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How do plant communities respond to an erupting bison *Bison bison athabascae* population?

Nicholas C. Larter

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Two distinct subpopulations of wood bison *Bison bison athabascae* inhabit the Mackenzie Bison Sanctuary and adjacent areas: the ML subpopulation which is increasing and inhabits the periphery of the bison range, and the MBS subpopulation which is stabilizing and inhabits the core area of the bison range. This system provided the unique opportunity to examine how the plant community responded to an erupting, indigenous herbivore population. The standing crop of sedges and grasses in willow savanna habitats located in the core area of the range (MBS) was consistently lower than that of willow savannas located at the periphery (ML). The difference in standing crop between areas appears to be a direct result of different grazing pressures between the two areas. Net primary production was similar between MBS and ML indicating that the vegetation in MBS showed at least some partial compensation in response to grazing. The species composition of willow savannas differed between areas. Willow savannas located in MBS showed an increase in more unpalatable or less preferred species compared to willow savannas located in ML. Forages were of similar quality between the areas.

Key words: bison, grazing, Northwest Territories, plant community dynamics

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Few studies have documented the plant community dynamics associated with an ungulate eruptive oscillation. It has often been implied that overgrazing is associated with the stabilization of the herbivore population, and consequently plant biomass is lower when the herbivore population stabilizes than when it was increasing (Holloway 1950, Riney 1964, Mech 1966). Available forage (as distinct from total plant biomass) was not measured in these papers. Where data on plant community dynamics were available, total plant biomass decreased and/or the presence of unpalatable species increased (Klein 1968, Caughley 1970, Kightley & Smith 1976, Jarman & Johnson 1977, Leader-Williams 1980). However, all these studies examined either populations of animals liberated onto islands with little historic grazing pressure, or those of exotic species introduced into a new habitat. It is possible that the observed changes in plant biomass and species composition occurred because the plants were not evolutionarily adapted to such grazing. Do such changes occur in plant communities that have evolved in the presence of indigenous grazers? So far data on plant communities during eruptions of indigenous grazers in their natural habitats are lacking to answer this question. In this paper I examine such a situation.

Large grazing animals can affect vegetation in a variety of ways, from altering species composition to affecting productivity and nutritional quality. The degree to which changes in the plant community occur seems closely related to the intensity of grazing pressure (Botkin, Mellio & Wu 1981, Lacey & van Poollen 1981, McNaughton 1983, 1985, Belsky 1986, Day & Detling 1990, Holland, Parton, Detling & Coppock 1992).

In interactive plant-herbivore systems, herbivores influence the amount of food to subsequent generations (Monro 1967). Caughley (1976) further subdivided interactive systems into interferential and laissez-faire systems. The key distinction between them is whether or not herbivores interfered with each other's search for food. In laissez-faire systems herbivores do not interfere with each other. Non-territorial ungulates are an example of this kind of grazing behaviour.

The Mackenzie wood bison *Bison bison athabascae* population is undergoing an eruptive increase following its liberation in 1963 (Gates & Larter 1990). From an initial 18 animals in 1963, the population increased in a sigmoidal fashion peaking at ca 2,400 animals in 1989. The 1992 estimate was ca 2,000 animals. The Mink Lake (ML) subpopulation, representing the leading front of the population, has shown a continual increase over the last three surveys (1987, 1989, and 1992), whereas the Mackenzie Bison Sanctuary (MBS) subpopulation has stabilized (Larter, Sinclair & Gates 1993, Larter 1994). Therefore, the plant communities located in MBS and ML should reflect the impact of the different grazing pressures exerted on them.

I predicted from previous studies that as the bison population stabilizes, plant species composition would change with unpalatable species becoming dominant, and the standing crop of forage would decrease as more of the initially total available plant biomass was cropped. This paper compares forage quantity, species composition, and forage quality of dry and wet meadows subjected to these different grazing pressures.

Methods

Study area

The Mackenzie wood bison inhabits an area exceeding 9,000 km², which includes the Bison Sanctuary (MBS) and adjacent areas located on the western side of Great Slave Lake (61°30'N, 117°00'W) in the Northwest Territories (Fig. 1). It is located in the Upper Mackenzie Section of the Boreal Forest Region (Rowe 1972) in the emerged bed of a once vast glacial lake.

