

**Effects of cattle grazing intensity on
vegetation structure, heterogeneity and plant
diversity in a northern mixed-grass prairie**

By: Tonya Lwiwski

A Thesis Submitted to the Faculty of Graduate Studies of
The University of Manitoba
In Partial Fulfillment of the Requirements
For the Degree of

Master of Natural Resource Management

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ABSTRACT

Re-introducing heterogeneity to native North American rangelands is imperative to maintaining grassland biodiversity, and it has been suggested that using a variety of cattle grazing intensities on the landscape could accomplish this. I used generalized linear mixed models to describe the effects of grazing intensity on vegetation structure, plant species diversity and plant communities over four years. I used the Mantel test and non-metric multidimensional scaling to illustrate changes in plant communities with varying grazing intensities and over time. Effects of grazing were cumulative and changed over time, upland and lowland habitats responded differently to grazing intensity, and heterogeneity was maximized at the landscape scale under a variety of grazing intensities. When conservation is the primary goal, a variety of grazing intensities on the landscape can be used to increase heterogeneity, and therefore grassland biodiversity.

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1.0 INTRODUCTION

1.1 Background

North American grasslands evolved with disturbances such as fire and grazing, and it is well documented that one of these disturbance regimes, or an interaction of both, is needed to maintain habitat heterogeneity and therefore biodiversity in these ecosystems (Collins and Barber 1986, Knapp et al. 1999, Fuhlendorf and Engle 2001, Hart 2001). Grazing and fire affect vegetation structure, which creates habitat for grassland species. Heterogeneous plant structure provides variable habitat conditions suitable for a range of grasslands species.

Historically, plains bison (*Bison bison*) grazed the western plains and their role as a keystone species in shaping this ecosystem has been acknowledged (Knapp et al. 1999). Domestic cattle are now the predominant grazer in the Great Plains. While the present management of cattle differs from the historic wide-ranging behaviour of the bison, both bison and cattle grazing have been shown to increase plant diversity in tall-grass prairie (Towne et al. 2005) and when managed similarly the two grazers have been considered functionally equivalent (Hartnett et al. 1997, Fuhlendorf and Engle 2001). However, current cattle grazing systems typically strive for uniform grazing of rangelands to optimize the use of forage (Teague and Dowhower 2003). These practices result in homogeneous rangelands, which may contribute to biodiversity loss in grassland ecosystems (Fuhlendorf and Engle 2001). To restore heterogeneity on rangelands with a long history of grazing, such as the mixed-grass prairie, Fuhlendorf and Engle (2001) suggest the re-introduction of historical spatial disturbances, such as the interaction of fire and grazing. The re-introduction of fire on grasslands, however, may not be socially acceptable in certain areas. In these cases, we must focus on grazing practices as the mechanism for disturbance.

Grazing can be used as a conservation tool to re-introduce heterogeneity on the landscape, whether in protected areas or on private rangelands. Many grasslands in protected areas are simply not grazed at all under the paradigm that the land is being protected by the removal of anthropogenic influence, in this case domestic grazing (Bai et al. 2001, Koper 2011). However, it is now recognized that these natural disturbances are necessary for overall rangeland health (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2012). Re-introducing grazing in a strategic way could transform cattle grazing into a successful ecosystem management tool. In a conservation setting, where not cattle gains but landscape heterogeneity is the primary goal, the use of multiple grazing intensities had been suggested as the solution (Fuhlendorf et al. 2012).

It was for this reason that Grasslands National Park (GNP) in southern Saskatchewan, Canada, initiated the Biodiversity And Grazing Management Area (BAGMA). This six-year project was designed to assess the effects of different grazing intensities ranging from no grazing to very high grazing intensity for the area on the plant communities of the native mixed-grass prairie. The focal point of my study included three important factors of heterogeneity: habitat heterogeneity, plant species diversity, and plant community differences (Fuhlendorf and Engle 2001, Symstad and Jonas 2011).

Habitat heterogeneity- I use the term habitat heterogeneity to refer to the variation in vegetation structure (Fuhlendorf and Engle 2001). Heterogeneity at the landscape scale is imperative to the survival of many imperilled grassland species (Fuhlendorf et al. 2012). Many grassland species, such as the burrowing owl, sage grouse, the Mormon metalmark butterfly, swift fox, chestnut-collared longspur and Sprague's pipit are listed under the Species at Risk Act, and all exhibit different habitat requirements (Government of Canada 2012). Ungrazed rangelands do exhibit natural variability, but do not provide habitat for species that evolved in

areas of heavy grazing. Conversely, at sustained high stocking rates forage availability can be reduced, resulting in the inability of cattle to graze selectively overriding any habitat patches that would otherwise be present (Fuhlendorf and Engle 2001). Continuous grazing at moderate grazing intensity, which is often suggested as a sustainable stocking rate (e.g. Biondini et al. 1998, Fuhlendorf and Engle 2001), does not provide sufficient habitat structural gradient between highly grazed and undergrazed patches needed to support the historic suite of grassland fauna and flora (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2012). Therefore, a variety of grazing intensities should increase heterogeneity at both the smaller scale (patches within a single grazing intensity) and the large landscape level (differences of patches among all the grazing intensity treatments; Fuhlendorf et al. 2012).

Plant diversity- Diversity is a quantitative measure of species within an area and can be represented by species richness (i.e. the number of species in a given area) and diversity indices, which describe the evenness of species distribution (Legendre and Legendre 2012). Plant species richness is hypothesized to vary with grazing intensity depending on the productivity and grazing history of rangeland (Michunas et al. 1988). In sub-humid grasslands (i.e. prairies with higher moisture content, such as tall-grass prairie) with a long history of grazing, under ungrazed conditions only a few species, predominately grasses, dominate the canopy (Milchunas et al. 1988). When grass cover is reduced by grazing, this then allows forb species to increase, as more light and nutrients are available, increasing species richness (Olf and Ritchie, 1998). At sustained high grazing intensities, species richness declines again as grazing-adapted species dominate (Milchunas et al. 1988). At continuous intermediate intensities, plants that exist under ungrazed conditions and grazed conditions may co-exist in a mosaic, and therefore diversity may potentially be maximized (Milchunas et al. 1988). Semi-arid grasslands (i.e. prairies with low

moisture availability, such as short-grass prairie) with a long history of grazing should have greater species richness at light grazing intensities, and richness should decline slightly as grazing intensity increases (Milchunas et al. 1988). This is because short-grass prairie plants co-evolved with both grazing and drought, and the plants have adapted to these stressors with their low stature and meristems low to the ground, and therefore most species are grazing-tolerant. As grazing intensity increases, the few grazing-intolerant present species will decline or disappear (Milchunas et al. 1988). However, the mixed-grass prairie of Grasslands National Park falls between the semi-arid and sub-humid grasslands classifications in terms of productivity. While the results of many studies support the theories postulated by Milchunas et al. (1988) of plant species richness in short-grass and tall-grass prairie, there have been few studies conducted in the mixed-grass prairie and the results are variable (e.g. Biondini et al. 1998, Bai et al. 2001, Willms et al. 2002).

Plant communities- Heterogeneity can also be described by the variety in plant communities across the landscape (Fuhlendorf and Engle 2001). Given the long history of grazing, grassland plants are believed to have evolved to include two broad pools of species: grazing-intolerant plants that dominate when grazing is absent and grazing-tolerant species that dominate when grazing is present (Cingolani et al. 2005). In sub-humid grasslands, it is predicted that these communities will overlap at intermediate grazing intensities (Milchunas et al. 1988). In semi-arid grasslands, distinct plant communities may be found along a gradient of grazing intensity with no net change in richness (Cingolani et al. 2005). The mixed-grass prairie should also follow these patterns, with grazing-tolerant species dominating when grazing is present and grazing-intolerant species dominating when grazing is absent, and these communities should overlap at intermediate grazing intensities, leading to an increase in heterogeneity.

Research objectives

As part of the BAGMA project, the focus of my study was to assess how different grazing intensities affect the mixed-grass prairie vegetation in Grasslands National Park, Saskatchewan, Canada, so that the Park may address future grazing strategies for optimal habitat management.

Specifically, my research objectives were:

- 1) To determine how a) habitat structure and b) structural heterogeneity changed with varying grazing intensities over time;
- 2) To assess how different grazing intensities affect plant species richness and diversity over time;
- 3) To determine the effects of differing grazing intensities on plant communities over time.

Hypotheses and predictions (prediction number in brackets)

Habitat structure and habitat heterogeneity - If the effects of livestock change at different stocking rates because, (i) at low stocking rates animals graze selectively but low grazing intensities are not high enough to induce many structural changes, (ii) at moderate stocking rates cattle can graze selectively, but highly grazed and ungrazed areas are absent, and (iii) selectivity is inhibited at high stocking rates, then I predict that, (1) habitat heterogeneity within a single pasture will be maximized at moderate grazing intensities but will be maximized on the landscape level using multiple grazing intensities (stocking rates).

Plant diversity - If plant communities in mixed-grass prairies that evolved with grazing are adapted to this stressor, then I predict that (2) grazing should increase plant diversity compared to the ungrazed control plots, as seen in previous studies (Manley et al. 1997, Hart 2001, Bai et al. 2001), but that plant diversity will peak at moderate grazing intensities because

of the patchy distribution of both grazing-tolerant and grazing-intolerant plant communities (Milchunas et al. 1988, Cingolani et al. 2005). If plant communities respond to selective grazing of grasses by exhibiting competitive release (i.e. as predominant species are grazed, competition is reduced allowing more species to grow), then I expect an increase in forb cover in grazed compared to ungrazed pastures, contributing to an increase in species richness.

Plant communities - If there are two distinct plant communities in the mixed-grass prairie where one community has evolved to tolerate grazing, another community has evolved that is intolerant of grazing, and that both can co-exist at moderate grazing intensities, then I predict that after a long period with no sustained grazing pressure, once grazing is introduced (3) these two distinct plant communities will begin to overlap, resulting in different communities among grazing intensities, contributing to spatial heterogeneity. I also predict that this effect will be more pronounced at higher grazing intensities and after longer grazing durations (Collins et al. 1998, Knapp et al. 1999, Cingolani et al. 2005).

Project significance

Rangelands have been called “biodiversity repositories” (Fuhlendorf and Engle 2001: 625) due to the fact that rangelands can encompass large numbers of native plants that create habitat for many grassland species, and therefore maintaining heterogeneity on these rangelands is pertinent to conserve biodiversity in the Great Plains. To my knowledge, there have been no studies conducted to assess how to explicitly increase heterogeneity by use of different grazing intensities. Most grazing studies have cattle gains as a primary focus, whereas in a conservation setting, the focus is not to maximize cattle gains but to increase heterogeneity, potentially for the benefit of species at risk. The importance of heterogeneity for the conservation of many

grassland populations has been identified (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2012), and now we must try to increase heterogeneity in rangelands.

As described by Power (2010) the preservation of native prairie within a matrix of agricultural land, such as the landscape surrounding Grasslands National Park, is essential to the success of agriculture. These native areas provide direct and indirect ecosystem services that benefit overall agricultural activities and food production. Such ecosystem services include increased pollination, natural pest control, soil conservation (e.g. less erosion) and carbon sequestration. Without the protection of such native lands, crop production may suffer due to decreased pollination and increased pest outbreaks as the native land provides food and habitat for natural pollinators and agricultural pest predators.

Collecting data prior to the introduction of grazing regimes is seldom an option in other long-term studies (Koper et al. 2008). As the entire study area of the BAGMA project was ungrazed prior to the study, data collected prior to grazing was necessary to document any trends that existed on the landscape prior to the introduction of the treatments (Koper et al. 2008). Without this information, pre-existing trends may be attributed to the grazing regimes, when in fact they may have been spurious patterns present on the landscape by chance.

While several studies have been conducted to assess the effects of grazing on vegetation communities and composition (Cid et al. 1991, Biondini and Manske 1996, Collins et al. 1998, Damhoureyeh and Hartnett 2002, Towne et al. 2005), grazing systems and grazing intensity are often confounded, (Manley et al. 1997, Teague and Dowhower 2003, Hickman et al. 2004) making any generalizations about grazing intensity under continuous grazing difficult. There have been few studies conducted to assess the impact of different grazing intensities on native mixed-grass prairie (e.g. Biondini et al. 1998, Bai et al. 2001, Vermeire et al. 2008). Comparison

among these studies is difficult due to different objectives, data collection, and study sizes. Extrapolation can be difficult as different grassland types with different mean productivity (e.g. tall-grass prairie, mixed-grass prairie and short-grass prairie) and grazing histories respond differently to the same management regimes (Milchunas et al. 1988).

Effects of grazing occur over long periods of time, and therefore require long-term studies (Manley et al. 1997). Although the proposed timeline for the BAGMA project was 12 years (2006-2017; Parks Canada 2006), it was terminated in 2012. This timeline is greater than some grazing studies (Cid et al. 1991) but not others (Biondini et al. 1998, Hart 2001). However, few, if any, studies collected data on the annual effects of grazing, which allows a glimpse of the potential cumulative effects of grazing, and this will be assessed in this study. The range of grazing intensities used in the current study encompasses a greater range of grazing intensities than have been used previously (Manley et al. 1997, Biondini et al. 1998, Hart 2001), and this will provide a clearer picture of how this process impacts the landscape.

CHAPTER 2: LITERATURE REVIEW

Mixed-grass prairie

Grasslands once covered 42% of the earth's productive surface (Anderson 2006). Today, vast amounts of grasslands have been altered by humans, and the conversion of these habitats for agricultural use is extensive (Samson et al. 2004, Anderson 2006). The Great Plains of North America, consisting of tall-grass prairie, mixed-grass prairie and short-grass prairie, covered approximately 162 million ha before European settlement (Samson and Knopf 1994). It is estimated that the Great Plains of North America has lost 70% of its native grasslands (Samson et al. 2004). The mixed-grass prairie region of the Great Plains, which encompasses Grasslands National Park (GNP), has only an estimated 29% of the area remaining compared to its historical extent (Samson et al. 2004).

History of grazing in the Great Plains of North America

Several million years ago, there was a diverse array of grazers in the grasslands of North America, including 32 genera of grazing megafauna (Anderson 2006). The fossil record indicates that the evolution of mammals with hypsodont teeth (teeth with high crowns and complex enamel patterns) and hoofs occurred at the same time as the evolution of grasses (Stebbins 1981). This indicates that grasses and grazers probably co-evolved. This co-evolution of grasses and grazers started approximately 45-55 million years ago in the Eocene era and is still present today (Stebbins 1981).

More recently, the Great Plains of North America were dominated by the plains bison (*Bison bison bison*; Samson and Knopf 1994, Knapp et al. 1999). It is estimated that bison numbers once reached 60 million in abundance, making them the most important herbivore on

the landscape (Samson and Knopf 1994). Bison were considered to play a key role in the development of the prairie ecosystem (Knapp et al. 1999). These extensive herds were driven to the brink of extinction in the 1800s due to widespread slaughter of the herbivore (Samson and Knopf 1994, Knapp et al. 1999).

Cattle and bison

More recently, bison have largely been replaced by the domestic cattle (*Bos taurus*). Key behaviour differences between the grazers time spent foraging (bison spend less time foraging than cattle; Plumb and Dodd 1993, Hartnett et al. 1997, Knapp et al. 1999) and wallowing (behaviour that bison undertake while cattle do not; Hartnett et al. 1997). However, despite these differences, bison and cattle are more similar to each other than to any other native ungulate species (Hartnett et al. 1997). While bison exhibit a more selective diet than do cattle, both select for C₄ grasses out of proportion to their availability (Hartnett et al. 1997, Plumb and Dodd 2005). Both grazers have also been shown to increase species diversity (Hartnett et al. 1997, Towne et al. 2005). While there are observed differences between cattle and bison, they are considered by some to be ecologically analogous (Hartnett et al. 1997) and it is thought that grazing management systems may have a larger effect on how the grazers affect their environment than any inherent differences between grazer species (Towne et al. 2005).

Grazing management systems

Traditional cattle grazing management systems have focused on the temporal and spatial distribution of grazing, as well as the stocking density (Fuhlendorf and Engle 2001). These grazing systems are designed to maximize livestock production over time (Heitschmidt and Taylor 1991). Grazing systems must assess the trade-off between the benefits of resting the

rangeland, the detrimental impacts of over-grazing the rangeland, and beef productivity (Heitschmidt and Taylor 1991). The two most commonly used grazing systems employed are rotational grazing and continuous grazing (Derner et al. 2008).

In a grazing system, spatial heterogeneity increases as the scale of the managed area increases (Fuhlendorf and Engle 2001, Teague and Dowhower 2003). Grazing ungulates are known to selectively graze areas that have been previously grazed (Teague and Dowhower 2003), which leads to natural variability in a rangeland. This can sometimes lead to the deterioration of these areas by overgrazing (Teague and Dowhower 2003). Many grazing management systems have been designed principally to promote the uniform distribution of grazing on the landscape (Hart 1978 *in* Fuhlendorf and Engle 2001).

