University of Alberta

Sustainable management of natural rangeland ecosystems

by

Johnny Montenegro-Ballestero

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
in
Soil Science

Renewable Resources

©Johnny Montenegro-Ballestero
Fall 2011
Edmonton, Alberta

Permission is hereby granted to the University of Alberta Libraries to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only. Where the thesis is converted to, or otherwise made available in digital form, the University of Alberta will advise potential users of the thesis of these terms.

The author reserves all other publication and other rights in association with the copyright in the thesis and, except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatsoever without the author's prior written permission.

ABSTRACT

Rangelands, an ecosystem widespread in Canada, are important source of land for animal production. Around 26 million ha are utilized for beef production and in Alberta this ecosystem accounts for 6.6 million ha providing up to 50% of total forage for livestock.

To improve our understanding of how topography and grazing influence the nutrient cycling in a semiarid grassland, in the first part of my thesis I investigated the effect of those two factors on litter decomposition through a field experiment. The results showed that topography affected shoot litter decomposition -was faster downslope, and associated with greater soil moisture-, and that grazing by altering litter chemical composition influenced its decomposition; the lignin content in the litter was linked with the remaining mass.

I also investigated topography and grazing effect on plant and soil carbon stock through the *ecosys*, a comprehensive mathematical model for natural and managed ecosystems. *Ecosys* modeled, as found in the field, a topographic effect on total aboveground plant carbon which was greater down slope, which was explained by better soil conditions at lower topographic location.

Simulated carbon balance under current climate showed that uplands independently of grazing, was net carbon source, and opposite to the condition found at lower locations. The average carbon balance without grazing from 2003 to 2005 showed that low and medium elevations were carbon sinks of 132 and 12 g C m^{-2} y^{-1} respectively, but adjacent uplands released 4 g C m^{-2} y^{-1}. Simulated grazing reduced net biome productivity at all topographic locations (35, 37 and 51 g of C m^{-2} y^{-1}) and upper and middle elevations were carbon sources, but low elevation was still carbon sink (81 g m^{-2} y^{-1}).

Under climate change soil organic carbon increased more without (13, 9, and 15g m^{-2} y^{-1}) than with grazing (10, 5, and 11g m^{-2} y^{-1} at upper, middle, and lower topographic locations), but all locations were carbon sink.

There was concluded that, if properly set, grazing will not turn into carbon source this grassland ecosystem, which will be benefit by climate change.

Acknowledgements

First the all, I am grateful to my supervisor, Dr. Robert F. Grant, for the great assistance and guidance that provided me over the time I was in this program. He was a continuous academic resource throughout my whole graduate program. My appreciation is extended to other committee members: Dr. Robert Hudson, Dr. Sylvie Quideau, Dr. Edward Bork, and Dr. James F. Cahill, for their support and constructive suggestions.

I would like to sincerely thanks to the staff of the Department of Renewable Resources, University of Alberta: Mrs. Sandy Nakashima and Amanda Brown for managing and supporting my graduate studies, Mr. Clive Figueiredo and Mrs. Monica Molina Ayala for the analyses of soil samples.

Also I would like to thanks to members of our research group: Dr. Muhammad Akbar, Dr. Dimitre Dimitrov, Dr. Tao Li, Dr. Kimlin Metivier, and Dr. Ziyu Wang, for the encouragement during the completion of this thesis, and also I extend it to my friends: Dr. Marcos Jimenez Casas, Virginia Jacob Cervantes, David Galvez, and Ana Yanci.

I am most grateful to my wife Laura Rodriguez and sons, Felipe and Ricardo, for their love, and encouragement year by year which supported me up to the end of my graduate program.

Finally, I have to thanks the Precision Ranching Initiative that economically supported this research, because without it could not be possible to complete my program. Also I am very thanks to the Government of Costa Rica and CONICIT which economically supported me during the study time.

TABLE OF CONTENTS

Chapter 1.0. Topography and grazing effect on soil quality and plant productivity of rangelands

Chapter 2.0. Effect of topography and grazing on shoot and root litter decomposition in a semiarid rangeland

Chapter 3.0. Effect of topography and grazing on plant carbon stock in a semiarid rangeland: measured and modeled results

Chapter 4.0. Effect of topography and grazing on net ecosystem productivity of a semiarid rangeland ecosystem

Chapter 5.0. Effects of grazing and climate change on the stability of a natural semiarid rangeland ecosystem: model predictions

LIST OF TABLES

LIST OF FIGURES

1.1. Topography and plant productivity

In semiarid ecosystems plant productivity is directly related with soil water content and greater plant growth has been reported in wetter years compared with dry years (Smoliak 1986, Eneboe *et al*. 2002). However, there is natural water redistribution associated with topography in any landscape.

Thus, soil moisture is associated with topography because water moves down slope due to gravitational forces. Martin and Timmer (2006) in Ontario, and Hairston and Grigal (1994) in Minnesota, found increases higher than 100% in soil moisture content at lower topographic locations compared with upper locations in forests. Similarly, Frank and Groffman (1998) in Yellowstone National Park, and Moran *et al*. (2000) in grasslands of southeast Arizona, detected increases of soil volumetric water greater than 100% down slope compared with hilltops. In an agricultural precision farming research center Pachepsky *et al*. (2001) found that available water was up to 27% greater down slope compared with uphill.

These changes in soil moisture along any hill slope influence plant distribution and productivity, which could be up two times higher at lower than upper slopes (Perez *et al*. 1998, Asamoah *et al*. 2004). Topography through its influence on soil water distribution also influences soil temperature (Martin and Trimmer 2006, Pachepsky *et al*. 2001). Water has a large heat capacity, so that during warming a wetter soil will have lower temperature than a drier soil. As temperature directly influences microbial activity, low temperature soils with great water content should decrease microbial activity and therefore litter decomposition. However, after wetter soils have been warmed, microbial activity should be higher than in drier soils, thus increasing decomposition (Cortez 1998, Dalias *et al*. 2001).

Litter decomposition is favored by the interaction of soil temperature with soil moisture (between wilting point and field capacity)(Chen *et al*. 2000). As lower topographic locations usually have greater soil water content than uphill, if soil temperature does not limit microbial activity, litter decomposition will be faster here than in adjacent uplands.

The decomposition of litter enables nutrients to be made available for plant uptake, therefore lower positions with rapid litter decomposition will have more rapid nutrient cycling and more soil available nutrients, which will stimulate plant growth and productivity more compared with elevated positions in which litter decomposes more slowly. Thus, plant productivity differs because rates of litter decomposition and hence nutrient cycling differ (Eneboe *et al*. 2002).

1.2. The topographic effect on quality of produced litter

The term litter quality describes how easily a plant material can decompose (Cortés 1998). In this sense, high initial N (1.5 to 2%) and P concentrations, C-to-N ratios less than 30 and low cellulose contents are indices of good quality, and have been positively correlated with decomposition rates (Giardina *et al*. 2001, Koukoura *et al*. 2003, Moretto and Distel 2003).

Topography affects plant species distribution by influencing soil properties over the landscape because different plant species require different soil conditions to grow (Scowcroft *et al*. 2000, Silver and Miya 2001). As plant species differ in nutrient concentration they produce litter that varies in chemical composition (Liu *et al*. 2006, Sariyidiz and Anderson 2003), and thus in decomposition rate (Koukoura *et al.* 2003), which shows that there is a relationship among topography, litterfall and plant productivity.

Thus, differences in plant productivity associated with topography are also reflected in the amount of litter incorporated to soil (Perez *et al*. 1998 and Asamoah *et al*. 2004). Greater plant biomass at lower locations implies greater incorporation of litterfall that in turn will increase microbial activity and associated nutrient mineralization and soil available nutrients.

1.3. Topography and soil development

Variability in soil water content caused by topography also influences the distribution of soil properties (Landi *et al.* 2004, Small and McCarthy 2005) that can affect litter decomposition and therefore plant productivity. These properties change along any slope as a result of water movement down slope that carries fine soil particles, plant material and mineral nutrients (Kachanoski *et al*. 1999, Ventera *et al.* 2003). Thus increases in the thickness of A_h horizon from 55 to 140% from top to bottom slopes have been reported by Gregorich and Anderson (1985), Pennock *et al*. (1987), Landi *et al*. (2004), and Martin and Timmer (2006).

The movement of water down slope also influences soil nutrient content, which increases down slope, and also affects soil texture along the hill. For instance, if texture is sandy/sandy-loam on the upland, it can change to loam at lower location (Seibert *et al*.

2007). Thus the combination of different factors (nutrients coming from upper locations, greater water holding capacity, and better soil structure as a result of greater soil carbon content down slope), stimulates plant growth at lower topographic locations. In consequence, more plant residues will be incorporated into the soil in those lower locations than at any other location. Over time this can increase soil carbon if the carbon incorporated into the soil is greater than that released as CO_2 from heterotrophic respiration.

1.4. Soil organic carbon

Soil carbon content, among other factors like temperature and soil moisture, are directly related with the amount of plant residues that have been incorporated into the soil over time. Thus, in landscapes with variable topography, where there is a soil fertility gradient down slope, there is also a gradient in plant growth and hence increasing soil organic carbon (SOC) because the plant residues incorporated into the soil are greater down hill as a result of better soil conditions for plant growth. in an agricultural field with soybean and corn crops, in the Great Plains of USA, and in a semiarid short grass steppe of Colorado there have been determined that soil carbon content was increased down slope from 4 to 42% (Honeycutt *et al.* 1990, Burke *et al.* 1999),Ritchie *et al.* 2006).

This increase in soil organic carbon and topsoil thickness down slope has positive implications for plant productivity and litter production because these two soil characteristics are related to soil water holding capacity an important determinant of plant growth. This likely explains why greater plant biomass has been found in lower locations in fields with variable topography (Perez *et al.* 1998, Asamoha *et al.* 2004). However these soil characteristics also contribute to better soil conditions for microbial activity and thus increases litter decomposition (Barnes *et al.* 1998). Because water moves down slope (sec. 1), bottom slope locations usually can provide enough soil moisture (relative water filled porosity higher than 0.3) for greater microbial activity (Brady and Weil 2002) and lower locations will have faster litter decomposition than upper slopes (Sariyildiz *et al.* 2005). This increases soil available nutrients, stimulates plant growth, and at the end of the growing season could incorporate high litterfall and hence contribute to high SOC.

Topographically induced gradients in soil resources also influence plant species distribution, the quality of litter, and hence decomposition (Scowcroft *et al.* 2000, Silver and Miya 2001).Species distribution is related with non-uniformity of soil resources because plant species differ in soil requirements, and so produce different litter quality that decomposes at different rates.

On upper slopes, where there is less available soil water, xeric species are more common compared with bottom slope positions where mesic species grow because there is more soil available water (Sebastia 2004). Xeric and mesic species have different potential grow rates, production of plant biomass and litterfall, and this is reflected in the SOC at each location.

However when there is grazing should be expected some effect on plant productivity, and hence in SOC, because the plant biomass instead of being completely incorporated to the soil is consumed by grazing animals, which reduces litterfall (Reeder and Schuman 2002, Snyman 2004) and nutrient cycling. Because it still is not clear if grazing affects litter decomposition, this kind of information is required to know if grazing could affect nutrient cycling, soil carbon and plant productivity in semiarid rangelands .

1.5. Grazing effects on litter quantity

Rangelands, widely spread in Canada, are a good food source for a wide variety of wild animals. Nowadays, this ecosystem is a key resource for animal production (Alberta Agriculture, Food and Rural Development 2005). However grazing, depending on its intensity, can adversely affect litter production (Baron *et al*. 2002, Snyman 2005), its chemical composition (Smit and Kooijman 2001), decomposition rate (Bardgett *et al*. 1996, 1997), SOC content (Derner *et al*. 2006) and plant productivity (Guillen *et al*. 2000).

Grazing is not something new for this ecosystem; wild animals have been part of rangelands evolutionary history by contributing to nutrient cycling, and keeping the ecosystem healthy (Hart 2001). However, commercial livestock farms have high grazing intensity that has caused around 50% of Prairie rangelands to be in less than good condition (Agriculture and Agri-Food Canada 2006). Good native range condition is that in which at least 50%-75% of biomass is made up of its natural vegetation. A decline in ecosystem condition probably is the result of selective grazing that decreases the number of grazing sensitive plant species (Schuman *et al*. 1999, Hart 2001, Reeder and Shuman 2002) following selective consumption of more palatable above ground plant biomass.

Usually animals eat foliage with higher chemical quality (Van Soest 1994) and thereby reduce the production of higher quality surface litter. Naeth *et al*. (1991) reported that heavy grazing (4.4 AUM ha^{-1}) reduced litter production by 91%; simulated heavy grazing on a rangeland reduced litter by 76% (Snyman and Preez 2005). Reeder and Schuman (2002) found that light and heavy grazing (10% and 40% of available biomass utilization) reduced above ground litter between 8% and 15% compared with ungrazed condition. Litter reduction as result of grazing also was reported by Mapfumo *et al.* (2002), Donkor *et al.* (2002), and Baron *et al.* (2002). This decrease in litter occurs because there is a reduction in plant biomass, and after grazing, plants retain their remaining foliage for longer (Schuman *et al.* 2000, Loeser *et al.* 2004) delaying senescent.

Grazing can also affect litter mineral concentration. McIntosh *et al.* (1997) found decreases from 69% to 74% in calcium, magnesium, phosphorous, sulphur, potassium, and nitrogen in grazed vs. ungrazed litter after 15 years of grazing with 0.6 sheep ha^{-1} in a semiarid rangeland. Similarly, Smit and Kooijman (2001) found reductions from 14% to 44% in Mg, Ca, K, P, and N concentrations in standing dead grass after grazing. According to them, in addition to direct nutrient removal by grazing, these chemical changes could be caused by increased nutrient translocation and retention from dying leaves under grazed conditions, by topsoil erosion and consequent nutrient loss, by nutrient leaching, and by N volatilization from urine patches. Changes in species composition associated with grazing (Schuman *et al.* 1999, Hart 2001, Reeder and Shuman 2002) also could be the cause of changes in litter nutrient concentration.

Decreases in nutrient concentration lead to decreased nutrient input to the soil (Smit and Kooijman 2001) that should reduce soil microbial activity (Bardgett *et al.* 1996, 1997) and hence decomposition rate. This will cause a reduction of soil available nutrients for plant uptake which will reduce plant biomass production.

Nutrient cycling will also be slowed and soil fertility lowered if litter production is reduced. In the Aspen Parkland ecosystem of Alberta, Irving (1992) found an average reduction of 40% in total above ground plant biomass over a two-year period by removing 86% of total above ground litter compared with plots from which litter was not removed. Similarly, Willms *et al.* (1993) showed that above ground plant production was reduced up to 38% when litter was completely removed from the ground in a rangeland on an Orthic Dark-Brown Chernozem located in Lethbridge, Alberta. This shows the direct link between litter decomposition and plant productivity because of nutrient cycling through litter. Nutrient cycling will also be altered when there is grazing because part of the biomass is consumed and litterfall is reduced (Donkor *et al.* 2004, Snyman 2005).

This shows that ecosystem productivity can be negatively affected if the grazing intensity applied is greater than that supported by the ecosystem (Snyman 2005, Schuman *et al*. 2000).

1.6. Grazing effects on soil quality

Grazing has a direct effect on soil organic carbon because changes in plant biomass from grazing influence the amount and distribution of litter incorporated into the soil. Thus, the soil carbon should decrease if carbon inputs from grazed litter are less than carbon outputs from heterotrophic respiration (Lal 2002).

In natural ecosystems a high proportion of total yearly growth is turned into litter and over time part of it becomes soil organic carbon, but when there is grazing part of that plant biomass is consumed. Even though a high percent of consumed plant biomass is returned to the soil as manure, its distribution is not uniform and affects less than 3% of the total grazed area over a growing season (Antil *et al*. 2001). This uneven distribution of animal waste contributes to increase spatial variability of plant productivity, and therefore the amount of litter incorporated to the soil.

Animal manure has a high nitrogen concentration with respect to that of carbon (and hence a small C:N ratio) (Antil *et al*. 2001), which increases microbial activity and litter decomposition in areas where animal waste is concentrated. In contrast, in the remaining area decomposition slows down because grazing animals reduce litter quality by consuming the highest quality forage and associated N (Aerts 1988, Olofsson and Oksaneu 2001, Koukoura *et al*. 2003). This implies a later reduction of plant residues incorporated to the soil and so a reduction of soil organic carbon because over time there is a reduction of litter quantity and quality.

Grazing has been found to have contrasting effects on SOC. After 16 years of heavy grazing (5.35 sheep ha^{-1}), Cao *et al*. (2004) reported that SOC was reduced by 6%. Similarly, Frank *et al*. (1995) found that SOC was reduced by 17% after 75 years of light grazing (2.6 ha steer^{-1})in the Northern Great Plains, USA. Derner *et al*. (2006) found that grazing by cattle removed approximately 40%–60% of above ground net primary productivity, and in turn reduced soil carbon in the upper 0.3 m of soil by 23 and 4 g C m^{-2} y^{-1} in mid and tall grass communities of the North American Great Plains. In the later experiment, there was a reduction in grazed plant biomass (41%-46% in above ground, and up to 78% below ground) compared with the ungrazed treatment. In all these experiments the reduction in plant biomass appeared responsible for the SOC reduction with grazing.

However, Dormaar *et al*. (1977) found increases from 1% to 3% in SOC at the A_h horizon after 22 years of heavy grazing (1.7 ha animal unit month (AUM) by ewes with lambs or at 0.2 ha AUM by cows with calves) compared with an ungrazed soil. Compared with an ungrazed exclosure light grazing (35% below the stocking rate recommended by the Natural Resources Conservation Service (NRCS, formerly the Soil Conservation Service) for the condition of the site), as determined by the biomass available in the paddock of a mixed grass rangeland, , increased soil carbon up to 34 g m^{-2} y^{-1} (Schuman *et al*. 1999). The same trend was found by Ganjegunte *et al*. (2005) with light grazing (0.16 to 0.23 steer ha^{-1}, 35% below than the NRCS recommended rate for the area). Recently Ingram *et al*. (2008), working in a northern mixed-grass rangeland with stocking rates similar than those applied by Schuman *et al*. (1999), found that 21-years of light grazing led to a significant increase of SOC (57g C m^{-2} y^{-1}). The increase of SOC in heavily grazed rangeland has been associated with changes in botanical composition (Schuman *et al*. 1999). In the experiment of Ganjegunte *et al*. (2005), grazing raised the proportion of blue grama, which allocates more carbon to the soil than do other grass species. Thus, the source of additional soil carbon with blue grama may be attributable to greater root-to-shoot ratio, root density and turnover, or possibly higher rates of root exudates from this grass species (Frank *et al*. 1995, Reeder *et al*. 2001).

According to Henderson *et al*. (2004), who studied the long term effect (up to 71 years) of good, fair, poor and poor-fair grazed areas in southern Alberta, there was no defined grazing trend on SOC when compared on an equivalent soil mass basis. Similar results were also previously reported by Michunas and Lauenroth (1993).

It is important to understand how grazing could affect litter decomposition, soil carbon, nutrient cycling, and plant growth because all are directly linked with ecosystem productivity over time. The variable results reported above indicate a need to generate this information for specific locations due to the existence of different factors that influence in different ways ecosystem response to a given grazing intensity. As discussed above, depending on its intensity grazing can influence botanical composition (section 5), quality and its decomposition (section 5), litter production, (section 5), and so the amount of SOC (section 6) which is the largest carbon pool in terrestrial ecosystems (Janzen 2004).

Semiarid grasslands hold an important amount of carbon in the soil (Agriculture and Agri-Food Canada 2000), and depending on grazing intensity, this ecosystem could lose part of this stored carbon because as noted earlier, grazing can reduce above ground plant carbon and later be reflected in lower soil carbon. How these carbon pools could be affected by grazing under climate change remains to be investigated.

1.7. Grazing and global warming

Anny large-scale change in stored soil carbon will have important implications for atmospheric CO2 concentrations. According to Lal (2002) grasses have large root biomass that contributes a high amount of carbon to the soil. If grazed and given sufficient rest, soil carbon should be increased from 10 to 30 g m^{-2} y^{-1} (Schuman *et al.* 2002). However, when these soils are converted into agriculture, there is a large carbon release to the atmosphere during the first years due to heterotrophic respiration. According to VanderBygaart *et al.* (2003), in an analysis of 50 studies regarding land use change across Canada, native soils lost an average of 24% of SOC following conversion to agriculture. This loss is estimated to be as much as 1 billion tons of carbon over the Canadian prairies during the 20th century. Thus, any large-scale change in this stored carbon will have important implications for atmospheric CO_2 concentration.

This reflects the importance of keeping perennial grasslands productivity to increase the SOC over time and therefore to contribute with the avoidance of increases in atmospheric CO_2. However, long-term grazing effects on plant productivity is not known until the effect is visible or after taken some measurements over time that demonstrate changes in key ecosystem parameters like SOC, and at that time could be too late for the ecosystem.

One way to anticipate grazing effects on plant productivity is through modeling, which allows anticipate possible consequences of applying different grazing intensities and then to choose the best option to protect the ecosystem.

1.8. Modelling ecosystem productivity and stability

Models are developed from scientific hypotheses that are thought to explain different processes, which are tested with quantitative data from experiments conducted under defined site conditions. Once tested, models allow the whole ecosystem to be studied under diverse site conditions through simulation of different scenarios by predicting results of different management strategies. In this way, both experimental and modeled results are useful to support decisions based on the best management that can be applied to preserve natural resources and the stability of ecosystems.

Models should account for the influence of weather variables such as radiation, temperature, humidity, wind speed, and precipitation on ecosystem behaviour, because they influence ecosystem energy and water balance including litter production, litter decomposition, nutrient cycling and SOC. These models have to consider soil variables and plant management, that in combination with climate, also determine plant growth and productivity. Grazing is a land management that has been frequently associated with degradation (van der Koppel *et al.* 1997, Van Auken 2000) and there is growing interest in developing grazing systems that protect grassland ecosystems.

Modelling results including grazing like those from Wang *et al.* (2008) found that grazing has to remove 40% or less live shoots to keep SOC stable or limit decreases in SOC and net primary productivity,. However, modelling results that address grassland ecosystem carbon balances are not common, and demonstrates the necessity of this kind of simulation to understand ecosystem processes better and design grazing intensities that contribute to keep the natural productivity of these ecosystems.

1.9. Ecosys model

Ecosys is a comprehensive mathematical model of natural and managed ecosystems (agriculture, forests, savannah, grassland, tundra, deserts) designed to provide a means to anticipate ecosystem behaviour under different environmental conditions (soils, climates and management practices). The design and scope of *ecosys*, in general terms, are based on the following guidelines:

1- It is constructed from basic scientific principles using parameters that may be determined independently of the model itself, and that function at spatial and temporal scales smaller than those at which the model is validated. It is therefore widely applicable, and will offer a predictive capability for ecosystem behavior with different soils, climate and management.

2- It integrates temporal scales from seconds to decades, allowing validation vs. data from experiments that range from short-term laboratory incubations to long-term field studies.

3- It integrates spatial scales ranging from mm to km in 1, 2 or 3 dimensions, as required, allowing the scaling up of micro scale phenomena to the landscape level.

4- It integrates biological scales, both plant and microbial, from the organ to the community, allowing the representation of complex biomes.

5- It simulates the transport and transformation of heat, water, carbon, oxygen, nitrogen, phosphorus and ionic solutes through soil-plant-atmosphere systems with the atmosphere as upper boundary and soil parental material as lower boundary.

In this research *ecosys* was used to model a semiarid rangeland in which hypotheses related with topography and grazing effects on plant productivity, litter decomposition, soil carbon, and ecosystem carbon balances at different topographic locations were tested.

To do this, a grazing experiment was established at the Kinsella Ranch experimental farm, in a semiarid ecosystem, characterized by topography with frequent hills and slopes up to 60°. Above-ground and below-ground biomass samples were measured from grazed and ungrazed plots along a topographic gradient**,** and used to evaluate the topographic and grazing effect on plant productivity. A litterbag experiment in open plots and exclosed areas along the topographic gradient, topography and grazing effects on litter decomposition were evaluated.

These experimental results, and other results coming from experiments carried out elsewhere, were compared with modeled results to test and validate *ecosys*. Based on agreement between modeled and experimental results, *ecosys* was used to simulate soil carbon levels over a long period of time at different topographic locations, and thereby to estimate topographic and grazing effects on SOC in this grassland ecosystem.

E*cosys* was utilized to test the hypothesis that there is a topographic influence on litter decomposition, plant productivity and nutrient cycling as well as net primary productivity (NPP), which in turn are also influenced by grazing animals. This research also tested the hypothesis that grazing animals reduce SOC by removing biomass, with grazing reducing LAI and subsequent net primary productivity, and hence litterfall and nutrient cycling.

Previous works in which *ecosys* was used to test hypotheses, which were fully coupled to simulate complex ecosystem behaviour, included the simulation of root growth (Grant 1998), water stress (Grant and Flanagan, 2007; Grant *et al.* 2006), soil temperature (Grant *et al.* 1995), plant phenology and photosynthesis (Grant 1989), changes in soil organic matter and soil carbon (Grant 1997, Grant *et al.* 2001), soil microbial respiration (Grant and Rochette 1994), and topography and climate effect on net ecosystem productivity of semiarid grasslands (Li *et al*. 2004, Grant 2004, Grant and Flanagan 2009). In these studies, *ecosys* was able to simulate experimental results coming from different experiments. However none of them have included the combined effects of topography and grazing.

1.10. Objectives and contents

This thesis is part of the Precision Ranching Initiative (PRI), a project developed to explore the effect of wild ungulate and livestock grazing on rangeland ecosystem and to understand the possible effects that this could have on ecosystem productivity. This initiative is to improve the productivity and sustainability of rangelands by grazing the right animal at the right place at the right time. The objective of this study within the PRI was to develop a better understanding of topography and grazing effects on carbon cycling in a natural rangeland ecosystem through field experiments and computer modeling.

This thesis is organized as follows; the first chapter gives a general introduction with a literature review regarding factors that influence plant productivity, while the remainder of the thesis consists of the following four chapters. Chapter 2, based on experimental results from a litterbag study, clarifies the influence that topography and grazing have on shoot and root litter decomposition, and on carbon cycling in a semiarid grassland. In Chapter 3, ecosystem productivity modeled by *ecosys* is compared with field experimental results, and the effect of topography and grazing on plant carbon stocks, a key component in the carbon cycle of terrestrial ecosystems, is discussed. In Chapter 4 *ecosys* is used to model the effects that grazing can have at different topographic locations on net ecosystem productivity through the estimation of ecosystem carbon balances. In Chapter 5 *ecosys* is used to predict the long-term effect of topography and grazing on soil carbon dynamics under current and climate change scenarios. Finally, Chapter 6 is a general overview.

2. References

Aerts, R. 1999. Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. Journal of Experimental Botany 50(330):29-37.

Agriculture and Agri-Food Canada. 2000. Lethbridge Research Centre Report: Western Range Science Seminar Report Managing range essential to maintaining soil carbon stores. http//sd.agr.ac/lethbridge/rep2000/rep0208b_e.htm

Amundson, R. 2001. The carbon budget in soils. Annu. Rev. Earth Planet Sci. 29:535-562.

Antil, R.S., Lovell, R.D., Hatch, D.J., Jarvis, S.D. 2001. Mineralization or nitrogen in permanent pastures amended with fertilizer or dung. Biology and fertility of soils 33(2):132-138.

Asamoha, S.; Bork, E.; Irving, B.; Price, M.; Hudson, R. 2004a. Seasonal herbage dynamics on aspen parkland landscape in central Alberta. Canadian Journal of Animal Science 84:149-153.

Ayres, M., Clause, T., MacLean, S., Redman, A., Reichardt, P. 1997. Diversity of structure and antiherbivore activity in condensed tannins. Ecology 78:1696-1712.

Baron, V.S.; Mapfumo, E.; Dick, A.C.; Naeth, M.A.; Okine, E.K.; Chanasyk, D.S. 2002. Grazing intensity impacts on pasture carbon and nitro flow. Journal Range Management 55:535-541.

Bending, G., Turner, M., Jones, J. 2002. Interactions between crop residue and soil organic matter quality and the functional diversity of soil microbial communities. Soil Biology ad Biochemistry 34:1073-1082.

Boddey, R., Macedo, R., Tarre, R., Ferreira, E., de Oliveira, O., de Rezende, C., Cantarutti, R., Pereira, J., Alvez, B., Urquiaga, S. 2004. Nitrogen cycling in Brachiaria pastures: the key to understanding the process of pasture decline. Agriculture, Ecosystems and Environment 103:389-403.

Brady, N., Weil, R. 2002. The nature and properties of soils. Prentice Hall, USA. 949 p.

Broder, M.W., Wagner, G.H. 1988. Microbial colonization and decomposition of corn, wheat and soybean residue. Soil Sci. Soc. Amer. J. 52: 112-117.

Burke, I., Lauenroth, W., Riggle, R., Brannen, P., Madigan, B., Beard, S. 1999. Spatial Variability of Soil Properties in the Shortgrass Steppe: The Relative Importance of Topography, Grazing, Microsite, and Plant Species in Controlling Spatial Patterns. Ecosystems 2: 422-438.

Cao, G., Tang, Y., Mo, W., Wang, Y., Li, Y., Zhao, X. 2004. Grazing intensity alters soil respiration in an alpine meadow on the Tibetan plateau. Soil Biology and Biochemistry 36:237-243.

Chen, H., Harmon, M.E., Sexton, J., Fasth, B. 2002. Fine-root decomposition and N dynamics in coniferous forests of the Pacific Northwest, U.S.A. Canadian Journal of Forest Research. 32:320-331.

Conant, R.T., Paustian, K., Elliott, E.T. 2001. Grassland management and conversion intro grassland:effects on soil carbon. Ecological Applications 11:343-355.

Cortez, J. 1998. Field composition of leaf litters: relationships between decomposition rates and soil moisture, soil temperature and earthworm activity. Soil biology and biogeochemistry 30(6):783-793.

Coûteaux, M.M., Aloui, A., Kurz-Besson, C. 2002. Pinus halepensis litter decomposition in laboratory microcosms as influenced by temperature and a millipede, Glomeris marginata. Applied Soil Ecology, 20(2):85-96.

Dalias, P., Anderson, J.M., Bottner, P., Couâteaux, M., M. 2001. Temperature responses of carbon mineralization in conifer forest soils from different regional climates incubated under standard laboratory conditions. Global Change Biology. 6:181-192.

Daliasa, P., Anderson, J., Bottnera, P., Couteaux, M. 2001. Long-term effects of temperature on carbon mineralisation processes. Soil Biology and Biochemistry 33:1049-1057.

Donkor, N., Gedir, J., Hudson, R., Bork, E., Chanasyk, D., Naeth, M. 2002. Impacts of grazing systems on soil compaction and pasture production in Alberta. Canadian Journal of Soil Science 82:1-8.

Dormaar, J., Johnston, A., Smoliak, S. 1977. Seasonal Variation in Chemical Characteristics of Soil Organic Matter of Grazed and Ungrazed Mixed Prairie and Fescue Grassland. Journal of Range Management 30(3):195-198.

Derner, J.D., Boutton, T.W., Briske, D.D. 2006. Grazing and ecosystem carbon storage in the North American Great Plains. Plant and Soil 280(1-2): 77-90.

Eneboe, E.; Sowell, B.; Heitszhmidt, R.; Karl, M.; Haferkamp, M. 2002. Droughts and grazing: iv. Blue grama and western wetgrass. Journal of Range Management 55:73-79.

Frank, A.B., Tanaka, D.L., Hofmann, L., Follet, R.F. 1995. Soil carbon and nitrogen of Northern Great Plains grasslands as influenced by long-term grazing. Journal of Range Management 48(5):470-474.

Fierer, N., Schimel, J., Cates, R., Zou, J. 2001. Influence of balsam poplar tannin fraction on carbon and nitrogen dynamics in Alaska taiga floodplain soils. Soil biology and biogeochemistry 33:1827-1839.

Ganjegunte, G., Vance, G., Preston, C., Schuman, G., Ingram, L., Stahl, P., Welker, J. 2005. Soil organic carbon composition in a Northern mixed-grass prairie: Effects of Grazing. Soil Science Society of America Journal 69:1746-1756.

Gill, R., Jackson, R. 2000. Global patterns of root turnover for terrestrial and aquatic habitats. Global Change Biology 7:849-882.

Gordon, W., Jackson, R. 2000. Nutrient concentration in fine roots. Ecology 81:275-280.

Grant R.F., Zhang Y. , Yuan F., Wang S., Hanson P.J., Gaumont-Guay, D., Chen J., Black T.A., Barr A., Baldocchi D.D., Arain A. 2006. Modelling water stress effects on CO2 and energy exchange in temperate and boreal deciduous forests. Ecological Modelling. accepted 9 Feb. 2006.

Grant, R. 1997. Changes in soil organic matter under different tillage and rotation: mathematical modeling in ECOSYS. Soil Science Society of American Journal 61(4)1159-1175,

Grant, R. 1998. Simulation in ecosys of root growth response to contrasting soil water and nitrogen. Ecological Modeling 107:237-264),

Grant, R. 2004. Modeling topographic effect on net ecosystem productivity of boreal black spruce forest. Tree Physiology 24:1-18.

Grant, R., Juma, N., Roberson, J., Izaurralde, R., McGill, W. 2001. Long-term changes in soil carbon under different fertilizer, manure and rotation: testing the mathematical model ecosys with data from the Brenton plots. Soil Science Society of American Journal 65:205-214

Grant, R.F. 1989. Simulation of carbon accumulation and partitioning in maize. Agron. J. 81:563-571.

Grant, R.F. 1989. Simulation of maize phenology. Agron. J. 81:451-457.

Grant, R.F. and Rochette, P. 1994. Soil microbial respiration at different temperatures and water potentials: Theory and mathematical modelling. Soil Sci. Soc. Amer. J. 58:1681-1690.

Grant, R.F., Izaurralde, R.C. and Chanasyk, D.S. 1995. Soil temperature under different surface managements: testing a simulation model. Agric. and For. Meteorol. 73: 89-113.

Guo, L.B., Sims, R.E.H. 2001. Effects of light, temperature, water and meatworks effluentirrigation on eucalypt leaf litter decomposition under controlled environmental conditions. Applied Soil Ecology 17:229–237.

Gillen, R., Eckroat, J.A., Mccollum III, T. 2000. Vegetation response to stocking rate in southern mixed-grass prairie. J. Range Manage. 53:471–478

Hamsa, M., Anderson, W. 2005. Soil compaction in cropping systems: A review of the nature, causes and possible solutions. Soil & Tillage Research 82:121-145.

Henderson, D.C., Ellert, B.H., Naeth M.A. 2004. Grazing and soil carbon along a gradient of Alberta rangelands. J. Range Manage. 57:402-410.

Honeycutt, C., Heil, R., Cole, C. 1990. Climatic and topographic relations of three Great Plains soils: II: carbon, nitrogen and phosphorus. Soil Science of American Journal 54:476-483.

Irvine, L., Kleczkowski, A., Lane, A., Pitchford, J., Caffrey, D., Chamberlain, P. 2006. An integrated data resource for modelling the soil ecosystem. Applied Soil Ecology 33:208–219).

Ingram, L., Schuman, G., Buyer, J., Vance, G., Ganjegunte, G., Welker, J., Derner, J. 2008. Grazing impacts on soil carbon and microbiol communities in a mixed-grass ecosystem. Soil Science Society of American Journal. 72(4):939-948.

Janzen, H. 2004. Carbon cycling in earth systems—a soil science perspective. Agriculture, Ecosystems and Environment 104:399–417.

John, B., Pandey, H., Tripathi, R. 2002. Decomposition of fine roots of Pinus kesiya and turnover of organic matter, N and P of coarse and fine pine roots and herbaceous roots and rhizomes in subtropical pine forest stands of different ages. Biology Fertility Soils 35:238-246.

Johnson, C.E., Ruiz-Mendez, J.J., Lawrence, G.B. 2000. Forest soil chemistry and terrain attributes in a Catskill watershed. Soil Science Society of America Journal 64:1804-1814.

Kalburtji, M., Mamolos, A., Kostopoulou, S. 1998. Litter dynamics of Dactylis glomerata and Vicia villosa with respect to climate and soil characteristics. Grass of forage 53(2):225-

Kirkegaard, J.A., Troedson, R.J., So, H.B., Kushwaha, B.L. 1992. The effect of compaction on the growth of pigeonpea on clay soils. II. Mechanisms of crop response and season effects on an oxisol in a humid coastal environment. Soil Tillage Res. 24:129–147.

Kogel-Knaber, I. 2002. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter.soil biology anmd biogeochemistry 34:139-162.

Koukoura, Z., Mamolos, A., Kalburtji, K. 2003. Decomposition of dominant plant species litter in a semi-arid grassland .Applied Soil Ecology 23:13-23.

Lal, R. 2002. Soil carbon dynamics in cropland and rangeland. Environmental Pollution 116 (3):353-362.

Lal, R. 2004. Agricultural activities and the global carbon cycle. Nutrient Cycling in Agroecosystems 70:103-116.

Landi, A., Mermut, A.R., Anderson, D.W. 2004. Carbon distribution in a hummocky landscape from Saskatchewan, Canada. Soil Science Society of America Journal 68(1):175-184.

Larcher, W. 2001. Physiological plant ecology. 4 ed. Springer-Verlag. 513 p.

LeCain, D., Morgan, J., Schuman, G., Reeder, J., Hart, R. 2002. Carbon exchange and species composition or grazed pastures and exclosures in the shortgrasses steppe of Colorado. Agriculture, ecosystems and environment 93:421-435.

Li, T., Grant, R., Flanagan, L. 2004. Climate impact on net ecosystem productivity of a semi-arid natural grassland: modeling and measurement. Agriculture Forest Meteorology 126:99-116),

Lindroth, R., Osier, T., Barnhill, H., Wood, S. 2002. Effects of genotype and nutrient on phytochemistry of trembling aspen (Populus tremuloides Michx.) during leaf senescence. Biochemical Systematics and Ecology 30:297-307.

Liu, P., Huang, J., Han, X., Sun, O., Zhou, Z. 2006. Differential responses of litter decomposition to increased soil nutrients and water between two contrasting grassland plant species of Inner Mongolia, China. Applied Soil Ecology 34:266–275.

Llacos, L. 1962. Water yield as influenced by degree of grazing in the California winter grasslands. Journal of Range Management 15:34-42.

Lorenz, K., Preston, C.M., Raspe, S., Morrison, I.K., Feger, K.H. 2000. Litter decomposition and humus characteristics in Canadian and German spruce ecosystems; information from tannin analysis and 13C CPMAS NMR. Soil biology and biogeochemistry 32:779-792.

Martin, W.K.E., Timmer, V.R. 2006. Capturing spatial variability of soil and litter properties in a forest stand by landform segmentation procedures. Geoderma 132:169-181.

Martinez, L., Zinck, J. 2004. Temporal variation of soil compaction and deterioration of soil quality in pasture areas of Colombian Amazonia. Soil and Tillage and Research 75:3-17.

Matches, A.G. 1992. Plant response to grazing: a review. J. Prod. Agr. 5:1-7.

Mapfumo, E., Chanasyk, D.S., Baron, V.S., Naeth, M.A. 2000. Grazing impacts on selected soil parameters under short-term forage sequences. Journal of Range Management 53(5): 466-470.

McIntosh, P., Allen, R., Scott, N. 1997. Effects of exclosure and management on biomass and soil nutrient pools in seasonally dry high country, New Zealand. Journal of Environment Management 51:169-186.

Milchunas, D., Lauenroth, W. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327-366.

Milton, S., Dean, W., du Plessis, M. 1994. A conceptual model of arid rangeland degradation. Bioscience 44:70-76.

Moore, T., Trofymow, J., Taylor, B., Prescott, C., Camire, C., Duschene, L., Fyles, J., Kozak, L., Kranabetter, M., Morrison, I., Siltanen, M., Smith, S., Titus, B., Visser, S., Wein, R.,Zolta, S. 1999. Litter decomposition rates in Canadian forests. Global Change Biology 5:75-82.

Moretto, A., Distel, R. 2003. Decomposition of and nutrient dynamics in leaf litter and roots of Poa ligularis and Stipa gyneriodes. Journal of Arid Environment 55:503-514.

Moretto, A., Distel, R., Didone, N. 2001. Decomposition and nutrient dynamic of leaf litter and roots from palatable and unpalatable grasses in a semi-arid grassland. Applied Soil Ecology 18:31-37.

Morley, F.H. 1981. Grazing animals. New York Elsevier Scientific Pub. Co., 411 p.

Naeth, M.A.; Bailey, A.W.; Pluth, D.J.; Chanasyk, D.S.; Hardin, R.T. 1991. Grazing impacts on litter and soil organic matter in mixed prairie and fescue grassland ecosystems of Alberta. Journal of Range Management 44(1): 7-12.

Olofsson, J., Oksanen, L. 2001. Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: a litterbag experiment. Oikos 96(3):507-515.

Pachepsky, Y.A., Timlin, D.J., Rawls, W.J. 2001. Soil water retention as related to topographic variables. Soil-Science-Society-of-America-Journal 65(6): 1787-1795.

Parton, W., Steward, J., Cole, C. 1988. Dynamics of C, N, P and S in grassland soils: a model. Biogeochemitry 5:109-131.

Pennock, D.J., Zebarth, B.J., De Jong, E. 1987. Landform classification and soil distribution in hummocky terrain, Saskatchewan, Canada. Geoderma 40:297-315.

Perez Corona, M.E., Vazquez de Aldana, B.R., Garcia Criado, B., Garcia Ciudad, A.1998. Variations in semiarid grasslands. Journal of Range Management 51:570-576.

Pietola, L., Horn, R., Yli-Halla, M. 2005. Effects of trampling by cattle on the hydraulic conductivity and mechanical properties of soil. Tillage and Research 82:99-108.

Prestonm, C.M., Trofymow, J.A. 2000. Variability in litter quality and its relationship to litter decay in Canadian forests. The Canadian Intersite Decomposition Experiment Working Group. Canadian Journal of Botany 78:1269-1287.

Reeder, J.D.; Franks, C.D.; Milchunas, D.G. 2001. Root biomass and microbial processes. In Follett, R.F.; Kimble, J.M.; Lal, R. Ed. The potential of U.S. grazing lands to sequester carbon and mitigate the greenhouse effect. Boca Raton, Florida, Lewis. p. 139-166.

Reeder, J., Schuman, G. 2002. Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands. Environmental Pollution 116:457-463.

Riedo, M., Grub, A., Rosset, M., Fuhrer, J. 1998. A pasture simulation model for dry matter production, and fluxes of carbon, nitrogen, water and energy. Ecological Modelling 105:141–183

Salamanca, E., Kaneko, N., Katagiri, S. 2003. Rainfall manipulation effects on litter decomposition and the microbial biomass of the forest floor. Applied Soil Ecology 22:271–281.

Sariyidiz, T., Anderson, J. 2003. Interactions between litter quality, decomposition and soil fertility: a laboratory study. Soil Biology and Biochemistry 35:391-399.

Sariyildiz, T., Anderson, J.M., Kucuk, M. 2005. Effects of tree species and topography on soil chemistry, litter quality, and decomposition in Northeast Turkey. Soil Biology and Biochemistry 37(9):1695-1706.

Schimel. J., Cates, R., Ruess, R. 1998. Polyphenols as regulators of `plant litter soil interactions in Northern California`s Pygmy Forest: a positive feedback. Biogeochemistry 42:221-234

Schuman, G.E., Herrick, J.E., Janzen, H.H. 2000. The dynamics of soil carbon in rangelands. In Follet, R.F., Kimble, J.M., Lal, R. The potential of U.S. grazing lands to sequester carbon to mitigate the greenhouse effect. Boca Raton, Lewis. p. 267-290.

Schuman, G.E., Reeder, J.D., Manley, J.T., Hart, R.H., Manley, W.A. 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecological Applications 9(1):65-71.

Scott-Denton, L.E., Sparks, K.L., Monson, R.K. 2003. Spatial and temporal controls of soil respiration rate in a high elevation sub-alpine forest. Soil biology and biogeochemistry 35:525-534.

Scowcroft, P., Turner, D., Vitousek, P. 2000. Decomposition of Metrosideros polymorpha leaf litter along elevational gradients in Hawaii. Global Change Biology 6:73-85.

Shariff, A., Biondini, M., Grygiel, C. 1994. Grazing intensity effects on litter decomposition and soil nitrogen mineralization. Journal of Range Management 47:444-449.

Silver, W.L., Miya, R.K. 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. Oecologia 129:407-419.

Smit, A., Kooijman, A. 2001. The impact of grazing on the input of organic matter and nutrients to the soil in a grass-encroached Scots pine forest. Forest, Ecology and Management 142:99-107.

Smoliak, S. 1986. Influence of climatic conditions on production of Stipa-Bouteloa prairie over a 50-year period. Journal of range management 39(2):100-103

Snyman, H.A., Preez. 2005. Rangeland degradation in a semi-arid South Africa I: influence on seasonal root distribution, root/shoot ratios and water-use efficiency. Journal of Arid Environments 60:457-481.

Southern Alberta Land Trust Society 2006. Conserving rangelands. http://www.salts-landtrust.org/conservingrangelands.html#e

Schulten, H.R., Schnitzer, M. 1997. Chemical model structures for soil organic matter and soils. Soil Sci., 162(2): 115-130.

Tardieu, F., 1994. Growth and functioning of roots and of root systems subjected to soil compaction. Towards a system with multiple signalling. Soil Tillage Res. 30, 217–243.

Tiessen, H., Cuevas, E., Chacon, P. . 2002. The role of soil organic matter in sustaining soil fertility. Nature 371:783 - 785; doi:10.1038/371783a0

Trofymo, J.A., Preston, C.M., Prescott, C.E. 1995. Litter quality and its potential effect on decay rates of materials from Canadian forests, Water Air Soil Poll., 82:215-226.

Towne, G., Hartnett, D., Cochran, R. 2005. Vegetation trends in tall grass prairie from bison and cattle grazing. Ecological applications 15(5):1550-1559.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics, 31:197–215.

van de Koppel, J., Rietkerk, M., Weissing, F.J. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. Trends in Ecology & Evolution, 12(9):352-356

Van der Krift, T.A.; Gioacchini, P.; Kuikman, P.J.; Berendse, F. 2001. Effects of high and low fertility plant species on dead root decomposition and nitrogen mineralization. Soil Biology and Biochemistry 33:2115-2124.

Van Soest, P.J. 1994. Nutritional ecology of the ruminant. 2nd ed. Ithaca Comstock Pub. 476 p.

Ventera, R.T., Lovett, G.M., Groffman, P.M., Schwarz, P.A. 2003. Landscape patterns of net nitrification in a northern hardwood conifer forest. Soil Sci. Soc. Am. J. 67:527-539.

Vivanco, L., Austin, A. 2006. Intrinsic effects of species on leaf litter and root decomposition: a comparison of temperate grasses from North and South America. Oecologia 150:97-107.

Wang, Ch., Wan, S., Xing, X., Zhang, L., Han, X. 2006. Temperature and soil moisture interactively affected soil net N mineralization in temperate grassland in Northern China. Soil Biology & Biochemistry. 38:1101–1110.

Wang, Y., Zhou, G., Jia, B. 2008. Modeling SOC and NPP responses of meadow steppe to different grazing intensities in Northeast China. Ecological modelling, 217:72–78

Wardle, D., Yeates, G., Nicholson, K., Bonner, K., Watson, R. 1999. Response of soil microbial biomass dynamics, activity and plant litter decomposition to agricultural intensification over a seven-year period. Soil biology and biogeochemistry 31(12):1707-1720.

Whallen, B. 1986. Above and below-ground dry mass of the three main vascular plants on hummocks on a subartic peat bog. Oikos 46:51-56.

Whitemore, A. 1991. A method for assessing the goodness of computer simulation of soil processes. Journal of soil science 42:289-299.

Willmott, C. J. 1981. On the validation of models. Physical Geography, 2(2):184−194.

Willmott, C. J. 1982. Some comments on the evaluation of model performance. Bulletin of the American Meteorological Society, 63(11):1309−1313.

Wright, A.; Hons, F.; Rouquette, F. 2004. Long-term management impacts on soil carbon and nitrogen dynamics of grazed Bermuda grass pastures. Soil Biology and Biochemistry 36:1809-1816.

Chapter 2.0. Effect of topography and grazing on shoot and root litter decomposition in a semiarid rangeland

1. Introduction: importance of litter decomposition

The decomposition of plant litter and the recycling of nutrients are vital for maintaining natural soil fertility. In fact, natural ecosystems rely on litter decomposition to produce plant biomass (Larcher 2001) because through it nutrients are released and made available for plant uptake. Due to the important role of litter decomposition in maintaining soil fertility, and hence the need to understand factors that influence this process, litter decomposition has been studied for different ecosystems (Berg 2000, Prescott *et al*. 2004, Smith and Bradford 2003, Quideau *et al*. 2005). Litter mass losses ranging from 40% to 90% in forest (Prescott *et al*. 2004, Hobbie 2000, Moore *et al*. 1999), and from 45% to 75% in grasslands (Moore *et al*. 1999, Koukoura *et al*. 2003, Smith and Bradford 2003) have been reported after two years of shoot litter incubation in the field.

Most of the information available refers to above ground litter. However, root litter decomposition is also very important because root litter can be several times greater than shoot litter (Wallen 1986, Gill and Jackson 2000, van der Kirft *et al*. 2001, Archer *et al*. 2002), and have greater nutrient concentration (Jackson *et al*. 1997, Gordon and Jackson 2000, Silver and Milla 2001). Roots can have a turnover rate up to 60% per year (Gill and Jackson 2000, Meelis and Wilson 2002), hence root decomposition recycles large amounts of nutrients.

Therefore, both kinds of litter are important for ecosystem functioning because of their direct influence on nutrient cycling and soil fertility. Litterfall also influences soil organic carbon (SOC) and if production of litterfall is reduced, soil conditions related to plant growth may be negatively affected. Over time reduced litterfall will decrease SOC which has direct environmental implications because the soil is the largest carbon pool in terrestrial ecosystems (Janzen 2004).

Even though litter decomposition is a very important process, there is not enough available information about it, and there are still ecosystems and site conditions in which it has not been fully studied and hence the rates at which it occurs are unknown. Two of those conditions are variable topography and grazing of ungulates in natural semiarid rangelands.

1.1. Topography and litter decomposition

1.1.1. Soil moisture

Topography has a direct influence on litter decomposition because it is directly linked with two soil properties connected with microbial activity: soil moisture and soil temperature (Hairston and Grigal 1994, Moran *et al*. 2000). If they increase or decrease so does microbial activity (Chen *et al*. 2000, Amudson 2001, Dalias *et al*. 2001), with the exception of high soil water contents that will slow down decomposition.

Microbial activity is highest when relative water-filled porosity (RWFP) is greater than 0.3 but less than 0.65 (Linn and Doran 1984). RWFP ranges from 0 (dry soil) to 1 (saturated soil), where field capacity (FC) usually has a value around 0.6, and permanent wilting point (WP) is around 0.3. In a lab experiment Linn and Doran (1984) found that microbial respiration, and hence decomposition, increased approximately 4.5 times when WFP was increased from 20 to 60%. Similarly increasing moisture from less than 40 to 80% of soil water holding capacity, increased decomposition in a chesnut forest from southern France by up to 200%. Cortés (1998),

Water moving down slope causes soil redistribution along the landscape and thereby increases the thickness (Pennock *et al*. 1987, Landi *et al*. 2004), organic carbon (Honeycutt *et al*. 1990, Burke *et al*. 1999, Norton *et al*. 2003), nitrogen (McCarthy 2005), and water contents (Martin and Timmer 2006, Pachepsky *et al*. 2001) of the near surface soil layers at lower topographic locations. As microbial activity also depends on the amount of organic matter incorporated into the soil, lower topographic locations with greater biomass production will have more microbial activity due to greater incorporation of plant residues into the soil (Petersen *et al*. 1988, Lal 2002, Lal 2004) hastening litter decomposition.

1.1.2. Soil temperature

Even with sufficient moisture and organic matter in the soil, microbial activity also depends on soil temperature. Thus, litter decomposition is strongly related to soil temperature because of its influence on microbial activity and enzymatic breakdown of polymers (Dalias *et al*. 2001, Wang *et al*. 2006). Soil temperature has a strong influence on organic matter decomposition because it induces changes in microbial activity (Dalias *et al*. 2001). Enzymes involved in polymer breakdown are stimulated by temperature, with an increase in soil temperature up to 35°C will enhance enzymatic activity (Chen *et al*. 2000) and decomposition rate. In general, microorganisms have a Q_{10} of about 2, thus for each increase of 10°C the microbial activity is doubled (Brady and Weil 2002). However, after reaching 35°C microbial activity decreases probably due to the denaturing of proteins (Chen *et al*. 2002) thus showing Arrhenius kinetics.

Several studies have demonstrated the effect of soil temperature (Dalias *et al*. 2001, Guo and Sims 2001, Couteaux *et al*. 2002, Wang *et al*. 2006) and its interaction with soil moisture (Chen *et al*. 2000) on litter decomposition. Thus, if lower topographic locations have good soil moisture and temperature for microbial activity, litter decomposition will be more rapid there. However, even though there are direct relationships among topography, soil conditions and microbial activity, there is limited information about their effects on litter decomposition in semiarid rangelands.

1.1.3. Topography and plant productivity

Differences in soil available resources (water, and nutrients) caused by topography are reflected in plant productivity and hence litter production. Perez *et al.* (1998) in a semiarid Mediterranean grassland ecosystem, Frank and Groffman (1998) in natural grasslands of Yellowstone National Park, USA, and Asamoah *et al*. (2004) in a semiarid grassland of Alberta, found up to 200% greater plant biomass at bottom slopes compared with the adjacent uplands. Usually plants that grow on fertile soils not only grow more (Perez *et al*. 1998), they also produce leaves with high nutrient (N, Ca, P) concentrations that may contribute higher quality litter (low C-to-N ratio, low lignin content) to the soil (Sariyidiz and Anderson 2002). This chemical composition stimulates litter decomposition (Moore *et al*. 1999). In contrast, plants that grow on low-fertility soils usually are located on elevated uplands, have slow growth rates, fibrous leaves and large investments in structural and storage organs (Grime *et al*. 1997). These tissues have low nutrient concentrations, and high concentrations of lignin and secondary compounds such as phenols that result in slow decomposition (Aerts 1999**).** Thus, the plant species from which the litter originates significantly influence its decomposition (Moretto and Distel 2003, Scowcroft *et al*. 2000, Silver and Miya 2001, Ross *et al*. 2002). In addition, plants may differ in nutrient concentrations depending on soil conditions (Liu *et al*. 2006, Sariyildiz and Anderson 2003), and there is a differentiation of litter chemical quality depending on where the plants grow.

This shows clearly that topography creates spatial variability in soil conditions, plant species and productivity over the landscape. This variability influences litter production, its chemical quality and decomposition, which controls nutrient release and recycling, that is reflected on plant growth. Therefore, topography should cause important variations in ecosystem productivity.

1.2. Grazing effect on litter decomposition

1.2.1. Grazing effect on botanical composition

Grazing affects plant diversity, particularly over time under heavy stocking rates in which a decrease in plant species has been observed (Schuman *et al*. 1999, Hart 2001, Reeder and Shuman 2002). Such grazing increases less palatable and more grazing resistant species (Hart 2001); that is why there is a replacement of C_3 by more grazing-tolerant grass species like Bouteloua (Reeder and Shuman 2002, LeCain *et al*. 2002). Grazing at moderate stocking rates also can cause changes in botanical composition (Berg *et al*. 1997). Towne *et al*. (2005) found that grazing with either bison or cattle increased spatial heterogeneity and promoted the biodiversity of tall grass prairies.

1.2.2. Grazing effect on litter quality

1.2.2.1. Direct effects

Grazing adversely affects litter quality and hence decomposition by altering the botanical composition of any field (Olofsson and Oksaneu 2001, Follet 2000, Scowcroft *et al*. 2000, Silver and Miya 2001, Koukoura *et al*. 2003). According to Vivanco and Austin (2006) there is higher nitrogen concentration (1.6 vs. 1.0%) and lower C-to-N ratio (29 vs. 50) in C_3 than in C_4 leaf litter. Thus, a change in the proportion of these species through grazing should influence litter decomposition rate.

Unpalatable plants that are not consumed by grazing animals usually have chemical compounds like tannins (Aerts 1999, Lindroth *et al.* 2002) that serve as defence against herbivores (Ayres *et al.* 1997, Kogel-Knabner 2002). These compounds will be present in litter (Koukoura *et al*. 2003), decreasing its quality and decomposition rate (Olofsson and Oksaneu 2001) through direct toxic effects (Bradley *et al.* 2000, Kogel-Knaber 2002), and through indirect effects on N-fixation reducing nodulation and the amount of leghemoglobin (Blum and Rice 1969) and N mineralization possibly because of their protein-binding properties (Schimel *et al*. 1996, Lorenz *et al*. 2000, Fierer *et al*. 2001).

Grazing, even if it does not change botanical composition, could influence litter quality and corresponding decomposition rates. According to Green and Detling (2000) and Baron *et al.* (2002) grazing increases litter quality by increasing nitrogen content in remaining plant tissue because grazing results in regrowth that is higher in leaf to stem ratios, and leaves have higher crude protein and lower acid detergent fibre than stems at most stages of grass development. These chemical characteristics will be reflected in the litterfall. This agrees with results found by Shariff *et al.* (1994) in which light grazing increased decomposition rate by 46% compared with an ungrazed treatment, possibly because of positive changes in litter chemical quality that stimulated microbial activity.

Good grazing systems usually contribute to an increase in the leaf-to-stem ratio (Matches 1992, Morley 1981), which is better for animal performance because the leaves have higher protein concentrations than stems. However, under highly intensive grazing, there is a reduction of the leaf-to-stem ratio because animals consume mainly leaves; this increases the amount of stems in litterfall, which in turn decreases the decomposition rate of this litter once it is incorporated into the soil (Koukoura *et al.* 2003). A reduction in decomposition rate also is caused by reduced litter production from animal consumption so that less litter is incorporated to the soil under grazing (Donkor *et al*. 2002).

Thus, different grazing intensites can cause negative (Smit and Kooijman 2001, Cao *et al*. 2004), positive (Couteaux *et al*. 1995, Chen *et al*. 2000, Olofsson and Oksanen 2001) or no effects (Smit *et al*. 2002) on litter decomposition.

1.2.2.2. Indirect effects

Grazing also affects litter decomposition by affecting the environment in which litter decomposition occurs. When the stocking rate is heavy and the utilization of available forage high ($\geq$50% y^{-1}) litterfall is reduced (Reeder and Schuman 2002), and animal traffic increases physical breakdown of plants and their direct incorporation into the soil (Schuman *et al.* 1999). This reduces soil coverage by plants allowing more sunlight to reach the soil surface. This raises soil temperature, which stimulates microbial activity and the enzymatic breakdown of polymers (Chen *et al*. 2000) accelerating organic matter decomposition (McIntosh *et al*. 1997). But if grazing is light and forage utilization small ($\leq$ 30%) soil temperature does not change because enough plant material covers the soil to insulate it from sunlight.

Grazing can also affect root litter decomposition through its effect on soil characteristics related with microbial activity. Grazing can increase bulk density (Donkor *et al*. 2002), and a compacted soil offers physical impedance to growing roots, decreasing their elongation and reducing their biomass (Hamza and Anderson 2005). The increase in bulk density caused by hoof action reduces soil aggregate size and compresses the soil surface. This effect is worse when soil moisture is high because the soil surface is easily sealed, which will reduce infiltration and associated soil moisture (Llacos 1962, Donkor *et al*. 2002, Martinez and Zinck 2004, Pietola *et al*. 2005). Also, the hard topsoil layer inhibits gas exchange with the atmosphere, reducing soil oxygen and constraining microbial respiration and therefore decomposition rate.

This change in soil environment with grazing is especially critical to root litter (Salamanca *et al*. 2003, Scott-Denton *et al*. 2003). Reduced microbial respiration (Cao *et al*. 2004) has been related with smaller microbial populations probably caused by suboptimal soil moisture and oxygen. This decreases root decomposition and nutrient cycling in different ways; one effect is through the reduction of root litter incorporated to the soil. This is important because the amount of carbon and nutrients returned to the soil from fine root turnover may equal or exceed that from leaf litter (Gordon and Jackson 2000).

Another grazing effect is related with root exudations. These are important energy sources for soil microorganisms, and plants with greater root biomass produce larger amounts of exudates than plants with small root biomass. Grazing has been related with reductions in root biomass (Mapfumo *et al*. 2000, Smit and Kooijman 2001) because grazing causes soil compaction and a compacted soil offers physical impedance for root growth (Kirkegaard *et al*. 1992, Tardieu 1994) decreasing the total root biomass. Additionally removal of leaves reduces photosynthates and the carbon transferred to roots, and so reduces root growth and exudation (van der Kirft *et al*. 2001).

1.3. Hypotheses and Objectives

Based on these previous results, the hypotheses for this research were 1) **that litter decomposition rates differ among topographic locations because topography creates gradients of soil moisture, temperature and fertility down slope which raise the decomposition rate at lower locations;** 2) **litter decomposition rates are reduced by wild ungulates grazing at moderate stocking rates because they consume the best available forage and lower the quality of the produced litter**. The objectives of this research were 1) to determine the decomposition rate of shoot and root litter at different topographic locations, and 2) to determine if litter decomposition rate is influenced by topography and wild grazing animals.

2. Materials and Methods

To test these hypotheses, a litterbag experiment was used to measure litter decomposition rates in the field under the following conditions.

2.1. Location and description of experimental field

The litter used to measure decomposition rates was collected at Kinsella Ranch, an experimental farm of 2247 hectares located 160 km southeast of Edmonton (53° 01' 13.7" N, 111° 32' 42.1" W), within the Aspen Parkland ecoregion (Strong 1992), Central Alberta, Canada. The average annual mean temperature and precipitation for the last 20 years were 2°C and 428 mm (Environment Canada 2006).

In this experimental field there is a strong topographic effect on soils across the landscape. The landform is a hummocky moraine with irregular hills and slopes up to 45°, and consists of calcareous parent material deposited over underlying marine shale (Howitt *et al*. 1988). Soils at upper topographic levels are well-drained Dark Brown, Black or Eluviated Black Chernozems; the depressional areas are poorly drained Gleysols (Wheeler 1976). A soil survey of Kinsella Ranch was done during September of 2003, and three soil profiles were examined at each of the upper, middle and lower topographic locations. These three topographic transects were selected based on their representativity of the experimental area. Results from this survey can be seen in Table 1, and they show a clear topographic trend in which N and C contents increased down slope.

Nutrient analyses were carried out at the soil lab of the Renewable Resources Department at the University of Alberta: Air-dry soil was ground to pass a 0.5 mm mesh. Soil pH was determined in water using a Fisher AR20 pH meter with glass and calomel reference electrodes calibrated to buffer pH 4 and 7; total C and N content was measured by dry combustion using a Costech 4010 Elemental Analyzer. Nitrate and ammonium were extracted with 2M KCl and then measured colorimetrically on a SmartChem - Discrete Wet Chemistry Analyzer, at 520nm the first, and at 630 nm the second. Phosphorus was determined using the Kelowna modified extractable method.

The vegetation, typical of rangeland ecosystems located in a semiarid region, is also influenced by topography (Wheeler 1976, Scheffler 1976). In that landscape, there are four dominant plant communities: grasses, shrubs, aspen trees, and riparian. The general distribution pattern is as follows: grasses dominated by fescue (*Festuca* spp.) are present at all topographic positions; forbs and shrubs (*Artemisia ludovisiana*, *A. frigida*,

Table 2-1. Physical and chemical soil properties at Kinsella Ranch experimental site, Central Alberta, Canada.

Topographic location	Depth cm	Bulk density	Clay	Silt %	Sand	pH	NO_3-N ppm	NH_4-N ppm	PO_4-P, ppm	Wt % N	Wt % C	WHC* $m^3\ cm^{-3}$	FC* $cm^3\ cm^{-3}$	PWP* $cm^3\ cm^{-3}$	K_{sat}* $mm\ h^{-1}$
Upper	Ah 0–10	1.19	18	28	54	7.03	3.41	3.65	3.84	0.31	3.40	0.14	0.294	0.155	42.6
	Bm 10–23	1.34	32	26	42	7.88	3.70	2.35	1.21	0.19	2.04	0.13	0.338	0.205	9.56
	Ck 23-50	1.63	30	25	45	8.51	3.04	1.56	0.83	0.13	2.21	0.11	0.316	0.201	0.86
Middle	Ah 0–22	1.07	13	35	52	5.94	2.75	2.14	1.85	0.36	4.23	0.16	0.299	0.142	64.65
	Btj 22-55	1.42	30	25	45	5.92	2.77	2.27	1.23	0.30	1.52	0.13	0.321	0.195	7.20
Lower	Ah 0 – 30	1.24	12	47	41	7.27	3.62	2.19	0.77	0.52	6.39	0.17	0.303	0.134	32.21
	Ahe 30 – 35	1.18	17	46	36	6.61	2.67	2.14	1.11	0.10	0.98	0.14	0.259	0.117	30.31
	Aeg 35 – 45	1.52	40	27	33	5.99	3.12	3.90	3.41	0.04	0.31	0.12	0.360	0.241	0.77
	Btjg 45 – 62	1.52	24	47	29	6.30	2.29	2.11	0.77	0.06	0.54	0.15	0.299	0.146	5.73
	Bcg 62 – 100	1.39	28	44	28	6.00	2.65	3.18	1.73	0.07	0.35	0.15	0.322	0.172	9.72
	Bg 100 - 116	1.60	27	47	26	5.88	5.13	2.24	1.16	0.07	0.67	0.15	0.321	0.169	1.27

*According to Saxton and Rawls (2006); WHC: water holding capacity, FC: field capacity, PWP: permanent wilting point,

K_{sat}: saturated hydraulic conductivity.

NO_3-N and NH_4-N were extracted with KCl 2M, and PO_4-P with the Kelowna modified method.

Symphoricarpos occidentalis and *Rosa woodsii*) are at the middle and upper hill positions on north facing slopes; aspen trees (*Populus* spp.) predominate in low locations and north slopes; and riparian communities are located in depressional areas but were not considered in this research. The study area has been grazed annually since 1995 using a rotational grazing regime at moderate stocking rate (~2 AUM ha^{-1}, Asamoah *et al*. 2004). Exclosure areas were established in 2003 to monitor grazing effects on plant productivity.

2.2. Soil moisture and temperature

The rate of litter decomposition is influenced by soil moisture and soil temperature, measurements of which were needed to test hypothesis 1. Because these two soil variables are influenced by topography, a transect 15m long with northeast aspect and 45° slope, covered by characteristic vegetation of Kinsella Ranch, was chosen to place three Time Domain Reflectometers (TDR, CR500 Campbell Scientific Inc.) and thermistors in fenced plots to get continuous hourly moisture and temperature data from three soil depths (0.05, 0.10, and 0.15m) at three different topographic locations: Upper (U), Middle (M), and Lower (L). Due to probe malfunction in the field during certain periods, there were some gaps in the gathered information, and data from the 0.05m depth at L were completely discarded.

To calibrate the TDR probes, soil was collected from each topographic location, and used to generate curves of soil moisture vs. TDR output for each probe. To do this, 20 L buckets were filled with each soil and wetted to saturation, then barley plants were grown under greenhouse conditions to dry the soil and TDR measurements were taken during drying. These curves were used to get a regression from which an equation was derived to convert the return time from the probes into volumetric soil water.

2.3. Site management

The 6.16 ha paddock in which the experiment was located was grazed during 2004 by two bison (*Bison bison*), two elk (*Cervus elaphus*) and two deer (*Odocoileus hemionus*) at 1.57 animal unit months ha^{-1} (AUM ha^{-1}). During 2005 one bison and one elk were added, increasing the stocking rate to 2.35 AUM ha^{-1}. There were two grazing periods each year, the first from June 1st to July 15th, and the second from September 1st to October 15th.

2.4. Shoot and root litter treatments

2.4.1. Effects of topography and grazing on litter decomposition

2.4.1.1. Topography

Slopes of different inclinations characterize this rangeland ecosystem. To capture the effect of topography on litter decomposition shoot litter was collected from three ungrazed and grazed plots at M located on the one single transect. Before collection, plots were cleaned by hand and raked, and all litter on the ground or standing was removed, so only current year's litter on the ground which was collected from June to July was utilized in this experiment

To study the effect of topography, a mix of grazed or ungrazed shoot litter collected in different plots at M, was placed in litterbags along a topographic transect (U, M, and L, see below) in which soil conditions (nutrient content, soil organic matter, water availability) were different along the hill (Table 1).

Distribution of litterbags to study topographic effect on decomposition:

1. Grazed shoot litter collected at M was placed under grazing condition at U
2. Ungrazed shoot litter collected at M was placed under ungrazed condition at U
3. Grazed shoot litter collected at M was placed under grazing condition at M
4. Ungrazed shoot litter collected at M was placed under ungrazed condition at M
5. Grazed shoot litter collected at M was placed under grazing condition at L
6. Ungrazed shoot litter collected at M was placed under ungrazed condition at L

Roots were taken from the same plots in which grazed shoot litter was collected. From these plots five soil cores (0.2*0.2*0.2m, wide, long, deep) were taken at random and placed in labeled plastic bags, and transported to a place to be washed. By using a screen of 1mm most of the finest roots was collected and subsequently air-dried.

To study topographic effects on root decomposition, a mix of grazed roots which were collected in different plots at M, were placed in litterbags along the same topographic transect (U, M, and L) in which composite shoot litter was placed, and distributed in similar way than was done with composite shoot litter. Litterbags with roots were buried at 0.15m depths.

2.4.1.2. Grazing

To study grazing effects on litter decomposition, shoot litter was collected from three ungrazed and grazed plots at U, M, and L located on one single transect. This litter was described as 'local' because it came from local plants growing at each topographic level, and was placed in litterbags at the same topographic location and condition (grazed or ungrazed) from which it was collected as follows:

1. Grazed shoot litter collected at U was placed under grazing condition at U
2. Ungrazed shoot litter collected at U was placed under ungrazed condition at U
3. Grazed shoot litter collected at M was placed under grazing condition at M
4. Ungrazed shoot litter collected at M was placed under ungrazed condition at M
5. Grazed shoot litter collected at L was placed under grazing condition at L
6. Ungrazed shoot litter collected at L was placed under grazed condition at L

Thus, litterbags filled with grazed shoot litter were placed at random in open plots in which animals were able to graze; the litterbags filled with ungrazed shoot litter were placed also at random but in fenced plots to avoid the grazing animals. Grazing effects in this experiment thus combined those of grazing before the experiment on litter quality, and of grazing during the experiment on litter decomposition. Litter samples were collected from July 20th to August 20th 2004, and the litter decomposition experiment began on August 24th 2004. .

