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Impacts of Ungulates on Rangeland Dynamics in Aspen-Boreal Ecosystems of Alberta

by

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ABSTRACT

The ability of rangelands to sustain livestock and wild herbivores is primarily a function of amount of forage, forage quality, and the efficiency by which the forage is harvested. A series of studies were conducted to assess the impact of these factors on rangeland dynamics in Aspen-Boreal ecosystems of Alberta.

The effects of defoliation time, frequency, and intensity on herbage yield and quality were determined by clipping trials. Plants were defoliated in early May, June or July; at 2-, 4- or 6-week intervals; and at 15, 10 or 5 cm from the soil surface. Herbage removal was greatest when initially defoliated in May. Greatest accumulated herbage yields were obtained at 10-cm defoliation height. Less frequent defoliation produced the greatest herbage yield. Average crude protein yield for forb and grass ranged from 1.5 to 3 g m^{-2}, and 6 to 10 g m^{-2}, respectively.

In a greenhouse experiment, aboveground phytomass decreased with increased water stress. Defoliation decreased both aboveground and belowground phytomass compared to a non-defoliated control. Root:shoot ratio increased with increasing water stress, defoliation intensity and frequency.

Seasonal dynamics of ungrazed pastures were determined by clipping and weighing green and dry vegetation and litter pools. Green herbage, standing dead and litter increased from spring to summer and decreased from summer to fall. Average growing conditions resulted in a peak phytomass of 350 g m^{-2}, and varied by year.

Investigation of the effects of intensive short-duration (SDG) and continuous (CG) grazing by wapiti (*Cervus elaphus*) on soil compaction and herbage yield indicated

that the SDG did not show any advantage over CG in improving soil physical characteristics and herbage production.

A preliminary computer simulation model of *Bromus-Poa* pastures grazed by farmed wildlife (specifically wapiti and bison) indicated that pasture condition benefited slightly from rotational grazing at high stocking densities but animal performance declined compared to continuous grazing. Proper use of the model, when the factors which influence bioeconomic efficiency are well-defined, will hopefully lead to a simple practical pasture simulator that could be used to evaluate continuous or rotational mixed species grazing systems in terms of pasture and animal productivity.

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CHAPTER 1

INTRODUCTION

The Aspen Parkland and Low Boreal Mixedwood ecoregions of western Canada cut across central Alberta, and are important areas for agricultural land use, especially livestock and wildlife production (Rowe 1972, Baron and Knowles 1984, Strong 1992). These areas contain forage resources suited to supporting beef enterprises, diversified livestock and free-ranging native ungulates (Telfer and Scotter 1975, Baron and Knowles 1984). Smooth brome (*Bromus inermis* Leyss.) and Kentucky bluegrass (*Poa pratensis* L.) are dominant cool-season grasses that are important forage resources in these ecosystems (Looman 1976). About 86% of western Canada's hay production is found in the Aspen Parkland (McCartney 1993). Similarly, 66% of western Canada's cattle herd is found in the Black and Gray-wooded soil zones of the Aspen Parkland (Coxworth 1992). The determination of forage quantity, forage and diet quality, and optimal stocking rates of grazing animals on these ranges are all important to the sustained ecological management and economic viability of this resource base.

Livestock/Wildlife Production

There is an inverse relationship between animal production per individual and production per unit land area with increasing grazing intensity. This relationship is the fundamental production response within all grazed systems (Briske and Heitschmidt 1991). This response originates from the combined effects of (i) decreasing efficiency of solar energy capture, (ii) increasing efficiency of forage harvest, and (iii) decreasing conversion efficiency (i.e., the efficeincy with which ingested energy is converted into animal products) as grazing intensity increases. Primary production decreases because of a reduction in the availability of leaf to intercept solar energy. Harvest efficiency increases as an increasing number of animals per unit land area consume plant material before it senesces and is transferred to litter. Conversion efficiency decreases as forage intake restrictions per individual animal limit nutrient and energy availability for growth (Van Soest 1982). The end result is that production per animal decreases as grazing intensity increases while production per unit land area increases. Animal production per unit area continues to increase with grazing intensity because it is dependent upon both individual animal performance and the total number of animals. Eventually, production per unit area decreases rapidly with increasing grazing intensity because increasing animal numbers are no longer able to compensate for the limited production per animal. Therefore, the grazing intensity that maximizes sustainable animal production per unit area is that which optimizes the processes of solar energy capture, harvest efficiency, and conversion efficiency within a system (Briske and Heitschmidt 1991).

Grazing Management

The primary objective of most grazing operations is to maximize livestock and/or wildlife production per unit area of rangeland while maintaining a sustained forage resource (Heitschmidt and Walker 1983). Rangeland productivity, relative to salable livestock products, is primarily a function of three factors: (a) amount of forage produced; (b) forage quality; and (c) the efficiency at which forage is harvested (Heitschmidt et al. 1982).

Grazing management practices are centered around the manipulation of these factors. For example, recommendations for increasing the quantity and quality of forage in the Aspen Parkland region (Tremblay 1995) include seeding more productive species such as alfalfa - in spite of the risk of bloat (Beacom 1991), and fertilization, which has only a 1 or 2 year benefit (Nuttall et al. 1991).

Grazing management also involves control over the timing, frequency, duration and selectivity of grazing activities. Information on the relative yield of grasses as plants develop following dormancy is useful to optimize total grazing potential and the quality of hay production. In some plants, defoliation has reduced herbage yield (Reed and Dwyer 1971, Buwai and Trlica 1977), decreased root phytomass (Ryle and Powell 1975, Detling et al. 1979, Richards 1984, Zhang and Romo 1994) and altered root:shoot ratios (Richards 1984, Christian and Wilson 1999). Plants may also respond to grazing or clipping by stimulating aboveground plant growth. This response has been observed in some species (e.g. Robbinson et al. 1952, McNaughton 1979, 1983). Such a stimulation is often referred to as overcompensation (Belsky 1986), which means that the accumulated production of defoliated plants exceeds the production of undefoliated plants. Defoliation may enhance growth through several interrelated mechanisms (McNaughton 1983) such as, increasing photosynthetic rate of the remaining tissue (Caldwell et al. 1981, Detling and Painter 1983, Wallace et al. 1984), changing the allocation pattern to a higher production of new leaf area (McNaughton and Chapin 1985), increasing nutrient uptake (Ruess 1984, McNaughton and Chapin 1985) and improving plant water use efficiency (Toft et al. 1987). Repeated defoliation can reduce total herbage phytomass as well (Reed and Dwyer 1971, Buwai and Trlica 1977, Zhang and Romo 1994). Frequent clipping has often resulted in reduced yield compared to less frequent harvests (e.g. Ethredge et al. 1973, Owensby et al. 1974).

Various parameters may be utilized to reflect forage quality. For example, low quality forage has been associated with reduced levels of crude protein, phosphorus, and dry matter digestibility, or increased levels of crude fiber and lignin (Streeter et al. 1968, Sims et al. 1971, Wallace et al. 1972). Herbage digestibility and crude protein concentration decrease, whereas fiber and lignin concentrations increase with maturation (Pritchard et al. 1963). Since herbage quality declines with advancing maturation (Cook and Harris 1968, Sims et al. 1971, Stoddart et al. 1975), any grazing management practice reducing or setting back plant development processes should increase the quality of forage available to the grazing animal (Heitschmidt et al. 1982).

Grazing Systems

Traditional methods of open range continuous grazing in the Aspen Parkland and Boreal regions are being increasingly replaced with higher intensity rotational grazing systems because of economic constraints, such as the availability and cost of land (Smith 1981). Nevertheless, some debate has occurred concerning the consistency of evidence for the value of rotational grazing (Cooke et al. 1965, Walton et al. 1981, Bailey et al. 1991, McCartney 1992). A key objective of grazing management is to optimize the efficiency of forage harvest by grazing livestock while allowing adequate rest for plants to recover following defoliation (McCollum et al. 1994). A grazing system should, therefore, provide the producer with profitable animal gains and the flexibility to adjust grazing to deal with variability in forage production and avoid reductions in pasture condition (Schellenberg et al. 1999).

Mismanagement of livestock, especially with high stocking rates, has caused severe degradation on much of the world's rangelands (Bari et al. 1993). Moderate stocking rates designed to use half the current year's forage production are generally accepted as proper grazing management (Stoddart et al. 1975).

Pasture Dynamics

The amount of herbage available to the grazing animal changes seasonally. Therefore, plant-herbivore dynamics on rangelands depend on pasture productivity and changes in phytomass with time, and the vegetation's responses to defoliation (Caughley 1976, 1982, Noy Meir 1975). Grazing may influence the dynamic interaction between plant growth rates and phytomass, as well as change the proportions of green herbage, standing dead, and fallen litter pools. Seasonal herbage production on pastures depends on the plant community type, local growing conditions and disturbance regime. Areas with a long history of heavy grazing are generally characterized by decreased annual production, increased losses of herbage over winter, and delayed spring growth (Willms et al. 1996).

Soil Water and Pasture Growth

Soil water on rangelands may be low due to low precipitation, poor infiltration, and/or high evapotranspiration (Naeth and Chanasyk 1995). Grazing or haying are common management practices that affect the productivity of pasture species. The effect of defoliation on the yield of these species may be explained by soil water content, because soil water availability generally limits growth in grasslands (Houston 1965, Anderson et al. 1970, Ogden and Loomis 1972). Williamson et al. (1989) stressed the need to understand the interactive role of soil water content and defoliation treatments as essential to understanding the relationship between grazing and forage production. Increases in the root:shoot ratio under drought have been reported for a number of crops (Malik et al. 1979, Turner and Begg 1978, Brar and Palazzo 1995). Earlier studies on prairie grasses were in general agreement that clipping of the shoots caused root reduction: e.g. Zhang and Romo (1994), Li and Redmann (1992) (*Agropyron dasystachyum*); Willms (1991) (*Festuca scabrella*); Smoliak et al. 1972 (*Stipa-Bouteloua*); Johnston (1961) (*Festuca spp.*); Harrison (1931) (*Bromus inermis*). Clipping or grazing can also change the distribution of roots in the soil by reducing the rooting depth and packing more roots in the soil surface (Willms 1991, Smoliak et al. 1972). Plant response to clipping or grazing often results in an increase in the root:shoot ratio (Dittmer 1973, Oesterheld and McNaughton 1988).

Trampling and Pasture Growth

Grazing animals may compact the soil (Knoll and Hopkins 1959, Lull 1959, McCarty and Mazurak 1976, Thurow et al. 1986). However, in some grazing studies there were no indications of compaction (Laycock and Conrad 1967, Skovlin et al. 1976, Gifford and Hawkins 1978, McGinty et al. 1979, Abdel-Magid et al. 1987). In Alberta, many fields are put into permanent perennial pasture for animal grazing and no cultivation practices are conducted after establishment, while others are planted to annual forages and grazed. Heavy stocking rates used in such grazing may lead to surface soil compaction (Mapfumo 1997). Soil pressures from animal hooves might be as much as 200 kPa, which is considerably greater than the pressure exerted on the soil surface by a tractor that ranges from 30 to 150 kPa (Proffitt et al. 1993).

The degree of compaction is affected by soil water content at the time of compaction (Gifford et al. 1977, Van Haveren 1983). Soil compaction often results from frequent traffic of heavy machinery particularly when the soil is wet (Thacker et al. 1994). In some rangelands, soil water in the Ah horizon decreases with increased grazing intensity (Johnston 1961, Johnston et al. 1971, Smoliak et al. 1972), whereas in others there is no effect (Lodge 1954). Reductions in soil water through grazing are attributed to altered rates of infiltration, combinations of soil compaction and sealing through animal trampling, reduced root channels through the soil, and reduced litter cover (Hagan and Peterson 1953, Hopkins 1954). Increases in soil water with removal of herbage through grazing is attributed to reduced evapotranspiration (Baker and Hunt 1961, Van Riper and Owen 1964).

Livestock trampling has both direct and indirect effects on vegetation and soils. The physical effects of animal hoof action include mechanical injury to or loss of vegetation as well as compaction of the soil surface. Goodloe (1969), Savory (1978), Savory and Parsons (1980), Savory (1983) and other proponents of rotational grazing systems have hypothesized that trampling hoof action of grazing animals under high animal density grazing might benefit soils and improve rangeland productivity in terms of livestock carrying capacity. However, research consistently indicates that the use of heavy stocking rates under rotational grazing show no significant soil improvement over continuously grazed pastures (Wood and Blackburn 1981, Blackburn 1984, Abdel-Magid et al. 1987, Heitschmidt et al. 1987, Dormaar et al. 1989, Naeth and Chanasyk 1995, Chanasyk and Naeth 1995). Researchers have repeatedly shown that as grazing intensity (e.g., stocking rates) is increased, the amount of standing herbage and litter cover decline and soil bulk density increases (Heitschmidt 1990).

Modeling of Pasture Growth and Use

Management of pastures systems for bioeconomic sustainability requires an understanding of many interacting factors. Computer simulation models have proven powerful tools for analyzing such complex interactions that characterize these systems. Several simulation models have been developed for evaluating pasture and beef cattle production systems. Some of the widely recognized models are: Texas A&M beef cattle simulation model (Sanders and Cartwright 1979, Cartwright and Doren 1986), Kentucky beef-forage model (Loewer et al. 1983, Lower and Smith 1986), the Cornell net carbohydrate and protein system (CNCPS), (Fox et al. 1995), and GRASSGRO (Cohen et al. 1995).

There is a large research database on factors affecting plant growth and quality, the growth of grazing animals, and other complex interactions that characterize grazing systems. Uncertainties due to weather, soil type, and many interactions at the farm level have always made the transfer of research results to the farmer more difficult. Computer simulation models have proven powerful tools for analyzing existing knowledge to predict the outcome of management strategies, and help the agricultural advisor/educator and the farmer make the best decisions for complex ecosystems (Cohen et al. 1995).

Range scientists in Australia and New Zealand have extensively studied pasture systems and developed grass growth models to understand pasture dynamics (Mothar et al. 1994). One of the widely recognized pasture simulation models in Australia is GrassGro (Donnelly et al. 1994). GrassGro is a Decision Support System for pasture and ruminant livestock production. It is capable of predicting from weather data the growth and composition of a pasture composed of one or more species of perennial and/or annual grasses, legumes and forbs. GrassGro also includes an animal biology model that predicts the consumption and assimilation of herbage by various classes of cattle and sheep and their subsequent production of weight gain, milk, wool and conceptus.

In the United States, crop modeling, particularly of grass growth, has received much attention in the last 30 years. Foremost among these models are the Texas A&M beef cattle simulation model (Sanders and Cartwright 1979, Sullivan et al. 1981, Bourden and Brinks 1987 a,b,c), the Cornell net carbohydrate and protein systems (CNCPS) (Fox et al. 1995), and the Kentucky beef-forage model (Loewer et al. 1983, Loewer and Smith 1986) developed at the University of Kentucky in the late 1970s. From the Kentucky beef-forage model, Parsch and Loewer (1995) developed GRAZE, a model for daily performance and interaction of other factors associated with beef-forage grazing systems. The plant component of the model reflects the relationships between plant growth and climate. The animal component of GRAZE describes animal growth, intake and response to environment. GRAZE is specific to beef cattle and does not include soil components to study the environmental impact of grazing. The dairy forage system model, DAFOSYM (Rotz et al. 1989) links forage quality and quantity from in-field production through harvest, storage, and feeding, and simulates animal performance based on the resulting feed supply. This approach is ideal for maximizing efficiency of pasture-based systems (Mohtar et al. 1997), but DAFOSYM currently does not include grazing as a harvest method, nor does it include crops other than alfalfa and corn. The comprehensive grazing system model, GRASIM (Mohtar et al. 1997) links the effects of climatic factors and pasture management on phytomass accumulation, nutrient flows, and animal intake for dairy cattle.

Knowledge about the effects of grazing on plant growth and quality, and animal intake exists in western Canada, but information specific to grass growth models is limited. Particularly relevant research is the GrassGro model for western Canadian pastures and rangelands (Cohen et al. 1995). Pasture parameter sets have been developed on two contrasting environments in Saskatchewan for 3 grass species: crested wheatgrass (*Agropyron cristatum*), smooth bromegrass (*Bromus inermis*) and Russian wild rye (*Psathyrostachys juncea*), but validation with field data has not been completed. Pang et al. (1996) completed simulation studies on the effects of cow size, milk production and calving season on the bioenergetic efficiency of beef production in Alberta. Most of the available models have been developed for beef cattle production systems. These models have proven immensely useful for management and planning. They also promise to be of even greater significance for wildlife production because of the great importance of range and pasture for wild ruminants, which are able to forage through snow and do not perform as well in feedlots. As a result, the impacts and responses to pasture use of wild ruminants are expected to be different than domestic livestock.

Objectives

This study had five main objectives:

(1) To investigate the effects of initial date of defoliation, defoliation intensity and frequency on season-long accumulated forage yield and quality of grassland herbage.

(2) To investigate the interactive role of soil moisture and defoliation treatments on herbage production.

(3) To describe seasonal changes in the live and dead phytomass of a grass community.

(4) To investigate the effects that grazing wapiti (*Cervus elaphus*) have on soil physical properties and to relate these to pasture production.

(5) To develop a preliminary rangeland dynamics model that captures the interaction between instantaneous initial growth rate (g) and vegetation phytomass (V), and could be

used to study the effects of climatic and edaphic factors as well as pasture management, on the production and quality of pastures and intake of farmed wildlife.

Research Strategy and Thesis Organization

The first, third and fourth objectives were accomplished using field studies, while the second was addressed in a greenhouse study and the last was programmed using Stella simulation software as a synthesis of the field and lab work. The model is used to explore the interaction between g and V and its application to grazing studies.

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CHAPTER 2

INFLUENCE OF DEFOLIATION REGIME ON BOREAL HAY MEADOW GRASSLAND YIELD AND QUALITY

INTRODUCTION

The Lower Boreal Mixedwood Ecoregion of Alberta represents a broad transition zone between the Aspen Parkland and Mid Boreal Mixedwood Ecoregion in the southern portion of the boreal forest (Strong 1992). Agriculture is a common land use, especially livestock and wildlife (e.g., diversified livestock production). This ecoregion has lower forage yields than the Aspen Parkland (Peters 1977), probably due to its cooler temperatures, decreased solar radiation associated with latitude, and frost damage (Strong 1992). To optimize productivity and profitability from limited land bases, traditional methods of open range continuous grazing are being replaced with grazing plans such as rotational, deferred, deferred rotational, high-intensity/low-frequency, and short-duration grazing. However, little information exists on the productivity and forage quality of the grasslands managed under these systems.

Current annual yields increase with seasonal growth towards the advancing reproductive cycle and are concomitant with decreases in protein and digestible contents, and increases in fiber concentrations (Sanderson and Wendin 1989, Kunelius et al. 1974, Pritchard et. al. 1963). Suleiman et al. (1999) reported an inverse relationship between crude protein and fiber concentration in prairie grasses in east-central Alberta until yields approached or reached maximum levels.

The timing, intensity, and frequency of defoliation interact in complex ways on production processes and affect herbage yield and quality in rangeland ecosystems (Oesterheld and McNaughton 1988, Heady and Child 1994, Zhang and Romo 1994). Mason and Lachance (1983) reported that total annual yields of timothy (*Phleum pratense L.*), tall fescue (*Festuca arundinacea* S.), reed canarygrass (*Phalaris arundinacea* L.) and Kentucky bluegrass (*Poa pratensis* L.) increased by delaying initial harvest date. Dovel (1996) showed that forage yields and regrowth following clipping of blue grass-clover, grass-sedge and sedge associations increased as clipping height decreased. Frequent defoliation reduces herbage yield (Reed and Dwyer 1971, Buwai and Trlica 1977). When tall wheatgrass (*Agropyron elongatum* (Host) Beauv.) was defoliated every 4 weeks, it produced more total herbage than if defoliated at 1 or 2-week intervals (Undersander and Naylor 1987).

