Impact of Grazing on Alberta's Northern Temperate Grasslands

By

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Abstract

Understanding factors affecting elemental carbon stocks on Alberta's grasslands is of special importance with recent policy shifts focusing on climate change and carbon (C) emissions. A large part of Alberta is native prairie utilized by the beef industry. This study examined soil and vegetation over more than a hundred Alberta grassland sites to better understand the effects that regional climate and grazing have on grassland C. Overall, grazing maintained plant production and increased vegetation diversity. In high precipitation environments, grazing tended to reduce woody species, favor introduced plants, and increase herb production as well as total C stores. Grazing decreased C mass in litter, but led to more C mass in soil, especially in regions with higher precipitation (>475mm). These results suggest that grazing is an important component for maintaining large C masses in soil.

“*Only the mountain has lived long enough to listen objectively to the howl of a wolf*.”

- Aldo Leopold

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Table of Contents

List of Tables

List of Figures

List of Symbols and Abbreviations

°C – Degrees Celsius
AEP- Alberta Environment and Parks
AHM- Annual Heat: Moisture index
ANOVA- Analysis of variance
BSE- Bovine Spongiform Encephalopathy
C- Carbon
cm- Centimeters
CO- Colorado
COOL- Country of Origin Labelling
COSEWIC- Committee on the Status of Endangered Wildlife in Canada
CT- Connecticut
g- grams
GDD- Growing Degree Days
ha - Hectare
Hr – Hour
Kg- kilogram
m – Metre
MAP- Mean Annual Precipitation
MAT- Mean Annual Temperature
MGSP- Mean Growing Season Precipitation
MI- Michigan
mm – Millimetre
mm- millimeters
n – Sample Size
N- Nitrogen
NC- North Carolina
OIE- Office International des Epizooties (World Organization for Animal Health)
OM- Organic Matter
PA- Pennsylvania
R^2 - Regression Goodness-of-fit Measure
RRA-Range Reference Area
SE – Standard Error
SOC- Soil Organic Carbon
SOM- Soil Organic Matter
SW- Southwest
USA- United States of America
VA- Virginia

Chapter 1. Introduction

Grasslands cover 40% of the global land surface (Lieth 1978), and provide a wide variety of ecological goods and services (EG&S), including forage for livestock, biodiversity, wildlife habitat, water purification, pollination and carbon storage, among others (Havstad et al. 2007; Hooper et al. 2005). Despite their perhaps obvious importance to society, many of these EG&S remain poorly understood, including plant diversity conservation and carbon storage.

The Alberta government defines rangelands as areas that support vegetation, native or introduced, that either have the potential to be grazed or is being grazed (AEP 2015). In this study the rangelands we focus on are grasslands native to south-central Alberta. Rangelands and their individual plant communities have adapted to specific climatic, geophysical and disturbance factors. Canadian rangelands east of the Rocky Mountains have historically been influenced by the presence of bison (Morgan 1980). In the last century cattle have replaced bison as the predominant herbivore of grasslands on the Canadian prairie.

Alberta rangelands provide a large amount of forage to the beef industry. Alberta has about 8.8 M ha of rangeland, which makes up about 43.2% of the provinces total farm land (Statistics Canada 2011). About 31% of Alberta is native grasslands and 12% is tame (i.e. introduced forage species). Large tracks of grassland in Alberta have been preserved because they are managed by Alberta Environment and Parks (AEP). AEP co-manages approximately 3.3 M ha of public rangeland (AEP 2015), which provides forage for approximately 14% of Alberta's beef herd (AEP 2015).

1.1 Grassland

Alberta's grasslands can be roughly broken down into six major sub-regions: the Dry Mixedgrass, Mixedgrass, Central Parkland, Foothills Fescue, Montane, and the Upper Foothills (Table 1.1; Downing and Pettapiece 2006).

1.1.1 Mixedgrass (and Dry Mixedgrass)

The mixedgrass prairies are found in some of the hottest and driest areas of the province. This area was influenced by grazing and sporadic fires and was limited by water and soil nutrients (Willms and Jefferson 1993). Production in the mixedgrass is highly variable largely due to changes in growing season moisture availability (Willms and Jefferson 1993).

When grazing is removed from the mixedgrass sub-region it does not necessarily affect the number of species that are present but rather their relative abundance (Willms et al. 2002). This change can be attributed to litter not being removed and subsequently accumulating in the community. Litter is known to strongly influence the relative abundance of species present by supporting more mesic moisture regimes that promote the growth of some species and deterring the growth of others (Willms et al. 1986; Smoliak 1965; Frank et al. 1995; Facelli and Pickett 1991). In drier areas of the Mixedgrass litter does not accumulate to a level that suppresses biomass (Schuman et al. 1999). Lightly grazed pastures produce more herb biomass than moderate or heavily grazed sites (Smoliak 1974; Bai et al. 2001).

1.1.2 Foothills Fescue

The foothill fescue sub-region is common along the eastern slopes of SW Alberta. When these areas are grazed lightly they do not undergo a decrease in production but experience an increase in diversity (Johnson 1960). The absence of grazing results in an increase in litter. In this region root biomass was found to be higher under light grazing than in protected areas. The difference in root biomass can either be attributed to an increase in plant density, and even though these plants have lower root mass per plant, their sum biomass may be greater (Troughton 1957).

In comparison to many of the other natural sub-regions the fescue foothills does not decline in forage yield even when it does undergo a decrease in its most productive species (Willms et al. 1985). While foothills rough fescue (*Festuca campestris*) decreases by 37%, it is replaced by Parry oat grass and other species to the extent that total forage yield is not affected (Willms et al. 1985). Typically grazed and non-grazed patches remain relatively stable and foothills rough fescue stands do not become the preferred area to graze unless there is an increase in grazing pressure (Willms et al. 1988). At the landscape level, this means grazing maintains more heterogeneity.

1.1.3 Central Parkland

The central parkland has similar plant communities to that found in the foothills fescue but they are not dominated by bunchgrass species like foothills rough fescue (*Festuca campestris)* to the same extent. This region is an ecological tension zone between the dry mixedwood boreal forest to the north and the mixedgrass to the south, and therefore vegetation can be highly variable. Moisture is a major driver of what plant species composition exists at any location in the landscape (Coupland and Brayshaw 1953), which is further modified by soil and other parameters (Wheeler 1976). In more xeric areas of the landscape, needlegrasses (*Stipa* spp.) dominate the community while in more mesic areas *Festuca hallii* dominates.

1.1.4 Upper Foothills & Montane

The Upper Foothills and Montane are the most mesic natural sub-regions observed in this study (Willoughby and Weerstra 2006). The Montane is a variable landscape that occurs along the western portion of the province and in the Cypress Hills. Conversely, grazed meadows in the Upper Foothills are largely restricted to floodplains in valley bottoms. Vegetation responses to grazing are similar to those within the Fescue Foothills.

1.2 Ecological Goods and Services

The earth's atmospheric C is increasing (Petit et al. 1999) and much of this increase can be tied to anthropogenic causes (IPCC 2013, 2001). As a result the importance of terrestrial C pools and the factors influencing them has gained more attention (Heimann and Reichstein 2008; Betts 2000). Grasslands store vast amounts of C in a relatively stable form belowground (Burke et al. 1997; Reeder and Schuman 2002; Scurlock and Hall 1998) and could play more of a role in the future (Desjardins et al 2001; Desjardins et al. 2005; Schuman et al. 2002). For this reason the response of grassland C pools to disturbance, including ongoing land use activities must be understood in order to develop strategies capable of maintaining and/or increasing these C pools.

Grassland C accumulates from vegetation growth on the landscape. Sequential annual vegetation growth/die-off cycles of phytomass both above- and belowground slowly add to the creation of soil organic matter (SOM), of which about 58% is C (i.e. SOC) (Pribyl 2010). A wide range of factors influence the creation of the C pool, a main one being the type of plant community present. Plant communities vary widely in composition and productivity, and are affected by many climatic variables like precipitation and temperature (Sims and Singh 1978), as well as disturbance events like fire and grazing (Wright and Bailey 1982; Morgan 1980). Since fire has largely been eliminated from the grassland regions of western Canada post-European settlement (Baker 1992), grazing, particularly by livestock, is now one of the main disturbances remaining.

1.2.1 Other Values

In addition to being a major source of forage for beef cattle, Alberta's grasslands provide habitat for a wide variety of wildlife. Many wildlife species, including both consumptive species (e.g. wapiti , deer, and sharp-tailed grouse) and non-consumptive species (e.g. grizzly bears, piping plover) call rangelands home, as well as some endangered species such as sage grouse (Aldridge and Brigham 2002), swift fox (COSEWIC 2009), and ferruginous hawks (COSEWIC 2008), among others. AEP's agricultural public land provides wildlife with native eco-systems that are managed in such a way that attempts to emulate natural disturbance events (i.e. grazing) that would have taken place prior to European settlement (Alberta Sustainable Resource Development 2007).

The remote nature of Alberta's rangelands has made them prime territory for recreation. Alberta's public rangelands are extensively used for recreational opportunities such as hiking, biking, ATVing, and hunting. As aforementioned, rangelands provide habitat for a large number of species that are hunted in Alberta. Alberta public land is purposefully protected to harbor wildlife to ensure that these recreational opportunities are available.

1.3 Threats to Alberta Grasslands

Globally grasslands face many threats like desertification (Schlesinger et al. 1990; Li et al. 2000) and shrub encroachment (Asner et al. 2004). Canadian grasslands are no different. Grasslands are also under decline due to urban-industrial sprawl and expanding intensive agriculture (Pitt and Hooper 1994) together with shrub encroachment (Bailey and Wroe 1974). Mixedgrass prairie is the ecoregion with the largest amount of intact, native prairie that hasn't been disturbed by cropping or heavy livestock use. Unfortunately, only about 50% of the ecoregion is in a native state (Hill et al. 2000). The aspen parkland is arguably the most productive grassland ecoregion with few limitations for crop production, and for that reason there is very little native grassland remaining. In fact, less than 5% of the Parkland is in a native state (Hill et al. 2000). Fescue foothills grasslands have more native cover than the aspen parkland with 30% of the area being in a native state (Hill et al. 2000). Typically, range condition decreases and biomass production increases with greater latitude (Hill et al. 2000) or elevation (east to west) due to more favorable growing conditions, primarily moisture availability.

1.4 Climate Change

Climate change is a threat to grasslands because of the way it can drastically alter weather patterns (IPCC 2001) and associated problems like drought (Sauchyn and Beadoin 1998). Changes to current weather patterns can have direct effects on local flora, not just by straining resources but also expanding opportunities for the entry of introduced plants (Doak and Moris 2010). Additionally, invasive species may be better suited to surviving under greater carbon dioxide concentrations or other conditions (i.e. changes to the seasonal timing of precipitation or growing season length) that are associated with climate change (Blumenthal et al. 2013).

1.5 Floristic Diversity and Productivity

Alberta rangelands are a large reservoir for floristic diversity. This is important because relatively little is understood about biodiversity functions at the ecosystem level (Hooper et al.

2005). For example certain combinations of species are very complimentary on their utilization of resources and therefore optimize productivity (in its broadest definition) (Hooper et al. 2005). Therefore, any addition or loss in that community could alter its function and have severe impacts on rare or endangered species.

On a global scale, the relationship between productivity of a plant community and the number of species found there is humpbacked in shaped (Fraser et al. 2015; West 1993). The same factors that produce low productivity also limit the number of species that can live there, but if resources are plentiful, highly competitive species dominate thereby decreasing the number of species present. The peak of the hump is indicative of high richness and intermediate levels of production. Fraser et al. (2015) also suggested litter played a major role in the creation of the humpback-shaped response.

1.6 Grasslands and Grazing

Grazing is an important part of the ecology of Alberta grasslands because these landscapes evolved with large animal herbivory and this continues to this day. Although all of the grasslands focused on in this study traditionally have had grazing on them, their specific response varies to changes in the intensity and timing of grazing (Willms et al. 2002; Johnson 1960; Coupland and Brayshaw 1953). Today livestock grazing is the main disturbance on these landscapes because fire has largely been suppressed (Baker 1992).

1.7 Carbon Storage in Grasslands

Understanding C storage in terrestrial ecosystems is becoming more of a priority as concerns over climate change increase globally. Presently, we know that 10-30% of the world's organic C is stored in grasslands (Schuman et al. 2002). Alberta's beef industry has experienced economic uncertainty in recent history from concerns over Bovine Spongiform Encephalopathy (BSE), intermittent droughts, and international trade issues like Country of Origin Labelling (COOL) for beef products, and guidelines for trade by the World Organization for Animal Health (known international as Office International des Epizooties- OIE). In Alberta, instability in the beef market and favorable returns from annual cropping has also led to an increase in the conversion of perennial grassland (both native and tame pasture) into cultivated land uses.

From a C storage perspective this trend is disconcerting because cultivation of native prairie can release up to 50% of soil C within the first few years (Burke et al. 1995; Lal 2002; Whalen et al. 2003). These changes to the C pool are not easily remedied by restoration, even after as long as nearly 50 years of recovery (Dormaar and Smoliak 1985), which may be because restoration of the plant community's original diversity may not be possible (Desserud and Naeth 2014). If an area is tilled and immediately planted back to perennial cover total C is not affected as much as compared to if annual crops were planted (Wang et al. 2010; Mapfumo et al. 2002; Whalen et al. 2003).

Within grasslands a larger proportion of the C is stored in soil than in aboveground biomass. Forests typically have large amounts of C associated with them (Bhatti et al. 2002) but much of this C is tied up in plant biomass aboveground, or as peat and surficial OM directly at the soil surface. This distribution of C leaves forested ecosystems susceptible to rapid short-term changes from disturbances such as fire, which can release large amounts of C. With global warming increasing the risk of severe fires we can expect that this will become a bigger problem (Krawchuk et al. 2009).

Grasslands are grazed by wildlife and livestock but their effects on soil organic C remain inconclusive. Some studies show that soil C increases with grazing (Schuman et al. 2009;

Dormaar et al. 1984; Reeder and Schuman 2002) while others indicate a decline in soil C with grazing (Naeth et al. 1991; Dormaar and Willms 1998; Liebig et al. 2006) and yet other investigations suggest no change (Willms et al. 2002; Henderson et al. 2004; Li et al. 2012). Some studies do not address changes in C directly with grazing, but rather suggest an impact of grazing via the physical breakdown of litter and therefore organic C (Naeth et al. 1991; Baron et al. 2002). Others factors, such as nitrogen (N) turnover, may indicate that grazing could increase C accumulation (Pineiro et al. 2010).

Soil C changes within the plant community situated thereon (Kuebbing et al. 2014; Liao et al. 2006; Connin et al. 1997) could make the maintenance of native plant communities essential to the protection and maintenance of C stores. Certain changes in disturbance regime, like the timing and intensity of grazing, may transform the plant community into another state (i.e. composition, structure and level of productivity), especially when invasive species are readily moving in (Bossdorf et al. 2005; Christian and Wilson 1999; Wilson et al. 1989; Blumenthal et al. 2013; Biondini et al. 1988). Plant species diversity also has a measurable impact on ecosystem function (Zak et al. 2003), including leading to direct increases in soil organic C (Steinbeiss et al. 2008). As different types of ecosystems respond variably to disturbance, their effects on soil organic C are not consistent (Jackson et al. 2002). What remains unknown is how large Alberta's grassland C pool may be and how exposure to different land use practices, including livestock grazing, affects these C levels.

1.8 Research Goals and Thesis Outline

Ultimately, this thesis reports on a study examining long-term grazing effects on native grasslands across Alberta. Additionally, this study evaluates whether C pools are impacted by grassland species diversity and associated grazing exposure across Alberta. In order for this to be determined, several initial questions need to be answered about plant communities and C pools.

Although fairly well established in other systems, one of the first patterns that needs to be evaluated is how plant communities across Alberta respond to grazing across a broad range of climatic conditions. This examination will be the basis for understanding fundamental differences between plant communities for the rest of the research. This will be explored in Chapter 2 as an assessment of grassland community responses to divergent agro-climatic conditions, long-term exposure to livestock (i.e. cattle) grazing, and the role of ecological site conditions. In this chapter summary results of the diversity measures will be compared to climatic and abiotic factors to identify their role in regulating grassland diversity. Later this thesis will delve into more specific plant community questions, such as how diversity and resistance to non-native plant presence may change with grazing exposure, climatic zone, and the combination of the two. More specifically my objectives are to:

1. Determine if long-term grazing has a consistent and predictable impact on plant community composition (i.e. richness, diversity, and evenness) in northern temperate grasslands, and determine if climatic conditions play a role in mitigating effects of grazing on composition.
2. Investigate if long-term grazing influences the resistance of northern temperate grasslands to plant invasions as exhibited by the ‘footprint’ of introduced species, and explore the role that natural sub-region and associated divergent growing conditions have on this relationship.

3. Assess if long-term grazing has a consistent and predictable impact on plant biomass in northern temperate grasslands, including whether biomass is associated with changes in plant species diversity.
4. Finally, determine the impact of long-term grazing on different plant functional groups, including the abundance of early seral (ruderal) and mid-seral (woody) species in the same.

After the groundwork has been set for understanding vegetation responses to grazing, these same treatments will be used to evaluate differences in grassland carbon stores (Chapter 3). First, it will be determined how the presence of grazing impacts total C and the size of different C pools across a broad range of climatic conditions. After that, focus will change to documenting the relationship between the size and stability of the grassland C pool and its inherent vegetation attributes, like diversity. In this chapter, many of the diversity measures introduced in Chapter 2 will be related to the total C pool for each associated site. In doing so, we will determine if vegetation diversity has an impact on total C pools. The specific objectives of this chapter were to:

1. Assess how the size, composition (above vs belowground, plant vs soil) and allocation of total C among grasslands varies in response to environmental conditions (climate and soils), as well as long-term exposure to grazing.
2. Determine whether the size, composition and allocation of C were a function of divergent plant species composition, including species diversity, and whether this in turn, is linked to long-term exposure to grazing.

Chapter 4 provides a short synthesis of the key research results, including highlighting implications for grassland management and strategies to maintain and/or enhance C storage as well as native biodiversity. It will also identify significant challenges associated with this research, and identify future research needs.

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Table 1.1 Summary of mean annual precipitation, growing degree days, mean annual temperature, the extent of disturbance and dominant soil types, for each of the six different sub-regions that contain the majority of Alberta's grasslands as described for the sub-regions in Downing and Pettapiece (2006). MAT=mean annual temperature; MAP=mean annual precipitation (mm); GDD= Growing Degree Days.

Natural Sub-region	GDD	MAT (^oC)	MAP (mm)	Total Area (km^2)	Area Disturbed (km^2)	Area Native (km^2)	Dominant Soil
Dry Mixedgrass	1318	4.2	333.3	46,937	NA	NA	Brown Chernozem
Mixedgrass	1217	3.9	394.1	20,072	10,036	10,036	Dark Brown Chernozem
Central Parkland	1092	2.7	441.2	53,706	51,021	2,685	Black Chernozem
Foothills Fescue	1052	3.0	469.6	13,623	9,536	4,087	Black Chernozem
Montane	708	2.3	588.6	8,768	NA	NA	Black Chernozem to Gray Luvisol
Upper Foothills	691	1.3	632.4	21,537	NA	NA	Brunisolic Gray Luvisol

Chapter 2: Regional Grassland Responses to Long-term Grazing Exposure in Alberta

2.1 Introduction

It is widely recognized that livestock grazing can impact plant community composition, including plant diversity (Milchunas and Lauenroth 1993; West1993) and biomass production (Sims and Singh 1978; Jones 2000; McNaughton et al. 1989; Milchunas et al. 1988). These responses reflect changes in the relative abundance of different plant species, and typically shifts towards species either more tolerant of defoliation or to those avoided by herbivores while foraging (Briske 1986, 1996). At even higher levels of disturbance, early-seral, ruderal plant species may colonize disturbed areas as less grazing tolerant species disappear from the community leaving vacant niches.

In general, diversity is a highly desirable characteristic of communities (Noss 1990), and in grasslands is considered an important attribute for increasing community resilience to environmental stress (Tilman 1997; Bai et al. 2007), as well as being responsible for increasing plant biomass (Tilman et al. 1996). Resulting patterns of grassland diversity responses to disturbance are thought to vary with both environmental (i.e. growing) conditions, primarily moisture availability, as well as the evolutionary history of grazing (Milchunas and Laurenroth 1993). More specifically, grasslands experiencing high moisture and a long adaptation period to herbivory tend to have greater plant diversity under exposure to moderate grazing (Bai et al. 2001; Hart 1978; Mack and Thompson 1982). However, the extent to which patterns in grassland diversity reflect changes in the presence and abundance of introduced plant species remains unclear, including whether long-term exposure to grazing alters the presence and abundance of introduced species and associated biodiversity.

Previously documented impacts of grazing on plant community composition, including increased numbers of invasive plant species (Hobbs and Huenneke 1992), raises the possibility that grazing induced changes in diversity are the result of the addition of non-native species rather than changes in the composition of endemic native flora. Given this, an understanding of diversity responses to long-term grazing, and how this may vary with environmental conditions, particularly regional climate, is important to understand plant diversity responses to grazing, interpret the role of plant invasions in regulating grassland diversity, and also assessing the susceptibility (and resistance) of grazed native plant communities to invasion by non-native plant species. The latter has particular implications for conserving native flora, which remains an important objective in the management of many grasslands (Burkinshaw and Bork 2009).

Resistance to invasion can be defined as a plant community's ability to prevent the successful colonization by an invasive species, either with or without environmental stresses such as moisture deficits and grazing by large herbivores. Resistance to invasion has three primary elements (Lodge 1993a, 1993b; Von Holle et al. 2003): environmental resistance (soil factors, temperature, etc.), biotic resistance (competition, availability of resources, presence of disease, etc.), and demographic resistance (volume of introduced propagules). Consistent with our understanding of competitiveness, plant communities with greater levels of diversity are considered more resistant to invasion (Elton 1958; Knops et al. 1999), and therefore should be easier to manage to conserve native flora. Evolutionary history also plays a key role in determining invasibility (Alpert et al. 2000); for example, systems with a long history of disturbance and competition may be less likely to be invaded.

Similar to invasive species, there is evidence that woody species can benefit from grazing (Asner et al. 2004; Archer et al. 1995; Dudwinnie 1977; Briggs et al. 2002), largely in response to a decline in the competitiveness of herbaceous species. However, studies examining the effect of livestock grazing on woody species are inconsistent, with other investigations indicating grazing decreases woody species presence in grasslands (Fitzgerald et al. 1984; Bork et al. 2013). From a global perspective livestock grazing is generally thought to promote shrub encroachment (Asner et al. 2004), although few data sets have examined this phenomenon across a wide range of environmental conditions in relation to long-term exposure to livestock grazing.

Previous studies examining the response of individual grassland communities are plentiful, but often sacrifice geographic (and environmental) spatial resolution in exchange for more detailed testing of localized treatments (e.g. on land use) within a few select locations. In general, few studies have addressed vegetation responses across a broad range of environmental and soil conditions, which would allow for a robust assessment of generalized plant community responses to livestock grazing. Such analyses have recently been done for boreal forests (Mayor et al. 2012) and indicate that plant diversity follows the hump-backed model, as observed in grasslands globally (Fraser et al. 2015). However, Mayor et al. (2012) also found divergent patterns in the response of native and introduced plant species to disturbance; while native flora followed the hump-backed model, introduced species generally increased linearly with disturbance. The lack of equivalent data from grasslands is due to the limited availability of suitable study sites (i.e. sites with long-term comparisons of grazed and non-grazed conditions, preferably with information on disturbance intensity), the challenges associated with maintaining the infrastructure required for representative non-grazed controls, and the high costs associated with field sampling.

Comparative studies on plant community responses to livestock grazing should ideally capture a wide range of spatial variability common in grasslands, and thereby lead to the differentiation of generalizable and regional specific effects of grazing on grassland composition and function. For this to be done, extensive data sets are required that cover a wide range of soil, climatic and vegetation conditions, and which facilitate direct comparison of grazed areas with adjacent non-grazed controls. In this study, we use a large data set (n=106 sites) covering a broad range of variation in soils, climate, and associated vegetation types, distributed across northern temperate grasslands in Alberta, Canada, in order to quantify the effect of long-term exposure to livestock grazing on total plant diversity, introduced species presence, peak biomass levels, and the abundance of various vegetation components. More specifically my objectives are to:

1. Determine if long-term grazing has a consistent and predictable impact on plant community composition (i.e. richness, diversity, and evenness) in northern temperate grasslands, and determine if climatic conditions play a role in mitigating effects of grazing on composition.
2. Investigate if long-term grazing influences the resistance of northern temperate grasslands to plant invasions as exhibited by the 'footprint' of introduced species, and explore the role that natural sub-region and associated divergent growing conditions have on this relationship.
3. Assess if long-term grazing has a consistent and predictable impact on plant biomass in northern temperate grasslands, including whether biomass is associated with changes in plant species diversity.
4. Finally, determine the impact that long-term grazing has on different plant functional groups, including the abundance of early seral (ruderal) and mid-seral (woody) species in the same.

2.2 Methods

2.2.1 Field Sites Study Design

We surveyed 106 grassland locations distributed throughout the south-central region of Alberta, Canada (Fig. 2.1). Sites were distributed across a wide range of grassland natural sub-regions, including the Dry Mixedgrass and Mixedgrass, Central Parkland, Foothills Fescue, Montane, and Upper Foothill sub-regions (Downing and Pettapiece 2006), and therefore represent a wide range of climatic and edaphic conditions, in turn creating high variation in the composition of plant communities. All study sites were part of the Rangeland Reference Area (RRA) program set up by Alberta Environment and Parks (AEP), which is an extensive network of cattle exclosures intended to monitor the ongoing condition of grasslands relative to cattle grazing.

Exclosures had minimum dimensions of 20 by 40 m, and were at least 15 years old, and up to 62 years, thereby providing a benchmark of grassland responses to long-term livestock protection (Weerstra and Willoughby 1998). While not intentionally excluding wild ungulates, vegetation therein expressed minimal use by wildlife, presumably because of their small size, which is known to deter their entry (Gross and Knight 2000). Precise data on the actual grazing intensity outside of the exclosures is not available because pastures were large and typically managed to have a moderate stocking rate by domestic beef cattle, and the extensive nature of grazing would create substantial heterogeneity in animal use, including in the areas next to exclosures.

2.2.2 Vegetation Sampling and Analysis

Monitoring of vegetation at each location was done within non-grazed exclosures and adjacent grazed grassland either annually (prairie and parkland regions) or every third year (montane and foothill regions) to assess plant species composition and above-ground biomass production. To do so, 15, 20 cm x 50 cm quadrats were systematically located 2 m apart along permanent transects (33m). The foliar cover of all plant species was assessed visually, together with ground cover (bare mineral soil, litter, rock, microphytes), at peak vegetation growth between late July and mid-August. Sampling was typically done earlier in the Mixedgrass due to more advanced phenology, and later in elevated regions of SW Alberta due to delayed growth in that region.

