Pyric herbivory in the northern mixed grass prairie: testing the use of fire as a land and livestock management tool on rangelands in Saskatchewan

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Abstract

The plant communities of the Great Plains of North America evolved with fire and grazing by bison. With the arrival of Europeans settlers, bison herds were hunted to near extinction, fires were suppressed, and the natural disturbance processes occurring on the prairies were altered. Cattle are now the main source of grazing disturbance on native prairie. Cattle and bison cause different impacts on grasslands and grassland community structure, due to differences in management practices, foraging preferences, and social behaviours. Fire is a natural disturbance which creates a landscape that is variable in vegetation structure, composition, and biomass. Both cattle and bison seek out recently burnt areas, leaving other areas on the landscape to recover from previous grazing. The attraction to burnt areas further promotes a heterogeneous landscape that varies in maturity, structure, and composition. Heterogenous landscapes are important to maintaining an environment that provides habitats to many at-risk grassland species. While the use of prescribed fire as a livestock and land management tool has been study extensively in the in the prairie ecosystems of the United States, few studies have examined the interaction of fire and grazing animals (i.e., pyric herbivory) in the northern mixed grass prairies in Canada. In this study, I examined the short-term effects of two spring prescribed fires on plant community structure in native prairie and tame forage pastures in the northern mixed grass prairie region. I also examined the influence of prescribed fire on cattle movement within these pastures by tracking their movements in the grazing season preceding and following the burns. Prescribed fire reduced total plant and litter biomass, however there were strong climatic influences on vegetation with significant season and annual changes in biomass. Burning homogenized vegetation composition in both pastures in the growing season following the prescribed fires. Finally, I saw a significant increase in cattle visitation to the recently burned areas within the pastures. Pyric herbivory in the northern mixed grass prairies of Canada appears to be a worthwhile land and livestock management tool to promote grassland conservation while maintaining a viable livestock operation.

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List of Abbreviations

ADF	acid detergent fibre
ANOVA	analysis of variance
AUM	animal unit month
e.g.	for example
GPS	Global Positioning System
GNP	Grasslands National Park
ha	hectares
I.D.	identification
i.e.	that is
ISA	indicator species analysis
km	kilometres
km/h	kilometres per hour
mm	millimetres
m^2	square metre
NDF	neutral detergent fibre
NMDS	non-metric multidimensional scaling
N8	native prairie pasture in this study
OMB	Old Man on His Back Heritage and Conservation Area
PERMANOVA	permutational multivariate analysis of variance
QGIS	Quantum Geographical Information System
SK	Saskatchewan
S5	tame forage pasture in this study
UHF	ultra high frequency
U.S.A.	United States of America
VHF	very high frequency
%	percent
°C	degrees Celsius

1.0 Introduction

1.1 General Introduction

The grasslands of the Great Plains of North America are threatened by a significant decline in biodiversity. The Great Plains are one of the most vulnerable ecosystems in the world due to rapid settlement and subsequent conversion to agricultural land within the past 200 years (Henwood, 2010; Hoekstra et al., 2005; Lark et al., 2019; Samson et al, 2004). Remaining tracts of grasslands provide critical habitat for wildlife species, many of which have experienced great declines in population and are now considered vulnerable or at-risk of extinction (Federal, Provincial, and Territorial Governments of Canada, 2010). Grasslands perform numerous ecological functions including, carbon storage, erosion control, water storage, and nutrient cycling (Samson et al., 2004; Samson and Knopf, 1994). In addition to the ecological services performed by grasslands, they are economically important as rangeland for grazing livestock (Carlyle, 2019; McDonald et al., 2019). Approximately 70% of the Great Plains have been converted to other land uses, and in remaining grassland habitat threats are ongoing and include habitat fragmentation, oil and gas development, continued conversion to agricultural land, invasion by exotic species, overgrazing, and the loss of natural fire cycles (Askins et al., 2007; Environment and Climate Change Canada, 2017; Fuhlendorf et al., 2006; Roch and Jaeger, 2014; Samson et al., 2004). Protecting the ecological and economic function of these landscapes is important to ensure the health and productivity of Great Plains grasslands and all the species which rely on them for their survival (Briske et al., 2020).

Grasslands evolved with frequent natural disturbances including frequent fires and grazing from large herd animals such as bison (*Bison bison*) and pronghorn (*Antilocapra americana*), as well as small mammals and insects (Coppedge and Shaw, 1998; Courtney, 1989; Fuhlendorf et al., 2010; Knapp et al., 1999). The relationship between grazing and fire, often called pyric herbivory, is considered a feedback loop where grazing animals are attracted to the nutritious regrowth from recently burned areas (Fuhlendorf and Engle, 2001). As the grazing animals are drawn to the regrowth, other areas of the landscape are left to ‘rest’ thus accumulating fuel, which in turn creates the ideal conditions to carry fire, perpetuating the fire-grazing relationship. With European settlement and the introduction of western agriculture to the prairies, fires have largely been removed from the landscape due to fire prevention and suppression measures. Conservationist and land managers are now recognizing the important role fire disturbance plays in a functioning grassland ecosystem and the use of prescribed fires are becoming increasingly more common. Prescribed fires are intentionally lit when weather and fuel conditions meet specific requirements in order to maintain control of the burn (Wright and Bailey, 1982). Reintroducing natural disturbance regimes, in the form of prescribed burning, will restore the dynamic nature of grasslands while providing both nutritious forage for livestock and habitat for native wildlife (Fuhlendorf and Engle, 2001; Fuhlendorf et al., 2012; Limb et al., 2011; Richardson et al., 2014). The combination of fire and grazing help to preserve biodiversity by creating heterogeneity across the landscape through space and time (Fuhlendorf and Engle, 2001).

The responses of northern mixed grass prairie ecosystems to fire have been studied extensively across the Great Plains (e.g., Engle and Bidwell, 2011; Gross and Romo, 2010; Redmann, 1978), as has the impact of grazing on grassland vegetation (Bai et al., 2001; Lwiwski et al., 2019; Milchunas et al., 1988). However, interactions between fire and grazing, or pyric herbivory, while extensively studied in the tallgrass prairie in the United States (Fuhlendorf and Engle, 2004; Fuhlendorf and Engle 2001; Knapp et al., 1999), have not been studied in detail in the northern mixed grass prairies in Canada.

1.2 Research Objectives

The objectives of my thesis research were to study the reintroduction of fire to an area of the northern mixed grass prairie in Saskatchewan that has experienced cattle grazing for the past 100 years with the goal to restore historic fire-grazing interactions. The study aimed to see how prescribed fire influences cattle movement within confined rangeland and determined the short-term effects of prescribed burning on plant communities in the northern mixed grass prairie. The findings of my project have the potential to influence livestock management strategies that will benefit wildlife species at risk habitat and guide environmentally sustainable management of grasslands in the mixed grass prairie. My specific objectives were to quantify 1) vegetation structure and composition; and 2) cattle movement in tame forage and native prairie pastures following prescribed fire.

1.3 Thesis Organization

This thesis is organized into four chapters. Chapter 1 provides a broad introduction to the research. Chapter 2 contains a literature review introducing the ecology of the native mixed grass prairie and ecological disturbance process including grazing and fire. Chapter 3 of this thesis is written as a stand-alone manuscript and presents research and analysis from data I collected in the field during the 2017 and 2018 growing seasons. This chapter examines the short-term effects of prescribed fire on vegetation and on cattle movement in northern mixed grass prairie. Chapter 4 provides a conclusion and synthesis of the research I conducted and provides my suggestions for future research directions and conservation strategies for the northern mixed grass prairie.

2.0 Literature Review

2.1 Ecology of Northern Mixed Grass Prairie

The historic range of the northern mixed grass prairie extends through south-eastern Alberta, southern Saskatchewan, and southwestern Manitoba and into the states of Montana, North Dakota, South Dakota, and north-eastern Wyoming (Askins et al., 2007). Dark brown and brown soils of the Chernozemic order are the dominant soil type in the northern mixed grass prairie (Acton et al., 1998; Coupland, 1950). Common vegetation communities within the mixed grass prairie are dominated by graminoids including needle grasses (*Stipa* spp.), wheat grasses *(Elymus* spp.), grama grasses *(Bouteloua* spp.), and June grasses *(Koeleria* spp.*)*, forbs including sage (*Artemisia* spp.), and shrubs including roses (*Rosa* spp.) (Acton et al., 1998; Coupland 1950, 1961). The climate of this region is classified as semi-arid to dry-subhumid with a mean annual precipitation ranging from 310 to 380 millimetres (mm) (Coupland, 1950, 1961; Mitchell and Csillag, 2001). Most precipitation is received during the growing season between April to July (Coupland, 1961). The temperature range in this region is extreme (40°C to -40°C), with a mean annual temperature from 0°C to 6°C, with an average of 125 frost-free days per year (Acton et al., 1998; Coupland, 1961). Precipitation is the primary driver in the productivity of the mixed grass prairie and changes to plant community structure and function are influenced by wet cycles and periodic droughts (Biondini et al., 1998; Heitschmidt and Haferkamp, 2005; Samson et al., 2004). Secondary drivers influencing grassland vegetation dynamics include fire and grazing by herbivores (Askins et al., 2007). The combination of fire and grazing dynamics result in grassland landscapes with spatial and temporal variation in structure, function, and diversity (Fuhlendorf et al., 2009; Fuhlendorf and Engle, 2001).

The mixed grass prairies in Canada have undergone drastic changes in the last 200 years; with 70% of this ecosystem converted to cropland or other uses (Federal, Provincial, and Territorial Governments of Canada, 2010; Fore et al., 2015; Roch and Jaeger, 2014). The mixed grass prairie that remains are mostly confined to areas with landscape characteristics which make them unsuitable for agriculture. These are generally areas that are too arid to support annual cropland, have rocky or saline soils, are too steep for farm equipment, and they are typically used as rangeland for livestock (Fore et al., 2015). Remaining native grasslands are highly fragmented by fences, roads, and oil and gas development, impacting the quality of habitat and isolating organisms genetically (Roch and Jaeger, 2014). These linear features further contribute to the degradation of prairie landscapes as they provide thousands of kilometers of paths where alien or invasive species can be introduced (Davis et al., 2000; Nasen et al., 2011). Smaller, fragmented blocks of native prairie impact the ability for natural fire disturbances to move across the landscape as they would have before European settlement. Following the dramatic loss of the native prairie, there are many grassland species that are listed as at risk that depend on the limited remaining mixed grass prairie for existence (e.g., Askins et al., 2007; Samson et al., 2004; Environment Canada, 2017).

2.2 Grazing in the Northern Mixed Grass Prairie

2.2.1 Ecological role of grazing

Grazing is an ecological process that results in the removal of biomass (i.e., a disturbance) to which plants on the northern mixed grass prairie have adapted to over thousands of years. Large ungulates including bison (*Bison bison*), pronghorn (*Antilocapra americana*), and elk (*Cervus canadensis*), rodents including gophers (*Geomys* spp.) and prairie dogs (*Cynomys* spp.), and insects grazed the prairies in great numbers before European settlement of the prairies (Knapp et al., 1999; Laliberte and Ripple, 2004; Samson et al., 2004). Bison are considered to be an ecological keystone species on the prairie (Knapp et al., 1999). Historians and Indigenous groups estimate 30 to 100 million roamed the Great Plains pre-European settlement (Isenberg, 2000; Knapp et al., 1999). By the 1880's, wild bison populations were reduced to near extinction, and in the following decades were largely replaced by intensively managed domestic cattle (*Bos taurus*) as the dominant grazer on the landscape. Habitat fragmentation and loss of habitat have impacted the distribution and abundance of other native animals on the Great Plains (Christie et al., 2017; COSEWIC, 2009, 2010; Davis et al., 2004). The presence of these animals, including past dominant grazers like bison and present cattle grazers, influences plant species composition and plant community structure through removal of biomass, selective grazing, trampling, and depositing nutrient-rich excrement and urine (Hobbs, 1996; Knapp et al., 1999).

Cattle are typically managed under extensive grazing systems to promote uniform grazing distribution and maximize animal weight gain (Fuhlendorf and Engle, 2001; Limb et al., 2011). Management systems include fencing to control the timing and distribution of grazing animals within an area which create a homogenous landscape that differs from the spatially and temporally heterogeneous patterns of the historic free-roaming bison (Fuhlendorf and Engle, 2001). Cattle are selective grazers; helping to create a mosaic of plant communities on the landscape, with differences in vegetation structure and composition (Allred et al., 2011). Dependent on the intensity and duration, selective grazing can be detrimental to plants that are not as tolerant to this form of disturbance and will be reduced or removed from the ecosystem (Briske, 1996; Government of Canada and Government of Saskatchewan, 2008). Conversely, plants that are tolerant of grazing or are not as nutritious or palatable to livestock will increase in abundance (Derner and Hart, 2007). Overall, cattle grazing reduces standing dead litter, and the biomass of grasses, increases the biomass of forbs, and alters plant species composition (Bai et al., 2001). Strategies for productive cattle grazing distribution and movement include strategic placement of mineral & salt blocks and fencing to restrict livestock to smaller areas for intense and uniform grazing pressure (Bailey et al., 2010; Government of Canada and Government of Saskatchewan, 2008). However, prolonged heavy grazing can lead to a decline in standing dead biomass, root biomass, litter biomass, and soil nitrogen mineralization (Biondini et al., 1989; Government of Canada and Government of Saskatchewan, 2008). Trampling of plant material can speed up the decomposition of litter by compacting the litter and increasing its contact with the soil and exposure to soil microbes. An important consideration in determining the impact grazing will have on a plant is timing in relation to its growth cycle (Bailey et al., 2010). Removing photosynthetically active plant tissue may weaken that plant over time as resources are allocated to replacing lost tissue instead of storing nutrients (Chapin et al., 1990; Romo, 2006). Conversely, grazing during seasons where plant tissue is dormant has less of an effect on the plant (Bailey et al., 2010).

2.2.2 Grazing systems

Many grazing management systems incorporate tame pasture to supplement livestock grazing on native prairie pasture. This style of range management is called a complimentary grazing system (Government of Canada and Government of Saskatchewan, 2008). Typically, tame pasture is composed of a forage mix of non-native species including crested wheatgrass (*Agropyron cristatum*), smooth brome (*Bromus inermus*), and alfalfa (*Medicago sativa*) (Bailey et al., 2010; Government of Canada and Government of Saskatchewan, 2008). These non-native grass and forb species become photosynthetically active earlier in the spring compared to species native to the northern mixed grass prairie and can tolerate intense early season grazing pressure (Smoliak et al., 1981). Crested wheatgrass reaches peak forage production in May, while native grasslands reach peak forage production in June (Schellenberg et al., 1999; Smoliak et al., 1981). Complimentary grazing systems take advantage of this high-quality early season forage on tame pasture and allow native pasture more time to accumulate forage and add to carbohydrate reserves, until early summer when the livestock can then be moved to the native pasture (Bailey et al., 2010; Government of Canada and Government of Saskatchewan, 2008). Using complementary grazing systems in the northern mixed grass prairie is more productive in terms of animal gains compared to grazing native prairie alone (Smoliak, 1968; Smoliak et al., 1981).

2.2.3 Forage quality

Regardless of whether the pasture is native or tame, the measures of quality and amount of forage available are important considerations in meeting the nutritional needs of the livestock. Forage quality is measured by the nutritional value and the palatability of the forage. Crude protein, acid detergent fibre (ADF), neutral detergent fibre (NDF) are measurements of forage quality. As a plant matures, forage quality declines due to a reduction in nutrients and decrease in palatability (Bailey et al., 2010; Government of Canada and Government of Saskatchewan, 2008). Young plants are more palatable and nutritious because they have a high leaf to stem ratio (McNaughton, 1984). Leaves are composed of cells that are high in protein and sugars, while stems have more rigid cells that have indigestible cellulose and lignin-rich cell walls (Jacobs, 2012). Indigestible fibre in plant stems increases NDF concentration and slows animal intake as it disproportionality results feeling of satiation during feeding. Crude protein is a measure of the amount of nitrogen from protein and non-protein sources and can be used to predict the amount of protein available (Jacobs, 2012). Crude protein is generally highest when plants are in the vegetative stage of growth and gradually declines after the plant has flowered and set seed (Smoliak and Bezeau, 1967). Disturbance impacts forage quality by predominantly removing mature, aboveground plant tissue, changing the phenological stage of the plant (Bailey et al., 2010; Government of Canada and Government of Saskatchewan, 2008). When actively growing plant tissue is removed by grazing, the plant will prioritize available resources to nutrient rich re-growth (Briske, 1996). Large herbivores take advantage of the palatable growth and continue to graze these disturbed areas forming grazing lawns (Fryxell, 1990; McNaughton, 1984).

