THE EFFECTS OF FIRE AND GRAZING IN THE NORTHERN MIXED-GRASS PRAIRIE: IMPLICATIONS FROM THE PAUTRE WILDFIRE

by

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ABSTRACT

Current federal recommendations pertaining to the management of post-fire grazing on rangelands interrupts historic disturbance regimes of the North American prairies by indicating that fire and grazing should be separated by at least two growing seasons. In contrast, some scholars suggest that North American prairie evolved under a tight linkage of fire and proximate post-fire grazing and should be well adapted to these combined disturbances. The Pautre wildfire of April 2013 provided an opportunity to test the effects of post-fire grazing in the northern mixed-grass prairie. One grazing allotment, burned in its entirety, and three burned and nonburned sites spanning a north-south gradient of the fire perimeter were selected as study locations. The effects of grazing versus rest, defoliation during the first spring, summer, or fall following the fire on burned and nonburned sites and the effects of fire on forage fiber digestibility were tested. Sites grazed during the first two growing seasons following the fire were found to recover similarly to sites rested during that same time. In addition, defoliation during any season following the fire produced no negative effects when compared to nondefoliation. Increases in forage fiber digestibility peaked shortly after fire and were short-lived, diminishing by the following year. These results lend support to the theory that fire and grazing were historically linked disturbances throughout the evolution of the North American prairies, indicating that the federal recommendation of rest is unnecessary in at least the northern mixed-grass prairie ecoregion. Historic, evolutionary patterns of disturbances, such as fire and grazing, may be useful in determining the most appropriate post-fire management regimes for specific ecoregions.

CHAPTER ONE

FIRE AND GRAZING AS ECOLOGICAL DRIVERS: A LITERATURE REVIEW

Introduction

Federal recommendations pertaining to post-fire livestock management decouple two natural disturbances that, in North American prairies, were historically linked. Natural disturbances and the disturbance regimes in which they occur, far from being stressors as the nomenclature might imply, are integral ecological processes essential to long-term ecosystem stability (Sousa 1984). Current recommendations state that rangelands be rested from grazing following fire for two growing seasons (Blaisdell et al. 1982; Bureau of Land Management 2007). However, during the evolution of the prairie biome, evidence suggests that fire and grazing co-occurred in an intimate interaction, with fire determining where grazing was likely to take place and vice versa (Fuhlendorf and Engle 2001). Fuhlendorf et al. (2009) suggest that the combination of fire and post-fire grazing be considered one perturbation and referred to as pyric herbivory. Evidence suggests that pyric herbivory may be an obligate ecological process, as conditions more closely matching what is thought to be the historic climax plant community (based on relic areas of native prairie) have been obtained when fire and grazing are applied in sequence rather than separately (Collins 1987; Fuhlendorf et al. 2009). Given this close interaction, deferral of grazing following fire may be unnecessary or even inappropriate in some North American prairies.

Fire and Grazing as Ecological Drivers

Both fire and grazing have been integral components of not only the natural history of grasslands, but of human history as well (Vogl 1979; Axelrod 1985; Pausas and Keeley 2009). Considered a major driving force in the evolution of terrestrial plant communities, fire should be considered a natural part of the landscape (Vogl 1979; Axelrod 1985; Biondini et al. 1989; Brockway et al. 2002; Pausas and Keeley 2009).

Vogl (1979) states that, "a basic assumption is that most grasslands have coexisted with fire through time and that fires are an inevitable part of those systems". The topography and annually senescent vegetation typical to grasslands facilitate this relationship with fire. Level to rolling terrain and dry, ignitable fuels enable the periodic spread of low intensity fires (Vogl 1979; Axelrod 1985). Humans have historically manipulated the natural environment and its attendant fire regimes in order to manage the land to better serve specific needs (Vogl 1979). Native Americans are believed to have used fire as a tool for a myriad of purposes (Axelrod 1985). Such purposes included influencing wildlife migration patterns to facilitate hunting (Old 1969), maintaining crops of forbs, nuts and fruits for gathering, clearing routes for travel and warfare, as well as several others (Axelrod 1985). Though all of these applications of fire changed the prairie landscape (Axelrod 1985), anthropogenic manipulation of the environment has had its strongest effect through fire suppression (Vogl 1979). In the 21st century, fire suppression has been so effective as to completely remove fire from most prairie systems (Brockway et al. 2002). Significant hesitation towards allowing fire to be restored to the landscape still exists (Brockway et al. 2002; Pausas and Keeley 2009). Especially in grasslands, this hesitation can be partially attributed to a lack of knowledge. Prairie and grassland fires, fire behavior and fire effects have not been as well studied and documented as in forest systems (Vogl 1979). Fire was, for a time, viewed as a destructive and damaging force (Old 1969) and was blamed for the condition of deteriorated ranges (Vogl 1979).

Anthropogenic application of grazing has undergone a similar shift in perceptions. Post-European settlement, the cultivation of large herds of cattle, sheep and horses began as westward expansion was encouraged by cheap abundant land, resulting not only in the removal or displacement of native grazers, but also in widespread, long-term overgrazing (Holechek 1981; Box 1995). Initially, rangelands were seen as a communal and inexhaustible resource, leading to severe overuse (Box 1995). While the prairies of the Great Plains evolved under significant grazing pressure from bison, the repeated, annual grazing of livestock was often at odds with the severe but infrequent grazing of bison (Fuhlendorf and Engle 2001). In the early, 1900's rangeland surveyors were already coming to the conclusion that livestock grazing was causing perceptible shifts in plant communities all across North America (Holechek 1981). Little attention was afforded to the role that manipulation of fire regimes may have played in the observed changes in these communities.

As a result of the manipulations of historical fire and grazing regimes, the interactions between fire and grazing were also interrupted. Modern scholars are concluding that while fire and grazing are important ecological drivers individually, they may render their most profound effects when combined (Collins 1987; Fuhlendorf and Engle 2004). This interaction is credited with controlling both the location and timing of fire and grazing events. Grazers, historically bison, were attracted to the relatively high quality forage that grew following fire when compared to nonburned areas (Vinton et al. 1993; Knapp et al. 1999; Vermeire et al. 2004; Fuhlendorf et al. 2009). Removal of this vegetation decreased the fuel available to carry a subsequent wildfire. As time since fire increased, the attractiveness of burned areas relative to nonburned areas diminished, reducing grazing pressure (Fuhlendorf et al. 2009). Fuels would eventually build up, increasing the probability of wildfire. The resultant cycle would cause fire and grazing to occur in a relatively predictable pattern in which the effects of fire and grazing rarely occurred individually. Unfortunately, most studies of the effects of fire and grazing do, in fact, focus on the effects of either fire or grazing, or pair the two in unlikely ways, resulting in a fair understanding of fire and grazing as individual processes, but a poor understanding of how fire and grazing interacted to maintain the prairies of North America.

With the restoration and conservation of grasslands becoming increasingly prioritized (Samson et al. 2004), the limited understanding of the interactions between fire and grazing (Vinton et al. 1993) and the shifting of ecosystem processes due to climate change (Mitchell and Csillag 2001), there is a crucial need to develop an understanding of how fire, grazing and post-fire grazing should be managed to not only allow for appropriate use of these economically important lands, but also to promote the maintenance of ecosystem stability.

Available knowledge pertaining to the effects of fire and grazing on productivity and community composition of grasslands and the effects of fire on grassland forage quality is summarized in the following sections.

The Northern Mixed-Grass Prairie

Grasslands represent an important biome dominating the arid regions of the world in which woodlands and forests could not exist (Axelrod 1985; Samson et al. 2004). Tallgrass, mixed-grass and shortgrass prairies constitute a large portion of North America's grasslands and cover a substantial portion of central North America, as shown in Figure 1.

The northern mixed-grass prairie begins near the eastern borders of the Dakotas and extends west into Montana and south into Wyoming and Nebraska (Wienk and Benkobi 2005). Typical soils are aridisols or mollisols ranging from clayey to silty-loam in texture (Wakimoto et al. 2005). Slopes tend to be gentle, resembling the rolling hills characteristic of many grasslands world-wide (Vogl 1979; Axelrod 1985; Wakimoto et al. 2005). The climate tends to be semi-arid with 254-508 mm of precipitation being the average (Wakimoto et al. 2005). Cycles of drought commonly occur in this region at least every 20 years (Engle and Bultsma 1984b). The mixed-grass prairie borders both the tall and shortgrass prairies and harbors tall, short and mid-statured grasses (Wakimoto et al. 2005). The northern mixed-grass prairie not only receives less precipitation than the average 835 mm received by the tallgrass prairie (Bark 1987) and more than the 320 mm received by the shortgrass prairie (Parton and Greenland 1987), but also experiences precipitation in a different form. The tall and shortgrass prairies receive most precipitation from summer to fall thunderstorms (Bark 1987; Parton and Greenland 1987) whereas the northern mixed-grass prairie receives most precipitation in the form of winter snow and spring rain (Wakimoto et al. 2005). Cool- (C3) and warm- (C4) season grasses occur in tandem (Wienk and Benkobi 2005). *Pascopyrum smithii* (Rydb.) Á. Löve, *Hesperostipa comata* (Trin. & Rupr.) Barkworth, *Nassella viridula* (Trin.) Barkworth and *Koeleria macrantha* (Ledeb.) Schult. are C3, mid- to short statured grasses typical of the northern mixed-grass prairie while *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths and *Bouteloua dactyloides* (Nutt.) J.T. Columbus represent the important C4 short grasses (Wakimoto et al. 2005; Wienk and Benkobi 2005). Common native forbs include *Grindelia squarrosa* (Pursh) Dunal, *Ratibida columnifera* (Nutt.) Wooton & Standl.and *Plantago patagonica* Jacq. The sedge, *Carex filifolia*, Nutt. and shrubs such as *Artemisia frigida* also frequently occur (Wakimoto et al. 2005).

Fire and Grazing Effects on Productivity and Community Composition

While many studies have addressed the effects of fire or the effects of grazing, far fewer studies address the effects of fire and grazing as interacting or complimentary forces. Those studies that do exists seem to be in disagreement as to the effects of post-fire grazing specifically. Observation by Bunting et al. (1998) and Jirik and Bunting (1994) on Great Basin bunchgrasses suggest that post-fire defoliation is injurious and that rest between fire and subsequent grazing is required to avoid additive mortality. However, observations by Vermeire et al. (2014) in the northern mixed-grass prairie and Bates et al. (2009) in the sagebrush steppe suggest that recovery following fire is similar between grazed and rested sites. This disagreement highlights not only the lack of knowledge as to proper post-fire grazing management, but serves as a reminder that ecoregions should be considered distinct entities with individualistic responses to disturbance.

Productivity

Maintaining and enhancing productivity of native rangelands used for livestock production purposes has been a longstanding goal of producers and managers. Stable or high productivity not only provides forage and habitat for livestock and wildlife, but is indicative of a functioning system. Uncharacteristically low or declining productivity can be indicative of disrupted ecosystem processes and overall community stress (Engle and Bultsma 1984a; Anderson et al. 2007).

Productivity of rangelands varies substantially in response to inter-year climatic variability and intra-year seasonal variability (White and Currie 1983). Effects of fire on productivity are largely dependent upon soil water availability after burning (Old 1969; Steuter 1987; Shay et al. 2001) and during and after grazing (Derner and Hart 2007). Consequently, drought may diminish any differences in productivity rendered between burned and nonburned areas (Engle and Bultsma 1984b) and may mask any effects of grazing management regimes (Derner and Hart 2007). Productivity will also vary drastically depending on topographic location (Gibson and Hulbert 1987). Lowland or sub-irrigated prairie sites are by and large expected to be more productive than upland or drier sites (Abrams and Hulbert 1987; Steuter 1987). As such, the effects of fire and grazing on productivity must be considered within a climatic, seasonal and topographic context.

White and Currie found that fire can have a positive or neutral influence on the productivity of key forage species such as *P. smithii*, *B. gracilis* and *C. filifolia* (1983). *P. smithii* productivity was ultimately increased by 10-15% and *B. gracilis* by 40% while *C. filifolia* was unaffected. Similarly, productivity of herbaceous pine understory was found to double following fire (Harris and Covington 1983).

Hulbert (1988) attributed the majority of increased production in a tallgrass prairie to the removal of standing and ground litter, as increases following fire were similar to those following mechanical litter removal. As standing and ground litter can inhibit productivity (Knapp and Seastedt 1986; Facelli and Pickett 1991), the combustion of these components can increase productivity by decreasing competition for light (Old 1969; Hulbert 1988), increasing nitrogen availability (Hobbs and Schimel 1984; Fenn et al. 1993; Neary et al. 1999), increasing the rate of microbial turn over (Fenn et al. 1993), and can ultimately result in increased tillering (Hulbert 1969).

Grazing inarguably reduces current standing crop (Clark et al. 1998; Clark et al. 2000). Immediate, short-term effects on productivity, on the other hand, will depend on several factors, including frequency, intensity and seasonality of defoliation. *P. smithii* production has been found to increase when compared to nondefoliated controls in the first season following a uniform clipping, but be less productive if clipped again the following year (Stroud et al. 1985). Additionally, uniformly clipping *P. smithii* was found to decrease productivity while clipping unevenly to simulate grazing had no such adverse effect. Seasonality of defoliation will determine the physiological status of tissue removed (Briske 1991). Physiologically active tissue will be allocated nutrients for growth and maintenance whereas senesced tissue contains fewer nutrients and is physiologically inactive (Briske 1991) As such, the removal of actively growing tissue may weaken a plant's potential productivity by depleting reserves (McLean and Wikeem 1985a; Mclean and Wikeem 1985b), whereas the removal of senesced tissue will have essentially no effect (McLean and Wikeem 1985a; Mclean and Wikeem 1985b; Briske 1991). Contrastingly, removal of active tissue may also increase productivity via compensatory growth, in which losses are recovered by sequestration and replacement of lost resources throughout the remainder of the growing season (McNaughton 1983).

Productivity and grazing have been described as negatively related by long-term studies (Ellison 1960; Jaramillo and Detling 1988; Milchunas and Lauenroth 1993; Derner and Hart 2007). In the mixed-grass prairie, this has been attributed to the increase of less productive short statured grasses, such as *Bouteloua gracilis*, under significant long-term grazing pressure (Ellison 1960). It has also been suggested that long-term grazing may favor the survival of diminutive, less productive morphs of tall or mid-statured species (Jaramillo and Detling 1988).

Community Composition

Community composition and biodiversity have been implicated as indicators of ecosystem health (Chapin III et al. 2000; Folke et al. 2004). This is based on the argument that adequate levels of biodiversity contribute to both the resistance and resilience of an ecosystem to disturbance (Tilman and Downing 1994; Chapin III et al.

2000; Folke et al. 2004; Zelikova et al. 2014). Resistance refers to an ecosystem's ability to maintain characteristics in the event of disturbance while resilience refers to the ability to recover from changes rendered by disturbance (Tilman and Downing 1994). In grasslands, adequate biodiversity can also ensure stable community productivity following disturbance (Tilman and Downing 1994; Hector et al. 2010; Fynn 2012). Community composition, like productivity, is primarily determined by state factors (state factors being climate, soil, topography, organisms, time and human influence) rather than by disturbances like fire or grazing.

While topographic position and climate ultimately have the strongest effect upon the type of vegetative community that exists in a location, fire has been implicated as a strong driver of vegetation gradients across sites with homogenous state factors (Abrams and Hulbert 1987; Gibson and Hulbert 1987; Steuter 1987). Lowland or sub-irrigated prairie sites are ubiquitously expected to be more diverse than upland or drier sites (Gibson and Hulbert 1987; Steuter 1987). Annual burning of these or similar ecological sites, however, represents a disturbance so severe that it is capable of obscuring the governing factor of topography and resulting in similar upland and lowland communities (Gibson and Hulbert 1987). In general, dormant season fire in prairie ecosystems may increase grass cover, decrease forb cover, decrease or eliminate shrubs or other woody components (Brockway et al. 2002) and decrease the presence of annuals (Vermeire et al. 2011)

Collins and Barber (1986) observed that diversity in a mixed-grass prairie reached minima on both undisturbed and severely disturbed sites. While burning alone either increased or had no effect upon diversity, maximum diversity resulted from the combined disturbance of fire, light grazing and bison wallowing. These results suggest that disturbances act cumulatively, though not necessarily additively, to produce distinct effects in grasslands (Collins and Barber 1986; Collins 1987; Biondini et al. 1989). Vinton et al. (1993) also documented an interaction between fire and grazing that differed from the effect of either disturbance on its own; grazed but nonburned patches were found to differ in species composition from that of the greater region, being only 34% similar, whereas burned and grazed patches closely resembled the greater region, being 91% similar. This indicates that fire and grazing in combination, not alone, interact to shape prairie grassland communities.

Fires in grasslands will render effects on diversity by differentially affecting plant functional groups. In general, fire may favor graminoids and reduce the presence of forbs (Harris and Covington 1983; Vinton et al. 1993). In a pine savanna understory community, grass-forb dominance was observed to reverse following fire. Initially dominated by 54% forbs versus 28% grasses, burning caused a decline in forbs to 28% and an increase in grass to 61% (Harris and Covington 1983). Diversity of a prairie forb community may decrease immediately following a fire, but forb density in some patches may increase. Burned patches, or other recently disturbed areas, can represent prime locations for the initiation of pioneering forbs (Biondini et al. 1989).

Shifts in the competitive interactions of plants may account for changes in community diversity or composition. As previously stated, burning removes litter and the shade of the canopy vegetation (Hulbert 1969; Hulbert 1988). This drastically reduces the competition for light, shifting the competitive interactions belowground for nutrients and water (Wilson and Shay 1990). Logically, this shift in competition may favor a different set of species. For example, when C3 annual grasses are reduced by early spring fire, C3 perennial grasses may be favored by the reduced competition for soil moisture and nutrients (Davies et al. 2009).

Heavy grazing was suggested by Collins and Barber (1986) to be a more severe disturbance than fire in a mixed-grass prairie and capable of producing a substantially stronger effect on community composition. Light to moderate grazing may be generally credited with increasing richness and diversity of grasslands (Collins 1987; Belsky 1992; Hickman et al. 2004; Towne et al. 2005). Towne et al. (2005) found a 29-37% increase in overall richness of grazed tallgrass prairie when compared to rested prairie. Towne et al. (2005) caution however, that increases in richness and diversity may not always be desirable, as they attributed some increased diversity to the introduction of non-native or invasive species.

Unlike fire, which consumes plants with less selectivity than grazing, responses of grass species to grazing largely depend on disparities in morphology; specifically, the stature of the species and the combination of dissimilar grass statures in a community. Short statured species respond negatively, or become less abundant, under no or very light grazing and may disappear as species of tall and mid-statures create a closed canopy, imposing limitation on light availability (Ellison 1960; Belsky 1992). Contrastingly, heavy grazing may result in a community dominated by short grasses (Fuhlendorf et al. 2001) as tall and mid-grasses are more accessible and selected at a higher rate than short grasses (Belsky 1992; Hickman et al. 2004). Forbs, in general, are reported as responding positively to long-term grazing (Collins 1987; Hickman et al. 2004; Towne et al. 2005).

Community altering effects of grazing must also be considered within the context of grazing pressure (Fuhlendorf et al. 2001; Hickman et al. 2004). Light or moderate grazing pressures will allow for selectivity, creating an opportunity for undesirable or unpalatable species to become competitively dominant (Collins 1987; Tallowin et al. 2005). These species may be those with grazing avoidance mechanisms, such as *Cirsium spp*. Mill., or with deterrent anti-quality compounds, such as *Centaurea maculosa* auct. non Lam. (Tallowin et al. 2005) or simply be less palatable grasses or forbs (Collins 1987). Light to moderate grazing pressures may maintain or decrease existing diversity and richness (Hickman et al. 2004). Conversely, heavy grazing pressures, which attempts to minimize selectivity and homogenize use, and can result in increased diversity and richness (Hickman et al. 2004).