Live above-ground biomass and litter were collected from within four, 0.5 x 0.5 m quadrats situated inside and outside of each exclosure; biomass samples were separated by hand into functional groups (grass + grass-likes, forbs, shrubs, and litter) in the field, then later dried for a minimum of two days at 55° C to stable mass, and weighed. In the Mixedgrass and Parkland sub-regions, biomass samples outside of exclosures were collected from under portable range cages (1.5 x 1.5 m in size) to provide an estimate of peak biomass for the year. For the purposes of this investigation, we used average cover and biomass data collected over a period of 12 years (2002 – 2014). The lone exception to this was biomass within the Montane and Upper Foothill sub-regions, which are not examined for biomass by AEP staff: hence, these areas were sampled only once and in the absence of cages. Despite this, biomass samples were considered to be representative of peak biomass at these locations and were non-grazed (personal observation) because grazing by livestock typically occurs later in the year. With the exception of the fore-mentioned data, all other sites were sampled at least 3 times (n=103 sites) during this period to account for inter-annual variation in vegetation composition and growth based on yearly growing conditions, with some locations sampled four (n=5) or five (n=4) times. The time period between the first and last sampling years within sites averaged 9.1 years. The time period (and number of sites in parentheses) over which data were collected across sites was as follows: five years (n= 1), six years (n=2), seven years (n=1), eight years (n=11), nine years (n= 74), ten years (n=10), eleven years (n=12), and twelve years (n=1).

2.2.3 Data Analysis

For analysis, all the quadrats (cover or biomass) sampled in each year were combined into either grazed or non-grazed treatments. These averages were then collapsed further into single averages over all the years data were collected, thereby providing a long-term estimate of plant composition and biomass for each plant community. All species were further characterized by growth form (grass, forb or woody), rhizomatous or bunchgrass habit in the case of grasses, longevity (perennial or annual/biennial), and origin (introduced or native/endemic). All plant nomenclature followed Moss (1983) and Budd (1987), including longevity and origin.

To assess plant biodiversity responses to long-term exposure to grazing and agro-climatic conditions, richness was determined as the total number of different vascular plant species found per community. In addition, mean cover values were used to determine Simpson's and Shannon's diversity, as well as species Evenness (Table 2.1). Both diversity metrics were assessed because each emphasizes a unique aspect of plant diversity (Table 2.1). In addition, to evaluate the presence of diversity comprised of introduced plant species, the contribution of introduced species to richness and Shannon's diversity were each quantified by adding up the contribution of all introduced species to the total value of each metric, as a percentage of total richness/diversity.

Biomass data were converted to kg/ha prior to analysis. To evaluate cover responses of different functional groups, the cover of species were tallied up for each community to general growth form (grasses, forbs and woody species), grass growth form (rhizomatous and bunchgrass), origin (native and introduced) and longevity (annual and perennial).

All data were analyzed using SAS (SAS institute Inc, Cary, NC, USA). Measures of diversity and richness (total and introduced plant species), individual biomass components, and various cover components (described above) were evaluated using a Mixed Model analysis of variance (ANOVA), with 2 grazing (long-term grazed and non-grazed) treatments and 6 agro-climatic regions (Dry Mixedgrass, Mixedgrass, Parkland, Foothills Fescue, Montane and Upper Foothills) as fixed factors. The interaction of grazing by region was also tested. Locations within regions were considered random in the analysis. Significant effects were considered at $p<0.05$ for main effects, and $p<0.10$ for interactions, unless noted otherwise. Where grazing x region interactions occurred, emphasis during interpretation was on isolating grazing effects within regions, with post-hoc mean comparisons conducted using a least significant difference test and an alpha of 5%.

To determine whether herbaceous biomass across grasslands was related to species richness, we regressed both herbaceous biomass and total biomass (herb + litter) against total plant species richness across all 106 sites. This was done separately for areas exposed to and protected from long-term grazing. When evaluating these relationships a linear fit was assumed unless the non-linear (polynomial) fit explained at least 3% more of the data.

To evaluate the association between introduced plant species presence and climatic conditions, Pearson correlations ($p < 0.05$) were performed between mean annual precipitation (MAP), mean summer (May through September, inclusive) precipitation (MGSP) or the annual heat: moisture index ($AHM=[MAT+10]/[MAP/1000]$), and the proportion of (Shannon's) diversity comprised of introduced species. This was done separately by grazing treatment.

Similarly, correlations were performed between the primary climatic metrics and the annual production of grass and herb (grass + forb) biomass components, as well as woody plant cover, stratified by grazing treatment. Climate metrics for the last decade for each site were interpolated from a province-wide climate data set using software designed to extract climate metrics for each location (Alberta Environment 2005; Mbogga et al. 2010).

2.3 Results

Results of the ANOVA analyses (F-statistics, degrees freedom, and associated p-values) for each of the response variables, relative to the treatments, are shown in Appendix 1. The dominant species within each sub-region are found in Appendix 2.

2.3.1 Biomass

Overall, long-term exposure to grazing altered forb biomass ($p < 0.0001$), with grazed areas (496 ± 34 kg/ha) greater than non-grazed (385 ± 34 kg/ha) areas. Although forb biomass varied among regions ($p < 0.0001$), no further grazing differences were evident in relation to the regions ($p = 0.31$), suggesting grazing effects were consistent across the latter. While grazing had no overall effect ($p = 0.66$) on grass biomass (grazed = 1700 ± 84 kg/ha; non-grazed = 1735 ± 84 kg/ha), distinct grazing x region effects were evident ($p = 0.01$), a pattern also evident for total herbaceous (grass + forb) biomass (grazing x region interaction; $p = 0.02$). Regional variation in grazing effects indicated that grazing had distinctly divergent effects on grass biomass, with grazing sharply increasing grass biomass in the Upper Foothills ($p = 0.02$), but decreasing grass biomass in the Mixedgrass ($p = 0.05$) and Central Parkland ($p= 0.02$) regions (Fig. 2.2A). Exposure to grazing did not alter total herb biomass in arid areas, but the Montane and Upper Foothill regions experienced an increase in herb biomass (Fig. 2.2B).

Correlations of grass and herb biomass with primary climatic variables surprisingly indicated that grass biomass had a weak negative association with MAP ($r = -0.185$), but only under non-grazed rather than grazed conditions (Table 2.2). In contrast, grass biomass was positively correlated with MGSP in the presence of livestock grazing ($r = +0.232$). A similar positive relationship for herb biomass was found with MGSP, both inside the exclosures ($r = +0.188$) and outside the exclosures ($r = +0.376$). Additionally, herb biomass was negatively correlated with AHM ($r = -0.309$) but only in the presence of livestock grazing (Table 2.2).

Finally, grazing reduced litter mass ($p < 0.0001$) by 52% across all sites (grazed = 1168 ± 116 kg/ha; non-grazed = 2432 ± 116 kg/ha), with further differences evident among regions (grazing x region interaction; $p = 0.01$). The interaction resulted due to the absence of a decrease in litter within the Upper Foothills, which contrasted with data from all other regions (Fig. 2.2C).

Root samples were collected and analyzed for both the 0-15 cm (shallow) depth and the 15-30 (deep) depth. Mass of roots was not found to be altered by grazing for either deep ($p=0.50$; Fig. 2.2E) or shallow ($p=0.22$; Fig. 2.2D) soil layers. While no interactions were evident of grazing with region ($p \geq 0.67$), it is noteworthy that grazing did tend to increase shallow root mass in the Montane ($p = 0.034$; Fig. 2.2D). The amount of root biomass in both depths was found to depend on natural sub-region (deep, $p=0.0016$; shallow, $p<0.0001$); in both regions root mass increased sharply in association with increasing precipitation from the Dry Mixedgrass to the Montane, only to markedly decline within the Upper Foothills.

2.3.2 Cover Responses

Total plant cover was not effected by grazing ($p = 0.20$) or grazing x region effects ($p = 0.30$), suggesting grazing did not alter the aggregate abundance of vegetation. Similar responses were observed for perennial cover in relation to grazing ($p = 0.27$) and grazing x region ($p =$

0.34). However, annual cover was effected by grazing (p = 0.03), with a smaller cover of annuals within exclosures (0.3 ± 0.2 %) compared to adjacent areas exposed to grazing (0.7 ± 0.2 %).

Among individual growth forms, forb cover was not impacted by grazing. A similar response occurred for grass cover, with the exception of a grazing x region interaction (p=0.0017). The latter was reflected by much greater live grass cover within the Upper Foothills sub-region in areas exposed to grazing (60.6 ± 4.1 %) compared to areas non-grazed (44.6 ± 4.1 %). The cover of rhizomatous grasses also demonstrated a grazing x region effect (p = 0.02), with rhizomatous grasses greater (p < 0.0003) in grazed areas (24.2 ± 2.1 %) than non-grazed areas (20.5 ± 2.3 %) of the Central Parkland. Bunchgrass had the opposite, but weaker, response to grazing where grazed areas (23.7± 2.1 %) had a lower (p=0.064) amount of cover than non-grazed areas (26.5 ± 2.1 %). Total woody cover was affected by grazing (p = 0.015), with grazing leading to a lower cover of woody species (5.4 ± 1.7 %) than areas inside exclosures (8.2 ± 1.7 %). Woody cover also had a grazing x region effect (p=0.005), with exposure to livestock grazing leading to pronounced reductions in woody cover within both the Montane and Upper Foothill sub-regions, of 30% and 60% in relative shrub cover, respectively (Fig. 2.3). Finally, correlation of woody cover with climatic variables indicated the former decreased in response to AHM but increased with precipitation (Table 2.2). The association with precipitation was particularly strong for MAP, regardless of grazing treatment. Notably, the relationship of woody cover to MGSP was substantially weaker under grazed conditions (Table 2.2).

2.3.3 Species Diversity and Native Species

Total species richness was greater in areas exposed to livestock grazing (p < 0.0001), with grazed areas (37.1 ± 1.2 species) having an overall average of 3.6 more plant species than non-grazed areas (33.5 ± 1.2 species). In addition to strong regional effects (Appendix 1), richness was influenced by a grazing x region interaction ($p = 0.051$). Grazing increased richness by about 20% within each of the Central Parkland and Foothills Fescue sub-regions (Table 2.3).

Grazing also had an impact on Simpson's diversity ($p= 0.0003$) although this difference was attributed to a grazing x region effect ($p = 0.0003$) with responses limited to the Central Parkland ($p = 0.0004$) and Mixedgrass ($p < 0.0001$) regions; in both these areas Simpson's diversity was higher in grazed than non-grazed areas (Table 2.3). Unlike Simpson's diversity, Shannon's diversity did not vary with grazing ($p = 0.68$) or grazing x region ($p = 0.21$) (Table 2.3). Finally, measures of species evenness varied marginally with grazing overall ($p = 0.0502$), with a further interaction of grazing x region ($p = 0.002$). Closer examination of these data indicated evenness differed only within the Mixedgrass region, where exposure to grazing led to increased evenness (Table 2.3).

Regression of total species richness against plant biomass revealed poor relationships between richness and herb mass plus litter when under grazing ($p = 0.006$; r^2 =-0.26) but was much weaker under grazing ($p = 0.79$; r^2 =0.03). When plant species richness was regressed without litter, a non-significant ($p = 0.30$) negative relationship was evident with total mass accounting for 7% of the variation in richness, but only for plant communities within exclosures and therefore not exposed to grazing (Fig. 2.4). Notably, exposure to grazing resulted in the loss of that relationship across the same study sites (Fig. 2.4).

Long-term grazing interacted with region ($p = 0.022$) to affect the proportion of total richness comprised of introduced species. Specifically, mesic regions such as the Montane and Upper Foothill sub-regions experienced increases in the relative abundance of introduced species (Table 2.4). Overall, the proportion of Shannon's diversity comprised of introduced diversity was approximately 4% higher (grazed = 13.5%; non-grazed = 9.4%) under grazing ($p = 0.0009$). However, the proportion of Shannon's diversity comprised of introduced species also mirrored introduced richness, with increases in the abundance of introduced diversity confined to the Montane and Upper Foothills (Table 2.4), in turn reflective of a grazing x region interaction ($p = 0.025$). Grazing had a particularly key role in increasing the abundance of introduced diversity within the Montane, where grazing increased diversity by 13% (Table 2.4). Finally, variation in the proportion of introduced Shannon's diversity was positively associated with MAP and MGSP, particularly the latter (summer rainfall), with the strongest relationship among communities exposed to long-term livestock grazing (Table 2.2; Fig. 2.5). The opposite pattern occurred with AHM (Table 2.2; Fig. 2.6), with introduced diversity lower under greater AHM, indicating there was a lower presence of introduced species in hotter, drier areas.

Finally, total cover of introduced plant species was greater ($p < 0.0001$) in grazed grasslands (grazed = 16.5 ± 2.3 %; non-grazed = 9.3 ± 2.3 %), although these effects varied with region as well (grazing x region interaction; $p < 0.0001$). More specifically, increases in the cover of introduced species were limited to the Montane and Upper Foothill regions (Table 2.4). Not surprisingly, total native cover showed a similar result with both strong effects of grazing ($p = 0.04$) and grazing x region ($p < 0.0001$). While native cover was greater in exclosures (73.2 ± 2.9 %) than in adjacent areas with grazing (68.6 ± 2.9 %), regional effects of grazing were divergent among regions. While grazing reduced native cover in both the Montane and Upper Foothill sub-regions, the opposite occurred in the Parkland where long-term grazing led to greater native cover than in adjacent non-grazed areas (Table 2.4). Although introduced cover was higher in grazed grasslands there was no evidence that it decreased overall range health (n =

64; grazed = 85.1 ± 2.9%; non-grazed = 84.5 ± 3.0%; p = 0.887) in these areas compared to non-grazed areas.

2.4 Discussion

2.4.1 Biomass and Growth Form Responses to Grazing

Not surprisingly, less total plant biomass was observed in areas more resource (i.e. water) limited for plant growth, with the lowest production in the mixedgrass regions of southeastern Alberta (Willms and Jefferson 1993; Smoliak 1986) and the greatest production in elevated Montane and Upper Foothill environments. This was further reinforced by the positive association of herb biomass with summer (May through September) moisture, and the negative association between herb biomass and AHM, a variable indicative of the magnitude of annual moisture deficit. It is notable however, that the reliance of herb biomass on summer moisture was stronger in grasslands exposed to long-term livestock grazing. This response may be a result of reductions in litter with ongoing grazing (discussed below), which could reduce plant growth by decreasing water availability. Several studies (Willms et al. 1986, 1993) have documented declines in seasonal biomass production with litter removal, with larger reductions (up to 60%) in more arid mixedgrass prairie. Litter is important for enhancing infiltration (Naeth and Chanasyk 1995), decreasing evaporation (Facelli and Pickett 1991) and stabilizing production (Deutsch et al. 2009). While annual summer grazing by cattle also has the potential to reduce the size and depth of root mass in grasslands (Smoliak 1965; Biondini et al. 1998), in turn increasing reliance of these plant communities on summer moisture supply, no change in root mass was found in the top 30 cm of soil.

Litter mass was consistently lower under long-term exposure to livestock grazing with the exception of the Upper Foothills region. By directly removing plant mass, herbivory accelerates biomass turnover via forage removal, digestion and decay (Baron et al. 2002; McInenly et al. 2010). As litter is a key factor regulating range health and biomass productivity through the amelioration of soil temperature and water loss (Facelli and Pickett 1991), litter conservation remains an important management objective on grasslands. Despite this widely held notion, we found similar total herbaceous biomass in areas with and without long-term exposure to cattle grazing in most regions. Two key exceptions to this were the Montane and Upper Foothills, where sustained livestock grazing surprisingly led to greater biomass production by up to 23%. In these high rainfall regions, abundant litter in the absence of grazing may be causing a decrease in production because of impaired nutrient cycling (Frank et al. 2000).

Given these results, existing litter levels did not appear to play a major role in regulating productivity in any of the grasslands across our study regions, potentially because residual litter mass may have been adequate to maintain production under grazing. In fact, the converse may have been the case, with litter increases in the absence of grazing accounting for observed net declines in grass biomass, at least in regions with high mean annual precipitation. This pattern may have occurred due to stagnation of plant growth in the absence of herbivore-induced nutrient cycling, which is known to stimulate plant growth (Frank et al. 2000, 2002; McInenly et al. 2010), the shading effect of high litter levels (Knapp and Seastedt 1986), or increases in competition from an expanding woody plant canopy (Bork and Burkinshaw 2009), or some combination thereof. Studies documenting negative impacts of litter accumulation are rare. For example, Deutsch et al. (2009) found that while very high litter loads (7- 10,000 kg/ha) altered current year plant morphology and phenology, it did not reduce total plant biomass production in either tame or native grasslands in the parkland of central Alberta. Litter may also be more important in aiding plant growth during dryer years (Deutsch et al. 2009), and in maintaining the growth of cool-season rather than warm-season grasses (Bork and Irving 2015). Finally, while the exclosures investigated here were not protected from wild ungulate grazing, previous studies have shown that wildlife are less likely to utilize exclosures as small as the ones employed here (Gross and Knight 2000), suggesting our non-grazed areas received little impact from any large herbivores.

While total herbaceous biomass remained independent of livestock grazing, the biomass of individual grass and forb components were found to respond to grazing. Forb biomass was 29% greater overall under exposure to grazing, and likely reflects the release of a variety of mid-seral species from high competition that would otherwise be sparse in grass dominated plant communities in the absence of grazing (Willms et al. 1985; Bork et al. 2012). Conversely, while grass biomass was also altered by grazing, this only occurred within select regions, and in markedly different ways. Exposure to livestock grazing sharply increased grass biomass in the Upper Foothills, but modestly reduced grass biomass in the Mixedgrass and Parkland. These disparate responses could reflect a number of factors, including regional differences in the grazing tolerance of vegetation (and hence, plant responses) or differences in stocking rates. While stocking rates on public land are generally set at low to moderate values across Alberta (Robertson et al. 1991), we are unable to rule out the possibility that localized stocking rates immediately outside exclosures were heavier than average near study exclosures in the Mixedgrass and Parkland regions, thereby leading to a decline in plant vigor and associated biomass production.

As previously discussed the decrease in grass biomass within the Upper Foothill exclosures could be because of excess litter or the plant community ‘stagnating’ under a less active nutrient cycle in the absence of large herbivores, both of which are disadvantages of using long-term exclosures as a benchmark to assess livestock grazing impacts (Frank et al. 2000). Litter accumulation in exclosures of the Upper Foothills appears less likely as a mechanism because litter masses remained low there compared to those in other regions. One other and more likely explanation for the reduced grass biomass in upper elevation exclosures is the associated increase in woody species cover. Both the Montane and Upper Foothills generally had more woody species, likely due to the abundant precipitation and reduced moisture stress (i.e. low AHM) at these locations, with a further increase evident inside exclosures in the absence of cattle. Interestingly, grazed areas were also those with more herb biomass and grass cover, suggesting exposure to livestock contributed to the maintenance of grassland composition and function. Woody species encroachment is known to decrease herb biomass in both the Parkland (Bailey and Wroe 1974; LaRade and Bork 2011) and Upper Foothill (Bork and Burkinshaw 2009) regions of Alberta, with woody species acting as strong competitors for light and moisture (Powell and Bork 2007).

Finally, an alternative explanation for the woody cover patterns at elevation is that livestock may be directly suppressing shrub encroachment by consuming the latter, and therefore limiting their growth and abundance. Cattle have been shown to impact tree generation in the region, particularly trembling aspen, both under intensively stocked private pastures (Fitzgerald and Bailey 1984) and under extensively managed silvopastures on public land (Kaufmann et al. 2013, 2014).

2.4.2. Diversity and Introduced Species Responses to Grazing

Increases in species richness, Simpson's diversity and evenness, in response to grazing, were dependent on region of sampling, occurring specifically within those environments having intermediate levels of moisture (i.e. Mixedgrass, Parkland and Foothills Fescue). Observed increases in richness and diversity were consistent with other studies that suggest moderate grazing releases a larger number of plant species (Milchunas et al. 1988; Milchunas and Laurenroth 1993). Mid-seral ecological conditions are thought to result in a combination of grazing tolerant and intolerant plant species (Grime 1973), thereby accounting for the net increase in the number of species and associated diversity under grazing. The lack of an increase in diversity under the lowest and greatest moisture regimes (i.e. in the Dry Mixedgrass and Montane/Upper Foothills, respectively) in this study was unexpected, as all these sub-regions coincide with areas where grazing can be expected to increase diversity (i.e. as per the model of Milchunas and Laurenroth 1993). For example, grazing is known to increase richness under moderate grazing in grasslands of Saskatchewan, including the Mixedgrass Prairie (Bai et al. 2001). The lack of an increase in the present study may reflect low grazing intensities in the Dry Mixedgrass prairie of Alberta, as stocking rates on public land in this region are typically very conservative (i.e. < 0.5 AUM/ha) (Adams et al. 2013), which could limit grazing-induced increases in diversity. While the same may be occurring in SW Alberta, high precipitation may mask grazing impacts, and the opposite may even be taking place. The Upper Foothills in particular has been experiencing shrub encroachment and an associated decline in carrying capacity (Burkinshaw and Bork 2009), and this may be increasing grazing intensity on isolated grasslands to the point of reducing the diversity of grasslands exposed to livestock. In any case, further study is required to understand the mechanisms behind when, where and why grazing induced changes to diversity may be expected. Additionally, we note that these responses are site specific and therefore cannot be used to consistently predict diversity increases at the landscape level (Stohlgren et al. 1999).

Interestingly, unlike Simpson's diversity, we saw no effect of grazing on Shannon's diversity. It is not uncommon for this pattern to occur because Simpson's index is more closely tied to species evenness (i.e. abundance) whereas Shannon's index is more closely tied to absolute richness (DeJong 1975), which in turn is a reflection of new species (including rare species) entering or leaving a community. In effect, as the Simpson's index weights all species based on abundance, this suggests our changes in diversity in response to grazing were primarily the result of changes in the abundance of existing plant species, rather than plant species gains and losses. This was further supported by the increase in evenness under grazing in the Mixedgrass, and suggests cattle grazing outside our exclosures created a more uniform composition of vegetation, particularly dominant plant species that are likely tolerant of grazing.

Richness demonstrated a non-linear relationship with total vegetation mass in the absence of grazing, peaking under intermediate biomass levels. This response is consistent with observations from Fraser et al. (2015), who observed a peak in plant richness at intermediate productivity within a global grassland dataset. Similar to the latter study, the inclusion of litter here improved this relationship. However, our data also revealed an important difference from Fraser et al. (2015), in that this relationship was weaker in grasslands not subject to livestock grazing, and instead richness declined linearly with phytomass. The loss of this relationship was unexpected and may reflect the key role that large mammal herbivory plays, even at moderate stocking rates, in regulating plant species composition and abundance, including species richness, within northern temperate grasslands. Further study is warranted evaluating the influence of grazing in mitigating diversity-biomass relationships in grasslands. Interestingly, previous studies have found that richness decreases at high biomass because woody species increase (Guo and Berry 1998). While the presence of woody species was greater under high biomass (and high moisture) here, the lack of any difference in richness between non-grazed and grazed grasslands did not support this notion.

Increasing attention is being paid to understanding and managing introduced species, particularly with species migration common globally (van Kleunen et al. 2015). Regionally, the conservation of native plant communities will depend on an understanding of how the presence of introduced vegetation contributes to diversity responses under grazing. We found that introduced richness, introduced cover and the contribution of introduced species to Shannon's diversity, all increased with simultaneous exposure to long-term grazing and greater moisture conditions. Introduced species presence was greatest within the Montane and Upper Foothill regions, and primarily under grazing, suggesting the combination of moist conditions and ongoing disturbance from livestock and other large herbivores may favor the establishment and propagation of introduced plants. Within grazed areas of the Upper Foothills introduced species comprised up to 34% of total cover, but remained at 8% cover in non-grazed areas. While the cause of this increase in introduced species remains unclear, a number of factors may play a role. As noted earlier, increased grazing pressure in a landscape of declining grassland in SW Alberta may favor the invasion of introduced plant species that possess superior defoliation tolerance (Willms et al. 1985; Bork et al. 2012). Linear increases in introduced vegetation have been found in relation to disturbance intensity within the adjacent boreal forest of northern Alberta (Mayor et al. 2012). Unfortunately, we do not have local stocking rate and grassland utilization data to fully assess the role of grazing intensity on introduced species presence at each of our study sites. Further testing is warranted.

Favorable moisture may also reduce the role of competition from the pre-existing native plant community in resisting invasions (Lamb and Cahill 2008); indeed our results showed a modest decline in native plant cover in grazed areas of the Montane and Upper Foothills. This suggests a decrease in native vegetation may have contributed to the increase within introduced species. In general, there is evidence that some introduced species are less competitive in environmentally stressed conditions, such as those with low moisture and nutrients (Nernberg and Dale 1997; MacDougall and Turkington 2005). These findings are corroborated by our decline in introduced diversity with low summer rainfall, specifically within all sub-regions drier than the Montane. Finally, it is important to note that native plant cover increased with exposure to grazing within the Central Parkland. As this response was independent of introduced plant abundance, this could reflect more conservative stocking rates in this region or a greater inherent tolerance to defoliation among the existing native vegetation.

2.5 Conclusion

The presence of long-term grazing did not decrease above-ground biomass production but rather increased it in certain regions. Furthermore, grazing increased vegetation diversity on the landscape. Together, these findings indicate that moderate grazing is an essential component in the maintenance of these grasslands.

In some cases grazing did lead to a plant community shift where introduced species cover took up a larger portion but this was most pronounced in wetter regions of the province. Further research will need to be done to determine whether the introduced species are negatively affecting ecological goods and services before this information will effect management.

Our research directly shows that livestock could be playing a role in inhibiting shrub encroachment in wetter portions of the province. As indicated by these results, a lack of moderate grazing on these landscapes could lead to a further reduction in grassland.

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Table 2.1 Summary of metrics used (Kent and Coker 1992) to evaluate the impact of grazing on grassland biodiversity

Diversity Measure	Formula	Variable description
Simpson's Diversity	$\lambda = \sum \frac{N(i)[N(i)-1]}{N[N-1]}$	N(i) = cover of species i N = total cover of all plant species
Evenness	$= \frac{\lambda}{Richness}$	Richness = species count
Richness	$= \sum s$	S = number of plant species
Shannon's Diversity	$H' = \sum[P(i)*\ln P(i)]$	P(i) = proportional abundance of a plant species relative to total plant cover

λ is used to signify Simpson's species diversity

Table 2.2 Correlations of key vegetation response variables with climatic factors assessed among the RRA sites across 6 natural sub-regions in Alberta under grazed and non-grazed conditions. Bolded p-values indicate significant correlations ($p < 0.05$).