2.2.4 Livestock behaviour

Livestock behaviour and movement within pastures are influenced by environmental factors, as well as the stocking rate, the species, the age, and the breed of the animal (Fynn et al., 2019; Government of Canada and Government of Saskatchewan, 2008; Launchbaugh and Howery, 2005). Grazing species allocate their time to activities differently based on the type of species (Fynn et al., 2019). For example, bison spend less time grazing, travel greater distances from water sources, and more time doing social activities such as wallowing compared to cattle (Allred et al., 2011; Kohl et al., 2013). Cattle typically spend mornings and evenings grazing and seek shade during the heat of the day. Furthermore, cattle generally stay within 2.5 km of a water source and avoid steep slopes (Bailey et al., 2010; Kohl et al., 2013). All livestock make decisions when foraging based on the quality and quantity of food available and will spend less time in areas where little or undesirable forage is encountered (Fynn et al., 2019). When livestock are introduced to a new range or pasture, they will spread out and evaluate the available forage (Government of Canada and Government of Saskatchewan, 2008). Livestock make selections of forage that is available to them, while livestock preference of forage is what they choose under unlimited forage options (Johnson, 1980). Green, leafy vegetation is favoured over older dry vegetation and selection of forage type will change with the growing season to meet nutritional demands (Government of Canada and Government of Saskatchewan, 2008; Launchbaugh and Howery, 2005). Livestock behaviour and forage selection are also influenced by the animal's knowledge and past experiences (Fynn et al., 2019; Launchbauch and Howery, 2005). Finally, livestock behaviour can be influenced by factors such as predators and human presence, which disrupt normal behavior.

2.3 Fire in the Northern Mixed Grass Prairie

2.3.1 Historic role of fire

Historically, fires were a common form of disturbance on the Great Plains, including the northern mixed grass prairie (Axelrod, 1985; Umbanhowar, 1996; Wright and Bailey 1982). Fires were naturally caused by lightning strikes or anthropogenically by Indigenous people (Nelson and England, 1971). The historical fire return interval for the northern mixed grass prairie is thought to have been between five and 25 years depending on moisture conditions and fuel load (Samson et al., 2004; Umbanhowar, 1996). Since European settlement of the prairies, this regular and natural phenomenon has been viewed as a threat to safety and property resulting in concerted efforts to prevent and suppress fires. This has thus interfered with the natural disturbance regime, resulting in many areas in the Canadian prairies that have not experienced fire in over 90 years (Romo, 2003). This is problematic for ecosystem balance as fire is an important disturbance in highly productive grasslands, as it prevents the encroachment of woody vegetation and invasive species that are not adapted to fire disturbance (Romo, 2003). In more arid grasslands, like the northern mixed grass prairie, fire disturbance creates heterogeneity within the landscape and promotes biodiversity (Romo, 2007). Grassland plants have adaptations to withstand or even benefit from fire, including vegetative buds beneath the soil surface and seeds and seedlings that benefit from the smoke and ash produced by fire (Abu et al., 2016; Coupland and Johnson, 1965; Ren and Bai, 2016; Russell et al., 2015).

2.3.2 Ecological role of fire

The impact, direction, magnitude, and form which a fire will burn across a landscape is influenced by many factors. These include the type and quantity of fuel or plant material burning, the level of cure, ambient temperature, wind, relative humidity, grazing history, fire return interval, and topography (Wright and Bailey, 1982). Plant communities that are dominated by grasses will burn hotter and more completely than plant communities dominated by forbs (Wragg et al., 2018). Additionally, grass species composition will affect how a fire will burn (Wright and Bailey, 1982). Bunchgrasses like *Stipa* accumulate large amounts of litter around the base of the plant, providing fuel for a hot, slow burn. In comparison, *Koeleria* and *Bouteloua* species have a small, tufted growth forms that produce smaller amounts of litter and are less likely to carry a flame. Rhizomatous species such as many *Elymus* species have even less litter around the base of the plant and growing points below the soil surface that are not damaged from the heat of the fire (Wright and Bailey, 1982). The more fuel available, the easier it is to carry a flame. As plant material matures and dries, it becomes more flammable. Fuel loads are influenced by seasonal growing conditions, grazing history, and the fire return interval. Fire and grazing disturbances reduce fuel loads, decreasing the intensity of the flame. Weather factors including air temperature, wind speed, and relative humidity affect the intensity and movement of the fire (Wright and Bailey, 1982). As the temperature increases, the fuel (i.e., plant matter) dries and becomes more flammable. Increasing wind speeds push flames across the landscape at a faster rate and increase the intensity of the fire. Relative humidity influences the intensity of a fire; as humidity drops, fuel becomes easier to burn which creates a more intense flame. The topography of the landscape also influences fire speed and intensity, with flames travelling uphill moving faster and more intensely than flames travelling downhill (Wright and Bailey, 1982).

The effective time for a plant community to recover from a fire event is dependent on factors such as type of plant species, the intensity, duration, and frequency as well as the season in which the fire occurs (Biondini et al., 1989; Pylypec and Romo, 2003; Russell et al., 2015). All fire events will result in a temporary reduction in standing biomass, with the recovery of the plant community influenced by the environmental conditions preceding and following the burn (Powell et al., 2018; Russell et al., 2015; Vermeire et al., 2014). It may take as long as several years for graminoid biomass to recover to the levels of unburned graminoid biomass when fires are succeeded by drought (Arterburn et al., 2018, Erichsen-Arychuk et al., 2002). Within the prairies, there is some evidence that a normal fire regime supports diversity via the intermediate disturbance hypothesis where species richness is highest in communities with moderate levels of disturbances and at intermediate time spans following disturbance (Collins et al., 1995; Vujnuvic et al., 2002). Evidence for this has been found in both the tallgrass prairie (Collins et al., 1995) and fescue prairie (Vujnuvic et al., 2002) where species richness was found to be highest at intermediate times since fire events.

The removal of litter due to fire events has a large number of effects which can alter the microclimate of the affected area. Litter acts as an insulator, regulating the temperature of the soil surface against solar radiation. Litter is a control on soil moisture and temperature which are thought to be a key driver of grassland productivity in semi-arid regions (De Jong and MacDonald, 1975, Deutsch et al., 2010; Facelli and Pickett, 1991; Hilger and Lamb, 2017). The absence of litter during the growing season decreases the amount of soil moisture available on the soil surface (Facelli and Pickett, 1991; Willms et al., 1986). In the winter months, burned areas have reduced snow trapping abilities due to the loss of aboveground plant biomass and plant litter (De Jong and MacDonald, 1975). The removal of litter can alter community composition and increase species richness by increasing the germination and flowering of forb species, due to an increase in available light, space, and nutrients (Harrison et al., 2003; Letts et al., 2015; Willms et al., 1986). In the tallgrass prairie where litter cover can be very dense, the removal of litter can substantially increase herbage production by increasing light availability (Blair, 1997).

Fire can increase nutrient availability by having a fertilizing effect on the landscape through the mineralization of aboveground plant matter (Redmann, 1991; Sharrow and Wright, 1977). Burning of grasslands results in higher amounts of copper, magnesium, nitrogen, and potassium in green leaf tissue from burned vegetation compared to unburned vegetation (Eby et al., 2014; Vermeire et al., 2020). Soil nitrogen can be enhanced through prescribed fire, due to soil temperature and microbial responses to burning, plant inputs into the ground, and rates of plant nitrogen uptake (Augustine et al., 2010).

2.3.3 Ecological effects of wildfire and prescribed fire

Even with best efforts to recreate the conditions of a wildfire, differences exist between wildfires and prescribed burns. The season of the fire will influence the fire behavior and severity and in turn, the impact a fire will have on the grassland ecosystem. Historically fires likely occurred in all seasons in the mixed grass prairie (Romo, 2003). Prescribed fires are usually conducted either in early spring before most vegetation has begun growing for the year or in the fall after the growing season has concluded. Prescribed fires conducted in fall may have a more consistent burn as fuel is more aerated relative to fuel in spring that has been compacted by snow over the winter (Wragg et al., 2018). Prescribed fires are also only conducted when specific weather condition criteria are met in order to maintain control of the burn (Wright and Bailey, 1982). For the northern mixed grass prairie, ideal prescribed burning conditions include consistent wind direction and speeds between 5 to 15 km/h to maintain a steady direction and push for the fire. Temperatures should be above 0°C but below 25°C to keep the intensity of the fire manageable. Relative humidity should be between 30-40% to allow for a steady and controlled rate of burn. Wildfires commonly occur in the summer months when vegetation is photosynthetically active and growth is at its peak (Higgins, 1984). Conditions that precede wildfires tend to be not ideal for optimal vegetation regrowth; such conditions include volatile high winds, low humidity, and high temperatures. A hotter and more complete burn can cause more damage to plants aboveground and will result in more volatilization of nutrients (Wragg et al., 2018). Vegetation is least affected by fires in the dormant season where fuel loads are low (Augustine et al., 2010). The season of burning can be important depending on the composition and density of the plant community. The diversity of forb species was affected by seasonality of burns in a northern mixed grass prairie community located in South Dakota (Biondini et al., 1989) while a study conducted in mixed grass prairie in Montana (Russell et al., 2015) showed no difference in plant densities following prescribed burns in summer, fall, and spring. Spring and fall fires in Montana stimulated bud activity in C_3 and C_4 grasses, while summer fires decreased bud activity in C_4 grasses (Russell et al., 2015; White and Currie, 1983). Summer fire in Montana increased the dominance of C_3 grasses and did not affect the abundance of C_4 grasses (Vermeire et al., 2011). Although most prescribed fires are conducted in spring and fall when the risk of the fire becoming uncontrolled is lower, it may be important for diversity to conduct prescribed fires in the summer when wildfires often occur naturally (Gross and Romo, 2010; Howe, 1994; Romo, 2003).

2.4 Fire and Grazing Interactions in the Northern Mixed Grass Prairie

The Great Plains of North America evolved over thousands of years with the removal of biomass from fires and herbivores grazing the land. The coupled effects of fire and grazing is termed pyric herbivory (Allred et al., 2011; Fuhlendorf et al., 2009). Disturbance through fire and grazing create a heterogeneous landscape with vegetation in various stages of succession based on the timing of fire (Fuhlendorf et al., 2009; Fuhlendorf and Engle, 2001). Grazing animals are attracted to recently burned patches, allowing unburned areas to rest and accumulate biomass (Allred et al., 2011; Fuhlendorf et al., 2009; Hobbs, 1996; Powell et al., 2018; Vermeire et al., 2004). The accumulation of biomass in the unburned areas provides fuel, increasing the probability of a fire event which will then attract livestock to the freshly burned area on the landscape. These disturbance patches result in a heterogeneous landscape which provide a variety of habitats suitable for many grassland birds (Askins et al., 2007; Fuhlendorf and Engle, 2004; Fuhlendorf et al., 2006), mammals (Fuhlendorf et al., 2010; Ricketts and Sandercock, 2016), and insects (Jonas and Joern, 2007).

The coupled effects of fire and grazing provide more beneficial ecosystem effects than either burning or grazing on their own. Even though there are some similarities between how a fire disturbance and grazing disturbance impacts the landscape, the effects of one disturbance cannot be replaced by the other. For example, both grazing and fire disturbance remove aboveground plant biomass; however, after a fire, the nutrients from plants are returned to the soil in an even distribution compared to highly concentrated releases of nutrients from urine and fecal deposits of grazers (Sharrow and Wright, 1977; Steinauer and Collins, 1995; Vermeire et al., 2020). Fire can completely remove aboveground material including litter, while standing dead material, litter, and untouched patches of unpalatable plant species are left on the landscape after grazing. By using fire and grazing in conjunction, land managers can influence the movement of livestock on the landscape, to focus grazing on areas that have been burnt (Coppedge and Shaw, 1998). Burning helps to rejuvenate stands of native and tame pasture that have become less palatable to grazers due to an accumulation of litter, or have senesced (Smoliak et al., 1981).

Pyric herbivory is well studied in tallgrass prairie where fire is needed to prevent the encroachment of woody vegetation (Fuhlendorf and Engle, 2004; Knapp et al., 1999; Svejcar, 1989). In the less productive mixed grass prairie, where tree encroachment is not a major factor, the fire-grazing interaction has been less studied (Powell et al., 2018). The mixed grass prairie has lower fuel loads compared to the tallgrass prairie and a more arid environment places strong limitations on woody species. The effects of burning in mixed grass prairie are therefore less pronounced than the tallgrass prairie, which reduces the potential to influence the behavior of grazing animals.

Pyric herbivory promotes biodiversity within the grassland ecosystem and has been shown to help stabilize livestock productivity against fluctuations in weather (Allred et al., 2014). Recently burnt areas provide nutritious regrowth which attracts livestock and allows for plant growth in the unburned areas (Allred et al., 2011; McGinty et al., 1983; Powell et al., 2018; Vermeire et al., 2004). Fires increase the palatability and crude protein content in the forage regrowth following a burn and can benefit livestock producers by improving annual cattle gains in the tallgrass and mixed grass prairie (Allred et al., 2014; Limb et al., 2011; Powell et al., 2018). Ungulate preference for burned sites decreases with time since fire (Allred et al., 2011; Powell et al., 2018). The crude protein content of forage decreases with time since fire, returning to non-burned levels in 120 days since fire (Powell et al., 2018).

Rest following fire or reductions in stocking rate following mixed grass prairie burning are not necessary to maintain resiliency of the plant communities present, or to prevent losses in livestock weight (Allred et al., 2014; Gates et al., 2017b; Limb et al., 2011; Vermeire et al., 2014). Pyric herbivory in the mixed grass prairies is likely a worthwhile land and livestock management tool to promote grassland conservation while maintaining a viable livestock operation.

Conserving northern mixed grass prairie requires the reintroduction of the natural fire-grazing disturbance regime to restore the historic spatial and temporal heterogeneity of these landscapes (Fuhlendorf and Engle, 2004; Powell et al., 2018). Including fire and grazing as part of rangeland management and prairie conservation will maintain or increase biodiversity in these ecosystems (Mori, 2009; Romo, 2007). Much of the northern mixed grass prairie has been lost though habitat conversion and the remaining tracts of grasslands act as a refuge for biodiversity (Federal, Provincial, and Territorial Governments of Canada, 2010; Hoekstra et al., 2005; Samson et al., 2004). The importance of managing rangeland to promote biodiversity and protect species at risk habitat has resulted in the creation of incentive programs for producers to improve habitat quality within this region of the Canadian prairies (Environment and Climate Change Canada, 2017; SODCAP, 2015). Although the historic spatial scale of the natural fire-grazing disturbance regime can not be replicated, reintroducing fire into rangelands can mimic the natural disturbance regimes and promote biodiversity within the ecosystem.

3.0 Pyric herbivory in the northern mixed grass prairie: testing the use of fire as a land and livestock management tool on rangelands in Saskatchewan

3.1 Abstract

While the use of prescribed fire as a livestock and land management tool has been study extensively in the in the prairie ecosystems of the United States, few studies have examined the interaction of fire and grazing animals (i.e., pyric herbivory) in the northern mixed grass prairies in Canada. In this study, I examined the short-term effects of two spring prescribed fires on plant community structure in native prairie and tame forage pastures in the northern mixed grass prairie region of Saskatchewan. I also examined the influence of prescribed fire on cattle movement within these pastures by tracking the movements of the cattle in the grazing seasons preceding and following the burns. Prescribed fire reduced total plant and litter biomass, however there were strong climatic influences on vegetation with significant season and annual changes in biomass. Burning homogenized vegetation composition in both pastures in the growing season following the prescribed fires. Finally, I saw a significant increase in cattle visitation to the recently burned areas within the pastures. Pyric herbivory in the northern mixed grass prairies of Canada appears to be a worthwhile land and livestock management tool to promote grassland conservation while maintaining a viable livestock operation.

3.2 Introduction

The rapid settlement and conversion of the Great Plains of North America has resulted in the dramatic loss of native prairie and in turn significant losses to biodiversity within these grassland ecosystems (Hoekstra et al., 2005; Lark et al., 2019; Samson and Knopf, 1994). As such, it is crucial that remaining grasslands are managed to maintain ecological function to prevent further losses to biodiversity (Briske et al., 2020; McDonald et al., 2019). Reintroducing fire to grassland ecosystems is one conservation management method that can be used to maintain natural landscape disturbances and create habitat heterogeneity (Fuhlendorf and Engle, 2001; Fuhlendorf et al., 2009). Habitat heterogeneity is then maintained through a feedback loop where grazing animals are attracted to the nutritious regrowth from recently burned areas, known as pyric herbivory (Fuhlendorf and Engle, 2001; Powell et al., 2018). As the grazing animals are drawn to the regrowth, other areas of the landscape are left to 'rest' thus accumulating fuel, which in turn creates the ideal conditions to carry fire, perpetuating the fire-grazing relationship. The combination of fire and grazing help to preserve biodiversity by creating heterogeneity across the landscape through space and time (Fuhlendorf and Engle, 2001).

Although the fire-grazing interaction has been well studied in many grassland biomes across the world (e.g., Archibald and Bond, 2004; Fuhlendorf and Engle, 2001; Huang et al., 2018), few studies have focused on the fire-grazing interaction in the northern mixed grass prairie (Powell et al., 2018). I conducted my research in the northern mixed grass prairie on Nature Conservancy Canada's Old Man on His Back Heritage and Conservation Area (OMB) property in southwest Saskatchewan. Through my study, fire was reintroduced to this landscape by conducting prescribed fires within a tame forage pasture and a native prairie pasture. I examined the short-term effects of fire on plant community structure and plant productivity and I tracked the movements of cattle grazing within these pastures to assess whether the fire influenced their movement.