The undulating topography supports largely forested habitats which include coniferous forest, dominated by black spruce *Picea mariana*, white spruce *P. glauca*, jack pine *Pinus banksiana*, and larch *Larix laricina*, and mixed deciduous-coniferous forest, dominated by white spruce, aspen *Populus tremuloides*, and balsam poplar *P. balsamifera*. Birch bog dominated by shrub birch *Betula glandulosa* is found in open, poorly drained areas of the forest. Shallow lakebeds originating from the scouring action of glaciers are widely dispersed throughout the area. These lakes are gradually filling in with sedges and grasses, while woody plants, notably willows *Salix* spp., are invading the lake margins. Wet sedge meadows (WM) were

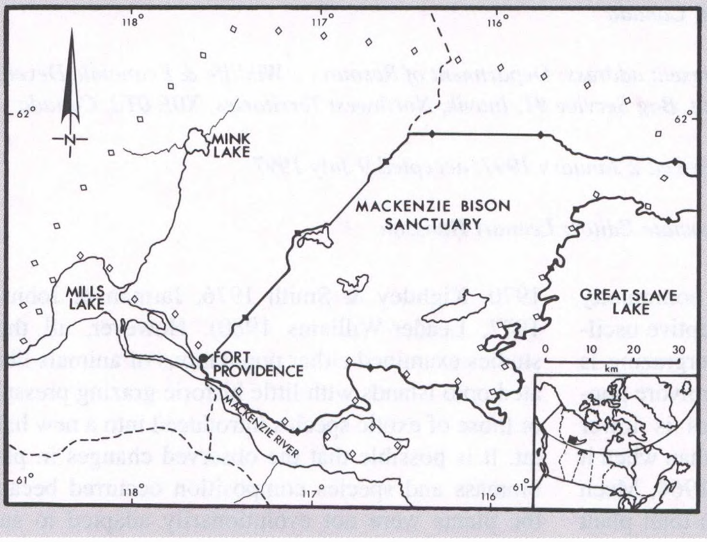

Figure 1. The study area, including the Mackenzie Bison Sanctuary and the areas on the western side of Great Slave Lake, Northwest Territories, Canada. The range of the bison population is indicated by the open diamonds. The area marked by solid diamonds is the Mackenzie Bison Sanctuary.

found where there was year-round standing water. They contained high biomass stands of sedge, dominated by *Carex atherodes* and *C. aquatilis*. Willow savannas (DM) were located in more mesic areas often bordering WM. Grass-sedge associations consisting of *Calamagrostis* spp., *Agropyron trachycaulum*, and *Carex atherodes* dominated the willow savanna plant community. *Hordeum jubatum*, *Phalaris arundinacea*, *Agrostis scabra*, and *C. aquatilis* were also present. Willow represented only a minor portion of the ground cover. DM and WM provide most of the forage used by bison, but represent <6% of the study area (Larter & Gates 1991a, Matthews 1991). Sedges, particularly *C. atherodes*, are a preferred and important forage for bison throughout the year. Grasses are less preferred tending to be utilized only during snow free periods (Larter 1988, Larter & Gates 1991a, 1991b). *P. arundinacea* is a highly unpalatable and avoided species (Audette, Vijayanagar & Bolan 1970, Hagman, Marten & Hovin 1975, Larter 1988).

Snow cover generally lasts from November to April. Snow depths show annual variability. By late winter (mid-March) accumulations of 40-65 cm can be found in various habitats (Larter & Gates 1991a).

Forage quantity

At the start of the 1990 growing season, two permanent line transects 200 m long were established in WM in ML and two in MBS. Concurrently, two permanent line transects were established in DM at ML (each 500 m long) and three in DM at MBS (300 m, 300 m, 225 m long, respectively). On these transects, 10 0.25 m^2 plots were randomly located, 5 plots/transect for WM in ML and MBS, 5 plots/transect for DM in ML, and 4, 4, and 2 plots/transect, respectively, for DM in MBS. All forage was clipped at a height of 3 cm above ground to represent forage available to grazing bison (Larter 1988). To estimate forage standing crop, 10 different randomly chosen plots were clipped at each of four times in 1990: 1) at the start of the growing season, early June, 2) at the peak of the growing season, mid-July, 3) at the middle of plant senescence, mid-August, and 4) at peak senescence before snow cover, mid-September (Larter 1988). Forage was dried at 60°C for 12 hours and subsequently weighed on an electronic balance.