Fire Effects on Forge Quality

Increases in forage quality represent factors that will increase the performance or efficiency of a foraging animal (Coleman and Moore 2003). Voluntary forage intake has been identified as the most limiting factor in animal performance (Allison 1985). Intake is primarily limited by physical fill of the rumen, digestibility of forage and passage rate. Hence, increases in forage quality can increase intake by decreasing rumen fill by less degradable fibers and increasing the extent and rate of digestion.

Within one growing season, forage quality is most dramatically affected by phenology and morphology (Arzani et al. 2004). Digestibility of forage will be greatest in spring or when new growth occurs and digestibility of leaves will be higher than digestibility of stems (Arzani et al. 2004). Thus, early season growth or growth with a high leaf to stem ratio will be of ubiquitously higher quality than later season growth, mature or dormant forage, or forage containing a large proportion of stems. As such, effects of fire upon forage quality should be assessed within the context of season or phenological stage.

Generally, fire has been indicated to increase relative forage quality by increasing the proportion of protein (Hilmon and Hughes 1965; Hobbs and Spowart 1984; Debyle et al. 1989; Mitchell et al. 1994; Dufek et al. 2014), decreasing anti-quality factors (Smith and Young 1959; Mitchell et al. 1994; Dufek et al. 2014) and increasing digestibility (Hobbs and Spowart 1984; Debyle et al. 1989; Mitchell et al. 1994; Dufek et al. 2014).

Observed post-fire increases in forage quality have been attributed to the removal of old standing dead material, increases in nitrogen availability, stimulated microbial activity and decreased competition for light. Senesced previous years' growth is expected to be of lower forage quality than newly produced plant tissues. Via combustion, fire removes dry, old dead material (Duvall 1970). The quality of regrowth following the fire is, thus, not diluted by low quality, old material (Hobbs and Spowart 1984). As such, less effort is required by animals to select for higher quality new growth (Duvall 1970; Hobbs and Spowart 1984). Combustion of aboveground vegetation also mineralizes nitrogen previously immobilized in plant tissues, potentially increasing nitrogen available for regrowth (Hobbs and Schimel 1984; Fenn et al. 1993; Neary et al. 1999). Nitrogen can increase forage quality as it is generally a limiting nutrient in grassland systems (Seastedt et al. 1991). Released nitrogen and increased soil temperatures via surface blackening can result in greater microbial activity (Fenn et al. 1993). Increasing the rate of microbial turnover increases nutrients available to post-fire regrowth (Coleman et al. 1983). Forage quality can also be enhanced by increasing the leafiness of vegetation. The leaves of forages are of universally higher nutritional value than stems, which contain greater portions of recalcitrant structural fibers (Arzani et al. 2004). Stem growth occurs in order to provide escape from the shade of canopy plants (Falster and Westoby 2003). Combustion of the plant canopy reduces shade, decreasing the need for stem elongation, increasing the resources which may be allocated to leaf tissue, ultimately increasing the leaf: stem ratio and increasing the relative forage quality (Arzani et al. 2004).

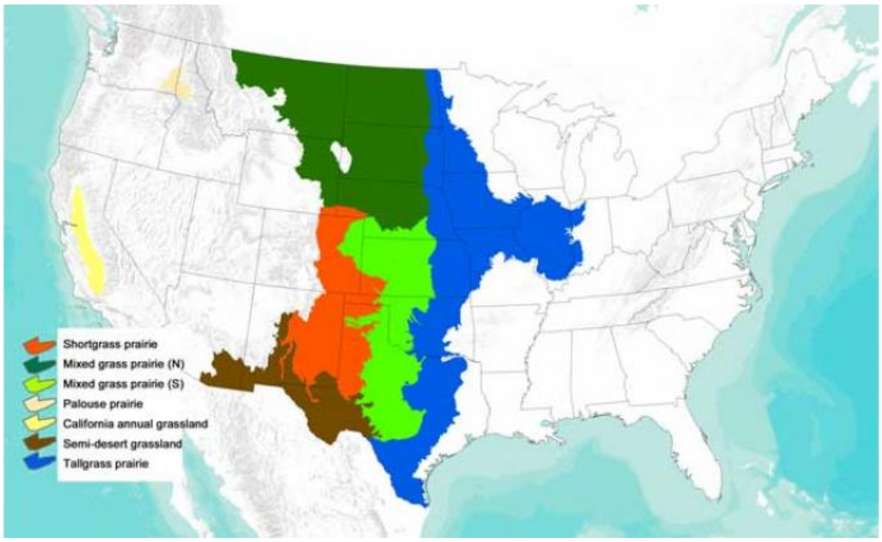
It is unclear how long post-fire increases in forage quality should be expected to last. Fire has been found to increase the quality of winter forage for up to two years in shrubby grasslands (Hobbs and Spowart 1984) whereas increases in the forage quality of desert grasslands have been observed to last for one to three years (McPherson et al. 1995), suggesting that the effects may not be transient. Conversely, studies of herbaceous pine forest understory (Wood 1988) and wiregrass rangelands (Hilmon and Hughes 1965) suggest that increases in forage quality disappear within the first growing season following fire. Given this disagreement, the longevity of increases in forage quality may be highly dependent on ecoregion.

Summary

Fire and grazing have been ecological drivers of ecosystem processes in the prairies of North America. Scholars of natural history suggest that fire and grazing as natural disturbances work in tandem, rather than individually, to maintain prairie stability. However, little actual evidence exists as to the combined effects of fire and grazing. The wealth of information as to the effects of fire or the effects of grazing may help to inform studies of post-fire grazing. In general, fire is credited with increasing productivity, favoring graminoids species and increasing forage quality. Livestock grazing is generally credited with decreasing long-term productivity and increasing diversity. The few available studies of post-fire grazing indicate that grazing following fire will not negatively impact some environments (Vinton et al. 1993; Bates et al. 2009; Vermeire et al. 2014). As such, post-fire grazing may be expected to have no impact on productivity in the short-term. Improper grazing management or chronic overstocking following fire or in the absence of fire may be expected to cause productivity declines. The combination of fire and grazing may have no impact on a plant community as fire may favor grass species while grazing may compensatorily favor forbs, resulting in no net community change. Additionally, fire can be expected to increase forage quality, but these dynamics may be secondary to the determinant factor of phenology.

Figures

Figure 1.1. The type and distribution of the grasslands of the United States. Mixed-grass prairie appears in green, with the northern mixed-grass prairie appearing in a darker green (Bagne et al. 2012).



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CHAPTER TWO

RECONSIDERING REST FOLLOWING FIRE: NORTHERN MIXED-GRASS PRAIRIE IS RESILIENT TO SPRING WILDIFRE AND RESISTANT TO MODERATE POST-FIRE GRAZING

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RECONSIDERING REST FOLLOWING FIRE: NORTHERN MIXED-GRASS PRAIRIE IS RESILIENT TO MODERATE GRAZING FOLLOWING SPRING WILDFIRE

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Abstract

Current federal post-fire land management recommendations suggest that rangelands be rested from grazing for two growing seasons following fire to allow for proper recovery, despite the lack of empirical literature supporting this recommendation. This project was designed to determine if grazing the first growing season following a spring wildfire alters later productivity and species composition of northern mixed-grass prairie. Following the April 2013 Pautre wildfire in northwestern South Dakota, 6- 100 m^2 exclosures were erected in three burned pastures to simulate two growing seasons of rest. Grazing exclosures were paired with sites grazed both the first and second growing seasons following the fire and replicated across loamy and sandy ecological sites. Prior to grazing the second growing season, five 2 m^2 cages were placed at each grazed site to assess first-year grazing effects. Following the second growing season, productivity and species composition were determined for exclosures and cages. Current-year productivity differed between ecological sites as loamy sites were more productive (Loamy= 2764 kg ha^{-1}, Sandy = 2356 kg ha^{-1}; P=0.0271), but was similar between grazing treatments (Rested= 2556 kg ha^{-1}, Grazed= 2564 kg ha^{-1}; P=0.9550). Ecological site strongly

determined species composition. Loamy sites consistently contained more *Pascopyrum smithii*, *Bouteloua gracilis* and *Carex duriuscula* than sandy sites (30 v 0%, 18 v 8%, 4 v 1%; *P*= 0.0004, 0.0457 and 0.0382 respectively). The effects of grazing exclusion manifested in only *Hesperostipa comata* and *Agropyron cristatum*. *H. comata* was more prevalent on rested sites (22 v 15%, *P*=0.0096). *A. cristatum* experienced a grazing treatment by ecological site interaction as it was reduced by grazing on sandy sites, but was not affected on loamy sites (*P*=0.0226). These results do not support the notion that a two growing season rest period following fire is required in the northern mixed-grass prairie.

Introduction

Current federal land management recommendations decouple the historic disturbances of fire and grazing in North American prairies. Natural disturbances and the disturbance regimes in which they occur, far from being stressors as the nomenclature might imply, are integral ecological processes essential to long term ecosystem stability (Sousa 1984). Scholars agree that prairies evolved under a tight, fire-grazing linkage, termed pyric herbivory, with herbivores being attracted to recently burned areas when given the freedom of selection (Anderson 2006; Fuhlendorf et al. 2009). Recent literature suggests that not only are prairies well adapted to fire and post-fire grazing, but that the combination of these disturbance may be necessary to the maintenance of ecological processes in these grasslands. However, current federal recommendations suggest that all rangelands should be rested from grazing following fire. Although this recommendation may be appropriate, essential or beneficial on some rangelands, it may be unnecessary or inappropriate when applied to all rangelands due to the large variety of rangeland ecosystems with individual disturbance regimes.

The Society for Range Management (1998) broadly define rangelands as, "land on which the indigenous vegetation (climax or natural potential) is predominantly grasses, grass-like plants, forbs, or shrubs and is managed as a natural ecosystem". In just the United States, this definition consequently includes not only every grassland from the sparse desert grasslands of the Southwest to the productive rolling prairies of the Midwest, but also shrublands such as the sagebrush steppe in the Great Basin and Pacific Northwest. United States Forest Service recommendations state, "Revegetated areas and areas that have been burned but not revegetated will be closed to livestock grazing for at least two growing seasons following the season in which the wildfire occurred to promote recovery of burned perennial plants and/or facilitate the establishment of seeded species. […] Livestock closures for less than two growing seasons may be justified, on a case-by-case basis, based on sound resource data and experience" (Blaisdell et al. 1982). The Bureau of Land Management employs an essentially identical recommendation (Bureau of Land Management 2007). The rationale for these recommendations rely on several assumptions. First, it is assumed that fire will reduce plant vigor and productivity, rendering plants less capable of surviving a grazing event. However, literature indicates that plants may respond negatively, neutrally or positively to fire (Russell et al. 2015). Additionally, it is assumed that fire will result in appreciable plant mortality, requiring the recruitment of new seedlings for recovery. In contrast, literature indicates that the plants of some ecoregions experience little mortality following fire (Benson and Hartnett 2006; Haile 2011) and that ecosystem recovery does not rely on seedling recruitment (Benson and Hartnett 2006). Lastly, this recommendation assumes an increased risk of soil erosion following fire due to bare ground resulting from litter combustion and plant mortality, indicating that burned sites should be protected from the increased erosion that can result from grazing (Naeth et al. 1991). Conversely, ground cover can actually build up to detrimental levels, limiting productivity, in under-disturbed prairies (Knapp and Seastedt 1986). Not only is there sparse empirical evidence to support this recommendation across the whole geographic region to which it is applied, but the underlying assumptions are in direct disagreement with the ecological realities of the northern mixed-grass prairies.

The few available references indicating that there may be a need for rest following fire originate primarily from the Great Basin and specifically assess the effects of fire and post-fire defoliation on caespitose grasses, primarily *Pseudoroegneria spicata* (Pursh) Á. Löve and *Festuca idahoensis*. Clipping following fire additively increased the mortality experienced by these species when compared to unclipped plants (Jirik and Bunting 1994). These studies suggest that rest from grazing for 1-3 years following fire will allow for plant vigor and seed production of these caespitose grasses to return to pre-fire levels while avoiding this additive mortality from defoliation (Patton et al. 1988; Bunting et al. 1998). The rest interval also allows for newly recruited seedlings to become sufficiently established to withstand a grazing event without mortality being inevitable, as recommended by the theory of rest-rotation grazing management (Hormay

1970). While these studies provide a valid indication of the response of Great Basin caespitose grasses to post-fire defoliation, the response of the rhizomatous and caespitose species of the northern mixed-grass prairie are not well documented.

Evidence suggests that the rhizomatous and caespitose species of the northern mixed-grass prairie do not respond to fire and grazing as do the two caespitose, Great Basin species, rendering the foundational assumptions of the post-fire grazing exclusion recommendation invalid. Research in the northern mixed-grass prairie indicate that vigor and productivity generally remain unaffected or are enhanced by fire (White and Currie 1983; Vermeire et al. 2014) with few, if any, plants experiencing mortality (Haile 2011). Furthermore, many northern mixed-grass species have a rhizomatous or stoloniferous, rather than caespitose, habit (e.g. *Pascopyrum smithii* (Rydb.) Á. Löve, *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths, *Bouteloua dactyloides* (Nutt.) J.T. Columbus, etc) (Wakimoto et al. 2005). A recent study indicates that, while neither the caespitose *Hesperostipa comata* (Trin. & Rupr.) Barkworth nor the rhizomatous *P. smithii* mixed-prairie grasses experience immediate mortality following fire, rhizomatous grasses are overall less susceptible than caespitose grasses (Russell et al. 2015). Rhizomatous grasses are also less reliant on the regular recruitment of seedlings for propagation (Cheplick 1998). Additionally, in the neighboring tallgrass prairie, composed of similar growth forms and subjected to similar disturbances as the northern mixed-grass prairie, Benson and Harttnett (2006) indicate that community recovery does not rely on germination of seed, but rather on asexual tillering by surviving plants. Seasonality of fire influences whether fire effects are negative, neutral or positive. In the neighboring southern shortgrass prairies, dormant season fire may have no effect on plant vigor or survival with effects essentially limited to the removal of litter, while fire during the peak of the summer growing season may limit productivity (Brockway et al. 2002). However, the evolutionary history of North American prairies suggest that most naturally ignited wildfires occurred during the summer season (Higgins 1984) suggesting that at least southern shortgrass prairie is well adapted to fire even in season most damaging to that ecoregion. Mixed-grass prairies may very well show a similar resilience. As such, adaptations to deal with the effects of fire should be equally as apparent in soil quality as they are in the vegetation.

Canopy and litter cover have been shown to moderate soil moisture and quality (Hulbert 1969) and reduce erosive potentials (Benkobi et al. 1993). Fire will readily consume existing litter while grazing effectively reduces litter via biomass removal, limiting future litter, and mechanical trampling of existing litter (Naeth et al. 1991), indicating that either fire, grazing or post-fire grazing could decrease soil moisture or quality and increase erosion. However, Knapp and Seastedt (1986) indicate that, in the tallgrass prairie, litter can accumulate to such a degree that it will inhibit productivity. Furthermore, in moisture limited systems such as North American prairies, decomposition of litter occurs at very limited rates, necessitating augmented recycling of litter via mineralization through fire or grazing to maintain sustainable nutrient cycling (Brockway et al. 2002).

Taking this all into account, it is probable that individual rangelands have the capacity to respond disparately to the same disturbance regimes. Concurrently, responses within one rangeland ecotype can be expected to differ as annual precipitation and ecological site change across the landscape. Precipitation patterns, not management regimes, have been shown to account for the majority of yearly variation in productivity on northern mixed-grass prairie (Derner and Hart 2007). Furthermore, ecological sites have been shown to maintain individuality unless severely or frequently disturbed (Gibson and Hulbert 1987). Thus, post-fire grazing considerations must be based upon the type of rangeland as well as the yearly and topographical variations within each rangeland type, indicating that the responses of Great Basin caespitose grasses may not be reflective of the adaptive capacity of the northern mixed-grass prairie to respond to fire and grazing.

Given the limited empirical support for current management recommendations, we evaluated the need for a two-year rest interval following a spring wildfire on two ecological sites within the northern mixed-grass prairie. The objective of this study is to quantify the effects of moderate post-fire grazing versus two years of rest on productivity, community composition and basal cover. White and Currie (1983) found no negative impact of fire on post-fire productivity and Vermeire et al. (2014) found no negative effects of grazing following summer fire on productivity, so we hypothesized that post-fire grazing following a spring wildfire would have no effect on subsequent-year productivity. Furthermore, we further hypothesized that post-fire grazing would have no effect on subsequent-year plant community composition as Vermeire et al. (2014) found minimal effects on community composition and Bates et al. (2009) found none when comparing grazed and rested sites following fire. Though Vermeire et al. (2014) found that moderate post-fire grazing may reduce litter mass, Bates et al. (2009) suggest that litter frequency under post-fire grazing will recover to levels comparable to rested sites within two years, leading us to hypothesize that while immediate basal cover composition may be affected by fire, subsequent-year basal cover composition would not be affected by post-fire grazing.

Methods

Wildfire & Study Sites

The Pautre fire (31 km southwest of Lemmon, SD ; lat 45° 52' 54" N long 102° 32' 52" W), occurred on 3 April 2013 and was contained on 7 April 2013, burning a 4322 ha mosaic of private, Grand River Grazing Co-op and Grand River National Grassland lands. This study was conducted on the Dyson grazing allotment located on the Grand River National Grassland portion of the burn (Figure 2.1). The Dyson allotment burned in its entirety and is comprised of North (143 ha), Southeast (74 ha) and Southwest (41 ha) pastures. Pastures were dominated by the C3 grasses *H. comata*, *Agropyron cristatum* (L.) Gaertn. and *P. smithii*, with a lesser component of the C4 grasses *B. gracilis* and *Aristida purpurea* Nutt. *Psoralidium tenuiflorum* (Pursh) Rydb., *Artemisia biennis* Willd. and *Artemisia ludoviciana* Nutt. were the most common forbs. *Artemisia frigida* Willd., the only woody shrub present, was rare.

Following the wildfire, six 10 x 10 m grazing exclosures were erected, with two exclosures located in each pasture. Within each pasture, one exclosure was built on a loamy ecological site (Reeder-Lantry loams: Fine-loamy, mixed, superactive, frigid

Typic Argiustolls and Fine-silty, mixed, superactive, calcareous, frigid Typic Ustorthents; 2-9% slopes) and the second on a sandy ecological site (Vebar-Cohagen fine sandy loams: Coarse-loamy, mixed, superactive, frigid Typic Haplustolls and Loamy, mixed, superactive, calcareous, frigid, shallow Typic Ustorthents; 6-25% slopes) (Soil Survey Staff USDA-NRCS 2008; Web Soil Survey 2015).

Precipitation averages 413 mm in Lodgepole, SD (approximately 12 km northeast of the study site) and 453 mm in Lemmon, SD with most occurring from April to September (National Climate Data Center 2015). During the study period from 2013-2014, precipitation was above average. Precipitation was 710 and 863 mm (190 and 172% of average) during 2013 and 474 and 457 mm (101 and 114% of average) during 2014 in Lodgepole and Lemmon, respectively.

<u>Post-Fire Grazing</u>

Moderate grazing was applied to pastures the first and second growing season following fire. Grazing occurred from 17 June to 31 October 2013 using 78 cow-calf pairs and 6 bulls (1.43 AUM ha^{-1}) and from 22 June to 30 September 2014 using 78 cow-calf pairs and 3 bulls (1.14 AUM ha^{-1}). Prior to the 2014 grazing season, five 2 x 1 m grazing exclosure cages were paired with each exclosure to prevent further grazing during the 2014 season and preserve the effects grazing during the 2013 growing season (Figure 2.2).