For composite litters a 3x2 factorial design (topographic locations x grazing) with five pseudoreps was implemented. There were six sampling times (1.-Oct. 26th 2004 after the 2nd grazing event (63 d after the start of the litterbag experiment), 2.-April 18th 2005 after the first winter (237 d), 3.-May 26th 2005 before the 1st grazing event (275 d), 4.-July 16th 2005 after the 1st grazing event (326 d), 5.-Oct. 15th 2005 after the 2nd grazing event (417 d), and 6.-April 16th 2006 after the second winter (600 d). For each litter type (grazed or ungrazed) five litter bags and two control bags were retrieved at each sampling time from each topographic location and from each treatment, and any weight increment in the control bags was subtracted from the weight of the litterbags retrieved on that sampling date. All results, once corrected for controls, were expressed as percent of the initial litter mass.

For local litter a nested design was utilized; the litter was nested into topography, so at any topographic location only litter coming from the same topographic location was placed. The total number of litterbags placed was 1008, of which 720 (3 topog.*2 litter types (grazed and ungrazed) *2 litter sources (local and composite) * 2 litter components (shoot and root) *6 dates *5 reps) were filled with litter; and 288 were used as control bags (3 topog. *2 litter types * 2 litter sources * 2 litter components *6 dates *2 reps).

2.4.2. Effects of aspect and grazing on litter decomposition

To study the effects of slope aspect and grazing on litter decomposition, a second litterbag experiment was started in August 2005 using the same litter collection protocol as in the previous experiment. Samples of litter types (ungrazed and grazed), sources (local and composite) and components (shoot and root) were placed in fenced and unfenced plots (2.0x2.0m) at U, M and L positions on six different slopes, three facing north and three facing south. Grazing effects in this experiment were thus resolved into those of grazing before the experiment on litter quality, and those of grazing during the experiment on litter decomposition. The treatments evaluated at each topographic position on each slope follow:

1. Previously grazed litter placed at grazed location (G-G).
2. Previously grazed litter placed at ungrazed location (G-UG).
3. Ungrazed litter placed at grazed location (UG-G).
4. Ungrazed litter placed at ungrazed location (UG-UG).

All litterbags with shoot litter were placed on top of the soil and in between the growing plants; small metal pins were placed in each corner to hold the bags on the ground. Litterbags with roots were buried at 0.15m depths. For composite litter a 2x3x4 factorial design (aspect, topographic location, and treatment) was implemented, with 2 sampling times (67 and 247 days after the start of the experiment). For local litter a nested design was utilized with litter nested into topography. For each litter component one litterbag was retrieved from each treatment of each aspect at each sampling time. The total number of litterbags in this experiment were 576 (3 topog * 2 aspect * 3 reps * 2 litter types * 2 litter sources * 4 treat * 2 sampling times).

2.5. Litterbags

To study the decomposition of these litters, the litterbag technique was utilized. The bags (0.15x0.15m) were made of dark 100% polyester fabric with 0.3x0.15mm mesh. The bags were filled with 3.00 g of shoot litter or 5.00 g of root litter clipped in pieces 5 cm long for the first experiment started in 2004, and with 2.00 g of shoot litter or 3.00 g of root litter for the second experiment started in 2005. To determine if exogenous material contaminated the litter in the bags during the decomposition experiment, control bags were included with the same size and fabric, but filled with polyester fabric clipped in pieces to get similar volume and shape as litter.

2.6. Statistical analysis

Statistical analysis utilized SAS (SAS Institute 2005) from which the Proc GLM procedure was run to get the ANOVA in which topography and grazing effect on litter were the analyzed variables. Means were compared using Duncan with a $P<0.05$.

2.7. Chemical analyses of litter

Proximate analysis was utilized to asses the quality of litter harvested at different dates because this analysis fractionates litter carbon compounds according to their potential degradability. These fractions consisted of water-soluble compounds (WSC including simple sugars, water-soluble phenols) with the fastest potential decomposition, non-polar compounds (NPC including soluble fats, waxes, oils) also with fast potential decomposition, acid-soluble carbohydrates (including cellulose, hemicellulose) with intermediate potential decomposition, and acid-insoluble residue known as Klason lignin (Lignin) with slowest potential decomposition, and ashes (Ash).

For these analyses, a homogeneous sample of each litter type was oven-dried at 65°C for 48 h and then ground to pass a mesh sieve of 0.5 mm using a Wiley mill. A sequential extraction was performed, first with dichloromethane to extract the NPC and then with hot distilled water to collect the WSC. Two replicates of each remaining litter sample were acid digested using H_2SO_4 and hemicellulose (cellulose and hemicellulose) content was determined as the difference between pre-and post-acid digested dry sample weights. The acid-insoluble residue was assumed to consist primarily of lignin and ash. This residue was placed in a pre-weighed dry crucible and kept in a muffle furnace for 24 h at 500°C to calculate ash content.

2.8. Estimating litter decomposition rate as functions of soil temperature and soil moisture

Measured soil temperature (T_s) and water content (θ) were used with scalar functions for T_s and θ effects on decomposition rates (f_t and f_θ respectively) developed in other studies to determine whether these two soil variables could explain variation in litter decomposition rates measured along a topographic gradient in the litter decomposition experiments described above. In f_θ, $\boldsymbol{\theta}$ was transformed to relative water filled porosity (RWFP) to estimate relative water-limited decomposition, with f_θ values close to zero at RWFP below 0.3 (wilting point), rising linearly from zero at RWFP 0.3 to one at RWFP 0.6 (field capacity), and declining from one at RWFP 0.75 to close to zero at RWFP 1.0 (saturation) (Schjønning *et al*. 2003**)**.

Similarly, f_t was formulated as an Arrhenius function (Stroo *et al*. 1989) which increased exponentially from near zero at 0 ^{o}C to 1 at 35°C but decreased thereafter. These functions were considered to be multiplicative (Andrén *et al*. 1992), so that when the soil temperature is close to 35°C, and RWFP around 0.6, the product of the two functions will give the maximum rate of litter decomposition.

2.9. Calculating decomposition rate constants

Decomposition rate constants (***k***) were calculated for each litter type in each treatment from the negative exponential decomposition function:

$$X/X_o = e^{-\boldsymbol{k} f_t f_\theta t} \qquad [1]$$

(Olson 1963), where X is the amount of litter remaining at time *t* from the initial quantity X_o. A single value of ***k*** was calculated for each litter type (grazed or ungrazed), source (composite only) and component (shoot or root), as well as for some carbon fractions derived from chemical analyses of these litters (see 2.8 below).

To derive ***k***, the hourly product of f_t and f_θ was multiplied by a test value of ***k*** to simulate hourly declines in X at ambient T_s and $\boldsymbol{\theta}$. This ***k*** was then adjusted to get the minimum root mean square for differences between modeled and measured X for a given litter type during the decomposition experiments. The resulting reference value of ***k*** was used with f_t and f_θ to test whether differences in X measured at U, M and L could be attributed to differences in T_s and $\boldsymbol{\theta}$.

Finally, as there were some gaps in measured T_s and θ during the experimental period, values simulated by *ecosys* (see chapter III for details) were used to gap-fill the data used in f_t and f_θ. There was good agreement between modeled and measured values; the RMSD during 2005 at U was 1.5°C and 1.8°C at 0.05 and 0.15 m depths, respectively. The RMSD at M was 2.7°C at 0.05 m and 2.8°C at 0.15 m depths;

meanwhile at L the RMSD was 1.4°C at 0.15 m depths (see Chapter III). These results reinforce the fact that algorithms used by *ecosys* to estimate soil temperature are able to reproduce field conditions and this is the reason why we use data generated for *ecosys* to gap-fill data

3. Results

3.1. Topography and relative water-filled porosity

RWFP measured at 0.05m and 0.15m remained higher and closer to 0.6 at L than at M and U (Figs. 1 and 2). The greater RWFP found at L (Fig. 2E,F) occurred because there was water recharge from upper locations (see Chapter III). Another factor that probably contributed to increase the RWFP was the fact that L had greater water holding capacity (Table 1) and so retained more available water than U during the growing season (Fig. 2).

The RWFP at 0.05m at U (Fig. 1C,D) rose with precipitation, but declined with plant water uptake and subsurface water movement (seepage, see Chapter III). The RWFP at 0.15m at U (Fig. 2A,B) showed the same trend as that found at 0.05m. The fact that only *ca*. 78% of long-term average rainfall was received during 2005 (Agriculture Canada 2006) could have contributed to the observed declines of RWFP during July and August of that year. The RWFP at 0.05m and 0.15m at M (Figs. 1E,F and 2C,D) had similar trends to those at U.

The RWFP did not rise with all rain events (Fig. 1). This could be caused by small rain events that were unable to wet the soil to the depth of the probes, slow infiltration rate and rapid plant uptake of rainwater, and some surficial water movement down hill.

3.2. Topography and soil temperature

The measured T_s was variable through the growing seasons of 2004 and 2005. During 2005 the average T_s at 0.05m depth in July, the warmest month, was the same at U and M (20±3°C) (Fig. 3B,D, but was 2°C lower at L (Fig. 3F). At 0.15m depth the average T_s was 1°C and 3°C lower at M and L than at U (20±2°C) (Fig. 4). For the whole growing season, the measured average T_s decreased 1°C from U to L

The decrease of T_s down slope could be explained from the interaction between θ and slope aspect at L. In the northern Temperate Zone, slope aspect is an important topographic factor influencing local site microclimate, mainly because it determines the intensity of solar radiation received at the ground surface which drives air and soil temperatures (Barnes *et al*. 1998). Because of the northeast aspect of the experimental transect, L received less direct and less intense sunlight than U (Lieffers and Larkin-Lieffers 1987) which, combined with a larger heat capacity from greater θ (Figs. 1 and 2) reduced T_s and its diurnal variation (Figs. 3 and 4). Conversely U, with more sunshine and lower θ than L, had higher T_s with more diurnal variation (Figs. 3 and 4). Thus, this landscape has cold slopes, which have west to north-west aspects, and warm slopes with south to south-east aspects (Lieffers and Larkin-Lieffers 1987).

3.3. Topographic effect on shoot and root litter decomposition

By influencing θ and T_s, topography also influences microbial activity. Thus, litter decomposition rate should be different if θ and T_s change with topographic location, as indicated in Figs. 1 to 4. A topographic effect on decomposition rates ($P<0.0001$) was found for composite shoot litter placed on the soil surface (Fig. 5A). Remaining mass measured during the first year of the litterbag study (Oct. 2004 – Oct. 2005) was smaller at L than at M and U. Better soil conditions at L (deeper soil layer, greater soil nitrogen, carbon and water holding capacity, Table 1) and greater RWFP compared with U (Figs. 1 and 2), were thought to stimulate litter decomposition at L. Cooler soil at L (Figs. 3, 4) apparently did not decrease decomposition, as was also found by Giardina and Ryan (2000). This means that θ likely limited decomposition more than did T_s. Topography no longer apparently influenced the rate of composite shoot litter mass loss after October 2005 (Fig. 5) probably because the less recalcitrant litter fractions had mostly finished decomposing. Similar results were showed by the experiment set in 2005 (Table 2).

Litter mass loss was also simulated from Eq. [1] with the decomposition functions developed for $\boldsymbol{\theta}$ and $\mathrm{T_s}$ (Section 2.9). The simulation showed that by using hourly $\boldsymbol{\theta}$ and $\mathrm{T_s}$ measured or gap-filled at each topographic location (Figs. 2 and 3), with a common reference $\boldsymbol{k}$ for the composite shoot litter ($0.000036\ \mathrm{h^{-1}}$), the simulated mass loss was similar among topographic locations during the first autumn and winter of the litterbag study (Fig. 5A). This similarity indicated that the more rapid mass loss measured at L during this period could not be attributed to topographic effects on $\boldsymbol{\theta}$ and $\mathrm{T_s}$. However during the following spring and summer (May – July 2005), the simulated litter mass loss was more rapid at L than at M and U, so that topographic effects on $\boldsymbol{\theta}$ and $\mathrm{T_s}$ largely explained the more rapid mass loss measured at L during this period (Fig. 5A). More rapid mass loss continued to be modelled at L during the second autumn and winter of the study (Nov. 2005 – April 2006), while mass losses in the litterbags apparently ceased at all locations. The slower mass loss measured later in the study could be explained by changes in the chemical composition of remaining litter as decomposition progressed. Recalcitrant C fractions became more concentrated following depletion of the more labile C fractions that drove decomposition early in the litterbag study, and therefore decomposition rates became less responsive to different θ and T_s among topographic locations in the field.

The RMSEs of measured remaining mass X were 6.1, 4.3, and 5.2%, at U, M and L respectively under ungrazed conditions. The RMSD's between measured and modeled X were 4.1, 4.2, and 4.6% at U, M, and L respectively, which means that modeled values were within the uncertainty ranges of those measured; a *t* test showed no statistical differences between modeled and measured remaining masses. This means that Eq. [1] reproduced the experimental results within the uncertainty of the experimental results, so that the model is not rejected.

Topography did not influence measured decomposition rates of composite root litter at 0.15m depth because variation among remaining litter masses was not consistent among topographic locations at different sampling times (Fig. 5B). The absence of a topographic effect may have been caused by offsetting effects of higher T_s and lower θ measured at 0.15 m on decomposition at U than at M and L (Fig. 4). The combined effects of f_t and f_θ on decomposition caused similar mass losses to be modelled at M and at L, but greater ones at U (Fig. 5B). This more rapid loss was attributed to higher T_s at U (Fig. 4) because θ at U remained high enough at 0.15 m so that decomposition was not greatly limited (Fig. 2). Decomposition of root litters in the second experiment were also not affected by topography (final remaining masses measured in April 2006 were 70.1±1.3, 71.4±1.2, 68.6±1.3 percent at U, M, and L).

3.4. Grazing effect on shoot and root litter decomposition

Local grazed shoot litter (coming from grazed condition and placed in a grazed condition) decomposed more slowly than did ungrazed litter (coming from ungrazed condition and placed in an ungrazed condition) at M but more rapidly at L ($P<0.0127$) during the first sampling time (October 2004), while at U there was no difference between grazing treatments (Fig. 6). Slower decomposition of grazed litter has been related with lower litter quality (Smit and Kooijman 2001), and particularly with greater lignin content. The contrasting results in Fig. 6 may therefore be explained by greater lignin content of grazed vs. ungrazed litter at M, but smaller lignin content at L (see section 3.7 below). This is supported by previous research result which showed that grazing could decrease nutrients (McIntosh *et al.* 1997, Smit and Kooijman 2001), reducing microbial activity (Cao *et al*. 2004) and hence decomposition rate.

Values of ***k*** were estimated for each litter type (grazed vs. ungrazed from each of U, M and L) by fitting the measured litter masses to the values estimated from f_t and f_θ for the whole experimental period (see Methods). These values were quite similar for ungrazed (0.000045 h^{-1}, 0.000045 h^{-1}, 0.000043 h^{-1}) and grazed (0.000042 h^{-1}, 0.000042 h^{-1}, 0.000053 h^{-1}) shoot litter decomposition at U, M, and L respectively (Fig. 6). These hourly ***k*** generally declined with greater litter lignin content (see section 3.7). Thus a greater ***k*** calculated for grazed vs. ungrazed litter at L corresponded with a smaller lignin content, while ***k*** and lignin content were similar at U for both litter types.

The comparison of modeled and measured remaining mass X showed good agreement (Figs. 6A). The RMSD's coming from a regression model of measured on modelled X were 6.8, 7.2, and 11.8% at U, M and L respectively for ungrazed litter; the corresponding RMSE's among replicated measurements for the same topographic locations were 11.4, 7.1, and 11.8%. For grazed litter, the RMSD's were 7.2, 3.9, and 9.4 for U, M and L, and the corresponding RMSE's were 16.1, 3.9, and 9.4. According to a *t* test, there were no statistical differences between modeled and measured X, so we can say that the fraction of the variation in X not explained by the model (RMSD) was similar to the random error from the measured values (RMSE). In terms of simulated results this means that the model is not disproven by the field results, and that improves confidence in using this model to do predictions in this environment.

Local root litter, grazed or not during the experimental time, showed similar decomposition rate between them at each topographic location (Fig. 7). The model also showed similar decomposition rates between grazing treatments especially during the first part of the experiment (Figs. 7A–7C).

In the second experiment started in August 2005, in which the grazing effect on decomposition was evaluated (section 2.4.2), we found that previously grazed litter, independently if grazed or not during the experiment, had greater mass loss at U and at L by October of 2005. At the end of the experimental that litter in which there was presence of grazing animals had greater mass loss in April 2006 ($P<0.05$) (Fig. 8). There was no significant effect of grazing on mass loss at M. Even though θ and T_s were not measured in this experiment, we can assume based on Carmi (1995) that grazing probably raised superficial θ, by reducing foliage and hence transpiration, and thereby stimulated microbial activity and so decomposition rate. The final results in this experiment showed that decomposition rates were similar to those at equivalent experimental time in the first experiment started in 2004 (Figs. 5 to 7).

Decomposition of root litter in the second experiment was not affected by grazing (masses remaining in April 2006 in percent were 71.0±1.4 with grazing and 69.5±2.8 without grazing). Also there was no effect of root litter source (grazed or not) on decomposition rate at any sampling time, the final values were: T1:71.0±1.4, T2:68.8±1.4, T3:70.8±1.5, T4:69.5±2.8 (see section 2.4.2 for treatment description). It is possible grazing was not heavy enough to reduce significantly the remaining plant foliage and did not influence soil bulk density (Table 3) nor soil environment and associated microbial activity at 0.15m depth. Final remaining root masses in this experiment were similar to those at equivalent experimental time for root litter established in the first experiment (Figs. 5B and 7).

3.5. Grazing, soil bulk density and root litter decomposition

There was no grazing effect on root litter decomposition in this experiment (Fig. 7). Bulk density controls soil pore space, infiltration rate and gas interchange with the atmosphere, soil conditions directly linked with microbial activity and hence decomposition. Grazing did not affect the bulk density at any topographic location (Table 3) which is in agreement with previous research results (Mapfumo *et al*. 1998, Donkor *et al*. 2002). Different reasons could explain this result: 1) grazing was done at moderate intensity, 2) the proportion of silt in the soil was high enough to prevent an increase of bulk density, and 3) the freeze-thaw cycles acted to stabilize bulk density (Donkor *et al*. 2002). So, if grazing did not affect soil density (Table 3), soil characteristics associated with grazing probably did not change and hence, microbial activity and root litter decomposition rate were not affected (decreased or stimulated).

On the other hand, bulk density decreased down slope (Table 3), influenced by SOC because soil carbon increased down slope (Table 1). Greater soil carbon is positively related with soil aggregation and increased macropore space (Brady and Weil 2002) that favors the microbial activity and decomposition rate, which may have contributed to more rapid shoot litter decomposition found at L vs. M and U (Fig. 5A) .

3.6. Slope aspect effect on litter decomposition

Slope aspect affects T_s and θ, and so affected litter decomposition early in the experiment. There was greater remaining mass of shoot litter ($P<0.05$) at south than at north slopes 67 days after the beginning of the experiment (Fig. 9). This result agrees with previous findings in which north-facing slopes have greater decomposition rates of shoot litter (Barnes *et al*. 1998, Mudrick *et al*. 1994, Sariyildiz *et al*. 2005). North-facing slopes would receive less solar radiation and thus experience slower ET and have higher θ, as was found for L in the first experiment (Figs. 1 and 2) in where decomposition was most rapid during the first 67 experimental days (Fig. 5A).

At the end of the experiment (247 experimental days), there was similar mass loss in both slopes (Fig. 9) probably because the more labile carbon compounds were exhausted early during the experiment, and the remaining and more recalcitrant litter components which have slower and similar decomposition rates become the greater components of the remaining mass (Barnes *et al*. 1998).

Aspect did not affect mass loss of local root litter at different topographic positions (67.3±1.9 N vs 65.2±1.9 S at U, 68.6±1.7 N vs 68.5±1.6 S at M, and 70.3±2.4 N vs 69.3±2.5 S at L), nor of composite root litter (70.7±1.0 at N vs. 69.4±1.1 at S), nor of grazed root litter (69.4±2.2 grazed and 74.7±4.8 ungrazed at N, vs. 70.6±2.2 grazed and 65.7±4.9 ungrazed at S), probably because at 0.15m depth aspect did not affect soil environment (moisture and temperature).

3.7. Litter quality and decomposition

Litter chemical composition or quality, as indicated by differences in readily available vs. recalcitrant fractions, has a big influence on litter decomposition (Hobbie 2000). Thus a proximate analysis was performed to classify litter components according to their degradability, and to relate them with their decomposition rate in the field.

3.7.1. Proximate analysis

3.7.1.1. Grazing effect on the initial chemical composition

According to the proximate analysis results, grazing at 2 AUM ha^{-1} during the previous 15 years, caused important differences ($P<0.0023$) in the initial chemical composition of composite (Table 4) and local shoot litter at each topographic location (Table 5) by increasing the initial lignin at M ($P<0.0034$) but decreasing it at L ($P<0.001$), without changing that at U. Grazing also influenced holocellulose, NPC, and WSC concentrations in different ways at each location (Table 5). This could be explained by differences in the amount of foliage consumed at each location, which would affect the quality of litter produced. In productivity locations like M, the remaining plant foliage after grazing, which is older, more lignified and with more support tissue, produces more coarse litter as showed by its great lignin content (Table 5).

Lignin has been related with slow decomposition rates (Moore *et al*. 1999, Sariyildiz and Anderson 2003, Moretto and Distel 2003) so that by decreasing lignin in the litter, grazing at L enhanced its quality and so its decomposability.

Our experimental results for decomposition rates of grazed vs. ungrazed Local litter (Fig. 6) can be explained by their initial concentrations of lignin (Table 5). Grazed litter at M and ungrazed litter at L had more lignin, and also had lower decomposition rates (Fig. 6B,C), than did ungrazed litter at M or grazed litter at L. At U in which these litter types had similar concentration of lignin (Table 5) there was no significant difference in decomposition rates (Fig. 6A).

At more productive locations like M and L in which there was more available plant foliage and better soil conditions for plant growth than at U (Table 1), grazing as suggested by Matches (1992) and Morley (1981) probably stimulated the plant growth and increased the leaf-to-stem ratio. Grazing animals consume mainly leaves with better quality than stems (Van Soest 1996), leaving plant material with low quality which is reflected in litter with higher lignin content at M. Higher grazing intensity at L than at M stimulated plant growth and so, the proportion of leaves in the plant. Leaf litter has less lignin than stem litter, which would improve litter chemical composition (Table 5).

The local root litter showed changes in its initial chemical composition that was related with topography (Table 6) thus there was more lignin in root litter at U than at L ($P<0.05$) (Table 6). This occurs because in drier environments plants tend to lignify more than in wetter conditions (Waisel *et al*. 1996), and U had less available soil water than L. However, these differences in chemical composition did not cause different decomposition rates (Fig. 7), indicating that not only chemical composition determine root litter decomposition (van der Krift *et al*. 2002). The fact that root litter was buried at 0.15m depth contributed to good soil environment, in terms of moisture and temperature (Figs. 2 and 4) for microbial activity and did less directly related decomposition with chemical composition. Thus, grazing did not cause any difference in root litter decomposition. There was no defined trend for holocellulose related with topography, and composite root litter had similar chemical composition to the litter at M (Table 6) because composite root litter was a mix of harvested roots at this topographic location.

3.7.1.2. Changes in litter quality during decomposition

Because litter carbon compounds have different decomposition rates, their proportions change as litter decomposes over time. Therefore changes in litter quality should explain changes in decomposition rates during the experiment at each topographic location.

3.7.1.2.1. Water soluble compounds and non-polar compounds

Independently of topographic location and grazing, the amount of WSC and NPC in remaining litter declined rapidly with decomposition (Fig. 10A,B). This influenced short-term litter mass loss (Berg 2000) after the first sampling period of 69 days (October 2004, Figs. 6-7). Chemical analyses showed that WSC decreased around 60% (Fig. 10A) and NPC decreased up to 52% (Fig. 10B) from initial values which were similar to decreases found by Quideau *et al*. (2005) with these compounds over a similar period (99 days). The daily decomposition rate constants (***k***) calculated from the change of these two components ranged from 0.001 to 0.002mg of NPC d^{-1}, and from 0.001 to 0.004mg of WSC d^{-1}. This shows that these two carbon compounds had faster decomposition rates compared with those of lignin and holocellulose (see next section). Over time, concentrations of WSC and NPC stabilized at 100–200 and 40–60 mg g^{-1} respectively (Fig. 10). This could be explained by:

- Litter contamination. During the cleaning process of retrieved litterbags new litter (shoot and root) was detected inside the bags. Fresh litter, that proportionally has more WSC and NPC than old litter, could increase these compounds. Even though all obvious new litter was removed, probably not all was eliminated.
- Soil contamination. The litterbags were cleaned using a brush; however after this process some fine soil particles were still inside the bags. The litterbag weight was corrected according to the increase of weight detected in the control litterbags, but this did not eliminate the soil. So, as soil contains NPC, it was extracted during the proximate analysis and included as coming from the remaining litter mass.
- Additional WSC and NPC could come from microbial residues produced during litter decomposition.

3.7.1.2.2. Lignin and holocellulose

During decomposition the total amount of lignin, which is the more recalcitrant organic compound (Berg 2000, John *et al*. 2002) to enzymatic breakdown (Sylver and Miya 2001, Chesson 1997), slowly decreased in grazed and ungrazed litter at any topographic location showing stability especially after the first experimental year (Fig. 10C). Thus, during the course of the experimental time there is no clear indication that topographic location and grazing influenced the amount of lignin in remaining litter (Fig.

10C,D). This result can be explained by the fact that during the litter decomposition process components like humic substances are generated (Preston *et al*. 1997), which proximate analysis identifies as lignin (Fig. 10).

Conversely, independent of topographic location and grazing treatment, the amount of holocellulose decreased steadily between 58% and 67% from the beginning of the experiment to the end 417 days later (Fig. 10D). According to this, litter decomposition after the initial mass decrease is driven by decomposition of holocellulose.

Litter contents of lignin and holocellulose showed similar trends to those reported by different researchers in which decomposition proceeds, the concentration of holocellulose declined in the remaining litter mass but that of lignin increased (Berg 2000). Holocellulose decomposition had an hourly ***k*** (calculated in the same way that earlier ***k*** values), depending on topographic location and kind of litter, in a range from 0.00011 to 0.00009. In the case of lignin, the range found in the ***k*** was between 0.0000022 and 0.0000086 (Fig. 10C). These ***k*´s** show clearly that holocellulose decomposed faster than lignin during the litterbag experiment, but both slower than WSC and NPC. That's why the overall ***k*** for total litter was 0.00099 as a result of the influence of the different proportion of each carbon compound present in the litter.

3.8. Litter quality, carbon and nitrogen content

Changes in litter carbon and nitrogen are indicators of microbial activity because during the decomposition process soil microorganisms use litter carbon as an energy source, and use both C and N in growth (Barnes *et al*. 1998). Additionally, declines in litter N indicate net mineralization by which N becomes available for plant uptake.

Shoot litter N decreased up to 48% from September 2004 to October 2005 ($P<0.05$) (Fig. 11A), commensurately with decreases in WSC and NPC. Shoot litter C decomposed relatively more rapidly than N (Fig. 11B) because some of the carbon was oxidized while N was immobilized, so that the C:N ratio declined from 33 to 21 during the 417 days of the experiment.

In root litter, N decreased up to 56% during the experiment ($P<0.001$) (Fig. 11C), while carbon decreased up to 62% (Fig. 11D), so that the C:N ratio also declined during decomposition.

4. Discussion

4.1. Topography and aspect effect on litter decomposition

At the end of the experimental period (600 days), remaining litter mass at all topographic locations (from 50% to 61% for shoot litter, and from 50% to 64% for root litter) were similar to those reported in the scientific literature under similar climatic conditions. Thus, at equivalent experimental times in which litter was in the field (around two years) the decomposition of fescue root litter (58%) (Moore *et al*. 1999), *Poa* grass root (60%) and shoot litter (55-65%) (Moretto and Distel 2003), *Festuca ovina* leaves (50-70%) (Koukoura 1998), and even tree root litter (20-60%) (Chen *et al*. 2002) were close to our experimental results. Similar remaining root litter mass to this experiment were also reported by King *et al*. (1997), Chen *et al*. (2000) and Gastine *et al*. (2003) after two years of litter incubation in the field under similar and even different climatic conditions.

Topography influenced shoot litter decomposition in the short term (Fig. 5A). More rapid decomposition at L vs. U (Fig. 5) was attributed to better soil properties (carbon and nitrogen content and soil thickness, see Table 1 and Fig. 2) at L vs. U that promoted microbial activity. Also microbial activity is directly related with θ (Cortez 1998), and because there is a natural redistribution of θ down slope (Landi *et al*. 2004, Johnson *et al*. 2000, Ventera *et al*. 2003) of the transect in the experiment (Fig. 2), greater θ at L compared with that at U would have sustained the faster litter decomposition rate found at L during the first part of this decomposition experiment. The measured RWFP (from 0.4 to 0.65, Fig. 2) was in the range that favors microbial activity.

Faster litter decomposition measured early in the field experiment (Figs. 5 and 6) has positive implications for plant growth. Natural ecosystems depend on nutrient cycling, and faster litter decomposition means more nutrient availability for plant uptake, and our results supports this because there was a faster release of N coming from shoot litter during the first experimental months (Fig. 11). If we consider that the growing season is short at this northern latitude (4-5 months), more soil nutrients coming from litter decomposition during the time of rapid plant uptake is good because plants will have better growth, they will produce more biomass and so, contribute to ecosystem productivity.

These results support my first hypothesis stating that topography creates a gradient down slope in soil properties (Table 1, Chapter II) and θ (Figs. 1 and 2) which increases litter decomposition at lower topographic locations. The field results

showed that there was a clear trend towards more rapid shoot litter mass loss at L during the first year (Fig. 5A). However, the long-term results do not support this hypothesis because any difference in litter decomposition related with topography disappeared at the end of the experiment after 600 days of decomposition. The observed stabilization in decomposition rate (Berg 2000) is related with changes in chemical composition because after labile chemical compounds have been decomposed (Fig 10 A,B), there is mainly lignin and cellulose in the remaining mass (Fig. 10C) and so decomposition rates decreased (Preston *et al*. 1997, Parton *et al*. 1998).

Even though there was rapid litter decomposition early in the experimental period, the remaining litter appears to immobilize much of the N mineralized during that time (Fig. 11), so much of the litter N was retained in the litterbags during the experiment, explaining the declines in the C-to-N ratio (Section 3.8). This also suggests that probably the remaining N could be linked to the more recalcitrant carbon fraction.

The mathematical functions used to simulate decomposition showed that apparently there was not a defined effect of θ or Ts on litter decomposition during the first autumn and winter (Fig. 5A) because the model showed similar decomposition at all topographic locations. Probably θ and soil temperature during this period were too similar to cause differences in modeled decomposition rate among topographic locations. However, the model reproduced the general result found in the field experiment from the following spring onwards (Fig. 5A), indicating that the effects of topography on decomposition could be at least partially explained by θ.

Slope aspect also influenced early shoot litter decomposition (Fig. 9). Even though soil moisture was not measured in this experiment, north aspects that receive less solar radiation tend to have more soil moisture, which increases microbial activity and the early decomposition rate (Barnes *et al*. 1998, Mudrick *et al*. 1994, Sariyildiz *et al*. 2005). This agrees with other findings that north aspects had greater litter decomposition than south aspects (Mudrick *et al*. 1994, Sariyildiz *et al*. 2005). This means that more nutrients are going to be mineralized and made available for plant uptake at north aspect slopes and therefore the plant growth and productivity should be greater in those slope aspects in which there will be more nutrient cycling compared with south aspect slopes.

Later, the aspect effect disappeared probably because labile carbon (NPC, WSC) was exhausted and thus, the combination of different factors (soil moisture, soil temperature, and litter chemical composition) at each aspect offset each other in the midterm. So, long-term decomposition became similar between aspects. This is in agreement with van der Krift *et al.* (2002) who stipulated that factors other than litter quality also influence decomposition process.

4.2. Grazing effect on litter decomposition

Grazing through its influence on litter chemical composition (Tables 4 to 6), affected the decomposition rate of shoot litter (Fig. 6) but not root litter (Fig. 7). This was mainly caused by differences in the concentration of shoot litter lignin (Table 5) which was affected differentially by grazing at each topographic location. This grazing effect on litter quality at M is consistent with other findings that showed that grazing decreased litter quality mainly by increasing the lignin concentration compared with the ungrazed litter (Giese *et al*. 2009). As stated earlier, differences in grazing intensities at each topographic location could cause the different lignin concentration found in the litter (Table 6) between grazing treatments. The grazing effect on litter quality is also demonstrated in NPC which was reduced by grazing (Table 6). The consistently lower NPC in grazed litter may mean lower N and hence slower nutrient cycling which over time will be reflected on the plant growth decreasing it.

Soil density was not changed by grazing (Table 3), therefore grazing during the experiment did not alter soil conditions (Donkor *et al*. 2002) or microbial activity (Waisel *et al.* 1996). This partially explains why there was no grazing effect on root decomposition rate. This result agrees with Giese *et al*. (2009) who did not find any difference in root litter decomposition when comparing grazed with ungrazed litter.

4.3. Implications of grazing on sustainability of topographically variable ecosystems

Grazed shoot litter decomposed more rapidly at L than did ungrazed shoot litter (Fig. 6), which means that nutrient cycling was more rapid under grazing at that location (Bardgett *et al.* 1997) which has been shown to have a positive and direct relationship with productivity (Brady and Weil 2002, Asamoah *et al*. 2004), and explains the spatial variability of plant productivity along slopes.

This result is consistent with previous research results that showed moderate grazing did not negatively affect soil fertility (Henderson *et al*. 2004).

More rapid cycling in combination with higher θ (Fig. 2) would stimulate plant growth which is very important for animal production. In fact, animal growth is based on plant biomass and its nutritive value, and highly fertile soils produce high quality plant biomass, the litter from which also decomposes faster (Moretto *et al*. 2001). Highly productive locations can therefore sustain more grazing animals and therefore be more productive than less productive locations.

However, we do not know if the evaluated grazing mix of wild ungulates should negatively affect nutrient cycling and ecosystem productivity over time. Thus, this kind of grazing has to be evaluated for longer time to know if it does not affect plant productivity. In this sense it is important to keep the grazing intensity according to the productivity to avoid significant reductions in plant biomass, litter, root biomass and microbial activity, as has been reported by different research (Derner *et al*. 2006, Donkor *et al*. 2002, Henderson *et al*. 2004, Reeder and Shuman 2002).

According to Jackson *et al.* (1997) and Silver and Milla (2001), roots have greater nutrient concentrations than above ground litter, and considering the fact that root litter is greater than above ground litter (Gill and Jackson 2000, van der Kirft *et al.* 2001), any reduction of root litter will affect more negatively nutrient cycling than would the same reduction in above ground litter. Therefore, we need to determine if grazing should cause important reductions in total plant biomass and with it the alteration of nutrient cycling in the ecosystem. This will be addressed in the next chapter.

5. Conclusions

Under the field and climatic conditions in which this research was carried out, the following may be concluded:

Topography

- There was a topographic effect on shoot litter decomposition: faster at lower topographic location during the first experimental year (Fig. 5A), but this effect disappeared during the second experimental year.

- The faster shoot litter decomposition at lower vs. middle and upper locations found during the first experimental months (Fig. 5A) was associated with greater soil water availability (Fig. 2).

- Soil temperature, which decreased an average of 1°C from upper to lower locations (Figs. 3 and 4), did not reduce the litter decomposition rate at the lower topography.

Grazing

- Grazing affected local shoot litter decomposition rate differently at each topographic location (Fig. 6). This effect was associated with the concentration of lignin in the litter (Table 5).

- Grazed and ungrazed root litter had similar decomposition rates.

- According to the experimental results, it is not clear if the grazing intensity (2 AUM ha^{-1}) in this experiment would alter nutrient cycling over time, so additional information and a longer evaluation period are required to confirm such alteration.

- Litter chemical composition was related with decomposition rate, with lignin content (Table 5) shown to be directly and positively linked with the percent of shoot litter remaining mass (Fig. 6).

Slope

- Northerly slope aspects hastened litter decomposition only during the early part of the experimental period; there was no slope aspect influence over longer period of time.

Table 2-2. Composite shoot remaining mass, %, according to topographic locations in the experiment established in August 2005

Topographic location	Remaining mass, % October	Remaining mass, % April
Upper	72.7±1.1 ^{a}	69.7±1.2^{a}
Middle	76.5±1.2 ^{b}	71.1±1.1^{a}
Lower	76.5±1.2 ^{b}	71.4±1.2^{a}

Means with the same letter are not different at $P<0.05$, ± 1 SE

Table 2-3. Grazing effect on soil bulk density at different topographic locations. Central Alberta, Canada

Topographic location	Treatment	Bulk density g cm^{-3}
Upper	Grazed	1.36^{a} ± 0.05
	Ungrazed	1.37^{a} ± 0.06
Middle	Grazed	1.27^{a} ± 0.04
	Ungrazed	1.23^{a} ± 0.03
Lower	Grazed	1.10^{a} ± 0.03
	Ungrazed	1.06^{a} ± 0.05

LSMeans with different letter at each topographic site are different at $P<0.05$, ± 1 SE

Table 2-4. Initial chemical composition of grazed and ungrazed composite shoot litter. Central Alberta, Canada.

Management	NPC, mg g^{-1}	WSC, mg g^{-1}	Holoc, mg g^{-1}	Lignin, mg g^{-1}	Ash, mg g^{-1}
Grazed	35^{a} ± 2	165^{a} ± 11	657^{a} ± 11	124^{a} ± 2	17^{a} ± 1
Ungrazed	57^{b} ± 1	152^{a} ± 11	637^{a} ± 10	132^{b} ± 1	22^{b} ± 1

LSMeans for treatments with same letter are not different at $P<0.05$, ± 1 SE; NPC: non-polar compounds, WSC: water soluble compounds, Holoc.: holocellulose, Ash: ashes.

Table 2-5. Initial chemical composition of Local shoot litter according to topography and grazing, Central Alberta, Canada.

Topographic location	Treatment	NPC, mg g^{-1}	WSC, mg g^{-1}	Holoc, mg g^{-1}	Lign, mg g^{-1}	Ash, mg g^{-1}
Upper	Grazed	37^{a}	190^{b}	603^{a}	149^{a}	21^{a}
	Ungrazed	46^{b}	128^{a}	654^{b}	150^{a}	22^{a}
Middle	Grazed	39^{a}	169^{a}	633^{b}	140^{b}	19^{a}
	Ungrazed	54^{b}	178^{a}	612^{a}	128^{a}	28^{b}
Lower	Grazed	45^{a}	220^{a}	552^{b}	165^{a}	18^{a}
	Ungrazed	54^{b}	213^{a}	528^{a}	188^{b}	17^{a}
S.E.		1	14	12	4	2

LSMeans for management with same letter within the same topographic level are not different at $P<0.05$, ± 1 SE;
NPC: non-polar compounds, WSC: water soluble compounds, Holoc.: holocellulose, Lign.: lignin, Ash: ashes.

Table 2-6. Initial chemical composition of local and composite grazed root litter according with topographic location. Central Alberta, Canada.

Topographic location	NPC, mg g^{-1}	WSC, mg g^{-1}	Holoc, mg g^{-1}	Lign, mg g^{-1}	Ash, mg g^{-1}
Upper	$17^{c} \pm 1$	$73^{a} \pm 5$	$613^{ab} \pm 2$	$268^{d} \pm 9$	$29^{a} \pm 7$
Middle	$13^{b} \pm 1$	$110^{b} \pm 7$	$603^{a} \pm 8$	$227^{b} \pm 9$	$47^{b} \pm 5$
Low	$9^{a} \pm 1$	$142^{c} \pm 2$	$619^{b} \pm 7$	$191^{a} \pm 3$	$39^{b} \pm 3$
Composite	$14^{b} \pm 1$	$119^{b} \pm 8$	$589^{a} \pm 6$	$248^{c} \pm 3$	$30^{a} \pm 1$

LSMeans for topography with same letter are not different at $P<0.05$, ± 1 SE.
NPC: non-polar compounds, WSC: water soluble compounds, Holoc.: holocellulose, Lign.: lignin, Ash: ashes.

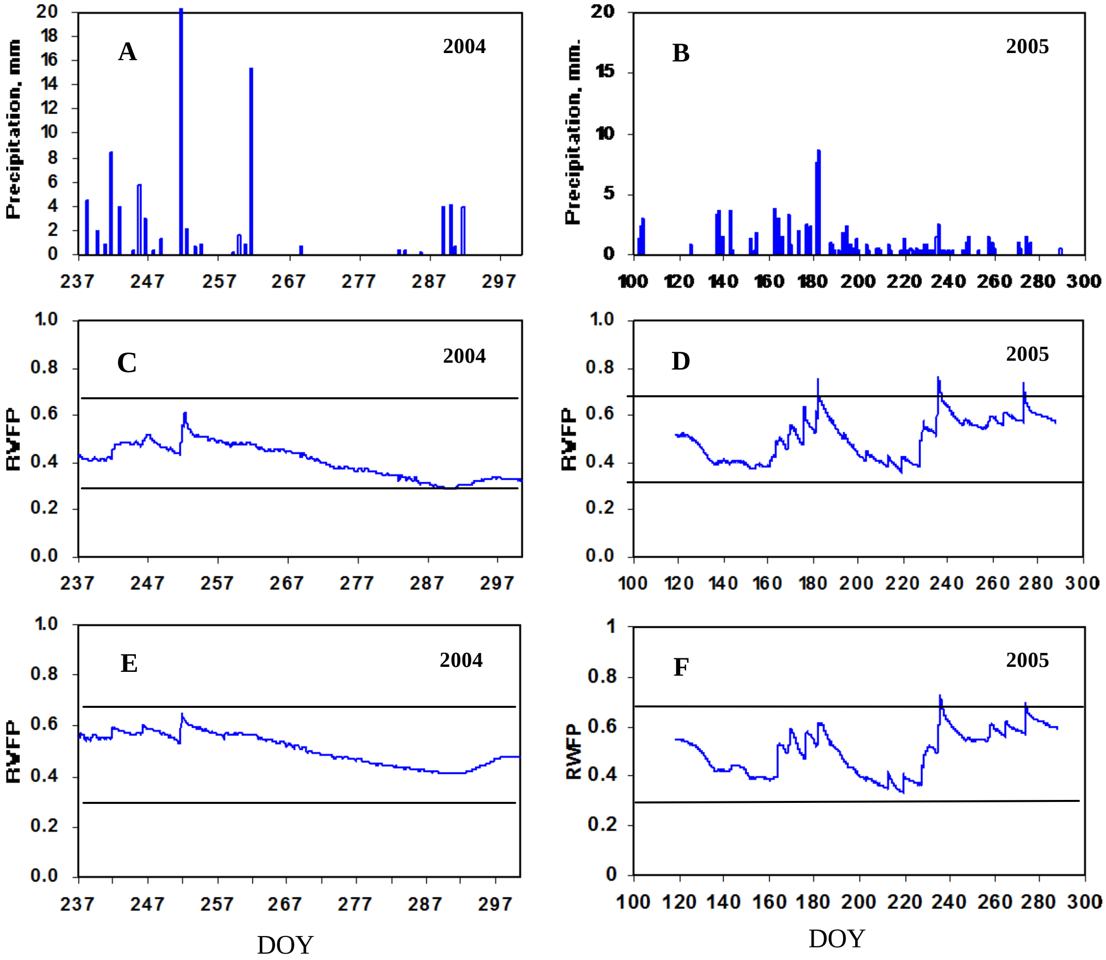

Figure 2-1. Precipitation (A, B), measured relative water-filled porosity (RWFP) at 0.05m depth at upper (C, D), and middle (E, F) topographic location during the growing season of 2004 and 2005. Central Alberta, Canada.

Data from the lower topographic position were discarded (see text).
Upper and lower solid lines represent field capacity and wilting points respectively.

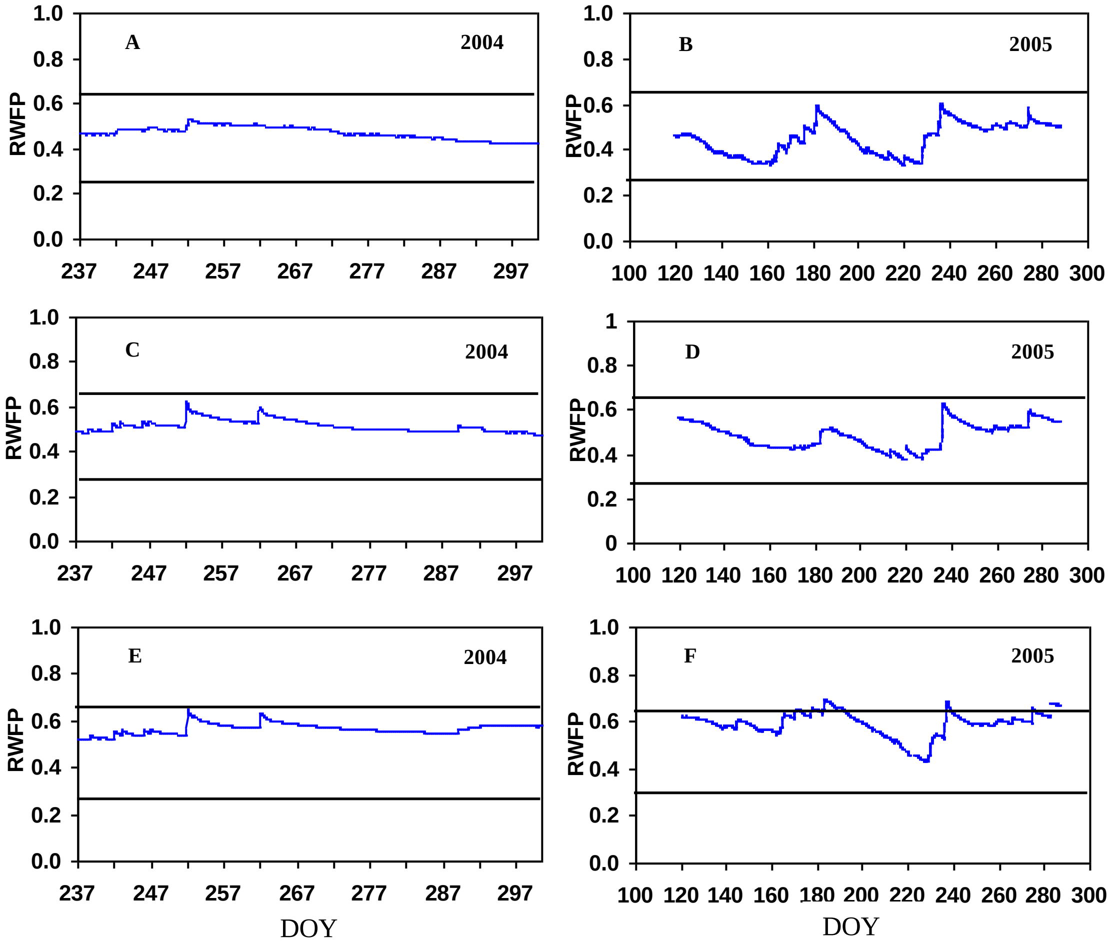

Figure 2-2. Relative water-filled porosity (RWFP) at 0.15 m depths at upper (A, B), middle (C, D) and lower (E, F) topographic locations during the growing season of 2004 and 2005. Central Alberta, Canada.

Upper and lower solid lines represent field capacity and wilting points respectively.
Lines show minimum and maximum limit for microbial activity

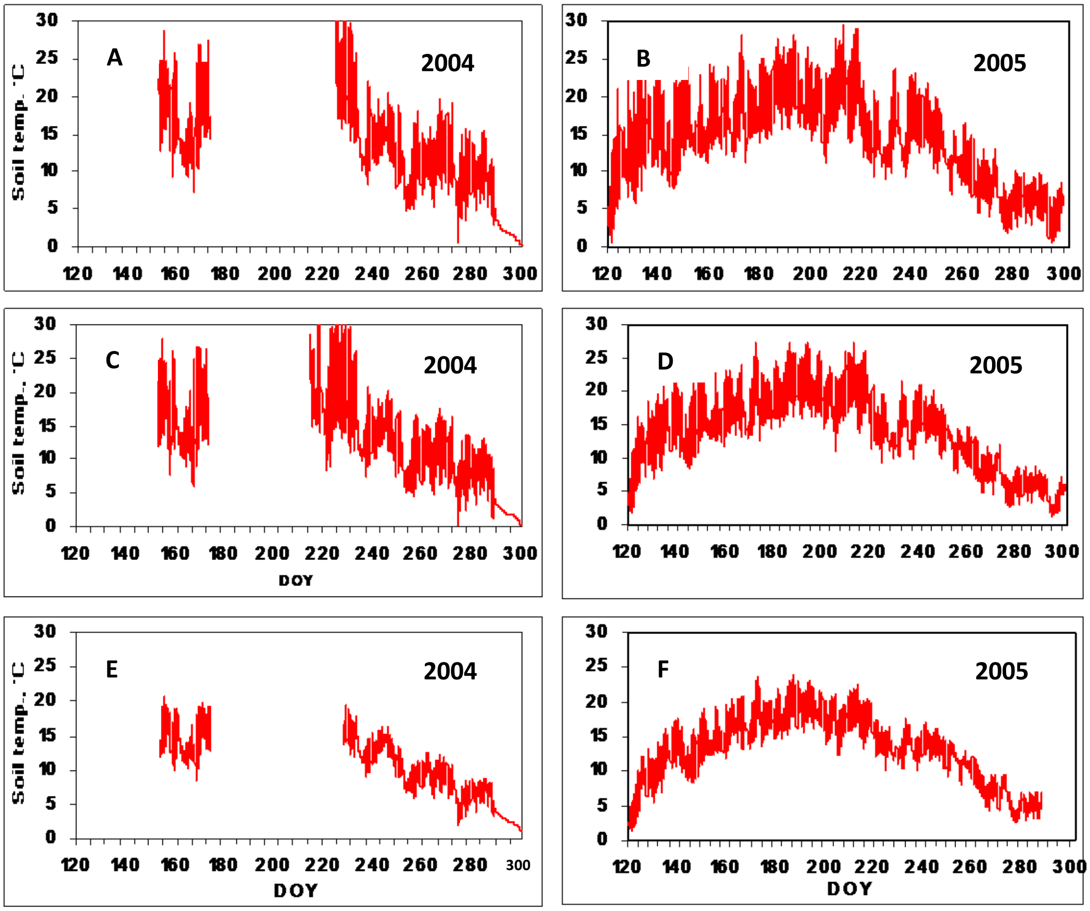

Figure 2-3. Measured soil temperature at 0.05 m depth at upper (A, B), middle (C, D), and low (E, F) topographic locations during the growing season of 2004 and 2005.

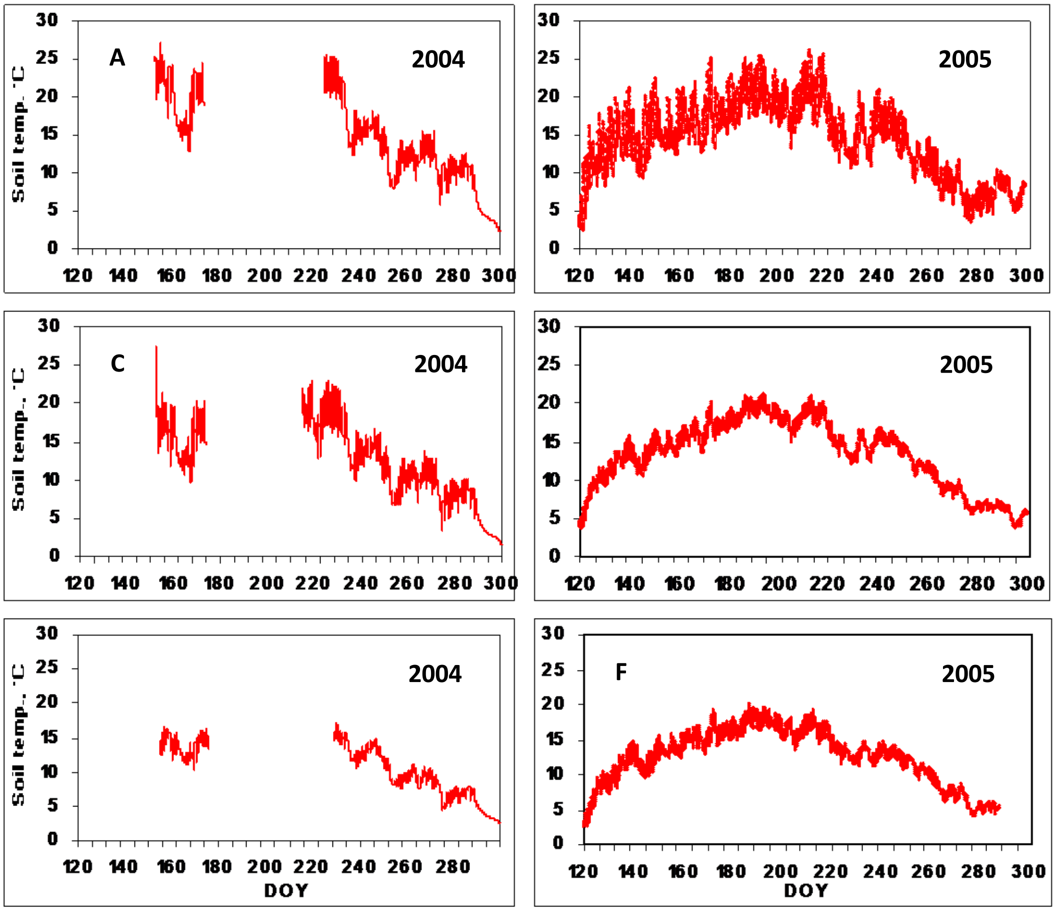

Figure 2-4. Measured soil temperature at 0.15 m depth at upper (A, B), middle (C, D) and lower (E, F) topographic locations during the growing season of 2004 and 2005. Central Alberta, Canada.

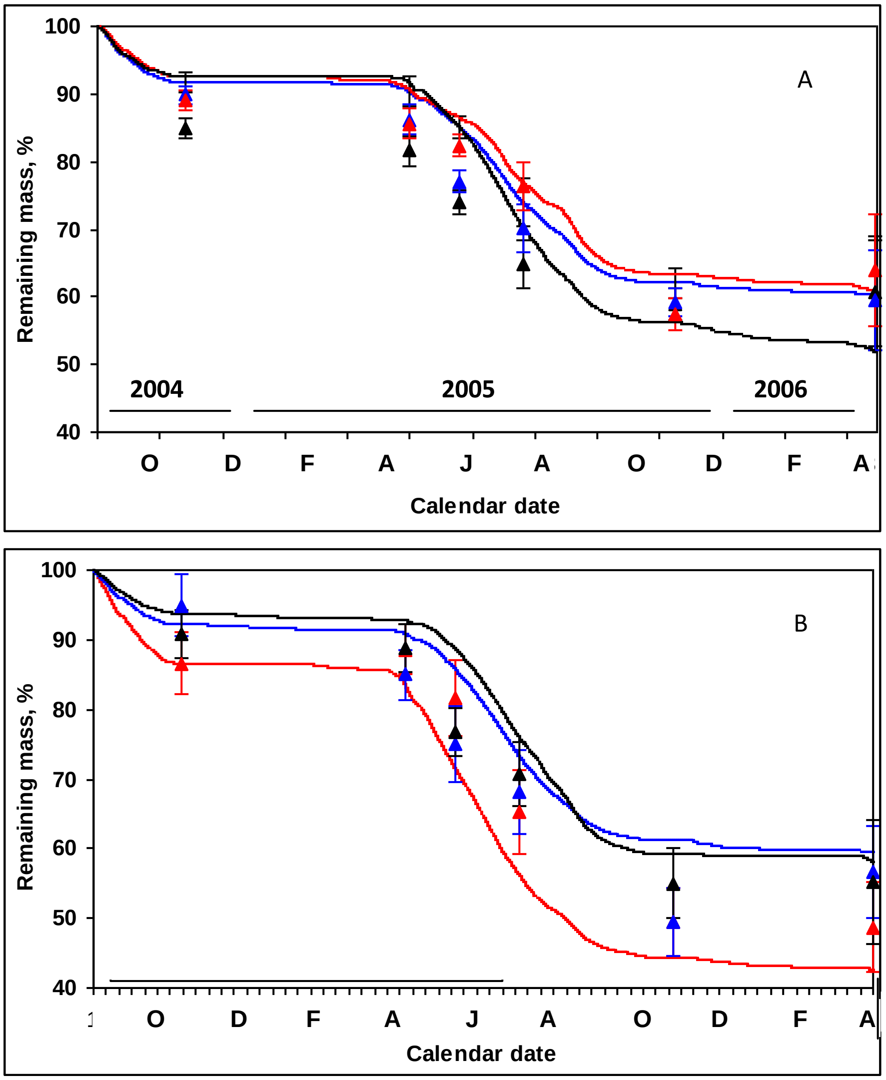

Figure 2-5. Topographic effect on ungrazed measured (dots) and modeled (lines) composite shoot (A) and root (B) litter remaining mass from 2004 to 2006. Central Alberta, Canada.

Red: upper, blue: middle, black: lower topographic locations

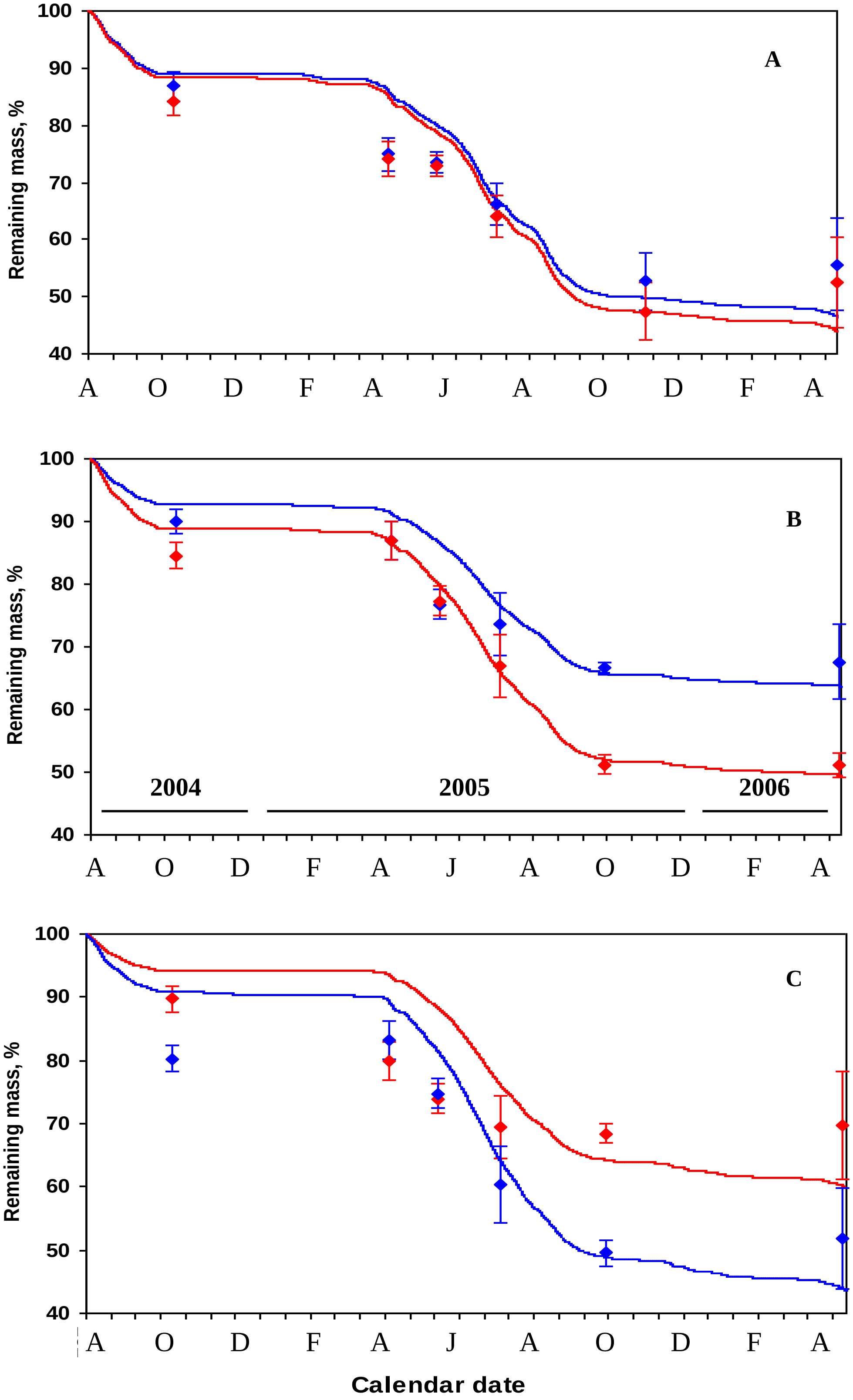

Figure 2-6. Grazing effect on measured (dots) and modeled (lines) Local shoot litter remaining mass at upper (A), middle (B), and low (C) topographic locations during 2004 and 2005. Central Alberta, Canada.

Red: ungrazed, blue: grazed

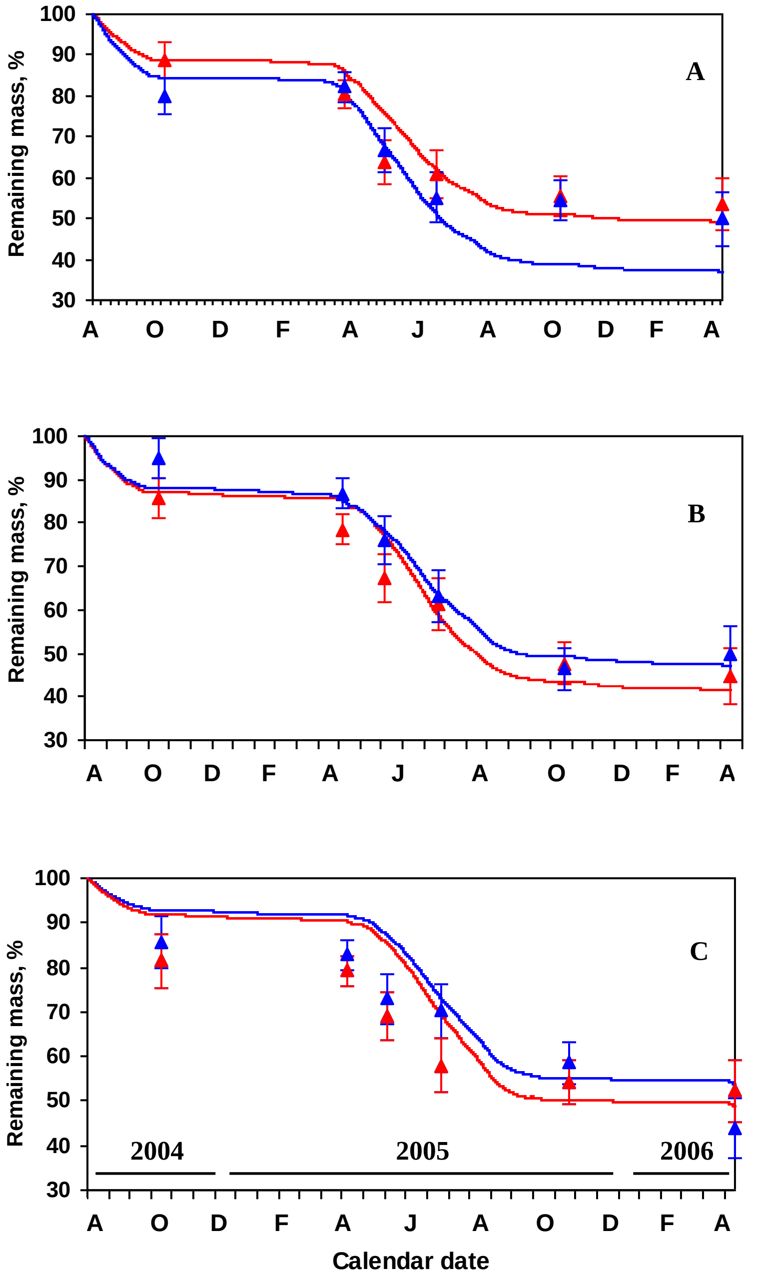

Figure 2-7. Grazing effect (measured: dots, modeled: lines) on Local root litter remaining mass at upper (A), middle (B), and lower (C) topographic locations from 2004 to 2006. Central Alberta, Canada.

Red: ungrazed, Blue: grazed

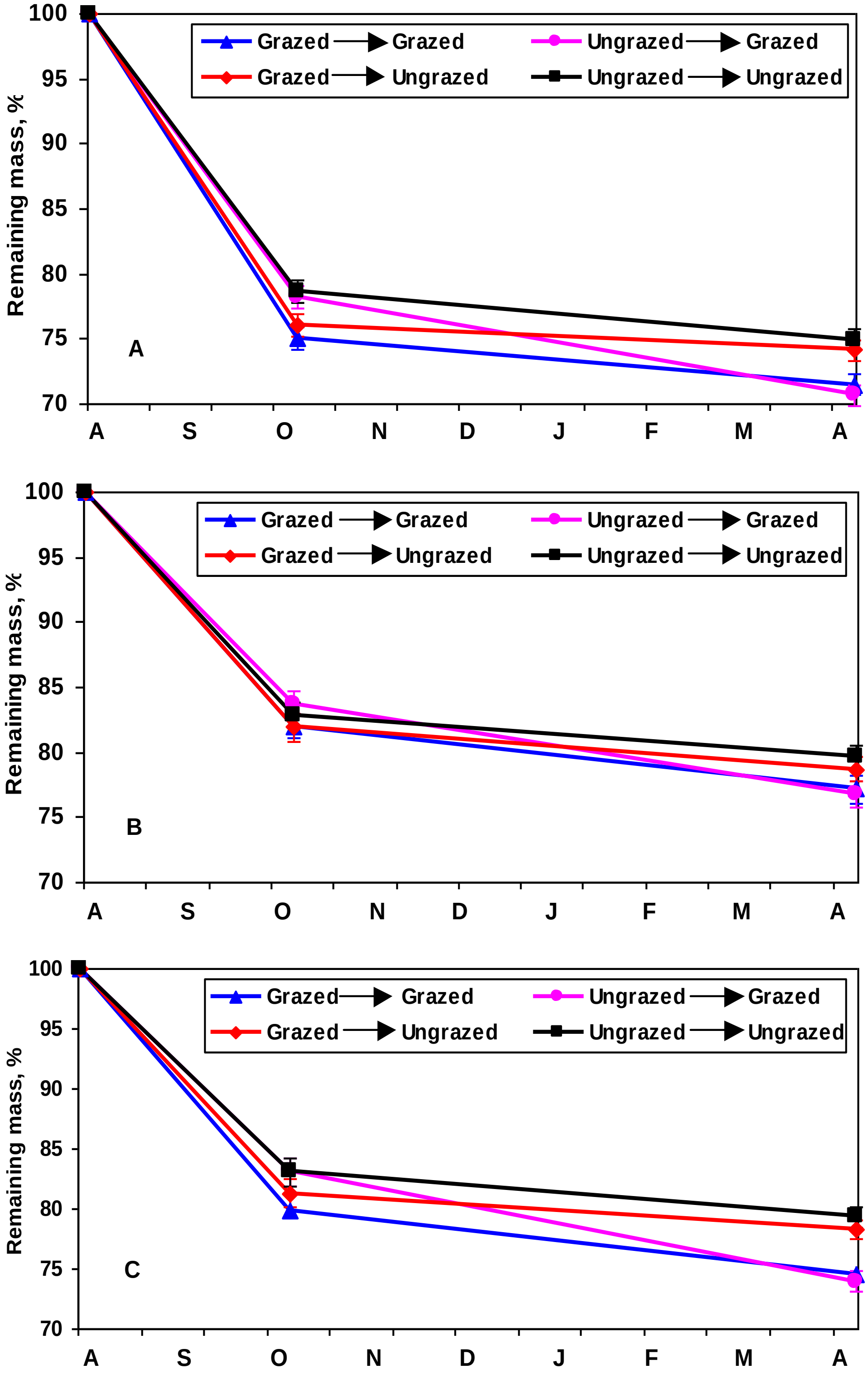

Figure 2-8. Grazing effect on Local litter mass loss at upper (A), middle (B) and lower (C) topographic locations during 2005 and 2006. Central Alberta, Canada.

