AN EXPLORATION OF THE EFFECTS OF CATTLE GRAZING, PRAIRIE DOG ACTIVITY, AND ECOLOGICAL SITE ON PLANT COMMUNITY COMPOSITION AND WESTERN WHEATGRASS VEGETATIVE REPRODUCTION IN NORTHERN MIXED GRASS PRAIRIE

A Dissertation
Submitted to the Graduate Faculty
of the
North Dakota State University
of Agriculture and Applied Science

By

Aaron Lee Field

In Partial Fulfillment of the Requirements
for the Degree of
DOCTOR OF PHILOSOPHY

Major Program:
Range Science

April 2017

Fargo, North Dakota

North Dakota State University
Graduate School

Title

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DOCTOR OF PHILOSOPHY

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ABSTRACT

Modern range scientists and managers are tasked with feeding more people than ever before while maintaining or improving the ecological function of over half of the world's land surface. Often, these tasks are in conflict. This disparity is evident in the relationship between rangeland livestock producers and black-tailed prairie dogs (*Cynomys ludoviciana*). Prairie dogs are considered a keystone species and an ecosystem engineer, but they also reduce available forage for livestock. In this disquisition we investigated the dynamic relationship between prairie dog activities and cattle grazing in respect to their combined and separate influences on plant community composition and western wheatgrass (*Pascopyrum smithii*) reproduction in northern mixed grass prairie. Our study took place on a private ranch in north-central South Dakota on the Standing Rock Indian Reservation, near McLaughlin. Using paired plots that either allowed or excluded cattle grazing, we were able to quantify the effects of different grazing intensities and grazing removal. While plant community composition and bare ground percentage were different among grazing regimes and ecological sites, removal of cattle grazing pressure did not change plant community composition over the three-year study in comparison to full use grazing (40 – 60% degree of disappearance). These findings show that short term (3 year) changes in grazing intensity did not lead to plant community change in northern mixed grass prairie. This was true regardless of ecological site and prairie dog occurrence. Western wheatgrass bud banks were also not influenced by herbivory type or intensity. This finding underscores the importance of aboveground tiller numbers as an indicator of reproductive capability rather than bud bank in western wheatgrass. Taken together, our results suggest that full use cattle grazing is a sustainable practice in northern mixed grass prairie. Our results also indicate that western wheatgrass vegetative reproduction is not likely to be inhibited or promoted by grazing.

ACKNOWLEDGEMENTS

There are many people who deserve acknowledgement and thanks for making it possible for me to complete this degree, and I will not be able to include all of them. I would first like to thank my major advisor, Dr. Kevin Sedivec. Without his guidance and patience over the last six years this would never have been possible. Kevin provided a stellar example of how to communicate with people of all walks of life, providing guidance with no hint of condescension or arrogance. He also showed me exactly what hard work looks like in academia.

I would next like to thank my graduate committee members: Drs. Christina Hargiss, Torre Hovick, Ben Geaumont, and John Hendrickson. You have each provided strong examples of success in a variety of roles within range science as well as direct instruction when it was needed. My personal goals for improvement and growth have been guided by strengths that I observed in each of you.

I would also like to thank Dennis Whitted for his support and instruction over the years. I'm not sure I would know a single plant if it wasn't for Dennis, and without having his office to stop by and talk about dogs or hunting I might have gone even more insane than I already have. To my officemates and fellow graduate students, especially Katherine Kral, thank you. Without you keeping me on track and showing me what a graduate student was capable of, the wheels may have fallen on a long time ago. To my parents, who have always expected the best from me, thank you for making me believe this was possible.

To the many I failed to mention by name, thank you. Whether it was a course you taught or a kind word you said, it made all the difference.

DEDICATION

I would like to dedicate this work to my wife, Jennifer. You, and later Allie and June, have given me a happy and wonderful family to go home to. Without that there would be no reason for any of this. Thank you for your love and support.

PREFACE

Chapter 1 provides a general introduction to the topics addressed within the dissertation. Chapters 2 and 3 of this dissertation were written as manuscripts that will be submitted to peer-reviewed journals. Chapter 2, “Effects of short term cattle exclusion on plant community composition: prairie dog and ecological site influences” will be submitted to *Rangeland Ecology and Management*. Chapter 3, “An exploration of the effects of cattle grazing, prairie dog activity, and ecological site on western wheatgrass vegetative reproduction in northern mixed grass prairie” will be submitted to *Rangeland Ecology and Management*. Chapter 4 serves a general conclusion to this dissertation and includes future directions for research.

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CHAPTER 1. GRAZING DISTURBANCE BY DOMESTIC LIVESTOCK AND PRAIRIE DOGS: IMPACTS ON PLANT COMMUNITY COMPOSITION AND BUD BANKS

Introduction

We are faced with the challenge of feeding more people than ever before. The United Nations Department of Economic and Social Affairs-Population Division (2015) estimates the current world population at over 7.3 billion people. This number is expected to rise to as many as 8.5 billion by 2030. It has also become evident that the energy intensive, monoculture based agricultural model which has led to the "green revolution" of the late 20th century cannot continue indefinitely (Pingali 2012). Most of the rangeland area that has not been cultivated is not suitable for farming or would yield marginal cropland (Kang et al. 2013) with minimal potential to produce high-yielding cereal grains (Pingali 2012). Most of this land area is poorly suited to row-crop agriculture or vegetable and fruit production without extensive inputs of water and fertilizer. These additions are typically not sustainable in the long term (Tilman et al. 2002). Conversion of these lands to intensive agricultural production also leads to a decrease in plant and animal diversity (Maestas et al. 2003). This loss of diversity is often tied to a decrease in ecological stability (Tilman et al. 2006), as well as a loss in production (Tilman et al. 2001).

The Role of Grazing Animals

The challenges of allowing human population growth while maintaining ecological stability make it more important now than ever to produce human food on rangelands without conversion to intensive methods. Cellulose is the primary carbohydrate produced by plants, and humans and other higher eukaryotes do not produce the enzymes necessary to digest it (Béguin and Aubert 1994). Ruminants (even-toed hoofed mammals of the suborder Ruminantia) typically have a stomach divided into four compartments and are able to regurgitate and re-chew partially digested food (American Heritage Science Dictionary 2016). This four-chambered stomach and its associated microbiota allows these animals to digest and metabolize cellulose. By then harvesting ruminant animals for meat, this meat can then be utilized by humans as a protein and calorie source. This process can allow human food production on land areas that could not we wish to maintain as rangeland for other ecological services such as water and air purification, biodiversity conservation, and outdoor recreation (Holechek 2011).

Grazing and browsing animals can take many forms. Historically, diverse communities of wild herbivores roamed freely across the landscape (Lamprey 1963). This freedom of movement typically encouraged a diversity of grazing pressure, with some areas being grazed heavily while others relatively untouched in a given year (England and De Vos 1969). These communities were often diverse in terms of herbivore size and diet selection (Lamprey 1963). Increased herbivore diversity can lead to higher secondary biomass production on a given land area (Gordon and Prins 2007). Modern examples can be observed in some parts of the African savannah, where nearly the full complement of wild herbivores are still intact.

However, in much of the world the full complement of native herbivores are no longer present, and many of those that remain are under threat (Ripple et al. 2015). Causes for decline include human over-hunting (Martin 1978, Ripple et al. 2015) and/or climate change (Grayson 2007) loss of habitat, disease, and competition with livestock (Ripple et al. 2015). It is also important to understand that relying on free-roaming communities of wild herbivores for human food production has historically only been successful if vast land areas were available per capita (Campbell 2011). The transient nature of these animals makes it impossible for large centralized populations to rely on them for food.

The domestication of livestock around 8500 B.C. allowed humans to harvest plant biomass through an animal without maintaining a transient lifestyle (Fitzhugh et al. 1978). Farmers and herders first selected animals for domestication based on their disposition (Zeder et al. 2006), if they were more precocious (Diamond 2002), and for a smaller size (Clutton-Brock 1992, from Mignon-Grastreau 2005). These characteristics allowed safer and easier handling, as well as lowered feed inputs.

Cattle (*Bos taurus* and *Bos indicus*) are the most common domestic ruminant today, with about 1.4 billion animals on earth at a given time (FAO 2014). Cattle have been bred to be tolerant of a wide range of environmental conditions and found on rangelands worldwide. They are among the easiest livestock species to keep in a fence, and are easier and safer to confine and transport than wild herbivores such as bison. These advantages have contributed to a largely single-species cattle grazing on many rangelands, especially in North America. Over 70% of the land area in the Western United States is grazed, primarily by cattle (Fleischner 1994).

Cattle grazing also has disadvantages. Cattle typically spend more time in shade or near water than native bison (*Bison bison*), use hillsides and hilltops less frequently, and spend more time in riparian areas (Van Vuren 1979, Van Vuren 1983, Steuter and Hittinger 1999, Allred et al. 2011, Kohl et al. 2013). Cattle are less winter hardy than native ungulates (Christopherson 1980). Cattle, especially British and Continental breeds, are also only able to forage 1-2 miles from a water source (Valentine 1947, Martin and Ward 1970, Martin and Ward 1973). These issues are amplified by single species, and often single breed management practices. Current models of meat production contribute to many environmental problems. This process is less energy efficient than most plant-based human diets and recent research into the sustainability of current models of meat production show some major problems. These include competition for human-edible feedstuffs (Schader et al. 2015) and high greenhouse gas emissions (Steinfeld 2006, Ripple et al. 2014, Caro et al. 2014). Despite these challenges, there is potential to reduce the negative effects of meat production through grazing and feed management, genetic selection, and manure management (Gerber et al. 2013). When ruminant meat is produced via sustainable grazing on rangelands that are unsuitable for cropping, it can contribute to food security and dietary quality (Smith et al. 2013, Eisler et al. 2014).

Currently, single-species cattle grazing is practiced on much of the world's rangeland area. This is especially true in North America on the grass-dominated Great Plains, where cattle grazing combined with feedlot finishing is the primary form of meat production. As range scientists and range managers, it is crucial that we understand the effects of this major driver of rangeland systems if we hope increase meat production without environmental degradation. Cattle grazing takes place on dynamic landscapes of varied scale, slope, aspect, soil type, and plant community composition. Grazing impacts vary depending on all of these factors. Additionally, rangeland livestock production impacts communities of people who depend on cattle for their livelihood. Any management changes that lead to a loss of income will be met with strong resistance. To understand sustainable meat production on rangelands we need to consider all of these factors together and ensure that all factors are given adequate weight in our management decisions.

Impacts of Fire and Grazing Disturbances on Plant Communities

Ecological disturbance is defined by Dodson et al. (1998) as "a relatively discrete event that disrupts the structure of an ecosystem, community or population, and changes resource availability or the physical environment." Northern mixed grass prairie (NMGP) plant species evolved under frequent and varied disturbances. The major disturbances in this ecosystem included fire, drought, and grazing by large herbivores (Anderson 1982) with occasional heavy defoliation by grasshoppers (Hewitt 1983) also played a role. Fire in the NMGP was historically characterized by low to moderate intensity fires that were fueled primarily by grasses. These fires were most often ignited American Indians or by lightning strikes (Nelson and England 1971). Lightning set fires were most common in July and August, but less frequent than anthropogenic fire (Higgins 1984). American Indians used fire to attract and herd wild animals, and these fires occurred throughout the year (Higgins 1986).

Fire intensity is influenced by temperature, fuel load, fuel type, fuel moisture, and humidity (Govender et al. 2006). In hot, dry conditions with heavy fuel loads fire on the NMGP would reach high intensities. Average historic fire return intervals under these conditions were about 5-7 years. Just prior to heavy European settlement in the northern plains, fire frequency and intensity spiked (Umbanhowar 1996). This was likely due to unintentional fires, often ignited by railroad activity. Since European settlement, fire suppression has led to less-frequent, but often more intense fires (Umbanhowar 1996). This shift can allow woody encroachment and invasive species establishment in many areas, as well as lowered plant vigor of many fire-dependent native species (Bragg 1995). Plant response to fire is dependent on fire intensity, fire frequency, and weather (Kruger 1984, Gibson and Hulbert 1987).

Large, native herbivores of the NMGP included bison (*Bison bison*), elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*) and others (Hanson 1984). Together, these herbivores exhibit a wide range of diet preference ranging from concentrate selectors, which prefer shrub-browse, to roughage selectors, which prefer grasses (Hofman 1973, Hofman 1989). While all of these species exhibited selective pressure on NMGP plants, none had as much impact as the bison. Bison bulls weigh approximately 1000 kg and cows weigh approximately 800 kg. Bison numbers on the Great Plains prior to European settlement have been estimated at 30-60 million animals (BSFW 1965, Stoddart et al. 1975, Epp and Dyck 2002), often moving in huge herds. After these herds passed, there was little to no usable forage for horses along their route, indicating very heavy grazing (England and De Vos 1969). However, it appears that once bison left an area they did not typically return for several years (England and De Vos 1969).

Plant Responses to Grazing

Plant responses to grazing or browsing largely depend on environmental conditions before and after the event, but also on their evolutionary history. Most plant species evolved with some sort of herbivory; however, the frequency and intensity of defoliation varies greatly among ecosystems and plant species. Mechanisms that reduce the probability or severity of grazing are known as grazing resistance (Briske and Richards 1994). Grazing resistance can be divided into two categories: avoidance and tolerance (Figure 1.1). Avoidance adaptations include mechanical mechanisms like prickles, thorns, or silica bodies as well as biochemical mechanisms such as secondary toxic or unpalatable compounds (Briske 1991).

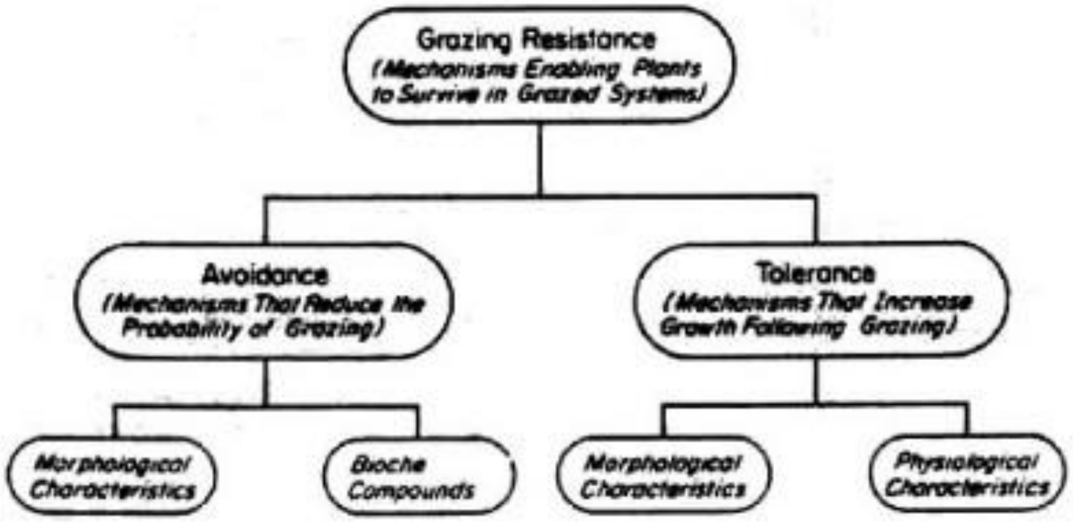

Figure 1.1: Organization of plant grazing resistance mechanisms. From Briske 1991. Adapted from Briske 1986.

Another way plants have evolved to survive grazing is through grazing tolerance, or the relative ability of a plant to tolerate grazing (Briske 1991). There are many factors that influence an individual or plant species' grazing tolerance. A major consideration is leaf replacement potential, defined by Briske (1991) as "the rate at which leaf area is re-established following defoliation". This trait is dependent on the number, source, and location of meristems on a plant after a grazing event (Briske 1991). If a plant's meristematic tissue is removed or severely damaged by herbivory, it will recover slowly irrelevant of the type and number of meristems present prior to grazing.

Proposed physiological mechanisms of grazing tolerance include compensatory photosynthesis and compensatory (or over-compensatory) growth (Briske 1991). Compensatory photosynthesis is defined as an increase in the photosynthetic rate of the foliage of a plant relative to similar-aged foliage on undefoliated plants (Nowak and Caldwell 1984). However, photosynthesis is a function of both photosynthetic rate and leaf area, so the impacts of compensatory photosynthesis are often limited (Briske 1991). When plants respond positively to damage, such as that caused by grazing, it is defined as compensatory growth (Belsky 1986). This process has been heavily debated as a potential mechanism by which forage production can be increased (see Belsky 1986 for an early review). Studies of compensatory growth led to McNaughton's (1979, 1983) "grazing optimization" hypothesis. McNaughton proposed that plants had co-evolved with their primary herbivores and were capable of replacing damaged tissue via compensatory growth without real damage to the plant. Subsequent discussion and debate of the theory has shown that while compensatory regrowth can occur under some conditions, it is largely limited to plants under mesic or humid conditions that evolved in the presence of heavy herbivory (Holechek et al. 2006) and should not be used as an excuse for overgrazing (Briske 1993).

Herbivore type has the potential to influence the ability of a plant to avoid or resist grazing. This is due to the herbivore preference for certain plant types or species (Heady 1964, Theron and Booysen 1966) as well as physiological differences between herbivores. These impacts are confounded by the fact that the impacts of grazing by different species is influenced by plant species diversity (Liu et al. 2015), at least in the short term. Plants on black-tailed prairie dog (*Cynomys ludovicianus*) towns are exposed to frequent grazing and clipping by both black-tailed prairie dogs and associated large herbivores. This is especially true for grasses (Fagerstone et al. 1981). This process provides a strong selective force for grazing tolerance or grazing avoidance. Due to these factors, grazing morphs of perennial plants do occur on prairie dog towns. These morphs are typically shorter and more prostrate than their less-frequently defoliated counterparts (Kemp 1937, Hickey 1961).

Prairie Dogs

Prairie dogs, especially black-tailed prairie dogs, were historically a major ecological force on North American rangelands. Historically, these rodents' distribution included areas from central Canada southward to Mexico, and from Illinois westward to the Great Basin (Figure 1.2). Other species including Utah prairie dogs (*Cynomys parvidens*), white-tailed prairie dog (*Cynomys leucurus*), Gunnison's prairie dog (*Cynomys gunnisoni*), and Mexican prairie dogs (*Cynomys mexicanus*) occupied and currently occupy smaller, but significant ranges. Black-tailed prairie dog form large colonies with extensive burrow systems. Individual colonies have been reported covering up to 120 ha^2 (Merriam 1902), although this expansion may have been somewhat inflated and/or due in part to overstocking by early ranchers (Virchow and Hygnstrom 2002). Estimates of total land area occupied by all species of prairie dog before European settlement range from under 40 million ha (Vermeire et al. 2004) to over 100 million ha (Miller 1994) with most recent estimates falling near 40 million ha. This area has been reduced by at least 90% since European settlement, with some estimates as high as 98% (see Miller et al. 2007 for a review).

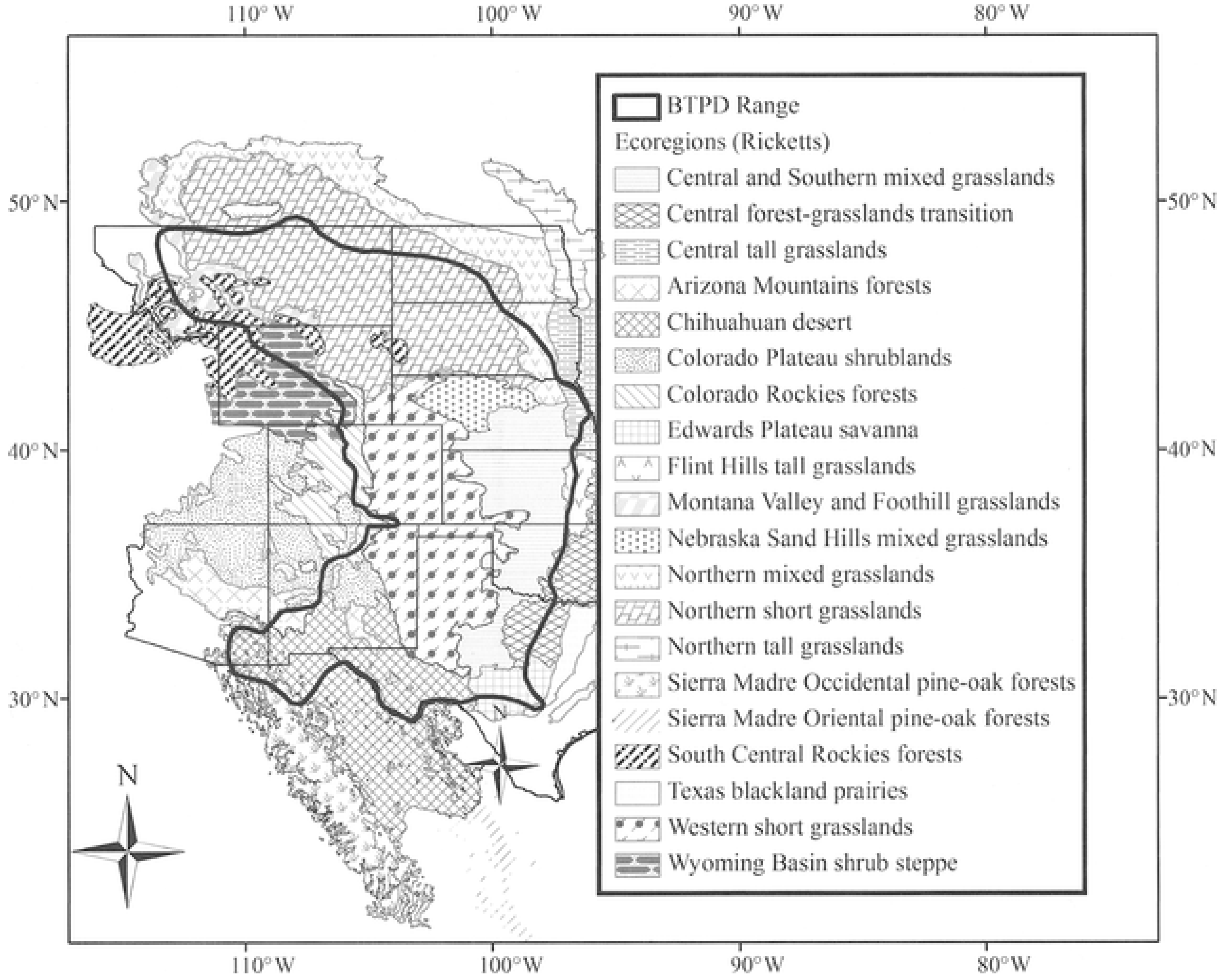

Figure 1.2: An outline of the historic range of black-tailed prairie dogs (*Cynomys ludovicianus*) within North America and the ecoregions (based on Ricketts et al. 1999) they encompassed. Taken directly from Facka et al. (2008).

