis inexpansa* and/or *C. neglecta*
HOJU - *Hordeum jubatum*
AGTR - *Agropyron trachycaulum*
SESP - *Senecio pauperculus* and/or *S. indecorus*
STPA - *Stachys palustris*
POSP - *Potentilla multifida* and/or *P. pensylvanica*
GEMA - *Geum macrophyllum*
RUCH - *Rubus chamaemorus*
ACMI - *Achillea millefolium*
CHAL - *Chenopodium album*
ANSP - *Antennaria microphylla* and/or *A. rosea*
ASPA - *Aster pansus*
STSP - *Stellaria longipes* and/or *S. crassifolia*
TXDU - *Taraxacum dumetorum*
PESA - *Petasites sagittatus*
FRVI - *Fragaria virginiana*
SOCA - *Solidago canadensis*
PONO - *Potentilla norvegica*

Table 4-2. Mean Vascular Plant Species Richness in Grazed and Ungrazed 0.25 sq m Microplots at 5 Study Sites in 1986.

Date	Ungrazed	Grazed	Probability
	Calais Lake East		
July 22	4.30±.30	5.59±.34	P≤.05
Aug. 21	3.50±.17	5.95±.49	P≤.01
	Lake 690		
July 10	3.50±.27	4.15±.36	P>.10
Aug. 9	4.50±.43	4.70±.35	P>.10
	Calais Lake West		
July 5	4.70±.50	6.15±.46	P≤.10
July 26	5.70±.52	6.95±.60	P>.10
	Lake 650		
July 14	3.20±.33	4.12±.44	P>.10
Aug. 14	4.50±.56	5.41±.45	P>.10
	Dieppe Lake		
July 20	5.60±.43	4.65±.35	P>.10
Aug. 17	5.70±.21	4.25±.36	P≤.01

Table 4-3. Mean Vascular Plant Species Richness in Grazed and Ungrazed* 0.25 sq m Microplots at 5 Study Sites in 1987.

Date	Ungrazed	Grazed	Probability
	Calais Lake East		
June 3	4.20±.33	5.12±.25	P≤.05
July 5	3.70±.37	5.52±.36	P≤.01
July 30	3.70±.40	5.24±.46	P≤.05
Aug. 21	4.20±.36	5.32±.28	P≤.05
	Lake 650		
June 13	2.50±.22	4.44±.34	P≤.001
July 12	2.53±.17	5.28±.41	P≤.001
Aug. 13	2.60±.27	5.50±.39	P≤.001
	Dieppe Lake		
Aug. 19	4.13±.36	4.92±.46	P>.10
	Lake 690		
Aug. 19	3.80±.31	4.48±.31	P>.10
	Calais Lake West		
Aug. 20	3.93±.30	6.12±.35	P≤.001

* Microplots Located in Permanent Exclosure Established September 1985.

Table 4-4. Mean Vascular Plant Species Richness in Ungrazed (Since Sept. 1985) 0.25 m^2 Microplots at 5 Study Sites in 1986 and 1987.

Date	1986	1987	Probability
	Calais Lake East		
July 25	4.3±0.3	3.7±0.4	P>.10
Aug. 21	3.5±0.2	4.2±0.4	P≤.10
	Lake 650		
July 12	3.2±0.3	2.5±0.2	P≤.05
Aug. 10	4.5±0.6	2.6±0.3	P≤.01
	Lake 690		
Aug. 14	4.5±0.4	3.8±0.3	P>.10
	Dieppe Lake		
Aug. 18	5.7±0.2	4.1±0.4	P≤.01

Table 4-5. Mean Vascular Plant Species Richness in Grazed 0.25 sq m Microplots at 5 Study Sites in 1986 and 1987.

Date	1986	1987	Probability
		Calais Lake East	
July 25	5.6±0.3	5.2±0.5	P>.10
Aug. 21	6.0±0.5	5.3±0.3	P>.10
		Lake 650	
July 12	4.1±0.4	5.3±0.4	P≤.10
Aug. 10	5.4±0.5	5.5±0.4	P>.10
		Lake 690	
Aug. 14	4.7±0.4	4.5±0.3	P>.10
		Dieppe Lake	
Aug. 18	4.3±0.4	4.9±0.4	P>.10

Table 4-6. Mean Vascular Plant Species Richness in 0.25 sq m Microplots Ungrazed Since 1985 and 1987 at 2 Study Sites in 1987.

Date	Ungrazed'85	Ungrazed'87	Probability
	Calais Lake East		
June 3	4.20±.33	4.73±.41	P>.10
July 4	3.70±.37	5.00±.43	P≤.05
July 29	3.70±.40	5.00±.45	P≤.05
Aug. 21	4.20±.36	4.47±.27	P>.10
	Lake 650		
June 14	2.50±.22	3.80±.35	P≤.01
July 10	2.53±.17	4.07±.25	P≤.001
Aug. 13	2.60±.27	4.71±.44	P≤.001

Table 4-7. Simpson's Vascular Plant Species Diversity Indices* for Ungrazed and Grazed Microplots 0.25 sq m at Five Study Sites in 1986.

Date	Ungrazed			Grazed			Probability
	Min.	Median	Max.	Min.	Median	Max.	
			Calais Lake East				
July 22	0.38	0.58	0.74	0.25	0.69	0.79	P>.10
Aug. 21	0.21	0.62	0.66	0.30	0.59	0.71	P>.10
			Lake 690				
July 10	0.40	0.57	0.67	0.08	0.49	0.80	P>.10
Aug. 9	0.27	0.57	0.70	0.12	0.51	0.75	P>.10
			Calais Lake West				
July 5	0.47	0.55	0.77	0.41	0.68	0.79	P≤.10
July 26	0.27	0.65	0.75	0.33	0.66	0.82	P>.10
			Lake 650				
July 14	0.06	0.31	0.50	0.00	0.57	0.77	P≤.05
Aug. 14	0.07	0.33	0.61	0.16	0.50	0.71	P≤.10
			Dieppe Lake				
July 20	0.36	0.57	0.69	0.16	0.51	0.75	P>.10
Aug. 17	0.26	0.55	0.67	0.04	0.47	0.67	P≤.10

*

$$D_j = 1 - \sum_i p_{ij}^2 \quad [1]$$

where, D_j = Simpson's Diversity Index
p_{ij} = the proportion of species i in plot j

Table 4-8. Simpson's Vascular Plant Species Diversity Indices for Ungrazed* and Grazed Microplots at Five Study Sites in 1987.

Date	Ungrazed			Grazed			Probability
	Min.	Median	Max.	Min.	Median	Max.	
Calais Lake East							
June 3	0.10	0.46	0.74	0.05	0.56	0.72	P>.10
July 5	0.12	0.44	0.73	0.20	0.61	0.75	P≤.05
July 30	0.32	0.46	0.57	0.00	0.56	0.73	P≤.05
Aug. 21	0.23	0.50	0.69	0.15	0.51	0.75	P>.10
Lake 650							
June 13	0.24	0.45	0.50	0.16	0.51	0.77	P≤.10
July 12	0.08	0.43	0.65	0.23	0.59	0.78	P≤.001
Aug. 13	0.00	0.27	0.62	0.24	0.62	0.78	P≤.001
Dieppe Lake							
Aug. 19	0.09	0.51	0.72	0.16	0.53	0.73	P>.10
Lake 690							
Aug. 19	0.25	0.59	0.68	0.06	0.59	0.81	P>.10
Calais Lake West							
Aug. 20	0.16	0.60	0.71	0.13	0.61	0.77	P>.10

* Permanent exclosure established September 1985.

Table 4-9. Simpson's VPS Diversity Indices for Ungrazed Microplots at Five Study Sites in 1986 and 1987.

Date	1986			1987			Probability
	Min.	Median	Max.	Min.	Median	Max.	
			Calais Lake East				
July 26	0.38	0.58	0.74	0.32	0.46	0.57	P≤.01
Aug. 21	0.21	0.62	0.66	0.23	0.50	0.69	P>.10
			Lake 650				
July 13	0.06	0.31	0.50	0.08	0.43	0.65	P≤.10
Aug. 13	0.07	0.33	0.61	0.00	0.27	0.62	P>.10
			Lake 690				
Aug. 9	0.27	0.56	0.70	0.25	0.59	0.68	P>.10
			Dieppe Lake				
Aug. 15	0.26	0.55	0.67	0.09	0.51	0.60	P>.10

Table 4-10. Simpson's VPS Diversity Indices for Grazed Microplots at Five Study Sites in 1986 and 1987.

Date	1986			1987			Probability
	Min.	Median	Max.	Min.	Median	Max.	
			Calais Lake East				
July 26	0.25	0.69	0.79	0.00	0.56	0.73	P>.10
Aug. 21	0.30	0.59	0.71	0.15	0.51	0.75	P>.10
			Lake 650				
July 13	0.00	0.57	0.77	0.23	0.59	0.78	P>.10
Aug. 17	0.16	0.50	0.71	0.24	0.62	0.78	P>.10
			Lake 690				
Aug. 9	0.12	0.51	0.75	0.06	0.59	0.81	P>.10
			Dieppe Lake				
Aug. 15	0.04	0.47	0.67	0.16	0.53	0.73	P≤.10

Table 4-11. Simpson's VPS Diversity Indices for Ungrazed'85 and Ungrazed'87 Microplots at Two Study Sites in 1987.

Date	Ungrazed'85			Ungrazed'87			Probability
	Min.	Median	Max.	Min.	Median	Max.	
Calais Lake East							
June 3	0.10	0.46	0.74	0.42	0.54	0.77	P>.10
July 4	0.12	0.44	0.55	0.12	0.53	0.68	P>.10
July 29	0.32	0.46	0.57	0.12	0.63	0.82	P≤.10
Aug. 21	0.23	0.50	0.69	0.16	0.61	0.80	P>.10
Lake 650							
June 14	0.24	0.45	0.46	0.33	0.53	0.59	P≤.05
July 10	0.08	0.43	0.65	0.16	0.58	0.76	P≤.01
Aug. 13	0.00	0.27	0.62	0.20	0.60	0.72	P≤.001

Table 4-12. Comparison of Median Number of Seed Heads (#/m ^{2}) in Ungrazed (n=10) and Grazed (n=15) Microplots at 5 Study Sites in 1986.

Date	Ungrazed			Grazed			Probability
	Min.	Median	Max.	Min.	Median	Max.	
				Calais Lake East			
June 9	0	0	0	0	0	0	P>.10
July 1	0	14	84	0	4	56	P≤.10
July 22	24	70	492	0	20	68	P≤.001
Aug. 21	0	74	400	20	16	328	P≤.10
				Lake 690			
June 12	0	0	0	0	0	0	P>.10
July 10	0	2	12	0	4	20	P>.10
Aug. 9	0	6	32	0	4	104	P>.10
				Calais Lake West			
June 14	0	0	0	0	0	0	P>.10
July 5	4	30	160	0	28	84	P>.10
July 26	64	166	424	0	50	284	P≤.01
				Lake 650			
June 17	0	0	0	0	0	0	P>.10
July 14	0	34	836	0	24	244	P>.10
Aug. 14	36	382	792	0	16	192	P≤.001
				Dieppe Lake			
June 26	0	0	0	0	0	60	P>.10
July 20	0	12	60	0	26	172	P>.10
Aug. 17	0	20	256	0	14	112	P>.10

Table 4-13. Comparison of Median Number of Seed Heads (#/m^2) in Ungrazed* (n=15) and Grazed (n=25) Microplots at 5 Study Sites in 1987.

Date	Ungrazed			Grazed			Probability
	Min.	Median	Max.	Min.	Median	Max.	
				Calais Lake East			
June 3	0	0	0	0	0	0	P>.10
July 5	0	1	56	0	20	96	P>.10
July 30	0	32	112	0	12	92	P>.10
Aug. 21	0	48	96	0	0	44	P≤.01
				Lake 650			
June 13	0	0	0	0	0	40	P>.10
July 12	0	0	24	0	8	84	P≤.001
Aug. 13	0	0	56	0	12	152	P≤.001
				Dieppe Lake			
Aug. 19	0	8	80	0	16	136	P>.10
				Lake 690			
Aug. 19	0	0	20	0	4	44	P>.10
				Calais Lake West			
Aug. 20	0	12	72	0	16	124	P>.10

*Permanent Exclosure Established September 1985

Table 4-14. Comparison of Median Number of Seed Heads (#/m^2) in Microplots (n=15) Ungrazed since Sept. 1985 and May 1987 at 2 Study Sites in 1987.