Sampling

At the end of the first growing season following the fire, August 2013, grazing utilization was measured by clipping eight 0.1 m^2 quadrats within each exclosure and eight quadrats from the grazed sites paired with each exclosure. The difference in standing biomass from within and outside of the exclosures was assumed to represent the grazing utilization during 2013. In August 2014, at the conclusion of the second growing season following the fire, standing biomass, community composition and basal cover were sampled. Ten quadrats were clipped from each exclosure while two quadrats were clipped from beneath each exclosure cage. Community composition was measured via the point-intercept method (Caratti 2006). Ten randomly distributed points were measured beneath each exclosure cage while fifty randomly distributed points were measured within each exclosure. Observations at each point delineated canopy and basal cover. Differences between the exclosures ("rested sites") and the exclosure cages ("grazed sites") were assumed to represent the effects of grazing the first growing season after fire.

Biomass samples were dried at 60˚C until loss in weight was no longer observed. Total standing biomass weights were recorded. Two samples from each exclosure and set of exclosure cages were then sorted and reweighed with respect to current-year production and old (past-year) standing dead biomass.

Statistical Analysis

The SAS MIXED procedure was used to perform analysis of variance (ANOVA) using the10 x 10 m exclosures (n=6) and grazed sites (n=6) as the experimental units

(Littell et al. 2006). Response variables for the mixed linear models included total standing biomass, old dead, current-year productivity, canopy composition by species and functional group (functional group here refers to plants with similar life strategies; groups used were cool season (C3) grasses, warm season (C4) grasses, annual grasses, sedges, shrubs and forbs), total canopy cover, basal cover composition, species richness and Shannon's diversity index (calculated using canopy frequency "hits" from the line-intercept transect). When necessary, effects on composition were compared against raw frequency data to determine if changes represented shifts in actual or relative abundance. Where outlier values were suspected, they were verified using the Generalized Extreme Studentized Deviate Test and removed from further analysis. Ecological site and grazing treatment were used as fixed-effect explanatory variables with pasture included as a random-effect variable. An α of 0.05 was used to identify significant effects and interactions while an α between 0.05 and 0.1 was used to identify trends or tendencies. The PDIFF option in SAS was used for mean separations when significant interactions between ecological site and grazing treatment were found. A list of all species observed can be found in Appendix A while a summary of ANOVA F-tests for the fixed and interacting effects of grazing and ecological site can be found in Appendix B.

Results

Biomass

In 2013, at the conclusion of the first growing season following the fire, average grazing utilization was 35% with the median being 47%. Grazed sites had less current-year standing biomass when compared to rested sites at the end of the grazing period (Figure 2.3 A; *P*= 0.0307). Median grazing utilization likely represents a more accurate utilization estimate as biomass data in 2013 were markedly skewed by one exclosure. Current-year standing biomass was similar between loamy and sandy ecological sites the first growing season after fire (Figure 2.3 B; *P*=0.7409).

In 2014, following the second post-fire grazing season, total standing biomass was 1.2 times greater on rested sites than grazed sites (Figure 2.3 A; *P*=0.0381). However, current-year productivity was similar between grazed and rested sites (Figure 2.3 A; *P*=0.7966) with old dead, which was greater on rested sites, accounting for the difference in total standing biomass (Figure 2.3 A; *P*<0.0001). Standing biomass was 1.2 times greater on loamy sites than sandy sites (Figure 2.3 B; *P*=0.0381). Total canopy tended to be less on grazed sites (98%) than on rested sites (100%) (*P*=0.0603).

Canopy Composition

With respect to canopy community composition (Table 2.1), only *A. cristatum* and *H. comata* were sensitive to grazing. Grazing and ecological site interacted in effects on *A. cristatum* with grazing causing a reduction on sandy sites and no effect on loamy sites where *A. cristatum* was uncommon. *H. comata* was the only species reduced by grazing on both ecological sites. C3 grasses decreased under grazing whereas C4 grasses experienced a concurrent relative increase. Based on observed frequency, C3 grasses decreased in actual abundance under grazing (38.2 v 58.2 hits, *P*=0.0051) while actual C4 grass abundance remained similar (19.5 v 12 hits, *P*=0.0948). Forbs trended toward greater abundance on grazed sites. Total species richness was lower on rested sites.

Grazing and site effects interacted with respect to Shannon's Diversity Index, resulting in grazing increasing the index on sandy sites and no apparent effect on loamy sites. *P. smithii*, *B. gracilis* and *Carex duriuscula* C.A. Mey. were, respectively, 8.8, 2.3 and 12.5 times more abundant on loamy than sandy ecological sites.

Basal Cover

The effect of grazing treatment on basal cover was limited to fecal matter, with fecal coverage appearing only on grazed sites (Table 2.2). Litter and bare ground were similar across grazed and rested sites. Basal cover composition differed between ecological sites across grazing treatments with respect to several plant species. *A. cristatum* appeared only on sandy sites while *A. purpurea* provided greater basal cover on sandy sites. Loamy sites exhibited greater *B. gracilis* basal cover.

Discussion

Results support the hypothesis that moderate grazing during the first year following fire will not alter subsequent-year community productivity. At the end of the first and second growing seasons, grazing predictably reduced standing biomass by 35 and 19%, respectively. At the conclusion of the first growing season, we can account for this reduction as actual use. At the conclusion of the second growing season, standing-dead from the previous year accounted for the deficit in total standing biomass. Rested sites had 691 $kg \cdot ha^{-1}$ (53%) more old dead material than grazed sites while current-year productivity remained similar across the grazed and rested sites. This finding agrees with observations of post-fire grazing in other areas of the northern mixed-grass prairie as well as sagebrush steppe that report no difference in current-year productivity (Bates et al. 2009; Vermeire et al. 2014).

Contrary to the hypothesis, community composition, as measured by canopy cover, did slightly shift under moderate post-fire grazing. On an individual species basis, only *A. cristatum* and *H. comata* were found to be sensitive to grazing. C3 grasses as a whole were 18.2% less prevalent after post-fire grazing. This reduction is primarily attributable to the dynamics of *A. cristatum* and *H. comata*. The shift in the relative abundance of C3 and C4 grasses observed following spring fire is well documented in the literature (Gibson and Hulbert 1987; Steuter 1987; Vinton et al. 1993; Ansley et al. 2010). However, many of these studies observe this decrease only after repeated burns. The reduction in C3 grasses in this case can be explained by the impact of grazing. C3 grasses are not only of a higher nutritional quality, but over-top the local C4 species, ultimately causing C3 grasses to be selectively preferred by grazers (Vinton et al. 1993; Coleman et al. 2004). The observed increase in Shannon's diversity index on grazed, sandy sites can be accounted for by the concurrent trend toward increased abundance of forbs on grazed sites. This agrees with the observations of Collins and Barber (1986) in which diversity was increased with the combined disturbances of fire and bison grazing when compared to fire alone, as predicted by the intermediate disturbance hypothesis. It is not unprecedented that this effect was only found on sandy sites as Gibson and Hulbert (1987) report a similar soil type by fire interaction.

The reduction of *A. cristatum* on sandy sites following post-fire grazing may be explained by the soil characteristics unique to sandy sites. Sandy sites, characterized by coarser textured soils, hold less moisture when compared to ecological sites with finer textured soils. In Canadian northern mixed-grass prairie, *A. cristatum* populations decreased after at least two years of defoliation when subjected to below average moisture versus remaining stable under average levels of moisture (Hansen and Wilson 2006). As moisture was above average during the study period, this explanation cannot fully account for the observed reductions in *A. cristatum*. The seasonality of the fire may have been an alternate contributing factor. *A. cristatum* resumes growth early in spring (Sedivec et al. 2010). Fire during the growing season has been indicated as most detrimental to prairie species (Brockway et al. 2002). Though an introduced species, *A. cristatum* appears to follow this trend, with spring burning being, in fact, one of the only disturbances capable of reducing *A. cristatum* production (Lodge 1960).

As a species especially resistant to disturbances such as grazing (Looman and Heinrichs 1973) and drought that can form persistent monocultures (Rogler and Lorenz 1983), this observed reduction in *A. cristatum* is somewhat unique. While valued by some producers as an early-season forage and as a competitor with more invasive species, some range managers and conservationists also struggle to reduce *A. cristatum* in attempts to restore native species (Cook and Harris 1952; Sedivec et al. 2010; Fansler and Mangold 2011). Managing *A. cristatum* for either maintenance or reductions was not the primary goal of this research, however, these preliminary results suggest that the role of post-fire grazing in maintaining, renovating or removing *A. cristatum* stands warrants future consideration.

The observed reduction in *H. comata* closely mimics the response observed by Vermeire et al. (2014) following summer fire with 50% post fire utilization. This correspondence of results suggests that *H. comata* may be more sensitive to post-fire grazing than the majority of mixed-prairie grasses. Russell et al. (2015) found that spring burns reduced the bud bank of *H. comata* the second growing season following spring fire. Additionally, *H. comata* has been reported to decrease under grazing pressure (Dormaar et al. 1994), suggesting that the reduction seen here may be a compound effect of fire and grazing. The results of this study and others imply that, while northern mixed-grass prairie may be generally resilient to fire and post-fire grazing, northern mixed-grass ranges dominated by *H. comata* may be less resistant.

We suspect that the observed reductions in *H. comata* and *A. cristatum* may be transient because observed reductions were based on measurements of the canopy. Neither the basal coverage of *H. comata* nor *A. cristatum* was found to change after one application of post-fire grazing. As basal cover is more resistant to change than canopy cover and is not affected by current defoliation, it may provide a more reliable indication of longer term vegetative trends (Cosgrove et al. 2001). Thus, the reductions in canopy cover indicate that these two species are susceptible to the immediate effect of post-fire grazing while the lack of change in basal cover indicates that longer-term position of these species in the community may be stable. However, previous research has indicated that repeated moderate grazing can result in ranges dominated by unselected, unpalatable species (Westoby et al. 1989). If the reductions in canopy cover of these two species likely resulted from selective grazing, declines in basal cover may result if these reductions in canopy cover are repeated. As the results of this study are indicative only of one year of grazing following fire, it is unclear what a pattern of successive burning and grazing events might have on the plant community composition, specifically with respect to basal cover.

The results of this study support the hypothesis that grazing the first growing season following fire will not affect the basal composition of the burned community. Neither litter, bare ground nor any other basal cover metric with the exception of fecal cover, differed between grazed or rested sites by the second growing season following the fire, indicating that grazing did not adversely affect the recovery of ground cover. The only observed impact, fecal cover, obviously results from the presence of animals versus the absence. While Bates et al. (2009) also found that litter had recovered similarly between grazed and ungrazed post-fire treatments, the results of this study seemingly contrast with those of Vermeire et al. (2014) which indicated that post-fire grazing depressed litter mass. However, the estimate of litter obtained through the point-intercept method indicates the frequency at which litter was encountered, providing no estimate of the thickness or density of the litter layer. While results indicate that litter provides the same amount of cover on grazed or rested sites within two growing seasons following fire, rested sites may have a thicker or denser litter layer due to the greater availability of old standing dead material. Reduced litter in prairies has been found to decrease the retention of soil moisture, indicating that depressed litter production via the removal of biomass by grazers could impact soil quality (Hulbert 1969). However, Vermeire et al. (2011) determined that a reduced litter layer following fire did not cause appreciable reductions in soil moisture when compared to nonburned sites.

By the second growing season following fire, ecological site had a greater impact on productivity, community composition on an individual species basis and basal cover composition than did grazing treatment. Gibson and Hulbert (1987) indicate that ecological site has a stronger deterministic effect on community composition than disturbance unless disturbance is severe or frequent. The results of this study suggest that fire combined with one season of post-fire grazing event does not represent a disturbance severe enough to override the effects of ecological site. Though the sandy and loamy sites tested at the Pautre fire had retained their individuality after post-fire grazing, the responses of the two sites, in most cases, were similar in direction and magnitude, indicating that though sites are unique, they can be managed similarly under post-fire grazing.

Implications

The results of this study indicate that moderate levels of post-fire grazing render few impacts on northern mixed-grass prairie vegetation, contrary to the assumptions of inevitable harm underlying the federal recommendation of post-fire rest. The observed reduction in total standing biomass, resulting from the loss of old dead vegetation, will minimally reduce desirable forage in moderately stocked pastures. The observed changes in community composition, including the reduction of *H. comata* and the concurrent reduction of C3 grasses is not unprecedented following fire or grazing nor is the shift in the C3:C4 ratio necessarily undesirable. A C3:C4 ratio closer to 1:1 can provide forage stability throughout a grazing season by ensuring that active growth of high quality forage occurs during both cool and warm seasons. Similarity of bare ground and litter between the grazed and rested treatments indicates that post-fire grazing will neither reduce subsequent-year soil moisture retention nor increase erosive potential. The limited and generally non-negative impacts of post-fire grazing provide no support for the recommendation that grazing be excluded for two growing seasons following fire in the northern mixed-grass prairie. While the results of this study are indicative of only one year of grazing, rather than annual or repeated grazing as might take place in a livestock production setting, we do have an indication that some post-fire grazing utilization will not render catastrophic results. Rather than the broadly recommended application of post-fire rest, data indicate that, in the northern mixed-grass prairie, post-burn grazing management should occur firstly on case-by-case basis, with rest applied if and when it is deemed appropriate, such as in communities dominated by caespitose grasses. Considerations should be based on historic disturbance regimes, which can provide insight as to the post-fire management regimes most appropriate for any given ecoregion, as well as the expected post-fire climatic conditions.

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Figures and Tables

Figure 2.1. The Dyson Grazing Allotment. T22N R13E Section 23, Grand River National Grasslands, SD.

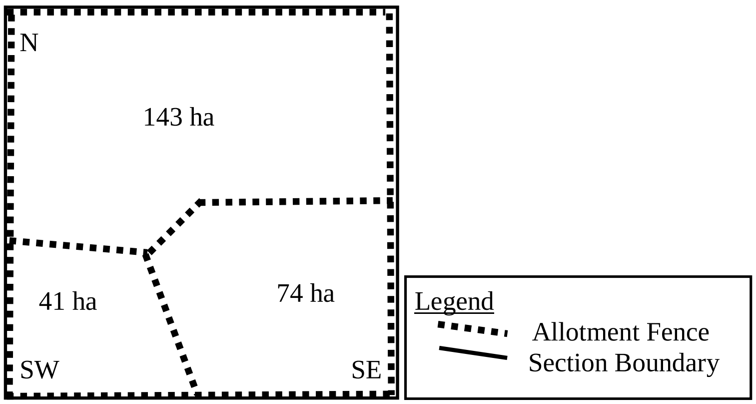

Figure 2.2. Exclosure Layout

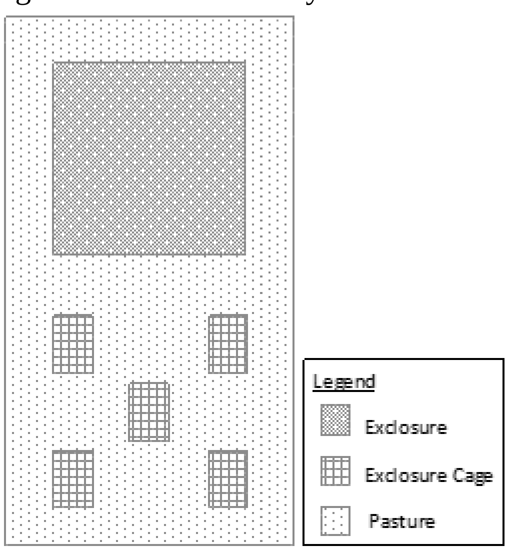

Figure 2.3. Grazing Treatment and Ecological Site Effects on Biomass. Estimates of biomass ± Std. Error of (A) grazed and rested sites and (B) sandy and loamy ecological sites.

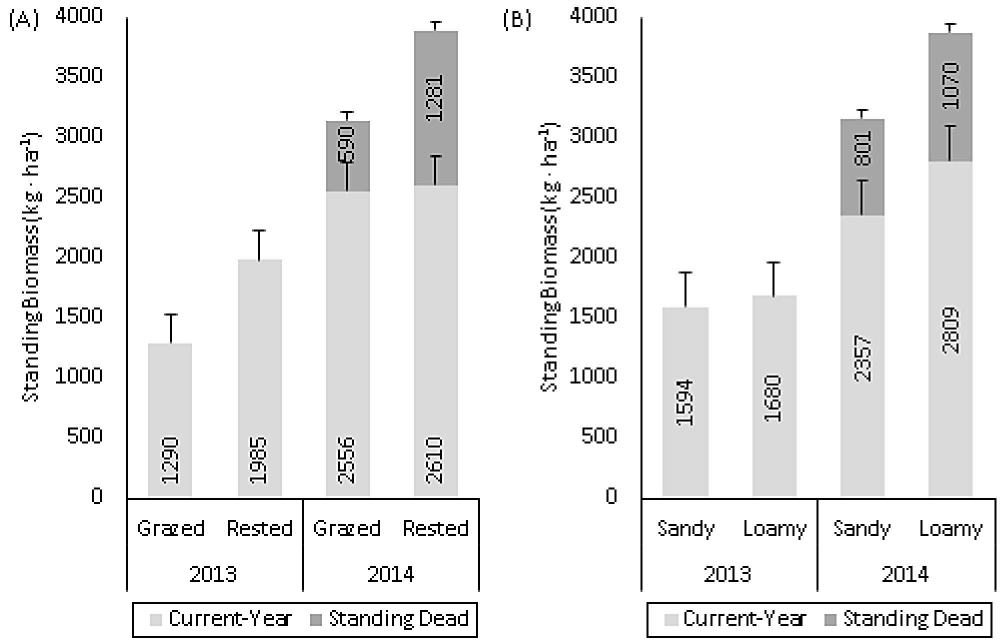

Table 2.1. Canopy Cover Composition. Estimates of community metrics ± Std. Error. % indicates percent canopy cover, spp indicates number of species, Shannon's Diversity index is indicated by unit-less values. [a,b] denote differences of $P<0.05$, [a*,b*] denote trends of $0.05<P<0.1$ and * indicates P-value for grazing treatment by ecological site interaction.

Metric	Years Rested	Ecological Site	Value	Std. Error	*P*-value
Agropyron cristatum	0	Sa	39.1% [a]	5.3	0.0268*
	2		62.6% [b]		
	0	L	1.8% [a]	5.3	
	2		1.0% [a]		
Hesperostipa comata	0		14.7%	3.1	0.0070
	2		22.2%		
Pascopyrum smithii		Sa	0.3%	4	0.0004
		L	29.7%		
Bouteloua gracilis		Sa	7.8%	4.2	0.0429
		L	17.7%		
Carex duriscula		Sa	4.4%	1.1	0.0377
		L	0.5%		
C3 grasses	0		54.9%	4.3	0.024
	2		73.1%		
C4 grasses	0		25.4%	3.5	0.0268
	2		13.9%		
Forbs	0		10.7% [a*]	2.8	0.087
	2		2.9% [b*]		
Richness	0		10 spp	1.2	0.0247
	2		8 spp		
Shannon's Diversity Index	0	Sa	1.9 [a]	0.16	0.0344*
	2		1.1 [b]		
	0	L	1.8 [a]	0.16	
	2		1.7 [a]		

Table 2.2: Basal Cover Composition. Estimates of community metrics ± Std. Error. % indicates percent cover.

Metric	Years Rested	Ecological Site	Value	Std. Error	*P*-value
Fecal	0		1.7%	0.47	0.0465
	2		0.0%		
Litter	0		20.7%	5.7	0.3205
	2		12.3%		
Bare Ground	0		30.0%	12.1	0.3194
	2		47.3%		
Agropyron cristatum		Sa	5.6%	0.91	0.0022
		L	0.0%		
Bouteloua gracilis		Sa	5.7%	7.0	0.0426
		L	25.7%		
Aristida purpurea		Sa	4.0%	1.2	0.0092
		L	0.7%		

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CHAPTER THREE

SEASON OF POST-FIRE DEFOLIATION: EFFECTS ON BIOMASS, COMMUNITY COMPOSITION AND GROUND COVER

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

Author: Emily A. Gates

Contributions: Collected and analyzed data. Wrote first draft of manuscript.