Grazing effects in willow savannas

During July 1991, five exclosures were erected in DM in each of ML and MBS. Each exclosure consisted of a 2.3 m × 1.7 m piece of 5 cm × 5 cm chain-link fencing. Once pegged into the ground it resulted in a domed exclosure of approximately 1.75 m^2. At the time these were erected, two 0.5 m × 0.5 m plots were clipped outside each exclosure, the position being 1 m from a randomly chosen corner. At the end of the growing season two, 0.25 m^2 plots were clipped inside the excluded area and two 0.25 m^2 plots were clipped 1 m from the corner of the exclosure that had not been previously clipped. Because grazing of WM during summer is rare (Larter 1988, Larter & Gates 1991a, 1991b), grazing effects in WM were not measured.

Forage composition of meadows

A measure of forage composition of both DM and WM was determined during the 1990 growing season using two methods, presence/absence measures recorded from the clip plots used to estimate forage quantity, and by the point-intercept method (Kershaw 1973). For the presence/absence measure all plots that were clipped in DM and WM over the course of the growing season were pooled. The number of times a forage occurred in a plot was tallied out of a possible 40 plots per site (ML and MBS). The forages recorded were: slough sedge *Carex atherodes*, water sedge *C. aquatilis*, grasses *Calamagrostis* spp., *Agropyron trachycaulum*, *Hordeum jubatum*, *Agrostis scabra*, and *Elymus innovatus*, forbs (non-woody dicotyledonous plants), and reed canarygrass *Phalaris arundinacea*. Data were reported as proportions. I used the proportion test (Zar 1984) to compare proportions between area.

For the point intercept method, a 1-m stick was placed perpendicularly to the transect at the location of the randomly placed plots used for the forage quantity estimate. At each of these 10 locations a nail, representing a point, was placed into the meadow substrate at 10 cm intervals along the stick. All forage plants that were intercepted by the nail as it was placed into the substrate were recorded. The same forages were recorded as described above. Data were pooled across the four sample times and recorded as a proportion of the number of point intercepts/400. I used the proportion test (Zar 1984) to compare proportions between area.

Forage quality - snow free season

Forage samples were gathered at the four times in 1989 and 1990 described above. Slough sedge, water sedge, grass, and willow were the forage types sampled. One composite sample of each forage type was collected from DM at ML and MBS. Only sedges were collected from WM in each area because grass and willows were absent. Composite samples of sedge and grass, respectively, were collected as follows. Numerous individual plants (constituting a minimum 35 g ground dry weight sample), were clipped at random from areas directly adjacent to permanently marked line transects (two transects per habitat per area except for three transects in DM at MBS). Current year's growth was clipped at 3 cm above ground level to represent forage available to grazing bison (Larter 1988). Composite willow samples were collected in a similar fashion. Current annual growth was clipped, with accompanying leaves. Each sample was dried at approximately 60°C in a propane oven for 12 hours, and ground in a cyclone mill through a 1-mm screen. A ≥1 g subsample of the ground forage described above was used for each of the forage quality analyses. Samples were analyzed for their fibre, lignin, nitrogen, carbon, aluminum, magnesium, potassium, manganese, chloride, and calcium content.

Forage quality - snow season

Snow season forage quality samples were collected during winter 1991-92. Different abiotic conditions associated with the growing season may profoundly affect forage quality on a yearly basis (Bell 1982, East 1984, Boutton, Tieszen & Imbamba 1988, Bø & Hjeljord 1991). This would be reflected in the quality of forage at the start of the snow season. I used mid-August 1991 samples as a reference for the rest of the winter samples because mid-September samples were unavailable. Forage samples were collected in mid-August, November, mid-February, and early April of 1991-92. Samples were collected as described above (snow free season). Because winter diet is almost exclusively sedge (Larter 1988), only slough sedge and water sedge were collected. Samples were prepared as above. These samples were analyzed for fibre, nitrogen, and carbon content only.