Rotational grazing is a popular concept with rangeland managers (Fuhlendorf and Engle 2001, Teague and Dowhower 2003). This type of grazing management was designed as a solution to overgrazing due to patch grazing (Teague and Dowhower 2003). Rotational grazing consists of smaller paddocks being grazed, sometimes intensively to maximize the amount of forage consumed, and then rested so that the plant communities may recover (Biondini and Manske 1996, Teague and Dowhower 2003). However, this does not allow for natural variability in grazing patches because it promotes even use of forage (Teague and Dowhower 2003).

Therefore, to maximize heterogeneity, continuous grazing should be the selected grazing system.

Stocking density

Stocking density or grazing intensity is an important management factor that changes the ecological effects of both rotational and continuous grazing systems. Most management systems strive to maximize the weight gain of the livestock without causing any long-term detrimental effects to the rangeland (Teague and Dowhower 2003).

The negative effects of heavy stocking rates have been known since the 1960's (Bement 1969). The major outcome of heavy stocking rates is the reduction of plant material. As stocking rates increase past a certain density, cattle gains decrease, primarily due to the scarcity of forage (Bement 1969, Derner et al. 2008). Although this can be reversed by reducing the stocking density (Bement 1969), sustained high grazing intensities can detrimentally alter and degrade a rangeland (Teague and Dowhower 2003).

Some studies have shown that plant communities respond differently to different stocking rates (Manley et al. 1997, Hart 2001), while others found no change in plant composition (Gillen et al. 2000). Decreases in graminoids and increases in forb cover has been recorded under higher stocking rates; however, in some instances the forbs that increased had lower palatability than the graminoids they replaced (Manley et al. 1997).

Importance of heterogeneity in grasslands

Heterogeneity may be defined as the variation in plant structure, composition, biomass and density of a rangeland (Fuhlendorf and Engle 2001). Many grazing systems strive to maximize uniform forage consumption and cattle gain; however, some question the impact of management regimes on native floral and faunal communities (Fuhlendorf and Engle 2001). Rangelands have been called "biodiversity repositories" (Fuhlendorf and Engle 2001: 625) due to the fact that they can encompass large numbers of native plants that create habitat for many grassland species. Therefore, maintaining heterogeneity on these rangelands is pertinent to conserve biodiversity in the Great Plains. In the United States, 61% of the land surface is covered by rangelands primarily managed for livestock (Fuhlendorf and Engle 2001). The conservation of grassland biodiversity is dependent on the sustained availability of heterogeneous habitats in these rangelands.

Measures of heterogeneity

As variability in the data increases, heterogeneity of the data increases. Two common measures of variability, are standard deviation (SD; the square-root of the variance), and the coefficient of variation (CV; the standard deviation of a variable divided by its mean; Quinn and Keough 2002). Standard deviation is a measure of spread within a data set, with larger values indicating a larger spread around the mean. A large SD value for a particular variable therefore signifies more heterogeneity of that variable in the study area. Standard deviation is sensitive to the scale on which the variable is measured i.e. if the mean is multiplied by a constant, the SD will also increase by the same factor. This differs from the coefficient of variation, in which both numerator (SD) and denominator (mean) in the same units, standardizes the measurement of heterogeneity rendering it insensitive to scale. Since CV is divided by the mean, it is a relative measure of variability. Because of this, CV is often used as a measure to compare heterogeneity among different systems with different means. In contrast, SD is a measure of absolute variability (Sørensen 2006). For this study we are more interested in the absolute variability, rather than the relative variability, so that we may detect and compare differences in heterogeneity among similar habitats.

Grazing theories

Grazing is considered an important process in the North American Great Plains, as the landscape evolved with a long history of grazing (Milchunas et al. 1988, Knapp et al. 1999). There have been many theories that have been developed to try to predict the effects of grazing on rangeland plant communities (Milchunas et al. 1988, Westoby et al. 1989).

Range succession models

The range succession model was the first model used to classify rangelands (Westoby et al. 1989, Briske et al. 2003, 2005). The range succession model projected that each rangeland had a single climax vegetation community in the absence of grazing (Clements 1936, Westoby et al. 1989, Briske et al. 2005). It had a single successional-grazing axis that was reversible (i.e. with the presence of grazing, the successional pathway of the system was set back along the succession-grazing continuum whereas in the absence of grazing, the successional pathway would continue and eventually result in the climax community, which is site-specific). Grazing intensity proportionately offset the secondary successional pathway, and resulted in a change in species composition (Briske et al. 2003). With this model, an optimal grazing intensity for a particular environment would be one that would allow the maximum gain in cattle while keeping the rangeland in an earlier successional stage (Westoby et al. 1989).

Milchunas et al. (1988) built on this model by accounting for the grazing history of the grassland as well as the annual average moisture levels of the area. Previous models of disturbance did not adequately address the various responses of grazing on different grassland communities (Milchunas et al. 1988). The historic use of grazing and moisture levels were used to develop hypotheses to determine how grassland plant communities respond to present forms of grazing, as these were key factors that influenced the adaptations of the current suite of species (Milchunas et al. 1988). This model was only applicable to climatically-driven grasslands (i.e. annual moisture levels only allow for grass development, and will not support trees).

Plants in semi-arid grasslands with a long history of grazing exhibit convergent evolution, as plant traits that can withstand drought are also adapted to surviving grazing pressure (Coughenour 1985, Belsky 1986, Milchunas et al. 1988). Grazing pressure and drought

both periodically cause damage to or loss of organs (i.e. leaves, shoots, roots etc.) in plants (Milchunas et al. 1988). In semi-arid grasslands that have a long history of grazing, such as the short-grass prairie, Milchunas et al. (1988) hypothesized that grazing will not have much of an effect on the plant communities. This is due to the evolution of plant communities with the selective pressure of grazing and drought. Over time, species richness may decline linearly with increasing grazing intensity, but only slightly. Rare species (mainly forbs) may be reduced in numbers or eliminated due to their reduced tolerance of grazing.

State-and-transition-model

Initial methods of assessing rangeland health were based on linear models that assumed plant communities followed predictable seral pathways that could be altered by grazing (Briske et al. 2005). While the model developed by Milchunas et al. (1988) was more complex than the previous range model, the model is still a linear model that is theoretically reversible. It was recognized, however, that not all vegetation communities follow linear, reversible pathways and that there is more than a single stable community type (Westoby et al. 1989). The state-and-transition model was developed, and recognizes that rangelands can have several separate climax communities or “states”. Rangelands can transition between these different states due to environmental factors (e.g. fire or drought) or management decisions (e.g. change in stocking density; Westoby et al. 1989). This model is not restricted to climatically determined rangelands, and each rangeland would have its own separate model. Unlike the range succession model, there is no mid-way point between states. Continuous and reversible dynamics as predicted by the succession model are possible within a stable vegetation community, but irreversible and discontinuous states occur when ecological thresholds are surpassed (Briske et al. 2005).

Cingolani et al. (2005) proposed a model that incorporates both the state-and-transition model and the climactically- and historical grazing-driven model of Milchunas et al. (1988). In this model, three components of the model developed by Milchunas et al. (1988) were modified (Cingolani et al. 2005). First, the gradient of productivity replaced “moisture content” in the model. Second, they suggested that there are two types of plant communities in areas with a long history of grazing; a community that dominates when there is high grazing intensity, and a community that becomes dominant when grazing is absent for a period of time. The first community would be adapted to grazing and exhibit grazing tolerant traits (such as low stature), while the second community type would be better competitors. This suggested change in the model allowed for species composition to change in the presence or absence of grazing, but with the diversity remaining the same. The final modification is the inclusion of system resilience into the model. Resilience, as defined by Cingolani et al. (2005), is the ability of the plant community to undergo reversible changes in response to significant variation in grazing intensity. Based on the theory by Milchunas et al. (1988), the suite of plants species found grasslands with a long history of grazing should have higher resilience due to the co-evolution of the plant communities with grazing.

Grassland communities that have a long history of grazing exhibit a high degree of resilience and tend to shift composition depending on the degree of grazing exerted on the grassland (Cingolani et al. 2005). It is important, therefore, to collect data on the plant communities and not simply record species richness to see if the composition is changing. However, when new pressures may arise that have no historical basis, such as heavy grazing for long periods of time resulting in soil erosion, or encroachment of woody species, which may then result in irreversible changes in the composition (Cingolani et al. 2005).

Plant responses to grazing

As described above, grasslands evolved with periodic fires and drought and the presence of grazing animals (Stebbins 1981, Knapp et al. 1999, Anderson 2006). Because of this, many grassland plants are adapted to tolerate these stressors (Coughenour 1985, Anderson 2006). Grazing, along with fire and drought, continues to be an important ecological process in grasslands. However, the effects of herbivory on the evolution of plants have started to receive attention only in the last 30 years (McNaughton 1983).

Plants employ different strategies to resist grazing (Briske 1991). Two mechanisms of grazing resistance include avoidance mechanisms, which decrease the severity and likelihood of being defoliated, and tolerance mechanisms that aid in regrowth following defoliation (Briske 1991).

Because of the simultaneous development of grasslands, grazers and semi-arid climates, it is difficult to distinguish whether plants evolved to tolerate grazing pressure, or to endure periodic droughts (Coughenour 1985, Milchunas et al. 1988, Milchunas and Lauenroth 1993). Coughenour (1985) calls these traits “exaptations”, which are traits that developed in response to one type of pressure (i.e. to tolerate a drier climate) but consequently allow for greater ability to cope with other pressures (i.e. grazing pressure). Coughenour (1985) has described these exaptations in detail, which include the presence of basal meristems, short stature, high shoot density, deciduous shoots, nutrient reserves found underground and rapid growth and transpiration. Basal meristems may be better to survive drought due to the protection of the basal sheath, but the low height of the meristems also provides protection from grazing. The smaller stature of grasses may be an adaptation to drier habitats as water limitation can restrict the height of plants. The short stature allows for less of the plant to be grazed in one bite compared to a

taller plant. The presence of many small shoots can respond better to the sudden availability of water, and spread the risk of death by drought. Many shoots also allows for quicker recovery following defoliation due to grazing. Plants with deciduous shoots allow for survival of drought by dropping their leaves, resulting in less water-losing transpiration. Deciduous leaves are metabolically less costly to produce than drought-resistant leaves, which results in less damage by grazing compared to the presence of drought-resistant leaves. Below-ground storage in perennial plants allows survival while still retaining nutrient reserves to enable subsequent growth when moisture returns the following season. The below-ground reserves also serves for re-growth following defoliation. These exaptations include both tolerance and avoidance mechanisms.

Compensatory growth

A controversial topic in the literature is whether plants exhibit compensatory growth following grazing (McNaughton 1979, Belsky 1986, Dyer et al. 1993, Painter and Belsky 1993). Compensatory growth may be defined as the positive response of a plant following defoliation or injury (Belsky 1986). Many studies have shown that plants subjected to grazing will exhibit compensatory growth following defoliation (Detling et al. 1979, McNaughton 1979, Williamson et al. 1989, Dyer et al. 1993). Empirical studies assessing the responses of plants following defoliation by grazing are well summarized by McNaughton (1979). A list of the possible plant responses to herbivory, and reasons for compensatory growth, include: the increased photosynthetic rate in the remaining tissue; the removal of older, less photosynthetically active tissues by grazing; increased photosynthetic capacity of leaves that were previously shaded by the grazed leaves; the remaining tissue may senesce at a later time, enabling more photosynthesis; hormonal responses to the grazing that include subsequent faster plant growth

and encourages tillering (McNaughton 1979). The response of plants to tissue damage is affected by many factors such as genetics, the frequency and intensity of herbivory, the developmental stage of the plant at the time of herbivory, the type of tissue that is damaged, and the environmental factors at the time of herbivory (McNaughton 1979). To support the theory of compensatory growth, McNaughton (1979) found that in the Serengeti, South Africa, even under very intense grazing, plants in grazed areas exhibited the same amount of growth as the ungrazed areas, suggesting that the suite of species found in the area exhibited compensatory growth and were well adapted to grazing.

However, compensatory growth also has its dissenters (Belsky 1986, Painter and Belsky 1993). Belsky (1986) conducted a detailed review of the evidence (or lack thereof) of compensatory growth in grazed plants. It was concluded that although over 40 papers had been cited in favour of plant benefits from grazing, there was no strong evidence that plants demonstrate any benefits derived from grazing (Belsky 1986). Only crop species or plants that were grown in lab conditions exhibited any conclusive evidence of compensatory growth (Belsky 1986). The methods that were used to obtain the results that support compensatory growth have also been questioned as the below-ground biomass is rarely taken into account in these studies (Painter and Belsky 1993). In studies that do account for underground biomass, the increase in above-ground biomass is offset by a decrease in below-ground biomass (Painter and Belsky 1993). Underground grazers (i.e. nematodes and other invertebrates) can also have a large impact on biomass, and cannot be ignored in these systems (Painter and Belsky 1993). The debate of plant compensation has not been resolved (Dyer et al. 1993, Painter and Belsky 1993).

Plant community response to grazing

Herbivore selection may affect the response of plant populations more than individual plant response to grazing, and therefore may have more of an effect on plant communities (Brown and Stuth 1993). Community response to grazing will also depend on the ability of an individual plant to respond to organ loss and its effect on competition (Milchunas and Lauenroth 1993).

In the Serengeti, there was evidence that certain grass species decreased in abundance or disappeared completely in the absence of grazing (McNaughton 1979). It was hypothesized that these species had a higher fitness when subjected to grazing pressure, but were out-competed when grazing was absent (McNaughton 1979). However, absolute fitness was not increased by grazing, as the ungrazed areas produced larger seed sets than did grazed plants (McNaughton 1979).

C₃ and C₄ plant response to grazing

A common way to distinguish between plants is by functional types (Wang et al. 2006). One widespread plant functional type used is the physiological functional type, which distinguishes plants based on their photosynthetic pathway (i.e. C₃ or C₄ pathways; Wang et al. 2006). These are also referred to as cool-season and warm-season plants, respectively. C₄ plants mostly belong to the grass family (Poaceae) but certain forbs also possess the C₄ pathways (Wang et al. 2006). In northern mixed-grass prairie, common C₄-grass species include *Bouteloua gracilis* (blue grama grass), *Distichlis spicata* (salt grass), *Muhlenbergia cuspidata* (plains muhly), *M. richardsonis* (mat muhly), and *Schyzachyrium scoparium* (little bluestem).

C₄ plants have a higher photosynthetic optimization point than do C₃ plants (Heckathorn et al. 1999, Moser et al. 2004). As such, the maximum photosynthetic rate of C₄ plants occurs at a higher temperature than C₃ plants, with an optimum temperature ranging between 35 and 38°C (Moser et al. 2004). C₄ plants have lower rates of stomatal conductance and are, therefore, able to conserve water more efficiently than C₃ plants (Heckathorn et al. 1999). Warm-season grasses require only one-third to one-half of the water required by cool-season grasses to produce the same amount of dry matter (Moser et al. 2004). In warm, dry areas this is an advantage in the event of leaf loss due to herbivory as the remaining leaves of the C₄ plant are able to undergo photosynthesis more efficiently than a C₃ plant due to the increased temperature caused by the loss of shade leaves (Heckathorn et al. 1999).

There is evidence that higher levels of herbivory may be sustained in ecosystems dominated by C₄ growth forms compared to C₃-dominated ecosystems (Heckathorn et al. 1999). An analysis of data conducted by Heckathorn et al. (1999) suggest that ecosystems that are dominated by both C₃ and C₄ plants produce on average 1.65 times more aboveground biomass than C₃ ecosystems, and C₄-dominated ecosystems produce 2.5 foliage than C₃ systems. There are many studies that classify the changes in plant functional group in response to fire management (Collins et al. 1998) or fire management plus grazing (Collins et al. 1998, Damhoueyeh and Harnett 2002, Collins and Smith 2006). There are others that assess the differences in plant responses to different grazers (i.e. cattle or bison; Damhoueyeh and Hartnett 2002; Towne et al. 2005). However, there is a paucity of information on how C₃ and C₄ plants respond to grazing in the absence of other factors (Jackson et al. 2010).

It has been found that grazing reduces the competitive ability of warm-season grasses (Collins et al. 1998, Jackson et al. 2010). In eastern tall-grass prairie, grazing increased C₃ forbs

and grasses where otherwise C₄ grasses would be dominant (Collins et al. 1998). Bison grazing C₄ grass monocultures in eastern tall-grass prairie decreased the abundance of C₄ grasses over six years, with C₃ grasses invading and becoming established and more numerous (Jackson et al. 2010). However, each warm-season grass declined at separate rates (Jackson et al. 2010). Conversely, in northern mixed-grass prairie C₄ grasses and forbs were found to increase while C₃ grasses were found to decrease under high stocking densities (Derner et al. 2008).

Effects of grazing in mixed-grass and short-grass prairies

There have been many studies conducted to assess the response of individual plant species or plant communities to different grazing intensities in all types of prairie (Manley et al. 1997, Biondini et al. 1998, Gillen et al. 2000, Hart 2001, Bai et al. 2001, Willms et al. 2002, Hickman et al. 2004, Vermeire et al. 2008). Some studies have used manipulative experiments (e.g. Manley et al. 1997, Biondini et al. 1998, Gillen et al. 2000, Hart 2001, Hickman et al. 2004), while others have been based on observations of prior effects (Bai et al. 2001). Reported findings will be limited to mixed-grass prairie and short-grass steppe.