Black-tailed prairie dog colonies are characterized by low vegetation, high annual forb diversity, and high bare ground percentage (Whicker and Detling 1988). These characteristics are caused by burrowing activity, feeding, and vegetation clipping. Black-tailed prairie dogs clip tall vegetation around their burrows to increase visibility and avoid predation (King 1955). Black-tailed prairie dogs are considered a “keystone species” (Kotliar 1999, Kotliar 2000) because of their disproportionate effect on their surroundings in relation to their abundance or biomass

(Power et al. 1996, Kotliar 2000). Up to 208 vertebrate wildlife species have been observed using prairie dog towns (Kotliar 1999); however, the literature only provides support for about eight vertebrate species depending on prairie dog towns for their survival or for maintaining their historic populations (Kotliar 1999). These species include Black-footed ferrets (*Mustela nigripes*), Burrowing Owls (*Athene cunicularia*), Mountain plovers (*Charadrius montanus*), Ferruginous hawks (*Buteo regalis*), Golden eagles (*Aquila chrysaetos*), Swift foxes (*Vulpes velox*), Horned larks (*Eremophila alpestris*), Deer mice (*Peromyscus spp.*), and Grasshopper mice (*Onychomys spp.*). More species may rely on prairie dogs, but quantitative data is lacking. This designation as a keystone species has been questioned by some who have demonstrated that intense grazing by other herbivores can produce many of the same conditions that promote high wildlife diversity as observed on prairie dog towns (Vermeire et al. 2004). While intense grazing may produce similar plant communities, prairie dog burrows are one of the key ways that the produce unique habitats. For some species, heavy grazing may a suitable replacement for prairie dog occupancy. For others, prairie dogs produce unique and critical habitat conditions (Kotliar et al. 2006).

Conflict between Prairie Dogs and Humans

Black-tailed prairie dogs have been considered a pest by many since European settlement, and have been systematically eradicated by both private landowners and government agencies, as well as other organizations (Bell 1921, Anderson et al. 1986, Mulhern and Knowles 1995). This eradication, along with the introduction of sylvatic plague, has led to a 90-99% reduction in black-tailed prairie dog range since European settlement (Mulhern and Knowles 1995, Vermeire et al. 2004, Miller et al. 2007). Competition for livestock forage is the primary reason for this conflict. Dietary overlap between prairie dogs and cattle can be as much as 68%

(Mellado et al. 2005). Although in a more arid environment than our study site, that degree of overlap may indicate competition for resources. In northern mixed prairie, the diet of black-tailed prairie dogs includes approximately 80% grasses and graminoids (Summers and Linder 1978, Fagerstone and Williams 1982, Uresk 1984). Cattle also select for grasses, which could contribute to competition in this system. However, competition is very difficult to document in nature. Prairie dogs can consume between 10% and nearly 100% of annual net primary production within towns ((Detling 2006). At the higher levels of consumption, and given high dietary overlap and inability of livestock to move outside of pasture fences, competition for forage and reduced livestock carrying capacity do occur on prairie dog towns.

Besides forage that is actually consumed, prairie dogs clip taller vegetation to improve sightlines and avoid predation (Kofford 1958, Hoogland 1995). This, combined with actual consumption has the potential to reduce livestock carrying capacity. Estimated reductions in large herbivore carrying capacity range from as low as 4-7% (Miller et al. 1994) to as high as 50-75% (Merriam 1902, Vermeire 2004). Both levels of reduction are possible depending on prairie dog density and the proportions of colonized and uncolonized areas. O'Meilia and colleagues (1982) found no difference in cattle weight gain between pasture with or without prairie dogs. However, these pastures were very heavily stocked and cattle gains may have been depressed in both pastures. Derner et al. (2006) found that as prairie dog colonization rates increased, cattle weight gains decreased. This led to a decrease in profitability in pastures that contained prairie dogs. However, considering that prairie dogs distribution has been reduced by over 90% since European settlement (Mulhern and Knowles 1995, Vermeire et al. 2004, Miller et al. 2007), large scale reductions in livestock carrying capacity due to prairie dogs are unlikely.

Shifts in plant community composition occur over time on prairie dog towns. These shifts are characterized by a reduction in grass dominance and an increase in forb and dwarf shrub cover and can occur in as little as two years (Coppock et al. 1983, Fahnestock and Detling 2002, Fahnestock et al. 2003). Increased cover of unpalatable forbs and shrubs could lead to decreased carrying capacity, decreased livestock weight gain, or increased grazing pressure on palatable plants.

Although livestock forage quantity is almost always reduced by prairie dog occupancy, there is still some question as to how much that could be offset by increased quality. The proportion of live plant material as compared to dead is higher on prairie dog colonies (Coppock et al. 1983, Whicker and Detling 1988, Detling 1998). Digestibility and protein levels of plants found on prairie dog colonies are typically higher than those found off colony (Coppock et al. 1983, Krueger 1986, Whicker and Detling 1988). Bison seem to select for prairie dog towns during at least part of the year (Coppock et al. 1983, Green 1998). Cattle select for sites with reduced litter and standing dead plant material (Willms et al. 1988), but do not seem to show preference for or avoidance of prairie dog towns (Guenther and Detling 2003). Research findings are still limited addressing the question of whether the increase in forage quality for cattle offsets some or all of the decrease in forage quantity caused by prairie dog activities.

Economics of Control

Prairie dogs are often targeted for removal with the goal of increasing forage for livestock. They are listed as some type of pest in at least six states (Van Putten and Miller 1999). As discussed above, prairie dogs do likely compete for forage and reduce livestock carrying capacity in many cases. Poisoning of prairie dogs is often justified by pointing to the potential for increased livestock production. This is often done despite a lack of economic justification

(Miller et al. 2007). Millions of acres of prairie dog towns have been poisoned since Merriam's (1902) calculation of range productivity losses associated with prairie dog activities (Bell 1921, Day and Nelson 1929, Anderson et al. 1986, Dunlap 1988). Roemer and Forrest (1996) document federal and state involvement in the poisoning of over 1 million acres of prairie dog colonies in Montana, South Dakota, and Wyoming during the time period of 1978-1992. Cattle production losses due to prairie dog activity can range from between \$2.23 and \$5.58 per hectare (Derner et al. 2006, Miller et al. 2007), but poisoning costs can range from \$3.81 to \$178 per hectare, depending on the chemical used and whether professional applicators were hired (Buhler 2006). If application costs are kept at the low end, and losses are valued at the high end this may be economically feasible; however, reapplication of pesticide is often required within a few years. Often, pesticide treatment costs exceeded forage gain value (Collins et al. 1984) and increases in plant production after prairie dog removal may take several years to occur (Uresk 1985). Private landowners and public land managers should perform cost-benefit analyses before applying prairie dog control. Positive profit margins from control are especially unlikely on public land, where contractors are typically hired for control and primary management goals are not profit driven.

Consequences of Control

Extreme reductions in black-tailed prairie dog range have had major consequences for other species. The effects of range reduction are most pronounced on species that depend on prairie dogs for food or prairie dog burrows for shelter. Species that have been impacted heavily include swift foxes, Mountain Plovers, and Ferruginous hawks, and black–footed ferrets (Miller et al. 1994). Western Burrowing Owls have also been negatively impacted (Klute et al. 2003).

Black-footed ferrets were once common across the Great Plains. However, by the late 1900's they were considered "the most endangered mammal in North America" (Clark 1987). Black-footed ferrets are primarily nocturnal and feed almost exclusively on prairie dogs (Dobson and Lyles 2000). Currently, black-footed ferrets are listed as an endangered species in the United States and are actively protected and supported by a captive breeding program (Dobson and Lyles 2000). However, due to huge reductions in their habitat, primary food source, as well as exposure to diseases such as sylvatic plague and canine distemper it seems unlikely that the black-footed ferret will be able to recover to population levels.

Western Burrowing Owls are diurnal, fossorial owls found in North and South America (Bent 1938, Coulumbe 1971). Weighing about 300 grams, Burrowing Owls feed on insects and small mammals, usually rodents (Haug 1985). Burrowing owls usually nest in black-tailed prairie dog burrows, but will use those of badgers (*Taxidea taxus*) or ground squirrels (*Spermophilus spp.*) in some parts of their range (Butts 1973, Ross 1974, Poulin et al. 2011). With the reduction of prairie dog range, especially black-tailed prairie dog range, Burrowing Owls have experienced steep declines in population due to habitat loss from agricultural and urban development and reduction of burrowing mammal populations (Klute et al. 2003). These decreases have led Burrowing Owls to be listed as endangered in Canada, and threatened in Mexico. The United States has not formally listed these birds as threatened or endangered, but they are considered a "species of conservation concern" (Klute et al. 2003).

Besides a direct loss on a prey source and nesting habitat, removing black-tailed prairie dog alters the environment in several other ways. Prairie dog activities increase bare ground percentage (Archer et al. 1987) and soil temperatures can average approximately 2.5°C higher within colonies than in uncolonized areas nearby (Archer and Detling 1986). Prairie dog towns are usually found in areas with deep soils and gentle slopes (Dahlsted et al. 1981). Black-tailed prairie dog burrowing activities are estimated to mix 200-225 kg per burrow (Whicker and Detling 1988). This activity brings mineral rich material to the surface, while moving carbon and nitrogen-heavy topsoil and excrement to lower horizons. Because of this, soil nutrients are very different near prairie dog burrows as compared to the surrounding area, with nitrogen levels being much higher in areas close to burrow entrances (Barth et al. 2014). These unique soil characteristics, along with heavy grazing and clipping, produce unique plant communities on prairie dog towns. These communities are typically represented by native and introduced annual forbs, and annual and perennial short grasses (Bonham and Lerwick 1976, Archer et al. 1987, Weltzin et al. 1997). Perennial plants found on prairie dog towns are often shorter and more prostrate than those found off town (Painter 1987).

Western Wheatgrass (*Pascopyrum smithii*)

Western wheatgrass (*Pascopyrum smithii* (Rydb.) Á. Löve) is a mid-statured (30-90 cm at the culm), cool-season, rhizomatous grass (Stubbendieck 2003). It is native to North America, and is found on most ecological sites in the NMGP. *Pascopyrum smithii* is relatively productive and moderately grazing tolerant, as well as very palatable (USDA-NRCS 2006), although palatability decreases as the growing season progresses (Hafenrichter et al. 1968). This grass also has high nutritional value, with good energy values and fair protein (Dittberner et al. 1983, Newell and Moline 1978, Table 1.1). These attributes make it an important forage grass in the NMGP.

Pascopyrum smithii is commonly identified by its steel-grey-blue color, spike inflorescence, 45 degree leaf attachment, and purple clasping auricles; but differentiation from similar species requires more detailed observation (Figures 1.3, 1.4). Similar species include thickspike wheatgrass (*Elymus lanceolatus*), intermediate wheatgrass (*Thinopyrum intermedium*), slender wheatgrass (*Elymus trachycaulus*), and quackgrass (*Elymus repens*). *Pascopyrum smithii* can be differentiated by its closely imbricate, solitary spikelets and its unequal glumes (Stubbendieck et al. 2003).

Table 1.1: *Pascopyrum smithii* crude protein levels by season of harvest. Adapted from Newell and Moline (1978).

Season	Crude Protein (%)
Early May	31.6
Regrowth: Early July	13
Late 1st Harvest: Early July	9.8
1st Harvest: Late July.	7.9

Pascopyrum smithii can be found in all soil textures, but is most common in fine-textured soils (Stubbendieck et al. 2003). It is an important component of the reference state in the loamy, thin loamy, and claypan ecological sites in our study area. *Pascopyrum smithii* provides important wildlife cover, especially in the northern portion of its range where it is able to produce more biomass (Dittberner et al. 1983, Table 1.2).

Table 1.2: Relative cover value of *Pascopyrum smithii* for wildlife in four states. Adapted from Dittberner et al. (1983).

	MT	ND	UT	WY
Pronghorn	Poor	Fair	Poor	Poor
Elk	Poor	----	Poor	Poor
Mule deer	Poor	Fair	Poor	Poor
White-tailed deer	Poor	Fair	----	Poor
Small mammals	Fair	Good	Fair	Good
Small nongame birds	Fair	Good	Fair	Good
Upland game birds	Fair	Good	Poor	Fair
Waterfowl	Good	Good	Poor	Fair

Figure 1.3: *Pascopyrum smithii* line drawing. From Gleason et al. (1913).

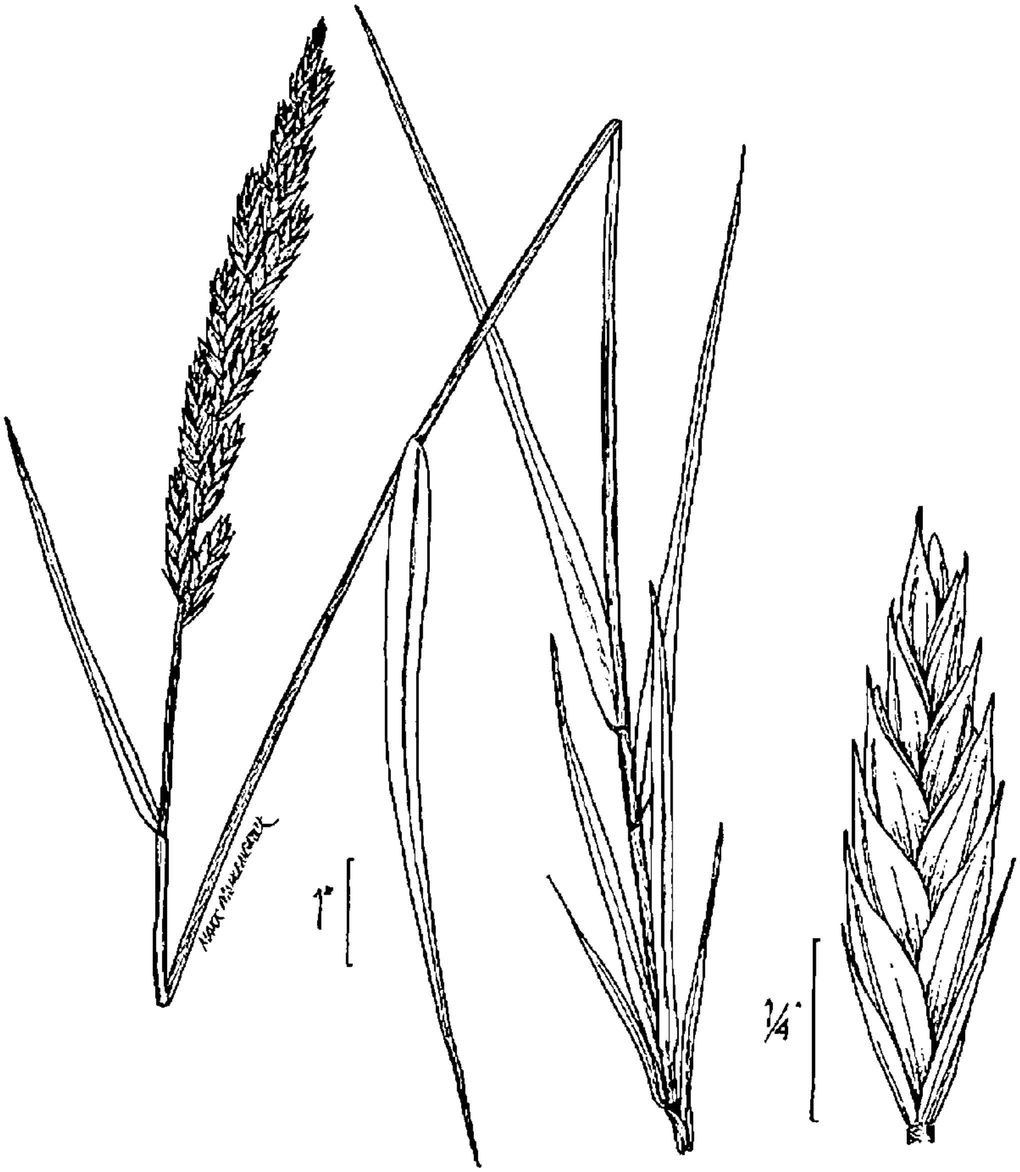

Figure 1.4: Line drawing of *Pascopyrum smithii*. From USDA-NRCS Plants Database (2016).

The rhizomatous growth form of *Pascopyrum smithii* promotes vegetative reproduction, often leading to uniform stands of the grass (Hafenrichter et al. 1968). This plant can also generate from seed, but that process is typically slow (Bultsma and Haas 1989). Peak germination takes place at alternating temperatures of 18.5 ºC for 8 hours and 10 ºC for 16 hours (Knipe 1973).

Pascopyrum smithii rhizomes can be found 1.3-5 cm below the soil surface (Coupland and Johnson 1965). This characteristic also makes *Pascopyrum smithii* fire-tolerant. *Pascopyrum smithii* grows in loose clusters little leafy material. This growth form promotes a fast burn with less chance of a lethal heat dosage impacting meristematic tissue (Tirmenstein 1999). Because of this, *Pascopyrum smithii* is generally fire tolerant (Tirmenstein 1999). However, spring burns after new growth can be harmful to the plant (Volland et al. 1981).

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CHAPTER 2. EFFECTS OF SHORT TERM CATTLE EXCLUSION ASSOCIATED WITH PRAIRIE DOG DISTURBANCE ON PLANT COMMUNITY COMPOSITION OF DIFFERENT ECOLOGICAL SITES IN A SEMI-ARID ENVIRONMENT

Abstract

Maintaining cattle and prairie dogs on rangelands is important ecologically, economically, and culturally. However, competition between these species, both actual and perceived, has led to conflict. Between 2012 and 2016 we explored the effects of short-term (three year) cattle exclusion on plant communities both on and off prairie dog towns, and among three common ecological sites in north-central South Dakota. Plant community composition differed between *on-town* and *off-town* sites, but did not differ between rangeland targeted for full use forage utilization and cattle exclusion. Litter basal cover was higher *off-town*, and bare ground basal cover higher *on-town*, but neither were affected by the removal of cattle grazing. Ecological site influenced plant community composition, bare ground, and litter basal cover but did not affect changes in these measures due to cattle grazing removal. Despite differences in community composition between *on-town* and *off-town* sites, inverse Simpson diversity and species richness were not different. Our results indicate that short-term cattle exclusion does not change plant community composition on these ecological sites, regardless of prairie dog occupancy or ecological site. Additionally, maintaining both *on-town* and *off-town* areas can increase plant species diversity at the ranch scale. Land managers should not expect changes in plant community to occur quickly after cessation of cattle grazing in northern mixed grass prairie. Managers tasked with maintaining or increasing plant diversity or community heterogeneity should consider prairie dogs as a contributor to these goals.

Introduction

Plant community composition is an important indicator of properly functioning rangelands (Pyke et al. 2002). Species composition plays an important role in shaping forage quantity and quality, wildlife cover and food sources, nutrient and water cycling, and drought tolerance (Hooper and Vitousek 1998, Fales and Fritz 2007). Diverse communities promote resilient ecosystems through these mechanisms (McNaughton 1977, Naeem and Li 1997, Chapin et al. 2000, Tilman et al. 2006). The major feature that impacts plant community composition in northern mixed grass prairie is precipitation (Biondini et al. 1998); however, grassland plant communities evolved under frequent and varied disturbance, which was often characterized by large mammal herbivory. In most grassland systems, herbivory influences plant species composition (e.g. Milchunas and Lauenroth 1993, Proulx and Mazumder 1998).

Historically, the primary herbivores in northern mixed grass prairie were bison (*Bison bison*) and black-tailed prairie dogs (*Cynomys ludovicianus*), with strong stochastic disturbance by grasshopper (*Acrididae spp.*) grazing (Whitman et al. 1943, Axelrod 1985, Wendtland and Dodd 1990, Detling 1998, Anderson 2006). These disturbances coupled with topographic and soil differences led to a diverse mix of tall, mid, and short stature grasses and forbs (Anderson 2006). Since European settlement, these disturbances have been greatly altered. Free-ranging bison have been almost entirely replaced by domestic cattle (Knapp et al. 2010) and prairie dog range reduced by as much as 98% (Miller et al. 2007). Where prairie dogs remain, plants on prairie dog towns are often subjected to grazing by both cattle and prairie dogs. Maintaining both prairie dogs and cattle on the landscape is important ecologically, culturally, and economically. When implemented properly, cattle grazing provides income and human food on landscapes that would be negatively impacted by other agricultural uses, while prairie dogs provide food or cover for many other wildlife species (Miller et al. 1994, Klute et al. 2003.)

Other influences on plant community composition, and changes in composition, are grazing intensity (Biondini et al. 1998) and ecological site (Biondini and Manske 1996). Neither full (50% utilization) nor heavy grazing (90% utilization) appear to cause plant community change in the short term (Biondini et al. 1998), but long tem heavy grazing can cause shifts to more grazing-tolerant, shortgrass communities (Brand and Goetz 1986). In contrast, long term absence of grazing in northern mixed grass prairie can cause increases in invasive cool-season grasses such as smooth brome (*Bromus inermis*) which can lead to near-monocultures, decreasing biodiversity and impacting ecological function (Murphy and Grant 2005).