Date	Ungrazed '85			Ungrazed '87			Probability
	Min.	Median	Max.	Min.	Median	Max.	
				Calais Lake East			
June 3	0	0	0	0	0	0	P>.10
July 4	0	1	56	0	0	60	P>.10
July 29	0	32	112	0	4	24	P>.10
Aug. 21	0	48	96	0	8	152	P>.10
				Lake 650			
June 14	0	0	0	0	0	0	P>.10
July 10	0	0	24	0	4	36	P≤.05
Aug. 13	0	0	56	0	60	356	P≤.001

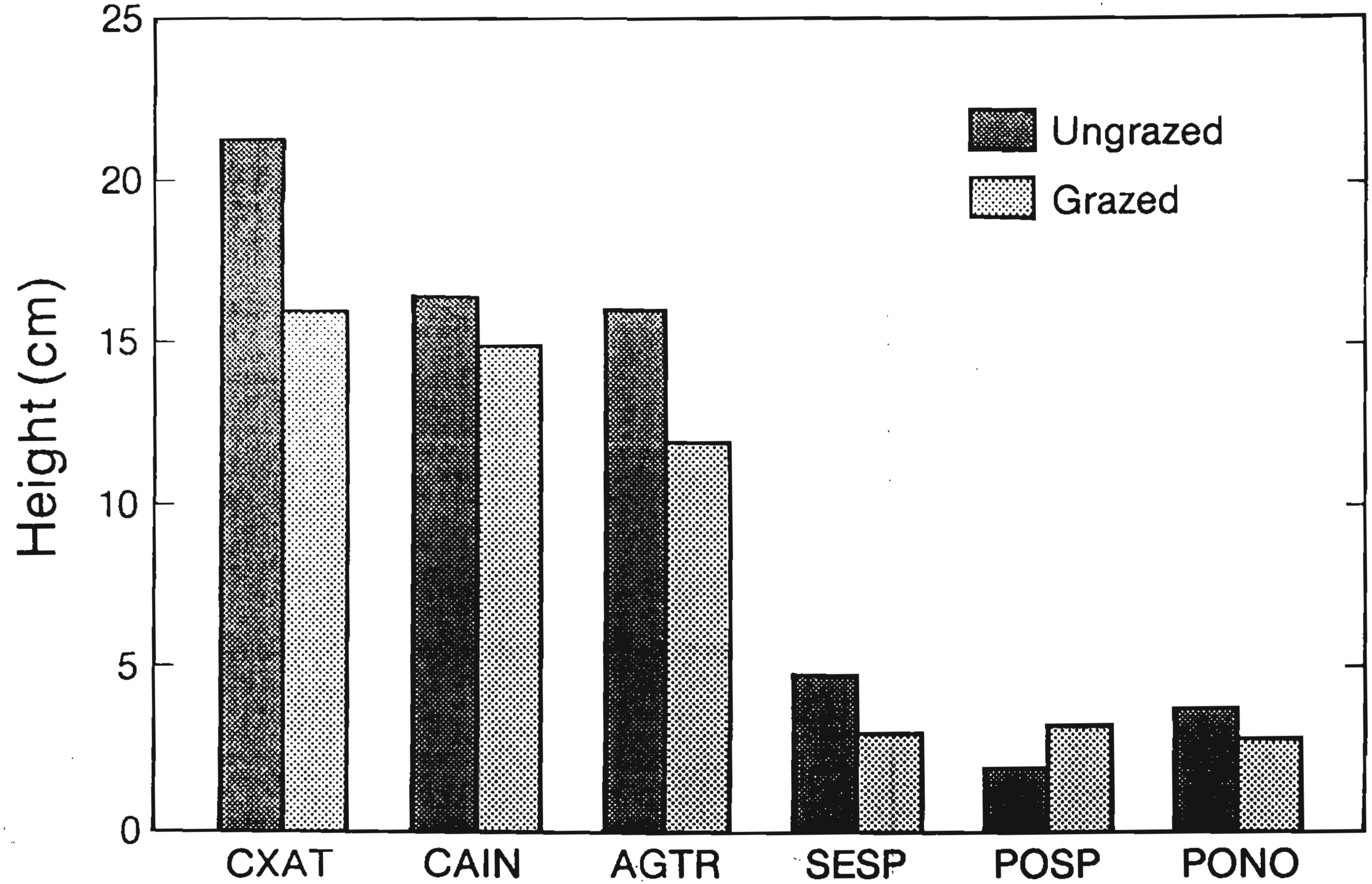

Fig. 4-1 Heights of graminoids and forbs in ungrazed '85 and grazed areas at Calais Lake East in June 1987. See Table 4-1 for full species names.

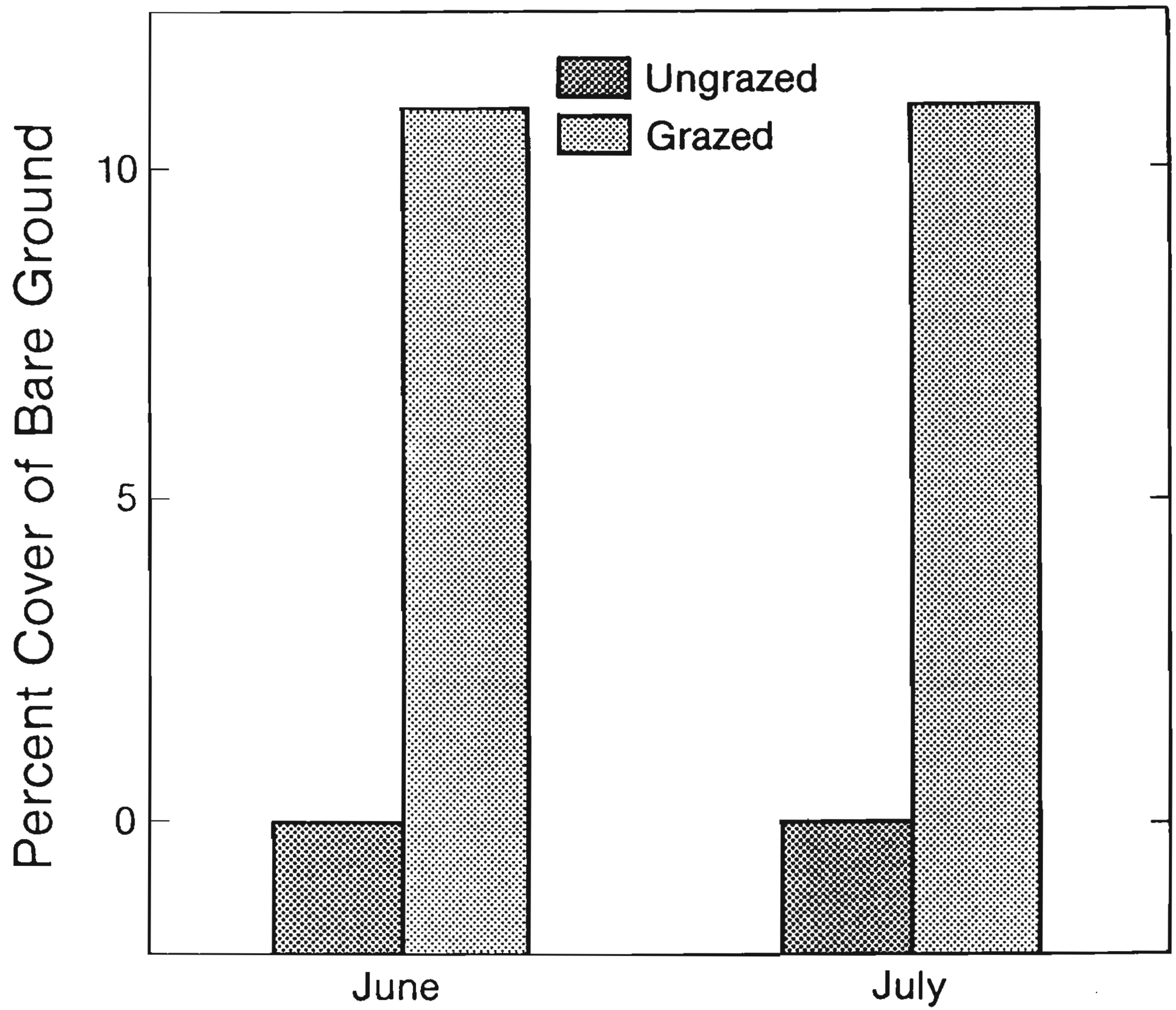

Fig. 4-2 Percent bare ground in ungrazed '85 and grazed areas at Lake 650 in 1987.

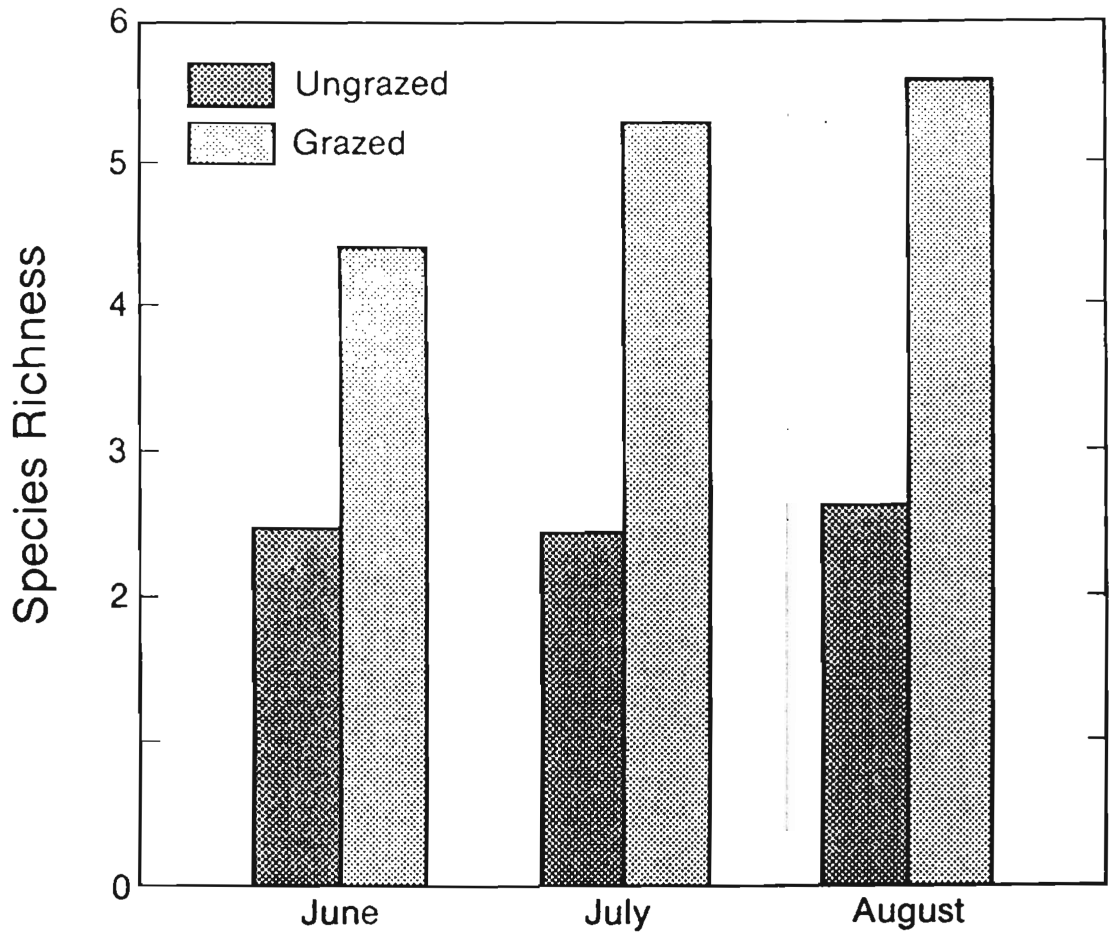

Fig. 4-3 Species richness (#/$0.25m^2$) in ungrazed '85 and grazed areas at Lake 650 in 1987.

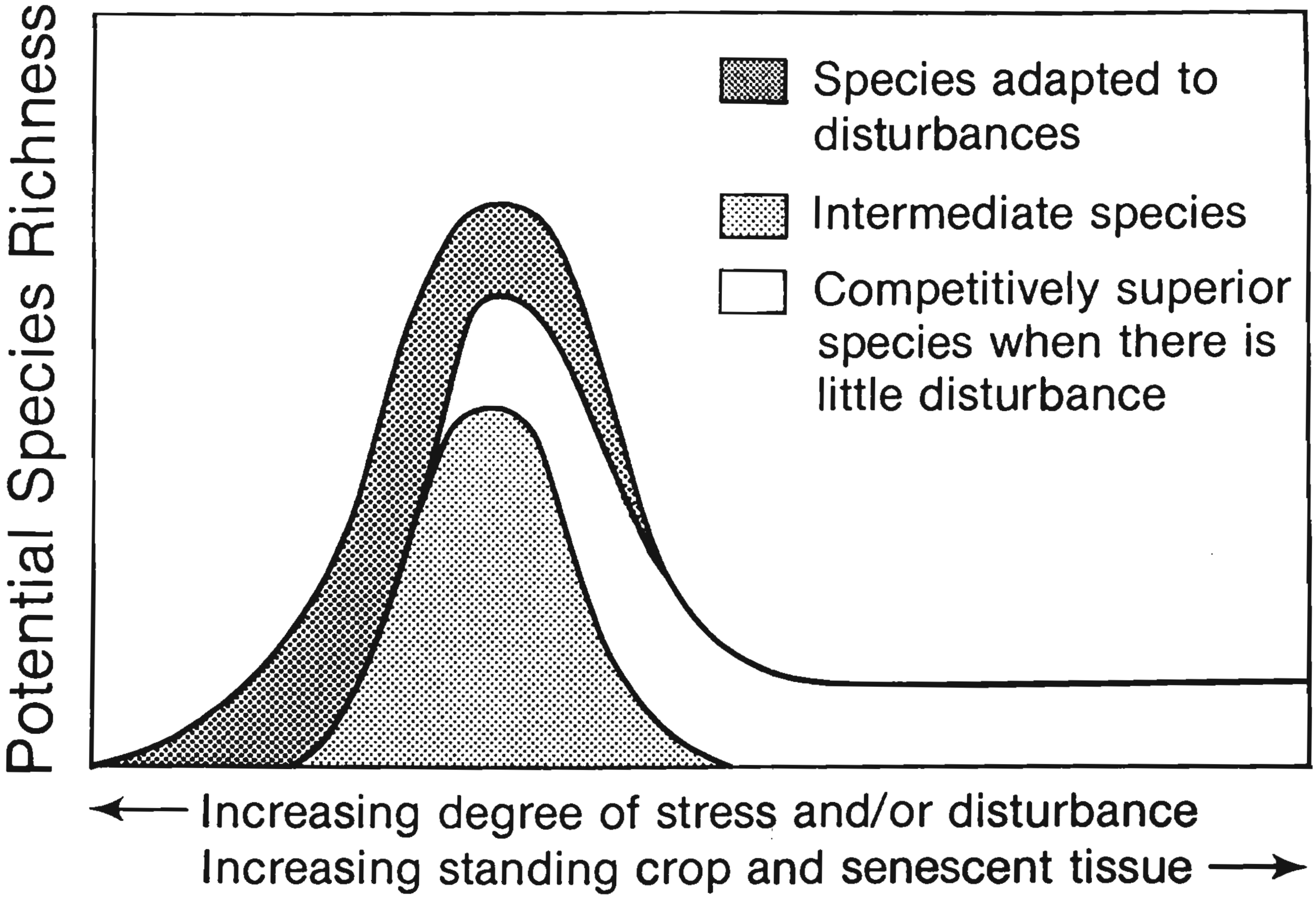

Fig. 4-4 Model describing impact of disturbance or stress on species richness. Modified after Grime, 1973