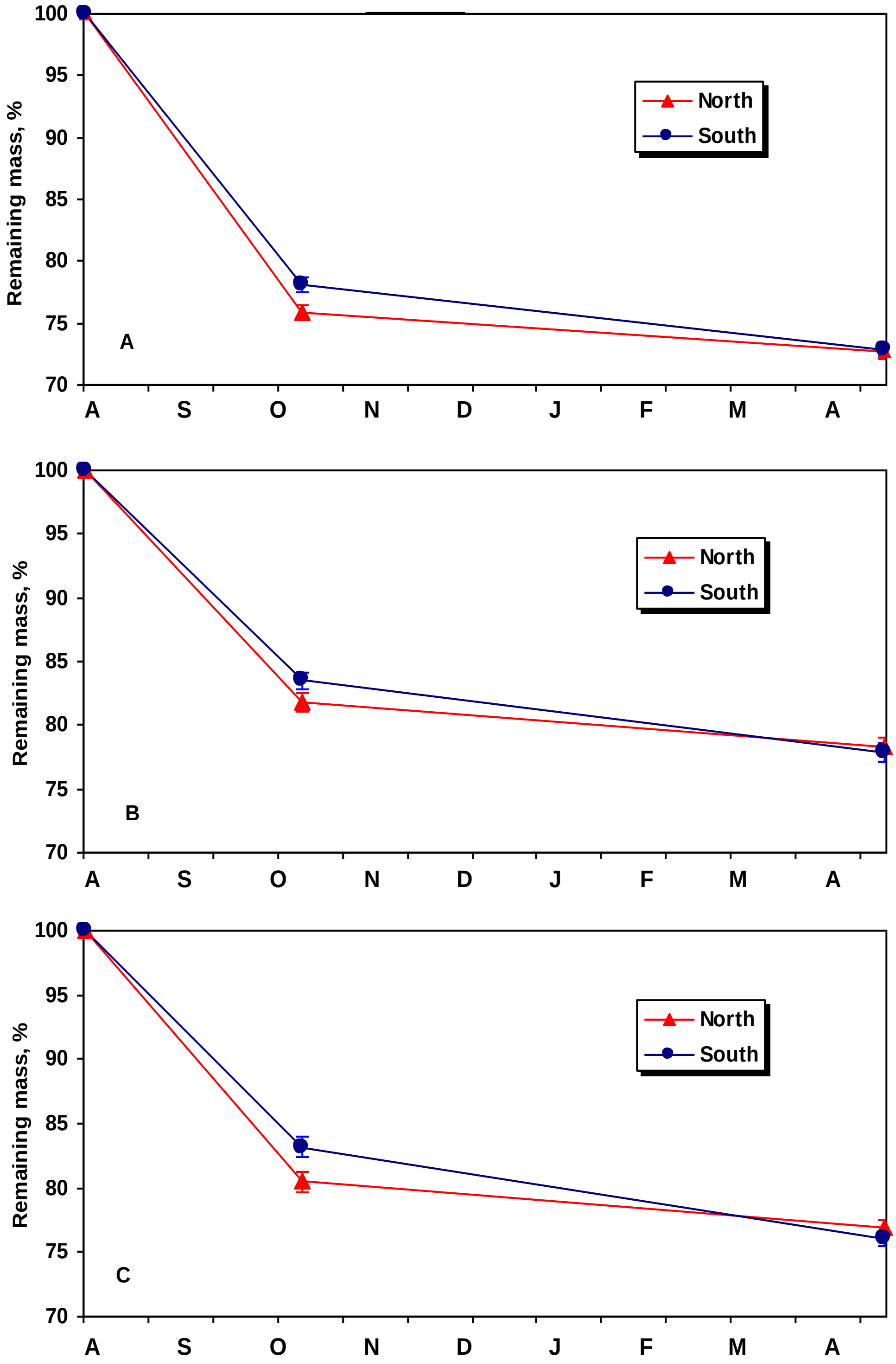

Figure 2-9. Aspect effect on Local litter mass loss at upper (A), middle (B) and lower (C) topographic locations during 2005 and 2006. Central Alberta, Canada.

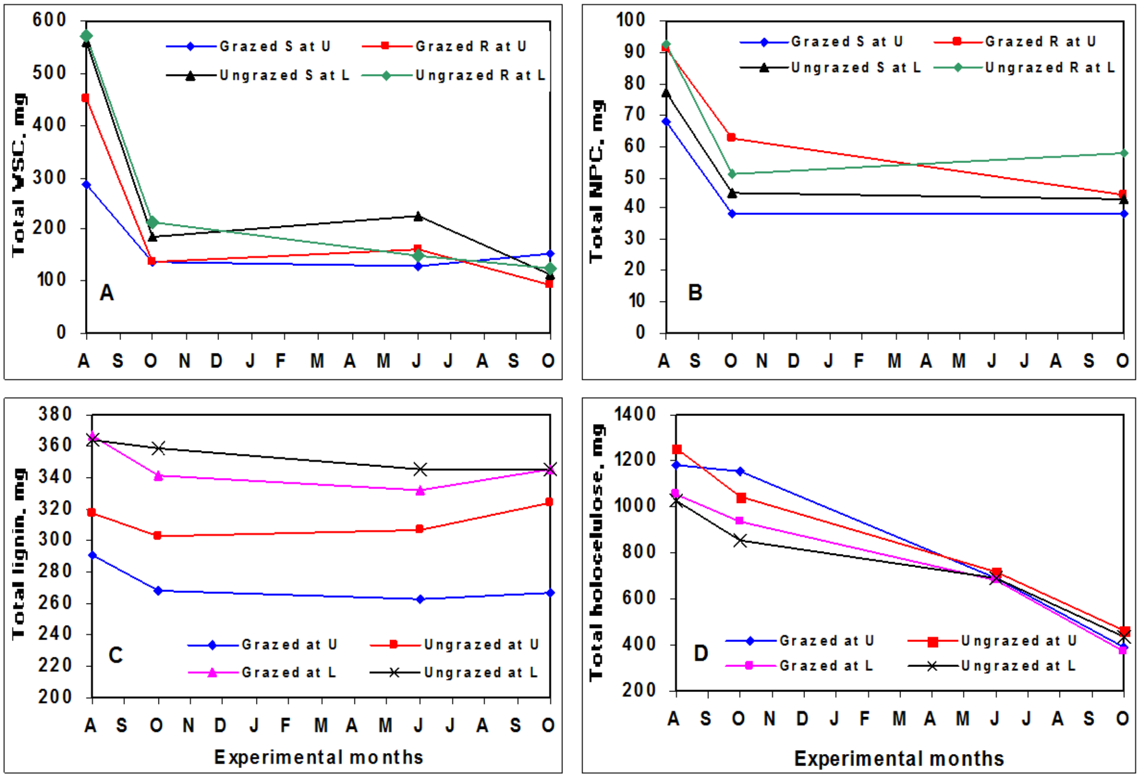

Figure 2-10. Total initial amount of different carbon compounds in some grazed and ungrazed shoot (S) and root (R) litter samples and its changes over 417 experimental days (from 2004 to 2005) at upper (U) and lower (L) topographic locations. Central Alberta, Canada.

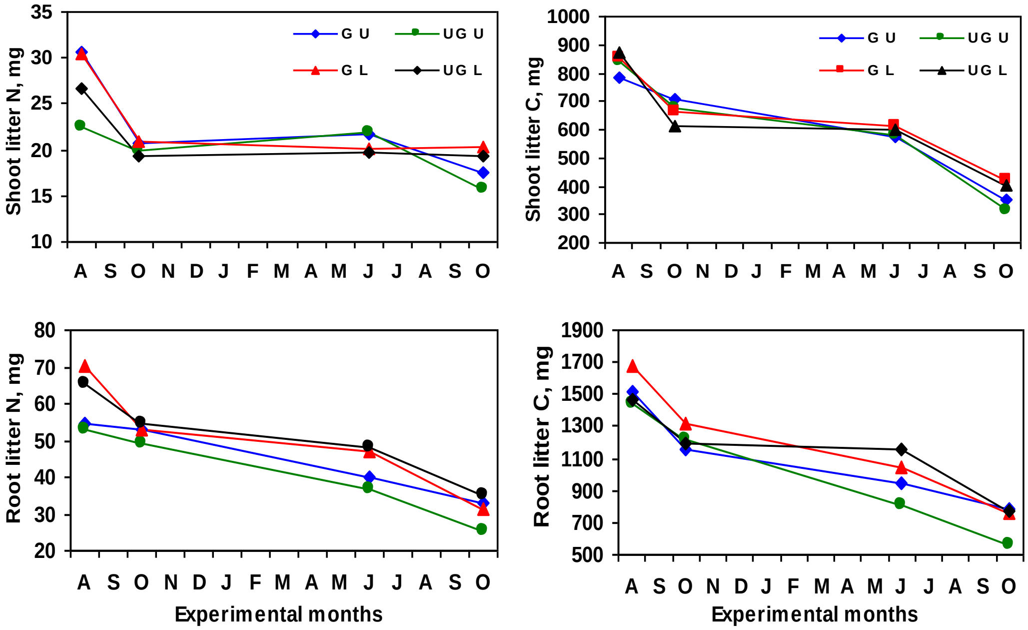

Figure 2-11. Total initial amount of nitrogen and carbon in some grazed (G) and ungrazed (UG) shoot and root litter samples and its changes over 417 experimental days (from 2004 to 2005) at upper (U) and lower (L) topographic locations. Central Alberta, Canada.

6. References

Alberta Agriculture, Food and Rural Development. 2005. http://www.salts-landtrust.org/conservingrangelands.html#top

Aber, J.D.; Melillo, J.M.; Nadelhoffer, K.J.; McClaugherty, C.A.; Pastor, J. 1985. Fine root turnover in forest ecosystems in relation to quality and form of nitrogen availability: a comparison of two methods. Oecologia 66:317-321.

Aerts, R. 1999. Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. Journal of Experimental Botany 50(330):29-37.

Agriculture and Agri-Food Canada. 2000. http://www.agr.gc.ca/pfra/land/range_e.htm

Andrén, O., Steen, E., Rajkai, K. 1992. Modelling the effects of moisture on barley straw and root decomposition in the field. Soil Biology and Biochemistry, 4(8):727-736.

Amundson, R. 2001. The carbon budget in soils. Annu. Rev. Earth Planet Sci. 29:535-562.

Archer, N.A.L.; Quinton, J.N.; Hess, T.M. 2002. Below-ground relationships of soil texture, roots and hydraulic conductivity in two-phase mosaic vegetation in South-east Spain. Journal of Arid Environments 52:535-553.

Asamoah, S.; Bork, E.; Irving, B.; Price, M.; Hudson, R. 2004. Seasonal herbage dynamics on aspen parkland landscape in central Alberta. Can. J. Animal Science 84:149-153.

Ayres, M.P., Clausen, T.P., MacLean, S.F. Jr., Redman, A.M., Reichardt, P.B., 1997. Diversity of structure and antiherbivore activity in condensed tannins. Ecology 78, 1696–1712

Bardgett, R.D.; Hobbs, P.J.; Frostegard, A. 1996. Changes in fungal:bacterial biomass ratios following reductions in the intensity of management on an upland grassland. Biology and Fertility of Soils 22: 261-264.

Bardgett, R.D.; Leemans, D.K.; Cook, R.; Hoobs, P.J. 1997. Seasonality in the soil biota of grazed and ungrazed hill grasslands. Soil Biology and Biochemistry 29:1285-1294.

Barnes, B.V.; Zak, D.R.; Denton, S.R.; Spurr, S.H. 1998. Forest ecology. 4 ed. New York, Wiley. 774 p.

Baron, V.S.; Mapfumo, E.; Dick, A.C.; Naeth, M.A.; Okine, E.K.; Chanasyk, D.S. 2002. Grazing intensity impacts on pasture carbon and nitro flow. Journal Range Management 55:535-541.

Berg, B. 2000. Litter decomposition and organic matter turnover in northern forest soils. Forest Ecology and Management 133(1-2):13-22.

Blum, U., Rice, E. 1969. Inhibition of symbiotic nitrogen-fixation by gallic and tannic acid, and possible roles in old-field successions. Bulletin of the Torrey Botanical Club 96(5):531-544

Boddey, R.M., Macedo, R., Tarre, R.M., Ferreira, E., de Oliveira, O.C., Rezende, C.D., Cantarutti, R.B., Pereira, J.M., Alves, B.J.R., Urquiaga, S., 2004. Nitrogen cycling in Brachiaria pastures: the key to understanding the process of pasture decline. Agric. Ecosyst. Environ. 103:389–403.

Brady, N.C.; Weil, R.R. 2002. The nature and properties of soils. New Jersey, Prentice Hall. 960 p.

Bragazza,_L., Siffi, C,. Iacumin, P., Gerdol, R. 2007. Mass loss and nutrient release during litter decay in peatland: The role of microbial adaptability to litter chemistry Soil Biology & Biochemistry 39:257–267

Burke, I.C.; Lauenroth, W.K.; Riggle, R.; Brannen, P.; Madigan, B.; Beard, S. 1999. Spatial variability of soil properties in the shortgrass steppe: the relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. Ecosystems 2(5): 422-438.

Carmi, A. 1995. Growth, water transport and transpiration in root-restricted plants of bean, and their relation to abscisic acid accumulation. Plant Science 107: 69-76

Cao, G.; Tang, Y.; Mo, W.; Wang, Y.; Li, Y.; Zhao, X. 2004. Grazing intensity alters soil respiration in an alpine meadow on the Tibetan plateau. Soil Biology and Biochemistry 36:237-243.

Chen, H.; Harmon, M.E.; Sexton, J.; Fasth, B. 2002. Fine-root decomposition and N dynamics in coniferous forests of the Pacific Northwest, U.S.A. Canadian Journal of Forest Research. 32:320-331.

Chen, H.; Harmon, M.E.; Griffiths, R.P.; Hicks, B. 2000. Effect of temperature and moisture on carbon respired from decomposing woody roots. Forest Ecology Management 138:51-64.

Chesson, A. 1997. Plant degradation by ruminants: paralales with litter decomposition in soils. In Driven by Nature. Plant litter quality and decomposition. Cadish, G.; Giller, K.E. Eds. CAB International. p. 47-66.

Cortez, J. 1998. Field composition of leaf litters: relationships between decomposition rates and soil moisture, soil temperature and earthworm activity. Soil biology and biogeochemistry 30(6):783-793.

Dalias, P.; Anderson, J.; Bottnera, P.; Couteaux, M. 2001. Long-term effects of temperature on carbon mineralisation processes. Soil Biology and Biochemistry 33:1049-1057.

Derner, J.D., Boutton, T.W., Briske, D.D. 2006. Grazing and ecosystem carbon storage in the North American Great Plains. Plant and soil 280(1-2):77-90.

Donkor, N.; Gedir, J.; Hudson, R.; Bork, E.; Chanasyk, D.; Naeth, M. 2002. Impacts of grazing systems on soil compaction and pasture production in Alberta. Canadian Journal of Soil Science 82:1-8.

Didkowsky, M.G. 2006. Scales of forage selection by ungulates in Aspen Parkland. Thesis MSc. University of Alberta. 86 p.

Environment Canada 2006 . http://www.ec.gc.ca/pdb/ghg/newsrelease2006_e.cfm

Frank, D.A.; Groffman, P. M. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone national park. Ecology 79(7):2229–2241.

Follet, R.F. 2001. Organic carbon pools in grazing land soils. In The potential of U.S. grazing lands to sequester carbon and mitigate the greenhouse effect. Boca Raton, Lewis. p. 65-86.

Frank, D.A.; Groffman, P. M. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone national park. Ecology 79(7):2229–2241.

Gastine, A.; Scherer-Lorenzen, M.; Leadley, P.W. 2003. No consistent effects of plant diversity on root biomass, soil biota and soil abiotic conditions in temperate grasslands communities. Applied Soil Ecology 24:101-111.

Giardina, C.P., Ryan, M.G. 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature, 404: 858-861.

Giese, M., Gao, Y., Zhao, Y., Pan, Q., Lin, S., Peth, S., Brueck, H. 2009. Effects of grazing and rainfall variability on root and shoot decomposition in a semi-arid grassland. Applied soil ecology 41:8-18.

Gill, R.; Jackson, R. 2000. Global patterns of root turnover for terrestrial and aquatic habitats. Global Change Biology 7:849-882.

Gordon, W.; Jackson, R. 2000. Nutrient concentration in fine roots. Ecology 81:275-280.

Gregorich, E.G.; Anderson, D.W. 1985. Effects of cultivation and erosion on soils of four toposequences in the Canadian Prairies Geoderma 36:343-354.

Grime, J. 1997. Biodiversity and ecosystem function: the debate deepens. Science 277:1260-1261.

Hamadi, Z., Steinberger, Y., Kutiel, P., Lavee, H., Barness, G. 2000. Decomposition of Avena sterilis litter under arid conditions. Journal of Arid Environments 46: 281–293

Hairston, A.B.; Grigal, D.F. 1994. Topographic variation in soil water and nitrogen for two forested landforms in Minnesota, USA. Geoderma 64:125-138.

Hart, R.H., 2001. Plant biodiversity on short grass steppe after 55 years of zero, light, moderate, or heavy cattle grazing. Plant Ecology 155(1): 111-118.

Henderson, D., Ellert, B., Naeth, M. 2004. Grazing and soil carbon along a gradient of Alberta rangelands. Journal of Range Management 57:402-410.

Hobbie, S.E. 2000. Interactions between litter lignin and soil nitrogen availability during leaf litter decomposition in a Hawaiian Montane. Forest. Ecosystems 3(5): 484-494.

Holechek, J.L.; Pieper, R.D.; Herbel, C.H. 2001. Range management: principles and practices. 4. ed. New Jersey, Prentice Hall. 587p.

Honeycutt, C.; Heil, R.; Cole, C. 1990. Climatic and topographic relations of three Great Plains soils: II: carbon, nitrogen and phosphorus. Soil Science of Am. Journal 54:476-483.

Howitt, R.; Findlayson, N.; Gowler, M.; Riddell, M.; McEwan, G. 1988. Soil survey of the County of Beaver, Alberta. No. 47. Edmonton, Alberta, Alberta Research Council.

Hutchinson, T.F.; Boerner, R.E.J.; Iverson, L.R.; Sutherland, S.; Sutherland, E.K. 1999. Landscape patterns of understory composition and richness across a moisture and nitrogen mineralization gradient in Ohio (U.S.A.) Quercus forests. Plant Ecology 144(2): 177-189.

IPCC. 2000. Intergovernmental Panel on Climate Change: Land Use, Land-Use Change, and Forestry. 2000. Special Report of the Intergovernmental Panel on Climate Change. Watson, R.T.; Noble, I.R.; Bolin, B.; Ravindranath, N.H.; Verardo, D.J; Dokken, D.J. Eds. Cambridge University Press. p. 375

Irving, B.D. 1992. The effect of litter on the herbage growth cycle, soil water, and soil temperature in the Aspen Parkland of Alberta. Thesis MSc. University of Alberta. 100 p.

Jackson, R.B.; Mooney, H.A.; Schulze, E.D. 1997. A global budget for fine root biomass, surface area, and nutrient contents. Ecology 94:7362-7366.

Janzen, H. 2004. Carbon cycling in earth systems-a soil science perspective. Agriculture, Ecosystems and Environment 104:399-417.

John, B.; Pandey, H.N.; Tripathi, R.S. 2002. Decomposition of fine roots of *Pinus kesiya* and turnover of organic matter, N and P of coarse and fine pine roots and herbaceous roots and rhizomes in subtropical pine forest stands of different ages. Biol. Fertil. Soils 35:238-246.

Johnson, C.E.; Ruiz-Mendez, J.J.; Lawrence, G.B. 2000. Forest soil chemistry and terrain attributes in a Catskill watershed. Soil Sci. Soc. Am. J. 64:1804-1814.

Kachanoski, R.; Carter M., 1999. Landscape position and soil redistribution under three soil types and land use practices in Prince Edward Island. Soil and Tillage Research 51(3-4):211-217.

King, J.; Lee, H.; Dougherty, P.; Strain, B. 1997. Decomposition of roots in loblolly pine: Effects of nutrient and water availability and root size class on mass loss and nutrient dynamics. Plant and Soil 195:171-184.

Koukoura, Z.; Mamolos, A.; Kalburtji, K. 2003. Decomposition of dominant plant species litter in a semi-arid grassland .Applied Soil Ecology 23:13-23.

Koukoura, Z. 1998. Decomposition and nutrient release from C_3 and C_4 plant litters in a natural grassland Acta Oecologica 19(2):115-123.

Lal, R. 2004. Agricultural activities and the global carbon cycle. Nutrient Cycling in Agroecosystems 70:103-116.

Landi, A.; Mermut, A.R.; Anderson, D.W. 2004. Carbon distribution in a hummocky landscape from Saskatchewan, Canada. Soil-Science-Society-of-America-Journal 68(1):175-184.

Larcher, W. 2001. Physiological plant ecology. Fourth edit. Springer-Verlag. 513 p.

Lindroth, R.; Osier, T.; Barnhill, H.; Wood, S. 2002. Effects of genotype and nutrient on phytochemistry of trembling aspen (Populus tremuloides Michx.) during leaf senescence. Biochemical Systematics and Ecology 30:297-307.

Linn, D. M., Doran, J. W. 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils. Soil Sci. Soc. Am. J. 48:1267-1272.

Lieffers, V.J., Larkin-Lieffers, P.A. 1987. Slope, aspect, and slope position as factors controlling grassland communities in the coulees of the Oldman River, Alberta. Can. J. Bot. 65: 1371 - 1378.

Liu, P., Huang, J., Han, X., Sun, O., Zhou, Z. 2006. Differential responses of litter decomposition to increased soil nutrients and water between two contrasting grassland plant species of Inner Mongolia, China. Applied Soil Ecology 34:266–275.

Loeser, M.; Crews T.; Sisk, T. 2004. Defoliation increased above-ground productivity in a semi-arid grassland. Journal of Range Management 57:442-447.

Mapfumo, E.; Naeth, M.A.; Baron, V.S.; Dick, A.C.; Chanasyk, D.S. 2002. Grazing impacts on litter and roots: perennial versus annual grasses. Journal Range Management 55:16-22.

Mapfumo, E.; Chanasyk, D.S.; Naeth, M.A.; Baron, V.S. 1999. Compaction under grazing of annual and perennial forages. Canadian Journal Soil Science 79:191-199.

Martin, W.K.E.; Timmer, V.R. 2006. Capturing spatial variability of soil and litter properties in a forest stand by landform segmentation procedures. Geoderma 132:169-181.

McIntosh, P.; Allen, R.; Scott, N. 1997. Effects of exclosure and management on biomass and soil nutrient pools in seasonally dry high country, New Zealand. Journal of Environment Management 51:169-186.

Meelis, P.; Wilson, S.D. 2002. Root dynamics and spatial pattern in prairie and forest. Ecology 83(5):1199-1203.

Moore, T.; Trofymow, J.; Taylor, B.; Prescott, C.; Camire, C.; Duschene, L.; Fyles, J.; Kozak, L.; Kranabetter, M.; Morrison, I.; Siltanen, M.; Smith, S.; Titus, B.; Visser, S.; Wein, R.; Zoltai, S. 1999. Litter decomposition rates in Canadian forests. Global Change Biology 5:75-82.

Moran, S.M.; Hymer, D.C.; Qi, J.; Sano, E.E. 2000. Soil moisture evaluation using multi-temporal synthetic aperture radar (SAR) in semiarid rangeland. Agricultural and Forest Meteorology 105:69-80.

Moretto, A.; Distel, R. 2003. Decomposition of and nutrient dynamics in leaf litter and roots of *Poa ligularis* and *Stipa gyneriodes*. Journal of Arid Environment 55:503-514.

Moretto, A.; Distel, R.; Didone, N. 2001. Decomposition and nutrient dynamic of leaf litter and roots from palatable and unpalatable grasses in a semi-arid grassland. Applied Soil Ecology 18:31-37.

Morley, F.H.W. 1981. Grazing animals. Amsterdam, Elsevier. 411 p.

Mudrick, D.A.., Hoosein, M., Hicks, R.R., Townsend, E.C. 1994. Decomposition of leaf litter in an Appalachian forest: effects of leaf species, aspect, slope position and time. Forest Ecology and Management 68:231-250.

Mueggler, W. F. 1967. Response of mountain grassland vegetation to clipping in southwestern Montana. Ecology 48: 942–949.

Naeth, M.A.; Bailey, A.W.; Pluth, D.J.; Chanasyk, D.S.; Hardin, R.T. 1991. Grazing impacts on litter and soil organic matter in mixed prairie and fescue grassland ecosystems of Alberta. Journal of Range Management 44(1): 7-12.

Olofsson, J.; Oksanen, L. 2001. Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: a litterbag experiment. Oikos 96(3):507-515.

Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322-331.

Parton, W., Silver, W., Burke, I., Grassens, L., Harmon, M.E., Currie, B., King, J., Adair, E., Brandt, L., Hart, S., Fasth, B. 2007. Global-scale similarity in nitrogen release pattern during long-term decomposition. Science, 315:361-364.

Pachepsky, Y.A.; Timlin, D.J.; Rawls, W.J. 2001. Soil water retention as related to topographic variables. Soil-Science-Society-of-America-Journal 65(6): 1787-1795.

Perez Corona, M.E.; Vazquez de Aldana, B.R.; Garcia Criado, B.; Garcia Ciudad, A.1998. Variations in semiarid grasslands. Journal Range Management 51:570-576.

Pennock, D.J., Zebarth, B.J., de Jong, E. 1987. Landform Classification and Soil Distribution in Hummocky Terrain, Saskatchewan, Canada. Geoderma, 40:297-315 297.

Prescott, C.E.; Vesterdal, L.; Preston, C.M.; Simard, S.W. 2004. Influence of initial chemistry on decomposition of foliar litter in contrasting forest types in British Columbia. Canadian Journal of Forest Research 34:1714-1729.

Preston, C.M.; Trofymow, J.A.; Sayer, B.G.; Niu-JunNing. 1997. 13C nuclear magnetic resonance spectroscopy with cross-polarization and magic-angle spinning investigation of the proximate-analysis fractions used to assess litter quality in decomposition studies. Canadian Journal of Botany 75(9):1601-1613.

Quideau, S.A.; Graham, R.C.; Oh, S.W.; Hendrix, P.F.; Wasylishen, R.E. 2005. Leaf litter decomposition in a chaparral ecosystem, Southern California. Soil-Biology-and-Biochemistry 37(11): 1988-1998.

Reeder, J.; Schuman, G. 2002. Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands. Environmental Pollution 116:457-463.

Ritchie, J.C.; McCarthy, G.W.; Venteris, E.R.; Kaspar, T.C. 2006. Soil and soil organic carbon redistribution on the landscape. Geomorphology (2006), doi:10.1016/j.geomorph.2006.07.021.

Ross, D.; Tate, K.; Newton, P.; Clark, H. 2002. Decomposability of C_3 and C_4 grass litter sampled under different concentrations of atmospheric carbon dioxide at a natural CO_2 spring. Plant and Soil 240:275-286.

Sariyildiz, T.; Anderson, J. 2003. Interactions between litter quality, decomposition and soil fertility: a laboratory study. Soil Biology and Biochemistry 35:391-399.

Sariyildiz, T., Anderson, J.M., Kucuk, M. 2005. Effects of tree species and topography on soil chemistry, litter quality, and decomposition in Northeast Turkey. Soil Biology and Biochemistry 37(9):1695-1706.

SAS Inst. Inc. 2005. Statistical analysis system. Release version 9. SAS Inst. Inc., Cary, NC.

Saxton, K.E., Rawls, W.J. 2006. Soil water characteristic estimates by texture and organic matter for hydrologic solutions. Soil Sci. Soc. Am. J., 70:1569-1578.

Schimel, J.P., Van Cleve, K., Cates, R.G., Clausen, T.P., Reichardt, P.B. 1996. Effects of balsam poplar (*Populus balsamifera*) tannins and low molecular weight phenolics on microbial activity in taiga floodplain soil: implications for changes in N cycling during succession. Can. J. Bot. 74, 84–90.

Sebastia, M.T. 2004. Role of topography and soils in grassland structuring at the landscape and community scales. Basic and Applied Ecology 5:331–346.

Seibert, J., Stendahl, J., Sorense, R. 2007. Topographical influence on soil properties in boreal forest. Geoderma 141:139-148.

Scheffler, E.J. 1976. Aspen forest vegetation in a portion of the east central Alberta parkland. M.Sc. Thesis. University of Alberta. 160 p.

Schjønning, P. Thomsena, I.K., Moldrupb, P., Christensena, B.T. 2003. Linking soil microbial activity to water- and air-phase contents and diffusivities. Soil Science Society of America Journal 67:156-165

Schuman, G.E.; Herrick, J.E.; Janzen, H.H. 2000. The Dynamics of soil carbon in rangelands. In Follet, R.F.; Kimble, J.M.; Lal, R. The potential of U.S. grazing lands to sequester carbon to mitigate the greenhouse effect. Boca Raton, Lewis. p. 267-290.

Schuman, G.E.; Reeder, J. D.; Manley, J.T.; Hart, R.H.; Manley, W.A. 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecological Applications 9(1):65–71.

Scowcroft, P.; Turner, D.; Vitousek, P. 2000. Decomposition of Metrosideros polymorpha leaf litter along elevational gradients in Hawaii. Global Change Biology 6:73-85.

Shariff, A., Biodini, M., Grygiel, C. 1994. Grazing intensity effects on litter decomposition and soil nitrogen mineralization. Journal of Range Management 47: 444-449.

Silver, W.L.; Miya, R.K. 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. Oecologia 129:407-419.

Small, C.J.; McCarthy, B.C. 2005. Relationship of understory diversity to soil nitrogen, topographic variation, and stand age in an eastern oak forest, USA. Forest Ecology and Management. 217(2-3):229-243.

Smit, A.; Kooijman, A. 2001. The impact of grazing on the input of organic matter and nutrients to the soil in a grass-encroached Scots pine forest. Forest, Ecology and Management 142:99-107.

Smith, V.C.; Bradford, M.A. 2003. Litter quality impacts on grassland litter decomposition are differently dependent on soil fauna across time. Applied-Soil-Ecology 24(2): 197-203.

Snyman, H.A. 2005. Rangeland degradation in a semi-arid South Africa I: influence on seasonal root distribution, root/shoot ratios and water-use efficiency. Journal of Arid Environments 60:457-481.

Snyman, H.A.; Preez, C.C. du. 2005. Rangeland degradation in a semi-arid South Africa - II: Influence on soil quality. Journal-of-Arid-Environments 60(3): 483-507.

Strong, W.L. 1992. Ecoregions and ecodistricts of Alberta. Alberta. Forestry, Lands and Wildlife, Edmonton, AB Publication T/224. Vol. 1.

Stroo, H.F., Bristow, K. L., Elliot, L.F., Papendick, R.I., Campbell, G.S. 1989. Predicting rates of wheat residue decomposition. Soil science Soc. Am. J. 53:91-99.

Vargas, D.N., Bertiller, M.B., Ares, J.O., Carrera, A.L., Sain, C.L. 2006. Soil C and N dynamics induced by leaf-litter decomposition of shrubs and perennial grasses of the Patagonian Monte Soil Biology & Biochemistry 38 (2006) 2401–2410

van der Krift, T.A.; Kuikman, P.J.; Berendse, F. 2002. The effect of living plants on root decomposition of four grass species. Oikos 96(1): 36-45.

Van der Krift, T.A.; Gioacchini, P.; Kuikman, P.J.; Berendse, F. 2001. Effects of high and low fertility plant species on dead root decomposition and nitrogen mineralization. Soil Biology and Biochemistry 33:2115-2124.

Van Soest, P. 1994. Nutritional ecology of the ruminant. Portland, Durham and Downey. 374 p.

Ventera, R.T.; Lovett, G.M.; Groffman, P.M.; Schwarz, P.A. 2003. Landscape patterns of net nitrification in a northern hardwood conifer forest. Soil Sci. Soc. Am. J. 67:527-539.

Vogt, K. 1991. Carbon budgets of temperate forest ecosystems. Tree-Physiology 9(1-2): 69-86.

Waisel, Y., Eshel, A., Kafkafi, U. 1996. Plants roots. The hidden half. Marcel Dekker, Inc., New York. 989 p.

Whallen, B. 1986. Above and below-ground dry mass of the three main vascular plants on hummocks on a subartic peat bog. Oikos 46:51-56.

Wheeler, G.W. 1976. Some grassland and shrubland communities in the Parklands of Central Alberta. Thesis MSc. University of Alberta. 75 p.

Willms, W.D.; McGinn, S.M.; Dormaar, J.F. 1993. Influence of litter on herbage production in the mixed prairie. Journal of Range Management 46:320-324.

Chapter 3.0. Effect of topography and grazing on plant carbon stock in a semiarid rangeland: Measured and modeled results

1. Introduction

Rangelands, a natural ecosystem widespread in Canada, are an important source of land for animal production and around 26 million ha of rangelands are utilized for beef production (Alberta Agriculture, Food and Rural Development 2005). In Alberta, rangelands account for 6.6 million ha and they provide up to 50% of total forage for livestock, a business worth close to $30 billion per year (Southern Alberta Land Trust Society 2006). Thus, this ecosystem plays an important role in the national economy.

At present, a large percent of grasslands all over the world is overused and has low productivity (Conant *et al*. 2001). Around 50% of rangelands located in the Canadian Prairies are in less than good condition (Agriculture and Agri-Food Canada 2000). As do other natural ecosystems, rangelands maintain soil fertility through nutrient cycling. However when there is grazing, nutrient redistribution occurs and nutrient cycling in the ecosystem is altered. According to Jewell *et al*. (2007), places in which animals gather to rest and ruminate can receive up to 50 kg more of P ha^{-1} year^{-1} than any other place on the farm. Similarly, Franzluebbers *et al*. (2000) found in Watkinsville, USA, that soil nitrogen increased up to 49 kg ha^{-1} in some soil patches due to redistribution of this nutrient by grazing animals. Such accumulation occurs at the expense of nutrients elsewhere in the rangeland.

This nutrient redistribution causes different nutrient cycling rates to occur over the landscape and so influences plant productivity (Barton *et al*. 1998). However, plant productivity is also often directly affected by topography, so to develop sustainable grazing systems it is necessary to know the magnitude of both grazing and topographic effects on plant productivity.

1.1. Topography and soil properties

Plant productivity is not evenly distributed over the landscape; in fact, there is spatial variation related with microsite soil properties caused by topographic variation (Landi *et al*. 2004, Hutchinson *et al*. 1999, Johnson *et al*. 2000, Ventera *et al*. 2003, Yimer *et al*. 2006). Topography influences the movement of water, fine organic matter, soil particles plus soluble carbon and nutrients from higher to lower elevations. As erosion is more rapid on upper hill sites compared with lower sites, the soils at shoulders tend to be shallower, whereas the soils on bottom-slope areas tend to be thicker due to soil deposition (Kachanoski *et al*. 1999, Landi *et al*. 2004, Ventera *et al*. 2003).

This variation in soil depth associated with topography is present in both uncultivated natural landscapes and in cultivated soils. Kachanoski and Carter (1999) found increases up to 20% down slope in the soil A horizon thickness of a grassland. This is in agreement with Landi *et al*. (2004) who found that A horizon thickness rose from 0.03 m in a sharply convex shoulder position to 0.26 m in a level position in a non-cultivated hummocky landscape of a Dark Brown Chernozem with glacial till parent material in Saskatchewan. For an agricultural Black Chernozem in southern Saskatchewan, Pennock *et al.* (1987) reported an increase in the A horizon from 0.15 m to 0.25 m from upper to lower topographic locations.

Even in forest soils such variation in soil thickness is possible. Martin and Timmer (2006) in southern Ontario, Canada, found that topsoil depth and moisture content increased around 40% from shoulder slopes to depressional areas. They concluded that topography plays a key role in creating localized micro-site conditions.

Like soil thickness, soil organic carbon also increases down slope. Schimel *et al*. (1985a, 1985b) in Colorado detected an increase of 53% in the amount of soil organic carbon down slope in the A horizon of a natural short grass steppe. In the same region, Norton *et al.* (2003) detected increases of 27% down hill in the organic carbon of agricultural soils. This is in agreement with findings reported by Small and McCarthy (2005). They found that soil carbon increased from 1.8% to 3.9%, and nitrogen from 0.12% to 0.27%, from upper slope positions to less xeric sites located at lower slopes in a forest ecosystem in Ohio, USA. Honeycutt *et al*. (1990) in the Great Plains and Burke *et al*. (1998) in a semiarid short grass steppe of Colorado, found that soil organic carbon content increased up to 42% from upper part of the landscape to the foot slope.

As soil carbon content is directly related with soil fertility and with soil water holding capacity this explains why slope-bottom sites are more productive than hilltops. In fact, soil water availability, soil organic carbon and mineral nitrogen have been shown to have positive and direct relationships with productivity (Eneboe *et al*. 2002, Bork *et al.* 2001, Brady and Weil 2002), and explain the spatial variability of plant productivity along slopes.

1.2. Topography and plant productivity

There is evidence that topography influences plant productivity through its effect on soil characteristics and thus on soil carbon content, which is directly linked with soil properties like porosity, structure and texture, water holding capacity, nutrient availability, and soil biodiversity (Karlen and Andrews 2000, Singer and Ewing 2000, Lal 2004). Thus, as soil properties usually are better at lower topographic locations the plant carbon is likely to be greater at lower slope positions than at upper (Norton *et al*. 2003, Small and McCarthy 2005).

In semiarid Mediterranean grasslands differences in above ground plant productivity during the growing season can be as great as 200% due to topography in which the upper locations have the smallest (90 g DM m^{-2}) and the lower locations the largest (280g DM m^{-2}) plant production (Perez *et al*. 1998). Similarly, Asamoah *et al.* (2004b) working in a semiarid grassland at Kinsella Ranch, Central Alberta, Canada, showed that total above ground plant biomass (without including litter) was greater at lower (479g DM m^{-2}) than at upper (193g DM m^{-2}) topographic positions. These differences in productivity should be the result of greater water holding capacity, soil carbon and soil nitrogen contents as they tend to increase down slope (Schimel *et al*. 1985b, Honeycutt *et al*. 1990, Small and McCarthy 2005), however in Asamoah's research soil nutrients were not determined.

1.3. Grazing effect on plant carbon stock and litter production

Grazing can reduce or increase plant productivity and hence litterfall and soil carbon (Loeser *et al*. 2004, Donkor *et al*. 2002). Grazing can decrease plant productivity because it involves consumption of above ground plant biomass and reduces the photosynthetic area. If this reduction is too large plants need to remobilize significant amounts of stored carbohydrates and use them as an energy source for plant regrowth because the reduced foliage cannot fix enough CO_2 to drive regrowth. If the remobilization of stored carbohydrates is frequent and depletes the carbohydrates that the plant is able to store before the next grazing event, there is a point at which the plant will be unable to drive regrowth as well as before because few reserves are available (Morley 1981, Van Soest 1994). Under this condition the plant will regrow less vigorously and hence will reduce its productivity.

There is evidence from several studies that grazing substantially reduces the above ground net primary productivity (ANPP) and/or total net primary productivity (NPP) if stocking rate exceeds the grazing capacity of grasslands (Conant and Paustian 2002).

According to Mueggler (1967) and Zhang and Romo (1994) who during three years clipped vegetation at 4 and 5 cm high to simulated grazing (with an initial defoliation in early-May, June, July, or August, and repeated at 2- or 6-week intervals until mid-September), above-ground plant productivity was reduced by 19% in mountain grasslands of Montana, and 32% in Saskatchewan.

Reductions from 24% to 42% in plant productivity were reported by Derner *et al*. (2006) when they evaluated the effect of moderate, continuous season-long (May–October) grazing by cattle that removed approximately 40–60% of above ground green biomass in north-central Colorado. Ferraro and Oesterheld (2002) reported in a comparison of 105 grazed and ungrazed grasslands and savannas that 72% of sites had their ANPP reduced 10-20% by grazing. Also Schuman *et al*. (1999) in Wyoming found that light grazing (0.19 steers ha^{-1}, 35% below the stocking rate recommended) reduced ANPP by 20%, and that heavy grazing (0.56 steer ha^{-1}, 33% higher than the recommended rate) reduced the ANPP by 53%.

According to Guillen *et al*. (2000), in a mixed grass prairie in Oklahoma the total ANPP averaged over 7 years decreased approximately 17.5 kg ha^{-1} y^{-1} for every animal unit day ha^{-1} increase in stocking rate. Biondini *et al*. (1998) working on a northern mixed-grass prairie in USA, found 17% reduction in ANPP with light grazing; and 44% with heavy grazing. Grazing intensities were defined as leaving after grazing standing plant material equivalent to 50% (light grazing) and 10% (heavy grazing) of the long-term average aboveground peak biomass of comparable ungrazed range sites.

Plant productivity is directly related with nutrient mineralization from litter incorporated into the soil, so if there is a reduction in plant biomass this will be reflected in less litterfall (Snyman 2005) and hence slower nutrient mineralization. According to Schuman *et al*. (2000) grazing could reduce litterfall by removing plant material and because grazed plants will keep their leaves longer to use them for photosynthesis during regrowth. Natural ecosystems depend on nutrient cycling to keep the soil fertile through incorporation and decomposition of litter (Larcher 2001). This dependence is supported by Barger *et al*. (2004) who found that above ground litter production is directly related with the range condition. So if grazing reduces litter production, ecosystem productivity should be negatively affected because less nutrients will be cycling and available in the soil for plant uptake.

A significant reduction in litterfall from grazing will alter different processes in the ecosystem, which include soil microbial activity because one of the main constraints of microbial activity is the mass of available litter for decomposition. When the addition of litter to the soil is reduced, microbial activity slows down and also the priming effect decreases, further reducing the decomposition rate (Brady and Weil 2002). As a result, the amount of nutrients made available in the soil through mineralization also will be reduced that in turn will limit the plant growth due to lower soil fertility. This will be reflected in less plant productivity.

Different researchers have found a reduction in litterfall as consequence of grazing. Donkor *et al.* (2002) working in a semiarid grassland ecosystem in Central Alberta, reported that after two grazing years with wapitis at 2.08 and 4.16 AUM ha^{-1}, average litterfall decreased by 66% and 75% respectively. Schuman *et al.* (1999) found at the High Plains Grasslands Research Station in Wyoming, that continuous light (0.19 steers ha^{-1}) and heavy grazing (0.56 steers ha^{-1}) decreased the total above ground litter (surface litter and standing dead plant biomass) of a native mixed-grass semiarid rangeland with rolling topography by 36% and 62% respectively. Similar trends were reported by Naeth (1988), Baron *et al.* (2002), Mapfumo *et al.* (2002), McIntosh *et al.* (1997) and Willms *et al.* (1993).

But grazing not only reduces above ground plant biomass, it also decreases root biomass (McIntosh *et al.* 1997, Smit and Kooijman 2001, Cao *et al.* 2004), which will negatively affect nutrient uptake because smaller mass of soil is explored (Snyman 2005). Additionally, as root biomass decreases there will be a reduction in root litterfall which will cause a comparatively large reduction in nutrient cycling because root litterfall is greater than above ground litterfall (van der Krift *et al.* 2001, Cao *et al.* 2004). Root turnover can be up to 60% per year (Gill and Jackson 2000, Meelis and Wilson 2002), and fine roots, which are the major proportion of roots turning over, have nutrient concentrations higher than shoot litter (Gordon and Jackson 2000, Dornbush *et al.* 2002). Thus, if there is a reduction of root biomass by grazing, plant productivity will also be reduced.

Plant productivity can be further reduced by adverse effects of grazing on soil quality if a field is overgrazed. Loss of plant diversity, increased soil compaction, decreased infiltration, increased soil erosion, and reduced litterfall are commonly associated with overgrazing (Trimble and Mendel 1995, Sivakumar 2007).

However there is no agreement in the scientific community about grazing effect on plant productivity because even though the studies cited above showed negative effects, there is also evidence that grazing animals can increase plant productivity (Schuman *et al.*

2002, Wright *et al*. 2004). This plant response is known as overcompensation because defoliated plants partially or fully compensate the removal of biomass (Belsky 1986). Biondini *et al*. (1998) found that grazing impact on ANPP was dependent on the year. According to this research, during wet years light grazing increased ANPP up to 44% and heavy grazing up to 20%. A similar trend was reported by Fahnestock and Detling (1999) simulating defoliation in a grassland located in Northern Wyoming. Loeser *et al*. (2004) reported that ANPP was increased 27% in a semiarid grassland when simulated light grazing (all plant material was clipped at 2.5 cm height twice a year) was compared with an ungrazed reference site in the same ecosystem. Frank *et al*. (2002) working in a rangeland of Yellowstone National Park, USA, found that grazers stimulated aboveground, belowground, and whole-grassland productivity by 21%, 35%, and 32%, respectively. In this research there was no reported grazing intensity because they studied grazing of herds of elk (*Cervus elaphus*), bison (*Bison bison*), and pronghorn (*Antilocapra americana*) that migrate annually from low-elevation winter range to high-elevation summer range during the plant growing season, and then return to the winter range during the first severe snow storms in the fall. Previously Frank and McNaughton (1993) utilizing information gathered in the same National Park detected increases of 48% in above ground productivity of grazed vegetation compared with the ungrazed counterpart.

These gains in productivity with grazing may be attributed to the increase in the photosynthetic rate of undamaged leaves of partially defoliated plants. This increase can lead to higher relative growth rates of grazed plants compared with ungrazed plants (Oesterheld and McNaughton 1991) and a decrease in the mesophyll resistance to CO_2 diffusion in new leaves which would improve carbon fixation (Schuman *et al*. 2002). Also a reduction of nutrient limitation should increase plant regrowth of grazed plants, and there is an extended photosynthetic capacity in the remaining leaves because the plant keeps the remaining foliage longer. Because there is a reduction of foliage, there is a lower respiration cost and so, more carbon can be allocated to growth. Moreover, there is an increase in the soil available water because removal of transpiring surface area may result in soil moisture conservation and less interception of the falling rain that allows more water to go directly to the soil surface to infiltrate (Loeser *et al*. 2004, Schuman *et al*. 2000, Georgiadis *et al*. 1989). More soil water means more plant growth especially in semiarid ecosystems in which water is the main limitation on plant productivity (Bork *et al*. 2001). Finally, herbivores remove nutrients from some poor grazed material and add to the field excreta rich in readily available nutrients which stimulate plant growth and soil microbe activity although on a limited area (Ruess 1987).

These plant responses to grazing explain earlier results under semiarid climatic conditions that showed increases in plant productivity after grazing (Frank and McNaughton 1993, Frank *et al*. 2002), and so increases in soil carbon content (Schuman *et al*. 2002, Bruce *et al*. 1999, Reeder and Schuman 2002).

1.4. Grazing and soil carbon stock

Carbon stock is the absolute quantity of carbon held within a pool at a specified time, which can be quantified by different methods (Nelson *et al*. 2000, Coomes *et al*. 2002, Baker *et al.* 2004). The carbon stock change is determined by the turnover of living biomass, dead plant material, and soil carbon pools. If over time there is a change (increase or decrease) in the carbon stock associated which a specific grazing intensity, we will know the effect of that grazing intensity on ecosystem productivity. Usually when grazing removal is greater than net ecosystem productivity the carbon stock is removed faster than it is being created. This causes a reduction of organic carbon incorporated into the soil and hence a reduction of soil organic carbon (Cao *et al*. 2004). As many natural ecosystems have been turned into grazing lands, the quantification of plant and soil carbon stocks has become important as an indicator of ecosystem stability.

Grazing can influence the plant productivity and therefore the soil carbon. When grazing intensity is set properly according to available biomass there is a potential to increase the soil carbon up to 30 g C m^{-2} y^{-1} (Schuman *et al*. 2002, Bruce *et al.* 1999). In the northern and central Great Plains of Wyoming and Colorado, Reeder and Schuman (2002) found, without taken into account the plant litter that was on the soil surface, an increase of 10 g C m^{-2} y^{-1} in the top 0.3m soil layer after 12 years of light grazing (5-15% utilization) of a semiarid grassland compared with an ungrazed exclosure. The increase of soil carbon with grazing could be caused by hoof action that incorporated standing litter directly to the soil (Schuman *et al*. 1999), by higher annual shoot turnover (Reeder and Schuman 2002), and by an increase of plant species like blue grama that allocate more carbon to roots and so increase soil carbon (Schuman *et al*. 2002).

Increased soil carbon with grazing could also occur because grazed plants start growing earlier than ungrazed plants during spring (April to June) in which there is more soil available water that allows plants to grow bigger (Schuman *et al.* 2000). Earlier growth may occur because grazing reduces surface litter, allowing earlier soil warming.

However Schuman *et al*. (2000) do not mention if soil carbon content under grazed and ungrazed conditions was measured based on soil mass or volume, so a possible increase of soil density because of grazing could have resulted in an apparent soil carbon increase.

However, grazing can also reduce soil carbon especially when grazing intensity is too high. In this sense Cao *et al.* (2004) found that soil under heavy grazing (5.35 sheep per hectare) had 33% less soil carbon in the top 0.1m-soil layer compared with light grazing (2.55 sheep per hectare) after 16 grazing years.

Even though topography and grazing influence plant productivity and soil carbon, there is still not enough available information about these influences in semiarid natural rangelands. This information is required to develop appropriate grazing systems and to apply the proper grazing intensity to prevent ecosystem degradation. One way to estimate topographic and grazing effects on plant productivity is through the determination of plant and soil carbon stocks at different topographic locations under grazed and ungrazed conditions and doing modelling.

1.5. Modeling plant and soil carbon stocks

Because grazing effects on plant productivity are complex, one way to study these effects is through process-based models which are combinations of hypotheses that interact to represent processes and thereby explain complex ecosystem behaviour. Models allow simulation of different scenarios by applying existing knowledge to predict results of different management strategies. Thus, experimental data and scientific hypotheses can be combined in a useful way to support decisions related with the best management that can be applied in any ecosystem. Therefore, topographic and grazing effects on plant carbon stock also can be studied with models in which hypotheses for these effects are realistically represented.

Different models have been utilized to simulate grassland productivity (Owensby *et al*. 1999, Li *et al*. 2004, Shen *et al*. 2005, Barrett *et al*. 2005) and grazing (Cohen *et al*. 1995, Diaz-Solis *et al*. 2006, Donkor *et al*. 2002, Donkor *et al.* 2007), but they did not take topography into account. Thus, still there is a lack of information about plant productivity and topography in natural ecosystems, and there are no studies showing the effect of wild animal grazing on plant carbon stocks along topographic gradients in semiarid natural rangelands.

Grazing effect on plant productivity was modeled by Teague and Foy (2002), utilizing the rangeland simulation model SPUR2.4 which modeled grazing from April to

October during 28-years in a place with a potential total above ground productivity that had a range from 500 to 1000kg C ha^{-1} y^{-1}. They showed good agreement of modeled with measured aboveground biomass under light continuous grazing (0.14 AU ha^{-1} y^{-1}) in which the simulated monthly value of total aboveground biomass (79g C m^{-2}) was within the standard error of measured monthly average of total aboveground biomass (81±9g C m^{-2} y^{-1}), which included live and dead plant material. However under moderate grazing (0.2 AU ha^{-1} y^{-1}) the modeled plant biomass (80g C m^{-2} y^{-1}) overestimated the measured value (57±9g C m^{-2} y^{-1}). That happened because the model overestimated the total wintergrass standing crop, one of four grass species growing at the simulated location. However the authors did not explicitly explain why there was that overestimation except that spatial variations associated with areas containing more than one soil series were not well simulated.

The effect of grazing on aboveground plant productivity also was modeled by Chen *et al*. (2007) in a semiarid grassland ecosystem in eastern Mongolia, and they showed that modeled plant biomass values were within the 95% confidence interval of measured data. In a prediction they found that over time (50 years) a modeled stocking rate of 0.4 sheep ha^{-1} decreased above ground net primary productivity (ANPP) around 27%. Greater simulated stocking rates (from 0.7 to 1.2 sheep ha^{-1}) and longer modeled time (100 years) would reduce the ANPP by 84%.

Donkor *et al.* (2007) simulated grazing of wapiti, deer, and bison in boreal grasslands of Alberta. The modeled results reproduced the measured green phytomass with low RMSE, with ungrazed and grazed phytomass of 4.1 and 2.1 kg DM ha^{-1} during 1997, and 2.3 and 4.2 kg DM ha^{-1} in 1998 respectively. In that research the measured results showed that plant productivity was reduced by 53% with short duration grazing and by 40% with continuous grazing over those two years.

Currently, there is no available information about simulating topographic interaction with grazing on plant productivity. This simulation is needed to improve our knowledge about which processes, if any, could be altered by grazing and thus to formulate improved grazing systems which are not going to negatively affect the stability of natural ecosystems.

Based on the above analyzed information, the hypotheses of this research were: 1) **Moderate grazing reduces the plant productivity in a semiarid ecosystem over time because the consumption of foliage reduces the leaf area index and hence plant photosynthetic capacity. Thus less photosyntates are produced which result in less**

plant growth that will be reflected in a reduction of plant and soil carbon stocks greater than that caused by grazing removal alone. 2) **Topography also influences plant productivity through its effects on soil characteristics. The movement of water and nutrients down slope influenced by topography creates a gradient in soil fertility and soil water content that increases from top to bottom slope. When water moves down hill, it carries soil particles and nutrients that are deposited at lower topographic locations increasing soil fertility there. Thus, better soil properties at lower topographic locations give better conditions for plant production which is reflected in greater plant and soil carbon stocks compared with upper slopes**.

These hypotheses were examined through the use of *ecosys* model, with the following objectives:

1.- To simulate the variation of plant carbon stock along a topographic gradient in a semiarid rangeland.

2.- To simulate the effect of wild grazing animals on the carbon stock of plants growing at different topographic locations in a rangeland ecosystem located at Kinsella Ranch in central Alberta, Canada.

3.- To compare our modeled results of plant carbon stock with experimental results coming from the rangeland ecosystem at Kinsella Ranch and from others under similar ecological conditions.

The importance of this research relies on an accurate simulation of grazing effects on plant productivity and its variability caused by topography. This simulation may provide a means to model the effect of different grazing intensities on productivity and to develop management strategies that can help to maintain the productive capacity of natural rangeland landscapes.

2. Methodology

2.1. Experimental field site

A grazing experiment was conducted at Kinsella Ranch, an experimental farm belonging to the University of Alberta (53° 01’ 13.7” N, 111° 32’ 42.1” W), located 160 km southeast of Edmonton within the Aspen Parkland ecoregion (Strong 1992), Central Alberta, Canada. The annual mean temperature is 2°C, and the mean annual precipitation from 1960 to 2005 was 428 mm (Environment Canada 2006). The topography with frequent hills and slopes up to 60° strongly affects soils across the landscape. Soils under well-drained uplands are dark brown, eluviated black or black Chernozems while

Gleysols are found in poorly drained lowlands (Wheeler 1976, Howitt *et al*. 1988). Results of a soil survey done at Kinsella Ranch are given in Table 1, Chapter II.

In this landscape there are four dominant plant communities: grasses, shrubs, aspen trees, and riparians. The vegetation is natural and typical of a rangeland ecosystem located in a semi-arid region influenced by topography (Wheeler 1976, Scheffler 1976). Grasses are present throughout the landscape, dominated by fescue (*Festuca* spp.). Different forbs and shrub species grow in response to soil available water at different topographic locations. At upper locations, the more xeric environments in this experimental field it is common to find *Artemisia* species, but the lower locations which have wetter soil conditions than uphill, *Symphoricarpos occidentalis* predominates.

Forbs (*Artemisia* spp.) and shrubs (*S. occidentalis* and *Rosa woodsii*) are characteristic of north facing slopes at middle and low parts of the hill; they also are present on hill tops in small quantities. Aspen trees (*Populus* spp.) predominate in lower positions facing north and around riparian areas in which there is more available soil water because they need good soil moisture to grow. Riparians located in depressional areas were not considered in this research.

Soil moisture (θ) and soil temperature (T_s) are important drivers of plant productivity. To know how different they can be along a topographic gradient, a transect 15 m long with a northeast aspect and a slope of 45° covered by characteristic vegetation of Kinsella Ranch was chosen. Along this transect data loggers (C5615, Campbell Scientific Inc.) with TDR probes (model CS616-L) and thermistors, were placed in fenced plots at each topographic location (U: upper, M: middle, L: lower) to get hourly soil moisture and temperature data (0.05m, and 0.15m soil depths).

To calibrate the TDR probes, soil was collected from each topographic location, and used to get curves of soil moisture vs. TDR output for each probe. To do this, 20 L buckets were filled with that soil and wetted to saturation, then barley plants were grown under greenhouse conditions to dry the soil while TDR measurements were taken. These curves were used to get a regression from which an equation was derived to convert the return time from the probes into volumetric soil water, as described in Chapter II.

There were some gaps in the measurements due to probe malfunction during certain periods, and all soil moisture data collected at 0.05 m depth at L were lost.

2.2 Grazing treatments

To test the hypothesis about grazing effects on plant carbon stocks, a grazing experiment was set during 2004 with two bison (*Bison bison*), two elk (*Cervus elaphus*) and two deer (*Odocoileus hemionus*), with two grazing periods, the first from June 1st to July 15th, and the second from September 1st to October 15th. This gave a stocking rate of 1.57 AUM ha^{-1} calculated as follows. The total animal weight of each animal species was divided by the corresponding weight of one animal unit (450 kg) and the result multiplied by 3, which is the time (in months) grazed. The result was divided by the grazing area. So, during 2004 the weight of 800 kg LW of bison, 540 kg LW of elk, and 106 kg LW of deer corresponded to 1.57 AUM ha^{-1}. To increase plant utilization during 2005, one bison and one elk were added during the same two grazing periods as in 2004, and so the experimental stocking was 2.57 AUM ha^{-1}.

Dry matter intake (DMI) rates were measured by Kuzyk and Hudson (2006) who utilized indigestible markers (double *n*-alkane ratio technique with capsules containing C_{32} and C_{36} given orally to bison, elk and, mule deer). Concentrations of even-chained *n*-alkanes were determined from freshly voided feces collected 7-10 days after commencement of the trial which was the recommended time for synthetic *n*-alkanes to achieve steady state. Odd-chained *n*-alkanes (C_{31}), which are normally found in plant cuticular wax, were analyzed from vegetation samples that were gathered using the simulated bite technique. DMI was calculated by pairing C_{32} with C_{31}:

$$\text{DMI (kg day}^{-1}) = (D_{32} x F_n / F_{32}) / H_n - (F_n / F_{32}) x H_{32}$$

where D_{32} is the release rate of synthetic C_{32} (mg day^{-1}), F_{32} and H_{32} are concentrations (mg kg^{-1} DM day^{-1}) of C_{32} recovered from fecal samples and vegetation respectively. F_n and H_n represent the respective concentrations (mg kg^{-1} DM day^{-1}) of natural odd-chained alkanes (C_{31}) in feces and vegetation. Further details about this trial can be found in Kuzyk and Hudson (2006).

2.3 Plant biomass sampling procedure

Hypotheses related with topographic and grazing effects on above ground plant carbon stock were tested with plant biomass data collected by Haddow (unpublished data) at M from grazed and ungrazed plots, and by Dewitt (2008) at U, M and L from grazed plots. Similarly, those of root carbon were tested with root biomass data coming from the same grazing treatments at M (Cahill 2007, personal communication). A general procedure related with the collection of these data follows.

2.3.1 Grazing effect on above ground plant biomass

To measure the grazing effect on aboveground plant biomass there were two groups of plots; the first consisted of 60 plots of 0.1 m^2 located at M, 30 of which were unfenced to allow the mixed grazing of bison, elk and deer; and the remaining 30 of which were fenced to prevent grazing. In these plots aboveground plant biomass was sampled from July 17th to July 26th (at peak biomass) and from October 15th to November 5th (at the end of the growing season) (Haddow unpublished data). All living and dead above-ground plant material from current year's growth was cut at 1.0cm height, deposited in bags and oven dried. Litter on the ground was not included as part of the sample. The proportion of live-to-dead plant material in these samples was not determined (Haddow unpublished data).

The second group of grazed plots (343 of 0.1 m^2), located at U, M and L were used to get only live plant biomass after grazing. They were sampled in 2005 (June 15th, July 1st and 15th; September 15th and October 1st and 15th, DeWitt 2008). From each plot all current aboveground plant material was collected by cutting it at ground level and drying in an oven.

2.3.2 Below ground biomass

Root biomass data were available only from M. According to Cahill (personal communication) root biomass was measured from soil samples taken in a cylinder 0.05m diameter and 0.15m long, and all roots regardless of diameter were taken from grazed and ungrazed plots. The roots, which included live and dead roots, were washed with cold tap water and oven dried. Root samples were collected June 30, July 31, and September 31 in 2003, the first day of each May, July, August, and October of 2004. In 2005 roots were sampled only the 1st of May and August.

All dry matter plant biomass data (above and below ground) was converted to C by using a factor of 0.45. The same conversion factor was used with any available data for DM used in comparisons with model results.

2.4 Model theory

In this research *ecosys*, a comprehensive mathematical model for natural and managed ecosystems, was utilized to simulate topographic and grazing effects on productivity of the natural rangeland ecosystem located at Kinsella Ranch, and then to test the two hypotheses described above. *Ecosys* is constructed from basic scientific principles using parameters that may be determined independently of the model itself. It integrates temporal scales from seconds to decades, and spatial scales from mm to km in 1, 2 or 3 dimensions. *Ecosys* also integrates biological scales, both plant and microbial, from the organ to the community, and simulates the transport and transformation of heat, water, carbon, oxygen, nitrogen, phosphorus and ionic solutes through soil-plant-atmosphere systems with the atmosphere as the upper boundary and soil parental material as the lower boundary (Grant 2001). Hypotheses and algorithms of *ecosys* relevant to the objectives of this study (those related with topography and grazing effect on plant carbon stock) are described below with reference to published papers.

2.4.1 Model description

In this research we investigated topographic and grazing effects on plant production. So, algorithms are needed to simulate water movement, nutrient movement, cycling and uptake, and plant growth as affected by topography and grazing, which were included in the appendix. These algorithms have been tested elsewhere. Therefore, I am including here just a brief description; further details can be found in previous papers used as references.

2.4.1.1. Surface flow

The redistribution of water in topographically variable landscapes occurs as surface and subsurface flows. Surface flow is calculated from runoff velocity, depth of mobile surface water and width of flow paths that develop when rates of precipitation exceed those of infiltration. Runoff velocity is calculated from hydraulic radius and slope of surface water, and from Manning’s roughness coefficient (D1, D4) according to Morgan *et al.* (1998). Changes in surface water come from differences in surface flows among adjacent landscape positions. Thus, surface flow modelling implements the kinematic wave theory of overland water flow (D2).

2.4.1.2. Subsurface flow

Subsurface water movement in soil is governed by a three-dimensional Richard's equation (Sharma *et al*. 1987, Somma *et al*. 1998), alternating with Green-Ampt flow (D5) during soil saturation. Water fluxes are the product of hydraulic conductances and water potential differences, including those caused by differences in elevation, in each landscape position. Changes in water content arise from differences in subsurface fluxes among adjacent landscape elements.

Model testing. These algorithms were tested in different ecosystems with good agreement between TDR measurements and modeled results. Grant *et al.* (2006) modeled with *ecosys* hourly soil water contents close to those measured by TDR probes over a three-year period under an aspen stand (see figure 1 of that paper). In a boreal black spruce forest, Grant (2004) showed that these algorithms simulated soil water content, associated with topographic position, which corresponded with soil water changes under a boreal black spruce stand. Grant and Flanagan (2007) looking at water deficits in a semiarid grassland also showed good agreement between modeled and measured θ values (see figures 1 and 5 in this reference).

2.4.1.3. Plant water relations

Topographically-driven water movement redistributes available soil water, thereby affecting plant water relations and hence plant growth. Plant water relations are modelled by coupling stomatally-limited canopy transpiration driven by surface energy exchange (B1a, B1b), with hydraulically limited root water uptake driven by water potential gradients (B3, B4). Canopy water potential determines transpiration by setting the osmotic potential and hence turgor potential which, with leaf carboxylation rate determines stomatal conductance (B2a, B2b) (Grant 2001). Canopy and root water potentials determine water uptake by setting soil–root–canopy potential gradients (Grant *et al*. 1999, Grant 2001). Changes in canopy water potential (B12) determine changes in canopy water content according to plant water potential–water content relationships.

Model testing. Water relations in *ecosys* have been tested with results from different experiments. During 2000 and 2001, when there was low precipitation (276mm and 216mm) over an ungrazed grassland ecosystem located at Lethbridge, Grant and Flanagan (2007) simulated with *ecosys* low soil water contents that forced declines in canopy water potential and canopy stomatal conductance. This reduced latent heat which indicated strong stomatal limitation to transpiration and forced canopy CO_2 fixation rates to decline. These declines were consistent with those in gross CO_2 uptake from eddy covariance fluxes. Modeled and measured latent heat and sensible heat during three full years with differing precipitation in a grassland located at Lethbridge showed good agreement ($R^2 = 0.7–0.8$).

Ecosys also simulated declines of 1 MPa in canopy water potential of wheat which were consistent with measured declines when irrigation was reduced from nonlimiting rates to one-half of evapotranspirational demand (Grant *et al.* 1999).

2.4.1.4. Nutrient uptake

Topographically-driven water movement also redistributes available soil nutrients in *ecosys*, thereby affecting plant nutrient status and hence plant growth. Nutrient uptake which controls plant nutrient status is calculated from aqueous concentrations of soil nutrients at root and mycorrhizal surfaces (A11a-A11e) as controlled by microbial nutrient transformations. The products of N and P uptake are added to root and mycorrhizal storage pools from which they are combined with storage C during plant growth (Grant 2004). The ratios of these nutrients determine those of N and P to C in new leaf growth, which in turn determines gross primary productivity (Grant *et al.* 2001). Competition among plant species for irradiance, water and nutrients also is modeled (Grant 1994a).

Previous testing. Nutrient uptake has been previously tested against field measurements of phytomass growth and phytomass nutrient content (N and P) under different fertilizer rates, in which *ecosys* accurately reproduced in a winter wheat crop the increase in uptake following fertilizer applications in May and June (Grant 1991). About 75% of the simulated cumulative N uptake was taken up before anthesis as commonly observed in field trials. The seasonal N uptake that increased from 13 to 20 and 25 g m^{-2} did not differ significantly from that measured. *Ecosys* was also able to reproduce the time course of leaf N content apparent in field trial and in others research (Grant 1991).

Grant and Robertson (1997) also tested modeled nutrient uptake with field data coming from fertilized and unfertilized barley treatments on two different soils. The results showed that shoot P and DM accumulations simulated at Breton in 1992 were close to those measured in fertilizer treatments during the entire season (see figure 5 of this reference). The simulated root P uptake that increased from 0.8 to 1.5g m^{-2} was about 0.2g m^{-2} higher than measured in barley.

2.4.1.5. Gross primary productivity

To simulate topographically-driven nutrient effects on plant productivity is important because these effects are required to estimate plant growth as it varies with slope position (Asamoah *et al*. 2004, Perez *et al.* 1998). Thus differences in gross primary productivity (GPP), in a landscape with variable topography, are the result of soil properties and nutrient contents which change along a topographic gradient mainly influenced by water movement down slope.

To estimate GPP, *ecosys* calculates CO_2 fixation with algorithms that considers dark and light-limited reaction rates (Grant 2001) according to Farquhar *et al.* (1980) as described in Grant *et al.* (1999). The maximum CO_2 fixation is calculated from specific activity and concentration of Rubisco or chlorophyll (Grant 2001) which is determined by N and P uptake and assimilation during leaf growth (C1) (Grant *et al.* 1989, 2001).

A carboxylation rate is used to calculate an initial leaf stomatal resistance required to maintain a fixed gradient between CO_2 concentration in the canopy boundary layer and that in the mesophyll (Grant 2001). Leaf resistance is used to calculate a mesophyll CO_2 concentration for each leaf surface at which gaseous diffusion equals a final carboxylation rate. GPP is the sum of all carboxylation rates for each species.

Model testing. The ability of *ecosys* to model plant growth has been tested against measured values, showing that above ground phytomass was comparable to measured field data. Grant and Flanagan (2007) in a semiarid grassland simulated GPP values (397, 844, and 636g C m^{-2}) under varying precipitation that were comparable with measured values (280, 816, and 636g C m^{-2}) from 2001 to 2003. Changes in modeled net ecosystem productivity from negative values (-100 g C m^{-2} y^{-1}, net C source) during drier years to positive values (+150g C m^{-2} y^{-1}, net C sink) during wetter years, were consistent with findings from eddy covariance studies of grasslands under variable precipitation at Lethbridge and elsewhere. Previously Li *et al*. (2004) utilizing *ecosys* simulated a semiarid grassland found that simulated GPP (627, 287, and 227g C m^{-2} y^{-1}) was close to that measured in 1998, 1999 and 2000 (373, 287, and 272g C m^{-2} y^{-1}).

2.4.1.6. Plant growth

Growth respiration drives plant growth (C6), through mobilization of storage C, N, and P which are the products of leaf CO_2 fixation and of root N and P uptake. Growth drives the extension of leaf area (C7) used to calculate CO_2 fixation, and of primary and secondary root and micorrhizal axes (Grant 1993, Grant 1998b) used to calculate root water (Grant *et al*. 1999b) and nutrient (Grant 1991, Grant and Robertson 1997) uptake.

The growth of shoots and roots in the model depends on transfers of storage C, N, and P among branches, roots, and mycorrhizae. These transfers are driven from concentration gradients within the plant (Grant 1998b). When root N or P uptake rates are low, storage N or P concentrations in roots and branches become low with respect to those of storage C. Such low ratios in branches reduce the specific activities and surficial concentrations of leaf rubisco and chlorophyll, which in turn reduce leaf CO_2 fixation rates. These low ratios also cause smaller root-to-shoot transfers of N and P and larger shoot-to-root transfers of C (Grant 1998b), thereby allowing more plant resources to be directed towards root growth.

The consequent increase in root/shoot ratios, and thus in N and P uptake, coupled with the decrease in C fixation rate redresses to some extent the storage C/N/P imbalance when N or P uptake is limited. The model thus implements the functional equilibrium between roots and shoots proposed by Thornley (1995).

Model testing. Plant growth with *ecosys* was successfully tested in different crops. The ability of *ecosys* to model plant growth has been tested against measured values, showing that above ground phytomass was comparable to measured field data.

Grant and Hesketh (1992) simulated with *ecosys*, at the agronomy farm of the University of Illinois (40°N) on a Flanagan silt loam soil, values of height (m) and LAI (m^2 m^{-2}) which were almost all in the standard deviation of measured values of maize. Grant (1994b) also showed that *ecosys* reproduced the average barley yields recorded at Lacombe and Vegreville in Central Alberta (measured was 434g DM m^{-2} while *ecosys* simulated 427g DM m^{-2}).

Also Li *et al*. (2004) using *ecosys* simulated, in an uncultivated mixed grass prairie with slopes less than 2% in Central Alberta, values of ungrazed above ground biomass peak (79, 52, and 36 g C m^{-2} y^{-1}) comparable with those measured (95, 53, and 41 m^{-2} y^{-1}) under declining precipitation from 1998 to 2000. However these researches did not include grazing and up to the current time in *ecosys*, the grazing effect on plant productivity has not been tested.

2.4.1.7. Grazing

To simulate grazing *ecosys* implements a removal of material from each plant species present in the plant biome during specified grazing periods according to animal consumption needs but limited by available forage. The consumption needs are based on inputs for animal weight per unit land area and a specific consumption rate for each plant species that are used to calculate animal consumption rate in g of carbon m^{-2} d^{-1} during each grazing period. The removal is allocated to leaves, non-foliar, non-woody and woody parts of each plant species according to user-selected coefficients. Therefore, browser animals such as deer can be simulated as well as typical grazers like bison or cattle, or a mix of them.

Removal of N and P in each plant part corresponds to that of C. The fraction of plant parts removed by grazing that leaves the ecosystem, as animal product or respiration, is set in the model according to results from metabolic studies. The remaining fraction is returned to the ground surface as manure the following day. Grazing removals from each plant species are allocated to each grid cell within a grazed landscape according to its current phytomass with respect to those of the other grid cells, so that at the same grazing intensity less productive locations are grazed less than more productive locations.