Herbage quality of cool-season grasses declines with advancing maturation (Hockensmith et al. 1997). Intra-annual quality of forage regrowth is likewise influenced by defoliation regime (Mason and Lachance 1983), with crude protein yield maximized in grasses harvested for the first time just before stem elongation. Mislevy et al. (1977) reported that in timothy and orchardgrass (*Dactylis glomerata* L.) regrowth, digestible protein ranged from 16 to 19% due to different initial defoliation regimes, species and phenology. Delaying the initial harvest date generally causes a decrease in the yield of crude protein regrowth (Bonin and Tomlin 1968, Mislevy et al. 1977).

Cumulative forage yield and quality information is important in optimizing season-long grazing potential or quality hay production. Despite the unique plant-animal interactions in actively grazed boreal regions, there is a paucity of information on the influence of defoliation regimes on herbage productivity and quality. This information is needed to formulate improved management decisions related to grazing and animal production in this environment.

It was hypothesized that varying the timing, intensity and frequency of defoliation would affect season-long accumulated herbage yield and quality. The objective of this study was to determine how accumulated herbage yield and quality were affected by initial date of defoliation, defoliation intensity as affected by stubble height and the frequency of defoliation within a boreal grassland. Collectively, this information would be used to provide recommendations on appropriate grazing regimes to optimize forage production and quality.

MATERIALS AND METHODS

Study Site

Research was conducted at Elk Island National Park (EINP) located 37 km east of Edmonton, Alta (53° 36′ N, 112° 51′W) in 1999. The park, 196 km^2 in size, is a vestige of natural landscape surrounded by agricultural fields. Plant communities inside the Park are biologically diverse, productive, and ecologically complex, providing wildlife with important habitat and forage. Elk Island National Park (EINP), home to many herbivore populations including bison (*Bison bison*), elk (*Cervus elaphus* L.), moose (*Alces alces* L.), whitetail deer (*Odocoileus virginiana* (Zimmerman)), and mule deer (*Odocoileus hemionus* (Raf.)), is intensively managed because of its limited size and fenced perimeter. Ungulate herbivory has heavily impacted vegetation (Bishoff 1981, Bork et al. 1997a, 1997b), with year-long stocking rates (e.g., 1600 elk, 500 plains bison and 350 wood bison) among the highest anywhere in north America. The study took place in a 256-ha fenced area, formerly cultivated and used for greenfed, oats and hay until 1967 (Blyth and Hudson 1987). The area is currently grazed only during the winter by bison and elk. Dominant grasses include *Bromus inermis* Leyss (Smooth brome), *Poa pratensis* L. (Kentucky bluegrass), *Calamagrostis canadensis* (Michx.) Beauv. (marsh reed grass), *Phleum pratense* L. (timothy), and dryland *Carex* spp. (sedges). Forbs such as *Solidago* spp. (goldenrod), *Epilobium angustifolium* L. (fireweed), *Trifolium* spp. (clovers) and *Medicago* spp. (alfalfa) are common as well (Table 2.1). These meadows are ungrazed in the summer (resulting in good range condition), and thus, provide the opportunity to study the effects of various summer defoliation regimes on forage yield and quality.

The climate of the area is cool continental, with cold winters and warm summers (Bowser et al. 1962). Mean temperatures average –16.5°C and +16.4°C for January and July, respectively (Blyth and Hudson 1987), with absolute temperatures ranging from –45 to +38 °C. Three quarters of the annual precipitation falls as rain during the summer growing period (May to August). In 1999 precipitation was 107% of the long-term average of 425 mm (Elk Island Automated weather station, 1999). Annual October to May snowfall ranges from 52 to 222 cm (Parks Canada, unpublished report, 1992).

Geologically, EINP and the surrounding area is predominantly glacial moraine. The topography is characterized by undulating hummocks with relief up to 10 m. Soils reflect the topography of the area: upland soils are Orthic Gray Luvisols or, less commonly, Dark Gray Luvisols or Dark Gray Chernozems (Crown 1977), under forest and grassland vegetation, respectively.

Experimental procedure

The experimental design was a 3 x 3 x 3 factorial design with six replications as blocks. Plots were 0.4 x 0.4 m with a 0.1-m buffer (clipped but not sampled). Twenty-seven defoliation treatments and an undefoliated control were imposed. Levels of the independent factors were: the dates of initial defoliation (May 17, June 10, and July 1), defoliation intensity (represented by 5-, 10-, and 15-cm stubble heights), and defoliation frequency (every two, four and six weeks after initial defoliation). The three initial dates simulated no deferment, early deferred grazing, and deferring grazing until heading (July 1). The latter date coincides with the Ducks Unlimited guideline for deferred grazing to protect nesting birds in Alberta. All clipped plant material was separated into grasses and forbs. Within each plot a 0.25 x 0.25 m area was clipped at ground level on September 30 to determine growing season-end regrowth phytomass, again divided into forb and grass components. Total dry matter yield of each component was calculated from the sum dry weight of plant material collected at each defoliation plus material harvested at the end of the growing season. Herbage samples were dried in a forced air oven at 60 °C for 72 h, cooled in a desiccator, and weighed. Dried samples were ground by component, in a Wiley mill to pass a 1-mm screen and stored in sealed containers for laboratory analyses.

Soil samples were randomly taken using a hand-driven auger from the Ah horizon of the study site, composited, dried, and analyzed for percent organic matter, pH, and texture. The experiment was conducted on a Gray Luvisolic soil of loam texture. On average, the soil (0-30 cm depth) contained 25% clay, 36% silt, 39% sand and 3% organic matter. Soil pH using distilled water was 5.2. Starting in May, the mean soil water content (from five readings) of the 0- to 30-cm depth increment at the study site was measured biweekly using the gravimetric (mass) method (ASTM 1980). Soil sampling sites were chosen randomly from the area among clip plots. Soil water content (in the 0- to 30-cm depth) varied during the growing season, increasing from approximately 15% (g/g x 100) in May to a peak of 32% in July.

Crude protein was determined using a LECO FP-428 Nitrogen Determinator (Sweeney and Rexroad 1987). Nitrogen values were multiplied by 6.25 to obtain crude protein (CP). Neutral detergent fiber (NDF) was determined using the ANKOM filter bag technique (Komarek 1993). Duplicate samples of the grass and forb components in each plot were analyzed separately. Means of the duplicates were used in the analysis.

Statistical Analyses

The yield and quality data were analyzed statistically using PROC GLM of SAS (SAS Institute, Inc. 1989) procedure for the randomized complete block design. Analyses of variance were performed on accumulated dry matter yields and quality of individual treatments summed across harvests to give a season-long total. Block treatment was not significant and the results were therefore presented as completely randomized design. All percentage data were tested for skewness and kurtosis before analysis (Snedecor and Cochran 1980). Preliminary tests prior to the ANOVA indicated the data were normally distributed. The effects of defoliation regimes on aboveground phytomass were compared to that of control plots using linear contrasts. Significance of main effects and interactions were determined with probability levels of 5% and 1%. Significant treatment effects were partitioned into orthogonal and polynomial components, and response surfaces fitted by least squares regression procedures (Snedecor and Cochran 1980).

Polynomials up to quadratic terms for initial defoliation, defoliation height and defoliation frequency, as well as their interactions, were introduced as independent variables in a stepwise regression procedure. Only regression coefficients that differed significantly from zero ($P \leq 0.05$) were retained in the model. Models with the highest R^2 were selected as best fit models.

RESULTS

Herbage Yield

Throughout the text the results will be discussed by main treatments, and when factors and their interactions are significant, only plots of the interaction are presented. The initial date of defoliation and its interaction with defoliation frequency significantly affected forb yield (Table 2.2). The greatest amount of forbs was harvested when initial defoliation occurred in May (Fig. 2.1). Forb yields following June and July initial defoliation were 17% and 34%, respectively, less than that associated with May initial defoliation. In contrast, the initial date of defoliation did not affect the yield of grass.

Defoliation frequency significantly affected grass yield but not the yield of forbs (Table 2.2); less frequent clipping (every 6 weeks) produced the greatest grass yield (Table 2.2). Increasing the defoliation frequency (from 6 to 2 weeks) reduced grass yield by 17%. Defoliation frequency also significantly affected forb yield due to an interaction with the date of initial defoliation. Defoliation at a 6-week frequency resulted in greater forb phytomass but only when defoliation began in June. At the 4-week frequency, forb phytomass was greater when defoliation began in May. Finally, when herbage was removed biweekly, forb phytomass was maximized when initial defoliation was delayed until July (Fig. 2.1). In general, forb yields increased when initial defoliation was deferred and plants were subsequently re-defoliated more often, or plants were defoliated early and allowed longer rest periods between defoliation events.

Defoliation height significantly affected both grass and forb yields (Table 2.2). Both components increased from 5 cm, peaking at 10 cm, and decreased with 15- cm defoliation height (Table 2.2). Taller clipping eight resulted in less grass and forb yields, 17 and 38%, respectively, relative to the moderate intensity clipping. Increasing defoliation intensity from 10 to 5 cm reduced grass and forb yields by 28 and 8%, respectively. At the end of the growing season, forb and grass phytomass across defoliation treatments averaged 62% and 83%, respectively of the control.

Forage Quality

Crude protein content in forbs and grasses ranged from 15 to 27%, and 10 to 19%, respectively. Initial date of defoliation and defoliation frequency significantly affected crude protein content in both grasses and forbs (Table 2.3). The interaction between defoliation frequency and defoliation height was a significant factor affecting grass crude protein content (Fig. 2.2); more frequent defoliation increased crude protein., but only at very intense defoliation levels (e.g., 5 cm). Forb crude protein concentration declined from initial defoliation in May through July and from 2- to 6-week frequency (Table 2.3).

Defoliation height significantly affected crude protein yield (CPY = herbage yield X crude protein content) of grasses (Table 2.3). Initial date of defoliation had an additional effect on CPY of forbs (Table 2.2). Crude protein yield of both forb and grass components peaked at 10-cm defoliation height (Table 2.3). Crude protein yield of forbs decreased with June or July clipping relative to May (Table 2.3).

The neutral detergent fiber (NDF) concentration in grass and forb herbage ranged from 63 to 50%, and 50 to 35%, respectively. Initial date of defoliation and defoliation frequency significantly affected the NDF in grasses (Table 2.4). Initial date of defoliation, defoliation frequency, and their interaction had significant effects on forbs (Table 2.4). Grass NDF increased with less frequent defoliation; and with later date of initial defoliation (May to July) (Fig 2.3). Forb NDF decreased with increasing defoliation frequency at the earliest date of initial defoliation, but NDF increased with less frequent defoliation following later dates of initial defoliation (Fig. 2.3).

DISCUSSION

Defoliation Effects on Forage Yield

The high production of forbs early in the year may be partly explained by the wet weather conditions, and probably these forbs are just plain "early growing" species. In other studies, the first cutting herbage (forb and grass) yields in early spring were almost twice that of subsequent harvests (Cooper 1979, Mason and Lachance 1983, DePeters and Kesler 1985).

The observation that date of initial defoliation did not affect grass yield is somewhat surprising because generally, as is typical of cool-season grasses, yield is highest from spring harvests and declines over summer (Undersander and Naylor 1987). The onset of moisture stress (after early July peak) and higher temperatures in mid-summer may depress herbage production in some cool-season species (Cooper 1979, Mason and Lachance 1983, DePeters and Kesler 1985, Dovel 1996). Moreover, the dominant grasses are exotic and productive species tolerant of defoliation, and cannot be harmed by grazing too early.

The effects of defoliation frequency on herbage yield in this study are basically in agreement with the findings of other researchers (Drawe et al. 1972, Eck et al. 1975, Mutz and Drawe 1983, Undersander and Naylor 1987, Zhang and Romo 1994), that clipping too frequently can decrease herbage yield. Frequent clipping, particularly at intense levels, may reduce photosynthetic area to the extent that insufficient photosynthate is available for rapid regrowth after clipping (Undersander and Naylor 1987). This suggests that under intensive management, pastures should be rested for longer periods to maximize herbage yields. The contrasting effects of defoliation regime on forbs and grasses may be due to some competitive interactions between forb and grass components in the sward, a problem highlighted by Fisher et al. (1996).

A study by Dovel (1996) found results similar to my study, in that raising the defoliation height from 5 to 15 cm reduced total forage by 63, 52 and 33% for sedge, grass-sedge and bluegrass-clover associations, respectively. Cooper (1956) found that raising defoliation height from 5 to 15 cm decreased yields of native wetland meadow hay by 78%. Despite these similar trends, my results do not support the findings in other studies that suggest between 2.5 and 5 cm as an optimal defoliation height (e.g., Reid 1966, Harrington and Binnie 1971, Dovel 1996), probably due to differences in environmental conditions and the specific tolerance of vegetation to defoliation.

At the end of the growing season, forb and grass phytomass across defoliation treatments averaged 62 and 83%, respectively of the control. As observed in studies elsewhere, repeated defoliation reduced the total herbage phtomass compared to the control (Reed and Dwyer 1971, Buwai and Trlica 1977, Zhang and Romo 1994).

Defoliation Effects on Herbage Quality

The higher crude protein content obtained from forbs compared to grasses supports the assertion that forbs contain more nutrients per unit dry matter than grasses and this increases forage nutrient concentrations above those of grass-only swards (Fisher et al. 1996). To maintain forb quality in this ecosystem, herbage must be defoliated early and often. To maintain grass quality, herbage must be defoliated early, often and intensely.

Results from this study agree with other studies that reported declines in crude protein as the growing season progressed and herbage matured (Kilchner and Troeson 1973, Mason and Lachance 1983, Kirby et al. 1989, Van Soest 1982, Fisher et al. 1996). Nevertheless, the CP content of forbs and grasses in this study falls well within the range of values considered adequate to meet protein requirements of all classes of grazing cattle (NRC 1984, 1989) and wild ruminants (Holter et al. 1979, Robbins 1983). Cows nursing calves and dry pregnant mature cows require total protein levels of 9.2 and 5.9%, respectively (NRC 1984,1989). Wild ruminants require protein levels between 5.5-9% (Holter et al. 1979). The significance effect of clipping height on CPY is relevant to farmers since they are interested in knowing which grazing regime will provide them with the highest CPY (both forage yield and crude protein). To maximize CPY of grasses, defoliation should be at moderate intensities above all else.

The neutral detergent fiber (NDF) values obtained from herbage in this study are consistent with results obtained elsewhere for average whole herbage NDF of smooth bromegrass and Kentucky bluegrass, 53.7 and 55.7%, respectively (Hockensmith et al. 1997). The increase in NDF concentration of herbage with maturation in this study agrees with Sanderson and Wendin (1989) who found that whole herbage NDF concentrations of smooth bromegrass and timothy increased with maturation. Earlier and more frequent defoliation of herbage is needed to keep fiber levels low and to increase digestibility.

CONCLUSIONS

The timing, intensity and frequency of defoliation affected herbage yield. Highest grass and forb yields were obtained at a 10-cm defoliation height. Less frequent (every 6 weeks) defoliation produced the highest grass yield. There was no apparent harmful effect on the plants by defoliating them as early as mid May as exemplified by the lack of an effect of initial date of clipping on grass yield. In contrast, the majority of forb yield was obtained after the initial date of defoliation in May.

Defoliation regime (initial date, intensity and defoliation) affected the quality of herbage in various ways. Crude protein (CP) content in forbs declined from the initial defoliation in May to July. Grass CP concentration was maximized by frequent and intense defoliation, but minimized under light and infrequent defoliation. Clipping height had a more dominant effect on CPY than the other factors. Initial defoliation had the most significant effect on the neutral detergent fiber (NDF) concentration in harvested herbage, mostly increasing the date of first harvest. These results indicate that to optimize animal production in the boreal ecosystem rotational grazing should result in greater forage yield than continuous grazing and may require appropriate grazing intensities.

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Table 2.1. Composition (canopy cover) of major species in the hay meadow grasslands at Elk Island National Park, Alberta.

Species	Composition (%)
Grasses and Sedges	
Agropyron cristatum	1.5
Avena fatua	3.0
Bromus inermis	35.2
Calamagrostis canadensis	4.1
Hordeum jubatum	1.9
Phleum pratense	4.7
Poa pratensis	20.1
Carex spp.	3.4
Other grasses	1.4
Forbs	
Achillea millefolium	1.5
Aster spp.	2.0
Cirsium arvense	1.9
Epilobium angustifolium	3.7
Lathyrus spp.	1.8
Medicago spp.	2.2
Solidago spp.	2.9
Taraxacum officinale	5.1
Trifolium spp.	2.6
Other forbs	1.0

Table 2.2. Summary of statistical significance from F tests for total accumulated grass and forb yield of hay meadow grasslands at Elk Island National Park, May 1 - Sept. 30, 1999. Mean yield in bold.

Source of variation	df	Grass yield	Forb yield
		$g\ m^{-2}$	
Initial Defoliation (I)	2	0.645	6.043**
Defoliation Frequency (F)	2	6.062**	0.594
2 weeks		**49.01b**	
4 weeks		**51.02b**	
6 weeks		**59.28a**	
Defoliation Height (H)	2	16.780**	7.011**
5 cm		**44.89c**	
10 cm		**62.81a**	
15 cm		**51.61b**	
IxF	4	0.616	4.867*
IxH	4	0.389	1.648
FxH	4	0.716	1.269
IxFxH	8	0.336	1.658

*, ** Significant at 0.5 and 0.01 level respectively.

Table 2.3. Summary of statistical significance from F tests grass and forb crude protein content (CP) and crude protein yield (CPY) of hay meadow grasslands at Elk Island National Park, clipped from May 1 - Sept. 30, 1999. Mean CP and CPY in bold.

		CP (%)		CPY (g m^{-2})	
Source of Variation	df	Grass	Forb	Grass	Forb
Initial Defoliation (I)	2	6.372**	16.941**	2.461	10.901**
May 17			**20.08a**		**2.61a**
June 10			**19.02a**		**1.63b**
July 1			**14.76b**		**1.69b**
Defoliation Frequency (F)	2	22.375**	14.546**	0.317	0.100
2 weeks			**19.54a**		
4 weeks			**17.30b**		
6 weeks			**17.03b**		
Defoliation Height (H)	2	2.418	0.338	10.657**	6.087**
5 cm				**6.80b**	**2.21a**
10 cm				**9.09a**	**2.27a**
15 cm				**7.50b**	**1.51b**
IxF	4	1.087	2.099	0.371	2.543
IxH	4	0.790	0.619	0.565	2.051
FxH	4	4.081*	1.329	1.094	0.985
IxFxH	8	1.526	1.099	0.510	1.045

* ** significant 0.5 and 0.01 level respectively.

Table 2.4. Summary of statistical significance from F tests for grass and forb neutral detergent fiber of hay meadow grasslands at Elk Island National Park, clipped from May 1 - Sept. 30, 1999. Mean NDF in bold.

		Neutral Detergent Fiber (%)	
Source of variation	df	Grass	Forb
Initial Defoliation (I)	2	3.618**	4.366**
May 17		**54.67a**	
June 10		**54.08a**	
July 1		**55.80a**	
Defoliation Frequency (F)	2	5.492**	4.361**
2 weeks		**53.71a**	
4 weeks		**55.06a**	
6 weeks		**55.78a**	
Defoliation Height (H)	2	2.447	2.010
IxF	4	0.986	3.071*
IxH	4	0.171	0.872
FxH	4	0.445	0.615
IxFxH	8	0.779	1.087

* ** Significant at 0.5 and 0.01 level respectively.