The objectives of my study were to study the reintroduction of fire to an area of the northern mixed grass prairie in Saskatchewan that has experienced cattle grazing for the past 100 years with the goal of restoring the historic fire-grazing interactions. My study aimed to see how prescribed fire influences cattle movement within confined rangelands and to determine the short-term effects of prescribed burning on plant communities in the northern mixed grass prairie. The findings of the study have the potential to influence livestock management strategies that will benefit wildlife species at risk habitat and guide environmentally sustainable management of grasslands in the northern mixed grass prairie.

3.3 Materials and Methods

3.3.1 Field Site

I conducted my research at Nature Conservancy Canada's Old Man on His Back Heritage and Conservation Area (OMB) property in southwestern Saskatchewan (49°12' N, 109°33' W, elevation 976 m). OMB is located 15 km west of Claydon, SK, 65 km east of the Alberta border and 23 km north of the U.S.A. border. OMB has a mean annual temperature of 4.7 °C and a mean annual precipitation of 385.0 mm (Government of Canada, 2019) (Figure 3.1). The property is located within the mixed prairie ecoregion in the brown soil zone and is dominated by Chernozemic and Solonetzic clay-loam soils (Saskatchewan Soil Survey, 1992). The dominant vegetation is native prairie dominated by species including needle and thread (*Hesperostipa comata*), northern wheatgrass (*Elymus lanceolatus*), and June grass (*Koeleria macrantha)*. The 5,300-hectare property is divided into several pastures for cattle grazing and two pastures for year-round bison grazing. Most of the property is native prairie however, some of the pastures have been cultivated and seeded to tame forage and some of those later restored to native prairie.

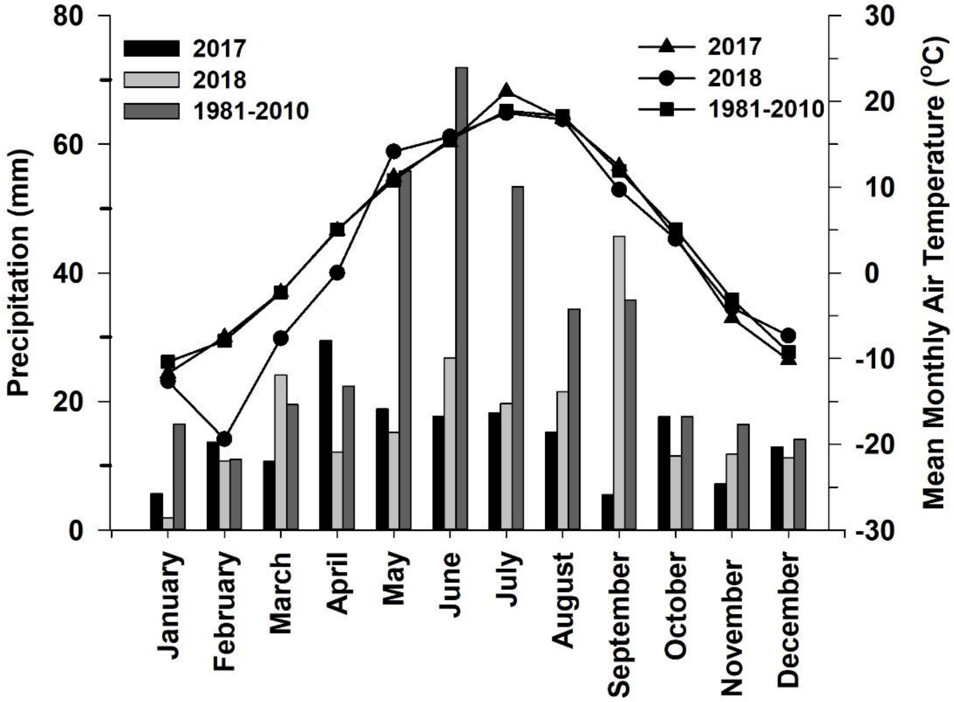

Figure 3.1. Precipitation and temperature data for Old Man on His Back region during the study period. Weather data collected and averaged from Eastend, SK and Val Marie, SK weather stations (Government of Canada, 2019).

This study focussed on two pastures: S5 - a 45 ha tame forage pasture that has been seeded to a tame and native seed mix, and N8 - a 151 ha pasture of native prairie (Figure 3.2). The tame forage pasture (S5) is dominated by non-native species including crested wheatgrass (*Agropyron cristatum*) and alfalfa (*Medicago sativa*) plants, with non-dominant native species including June grass (*Koeleria macrantha*) and broomweed (*Gutierrezia sarothrae)*. Both pastures are typically grazed by 45 heifers and 2 bulls and are currently managed with a deferred-rotation plan. The frequency and duration of grazing in the pastures are adjusted based on the seasonal weather conditions and the plant community productivity. In general, the tame forage pasture (S5) is grazed from June to July, then the herd is moved to the native pasture (N8) to graze from July to October. In 2017 and 2018, the stocking rate for the tame forage pasture (S5) was 1.0 AUMs/ha. The native pasture was stocked at 0.8 AUMs/ha in 2017 and 0.6 AUMs/ha in 2018. Variation in the location of salt and mineral block placement is an encouraged practice for better livestock distribution at OMB but was not done during the 2017 and 2018 fieldwork. The OMB property has been grazed by cattle since the early 1900s and there have been no recorded fires within the property in recent memory.

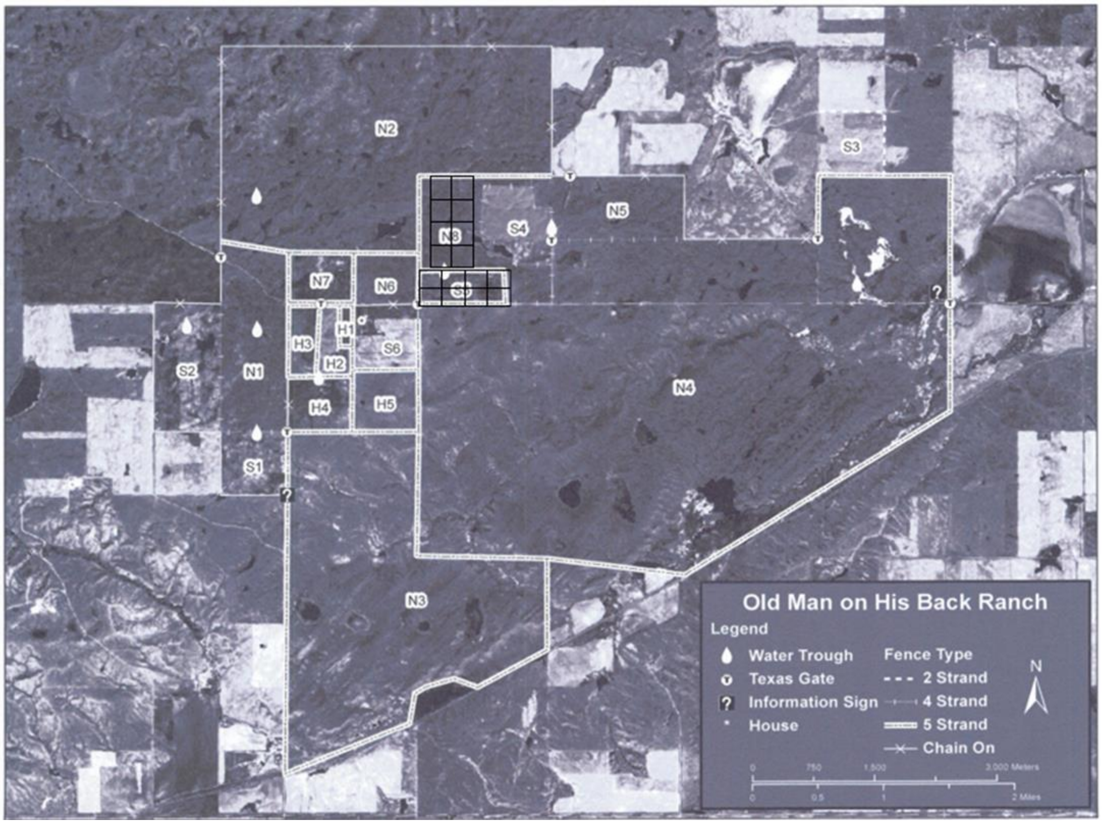

Figure 3.2. Location of permanent research units and treatment blocks (black grid) within the Old Man on His Back Property (Nature Conservancy of Canada, 2020).

3.3.2 Study Design

Permanent research units were established at OMB in the spring of 2017. The permanent research units used by this project are found within the native prairie (N8) and tame forage (S5) pastures. The locations of the research units within the pastures were chosen based on distance from fences and water troughs, as well as ability to access plots with minimal land disturbance. The permanent research unit in the native pasture (N8) was 72 ha, and in the tame forage pasture (S5) the permanent research unit was 41.6 ha. Eight treatment blocks were contained within each of the permanent research units and act as the boundaries for prescribed fire units. The treatment blocks in N8 were each 9 ha in size, and in S5 the treatment blocks were each 5.2 ha in size (Figure 3.3). Within each treatment block in pasture S5, there were six permanent 4.0 m^2 sample plots, for a total of 48 sampling plots in the tame forage pasture (S5) (Figure 3.3). Pasture N8 had up to 18 permanent 4.0 m^2 sample plots within each treatment block, for a total of 122 sampling plots in the native pasture (Figure 3.3). All sample plots were laid out in a grid pattern and were located at least 50 m apart. Each sample plot was identified with a physical marker and assigned a unique number. Within the 4.0 m^2 sample plots, there were four 0.25 m^2 subplots for biomass collection and one 1.0 m^2 permanent subplot for recording canopy cover (Figure 3.4). Sampling within the four 0.25 m^2 biomass subplots was systematic to avoid re-clipping vegetation over time.

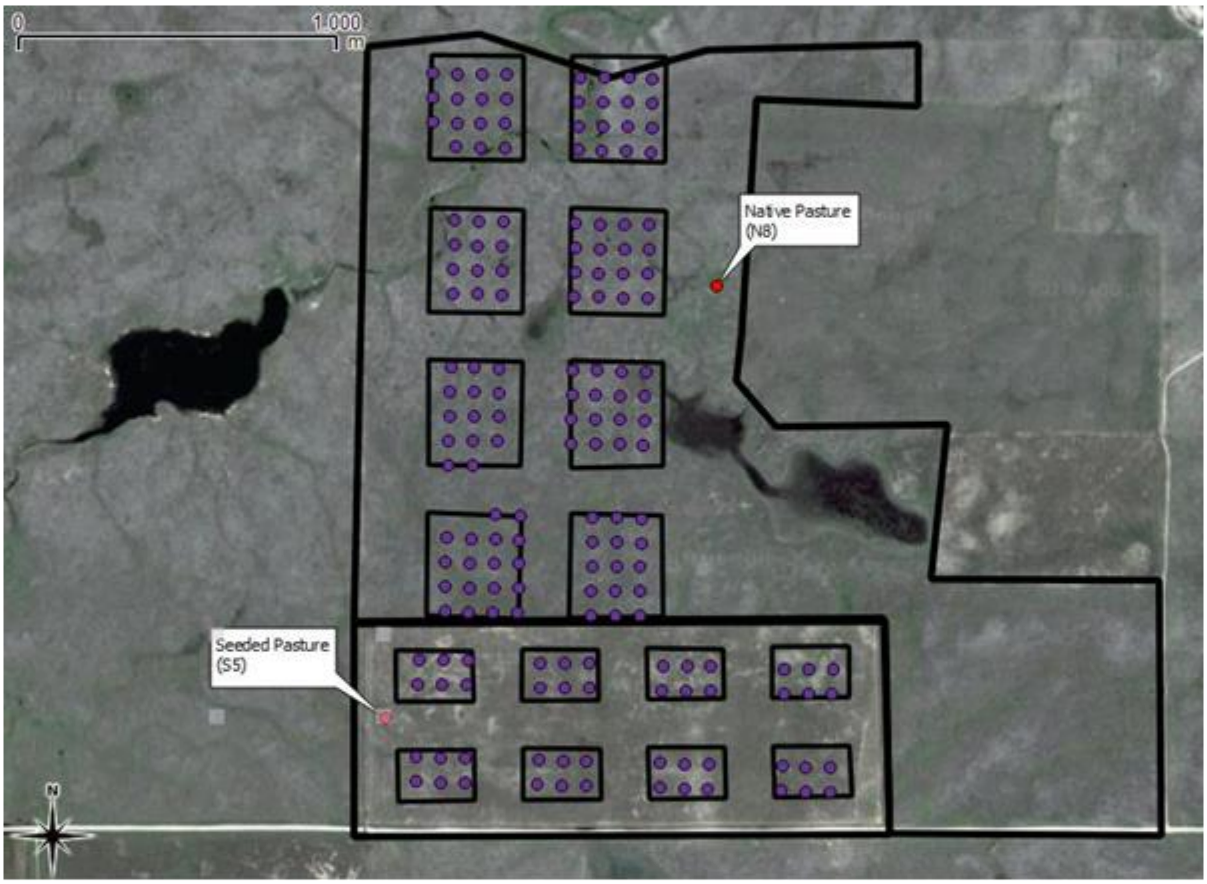

Figure 3.3. Treatment blocks (black squares) and locations of sampling plots (purple dots) in pastures N8 and S5.

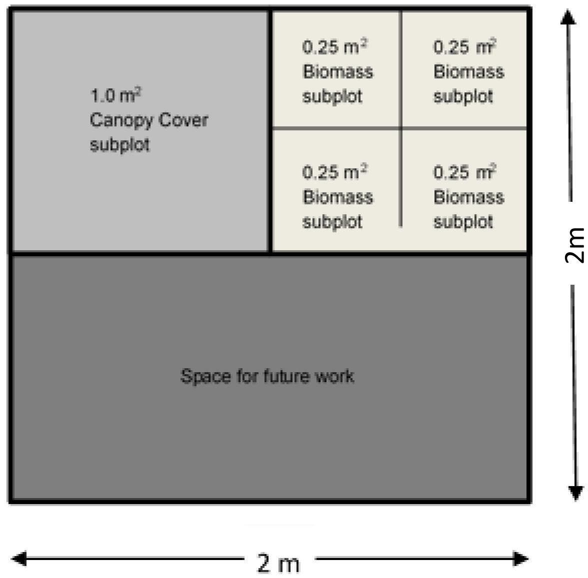

Figure 3.4. Layout of each 4.0m^2 sampling plot.

3.3.2.1 Prescribed fire

One treatment block in the tame forage pasture (S5) and one treatment block in the native pasture (N8), were burned with prescribed fire between April 26 and 28, 2018 (Figure 3.5). The burn in S5 was conducted over 2.5 hours on the morning of April 26, 2018. The average windspeed was between 1.6-10 km/h, the temperature was between 5.8-15.1°C, and the relative humidity was between 33-42% during the burning period. The burn unit was 5.2 ha and consisted of areas with complete and partial combustion of the vegetation. Prescribed burning began in the N8 treatment block in the evening of April 26, 2018. Due to changing weather conditions and wind directions, the burn in N8 had to be conducted over multiple mornings and evenings to meet conditions for safe and effective burning. The prescribed fire in N8 was completed on the morning of April 28, 2018. The average windspeed varied between 1.4-21.3 km/h, the relative humidity was between 18.4-60.5%, and the temperature was between 5.1-22.5°C during the burning period. The burn unit was 9 ha and consisted of areas with complete and partial combustion of the vegetation.

Figure 3.5. Selection of treatment blocks for spring 2018 prescribed fire treatments (outlined in pink) and selected adjacent control blocks (outlined in green).

3.3.2.2 Vegetation sampling

Vegetation sampling occurred in July 2017, by randomly selecting half of the sampling plots within pastures S5 and N8. Vegetation sampling in 2018 was more intensive to gather vegetation data following the spring 2018 prescribed burn treatments. In June 2018 vegetation samples were collected from all sampling plots within the burn treatment block, and all sampling plots within an adjacent unburnt control treatment block in both the tame forage (S5) and native pasture (N8) (Figure 3.5). These plots were sampled again in July and August 2018. The rest of the treatment blocks within the tame forage (S5) and native pasture (N8) were sampled in July 2018, following the same random sampling plot selection as in July 2017.

For each sample plot visited, canopy percent cover was visually estimated for each plant species occupying the 1.0 m^2 permanent subplot. Visual estimates were done using the same observers for all subplots and the unique sample plot number corresponding to the subplot was recorded. Litter biomass from within the 0.25 m^2 subplot area was hand-raked and placed in a paper bag. After the litter was collected, the standing biomass rooted within the 0.25 m^2 subplot was clipped at ground level and placed in a paper bag. If a shrub was rooted with the biomass subplot, the stems and leaves of the current year's growth were clipped from the plant. All litter and biomass samples collected were oven dried at 80°C for 48 hours. Litter samples were weighed, and the mass were recorded. Biomass samples were sorted into graminoid, forb, and shrub. The mass of each of these plant classifications were weighed and recorded for each biomass subplot.