Primary Response	Climatic Factor[1]	Non-Grazed		Grazed	
		r	p-value	*r*	p-value
Grass Biomass	Mean annual precip.	**-0.185**	**0.058**	-0.003	0.98
	Mean growing season precip.	-0.016	0.87	**+0.232**	**0.016**
	Annual Heat: Moisture index	+0.032	0.75	-0.125	0.20
Herb Biomass	Mean annual precip.	+0.021	0.83	**+0.187**	**0.055**
	Mean growing season precip.	**+0.188**	**0.054**	**+0.376**	**< 0.0001**
	Annual Heat: Moisture index	-0.154	0.11	**-0.309**	**0.001**
Woody Cover	Mean annual precip.	**+0.401**	**< 0.0001**	**+0.401**	**< 0.0001**
	Mean growing season precip.	**+0.259**	**0.007**	+0.166	0.09
	Annual Heat: Moisture index	**-0.382**	**< 0.0001**	**-0.330**	**< 0.001**
Introduced Shannon's Diversity	Mean annual precip.	**+0.22**	**0.02**	**+0.36**	**0.0002**
	Mean growing season precip.	**+0.25**	**0.009**	**+0.505**	**< 0.0001**
	Annual Heat: Moisture index	**-0.21**	**0.025**	**-0.39**	**<0.0001**

[1] MAP and MGSP represent precipitation ranges from 295 to 947 mm, and 199 to 417 mm, respectively. AHM varies from 14 to 53, 14 is the coldest/wettest and 53 is the warmest/driest.

Table 2.3 Regional variation in overall mean (± SE) plant biodiversity responses to long-term livestock grazing across 106 grassland locations in Alberta.

		Agro-climatic Natural Sub-region					
Response	Grazing	Dry Mixedgrass (n=16)	Mesic Mixedgrass (n=9)	Central Parkland (n=25)	Foothills Fescue (n=7)	Montane (n=37)	Upper Foothills (n=11)
Richness	Non-grazed	26.3 (±2.6)	25.7 (±3.5)	29.8(±2.1)*[1]	42.3(±4.0)*	38.7 (±1.)	38.1 (±3.2)
	Grazed	26.5 (±2.6)	29.7 (±3.5)	35.9 (±2.1)*	50.4(±4.0)*	40.6 (±1.7)	39.3 (±3.2)
Simpson's Diversity	Non-grazed	0.813 (±0.024)	0.666 (±0.033)*	0.749 (±0.020)*	0.844 (±0.038)	0.854 (±0.016)	0.872 (±0.030)
	Grazed	0.803 (±0.024)	0.808 (±0.033)*	0.818 (±0.020)*	0.886 (±0.038)	0.853 (±0.016)	0.862 (±0.030)
Shannon's Diversity	Non-grazed	2.561 (±0.122)	2.092 (±0.168)	2.233 (±0.101)	2.608 (±0.191)	2.473 (±0.082)	2.376 (±0.152)
	Grazed	2.235 (±0.122)	2.147 (±0.168)	2.208 (±0.101)	2.474 (±0.191)	2.349 (±0.082)	2.733 (±0.152)
Evenness	Non-grazed	0.250 (±0.007)	0.205 (±0.009)*	0.223 (±0.005)	0.228 (±0.010)	0.2396 (±0.004)	0.240 (±0.008)
	Grazed	0.249 (±0.007)	0.242 (±0.009)*	0.231 (±0.005)	0.227 (±0.010)	0.236 (±0.004)	0.236 (±0.008)

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[1] Within a response and sub-region, grazing treatment means denoted with an asterisk differ, $p < 0.05$.

Table 2.4 Regional variation in mean (± SE) introduced plant richness and diversity, as well as introduced and native cover metrics, in response to long-term livestock grazing across 106 RRAs in Alberta.

Introduced Diversity Metric	Grazing	Agro-climatic Natural Sub-region					
		Dry Mixedgrass (n=16)	Mesic Mixedgrass (n=9)	Central Parkland (n=25)	Foothills Fescue (n=7)	Montane (n=37)	Upper Foothills (n=11)
% Introduced	Non-grazed	0.117 (±0.021)	0.116 (±0.029)	0.106 (±0.018)	0.094 (±0.033)	0.118 (±0.014)*	0.084 (±0.026)
Richness	Grazed	0.121 (±0.021)	0.099 (±0.029)	0.0901 (±0.018)	0.088 (±0.033)	0.141 (±0.014)*	0.108 (±0.026)
Proportion Introduced Shannon's	Non-grazed	0.072 (±0.029)	0.039 (±0.040)	0.113 (±0.024)	0.109 (±0.045)	0.156 (±0.020)*	0.077 (±0.036)*
Diversity	Grazed	0.100 (±0.029)	0.038 (±0.040)	0.111 (±0.024)	0.159 (±0.045)	0.196 (±0.020)*	0.208 (±0.036)*
Introduced	Non-grazed	3.6 (±4.7)	1.5 (±6.6)	10.6 (±4.0)	7.5 (±7.5)	24.0 (±3.3)	8.7 (±6.0)*
Cover (%)	Grazed	4.7 (±4.7)	1.3 (±6.6)	9.6 (±4.0)	12.8 (±7.5)	32.2 (±3.3)*	38.3 (±6.0)*
Native	Non-grazed	56.8 (±6.1)	62.3 (±8.3)	63.8 (±5.0)*	68.0 (±9.4)	86.7 (±4.1)*	101.3 (±7.5)*
Cover (%)	Grazed	55.0 (±6.1)	63.9 (±8.3)	74.9 (±5.0)*	64.2 (±9.4)	78.5 (±4.1)*	74.7 (±7.5)*

[1] Within a response and sub-region, grazing treatment means denoted with an asterisk differ, $p < 0.05$.

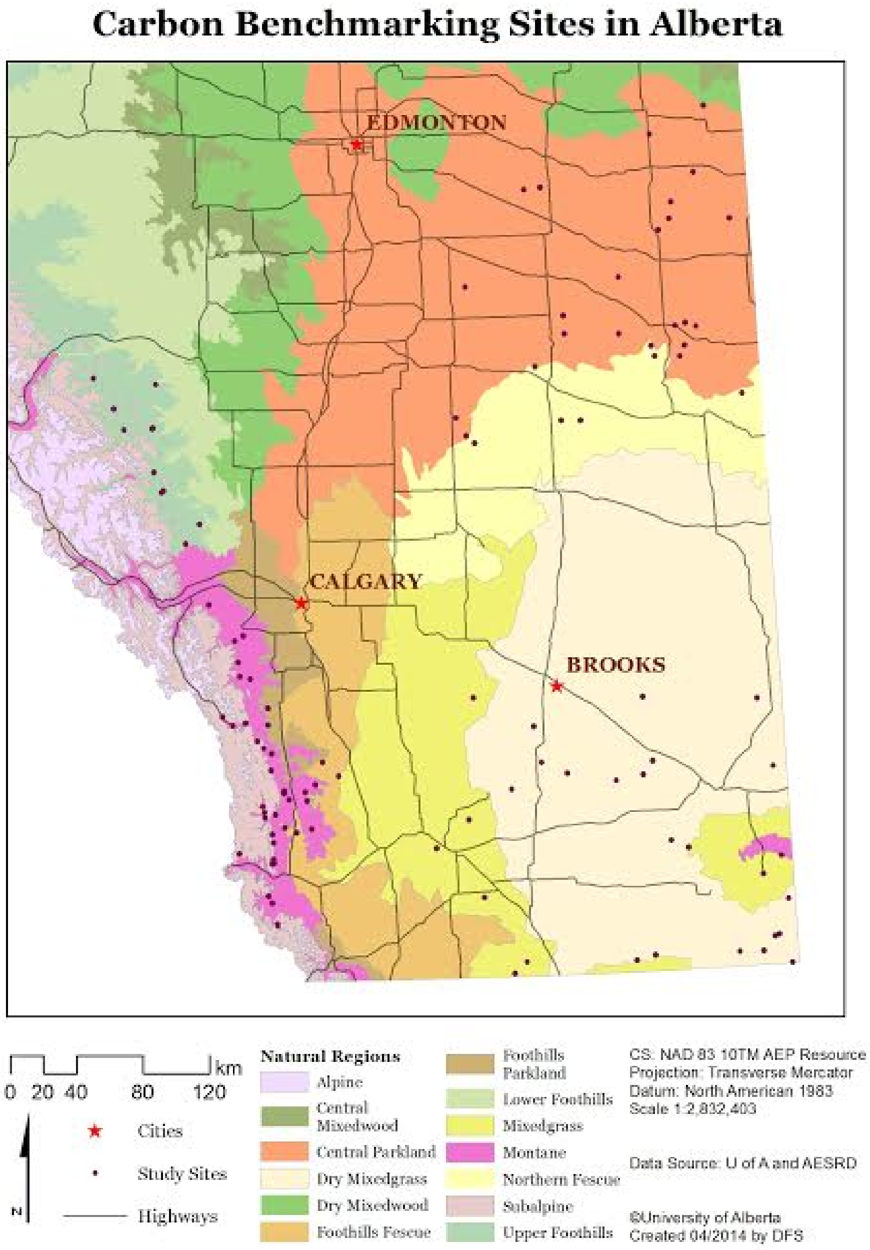
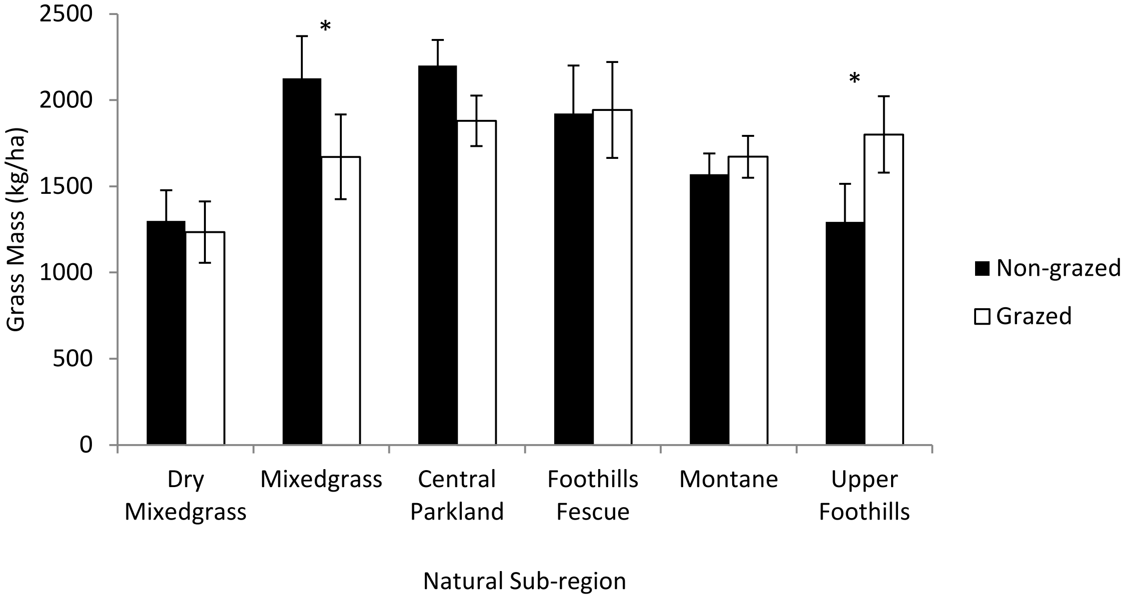


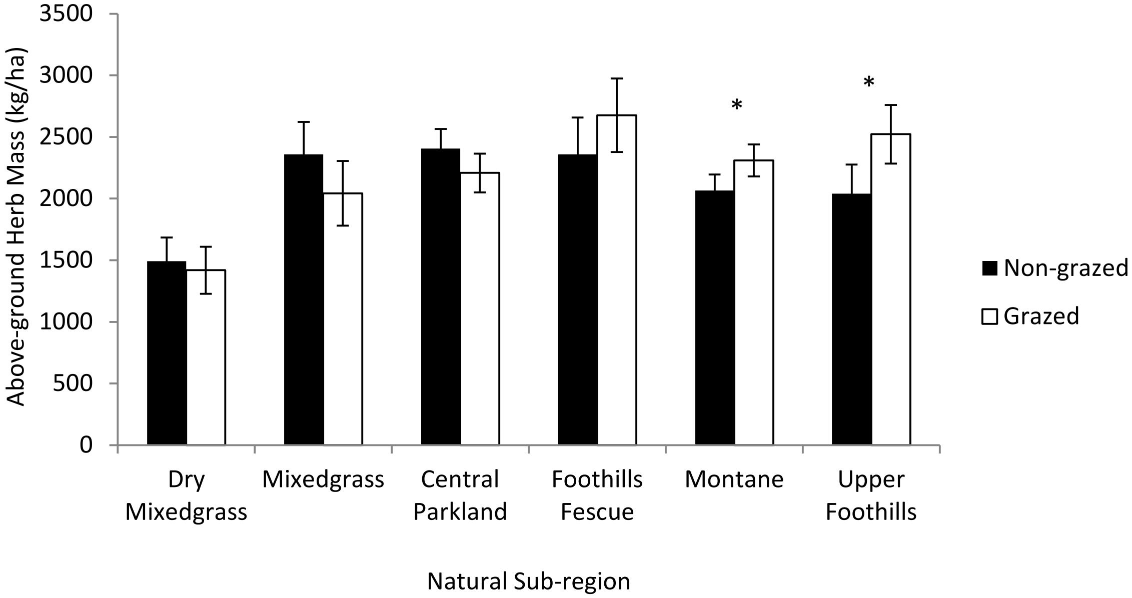
Figure 2.1 Map of the natural sub-regions of Alberta and the distribution of study sites.

(A)



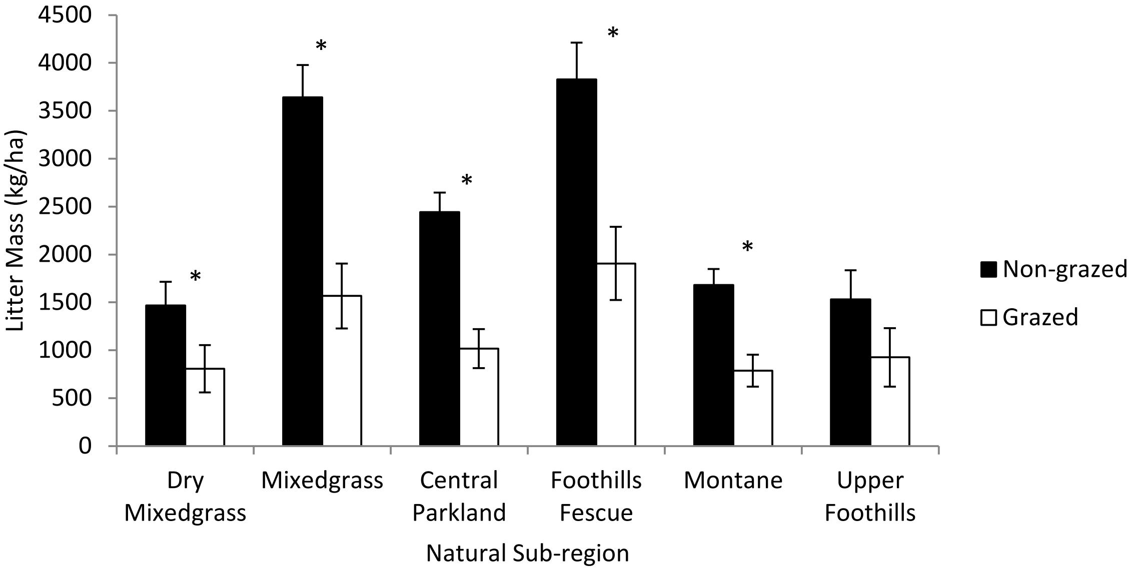
2500
2000
1500
1000
500
0
Grass Mass (kg/ha)
*
*
Dry Mixedgrass
Mixedgrass
Central Parkland
Foothills Fescue
Montane
Upper Foothills
Natural Sub-region
■ Non-grazed
☐ Grazed

(B)

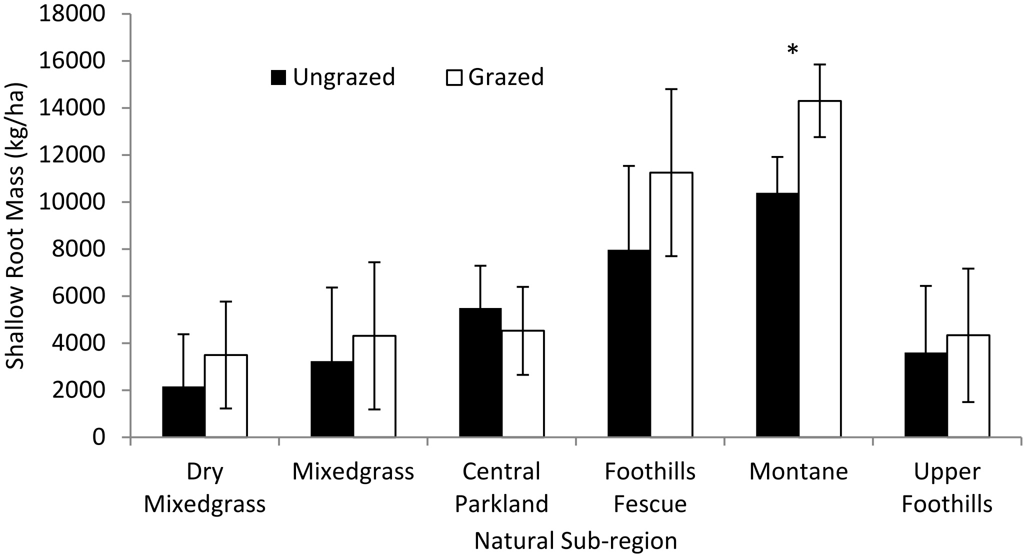


3500
3000
2500
2000
1500
1000
500
0
Above-ground Herb Mass (kg/ha)
*
*
Dry Mixedgrass
Mixedgrass
Central Parkland
Foothills Fescue
Montane
Upper Foothills
Natural Sub-region
■ Non-grazed
☐ Grazed

(C)


Litter Mass (kg/ha)
4500
4000
3500
3000
2500
2000
1500
1000
500
0
*
*
*
*
*
Dry Mixedgrass
Mixedgrass
Central Parkland
Foothills Fescue
Montane
Upper Foothills
Natural Sub-region
■ Non-grazed
☐ Grazed

(D)


Shallow Root Mass (kg/ha)
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
■ Ungrazed
☐ Grazed
*
Dry Mixedgrass
Mixedgrass
Central Parkland
Foothills Fescue
Montane
Upper Foothills
Natural Sub-region

(E)

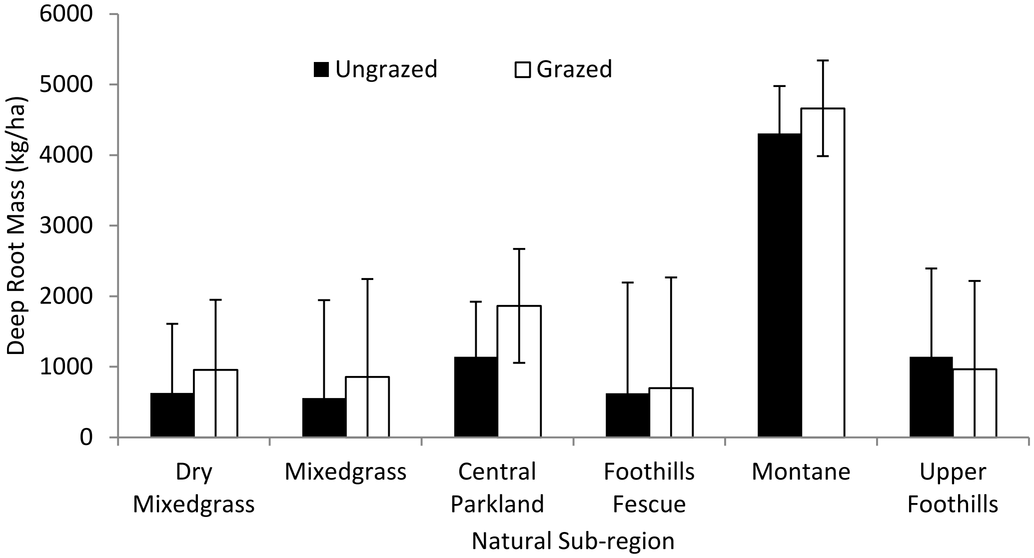


Figure 2.2 Mean (± 1 SE) biomass of (A) grasses, (B) total herbs (grass + forb), (C) litter, (D) shallow roots (0-15 cm), and (E) deep roots (15-30 cm) for both grazed and non-grazed conditions in each natural sub-region. * Indicates a significant difference between grazing treatments within a region (alpha<0.05).

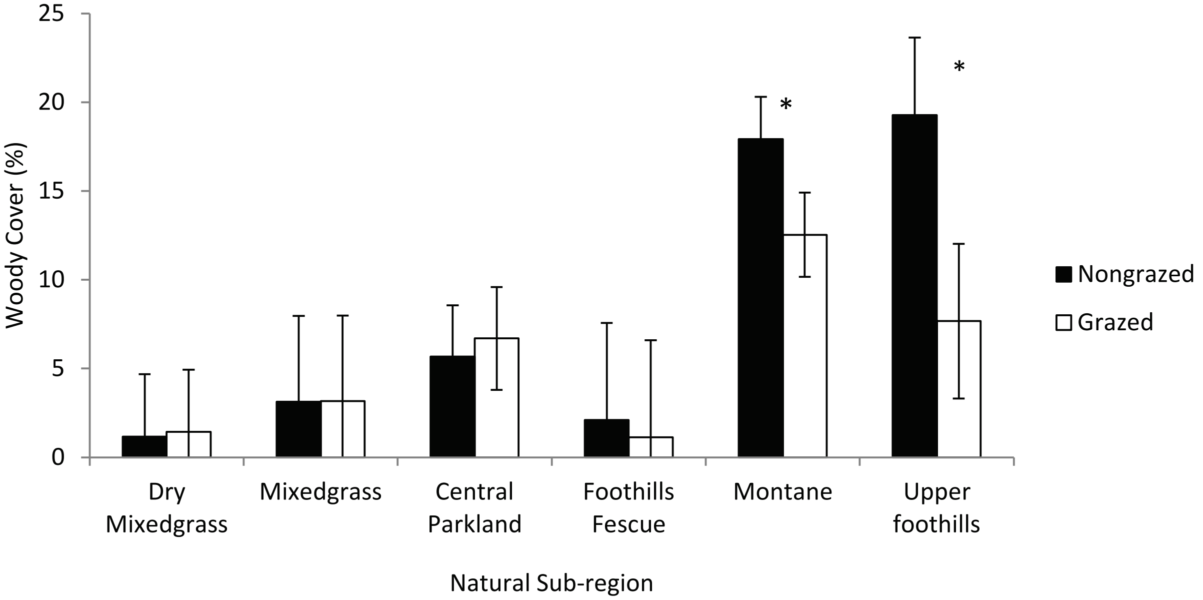


Figure 2.3 Mean woody cover (± 1 SE) in relation to protection from grazing (non-grazed) and long-term exposure to grazing within each natural sub-region. * Indicates significant differences between grazing treatments within a region (alpha<0.05).

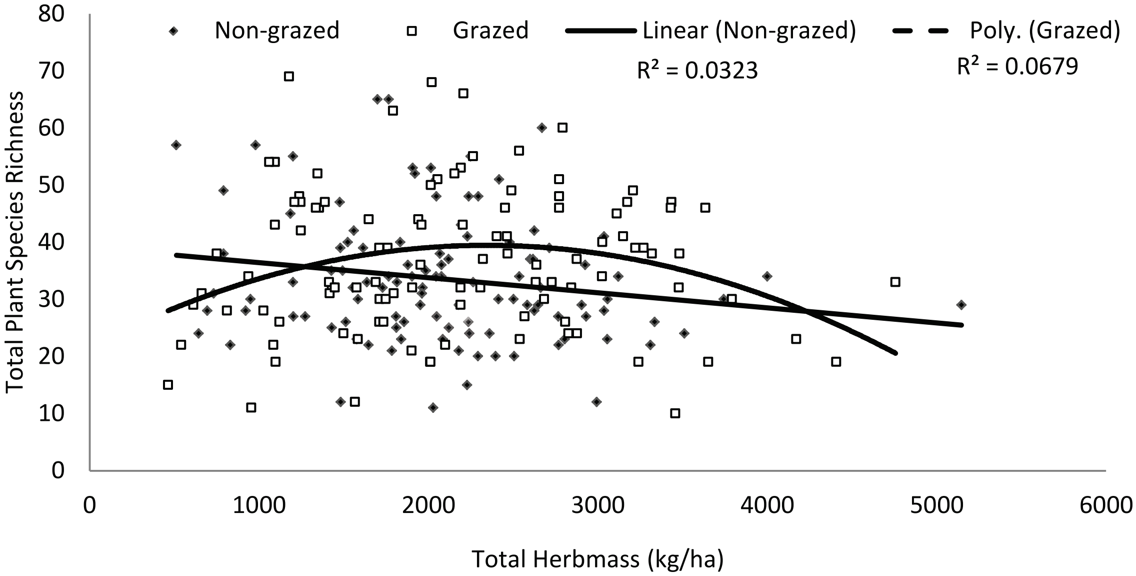


Figure 2.4 Total species richness plotted against total above-ground herb mass (grass + forb) for each of the non-grazed and grazed treatments sampled in Alberta grasslands.

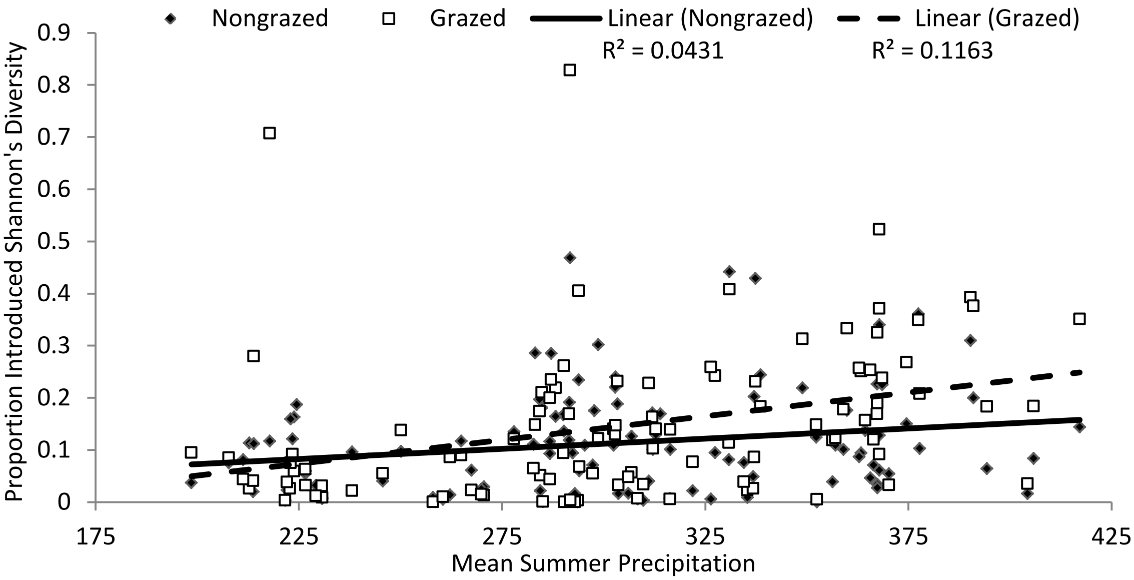


Figure 2.5 Relationship between the proportion of introduced Shannon's diversity and mean summer precipitation (mm) for each of the non-grazed and grazed treatments in Alberta grasslands.