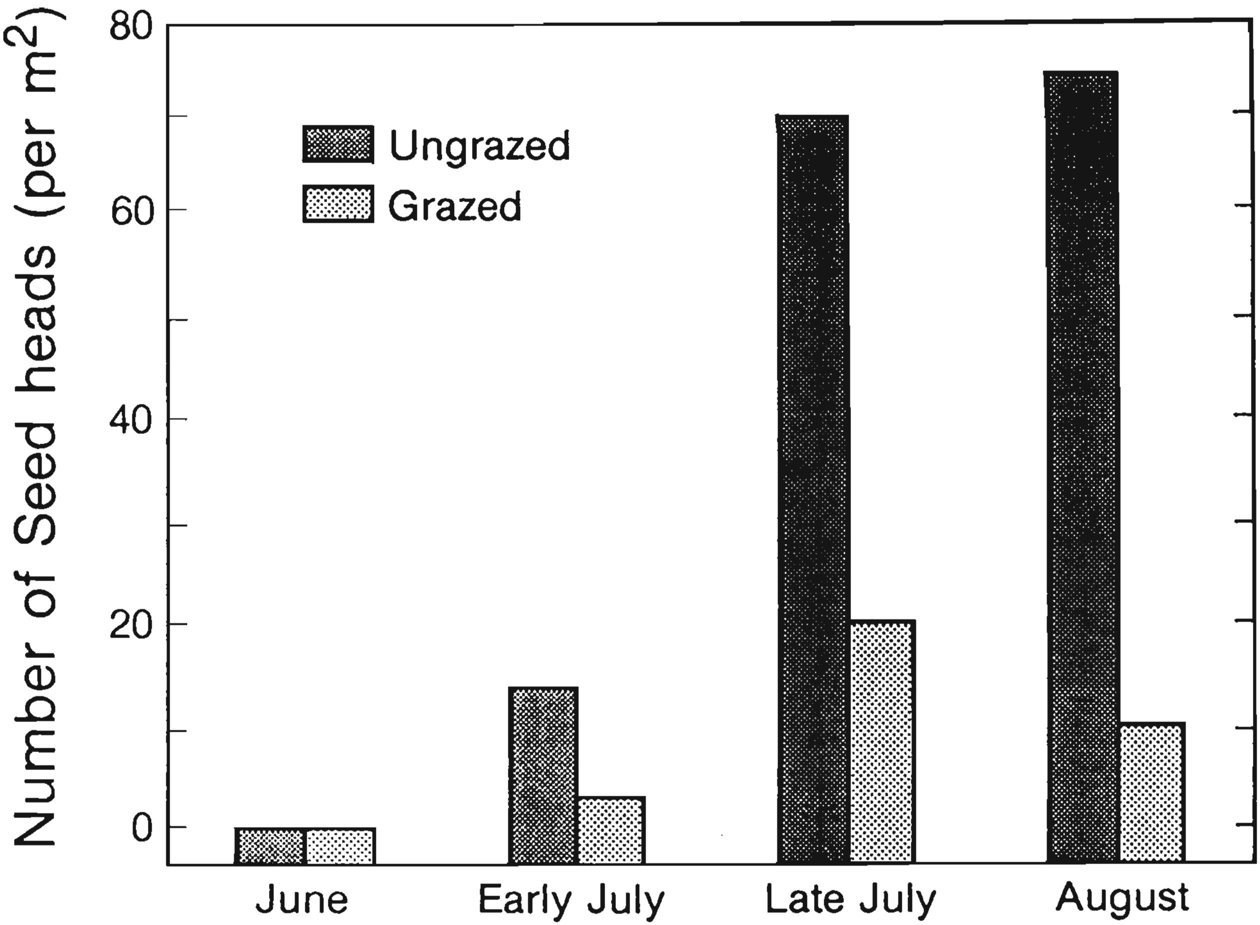

Fig. 4-5 Seed head density in ungrazed and grazed areas at Calais Lake East in 1986.

4.4 Discussion

4.4.1 Species Composition and Physiognomy

By reducing the height and % cover of graminoid species and by increasing the cover of bare ground in plots, Wood Bison altered the competitive interactions between plant species within the Shrub Meadow c.t. This trend has been reported elsewhere (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). This resulted in the shift in species composition and physiognomy observed in the Shrub Meadow c.t. after areas had been protected from grazing. Wood Bison selectively removed competitively superior, erect graminoids (see Chapter 3), thereby freeing resources (light, space, and nutrients) for grazing-tolerant, prostrate forbs. Similar trends have been reported in both terrestrial and marine ecosystems (Connell 1961; Paine 1966, 1971; Belsky 1986a; Hay 1986). Since species richness and diversity of grazed plots remained constant from 1986 to 1987, I conclude that lower precipitation amounts in 1987 (see Chapter 2) were not responsible for the decreases observed in ungrazed plots.

Wood Bison probably increased the % cover of prostrate genotypes and decreased the % cover of erect genotypes within this c.t. Ungrazed graminoids are erect because it is to their competitive advantage to get as much light as possible (McNaughton 1979b, 1984; Noy-Meir et al. 1989), yet graminoids were able to regenerate in shade beneath dense canopies of live plants or beneath thick layers of litter. Forbs are more resistant to trampling and grazing because of their prostrate growth form. Most of their leaf areas were inaccessible to Wood Bison in my study. Unlike graminoids, forb species direct their resources into lateral spread. This has also been reported in other studies (Jameson 1963; Harper 1977; McNaughton 1983a; Belsky 1986b). This explains why forbs were relatively uncommon inside the permanent exclosures and why species richness decreased in ungrazed plots from 1986 to 1987.

This shift in the abundance of prostrate forbs and of graminoids in grazed plots is commonly referred to as retrogressive succession (Ellison 1960; Facelii et al. 1989). Wood Bison, however, did not transform the Shrub Meadow c.t. into the c.t. from which it probably arose (the Wet Sedge Meadow c.t). Wood Bison may be suppressing the invasion of willows (Sharrow et al. 1989), thus inhibiting the succession of the Shrub Meadow c.t. into a willow-dominated c.t. Wood Bison are not responsible for a complete reversal of the successional processes occurring in the Shrub Meadow c.t., which is what the term "retrogressive succession" implies. A distinction should be made between a reversal in direction along a successional gradient and the changes that occur within a c.t. in response to a disturbance. Stable communities that result from natural or man-deflected successional processes have been called "plateaus" (Whittaker and Levin 1977).

It is well documented that the intensity of grazing can affect the species composition of meadows. Moderate grazing intensities result in more diverse, species-rich meadows than heavy or light grazing intensities (Paine 1977; Connell 1978; Lubchenco 1978; Edroma 1981; Helle and Aspi 1983; Hixon and Brostoff 1983) in communities where competition causes mortality (Peterson 1982) (see Figure 4-4). The decreased number of forb species observed in ungrazed plots suggests that competitive exclusion occurred (caused mortality) in the Shrub Meadow c.t. The usual relations among grazing intensity, species richness and species diversity estimates were not observed in this study. Perhaps, this is in part because of the small number of sites examined. Since these study sites were fairly similar to each other (with the exception of Lake 650, see Chapter 2) their richness and diversity were probably in part a reflection of variations in seed source availability between them. It is possible that a more species-rich seed source was available at lightly grazed Calais Lake West. Forb species were the main contributors to the species richness and diversity increases observed in grazed plots (Table 4-1).

In addition, differences in species richness and diversity estimates observed between study sites indicate that the species composition and structure of swards were influenced by more than just the presence or absence of Wood Bison. Soil characteristics (Anderson and Talbot 1965; de Wit 1978; Belsky 1986b), the type of grazer (Harper 1977), the non-random deposition of dung (Peterson et al. 1956), the ecotypic variation of the swards' plant species (Detling and Painter 1983), the grazing history (Noble and Slatyer 1980), and climate (McNaughton 1983b) can all influence the species composition of a site and thus its response to grazing. These factors can also interact in complex ways that remain unresolved (McNaughton 1983b).

4.4.2 Resistance to Disturbance

Some researchers have found that the resistance of ecosystems to disturbance increases as species diversity and richness increase (MacArthur 1955; Elton 1958; Ellison 1960; Holling 1973; Whittaker and Levin 1977; McNaughton 1985). However, there has been considerable debate over this because of a lack of testable hypotheses (May 1971; Goodman 1975). Within the Shrub Meadow c.t., the forb species that colonized disturbed sites may have served as a buffer against other perturbations. Because each species responds differently to disturbance (e.g. weather, insect pests, fire, grazing, etc.) it is an advantage for a c.t. to be heterogeneous. Grazed vegetation responded to disturbance by increasing in species diversity and richness (Figure 4-3). This probably increased the vegetation's resistance to further disturbance. Therefore, Shrub Meadow vegetation that grew at sites where disturbance (i.e. grazing) was common was probably better equipped to deal with most kinds of perturbation relative to vegetation that rarely experienced disturbance (i.e. a positive feedback mechanism). For example, forbs probably increase the resistance of Shrub Meadow vegetation to grazing by reducing grazing intensities (McNaughton 1985). Since forbs were not an important forage (see Chapter 3), Wood Bison probably avoid forb-dominated areas thus reducing further disturbance. If the grazing intensity is reduced at overgrazed, forb-dominated sites, interspecific competition should increase (Connell 1961; MacArthur and Wilson 1967; MacArthur 1972; Schoener 1974), and competitively superior graminoids would become more abundant. This hypothesis could be tested by determining the grazing intensities and examining the species composition and structure of previously overexploited sites.

4.4.3 Reproductive Output

Although Wood Bison may have increased the resistance of Shrub Meadow vegetation to perturbation, Wood Bison probably reduced the absolute fitness of genets in this c.t. "Fitness" has been defined as the contribution that a genotype makes to the next generation (Belsky 1986a). Although grazing may stimulate vegetative reproduction (Jameson 1963; Belsky 1986b), the lower numbers of seed heads produced in grazed plots relative to ungrazed plots indicates that the overall fitness of grazed genets was lower than ungrazed genets (Figure 4-5). To be completely thorough, however, the number of seeds and the survival of seedlings from grazed and ungrazed areas should have been examined. Grazing may have also slowed the rate at which a genet's descendents occupied a habitable site (Harper 1977). Grazing may have increased plant fitness at one of the study sites, however. The thick layer of litter that accumulated in ungrazed plots at productive Lake 650 had a similar effect on genet fitness by reducing seed head formation. In both of these cases (i.e. grazing and litter accumulation), the phenology of these relatively sterile plants was delayed relative to other plants. The accumulation of litter may have slowed growth by changing the microclimate of ungrazed plots as well as creating a physical barrier. Grazing (Hurlburt 1955; McNaughton 1979a, 1985; Grayson and Hassall 1985; Belsky 1986b) and litter accumulation (Curtis and Partch 1950; Weaver and Rowland 1952) have had similar effects in other studies.

Alternatively, the smaller numbers of seed heads observed in 1987 relative to 1986 may be attributable to lower precipitation amounts in 1987 (see Chapter 2). Plants were not able to develop as quickly during the drier growing season. Therefore, the relative "fitness" of Shrub Meadow genotypes depends on several factors and their interactions including climate, grazing frequency and intensity (Jameson 1963; Pyke 1986), site characteristics (McKendrick et al. 1980), the tissue defoliated (McNaughton 1979b; Inouye 1982), the time of defoliation (Roberts 1959; Dyer 1975), plant developmental stage (Hendrix 1979; McNaughton 1983a; Paige and Whitham 1987) and the genetic constitution of individuals (Hendrix 1979).

Although grazing and clipping have been reported to increase seed production in some systems (Binnie and Clifford 1980; Richards 1983; Solomon 1983; Ambasht et al. 1984; Paige and Whitham 1987) through physiological changes (see Chapter 2), most studies show decreased seed production (Belsky 1986a). Therefore, it is inappropriate to conclude that the relationship between grasses and grazers is mutualistic (McNaughton 1979b, 1986; Lam and Dudgeon 1985). Antiherbivore defenses such as secondary compounds, spines, silicification, and low plant food quality further indicate that grazing is not completely beneficial for graminoids and forbs. These defenses are probably more wide-spread in areas where herbivory causes mortality (e.g. nutrient poor sites). As well, some effects of herbivory (e.g., increases in productivity and nutrient turnover rates, increases in resistance to disturbance, and the extension of periods of active growth) may serve to partially counteract losses in fitness.

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5. GENERAL DISCUSSION AND CONCLUSION

5.1 Impacts of Wood Bison on Primary Summer Range

The results of this study indicate that in 1986 and 1987 Wood Bison were not having adverse effects on their primary summer range, the Shrub Meadow c.t. Exact- and over-compensation observed in grazed plots indicate that plants within this community type had sufficient carbohydrate and nutrient reserves to withstand moderate artificial and natural grazing intensities for at least several growing seasons. None of the results showed that natural or artificial grazing depleted these reserves.

Natural and artificial grazing appeared to increase productivity relative to ungrazed plots by improving the microclimate for rapid growth. The rapid accumulation of dead tissue observed in ungrazed plots may have decreased productivity rates by decreasing light intensities, by creating a cooler microclimate and by physically obstructing new growth. Grazing may also stimulate photosynthetic rates (McNaughton 1979) and thus increase the productivity of plants. These physiological mechanisms were not examined in this study. Wood Bison may have also increased the productivity of vegetation at the Lake 650 study site by importing nutrients in the form of feces and urine from other swards. An intensive description and comparison of the soils within stands of this c.t. could prove or disprove this

Wood Bison selected Carex atherodes over all other species within the Shrub Meadow community type. Species with similar abundances had very different grazing ratings suggesting that Wood Bison are selective feeders. Species grazing ratings did not show a clear functional response to changes in species abundance, however grazing ratings were not proportional to cover. Factors such as grazing intensity and palatability of plant species play an important role in explaining spatial and temporal variation in species grazing ratings. However, species abundance did play a role in influencing Wood Bison food habits. Some forb species may have escaped herbivory because of their relative rarity. As well, intense grazing reduced the abundance of Agropyron trachycaulum at Lake 650 in July 1987. In August, the grazing rating of A. trachycaulum was very low perhaps because there was very little A. trachycaulum left to be grazed.

Wood Bison shifted the species composition and structure of meadows by altering the competitive interactions between plant species. By preferentially removing competitively superior dominants (e.g. Carex atherodes), Wood Bison freed resources for competitively inferior, grazing-tolerant forbs. This suggests that Wood Bison are responsible for maintaining an assemblage of plant species indicative of moderate disturbance. However, Wood Bison are not responsible for reversing successional processes (i.e., converting the subhygric Shrub Meadow c.t. into the subhydric Sedge Meadow c.t.).

The species structure of grazed plots suggested that Shrub Meadows were not overgrazed. Since grazed areas were more species-rich and diverse than ungrazed areas, Wood Bison grazed this c.t. at moderate intensities (grazing intensity data agreed with this). At higher grazing intensities, sites would become forb-dominated. Species richness and diversity may also decrease at overgrazed sites because only a few grazing-tolerant species (e.g. Antennaria microphylla) can withstand such high grazing intensities (Grime 1973). Moderate grazing intensities may have increased the resistance of Shrub Meadow vegetation to disturbance. Since each species has a different growth response to disturbance, more heterogeneous, species-rich communities tend to be more stable after disturbance than homogeneous, species-poor communities (Odum 1953; Clarke 1962; Connell and Orias 1964; Paine 1966; Holling 1973; Whittaker and Levin 1977). Therefore, grazed vegetation may be better able to cope with climatic fluctuations, insect and fungal pests, and grazing itself than ungrazed vegetation.