Grazing in the model removes structural C, N and P from leaves, petioles or sheaths, and stems at successive nodes starting from the top of the canopy. Grazing thereby reduces leaf area used to calculate radiation interception and thereby reduces CO_2 fixation that maintains nonstructural C pools. Grazing also removes some of the nonstructural C, N and P pools. These pools drive the formation of new structural C, N and P in shoots and roots, so that reduction of these pools by grazing slows subsequent regrowth. These removals also reduce plant height and hence competitive access to radiation. Consequently grazing in the model reduces plant biomass directly through removal, and indirectly through subsequent reductions in plant regrowth. This part of the model has not been tested yet, and this research will be the first time in which grazed model results will be compared with measured field data.

2.5 Model experiment

2.5.1. Testing modelled topographic effect on plant growth

To test the hypothesis about the effect of topography on plant growth, *ecosys* was initialized with model inputs set to represent a field transect (15m long with northeast aspect and gradient of 15° at upper (U), 45° at middle (M) and 15° at lower (L) slope positions (Figure 1A) at Kinsella Ranch in which a decomposition experiment had been conducted (see Chapter II). These inputs included soil properties at U, M and L of a Black Chernozem from the soil survey carried out in September 2003 (Table 1, Chapter

II). Field capacity, permanent wilting point, and saturated hydraulic conductivity utilized for each topographic level in this model run were set using the soil physical properties from the soil survey as input to the Soil-Plant-Air-Water (SPAW) hydrology software (ver. 6.02.67) (Saxton and Rawls 2005) (Table 1, Chapter II). These slopes and soil hydrological properties were used by *ecosys* to simulate the topographic influence on water movement.

Model inputs also included biological properties of plant functional types distributed along the topographic transect (Fig. 1A) using values from earlier studies (Grant 1998, 2004, 2006, 2007). In the model run, grasses and shrubs, present in all topographic locations, and aspen trees, present only at L, were planted in a bare soil. The initial densities were 100 and 10 seeds m^{-2} for grasses and shrubs respectively at all topographic locations; aspen trees were established at a density of 0.2 seeds m^{-2}. There was no disturbance of those plants over time, except for aspen trees that were thinned an annual rate of 7 % with the thinned plant material left as surface litter. These seed densities were chosen to approximate the plant densities observed at Kinsella Ranch experimental rangeland (Section 2.1).

The model was driven by continuous hourly surface boundary conditions for solar radiation, air temperature, precipitation, humidity, and wind speed recorded at Viking (16 km north of the experimental site) from 1996 to 2002 by Len Kryzanowski (Alberta Agriculture, Food and Rural Development, Edmonton, Alberta, Canada), at Holden (52 km away from the experimental site) from 2003 to 2004 (Agriculture Canada 2005), and at Kinsella Ranch, approximately 1 km south from the experimental field in 2005.

The model was spun up over 54 years by repeating the climate record from 1997 to 2005 six times, with grazing during the two last years of each 9-year cycle. The modeled years taken for this research (2004 and 2005) came from the end of the sixth cycle after the model results had stabilized during previous cycles. The atmospheric CO_2 concentration in the model was kept at 370 µmol mol^{-1} for the whole simulated period. Atmospheric N deposition occurred during model runs as NH_4^+ and NO_3^- in precipitation (each 0.5 mg N L^{-1}) and through adsorption (or volatilization) of NH_3^+ (atmospheric concentration 0.005 µmol mol^{-1}).

2.5.2. Testing modelled effects of grazing on plant growth

Simulated grazing intensity, expressed as live weight m^{-2}, reproduced the field grazing intensity which started in 2004 with two 45 days grazing periods (the first from

June 1st to July 15th, and the second from September 1st to October 15th). The stocking rate in the field during 2004 was 1.57 AUM ha^{-1}, increased to 2.35 AUM ha^{-1} in 2005 to have greater forage utilization. To transform AUM into total live weight (LW) m^{-2}, the weight of each animal of each species grazing in the mix was added, and the total LW for each year was divided by the grazed area in m^2, and the result in g LW m^{-2} used as input to the model. Thus, according to the calculation in Section 2.3, 1.57 AUM ha^{-1} represented a LW of 1440 kg for the mix of three grazing animal species (bison, elk, and deer) in 2004; as the paddock was 6.16 ha in area, the stocking rate used in the model was 23.38g LW m^{-2}. The corresponding LW in 2005 was 2164 kg, so the model stocking rate was 35.13g LW m^{-2}. These stocking rates were allocated among the plant functional types at each topographic location according to grazing preferences derived from Didkowsky (2006) (Table 1).

Another factor that influenced grazing location was the animal behaviour, and this was taken into consideration in the simulation. Bison are basically grass eaters, and according to observations made on the field, they grazed the whole paddock because grasses were present at all topographic locations. Deer, highly selective browsers (Holecheck *et al*. 2001), prefer to be closer to forest to get quick protection if they need it, so they grazed preferentially at L and M due to the nearness of aspen trees. Elk, which are a mix of browser and grazer, expended more time at M because of the greater foliage availability there but also grazed L and U.

Dry matter intake was set at 2.5% of LW per day (Van Soest 1994, Morley 1981), of which 40% was removed as animal product or released as respiration (Whitehead 1995, Van Soest 1994, Baron *et al*. 2002). Modeled dry matter intake was compared with measured values from Kuzyk and Hudson (2006) taken at the same modeled locations with a mix of wild grazing animals.

Total consumption per grazing year, according to these inputs, was 36g C m^{-2} y^{-1} (35.13g LW m^{-2} x 0.025g DM g LW^{-1} d^{-1} x 0.45g C g DM^{-1} x 90 d y^{-1}) from which 40% or 14.4g of C m^{-2} y^{-1} was removed as respired CO_2 and animal biomass The consumption of each plant species was distributed across U, M and L according to the relative availability of biomass for grazing at each topographic position.

3. Results

Plant growth depends, among other factors, on soil water availability which is especially true in semiarid ecosystems where there is a strong correlation between soil moisture and plant productivity (Bork *et al.* 2001). Therefore modelled soil volumetric water content (**θ**) was first tested against field measurements.

3.1. Modeled and measured volumetric soil water content

Ecosys simulated the same trend in **θ** as that measured during 2005 (Figs. 1 and 2). Both groups of data (modeled and measured) had periods in which **θ** decreased below 50% of water holding capacity at U and M during a period of low precipitation in July and August (Figs. 1B,C and 2A,B), but remained high at L (Fig. 2C). The modeled decreases at U and M were caused by rapid transpiration from plant biomass because those months had high mean temperature (15.1°C) compared to the remaining growing season (8.0°C). These decreases were also caused by surface (Q_r) and subsurface (Q_w) flows down gravimetric water potential (Ψ_g) gradients from U and M, to L. In the simulation, θ at L remained close to field capacity during most of the growing season (Fig. 2C), except during August when **θ** declined slightly, while receiving Q_r and Q_w from upslope positions and losing Q_r through its lower boundary.

The lower values of θ (around 0.25 m^3 m^{-3}) at U (Fig. 1B) were recorded by the probes and modeled by *ecosys*, which suggest that algorithms used by this model to estimate θ are able to reproduce field conditions. Differences between modeled and measured values were reflected in the root means square difference (RMSD), the residual term from the regression of measured on modelled values, which was used to determine how well the model fitted the measured data. If the RMSD is close to the uncertainty in the measured values, then further model improvement would be difficult to verify.

RMSD for the whole growing season of 2005 at U was 0.03 m^3 m^{-3} at 0.05m and at 0.15m depths); the corresponding values at M were 0.04 m^3 m^{-3} and 0.03 m^3 m^{-3} respectively. Modeled θ at 0.05m depth at L could not be compared with measured values because probes malfunctioned. At 0.15m depths the RMSD was 0.02 m^3 m^{-3}. These RMSD's could be partly attributed to some discrepancies between modeled and measured θ. Some rain events did not increase the measured θ but did increase the modelled (Fig. 1) which could have been caused by slow infiltration and rapid plant uptake in the field, so that small rain events were unable to wet the soil deeply enough to be recorded by the probes. The algorithms in *ecosys* might have allowed faster infiltration than in the field and so simulated θ increased with each rain event, (Figs. 1 and 2) possibly due to soil properties estimated from SPAW (Saxton *et al.* 2005). There may also have been spatial variation in infiltration in the field caused by macropores and soil cracks that altered the normal pattern of soil infiltration which was not reproduced by the model.

3.2. Modeled and measured soil temperature

Topographic variation in soil temperature may affect plant productivity through its effect on organic matter decomposition, which is the main source of soil nutrients in natural ecosystems and so determining the plant growth. Soil warming during spring at 0.05 m was fastest in U, slower in M, and slowest in L where modeled thawing was delayed by 3 days with respect to that at U (Figs. 3 – 5). Later warming at L was caused in the model by higher $\boldsymbol{\theta}$ (Fig. 1) which raised soil heat capacity and thermal conductivity, causing greater ice accumulation during winter which delayed thawing in spring, and lowered T_s in summer by 1°C (Fig. 3). The modeled hourly T_s at 0.05 m during 2004 (Fig. 3) and 2005 (Fig. 4) and at 0.15cm depths in 2005 (Fig. 5) showed a similar trend to that measured.

The average measured and modeled T_s during the growing season decreased from U to L by 1°C at 0.05m depth. This was related with lower bulk density (Table 4, Chapter II) and higher θ (Figs. 1 and 2) down slope. As θ increases, more energy is required to warm the soil. Also as bulk density decreases, a decrease of thermal conductivity is expected (Presley and Christensen 1997) because air has lower conductivity than soil, which decreases the soil heat flux. As *ecosys* take these factors in algorithms used to do the calculations, the modeled results are very close to measured values.

There was good agreement between modeled and measured values; the RMSD during 2005 at U was 1.5°C and 1.8°C at 0.05 and 0.15 m depths respectively. The RMSD at M was 2.7°C at 0.05 m and 2.8°C at 0.15 m depths; meanwhile at L the RMSDs was 1.4°C at 0.15 m depths. These results reinforce the fact that algorithms used by *ecosys* to estimate soil temperature are able to reproduce field conditions.

3.3. Modeled and measured animal consumption

During 2004 and 2005 the simulated consumption (calculated as animal live weight per m^2 multiplied by specific grazing rate in Table 1) during the two grazing periods of 45 days, was 23.3 and 33.3 g C m^{-2} respectively for each year. These values were slightly smaller than those in table 1 because grazing in the model is reduced if at any time the plant biomass is insufficient for the grazing rate imposed by the model inputs. Measured values of animal consumption at the experimental field during 2005, with a mix of grazing ungulates (bison, elk and deer) with equal total weight to that used by *ecosys*, were in a range from 30.0 to 43.4 g C m^{-2} (Kuzyk and Hudson 2006). So, the algorithms used by *ecosys* to simulate animal consumption reproduced the actual measured animal consumption.

3.4. Modeled and measured changes in shoot carbon stock with grazing and topography

Modeled and measured grazing in this ecosystem caused a decrease of plant carbon stock (Fig. 6), directly through removal of above ground biomass, and indirectly through decrease in the leaf area index and the subsequent reduction of carbon fixation and growth. This difference might also be attributed to soil properties provided to the model which come from the lab soil analyses. At M the soil has a large amount of N below 22cm depth (Table 1, Chapter II) which contributed to greater modeled plant growth and so higher values than measured. Other reasons why modelled values could be larger could be: other herbivores such as rabbits were not taken into consideration by *ecosys* model. Regarding to insects, they were not included in the simulation because even though there is some evidence that insects depress primary productivity (Coupe and Cahill 2003), newer results showed that insects do not have effect on ecosystem function, community structure or plant biomass (Coupe, *et al*. 2009). Also nutrient limitations not accounted for in the model contributed with the difference between grazed and ungrazed plant carbon stock showed in Fig. 6.

The greater modeled vs. measured values also could be explained by spatial variability of grazing intensity. According to plant utilization data from Haddow (unpublished data), some grazed plots used to measure animal utilization had nothing left to be measured, so they were completely utilized. This over consumption reduced the average weight of collected plant material which was not balanced off by less grazed plots and so, influenced the difference between measured and modeled values.

During the two years of field experimentation, there were no statistical differences between measured ungrazed and grazed values of carbon stock at M, but there was a trend in which grazed values tended to be smaller (Fig. 6). This trend was more evident in

2005 because that year the stocking rate was 0.8 AUM ha^{-1} heavier than in 2004 (Table 1).

As a result of the two grazing event each year, there was modeled a decrease in the available grass forage by 17% in 2004 and 25% in 2005, which was similar to measured decreases at the field experimental grazing of 18% in 2004 and 36% in 2005 (Fig. 6A,B). Grazed shrub biomass in the field experiment was similar to ungrazed biomasses during 2004 but was 37% lower after the first grazing in 2005 (Fig. 6C,D). However grazed shrub biomass in the model was slightly larger than ungrazed biomasses during both years because of reduced competition for light and nutrients from the grazed grass. The modelled response of shrub vs. grass biomass to grazing was determined by the allocation of grazing intensity to shrubs vs. grasses in Table 1. These modeled results agree with the general observation that grazing decreases total plant growth (Zhang and Romo 1994, Conant and Paustian 2002), although it may change species composition.

The greater modeled than measured ungrazed grass and shrub biomass found during the first grazing period at M (Fig. 6) was also found when grazed biomass of grass (Fig. 7) and shrub (Fig. 8) in the model was compared with those measured in the field for DeWitt (2008) at U, M and L after grazing by a mix of wild ungulates at Kinsella Ranch during 2005. There was modeled more plant grow at M than at U which was the result of better soil conditions (Table 1 Chapter II) and more available soil water (Figs. 1 and 2) which stimulated the plant growth. In *ecosys*, low θ and hence low soil water potential (Ψ_s) at U caused low soil and root hydraulic conductance's. These conditions forced canopy water potential (Ψ_c), canopy turgor potential and hence canopy conductance to decrease, thereby reducing canopy transpiration during equilibration with root water uptake. This caused a reduction in plant growth at U.

At L, even though there was more soil moisture (Figs. 1 and 2) and good soil conditions for plant grow than at U, the low values of plant carbon simulated are mainly the result of aspen shade that reduced the sunlight going to the understory limiting the photosynthesis of grass and shrubs growing there and hence reducing its growth.

The RMSD between modelled and measured biomasses for grazed grass (Fig. 7) was 47, 75 and 16 g C m^{-2} at U, M and L; smaller RMSD values were estimated with grazed shrubs (Fig. 8) (18, 26, and 10 g C m^{-2} at U, M, and L respectively). For grasses there was not statistical difference between root mean square error (RMSE), from replicated biomass measurements, to measured values. This means that the fraction of variation not explained by the model (RMSD) is similar to the random error of measured values

(RMSE). However there was statistical difference between RMSE and RMSD in the case if shrubs, which means that the model did explain many of the variation in the measured values.

3.5. Modeled grazing and topographic effects on plant carbon stock

3.5.1. Above ground carbon

The simulated grazing increased the shrub carbon stock by 16%, 7%, and 54%, respectively at U, M, and L (Fig. 9D,E,F), and that of grass by 51% at L (Fig. 9C) during 2005. This increase could be explained by the fact that simulated grazing decreased the competition for light and soil nutrients by grass at U and M, and by aspen trees at L, thus more available resources stimulated plant growth.

However during the same year (2005) grazing decreased the grass carbon stock by 33% and 25% at U and M (Fig. 9A,B). This shows that grazing can have different effects on growth of different species depending on the intensity with which each species is grazed. These modeled results are consistent with experimental field measurements showing that grazing can stimulate (Schuman *et al*. 2002, Wright *et al*. 2004, Loeser *et al*. 2004) or decrease plant growth (Derner *et al*. 2006, Conant and Paustian 2002, Ferraro and Oesterheld 2002).

Modeled grazing reduced plant carbon differently at U, M and L because animal consumption was not the same in each topographic location. Even though average animal consumption for the grazed area was set at the beginning of modeled run, *ecosys* also allocated consumption at different topographic positions within the grazing area according to available forage. Thus in the simulation, animals grazed more where there was more forage to meet their requirements. As M had greater modeled plant growth than U (Fig. 9B vs. 9A), animal consumption was 13% greater at M.

Under field conditions, experimental results showed that productivity increased from upper to lower landscape positions at Kinsella Ranch (Asamoah *et al*. 2004), and in other experimental field (Perez *et at*. 1998). The model simulated this trend (Fig. 9), so the algorithms used to simulate topographic effects on water and nutrient transport were able to reproduce topographic effects on plant growth at the experimental field and previously reported in the literature. According to Asamoah *et al*. (2004) the above ground peak of biomass in Kinsella Ranch should be from late July in the meadows to September in the uplands (85g C m^{-2}), which is similar to our modeled peak of above ground biomass at U (98g C m^{-2}). Unfortunately there is no available information about measured root biomass peak at this site, and root biomass measurements at the experimental field (Fig. 10) were not frequent enough to corroborate if a delay in root growth is present in the experimental field.

In the simulated topographic gradient, grass and shrub carbon stocks were greater at M than at any other topographic location (Fig. 9). This is the result of different soil properties at each topographic location (Table 1, Chapter II) as a result of the influence of water movement down slope (Kachanoski and Carter 1999, Landi *et al*. 2004, Martin and Timmer 2006). The soil at M, compared with that at U, had more organic C and total N in the A_h horizon, and greater topsoil thickness (Table 1 Chapter II), characteristics directly related with soil fertility. Also the $\boldsymbol{\theta}$ was greater at M than at U (Figs. 1 and 2), indicating less soil limitations for plant growth at M.

Grasses and shrubs modelled at L did not grow as well as those at M and U because even though there was good $\boldsymbol{\theta}$ during the whole growing season (Fig. 2) and soil had great amount of N (Table 1 Chapter II), competition for nutrients and light by aspen trees negatively affected grass and shrub growth. The modeled plant growth followed that measured in the experimental field (Figs. 7 and 8).

3.5.2. Below ground carbon

Modeled root growth was driven by carbon transfer from shoots, so that seasonal trends in root biomass (Fig. 10) followed those in above ground biomass (Figs. 7 and 8). As temperature increased during spring time shoots and then roots regrew. As shoots grew, leaf area index increased and hence photosynthates also increased, part of which were allocated below-ground to drive root growth. Therefore root growth driven by shoot primary productivity was delayed with respect to shoot growth. Thus, the modeled peak of above ground biomass at M was during August (Fig. 6) and root biomass peaked during September (Fig. 10). After the biomass peaked, shoot and root biomass declined because climatic conditions became less favorable to growth (Figs. 3 to 5).

The measured root biomass used to compare with modeled results was gathered only at M (Dr. J.C. Cahill, personal communication) and *ecosys* simulated values close to those measured (Fig. 10). The modelled root carbon values were within the standard deviation of the measured values during each year of the field experiment, indicating acceptable agreement between modelled and measured results. In fact, the RMSDs of the modeled vs. measured values were 69 and 77g C m^{-2} respectively for ungrazed and grazed treatments during 2003, the base line year in which three samplings were carried out. The agreement in 2004, in which four samplings were performed, showed a RMSD of 85 and 108g C m^{-2} for grazed and ungrazed treatments respectively. In 2005, with only two sampling times, the RMSD was 146g C m^{-2} for grazed and 87g C m^{-2} for ungrazed. The differences between modeled and measured values could be caused by the fact that *ecosys* results only included root diameters <1mm while measured values took into consideration any root diameter present in the soil core which explains why in general measured values were greater than simulated (Fig. 10).

Modeled grazing at M reduced total live and dead root C between 4% and 22% compared with ungrazed values (Fig. 10). Measured root carbon also was reduced between 6% and 20% by grazing but without statistical significance. Reduced root C from grazing in grasses was the result of animal consumption that decreased above ground biomass (Fig. 9), the leaf area index and hence photosynthates. This reduced the carbon allocated to the roots, and consequently their growth and biomass. Similar findings in which root C decreased with grazing in field experiments were reported by Wang *et al*. (1997) and Han *et al*. (2008). Thus, there was a clear relationship between above and below ground plant carbon stocks across topographic positions, so if shoots were increased or reduced the roots were affected in the same way.

Plants with great above ground biomass require more nutrient and water, and will allocate more carbon below ground than plants with small biomass. At M in which there was greater modeled above ground carbon (Fig. 9) there was also greater root C (Fig. 11). U and L with less shoot C than M (Fig. 9) have less root carbon (Fig. 11). In the simulated transect grass root carbon was reduced by grazing at U (42%) and M (35%), but increased at L (34%) (Fig. 11A,B,C); the aspen root C also was decreased 26% by grazing (Fig. 11G). Modeled grazing increased the shrub root C by 24%, 22% and, 39% at U, M and, L respectively (Fig. 11D,E.F). The increase of shrub root carbon at U and M was related with the reduction that grazing caused in grasses which decreased the competition for light, water and nutrients allowing the increase in shoot (Fig. 9) and root (Fig. 11) carbon of shrubs. The increase in grass and shrubs with grazing at L (Fig. 11C,F) is explained by reduction of aspen shoot carbon caused by modeled grazing and browsing (Fig. 9) that reduced competition for available resources.

These changes in above and below ground biomass also changed the root-to-shoot (R:S) ratio. Unfortunately we do not have field samples to calculate this ratio and then to compare it with modeled results. Root samples were not taken at the time of peak biomass (DOY 202) (Fig. 6) (Haddow unpublished data) at M location. So, to compare modeled with measured R:S, I took measured root biomass at DOY 182 and DOY 121 (Fig. 10) and through lineal inference calculated root biomass at DOY 202. The measured ungrazed R:S ratio at DOY 202 was 5.0 in 2004 and 5.1 in 2005, while grazed R:S was 5.4 and 6.3 in those same years. These ratios were similar to our modeled R:S with values for ungrazed R:S of 4.3 and 4.7, and grazed R:S of 4.8 and 8.5 in 2004 and 2005 respectively. The modeled R:S along the topographic transect during the growing season of 2005 without grazing was similar at U and at M (5.6), and higher at L (6.7). Under simulated grazing, U had the smaller ratio (6.8) followed by M (7.4), and L (10.4). These ratios were similar to those measured by Schiborra *et al*. (2009) who found a range from 3.0 to 11.7 in a semiarid grassland in a Chernozem soil. Previously Jackson (1996) reported a R:S ratio of 3.7 for temperate grasslands.

An important fact to note is that modeled grass or shrub root carbon, grazed or not (Fig. 11) is larger than modeled shoot carbon (Fig. 9); the measured biomass also showed the same trend, and this indicates that belowground biomass is the most important plant component of rangeland ecosystem. For instance in 2005, root growth at M was larger than shoot growth (88g C m^{-2} with grazing, and 113g C m^{-2} without grazing). The root carbon measured and modelled at Kinsella reflects the plant's response to semiarid conditions in which C is mainly invested in roots because more root biomass will enable more soil to be explored and thus the plants can have access to more water and nutrients and hence, to produce and sustain more above ground biomass. The large root biomass has other important implications for ecosystem productivity because it generates more exudates and residues incorporated into the soil which will increase the soil organic carbon (SOC) through time. As SOC is directly linked with soil fertility, soils with greater SOC provide better condition for plant growth and so increase the ecosystem productivity. This issue will be focused in the next chapter of this thesis.

4 Discussion

There is limited information about the effect of topography on plant production in semiarid ecosystems. So, it was difficult to get experimental data to compare with our simulated results. Therefore, it is necessary to generate information regarding plant growth along topographic gradients, and how such growth could be affected by grazing. This information could be used to develop good grazing systems that should keep rangeland productivity stable over time. This information could also be used to test model results, and after their validation, models can be very useful to develop management practices that could protect the ecosystem over time.

4.1. Topography and plant carbon stock

Kinsella Ranch has variable topography which influences plant productivity (Fig. 9) because plant growth is influenced by soil properties like fertility and water availability that vary with topography. In this grass-dominated semiarid ecosystem, θ is influenced first by climatic conditions especially rainfall, and secondly by topography that creates a gradient down slope (Fig. 2). Thus plant productivity depends on different factors of which soil moisture is critical (Eneboe *et al*. 2002).

As a result of topographic influence, the soil properties change along the slope and more soil C and N (two key nutrients for plant growth) were found at M and L than at U (Table 1, Chapter II); they increased respectively, 47% and 67% from top to down slope. This agrees with increases of soil carbon (from 27% to 53%) and nitrogen (up to 125%) down slope in semiarid environments reported by Schimel *et al*. (1985a, 1985b) and Norton *et al*. (2003).

The gradient in soil properties along the topographic transect found in the soil survey, and used as input to *ecosys*, was reflected in the modeled plant carbon stock (Figs. 9 and 11). **So, better soil properties at M were translated by *ecosys* into 52% greater plant carbon stock than at U.** This increase is in agreement with previous research carried out in Kinsella by Asamoah *et al*. (2004) who found 76% more above ground plant biomass at lower topographic locations compared with upper hill. Similarly Perez *et al*. (1998) in Spain reported under similar climatic conditions more than 100% greater above ground biomass down slope than at upper hill positions.

The simulated root carbon was close to values reported in the literature. Under grazed conditions in a grassland located in a temperate climate, Pucheta *et al*. (2004) found fine root (diameter less than 1mm) values of 225.5±52.9 and 271.5±70.5g of C m^{-2} in summer and autumn respectively. At comparable times *ecosys* simulated 224 and 304g of C m^{-2} at M.

The modeled results showed that L had smaller grass carbon stock than U and M. This is partially explained by the shade of aspen trees that reduced the sunlight and so the photosynthetic rate. Thus averaged over the whole growing season, U (55g C m^{-2}) and M (107g C m^{-2}) had greater modeled daily above ground plant carbon than L (36g C m^{-2}). This trend is similar than that reported by Asamoah *et*

***al*. (2004)** who found at Kinsella Ranch that upland produced less plant biomass than meadows (69 vs. 187g of C m^{-2}) but similar than aspen forest (82g of C m^{-2}) at the first rotation period starting in June. The second rotation performed in July 18th showed that upland produce less plant biomass than meadows (103 vs. 243g of C m^{-2}) but more than aspen forest (87g of C m^{-2})

Topographic effects on soil nutrient status (Table 1 in Ch. 2) were apparent in those on plant nutrient status. The modeled ungrazed grass leaf N:C ratio was 0.03 at U and M, and 0.06 at L which reflects the amount of soil N along the topographic transect (Table 1, Chapter II) and the sensitivity of *ecosys* to soil fertility. The same trend was simulated with shrubs along the hill. To calculate these ratio *ecosys* takes into account the plant growth and hence total plant uptake, distributing the available resource among all plant species and total biomass at each topographic location. Grazing by consuming part of this foliage reduced the N:C ratio at L (0.04) but not at M and U. In general, modeled N:C ratios were similar to those reported by Asamoah *et al.* (2004) at Kinsella Ranch who found leaf N:C ratios in a range from 0.05 at the beginning of the first rotational period (1st of June) to 0.03 at July 30th (the second rotational period) in which also found larger ratios in riparian biomass than in uphill location.

Thus, soil properties directly linked with soil fertility and influenced by topography, explained the modeled difference in plant carbon stock and therefore supported the topographic effect on plant growth modelled along the transect. This is corroborated by measured biomass that showed greater values down slope (64 and 95g of C m^{-2} at first and second rotational period) than at uphill (172 and 224g of C m^{-2} in those same rotational periods, Asamoah *et al*. 2004). These results support the hypothesis that there is a gradient down slope in plant carbon stock which is the result of soil properties that change with topography.

4.2. Grazing and plant carbon stock

The modeled reduction in above ground grass carbon stock by grazing, from 23% to 33% during 2005 in this research (Fig. 9), is in the range that has been reported by different researchers under similar climatic conditions to those at Kinsella. Thus, Schuman *et al*. (1999) in Wyoming in which grazing was 35% below the recommended stocking rate for a mixed-grass rangeland, found that grazing reduced the live above ground biomass from 9% to 40%. Derner *et al*. (2006) with moderated grazing (that removed approximately 40–60% of above ground green biomass) in the Central

Plains of north-central Colorado found that available plant biomass was reduced between 24% and 47%. Greater plant reductions (57%) were found in a meta-analysis performed by Ferraro and Oesterheld (2002) in which they analyzed available information related with grazing effect on grass growth. Thus in the above research results, as well as in this research, apparently grazing cause a general reduction of above ground plant biomass that could be the result of different conditions, in which time of recovering from the last grazing event is critical for plant regrowth. So, probably at Kinsella Ranch resting or recovering time has to be increased to avoid reduction in plant biomass available for animal intake and therefore, in this way to keep stable the animal and ecosystem production over time.

Because root growth depends on carbon transferred from the leaves, grazing reduces carbon allocated to the roots which in turn reduces root growth (van der Krift *et al.* 2001, Cao *et al.* 2004). **The measured total root biomass (live and dead roots) at M was decreased by grazing between 10% and 14%, and during three years (from 2003 to 2005) measured root carbon was consistently lower under grazing (Fig. 10); *ecosys* modeled the same trend (Figs. 6 and 11) with root carbon reductions between 4% and 22%. Similar reductions in root biomass as a result of grazing have been reported in the literature under similar climatic conditions to those at Kinsella.** Utilizing medium grazing intensity (1.63 AUM ha^{-1}) Mapfumo *et al.* (2002) found in a semiarid ecosystem located in Lacombe with a long-term (89 years) mean annual precipitation of 362mm, a reduction of 24% in root carbon. Schuman (1999) reported that even light grazing (35% below the stocking rate recommended in Wyoming) decreased root biomass up to 31%.

The reduction of root carbon has implications for grazing and for ecosystem stability over time. A decrease in root growth reduces the volume of explored soil which will limit access to soil resources needed for plant growth (Snyman 2005). Therefore, plants will have reduced foliage and less photosynthates. Reduced root growth means less root litterfall and exudates incorporated to the soil, which is the greater source of plant C in the ecosystem (Figs. 9 and 11) with the greatest turnover (Jackson *et al.* 1996). Declines in root carbon stocks with grazing may be as great as, or even greater than, those in shoot carbon stocks commonly measured in earlier studies. Thus the impacts of grazing on ecosystem plant carbon stocks may have been underestimated in some earlier studies in which only impacts on shoot C were considered.

***Ecosys* modeled a functional equilibrium between roots and shoots which maintained a balance between CO_2 fixation and nutrient uptake (like N) (Grant 1993). Thus, as grazing caused reductions in both above- and below-ground biomass, grazing probably has to be adjusted and likely decreased over time to avoid important plant carbon stock reductions which will reduce the animal production and farmer income. Less total plant biomass production means that plant residues incorporated into the soil also will be reduced, and that in the long term will reduce SOC.** However this has to be evaluated through longer field grazing research or by simulation. The next chapter of this thesis will address the grazing effect on net ecosystem productivity through modelling.

The modeled results showed that total plant carbon stock was negatively affected by wild ungulates grazing at moderate intensity, which is in agreement with measured experimental values, and supports our hypothesis of reductions in plant carbon stock because of grazing. So, if this grazing intensity is maintained without change, over time the total plant carbon stock would continue decreasing or would stabilize at lower levels. Under this condition, the net biome productivity of the ecosystem will determine if the applied grazing could affect in some way ecosystem stability over time. An ecosystem carbon balance can tell us how the ecosystem is evolving with the applied treatment or management; this will be examined in the next chapter of this thesis.

Based on the fact that *ecosys* reproduced field conditions with similar results that those coming from experimental fields, with confidence we can use *ecosys* to do simulation in semiarid grassland ecosystems.

5. Conclusions

According to the modeled results, it can be concluded that:

***Ecosys* simulated above and below plant biomass that was within the uncertainly of field measurements carried out in Kinsella Ranch experimental field,** and from reported results from scientific literature that came from similar conditions.

***Ecosys* simulated a clear topographic effect on plant carbon stock which increased down slope from U to M to L.** This increase was caused by better soil properties and more soil available water at M and at L. However, as was shown by previous measured values at Kinsella, modeled grass and shrub C stocks declined at L due to the competition with aspen trees for available soil resources and sunlight.

Grazing animals decreased the measured and modeled above ground plant carbon stock compared with those in ungrazed exclosures. This reduction was not uniform because grazing intensity was not the same at all topographic locations. This is a clear indication that plant response to grazing depend on the interaction of factors in which soil properties linked with topography and grazing intensity define the growth rate after grazing.

Based on the fact that the evaluated grazing intensity reduced root carbon stock but without statistical significance as shown by measured values, it should be thought that continuing the grazing of this mix of wild animals at moderate intensity should not cause negative effects on this ecosystem over time. However a longer period of evaluation is required to know for sure what should be the effect of grazing in the long term on this ecosystem.

Finally, due to the limited availability of field experiment data related with topographic effect on plant growth in semiarid grasslands, there is a need to generate this kind of data, which will allow not only better understanding of this ecosystem, also will allow to test modeled results.

Table 3-1. Grazing intensity of different plant species used by *ecosys* to simulate grazing in early and late summer of 2004 and 2005.

Year	Grasses		Shrubs		Aspen[2]		Total Grazing Intensity[3]	Total Consumption[4]
	U,M	L	U,M	L	U,M	L		
	Animal weight $\mathrm{g\ m^{-2}}$							$\mathrm{g\ C\ m^{-2}}$ $\mathrm{45\ d^{-1}}$
Early summer (from June 1st to July 15th)								
2004	16.9	13.2	6.5	8.5	0	2.2	23.4	11.8
2005	25.3	18.9	9.8	13.5	0	2.6	35.1	17.8
Late summer (from September 1st to October 15th)								
2004	19.8	16.8	3.6	4.4	0	2.2	23.4	11.8
2005	29.7	25.9	5.4	6.6	0	2.6	35.1	17.8

[1] based on observations of grazing by bison, elk and deer from Didkowsky (2006)

[2] Located only at lower topographic position.

[3] Total animal live weights: 234 $\mathrm{kg\ ha^{-1}}$ in 2004 and 351 $\mathrm{kg\ ha^{-1}}$ in 2005,

[4] These numbers represent the animal consumption: 2.5% of body weight as dry matter and expressed as carbon in each square meter during a 45-day grazing period.

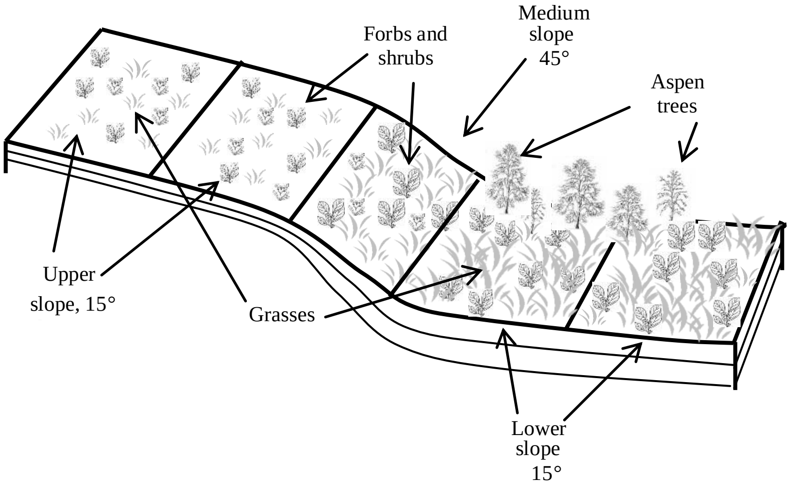

Figure 3-1A. Topography and plant distribution across the field transect modeled with *ecosys*

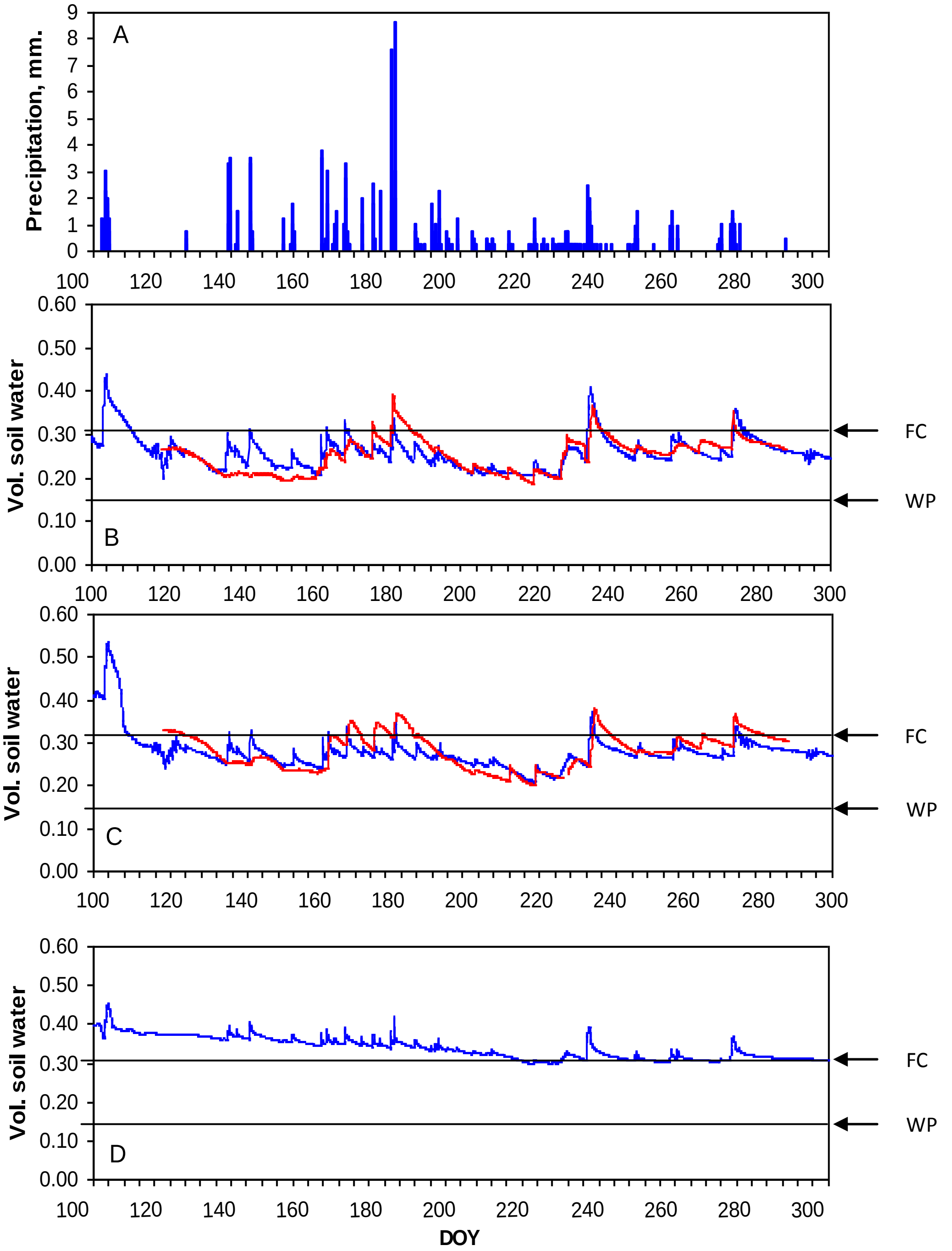

Figure 3-1. Precipitation (A), modeled (blue line) and measured (red line) volumetric soil water at 0.05 m depth at upper (B), middle (C), and lower (D) topographic locations during the growing season of 2005. Central Alberta, Canada.

DOY: day of the year; FC: field capacity, WP: wilting point

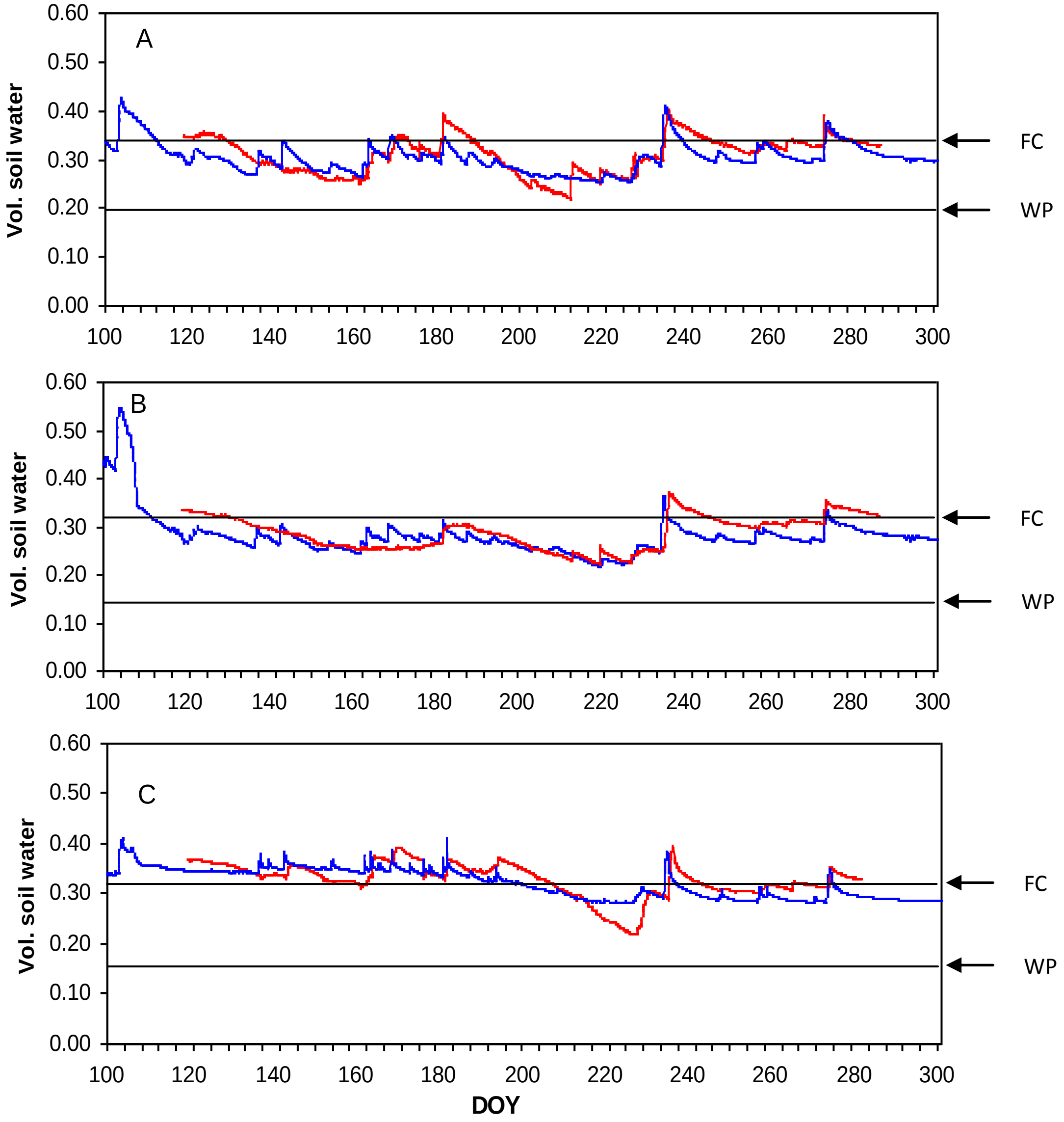

Figure 3-2. Modeled (blue line) and measured (red line) volumetric soil water at 0.15 m depth at upper (A), middle (B), and lower (C) topographic locations during the growing season of 2005. Central Alberta, Canada.

DOY: day of the year; FC: field capacity, WP: wilting point

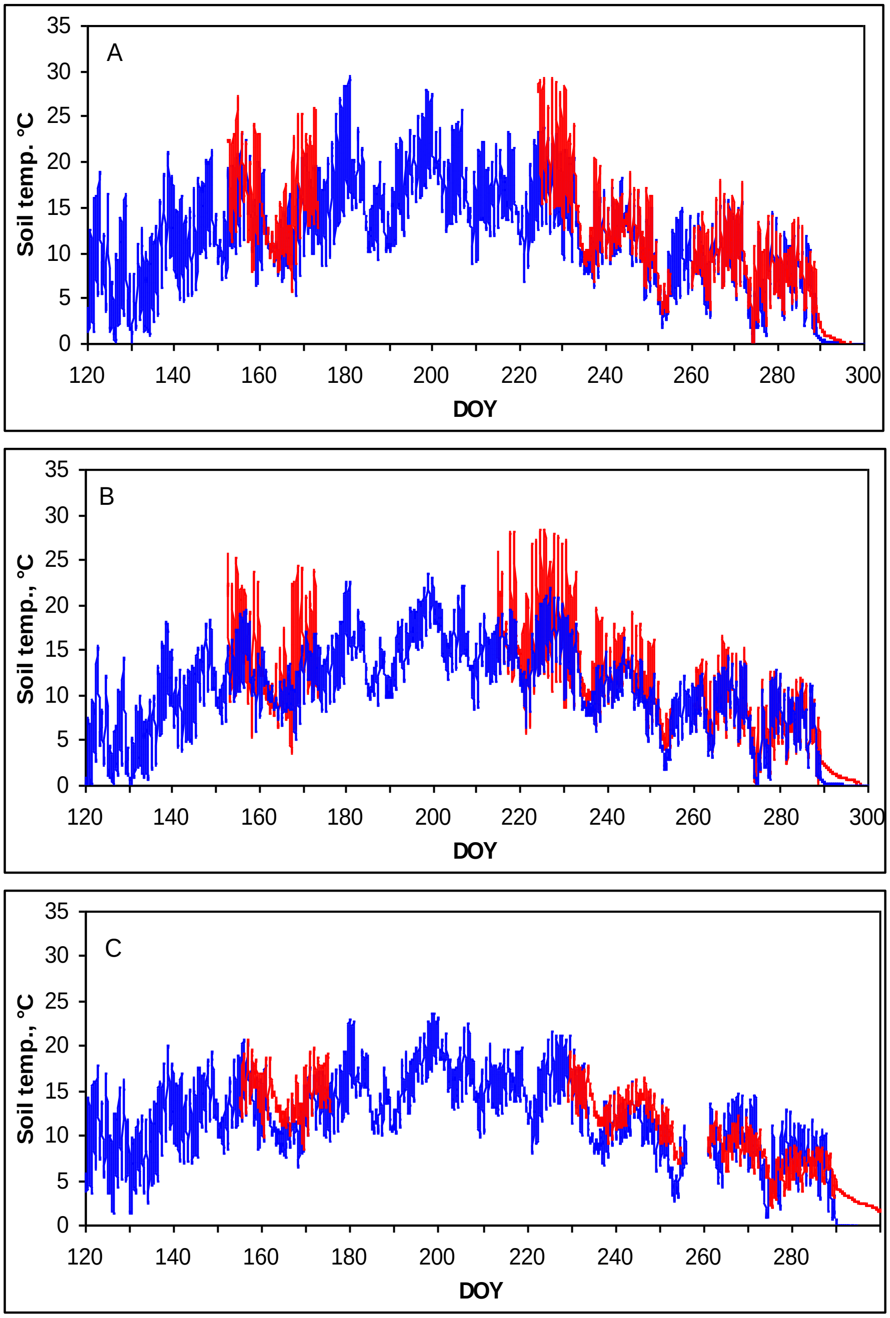

Figure 3-3. Modeled (blue line) and measured (red line) soil temperature at 0.05 m depth at upper (A), middle (B), and lower (C) topographic locations during the growing season of 2004. Central Alberta, Canada.

DOY: day of the year

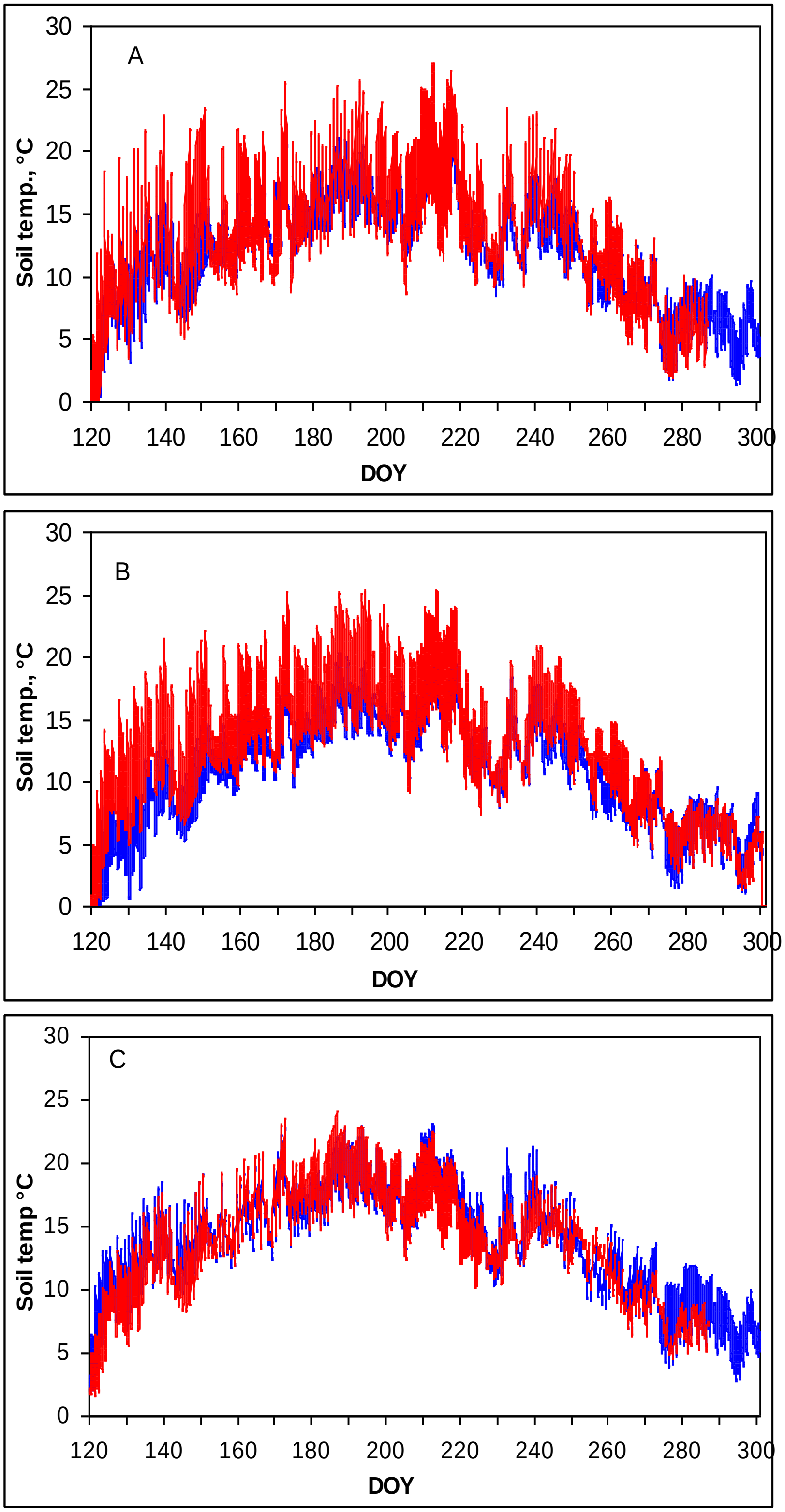

Figure 3-4. Modeled (blue line) and measured (red line) soil temperature at 0.05 m depth at upper (A), middle (B), and lower (C) topographic locations during the growing season of 2005. Central Alberta, Canada.

DOY: day of the year

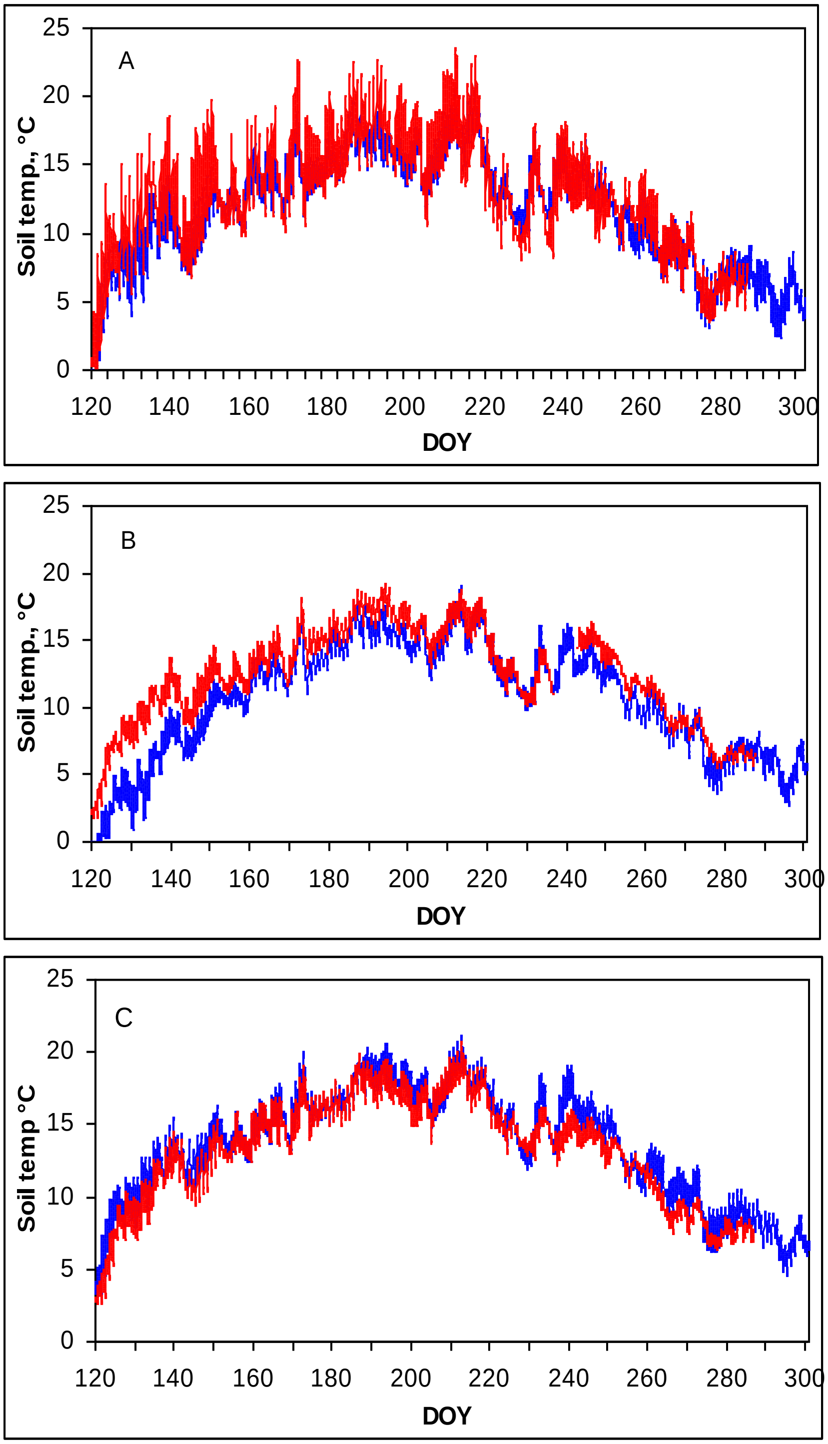

Figure 3-5. Modeled (blue line) and measured (red line) hourly soil temperature at 0.15 m depth at upper (A), middle (B), and lower (C) topographic locations during the growing season of 2005. Central Alberta, Canada.

DOY: day of the year

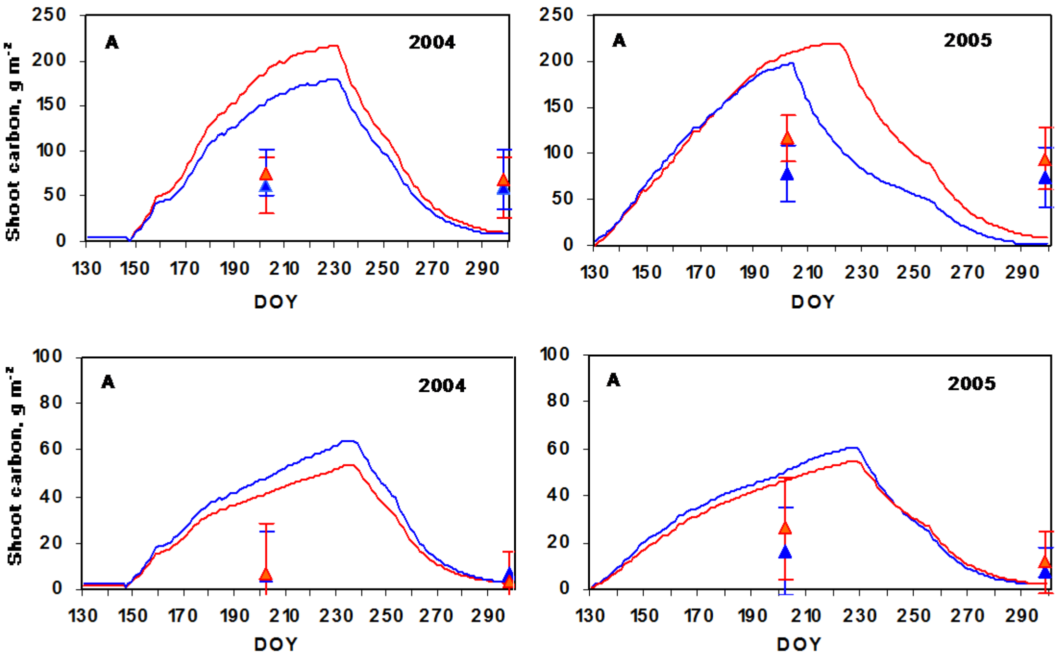

Figure 3-6. Modeled (lines) and measured (dots) ungrazed (red) and grazed (blue) live shoot carbon, g m^{-2}, of A, B) grasses and C, D) shrubs at middle topographic location during the growing season of 2004 and 2005. Central Alberta, Canada.

Measured data come from Haddow unpublished data

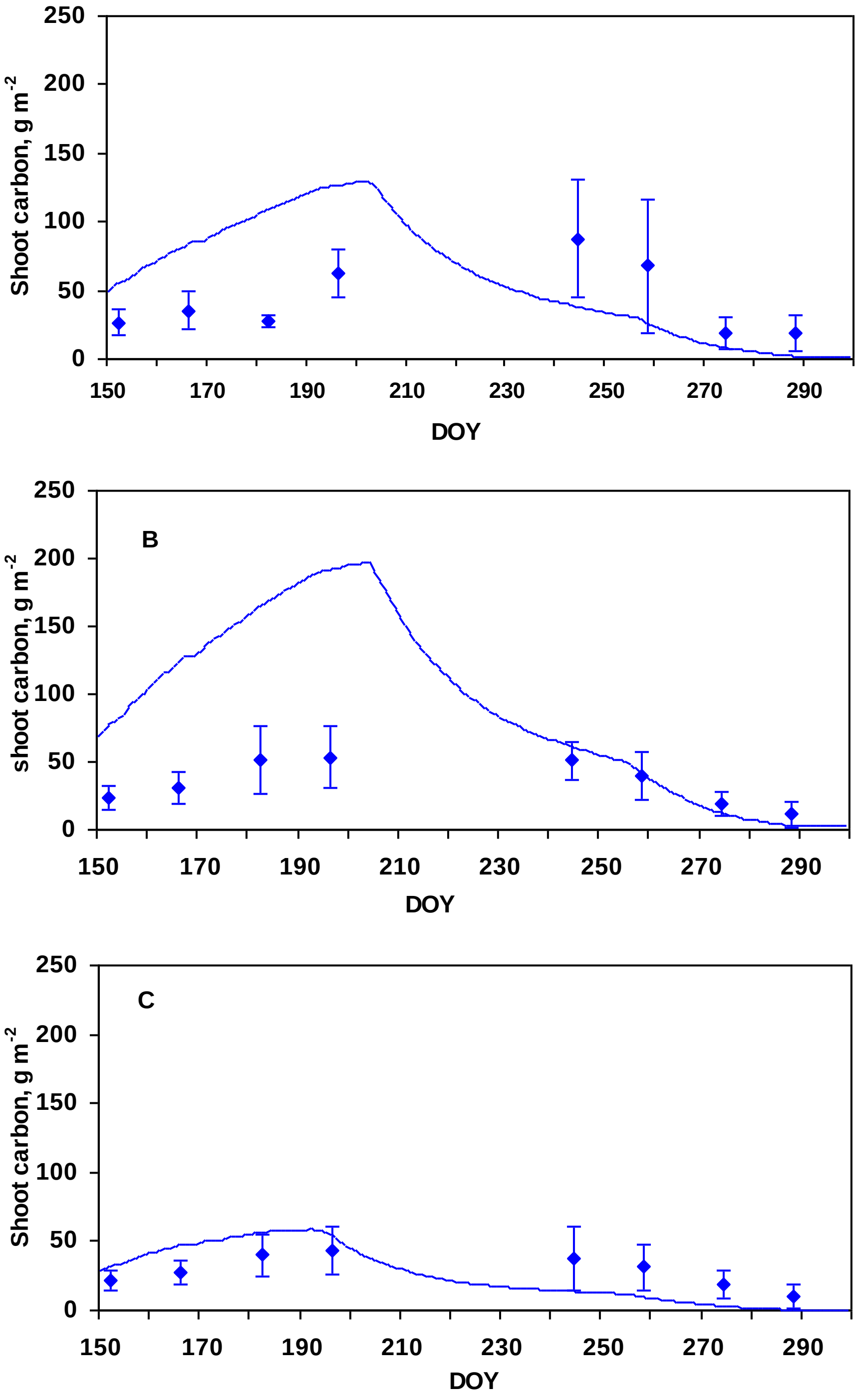

Figure 3- 7. Modeled (lines) and measured (dots) above ground grazed live shoot grass carbon, g m^{-2}, during 2005 at upper (A), middle (B), and lower (C) topographic locations. Central Alberta, Canada.

DOY: day of the year
Comparison data come from Dewitt (2008).

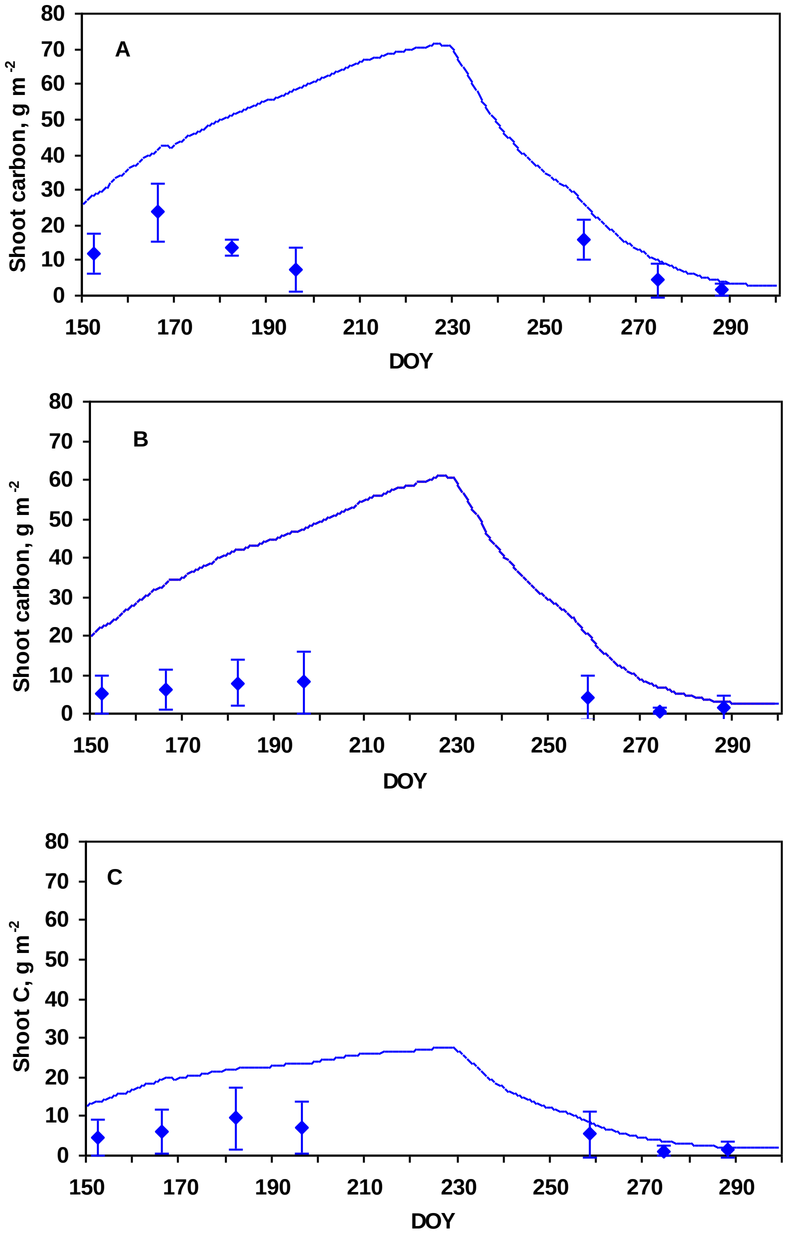

Figure 3- 8. Modeled (lines) and measured (dots) above ground grazed live shoot shrub carbon, g m^{-2}, during 2005 at A) upper, B) middle and C) lower topographic locations. Central Alberta, Canada.

DOY: day of the year
Comparison data come from Dewitt (2008)

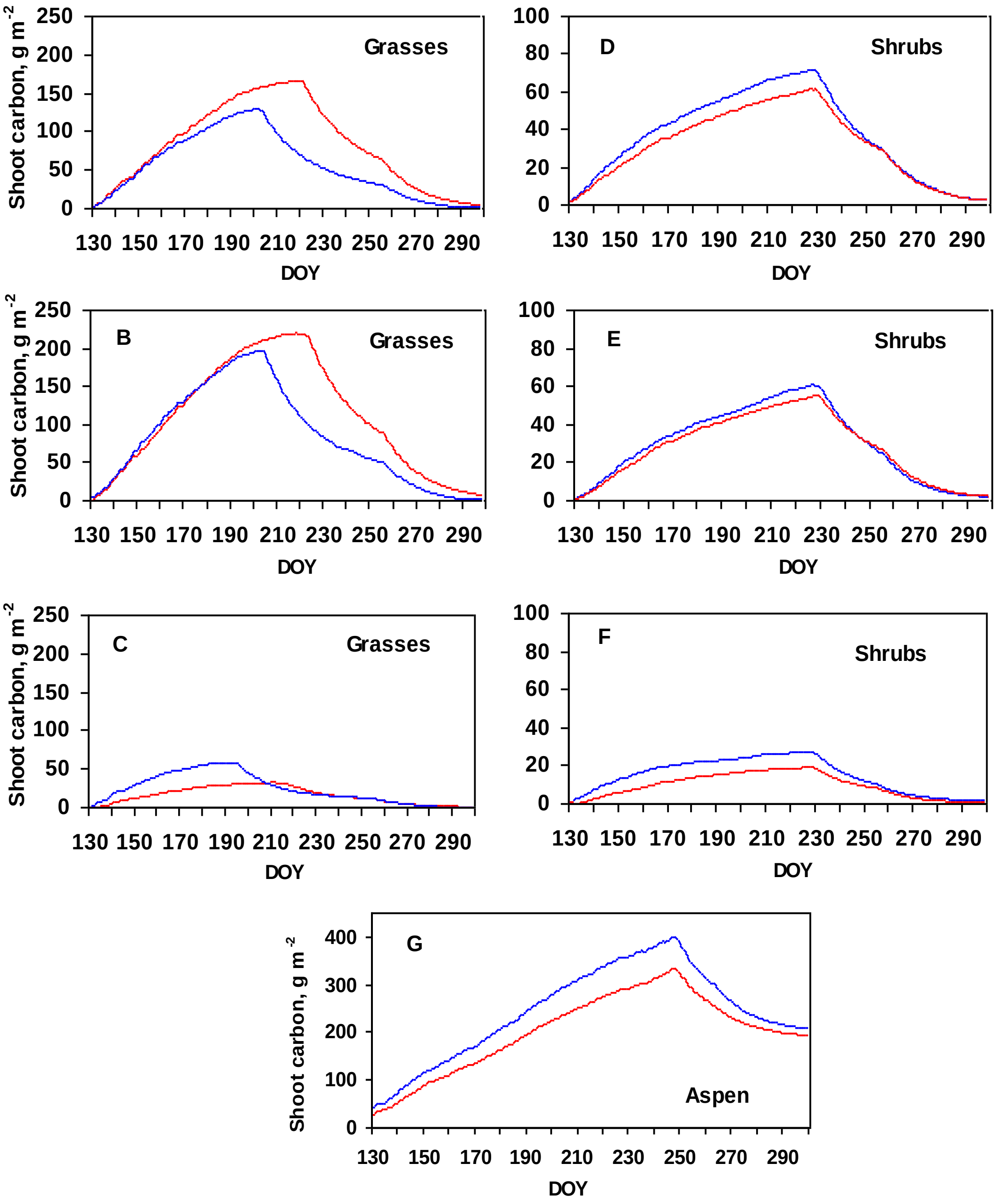

Figure 3-9. Modeled grass, shrubs and aspen live shoot carbon, g m^{-2}, under ungrazed (red) and grazed (blue) treatment according to upper (A, D), middle (B, E), and lower (C, F, G) topographic locations during the growing season of 2005. Central Alberta, Canada.