Biondini et al. (1998) studied the effects of two grazing intensities (50% and 90% aboveground biomass removal) and compared them with ungrazed exclosures over seven years in northern mixed-grass prairie. An increase in average species richness was found over time; however, the increase was not statistically correlated with grazing treatments. A decrease in standing dead vegetation was seen over time in the pastures with high grazing intensity. It was concluded that climate effects, such as the amount of precipitation, had a greater influence on the plant communities than grazing intensity (Biondini et al. 1998).

Hart (2001) assessed the impacts of three grazing intensities (20%, 40%, 60% biomass removal) with control exclosures over 55 years in short-grass steppe, and found that plant

diversity increased with moderate grazing (40% biomass removal), but decreased at heavy grazing intensities (60% biomass removal).

In mixed-grass prairie in southern Saskatchewan, Bai et al. (2001) compared protected areas, with no grazing present, to nearby pastures with differing levels of grazing. Consistent with other studies, Bai et al. (2001) concluded that plant diversity was maximized with moderate grazing and decreased with heavy grazing. However, grazing intensities were visually assessed based on grassland condition, and no numerical grazing intensities were given, making comparisons to other regions or studies difficult (Bai et al. 2001).

Willms et al. (2002) compared species diversity of grazed pastures to exclosures that had been protected from grazing for 70 years in the northern mixed-grass prairie of Alberta. A slight decline in species diversity was detected in ungrazed areas compared to grazed pastures, but species richness remained the same, indicating the change in abundance of a particular species (Willms et al. 2002).

3.0 EFFECTS OF CATTLE GRAZING INTENSITY ON VEGETATION STRUCTURE, HETEROGENEITY, AND PLANT DIVERSITY, IN A NORTHERN MIXED-GRASS PRAIRIE

3.1 Introduction

North American grasslands evolved with disturbances such as fire and grazing, and one of these disturbance regimes, or an interaction between them, is needed to maintain habitat heterogeneity and therefore biodiversity in these ecosystems (Collins and Barber 1986, Knapp et al. 1999, Fuhlendorf and Engle 2001, Hart 2001, Fuhlendorf et al. 2012). Grazing and fire affect vegetation structure, which creates habitat for grassland species. Since fire is associated with crop and property damage, and therefore is suppressed by many human communities, the only ecological disturbance that can feasibly be used to promote ecological heterogeneity at a large spatial scale across most of the North American Great Plains is grazing by livestock. However, typical management of cattle grazing is leading to a decrease in heterogeneity (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2012) by encouraging uniform grazing in order to maximize the use of forage (Teague and Dowhower 2003). These practices result in homogeneous rangelands, which may contribute to biodiversity loss in grassland ecosystems (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2012). However, strategic grazing management could transform cattle grazing into an ecosystem management tool that can restore heterogeneity on rangelands with a long history of grazing, such as the mixed-grass prairie. The purpose of this study was to assess how grazing can be used as a conservation tool by evaluating the effects of a range of grazing intensities over time on vegetation structure and three components of heterogeneity (Fuhlendorf and Engle 2001, Symstad and Jonas 2011): habitat heterogeneity, plant species diversity, and changes in plant community composition.

Different grazing intensities or stocking rates (i.e. how many cattle per area and time unit) can impact the same area differently. Extreme stocking rates are detrimental to rangelands and can decrease productivity and increase erosion (Bement 1969). As a consequence, many studies have been conducted to assess the impacts of different stocking rates on a variety of vegetation and structure components, albeit not for the purpose of increasing heterogeneity (e.g. Manley et al. 1997, Gillen et al. 2000, Hart 2001, Vermeire et al. 2008). Many studies suggest that grazing at a moderate stocking rate is sustainable (e.g. Biondini et al. 1998), because it results in predictable cattle gains and does not lead to deterioration of the rangeland. This had been termed “managing for the middle” (Fuhlendorf et al. 2012). However, this does not allow species that evolved with low or very high grazing intensities to persist on these rangelands. The importance of re-introducing “pattern and process” in grasslands has been identified, and includes managing rangelands to include historical variation in grazing intensity across the landscape (Fuhlendorf et al. 2012). However, few studies have empirically assessed the use of a variety of grazing intensities in a conservation setting with the objective of restoring heterogeneity to the landscape.

Heterogeneity on the landscape scale is imperative to the survival of many imperilled grassland species (Fuhlendorf et al. 2012), both because different species at risk require different habitat conditions (e.g. Baird’s sparrow versus chestnut-collared longspur; Davis 2004), and because some species require both short and tall vegetation to complete all life history stages (e.g. burrowing owl). Heterogeneity can be described as the variation in plant structure and composition (Fuhlendorf and Engle 2001). Ungrazed rangelands are naturally variable, but do not provide habitat for species that evolved in areas of heavy grazing. Conversely, at sustained high stocking rates, forage availability is reduced, decreasing the opportunity for cattle to graze

selectively, leading to little patchiness (Fuhlendorf and Engle 2001). Continuous grazing at a moderate grazing intensity, which is generally recommended as sustainable (e.g. Biondini et al. 1998, Fuhlendorf and Engle 2001), does not lead to a habitat structural gradient between highly grazed and undergrazed patches which is sufficient to support the historic suite of grasslands species (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2012). Therefore, a variety of grazing intensities should increase heterogeneity at both the smaller scale (patches within a single pasture) and the large landscape level (variability among pastures; Fuhlendorf et al. 2012).

However, effects of grazing on species diversity might differ from effects of grazing on vegetation structure. Diversity is a quantitative measure of species within an area and can be represented by species richness (i.e. the number of species in a given area) and diversity indices, which describe the evenness of species distribution (Legendre and Legendre 2012). Plant species richness is hypothesized to vary with grazing intensity depending on the productivity and grazing history of rangeland (Michunas et al. 1988). In sub-humid grasslands (i.e. prairies with higher moisture content, such as tall-grass prairie) with a long history of grazing, under ungrazed conditions only a few species, predominately grasses, dominate the canopy (Milchunas et al. 1988). When grass cover is reduced by grazing, this then allows forb species to increase, as more light and nutrients are available, increasing species richness (Olf and Ritchie, 1998). At sustained high grazing intensities, species richness declines again as grazing-adapted species dominate (Milchunas et al. 1988). At intermediate intensities, plants that exist under ungrazed conditions and grazed conditions may co-exist in a mosaic, and therefore diversity may potentially be maximized (Milchunas et al. 1988). In contrast, semi-arid grasslands (i.e. prairies with low moisture availability, such as short-grass prairie) with a long history of grazing should have greater species richness at light grazing intensities, and richness should decline slightly as

grazing intensity increases (Milchunas et al. 1988). This is because short-grass prairie plants co-evolved with both grazing and drought, and the plants have adapted to these stressors with their low stature and meristems low to the ground, and therefore most species are grazing-tolerant. As grazing intensity increases, the few grazing-intolerant present species will decline or disappear (Milchunas et al. 1988). However, the mixed-grass prairie of Grasslands National Park falls between the semi-arid and sub-humid grasslands classifications in terms of productivity. While the results of many studies support the theories postulated by Milchunas et al. (1988) of plant species richness in short-grass and tall-grass prairie, there have been few studies conducted in the mixed-grass prairie and the results are mixed (e.g. Biondini et al. 1998, Bai et al. 2001, Willms et al. 2002).

Plant community composition is also thought to vary with disturbance intensity. Because of the long history of grazing, grassland plants are believed to have evolved to include two broad pools of species: grazing-intolerant plants that dominate when grazing is absent and grazing-tolerant species that dominate when grazing is present (Cingolani et al. 2005). In sub-humid grasslands, it is predicted that these communities will overlap at intermediate grazing intensities (Milchunas et al. 1988). In semi-arid grasslands, distinct plant communities may be found along a gradient of grazing intensity with no net change in richness (Cingolani et al. 2005). The mixed-grass prairie should also follow these patterns, with grazing-tolerant species dominating when grazing is present and grazing-intolerant species dominating when grazing is absent and these communities should overlap at intermediate grazing intensities, leading to an increase in heterogeneity.

The effects of grazing may change over time. Grazing can have short-term effects on a rangeland that can be detected within a single year of grazing, such as a decrease in biomass and

litter cover (Biondini et al. 1998, Derner and Hart 2007), but can have different long-term effects. While no changes in plant species composition were reported in a Wyoming mixed-grass prairie study after six years of grazing, these changes were “substantial” after twelve years (Hart et al. 1988, Manley et al. 1997). However, the effects of grazing period are not well understood. Further, in some studies, the effects of the temporal component have not been assessed, because the study area was grazed prior to the initiation of the study (e.g. Gillen et al. 2000).

Grasslands National Park (GNP) in southern Saskatchewan, Canada, initiated an adaptive management, large-scale grazing experiment known as the Biodiversity and Grazing Management Area (BAGMA) to assess the effects of different grazing intensities ranging from no grazing to very high grazing intensity for the area on grassland bird species, plant communities and habitat structure of the native mixed-grass prairie (Koper et al. 2008). The focus of my study was to assess the impact of different grazing intensities affect the mixed-grass prairie vegetation. More specifically, my objectives were to determine how habitat structure, habitat heterogeneity, plant species diversity and plant communities changed with varying grazing intensities over four years following the re-introduction of livestock grazing.

3.2 Methods

3.2.1 Study Site

BAGMA comprises a 26.5 km² area in and adjacent to the East Block of Grasslands National Park, in southern Saskatchewan, Canada, at approximately lat 49°01'00"N and long 106°49'00"W (Koper et al. 2008). This area had only intermittent and light livestock grazing from the 1930s until Parks Canada purchased the land in 1990-1991, when livestock grazing ceased (Parks Canada 2006). The region is unfragmented by cultivation, has few seeded forage crops, with few cross-fences present (Henderson 2005, Parks Canada 2006). Mean annual

precipitation is approximately 350 mm (Parks Canada 2006). Mean annual temperature is 3.8 °C, with reported extreme temperatures of -49 °C and +41 °C in January and August, respectively (Henderson 2005).

The experimental area is characteristic of northern mixed-grass prairie and includes upland and lowland habitat areas. Upland areas were dominated by grasses such as blue grama grass (*Bouteloua gracilis*), speargrass (*Hesperostipa comata*), northern and western wheatgrasses (*Elymus lanceolatus* and *Pascopyrum smithii*), and June grass (*Koeleria macrantha*). Pasture sage (*Artemisia frigida*), scarlet mallow (*Sphaeralcea coccinea*), and moss phlox (*Phlox hoodii*) were the dominant forbs found in the area. Clubmoss (*Selaginella densa*) was also found throughout the upland areas. Lowland areas were also dominated by grass, with an additional shrub component such as western snowberry (*Symphoricarpos occidentalis*), wild prickly rose (*Rosa acicularis*) and silver sagebrush (*Artemisia cana*). Predominant forbs in the lowlands included Canada goldenrod (*Solidago canadensis*) and wild licorice (*Glycyrrhiza lepidota*).

The study area consisted of nine pastures, each approximately 300 ha in area (pastures 1-9, Fig. 1). Six of the pastures were grazed at a range of grazing intensities (stocking rates); two were grazed with the intention of removing approximately 70% biomass (Pastures 4, 8; Fig. 1), and the remaining four were grazed aiming for approximately 57% (Pasture 3), 45% (Pasture 7), 32% (Pasture 6) and 20% (Pasture 2) biomass removal, respectively. It should be noted that while these were the intended percentages of biomass removal, data were not collected to determine the actual biomass produced within a year, and therefore these values are approximate. While the exact amount of biomass removal is not known, the gradient of grazing intensities is still retained which is fundamental to this study. The four-year average of the stocking rates were 0.83 and 0.77, 0.69, 0.56, 0.38, and 0.24 animal unit months per hectare (AUMs/ha; Figure 1).

The location of each pasture and associated stocking rate can be seen in Figure 1. The remaining three pastures (Pastures 1, 5, 9) were ungrazed and are considered control pastures. Two years of baseline data were collected in the summers of 2006 and 2007 on the ungrazed prairie before cattle were re-introduced to the park in 2008. For this study, the two years of pre-grazing (2006-2007) and four years of grazing (2008-2011) data were analysed, providing a total of six years of data.

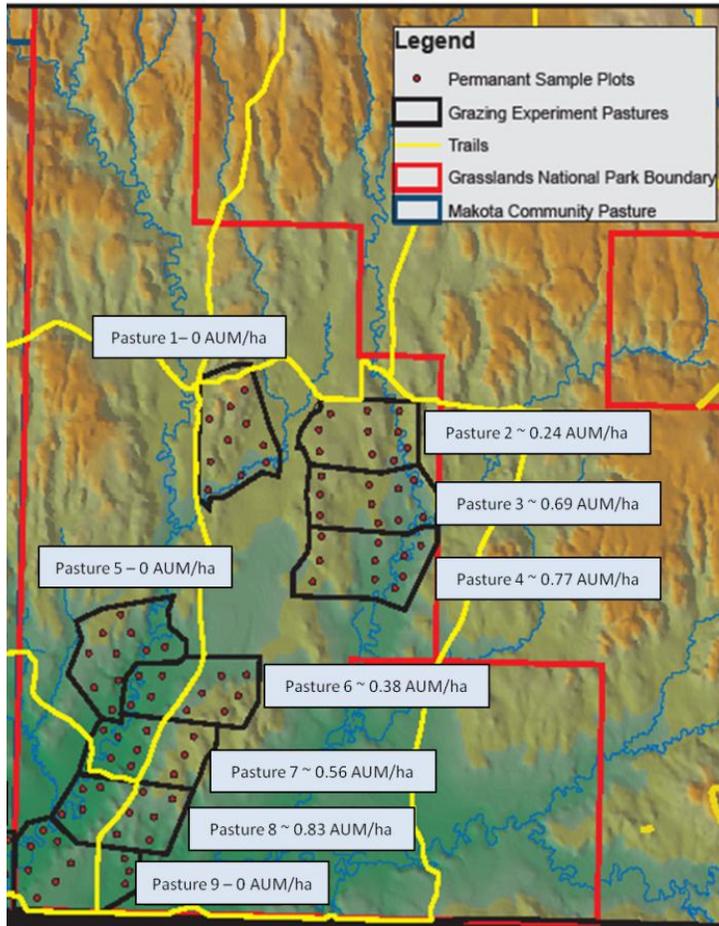


Figure 1. Study area and treatment locations of the Biodiversity and Grazing Management Area in the East Block of Grasslands National Park in Saskatchewan, Canada. Average stocking rates from 2008-2011 are presented (Modified from Parks Canada, 2012).

3.2.2 Vegetation Sampling

Each pasture included 10 permanent 50-m x 20-m plots; six were located in upland areas, and four were located in lowland areas. Ten 50-cm x 10-cm modified Daubenmire frames were located in permanent positions within the larger plot (Daubenmire 1959). Species richness was recorded within the larger plot. Within each of the smaller frames, an estimate of aerial cover for each plant species present was assessed and assigned to cover class (i.e. less than 0.1% cover, between 0.1 and 1% cover etc.). Cover of vegetation structure components such as bare ground

cover, litter and *Selaginella densa* were also assessed. *S. densa* is a clubmoss that is interspersed throughout the grasses, and covers a large portion of the study area. The depth of litter present at the centre of the frame was measured. All cover classes were then converted to the midpoint of the percent cover, and plants were grouped by growth form (i.e. grasses, forbs and shrubs) for analysis. All measurements were taken in the middle of the growing season, from approximately middle of June to the middle of August. Upland plots were the first to be surveyed, followed by lowlands, to coordinate with different plant phenologies in these two habitats.

3.2.3 Statistical analysis

Diversity indices- Species richness of each plot was calculated using the species count from the larger plot. Shannon's diversity index (H') is a measure of species heterogeneity and is calculated as follows:

$$H' = -\sum(p_i)(\log_2 p_i) \quad (1)$$

where p_i is the proportion of individuals of species i found in the community. Shannon's diversity index was calculated on a per-plot basis, and was converted back to units of species using the equation (Krebs, 1999):

$$2^{H'} \quad (2)$$

I also calculated Simpson's diversity index to account for the difference Simpson's and Shannon's indices, as these indices give more weight to common and rare species, respectively. However, since both Shannon's and Simpson's diversity indices showed similar trends, I only report the results of Shannon's index.

Habitat structure model selection- To assess the response and change over time of habitat structure to the different grazing treatments, I used generalized linear mixed models (GLMMs) modelled using the GLIMMIX procedure in SAS[®] 9.2 software (SAS Institute Inc. 2008). One or

more random variables were included in the models to account for nesting of years within frames, frames within plots, and plots within sites. The appropriate distribution that best fit each response variable was chosen using Generalized Linear Models in the GENMOD procedure, prior to the GLMM analyses. Upland and lowland plots were analysed separately.