Although Wood Bison appear to have beneficial effects upon the Shrub Meadow c.t., this should not be confused with mutualism between grasses and grazers (Owen and Wiegert 1976; Owen 1980). Since Wood Bison decreased the sexual reproduction of Shrub Meadow vegetation, the absolute fitness of grazed genets may have decreased. However, the heavy accumulation of litter associated with the lack of grazing inside the permanent exclosure at Lake 650 set the phenology of plants back, resulting in fewer inflorescences.

5.2 Carrying Capacity

Since grazing by Wood Bison did not have any adverse effects on Shrub Meadow vegetation, its preferred summer range, the population size of Wood Bison in 1986 and 1987 was below the carrying capacity (Wildlife Society 1980) of its summer range. Palatable dominants (e.g., Carex atherodes) were common relative to forbs even in heavily grazed areas, implying that these meadows were valuable to Wood Bison as a food source. If large areas of the Shrub Meadow c.t. become forb-dominated in the future, Wood Bison numbers should be reduced if they don't decline naturally.

Because Wood Bison stimulate productivity rates at some sites, moderate grazing intensities may increase the carrying capacity of the Shrub Meadow c.t. above control (i.e., ungrazed) levels. In addition, Wood Bison may inhibit the invasion of willows (Wein unpubl. man.; Sharrow et al. 1989). Since willow-dominated c.t.'s are less valuable as a forage source (Larter 1988), Wood Bison could be reducing the rate of high quality food lost to willow invasion. However, the inundation of water in the Shrub Meadow c.t. during the spring and summer (Larter pers. comm 1988) probably plays a much more important role in reducing willow cover (Doherty 1978) and thus in inhibiting the conversion of the Shrub Meadow c.t. into a willow dominated c.t. Fire is also an important mechanism that could reduce the % cover of willows growing in peaty soils (Wein, unpubl. man.).

Fire kills the roots of willows growing in organic soils such as those found within the Shrub Meadow c.t. (see Chapter 2). However, fire often increases the abundance of willows growing in mineral soils (Wein pers. comm. 1990).

As well as productivity rates, food quality of Shrub Meadow vegetation may also increase in response to grazing. Rapidly growing graminoids are commonly reported to be more nutritious than ungrazed plants (Albertson et al. 1953; Thaine 1954; Jameson 1963; McNaughton 1976, 1984, 1985; Prins et al. 1980). Grazing may also increase plant quality by decreasing the absolute and relative quantities of standing dead tissue in plots (Stoner et al. 1982; McNaughton 1985). Increases in plant quality may have also increased the carrying capacity of the Shrub Meadow c.t. relative to control levels.

The ability of Wood Bison to feed in c.t.'s other than the Shrub Meadow c.t. (Larter 1988) is additional support for the hypothesis that this population can continue to grow without adversely affecting summer range. However, Gates and Larter (1990) point out that females in the MBS herd may be dispersing to new habitat patches in a pattern suggesting pressure threshold dispersal. That is, resources such as food may be limiting. It is unlikely that a lack of forage within Shrub Meadow c.t. is responsible for this dispersal, given its good condition. Winter forage availability and quality as well as snow, ice and adverse weather conditions are more likely to limit further growth of the MBS Wood Bison population.

The differences in productivity observed between the summers of 1986 and 1987 suggest that precipitation may also play an important role in limiting the population size of the Mackenzie herd in the future. Wood Bison were in poorer condition during the winter of 1987-88 than in the previous winter (C. Gates, unpubl. data). Because snow and ice conditions were poor in 1987-88, Wood Bison moved into the Shrub Meadow c.t. to feed in winter (Larter 1988). Larter suggested that lower standing crops within the Shrub Meadow c.t. in 1987 may have contributed to the poorer condition of Wood Bison. Since precipitation limits the productivity of Shrub Meadow vegetation, summer rainfall amounts could limit Wood Bison numbers if they do not have access to Sedge Meadow vegetation during the winter. Rainfall amounts probably do not influence the productivity of Sedge Meadows since these areas are saturated with water with the exception of peripheral areas during dry years (pers. obs. 1986-87).

5.3 Conclusions

1. Wood Bison were not adversely affecting their primary summer range, the Shrub Meadow c.t., in 1986 and 1987.
2. Extrinsic and possibly intrinsic mechanisms of overcompensation were operating in grazed areas.
3. Forage quality should be studied to determine if Wood Bison are responsible for affecting the amount of protein and acid detergent fiber in plant tissue.

4. An intensive examination of the soils within the Shrub Meadow c.t. should be conducted to determine if Wood Bison are importing nutrients into the Lake 650 study site.
5. Wood Bison select Carex atherodes, and to a lesser degree Agropyron trachycaulum, over all other species and avoid forb-dominated areas, reflecting their preference for high quality graminoids and their physiological requirements for large quantities of forage.
6. The Shrub Meadow c.t. does not appear to be in danger of being overgrazed in the near future. However, summer range condition should be evaluated at least every two years to test this conclusion.
7. The species composition of Shrub Meadow vegetation should be used as an index of range condition. If grazing intensities become high, the abundance of forb species would increase and the abundance of graminoid species would decrease.

5.4 References

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APPENDICES

Appendix 2a-1. Green Control Productivity (g $m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established August 1985, n=10) and Green Apparent Productivity of Grazed (n=20) Shrub Meadow Vegetation at Five Study Sites in 1986.

Period of Growth	95% Confidence Intervals						Probability
	Control '85			Apparent			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 9-Aug.21	1.62	2.27	3.17	0.78	1.10	1.53	P>.10
June 9-July 1	2.97	4.00	5.39	-1.19	-0.74	-0.47	P≤.01
June 9-July 22	2.54	3.32	4.22	0.47	0.79	1.18	P≤.001
July 1-July 22	1.20	2.33	3.82	1.50	2.37	3.43	P>.10
July 1-Aug.21	1.12	1.63	2.37	1.25	1.93	2.98	P≤.01
July 22-Aug.21	0.36	1.17	2.46	0.97	1.55	2.26	P>.10
			Lake 690				
June 12-Aug.9	1.23	1.70	2.17	0.87	1.20	1.52	P≤.10
June 12-July 10	1.22	1.62	2.16	0.38	0.64	1.09	P>.10
July 10-Aug.9	1.09	1.46	1.95	1.28	1.78	2.48	P>.10
			Calais Lake West				
June 14-July 26	1.28	2.04	2.97	0.44	0.86	1.41	P>.10
June 14-July 5	2.00	3.16	4.58	1.60	2.50	3.59	P>.10
July 5-July 26	-0.92	1.01	2.95	-2.22	-0.61	1.00	P>.10
			Lake 650				
June 17-Aug.14	3.29	5.39	8.01	0.38	0.81	1.39	P≤.01
June 17-July 14	Not Available			1.10	2.46	4.37	
July 14-Aug.14	Not Available			-1.54	-0.54	-0.05	
			Dieppe Lake				
June 26-Aug.17	1.30	1.81	2.52	0.65	1.02	1.61	P>.10
June 26-July 20	2.01	2.68	3.56	1.27	1.99	3.12	P>.10
July 20-Aug.17	0.76	1.06	1.47	0.13	0.19	0.28	P>.10

Appendix 2a-2. Total Control Productivity (g $m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established Aug. 1985, n=10) and Total Apparent Productivity of Grazed (n=20) Shrub Meadow Vegetation at Five Study Sites in 1986.

Period of Growth	95% Confidence Intervals						Probability
	Control '85			Apparent			
	L1	Mean	L2	L1	Mean	L2	
				Calais Lake East			
June 9-Aug.21	2.09	2.76	3.64	0.81	1.13	1.58	P>.10
June 9-July 1	2.40	3.84	5.61	-1.73	-0.99	-0.46	P≤.001
June 9-July 22	2.35	3.17	4.11	0.38	0.69	1.08	P≤.001
July 1-July 22	1.18	2.36	3.94	1.57	2.50	3.64	P>.10
July 1-Aug.21	1.68	2.33	3.21	1.36	2.11	3.25	P≤.05
July 22-Aug.21	1.66	2.15	2.79	1.28	1.68	2.20	P>.10
				Lake 690			
June 12-Aug.9	1.31	1.70	2.21	0.74	1.03	1.43	P>.10
June 12-July 10	1.32	1.77	2.38	0.03	0.05	0.08	P>.10
July 10-Aug.9	1.14	1.46	1.87	1.42	1.99	2.78	P>.10
				Calais Lake West			
June 14-July 26	1.45	2.32	3.39	0.70	1.15	1.70	P>.10
June 14-July 5	2.11	3.30	4.75	1.41	2.38	3.61	P>.10
July 5-July 26	-1.14	1.46	4.07	-1.86	-0.18	1.49	P>.10
				Lake 650			
June 17-Aug.14	3.69	6.00	8.86	0.47	0.96	1.61	P≤.001
June 17-July 14	4.94	7.59	10.81	1.45	3.02	5.14	P>.10
July 14-Aug.14	2.20	4.57	7.78	-1.41	-0.44	-0.02	P≤.10
				Dieppe Lake			
June 26-Aug.17	1.34	1.74	2.27	0.88	1.38	2.15	P>.10
June 26-July 20	2.55	3.45	4.67	1.41	2.25	3.59	P>.10
July 20-Aug.17	0.20	0.28	0.38	0.45	0.63	0.89	P>.10

Appendix 2a-3. Green Control Productivity (g $m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Estalished Aug. 1985, n=10) and Green Apparent Productivity of Grazed (n=25) Shrub Meadow Vegetation at Two Study Sites in 1987.

Period of Growth	95% Confidence Intervals						Probability
	Control '85			Apparent			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 4-Aug.21	0.19	0.26	0.36	0.13	0.18	0.26	P>.10
June 4-July 5	0.68	1.13	1.69	0.64	0.96	1.34	P>.10
June 4-July 31	0.54	0.76	1.08	0.47	0.62	0.83	P>.10
July 5-July 31	0.29	0.40	0.56	0.23	0.33	0.46	P>.10
July 5-Aug.21	-0.30	-0.22	-0.16	-0.47	-0.32	-0.21	P>.10
July 31-Aug.21	-1.30	-0.93	-0.66	-1.61	-1.12	-0.78	P>.10
			Lake 650				
June 14-Aug.13	0.14	0.48	1.02	-0.90	-0.64	-0.42	P≤.001
June 14-July 12	0.98	1.86	3.02	-1.38	-0.96	-0.61	P≤.001
July 12-Aug.13	-1.48	-0.76	-0.27	-0.58	-0.31	-0.12	P>.10

Appendix 2a-4. Total Control Productivity (g $m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established Aug. 1985, n=10) and Total Apparent Productivity of Grazed (n=25) Shrub Meadow Vegetation at Two Study Sites in 1987.

Period of Growth	95% Confidence Intervals						Probability
	Control '85			Apparent			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 4-Aug.21	0.39	0.59	0.89	0.17	0.24	0.33	P>.10
June 4-July 5	0.56	0.93	1.40	0.79	1.27	1.86	P>.10
June 4-July 31	0.47	0.82	1.26	0.58	0.85	1.15	P>.10
July 5-July 31	0.24	0.69	1.36	0.03	0.27	0.72	P>.10
July 5-Aug.21	0.27	0.41	0.62	-0.54	-0.36	-0.24	P>.10
July 31-Aug.21	0.08	0.12	0.19	-1.81	-1.25	-0.87	P>.10
			Lake 650				
June 14-Aug.13	0.08	0.43	1.06	-1.09	-0.74	-0.46	P≤.05
June 14-July 12	2.09	4.43	7.63	-2.05	-1.46	-0.97	P≤.001
July 12-Aug.13	-4.29	-3.03	-2.14	-0.16	-0.11	-0.07	P>.10

Appendix 2a-5. Green Control Productivity ($g\ m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established May 1987, n=15) and Green Apparent Productivity of Grazed (n=25) Shrub Meadow Vegetation at Two Study Sites in 1987.

Period of Growth	95% Confidence Intervals						Probability
	Control '87			Apparent			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 4-Aug.21	0.30	0.46	0.67	0.13	0.23	0.36	P>.10
June 4-July 6	1.56	2.49	3.65	0.64	0.96	1.34	P≤.05
June 4-July 31	0.52	0.80	1.26	0.47	0.62	0.83	P>.10
July 6-July 31	-1.54	-0.97	-0.60	0.23	0.33	0.46	P>.10
July 6-Aug.21	-1.38	-0.83	-0.42	-0.59	-0.32	-0.13	P>.10
July 31-Aug.21	-0.56	-0.37	-0.25	-1.61	-1.12	-0.78	P>.10
			Lake 650				
June 13-Aug.18	0.94	1.31	1.74	-0.90	-0.64	-0.42	P≤.001
June 13-July 13	0.96	1.67	2.57	-1.43	-0.99	-0.63	P≤.001
July 13-Aug.18	0.61	1.06	1.62	-0.58	-0.31	-0.12	P≤.05

Appendix 2a-6. Total Control Productivity (g $m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established May 1987, n=15) and Total Apparent Productivity of Grazed (n=25) Shrub Meadow Vegetation at Two Study Sites in 1987.

Period of Growth	95% Confidence Intervals						Probability
	Control '87			Apparent			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 4-Aug.21	0.34	0.56	0.83	0.18	0.30	0.46	P>.10
June 4-July 6	1.38	2.35	3.57	0.76	1.27	1.91	P>.10
June 4-July 31	0.49	0.92	1.49	0.56	0.85	1.18	P>.10
July 6-July 31	-1.81	-0.79	-0.18	0.03	0.27	0.72	P>.10
July 6-Aug.21	-1.09	-0.59	-0.24	-0.80	-0.42	-0.17	P>.10
July 31-Aug.21	-1.01	-0.37	-0.04	-2.14	-1.29	-0.65	P>.10
			Lake 650				
June 13-Aug.18	0.85	1.34	1.94	-1.09	-0.74	-0.46	P≤.001
June 13-July 13	0.57	1.29	2.29	-2.11	-1.50	-1.00	P≤.001
July 13-Aug.18	0.75	1.38	2.19	-0.15	-0.02	0.01	P≤.10

Appendix 2a-7. Total Control Productivity (g $m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established in Aug. 1985, n=10) and Total Actual Productivity of Grazed (n=25) Shrub Meadow Vegetation at Two Study Sites in 1987.