Ecological sites are defined as a distinctive kind of land with specific soil and physical characteristics that differ from other kinds of land in its ability to produce a distinctive kind and amount of vegetation and its ability to respond similarly to management actions and natural disturbances (USDA-NRCS 2006). In our study area, the three most common ecological sites were claypan, loamy, and thin loamy. Claypan sites are usually found at the toe slope of hills and characterized by higher levels of bare ground and lower phytomass production. Loamy sites are found on gentle slopes and highly productive, often associated with the backslope. Thin loamy sites are found on shoulder slopes, or the summit, and usually less productive than loamy sites, largely due to greater runoff. These ecological sites are a useful classification system for rangelands, allowing producers and managers to make focused decisions. As stated in the definition, they also have the potential to respond differently to disturbances, including prairie dog and cattle grazing

Prairie dog activity has a substantial impact on plant community composition and function (Archer et al. 1987, Coppock et al. 1983, Fahnestock and Detling 2002, Fahnestock et al. 2003). Vegetation on prairie dog towns is characterized by grazing-tolerant grasses, annual forbs, high percentages of bare ground, and high plant species diversity (Archer et al. 1987). Prairie dogs grazing and clipping can also produce grazing morphs of perennial plants. These morphs are shorter and more prostrate than their less-frequently defoliated counterparts (Kemp 1937, Hickey 1961). Plant community and basal cover shifts can occur in as few as two years following prairie dog habitation (Archer et al. 1987), and are often viewed unfavorably by livestock producers due to a high dietary overlap (~60%) between cattle and prairie dogs (Uresk 1984). Cattle grazing can increase prairie dog density and extent by creating short stature vegetation (Davidson et al. 2010), which prairie dogs prefer due to increased predator visibility (Hoogland 1995). Additionally, the low vegetation around cattle point attractants (water, mineral, etc.) encourages prairie dog colonization and create increased impacts in areas where cattle and prairie dogs co-exist (Licht and Sanchez 1993).

This study evaluated the effects of prairie dog and cattle grazing on the plant community composition of three common ecological sites in the semi-arid mixed grass prairie of the Northern Great Plains. Our specific objectives were to determine:

1. Whether short-term cattle exclusion would lead to plant community shifts or changes in plant species diversity.
2. Whether short-term cattle exclusion would lead to changes in basal bare-ground and litter cover.
3. If ecological site or prairie dog activity influence these plant community changes.

4. What plant species were most associated with prairie dog presence or absence, ecological site, and cattle grazing regime.

We hypothesized that cattle exclusion would not lead to plant community and species diversity shifts during our three year study, but bare ground percentage would be higher under cattle grazing and litter basal cover would increase in cattle exclosures. We expected this change to be more pronounced off prairie dog towns (*off-town*) than on prairie dog towns (*on-town*).

Materials and Methods

Study Area

This study was conducted in north central South Dakota on the Standing Rock Indian Reservation approximately 24 km southeast of the city of McLaughlin. This region is characterized by northern mixed grass prairie (NMGP) with a diverse mixture of short, mid and tall grass species, as well as a combination of both warm and cool season grasses. Forb and shrub species play a lesser but significant role in the overall plant community. The NMGP includes the western halves of North and South Dakota, the eastern two-thirds of Montana, and parts of Wyoming, Alberta, and Saskatchewan (Holechek et al. 2011). Our study site consisted of approximately 1400 ha of private land, most of which had never been cultivated. The study site has been stocked with livestock at a similar yearly stocking rate from the 1940s until the early 2000s. The study site was grazed season-long with approximately 300 cows with calves and 100 horses throughout the season (Ricky McLaughlin, personal communication, from Hendrickson et al. 2016). Black-tailed prairie dogs (*Cynomys ludoviciana*) occupy approximately 800 ha of the site (Barth et al. 2014).

The climate of the NMGP region is characterized by long, cold winters and warm summers. Growing season temperature at the study site averages 23 ºC. Temperatures during the study period were close to the 30-year average. Most of the annual precipitation in this region falls during or just before the growing season (late April – late September), allowing greater production than may be expected based on annual rainfall totals. The 30-year average annual precipitation for the study area is 43.9 cm and 30-year average growing season precipitation 29.9 cm. Precipitation during the study period was close to the 30-year long term average (Figure 2.1). Growing season precipitation on the site was slightly below average in 2012 (27.0 cm), but was above average in 2013, 2014, and 2015 (50.1, 40.9, and 36.7 cm, respectively). Precipitation data from April 2013 was not available and data from May 2013 represents only part of the month.

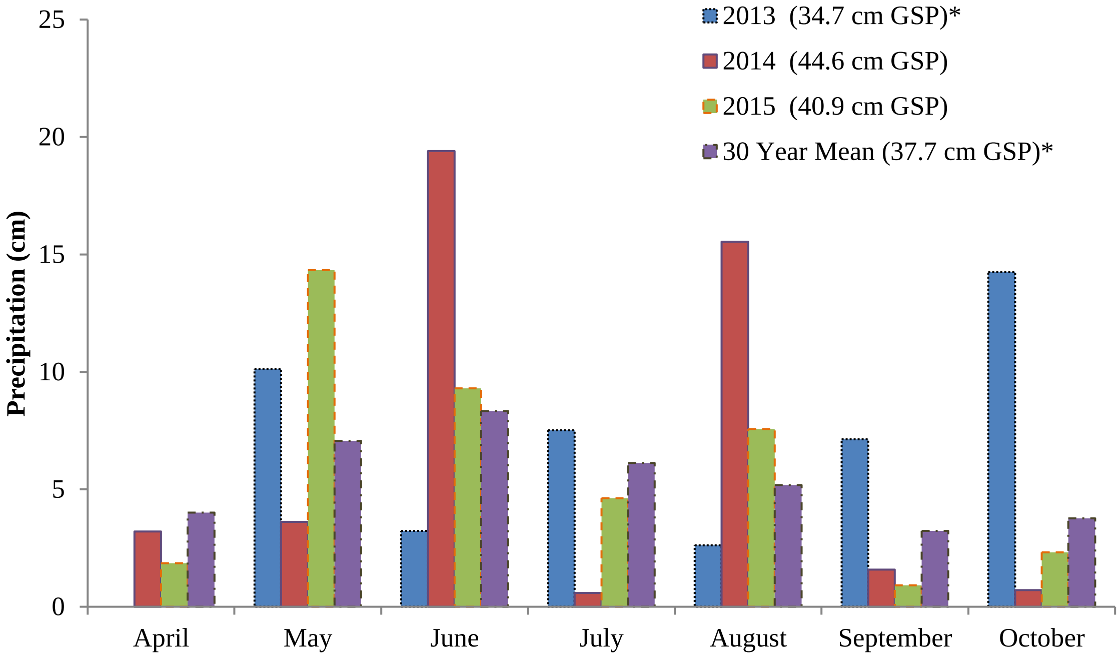

Figure 2.1: Extended growing season precipitation (GSP) by month from Mahto Weather Station at research site. Asterisks reflect missing or partial data in April and May of 2013. Thirty year average from McLaughlin, SD, weather station approximately 11 km northwest of study site.

Soils of the study area are varied and represent several orders and many series due to the broken topography and wide variety of slopes. These soils also formed from a variety of parent materials including glacial till, lacustrine sediments, and alluvial deposits. Common orders include Mollisols, Entisols, Vertisols, and Inceptisols (USDA-NRCS 2016). The dominant series on the site are Cabba, Reeder, Wayden, Opal, and Dupree. Cabba series is classified as a loamy, mixed, superactive, calcareous, frigid, shallow Typic Ustorthent and found on hills, escarpments, and sedimentary plains (USDA, NRCS 2016). Reeder series is a fine-loamy, mixed, superactive, frigid Typic Argiustoll and found primarily on upland sites. Wayden series is a clayey, smectitic, calcareous, frigid, shallow Typic Ustorthent. Opal series is a fine, smectitic, mesic Leptic Haplustert and typically found on lower slopes. Dupree series is a clayey, smectitic, mesic, shallow Typic Haplustepts and found on a variety of slopes. (USDA-NRCS 2016)

The study area is located on the border of Major Land Resource Areas (MLRAs) 54: Rolling Soft Shale Plain, and 63A: Northern Rolling Pierre Shale Plains. These MLRAs vary somewhat in geology, but historic plant communities and expected production are very similar between the two. Due to the relatively gentle topography and lack of Missouri River influence on our site's development, the following abbreviated ecological site descriptions are taken from MLRA 54 (USDA-NRCS 2016). Our study area comprised several ecological sites, but the three most common ecological sites were the loamy, thin loamy, and claypan ecological sites.

The loamy ecological site is the most common ecological site in South Dakota. These sites are on uplands with a surface soil layer of loam or silt-loam (Sedivec and Printz 2012). The plant community is comprised of about 85% grasses and grass-like plants, 10% forbs, and 5% shrubs. The plant community is dominated by western wheatgrass (*Pascopyrum smithii*) and green needlegrass (*Nassella viridula*) with common forbs including Missouri goldenrod (*Solidago* *missouriensis*) (USDA-NRCS 2003). The combination of gentle slopes and optimal available water content make these sites one of the most productive ecological sites in MLRA 54 and 58C, with annual production averaging about 2400 kg/ha.

The thin loamy ecological site was the second most common site in our study area. These soils are also loamy in texture, but include high levels of calcium carbonate to the surface and found on ridges and knolls (Sedivec and Printz 2012). The plant community is comprised of about 85% grasses or grass-like plants including needle-and-thread (*Hesperostipa comata*), green needlegrass, western wheatgrass, little bluestem (*Schizachyrium scoparium*), and sideoats grama (*Bouteloua curtipendula*). The increased slope, and consequently increased runoff, of the thin loamy site leads to less production, averaging about 1500 kg/ha in MLRA 54.

The claypan ecological site is the third most common ecological site in our study area. In a claypan ecological site the surface layer ranges from 15 to 35 cm and followed by an argillic horizon (USDA-NRCS 2011, Field Office Technical Guide, Soil Field Guide to Identifying Ecological Sites, Version 1.7). The dense argillic horizon in these sites often restricts water and root movement, inhibiting the growth of some plant species. Above-ground biomass production averages about 1500 kg/ha. Historic native plant communities for this ecological site are comprised mostly of grasses, with forbs and shrubs making up 10-20% of the cover. Western wheatgrass is typically the dominant grass.

Experimental Design

We stratified our study area by ecological site and the three most common ecological sites were selected for the study; including claypan, loamy and thin loamy. Plots 40 m x 40 m in size were distributed on each ecological site *on-town* and *off-town* using a randomized block design. Fifty of these 40 m x 40 m plots were developed and permanently marked to test either grazed by cattle only, impacted by prairie dogs only, or impacted by both in 2012. Of the 50 plots, 32 were located *on-town* and 18 plots *off-town*. Each 40 m x 40 m plot was paired with another of the same ecological site and prairie dog occupancy, and cattle exclusion was randomly assigned to one member of the pair. Plot distribution among the three ecological sites included 18 plots located on claypan, 18 on loamy, and 14 on thin loamy. Cattle grazing was performed using yearling angus and angus-cross heifers and occurred from 1 June through 15 October, at which point approximately 40 to 60% of plant growth removed in all years. The degree of disappearance, or plant growth removed, was determined by clipping the paired grazed and un-grazed sites at the end of the grazing period.

Sampling Methods

Vegetative data were collected pre-treatment (2012) and three years after treatment (2015) at the peak of the growing season (mid-July). Three, 20m transects were laid out within each plot, each beginning 10m from the south edge of the plot and ending 10m from the north edge. Transects were spaced 10m apart and the two outer transects were placed 10m from the east and west edges of the plot (Figure 2.2). Bare ground and litter cover were estimated using a ten-point pin frame every two meters on each transect, totaling 30 readings per plot. We estimated canopy cover (totaling 100% per frame) for each plant species within $0.25m^2$ frame. Cover was estimated at four points, five meters apart on each transect, totaling 12 points per plot.

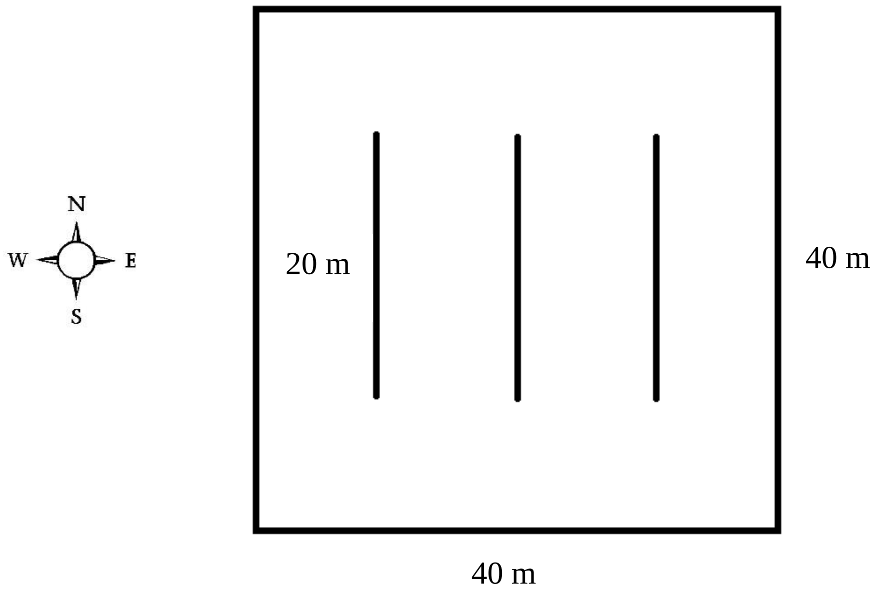

Figure 2.2: Plot layout for species composition and basal cover determination near McLaughlin, SD. Interior vertical lines indicate transects. Exterior box indicates perimeter of the plot.

Statistical Analysis

All analyses were completed in program R, version 3.2.0. Results for bare ground and litter basal cover were averaged among the ten-pin point frame readings within each plot and compared among treatments using ANOVA (function aov) and a posthoc Tukey test when necessary (function TukeyHSD). Canopy cover for each species present was averaged among readings to produce an average canopy cover for each plot. Canopy cover data were used for community composition, indicator species, and diversity analyses.

We used function metaMDS (Nonmetric Multidimensional Scaling (NMDS) with Stable Solution from Random Starts, Axis Scaling and Species Scores: *vegan* package 2.2.1, R version 3.2.0, three dimensions) to ordinate our community (cover) data and function envfit to test for differences among groups. Function envfit uses permutation of environmental variables to test for significance and provides a goodness of fit statistic (r^2) based on the unconstrained ordination

(Oksanen et al. 2015). NMDS is considered to be a robust unconstrained ordination method for community ecology (Minchin 1987, McCune and Grace 2002). We chose the Bray-Curtis dissimilarity for our ordination based on the results of the strength test function *rankindex* (Oksanen et al. 2015, *vegan* package 1.16-32). Plant community composition tables were produced using each species' average canopy cover *on-town* and *off-town*, and within ecological site to provide a clearer picture of any differences.

Diversity measures were calculated using the package BiodiversityR and compared among groups using ANOVA (function aov) and a posthoc Tukey test when necessary (function TukeyHSD). Comparisons that produced p values <0.05 were considered statistically different. Summary statistics were determined using the function describeBy. All comparisons of basal cover, plant community composition, and diversity were made within year to avoid confounding results with observer bias. We used Dufrene-Legendre Indicator Species Analysis (function indval in Package labsdv, Dufrene and Legendre 1997) to identify individual species which were strongly associated with our treatments (p<0.05). These associations are based on fidelity to group and abundance.

Results

Basal Bare Ground and Litter Cover

No difference in percent bare ground was observed between cattle grazed and un-grazed plots pre-treatment (2012, p=0.44, Table 2.1), or three years of treatment (2015, p=0.82, Table 2.2). Litter cover also did not differ between cattle grazed and un-grazed plots in either 2012 (p=0.29, Table 2.3) or 2015 (p=0.61, Table 2.4). Pre-treatment bare ground basal cover was higher *on-town* than *off-town* (p<0.01). This pattern remained after three years of treatment (p<0.01). Litter basal cover was lower *on-town* than *off*-town before treatment (p<0.01) and after three years of treatment (p<0.01).

Table 2.1: Mean percent bare ground basal cover on the cattle grazing and prairie dog treatments near McLaughlin, SD in 2012.

2012 Bare Ground Basal Cover (%)	**n**	**Mean**	**SD**	**SE**	**p**
Cattle Grazed	25	1.61	2.34	0.47	0.44
Ungrazed	25	1.75	2.42	0.48	
Off-town	18	0.10	0.10	0.02	<0.01
On-town	32	2.57	2.55	0.45	

Table 2.2: Mean percent litter basal cover on the cattle grazing and prairie dog treatments near McLaughlin, SD in 2012.

2012 Litter Basal Cover (%)	**n**	**Mean**	**SD**	**SE**	**p**
Cattle Grazed	25	7.73	2.34	0.47	0.29
Ungrazed	25	7.54	2.40	0.48	
Off-town	18	9.38	0.28	0.07	<0.01
On-town	32	6.65	2.43	0.43	

Table 2.3: Mean percent bare ground basal cover on the cattle grazing and prairie dog treatments near McLaughlin, SD in 2015.

2015 Bare Ground Basal Cover (%)	**n**	**Mean**	**SD**	**SE**	**p**
Cattle Grazed	25	1.24	1.66	0.33	0.82
Ungrazed	25	1.19	1.95	0.39	
Off-town	18	0.12	0.24	0.06	<0.01
On-town	32	1.83	1.99	0.35	

Table 2.4: Mean percent litter basal cover on the cattle grazing and prairie dog treatments near McLaughlin, SD in 2015.

2015 Litter Basal Cover (%)	**n**	**Mean**	**SD**	**SE**	**p**
Cattle Grazed	25	8.64	1.95	0.39	0.61
Ungrazed	25	8.79	1.94	0.39	
Off-town	18	9.87	0.23	0.06	<0.01
On-town	32	8.06	2.15	0.38	

Pre-treatment, *on-town* cattle grazed and un-grazed plots did not differ in either bare ground percentage (p=0.81, Table 2.5) or litter cover (p=0.75; Table 2.5). *Off-town* cattle grazed and un-grazed plots also did not differ in either bare ground percentage (p=0.43, Table 2.5) or litter cover (p=0.75, Table 2.5) in 2012. After treatment, *on-town* cattle grazed and un-grazed plots did not differ in either bare ground percentage (p=0.97, Table 2.5) or litter cover (p=0.75; Table 2.5). *Off-town* cattle grazed and un-grazed plots also did not differ in either bare ground percentage (p=0.51, Table 2.5) or litter cover (p=0.62, Table 2.5) after three years of treatment.

Table 2.5: Summary statistics of average percent bare ground and litter basal cover classified by prairie dog presence and cattle grazing treatment near McLaughlin, SD in 2012 and 2015.

	Measure	**Prairie Dogs**	**Cattle**	**n**	**Mean**	**SD**	**SE**	**p**
2012 Pre-treatment	Bare ground	*On-town*	Un-grazed	16	26.7	26.2	6.5	0.81
			Grazed	16	24.7	25.6	6.4	
		Off-town	Un-grazed	9	1.1	1.0	0.3	0.43
			Grazed	9	0.8	1.0	0.3	
	Litter	*On-town*	Un-grazed	16	65.2	24.6	6.1	0.75
			Grazed	16	67.8	24.8	6.2	
		Off-town	Un-grazed	9	93.6	3.6	1.2	0.75
			Grazed	9	94.0	1.9	0.6	
2015 Post-treatment	Bare ground	*On-town*	Un-grazed	16	18.2	22.1	5.5	0.97
			Grazed	16	18.4	18.0	4.5	
		Off-town	Un-grazed	9	0.8	1.1	0.4	0.51
			Grazed	9	1.6	3.2	1.1	
	Litter	*On-town*	Un-grazed	16	81.6	22.1	5.5	0.75
			Grazed	16	79.6	21.6	5.4	
		Off-town	Un-grazed	9	99.0	1.1	0.4	0.62
			Grazed	9	98.4	3.2	1.1	

Ecological site influenced bare ground and litter basal cover in both 2012 and 2015. In 2012, bare ground percentage was higher on the claypan ecological site than the loamy ecological site (p=0.039, Table 2.6). There were no differences between the thin loamy and claypan site (p=0.124, Table 2.6) or between the loamy and thin loamy ecological site (p=0.929, Table 2.6). In 2015, bare ground percentage was higher on the claypan ecological site than the thin loamy (p=0.013, Table 2.7) or the loamy ecological site (p=0.011, Table 2.7). There was no difference in bare ground basal cover between the thin loamy and loamy ecological site in 2015 (p=0.99, Table 2.7).

Table 2.6: Mean percent bare ground basal cover on ecological site treatments near McLaughlin, SD in 2012. Shared letters in the far right column indicate no difference (p>0.05).

2012 Bare Ground Basal Cover (%)	n	Mean	SD	SE	Sig.
Thin Loamy	14	1.10	1.53	0.41	AB
Loamy	18	1.08	1.10	0.26	A
Claypan	18	2.73	3.35	0.79	B

Table 2.7: Mean percent bare ground basal cover on ecological site treatments near McLaughlin, SD in 2015. Shared letters in the far right column indicate no difference (p>0.05).

2015 Bare Ground Basal Cover (%)	n	Mean	SD	SE	Sig.
Thin Loamy	14	0.53	0.55	0.15	A
Loamy	18	0.71	0.87	0.21	A
Claypan	18	2.26	2.54	0.60	B

Litter basal cover did not differ among ecological sites in 2012 (p=0.102, Table 2.8). In 2015, litter basal cover was lower on claypan sites than on thin loamy (p=0.014, Table 2.9) or loamy sites (p=0.011, Table 2.9). Litter basal cover on the loamy ecological site was not different than the thin loamy site in 2015 (p=0.993, Table 2.9).