Co-Author: Lance T. Vermeire

Contributions: Conceived of and implemented study design. Collaborated on data collection and analysis. Provided feedback on manuscript drafts.

Co-Author: Clayton B. Marlow

Contributions: Provided feedback on statistical analysis and manuscript drafts.

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Contributions: Provided feedback on statistical analysis and manuscript drafts.

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SEASON OF POST-FIRE DEFOLIATION: EFFECTS ON BIOMASS, COMMUNITY COMPOSITION AND GROUND COVER IN THE NORTHERN MIXED-GRASS PRAIRIE

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Abstract

In the lexicon of North American prairie ecology, it is acknowledged that defoliation events via bison grazing consistently followed fire. Given this evolutionary fire-grazing interaction, our objective was to determine whether seasonal timing of defoliation following fire altered subsequent productivity and species composition. Following the April 2013 Pautre wildfire in the Grand River National Grasslands of South Dakota, we installed exclosures in three locations along the border of the fire. Grazing exclosures were paired across the fire line to create a "burned" and "nonburned" exclosure at each location. Four plots were demarcated in each exclosure. Three plots were defoliated via mowing to 6cm either 2, 4 or 6 months following the fire with the fourth maintained as a control. Productivity and species composition data were collected in November 2013, June 2014, August 2014 and July 2015. Fire increased productivity 38% during the 2013 growing season following the fire (P=0.0330). During the 2014 growing season, there was a tendency for burned sites to maintain greater production (P=0.0832). June defoliation resulted in the greatest current-year productivity regardless of fire treatment, while all other treatments resulted in similar productivity (P=0.0299).

Fire and defoliation effects were undetectable in 2015. Community composition was not affected by fire in 2013. *Melilotus officinalis* was increased by spring defoliation in 2015 (P=0.0488) and by fire in 2015 (P=0.0162). Litter was initially reduced by fire, but recovered to nonburned levels by 2015. Initial results suggest that fire effects on productivity are limited to the first growing season following fire whereas defoliation effects manifest the second growing season following fire. Additionally, both fire and timing of defoliation will disparately affect community composition.

Introduction

Current federal post-fire land management recommendations decouple two natural disturbances that, in the prairies of North America, were historically linked. Federal recommendations state that grazing be deferred following fire, preferably for two growing seasons (Blaisdell et al. 1982; Bureau of Land Management 2007). If grazing does occur the first growing season following fire, the recommended approach is to defer grazing until after seed set, when vegetation has completed active growth and dormancy is imminent. However, during the evolution of the Great Plains ecoregion, evidence suggests that fire and grazing were intimately linked, with fire determining where grazing was likely to take place and vice versa (Fuhlendorf and Engle 2001). Scholars, such as Fuhlendorf et al. (2009), suggest that these coupled disturbances be considered one perturbation: pyric herbivory. Evidence suggest that pyric herbivory may be an obligate ecological process, as more native conditions have been obtained when fire and grazing are applied in sequence rather than separately (Vinton et al. 1993). Given this close interaction, deferral of grazing following fire may be unnecessary or disadvantageous.

Grazers are attracted to the relatively high quality forage that grows following fire (Vinton et al. 1993; Knapp et al. 1999; Fuhlendorf and Engle 2001; Vermeire et al. 2004). The degree to which forage quality is increased is likely largest soon after the resumption of growth (Hilmon and Hughes 1965; McPherson et al. 1995). Thus, grazers are likely most attracted to regrowth shortly following fire, with no natural deferment period. Foraging focuses on these areas until the level forage quality diminishes relative to adjacent nonburned areas (Fuhlendorf et al. 2009), suggesting that northern mixed-grass prairie is well adapted to withstand fire as well as one or more defoliation events immediately following fire.

The federal agencies base the recommendation for two years of rest on several assumptions. First, this recommendation assumes that the vigor of plants will be lessened by fire, rendering the remaining tissues less able to withstand subsequent damage via defoliation. This seem to follow the findings of Bunting et al. (1998), Jirik and Bunting (1998) and Bailey and Anderson (1978) who recommend that 1-3 years of rest from defoliation following fire may be needed to avoid additive mortality in the bunchgrasses *Pseudoroegneria spicata* (Pursh) Á. Löve and/ or *Festuca idahoensis* Elmer in the Great Basin. Second, this recommendation assumes that establishment of new plants via seed will constitute an important facet of recovery. If mature plants experience mortality directly from fire, they will need to be replaced by the recruitment of new individuals, possibly via the production and germination of seed. Third, this recommendation assumes that if defoliation must occur the first growing season following fire, it should be deferred until after seed set and the cessation of active growth. This implies that the removal of actively growing tissue should be considered more detrimental post-fire than the removal of senesced or dormant. This recommendation again comes from observations of bunchgrasses *P. spicata* and *Festuca campestris* Rydb. made by Mclean and Wikeem (1985a; 1985b). Fourth and Lastly, this recommendation seeks to protect soil stability and health by providing a protected interval in which litter can recover and lessen erosion as heavy intensity grazing has been implicated in reducing standing and fallen litter and increasing bare ground (Naeth et al. 1991). However, these assumptions are in disagreement with many of the ecological observations in North American prairies.

Few, if any of dominant native prairie grasses actually experience mortality following fire (Brockway et al. 2002; Haile 2011). Additionally, surviving plants are often more productive (White and Currie 1983) and of higher forage quality than nonburned counterparts (Hobbs and Spowart 1984). As few plants experience mortality following fire, there is little need for replacement of lost plants in the recovery process. For example, 99% of community recovery in tallgrass prairie has been attributed to tillering of surviving plants, rather than being dependent upon the establishment of new seedlings (Benson and Hartnett 2006). Thus, rest designed to protect seedlings may not be necessary if seedlings contribute so little to population recovery. Lastly, litter is inarguably removed or reduced by fire, potentially increasing erosion potential (Benkobi et al. 1993) and degrading soil conditions (Hulbert 1969). In contrast, Bates et al. (2009) indicate that post-fire grazing did not impede recovery of litter frequency and, thus, did not prolong the risk of erosion or degraded soil quality on burned, grazed sites compared to burned, rested sites. Moreover, even though litter is temporarily decreased by fire, Vermeire et al. (2011) indicate comparable soil moisture retention between burned and nonburned sites, indicating that the benefits gained from litter may be regained even before litter recovers to pre-burn levels.

Due to these ecological realities in the northern mixed-grass prairie, this ecoregion should be well adapted to withstand grazing the first growing season following a fire. However, post-fire grazing effects may depend not only on whether or not defoliation occurs following a fire, but also on the time of the year during which grazing takes place. Grazing systems are designed to control the season, intensity and frequency of defoliation to minimize the effects of grazing on a plant community (Briske et al. 2011). The season of defoliation, in particular, will determine whether actively growing or senesced tissue is removed as resources and nutrients are allocated to active plant tissues for growth and maintenance (Briske 1991). As such, the removal of actively growing tissue may weaken a plant's potential productivity by depleting reserves (McLean and Wikeem 1985a; Mclean and Wikeem 1985b). Alternatively, a plant may respond with increased productivity via compensatory growth, in which losses are recovered through regrowth and subsequent sequestration and replacement of lost resources (McNaughton 1983). In contrast, removal of senesced tissue during the dormant season will have essentially no effect, as these tissues are no longer physiologically active nor tied to the remaining, live portion of the plant (McLean and Wikeem 1985a; Mclean and Wikeem 1985b; Briske 1991). Given the general lack of information on the effects of immediate defoliation following fire, it is unclear if defoliation in one season post-fire should be considered more detrimental than another. This knowledge gap must be filled if post-fire grazing without a two-year rest period is to be considered a viable management strategy.

Based on the available literature, we hypothesized that fire would increase current year productivity (White and Currie 1983). Concurrently, we hypothesized that post-fire defoliation would not negatively impact subsequent-year productivity, nor would it negatively impact subsequent-year community composition (Bates et al. 2009; Vermeire et al. 2014). Additionally, we hypothesized that season of defoliation during the first post-fire growing season would not affect subsequent-year productivity or community composition. Finally, we hypothesized that while litter would initially be reduced by fire, season of defoliation will not impact the rate of recovery. We expected recovery of the litter layer to occur within two years (Bates et al. 2009).

Methods

Wildfire & Study Sites

The Pautre fire occurred on 3 April 2013, approximately 12 km northeast of Lodgepole, SD (45° 52' 54" N 102° 32' 52" W), with total containment declared on 7 April 2013, burning a total of 4322 ha of Grand River National Grassland, Grand River Grazing Co-op and private lands (Figure 3.1 A). Study sites were selected from the burned portion of the Grand River National Grassland. Three sites were selected along the perimeter of the wildfire in order to span the north-south gradient of the burn, with one site located in the "3B" pasture and two sites at the northern and southern ends of the "4B" pasture (N4B and S4B, respectively) (Figure 3.1B).

Dominant soil types in the area include Reeder-Lantry loams (Fine-loamy, mixed, superactive, frigid Typic Argiustolls and Fine-silty, mixed, superactive, calcareous, frigid Typic Ustorthents; 2-9% slopes), Amor-Cabba loams (Fine-loamy, mixed, superactive, frigid Typic Haplustolls and Loamy, mixed, superactive, calcareous, frigid, shallow Typic Ustorthents; 6-15% slopes) and the Vebar-Chogen complex (Coarse-loamy, mixed, superactive, frigid Typic Haplustolls and Loamy, mixed, superactive, calcareous, frigid, shallow Typic Ustorthents; 6-25% slopes) (Soil Survey Staff USDA-NRCS 2008; Web Soil Survey 2015).

The three sites captured the wide range of community compositions possible in the northern mixed-grass prairie. The 3B pasture was dominated by the introduced, cool-season (C3) grass *Agropyron cristatum* (L.) Gaertn. with lesser components of the native, C3 grass *Hesperostipa comata* (Trin. & Rupr.) Barkworth and warm-season (C4) grass *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths. The N4B and S4B pastures contained dominant components of C3 native grasses *H. comata*, *Pascopyrum smithii* (Rydb.) Á. Löve, *Koeleria macrantha* (Ledeb.) Schult. and *Nassella viridula* (Trin.) Barkworth. The N4B pasture had a notable constituent of the introduced C3 grass *Poa compressa* L. Common forbs across all pastures included natives *Grindelia squarrosa* (Pursh) Dunal, *Ratibida columnifera* (Nutt.) Wooton & Standl., *Plantago patagonica* Jacq., and the invasive *Melilotus officinalis* (L.) Lam. The only shrubs encountered, *Artemisia frigida* Willd. and *Symphoricarpos albus* (L.) S.F. Blake, were rare.

Precipitation averages 413 mm in Lodgepole, SD and 453 mm in Lemmon, SD (approximately 31 km northeast of the study location) with most occurring from April to September (National Climate Data Center 2015). During the study period from 2013-2015, precipitation ranged from above to below average. In 2013 precipitation was 710 and 863 mm (190 and 172% of average), 474 and 457 mm (101 and 114% of average) in 2014 and 259 and 327 mm (72 and 63% of average) during 2015 in Lodgepole and Lemmon, respectively.

Defoliation Treatments

Following the wildfire, two 15 x 15 m exclosures were erected at each of the 3B, N4B and S4B study sites, with one exclosure located on each of the burned and nonburned sides of the fire perimeter (Figure 3.2). Within each exclosure, four plots of equal area were delineated. Three of the four plots were defoliated via mowing to 6 cm in either June, August or November 2013 (referred to hereafter as spring (Spr), summer (Sum) or fall (Fall) defoliation, respectively). The fourth plot in each exclosure was maintained as a nondefoliated control (Con). The fifth, smaller plot, was used in a companion study. Mowed clippings were removed from the exclosures and disposed of away from the study sites. Mowing was used as a proxy for defoliation by grazing and would most closely mimic a severe or heavy defoliation event in which use was uniform and selectivity minimal.

Sampling

In November 2013, biomass, community composition and basal cover were sampled in the burned and nonburned control plots only. Biomass was determined by clipping Eight 0.1 m^2 quadrats from each plot and drying the samples at 60˚C until no additional loss in weight was detected. Canopy and basal cover composition were measured via the point-intercept method (Caratti 2006). Observations were made along a 10 m transect at 20 cm intervals for a total of fifty observations. Canopy and basal observations were delineated at each point. Canopy composition and basal coverage were measured in all plots in June 2014, August 2014, and July 2015. Biomass was measured in all plots in August 2014 and July 2015.

Statistical Analysis

Where outlier values were suspected, they were identified using the Generalized Extreme Studentized Deviate test and removed from further analysis. The SAS mixed procedure was used to perform analysis of variance (ANOVA) in order to test for fixed effects as well as interactions between fixed effects across the factorial of defoliation and fire treatments (Littell et al. 2006). Plot was the experimental unit. Defoliation treatment and fire treatment were used as fixed effects. Pasture was included as a random-effect, stratifying the comparisons within each set of paired exclosures. Response variables for the mixed linear models included total standing biomass, old standing dead, current-year productivity, species richness, Shannon's diversity index (calculated using canopy frequency "hits" from the line-intercept transect), community composition by species and functional group (functional group here refers to plants with similar life strategies; groups used were cool season (C3) grasses, warm season (C4) grasses, annual grasses, sedges, shrubs and forbs) and basal cover composition. Raw frequency data were used to confirm that any observed shifts in composition were due to shifts in actual as opposed to relative abundance. Changes in composition due only to relative abundance will be mentioned, but reported in terms of actual abundance only. An $\alpha < 0.05$ was used to identify significant differences while an $0.05 < \alpha < 0.1$ was used to identify “trends” or “tendencies”. The PDIFF option of SAS was used to perform mean separations when defoliation and fire interacted in their effects.

Canopy cover estimates were used to present community composition assessments by functional group. Effects on individual species are presented only if a difference or trend was observed with respect to main effects or interactions. Basal cover estimates of litter and bare ground will be presented regardless of significance, whereas basal cover of individual species will be presented only if a difference or trend in main effects or interactions is observed. If no interaction is explicitly stated, discussion pertains to the main effect of fire across all defoliation treatments or the main effect of defoliation across burned and nonburned treatments. A list of species observed can be found in Appendix A while a summary of the ANOVA F-tests pertaining to main effects of defoliation, fire and interactions between fire and defoliation can be found in Appendix B.

Results

Biomass

Fire Effects. Standing biomass was reduced on burned sites by 25% in 2013, the first growing season following the fire (Figure 3.3). This reduction can be attributed to the total removal of old standing dead from the burned sites. Current-year production, in contrast, increased by 38% on burned sites. By 2014, two growing seasons after fire, a trend toward an increase of 10% in current-year production remained while old standing dead and standing biomass were similar between burned and nonburned sites. In 2015, three growing seasons post-fire, current-year production and standing biomass were similar between burned and nonburned sites.

Defoliation Effects. In 2014, control plots and spring defoliated plots, while similar to one another, contained an average of 19% greater standing biomass than both summer and fall defoliated plots (Figure 3.4). Control, summer defoliated and fall defoliated plots yielded similar current-year production while spring defoliated plots contained an average of 18% greater current-year production than all other treatments. Control plots contained an average 40% more old standing dead than any defoliated plots. By 2015, current-year production and standing biomass were similar across all treatments. Fire and defoliation interacted in their effects on old standing dead in 2015 (Figure 3.5). Nonburned-spring defoliated plots contained 24-47% more standing dead than all other treatments with the exception of burned-summer defoliated plots. Burned-summer defoliated plots contained 7-35% greater old standing dead than the remaining treatments. Burned-fall and spring defoliated plots, and nonburned-summer and fall defoliated plots, and nonburned nondefoliated plots all contained similar old standing dead. While similar to all other treatments, burned-nondefoliated plots contained less standing dead than nonburned-spring defoliated, burned-summer and fall defoliated plots.

Community Composition

Fire Effects. A total of 43 species were observed across the three study sites, 35 of which were native. Species richness and Shannon's diversity index were unaffected by fire in 2013, 2014 and 2015 (4.3 vs 5.6 species, 11.7 vs 11.8 species and 8.3 vs 8.0 species; P= 0.4557, 0.8869, 0.7759 and 1.1 vs 0.7, 1.7 vs 1.7 and 1.4 vs 1.4; P= 0.2801, 0.7516, 0.9803, respectively). In 2013, no differences in composition on the basis of individual species or functional groups were observed (Figure 3.6 & Table 3.1). In 2014, no shifts in composition with respect to functional groups were observed. *Sphaeralcea coccinea* (Nutt.) Rydb. was more abundant on nonburned sites in 2014. In 2015 an apparent reduction in C3 grass cover and an increase in forb cover on burned sites was observed. However, the apparent reduction in C3 grasses was attributable to a shift in relative rather than actual abundance, with actual abundance remaining similar. *K. macrantha* was greater on nonburned sites while *A. frigida* and *Asclepias incarnata* trended toward greater abundance on nonburned sites. *M. officinalis* was more abundant on burned than nonburned sites.

Defoliation Effects. Species richness in 2014 had a tendency to be higher in fall defoliation plots when compared to spring defoliated plots, but was similar across all other comparisons of defoliation treatments (11 species in spring defoliated plots vs 11, 11, and 13 species in control, spring and fall defoliated plots, respectively; *P*=0.0878). Richness was similar across all defoliation treatments in 2015 (8 species in all treatments; *P*=0.9429). Shannon's diversity index was greater in summer and fall defoliated plots when compared to the control in 2014 (1.5, 1.7, 1.8 and 1.9 in the control, spring, summer and fall defoliated plots, respectively; *P*= 0.0253) but was similar across all defoliation treatments in 2015 (1.3, 1.3, 1.5 and 1.6 in the control, spring, summer and fall defoliated plots, respectively; *P*= 0.4973). In 2014, no differences across defoliation treatments was observed in C3 grasses, C4 grasses, annual grasses, sedges or shrubs (Figure 3.7). A trend toward increased forbs in spring defoliated plots was apparent. This trend is primarily attributable to the large, 14% average increase of *M. officinalis* in spring defoliated plots when compared to all other treatments (Table 3.1). *K. macrantha* was also slightly increased in summer defoliated plots when compared to control and spring defoliated plots. In 2015, no effects of defoliation treatments were observed with respect to either functional group or individual species.

Basal Cover

Fire Effects. Litter was completely eliminated by fire and bare ground increased by 54% when compared to nonburned sites in 2013 (Figure 3.8). No differences in other basal cover components were observed. In 2014, litter on burned sites was 15% less while bare ground was 11.3% greater. By 2015, litter and bare ground were similar between burned and nonburned sites. *B. gracilis* and fecal material provided greater cover on nonburned sites in 2014 (Table 3.2). Basal cover of *M. officinalis* was 4% greater on burned sites in 2015.

Defoliation Effects. Summer defoliation decreased litter abundance by 27% when compared to spring and fall defoliation, but remained similar to control plots. Bare ground was similar among all treatments, averaging 17%. *K. macrantha* trended toward greater basal cover in summer defoliated plots when compared to the control while *N. viridula* trended toward greater abundance in control and fall defoliated plots (Table 3.2). The sedge *Carex duriuscula* C.A. Mey. was more abundant in summer defoliated than nondefoliated and fall defoliated plots.

Discussion

The lack of compounding, interacting effects caused by both fire and defoliation should alleviate the concern that defoliation following fire, especially during active growth, will exacerbate any negative effects of fire. Most observed effects could be attributed to fire or defoliation independently. In the only case of fire by defoliation interaction, old standing dead in 2015, all combinations of burned and defoliated treatments either out produced or were similar to the burned and nonburned nondefoliated controls. This suggests that post-fire defoliation does not produce negative effects at the community level when compared to sites that have been rested. Vermeire et al. (2014) in the mixed-grass prairie and Bates et al. (2009) in the sagebrush steppe similarly reported that sites grazed post-fire recovered similarly to rested sites, indicating that, at least in these systems, two years of rest following fire may be unnecessary.