3.3.2.3 Cattle Movement

Spatial data on the movements of cattle with the pastures were collected using Lotek 7000MU and Lotek Litetrack420 UHF direct-downloadable GPS/VHF collars (Lotek Wireless Inc., 2020) as approved under University of Saskatchewan Animal Care Protocol 20170045. Seven collars were fitted to yearling heifers before they were turned out to OMB pastures in both the 2017 and 2018 grazing seasons. The GPS collars were programmed to record a geospatial fix every 15 minutes for the duration of the June to October grazing season. Collar data was periodically downloaded throughout the summer to prevent loss of data in the case of collar failure. Due to adjustments in grazing management, the duration and time period the cattle were in the tame forage (S5) and native (N8) pastures were not identical year to year, but both pastures had a month of overlap in usage between 2017 and 2018. Cattle were in the tame forage pasture (S5) between June 5 and July 8 in 2017 and 2018. The cattle were in the native pasture (N8) between July 25 and August 23 in 2017 and 2018. Collar data was processed using QGIS software (QGIS Development Team, 2019).

On Lotek Litetrack420 UHF and two Lotek 7000MU collars were tested for accuracy by placing them on the ground in an empty pasture for 13 consecutive days during the summer of 2018. The collars were programmed to record a geospatial fix every 15 minutes. Among the three collars, accuracy within 15 m was 96.8%.

3.4 Statistical Analyses

3.4.1 Univariate Analyses

The effects of the prescribed fires on plant community productivity, plant species richness, plant species evenness, and percent cover of exposed bare ground were examined using linear mixed effects models. The tame forage (S5) and native (N8) pastures were analyzed separately due to differences in species composition, grazing intensity, and pasture size. Within each pasture two models were used for each variable. The first model compared the seasonal effects of the burn treatment to the adjacent control block. The fixed effects were burn treatment, vegetation sampling month, and the treatment by month interaction. The second model compared the annual effects of the burn treatment. The fixed effects were burn treatment, year, and the treatment by year interaction. The second model only used July data as monthly sampling was not done in the pre-burn year and used all seven unburned (control) blocks. Sampling plot I.D. was used as a random factor to account for the repeat sampling of individual sampling plots. The mixed effects models were fit using R statistical software and the LMER function from the lme4 package (Bates et al., 2015; R Development Core Team, 2019). Biomass and percent cover of exposed bare ground values were transformed using log +1 to improve heteroskedacity in the models.

3.4.2 Multivariate Analyses

The effects of the prescribed fires on plant community composition were examined using ordination, permutational multivariate analysis of variance (PERMANOVA), and indicator species analysis (ISA) (Legendre and Legendre, 1998). The PERMANOVA and ISA models fit were the same as for the univariate analyses, with the tame forage pasture (S5) and the native pasture (N8) analyzed separately, and separate models comparing year-to-year and within season, due to the differences in species composition between these pastures. PERMANOVA models were fit to test whether the plant community composition differed between the burn treatment and the control. The PERMANOVA was performed using the adonis function in vegan package in R (Oksanen et al., 2019; R Development Core Team, 2019). ISA was used to identify species that may have individually responded to the burn treatments using the multipatt function in the indicspecies package in R (De Caceres and Legendre, 2009; R Development Core Team, 2019). The indicator species analysis identifies species that are significantly associated (i.e. more frequent and/or abundant) within a treatment. Overall compositional changes were visualized using a non-metric multidimensional scaling (NMDS) ordination of the percent cover for all species. The NMDS analysis was done using Bray-Curtis distances and the metaMDS function in the vegan package using R statistical software (Oksanen et al., 2019; R Development Core Team, 2019).

3.4.3 Cattle Movement Analyses

The effects of prescribed fire on cattle movement were examined using GPS tracking data from the 2017 and 2018 grazing periods. GPS data from seven heifers were combined and sorted into time periods where the cattle were in tame forage (S5) and native (N8) pastures during the same period in 2017 and 2018. For pasture S5 this was between June 5 and July 8, and for pasture N8 this was between July 25 and August 23. GPS points that were greater than 15 m outside of the pasture boundaries were removed from the data set, and GPS points that were collected using less than three satellites were also removed from the data set. GPS data was imported into QGIS and counts of GPS fixes recorded within each treatment block in S5 and N8 were counted in 2017 and 2018 data (QGIS Development Team, 2019). Chi-square goodness of fit tests were used to test whether the number of GPS fixes recorded within each treatment block in 2018 differed from the number of GPS fixes recorded in 2017. Using R statistical software these collar counts were then used to create mosaic plots to compare whether the observed number of counts was different than the expected number of counts (R Development Core Team, 2019). Heatmaps were created for each year in both the tame forage and native pastures in QGIS (QGIS Development Team, 2019). The heatmaps in each pasture were subtracted from each other to create a heatmap showing the differences between 2018 and 2017 grazing seasons to visualise changes in usage among the treatment blocks.

3.5 Results

Prescribed fire had statistically significant effects on plant productivity and plant community structure in both the tame forage and native pastures. Many of the significant fire effects interacted with year-to-year and seasonal patterns.

3.5.1 Tame Forage Pasture (S5)

The burned plots had more bare ground exposed and less litter biomass compared to the control plots (Table 3.1, Figure 3.6). Total, graminoid, and forb biomass decreased once grazing began (July and August 2018) in both burned and unburned treatments. Species richness was highest in the month of July in 2018, but there were no differences in species evenness between months or treatments. Substantial year-to-year variation was also observed with higher total and forb biomass, and less bare ground in July 2017 compared to July 2018. Graminoid biomass was lower and exposed bare ground was higher in the burned treatments compared to the unburned treatments in both sampling years. There were no significant effects of year or treatment on litter biomass, species evenness, and species richness.

Table 3.1. ANOVA results for mixed effects models from the tame forage pasture (S5) in a) 2018; b) July 2017 and July 2018. Bolded terms are significant.

Model	Component		Sum Sq	Mean Sq	Num DF	Den DF	F. value	P
a) S5 2018	forb	treatment	0.61	0.61	1	30	0.74	0.3960
		month	**5.68**	**2.84**	**2**	**30**	**3.48**	**0.0437**
		treatment:month	0.11	0.06	2	30	0.07	0.9330
	graminoid	treatment	0.71	0.71	1	10	2.87	0.1207
		month	**3.32**	**1.66**	**2**	**19**	**6.70**	**0.0062**
		treatment:month	0.32	0.16	2	19	0.65	0.5336
	litter	treatment	1.44	1.44	1	10	2.19	0.1695
		month	1.59	0.80	2	20	1.21	0.3192
		treatment:month	**9.00**	**4.50**	**2**	**20**	**6.84**	**0.0056**
	total	treatment	1.00	1.00	1	10	4.08	0.0711
		month	**4.96**	**2.48**	**2**	**20**	**10.13**	**0.0009**
		treatment:month	0.08	0.04	2	20	0.17	0.8468
	evenness	treatment	0.02	0.02	1	10	1.09	0.3200
		month	0.05	0.03	2	20	1.56	0.2337
		treatment:month	0.06	0.03	2	20	1.90	0.1757
	richness	treatment	0.01	0.01	1	10	<0.01	0.9460
		month	**24.39**	**12.19**	**2**	**20**	**7.65**	**0.0034**
		treatment:month	2.39	1.19	2	20	0.75	0.4856
	% bare ground cover	**treatment**	**0.73**	**0.73**	**1**	**10**	**5.03**	**0.0488**
		month	**1.79**	**0.89**	**2**	**20**	**6.17**	**0.0082**
		treatment:month	**1.11**	**0.56**	**2**	**20**	**3.84**	**0.0388**
b) S5 July 2017, 2018	forb	treatment	0.10	0.10	1	48	0.23	0.6358
		year	**4.05**	**4.05**	**1**	**48**	**9.25**	**0.0038**
		treatment:year	<0.01	<0.01	1	48	0.01	0.9268
	graminoid	**treatment**	**1.01**	**1.01**	**1**	**22**	**5.03**	**0.0355**
		year	0.89	0.89	1	8	4.39	0.0674
		treatment:year	<0.01	<0.01	1	8	<0.01	0.9581

Table 3.1 continued

Model	Component		Sum Sq	Mean Sq	Num DF	Den DF	F. value	P
b) S5 July 2017, 2018	litter	treatment	0.75	0.75	1	37	1.27	0.2674
		year	1.82	1.82	1	37	3.09	0.0871
		treatment:year	0.39	0.39	1	37	0.67	0.4197
	total	treatment	0.44	0.44	1	49	0.91	0.3452
		year	**3.27**	**3.27**	**1**	**49**	**6.78**	**0.0122**
		treatment:year	0.07	0.07	1	49	0.14	0.7141
	evenness	treatment	0.02	0.02	1	35.867	1.66	0.2055
		year	0.01	0.01	1	15.289	0.56	0.4656
		treatment:year	0.01	0.01	1	15.289	1.10	0.3102
	richness	treatment	0.02	0.02	1	35.867	1.66	0.2055
		year	0.01	0.01	1	51.289	0.56	0.4656
		treatment:year	0.01	0.01	1	15.289	1.10	0.3102
	% bare ground cover	**treatment**	**0.46**	**0.46**	**1**	**37.327**	**4.89**	**0.0333**
		year	**0.65**	**0.65**	**1**	**15.514**	**6.91**	**0.0186**
		treatment:year	0.30	0.30	1	15.514	3.18	0.0943

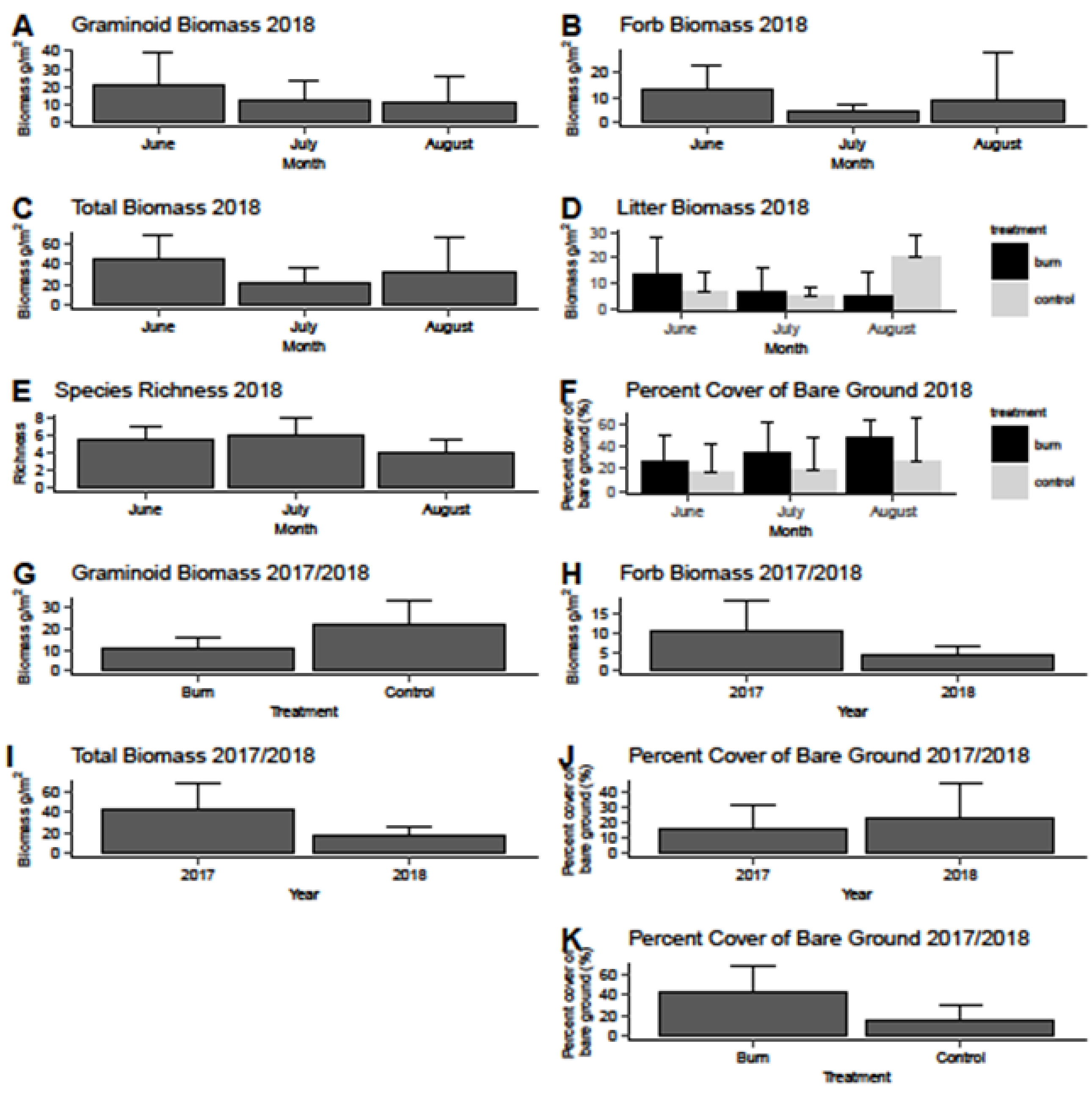

Figure 3.6. Linear mixed effects models in the tame forage pasture (S5) examining A) graminoid biomass 2018, B) forb biomass 2018, C) total biomass 2018, D) litter biomass 2018, E) species evenness 2018, F) percent cover of bare ground 2018, G) graminoid biomass July 2017 and July 2018, H) forb biomass July 2017 and July 2018, I) total biomass July 2017 and July 2018, J) percent cover of bare ground July 2017 and July 2018, K) percent cover of bare ground July 2017 and July 2018. Error bars represent standard error around the mean.

The two-dimensional NMDS model for the tame forage pasture (S5) in 2018 had a final stress of 0.156 (Figure 3.7) and the July 2017 - 2018 NMDS model had a final stress of 0.199 (Figure 3.8). The burn treatment homogenized species composition as indicated by the clustering of burn plots in the ordinations and the significant burn effect in the PERMANOVA (Table 3.2).

Table 3.2. PERMANOVA results based on Bray-Curtis dissimilarities using plant community composition data from the tame forage pasture (S5) a) 2018 biomass; b) July 2017 and July 2018 biomass. Bolded terms are significant.

Model	DF	Sum Sq	Mean Sq	F Model	r^2	P
a) S5 2018						
treatment	**1**	**0.92**	**0.92**	**6.40**	**0.1524**	**0.0020**
month	**2**	**0.75**	**0.28**	**2.63**	**0.1252**	**0.0270**
treatment*month	2	0.05	0.02	0.17	0.0082	0.9970
b) S5 July 2017, 2018						
treatment	**1**	**0.71**	**0.71**	**6.79**	**0.1085**	**0.0010**
year	**1**	**0.52**	**0.52**	**4.98**	**0.0795**	**0.0020**
treatment*year	1	0.09	0.09	0.85	0.0136	0.4560

In the 2018 growing season Russian wild-rye (*Psathyrostachys juncea*) was more common in the burn treatment and June grass (*Koeleria macrantha)*, scarlet mallow (*Sphaeralcea coccinea ssp. coccinea)*, and yarrow (*Achillea millefolium)* were more common in the control treatment (Table 3.3). Significant month effects in the 2018 growing season included Russian wild-rye being more common in June and July than in August and Sedge species (*Carex sp.*) more common in July. Significant burn treatment effects between July 2017 and July 2018 included Russian wild-rye, northern wheatgrass (*Elymus lanceolatus var. lanceolatus)* and broomweed (*Gutierrezia sarothrae)* being more common in the burn treatment. There were no species significantly more frequent or abundant in the unburned control in either of the seasonal or between year analyses.