Table 2.8: Mean percent litter basal cover on ecological site treatments near McLaughlin, SD in 2012.

2012 Litter Basal Cover (%)	n	Mean	SD	SE	Sig.
Thin Loamy	14	8.13	1.64	0.44	A
Loamy	18	8.11	1.23	0.29	A
Claypan	18	6.78	3.33	0.79	A

Table 2.9: Mean percent litter basal cover on ecological site treatments near McLaughlin, SD in 2015.

2015 Litter Basal Cover (%)	n	Mean	SD	SE	Sig.
Thin Loamy	14	9.46	0.55	0.15	A
Loamy	18	9.22	0.88	0.21	A
Claypan	18	7.62	2.78	0.65	B

Community Composition

Plant community composition was different between *on-town* and *off-town* sites in 2012 (r^2=0.347, p≤0.01, Figure 2.3, Appendix 1) and 2015 (r^2=0.481, p≤0.01, Figure 2.4). Plant community composition was also different among ecological sites in 2012 (r^2=0.131, p≤0.01, Tables 2.10-2.15) and 2015 (r^2=0.191, p≤0.01). Prior to study initiation, there was no difference in plant community composition between our cattle grazed and un-grazed plots (r^2=0.005, p=0.848). We saw no evidence of plant community composition changes due to three years of cattle exclusion (r^2=0.002, p=0.981).

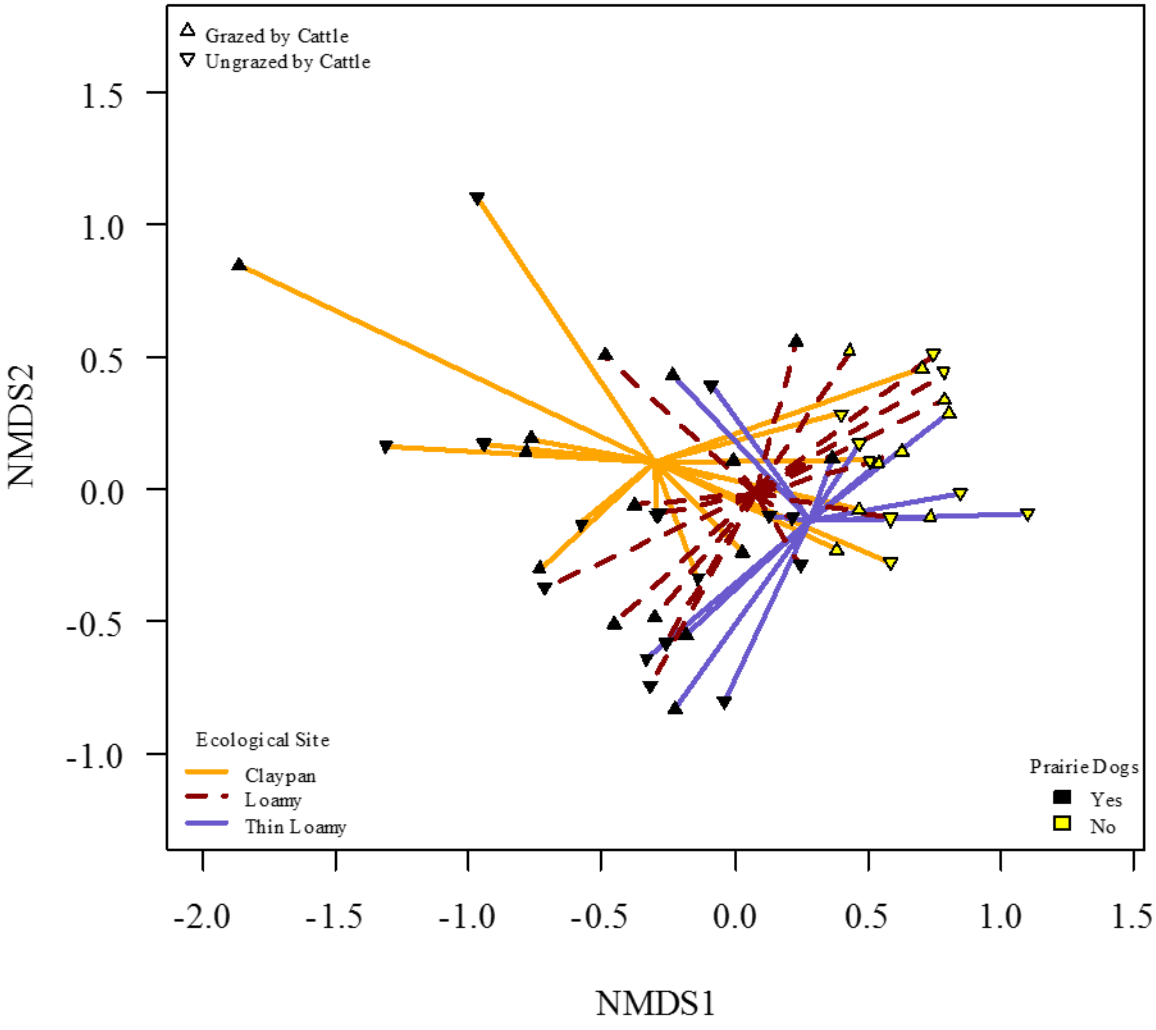

Figure 2.3: Non Metric Multidimensional Scaling (NMDS) ordination of plant community data by cattle grazing treatment and prairie dog presence treatment by ecological site near McLaughlin, SD using Bray-Curtis dissimilarity in 2012. Triangle shaped points represent plots; colored vectors connect plots on the same ecological site; point direction indicates cattle presence; fill indicates prairie dog presence. Stress =0.129. Ordinated in three dimensions.

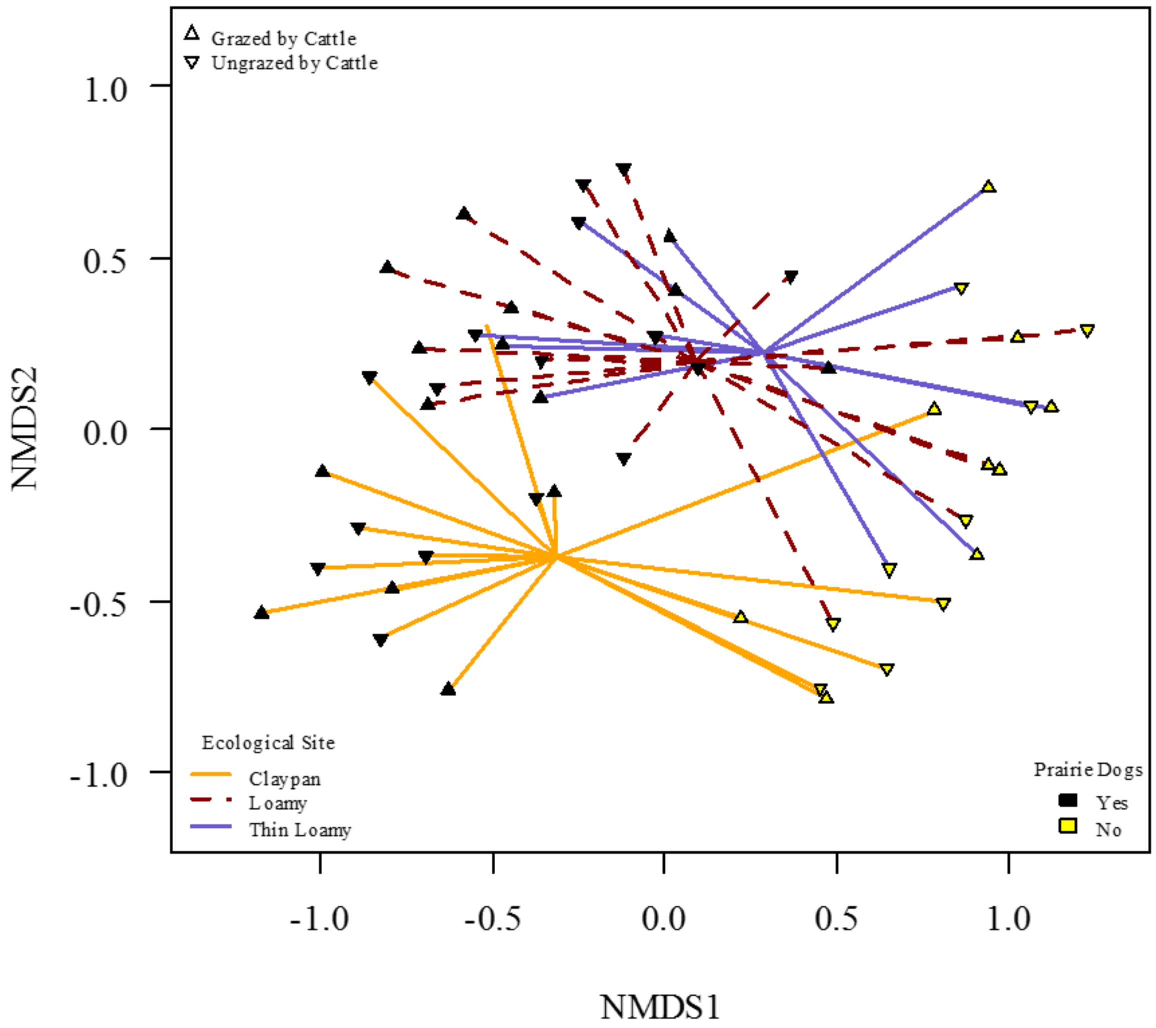

Figure 2.4: Non Metric Multidimensional Scaling (NMDS) ordination of plant community data by cattle grazing treatment and prairie dog presence treatment by ecological site near McLaughlin, SD using Bray-Curtis dissimilarity in 2015. Triangle shaped points represent plots; colored vectors connect plots on the same ecological site; point direction indicates cattle presence; fill indicates prairie dog presence. Stress=0.135. Ordinated in three dimensions.

Table 2.10: Species composition of the thin loamy ecological site by *on-town* and *off-town* prairie dog treatments in 2012. Species that comprised 1.0 percent cover or greater are shown.

***On-town* Thin Loamy (n=8)**		***Off-town* Thin Loamy (n=6)**	
Species	**Mean Cover (%)**	**Species**	**Mean Cover (%)**
Agrostis scabra	15.6	*Nassella viridula*	13.2
Pascopyrum smithii	11.4	*Pascopyrum smithii*	9.5
Bouteloua gracilis	10.7	*Poa pratensis*	8.1
Dicanthelium oligosanthes	3.5	*Bouteloua gracilis*	7.4
Carex filifolia	3.3	*Carex filifolia*	6.1
Schedonnardus paniculatus	2.1	*Bouteloua curtipendula*	4.5
Conyza ramosissima	1.8	*Melilotus officinalis*	2.9
Solidago missouriensis	1.4	*Artemisia dracunculoides*	2.3
Nassella viridula	1.2	*Artemisia frigida*	2.2
Sphaeralcea coccinea	1.2	*Bromus inermis*	2.1
Poa pratensis	<1.0	*Hesperostipa comata*	1.5
Hesperostipa comata	<1.0	*Agrostis scabra*	1.3
Dyssodia papposa	<1.0	*Koeleria macrantha*	1.3
Artemisia frigida	<1.0		
Artemisia dracunculoides	<1.0		
Koeleria macrantha	<1.0		
Melilotus officinalis	<1.0		

Table 2.11: Species composition of the loamy ecological site by *on-town* and *off-town* prairie dog treatments in 2012. Species that comprised 1.0 percent cover or greater are shown.

***On-town* Loamy (n=12)**		***Off-town* Loamy (n=6)**	
Species	**Mean Cover (%)**	**Species**	**Mean Cover (%)**
Agrostis scabra	16.5	*Nassella viridula*	28.4
Pascopyrum smithii	14.3	*Pascopyrum smithii*	15.8
Bouteloua gracilis	7.3	*Poa pratensis*	9.9
Conyza ramosissima	2.8	*Bouteloua gracilis*	4.9
Schedonnardus paniculatus	2.1	*Bouteloua curtipendula*	4.1
Nassella viridula	1.8	*Carex filifolia*	3.8
Dicanthelium oligosanthes	1.8	*Artemisia frigida*	1.2
Lotus unifolia	1.0	*Dicanthelium oligosanthes*	<1.0
Artemisia frigida	<1.0	*Lotus unifolia*	<1.0
Carex filifolia	<1.0	*Conyza ramosissima*	<1.0
Poa pratensis	<1.0	*Schedonnardus paniculatus*	<1.0

Table 2.12: Species composition of the claypan ecological site by *on-town* and *off-town* prairie dog treatments in 2012. Species that comprised 1.0 percent cover or greater are shown.

***On-town* Claypan (n=12)**		***Off-town* Claypan (n=6)**	
Species	**Mean Cover (%)**	**Species**	**Mean Cover (%)**
Pascopyrum smithii	15.5	*Pascopyrum smithii*	21.0
Bouteloua gracilis	4.3	*Poa pratensis*	15.7
Agrostis scabra	4.3	*Nassella viridula*	9.6
Schedonnardus paniculatus	4.1	*Bouteloua gracilis*	5.9
Dyssodia papposa	2.6	*Carex filifolia*	2.9
Bassia scoparia	2.0	*Carex inops*	1.7
Nassella viridula	1.1	*Sphaeralcea coccinea*	1.2
Conyza ramosissima	1.1	*Achillea millefolium*	1.1
Sphaeralcea coccinea	<1.0	*Bassia scoparia*	<1.0
Poa pratensis	<1.0		
Achillea millefolium	<1.0		
Carex filifolia	<1.0		

Table 2.13: Species composition of the thin loamy ecological site by on-town and off-town prairie dog treatments in 2015. Species that comprised 1.0 percent cover or greater are shown.

***On-town* Thin Loamy (n=8)**		***Off-town* Thin Loamy (n=6)**	
Species	**Mean Cover (%)**	**Species**	**Mean Cover (%)**
Conyza ramosissima	25.4	*Poa pratensis*	16.1
Calamagrostis montanum	13.2	*Bouteloua curtipendula*	14.6
Schedonnardus paniculatus	11.3	*Hesperostipa comata*	12.4
Agrostis scabra	9.5	*Lactuca tatarica*	6.6
Pascopyrum smithii	7.9	*Bromus inermis*	5.5
Bouteloua gracilis	4.6	*Nassella viridula*	5.4
Carex filifolia	3.7	*Amorpha nana*	4.6
Dicanthelium wilcoxianum	3.4	*Schizachyrium scoparium*	4.4
Muhlenbergia cuspidata	2.5	*Symphoricarpos occidentalis*	4.2
Amorpha cana	2.4	*Melilotus officinalis*	3.9
Solidago missouriensis	2.2	*Carex filifolia*	3.7
Aristida purpurea	2.1	*Pascopyrum smithii*	3.7
Lactuca tatarica	1.9	*Anemone canadensis*	3.6
Lotus unifolia	1.5	*Ratibida columnifera*	3.3
Plantago elongata	1.5	*Pediomelum argophyllum*	2.8
Poa pratensis	<1.0	*Bouteloua gracilis*	2.5
Schizachyrium scoparium	<1.0	*Muhlenbergia cuspidata*	2.5
Ratibida columnifera	<1.0	*Rosa arkansana*	1.6
Anemone canadensis	<1.0	*Artemisia dracunculoides*	1.5
Pediomelum argophyllum	<1.0	*Cirsium flodmanii*	1.5
Amorpha nana	<1.0	*Achillea millefolium*	1.3
Achillea millefolium	<1.0	*Artemisia ludoviciana*	1.3
Artemisia ludoviciana	<1.0	*Antennaria neglecta*	1.0
Rosa arkansana	<1.0	*Aristida purpurea*	1.0
Hesperostipa comata	<1.0	*Lotus unifolia*	<1.0
Symphoricarpos occidentalis	<1.0	*Solidago missouriensis*	<1.0

Table 2.14: Species composition of the loamy ecological site by on-town and off-town prairie dog treatments in 2015. Species that comprised 1.0 percent cover or greater are shown.

***On-town* Loamy (n=12)**		***Off-town* Loamy (n=6)**	
Species	**Mean Cover (%)**	**Species**	**Mean Cover (%)**
Agrostis scabra	19.2	*Poa pratensis*	30.5
Calamagrostis montanum	18.7	*Nassella viridula*	8.0
Conyza ramosissima	18.3	*Amorpha nana*	6.8
Pascopyrum smithii	8.8	*Pascopyrum smithii*	5.8
Bouteloua gracilis	8.6	*Schizachyrium scoparium*	4.3
Poa pratensis	6.7	*Melilotus officinalis*	3.9
Schedonnardus paniculatus	5.9	*Amorpha cana*	3.8
Bouteloua curtipendula	4.8	*Bouteloua curtipendula*	3.7
Amorpha cana	3.8	*Lactuca tatarica*	3.7
Solidago missouriensis	3.3	*Bromus inermis*	3.5
Nassella viridula	2.9	*Bouteloua gracilis*	3.2
Cirsium arvense	2.6	*Pediomelum argophyllum*	2.9
Asclepias pumila	2.5	*Symphoricarpos occidentalis*	2.2
Dicanthelium wilcoxianum	2.4	*Carex inops*	1.9
Polygonum achoreum	2.2	*Hesperostipa comata*	1.8
Calamovilfa longifolia	2.1	*Artemisia dracunculoides*	1.8
Verbena bracteata	1.5	*Rosa arkansana*	1.6
Carex inops	1.5	*Galium boreale*	1.4
Oxalis stricta	1.3	*Bromus arvense*	1.1
Andropogon gerardii	1.3	*Artemisia frigida*	<1.0
Rosa arkana	1.3	*Solidago missouriensis*	<1.0
Anemone canadensis	1.2		
Artemisia frigida	1.1		
Plantago elongata	1.0		
Lactuca tatarica	<1.0		
Hesperostipa comata	<1.0		
Melilotus officinalis	<1.0		
Galium boreale	<1.0		
Pediomelum argophyllum	<1.0		

Table 2.15: Species composition of the claypan ecological site by on-town and off-town prairie dog treatments in 2015. Species that comprised 1.0 percent cover or greater are shown.

***On-town* Claypan (n=12)**		***Off-town* Claypan (n=6)**	
Species	**Mean Cover (%)**	**Species**	**Mean Cover (%)**
Distichlis spicata	18.7	*Poa pratensis*	32.2
Agrostis scabra	15.1	*Pascopyrum smithii*	16.3
Schedonnardus paniculatus	12.2	*Nassella viridula*	9.6
Pascopyrum smithii	12.1	*Bouteloua curtipendula*	6.6
Bouteloua gracilis	7.3	*Lactuca tatarica*	6.4
Conyza ramosissima	7.2	*Muhlenbergia cuspidata*	5.5
Cirsium arvense	4.2	*Hesperostipa comata*	4.0
Plantago elongata	2.7	*Bromus inermis*	3.4
Bouteloua dactyloides	2.6	*Amorpha nana*	2.5
Dyssodia papposa	2.3	*Bouteloua dactyloides*	2.5
Carex inops	2.0	*Artemisia frigida*	2.1
Bassia scoparia	2.0	*Carex filifolia*	2.1
Astragalus adsurgens	1.8	*Symphoricarpos occidentalis*	1.9
Solidago missouriensis	1.8	*Bouteloua gracilis*	1.8
Chamaesyce glyptosperma	1.3	*Ratibida columnifera*	1.3
Asclepias pumila	1.2	*Pediomelum argophyllum*	1.2
Artemisia frigida	<1.0	*Achillea millefolium*	1.1
Achillea millefolium	<1.0	*Artemisia cana*	1.1
Carex filifolia	<1.0	*Asclepias pumila*	<1.0
Lactuca tatarica	<1.0	*Carex inops*	<1.0

Indicator Species

Pre-treatment there were 10 species that were strongly associated with prairie dog presence and 16 species strongly associated with prairie dog absence (Table 2.16). There were also six species that were found to be strongly associated with the thin loamy ecological site (Table 2.17). No species showed significant associations with the loamy or claypan ecological sites. We also found no species to be strongly associated with cattle grazing or cattle exclusion.

Table 2.16: Statistically significant indicator species categorized by prairie dog presence near McLaughlin, SD in 2012.

Associated Category	Species	Indicator Value	p-value
Off-town	*Poa pratensis*	0.96	0.001
	Nassella viridula	0.92	0.001
	Carex filifolia	0.80	0.001
	Artemisia dracunculoides	0.68	0.001
	Carex inops	0.65	0.001
	Artemisia frigida	0.64	0.001
	Achillea millefolium	0.41	0.008
	Artemisia ludoviciana	0.39	0.008
	Bouteloua curtipendula	0.39	0.001
	Echinacea angustifolia	0.37	0.002
	Koeleria macrantha	0.32	0.004
	Bromus inermis	0.28	0.005
	Bromus arvense	0.17	0.047
	Lygodesmia juncea	0.17	0.034
	Pediomelum argophyllum	0.16	0.044
	Rosa woodsii	0.16	0.042
On-town	*Schedonnardus paniculatus*	0.69	0.001
	Dyssodia papposa	0.66	0.002
	Lotus unifolia	0.61	0.001
	Agrostis scabra	0.60	0.001
	Conyza ramosissima	0.56	0.001
	Solidago missouriensis	0.49	0.011
	Plantago elongata	0.44	0.004
	Cirsium arvense	0.28	0.040
	Amorpha nana	0.25	0.036
	Verbena bracteata	0.25	0.039

Table 2.17: Statistically significant indicator species categorized by ecological site near McLaughlin, SD in 2012.

Associated Category	Species	Indicator Value	p-value
Thin Loamy Ecological Site	*Carex filifolia*	0.54	0.003
	Artemisia dracunculoides	0.46	0.012
	Ratibida columnifera	0.39	0.050
	Echinacea angustifolia	0.36	0.007
	Dicanthelium wilcoxianum	0.36	0.048
	Koeleria macrantha	0.33	0.006
Loamy Ecological Site	No Indicator Species	-	-
Claypan Ecological Site	No Indicator Species	-	-

Post-treatment, 15 species were found to be associated with prairie dog presence and 19 species associated with prairie dog absence (Table 2.18). The thin loamy and claypan ecological sites each showed significant associations with six species (Table 2.19). No species showed significant associations with the loamy ecological site, cattle grazing, or cattle exclusion.