Forage quality analyses

Forage fibre content was determined by the *in vitro* acid-pepsin digestibility technique following Tilley & Terry (1963) and Spalinger (1980). Larter (1992) found this simple method gave an index of forage quality comparable to that of the more complicated acid-detergent fibre analyses (van Soest 1967). Mean percent digested, from four runs of each forage sample, were used. High digestibility values indicate low fibre content and vice versa (Larter 1992).

Percent lignin content was determined by the acid-detergent lignin technique (van Soest 1963). Lignin analysis was limited to slough sedge and willow. Each sample was run through this technique once. Duplicate samples (N = 29) were run to determine precision of the measurement which was 92.4%.

Nitrogen content was determined by the micro-Kjeldahl technique (Nelson & Sommers 1973). Each sample was run through this technique once. Duplicate samples (N = 63) were run to determine precision of the measurement which was 98.3%. Percent crude protein was determined by the standard conversion (6.25 × percent nitrogen).

Carbon content was determined using an induction furnace carbon analyzer (LECO). A 50-mg sample was heated to 3,000°C in an induction furnace which liberated CO_2 from the combustion. Measurement of the liberated CO_2 provided an estimate of percent carbon of the forage sample. Each sample was run through this technique once. Duplicate samples (N = 9) were run to determine the precision of the measurement which was 98.6%. The carbon/nitrogen ratio (C/N) was determined by dividing percent carbon by percent nitrogen.

Aluminum, magnesium, potassium, manganese, chloride, and calcium content was determined using instrumental neutron activation analysis (INAA) (Bortolotti & Barlow 1985). Briefly, the dried, ground samples were irradiated by a neutron flux, the gamma rays resulting from their artificially produced radio-isotopes were counted using a gamma ray spectrometer, and the gamma ray peaks converted into chemical concentrations. Results were expressed in parts per million (ppm).

Statistical analysis of quality measures

I used ANOVA to determine which factors, if any, explained significant variability in mean digestibility, lignin, nitrogen, carbon, aluminum, magnesium, potassium, manganese, chloride, and calcium content, and C/N ratio. There were a maximum of five factors used: forage type, sampling time in the growing season, meadow type (DM or WM), meadow location (MBS or ML), and year. Data were lumped across factors that did not explain significant ($P > 0.05$) variability and reanalyzed with a reduced model ANOVA. Data on percent digested were normalized using a square root transformation prior to ANOVA.

Results

Forage quantity

There were significant differences in standing crop of different meadow communities between areas (Fig. 2). DM in MBS had lower standing crop than those in ML at all sampling times except at the start and end of the growing season. These differences were significant in both mid-July (one-tailed, t = -7.19, $P < 0.0001$) and mid-August (one-tailed, t = -4.16, $P < 0.001$) (see Fig. 2a). WM in MBS and ML had similar standing crop at all times regardless of location except for mid-August (see Fig. 2b), when available standing crop was significantly lower in ML (one-tailed, t = 4.95, $P < 0.001$).

Grazing effects in willow savannas

Standing crop in grazed areas of DM showed no yearly variation in either MBS or ML (Fig. 3). Areas excluded from grazing in MBS had a standing crop three times greater (one-tailed, t = -3.24, $P < 0.004$) than that in areas where grazers were present (see Fig. 3a). In contrast, areas excluded from grazing in ML showed only a slight, and non-significant increase (one-tailed, t = -0.66, P = 0.26) in standing crop from areas where grazers were present (see Fig. 3b). Excluded areas in MBS had an August standing crop similar to that found in both the grazed (two-tailed, t = -0.58, P = 0.57) and ungrazed (two-tailed, t = -0.96, P = 0.35) areas in ML.