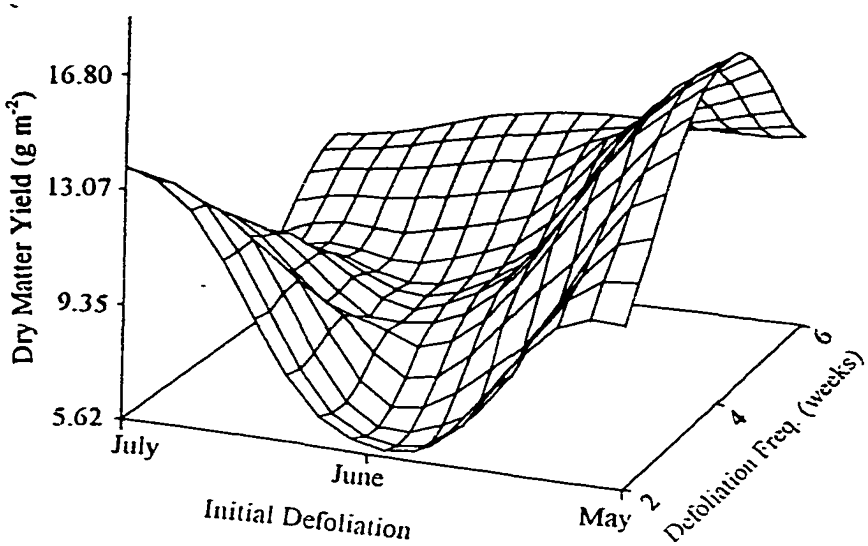

Fig. 2.1. Yield of forb component (Yield = 5.56 + 1.32 (I) + 3.97 (F) - 0.61(IF), R^2 = 0.73) of hay meadows in Elk Island National Park, AB. as affected by initial date of defoliation, defoliation frequency and defoliation height.

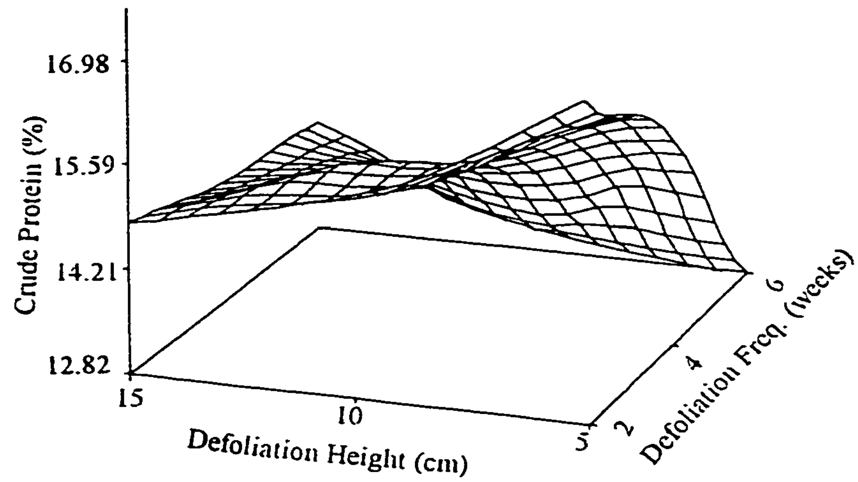

Fig. 2.2 Crude protein concentration of grass (Crude Protein = 33.75 – 0.04 (F) + 0.27 (H) - 0.06 (FH), $R^2 = 0.43$) of hay meadows in Elk Island National Park, AB. as affected by initial date of defoliation, defoliation frequency and defoliation height.

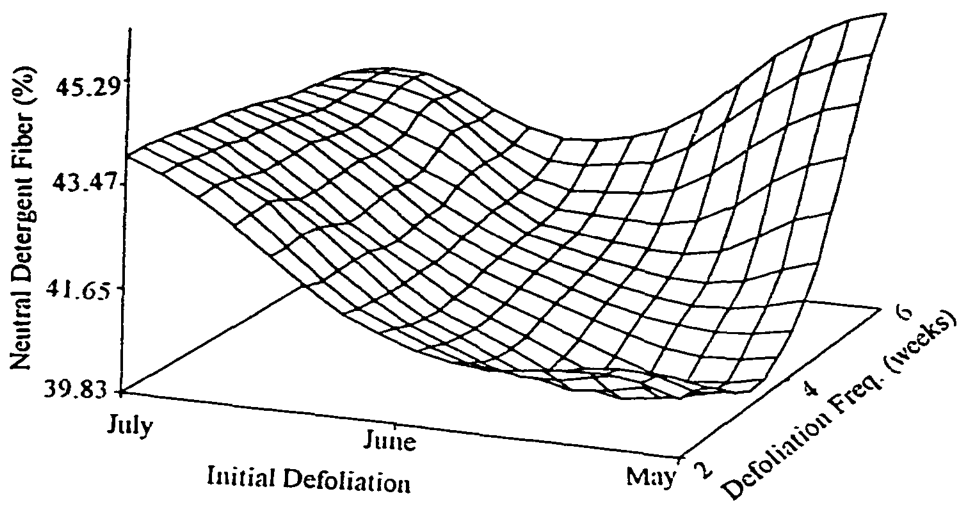

Fig. 2.3. Neutral Detergent Fiber concentration of forb (NDF = 22.18 + 3.27 (I) + 4.23 (F) - 0.63 (IF), R^2 = 0.11) of hay meadows in Elk Island National Park, AB. as affected by initial date of defoliation, defoliation frequency and defoliation height.

CHAPTER 3

VEGETATION RESPONSES TO DEFOLIATION AND SOIL WATER REGIMES IN A BROMUS-POA COMMUNITY

INTRODUCTION

Smooth brome (*Bromus inermis* Leyss.) and Kentucky bluegrass (*Poa pratensis* L.) are dominant cool-season grasses that are important forage resources in the Boreal Ecosystems of central Alberta (Looman 1976). Grazing or haying are common management practices that affect the productivity of these species. The effect of defoliation regimes on the yield of these species may be explained by soil water content, because soil water availability often limits growth in grasslands (Anderson et al. 1970, Ogden and Loomis 1972). Williamson et al. (1989) stressed the need to understand the interactive role of soil water content and defoliation treatments is essential to understanding the relationship between grazing and forage production.

Plant responses to defoliation have economic implications (McNaughton et al. 1983). Recovery time and amount of forage left after grazing affect regrowth (Oesterheld and McNaughton 1988, Dovel 1996). In some plants defoliation has reduced herbage yield (Reed and Dwyer 1971, Buwai and Trlica 1977), decreased root phytomass (Ryle and Powell 1975, Detling et al. 1979, Richards 1984, Zhang and Romo 1994) and altered root:shoot ratios (Richards 1984, Christian and Wilson 1999). Plants may also adapt to grazing or clipping by stimulating aboveground plant growth. This response has been observed in some species (e.g., Robbinson et al. 1952, McNaughton 1979, 1983, Barker and Kidar 1989). Such a stimulation is often referred to as overcompensation (Belsky

1986), which means that the production of defoliated plants exceeds the production of undefoliated plants. This phenomenon has led to herbivore optimization models, which predict that the level of overcompensation is dependent on the intensity of defoliation (McNaughton 1979, Hik and Jefferies 1990).

Agronomists define field capacity as the upper limit for soil water content that provides a balance between good aeration and uptake of water by plants, and wilting point as the lower limit for soil water below which plants can not extract water (Hillel 1980). The practical working definition of field capacity is the moisture content of the soil that has drained for 2-3 days after a rain or irrigation (Hillel 1980). The soil moisture status of potted plants can be manipulated in a number of ways. The most common method is that in which pots are fitted with tensiometers or resistance blocks and allowed to dry to required soil moisture potentials (Sands and Rutter 1959, Javis and Javis 1963, Hillel 1980). Whenever this potential is reached water is added to the soil so that the plants effectively undergo cycles of drying to a required potential. An alternative method requiring less instrumentation yet maintaining a uniform moisture status is that in which soil water content is maintained by regular addition of water to a predetermined weight (Migahid 1937, Read and Bartlett 1972). Provided that a highly uniform medium giving optimal distribution of irrigation water is available for all pots, this procedure (gravimetric method) has a number of advantages, particularly in terms of large-scale replication without undue demands of instrumentation (Read and Bartlett 1972).

The interactions of defoliation intensity and frequency, with watering regimes as affecting plant growth have received limited attention (McNaughton et al. 1983, Wallace et al. 1984, Toft et al. 1987). Most research in western Canada has focussed on the benefits of fertilizer, legumes, and grazing regimes on pasture productivity (e.g., Johnston et al. 1971; Smoliak et al. 1972; Ukrainetz et al. 1988; Pearen and Baron 1996; McCartney et al. 1999). Little information exists however, on the interactive role of soil water and defoliation treatments on forage production in western Canada. Research evaluating these effects is warranted because most prairie grasses grow in environments where water stress may influence herbage productivity and animal production. Such knowledge is critical to decisions on whether soil water regimes modify (e.g., ameliorate or amplify) the effects of defoliation. This research would provide insight towards developing drought management strategies beneficial for farmers and ranchers, and would provide a database for modeling pasture growth and productivity. The objective of this study was to measure growth responses in *Bromus-Poa* swards to variations in defoliation frequency and intensity under varying moisture regimes.

This study was conducted to test the following hypotheses:

(1) Intensity and frequency of defoliation affect herbage yield and quality.

(2) Plants may fully compensate or overcompensate for the defoliation of aboveground phytomass.

(3) Soil water regimes can affect herbage production.

(4) Interaction of soil water and defoliation regime affect herbage production.

MATERIALS AND METHODS

Experimental procedure

A hand-driven Uhland soil core sampler was used to collect ninety-six samples of Aspen Boreal grassland sods (14-cm diameter, 15-cm long) from a Luvisolic loam soil at Ministik Wildlife Research Station near Edmonton, Alberta, in June 1999. On average, the soil contained 25% clay, 33% silt and 42% sand. Organic matter content was 2.1%. Soil pH using distilled water was 5.5. Smooth brome (Bromus inermis) and Kentucky bluegrass (Poa pratensis) dominated vegetation. From field baseline studies, these two species comprised 42 and 22% cover, respectively. Each sod contained variable amounts of each of the two species. Forbs were removed because not all sods contained them. Each sod core was placed carefully in a 15-cm diameter cylindrical pot (15 cm high) with as little disturbance as possible. Caps with three holes were fitted at the bottom of the pots to allow free drainage. Samples were transported to a greenhouse on the University of Alberta campus in Edmonton. The water content of the soil at field capacity was determined on ten replicate samples. These pots were brought to field capacity by standing them with their bases in water until the waterfront reached the top of the pot. They were removed and left to stand on a grid until freely draining water had passed through the basal draining holes. At this water content, the pots were weighed. Using this figure and the value of water content at field capacity, the weight at which any pot was to be maintained to provide a required water regime was determined. Each sod was watered every 2-3 days with distilled water to maintain favorable moisture levels (field capacity) during the acclimation period of 3 weeks in the green house prior to defoliation treatments. The greenhouse was maintained at an air temperature of 23 °C, with an 18- hr. photoperiod. The temperature control was set at 25 °C; the emergency vent was set at 32 °C.

Studies of plant response to defoliation in soils of different moisture regimes were subsequently conducted on the sods. A completely random design with four replicates of a factorial arrangement of treatments (moisture level, defoliation intensity and defoliation frequency) was used. Soil water conditions within the sods were maintained at one of 3 levels by adding water to the soil every 3 days after weighing: field capacity, moderate water stress maintained at 50% field capacity, or severe water stress on plants watered to 20% field capacity. Within a watering regime (moisture level), sods were randomly assigned to one of 4 clipping intensities (height) X 2 clipping frequencies, with 4 replications of each treatment combination. The 4 clipping intensities were achieved by clipping sods at heights of 15, 7.5, 2.5, or undefoliated (control) cm above the soil surface. After sods were initially defoliated on July 1, they were defoliated again at 2- or 4-week intervals for the 92-day duration of the experiment. Total accumulated shoot phytomass was calculated from the sum of dry weight of plant material collected at each clipping, plus material harvested at the termination of the experiment to the soil surface. Herbage samples were sorted into live and dead categories, dried in a forced air oven at 60 °C for 72 h, cooled in a desiccator, and weighed. Dried samples were ground in a Wiley mill to pass a 1-mm screen and stored in sealed containers for laboratory analyses.

Total root phytomass in the sods was measured at the end of the experiment. Belowground material was separated from the soil by soaking each core in water for 12 hours. These samples were hand washed over a set of three sieves of sizes 6.3, 2.0, and 1.18 mm, and separated into roots and crown. Samples were oven dried at 60 °C for 72 hours and weighed.

Crude protein in aboveground accumulated production was determined using a LECO FP-428 Nitrogen Determinator (Sweeney and Rexroad 1987). Nitrogen values were multiplied by 6.25 to obtain percent crude protein (CP). Neutral detergent fiber

(NDF) in shoots was determined using the ANKOM filter bag technique (Komarek 1993). Means of the duplicates were used in the analysis.

Statistical Analyses

The yield and quality data were analyzed statistically using PROC GLM of SAS (SAS Institute, Inc. 1989). Analyses of variance for dry matter yields and quality of individual treatments were summed across harvests to give an entire period total. Significance of main effects and interactions were determined with probability levels of 5 and 1%.

RESULTS

Herbage Yield Response

Watering regime, clipping frequency and clipping height significantly affected shoot phytomass (Table 3.1). Shoot phytomass generally decreased under increasing defoliation intensity compared to the non-defoliated control (Table 3.2). This was evident in both live and dead categories. Live shoot was greater when plants were clipped less frequently (e.g., every 4 weeks rather than 2 weeks).

Live shoot phytomass increased with decreased water stress among the three soil water regimes (Table 3.3). Severe water stress caused an additional decrease in the aboveground live phytomass over moderate stress, but there was little difference in aboveground standing dead among the two. Therefore, most of the differences in total aboveground phytomass among plants within the 3 soil water regimes were the result of greater live phytomass under less severe water stress.

Clipping frequency and height had a significant effect on belowground phytomass, whereas soil water regime did not (Table 3.1). Increasing defoliation reduced root and crown phytomass compared to the control (Table 3.2). The root:shoot ratio increased with more intense and less frequent clipping (Table 3.2). Watering regimes had a significant effect on the root:shoot ratio. In the severe water stress treatment the root:shoot ratio was significantly greater than in plants maintained at field capacity (Table 3.3).

Herbage Quality response

The crude protein (CP) content of the accumulated shoot phytomass ranged from 12 to 23%. Frequency of clipping and clipping height had significant effects on shoot crude protein (Table 3.4), increasing in the plants clipped more frequently (Table 3.5). Clipping height had a non-linear effect on CP, peaking at 7.5 cm defoliation, and at a minimum with the season-end defoliation only (Table 3.5). Watering regime, clipping frequency and clipping height significantly affected crude protein yield (CPY) (herbage yield X crude protein content) in the plants (Table 3.4). Crude protein yield of plants clipped at the 15-cm height and control were not significantly different, while CPY of plants clipped at 7.5-cm height was significantly greater than all other treatments (Table 3.6). This represents total compensation in plants clipped at 15-cm height and overcompensation in plants clipped at 7.5-cm height. Crude protein yield of herbage was also greater when plants were clipped every 4 weeks rather than 2 weeks (Table 3.6). Though water regime did not significantly affect crude protein (Table 3.4), CPY decreased with increasing water stress (Table 3.6).

The neutral detergent fiber (NDF) concentration in harvested shoots ranged from 50 to 60% with only clipping frequency significantly affecting NDF in aboveground herbage (Table 3.4). Increasing the clipping frequency from 4 to 2 weeks decreased NDF (Table 3.5).

DISCUSSION

Herbage Yield Response to Defoliation and Watering Regimes

As observed in studies elsewhere (Reed and Dwyer 1971, Buwai and Trlica 1977, Zhang and Romo 1994), repeated defoliation during growth reduced accumulated shoot phytomass under increasing defoliation intensity compared to the non-defoliated control. Accumulated shoot phytomass was greater when plants were clipped every 4 weeks rather than 2 weeks. Frequent clipping resulted in reduced yield compared to less frequent harvests. This is consistent with results from many studies (e.g., Ethredge et al. 1973, Owensby et al. 1974). In Saskatchewan, when northern wheatgrass (*Agropyron dasystachyum* (Hook), Scribn.) was defoliated at a 6-week interval, yields were generally greater than when herbage was removed biweekly (Zhang and Romo 1994). Thus, longer recovery time is needed to maximize forage yields.

Soil water availability often limits growth in grasslands (Anderson et al. 1970, Ogden and Loomis 1972). The influence of soil water on shoot production observed here followed the same trend reported in other studies (e.g. Levitt 1980, Abdel-Magid et al. 1987); aboveground production was reduced with increasing water stress, highlighting the drought susceptibility of *Bromus-Poa* swards in central Alberta.

Defoliation reduced root and crown phytomass compared to the control. This is despite the grasses being increasingly tolerant of defoliation (e.g., formation of rhizomes, etc.). Previous studies on prairie grasses are in general agreement that clipping of the shoots inhibited root production: e.g. Zhang and Romo (1994), Li and Redmann (1992) (*Agropyron dasystachyum*); Smoliak et al. 1972 (*Stipa-Bouteloua);* Harrison (1931) (*Poa* *pratensis*). As expected, the root:shoot ratio increased with clipping intensity and frequency. Plant response to clipping or grazing has often resulted in increased root:shoot ratios (Dittmer 1973, Oesterheld and McNaughton 1988). In spite of the inability of statistical analyses to distinguish between the effects of watering regimes on root phytomass, watering regimes had a significant effect on the root:shoot ratio. This is similar to many previous observations on a number of crops (e.g., Malik et al. 1979, Turner and Begg 1978, Brar and Palazzo 1995) that the root:shoot ratio of vegetation increases under drought. This increases the survivability of plants because it allows a large root system to obtain water for a smaller shoot. Roots of Bromus-Poa plants appear to be relatively more susceptible to defoliation intensity rather than drought, but it does not appear producers can make their stand more drought resistant by increasing root phytomass, as documented under field conditions (Johnston et. al 1971).

Though defoliation regimes and soil water affected forage production individually, there was no interaction between the two. This seems to support the null hypothesis that there is no interactive role of soil water and defoliation regimes. It remains to be seen whether or not plant community responses to defoliation and soil water conditions will interact under field conditions.

Herbage Quality Response to Defoliation and Watering Regimes

The average crude protein (CP) content observed in plants in this study (10-18%) was greater than the 9% observed by (Kilcher and Troelsen 1973) for irrigated smooth bromegrass. The CP content of plants falls well within the NRC (1984, 1989) range of values considered adequate to meet protein requirement of all classes of grazing cattle (NRC 1984, 1989); cows nursing calves and dry pregnant mature cows require total protein level of 9.2 and 5.9%, respectively. In addition, grazing animals are selective and generally consume forage of higher nutritive value than non-selectively clipped herbage. Lowering clipping height up to a point (7.5 cm) produced herbage with higher CP content and CPY, similar to results obtained from studies in Kentucky bluegrass/white clover pastures (Robinson et al. 1952, Dovel 1996). Therefore, optimum clipping height for this vegetation is 7.5 cm above ground level. Also, more frequent defoliation increased CP due to constant clipping of regrowth on these plants well adapted to defoliation.

The decreased crude protein yield with increasing water stress has economic importance for the rancher striving for quality forage production with the onset of drought. The NDF concentrations in herbage are consistent with results obtained elsewhere for average whole herbage NDF of smooth bromegrass and Kentucky bluegrass, 53.7 and 55.7%, respectively (Hockensmith et al. 1997).

