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RESILIENCE AND HETEROGENEITY FOLLOWING
FIRE IN THE NEBRASKA SANDHILLS

by

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A THESIS

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RESILIENCE AND HETEROGENEITY FOLLOWING
FIRE IN THE NEBRASKA SANDHILLS

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University of Nebraska, 2016

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The Nebraska Sandhills grassland is an expansive, semi-arid ecosystem characterized by vegetation-stabilized rolling sand dunes. The Sandhills grassland is managed for livestock production by seeking to minimize disturbances, such as fire, that increase bare ground. The increase in bare ground following fire has contributed to the fear of fire leading to the emergence of a mobile sand dune state. We tracked vegetation response following a growing season wildfire that occurred during extreme drought conditions. In wildfire and drought conditions are when one would expect resilience to be overcome leading to a lack of vegetation recovery and a transition to a mobile sand dune state. However, aboveground herbaceous biomass recovered to unburned levels after two years and resisted a transition to an undesirable plant community. Next, we assessed the potential for focal fire and grazing to create heterogeneity of grassland structure and composition in order to increase biodiversity. Using patch burning, discrete patches were burned annually and grazers were allowed to select between recently burned and unburned areas. We found the Sandhills grassland is spatially homogeneous in vegetation structure and composition with greater structural heterogeneity emerging temporally in the transition from growing to dormant season.

However, temporal heterogeneity manifests as an artifact of how vegetation was classified. Although live herbaceous vegetation decreases in the transition to dormant season, grassland vegetation structure is only slightly affected because herbaceous standing dead vegetation increases as a result of herbaceous vegetation senescence.

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CHAPTER I

RESILIENCE OF SANDHILLS GRASSLAND TO WILDFIRE

INTRODUCTION

In sandy soil ecosystems, a major concern is that a destabilizing event or feedback will overcome the resilience of vegetated sand dunes and shift a stabilized dune into a mobile sand dune state. Many mobile sand dunes occur where precipitation is insufficient to support vegetation (Lancaster, 1988; Mason et al., 2004; Miao et al., 2007; Muhs and Wolfe, 1999; Roskin et al., 2011; Sridhar et al., 2006). Where vegetation is present and sand dunes are stable, fine root biomass holds the soil particles in place, providing protection against erosion and preventing the soil from becoming mobile (Hartman, 2015; Stubbendieck et al., 1989). It has often been suggested that sandy soil ecosystems are sensitive to destabilization when a feedback decreases aboveground biomass, increasing the amount of bare ground and, the potential for erosion (Forman, 2001; Mason et al., 2004; Muhs and Wolfe, 1999). Such concerns are evident in agency frameworks meant to guide land management actions. For example, state-and-transition models (STMs) within Ecological Site Descriptions (ESD) and Landscape Fire and Resource Planning Tools (LANDFIRE) show a transitional pathway from a stable grassland state to a mobile sand dune state following wildfire in sandy soil ecosystems (LANDFIRE, 2016; USDA-NRCS, 2015a; Figure 1-1).

Concerns over destabilization have led to management that aims to avoid an undesirable state change toward mobile sand dunes in the Nebraska Sandhills. The

Sandhills are the largest sand dune field in the Western Hemisphere and one of the largest stabilized sandy soil ecosystems in the world (Ahlbrandt and Fryberger, 1980). The sandy textured soil is stabilized by fine root biomass of predominantly herbaceous vegetation (Ahlbrandt and Fryberger, 1980; Bleed and Flowerday, 1991). Although the Sandhills grassland currently stabilizes the sand dunes, small-scale destabilization occurs in the form of localized blowouts (a discrete depression with little to no vegetation) that act as reminders of the potential for destabilization (Stubbendieck et al., 1989). Management actions and policies therefore avoid feedbacks that consume aboveground biomass and increase bare ground (Stubbendieck, 1998). Livestock producers seek uniform grazing distribution through moderate grazing pressure and adequate rest to prevent highly disturbed areas (Holechek et al., 2011). While fire has been attributed to blowout formation and short-term destabilization (Pool, 1912; Stubbendieck et al., 1989), few studies have assessed the potential for broad-scale destabilization of Sandhills grassland following wildfire. None of the studies conducted have shown that wildfire causes broad-scale destabilization (Pfeiffer and Steuter, 1994), whereas evidence does demonstrate that Sandhills grassland recovers following wildfire (Volesky and Connot, 2000). Scientific evidence of grassland recovery, or lack thereof, is lacking for more extreme conditions, such as when a high intensity wildfire occurs during severe drought. This has led to a prevailing hypothesis that a threshold will be crossed in more extreme conditions and destabilization will manifest when a wildfire occurs during drought.

The ongoing debate is whether fire operates as a positive feedback in stabilized sandy soil ecosystems. Positive feedbacks are forces that move a system to an alternative

stable state (Twidwell et al., 2013b). If fire operates as a positive feedback, we would not expect biomass to recover, signaling the potential for a long-term shift away from pre-feedback conditions. This would be consistent with purviews that wildfire will overcome the resilience of Sandhills grassland and lead to the emergence of an alternative, destabilized state. Biomass recovery following a feedback has been used as a key indicator to assess whether resilience of the pre-feedback state has, or has not, been overcome (Allen et al., 2005; Folke et al., 2004; Wonkka et al., 2015). In July 2012, a wildfire occurred during a 9-month drought when precipitation levels were 72% below the historical average (HPRCC, 2015). In 2012, the northcentral Sandhills experienced the second lowest amount of annual precipitation, the third lowest amount of growing season (April to September) precipitation, and the lowest May to September precipitation. Coinciding with extreme drought conditions, more wildfires occurred in Nebraska during 2012 than any year on record, more than doubling the area burned compared to any other year (since 1964; Nebraska Forest Service, 2016).

The objective of this study is to determine whether wildfire during severe drought conditions was able to overcome the resilience of Sandhills grassland, leading to the emergence of an alternative, mobile sand dune state. Based on current expectations, the combination of wildfire and drought conditions observed in 2012 will lead to a lack of herbaceous biomass recovery and the emergence of a mobile sand dune state (USDA-NRCS, 2015a). We tracked aboveground biomass response and plant community composition in adjacent burned and unburned areas 2 and 3 years following the wildfire. The primary consideration is whether grassland biomass will rapidly recover. Rapid

recovery of grassland biomass to pre-feedback levels signals the resilience of the existing state has not been overcome, and clearly indicates that the system is still stabilized by grassland vegetation. If resilience has not been overcome, a secondary consideration is whether the plant community has undergone a shift in species composition that could undermine future resilience of the state (e.g., an increase in exotic invasive species). Alternatively, if fire is operating as a positive feedback we do not expect biomass to recover. The lack of biomass recovery signifies the potential for a long-term shift away from pre-wildfire conditions and provides evidence that the resilience of the previous state might have been overcome and an alternative state has emerged (Allen et al., 2005; Folke et al., 2004).

METHODS

This research was conducted in the 5.7 million ha Nebraska Sandhills ecoregion at The Nature Conservancy's Niobrara Valley Preserve. The Niobrara Valley Preserve is located 43 kilometers northwest of Ainsworth, Nebraska. Mean annual precipitation for the site is 591 mm (HPRCC, 2015). Mean annual temperature is 10°C, ranging from -3°C in January to 24°C in July. Soils at the site are characteristic of Sandhills soils, classified as Valentine fine sands (mixed, mesic Typic Ustipsamments) featuring a low water-holding capacity and a high risk of wind erosion (USDA-NRCS, 2015b). The Sandhills are comprised of upland prairie dunes that account for 90% of the land area, with intervening subirrigated and wetland areas (Pfeiffer and Steuter, 1994; Schacht et al., 2000). The study site features predominantly upland dunes of sands, choppy sands, and

sandy ecological sites with intervening dry interdune regions and no subirrigated or wetland sites. Sand dunes of 9 to 60% slopes are oriented east to west, and thus comprised of predominately north and south-facing upland slopes (Schacht et al., 2000; Steinauer and Bragg, 1987).

Upland vegetation at the site is characterized as Sandhills mixed-grass prairie that is dominated by perennial graminoids, including sand bluestem (*Andropogon hallii* Hack.), little bluestem (*Schizachyrium scoparium* [Michx.] Nash), and prairie sandreed (*Calamovilfa longifolia* [Hook.] Scribn.). Cool-season graminoids, including sedge (*Carex* spp.), Scribner panicum (*Panicum oligosanthus* J. A. Shules subsp. *scribnerianum* [Nash] Fern.), needlegrasses (*Hesperostipa comata* [Trin. & Rupr.] Barkw. and *Hesperostipa spartea* [Trin.] Barkw.), and prairie junegrass (*Koeleria macrantha* [Ledeb.] J. A. Shultes) are common. Secondary to graminoids are forbs, which are found throughout and are comprised primarily of perennial species such as western ragweed (*Ambrosia psilostachya* DC.) and stiff sunflower (*Helianthus pauciflorus* Nutt.); some annual forbs also occur. Shrubs are also common, but account for a small portion of the community.

The preserve includes a 5217 ha west bison unit and a 3935 ha east bison unit that have been grazed year-round by independent bison herds since 1988 and 1986, respectively (Figure 1-2). The stocking rate of both units is 1 AUM ha⁻¹ (Biondini et al., 1999; Pfeiffer and Steuter, 1994), which is low relative to a moderate Sandhills stocking rate of 1.8 AUM ha⁻¹. Following a July 2012 wildfire, the stocking rates were reduced to 0.69 AUM ha⁻¹ and 0.49 AUM ha⁻¹, before increasing to 1.09 AUM ha⁻¹ and 1.12 AUM

ha⁻¹, respectively, by 2015. Both units were heavily grazed by cattle prior to being established (Steinauer and Bragg, 1987). Prescribed fire has been used intermittently in both units since 1991 at a return interval of 7.5 to 10 years (Biondini et al., 1999).

The Fairfield Creek Wildfire (part of the Region 24 Complex) burned major portions of the west and east bison units in late July 2012, resulting in burned and unburned areas in both (Figure 1-2). Precipitation levels were 75% below average for the 60 days prior to the wildfire. At the time of the fire, temperatures exceeded 38°C, relative humidity was below 15%, and winds were recorded up to 40 km hour⁻¹ (NOAA, 2012). Following the wildfire, departures from the mean annual precipitation in 2013, 2014, and 2015 were -1.73%, -11.48%, and 0.55%, respectively.

Grassland biomass and herbaceous species composition were tracked following the wildfire. In 2013, a pilot study was conducted to track the response of herbaceous biomass (the results of this pilot study are reported in Appendix I). A more rigorous field study was then conducted in 2014 and 2015. One hundred samples were collected in burned and unburned areas within each bison unit. Samples were collected in a 0.1 m² quadrat at 3 m intervals along a 300 m, north/south transect. Transects were randomly positioned, but excluded minor components of the landscape (e.g., patches of trees and large shrub islands). Sampling of herbaceous vegetation occurred near peak annual production in late July/early August. Aboveground herbaceous biomass within each quadrat was clipped at ground level using hand shears and sorted to live, standing dead, and litter. Herbaceous standing dead biomass and herbaceous litter biomass consisted of previous-years' growth, differentiated by the attachment to the soil or not, respectively.

Samples were transported to Lincoln, NE, oven-dried at 60°C for a minimum of 48 hours to remove all moisture, and then weighed to determine aboveground productivity. Plant community composition was sampled along the same transects by estimating percentage foliar cover of all live herbaceous species within each quadrat.

We tested for differences in aboveground herbaceous biomass between burned and unburned areas using one-way analysis of variance (significance level of <0.05) in the R statistical computing package (R Core Team, 2014). This comparison was used to infer whether wildfire overcame the resilience of Sandhills grassland resulting in a lack of grassland vegetation recovery and a transition to a mobile sand dune state. We assumed burned and unburned areas were similar prior to the wildfire based on close proximity and similar management and topography, which is consistent with other post-wildfire assessments (Fule et al., 2004). Generalized linear models were used with Poisson error distribution because data were normally distributed. Like other wildfire studies, samples ($n=200$) were pseudoreplicated because only one wildfire event occurred on the landscape (Fulé et al., 2005; Hurlbert, 1984; Laughlin and Fule, 2008; van Mantgem et al., 2001; Wiens and Parker, 1995). An important distinction here is that concerns of false positive results (type I error) from pseudoreplication do not apply to non-significant results (Heffner et al., 1996; Hurlbert, 1984). Data collected two and three years following the wildfire were first analyzed separately to test for difference between burned and unburned areas. Analysis was conducted for total herbaceous biomass, live herbaceous biomass, dead herbaceous biomass, herbaceous standing dead biomass, and litter biomass. Total herbaceous biomass is an aggregate of live herbaceous biomass and

dead herbaceous biomass. Dead herbaceous biomass is an aggregate of herbaceous standing dead biomass and herbaceous litter biomass.

We used nonmetric multidimensional scaling (NMDS) to assess plant community composition between burned and unburned areas, two and three years following the wildfire. NMDS is an unconstrained, distance-based ordination technique in which samples are represented in ordination space based on their similarity which corresponds to the distance between points (Debinski et al., 2011; Moranz et al., 2012). NMDS was performed using the *vegan* package (Oksanen et al., 2016) of the R statistical computing software (R Core Team, 2014) with Bray-Curtis distances (McGranahan et al., 2013a). We then calculated relative abundance of herbaceous species to detect differences between burned and unburned areas over time. Species that occurred in less than 5% of samples for both years were omitted from analysis to focus on relationships between dominant species in burned and unburned areas over time (as done elsewhere; Laughlin and Fule, 2008; McCune et al., 2002; Taylor et al., 2011)

RESULTS

Aboveground herbaceous biomass recovered to levels similar to unburned areas within two and three years following wildfire (Figure 1-3; Table 1-1), indicating that the resilience of Sandhills grassland to the combination of wildfire and drought was not overcome. Total herbaceous biomass and live herbaceous biomass in burned areas did not differ from unburned areas after two or three years. Dead herbaceous biomass was significantly lower in burned areas after two and three years. Differences in dead

herbaceous biomass were the result of a significant difference in litter. Standing dead biomass was not different in burned and unburned areas after two or three years.

NMDS ordination revealed plant community composition in burned and unburned areas did not differ two and three years following the wildfire (Figure 1-4). Relative abundance of grasses and forbs were similar in burned and unburned areas during this study (Table 1-2). The relative abundance of the plant community across the study site was dominated by graminoid species (Table 1-2). The warm-season graminoid species were the most dominant functional group two and three years following the wildfire. Dominant warm-season graminoids include sand bluestem, little bluestem, and prairie sandreed. Cool-season graminoid species were the second most dominant functional group, comprised mostly by sedge, Scribner panicum, and needlegrasses. Perennial forbs western ragweed and stiff sunflower were the most abundant forb and annual forbs made up only a small portion of the community.

DISCUSSION

Our study provides evidence that counters the perspective that Sandhills grassland is highly vulnerable to destabilization when wildfires occur during severe drought conditions (LANDFIRE, 2016; USDA-NRCS, 2015a). Two years following wildfire, aboveground herbaceous biomass in burned areas maintained the stability of the sand dunes and had recovered to levels that did not differ from unburned areas. Instead, long-term drivers that change the amount of root biomass, such as long-term changes in precipitation or long-term overgrazing, are associated with broad-scale destabilization of

sandy soil ecosystems rather than short-term or stochastic events such as fire (Miao et al., 2007; Pfeiffer and Steuter, 1994). In a recent experimental manipulation aimed at understanding destabilization in the Sandhills (Hartman, 2015; Wang et al., 2015), continual herbicide applications were required for 5 years before belowground root biomass was sufficiently lost to trigger destabilization. Destabilization only occurred earlier when continual herbicide application was combined with shallow disking and raking that removed aboveground and belowground plant material. Fire, by itself, does not create this type or severity of disturbance to belowground plant components in grasslands. Megadroughts spanning multiple decades, not fire, are considered to be the primary driver of broad-scale destabilization in the past (Mason et al., 2004; Miao et al., 2007; Schmeisser et al., 2009).

Post-wildfire studies in the Sandhills suggest that diversity plays an important role in stabilizing herbaceous biomass following wildfire. In this study and others, transient increases in forbs immediately following fire compensate for reductions in grass biomass in previous post-wildfire studies (Pfeiffer and Steuter, 1994; Steuter et al., 1995; Volesky and Connot, 2000). Grass biomass then recovered and displaced forbs in subsequent years (Pfeiffer and Steuter, 1994; Steuter et al., 1995; Volesky and Connot, 2000). All of these post-wildfire studies were conducted in Sandhills grassland with a relatively high diversity of functional groups at low stocking rates. Based on current evidence, it is unlikely that wildfire will overcome the resilience of a high diversity Sandhills grassland when grazing pressure is managed to avoid degradation. Avoiding management actions that reduce diversity, like overgrazing or using herbicides to eradicate all weeds, should

be a future consideration of management efforts. Actions that reduced diversity in the Sandhills have been shown to be less stable, in terms of their productivity, during periods of drought (Fay et al., 2015), but these actions might reduce the resilience of the Sandhills to wildfire by removing species central to the stability of sand dunes during periods of environmental extremes. We note, however, that no empirical evidence exists to indicate that wildfire in low diversity Sandhills grassland will result in destabilization, but it is in one of the only plausible contexts that remains untested.

In cases where vegetation biomass is used as an indicator for resilience, a secondary indicator important to rangeland managers is to detect changes in species composition. Changes in species composition can result in less palatable forage resources and changes in how disturbance regimes function in the future (e.g., McGranahan et al., 2012). We did not observe shifts in plant community composition and the relative abundance of species functional groups remained similar in burned and unburned areas throughout the study. These findings are consistent with evidence from other Great Plains grasslands that fire during drought has not resulted in long-term significant shifts in the plant community (Ansley et al., 2010; Rideout-Hanzak et al., 2011; Taylor et al., 2011; Towne and Kemp, 2008; Twidwell et al., 2012). These findings contrast with other regions, which are experiencing large shifts from native to exotic species dominance or to less preferred forage species (Knapp, 1996).

IMPLICATIONS

Our study adds to mounting evidence that fire as an infrequent event does not act as a destabilizing (positive) feedback in the Sandhills grassland. Multiple lines of evidence show a well-established and diverse Sandhills grassland readily recovers following fire (Bragg, 1998; Morrison et al., 1986; Pfeiffer and Steuter, 1994; Volesky and Connot, 2000). Like other grasslands around the world, the Sandhills grassland consists of fuels that readily support fire (Guyette et al., 2012). The major concern here is that policies and statutes that exaggerate, without scientific evidence, concerns over destabilization are promoting fire prevention to avoid a known type of state change (active sand dunes) but are actually contributing to the emergence of another by constraining the ability to prevent woody invasions (e.g., Sandhills grassland conversion to juniper woodland; Eggemeyer et al., 2006). Since European settlement, anthropogenic influences have decreased the occurrence of fire in the Sandhills and increased concerns over expanding *Juniperus virginiana* invasion (Bragg, 1985; Eggemeyer et al., 2006; Steinauer and Bragg, 1987). Given the evidence that indicates fire is not a positive feedback, and may even act as a negative (stabilizing) feedback (e.g., to prevent juniper invasions; Twidwell et al., 2013b, 2012, 2009), we recommend that STMs be modified to account for the present scientific consensus.

Instead of considering fire solely as a destabilizing feedback, principles of ecological stewardship suggest fire should be viewed with the same mentality that is used for grazing. Unlike fire, there is evidence that grazing can lead to small-scale active sand dunes (blowouts) when concentrated grazing removes aboveground forage and disrupts

fine root biomass (Stubbendieck et al., 1989). But instead of excluding grazers from the Sandhills, grazing is closely managed by monitoring grazing pressure and forage supply. We suggest a similar approach to fire management is warranted and more flexible legislation be enacted due to the recognized importance of fire-drought interactions in Great Plains grasslands (Twidwell et al., 2016a). Although fire and grazing increase bare ground, this does not in turn equate to erosion. Instead, broad-scale destabilization in the past has been linked to megadrought and the removal of belowground fine root biomass (Miao et al., 2007). Moving forward, it is important to understand the influence of social factors that influence our understanding of fire and its effects in rangelands (Twidwell et al., 2016b). Potential trade-offs to ecosystem services and unexpected transformations can result from overemphasizing a transition that has no empirical support (fire induced destabilization) while inadvertently setting the stage for an alternative state change (e.g., woody invasions as a result of fire exclusion).

While evidence is mounting that fire is not a dominant driver of Sandhills destabilization, additional research would clearly benefit our understanding of how to manage this system to avoid undesirable tipping points. Additional studies are needed that characterize relative ecosystem resilience. Resilience is defined as a measure of the amount of change an ecological state can absorb and continue to persist (Holling, 1973). Improving our understanding and characterization of resilience would benefit STM development and their utility. Difficulty in quantifying resilience and identifying the location of thresholds is a current limiting component of agency initiatives that operationalize the state-and-transition framework (e.g., ESDs; Twidwell et al., 2013a).

However, studies have recently been conducted to quantify the threshold between states by determining the amount of disturbance required to restore grasslands and overcome the resilience of a juniper woodland (Twidwell et al., 2013b). Similarly, Wonkka et al. (2015) monitored vegetation change following restoration actions to characterize whether resilience of a woody-invaded rangeland had been overcome. Moving forward, it is important to address the challenge of quantifying resilience of ecological states, thresholds between states, and how external system components contribute to resilience (Allen et al., 2016). We also need to better understand the role of functional diversity and adaptive capacity (as done in Elmqvist et al., 2003) and how they contribute to resilience of the Sandhills to wildfire and other drivers. To date, our understanding of the role of fire and drought in the Sandhills is built on a handful of post-wildfire studies, like this one. Alternative studies focused on the nexus of resilience, diversity, and disturbance would answer important management questions by identifying the context and interactions required to cause destabilization and ultimately to explain why fire has not caused broad-scale destabilization in modern Sandhills landscapes.

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data collection; Carissa Wonkka for analytical support; and Jeremy Hiller and the Niobrara Valley Preserve staff for technical support.