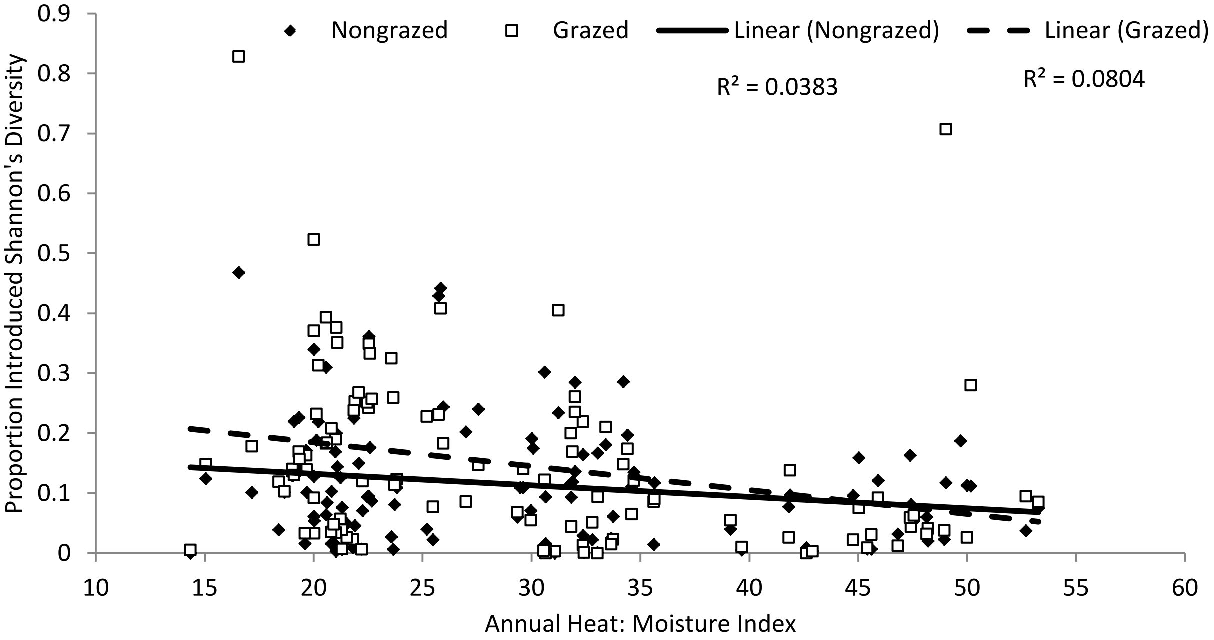


Figure 2.6 Relationship between the proportion of introduced Shannon's diversity and AHM (annual heat:moisture index) for each of the non-grazed and grazed treatments in grasslands across Alberta.

Chapter 3. Regional Carbon Responses to Long-term Grazing Exposure in Southern Alberta Grasslands

3.1 Introduction

It is well documented that levels of carbon (C) in the Earth's atmosphere are increasing (Petit et al. 1999), reflecting anthropogenic emissions from the burning of fossil fuels coupled with large-scale changes in land use (IPCC 2001). Increases in atmospheric C, in turn, are known to lead to climate change, as exemplified by changes in air temperature, growing season length, and rainfall intensity and frequency (IPCC 2001). Climate change has the potential to drastically affect weather patterns (IPCC 2001) and ultimately cause economically deleterious events like drought (Sauchyn and Beadoin 1998), with significant implications for the productivity and sustainability of agricultural systems.

As climate change becomes more of a global concern, understanding the size, stability and inherent properties of the earth's C pools is becoming more of a priority (Betts 2000). Grasslands cover between 20% (Lieth 1978) and 40% (Wang and Fang 2009) of the global land surface and store vast amounts of C in a relatively stable form below-ground (Burke et al. 1997). At present, 10-30% of the world's organic C is stored within grasslands (Schuman et al. 2002). Globally, grasslands face many challenges including desertification (Schlesinger et al. 1990; Li et al. 2000) and shrub encroachment. Locally in Alberta, grasslands face similar issues like shrub and tree encroachment (Bailey and Wroe 1974; Bork and Burkinshaw 2009) but are also being increasingly altered by the expansion of cultivated agriculture and urban-industrial development (Pitt and Hooper 1994). As a result, many of Alberta's grasslands have been altered by human activity (Hill et al. 2000) and are no longer in a native state, potentially altering their ability to provide ecological goods and services such as C storage.

At its simplest, grassland C accumulates from plant growth (phytomass) that subsequently dies-back both above and belowground, as shoots and roots, respectively. Aboveground phytomass contributes to the accumulation of litter and surface mulch organic C pools. Similarly, root turnover slowly adds to the size of the below-ground C pool. Carbon pools ultimately can be expected to stabilize at a level that is in equilibrium with C release through respiration (Flanagan et al. 2002; Schulze et al. 2000), the by-product of decomposition processes. Cultivation remains a significant threat to grassland C, as the former is known to reduce soil organic C stores by 30 to 50% (Burke et al. 1995; Lal, 2002). In northern temperate grasslands of Western Canada, soil C declines have been well documented from the conversion of grassland into both simplified swards of introduced forages as well as annual cropland systems (Dormaar et al. 1994; Whalen et al. 2003). Although tilling has an immediate impact on soil C, its effect can be reduced if seeded back to perennial cover (Wang et al. 2010; Mapfumo et al. 2002). However, the degree of carbon decline also has varied with agro-climatic conditions, with larger reductions in drier regions such as the Mixedgrass Prairie relative to the Foothills Fescue (Whalen et al. 2003). Given these patterns and the fact that conversion of cropland to grassland could reduce carbon levels (Desjardin et al. 2005) by allowing soil organic matter (and carbon) to rebuild over time, grassland conservation and/or restoration could be an important part of atmospheric carbon mitigation in the future.

Aside from cultivation, a wide range of other factors contribute to the creation of carbon pools in grasslands, including disturbance and the associated plant community present (Kuebbing et al. 2014; Liao et al. 2006; Connin et al. 1997). Plant communities are highly variable themselves and are heavily influenced by climatic factors like precipitation and temperature (Sims and Singh 1978). Historical disturbances such as fire (Nelson and England, 1971; Wright and Bailey, 1982) and grazing (Morgan, 1980) have been important ecological processes in the region, and play a major role in determining what plant species are present and their associated productivity (Bogen et al. 2003; Willms et al.1985). For many grasslands, including in North America, fire has been largely eliminated by fire suppression (Baker, 1992), leaving grazing as the primary disturbance on the contemporary grassland landscape. Although wild ungulates such as bison were the main grazing disturbance historically across the northern plains of North America (Morgan, 1980), in the last century this land use has effectively been replaced by livestock, namely cattle.

Livestock effects on grassland carbon are inconclusive. Some studies suggest that grazing increases soil carbon (Schuman et al. 2009; Dormaar et al. 1984; Reeder and Schuman 2002) while others indicate it causes a decline (Naeth et al. 1991; Dormaar and Willms, 1998; Liebig et al. 2006). Yet other investigations suggest that levels of soil carbon remain independent of grazing (Willms et al. 2002; Henderson et al. 2004; Li et al. 2012). The lack of consensus in this regard suggests more work needs to be done before a firm policy can be developed linking grazing activities to grassland carbon conservation and management. Grazing aside, evidence exists showing that attributes of the plant community, such as high species diversity, may translate to increases in soil carbon (Steinbeiss et al. 2008). Given this, grazing-induced changes in grassland carbon may depend on plant community diversity, which in turn, may be linked to climatic conditions (Willms et al. 2002; Willms et al. 1986; Facelli and Pickett, 1991; Johnson, 1961; Coupland and Brayshaw, 1953). Consequently, the relationship between diversity, livestock grazing, and soil carbon needs to be explored in northern temperate grasslands.

To understand how livestock grazing as a primary land use alters the size, composition and stability of grassland carbon pools, extensive data sets are needed that cover a wide range of soil, climatic and vegetation conditions, and which facilitate direct comparison of grazed areas with adjacent non-grazed controls. In this study, a large, spatially diverse data set from 106 sites spread across northern temperate grasslands in Alberta, Canada, and covering a wide variation in soil, vegetation and climatic conditions, was used to quantify the effect of long-term exposure to livestock grazing on key properties of grassland carbon. The specific objectives were to:

1. Assess how the size, composition (above- vs belowground, plant vs soil) and allocation of total C among grasslands varies in response to environmental conditions (climate and soils), as well as long-term exposure to grazing.
2. Determine whether the size and allocation of carbon was a function of divergent plant species composition, including species diversity, and whether this in turn, is linked to long-term exposure to grazing.

3.2 Methods

3.2.1 Field Sites

All study sites were part of the Rangeland Reference Area (RRA) program established by Alberta Environment and Parks (AEP), which is an extensive network of sites intended to monitor the ongoing health and condition of grasslands relative to livestock (namely cattle) grazing. We surveyed 106 grassland locations distributed throughout the southern and central regions of Alberta, Canada (Fig. 2.1). Sites were broadly distributed across several different natural sub-regions (Downing and Pettapiece 2006), including the Dry Mixedgrass and Mixedgrass, Parkland, Foothills Fescue, Montane, and Upper Foothills. The broad distribution of these sites captures a wide range of climatic and edaphic variation typical of these grasslands.

Vegetation monitoring at each RRA was done within grazed and non-grazed conditions either annually (prairie and parkland) or every third year (montane and foothill) to assess species composition and above-ground biomass production. Within each location, the non-grazed transect was situated inside a fenced area that excluded cattle. Exclosures had minimum dimensions of 20 by 40 m, and were at least 15 years old and up to 62 years, thereby providing a benchmark of grassland responses to long-term livestock protection (Weerstra and Willoughby 1998). While not intentionally excluding wild ungulates, vegetation therein expressed minimal use by wildlife, presumably because of their small size, which is known to deter their entry (Gross and Knight 2000).

Transects outside of each exclosure were similar in range type to those inside, but were in areas exposed to livestock grazing, bringing the total number of plant communities sampled to 212. Grazed areas were typically managed to have a moderate stocking rate by domestic beef cattle, although actual use levels within grazed areas immediately outside exclosures may have varied because of large pasture sizes and variable use patterns therein by livestock.

3.2.2 Soil Sampling

At all RRAs ten soil cores (3.25 cm diameter) were randomly sampled both inside and outside each exclosure to a depth of 30 cm using a JMC Backsaver Handle with a 39.6 cm dry sampling tube (JMC Soil Samplers, Newton, IA, USA). The sample size (n=10) of cores within each community was determined based on preliminary sampling of four communities in 2012, which suggested a minimum of eight cores would be sufficient to capture the ‘within plant community’ variation in soil C (see Appendix 3 for overview). During sampling, care was taken to not disturb the permanent transect used by AEP for vegetation sampling. Cores were taken parallel to the transect, after which mulch depth, Ah depth, and presence of rocks was recorded.

Each core was divided into the overlying surface mulch layer, and the 0-15 and 15-30 cm mineral layers, with cores then composited by layers within each ‘plant community’. Samples were subsequently air-dried initially to ensure preservation, and then brought back to the University of Alberta for assessment of soil and vegetation properties. In addition to the subsampled cores, a single large diameter (10.8 cm) core was randomly collected from each plant community (inside and outside each exclosure) using a Pro II Golf Green Hole Cutter (TJB-INC, Hamden, CT, USA) to assess bulk density. Bulk density was done for both the 0-15 cm and the 15-30 cm depths.

3.2.3 Root Mass

Root biomass was assessed from bulked soil cores removed for the assessment of soil properties. Roots were extracted from soil by hand by carefully running soil samples through a 2 mm sieve. Resulting root samples were picked clean of visible soil, then washed with water to remove any microscopic soil, and dried (at 55 °C) in preparation for weighing. Root biomass and surface mulch were ground separately to prepare samples for C and N analysis, first through a Wiley Mill to 0.5 mm size, then through a ball mill to a fine powder (Thomas Scientific, Swedesboro, NJ, USA). The ball mill had a mesh size of roughly 0.25 mm^2, which homogenized the sample. Concentrations of C and N were measured following a standard protocol for a LECO TruSpec CN elemental analyzer (LECO Corporation, St. Joseph, MI, USA). Each day drift calibrations were measured using commercially available standards spanning the range of expected C and N values to ensure that the LECO was both accurate and precise. Again, relevant standards were checked every tenth sample.

3.2.4 Soil Biophysical Characterization

Soil texture was assessed with the hydrometer method on 40 g of soil from the composited soil (Kroetsch and Wang 2006). The entire texturing process took place over several days. First, organic matter was removed using digestion with hydrogen peroxide (Kroetsch and Wang 2006; Mikutta et al. 2005). The peroxide reaction was controlled with minimal use of ethanol. Resulting samples were then dried (at 55°C) overnight (approximately 24 hours). Next, two 40 g samples of the treated soil were weighed and placed in a beaker with 4 g of sodium hexametaphosphate and 100 mL of water. These samples were left overnight to allow proper dispersion of clay. On the final day samples were washed with HCl to remove carbonates (Kroetsch and Wang 2006). Hydrochloric acid was added drop-wise until pH remained between 3.5 and 4.0 for ten minutes. After the pre-treatments were completed samples were mixed for five minutes in a mixer (Hamilton Beach Commercial, Glen Allen, VA, USA). Last, samples were dropped into 1000 mL sedimentation tubes and mixed vigorously. Density measures were taken with an ASTM Soil Hydrometer 152H (H-B Instrument Company, Collegeville, PA, USA) at two minutes and seven hours (Kroetsch and Wang 2006) then run through a standard formula (Kroetsch and Wang 2006) to calculate percent sand, silt, and clay.

Soil organic matter content was assessed with loss-on-ignition (LOI) by weighing approximately 15 g of soil, heating to 350 °C for a minimum of 3 hours, and then reweighing to determine OM loss (Robertson 1999). Soil pH was assessed for each soil with a Fisher Scientific Accument benchtop pH meter in a 2:1 mixture of deionised water (80 mL water to 40 g soil). The meter was calibrated following protocols set out by the manufacturer within our expected soil pH range (4.0, 7.0, and 10.0). Calibrations were done before assessing samples for pH, and again after every tenth sample. Finally, salinity was assessed at the same time as pH with a standard salinity probe (Hach, Loveland, CO, USA). Internal calibration was done with water at a known temperature. A summary of soil biophysical characteristics can be found in Appendix 4.

3.2.5 Carbon and Nitrogen Analysis

Soils were sieved to 2 mm to remove coarse debris (rocks and roots), which were then dried and weighed. Mineral soils were kept as separate depth classes (0-15 cm and 15-30 cm) for every site, from inside and outside of the exclosure. Each mineral soil was then ground in a Wiley Mill and ball ground (mesh size of 0.25 mm^2) before C and N analysis. Determination of C and N concentration were done following standard protocols of a LECO TruSpec CN elemental analyzer (LECO Corporation, St. Joseph, MI, USA). On every separate day of use, drift calibrations were measured using commercially available standards spanning the range of relevant C and N values to ensure that the LECO was both accurate and precise. Standards were checked every tenth sample.

3.2.6 Aboveground Vegetation Sampling and Analysis

Four vegetation samples were collected at all RRAs both inside and outside of the exclosure. Samples were collected within a 50 cm x 50 cm quadrat and separated into grass (and grass-likes), forb, shrub and litter components through sorting in the field. These samples were then bagged and dried at 55°C for 48 hours once brought back to the University of Alberta.

All shoot biomass and litter samples were then ground separately through a Wiley Mill to 0.5 mm size to prepare samples for carbon/nitrogen (CN) analysis. Shoot biomass samples were first subsampled after thorough mixing for processing if the sample was large (e.g. > 50 g). Concentrations of C and N were measured following standard protocols of a LECO TruSpec CN elemental analyzer (LECO Corporation, St. Joseph, MI, USA). Each day drift calibrations were measured using commercially available standards spanning the range of expected C and N values to ensure that the LECO readings were accurate and precise.

3.2.7 Soil Bulk Density

The 10.8 cm bulk core that was previously mentioned was used to calculate bulk density. Cores were stored in a plastic bag until they could be returned to the University of Alberta to be dried at 105°C, weighed and sieved (2 mm) to remove any large fragments. To calculate the density of soil, rock (i.e. coarse fragment) weights were subtracted from the total weight. This corrected weight was then divided by corrected core volume (bulk core volume less rock volume) to calculate the actual soil bulk density (Ellert and Bettany 1995).

3.2.8 Data Analysis

Replicates of C and N data were averaged and standardized compared to commercially available controls to account for daily changes. Data points were then converted to a mass per square meter basis by combining CN concentration data for vegetation, roots, litter and mulch, as well as various soil components, with each respective biomass component for each plant community, as well as bulk density for soil.

All data were analyzed using SAS (SAS institute Inc, Cary, NC, USA). Masses and percentages were evaluated using a Mixed Model analysis of variance (ANOVA), with 2 grazing (long-term grazed and non-grazed) treatments and 6 agro-climatic regions (Dry Mixedgrass, Mixedgrass, Parkland, Foothills Fescue, Montane and Upper Foothills) as fixed factors. The interaction of grazing by region was also tested. Locations within regions were considered random in the analysis. Significant effects were considered at $p < 0.05$ for main effects, unless noted otherwise. Where grazing by region interactions occurred, emphasis during interpretation was on isolating grazing effects within regions, with post-hoc mean comparisons conducted using a least significant difference test and an alpha of 5%. Last, given the variation in the number of study sites observed among different sub-regions and associated impacts on the ability to detect grazing by sub-region effects in the primary ANOVA analysis with Mixed Models, we conducted follow up pairwise comparisons of grazing impacts within individual sub-regions on primary C pools where deemed appropriate to more fully understand the nature of these responses (or lack thereof).

To evaluate the association between climatic factors and total carbon pools, Pearson correlations ($p < 0.05$) were performed between mean annual precipitation (MAP), mean summer (May through September, inclusive) precipitation (MGSP) or annual heat: moisture index (AHM=[MAT+10]/[MAP/1000]), and the total carbon pool for each site. This was done separately by grazing treatment. Similarly, correlations were performed between the species diversity metrics and the total carbon pool. Climate metrics for the last decade for each site were interpolated from a province-wide climate data set using software designed to extract climate metrics for each location (Alberta Environment 2005; Mbogga et al. 2010).

To determine whether species diversity and induced diversity were related to ecosystem C, we regressed Simpson's Diversity, Shannon's Diversity and the richness of introduced species as a proportion of total, against ecosystem C across all 106 sites. This was done separately for areas exposed to and protected from long-term grazing. When evaluating these relationships a linear fit was assumed except where a non-linear (polynomial) trend-line increased the model R^2 by 0.03 (i.e. 3% more).

3.3 Results

Summary results for all ANOVA analyses, including carbon and nitrogen concentrations, C and N mass for vegetation and soil, as well as C:N ratios, are provided in Appendix 5.

3.3.1. Carbon Mass

3.3.1.1. Total Ecosystem Carbon

In terms of the total C pool, we observed a trend for C to be greater under long-term exposure to grazing (12300± 422 g/m^2) than in non-grazed areas (11726± 421 g/m^2), although this difference remained non-significant overall ($p=0.15$). Total C also varied among natural sub-regions ($p<0.0001$; Fig. 3.1a), and while there was no clear evidence that grazing effects on total C were dependent on sub-region ($p=0.25$), total C was nevertheless greater within the Montane region under grazing (Fig. 3.1a). At a minimum, these results indicate that livestock exposure maintained, and potentially increased, the size of the ecosystem C pool in grasslands of south-central Alberta.

3.3.1.2 Vegetation Carbon Mass

While total vegetation C mass did not vary with exposure to grazing ($p=0.76$), the latter did vary with region ($p=0.01$). The aggregate C profile of all vegetation components, both live (grass, forb, and root mass) and dead (litter and mulch), are shown in Fig. 3.1b in relation to various combinations of grazing and region. Regardless of grazing history, the largest proportion of measured C mass within vegetation was situated within the surface mulch pool (approximately 81.1%), followed by loose surface litter (~3.5%), roots within the upper 30 cm of soil (~8.6%) and then current year's live vegetation (~4.4%; Fig. 3.1b). Notably, dead vegetation C pools (litter + mulch) comprised approximately 86.6% of the total vegetation C pool - the vast majority of all phytomass-based carbon. Across all natural sub-regions, the size of the vegetation C pool tended to follow ambient precipitation, being greater within those regions with greater rainfall (Fig. 3.1b). Specific effects of grazing on vegetation C mass indicated a negative effect of grazing in the Dry Mixedgrass and Upper Foothills, and while the opposite occurred in the Parkland and Foothills Fescue, these differences remained non-significant (Fig. 3.1b).

Effects of long-term grazing on total aboveground C mass of herbs (grasses + forbs) indicated grazing effects were contingent on natural sub-region ($p=0.052$). Changes in herbaceous C mass were limited to the Montane and Upper Foothill regions, where grazing led to greater C (Table 3.1) relative to non-grazed areas. Within growth forms, grazing led to an overall increase ($p=0.005$) in the C mass of forbs (22.0 ± 1.5 g/m^2) relative to areas protected from livestock (16.8 ± 1.5 g/m^2). However, similar to total herbs, grass C mass was subject to an interaction of grazing by region ($p=0.02$). While grass C mass was greater in areas exposed to livestock in the Upper Foothills (Table 3.1), the opposite was evident in the Parkland (Table 3.1) where grazing reduced standing C mass in herb vegetation ($p=0.03$). Although litter C mass was generally 50.2% lower under grazing, this response also varied with natural sub-region ($p=0.028$); litter C was lower under grazing in all regions except the Upper Foothills (Table 3.1). Finally, C mass within the mulch layer was also effected by the interaction of grazing by sub-region ($p=0.019$), with grazing leading to a decline in mulch C mass only in the Upper Foothills (Table 3.1).

There was no evidence that the C mass of roots in the shallow (0-15 cm) or deep (15-30 m) soil layers responded to grazing exposure, either alone ($p\geq0.18$) or in combination with region ($p\geq0.78$). The same was evident for total root C mass (Fig. 3.2) down to a 30 cm depth in relation to grazing ($p=0.09$), although the trend was for C mass to be greater (by 33%) in roots of areas subject to livestock grazing. The Montane was the only region to show evidence of grazing increasing ($p= 0.02$) overall root carbon from 289.6 (±40.6) g/m^2 to 403.4 (±41.1) g/m^2 (Fig. 3.2).

3.3.1.3 Soil Carbon Mass

Total soil C values for both the shallow (0-15 cm) and deep (15-30 cm) soil layers varied significantly by region ($p<0.0001$), but soil C response to grazing was less consistent. In the shallow layer grazed areas had greater ($p=0.038$) soil C (6568±290.6g/m^2) relative to those non-grazed (6005.3±287.0 g/m^2), but this effect disappeared in the deeper layer ($p=0.996$). Neither soil layer showed evidence of a grazing by region interaction suggesting soil responses were consistent across regions.

3.3.1.4 Carbon Allocation Pools

Belowground carbon is the combination of all soil C and roots. Grazing interacted with sub-region ($p=0.01$), and reflected a large increase ($p=0.05$) in belowground C under grazing within the Foothills Fescue (Table 3.1). While belowground C was marginally lower with grazing in the Dry Mixedgrass ($p=0.08$), it was prominently lower in the Upper Foothills ($p=0.01$). Total aboveground C also responded to an interaction of grazing by sub-region ($p=0.015$), with strongly divergent responses among regions. While aboveground C declined in drier regions (Dry Mixedgrass, Mixedgrass and Parkland), aboveground C increased in the Foothills Fescue and Montane, with a similar (though non-significant) trend in the Upper Foothills (Table 3.1).

The dead C pool is comprised of surface mulch and litter. This C pool varied with the interaction of grazing by sub-region ($p=0.024$), and reflected declines in C under grazing within the most extreme climates studied here (Dry Mixedgrass and Upper Foothills). In contrast, the live C pool (total root C and shoot C) tended to be greater ($p=0.080$) under grazing (337.2±29.1 g/m^2) compared to in adjacent fenced areas (272.4±28.4 g/m^2), an effect that appeared to be consistent across study sites.

3.3.2 Carbon Concentrations

Overall, long-term exposure to grazing decreased the C concentrations of grass and grass-likes (p=0.0025), with non-grazed (44.3 ± 0.1%) areas greater than grazed (44.0 ± 0.1%) areas. Grass C concentrations in response to grazing did not vary further by region (p=0.32). Conversely, although forb C concentration had a response to grazing (p=0.01), this varied further by region (p <0.0001). While forbs in the Dry Mixedgrass and Parkland both increased in C concentration under grazing, the opposite occurred in the Montane and Upper Foothills (Fig. 3.3a). An interaction of grazing by region was also evident on litter carbon concentration (p=0.002); although grazing increased litter C concentration in the Parkland, it decreased C concentrations of litter in the Upper Foothills (Fig. 3.3b). Carbon concentrations in the surface mulch (i.e. LFH) layer of grasslands did not respond to grazing (p≥0.12).

Below ground, the C concentration of both shallow (0-15 cm) and deep (15-30 cm) roots did not demonstrate overall grazing effects (p=0.92 and p=0.39, respectively) but were effected by grazing by region (p=0.0031 and p=0.0398, respectively), indicating grazing impacts were inconsistent across regions. For shallow roots the Parkland had a 13.8% increase (p=0.0003) in C concentration (Fig. 3.4a), while the Mixedgrass experienced the opposite (17.0% decrease; p=0.02). Among deeper roots, grazing reduced C concentrations but only in the Parkland (p=0.01; Fig. 3.4b).

3.3.3 Nitrogen Concentrations

Long-term exposure to grazing led to a widespread increase (p=0.0137) in N concentration of current year grass biomass (1.49% ±0.03) relative to non-grazed areas (1.42% ±0.03). While N concentration of forbs varied among regions (p<0.0001) it demonstrated no effect of grazing (p=0.966) exposure or the interaction of grazing and region (p=0.299).

Similarly, N concentrations of the surface mulch layer remained unaffected by grazing ($p \geq 0.20$). Concentrations of N within litter were altered by the interaction between grazing and region ($p=0.025$); the Upper Foothills was the only sub-region where litter N concentration varied with grazing ($p=0.004$), with non-grazed areas (1.37% ± 0.097) lower in litter N than grazed areas (1.63% ± 0.10).