Period of Growth	95% Confidence Intervals						Probability
	Control '85			Actual			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 3-July 30	0.58	0.79	1.07	0.69	1.09	1.72	P>.10
June 3-July 2	0.69	0.89	1.16	1.30	1.71	2.25	P≤.05
July 5-July 30	0.49	0.67	0.92	0.26	0.37	0.53	P>.10
			Lake 650				
June 13-Aug.13	0.08	0.43	1.06	1.19	1.85	2.66	P>.10
June 13-July 12	2.09	4.43	7.63	0.94	1.60	2.43	P>.10
July 12-Aug.13	-5.02	-3.15	-1.72	1.41	2.08	2.88	P≤.001

Appendix 2a-8. Green Control Productivity (g $m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established in May 1987, n=15) and Green Actual Productivity of Grazed (n=25) Shrub Meadow Vegetation at Two Study Sites in 1987.

Period of Growth	95% Confidence Intervals						Probability
	Control '87			Actual			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 4-July 30	0.56	0.80	1.16	0.70	1.07	1.63	P>.10
June 4-July 3	1.45	2.28	3.58	1.16	1.53	2.03	P>.10
July 6-July 30	-1.55	-0.97	-0.60	0.38	0.53	0.73	P≤.10
			Lake 650				
June 14-Aug.18	0.94	1.31	1.74	0.98	1.49	2.11	P>.10
June 13-July 12	0.96	1.67	2.57	1.02	1.59	2.29	P>.10
July 13-Aug.18	0.61	1.06	1.62	0.94	1.41	1.97	P>.10

Appendix 2a-9. Total Control Productivity ($g\ m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established in May 1987, n=10) and Total Actual Productivity of Grazed (n=25) Shrub Meadow Vegetation at Two Study Sites in 1987.

Period of Growth	95% Confidence Intervals						Probability
	Control '87			Actual			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 4-July 30	0.55	0.87	1.36	0.69	1.09	1.72	P>.10
June 4-July 3	1.38	2.35	3.57	1.29	1.81	2.41	P>.10
July 6-July 3	-1.03	-0.65	-0.41	0.26	0.37	0.53	P>.10
			Lake 650				
June 14-Aug.18	0.85	1.34	1.94	1.19	1.85	2.66	P>.10
June 13-July 12	0.57	1.29	2.29	0.94	1.60	2.43	P>.10
July 13-Aug.18	0.75	1.38	2.19	1.41	2.08	2.88	P≤.10

Appendix 2a-10. Green Apparent Productivity (g $m^{-2}d^{-1}$) of Grazed (n=25) and Green Actual Productivity of Grazed (n=25) Shrub Meadow Vegetation at Two Study Sites in 1987.

Period of Growth	95% Confidence Intervals						Probability
	Apparent			Actual			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 3-July 31	0.47	0.62	0.83	0.70	1.07	1.63	P>.10
June 3-July 3	0.62	0.84	1.15	1.16	1.53	2.03	P≤.10
July 7-July 31	0.23	0.33	0.46	0.38	0.53	0.73	P>.10
			Lake 650				
June 13-Aug.18	-0.90	-0.64	-0.42	0.98	1.49	2.11	P≤.001
June 13-Jul.14	-1.42	-0.99	-0.63	1.02	1.59	2.29	P≤.001
July 15-Aug.18	-0.58	-0.31	-0.12	0.94	1.41	1.97	P≤.001

Appendix 2a-11. Total Apparent Productivity (g $m^{-2}d^{-1}$) (n=25) and Total Actual Productivity of Grazed (n=25) Shrub Meadow Vegetation at Two Study Sites in 1987.

Period of Growth	95% Confidence Intervals						Probability
	Apparent			Actual			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 3-July 31	0.56	0.75	1.01	0.69	1.09	1.73	P>.10
June 3-July 3	0.73	1.04	1.47	1.30	1.71	2.25	P>.10
July 7-July 31	0.24	0.35	0.52	0.26	0.37	0.53	P>.10
			Lake 650				
June 13-Aug.18	-1.09	-0.74	-0.46	1.19	1.85	2.66	P≤.001
June 13-Jul.14	-2.11	-1.50	-1.00	0.94	1.60	2.43	P≤.001
July 15-Aug.18	-0.15	-0.02	0.01	1.41	2.08	2.88	P≤.001

Appendix 2a-12. Cumulative Green Biomass Estimates (g m^{-2}) (n=10) of Artificially Grazed Control Plots* (Permanent Exclosure Established Aug. 1985) at Calais Lake East in 1986.

Date of Clips		95% Confidence Intervals						Prob.
Clip1	Clip2	Clip1			Clip2			
		L1	Mean	L2	L1	Mean	L2	
June 9 July 9 July 22 Aug. 21	July 1 July 22 Aug. 21	195.66	234.82	277.54	190.62	236.35	286.99	P>.10
June 9 July 9 July 22 Aug. 21	July 22 Aug. 21	195.66	234.82	277.54	189.35	228.42	271.14	P>.10
June 9 July 9 July 22 Aug. 21	Aug. 21	195.66	234.82	277.54	179.49	252.31	337.47	P>.10
July 1 July 22 Aug. 21	July 22 Aug. 21	190.60	233.42	285.82	185.91	222.87	267.14	P>.10
July 1 July 22 Aug. 21	Aug. 21	190.60	233.42	285.82	180.18	244.47	331.58	P>.10
July 22 Aug. 21	Aug. 21	185.91	222.87	267.14	179.38	244.47	333.06	P>.10

* Dates beneath "clip1" and "clip2" columns refer to dates plots were (re)clipped.

Appendix 2a-13. Cumulative Green Biomass Estimates (g m^{-2}) (n=10) of Artificially Grazed Control Plots* (Permanent Exclosure Established Aug. 1985) at Calais Lake West and Lake 690 in 1986.

Date of Clips		95% Confidence Intervals						Prob.
		Clip1			Clip2			
Clip1	Clip2	L1	Mean	L2	L1	Mean	L2	
				Calais Lake West				
June 14 July 9 July 26	July 5 July 26	164.34	230.63	323.50	171.11	207.11	250.65	P>.10
June 14 July 9 July 26	July 26	162.52	228.09	319.94	144.01	180.97	227.35	P>.10
July 5 July 26	July 26	171.79	207.93	251.64	144.01	180.97	227.35	P>.10
				Lake 690				
June 12 July 10 Aug. 9	July 10 Aug. 9	148.03	180.97	221.19	150.39	185.21	228.04	P>.10
June 12 July 10 Aug. 9	Aug. 9	148.03	180.97	221.19	130.35	157.49	190.23	P>.10
July 10 Aug. 9	Aug. 9	146.65	192.00	237.35	136.62	163.80	190.98	P>.10

* See footnote Appendix 2a-12

Appendix 2a-14. Cumulative Green and Total Biomass* (g m^{-2}) (n=10) of Artificially Grazed Control Plots (Permanent Exclosure Established Aug. 1985) at Lake 650 and Dieppe Lake in 1986.

Date of Clips		95% Confidence Intervals						Prob.
Clip1	Clip2	Clip1			Clip2			
		L1	Mean	L2	L1	Mean	L2	
				Lake 650				
June 17 July 14 Aug. 13	July 14 Aug. 13	267.36*	348.44*	440.23*	318.14*	384.05*	456.15*	P>.10
June 17 July 14 Aug. 13	Aug. 13	254.23	324.94	404.30	285.25	414.44	567.65	P>.10
July 14 Aug. 13	Aug. 13	318.87*	384.05*	456.15	322.87*	460.46*	622.37*	P>.10
				Dieppe Lake				
June 26 July 20 Aug. 17	July 20 Aug. 17	118.24	140.16	163.93	142.16	166.69	193.16	P≤.10
June 26 July 20 Aug. 17	Aug. 17	118.64	140.16	163.46	118.15	161.81	212.29	P>.10
July 20 Aug. 17	Aug. 17	140.95	164.96	193.03	118.73	157.49	208.80	P>.10

*These confidence intervals include dead and live plant tissue (i.e. total biomass).

Appendix 2a-15. Green Productivity (g $m^{-2}d^{-1}$) of Artificially Grazed (n=15) and Green Control Productivity of Ungrazed (n=15) Shrub Meadow Vegetation at Two Study Sites in 1987.

Period of Growth	95% Confidence Intervals						Prob.
	Art. Grazed			Control			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 4-Aug. 21	0.41*	0.70*	1.07*	0.13*	0.26*	0.44	P≤.01
June 5-Aug. 21	0.64**	0.80**	0.98**	0.30**	0.47**	0.67	P≤.05
			Lake 650				
June 14-Aug.10	0.63*	1.06*	1.59*	0.14*	0.48*	1.02*	P>.10
June 14-Aug.15	0.99**	1.58**	2.30**	0.94**	1.31**	1.73**	P>.10

Artificially grazed plots clipped at beginning and end of period of growth.

* Exclosure established September 1985.

** Exclosure established May 1987.

Appendix 2a-16. Cumulative Green Biomass Estimates (g m^{-2}) (n=15) of Artificially Grazed Control Plots (Permanent Exclosure Established May 1987) in 1987.

Date of Clips		95% Confidence Intervals						Prob.
Clip1	Clip2	Clip1			Clip2			
		L1	Mean	L2	L1	Mean	L2	
				Calais Lake East				
June 5 Aug. 21	July 5 Aug. 22	73.83	92.33	115.39	85.88	116.49	157.88	P>.10
June 5 Aug. 21	July 30 Aug. 22	73.83	92.33	115.39	54.26	76.62	108.04	P>.10
June 5 Aug. 21	Aug. 21	76.51	95.54	116.66	54.74	68.56	83.91	P≤.05
July 5 Aug. 22	July 30 Aug. 22	85.88	116.49	157.88	54.26	76.62	108.04	P≤.10
July 5 Aug. 22	Aug. 21	85.88	116.49	157.88	52.82	66.61	83.93	P≤.01
July 30 Aug. 22	Aug. 21	54.26	76.62	108.04	52.82	66.61	83.93	P>.10
				Lake 650				
June 14 Aug. 12	July 12 Aug. 12	130.27	164.11	201.83	124.16	159.52	199.30	P>.10
July 12 Aug. 12	Aug. 18	124.16	159.52	199.30	128.48	150.79	174.88	P>.10
June 14 Aug. 18	Aug. 18	132.55	167.60	202.65	131.13	153.49	175.85	P>.10

Appendix 2b-1. Total Control Productivity (g $m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established in Aug. 1985, n=10 and Permanent Exclosure Established in May 1987, n=15) Shrub Meadow Vegetation at Two Study Sites in 1987.

Period of Growth	95% Confidence Intervals						Prob.
	Control '85			Control '87			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 3-Aug.21	0.29	0.72	1.34	0.33	0.55	0.82	P>.10
June 3-Jul. 4	0.19	0.95	1.70	1.26	2.52	3.77	P≤.10
June 3-Jul.29	0.47	0.82	1.26	0.49	0.92	1.49	P>.10
July 4-Jul.29	0.24	0.69	1.36	-1.81	-0.79	-0.18	P>.10
July 4-Aug.21	0.27	0.41	0.62	-0.65	-0.44	-0.29	P>.10
July 29-Aug.21	0.08	0.12	0.19	-0.28	-0.19	-0.13	P>.10
			Lake 650				
June 14-Aug.13	0.08	0.43	1.06	0.85	1.34	1.94	P>.10
June 14-Jul.10	2.09	4.43	7.63	0.57	1.29	2.29	P>.10
July 10-Aug.13	-4.29	-3.03	-2.14	1.00	1.37	1.86	P≤.001

Appendix 2b-2. Comparison of Percent Standing Dead Tissue in Control'85 Plots and Grazed Plots in 1986.

Date	Study Site	Control'85	Grazed	Probability
June 9	C.L.East	.17±.10	.22±.09	P>.10
July 1	C.L.East	.04±.05	.18±.09	P>.10
July 22	C.L.East	.04±.05	.10±.07	P>.10
Aug. 21	C.L.East	.17±.10	.11±.07	P>.10
June 12	Lake 690	.24±.11	.41±.11	P>.10
July 10	Lake 690	.16±.09	.15±.08	P>.10
Aug. 9	Lake 690	.12±.09	.15±.08	P>.10
June 14	C.L.West	.12±.09	.17±.08	P>.10
July 5	C.L.West	.09±.07	.08±.06	P>.10
July 26	C.L.West	.08±.07	.11±.07	P>.10
June 17	Lake 650	.10±.08	.14±.09	P>.10
July 14	Lake 650	*******	.10±.07	*****
Aug. 14	Lake 650	.10±.08	.14±.08	P>.10
June 26	Dieppe L.	.21±.11	.17±.08	P>.10
July 20	Dieppe L.	.25±.11	.15±.08	P>.10
Aug. 17	Dieppe L.	.16±.09	.20±.09	P>.10

Appendix 2b-3. Standing Crop Biomass (g m^{-2}) of Standing Dead Plant Tissue in Ungrazed (Permanent Exclosure Established in May 1987, n=15) and Grazed (n=25) Meadows in 1987.

Date	95% Confidence Intervals						Probability
	Ungrazed			Grazed			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 4	8.92	15.26	23.22	7.83	10.59	13.75	P>.10
July 6	1.49	3.25	6.23	8.02	14.14	24.39	P≤.01
July 31	11.33	16.97	23.72	13.60	19.93	27.44	P>.10
Aug. 21	15.82	22.25	29.76	11.16	15.58	20.71	P>.10
			Lake 650				
June 13	16.47	25.92	40.48	13.26	18.95	26.92	P>.10
July 13	6.79	16.15	29.31	3.91	6.84	10.53	P≤.05
Aug. 13	9.20	18.95	38.04	7.97	12.80	20.25	P>.10

Appendix 2b-4. Comparison of Percent Standing Dead Tissue in Control'87 Plots (n=15) and Grazed Plots (n=25) in 1987.

Date	Study Site	Control'87	Grazed	Probability
June 4	C.L.East	$.34 \pm .11$	$.30 \pm .09$	$P > .10$
July 6	C.L.East	$.10 \pm .07$	$.10 \pm .06$	$P > .10$
July 31	C.L.East	$.17 \pm .08$	$.25 \pm .09$	$P > .10$
Aug. 21	C.L.East	$.25 \pm .10$	$.26 \pm .09$	$P > .10$
June 13	Lake 650	$.33 \pm .11$	$.23 \pm .08$	$P > .10$
July 13	Lake 650	$.16 \pm .08$	$.14 \pm .07$	$P > .10$
Aug. 13	Lake 650	$.19 \pm .09$	$.33 \pm .09$	$P > .10$

Appendix 2b-5. Standing Crop Biomass (g m^{-2}) of Standing Dead Plant Tissue in Ungrazed (Permanent Exclosure Estabished Aug. 1985, n=10) Meadows at Five Study Sites in 1986 and 1987.