The hypothesis that burning increases current-year productivity and does not negatively impact subsequent-year productivity is supported by the data. While more modest increases in productivity might be expected, the 38% increase in current-year productivity the first growing season following fire is not unprecedented in the literature. In the mixed-grass prairie, White and Currie (1983) observed a 10-15% increase in the productivity of spring burned *Carex filifolia* Nutt. when compared to nonburned controls while *B. gracilis* production increased by 40%. In pine savanna herbaceous understory, Harris and Covington (1983) observed increases in herbage yield following fire, ranging in magnitude from 10-55%. The increase following the Pautre fire likely stems from the removal of litter and standing dead material. If the nonburned sites are representative of the conditions prior to fire, this area had approximately 1400 $kg \cdot ha^{-1}$ of old, standing dead material at the time of the fire, or 48% of the standing biomass and 40% litter basal cover. While modest amounts of old standing dead material and litter have beneficial effects on soil retention, quality and moisture (Hulbert 1969; Benkobi et al. 1993), over accumulation can lead to depressed production by immobilizing valuable nutrients, decreasing light availability and decreasing soil moisture via interception (Knapp and Seastedt 1986; Facelli and Pickett 1991). In a Kansas prairie, Hulbert (1969) found that removal of litter had the potential to double productivity. The increased productivity on burned sites in the Pautre fire was short lived, with the degree of increased productivity diminishing the second growing season following fire and disappearing by the third. This is likely due to the relatively rapid recovery of litter and old standing dead material on the burned sites resulting in inhibition of growth. However, defoliation pressure was applied only in one of the three study years following fire on the burned and nonburned sites. Had defoliation been applied seasonally in the other two years on the burned sites, such as might occur under a livestock grazing system, fire effects on productivity may have been extended. Annual removal of biomass, via mowing or grazing, has the potential to curb or slow the resurgence of standing dead and litter following fire, potentially elongating the period in which productivity is less inhibited by litter and standing dead.

Defoliation had a more modest and shorter lived but relatively positive effect on productivity. Spring defoliation, the only treatment to substantially influence productivity in comparison to the control, resulted in a 19% increase observable during only the 2014 growing season. This boost in productivity is similar to the “overcompensation” via compensatory growth observed by Oesterheld and McNaughton (1991) when plants were stressed prior to defoliation and had an adequate growth period in which to recover biomass. The increase in *M. officinalis* in spring defoliated plots could also have contributed to the increase in productivity. Importantly, no defoliation treatment resulted in production less than the controls on either burned or nonburned sites in 2014 or 2015. This indicates that not only is rest from defoliation for two growing seasons to protect future vigor following fire unnecessary when that defoliation is relatively uniform, but deferral from grazing until after seed-set the first growing season following fire is also not required. Grazing might be applied as early as two months following a spring wildfire in the northern mixed-grass prairie with no deleterious effects on subsequent-year productivity if that grazing is managed toward equivalent animal densities, time spent in pastures and use of all species.

Community composition with respect to functional groups, remained relatively stable throughout the study period, lending some support to the hypothesis that neither fire nor defoliation will negatively impact the plant community as a whole. However, a few minor or introduced components of the community did respond to either fire or defoliation, indicating that staticity should not be expected. The cover of C3 grasses, which make up a majority of the community, C4 grasses, annual grasses and sedges remained unaffected by fire or defoliation throughout the study period. A trend toward increased forbs in spring defoliated plots in 2014 and an increase in burned plots in 2015 can be attributed to the invasive forb, *M. officinalis*. In comparison, native species exhibited few responses. Of the thirty-five native species observed, only eight (*K. macrantha*, *N. viridula*, *C. duriuscula*, and *B. gracilis* in 2014 and *A. frigida*, *A. incarnata*, and *D. pinnata* in 2015) responded to either fire or defoliation. Neither richness, nor Shannon's diversity index were affected by fire during the study period. Defoliation resulted in richness that was similar to or greater than nondefoliated plots. These results indicate that while non-native and minor components of the community can be temporarily affected by fire or defoliation, the community as a whole remains relatively stable with no negative effects on richness or diversity. As diversity is considered an indicator of ecosystem health (Chapin III et al. 2000; Folke et al. 2004), the maintenance or increases in diversity observed here in response to fire and defoliation indicate that the northern mixed-grass prairie is well adapted to these disturbances at the community level.

A. frigida, one of only two shrubs observed, was reduced by fire in 2015, causing the concurrent trend toward reduced shrubs. The removal of woody plants is an expected effect of fire as is the lag in recovery of shrubs when compared to herbaceous community components (Beck et al. 2009). Reductions in *A. frigida* have been reported following heavy, season-long grazing as well, indicating that post-fire grazing may further prolong recovery of this particular species (Jinhua et al. 2005).

K. macrantha, the only native C3 grass responding to defoliation treatment in canopy measurements, was similar to or greater than the control in all defoliation treatments. Correspondingly, in an Alberta, Canada prairie, *K. macrantha* increased in response to light, rotational grazing (Smoliak 1965). This increase in *K. macrantha* was corroborated by basal cover estimates, suggesting that the trend toward increased basal cover under the respective treatments may be persistent. Basal cover is a resistant measure, more indicative of long-term change than canopy measurements (Cosgrove et al. 2001). As such, these basal cover dynamics suggest that *K. macrantha* increased not only in foliage, but in either diameter or number of bunches as well. *K. macrantha* is a palatable native forage, making this a desirable shift. The native sedge, *C. duriuscula*, was similarly equivalent to or greater than the control under all seasons of defoliation. *C. duriuscula* may be a palatable early season forage like its relative, *C. filifolia* (White and Currie 1983), and, as a rhizomatous species, provides soil stability (Morgan and Rickson 2003).

N. viridula, another palatable, native C3 grass, trended toward decreased basal cover in response to defoliation during summer, when compared to control and fall defoliation in 2014. *N. viridula* has been documented to decrease under grazing pressure, particularly when defoliation is severe or applied during the growing season, as it was in this case (Reed and Peterson 1961). Though decreases in *N. viridula* by any defoliation when compared to rest may be expected, decreases in this desirable, climax species can be minimized by application of light to moderate defoliation, which, at high animal densities, may be accomplished in a matter of days.

B. gracilis, the only native C4 species observed to respond to fire, trended toward depressed basal cover on burned site in 2014. This is in contrast to expectations, as *B. gracilis* is generally reported as favored or unaffected by dormant season fire (Ford 1999). However, some studies have observed temporary reductions, lasting one or two years post-fire, attributed to decreased tillering (Launchbaugh 1964; Whisenant and Uresk 1989). As this tendency toward reduced basal cover on burned sites was not observed in either 2013 nor 2015, we suspect the status of *B. gracilis* following fire is not at risk.

Native forbs, generally expected to increase following a dormant season fire (Biondini et al. 1989) both decreased (*S. coccinea* in 2014 and *A. incarnata* trend in 2015) and increased (*D. pinnata* trend in 2015), following fire. However, the increase in forbs reported by Biondini et al. (1989) occurred after repeated dormant season fires. As these data represent the effects of only one spring wildfire, the disturbance may not have been severe or frequent enough to produce a clear trend in the dynamics of the forb community. The slight shifts observed may be due to the temporary shift from competition for above ground resources, light, to competition for belowground resources caused by the removal of vegetation by the fire. Defoliation, contrastingly, had no effect on native forbs. This contrasts with the findings of Mueggler (1967), who found that defoliation in mountain grasslands resulted in an overall negative effect on forbs. This disparity may stem from the more extensive history of grazing in prairies when compared to mountain grasslands, indicating that prairie forbs should, in fact, withstand defoliation better.

As a biennial species, the increases in *M. officinalis* due to spring defoliation in 2014 and fire in 2015 can be attributed to factors that either enhanced germination or seedling establishment in the year prior to flowering. *M. officinalis* emergence peaks in March and April (Van Assche et al. 2003). Seedlings emerging during this period on nonburned sites or in mid-late April following the fire on burned sites in 2013 would be released from light competition via the removal of the overstory vegetation. This increased light availability may have allowed for more seedlings to establish, over-winter and flower in 2014. Fire effects were possibly delayed to 2015 if germination was enhanced by a combination of factors rather than by fire alone. Germination may have been enhanced through heat treatment via fire (Kline 1984; Van Assche et al. 2003) but also by subsequent cold stratification during the 2013-2014 winter (Martin 1945). This combined effect may have succeeded in breaking the coats of hard seed, allowing high germination success in 2014 and flowering in 2015 (Van Assche et al. 2003). Due to its biennial nature, without another fire, severe defoliation or alternative germination enhancing event, the surges in *M. officinalis* should be short-lived.

The large increases in *M. officinalis* can be considered a negative impact on the plant community not only because strong competition for light is imposed on native plants, but also due to the potential toxicity to livestock. Coumarin, the blood thinning agent responsible for “sweet clover disease” has been deemed unsafe for cows about to give birth (Radostits et al. 1980) and calves less than two weeks old (Fraser and Nelson 1959). Molded *M. officinalis* poses the greatest toxic threat, grazing of old, standing dead *M. officinalis* stems or fallen litter during a moist fall or spring may pose the greatest danger in a rangeland setting. As such, in areas invaded by *M. officinalis*, prior planning may be needed to provide alternative pasture, nonburned and rested from severe defoliation, for calving females or calves less than two weeks old during the second and third growing seasons following a severe defoliation or fire event.

Litter, identified as a moderator of soil moisture, temperature, (Hulbert 1969) and erosive potential (Benkobi et al. 1993) was eliminated by fire in 2013, reduced compared to nonburned plots in 2014 and comparable across burned and nonburned sites by 2015. Bare ground displayed the inverse dynamics. Summer defoliation, the only defoliation treatment to impact litter, slightly depressed cover in 2014 while litter was, again, comparable across all defoliation treatments by 2015. This indicates that, given adequate moisture, full litter recovery can be expected within three growing seasons following fire regardless of defoliation the first growing season following the fire. Neither the chance of degraded soil conditions nor increased erosive potential are greatly exacerbated following fire by the application of post-fire defoliation at any point during the first growing season. This agrees with the results of Bates et al. (2009) in the sagebrush steppe, reporting that litter cover accumulated similarly following fire under grazing or rest but seems to disagree with the results of Vermeire et al. (2014) who report that 50% post-fire utilization will result in depressed litter biomass two years following fire. These results may not be incompatible, as a thinner or less dense litter layer may cover a similar area of the soil surface. Benefits of litter cover may be recovered by the second growing season following fire even if litter cover or mass is reduced, as was observed in burned and summer defoliated plots, as Vermeire et al. (2011) indicate that a reduced litter layer on burned sites will provide soil moisture retention comparable to nonburned sites. Vermeire et al. (2014) further indicate that post-fire utilization of 17-34% will result in similar litter recovery across burned sites that are grazed or rested. As such, swifter litter recovery can be encouraged following fire by application of lighter defoliation or grazing pressures than those employed in this study.

The defoliation via mowing used in this study is more indicative of a short-duration, high-intensity grazing event rather than the more typical moderate use employed by producers and federal managers. Moderate grazing, in contrast to mowing or high-intensity grazing, allows for selectivity, imposing competition on palatable grazed plants from the less palatable plants left ungrazed (Mueggler 1972). The results of this study are also not indicative of repeated or annual defoliation as would more likely occur in a livestock production type setting. Regardless, the results presented here represent an important first step toward evaluative the effects of post-fire grazing at all season within the first growing season following fire.

Implications

In no case did defoliation at any time during the first growing season following the Pautre fire depress productivity in comparison to the control. Additionally, in only one case, *N. viridula* basal cover, was a trend toward decreased cover due to defoliation observed. These observations indicate that exclusion of defoliation for two growing seasons following fire may benefit minor species, but is not necessary for the community as a whole. Additionally, defoliation need not be deferred until after seed set the first growing season following the fire. While a small number of minor, native species increased or decreased in response to fire or defoliation, the magnitude of the effects was small. With the exception of dynamics driven by *M. officinalis*, the community composition with respect to functional group remained relatively similar across fire and defoliation treatments throughout the study period. While litter initially decreased and bare ground increased due to fire, both were comparable to nonburned sites within three growing seasons following the fire, regardless of defoliation treatment. These results indicate that native, northern mixed-grass prairie is resilient to spring wildfire and resistant to post-fire defoliation between late spring and early fall during the first post-fire growing season. As such, less emphasis on post-fire rest may be appropriate in this system. However, the large scale dynamics driven by *M. officinalis* are a reminder that while the native vegetation of this system may be well adapted to and respond neutrally or positively to fire and post-fire defoliation, the presence of prolific, invasive species can add a confounding, potentially undesirable dynamic to a system's response. Additionally, the results of this study are based on only one application of post-fire grazing. As the effects of repeated grazing following fire were not quantified, prudent grazing management, including the incorporation of deferral or rest on a regular basis, as well as persistent monitoring to maintain sensitive species such as *N. viridula* may be advisable.

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Figures and Tables

Figure 3.1. Locations of (A) the Pautre wildfire and (B) the 3B, N4B and S4B study sites. Data: USGS and ESRI. Map Authors: Narciso Garcia-Neto and Emily Gates.

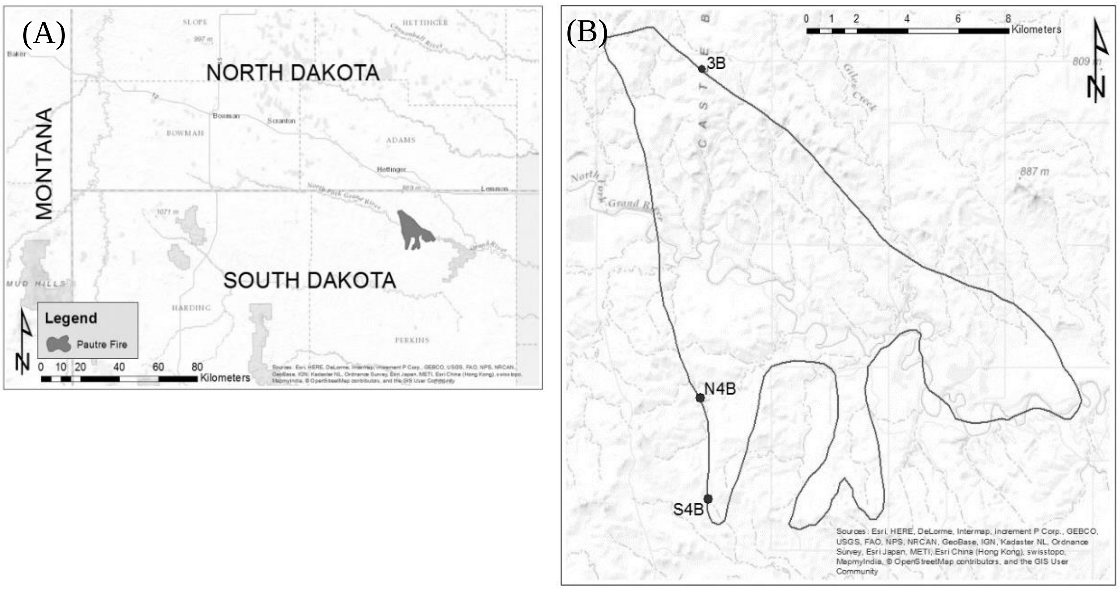

Figure 3.2. Exclosure and Plot Design.

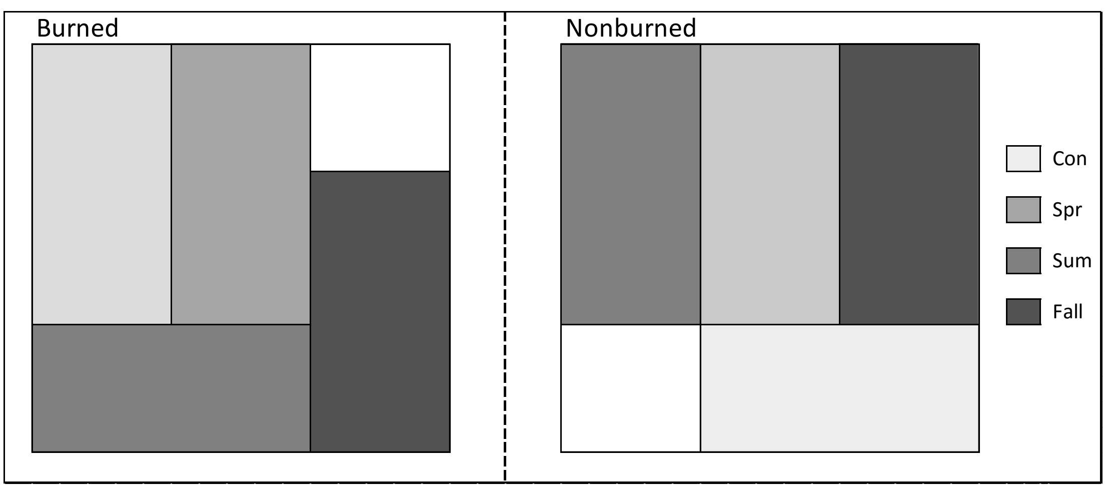

Figure 3.3. Fire Effects on Biomass. Estimates of biomass ± Std. Error of burned and unburned plots across defoliation treatments. [a,b] denote differences of $P<0.05$. [a*,b*] denote differences of $0.05<P<0.1$.

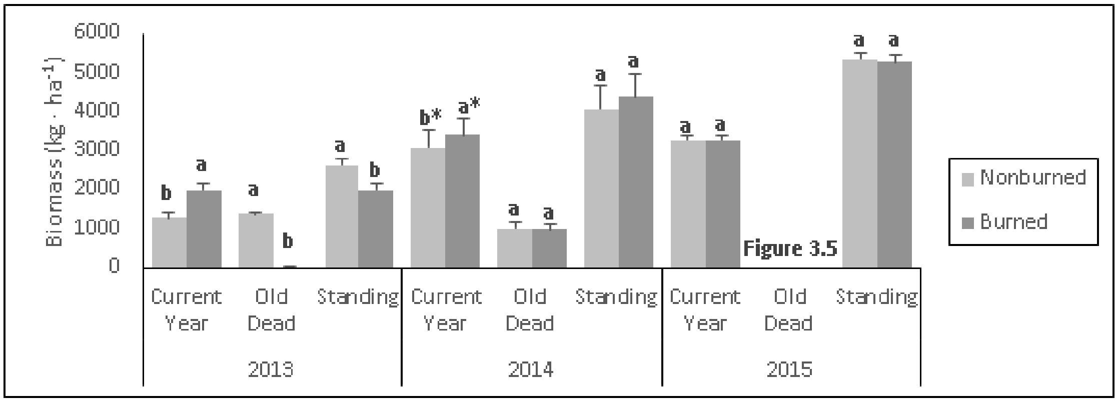

Figure 3.4. Defoliation Effects on Biomass. Estimates of biomass ± Std. Error of spring (Spr), summer (Sum) and Fall defoliated plots and nondefoliated (Con) plots across fire treatments. [a,b] denote differences of $P<0.05$.