Concentrations of N within roots were altered by the interaction of grazing by region in both the shallow ($p=0.0025$) and deeper ($p=0.066$) soil profile, with divergent results between layers. Within the 0-15 cm layer, root N concentration was reduced with exposure to grazing in the Mixedgrass and Foothills Fescue sub-regions (Fig. 3.5a). In contrast, root N concentrations in the 15-30 cm soil layer were greater under grazing, although this response was limited to the Parkland, Foothills Fescue and Upper Foothill areas (Fig. 3.5b). Notably, overall grazing effects suggested that grazing decreased root N at shallow depths (from 0.89% ±0.02 to 0.82% ±0.03; $p=0.026$), while increasing root N (from 0.65±0.02 to 0.76±0.02; $p=0.0002$) deeper down.

3.3.4 Nitrogen Mass

Nitrogen mass represents the combination of N concentration and mass, and therefore represents crude protein yield. The mass of forb N in above-ground shoots varied by grazing ($p=0.0053$) where grazed areas (0.91 ± 0.07 g/m^2) had greater N mass than non-grazed areas (0.72 ± 0.07 g/m^2). Grass N mass showed regional differences ($p< 0.0032$), but more importantly, a grazing by region interaction ($p=0.0279$); the wettest region, the Upper Foothills, was the only natural sub-region to display a difference ($p=0.0036$) whereby grazed areas (3.69 ± 0.37 g/m^2) had greater grass N mass than non-grazed (2.63 ± 0.37 g/m^2) areas. There was little variance overall between grazed and non-grazed areas. Similarly, the N mass of both shallow and deep roots displayed no effects of grazing, alone or in combination with region. Litter N mass followed similar trends to that of carbon, with both grazing ($p<0.0001$) and grazing by region interaction ($p=0.015$) effects. Grazing led to a sharp decline in litter N mass among the Mixedgrass, Parkland, Foothills Fescue and Montane sub-regions, with no difference in the driest (Dry Mixedgrass) and wettest (Upper Foothill) areas (Fig. 3.6).

Soil N mass exhibited an impact from the long-term effects of grazing, but only in the shallow layer, where grazed areas (604.5± 28.1 g/m^2) had greater ($p=0.025$) soil N mass compared to non-grazed areas (543.2±28.5 g/m^2). There was no evidence to suggest that grazing responses varied by region (shallow, $p=0.969$; deep, $p=0.372$).

3.3.5 Carbon to Nitrogen (C:N) Ratios

Relatively few changes in C:N ratio were evident among the vegetation biomass components sampled. The C:N ratio of forbs, surface mulch, and shallow roots in the 0-15 cm depth of soil, were not affected by grazing (min $p\geq0.66$). The C:N ratio of grasses tended to increase ($p=0.025$) in non-grazed areas (33.2 ± 0.6) compared to adjacent grazed (31.4 ± 0.6) areas. A similar response was observed on the C:N ratio of deep root biomass ($p=0.0021$), with C:N ratios markedly greater inside exclosures (54.4±2.6) than outside (44.8±2.5). The lone grazing by region interaction evident was weak and occurred for litter C:N ratios ($p=0.083$); however, this response was driven by a lower C:N ratio in grazed areas of the Upper Foothills (grazing = 27.7 ± 3.1; non-grazed = 33.0 ±3.0).

Conversely, soil C:N ratios showed no evidence of being impacted by grazing, either alone or in combination with region ($p\geq0.17$). The only region where any difference was found between areas inside and outside exclosures was the Parkland, where the deeper horizon had a greater C:N ratio ($p=0.011$) under grazing (12.7±1.9) compared to without grazing (8.8±1.9).

3.3.6 Linkages of Total Carbon to Vegetation and Climate

Although an obvious trend was evident for the wetter natural sub-regions to contain more carbon, this also held true for total carbon regressed against MAP and MGSP (Table 3.2). Total C in both the non-grazed and grazed treatments demonstrated strong positive relationships with moisture, particularly MGSP. In contrast, total C declined with increasingly larger moisture deficits, as represented by AHM (Table 3.2).

As might be expected, total C was positively related to total live vegetation cover in both grazed and non-grazed areas (Table 3.3). Among all primary metrics of biodiversity, only Simpson’s diversity had a positive relationship with total C pool size, and only in non-grazed areas (r^2=+0.208, p=0.028). Interestingly, total C was not associated with richness or Shannon’s diversity (Table 3.3).

More notable relationships were found when comparing total C mass to introduced species abundance (Table 3.3). Richness of introduced vegetation was positively related to total C mass in grazed areas (r^2=+0.195, p=0.039) but there was no evidence of a similar relationship in non-grazed areas (r^2=+0.146, p=0.125). Similarly, total C mass was positively related to the absolute and relative contribution of introduced plant species to Shannon’s diversity, a pattern evident for both non-grazed and grazed areas (Table 3.3). In both cases, however, a stronger positive association was evident between total C mass and the footprint of introduced species for grazed areas, peaking at *r*=+0.390 (p<0.0001). Similarly, relative measures of introduced species diversity led to stronger associations with total C mass than absolute measures of Shannon’s diversity (Table 3.3). When introduced Shannon’s diversity was regressed against total ecosystem C, it showed at an intermediate amount of diversity there was the largest amount of ecosystem C (R^2= 0.208, p<0.0001). Areas with low and high proportions of introduced species' diversity had lower total ecosystem C compared to areas with a moderate presence of introduced species (Fig. 3.7B).

3.4 Discussion

3.4.1 Ecosystem Carbon

We found C pools inherently increased with moisture, particularly MGSP from May through September, inclusive. In the current study, total C mass varied from approximately 7550 g/m^2 (~78 t/ha) in Dry Mixedgrass prairie to about 18299 g/m^2 (~183 t/ha) in the Upper Foothills. These results are consistent with other studies indicating soil carbon is greater in areas with higher rainfall (McSherry et al. 2013; Cole et al. 1993), likely in response to greater C inputs associated with enhanced primary productivity and carbon deposition (Derner and Schuman 2007; Sim and Singh 1978). Numerous studies across western Canada indicate that grassland biomass is heavily dependent on moisture (Coupland and Brayshaw 1953; Smoliak 1965; Sims and Singh 1978), with summer precipitation being particularly important in grasslands due to the shallow nature of roots within these ecosystems. The only natural sub-region that did not follow the trend of increasing carbon in direct relation to increasing moisture was the Montane, which had ecosystem C levels at or slightly below those of the Foothills Fescue.

While total ecosystem C did not respond uniformly to grazing, we did find limited evidence that grazing may increase total C under select conditions (i.e. grasslands in the Montane). It is notable that the lone region demonstrating a grazing response was that having the largest sample size (n=37), suggesting that larger sample sizes may have been necessary to detect differences in soil and/or total ecosystem C in other sub-regions. Moreover, we did observe a generalized increase in shallow soil C under grazing. These results are consistent with several soil C studies indicating grazing can increase the size of the stocks (Schuman et al. 2009; Dormaar et al. 1984; Reeder and Schuman 2002; Wang et al. 2014). A reason for the increase in ecosystem C within the Montane could be the large increases in root production under grazing (+23%) reported in Chapter 2. Naeth et al. (1991) found that grazing increased root production in the Mixedgrass Prairie and Parkland, but not in the Foothills, which in turn may have led to greater ecosystem C (Derner and Schuman 2007). Additionally, since the response documented in the Montane does not seem to follow the earlier mentioned moisture trend within the other sites, it could be that some other mechanism accounts for the increase in C. Personal observation indicated that the Montane sites are on rockier areas with significant slopes compared to the rolling meadows of the Fescue Foothills or the riparian floodplain meadows of the Upper Foothills. For the rest of the sub-regions, there was no clear difference between grazed and non-grazed ecosystem C. This lack of a response could be due to the light grazing intensity from livestock on Alberta public lands, whereas other studies used much higher grazing intensities (e.g. Reeder and Schuman 2002). More extreme results may be occur under heavier grazing scenarios. Additionally, there appeared to be a balance of aboveground and belowground C accumulation among sites, discussed further below.

3.4.2 Vegetative Carbon

Within vegetation, the vast majority of C was situated within the dead vegetation components, particularly the mulch layer situated on the soil surface, with live vegetation apparently representing only a small component of the ecosystem. Nevertheless, live biomass additions over time remained important in modifying grassland C by progressively adding biomass (and C) to litter, and eventually the mulch layer. The mulch layer was particularly pronounced within the more mesic regions of Alberta, and represents an important pool of C.

Despite its size and potential importance in storing C, both litter and mulch C remain susceptible to rapid loss in the event of disturbance. For example, large fire events are known to remove litter and even surface mulch (Bork et al. 2002), and thus should not be considered a protected C pool in the long-term.

Findings of reduced C mass in dead vegetation components under grazing is not surprising given that herbivory accelerates biomass turnover (Baron et al. 2002) via forage removal, digestion and decay. However, our results also indicate that grazing often increased C stored in live vegetation, particularly areas with high precipitation (i.e. ≥450 mm), and parallels the increase in herb productivity found in the Upper Foothills under grazing (Chapter 2). Similarly, increased forb C mass directly reflects the increase in species diversity commonly found under moderate grazing (Bai et al. 2001). In any case, our results appear to show that changes in live aboveground vegetation are able to compensate for changes (typically reductions) in C mass within senescent vegetation (litter and mulch), thereby maintaining C mass.

Reasons for the decline in total vegetation C within the Dry Mixedgrass and Upper Foothills under grazing are unknown, but appear to reflect a reduction in dead C pools, which in turn, may reflect a generalized decline in the vigor of vegetation and C inputs under grazing. Previous studies have assessed the impact of grazing on soil C in the Dry Mixedgrass, and suggest increases in soil C are because of species composition shifts in favour of grazing tolerant species, both native and introduced. A species composition shift could change litter inputs (Naeth et al. 1991; Wolkovich et al. 2010) and chemistry (Gariboldi et al. 2007). In the Dry Mixedgrass, species like *Bouteloua gracilis* increase under grazing (Coupland 1961). This warm-season species has greater structural carbohydrates and abundant roots in the top soil (Lutwick and Dormaar 1974); this could lead to an increase in C stores due to slower decomposition of the litter from this species. Additionally, litter C was markedly reduced under grazing in most regions, including the Dry Mixedgrass. Within the Upper Foothills, although grazing did not change litter levels, grazing led to a reduction in vegetation C largely due to a 22% reduction in the C mass within the mulch layer, suggesting turnover of litter was particularly rapid within this high rainfall environment. Part of the explanation for these changes can be found in the make-up of the litter within the Upper Foothills. The latter underwent a decrease in the C concentration of litter and an increase in N concentration under grazing, which in turn, resulted in an decrease in C:N ratio. Studies suggest higher N values allow for increased microbial activity (Flanagan and van Cleve, 1983; Melin, 1930; Taylor et al. 1989), which in turn would lead to faster breakdown of the litter, thereby accounting for the reduced mulch C in the Upper Foothills. As Upper Foothill sites were consistently in low lying areas with adequate moisture, coupled with increased N levels, potentially brought on by grazing itself (Frank et al. 2000), this could explain higher breakdown rates.

Interestingly, total vegetation C remained relatively stable in relation to grazing in most areas, primarily due to divergent responses between the live (herb and root mass) and dead (litter and mulch) C pools. Reductions in the dead C pool were typically offset by increases in C mass within live vegetation. Live vegetation mass was larger within the Mixedgrass and Upper Foothills under grazing, and in the case of the latter, would help account for the reduced mulch C mass. Moreover, forb mass and associated C was also generally greater under grazing, which would help offset the observed reduction in C within the litter and/or mulch layers under grazing. The Dry Mixedgrass was somewhat of an anomaly with no difference in herb production (Chapter 2), although it did undergo a decrease in the dead carbon mass of vegetation (significantly lower litter) under grazing. In the Dry Mixedgrass, best livestock management practices suggest deferred grazing on native prairie (Clark et al. 1943). Under this practice herb biomass may be removed late in the season, in which case direct effects of grazing on herb biomass would not be reflected at our time of sampling at peak biomass in mid-summer.

3.4.3 Soil Carbon Pool

The soil C pools were the largest C pools (>80%) and remained regionally dependent, with only the upper horizon (0-15 cm) showing a response to grazing. In fact, the shallow soil horizon experienced a net increase in soil carbon under grazing, but this relationship was lost for the deeper horizon. As root turnover is a major component of nutrient cycling and C balance (Pendal et al. 2004; Chen et al. 2006) the most likely explanation for the increase in shallow soil C would come from changes in root cycling. In some wetter ecosystems, low levels of grazing can lead to compensatory growth of vegetation (McNaughton et al. 1998) including increases in root growth (Sims and Singh, 1978; Frank et al. 2002). Bai et al. (2015) reported that root production and die-off were both positively linked to livestock grazing, and could account for the increases in shallow C observed here.

Changes in root dynamics under grazing may be due to changes in species composition. Reeder and Schuman (2002) found that some species like *Bouteloua gracilis*, increase under heavy grazing. This species is known for a high root-to shoot ratio (Coupland and Van Dyne 1979), which could explain some of the changes in root dynamics and ultimately soil C. The generalized increase in shallow C and the greater belowground C within the Foothills under grazing reflects some potential for enhanced C storage under grazing. In Chapter 2 the wetter regions showed higher levels of introduced species, which can be highly productive and may produce more biomass than communities that are solely dominated by native species (Ehrenfeld 2003). Additionally, introduced species could have effects on C due to impacts on the microbial communities (Semmartin et al. 2010) or changes to litter chemistry (Wolkovich et al. 2010). Our study was limited to the depth we could extract soil cores from, thereby not allowing us to capture the full extent of root growth, which is up to 2 m in some range species (Coupland and Johnson 1965). Our results still shed insight into grassland C responses to grazing because the majority of root mass is situated in the top 30 cm of soil in grasslands (Jackson et al. 1996).

In the upper layer of the Fescue Foothills and Central Parkland soil there was little evidence of increased root mass under grazing, whereas there was root mass changes in the lower horizon. For the Central Parkland C percentages increased in the upper horizon and decreased in the lower horizon. For nitrogen (N) an opposite response was observed in the Fescue Foothills, where N decreased in the shallow horizon and increased in the deeper layer. While our data do not quantify root production or turnover *per-se*, the difference in C and N concentration could suggest there was less active root growth taking place in the upper horizons and more in the lower horizons, although it should be noted that our sampling of roots was done at only a single time (i.e. mid-summer of one year), and thus, is not able to detect patterns over the course of a year or between years.

Livestock grazing has been shown to impact the availability of nutrients and soil characteristics, like decreased soil moisture and increased bulk density (Steffens et al. 2008; Brueck et al. 2013), although this response is typically only observed under high intensity grazing. Some investigators speculate that this could lead to root die-off because of decreased nutrient availability (Bai et al. 2015). Bai et al. (2015) found that shallower soil horizons had higher root production and mortality than deeper ones.

3.4.4 Diversity

In Chapter 2 we established that diversity tended to increase with precipitation, as did the presence of introduced plant species, particularly under grazing. Similarly, our study suggested that the size of the total carbon pool was closely tied to MAP and MGSP (Table 3.2). Therefore we might expect a strong association between various diversity metrics and the size of the total C pool. Steinbeiss et al. (2008) found that species diversity was associated with increases in C, therefore natural sub-regions with higher moisture can be expected to have larger species diversity and more carbon. This relationship was only apparent for Simpson's Diversity in non-grazed areas however, and was lost under grazing. As Simpson's diversity is closely tied to evenness and therefore species relative abundance, whereas Shannon's index is more closely tied to richness (DeJong 1975), our results suggest that just having more species in a plant community does not enhance the carbon pool. Instead, a more balanced mixture of species (by cover or biomass) is needed to support increases in ecosystem C, presumably because of greater aggregate inputs of phytomass.

We also found strong relationships between total C pool size and the abundance of introduced species. Moreover, while these were apparent regardless of disturbance history, they were particularly strong under grazing. The proliferation of grazing-tolerant introduced species under exposure to livestock may therefore be playing a role in enhancing the storage of carbon in grasslands. This increase in C could arise from greater above and belowground production (Fink and Wilson 2011), which could reflect greater root production to support ongoing shoot growth (Bai et al. 2015; Sims and Singh 1978; Frank et al. 2002). As increases in the abundance of introduced species were confined largely to moist regions (Chapter 2), increases in soil C mass with grazing were limited to the Montane and Upper Foothills, highlighting the key role of growing conditions in promoting plant growth and C accumulation in Alberta grasslands.

Interestingly, other studies have found that the presence of introduced plant species can lead to a decline in soil C. In western Canada these are particularly well document in the arid prairie regions where the introduction of species such as crested wheatgrass (*Agropyron cristatum*) is known to have decreased soil C levels (Dormaar et al. 1995; Christian and Wilson 1999). Christian and Wilson (1999) found that introduced species do not store carbon at similar rates because of differences in root growth. In the current study however, presence of crested wheatgrass was relatively limited across the study sites, potentially because arid grasslands may be more resistant to invasion by introduced species (Chapter 2), which in turn, could prevent changes in ecosystem C.

3.5 Conclusion

Rangelands are an important pool of C, with significant C contained in soil organic matter, surface mulch, and live vegetation. While grazing altered the allocation of C within grasslands, largely by shifting C from dead to live vegetation pools, total ecosystem C remained relatively stable, with some evidence suggesting grazing may increase C in the shallow soil layer. Ecosystem C levels in mesic regions of Alberta also appeared to be favorably impacted under grazing by both high levels of current annual herb production (shoots and roots), potentially coupled with the introduction of grazing tolerant vegetation. At a minimum, these results indicate long-term livestock grazing did not reduce or compromise ecosystem C levels in vegetation and surface soils (to 30 cm depth) of grasslands, with some potential to enhance C stores under select conditions. Further work is warranted to more fully understand where and how grazing may alter grassland ecosystem C in Alberta, and thereby support the development of innovative policies that reward landowners and rangeland managers who are conserving and/or increasing this important environmental service.

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Table 3.1 Variation in mean (± SE) carbon mass (g/m2) for several vegetation and soil pools in response to long-term livestock grazing across 106 Rangeland Reference Areas distributed across 6 natural sub-regions in Alberta.

		Natural Sub-region (// Agro-climatic Zone)					
Vegetation /Soil Pool	Grazing Treatment	Dry Mixedgrass (n=16)	Mesic Mixedgrass (n=9)	Parkland (n=25)	Foothills Fescue (n=7)	Montane (n=37)	Upper Foothills (n=11)
Grass Carbon	Non-grazed	58.21 (±7.61)	93.64 (±10.54)	97.06 (±5.97)*	86.14 (±12.91)	69.12 (±5.11)	57.15 (±9.53)*
	Grazed	55.23 (±7.61)	75.19 (±11.00)	83.52 (±6.32*	87.21 (±12.91)	73.68 (±5.16)	78.59 (±9.53)*
Forb Carbon	Non-grazed	8.14 (±3.15)	10.47 (±4.34)	8.95 (±2.46)*	18.51 (±5.32)*	22.00 (±2.11)*	32.92 (±3.93)
	Grazed	8.33 (±3.15)	17.26 (±4.58)	14.85 (±2.64)*	32.27 (±5.31)*	27.95 (±4.58)*	31.33 (±3.93)
Total Herb Carbon	Non-grazed	66.41 (±8.12)	104.11 (±11.27)	106.00 (±6.39)	104.65 (±13.80)	91.19 (±5.46)*	90.07 (±10.19)*
	Grazed	63.55 (±8.12)	92.69 (±11.73)	98.43 (±6.74)	119.48 (±13.80)	101.59 (±5.51)*	109.91 (±10.19)*
Litter Carbon	Non-grazed	59.60 (±10.21)*	149.01 (±14.05)*	99.35 (±7.97)*	165.12 (±17.21)*	72.55 (±6.83)*	65.32 (±12.71)
	Grazed	34.1 (±10.21)*	66.72 (±14.87)*	42.97 (±8.58)*	84.50 (±17.21)*	34.18 (±7.01)*	41.74 (±13.30)
Shallow Root Carbon	Non-grazed	91.46 (±55.70)	92.91 (±78.77)	151.78 (±44.64)	206.87 (±83.55)	226.95 (±38.34)*	128.44 (±71.25)
	Grazed	132.68 (±55.70)	96.53 (±55.70)	167.41 (±47.19)	332.61 (±83.55)	339.10 (±38.84)*	158.30 (±71.25)
Deep Root Carbon	Non-grazed	24.57 (±24.57)	19.86 (±19.86)	40.96 (±10.34)	21.11 (±19.36)	62.62 (±8.88)	26.85 (±16.51)
	Grazed	38.07 (±38.07)	27.43 (±18.25)	54.17 (±10.92)	16.35 (±19.36)	64.23 (±9.00)	31.33 (±16.51)
LFH/ Mulch Layer Carbon	Non-grazed	950.88 (±263.15)*	889.65 (±372.14)	1408.13 (±201.3)*	1657.09 (±394.72)	1858.74 (±181.11)	3401.57 (±336.62)*
	Grazed	445.64 (±263.15)*	951.56 (±372.14)	1834.31 (±218.8)*	2227.44 (±394.72)	1859.39 (±182.85)	2548.89 (±336.62)*
Total Aboveground Carbon	Non-grazed	126.46 (±16.01)*	253.12 (±22.64)*	199.82 (±12.61)*	212.54 (±24.02)*	165.52 (±11.02)*	150.63 (±20.48)
	Grazed	92.98 (±16.01)*	157.43 (±23.6)*	137.68 (±13.51)*	168.56 (±24.02)*	143.92 (±11.12)*	143.44 (±20.48)

Total Belowground Carbon	Non-grazed	1066.91 (±269.74)	1002.42 (±381.47)	1724.01 (±217.85)	2154.37 (±432.54)*	2148.31 (±185.65)	3556.85 (±345.05)*
	Grazed	616.39 (±269.74)	1075.52 (±381.47)	2052.03 (±223.89)	2944.47 (±432.54)*	2263.32 (±187.36)	2738.52 (±345.05)*
Live Vegetation Carbon	Non-grazed	180.14 (±60.28)	216.88 (±85.25)	297.38 (±48.30)	319.44 (±90.42)	380.75 (±41.49)*	239.93 (±77.11)
	Grazed	230.49 (±60.28)	225.66 (±90.23)	322.07 (±52.04)	445.51 (±90.42)	505.98 (±42.03)*	293.65 (±77.11)
Dead Vegetation Carbon	Non-grazed	1013.23 (±262.99)*	1028.66 (±371.93)	1504.31 (±207.20)	1778.17 (±394.49)	1933.08 (±181.00)	3467.56 (±336.42)*
	Grazed	478.88 (±262.99)*	1078.25 (±388.66)	1871.14 (±219.05)	2299.45 (±394.49)	1900.83 (±182.80)	2717.61 (±348.58)*

[1] Within a response and sub-region, grazing treatment means denoted with an asterisk differ, $p<0.05$.

Table 3.2 Correlations of total carbon mass with major climatic factors assessed among the 106 RRA sites across 6 natural sub-regions in Alberta under grazed and non-grazed conditions. Bolded p-values indicate significant correlations at $p < 0.0001$.

Primary Response	Climatic Factor[1]	Non-Grazed		Grazed	
		r	p-value	*r*	p-value
Carbon Pool	Mean annual precip (MAP)	**+0.424**	**< 0.0001**	**+0.387**	**< 0.0001**
	Mean summer precip (MGSP)	**+0.563**	**< 0.0001**	**+0.528**	**< 0.0001**
	Annual Heat: Moisture index (AHM)	**-0.461**	**< 0.0001**	**-0.468**	**< 0.0001**

[1] MAP and MGSP represent precipitation falling from 295 to 947 mm, and 199 to 417 mm, respectively. MGSP is precipitation falling from May through September, inclusive. AHM varies from 14 to 53, 14 is the coldest/wettest and 53 is the warmest/driest.

Table 3.3 Correlations of total carbon pool size with various vegetation characteristics assessed among 106 RRA sites across 6 natural sub-regions in Alberta under grazed and non-grazed conditions. Bolded p-values indicate significant correlations, $p \leq 0.05$

Primary Response	Vegetation Parameter	Non-Grazed		Grazed	
		r	p-value	*r*	p-value
Total Carbon	Simpson's Diversity	**+0.195**	**0.039**	+0.141	0.150
	Shannon's Diversity	+0.011	0.911	+0.086	0.378
	Richness	+0.138	0.148	+0.0532	0.588
	Richness of Introduced	+0.146	0.125	**+0.297**	**0.002**
	Shannon's Diversity Introduced	**+0.208**	**0.028**	**+0.390**	**< 0.0001**
	Proportion of Shannon's Diversity that is Introduced	**+0.206**	**0.029**	**+0.321**	**0.0008**
	Percent Introduced Richness	+0.080	0.402	**+0.186**	**0.056**
	Total Vegetation Cover	**0.329**	**0.0004**	**0.408**	**<0.0001**

Table 3.4 Variation in mean (± SE) nitrogen concentration (%) for several vegetation and soil pools in response to long-term livestock grazing across 106 RRAs distributed across 6 natural sub-regions in Alberta.

		Natural Sub-region (// Agro-climatic Zone)					
Vegetation/ Soil Pool	Grazing Treatment	Dry Mixedgrass (n=16)	Mesic Mixedgrass (n=9)	Parkland (n=25)	Foothills Fescue (n=7)	Montane (n=37)	Upper Foothills (n=11)
Grass Nitrogen	Non-grazed	1.18 (±0.05)	1.17 (±0.08)	1.23 (±0.04)	**1.33** **(±0.09)***	1.60 (±0.04)	2.01 (±0.07)
	Grazed	1.25 (±0.06)	1.20 (±0.08)	1.28 (±0.05)	**1.50** **(±0.09)***	1.63 (±0.04)	2.08 (±0.07)
Forb Nitrogen	Non-grazed	1.50 (±0.07)	1.59 (±0.10)	1.55 (±0.05)	1.61 (±0.11)	1.96 (±0.05)	2.35 (±0.09)
	Grazed	1.47 (±0.07)	1.57 (±0.10)	1.62 (±0.06)	1.48 (±0.11)	1.93 (±0.05)	2.51 (±0.09)
Litter Nitrogen	Non-grazed	1.09 (±0.08)	1.32 (±0.11)	1.32 (±0.06)	1.29 (±0.12)	1.22 (±0.05)	**1.37** **(±0.05)***
	Grazed	1.16 (±0.08)	1.18 (±0.11)	1.25 (±0.06)	1.27 (±0.12)	1.22 (±0.05)	**1.63** **(±0.10)***
Shallow Root Nitrogen	Non-grazed	0.84 (±0.05)	**0.88** **(±0.07)***	0.78 (±0.04)	**1.07** **(±0.08)***	0.83 (±0.03)	0.96 (±0.06)
	Grazed	0.73 (±0.05)	**0.67** **(±0.07)***	0.84 (±0.04)	**0.75** **(±0.08)***	0.87 (±0.03)	1.06 (±0.07)
Deep Root Nitrogen	Non-grazed	0.71 (±0.05)	0.65 (±0.07)	**0.57** **(±0.04)***	**0.68** **(±0.08)***	0.59 (±0.03)	**0.70** **(±0.06)***
	Grazed	0.75 (±0.05)	0.69 (±0.07)	**0.67** **(±0.04)***	**0.86** **(±0.08)***	0.61 (±0.03)	**0.95** **(±0.06)***
LFH/Mulch Horizon Nitrogen	Non-grazed	0.69 (±0.11)	0.68 (±0.15)	0.95 (±0.09)	1.03 (±0.18)	1.05 (±0.07)	1.62 (±0.14)
	Grazed	0.63 (±0.11)	0.68 (±0.15)	1.03 (±0.09)	1.23 (±0.17)	1.05 (±0.08)	1.77 (±0.14)

[1] Within a carbon pool and sub-region, grazing treatment means denoted with an asterisk differ, $p < 0.05$.