DOY: day of the year

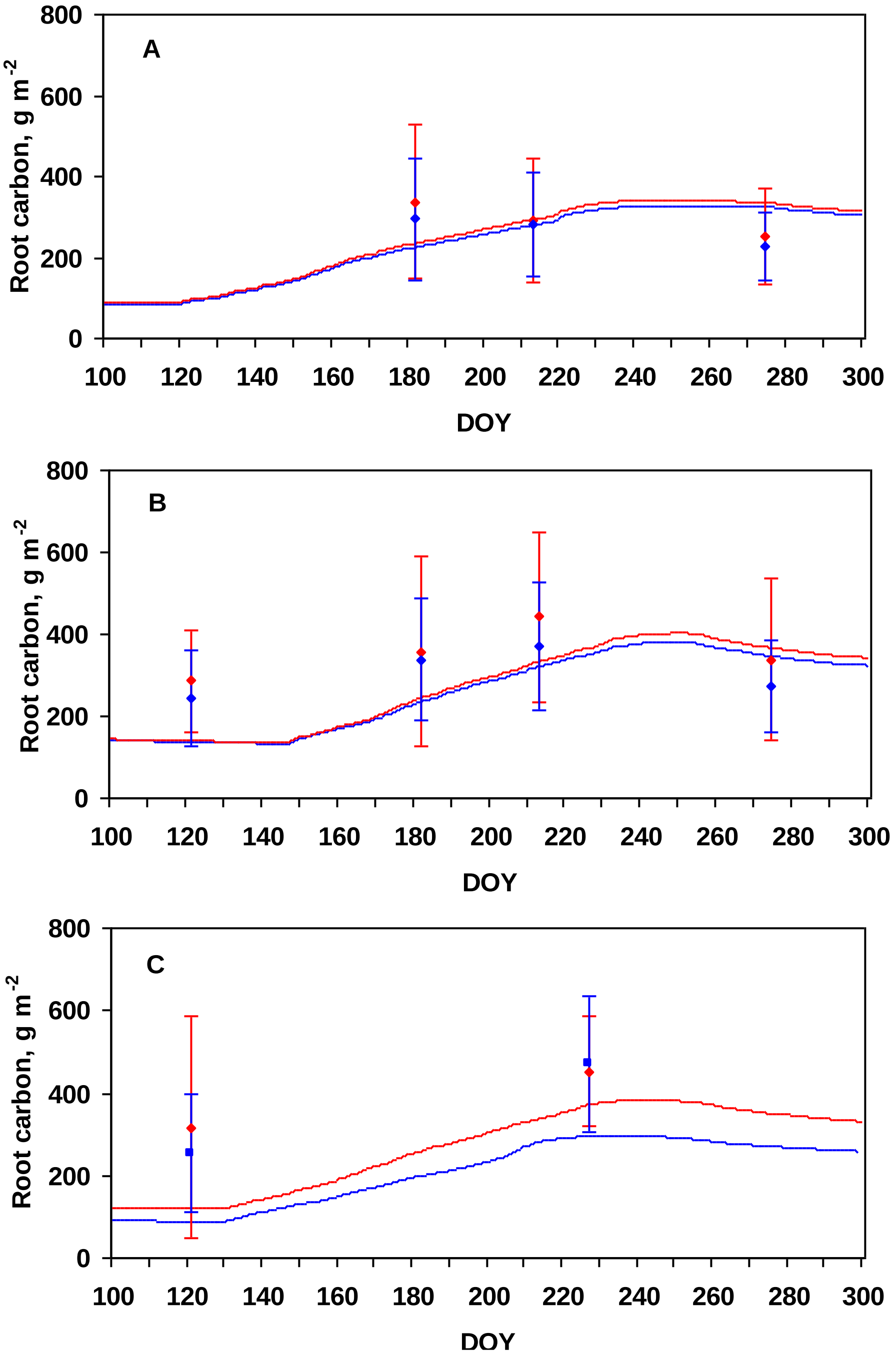

Figure 3-10. Ungrazed (red) and grazed (blue) measured (dots) and modeled (lines) total live and dead root carbon, g m^{-2}, at middle slope during the growing season of 2003 (A), 2004 (B), and 2005 (C). Central Alberta, Canada.

Comparison data come from Cahill
DOY: day of the year

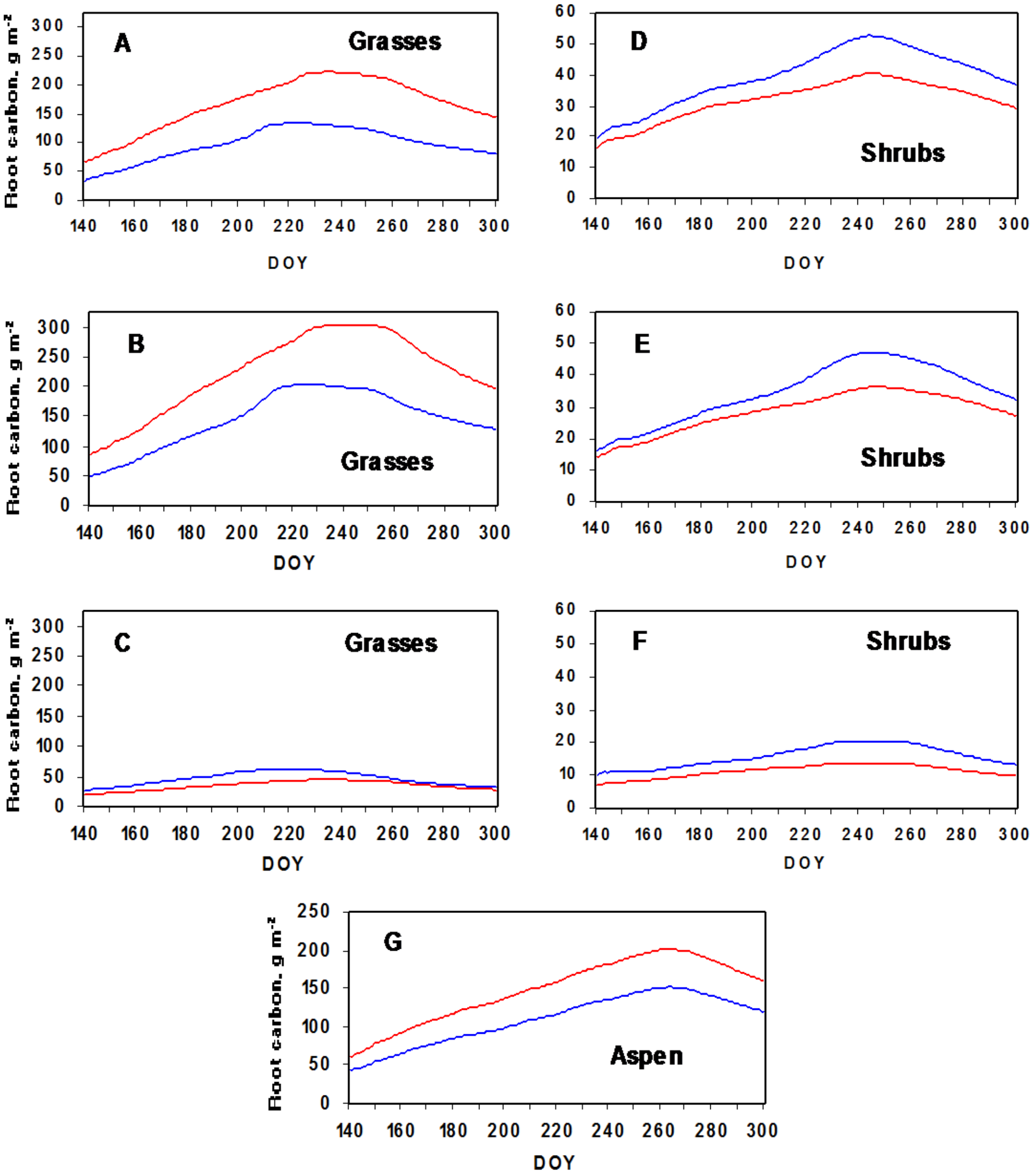

Figure 3-11. Modeled grass, shrubs, and aspen live root carbon, g m^{-2}, under grazed (blue lines) and ungrazed (red lines) treatments according to upper (A, D), middle (B, E) and lower (C, F, G) topographic locations during the growing season of 2005. Central Alberta, Canada.

DOY: day of the year

6. References

Agriculture and Agri-Food Canada. 2000. http://res2.agr.ca/Lethbridge/rep2000/rep0208b_e.htm

Alberta Agriculture, Food and Rural Development. 2005. http://www.salts-landtrust.org/conservingrangelands.html#top

Asamoah, S.; Bork, E.; Irving, B.; Price, M.; Hudson, R. 2004. Cattle herbage utilization patterns under high-density rotational grazing in the Aspen Parkland. Canadian Journal of Animal Science 83:541-550.

Asamoah, S.; Bork, E.; Irving, B.; Price, M.; Hudson, R. 2004b. Seasonal herbage dynamics on aspen parkland landscape in central Alberta. Canadian Journal of Animal Science 84:149-153.

Baker, T.R.; Phillips, O.L.; Malhi, Y.; Almeida, S.; Arroyo, L.; DiFiore, A.; Erwin, T.; Killeen, T.J.; Laurance, S.G.; Laurance, W.F.; Lewis, S.L.; Lloyd, J.; Monteagudo, A.; Neill, D.A.; Patino, S.; Pitman, N.C.A.; Silva, M.; Vasquez Martinez, R. 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biology 10:545-562.

Barger, N.; Ojima, D.; Belnap, J.; Shiping, W.; Yanfen, W.; Chen, Z. 2004. Changes in plant functional groups, litter quality, and soil carbon and nitrogen mineralization with sheep grazing in an inner Mongolian grasslands. Journal Range Management 57:613-619.

Barnes, B.V.; Zak, D.R.; Denton, S.R.; Spurr, S.H. 1998. Forest ecology. 4 ed. New York, Wiley. 774 p.

Baron, V.S.; Mapfumo, E.; Dick, A.C.; Naeth, M.A.; Okine, E.K.; Chanasyk, D.S. 2002. Grazing intensity impacts on pasture carbon and nitro flow. Journal Range Management 55:535-541.

Barrett, P.; Laidlawb, A.; Mayne, C. 2005. GrazeGro: a European herbage growth model to predict pasture production in perennial ryegrass swards for decision support. European Journal of Agronomy 23:37-56.

Biondini, M.E., Patton, B. D., Nyren, P. E. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. Ecological Applications, 8(2):469–479.

Bork, E.; Thomas, T.; Mcdougall, B. 2001. Herbage response to precipitation in central Alberta boreal grasslands. Journal of Range Management 54:243-248.

Brady, N.; Weil, R. 2002. The nature and properties of soils. Prentice Hall, USA. 949 p.

Bruce, J.P.; Frome, M.; Haites, E.; Janzen, H.; Lal, R.; Paustian, K. 1999. Carbon sequestration in soils. Journal of Soil and Water Conservation 54(1): 382-389.

Burke, I.C.; Lauenroth, W.K.; Vinton, M.A.; Hook, P.B.; Kelly, R.H.; Epstein, H.E.; Aguiar, M.R.; Robles, M.D.; Aguilera, M.O.; Murphy, K.L.; Gill, R.A. 1998. Plant-soil interactions in temperate grasslands. Biogeochemistry 42:121-43.

Burton, A.J.; Pregitzer, K.S.; Ruess, R.W.; Hendrick, R.L.; Allen, M.F. 1998. Root respiration in North American forests: effects of nitrogen concentration and temperature across biomes. Oecologia 131(4): 559-568.

Cahill, J., et al. 2007. Paper in preparation.

Cao, G.; Tang, Y.; Mo, W.; Wang, Y.; Li, Y.; Zhao, X. 2004. Grazing intensity alters soil respiration in an alpine meadow on the Tibetan plateau. Soil Biology and Biochemistry 36:237-243.

Chanasyk, D.S.; Naeth, M.A. 1995. Grazing impacts on bulk density and soil strength in the foothills fescue grasslands of Alberta, Canada. Canadian Journal of Soil Science 75(4): 551-557.

Chen, Y.; Lee, G.; Lee, P.; Oikawa, T. 2007. Model analysis of grazing effect on above-ground biomass and above-ground net primary production of a Mongolian grassland ecosystem. Journal of Hydrology 333:155-164.

Cohen, R.; Donnelly, J.; Moore, A.; Leech, F.; Bruynooghe, J.; Lardner, H. 1995. GrassGro – a computer decision support system for pasture and livestock management. American Society of Animal Science 46:376-379.

Conant, R.T.; Paustian, K.; Elliott, E.T. 2001. Grassland management and conversion intro grassland:effects on soil carbon. Ecological Applications 11:343-355.

Coomes, D.A.; Allen, R.B; Scott, N.A. Goulding, C.; Beets, P. 2002. Designing systems to monitor carbon stocks in forests and shrub lands. Forest Ecology and Management 164:89-108.

Coupea, M., Cahill, J. 2003. Effects of insects on primary production in temperate herbaceous communities: a meta-analysis. Ecological entomology 20:511-521.

Coupe, M., Stacey, J., Cahill, J. 2009. Limited effects of above-and belowground insect on community structure abd function in a species-rich grassland. Journal of Vegetation Science 20:121-129

Derner, J.D.; Boutton, T.W.; Briske, D.D. 2006. Grazing and ecosystem carbon storage in the North American Great Plains. Plant and Soil 280(1-2): 77-90.

DeWitt, P. 2008. Ungulate guild dynamics: mechanisms and consequences for aspen-parklands. MSc thesis, Biological Sciences, University of Alberta.

Diaz-Solis, H.; Kothmann, M.; Grant, W.; De Luna-Villarreal, R. 2006. Use of irrigated pastures in semi-arid grazinglands: A dynamic model for stocking rate decisions. Agricultural Systems 88:316-331.

Didkowsky, M.G. 2006. Scales of forage selection by ungulates in Aspen Parkland. Thesis MSc. University of Alberta. 86 p.

Donkor, N.; Gedir, J.; Hudson, R.; Bork, E.; Chanasyk, D.; Naeth, M. 2002. Impacts of grazing systems on soil compaction and pasture production in Alberta. Canadian Journal of Soil Science 82:1-8.

Donkor, N.; Hudson, R.; Bork, E. 2007. Simulation and quantification of pasture condition and animal performance on boreal grasslands in Alberta. Agricultural Systems. 93(1-3):229-251.

Dornbush, M.E.; Isenhart, T.M.; Raich, J.W. 2002. Quantifying fine-root decomposition: an alternative to buried litterbags. Ecology 83(11): 2985-2990.

Eneboe, E.; Sowell, B.; Heitszhmidt, R.; Karl, M.; Haferkamp, M. 2002. Droughts and grazing: iv. Blue grama and western wetgrass. Journal of Range Management 55:73-79.

Environment Canada 2006. http://www.ec.gc.ca/pdb/ghg/newsrelease2006_e.cfm

Farquhar, G.; Von Cammerer, S.; Berry, J. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 149:78-90.

Ferraro, D., Oesterheld, M. 2002. Effect of defoliation on grass growth. A quantitative review. Oikos. 98:125-133.

Frank, D.A.; Groffman, P.M. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone national park. Ecology 79(7):2229-2241.

Frank, D.A.; Kuns, M.; Guido, D. 2002. Consumer control of grassland plant production. Ecology 83(3):602–606.

Frank, D.A.; McNaughton, S.J. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oecologia 96(2): 157-161.

Georgiadis, N.J.; Ruess, R.W.; McNaughton, S.J.; Western, D. 1989. Ecological conditions that determine when grazing stimulate grass production. Oecologia 81(3):316-322.

Gill, R.; Jackson, R. 2000. Global patterns of root turnover for terrestrial and aquatic habitats. Global Change Biology 7:849-882.

Gillen, R., Eckroat, J.A., Mccollum III, T. 2000. Vegetation response to stocking rate in southern mixed-grass prairie. J. Range Manage. 53:471–478

Gordon, W.; Jackson, R. 2000. Nutrient concentration in fine roots. Ecology 81:275-280.

Grant, R. 1997. Changes in soil organic matter under different tillage and rotation: mathematical modeling in ECOSYS. Soil Science Society of America Journal 61(4):1159-1175.

Grant, R., Juma, N., Roberson, J., Izaurralde, R., McGill, W. 2001c. Long-term changes in soil carbon under different fertilizer, manure and rotation: testing the mathematical model ecosys with data from the Brenton plots. Soil Science Society of American Journal 65:205-214

Grant, R., Kimball, G., Wall, G. 2004. How elevated CO_2 affects water relations, water use and growth of irrigated sorghum: testing a model with results from a Free Air CO_2 enrichment (FACE) experiment. Agron. J. 96:1693-1705.

Grant, R.F. 1989. Test of a simple biochemical model for photosynthesis of maize and soybean leaves. Agric. For. Meteorol. 48: 59–74.

Grant, R.F. 1991. The distribution of water and nitrogen in the soil-crop system: a simulation study with validation from a winter wheat field trial. Fer Res. 27:199-214.

Grant, R.F. 1993. Simulation model of soil compaction and root growth. I. Model development. Plant Soil 150:1-14.

Grant, R.F. 1994a. Simulation of ecological controls on nitrification. Soil Biology & Biochemistry 26:305-315.

Grant, R.F. 1994b. Simulation of competition between barley (*Hordeum vulgare* L.) and wild oat (*Avena fatua* L.) under different managements and climates. Ecological Modelling 71:269–287.

Grant, R.F. 1998. Simulation in ecosys of root growth response to contrasting soil water and nitrogen. Ecological Modelling 107:237–264.

Grant, R.F. 2001. A review of the Canadian ecosystem model ecosys. In Modeling Carbon and Nitrogen Dynamics for Soil Management. Shaffer, M. Ed. Boca Raton, FL, CRC Press. p 175-264.

Grant, R.F. 2004. Modeling topographic effects on net ecosystem productivity of boreal black spruce forests. Tree Physiology 24:1-18.

Grant, R.F., B.A. Kimball, T.J. Brooks, Wall, G.W., Pinter, P.J., Hunsaker, D.J., Adamsen, F.J., Lamorte, R.L., Leavitt, S.W., Thompson, T.L., Matthias, A.D. 2001b. CO_2 effects on mass and energy exchange of wheat under different N fertilization: model theory and testing with a Free Air CO2 Enrichment (FACE) experiment. Agron. J. 93:638–649.

Grant, R.F., Black, T.A., Gaumont-Guay, D., Klujn, N., Barr, A.G., Morgenstern, Nesic, K.Z. 2006. Net ecosystem productivity of boreal aspen forests under drought and climate change: Mathematical modelling with Ecosys. Agricultural and Forest Meteorology 140:152–170.

Grant, R.F., Flanagan, L.B. 2007. Modelling stomatal and nonstomatal effects of water deficits on CO_2 fixation in a semi-arid grassland. J. Geophys. Res. 112, G03011, doi:10.1029/2006JG000302

Grant, R.F., Kimball, B.A., Brooks, T.J., Wall, G.W., Pinter Jr., P.J., Hunsaker, D.J., Adamsen, F.J., Lamorte, R.L., Leavitt, S.W., Thompson, T.L., Matthias, A.D., 2001. Modeling interactions among carbon dioxide, nitrogen, and climate on energy exchange of wheat in a free air carbon dioxide experiment. Agron. J. 93, 638–649.

Grant, R.F., R.L. Garcia, P.J. Pinter, D. Hunsaker, G.W. Wall, B.A. Kimball and R.L. LaMorte. 1995a. Interaction between atmospheric CO_2 concentration and water deficit on gas exchange and crop growth: Testing of ecosys with data from the Free Air CO_2 Enrichment (FACE) experiment. Global Change Biol. 1:443–454.

Grant, R.F., T.A. Black, G. den Hartog, J.A. Berry, S.T. Gower, H.H. Neumann, P.D. Blanken, P.C. Yang and C. Russell. 1999a. Diurnal and annual exchanges of mass and energy between an aspen- hazelnut forest and the atmosphere: testing the mathematical model ecosys with data from the BOREAS experiment. J. Geophys. Res. 104:27,699–27,717.

Grant, R.F.; Goulden, M.L.; Wofsy, S.C.; Berry, J.A. 2001. Carbon and energy exchange by a black spruce – moss ecosystem under changing climate: testing the mathematical model Ecosys with data from the BOREAS experiment. Journal of geophysical Research 106:22605-33621.

Grant, R.F.; Hesketh, J. 1992. Canopy structure of maize (*Zea mays*) at different populations: simulation and experimental verification. Biotronics 21:11-24.

Grant, R.F.; Juma, N.G.; McGill, W.B. 1993a. Simulation of carbon and nitrogen transformations in soils. I: Mineralization. Soil Biology and Biochemistry 25:1317–1329.

Grant, R.F.; Nyborg, M. Laidlaw, J. 1993b. Evolution of nitrous oxide from soil. I: Model development. Soil Science 156:259-265.

Grant, R.F.; Robertson, J.A. 1997. Phosphorus uptake by root systems: mathematical modelling in ecosys. Plant and Soil. 188:279-297.

Grant, R.F.; Rochette, P. 1994. Soil microbial respiration at different temperatures and water potentials: theory and mathematical modelling. Soil Science of Society of America Journal 58:1681–1690.

Grant, R.F.; Wall, G.W.; Kimball, B.A.; Frumau, K.F.A.; Pinter Jr, P.J.; Hunsaker, D.J.; Lamorte, R.L. 1999b. Crop water relations under different CO_2 and irrigation: testing of ecosys with the free air CO2 enrichment (FACE) experiment. Agricultural and Forest Meteorology 95(1):27-51.

Green, R.E.; Corey, R.B. 1971. Calculation of hydraulic conductivity: a further evaluation of some predictive methods. Soil Science Society of America Proceedings 35:3–8.

Grime, J. 1997. Biodiversity and ecosystem function: the debate deepens. Science 277:1260-1261.

Han, G., Hao, X., Zhao, M., Wang, M., Ellert, B.H., Willms, W., Wang, M. 2008. Effect of grazing intensity on carbon and nitrogen in soil and vegetation in a meadow steppe in Inner Mongolia. Agriculture, Ecosystems and Environment 125:21–32

Haddow, R. 2006. Thesis M Sc. In preparation

Hamzaa, M.A., Anderson, W.K.. 2005. Soil compaction in cropping systems. A review of the nature, causes and possible solutions. Soil & Tillage Research, 82:121–145.

Holechek, J.L.; Pieper, R.D.; Herbel, C.H. 2001. Range management: principles and practices. 4. ed. New Jersey, Prentice Hall. 587p.

Honeycutt, C.; Heil, R.; Cole, C. 1990. Climatic and topographic relations of three Great Plains soils: II: carbon, nitrogen and phosphorus. Soil Science of American Journal 54:476-483.

Howitt, R.; Findlayson, N.; Gowler, M.; Riddell, M.; McEwan, G. 1988. Soil survey of the County of Beaver, Alberta. N0. 47. Edmonton, Alberta, Alberta Research Council.

Hutchinson, T.F.; Boerner, R.E.J.; Iverson, L.R.; Sutherland, S.; Sutherland, E.K. 1999. Landscape patterns of understory composition and richness across a moisture and nitrogen mineralization gradient in Ohio (U.S.A.) Quercus forests. Plant Ecology 144(2): 177-189.

Irving, B.D.; Rutledge, P.L.; Bailey, A.W.; Naeth, M.A.; Chanasyk, D.S. 1995. Grass utilization and grazing distribution within intensively managed fields in Central Alberta. Journal of Range Management 48(4): 358-361.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D. 1996. A global analysis of root distributions for terrestrial biomes. Oecología 108: 389-411

Janzen, H. 2004. Carbon cycling in earth systems: a soil science perspective. Agriculture, Ecosystems and Environment 104:399-417.

Janzen, H.H.; Campbell, C.A.; Izaurralde, R.C.; Ellert, B.H.; Juma, N.; McGill, W.B.; Zentner, R.P. 1998. Management effects on soil C storage on the Canadian prairies. Soil & Tillage Research 47:181-195

Johnson, C.E.; Ruiz-Mendez, J.J.; Lawrence, G.B. 2000. Forest soil chemistry and terrain attributes in a Catskill watershed. Soil Science Society of America Journal 64:1804-1814.

Kachanoski, R.; Carter, M., 1999. Landscape position and soil redistribution under three soil types and land use practices in Prince Edward Island. Soil and Tillage Research 51(3-4):211-217.

Karlen, D.L.; Andrews, S.S. 2000. The soil quality concept: a tool for evaluating sustainability. DIAS-Report, Plant Production 38:15-26.

Kirkegaard, J.A., Troedson, R.J., So, H.B., Kushwaha, B.L. 1992. The effect of compaction on the growth of pigeonpea on clay soils. II. Mechanisms of crop response and season effects on an oxisol in a humid coastal environment. Soil Tillage Res. 24:129–147.

Kirkegaard, J.A., Troedson, R.J., So, H.B., Kushwaha, B.L., 1992. The effect of compaction on the growth of pigeonpea on clay soils. II. Mechanisms of crop response and season effects on an oxisol in a humid coastal environment. Soil Tillage Res. 24, 129–147.

Kuzyk, G.W.; Hudson, R.J. 2007. Animal-unit equivalence of bison, elk and mule deer in the aspen parkland of Alberta. In press.

Lal, R. 2002. Soil carbon dynamics in cropland and rangeland. Environmental Pollution 116 (3):353-362.

Lal, R. 2004. Agricultural activities and the global carbon cycle. Nutrient Cycling in Agroecosystems 70:103-116.

Landi, A.; Mermut, A.R.; Anderson, D.W. 2004. Carbon distribution in a hummocky landscape from Saskatchewan, Canada. Soil Science Society of America Journal 68(1):175-184.

Larcher, W. 2001. Physiological plant ecology. 4 ed. Springer-Verlag. 513 p.

Li, T.; Grant, R.F.; Flanang, L.B. 2004. Climate impact on net ecosystem productivity of a semiarid natural grassland: modeling and measurement. Agricultural and Forest Meteorology 126:99-116.

Lizama, H.M.; Suzuki, I. 1990. Kinetics of sulfur and pyrite oxidation by Thiobacillus thiooxidans. Competitive inhibition by increasing concentrations of cells. Canadian Journal of Microbiology 37:182–187.

Loeser, M.; Crews, T.; Sisk, T. 2004. Defoliation increased above-ground productivity in a semi-arid grassland. Journal of Range Management 57:442-447.

Mapfumo, E.; Chanasyk, D.S.; Baron, V.S.; Naeth, M.A. 2000. Grazing impacts on selected soil parameters under short-term forage sequences. Journal of Range Management 53(5): 466-470.

Mapfumo, E.; Chanasyk, D.S.; Naeth, M.A.; Baron, V.S. 1999. Compaction under grazing of annual and perennial forages. Canadian Journal Soil Science 79:191-199.

Mapfumo, E.; Naeth, M.A.; Baron, V.S.; Dick, A.C.; Chanasyk, D.S. 2002. Grazing impacts on litter and roots: perennial versus annual grasses. Journal Range Management 55:16-22.

Martin, W.K.E.; Timmer, V.R. 2006. Capturing spatial variability of soil and litter properties in a forest stand by landform segmentation procedures. Geoderma 132:169-181.

McGill, W.B.; Hunt, H.W.; Woodmansee, R.G.; Reuss, J.O. 1981. Phoenix, a model of the dynamics of carbon and nitrogen in grassland soils. In Terrestrial Nitrogen Cycles. Clark, F.E. Rosswall, T. Eds. Ecol. Bull. 33:49-115.

McIntosh, P.; Allen, R.; Scott, N. 1997. Effects of exclosure and management on biomass and soil nutrient pools in seasonally dry high country, New Zealand. Journal of Environment Management 51:169-186.

Meelis, P.; Wilson, S.D. 2002. Root dynamics and spatial pattern in prairie and forest. Ecology 83(5):1199-1203.

Moore, T.; Trofymow, J.; Taylor, B.; Prescott, C.; Camire, C.; Duschene, L.; Fyles, J.; Kozak, L.; Kranabetter, M.; Morrison, I.; Siltanen, M.; Smith, S.; Titus, B.; Visser, S.; Wein, R.; Zoltai, S. 1999. Litter decomposition rates in Canadian forests. Global Change Biology 5:75-82.

Morgan, R.; Quinton, J.; Smith, R., Govers, G., Poese, J., Auerswald, K., Chisci, G., Torri, D., Styczen, M. 1998. The European Soil Erosion Model (EUROSEM): a dynamic approach for predicting sediment transport from fields and small carchments. Earth Surface Processes and Landforms. 23:527-544.

Morley, F.H.W. 1981. Grazing animals. Amsterdam, Elsevier. 411 p.

Mueggler, W. 1965. Cattle distribution on steep slopes. Journal of Range Management, 18(5):255-257.

Mueggler, W. F. 1967. Response of mountain grassland vegetation to clipping in southwestern Montana. Ecology 48: 942–949.

Naeth, M.A. 1988. The impact of grazing on litter and hydrology in mixed prairie and fescue grassland ecosystems of Alberta. Thesis Ph.D. University of Alberta. 173 p.

Nelson, R.F.; Kimes, D.S.; Salas, W.A.; Routhier, M. 2000. Secondary forest age and tropical forest biomass estimation using thematic mapper imagery. Bioscience 50:419-431.

Norton, J.B.; Sandor, J.A.; White, C.S. 2003. Hillslope soils and organic matter dynamics within a Native American agroecosystem on the Colorado Plateau. Soil Science Society of America Journal 67(1): 225-234.

Oesterheld, M., McNaughton, J.S. 1991. Effect of stress and time for recovery on the amount of compensatory growth after grazing. Oecologia 85:305-313

Owensby, C.; Ham. J.; Knapp, A.; Auen, L. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO_2. Global Change Biology 5:497-506

Pennock, D.J.; Zebarth, B.J.; De Jong, E. 1987. Landform Classification and Soil Distribution in Hummocky Terrain, Saskatchewan, Canada. Geoderma 40:297-315.

Perez Corona, M.E.; Vazquez de Aldana, B.R.; Garcia Criado, B.; Garcia Ciudad, A.1998. Variations in semiarid grasslands. Journal of Range Management 51:570-576.

Pinchak, W.E.; Smith, M.A.; Hart, R.H.; Waggoner, J.W. 1991. Beef cattle distribution patterns on foot hill range. Journal of Range Management 44(3):267-275.

Presley, P., Christensen, P. 1997. Thermal conductivity measurements of particulate materials. Journal of geophysical research. 102:6535-6549.

Pucheta, E.; Bonamici, I.; Cabido, M.; Diaz, S. 2004. Below-ground biomass and productivity of a grazed site and a neighbouring ungrazed exclosure in a grassland in Central Argentina. Austral Ecology 29:201-208.

Reeder, J.; Schuman, G. 2002. Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands. Environmental Pollution 116:457-463.

Riedo, M.; Grub, A.; Rosset, M.; Fuhrer, J. 1998. A pasture simulation model for dry matter production and fluxes of carbon, nitrogen, water and energy. Ecological Modelling 105:141-183.

Rosef, L.; Bonesmo, H. 2005. Seasonal variation in productivity in semi natural grasslands. Acta Agriculturae Scandinavica. B-Soil and Plant 55:36-43.

Ruess, R.W. 1987. The role of large herbivores in nutrient cycling of tropical savannas. In: Walker BH (ed) Determinants of tropical savannas. IRL Press Limited, Oxford. pp 67-91.

Saxton, K.E.; Rawls, W.J. 2005. SPAW, Soil-Plant-Atmosphere-Water Field & Pond Hydrology. Version. 6.02.67. http://www.bsyse.wsu.edu/saxton

Scheffler, E.J. 1976. Aspen forest vegetation in a portion of the east central Alberta parkland. M.Sc. Thesis. University of Alberta. 160 p.

Schiborra, A., Gierus, M., Wei Wana, H., Fei Bai, Y., Taube, F. 2009. Short-term responses of a Stipa grandis/Leymus chinensis community to frequent defoliation in the semi-arid grasslands of Inner Mongolia, China. Agriculture, Ecosystems and Environment 132:82–90

Schimel, D.S.; Coleman, D.C.; Horton, K.A. 1985a. Soil organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. Geoderma 36:201–14.

Schimel, D.S.; Stillwell, M.A.; Woodmansee, R.G. 1985b. Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. Ecology 66:276-82.

Schuman, G.E.; Janzen, H.H.; Herrick, J.E. 2002. Soil carbon dynamics and potential carbon sequestration by rangelands. Environmental Pollution 116(3): 391-396.

Schuman, G.E.; Herrick, J.E.; Janzen, H.H. 2000. The Dynamics of soil carbon in rangelands. In Follet, R.F.; Kimble, J.M.; Lal, R. The potential of U.S. grazing lands to sequester carbon to mitigate the greenhouse effect. Boca Raton, Lewis. p. 267-290.

Schuman, G.E.; Reeder, J.D.; Manley, J.T.; Hart, R.H.; Manley, W.A. 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecological Applications 9(1):65-71.

Schwab, G.O.; Fangmeier, D.D.; Elliot, W.J. 1996. Soil and water management systems 4 ed. New York, Wiley. 371 p.

Shaffer, M.; Larson, W. 1987. NTRM, a soil-crop simulation model for nitrogen, tillage and crop-residue management. USDA Conservation Research Report 34-1. National Technical Information Service, Springfield, Virginia.

Sharma, M.; Luxmoore, R.; DeAngelis, R.; Ward, R.; Yeh, G. 1987. Subsurface water flow simulated for hillslope with spatially dependent soil hydraulic characteristics. Water Resource Research. 23(8):1523-1530.

Shen, W.; Wu, J.; Kemp, P.R.; Reynolds, J.F.; Grimm, N.B. 2005. Simulating the dynamics of primary productivity of a Sonoran ecosystem: Model parameterization and validation. Ecological Modeling 189(1-2):1-24.

Singer, M.J.; Ewing, S.A. 2000. Soil quality In: Summer, M. Ed. Handbook of Soil Sciences. Florida, Boca Raton. p. 271-298.

Sivakumar, M.V. 2007. Interactions between climate and desertification. Agricultural and Forest Meteorology 142:143–155.

Small, C.J.; McCarthy, B.C. 2005. Relationship of understory diversity to soil nitrogen, topographic variation, and stand age in an eastern oak forest, USA. Forest Ecology and Management 217(2-3):229-243.

Smit, A.; Kooijman, A. 2001. The impact of grazing on the input of organic matter and nutrients to the soil in a grass-encroached Scots pine forest. Forest, Ecology and Management 142:99-107.

Snyman, H.A. 2005. Rangeland degradation in a semi-arid South Africa I: influence on seasonal root distribution, root/shoot ratios and water-use efficiency. Journal of Arid Environments 60:457-481.

Somma, E.; Hopmans, J.; Clausniter, V. 1998. Transient three-dimensional modeling of soil water and solute transport with simultaneous root growth, root water and nutrient uptake. Plant and Soil 202:281-293.

Southern Alberta Land Trust Society 2006. Conserving rangelands. http://www.salts-landtrust.org/conservingrangelands.html#e

Stepniewski, W., Przywara, G., 1992. The influence of soil oxygen availability on yield and nutrient uptake (N,P,K,Ca,Mg,Na) by winter rye (Secale cereale). Plant Soil 143(2):267–274.

Strong, W.L. 1992. Ecoregions and ecodistricts of Alberta. Alberta. Forestry, Lands and Wildlife, Edmonton, AB Publication T/224. Vol. 1.

Tardieu, F., 1994. Growth and functioning of roots and of root systems subjected to soil compaction. Towards a system with multiple signalling. Soil Tillage Res. 30, 217–243.

Tate, K.; Dubley, D.; McDougald, N.; George, M. 2004. Effect of Canopo and grazing on soil bulk density. Journal of Range Management 57:411-417.

Taylor, S.A., Ashcroft, G.L. 1972. Physical edaphology. WH Freeman and Company, San Francisco, USA, pp. 533.

Teague, W.R., Foy, J. K. 2002. Validation of SPUR2.4 rangeland simulation model using a cow-calf field experiment. Agricultural Systems 74(2):287-302

Thornley, J.H.M. 1995. Shoot:root allocation with respect to C, N and P: an investigation and comparison of resistance and teleonomic models. Annals of Botany 75(4): 391-405

Tracol, Y., Mougin, E., Hiernaux, P., Jarlan, L. 2006. Testing a sahelian grassland functioning model against herbage mass measurements. Ecological Modelling 193:437–446.

Trimble, S. W., Mendel, A. C. 1995. The cow as a geomorphic agent. A critical review .Geomorphology 13:233-253.

Van der Krift, T.A.; Gioacchini, P.; Kuikman, P.J.; Berendse, F. 2001. Effects of high and low fertility plant species on dead root decomposition and nitrogen mineralization. Soil Biology and Biochemistry 33:2115-2124.

Van Soest, P. 1994. Nutritional ecology of the ruminant. Portland, Durham and Downey. 374 p.

Ventera, R.T.; Lovett, G.M.; Groffman, P.M.; Schwarz, P.A. 2003. Landscape patterns of net nitrification in a northern hardwood conifer forest. Soil Sci. Soc. Am. J. 67:527-539.

Wang, R., Ripley, E.A., 1997. Effects of grazing on a Leymus chinensis grassland on the Songnen plain of north-eastern China. J. Arid Environ. 36:307–318.

Wheeler, G.W. 1976. Some grassland and shrubland communities in the Parklands of Central Alberta. Thesis MSc. University of Alberta. 75 p.

Whitehead, D. 1995. Consumption, digestion and excretion of nitrogen by ruminant livestock. In Whitehead, D. Ed. Grassland nitrogen. Wallingford, Oxon, CAB International. p 59-81.

Willms, W.D.; McGinn, S.M.; Dormaar, J.F. 1993. Influence of litter on herbage production in the mixed prairie. Journal of Range Management 46:320-324.

Wright, A.; Hons, F.; Rouquette, F. 2004. Long-term management impacts on soil carbon and nitrogen dynamics of grazed bermudagrass pastures. Soil Biology and Biochemistry 36:1809-1816

Yimer, F.; Stig, L.; Abdu Abdelkadir. 2006. Soil organic carbon and total nitrogen stocks as affected by topographic aspect and vegetation community in the Bale mountains, Ethiopia., doi:10.1016/j.geoderma.2006.01.005.

Zhang, J., Romo, J. T. 1994. Defoliation of a northern wheatgrass community: Above- and belowground phytomass productivity. Journal of Range Management 47:279–294.

Chapter 4.0. Effect of topography and grazing on net biome productivity of a semiarid rangeland ecosystem

1. Introduction

Net ecosystem productivity (NEP), defined as the difference between gross primary productivity (GPP) and ecosystem respiration (R_e which is the sum of autotrophic R_a plus heterotrophic respiration R_h), is a way to summarize carbon fluxes in an ecosystem. The net biome productivity (NBP = NEP - removals from grazing, harvesting, fire or other disturbances) provides an indication whether the ecosystem is aggrading and hence a carbon sink (NBP > 0), or degrading and hence a carbon source (NBP < 0). Thus, NBP represents the carbon balance of uptake and losses between the ecosystem and atmosphere following the aggregation of all carbon fluxes (Lal 2004).

NBP in managed ecosystems gives us a complete carbon balance and reflects the effect of any land use practice or other disturbance. Consequently, different treatments can be compared to understand the effect of each one on ecosystem stability. NBP can be measured by meteorological and ecological techniques, or modeled (Nelson *et al*. 2000, Coomes *et al*. 2002, Baker *et al*. 2004).

The ability of an ecosystem to be a net carbon sink depends on the amount of carbon fixed through photosynthesis, part of which is incorporated into the soil from above and belowground litterfall. This leads to an increase in the soil carbon pool over time if the carbon emitted by R_h is smaller than that incorporated into the soil from litterfall (Law *et al*. 2001).

Under stable climatic conditions and without any important disturbance like fire or heavy grazing, NBP in water limited ecosystems like semiarid natural ecosystems varies over time depending on changes in annual precipitation (Bork *et al.* 2001). During years in which precipitation is above average, plants grow more (Smoliak 1986), and presumably leads to greater carbon fixation. Under this condition semiarid rangeland ecosystems usually are a carbon sink. Thus, depending on plant species composition and management, it has been reported that high soil moisture increases soil organic carbon (SOC) from 15 to 150 g C m^{-2} y^{-1} (Anderson 1977, Li *et al.* 2004, Thuille *et al*. 2000, Zhang *et al*. 2005, Ganjegunte *et al*. 2005, Grant and Flanagan 2007).

However, during dry years in which the precipitation is less than average, limited water is known to constrain plant growth (Bork *et al.* 2001, Smoliak 1986) and hence the carbon fixed. Under this condition the ecosystem usually becomes a carbon source. According to Zhang *et al*. (2005), who simulated and compared modeled results with measured data within a cool, semiarid grassland site near Lethbridge, Canada, this ecosystem could be a source of up to 17g C m^{-2} y^{-1}, and even greater source of carbon during drought years (Flanagan *et al*. 2002). Higher emissions (97g C m^{-2} y^{-1}) were reported by Novick *et al*. (2004) who worked under drought conditions to asses the NEP of a southeastern United States warm-temperate grassland ecosystem. Similarly, Li *et al*. (2004) and Grant and Flanagan (2007) found that a semiarid grassland near Lethbridge was a carbon source (33 and 100 g C m^{-2} y^{-1}) during dry years.

However, NEP may also be affected by spatial variation in plant productivity over the landscape, independent of climatic conditions. This variation results from uneven distribution of soil resources because of topography, which needs to be known to understand the carbon balance in the whole ecosystem.

1.1. Topography and net ecosystem productivity

Variation in NEP along any slope occurs because plant productivity depends on soil properties, which in turn varies over the landscape as a result of topography (Honeycutt *et al*. 1990, Martin and Timmer 2006). Milne in 1935 highlighted the influence of topography on soil characteristics, and more recently similar findings were pointed out by other researchers (Hutchitson *et al*. 1999, Johnson *et al*. 2000, Ventera *et al*. 2003, Landi *et al*. 2004).

Slope length and gradient affect water runoff that carries soil, minerals and plant material down hill depositing them at lower parts of the slope, increasing soil thickness. Increases of 40% (Martin and Timmer 2006), 56% (Landi *et al*. 2004), and 140% (Gregorich and Anderson 1985) in Ah soil horizon thickness have been associated with topography. As a result, bottom slope positions that have more nutrients and available water (Eneboe *et al*. 2002) also have high biomass production and greater SOC, which is reflected in greater NEP.

Therefore soil characteristics define plant growth, which is directly related with NEP and corresponding SOC. Thus, locations with higher SOC have been accumulating more carbon over time, which means that on average its NEP was larger (carbon sinks) than locations with lower SOC.

Greater plant biomass, up to 2.6 times higher in Central Alberta, Canada, and up to 1.8 times higher in Spain, were found at lower topographic locations of semiarid rangeland ecosystems compared with adjacent upslope positions (Asamoah *et al*. 2004, Perez *et al*. 1998). This gradient in plant productivity down slope over time is reflected in

SOC. As more litter is incorporated into the soil at lower topographic locations, these locations accumulate more soil carbon. In fact, when evaluating the carbon content (g m^{-2}) there was found between 42 and 139% more carbon in the A horizon at lower topographic positions of a semiarid environment compared with adjacent elevated positions (Burke *et al*. 1999, Schimel *et al*. 1985). Similarly, Pierson and Mulla (1990), Malo *et al*. (1974) and Gregorich and Anderson (1985) reported greater soil carbon at lower topographic locations compared with hills tops. In the present investigation SOC increased 66% from upper to lower slopes (see Table 1, Chapter II). This agrees with earlier statements by Cole (1986) and Houghton *et al*. (1999) who pointed out that when soils limit grassland productivity (as at uphill locations), they also limit the potential of grassland to capture and store carbon.

In summary, there is substantial variability in plant productivity over the landscape as a result of soil properties that change with topography, and which in turn is reflected in NEP. This variability should be characterized when proposing specific grazing management practices to avoid ecosystem degradation. This information is also needed to develop simulation models that will allow better understanding of ecosystem processes, which can then be used to improve predictions of grazing effects on ecosystem productivity and stability.

1.2. Grazing and net biome productivity

Depending on intensity, grazing could decrease plant biomass and thereby reduce litterfall (Donkor *et al*. 2004, Henderson *et al*. 2004). This in turn would reduce soil carbon, available soil nutrients and hence plant productivity and NEP. Therefore, if any applied ecosystem management reduces plant growth and associated plant productivity, that management is also likely to decrease NEP.

Reductions from 9% to 42% in above ground biomass (AGB) have been reported as a result of grazing in which animal consumption was between 40% and 60% of available foliage (Derner *et al*. 2006). A similar range of decline has been reported with stocking rates that were 35% below or 33% higher than recommended for specific grassland conditions at the High Plains of Wyoming (Schuman *et al*. 1999). Decreases of 10% to 28% in AGB because of grazing were also found by Biondini *et al*. (1998), Fahnestock and Detling (1999) and Ferraro and Oesterheld (2002).

In natural ecosystems there is a direct relationship between plant biomass and litterfall because biomass produced during the growing season is turned into litter except when coinciding with a disturbance event like fire or grazing. By reducing AGB, grazing reduces litterfall. Henderson *et al*. (2004) determined through a study of various grasslands in southern Alberta, Canada, that on average grazed paddocks had 65% less litterfall and 30% less above ground vegetation than their ungrazed counterparts. In Lacombe, Alberta, grazing at different intensities (from 1.5 to 4 animal unit months ha^{-1}) depending on climatic conditions reduced the amount of litterfall by 38% to 61% (Mapfumo *et al*. 2002). Similarly, Snyman (2005) in a semiarid rangeland found decreases in above ground litterfall from 38% to 76% when plants were clipped to simulate moderate or poor range condition as a result of grazing. The reduction in litter was associated with decreases of 30% and 70% in AGB which strongly reduced photosynthetic area and subsequent plant regrowth after grazing.

When plants have a reduced leaf area index after grazing, they cannot produce sufficient photosynthates to allow rapid and vigorous regrowth (Holecheck *et al*. 2001). Under this condition the plant remobilizes carbon from reserves to balance the deficit, but if grazing continues the plant is unable to completely restore reserves to previous levels. Thus, current plant growth and its future productivity are both typically reduced over time with grazing, and NBP is consequently reduced.

Reductions in plant biomass caused by grazing could be related to changes in nitrogen (N) cycling in the ecosystem. When grazed foliage has N content above 1.5%, grazing animals usually consume more N than they can utilize, and excrete the excess mainly through urine as urea. This N compound stimulates soil microbial activity and forage production. But if N content in grazed foliage is lower than 1.15%, animals excrete only limited N as non-digestible compounds in feces that mineralize slowly. This decreases microbial activity and soil N availability, reducing subsequent forage production (Pastor *et al*. 2006, Van Soest 1998) and eventually NBP.

Thus, grazing could result in reductions of NBP because the slowing of N cycling reduces the growth of plants with high digestibility instead giving rise to more resistant, slower growing and grazing tolerant species that require less N to grow and have lower forage quality for animal consumption. This further reduces site productivity, NBP and further decreases animal production.

However, grazing can also increase plant productivity and in doing so, raise NBP. Loeser *et al*. (2004) in semiarid grasslands of Arizona found that grazing 200 cow-calf pairs ha^{-1} for 8 hours per year raised the AGB by 20% compared with ungrazed plots. Similarly, Frank and McNaughton (1993) and Frank *et al*. (2002) measured the effect of large migratory herds of elk and bison (these studies did not define the stocking rate) in Yellowstone National Park, and found that grazing increased the ABG from 20% to 48%. These increases in biomass could be explained by an increase in photosynthetic efficiency. The remaining ungrazed leaves that were shaded or partially shaded before grazing had large intercellular spaces. In those leaves beneath the stomata there was a large substomatal cavity which reduced mesophyll resistance to CO_2 diffusion (Larcher 2003) and increased the amount of CO_2 fixed. Additionally, grazed plants tended to keep their leaves longer (Schuman *et al.* 2000), which increased plant biomass because a longer life span of leaves meant they photosynthesized longer and produced more photosyntates which promoted plant biomass accumulations.

1.3. Grazing and soil carbon

SOC is recognized as a key parameter closely related with soil fertility, and is directly linked with many soil properties like porosity, water holding capacity, nutrient availability, and structure (Karlen and Andrews 2000, Singer and Ewing 2000). Therefore, as SOC depends on litterfall that comes from plant biomass, and plant growth depends on soil fertility, which is determined by organic matter and associated litterfall, if there is a decrease in plant growth because of grazing, there will also be a reduction of litterfall that will reduce SOC over time.

In accordance with this, Liebig *et al.* (2006) found that in moderately (2.6 ha steer^{-1}) and heavily (0.9 ha steer^{-1}) grazed grassland in the Northern Great Plains there was reduced the carbon content to a depth of 1 m by 10g m^{-2} y^{-1} after 87 years. According to Frank *et al.* (1995) SOC was reduced by 32g C m^{-2} y^{-1} in the top meter after 75 years of moderate grazing (2.6 ha steer^{-1}) in the Northern Great Plains. More recently, Derner *et al.* (2006) found that when cattle removed 40–60% of AGB they also reduced the SOC in the upper 0.3m of soil by 23 and 4g C m^{-2} y^{-1} in mid grass and tall grass communities, respectively.

However, depending on grazing intensity there could also be an increase of SOC. Derner *et al.* (2006) found that grazing increased SOC in a short grass community by 14g C m^{-2} y^{-1}. This increase was the result of an increase of blue grama that has a high root:shoot ratio, and therefore incorporated a large amount of carbon into the soil. Reeder *et al.* (2004) also reported an increase of 13g C m^{-2} y^{-1} in SOC content (up to 0.9m depth) when evaluating the effect of heavy stocking (i.e. from 60% to 75% of available foliage was utilized) in a short grass steppe of northeastern Colorado. Similar increases in SOC with grazing have also been reported by Ganjegunte *et al*. (2005), Smoliak *et al*. (1972), Dormaar *et al*. (1997), and Reeder and Schuman (2002).

Changes in plant species over time because of grazing explain part of the previous results. Increases in C_4 grass species, like *B. gracilis*, accounted for soil carbon gains in many of those studies because this grass species allocate from 75% to 98% of their root biomass to the 0 to 30-cm depth of the soil profile (Reeder *et al.* 2001). With its high root:shoot ratio, species such as *B. gracilis* transfer more of its photosynthate C to belowground biomass than do other grass species (Reeder *et al*. 2004). Therefore, the amount and distribution of SOC in grasslands depends on plant species composition, which in turn, could be strongly modified by grazing. The decomposability and root system distribution patterns of different plant species comprising the vegetation community will also influence SOC because root residues are the primary source of organic matter contribution to the soil.

However, there are also studies showing no change in SOC as result of grazing (Milchunas and Lauenroth 1993, McIntosh *et al*. 1997, Henderson *et al*. 2004). Differences in sampling procedures, physiological characteristics of grazed plants (C_3 vs. C_4), and differences in the plant species composition between locations could explain these apparent inconsistent results for grazing effect on SOC (Schuman *et al*. 1999).

1.4. Hypotheses for topographic and grazing effects on NEP

Based on this, the hypotheses of this research were: 1) **net ecosystem productivity (NEP) is greater at lower topographic locations because the soil available resources that arise (i.e. water accumulation with redistribution across the landscape) allows plants to grow better and contribute to greater NEP relative to upper positions**; 2) **grazing at moderate stocking rates decreases NEP at all topographic locations because animal consumption reduces above ground biomass and hence foliar area. This reduction in area causes a decrease in plant photosynthesis and hence growth, which in turn will reduce NEP and hence NBP**.

The hypotheses were tested by 1) using results from field research and a terrestrial ecosystem model to construct a carbon budget at different topographic locations under grazed and ungrazed conditions, and 2) comparing these budgets to determine if grazing of a mix of wild ungulates affects NEP along a topographic gradient.

2. Materials and Methods

2.1. Field experiment

This section briefly describes the experimental field condition that was simulated. Further details can be found in Dewitt (2009), Haddow (2007) and in previous chapters of this thesis.

2.1.1. Location and description of experimental conditions

The experimental field was located at the Kinsella Research Ranch, an experimental farm that belongs to the University of Alberta, located 160 km southeast of Edmonton (53° 01' 13.7" N, 111° 32' 42.1" W), within the Aspen Parkland ecoregion (Strong 1992), in Central Alberta, Canada. The annual mean temperature is 2°C, and the long-term mean annual precipitation is 428 mm (Environment Canada 2006).

The landform across the experimental farm is hummocky moraine (Howitt *et al.* 1988) with strong effects of topography on soils across the landscape. Soils in well-drained uplands are Dark Brown, Eluviated Black or Black Chernozems, while those in poorly drained lowlands are Gleysols (Wheeler 1976). Results of a soil survey for key soil properties according to topographic location can be seen in Table 1 of Chapter II.

The main plants present at the experimental site are described by Dewitt (2009). The main grasses present were *Festuca* and *Poa* spp, forbs and shrubs included *Symphoricarpos occidentalis*, *Achillea millefolium*, *Artemisia* spp, and aspen (*Populus* spp.) trees. In this location a topographic transect was established and divided into upper (U), middle (M), and lower (L) hill positions to study the effects of topography and grazing on NEP. Three groups of plants were distributed along the slope: grasses at all topographic locations, shrubs at M and L while aspen trees were present only at L.

2.1.2. Treatments and experimental designs

To assess the grazing effect of wild ungulates on plant productivity, AGB samples were taken from unfenced 0.1 m^2 plots located at the most representative area in the experimental field which was M. These plots were paired with those in exclosed areas (8x8 m) from which large ungulate grazing was removed and AGB samples were also collected (Haddow personal communication). Samples were collected during 2003, 2004 and 2005, from July 17th to July 26th. These samples, a mix of all live plant material from current year's growth, were oven-dried to get the dry weight.

Root samples were also collected from the two grazing treatments at M. Metal cylinders (0.05m diameter x 0.15m long) were used to harvest the roots, and the diameter of all roots in the core were taken. Root samples were collected three times in 2003 (June 30th, July 31th, September 30Th), four times during 2004 (01st of May, July, August, and October), and two times during 2005 (May 15th and August 15th). All roots were washed with cold water and oven-dried (Dr. Cahill, personal communication).

Plant dry matter (above and below ground) was transformed into carbon by using a factor of 0.45 (i.e. carbon was assumed to comprise 45% of all biomass, Grant 2001).

2.1.3. Grazing treatments

A mix of wild ungulates, bison (*Bison bison*), elk (*Cervus elaphus*) and deer (*Odocoileus hemionus*), grazed the experimental farm at a stocking rate of 1.57 animal unit months (AUM) ha^{-1} during 2004. This stocking rate was raised to 2.35 AUM ha^{-1} in 2005 by adding 1 bison and 1 elk.

There were two grazing periods of 45 days, the first from June 1st to July 15th, and the second from August 1st to October 15th. The proportion of plant consumption (Table 2, Chapter III) was estimated according to the grazed period (June or September) based on Didkowsky (2006). Daily dry matter consumed was estimated to be 2.5% of body mass (Morley 1981, Van Soest 1996).

Total consumption per grazing year, according to these inputs, in 2004 was 23.7g C m^{-2} y^{-1} (23.38g LW m^{-2} x 0.025g DM g LW^{-1} d^{-1} x 0.45g C g DM^{-1} x 90 d y^{-1}) from which 40% or 9.47g of C m^{-2} y^{-1} was removed as respired CO_2 and animal biomass. This consumption was assumed to be distributed across topographic positions according to the relative availability of biomass for grazing. Similarly in 2005 the total consumption was 36g C m^{-2} y^{-1} from which 40% (14.4g of C m^{-2} y^{-1}) was removed from the ecosystem.

2.2. Model theory

In this research *ecosys*, a comprehensive mathematical model for natural and managed terrestrial ecosystems was used because it has been successfully tested in ungrazed semiarid grassland ecosystems (Li *et al*. 2004, Grant and Flanagan 2007) like Kinsella, and demonstrated its capability of reproducing field experimental results. Also *ecosys* demonstrated its capability to implement hypotheses in which topographically driven water movement explained topographic effects on the productivity of boreal black spruce forests through topographic effects on soil O_2 and nutrient status (Grant 2004). In the current study, this model will be used to test similar hypotheses relative to topography and its impacts on NEP in semiarid grasslands.

The mathematical model *ecosys* (Grant 2001) uses basic principles to simulate vertical and lateral water redistribution within complex landscapes, and its effects on soil gas transfers (Grant and Roulet 2002, Grant and Pattey 2003) and plant primary productivity. The model uses the energetics of oxidation–reduction reactions to drive microbial activity. These energetics depend on the availability of electron acceptors with differing energy yields (O_2, NO^-_3, NO^-_2, N_2O or reduced C) (Grant 1998a, Grant and Pattey 1999), so that the effect of soil gas exchange on nutrient mineralization can be simulated (Grant *et al*. 2003). Nutrient uptake by plants in *ecosys* is driven by soil nutrient concentrations and root O_2 uptake (Grant and Robertson 1997), and is fully coupled to CO_2 fixation and plant growth. *Ecosys* is thus well suited to test hypotheses related with topographically driven productivity in different ecosystems. The successful evaluation of these hypotheses improves the estimates of NPP and NEP for semiarid grasslands with variable topography.

Ecosys integrates biological scales, both plant and microbial, from the organ to the community, and simulates the transport and transformation of heat, water, carbon, oxygen, nitrogen, phosphorus and ionic solutes through soil-plant-atmosphere systems with the atmosphere as the upper boundary and soil parental material as the lower boundary (Grant 2001). *Ecosys* has different options to introduce a full range of management practices that includes tillage, fertilization, irrigation, planting, harvesting, and grazing. Options are also provided to introduce changes in atmospheric boundary conditions. All these options allow *ecosys* to simulate a wide range of management conditions and disturbances.

Hypotheses and algorithms of *ecosys* relevant to the objectives of this study are described below; references related with the *ecosys* test can be seen in a previous chapter of this thesis.

2.3. Model description

2.3.1. Organic matter decomposition

Organic transformations in *ecosys* (A1 – A2) are based on four organic matter–microbe complexes: plant litterfall, animal manure, particulate organic matter, and humus, from which C, N, and P are released and transformed. Plant litterfall and animal manure are partitioned into carbohydrate, protein, cellulose, and lignin components based on results from proximate analyses (e.g. Ch. III), each of which has different vulnerability to their heterotrophic decomposers. Particulate organic matter and humus also have different vulnerability to their decomposers. The rate at which each component is decomposed is affected by temperature and water content of surface detritus and those of a spatially resolved soil profile (Grant and Rochette 1994). Thus, microbial biomass in *ecosys* is an active agent of organic matter transformation rather than a passive organic state as in most other ecosystem models.

Heterotrophic respiration (R_h in g C m^{-2} h^{-1}) is conducted by microbial biomass of each heterotrophic microbial functional type in each organic matter-microbial complexes of each soil layer consuming DOC according to Michaelis-Menten kinetics (Km_{DOC} = 36 g C m^{-3}). R_h is driven by maximum specific rate R'_h (= 0.15 g g^{-1} h^{-1} at 25°C) and constrained by DOC concentration ([DOC] = DOC/θ in g C m^{-3}), and by microbial N and P concentrations CN and CP with respect to maximum values C'_N and C'_P.

Along a modelled topographic gradient in which plant productivity is influenced by soil conditions that change down slope, there are differences in the amount of litterfall incorporated into the soil. This creates differences in the rates of modelled heterotrophic activity and hence in the amounts of available nutrients that are released through mineralization of organic matter, which in turn affects modelled plant productivity.

2.3.2. Nutrient uptake

Nutrient uptake is calculated for each plant species by solving for the aqueous concentrations at both root and mycorrhizal surfaces in each rooted soil layer at which radial convective–dispersive transport from the soil solution equals active uptake by these surfaces. These concentrations change in the model when soluble nutrients like N move downslope, thereby affecting uptake and hence plant productivity.

Active uptake is calculated from length densities and surface areas (Itoh and Barber 1983) given by a root and mycorrhizal growth submodel (Grant 1998b, Grant and Robertson 1997). The products of N and P uptake are added to storage pools, and from there they can be mobilized through growth respiration to form new plant biomass. Modeling of plant N and P uptake (A11a – A11f) is described in more detail elsewhere (Grant 1998b, Grant and Robertson 1997).

2.3.3. Water transport

2.3.3.1. Surface flow

Surface flow is calculated as the product of runoff velocity, depth of mobile surface water and the width of flow paths in each landscape position. Changes in the depth of surface water arise from differences in surface flows among adjacent landscape positions. Runoff velocity is calculated from the hydraulic radius, considering microtopographic roughness and particle size (D1 – D4) according to Morgan *et al*. (1998b). The depth of mobile surface water is the positive difference between depth of surface water and the maximum depth of surface storage, calculated from microtopographic roughness and slope according to Shaffer and Larson (1987). The amount of surface water arises from the difference between rates of precipitation and infiltration (described in the next paragraph). The calculation of hydraulic radius assumes overland flow through triangular channels (Schwab *et al.* 1996). The slopes are the elevational gradients of water surfaces calculated from the sum of ground surface elevation, determined by topography, and depth of surface water, allowing surface water to be transported downhill. This implements the kinematic wave theory of overland water flow in which changes in horizontal flow plus changes in surface water depth equal the difference between rainfall and infiltration (D2).

2.3.3.2. Subsurface flow

Water fluxes are the product of hydraulic conductance and water potential differences along topographic locations. Water potentials are the sum of matric, osmotic (multiplied by a reflection coefficient) and gravitational components determined by topographic position. Conductance is calculated from the geometric means of the hydraulic conductivities (Green and Corey 1971) of adjacent landscape positions, unless water potential of one of the positions exceeds its air entry potential. In these cases conductance is calculated from hydraulic conductivity of the saturated position only, and water potential of the unsaturated position is calculated from a water content that excludes water added while water potential of the first position is greater than entry potential, thereby simulating a wetting front. The water movement between adjacent locations therefore alternates between Richard’s and Green–Ampt flow (D5) which depend on water potential vs. air entry potential in each location. The wet front in a topographic gradient may advance down slope and transfer soil moisture to lower locations. This transfer may influence plant productivity in environments in which soil available water is critical for plant growth.

Water may also move through macropores driven by gravitational gradients and conductance calculated from Poiseuille–Hagen theory using set numbers and radii of macropore channels. This water movement also influences soil available water for plant uptake and thus, has a direct link with plant growth. These water movements also drive nutrient transport, and hence plant nutrient uptake as described in Sec. 2.3.2.

2.3.4. Gross primary productivity

Carbon dioxide fixation is calculated in *ecosys* from coupled algorithms for carboxylation and diffusion. Carboxylation rates are driven by absorbed irradiance, canopy temperature, and atmospheric CO_2 concentration. Diffusion rates are driven by CO_2 concentration differences between the atmosphere and mesophyll, and constrained by stomatal resistance (C1).

Maximum carboxylation rates are determined by specific activities and surficial concentrations of rubisco and chlorophyll, which are determined by N and P uptake and assimilation during leaf growth (Grant 2001). Carboxylation rate is used to calculate the leaf stomatal resistance required to maintain a fixed gradient between CO_2 concentration in the canopy boundary layer and that in the mesophyll.

Stomatal resistance also rises exponentially with declining canopy turgor, which may reduce diffusion and hence carboxylation. Canopy turgor is calculated in a scheme for canopy water potential in which root water uptake is equilibrated with canopy transpiration and changes in plant water storage (Grant 2001). Root water uptake is governed by water potential gradients and hydraulic resistances in the soil and roots, calculated from soil hydraulic conductivities and root length densities (Grant 1998b), both of which may be affected by changes in soil water content with topographic position. Canopy transpiration is calculated from air–canopy vapor pressure differences, and from canopy resistances. Turgor-limited stomatal resistance is used to calculate a mesophyll CO_2 concentration for each leaf surface at which rates of diffusion and carboxylation are equal.

2.3.5. Autotrophic respiration and litterfall

Autotrophic respiration (R_a) is driven by first-order oxidation of non-structural carbon that comes from GPP, depending on temperature in shoots, and also on oxygen uptake in roots as controlled by soil water content (Grant *et al*. 1999). R_a is used for maintenance (R_m) and growth (R_g) respiration. If oxidation of non-structural carbon is less than R_m, the difference will be taken from remobilizable carbon in leaves and roots, causing senescence and litterfall (C2, C4). Carbon oxidized in excess of R_m is used for growth respiration (Grant *et al*. 1999), which drives the growth of new biomass. Net primary productivity (NPP) is the difference between GPP (2.4.4) and R_a.

2.4. Model experiment

2.4.1. Model initialization

A topographic transect with variable topography and with the typical communities of plants that grow at upper (U), mid (M) and lower (L) topographic locations of Kinsella Ranch was simulated with *ecosys* (see diagram 1, Chapter III). Based on field observations, the simulated transect had a slope of 15° at U, 45° at M, and 15° at L. The physical-chemical characteristics of the soil at each topographic location used to initialize the model were obtained from a topographic soil survey carried out in September 2003 at Kinsella (Table 1, Chapter II). Field capacity, wilting point, and saturated hydraulic conductivity used in the model for each soil were set by using the soil physical properties from the soil survey as input to the Soil-Plant-Air-Water (SPAW) hydrology software (ver. 6.02.67) (Saxton and Rawls 2005) (Table 1, Chapter II).

The model was initialized at all topographic locations with physiological properties of C_3 grasses and shrubs used in earlier studies (Grant 1998, 2004, 2006, 2008). Aspen trees were included only at L in the model, based on field observations. These groups of plants in the simulation were planted in May of the first year of the model run on a bare soil with initial densities of 100 seeds m^{-2} for grasses and 10 seeds m^{-2} for shrubs at all topographic locations. Aspen trees at L were planted with 0.2 seeds m^{-2}. All seeds were planted 0.025 m below the soil surface. These seed densities were chosen to approximate the plant densities observed at Kinsella Ranch experimental rangeland (See section 2.1 Chapter III).

2.4.2. Model Run

The model was then run under six repeating 9-year sequences of hourly meteorological data (solar radiation, air temperature, precipitation, humidity, and wind speed) recorded at Viking from 1996 to 2002, Holden from 2003 to 2004, and Kinsella in 2005, located 16, 36, and 1 km away respectively, from the experimental site. During the run, the model simulated interconnected grid cells along the topographic gradient on which the plants were distributed (see diagram 1, Chapter III). The influence of topography on water flow is described above in the model description section. During the run, aspen trees were thinned at an annual rate of 7% after the second year of growth to simulate natural mortality, with all thinned plant material including the woody parts left on the ground. Grazing was done exactly as was explained in chapter III of this thesis.

The atmospheric CO_2 concentration in the model was kept constant at 370 µmol mol^{-1} for the whole simulated period. The atmospheric N deposition occurred during model runs through N in precipitation (0.5 µmol mol^{-1}), and through adsorption (or volatilization) of NH_3 (atmospheric concentration 0.005 µmol mol^{-1}).

Grazing was modeled only during the last two years of the model run under weather data recorded during 2004 and 2005. Further details about this simulated grazing can be found in Chapter III, here there is only a brief description of it.

There were two grazing periods each year, the first from June 1st to July 15th, and the second from September 1st to October 15th, in 6.16 ha of grazed area with 1.57 and 2.35 AUM ha^{-1} during 2004 and 2005 respectively. The input to the model was given in g of animal live weight (LW) m^{-2} present during grazing. Thus in 2004 and in 2005 the inputs were 23.4 and 35.1g of LW m^{-2}, for each day in the two grazing periods. These inputs were multiplied by a specific grazing rate of 0.025 g DM per g LW per day, which was converted into carbon using a factor of 0.45. This daily consumption rate was applied to the plants at U, M and L during each day of the two grazing periods. This rate was multiplied by 90 (total grazing days) to obtain the annual consumption presented in tables 2 to 4.

From daily consumption in the model, 40% of C was removed from the ecosystem as animal weight, or respired as CO_2 or CH_4 (Whitehead 1995, Van Soest 1994, Baron *et al*. 2002). The remaining C was returned to the ecosystem as animal waste.

Animal consumption was distributed among plant types (grasses, shrubs, and aspen trees) in the model according to Didkowsky (2006) (see table 2, Chapter III) and the proportions of leaf, petiole and stem consumed were specified during each grazing period. Grazing in the model started at the uppermost canopy layer, and continued downward through successive canopy layers until the amount of plant material specified by the inputs for the daily grazing rate was reached. This modelled consumption was not evenly distributed over the landscape because topography influenced plant productivity and hence the grazing pattern (Pinchak *et al*. 1991, Irving *et al*. 1995, Asamoah *et al*.

2004b). *Ecosys* distributed grazing among locations within user-defined paddocks consisting of different landscape positions based on available forage, plant species, and grazing behaviour at each position during each day.

2.4.3 Model testing

To test *ecosys* results, modeled and measured ungrazed and grazed AGB at M were compared at peak of biomass of 2005 on day 202 of the year which represented the central day of the sampling period (from July 17th to 26th) from which AGB samples were taken by Haddow (personal communication). Similarly, modeled root biomass was compared to measured root biomass sampled on DOY's 182, 213, and 274 in 2003, DOY's 121, 182, 213, and 274 in 2004, and DOY's 121, and 227 during 2005. Thus, it is proposed that if the model has good agreement with measured grazing effects at M, the same should also occur in the two remaining topographic locations (U and L).

Modeled shoot and root litter decomposition were tested against observations from a litter decomposition study conducted at Kinsella Ranch during 2004 and 2005 (Ch. 2) as follows: for each two consecutive sampling dates in the field study, surface and subsurface litter C stocks from model output for the later date were subtracted from those of the earlier date at each topographic location. To these differences were added total shoot or root litterfall from model output for all plant species between these dates. The change in surface or subsurface litter stock plus shoot or root litterfall represented shoot or root decomposition modelled between the two sampling dates. This decomposition was divided into the total surface or subsurface litter stock during the sampling period to get relative decomposition rates. These rates were tested against those measured in the field study by comparing root mean squares for differences between modelled and measured rates (RMSD) with root mean squares for errors of measured rates (RMSE).

To estimate the sensitivity of the semiarid rangeland at Kinsella to greater grazing intensity, simulated grazing intensities were doubled to 46.8 and 70.2 g LW m^{-2} in 2004 and 2005 by doing another model run with all other inputs unchanged. The results of this run were compared with the previous one done with moderate grazing in terms of changes in both SOC and NBP.

3. Results

3.1. Animal consumption

The mix of animals removed an average of 23.3 and 33.3 g C m^{-2} at the three topographic locations during 90-grazing days in 2004 and 2005 (from 1st of June to July 15th, and from September 1st to October 15th) (Tables 2 to 4). To get this consumption, the total animal weight (in kilograms) was multiplied by the daily consumption rate (2.5%) to get the consumed dry matter, and this result was translated into carbon by multiplying it by 0.45 (common factor used to transform plant organic matter into carbon). This daily carbon consumed was multiplied by 90 (i.e. total grazing days) and this total divided by the grazed area (6.16 ha) and by 10 (to transform kg of C ha^{-1} into g of C m^{-2}). Finally, the result was multiplied by 40%, which represented the carbon loss from respiration, methane, and also carbon gained as animal weight (Tables 2 to 4). Animal consumption was smaller at L (Table 4) than at M and U (Tables 2 and 3) because L had less available foliage due to shading from aspen. In similar way there was smaller grazing consumption at U with respect of that at M because of lower plant productivity at U.

The modeled daily animal consumption was in the range of measured animal consumption (from 2.07% to 2.98% of body weight) in a grazing experiment with the same mix of wild ungulates (Kuzyk and Hudson 2007).

3.2. Model test

Ecosys simulated shoot litter decomposition rates at U without grazing, from DOY 231 to DOY 300 in 2004, similar to those measured (Table 1), but from DOY 147 to 289 in 2005, *ecosys* underestimated the decomposition rate. The reason for this difference may be related with changes in litter chemical composition as decomposition proceeds. During the first experimental year (from August to October 2004) the model simulated decomposition mostly based on faster decomposable carbon compounds (NPC and WSC). However, from May to October 2005 the remaining modeled litter has higher concentration of more recalcitrant carbon compounds (holocelulose and lignin, Fig. 10 Chap. II) with slower decomposition and that may explain the smaller modeled ungrazed shoot decomposition rate at U compared with measured values (Table 1). Modeled shoot litter decomposition with grazing was within the standard deviation of measured values in both years (Table 1).

Regarding root litter, *ecosys* simulated decomposition values in 2004 and 2005 which were similar than, and within the standard deviation range of measured values (Table 1).