CONCLUSIONS

Defoliation height and frequency affected both aboveground and belowground phytomass yield and forage quality. Long rest and moderate defoliation intensity result in maximum shoot yield and CPY in this vegetation. The root:shoot ratios rather than root increased with increasing defoliation intensity and frequency due to change in shoot phytomass. Both defoliation intensity and frequency affected crude protein and crude protein yield, while only defoliation frequency affected NDF. Based on CPY estimates alone, *Bromus-Poa* plants compensated and overcompensated for aboveground phytomass removed at the 15- and 7.5-cm height, respectively. However, because there was no water x defoliation interaction interpretation of this becomes problematic.

This vegetation is drought susceptible with impacts mostly aboveground, not belowground. Soil water regime affected aboveground phytomass and root:shoot ratios but not belowground phytomass. Soil water regime affected crude protein yield, decreasing with increasing water stress.

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Table 3.1. Summary of statistical significance from F tests for total accumulated shoot and end of trial belowground phytomass of *Bromus-Poa* sods.

Source of Variation	df	Shoot phytomass	Belowground phytomass
Water regime (W)	2	4.96*	2.25
Clipping frequency (F)	1	4.55*	4.52*
Clipping height (H)	2	6.54**	4.35*
WxF	2	1.25	1.5
WxH	4	0.18	0.07
FxH	2	0.56	0.13
WxFxH	4	0.80	0.09

* $P \leq 0.05$, ** $P \leq 0.01$

Table 3.2. Accumulated shoot and end of trial belowground phytomass (g) and root:shoot ratios of *Bromus-Poa* sods as affected by clipping height and clipping frequency.

	Clipping Height (cm)			Control	Clipping Frequency (Weeks)	
Variable	2.5	7.5	15	∞	4	2
Shoot phytomass						
Live	9.49c[1]	13.36b	11.61b	15.39aZ	12.92Y	7.85X
Dead	5.01c	6.06b	6.12b	9.81aY	9.03Y	4.22X
Total	14.50c	19.40b	17.73b	25.2aZ	21.92Y	12.10X
Belowgrond phytomass						
Roots	7.58c[1]	9.90b	7.80bc	11.08aZ	9.23Y	6.01X
Crowns	5.72b	7.10b	6.40b	8.22aY	8.02Y	5.58X
Total	13.30c	17.0b	14.20c	19.30aZ	17.25Y	11.59X
Root:shoot ratio	0.52a	0.51a	0.44a	0.44aX	0.42X	0.50X

[1]Means for either clipping height (lower case comparison) or clipping frequency (upper case comparisons) followed by the same letter are not significantly different ($P \leq 0.05$). The same control was used for both sets of data.

Table 3.3. Accumulated shoot and end of trial belowground phytomass (g) and root:shoot ratios of *Bromus-Poa* sods as affected by soil water regime.

	Soil water regime [2]		
Variable	Field capacity	Moderate stress	Severe stress
Shoot phytomass			
Live	13.05a[1]	11.31b	6.28c
Dead	9.25a	7.25b	7.48b
Total	22.30a	18.56b	13.76c
Belowground phytomass			
Roots	9.55a	9.70a	9.50a
Crowns	8.10a	7.80a	7.50a
Total	17.66a	17.5a	17.0a
Root:shoot ratio	0.43b	0.52ab	0.69a

[1] Means in a row followed by the same letter are not significantly different ($P \leq 0.05$).
[2] Moderate and severe stress represent 50 and 20% field capacity, respectively.

Table 3.4. Summary of statistical significance from F tests for crude protein content (CP), neutral detergent fiber (NDF), and crude protein yield (CPY) of accumulated shoot of *Bromus-Poa* sods.

Source of Variation	CP	NDF	CPY
Water regime (W)	0.76	0.40	4.67**
Clipping frequency (F)	4.00*	6.28**	3.33*
Clipping height (H)	3.11*	0.48	6.55**
WxF	0.40	0.69	0.99
WxH	0.42	0.69	0.20
FxH	0.94	0.06	0.71
WxFxH	1.96	0.70	0.17

* $P \leq 0.05$, ** $P \leq 0.01$.

Table 3.5. Crude protein (CP) (%) and neutral detergent fiber (NDF) (%) contents in total accumulated shoot phytomass of *Bromus-Poa* sods as affected by clipping height and clipping frequency.

	Clipping Height (cm)			Control	Clipping Frequency (Weeks)	
Variable	2.5	7.5	15	∝	4	2
CP	15.25b	17.91a	13.27c[1]	10.0dZ	13.19Y	16.49X
NDF	58.95a	59.49a	59.61a	60.0aZ	55.0Y	50.0X

[1]Means for either clipping height (lower case comparisons) or clipping frequency (upper case comparisons) followed by the same letter are not significantly different ($P \leq 0.05$). The same control was used for both sets of data

Table 3.6. Crude Protein Yield (CPY) (g) of *Bromus-Poa* sods as affected by clipping height, clipping frequency and water regime.

Variable	CPY
Clipping Height (cm)	
2.5	2.21c[1]
7.5	3.47a
15	2.35bc
Control (∝)	2.52bZ
Clipping Frequency (weeks)	
4	2.89Y
2	1.99X
Water regime (g kg^{-1})[2]	
Field Capacity	3.35a
Moderate Stress	2.60b
Severe Stress	1.92c

[1]Means for either clipping height, clipping frequency or water regime followed by the same letter are not significantly different ($P \leq 0.05$).
The same control was used for clipping height and clipping frequency data.
[2] Moderate and severe stress represent 50 and 20% field capacity, respectively.

CHAPTER 4

SEASONAL DYNAMICS AND DEFOLIATION IMPACT ON HERBAGE YIELD IN ASPEN BOREAL HABITATS OF ALBERTA

INTRODUCTION

Plant-herbivore dynamics on rangelands depend on pasture productivity, changes in phytomass with time, and the vegetation's responses to defoliation (Caughley 1976, 1982, Noy Meir 1975). Grazing may influence the dynamic interaction between plant growth rates and phytomass, as well as change the proportions of green herbage, standing dead, and fallen litter pools.

There is no definitive description or terminology for live and dead vegetation material in range ecosystems. Range ecologists have used different terms for vegetation components, e.g., above- and below ground phytomass, dead-shoot phytomass, recent dead, old-dead, mulch, litter, standing litter, ground litter, and standing dead (Odum 1960, Golley 1965, Tomanek 1969, Coupland 1979, Heitschmidt et al. 1982). For this study, green herbage refers to green photosynthesizing material of growing plants; standing dead refers to cured or dried plant material still attached to the standing plant; and fallen litter consists of detached undecayed plant residuum lying on the soil surface (Dyksterhuis and Schmutz 1947).

The timing, intensity, and frequency of defoliation interact in complex ways on production processes and herbage yield in rangeland ecosystems (Oesterheld and McNaughton 1988, Heady and Child 1994, Zhang and Romo 1994). Defoliation by animals may have both negative and positive effects on plant growth. Grazing decreases the photosynthetic capacity of plants through a reduction of leaf area. However, defoliation may enhance plant growth through interrelated mechanisms such as increasing the relative allocation pattern of carbohydrates to the production of new leaf area and increasing the photosynthetic rate of remaining tissue (McNaughton 1983).

Smooth bromegrass (*Bromus inermis* Leyss) and Kentucky bluegrass (*Poa pratensis* L.) are dominant in many pastures of the Aspen Parkland and Boreal-Mixedwood in western Canada (Looman 1976) and are preferred by many grazing animals, e.g., cattle and elk. Despite the abundance of these introduced perennial grass species, little information is available on the seasonal dynamics of available herbage and the influence of defoliation on aboveground phytomass production. Therefore, the objectives of this study were to investigate: 1) seasonal changes in the live and dead phytomass components of a *Bromus-Poa* community; and 2) the effects of initial timing, height and frequency of clipping on accumulated herbage removal.

The study reported herein was conducted to test the following hypotheses:

(1) Amounts of herbage available for grazing change seasonally.

(2) Initial timing, height and frequency of clipping would affect accumulated herbage removal.

MATERIALS AND METHODS

Study Site

Field research was conducted at the University of Alberta Ministik Wildlife Research Station (53° 18′N, 114° 35′W), located 48 km southeast of Edmonton, Alberta on the Cooking Lake glacial moraine. Vegetation is classified as boreal aspen forest (Rowe 1972, Strong 1992), although homesteading in the early 1900s created characteristics more similar to those of the Aspen Parkland. Major vegetation types include balsam poplar (*Populus balsamifera*) and trembling aspen (*P. tremuloides*) forests, *Bromus-Poa* grasslands and sedge (*Carex* spp.) wetlands. Seeded some fifty years ago, the grasslands are dominated by smooth brome (*Bromus inermis* Leyss) and Kentucky bluegrass (*Poa pratensis* L.). Smooth brome is a tall, leafy, rhizomatous, cool-season perennial that is long-lived and grows rapidly (Hardy 1989). In contrast, Kentucky blue grass is a short-statured, long-lived, cool-season perennial that spreads via extensive rhizomes. Dicotyledonous plants include white clover (*Trifolium repens L.*) and dandelion (*Taraxacum officinale*). Grasses typically initiate growth in late-April or early May following snow melt, with swards dominated by vegetative graminoids in mid-May. Grasses head in June with seed-ripe by mid-August. The dominant dicot, dandelion, emerges in early-May, becomes the most visible dicot in early-June and persists to autumn. Following dandelion, clovers reach their peak phytomass in July, and survive until the end of the frost-free period. Grasses senesce in late-September and October. The pastures used in this study were grazed by Rocky Mountain wapiti (*Cervus elaphus* nelsoni) at a stocking rate of approximately 2.0 AUM ha^{-1} in the years prior to the study.

Average annual precipitation of the area varies from 400 to 450 mm with 334 mm falling during the growing season (April to September). Mean temperatures average -17.3 °C and +17.4 °C for January and July, respectively, with absolute temperatures ranging from –49 to +32 °C (Olson 1985).

Soils are mainly moderately well- to well-drained Luvisols. The upland Cooking Lake loam, which predominates in the region (Bowser et al. 1962), is a fairly well-drained Orthic Gray Luvisolic soil developed on glacial till of the Edmonton formation, underlying forested areas. The Uncas loam, an Orthic Dark Gray Luvisolic soil, also developed from glacial till, is found on less densely forested areas. Sandy loams are also present on the area, though in low proportions.

Experimental Procedure

A 20 x 60-m exclosure was established in April 1997 to protect plots from grazing. To ascertain the vegetation growth curve for the area thirty plots, each 40 x 40 cm, were permanently marked within the site. Clip samples were obtained at monthly intervals from 5 randomly selected plots from April to September. All phytomass within each plot was harvested to ground level and litter removed to mineral soil. Sampling was subsequently repeated on the same plots on the same dates in 1998. All harvested material was hand sorted into components of live green plant material, dry plant material (standing dead), and fallen litter, dried at 60 °C, and weighed. Measurements were not made from October to March because snow cover and freezing temperatures limited field activities.

To describe the plant community in the study area, five 10-m line transects were marked across the exclosure at five regular intervals in 1998. A 30 x 30 cm quadrat was used to systematically sample along each transect in midsummer (n = 20 quadrats). Within each quadrat, all plant species were identified and their percent cover estimated (Daubenmire 1959).

To establish the relationship between plant growth and herbage removed, clipping treatments with 3 initiation dates, 3 heights and 3 frequencies (e.g., intervals) were replicated 6 times in a completely randomized design over the two years (1997 and 1998). All plots were 40 x 40 cm permanently marked, with a 10-cm clipped buffer maintained on all sides. Levels of the independent factors were: date of initial clipping (May 20, June 22, and July 22); heavy, moderate, and light intensities (clipping heights of

2.5, 7.5, and 15 cm from ground level); clipping frequency (three, six and nine week intervals after initial defoliation); and time (first and second years growth). Sub-plots of 20 x 20 cm were clipped on each plot at ground level at the end of September in each year to determine residual (seson-end) phytomass. Aboveground phytomass was calculated from the sum of plant material collected at each clipping date plus residual phytomass. Treatments were imposed on the same plots each year. All samples were oven-dried at 60 °C and weighed. Mean percent soil water content (from five readings) of the 0 to 30 cm soil increment at the study site was measured biweekly using gravimetric (mass) method (ASTM 1980). Soil sampling sites were chosen randomly from the area between clip plots.

Statistical Analyses

Comparisons of spring, summer and fall phytomass of green herbage, standing dead and fallen litter herbage components were made. The effects of date of initial clipping, clipping height, clipping frequency and year were analyzed with a factorial analysis of variance using PROC GLM of SAS (SAS Institute, Inc. 1989). Preliminary tests prior to the ANOVA indicated no deviation from normality. Post-hoc mean comparisons were done on all significant treatment means and their interactions using Tukey's method ($P \leq 0.05$).

RESULTS

Weather and soil water

Total annual precipitation at the Ministik area for 1997 and 1998 was 494 and 429 mm, compared to a long-term average of 425 mm. Growing season precipitation (April to September) in 1997 was 26% above the long-term average (Table 4.1). Growing season precipitation for 1998 was slightly above average. Average air temperatures experienced during the growing season in 1997 were normal, but exceeded the average in 1998 (Table 4.1). Soil water content varied during the entire growing season for both years. Soil water content in the top 30 cm of soil increased from approximately 14% of soil weight in April to a peak of 26% in June (Table 4.1). Overall, weather conditions at Ministik during the growing season of 1997 were more favorable for herbage production than in 1998.

Plant Composition and Seasonal Changes of Herbage Phytomass

Plant species composition data showed a community dominated by Kentucky bluegrass and smooth brome (Table 4.2). The three phytomass pools of green herbage, standing dead, and fallen litter generally increased from spring to summer and subsequently decreased from summer to fall (Table 4.3). In 1997, green herbage increased by 107% and decreased by 39% from spring to summer and from summer to fall, respectively. The same trend was observed in 1998 with a 105% increase and 26% decrease, respectively. Standing dead and litter followed the same trends, peaking in midsummer during both year, although summer and fall pools of standing dead and litter were generally not significant from one another. Seasonal accumulation of herbage phytomass was generally greater in 1997 than 1998, likely due to the higher precipitation in 1997. Weathering losses of green herbage, standing dead and fallen litter over winter (i.e., between fall 1997 and spring 1998) expressed as a proportion of the fall 1997 estimate were 34, 52 and 51%, respectively (Table 4.3). Dry matter losses of total herbage (all 3 pools) over winter was 58% of 1997 summer green phytomass.

Defoliation Effects on Aboveground Productivity

Clipping date, height and frequency all had significant effects on accumulated aboveground herbage removal between years (Table 4.4), and within years (data not shown). The effect of year on aboveground forage removal was independent of clipping height and frequency. Clipping date affected forage yield the most, with yield values differing significantly among all three dates investigated but peaking with May clipping (Table 4.5). Herbage yield following July clipping was less than half that of May. Heavy and moderate clipping intensities increased herbage removal relative to the light intensity clipping (Table 4.5). Raising the clipping height from 7.5 to 15 cm reduced herbage yield by 27%. The greatest accumulated herbage yield was found with longer regrowth periods (e.g., six or nine weeks rest) (Table 4.5). The significant interaction between clipping date and clipping frequency (Table 4.4) was attributed to the increased positive effect of longer recovery times following May clipping, as well as a contrasting reduction in forage yield with longer recovery times following later initial dates of defoliation.

DISCUSSION

Seasonal herbage production on pastures is influenced by plant community type, local growing conditions, and disturbance regime. Areas with a history of grazing are generally characterized by reduced litter (Willms et al. 1986), decreased annual production, increased losses of herbage over winter, and delayed spring growth (Willms et al. 1996). The maximum seasonal phytomass of each herbage component documented in summer coincided with wet soil conditions. In this study, there were over-winter losses of total herbage, standing dead and fallen litter. These losses are of economic importance in this area because grazing animals such as elk forage through snow during winter months, and hence it is necessary to maintain a high proportion of herbage on winter ranges to ensure adequate grazing opportunities. Low spring yield in the *Bromus-Poa* community was likely due to dry soil conditions or slow growth of plants. High herbage yield in summer was dependent on precipitation during the growing season. Shallow-rooted, rhizomatous species (like those dominant in this community) are most productive with frequent showers since moisture conservation tends to be inefficient with reduced litter (Willms et al. 1996). Clipping or grazing can also change the distribution of roots in the soil by reducing the rooting depth and packing more roots in the soil surface (Willms 1991, Smoliak et al. 1972). Herbage yield response to precipitation late in the growing season also tends to be low because many species have completed their growth cycle and the onset of cooler temperatures may impede growth.

Numerous studies have demonstrated the effects of fertilizer, legumes, and grazing on pastures (Johnston et al. 1971; Smoliak et al. 1972; Ukrainetz et al. 1988; Pearen and Baron 1996; McCartney et al. 1999). Most of these studies have taken place on nutrient rich soils in the Black Chernozemic soil zone, rather than the less fertile Gray Luvisolic soils of the Boreal Mixedwood where many commercial game ranching enterprises are located (McCartney et al. 1999). By conducting studies on the latter, the effects of defoliation on pasture growth and productivity can be established for an area representative of a large region of central Alberta important for commercial livestock production.

In addition to the within-year seasonal variation of herbage yield and overwinter losses in phytomass, the influence of initial timing, height and frequency of clipping affected phytomass yield both within and between years in this boreal environment.

These variable responses are attributed to differences in environmental conditions between years and the cumulative effects of defoliation in current and preceding years (Zhang and Romo 1994).

The greatest herbage harvested was associated with clipping initiated in May, and peaked with at least six weeks rest (regrowth). Increases in herbage yield should be more pronounced during the early active growth period of plants than later on when growth is constrained by seed herd production. This trend is particularly prevalent because the dominant grasses are all C3 species, which typically produce maximum growth by July (Zhang and Romo 1994). This pattern is also indicative of species well adapted to withstand herbivory (e.g., rhizomatous species). The decline in herbage yield associated with initial clipping in July may be due to lower soil moisture availability after mid-summer. In addition, higher temperatures in late-summer can depress forage production of cool-season species (Cooper 1979; DePeters and Kesler 1985; Mason and Lachance 1983). These results agree with other studies (e.g., Cooper 1956; DePeters and Kesley 1985; Dovel 1996), wherein pasture regrowth from defoliation in spring represented nearly half of the total growing season yield. It contrasts, however, with studies conducted on native bunchgrass rangelands in Alberta that indicate spring defoliation can decrease total yields (Mclean and Wikeem 1985, Willms and Fraser 1992).

Moderate defoliation at all times appeared to increase herbage yield in this study, though not significantly. Similar results have been obtained in other studies (Robinson et al. 1952; Cooper 1956). Studies examining the effect of clipping height on yield of individual grass species suggest between 2.5 and 5 cm as an optimal clipping height (e.g., Reid 1966). Intensity of defoliation directly controls the herbage remaining for optimal regrowth (Heady and Child 1994). In a study adjacent to my research site that examined remaining herbage (stubble) in response to defoliation heights, Okello (1996) recorded season-long herbage stubble of 90, 120, and 170 g m^{-2} from 2.5, 7.5, and 15 cm defoliation heights. Remaining herbage values for these pastures at the 7.5-cm clipping height exceeded the recommended level of 100 g m^{-2} for optimizing forage production in many pastures (Smethen 1990). Thus, a relatively intense defoliation height between 2.5 and 7.5 cm may be needed to optimize forage production on these particular pastures. I agree, however, with Dovel's (1996) assertion that factors other than forage yield, such as type of vegetation, stand vigor and animal performance must also be considered in determining the optimum defoliation intensity (e.g., height).

Frequent clipping has often resulted in reduced yield compared to less frequent harvests (Ethredge et al. 1973, Owensby et al. 1974). In this study, the greatest yield was obtained from clipping no less than six weeks after initial defoliation. Rotational grazing is an important option for increasing pasture production in the Aspen Parkland (see McCartney 1999). It is obvious from these data that pastures should be rested for six weeks during rotational grazing if season-long yields are to be maintained.