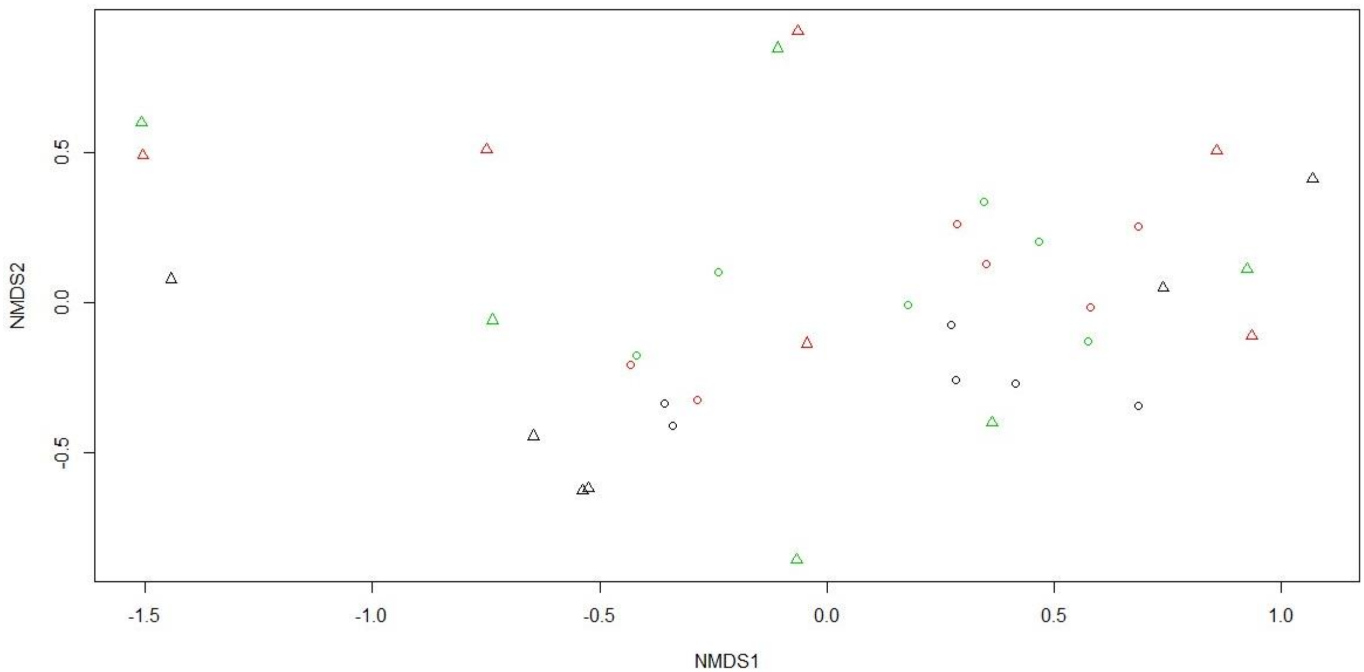

Figure 3.7. Plot scores from a NMDS run on the species data collected from the tame forage pasture (S5) in June (green), July (red), and August (black) 2018 in the burn treatment block (circles) and control treatment block (triangles).

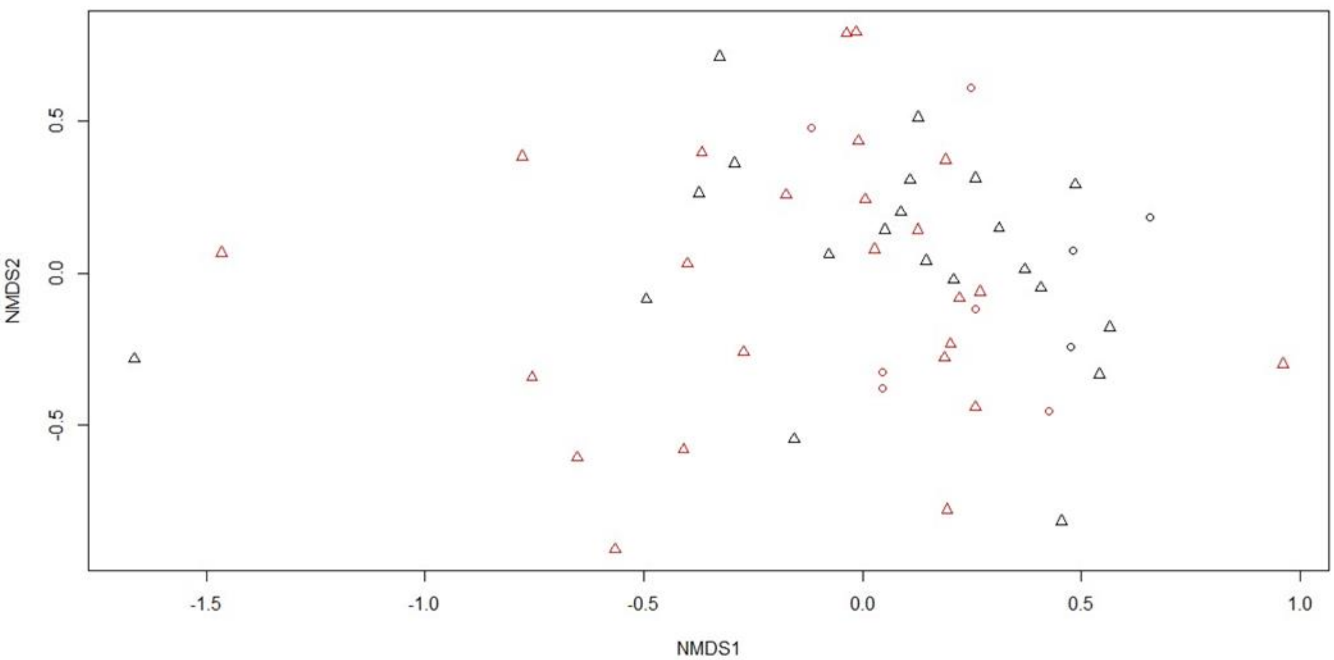

Figure 3.8. Plot scores from NMDS model of species in the tame forage pasture (S5) in July 2017 (black), July 2018 (red) and burn treatment block (circles) and control treatment blocks (triangles).

Table 3.3. Species indicator analysis results showing species significantly more frequent and abundant treatment combinations in the tame forage pasture (S5) in a) 2018; b) July 2017 and July 2018. Bolded terms are significant.

Model	Treatment	Indicator Value	P	Species
a) S5 2018	**burn**	**0.785**	**0.0050**	***Psathyrostachys juncea***
	control	**0.644**	**0.0300**	***Koeleria macrantha***
	control	**0.577**	**0.0450**	***Sphaeralcea coccinea ssp. coccinea***
	control	**0.527**	**0.0300**	***Achillea millefolium***
	June+July	**0.785**	**0.0300**	***Psathyrostachys juncea***
	July	**0.645**	**0.0050**	***Carex species***
b) S5 July 2017, 2018	**burn**	**0.749**	**0.0100**	***Psathyrostachys juncea***
	burn	**0.716**	**0.0300**	***Gutierrezia sarothrae***
	burn	**0.525**	**0.0500**	***Elymus lanceolatus var. lanceolatus***

3.5.2 Native Pasture (N8)

The burned plots had less total, graminoid, and litter biomass and higher species richness compared to the control sampling plots in the 2018 growing season (Figure 3.9, Table 3.4). Forb biomass and species evenness in 2018 did not differ by treatments and was lowest in the month of August, and highest in the month of June, respectively. There were no significant burn or month effects on exposed bare ground. Substantial year-to-year variation was also observed with higher total, graminoid, and litter biomass and less bare ground in July 2017 compared to July 2018. Total, graminoid, and litter biomass were lower in the burned treatment compared to the unburned treatment in both sampling years. There were no significant year or treatment effects on forb biomass, species evenness, and species richness in July 2017- 2018.

Table 3.4. ANOVA results for mixed effects models in the native prairie pasture (N8) a) 2018; b) July 2017 and July 2018. Bolded terms are significant.

Model	Component		Sum Sq	Mean Sq	Num DF	Den DF	F. value	P
a) N8 2018	forb	treatment	0.85	0.85	1	28	2.75	0.1087
		month	**2.90**	**1.45**	**2**	**56**	**4.66**	**0.0134**
		treatment:month	0.74	0.37	2	56	1.19	0.3106
	graminoid	**treatment**	**0.63**	**0.63**	**1**	**28**	**6.41**	**0.0172**
		month	0.05	0.03	2	56	0.23	0.7699
		treatment:month	**1.10**	**0.55**	**2**	**56**	**5.59**	**0.0061**
	litter	**treatment**	**10.42**	**10.42**	**1**	**28**	**21.47**	**<0.0001**
		month	**8.56**	**4.28**	**2**	**56**	**8.82**	**0.0005**
		treatment:month	**4.78**	**2.39**	**2**	**56**	**4.92**	**0.0107**
	total	**treatment**	**0.65**	**0.65**	**1**	**28**	**7.67**	**0.0099**
		month	0.45	0.22	2	56	2.63	0.0809
		treatment:month	**0.79**	**0.40**	**2**	**56**	**4.65**	**0.0135**
	evenness	treatment	<0.01	<0.01	1	28	0.23	0.6323
		month	**0.11**	**0.06**	**2**	**57**	**3.70**	**0.0307**
		treatment:month	0.05	0.02	2	57	1.60	0.2104
	richness	**treatment**	**11.69**	**11.69**	**1**	**28**	**6.05**	**0.0204**
		month	**43.47**	**21.73**	**2**	**57**	**11.24**	**<0.0001**
		treatment:month	5.17	2.58	2	57	1.34	0.2710

(Continued on next page)

Table 3.4 continued

Model	Component		Sum Sq	Mean Sq	Num DF	Den DF	F. value	P
a) N8 2018	bare ground cover	treatment	0.23	0.23	1	28	1.18	0.2865
		month	0.03	0.02	2	57	0.08	0.9201
		treatment:month	0.27	0.14	2	57	0.71	0.4968
b) N8 July 2017, 2018	forb	treatment	0.22	0.22	1	97	0.92	0.3404
		year	0.05	0.05	1	39	0.19	0.6682
		treatment:year	0.83	0.83	1	39	3.42	0.0722
	graminoid	treatment	<0.01	<0.01	1	101	0.01	0.9286
		year	**14.33**	**14.33**	**1**	**36**	**202.73**	**<0.0001**
		treatment:year	**2.05**	**2.05**	**1**	**36**	**28.98**	**<0.0001**
	litter	treatment	0.67	0.67	1	92	1.89	0.1728
		year	**2.72**	**2.72**	**1**	**41**	**7.61**	**<0.0001**
		treatment:year	**10.05**	**10.05**	**1**	**41**	**28.14**	**<0.0001**
	total	treatment	0.02	0.02	1	100	0.18	0.6734
		year	**9.06**	**9.06**	**1**	**40**	**85.56**	**<0.0001**
		treatment:year	**2.38**	**2.38**	**1**	**40**	**22.44**	**<0.0001**
	evenness	treatment	0.03	0.03	1	96.34	3.41	0.0679
		year	<0.01	<0.01	1	45.674	0.12	0.7261
		treatment:year	0.02	0.02	1	45.674	2.77	0.1030
	richness	treatment	1.64	1.64	1	97.098	0.78	0.3788
		year	0.15	0.15	1	40.976	0.07	0.7890
		treatment:year	2.42	2.42	1	40.976	1.15	0.2897
	bare ground cover	treatment	0.26	0.26	1	98.128	1.90	0.1717
		year	**1.29**	**1.29**	**1**	**41.026**	**9.31**	**0.0040**
		treatment:year	0.03	0.03	1	41.026	0.23	0.6342

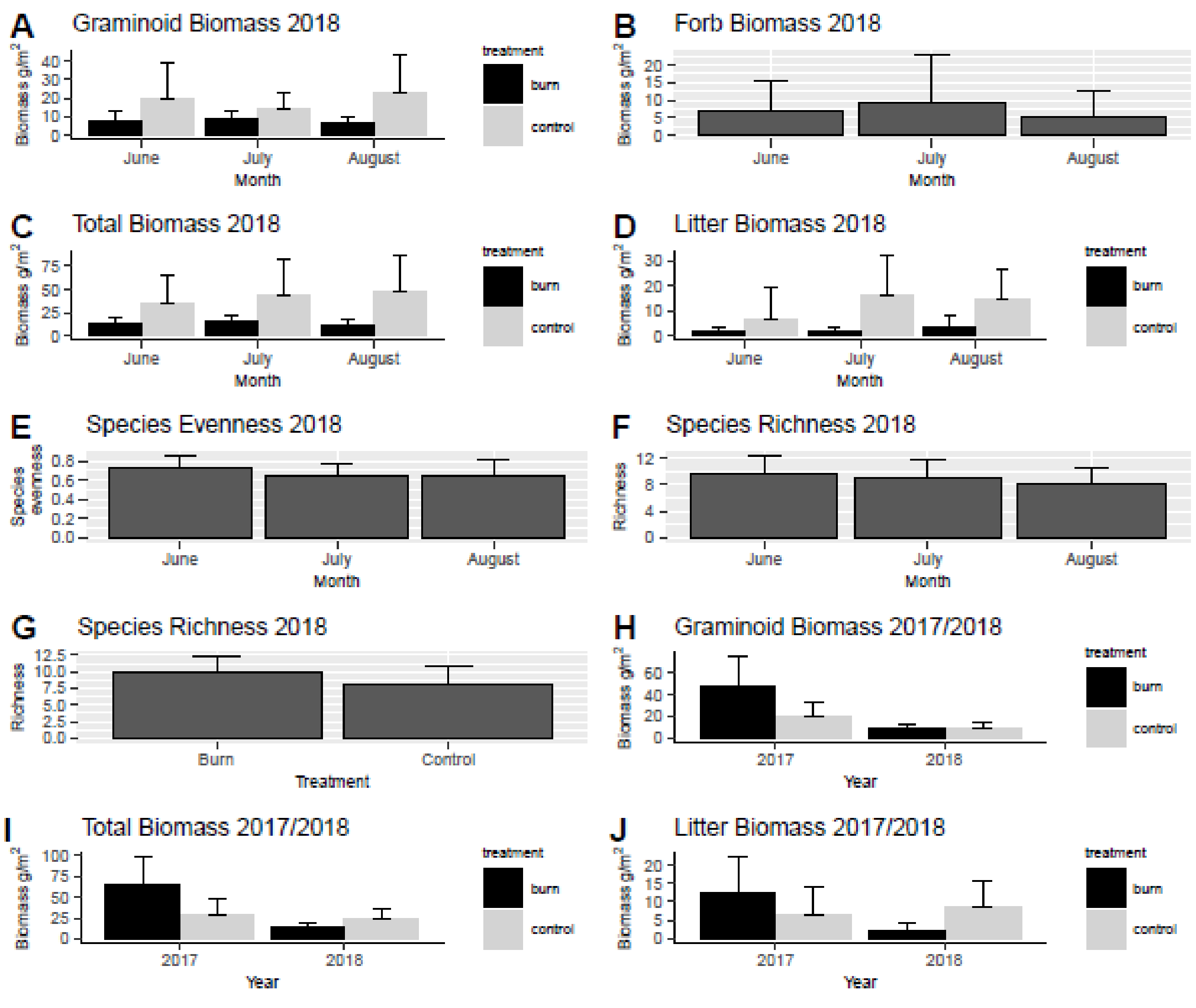

Figure 3.9. Linear mixed effects models in the native pasture (N8) examining A) graminoid biomass 2018, B) forb biomass 2018, C) total biomass 2018, D) litter biomass 2018, E) species evenness 2018, F) species richness 2018, G) species richness 2018, H) graminoid biomass July 2017 and July 2018, I) total biomass July 2017 and July 2018, J) litter biomass July 2017 and July 2018. Error bars represent standard error around the mean.

The two-dimensional NMDS model for the native pasture in 2018 had a final stress of 0.226 (Figure 3.10) and the July 2017 - 2018 model had a final stress of 0.247 (Figure 3.11). The burn treatment homogenized species composition as indicated by the clustering of burn plots in the ordinations and the significant burn effect in the PERMANOVA (Table 3.5).

Table 3.5. PERMANOVA results based on Bray-Curtis dissimilarities using plant community composition data from the native pasture (N8) a) 2018 biomass; b) July 2017 and July 2018 biomass. Bolded terms are significant.

Model	DF	Sum Sq	Mean Sq	F Model	r^2	P
a) N8 2018						
treatment	**1**	**2.43**	**2.43**	**8.44**	**0.0846**	**0.0010**
month	**2**	**1.28**	**0.64**	**2.22**	**0.0446**	**0.0030**
treatment*month	2	0.83	0.42	1.45	0.0291	0.0790
b) N8 July 2017, 2018						
treatment	**1**	**1.50**	**1.53**	**5.27**	**0.0384**	**0.0010**
month	**1**	**0.90**	**0.92**	**3.17**	**0.0231**	**0.0010**
treatment*month	1	0.20	0.25	0.87	0.0064	0.5980

In the 2018 growing season American vetch (*Vicia americana*), scarlet mallow, and hairy wild-parsley (*Lomatium foeniculaceum)* were more common in the burn treatment and grass-leaved death camas (*Zygadenus venenosus)*, slender wheatgrass (*Elymus trachycaulus ssp. trachycaulus*), green needle-grass (*Nassella viridula*), golden bean (*Thermopsis rhombifolia*) and sedge species were more common in the control treatment (Table 3.6). Significant month effects in the 2018 growing season included early blue-grass (*Poa cusickii)* being more common in June, western wheatgrass (*Pascopyrum smithii)* was more common in June and July, and slender wheatgrass was more common in July and August. Significant burn treatment effects between July 2017 and July 2018 included northern wheatgrass being more common in the burn treatment. There were no species significantly and more frequent and abundant in the control treatment. Significant year effects included inland blue-grass (*Poa interior*) being more frequent and abundant in 2017, and hairy golden-aster (*Heterotheca villosa*), prairie coneflower (*Ratibida columnifera*), Colorado rubberweed (*Hymenoxys richardsonii* var. *richardsonii*), inland salt grass (*Distichlis spicata* var. *stricta*) and mat muhly (*Muhlenbergia richardsonis*) more frequent and abundant in 2018.