TABLES

Table 1-1. One-way analysis of variance testing for differences of aboveground herbaceous biomass in adjacent burned and unburned areas two and three years following a growing season wildfire in Nebraska Sandhills grassland.

	Df	Sum Sq	Mean Sq	F value	<i>P</i> *
Year 2 burned vs. unburned					
total herbaceous biomass	1	522	522.1	1.941	0.164
live herbaceous biomass	1	58	57.8	0.574	0.449
dead herbaceous biomass	1	858	858.5	8.819	0.003
standing dead biomass	1	9	9.3	0.184	0.668
litter biomass	1	705	704.9	23.390	1.890E-06
Year 3 burned vs. unburned					
total herbaceous biomass	1	190	190.4	0.611	0.435
live herbaceous biomass	1	24	23.6	0.130	0.719
dead herbaceous biomass	1	345	345	5.817	0.017
standing dead biomass	1	72	72.1	3.346	0.068
litter biomass	1	92	92.0	3.372	0.067
*Bold <i>P</i> values indicate statistically significant results ($P < 0.05$)					

Table 1-2. Herbaceous species abundance (%) of Nebraska Sandhills grassland in adjacent burned and unburned areas two and three years following a growing season wildfire that occurred during severe drought.

Scientific name	Common name	Acronym	Growth form	Life span	Season	2014		2015	
						Burned	Unburned	Burned	Unburned
<i>Andropogon hallii</i> Hack.	sand bluestem	ANHA	graminoid	perennial	warm	17.1	13.6	18.5	17.2
<i>Schizachyrium scoparium</i> (Michx.) Nash	little bluestem	SCSC	graminoid	perennial	warm	8.2	15.8	7.3	9.8
<i>Calamovilfa longifolia</i> (Hook.) Scribn.	prairie sandreed	CALO	graminoid	perennial	warm	8.2	9.2	4.9	3.1
<i>Sporobolus cryptandrus</i> (Torr.)	sand dropseed	SPCR	graminoid	perennial	warm	6.8	3.6	3.8	1.8
<i>Bouteloua hirsuta</i> Lag.	hairy grama	BOHI2	graminoid	perennial	warm	3.5	5.4	2.6	2.9
<i>Eragrostis trichodes</i> (Nutt.) Wood	sand lovegrass	ERTR3	graminoid	perennial	warm	0.3	0.1	3.5	8.1
<i>Panicum virgatum</i> L.	switchgrass	PAVI2	graminoid	perennial	warm	2.6	2.4	5.5	0.1
<i>Muhlenbergia pungens</i> Thurb.	sandhill muhly	MUPU2	graminoid	perennial	warm	0.3	2.5	0.4	0.5
<i>Paspalum setaceum</i> Michx.	sand paspalum	PASE5	graminoid	perennial	warm	0.4	0.1	0.4	1.7
<i>Bouteloua curtipendula</i> (Michx.) Torr.	sideoats grama	BOCU	graminoid	perennial	warm	0.5	1.8	0	0
<i>Carex</i> spp.	sedge	CAREX	graminoid	perennial	cool	17.4	17.2	10.4	11.3
<i>Panicum oligosanthos</i> J. A. Shultes subsp. <i>scribnerianum</i> (Nash) Fern.	Scribner panicum	DIOLS	graminoid	perennial	cool	6	3.5	10.5	10.2
<i>Hesperostipa</i> spp.	needleandthread or porcupinegrass	HECOC8/HESP11	graminoid	perennial	cool	4.6	6.3	4.5	0.8
<i>Panicum wilcoxianum</i> Vasey Freckman	Wilcox panicum	DIWI5	graminoid	perennial	cool	1	0.2	2.7	6.3
<i>Koeleria macrantha</i> (Ledeb.) J. A. Shultes	prairie junegrass	KOMA	graminoid	perennial	cool	2.9	1.2	1.6	2.6
<i>Vulpia octoflora</i> (Walt.) Rydb.	sixweeds fescue	VUOC	graminoid	annual	cool	1.3	1.5	0	0
<i>Ambrosia psilostachya</i> DC.	western ragweed	AMPS	forb	perennial	warm	5.1	5.1	10.5	11.2
<i>Helianthus pauciflorus</i> Nutt.	stiff sunflower	HEPA19	forb	perennial	warm	3.5	1.4	7.1	9
<i>Artemisia ludoviciana</i> Nutt.	cudweed sagewort	ARLU	forb	perennial	warm	3.4	0.8	4.8	0.8
<i>Tradescantia bracteata</i> Small ex Britt.	bracted spiderwort	TRBR	forb	perennial	cool	0.5	5.1	0	0.4

<i>Lygodesmia juncea</i> (Pursh) D. Don ex Hook.	rush skeletonplant	LYJU	forb	perennial	warm	0.3	0.9	0.3	0.1
<i>Helianthus annuus</i> L.	common sunflower	HEAN3	forb	annual	warm	2.8	0.6	0.1	1.6
<i>Plantago patagonica</i> Jacq.	woolly plantain	PLPA2	forb	annual	cool	2	0.8	0.1	0.1
<i>Eriogonum annuum</i> Nutt.	annual buckwheat	ERAN4	forb	annual	warm	1.2	1.1	0.4	0.1

Names are from (Stubbendieck and Kottas, 2007, 2005).

FIGURES

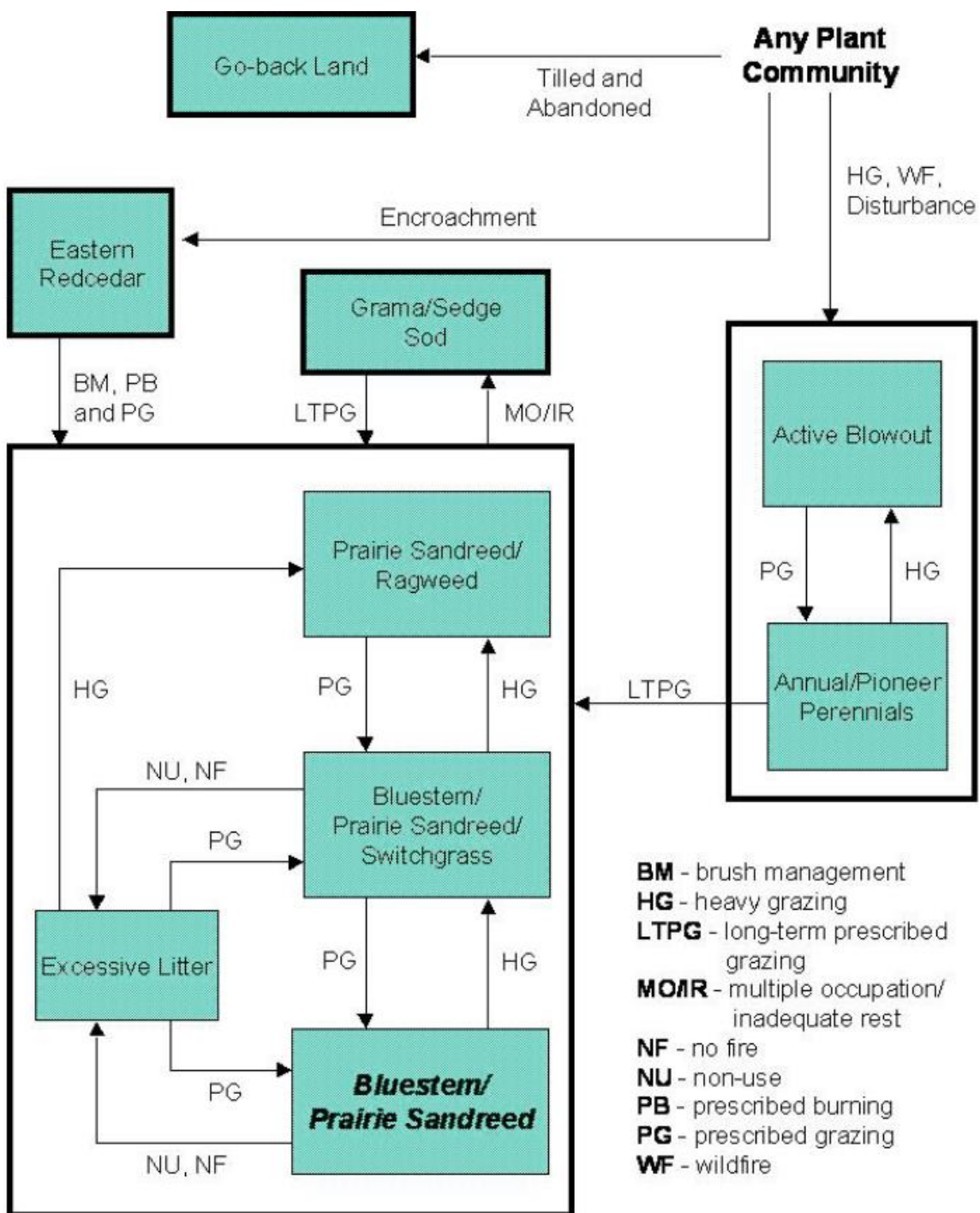


Figure 1-1. State-and-transition models (STM) characterize fire as a destabilizing feedback in sandy soil ecosystems. Shown here is an example of an STM that shows a

transitional pathway from a stabilized grassland state to a mobile sand dune state following wildfire. This STM (Sands Medium P.Z. 17-22; MLRA 065-Nebraska Sandhills) is from the Ecological Site Description (ESD) Database developed by the United States Department of Agriculture Natural Resources Conservation Service (USDA NRCS).

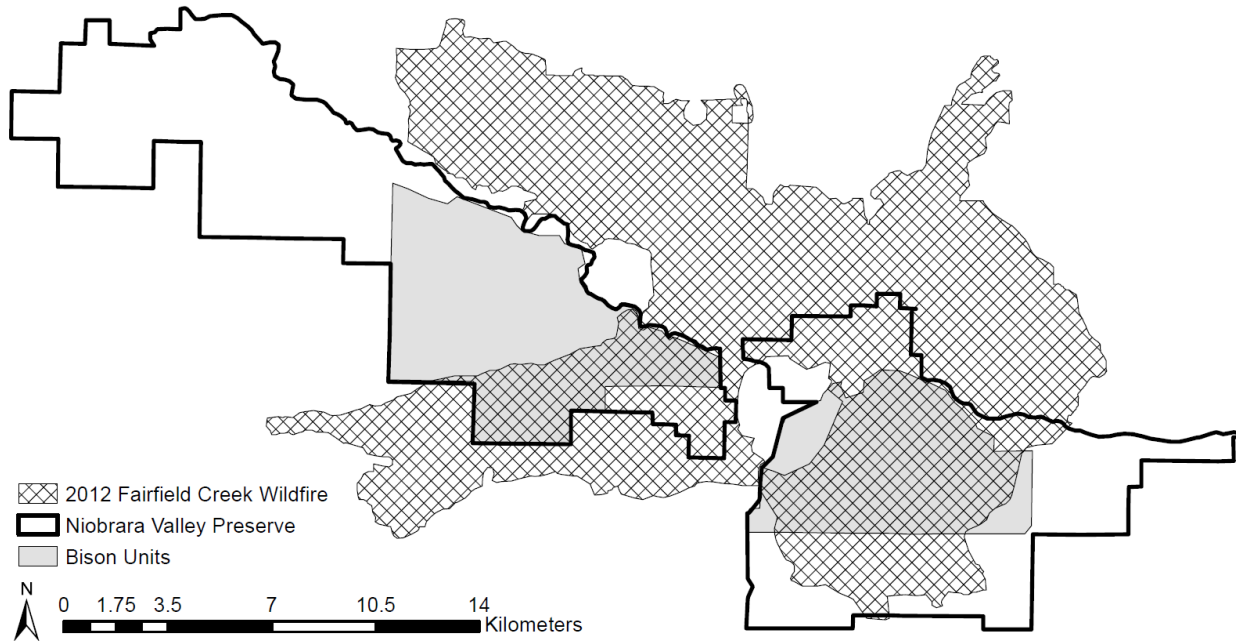


Figure 1-2. Map of the study site depicting the extent of the 2012 Fairfield Creek Wildfire on bison units at The Nature Conservancy's Niobrara Valley Preserve.

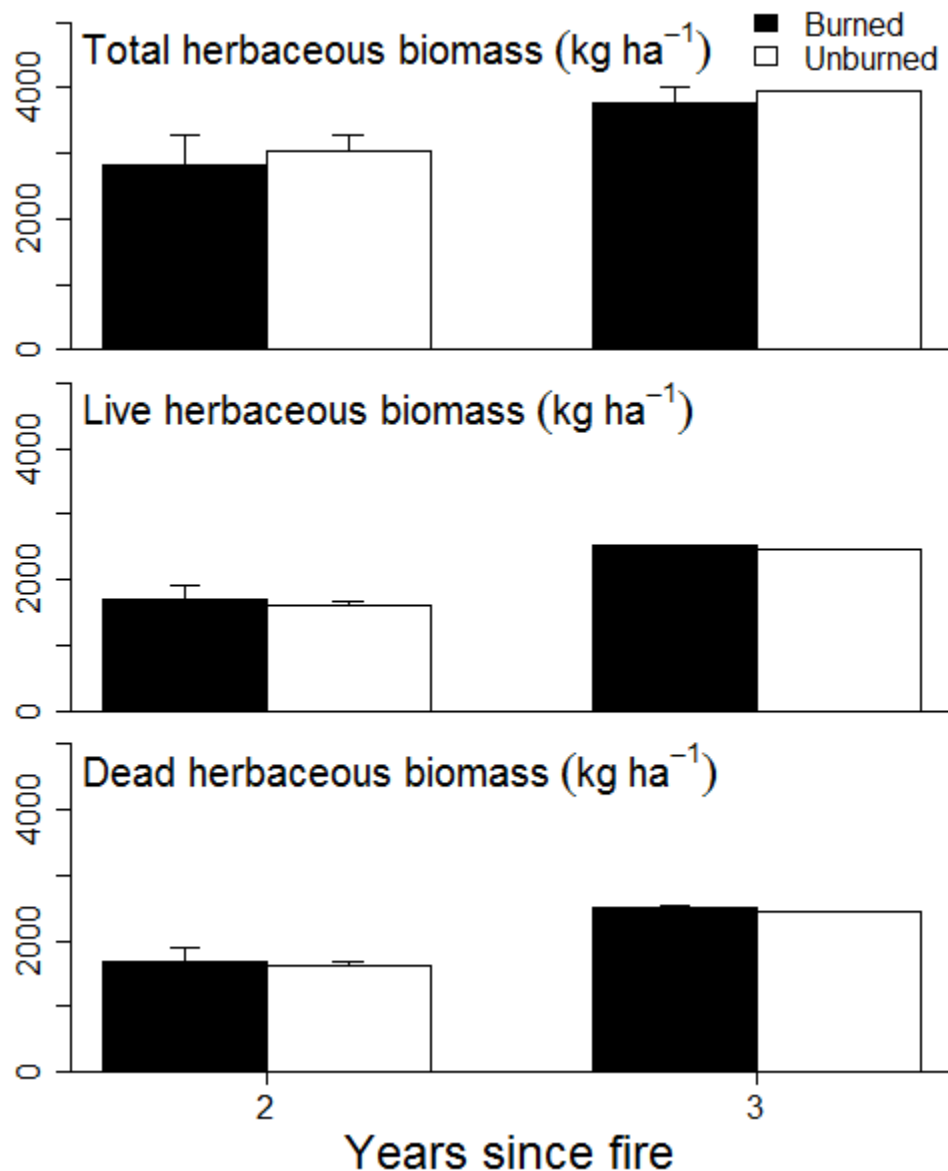


Figure 1-3. Mean and standard error of total herbaceous biomass, live herbaceous biomass, and dead herbaceous biomass from adjacent burned and unburned areas two and three years following a growing season wildfire in the Nebraska Sandhills grassland. Standard error bars are absent 3 years following wildfire in the unburned area because a

prescribed burn was conducted in the area resulting in an irregularity of treatment applications.

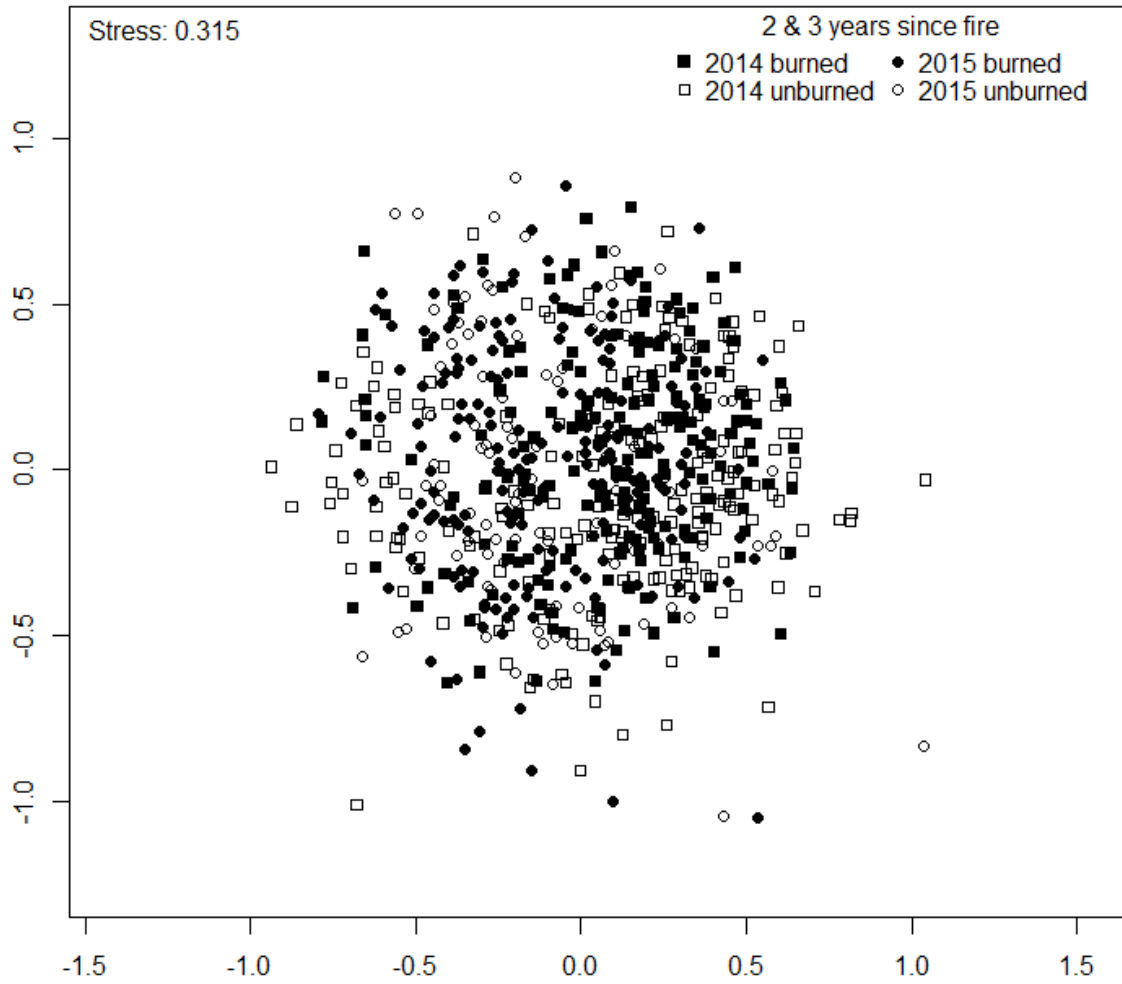


Figure 1-4. NMDS ordination of Nebraska Sandhills plant community composition from adjacent burned and unburned areas two and three years following a growing season wildfire. The distance between points in ordination space corresponds to differences between samples (Debinski et al., 2011; Moranz et al., 2012).

(A) 2013 April



(B) 2015 August

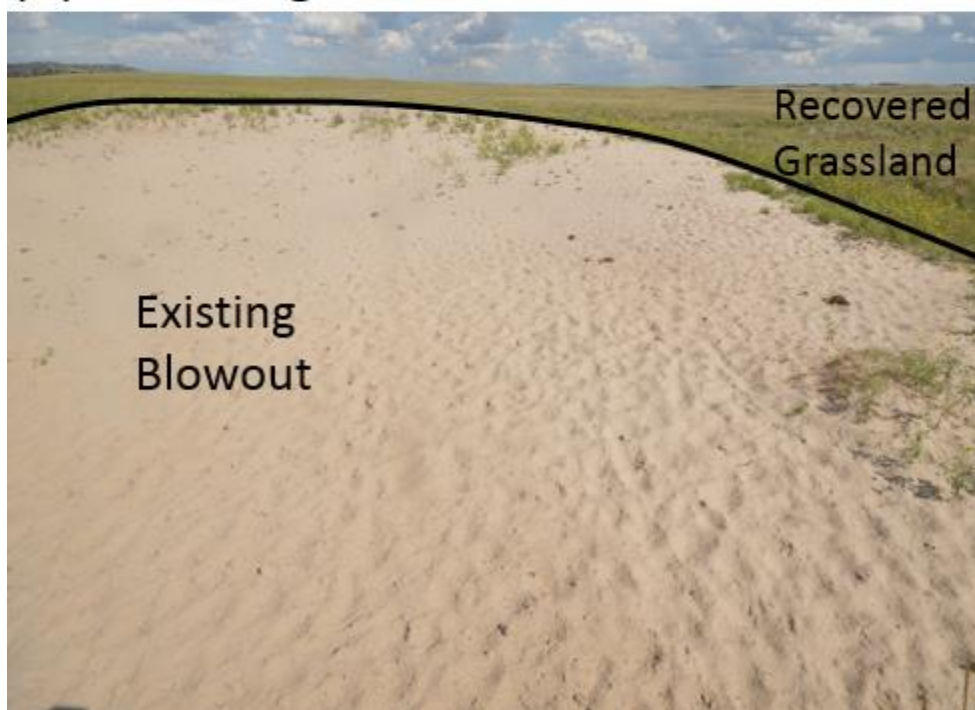


Figure 1-5. Pictures showing (A) an existing blowout next to burned grassland 9-months after the 2012 wildfire and before the start of the growing season, and (B) recovery of Sandhills grassland 3 year after the wildfire. Time lapse video showing more rapid recovery is available at <https://www.youtube.com/watch?v=YqMMIvAKuf0>.