The interaction between initial defoliation date and clipping frequency may be related to the phenology of plants within the study area. Plants tend to grow rapidly in the early part of the growing season, with defoliation causing photosynthates to be translocated to defoliated sites for tissue repair rather than growth (McNaughton 1979). Changes in below ground phytomass may also parallel aboveground phytomass, with root development requiring re-initiation (e.g., Johnston, 1961, Johnston et al. 1971). This trend changes, however, as plants mature: growth rates decline and products of photosynthesis are preferentially utilized for reproduction (Harper 1977; Krebs 1985). Also, compensation in the defoliated plants along the growing cycle depends on the length of time available for recovery (Hilbert et al. 1981). Hence, it appears from these results that longer recovery times are more beneficial during early defoliation and vice versa.

Pasture response to defoliation varied with the growing cycle of major plants and corresponded with precipitation and soil moisture conditions. Williamson et al. (1989) stressed the need to understand the interactive role of soil water content and defoliation treatments as essential to understanding the relationship of grazing and herbage production. Maximum herbage production under defoliation may occur under certain hydrologic conditions, such as when water remains non-limiting despite grazing induced changes in root phytomass. Defoliation may also result in less water uptake and increased soil water availability later in the growing season, subsequently increasing productivity. In contrast, the lack of defoliation early in the growing season, may result in early maturation of the herbage and less efficient use of any remaining soil moisture in mid- to late summer.

CONCLUSIONS

Maximum summer yield, rapid loss of green herbage late in the growing season, and dry matter losses in the standing dead and fallen litter pools over winter characterized the seasonal changes in herbage phytomass on this Boreal grassland. The amount of herbage harvested was affected by initial clipping date, clipping height and frequency of clipping. Pasture response to clipping varied with the growth cycle of major plants and also corresponded with the soil water conditions of the area. The interaction between clipping date and frequency demonstrates the importance of temporal rest and resource allocation for the sustained productivity of herbage plants.

The defoliation intensities adopted in this study are consistent with field observations of livestock and wildlife grazing. However, I acknowledge that clipping is not equivalent to grazing as it excludes trampling impacts, shredding and the behavioral role of the grazing animal as an ecosystem regulator, selectively facilitating energy flow and the local cycling, redistribution and transformation of nutrients on the landscape. Hence, work is needed with actual grazing systems under field studies to further validate these findings.

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Table 4.1. Monthly precipitation, soil water and average temperatures for Ministik Wildlife Research Station, Alberta, during the growing seasons of 1997 and 1998.

	Precipitation (mm)							Air Temperature (°C)		
Year	April	May	June	July	Aug.	Sept.	Total	Max.	Min	Daily
1997	38	69	149	28	52	84	420	19	7	13
1998	34	38	111	89	21	50	343	21	9	15
1961-1990	10	40	77	89	78	40	334	18.6	7.4	13
	Soil water (g/100g)									
1997	15	19	28	22	17	16				
1998	13	16	22	19	12	13				

Max = average maximum daily temperature, Min = average minimum daily temperature, Daily = average daily temperature.

Table 4.2. Composition (canopy cover) of major species in the *Bromus–Poa* community at Ministik Wildlife Research Station, Alberta.

Speecies	Composition (%)
Grasses and Sedges	
Bromus inermis	41.3
Phleum pratense	5.8
Poa pratensis	22.1
Carex spp.	4.8
Other grasses	2.4
Forbs	
Achillea millefolium	1.5
Aster spp.	4.9
Cirsium arvense	1.9
Lathyrus spp.	2.2
Taraxacum officinale	8.8
Trifolium spp.	3.1
Other forbs	1.2

Table 4.3. Seasonal changes of herbage phytomass (g m^{-2}) components on the *Bromus-Poa* community at Ministik Wildlife Research Station, Alberta in 1997 and 1998 (n = 5).

Sampling period interval	Green herbage	Standing dead	Fallen litter
1997			
Spring (15 Apr-3 June)	96b[1]	77c	22b
Summer (4 June-31 Jul)	208a	135a	44a
Fall (1Aug-30 Sep)	127b	113b	35a
SEM	11	8	6
1998			
Spring (15 Apr-3 June)	84c	54b	17b
Summer(4 June-31 Jul)	178a	90a	45a
Fall (1Aug-30 Sep)	121b	74a	38a
SEM	13	9	7

[1]Within columns in a given year, means with different letters are significantly different ($P \leq 0.05$).

Table 4.4. Analysis of Variance (F-values) of total accumulated dry matter yield from clipping treatments at Ministik Wildlife Research Station in Alberta, 1997 and 1998.

Source of Variation	df	Yield (g m^{-2})
Year (Y)	1	4.50 *
Clipping Date (D)	2	65.22 **
Clipping Height (H)	2	20.75 **
Clipping Frequency (F)	2	31.63 **
YxD	2	4.41 *
YxH	2	2.98
YxF	2	2.60
DxH	4	0.58
DxF	4	17.05 **
HxF	4	1.49
YxDxH	4	1.65
YxDxF	4	0.82
YxHxF	4	0.56
DxHxF	8	1.34
YxDxHxF	8	0.89

* $P \leq 0.05$, ** $P \leq 0.01$.

Table 4.5. Effects of clipping date, height, and frequency on total accumulated dry matter yield (SD in parenthesis) of *Bromus-Poa* pasture in Alberta.

Treatments	df	Yield (g m^{-2})
Clipping Date (D)	2	
May 20		147.97 (12.37)a
June 22		95.27 (6.07)b
July 22		59.15 (4.07)c
Clipping Height	2	
2.5 cm		104.22 (10.61)a
7.5 cm		113.06 (10.04)a
15 cm		84.47 (7.75)b
Clipping Frequency	2	
3 weeks		64.33 (3.11)b
6 weeks		119.31 (6.54)a
9 weeks		118.75 (5.56)a

Within treatments, means with different letters are significantly ($P \leq 0.05$) different.

CHAPTER 5

IMPACTS OF WAPITI GRAZING AND TRAMPLING ON SOIL COMPACTION AND PASTURE PRODUCTION IN ASPEN BOREAL ECOSYSTEMS OF ALBERTA

INTRODUCTION

Wapiti and other diversified ruminant livestock are raised in pasture-based systems and provide the opportunity to enhance the efficient and sustainable use of these areas. Determining an optimal grazing rotation to ensure sustainable pasture use goes beyond the simple examination of vegetation removal. Modification of soil physical properties by hoof action, in concert with reduced vegetation cover, often results in increased bulk density and penetration resistance of soils (Rauzi and Hanson 1966, Hansen et al. 1970, Gifford and Hawkins 1978, Wood and Blackburn 1981, Blackburn 1984).

Several studies (e.g., Heydon et al. 1993) have demonstrated differences in foraging rates between deer grazing pastures with high and low forage availability, whereas others have shown little difference (e.g., Niezen et al. 1993, Gedir and Hudson 2000). The disparity in foraging behavior could ultimately affect pasture regrowth because treading is a key factor in pasture damage (Brown and Evans 1973). Consequently, manipulating variables that result in reduced animal travel, including forage availability (Abdel-Magid et al. 1987), could minimize pasture soil damage.

Goodloe (1969), Savory (1978, 1983), and Savory and Parsons (1980) along with other proponents of intensive rotational grazing systems have hypothesized that trampling by grazing animals under short-duration grazing might benefit certain soils through hoof action, and improve rangeland productivity in terms of nutrient cycling, water infiltration, and ultimately, livestock carrying capacity. However, research indicates that the use of heavy stocking rates under rotational grazing have consistently shown no significant hydrologic and carrying capacity improvement over continuously grazed pastures (Wood and Blackburn 1981, Blackburn 1984, Abdel-Magid et al. 1987, Heitschmidt et al. 1987, Dormaar et al. 1989, Chanasyk and Naeth 1995). The negative effect of continuous season-long grazing on soil physical properties has also received considerable attention (e.g., McCarty and Mazurak 1976, Thurow et al. 1986). Grazing animals may compact soil, mechanically disrupt soil aggregates and reduce soil aggregate stability (Knoll and Hopkins 1959, Beckmann and Smith 1974, Willatt and Pullar 1983).

The degree of compaction is affected by soil water content at the time of compaction (Gifford et al. 1977, Van Haveren 1983). In some rangelands, soil water in the Ah horizon decreased with increased grazing intensity (Johnston 1961, Johnston et al. 1971, Smoliak et al. 1972), whereas in others there was no effect (Lodge 1954). Reductions in soil water through grazing are attributed to altered rates of infiltration, combinations of soil compaction and sealing through animal trampling, reduced root channels through the soil, and reduced litter cover (Hagan and Peterson 1953, Hopkins 1954). Increased soil water with removal of herbage through grazing is attributed to reduced evapotranspiration (Baker and Hunt 1961, Van Riper and Owen 1964, Naeth and Chanasyk 1995). Despite numerous studies of the effects of cattle grazing on soil physical properties (e.g. Bryant et al. 1972, Naeth et al. 1990, Mulholland and Fullen 1991, Mapfumo et al. 1999), little information is available on the effect of farmed wapiti and other wildlife on soil properties. Moreover, animal trampling impacts on Luvisolic soils in aspen boreal forest ecosystems in Alberta have received little attention.

The purpose of this study was to investigate the effects of wapiti (*Cervus elaphus canadensis*) grazing on soil physical properties in an aspen boreal forest ecosystem and to relate these to *Bromus-Poa* pasture production. This was achieved by measuring soil bulk density, penetration resistance (soil strength) and soil water, and relating this to pasture production in an intensive short-duration and continuous grazing system. Specific objectives included testing of the following hypotheses: (1) Grazing would compact the soil by increasing both bulk density and penetration resistance and that these impacts would be related to grazing systems. (2) Natural processes would alleviate this compaction. (3) Grazing and trampling would reduce growth and pasture production.

MATERIALS AND METHODS

Study Site

The study was conducted at the Ministik Wildlife Research Station, located 50 km southeast of Edmonton, Alberta, Canada (53° 18′N, 114° 35′W). Vegetation of the area is classified as Boreal Mixed-Wood forest (Strong 1992), although homesteading (logging and clearing) in the early 1900s created characteristics more similar to those of Aspen Parkland. Major vegetation types include balsam poplar (*Populus balsamifera*) and trembling aspen (*P. tremuloides*) forests, *Carex* wetlands, and grasslands primarily composed of Kentucky bluegrass (*Poa pratensis*), smooth brome (*Bromus inermis*), Dutch white clover (*Trifolium repens*), and dandelion (*Taraxacum officinale*).

The climate is continental, typical of northern boreal forest regions. Ambient temperatures are characterized by seasonal extremes, ranging from a minimum of –49 °C in winter to temperatures exceeding 32 °C in summer (Olson 1985). Snow cover is usually established in late November, and normally remains into April. The growing season typically extends from May until September. Grasses become senescent in October and by the end of the month deciduous trees have shed their leaves.

The Ministik area is underlain by the Edmonton Formation, an Upper Cretaceous bedrock of shales, sandstones, and coal interbedding (Bayrock 1972). The area exhibits gently rolling hills and shallow depressions, typical of hummocky dead-ice moraine. Numerous sloughs are characteristic of the area. The study was conducted on a Luvisolic soil of loam texture. On average, the soil (0-15 cm depth) contained 25% clay, 33% silt, 42% sand and 2.1% organic matter. Soil pH using distilled water was 5.5.

Experimental procedures

Study plots were located in an area that had been continuously grazed in summer by wapiti until the end of 1996, but subsequently rested for this study. The previous stocking rate was near 2.0 AUM ha^{-1} (with approximately 50% herbage utilized), which is considered moderate for wapiti hinds under yearlong continuous grazing at the station. Grazing trials were established in 1997 and run for 2 years from early May to late September. The grazing treatments studied were: continuous grazing (CG) stocked at a moderate rate of 2.08 AUM ha^{-1}; and short-duration grazing (SDG) stocked at a high rate of 4.16 AUM ha^{-1} (with approximately 75% herbage utilized). Both treatments were stocked with wapiti hinds that weighed an average of 290 kg. The two CG replicate pastures, each 2.2 ha in size, were stocked with five wapiti hinds while the two 1.5-ha SDG pastures were rotationally grazed by 15 wapiti hinds. Animal movement between SDG pastures was timed to prevent excessive use during periods of rapid forage growth and to allow recovery following grazing. Grazing periods in the SDG pastures varied from 7 to 10 days, with 30 to 40 days of rest between grazing periods. There were only 2 paddocks in the SDG because of logistic constraints and conflict of interests from concurrent research being carried out at the station. During the rest periods, the 15 animals were moved to other pastures for concurrent behavioral studies. All pastures were considered to be nearly equal in carrying capacity when the trial began, and the overall range condition was considered good.

Immediately after every grazing period (within 1-2 days), ten 40 x 40 cm plots were clipped at ground level in the SDG treatment. Vegetation in the CG treatment and in the ungrazed control (UNG) area adjacent to the grazed pastures was sampled in an identical manner. Data from May to June sampling dates (May 10, May 20, June 19 and June 29) were pooled into (spring), while those from August to September (August 3, August 13, September 17 and September 28) were pooled into (fall) estimates. Herbage was hand sorted into components of green herbage, standing dead and fallen litter, dried at 60°C, and weighed.

To evaluate the combined effect of defoliation and trampling on soil compaction, bulk density and penetration resistance were measured in the treatment areas at the end of each grazing period. Soil water was also measured in each pasture with five sample sites randomly chosen for core sampling. Around each sample site penetration resistance was measured to a 15-cm depth at 2.5-cm intervals at five different locations, using a small hand-pushed cone penetrometer (30° angle and basal area of 3.2 cm^2). A 7.5-cm diameter hand-driven Uhland core sampler was used to collect 15-cm long samples for bulk density measurements. Each sample was sectioned into six segments of 2.5-cm depth intervals. Moist soil samples were immediately weighed and later oven dried at 105 °C to determine dry bulk density and gravimetric water content. The same soil parameters were measured in the UNG pasture. The soil water contents, bulk densities and penetration resistances measured in the UNG pasture (averaged data) were then compared with corresponding values obtained in the grazed treatments.

Statistical Analyses

Statistical analyses were conducted using the SAS generalized linear models procedure (SAS Institute, Inc. 1989) to compare bulk density, penetration resistance, soil water and herbage production among the three treatments. Post-hoc mean comparisons were done on all significant treatment means using Tukey's method ($P \leq 0.05$). To compare bulk densities between spring and fall for each depth interval, the Student's t-test for paired samples (Snedecor and Cochran 1989) was used. To compare the time trends in responses to the three treatments, the GLM procedure (Repeated Measures Analysis of Variance) was used.

RESULTS

Bulk Density

Overall, grazing by wapiti, regardless of the type of grazing system (e.g. CG or SDG), had the effect of increasing soil bulk density (BD). These differences were most pronounced at soil depths less than 10 cm, but also varied temporarily, with the most pronounced difference in fall 1998, followed by spring 1998, fall 1997, and finally spring 1997 (Table 5.1).

Comparison of the two grazing systems indicates that SDG generally had greater BD than the CG pastures. These differences were most evident at the soil depths down to 7.5 cm in spring of 1997, 10 cm in fall of 1997, 5 cm in spring of 1998, and 12.5 cm in the fall of 1998 (Table 5.1). Relative to SDG, the CG pastures wee much more similar to the UNG treatment, with only occasional increases in BD (e.g., 0-2.5 and 7.5-10 cm in fall 1997, and 0-2.5 cm in spring 1998, and 0-5 cm in fall 1998 (Table 5.1).

Bulk densities in the 0 to 7.5-cm and 12.5 to 15-cm depth intervals were significantly ($P \leq 0.05$) lower in the spring of 1998 than in the fall of 1997 (Table 5.2). For the 7.5- to 12.5-cm interval, BD were similar between the two times.

Over winter change in BD between fall 1997 and spring 1998 was significantly greater for SDG than that for CG and UNG for the surface 2.5-cm (Table 5.3). At depths between 2.5- to 15-cm, the changes in BD were similar between all three grazing treatments. Changes in BD below 7.5cm soil depth were generally small (Table 5.3). The repeated measures analysis of variance failed to show significant year by grazing time interaction or their interactions with grazing system (data not shown).

Penetration Resistance

Generally, differences in penetration resistance (PR) occurred between grazing treatments (SDG > CG ≥ UNG). Also, PR in fall 1998 > fall 1997 > spring 1998 > spring 1997. Comparison of the two grazing systems indicates that SDG generally had greater PR the CG pastures. These differences were most evident at the soil depths down to 5 cm in spring 1997, 7.5 cm in fall 1997, 5 cm in spring 1998, and 10 cm in fall 1998 (Table 5.4). Relative to SDG, the CG was much more similar to the ungrazed treatment at the surface, with exceptional increase in PR in spring 1998 (Table 5.4). The repeated measures analysis of variance failed to show significance in year by grazing time interactions or their interactions with grazing system (data not shown).

In general, the PR measured in spring and fall1997 were lower than spring and fall 1998. In the fall of both years, PR measured deeper than 2.5-cm were greater than 2 MPa, while PR in spring of both years were generally less than 2 MPa.

Soil Water

Generally, grazing reduced soil water up to a depth of 15 cm in fall and up to 7.5 cm depth in spring (Table 5.5). In addition, soil water content under SDG was significantly ($P<0.05$) lower than CG. This trend occurred in the top 5 cm of soil regardless of sampling time, but extended to 7.5 and 10 cm in spring of 1997 and 1998, respectively. By the fall of 1998, the SDG treatment remained lower in soil water at all depths sampled. Because of high precipitation in 1997 (Table 5.6), especially at the time of sampling, soil water content was generally higher in 1997 than in 1998. The repeated measures analysis of variance failed to show significance in year by grazing time interactions or their interactions with grazing system (data not shown).

Herbage available under grazing

Live green, standing dead and litter phytomass was generally greater in the CG than the SDG treatment (Table 5.7). Grazing under SDG resulted in less herbage on the pastures than that of CG by 16% and 26%, respectively in spring and fall 1997 (Table 5.7). The same trend was observed in spring and fall 1998; a decrease of 22% and 24%, respectively. Herbage available on pastures was generally greater in 1997 than 1998, likely because of high precipitation in 1997. As expected, grazing treatments reduced herbage on grazed pastures compared to UNG pasture. Herbage reduction was evident in all three herbage pools (green herbage, standing dead and fallen litter). In the absence of grazing, there was trend towards standing dead and litter accumulation, e.g., by the fall of 1998 (Table 5.7).

DISCUSSION

Grazing impacts on soil physical properties

Short-duration grazing is a relatively new concept for western Canada and controlled research studies are few (Dormaar et al. 1989). From the standpoint of livestock distribution and production, the grazing system is encouraging. Nevertheless, the hypothesis of potential benefit to soil physical properties from intensive livestock activity at high stocking rates is questionable (Heitschmidt et al. 1987, Dormaar et al. 1989).

Soil bulk densities were significantly greater up to 10-cm depth in the SDG pastures than those in the CG pastures and UNG pasture due to trampling. Greater amounts of fallen litter, and a lower stocking rate and density in the CG pasture may have reduced trampling effects on the soil. Although it is recognized that stocking rate and grazing system covaried in this study, stocking rate was more likely the principal factor that caused differences to occur between treatments because the time trends in responses to grazing treatments were not significant. Other studies on Alberta pastures containing Orthic Black Chernozems found trampling associated with very heavy grazing caused significantly greater bulk densities in the top 7.5-cm (Naeth et al. 1990, Chanasyk and Naeth 1995) and 2.5-3 cm of soil (Dormaar et al. 1989, Mapfumo et al. 1999). Differences in the depth of compaction in our study and others could be due to differences in soil type. Soil properties such as texture, organic matter, water content and other environmental conditions govern the degree to which compaction occurs (Mapfumo et al. 1999). For example, my soil was Luvisolic with an organic matter content of 2.1%

compared to as high as 9.5% in the study area of Mapfumo et al. (1999). These characteristics, combined with a greater clay content (25% compared to 15% in others) may have resulted in greater soil water and greater potential for compaction in general. Hence, the variation of these factors makes it difficult to compare results of grazing impacts on actual BD values among sites.