At M *ecosys* simulated ungrazed shoot litter decomposition rate, from DOY 231 to DOY 300 in 2004, that was similar to that measured (Table 1). The modeled and measured shoot litter decomposition from DOY 147 to 289 in 2005 were also similar. The simulated decomposition rate of grazed shoot litter during 2004 was larger than the measured rate (Table 1). However, during 2005 (from May to October) the simulated decomposition rate was similar to that measured (Table 1). Modeled root litter decomposition rates without grazing in both 2004 and 2005 were similar to those measured (Table 1); however the simulated grazed values were out of the standard deviation range of measured values, larger in 2004 but smaller in 2005.

Simulated shoot litter decomposition at L, from DOY 231 to DOY 300 in 2004, with and without grazing were similar to that measured (Table 1). However during 2005, the ungrazed modeled value was out of standard deviation range of measured values. Simulated root litter decomposition, with the exception of ungrazed values in 2004, were within the uncertainty range of measured values (Table 1).

In general, the trend regarding topographic or grazing effects on litter decomposition found in the field experiment (Chapter II) was the same modeled by *ecosys.* Thus, shoot litter decomposition was faster at L but root litter decomposition did not show a defined trend relatuive to topography or grazing.

The root means square difference (RMSD) between modeled and measured decomposition rates during the measurement periods in 2004 and 2005 were calculated and compared to those of root mean square error (RMSE) (Table 1). They showed that the modelled – measured differences (RMSD) were similar to the experimental error (RMSE). This similarity indicated that algorithms used by *ecosys* to simulate litter decomposition were able to reproduce the decomposition rates measured in semiarid grasslands but also that the simulation done by *ecosys* is reliable and so, we continue analyzing the carbon balance.

3.3. Carbon budget

3.3.1. C Budget at M

Measured above ground biomass (AGB) at day of year (DOY) 202 was reduced 20% by grazing in 2004 under the 1.57 AUM stocking, and by 35% by grazing in 2005 when stocking was increased to 2.35 AUM (Table 2). Modeled AGB showed the same response to grazing as did measured AGB because grazing reduced the modeled AGB by 12% and 42% on DOY 202 in 2004 and 2005. These reductions were modelled from animal consumption of foliage which reduced the leaf area index (LAI) by 19% in 2004 and 32% in 2005, and hence reduced GPP and NPP (Table 2). These reductions also can be seen in the below-ground biomasses at different sampling dates which were smaller with grazing than without (Table 2). This has implications for the carbon budget because there was less litterfall incorporated into the soil and hence less carbon going into the ecosystem.

The simulated AGB values were greater than those measured (Table 2; Fig. 6 in Chapter III) which were attributed in the model to great organic nitrogen content measured in the soils (Table 1, Chapter II). Regarding to below ground plant biomass, *ecosys* simulated root biomasses from 2003 to 2005 that, with few exceptions, were in the standard deviation range of measured values (Table 2). Both measured and modeled values indicated that grazing tended to decrease root biomass, and measured decreases did not have statistical significance.

Growth of shoot and root biomass in the model were driven in part by nutrient mineralization from decomposing shoot and root litter. Thus litter decomposition influenced plant productivity which affected net ecosystem productivity (NEP) in both grazing treatments. Without grazing, NEP changed from positive (carbon sink) during 2003 and 2004, to negative (carbon source) in 2005 (Table 2). As a result, under the conditions of this simulation there was a strong year effect on the carbon budget. The reduction in modeled NEP from 2003 to 2005 can be explained by an increase in heterotrophic respiration (R_h) (from 372g C m^{-2} in 2003 to 405g C m^{-2} in 2004 and to 545g C m^{-2} in 2005, Table 2). This increase may be attributed to the effects of antecedent weather on productivity. As 2002 was a dry year (annual rainfall 227mm, growing season rainfall 100mm), low θ limited plant growth and hence litterfall (153g C m^{-2}), causing lower R_h and thereby raising NEP in 2003 (Table 2): litterfall occurs mainly after July and thus decomposition is most rapid during the following year (see Figs. 5-7 in Chapter II).

Higher precipitation during the growing season of 2003 (189mm) and 2004 (138mm) compared to that in 2002, raised productivity and litterfall, and hence R_h in 2004 and 2005 (Table 2). The rise in 2005 was further increased by greater rainfall during the growing season (164mm) compared to that in 2004, which meant more soil water (Figs. 1 and 2, Chapter II), and by higher soil temperature which depending on topographic location was from 0.1 to 0.6°C above that in 2004 (Figs. 3 and 4 in Chapter II). Thus the combination of these factors (previous litterfall, rainfall, and soil temperature) raised R_h

and reduced NEP to the point that the ecosystem became a carbon source in 2005 (Table 2).

Grazing in 2004 and 2005 decreased GPP and hence R_a by removing AGB, and even though the presence of grazing animals decreased R_h, because litterfall was reduced, (Table 2) the reduction in R_h was smaller than in NPP, thereby reducing net biome productivity (NBP = NEP – carbon consumed by grazing animals and not returned as manure), changing M from a carbon sink to carbon source in 2004, and to a greater C source in 2005. This can be seen in negative changes in plant carbon in 2004, which means that grazing reduced ecosystem C stocks at the experimental stocking rate tested, and if this reduction were sustained, grazing intensity would have to be decreased and adjusted to the natural productivity under current climatic conditions to avoid ecosystem degradation.

3.3.2. C Budget at U

As showed by the NBP, this location was modeled to be a carbon sink in 2003, and a source in 2004 and 2005 whether grazed or not (Table 3). The small R_h in 2003 reflects the low litterfall incorporated in 2002 (144g C m^{-2}) and carried over from that year. This contributed to reduced loss of carbon and so to have positive NBP in 2003. However a reduction of 17% in GPP from 2003 to 2004 (Table 3) was the result of lower rainfall (41mm less) and cooler temperatures (1.3°C less) during the growing season of 2004 (which also caused 10% reduction in GPP at M, Table 3) compared to that in 2003. However R_h increased because there was more litterfall in 2003 so that total respiration ($R_t = R_a + R_h$) was bigger than GPP (Table 3), causing a negative NEP. The decline in GPP that led to the negative NEP in 2004 can be seen as negative changes in above and below ground plant biomass in the model (Table 3). NEP was even more negative during 2005 than in 2004 as a result of a further rise in R_h due to higher θ (Figs. 3 and 4, chapter II), soil temperatures (Figs. 1 and 2, Chapter II) and increased litterfall from 2004 (Table 3), all of which appeared to stimulate microbial activity and the subsequent release of carbon from the ecosystem.

Grazing at U further increased the loss of carbon (Table 3) by reducing NPP more than R_h because plant residues carried over from previous year’s sustained microbial activity. The reduction in LAI from grazing also reduced subsequent plant growth (10% in 2004 and 21% in 2005) and so further decreased the LAI (25% and 40% in those years). Thus, less CO_2 was fixed reducing GPP, NPP and so the changes in plant carbon became negative (Table 3). This explains why NBP become more negative with grazing.

According to these model results, U only should be grazed during those years in which precipitation is above average, as in 2003, because that was the only year in which NEP was positive without grazing. If grazing intensity were adjusted to productivity in these years, it would be possible that moderate grazing would reduce the carbon input, but not enough to turn U into a carbon source.

3.3.3. C Budget at L

The modeled ungrazed GPP decreased by 15% from 2003 to 2004 as a result of lower rainfall and cooler temperatures during the growing season of 2004 (as showed in Sections 3.1.1. and 3.1.2.). However, GPP increased 12% in 2005 with respect to that in 2004 (Table 4) because rainfall was 26mm greater during the growing season of 2005 compared to that in 2004. This rain increased available soil water down slope with respect to that at U and M (Fig. 2, Chapter III) and so, NPP was greater (Bork *et al*. 2001, Eneboe *et al*. 2002). The change in plant carbon showed positive values indicating greater plant growth (Table 4). However much of NPP at L came from aspen, in which was simulated to have the greatest LAI value, that shaded the grass and shrubs reducing their growth.

Grazing reduced GPP (11% in 2004 and 9% in 2005) and NPP (14% in 2004 and 11% in 2005) however the presence of grazing animals did not change R_h and because of that reduced NBP (Table 4). Simulated grazing lowered the carbon sink by 89g m^{-2} in 2004 and by 77g m^{-2} in 2005.

3.4. Topographic effect on net ecosystem productivity

Topography strongly influenced NEP, with L having the greatest NEP because of aspen (Table 4), M intermediate (Table 2) and U the smallest (Table 3). This effect is explained by θ and soil properties (Table 1, Chapter II) associated with topography, and simulated by *ecosys*.

Topographic effects on θ were driven by surface water movement and associated nutrient movement modeled from elevational gradients and microtopography, and subsurface water movement and associated nutrient movement modeled from gravimetric water potential gradients and soil hydraulic conductivities. Thus, θ modeled at L remained higher than at any other topographic location because it received water from upper locations (Figs. 1 and 2 Ch III). This was reflected in the annual carbon budget (Tables 2-4) which showed that plant productivity and NEP in semiarid ecosystems was directly related with soil moisture which depends on rainfall (Eneboe *et al*. 2002, Bork *et al*. 2001), and soil properties related with fertility. Thus, independent of rainfall, there was a trend for greater NBP down slope (Tables 2-4).

From the analyzed years, and showed in previous sections, 2003 had the highest annual and seasonal rainfall and showed positive NBP at all topographic locations with greater values down hill (Tables 2-4). The following years even though there was less rainfall, NBP showed the same topographic trend as that for 2003. So, independently of interannual variability associated with rainfall, the trend clearly showed that carbon released to the atmosphere was greater at U than at any other topographic location. Probably over a long period of time these differences in NBP among topographic locations contributed to build the differences in soil organic carbon found in the field (Table 1 Chapter II).

When the carbon flux is averaged for the three years U was a source of 4 g C m^{-2} y^{-1}, but M and L were carbon sinks of 12 and 132g C m^{-2} y^{-1} respectively, in which L location has a direct effect of aspen trees which storage carbon in their wood. These interannual and topographic variations in NBP followed the same trend previously found by Flanagan *et al*. (2002) in a semiarid grassland, and those reported by Meyers (2001) and Suyker *et al*. (2003) for more humid grasslands environments in which there was high carbon uptake and those ecosystems were carbon sinks with positive NEP during wetter years, but under dry conditions they were carbon sources with negative NEP.

3.5. Grazing effect on net ecosystem productivity

Ecosys simulated an adverse effect of grazing on NBP at all topographic positions (Tables 2-4). Grazing increased the C source at U by 44 and 71g C m^{-2} y^{-1} (Table 3). At M, modeled grazing reduced NBP by 52 and 94g C m^{-2} y^{-1} in 2004 and 2005 (Table 2), turning the rangeland into a carbon source from a carbon sink in 2004. At L, grazing decreased the carbon sink by 89 and 77g C m^{-2} y^{-1} which is mainly the result of a reduction in GPP (Table 4). Simulated grazing reduced the carbon at all topographic locations because animal consumption decreased the LAI by 12% and 15% during 2004 and 2005. Thus, the plants reduced their growth (reflected in smaller GPP, Tables 2-4) the produced litterfall by 16%, 14% and 9% at U, M, and L respectively (Tables 2-4), which lowered soil C inputs more than R_h.

3.6. Effect of doubled grazing intensity

Declines in NBP modelled under grazing (Tables 2-4) suggested that more intensive grazing would accelerate ecosystem degradation. To assess this possibility, the effect of doubled grazing intensity on NBP and SOC was simulated and compared to previous model results.

Doubled grazing intensity in the model reduced NBP and therefore increased the loss of carbon from the ecosystem from 14g m^{-2} y^{-1} at U in 2004 to more than 200g m^{-2} y^{-1} at L in 2005 (Table 5) compared to that modelled under the grazing intensities set in the field experiment, and all topographic locations became carbon sources. The greatest carbon reduction was simulated at L because NPP was more strongly decreased by grazing there than at any other location. Animal consumption reduced plant residues incorporated into the soil and hence SOC. In fact on average, simulated double grazing intensity reduced the incorporation of litter carbon at U, M, and L by 21, 43, and 63 g m^{-2} y^{-1} respectively from that simulated under the actual intensity. These carbon losses were reflected in decreases of SOC. There was modeled a change in the soil carbon from 18 to more than 100g of SOC m^{-2} y^{-1}, which clearly shows that is not good idea to increase the grazing intensity more than the already applied in the experimental field. These modeled results agree with previous filed measurements done by Willms *et al*. (1985) who worked on a grassland in southwest Alberta and found that the increase of grazing rate up to 4.8 AUM ha^{-1}, similar than our simulated double grazing, caused severe grassland deterioration that reduced productivity 47% (from 1011 to 538 kg of C ha^{-1} y^{-1}). This heavily grazed grassland required more than 32 years to get back to a stable range condition.

Thus, increased carbon lost from the ecosystem as a consequence of increased grazing intensity shows that if grazing is not properly set, it can compromise ecosystem productivity over time, which will be reflected in soil carbon loss.

4. Discussion

4.1. Topography and net ecosystem productivity

Modeled NEP rose downslope from U to M and L (Tables 2 to 4, Fig. 1). This was the result of rises in soil moisture (Fig. 2, Chapter III) and better soil properties that affected plant water and nutrient status (Table 1, Chapter III). In fact soil resources are not evenly distributed over the landscape (Landi *et al*. 2004, Hutchitson *et* *al*. 1999, Johnson *et al*. 2000, Ventera *et al*. 2003) and soil properties change along any slope as a result of water movement down slope that carries fine soil particles, plant material and mineral nutrients (Kachanoski *et al*. 1999, Ventera *et al.* 2003) which stimulates plant growth. In agreement with this, Honeycutt *et al.* (1990) and Burke *et al.* (1999) reported 23% and 42% more soil carbon at lower topographic locations than upslope, and up to more than 100% soil nitrogen has been reported at low topographic locations (Small and McCarthy 2005). Similarly, the N gradient associated with topography found in the field of this research (Table 1, Chapter II) supports the modeled finding regarding greater GPP, NPP and NEP at L (Tables 2-4) because nitrogen is known to be closely and positively related with plant growth and productivity. Also this field data supports the modeled results related with the increase in soil N, which showed that from 2003 to 2005 the increase was on average 0.7g of N m^{-2} greater at L than at U.

Growing plant species are related with soil available resources and those species associated with resource-rich habitats (high fertile soils with large water holding capacity) tend to be have nutrient-rich leaves (low C-to-N ratio, low lignin content (Moore *et al*. 1999). This is in agreement to which was simulated and for example during 2005, the leaf N:C ratio in modeled grass at L (0.10) was double that at U (0.05) indicating that this nutrient was less limiting to plant growth at L. Also the minimum value of canopy water potential modelled at L was higher (-0.81 MPa) than at U (-1.32 MPa), and in average during July those values corresponded to -0.029 MPa at U and -0.10 MPa at L, thus there was less water at U than at L. Thus, better soil conditions allowed plants to grow better at L, which increased carbon going into the ecosystem and so NBP was greater down slope. **These modeled results show that there was a clear influence of topography on net ecosystem productivity, and therefore supports my first hypothesis that better available soil resources at L (Table 1 and Fig. 2, Chapter III) allow greater NPP and hence NEP at L than at U.**

These modelled results are consistent with reports in the scientific literature. In fact Asamoah *et al*. (2004) working at Kinsella found under grazed conditions greater above ground green biomass down slope (254g C m^{-2} y^{-1}) than uphill (94g C m^{-2} y^{-1}). Research done by Perez *et al*. (1998) in semiarid grasslands of Spain also found smaller above ground green biomass uphill (94g C m^{-2} y^{-1}) compared to that down hill (275g C m^{-2} y^{-1}).

In this research **NEP modelled without grazing varied with topography from U to L (from -24 to +96g C m^{-2} y^{-1} during 2004, and from +32 to -119g C m^{-2} y^{-1} during 2005, Tables 1-4), which was related with changes in precipitation (2005 had below-**

average precipitation). These values were greater than those simulated by Li *et al*. (2004) who modeled in a similar semiarid grassland, a range of NEP from +59g C m^{-2} y^{-1} in 1998 to –33 g C m^{-2} y^{-1} in 2000. The variation in NEP was explained based on changes in the amount of rainfall in those years taken into account for Li. Similarly Grant and Flanagan (2007) found variations in NEP that were closely related with precipitation. Previously Dugas *et al*. (1999) measured annual carbon fluxes in an ungrazed natural prairie in Texas and found that fluxes varied from 50 to 80g C m^{-2} y^{-1}. These results support this research because in the same way that we found, they reported variations on NEP caused by precipitation, and the values of NEP reported in those studies for grasslands located in similar ecological conditions were into our modeled range of NEP.

Results from Frank *et al*. (2001) in Yellowstone National Park, from Suyker and Verma (2001), and Suyker *et al*. (2003) working on a native tallgrass prairie of north-central Oklahoma, USA, ecosystems warmer than Kinsella in which NBP was estimated based on eddy covariance technique, showed NBP values from -36 to 51g of C m^{-2} y^{-1} that were in the range of those modeled in this research, and in which the variation found was related with precipitation

Because there is a clear topographic influence on plant productivity, which increase downhill, this variation needs to be considered when estimates of grassland productivity are going to be done to determine an appropriated grazing intensity. Thus, improved scientific information related with carbon budgets at different topographic locations is needed for better-constrained tests of model results, and thereby improve our understanding of processes related to ecosystem productivity and stability. Such understanding can contribute to designing grazing systems that will better protect and preserve this ecosystem.

4.2. Grazing and net biome productivity

The NBP simulated with grazing, averaged for all topographic locations during 2004 and 2005, was -80g C m^{-2} y^{-1} with a range from -182 to +10g C m^{-2} y^{-1} (Tables 2 to 4). There are few available studies in which grazing effects on NBP have been calculated. One of those is the study done by Frank (2002) in the Northern Great Plains in North Dakota (long term annual average precipitation of 404mm similar to that at Kinsella), on a loam, silt loam, and silty clay loam Entic and Typic Haploboroll soils. The measured NBP during three years in that grazed prairie ranged from -19 to +51g C m^{-2} y^{-1}. This study showed that NBP changed with time, as was simulated in this research, because climatic conditions also changed and influenced plant growth. NBP variations with time were also found in Germany by Prescher *et al*. (2010) under simulated grazing done through foliage cutting. The NBP had a range from -28 to +25 g of carbon m^{-2} y^{-1}, in which those variations were associated with variable amounts of exported carbon as cut foliage and also with variable climate.

This shows that the implementation of grazing intensity, and grassland productivity, are important to get a positive (sink) or negative (source) net productivity but it is not only the grazing animals that influence the final carbon balance because the climate has a large influence regulating the response of plants to grazing and hence on NEP (Meyers 2001, Flanagan *et al*. 2002, Suyker *et al*. 2003) and NBP. Thus, a given grazing intensity can produce positive or negative carbon balance depending on the seasonal climate (Bork et al. 2001, Eneboe et al. 2004). In fact plant growth in semiarid ecosystems is directly linked with soil water (Bork *et al*. 2001) and therefore with the carbon going into the ecosystem. Thus, the development of sustainable grazing systems requires consideration not only the amount of available forage, but also the climatic conditions that influence soil moisture and hence plant growth and NBP.

Modeled results also showed that grazing caused great reductions in NBP. At U grazing reduced NBP by 52 and 94g of C m^{-2} y^{-1} compared to that without grazing during 2004 and 2005, respectively. Grazing also reduced the NBP at M (44 and 71g of C m^{-2} y^{-1}) and at L (89 and 71 of C m^{-2} y^{-1}) in those same years (Tables 2-4). These modeled results suggest that a small removal of plant biomass by grazing results in a much larger loss of NPP. Thus, in each grazing year (2004 and 2005) each gram of C per square meter consumed by grazing animals reduced by about 2g of C m^{-2} y^{-1} the NBP at U and M locations. To get these numbers, the difference between ungrazed and grazed NBP was obtained, and the result divided by the total animal consumption in the year at each topographic location. **At L the result showed different values for each grazing year, in 2004 each gram of C consumed by grazing animals produced the loss of 7g of C m^{-2} y^{-1} in NBP; in 2005 this value corresponded to a loss of 4g of C m^{-2} y^{-1} in NBP.** This could be explained by the fact that at lower location R_h was not reduced in the presence of grazing animals as in the remaining topographic locations in which R_h decreased (Tables 2-4). This increased carbon loss from the ecosystem which reduced NEP and then NBP.

Measured changes in NBP with grazing are scarce and because of that, we calculated the change in AGB associated with changes in stocking rate. According to Willms *et al*. (1985) who worked on a rough fescue grassland in southwest Alberta, there is a decrease in AGB as stocking rate increases. Those data showed that taking the stocking rate of 1.2 AUM ha^{-1} used in this research as reference point, the increase above that of 0.4, 1.2, and 3.6 AUM ha^{-1} decreased grassland biomass by 1.3, 15.0 and 46.3g of C m^{-2} y^{-1}. Similarly in the study carried out by Baron *et al*. (2002) at Lacombe, Albert, and taken light grazing as a reference, the increase in grazing intensity to medium or heavy grazing decreased AGB by 1 and 11g of C m^{-2} y^{-1} respectively. In this research light, medium and heavy grazing was defined as pregrazing canopy height of 26, 17, and 13cm respectively. Thus, our modeled results showed the same trend than those research results in which the decline in plant biomass was greater that only the carbon removed by grazing animals.

Changes in NBP also typically parallel those changes in SOC, so we can do some comparison based on SOC because semiarid grasslands only store carbon in the soil, excepting those in which there is the presence of trees. Studies by Frank *et al*. (1995) and Liebig *et al*. (2006) with moderate grazing (2.6 ha steer^{-1}), and Derner *et al*. 2006 with moderate, continuous season-long (May–October) grazing by cattle (that removed approximately 40–60% of ANPP) found SOC reductions from 4 to 32g C m^{-2} y^{-1} which should indicate that those ecosystems were carbon sources. The SOC reductions in this simulation, in which grazing took place only in the last two years of nine modeled years, depending on topographic location were between 3 and 7g C m^{-2} in 2005, and in the range found by those researchers. This modeled carbon reduction caused important reductions in NBP as commented above, and we could say that in the studies cited above in this paragraph there was also reductions in NBP.

Thus the modeled result plus these reported results in the scientific literature support our second hypothesis which stated that moderate grazing, independently of rainfall (the year effect), will decrease the NBP.

4.3. Grazing implications for ecosystem sustainability

The simulated results showed that this ecosystem would be degraded if the current grazing intensity is maintained. The carbon released from the ecosystem, additionally to the weather effect, was directly related with grazing intensity because as intensity increased from 2004 to 2005, the carbon loss also increased by an average of 15g C m^{-2} y^{-1}, which was apparent in more negative values of NBP in

2005 (Tables 2-4, and section 3.5). Also the release of carbon increased further when double grazing intensity was simulated (Table 5).

Even though the modeled grazing varied with AGB along the transect, apparently the intensity was greater at some topographic locations than the ecosystem can sustain, as indicated by the negative NBP. Therefore, a possible way to avoid the consequent decline in ecosystem C stocks should be applying a variable stocking rate, adjusting it every growing season to the expected grassland productivity. Also could be given more resting time to the grassland in order to allow the plants to fully recover their foliage after grazing, or delaying the first grazing of the season (not start the 1st of June as was done in this research).

In summary, the implementation of constant stocking rates should be avoided where possible because plant productivity varies with time, and so does corresponding NBP. A constant grazing intensity, if greater than natural ecosystem productivity, will cause degradation. **Therefore, the best way to achieve ecosystem stability is implementing a grazing system that avoids sustained negative NBP. Thus the number of AUM to be included at any paddock or farm for a defined period of time there has to be based on field measurements of available forage which has taken into consideration the plant productivity associated with topography.** In the field experiment the grazing was set to get a utilization of about 40-50%, and with that intensity the carbon balance proved to be negative (i.e. a carbon source). That implies that grazing probably would have to be reduced to forage utilization levels around 30-35% to avoid carbon losses.

In this sense, modeling can simulate different conditions related with variable landscape topography and generate in advance the necessary information to contribute planning for ecosystem stability over time at the same time that preserves the stability of this ecosystem while it is producing.

When any grassland ecosystem is grazed at a given intensity, and it is greater than its natural productivity, over time there will be changes in its botanical composition (Holechek *et al*. 2001). Thus, grazing tolerant species become more frequent. Those species normally have low productivity and have less nutritive value for animal production, which will reduce even more the potential of the grassland to support grazing animals. As a result the net farmer income could be significantly reduced. In consequence to avoid this scenario, there has to be a grazing system developed that can keep the grassland ecosystem stable over time while allowing for ongoing grazing capable of generating acceptable profit.

5. Conclusions

According to the results from this research the followed conclusions can be made:

There was a strong topographic influence on net ecosystem productivity (NEP), it was greater at M and L than at U; this was the result of soil resources associated with topography which increased the N:C ratio in leaves and the canopy water potential down slope. L had the greatest NEP, but this location was influenced by aspen trees that were not present at any other topographic location.

Modeled NEP was strongly influenced by changes in precipitation. The greatest interannual NEP variation was simulated at U (Table 3) which was the place with less soil moisture (Fig. 2, Chapter III).

The extent to which grazing affects NBP depends on its intensity, and at least with the simulated intensities, in 2004 and 2005 the grazing effect on NBP was smaller than that caused by precipitation.

***Ecosys* was able to simulate field conditions**, with comparable results between those coming from Kinsella Ranch and from the scientific literature.

To design a grazing system that is not going to negatively affect ecosystem stability, it has to take into consideration plant productivity associated with topography and precipitation.

It is necessary to generate more experimental data in this environment to confidently test hypotheses through modeling. This should give us better understanding of different processes that will help us to design managements that contribute to keep the ecosystem stable over time.

Table 4-1. Measured and modeled shoot and root litter decomposition rate, in %, during the growing season of 2004 (from DOY 231 to DOY 300) and 2005 (from DOY 147 to DOY 289), within a fescue grassland near Central Alberta, Canada.

Shoot litter		**Measured**			**Modeled**		**RMSD**	**RMSE**
2004	U	M	L	U	M	L		
Grazed	14±6	12±5	22±2	20	20	24	6	2
Ungrazed	15±6	19±2	28±3	18	18	30	2	3
2005								
Grazed	21±10	17±10	22±1	16	18	22	3	3
Ungrazed	26±4	14±6	23±6	15	15	11	9	8

Root litter		**Measured**			**Modeled**		**RMSD**	**RMSE**
2004	U	M	L	U	M	L		
Grazed	14±9	3±2	14±4	14	14	11	7	8
Ungrazed	14±13	17±7	23±8	16	17	12	6	3
2005								
Grazed	12±9	30±4	19±9	18	20	26	8	12
Ungrazed	12±15	20±11	15±4	22	24	12	7	6

Table 4-2. Modeled carbon balance from 2003 to 2005 at the middle topographic location under grazed and ungrazed conditions, within a fescue grassland near Central Alberta, Canada[a].

Year	2003		2004		2005	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
	C Fluxes (g C m^{-2} y^{-1})					
GPP	983		882	825	897	740
R_a	496		458	442	450	384
Shoot	251		217	214	208	200
Root	245		241	228	242	184
NPP	487		424	383	447	356
R_h	372		405	403	545	529
R_t	868		863	845	995	913
NEP	115		19	-20	-98	-173
Litterfall	414		450	438	443	359
Changes in plant carbon						
AGB	1		1	-5	0	-7
BGB	66		-24	-51	3	-4
Carbon removed by grazing animals[b]	---		---	13	---	19
NBP	115		19	-33	-98	-192
AGB at DOY 202[c] (g C m^{-2})						
DOY202 Measured Modeled	--- 285		87±18 228	70±31 201	150±30 254	98±37 146
Root biomass (g C m^{-2})						
DOY 121 Measured Modeled	--- ---		286±124 140	242±117 137	317±270 121	254±142 89
DOY 182 Measured Modeled	338±189 234	295±150 224	358±231 244	337±149 236	---	---
DOY 213 Measured Modeled	290±152 293	281±128 280	442±209 332	371±156 320	---	---
DOY227 Measured Modeled	---	---	---	---	453±133 373	471±164 296
DOY 274 Measured Modeled	252±120 336	228±84 325	339±198 368	275±112 347	---	---

[a] Positive and negative values are C gains or losses from atmosphere.

[b] This carbon loss represents 40% of the animal consumption

[c] Modeled AGB includes only live plant material; root biomass includes live and litter root

GPP: gross primary productivity, NPP: net primary productivity, AGB: above ground plant biomass

NEP: net ecosystem productivity, NBP: net biome productivity; R_a, R_h, R_t : Autotrophic, heterotrophic, and total respiration.

Measured AGB values ±1STD comes from personal communication Rae, and Cahill

Table 4.3. Modeled carbon balance from 2003 to 2005 at upper topographic location under grazed and ungrazed treatment within a fescue grassland nearCentral Alberta, Canada[a]*.

Year	2003	2004		2005	
		$g\ C\ m^{-2}\ y^{-1}$			
	Ungrazed	Ungrazed	Grazed	Ungrazed	Grazed
GPP	841	696	629	709	558
R_a	419	368	345	366	300
Shoot	221	179	175	164	153
Root	198	189	170	202	147
NPP	422	328	284	343	258
R_h	292	352	342	462	434
R_t	711	720	687	828	734
NEP	130	-24	-58	-119	-176
Litterfall	351	360	342	341	269
Changes in plant carbon					
AGB	5	-3	-1	-1	-4
BGB	58	-23	-43	7	-5
Carbon removed from the ecosystem by grazing animals[b]	---	---	10	---	14
NBP	130	-24	-68	-119	-190
AGB at DOY 202[c] ($g\ C\ m^{-2}$)	253	203	176	210	191
Root biomass at DOY 213	221	253	234	263	200

[a] Positive and negative values are C gains or losses from atmosphere.

[b] This carbon loss represents 40% of the animal consumption

[c] Modeled AGB includes only live plant material; root biomass includes live and litter root

GPP: gross primary productivity, NPP: net primary productivity, AGB: above ground plant biomass
NEP: net ecosystem productivity, NBP: net biome productivity
R_a, R_h, R_t: Autotrophic, heterotrophic, and total respiration.

Table 4-4. Modeled carbon balance from 2003 to 2005 at lower topographic location under grazed and ungrazed treatment, in a fescue grassland of Central Alberta, Canada[c]*

Year	2003	2004		2005	
		$g\ C\ m^{-2}\ y^{-1}$			
	Ungrazed	Ungrazed	Grazed	Ungrazed	Grazed
GPP	1192	1012	901	1139	1038
R_a	582	495	459	535	503
Shoot	390	330	308	344	228
Root	192	165	251	191	275
NPP	610	517	442	604	535
R_h	342	421	429	572	573
R_t	924	916	888	1107	1076
NEP	268	96	12	32	-38
Litterfall	400	392	374	404	367
Changes in plant carbon	229	141	92	209	192
AGB	195	170	130	191	180
BGB	41	-21	33	-15	11
Carbon removed from the ecosystem by grazing animals[b]	---	---	5	---	7
NBP	268	96	7	32	-45
AGB at DOY 202[c] ($gC\ m^{-2}$)	1312	1473	1005	1673	1259
Root biomass at DOY 213	228	215	218	237	218

[a] Positive and negative values are C gains or losses from atmosphere.

[b] This carbon loss represents 40% of the animal consumption

[c] Modeled AGB includes only live plant material; root biomass includes live and litter root

GPP: gross primary productivity, NPP: net primary productivity, AGB: above ground plant biomass

NEP: net ecosystem productivity, NBP: net biome productivity

R_a, R_h, R_t: Autotrophic, heterotrophic, and total respiration.

Table 4-5. Modeled net ecosystem and biome productivity during 2004 and 2005 at different topographic locations under doubled grazed treatment in a fescue grassland. Central Central Alberta, Canada[a].

Year	**2004**	**2005**
Topography		
U	**g C m^{-2} y^{-1}**	**g C m^{-2} y^{-1}**
NEP	-67	-215
NBP	-82	-236
M		
NEP	-47	-207
NBP	-66	-234
L		
NEP	-107	-290
NBP	-129	-318

[a] Positive and negative values are C gains or losses from atmosphere.
NEP: net ecosystem productivity,
NBP: net biome productivity

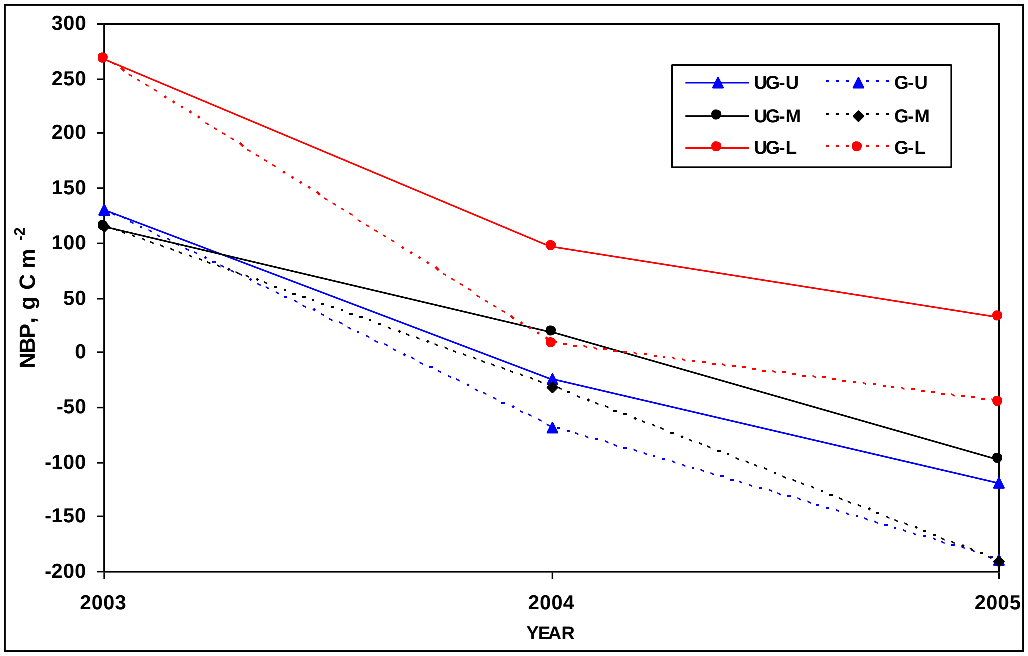

Figure 4-1. Topographic and grazing effect on net biome productivity from 2003 to 2005, in a fescue grassland of Central Alberta, Canada.

6. References

Agriculture and Agri-Food Canada 2000. http://res2.agr.ca/Lethbridge/rep2000/rep0208b_e.htm

Allard, V., Soussana, J., Falcimagne, R., Berbigier, P., Bonnefond, J.M., Ceschia, E., D'hour, P., Henault, C., Laville, P., Martin, C., Pinare`s-Patino, C. 2007. The role of grazing management for the net biome productivity and greenhouse gas budget (CO_2, N_2O and CH4) of semi-natural grassland. Agriculture, Ecosystems and Environment 121:47–58.

Anderson, D.W. 1977. Early stage of soil formation on glacial till mine spoils in a semi-arid climate. Geoderma 19:11-19.

Asamoha, S.; Bork, E.; Irving, B.; Price, M.; Hudson, R. 2004a. Seasonal herbage dynamics on aspen parkland landscape in central Alberta. Canadian Journal of Animal Science 84:149-153.

Asamoha, S.; Bork, E.; Irving, B.; Price, M.; Hudson, R. 2004b. Cattle herbage utilization patterns under high-density rotational grazing in the aspen parkland. Canadian Journal of Animal Science 83:514-550.

Baron, V.S., Mapfumo, E., Dick, A.C., Naeth, M.A., Okine, E.K., Chanasyk, D.S 2002. Grazing intensity impacts on pasture carbon and nitro flows. Journal of Range Management 55:535-541.

Baker, T.R.; Phillips, O.L.; Malhi, Y.; Almeida, S.; Arroyo, L.; DiFiore, A.; Erwin, T.; Killeen, T.J.; Laurance, S.G.; Laurance, W.F.; Lewis, S.L.; Lloyd, J.; Monteagudo, A.; Neill, D.A.; Patino, S.; Pitman, N.C.A.; Silva, M.; Vasquez Martinez, R. 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biology 10:545-562.

Ball, J.T. 1988. An analysis of stomatal conductance. Ph.D. Thesis. California, Stanford University.

Biondini, M.E.; Patton, B.D.; Nyren, P.E. 1998. Grazing intensity and ecosystem processes in a Northern mixed grass prairie, USA. Ecological applications 8(2):469-479.

Boddey, R.M.; Macedo, R.; Tarre, R.M.; Ferreira, E.; Oliveira, O.C. de; Rezende, C. de P.; Cantarutti, R.B.; Pereira, J.M.; Alves, B.J.R.; Urquiaga, S. 2004. Nitrogen cycling in Brachiaria pastures: the key to understanding the process of pasture decline. Agriculture Ecosystems and Environment 103(2):389-403.

Bork, E.; Thomas, T.; Mcdougall, B. 2001. Herbage response to precipitation in central Alberta boreal grasslands. Journal of Range Management 54:243-248.

Burke, I.; Lauenroth, W.; Riggle, R.; Brannen, P.; Madigan, B.; Beard, S. 1999. Spatial variability of soil properties in the shortgrass steppe: The relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. Ecosystems 2(5): 422-438.

Cao, G.; Tang, Y.; Mo, W.; Wang, Y.; Li, Y.; Zhao, X. 2004. Grazing intensity alters soil respiration in an alpine meadow on the Tibetan plateau. Soil Biology and Biochemistry 36:237-243.

Choudhury, B.J.; Reginato, R.J.; Idso, S.B. 1986. An analysis of infrared temperature observations over wheat and calculation of latent heat flux. Agric. For. Meteorol. 37:75-88.

Cole, V. 1996. Agricultural options for mitigation of greenhouse gas emissions. In: Watson, R.T. et al. (Eds.), Climate Change 1995. Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses. Cambridge University Press, Cambridge, pp. 747–771.

Coomes, D.A.; Allen, R.B; Scott, N.A. Goulding, C.; Beets, P. 2002. Designing systems to monitor carbon stocks in forests and shrub lands. Forest Ecology and Management 164:89-108.

Derner, J.D.; Boutton, T.W.; Briske, D.D. 2006. Grazing and ecosystem carbon storage in the North American Great Plains. Plant and Soil 280(1-2): 77-90.

Didkowsky, M.G. 2006. Scales of forage selection by ungulates in Aspen Parkland. Thesis MSc. University of Alberta. 86 p.

Prescher, Anne-Katrin, Grünwald, T., Bernhofer, C. 2010. Land use regulates carbon budgets in eastern Germany: From NEE to NBP. Agricultural and Forest Meteorology. 150 (7-8):1016-1025

Dormaar, J.; Johnston, A.; Smoliak, S. 1997. Seasonal variation in chemical characteristics of soil organic matter of grazed and ungrazed mixed prairie and fescue grasslands. Journal of Range Management 30:195-198.

Dugas, W.A., Heuer, M.L., Mayeux, H.S. 1999. Carbon dioxide fluxes over bermudagrass, native prairie, and sorghum. Agricultural and Forest Meteorology. 93:121-139.

Eneboe, E.; Sowell, B.; Heitszhmidt, R.; Karl, M.; Haferkamp, M. 2002. Droughts and grazing: iv. Blue grama and western wetgrass. Journal of Range Management 55:73-79.

Environment Canada 2006. http://www.ec.gc.ca/pdb/ghg/newsrelease2006_e.cfm

Fahnestock, J.T.; Detling, J.K. 1999. Plant responses to defoliation and resources supplementation in the Pryor mountains. Journal of Range Management 52:263-270.

Farquhar, G.; Von Cammerer, S.; Berry, J. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species. Planta 149:78-90.

Ferraro, D.O.; Oesterheled, M. 2002. Effect of defoliation on grass growth: A quantitative review. Oikos 98:125-133.

Flanagan, L.B.; Weber, L.A.; Carlson, P.J. 2002. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a Northern temperate grassland. Global Change Biology 8:599-615.

Frank, A.B.; Tanaka, D.L.; Hofmann, L.; Follett, R.F. 1995. Soil carbon and nitrogen of Northern Great Plains grasslands as influenced by long-term grazing. Journal of Range Management 48:470-474.

Frank A.B. 2002. Carbon dioxide fluxes over a grazed prairie and seeded pasture in the Northern Great Plains. Environmental Pollution 116:397–403.

Frank, A.B.; Sims, P.L.; Bradford, J.A.; Mielnick, P.C.; Dugas, W.A.; Mayeux, H.S. 2001. Carbon dioxide fluxes over three great plains grasslands. In Follet, R.F.; Kimble, J.M.; Lal, R. Ed. The potential of US grasslands to sequester carbon and mitigate the greenhouse effect. Boca Raton, Lewis. p. 167-182.

Frank, D.A.; McNaughton, S.J. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oecologia 96(2): 157-161.

Frank, D.A.; Kuns, M.; Guido, D. 2002. Consumer control of grassland plant production. Ecology 83(3):602–606.

Frank, D.A.; Groffman, P.M. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone national park. Ecology 79(7):2229-2241.

Ganjegunte, G.; Vance, G.; Preston, C.; Schuman, G.; Ingram, L.; Stahl, P.; Welker, J. 2005. Soil organic carbon composition in a Northern mixed-grass prairie: Effects of Grazing. Soil Science Society of America Journal 69:1746-1756.

Grant, R.F. 2001. A review of the Canadian ecosystem model ecosys. In Modeling Carbon and Nitrogen Dynamics for Soil Management. Shaffer, M. Ed. Boca Raton, FL, CRC Press. p 175-264.

Grant, R.F. 1998a. Simulation in ecosys of root growth response to contrasting soil water and nitrogen. Ecological Modelling 107:237–264.

Grant, R.F. 1994b. Simulation of ecological controls on nitrification. Soil Biology & Biochemestry 26:305-315.

Grant, R.F. 1993. Simulation model of soil compaction and root growth. I. Model development. Plant Soil 150:1-14.

Grant, R. F., Flanagan, L. B. 2007. Modeling stomatal and nonstomatal effects of water deficits on CO2 fixation in a semiarid grassland. Journal of Geophysical Research, 112, G03011, doi:10.1029/2006JG000302.

Grant, R.F.; Heaney, D.J. 1997. Inorganic phosphorus transformation and transport in soils: mathematical modeling in ecosys. Soil Science Society of America Journal 61(3):752-764.

Grant, R.F.; Hesketh, J. 1992. Canopy structure of maize (*Zea mays*) at different populations: simulation and experimental verification. Biotronics 21:11-24.

Grant, R.F.; Nalder, I.A. 2000. Climate change effects on net carbon exchange of a boreal aspen–hazelnut forest: Estimates from the ecosystem model ecosys. Global Change Biol. 6:183-200.

Grant, R.F.; Robertson, J.A. 1997. Phosphorus uptake by root systems: mathematical modelling in ecosys. Plant Soil 188:279-297.

Grant, R.F.; Wall, G.W.; Kimball, B.A.; Frumau, K.F.A.; Pinter Jr, P.J.; Hunsaker, D.J.; Lamorte, R.L. 1999b Crop water relations under different CO_2 and irrigation: testing of ecosys with the free air CO_2 enrichment (FACE) experiment. Agricultural and Forest Meteorology 95(1):27-51.

Grant, R.F. 2004. Modeling topographic effects on net ecosystem productivity of boreal black spruce forests. Tree Physiology 24:1–18.

Gregorich, E.G.; Anderson, D.W. 1985. Effects of cultivation and erosion on soils of four toposequences in the Canadian Prairies Geoderma 36:343-354.

Haddow, R. nd. Thesis M Sc. In preparation

Henderson, D.; Ellert, B.; Naeth M. 2004. Grazing and soil carbon along a gradient of Alberta rangelands. Journal of Range Management 57:402-410.

Holechek, J.L.; Pieper, R.D.; Herbel, C.H. 2001. Range management: principles and practices. 4. ed. New Jersey, Prentice Hall. 587p.

Honeycutt, C.; Heil, R.; Cole, C. 1990. Climatic and topographic relations of three Great Plains soils: II: carbon, nitrogen and phosphorus. Soil Science of American Journal 54:476-483.

Houghton, R.A., Hacker, J.L., Lawrence, K.T. 1999. The US carbon budget: contributions from land-use change. Science. 285:574–578.

Howitt, R.; Findlayson, N.; Gowler, M.; Riddell, M.; McEwan, G. 1988. Soil survey of the County of Beaver, Alberta. N0. 47. Edmonton, Alberta, Alberta Research Council.

Hutchinson, T.F.; Boerner, R.E.J.; Iverson, L.R.; Sutherland, S.; Sutherland, E.K. 1999. Landscape patterns of understory composition and richness across a moisture and nitrogen mineralization gradient in Ohio (U.S.A.) Quercus forests. Plant Ecology 144(2): 177-189.

Irving, B.D., Rutledge, P.L., Bailey, A.W., Naeth, M.A., Chanasyk, D.S. 1995. Grass utilization and grazing distribution within intensively managed fields in Central Alberta. Journal of Range Management 48(4): 358-361.

Irving, B.D. 1992. The effect of litter on the herbage growth cycle, soil water, and soil temperature in the Aspen Parkland of Alberta. Thesis MSc. University of Alberta. 100 p.

Itoh, S.; Barber, S.A. 1983. Phosphorus uptake by six plant species as related to root hairs. Agronomy Journal 75(3):457-461.

Johnson, C.E.; Ruiz-Mendez, J.J.; Lawrence, G.B. 2000. Forest soil chemistry and terrain attributes in a Catskill watershed. Soil Science Society of America Journal 64:1804-1814.

Kachanoski, R.; Carter, M., 1999. Landscape position and soil redistribution under three soil types and land use practices in Prince Edward Island. Soil and Tillage Research 51(3-4):211-217.

Karlen, D.L.; Andrews, S.S. 2000. The soil quality concept: a tool for evaluating sustainability. DIAS-Report, Plant Production 38:15-26.

Kuzyk, G.W.; Hudson, R.J. 2007. Animal-unit equivalence of bison, elk and mule deer in the aspen parkland of Alberta. In press.

Larcher, W. 2003. Physiological plant ecology: ecophysiology and stress physiology of functional groups. 4 ed. Berlin, Springer-Verlag. 513 p.

Lal, R. 2004. Agricultural activities and the global carbon cycle. Nutrient Cycling in Agroecosystems 70:103-116.

Landi, A.; Mermut, A.R.; Anderson, D.W. 2004. Carbon distribution in a hummocky landscape from Saskatchewan, Canada. Soil Science Society of America Journal 68(1):175-184.

Law, B.; Thornton, P.; Irvine, J.; Anthoni, P.; Van, T. 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Global Change Biology 7:755-77.

Li, T.; Grant, R.F.; Flanang, L.B. 2004. Climate impact on net ecosystem productivity of a semiarid natural grassland: modeling and measurement. Agricultural and Forest Meteorology 126:99-116.

Liebig, M.A.; Gross, J.R.; Kronberg, S.L.; Hanson, J.D.; Frank, A.B.; Phillips, R.L. 2006. Soil response to long-term grazing in the northernGreat Plains of North America. Agriculture, Ecosystems and Environment 115:270-276.

Loeser, M.; Crews, T.; Sisk, T. 2004. Defoliation increased above-ground productivity in a semi-arid grassland. Journal of Range Management 57:442-447.

Malo, D.D., Worcester, B.K.; Cassel, D.K.; Matzdorf, K.D. 1974. Soil-landscape relationships in a closed drainage system. Soil Science Society of America Proceedings 38(5):813-818.

Mapfumo, E.; Naeth, M.A.; Baron, V.S.; Dick, A.C.; Chanasyk, D.S. 2002. Grazing impacts on litter and roots: perennial versus annual grasses. Journal Range Management 55:16-22.

Martin, W.K.E.; Timmer, V.R. 2006. Capturing spatial variability of soil and litter properties in a forest stand by landform segmentation procedures. Geoderma 132:169-181.

McIntosh, P.; Allen, R.; Scott, N. 1997. Effects of exclosure and management on biomass and soil nutrient pools in seasonally dry high country, New Zealand. Journal of Environment Management 51:169-186.

Meyers, T. 2001. A comparison of summertime water and CO_2 fluxes over rangeland for well watered and drought conditions. Agric. For. Meteorol. 106, 205–214.

Mielnick, P.C., Dugas, W.A., 2000. Soil CO_2 flux in a tallgrass prairie. Soil biology and biochemistry 32: 221–228.

Milchunas, D.; Lauenroth, W. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327-366.

Moore, T.; Trofymow, J.; Taylor, B.; Prescott, C.; Camire, C.; Duschene, L.; Fyles, J.; Kozak, L.; Kranabetter, M.; Morrison, I.; Siltanen, M.; Smith, S.; Titus, B.; Visser, S.; Wein, R.; Zoltai, S. 1999. Litter decomposition rates in Canadian forests. Global Change Biology 5:75-82.

Nelson, R.F.; Kimes, D.S.; Salas, W.A.; Routhier, M. 2000. Secondary forest age and tropical forest biomass estimation using thematic mapper imagery. Bioscience 50:419-431.

Nouvellon, Y., Rambal, S., Lo Seen, D., Moran, M.S., Lhomme, J.P., Bégué, A., Chehbouni, A.G., Kerr, Y. 2000. Modelling of daily fluxes of water and carbon from shortgrass steppesAgricultural and Forest Meteorology 100:137–153

Novick, K.; Stoy, P.; Katul, G.; Ellsworth, D.; Siqueira, M.; Juang, J.; Oren, R. 2004. Carbon dioxide and water vapor exchange in a warm temperate grassland. Oecologia 138: 259-274.

Ottoni, T.B.; Matthias, A.D.; Guerra, A.F.; Slack, D.C. 1992. Comparison of three resistance methods for estimating heat flux under stable conditions. Agric. For. Meteorol. 58:1-18.

Pachepsky, Y.A.; Timlin, D.J.; Rawls, W.J. 2001. Soil water retention as related to topographic variables. Soil-Science-Society-of-America-Journal 65(6): 1787-1795.

Pastor, J.; Cohen, Y.; Hobbs, T. 2006. The roles of large herbivores in ecosystem nutrient cycles. In Large herbivore ecology, ecosystem dynamics and conservation. Danell, K.; Bergstrom, R.; Duncan, P.; Pastor, J. Eds. p. 289-325.

Perez Corona, M.E.; Vazquez de Aldana, B.R.; Garcia Criado, B.; Garcia Ciudad, A.1998. Variations in semiarid grasslands. Journal of Range Management 51(3):570-576.

Perrier, A. 1982. Land surface processes: Vegetation. In Eagleson, P.S. Ed. Atmospheric general circulation models. Cambridge Univ. Press. p. 395-448.

Pierson, F.B.; Mulla, D.J. 1990. Aggregate stability in the Palouse region of Washington: effect of landscape position. Soil-Science-Society-of-America-Journal 54(5):1407-1412.

Pinchak, W.E., Smith, M.A., Hart, R.H., Waggoner, J.M. 1991. Beef cattle distribution patterns on foot hill range. Journal of Range Management 44(3): 267-275.

Prescher, A.K., Grünwald , T., Bernhofer, C. 2010. Land use regulates carbon budgets in eastern Germany: From NEE to NBP. Agricultural and Forest Meteorology 150:1016-1025.

Reeder, J.; Schuman, G. 2002. Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands. Environmental Pollution 116:457-463.

Reeder, J.D.; Franks, C.D.; Milchunas, D.G. 2001. Root biomass and microbial processes. In Follett, R.F.; Kimble, J.M.; Lal, R. Ed. The potential of U.S. grazing lands to sequester carbon and mitigate the greenhouse effect. Boca Raton, Florida, Lewis. p. 139-166.

Reeder, J.D.; Schuman, G.E.; Morgan, J.A.; LeCain, D.R. 2004. Response of organic and inorganic carbon and nitrogen to long-term grazing of the shortgrass steppe. Environment Management 33(4):485-495.

Ritchie, J.C.; McCarthy, G.W.; Venteris, E.R.; Kaspar, T.C. 2006. Soil and soil organic carbon redistribution on the landscape. Geomorphology (2006), doi:10.1016/j.geomorph.2006.07.021.

Saxton, K.E.; Rawls, W.J. 2005. SPAW, Soil-Plant-Atmosphere-Water Field & Pond Hydrology. Version. 6.02.67. http://www.bsyse.wsu.edu/saxton

Small, C.J.; McCarthy, B.C. 2005. Relationship of understory diversity to soil nitrogen, topographic variation, and stand age in an eastern oak forest, USA. Forest Ecology and Management 217(2-3):229-243.

Smoliak S.; Dormaar, J.F.; Johnston, A. 1972. Long-term grazing effects on Stipa-Bouteloua prairie soils. Journal of Range Management 25:246-250.

Smoliak, S. 1986. Influence of climatic conditions on production of Stipa-Bouteluoa prairie over a 50-year period. Journal of range management 39(2):100-103.

Schimel, D.S.; Stillwell, M.A.; Woodmansee, R.G. 1985. Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. Ecology 66:276-82.

Schuman, G.E.; Reeder, J.D.; Manley, J.T.; Hart, R.H.; Manley, W.A. 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecological Applications 9(1):65-71.

Schuman, G.E.; Janzen, H.H.; Herrick, J.E. 2002. Soil carbon dynamics and potential carbon sequestration by rangelands. Environmental Pollution 116(3): 391-396.

Schuman, G.E.; Herrick, J.E.; Janzen, H.H. 2000. The dynamics of soil carbon in rangelands. In Follet, R.F.; Kimble, J.M.; Lal, R. The potential of U.S. grazing lands to sequester carbon to mitigate the greenhouse effect. Boca Raton, Lewis. p. 267-290.

Singer, M.J.; Ewing, S.A. 2000. Soil quality In: Summer, M. Ed. Handbook of Soil Sciences. Florida, Boca Raton. p. 271-298.

Smit, A.; Kooijman, A. 2001. The impact of grazing on the input of organic matter and nutrients to the soil in a grass-encroached Scots pine forest. Forest, Ecology and Management 142:99-107.

Snyman, H.A. 2005. Rangeland degradation in a semi-arid South Africa I: influence on seasonal root distribution, root/shoot ratios and water-use efficiency. Journal of Arid Environments 60:457-481.

Snyman, H.A.; du Preez, C.C. 2005. Rangeland degradation in a semi-arid South Africa II: influence on soil quality. Journal of Arid Environments 60:483-507.

Stitt, M. 1991. Rising CO_2 levels and their potential significance for carbon flow in photosynthetic cells. Plant Cell Environ. 14:741-762.

Strong, W.L. 1992. Ecoregions and ecodistricts of Alberta. Alberta. Forestry, Lands and Wildlife, Edmonton, AB Publication T/224. Vol. 1.

Suyker, A.E.; Verma, S.B. 2001. Year-round observations of the net ecosystem exchanges of carbon dioxide in a native tallgrass prairie. Global Change Biology 7:279-289.

Suyker, A.E.; Verma, S.B.; Burba, G.G. 2003. Interannual variability in net CO_2 exchange of a native tallgrass praire. Global Change Biology 9:255-265.

Thornley, J.H.M. 1995. Shoot:root allocation with respect to C, N and P: an investigation and comparison of resistance and teleonomic models. Annals of Botany 75(4): 391-405

Thuille, A.; Buchmann, N.; Schulze, E.D. 2000. Carbon stocks and soil respiration rates during deforestation, grassland use and subsequent Norway spruce afforestation in the Southern Alps, Italy. Tree Physiology 20:849-857.

Van Bavel, C.H.M.; Hillel, D.I. 1976. Calculating potential and actual evaporation from a bare soil surface by simulation of concurrent flow of water and heat. Agric. Meteorol. 17:453-476.

Van Soest, P. 1994. Nutritional ecology of ruminant. Portland, Durham and Downey. 374 p.

Ventera, R.T.; Lovett, G.M.; Groffman, P.M.; Schwarz, P.A. 2003. Landscape patterns of net nitrification in a northern hardwood conifer forest. Soil Sci. Soc. Am. J. 67:527-539.

Wheeler, G.W. 1976. Some grassland and shrubland communities in the Parklands of Central Alberta. Thesis MSc. University of Alberta. 75 p.

Whitehead, D. 1995. Consumption, digestion and excretion of nitrogen by ruminant livestock. In Whitehead, D. ed. Grassland nitrogen. Wallingford, Oxon, CAB International. p 59-81.

Willms, W., Smoliak, S., Dormaar, J. 1985. Effects of stocking rate on a rough fescue grassland vegetation. Journal Range Management 38(3):220-225.

Wright, A.; Hons, F.; Rouquette, F. 2004. Long-term management impacts on soil carbon and nitrogen dynamics of grazed bermudagrass pastures. Soil Biology and Biochemistry 36:1809-1816.

Xu, L., Baldocchi, D.D. 2004. Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. Agricultural and Forest Meteorology 123(1-2): 79–96.

Zhang, Y.; Grant, R.F.; Flanang, L.B.; Wang, S.; Verseghy, D.L. 2005. Modelling CO2 and energy exchanges in a northern semiarid grassland using the carbon- and nitrogen- couplet Canadian Land Surface Skin (C-Class). Ecological Modelling 181:591-614.

Zur, B.; Jones, J.W. 1981. A model for the water relations, photosynthesis and expansive growth of crops. Water Resour. Res. 17: 311-320.

Chapter 5.0. Effects of grazing and climate change on the stability of a semiarid rangeland ecosystem: model predictions

1. Introduction

Rangelands are a major ecosystem type found on all continents worldwide. They comprise about 50% of the world's land area (Allen-Díaz 1996) and provide the major source of feed for domestic and wild ruminant animals because they are usually grazed (Holechek *et al*. 2001). In Alberta, rangelands have been estimated at 7.4 million hectares and they provide about 20% of the forage required by the Alberta beef cattle herd (Alberta Government 2006). Thus, they play an important role in the provincial economy. Because of this, we need to know in advance if this ecosystem should be affected by climate change, and if so, to develop a good grazing system that can contribute to maintain the ecosystem stability by maintaining soil organic carbon (SOC). This will allow sustainable grazing in Alberta's grasslands.

Terrestrial ecosystems interact with global climate through carbon fixation, and its release back to the atmosphere through plant and soil microbial respiration. Therefore, carbon (C) stocks in rangeland plants and soils are affected by changes in the global atmospheric concentration of CO_2 and temperature. These stocks could be affected by grazing animals through the consumption of plant biomass which will reduce the amount of plant residues incorporated into the soil (Donkor *et al*. 2002, Snyman and Preez 2005), and thereby reduce soil carbon over time (Derner *et al*. 2006) if the C going into the soil is less than that going out. Declines in SOC over time means that grazing would contribute to the increase of atmospheric C because it is transferred from a terrestrial pool to the atmospheric pool.

According to IPCC (2006) the global average surface temperature increased over the 20th century by ~0.6°C and is projected to increase between 1.4 and 5.8°C over the period 1990–2100. The continuous increase in atmospheric CO_2 is also well documented (IPCC 2006), and is predicted to double in the next century. Because climate change influences plant growth through increases of temperature and atmospheric CO_2 concentration, which enhances water use efficiency but also stimulates CO_2 fixation and soil microbial activity (Morgan *et al*. 2001, 2004), we need to know how grassland ecosystems will respond to new climatic conditions because this response is directly linked with the C stored in soils, and hence with ecosystem carbon balance and its stability over time.

This response is important because rangelands store a huge amount of carbon in the soil, and according to Agriculture and Agri-Food Canada (2000) western Canadian rangelands alone hold around 2.5 billion tons of C to one-meter depth. Thus, any disturbance in the carbon of this ecosystem could impact the global carbon balance (Schuman *et al*. 2002) and could increase or reduce the annual Canadian agriculture emission of greenhouse gases (Environment Canada 2006). How this C pool could be increased or reduced because of grazing under a new climatic regime is not clear yet. Therefore, under specific growing conditions and grazing intensity some questions that need to be answered will be, How will global warming affect the carbon balance of semiarid grassland ecosystems? Could grazing under climate change negatively influence the carbon balance?

1.1. Climate change, grazing and net ecosystem productivity

The increase of atmospheric CO_2 and temperature because of climate change will have site-specific effects on ecosystem productivity, depending on the availability of other resources (Eneboe *et al*. 2002, Thornley and Cannell 1997). Greater atmospheric concentration of CO_2 stimulates plant growth through carbon fertilization and better water use efficiency (Larcher 2003, Morgan *et al*. 2004), and this will increase the carbon in the ecosystem as more plant biomass will be produced and incorporated into the soil. In cooler climates warming may increase CO_2 fixation because growing season becomes longer (Rustad *et al*. 2001). This would increase the net ecosystem productivity (NEP). However, the increase in temperature may also reduce the net amount of carbon fixed because more energy is required for autotrophic respiration (R_a). Also greater temperature will stimulate microbial activity which in combination of more litterfall incorporated into the soil will increase heterotrophic respiration (R_h), and so the carbon released to the atmosphere (Pepper *et al*. 2005) decreasing NEP. Higher temperature can also increase soil available nitrogen (N) through faster mineralization (Dijkstra *et al*. 2008) which can enhance plant growth and hence C accumulation in grassland soils (Coughenour and Chen 1997).

Different researchers have studied the effect of climate change through experiments in grasslands. Campbell and Smith (2000), in a synthesis of global change research in rangelands, pointed out that grasslands increased above ground plant productivity by an average of 17% (range 0 – 30%) under doubled atmospheric CO_2, depending on temperature, nitrogen inputs, defoliation intervals and water availability. Increases in plant productivity of tall grass prairie were also reported by Owensby *et al.* (1999). They determined above— and belowground biomass production, plant community species composition, and water status of a tallgrass prairie ecosystem in Kansas. The ecosystem was sampled at ambient and twice—ambient CO_2 concentrations in open—top chambers during the entire growing season from 1989 through 1991. They showed that plants growing in doubled atmospheric CO_2 had up to 100% greater peak biomass when precipitation was below average compared with plants growing under normal atmospheric CO_2.

Morgan *et al.* (2001) utilizing open-top chambers in a native rangeland pastures with a mixture of C_3 and C_4 grass species in north-eastern Colorado, found increases between 27% and 43% in above ground phytomass when plants grew under doubled (720 ppm) atmospheric CO_2. The increase of plant productivity in the last two experiments (Owensby *et al.* 1999; Morgan *et al.* 2001) was attributed to better water use efficiency. Picon-Cochard *et al.* (2004), using open-top chambers in south-eastern France, also found that aboveground plant production of a semi-natural grasslands was increased between 7% and 15% under elevated CO_2 (600 ppm). Allard *et al.* (2006) in controlled environments detected that plant biomass increased 24% when plants grew under atmospheric CO_2 concentration of 700 ppm compared with 460 ppm. However, this increase was mostly due to high nitrogen availability from fertilizer. When N was not applied the increase in plant biomass was only 3%.

Climate change also is expected to increase the average temperature and this has been taken into account in different research. Rustad *et al.* (2001) evaluated the effect that warming should produce on above ground plant growth as part of the Global Change in Terrestrial Ecosystem, a Network of Experimental Warming Experiments. They found that 2-9 years of experimental warming in the range 0.3-6.0°C increased plant productivity by 19% with the greatest temperature response in colder ecosystems characterized by low mean annual precipitation. Thus, warming increased plant productivity through a direct effect of either increased rates of photosynthesis at higher temperatures and longer growing seasons (Rustad *et al.* 2001), and through an indirect effect of greater nutrient availability which resulted from increased rates of litter decomposition and N mineralization (Dijkstra *et al.* 2008).

All those possible effects of climate change on terrestrial ecosystems raise the question, How might climate change effects on grassland ecosystems be altered by grazing animals? The answer is not known yet and this needs to be addressed to understand how grazing systems have to be adapted to the new climate regime without compromising ecosystem stability. Modeling may be used to estimate possible grazing effects on soil organic carbon and plant productivity under changing climates and so to determine in advance grazing intensities that will not degrade the ecosystem.

1.2. Grazing effect on soil carbon

The SOC has a direct relationship with the atmospheric CO_2 because there is carbon transfer between terrestrial and atmospheric carbon pools. Thus, if terrestrial ecosystems increase C storage in the soil, that could contribute decreasing atmospheric CO_2. However, if the opposite situation occurs, the atmospheric concentration of CO_2 will be increased. In this sense grasslands have great potential to storage carbon in the soil when appropriate grazing intensity is applied (Schuman *et al.* 1999, 2002, Reeder *et al.* 2004). This has great importance because of the area covered by grasslands (Allen-Díaz 1996) this ecosystem could have a key role as carbon sink with positive carbon budgets which will contribute positively to control climate change.

Under current climate different researchers have pointed out the potential and importance of fixing carbon in grasslands soils, which depending on the intensity and amount of available foliage, there could be increases or decreases of plant productivity and so the SOC (Frank *et al*. 1995, Reeder *et al*. 2004, Ganjegunte *et al*. 2005, Liebig *et al*. 2006, Schuman *et al*. 1999, Wright *et al*. 2004, Derner *et al*. 2006) and NBP.

According to Lal (2002) grazing lands can keep high levels of soil carbon and even increase it because the large root biomass of grasses incorporates large amounts of organic matter into the soil. In agreement with this Schuman *et al*. (1999) found that compared with ungrazed condition, continuous season-long grazing at light (0.2 steers ha^{-1}) and heavy (0.56 steers ha^{-1}) stocking rates near Cheyenne, Wyoming, raised soil carbon from 10 to 30g m^{-2} y^{-1}. Similar results were reported by Bruce *et al*. (1999) and Derner *et al*. (2006).

In a semi-arid grassland located in the Central Plains, Reeder and Schuman (2002) showed that after 55 years of light (5–15% utilization) and heavy grazing (35–45% utilization) the soil carbon in the top 0.6 m soil layer was increased by 5 and 18 g m^{-2} y^{-1} respectively. The greater soil carbon was the result of higher annual shoot turnover and carbon redistribution within the plant–soil system as a result of changes in plant species composition. Increases in blue grama (*Bouteloua gracilis*) because of grazing have been related with increases in soil carbon because this species has high root-to-shoot ratio and reallocates more carbon belowground than do cool-season midgrass species (Reeder and Schuman 2002, Derner *et al*. 2006). Previous research carried out by Schuman *et al*. (1999) showed similar trends.

These research results show that grazing compared with the ungrazed condition did not cause negative effect on the ecosystem, on the contrary, the measured increase of SOC with grazing means that those grassland ecosystems had a positive carbon balance (carbon sink) with positive NBP.

However, in some studies grazing did not show any influence on soil carbon. McIntosh *et al*. (1997) did not find any difference in soil carbon compared with an ungrazed exclosure in the upper 0.075 m soil layer in a grassland composed of *Festuca* and *Poa* grazed over 15 years with 0.6 sheep ha^{-1}. Milchunas and Lauenroth (1993) analyzed available scientific information and did not find a definite trend in SOC related with grazing. Recently Henderson *et al*. (2004) also did not find any relationship between soil carbon and grazing along an Alberta rangelands gradient. Decreases in soil carbon with grazing also have been reported. Derner *et al*. (2006) found a reduction of 4 g C m^{-2} y^{-1} in a mid grass community located in Kansas.

So far there is little available information regarding to combined grazing and climate change effects on soil carbon. This has to be solved through modeling studies which can give us in advance possible SOC changes over long periods of time as a result of grazing intensities under climate change scenarios.

1.3. Models and climate change effect on grassland ecosystem

The long term grazing effect on grassland productivity under climate change is complex because there are different factors that influence the ecosystem response. Thus models have been used to study the impact of climate change on grasslands and to get a better understanding of which processes could be altered. Models are technological tools that help us to understand processes, test hypotheses and contribute to support decisions related with agroecosystem management. Thus, mathematical computer models could be used to take decisions about the best management to preserve ecosystems. Recently models have been used to project possible climate change effects on specific processes like litter decomposition (Sindhøj *et al*. 2006), organic carbon turnover (Jones *et al*. 2004), and grassland productivity (Zhang *et al*. 2006, Coughenour and Chen 1997, Li *et al*. 2004), as well as on general ecosystem behavior (Cao and Woodward 1998, Levy *et al*. 2004).

According to Thornley and Cannell (1997), who used the Hurley pasture model, the net effect of CO_2 and temperature increases in humid, temperate grasslands is to raise their carbon stocks. This is in agreement with the prediction of CEVSA model for terrestrial ecosystems (Cao and Woodward 1998) which found an increase of C fixed with greater atmospheric CO_2 concentration. Simulations with the grassland ecosystem model (GEM) predicted increased productivity and C storage in plant residue and soil organic matter for temperate grasslands in response to doubled CO_2 (Hunt *et al.* 1991). Much of this change in productivity was attributed to the increase of atmospheric CO_2. The increase of temperature by itself stimulated microbial activity and so heterotrophic respiration, and caused the evaluated ecosystems to become C sources.

However, Parton *et al*. (1995) using the CENTURY model simulated a C net loss which was caused by the combination of increased temperature and CO_2. This shows that there is not complete agreement about climate change impacts on grassland ecosystems. In addition to this, if we consider that grazing consumes plant biomass and so reduces net biome productivity (NBP) and total carbon in the system, the grassland response to climate change becomes more uncertain. Thus, we require more research to generate information related to grazing and climate change effects on semiarid grassland ecosystems.

According to Levy *et al*. (2004), who simulated with the coupled atmospheric-land surface model (HyLand) an increase up to 970 ppm of atmospheric CO_2 by 2100, the terrestrial biosphere will be a net carbon sink (from 2 to 6 Pg C y^{-1}) during the 21st century. The increase of CO_2 will strongly influence the vegetation which will enhance the net primary productivity.

This is in agreement with previous research carried out by Coughenour and Chen (1997) in short and tall grasslands located in Colorado, who simulated without grazing the effect of doubling the CO_2 concentration (700 ppm) by using GRASS-CSOM model. They found that soil carbon should increase between 6 and 9 g m^{-2} y^{-1}.

Meanwhile Riedo *et al.* (2000) modelling different scenarios of grazing under climate change found that doubling the atmospheric CO_2 from 350 to 700 ppm in which grazing was set to get a leaf area near to a value of 2, simulated up to 15% of increase in plant biomass.

Increased plant productivity and hence carbon inputs to the soil under climate change could be explained by possible greater nitrogen availability (Kicklighter *et al*. 1999, Schimel *et al*. 1994, Zhuang *et al*. 2003, Dijkstra *et al*. 2008). However, previous modeled results reviewed by Parton and Ojima (1994) showed that soil carbon decreased under climate change conditions. In fact studies with models that include coupled C/N cycles (Schimel *et al*. 1994, Clein *et al*. 2002) suggest that possibly future N limitation will reduce the CO_2 fertilization effect, and hence will limit plant productivity (Schimel *et al*. 1994, Clein *et al*. 2002, Zhuang *et al*. 2003) also net primary productivity (Reich *et al*. 2006, Van Groenigen *et al*. 2006) which later will be reflected in less carbon input to the soil and so in soil organic carbon reductions. However under climate change there could be more rapid C cycling which will drive faster symbiotic and non-symbiotic nitrogen fixation.