CHAPTER II
RESTORATION OF HISTORICAL FIRE-GRAZER INTERACTIONS TO
INCREASE HETEROGENEITY IN SANDHILLS GRASSLAND

INTRODUCTION

The rangeland discipline has undergone a recent ideological shift to embrace heterogeneity as a fundamental principle for rangeland management (Fuhlendorf et al., 2012). Heterogeneity is the spatial and temporal variability in vegetation structure and composition essential for ecosystem function (Fuhlendorf and Engle, 2004; Wu and Loucks, 1995). Environmental heterogeneity begets greater diversity across multiple trophic levels (MacArthur and MacArthur, 1961; Tews et al., 2004), causing academics and natural resource professionals to question the appropriateness of rangeland practices that seek to promote uniform grassland structure and composition (Fuhlendorf et al., 2012). In rangelands, soil and topographic features contribute to inherent diversity of vegetation due to resource availability and plant species competition (Fuhlendorf and Engle, 2001; Patten and Ellis, 1995; Winter et al., 2011). Grassland species evolved within a dynamic, disturbance-driven spatially and temporally heterogeneous landscape with specialist niche space for flora and fauna (Biondini et al., 1989; Fuhlendorf and Engle, 2004; Devan A. McGranahan et al., 2012; Tews et al., 2004). Inherent and disturbance-driven heterogeneity has long-been minimized in utilitarian rangeland management systems that have sought to “manage for the middle” and promote uniform grazing distribution (Fuhlendorf et al., 2012; Twidwell et al., 2013a).

Management for the middle seeks to decrease spatial heterogeneity by utilizing moderate grazing pressure in order to minimize overgrazing and underutilization (Fuhlendorf et al., 2009). The rangeland discipline countered long-term overgrazing and increased livestock production by adopting utilitarian ideals that promoted uniform grazing at a moderate grazing pressure using fencing and water development to avoid too little or too heavy of grazing utilization and disturbance (Dunn et al., 2010; Fuhlendorf et al., 2012, 2009, 2006; Holechek et al., 2011). Therefore, heterogeneity of grassland vegetation managed for spatially uniformity is limited to variability associated with phenological changes over time. Restoration of spatial heterogeneity in rangelands has been proposed as an alternative approach to traditional rangeland management better suited for managing for multiple ecosystem services (Fuhlendorf et al., 2012).

Patch burning has been introduced as a way to transition away from homogeneous rangeland management in an effort to increase biodiversity and ecosystem service provisioning while still sustaining production value (Fuhlendorf and Engle, 2004, 2001). Patch burning attempts to increase heterogeneity in rangelands managed for uniformity over the last century by restoring the fire-grazing interaction (Fuhlendorf et al., 2009; Fuhlendorf and Engle, 2001). By applying spatially and temporally discrete fires and allowing grazers unrestricted access to burned and unburned areas, preferential grazer selection of burned areas creates a heterogeneous landscape of vegetation structure, composition, and biomass in various stages of recovery (Anderson et al., 2006; Fuhlendorf et al., 2006; Fuhlendorf and Engle, 2001). Application of patch burning in tallgrass, mixed-grass, and shortgrass prairies has increased the diversity of small

(Fuhlendorf et al., 2010) and large mammal communities (Augustine and Derner, 2015; Meek et al., 2008), increased desirable invertebrate species (Debinski et al., 2011), and decreased insects harmful to livestock (Polito et al., 2013; Scasta et al., 2012) all while improving cattle production (Allred et al., 2014, 2011a; Fuhlendorf and Engle, 2004; Limb et al., 2011; Vermeire et al., 2004), reducing invasive species (Cummings et al., 2007), and contributing to grassland restoration (McGranahan et al., 2014). Although studies have occurred across precipitation, productivity, and topographic gradients (Augustine and Derner, 2014; McGranahan et al., 2012; Winter et al., 2011), few studies have occurred in ecosystems consisting of predominantly sandy soil.

Restoring the fire-grazer interaction in the Sandhills of Nebraska is a relatively new idea for increasing heterogeneity, but patch burning has been controversial because the system has a long history of “managing for the middle” (Biondini et al., 1999; Steuter and Hidinger, 1999). Although fire occurred in the Sandhills more frequently prior to EuroAmerican settlement (Steinauer and Bragg, 1987), fire continues to drive grazing site selection irrespective of topographic features (Biondini et al., 1999). However, concerns over disturbances that increase bare ground has limited the application of fire in the Sandhills (Stubbendieck, 1998). Management of the Sandhills reflects the ideology of the rangeland discipline resulting in a structurally homogeneous grassland landscape with the greatest differences in structure and composition occurring as a result of topographic position (i.e., dune vs. interdune; Biondini et al., 1999; Schacht et al., 2000; Steuter et al., 1995), pastoral management history (e.g., differences in timing and intensity of grazing) or the occasional blowout (Stubbendieck et al., 1989).

The goal of this project was to determine the degree of heterogeneity in Nebraska Sandhills grassland where fire was reintroduced to a grazed landscape in an effort to restore historical fire-grazing interactions and increase landscape-level heterogeneity. The Sandhills of Nebraska is an expansive ecoregion where land managers have a long history of “managing for the middle” and preventing disturbances (e.g., fire) that expose bare ground. The primary expectation is that patch burning will create a landscape that is structurally and compositionally more dynamic in space. An alternative expectation, given the long-term management legacy in the Sandhills and that patch burning has recently been implemented, is that grassland structure and composition will continue to be similar in space and dynamic only in time. In this latter case, grassland structure and composition would be spatially homogeneous, irrespective of environmental gradients (e.g., topographic position, pastoral management history, and time since focal fire and grazing), and all patches would change as a result of differences resulting from temporal (intra-annual) sources of variation (e.g., plant senescence).

METHODS

This study was conducted in the Nebraska Sandhills ecoregion at The Nature Conservancy’s Niobrara Valley Preserve located in north-central Nebraska. The Sandhills are a contiguous, 5.6 million ha grassland ecoregion that support 500,000 cattle and Nebraska’s 7.2 billion dollar a year cattle industry. The study site receives 591 mm of precipitation annually, with 77% occurring during the April through September growing season (HPRCC, 2015). The mean annual temperature for the site is 10°C, ranging from -

3°C in January to 24°C in July, with an average frost free period of 152 days (HPRCC, 2015). Soils at the site are characteristic of Sandhills soils, comprised of Valentine fine sands (mixed, mesic Typic Ustipsamments; 83%) and Valent fine sand (mixed, mesic Ustic Torripsamments; 21%) featuring a high risk of wind erosion, low water-holding capacity and rapid infiltration of precipitation, with little or no runoff (USDA-NRCS, 2015b). Sands ecological site is the most common, but sandy, choppy sands and shallow to gravel also occur (Pfeiffer and Steuter, 1994; Steuter et al., 1995; USDA, 2013). Vegetation stabilized sand dunes of 0 to 80% slope are comprised of north and south-facing, gently-rolling dunes (Schacht et al., 2000; Steinauer and Bragg, 1987; USDA-NRCS, 2015b).

Vegetation at the study site is representative of the Sandhills and is characterized as Sandhills mixed-grass prairie (Kaul, 1998; Schacht et al., 2000). Differences in topographic features of unburned Sandhills grassland drives grazing site selection and both alter plant community composition because of differences in microclimate conditions and preferential grazing selection for interdune regions before the reduction in forage necessitates movement to upland dunes (Bragg, 1978; Schacht et al., 2000; Steuter et al., 1995). Warm-season graminoids dominate the Sandhills plant community on both south and north dunes; however, their deep root systems and low transpiration rates make them better adapted to the drier, south-facing slopes (Schacht et al., 2000; Steuter, 1987). Dominant warm-season graminoids include sand bluestem (*Andropogon hallii* Hack.), little bluestem (*Schizachyrium scoparium* [Michx.] Nash), and prairie sandreed (*Calamovilfa longifolia* [Hook.] Scribn.). Cool-season graminoids are found on north

dunes and dominate interdune regions that feature lower light intensities, lower temperatures, and high water availability due to greater organic matter content (Doliner and Jolliffe, 1979; Schacht et al., 2000). Interdunes are ideal for cool-season species because of lower water use efficiencies and available moisture at the soil surface during their growing season for the shallow root system (Schacht et al., 2000). Common cool-season graminoids include sedge (*Carex* spp.), Scribner panicum (*Panicum oligosanthus* J. A. Shules subsp. *scribnerianum* [Nash] Fern.), needlegrasses (*Hesperostipa* spp.), and prairie junegrass (*Koeleria macrantha* [Ledeb.] J.A. Shultes. Western ragweed (*Ambrosia psilostachya* DC.) and stiff sunflower (*Helianthus pauciflorus* Nutt.) are common perennial forbs. Annual forbs and shrubs also occur frequently (Schacht et al., 2000).

The preserve includes two independent units that have been grazed year-round by bison for over 20 years (Figure 2-1). The 5217 ha west bison unit and the 3935 ha east bison unit, established in 1988 and 1986, respectively, range from 2.5 km to 24 km apart. The original 975 ha east bison unit has expanded several times with the most recent addition of 953 ha in the fall of 2012. Grazing pressure in each unit has remained relatively low at 1 AUM ha⁻¹ for the entire year to follow conservation-based management (Biondini et al., 1999; Pfeiffer and Steuter, 1994). In 2012, during a prolonged drought, both herds were reduced to 0.69 AUM ha⁻¹ in the west bison unit and 0.49 AUM ha⁻¹ in the east bison unit (stocking rates based on bison numbers at fall round-ups). By 2015, stocking rates had increased to 1.09 AUM ha⁻¹ in the west bison unit and 1.12 AUM ha⁻¹ in the east bison unit. Since 1991, growing and dormant season fires have occurred inconsistently across both units based on the location of high fine fuel

loads with the intent of increasing biological diversity (Biondini et al., 1999; Pfeiffer and Steuter, 1994). Prior to being established, both units were grazed by cattle (Steinauer and Bragg, 1987).

We tracked vegetation structure and plant community composition in discrete fire patches that varied in space and time (fire patch size range: 188 ha to 3,436 ha; Figure 2-1). Fire patches include prescribed fires conducted in March 2012, 2013 and 2015, a prescribed fire conducted in September 2014, and a July 2012 wildfire. In March, the vegetation is primarily dormant and fires were conducted during mild conditions of below 26°C, below 32 km hour⁻¹, and above 20% relative humidity. In September, some live vegetation is present, but is transitioning from growing to dormant season. The fire was conducted during very mild conditions of below 15°C, below 16 km hour⁻¹, and above 60% relative humidity. The Fairfield Creek Wildfire (part of the Region 24 Complex) burned in late July 2012 when precipitation levels were 75% below average for the 60 days prior to the wildfire. At the time of the wildfire, temperatures exceeded 38°C, relative humidity was below 15%, and winds were recorded up to 40 km hour⁻¹ (NOAA, 2012). Bison were allowed immediate access to burned and unburned areas following all fires.

Within each patch, two, 300-m transects were sampled using a 0.1-m² quadrat placed at 3-m intervals. Transect locations were recorded using a handheld GPS unit to allow repeated sampling. Topographic position was recorded for each quadrat (north dune, south dune, or interdune). Vegetation structure was sampled along each transect over six periods spanning three seasons of vegetation growth. Sampling periods included

early growing season in June 2014 and 2015, late growing season in August 2014 and 2015, and dormant season in December 2014 and January 2016. Estimates of percentage foliar cover, litter cover, and bare ground were recorded using cover classes modified from Daubenmire (1959). Measurements of vegetation height and litter depth occurred at three points within each quadrat. Cover and height were recorded for live herbaceous vegetation (live graminoids and live forbs), live graminoids, live forbs, herbaceous standing dead vegetation (characterized as previous years' growth attached at the plant base), and shrub vegetation. Visual obstruction reading (VOR) was measured at a 4-m distance from the center of the quadrat, at a height of 1 m, in the four cardinal directions by recording complete coverage of 5-cm segments (Robel et al., 1970). Plant community composition was sampled along one transect during August sampling periods by estimating percentage foliar of each species using classes modified from Daubenmire (1959).

We used an unconstrained, distance-based ordination technique known as nonmetric multidimensional scaling (NMDS) to visually describe heterogeneity based on differences in vegetation structure and plant community. NMDS plots samples in ordination space with the distance between samples corresponding to the similarity among samples (Debinski et al., 2011; Moranz et al., 2012). Vegetation structure metrics and plant community composition were analyzed separately and species that occurred in less than 5% of samples for both years were omitted from analysis to focus on relationships between dominant species (Biondini et al., 1989; Laughlin and Fule, 2008; McCune et al., 2002; Taylor et al., 2011). Data were plotted in ordination space over time

according to sampling period and colored envelopes were added to describe spatial landscape features (e.g., bison units, fire patches, and topographic positions). Vegetation structure in each fire patch was plotted by sampling period to describe temporal variability. We used linear regression to determine a relationship between structural metrics and time since fire. We used boxplots of structural metrics to evaluate changes in time related to phenology. To assess phenological changes of herbaceous vegetation structural metrics over time, we plotted respective means of live herbaceous, herbaceous standing dead, and live and dead vegetation. All analyses were performed using the R statistical computing software (R Core Team, 2014). NMDS was performed using with Bray-Curtis distances in the vegan package (Oksanen et al., 2016).

RESULTS

The structure and composition of this Sandhills grassland exhibited greater temporal variability than spatial variability, which is indicative of a homogeneous grassland at the landscape-scale. Distribution of vegetation structural metrics differed between growing and dormant season sampling periods (Figure 2-2). Metrics of live vegetation (live herbaceous vegetation, live grasses, live forbs, live shrubs) were lowest during dormant sampling periods and herbaceous standing dead metrics were greater in the dormant season (Figure 2-6). Litter structural metrics, bare ground, and VOR did not vary over time. NMDS ordination showed structural metrics during growing season sampling periods were similar within each fire patch, but differences in structural metrics between growing and dormant season occurred during both years of the study, including

some separation between years for the dormant season sampling periods (Figure 2-4). All landscape features assessed in this study (bison unit, fire patch, or topographic position) did not contribute to spatial contrasts (Figure 2-2). This pattern of homogeneity occurred even after accounting for nested hierarchies among landscape features (e.g., fire patches located within individual bison units; Appendix 2-1 and Appendix 2-2). Grassland community composition was not temporally dynamic over the two years of this study or associated with landscape features (Figure 2-3).

Patch burning did not create a landscape that was structurally and compositionally more dynamic in space. Vegetation structure and composition were each similar across patches of different histories of time since fire (Figure 2-2 and 2-3, respectively). The lack of spatial patch contrasts is attributed to rapid growth of vegetation following fire. Vegetation structure rebounded quickly to levels of unburned areas for most structural measures (Figure 2-5). Following fire, structural metrics of live herbaceous and live graminoids returned to unburned levels after 300 days. Live forbs and live shrubs remained within unburned levels irrespective of days since fire. Herbaceous standing dead metrics and litter cover significantly increased following fire, returning to unburned levels after 450 days. Further, structural metrics of live herbaceous vegetation were greatest during growing season sampling periods and lowest during dormant sampling periods. Conversely, structural metrics of herbaceous standing dead vegetation during dormant sampling periods were similar or greater than during growing season sampling periods (Figure 2-7). Bare ground was greatest immediately following fire before significantly decreasing with time, returning to unburned levels after 300 days. Litter

depth and visual obstruction readings were variable, but did not significantly change after fire.

DISCUSSION

Patch burning has been introduced as a method for increasing spatial heterogeneity and biodiversity in rangelands (Fuhlendorf and Engle, 2001). We applied patch burning in a sandy soil, mixed-grass landscape that has been managed for uniformity in order to assess the ability for patch burning to create spatial heterogeneity. However, vegetation structure and plant community composition were spatially uniform across landscape features as a result of rapid vegetation recovery in the subsequent growing season following fire that limited the ability to create lasting variability. Instead, heterogeneity emerged temporally according to growing and dormant season conditions. Senescence of live herbaceous vegetation resulted in an inverse relationship between live and herbaceous standing dead vegetation where live herbaceous vegetation decreased and herbaceous standing dead increased in the transition from growing to dormant season (i.e., live herbaceous vegetation transitioned to become herbaceous standing dead vegetation; Figure 2-7). Therefore, temporal heterogeneity manifested as artifact of how vegetation structural metrics were classified in this study.

For patch burning to increase spatial heterogeneity, Allred et al. (2011) and McGranahan et al. (2012) hypothesize three major conditions are required: (a) discrete fires must be applied in patches on the landscape, (b) fire must be the primary driver of grazing selection and (c) forage demand must correspond at a moderate grazing pressure

to forage supply. Grazers preferentially select for areas recently burned and avoid areas with greater time since fire (Allred et al., 2011a; Fuhlendorf and Engle, 2004). However, fire can only drive grazing site selection when applied in patches on a landscape, allowing grazers unrestricted access to select between recently burned areas and areas not recently burned (Allred et al., 2011a). Application of fire on the entire landscape, eliminating unburned areas and creating a homogeneously burned landscape, removes the ability of fire to influence grazing selection (Allred et al., 2011a). Spatially discrete fires lose the ability to attract grazers and influence vegetation dynamics when fire intensity is constrained, such as by increased fuel moisture of an invasive species or unfavorable weather conditions (McGranahan et al., 2014). In a patch burned landscape, the ability for fire to reduce grazing selectivity at the plant level is lost when stocking rate does not adequately match the forage production of the burned area. Overstocking results in more uniform grazing as animals graze unburned areas because of depleted forage supply in burned areas. Understocking enables selective grazing in burned areas as vegetation growth exceeds grazing demand creating small-scale variability within a patch rather than broad scale variability between patches (Cummings et al., 2007; Fuhlendorf et al., 2009; Fuhlendorf and Engle, 2004).

In our study, a low stocking rate and the rapid growth of live herbaceous vegetation following fire constrained the ability of patch burning to create spatial heterogeneity. Bison were stocked an average of 0.85 AUM ha⁻¹ over the course of this study compared to a moderate Sandhills stocking rate of 1.8 AUM ha⁻¹. As a result, fire did not have the ability to modify grazing behavior or create spatial variability because

vegetation growth exceeded grazing demand and allowed grazers to selectively graze, thus, failing to reduce plant-level grazing selectivity.

The balance between forage supply and demand is complicated in semi-arid climates. Annual precipitation variability coincides with variable annual forage production complicating the ability for managers to maintain a constant annual grazing pressure. Lower and variable annual precipitation also fosters slower vegetation growth following fire which decreases grazer attraction to recently burned areas (Augustine and Derner, 2014; McGranahan et al., 2013b). Distance to water in semi-arid grasslands constrains grazing distribution because animals focally graze near water sources to conserve energy (Allred et al., 2011a). During our study, precipitation variability, including one of the driest years on record, created a dynamic system of variable forage production and relatively constant annual stocking rate on a patch burned landscape. In other prairie ecosystems, greater landscape-level heterogeneity has occurred in years where forage supply equals forage demand, because grazers have the ability to create grazing lawns of short vegetation structure in recently burned areas compared to areas not recently burned (Fuhlendorf and Engle, 2001; Fuhlendorf and Smeins, 1999). Conversely, homogeneity is expected when annual precipitation is at the extremes because vegetation growth exceeded grazing pressure during wet years and inadequate growth during dry years results in overgrazing (Fuhlendorf and Engle, 2001).

Patch burning in the tallgrass prairie has resulted in greater crude protein content from vegetation regrowth in burned areas compared to vegetation in areas not burned (Allred et al., 2011a; Sensenig et al., 2010). Increased forage quality has been prolonged

by focal fire and grazing that created a grazing lawn of short statured vegetation (Hobbs et al., 1991) and growing season fires that have extended the period of increased forage quality past the average growing season (Allred et al., 2011a; Biondini et al., 1999; Fuhlendorf et al., 2009; Milchunas et al., 1995). However, in the Sandhills, grazer attraction to recently burned areas decreases during the dormant season (Biondini et al., 1999) and forage growth can be limited following summer fire in years where precipitation is low (Pfeiffer and Steuter, 1994). These factors are more common to the semi-arid climates associated with lower and more variable precipitation and colder dormant season temperatures. Plant community composition and net primary production differences between Sandhills and tallgrass prairies correspond to lower forage production in the Sandhills that restricts the ability to create grazing lawns because of lower grazing pressure associated with lower forage supply. Further, the growing season is shorter and available resources are lower in the Sandhills compared to the tallgrass prairie at lower latitudes (Allred et al., 2011a), thus restricting the ability for vegetation to recover intrannually following fire or grazing (Pfeiffer and Steuter, 1994).

As expected, long-term management for uniformity resulted in spatially homogeneous grassland structure and composition, irrespective of landscape factors (e.g., pastoral management history, time since focal fire and grazing, and topographic position). Although landscape management histories, season of fire, and topographic features contribute to Sandhills grassland variability (Barnes et al., 1984; Biondini et al., 1989; Schacht et al., 2000), we found no differences in vegetation structure or plant community composition across topographic features or between areas burned during different

seasons. Previous studies have shown moderate cattle grazing influences plant community composition (Bragg, 1978; Schacht et al., 2000; Steuter et al., 1995). In our study, using conservation-based management, bison grazing pressure has remained low for nearly 30 years (Biondini et al., 1999; Pfeiffer and Steuter, 1994; Steuter et al., 1995). Further, bison have exhibited greater grazing distribution compared to cattle who focus grazing near water sources (Allred et al., 2011b) and in interdune regions (Schacht et al., 2000; Stubbendieck and Reece, 1992). The replacement of heavy cattle grazing with light bison grazing has allowed warm-season species to replace grazing-tolerant cool-season species in the interdune regions and decreased variability of plant community composition associated with topographic position that was reported in previous studies (Barnes et al., 1984; Schacht et al., 2000).