Date	95% Confidence Intervals						Probability
	1986			1987			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 7	6.77	11.59	19.41	14.38	18.95	24.89	P≤.10
July 2	3.13	5.92	10.59	9.20	11.02	13.18	P≤.05
July 26	4.90	7.13	10.21	12.50	19.42	29.87	P≤.001
Aug. 21	21.53	39.74	72.66	19.91	37.90	71.37	P>.10
			Lake 650				
June 16	3.31	9.80	19.46	20.27	54.56	105.24	P≤.01
July 12	Not Available			47.35	86.10	155.89	NA
Aug. 11	27.63	40.69	59.69	32.38	45.77	64.54	P>.10
			Dieppe Lake				
Aug. 18	21.71	28.44	36.07	15.09	19.75	25.02	P≤.05
			Lake 690				
Aug. 14	18.13	21.91	26.44	12.78	16.38	20.91	P≤.10

Appendix 2b-6. Standing Crop Biomass (g m^{-2}) of Standing Dead Plant Tissue in Ungrazed (Permanent Exclosure Estabished Aug. 1985, n=10 and Permanent Exclosure Established May 1987) Meadows at Two Study Sites in 1986 and 1987, respectively.

Date	95% Confidence Intervals						Probability
	1986			1987			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 7	6.77	11.59	19.41	7.33	12.80	21.88	P>.10
July 3	3.16	5.97	10.67	1.49	3.25	6.23	P>.10
July 26	4.92	7.17	10.26	10.99	15.60	21.97	P≤.01
Aug. 21	21.53	39.74	72.66	14.41	20.38	28.67	P≤.05
			Lake 650				
June 16	3.37	7.77	16.61	16.47	25.92	40.48	P≤.01
July 12	Not Available			6.79	16.15	29.31	NA
Aug. 16	27.63	40.69	59.69	9.20	18.95	38.04	P≤.10

Appendix 2b-7. Comparison of Percent Standing Dead Tissue in 1986 (n=10) (Permanent Exclosure Established September 1985) and 1987 (n=15) (Permanent Exclosure Established May 1987).

Date	Study Site	1986	1987	Probability
June 7	C.L.East	.17±.10	.34±.11	P>.10
July 3	C.L.East	.04±.05	.10±.07	P>.10
July 26	C.L.East	.04±.05	.17±.08	P>.10
Aug. 21	C.L.East	.17±.10	.25±.10	P>.10
June 16	Lake 650	.10±.08	.33±.11	P>.10
July 13	Lake 650	*******	.16±.08	*****
Aug. 16	Lake 650	.10±.08	.19±.09	P>.10

Appendix 2c-1. Green Control Productivity (g $m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established Aug. 1985, n=10) Shrub Meadow Vegetation at Two Study Sites, in 1986 and 1987.

Period of Growth	95% Confidence Intervals						Probability
	1986			1987			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 6-Aug. 21	1.67	2.35	3.29	0.19	0.26	0.36	P≤.001
June 6-July 2	2.81	4.18	5.82	0.68	1.13	1.69	P≤.01
June 6-July 25	2.54	3.33	4.22	0.45	0.78	1.19	P≤.001
July 4-July 25	1.75	2.35	3.15	0.29	0.40	0.56	P>.10
July 2-Aug. 21	1.13	1.63	2.37	-0.30	-0.22	-0.17	P≤.05
July 25-Aug.21	0.76	1.06	1.48	-1.30	-0.93	-0.66	P≤.10
			Lake 650				
June 15-Aug. 10	3.29	5.39	8.01	0.14	0.48	1.02	P≤.001
June 15-July 12	Not Available			0.98	1.86	3.02	NA
July 12-Aug. 10	Not Available			-1.48	-0.76	-0.27	NA

Appendix 2c-2. Total Control Productivity (g $m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established Aug. 1985, n=10) Shrub Meadow Vegetation at Two Study Sites, in 1986 and 1987.

Period of Growth	95% Confidence Intervals 1986 L1	Mean	L2	1987 L1	Mean	L2	Probability
			Calais Lake East				
June 6-Aug.21	2.08	2.76	3.66	0.39	0.59	0.89	P≤.01
June 6-July 2	2.40	3.84	5.61	0.56	0.93	1.40	P≤.05
June 6-July 25	2.43	3.18	4.16	0.58	0.79	1.07	P≤.01
July 4-July 25	1.88	2.46	3.22	0.49	0.67	0.92	P>.10
July 2-Aug.21	1.70	2.33	3.19	0.27	0.41	0.62	P>.10
July 25-Aug.21	1.66	2.15	2.79	0.08	0.12	0.19	P>.10
			Lake 650				
June 15-Aug.10	3.69	6.00	8.86	0.08	0.43	1.06	P≤.001
June 15-July 12	4.94	7.59	10.81	2.09	4.43	7.63	P>.10
July 12-Aug.10	2.77	4.01	5.80	-4.29	-3.03	-2.14	P≤.01

Appendix 2c-3. Green Control Productivity (g $m^{-2}d^{-1}$) of Ungrazed Shrub Meadow Vegetation at Two Study Sites in 1986 (Permanent Exclosure Established Aug. 1985, n=10) and in 1987 (Permanent Exclosure Established May 1987, n=15).

Period of Growth	95% Confidence Intervals						Prob.
	1986			1987			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 7-Aug.21	1.27	2.36	3.45	0.25	0.47	0.68	P≤.001
June 7-July 3	2.81	4.18	5.82	1.56	2.49	3.65	P>.10
June 7-July 26	2.54	3.33	4.22	0.51	0.90	1.39	P≤.001
July 3-July 26	1.75	2.35	3.15	-1.55	-0.97	-0.60	P≤.10
July 3-Aug.21	0.83	1.69	2.86	-1.38	-0.83	-0.42	P≤.01
July 26-Aug.21	0.36	1.17	2.46	-1.32	-0.61	-0.17	P>.10
			Lake 650				
June 15-Aug.15	3.29	5.39	8.01	0.94	1.31	1.74	P≤.001
June 15-July 12	Not Available			0.96	1.67	2.57	NA
July 12-Aug.15	Not Available			0.61	1.06	1.62	NA

Appendix 2c-4. Total Control Productivity (g $m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established Aug. 1985, n=10 and Permanent Exclosure Established May 1987, n=15) Shrub Meadow Vegetation at Two Study Sites, in 1986 and 1987, respectively.

Period of Growth	95% Confidence Intervals						Probability
	1986			1987			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 7-Aug.21	2.08	2.79	3.60	0.34	0.56	0.83	P≤.001
June 7-July 3	2.40	3.84	5.61	1.38	2.35	3.57	P>.10
June 7-July 26	2.43	3.18	4.16	0.55	0.87	1.36	P>.10
July 3-July 26	1.81	2.46	3.32	-1.03	-0.65	-0.41	P>.10
July 3-Aug.21	1.58	2.33	3.24	-1.09	-0.59	-0.24	P≤.001
July 26-Aug.21	1.21	2.24	3.59	-1.01	-0.37	-0.04	P>.10
			Lake 650				
June 15-Aug.15	3.70	6.01	8.87	0.85	1.34	1.94	P≤.001
June 15-July 12	4.94	7.59	10.81	0.57	1.29	2.29	P≤.01
July 12-Aug.15	2.20	4.57	7.78	0.75	1.38	2.19	P>.10

Appendix 2c-5. Total Standing Crop Biomass (g m^{-2}) of Control Vegetation (Permanent Exclosure Established in Aug. 1985) for 1986 (n=10) and 1987 (n=10) with Corresponding Cumulative (since June 1) Precipitation Data (mm).

Date	95% Confidence Intervals								Prob.
	1986				1987				
	L1	Mean	L2	Precip	L1	Mean	L2	Precip	
Calais Lake East									
June 7	70.36	90.72	111.08	10.6	61.46	75.50	89.54	5.6	P>.10
July 2	129.34	173.21	223.46	43.2	82.85	101.51	122.05	31.2	P≤.01
July 26	185.16	225.10	268.93	83.9	87.41	119.18	155.85	54.4	P≤.001
Aug. 21	232.91	287.40	354.59	NA	79.86	119.23	177.76	94.1	P≤.001
Lake 650									
June 16	73.20	129.49	185.78	13.7	75.94	139.93	203.92	5.6	P>.10
July 12	267.39	323.50	384.94	79.3	177.68	240.06	311.80	40.8	P≤.10
Aug. 11	322.87	460.46	622.37	142.8	114.35	148.58	187.28	82.4	P≤.001
Dieppe Lake									
Aug. 18	140.97	175.86	214.58	156.1	81.31	93.59	106.73	90.9	P≤.001
Lake 690									
Aug. 14	159.77	186.45	213.13	114.2	98.32	115.89	133.40	90.9	P≤.001

Appendix 2c-6. Green Standing Crop Biomass (g m^{-2}) of Control Vegetation for 1986 (Permanent Exclosure Established in Aug. 1985, n=10) and 1987 (Permanent Exclosure Established May 1987, n=15) with Corresponding Cumulative (since June 1) Precipitation Data (mm).

Date	95% Confidence Intervals								Prob.
	1986				1987				
	L1	Mean	L2	Precip	L1	Mean	L2	Precip	
				Calais Lake East					
June 7	61.03	75.23	89.43	10.6	25.02	35.02	45.02	5.6	P≤.001
July 3	125.56	170.86	216.16	43.2	81.49	116.02	150.55	34.8	P≤.05
July 26	177.87	217.06	260.14	83.9	55.60	81.95	113.35	73.0	P≤.001
Aug. 21	179.38	244.47	333.06	NA	52.82	66.61	83.93	94.1	P≤.001
				Lake 650					
June 16	63.90	107.24	161.68	13.7	48.52	65.60	85.22	5.6	P≤.05
July 11	Not Available			79.3	88.19	115.62	143.05	40.8	NA
Aug. 16	277.56	397.11	567.95	142.8	124.25	146.91	173.67	87.9	P≤.001

Appendix 2c-7. Total Standing Crop Biomass (g m^{-2}) of Control Vegetation for 1986 (Permanent Exclosure Established in Aug. 1985, n=10) and 1987 (Permanent Exclosure Established in May 1987, n=15) with Corresponding Cumulative (since June 1) Precipitation Data (mm).

Date	95% Confidence Intervals								Prob.
	1986				1987				
	L1	Mean	L2	Precip	L1	Mean	L2	Precip	
				Calais Lake East					
June 7	70.36	90.72	111.08	10.6	37.08	52.80	68.52	5.6	P≤.01
July 3	128.83	178.71	228.59	43.2	91.96	128.26	164.56	34.8	P≤.10
July 26	186.58	228.46	270.34	83.9	71.69	108.31	144.93	73.0	P≤.001
Aug. 21	230.61	292.25	361.18	NA	73.30	91.66	112.05	94.1	P≤.001
				Lake 650					
June 16	73.20	129.49	185.78	13.7	74.03	103.08	132.13	5.6	P>.10
July 13	271.89	328.11	384.33	79.3	104.27	137.54	170.81	40.8	P≤.001
Aug. 16	308.00	435.52	615.66	142.8	145.56	176.83	214.77	87.9	P≤.001

Appendix 2c-8. Green Apparent Productivity (g $m^{-2}d^{-1}$) of Grazed Shrub Meadow Vegetation at Two Study Sites in 1986 (n=20) and 1987 (n=25).

Period of Growth	95% Confidence Intervals 1986 L1	1986 Mean	1986 L2	1987 L1	1987 Mean	1987 L2	Probability
			Calais Lake East				
June 6-Aug.21	0.79	1.10	1.53	0.13	0.18	0.26	P≤.01
June 6-July 4	-1.27	-0.69	-0.29	0.64	0.96	1.34	P≤.001
June 6-July 27	0.57	0.81	1.15	0.47	0.62	0.83	P>.10
July 4-July 27	1.56	2.47	3.92	0.23	0.33	0.46	P≤.001
July 4-Aug.21	1.26	1.93	2.96	-0.47	-0.32	-0.21	P≤.001
July 27-Aug.21	1.14	1.50	1.98	-1.61	-1.12	-0.78	P≤.01
			Lake 650				
June 15-Aug.16	0.38	0.81	1.38	-0.90	-0.64	-0.42	P≤.001
June 15-July 14	1.10	2.46	4.37	-1.42	-0.99	-0.63	P≤.001
July 14-Aug.16	-1.54	-0.54	-0.05	-0.58	-0.31	-0.12	P>.10

Appendix 2c-9. Total Apparent Productivity (g $m^{-2}d^{-1}$) of Grazed Shrub Meadow Vegetation at Two Study Sites, in 1986 (n=20) and 1987 (n=25).

Period of Growth	95% Confidence Intervals						Probability
	1986			1987			
	L1	Mean	L2	L1	Mean	L2	
			Calais Lake East				
June 6-Aug.21	0.79	1.13	1.53	0.18	0.30	0.46	P≤.01
June 6-July 4	-1.73	-0.99	-0.46	0.79	1.27	1.86	P≤.001
June 6-July 27	0.38	0.69	1.08	0.58	0.85	1.15	P>.10
July 5-July 27	1.66	2.63	4.17	0.24	0.35	0.52	P≤.01
July 5-Aug.21	1.37	2.11	3.25	-0.54	-0.36	-0.24	P≤.001
July 27-Aug.21	1.29	1.68	2.20	-1.81	-1.25	-0.87	P≤.01
			Lake 650				
June 15-Aug.16	-1.60	-0.96	-0.48	-1.09	-0.74	-0.46	P≤.001
June 15-July 14	1.17	2.66	4.76	-2.11	-1.50	-1.00	P≤.001
July 14-Aug.16	-1.41	-0.44	-0.02	-0.15	-0.02	0.01	P>.10

Appendix 2c-10. Cumulative Heat Sums ($0^{o}C$ base) from May 17, 1986-1987. Dry Bulb Air Temperature Data Recorded at 1200hrs in Fort Providence, N.W.T.