The idea that benefit can be derived from short-term, high intensity physical impact of livestock is the principal foundation upon which many proponents of SDG base their support. The physical impact is believed to chip or churn the soil and break up surface crusting without compacting the soil (Goodloe 1969, Savory and Parsons 1980). However, trampling due to SDG on Black Chernozems in Alberta (Dormaar et al. 1989, Chanasyk and Naeth 1995) and this study conducted on Luvisolic soil had no clear advantage for breaking up surface crusting and improving soil properties that are normally correlated to water infiltration. Trampling a dry soil did, indeed, chip and churn the soil surface in other studies (e.g. Warren et al. 1986). However, the hoof action reduced the size of naturally occurring soil aggregates and increased density of the surface soil layer.

The observed decrease in BD in the top 7.5cm and 12.5 to 15-cm over winter is consistent with the study by Mapfumo et al. (1999) in central Alberta on Chernozemic soil. They found a decrease in BD over winter in the top 2.5-cm. These observations support the assertion that freeze-thaw activities can alleviate the effect of animal trampling on soils (Abdel-Magid 1987), and is likely a very important mitigator of soil compaction in central Alberta where moisture is abundant and winters are long and cold.

Penetration resistance is frequently used to measure soil strength. Animal hooves can exert pressure up to 200 kPa, which is considerably greater than the pressure exerted on the soil surface by a tractor, which can range from 30 to 150 kPa (Proffitt et al. 1993). The maximum depth of soil at which changes in PR occurred in this study was 10 cm. The PR was also significantly greater under SDG than CG.

In many studies, root elongation has been linearly related to PR up to 2 MPa, which has been used as the threshold beyond which root growth becomes restricted (Taylor et al. 1966, Graecen 1986, Naeth et al. 1991). If we accept this value as critical for limiting growth, then root growth was most likely affected in the fall of both years at depths of 2.5- to 15-cm for both grazed treatments. Additionally, root growth was less likely affected in the spring of each year because of PR values around 2 MPa. An empirical linear relationship between PR, BD and soil moisture was observed in all experimental periods (not shown). This observation is consistent with other field studies that report PR increases with increased BD and decreased soil water content (Malqueen et al. 1977, Ehlers et al. 1983, Busscher et al. 1987, Mapfumo and Chanasyk 1998). These relationships have ramifications to pasture production because this study has also shown that soil water differences explain variation in pasture production in each year.

The influence of soil water on pasture phytomass production followed the same pattern as that reported by Levitt (1980); aboveground production was reduced with increasing water stress. Soil water was generally reduced at all depths by grazing. This agrees with studies in native rangeland grassland ecosystems in Alberta in which grazing decreased soil water to a 10-cm depth (Smoliak et al. 1972) and to a 30-cm depth (Johnston 1961, Johnston et al. 1971, 1972, Naeth et al. 1991). Soil water was greater in ungrazed exclosures compared to short-duration grazed treatments near Fort Macleod, Alberta (Dormaar et al. 1989). Reduced soil water under grazing is generally attributed to reduced infiltration rates as trampling compacts and seals the soil surface (Llacos 1962), a finding backed up by the changes in BD and PR. Grazing also reduces litter, which affects soil water through increased evaporation and reduced infiltration (Tomanek 1969, Naeth et al. 1991).

Grazing impacts on pasture production

The results of this study show that differences occurred between grazing treatments relative to quantity (CG>SDG) of standing crop (green and standing dead) and fallen litter (CG>SDG). These results agree with findings of other studies (e.g. Holechek 1980, Heitschmidt et al. 1987) which indicated that SDG reduced the accumulation of standing dead vegetation and fallen litter. My study indicated that greater litter appeared to be removed by trampling and or consumption under SDG than CG. As grazing animals trample and remove live vegetation and litter mass, production is reduced, especially in xeric ecosystems (Johnston et al. 1971, Willms et al. 1986). Though Savory and Parsons (1980) suggest SDG can increase forage production through hoof action, there is abundant literature suggesting that the amount of physical animal impact attained at high stocking rates deters plant succession by reducing the amount of protective plant cover (e.g. Heitschmidt and Walker 1983). My results, therefore, support the conclusion that high intensity rotational grazing systems do not eliminate the potential hazards commonly associated with excessive rates of stocking on rangelands (Heitschmidt et al. 1987, Dormaar et al. 1989). These results also clearly demontrate that the dangers of high stocking apply to diversified livestock such as wapiti, and tame pastures as well as native grasslands (e.g., Willms et al. 1985, Dormaar et al. 1989), including Luvisolic soils in the more mesic Boreal Mixed region of Alberta.

CONCLUSIONS

Wapiti grazing effects on BD and PR were evident in the top 10 cm of the Luvisolic soil examined here. In general, grazing effects on soil properties were more evident in fall than in spring. Natural alleviation processes such as freezing and thawing activities likely reduced the effects of animal trampling in spring, as BD decreased over winter, especially in the upper 7.5-cm. High intensive SDG compacted the soil more than moderately stocked CG, indicating the former has no advantage over the latter on soil physical properties, at least in the short term. Moreover, SDG removed more green herbage and standing dead material and reduced fallen litter more than that of CG. Long-term evaluation of the effects of grazing systems on soil physical characteristics may help to address seasonal, yearly, and inherent variability in these ecosystems.

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Table 5.1. Mean bulk densities (Mg m^{-3}) at different depth intervals (cm) for *Bromus-Poa* pasture under short-duration and continuous grazing by wapiti versus ungrazed pasture at Ministik Wildlife Research Station, Alberta

Sampling Time	Grazing System	Depth intervals					
		cm					
		0-2.5	2.5-5	5-7.5	7.5-10	10-12.5	12.5-15
Spring (May - June) 1997							
	Short-duration	1.05a	1.07a	1.10a	1.15a	1.18a	1.21a
	Continuous	0.75b	0.90b	0.85b	1.16a	1.20a	1.22a
	Ungrazed	0.85b	0.90b	0.90b	1.02a	1.15a	1.07a
Fall (August - September) 1997							
	Short-duration	1.41a	1.41a	1.37a	1.26a	1.25a	1.27a
	Continuous	1.10b	1.21b	1.18b	1.19b	1.22a	1.23a
	Ungrazed	0.95c	1.15b	1.11b	1.08c	1.10a	1.14a
Spring (May - June) 1998							
	Short-duration	1.05a	1.08a	1.12a	1.16a	1.18a	1.20a
	Continuous	0.98b	0.91b	0.95ab	1.14ab	1.16a	1.17a
	Ungrazed	0.81c	0.87b	0.90b	1.05b	1.11a	1.10a
Fall (August - September) 1998							
	Short-duration	1.38a	1.37a	1.35a	1.30a	1.24a	1.20a
	Continuous	1.24b	1.21b	1.17b	1.19ab	1.14b	1.13a
	Ungrazed	0.96c	1.07c	1.11b	1.05b	1.09b	1.04b

Within each sampling time and depth interval, means followed by the same letter are not significantly different ($P \leq 0.05$).

Table 5.2. Average bulk densities in spring and fall at each depth interval (cm) averaged across grazing intensity, and the significance levels obtained using Student's *t*-test.

Bulk density (Mg m^{-3})			
Depth interval	Fall 1997	Spring 1998	Significance level (α)
0-2.5	1.15	0.95	0.014
2.5-5	1.26	0.95	0.002
5-7.5	1.22	0.99	0.003
7.5-10	1.18	1.12	0.102
10-12.5	1.19	1.15	0.253
12.5-15	1.21	1.16	0.023

Table 5.3. Changes in average bulk densities[z] over winter (Fall 1998 vs. Spring 1998) at different depths (cm) for *Bromus-Poa* pasture under short-duration and continuous grazing by wapiti versus ungrazed pasture at Ministik Wildlife Research Station, Alberta.

Grazing System	0-2.5	2.5-5	0-2.5	7.5-10	10-12.5	12.5-15
			Depth interval			
Short-duration	-0.36a[y]	-0.33a	-0.25a	-0.10a	-0.07a	-0.07a
Continuous	-0.12b	-0.30a	-0.23a	-0.05a	-0.06a	-0.06a
Ungrazed	-0.10b	-0.20a	-0.21a	-0.03a	+0.01a	-0.04a

[z] Change in bulk density = spring bulk density – previous fall bulk density for a given depth interval.

[y] Over winter decreases in bulk density have minus (-) signs.

a,b Within columns, means followed by the same letter are not significantly different from each other at 0.05 probability level.

Table 5.4. Mean penetration resistance (MPa) at various soil depths for *Bromus-Poa* pasture under short-duration and continuous grazing by wapiti versus ungrazed pastures at Ministik Wildlife Research Station, Alberta

Grazing Time	Grazing System	Depth						
		cm						
		surface	2.5	5	7.5	10	12.5	15
Spring (May - June) 1997								
	Short-duration	1.27a	1.64a	1.78a	1.77a	1.84a	1.92a	1.95a
	Continuous	0.92b	1.42b	1.54b	1.41a	1.50a	1.68a	1.75a
	Ungrazed	0.85b	1.29c	1.47b	1.32a	1.31b	1.41b	1.55b
Fall (August - September) 1997								
	Short-duration	1.61a	3.40a	2.98a	2.70a	2.85a	3.00a	3.35a
	Continuous	1.45b	2.66b	2.50b	2.45b	2.90a	3.18a	3.10a
	Ungrazed	1.35b	1.97b	1.81c	1.97c	1.90b	1.95b	1.91b
Spring (May - June) 1998								
	Short-duration	1.56a	2.60a	2.14a	1.96a	2.05a	2.00a	1.86a
	Continuous	1.20b	2.18b	1.74b	1.52a	1.55ab	1.60ab	1.46a
	Ungrazed	1.11c	1.58c	1.52c	1.42a	1.41b	1.44b	1.45a
Fall (August - September) 1998								
	Short-duration	1.95a	3.58a	3.86a	3.93a	4.02a	3.54a	3.45a
	Continuous	1.42b	2.56b	3.18b	2.98b	3.06b	3.02a	3.20a
	Ungrazed	1.36b	1.98c	1.95c	1.91c	1.99c	1.99b	1.98b

Within each sampling time and depth interval, means followed by the same letter are not significantly different ($P \leq 0.05$).

Table 5.5. Mean moisture content (g/100 g) at different depth intervals (cm) for *Bromus-Poa* pasture under short-duration and continuous grazing by wapiti versus ungrazed pasture at Ministik Wildlife Research Station, Alberta

Sampling Time	Grazing System	Depth Intervals cm					
		0-2.5	2.5-5	5-7.5	7.5-10	10-12.5	12.5-15
Spring (May - June) 1997							
	Short-duration	22.7c	23.0c	24.3c	24.5a	23.8a	22.8a
	Continuous	25.2b	26.4b	27.6b	26.9a	25.5a	23.9a
	Ungrazed	31.3a	30.5a	29.8a	28.4a	27.1a	25.2a
Fall (August - September) 1997							
	Short-duration	13.7c	15.8b	16.1a	15.3a	15.2b	14.8b
	Continuous	14.8b	17.4a	16.5a	16.4a	15.9b	15.7b
	Ungrazed	18.5a	18.0a	17.2a	17.7a	18.3a	17.5a
Spring (May - June) 1998							
	Short-duration	22.5c	22.1c	23.8c	24.3b	23.3a	22.2a
	Continuous	26.0b	25.4b	26.2b	24.0a	23.0a	22.8a
	Ungrazed	30.0a	27.5a	28.5a	26.1a	24.1a	23.0a
Fall (August - September) 1998							
	Short-duration	11.3b	12.8b	13.3b	13.3b	13.0b	12.7c
	Continuous	14.1a	15.7a	16.5a	16.1a	16.0a	15.8b
	Ungrazed	15.0a	16.8a	17.2a	17.5a	18.1a	18.4a

Within each sampling time and depth, means followed by the same letter are not significantly different ($P \leq 0.05$).

Table 5.6. Monthly precipitation for Ministik Wildlife Research Station, Alberta, during the growing seasons of 1997 and 1998.

	Precipitation (mm)						
Year	April	May	June	July	Aug.	Sept.	Total
1997	38	69	149	28	52	84	420
1998	34	38	111	89	21	50	343
1961-1990	10	40	77	89	78	40	334

Table 5.7. Herbage availability (g m^{-2}) on *Bromus-Poa* pasture under short-duration and continuous grazing by wapiti versus ungrazed at Ministik Wildlife Research Station, Alberta

Sampling Time	Grazing System	Herbage component		
		Green herbage	Standing dead	Fallen litter
Spring (May - June) 1997				
	Short-duration	60c[z]	46c	16b
	Continuous	71b	55b	19b
	Ungrazed	90a	70a	55a
Fall (August - September) 1997				
	Short-duration	68c	77c	23c
	Continuous	89b	103b	35b
	Ungrazed	105a	134a	85a
Spring (May - June) 1998				
	Short-duration	51c	33c	12b
	Continuous	65b	42b	16b
	Ungrazed	81a	79a	65a
Fall (August - September) 1998				
	Short-duration	55c	61b	21b
	Continuous	74b	73b	33b
	Ungrazed	90a	117a	93a

[z] For each sampling time and within each column, means followed by the same letter are not significantly different ($P \leq 0.05$).

CHAPTER 6

SYNTHESIS

GENERAL DISCUSSION

The model presented in this section is a natural outcome of my thesis research and serves as a synthesis for the field and laboratory work described in the previous chapters. The model attempts to integrate what has been learned and provides a framework for the field studies. This is done through exploring the interaction between instantaneous initial growth rate (g) and vegetation phytomass (V) and its application to grazing studies.

PASTURE MODEL FOR FARMED WILDLIFE

Management of pasture-based systems for bioeconomic sustainability involves many interacting factors. Simulation models, such as Texas A&M beef cattle simulation model (Sanders and Cartwright 1979, Cartwright and Doren 1986), Kentucky beef-forage model (Loewer et al. 1983, Lower and Smith 1986), Cornell net carbohydrate and protein systems (Fox et al. 1995) and GRASSGRO (Cohen et al. 1995), have been developed for evaluating pasture and beef cattle production. These have been immensely useful in management and planning of livestock production.

Their value for wildlife production systems is expected to be even greater because of the greater importance of range and pasture for wild ruminants, which are able to forage through snow and tend to be finished on pasture (they perform poorer than cattle in feedlots). I expect both the impacts and responses to pasture use of wild ruminants to be different than domestic livestock. I also expect considerable gains by common-use or leader-follower grazing by several wildlife species. Simulation modelling could evaluate these differences in management.

Hudson and Gedir (1998) attempted to develop dynamic feeding standards for farmed deer along the lines of the National Research Council Nutrient Requirements for farmed wildlife. That model focussed on the bioenergetics and behaviour of wapiti (elk, *Cervus elaphus*) but used a very simplistic treatment of pasture production, particularly the feedback effects of grazing. This study attempts to fill this important information gap (pasture production) by modeling the dynamics of pastures grazed by wapiti and/or bison to help evaluate stocking and rotational grazing strategies. This study provides a model of seasonal pasture production and utilisation for management of farmed game. This should improve sustainability of pasture production and encourage a more strategic approach to supplemental feeding. The operational objectives were: 1. To develop and calibrate a computer simulation model to predict pasture condition and animal performance when wild ruminants (wapiti and bison) are grazed together or in a leader-follower system, and 2. To illustrate the application of this model in the evaluation of grazing management systems that optimise animal production, minimise supplemental feeding, and ensure sustainability of range/pastures grazed by farmed wildlife/diversified livestock.

The model was developed using functional relationships derived from studies of pasture dynamics at the Ministik Research Station in 1997 and 1998, and Elk Island National Park and the University of Alberta greenhouse in 1999 (Chapters 2-5). It is a proof-of-concept model that should be tested using independent data sets from a variety of field conditions. The model is constructed around two key relationships; namely, that existing between pasture growth rate and accumulated phytomass, and between foraging rates and sward characteristics. These are key elements of the plant-animal interaction and central considerations for management decisions.

MODEL DEVELOPMENT

The high costs of containment of wild ruminants have lead to rather intensive (e.g., small landbase) pasture use. Pastures are typically grazed year round although supplemental feed is offered when pasture supplies are considered to fall short of animal requirements.

My interest in this preliminary study was to develop an appropriate model scope, structure and resolution rather than to conduct a thorough analysis of functional relationships and validation. I considered that a useful model for farmed game on pasture must:

1. Simulate the dynamics of herbage pools, and nutrient intake by wild ruminants in all seasons of the year.

2. Represent the feedback effects of grazing on the rate of pasture production and the effects of pasture characteristics on habitat and forage selection and intake. Pastures typically are grazed throughout the growing season.

3. Allow for rotational grazing of paddocks by the same or different species. Leader-follower grazing by wapiti and bison is being explored as a means to manage pastures.

4. Account for selection of mixed open and closed habitats. Wapiti, in particular, use a wide variety of forages in a diversity of habitats at various times of year. Closed habitats provide security and thermal shelter and should be provided in paddocks.

5. Provide summary measures of pasture and animal performance to evaluate grazing strategies.

Modeling Approach

The model is a dynamic deterministic simulation and is programmed using STELLA simulation software by High Performance Systems. STELLA was selected for its simplicity, graphic object orientation, strict adherence to systems dynamics conventions, and availability of a free player for both MS-Windows and Mac OS. Versions beginning with 5.0 Research allow subscripted variables, offering new scope for dealing with distributed systems.

The pasture model predicts snow pack, soil moisture, forage yield and quality, and habitat/forage selection and nutrient intake rates of wapiti and bison managed in a mixed or leader-follower grazing system. The model defines the seasonal environment experienced by the grazing animal and driving forage production in terms of temperature, precipitation, snow pack, forage biomass and quality. Season, temperature, soil moisture and forage removals influence pasture dynamics. Pools of green forage, dry forage and litter determine foraging rates and diet quality. The model operates on a daily time step. In the base case, animals are assumed to have access to several paddocks each containing several habitats or pasture types with different parameters. Default settings assume that these are open and wooded habitats in the aspen parkland of western Canada.

The model is organized into four submodels: edaphic factors, below ground phytomass, aboveground vegetation growth and use, and mixed species grazing strategy.

Edaphic factors

The edaphic submodel simulates soil moisture within the rooting zone, a driving factor in plant growth, as the balance of precipitation, percolation, and evapotranspiration. It has the dimensions of paddock and habitat because green phytomass, a key determinant, varies in these dimensions. Snowpack (cm) also is modeled because it influences both soil moisture and access by grazing animals (Figure 6.1). Soil water in excess of field capacity is lost through runoff and percolation. The soil water pool is further reduced by evapotranspiration which is influenced by both ambient temperature and green phytomass. Water in excess of the permanent wilting point is available to support plant growth.

Below-ground phytomass

The belowground root phytomass submodel accounts for the cumulative effects of growing conditions and grazing and similarly has dimensions of paddock and habitat (Figure 6.2). This allows the carryover effects of heavy grazing on root development into subsequent years. Net root production depends on the photosynthetic capacity of green phytomass. Loss of root phytomass is independent of ambient temperature.

Vegetation growth and utilisation

The vegetation-pool submodel accounts for pasture growth, use (habitat selection), stocking rates and animal intake (Figure 6.3). A key feature of the pasture model is the explicit treatment of the impacts of grazing on regrowth of vegetation. Subject to temperature and soil moisture, the rate of pasture growth is defined in terms of the regenerative power of green plant tissue and feedback from accumulated green and dry biomass. By removing accumulated biomass, grazing can stimulate forage growth but heavy grazing ultimately reduces regenerative capacity.