Our findings highlight the success of “management for the middle” in creating spatially and temporally uniform landscapes where moderate grazing by cattle attempted to optimize cattle production by reducing variability. Although bison units have been managed independently and fire has been applied to increase biodiversity, the low stocking rates in both units likely contributed to the lack of spatial heterogeneity in this study (Fuhlendorf and Engle, 2004). Further, in other grassland systems, conservation-based management using light grazing pressure also resulted in the loss of diversity as a few species became dominant by outcompeting for resources (Briggs and Knapp, 1995; Collins, 1992; Fuhlendorf et al., 2009). Patch burning has increased heterogeneity and biodiversity in other ecoregions, but alternative patterns of heterogeneity have emerged at multiple scales across patch burning studies (Augustine and Derner, 2014; McGranahan

et al., 2012; McGranahan et al., 2013b; Winter et al., 2011). Further research is needed in the Sandhills to identify how fire and grazing interact in a system characterized by high precipitation variability, contrasting topographic features, and sites with different management histories in order to advance our understanding of how patch burning creates heterogeneity.

ACKNOWLEDGEMENTS

We are grateful to the Nebraska Environmental Trust, University of Nebraska-Lincoln, and The Nature Conservancy for funding and support. We thank the staff of the Niobrara Valley Preserve for logistical support. We thank Doug Tosoni, Vicki Simonsen, Christine Bielski, Torie Lindsey, Brad Schick, Kyle Schumacher, Carissa Wonkka, Cheryl Dunn, Amanda Hefner, and Jeremy Hiller for assisting with data collection, data analysis, and technical support.

FIGURES

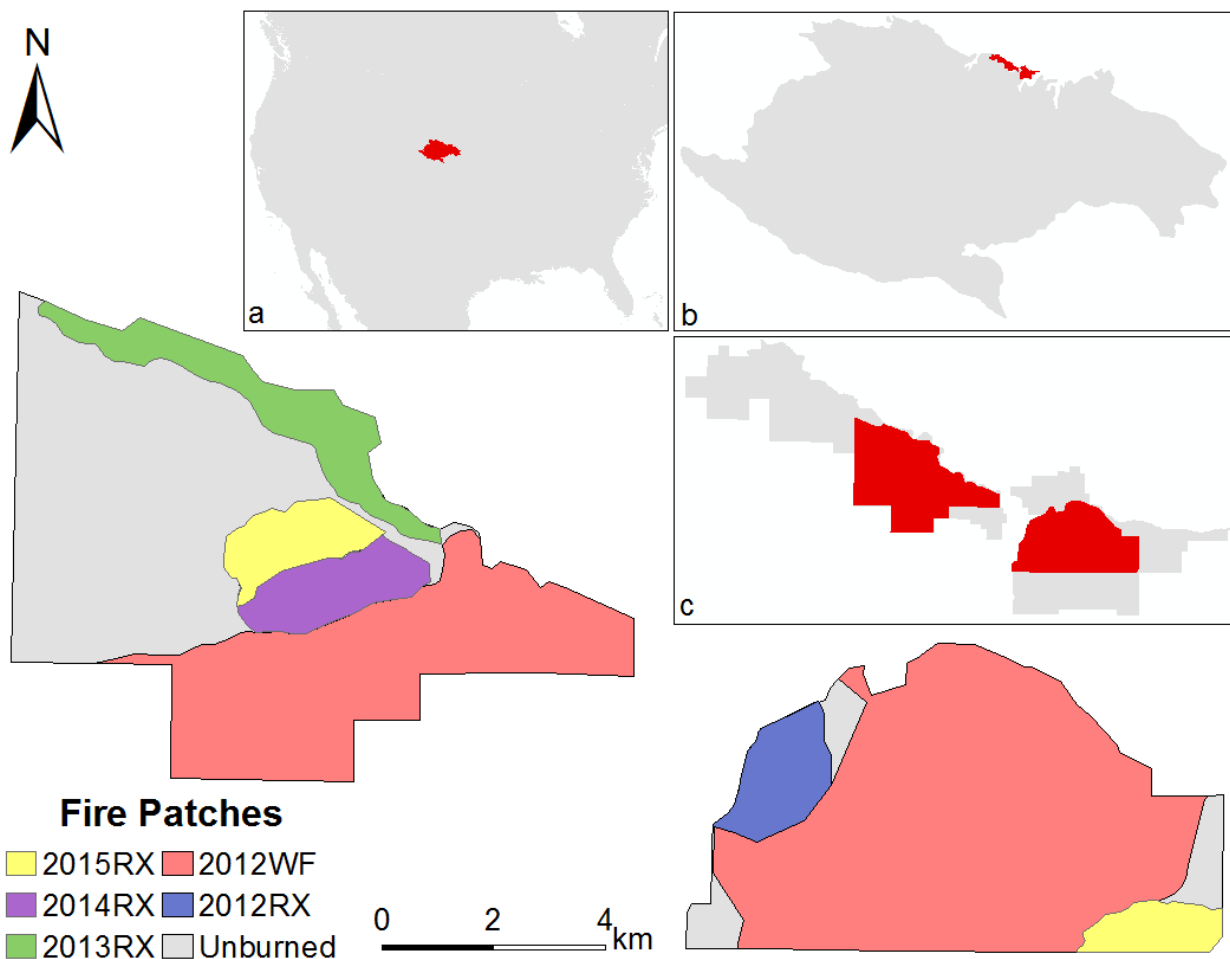


Figure 2-1. Map of fire patches within bison units at the Niobrara Valley Preserve. RX represents patches burned using prescribed fire in March (2015RX, 2013RX, and 2012RX) or September (2014RX) of each respective year. WF represents the Fairfield Creek Wildfire that burned in July 2012. The unburned patch has not burned since prior to 2012. Bison have unrestricted access to all fire patches within each unit. Insets illustrate the location of (a) the Nebraska Sandhills in central North America, (b) the

Niobrara Valley Preserve in the northern Sandhills, and (c) the bison units at the Niobrara Valley Preserve.

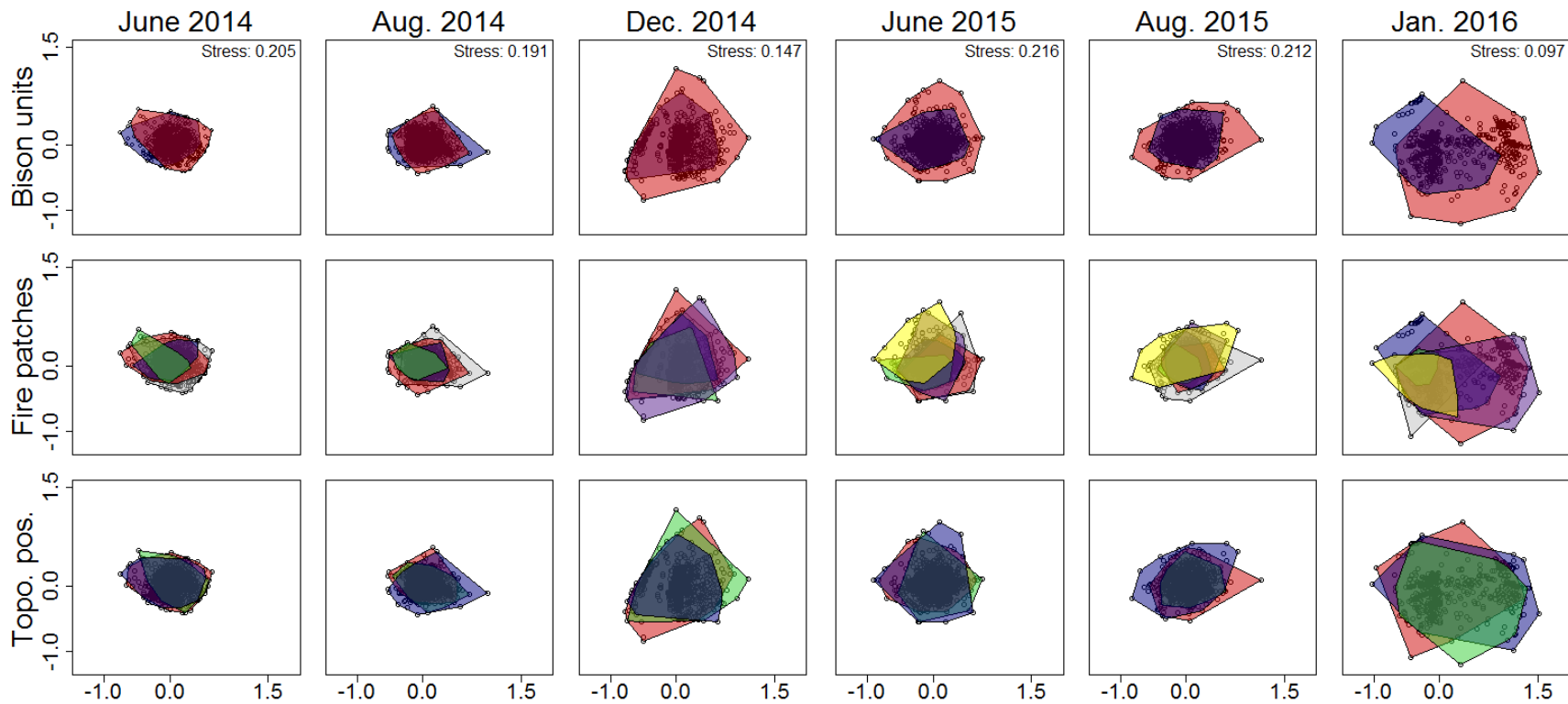


Figure 2-2. NMDS ordination of vegetation structure metrics collected over six sampling periods in Sandhills grassland managed with patch burning. Ordinations were duplicated for each sampling period with color envelopes corresponding to functional patch types. Bison unit color envelopes are red for the west and blue for the east. Fire patch color envelopes are red for 2012WF, blue for 2012RX,

green for 2013RX, purple for 2014RX, yellow for 2015RX, and gray for the area unburned since 2012. Topographic position color envelopes are red for north dunes, blue for south dunes, and green for interdunes.

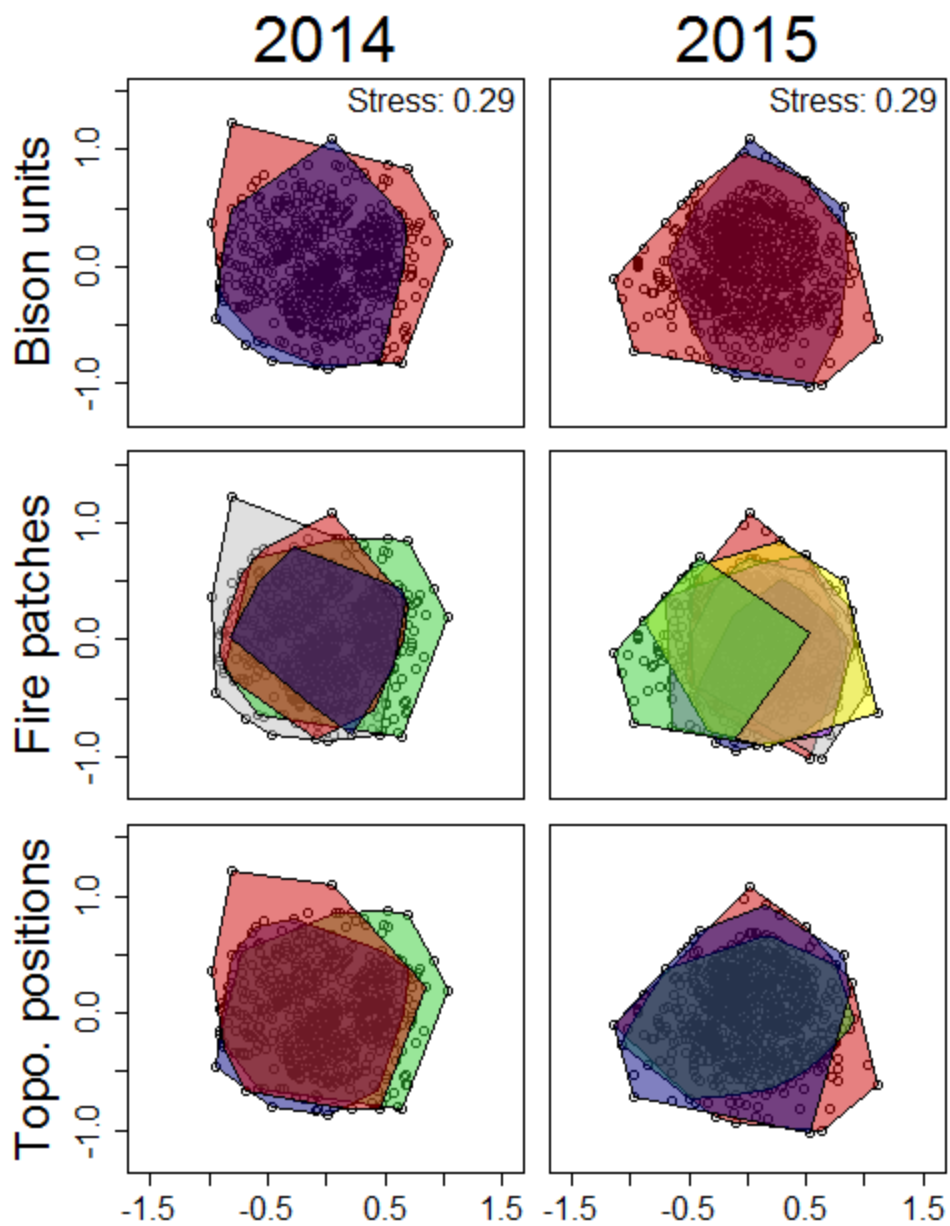


Figure 2-3. NMDS ordination of Nebraska Sandhills plant community composition collected in discrete fire patches during August 2014 and 2015. Ordinations were duplicated for each sampling period with color envelopes corresponding to functional patch types. Color envelopes for bison units are red for the west bison unit and blue for

the east bison unit. Color envelopes for fire patches are red for the 2012 wildfire, blue for the 2012 prescribed fire, green for the 2013 prescribed fire, purple for the 2014 prescribed fire, yellow for the 2015 prescribed fire, and gray for the area unburned prior to 2012. Color envelopes for topographic positions are red for north dunes, blue for south dunes, and green for interdunes.

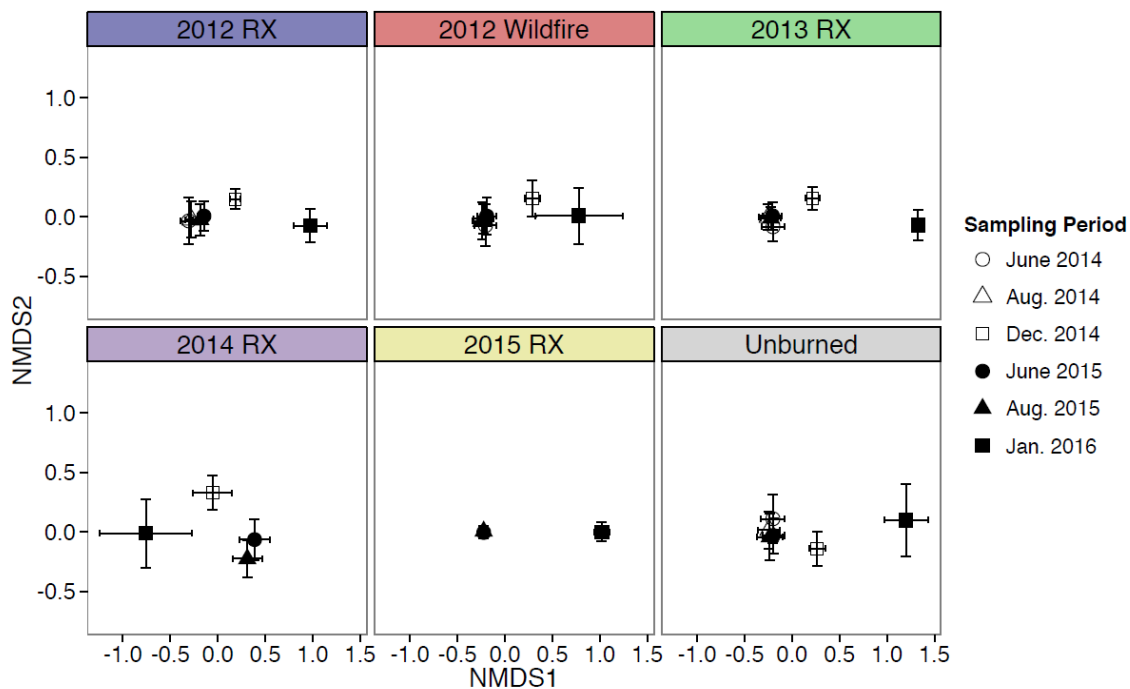


Figure 2-4. NMDS ordination of vegetation structural metrics from discrete fire patches in a Nebraska Sandhills grassland managed with patch burning. Shapes correspond to the six data sampling periods in the early growing, late growing and dormant seasons that were replicated.

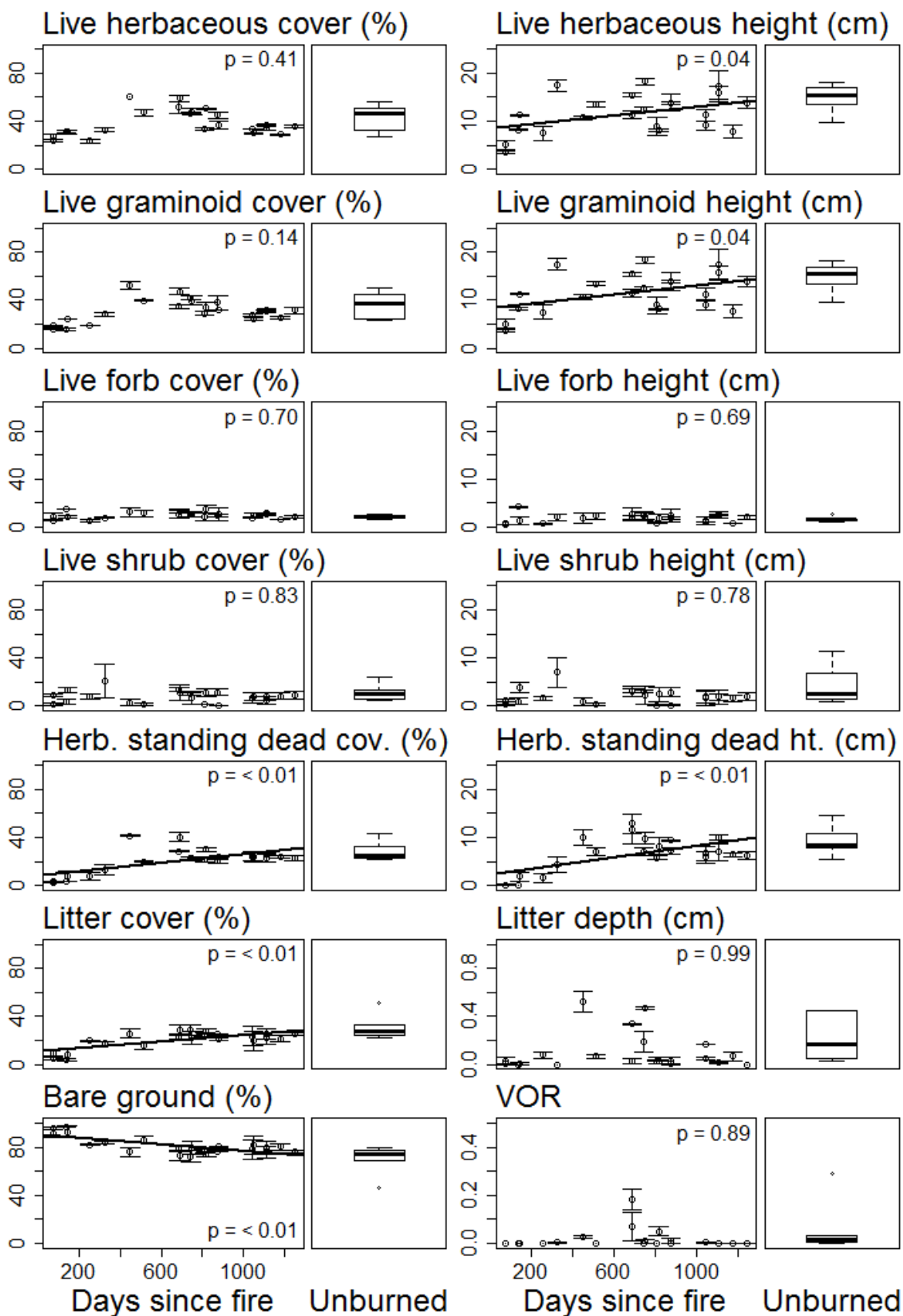


Figure 2-5. Mean ($n=2$) and standard error of structural metrics of growing season vegetation following fire in the Nebraska Sandhills grassland.