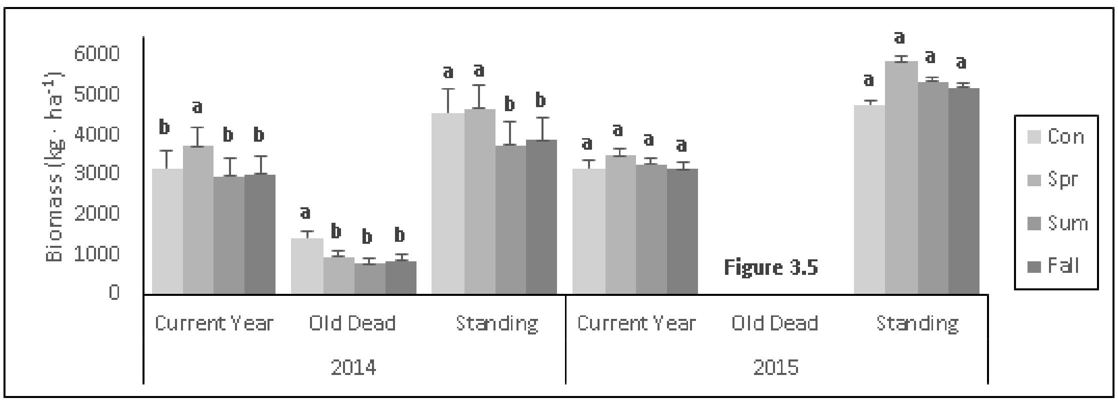

Figure 3.5. 2015 Fire x Defoliation Interaction. Effects on Old Dead. Estimates of biomass ± Std. Error of burned (B) and nonburned (NB) and spring (Spr), summer (Sum) and Fall defoliated plots and nondefoliated (Con) plots. [a,b] denote differences of $P<0.05$.

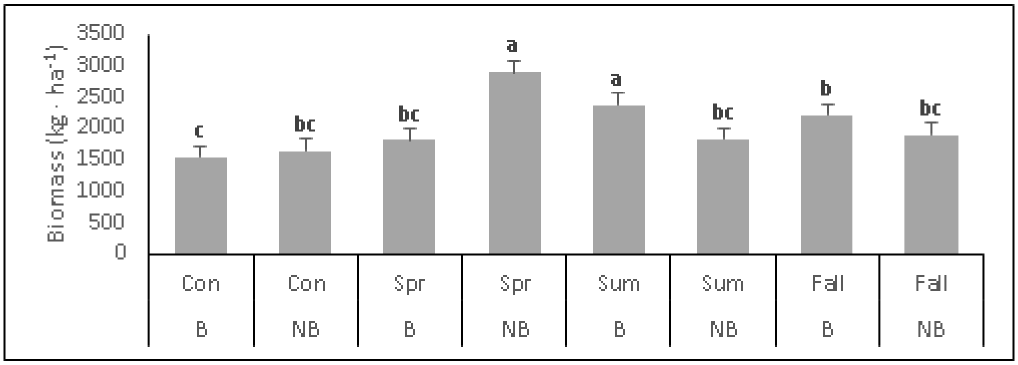

Figure 3.6. Fire Effects on Canopy Community Composition by Functional Group. Estimates of cover ± Std. Error of cool season grasses (C3), warm season grasses (C4), annual grasses, sedges, shrubs and forbs in burned and nonburned plots across defoliation treatments. [a,b] denote differences of $P<0.05$ while [a*,b*] denote trends of $0.05<P<0.1$.

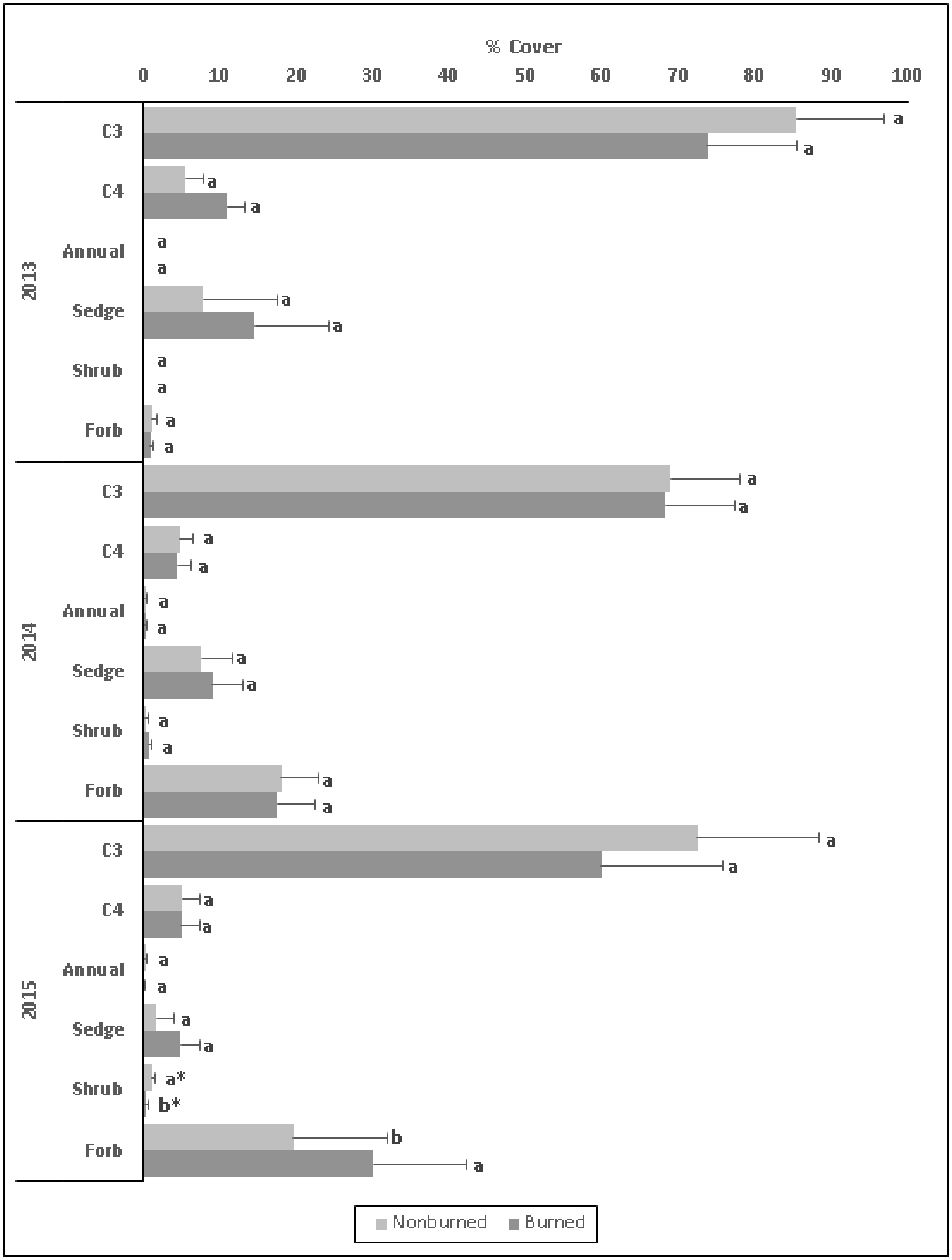

Figure 3.7. Defoliation Effects on Canopy Community Composition by Functional Group. Estimates of cover ± Std. Error of cool season grasses (C3), warm season grasses (C4), annual grasses, sedges, shrubs and forbs in spring (Spr), summer (Sum) and Fall defoliated plots and nondefoliated (Con) plots. [a,b] denote differences of $P<0.05$ while [a*,b*] denote trends of $0.05<P<0.1$.

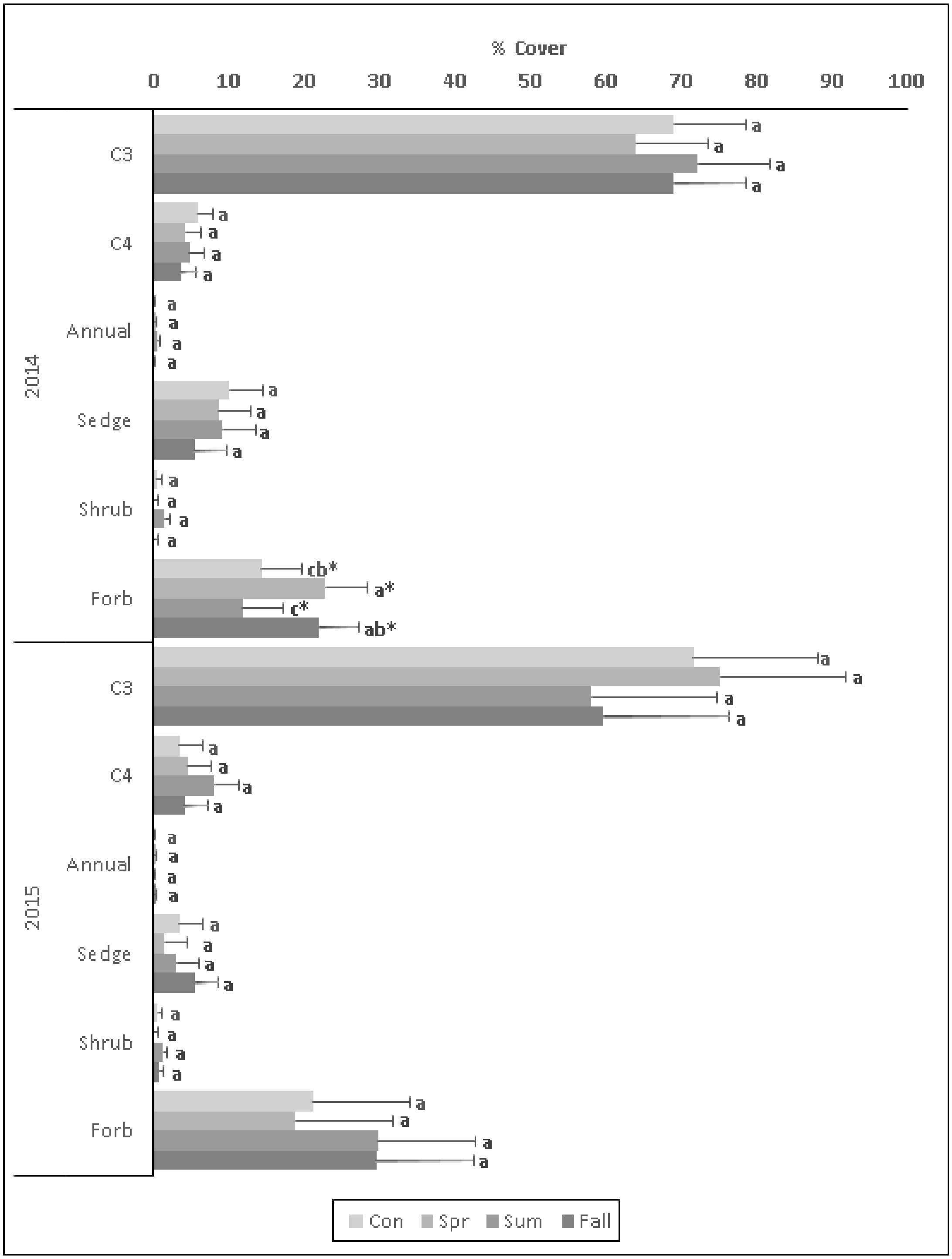

Table 3.1. Effects on Canopy Cover of Individual Species. Estimates of canopy cover ± Std. Error in burned (B) and nonburned (NB) and spring (Spr), summer (Sum) and Fall defoliated plots and nondefoliated (Con) plots. [a,b] denote differences of $P<0.05$ while [a*,b*] denote trends of $0.05<P<0.1$.

Year	Metric	Treatment	Burn	Value	Std. Error	*P*-value
2014	*Koeleria macrantha*	Con		2.93% [b*]	1.8	0.0564
		Spr		3.87% [b*]		
		Sum		7.97% [a*]		
		Fall		5.81% [ab*]		
	Melilotus officinalis	Con		6.75% [b]	6.7	0.0488
		Spr		22.48% [a]		
		Sum		9.56% [b]		
		Fall		9.26% [b]		
	Sphaeralcea coccinea		NB	1.91%	0.7	0.0184
			B	0.05%		
2015	*Koeleria macrantha*		NB	2.10%	1.0	0.0217
			B	0.00%		
	Artemisia frigida		NB	1.57%	0.6	0.0647
			B	0.23%		
	Asclepias incarnata		NB	2.80%	1.3	0.0849
			B	0.08%		
	Descurainia pinnata		NB	0.17%	0.7	0.0542
			B	1.40%		
	Melilotus officinalis		NB	9.59%	12.4	0.0162
			B	21.33%		

Figure 3.8. Fire Effects on Litter and Bare Ground. Estimates of cover ± Std. Error in burned and nonburned plots. [a,b] denote differences of $P<0.05$.

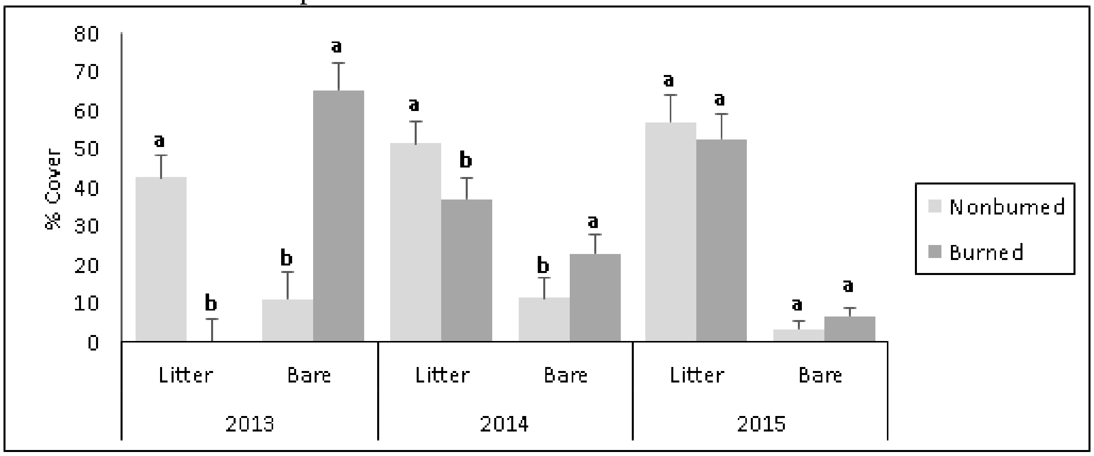

Figure 3.9. Defoliation Effects on Litter and Bare Ground. Estimates of cover ± Std. Error in spring (Spr), summer (Sum) and Fall defoliated plots and nondefoliated (Con) plots. [a,b] denote differences of $P<0.05$.

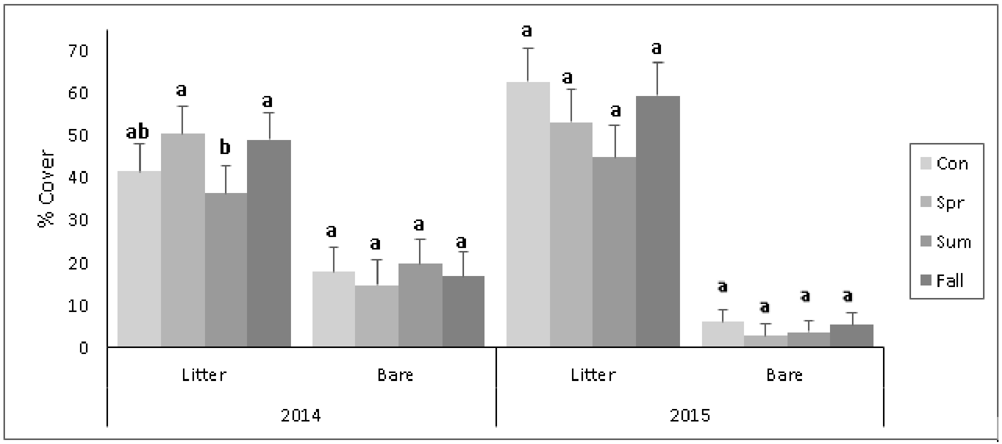

Table 3.2. Effects on Basal Cover of Individual Metrics. Estimates of basal cover ± Std. Error in burned (B) and nonburned (NB) and spring (Spr), summer (Sum) and Fall defoliated plots and nondefoliated (Con) plots. [a,b] denote differences of $P<0.05$ while [a*,b*] denote trends of $0.05<P<0.1$.

Year	Metric	Treatment	Burn	Value	Std. Error	*P*-value
2014	*Koeleria macrantha*	Con		1.00% [b*]	0.8	0.0928
		Spr		1.50% [ab*]		
		Sum		3.67% [a*]		
		Fall		2.50% [ab*]		
	Nassella viridula	Con		4.17 % [b*]	1.9	0.0812
		Spr		2.17% [ab*]		
		Sum		1.17% [a*]		
		Fall		3.67% [b*]		
	Carex duriuscula	Con		0.17% [b]	0.6	0.0083
		Spr		1.33% [ab]		
		Sum		2.33% [a]		
		Fall		0.50% [b]		
	Bouteloua gracilis		NB	7.75%	1.8	0.0829
			B	4.67%		
	Fecal		NB	0.92%	0.3	0.0365
			B	0.08%		
2015	*Melilotus officinalis*		NB	0.33%	2.2	0.0953
			B	4.50%		

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CHAPTER FOUR

FORAGE FIBER DIGESTIBILITY DYNAMICS IN THE NORTHERN MIXED-GRASS PRAIRIE FOLLOWING SPRING WILDFIRE

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

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Contributions: Conceived of and implemented study design. Collaborated on data collection and analysis. Provided feedback on manuscript drafts.

Co-Author: Clayton B. Marlow

Contributions: Provided feedback on statistical analysis and manuscript drafts.

Co-Author: Richard C. Waterman

Contributions: Advised on laboratory procedures. Collaborated on data analysis. Provided feedback on statistical analysis and manuscript drafts.

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FORAGE FIBER DIGESTIBILITY DYNAMICS IN THE NORTHERN MIXED-GRASS PRAIRIE FOLLOWING SPRING WILDFIRE

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Abstract

Forage quality plays an important role in determining grazing distribution in both natural systems and livestock production systems. Fire is a known modifier of forage quality, but the dynamics of forage quality following fire have not been well characterized. Here, we aim to quantify the magnitude and longevity of fire effects on forage digestibility in order to speculate when historic post-fire grazing would have likely ocurred and to determine when the greatest benefit might be gained from post-fire grazing. Following the Pautre wildifre of April 2013, exclosures were erected on the burned and nonburned sides of the fire perimeter at three locations spanning a north-south gradient of the burned area. Samples were collected in June, August and November 2013 and June and August 2014 and analyzed for dry matter (DM), ash, acid detergent fiber (ADF) , neutral detergent fiber (NDF) , *in vitro* dry mattter dissappearance (IVDMD), *in vitro* neutral detergent fiber dissappearance (IVNDFD) and gas production. DM and ash were unaffected in either year. Fire decreased ADF and NDF and increased IVDMD during June and/or August of the 2013 growing season with effects diminishing by November. IVNDFD and gas production were increased by fire across all 2013

samples. No fire effects were apparent in 2014, with only June to August phenological differences in forage digestibility apparent. This suggests that the dynamics of forage digestibility following fire are largely driven by phenology, peak increases in forage digestibility occur soon within the first growing season following fire and any increases are short-lived.

Introduction

Fire and grazing have played pivotal roles in shaping the ecosystem dynamics of the North American prairies (Biondini et al. 1999; Fuhlendorf and Engle 2001; Anderson 2006). Recent fire attracted free-roaming grazers (Biondini et al. 1999; Fuhlendorf et al. 2009) and the ensuing grazing decreased the likelihood of a proximate fire. Areas left ungrazed for extended periods of time, comparatively, experienced increased probabilities of fire the longer grazing was absent. Fire, generally preceded by this long period of absent grazers, would be followed by an increase in visitation by grazers, resulting in a cyclical pattern of feedback. It has been proposed that this linkage be referred to as pyric herbivory (Fuhlendorf et al. 2009). An important intermediary factor driving this linkage is forage quality. Grazers would be attracted to recently burned areas as the forage quality found there is generally improved when compared to nonburned areas (Bailey et al. 1996; Fuhlendorf and Engle 2004; Fuhlendorf et al. 2009). Several studies indicate that fire in grassland systems can improve forage quality by increasing protein content (Hilmon and Hughes 1965; Hobbs and Spowart 1984; Debyle et al. 1989; Mitchell et al. 1994; Dufek et al. 2014), decreasing anti-quality factors (Smith and Young

1959; Mitchell et al. 1994; Dufek et al. 2014), and improving digestibility (Hobbs and Spowart 1984; Debyle et al. 1989; Mitchell et al. 1994; Dufek et al. 2014). However, the dynamics of these expected shifts within the growing season immediately following fire and the longevity of such effects is less clear.