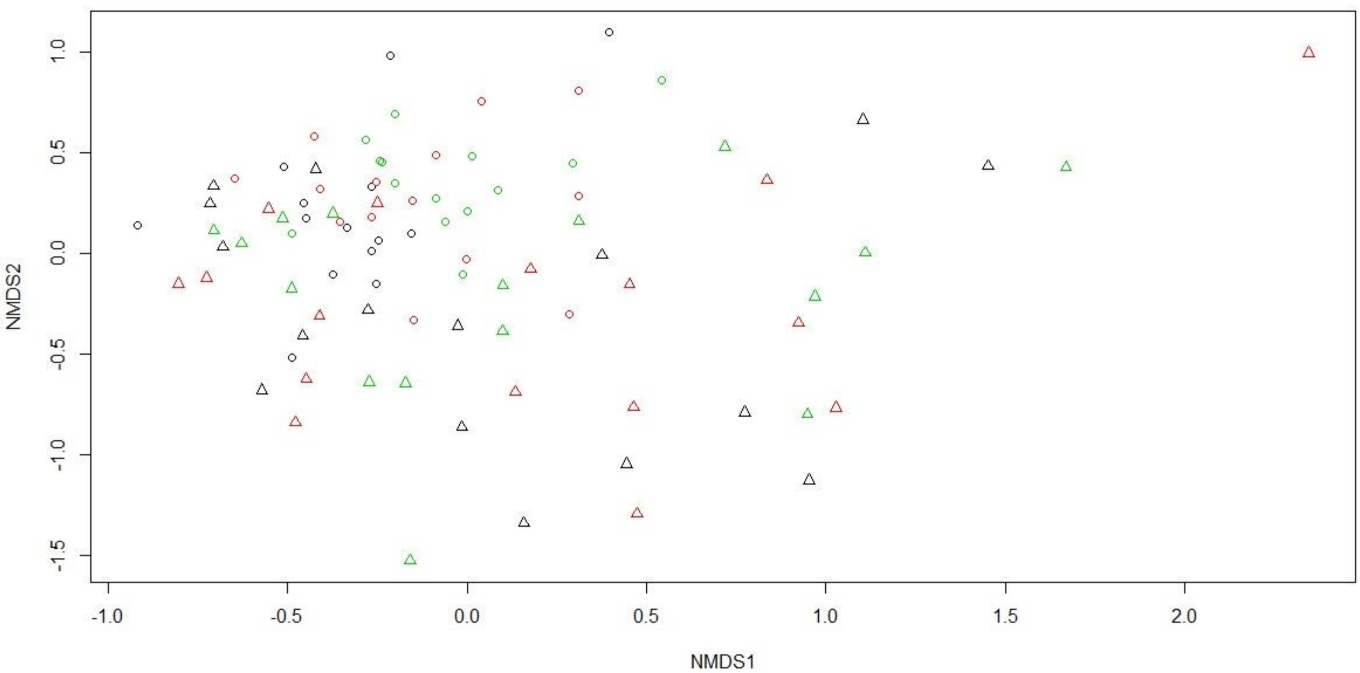

Figure 3.10. Plot scores from NMDS model of species in the native pasture (N8) in June (green), July (red), August (black) 2018 and burn treatment block (circles) and control treatment block (triangles).

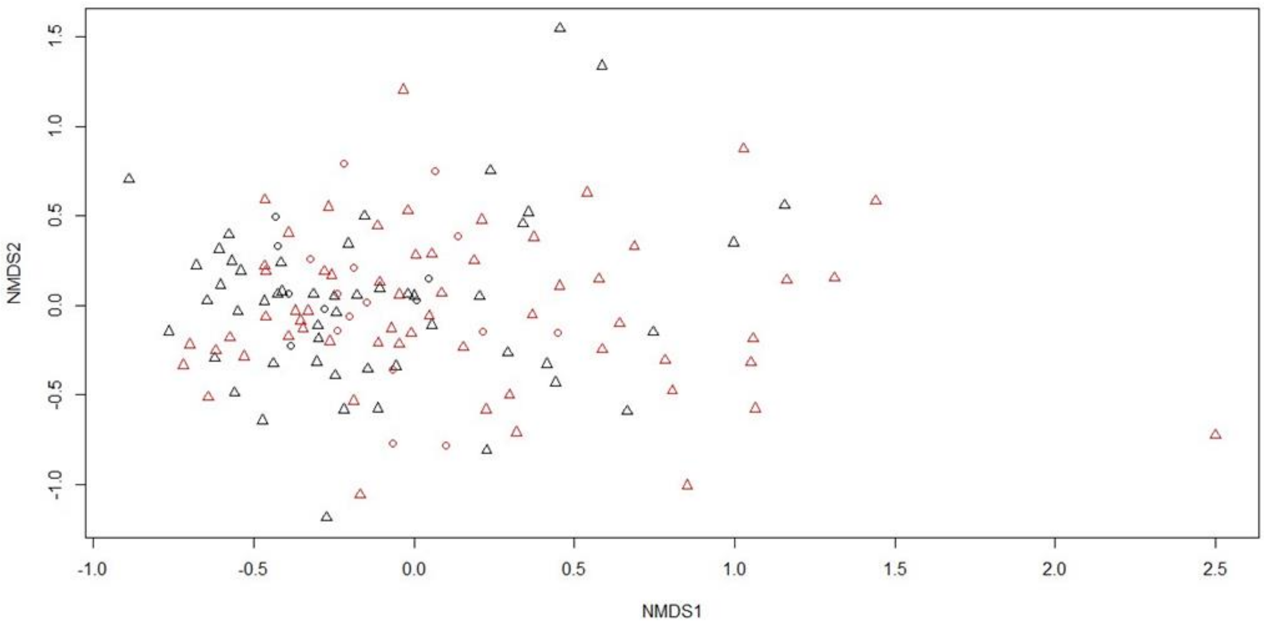

Figure 3.11. Plot scores from NMDS model of species in the native pasture (N8) in July 2017 (black), July 2018 (red) and burn treatment block (circles) and control treatment block (triangles).

Table 3.6 Species indicator analysis results showing species significantly more frequent and abundant treatment combinations from the native pasture (N8) in a) 2018; b) July 2017 and July 2018. Bolded terms are significant.

Model	Treatment	Indicator Value	P	Species
a) N8 2018	**Burn**	**0.787**	**0.0050**	***Sphaeralcea coccinea ssp. coccinea***
	Burn	**0.602**	**0.0050**	***Vicia americana***
	Burn	**0.408**	**0.0100**	***Lomatium foeniculaceum***
	Control	**0.673**	**0.0050**	***Elymus trachycaulus ssp. trachycaulus***
	Control	**0.577**	**0.0050**	***Carex species***
	Control	**0.408**	**0.0450**	***Thermopsis rhombifolia***
	Control	**0.382**	**0.0150**	***Nassella viridula***
	Control	**0.382**	**0.0200**	***Zygadenus venenosus***
	June	**0.548**	**0.0050**	***Poa cusickii***
	June+July	**0.679**	**0.0200**	***Pascopyrum smithii***
	July+August	**0.751**	**0.0050**	***Elymus trachycaulus* ssp. *trachycaulus***
b) N8 July 2017, 2018	**Burn**	**0.644**	**0.0250**	***Elymus lanceolatus var. lanceolatus***
	2017	**0.428**	**0.0300**	***Poa interior***
	2018	**0.576**	**0.0100**	***Heterotheca villosa***
	2018	**0.494**	**0.0150**	***Ratibida columnifera***
	2018	**0.435**	**0.0200**	***Hymenoxys richardsonii var. richardsonii***
	2018	**0.386**	**0.0100**	***Distichlis spicata var. stricta***
	2018	**0.321**	**0.0350**	***Muhlenbergia richardsonis***

3.5.3 Cattle Movement

Prescribed fire had significant effects on cattle movement in both the native and tame forage pastures (Tables 3.7 and 3.8). Overall, there was substantial variation in visitation rates between years (Table 3.8).

Table 3.7. Chi-square goodness of fit tests to test whether the number of GPS fixes recorded within each treatment block in 2018 differed from the number of GPS fixes recorded in 2017. Bolded terms are significant.

Pasture	χ-square	df	P
S5	**1335.1**	**7**	**<0.001**
N8	**1127.4**	**7**	**<0.001**

Table 3.8. Percentages of GPS collar counts from 2017 and 2018 in the tame forage (S5) and native prairie (N8) pastures and the percentage of frequencies expected during this time period assuming that the movement of the cattle across the pasture are random.

Pasture	Treatment block	Percentage (%) of total counts in 2017	Percentage (%) of expected frequency 2017	Percentage (%) of total counts in 2018	Percentage (%) of expected frequency 2018
S5	control1	7	8	9	8
	control2	8	8	8	8
	control3	9	7	5	7
	control4	13	13	14	13
	control5	11	9	6	9
	control6	34	26	18	26
	burn	4	8	11	8
	control8	14	21	28	21
N8	control1	20	14	8	14
	control2	9	14	17	14
	control3	6	5	5	5
	control4	14	8	3	8
	burn	8	10	13	10
	control6	6	6	5	6
	control7	31	38	43	38
	control8	6	5	5	5

3.5.3.1 Tame forage pasture (S5)

In the tame forage pasture (S5) the cattle had lower than expected visitation to the burn treatment block in 2017, while in after the prescribed fire treatment in 2018, the cattle had higher than expected visitation rates (Figure 3.12 and 3.14). Overall, there was substantial variation in visitation rates between years with four of the seven control treatment blocks having significant variation in visitation between years. (Figure 3.12).

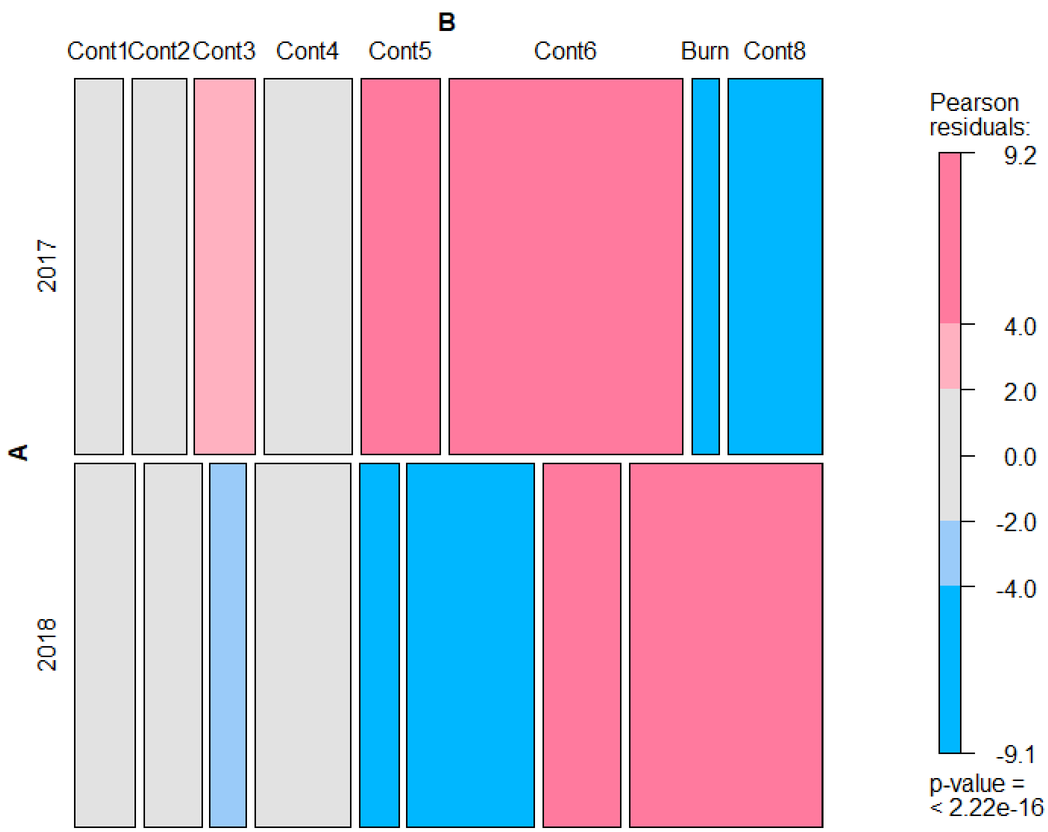

Figure 3.12: A mosaic plot illustrating count data collected in the tame forage pasture (S5) from seven heifers fitted with GPS collars from June 5 to July 8 in 2017 and 2018. Each treatment block within pasture S5 are represented along the y-axis (7 control blocks, 1 burn block). The year of data collection is along the x-axis (2017 and 2018). The sizes of the tiles are scaled to the relative frequencies of the collar count data. Warmer coloured cells indicate a higher than expected frequency, cooler coloured cells indicate a lower than expected frequency.

3.5.3.2 Native pasture (N8)

In the native pasture (N8) the cattle had lower than expected visitation to the burn treatment block in 2017, while in 2018, after the prescribed fire treatment, the cattle had higher than expected visitation rates (Figure 3.13 and 3.14). Overall, there was substantial variation in visitation rates between years with four of the seven control treatment blocks having significant variation in visitation between years. (Figure 3.13).

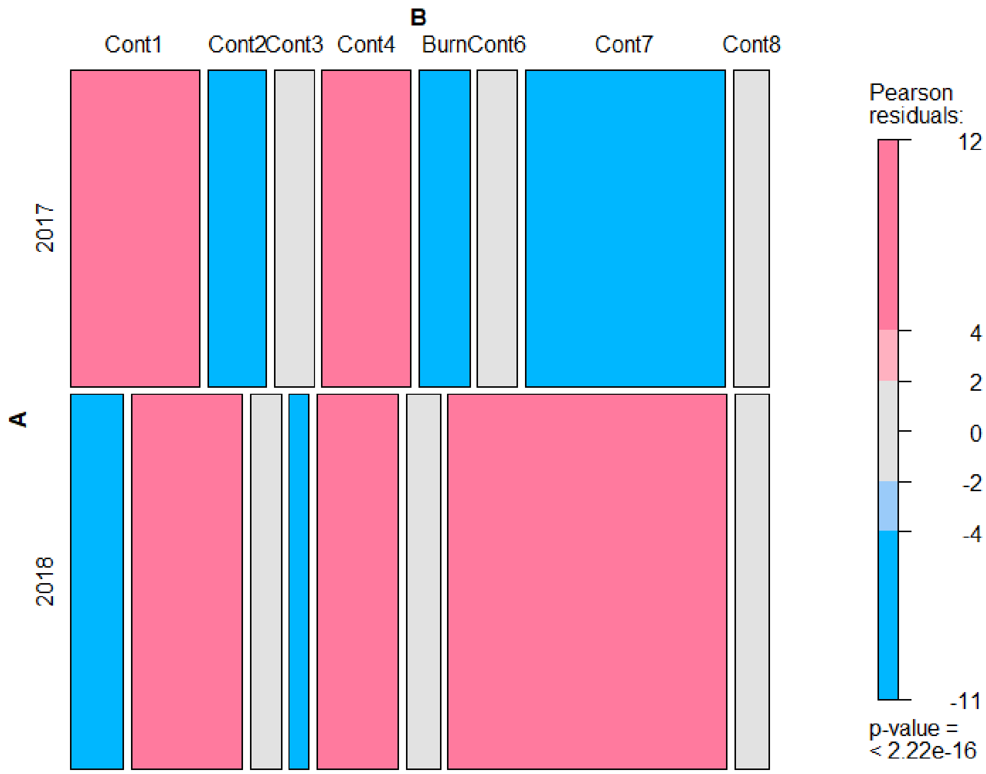

Figure 3.13: A mosaic plot illustrating count data collected in the native pasture (N8) from 7 heifers fitted with GPS collars from July 24 to August 23 in 2017 and 2018. Each treatment block within pasture N8 are represented along the y-axis (7 control blocks, 1 burn block). The year of data collection is along the x-axis (2017 and 2018). The sizes of the tiles are scaled to the relative frequencies of the collar count data. Warmer coloured cells indicate a higher than expected frequency, cooler coloured cells indicate a lower than expected frequency.