Table 2.18: Statistically significant indicator species categorized by prairie dog presence near McLaughlin, SD in 2015.

Associated Category	Species	Indicator Value	p-value
Off-town	*Poa pratensis*	0.98	0.001
	Nassella viridula	0.98	0.001
	Pediomelum argophyllum	0.76	0.001
	Artemisia dracunculoides	0.67	0.001
	Hesperostipa comata	0.61	0.001
	Rosa arkansana	0.50	0.001
	Bouteloua curtipendula	0.47	0.001
	Echinacea angustifolia	0.46	0.001
	Koeleria macrantha	0.33	0.002
	Artemisia ludoviciana	0.30	0.009
	Amorpha nana	0.28	0.004
	Symphoricarpos occidentalis	0.27	0.014
	Artemisia cana	0.22	0.020
	Bromus inermis	0.22	0.011
	Sisyrinchium montanum	0.22	0.015
	Bromus arvense	0.21	0.016
	Muhlenbergia cuspidata	0.19	0.044
	Schizachyrium scoparium	0.16	0.042
	Erigeron strigosus	0.15	0.038
On-town	*Conyza ramosissima*	0.88	0.001
	Schedonnardus paniculatus	0.88	0.001
	Dyssodia papposa	0.81	0.001
	Plantago elongata	0.69	0.001
	Hedeoma hispida	0.67	0.001
	Agrostis scabra	0.63	0.001
	Glycyrrhiza lepidota	0.59	0.001
	Dicanthelium wilcoxianum	0.56	0.001
	Oxalis stricta	0.53	0.001
	Sphaeralcea coccinea	0.49	0.032
	Conyza canadensis	0.49	0.003
	Verbena bracteata	0.47	0.005
	Solidago missouriensis	0.36	0.039
	Setaria glauca	0.34	0.013
	Cirsium arvense	0.28	0.020

Table 2.19: Statistically significant indicator species categorized by ecological site near McLaughlin, SD in 2015.

Associated Category	Species	Indicator Value	p-value
Thin Loamy Ecological Site	*Carex filifolia*	0.71	0.001
	Ratibida columnifera	0.56	0.002
	Hesperostipa comata	0.43	0.016
	Conyza canadensis	0.36	0.030
	Solidago missouriensis	0.33	0.038
	Echinacea angustifolia	0.26	0.050
Claypan Ecological Site	*Pascopyrum smithii*	0.51	0.018
	Dyssodia papposa	0.45	0.030
	Hedeoma hispida	0.44	0.033
	Plantago elongata	0.41	0.030
	Bouteloua dactyloides	0.28	0.015
	Artemisia cana	0.22	0.029
Loamy Ecological Site	No Indicator Species	-	-

Plant Diversity

Overall Comparisons: Pre-treatment (2012)

Plant community composition prior to the cattle grazing treatments was not different in plant species richness (p=0.787) or inverse Simpson diversity (p=0.971) between cattle grazing exclosures and paired un-grazed plots (Table 2.20, Figure 2.5). There were also no detectable differences in species richness (p=0.833) or inverse Simpson diversity (p=0.081) between *on-town* and *off-town* sites (Table 2.20, Figure 2.5) prior to study treatments in 2012. There was a difference in species richness among ecological sites (Table 2.20, Figure 2.5), with the claypan ecological site having lower species richness than the thin loamy (p<0.001) and loamy ecological sites (p=0.003). The thin loamy and loamy ecological sites were not different in species richness (p=0.734). Ecological sites also influenced inverse Simpson diversity, with the thin loamy ecological site with higher values than the claypan (p=0.006) and loamy (p=0.02) ecological sites. Inverse Simpson diversity was not different between the loamy and claypan ecological sites (p=0.870).

Table 2.20: Summary statistics of species richness and inverse Simpson diversity by prairie dog presence, cattle grazing occurrence, and ecological site near McLaughlin, SD in 2012. The far right column (Sig.) displays p-values for comparisons between two groups and letters for comparisons among three groups. Shared letters indicate no difference (p>0.05).

Measure	Category	n	Mean	SD	SE	Med	Min	Max	Range	Sig.
Species Richness	Cattle Grazed	25	14.4	5.3	1.1	15.0	3.0	28.0	25.0	p=0.787
	Un-grazed	25	14.9	6.2	1.2	14.0	4.0	31.0	27.0	
Inv. Simp. Diversity	Cattle Grazed	25	4.2	1.8	0.4	3.9	1.5	8.9	7.4	p=0.971
	Un-grazed	25	4.3	1.9	0.4	4.6	1.5	8.1	6.5	
Species Richness	Off-Town	32	14.5	6.5	1.2	13.0	3.0	31.0	28.0	p=0.833
	On-Town	18	14.9	4.0	0.9	15.0	8.0	23.0	15.0	
Inv. Simp. Diversity	Off-Town	32	3.9	1.9	0.3	3.6	1.5	8.9	7.4	p=0.081
	On-Town	18	4.9	1.6	0.4	5.1	1.8	7.9	6.0	
Species Richness	Thin Loamy	14	17.6	6.2	1.7	16.0	11.0	31.0	20.0	B
	Loamy	18	16.3	4.6	1.1	15.0	10.0	28.0	18.0	B
	Claypan	18	10.7	4.0	0.9	10.0	3.0	17.0	14.0	A
Inv. Simp. Diversity	Thin Loamy	14	5.6	2.0	0.5	5.8	1.9	8.9	7.0	C
	Loamy	18	3.9	1.6	0.4	3.6	1.8	7.0	5.2	D
	Claypan	18	3.6	1.5	0.4	3.8	1.5	6.1	4.6	D

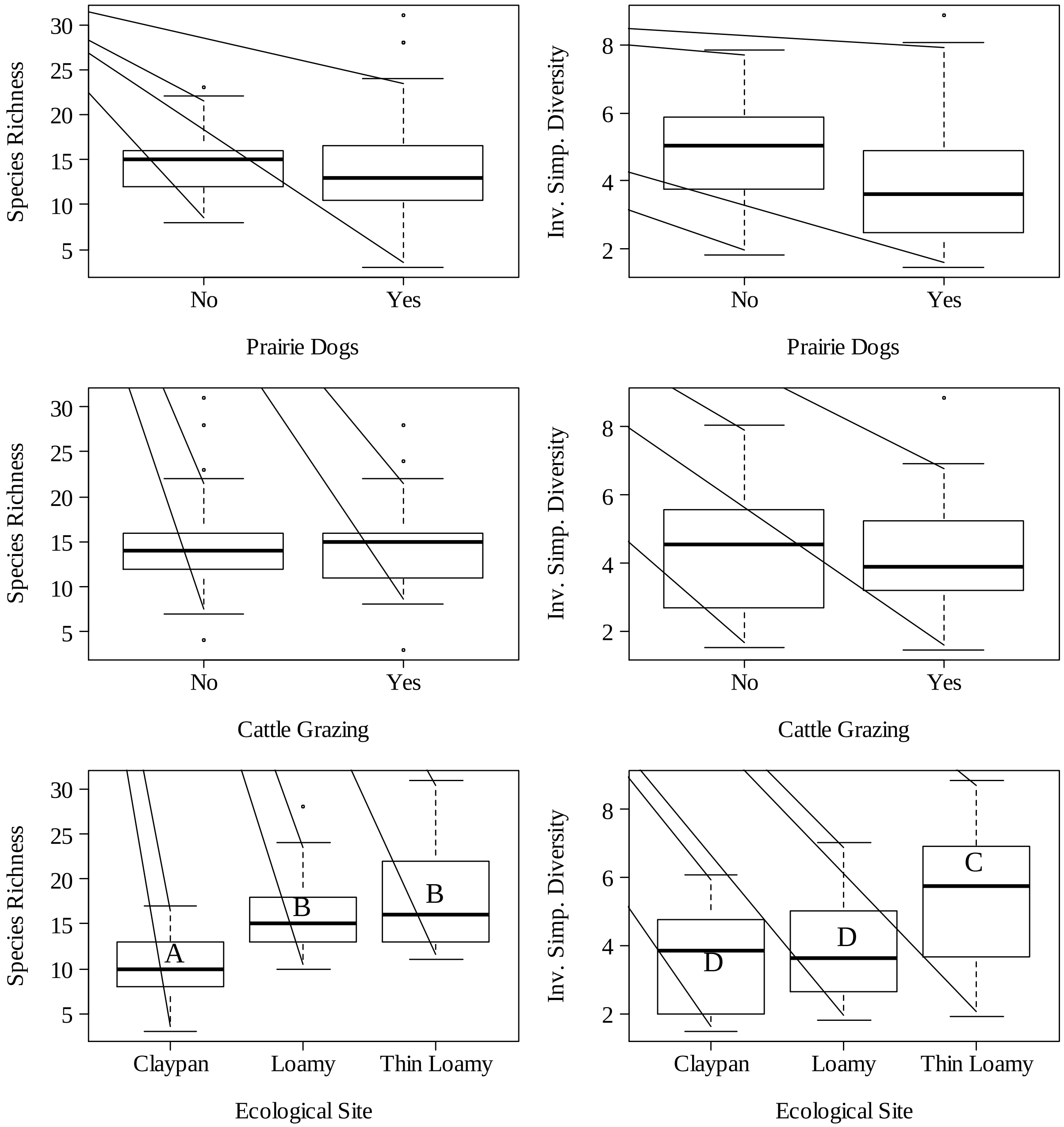

Figure 2.5: Box and whisker plots displaying species richness and inverse Simpson diversity by prairie dog presence, cattle grazing occurrence, and ecological site near McLaughlin, SD in 2012. Letters in plots indicate statistically significant differences, with shared letters or lack of letters indicating no difference (p>0.05).

Overall Comparisons: Post-treatment (2015)

Plant species richness (p=0.438) and inverse Simpson diversity (p=0.612) were not different between cattle grazing and un-grazed treatments three years after treatment (2015; Table 2.21, Figure 2.6). There was also no differences in species richness (p=0.284) or inverse Simpson Diversity (p=0.328) between *on-town* and *off-town* treatments (Table 2.21, Figure 2.6) after three years of treatment.

Ecological site did influence species richness (Table 2.21, Figure 2.6), with the claypan ecological site having lower species richness than both the thin loamy plots (p<0.001) and loamy ecological sites (p<0.001) three years following treatments. The thin loamy and loamy ecological sites were not different in species richness (p=0.773). Type of ecological site also influenced inverse Simpson diversity, with the thin loamy ecological site having a higher value than the claypan ecological sites (p=0.008), but not different than loamy ecological sites (p=0.13). Inverse Simpson diversity was not different between the loamy and claypan ecological sites (p=0.436).

Table 2.21: Summary statistics of species richness and inverse Simpson diversity by prairie dog presence, cattle grazing occurrence, and ecological site near McLaughlin, SD in 2015. The far right column (Sig.) displays p-values for comparisons between two groups and letters for comparisons among three groups. Shared letters indicate no difference (p>0.05).

Measure	Category	n	Mean	SD	SE	Med	Min	Max	Range	Sig.
Species Richness	Cattle Grazed	25	18.5	5.3	1.1	19.0	8.0	28.0	20.0	p=0.438
	Ungrazed	25	17.3	5.6	1.1	17.0	8.0	30.0	22.0	
Inv. Simp. Diversity	Cattle Grazed	25	4.2	2.0	0.4	3.2	1.5	10.2	8.6	p=0.612
	Ungrazed	25	3.9	1.5	0.3	3.8	1.4	9.2	7.8	
Species Richness	Off-Town	18	16.8	4.6	1.1	15.5	8.0	26.0	18.0	p=0.284
	On-Town	32	18.5	5.8	1.0	19.5	8.0	30.0	22.0	
Inv. Simp. Diversity	Off-Town	18	4.4	2.1	0.5	3.7	1.5	10.2	8.6	p=0.328
	On-Town	32	3.8	1.5	0.3	3.5	1.4	9.2	7.8	
Species Richness	Thin Loamy	14	21.1	3.7	1.0	20.5	14.0	26.0	12.0	B
	Loamy	18	20.1	4.8	1.1	19.5	14.0	30.0	16.0	A
	Claypan	18	13.2	3.9	0.9	12.5	8.0	21.0	13.0	A
Inv. Simp. Diversity	Thin Loamy	14	5.1	2.3	0.6	4.7	2.0	10.2	8.2	D
	Loamy	18	4.0	1.6	0.4	3.5	1.5	8.3	6.7	C
	Claypan	18	3.3	1.0	0.2	3.0	1.4	5.3	3.9	CD

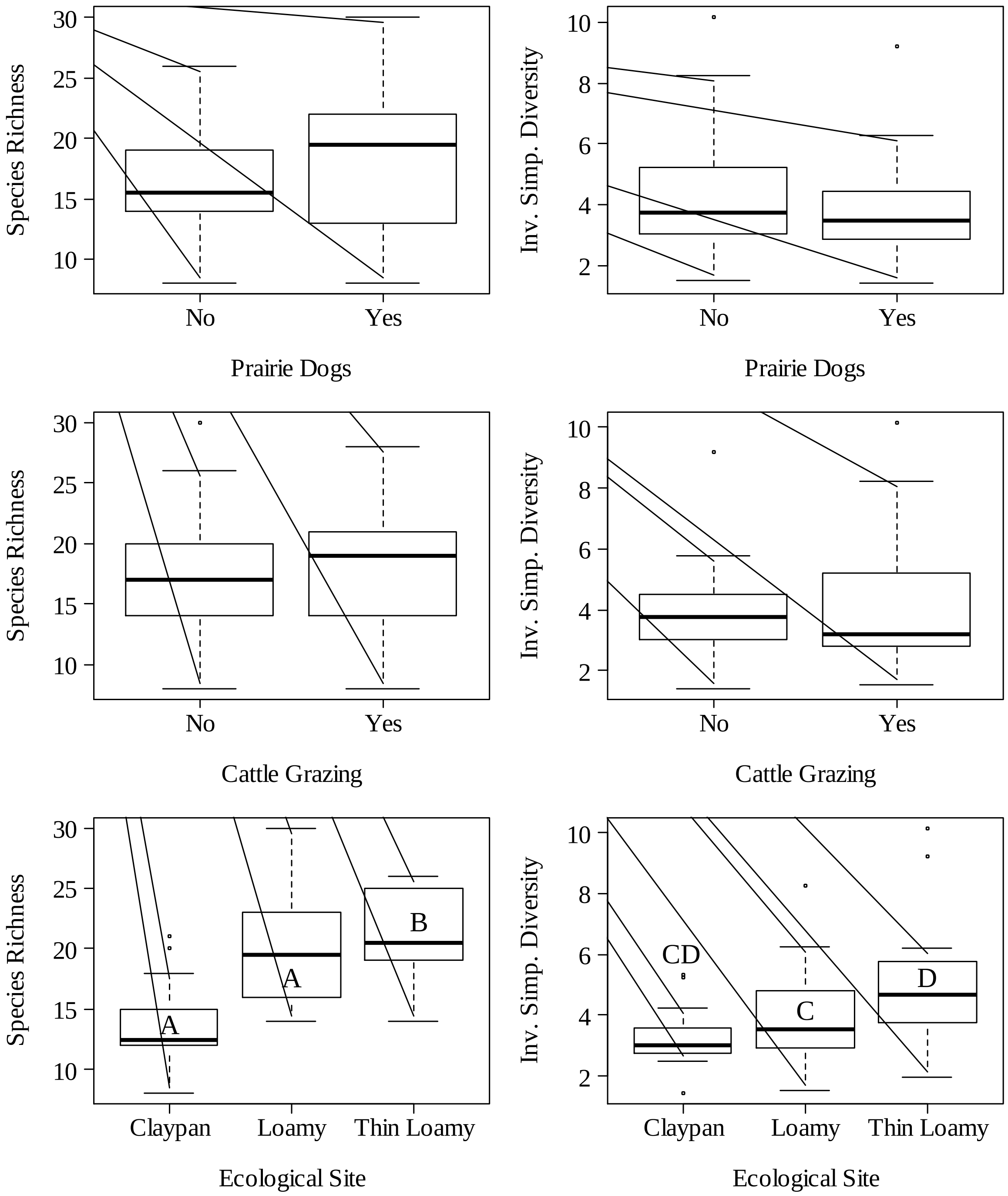

Figure 2.6: Box and whisker plots displaying species richness and inverse Simpson diversity by prairie dog presence, cattle grazing occurrence, and ecological site near McLaughlin, SD in 2015. Letters in plots indicate statistically significant differences, with shared letters or lack of letters indicating no difference (p>0.05).

On-town Comparisons: Pre-treatment (2012)

When analysis was restricted to only the *on-town* treatments, no differences were found between cattle-grazed and un-grazed treatments for either species richness (p=0.978) or inverse Simpson diversity (p=0.856, Table 2.22, Figure 2.7). The claypan ecological site had lower species richness than the thin loamy (p=0.001) and loamy ecological sites (p=0.009). Species richness was not different between the thin loamy and loamy ecological sites (p=0.509). The thin loamy ecological site had a higher inverse Simpson diversity than the claypan ecological site (p=0.031), but not different from the loamy ecological site (p=0.179). The inverse Simpson diversity on the loamy ecological site was not different that the claypan ecological site (p=0.613).

Table 2.22: Summary statistics of species richness and inverse Simpson diversity of *on-town* plots categorized by cattle grazing occurrence and ecological site near McLaughlin, SD in 2012. The far right column (Sig.) displays p-values for comparisons between two groups and letters for comparisons among three groups. Shared letters indicate no difference (p>0.05).

Measure	Category	n	Mean	SD	SE	Median	Min	Max	Range	Sig.
Species Richness	Cattle Grazed	16	14.5	5.9	1.5	14.5	3.0	28.0	25.0	p=0.978
	Un-grazed	16	14.6	7.3	1.8	13.0	4.0	31.0	27.0	
Inv. Simp. Diversity	Cattle Grazed	16	4.0	1.8	0.5	3.7	1.5	8.9	7.4	p=0.856
	Un-grazed	16	3.9	2.0	0.5	3.6	1.5	8.1	6.5	
Species Richness	Thin Loamy	8	19.1	7.4	2.6	17.0	11.0	31.0	20.0	B
	Loamy	12	16.4	4.9	1.4	15.0	12.0	28.0	16.0	B
	Claypan	12	9.6	3.9	1.1	10.0	3.0	16.0	13.0	A
Inv. Simp. Diversity	Thin Loamy	8	5.3	2.3	0.8	5.0	1.9	8.9	7.0	D
	Loamy	12	3.8	1.5	0.4	3.5	1.8	7.0	5.2	CD
	Claypan	12	3.1	1.5	0.4	2.7	1.5	6.1	4.6	C

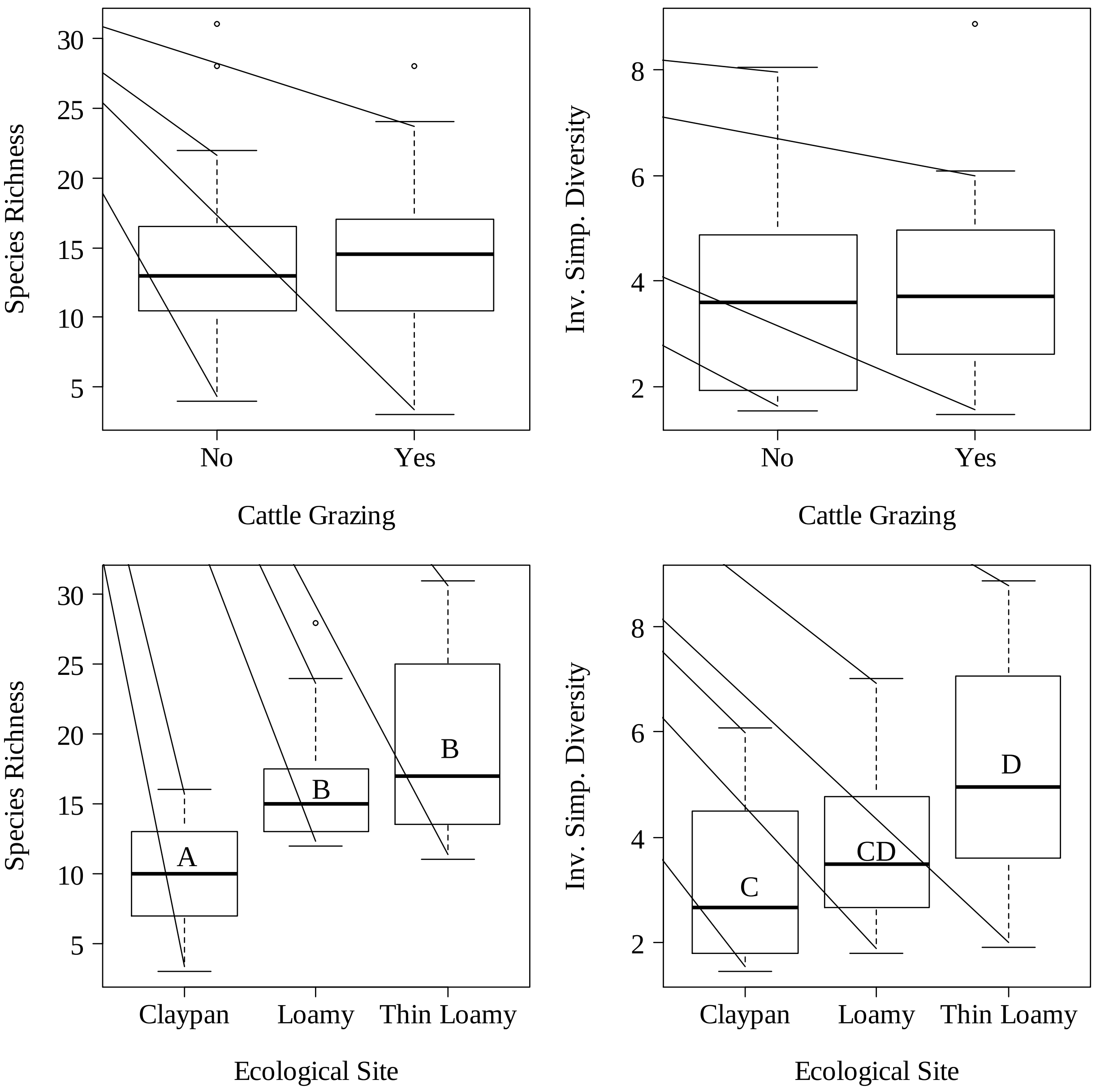

Figure 2.7: Box and whisker plots showing species richness and inverse Simpson diversity for *on-town* treatments by cattle grazing occurrence and ecological site near McLaughlin, SD in 2012. Letters in plots indicate statistically significant differences, with shared letters or lack of letters indicating no difference (p>0.05).