Forage composition of meadows

Using presence/absence data, DM in MBS had significantly more grass (Z = 1.98, $P < 0.025$), forbs (Z = 5.82, $P < 0.0001$), and reed canarygrass (Z = 2.77, $P < 0.003$), and less slough (Z = 2.91, $P < 0.002$) and water sedge (Z = 2.22, $P < 0.014$) than DM in ML (Fig. 4). These differences were similar in point intercept data, but not all differences were significant (Z = 1.46, $P < 0.075$ for slough sedge and Z = 1.00, $P < 0.16$ for reed canarygrass). WM had similar composi-

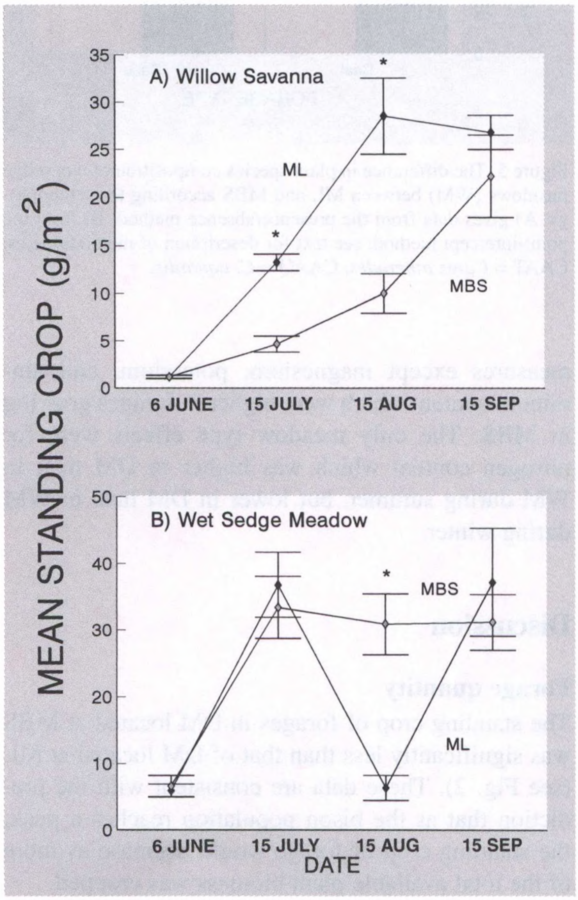

Figure 2. Mean (±SE) standing crop (g/m² dry weight) on the two locations, Mink Lake (ML) and Mackenzie Bison Sanctuary (MBS), for A) willow savannas (DM) and B) wet sedge meadows (WM). * indicates significant differences ($P < 0.05$) between the two areas.

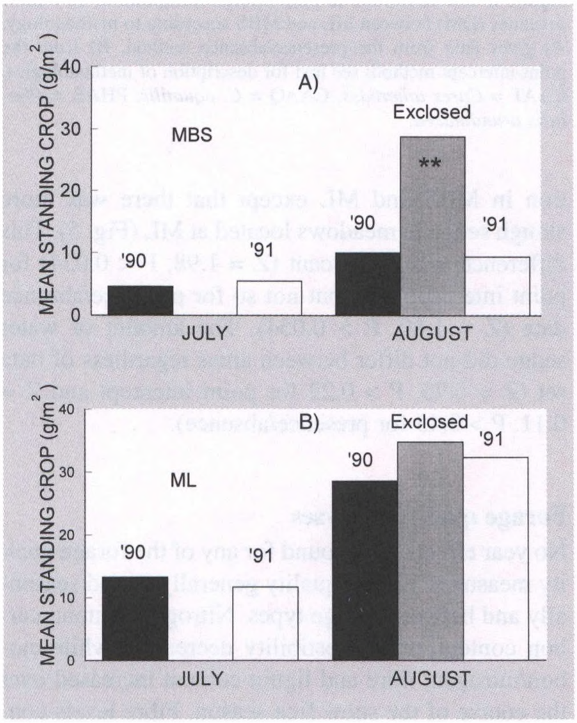

Figure 3. Comparison of the mean standing crop (g/m² dry weight) of areas where animals were either permitted to graze or excluded from grazing. Data from willow savannas (DM) in A) MBS, and B) ML. Exclosures were erected in July, 1991. ** indicates significant difference between grazed and excluded areas ($P < 0.01$).