For the base scenario, in each of two paddocks and two habitats (open and wooded), change in vegetation components is traced through green material, standing dead and litter pools. The regeneration of new green vegetation is controlled by soil moisture, temperature and accumulated plant biomass. It matures and persists in the standing dead pool until it becomes litter, which ultimately decays. Grazing animals remove material from green and standing dead pools of each habitat according to the rules established for the species. The two habitats differ in maximum forage and rate of snow accumulation and melt. Biological processes are summarized in computational blocks that interface edaphic environment, pasture growth and animal use.

Interaction and Interface

Interaction is through a control panel. The model invites inputs in several ways. Graphical parameters such as seasonal (monthly) temperature, precipitation and digestibility, of each forage pool can be sketched to represent the year beginning September 1. Numerical parameters describing the animal, pasture and management are entered in a tabular form with a page tab. There also is a switch to compare continuous and rotational grazing.

Major tracking variables are summarized in graphic pads monitoring general parameters (weight, intake, conceptus weight, and milk production), activity budgets, feeding constraints, digestive kinetics, body composition and energy and nitrogen balance.

Monthly precipitation and average temperatures for Ministik Wildlife Research Station were presented in Table 4.1 in Chapter 4. Soil water measured at the site is used in the pasture simulation. These values describe the conditions under which functional relationships and calibration information were derived.

Functional Relationships

The dynamics and general stability of grazing ecosystems are determined by two processes; namely, (1) plant growth and (2) grazing efficiency. In turn, these two linked processes are influenced by edaphic factors such as soil moisture, and snow cover.

Snow pack and soil moisture

Climatic and edaphic conditions are site-specific and were supplied as inputs to the model. However, I modeled snow pack in each habitat type from precipitation during cold weather modified by interception by the forest canopy and differential rates of melt. This crude approach was tuned to fit empirical data. Snow cover in grassland areas during winter months significantly exceeded that in wooded areas (Figure 6.4). The snow densities were not significantly different at 0.27 and 0.26 g cm^{-3}, respectively. Greater interception within aspen forests reduces snow accumulation. Wind in open areas results in a redistribution of snow creating higher spatial variance despite the overall greater snow depths. Such topographic effects are not specified in the model. Snowmelt proceeds most rapidly in open areas but the larger snowpack means that the ground is bare at about the same date as wooded areas in early April.

Soil moisture within the rooting zone, a driving factor in plant growth, was modeled simplistically as the balance of precipitation, runoff/percolation, and evapotranspiration. Precipitation is generated from monthly means. Runoff and percolation are related to site characteristics such as topography and soil texture. Evapotranspiration is considered to be most strongly influenced by air temperature and green phytomass. Soil fertility and the influence of animals on nutrient recycling are not explicitly represented. Rather, the general productivity of the site is established by parameters defining plant growth.

Plant growth

Growth of pasture is typically sigmoidal. Relative growth is described:

$$G = g\,V\,(1 - V/K)$$

where G is change in herbage phytomass over a given period of time (primary productivity), g is instantaneous initial growth rate, V is herbage phytomass (per unit area) and K is the maximum grazable vegetation (carrying capacity). The curve generally is convex. The increase in gradient in the low phytomass range expresses the increase in photosynthesis capacity with increasing leaf area. The plateau and the decline in higher phytomass range expresses self-interference (shading, competition). When V = K, maintenance losses equal photosynthesis and G = 0 (Noy-Meir 1975).

This idealized pattern is modified by the genetic potential of plants, soil moisture, soil nutrients, air temperature and light. Okello (1996) determined forage productivity of ungrazed (protected) and continuously grazed (irrigated, unirrigated and manured) pastures at Ministik by clipping and weighing herbage phytomass. Irrigation was done using a sprinkler in the evenings at least every two days except when it had rained heavily. To evaluate nutrient enrichment he selected a "manured plot" with a high concentration of fecal pellets (and possibly urine deposits) from previous winter accumulation. These field trials suggest that the parameter K is more sensitive than g to site factors (Figure 6.5). Using this graph, values for g and K can be assigned to reflect general site-specific growing conditions. Linking K to soil moisture levels captures dynamic effects. At the present time, this is done in a rather simplistic way by allowing the initial value of K to be increased by 20% as soil moisture increases from 50 to 100% of field capacity.

Plant consumption

Functional response is expressed as the daily rate of consumption of vegetation by a herbivore per unit area, c. This relationship has the shape of a saturation curve when consumption is plotted against some measure of vegetation. Consumption increases at low V and reaches a plateau at high V. At low V, intake is limited by herbage availability and increases with it while, at high V, a saturation of intake capacity is reached. One form of this relationship is the Michaelis-Menton equation (Wilmshurst et al. 1995):

$$c = c_{max} V / (V + K)$$

This relationship has also been expressed as a first-order exponential equation (Caughley and Sinclair 1994): Intake = c (1 – Exp (-b V), where c is a constant and b is the slope of the curve that indicates grazing efficiency of a herbivore.

Pasture phytomass/structure and snow cover are the most important determinants of foraging rates and daily intakes. The feeding rate on foliage and browse is not very sensitive to biomass because of the clumped distribution of these forages. However, intake on grass pastures is determined largely by standing crop although different maximum feeding rates occur on green and dry forage. For example, the maximum feeding rate of wapiti (15 g/min or 9 kg/d) is reduced to 50% at about 500 kg/ha on cured pasture and below 400 kg/ha on green swards (Figure. 6.6). Bison have much higher feeding rates (55 g/min or 15 kg/d) than wapiti and forage efficiently on short dense swards (800 kg/ha) (Hudson and Frank 1987).

Resource Use Behaviour

Grazing animals are able to select diets both by selecting feeding habitats and green/dry pools within each habitat. Spatial behaviour of wapiti on seasonal pastures responds largely to foraging opportunities (Watkins et al. 1991; Wilmshurst et al. 1995) and the same will be assumed of bison. Time spent grazing in each of two habitats is considered linearly proportional to the relative green forage pools.

Grass swards offer modest opportunity for selection within a feeding patch because green and dry forage are intermixed. Selectivity is allowed by assigning a preference factor for green:dry pools and applies this to the size of the respective forage pools. From these rules regarding resource use, seasonal diets are composed. Bison are expected to be less selective than wapiti because they are more tolerant of low quality feeds and are less able to be selective with their wider muzzles and incisor bars.

EVALUATION AND APPLICATION

Models are never completely validated since critical proof must come from long-term studies. They are not right or wrong, simply more or less useful in ordering current information and guiding management or future research. Confidence is gained as models provide realistic predictions under a growing range of circumstances. This section displays simulations of phytomass dynamics under conditions for which I have at least some empirical data.

Management Scenario

Because of the relatively high costs of containment, wapiti and bison tend to be heavily stocked. Although bison are finished in feedlots, the production system is largely pasture-based. Wild ruminants are able to forage through snow allowing year-round grazing.

Game farmers usually begin their operations with a paddock the minimum size required for licensing (e.g. 10 acres in Alberta). They expand with additional paddocks as herd size increases. Some farmers raise several species that are often grazed in tandem. Deer farmers often use bison to 'clean' deer paddocks; others will hay paddocks in late summer. Wapiti often are grazed first in a rotation to open the vegetation and improve conditions for bison that follow the sequence. Stags are sometimes grazed with bison on larger paddocks. Many game farmers fear that wapiti calves will be injured or killed by bison so cow-calf groups usually are grazed separately.

As farms expand, managers may opt to simply open gates to continuously-graze larger areas. However, many like to take the opportunity to control parasites by pasture rotation. Whether rotational grazing has the additional benefit of improving animal performance and pasture productivity is unknown.

Several constraints and rotation rules may be applied. On many farms, winter or calving paddocks are constrained by access or facilities. Managers may decide to rotate herds according to predetermined calendar periods (e.g., every 2 weeks) or apply more complex rules such as to move animals to the 'best' pasture despite its grazing history. This model is designed to explore the impacts of single or mixed species grazing strategies using the dual criteria of animals and pastures.

Empirical Data used for Calibration

Ungrazed swards

Before going on to the more complex picture expressed by grazed swards, I explored concordance of the model with growing-season development of forage pools in protected plots. Protected plots were monitored at Ministik Wildlife Research Station in 1997 and 1998 and in Elk Island National Park in 1999, both located east of Edmonton, Alberta in the Cooking Lake glacial moraine. Vegetation is classified as

Boreal Aspen Mixed Wood forest (Rowe 1972). The experimental pastures were primarily composed of Kentucky bluegrass, smooth brome, white clover and dandelion. Accumulation of green, dry and litter pools are shown in Fig. 6.7.

The model was able to reproduce these general dynamics of vegetation pools. The difference in pasture production between wet and dry years at Ministik was easy to mimic. The greater accumulation of litter at Elk Island than Ministik apparently was due to accumulation for several years before the plots were monitored at Elk Island.

Clipped swards

Grazing may influence the dynamic interaction between plant growth rates and phytomass, as well as change the proportions of green herbage, standing dead, and fallen litter pools. Clipping experiments were conducted to evaluate the effects of timing and intensity of defoliation in the field. Similar clipping experiments were conducted with potted sods in the greenhouse where light, temperature and moisture could be tightly controlled (Table 6.1). This was particularly useful for developing functional relationships that drive plant growth.

Grazed Swards

Because grazing is expected to have long-term cumulative effects on plant growth, I explored the seasonal dynamics of live and dead components of pasture over two years after wapiti had grazed continuously in the previous years. Green herbage, standing dead and fallen litter increased from spring to summer by an average of 106, 71, and 133%, respectively; and decreased from summer to fall by an average of 33, 17, and 16%, respectively. Weathering losses of green herbage, standing dead and fallen litter over winter were 34, 52 and 51%, respectively. Dry matter losses of total herbage (all 3 pools) over winter, expressed as the proportion of 1997 peak summer green herbage was 58%. The effects of wet (1997) and dry (1998) years on pasture production are apparent.

The effects of stocking rate (grazing intensity) on average pasture production is evident in this ecosystem (from experiment described in chapter 5). At the high grazing intensity (high intensive short-duration) grazing, pasture growth is limited more by the amount of green photosynthetic material and reduced soil moisture than lower stocking rate (continuous grazing).

In the factorial experiment with potted sods in the greenhouse involving treatments of moisture level, clipping height and clipping frequency (experiment described in chapter 3) defoliation affected the quality of pastures. Moderate clipping intensity and high clipping frequency improved quality of grassland herbage.

Predictions

As the model is refined and tested, it will be used to explore the benefits of mixed species grazing and rather complex grazing rotations. The following simulations introduce the features of the model, illustrate its robustness and demonstrate its potential to evaluate grazing management decisions.

The first comparison is of the dynamics of ungrazed and moderately (continuously) grazed pastures (Fig. 6.8). These results are for average growing conditions for the Beaver Hills and result in a peak biomass accumulation of 3500 kg/ha for ungrazed swards and 2800 kg/ha for moderately grazed swards at peak biomass. The effect of grazing on extending the growing season and enhancing pasture quality (ratio of green to dry) is clear. Peak green biomass of ungrazed swards occurs 260 days after September 30, i.e., June 20. Peak green biomass of grazed swards was delayed 40 days to about July 30. Total plant growth was also 30% higher with moderate grazing. This level of grazing was insufficient to reduce root biomass enough that residual effects were encountered in subsequent years. A more detailed trace of vegetation pools, soil moisture and snow pack is illustrated in Fig. 6.9 for an ungrazed pasture. These trends accurately predict the features of the ungrazed pastures in the Beaver Hills (encompassing Ministik and Elk Island National Park).

Rotational grazing of wapiti (simulated) resulted in slight improvements in pasture production and biomass accumulation. However, compared with continuous grazing, it had a strongly negative effect on intake of metabolizable energy. Generally, the penalty in terms of animal intake was greater for rotational grazing at high stocking rates. Of course, there are other reasons for grazing rotations such as parasite control, maintenance of range condition, etc. The benefits of including both wapiti and bison in a grazing system were strong. Compared with 50 wapiti on 30 ha, 25 wapiti and an equivalent metabolic mass of bison resulted in greater metabolizable energy intake and greater primary production.

CONCLUSIONS

Computer simulation of grazing systems for farmed wild ruminants is more important than for domestic cattle and sheep. The physical, physiological and behavioural adaptations of wild ruminants make grazing possible year round. By grazing 'lighter but longer', pasture plants are better able to resist the damaging effects of herbivory. The challenge of making the most effective and sustainable use of the adaptations of both animals and plants is sufficiently complex to benefit from the structured approach offered by systems dynamics models. This study provides a modeling framework and preliminary data to drive a general mixed species grazing simulation model. The goal was to establish a simple, practical pasture simulator that could be used to evaluate continuous or rotational mixed species grazing systems in terms of pasture productivity. It has met the objective of providing an appropriate framework but has the following limitations at its present stage of development.

This version is limited to wapiti and/or bison grazing *Bromus-Poa* pastures typical of the Aspen Parkland from southern Manitoba to western Alberta. Following modest local calibration, it should work for any pasture where most production is vegetative. This version deals only with forage from a mixed sward rather than foliage and browse as food sources. Therefore, it is not suitable for browsers such as white-tail and mule deer. Effects of hoof action and trampling on forage losses, tillering, soil compaction and soil moisture need further study to understand the long-term effects of grazing on pasture soils.

The model suggests there is a considerable potential for improving productivity and sustainability through mixed species grazing systems, especially those based on wild ruminants. Currently, pastures in the parkland are used mainly to bridge winter feeding periods, with minimal efforts to improving their production efficiency and sustainability.

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Table 6.1. Phytomass accumulation (g/pot) of green herbage, standing dead and fallen dead of *Bromus-Poa* sward in a greenhouse under constant temperature and unlimited soil moisture.

Sampling date	Green herbage	Standing dead	Fallen litter
July 1	8.9a	2.8b	0.38c
July 15	11.6a	1.6b	0.7b
July 29	11a	1.7b	0.43c
August 12	13.7a	4.3b	0.5c
August 26	16.4a	2.8b	0.67c
Sept. 7	15.5a	2.9b	0.81c
Sept. 21	8.1a	1.2b	0.4b
Sept. 30	7.6a	2.4b	0.23c

Within rows, means with different letters are significantly ($P \leq 0.05$) different.

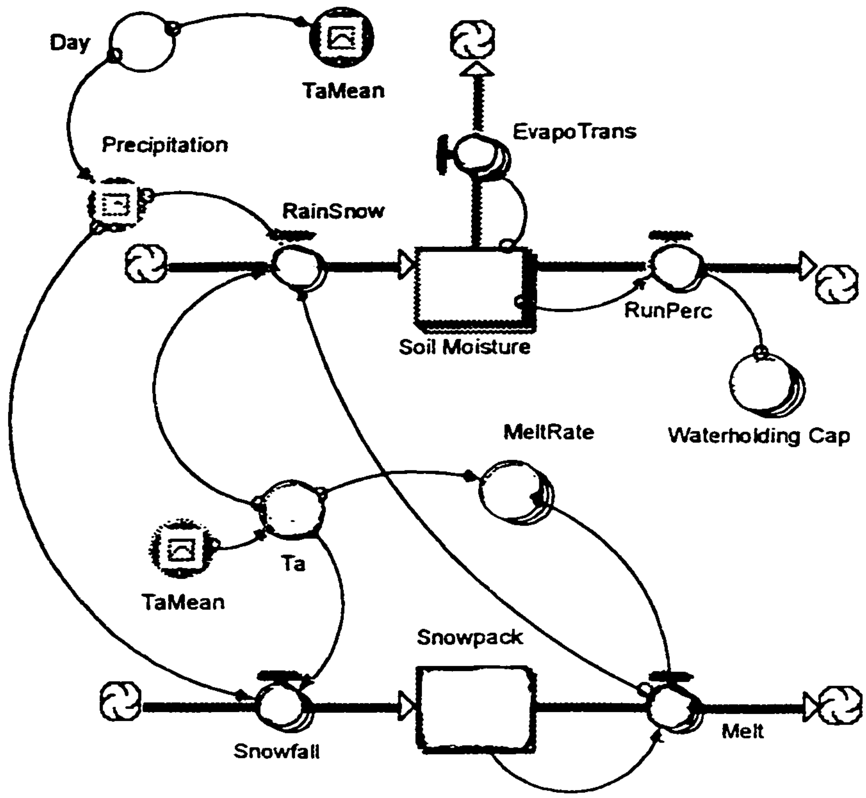

Figure 6.1. Edaphic factors and snow pack influencing pasture production and grazing efficiency in a STELLA model.

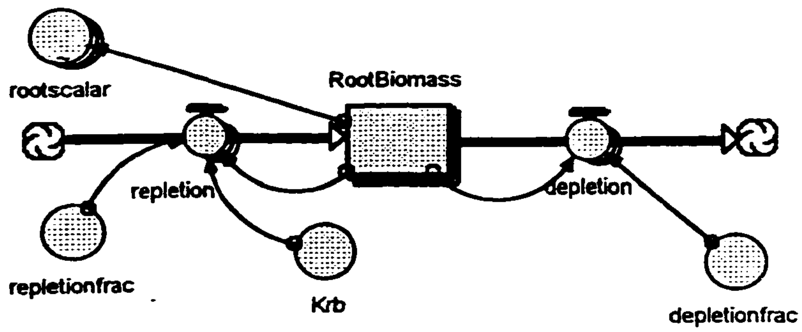

Figure 6.2. Below ground phytomass influences longer term effects of grazing.

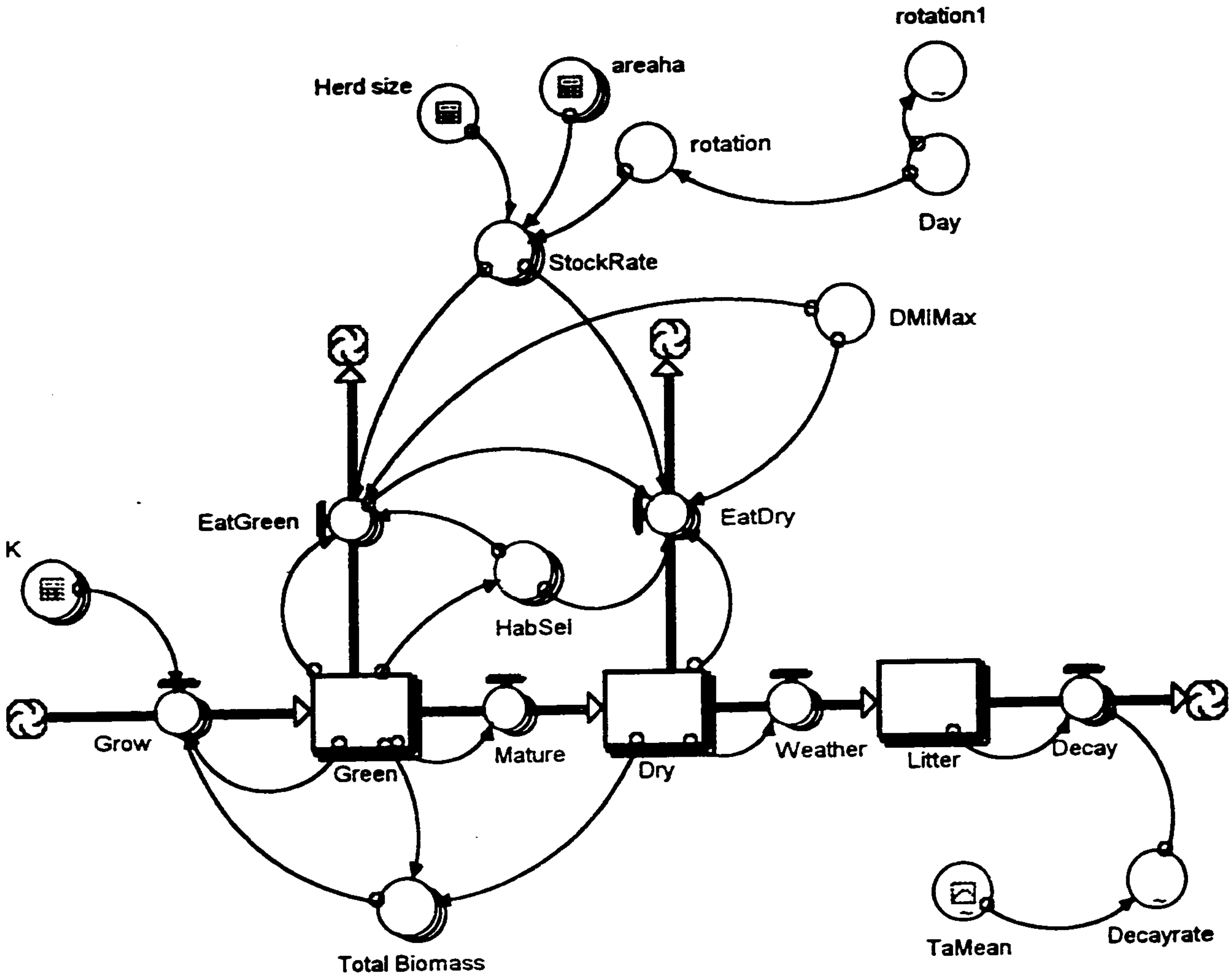

Figure 6.3. Phytomass pools defining forage supplies for grazing animals and the health of pasture.