On-town Comparisons: Post-treatment (2015)

When analysis was restricted to only *on-town* treatments, there were no differences between cattle-grazed and un-grazed treatments plots for species richness (p=0.675) or Inverse

Simpson Diversity (p=0.960, Table 2.23, Figure 2.8). Claypan ecological sites had lower species richness than the thin loamy (p<0.001) and loamy ecological sites (p<0.001). Species richness did not differ between the thin loamy and loamy ecological sites (p=0.890). No differences in inverse Simpson diversity were observed among ecological sites (p=0.116).

Table 2.23: Summary statistics of species richness and inverse Simpson diversity of *on-town* plots categorized by cattle grazing occurrence and ecological site near McLaughlin, SD in 2015. The far right column (Sig.) displays p-values for comparisons between two groups and letters for comparisons among three groups. Shared letters indicate no difference (p>0.05).

Measure	Category	n	Mean	SD	SE	Median	Min	Max	Range	Sig.
Species Richness	Cattle Grazed	16	18.9	5.4	1.4	20.0	8.0	28.0	20.0	p=0.675
	Un-grazed	16	18.1	6.2	1.6	19.0	8.0	30.0	22.0	
Inv. Simp. Diversity	Cattle Grazed	16	3.9	1.4	0.4	3.0	2.3	6.3	3.9	p=0.960
	Un-grazed	16	3.8	1.7	0.4	3.7	1.4	9.2	7.8	
Species Richness	Thin Loamy	8	22.4	2.9	1.0	21.5	19.0	26.0	7.0	B
	Loamy	12	21.6	4.2	1.2	20.5	15.0	30.0	15.0	B
	Claypan	12	12.8	3.8	1.1	12.0	8.0	20.0	12.0	A
Inv. Simp. Diversity	Thin Loamy	8	4.6	2.3	0.8	4.3	2.0	9.2	7.3	p=0.116
	Loamy	12	3.9	1.1	0.3	3.7	2.8	6.3	3.5	
	Claypan	12	3.2	1.0	0.3	3.0	1.4	5.3	3.9	

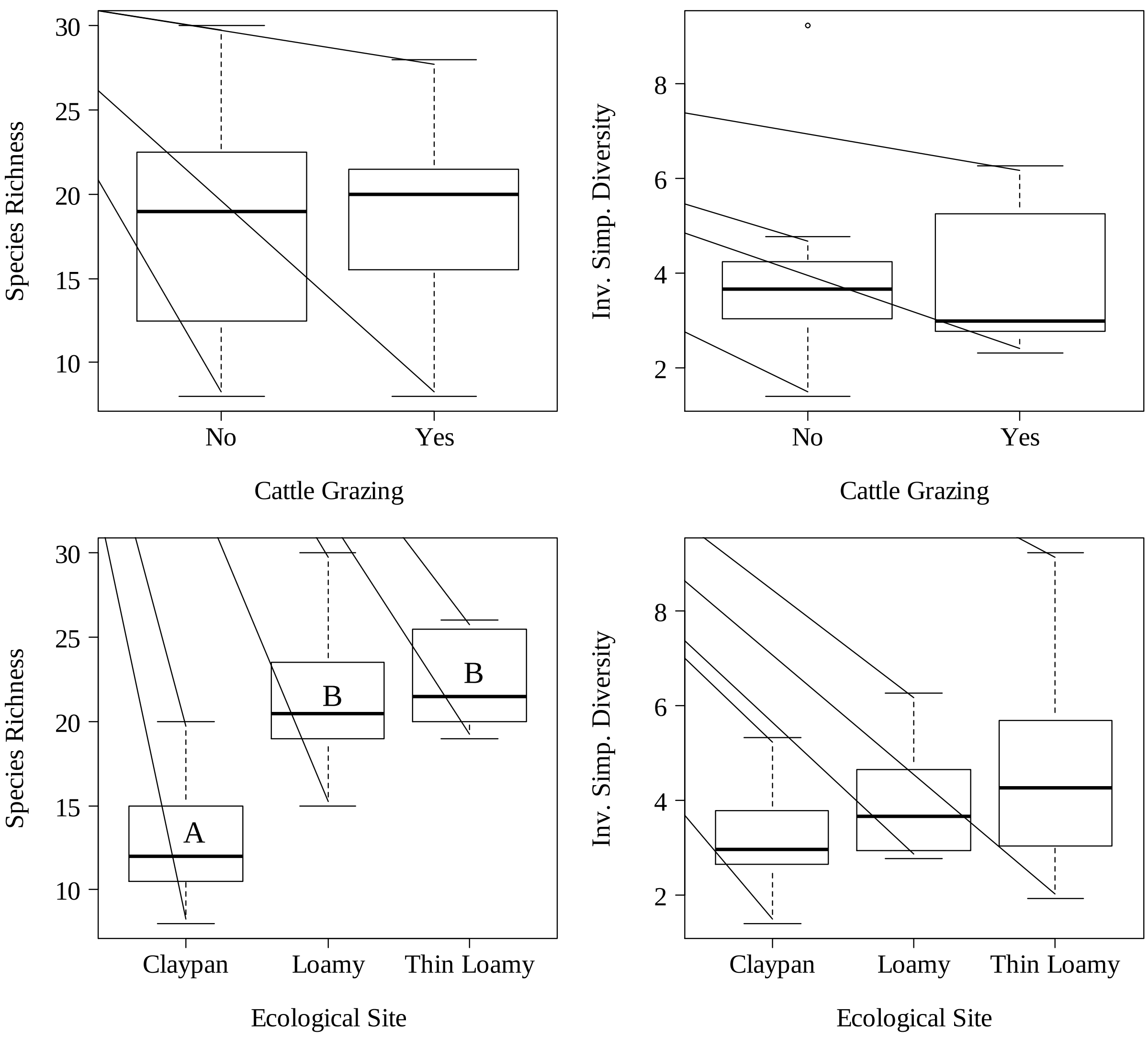

Figure 2.8: Box and whisker plots showing species richness and inverse Simpson diversity for on-town treatments by cattle grazing occurrence and ecological site near McLaughlin, SD in 2015. Letters in plots indicate statistically significant differences, with shared letters or lack of letters indicating no difference (p>0.05).

Off-town Comparisons: Pre-treatment (2012)

When analysis was restricted to only *off-town* treatments, there was no difference between cattle-grazed and un-grazed plots for plant species richness (p=0.568) or inverse

Simpson diversity (p=0.734, Table 2.24, Figure 2.9). Neither species richness (p=0.309) nor inverse Simpson diversity (p=0.110) differed among ecological sites.

Table 2.24: Summary statistics of species richness and inverse Simpson diversity of *off-town* plots categorized by cattle grazing occurrence and ecological site near McLaughlin, SD in 2012. The far right column (Sig.) displays p-values for comparisons between two groups and letters for comparisons among three groups. Shared letters indicate no difference (p>0.05).

Measure	Category	n	Mean	SD	Median	Min	Max	Range	SE	Sig.
Species Richness	Cattle Grazed	9	14.3	4.2	16.0	8.0	22.0	14.0	1.4	p=0.568
	Un-grazed	9	15.4	3.8	15.0	10.0	23.0	13.0	1.3	
Inv. Simp. Diversity	Cattle Grazed	9	4.7	1.7	5.1	1.8	6.9	5.1	0.6	p=0.734
	Un-grazed	9	5.0	1.6	5.0	2.2	7.9	5.7	0.5	
Species Richness	Thin Loamy	6	15.7	3.9	15.0	12.0	23.0	11.0	1.6	p=0.309
	Loamy	6	16.2	4.3	15.5	10.0	22.0	12.0	1.8	
	Claypan	6	12.8	3.4	13.5	8.0	17.0	9.0	1.4	
Inv. Simp. Diversity	Thin Loamy	6	6.0	1.6	6.1	3.2	7.9	4.6	0.6	p=0.110
	Loamy	6	4.1	1.9	4.2	1.8	6.9	5.1	0.8	
	Claypan	6	4.6	0.8	4.6	3.8	5.6	1.8	0.3	

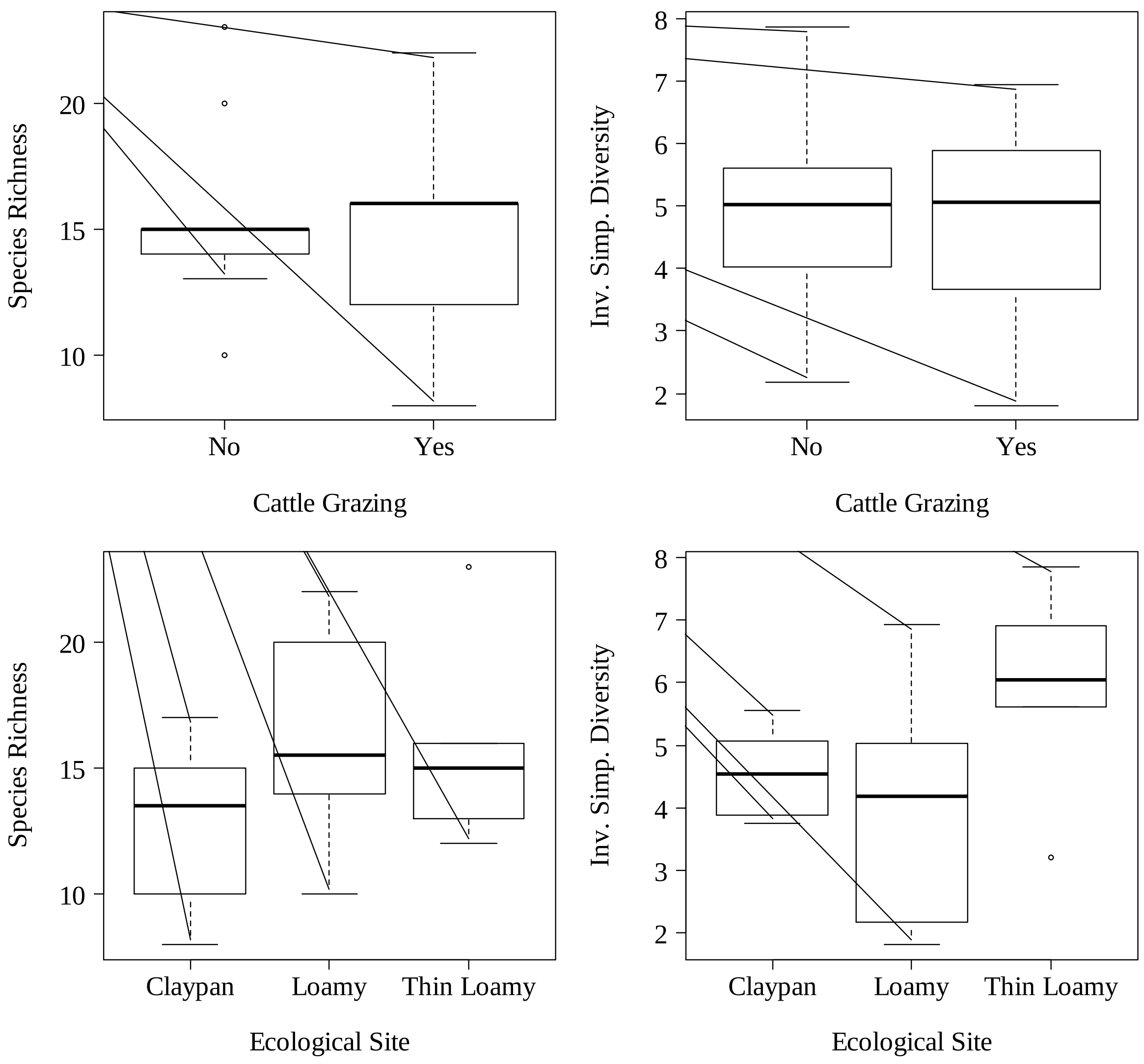

Figure 2.9: Box and whisker plots showing species richness and inverse Simpson diversity for *off-town* treatments by cattle grazing occurrence and ecological site near McLaughlin, SD in 2012. Letters in plots indicate statistically significant differences, with shared letters or lack of letters indicating no difference (p>0.05).

Off-town Comparisons: Post-treatment (2015)

When analysis was restricted to only *off-town* treatments, there was no difference between cattle-grazed and un-grazed treatments for either species richness (p=0.432) or Inverse Simpson Diversity (p=0.524, Table 2.25, Figure 2.9). Neither species richness (p=0.134) nor Inverse Simpson Diversity (p=0.144) differed among ecological sites (Figure 2.10).

Table 2.25: Summary statistics of species richness and inverse Simpson diversity of *off-town* plots categorized by cattle grazing occurrence and ecological site near McLaughlin, SD in 2015. The far right column (Sig.) displays p-values for comparisons between two groups and letters for comparisons among three groups. Shared letters indicate no difference (p>0.05).

Measure	Category	n	Mean	SD	SE	Med	Min	Max	Range	Sig.
Species Richness	Cattle Grazed	9	17.7	5.1	1.7	16.0	12.0	26.0	14.0	p=0.432
	Un-grazed	9	15.9	4.2	1.4	15.0	8.0	23.0	15.0	
Inv. Simp. Diversity	Cattle Grazed	9	4.7	2.8	1.0	3.7	1.5	10.2	8.6	p=0.524
	Un-grazed	9	4.0	1.2	0.4	3.8	2.6	5.8	3.2	

Species Richness	Thin Loamy	6	19.3	4.1	1.7	19.0	14.0	25.0	11.0	p=0.134
	Loamy	6	17.0	4.6	1.9	15.5	14.0	26.0	12.0	
	Claypan	6	14.0	4.2	1.7	14.0	8.0	21.0	13.0	
Inv. Simp. Diversity	Thin Loamy	6	5.7	2.3	0.9	5.1	3.7	10.2	6.5	p=0.144
	Loamy	6	4.0	2.4	1.0	3.4	1.5	8.3	6.7	
	Claypan	6	3.4	1.0	0.4	3.1	2.6	5.2	2.6	

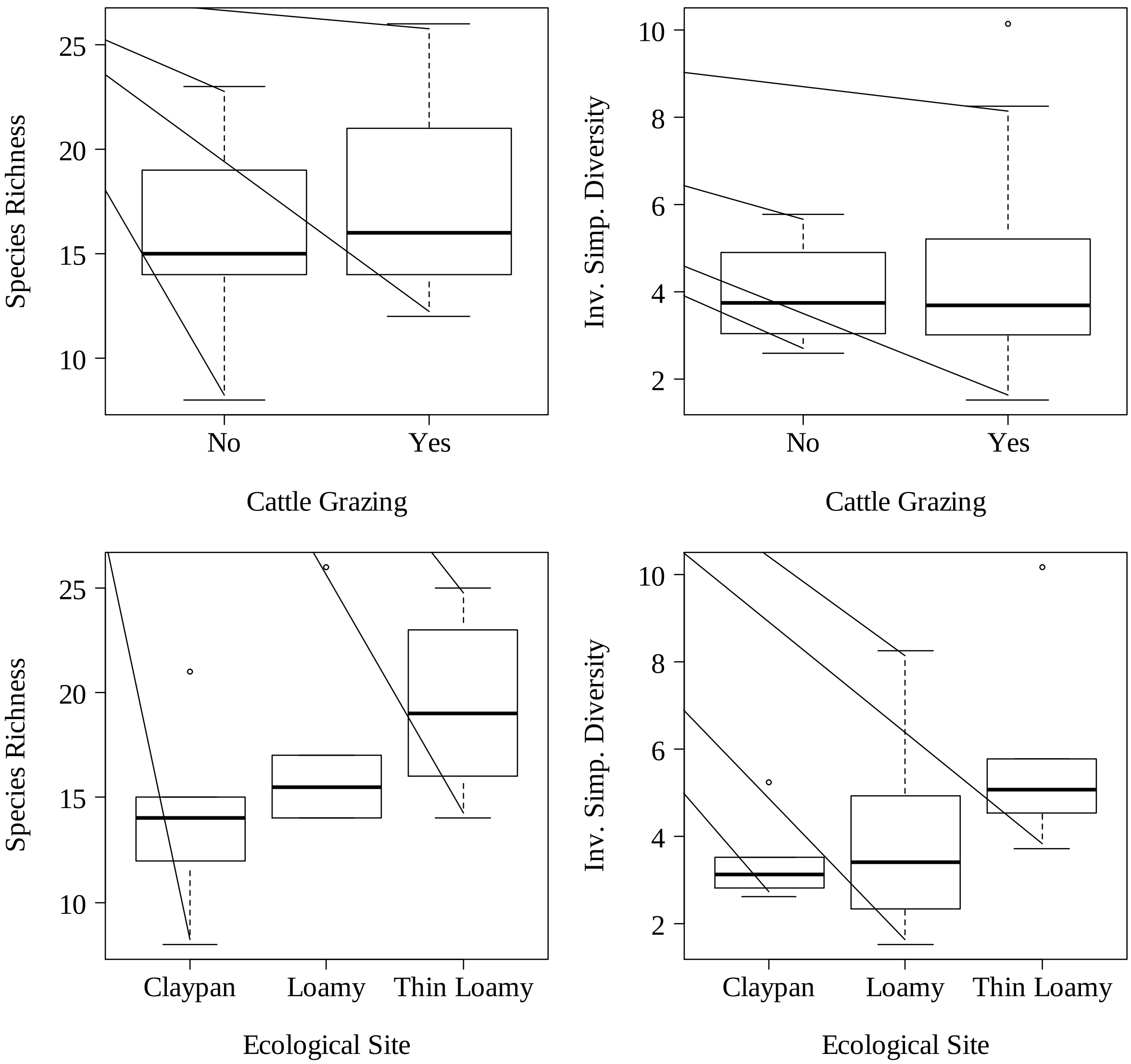

Figure 2.10: Box and whisker plots showing species richness and inverse Simpson diversity for *off-town* treatments by cattle grazing occurrence and ecological site near McLaughlin, SD in 2015. Letters in plots indicate statistically significant differences, with shared letters or lack of letters indicating no difference (p>0.05).

Discussion

Three years of cattle exclusion led to no differences in bare ground and litter basal cover, plant community composition, alpha diversity, or species richness when compared to areas that were grazed at full use. We also found no examples of individual species that were more strongly associated with cattle grazed or un-grazed areas after the same time period. These findings were the same whether *on* or *off* black-tailed prairie dog towns, and at any of the three ecological sites examined. Prairie dog presence and ecological site influenced plant community composition as well as basal cover, but alpha diversity and species richness were not different *on* vs. *off-town.*

The finding of no differences in bare ground or litter percentage between cattle excluded and non-excluded plots was somewhat surprising, especially in *off-town* areas where prairie dogs grazing was not a factor. Intuitively, removing cattle grazing pressure should allow plants to retain more aboveground biomass, leading to higher litter cover; however, previous work in the region has found basal cover to be relatively static and unaffected by cattle grazing removal (Biondini and Manske 1996). This seems to indicate that removing or reducing cattle grazing from this system is not an effective means of reducing bare ground percentage, at least when compared to full use utilization. Bare ground percentage is likely to be more strongly influenced by precipitation and soil properties than grazing pressure (Biondini and Manske 1996).

Removing cattle grazing pressure for three years also did not cause plant community changes when compared to full use grazing over the same period. This finding was similar to Fahnestock and Detling (2002) who also reported that 3 years of bison (*Bison bison*) exclusion did not change plant community species composition on or off prairie dog towns. While cattle and bison do not have identical grazing habits (Plumb and Dodd 1993), cattle spend more time grazing and being less selective, they have many similarities and both attracted to prairie dog towns under certain conditions (Chipault and Detling 2013). Comparisons of plant communities under moderate, heavy, and no grazing by cattle showed that shifts over an eight year period were more strongly controlled by precipitation than cattle grazing (Biondini and Manske 1998). Species composition changes due to cattle grazing removal over a period of six years have been reported in the region, but were highly dependent on range site and may have been influenced by drought (Biondini and Manske 1996).

A lack of difference between the plant communities of cattle grazed and un-grazed areas does not rule out changes in individual species abundance or fidelity; however, our indicator species analysis (Dufrene and Legendre 1997) demonstrated that cattle grazing removal did not cause changes to these measures. Although rangeland plant species have long been classified as "increasers" or "decreasers" based on their response to cattle grazing (Dyksterhuis 1958), these responses are more visible over long time scales and under heavy grazing (Holechek 1999).

The results of our indicator species analysis did demonstrate that ecological site was a strong predictor of individual species occurrence, as was prairie dog occurrence. Plant community differences among ecological sites are expected due to different soil chemical and physical properties at these sites (USDA-NRCS 2006). The steep slopes of the thin loamy ecological site and the dense argillic horizon of the claypan site inhibit the growth of many species. The loamy site is more favorable for most species, resulting in higher production and growth of less-drought tolerant species. Because of these differences, several species showed strong fidelity to the thin loamy and claypan ecological sites, but none to the loamy ecological site.