Table 3.5 Variation in mean (± SE) carbon concentration (%) for several vegetation and soil pools in response to long-term livestock grazing across 106 RRAs distributed across 6 natural sub-regions in Alberta.

		Natural Sub-region (// Agro-climatic Zone)					
Vegetation /Soil Pool	Grazing Treatment	Dry Mixedgrass (n=16)	Mesic Mixedgrass (n=9)	Parkland (n=25)	Foothills Fescue (n=7)	Montane (n=37)	Upper Foothills (n=11)
Grass Carbon	Non-grazed	44.04 (±0.19)	44.22 (±0.27)	**44.02** **(±0.15)***	44.98 (±0.31)	44.32 (±0.13)	44.17 (±0.24)
	Grazed	43.96 (±0.19)	43.90 (±0.28)	**43.64** **(±0.16)***	44.55 (±0.31)	44.31 (±0.13)	43.86 (±0.24)
Forb Carbon	Non-grazed	**43.75** **(±0.32)***	45.28 (±0.45)	44.43 (±0.26)	44.79 (±0.51)	**44.55** **(±0.22)***	**44.25** **(±0.41)***
	Grazed	**45.68** **(±0.33)***	45.70 (±0.47)	45.18 (±0.27)	45.43 (±0.51)	**43.88** **(±0.22)***	**43.48** **(±0.41)***
Litter Carbon	Non-grazed	42.02 (±0.43)	41.56 (±0.60)	**40.90** **(±0.34)***	43.23 (±0.68)	43.43 (±0.29)	**42.56** **(±0.55)***
	Grazed	42.59 (±0.43)	42.38 (±0.63)	**42.02** **(±0.36)***	43.62 (±0.68)	43.24 (±0.29)	**41.56** **(±0.56)***
Shallow Root Carbon	Non-grazed	42.07 (±1.79)	**35.0** **(±2.46)***	**32.71** **(±1.40)***	32.61 (±3.22)	27.29 (±1.23)	36.75 (±2.23)
	Grazed	40.73 (±1.8293)	**29.06** **(±2.57)***	**37.96** **(±1.47)***	33.17 (±3.01)	27.90 (±1.22)	38.10 (±2.23)
Deep Root Carbon	Non-grazed	38.50 (±2.29)	34.52 (±3.39)	**36.28** **(±1.95)***	34.66 (±4.12)	23.36 (±1.69)	33.25 (±2.89)
	Grazed	41.63 (±2.43)	32.11 (±3.39)	**31.47** **(±2.06)***	32.02 (±3.91)	21.84 (±1.66)	36.48 (±2.97)
LFH/Mulch Carbon	Non-grazed	9.65 (±1.45)	9.15 (±2.05)	13.03 (±1.14)	14.0891 (±2.4422)	15.24 (±1.00)	20.66 (±1.86)
	Grazed	9.81 (±1.54)	9.79 (±2.05)	13.92 (±1.21)	17.3343 (±2.3262)	14.59 (±1.01)	22.27 (±1.91)

[1] Within a carbon pool and sub-region, grazing treatment means denoted with an asterisk differ, p < 0.05.

Table 3.6 Variation in mean (± SE) C:N ratios for several vegetation pools in response to long-term livestock grazing across 106 RRAs distributed across 6 natural sub-regions in Alberta.

		Natural Sub-region (// Agro-climatic Zone)					
Vegetation Pool	Grazing	Dry Mixedgrass (n=16)	Mesic Mixedgrass (n=9)	Parkland (n=25)	Foothills Fescue (n=7)	Montane (n=37)	Upper Foothills (n=11)
Grass C:N	Non-grazed	**38.48** **(±1.17)***	38.42 (±1.65)	36.27 (±0.93)	**35.53** **(±1.87)***	28.47 (±0.80)	22.11 (±1.49)
	Grazed	**35.80** **(±1.19)***	37.88 (±1.72)	34.75 (±0.99)	**30.75** **(±1.87)***	27.99 (±0.81)	21.46 (±1.49)
Forb C:N	Non-grazed	29.89 (±1.04)	29.72 (±1.48)	29.48 (±0.84)	28.71 (±1.67)	23.38 (±0.72)	19.46 (±1.34)
	Grazed	31.63 (±1.07)	29.54 (±1.55)	28.39 (±0.89)	30.96 (±1.67)	23.34 (±0.72)	17.60 (±1.34)
Litter C:N	Non-grazed	41.18 (±2.34)	32.54 (±3.31)	33.12 (±1.87)	34.61 (±3.75)	38.46 (±1.60)	**33.02** **(±2.99)***
	Grazed	38.62 (±2.38)	36.85 (±3.42)	35.24 (±1.96)	35.77 (±3.75)	38.56 (±1.61)	**27.69** **(±3.08)***
Shallow Root C:N	Non-grazed	53.8 (±3.6209)	39.36 (±5.28)	44.94 (±2.87)	33.27 (±6.62)	33.47 (±2.52)	41.98 (±4.50)
	Grazed	59.89 (±3.83)	41.36 (±5.61)	47.66 (±3.22)	46.93 (±6.09)	32.86 (±2.59)	39.11 (±4.93)
Deep Root C:N	Non-grazed	66.57 (±5.01)	54.77 (±7.32)	**64.78** **(±4.29)***	51.29 (±9.19)	40.07 (±3.76)	48.64 (±6.24)
	Grazed	60.75 (±5.48)	46.59 (±7.32)	**48.64** **(±4.69)***	38.94 (±8.45)	34.90 (±3.65)	38.99 (±6.52)
LFH/Mulch C:N	Non-grazed	14.83 (±0.69)	12.16 (±0.98)	14.01 (±0.55)	11.77 (±1.18)	14.54 (±0.48)	12.80 (±0.89)
	Grazed	15.53 (±0.74)	12.86 (±0.98)	14.16 (±0.59)	12.02 (±1.11)	13.81 (±0.48)	12.62 (±0.92)

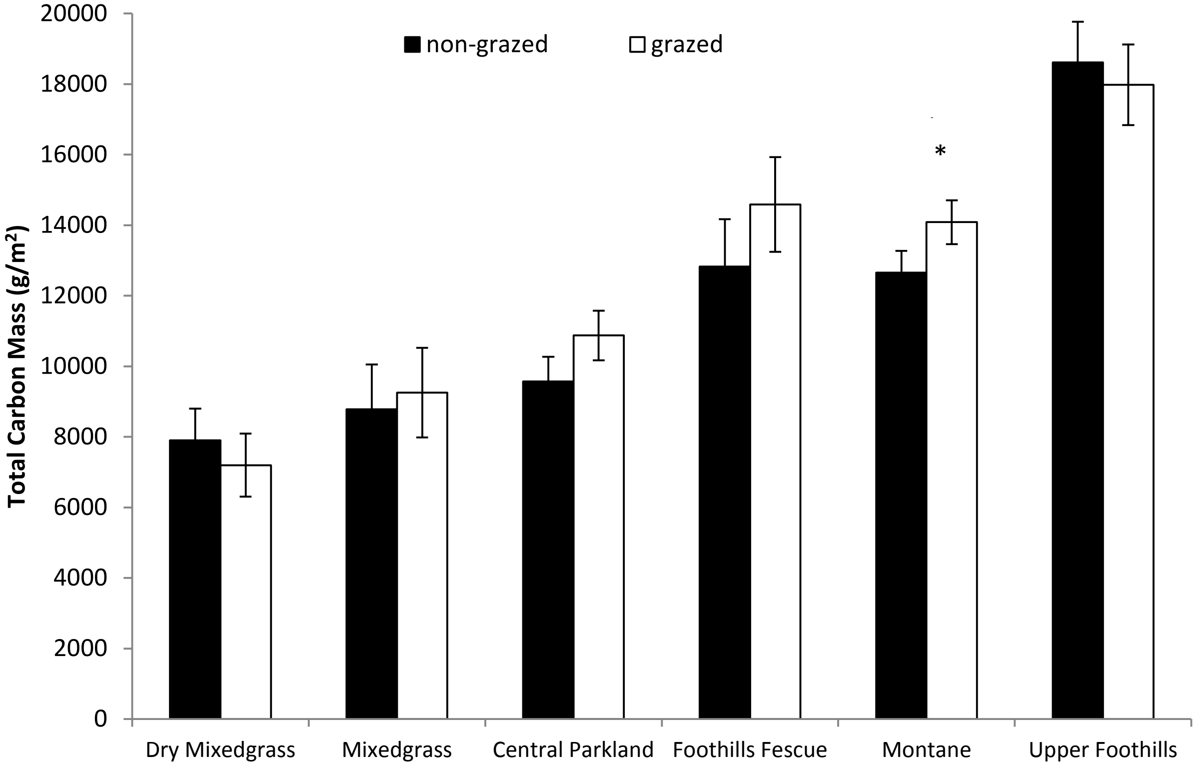
[1] Within a response and sub-region, grazing treatment means denoted with an asterisk differ, $p < 0.05$.

Table 3.7 Variation in mean (± SE) nitrogen mass (g/m2) for several vegetation pools in response to long-term livestock grazing across 106 RRAs distributed across 6 natural sub-regions in Alberta.

		Natural Sub-region (// Agro-climatic Zone)					
Vegetation Pool	Grazing Treatment	Dry Mixedgrass (n=16)	Mesic Mixedgrass (n=9)	Parkland (n=25)	Foothills Fescue (n=7)	Montane (n=37)	Upper Foothills (n=11)
Grass Nitrogen	Non-grazed	1.53 (±0.29)	2.50 (±0.41)	2.76 (±0.23)	2.58 (±0.50)	2.44 (±0.20)	**2.63** **(±0.37)***
	Grazed	1.60 (±0.29)	2.06 (±0.42)	2.46 (±0.24)	2.96 (±0.50)	2.75 (±0.20)	**3.69** **(±0.37)***
Forb Nitrogen	Non-grazed	0.27 (±0.15)	0.36 (±0.20)	0.31 (±0.11)	0.66 (±0.25)	**0.96** **(±0.10)***	1.73 (±0.18)
	Grazed	0.27 (±0.15)	0.61 (±0.21)	0.53 (±0.12)	1.08 (±0.25)	**1.22** **(±0.10)***	1.78 (±0.18)
Litter Nitrogen	Non-grazed	1.56 (±0.42)	**4.81** **(±0.57)***	**3.56** **(±0.32)***	**4.94** **(±0.70)***	**2.24** **(±0.28)***	2.24 (±0.28)
	Grazed	0.99 (±0.42)	**1.85** **(±0.61)***	**1.26** **(±0.35)***	**2.48** **(±0.70)***	**0.94** **(±0.29)***	1.75 (±0.54)

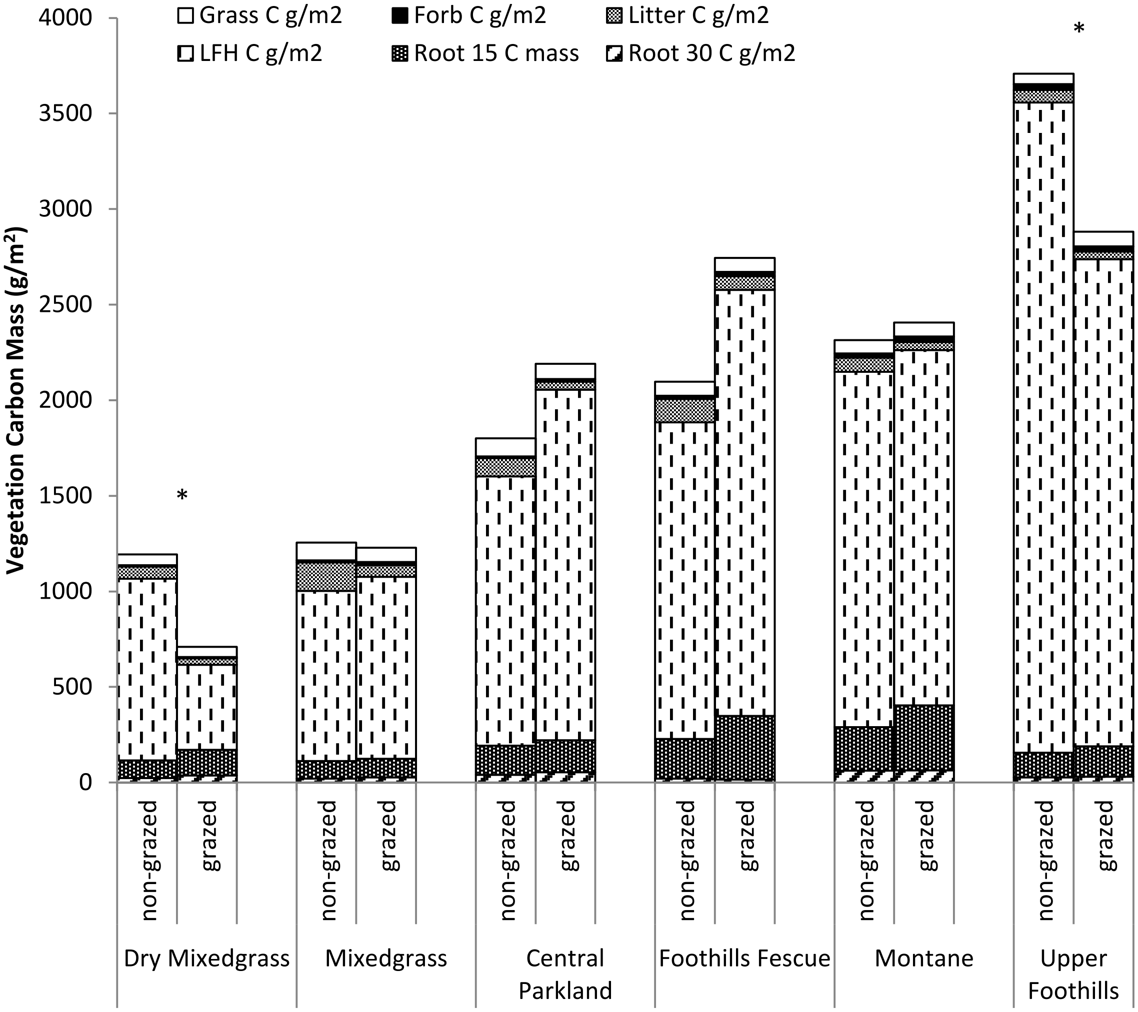
[1] Within a response and sub-region, grazing treatment means denoted with an asterisk differ, $p < 0.05$.

(A)



Total Carbon Mass (g/m²)
20000
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
■ non-grazed
□ grazed
*
Dry Mixedgrass
Mixedgrass
Central Parkland
Foothills Fescue
Montane
Upper Foothills

(B)


☐ Grass C g/m2
■ Forb C g/m2
▨ Litter C g/m2
☐ LFH C g/m2
▨ Root 15 C mass
◪ Root 30 C g/m2
Vegetation Carbon Mass (g/m²)
4000
3500
3000
2500
2000
1500
1000
500
0
*
*
non-grazed
grazed
Dry Mixedgrass
Mixedgrass
Central Parkland
Foothills Fescue
Montane
Upper Foothills

(C)

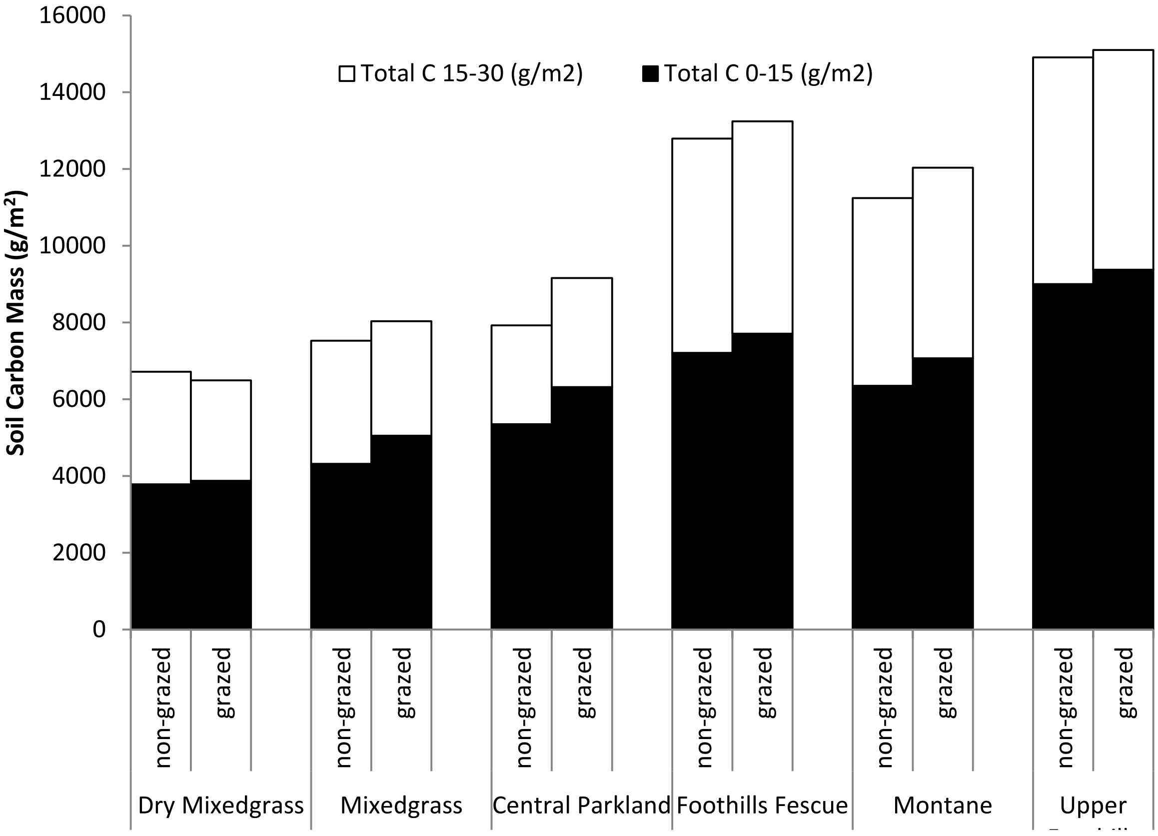


Figure 3.1 Estimates of (A) total grassland carbon mass (g/m^2), (B) the total vegetation carbon mass (deep and shallow roots, forbs, grass, mulch, and litter; g/m^2), and (C) soil carbon mass (deep and shallow; g/m^2) for both grazed and non-grazed conditions in each natural sub-region (natural sub-regions are arranged from driest to wettest, left to right). * Indicates significant differences between grazing treatments within a region (alpha<0.05).

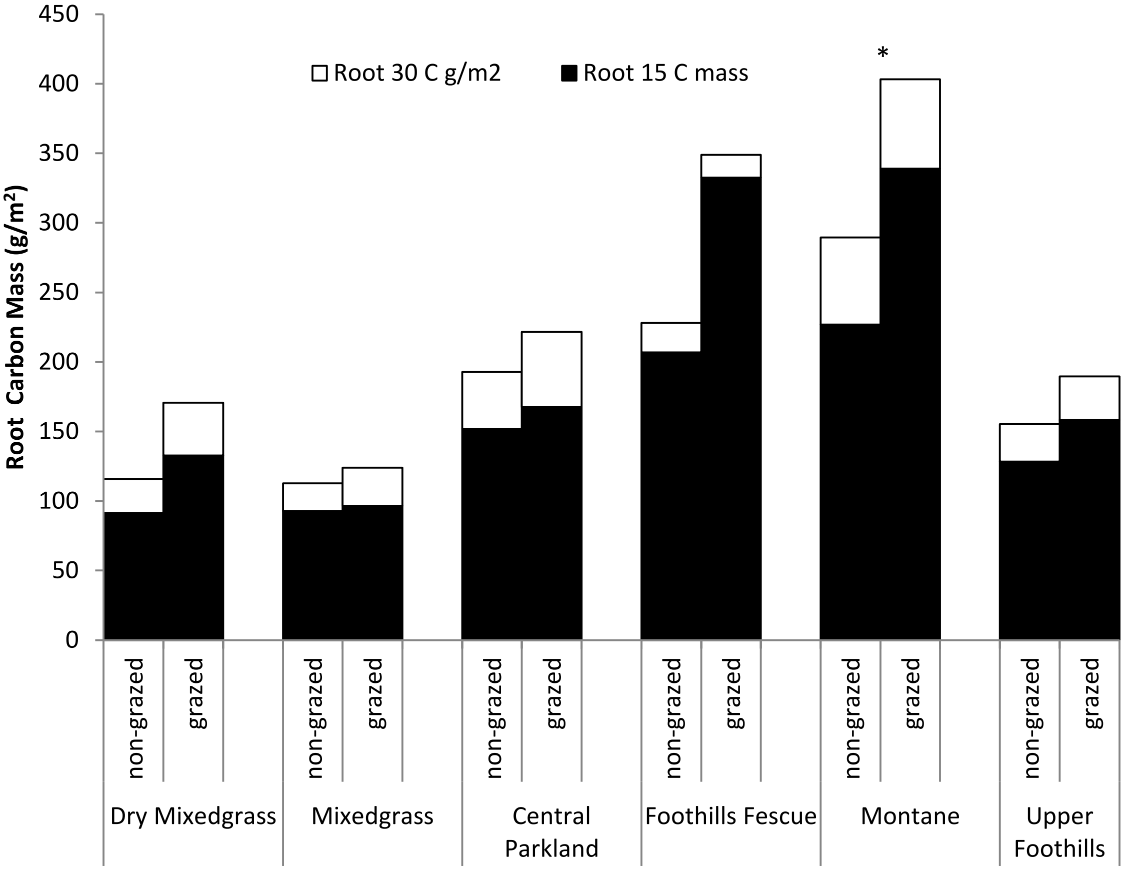


Figure 3.2 Shallow and deep root carbon mass (g/m^2) within the 0-15 cm and 15-30 cm soil layers, respectively, for both grazed and non-grazed conditions in each natural sub-region (natural sub-regions are arranged from driest to wettest, left to right). * Indicates significant differences between grazing treatments within a region (alpha<0.05).

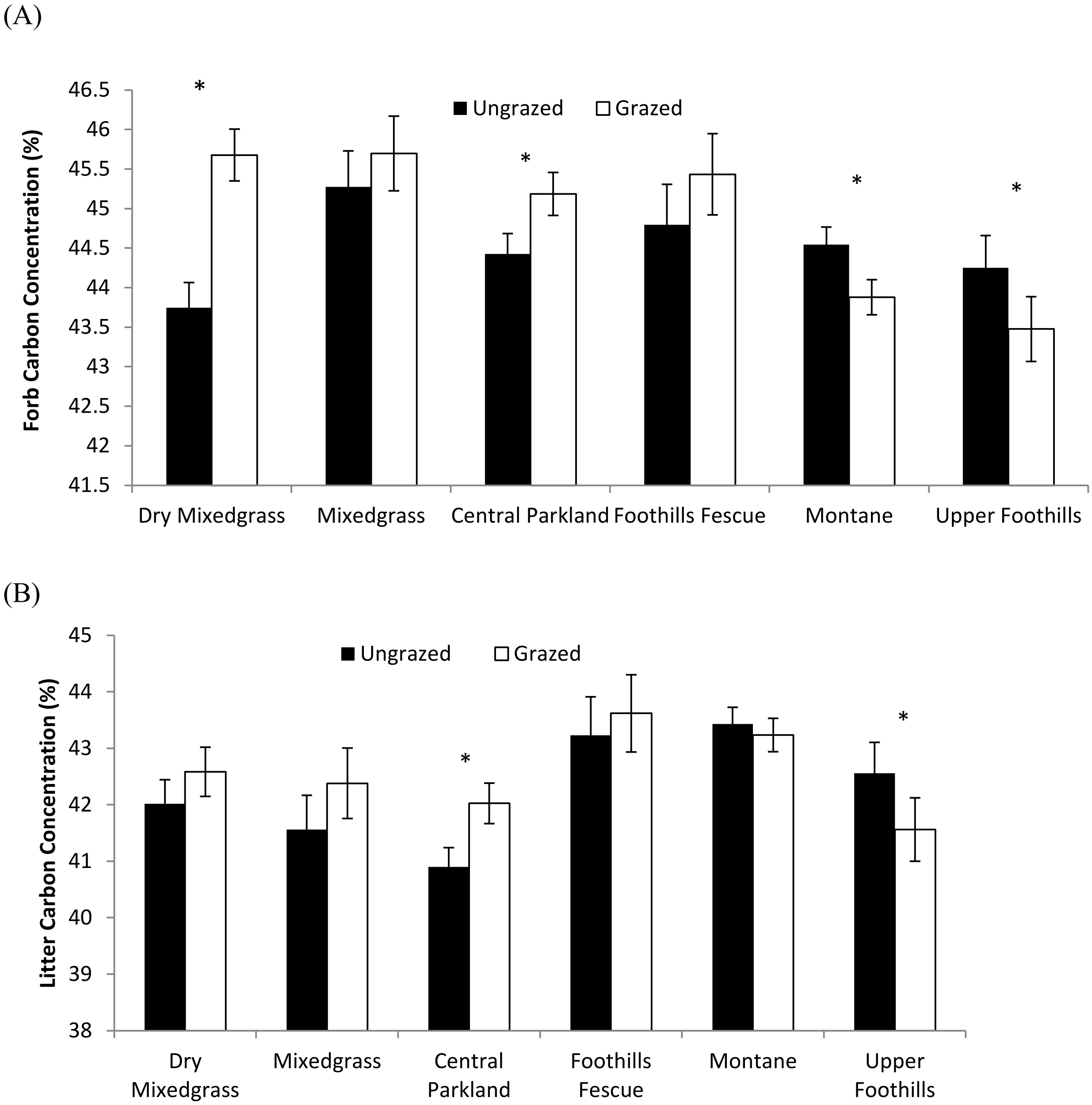


Figure 3.3 Concentration of carbon (%) in (A) forb and (B) litter mass for both grazed and non-grazed conditions within each natural sub-region (natural sub-regions arranged from driest to wettest, left to right). * Indicates significant differences between grazing treatments within a region (alpha<0.05).