Thus, apparently there is lack of consensus about climate change effects on ecosystem productivity; however that could be explained by the fact that there are site-specific responses to climate change because of differences in available resources. The effects also could change due to management. Therefore, more research utilizing well-integrated models combined with field research (e.g. Morgan 2002) is needed that can give us the plant growth response to climate change under different available resources. Thus, models can allow us to get better knowledge of ecosystem response to grazing and provide estimates of future results with some simulated grazing intensities.

Ecosys is one of those models used to estimate grassland productivity (Li *et al*. 2004). This model, which was utilized in this research, is used to test these hypotheses described below, to simulate effects of CO_2, temperature and soil moisture on carbon exchanges of terrestrial ecosystems (Grant *et al*. 2001).

Based on the previous information, the hypotheses for this research were that 1) **under current climatic conditions, long term moderate grazing intensity will reduce significantly the soil carbon, because grazing reduces the plant biomass and hence the total plant residue. As soil carbon depends on the amount of litterfall incorporated into the soil, if the litter is reduced significantly the soil carbon also will be reduced over time** 2) **Climate change will increase the soil carbon under grazed or ungrazed conditions. The predicted increases of temperature and precipitation during climate change, plus the increase of atmospheric CO_2, will stimulate the plant carbon fixation and so the plant productivity. Thus, more litter will be produced and incorporated into the soil. As a result, the soil carbon will be increased in the whole ecosystem.**

These hypotheses were tested by using the *ecosys* model which has been previously used to simulate different ecosystem processes under current and climate change scenarios with high confidence. For instance, here in Canada, long-term predictions done with *ecosys* model under climate change scenario showed that soil carbon sequestration in a semi-arid ungrazed grassland was increased by 2 g C m^{-2} y^{-1} more than under current climate (Li *et al*. 2004). More research results and references related with different simulations carried out with *ecosys* are given in each section below.

The objectives of this research were to predict the long term grazing effect of a mix of wild ungulates under current climate and climate change (Table 1) on soil carbon and on carbon balance of a semiarid grassland in Central Alberta, Canada.

2. Methodology

2.1. Model theory

Ecosys, the terrestrial ecosystem model used in this research, simulates the dynamics of carbon, nitrogen, phosphorus, heat and water, and the effects of management practices such as tillage methods, fertilizer and irrigation on these dynamics (Grant *et al*. 2001a). This model has been tested in different ecosystems, with different crops, managements, and climate change scenarios. In each one of the following model description sections, references are provided for *ecosys* results that show good agreement between modeled and measured values from model tests relevant to the objectives of the current study. Those previous results give us confidence about the use of *ecosys* to do this research. Previous chapters of this thesis also have others references about tests of *ecosys*.

A general description of the main *ecosys* hypotheses and algorithms relevant to the modelling climate change impacts on productivity follow. Further details can be seen in Chapters III and IV of this thesis.

2.2. Model description

2.2.1. Energy Exchange

Under climate change there will be higher vapor pressure deficits which will raise evapotranspiration rates, but unless precipitation rises commensurately, this rise may be constrained by declining soil water content. In *ecosys*, evapotranspiration is driven by latent heat fluxes modelled through closure schemes of hourly energy exchange between the atmosphere and plant canopy, snow, litter and soil surfaces (Eqs. B1a, D6), Grant 2001). Surface energy exchanges (D6) are coupled to subsurface conductive, convective and latent heat transfer (D7) using forward differencing schemes with heat capacities and thermal conductivities (Grant 2001). If intercepted precipitation is present on leaf or stem surfaces, latent heat is calculated from evaporation caused by canopy-atmosphere vapor density gradients and aerodynamic conductance (Grant 2001). If there is no intercepted precipitation, latent heat flux is calculated from transpiration which is also controlled by stomatal conductance (Grant 2001).

Total energy exchange is calculated as the sum of exchanges for all plant and ground surfaces. Surface energy exchange is coupled with soil heat and water transfers, including runoff, infiltration, macro and micropore flow. The exponential function used to calculate stomatal resistance from canopy turgor potential (B2b)(Grant and Flanagan 2007) causes stomatal resistance to become more sensitive to canopy turgor potential as canopy water potential and canopy turgor potential decline. In wet soil, canopy turgor potential may be high enough that stomatal resistance is not very sensitive to diurnal variation in vapor pressure deficit as found experimentally (Garcia *et al*. 1998). However, in drying soil with low canopy turgor potential, stomatal resistance becomes more sensitive to vapor pressure deficit (Wever *et al*. 2002). This sensitivity under climate change is very important because it will define the water use efficiency and so, the plant growth and productivity.

Reductions in stomatal conductance under elevated atmospheric CO_2 (C_a) should cause significant reductions in transpiration, which are manifested in field experiments as reductions in latent heat fluxes and increases in sensible heat fluxes and canopy temperatures (Grant *et al*. 1999, Grant and Flanagan 2007).

The canopy water potential determines transpiration by setting the osmotic potential and turgor potential (B1 - B2) (Grant 2001) which, with leaf carboxylation rate described under gross primary productivity below, determines stomatal conductance.

Energy exchange was successfully tested by Grant *et al*. (1995) with data for diurnal gas exchange and seasonal wheat growth measured under high and low irrigation at C_a=370 and 550 μmol mol^{-1} in the Free Air CO_2 Enrichment (FACE) experiment near Phoenix, AZ. Also Grant and Flanagan (2007) simulated hourly CO_2 fluxes in a semiarid grassland that had a RMSD of 0.9, 2.6 and 2.4 μmol m^{-2} s^{-1} when compared with eddy covariance measurements during a drought from 2001 to 2003 at Lethbridge, Alberta, Canada. Latent and sensible heat also were well simulated with *ecosys*, showing values of RMSD in the range from 18 to 44 W m^{-2}. This shows that *ecosys* is well suited to reproduce experimental data under variable climatic conditions, so a climate change scenario will be well simulated after the model validation.

2.2.2. Water relations

NEP of grasslands in North America is strongly controlled by ecosystem water status which is in turn controlled by the relationship between precipitation and potential evapotranspiration that are believed to change with climate change. So, if a model is going to do reliable predictions it has to simulate accurately water deficit effects on GPP.

Following closure of the energy balance, a convergence solution is sought for a canopy water potential (B5) at which the difference between transpiration and root water uptake equals the difference between canopy water contents at its previous and current water potential (Grant *et al.* 1999b). Canopy water potential controls transpiration by determining canopy turgor (Grant *et al.* 1999b) which affects stomatal conductance.

At the leaf level, a maximum conductance is first calculated for each leaf surface that allows a set C_i:C_a ratio to be maintained at an initial mesophyll carboxylation rate calculated under ambient irradiance, temperature, C_a and full turgor. This assumption (constant C_i:C_a), which has been verified by experimental research, requires that reduced stomatal conductance be modelled under higher C_a to equilibrate diffusive and biochemical CO_2 fluxes. The leaf-level maximum conductance is then aggregated by leaf surface area to the canopy-level for use in the canopy energy balance convergence scheme.

Canopy water potential controls root water uptake by determining canopy-root-soil water potential gradients through a hydraulic scheme based on soil-root and root-canopy hydraulic conductances in each rooted soil layer. Soil-root conductance is calculated from root length given by a root growth submodel (Grant 1993b, Grant and Robertson 1997, Grant 1998b), and from soil-root hydraulic conductivity calculated according to Cowan (1965). Root-canopy conductance is calculated from radial and axial conductances (Reid and Huck 1990) of primary and secondary roots (Grant 1998b). The root densities used to calculate root conductance is driven from shoot-root C transfers likely to be increased under climate change.

Under climate change, in which an increase of temperature is expected, atmospheric vapor pressure deficits and hence transpiration rates will rise and so the canopy water potential and stomatal conductance will decrease, depending on θ. *Ecosys* simulates θ through water fluxes which are the product of hydraulic conductance and water potential differences among adjacent grid cells in each topographic location. Changes in soil water content arise from differences in water fluxes among adjacent landscape elements.

Previous model results. Grant and Flanagan (2007) simulating with *ecosys* hourly CO_2 and energy exchange during soil drying achieved good agreement between modeled and measured values in a semiarid ungrazed grassland located west Lethbridge, Alberta. They modeled declines of canopy CO_2 fixation rates that were consistent with those of gross CO_2 uptake calculated from eddy covariance fluxes. The strong decline in precipitation and so in θ in the simulated years was the main reason why CO_2 fixation declined. Also Li *et al*. (2004) in the same location estimated a rainfall compensation point above which the grassland was carbon sink, and below a carbon source. During soil drying declining hydraulic conductivity raised soil-root resistances which in combination with declining soil water potential forced declines in root and canopy water potentials and hence turgor water potential which forced rises in canopy stomatal resistance that reduced latent heat and raised H.

This showed the capability of *ecosys* to reproduce experimental data under the influence of drought or rainy conditions. So changes in water status under climate change should be simulated with confidence by *ecosys*.

2.2.3. Gross Primary Productivity

Gross primary productivity (GPP), the total plant growth over a period of time, is strongly influenced by available soil resources and climatic conditions. So, as climate is going to change we need to know how it could influence CO_2 fixation, a key plant process directly associated with plant grow and hence with GPP.

The carboxilation efficiency of RuBP carboxylase, the enzyme that catalyze the CO_2 fixation, depends on the CO_2 concentration in the medium surrounding the plant, thus the higher concentration of CO_2 the more efficient is the catalytic activity of Rubisco. Therefore, we need to take this condition into account when modeling plant growth under climate change scenarios.

After successful convergence for canopy temperature and water potential, a convergence solution is used to calculate gaseous CO_2 concentration and its aqueous equivalent in the mesophyll of each leaf surface in each canopy. These are the concentrations at which the diffusion rate of gaseous CO_2 equals the carboxylation rate of aqueous CO_2 within each leaf surface (Grant *et al.* 1999b).

The diffusion rate is calculated from the CO_2 concentration gradient across the stomata multiplied by the stomatal conductance from the convergence solutions for energy exchange and water transfer described above. Leaf resistance is used to calculate a mesophyll CO_2 concentration for each leaf surface at which gaseous diffusion equals a final carboxylation rate calculated in the same way as the initial carboxylation rate. The carboxylation rate is the minimum of that from the dark and light reactions calculated according to Farquhar *et al*. (1980). These reactions are driven by the product of the specific activities and areal concentrations of rubisco or chlorophyll at each node. These concentrations are determined by the growth of each leaf as affected by environmental conditions (CO_2, radiation, temperature, water, N, P). The CO_2 fixation rate of each leaf surface is added to arrive at a value for gross CO_2 fixation by each canopy.

The sensitivity of CO_2 fixation to C_a is determined by the aqueous concentrations of CO_2 and O_2 used in Michaelis-Menten functions to calculate rubisco activity (Grant 1992a). The sensitivity of fixation to T_c is determined by parameters for Arrhenius functions (Bernacchi *et al*. 2001, 2003) which should allow the effects of rising temperatures on carboxylation rates to be accurately modelled during climate change. The algorithms used by ecosys to simulate GPP are in the appendix (C1).

Previous model test. Li *et al*. (2004) utilizing *ecosys* simulated a semiarid grassland and found that simulated GPP (627, 287, and 227g C m^{-2} y^{-1}) was close to that measured with eddy covariance (EC) in 1998, 1999 and 2000 (373, 287, and 272 g C m^{-2} y^{-1}). In that research data from 1998 were incomplete, which probably caused the greater divergence in modeled vrs measured values. The GPP was derived from EC measurements but was not itself measured. Recently Grant and Flanagan (2007) in a semiarid grassland simulated GPP values that were comparable with measured values (397 vs. 280g C m^{-2} in 2001, 844 vs. 816g C m^{-2} in 2002, and 636 vs. 685g C m^{-2} in 2003). Changes in modeled NEP from negative values (-100g C m^{-2} y^{-1}, net C source) during drier years to positive values (+150g C m^{-2} y^{-1}, net C sink) during wetter years were consistent with findings from other eddy covariance studies of grasslands under variable precipitation at Lethbridge and elsewhere. The good agreement with measured data gives us confidence to use *ecosys* for simulating scenarios related with climate change

2.2.4. Nutrient uptake

Accurate predictions of plant and ecosystem responses to global change require a better understanding of the mechanisms that control acquisition of growth-limiting resources. One such key mechanism is root capacity to acquire nutrients.

Nutrient uptake (N and P) is calculated hourly for each plant species by solving for aqueous concentrations at root and mycorrhizal surfaces in each soil layer at which radial transport by mass flow and diffusion from the soil solution to the surfaces equals active uptake by the surfaces (Grant and Robertson 1997). The aqueous concentrations of nutrients in each soil layer are controlled by precipitation, adsorption and ion pairing reactions, solute transport (Grant and Heaney 1997) and microbial activity (Grant *et al.* 1993a, b) (Eqs A11a – A11f).

Mass flow is calculated from root water uptake described above, and diffusion is calculated from root length densities (Grant 1993b, Grant and Robertson 1997, Grant 1998b). Active root uptake is calculated from root surface area (Itho and Barber 1983) and is constrained by root oxygen uptake, by solution N and P concentrations, and by C and nutrient storage.

The solution concentration of N and P that occur in the model depend on site conditions. Under nutrient-limited conditions found in most natural ecosystems, rates of nutrient transport to and uptake by root and mycorrhizal surfaces are constrained by rates of nutrient mineralization, desorption, and dissolution from organic and inorganic sources (Grant and Robertson 1997).

Under climate change, microbial activity will increase because of higher soil temperature and so there will be faster mineralization that will stimulate plant uptake due to more rapid nutrient released from plant residues and soil humus.

Previous model test. *Ecosys* simulated N uptake which did not differ from measured field values coming from wheat (Grant 1991) in which about 75% of simulated cumulative N uptake at the end of the season was taken up before anthesis (day 170), as commonly observed in field trials. In a fertilized barley experiment at the Brenton Plots located in Central Alberta, Grant and Robertson (1997) simulated with *ecosys* similar P uptake to that measured during 1991 and 1992.

2.2.5. Autotrophic respiration

Autotrophic respiration (R_a), the sum of maintenance (R_m) and growth (R_g) respiration, is driven by the oxidation of the non-structural carbon product of gross primary productivity. R_a depends on the size of the non-structural carbon pool, temperature, and oxygen uptake (in roots) (Grant *et al.* 1999). R_a is first used to meet requirements for maintenance respiration R_m, a temperature-dependent function (Q_{10} = 2.25) of structural N content (specific rate = 0.1125g C g N^{-1} h^{-1} at 25°C). If oxidation of non-structural carbon is less than R_m, the difference will be taken from remobilizable carbon in leaves and organs of support, causing senescence and litterfall (C2 – C4). Carbon oxidized in excess of R_m is used for R_g (C6) (Grant *et al.* 1999.

Growth respiration drives growth of vegetative and reproductive organs through mobilization of storage C, N, and P; this growth is used to simulate lengths, areas, and volumes of individual internodes, sheaths or petioles, and leaves (Grant 1994b, Grant and Hesketh 1992) from which heights and areas of leaf and stem surfaces are calculated for irradiance interception (C7). R_g also drives extension of primary and secondary root axes and of micorrhizal axes of each plant species in each soil layer through mobilization of storage C, N, and P (Grant 1993, Grant 1998b). This growth is used to calculate lengths and areas of root and mycorrhizal axes from which root uptake of water (Grant *et al.* 1999b) and nutrients is calculated (Grant 1991, Grant and Robertson 1997).

Transfer of storage C, N, and P among different shoot branches and root axes are driven from concentration gradients that are created by the proximity to the site of resource acquisition and by the rate of resource consumption of each branch and axis (Grant 1998b). For perennial plant species, soluble C, N and P are withdrawn from storage pools in shoot branches into a long-term storage pool in the crown during autumn, causing leaf senescence. Soluble C, N, and P are remobilized from this pool to drive leaf and twig growth the following spring. The timing of withdrawal and remobilization is determined by duration of exposure to cooling or warming temperatures under shortening or lengthening photoperiods, respectively.

R_a is sensitive to increases in temperature (Ryan 1991) and under a climate change scenario the response of NPP to rising temperatures will be determined by differences in the responses of R_a and the photosynthetic rate.

Model test. Annual carbon budgets modelled by *ecosys* during 3 years of drought (from 2001 to 2003), showed that simulated R_a values (921, 699, and 786 g C m^{-2} y^{-1}) were similar to those calculated from eddy covariance flux or biometric measurements (836, 667, and 731 g C m^{-2}) for an aspen site (Grant *et al.* 2006).

2.2.6. Heterotrophic respiration

Microbial activity is affected among other factors by soil temperature and soil water content; thus if soil temperature rises the activity of microorganisms also will increase up to a point (usually 35°C) in which microbial activity is depressed. Therefore as climate change will increase soil temperature over time, we need to know how these increases will affect microbial activity and hence litter decomposition and SOC.

Microbial activity in *ecosys* is represented as a parallel set of substrate-microbe complexes (coarse woody litter, fine nonwoody litter, animal manure, particulate organic matter (POM), and humus) (Grant *et al.* 1993a, b) which include the rhizosphere (Grant 1993c), plant residues, animal manure (Grant and Rochette 1994), and native organic matter (Grant *et al.* 1993a, b). Within each complex, the activities of obligate aerobic, facultative anaerobic, and obligate anaerobic heterotrophs are simulated at temperatures and water contents of plant surface residue and of a soil profile (A1 – A4) (Grant *et al.* 2001, 2001a, Grant *et al.* 2009). The possible changes of temperature and moisture caused by climate change and their impacts on microbial activity and hence R_h will thus be simulated by *ecosys*.

Plant residues are partitioned into carbohydrate, protein, cellulose, and lignin fractions according to Trofymow *et al.* (1995), each of which differs in vulnerability to hydrolysis by heterotrophic decomposers. Soil organic matter is also partitioned into fractions of differing vulnerability to hydrolysis. Hydrolysis rate is controlled by soil temperature through an Arrhenius function (A1) (Grant and Flanagan 2007), and by $\boldsymbol{\theta}$ through its effect on aqueous microbial concentrations through an inhibition constant (in g C m^{-3}) based on competitive kinetics proposed by Lizama and Suzuki (1990).

Heterotrophic respiration (R_h) is driven by the microbial biomass of each heterotrophic microbial functional type in each organic matter–microbe complex of each soil layer consuming dissolved organic carbon (DOC) according to Michaelis-Menten kinetics (A10)(Grant and Flanagan 2007). R_h is driven by maximum specific rate of microbial DOC oxidation and constrained by DOC concentration, and by microbial N and P concentrations (A5 – A7).

All heterotrophic populations conduct C oxidation to support growth and maintenance processes, the total of which drives CO_2 emission from the soil surface. This oxidation is coupled to the reduction of O_2 by all aerobic populations (Grant *et al.* 1993c,d, Grant and Pattey 1999) in each substrate-microbe complex. The energetic of these oxidation-reduction reactions determine the microbial growth from which total microbial activity is calculated.

Previous model test. The simulation model *ecosys* predicted changes in soil C by calculating C added through litterfall from plant communities and C lost through oxidation by microbial communities. Heterotrophic microbial activity in the model gave changes in mineralization, immobilization and stabilization of C and N in different soils that were within 10% of recorded changes over time scales of hours, days and years following laboratory amendments of glucose, cellulose, lignin and plant residues (Grant *et al*. 1993a, b).

Modeled changes in soil carbon during 14 simulated years at Swift Current, SK, under different tillage and production systems were within standard errors of measured values (Grant 1997, Grant *et al.* 1997). *Ecosys* predicted that between 14 and 20 g m^{-2} yr^{-1} of more C would be sequestered in the upper 0.15m of soil in continuous wheat than in wheat-fallow. These modeled increases were comparable with those measured of 9 and 19g C m^{-2} yr^{-1}.

2.3. Model experiment

2.3.1. Model runs

Ecosys was initialized with soil properties given in Table 1 of Chapter II from a soil survey carried out in Kinsella Ranch and with physiological properties of C_3 grasses, shrubs, and aspen trees (see previous chapters). Those plant species were distributed along a simulated 15-m long transect with northeast aspect at upper (U), middle (M) and lower (L) topographic locations. There was no management of these plants except for the aspen trees that were thinned at 7% per year from 1998 to 2015. The thinning was done to simulate the mortality that occurs in natural ecosystems, so that all modeled thinned plant material was added to surface residue. A diagram showing plant distribution and slope can be seen in Fig. 1A, Chapter III.

Ecosys was seeded with different amount of grass or shrubs seeds at each topographic location selected to reproduce species composition, and then run for 100 years under repeating a 9-year sequence of hourly meteorological data (short-wave radiation, air temperature, relative humidity, wind speed and precipitation) recorded from 1997 to 2005 at Kinsella Ranch or at nearby weather stations. *Ecosys* was set with actual concentrations of NH_4^+ and NO_3^- in precipitation (0.5 mg N L^{-1}), and of CO_2 and NH_3 in the atmosphere (370 and 0.005 μmol mol^{-1}, respectively).

To examine the climate change effect on this ecosystem *ecosys* was run over 100 years using the same repeating a 9-year sequence of hourly meteorological data as for current climate but with atmospheric CO_2, temperature and precipitation increased hourly at rates corresponding to projections from the Second Generation Coupled Global

Climate Model (CGCM2) for Central Alberta (Environment Canada 2007) (Table 1). At the end of this modeled run the CO_2 concentration was double the current value.

These modeled results were utilized to build a carbon budget after 100 years of climate change for each topographic location with and without grazing; similarly the changes in soil organic carbon were analyzed over the simulated century. These modeled results were compared to those generated with current climate.

There were four model runs, two under current climate and two with the climate change scenario (Table 1), and in each climate scenario one run was with grazing and another without grazing.

2.3.2. Grazing treatments

Grazing in the model runs described above was based on a field experiment carried out at Kinsella Ranch during 2004 and 2005, in which there were two 45-day grazing periods, the first from June 1st to July 15th, and the second from August 1st to October 15th in each year.

In *ecosys* the simulated grazing started in 2004 with a mix of wild ungulates during each grazing period and continued so over the simulated period up to the end of the modeled run. The modeled stocking rate was 2.35 animal units month (AUM) with a total animal live weight (LW) of 2164 kg which correspond to that utilized at Kinsella during 2005 with the three animal species. As the paddock in which animals grazed on the field had 6.16 ha size, the input used in the model to represent this weight was 35.13g LW m^{-2}. This value was divided among plant species growing at U, M and L according to grazing behavior of each animal species (Didkowsky 2006) to get a similar grazing intensity to that observed at Kinsella.

The daily animal consumption was set at 2.5% of their live weight as dry matter which is a normal value for grazing animals (Morley 1981). This consumption was distributed among plant types (grasses, shrubs, and aspen trees) according to observations at Kinsella by Didkowsky (2006) (see table 2, Chapter III) with specified proportions of leaf, petiole and stem consumed each grazing day. These observations showed that grazing by each animal species at each topographic location depended on forage availability and grazing behavior. Bison which are grass eaters grazed more at L and M because of greater grass availability there; elk that are grass eaters and browsers grazed and browsed at L and M in which grasses and shrubs were more abundant. Deer that are basically browsers grazed more at L because the presence of aspen trees gave protection to them (Holechek *et al*. 2001). These observations were taken into consideration when setting inputs to the model for different grazing intensities of different plant species present in each topographic location. Total consumption per grazing year, according to these inputs, was done in the same way as in the previous chapter of this thesis.

Grazing for each day started at the uppermost canopy layer, and continued downward through successive canopy layers until the amount of plant material specified by the inputs for grazing intensity was removed. Grazing of each plant species was distributed according to the available forage in each grid cell, so that greater animal consumption occurred in those grid cells in which there was more forage.

The proportion of consumed carbon returned to the ecosystem as manure was set to 60% (Whitehead 1995, Van Soest 1994, Baron *et al*. 2002); the remaining carbon left the ecosystem as respiration, methane, and live weight. Further details of this grazing simulation can be seen in chapters III and IV of this thesis.

3. Results

An important indicator of how any ecosystem is evolving in ecological terms is the change in soil carbon (SOC) where gains indicate ecosystem aggradation, and losses indicate ecosystem degradation (Janzen 2004, Lal 2004). These changes in natural semiarid ecosystems are directly related with climate of which one of the more important variables is precipitation because it is related with soil available water, plant growth, and so with plant productivity (Bork *et al*. 2001) which ultimately defines the amount of carbon going to the ecosystem. Changes in SOC with climate can be assessed by doing a carbon budget.

3.1. Grazing effect on annual carbon budget

3.1.1. Current climate

Under current climate the annual carbon budget, averaged over the last nine simulated years which included continuous grazing during the entire 9-year cycle of weather data after 2004 showed that U probably will be carbon source whether grazed or not (negative NBP, Table 2). This condition changed at M because the ungrazed treatment was carbon sink mean while grazing treatment translated into carbon source this part of the ecosystem.

In these two locations modeled grazing reduced gross primary productivity (GPP), and also R_a because less foliage required less carbohydrate to be used in maintenance and growth. The reduction of GPP was the result of the combination of different factors. One of those was the reduction of leaf area index (LAI), from 1.71 to 1.11 m^2 m^{-2} with grazing, which reduced photosynthetic area and so postgrazing photosynthate production which then drove less plant growth. The LAI reductions caused by grazing were similar at U (0.19 m^2 m^{-2}) and M (0.17 m^2 m^{-2}) but it was greater at L (0.24 m^2 m^{-2}). Greater soil nutrients at L and M vs. U (Table 1, Chapter II) contributed to different plant responses to grazing and so to different GPP.

Another factor that influenced GPP should be the nutrient redistribution that usually occurs throughout feces of grazing animals because the animal waste is deposited in small patches of less than 3% of the total grazed area (Morley 1964) which change nutrient availability in the landscape and that is reflected as less plant growth (GPP).

The reduction of plant biomass from simulated grazing caused reduction of litterfall. In fact *ecosys* modeled 19% and 9% reduction of litter carbon with grazing at U and M compared to that without grazing (Tables 2 and 3). This decrease in litterfall explains the smaller R_h simulated with grazing in these two locations (Tables 2 and 3). However, although grazing reduced total ecosystem respiration ($R_t = R_a + R_h$) at U and M (Tables 2 and 3), it reduced GPP more, so that with animal consumption NBP became negative, which over time was reflected in less soil carbon (Figs. 1A, 1B). According to these modeled results the grazing intensity has to be slightly reduced at these two topographic locations (U and M) to avoid the modeled soil carbon loss (Tables 2 and 3).

The L location, from an environmental point of view, was more productive than U or M because both treatments at L were net carbon sinks (Table 4). Better soil properties at L, compared with those at U and M (Table 1, Chapter III) allowed greater plant productivity which was reflected in greater NPP and NEP than at those topographic locations (Table 4 vs. Tables 2 and 3). Grazing animals did not turn negative the NBP at L because grazing, as reported in previous research, reduced the litterfall (Donkor *et al*. 2002) which prevented an increase in R_h and thus raised NEP (Table 4). The positive NBP shows that after grazing still there was enough plant material that once incorporated as litter increased the soil carbon over time. This shows that modeled grazing intensity was appropriate to the natural productivity of this topographic location. The simulated grazing intensity at L could even be slightly increased because there is remaining plant material which if consumed by grazing animals would not cause stability problems at this location. This increase should first be modeled to project the ecosystem response to higher grazing intensity.

3.1.2. Climate change

Under climate change, GPP with grazing at U (1093g C m^{-2} y^{-1}) was greater than that under current climate (486g C m^{-2} y^{-1}) (Table 2). Climate change increased GPP at U more than it did R_t, which resulted in an increase of NBP so that this ecosystem became a carbon sink (Table 2). The simulated results with grazing showed similar trends at M and L (Tables 3 and 4) to that at U. Thus after 100 years of modeled climate change, and assuming an area distribution in proportion of 10% 50%, and 40% of U, M, and L, the rangeland landscape had a NBP of 35g of C m^{-2} y^{-1}, which was 21g C m^{-2} smaller than that without grazing.

The increase in GPP under climate change was explained by different factors and processes in the model. One of those was the growing season length, which depending on topographic location and compared with current climate, was increased from 2 to 14 days. Also the elevated C_a (Table 1) raised CO_2 fixation (C1) (Grant 2001). The higher atmospheric CO_2 concentration reduced plant transpiration and improved water use efficiency, which is a particular benefit in water-limited ecosystems. Greater precipitation (104mm more during the growing season from Table 1) increased soil available water relative to earlier values in the upper 0.45m, by 8% after 100 years of climate change which raised ψ_c and hence stimulated plant growth. Due to U was the drier environment under current climate, the increase in precipitation and so the available soil moisture with climate change stimulated more the plant grow at U than at any other topographic location (Tables 2-4). The increase in air temperature with climate change raised soil temperature which stimulated microbial activity and hence decomposition and mineralization (A1, A2), increasing N uptake and plant growth (as showed by Dijkstra *et al*. 2008) and thereby GPP (A1) and NBP (Tables 2, 3 and 4). The increase in air temperature also affected CO_2 fixation rates through interactions among (1) carboxylation, oxygenation and electron transport kinetics according to Arrhenius functions (Eq. 21 in Li *et al*. 2004) with parameters from Bernacchi *et al*. (2001, 2003), (2) declining aqueous CO_2 versus O_2 concentrations caused by declining gaseous solubility, and (3) declining turgor potentials and hence stomatal conductance's caused by increasing vapor pressure differences and hence transpiration rates. However, this last effect could be offset by higher C_a and hence lower conductance that would reduce transpiration. The net effect of these interactions was to raise simulated leaf CO_2 fixation and stomatal conductance with temperature.

According to these simulated results grazing under climate change should not adversely affect the stability of any topographic location because even though animal consumption reduced NBP respectively by 21 and 36g C m^{-2} y^{-1} at M and L compared with the ungrazed condition (Tables 3 and 4), still those locations were carbon sinks as showed by positive NBP. At U the NBP also was reduced by 11g C m^{-2} y^{-1} but similarly to M and L, there was enough carbon left to be a carbon sink. The greater increase in plant growth and so in the carbon sink can be partially explained by more available N coming from manure (Holland *et al*. 1992),

This means that under the simulated climate change scenario (Table 1) the whole ecosystem can be grazed at the current simulated intensity without compromising its stability over time. Under this scenario grazing could be intensified to take advantage of the greater plant productivity.

3.2. Grazing effect on soil carbon

3.2.1. Current climate

In *ecosys* the change in SOC should be equal to litterfall minus R_h minus DOC (dissolved organic carbon) and DIC (dissolved inorganic carbon), however the last two fractions of carbon (DOS ans DIC) were not included in the budget showed in Tables 2 to 4. Under current climate grazing decreased the SOC at all topographic locations (Tables 2 to 4). This is partially the result of less plant residues incorporated into the soil because the plant grow less because of LAI reduction during the growing season with grazing (as analyzed in section 3.1.1) which decreased GPP.

The grazing effect also was reflected in the modeled litterfall, which was reduced by 19%, 9%, and 10% at U, M, and L respectively, and this contributed to the decrease of SOC (Fig. 1). Differences in litter production with grazing at each topographic location are the result of different plant biomass and animal consumption. Thus, after the simulated century of current climate the soil carbon with grazing decreased 4 g m^{-2} y^{-1} at U and M with respect of that without grazing, and thus these locations became carbon sources (Figs. 1A and 1B). At L, grazing also reduced the SOC by 2g m^{-2} y^{-1} (Fig. 1C) with respect to that without grazing but did not turn this location into carbon source because it still increased the SOC and has a positive NBP (Table 4). Looking at the whole simulated grazed paddock, if we assume that the total grazed area (6.16ha) has a proportion of 10% 50%, and 40% of U, M, and L, grazing could cause a loss of 3g of soil per m^{-2} y^{-1} during the simulated century.

Regarding with plant growth, better soil conditions at L compared to those at U (Table 1, Chapter III), allowed even with grazing greater plant growth which incorporated more plant residues into the soil down hill which increased the soil carbon. Thus, over a hundred years the simulated grazing intensity at L did not cause degradation under the climatic and soil conditions utilized in the simulation as showed by the increase of SOC (Fig. 1).

Therefore, if we define sustainability as a condition in which any ecosystem has an average carbon budget close to zero or positive (carbon sink), any applied treatment that causes sustained carbon release from the ecosystem will adversely affect its stability. According to these model results, U should not be grazed because it increases the carbon loss (Table 2) and so accelerates the degradation of this part of the ecosystem. The modeled grazing was greater at M than at U (Tables 2 and 3), and turned it into a carbon source as shown by the negative value of NBP (Table 3). However, this location could be grazed at lighter intensity to avoid C loss and hence degradation. Grazing did not adversely affect L, where grazing still could be intensified without causing ecosystem degradation because both, NBP and SOC showed positive values (Table 4).

3.2.2. Climate change

Climate change, compared with current climate, was good for this environment because the SOC at U without grazing increased by 13 g m^{-2} y^{-1} (Table 2), with grazing this location was also carbon sink of 10 g m^{-2} y^{-1} (Fig. 1A). This is supported by the fact that NBP was positive with both treatments at this location. The modeled soil carbon also increased at M without (9 g m^{-2} y^{-1}) and with (5 g m^{-2} y^{-1}) grazing (Fig. 1B, table 3). At L the increase of soil carbon was greater than at any other topographic location, in which the gain in SOC was bigger without grazing (15g m^{-2} y^{-1}) than with grazing (11g m^{-2} y^{-1}) animals (Fig. 1C, table 4).

The simulated gain in SOC under climate change, whether grazed or not, is the result of greater GPP compared with that under current climate. During the last 9 years of modeled climate change *ecosys* simulated at U without and with grazing an average of 277 and 304g of total litterfall carbon m^{-2} y^{-1} more than under current climate. At M the simulated total litterfall carbon was increased by climate change under no grazing and grazed treatment by 168 and 151g m^{-2} y^{-1} compared to that with current climate. At L litterfall carbon under climate change was 161 and 176g m^{-2} y^{-1} greater than that under current climate without and with grazing respectively. Even though the incorporation of litterfall was greater under climate change than with current climate, R_h was not high enough to offset NPP and so, NEP and NBP became positive (carbon sink) under this simulated scenario. These increases of litterfall with climate change were reflected in the soil carbon increases (Fig. 1).

4. Discussion

4.1. Grazing effect on soil carbon

4.1.1. Current climate

Under current climate reductions in plant growth with grazing were observed by Ferraro and Oesterheld (2002) when they did a meta-analysis for grazed from North American prairies. According to that analysis, grazing reduced plant biomass between 44% and 57%, but at ecosystem level grazing reduced ANPP by 10-20%, which is in the range of our modeled reduction in NPP (from 8% to 17% smaller NPP with grazing than that without grazing, tables 2 and 3). Simulated results in other studies also show that grazing decreases NPP (Wanga *et al*. 2008).

Reductions in NPP because of grazing have been related with decreases of litterfall. Reductions of 27-28% in litterfall (Dormaar *et al*. 1997, Schuman *et al*. 1999) because of grazing in semiarid ecosystems of Alberta, Canada, and Wyoming, USA, are similar to reductions simulated in this research which were from 9% to 19%. Similar decreases in litterfall as a result of grazing have been reported by different researchers (Donkor *et al*. 2002, Henderson *et al*. 2004).

Declines in NPP and consequently in litterfall with grazing lead to reductions in SOC. Modeled changes in SOC with grazing in this research were similar to those coming from field measurements reported in the literature. Our simulated decrease of 2g C m^{-2} y^{-1} with the set grazing intensity at L is consistent with that reported by Reeder and Schuman (2002). They measured in semi-arid mixed-grass and short-grass rangelands under comparable climatic conditions in Wyoming decreases of 2g C m^{-2} y^{-1} in the top 0.6m depth with moderate grazing (up to 40% of utilization) compared with the SOC without grazing. Similarly, Frank *et al*. (1995) reported, after 76 years of moderate grazing (≈0.4 AUM ha^{-1}) in Northern Great Plains compared with ungrazed exclosures, carbon losses of 2.4g m^{-2} y^{-1} in the soil profile (up to 1.07m depth) which were similar to our modeled carbon losses with grazing vs. no grazing at L (Fig. 1, table 4).

The modeled carbon losses (4g C m^{-2} y^{-1}, Fig. 1) at M and U (section 3.2.1.) with grazing compared to that without grazing in this research were similar to those measured by Derner *et al.* (2006) in a mid grass community (4g C m^{-2} y^{-1}) in west-central Kansas at Fort Hays State University (38°52´ N, 99°23´W) when comparing the SOC under ungrazed and moderate grazing. In this last research the animal consumption was 40-60% of above ground plant biomass which was similar to that set in the experimental field which was the base of that used in this research.

Thus, the modeled results, corroborated by those field experimental results reported in scientific literature and commented above, support our first hypothesis which stipulated that under current climate moderate grazing will decrease soil organic carbon compared to that of ungrazed rangeland.

Even though grazing lowers SOC in comparison with that in ungrazed exclosures, it can still allow long-term gains in SOC. Derner *et al.* (2006) found, after 55 years of grazing at the Flint Hills of eastern Kansas with grazing removals between 40 and 60% of above ground plant foliage, SOC increases of around 1g m^{-2} y^{-1}. With similar grazing intensity in this study *ecosys* simulated carbon gains at L (Table 4) that were comparable to the field result of Derner *et al*. (2006). The simulated changes in soil carbon by *ecosys* with grazing also were in the range of those reported by Schuman *et al*. (2002) who found that the estimated rate of soil C gain to be achieved in dry-temperate ecozones by management of grazing lands is around 1 g C m^{-2} y^{-1}. This value is similar to that modeled with *ecosys* of 2g C m^{-2} y^{-1} at L (Fig. 1C, section 3.2.1, Table 4).

Increases of SOC have been reported as a result of grazing due to changes in grassland botanical composition. Thus Reeder and Schuman (2002) and Schuman *et al*. (1999) found increases of 18 and 23g C m^{-2} y^{-1} respectively, in semi-arid grassland soils grazed less than 50% of annual available biomass. These increases were explained by grazing-induced increment of blue grama, a grass specie that has higher root-to-shoot ratio and that transfers more C belowground than do other grass species. Our simulated long-term gains of soil carbon with grazing were smaller than those measured because in the model there was not any important change of grass species because of grazing.

Because of the similarity between reductions in NPP, litterfall and SOC with grazing modeled in *ecosys* and those reported in the scientific literature under similar ecological conditions, we have enough confidence in the simulated *ecosys* results with grazing under current climate and support those that we obtained under the transient climate change scenario.

4.1.2. Climate change

There is a coupling between the stimulatory effect of CO_2 on plant growth and accompanying long-term changes in soil carbon, nitrogen and water availability resulting from elevated CO_2 (Williams *et al*. 2004, Ross *et al*. 2004). Therefore prediction of long-term effects on plant productivity using models must take into account the changes in these components of semiarid grassland ecosystems.

The simulated results by *ecosys* showed that more plant biomass is produced with growth under elevated CO_2 compared with current climate and without grazing animals. The warming under climate change scenario increased plant productivity through a direct effect of either increased rates of photosynthesis at higher temperatures (Rustad *et al*. 2001) and longer growing seasons (as commented above section 3.1.2.) and through an indirect effect of greater nutrient availability which resulted from increased rates of litter decomposition and N mineralization (Dijkstra *et al*. 2008).

For water-limited ecosystems like the modeled grassland, elevated CO_2 can result in greater water availability for longer in the growing season (Campbell *et al.* 1997, Owensby *et al.* 1997). The experimental results suggest that the hydrological consequences of elevated CO_2 in water-limited systems can be as significant as the direct CO_2 fertilization effect on photosynthesis. This is in agreement to which was found by different researchers. According to Cambell and Smith (2000), Marissink *et al.* (2002) and Morgan *et al.* (2001), under greater CO_2 concentration there is a decrease of leaf conductance and greater plant water status, which contribute with the increase of plant growth. Related to this, Owensby *et al.* (1999) found in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO_2 that volumetric soil water content of the 0–100 cm soil layer was generally higher in elevated CO_2 plots than under ambient.

With greater CO_2 concentration, and the increases in temperature and precipitation, *ecosys* simulated that NPP with grazing increased from 38% to 129% (Tables 2 to 4) compared with grazed condition under current climate. This increase in NPP had the same trend as experimental observations carried out in semiarid grasslands. According to Picon-Cochard *et al.* (2004) an increase of CO_2 up to 600 ppm, using the mini-FACE (Free Air CO_2 Enrichment) exposure system, raised the above ground plant biomass up to 47%. A similar trend (increases from 17% to 108% in above ground plant biomass) was found in other field research results with increased concentration of CO_2 by Owensby *et al.* (1999) with open-top chambers (which also rise air temperatures by1-2°C), and in the Global Change and Terrestrial Ecosystems (GCTE) Pastures and Rangelands Core Research Project 1 network, a world-wide network of 83 full-time equivalent researchers established in different pasture and rangelands systems (Campbell and Smith 2000). Marissink *et al.* (2002) working on a semi-natural grassland (annual average precipitation and temperature of 527mm and 5.5°C) in Sweden found that doubling the CO_2 concentration (from 350 to 700 µmol mol^{-1} but keeping the same precipitation in both treatments), increased the above ground plant productivity on average by 36%. Similarly Morgan *et al.* (2001) in a shortgrass steppe in north-eastern Colorado, USA (320mm, 15.6°C in summer and 0.6°C in winter), detected that aboveground productivity was enhanced between 26% and 47% at elevated CO_2 (720±20 µmol mol^{-1}), and above ground plant biomass from 17% to 88% compared with those under ambient (360 µmol mol^{-1}) conditions (Morgan *et al.* 2004).

Measured results elsewhere have showed that elevated C_a and temperature increase grassland productivity and hence soil carbon (Coughenour and Chan 1997, Morgan *et al.*

2001, 2004) which agrees with our modeled results that showed soil carbon increased over a hundred years (Fig. 1) under the simulated climate change scenario. Thus greater plant biomass increased the amount of plant residues incorporated into the soil as litterfall which over time also increased the soil carbon (Fig. 1) at all topographic locations whether grazed or not.

Under no grazing, *ecosys* simulated increases in SOC from 9 to 15 g m^{-2} y^{-1} depending on topographic location after doubling CO$_2$ concentration and changing precipitation and temperature over 100 years (Fig. 1, Table 1). Similar increases (between 6 and 13g C m^{-2} y^{-1}) were simulated by Coughenour and Chen (1997) using the GRASS-CSOM model in which CO$_2$ concentration was gradually increased over the modeled run.

The modeled changes in soil carbon in our research were greater that reported by Jones *et al.* (2005). They simulated between 3 and 7 g C m^{-2} y^{-1} of net soil carbon loss in Saskatchewan, Canada, as a result of climate change without grazing with RothC and HadCM3LC models over 250 years (from 1850 to 2100). According to them, the SOC reduction was the result of greater temperature rises at the end of the 21st century (it was 3°C higher than simulated in the climate change scenario in this study as presented in Table 1), which increased the microbial activity and reduced the SOC because there was an increase of litter decomposition. Jones *et al.* (2005) also mentioned that there were reductions in carbon input to the soil because the simulated dry condition at Saskatchewan limited plant growth.

When there was grazing, and depending on topographic location, *ecosys* simulated that soil carbon under climate change increased from 5 to 11g C m^{-2} y^{-1}, which was from 6 to 22g C m^{-2} y^{-1} greater than changes in SOC with grazing under current climate (Tables 2 to 4). These results are similar to those modeled by Thornley and Cannell (1997) with the Hurley Pasture Model under the combined effect of continuous grazing (10 sheep ha^{-1}), double CO$_2$ and 5°C increase in air and soil temperature. According to them, temperate grasslands should accumulate about 5g C m^{-2} y^{-1} for several decades under the influence of climate change. With grazing heavier than in this simulation, Pepper *et al.* (2005) found small soil carbon increases (1 g m^{-2} y^{-1}) by simulating the effect of climate change in a short grassland of Colorado with a grazing intensity in which 50% of NPP was consumed. The higher animal consumption explains the smaller SOC compared with our modeled results. Additionally, high R_h due to the increase of temperature reduced NEP and so, limited the gains in SOC (Pepper *et al*. 2005).

Unfortunately there is little available information related with climate change and grazing effect on soil carbon to do more comparisons with modeled results coming from *ecosys*.

The simulated soil carbon results, under climate change scenario (Tables 2 to 4), supports the second hypothesis stating that climate change will increase SOC. Even though the increase of soil carbon was smaller with grazing than without, in both treatments the soil carbon increased over time (Fig. 1) as shown by positive NBP (Tables 2 to 4) in the three topographic locations. According to the carbon budget predicted by *ecosys* this ecosystem will be a net carbon sink during the next century; under the simulated climate change increases in GPP will be greater than those in R_t and so increase NEP and NBP at all topographic locations.

Thus, the modeled results agree with the trend of previous research results, and the simulated values are close to those reported in the literature which gives us confidence in the simulation done in this research.

5. Conclusions

Based on the conditions of this simulation, it can be concluded that:

- **The grazing intensity (2.35 AUM) simulated with *ecosys* under current climate over a hundred years, reduced the soil carbon at all topographic locations from that without grazing** (Fig. 1).

- **The simulated climate change will have a beneficial effect in this ecosystem because grazed or not the soil carbon will increase at all topographic locations** (Fig. 1).

- **The carbon budget showed that grazing should reduce the amount of carbon captured in the ecosystem but if the intensity is properly set, it should be possible not to endanger the ecosystem stability because still it will be aggrading as shown by positive NBP** (Tables 2 to 4).

- **Because of the stimulus that climate change is going to cause in the plant growth in this ecosystem, grazing intensity could be increased to take advantage of the simulated additional plant biomass produced.** This grazing increase should be evaluated by simulation to get in advance important information about the grazing intensity that should be applied without endanger the site productivity over time.

- **The results of *ecosys* model were comparable with those reported in the scientific literature** (sections 4.1.1 and 4.1.2), so *ecosys* can be confidently used to simulate grazing effects on productivity in semiarid temperate grassland ecosystems under current climate and climate change scenarios.

Table 5-1.Annual rises in temperature (maximum and minimum), precipitation and atmospheric CO_2 concentration used in the modeled climate change scenario.

Season	Temp. maximum + deg. C	Temp. minimum +deg. C	Precipitation	CO_2
January–March	0.017	0.022	1.001	1.007
April–June	0.017	0.018	1.006	1.007
July–September	0.013	0.014	0.998	1.007
October–December	0.014	0.014	1.004	1.007

According with the Second Generation Coupled Global Climate Model (CGCM2) for Central Alberta (Environment Canada 2007)

Table 5-2. Average modeled carbon balance for grazed and ungrazed treatments during the last nine of a hundred simulated years at upper topographic location under normal and climate change scenario*.

Scenario	Current Climate**		Climate change	
Treatment	UG	G	UG	G
	$g\ C\ m^{-2}\ y^{-1}$			
GPP	595	486	1078	1093
R_a	309	250	503	551
NPP	286	236	575	542
R_h	287	244	527	499
R_t	596	494	1030	1050
NEP	-1	-8	48	43
Removal	---	6	---	6
NBP	-1	-14	48	37
Litterfall	276	223	553	527
Δ SOC***	-8	-12	13	10

* Positive and negative values are C gains or losses respectively.
** Current: the current climate; Clim. change: climate change scenario according to table 1
*** Averaged over the total simulated time.
GPP: gross primary productivity; NPP, NEP, NBP: net primary, ecosystem, and biome productivity. UG: ungrazed; G: grazed; R_a, R_h, R_t: Autotrophic, heterotrophic, and total respiration. Removals represent animal consumption less return by manure

The carbon budget is not quite balanced because the flux of organic (DOC) and inorganic (DIC) carbon leaving the ecosystem in runoff and leaching was not included. DOC and DIC do not represent important carbon losses in this semiarid ecosystem.

Table 5-3. Average modeled carbon balance for grazed and ungrazed treatments during the last nine of a hundred simulated years at middle topographic location under normal and climate change scenario*.

Scenario	Current**	Current	Clim. change	Clim. change
	g C m^{-2} y^{-1}			
Treatment	UG	G	UG	G
GPP	834	738	1150	1044
R_a	442	354	555	506
NPP	420	384	595	538
R_h	416	381	565	519
R_t	830	735	1120	1025
NEP	4	-3	30	19
Removal	---	10	---	10
NBP	4	-13	30	9
Litterfall	413	374	581	525
SOC***	3	-1	9	5

* Positive and negative values are C gains or losses respectively.

** Current: the current climate; Clim. change: climate change scenario according to table 1

*** Averaged over the total simulated time.

GPP: gross primary productivity; NPP, NEP, NBP: net primary, ecosystem, and biome productivity. UG: ungrazed; G: grazed; R_a, R_h, R_t: Autotrophic, heterotrophic, and total respiration. Removals represent animal consumption less return by manure.

Table 5-4. Average modeled carbon balance for grazed and ungrazed treatments during the last nine of a hundred simulated years at lower topographic location under normal and climate change scenario*.

Scenario	Current**	Current	Clim. change	Clim. change
	G C m^{-2} y^{-1}			
Treatment	UG	G	UG	G
GPP	1077	1092	1546	1465
R_a	523	581	793	761
NPP	554	511	753	704
R_h	533	479	663	628
R_t	1056	1060	1456	1389
NEP	21	32	90	76
Removal	---	22	---	22
NBP	21	10	90	54
Litterfall	515	463	676	639
SOC***	4	2	15	11

* Positive and negative values are C gains or losses respectively.

** Current: the current climate; Clim. change: climate change scenario according to table 1

*** Averaged over the total simulated time.

GPP: gross primary productivity; NPP, NEP, NBP: net primary, ecosystem, and biome productivity. UG: ungrazed; G: grazed; R_a, R_h, R_t: Autotrophic, heterotrophic, and total respiration. Removals represent animal consumption less return by manure

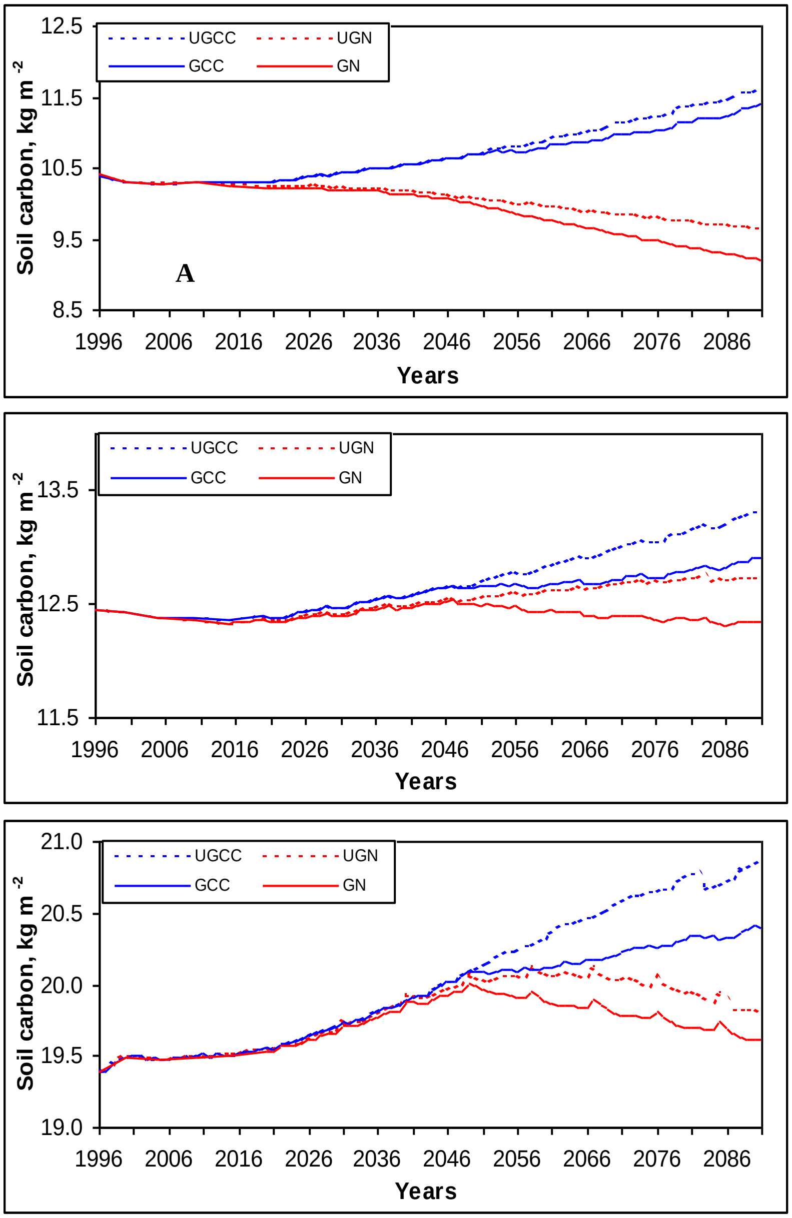

Figure 5-1. Simulated long-term effect of grazing under current and climate change scenario at different topographic locations (U:upper, M:middle, L:lower).

Climate change scenario according with Table 5-1
UGCC: ungrazed under climate change scenario
GCC: grazed under climate change scenario
UGN: ungrazed under current climate
GN: grazed under current climate

6. References

Agriculture and Agri-Food Canada. 2000. http://res2.agr.ca/Lethbridge/rep2000/rep0208b_e.htm

Alberta Government. 2006. Sustainable resource development.

http://www.srd.gov.ab.ca/land/m_rm_rangepasture.html

Allard, V., Robin, C., Newton, P., Lieffering, M., Soussana, J. 2006. Short and long-term effects of elevated CO_2 on Lolium perenne rhizodeposition and its consequences on soil organic matter turnover and plant N yield. Soil Biology & Biochemistry 38(6):1178-1187.

Allen-Diaz, B. 1996. Rangelands in a changing climate: Impacts, adaptations, and mitigation. p. 131–158. In R.T. Watson et al. (ed.) Climate change 1995. Impacts, adaptation, and mitigation of climate change: Scientific technical analyses. Published for the Intergovernmental Panel on Climate Change. Cambridge Univ. Press, Cambridge, UK.

Asamoah, S., Bork, E., Irving, B., Price, M., Hudson, R. 2004. Seasonal herbage dynamics on aspen parkland landscape in central Alberta. Canadian Journal of Animal Science 84:149-153.

Bernacchi, C.J., Singsaas, E.L., Pimentel, C., Portis, A.L., Long, S.P. 2001. Improved temperature response functions for models of rubisco-limited photosynthesis. Plant, Cell and Environment 24:253-259.

Bernacchi, C.J., Pimentel, C., Long, S.P. 2003. In vivo temperature response functions of parameters required to model RuBP-limited photosynthesis. Plant, Cell and Environment 26:1419–1430.

Bork, E., Thomas, T., McDougall, B. 2001. Herbage response to precipitation in central Alberta boreal grasslands. Journal of Range Management 54:243–248.

Bowes, G. 1991. Growth at elevated CO_2: Photosynthetic responses mediated through Rubisco. Plant Cell Environ. 14:795–806.

Bruce, J.P., Frome, M., Haites, E., Janzen, H., Lal, R., Paustian, K. 1999. Carbon sequestration in soils. Journal of Soil and Water Conservation 54(1): 382-389.

Campbell, B.D., Smith, D.M.S. 2000. A synthesis of recent global change research on pasture and rangeland production: reduced uncertainties and their management implications. Agriculture,-Ecosystems-and-Environment 82(1/3): 39-55.

Campbell, B., Stafford Smith, D., McKeon, G. 1997. Elevated CO_2 and water supply interactions in grasslands: a pastures and rangelands management perspective. Global Change Biol. 3: 177–187.

Cao, M., Woodward, I. 1998. Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. Global Change Biology 4:185-198.

Cao, G., Tang, Y., Mo, W., Wang, Y., Li, Y., Zhao, X. 2004. Grazing intensity alters soil respiration in an alpine meadow on the Tibetan plateau. Soil Biology and Biochemistry 36:237-243.

Clein, J.S., McGuire, A.D., Zhang, X. 2002. Historical and projected carbon balance of mature black spruce ecosystems across North America: the role of carbon–nitrogen interactions. Plant and Soil, 242, 15–32.

Coughenour, M., Chen, D. 1997. Assessment of grassland ecosystem responses to atmospheric change using linked plant–soil process models. Ecological Applications 7(3):802–827.

Cowan. I.R. 1996. Transport of water in the soil-plant-atmosphere system. Journal of applied Ecology 2:221-239.

Derner, J.D., Boutton, T.W., Briske, D.D. 2006. Grazing and ecosystem carbon storage in the North American Great Plains. Plant and Soil 280(1-2): 77-90.

Dormaar, J., Adams, B., Willms, D. 1997. Impacts of rotational grazing on mixed prairie soils and vegetation. J. Range Manage.50:647451

Donkor, N., Gedir, J., Hudson, R., Bork, E., Chanasyk, D., Naeth, M. 2002. Impacts of grazing systems on soil compaction and pasture production in Alberta. Canadian Journal of Soil Science 82:1-8.

Didkowsky, M.G. 2006. Scales of forage selection by ungulates in Aspen Parkland. Thesis MSc. University of Alberta. 86 p.

Dijkstra, F., Pendall, E., Mosier, A., King, J., Milchunas, D., Morgan, J. 2008. Long-term enhancement of N availability and plant growth under elevated CO_2 in a semi-arid grassland. Functional ecology 22:975-982.

Drake, B.G., Gonzàlez-Meler, M.A., Long, S.P. 1997. More efficient plants: a consequence of rising atmospheric CO_2? Annual Review of Plant Physiology and Plant Molecular Biology, 48, 609–639.

Fang, J.Y., Piao, S.L., Tang, Z.Y., Peng, C.H., Wei, J. 2001. Interannual variability in net primary production and precipitation. Science, 293, 1723a.

Ferraro, D., Oesterheld, M. 2002. Effect of defoliation on grass growth. A quantitative review. Oikos. 98:125-133.

Eneboe, E., Sowell, B., Heitszhmidt, R., Karl, M., Haferkamp, M. 2002. Droughts and grazing: iv. Blue grama and western wetgrass. Journal of Range Management 55:73-79.

Environment Canada 2006. http://www.ec.gc.ca/pdb/ghg/newsrelease2006_e.cfm

Environment Canada. 2007. http://www.cccma.ec.gc.ca/models/cgcm2.shtml.

Farquhar, G., Von Cammerer, S., Berry, J. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species. Planta 149:78-90.

Frank, D.A., Kuns, M., Guido, D. 2002. Consumer control of grassland plant production. Ecology 83(3):602–606.

Frank, A.B., Tanaka, D.L., Hofmann, L., Follett, R.F. 1995. Soil carbon and nitrogen of Northern Great Plains grasslands as influenced by long-term grazing. Journal of Range Management 48:470-474.

Frank, D.A., McNaughton, S. J. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oecologia. 96:157-161.

Fynn, R., O'connor, T. 2000. Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa. Journal of Applied Ecology 37:491-507.

Ganjegunte, G., Vance, G., Preston, C., Schuman, G., Ingram, L., Stahl, P., Welker, J. 2005. Soil organic carbon composition in a Northern mixed-grass prairie: effects of grazing. Soil Science Society of America Journal 69:1746-1756.

Garcia, R.L., Long, S.P., Wall, G.W., Osborne, C.P., Kimball, B.A., Nie, G.Y., Pinter P.J.Jr., LaMorte, R.L., Wechsung, F., 1998. Photosynthesis and conductance of spring-wheat leaves: field response to continuous free-air CO2 enrichment. Plant Cell Environ. 21, 659–669.

Giardina, C., Ryan, M. 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature. 404:858-861.

Goverde, M., Arnone, J.A., Erhardt, A. 2002. Species-specific reactions to elevated CO_2 and nutrient availability in four grass species. Basic Appl. Ecol. 3:221–227.

Grant, R.F. 1993. Simulation model of soil compaction and root growth. I. Model development. Plant Soil 150:1-14.

Grant, R.F. 1993b. Simulation model of soil compaction and root growth. I. Model performance and validation. Plant Soil 150:15-24.

Grant, R.F. 1991. The distribution of water and nitrogen in the soil-crop system: A simulation study with validation from a winter wheat field trial. Nutrient Cycling in Agroecosystems. Volume 27(2-3):199-213

Grant, R.F., Nyborg, M., Laidlaw, J. 1993c. Evolution of nitrous oxide from soil: I. Model development. Soil Sci. 156:259–265

Grant, R.F., Nyborg, M., Laidlaw, J. 1993d. Evolution of nitrous oxide from soil: II. Experimental results and model testing. Soil Sci. 156:266–277

Grant, R.F. 1994b. Simulation of ecological controls on nitrification. Soil Biology & Biochemestry 26:305-315.

Grant, R.F., Rochette, P. 1994. Soil microbial respiration at different temperatures and water potentials: Theory and mathematical modelling. Soil Science society of America Journal 58:1681-1690.

Grant, R.F. 1989. Test of a simple biochemical model for photosynthesis of maize and soybean leaves. Agricultural and Forest Meteorology. 48:59:74

Grant, R.F. 1992a. Simulation of carbon dioxide and water deficit effects upon photosynthesis of soybean leaves with testing from growth chamber studies. Crop Science 32:1313-1321.

Grant, R., Black, T., den Hartog, G., Berry, J., Neumann, H., Blanken, P., Yang, P., Russell, C., and Nalder, I. 1999a. Diurnal and annual exchanges of mass and energy between an aspen-hazelnut forest and the atmosphere: Testing the mathematical model Ecosys with data from the BOREAS experiment. J. Geophys. Res., 104(D22):27699-27717.

Grant, R.F., Garcia, R.L., Pinter, P.J., Jr., Hunsaker, D., Wall, G.W., Kimball, B.A., LaMorte, R.L. 1995a. Interaction between atmospheric CO_2 concentration and water deficit on gas exchange and crop growth: Testing of ecosys with data from the Free Air CO_2 Enrichment (FACE) experiment. Global Change Biol. 1:443–454.

Grant, R.F., Arain, A., Arora, V., Barr, A., Black, T.A., Chen, J., Wang, S., Yuan, F., Zhang, Y. 2005. Intercomparison of techniques to model high temperature effects on CO_2 and energy exchange in temperate and boreal coniferous forests. Ecological Modelling 188:217-252.

Grant, R.F., Kimball, B.A., Pinter, P.J. Jr., Wall, G.W., Garcia, R.L., LaMorte, R.L., 1995c. CO_2 effects on crop energy balance: Testing ecosys with a Free-Air CO_2 Enrichment (FACE) Experiment. Agron. J. 87, 446-457.

Grant, R.F. 1995b. Mathematical modelling of nitrous oxide evolution during denitrification. Soil Biology & Biochemestry 27:1117–1125.

Grant, R.F. 1998a. Simulation in ecosys of root growth response to contrasting soil water and nitrogen. Ecological Modelling 107:237–264.

Grant, R.F. 1998b. Mathematical modelling of methanogenesis in ecosys. Soil Biol. Biochem. 30:883-896.

Grant, R.F., Wall, G.W., Kimball, B.A., Frumau, K.F.A., Pinter Jr., P.J.., Hunsaker, D.J., Lamorte, R.L.. 1999b. Crop water relations under different CO_2 and irrigation: Testing of ecosys with the free air CO_2 enrichment (FACE) experiment. Agric. For. Meteorol. 95:27–51

Grant, R.F., Black, T.A., Gaumont-Guay, D., Klujn, N., Barr, A.G., Morgenstern, K., Nesic, Z. 2006. Net ecosystem productivity of boreal aspen forests under drought and climate change: Mathematical modelling with Ecosys. Agricultural and Forest Meteorology, 140:152-170.

Grant, R.F. 2001. A review of the Canadian Ecosystem model ecosys. In: Shaffer, M.J.; Ma, L.W.; Hansen, S. Eds. Modeling Carbon and Nitrogen Dynamics for Soil Management. Boca Raton, Florida, CRC Press. p. 173–264.

Grant, R. F., Flanagan, L. B. 2007. Modeling stomatal and nonstomatal effects of water deficits on CO_2 fixation in a semiarid grassland. Journal of Geophysical Research, 112, G03011, doi:10.1029/2006JG000302.

Grant, R.F., Kimball, B.A., Brooks, T.J., Wall, G.W., Pinter, P.J., Hunsaker, D.J., Adamsen, F.J., Lamorte, R.L., Leavitt, S.W., Thompson, T.L., Matthias, A.D. 2001. Modeling interactions among carbon dioxide, nitrogen, and climate on energy exchange of wheat in a Free Air Carbon Dioxide Experiment. Agronomy Journal 93(3):638-649.

Grant, R.F., Juma, N.G., Robertson, J.A., Izarralde, R.C., McGill, W.B. 2001a. Long-term changes in soil carbon under different fertilizer manure, and rotation: testing the mathematical model ecosys with data from the Brenton plots. Soil Science Soc. Am. J. 65:205-214.

Grant, R.F. 2004. Modeling topographic effects on net ecosystem productivity of boreal black spruce forests. Tree Physiology 24:1-18.

Grant, R.F., Heaney, D.J. 1997. Inorganic phosphorus transformation and transport in soils: mathematical modeling in ecosys. Soil Science Society of America Journal 61(3):752-764.

Grant, R.F., Hesketh, J. 1992. Canopy structure of maize (Zea mays) at different populations: simulation and experimental verification. Biotronics 21:11-24.

Grant, R.F. 1992b. Simulation of carbon dioxide and water deficit effects upon photosynthesis and transpiration of soybean canopies with testing from growth chamber studies. Crop Science 32:1322-1328.

Grant, R.F., Barr, A.G., Black, T.A., Margolis, H.A., Dunn, A.L., Metsaranta, J., Wang, S., McCaughey, J.H., Bourque, C.A. 2009. Interannual variation in net ecosystem productivity of Canadian forests as affected by regional weather patterns – A Fluxnet-Canada synthesis. Agricultural and Forest Meteorology, 149:2022–2039

Grant, R.F. 1997. Changes in soil organic matter under different tillage and rotation: mathematical modelling in Ecosys. Soil Science Society of America Journal 61:1159-1174.

Grant, R.F.; Robertson, J.A. 1997. Phosphorus uptake by root systems: mathematical modelling in ecosys. Plant Soil 188:279-297.

Grant, R.F., Rochette, P. 1994. Soil microbial respiration at different water potentials and temperatures: theory and mathematical modeling. Soil Science Society of America Journal 58:1681–1690.

Henderson, D., Ellert, B., Naeth M. 2004. Grazing and soil carbon along a gradient of Alberta rangelands. Journal of Range Management 57:402-410.

Holechek, J., Pieper, R., Herbel, C. 2001. Range management, principles and practices. New Jersey, Prentice Hall. 587 p.

Holland E., Parton, W., Detling, J., Coppock, D. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. The American Naturalist 140:685-705.

Hunsaker, D.J., Kimball, B.A., Pinter Jr., P.J., LaMorte, R.L., Wall, G.W., 1996. Carbon dioxide enrichment and irrigation effects on wheat evapotranspiration and water use efficiency. Trans. ASAE 39:1345-1355.

Hunt, H.W., Trlica, M.J., Redente, E.F., Moore, J.C., Detling, J.K., Kittel, T.G.F., Walter, D.E., Fowler, M.C., Klein, D.A., Elliott, E.T., 1991. Simulation model for the effects of climate change on temperate grassland ecosystems. Ecol. Model. 53, 205–246.

Intergovernmental Panel on Climate Change (IPCC). 2006. Technical summary. In Climate Change 2001: The Scientific Basis. Houghton J.T.; Ding, Y.; Griggs, D.J.; Noguer, M. Eds. Cambridge, University Press. p. 21–83.

Itoh, S., Barber, S.A. 1983. Phosphorus uptake by six plant species as related to root hairs. Agronomy Journal 75(3):457-461.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108:389-411

Jones, C., McConnell, C., Coleman, K., Cox, P., Falloon, P., Jenkinson, D., Powlson, D.2005. Global climate change and soil carbon stocks; predictions from two contrasting models for the turnover of organic carbon in soil. Global Change Biology. 11:154–166.

Jones, M.B., Donnelly, A. 2004. Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO_2. New Phytologist 164(3): 423-439.

Kicklighter D.W., Bruno M., Donges S. 1999. A first-order analysis of the potential role of CO_2 fertilization to affect the global carbon budget: a comparison of four terrestrial biosphere models. Tellus, 51B, 343–366.

Kimmins, J.P. 1987. Forest ecology. New York, McMillan. 531 p.

Kimball, B.A., Pinter Jr., P.J., Garcia, R.L., LaMorte, R.L., Wall, G.W., Hunsaker, D.J., Wechsung, G., Wechsung, F., Kartschall, T., 1995. Productivity and water use of wheat under free-air CO_2 enrichment. Global Change Biol. 1, 429±442.

Kuzyk, G.W., Hudson, R.J. 2007. Animal-unit equivalence of bison, elk and mule deer in the aspen parkland of Alberta. In press.

Lal, R. 2004. Agricultural activities and the global carbon cycle. Nutrient Cycling in Agroecosystems 70:103-116.

Lal, R. 2002. Soil carbon dynamics in cropland and rangeland. Environmental Pollution 116 (3):353-362.

Landi, A.; Mermut, A.R.; Anderson, D.W. 2004. Carbon distribution in a hummocky landscape from Saskatchewan, Canada. Soil Science Society of America Journal 68(1):175-184.

Larcher, W. 2003. Physiological plant ecology: ecophysiology and stress physiology of functional groups. 4th ed. Berlin, Springer-Verlag. 513 p.

Levy, P.E., Cannell, M.G.R., Friend, A.D. 2004. Modelling the impact of future changes in climate, CO_2 concentration and land use on natural ecosystems and the terrestrial carbon sink. Global Environmental Change 14:21–30.

Li, T., Grant, R.; Flanagan, L. 2004. Climate impact on net ecosystem productivity of a semi-arid natural grassland: modeling and measurement. Agricultural and Forest Meteorology 126(1-2):99-116.

Liebig, M.A., Gross, J.R., Kronberg, S.L., Hanson, J.D., Frank, A.B., Phillips, R.L. 2006. Soil response to long-term grazing in the northern Great Plains of North America. Agriculture, Ecosystems and Environment 115:270-276.

Lizama, H.M., Suzuki, I. 1990. Kinetics of sulfur and pyrite oxidation by Thiobacillus thiooxidans. Competitive inhibition by increasing concentrations of cells. Canadian Journal of Microbiology 37:182–187.

Loeser, M., Crews, T., Sisk, T. 2004. Defoliation increased above-ground productivity in a semi-arid grassland. Journal of Range Management 57:442-447.

Makino, A., Harada, M., Sato, T., Nakano, H., Mae, T. 1997. Growth and N allocation in rice plants under CO_2 enrichment. Plant-Physiology115(1): 199-203.