Prairie dog presence or absence was a strong predictor of plant community composition. Indicator species analysis identified 15 species significantly associated with prairie dog presence, and 19 species associated with their absence. The majority of these species represent plant types commonly reported (*Conyza ramosissima, Schedonnardus paniculatus, Dyssodia papposa, Plantago elongata*) or rarely reported (*Nassella viridula, Pediomelum argophyllum, Artemisia dracunculoides, Hesperostipa comata*) on prairie dog towns (King 1955, Uresk 1984, Fahnestock et al. 2003, Johnson-Nistler et al. 2004). These plant communities, along with prairie dog burrowing activities, create a unique combination that is not replicated by cattle grazing alone (see Miler et al. 2007 for a review), although very heavy cattle grazing can produce some similarities (Kotliar et al. 1999, Vermeire 2004).

One species of particular interest that was identified by our indicator species analysis as showing high fidelity and abundance *off-town* was Kentucky bluegrass (*Poa pratensis*). Kentucky bluegrass is a common invasive species in northern mixed grass prairie that has been increasing in abundance (Murphy and Grant 2005) and increases under a lack of herbivory (Grant et al. 2009). We found almost no Kentucky bluegrass *on-town* in our study, but it was among the most common species *off-town.* It is possible that the intense grazing and clipping activities of these mammals prevents Kentucky bluegrass establishment or reproduction. Prairie dog towns often have elevated soil temperatures and lower soil moisture compared to nearby *off-town* areas (Archer and Detling 1986), which may place Kentucky bluegrass at a competitive disadvantage with native species. While our results do not show that black-tailed prairie dogs reduce or eliminate Kentucky bluegrass, the role of prairie dog colonies as a barrier to Kentucky bluegrass expansion should be investigated further.

Conclusions

Our findings show short term cattle exclusion does not lead to plant community species composition changes, or changes in bare ground basal cover in this ecosystem, regardless of ecological site or prairie dog activity. This supports the findings of Biondini et al. (1998) which showed moderate grazing is sustainable in this ecosystem and those of Fahnestock and Detling (2002) that short term exclusion of large ungulates does not change plant communities. Longer term grazing exclusion can change plant communities in this ecosystem (Brand and Goetz 1986), and more research is needed to determine the long term effects of grazing exclusion under different prairie dog activity and on different ecological sites. Land managers seeking to shift plant communities or reduce bare ground in the northern Great Plains are limited largely by precipitation. Shifts caused by cattle exclusion should not be expected in the short-term. Additionally, plant communities on black tailed prairie dog towns add to ranch-scale plant diversity. Prairie dogs are a valuable wildlife species for land managers seeking to increase plant diversity and plant community heterogeneity.

Acknowledgments

The authors would like to acknowledge the McLaughlin family for their continued support and cooperation at the study site. We would also like to acknowledge the work of our dedicated technicians, without whom this study would not have been possible. We would especially like to thank Dennis Whitted for his assistance in plant identification. Finally, this study would not have been possible without funding through the United States Department of Agriculture's National Institute of Food and Agriculture.

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CHAPTER 3. AN EXPLORATION OF THE EFFECTS OF CATTLE GRAZING, PRAIRIE DOG ACTIVITY, AND LANDSCAPE POSITION ON WESTERN WHEATGRASS VEGETATIVE REPRODUCTION IN NORTHERN MIXED GRASS PRAIRIE

Abstract

Vegetative reproduction of grasses is important for the persistence of many prairie grasses, but is not well understood for many species in northern mixed grass prairie. This is particularly true for fine-scale assessments of the impacts of disturbance in different soil and topographic conditions. Our objective was to quantify the effects of grazing disturbance by cattle and black-tailed prairie dogs (*Cynomys ludovicianus*) on western wheatgrass vegetative reproduction at three different ecological sites in northern mixed grass prairie. Our findings indicate that defoliation by cattle or prairie dogs had little impact on the number of buds, rhizomes, or juvenile tillers produced by individual western wheatgrass ramets. Defoliation impacts on western wheatgrass reproduction may be controlled by tiller mortality rather than bud bank changes. Additionally, aboveground tiller counts may be a suitable alternative to bud bank quantification for western wheatgrass.

Introduction

Western wheatgrass (*Pascopyrum smithii*) is an important cool-season (C_3), rhizomatous grass in the Northern Plains for both its forage and cover value. Western wheatgrass is long-lived, tolerates variety of soil conditions, moisture levels, and disturbance regimes (USDA-NRCS 2017a). Reproduction occurs both by seed (sexually) and vegetatively (asexually), but sexual reproduction is much less common (Karl et al. 1999). Vegetative reproduction in *Pascopyrum smithii* originates from axillary buds at the base of the plant. Axillary buds are defined as “rudimentary apical meristems differentiated from the apical meristems of parental tillers that can potentially grow out to produce juvenile tillers” (Hendrickson and Briske 1997, from Sharman 1945, Langer 1963). Each bud can behave in one of four ways: death, differentiation, active maintenance, and dormancy.

Buds that die have either been damaged by an external factor or have simply not been maintained by the parent tiller. Western wheatgrass buds have the potential to live at least two years (Ott and Hartnett 2015). Differentiation is the process by which an apical bud forms into a living juvenile tiller or rhizome, and this process is typically inhibited by auxin and promoted by cytokynin (Phillips 1975, Cline 1994, Tamas 1995, Napoli et al. 1999), but the exact mechanism is not known (Tomlinson and O’Connor 2004). Tillers and rhizomes are actively growing to form a new clonal outgrowth of the parent tiller. Active maintenance of buds allows a plant to maintain a reserve of potential juvenile tillers in some grass species, but in others active buds differentiate quickly or die (Ott and Hartnett 2012). These buds maintain both membrane integrity and the ability to actively transport materials into their cells. Dormancy is a mechanism by which a plant maintains its buds’ membrane integrity, but little respiratory activity. These buds presumably require less input from the parent plant (Hendrickson and Briske 1997), but are also rarely able to be activated in order to produce juvenile tillers (Heidemann and Van Riper 1967, Haslam 1969).

Taken together, active and dormant buds, rhizomes, and juvenile tillers can be considered “potential tiller recruits” (Ott and Hartnett 2015) which, when maintained over time, can also be called a “bud bank” (*sensu* Harper 1977). If there are not enough buds to replace aboveground tillers, primary production can be meristem limited (Dalgleish and Hartnett 2006). Recently formed axillary buds (distal) are much more likely to differentiate than older buds (proximal) or dormant buds (Hendrickson and Briske 1997), but dormant buds can be activated under some conditions (Heidemann and Van Riper 1967, Haslam 1969). Ott and Hartnett (2012) found no evidence of a bud bank accumulating over time in *Dicanthelium oliganthe*, a C_3 grass, but found contributions to outgrowth from buds over two years old from *Andropogon gerardii*, a C_4 grass. These findings indicate that bud-bank dynamics are species specific. This bank of active and dormant buds allows a grass such as *Pascopyrum smithii* to respond appropriately to environmental conditions and disturbance in order to maximize its reproductive output.

Maximizing reproductive output is important not only to individual *Pascopyrum smithii* tillers, but also to livestock producers and wildlife which use this species for both forage and shelter (Dittberner et al. 1983, Newell and Moline 1978). If we can understand the effects of disturbance on the vegetative (asexual) reproduction of this species, it may be possible to alter our management to increase the resilience and production of *Pascopyrum smithii* at a landscape level. This would help to maximize our ability to produce food and fiber on limited acreages while maintaining ecological integrity.

The objectives of our study were to determine the effects of cattle-grazing and cattle exclusion, prairie dog activities, and ecological site on the vegetative reproduction of western wheatgrass. We intended to use this information to help guide management for western wheatgrass persistence in northern mixed grass prairie. A second objective was to determine whether bud bank surveys were a necessary component of western wheatgrass population viability estimates.

Materials and Methods

Study Area and Sites

The study was conducted on the Standing Rock Indian Reservation approximately 30 km southeast of McLaughlin in north central South Dakota. Thirty-six permanent 40 x 40 m plots were systematically located on the site during summer of 2012 to represent the three most common ecological sites on the study area. Sites that most closely represented the historic climax plant community for each ecological site (see descriptions within USDA–NRCS 2017b). Twelve plots each were located on loamy, thin loamy, and claypan ecological sites (USDA–NRCS 2017b). These plots were arranged in pairs, with one member of each pair protected from cattle grazing by a four-strand barbed wire exclosure and the other being unprotected. Of the 12 plots on each ecological site, eight were located within black-tailed prairie dog (*Cynomys ludovicianus*) colonies (*on-town*) and six were located on sites outside of colony boundaries (*off-town*).

Cattle grazing with yearling Angus and angus-cross heifers occurred from 1 June until approximately 40 to 60 % disappearance of herbage occurred at a site-wide level (approximately 15 October). Before our study was initiated, the study site was grazed season-long by cattle and horses at unknown stocking rates. Average growing season precipitation (May through September) is 29.9 cm. Growing season precipitation on the site was slightly below average in 2012, but was above average in 2013, 2014, and 2015 (Figure 3.1).

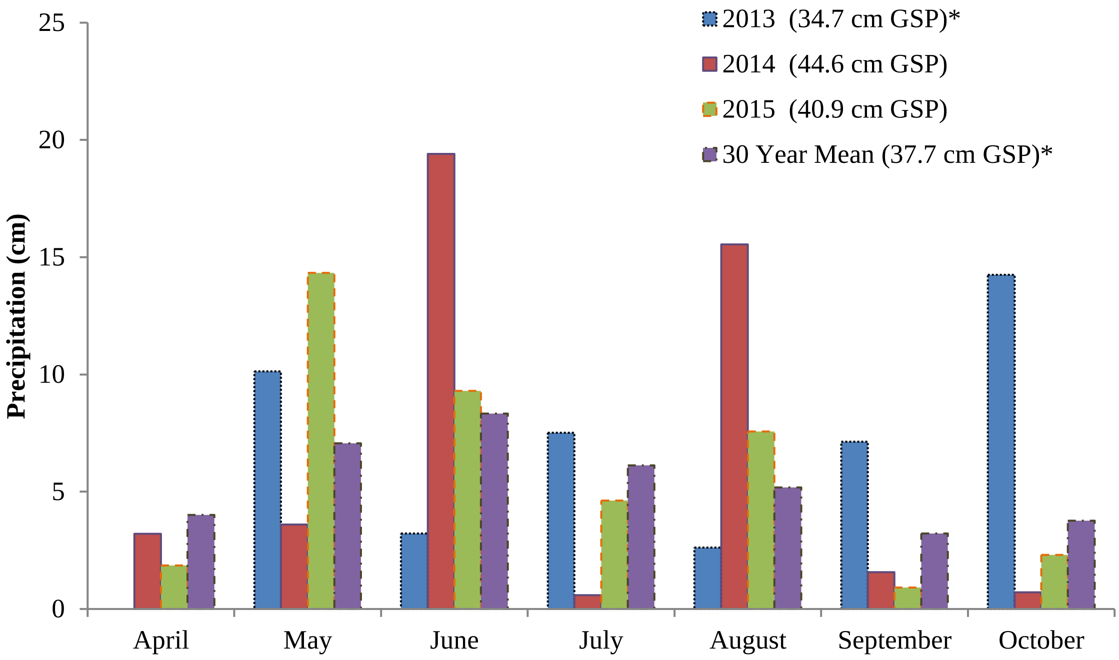

Figure 3.1: Extended growing season precipitation (GSP) by month from Mahto Weather Station at research site. Asterisks reflect missing or partial data in April and May of 2013. Thirty year average from McLaughlin Weather Station approximately 11 km northwest of study site.

Field Sampling and Laboratory Methods

Three *Pascopyrum smithii* tillers in the elongation growth stage were destructively sampled from each plot in each collection period. During the elongation growth stage, culms begin to elongate and nodes become palpable (Moore et al. 1991) and culms were collected at this time to avoid confounding effects of growth stage. Destructive sampling involved identifying and marking a western wheatgrass tiller in the elongation phase and then digging up the individual tiller and separating its root mass from neighboring plants. The collection periods occurred at three seasons: spring (May-June), summer (July-August), and fall (October-November). This sample collection procedure was repeated in 2013, 2014, and 2015. Tillers were partially cleaned in the field and maintained in sealable plastic zip-top bags containing paper towels and moistened with distilled water until processing. Tillers were cleaned, processed, and examined in the lab within one week of collection and maintained under refrigeration until processed. Initial examination classified all potential outgrowth positions from root crown to the soil surface as tillers, rhizomes, buds, or leaf scars. Only those positions within the basal 20mm of the parent tiller were evaluated (Hendrickson and Briske 1997). Axillary buds that were contained within the prophyll were classified as buds, while those that had elongated past the prophyll were classified as tillers (Ott and Hartnett 2015). Bud viability (*active*, *dormant*, or *dead*) was assessed using a double staining procedure (Busso et al. 1989). Buds were stained with a 2,3,5-triphenyl tetrazolium chloride (TTC) solution (Hendrickson and Briske 1997). Live, active buds transport TTC through their outer membranes and stain varying shades of pink. Buds that did not stain with TTC were placed in a 0.25% w/v solution of Evan's blue dye for 20 minutes. Buds with compromised membranes stain dark blue and were classified as dead (Gaff and Okong'o-ogola 1971). Buds that did not stain with either TTC or Evan's Blue were classified as dormant (e.g. Busso et al. 1989).

Statistical Analysis

Due to low numbers and non-normal distribution, comparisons for active buds, juvenile tillers, rhizomes, and dormant buds were not appropriate individually. Therefore, we made comparisons of potential tiller recruits among treatments. We defined potential tiller recruits as live juvenile tillers, live rhizomes, active buds, and dormant buds. All of these classifications have the potential to produce new juvenile tillers, although recently formed axillary buds (proximal) are more likely to differentiate than older buds (distal) or dormant buds (Hendrickson and Briske 1997).

The plot average of positions was calculated using the three tillers assessed and used as the response for statistical analysis, thus using Poisson distribution for count data was not necessary. Treatments were compared using generalized linear mixed modelling (GLIMMIX procedure of SAS) and ANOVA, with plots used as sample units. Collection year was treated as a random effect as well as cattle grazing by exclusion since the exclosure was nested within the grazing area. Season of collection (spring, summer, fall), defoliation treatment (no grazing, cattle only, prairie dog only, or cattle and prairie dogs together), and ecological site (claypan, loamy, and thin loamy) were treated as fixed effects. Due to strong seasonal differences, comparisons among ecological sites and defoliation treatment were analyzed within season. Due to strength of seasonal effect, combined with unequal seasonal sampling among years, year effect was not determined. Although statistical comparisons active bud, juvenile tiller, rhizome, and dormant bud numbers were not made among treatments, summary statistics for these categories were calculated for using function describeBy (*psych* package, program R, version 3.2.0).

Results

Counts ranged from zero to 14 potential tiller recruits per tiller (median=3, mean=2.9, standard error= 0.05). Counts per plot ranged from three to 19 potential tiller recruits (median=9, mean=8.9, standard error= 0.19) Overall, each sample tiller averaged 2.9 potential tiller recruits (Table 3.1). Potential tiller recruits were comprised primarily of active buds (mean=1.47 tiller^{-1}, Table 3.2) and juvenile tillers (mean=1.02 tiller^{-1}, Table 3.3). Rhizomes were less common (mean=0.38 tiller^{-1}, Table 3.4). There were very few dormant buds in any collection period (mean=0.07 tiller^{-1}, Table 3.5). Neither ecological site nor defoliation treatment influenced potential tiller recruits per tiller (p=0.89, p=0.65, Table 3.1) and there were no interactions among treatments. Season of collection influenced the number of potential tiller recruits per tiller^{1} ($p<0.001$). There was an average of 1.3 more potential tiller recruits per tiller in the fall than summer, with spring averages intermediate (Table 3.1).

Table 3.1: Summary statistics for potential tiller recruits per parent tiller of *Pascopyrum smithii* classified by defoliation treatment, ecological site, and collection season in the northern mixed grass prairie of South Dakota.

		Mean	**SD**	**SE**	**Median**	**Min**	**Max**	**Range**
Defoliation Treatment	No Grazing	2.89	1.37	0.56	3	1	8	7
	Cattle Only	2.80	1.43	0.58	3	0	7	7
	PD Only	3.01	1.51	0.44	3	0	8	8
	Both	3.00	1.61	0.46	3	0	14	14
Ecological Site	Claypan	2.96	1.48	0.43	3	0	8	8
	Loamy	2.95	1.43	0.41	3	1	8	7
	Thin Loamy	2.93	1.61	0.46	3	0	14	14
Collection Season	Spring	2.76	1.20	0.20	3	0	7	7
	Summer	2.53	1.37	0.23	2	1	8	7
	Fall	3.42	1.66	0.28	3	0	14	14

Table 3.2: Summary statistics for active buds per parent tiller of *Pascopyrum smithii* classified by defoliation treatment, ecological site, and collection season in the northern mixed grass prairie of South Dakota.

		Mean	**SD**	**SE**	**Median**	**Min**	**Max**	**Range**
Defoliation Treatment	No Grazing	1.41	1.19	0.49	1	0	6	6
	Cattle Only	1.47	1.27	0.52	1	0	6	6
	PD Only	1.45	1.30	0.38	1	0	6	6
	Both	1.52	1.36	0.39	1	0	8	8
Ecological Site	Claypan	1.52	1.38	0.40	1	0	8	8
	Loamy	1.49	1.28	0.37	1	0	6	6
	Thin Loamy	1.40	1.22	0.35	1	0	6	6
Collection Season	Spring	1.44	1.05	0.18	1	0	5	5
	Summer	1.38	1.34	0.22	1	0	8	8
	Fall	1.56	1.40	0.23	1	0	6	6

Table 3.3: Summary statistics for juvenile tillers per parent tiller of *Pascopyrum smithii* classified by defoliation treatment, ecological site, and collection season in the northern mixed grass prairie of South Dakota.

		Mean	**SD**	**SE**	**Median**	**Min**	**Max**	**Range**
Defoliation Treatment	No Grazing	0.94	0.67	0.27	1	0	3	3
	Cattle Only	0.93	0.81	0.33	1	0	5	5
	PD Only	1.08	0.77	0.22	1	0	3	3
	Both	1.06	0.77	0.22	1	0	3	3
Ecological Site	Claypan	1.02	0.76	0.22	1	0	4	4
	Loamy	1.00	0.76	0.22	1	0	3	3
	Thin Loamy	1.05	0.77	0.22	1	0	5	5
Collection Season	Spring	0.98	0.73	0.12	1	0	3	3
	Summer	0.91	0.70	0.12	1	0	3	3
	Fall	1.14	0.82	0.14	1	0	5	5

Table 3.4: Summary statistics for rhizomes per parent tiller of *Pascopyrum smithii* classified by defoliation treatment, ecological site, and collection season in the northern mixed grass prairie of South Dakota.

		Mean	**SD**	**SE**	**Median**	**Min**	**Max**	**Range**
Defoliation Treatment	No Grazing	0.47	0.72	0.29	0	0	3	3
	Cattle Only	0.33	0.62	0.25	0	0	4	4
	PD Only	0.43	0.66	0.19	0	0	3	3
	Both	0.31	0.62	0.18	0	0	4	4
Ecological Site	Claypan	0.36	0.61	0.18	0	0	3	3
	Loamy	0.42	0.70	0.20	0	0	4	4
	Thin Loamy	0.36	0.65	0.19	0	0	4	4
Collection Season	Spring	0.31	0.54	0.09	0	0	3	3
	Summer	0.20	0.51	0.09	0	0	4	4
	Fall	0.57	0.77	0.13	0	0	4	4

Table 3.5: Summary statistics for dormant buds per parent tiller of *Pascopyrum smithii* classified by defoliation treatment, ecological site, and collection season in the northern mixed grass prairie of South Dakota.

		Mean	**SD**	**SE**	**Median**	**Min**	**Max**	**Range**
Defoliation Treatment	No Grazing	0.07	0.29	0.12	0	0	2	2
	Cattle Only	0.07	0.30	0.12	0	0	2	2
	PD Only	0.05	0.24	0.07	0	0	2	2
	Both	0.11	0.61	0.18	0	0	8	8
Ecological Site	Claypan	0.06	0.28	0.08	0	0	3	3
	Loamy	0.05	0.23	0.07	0	0	2	2
	Thin Loamy	0.12	0.61	0.18	0	0	8	8
Collection Season	Spring	0.04	0.25	0.04	0	0	3	3
	Summer	0.03	0.19	0.03	0	0	2	2
	Fall	0.14	0.59	0.10	0	0	8	8

When analysis was constrained to the spring collection period, neither ecological site (p=0.72) nor defoliation treatment (p=0.99) influenced potential tiller recruits per tiller (Table 3.6). The same pattern held true when analysis was constrained to the summer collection periods, with neither ecological site (p=0.70) nor defoliation treatment (p=0.62) influencing potential tiller recruit numbers (Table 3.7). Within the fall collection period, neither ecological site (p=0.66) nor defoliation treatment (p=0.70) influenced potential tiller recruit numbers (Table 3.8).

Table 3.6: Summary statistics for types of potential tiller recruits per parent tiller of *Pascopyrum smithii* within the spring collection period classified by defoliation treatment and ecological site in the northern mixed grass prairie of South Dakota.