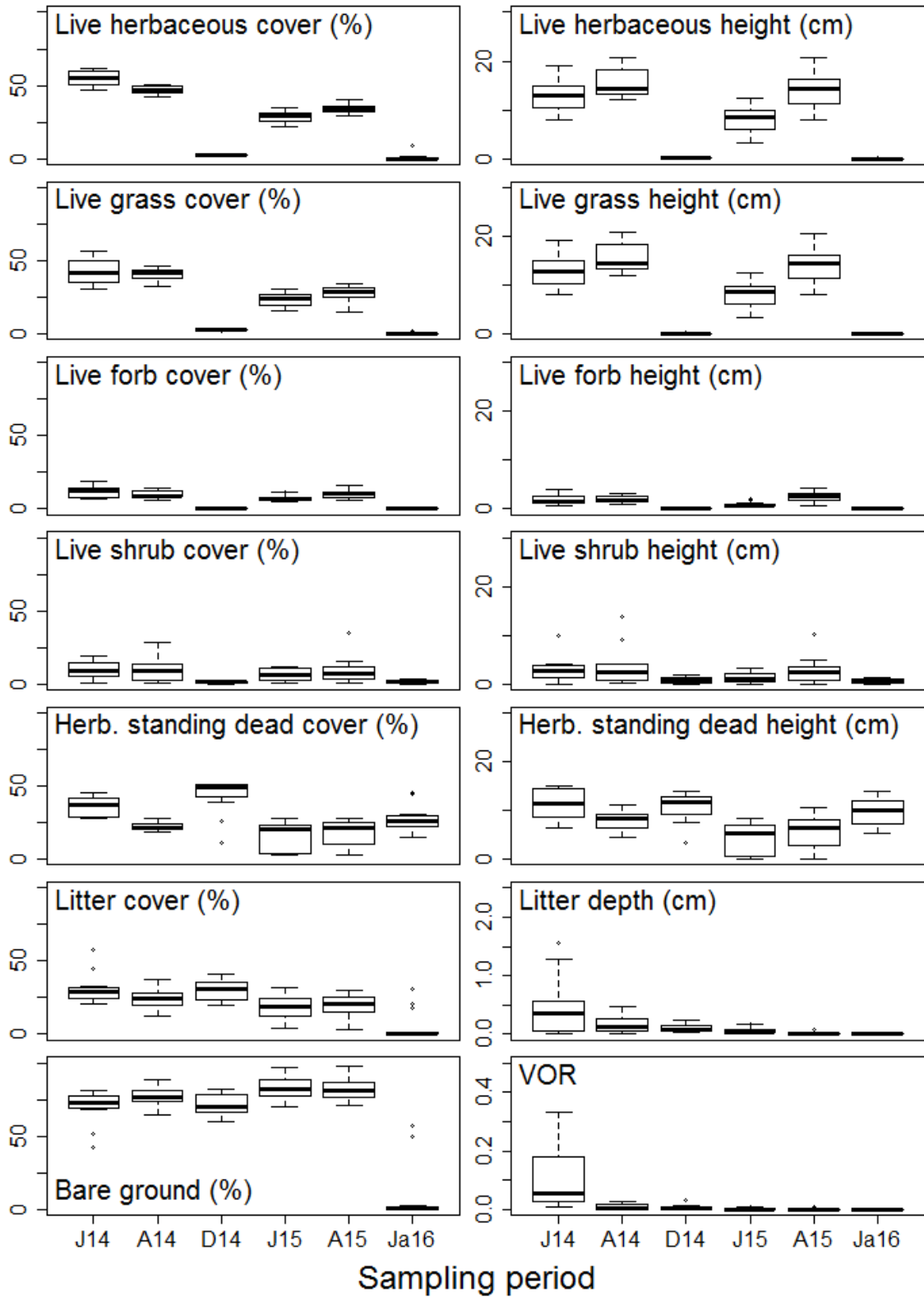


Figure 2-6. Mean and standard error of vegetation structural metrics collected over six sampling periods in a Nebraska Sandhills grassland managed with patch burning.

Abbreviation of sampling periods are: J14 = June 2014, A14 = August 2014, D14 = December 2014, J15 = June 2015, A15 = August 2015, Ja16 = January 2016.

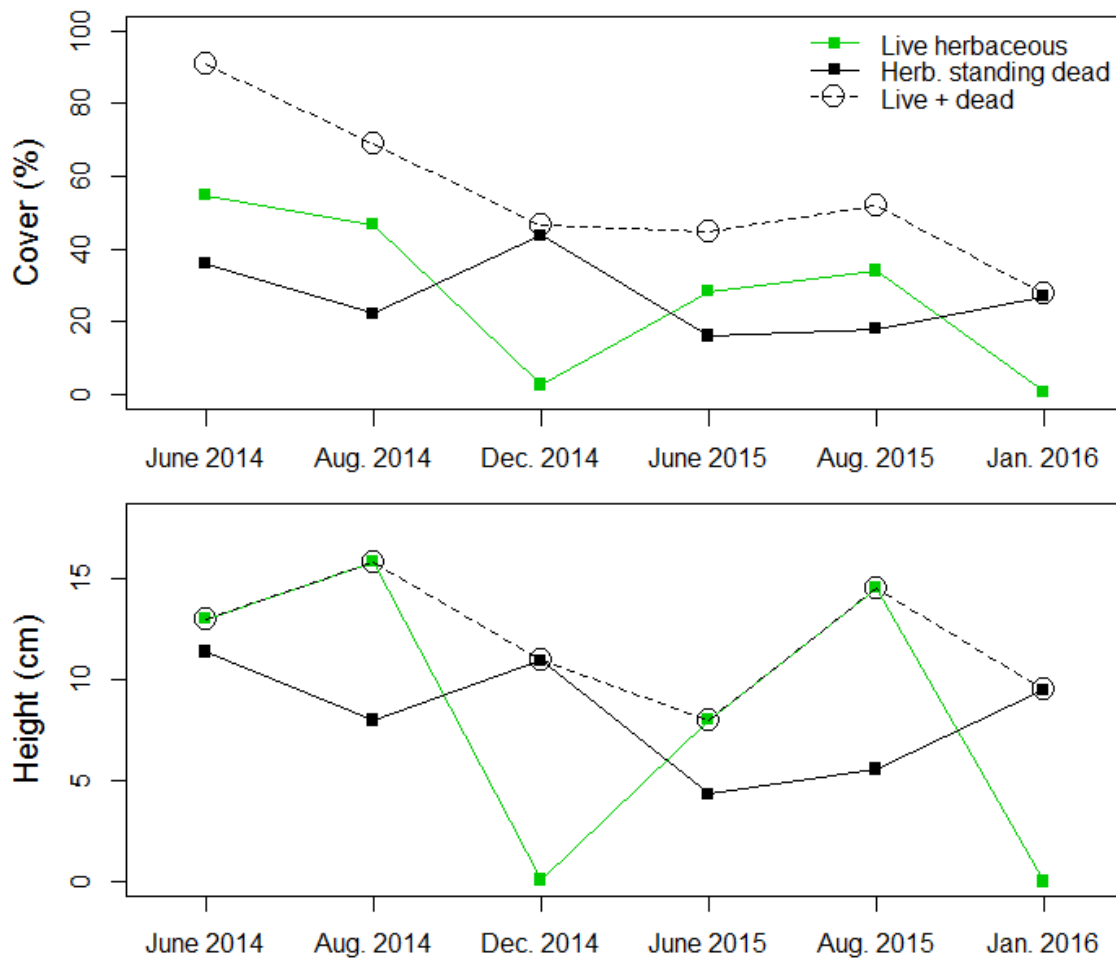
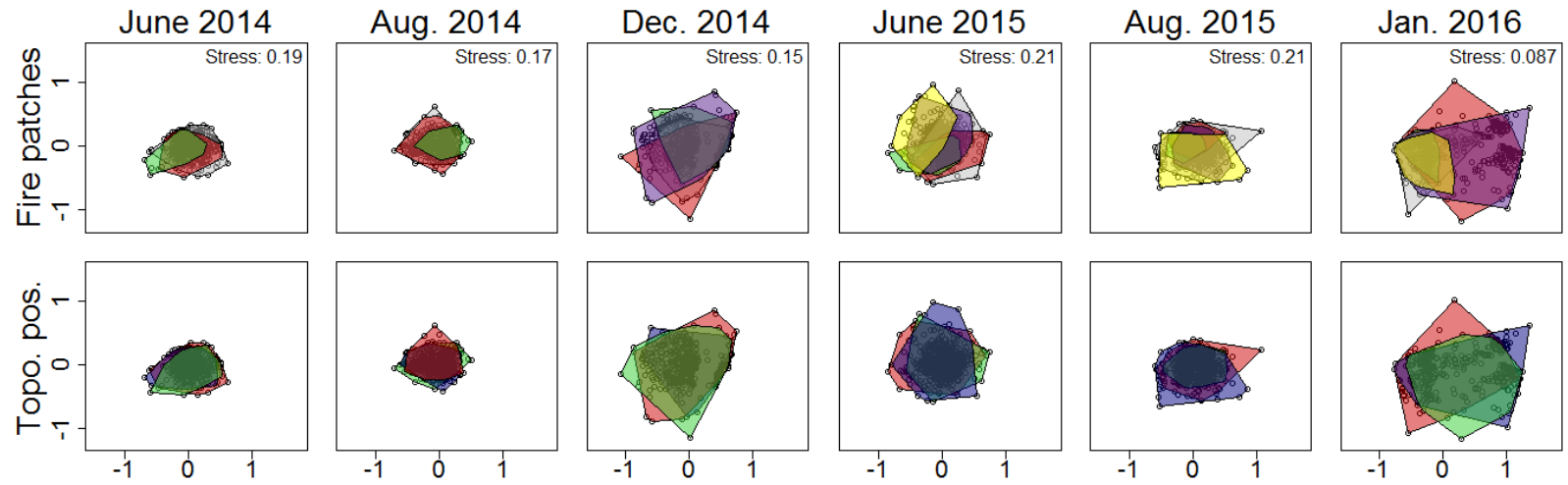
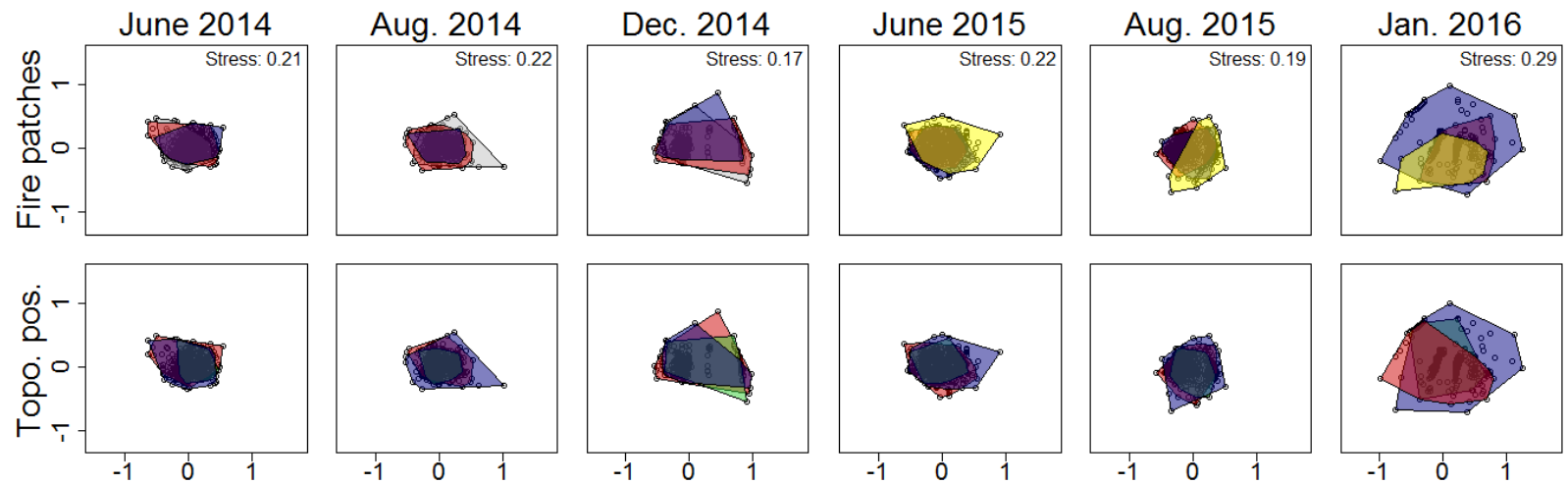


Figure 2-7. Structural metrics of live herbaceous and herbaceous standing dead vegetation in the transition from growing to dormant season in a Nebraska Sandhills grassland managed with patch burning.

(a) West bison unit

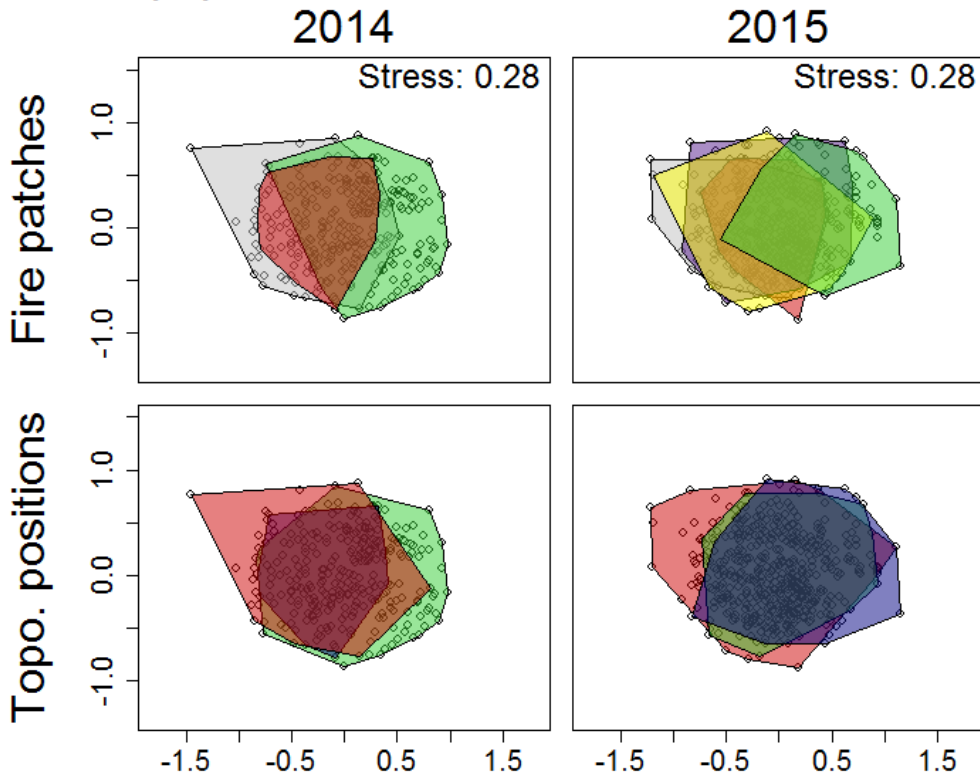


(b) East bison unit

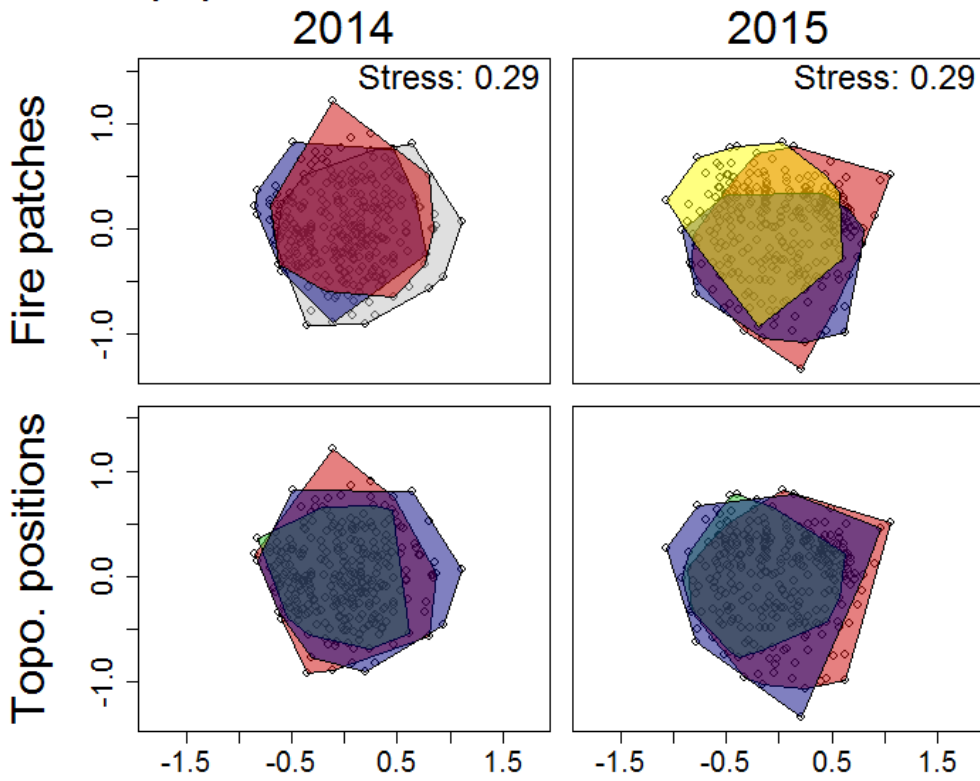


Appendix 2-1. NMDS ordination of vegetation structural metrics from six sampling periods in independent bison units in the Nebraska Sandhills grassland. Ordinations were duplicated for each sampling period in each bison unit with color envelopes corresponding to functional patch types. Color envelopes for fire patches are red for the 2012 wildfire, blue for the 2012 prescribed fire, green for the 2013 prescribed fire, purple for the 2014 prescribed fire, yellow for the 2015 prescribed fire, and gray for the area unburned prior to 2012. Color envelopes for topographic positions are red for north dunes, blue for south dunes, and green for interdunes.

(a) West bison unit



(b) East bison unit



Appendix 2-2. NMDS ordination of plant community composition over two years from independent bison units in the Nebraska Sandhills grassland. Ordinations were duplicated for each sampling year in each bison unit with color envelopes corresponding to functional patch types. Color envelopes for fire patches are red for the 2012 wildfire, blue for the 2012 prescribed fire, green for the 2013 prescribed fire, purple for the 2014 prescribed fire, yellow for the 2015 prescribed fire, and gray for the area unburned prior to 2012. Color envelopes for topographic positions are red for north dunes, blue for south dunes, and green for interdunes.

CHAPTER III
GRAZING FOR HETEROGENEITY WITHOUT FIRE: INITIAL
FINDINGS IN SANDHILLS GRASSLAND

INTRODUCTION

Patch-burn grazing (PBG) mimics the fire-grazer interaction on rangelands by allowing grazers unrestricted access to select between spatially and temporally discrete fire patches (Fuhlendorf and Engle, 2004, 2001). PBG attempts to create heterogeneity of rangeland vegetation to increase biodiversity of grassland flora and fauna (Fuhlendorf and Engle, 2004, 2001). However, general recommendations on rangelands, including those recommendations based on soil health, are to manage against disturbances, such as fire, that expose bare ground (USDA-NRCS, 2015a). Therefore, to increase grassland heterogeneity, managers desire a strategy for creating heterogeneity that does not rely on fire.

The objective of this study is to contrast attempts to use grazing without fire to manage for heterogeneity compared to PBG. Three heterogeneity treatments excluding fire employ fencing and cattle grazing from May to November to create discrete disturbance patches. These include: rotational grazing, patch-grazing, and season-long grazing. Rotational grazing (RG) is the movement of cattle between 3 separate patches with one grazing period in each patch throughout the course of the grazing season. Patch-grazing (PG) uses fencing and variable stocking rates to vary the level of disturbance in 6

discrete patches. Season-long grazing (SLG) uses one contiguous patch that is grazed for the duration grazing season.

METHODS

This study was conducted in the Sandhills ecoregion at The Nature Conservancy's Niobrara Valley Preserve in north-central Nebraska. Management of the preserve seeks to promote native flora and fauna by increasing grassland biodiversity. Cattle grazing is used to create grassland variability on portions of the preserve. Cattle graze during the May to November grazing season in each heterogeneity treatment. Discrete fires were applied in the PBG treatment in 2014 and 2015 during March. Grazing pressure was kept constant in the RG and SLG treatments. Grazing pressure varies spatially and temporally between patches in the PG treatment.

In mid-June 2014 and 2015, we sampled vegetation structural metrics in focal patches within each unit that were delineated by time since focal disturbance (Figure 3-1). Sampling occurred at 15 random points distributed across each patch using a 0.1 m² quadrat. Estimates of percentage foliar cover and height measurements were recorded for live herbaceous vegetation, live graminoids, live forbs, herbaceous standing dead vegetation, and shrub vegetation using cover classes modified from Daubenmire (1959). Litter depth and estimates of percentage litter cover and bare ground were also recorded. Height and depth measurements were taken from three points within each quadrat. Visual obstruction reading was measured at a 4 m distance from the center of the quadrat, at a height of 1 m, in the four cardinal directions by recording complete coverage of 5 cm

segments (Robel et al., 1970). Topographic position was also recorded for each quadrat as either north dune, south dune, or interdune. Only data collected in 2015 was used for analysis.

RESULTS

Mean vegetation structure was similar at the landscape level across heterogeneity treatments (Figure 3-2), making comparisons between heterogeneity treatments appropriate. PBG increased bare ground and decreased herbaceous standing dead structural metrics and litter cover while maintaining similar levels of live herbaceous cover (Figure 3-3). Herbaceous standing dead structural metrics, litter cover, and bare ground were similar between patches in treatments that excluded fire. Live shrub cover and height were greater with greater time since focal disturbance in the patch-burn grazing treatment. Live herbaceous vegetation and live forbs were greater with greater time since focal disturbance in the RG treatment. Height of live herbaceous vegetation, live graminoids, and live forbs were slightly greater with time since focal disturbance in PBG and RG (Figure 3-4). Vegetation structural metrics were highly variable in PG patches irrespective of time since focal disturbance. Litter depth and VOR were near zero in all treatments.

CONCLUSIONS

- PBG reduced litter and increased bare ground while maintaining levels of live vegetation similar to other treatments.

- RG and PG treatments created variability of several vegetation classes between patches, but failed to reduce litter and increase bare ground.
- Moving forward, there is a need to identify heterogeneity *of what* and *for what*. Organisms are responding to different types of heterogeneity and not simply spatial differences in the height or cover of vegetation. Identifying species that respond to differences in bare ground, or those species that respond to the occurrence of bare ground that corresponds to high vegetation structural metrics could identify tradeoffs of using grazing practices without fire.

ACKNOWLEDGEMENTS

We are grateful to the Nebraska Environmental Trust, University of Nebraska-Lincoln, and The Nature Conservancy for funding. We thank the staff of the Niobrara Valley Preserve for logistical support. We thank Doug Tosoni and Vicki Simonsen for assisting with data collection.

TABLES

Table 3-1. Mean and standard error of structural metrics of patches occurring in four heterogeneity treatments.