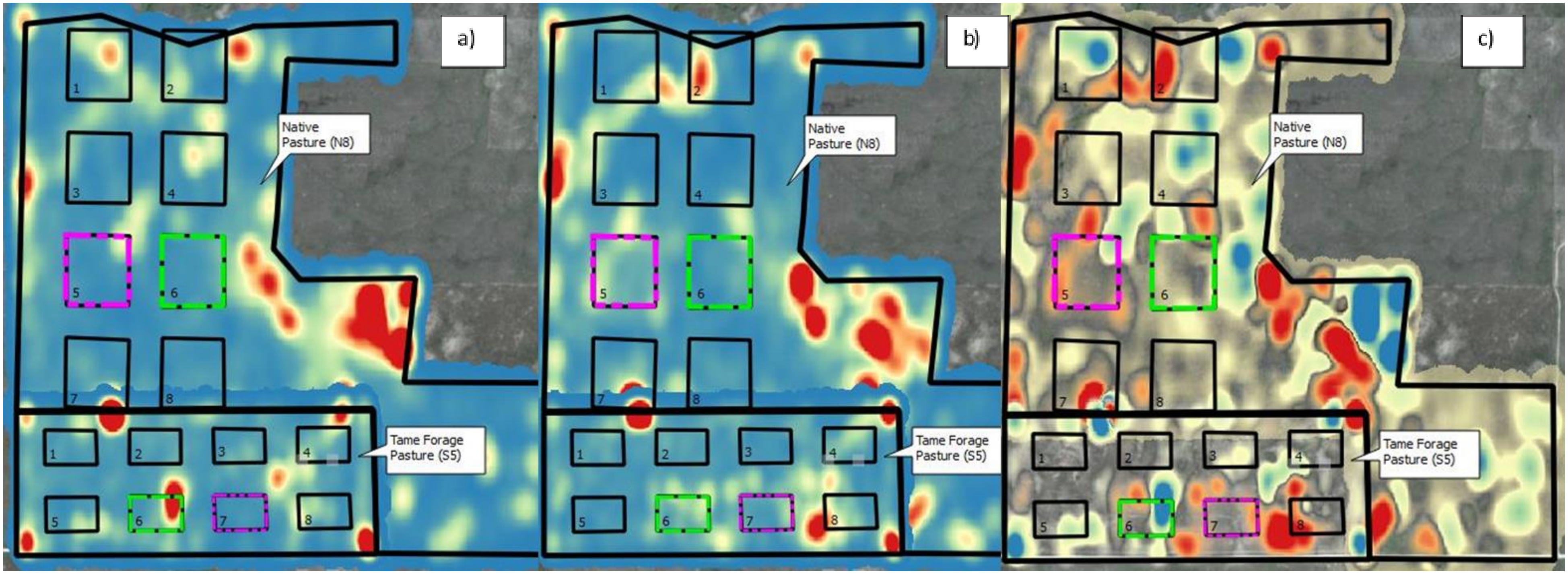

Figure 3.14. Heatmaps created from grazing period in a) 2017; b) 2018; where warmer colours indicate more frequent visitation; c) subtraction of 2018 heatmap from 2017 heatmap; where warmer colours show an increase in usage in 2018 and cooler colours show a decrease of usage in 2018. Burn treatment blocks are outlined in pink, 2018 control block outlined in green, and 2017-2018 control blocks outlined in black. Treatment blocks in each pasture are numbered in the bottom left corner of each block.

3.6 Discussion

My study demonstrated that, in the short-term, prescribed fire had significant effects on plant productivity and plant community structure in both tame forage and native prairie pastures but has little influence the movement of cattle within the pastures. My results are consistent with burning effects on vegetation across the Great Plains (e.g., White and Currie, 1983; Fuhlendorf and Engle, 2001; Powell et al., 2018; Shay et al., 2001), however the effect of burning on livestock movement here was much less pronounced than in similar studies (e.g., Allred et al., 2011; Augustine and Derner, 2014; Powell et al., 2018; Vermeire et al., 2004).

3.6.1 Vegetation Structure

Many of the significant effects of fire on plant productivity and plant community structure interacted with year-to-year and seasonal patterns. Burning in the native prairie pasture reduced biomass more strongly than in the tame forage pasture. Bare ground cover increased in the tame forage pasture with burning but did not significantly change in cover in the native pasture. The importance of year-to-year effects is expected, because precipitation is the dominant driver of plant productivity in the mixed grass prairie (Biondini et al., 1998; Maurer et al., 2020; Samson et al., 2004; Wiles et al., 2011) and biomass is more responsive to precipitation than to fire (Maurer et al., 2020; Vermeire et al., 2011; Vermeire et al., 2014). Growing conditions in 2016, the year prior to the start of the study, were extremely wet with 134% of the average precipitation (Government of Canada, 2019). The year when the study was initiated was the driest on record (47% of average precipitation), while 2018 was also below normal precipitation (58% of average). Soil moisture plays an important role in the production of prairie vegetation (Coupland, 1958; Deutsch et al., 2010) and it is probable the soil moisture from 2016 carried over to 2017 and allowed for more favorable growing conditions despite the drought. After two dry summers this moisture carryover was likely exhausted and biomass in 2018 was consequently lower. Fire-driven reductions in productivity are also not surprising as other studies have found that biomass in northern mixed grass prairie and tame forage can decrease for up four years after burning (Gates et al., 2017b; Lodge, 1960; Powell, 2017; Redmann, 1978; Romo et al., 1993). This is not universal, however, as some studies have reported no post-fire changes in biomass (Shay et al., 2001).

Litter biomass in the native prairie pasture declined after burning and in the second year of my study, while the litter biomass in the tame forage pasture did not significantly differ year-to-year or between burn treatments. The litter biomass in the tame forage pasture did not noticeably decline after burning, because the heavy grazing intensity within this small pasture prevents the accumulation of litter (Biondini et al., 1998). Litter plays an important role in forage production in the mixed grass prairie, with increasing litter biomass improving plant productivity (Deutsch et al., 2010; Hilger and Lamb, 2017). Litter acts to insulate the soil surface, improve soil moisture in the growing season, and trap snow in the dormant season (e.g., Facelli and Pickett, 1991; Willms et al., 1986). Redman et al., (1978) found that the removal of litter from fire decreased the productivity of cool season grasses in the northern mixed grass prairie. Declines in litter biomass are common following burning and are noticeable several years after burning in the northern prairies (Mori, 2009; Shay et al., 2001; Vermeire et al., 2011).

The cover of bare ground increased with burning throughout the growing season in the tame forage pasture and both pastures had an increase in bare ground in the second year of my study. This annual increase in bare ground could be a result of back to back years of below normal precipitation and intensive grazing. The amount of bare ground present on a site can be influenced by the history of the site and the grazing intensity on the site (Fuhlendorf et al., 2002). Burning increases the amount of bare ground on a site, because it partially or completely removes standing and dead vegetation. Increased amounts of bare soil are common after burning and can continue to be detectable up to four years after burning (Erichsen-Arychuk et al., 2002; Gates et al., 2017a; Gross, 2005; Mori, 2009; Shay et al., 2001). The tame forage pasture would be expected to have more bare ground present than the native prairie pasture because it has been cultivated and the protective moss and lichen layer over the soil has been removed (Weber et al., 2016). Burning in the native prairie pasture did not result in an increase in bare ground as these protective biological soil crusts that cover the ground remained largely intact after burning. This moss and lichen layer of vegetation found on native prairie can take decades to centuries to establish and function to hold in soil moisture and stabilize the soil surface (Concostrina-Zubiri et al., 2014; Weber et al., 2016).

In the short-term, prescribed burning did not have a significant effect on species richness or species evenness in the tame forage and the native prairie pastures. Vegetation is generally least affected by fires in the dormant season with low fuel loads (Augustine et al., 2010; Coupland and Johnson, 1965). Fires that occur during the dormant season are generally less intense than fires that occur during the summer months (Wright and Bailey, 1982). A single burn may not be a significant enough disturbance to initiate changes to species richness and species evenness, as similar results have been found in the tallgrass prairie (Dickson et al., 2019), mixed grass (Gates et al., 2017a) and fescue prairie (Mori, 2009). My study found plant community composition were homogenized with burning in both the tame forage and native prairie pastures. The tame forage species Russian wild-rye (*Psathyrostachys juncea*) was more common within the burned patch of the tame pasture and several forb species were more commonly associated with the burned area in the native pasture. Fire can result in a competitive release of subdominant forb species through an increase in available light, space, and nutrients (Gates et al., 2017a; Harrison et al., 2003; Willms et al., 1986). However, this is not always the case as declines in the abundance of forbs have been recorded after burning in consecutive years (Shay et al., 2001).

3.6.2 Cattle Movement

Cattle movement in summer 2018 appears to have been influenced by the spring 2018 prescribed burns in the native prairie and tame forage pastures. There was a slight increase in cattle visitation within the burned treatment blocks in 2018 compared to the same time period during 2017. Although there was a significant increase in visitation to the burned areas, there was substantial variation in visitation to unburned areas of the pastures between the study years. In both pastures, the cattle visitation was heavily focussed near water sources and areas of low topography. The attraction to the burned areas could have been obscured by these other landscape features within the pastures, or in the case of the tame pasture by the heavy stocking rate that resulted in almost all available forage being eaten. The attraction of grazing animals to recently burned areas is well documented in the tallgrass prairie (Allred et al., 2001; Coppedge and Shaw, 1998; Knapp et al., 1999), fescue prairie (Mori, 2009), shortgrass prairie (Augustine and Derner, 2014), and mixed grass prairie (Erichsen-Arychuk et al., 2002; Powell et al., 2018). Vegetation growth following fire is more palatable to grazing animals and has higher crude protein content compared to the surrounding unburned vegetation (Allred et al., 2011; McGinty et al., 1983; Powell et al., 2018; Smoliak et al., 1981; Vermeire et al., 2004). This preferred selection for landscape areas that have been burned decreases with time since fire (Allred et al., 2011), as the nutritional content returns to unburned levels within 120 days in the mixed grass prairie (Powell et al., 2018). In periods of drought, the increase in nutritional content after fire is less predictable and less pronounced compared to non-drought conditions (Bielski et al., 2018). The limited strength of the attraction to burned areas in my study could be a result of the drought conditions and the limited amount of time the cattle had access to the burned areas within the pastures. Additionally, the size of the pastures (45 ha tame forage; 151 ha native prairie) and the area burned within the pastures (5 ha in tame forage; 9 ha in native prairie) were considerably smaller than many pyric herbivory studies (Allred et al., 2011; Arterburn et al., 2019; Powell et al., 2018). Although smaller burned areas can facilitate a higher concentration of grazing compared to larger burned areas, the cattle in my study did not form a concentrated grazing lawn within the burned patches. Further research manipulating the season of the prescribed burn, the elapsed time between burning and the commencement of grazing, and the size of the burn are required. Further exploration of these data would benefit from the use of resource selection function analysis to examine the spatial data and assess the influence of habitat characteristics (i.e. vegetation community, slope, distance to water, etc) on cattle movement within the pastures (McLoughlin et al., 2010).

The influence of fire on the movement of cattle was less pronounced in mesic areas where precipitation is a limiting factor in plant growth. In my study, drought conditions through both grazing seasons studied likely decreased the length of time the burned areas were attractive on the landscape. Additionally, the natural topedaphic variability within the pastures likely played a more important role in the distribution of cattle within the pastures. Some areas on the landscape are more desirable for grazing based on the vegetation it can support due to topedaphic effects. Furthermore, cattle select areas close to water and avoid areas with steep slopes (Allred et al., 2011). Finally, the heavy grazing intensity from the previous growing season reduced the amount of fuel available to burn a contiguous area. Therefore, incomplete combustion was evident as some areas within the burned patch did not burn at all and this may have lessened attraction to the burned area.

Generally, reduced stocking rates are recommended when grazing pastures that have been burned (Erichsen-Arychuk et al., 2002), though some recent studies suggest that there is no need for rest after burning (Augustine et al., 2010; Gates et al., 2017b; Vermeire et al., 2018). My research in the northern mixed grass prairie of Saskatchewan suggests that both native prairie and tame forage pastures are resilient to pyric herbivory in the first growing season after fire. In both pastures, burning caused few short-term changes in plant community structure as a result of burning after one growing season. Managing pastures for heterogeneity by conducting prescribed burning in portions of a pasture can be used as a tool to maximise forage quality in burned patches and maintain forage quantity in unburned patches (Allred et al., 2014; Augustine et al., 2010; Powell et al., 2018). Economic benefits to cattle producers can also occur as a result of patch burn grazing due to the increase in forage quality after fire (Powell et al., 2018; Scasta et al., 2016). In the tallgrass prairie, pastures with two or more patches created by fire-grazing interaction had greater stability in livestock weight gains and did not depend on the precipitation in a six-year study (Allred et al., 2014; Svejcar, 1989). In addition to the economic benefits for livestock producers, patch burning and grazing promotes heterogeneity within the landscape and provides habitat to grassland song birds, many of which are experiencing sharp declines in population (Duchardt et al., 2016; Environment and Climate Change Canada, 2017; Pylypec, 2017). Federally listed species such as the Chestnut-collared Longspur (*Calcarius ornatus*) prefer sparsely vegetated habitats which can be created through patch burning and grazing, while Sprague's Pipit (*Anthus spragueii*) utilize undisturbed areas with mature vegetation (COSEWIC, 2009, 2010; Davis, 2004). Restoring the natural fire-grazing relationship in the northern mixed grass prairie aligns with federal species at risk action plans for multiple at-risk species and appears to be a viable means to utilize rangeland for cattle production. Furthermore, the importance of managing rangeland for conservation of species at risk has resulted in the creation of incentive programs for producers to improve habitat quality within this region of the Canadian prairies (Environment and Climate Change Canada, 2017; SODCAP, 2015).

Long-term studies are required to fully assess the effects of pyric herbivory in the mixed-grass prairie through periods of natural climatic variability (i.e., wet and dry cycles) and to evaluate the recovery of the vegetation over time. Further research into the impacts of location, frequency, and timing of burns, as well as size of pasture, stocking rate, and grazing intensity are needed to full understand the interactions between fire and grazing through space and time in the northern mixed grass prairie (Allred et al., 2011; Fuhlendorf and Engle, 2001; Gross and Romo, 2010; Howe, 1994; Romo, 2003).

4.0 Conclusion

4.1 General Conclusions

The rapid settlement and conversion of the Great Plains of North America has resulted in the dramatic loss of native prairie, and in turn significant losses to biodiversity within these grassland ecosystems (Hoekstra et al., 2005; Samson and Knopf, 1994). As such, it is crucial that remaining grasslands are managed to maintain ecological function to prevent further losses to biodiversity. Reintroducing fire to grassland ecosystems is one conservation management method to maintain natural landscape disturbances and create habitat heterogeneity (Fuhlendorf and Engle, 2001; Fuhlendorf et al., 2009). Habitat heterogeneity is then maintained by grazing animals which are attracted to the vegetation regrowth after fire, further promoting diversity in vegetation structure and composition (Powell et al., 2018).

Although the fire-grazing interaction has been well studied in the grassland biomes of the across the world (e.g., Archibald and Bond, 2004; Fuhlendorf and Engle, 2001; Huang et al., 2018), few studies have focused on the fire-grazing interaction in the northern mixed grass prairie (Powell et al., 2018). I conducted my research in the northern mixed grass prairie on Nature Conservancy Canada's Old Man on His Back Heritage and Conservation Area (OMB) property in southwest Saskatchewan. Through my study, fire was reintroduced to this landscape by conducting prescribed fires within a tame forage pasture and a native prairie pasture. I examined the short-term effects of fire on plant community structure and plant productivity and I tracked the movements of cattle grazing within these pastures to assess whether the fire influenced their movement. I found that many of the significant effects of fire on plant community productivity and plant community structure interacted with year-to-year and seasonal patterns. In general, precipitation is the dominant driver of productivity in more arid regions of the Great Plains (Maurer et al., 2020; Samson et al., 2004; Wiles et al., 2001) and plant biomass is more responsive to precipitation than to disturbance events such as fire (Vermeire et al., 2011, 2014). My study demonstrates that in the short-term, consistent with many other studies (e.g., Fuhlendorf and Engle, 2001; Powell et al., 2018; Shay et al., 2001; White and Currie, 1983), the plant communities of the northern mixed grass prairie are resilient to burning. Evidence for pyric herbivory, however, was weak in my study. There was a significant increase in cattle visitation to the areas that were burned in the spring prescribed fires, however this attraction is masked by substantial year-to-year variability in visitation, and is generally weaker than effects seen in pyric herbivory studies in more mesic grasslands (e.g., Augustine and Derner, 2014; Powell et al., 2018; Vermeire et al., 2004).

Limitations to my study include the use of only a single burn in each pasture type. Replication of burns within the tame forage and native prairie pastures would help to minimize the topoedaphic effects on vegetation composition and increase statistical power. Replicate burns were planned for this study but could not be implemented due to narrow windows of weather within the prescribed fire parameters. Additional limitations include the lack of grazing exclusion areas within the pastures, so comparisons could not be made between undisturbed vegetation, grazed vegetation, and burnt vegetation. These limitations are primarily driven by the large logistical challenges in designing and implementing large-scale experimental grazing and burning studies. Future pyric herbivory research in the northern mixed grass prairie should focus on manipulating burn frequency, timing, and the size of the burn patch. Further research into the effects of fires on cattle distribution should be further examined through manipulating pasture size, the lag time for the cattle to have access to the burn, and the breed and age of the livestock. My study was initiated during a drought period that was preceded by a wet cycle. A long-term study that encompasses both wet and dry cycles is required to determine the effects of pyric herbivory in the northern mixed grass prairie. This opportunity exists in the nearby 90,700 ha, Grasslands National Park (GNP). GNP has a robust prescribed fire program that outlines at least 75 ha of burning per year to achieve specific ecosystem objectives (Government of Canada, 2018). Therefore, GNP would be an ideal location to build on fire and grazing research in the northern mixed grass prairie. The prescribed fire program combined with wildfires that have occurred within the park and grazing from the Parks' bison and cattle, this site could be used to further examine spatial and temporal effects of pyric herbivory at a larger scale.

