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Understanding spatial dynamics of Tallgrass prairie dominated by tall fescue

Callie Griffith  
University of Nebraska - Lincoln

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Understanding spatial dynamics of Tallgrass prairie dominated by tall fescue

Callie D. Griffith M.S.

University of Nebraska, 2018

Advisers: Walter H. Schacht and Dirac Twidwell

This study was conducted on restored tallgrass prairie and invaded tallgrass prairie located in the Grand River Grasslands of southern Iowa to determine differences in heterogeneity of plant structure and functional group composition at different scales. Restored tallgrass prairies were seeded with a species-rich seeding mixture and managed by burning the entire prairie, every three years. Data were collected in August 2014 and 2015 to compare heterogeneity of restoration of native plant structure and functional group composition to the heterogeneity of invaded tallgrass prairies that were managed with patch burning and conventionally grazed. Invaded tallgrass prairies were managed with patch-burning to create a fire-grazing interaction where grazers preferentially grazed patches of the landscape that had been recently burned. We quantified structural heterogeneity in invaded landscapes managed with patch burn grazing under two different grazing strategies. The grazing strategies we compared were 1) season-long stocking (April – September) and 2) intensive early stocking (April – July). Data were collected early, late, and after the growing season in 2014 and 2015 to determine how heterogeneity changed throughout the year. Heterogeneity was higher in invaded patch-burned sites than in restored tallgrass prairie. Patch burning created patch-level heterogeneity in litter and bare ground measurements but not in structure or plant functional group composition. IES did not increase among-patch heterogeneity compared to SLS, but it did increase within-patch heterogeneity. Tall fescue forage quality is
higher than many native grasses, and has low amounts of standing dead post-fire. These characteristics shifted grazers focus from recently burned patches, as is typically seen in native grasslands managed with patch-burning, and created conditions whereby grazers patchily grazed throughout the pasture.

**Key Words** heterogeneity; tall fescue; patch-burning; patch-burn grazing; pyric herbivory; invasion; intensive-early stocking
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CHAPTER I

Heterogeneity of invaded tallgrass prairie: evaluation of alternative restoration strategies in tall fescue dominated grasslands

ABSTRACT

Determining the best method of restoring tallgrass prairie on areas dominated by non-native cool-season grasses is critical to the existence of the flora and fauna native to this ecosystem. In this study, conducted in Iowa’s Grand River Grasslands, we quantified temporal heterogeneity of the plant community and spatial heterogeneity at three scales: point, patch, and pasture. We compared the temporal and spatial heterogeneity of two contrasting restoration perspectives used to restore tallgrass prairie on tall fescue dominated grasslands. Restoration perspectives were 1) The Biodiversity and Ecosystem Function (BEF) perspective, which prioritizes increasing biodiversity and restoring dominant native species, and 2) Restoration of Pattern and Process (RPP) perspective which prioritizes the restoration of ecosystem processes that will increase biodiversity. Data was collected early and late in the growing season in 2014 and 2015 to determine how the restoration treatments influenced temporal heterogeneity. We measured visual obstruction, plant height, and canopy cover of vegetation functional groups every 3-m on 300-m long transects permanently located in each patch of each pasture. We used NDMS with Bray-Curtis distances to show how the plant community changed during the course of the two-year study. Results showed that BEF sites were virtually one homogeneous patch, resulting in no patch-level heterogeneity for all plant measurements. In contrast, patch-scale heterogeneity was constrained without the removal of tall fescue and re-establishment of native species in RPP treatments and patch-scale heterogeneity was only higher for bare-ground and litter measurements. The NDMS showed little temporal heterogeneity occurring during the duration of this study. Prioritizing a single restoration ideology of composition without pattern-process (BEF) or restoration of pattern-process without composition (RPP) does not support sufficient spatial complexity known to be important for multiple taxa in tallgrass prairie.
INTRODUCTION

Tallgrass prairie is among the most endangered ecosystems in North America with as little as 1% of the original tall grass prairie remaining (Samson and Knopf 1994; Smith 1998). Loss of tallgrass prairie has been primarily due to conversion to cropland; and most of the remaining prairie has been invaded by exotic species resulting in a loss of species diversity at all trophic levels (Burns and Chamblee 1979; D’Antonio and Vitousek 1992; Ball et al. 1993; Knopf 1994; Noss et al. 1995). Non-native cool-season grasses have been introduced in millions of ha of tallgrass prairie remnants in central United States (Ball et al. 1993; Grant et al. 2009). These non-native dominated ecosystems present a problem for landowners and advisors concerned with restoring and preserving tallgrass prairie biodiversity (McGranahan et al. 2012). Furthermore, remaining tallgrass prairie tracts are in small fragments which are highly susceptible to invasion (Hobbs & Huenneke 1992; Madson 1990).

Tall fescue (Schedonorus arundinaceus (Schreb.)), is a Eurasian cool-season grass that has been introduced to over 14 million ha in the United States (Fribourg et al. 1991). In the Grand River Grasslands (GRG) of southern Iowa, tall fescue is one of the biggest threats to restoring native tallgrass prairie (McGranahan 2012). Tall fescue has the potential to decrease livestock production, limit heterogeneity in vegetation composition and structure, lower plant species richness, and reduce habitat quality for several wildlife species (Madej and Clay 1991, Barnes et al 1995, Cid and Brizuela 1998, Thompson et al. 2001, Shepherd 2005; McGranahan et al. 2012; Lyons et. al. 2015 Finch et al. 2016).

Finding successful restoration practices is critical to meet management goals of
biodiversity in these areas. Often in these areas, restoration efforts are focused on one of
two contrasting perspectives (Table 1-1).