System	Acronym	Patch	(%)						
			Live herbaceous	Live graminoid	Live forb	Live shrub	Herb. standing dead	Litter	Bare ground
Patch-burn grazing	PBG	2014 Rx	33 + 2	21 + 2	12 + 2	4 + 2	13 + 1	9 + 1	92 + 1
Patch-burn grazing	PBG	2015 Rx	35 + 1	26 + 2	11 + 2	0 + 0	3 + 0	3 + 0	97 + 0
Patch-burn grazing	PBG	Unburned	35 + 1	26 + 2	10 + 1	5 + 2	26 + 3	20 + 4	81 + 4
Rotational grazing	RG	1	24 + 2	20 + 2	4 + 1	5 + 2	16 + 0	13 + 3	87 + 2
Rotational grazing	RG	2	39 + 1	21 + 2	20 + 2	0 + 0	18 + 1	12 + 3	88 + 3
Rotational grazing	RG	3	27 + 2	18 + 1	11 + 2	0 + 0	19 + 2	13 + 2	88 + 2
Patch-grazing	PG	1	46 + 3	40 + 4	20 + 2	2 + 1	25 + 3	32 + 5	68 + 5
Patch-grazing	PG	2	35 + 4	25 + 4	15 + 2	6 + 2	26 + 3	23 + 2	78 + 2
Patch-grazing	PG	3	35 + 1	29 + 2	11 + 2	1 + 1	18 + 2	16 + 0	86 + 0
Patch-grazing	PG	4	38 + 2	23 + 2	15 + 1	3 + 1	23 + 2	17 + 1	84 + 1
Patch-grazing	PG	5	35 + 3	33 + 3	9 + 1	5 + 2	32 + 3	21 + 2	79 + 2
Patch-grazing	PG	6	40 + 3	35 + 4	8 + 3	4 + 1	18 + 1	18 + 1	82 + 2
Season-long grazing	SLG	1	35 + 1	20 + 2	11 + 1	1 + 1	20 + 2	13 + 2	88 + 2

System	Acronym	Patch	(cm)						
			Live herbaceous	Live graminoid	Live forb	Live shrub	Herb. standing dead	Litter	VOR
Patch-burn grazing	PBG	2014 Rx	9 + 1	9 + 1	1 + 0	0 + 0	2 + 0	0 + 0	0 + 0
Patch-burn grazing	PBG	2015 Rx	8 + 0	8 + 0	1 + 0	0 + 0	0 + 0	0 + 0	0 + 0
Patch-burn grazing	PBG	Unburned	19 + 1	19 + 1	3 + 1	1 + 1	4 + 1	0 + 0	0 + 0
Rotational grazing	RG	1	10 + 0	10 + 0	0 + 0	0 + 0	7 + 2	0 + 0	0 + 0
Rotational grazing	RG	2	14 + 1	14 + 1	2 + 0	0 + 0	3 + 1	0 + 0	0 + 0
Rotational grazing	RG	3	11 + 1	10 + 1	1 + 0	0 + 0	5 + 1	0 + 0	0 + 0
Patch-grazing	PG	1	18 + 2	18 + 2	6 + 1	0 + 0	8 + 2	0 + 0	0 + 0
Patch-grazing	PG	2	10 + 1	10 + 1	1 + 0	0 + 0	6 + 1	0 + 0	0 + 0
Patch-grazing	PG	3	12 + 1	12 + 1	2 + 0	0 + 0	2 + 0	0 + 0	0 + 0
Patch-grazing	PG	4	12 + 1	11 + 1	4 + 1	0 + 0	3 + 1	0 + 0	0 + 0
Patch-grazing	PG	5	15 + 1	15 + 1	0 + 0	2 + 0	7 + 1	0 + 0	0 + 0

Patch-grazing	PG	6	18 + 1	17 + 1	1 + 0	0 + 0	6 + 1	0 + 0	0 + 0
Season-long grazing	SLG	1	17 + 2	16 + 2	3 + 1	0 + 0	5 + 0	0 + 0	0 + 0

FIGURES

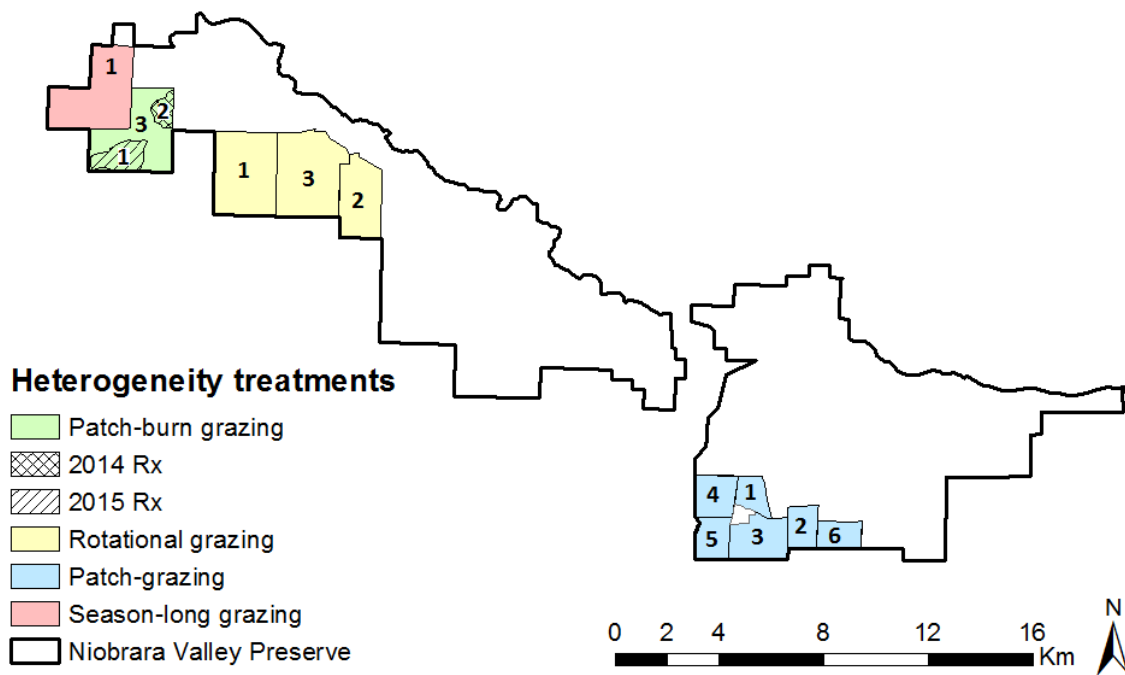


Figure 3-1. Heterogeneity treatments and associated patches applied at the Niobrara Valley Preserve in the Nebraska Sandhills grassland. Numbers delineate the most recently disturbed patch.

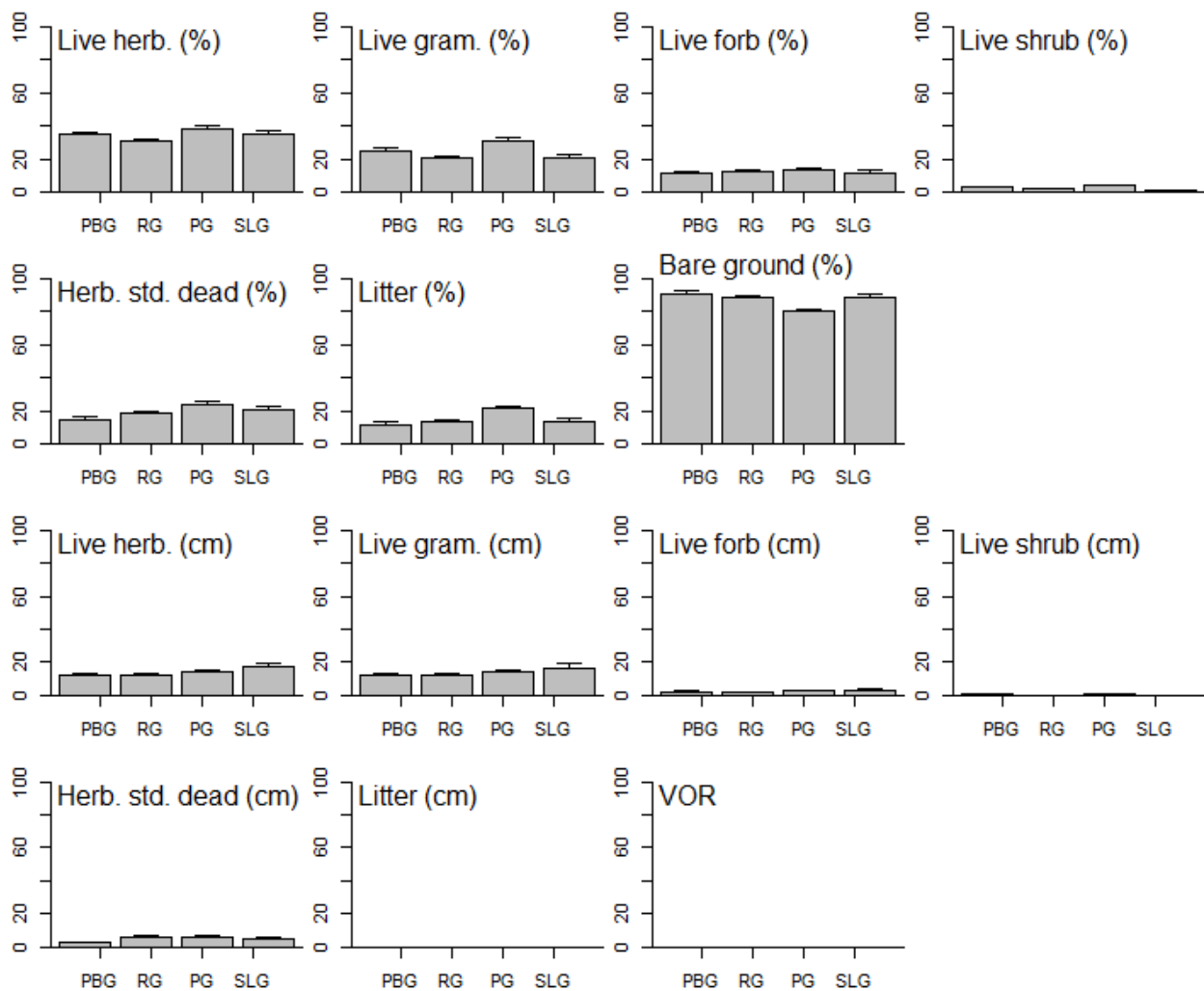


Figure 3-2. Mean and standard error of Nebraska Sandhills vegetation structure for each heterogeneity treatment. Data collected in June 2015.

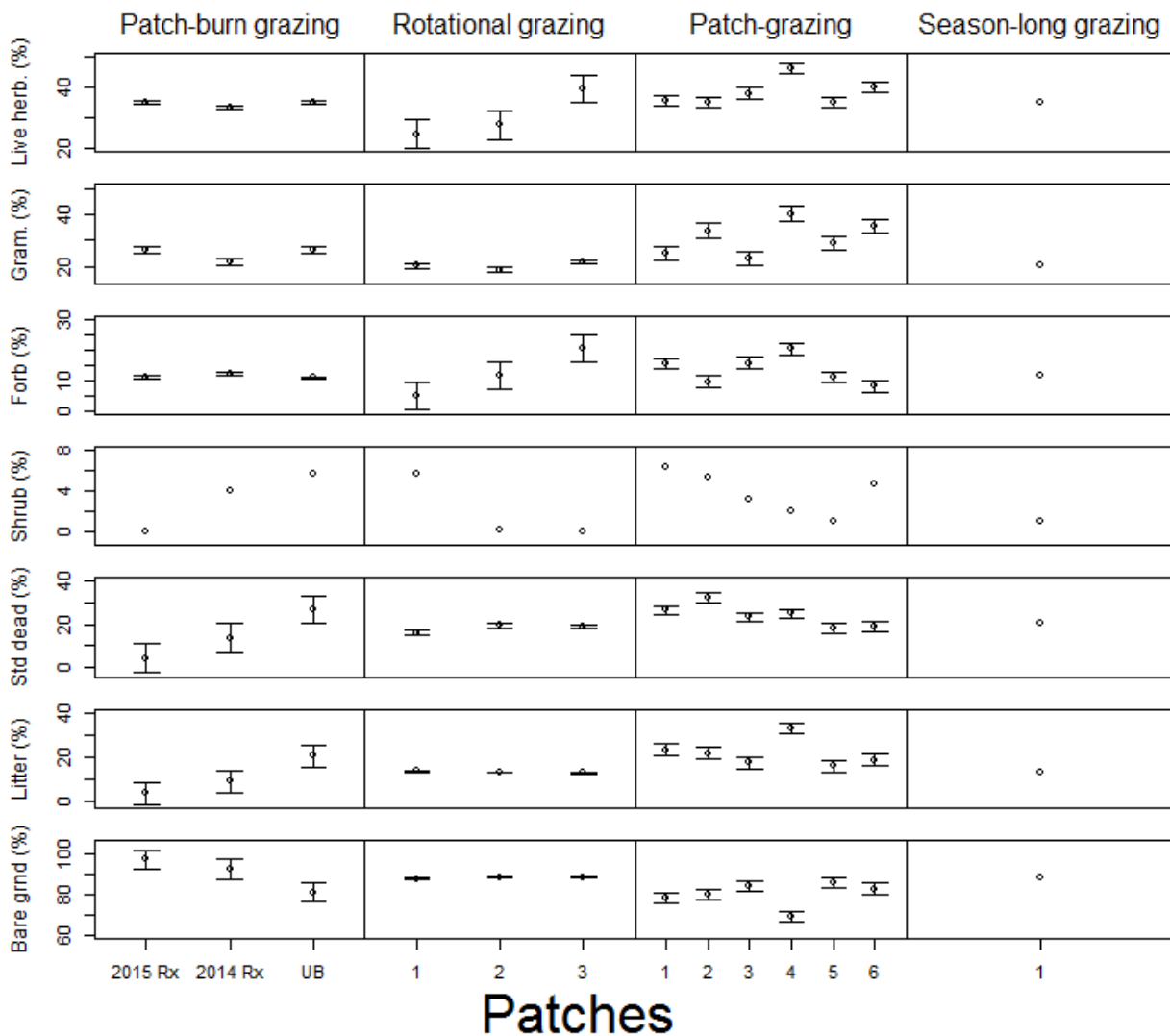


Figure 3-3. Percentage cover of Sandhills vegetation and bare ground within each heterogeneity treatment. Patches on the x-axis are organized by time since focal disturbance within each treatment increasing from left to right. The number of each patch corresponds to the mapped location shown in Figure 3-1.

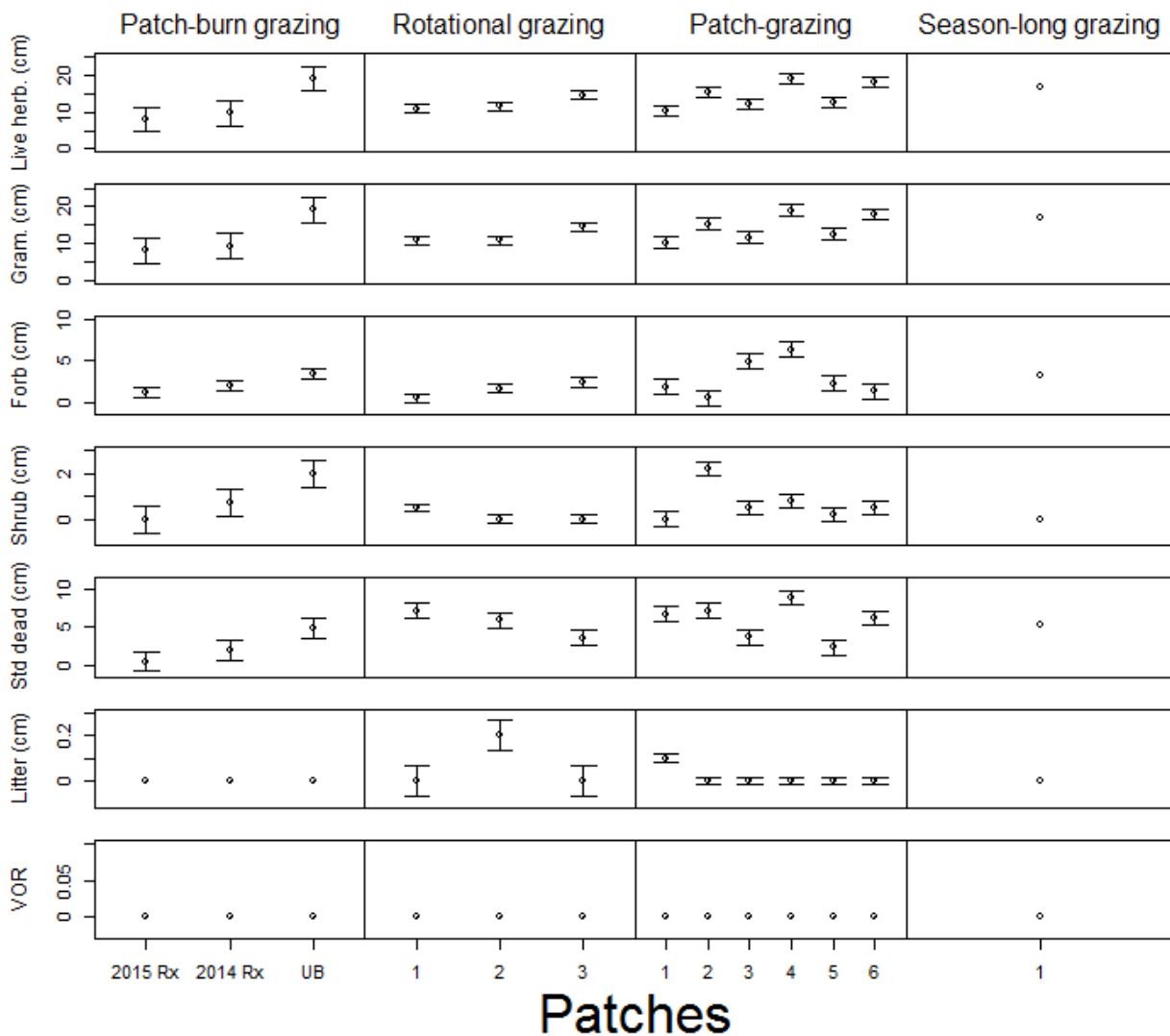


Figure 3-4. Sandhills vegetation height, litter depth, and visual obstruction reading (VOR) within each heterogeneity treatment. Patches on the x-axis are organized by time since focal disturbance within each treatment increasing from left to right. The number of each patch corresponds to the mapped location shown in Figure 3-1.

APPENDIX I
THE IMPACTS OF GRAZING AND WILDFIRE ON
NEBRASKA SANDHILLS GRASSLAND: A PILOT STUDY

OBJECTIVE

This pilot study was conducted to assess the first year response of Sandhills grassland following a growing-season wildfire during drought conditions and grazing.

METHODS

This study was conducted in the Nebraska Sandhills ecoregion at the Niobrara Valley Preserve in north-central Nebraska. The study site features predominantly upland dunes of sands, choppy sands, and sandy ecological sites with intervening dry interdune regions. Sand dunes of 9 to 60% slopes are oriented east to west, and thus comprised of predominately north and south-facing upland slopes separated by an interdune region (Schacht et al., 2000; Steinauer and Bragg, 1987).

Upland vegetation at the site is characterized as Sandhills mixed-grass prairie that is dominated by perennial graminoids, including sand bluestem (*Andropogon hallii* Hack.), little bluestem (*Schizachyrium scoparium* [Michx.] Nash), and prairie sandreed (*Calamovilfa longifolia* [Hook.] Scribn.). Cool-season graminoids, including sedge (*Carex* spp.), Scribner panicum (*Panicum oligosanthos* J. A. Shules subsp. *scribnerianum* [Nash] Fern.), needlegrasses (*Hesperostipa comata* [Trin. & Rupr.] Barkw. and *Hesperostipa spartea* [Trin.] Barkw.), and prairie junegrass (*Koeleria macrantha*

[Ledeb.] J. A. Shultes) are common. Secondary to graminoids are forbs which are found throughout, comprised primarily of perennial species such as western ragweed (*Ambrosia psilostachya* DC.) and stiff sunflower (*Helianthus pauciflorus* Nutt.), but annual forbs also occur. Shrubs are also common, but account only for a small portion of the community.

The preserve is 22,000 ha natural area managed with bison and cattle grazing, and fire. Two discrete units, the 5217 ha west bison unit and the 3935 ha east bison unit, have been grazed year-round by bison since 1988 and 1986, respectively. Both units were heavily grazed by cattle prior to being established (Steinauer and Bragg, 1987).

Prescribed fire has been used intermittently in both units since 1991 at an return interval of 7.5 to 10 years (Biondini et al., 1999). The stocking rate of both units has remained low at 1 AUM ha⁻¹ (Biondini et al., 1999; Pfeiffer and Steuter, 1994) relative to a moderate Sandhills stocking rate of 1.8 AUM ha⁻¹. Following a July 2012 wildfire, the stocking rates were reduced to 0.69 AUM ha⁻¹ and 0.49 AUM ha⁻¹ in the west and east bison units, respectively. The east bison unit was expanded by 953 ha in July 2012. Cattle graze the remaining portion of the preserve, including adjacent to both bison units.

In July 2012, the Fairfield Creek Wildfire (part of the Region 24 Complex) burned major portions of the preserve that are grazed by bison and cattle, resulting in burned and unburned areas in both west and east bison units and several cattle-grazed units. Precipitation levels were 75% below average for the 60 days prior to the wildfire. At the time of the fire, temperatures exceeded 38°C, relative humidity was below 15%, and winds were recorded up to 40 km hour⁻¹ (NOAA, 2012). Precipitation in 2013 was

1.73% below the mean annual precipitation for the area. Following the wildfire, bison were allowed unrestricted access to burned and unburned areas immediately following the wildfire. The east bison herd was fed supplemental hay through the winter of 2012/2013 as a result of forage loss. Cattle were rotated through several units beginning in May and ending in November. Therefore, cattle were not present during the dormant season.