To evaluate how response variables responded to grazing and if this response varied by year, grazing intensity, year since grazing was introduced, and the interaction between these main effects were tested. The interaction of AUMs \times AUMs was also included as the quadratic variable to allow the response to grazing intensity to follow a curvilinear trend. To choose the appropriate model that best described each response variable, Akaike's Information Criterion (AIC) was used within a hierarchical framework. Low AIC values have a higher likelihood of a model being true (Burnham and Anderson 2001). These AIC values can be compared among different models and given "weights", with lower AIC values having higher relative weights (Burnham and Anderson 2001). Therefore, the model with the highest AIC weight was selected to go on to the next round of testing, unless the difference of the AIC values was less than two AIC units ($\Delta \text{AIC} < 2$), in which case the model with the fewest parameters (i.e. simpler model) was chosen (Arnold 2010). The first set of comparisons included 1) the null hypothesis; 2) years since grazing ("year") and grazing intensity (AUMs/ha; "AUM"); and 3) the interaction of year \times AUM as well as both main effects. The model with the highest AIC weight went on to the next round of testing, which included the quadratic term. If the inclusion of the quadratic term resulted in a higher AIC weight, the model was then tested with an interaction between year and the quadratic term.

Data were analysed at the smallest spatial scale possible (i.e. frame scale). Certain variables (i.e. species richness, Shannon's diversity index) could only be assessed at the plot

scale because their calculation used data from multiple within-plot subsamples. At the frame scale, the response variables tested were litter depth, litter cover, bare cover, *S. densa* cover, grass cover, forb cover, shrub cover, and C₄ grass cover. Because of the paucity of C₄ grasses in our study site, overall grass cover reflects mostly trends of C₃ grasses, and it is for this reason C₃ grasses were not assessed separately. Assessing the effects of grazing intensity on habitat structure is an important step in answering the main question of whether a range of grazing intensities influence habitat heterogeneity.

Habitat heterogeneity- Standard deviation is a measure of absolute variability (Sørensen 2006), and I used this as a measure of heterogeneity on the landscape. To assess the impact of grazing intensity on habitat heterogeneity, I used the standard deviation of the same response variables as above, in models chosen with the same AIC procedure as described above.

Plant diversity - To determine how plant diversity changed in response to grazing intensity and time, I used GLMMs with species richness, Shannon's and Simpson's diversity indices as response variables, in models chosen with the same AIC procedure as described above.

Plant community analyses - To determine whether plant communities changed in response to grazing intensity and time, I used the Mantel test. The Mantel test calculates a similarity matrix between two sets of data and determines whether a correlation between the data sets exist (Quinn and Keough 2002). It is used to assess whether plant communities are more similar as environmental conditions (i.e. grazing intensities or years since grazing started) are more similar. The null hypothesis is that no correlation exists between the two matrices and this is measured by the Mantel statistic, the *rM*. A large *rM* value with a *p*-value of <0.05 indicates a high correlation between two matrices. To separate the confounding effects of grazing intensity and time, I conducted the Mantel test twice; first, to evaluate whether plant communities changed as time-

since-grazing changed within a particular treatment, and second, to evaluate whether plant communities differed among the different stocking rates within each year. To give equal weight to both rare and abundant species, the Bray-Curtis distance index was used (Legendre and Legendre 2012).

To visualize trends in plant communities with different grazing intensities and time, non-metric multidimensional scaling (NMS) was used. NMS is an ordination method that calculates pair-wise distances among all objects (e.g. plant communities) and arranges the objects in n -dimensional space based on the rank of the distance measures (Kenkel et al 2002). NMS makes no assumption regarding the underlying structure of the data, and therefore, is suited to most data. The Bray-Curtis distance measure was used (Legendre and Legendre 2012). The stress value is a measure of goodness-of-fit of the number of dimensions that were chosen (Legendre and Legendre 2012). With a possible range of values from 0-100 (McCune and Mefford 2011), a smaller value indicates that the appropriate number of dimensions were chosen (Legendre and Legendre 2012). Relative weights of the influence of independent variables are also given. Both the Mantel test and NMS were run using PC-ORD 6.0 (McCune and Mefford 2011).

I analysed species relative cover data at the frame scale, and species occurrence at the plot scale, to answer two related but distinct questions. I analysed the relative cover data to assess whether there were changes in species abundance across the plant community, whereas I analysed species occurrence to assess whether the types of species that are present changed with grazing treatment and time.

3.3 Results

Over a six year period, 256 different plant species were identified (for complete species list, see appendix A). The highest number of species identified in 2010 (212 species), and the

lowest number (165 species) in 2006. Upland and lowland plots over all years had a total of 198 and 232 species identified, respectively. Average species richness in upland habitat was 43.4 species per plot (SD = 7.3, range 26 - 61 species per plot). Species richness was more variable in lowland plots, where both the highest (82 species) and lowest (12 species) species richness per plot were recorded. Average species richness in lowland plots was 42.3 species (SD = 13.7).

3.3.1 Habitat structure

Upland - All measures of habitat structure were influenced by grazing intensity (Table 1, Figs 2-9). All variables except *S. densa* cover and shrub cover responded linearly to grazing intensity with a varying effect by year (Table 1). Grass cover and litter cover responded negatively in a non-linear fashion to the interaction of grazing intensity and year. The main effect of year since grazing was not significant in influencing litter depth.

Bare ground cover and C₄ grass cover increased as grazing intensity increased, and this response varied by year (Table 1; Fig. 2, 3). Prior to the grazing treatments, C₄ grass cover increased in pastures in the high grazing treatment pastures, even though there were no cattle present to create this pattern; thus, the pre-existing pattern was spurious. After four years of grazing, however, the effect of grazing dominated, thereby overshadowing this trend (Table 1; Fig. 3).

Forb cover varied with grazing intensity over the years, as the initial trend of decreasing forb cover with increasing grazing intensity was reversed after the fourth year of grazing (Table 1; Fig. 4). Grass cover exhibited a non-linear negative response to grazing intensity, and varied by year (Table 1; Fig. 5).

Grass cover, litter cover and *S. densa* cover varied over the years in the ungrazed control pastures (Table 1; Figs. 5, 7, 8). However, clear negative (grass and litter cover) and positive (*S.*

densa cover) relationships with grazing intensity in the grazed pastures suggest that grazing intensity explains some of the variability observed over time. The apparent initial trend in litter depth was likely spurious as it became less obvious over time (Table 1; Fig. 6).

Lowland - All variables except litter cover and grass cover responded to grazing intensity and changed over time. Grass cover responded to the main effects of grazing intensity and year since grazing, but not an interaction of the two main effects. Litter cover responded only to year, with no effect of grazing intensity (Table 2). In contrast to upland trends of the same response variables, litter depth and bare ground cover responded non-linearly to grazing intensity and this non-linear relationship changed over time.

3.3.2 Structural heterogeneity

Upland - Effects of grazing on upland heterogeneity were linear for all response variables. Trends seen for heterogeneity were similar to the mean trends in the same response variable (e.g., effect of grazing on SD of forb cover was the same as the effect of grazing on forb cover). Heterogeneity of bare ground and *S. densa* cover increased with increasing stocking rate and over time, whereas heterogeneity of litter depth decreased with increasing grazing intensity (Table 3). Heterogeneity of shrub cover and C₄ grass cover decreased over time, but grazing intensity had no effect.

Contrary to my predictions, heterogeneity was highest in the ungrazed control pastures in all years after grazing was introduced, for forb, grass and litter cover and litter depth (Figs. 4-7). Heterogeneity of litter depth was the only response variable that increased with increasing grazing intensity, and this response became more pronounced over time (Fig. 2).

Lowland - Heterogeneity of all response variables except grass cover responded linearly to grazing intensity and year since onset of grazing (Table 4). *S. densa* cover, forb, grass and shrub

cover increased over time. Litter cover, bare cover and C₄ grass cover decreased over time. Grass cover remained unchanged over time. The effect of grazing intensity varied by year for heterogeneity of litter depth, forb cover, and shrub cover.

Similar to upland heterogeneity trends, heterogeneity of bare ground, C₄ grasses, litter cover and litter depth was most pronounced before grazing was introduced, and continued to be highest in the ungrazed control pastures throughout the study (Figs. 2, 3, 6, 7). Heterogeneity of litter depth increased in ungrazed control pastures by 25% over the study period (Fig. 6). The first year of grazing reduced SD of litter depth by 20 mm between ungrazed control and the heaviest grazed pastures, but this difference became less pronounced over time.

3.3.3 Plant diversity

Upland- Species richness increased as grazing intensity increased, and this effect became more pronounced over time (Table 1). Species richness in the ungrazed control plots also increased with each year, though this increase was less than the increase induced by grazing (Fig. 10). Shannon's diversity index exhibited a variable response to grazing intensity over the course of the study (Table 1). A spurious trend was present where diversity slightly decreased as future grazing intensity increased for the two pre-grazing years, and this trend was still apparent after two years of grazing (Fig. 11). However, in year three and four post-grazing, this trend reversed so that diversity increased as grazing intensity increased.

Lowland- Species richness in lowland plots show an opposite trend from upland plots. Species richness decreased with increasing grazing intensity once grazing was introduced (Fig. 10). Surprisingly, this trend was greatest after the first year of grazing (13% decrease), and became less prominent as grazing continued. Species richness in the ungrazed control pastures increased

by 40% over four years of grazing. Shannon's diversity index did not show any correlation with year or grazing intensity in lowland plots.

3.3.4 Plant composition

3.3.4.1 Plant species relative cover

Upland

Effects of grazing intensity - The Mantel test suggested no pre-existing differences of species relative cover across the landscape prior to the introduction of grazing (Table 5). Small changes in relative cover were detected among different grazing intensities in subsequent years.

Conversely, NMS results suggested that no changes in plant species relative cover could be attributed to grazing intensity when all years were included in the model (Table 6). Further, when grazing intensity was tested within each year to remove the effect of annual variability, species relative cover was different among grazing intensities after three years of grazing (Table 8).

Effects of year - The results from the Mantel test suggest that plant communities changed over time in all treatments except the lowest grazing treatment, but including the ungrazed control pastures. The NMS results also suggested that species relative cover changed over time in the ungrazed control pastures (Table 6). In experimental plots, a slight change in species relative cover was detected among years at the larger pasture scale, but no changes were detected at the smaller plot scale (Table 6, Fig 12).

Lowland

Effects of grazing intensity - The Mantel test suggested that grazing intensity was not correlated with changes in species relative cover in lowland plots (Table 5); however, the NMS results

indicate that species relative cover in the experimental plots were different among the different grazing intensities (Table 6).

Effects of year- Neither the Mantel nor NMS tests suggested any changes in species relative cover over time (Tables 6, 7).

3.3.4.2 *Plant species occurrence*

Upland

Effects of grazing intensity - Results from the Mantel test suggest that plant species occurrence was significantly correlated with future stocking rate prior to the commencement of the grazing treatments (Table 5). This trend continued once grazing was introduced, and is, therefore, spurious, and cannot be attributed to grazing. The results from NMS also support this result, as changes in plant species occurrence could not be attributed to grazing intensity (Table 6).

Change in species occurrence were not apparent among grazing intensities within years, also suggesting that grazing intensity did not influence plant species occurrence (data not shown).

Effects of year - The Mantel test suggested that changes in species occurrence occurred in both control plots and experimental plots (Table 7), consistent with results of the NMS analysis (Table 6, Fig. 13).

Lowland

Effects of grazing intensity - Both the Mantel test and NMS suggested that there was no correlation between grazing intensity and changes in species occurrence in lowland plots (Table 5, 6).

Effects of year - Both the Mantel test and NMS indicate that species occurrence varied among years in control plots, suggesting that annual variability may account for changes in species occurrence in experimental plots (Tables 8, 9).

Table 1. Models selected by AIC, AIC weights and parameter estimates for response variables in upland plots for data collected from 2006-2011 in Grasslands National Park in Saskatchewan, Canada.

Variable	Model chosen	AIC Weight	Variable	Parameter Estimate	Standard Error	p-value
Litter depth	AUM year AUM*year	0.72	AUM	-2.4896	0.1195	<0.0001
			year	0.009424	0.01636	0.5646
			AUM*year	0.2911	0.04204	<0.0001
Litter cover	AUM year AUM*year AUM*AUM	0.68	AUM	1.3802	0.221	<0.0001
			year	-0.1448	0.01157	<0.0001
			AUM*year	-0.3313	0.02944	<0.0001
			AUM*AUM	-1.1618	0.3046	0.0001
Bare cover	AUM year AUM*year	0.39 (Δ AIC <2)	AUM	-0.2104	0.1833	0.2511
			year	-0.2809	0.03353	<0.0001
			AUM*year	0.884	0.07642	<0.0001
<i>Selaginella densa</i> cover	AUM year	0.7	AUM	0.4427	0.09779	<0.0001
			year	0.4164	0.01694	<0.0001
Forb cover	AUM year AUM*year	0.7	AUM	-1.2113	0.09895	<0.0001
			year	0.05575	0.01364	<0.0001
			AUM*year	0.3405	0.03719	<0.0001
Grass cover	AUM year AUM*year AUM*AUM year*AUM*AUM	0.96	AUM	0.9943	0.3226	0.0021
			year	0.08405	0.01078	<0.0001
			AUM*year	-0.3732	0.1125	0.0009
			AUM*AUM	-1.6542	0.4549	0.0003
Shrub cover	AUM year AUM*AUM	0.78	year*AUM*AUM	0.4315	0.1508	0.0042
			AUM	-2.5153	0.8866	0.0046
			year	0.4805	0.04244	<0.0001
			AUM*AUM	2.4478	1.1565	0.0344

C ₄ cover	AUM year AUM*year	0.5	AUM	-0.5001	0.1502	0.0009
			year	-0.2181	0.02473	<0.0001
			AUM*year	0.1755	0.06178	0.0045
Richness	AUM year AUM*year	0.74	AUM	-0.03477	0.06262	0.5791
			year	0.03895	0.00889	<0.0001
			AUM*year	0.0472	0.02405	0.0506
Shannon diversity	AUM year AUM*year	0.73	AUM	-0.2257	0.08494	0.0083
			year	-0.01604	0.01225	0.1914
			AUM*year	0.1328	0.03291	<0.0001

* terms in grey type are those which the standard deviation included 0

Table 2. Models selected by AIC, AIC weights and parameter estimates for response variables in lowland plots for data collected from 2006-2011 in Grasslands National Park in Saskatchewan, Canada.

Variable	Model Chosen	AIC Weight	Variable	Estimate	Standard Error	<i>p</i> -value
Litter depth	AUM year AUM*year AUM*AUM AUM*AUM*year	0.9	AUM	-6.1493	0.8273	<0.0001
			year	0.05916	0.02639	0.0251
			AUM*year	1.0474	0.2693	0.0001
			AUM*AUM	5.2308	1.1333	<0.0001
			AUM*AUM*year	-0.9036	0.3543	0.0108
Litter cover	AUM year	0.69	AUM	-0.0335	0.07363	0.6494
			year	-0.165	0.01213	<0.0001
Bare cover	AUM year AUM*year AUM*AUM	0.42 (Δ AIC <2)	AUM	1.8764	0.7036	0.0077
			year	-0.0694	0.03477	0.0459
			AUM*year	0.4284	0.08679	<0.0001
			AUM*AUM	-2.6794	0.9373	0.0043
<i>Selaginella densa</i> cover	AUM year AUM*year	0.72	AUM	-0.2885	0.2553	0.2585
			year	0.2359	0.04136	<0.0001
			AUM*year	0.2623	0.09823	0.0076
Forb cover	AUM year AUM*year	0.51	AUM	-2.0035	0.1707	<0.0001
			year	-0.0665	0.02314	0.0041
			AUM*year	0.577	0.06417	<0.0001
Grass cover	AUM year	0.65	AUM	-0.1013	0.06334	0.1099
			year	0.03205	0.01062	0.0026
Shrub cover	AUM year AUM*year	0.7	AUM	1.0408	0.2546	<0.0001
			year	-0.2327	0.04343	<0.0001
			AUM*year	-0.2908	0.107	0.0066

C ₄ cover	AUM year AUM*year	0.73	AUM	-0.4518	0.1902	0.0176
			year	-0.243	0.03147	<0.0002
			AUM*year	0.288	0.07757	0.0002
Richness	AUM year	0.73	AUM	-0.1827	0.08995	0.0435
			year	0.09066	0.01499	<0.0001
Shannon diversity	Null					

* terms in grey type are those which the standard deviation included 0

Table 3. Models selected by AIC, AIC weights and parameter estimates for the standard deviation of response variables in upland plots for data collected from 2006-2011 in Grasslands National Park in Saskatchewan, Canada.