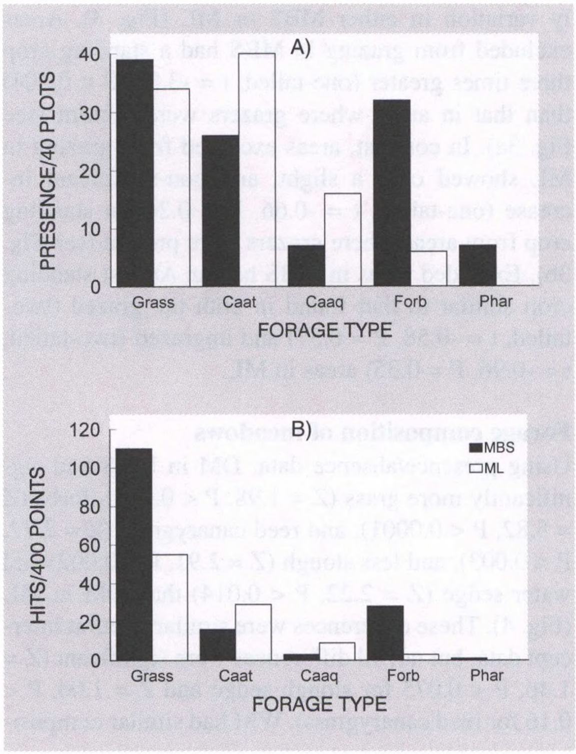

Figure 4. The difference in plant species composition of willow savannas (DM) between ML and MBS according to methodology. A) gives data from the presence/absence method, B) from the point-intercept method; see text for description of methodologies. CAAT = *Carex atherodes*, CAAQ = *C. aquatilis*, PHAR = *Phalaris arundinacea*.

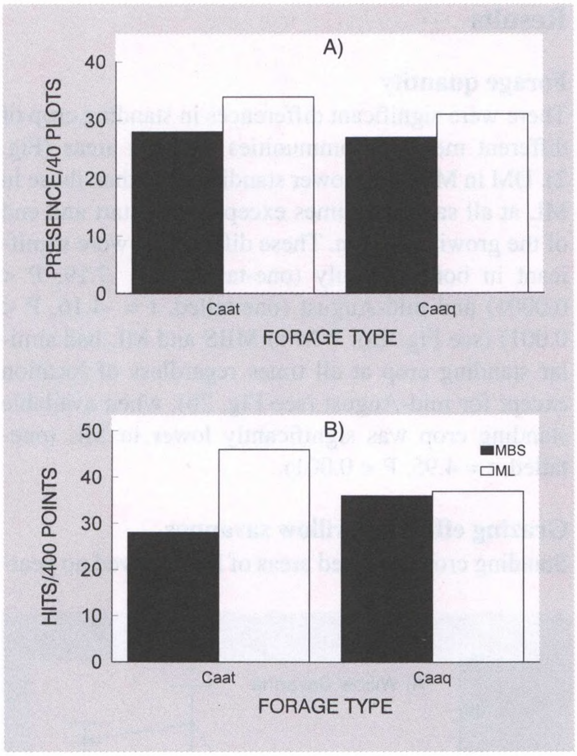

Figure 5. The difference in plant species composition of wet sedge meadows (WM) between ML and MBS according to methodology. A) gives data from the presence/absence method, B) from the point-intercept method; see text for description of methodologies. CAAT = *Carex atherodes*, CAAQ = *C. aquatilis*.

tion in MBS and ML except that there was more slough sedge in meadows located at ML (Fig. 5). This difference was significant (Z = 1.98, P < 0.024) for point intercept data, but not so for presence/absence data (Z = 1.60, P > 0.054). The amount of water sedge did not differ between areas regardless of data set (Z = 0.75, P > 0.22 for point intercept and Z = 0.11, P > 0.45 for presence/absence).

Forage quality analyses

No year effects were found for any of the forage quality measures. Forage quality generally varied seasonally and between forage types. Nitrogen content, carbon content, and digestibility decreased, while carbon/nitrogen, fibre and lignin content increased over the course of the snow free season. Fibre levels continued to rise during the snow season, peaking in midwinter (February), while nitrogen content continued its decline through late-winter (early April). There were no meadow location effects for most quality measures except magnesium, potassium, and aluminum content which were higher in forages growing in MBS. The only meadow type effects were for nitrogen content which was higher in DM than in WM during summer, but lower in DM than in WM during winter.