In June 2013, 50 m transects were established in bison and cattle grazed areas that were burned and unburned during the 2012 wildfire. Sandhills plant communities differ according to topographic position (Barnes et al., 1984; Schacht et al., 2000), so transects were established along well defined north and south facing dune slopes of 100 m length or longer. Three transects were established in each treatment combination resulting in 24 total transects. Transects were oriented parallel to the dune top to keep transects in the same vegetation community. We marked each transect to allow repeat sampling by recording locations with a handheld GPS and marking the ends of each transect with a 30 cm rebar stake driven below the soil surface. Three grazing exclosures were established adjacent to each transect to eliminate grazing of the enclosed vegetation beginning in June. Therefore, following the wildfire and prior to establishment of exclosures in the bison units, these areas were exposed to grazing from July 2012 to June 2013.

In mid-June and early August, we sampled plant community composition at 2 m intervals along each transect using a 0.1 m² quadrat. Aboveground biomass was sampled in early August by clipping vegetation to ground level within a 0.25 m² quadrat. Aboveground biomass collected within each exclosure was sorted by functional groups:

warm-season grasses, cool-season grasses, sedges, forbs, shrubs, and succulents.

Aboveground biomass was collected at a distance of 1 m outside of each enclosure but was not sorted. Samples were transported to Lincoln, NE, oven-dried at 60° C for a minimum of 48 hours to remove all moisture, and then weighed to determine aboveground productivity. In early August, we also sampled for species composition along 12 transects in a northern mixed-grass prairie (not Sandhills). Transects were split between burned and unburned areas, both of which were grazed by cattle immediately following the fire. Transects were marked using the same methods.

RESULTS

Warm-season grasses and annual forbs were the dominant functional groups on all sites (Figure A-1 and Figure A-2). Grazing from August 2012 through May 2013 resulted in lower plant biomass in August 2013. Plant biomass in August 2013 was unaffected by the wildfire in July 2012. The July wildfire tended to favor cool-season grasses. Biomass was greatest on the burned north slopes and lowest on the burned south slopes (Figure A-2). Biomass on the unburned south slopes was greater than biomass on the unburned north slopes (Figure A-2). Total aboveground biomass in burned areas grazed by bison immediately following the fire did not differ from unburned and grazed areas (Figure A-3).

Frequency of occurrence of warm-season grasses did not differ between treatment combinations (Figure A-4). Little bluestem was lower in burned areas compared to unburned areas (Figure A-5). Sand bluestem was similar in burned and unburned areas

(Figure A-5). Cool-season grasses were lower in unburned and grazed areas (Figure A-4). Porcupine grass was lower in unburned and grazed areas (Figure A-5). Forbs were similar among treatment combinations (Figure A-4). Western ragweed was greater in burned areas than unburned areas (Figure A-5). Spotted spurge was lower in ungrazed areas that were not burned and similar in grazed and ungrazed areas that were burned (Figure A-5). Shrubs, including rose, were greater in burned areas compared to unburned areas (Figure A-4 and Figure A-5).

CONCLUSIONS

- Aboveground biomass in burned and unburned areas grazed by bison were not different one year following a growing season wildfire and drought.
- Aboveground biomass was greater in areas excluded from grazing starting in June 2013 compared to grazed areas.
- Plant community composition was similar in burned and unburned areas, although cool-season grasses were more abundant in burned areas than unburned areas.

ACKNOWLEDGEMENTS

We would like to thank the Nebraska Environmental Trust, The Nature Conservancy, the Center for Grassland Studies, the US Forest Service, and the Nebraska Forest Service for financial support. We thank the staff of the Niobrara Valley Preserve for logistical support. We would like to thank Laura Snell, Amanda Hefner, Cameron Oden, McKinzie Peterson, Jon Soper, Ben Beckman, and Miles Redden for assistance

collecting data. I would also like to thank Heidi Hillhouse for assistance with data analysis and Jeremy Hiller for technical support.

FIGURES

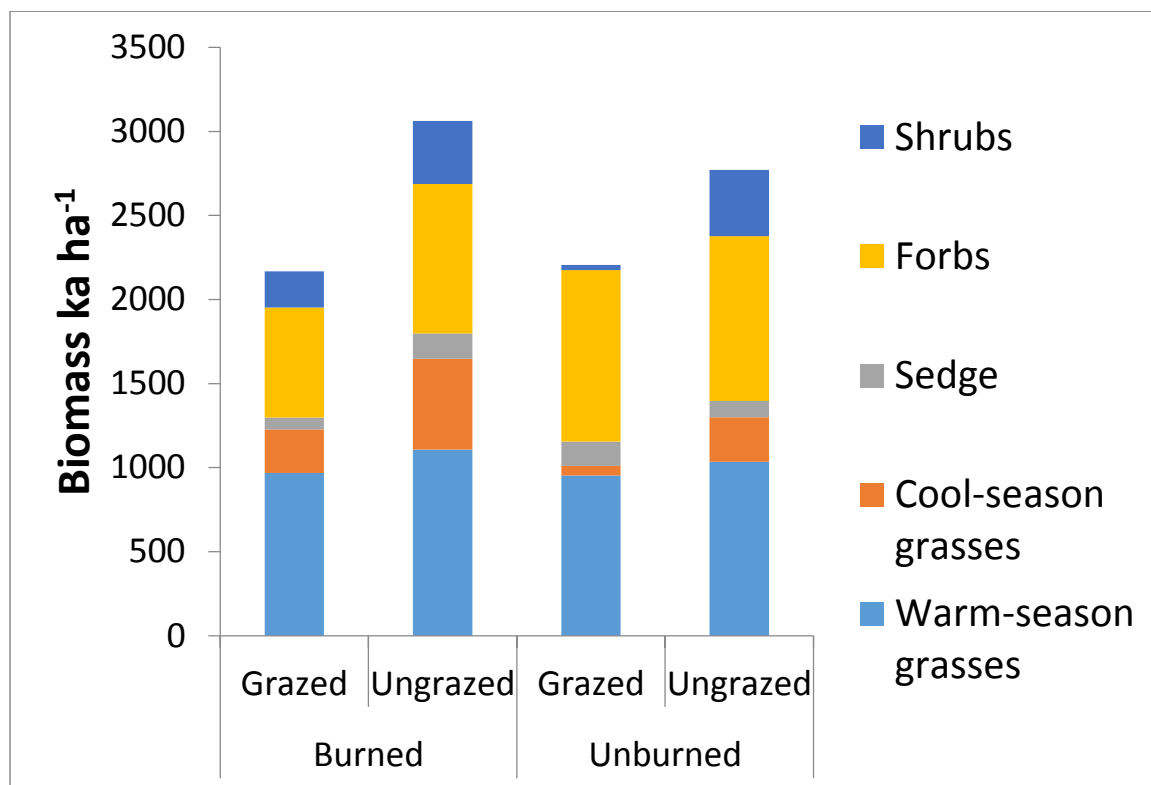


Figure A-1. Sandhills aboveground biomass by plant functional group in fire and grazing treatment combinations.

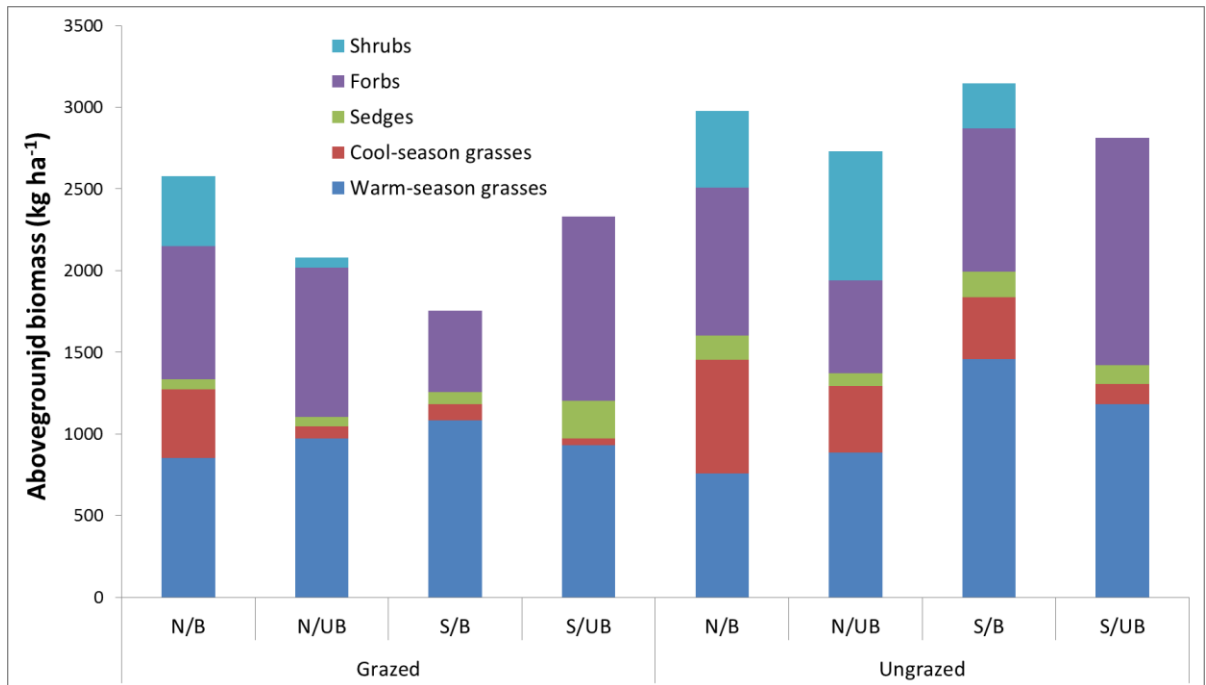


Figure A-2. Sandhills aboveground biomass in fire and grazing treatment combinations on north and south dune slopes. N signifies north slopes and S signifies south slopes. B signifies burned areas and UB signifies unburned areas.

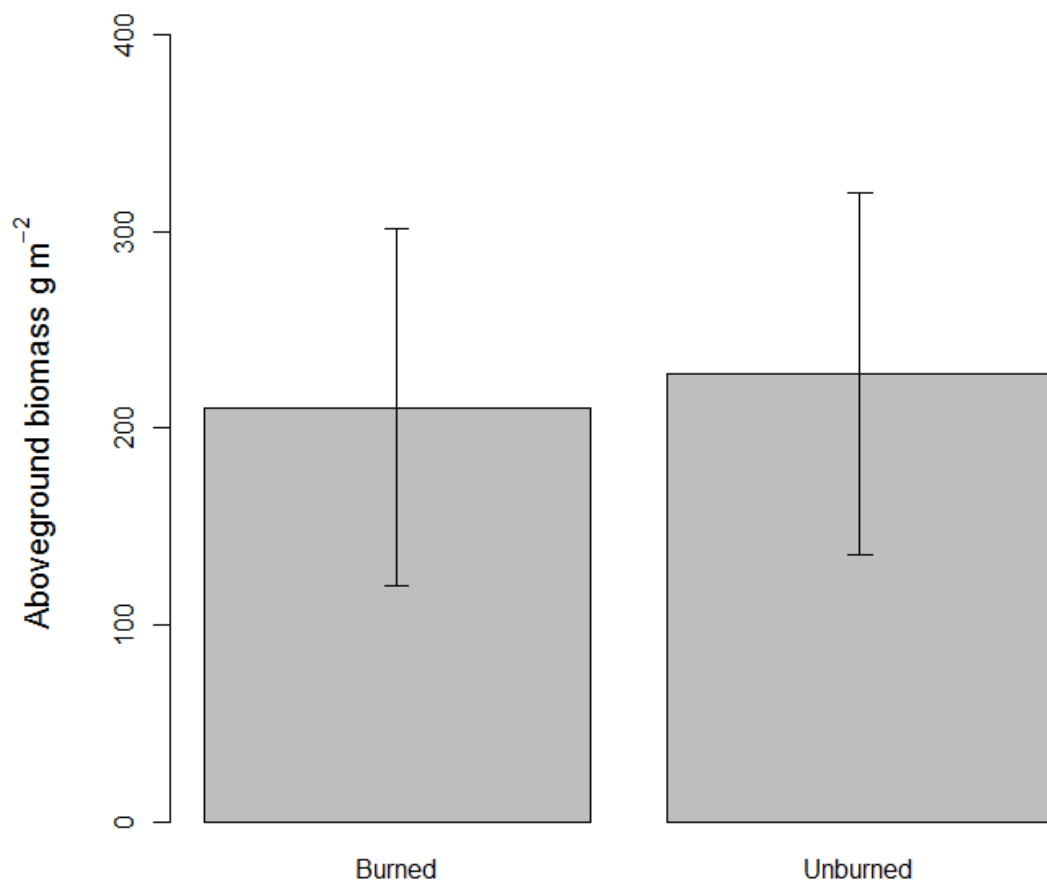


Figure A-3. Sandhills aboveground biomass in burned and unburned areas that were grazed by bison immediately following the fire.

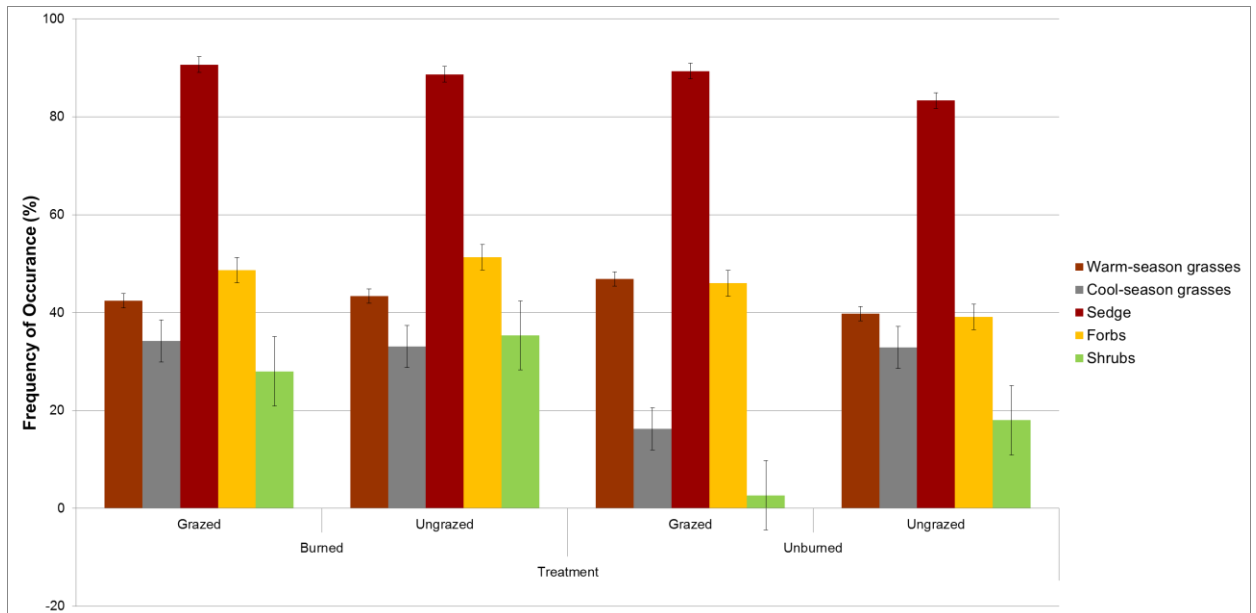


Figure A-4. Frequency of occurrence of Sandhills plant functional groups following fire and grazing treatment combinations.

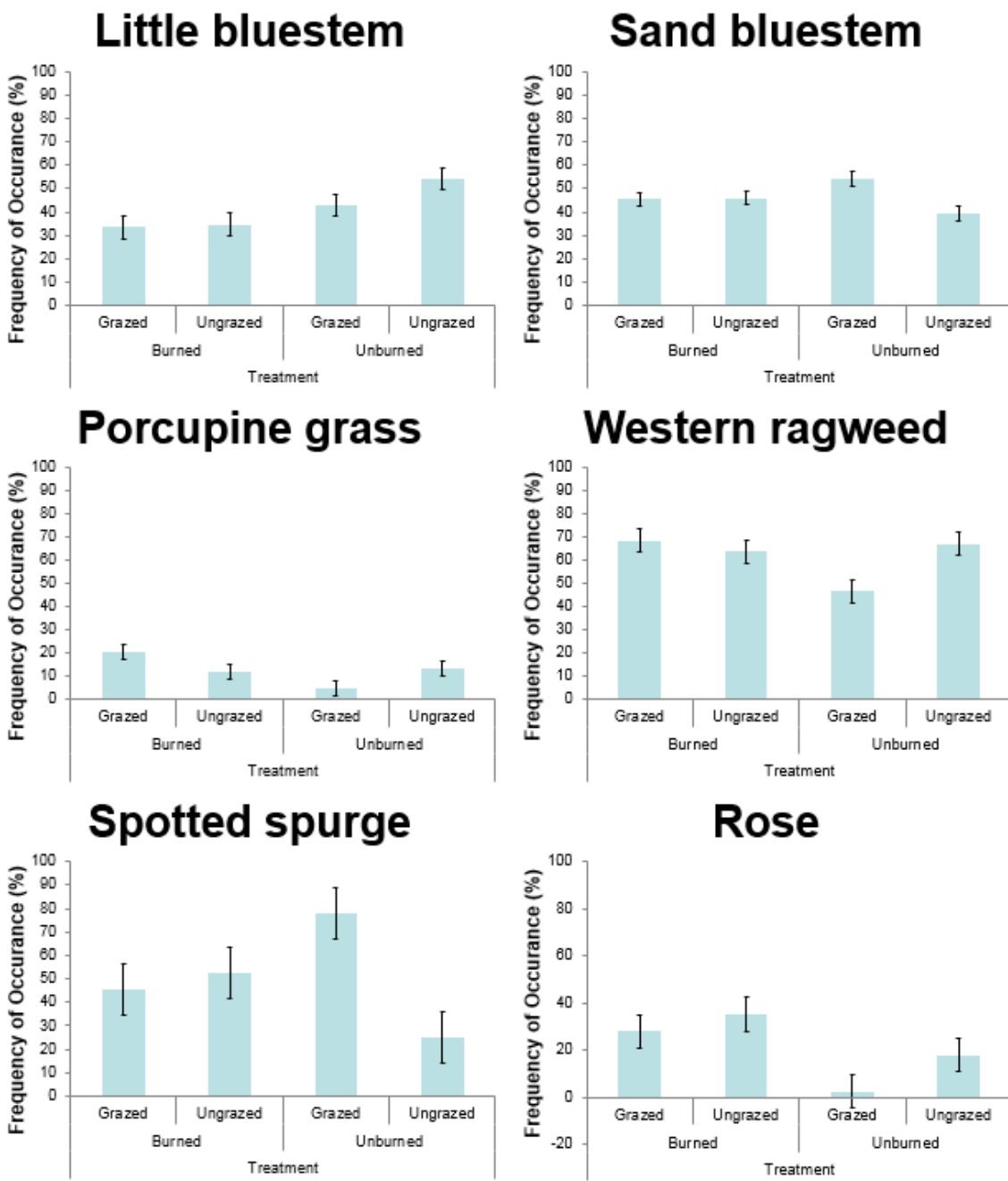


Figure A-5. Frequency of occurrence for selected Sandhills grassland species following fire and grazing treatment combinations.

LITERATURE CITED

- Ahlbrandt, T.S., Fryberger, S.G., 1980. Eolian deposits in the Nebraska sand hills. US Geol. Surv. Prof. Pap. 1120, 1–24.
- Allen, C.R., Angeler, D.G., Cumming, G.S., Folke, C., Twidwell, D., Uden, D.R., 2016. REVIEW: Quantifying spatial resilience. *J. Appl. Ecol.* 53, 625–635.
- Allen, C.R., Gunderson, L., Johnson, A.R., 2005. The Use of Discontinuities and Functional Groups to Assess Relative Resilience in Complex Systems. *Ecosystems* 8, 958–966. doi:10.1007/s10021-005-0147-x
- Allred, B.W., Fuhlendorf, S.D., Engle, D.M., Elmore, R.D., 2011a. Ungulate preference for burned patches reveals strength of fire–grazing interaction. *Ecol. Evol.* 1, 132–144. doi:10.1002/ece3.12
- Allred, B.W., Fuhlendorf, S.D., Hamilton, R.G., 2011b. The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. *Ecosphere* 2, art26. doi:10.1890/ES10-00152.1
- Allred, B.W., Scasta, J.D., Hovick, T.J., Fuhlendorf, S.D., Hamilton, R.G., 2014. Spatial heterogeneity stabilizes livestock productivity in a changing climate. *Agric. Ecosyst. Environ.* 193, 37–41.
- Anderson, R.H., Fuhlendorf, S.D., Engle, D.M., 2006. Soil Nitrogen Availability in Tallgrass Prairie Under the Fire–Grazing Interaction. *Rangel. Ecol. Manag.* 59, 625–631. doi:10.2111/05-088R2.1
- Ansley, R.J., Boutton, T.W., Mirik, M., Castellano, M.J., Kramp, B.A., 2010. Restoration of C4 grasses with seasonal fires in a C3/C4 grassland invaded by *Prosopis glandulosa*, a fire-resistant shrub. *Appl. Veg. Sci.* 13, 520–530. doi:10.1111/j.1654-109X.2010.01091.x
- Augustine, D.J., Derner, J.D., 2015. Patch Burn Grazing Management in a Semiarid Grassland: Consequences for Pronghorn, Plains Pricklypear, and Wind Erosion. *Rangel. Ecol. Manag.* 68, 40–47. doi:10.1016/j.rama.2014.12.010
- Augustine, D.J., Derner, J.D., 2014. Controls over the strength and timing of fire–grazer interactions in a semi-arid rangeland. *J. Appl. Ecol.* 51, 242–250. doi:10.1111/1365-2664.12186
- Barnes, P., Harrison, A., Heinisch, S., 1984. Vegetation Patterns in Relation to Topography and Edaphic Variation Nebraska Sandhills Prairie. *Fac. Publ. Biol. Sci.*

- Biondini, M.E., Steuter, A.A., Grygiel, C.E., 1989. Seasonal fire effects on the diversity patterns, spatial distribution and community structure of forbs in the Northern Mixed Prairie, USA. *Vegetatio* 85, 21–31. doi:10.1007/BF00042252
- Biondini, M.E., Steuter, A.A., Hamilton, R.G., 1999. Bison Use of Fire-Managed Remnant Prairies. *J. Range Manag.* 52, 454–461. doi:10.2307/4003772
- Bleed, A., Flowerday, C., 1991. The Nebraska Sand Hills. *Rangelands* 13, 53–55.
- Bragg, T.B., 1998. Fire in the Nebraska Sandhills prairie, in: *Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription*. Tall Timbers Fire Ecol. Conf. Proc. (TL Pruden and LA Brennan, Eds.). pp. 179–194.
- Bragg, T.B., 1985. A preliminary fire history of the oak/pine forest of northcentral Nebraska, in: *Proceedings 95th Annual Meeting of the Nebraska Academy of Sciences*, Lincoln, Nebraska.
- Bragg, T.B., 1978. Effects of burning, cattle grazing, and topography on vegetation of the choppy sands range site in the Nebraska Sandhills prairie. *Proc First Intl Rangel. Cong* 248–253.
- Briggs, J.M., Knapp, A.K., 1995. Interannual Variability in Primary Production in Tallgrass Prairie: Climate, Soil Moisture, Topographic Position, and Fire as Determinants of Aboveground Biomass. *Am. J. Bot.* 82, 1024–1030. doi:10.2307/2446232
- Collins, S.L., 1992. Fire Frequency and Community Heterogeneity in Tallgrass Prairie Vegetation, in: *Ecosystem Management*. Springer New York, pp. 99–105.
- Cummings, D.C., Fuhlendorf, S.D., Engle, D.M., 2007. Is Altering Grazing Selectivity of Invasive Forage Species With Patch Burning More Effective Than Herbicide Treatments? *Rangel. Ecol. Manag.* 60, 253–260. doi:10.2111/1551-5028(2007)60[253:IAGSOI]2.0.CO;2
- Daubenmire, R.F., 1959. Canopy coverage method of vegetation analysis. *Northwest Sci.* 33, 43–64.
- Debinski, D.M., Moranz, R.A., Delaney, J.T., Miller, J.R., Engle, D.M., Winkler, L.B., McGranahan, D.A., Barney, R.J., Trager, J.C., Stephenson, A.L., others, 2011. A cross-taxonomic comparison of insect responses to grassland management and land-use legacies. *Ecosphere* 2, art131.