Current federal post-fire grazing management recommendations suggest that grazing be excluded at least through the active growing period of the first growing season following a fire and preferably for two full growing seasons (Blaisdell et al. 1982; Bureau of Land Management 2007). However, the evolutionary link between fire and grazing suggests that North American prairies should be well adapted to grazing following fire at the point when the forage quality of the burned areas is highest, and thus most comparatively attractive, relative to nonburned areas. Some literature suggests that this peak occurs soon after fire and is short lived, disappearing within one to three years following fire (Hilmon and Hughes 1965; McPherson et al. 1995). If this is the case, historic grazers would be naturally attracted to burned areas before the cessation of active growth during the first growing season, as this may be the time in which increases in forage quality are maximized. As time since fire increases, forage quality is expected to decline relative to adjacent nonburned areas, causing grazing utilization to shift to other, possibly recently burned, locations Determining the dynamics of forage quality following fire will not only provide insight as to when grazing would have naturally occurred following fire during the evolutionary history of the northern Great Plains, but will also indicate how prescribed fire might best be used to manipulate grazing distribution (Vermeire et al. 2004) or improve animal performance (Svejcar 1989). Waterman and

Vermeire (2011) indicate that animal performance and diet quality can be improved by grazing during the spring or early summer during the growing season following a summer fire when compared with the deferment of grazing until late summer. This indicates that deferment of grazing until after seed set or for two years causes lost opportunity with regards to animal productivity.

Increases in forage quality have been attributed to the removal of senesced or old standing dead material, increases in nitrogen availability, stimulated microbial activity, reduced competition for light increasing and increased leaf: stem ratios. Forages of advanced phenological stage, including senesced material and old dead material from previous-years' growth, are of lower forage quality than actively growing material. Fire efficiently removes old dead material (Duvall 1970). As a result, the forage quality of vegetation regrowth following fire is relatively high as it will not be diluted by low quality senescent material (Hobbs and Spowart 1984). Additionally, removal of old standing dead material will decrease the effort expended to select for new growth (Duvall 1970; Hobbs and Spowart 1984). Combustion of above-ground vegetation, standing dead, and litter will also mineralize nitrogen previously immobilized in plant tissues, potentially increasing availability for subsequent regrowth (Hobbs and Schimel 1984; Fenn et al. 1993; Neary et al. 1999). Increases in nitrogen availability may increase forage quality as it is generally a limiting nutrient (Seastedt et al. 1991). Release of nitrogen as well as increased soil temperatures, stemming from decreased soil albedo, can also stimulate microbial activity (Fenn et al. 1993). Greater microbial activity, in turn, increases mineralization and the rate of soil nutrient turnover, releasing nutrients for post-fire regrowth (Coleman et al. 1983). Forage quality can also be amplified by increasing the leafiness of vegetation.

The leaves of forages are of higher nutritional value than stems, which contain high proportions of structural fibers (Arzani et al. 2004). Stem growth occurs in order to raise the current year's leaves above the shade of litter and overstory vegetation, increasing light accessibility (Falster and Westoby 2003). When this occurs across the entire vegetation community, light available for photosynthesis is decreased. Removal of the plant canopy via fire decreases competition for light, thereby increasing the leaf: stem ratio and increasing the relative forage quality (Arzani et al. 2004).

Increases in forage quality are represent alterations that enhance an animal's performance or efficiency (Coleman and Moore 2003). As voluntary forage intake is the major factor limiting animal performance, increases in forage quality should be equivalent to changes that allow for increased voluntary forage intake (Allison 1985). Potential intake is primarily limited by the physical space of the rumen, forage digestibility and rate of passage through the gastrointestinal tract. Intake can be increased by decreasing the less digestible fiber fractions and decreasing the rumen space and digestion time required for digestion of high fiber feeds. Greater digestibility can increase the nutrition gained per volume of forage ingested while faster passage will decrease the time that less digestible fibers remain in the rumen, increasing the rumen space available for fresh intake.

We examined the effects of fire on the composition and digestibility of forage. Dry matter, ash, acid detergent fiber (ADF) and neutral detergent fiber (NDF) fractions were measured to provide an indication of the composition and relative recalcitrance of the forage sampled. NDF, a strong predictor of intake limitation due to fibrous fill, is indicative of the potential to increase intake while ADF is indicative of the fraction of forage sampled that may ultimately be indigestible (Van Soest 1965). *In vitro* dry matter disappearance (IVDMD) and *in vitro* NDF disappearance (IVNDFD) were also measured to indicate the relative extent of digestion (digestibility) in order to provide an estimate of the potential energy that could be gained from ingested forage. IVNDFD, specifically, indicated if the digestibility of the less degradable structural fibers, was increased. Methane gas production analysis was used to indicate if the relative extent or rate of digestion was responsive to fire.

In accordance with previous literature, we hypothesized that fire will increase relative forage digestibility by decreasing ADF and NDF (Smith and Young 1959; Dufek et al. 2014) and increasing the rate and volume of gas production (Dufek et al. 2014), IVDMD (Hobbs and Spowart 1984; Dufek et al. 2014) and IVNDFD (Dufek et al. 2014) relative to nonburned sites. We expected that forage digestibility will decrease with advancing season, and that any effects of fire will be within the context of seasonal forage conditions (Hobbs and Spowart 1984; Arzani et al. 2004).

Methods

Wildfire and Study Sites

In the area 31 km southwest of Lemmon, SD (45° 52' 54" N 102° 32' 52" W), the Pautre fire began on 3 April 2013, and ended on 7 April 2013, burning a total of 4322 ha consisting of Grand River Grazing Co-op, Grand River National Grassland and private lands (Figure 4.1A). Study sites were selected from the portion of the Grand River National Grassland that lay within the burn perimeter. Three sites were selected along the perimeter of the wildfire to capture the north-south gradient of the burn. One site was located in the "3B" pasture and two sites at the northern and southern ends of the "4B" pasture (N4B and S4B, respectively) (Figure 4.1B).

The dominant soil series in this area are Reeder-Lantry loams (Fine-loamy, mixed, superactive, frigid Typic Argiustolls and Fine-silty, mixed, superactive, calcareous, frigid Typic Ustorthents; 2-9% slopes) and Amor-Cabba loams (Fine-loamy, mixed, superactive, frigid Typic Haplustolls and Loamy, mixed, superactive, calcareous, frigid, shallow Typic Ustorthents; 6-15% slopes) (Soil Survey Staff USDA-NRCS 2008; Web Soil Survey 2015).

The three sites typified the wide range of possible northern mixed-grass prairie community compositions. Vegetation in the 3B pasture was dominated by the cool season (C3) introduced species *Agropyron cristatum* (L.) Gaertn, while the N4B pasture contained an even mix of the introduced C3 grass *Poa compressa* L. and more typical native C3 grasses such as *Nassella viridula* (Trin.) Barkworth and *Hesperostipa comata* (Trin. & Rupr.) Barkworth. The S4B pasture community was more classically composed of native northern mixed-grass prairie species such as C3 the native grasses *H. comata*, *Pascopyrum smithii* (Rydb.) Á. Löve, *Koeleria macrantha* (Ledeb.) Schult. and *N. viridula*. Common forbs across all pastures included natives *Grindelia squarrosa* (Pursh)

Dunal, *Ratibida columnifera* (Nutt.) Wooton & Standl., *Plantago patagonica* Jacq., and the invasive *Melilotus officinalis* (L.) Lam. Shrubs were rare.

Precipitation averages and 453 mm in Lemmon, SD and 413 mm in Lodgepole, SD (approximately 12 km Northeast of the study location) with most occurring from April to September (National Climate Data Center 2015). During the 2013-2014 study period, precipitation was well above average. In 2013, precipitation was 863 and 710 mm (172 and 190% of average), and 457 and 474 mm (114 and 101 % of average) in 2014 in Lemmon and Lodgepole, respectively.

Sample Collection and Preparation

Samples were collected the first (2013) and second (2014) growing seasons following the Pautre fire. Samples were collected in June, August and November in 2013 and June and August in 2014. Persistent snow and ice cover caused November sampling in 2014 to be impractical. Forage samples were collected from within 15 x 15 m exclosures erected on the burned and nonburned sides of the fire perimeter at the three study sites. At the N4B and S4B sites, a strip of vegetation from within each exclosure was mowed to 6 cm, creating a homogenous mixture of vegetation from each site, from which approximately a 1 dm^3 grab sample was taken. At the 3B sites, only *A. cristatum* was sampled as it was the overwhelmingly dominant forage species at this site. Approximately 1 dm^3 of *A. cristatum* was collected from each exclosure by clipping full bunches to 6 cm. Samples were immediately placed on ice for transport to the Fort Keogh Livestock and Range Research Laboratory (LARRL) in Miles City, MT, where all subsequent processing and analysis was done. Samples were frozen, lyophilized and ground to 2 mm for use in all subsequent analyses.

Analyses performed included DM, ash, ADF (ANKOM Technology 2014), NDF (ANKOM Technology 2015), IVDMD (Tilley and Terry 1963), IVNDFD, and *in vitro* gas production (Menke et al. 1979; Blümmel and Ørskov 1993).

Rumen Liquor Collection and Preparation

Rumen liquor used for all *in vitro* fermentation techniques was collected from two cannulated cows selected from the standing cannulated herd at the LARRL. Use, treatment and handling of these animals was approved by the LARRL Institutional Animal Care and Use Committee (IACUC No. 021308-1). Prior to the collection of rumen liquor, the two cows were fed a standard hay diet for at least 10 days with ad libitum access to water. Approximately 1 L, about 500 mL from each cow, of rumen liquor and some fiber was collected and stored in an insulated Dewar that had been warmed to 38˚C for at least 8 hours prior to collection, for transport to the lab. Rumen liquor was strained through four layers of cheese cloth into a 4 L beaker. Adequate rumen liquor for the ensuing procedure was measured and combined with McDougal's solution in a 1:2 ratio of rumen liquor to McDougal's solution in a 4 L flask under constant CO_2 bubbling. This rumen liquor, McDougal's solution mixture will be discussed as "inoculum".

In Vitro Fermentation Procedures

Techniques described by Tilley and Terry (1963) were used to estimate IVDMD and IVNDFD. Samples (500 mg) were weighed in duplicate and placed into a 90 mL culture tube. Tubes were randomly assigned a position in a metal rack and placed in a 38˚C water bath. Tubes were filled with 30 mL of inoculum, bathed in CO_2 to ensure that the tube was oxygen free, capped tightly and agitated. Racks were placed in a 38 ˚C incubator and agitated at approximately 4, 8, 24, 28 and 32 hours during a 48-hour incubation. Once removed from the incubator, caps were immediately unsealed and samples filtered under suction onto pre-weighed Whatman® No. 1-10mm diameter filter papers to determine IVDMD. Samples for the IVNDFD procedure were then scraped from filter papers post-drying, reweighed, placed into pre-weighed ANKOM F57 filter bags and analyzed for NDF following the ANKOM NDF method (ANKOM Technology 2015).

Techniques described by Menke et al. (1979) were used to estimate 96-hour methane gas production. Samples (250 mg) were weighed in triplicate and placed into 100 mL gas production syringes. Syringes were then filled with 20 mL of inoculum, voided of excess air and placed into a 38˚C water bath. Gas production was recorded at 0, 2, 4, 6, 8, 10, 12, 14, 24, 30, 34, 48, 54, 60, 72 and 96 hours during the fermentation. If at any time a syringe had accumulated ≥ 85 mL of gas, 10 mL was released to ensure that the plungers were not ejected.

Data Analysis

Gas production measurements were fitted with the equations described by Blümmel and Ørskov (1993) via nonlinear regression using GraphPad Prism (Motulsky 1996). The equations and associated variables used were:

$$G=AGP\ (1\text{-}e^{-K[T-Lag]})$$

where G is equal to total gas production (mL·g^{-1} DM) at time T (hours), AGP denotes the asymptotic or maximum gas production (mL·g^{-1} DM), K denotes the fractional fermentation rate (h^{-1}) and lag is the interval between the start of fermentation and the onset of gas production and

$$AFR=\frac{A\cdot K}{2[\ln(2)+K\cdot Lag]}$$

Where AFR denotes the average rate of fermentation (mL· h^{-1}).

Data were analyzed using SAS MIXED procedure analysis of variance (Littell et al. 2006) using the exclosures as the experimental unit. Fire treatment and sample month (indicative of phenological stage) were included as fixed-effect variables while study site was included as a random variable. Response variables included DM, ash, ADF, NDF, IVDMD, IVNDFD, AGP, K, Lag and AFR. Test significance was determined using an α of 0.05. Mean separations were conducted using the PDIFF option of SAS when significant interactions were found.

Results

In 2013, DM and ash were unaffected by fire or sampling month (Table 4.1). Fire increased IVNDFD by 8.5% relative to nonburned sites. IVNDFD also decreased an average 17% from June to August and November. AGP was similarly increased 6.8

$mL \cdot g^{-1}$ OM by fire but decreased 6.4 $mL \cdot g^{-1}$ OM between June and August to November. K followed a similar pattern, with the fractional fermentation rate increasing due to fire by 1% $\cdot$ h^{-1} and decreasing 2% $\cdot$ h^{-1} from June to August and November. Lag was unaffected by fire but increased from 0.67 h in August to 1.98 h in November.

Fire and sampling month interacted in their effects on ADF, NDF, IVDMD, and AFR (P= 0.0159, 0.0197, 0.0425, 0.0076, respectively; Figure 4.2 A-D). ADF was decreased by fire in June sampled plots by 9.2-15.3% when compared to all other treatments (Figure 4.2 A). ADF was also decreased in burned plots sampled in August by 4.3% when compared to nonburned plots sampled in the same month. Burned and nonburned plots yielded similar ADF in November. Burned plots sampled in June had 9.1% les NDF when compared that the next lowest estimated NDF, which occurred in burned plots sampled in August (Figure 4.2 B). Burned plots sampled in August were similar in NDF content to nonburned June and August sampled plots, which averaged 65.1% NDF. Nonburned plots sampled in August and both burned and nonburned plots sampled in November contained the greatest concentrations of NDF at an average of 70.2%.

A similar pattern was measured for IVDMD (Figure 4.2 C). Burned plots sampled in June generated the greatest IVDMD of 72.9% compared to all other treatments, yielding 12.1% greater disappearance than the next highest estimate. Burned plots sampled in August and nonburned plots sampled in June were similar to one another and yielded the next highest IVDMD, averaging 58.7%. Nonburned plots sampled in June and August were also similar with regards to IVDMD, averaging 54.2%. Nonburned plots sampled in August and both burned and nonburned plots sampled in November were similar and yielded the lowest IVDMD observed at an average of 48.2%. The most rapid AFR was observed in burned plots sampled in June at 2.63 mL gas · h^{-1} while nonburned plots sampled in June and burned plots sampled in August had an AFR that was 0.9 mL gas · h^{-1} slower (Figure 4.2 D). Burned and nonburned plots sampled in August were similar while nonburned plots sampled in August were also similar to burned plots sampled in November. Burned and nonburned plots sampled in November yielded the lowest observed AFR, at an average of 1.23 mL gas · h^{-1}.

In 2014, there were no substantial fire effects on DM, ash, ADF, NDF, IVDMD, IVNDFD, AGP, K, lag or AFR (Table 4.2), with only a trend toward greater IVNDFD in nonburned plots. Sampling month rendered differences in ADF, NDF, IVDMD, IVNDFD, AGP, K, lag and AFR. ADF and NDF of plots sampled in June was 6.42 and 2.1% lower than that of plots sampled in August, respectively. Measurements of IVDMD and IVNDFD were decreased by 9.5% and 11%, respectively, from June to August. AGP and AFR were similarly higher in June than in August while K and lag were unaffected by sampling month in 2014.

Discussion

Fire had a clear effect on several forage digestibility factors in 2013. However, this effect was short-lived overall, with several effects becoming indiscernible by November of 2013 and no fire effects lasting to 2014. Additionally, fire effects on forage digestibility were often dependent on the phenological stage of the most abundant vegetation in the community during the sampling month.

Sampling month, which is somewhat indicative of phenology, played a clear and deterministic role in forage quality in both 2013 and 2014. In 2013, forage of new growth sampled in June was almost always less fibrous and more digestible than the forage sampled in August, which contained senescent or flowering vegetation from cool season species, or the dormant forage sampled in November. Similarly, the samples taken in June 2014 were generally more digestible than those taken in August 2014. These observations are consistent with prior information on seasonal forage quality (Arzani et al. 2004).

However, fire increased IVNDFD, AGP and K within the context of this seasonal gradient in 2013. While fire resulted in samples with lower NDF to begin with, these observations also indicate that a greater portion NDF of the forage may have been ultimately degradable. Essentially, a greater proportion of the forage sample was ultimately fermented and a greater percent of the original forage was fermented each hour during the fermentation period. This increases the potential energy available to an animal per unit of forage ingested while also decreasing the time spent digesting that forage.

In 2013, ADF, NDF, IVDMD and AFR were also affected by fire, but with an interacting effect of sampling month. Concentrations of ADF and NDF were decreased while IVDMD was increased by burning in June when compared to the nonburned sample taken in the same month. Fire, in fact, yielded similar ADF, NDF and IVDMD values in burned plots sampled in August when compared to nonburned plots sampled in

June, indicating that fire can potentially extend relatively high forage quality, such as might be expected from active spring growth, into the summer. Additionally, AFR was dramatically increased by fire in June sampled plots when compared to nonburned plots in the same month, but this difference diminished in the summer and disappeared in the fall. This indicates that while fire may initially increase the rate of fermentation and passage and ultimately voluntary forage intake and overall animal performance, the effect is very short-lived. The interaction between fire and sampling month observed indicates the window of opportunity for livestock producers to take advantage of increased forage digestibility may be limited to the first active growing season following fire with respect to some forage quality metrics. This agrees with the results of Waterman and Vermeire (2011) who observed that ewes grazing following a summer fire had positive average daily gains when grazing in spring or early summer, but had significantly smaller or negative average daily gains when grazing was deferred until late summer.

The magnitude and direction of fire effects on the gas production variables compare to those seen by Dufek et al. (2014) in which fall fire increased the quality of the native, but weedy *Aristida purpurea* Nutt. by increasing AGP by 8.8 mL $\cdot g^{-1}$, decreasing lag by 0.5 h and increasing K and AFR differentially depending on sampling month. Several others have observed similar increases in digestibility (Hobbs and Spowart 1984; Debyle et al. 1989; Mitchell et al. 1994) and decreases in NDF (Smith and Young 1959; Smith et al. 1960; Mitchell et al. 1994).

The short-lived nature of the observed fire effects is in contrast with some observations but in agreement with others. Fire has been found to increase the quality of winter forage for up to two years in shrubby grasslands, suggesting that the effect lasted well past senescence in the first year following fire as well as into subsequent years (Hobbs and Spowart 1984). Additionally, increases in the forage quality of desert grasslands have been observed to last for one to three years (McPherson et al. 1995). Conversely, studies of herbaceous pine forest understory (Wood 1988) and southern wiregrass ranges (Hilmon and Hughes 1965) agree with the finding that fire driven increases in forage quality diminish by senescence the first growing season following fire. This disagreement across studies strongly indicates that the longevity of fire effects on forage quality is highly dependent on the biome and the respective variations in climate, vegetation and disturbance regimes in distinct systems. These variations are reflected in productivity and the subsequent accumulation of standing dead material

Much of the difference in forage digestibility between burned and nonburned sites in this study can be attributed to the accumulation of old, standing dead material, which is consistently of lower quality and digestibility when compared to living plant tissue (Arzani et al. 2004). As samples were a homogenous mix of vegetation, the measurements of quality obtained represent the quality of all available forage, rather than being a representative of actual diet quality (Hardison et al. 1954). In 2013, burned samples contained no old, standing dead material while nonburned sample contained $\geq$1000 kg $\cdot$ ha^{-1}, or around 50% of the total standing biomass (see Chapter 3, Figure 3.1). If the quality of the current year's growth were unaffected by fire, this difference in standing dead material alone would result in the burned sites yielding higher quality. A grazing animal would be much more selective than the sample taken, obtaining predominately the newer, higher quality portion of the forage available and avoiding much of the old, standing dead material. However, the removal of old, standing dead material does decrease the effort needed to select for the higher quality portion of the available forage (Duvall 1970), allowing for increased foraging efficiency on burned landscapes.