Variable	Model Chosen	AIC Weight	Variable	Estimate	Standard Error	<i>p</i> -value
Litter depth	AUM year AUM*year	0.61	AUM	-1.6313	0.2033	<0.0001
			year	0.02578	0.02966	0.3855
			AUM*year	0.2569	0.07649	0.0009
Litter cover	AUM year	0.68	AUM	-0.1054	0.07639	0.1686
			year	0.0953	0.01649	<0.0001
Bare cover	AUM year AUM*year	0.41 (Δ AIC <2)	AUM	-0.3371	0.4699	0.4737
			year	-0.1869	0.07752	0.0165
			AUM*year	0.5497	0.1938	0.0049
			AUM	0.7688	0.2058	0.0002
<i>Selaginella densa</i> cover	AUM year AUM*year	0.71	year	0.3964	0.02924	<0.0001
			AUM*year	-0.1856	0.08127	0.0231
			AUM	-0.5228	0.125	<0.0001
Forb cover	AUM year	0.51 (Δ AIC <2)	year	0.08869	0.02411	<0.0001
			AUM	-0.1303	0.09177	0.1567
Grass cover	AUM year	0.69	year	0.1183	0.01759	<0.0001
			AUM	0.196	0.2474	0.4288
Shrub cover	AUM year	0.71	year	-0.0591	0.04663	0.2059
			AUM	0.1186	0.1775	0.5047
C ₄ cover	AUM year	0.56	year	-0.1529	0.03382	<0.0001

* terms in grey type are those which the standard deviation included 0

Table 4. Models selected by AIC, AIC weights and parameter estimates for the standard deviation of response variables in lowland plots for data collected from 2006-2011 in Grasslands National Park in Saskatchewan, Canada.

Variable	Model Chosen	AIC Weight	Variable	Estimate	Standard Error	p-value
Litter depth	AUM year AUM*year	0.69	AUM	-1.475	0.2368	<0.0001
			year	-0.0539	0.03268	0.1016
			AUM*year	0.2839	0.09016	0.002
Litter cover	AUM year	0.69	AUM	0.07356	0.09918	0.4593
			year	0.06564	0.01702	0.0002
Bare cover	AUM year	0.48 (Δ AIC <2)	AUM	0.3466	0.2127	0.1049
			year	0.06151	0.03407	0.0726
<i>Selaginella densa</i> cover	AUM year	0.67	AUM	0.2266	0.2598	0.3843
Forb cover	AUM year AUM*year	0.72	year	0.3542	0.04249	<0.0001
			AUM	-1.4727	0.3245	<0.0001
			year	-0.0885	0.04225	0.0377
			AUM*year	0.4319	0.1212	0.0005
Grass cover	null					
Shrub cover	AUM year AUM*year	0.74	AUM	1.1676	0.3281	0.0005
			year	-0.2685	0.05205	<0.0001
			AUM*year	-0.3528	0.1376	0.0111
C ₄ cover	AUM year	0.74	AUM	0.2381	0.2439	0.3301
			year	-0.1055	0.04027	0.0096

* terms in grey type are those which the standard deviation included 0

Table 5. Mantel test results comparing plant species relative abundance and plant species occurrence among six experimental grazing intensities within a year for 2006-2011, collected in Grasslands National Park, Saskatchewan, Canada. Grazing was not present in 2006 and 2007, but data was collected to detect any spurious trends.

		Upland						Lowland						
		2006	2007	2008	2009	2010	2011	2006	2007	2008	2009	2010	2011	
Species relative cover	<i>n</i>	54	54	54	54	54	54	<i>n</i>	36	36	36	36	36	36
	rM	0.038	0.023	0.058	0.093	0.085	0.081	rM	0.066	-0.014	0.057	0.053	0.021	0.050
	<i>p</i>	0.080	0.178	0.025	0.003	0.006	0.006	<i>p</i>	0.060	0.388	0.070	0.086	0.248	0.085
Species occurrence	<i>n</i>	54	54	54	54	54	53	<i>n</i>	36	36	36	36	36	36
	rM	0.048	0.049	0.103	0.061	0.075	0.088	rM	0.049	-0.034	-0.009	0.003	0.002	-0.001
	<i>p</i>	0.042	0.041	0.001	0.018	0.010	0.004	<i>p</i>	0.090	0.159	0.427	0.427	0.428	0.053

* Bold type indicate significant p-values

Table 6. Relative weights and stress of year-since-grazing and grazing intensity on plant communities using non-metric multidimensional scaling in Grasslands National Park, Saskatchewan, Canada.

		Upland				Lowland			
		Plot Scale		Pasture Scale		Plot scale		Pasture Scale	
		Year since grazing	Grazing intensity						
Species relative cover	Axis 1	0.043	0.001	0.115	0.27	0	0.007	0.003	0
	Axis 2	0	0.036	0.126	0.037	0.024	0.01	0.003	0.028
	Axis 3	0.016	0	0.003	0.06	0.006	0.02	0.051	0.148
	Stress	16.92		13.94		14.98		12.56	
Species occurrence	Axis 1	0.014	0.025	-	-	0.003	0.022	-	-
	Axis 2	0.014	0.021	-	-	-0.025	0.003	-	-
	Axis 3	0.346	0.029	-	-	0.655	0.003	-	-
	Stress	18.92		-		16.4		-	

Table 7. Mantel test results showing plant community trends over time within grazing treatments over six years (2006-2011), collected in Grasslands National Park, Saskatchewan, Canada.

	Upland (AUMs/ha)						Lowland (AUMs/ha)							
		0	0.24	0.38	0.56	0.69	0.8		0	0.24	0.38	0.56	0.69	0.8
Species relative cover	<i>n</i>	108	36	36	36	36	71	<i>n</i>	72	24	24	24	24	48
	rM	0.161	0.106	0.13	0.196	0.117	0.107	rM	0.016	-0.043	-0.018	-0.072	-0.007	0.048
	<i>p</i>	0.0001	0.049	0.012	0.0001	0.023	0.001	<i>p</i>	0.616	0.532	0.777	0.295	0.924	0.227
Species occurrence	<i>n</i>	108	36	36	36	36	71	<i>n</i>	72	24	24	24	24	48
	rM	0.136	0.053	0.223	0.242	0.102	0.119	rM	0.123	0.079	0.569	0.11	0.167	0.234
	<i>p</i>	0.0001	0.326	0.0001	0.0001	0.040	0.0001	<i>p</i>	0.0001	0.215	0.373	0.088	0.012	0.000

*Bolder terms are statistically significant, and indicate that plant communities are changing over time.

Table 8. Relative weights of effects of grazing intensity on plant communities within a single year using non-metric multidimensional scaling in Grasslands National Park, Saskatchewan, Canada.

	Upland					Lowland				
	pre-grazing	2008	2009	2010	2011	pre-grazing	2008	2009	2010	2011
Axis 1	0.035	0.001	0.031	0	0.008	0.033	0.063	0	0.013	0.012
Axis 2	0.013	0.059	0.025	0.18	0.102	0.029	0.011	0.04	0.005	0.022
Axis 3	0	0.015	0.008	0.082	0.094	0.002	0.031	-	-	-
Stress	15.59	13.85	12.48	13.45	14.23	14.65	11.86	16.28	15.98	14.89

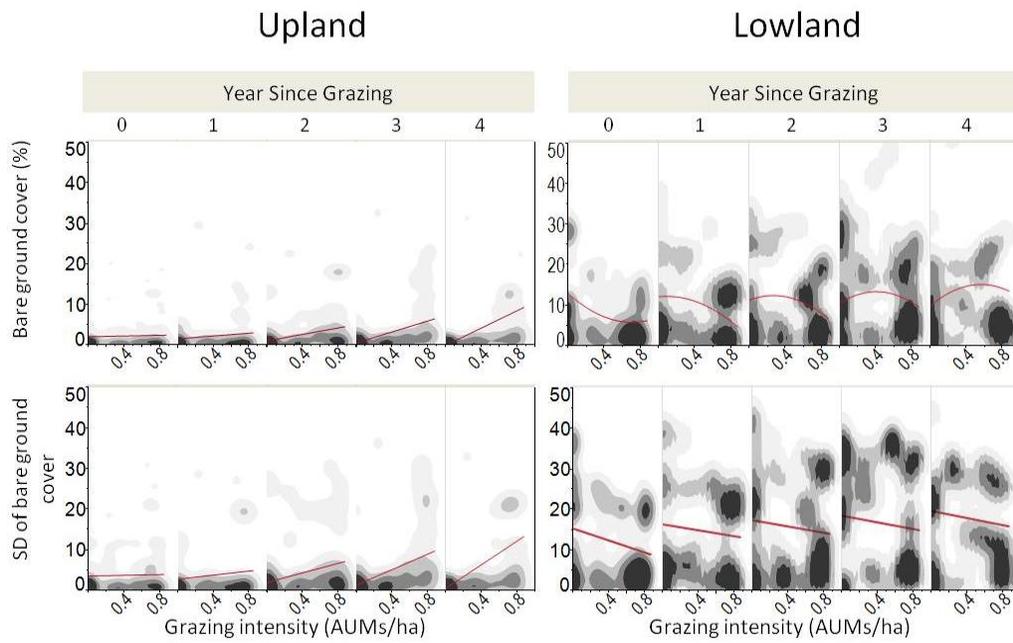


Figure 2. Percent cover and standard deviation of bare ground in response to grazing intensity in upland and lowland plots based on best AIC models for data collected from 2006-2011 in Grasslands National Park, Saskatchewan, Canada.

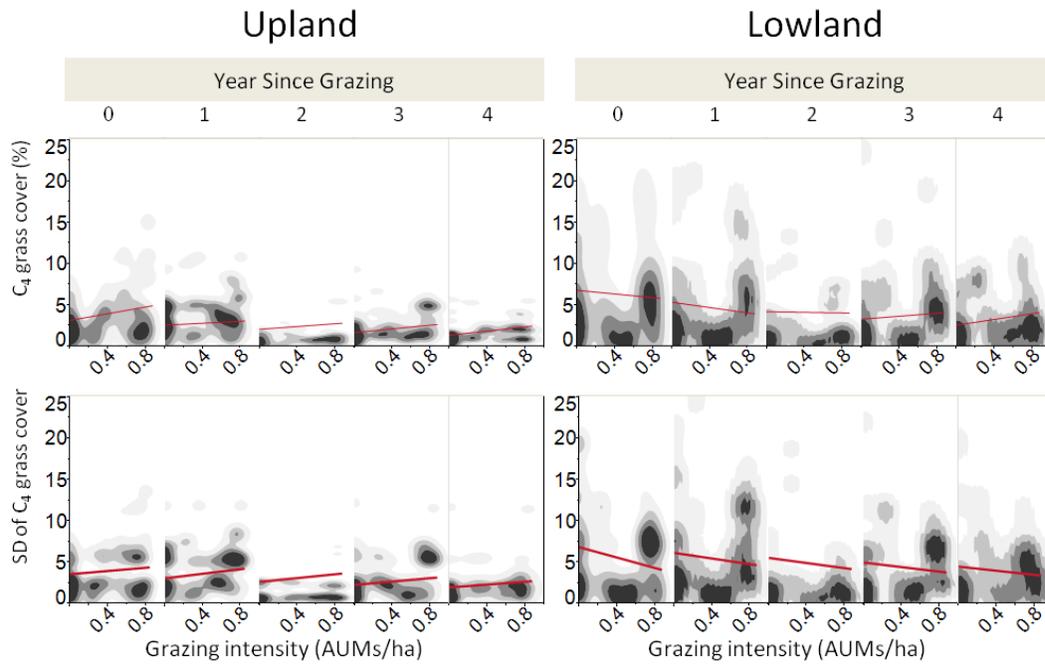


Figure 3. Percent cover and standard deviation of C_4 grass cover in response to grazing intensity in upland and lowland plots based on best AIC models for data collected from 2006-2011 in Grasslands National Park, Saskatchewan, Canada.

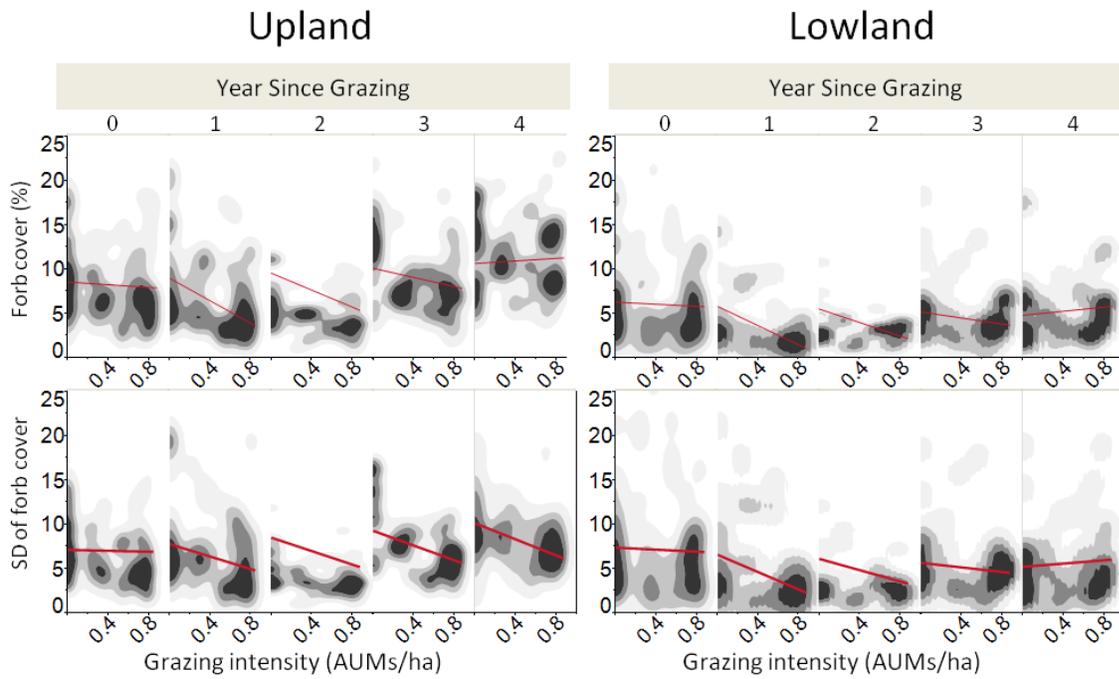


Figure 4. Percent cover and standard deviation of forb cover in response to grazing intensity in upland and lowland plots based on best AIC models for data collected from 2006-2011 in Grasslands National Park, Saskatchewan, Canada.

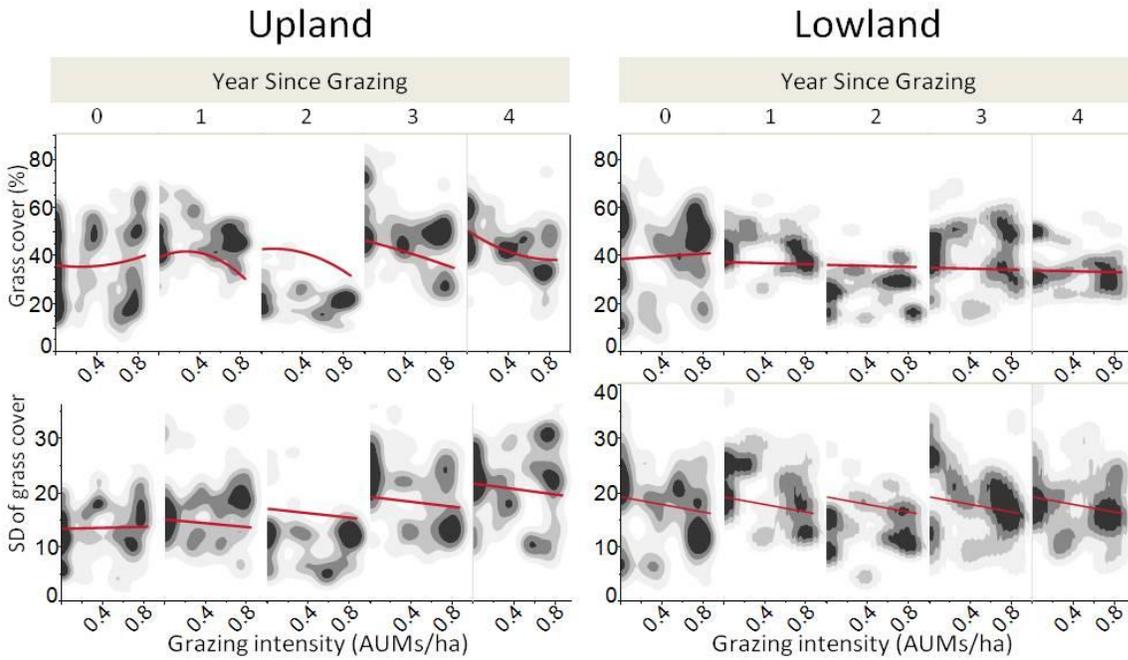


Figure 5. Percent cover and standard deviation of grass cover in response to grazing intensity in upland and lowland plots based on best AIC models for data collected from 2006-2011 in Grasslands National Park, Saskatchewan, Canada.