Discussion

Forage quantity

The standing crop of forages in DM located at MBS was significantly less than that of DM located at ML (see Fig. 2). These data are consistent with the prediction that as the bison population reaches a peak, the standing crop of forage would decrease as more of the total available plant biomass was cropped.

There were no significant differences in WM standing crop between areas except for the August sampling time (see Fig. 2). This difference likely resulted from unusually heavy rainfall on the Horn Plateau during early August. Water levels around ML rose drastically (1.5 m) during early August flooding much of the area adjacent to Mink Lake, but had subsided by September. Forage availability in WM in ML was directly affected by the change in water levels (see Fig. 2), not by grazing. Because WM were essentially ungrazed during the snow free season (Larter & Gates 1991a, 1991b), one would not expect to see differences in standing crop between area during this season. During winter, WM were heavily grazed (Larter & Gates 1991a, 1991b). Therefore one would predict differences between area in standing crop of WM during the snow season to be similar to those found in DM during the snow free season. Although standing crop of WM was not measured, anecdotal observations during April indicated that WM in the MBS were more heavily utilized, and had a much lower standing crop of sedge material than WM in ML.

Grazing effects in willow savannas

Standing crop during early to mid-senescence (August) was lower in MBS than in ML, yet by peak senescence (September) there was no significant difference in standing crop between areas (see Fig. 2). Standing crop in ML remained constant between mid and peak senescence. Knapp & Seastedt (1986) describe this as vegetation ‘stagnation' in lightly grazed areas like ML. In contrast, in MBS with heavy grazing, the standing crop increased between mid and peak senescence. These data imply that primary productivity was increasing in response to grazing. The exclosure experiment also indicates that vegetation in DM was responding by at least partially or possibly exactly compensating for forage removed by grazing (*sensu* Belsky 1986) at MBS but not at ML. Because exclosures were erected one month into the growing season, the vegetation had already been subjected to some removal by grazing. Yet after only six weeks of exclusion from grazing, the standing crop of vegetation in MBS had completely recovered to the levels found in grazed and excluded areas in the less heavily grazed DM of ML (see Fig. 3). Therefore, even though the standing crop was generally lower in heavily grazed areas, the effect of high grazing pressures on the vegetation in DM's was to stimulate primary productivity to levels that showed, at worst, partial compensation for the loss due to grazing. Because I did not measure primary productivity directly the extent of compensation cannot be measured directly. Partial compensation is occurring, but one can only speculate about exact compensation. These data are consistent with the findings of Cargill & Jefferies (1984), Frank & McNaughton (1993) and McNaughton (1976, 1979a, 1979b, 1985) in other grassland grazing systems.

Caughley's (1976) laissez-faire interactive system assumes a fixed rate of increase of plants regardless of grazing intensity and predicts the vegetation and herbivore population dynamics to follow the classic four stages of an eruptive oscillation described by Riney (1964). These stages are: 1) an initial increase in population size when resources are abundant, 2) a levelling off in animal numbers in response to decreasing forage availability, 3) a decline in animal numbers because the population has increased beyond the carrying capacity of the environment, and 4) a phase of relative stability with population density remaining lower than peak density because the carrying capacity of the environment has been reduced by the impact of peak population density. The population dynamics of the bison eruption have followed the four stage scenario to some extent. The MBS subpopulation is stabilizing or indicating the start of a decline while the ML subpopulation continues to increase (Larter et al. 1993, Larter 1994). Although there was heavy use of DM in MBS there was no evidence of overgrazing and severe mortality of bison (Larter 1994). Possibly the lack of overgrazing and severe herbivore mortality predicted in the four stage scenario is related to partial compensation and increased primary productivity of vegetation in DM located in MBS. This vegetation system has historically been grazed. Most systems supporting the model of overgrazing and severe herbivore mortality were based upon either populations of animals liberated onto islands with little historic grazing pressure (i.e. Klein 1968), or those of exotic species introduced into a new habitat (i.e. Caughley 1970). It is possible that the plants associated with these systems were not evolutionarily adapted to such grazing and could not respond to increased grazing removal with increased primary productivity and partial compensation.