In the northern mixed-grass prairie specifically, the duration of the interval in which forage quality is increased following fire is an important indicator of the historical linkage between grazing and fire. Gazers given the freedom of selection will seek out areas that are of higher forage quality relative to other potential foraging locations (Senft et al. 1985; Bailey et al. 1996). In this study, forage digestibility, with respect to some metrics, was only enhanced during June or August, and with respect to all metrics, was only enhanced during the first growing season following the fire. This indicates that over the evolutionary time-line of this ecoregion, free-ranging grazers would have been attracted to burned areas at least within the first growing season following a spring wildfire, if not within the immediate one to three months of growth following fire.

This clue to the historical timing of post-fire grazing not only indicates that northern mixed-grass prairie likely evolved with significant post-fire grazing utilization, but also provides insight into how fire can be effectively used as a livestock management tool in this ecoregion (Fuhlendorf and Engle 2001). Prescribed fire has been proposed as a tool for managing grazing distribution (Fuhlendorf and Engle 2001; Vermeire et al. 2004). As grazers are attracted to these areas due to the increased nutritional potentials, this technique may be most effective when the quality of burned areas is greatest relative to nonburned areas. The results of this study suggest that burning of northern mixed-grass prairie as a tool to manage grazing distribution will be most effective before senescence the first growing season following fire. Additionally, studies have reported increased diet quality of cattle grazing burned pastures, resulting in maintenance or gains in weight (Angell et al. 1986; Svejcar 1989). These benefits too would be optimized by the application of grazing shortly following fire and may be missed altogether via deferment.

Application of post-fire grazing would manipulate forage quality dynamics and potentially extend the period for which available forage quality of a burned site is increased relative to nonburned sites. When given the freedom of selection, grazer may create "grazing lawns" on attractive areas by persistently revisiting these areas and removing subsequent regrowth (McNaughton 1984). As such, senescence is delayed and subsequent buildup of old, standing dead material is inhibited, influencing the quality of the available forage by manipulating the ratio of current-year's growth to old, standing dead. This pattern can potentially enhance forage quality and foraging conditions over several years, but has the potential, if allowed, to lead to serious overuse.

Implications

Forage quality in the northern mixed-grass prairie increases following spring wildfire. However, the increases are short-lived, with some improvements lasting only a few months and none lasting into the following year. This indicates that not only would grazers have historically utilized burned areas within the first growing season following fire, but also that the use of prescribed fire as a management technique renders the most benefit within the first growing season following application. As such, prescribed fires with the intention of increasing forage quality or foraging conditions may need to be applied on a regular basis.

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Figures and Tables

Figure 4.1. Locations of (A) the Pautre wildfire and (B) the 3B, N4B and S4B study sites. Data: USGS and ESRI. Map Authors: Narciso Garcia-Neto and Emily Gates

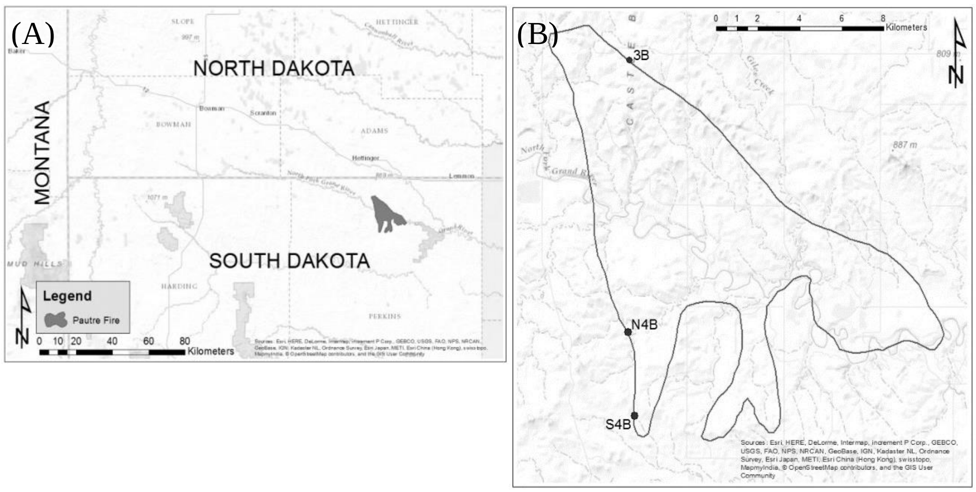

Table 1. 2013 Estimates ± Std. Error.

Metric	Fire Treatment: B	NB	Std. Error	*P*-value	Sampling Month: Jun	Aug	Nov	Std. Error	*P*-value
					% DM				
DM	91.62	91.71	0.2	0.6286	91.40	91.80	91.78	0.2	0.1885
Ash	12.33	13.10	1.0	0.4761	12.17	13.23	12.75	1.1	0.7114
IVNDFD	39.10	30.60	2.5	0.0218	46.20 ^{a}	30.61 ^{b}	27.72 ^{b}	3.0	0.0015
					mL·g-1 OM				
AGP	71.45	64.65	3.3	0.0028	71.52 ^{a}	68.84 ^{a}	63.78 ^{b}	3.73	0.0132
					h-1				
K	0.04	0.03	0.001	0.0340	0.05 ^{a}	0.03 ^{b}	0.03 ^{b}	0.001	<0.0001
					h				
Lag	1.20	1.47	0.3	0.4369	1.35 ^{ab}	0.67 ^{b}	1.98 ^{a}	0.3	0.0268

^{a,b} Differing letters indicate differences at P<0.05

Figure 4.2. 2013 Estimates ± Std. Error for the fire by sampling month interactions of (A) ADF, (B) NDF, (C) IVDMD and (D) AFR observed in 2013. [a,b] Differing letters indicate differences at P<0.05.

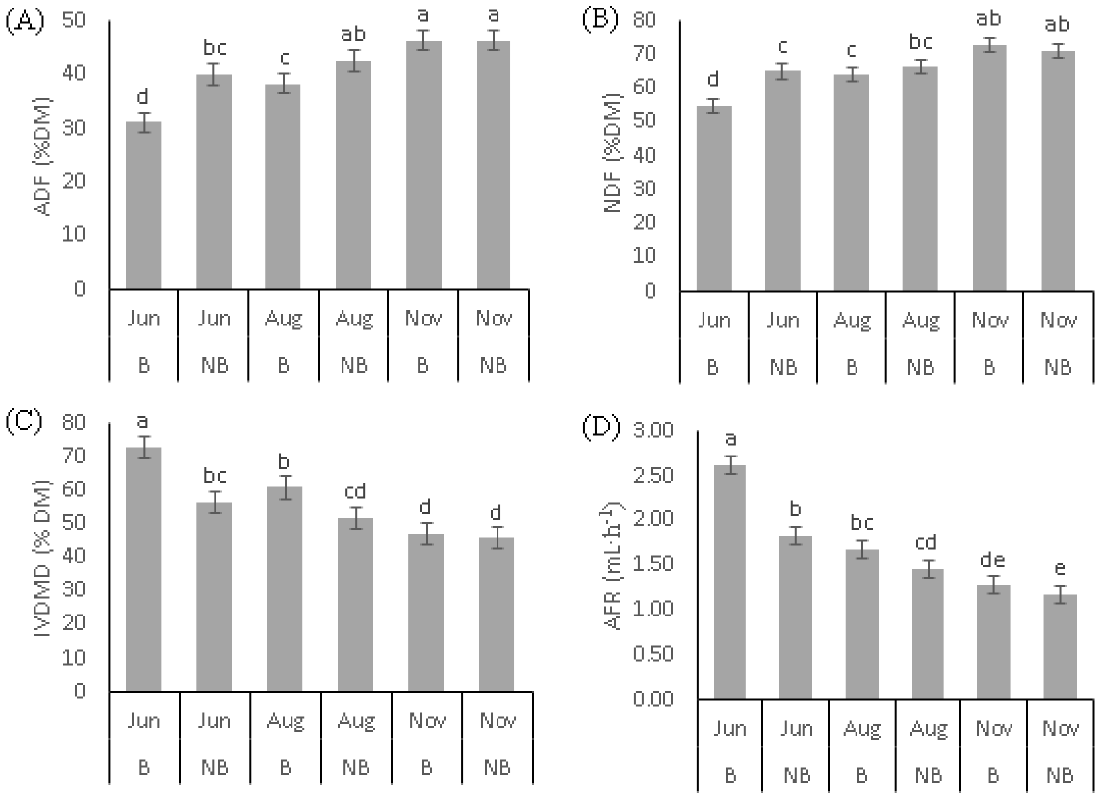

Table 2. 2014 Estimates ± Std. Error.

	Fire Treatment				Sampling Month			
Metric	B	NB	Std. Error	*P*- value	Jun	Aug	Std. Error	*P*- value
				% DM				
DM	91.34	91.25	0.2	0.7413	91.14	91.45	0.2	0.2771
Ash	14.71	14.86	0.9	0.6685	15.08	14.49	0.9	0.1327
NDF	66.64	66.35	2.7	0.7988	66.43	68.55	2.7	0.0094
IVDMD	49.12	50.42	2.0	0.4025	54.46	45.08	2.0	0.0006
IVNDFD	40.38	46.92	4.0	0.0984	49.23	38.23	4.0	0.0156
				$mL \cdot g^{-1}$ OM				
AGP	80.66	84.73	3.1	0.3181	89.45	75.93	3.1	0.0111
				h^{-1}				
K	0.05	0.05	0.006	0.9695	0.05	0.05	0.006	0.8560
				h				
Lag	0.04	0.08	0.06	0.6349	0.03	0.03	0.06	0.4298
				$mL \cdot h^{-1}$				
AFR	2.72	2.90	0.3	0.3459	3.09	2.53	0.3	0.0221

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CHAPTER FIVE

CONCLUSIONS

The implications from the Pautre fire, presented in chapters two, three and four, indicate that northern mixed-grass prairis is well adapted to the disturbances of fire, grazing and post-fire grazing. This is at odds with federal post-fire grazing reccommendations, which seek to protect rangelands from any detrimental effects of post-fire grazing by dictating rest from grazing for two growing seasons following fire. The results presented in chapter two indicate that northern mixed-grass prairie will recover similarly when grazed during the first two growing seasons following spring fire as when rested during that same period. This indicates that post-fire grazing will not impede recovery of northern mixed-grass prairie in the short term. Importantly, further work will be needed to determine the longer term impacts of repeated or annual grazing following fire. Results presented in chapter three further indicate that defoliation during the spring, summer or fall during the first year following a spring fire will not negatively impact productivity, community composition or basal cover when compared to nondefoliated or rested sites. This indicates that some actively growing plants do not require rest following fire in order to recover. Again, additional work is needed to determine if the caespitose and rhizomatous graminoid species of the northern mixed-grass prairie will respond similarly to fire and grazing or if caespitose dominated communities may be less resistant to post-fire grazing. The nutritional analyses presented in chapter four demonstrate that peak increases in forage quality occur shortly after spring fire and do not persist into the following year, suggesting that during the evolution of the northern mixed-grass prairie, free-roaming grazers would have been most attracted to burned areas soon after fire. Additionally, this demonstrates that the period during which livestock producers might best take advantage of increased forage quality may be incompatible with the reccomendation of deferment of grazing following fire. The creation of “grazing lawns” on previously burned areas may potentially imapct these dynamics for years following fire, however, as grazers return to well grazed sites of previous fires. As such, the role of post-fire grazing on post-fire forage quality dynamics over extended periods should also be evaluated.

Studies of the Pautre fire indicate that, in the northern mixed-grass prairie, neither grazing within the first growing season following fire nor defoliation during active growth the first growing season following fire will decrease productivity nor shift species composition toward less desirable species. Additionally the largest increases in forage quality occurr shortly after fire. Given these observations, post-fire grazing could be more appropriately and beneficially managed on a case-by-case basis using evolutionary pressures and historic disturbance regimes to inform managers as to what management regimes should be most appropriate for their specific ecoregion. The results of the studies presented here indicate that post-fire grazing without rest may indeed be a viable strategy in the northern mixed-grass prairie.

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APPENDICES

APPENDIX A

OBSERVED SPECIES

APPENDIX A

Chapter 2:	*Achillea milefolium*	*Grindelia squarrosa*
	Agrpyron cristatum	*Hesperostipa comata*
	Pseudoroegeneria spicata	*Koeleria macrantha*
	Atermisia biennis	*Liatris punctata*
	Artemisia campestris	*Melilotus officinalis*
	Artemisia frigida	*Nassella viridula*
	Atremisia ludoviciana	*Pascopyrum smithii*
	Aristida purpurea	*Plantago patagonica*
	Bouteloua gracilis	*Poa secunda*
	Bromus tectorum	*Psoralidium tenuiflorum*
	Carex duriuscula	*Ratibida columnifera*
	Carex filifolia	*Schizachyrium scoparium*
	Calomovilfa longifolia	*Spharalcea coccinea*
	Chondrilla juncea	*Sporobolus cryptandrus*
	Cirsium undulatum	*Taraxacum officinale*
	Eriogonum umbellatum	*Vulpia octoflora*
Chapter 3:	*Achillea milefolium*	*Koeleria macrantha*
	Agrpyron cristatum	*Kochia scoparia*
	Pseudoroegeneria spicata	*Lactuca serriola*
	Artemisia campestris	*Liatris punctata*
	Artemisia frigida	*Melilotus officinalis*
	Atremisia ludoviciana	*Medicago sativa*
	Asclepias incarnata	*Nassella viridula*
	Bouteloua gracilis	*Oxytropis lambertii*
	Bromus tectorum	*Pascopyrum smithii*
	Buchloe dactyloides	*Phlox hoodii*
	Carex duriuscula	*Plantago patagonica*
	Carex filifolia	*Poa compressa*
	Chondrilla juncea	*Psoralidium tennuiflorum*
	Cirsium undulatum	*Ratibida columnifera*
	Conyza canadensis	*Spharalcea coccinea*
	Dalea purpurea	*Symphoricarpos albus*
	Descurinia pinata	*Taraxacum officinale*
	Erysimum asperum	*Tragopogon dubius*
	Eriogonum umbellatum	*Vicia americana*
	Grindelia squarrosa	*Vulpia octoflora*
	Hesperostipa comata	*Wyethia amplexicaulis*

APPENDIX B

SUMMARY OF F-TESTS FOR MAIN AND INTERACTING EFFECTS

APPENDIX B

Chapter 2:		Grazing Treatment		Ecological Site		Grazing Treatment * Ecological Site Interaction	
		F-value	*P*-value	F-value	*P*-value	F-value	*P*-value
2013	Standing Biomass	7.90	0.0307	0.12	0.7409	0.14	0.7198
2014	Standing Biomass	7.48	0.0340	7.02	0.0381	0.01	0.9173
2014	Current-Year Biomass	0.80	0.7966	0.07	0.0676	0.56	0.5634
2014	Old Dead Biomass	89.22	<0.0001	13.66	0.0101	1.67	0.2437
2014	Canopy Cover	5.33	0.0603	1.33	0.2921	1.33	0.2921
2014	Richness	8.87	0.0247	0.42	0.5414	1.36	0.2882
2014	Shannon's Diversity Index	16.14	0.0070	3.87	0.0968	7.43	0.0344
2014	C3 Grasses	9.00	0.0240	5.86	0.0518	2.07	0.2005
2014	C4 Grasses	8.50	0.0268	0.62	0.4611	0.05	0.8234
2014	Annual Grasses	0.12	0.7374	0.08	0.7860	0.64	0.4543
2014	Sedges	0.36	0.5726	5.52	0.0572	0.51	0.5002
2014	Shrubs	1.77	0.2314	1.77	0.2314	1.77	0.2314
2014	Forbs	4.18	0.0870	0.02	0.8972	0.79	0.4083
2014	Litter	1.17	0.3205	0.32	0.5938	1.17	0.3205
2014	Bare Ground	1.18	0.3194	4.53	0.0773	1.09	0.3368

APPENDIX B – CONTINUED

Chapter 3:		Fire Treatment		Defoliation Treatment		Fire Treatment * Defoliation Treatment Interaction	
		F-value	*P*-value	F-value	*P*-value	F-value	*P*-value
2013	Standing Biomass	10.22	0.0377	-	-	-	-
	Current-Year Biomass	10.50	0.0330	-	-	-	-
	Old Dead Biomass	10.73	<0.0001	-	-	-	-
	Richness	0.84	0.4557	-	-	-	-
	Shannon's Diversity Index	2.15	0.2801	-	-	-	-
	C3 Grasses	0.85	0.4540	-	-	-	-
	C4 Grasses	2.63	0.2462	-	-	-	-
	Annual Grasses	-	-	-	-	-	-
	Sedges	0.52	0.5452	-	-	-	-
	Shrubs	-	-	-	-	-	-
	Forbs	3.99	0.1839	-	-	-	-
	Litter	26.09	0.0363	-	-	-	-
	Bare Ground	28.53	0.0333	-	-	-	-
2014	Standing Biomass	1.79	0.2022	4.20	0.0258	0.22	0.8786
	Current-Year Biomass	3.48	0.0832	4.00	0.0299	0.77	0.5288
	Old Dead Biomass	0.06	0.8074	22.13	<0.0001	3.11	0.0606
	Richness	2.67	0.0878	0.02	0.8864	1.26	0.3254
	Shannon's Diversity Index	0.10	0.7516	4.22	0.0253	0.11	0.9493
	C3 Grasses	0.51	0.6798	0.02	0.8767	1.01	0.4170
	C4 Grasses	0.69	0.5752	0.13	0.7220	0.82	0.5022
	Annual Grasses	1.87	0.1814	0.89	0.3606	0.30	0.8263
	Sedges	0.72	0.5589	0.34	0.5677	0.70	0.5664
	Shrubs	0.98	0.4287	0.55	0.4708	0.96	0.4393
	Forbs	2.88	0.0733	0.03	0.8627	2.17	0.1376
	Litter	2.44	0.1080	11.60	0.0043	0.44	0.7282
	Bare Ground	0.24	0.8664	7.12	0.0183	0.42	0.7443
2015	Standing Biomass	0.03	0.8544	1.43	0.2765	0.51	0.6803
	Current-Year Biomass	0.00	0.9703	0.19	0.9021	0.07	0.9725
	Old Dead Biomass	3.00	0.5950	4.24	0.0251	5.51	0.0104
	Richness	0.13	0.9429	0.08	0.7759	0.80	0.5143
	Shannon's Diversity Index	0.0006	0.9803	0.83	0.4973	0.14	0.9336
	C3 Grasses	2.25	0.1312	4.68	*0.0498	0.33	0.8067

APPENDIX B – CONTINUED

	C4 Grasses	0.60	0.6275	0.00	0.9652	0.20	0.8977
	Annual Grasses	0.74	0.5462	1.90	0.1912	0.74	0.5462
	Sedges	0.50	0.6861	1.61	0.2269	0.66	0.5939
	Shrubs	1.32	0.3097	3.65	0.0784	0.88	0.4778
	Forbs	1.59	0.2390	5.09	0.0419	0.55	0.6558
	Litter	2.27	0.1256	0.73	0.4069	0.39	0.7628
	Bare Ground	0.19	0.9031	1.94	0.1854	0.27	0.8448

* Estimate of relative composition in disagreement with actual composition. No change in actual composition observed.