Marissink, M., Pettersson, R., Sindhøj, E. 2002. Above-ground plant production under elevated carbon dioxide in a Swedish semi-natural grassland. Agriculture, Ecosystems and Environment 93:107–120.

McGill, W.B., Hunt, H.W., Woodmansee, R.G., Reuss, J.O. 1981. Phoenix, a model of the dynamics of carbon and nitrogen in grassland soils. In Terrestrial Nitrogen Cycles. Clark, F.E., Rosswall, T. Eds. Ecology Bulletin 33:49-115.

McIntosh, P.D., Allen, R.B., Scott, N. 1997. Effects of exclosure and management on biomass and soil nutrient pools in seasonally dry high country, New Zealand. Journal of Environmental Management 51:169–186.

Milchunas, D.G., Lauenroth, W.K. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63(4):327–366.

Morgan, J. 2002. Looking beneath the surface. Science 298:1903-1904.

Morgan, J., Lecain, D., Mosier, A., Milchunas, D. 2001. Elevated CO_2 enhances water relations and productivity and affects gas exchange in C_3 and C_4 grasses of the Colorado shortgrass steppe. Global Change Biology 7: 451-466.

Morgan, J., Pataki, D., Korner, H., DelGrosso, S., Grunzewig, J., Knapp, A., Mosier, A., Newton, P., Niklaus, P., Nippert, J., Nowak, R., Parton, W., Polley, H., Shaw, M. 2004. Water relations in grasslands and desert ecosystems to elevated atmospheric CO_2. Oecologia 140:11-25

Morley, F.H.W. 1981. Grazing animals. Amsterdam, Elsevier. 411 p.

Nelson, J.A., Morgan, J.A., LeCain, D.R., Mosier, A.R., Milchunas, D.G., Parton, B.A. 2004. Elevated CO_2 increases soil moisture and enhances plant water relations in a long-term field study in semi-arid shortgrass steppe of Colorado. Plant and Soil 259: 169–179.

Owensby, C.E., Ham, J.M., Knapp, A.K., Auen, L.M. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO_2. Global Change Biology 5(5): 497-506.

Owensby, C., Ham, J., Knapp, A., Bremer, D., Auen, L. 1997. Water vapour fluxes and their impact under elevated CO_2 in a C_4-tallgrass prairie. Global Clim. Change 3:189–195.

Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Schimel, D.S., Hall, D.O., Scopegram Group Members, 1995. Impact of climate change on grassland production and soil carbon worldwide. Global Change Biol. 1, 13–22.

Parton, W.J., Ojima, D.S. 1996. Environmental change in grasslands: Assessment using models. Climatic Change 28:111-141.

Pepper, D.A., Del Grosso , S.J., McMurtrie, R.E., Parton, W.J. 2005. Simulated carbon sink response of shortgrass steppe, tallgrass prairie and forest ecosystems to rising [CO_2], temperature and nitrogen input. Global Biogeochemical Cycles. 19 GB1004, doi:10.1029/2004GB002226.

Perez Corona, M.E., Vazquez de Aldana, B.R., Garcia Criado, B., Garcia Ciudad, A.1998. Variations in semiarid grasslands. Journal of Range Management 51(5):570-576.

Picon-Cochard, C., Teyssonneyre, F., Besle, J., Soussana, J. 2004. Effects of elevated CO_2 and cutting frequency on the productivity and herbage quality of a semi-natural grassland. European Journal of Agronomy 20:363–377.

Reeder J.D., Schuman, G.E. 2002. Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands. Environmental Pollution 116: 457–463.

Reich, P.B., Hobbie, S.E., Lee, T., Ellsworth, D.S., West, J.B., Tilman, D., Knops, J.M.H., Naeem, S., Trost, J. 2006. Nitrogen limitation constrains sustainability of ecosystem response to CO_2. Nature, 440, 922–925.

Reid, J.B., Huck, M.G. 1990. Diurnal variation of crop hydraulic resistance: a new analysis. Agronomy Journal 82:827-834.

Riedo, M., Gyalistras, D., Fuhrer, J. 2000. Net primary production and carbon stocks in differently managed grasslands: simulation of site-specific sensitivity to an increase in atmospheric CO_2 and to climate change Ecological Modelling 134:207–227.

Rogers, G.S., L. Payne, P. Milham, and J. Conroy. 1993. Nitrogen and phosphorus requirements of cotton and wheat under changing CO_2 concentrations. p. 257–260 In J. Barrow (ed.) Plant nutrition: From genetic engineering to field practice. Kluwer Academic Publ., Dordrecht, the Netherlands.

Ross, D., Newton, P., Tate, K. 2004. Elevated [CO_2] effects on herbage production and soil carbon and nitrogen pools and mineralization in a species-rich, grazed pasture on a seasonally dry sand. Plant and Soil 260: 183–196.

Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J., Gurevitch, J. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543–562.

Ryan, M.G. 1991. Effects of climate change on plant respiration. Ecol. Appl. 1:157–167.

Saliendra, N.Z., Meinzer, F.C. 1991. Symplast volume, turgor, stomatal conductance and growth in relation to osmotic and elastic adjustment in droughted sugarcane. Journal of Experimental Botany 42(243): 1251-1259.

Schimel, D.S., Braswell, B.H., Holland, E.A. 1994. Climatic, edaphic and biotic controls over storage and turnover of carbon in soils. Global Biogeochemical Cycles, 8, 279–293.

Schuman, G., Reeder, J., Manley, J., Hart, R., Manley, W. 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecological Applications 9:65-71.

Schuman, G.E., Herrick, J.E., Janzen, H.H. 2000. The Dynamics of soil carbon in rangelands. In Follet, R.F., Kimble, J.M., Lal, R. The potential of U.S. grazing lands to sequester carbon to mitigate the greenhouse effect. Boca Raton, Florida, Lewis. p. 267-290.

Schuman, G.E., Janzen, H.H., Herrick, J.E. 2002. Soil carbon dynamics and potential carbon sequestration by rangelands. Environmental Pollution 116(3): 391-396.

Sindhøj, E., Andren, O., Katterer, T., Gunnarsson, S., Pettersson, R. 2006. Projections of 30-year soil carbon balances for a semi-natural grassland under elevated CO_2 based on measured root decomposability. Agriculture, Ecosystems and Environment 114:360–368.

Snyman, H.A., Preez, C.C. du. 2005. Rangeland degradation in a semi-arid South Africa - II: Influence on soil quality. Journal-of-Arid-Environments 60(3): 483-507.

Stitt, M. 1991. Rising CO_2 levels and their potential significance for carbon flow in photosynthetic cells. Plant Cell Environ. 14:741-762.

Thornley, J.H.M. 1995. Shoot:root allocation with respect to C, N and P: an investigation and comparison of resistance and teleonomic models. Annals of Botany 75(4): 391-405

Thornley, J.H.M., Cannell, M.G.R. 1997. Temperate grassland responses to climate change: an analysis using the Hurley Pasture Model. Annals of Botany 80(2): 205-221.

Thuille, A.., Buchmann, N., Schulze, E. 2000. Carbon stocks and soil respiration rates during deforestation, grassland use and subsequent Norway spruce afforestation in the Southern Alps, Italy. Tree Physiology 20:849–857.

Twine, T.E., Kucharik, Ch.J. 2009. Climate impacts on net primary productivity trends in natural and managed ecosystems of the central and eastern United States. Agricultural and Forest Meteorology 149:2143–2161.

Van Groenigen, K.J., Six, J., Hungate, B.A., De Graaff, M.A., Van Breemen, N., Van Kessel, C. 2006. Element interactions limit soil carbon storage. Proceedings of the National Academy of Sciences of the United States of America, 103: 6571–6574.

van Kessel, C., Boots, B., De Graaff, M., Harris, D., Blum, H., Six, J. 2006. Total soil C and N sequestration in a grassland following 10 years of free air CO_2 enrichment. Global Change Biology 12:2187–2199.

Van Soest, P. 1994. Nutritional ecology of the ruminant. Portland, Durham and Downey. 374 p.

Ventera, R.T., Lovett, G.M., Groffman, P.M., Schwarz, P.A. 2003. Landscape patterns of net nitrification in a northern hardwood conifer forest. Soil Sci. Soc. Am. J. 67:527-539.

Volk, M., Niklaus, P.A., Korner, C. 2000. Soil moisture effects determine CO_2 responses of grassland species. Oecologia, 125(3):380-388.

Wanga, Y., Zhoua, G., Jia, B. 2008. Modeling SOC and NPP responses of meadow steppe to different grazing intensities in Northeast China. Ecological Modelling. 217:72–78

Wever, L.A., Flanagan, L.B., Carlson, P.J. 2002. Seasonal and interannual variation in evapotranspiration, energy balance and surface conductance in northern temperate grassland, Agric. For. Meteorol., 112:31– 49.

Williams, M.A., Rice, C.W., Omay, A., Owensby, C. 2004. Carbon and nitrogen pools in a tallgrass prairie soil under elevated carbon dioxide. Soil Science Society of America Journal 68:148–153.

Wright, A., Hons, F., Rouquette, F. 2004. Long-term management impacts on soil carbon and nitrogen dynamics of grazed bermuda grass pastures. Soil Biology and Biochemistry 36:1809-1816.

Zhang, L., Wylie, B., Loveland, T., Fosnight, E., Tieszen, L.L., Ji, L., Gilmanov, T. 2006. Evaluation and comparison of gross primary production estimates for the Northern Great Plains grasslands. Remote Sensing of Environment:10.1016/j.rse.2006.08.012.

Zhang, Y., Grant, R.F., Flanagan, L.B., Wang, S., Verseghy, D.L. 2005. Modelling CO_2 and energy exchanges in a northern semiarid grassland using the carbon- and nitrogen-coupled Canadian Land Surface Scheme (C-CLASS). Ecological Modelling, 181: 591-614.

Zhuang, Q., McGuire, J.M., Clein, J.S. 2003. Carbon cycling in extratropical terrestrial ecosystems of the Northern Hemisphere during the 20th century: a modeling analysis of the influences of soil thermal dynamics. Tellus, 55B, 751–776.

Chapter 6.0. General overview

Rangelands, a natural ecosystem widespread in Canada, are an important source of land for animal production and around 26 million ha of them are utilized for beef production (Alberta Agriculture, Food and Rural Development 2005). In Alberta, rangelands account for 6.6 million ha and they provide up to 50% of total forage for livestock, a business worth close to $30 billion per year (Southern Alberta Land Trust Society 2006). Thus, this ecosystem plays an important role in the national economy.

At present, a large percent of grasslands all over the world is overused and has low productivity (Conant *et al*. 2001), and around 50% of rangelands located in the Canadian Prairies are in less than good condition (Agriculture and Agri-Food Canada 2000). As do other natural ecosystems, rangelands maintain soil fertility through nutrient cycling which is based on litter decomposition. However when there is grazing, nutrient redistribution occurs and nutrient cycling in the ecosystem is altered. This nutrient redistribution causes different nutrient cycling rates to occur over the landscape and that influences plant productivity (Perez *et al*. 1998, Asamoah *et al*. 2004) which also is affected by topography. Therefore, to develop sustainable grazing systems it is necessary to know the magnitude of grazing and topography effects on plant productivity.

Topography influences water movement, and with it redistributes soil nutrients and soil particles in any landscape, altering soil conditions along a topographic gradient (Kachanoski *et al*. 1999) and thus influencing microbial activity and decomposition. In consequence there will be more rapid nutrient cycling and more soil available nutrients in lower topographic locations compared with those adjacent uplands, and this is reflected in plant productivity. Additionally when there is grazing it can change litter chemical composition which affects decomposition and with it the release of nutrients. Thus both factors can influence nutrient cycling and therefore also influence plant productivity.

Aspect is another factor that influences microbial activity because depending on it, slopes receive different sunlight which is directly linked to soil temperature and soil moisture, and hence with microbial activity and decomposition. That is going to be reflected in plant productivity.

For these reasons I investigated the influence of topography, grazing and aspect, on shoot litter and root decomposition through different litterbag experiments established in a grassland with variable topography located at Kinsella Ranch Experimental Station, Central Alberta.

To set these experiments there was collected shoot litter and roots from upper (U), middle (M), and lower (L) topographic locations. These plant materials, denominated Local, were placed on top of the soil in the same topographic location (U, M, L) or condition (grazed or ungrazed) in which it was collected. A mix of each material (shoot or roots, grazed or ungrazed) collected at M, and named composite, was also placed along a topographic transect under grazing and ungrazed condition. Roots were buried at 0.15m depth.

Data loggers were placed at those topographic locations to get soil moisture (θ) and temperature (T_s). These data were used with scalar functions (f_θ and f_t respectively) to determine if these two soil variables could explain variations in litter decomposition measured in the field experiments described above. θ was transformed into relative water filled porosity (RWFP), and T_s was formulated as an Arrhenius function (Stroo *et al*. 1989). These functions were considered to be multiplicative (Andrén *et al*. 1992), so that when soil temperature was close to 25°C and RWFP around 0.6, the product of the two functions will give the maximum rate of litter decomposition. To derive a $\boldsymbol{k}$, the hourly product of f_θ and f_t was multiplied by a test value of $\boldsymbol{k}$ to simulate hourly declines in remaining mass (X). This $\boldsymbol{k}$ was then adjusted to get the minimum root mean square for differences between modeled and measured X for a given litter type during the decomposition experiments. The resulting reference value of $\boldsymbol{k}$ was used with f_θ and f_t to test whether differences in X measured at U, M and L could be attributed to differences in T_s and θ.

A topographic effect on decomposition ($P<0.0001$) was found for composite shoot litter because measured remaining mass during the first year (Oct. 2004 – Oct. 2005) was smaller at L than at M and U. Better soil conditions at L (deeper soil layer, greater soil nitrogen, carbon and water holding capacity) and greater RWFP compared with U, stimulated litter decomposition. Cooler soil at L did not decrease decomposition, as also found by Giardina and Ryan (2000). This means that θ probably limited decomposition more than did T_s. Topography no longer apparently influenced composite shoot litter mass loss after October 2005 probably because the less recalcitrant litter fractions had mostly finished decomposing.

The simulated mass loss with the decomposition functions developed for θ and T_s was similar among topographic locations during the first autumn and winter of the litterbag study, which indicated that faster mass loss measured at L could not be attributed to topographic effects on θ and T_s. However during the following spring and summer (May – July 2005), the simulated litter mass loss was more rapid at L than at M and U, so that topographic effects on θ and T_s largely explained the more rapid mass loss measured at L during this period. There was not any topographic effect on root decomposition which may have been caused by offsetting effects of higher T_s and lower θ at the 0.15 m depth to which the root litter was placed along the hill. The modeled root decomposition showed the same trend than measured; and simulated values were in the standard deviation range of measured values.

Regarding to grazing, there was effect of it on shoot litter decomposition. Local grazed shoot litter (coming from grazed condition and placed in a grazed condition) decomposed more slowly than did ungrazed litter (coming from ungrazed condition and placed in an ungrazed condition) at M but more rapidly at L ($P<0.0127$) during the first sampling time (October 2004), while at U there was no difference between grazing treatments. Those contrasting results may be explained by greater lignin content of grazed vs. ungrazed shoot litter at M, but smaller lignin content at L. Previous research results showed that grazing could decrease nutrients lowering litter quality (McIntosh *et al*. 1997, Smit and Kooijman 2001), reducing microbial activity (Cao *et al*. 2004) and hence decomposition rate. The comparisons of modeled vs measured shoot litter and root remaining mass showed good agreement without statistical differences.

We also found an aspect effect on litter decomposition. There was greater remaining mass of shoot litter ($P<0.05$) at south than at north slopes 67 days after the beginning of the experiment which agrees with previous findings (Barnes *et al*. 1998, Mudrick *et al*. 1994, Sariyildiz *et al*. 2005). At the end of the experimental time (247 experimental days), there was similar mass loss in both aspects probably because the more labile carbon compounds were exhausted, and the remaining and more recalcitrant litter components with slower and similar decomposition rates became the greater components of the remaining mass (Barnes *et al*. 1998). Aspect did not affect mass loss of local root litter at different topographic positions (67.3±1.9 N vs 65.2±1.9 S at U, 68.6±1.7 N vs 68.5±1.6 S at M, and 70.3±2.4 N vs 69.3±2.5 S at L), nor of composite root litter (70.7±1.0 at N vs. 69.4±1.1 at S), grazed or not (69.4±2.2 grazed and 74.7±4.8 ungrazed at N, vs. 70.6±2.2 grazed and 65.7±4.9 ungrazed at S), probably because at 0.15m depth aspect did not affect soil environment (moisture and temperature).

According to proximate analysis results, grazing caused important differences ($P<0.0023$) in the initial chemical composition of local shoot litter at each topographic location. Grazing increased the initial lignin at M ($P<0.0034$) but decreased it at L

(P<0.001), without changing that at U, which explain the different decomposition rates found in the field. Grazing also influenced concentrations of holocellulose, non-polar compounds, and water-soluble compounds in different ways at each location. This was explained by differences in the amount of foliage produced and consumed at each topographic location, which would affect the quality of litter produced. Differences in chemical composition of roots did not cause different decomposition rates indicating that factors other than chemical composition determine root decomposition (van der Krift *et al*. 2002).

These results showed that shoot litter decomposition differs along a topographic gradient in this semiarid grassland ecosystem, which could possibly explain differences in plant productivity along the hill. Therefore, to develop sustainable grazing systems that may keep stable ecosystem productivity over time with animal production, it is important to know how variable is plant productivity in landscapes with variable topography. Modeling is a good way to get this knowledge because through simulation it is possible to reproduce field conditions and test hypotheses that contribute with our understanding of different processes that influence the plant growth and its productivity.

There is evidence that topography influences plant productivity through its effect on soil characteristics and hence on soil carbon content, which is directly linked with good soil properties (structure and texture, water holding capacity, nutrient availability, and soil biodiversity (Karlen and Andrews 2000, Singer and Ewing 2000, Lal 2004) and litter decomposition. Thus, as soil properties usually are better at lower topographic locations the plant biomass is likely to be greater at lower than at upper slope positions (Norton *et al*. 2003, Small and McCarthy 2005).

In semiarid grasslands differences in above ground plant productivity has been found to be related with topography (Perez *et al*. 1998, Asamoah *et al*. 2004), probably that is the result of greater water holding capacity, soil carbon and soil nitrogen contents as they increase down slope (Schimel *et al*. 1985b, Honeycutt *et al*. 1990, Small and McCarthy 2005). Moreover when there is grazing, depending on its intensity it can reduce or increase plant productivity, and hence litterfall, its decomposition, and soil carbon (Loeser *et al*. 2004, Donkor *et al*. 2002). Grazing decreases plant productivity because it involves consumption of above ground plant biomass and reduces the photosynthetic area. If this reduction is too large plants need to remobilize significant amounts of stored carbohydrates and use them as energy source for plant regrowth because the reduced foliage cannot fix enough CO_2. However there is evidence showing that grazing can increase plant productivity (Schuman *et al.* 2002, Wright *et al.* 2004). This plant response is known as overcompensation because defoliated plants partially or fully compensate the removal of biomass (Belsky 1986), and usually this occurs under moderate and light grazing.

Even though topography and grazing influence plant productivity and soil carbon, there is still not enough available information about these influences in semiarid grasslands. This information is required to develop appropriate grazing intensity to prevent ecosystem degradation. One way to do this is through simulation of plant and soil carbon stocks at different topographic locations under grazed and ungrazed conditions. Different models have been utilized to simulate grassland productivity (Owensby *et al.* 1999, Li *et al.* 2004, Shen *et al.* 2005, Barrett *et al.* 2005) and grazing (Cohen *et al.* 1995, Diaz-Solis *et al.* 2006, Donkor *et al.* 2002, Donkor *et al.* 2007), but they did not take topography into account.

In this research *ecosys*, a comprehensive mathematical model for natural and managed ecosystems was utilized to simulate a grassland ecosystem located at Kinsella Ranch, because it has the capability of taken into consideration topography and grazing effects on plant productivity. Previous model tests showed good agreement of model vs measured data coming from different field experiments carried out under similar climatic conditions to those of this research (Li *et al.* 2004, Grant and Flanagan 2007).

Ecosys simulated, as found in the field, a topographic effect on total aboveground plant biomass which was greater at M and at L than at U. The modeled grazing decreased the grass carbon at U (33%) and at M (23%), but increased it at L (51%) and increased shrub carbon (16%, 7%, and 54%, at U, M, and L). Modeled grazing reduced plant carbon differently because animal consumption was not the same at each topographic location. Even though average animal consumption was set at the beginning of modeled run, *ecosys* also allocated consumption at different topographic positions according to available forage. Thus, in the simulation animals grazed more where there was more forage to meet their requirements. As M had greater modeled plant growth than U, animal consumption was 13% greater at M. Modeled grass carbon decreases at M with grazing (17% and 25%) during 2004 and 2005 were similar to those measured (18% and 36%).

Modeled grazing at M, compared with modeled ungrazed values, reduced total root biomass between 4% and 22%. Measured root biomass also was reduced by grazing, between 6% and 20%, but without statistical significance. Modelled root biomass was within the standard deviation range of measured root biomass at M (the only place in which root biomass was measured at Kinsella Ranch) from 2003 to 2005 that indicated good agreement between modelled and measured results. In the simulated topographic transect grass root carbon was reduced by grazing at U (42%) and M (35%), but increased at L (34%); the aspen root carbon also was decreased 26% by grazing. Modeled grazing increased the shrub root carbon by 24%, 22% and, 39% at U, M and, L respectively. Reduced root carbon from grazing in grasses was the result of animal consumption that decreased above ground biomass, the leaf area index and hence photosynthates. This reduced the carbon allocated to the roots, and consequently their growth and biomass. Similar findings in field experiments were reported by Han *et al.* (2008).

The increase of shrub root carbon at U and M was related with the reduction that grazing caused in grasses which decreased the competition for light, water and nutrients allowing the increase in shoot and root carbon of shrubs. The increase in grass and shrubs with grazing at L is explained by reduction of aspen shoot carbon caused by modeled grazing and browsing that reduced competition for available resources. This also shows that grazing can have different effects on growth of different species depending on the intensity with which each species is grazed. These modeled results are consistent with field measurements showing that grazing can stimulate (Schuman *et al*. 2002, Wright *et al*. 2004, Loeser *et al.* 2004) or decrease (Derner *et al.* 2006, Conant and Paustian 2002, Ferraro and Oesterheld 2002) plant growth.

During 2005 the total simulated consumption (calculated as animal live weight per m^2 multiplied by specific grazing rate) was 33.3 g C m^{-2}. Measured values of animal consumption at the experimental field in 2005, with equal total weight to that used by *ecosys*, were in a range from 30.0 to 43.4 g C m^{-2} (Kuzyk and Hudson 2007). Therefore, algorithms used by *ecosys* to simulate animal consumption reproduced the actual measured animal consumption.

Grazing by affecting plant biomass also influences root biomass and with it the root-to-shoot ratio (R:S). The measured ungrazed R:S ratio at M, at DOY 202, was 5.0 in 2004 and 5.1 in 2005, while grazed R:S was 5.4 and 6.3 in those same years. These ratios were similar to those modeled without grazing (4.3 and 4.7), and with grazing (4.8 and 8.5) in 2004 and 2005 respectively. The modeled R:S along the topographic transect during the growing season of 2005 without grazing was similar at U and at M (5.6), and higher at L (6.7). Under simulated grazing, U had the smaller ratio (6.8) followed by M (7.4), and L (10.4). These ratios were similar to those measured by Schiborra *et al.* (2009) who found a range from 3.0 to 11.7 in a semiarid grassland in a Chernozem soil. Previously Jackson (1996) reported a R:S ratio of 3.7 for temperate grasslands.

Because grazing reduces above and below ground plant biomass, to get better understanding of grazing effects along a topographic gradient on this grassland ecosystem, there was simulated with *ecosys* a carbon balance at different topographic locations (U, M, and L) with and without grazing, which will indicate if an ecosystem is carbon sink (NBP > 0) or source (NBP < 0). A grassland ecosystem is carbon sink if the amount of carbon fixed through photosynthesis, part of which is incorporated into the soil from above and belowground litterfall, leads to an increase in the soil carbon pool over time (Law *et al*. 2001).

Under stable climatic conditions and without any important disturbance like fire or heavy grazing, NBP in water limited ecosystems like semiarid natural ecosystems varies over time depending on changes in annual precipitation (Bork *et al*. 2001). However, net ecosystem productivity (NEP) may also be affected by spatial variation in plant productivity over the landscape, independent of climatic conditions. This variation results from uneven distribution of soil resources because of topography, which needs to be known to understand the carbon balance in the whole ecosystem.

Therefore, there is variability in plant productivity over the landscape as a result of soil properties that change with topography and that has to be reflected in NEP. This variability should be characterized when proposing grazing systems to avoid ecosystem degradation. This information is also needed to develop simulation models that will allow better understanding of ecosystem processes, which can then be used to improve predictions of grazing effects on ecosystem productivity and stability. Based on this, through *ecosys* model, the influence of topography and grazing on NEP was investigated, and the results showed as carbon balances at different topographic locations.

The simulated carbon balance at M without grazing showed that NEP changed from positive (carbon sink) during 2003 (115 g C m^{-2} y^{-1}) and 2004 (19 g C m^{-2} y^{-1}), to negative (carbon source) in 2005 (-98 g C m^{-2} y^{-1}) showing that there was a strong year effect which was attributed to the effects of antecedent weather on productivity. 2002 was a dry year (annual rainfall was 46% below average, and growing season rainfall 100mm), and low θ limited plant growth and hence litterfall, which occurs mainly after July. As litterfall is carried over the next growing season, reduced litterfall in 2002 reduced R_h in 2003. Also more precipitation during the growing season (189mm) compared to that in 2002, raised plant productivity. Thus, the carbon balance showed positive NEP.

Greater rainfall during the growing season of 2004 (138mm) and 2005 (164mm), compared to that in 2002, in combination with greater amount of litterfall because of less θ limitation for plant growth, stimulated microbial activity and hence R_h. Thus the combination of different factors (previous litterfall, rainfall, and soil temperature) raised R_h and reduced NEP to the point that it became negative and this ecosystem became a carbon source in 2005.

Modeled grazing in 2004 and 2005 decreased gross primary productivity (GPP), and hence autotrophic respiration (R_a) by removing above ground biomass, which reduced litterfall. That decreased R_h but less than it did NPP, thereby reducing net biome productivity (NBP = NEP – carbon consumed by grazing animals and not returned as manure), changing M from carbon sink without grazing to carbon source with grazing in 2004 (-33 g C m^{-2} y^{-1}), and to a greater carbon source in 2005 (-192 g C m^{-2} y^{-1}). If this reduction were sustained, grazing intensity would have to be decreased to avoid ecosystem degradation.

Simulated carbon balance without grazing showed that, averaged from 2003 to 2005, U was source of 4 g C m^{-2} y^{-1}, but M and L were carbon sinks of 12 and 132 g C m^{-2} y^{-1} respectively. Simulated grazing, compared with the ungrazed condition, reduced NBP by 35 and 37 g C m^{-2} y^{-1} at U and M, turning these two locations into carbon sources. At L, grazing reduced NBP by 51 g C m^{-2} y^{-1} but still it was a carbon sink (81g C m^{-2} y^{-1}). Simulated grazing caused smaller variations in NEP than did rainfall. Thus, the simulated adverse effect of grazing on NBP at all topographic positions was the result of animal consumption that decreased the leaf area index by 12% and 15% during 2004 and 2005. In consequence, the plants reduced their growth (reflected in smaller GPP) and hence litterfall (16%, 14% and 9% at U, M, and L respectively), so that C inputs were lowered.

Based on these results and knowing that climate is changing, there was investigated the effect that moderate long term grazing (2.35 AUM ha^{-1}) should cause on carbon balance through the use of *ecosys* model. Climatic projections were done under current climatic conditions, and with projections of a GCM for Central Alberta to examine the climate change effect; there were analyzed carbon budgets and soil organic carbon (SOC) changes at different topographic locations over a simulated century.

Under current climate the carbon budget showed that U, whether grazed or not, probably will be a carbon source (NEP=-1 g C m^{-2} y^{-1} and NBP=-14 g C m^{-2} y^{-1}); the M location without grazing should be a carbon sink (NEP = 4 g C m^{-2} y^{-1}) but a C source (-13 g C m^{-2} y^{-1}) with grazing. At L, NEP and NBP were positive (21 and 10 g C m^{-2} y^{-1})

showing that grazing can be kept at this topographic location at the simulated intensity because it is not going to cause any net carbon loss. At the end of the simulated century, grazing decreased the soil carbon at U and M (4 g m^{-2} y^{-1} at each topographic location) and at L (2 g m^{-2} y^{-1}) compared with that without grazing, but L location was the only place that with grazing still increased SOC. This reinforces the finding that grazing can be maintained in this part of the ecosystem.

Under climate change, grazing reduced NBP by 11, 21 and 36 g C m^{-2} y^{-1} at U, M and L compared with the ungrazed condition. However, all topographic locations had positive NBP with and without grazing, and therefore were carbon sinks. The SOC increased in both grazing treatments, but more without (13, 9, and 15 g m^{-2} y^{-1} at U, M and L) than with grazing (10, 5, and 11 g m^{-2} y^{-1}) in those same topographic locations compared with without climate change condition. This is an indication that climate change should benefit this ecosystem because grazed or not soil carbon will increase at all topographic locations. Moreover because of the stimulus that climate change is going to cause in the plant growth in this ecosystem, grazing intensity could be increased to take advantage of the simulated additional plant biomass produced.

Finally, because *ecosys* results were comparable with those reported in scientific literature, this model can be confidently used to simulate grazing effects on semiarid temperate grassland ecosystems under current and climate change scenario.

References

Agriculture and Agri-Food Canada. 2000. http://res2.agr.ca/Lethbridge/rep2000/rep0208b_e.htm

Alberta Agriculture, Food and Rural Development. 2005. http://www.salts-landtrust.org/conservingrangelands.html#top

Andrén, O., Steen, E., Rajkai, K. 1992. Modelling the effects of moisture on barley straw and root decomposition in the field. Soil Biology and Biochemistry, 4(8):727-736.

Asamoah, S., Bork, E., Irving, B., Price, M., Hudson, R. 2004. Seasonal herbage dynamics on aspen parkland landscape in central Alberta. Canadian Journal of Animal Science 84:149-153.

Barnes, B.V.; Zak, D.R.; Denton, S.R.; Spurr, S.H. 1998. Forest ecology. 4 ed. New York, Wiley. 774 p.

Barrett, P.; Laidlawb, A.; Mayne, C. 2005. GrazeGro: a European herbage growth model to predict pasture production in perennial ryegrass swards for decision support. European Journal of Agronomy 23:37-56.

Belsky, A. 1986. Does herbivory benefit plants? A review of the evidence. The American Naturalist 127(6):870-892.

Bork, E., Thomas, T., McDougall, B. 2001. Herbage response to precipitation in central Alberta boreal grasslands. Journal of Range Management 54:243–248.

Cao, G., Tang, Y., Mo, W., Wang, Y., Li, Y., Zhao, X. 2004. Grazing intensity alters soil respiration in an alpine meadow on the Tibetan plateau. Soil Biology and Biochemistry 36:237-243.

Cohen, R.; Donnelly, J.; Moore, A.; Leech, F.; Bruynooghe, J.; Lardner, H. 1995. GrassGro – a computer decision support system for pasture and livestock management. American Society of Animal Science 46:376-379.

Conant, R.T.; Paustian, K.; Elliott, E.T. 2001. Grassland management and conversion intro grassland:effects on soil carbon. Ecological Applications 11:343-355.

Derner, J.D., Boutton, T.W., Briske, D.D. 2006. Grazing and ecosystem carbon storage in the North American Great Plains. Plant and Soil 280(1-2): 77-90.

Diaz-Solis, H.; Kothmann, M.; Grant, W.; De Luna-Villarreal, R. 2006. Use of irrigated pastures in semi-arid grazinglands: A dynamic model for stocking rate decisions. Agricultural Systems 88:316-331.

Donkor, N.; Gedir, J.; Hudson, R.; Bork, E.; Chanasyk, D.; Naeth, M. 2002. Impacts of grazing systems on soil compaction and pasture production in Alberta. Canadian Journal of Soil Science 82:1-8.

Donkor, N.; Hudson, R.; Bork, E. 2007. Simulation and quantification of pasture condition and animal performance on boreal grasslands in Alberta. Agricultural Systems. 93(1-3):229-251.

Ferraro, D., Oesterheld, M. 2002. Effect of defoliation on grass growth. A quantitative review. Oikos. 98:125-133.

Giardina, C., Ryan, M. 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature. 404:858-861.

Grant, R. F., Flanagan, L. B. 2007. Modeling stomatal and nonstomatal effects of water deficits on CO_2 fixation in a semiarid grassland. Journal of Geophysical Research, 112, G03011, doi:10.1029/2006JG000302.

Han, G., Hao, X., Zhao, M., Wang, M., Ellert, B.H., Willms, W., Wang, M. 2008. Effect of grazing intensity on carbon and nitrogen in soil and vegetation in a meadow steppe in Inner Mongolia. Agriculture, Ecosystems and Environment 125:21–32

Honeycutt, C.; Heil, R.; Cole, C. 1990. Climatic and topographic relations of three Great Plains soils: II: carbon, nitrogen and phosphorus. Soil Science of American Journal 54:476-483.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108:389-411

Kachanoski, R.; Carter M., 1999. Landscape position and soil redistribution under three soil types and land use practices in Prince Edward Island. Soil and Tillage Research 51(3-4):211-217.

Karlen, D.L.; Andrews, S.S. 2000. The soil quality concept: a tool for evaluating sustainability. DIAS-Report, Plant Production 38:15-26.

Kuzyk, G.W., Hudson, R.J. 2007. Animal-unit equivalence of bison, elk and mule deer in the aspen parkland of Alberta. In press.

Lal, R. 2004. Agricultural activities and the global carbon cycle. Nutrient Cycling in Agroecosystems 70:103-116.

Law, B.; Thornton, P.; Irvine, J.; Anthoni, P.; Van, T. 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Global Change Biology 7:755-77.

Li, T., Grant, R.; Flanagan, L. 2004. Climate impact on net ecosystem productivity of a semi-arid natural grassland: modeling and measurement. Agricultural and Forest Meteorology 126(1-2):99-116.

Loeser, M., Crews, T., Sisk, T. 2004. Defoliation increased above-ground productivity in a semi-arid grassland. Journal of Range Management 57:442-447.

McIntosh, P.D., Allen, R.B., Scott, N. 1997. Effects of exclosure and management on biomass and soil nutrient pools in seasonally dry high country, New Zealand. Journal of Environmental Management 51:169–186.

Mudrick, D.A.., Hoosein, M., Hicks, R.R., Townsend, E.C. 1994. Decomposition of leaf litter in an Appalachian forest: effects of leaf species, aspect, slope position and time. Forest Ecology and Management 68:231-250.

Norton, J.B.; Sandor, J.A.; White, C.S. 2003. Hillslope soils and organic matter dynamics within a Native American agroecosystem on the Colorado Plateau. Soil Science Society of America Journal 67(1): 225-234.

Owensby, C.E., Ham, J.M., Knapp, A.K., Auen, L.M. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO_2. Global Change Biology 5(5): 497-506.

Perez Corona, M.E., Vazquez de Aldana, B.R., Garcia Criado, B., Garcia Ciudad, A.1998. Variations in semiarid grasslands. Journal of Range Management 51(5):570-576.

Sariyildiz, T., Anderson, J.M., Kucuk, M. 2005. Effects of tree species and topography on soil chemistry, litter quality, and decomposition in Northeast Turkey. Soil Biology and Biochemistry 37(9):1695-1706.

Schiborra, A., Gierus, M., Wei Wana, H., Fei Bai, Y., Taube, F. 2009. Short-term responses of a Stipa grandis/Leymus chinensis community to frequent defoliation in the semi-arid grasslands of Inner Mongolia, China. Agriculture, Ecosystems and Environment 132:82–90

Schimel, D.S.; Stillwell, M.A.; Woodmansee, R.G. 1985. Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. Ecology 66:276-82.

Schuman, G.E.; Janzen, H.H.; Herrick, J.E. 2002. Soil carbon dynamics and potential carbon sequestration by rangelands. Environmental Pollution 116(3): 391-396.

Shen, W.; Wu, J.; Kemp, P.R.; Reynolds, J.F.; Grimm, N.B. 2005. Simulating the dynamics of primary productivity of a Sonoran ecosystem: Model parameterization and validation. Ecological Modeling 189(1-2):1-24.

Singer, M.J.; Ewing, S.A. 2000. Soil quality In: Summer, M. Ed. Handbook of Soil Sciences. Florida, Boca Raton. p. 271-298.

Small, C.J.; McCarthy, B.C. 2005. Relationship of understory diversity to soil nitrogen, topographic variation, and stand age in an eastern oak forest, USA. Forest Ecology and Management 217(2-3):229-243.

Smit, A.; Kooijman, A. 2001. The impact of grazing on the input of organic matter and nutrients to the soil in a grass-encroached Scots pine forest. Forest, Ecology and Management 142:99-107.

Southern Alberta Land Trust Society 2006. Conserving rangelands. http://www.salts-landtrust.org/conservingrangelands.html#e

Stroo, H.F., Bristow, K. L., Elliot, L.F., Papendick, R.I., Campbell, G.S. 1989. Predicting rates of wheat residue decomposition. Soil science Soc. Am. J. 53:91-99.

van der Krift, T.A.; Kuikman, P.J.; Berendse, F. 2002. The effect of living plants on root decomposition of four grass species. Oikos 96(1): 36-45.

Wright, A., Hons, F., Rouquette, F. 2004. Long-term management impacts on soil carbon and nitrogen dynamics of grazed bermuda grass pastures. Soil Biology and Biochemistry 36:1809-1816.

Key governing equations used in *ecosys.* Variables input to the model appear in bold with values given in the definition of variables below.

Heterotrophic respiration

Decomposition

$D_{Si,j,l,\mathrm{C}} = D'_{Si,j,l,\mathrm{C}}\, \Sigma_n M_{i,n,a,l,\mathrm{C}}\ \ f_{\mathrm{tg}l}$	decomp'n of SOC	[A1]
$D_{Zi,j,l,\mathrm{C}} = D'_{Zi,j,l,\mathrm{C}}\, \Sigma_n M_{i,n,a,l,\mathrm{C}}\ f_{\mathrm{tg}l}$	decomp'n of microbial residues	[A2]
$D'_{Si,j,l,\mathrm{C}} = \{\boldsymbol{D}_{Sj,\mathrm{C}}[S_{i,j,l,\mathrm{C}}]\}/\{[S_{i,j,l,\mathrm{C}}] + \boldsymbol{K}_{\mathbf{m}\boldsymbol{D}}(1.0 + [\Sigma_n M_{i,n,a,l,\mathrm{C}}]/\boldsymbol{K}_{\mathbf{i}\boldsymbol{D}})\}$	substrate and water	
$D'_{Zi,j,l,\mathrm{C}} = \{\boldsymbol{D}_{Zj,\mathrm{C}}[Z_{i,j,l,\mathrm{C}}]\}/\{[Z_{i,j,l,\mathrm{C}}] + \boldsymbol{K}_{\mathbf{m}\boldsymbol{D}}(1.0 + [\Sigma_n M_{i,n,a,l,\mathrm{C}}]/\boldsymbol{K}_{\mathbf{i}\boldsymbol{D}})\}$	constraint on D	
$f_{\mathrm{tg}l} = T_{\mathrm{s}l}\{e^{[B - \boldsymbol{H}_\mathbf{a}/(\boldsymbol{R}T_{\mathrm{s}l})]}\}/\{1 + e^{[(\boldsymbol{H}_\mathbf{dl} - \boldsymbol{S}T_{\mathrm{s}l})/(\boldsymbol{R}T_{\mathrm{s}l})]} + e^{[(\boldsymbol{S}T_{\mathrm{s}l} - \boldsymbol{H}_\mathbf{dh})/(\boldsymbol{R}T_{\mathrm{s}l})]}\}$	Arrhenius function for D and R_h	
$D_{Si,j,l,\mathrm{N,P}} = D_{Si,j,l,\mathrm{C}}(S_{i,j,l,\mathrm{N,P}}/S_{i,j,l,\mathrm{C}})$	N and P coupled with C	[A3]
$D_{Zi,j,l,\mathrm{N,P}} = D_{Zi,j,l,\mathrm{C}}(Z_{i,j,l,\mathrm{N,P}}/Z_{i,j,l,\mathrm{C}})$	during D	[A4]

Microbial growth

$R_\mathrm{h} = \Sigma_i \Sigma_n \Sigma_l R_{\mathrm{h}i,n,l}$		[A5]
$\boldsymbol{R}_{\mathrm{h}i,n,l} = \boldsymbol{R}'_{\mathrm{h}n} \min\{C_{\mathrm{N}i,n,l,a}/\boldsymbol{C}_{\mathbf{N}j}, C_{\mathrm{P}i,n,l,a}/\boldsymbol{C}_{\mathbf{P}j}\}$	R_h constrained by microbial N, P	[A6]
$R_\mathrm{h}'{}_{i,n,l} = M_{i,n,a,l,\mathrm{C}}\ \{\boldsymbol{R}_{\mathrm{h}i,n,l}\ [Q_{i,l,\mathrm{C}}]\}/\{(\boldsymbol{K}_{\mathbf{m}\boldsymbol{Q}\mathbf{C}} + [Q_{i,l,\mathrm{C}}])\} f_{\mathrm{tg}l}\ f_{\psi\mathrm{g}l}$	R_h constrained by substrate DOC	[A7]
$R_{\mathrm{h}i,n,l} = R_\mathrm{h}'{}_{i,n,l}(U_{\mathrm{O2}i,n,l}/U'_{\mathrm{O2}i,n,l})$	R_h constrained by O_2	[A8]
$f_{\psi\mathrm{g}l} = 1.0 - 6.67(1.0 - e^{(M\psi_\mathrm{s}/(\boldsymbol{R}T_{\mathrm{s}l})})$	ψ_s constraints on microbial growth	
$U'_{\mathrm{O2}i,n,l} = 2.67 R_\mathrm{h}'{}_{i,n,l}$		
$U_{\mathrm{O2}i,n,l} = U'_{\mathrm{O2}i,n,l}[\mathrm{O}_{2\mathrm{m}i,n,l}]/([\mathrm{O}_{2\mathrm{m}i,n,l}] + \boldsymbol{K}_{\mathbf{O_2}})$	active uptake coupled	
$= 4\pi n\, M_{i,n,a,l,\mathrm{C}}\ D_{\mathrm{sO2}l}[\mathbf{r_m} r_{\mathrm{w}l}/(r_{\mathrm{w}l} - \mathbf{r_m})]([\mathrm{O}_{2\mathrm{s}l}] - [\mathrm{O}_{2\mathrm{m}i,n,l}]$	with diffusion of O_2	
$D_{Mi,n,j,l,\mathrm{C}} = \boldsymbol{D}_{Mi,j} M_{i,n,j,\mathrm{C}}\, f_\mathrm{tg}$	first-order decay of microbial C,	[A9]
$D_{Mi,n,j,\mathrm{N,P}} = \boldsymbol{D}_{Mi,j} M_{i,n,j,l,\mathrm{N,P}}\, f_{\mathrm{tg}l}\ f_{\mathrm{d}i,n,l\mathrm{N,P}}$	partial recycling of microbial N, P	[A10]

Root and mycorrhizal nutrient uptake

$U_{\mathrm{NH}_{4i,r,l}} = \{U_{\mathrm{w}_{i,r,l}}[\mathrm{NH_4}^+{}_l] + 2\pi L_{i,r,l} D_{\mathrm{eNH}_{4l}}\ ([\mathrm{NH_4}^+{}_l] - [\mathrm{NH_4}^+{}_{i,r,l}])\ /\ \ln(d_{i,r,l}/r_{i,r,l})\}$	root uptake from mass flow + diffusion coupled with active uptake of	[A11a]
$= \boldsymbol{U}'_{\mathbf{NH_4}}\ A_{i,r,l}\ ([\mathrm{NH_4}^+{}_{i,r,l}] - [\mathbf{NH_4}^+{}_\mathbf{mn}])/([\mathrm{NH_4}^+{}_{i,r,l}] - [\mathbf{NH_4}^+{}_\mathbf{mn}] + \boldsymbol{K}_{\mathbf{NH_4}})\, f_{\mathrm{ti}l}$	NH_4^+, NO_3^- and $H_2PO_4^-$,	[A11b]

$U_{\mathrm{NO}_{3i,r,l}} = \{U_{\mathrm{w}_{i,r,l}}[\mathrm{NO_3}^{-}{}_{l}] + 2\pi L_{i,r,l}\, D_{\mathrm{eNO}_{3l}}\, ([\mathrm{NO_3}^{-}{}_{l}] - [\mathrm{NO_3}^{-}{}_{i,r,l}]) / \ln(d_{i,r,l} / r_{i,r,l})\}$ [A11c]

$= \boldsymbol{U'}_{\mathbf{NO_3}}\, A_{i,r,l}\, ([\mathrm{NO_3}^{-}{}_{i,r,l}] - \mathbf{[NO_3^{-}{}_{mn}]})/([\mathrm{NO_3}^{-}{}_{i,r,l}] - \mathbf{[NO_3^{-}{}_{mn}]} + \boldsymbol{K}_{\mathbf{NO_3}})\, f_{\mathrm{t}_{il}}$ [A11d]

$U_{\mathrm{PO}_{4i,r,l}} = \{U_{\mathrm{w}_{i,r,l}}[\mathrm{H_2PO_4}^{-}{}_{l}] + 2\pi L_{i,r,l} D_{\mathrm{ePO}_{4l}}\, ([\mathrm{H_2PO_4}^{-}{}_{l}] - [\mathrm{H_2PO_4}^{-}{}_{i,r,l}]) / \ln(d_{i,r,l} / r_{i,r,l})\}$ [A11e]

$= U'_{\mathrm{PO_4}}\, \boldsymbol{A}_{\boldsymbol{i,r,l}}\, (\mathbf{[H_2PO_4}^{\square}{}_{\boldsymbol{i,r,l}}\mathbf{]} - [\mathrm{H_2PO_4}^{\square}{}_{\mathrm{mn}}])/(\mathbf{[H_2PO_4}^{\square}{}_{\boldsymbol{i,r,l}}\mathbf{]} - [\mathrm{H_2PO_4}^{\square}{}_{\mathrm{mn}}] + K_{\mathrm{PO_4}})\, f_{\mathrm{t}_{\mathrm{g}\boldsymbol{l}}}$ [A11f]

Plant water relations

Canopy transpiration

$\boldsymbol{L}E_{\mathrm{c}i} = L\, (e_{\mathrm{a}} - e_{\mathrm{c}i(T_{\mathrm{c}i}, \psi_{\mathrm{c}i})})/(r_{\mathrm{a}i} + r_{\mathrm{c}i})$	*LE* and *H* from canopy energy balance	[B1a]
$H_{\mathrm{c}i} = \rho C_{\mathrm{p}}(T_{\mathrm{a}} - T_{\mathrm{c}i})/r_{\mathrm{a}i}$		[B1b]
$r_{\mathrm{cmin}i} = 0.64\, (C_{\mathrm{b}} - \boldsymbol{C}_{\mathbf{i}}\mathbf{'}_{\boldsymbol{i}})/ V_{\mathrm{c}}'_{i}$	r_{c} driven by rates of carboxylation *vs.* diffusion	[B2a]
$r_{\mathrm{c}i} = r_{\mathrm{cmin}i} + (\boldsymbol{r}_{\mathbf{cmax}\boldsymbol{i}} - r_{\mathrm{cmin}i})\, e^{(-\boldsymbol{\beta}\, \psi_{\mathrm{t}i})}$	r_{c} constrained by water status	[B2b]
$\psi_{\mathrm{t}i} = \psi_{\mathrm{c}i} - \psi_{\pi i}$		[B3]

Root and mycorrhizal water uptake

$U_{\mathrm{w}i} = \Sigma_{l}\, \Sigma_{\mathrm{r}}\, U_{\mathrm{w}i,r,l}$		[B4]
$U_{\mathrm{w}i,r,l} = (\psi_{\mathrm{c}}'_{i} - \psi_{\mathrm{s}}'_{l})/(\Omega_{\mathrm{s}i,r,l} + \Omega_{\mathrm{r}i,r,l} + \Sigma_{x}\, \Omega_{\mathrm{a}i,r,l,x})$	U_{w} along hydraulic gradient	
$\psi_{\mathrm{c}}'_{i} = \psi_{\mathrm{c}i} + 0.01\, z_{\mathrm{b}i}$		
$\psi_{\mathrm{s}}'_{l} = \psi_{\mathrm{s}l} - 0.01\, z_{l}$		
$\Omega_{\mathrm{s}i,r,l} = \ln\{(d_{i,r,l}/r_{i,r,l})/(2\pi\, L_{i,r,l}\, \kappa_{\mathrm{r}i,r,l})\}\ \theta_{\mathrm{w}l}/\theta_{\mathrm{p}l}$		
$\Omega_{\mathrm{r}i,r,l} = \boldsymbol{\Omega'}_{\mathbf{r}\mathbf{i},\mathbf{r}}/L_{i,r,l}$		
$\Omega_{\mathrm{a}i,r,l,x=1} = \boldsymbol{\Omega'}_{\mathbf{ai,r}}\, z_{l} /\{n_{i,r,l,1}\, (r_{i,r,l,1} / \mathbf{r'}_{i,r})^{4}\} + \boldsymbol{\gamma\Omega'}_{\mathbf{ai,r}}\, z_{\mathrm{b}i} /\{n_{i,r,l,1}\, (r_{\mathrm{b}i} / r_{\mathrm{b}}'_{i})^{4}\}\Sigma_{i,r,l}\, (M_{i,r,l}) / M_{i,r,l}$		
$\Omega_{\mathrm{a}i,r,l,x=2} = \boldsymbol{\Omega}_{\mathbf{ai,r}}\, (L_{i,r,l,2} / n_{i,r,l,2}) / \{n_{i,r,l,2}\, (r_{i,r,l,2} / r'_{i,r})^{4}\}$		

Canopy water potential

$(e_{\mathrm{a}} - e_{i(T_{\mathrm{c}i})})/(r_{\mathrm{a}i} + r_{\mathrm{c}i})$ [B1] $= \Sigma_{l}\, \Sigma_{\mathrm{r}}(\psi_{\mathrm{c}}'_{i} - \psi_{\mathrm{s}}'_{l})/(\Omega_{\mathrm{s}i,r,l} + \Omega_{\mathrm{r}i,r,l} + \Sigma_{x}\, \Omega_{\mathrm{a}i,r,l,x}) + X_{\mathrm{c}i}\, \delta\psi_{\mathrm{c}i}/\delta t$	ψ_{c} solved when transpiration from [B1-B4] (LHS) equals uptake from [B5-B13] + change in storage (RHS)	[B5]

Gross primary productivity and autotrophic respiration

Gross primary productivity

$GPP = \Sigma_{i,j,k,l,m,n,o} (V_{\mathrm{c}i,j,k,l,m,n,o} = V_{\mathrm{g}i,j,k,l,m,n,o}) A_{i,j,k,l,m,n,o}$	solve for $C_{\mathrm{i}i,j,k,l,m,n,o}$ at which $V_{\mathrm{c}i,j,k,l,m,n,o} = V_{\mathrm{g}i,j,k,l,m,n,o}$	[C1]
$V_{\mathrm{g}i,j,k,l,m,n,o} = (C_\mathrm{b} - C_{\mathrm{i}i,j,k,l,m,n,o})/r_{\mathrm{l}i,j,k,l,m,n,o}$	diffusion	
$V_{\mathrm{c}i,j,k,l,m,n,o} = min\{V_{\mathrm{b}i,j,k,l,m,n,o}, V_{\mathrm{j}i,j,k,l,m,n,o}\}$	carboxylation	
$r_{\mathrm{l}i,j,k,l,m,n,o} = r_{\mathrm{lmin}i,j,k,l,m,n,o} + (r_{\mathrm{lmax}i} - r_{\mathrm{lmin}i,j,k,l,m,n,o})\, e^{(-\boldsymbol{\beta}\psi_{\mathrm{t}i})}$	r_l is leaf-level equivalent of r_c	
$r_{\mathrm{lmin}i,j,k,l,m,n,o} = (C_\mathrm{b} - \boldsymbol{C_\mathrm{i}'}_{\boldsymbol{i}})/ V_\mathrm{c}'_{i,j,k,l,m,n,o}$		
$V_{\mathrm{b}i,j,k,l,m,n,o} = V_{\mathrm{bmax}i,j,k}(C_{\mathrm{c}i,j,k,l,m,n,o} - \Gamma_{i,j,k})/(C_{\mathrm{c}i,j,k,l,m,n,o}) + K_{\mathrm{c}_i})\, f_{\psi\, i,j,k,l,m,n,o}\, f_{\mathrm{NP}\boldsymbol{i}}$	$\mathrm{CO_2}$, water, temperature and nutrient constraints on V_b	
$V_{\mathrm{bmax}_{i,j,k}} = \boldsymbol{V_\mathrm{b}'}_i \boldsymbol{F}_{\mathbf{rubisco}_i} M_{i,j,k,prot}/A_{i,j,k}\, f_{\mathrm{tb}\boldsymbol{i}}$		
$\Gamma_{i,j,k} = 0.5\, O_\mathrm{c}\, V_{\mathrm{omax}_{i,j,k}}\, \boldsymbol{K}_{\mathbf{c}_i} /(V_{\mathrm{bmax}_{i,j,k}}\, \boldsymbol{K}_{\mathbf{o}_i})$		
$V_{\mathrm{omax}_{i,j,k}} = \boldsymbol{V_\mathrm{o}'}_i \boldsymbol{F}_{\mathbf{rubisco}_i} M_{i,j,k,prot}/A_{i,j,k}\, f_{\mathrm{to}\boldsymbol{i}}$		
$K_{\mathrm{c}_i} = \boldsymbol{K}_{\mathbf{c}_i} f_{\mathrm{tkc}i} (1 + O_\mathrm{c}/ \boldsymbol{K}_{\mathbf{o}_i} f_{\mathrm{tko}i})$		
$V_{\mathrm{j}i,j,k,l,m,n,o} = J_{i,j,k,l,m,n,o}\, Y_{i,j,k,l,m,n,o}\, f_{\psi\, i,j,k,l,m,n,o}\, f_{\mathrm{NP}\boldsymbol{i}}$		
$J_{i,j,k,l,m,n,o} = (\boldsymbol{\varepsilon} I_{i,l,m,n,o} + J_{\mathrm{max}i,j,k} - ((\boldsymbol{\varepsilon} I_{i,l,m,n,o} + J_{\mathrm{max}i,j,k})^2 - 4\boldsymbol{\alpha\varepsilon} I_{i,l,m,n,o} J_{\mathrm{max}i,j,k})^{0.5})/(2\boldsymbol{\alpha})$	water, temperature and nutrient constraints on V_j	
$J_{\mathrm{max}i,j,k} = \boldsymbol{V_\mathrm{j}'}_i \boldsymbol{F}_{\mathbf{chlorophyll}_i} M_{i,j,k,prot}/A_{i,j,k}\, f_{\mathrm{tj}i}$		
$f_{\psi\, i,j,k,l,m,n,o} = (r_{\mathrm{lmin}_{i,j,k,l,m,n,o}} / r_{\mathrm{l}_{i,j,k,l,m,n,o}})^{0.5}$	non-stomatal effect related to stomatal effect	
$f_{\mathrm{tb}\boldsymbol{i}} = \exp[\boldsymbol{B}_\mathbf{v} - \boldsymbol{H}_\mathbf{av}/(\boldsymbol{R}T_{\mathrm{c}i})]/\{1 + \exp[(\boldsymbol{H}_\mathbf{dl} - \boldsymbol{S}T_{\mathrm{c}i})/(\boldsymbol{R}T_{\mathrm{c}i})] + \exp[(\boldsymbol{S}T_{\mathrm{c}i} - \boldsymbol{H}_\mathbf{dh})/(\boldsymbol{R}T_{\mathrm{c}i})]\}$	Arrhenius functions for carboxylation, oxygenation and electron transport	
$f_{\mathrm{to}\boldsymbol{i}} = \exp[\boldsymbol{B}_\mathbf{o} - \boldsymbol{H}_\mathbf{ao}/(\boldsymbol{R}T_{\mathrm{c}i})]/\{1 + \exp[(\boldsymbol{H}_\mathbf{dl} - \boldsymbol{S}T_{\mathrm{c}i})/(\boldsymbol{R}T_{\mathrm{c}i})] + \exp[(\boldsymbol{S}T_{\mathrm{c}i} - \boldsymbol{H}_\mathbf{dh})/(\boldsymbol{R}T_{\mathrm{c}i})]]$		
$f_{\mathrm{tj}\boldsymbol{i}} = \exp[\boldsymbol{B}_\mathbf{j} - \boldsymbol{H}_\mathbf{aj}/(\boldsymbol{R}T_{\mathrm{c}i})]/\{1 + \exp[(\boldsymbol{H}_\mathbf{dl} - \boldsymbol{S}T_{\mathrm{c}i})/(\boldsymbol{R}T_{\mathrm{c}i})] + \exp[(\boldsymbol{S}T_{\mathrm{c}i} - \boldsymbol{H}_\mathbf{dh})/(\boldsymbol{R}T_{\mathrm{c}i})]\}$	temperature sensitivity of $\boldsymbol{K}_{\mathbf{c}_i}$, $\boldsymbol{K}_{\mathbf{o}_i}$	
$f_{\mathrm{tkc}i} = \exp[\boldsymbol{B}_\mathbf{kc} - \boldsymbol{H}_\mathbf{akc}/(\boldsymbol{R}T_{\mathrm{c}i})]$		
$f_{\mathrm{tko}i} = \exp[\boldsymbol{B}_\mathbf{ko} - \boldsymbol{H}_\mathbf{ako}/(\boldsymbol{R}T_{\mathrm{c}i})]$		
$f_{\mathrm{NP}\boldsymbol{i}} = min\{\sigma_{\mathrm{N}i,j}/(\sigma_{\mathrm{N}i,j} + \sigma_{\mathrm{C}i,j}/\boldsymbol{K}_{\mathbf{I}\sigma_\mathbf{N}}), \sigma_{\mathrm{P}i,j}/(\sigma_{\mathrm{P}i,j} + \sigma_{\mathrm{C}i,j}/\boldsymbol{K}_{\mathbf{I}\sigma_\mathbf{P}})\}$	product inhibition of V_b, V_j determined by σ_N and σ_P *vs.* σ_C	

Autotrophic respiration and growth

$R_\mathrm{a} = \Sigma_i\Sigma_j (R_{\mathrm{c}i,j} + R_{\mathrm{s}i,j}) + \Sigma_i\Sigma_l\Sigma_z (R_{\mathrm{c}i,r,l} + R_{\mathrm{s}i,r,l})$		[C2]
$R_{\mathrm{c}i,j} = \boldsymbol{R}_\mathrm{c}'\sigma_{\mathrm{C}i,j}\ f_{\mathrm{ta}i}$	O_2 constraint on root respiration from active uptake coupled with diffusion of O_2 as for heterotrophic respiration in [A17]	
$R_{\mathrm{c}\,i,r,l} = \boldsymbol{R}_\mathrm{c}'\sigma_{\mathrm{C}\,i,r,l}\ f_{\mathrm{ta}\,i,l}\ (U_{\mathrm{O2}i,r,l}/U'_{\mathrm{O2}i,r,l})$		
$U_{\mathrm{O2}i,r,l} = U'_{\mathrm{O2}i,l.r}[\mathrm{O}_{2\mathrm{r}i,r,l}]/([\mathrm{O}_{2\mathrm{r}i,r,l}] + \boldsymbol{K}_{\mathbf{O_2}})$		
$= U_{\mathrm{w}_{i,r,l}}[\mathrm{O}_{2\mathrm{s}l}] + 2\pi L_{i,r,l}\, D_{\mathrm{sO2}}([\mathrm{O}_{2\mathrm{s}l}] - [\mathrm{O}_{2\mathrm{r}i,r,l}]) \ln\{(r_{\mathrm{w}l} + r_{\mathrm{r}i,r,l})/$		
$r_{\mathrm{r}i,r,l}\}$		
$+ 2\pi L_{i,r,l}\, D_{\mathrm{rO2}}([\mathrm{O}_{2\mathrm{q}i,r,l}] - [\mathrm{O}_{2\,\mathrm{r}i,r,l}]) \ln(r_{\mathrm{q}i,r,l})/ r_{\mathrm{r}i,r,l})$		
$R_{\mathrm{s}i,j} = -\,min\{0.0, R_{\mathrm{c}i,j} - R_{\mathrm{m}i,j}\}$	remobilization when R_m > R_c	
$R_{\mathrm{m}i,j} = \Sigma_z (\mathrm{N}_{i,j,z}\, \boldsymbol{R}_\mathbf{m}'\ f_{\mathrm{tm}i})$		
$R_{\mathrm{g}i,j} = max\{0.0, min\{(R_{\mathrm{c}i,j} - R_{\mathrm{m}i,j})\ min\{1.0, max\{0.0, \psi_{\mathrm{t}i} - \psi_\mathrm{t}'\}\}$	growth when $R_\mathrm{m} < R_\mathrm{c}$	[C3]
$l_{i,j,z,\mathrm{C}} = R_{\mathrm{s}i,j}\ \mathrm{C}_{i,j,z=l,non\text{-}remobilizable}/\mathrm{C}_{i,j,z=l,remobilizable}$	remobilization drives litterfall	[C4]
$l_{i,j,z,\mathrm{N,P}} = l_{i,j,z,\mathrm{C}}\ \mathbf{N{,}P}_\mathbf{protein}\ \mathrm{N}_{i,j,z=l,non\text{-}remobilizable}/\mathrm{N}_{i,j,z=l,remobilizable}$		[C5]
$\delta M_{Bi,j,\mathrm{C}}/\delta t = \Sigma_z[R_{\mathrm{g}i,j,z}(1 - \boldsymbol{Y}_{\mathbf{g}i,z})/\boldsymbol{Y}_{\mathbf{g}i,z}] - R_{\mathrm{s}i,j} - l_{i,j,\mathrm{C}}$	phytomass growth driven by R_g	[C6]
$\delta A_{i,j,k,n}/\delta t = \chi\,(M_{i,j,k,n}/y_i)^{-0.33}\ \ \delta M_{\mathrm{L}i,j,k,n}/\delta t\ \min\{1, \max\{0, \psi_{\mathrm{t}i} - \psi_\mathrm{t}'\}$	leaf area growth driven by 3D leaf mass growth	[C7]
$f_{\mathrm{ta}i} = T_{\mathrm{c}i}\{\exp[\boldsymbol{B}_\mathbf{v} - \boldsymbol{H}_\mathbf{av}/(\boldsymbol{R}T_{\mathrm{c}i})]\}/\{1 + \exp[(\boldsymbol{H}_\mathbf{dl} - \boldsymbol{S}T_{\mathrm{c}i})/(\boldsymbol{R}T_{\mathrm{c}i})] +$	Arrhenius function for R_a	[C8]
$\exp[(\boldsymbol{S}T_{\mathrm{c}i} - \boldsymbol{H}_\mathbf{dh})/(\boldsymbol{R}T_{\mathrm{c}i})]\}$		
$f_{\mathrm{tm}i} = e^{(0.0811*(T_{ci} - 298.15))}$	temperature function for R_m	[C9]

Soil water and heat fluxes

Surface water flux

$Q_{\mathrm{r},x(x,y)} = v_{x(x,y)}d_{x,y}L_{y(x,y)}$ $Q_{\mathrm{r},y(x,y)} = v_{y(x,y)}d_{x,y}L_{x(x,y)}$	2D Manning equation in x (EW) and y (NS) directions	[D1]
$\Delta(d_{\mathrm{w}(x,y)}A_{x,y})/\Delta t = Q_{\mathrm{r},x(x,y)} - Q_{\mathrm{r},x+1(x,y)} + Q_{\mathrm{r},y(x,y)} - Q_{\mathrm{r},y+1(x,y)}$	2D kinematic wave theory for overland flow	[D2]
$v_{x(x,y)} = R^{0.67}s_{x(x,y)}{}^{0.5}/z_{\mathrm{r}(x,y)}$	E slope	
$v_{x(x,y)} = R^{0.67}s_{y(x,y)}{}^{0.5}/z_{\mathrm{r}(x,y)}$	S slope	
$v_{y(x,y)} = -R^{0.67}s_{x(x,y)}{}^{0.5}/z_{\mathrm{r}(x,y)}$	W slope	
$v_{y(x,y)} = -R^{0.67}s_{y(x,y)}{}^{0.5}/z_{\mathrm{r}(x,y)}$	N slope	
$d_{x,y} = \max(0, d_{\mathrm{w}(x,y)} + d_{\mathrm{i}(x,y)} - d_{\mathrm{s}(x,y)})d_{\mathrm{w}(x,y)}/(d_{\mathrm{w}(x,y)} + d_{\mathrm{i}(x,y)})$	E slope	
	S slope	
$d_{x,y} = \max(0, d_{\mathrm{w}(x+1,y)} + d_{\mathrm{i}(x+1,y)} - d_{\mathrm{s}(x+1,y)})d_{\mathrm{w}(x+1,y)}/(d_{\mathrm{w}(x+1,y)} + d_{\mathrm{i}(x+1,y)})$	W slope	
$d_{x,y} = \max(0, d_{\mathrm{w}(x,y+1)} + d_{\mathrm{i}(x,y+1)} - d_{\mathrm{s}(x,y+1)})d_{\mathrm{w}(x,y+1)}/(d_{\mathrm{w}(x,y+1)} + d_{\mathrm{i}(x,y+1)})$	N slope	
$R = s_\mathrm{r}d/[2(s_\mathrm{r}{}^2 + 1)0.5]$	wetted perimeter	[D3]
$s_{x(x,y)} = 2abs[(Z + d_\mathrm{s} + d)_{x,y} - (Z + d_\mathrm{s} + d)_{x+1,y}]/(L_{x(x,y)} + L_{x(x+1,y)})$ $s_{y(x,y)} = 2abs[(Z + d_\mathrm{s} + d)_{x,y} - (Z + d_\mathrm{s} + d)_{x,y+1}]/(L_{y(x,y)} + L_{y(x,y+1)})$	2D slope from topography and pooled surface water in x (EW) and y (NS) directions	[D4]

Subsurface water flux

$Q_{\mathrm{w},x(x,y,z)} = K'_x(\psi_{x,y,z} - \psi_{x+1,y,z})$ $Q_{\mathrm{w},y(x,y,z)} = K'_y(\psi_{x,y,z} - \psi_{x,y+1,z})$ $Q_{\mathrm{w},z(x,y,z)} = K'_z(\psi_{x,y,z} - \psi_{x,y,z+1})$	3D Richard's or Green-Ampt equation depending on saturation of source or target cell in x (EW), y (NS) and z (vertical) directions	[D5]
$K'_x = 2K_{x,y,z}K_{x+1,y,z}/(K_{x,y,z}L_{x,(x+1,y,z)} + K_{x+1,y,z}L_{x,(x,y,z)})$	in x if source and target cells are unsaturated	
$= 2K_{x,y,z}/(L_{x(x+1,y,z)} + L_{x(x,y,z)})$	in x if source cell is saturated	
$= 2K_{x+1,y,z}/(L_{x(x+1,y,z)} + L_{x(x,y,z)})$	in x if target cell is saturated	
$K'_y = 2K_{x,y,z}K_{x,y+1,z}/(K_{x,y,z}L_{y(x,y+1,z)} + K_{x,y+1,z}L_{y(x,y,z)})$	in $y$if source and target cells are unsaturated	
$= 2K_{x,y,z}/(L_{y(x,y+1,z)} + L_{y(x,y,z)})$	in y if source cell is saturated	
$= 2K_{x,y+1,z}/(L_{y(x,y+1,z)} + L_{y(x,y,z)})$	in y if target cell is saturated	
$K'_z = 2K_{x,y,z}K_{x,y,z+1}/(K_{x,y,z}L_{z(x,y,z+1)} + K_{x,y,z+1}L_{z(x,y,z)})$	in z if source and target cells are unsaturated	
$= 2K_{x,y,z}/(L_{z(x,y,z+1)} + L_{z(x,y,z)})$	in z if source cell is saturated	
$= 2K_{x,y,z+1}/(L_{z(x,y,z+1)} + L_{z(x,y,z)})$	in z if target cell is saturated	

Surface heat flux

$R_n + \lambda E + H + G = 0$	for each canopy, snow, residue and soil surface, depending on exposure	[D6]

Subsurface heat flux

$G_{x(x,y,z)} = 2\,\kappa_{(x,y,z),(x+1,y,z)}\,(T_{(x,y,z)} - T_{(x+1,y,z)})/(L_{x\,(x,y,z)} + L_{x\,(x+1,y,z)}) + c_w T_{(x,y,z)}\,Q_{\mathrm{w},x(x,y,z)}$ $G_{y(x,y,z)} = 2\,\kappa_{(x,y,z),(x,y+1,z)}\,(T_{(x,y,z)} - T_{(x,y+1,z)})/(L_{y\,(x,y,z)} + L_{y\,(x,y+1,z)}) + c_w T_{(x,y,z)}\,Q_{\mathrm{w},y(x,y,z)}$ $G_{z(x,y,z)} = 2\,\kappa_{(x,y,z),(x,y,z+1)}\,(T_{(x,y,z)} - T_{(x,y,z+1)})/(L_{z\,(x,y,z)} + L_{z\,(x,y,z+1)}) + c_w T_{(x,y,z)}\,Q_{\mathrm{w},z(x,y,z)}$	3D conductive – convective heat flux among snowpack, surface residue and soil layers in x (EW), y (NS) and z (vertical) directions	[D7]

The following are the uncertainties associated with the results of this thesis, which could be related with:

1. The determination of dry weight of shoots and root litterbags.
2. Sampling manipulation during proximate analyses.
3. Soil data used as input to *ecosys* model (soil hydraulic conductivity, permanent wilting point, and field capacity) that were estimated through the use of SPAW (Saxton and Rawls 2006).
4. The use of a general average carbon value of 0.45 (to convert dry matter into carbon of all simulated plant species).
5. The simulated soil water availability which influenced the modeled plant growth over the topographic transect
6. The algorithms used by *ecosys* to simulate plant and root growth were the same at different topographic locations and for different plant species.
7. The simulated grazing distribution over the landscape was based on field observations because there were no experimental data available to use in simulation.

Finally, sensitive analysis was not done in this research because earlier *ecosys* results showed good agreement with field experimental results. In this thesis, simulated results were coincident with research carried out in similar ecosystems, and also showed the same trend than found by other models.