Forage composition of meadows

There was a higher occurrence of unpalatable species in MBS than in ML, a finding consistent with the prediction that as the bison population reaches a peak, plant species composition would change with unpalatable species becoming dominant.

DM in MBS had significantly more reed canarygrass, forb, and grass, and significantly less sedge (both *C. atherodes* and *C. aquatilis*) than DM in ML. Reed canarygrass is a highly unpalatable species which increases its substantial alkaloid content with foliage removal (Woods & Clarke 1971). Alkaloids have been negatively correlated with palatability when offered to sheep and cattle (Marten, Jordan & Hovin 1976). It also has a high silica content (van Soest 1967). Silica has many detrimental effects to mammals, ranging from increased tooth wear to silica urolithiasis (Baker, Jones & Wardrop 1959, Bailey 1981, van Soest 1982). Wood bison avoid foraging on this species (Larter 1988).

Forbs could be a valuable food source (Belovsky 1986, Renecker & Hudson 1988), but are rarely grazed by wood bison (Larter 1988, Larter & Gates 1991a, 1991b). Smith (1990) found that the majority of forb species present were of the prostrate growth form. Wood bison grazing removed the competitively superior erect graminoids leaving the prostrate forbs which could escape grazing below 3 cm height (pers. obs.). Forbs were consumed if they reached a sufficient height (Smith 1990, pers. obs.), but patches of DM with higher densities of forb growth were grazed less frequently than those with lower forb densities (Smith 1990). DM in MBS had significantly higher forb densities than those in ML.

Grass is generally of equal or superior nutritional quality to sedge (Larter 1988, Larter & Gates 1991a). However, grass tussocks, unlike sedge plants, are a mixture of live green and dead material which bison, with their large mouths, cannot sort (Hanley 1982). Because of this unsorted mix of live and dead material, grass that is eaten by bison is of lower quality than similar forage of sedge. DM in MBS have a higher grass component than those in ML.

Sedges, in particular *C. atherodes*, appear to be a preferred and important forage for bison throughout the year (Reynolds, Hansen & Peden 1978, Hawley, Peden, Reynolds & Stricklin 1981, Larter 1988, Larter & Gates 1991a, 1991b). DM in ML had more sedge, both *C. atherodes* and *C. aquatilis*, than those in MBS.

Although there was more of the preferred sedge, *C. atherodes*, in WM in ML than in MBS, this difference was not significant in either data set. WM are primary winter foraging areas, rarely used for summer foraging (Larter 1988, Larter & Gates 1991a, 1991b). Because foraging does not occur during the growing season, removal of one species, *C. atherodes*, during winter will not provide a competitive advantage to the other species, *C. aquatilis*. This situation, therefore differs from that where forbs benefit from the constant grazing of graminoids during the growing season. Possibly winter grazing has a positive effect on sedges by removing the dead leaf matter from the previous summer's growth, so that with the onset of spring there is more light and possibly heat available for the young growing shoots. The carbon/nitrogen ratio of forages in WM is higher than for forages in DM, indicating that WM are more nutrient limited, and this could reduce the rate of change in sedge species composition. Therefore, the differences in occurrence of *C. atherodes* may not yet be statistically detectable.

Forage quality analyses

Generally, there were no major differences in forage quality between the two areas. At any given time the quality of a forage type was similar whether growing in MBS or ML. The increased content of three positively charged elements in forages growing in MBS may be a direct result of a more calcareous, lacustrine substrate. Higher contents of these cations may have affected forage quality, but any noticeable shift in the use of these forages was not evident when comparing previous diet data (Larter 1988, Larter & Gates 1991a) with current diet data (Larter 1994).

Crude protein proportions in the forage were highest at the start of the growing season and declined throughout the year. The amount of crude protein was highest in mid-July (Larter & Gates 1991a). At this time crude protein levels were lower than at the start of the growing season, but the quantity of forage was higher. Wood bison in ML may have had access to forage of similar crude protein content to forages in the MBS, but the total amount of crude protein was probably much greater in ML because of the higher standing crop in DM.

Lower nitrogen levels in DM than in WM during winter likely occur because sedge in wet sedge meadows still have green material present in the vicinity of the forage/water interface when these meadows freeze up. Sedge in DM is completely senesced and thoroughly weathered prior to freeze up.

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