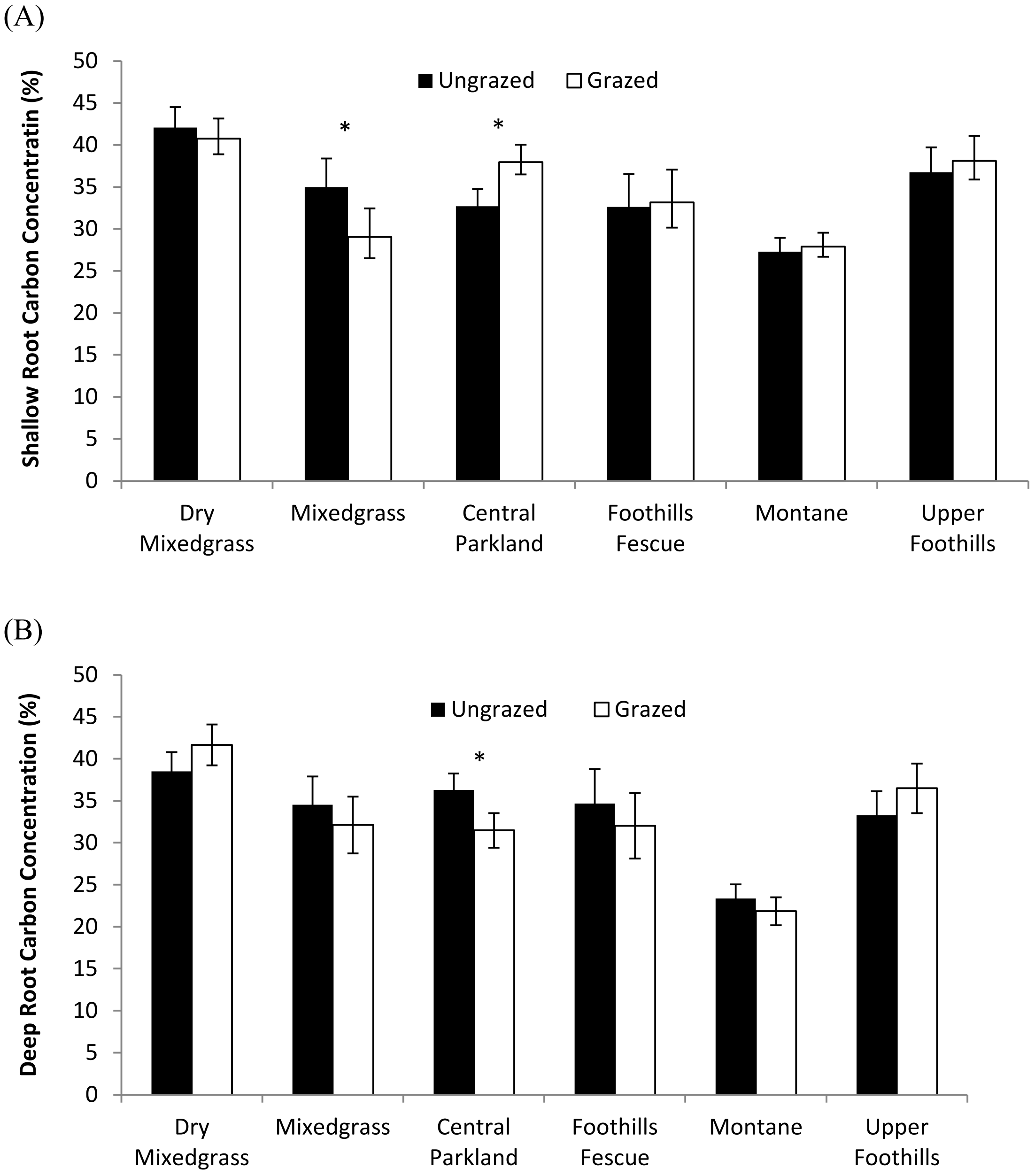


Figure 3.4 Concentration of carbon (%) within the (A) shallow root (0-15 cm) and (B) deeper root (15-30 cm) layer for both grazed and non-grazed conditions within each natural sub-region (natural sub-regions are arranged from driest to wettest, left to right). * Indicates significant differences between grazing treatments within a region (alpha<0.05).

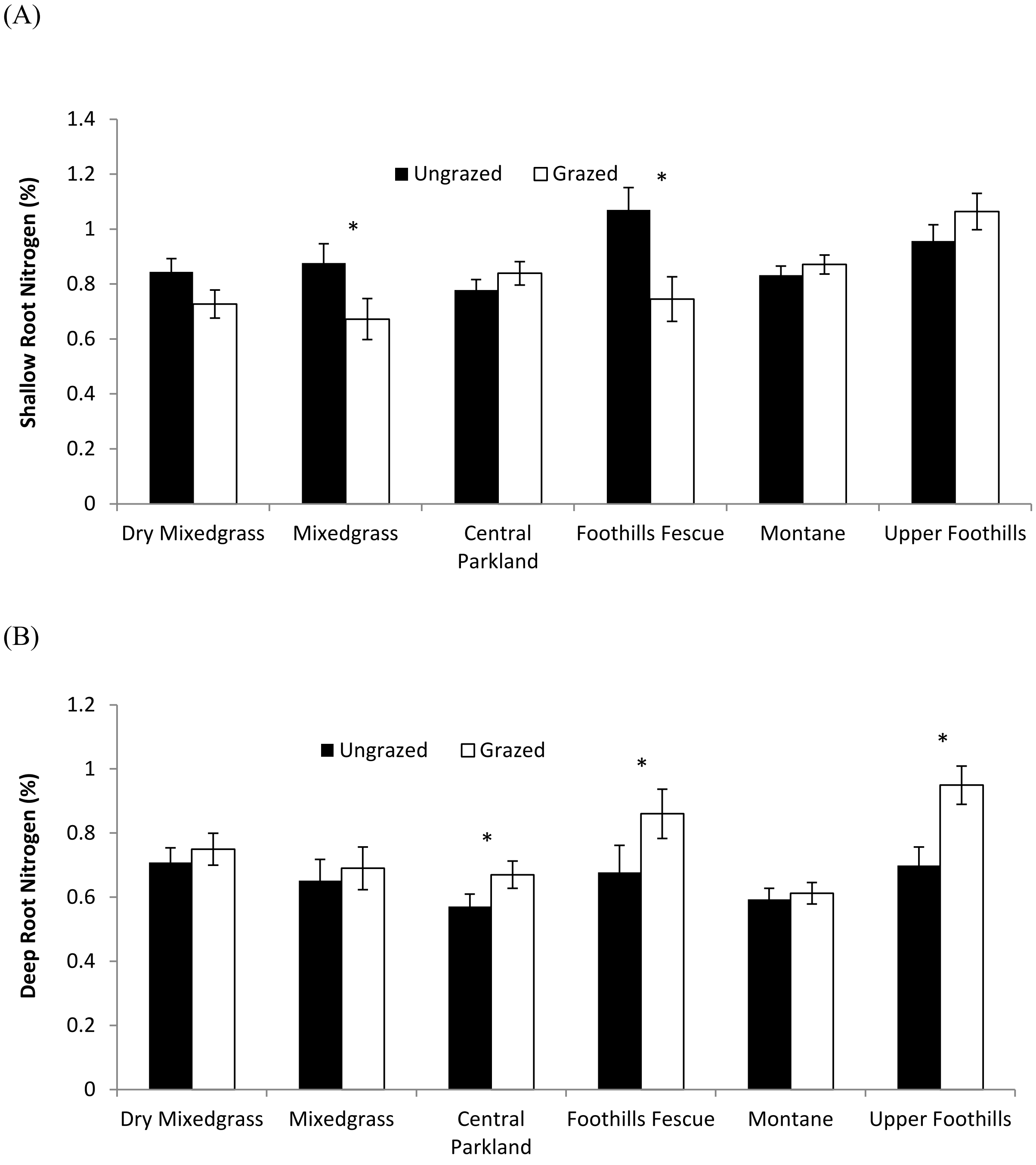


Figure 3.5 Nitrogen concentration (%) of (A) shallow roots (0-15 cm) and (B) deeper roots (15-30 cm) for both grazed and non-grazed conditions within each natural sub-region (regions are arranged from driest to wettest, left to right). * Indicates significant differences between grazing treatments within a region (alpha<0.05).

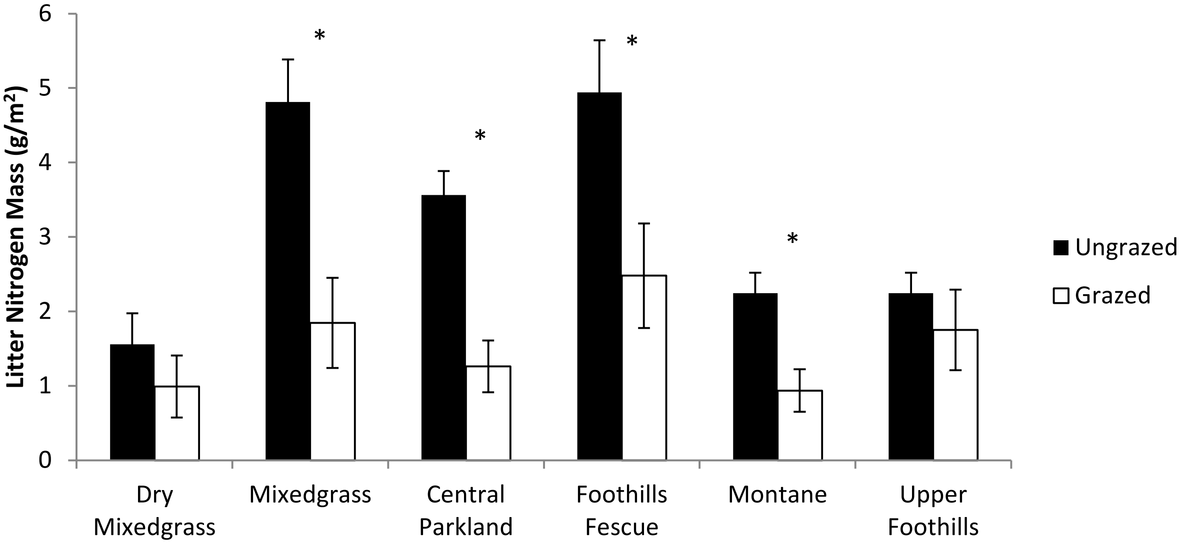
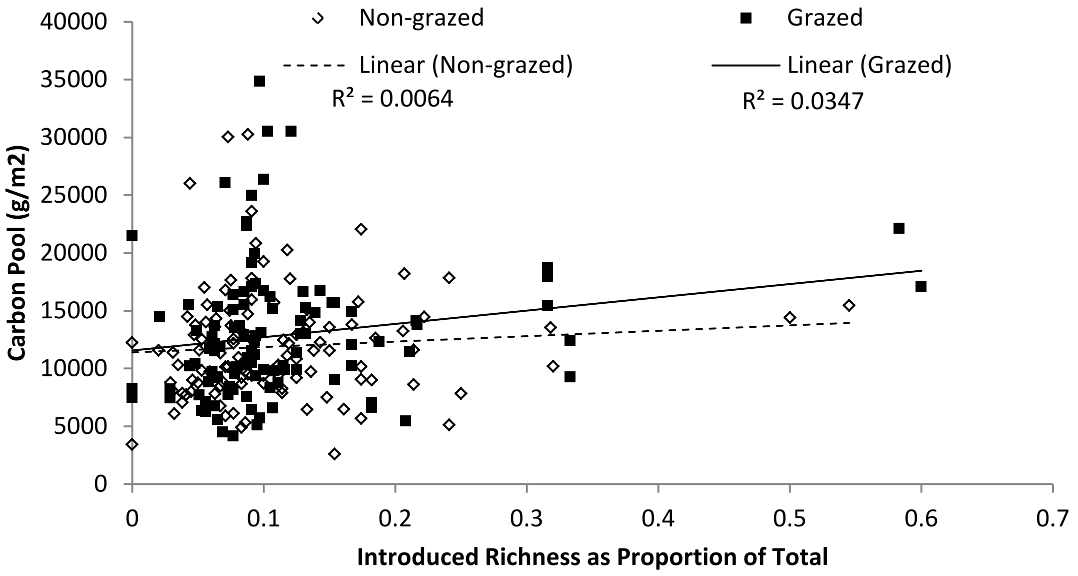
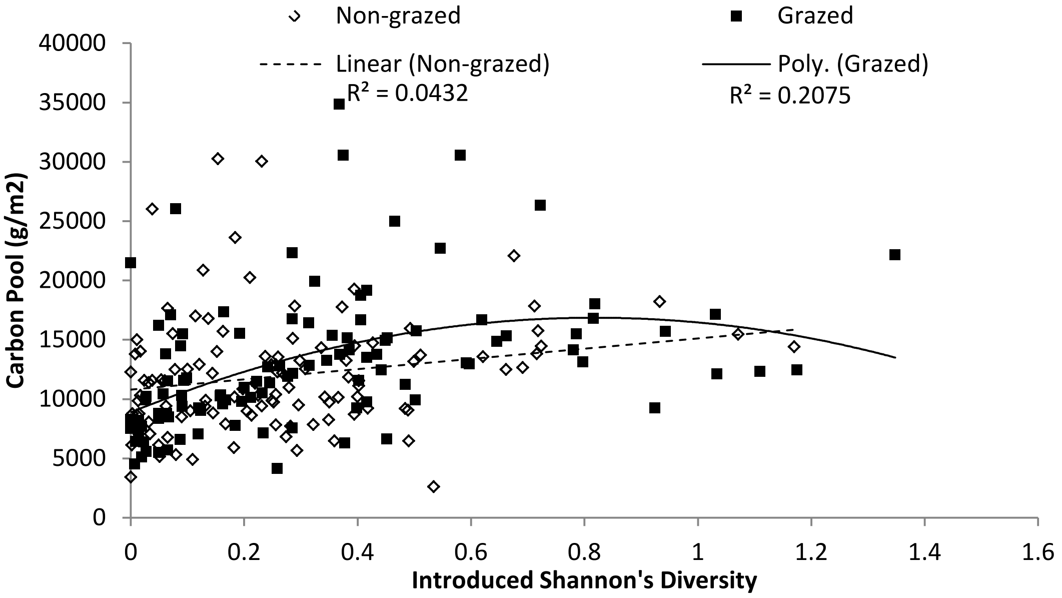


Figure 3.6: Mass of nitrogen (g/m^2) held in litter of both grazed and non-grazed plots within each natural sub-region (regions are arranged from driest to wettest, left to right). * Indicates significant differences between grazing treatments within a region (alpha= 0.05).

(A)


Non-grazed
Grazed
Linear (Non-grazed)
Linear (Grazed)
R² = 0.0064
R² = 0.0347
Carbon Pool (g/m2)
40000
35000
30000
25000
20000
15000
10000
5000
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Introduced Richness as Proportion of Total

(B)


Non-grazed
Grazed
Linear (Non-grazed)
Poly. (Grazed)
R² = 0.0432
R² = 0.2075
Carbon Pool (g/m2)
40000
35000
30000
25000
20000
15000
10000
5000
0
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
Introduced Shannon's Diversity

(C)

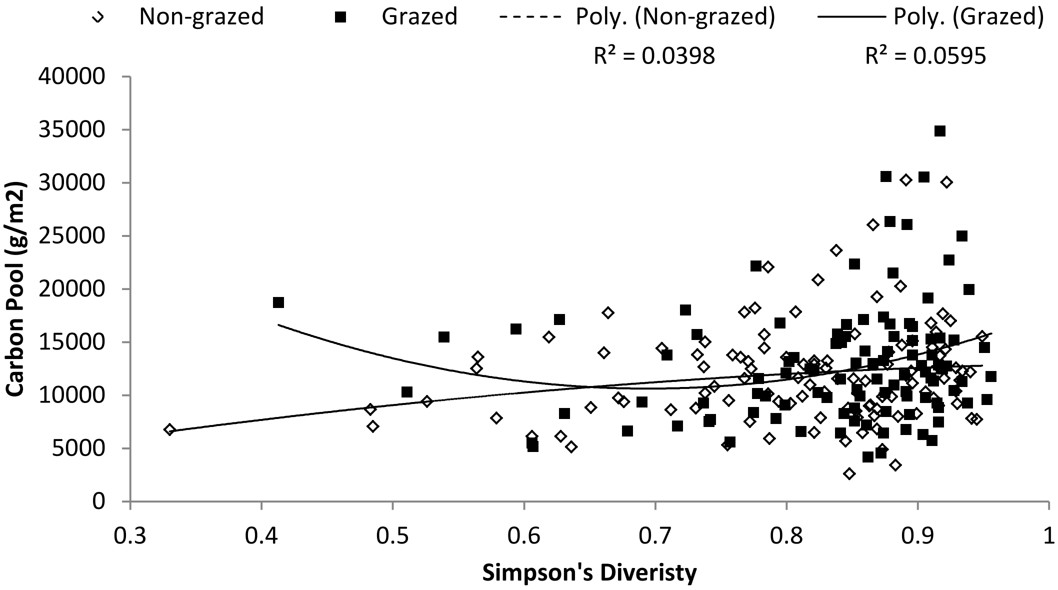


Figure 3.7 Relationship of ecosystem C mass (g/m^2) to (A) introduced species richness as a proportion of total richness, (B) introduced Shannon's Diversity, and (C) Simpson's Diversity, for each of the grazed and non-grazed grasslands. Line of best fits was selected with the highest r^2 with a minimum of 0.03 increase from the linear fit.

Chapter 4 Synthesis

4.1 Introduction

Livestock industries, specifically beef production, have been under a lot of pressure from environmental advocates, to justify the 'sustainability' of their product. As the Canadian population becomes more urban and has more generations removed from first-hand job experience related to livestock production, these industries will only face more questions about environmental impact. Not only will industries have to defend their management practices but they must do so in a way that's tangible to an audience lacking understanding of the Canadian beef industry and in a way that provides quantifiable evidence to support their social license to operate, particularly on public lands. Unfortunately, the role of the Canadian beef industry in conserving ecological goods and service on rangeland landscapes remains relatively poorly understood. Future initiatives by the beef industry could align with Canadian and Albertan commitments for decreasing greenhouse gas emissions.

Optimizing ecological goods and services is the goal of many land management organizations including Environment and Parks. Environment and Parks has a multiple-use mandate, meaning that all land-uses need to be in balance on the landscape. Therefore Environment and Parks does not just have to justify the potential impacts of livestock grazing, it also has to defend grazing against competing land uses. In this thesis, I set out to examine the effects of cattle grazing on vegetation diversity and carbon stocks. I found that depending on the environment, grazing could be beneficial to forage production, vegetation diversity and carbon storage. This study has outlined three benefits that livestock grazing has on the landscape and why grazing should be maintained as an ongoing land management tool.

4.2 Biomass

Concerns of livestock grazing decreasing biomass production on Alberta grasslands are not justified by our study. There was no significant decline in herbage production due to grazing suggesting that existing levels of low to moderate grazing are compatible with the long-term maintenance and function of Alberta grasslands. In fact, the only exception to this was in the Upper Foothills where grazing increased herbage production. Although biomass production is important for livestock producers for use as forage, it is also important to the naturalist for habitat. Ultimately, our results indicate that forage resources are not being pulled away from other demands, such as habitat, but are being maintained and even enhanced.

4.3 Diversity

Diversity is a desirable characteristic of a plant community (Noss 1990) with many benefits to production, resistance to invasion, and wildlife. Pressure to provide more habitats in a shrinking land base will become more and more of a problem with increased urban-industrial sprawl and expansion of intensive agriculture (Pitt and Hooper 1994). Land-uses will ultimately need to overlap, especially when uses are mutually beneficial to each other. For example, livestock grazing may be utilized as a mechanism in which to increase floristic diversity across the landscape, and in doing so, provide a more suitable habitat for not only plant species, but other wildlife as well, including potentially key species of concern. From a naturalists perspective an opportunity has opened up for conservation of a species or plant community, and from a cattlemen's perspective they will have access to a reliable forage base.

Similarly, many of Alberta's landscapes are threatened by encroachment of shrubs and although some would argue that shrub encroachment is a product of fire suppression, our data shows that grazing by livestock also plays a role in suppressing shrub advancement in wetter regions. For the Montane and Upper Foothill natural sub-regions, grazing should be looked at as an ongoing management tool to help control shrubs and woody cover. Other options, for example burning, carry an inherent risk with them and can also be expensive to implement. Cattle are typically profit generating, and therefore are a much more economical solution to help combat shrub encroachment.

4.4 Carbon

Throughout this thesis, we have heavily emphasized that atmospheric C has been increasing, and grasslands are and will continue to be, a major sink in the future (Desjardin et al. 2005). Our research suggests that more C is found in soil that has been grazed, and therefore grazing may be a key natural process to help increase current grassland carbon stocks.

Knowing that grazing increases C stocks in the soil can help livestock producers start a carbon offsets program similar to what is paid to landowners for converting conventionally cropped fields to reduced-till practices. Although more research is need to understand the mechanism for change over time, land managers that have moderate grazing on their land could be compensated for continuing to maintain grasslands, or perhaps improving C via targeted management practices. A compensation program could either be facilitated by government or by industry, but the most plausible would be a voluntary program where companies could buy credits from ranchers for their C credits coming from grazing practices that could increase C storage. Industrial organizations could use these credits as both a way to meet government requirements (Wang et al. 2014) and create positive optics for conserving the landscape. For C credits to work properly however, more research will need to look into indicators or large C pools so rapid assessments of the land base can be performed. Similarly, further research will have to be done on the effects of stocking rate on C pools in grassland.

Further research should be put into when, where and how ecosystem carbon is changing under grazing, and what is the difference in sequestration rates compared to non-grazed situations, as well as other alternate land uses. Knowing the answer to these questions would help policy developers make well-informed policies that directly tie to the benefits of livestock grazing. Additionally, the stability of the carbon being stored may also be important to understanding if livestock grazing has a long-term effect on carbon stocks.

4.5 Conclusions

For a contemporary rangeland manager there is currently only one major economic opportunity to be generated from grassland ecosystems (excluding urban-industrial development activities), that being livestock production. Unlike conserving biodiversity and pristine habitat, livestock grazing provides a real tangible economic benefit for use of a landscape. Livestock has a direct economic benefit from the sale of stock but also the storage of carbon, an element that has a direct value on the open market. This is unlike many ecological goods and services that have more abstract returns to a disengaged audience. Land management groups focusing on habitat could utilize livestock grazing to maintain habitat through the suppression of shrubs and increasing diversity, as well as simultaneously supporting the beef industry. In some cases conservation groups are at odds with beef producers, but this would provide an opportunity for relationship building and to secure social license to operate on public land.

The general expectations among the public may be that ecosystems not be disturbed by agricultural practices. However, that doesn’t necessarily translate into higher prices for ecologically sustainable management of livestock. Similarly, producers are not paid for the retention and/or increase in diversity and preservation of ecosystems. Cattlemen therefore have the opportunity to increase their marketability by showing what their (typical) practices do for society, including why they are a source of protein that is compatible with a plethora of other social land uses. Native prairie has obvious value in carbon storage and te maintenance of vegetation diversity, and our research shows that livestock grazing is compatible with their maintenance.

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Appendix 1. Summary ANOVA results (F-stats, df and P-values) for the effects of sub-region, grazing and grazing x sub-region, on measures of total vegetation diversity, introduced species abundance, individual vegetation (grass, forb, total herb, litter, and deep and shallow root) masses, and various cover metrics. Significant grazing impacts are bolded.

Parameter	Sub-region		Grazing		Grazing x Sub-region	
	F-stat[1]	P-value	F-stat	P-value	F-stat	P-value
			Overall Diversity			
Simpson's Diversity	4.54 $_{5,100}$	0.0009	13.00 $_{1,100}$	**0.0005**	5.22 $_{5,100}$	**0.0003**
Shannon's Diversity	2.63 $_{5,100}$	0.0283	0.17 $_{1,100}$	0.6801	1.45 $_{5,100}$	0.2137
Total Richness	7.47 $_{5,100}$	<0.0001	17.47 $_{1,100}$	**<0.0001**	2.29 $_{5,100}$	**0.0514**
Evenness	2.55 $_{5,100}$	0.0324	3.93 $_{1,100}$	**0.0502**	4.01 $_{5,100}$	**0.0024**
			Presence of Introduced Species			
Introduced Species Richness	2.05 $_{5,100}$	0.0775	4.38 $_{1,100}$	**0.039**	1.77 $_{5,100}$	0.1263
Proportion Introduced Richness	0.64 $_{5,100}$	0.6705	0.13 $_{1,100}$	0.7174	2.77 $_{5,100}$	**0.0218**
Introduced Simpson's Diversity	2.90 $_{5,100}$	0.0174	3.28 $_{1,100}$	0.0732	1.82 $_{5,100}$	0.1154
Introduced Shannon's Diversity	4.99 $_{5,100}$	0.0004	19.27 $_{1,100}$	**<0.0001**	10.86$_{5,100}$	**<0.0001**
Prop. Introduced Shannon's Div.	3.46 $_{5,100}$	0.0063	11.64 $_{1,100}$	**0.0009**	2.70 $_{5,100}$	**0.0247**
Introduced Cover	4.70 $_{5,100}$	0.0007	4.23 $_{1,100}$	**0.0424**	6.35 $_{5,100}$	**<0.0001**
Native Cover	6.63 $_{5,100}$	<0.0001	21.39 $_{1,100}$	**<0.0001**	8.94 $_{5,100}$	**<0.0001**
			Mass			
Grass Mass	3.46 $_{5,100}$	0.0063	0.20 $_{1,100}$	0.6548	3.19 $_{5,100}$	**0.0103**
Forb Mass	12.68 $_{5,100}$	<0.0001	7.85 $_{1,100}$	**0.0061**	1.21 $_{5,100}$	0.3096
Total Herb Mass	4.01 $_{5,100}$	0.0023	0.89 $_{1,100}$	0.3473	2.82 $_{5,100}$	**0.0201**
Litter Mass	9.26 $_{5,100}$	<0.0001	82.98 $_{1,100}$	**<0.0001**	3.18 $_{5,100}$	**0.0106**
Shallow Root Mass	5.99 $_{5,106}$	<0.0001	1.53 $_{1,102}$	0.2195	0.64 $_{5,103}$	0.6677
Deep Root Mass	4.20 $_{5,107}$	0.0016	9.26 $_{5,101}$	0.5016	0.12 $_{5,101}$	0.9880
			Vegetation Cover			
Vegetation Cover	37.22 $_{5,100}$	<0.0001	1.71 $_{1,100}$	0.1945	1.26 $_{5,100}$	0.2888
Perennial Cover	37.08 $_{5,100}$	<0.0001	1.21 $_{1,100}$	0.2734	1.14 $_{5,100}$	0.3439
Annual Cover	1.29 $_{5,100}$	0.2737	4.70 $_{1,100}$	**0.0326**	0.49 $_{5,100}$	0.7835
Forb Cover	24.15 $_{5,100}$	<0.0001	2.65 $_{1,100}$	0.1064	0.96 $_{5,100}$	0.4491
Grass Cover	2.58 $_{5,100}$	0.0305	3.45 $_{1,100}$	0.0661	4.20 $_{5,100}$	**0.0017**
Woody Cover	3.83 $_{5,100}$	0.0032	6.12 $_{1,100}$	**0.0151**	3.57 $_{5,100}$	**0.0051**
Rhizome Cover	3.58 $_{5,100}$	0.0051	3.51 $_{1,100}$	0.0641	1.27 $_{5,100}$	0.2836
Bunchgrass Cover	2.51 $_{5,100}$	0.0350	1.86 $_{1,100}$	0.1761	2.76 $_{5,100}$	**0.0222**
Range Health	6.18 $_{4,54.9}$	0.0004	0.02 $_{1,53.2}$	0.8866	0.34 $_{4,54.1}$	0.8472

[1] Numerator and denominator degrees freedom shown for each F-statistic.