			Mean	**SD**	**SE**	**Med**	**Min**	**Max**
Potential Tiller Recruits	Defoliation Treatment	No Grazing	2.81	1.01	0.41	3	1	5
		Cattle Only	2.69	1.14	0.47	3	1	6
		PD Only	2.75	1.41	0.41	3	1	7
		Both	2.78	1.12	0.32	3	0	6
	Ecological Site	Claypan	2.79	1.14	0.33	3	1	6
		Loamy	2.82	1.29	0.37	3	1	7
		Thin Loamy	2.67	1.19	0.34	3	0	5
Active Buds	Defoliation Treatment	No Grazing	1.58	0.94	0.38	2	0	4
		Cattle Only	1.56	1.11	0.45	1	0	4
		PD Only	1.33	1.19	0.34	1	0	5
		Both	1.40	0.91	0.26	1	0	4
	Ecological Site	Claypan	1.61	1.22	0.35	2	0	5
		Loamy	1.33	0.95	0.27	1	0	4
		Thin Loamy	1.36	0.94	0.27	1	0	4
Juv. Tillers	Defoliation Treatment	No Grazing	0.86	0.59	0.24	1	0	2
		Cattle Only	0.83	0.65	0.27	1	0	2
		PD Only	1.04	0.78	0.23	1	0	3
		Both	1.06	0.79	0.23	1	0	3
	Ecological Site	Claypan	0.22	0.45	0.13	0	0	2
		Loamy	0.39	0.62	0.18	0	0	3
		Thin Loamy	0.31	0.52	0.15	0	0	2
Rhizomes	Defoliation Treatment	No Grazing	0.31	0.62	0.25	0	0	2
		Cattle Only	0.28	0.45	0.18	0	0	1
		PD Only	0.36	0.59	0.17	0	0	3
		Both	0.26	0.47	0.14	0	0	2
	Ecological Site	Claypan	0.22	0.45	0.13	0	0	2
		Loamy	0.39	0.62	0.18	0	0	3
		Thin Loamy	0.31	0.52	0.15	0	0	2
Dormant Buds	Defoliation Treatment	No Grazing	0.06	0.23	0.09	0	0	1
		Cattle Only	0.03	0.17	0.07	0	0	1
		PD Only	0.01	0.12	0.03	0	0	1
		Both	0.06	0.37	0.11	0	0	3
	Ecological Site	Claypan	0.00	0.00	0.00	0	0	0
		Loamy	0.06	0.23	0.07	0	0	1
		Thin Loamy	0.06	0.37	0.11	0	0	3

Table 3.7: Summary statistics for types of potential tiller recruits per parent tiller of *Pascopyrum smithii* within the summer collection period classified by defoliation treatment and ecological site in the northern mixed grass prairie of South Dakota.

			Mean	SD	SE	Med	Min	Max
Potential Tiller Recruits	Defoliation Treatment	No Grazing	2.50	1.28	0.52	2	1	6
		Cattle Only	2.60	1.53	0.62	2	1	7
		PD Only	2.63	1.37	0.40	2	1	7
		Both	2.40	1.35	0.39	2	1	8
	Ecological Site	Claypan	2.61	1.54	0.44	2	1	8
		Loamy	2.55	1.40	0.40	2	1	7
		Thin Loamy	2.43	1.19	0.34	2	1	5
Active Buds	Defoliation Treatment	No Grazing	1.26	1.27	0.52	1	0	5
		Cattle Only	1.44	1.41	0.58	1	0	6
		PD Only	1.43	1.27	0.37	1	0	6
		Both	1.38	1.41	0.41	1	0	8
	Ecological Site	Claypan	1.49	1.60	0.46	1	0	8
		Loamy	1.37	1.33	0.38	1	0	6
		Thin Loamy	1.30	1.08	0.31	1	0	5
Juv. Tillers	Defoliation Treatment	No Grazing	0.96	0.76	0.31	1	0	3
		Cattle Only	0.81	0.64	0.26	1	0	3
		PD Only	0.96	0.73	0.21	1	0	3
		Both	0.88	0.66	0.19	1	0	2
	Ecological Site	Claypan	0.89	0.72	0.21	1	0	3
		Loamy	0.95	0.75	0.22	1	0	3
		Thin Loamy	0.88	0.63	0.18	1	0	2
Rhizomes	Defoliation Treatment	No Grazing	0.24	0.52	0.21	0	0	2
		Cattle Only	0.33	0.75	0.31	0	0	4
		PD Only	0.21	0.44	0.13	0	0	2
		Both	0.11	0.35	0.10	0	0	2
	Ecological Site	Claypan	0.18	0.42	0.12	0	0	2
		Loamy	0.22	0.60	0.17	0	0	4
		Thin Loamy	0.21	0.48	0.14	0	0	2
Dormant Buds	Defoliation Treatment	No Grazing	0.04	0.21	0.09	0	0	1
		Cattle Only	0.02	0.14	0.06	0	0	1
		PD Only	0.02	0.16	0.05	0	0	1
		Both	0.04	0.24	0.07	0	0	2
	Ecological Site	Claypan	0.05	0.22	0.06	0	0	1
		Loamy	0.00	0.00	0.00	0	0	0
		Thin Loamy	0.04	0.25	0.07	0	0	2

Table 3.8: Summary statistics for types of potential tiller recruits per parent tiller of *Pascopyrum smithii* within the fall collection period classified by defoliation treatment and ecological site in the northern mixed grass prairie of South Dakota.

			Mean	SD	SE	Med	Min	Max
Potential Tiller Recruits	Defoliation Treatment	No Grazing	3.28	1.57	0.64	3	1	8
		Cattle Only	3.06	1.51	0.62	3	0	7
		PD Only	3.47	1.56	0.45	3	0	8
		Both	3.61	1.85	0.53	3	1	14
	Ecological Site	Claypan	3.34	1.55	0.45	3	0	8
		Loamy	3.37	1.44	0.42	3	1	8
		Thin Loamy	3.53	1.96	0.57	3	0	14
Active Buds	Defoliation Treatment	No Grazing	1.42	1.26	0.51	1	0	6
		Cattle Only	1.44	1.25	0.51	1	0	5
		PD Only	1.54	1.40	0.40	1	0	6
		Both	1.71	1.54	0.44	1	0	6
	Ecological Site	Claypan	1.49	1.32	0.38	1	0	6
		Loamy	1.68	1.40	0.40	1	0	6
		Thin Loamy	1.51	1.48	0.43	1	0	6
Juv. Tillers	Defoliation Treatment	No Grazing	0.98	0.64	0.26	1	0	2
		Cattle Only	1.11	1.00	0.41	1	0	5
		PD Only	1.19	0.78	0.23	1	0	3
		Both	1.19	0.83	0.24	1	0	3
	Ecological Site	Claypan	1.16	0.80	0.23	1	0	4
		Loamy	1.01	0.81	0.23	1	0	3
		Thin Loamy	1.26	0.83	0.24	1	0	5
Rhizomes	Defoliation Treatment	No Grazing	0.77	0.82	0.33	1	0	3
		Cattle Only	0.37	0.59	0.24	0	0	2
		PD Only	0.64	0.77	0.22	0	0	3
		Both	0.50	0.80	0.23	0	0	4
	Ecological Site	Claypan	0.58	0.75	0.22	0	0	3
		Loamy	0.60	0.78	0.23	0	0	3
		Thin Loamy	0.53	0.79	0.23	0	0	4
Dormant Buds	Defoliation Treatment	No Grazing	0.11	0.38	0.16	0	0	2
		Cattle Only	0.13	0.44	0.18	0	0	2
		PD Only	0.09	0.32	0.09	0	0	2
		Both	0.20	0.87	0.25	0	0	8
	Ecological Site	Claypan	0.11	0.39	0.11	0	0	3
		Loamy	0.08	0.31	0.09	0	0	2
		Thin Loamy	0.22	0.88	0.25	0	0	8

Discussion

Our results show individual tillers each producing two to three potential tiller recruits. This was similar to findings of Ott and Hartnett (2015), as well as those found by Russell et al. (2015) in their unburned treatment. Plant primary production can be meristem limited under certain disturbance regimes (Dalgleish and Hartnett 2006), and with only two or three potential tiller recruits per tiller *Pascopyrum smithii* could face this issue. To avoid population reductions, tiller recruitment must exceed or equal tiller death. This means that at the population level, each parent tiller must average at least one juvenile tiller during its lifetime. If this is not achieved, population size will decrease. In our study, no combination of grazing, prairie dog activity, and ecological site led to average potential tiller recruits per tiller below 2.0. *Pascopyrum smithii* buds can live at least two years (Ott and Hartnett 2015). It would be possible to use potential tiller recruit counts and survival rates paired with parent tiller longevity estimates to determine *Pascopyrum smithii* population persistence, but aboveground tiller density estimates over time would be a more practical option.

Neither cattle grazing, prairie dog activity, nor the combination of the two affected the production and/or maintenance of potential tiller recruits. The intense defoliation pressure of prairie dog activity did not depress or stimulate vegetative reproduction on a per-tiller basis. This despite the fact that *Pascopyrum smithii* is only moderately grazing tolerant due to its early elevated growth points (Branson 1953). Grazing morphs of perennial plants do occur on prairie dog towns. These morphs are typically shorter and more prostrate than their less-frequently defoliated counterparts (Kemp 1937, Hickey 1961). These growth characteristics could have mediated the effects of heavy grazing on individual tillers in our study. It is also possible that although grazing intensity was high on-town, it did not reach the level of intensity required to impede bud production on *Pascopyrum smithii*. This result could also be due to the favorable growing season precipitation levels during our study period allowing plants to avoid drought stress. In a greenhouse experiment, Russell et al. (2013) found that moderate clipping did not affect tiller number or axillary bud counts in western wheatgrass. However, fire can increase active bud counts, and summer and fall fires increase tillering in this species (Russell et al. 2015). Our findings and studies reported by others indicate that *Pascopyrum smithii* may more rely on regenerative axillary bud development to recover after fire than after herbivory. This strategy may be based on more frequent grazing disturbance than fire disturbance.

Ecological site did not influence tiller or bud production. Because growing season precipitation was above average during our study period, it is likely that plants were not heavily water stressed in any location. While each ecological site in our study is capable of producing a different type and amount of vegetation, *Pascopyrum smithii* is commonly found in each of these ecological sites and may be able to reproduce with the same degree of success in each.

The main driver of bud and tiller production in our study was season. We expected harvesting study tillers at the same growth stage (elongation) would allow us to use multiple collection periods within a year as a form of replication. However, statistical analysis showed that this was not the case. Ott and Hartnett (2012) found a similar pattern of lower overall bud bank in summer for a C_3 grass (*Dichanthelium oligosanthes*). They concluded that buds produced in the previous year were dying off and new buds were just beginning to be produced at this time. This pattern may hold true for *Pascopyrum smithii,* but very few dead buds were found in our study, regardless of season. It is possible that the short lifespan common to C_3 grasses and their buds (Ott and Hartnett 2012) leads to rapid decomposition of dead buds. Ott and Hartnett (2015) demonstrated that *Pascopyrum smithii* is highly plastic in its tiller recruitment timing, with recruitment occurring either in the spring or fall. Our data also indicated fewer potential tiller recruits in mid-summer than in spring or fall.

Pascopyrum smithii bud bank varies according to season, but does not appear to vary based on ecological site or defoliation type or intensity, at least on a per-tiller basis. However, we cannot say conclusively that *Pascopyrum smithii* vegetative reproduction was not affected at a population level. If defoliation intensity or ecological site influences parent tiller density, it is possible that overall reproduction is dependent on these factors. Further study is needed to determine whether vegetative reproduction of *Pascopyrum smithii* can be maximized through grazing manipulation. Based on our results, *Pascopyrum smithii* axillary bud dynamics are very tolerant of herbivory and above ground tiller density is likely to be a more practical indicator of *Pascopyrum smithii* reproduction than bud bank dynamics.

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CHAPTER 4. GENERAL CONCLUSIONS AND FUTURE DIRECTIONS

Sustainable or regenerative food production in northern mixed grass prairie will continue to gain importance in the coming years Plant community composition is a critical component of rangeland function, and strongly influences the goods and services that rangelands are able to provide. As our understanding of and appreciation for the roles of heterogeneity and biodiversity continue to grow, I believe that we will begin to appreciate the role of prairie dogs more fully. Despite the challenge of lost forage, the value of these mammals will only grow. Ecological education that promotes an understanding of the value of biodiversity needs to be promoted. By the same token, the daily struggles of livestock producers dealing with mammalian competitors for forage should not be ignored. Programs that employ the “carrot” rather than the “stick” may be more successful in the conservation of prairie dogs, because these programs are more likely to gain support from ranching and livestock groups, and therefore the legislatures of states with strong agricultural economies.

Cattle grazing at a full use stocking rates did not change the plant community in this study. This is not a surprising finding based on previous work, but looking within ecological site and incorporating prairie dog activity into the discussion adds detail to our understanding of the process. Longer term full use grazing could still lead to plant community change on some ecological sites, especially if there are impediments to livestock distribution. On prairie dog towns, changes in plant community are much more likely to be driven by prairie dogs except under very low prairie dog densities or very high cattle stocking rates.

Underground bud bank dynamics are a major driver of plant species persistence and plant community change, particularly in grassland settings where the vast majority of reproduction occurs vegetatively. However, it appears that for western wheatgrass, grazing is not the primary driver of these dynamics, at least at the tiller level. This was true at all three ecological sites that we investigated. Other factors including precipitation, temperature, and soil characteristics may play a more important role. Future research on this species should be directed at grazing and/or ecological site impacts on above-ground tiller densities.

APPENDIX. PLANT SPECIES ENCOUNTERED ON THE MCLAUGHLIN STUDY SITE DURING THE STUDY PERIOD (2012-2015)

Species	**Common**	**Plant Type**	***Off-Town***	***On-Town***
Achillea millefolium	Western yarrow	Forb	X	X
Agropyron cristatum	Crested wheatgrass	Grass	X	X
Agrostis scabra	Rough bentgrass	Grass		X
Amaranthus albus	Prostrate pigweed	Forb		X
Amaranthus retroflexus	Redroot amaranth	Forb	X	X
Ambrosia psilostachya	Western ragweed	Forb	X	X
Amorpha canescens	Leadplant	Shrub	X	X
Amorpha nana	Dwarf false indigo	Shrup	X	X
Andropogon gerardii	Big bluestem	Grass		
Androsace occidentalis	Western rockjasmine	Forb	X	X
Anemone canadensis	Canadian anemone	Forb	X	X
Antennaria neglecta	Field pussytoes	Forb	X	X
Antennaria parvifolia	Small-leaf pussytoes	Forb		X
Arabis hirsuta	Hairy rockcress	Forb	X	
Aristida purpurea	Purple threeawn	Grass	X	X
Artemisia absinthium	Absithium	Subshrub	X	X
Artemisa cana	Silver sagebrush	Shrub	X	X
Artemisia dracunculoides	Green sagewort	Subshrub	X	X
Artemisia frigida	Fringed sagewort	Subshrub	X	X
Artemisia ludoviciana	White sagewort	Forb	X	X
Asclepias pumila	Plains milkweed	Forb		X
Asclepias verticillata	Whorled milkweed	Forb	X	X
Astragalus agrestis	Purple milkvetch	Forb		X
Astragalus crassicarpus	Groundplum milkvetch	Forb		X
Astragalus laxmannii	Standing milkvetch	Forb	X	
Atriplex argentea	Silverscale saltbush	Forb		X
Bassia scoparia	Kochia	Forb	X	X
Bouteloua curtipendula	Sideoats grama	Grass	X	X
Bouteloua dactyloides	Buffalograss	Grass	X	X
Bouteloua gracilis	Blue grama	Grass	X	X
Brickellia eupatoroides	False boneset	Forb		X
Bromus arvensis	Field brome	Grass	X	X
Bromus inermis	Smooth brome	Grass	X	X
Bromus tectorum	Cheatgrass	Grass	X	

Species	**Common**	**Plant Type**	***Off-Town***	***On-Town***
Calamovilfa longifolia	Prairie sandreed	Grass	X	X
Calmagrostis montanensis	Plains reedgrass	Grass	X	X
Calylophus serrulatus	Yellow sundrops	Forb		X
Carex duriuscula	Needleleaf sedge	Sedge	X	X
Carex filifolia	Threadleaf sedge	Sedge	X	X
Carex inops	Sun sedge	Sedge	X	X
Chamaesyce glyptosperma	Ribseed sandmat	Forb		
Chamaesyce serpens	Matted sandmat	Forb		X
Chenopodium subglabrum	Smooth goosefoot	Forb	X	
Cirsium arvense	Canada thistle	Forb	X	X
Cirsium flodmanii	Flodman's thistle	Forb	X	X
Cirsium undulata	Wavyleaf thistle	Forb		X
Collomia linearis	Tiny trumpet	Forb		X
Convolvulus arvensis	Field bindweed	Forb	X	X
Conyza canadensis	Canadian horseweed	Forb	X	X
Conyza ramosissima	Dwarf horseweed	Forb		X
Dalea candida	White prairie clover	Forb		X
Dalea purpurea	Purple prairie clover	Forb	X	X
Descurainia sophia	Flixweed	Forb	X	X
Dichanthelium oligosanthes	Scribner's rosette grass	Grass	X	X
Dichanthelium wilcoxianum	Fall rosette grass	Grass	X	X
Distichlis spicata	Inland saltgrass	Grass		X
Dyssodia papposa	Fetid marigold	Forb		X
Echinacea angustifolia	Black samson	Forb	X	X
Echinochloa crus-gali	Barnyardgrass	Grass		X
Elymus repens	Quackgrass	Grass	X	
Erigeron canus	Hoary fleabane	Forb		X
Erigeron strigosus	Prairie fleabane	Forb	X	
Galium boreale	Northern bedstraw	Forb	X	X
Glycyrrhiza lepidota	American licorice	Forb	X	
Grindelia squarrosa	Curlycup gumweed	Forb	X	X
Hedeoma hispida	Rough false pennyroyal	Forb	X	X
Hesperostipa comata	Needle-and-thread	Grass	X	X
Hesperostipa spartina	Porcupinegrass	Grass		X
Heterotheca villosa	Hairy false goldenaster	Forb		X
Hordeum jubatum	Foxtail barley	Grass		X
Juncus arcticus	Mountain rush	Rush		X

Species	**Common**	**Plant Type**	***Off-Town***	***On-Town***
Koeleria macrantha	Prairie junegrass	Grass	X	X
Krascheninnikovia lanata	Winterfat	Shrub		X
Lactuca serriola	Prickly lettuce	Forb		X
Lactuca tatarica	Blue lettuce	Forb	X	X
Lepidium densiflorum	Common pepperweed	Forb	X	X
Liatris punctata	Dotted blazing star	Forb	X	X
Linum lewisii	Prairie flax	Forb		X
Linum rigidum	Stiffstem flax	Forb	X	X
Lithospermum incisum	Narrowleaf stoneseed	Forb	X	X
Lotus unifoliolatus	Bird's-foot trefoil	Forb		X
Lygodesmia juncea	Rush skeletonplant	Forb		X
Machaeranthera pinnatifida	Lacy tansyaster	Forb	X	X
Medicago lupulina	Black medick	Forb		X
Melilotus officinalis	Sweetclover	Forb	X	X
Mirablis nyctaginea	Heartleaf four o'clock	Forb		X
Muhlenbergia cuspidata	Plains muhly	Grass	X	X
Munroa squarrosa	False buffalograss	Grass		X
Nassella viridula	Green needlegrass	Grass	X	X
Oenothera suffrutescens	Scarlet beeblossom	Forb		
Opuntia fragilis	Brittle pricklypear	Shrub	X	
Opuntia polyacantha	Plains pricklypear	Shrub	X	
Oxalis stricta	Common yellow oxalis	Forb		X
Oxytropis lambertii	Purple locoweed	Forb		X
Pascopyrum smithii	Western wheatgrass	Grass	X	X
Pediomelum argophyllum	Silverleaf Indian breadroot	Forb	X	X
Pediomelum esculentum	Large Indian breadroot	Forb		X
Penstemon gracilis	Lilac penstemon	Forb	X	X
Phlox hoodii	Spiny phlox	Forb	X	X
Plantago elongata	Prairie plantain	Forb	X	X
Plantago patagonica	Woolly plantain	Forb		X
Poa compressa	Canada bluegrass	Grass	X	
Poa pratensis	Kentucky bluegrass	Grass	X	X
Polygonum achoreum	Leathery knotweed	Forb		X
Polygala alba	White milkwort	Forb		X

Species	**Common**	**Plant Type**	***Off-Town***	***On-Town***
Polygonum aviculare	Prostrate knotweed	Forb		X
Polygonum convolvulvus	Black bindweed	Forb	X	X
Polygonum ramosissimum	Bushy knotweed	Forb	X	X
Potentilla pensylvanica	Pennsylvania cinquefoli	Forb		X
Psoralidium tenuiflorum	Slimflower scurfea	Forb		
Pulsatilla patens	Cutleaf anemone	Forb		X
Ratibida columnifera	Prairie coneflower	Forb	X	X
Rosa arkansana	Prairie rose	Shrub	X	X
Rosa woodsii	Woods' rose	Shrub	X	
Salsola tragus	Russian thistle	Forb		X
Schedonnardus paniculatus	Tumblegrass	Grass	X	X
Schizachyrium scoparium	Little bluestem	Grass	X	X
Selaginella densa	Lesser spikemoss	Forb		
Setaroa pumila	Yellow foxtail	Grass		
Sisyrinchium montanum	Strict blue-eyed grass	Forb		
Solidago missouriensis	Missouri goldenrod	Forb	X	X
Solidago mollis	Soft goldenrod	Forb	X	X
Solanum rostratum	Buffalobur nightshade	Forb		X
Solanum triflorum	Cutleaf nightshade	Forb		X
Sphaeralcea coccinea	Scarlet globemallow	Forb	X	X
Symphyotrichum ericoides	White heath aster	Forb	X	X
Symphyotrichum falcatum	White prairie aster	Forb	X	X
Symphyotrichum oblongifolium	Aromatic aster	Forb	X	
Symphoricarpos occidentalis	Western snowberry	Shrub	X	X
Taraxacum officinale	Common dandelion	Forb	X	X
Tetraneuris acaulis	Stemless four-nerve daisy	Forb	X	
Thlaspi arvense	Field pennycress	Forb		
Tradescantia bracteata	Longbract spiderwort	Forb	X	X
Tragopogon dubius	Yellow salsify	Forb	X	X
Verbena bracteata	Bigbract verbena	Forb		X
Vicia americana	American vetch	Forb	X	X
Vulpia octoflora	Sixweeks fescue	Grass	X	X
		n=137	**n=86**	**n=116**