Date	1986	1987	Date	1986	1987
May 17	14.0	8.0	July 5	764.5	897.5
May 18	25.5	15.0	July 6	783.5	909.0
May 19	43.5	17.0	July 7	803.0	926.0
May 20	61.5	29.0	July 8	826.0	947.0
May 21	76.0	46.0	July 9	849.0	965.0
May 22	89.0	61.0	July 10	872.5	987.0
May 23	100.0	76.0	July 11	895.5	1011.0
May 24	113.5	95.5	July 12	917.0	1035.5
May 25	133.0	109.0	July 13	942.0	1058.5
May 26	149.5	126.5	July 14	966.0	1075.5
May 27	166.5	148.5	July 15	982.0	1096.0
May 28	173.5	174.0	July 16	1001.0	1116.5
May 29	182.5	199.0	July 17	1023.0	1141.5
May 30	195.5	216.5	July 18	1036.0	1169.0
May 31	206.5	235.5	July 19	1054.0	1184.0
June 1	218.5	251.5	July 20	1070.5	1198.5
June 2	229.5	264.5	July 21	1086.5	1221.5
June 3	236.5	274.5	July 22	1095.5	1235.0
June 4	250.5	289.0	July 23	1112.0	1250.5
June 5	266.5	306.0	July 24	1130.5	1273.5
June 6	279.5	321.0	July 25	1148.0	1300.5
June 7	303.0	339.0	July 26	1171.0	1321.5
June 8	318.0	365.5	July 27	1194.5	1340.5
June 9	331.5	394.0	July 28	1212.5	1364.0
June 10	345.5	413.5	July 29	1230.5	1389.0
June 11	358.0	436.5	July 30	1249.5	1409.5
June 12	363.0	458.0	July 31	1273.5	1432.5
June 13	375.5	480.0	Aug. 1	1317.5	1454.5
June 14	391.5	495.0	Aug. 2	1341.5	1471.5
June 15	402.5	507.5	Aug. 3	1367.0	1489.5
June 16	418.5	521.5	Aug. 4	1388.0	1509.5
June 17	439.5	541.0	Aug. 5	1406.5	1529.5
June 18	464.0	562.0	Aug. 6	1419.5	1550.0
June 19	483.5	584.0	Aug. 7	1437.0	1569.5
June 20	493.0	609.0	Aug. 8	1451.5	1586.0
June 21	502.0	634.0	Aug. 9	1472.0	1604.0
June 22	514.5	648.0	Aug. 10	1498.5	1620.0
June 23	533.5	656.5	Aug. 11	1523.5	1632.5
June 24	550.5	671.0	Aug. 12	1538.5	1641.0
June 25	566.0	692.5	Aug. 13	1559.5	1653.0
June 26	582.0	712.5	Aug. 14	1569.5	1666.5
June 27	602.0	732.5	Aug. 15	NA	1685.5
June 28	624.5	757.5	Aug. 16	NA	1703.5
June 29	649.0	780.5	Aug. 17	NA	1719.5
June 30	670.0	801.5	Aug. 18	NA	1735.5
July 1	692.0	823.0	Aug. 19	NA	1756.0
July 2	708.0	838.5	Aug. 20	NA	1770.0
July 3	726.0	855.5	Aug. 21	NA	1785.0
July 4	746.0	876.5	Aug. 22	NA	1801.5

Appendix 2c-11. Grazing Intensity* and Fecal Pats (pats/hectare) at Five Study Sites in 1986 and 1987.

1986			1987		
Date	Grazing Intensity	Fecal Pats	Date	Grazing Intensity	Fecal Pats
	Calais Lake East			Calais Lake East	
June 9	0.27±0.08	29	June 4	0.48±0.08	600
July 1	0.75±0.08	212	July 5	0.12±0.05	98
July 22	0.59±0.09	278	July 30	0.23±0.07	176
Aug. 21	0.50±0.09	15	Aug. 21	0.53±0.08	44
	Lake 690			Lake 690	
June 12	0.04±0.04	6	Aug. 19	0.16±0.06	97
10	0.41±0.09	239			
Aug. 9	0.27±0.08	0			
	Calais Lake West			Calais Lake West	
June 14	0.40±0.09	86	Aug. 20	−0.28±0.09	0
July 5	0.33±0.09	103			
July 26	0.45±0.09	215			
	Lake 650			Lake 650	
June 17	0.69±0.09	147	June 13	0.21±0.06	309
July 14	0.62±0.09	431	July 12	0.76±0.07	142
Aug. 14	0.79±0.08	175	Aug. 13	0.58±0.08	146
	Dieppe Lake			Dieppe Lake	
June 26	0.49±0.09	25	Aug. 19	0.16±0.06	25
July 20	0.43±0.09	44			
Aug. 17	0.35±0.09	38			

$$* \text{ Grazing Intensity} = 1 - \frac{\text{Mean Standing Crop of Grazed Vegetation}}{\text{Mean Standing Crop of Ungrazed Vegetation}}$$

(Permanent Exclosure Established Sept. 1985)

Appendix 2c-12. Grazing Intensity and Fecal Pats (pats/hectare) at Five Study Sites in 1986* and at Two Study Sites in 1987**.

1986			1987		
Date	Grazing Intensity	Fecal Pats	Date	Grazing Intensity	Fecal Pats
	Calais Lake East			Calais Lake East	
June 9	0.27±0.08	29	June 4	0.25±0.07	600
July 1	0.75±0.08	212	July 6	0.29±0.07	98
July 22	0.59±0.09	278	July 31	0.13±0.05	176
Aug. 21	0.50±0.09	15	Aug. 21	0.28±0.07	44
	Lake 690			Lake 650	
June 12	0.04±0.04	6	June 13	-0.07±0.04	309
July 10	0.41±0.09	239	July 13	0.55±0.08	142
Aug. 9	0.27±0.08	0	Aug. 13	0.66±0.07	146
	Calais Lake West				
June 14	0.40±0.09	86			
July 5	0.33±0.09	103			
July 26	0.45±0.09	215			
	Lake 650				
June 17	0.69±0.09	147			
July 14	0.62±0.09	431			
Aug. 14	0.79±0.08	175			
	Dieppe Lake				
June 26	0.49±0.09	25			
July 20	0.43±0.09	44			
Aug. 17	0.35±0.09	38			

$$\text{* Grazing Intensity} = 1 - \frac{\text{Mean Standing Crop of Grazed Vegetation}}{\text{Mean Standing Crop of Ungrazed Vegetation}}$$

(Permanent Exclosure Established Sept. 1985)

$$\text{** Grazing Intensity} = 1 - \frac{\text{Mean Standing Crop of Grazed Vegetation}}{\text{Mean Standing Crop of Ungrazed Vegetation}}$$

(Permanent Exclosure Established May 1987)

Appendix 2c-13. Comparison of Grazing Intensities (G)[a] at Five Study Sites in 1986.

Date	Study Site 1	G	Date	Study Site 2	G	Probability
Early Summer						
June 9	C.L.East	0.27±.08	June 12	Lake 690	0.04±.04	P≤.05
			June 14	C.L.West	0.40±.09	P>.10
			June 17	Lake 650	0.69±.09	P≤.01
			June 26	Dieppe L.	0.49±.09	P≤.10
June 12	Lake 690	0.04±.04	June 14	C.L.West	0.40±.09	P≤.001
			June 17	Lake 650	0.69±.09	P≤.001
			June 26	Dieppe L.	0.49±.09	P≤.001
June 14	C.L.West	0.40±.09	June 17	Lake 650	0.69±.09	P≤.05
			June 26	Dieppe L.	0.49±.09	P>.10
June 17	Lake 650	0.69±.09	June 26	Dieppe L.	0.49±.09	P>.10
Middle Summer						
July 1	C.L.East	0.75±.08	July 5	C.L.West	0.33±.09	P≤.001
			July 10	Lake 690	0.41±.09	P≤.01
			July 14	Lake 650	0.62±.09	P>.10
			July 20	Dieppe L.	0.43±.09	P≤.05
July 5	C.L.West	0.33±.09	July 10	Lake 690	0.41±.09	P>.10
			July 14	Lake 650	0.62±.09	P≤.05
			July 20	Dieppe L.	0.43±.09	P>.10
July 10	Lake 690	0.41±.09	July 14	Lake 650	0.62±.09	P>.10
			July 20	Dieppe L.	0.43±.09	P>.10
July 14	Lake 650	0.62±.09	July 20	Dieppe L.	0.43±.09	P>.10
Late Summer						
July 22	C.L.East	0.59±.09	July 26	C.L.West	0.45±.09	P>.10
			Aug. 9	Lake 690	0.27±.08	P≤.05
			Aug. 14	Lake 650	0.79±.08	P>.10
			Aug. 17	Dieppe L.	0.35±.09	P≤.10
July 26	C.L.West	0.45±.09	Aug. 9	Lake 690	0.27±.08	P>.10
			Aug. 14	Lake 650	0.79±.08	P≤.01
			Aug. 17	Dieppe L.	0.35±.09	P>.10
Aug. 9	Lake 690	0.27±.08	Aug. 14	Lake 650	0.79±.08	P≤.001
			Aug. 17	Dieppe L.	0.35±.09	P>.10
Aug. 14	Lake 650	0.79±.08	Aug. 17	Dieppe L.	0.35±.09	P≤.001

[a]G= 1-(Mean Standing Crop of Grazed/Mean Standing Crop of Ungrazed)

Appendix 2c-14a. Comparison of Grazing Intensities (G) at Five Study Sites in 1987 (Permanent Exclosure Established Sept. 1985).

Date	Study Site 1	GI	Date	Study Site 2	GI	Probability
June 4	C.L.East	0.48±.08	June 13	Lake 650	0.21±.06	P≤.01
July 5	C.L.East	0.12±.05	July 12	Lake 650	0.76±.07	P≤.001
July 30	C.L.East	0.23±.07	Aug. 13	Lake 650	0.58±.08	P≤.01
Aug. 21	C.L.East	0.53±.08	Aug. 13	Lake 650	0.58±.08	P>.10
			Aug. 20	C.L.West	-0.28±.09	P≤.001
			Aug. 19	Lake 690	0.16±.06	P≤.001
			Aug. 19	Dieppe L.	0.16±.06	P≤.001
Aug. 13	Lake 650	0.58±.08	Aug. 20	C.L.West	-0.28±.09	P≤.001
			Aug. 19	Lake 690	0.16±.06	P≤.001
			Aug. 19	Dieppe L.	0.16±.06	P≤.001
Aug. 20	C.L.West	-0.28±.09	Aug. 19	Lake 690	0.16±.06	P≤.001
Aug. 20	C.L.West	-0.28±.09	Aug. 19	Dieppe L.	0.16±.06	P≤.001
Aug. 19	Lake 690	0.16±.06	Aug. 19	Dieppe L.	0.16±.06	P>.10

Appendix 2c-14b. Comparison of Grazing Intensities (G) at Two Study Sites in 1987 (Permanent Exclosure Established May 1987).

Date	Study Site 1	GI	Date	Study Site 2	GI	Probability
June 4	C.L.East	0.25±.07	June 13	Lake 650	-0.07±.04	P≤.001
July 6	C.L.East	0.29±.07	July 13	Lake 650	0.55±.08	P≤.05
July 31	C.L.East	0.13±.05	Aug. 13	Lake 650	0.66±.07	P≤.001
Aug. 21	C.L.East	0.28±.07	Aug. 13	Lake 650	0.66±.07	P≤.001

Appendix 2c-15. Comparison of Green Consumption Estimates* (C_g) (g/sq m/day) of Two Study Sites in 1987.

Study Site	Period of Growth	95% Confidence Interval			Probability
		L1	Mean	L2	
C.L.East	June 3-July 31	0.28	0.37	0.48	
Lake 650	June 13-Aug.18	1.96	2.13	2.31	$P \leq .05$
C.L.East	June 3-July 4	0.57	0.65	0.73	
Lake 650	June 13-July 14	2.40	2.58	2.79	$P \leq .05$
C.L.East	July 7-July 31	0.06	0.09	0.14	
Lake 650	July 15-Aug.18	1.58	1.72	1.86	$P \leq .05$

C_g = Green Actual Productivity - Green Apparent Productivity

Appendix 2-16a. Green Control Productivity Estimates (g $m^{-2}d^{-1}$) of Ungrazed (Permanent Exclosure Established Sept. 1985, n=10) Shrub Meadow Vegetation among Five Study Sites in 1986.

Study Site	Period of Growth	95% Confidence Interval L1	Mean	L2	Probability
C.L.East	June 9-Aug.21	1.63	2.44	3.41	
Lake 690	June 12-Aug.9	1.28	1.68	2.12	P>.10
C.L.East	June 9-July 1	2.81	4.18	5.82	
Lake 690	June 12-July 10	1.10	1.69	2.42	P≤.05
C.L.East	July 1-Aug.21	0.92	1.69	2.70	
Lake 690	July 10-Aug.9	0.86	1.49	2.30	P>.10
C.L.East	June 9-July 22	2.54	3.33	4.22	
C.L.West	June 14-July 26	1.28	2.04	2.97	P≤.05
C.L.East	June 9-July 1	2.81	4.18	5.82	
C.L.West	June 14-July 5	1.99	3.15	4.57	P>.10
C.L.East	July 1-July 22	1.20	2.33	3.82	
C.L.West	July 5-July 26	0.31	0.93	1.88	P>.10
C.L.East	June 9-Aug.21	1.63	2.44	3.41	
Lake 650	June 17-Aug.13	3.29	5.39	8.01	P≤.05
C.L.East	June 9-July 22	2.35*	3.17*	4.11*	
Lake 650	June 17-July 14	4.94*	7.59*	10.81*	P≤.05
C.L.East	July 22-Aug.21	1.24*	2.24*	3.53*	
Lake 650	July 14-Aug.13	2.20*	4.57*	7.78*	P>.10
C.L.East	July 1-Aug.21	0.92	1.69	2.70	
Dieppe Lake	June 26-Aug.17	1.20	1.86	2.65	P>.10
C.L.East	July 1-July 22	1.20	2.33	3.82	
Dieppe Lake	June 26-July 20	1.83	2.67	3.66	P>.10
C.L.East	July 22-Aug.21	0.36	1.17	2.46	
Dieppe Lake	July 20-Aug.17	0.48	1.16	2.13	P>.10
Lake 690	June 12-Aug.9	1.29	1.68	2.12	
C.L.West	June 14-July 26	1.28	2.04	2.97	P>.10
Lake 690	June 12-July 10	1.11	1.71	2.43	
C.L.West	June 14-July 5	1.99	3.15	4.57	P>.10
Lake 690	July 10-Aug.9	0.86	1.49	2.30	
C.L.West	July 5-July 26	0.31	0.93	1.88	P>.10