Appendix 2. Dominant plant species found in 106 rangeland reference areas for both grazed and non-grazed across southern Alberta. Only species above a specific cut-off abundance (%) are shown, with the cut-off specified.

Sub-region	Functional group (cut off percent)	Treatment	Dominant Species
Dry Mixedgrass	Introduced Forbs (>0.3)	Grazed	*Traxacum officinale* *Tragapogon dubius*
	Introduced Forbs (>0.3)	Non-grazed	*Traxacum officinale* *Tragapogon dubius* *Melilotus officinale*
Mixedgrass	Introduced Forbs (>0.3)	Grazed	*Traxacum officinale*
	Introduced Forbs (>0.3)	Non-grazed	*Traxacum officinale* *Tragapogon dubius*
Parkland	Introduced Forbs (>0.3)	Grazed	*Traxacum officinale*
	Introduced Forbs (>0.3)	Non-grazed	Sonchus arvensis
Fescue Foothills	Introduced Forbs (>0.3)	Grazed	*Traxacum officinale*
	Introduced Forbs (>0.3)	Non-grazed	*Traxacum officinale* *Cirsium arvense*
Montane	Introduced Forbs (>0.3)	Grazed	*Traxacum officinale* *Trifolium repens* *Cirsium arvense* *Ranunculus acris* *Trifolium pratense*
	Introduced Forbs (>0.3)	Non-grazed	*Cirsium arvense* *Traxacum officinale*
Upper Foothills	Introduced Forbs (>0.3)	Grazed	*Traxacum officinale* *Trifolium repens* *Trifolium pratense*
	Introduced Forbs (>0.3)	Non-grazed	*Traxacum officinale*
Dry Mixedgrass	Introduced Grasses (>0.3)	Grazed	*Agropyron cristatum* *Poa pratensis*
	Introduced Grasses (>0.3)	Non-grazed	*Poa pratensis*

Mixedgrass	Introduced Grasses (>0.3)	Grazed	N/A*
	Introduced Grasses (>0.3)	Non-grazed	*Agropyron cristatum*
Parkland	Introduced Grasses (>0.3)	Grazed	*Poa Pratensis*
	Introduced Grasses (>0.3)	Non-grazed	*Poa Pratensis* *Poa Compressa*
Fescue Foothills	Introduced Grasses (>0.3)	Grazed	*Poa pratensis* *Bromus inermis*
	Introduced Grasses (>0.3)	Non-grazed	*Poa pratensis*
Montane	Introduced Grasses (>0.3)	Grazed	*Poa pratensis* *Bromus inermis*
	Introduced Grasses (>0.3)	Non-grazed	*Poa pratensis* *Bromus inermis*
Upper Foothills	Introduced Grasses (>0.3)	Grazed	*Poa pratensis* *Festuca rubra*
	Introduced Grasses (>0.3)	Non-grazed	*Poa pratensis* *Bromus inermis*
Dry Mixedgrass	Native Forbs (>1.0)	Grazed	*Selaginella densa* *Artemisia frigida* *Sphaeralcea coccinea*
	Native Forbs (>1.0)	Non-grazed	*Artemisia ludoviciana* *Selaginella densa* *Artemisia frigida* *Vicia americana* *Thermopsis rhombifolia*
Mixedgrass	Native Forbs (>1.0)	Grazed	*Thermopsis rhombifolia* *Selaginella densa* *Vicia americana* *Artemisia ludoviciana*
	Native Forbs (>1.0)	Non-grazed	*Achillea millefolium* *Galium boreale* *Geum triflorum* *Artemisia frigida*

Parkland	Native Forbs (>1.0)	Grazed	*Artemisia frigida* *Achillea millefolium* *Aster falcatus* *Antennaria parvifolia* *Solidago missouriensis* *Geum triflorum* *Artemisia ludoviciana*
	Native Forbs (>1.0)	Non-grazed	*Lupinus sericeus* *Galium boreale* *Thermopsis rhombifolia* *Geum triflorum* *Solidago missouriensis* *Agoseris glauca* *Achillea millefolium*
Fescue Foothills	Native Forbs (>1.0)	Grazed	*Lupinus sericeus* *Galium boreale* *Thermopsis rhombifolia* *Geum triflorum* *Achillea millefolium*
	Native Forbs (>1.0)	Non-grazed	*Geum triflorum* *Potentilla gracilis* *Achillea millefolium* *Galium boreale* *Penstemon confertus* *Fragaria virginiana* *Lupinus sericeus* *Thalictrum venulosum* *Vicia americana*
Montane	Native Forbs (>1.0)	Grazed	*Penstemon confertus* *Achillea millefolium* *Galium boreale* *Geranium viscosissimum* *Fragaria virginiana* *Potentilla gracilis* *Epilobium angustifolium* *Vicia Americana* *Geum trifolium* *Lupinus sericeus* *Aster laevis*
	Native Forbs (>1.0)	Non-grazed	*Achillea millefolium* *Potentilla gracilis*

			Geum trifolium *Thalictrum venulosum* *Fragaria virginiana* *Aster laevis* *Galium boreale* *Vicia Americana* *Mertensia paniculata*
Upper Foothills	Native Forbs (>1.0)	Grazed	*Thalictrum venulosum* *Epilobium angustifolium* *Penstemon procerus* *Geum trifolium* *Mertensia paniculata* *Delphinium glaucum* *Achillea millefolium* *Galium boreale* *Vicia Americana* *Aster laevis* *Potentilla gracilis* *Valeriana sitchensis*
	Native Forbs (>1.0)	Non-grazed	*Stipa comata* *Bouteloua gracilis* *Carex spp* *Agropyron smithii* *Koeleria macrantha* *Agropyron dasystachyum* *Danthonia parryi*
Dry Mixedgrass	Native Grasses (>1.0)	Grazed	*Stipa comata* *Carex spp* *Bouteloua gracilis* *Agropyron smithii* *Agropyron dasystachyum* *Koeleria macrantha*
	Native Grasses (>1.0)	Non-grazed	*Festuca hallii* *Bouteloua gracilis* *Stipa comata* *Agropyron smithii* *Festuca idahoensis* *Stipa curtiseta* *Poa sandbergii* *Carex spp* *Agropyron dasystachyum*

			Danthonia intermedia
Mixedgrass	Native Grasses (>1.0)	Grazed	*Festuca hallii*
			Stipa comata
			Agropyron dasystachyum
			Carex spp
			Agropyron smithii
			Bouteloua gracilis
			Festuca idahoensis
			Stipa curtiseta
			Koeleria macrantha
	Native Grasses (>1.0)	Non-grazed	*Festuca hallii*
			Carex spp
			Stipa curtiseta
			Agropyron smithii
			Agropyron dasystachyum
			Koeleria macrantha
			Poa cusickii
			Agropyron subsecundum
			Danthonia intermedia
Parkland	Native Grasses (>1.0)	Grazed	*Festuca hallii*
			Carex spp
			Stipa curtiseta
			Agropyron smithii
			Poa cusickii
	Native Grasses (>1.0)	Non-grazed	*Festuca campestris*
			Danthonia parryi
			Carex spp
			Festuca idahoensis
			Agropyron dasystachyum
			Stipa curtiseta
Fescue Foothills	Native Grasses (>1.0)	Grazed	*Festuca campestris*
			Danthonia parryi
			Carex spp
			Festuca idahoensis
			Agropyron dasystachyum
			Agropyron smithii
	Native Grasses (>1.0)	Non-grazed	*Festuca campestris*
			Phleum pretense
			Danthonia parryi
			Carex obtusata

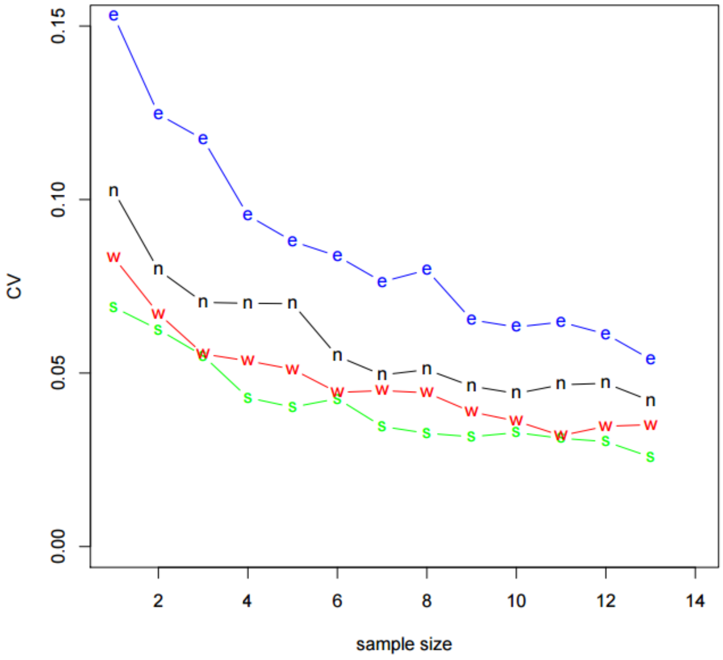
			Festuca idahoensis *Agropyron trachycaulum*
Montane	Native Grasses (>1.0)	Grazed	*Festuca campestris* *Danthonia parryi* *Carex obtusata* *Carex preslii* *Phleum pretense* *Festuca idahoensis* *Agropyron trachycaulum*
	Native Grasses (>1.0)	Non-grazed	*Deschampsia cespitosa* *Festuca campestris* *Elymus innovatus* *Agropyron trachycaulum* *Carex preslii* *Carex obtusata* *Carex praegracilis* *Danthonia parryi* *Phleum pretense* *Festuca saximontana*
Upper Foothills	Native Grasses (>1.0)	Grazed	*Festuca campestris* *Elymus innovatus* *Deschampsia cespitosa* *Carex atherodes* *Carex preslii* *Agropyron trachycaulum* *Bromus ciliates* *Carex praegracilis* *Carex obtusata* *Danthonia parryi*
	Native Grasses (>1.0)	Non-grazed	*Artemisia cana*
Dry Mixedgrass	Native Woody (>0.3)	Grazed	*Eurotia lanata* *Artemisia cana*
	Native Woody (>0.3)	Non-grazed	*Potentilla fruticosa* *Eurotia lanata*
Mixedgrass	Native Woody (>0.3)	Grazed	*Eurotia lanata* *Potentilla fruticosa*
	Native Woody (>0.3)	Non-grazed	*Juniperus horizontalis* *Rosa arkansana*

			Elaeagnus commutate *Rosa acicularis* *Symphoricarpos occidentalis*
Parkland	Native Woody (>0.3)	Grazed	*Juniperus horizontalis* *Symphoricarpos occidentalis* *Rosa arkansana* *Rosa acicularis*
	Native Woody (>0.3)	Non-grazed	*Potentilla fruticosa*
Fescue Foothills	Native Woody (>0.3)	Grazed	*Potentilla fruticosa* *Rosa arkansana*
	Native Woody (>0.3)	Non-grazed	*Symphoricarpos occidentalis* *Potentilla fruticosa* *Rosa acicularis* *Arctostaphylos uva-ursi* *Amelanchier alnifolia* *Rosa arkansana* *Populus tremuloides* *Rhamnus alnifolia* *Vaccinium caespitosum*
Montane	Native Woody (>0.3)	Grazed	*Potentilla fruticosa* *Symphoricarpos occidentalis* *Rosa acicularis* *Juniperus horizontalis* *Amelanchier alnifolia* *Arctostaphylos uva-ursi* *Populus tremuloides* *Salix myrtillifolia* *Rubus parviflorus*
	Native Woody (>0.3)	Non-grazed	*Betula glandulosa* *Potentilla fruticosa* *Arctostaphylos uva-ursi* *Vaccinium caespitosum*
Upper Foothills	Native Woody (>0.3)	Grazed	*Betula glandulosa* *Potentilla fruticosa* *Salix myrtillifolia* *Arctostaphylos uva-ursi* *Salix bebbiana* *Salix petiolaris* *Salix brachycarpa*

		Ribes oxyacanthoides *Ribes lacustre* *Vaccinium caespitosum* *Salix maccalliana* *Rosa acicularis*
Native Woody (>0.3)	Non-grazed	*Betula glandulosa* *Potentilla fruticosa* *Salix myrtillifolia* *Arctostaphylos uva-ursi* *Salix bebbiana* *Salix petiolaris* *Salix brachycarpa* *Ribes oxyacanthoides* *Ribes lacustre* *Vaccinium caespitosum* *Salix maccalliana* *Rosa acicularis*

*N/A signifies no species present were present that had above 0.05% cover.

Appendix 3. Summary of preliminary data collected at four test sites (two in the Parkland, two in the Mixedgrass)**. C**oefficient**s** of variation (CV= standard deviation/mean) were compared to sample size. As you can see there is increasingly less benefit to adding more samples after approximately 8 soil sub-samples. Therefore, 10 samples was determined to be an appropriate sample size.



Appendix 4. Variation in mean (± SE) soil physical characteristics across 106 RRAs for both grazed and non-grazed areas distributed across 6 natural sub-regions in Alberta.

Parameter		Sub-Region					
	Treatment	Dry Mixedgrass	Mixed grass	Parkland	Fescue Foothills	Montane	Upper Foothills
pH (0-15 cm)	Grazed	7.04 (±0.16)	6.54 (±0.23)	6.09 (±0.13)	6.31 (±0.25)	5.68 (±0.12)	6.08 (±0.22)
pH (0-15 cm)	Non-grazed	7.31 (±0.17)	6.44 (±0.24)	6.25 (±0.13)	6.18 (±0.25)	5.68 (±0.12)	5.99 (±0.21)
pH (15-30 cm)	Grazed	7.96 (±0.19)	7.17 (±0.26)	7.02 (±0.15)	6.37 (±0.31)	6.13 (±0.13)	6.90 (±0.26)
pH (15-30 cm)	Non-grazed	8.02 (±0.19)	7.16 (±0.27)	7.15 (±0.15)	6.54 (±0.31)	6.13 (±0.13)	6.94 (±0.26)
Salinity 0-15 cm (EC;mS/m-2)	Grazed	398.72 (±53.90)	319.68 (±67.81)	264.09 (±42.22)	511.08 (±80.84)	172.19 (±37.42)	268.73 (±68.94)
Salinity 0-15 cm (EC;mS/m-2)	Non-grazed	289.09 (±53.90)	309.41 (±76.22)	265.25 (±41.75)	298.76 (±80.84)	193.56 (±33.18)	222.55 (±61.34)
Salinity 15-30 cm (EC;mS/m-2)	Grazed	319.14 (±53.78)	361.76 (±76.06)	370.48 (±42.79)	296.92 (±90.17)	140.13 (±37.29)	137.85 (±72.15)
Salinity 15-30 cm (EC;mS/m-2)	Non-grazed	275.09 (±53.78)	234.14 (±76.06)	305.41 (±42.36)	329.21 (±86.24)	151.03 (±37.58)	162.43 (±72.15)
Organic Matter % (0-15 cm)	Grazed	3.29 (±0.59)	4.85 (±0.83)	4.88 (±0.47)	10.04 (±0.89)	9.57 (±0.41)	9.65 (±0.76)
Organic Matter % (0-15 cm)	Non-grazed	2.80 (±0.59)	5.07 (±0.83)	4.71 (±0.47)	9.40 (±0.89)	9.58 (±0.41)	7.83 (±0.76)
Organic Matter % (15-30 cm)	Grazed	1.97 (±0.39)	2.92 (±0.57)	2.72 (±0.31)	5.40 (±0.67)	5.78 (±0.27)	5.32 (±0.49)
Organic Matter % (15-30 cm)	Non-grazed	2.42 (±0.39)	3.08 (±0.54)	2.70 (±0.30)	5.35 (±0.67)	5.74 (±0.27)	4.81 (±0.50)
Bulk Density 0-15 cm (g/cm^3)	Grazed	1.50 (±0.06)	1.18 (±0.11)	1.44 (±0.06)	0.85 (±0.12)	0.85 (±0.05)	1.05 (±0.10)

Bulk Density 0-15 cm (g/cm^3)	Non-grazed	1.51 (±0.08)	1.08 (±0.10)	1.31 (±0.06)	0.93 (±0.12)	0.79 (±0.05)	1.13 (±0.10)
Bulk Density 15-30 cm (g/cm^3)	Grazed	1.20 (±0.02)	1.17 (±0.03)	1.17 (±0.02)	1.03 (±0.04)	1.01 (±0.02)	1.04 (±0.03)
Bulk Density 15-30 cm (g/cm^3)	Non-grazed	1.19 (±0.02)	1.16 (±0.03)	1.16 (±0.02)	1.03 (±0.04)	1.01 (±0.02)	1.05 (±0.03)
Percent Sand	Grazed	57.95 (±2.92)	50.51 (±5.89)	64.75 (±3.29)	48.73 (±6.00)	50.55 (±1.79)	46.09 (±2.25)
Percent Sand	Non-grazed	59.04 (±3.03)	50.48 (±5.76)	61.89 (±3.44)	52.92 (±5.21)	48.35 (±1.72)	48.74 (±3.09)
Percent Silt	Grazed	23.12 (±2.18)	22.10 (±3.62)	16.51 (±2.14)	27.56 (±7.24)	29.88 (±2.08)	33.26 (±2.35)
Percent Silt	Non-grazed	20.45 (±1.87)	24.08 (±4.39)	14.64 (±2.00)	23.31 (±6.47)	31.37 (±1.85)	29.79 (±3.43)
Percent Clay	Grazed	19.21 (±1.35)	27.38 (±3.38)	18.73 (±1.66)	23.71 (±3.39)	19.57 (±1.52)	20.64 (±2.59)
Percent Clay	Non-grazed	20.50 (±1.45)	25.44 (±3.46)	23.47 (±2.29)	23.77 (±2.14)	20.27 (±1.67)	21.48 (±2.38)

Appendix 5. Summary ANOVA results (F-stats, df and P-values) for the effects of grazing, sub-region, and grazing x sub-region, on various measures of vegetation (grass, forb, total herb, litter, LFH/mulch, and deep and shallow roots) carbon and nitrogen concentration (%), mass (g/m2), and C:N ratio, as well as mineral soil C and N concentrations, masses, and C:N ratios. Significant grazing impacts are bolded.

Response	Grazing		Sub-region		Grazing x Sub-region	
	F-stat[1]	P-value	F-stat	P-value	F-stat	P-value
-------------------- *Carbon Mass* --------------------						
Total Ecosystem (Veg + Soil) Carbon (g/m^2)	2.11 $_{1,106}$	0.1497	19.27 $_{5,108}$	<0.0001	1.34 $_{5,106}$	0.2546
Total Vegetation Carbon (g/m^2)	0.09 $_{1,99}$	0.7590	8.86 $_{5,107}$	<0.0001	3.06 $_{5,99}$	**0.0130**
Live Veg C Component (g/m^2)	3.13 $_{1,99}$	0.0797	4.82 $_{5,107}$	0.0005	0.44 $_{5,99}$	0.8205
Dead Veg C Component (g/m^2)	0.27 $_{1,100}$	0.6055	9.22 $_{5,107}$	<0.0001	1.14 $_{5,100}$	**0.0243**
Aboveground C (g/m^2)	35.71 $_{1,100}$	**<0.0001**	4.21 $_{5,107}$	0.0016	2.96 $_{5,100}$	**0.0154**
Belowground C (g/m^2)	0.00 $_{1,99}$	0.9595	9.85 $_{1,106}$	<0.0001	3.23 $_{5,99}$	**0.0097**
Total Herbaceous Carbon (g/m^2)	1.10 $_{1,99.5}$	0.2961	4.29 $_{5,106}$	0.0013	2.29 $_{5,100}$	**0.0517**
Grass Carbon (g/m^2)	0.13 $_{1,99.1}$	0.7164	3.85 $_{5,105}$	0.0030	2.84 $_{5,99.7}$	**0.0192**
Forb Carbon (g/m^2)	8.13 $_{1,102}$	**0.0053**	12.71 $_{5,106}$	<0.0001	1.20 $_{5,103}$	0.3167
Litter Carbon (g/m^2)	69.12 $_{1,98.2}$	**<0.0001**	9.08 $_{5,102}$	<0.0001	2.64 $_{5,99.1}$	**0.0279**
LFH/Mulch Carbon (g/m^2)	0.01 $_{1,93.1}$	0.9245	9.82 $_{5,102}$	<0.0001	2.87 $_{5,93.5}$	**0.0186**
Roots Shallow Carbon (g/m^2)	2.52 $_{1,101}$	0.1153	3.83 $_{5,107}$	0.0031	0.49 $_{5,101}$	0.7850
Roots Deep Carbon (g/m^2)	0.59 $_{1,101}$	0.4450	3.20 $_{5,107}$	0.0099	0.17 $_{5,101}$	0.9743
Total Root C (g/m^2)	2.92 $_{1,101}$	0.0908	4.44 $_{5,107}$	0.0010	0.37 $_{5,101}$	0.8710
Total Shallow Soil Carbon (0-15 cm; g/m^2)	4.41 $_{1,106}$	**0.0381**	9.30 $_{5,108}$	<0.0001	0.35 $_{5,105}$	0.8794
Total Deep Soil Carbon (15-30 cm; g/m^2)	0.00 $_{1,100}$	0.9963	18.97 $_{5,105}$	<0.0001	1.10 $_{5,101}$	0.3629
-------------------- *Carbon Percentage* --------------------						
Grass Carbon (%)	9.59 $_{1,99.7}$	**0.0025**	2.67 $_{5,106}$	0.0258	1.18 $_{5,100}$	0.3247
Forb Carbon (%)	6.56 $_{1,101}$	**0.0119**	3.05 $_{5,107}$	0.0131	11.70 $_{5,101}$	**<0.00**
Litter Carbon (%)	2.65 $_{1,101}$	0.1069	4.95 $_{5,108}$	0.0004	4.11 $_{5,101}$	**0.0019**
LFH/Mulch Carbon (%)	2.43 $_{1,93.8}$	0.1223	7.54 $_{5,104}$	<0.0001	0.79 $_{5,94.1}$	0.5611
Roots Shallow Carbon (%)	0.01 $_{1,94.5}$	0.9246	12.33 $_{5,101}$	<0.0001	3.87 $_{5,94.7}$	**0.0031**
Roots Deep Carbon (%)	0.75 $_{1,78.6}$	0.3884	10.89 $_{5,97.1}$	<0.0001	2.46 $_{5,79.5}$	**0.0398**
-------------------- *Nitrogen Percentage* --------------------						

Grass Nitrogen (%)	6.30 $_{1,101}$	**0.0137**	38.03 $_{5,106}$	<0.0001	0.51 $_{5,101}$	0.7650
Forb Nitrogen (%)	0.00 $_{1,102}$	0.9663	30.84 $_{5,106}$	<0.0001	1.23 $_{5,102}$	0.2994
Litter Nitrogen (%)	0.28 $_{1,98.9}$	0.5953	2.44 $_{5,106}$	0.0387	2.70 $_{5,99.2}$	**0.0247**
LHF/Mulch Nitrogen (%)	1.66 $_{1,96.8}$	0.2000	9.95 $_{5,107}$	<0.0001	0.64 $_{5,97.1}$	0.6699
Roots Shallow Nitrogen (%)	5.13 $_{1,95.1}$	**0.0258**	3.89 $_{5,98.5}$	0.0029	3.99 $_{5,96.4}$	**0.0025**
Roots Deep Nitrogen (%)	15.02$_{1,82.3}$	**0.0002**	6.64 $_{5,95.2}$	0.0007	2.16 $_{5,83.9}$	0.0659
		-------------------- *Carbon to Nitrogen Ratio* --------------------				
Grass C:N	9.62 $_{1,98.6}$	**0.0025**	30.85 $_{5,104}$	<0.0001	1.24 $_{5,99}$	0.2967
Forb C:N	0.07 $_{1,101}$	0.7907	23.87 $_{5,106}$	<0.0001	1.48 $_{5,102}$	0.2027
Litter C:N	0.00 $_{1,97.7}$	0.9752	2.33 $_{5,105}$	0.0471	2.02 $_{5,97.9}$	0.0829
LFH/Mulch C:N	0.19 $_{1,98.7}$	0.6636	2.78 $_{5,108}$	0.0211	0.78 $_{5,99.}$	0.5650
Roots Shallow C:N	2.60 $_{1,94.1}$	0.1103	9.16 $_{5,100}$	<0.0001	0.97 $_{5,94.1}$	0.4401
Roots Deep C:N	10.11$_{1,85.1}$	**0.0021**	6.64 $_{5,95.2}$	<0.0001	0.57 $_{5,86.6}$	0.7260
Shallow Soil C:N (0-15 cm)	0.84 $_{1,107}$	0.3602	0.87 $_{5,109}$	0.5050	0.45 $_{5,106}$	0.8123
Deep Soil C:N (15-30 cm)	0.02 $_{1,101}$	0.8897	1.73 $_{5,108}$	0.1344	1.59 $_{5,101}$	0.1708
		-------------------- *Nitrogen Masses* --------------------				
Grass Nitrogen (g/m^2)	1.59 $_{1,99.4}$	0.2104	3.83 $_{5,105}$	0.0032	2.64 $_{5,100}$	**0.0279**
Forb Nitrogen (g/m^2)	5.50 $_{1,103}$	**0.0210**	19.48 $_{5,107}$	<0.0001	0.56 $_{5,104}$	0.7331
Litter Nitrogen (g/m^2)	45.14 $_{1,99.4}$	**<0.0001**	5.68 $_{5,103}$	0.0001	2.97 $_{5,100}$	**0.0153**
Roots Shallow Nitrogen (g/m^2)	1.54 $_{1,39.2}$	0.2218	4.00 $_{5,42.4}$	0.0046	0.42 $_{5,39}$	0.8322
Total Shallow Soil Nitrogen (0-15 cm; g/m^2)	5.19 $_{1,106}$	**0.0247**	10.58 $_{5,108}$	<0.0001	0.18 $_{5,106}$	0.9691
Total Deep Soil Nitrogen (15-30 cm; g/m^2)	0.29 $_{1,99.3}$	0.5909	24.44 $_{5,105}$	<0.0001	1.09 $_{5,99.9}$	0.3723

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[1] Numerator and denominator degrees freedom shown for each F-statistic.