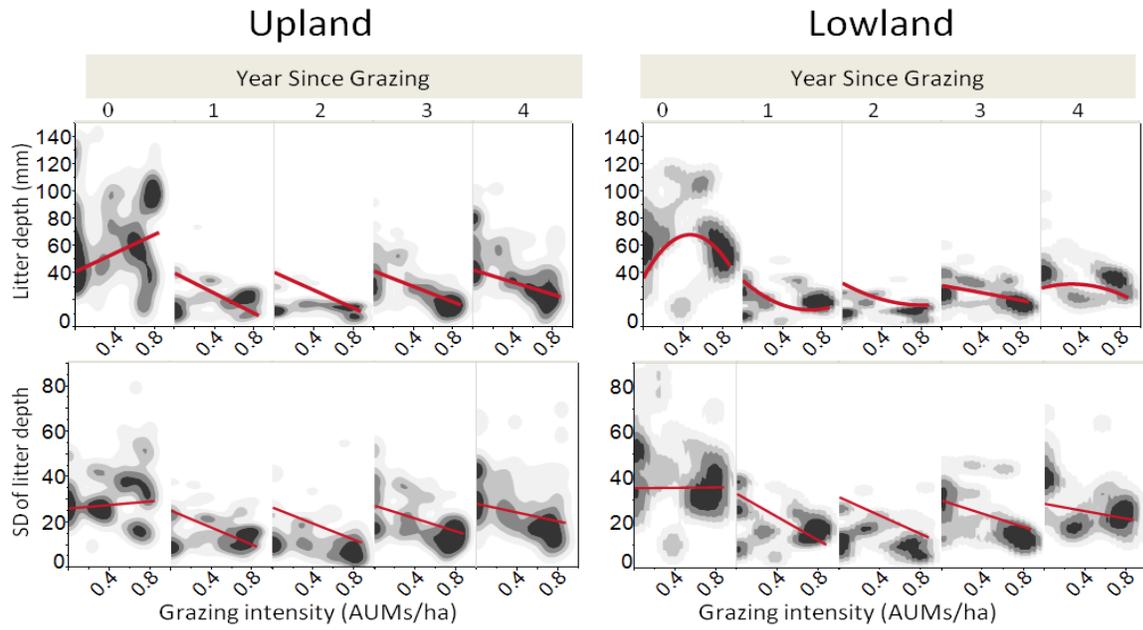


Figure 6. Depth and standard deviation of litter depth in response to grazing intensity in upland and lowland plots based on best AIC models for data collected from 2007-2011 in Grasslands National Park, Saskatchewan, Canada.

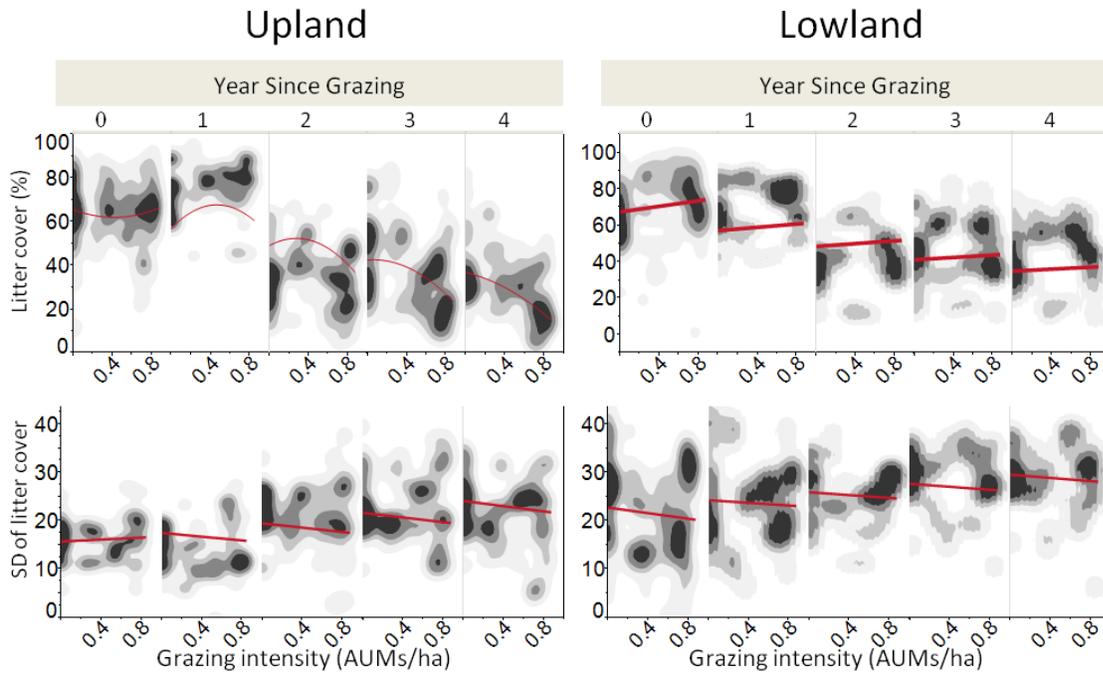


Figure 7. Percent cover and standard deviation of litter cover in response to grazing intensity in upland and lowland plots based on best AIC models for data collected from 2006-2011 in Grasslands National Park, Saskatchewan, Canada.

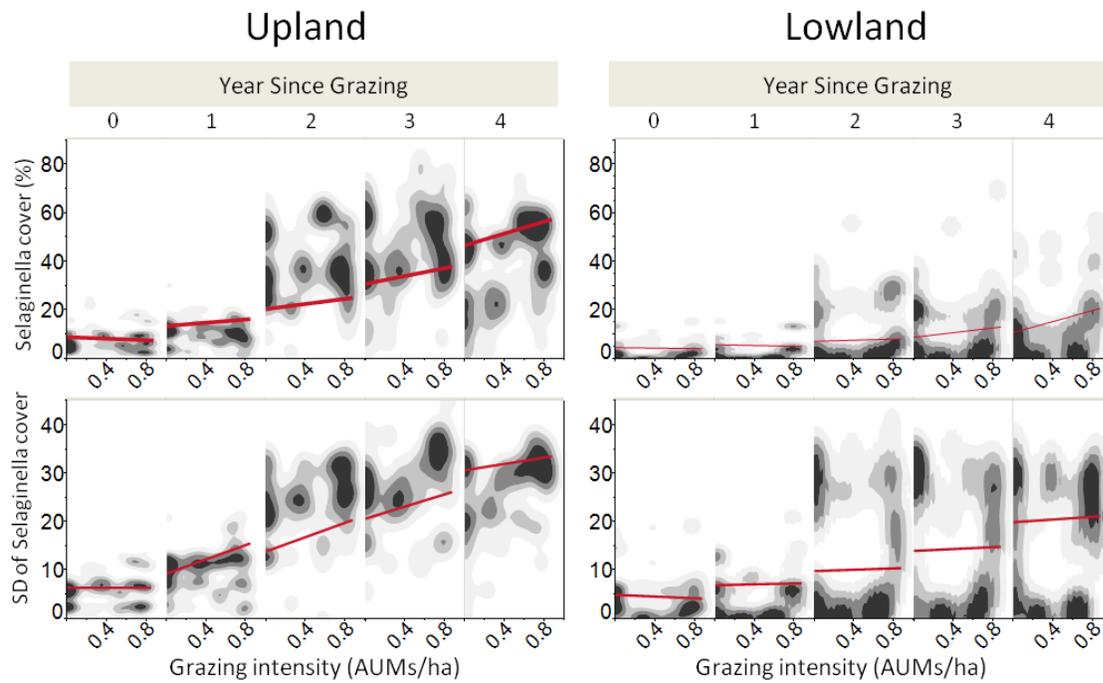


Figure 8. Percent cover and standard deviation of *Selaginella densa* cover in response to grazing intensity in upland and lowland plots based on best AIC models for data collected from 2006-2011 in Grasslands National Park, Saskatchewan, Canada.

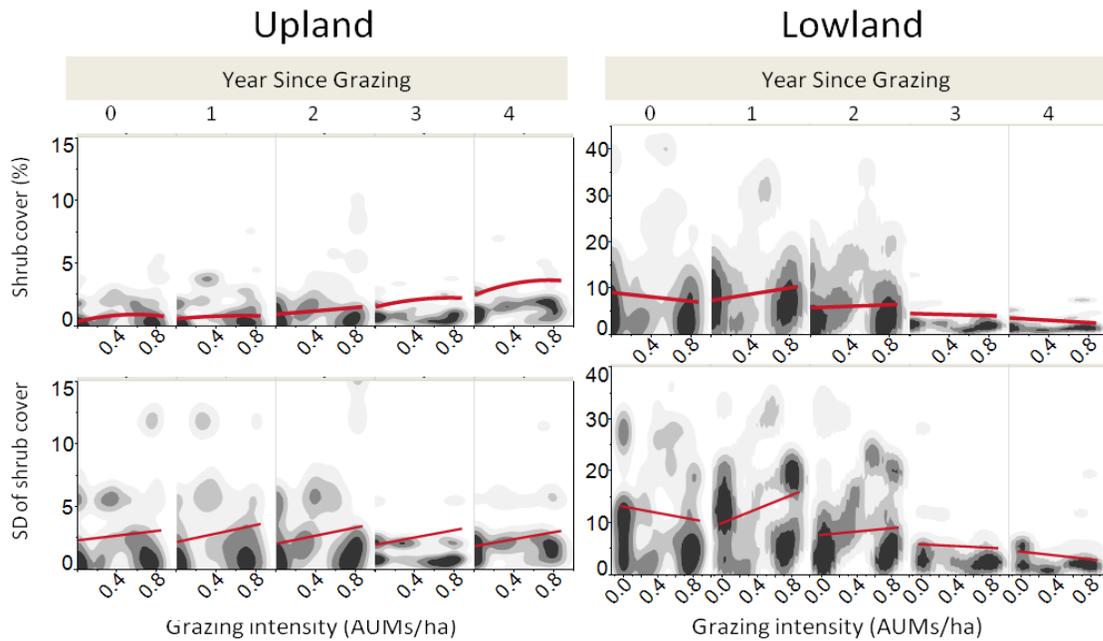


Figure 9. Percent cover and standard deviation of shrub cover in response to grazing intensity in upland and lowland plots based on best AIC models for data collected from 2006-2011 in Grasslands National Park, Saskatchewan, Canada.

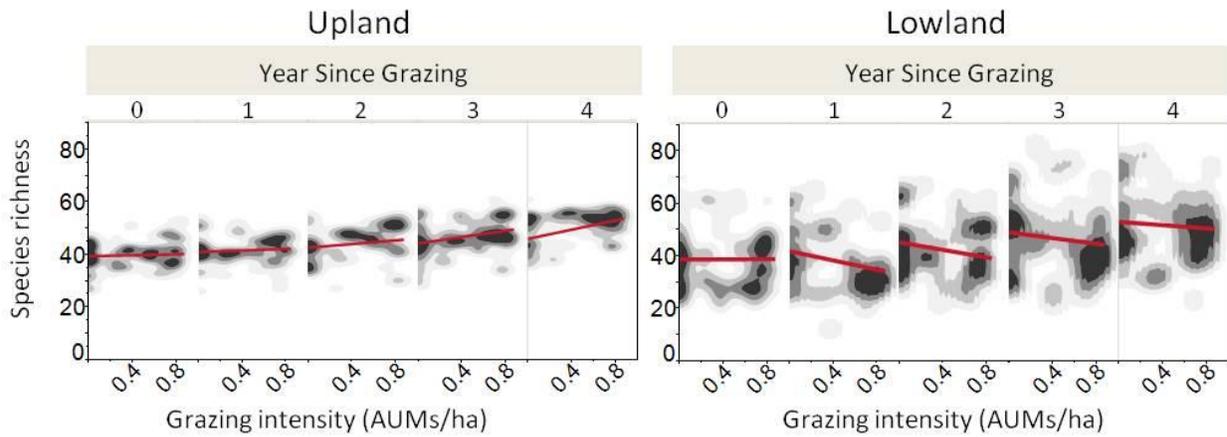


Figure 10. Species richness in response to grazing intensity in upland and lowland plots based on best AIC models for data collected from 2006-2011 in Grasslands National Park, Saskatchewan, Canada.

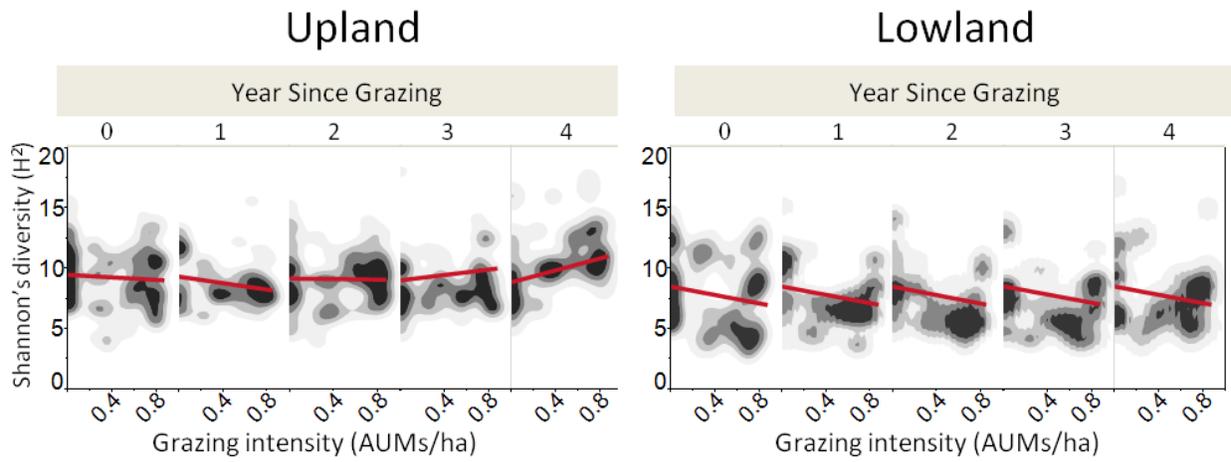


Figure 11. Shannon's diversity index in response to grazing intensity in upland and lowland plots based on best AIC models for data collected from 2006-2011 in Grasslands National Park, Saskatchewan, Canada.

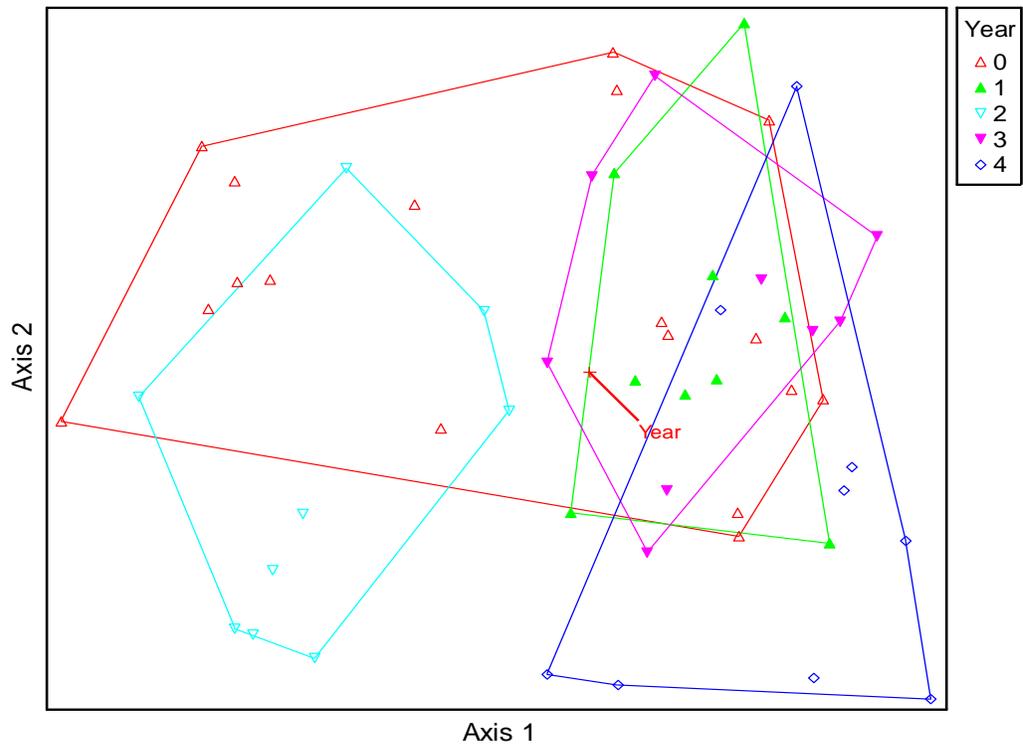


Figure 12. Non-metric multidimensional biplot depicting the change in plant species relative cover with year at the larger pasture scale in upland treatment pastures in Grasslands National Park, Saskatchewan, Canada. “Year” indicates the number of years since grazing commenced, “0” the pre-grazing data, and “1-4” the number of years of grazing.