(Continued)

Appendix 2c-16 Concluded**

Study Site	Period of Growth	95% Confidence Interval			Probability
		L1	Mean	L2	
Lake 690	June 12-Aug.9	1.28	1.68	2.12	
Lake 650	June 17-Aug.13	3.29	5.39	8.01	P≤.05
Lake 690	June 12-July 10	1.13*	1.79*	2.60*	
Lake 650	June 17-July 14	4.94*	7.59*	10.81*	P≤.01
Lake 690	July 10-Aug.9	0.90*	1.50*	2.26*	
Lake 650	July 14-Aug.13	2.20*	4.57*	7.78*	P>.10
Lake 690	June 12-Aug.9	1.28	1.68	2.12	
Dieppe Lake	June 26-Aug.17	1.20	1.86	2.65	P>.10
Lake 690	June 12-July 10	1.10	1.69	2.42	
Dieppe Lake	June 26-July 20	1.83	2.67	3.66	P>.10
Lake 690	July 10-Aug.9	0.86	1.49	2.30	
Dieppe Lake	July 20-Aug.17	0.48	1.16	2.13	P>.10
C.L.West	June 14-July 26	1.28	2.04	2.97	
Lake 650	June 17-Aug.13	3.29	5.39	8.01	P≤.05
C.L.West	June 14-July 5	2.11*	3.30*	4.75*	
Lake 650	June 17-July 14	4.94*	7.59*	10.81*	P≤.10
C.L.West	July 5-July 26	0.57*	1.34*	2.44*	
Lake 650	July 14-Aug.13	2.20*	4.57*	7.78*	P>.10
Lake 650	June 17-Aug.13	3.29	5.39	8.01	
Dieppe Lake	June 26-Aug.17	1.20	1.86	2.65	P≤.05
Lake 650	June 17-July 14	4.94*	7.59*	10.81*	
Dieppe Lake	June 26-July 20	2.39*	3.66*	5.20*	P>.10
Lake 650	July 14-Aug.13	3.23*	4.57*	6.13*	
Dieppe Lake	July 20-Aug.17	0.02*	0.18*	0.49*	P≤.01

* These estimates include dead and live biomass (i.e. total productivity)

** Dieppe and Calais Lake West were not compared because periods of growth were very different.

Appendix 4-1. Median Heights (cm) of Major Graminoid and Forb Species in Grazed and Ungrazed Areas at 5 Study Sites in 1986.

Date	Species	Ungrazed			Grazed			Probability
		Min.	Median	Max.	Min.	Median	Max.	
				Calais Lake East				
July 1	CXAT	24	37.0	56	10	19.5	39	P≤.001
	CAIN	27	29.0	32	3	16.5	38	P≤.001
	SESP	5	40.0	54	2	7.0	31	P≤.01
	GEMA	2	17.0	42	2	6.0	18	P≤.05
Aug. 21	CXAT	27	35.0	53	17	32.0	42	P>.10
	CAIN	25	38.0	43	12	25.5	37	P>.10
	HOJU	45	47.5	50	30	37.0	52	P>.10
	AGTR	35	41.0	49	19	35.0	68	P>.10
	SESP	2	4.5	9	2	3.0	33	P>.10
				Lake 690				
July 10	CXAT	39	45.0	53	16	29.0	46	P≤.001
	CAIN	28	38.0	44	11	30.0	47	P≤.05
	HOJU	36	38.0	40	15	29.0	30	P>.10
	STPA	15	19.5	24	5	9.0	15	P≤.05
Aug. 9	CXAT	34	44.5	51	25	35.0	53	P≤.01
	CAIN	30	42.5	50	12	31.0	49	P≤.05
	HOJU	27	38.5	44	16	28.0	43	P>.10
	STPA	10	18.0	22	5	15.0	24	P>.10
				Calais Lake West				
July 5	CXAT	37	46.5	51	21	32.0	48	P≤.001
	CXAQ	51	54.0	61	30	32.0	47	P≤.05
	CAIN	30	41.0	57	12	28.0	48	P≤.001
	AGTR	31	37.0	56	17	37.0	50	P>.10
	SESP	2	38.5	53	2	5.0	44	P>.10
	GEMA	2	2.0	26	2	9.0	28	P>.10
July 27	CXAT	35	43.5	52	17	30.0	52	P≤.001
	CAIN	19	35.0	52	12	30.0	40	P>.10
	HOJU	36	45.0	50	23	28.0	50	P≤.10
	AGTR	25	50.5	55	12	27.0	60	P≤.01
	SESP	2	2.0	47	2	3.0	39	P>.10
	GEMA	2	2.0	2	2	3.0	11	P>.10
	PONO	2	23.5	45	2	5.5	16	P>.10

Continued

Appendix 4-1. concluded

Date	Species	Ungrazed Min.	Ungrazed Median	Ungrazed Max.	Grazed Min.	Grazed Median	Grazed Max.	Probability
				Lake 650				
July 14	CXAT	22	52.5	68	6	39.0	58	P≤.10
	CAIN	40	47.5	55	34	50.0	60	P>.10
	HOJU	54	56.0	58	27	46.0	55	P≤.05
	AGTR	35	60.0	76	9	20.0	57	P≤.001
	PONO	1	29.5	58	2	19.0	22	P>.10
Aug. 14	CXAT	30	50.0	63	7	22.0	60	P≤.01
	CAIN	40	55.0	75	15	37.0	82	P>.10
	HOJU	45	53.0	59	9	28.0	38	P≤.05
	AGTR	39	57.0	62	15	26.0	52	P≤.001
	GEMA	2	2.0	58	2	2.0	9	P>.10
	PONO	6	33.0	60	2	3.5	19	P>.10
				Dieppe Lake				
July 20	CXAT	37	43.0	48	18	28.0	56	P≤.01
	CXAQ	35	42.0	51	25	29.0	35	P≤.05
	CAIN	22	44.0	54	19	32.0	51	P≤.05
	SESP	2	25.0	45	2	9.0	28	P>.10
	GEMA	2	2.0	3	2	2.0	6	P>.10
	PONO	2	12.0	42	2	2.0	25	P>.10
Aug. 17	CXAT	33	36.5	45	19	30.0	45	P≤.001
	CXAQ	34	37.0	41	26	41.5	55	P>.10
	CAIN	36	42.0	55	20	34.5	55	P≤.01
	SESP	2	3.0	30	2	2.0	3	P>.10
	GEMA	2	2.0	2	2	2.0	27	P>.10
	PONO	2	45.0	55	2	6.0	50	P>.10

Appendix 4-2. Median Heights (cm) of Major Graminoid and Forb Species in Grazed and Ungrazed Areas* at 2 Study Sites in 1987.

Date	Species	Ungrazed			Grazed			Probability
		Min.	Median	Max.	Min.	Median	Max.	
				Calais Lake East				
June 3	CXAT	18	21.5	24	8	16.0	23	P≤.001
	CAIN	14	16.5	22	5	15.0	20	P>.10
	AGTR	12	16.0	28	6	12.0	17	P≤.05
	SESP	3	5.0	6	2	3.0	10	P>.10
	POSP	2	2.0	3	2	3.5	5	P>.10
	PONO	3	4.0	5	3	3.0	3	P>.10
July 5	CXAT	22	26.5	30	13	24.0	40	P>.10
	CAIN	17	19.5	21	10	23.0	38	P>.10
	AGTR	12	21.0	27	11	20.0	45	P>.10
	SESP	2	15.0	22	2	16.0	33	P>.10
	GEMA	5	10.0	17	2	3.0	10	P≤.10
				Lake 650				
June 13	CXAT	22	29.0	31	7	20.0	37	P≤.10
	AGTR	8	18.5	30	6	20.0	30	P>.10
	GEMA	2	2.0	10	2	7.0	19	P>.10
July 12	CXAT	30	35.5	41	7	16.0	29	P≤.001
	CAIN	30	31.0	40	5	24.0	35	P≤.05
	AGTR	3	35.0	45	10	19.5	27	P≤.001

* Plots are located inside the permanent exclosure established Sept. 1985.

Appendix 4-3. Median % Cover Estimates for Bare Ground in Grazed and Ungrazed Areas at 5 Study Sites in 1986.

Date	Ungrazed			Grazed			Probability
	Min.	Median	Max.	Min.	Median	Max.	
			Calais Lake East				
July 1	0	0.5	21.0	0	3.0	86.0	P≤.05
July 22	0	0.4	3.0	0	3.0	63.0	P>.10
Aug. 21	0	0.0	3.0	0	0.8	86.0	P≤.10
			Lake 690				
July 10	0	0.0	3.0	0	0.7	86.0	P≤.05
Aug. 9	0	0.0	0.5	0	0.0	3.0	P>.10
			Calais Lake West				
July 5	0	0.5	0.3	0	0.8	63.0	P>.10
July 26	0	0.0	38.0	0	0.7	86.0	P>.10
			Lake 650				
July 14	0	3.0	11.0	0	11.0	86.0	P≤.05
Aug. 14	0	0.4	38.0	0	11.0	21.0	P>.10
			Dieppe Lake				
July 20	0	0.0	0.5	0	3.0	86.0	P≤.001
Aug. 17	0	0.0	0.3	0	0.7	38.0	P≤.10

Appendix 4-4. Median % Cover Estimates for Bare Ground in Grazed and Ungrazed Areas at 2 Study Sites in 1987.

Date	Ungrazed			Grazed			Probability
	Min.	Median	Max.	Min.	Median	Max.	
Calais Lake East							
June 4	0	0.0	11.0	0	3.0	21.0	$P \leq .05$
July 5	0	0.0	3.0	0	0.8	98.0	$P > .10$
Lake 650							
June 13	0	0.0	0.5	0	3.0	63.0	$P \leq .01$
July 12	0	0.0	3.0	0	3.0	38.0	$P \leq .05$

Appendix 4-5. Median % Cover Estimates for Bare Ground in Areas Ungrazed Since September 1985 and May 1987 at 2 Study Sites in 1987.

Date	Ungrazed'85			Ungrazed'87			Probability
	Min.	Median	Max.	Min.	Median	Max.	
				Calais Lake East			
June 4	0	0.0	11.0	0	0.0	11	P>.10
July 4	0	0.0	3.0	0	0.0	11	P>.10
				Lake 650			
June 13	0	0.0	0.5	0	0.0	38	P>.10
July 12	0	0.0	3.0	0	0.0	11	P>.10

Appendix 4-6. Comparison of Median Number of Seed Heads (#/sq m) in Plots Ungrazed (n=20) for 30 ca. days* and since September 1985 at Two Study Sites in 1987.

Date	Ungrazed 30 days			Ungrazed'85			Probability
	Min.	Median	Max.	Min.	Median	Max.	
				Calais Lake East			
July 2	0	28	240	0	1	56	$P \leq .10$
July 31	0	20	96	0	32	112	$P > .10$
				Lake 650			
July 14	0	20	88	0	0	24	$P \leq .001$
Aug. 18	8	20	432	0	0	56	$P \leq .001$

* Moveable Exclosure - Ungrazed for ca. 30 days.

Appendix 4-7. Median Number of Seed Heads (#/m^2) in Microplots* Artificially Grazed at Different Frequencies** in 1985 Exclosure Throughout the 1986 Growing Season.

Date of Clips		Median Number of Seed Heads						Probability
		Clip 1			Clip 2			
Clip 1	Clip 2	Min.	Median	Max.	Min.	Median	Max.	
		Calais Lake East						
June 9 July 9 July 22 Aug. 21	Aug. 21	0	8	24	0	74	400	P≤.05
July 1 July 29 Aug. 21	Aug. 21	8	20	84	0	74	400	P>.10
July 22 Aug. 21	Aug. 21	24	72	160	0	74	400	P>.10
		Calais Lake West						
June 14 July 9 July 26	July 26	0	4	56	64	166	424	P≤.001
July 5 July 26	July 26	4	38	168	64	166	424	P>.10
		Lake 690						
June 12 July 10 Aug. 9	Aug. 9	0	0	0	0	6	32	P≤.05
July 10 Aug. 9	Aug. 9	0	2	36	0	6	32	P>.10
		Dieppe Lake						
June 26 July 20 Aug. 17	Aug. 17	0	0	72	0	20	256	P>.10
July 20 Aug. 17	Aug. 17	0	20	60	0	20	256	P>.10
		Lake 650						
June 17 July 14 Aug. 13	Aug. 13	40	308	672	36	382	792	P>.10
July 14 Aug. 13	Aug. 13	0	42	384	36	382	792	P≤.05

* Microplots located in permanent exclosure established in September 1985

** Dates beneath "clip1" and "clip2" columns refer to days when microplots were (re)clipped.

Appendix 4-8. Median Number of Seed Heads (g/m^2) in Microplots* Artificially Grazed at Different Times** in May 1987 Exclosure During the 1987 Growing Season.

Date of Clips		Median Number of Seed Heads						Probability
Clip 1	Clip 2	Clip 1			Clip 2			
		Min.	Median	Max.	Min.	Median	Max.	
		Calais Lake East						
June 5								
Aug. 21	Aug. 21	0	0	24	0	8	152	P≤.10
July 5								
Aug. 21	Aug. 21	0	0	60	0	8	152	P>.10
July 30								
Aug. 22	Aug. 21	0	4	24	0	8	152	P>.10
		Lake 650						
June 14								
Aug. 12	Aug. 18	0	52	220	12	60	356	P>.10
July 12								
Aug. 12	Aug. 18	0	4	60	12	60	356	P≤.001

* Microplots are located inside of permanent exclosure established in May 1987.

** See footnote Appendix 4-7.

Appendix 4-9. Median Number of Seed Heads (g/m^2) in Plots* Artificially Grazed at Different Times in Sept. 1985 Exclosure During the 1987 Growing Season.

Date of Clips		Median Number of Seed Heads						Probability
Clip 1	Clip 2	Clip 1			Clip 2			
		Min.	Median	Max.	Min.	Median	Max.	
		Calais Lake East						
June 4 Aug. 21	Aug. 21	0	0	32	0	48	96	P≤.01
July 3 Aug. 22	Aug. 21	0	1	56	0	48	96	P≤.05
July 29 Aug. 22	Aug. 21	0	32	112	0	48	96	P>.10
		Lake 650						
June 14 Aug. 12	Aug. 8	0	0	0	0	0	0	P>.10
July 10 Aug. 12	Aug. 8	0	0	4	0	0	0	P>.10

*Plots are located inside permanent exclosure established September 1985.