OMB is in the South of the Divide area that is important habitat for nine federally listed species at risk (Environment and Climate Change Canada, 2017). The 5,300 ha OMB property is managed by Nature Conservancy Canada and is divided into several pastures for cattle and bison grazing. Reintroducing fire to the grasslands within the OMB property aligns with Action Plan and Recovery Strategies for several of the federally listed species known to occur in the area (Environment and Climate Change Canada, 2017). Prescribed burning as a conservation tool would also be beneficial to implement to the neighbouring 20,000 ha Govenlock pasture, recently transfered from the Prairie Farm Rehabilitation Administration to Environment and Climate Change Canada. Furthermore, nearby Grasslands National Park has a robust prescribed fire program, and although the area encompassed by these grasslands are relatively small compared to their historical extent, restoring these disturbance patterns will benefit the structure and function of these ecosystems.

An additional benefit of using pyric herbivory as a land management tool is the creation of natural fire breaks in the landscape which reduce the need to plough the land to create fire breaks (Starns et al., 2019). Fire breaks created by ploughing the land add linear disturbances within grasslands, open the landscape to invasion from non-native and invasive species, and negatively impact habitat quality for many species at risk (Environment and Climate Change Canada, 2017).

Fire breaks are used to stop or slow down the spread of wildfires. Wildfires generally occur in the summer months when air temperature and wind speeds are high and relative humidity is low. These conditions create intense burns which are extremely dangerous and difficult to subdue. Wildfires are predicted to become more frequent and increase as a result of global climate change causing more extreme fluctuations in wet and dry periods along with an average increase in air temperature (Intergovernal Panel on Climate Change, 2007; Flannigan et al., 2009; Kulshreshtha, 2011; Shepherd and McGinn, 2003). These conditions are ideal for wildfires as wet years accumulate vegetative biomass followed by drought where the vegetation cures and becomes perfect fuel for igniting. Such events occurred during the initiation of my study where 2016 had 134% of the average yearly precipitation followed by drought in 2017 with only 47% of the average yearly precipitation (Government of Canada, 2019). As a result of these conditions, there were several devastating wildfires in southern Alberta and in Saskatchewan in the fall of 2017.

Using prescribed fire as a tool to remove accumulated biomass creates a natural fuel break in the landscape that can stop or slow down a wildfire. An example of this occurred in the spring of 2019 at Cranberry Flats, a conservation grassland managed by Meewasin Valley Authority near Saskatoon, Saskatchewan (R. Grilz pers. com., 2020). A wildfire burning on a trajectory that threatened several acreages was deflected by a prescribed fire patch less than 1 ha in area that had been created the previous fall. Ultimately the slowed fire could be safely contained by firefighting crews without the use of ploughed firebreaks, in part due to the consistent prescribed burning program implemented by the Meewasin conservation group (R. Grilz pers. com., 2020). This is one example that shows that by using a proactive approach to conducting prescribed fires under safe weather conditions, land managers and conservation groups can potentially reduce the severity and destructiveness of wildfires.

4.2 Management Implications

Based on results from my research, I recommend that prescribed fires continue to be used as a management tool within OMB to promote species at risk habitat by creating habitat diversity within pastures. By combining Indigenous ways of knowing with contemporary research, fire can be effectively utilized as a land management tool (Miller et al., 2010). By engaging both Indigenous and non-Indigenous communities and stakeholders, rangeland management can also be another avenue from which partnerships are strengthened towards reconciliation.

Given that a primary management goal is to create habitat diversity for species at risk (Nature Conservancy Canada, 2011), cattle stocking rates will have to be monitored closely and may need to be adjusted to create heterogeneity in vegetation structure (McGranahan et al., 2012; Richardson, 2012). Too high of a stocking rate will result in uniform vegetation structure despite the presence of burned patches and too low of a stocking rate will not provide enough grazing pressure to maintain some areas of vegetation at low vegetation height (Arterburn et al., 2019; Richardson, 2012; Scasta et al., 2016). Intermediate cattle stocking rates after patch burning generally results in the greatest habitat heterogeneity (Scasta et al., 2016).

Managing for habitat heterogeneity is important for grassland birds. For example, the short vegetation structure created in burned patches is thought to benefit species such as the at risk Chestnut-collared Longspur which prefers sparsely vegetated areas (COSEWIC, 2009; Davis, 2004). Other species such as the threatened Sprague’s Pipit selects habitats which have tall vegetation structure (COSEWIC, 2010; Davis, 2004). This requires pasture areas with low grazing intensity and no recent fire. In the case of OMB, the grazing intensity in the tame forage pasture was too heavy to create spatially discrete patches of vegetation as a result of the fire and grazing. Instead, this pasture is grazed to a uniform low vegetation height and there were no differences between total biomass and litter biomass in the burned areas compared to the unburned areas. Additionally, maintaining vegetation cover is important to facilitate prescribed burning, as there needs to be enough fuel continuity to create a distinctly burned patch (McGranahan et al., 2012).

Heavy grazing intensity will reduce productivity and prevent the accumulation of litter within the pasture (Biondini et al., 1989; Government of Canada and Government of Saskatchewan, 2008). Litter carryover is also very important for soil moisture retention under most climatic conditions (Deutsch et al., 2010; Hilger and Lamb, 2017). including dry periods which are predicted to occur more frequently due to global climate change, along with an average increase in air temperature (Intergovernmental Panel on Climate Change, 2007; Kulshreshtha, 2011; Shepherd and McGinn, 2003). Intensive grazing generally deteriorates the range condition and can increase cover of bare ground. In both the tame forage and native prairie pastures, bare ground increased as my study progressed. Bare ground can open the landscape to invasion of non-native and invasive species, which can compromise the structure and function of the grassland (Bailey et al., 2010; Government of Canada and Government of Saskatchewan, 2008). An increase in bare ground and the invasion of non-native species is of particular concern to native prairie pastures as they are a more sensitive ecosystem than tame forage pastures which can be more easily rejuvenated with herbicide and reseeding (Government of Canada and Government of Saskatchewan, 2008; Omokanye et al., 2019). Therefore, I recommend stocking rates and grazing duration within these pastures be adjusted to increase litter carryover and prevent the exposure of bare ground.

4.3 Conclusion

Overcoming the social perception that prescribed burning is dangerous will be an important factor to utilizing fire as a tool in the northern mixed grass prairie. This project demonstrates that the public fear of fire can be overcome through communication and participation by the local community members, rural municipalities, First Nations, local fire departments, and conservation groups. Furthermore, interagency collaboration and community participation reduces equipment costs, allows for a larger crew on the fire line, and trains and exposes more people to prescribed fires. Reintroducing fires to the northern mixed grass prairie is an important tool land managers and conservation groups can implement to maintain ecological function and biodiversity in these endangered ecosystems.

5.0 References

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6.0 Appendix

Appendix A: Ordination species scores from NMDS analyses comparing burned and unburned pastures.

Table A.1. Species scores for 2018 tame forage pasture (S5) ordination.

NMDS1	NMDS2
-0.35905818	-0.336277534
-0.28608929	-0.318249452
-0.23950301	0.102078082
0.27252869	-0.075508637
0.35130769	0.129246577
0.3454393	0.336783377
0.41456767	-0.268078238
0.68649701	0.255309449
0.46592859	0.200725453
0.28437208	-0.256143539
0.28611975	0.260170675
0.17806804	-0.007962941
0.68359942	-0.344123665
0.57856394	-0.017431699
0.57283733	-0.127379897
-0.33853002	-0.409248337
-0.4328986	-0.206287527
-0.42074718	-0.173486415
0.74046473	0.048325142
0.93404046	-0.111572952
0.36351429	-0.400923553
-0.52505481	-0.619088631
-0.04487211	-0.1351712
-0.06686803	-0.856765722
-0.53787314	-0.625418932
-0.74795968	0.514450924
-0.73702101	-0.057209474
1.0695655	0.409795264
0.85871408	0.506077811
0.92384152	0.110699951
-0.64534952	-0.444709331
-0.06317019	0.9050305
-0.10800098	0.847644065
-1.44310131	0.07806206
-1.50531491	0.488631527
-1.5085581	0.598006816

Table A.2. Species scores for July 2017 and July 2018 tame forage pasture (S5) ordination.

NMDS1	NMDS2
-0.1502151	-0.54892274
-0.56567411	-0.9110478
0.55826294	-0.17907426
0.20842034	-0.27303256
0.97968061	-0.24764564
0.05661307	0.29988226
0.11065616	0.29344683
-0.77776263	0.38839267
0.48528524	0.28672101
0.35962348	0.01337044
0.15274915	0.15858585
-0.27487201	-0.26634693
0.40919965	-0.03394192
0.45327229	-0.81977583
0.21199751	-0.77676143
-0.6376988	-0.61893807
-1.66656971	-0.27976377
-1.46920193	0.06567333
-0.40292157	0.02868637
0.01412638	0.01044592
-0.17823775	0.26077937
0.04247088	0.14740999
0.20773474	-0.01531903
0.25643513	-0.06016512
0.54177409	-0.34247594
0.20187044	-0.23044716
0.16704425	0.51465332
-0.39949485	-0.59103085
0.27625473	0.30481672
0.15984325	0.05252819
0.20452535	0.37340659
-0.35053059	0.69739585
-0.04490019	0.78953406
-0.32955538	0.31832639
-0.09373507	0.06006242
0.04109854	0.10188479
-0.0174489	0.43363992
-0.49688396	-0.09404353
-0.74862485	-0.34518887
-0.32639385	0.42933038
0.10550713	0.20891157

Table A.2. continued

NMDS1	NMDS2
0.22445769	-0.07914549
-0.38332931	0.25714054
-0.02231621	0.79356359
0.28545476	-0.43074965
0.26114431	0.610432
0.64999055	0.18379101
0.0694736	-0.33142545
0.44697116	-0.44275476
0.47095021	0.07542457
0.07380853	-0.38245268
0.47758194	-0.2401567
0.26835786	-0.11000232
-0.09626919	0.49237256

Table A.3. Species scores for 2018 native pasture (N8) ordination.

NMDS1	NMDS2
-0.22998637	-0.174159347
-0.62526779	-0.508264664
-0.27147489	-0.218906618
-0.34118211	0.944972595
-0.06908444	0.788895741
-0.03846059	0.481533059
-0.34994415	-0.136877566
0.20650257	0.38331884
0.14415872	0.557277877
-0.27253978	0.039429165
-0.2849999	0.230244225
-0.21759159	0.239628818
-0.54919919	0.363606681
-0.12419535	0.557767343
0.01140772	0.242128275
-0.91657288	0.078738387
-0.66747457	0.346020812
-0.53389665	-0.00144582
-0.07781657	0.128843137
0.10485515	0.029793522
0.08176376	0.317790933
-0.43051889	0.144037487
-0.36525993	0.141803113
-0.2802575	0.55303613
0.33314177	1.110168374
0.26490956	0.838679383
0.47922681	0.892249794
-0.47968093	0.199897803
-0.45547875	0.268830101
-0.22965888	0.416475277
-0.13284909	-0.550557275
-0.11041381	-0.338391839
-0.23618752	0.427147768
-0.26735322	0.301243289
-0.31565113	0.317005203
-0.23397751	0.323453613
-0.24513568	-0.002466706
-0.32495517	0.147003301
-0.14101632	0.156054988
-0.35679472	0.088701155
-0.34392047	0.473749494
-0.45850491	0.624570056

Table A.3. continued

NMDS 1	NMDS2
0.26892662	-1.334754615
0.68398587	-1.1779578
1.08012522	-0.971602532
-0.73341205	0.24157021
-0.54066784	0.180513301
-0.52954359	0.139384881
-0.13166259	-0.421000759
0.06634583	-0.842472381
-0.07891105	-0.084847263
0.95840361	-1.156564987
1.12429037	-0.586873489
1.04511429	-0.624911149
1.45042286	0.454459295
2.24482355	1.033833588
1.60691032	0.633927859
0.84653382	-0.725817435
0.98189942	-0.165897135
0.97882153	-0.087075338
-0.18827122	-1.254415192
-0.50611354	-0.985650926
-0.8964642	-0.954037964
-0.47559905	0.374000682
-0.17070454	0.225006511
-0.46106002	0.041535456
0.36134326	0.132491647
0.487376	-0.036220229
0.27499828	0.249427111
1.05974668	0.676909532
0.86257422	0.391206398
0.73339691	0.535187576
0.16451479	-0.22240581
0.28039583	0.008875674
0.20396465	-0.075949786
-0.64377026	0.025285176
-0.76068655	-0.178811379
-0.66184581	0.10312699
-0.38263725	-0.363913329
-0.36178327	-0.37693235
0.06546177	-0.380337889
-0.74889574	0.171007675
-0.68016491	-0.213064839

Table A.3. continued

NMDS 1	NMDS2
-0.64640931	-0.053744077
0.27966149	-0.774670983
0.35811089	-0.591031204
0.40631945	-0.321062586
-0.13012629	-0.747061506
-0.04727502	-0.643115512
0.25287176	-0.488575018

Table A.4. Species scores for July 2017 and July 2018 native pasture (N8) ordination.

NMDS1	NMDS2
-0.549342809	-0.03520121
-0.353452076	-0.08634597
0.665387195	-0.59178593
0.455740097	1.54717378
-0.154886953	0.49737645
-0.01847964	0.52762974
-0.205552713	0.34277528
-0.178043879	0.05517533
-0.267774605	0.54873445
-0.244729351	-0.39237538
0.291489657	-0.26507569
0.297882656	-0.50249374
-0.465753982	0.21953041
2.88613E-05	0.05268129
0.086749367	0.06706801
-0.019076511	0.06163054
0.00617031	0.27892564
-0.57784408	0.39553066
-0.678365755	0.22334082
-0.242515904	-0.04238033
-0.462777625	-0.06579797
0.37375277	0.38116254
-0.107656375	0.12963573
-0.298087904	-0.18746429
-0.187648651	-0.5353648
-0.071079044	-0.13001195
-0.540291438	0.19121828
-0.25761179	0.16754588
-0.329629582	-0.03147032
-0.391288424	0.40452312
-0.299516432	-0.11395349
-0.26320646	-0.20094968
2.500696907	-0.72602359
1.161863032	0.13935533
0.23810496	0.7524738
-0.034119171	1.20292994
-0.472215839	-0.6444009
0.047122217	-0.05852762
0.203451354	0.04934666
0.575769816	0.14553143
1.057745674	-0.18628897
0.368983142	-0.05255228
-0.530766408	-0.28655006
-0.113404119	0.44369069
-0.425463472	0.063322
-0.463572975	0.18974788

Table A.4. continued

NMDS1	NMDS2
0.357035396	0.5185747
0.687147217	0.3273815
0.341070223	0.45398297
0.211180155	0.4780971
0.585697149	1.33715954
1.028647027	0.8750572
-0.312550266	0.0631812
-0.369820468	-0.03202209
0.539213589	0.62831337
1.440891665	0.58191823
-0.699702574	-0.22016083
0.154418241	-0.2351724
-0.303104156	-0.31702698
-0.111613998	-0.21181128
0.186590124	0.25025202
-0.411628137	0.07810712
0.224336562	-0.58335715
-0.05530366	-0.34115876
-0.047230931	0.05925999
-0.765183271	-0.14636583
-0.34611577	-0.12892757
-0.608088285	0.31392605
0.226877774	-0.81232403
-0.622634701	-0.29541016
-0.720349577	-0.33577717
-0.574467937	-0.18125158
-0.603577048	0.11386265
-0.464766873	0.58893591
0.054395269	0.28483226
-0.219020343	-0.58360296
-0.273131902	-1.18703459
-0.167015969	-1.05975101
-0.645430932	0.02585029
-0.280890588	0.18962268
-0.144761212	-0.3550419
-0.008597997	-0.15746987
-0.414511956	0.23829864
-0.107815464	0.09438265
1.064899098	-0.57844086
-0.888335769	0.7027855
-0.617401636	-0.25307925

Table A.4. continued

NMDS1	NMDS2
-0.439588688	-0.32763945
0.783529943	-0.30586608
0.441449194	-0.43104907
1.051466096	-0.32058815
0.414087023	-0.32844632
0.805670901	-0.47622975
0.318909181	-0.71058215
-0.641436641	-0.51224871
-0.247981326	0.04922264
1.156598495	0.55942681
-0.568922533	0.24623682
0.746595261	-0.15093709
0.640129884	-0.10321757
0.995672639	0.34870977
1.311584595	0.15352656
-0.559542954	-0.4885551
-0.467528244	0.02181585
-0.39251853	-0.17413096
0.054538849	-0.11024074
0.58681574	-0.24853244
0.453804524	0.10812813
-0.112496818	-0.57807394
-0.046213583	-0.2166513
0.852661777	-1.00847424
-0.432455111	0.49395608
-0.217429695	0.79154691
0.099588717	-0.78357727
0.064388776	0.74787654
-0.42583488	0.33352225
-0.189089043	0.20817078
0.008079203	0.0276506
0.448028593	-0.15174427
-0.067354428	-0.36003167
0.046781025	0.15088848
0.214080997	-0.14663258
-0.389864696	0.06243441
-0.238808034	0.06550359
-0.067072964	-0.76925836
-0.385135598	-0.22846744
-0.23893074	-0.14344846
0.136376551	0.38760646

Table A.4. continued

NMDS1	NMDS2
-0.278778902	-0.01781036
-0.200300135	-0.06505064
-0.147088803	0.01304676
-0.322597739	0.25657783