- Doliner, L.H., Jolliffe, P.A., 1979. Ecological evidence concerning the adaptive significance of the C₄ dicarboxylic acid pathway of photosynthesis. *Oecologia* 38, 23–34.
- Dunn, B.H., Smart, A.J., Gates, R.N., Johnson, P.S., Beutler, M.K., Diersen, M.A., Janssen, L.L., 2010. Long-term production and profitability from grazing cattle in the northern mixed grass prairie. *Rangel. Ecol. Manag.* 63, 233–242.
- Eggemeyer, K.D., Awada, T., Wedin, D.A., Harvey, F.E., Zhou, X., 2006. Ecophysiology of Two Native Invasive Woody Species and Two Dominant Warm-Season Grasses in the Semiarid Grasslands of the Nebraska Sandhills. *Int. J. Plant Sci.* 167, 991–999. doi:10.1086/505797
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., Norberg, J., 2003. Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* 1, 488–494. doi:10.1890/1540-9295(2003)001[0488:RDECAR]2.0.CO;2
- Fay, P.A., Prober, S.M., Harpole, W.S., Knops, J.M.H., Bakker, J.D., Borer, E.T., Lind, E.M., MacDougall, A.S., Seabloom, E.W., Wragg, P.D., Adler, P.B., Blumenthal, D.M., Buckley, Y.M., Chu, C., Cleland, E.E., Collins, S.L., Davies, K.F., Du, G., Feng, X., Firn, J., Gruner, D.S., Hagenah, N., Hautier, Y., Heckman, R.W., Jin, V.L., Kirkman, K.P., Klein, J., Ladwig, L.M., Li, Q., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Morgan, J.W., Risch, A.C., Schütz, M., Stevens, C.J., Wedin, D.A., Yang, L.H., 2015. Grassland productivity limited by multiple nutrients. *Nat. Plants* 1, 15080. doi:10.1038/nplants.2015.80
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. Syst.* 35, 557–581.
- Forman, 2001. Temporal and spatial patterns of Holocene dune activity on the Great Plains of North America: megadroughts and climate links. *Glob. Planet. Change* 29, 1–29.
- Fuhlendorf, S.D., Engle, D.M., 2004. Application of the fire–grazing interaction to restore a shifting mosaic on tallgrass prairie. *J. Appl. Ecol.* 41, 604–614. doi:10.1111/j.0021-8901.2004.00937.x
- Fuhlendorf, S.D., Engle, D.M., 2001. Restoring Heterogeneity on Rangelands: Ecosystem Management Based on Evolutionary Grazing Patterns We propose a paradigm that enhances heterogeneity instead of homogeneity to promote biological diversity and wildlife habitat on rangelands grazed by livestock. *BioScience* 51, 625–632. doi:10.1641/0006-3568(2001)051[0625:RHOREM]2.0.CO;2

- Fuhlendorf, S.D., Engle, D.M., Elmore, R.D., Limb, R.F., Bidwell, T.G., 2012. Conservation of pattern and process: developing an alternative paradigm of rangeland management. *Rangel. Ecol. Manag.* 65, 579–589.
- Fuhlendorf, S.D., Engle, D.M., Kerby, J., Hamilton, R., 2009. Pyric Herbivory: Rewilding Landscapes through the Recoupling of Fire and Grazing. *Conserv. Biol.* 23, 588–598. doi:10.1111/j.1523-1739.2008.01139.x
- Fuhlendorf, S.D., Harrell, W.C., Engle, D.M., Hamilton, R.G., Davis, C.A., Leslie, D.M., 2006. Should heterogeneity be the basis for conservation? grassland bird response to fire and grazing. *Ecol. Appl.* 16, 1706–1716. doi:10.1890/1051-0761(2006)016[1706:SHBTBF]2.0.CO;2
- Fuhlendorf, S.D., Smeins, F.E., 1999. Scaling Effects of Grazing in a Semi-Arid Grassland. *J. Veg. Sci.* 10, 731–738. doi:10.2307/3237088
- Fuhlendorf, S.D., Townsend, D.E., Elmore, R.D., Engle, D.M., 2010. Pyric-herbivory to promote rangeland heterogeneity: evidence from small mammal communities. *Rangel. Ecol. Manag.* 63, 670–678.
- Fule, P.Z., Cocks, A.E., Heinlein, T.A., Covington, W.W., 2004. Effects of an intense prescribed forest fire: is it ecological restoration? *Restor. Ecol.* 12, 220–230.
- Fulé, P.Z., Laughlin, D.C., Covington, W.W., 2005. Pine-oak forest dynamics five years after ecological restoration treatments, Arizona, USA. *For. Ecol. Manag.* 218, 129–145.
- Guyette, R.P., Stambaugh, M.C., Dey, D.C., Muzika, R.-M., 2012. Predicting fire frequency with chemistry and climate. *Ecosystems* 15, 322–335.
- Hartman, J., 2015. A DESERT IN DISGUISE: THE RESILIENCE OF THE NEBRASKA SANDHILLS. Diss. Theses Nat. Resour.
- Heffner, R.A., Butler, M.J., Reilly, C.K., 1996. Pseudoreplication Revisited. *Ecology* 77, 2558–2562. doi:10.2307/2265754
- Hobbs, N.T., Schimel, D.S., Owensby, C.E., Ojima, D.S., 1991. Fire and Grazing in the Tallgrass Prairie: Contingent Effects on Nitrogen Budgets. *Ecology* 72, 1374–1382. doi:10.2307/1941109
- Holechek, J.L., Pieper, R.D., Herbel, C.H., 2011. Range management: principles and practices.

- Holling, C.S., 1973. Resilience and Stability of Ecological Systems. *Annu. Rev. Ecol. Syst.* 4, 1–23.
- HPRCC, 2015. High Plains Regional Climate Center. <http://www.hprcc.unl.edu/> (accessed 3.25.16).
- Hurlbert, S.H., 1984. Pseudoreplication and the Design of Ecological Field Experiments. *Ecol. Monogr.* 54, 187–211. doi:10.2307/1942661
- Kaul, R., 1998. Plants, in: In “An Atlas of the Sand Hills” (A. Bleed and C. Flowerday, Eds.), Resource Atlas 5a.
- Knapp, P.A., 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert: history, persistence, and influences to human activities. *Glob. Environ. Change* 6, 37–52.
- Lancaster, N., 1988. Development of linear dunes in the southwestern Kalahari, southern Africa. *J. Arid Environ.* 14, 233–244.
- LANDFIRE, 2016. <http://www.landfire.gov/> (accessed 7.11.16).
- Laughlin, D.C., Fule, P.Z., 2008. Wildland fire effects on understory plant communities in two fire-prone forests. *Can. J. For. Res.* 38, 133–142.
- Limb, R.F., Fuhlendorf, S.D., Engle, D.M., Weir, J.R., Elmore, R.D., Bidwell, T.G., 2011. Pyric–Herbivory and Cattle Performance in Grassland Ecosystems. *Rangel. Ecol. Manag.* 64, 659–663. doi:10.2111/REM-D-10-00192.1
- MacArthur, R.H., MacArthur, J.W., 1961. On Bird Species Diversity. *Ecology* 42, 594–598. doi:10.2307/1932254
- Mason, J.A., Swinehart, J.B., Goble, R.J., Loope, D.B., 2004. Late-Holocene dune activity linked to hydrological drought, Nebraska Sand Hills, USA. *The Holocene* 14, 209–217. doi:10.1191/0959683604hl677rp
- McCune, B., Grace, J.B., Urban, D.L., 2002. Analysis of ecological communities. MjM software design Gleneden Beach, OR.
- McGranahan, D.A., Engle, D.M., Fuhlendorf, S.D., Miller, J.R., Debinski, D.M., 2013a. Multivariate Analysis of Rangeland Vegetation and Soil Organic Carbon Describes Degradation, Informs Restoration and Conservation. *Land* 2, 328–350. doi:10.3390/land2030328

- McGranahan, D.A., Engle, D.M., Fuhlendorf, S.D., Miller, J.R., Debinski, D.M., 2012. An Invasive Cool-Season Grass Complicates Prescribed Fire Management in a Native Warm-Season Grassland. *Nat. Areas J.* 32, 208–214. doi:10.3375/043.032.0214
- McGranahan, D.A., Engle, D.M., Fuhlendorf, S.D., Winter, S.J., Miller, J.R., Debinski, D.M., 2012. Spatial heterogeneity across five rangelands managed with pyric-herbivory. *J. Appl. Ecol.* 49, 903–910. doi:10.1111/j.1365-2664.2012.02168.x
- McGranahan, D.A., Engle, D.M., Fuhlendorf, S.D., Winter, S.L., Miller, J.R., Debinski, D.M., 2013b. Inconsistent outcomes of heterogeneity-based management underscore importance of matching evaluation to conservation objectives. *Environ. Sci. Policy* 31, 53–60. doi:10.1016/j.envsci.2013.03.005
- McGranahan, D.A., Henderson, C.B., Hill, J.S., Raicovich, G.M., Wilson, W.N., Smith, C.K., 2014. Patch Burning Improves Forage Quality and Creates Grass-bank in Old-field Pasture: Results of a Demonstration Trial. *Southeast. Nat.* 13, 200–207.
- Meek, M.G., Cooper, S.M., Owens, M.K., Cooper, R.M., Wappel, A.L., 2008. White-tailed deer distribution in response to patch burning on rangeland. *J. Arid Environ.* 72, 2026–2033.
- Miao, X., Mason, J.A., Swinehart, J.B., Loope, D.B., Hanson, P.R., Goble, R.J., Liu, X., 2007. A 10,000 year record of dune activity, dust storms, and severe drought in the central Great Plains. *Geology* 35, 119–122. doi:10.1130/G23133A.1
- Milchunas, D.G., Varnamkhasti, A.S., Lauenroth, W.K., Goetz, H., 1995. Forage Quality in Relation to Long-Term Grazing History, Current-Year Defoliation, and Water Resource. *Oecologia* 101, 366–374.
- Moranz, R.A., Debinski, D.M., McGranahan, D.A., Engle, D.M., Miller, J.R., 2012. Untangling the effects of fire, grazing, and land-use legacies on grassland butterfly communities. *Biodivers. Conserv.* 21, 2719–2746.
- Morrison, L.C., DuBois, J.D., Kapustka, L.A., 1986. The vegetational response of a Nebraska Sandhills grassland to a naturally occurring fall burn. *Prairie Nat.* 18, 179–184.
- Muhs, D.R., Wolfe, S.A., 1999. Sand dunes of the northern Great Plains of Canada and the United States, in: *Holocene Climate and Environmental Change in the Palliser Triangle; a Geoscientific Context for Evaluation of the Impacts of Climate Change on the Southern Canadian Prairies*. Geological Survey of Canada.

- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. *vegan*: Community Ecology Package.
- Patten, R.S., Ellis, J.E., 1995. Patterns of species and community distributions related to environmental gradients in an arid tropical ecosystem. *Vegetatio* 117, 69–79.
- Pfeiffer, K.E., Steuter, A.A., 1994. Preliminary Response of Sandhills Prairie to Fire and Bison Grazing. *J. Range Manag.* 47, 395–397. doi:10.2307/4002337
- Polito, V.J., Baum, K.A., Payton, M.E., Little, S.E., Fuhlendorf, S.D., Reichard, M.V., 2013. Tick abundance and levels of infestation on cattle in response to patch burning. *Rangel. Ecol. Manag.* 66, 545–552.
- Pool, R.J., 1912. Glimpses of the Great American Desert, in: *Popular Science Monthly*.
- R Core Team, 2014. *R: The R Project for Statistical Computing*.
- Rideout-Hanzak, S., Wester, D.B., Britton, C.M., Whitlaw, H., 2011. Biomass not linked to perennial grass mortality following severe wildfire in the southern High Plains. *Rangel. Ecol. Manag.* 64, 47–55.
- Robel, R.J., Briggs, J.N., Dayton, A.D., Hulbert, L.C., 1970. Relationships between Visual Obstruction Measurements and Weight of Grassland Vegetation. *J. Range Manag.* 23, 295–297. doi:10.2307/3896225
- Roskin, J., Tsoar, H., Porat, N., Blumberg, D.G., 2011. Palaeoclimate interpretations of Late Pleistocene vegetated linear dune mobilization episodes: evidence from the northwestern Negev dunefield, Israel. *Quat. Sci. Rev.* 30, 3364–3380. doi:10.1016/j.quascirev.2011.08.014
- Scasta, J.D., Engle, D.M., Talley, J.L., Weir, J.R., Stansberry, J.C., Fuhlendorf, S.D., Harr, R.N., 2012. Pyric-herbivory to manage horn flies (Diptera: Muscidae) on cattle. *Southwest. Entomol.* 37, 325–334.
- Schacht, W.H., Volesky, J.D., Bauer, D., Smart, A., Mousel, E., 2000. Plant community patterns on upland prairie in the eastern Nebraska sandhills. *Agron. Publ.* 339.
- Schmeisser, R.L., Loope, D.B., Wedin, D.A., 2009. Clues to the Medieval Destabilization of the Nebraska Sand Hills, Usa, from Ancient Pocket Gopher Burrows. *Palaios* 24, 809–817. doi:10.2110/palo.2009.p09-037r

- Sensenig, R.L., Demment, M.W., Laca, E.A., 2010. Allometric scaling predicts preferences for burned patches in a guild of East African grazers. *Ecology* 91, 2898–2907. doi:10.1890/09-1673.1
- Sridhar, V., Loope, D.B., Swinehart, J.B., Mason, J.A., Oglesby, R.J., Rowe, C.M., 2006. Large Wind Shift on the Great Plains During the Medieval Warm Period. *Science* 313, 345–347. doi:10.1126/science.1128941
- Steinauer, E.M., Bragg, T.B., 1987. Ponderosa Pine (*Pinus ponderosa*) Invasion of Nebraska Sandhills Prairie. *Am. Midl. Nat.* 118, 358–365. doi:10.2307/2425792
- Steuter, A.A., 1987. C3/ C4 Production Shift on Seasonal Burns: Northern Mixed Prairie. *J. Range Manag.* 40, 27–31. doi:10.2307/3899356
- Steuter, A.A., Steinauer, E.M., Hill, G.L., Bowers, P.A., Tieszen, L.L., 1995. Distribution and Diet of Bison and Pocket Gophers in a Sandhills Prairie. *Ecol. Appl.* 5, 756–766. doi:10.2307/1941983
- Steuter, A., Hidinger, L., 1999. Comparative Ecology of Bison and Cattle on Mixed-Grass Prairie. *Gt. Plains Res. J. Nat. Soc. Sci.*
- Stubbendieck, J., 1998. Range Management, in: *An Atlas of the Sand Hills.*
- Stubbendieck, J., Flessner, T.R., Weedon, R., 1989. Blowouts in the Nebraska Sandhills: The Habitat of *Penstemon haydenii*. *Proc. North Am. Prairie Conf.*
- Stubbendieck, J.L., Reece, P.E., 1992. EC92-124 Nebraska Handbook of Range Management. *Hist. Mater. Univ. Neb.-Linc. Ext.* 1624.
- Taylor, C.A., Twidwell, D., Garza, N.E., Rosser, C., Hoffman, J.K., Brooks, T.D., 2011. Long-Term Effects of Fire, Livestock Herbivory Removal, and Weather Variability in Texas Semiarid Savanna. *Rangel. Ecol. Manag.* 65, 21–30. doi:10.2111/REM-D-10-00124.1
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.* 31, 79–92. doi:10.1046/j.0305-0270.2003.00994.x
- Towne, E.G., Kemp, K.E., 2008. Long-Term Response Patterns of Tallgrass Prairie to Frequent Summer Burning. *Rangel. Ecol. Manag.* 61, 509–520. doi:10.2111/08-043.1

- Twidwell, D., Allred, B.W., Fuhlendorf, S.D., 2013a. National-scale assessment of ecological content in the world's largest land management framework. *Ecosphere* 4, art94.
- Twidwell, D., Fuhlendorf, S.D., Engle, D.M., Taylor, C.A., 2009. Surface Fuel Sampling Strategies: Linking Fuel Measurements and Fire Effects. *Rangel. Ecol. Manag.* 62, 223–229. doi:10.2111/08-124R2.1
- Twidwell, D., Fuhlendorf, S.D., Taylor, C.A., Rogers, W.E., 2013b. Refining thresholds in coupled fire–vegetation models to improve management of encroaching woody plants in grasslands. *J. Appl. Ecol.* 50, 603–613.
- Twidwell, D., Rogers, W.E., McMahan, E.A., Thomas, B.R., Kreuter, U.P., Blankenship, T.L., 2012. Prescribed Extreme Fire Effects on Richness and Invasion in Coastal Prairie. *Invasive Plant Sci. Manag.* 5, 330–340. doi:10.1614/IPSM-D-12-00017.1
- Twidwell, D., Rogers, W.E., Wonkka, C.L., Taylor, C.A., Kreuter, U.P., 2016a. Extreme prescribed fire during drought reduces survival and density of woody resprouters. *J. Appl. Ecol.*
- Twidwell, D., West, A.S., Hiatt, W.B., Ramirez, A.L., Winter, J.T., Engle, D.M., Fuhlendorf, S.D., Carlson, J.D., 2016b. Plant invasions or fire policy: which has altered fire behavior more in tallgrass prairie? *Ecosystems* 19, 356–368.
- USDA, 2013. Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. <http://websoilsurvey.nrcs.usda.gov/> (accessed 5.24.16).
- USDA-NRCS, 2015a. Official Ecological Site Descriptions
<https://esis.sc.egov.usda.gov/ESDReport/fsReport.aspx?id=R065XY033NE&rptLevel=communities&approved=yes&repType=regular&scrns=&comm=> (accessed 5.21.15).
- USDA-NRCS, 2015b. Official Soil Series Descriptions
https://soilseries.sc.egov.usda.gov/OSD_Docs/V/VALENTINE.html (accessed 5.22.15).
- van Mantgem, P., Schwartz, M.W., Keifer, M., 2001. Monitoring wildfire effects: Coming to terms with pseudoreplication. *Nat. Areas J.* 21, 266–273.
- Vermeire, L.T., Mitchell, R.B., Fuhlendorf, S.D., Gillen, R.L., 2004. Patch burning effects on grazing distribution. *Rangel. Ecol. Manag.* 57, 248–252.

- Volesky, J.D., Connot, S.B., 2000. Vegetation Response to Late Growing-Season Wildfire on Nebraska Sandhills Rangeland. *J. Range Manag.* 53, 421–426. doi:10.2307/4003754
- Wang, T., Wedin, D.A., Franz, T.E., Hiller, J., 2015. Effect of vegetation on the temporal stability of soil moisture in grass-stabilized semi-arid sand dunes. *J. Hydrol.* 521, 447–459.
- Wiens, J.A., Parker, K.R., 1995. Analyzing the Effects of Accidental Environmental Impacts: Approaches and Assumptions. *Ecol. Appl.* 5, 1069. doi:10.2307/2269355
- Winter, S.L., Fuhlendorf, S.D., Goad, C.L., Davis, C.A., Hickman, K.R., 2011. Topoedaphic Variability and Patch Burning in Sand Sagebrush Shrubland. *Rangel. Ecol. Manag.* 64, 633–640. doi:10.2111/REM-D-11-00068.1
- Wonkka, C.L., Twidwell, D., West, J.B., Rogers, W.E., 2015. Shrubland resilience varies across soil types: implications for operationalizing resilience in ecological restoration. *Ecol. Appl.* doi:10.1890/15-0066.1
- Wu, J., Loucks, O.L., 1995. From Balance of Nature to Hierarchical Patch Dynamics: A Paradigm Shift in Ecology. *Q. Rev. Biol.* 70, 439–466.