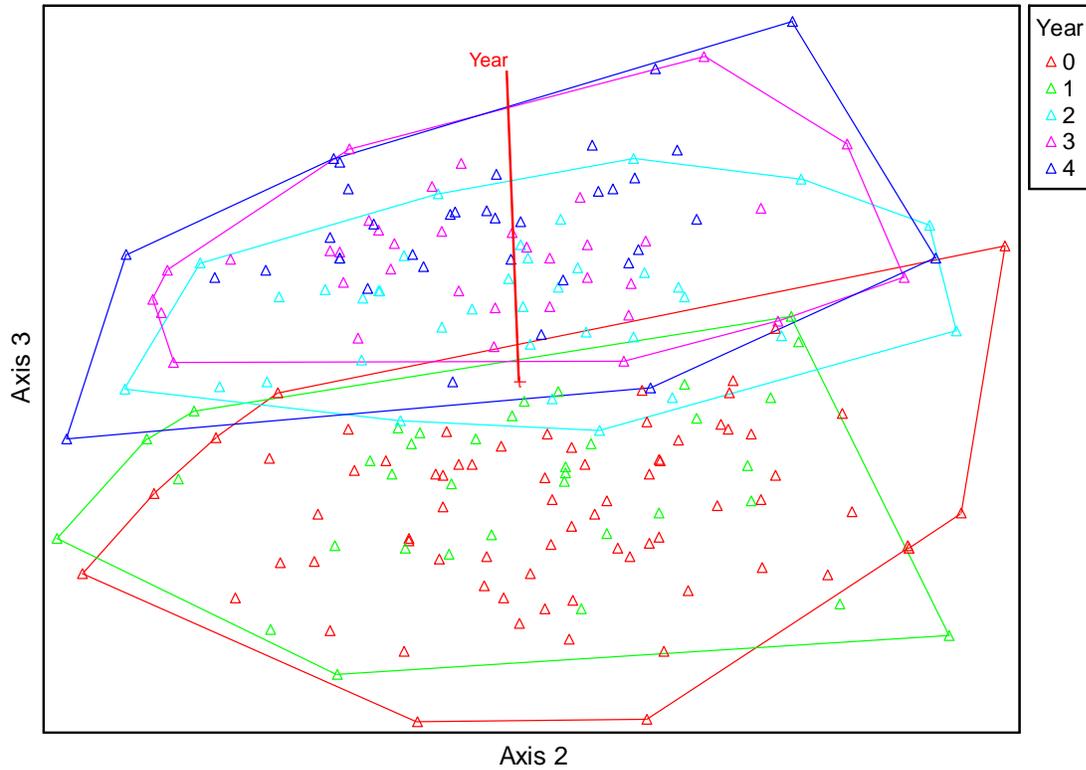


Figure 13. Non-metric multidimensional biplot depicting the change in plant species occurrence among years at the pasture scale in upland treatment pastures in Grasslands National Park, Saskatchewan, Canada. “Year” indicates the number of years since grazing commenced, “0” the pre-grazing data, and “1-4” the number of years of grazing.

3.4 Discussion

3.4.1 Habitat structure

Grazing intensity influenced many habitat structure variables, and these effects increased over time, suggesting that livestock grazing had a cumulative effect in the first few years following its introduction to this landscape. Few other manipulative grazing studies have been designed to describe these cumulative changes in habitat structure. In upland habitats, the amount of bare ground increased over time in the most intensely grazed pastures. Although this trend has been reported in other studies (Manley et al. 1997, Bai et al. 2001), our results show that the increase in bare ground cover is a gradual process. Bare ground cover has been reported to decrease with light grazing over time (Hart et al. 1988, Manley et al. 1997), suggesting that this trend may be reversible if the stocking rate is reduced. Biondini et al. (1998) found no evidence of cumulative effects of grazing on plant species biomass and composition after eight years of grazing. In contrast, Manley et al. (1997) reported a steady increase in cool-season (C_3) graminoid cover over a ten-year period under high grazing intensities. However, it is possible that effects of grazing may increase further after a longer grazing duration, stressing the importance of long-term studies. Contrary to the above trends, some habitat structure variables, such as litter depth, did not exhibit much change beyond a single year of grazing, demonstrating that some elements of habitat structure are more sensitive to grazing duration than others.

The change in forb cover over time is consistent with trends reported in other studies. Manley et al. (1997) reported a decrease in total plant cover after two years of grazing on a study site that was previously ungrazed. The initial decrease seen in forb cover under high grazing intensity in the present study may be due to the loss of cover of grazing-intolerant forb species. My results suggest that as grazing continued, the reduction in grazing-intolerant plants may have

given grazing-tolerant species an opportunity to colonize the area or to increase in abundance, thus allowing for a subsequent increase in forb cover (Milchunas et al. 1988, Cingolani et al. 2005).

The importance of collecting data prior to beginning any experiment (Underwood 1994) is demonstrated by the fact that some variables, such as C₄ grass and litter depth in upland plots, had spurious pre-existing trends on the landscape before grazing was introduced. In upland plots, the increase in C₄ grasses with increasing grazing intensity in subsequent years may be a residual effect from the patchy distribution of species prior to the introduction of grazing. The decrease in C₄ cover at the highest stocking rates over time suggests a reversal of this trend, but without the pre-grazing data, this trend may have been overlooked (Fig. 3).

Natural yearly variation had a large effect on habitat structure variables. Grass, litter and *S. densa* cover, for example, increased over time in upland control pastures, despite experiencing no change in their grazing regimes over time. However, despite this annual variation, grass and litter cover clearly decreased with increasing grazing intensity, suggesting that grazing caused significant structural changes to the vegetation. This differs from other studies that concluded that annual variation had the largest impact on the landscape, with a minor role attributed to grazing (Biondini et al. 1998, Vermeire et al. 2008).

While *S. densa* cover increased in control plots over time, it also increased with increasing grazing intensity, indicating that grazing did induce these changes. The increase in control plots may be due to observer bias as *S. densa*, when desiccated, can appear to be dead. Despite efforts to ensure data collection was consistent across years, data collection protocols may have changed over the years to include *S. densa* that appeared to be dead when assessing cover due to ambiguity in the protocols. It is also likely that as litter cover decreased in both

ungrazed control and grazed pastures, *S. densa* was uncovered when it was previously obscured by the litter. The decrease in litter cover in upland control pastures is a trend that is difficult to explain. Since the plots were permanent plots that were returned to year after year, it is possible that repeated annual visits to the plots resulted in compaction of the vegetation.

My results show that vegetation and structure in upland and lowland plots respond differently to grazing intensity. In particular, the opposite trend in species richness in response to grazing intensities in uplands compared with lowland sites was an unexpected result. Litter cover, grass cover, *S. densa* cover and Shannon's diversity all exhibited a smaller magnitude of change in response to grazing in lowland plots compared to upland plots. It has long been recognized that livestock use lowland areas disproportionately compared to upland areas, and it has thus been suggested that upland and lowland areas be considered as separate management units (Kauffman and Krueger 1984). However, there is a paucity of information regarding the impacts of the same management practices in upland and lowland habitats. I was also not able to find any studies that assessed the effects of grazing in lowland areas in ecosystems that were predominantly grassland, and therefore the closest comparison of these habitats in the literature is riparian areas. There are many studies that assess the effects of grazing on riparian areas in montane areas (e.g. Popolizio et al. 1994, Green and Kauffman 1995, Lucas et al. 2004), but none of these compare the effects of grazing in upland areas.

3.4.2 Structural heterogeneity

Contrary to my predictions, heterogeneity was not maximized with moderate grazing. These results are not consistent with theoretical predictions that heterogeneity on grazed pastures is higher than ungrazed pastures due to the patches created by the selectivity of cattle (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2012). In my study, interestingly, heterogeneity

was highest before grazing was even introduced for C₄ grass cover, litter depth, and bare cover in lowlands. This suggests that all grazing reduced heterogeneity of litter depth and bare ground cover in lowland areas, in contrast to results of previous research (Fuhlendorf and Smeins 1999). In my study area, lowland areas are naturally more heterogeneous than upland areas, as there are distinct micro-habitats, such as mud-flat areas, and areas that cross stream banks. In particular, the presence or absence of a mud-flat within a plot would likely affect the presence of litter depth and bare ground cover. Responses to grazing of heterogeneity of bare ground cover, C₄ grasses and *S. densa* in upland habitats were also surprising and contradicted previous research conducted in Texas (Fuhlendorf and Smeins 1999), as heterogeneity was maximized at the highest grazing intensities. This demonstrates that effects of grazing may vary regionally and that management strategies to promote biodiversity must be site specific.

My results are consistent with the theory that heterogeneity at the landscape scale is maximized by the use a variety of grazing intensities (Hart 2001, Fuhlendorf and Engle 2001, Fuhlendorf et al. 2012). However, my results also demonstrate that different structural and compositional elements varied in their response to both grazing intensity and duration. Vegetation structure tended to respond strongly and cumulatively to grazing intensity and duration. Compositional diversity showed a smaller immediate response to introduction of grazing to this landscape, which increased with grazing duration and may presumably continue to increase with more years of grazing. It is clear that no one single grazing intensity will meet the habitat needs of all prairie wildlife.

3.4.3 Plant diversity

In contrast to my prediction that richness would be maximized at moderate grazing intensities, my results suggest that richness in upland plots was maximised at high grazing

intensities, and that this effect may increase with grazing duration beyond 4 years, consistent with a previous study in a northern mixed-grass prairie (Bai et al. 2001). Conversely, Hart (2001) found that species richness was lowest in lightly grazed pastures, compared to ungrazed and heavy grazed pastures in the short-grass steppe. Interestingly, Willms et al. (2002) detected no differences in species richness in grazed compared to ungrazed pastures in another northern dry mixed-grass prairie. As summarized by Symstad and Jonas (2011), few other grazing studies in mixed-grass prairie evaluated effects on species richness. The increase in species richness with increasing stocking rate may be caused by the availability of newly defoliated areas, within which there is a decrease in competition for soil and light resources, for new species to colonize (Olf and Ritchie 1998). It is likely that the increase in richness is being driven by an overlap in grazing-intolerant and grazing-resistant species (Cingolani et al. 2005). It is possible that the grazing-tolerant plants have not had sufficient duration of grazing to increase in cover and become better competitors than the grazing-intolerant species, which would lead to the local extirpation of the grazing-intolerant species. However, I caution that it is also possible that the actual grazing intensity was lower than intended in upland habitats, even in the pastures with the highest stocking rates. Unusually high precipitation levels in 2010 may have increased biomass production such that cattle removed much less than 70% of the biomass produced annually. This would imply that the highest stocking rate in the study may be comparable to moderate stocking rates in other studies, and we cannot predict what the effects of higher stocking rates on species richness.

Since the mixed-grass prairie falls in between the moisture/biomass production of the tall-grass and short-grass prairies, it is not clear which theories would directly relate to our study area. Our species richness results are more consistent with theories proposed to explain tall-grass

prairie responses to grazing pressure, rather than short-grass prairie responses (Milchunas et al. 1988). This supports the few studies in upland mixed-grass prairies that have reported that grazing does not negatively affect overall species richness (Symstad and Jonas 2011).

Negative effects of grazing intensity on species diversity in lowland habitats were inconsistent both with our results in upland habitats, and with the literature. A review of the effects of cattle grazing in riparian areas, mostly in montane areas, found that species richness was higher in grazed than ungrazed areas, in some instances due to increased forb cover (Kauffman and Krueger 1984). In montane areas, studies have also shown that riparian species richness and diversity increases with light or moderate grazing compared to ungrazed areas (Popolizio et al. 1994, Green and Kauffman 1995, Lucas et al. 2004). The decrease in richness with higher stocking rates is perhaps due to some lowland plants being less well adapted to grazing than upland plants, which could lead to a higher proportion of grazing-intolerant plants disappearing at high grazing intensities. This would be somewhat consistent with the hypothesis of Cingolani et al. (2005), in that there are different suites of grazing-tolerant and grazing-intolerant plant species. If plants that evolved with drought stress are more adapted to grazing stress because the mechanisms of stress avoidance are the same (Coughenour 1985, Milchunas et al. 1988), then plant communities in riparian areas might be less adapted to grazing. Another possible explanation for the difference in effects of grazing in lowland and upland habitats may be that since cattle spend more time in riparian areas, (Kauffman and Krueger 1984) the grazing intensity in lowlands was actually higher than in the upland habitats. Conversely, it has been reported that grazing can induce a decrease in species richness in areas with nutrient-poor soils (Proulx and Mazumder 1998). If the soils in lowland habitats are nutrient-poor, new plant species may be resource-limited and thus unable to germinate, possibly leading to a decrease in species

richness (Proulx and Mazumder 1998). The trend of decreasing species richness with increasing grazing intensity in lowland plots is not one that is easily explained.

Effects of grazing intensity on upland species diversity is similar to the effects we detected on forb cover, and it is likely that the change in forb cover drove this change in diversity. Bai et al. (2001) also detected a positive correlation between Shannon's diversity index and forb cover, consistent with this interpretation. Hart (2001) reported that plant diversity in short-grass steppe was maximized under light and moderate grazing after 55 years of grazing. Perhaps after a period of prolonged grazing, species diversity would be maximized under moderate grazing.

3.4.4 Plant species composition

3.4.4.1 Plant species relative cover

Effects of grazing - After four years of grazing, small differences in plant relative cover were detected among grazing intensities in upland plots. This suggests that plant species respond differently to different grazing intensities, after only a few years of grazing. After six years of grazing, Hart et al. (1988) found no significant difference in relative cover of any plant species or guild at any grazing intensity in a Wyoming mixed-grass prairie. However, as a continuation of the same long-term study, Manley et al. (1997) found that forb cover increased under heavy grazing, suggesting that plant species community changes may take longer than four years to appear. If plant relative cover in my study site continues to change in the future, this effect would be consistent with theory proposed by Cingolani et al. (2005) for semi-arid grasslands. This change in relative cover may be due to the decrease in plant species that are better competitors for soil resources, and an increase in plant species that are less successful competitors but that can withstand grazing (Cingolani et al. 2005).

Conversely, in lowland plots after four years of grazing, the different grazing treatments did not induce clear changes in species occurrence. This is somewhat surprising, since overall species richness decreased as grazing intensity increased. A possible explanation may be that plant species that disappeared in lowland plots were rare species that contributed little to overall plant cover, and therefore their disappearance had few strong ecological consequences. The results of my study are contrary to that observed by Jackson and Allan-Diaz (2006) in which plant communities along a stream-fed creek in an oak-savanna grassland, where plant communities under no, light, and moderate grazing developed into three distinct communities over time. However, the differences seen among the different communities may have been driven by natural variability due to a moisture gradient (Jackson and Allan-Diaz 2006).

Effects of year - Since species relative cover changed in ungrazed upland plots over time, no changes in species relative cover can be attributed to grazing.

3.4.4.2 *Plant species occurrence*

Effects of grazing - In upland plots, the Mantel test results suggest that species occurrence was inherently different among treatment sites before grazing was introduced. The very low rM values indicate that the differences among treatments were small, and these small differences may have been insufficient to be detected by NMS.

While the Mantel test results and NMS results at the plot scale show that no changes in species occurrence were detected in lowlands at the smaller plot scale, small changes were detected at the larger pasture scale. This may, however, simply be a reflection of inherent differences among pastures, as combining the plot scale data masks inter-plot environmental variability (Fuhlendorf and Smeins 1996).

Effects of year - The change in plant occurrence across time cannot be attributed to grazing, as control plots also varied, consistent with results of some other studies (Biondini and Manske 1996). The large effect of year may be driven by the fact that the majority of this study was conducted during a wet cycle, where precipitation far exceeded normal values. The effects of high stocking rates may have been mitigated with the additional moisture (Biondini et al. 1998, Gillen et al. 2000). High grazing intensities may be sustainable during a wet cycle, but this may not be true in drier years.

3.5 Conclusion

There is no one grazing intensity that would maximize all biological components that contribute to ecosystem heterogeneity, either within or among pastures. Thus, the grazing prescriptions must be designed to address specific management goals. For example, grassland songbirds such as the Sprague's pipit and chestnut collared longspur are both species at risk (Government of Canada 2012) but have different habitat requirements, and a stocking rate that would benefit one species could be detrimental to the other (Fuhlendorf and Engle 2001). Heterogeneity of litter depth and cover may play a particularly important role in affecting habitat suitability for wildlife, as litter can affect soil moisture (Deutsch et al. 2009), invertebrate communities (Eschen et al. 2012), and nest site selection of grassland birds (Davis 2004).

Natural temporal and spatial variation are very important in mitigating or enhancing effects of grazing intensity (Biondini and Manske 1996, Biondini et al. 1998, Vermeire et al. 2008). In my study, inherent natural variation among study treatments, despite initial careful selection of similar sites for the study, was apparent in plant communities. However, since data were collected before the grazing treatments started, these pre-existing trends were recognized so I was able to determine which trends with grazing intensity were spurious. Without this

information, I may have made incorrect conclusions about grazing. The natural yearly variation was also apparent in many instances and while this is a factor that cannot be predicted, management plans must be adapted accordingly.

My results also show that grazing can have cumulative effects; because of this, frequent (i.e. annual) monitoring is necessary, as effects seen in one year may increase over time, or have an opposite effect in subsequent years (e.g. forb cover). This also emphasizes the importance of long-term grazing studies (Hart et al. 1988, Manley et al. 1997, Derner and Hart 2007). The four years of grazing is only a very short period of time of a process that helped shape the Great Plains over millennia. My study also took place during a wet cycle, and effects of grazing might be different under drier conditions.

There is a substantial gap in the literature that has prevented us from understanding the effects of different grazing intensities in lowland grassland areas. It has long been known that since cattle spend a disproportionate amount of time in riparian areas, these habitats can become degraded (Kauffman and Krueger 1984). My results indicate that upland and lowland habitats sometimes did not respond similarly to grazing intensity. This demonstrates the need to manage the habitats differently, perhaps by fencing off lowland areas, or at the least be aware that the effects of grazing may differ between habitats. Many pastures include both of these broad habitat types, and it is therefore perhaps important to consider these two habitats types as separate management units (Kauffman and Krueger 1985). Since so little focus has been how upland and lowland habitats respond differently to grazing and grazing intensities, and because many managed rangelands likely have both habitat types present, future studies should make an effort to incorporate both habitats into the study design.