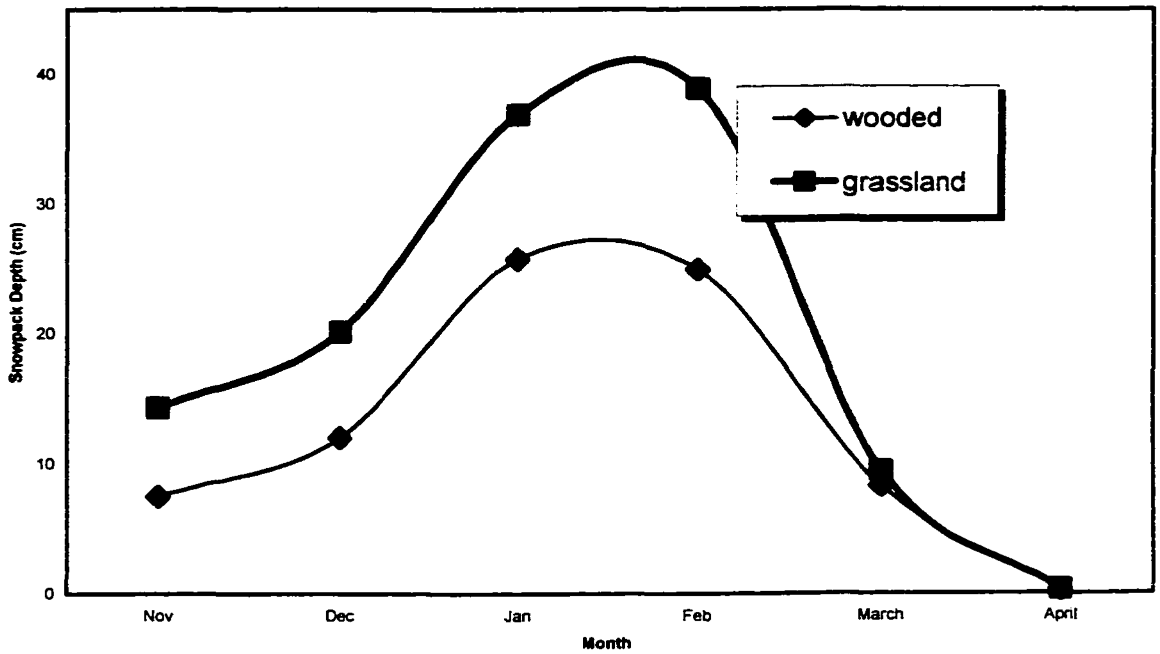

Figure 6.4. Representative snowpack depth (cm) in open and closed habitats measured at Ministik wildlife Research Station, AB.

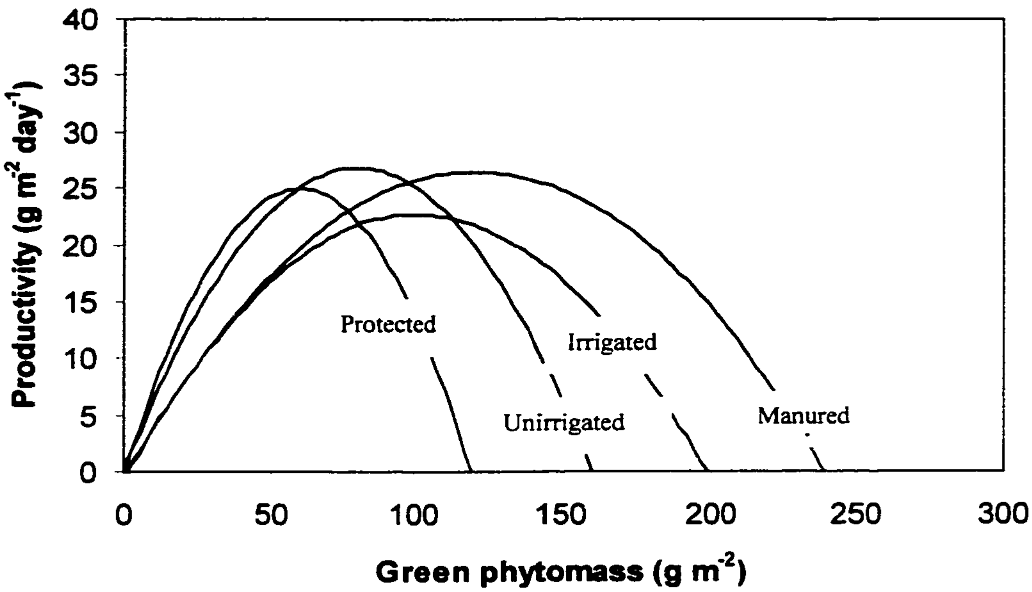

Figure 6.5. Effects of soil moisture and nutrients on parameters of plant growth. The use of manure and irrigation produced more green herbage than unirrigated and protected plots. Manured: (261.1 ± 25.5, r = 0.47, K = 227), where r is the rate of increase and K is the maximum green phytomass; irrigated: (197.7 ± 6.2, r = 0.48, K =198); unirrigated: (164.8 ± 6.9, r = 0.69, K = 161); and protected (123.5 ± 6.7, r = 0.85, K = 123). Adapted from Okello (1996).

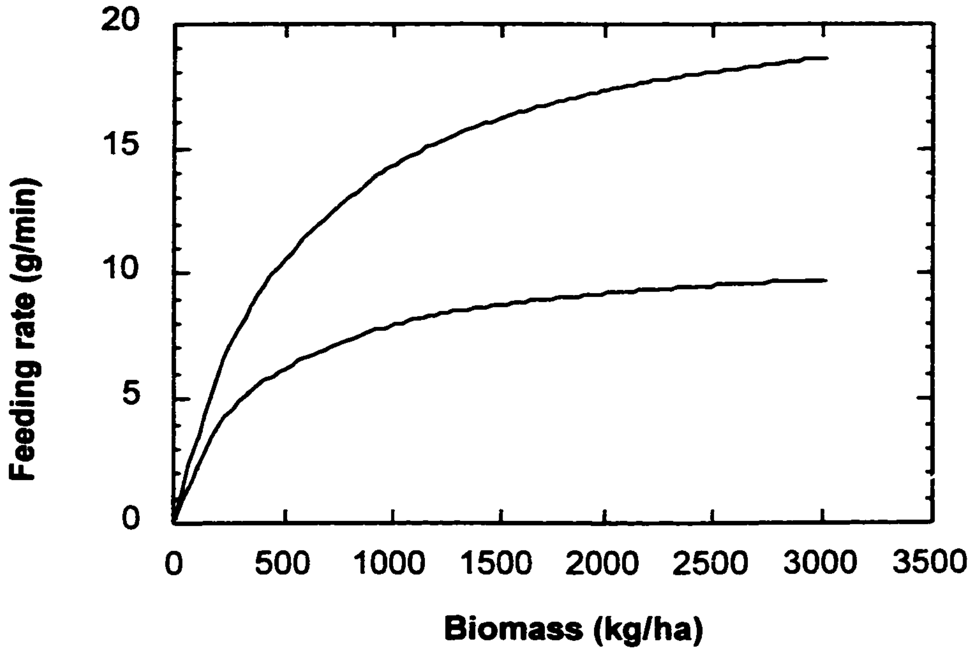

Figure 6.6. Feeding rate of wapiti on Poa/Brome pastures (adapted from Hudson and Watkins 1986). Cured pasture (top), Y=22X/(533+X). Green pasture (bottom), Y=11X/(385+X).

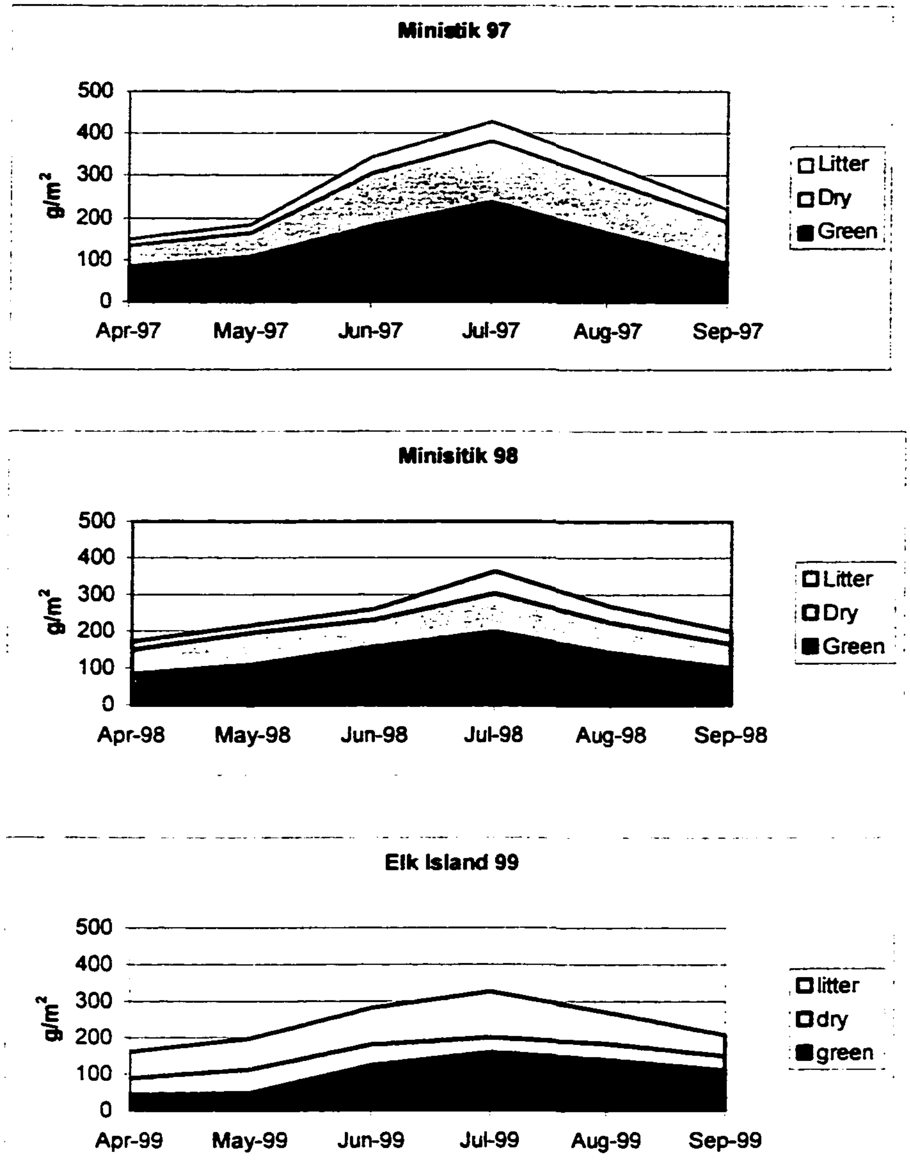

Figure 6.7. Accumulation of phytomass pools (field data) of protected plots at Ministik and Elk Island National Park.

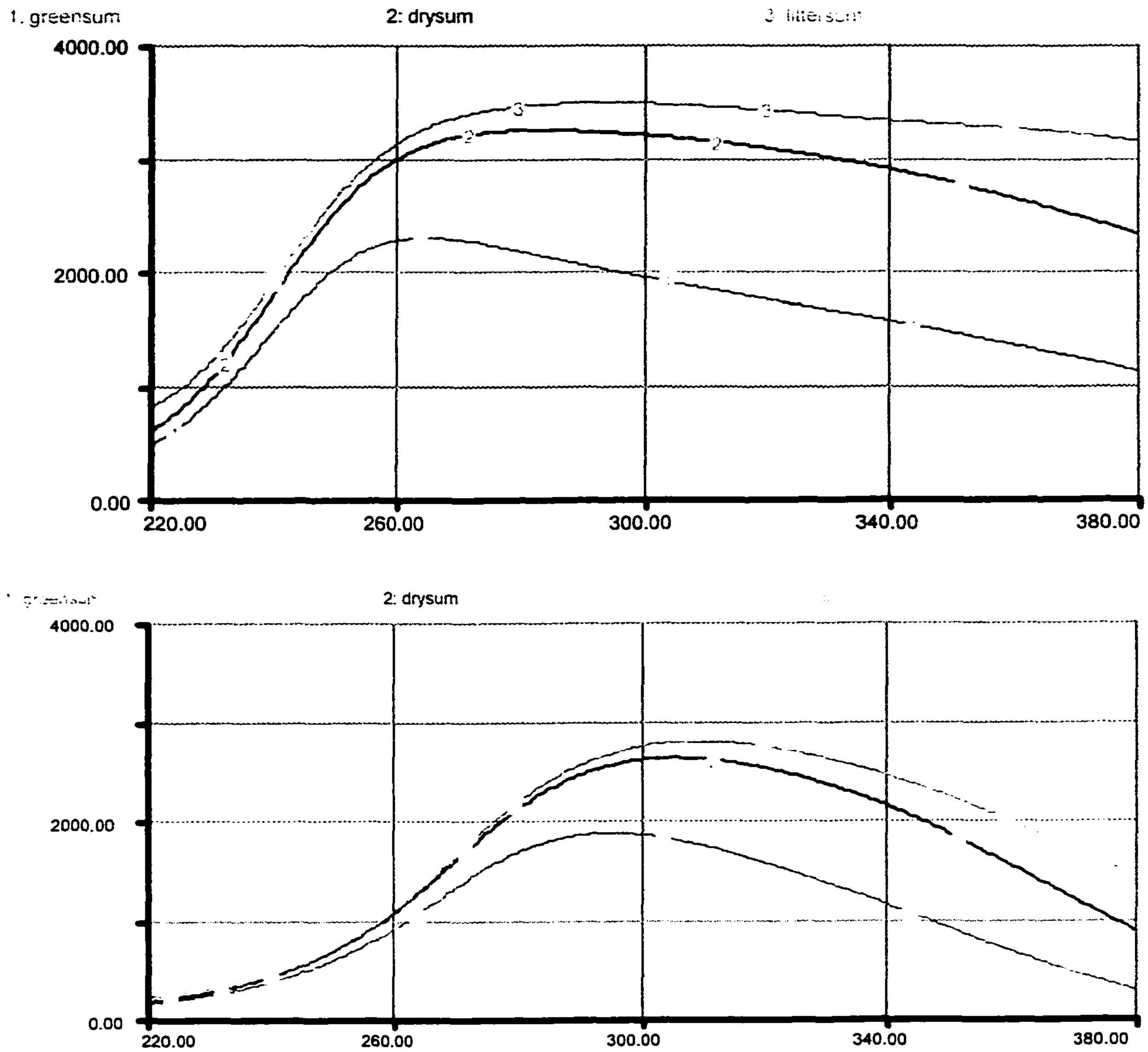

Figure 6.8. Vegetation pools of ungrazed (above) and moderately grazed (below) pastures. Dates are days from 30 September. Dates are days from 30 September. Green phytomass (1:greensum, kg/ha), standing dead phytomass (2:drysum, kg/ha), and fallen litter phytomass (3:littersum, kg/ha).

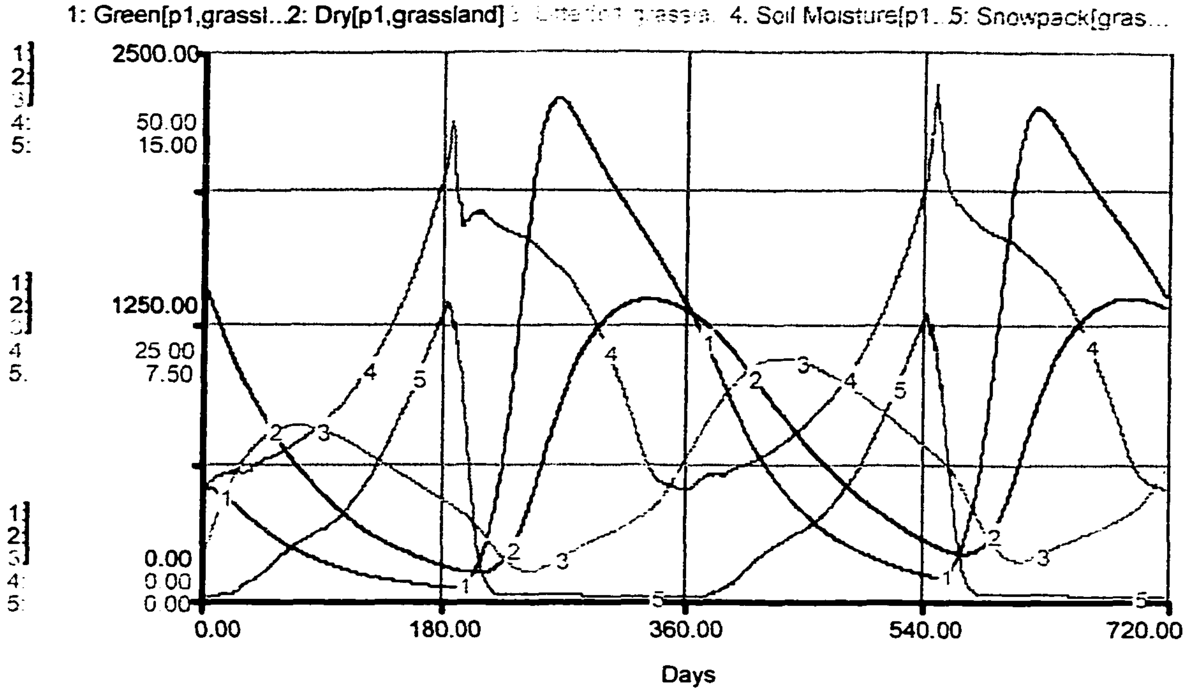

Figure 6.9. Vegetation pools, soil moisture and snow pack for an ungrazed sward over 2 years. Green phytomass (1:Green[p1,grassl..., kg/ha), standing dead phytomass (2:Dry[p1,grassland], kg/ha), fallen litter phytomass (3:Litter[p1,grassla..., kg/ha), soil moisture (Soil Moisture[p1..., g/100g), and snow pack (snowpack[grass..., cm).