3.6 Management Implications

Grasslands National Park – For a conservation plan that provides suitable habitat for all grassland species including species at risk, a gradient of grazing intensities, including either ungrazed or very lightly grazed areas, and heavily grazed areas (ensuring no rangeland degradation) should be used across the landscape concurrently (see also Fuhlendorf et al. 2012). The range of intensities that can be used will depend on the size of the area intended to be grazed as well as the fencing that is already on the landscape. The results of this study did not assess the optimal number of intensities to be used, but as long as some areas are both lightly grazed and highly grazed, it will complement private ranching in the surrounding landscape, as these are often stocked at moderate intensities.

Natural variation must be taken into account when developing management plans. For instance, as moisture increases or decreases within a year, grazing intensities change. During wet years, stocking rates can afford to be higher than in dry years. However, care must be taken that high stocking rates do not become severe and thus degrade rangelands, particularly in dry years. This also emphasizes the importance of regular monitoring efforts. In dry years, monitoring may be necessary on a bi-weekly to monthly basis to ensure that rangelands are not being degraded with the prescribed stocking rates. Nonetheless, effects of grazing intensity on vegetation structure and plant communities can exceed some effects of environmental variability as depicted by grass and litter cover in upland plots that increased with increasing grazing intensity even though yearly variation was also influencing cover in ungrazed control plots.

It may not be feasible to separate upland and lowland areas by fences, and therefore treating these habitats as separate management units may not be possible. Since upland and lowland areas seem to respond differently to grazing, it is important to monitor both areas, especially lowland areas to ensure that the stream banks do not become eroded.

Private ranchers – Even if conservation and ranching have divergent objectives, it is perhaps possible to come to a common understanding regarding conservation. For private ranchers, economics is undoubtedly and understandably an important factor regarding the stocking rate that is used on private land. Since higher stocking rates may lead to less cattle gains (Manley et al. 1997), it is important to stress that any variation in the grazing intensity will open up different habitat patches, and therefore any concurrent use of any number of different grazing intensities is better than a single intensity. Manley et al. (1997) suggest that temporary (i.e. one grazing season) high stocking rates when cattle prices are good should not negatively impact rangelands, but stocking rates sustained at high levels may be detrimental.

Conservation Agencies – While this study contributes to the understanding of the importance of grazing for heterogeneity and conservation, most importantly we must ensure that our native grasslands remain native grasslands. It is pertinent to define the relevance and importance of cattle grazing. Most rangelands are considered to be “marginal lands,” as they were unable to be cultivated, mostly due to undesirable soil conditions (Herrick et al. 2012). These lands are increasingly coming under pressure to be converted to cropland due to improved technologies and increasingly attractive crop prices (Herrick et al. 2012). On private lands, as long as rangelands that support cattle production can be at least as profitable as crop production, this discourages the conversion of native rangeland to cultivated land (Rashford et al. 2011). Policies must be developed that makes ranching and cattle production more profitable than plowing up marginal land. As long as cattle are grazing native prairie, whether in protected areas or on private ranches, that is land that can provide habitat to grassland species. In effect, simply grazing is contributing to grassland species conservation.

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APPENDIX A.

Plant species name, number of plots in which they were observed and life form of plants identified in the experimental plots of the Biodiversity And Grazing Management Area in the East Block of Grasslands National Park from 2006-2011.

Species name	# of plots (out of a possible 539)	Life- form
<i>Achillea millefolium</i>	485	Forb
<i>Agoseris glauca</i>	205	Forb
<i>Agropyron cristatum</i>	25	Grass
<i>Agropyron repens</i>	1	Grass
<i>Agrostis scabra</i>	48	Forb
<i>Alisma plantago-aquatica</i>	1	Forb
<i>Allium textile</i>	225	Forb
<i>Alopecurus aequalis</i>	13	Grass
<i>Androsace septentrionalis</i>	216	Forb
<i>Antennaria</i> spp.	348	Forb
<i>Arabis divaricarpa/holboellii</i>	289	Forb
<i>Arabis hirsuta</i>	68	Forb
<i>Argentina anserina</i>	23	Forb
<i>Arnica fulgens</i>	109	Forb
<i>Artemisia campestris</i>	5	Forb
<i>Artemisia cana</i>	518	Shrub
<i>Artemisia frigida</i>	531	Forb
<i>Artemisia ludoviciana</i>	183	Forb
<i>Asclepias speciosa</i>	3	Forb
<i>Astragalus agrestis</i>	207	Forb
<i>Astragalus bisulcatus</i>	42	Forb
<i>Astragalus crassicaarpus</i>	80	Forb
<i>Astragalus drummondii</i>	1	Forb
<i>Astragalus flexuosus</i>	44	Forb
<i>Astragalus gilviflorus</i>	40	Forb
<i>Astragalus laxmanii</i>	118	Forb
<i>Astragalus lotiflorus</i>	42	Forb
<i>Astragalus missouriensis</i>	9	Forb
<i>Astragalus pectinatus</i>	235	Forb
<i>Astragalus purshii</i>	14	Forb
<i>Atriplex nuttallii</i>	235	Shrub
<i>Atriplex prostrata</i>	29	Forb
<i>Beckmannia syzigachne</i>	17	Grass

<i>Bouteloua gracilis</i>	494	Grass
<i>Bromus inermis</i>	5	Grass
<i>Calamagrostis inexpansa/stricta</i>	24	Grass
<i>Calamagrostis montanensis</i>	410	Grass
<i>Campanula rotundifolia</i>	4	Forb
<i>Carex aquatilis</i>	13	Other
<i>Carex diurscula</i>	517	Other
<i>Carex filifolia</i>	282	Other
<i>Carex obtusata</i>	1	Other
<i>Carex pensylvanica</i>	279	Other
<i>Carex praegracilis</i>	8	Other
<i>Carex praticola</i>	19	Other
<i>Carex rostrata</i>	2	Other
<i>Carex sprengei</i>	1	Other
<i>Cerastium arvense</i>	99	Forb
<i>Chamaerhodos nuttallii</i>	29	Forb
<i>Chenopodium album</i>	108	Forb
<i>Chenopodium capitatum</i>	9	Forb
<i>Chenopodium pratericola</i>	120	Forb
<i>Chenopodium rubrum</i>	9	Forb
<i>Cicuta maculata</i>	14	Forb
<i>Cirsium drummondii</i>	5	Forb
<i>Cirsium flodmannii</i>	165	Forb
<i>Collomia linearis</i>	140	Forb
<i>Comandra pallida</i>	121	Forb
<i>Conyza canadensis</i>	66	Forb
<i>Coreopsis tinctoria</i>	6	Forb
<i>Crepis tectorum</i>	209	Forb
<i>Cryptantha celosiodes</i>	28	Forb
<i>Cymopterus acaulis</i>	6	Forb
<i>Dalea candida</i>	29	Forb
<i>Dalea purpurea</i>	72	Forb
<i>Danthonia unispicata</i>	8	Grass
<i>Deschampsia caespitosa</i>	20	Grass
<i>Descurainia sophia</i>	70	Forb
<i>Distichlis spicata</i>	165	Grass
<i>Draba nemorosa</i>	183	Forb
<i>Eleocharis acicularis</i>	19	Other
<i>Eleocharis palustris</i>	29	Other
<i>Elymus canadensis</i>	20	Grass
<i>Elymus lanceolatus</i>	534	Grass

<i>Elymus trachycaulus</i>	143	Grass
<i>Epilobium brachycarpum</i>	2	Forb
<i>Epilobium ciliatum</i>	5	Forb
<i>Equisetum arvense</i>	22	Other
<i>Equisetum hyemale</i>	21	Other
<i>Ericameria nauseosa</i>	181	Shrub
<i>Erigeron asper</i>	15	Forb
<i>Erigeron caespitosus</i>	97	Forb
<i>Erigeron compositus</i>	4	Forb
<i>Erigeron pumilus</i>	33	Forb
<i>Eriogonum flavum</i>	18	Forb
<i>Eriogonum pauciflorum</i>	17	Forb
<i>Eriogonum umbellatum</i>	5	Forb
<i>Erysimum inconspicuum</i>	347	Forb
<i>Escobaria vivipara</i>	137	Shrub
<i>Euphorbia serpyllifolia</i>	1	Forb
<i>Gaillardia aristata</i>	220	Forb
<i>Galium boreale</i>	29	Forb
<i>Gaura coccinea</i>	153	Forb
<i>Gentiana affinis</i>	12	Forb
<i>Geum macrophyllum</i>	3	Forb
<i>Geum triflorum</i>	200	Forb
<i>Glaux maritima</i>	42	Forb
<i>Glyceria grandis</i>	7	Grass
<i>Glycyrrhiza lepidota</i>	129	Forb
<i>Gnaphalium palustre</i>	52	Forb
<i>Grindelia squarrosa</i>	172	Forb
<i>Gutierrezia sarothrae</i>	310	Shrub
<i>Haplopappus lanceolatus</i>	15	Forb
<i>Hedeoma hispida</i>	141	Forb
<i>Helianthus annuus</i>	4	Forb
<i>Helianthus nuttallii</i>	18	Forb
<i>Helictrotrichon hookeri</i>	1	Forb
<i>Hesperostipa comata</i>	457	Grass
<i>Hesperostipa curtiseta</i>	267	Grass
<i>Heterotheca villosa</i>	322	Forb
<i>Heuchera richardsonii</i>	6	Forb
<i>Hordeum jubatum</i>	59	Grass
<i>Hymenopappus filifolius</i>	6	Forb
<i>Hymenoxys richardsonis</i>	175	Forb
<i>Juncus alpinoarticulatus</i>	2	Other

<i>Juncus balticus</i>	48	Other
<i>Kochia scoparia</i>	2	Forb
<i>Koeleria macrantha</i>	495	Grass
<i>Krascheninnikovia lanata</i>	42	Shrub
<i>Lactuca tatarica</i>	29	Forb
<i>Lappula echinata/occidentalis</i>	68	Forb
<i>Lepidium densiflorum</i>	133	Forb
<i>Lesquerella arenosa</i>	14	Forb
<i>Liatris punctata</i>	70	Forb
<i>Linum lewisii</i>	83	Forb
<i>Linum rigidum</i>	129	Forb
<i>Lithospermum incisum</i>	66	Forb
<i>Lomatium macrocarpum</i>	16	Forb
<i>Lycopus asper</i>	17	Forb
<i>Lygodesmia juncea</i>	55	Forb
<i>Machaeranthera canescens</i>	71	Forb
<i>Machaeranthera grindeloides</i>	15	Forb
<i>Machaeranthera pinnatifida</i>	184	Forb
<i>Medicago sativa</i>	7	Forb
<i>Melilotus officinale</i>	5	Forb
<i>Mentha arvensis</i>	18	Forb
<i>Mertensia lanceolata</i>	75	Forb
<i>Minuartia stricta</i>	2	Forb
<i>Mirabilis hirsuta</i>	10	Forb
<i>Monolepis nuttalliana</i>	19	Forb
<i>Muhlenbergia cuspidata</i>	91	Grass
<i>Muhlenbergia richardsonis</i>	60	Grass
<i>Musineon divaricatum</i>	40	Forb
<i>Myosurus minima</i>	9	Forb
<i>Nasella viridula</i>	218	Grass
<i>Navarretia minima</i>	6	Grass
<i>Oenothera caespitosa</i>	19	Forb
<i>Oenothera nuttallii</i>	2	Forb
<i>Oligoneuron rigidum</i>	128	Forb
<i>Opuntia fragilis</i>	174	Shrub
<i>Opuntia polyacantha</i>	314	Shrub
<i>Orobanche fasciculata</i>	27	Forb
<i>Orthocarpus luteus</i>	53	Forb
<i>Oxalis stricta</i>	1	Forb
<i>Oxytropis sericea</i>	73	Forb
<i>Oxytropis splendens</i>	1	Forb

<i>Packera cana</i>	167	Forb
<i>Parietaria pensylvanica</i>	13	Forb
<i>Paronychia sessiflora</i>	18	Forb
<i>Pascopyrum smithii</i>	512	Grass
<i>Pediomelum agrophyllum</i>	362	Forb
<i>Pediomelum esculentum</i>	4	Forb
<i>Penstemon albidus</i>	200	Forb
<i>Penstemon gracilis</i>	39	Forb
<i>Penstemon nitidus</i>	9	Forb
<i>Penstemon procerus</i>	48	Forb
<i>Phalaris arundinaceae</i>	1	Grass
<i>Phlox hoodii</i>	361	Forb
<i>Physaria didymocarpa</i>	1	Forb
<i>Plantago elongata</i>	134	Forb
<i>Plantago eriopoda</i>	28	Forb
<i>Plantago major</i>	2	Forb
<i>Plantago patagonica</i>	105	Forb
<i>Poa compressa/pratensis</i>	101	Grass
<i>Poa palustris</i>	28	Grass
<i>Poa secunda</i>	406	Grass
<i>Polygonum amphibium</i>	9	Forb
<i>Polygonum aviculare</i>	69	Forb
<i>Polygonum convolvulus</i>	9	Forb
<i>Potentilla arguta</i>	23	Forb
<i>Potentilla concinna</i>	46	Forb
<i>Potentilla gracilis</i>	22	Forb
<i>Potentilla hippiana</i>	96	Forb
<i>Potentilla pensylvanica</i>	324	Forb
<i>Puccinellia nuttalliana</i>	121	Grass
<i>Pulsatilla patens</i>	283	Forb
<i>Ranunculus cymbalaria</i>	8	Forb
<i>Ranunculus macounii</i>	2	Forb
<i>Ranunculus rhomboides</i>	19	Forb
<i>Ratibida columnifera</i>	342	Forb
<i>Ribes oxyacanthoides</i>	5	Shrub
<i>Rosa acicularis</i>	44	Shrub
<i>Rosa arkansana</i>	90	Shrub
<i>Rosa woodsii</i>	21	Shrub
<i>Rumex crispus</i>	20	Forb
<i>Rumex occidentalis</i>	45	Forb
<i>Sagittaria cuneata</i>	15	Forb

<i>Salicornia rubra</i>	14	Forb
<i>Salix exigua</i>	7	Shrub
<i>Sarcobatus vermiculatus</i>	134	Shrub
<i>Schedonnardus paniculatus</i>	19	Grass
<i>Schoenoplectus americanus</i>	14	Other
<i>Schoenoplectus pungens</i>	22	Other
<i>Schyzachyrium scoparium</i>	25	Grass
<i>Senecio integerrimus</i>	59	Forb
<i>Silene pratensis</i>	69	Forb
<i>Sisyrinchium montanum</i>	6	Forb
<i>Smilacina stellata</i>	11	Forb
<i>Solanum triflorum</i>	22	Forb
<i>Solidago canadensis</i>	11	Forb
<i>Solidago missouriensis</i>	371	Forb
<i>Solidago mollis</i>	182	Forb
<i>Solidago simplex</i>	2	Forb
<i>Sonchus arvensis</i>	18	Forb
<i>Spartina gracilis</i>	16	Grass
<i>Sphaeralcea coccinea</i>	449	Forb
<i>Stachys palustris</i>	1	Forb
<i>Stellaria longifolia</i>	1	Forb
<i>Suaeda maritima</i>	16	Forb
<i>Symphoricarpos occidentalis</i>	260	Shrub
<i>Symphyotrichum ciliolatum</i>	1	Forb
<i>Symphyotrichum ericoides/falcatum</i>	175	Forb
<i>Symphyotrichum laeve</i>	22	Forb
<i>Symphyotrichum lanceolatum</i>	26	Forb
<i>Taraxacum officinale</i>	447	Forb
<i>Thalictrum venulosum</i>	11	Forb
<i>Thermopsis rhombifolia</i>	168	Forb
<i>Thlaspi arvense</i>	2	Forb
<i>Townsendia nuttallii</i>	27	Forb
<i>Toxicodendron radicans</i>	1	Forb
<i>Tragopogon dubius</i>	433	Forb
<i>Triglochin maritima</i>	18	Forb
<i>Triglochin palustris</i>	2	Forb
Unknown 08-01	3	Forb
Unknown 09-01	14	Forb
Unknown 09-02	10	Other
Unknown 09-03	1	Other
Unknown 09-06	2	Forb

Unknown 10-01	1	Forb
Unknown 10-03	3	Forb
Unknown 10-05	1	Forb
Unknown 11-01	1	Forb
Unknown 11-04	1	Forb
Unknown 11-05	1	Forb
Unknown 11-09	2	Forb
<i>Urtica dioica</i>	2	Forb
<i>Verbascum thapsus</i>	1	Forb
<i>Veronica peregrina</i>	59	Forb
<i>Vicia americana</i>	262	Forb
<i>Viola adunca</i>	26	Forb
<i>Viola canadensis</i>	4	Forb
<i>Viola nuttallii</i>	63	Forb
<i>Xanthium strumarium</i>	4	Forb
<i>Zizia aptera</i>	6	Forb
<i>Zygadenus gramineus</i>	63	Forb

*"Other" life forms include sedges, rushes and horsetails.