The first, more common restoration perspective in invaded grasslands is the
Biodiversity and Ecosystem Function (BEF) perspective, which prioritizes increasing
biodiversity and restoring dominant native species (Falk et al. 2006). This perspective
operates under the idea that increasing native species diversity is critical to an
ecosystem’s resilience. Interventions under the BEF perspective often involve landscapes
invaded by non-native vegetation, and require herbicide application to control non-native
species followed by reseeding with native seeding mixtures (Washburn and Barnes 2000;
is often defined as reaching a predefined target species diversity, or reaching a floristic
community similar to target grasslands (Martin et al. 2005; Rowe, 2010; Larson et al.
2011). This type of restoration effort is costly, and has the potential to contribute to the
loss of local genetics by spraying non-target species such as native forbs and grasses, and
seeding with commercially available seeds that can outcompete native plants with local
Additionally, the follow-up management of these areas focuses on maintaining the
ecosystem by limiting disturbances such as fire and grazing. Restricting disturbances on
these restored areas can result in more uniform grassland environments that are unable to
maintain planted levels of diversity as species are lost over time (Sluis 2002).

The second restoration perspective focuses on the restoration of pattern and processes
(now referred to as the Restoration of Pattern and Process [or RPP] perspective). This
perspective prioritizes the restoration of ecosystem processes that will increase
biodiversity of higher taxa by creating sufficient structural heterogeneity in plant
communities (Fuhlendorf and Engle 2004). This perspective was born in response to the
need of restoring large areas where reseeding native vegetation was difficult or costly.
Restoration practices under the RPP perspective includes restoring topsoil and allowing
plant succession to reclaim old mine sites, restoring natural water flow and hydraulic
regimes to river and wetland systems (Palmer et al. 2007; Middleton 1998, 2002), and
restoring natural disturbance regimes to disturbance-adapted communities (Collins et al.
2000; Fuhlendorf and Engle 2004). A restoration practice under the RPP perspective that
has become increasingly popular in recent years is restoring the disturbance processes
called pyric herbivory (Fuhlendorf and Engle 2004). Pyric herbivory is the ecological
interaction of fire and grazing and is characterized as a single disturbance process
because it affects ecosystems differently than applying fire or grazing separately
(Fuhlendorf and Engle 2001). Through this process, each year discrete areas of a
landscape are burned and grazers are allowed access to all burned and unburned areas.
Grazers preferentially graze on recently burned areas and leave unburned portions of the
landscape largely undisturbed. This interaction produces a landscape that is
heterogeneous across many spatio-temporal scales as the occurrence of fire and grazing
shift throughout time and space on the landscape (Fuhlendorf et al. 2009). Heterogeneity
created by pyric herbivory is critical to grassland species diversity and abiotic processes
such as nutrient cycling (Anderson et al. 2006, Fuhlendorf et al. 2009).
When applied as a management tool, termed patch-burn grazing, restoring pyric herbivory on grasslands increases heterogeneity among burn patches by creating patches of short vegetation in recently burned areas and patches of tall ungrazed or lightly grazed vegetation in areas that have not been grazed for one year or more. This heterogeneity between burn patches (now referred to as patch-scale heterogeneity) can positively influence mammal (Fuhlendorf et. al. 2010), bird (Fuhlendorf et al. 2006; Coppedge et al. 2008; Bouwman and Hoffman 2007), and invertebrate (Engle et al. 2008; Debinski et al. 2011; Doxon et al. 2011) diversity. Patch burning also has the potential to help control exotic species which may aid in increasing the dominance of native species (Fuhlendorf and Engle 2004; Cummings et al. 2007). Under the RPP perspective, restoration success is often defined as increasing heterogeneity in vegetation characteristics such as height, percentage canopy cover, and plant diversity (Fuhlendorf et al. 2006; Engle et al. 2008; Fuhlendorf et al. 2010; Doxon et al. 2011). Because increasing patch-scale heterogeneity is shown to increase diversity in higher taxa, managing areas for patch-scale heterogeneity is a common goal in the RPP method. Creating heterogeneity at larger or smaller scales, however, may be beneficial to certain species, which warrants examination. Restoring processes without changing botanical composition could provide a more cost effective way to restore invaded grasslands compared to the alternative method of restoration which includes costly modes of removing exotic species and increasing native plant species (Mack et al. 2000).

Given the recognition that restoring the diversity of native plants (BEF method) is not sufficient to meet grassland restoration targets for higher order taxa, we established a
study to compare BEF restored and RPP restored tall-fescue invaded grassland in terms of heterogeneity of vegetation structure and composition. We compared spatial and temporal heterogeneity from patch-burn grazing in tall fescue grasslands (RPP perspective) to grasslands that were restored under the BEF perspective which prioritized the establishment of native plant species. To evaluate spatial heterogeneity differences between treatments, we compared standard deviations of plant composition and structure measurements at three different scales: (a) point, (b) patch, and (c) pasture. Because tall fescue has the potential to decrease heterogeneity in grazed pastures, and it was abundant in the RPP pastures, we expected grasslands restored under the BEF perspective to have higher point-scale and pasture-scale heterogeneity. However, because patch-burning has the potential to increase patch-level heterogeneity, we expected the RPP treatment to have higher heterogeneity at the patch-scale than the BEF treatment. To compare temporal heterogeneity we used non-metric multidimensional scaling (NMDS) to plot vegetation composition and structure measurements across four sampling periods. Because an increase in spatial heterogeneity often correlates to a decrease in temporal heterogeneity we expected temporal heterogeneity to be higher in the BEF treatment.

METHODS

Study area and design

This study was conducted in the Grand River Grasslands of southern Iowa (USA) to examine heterogeneity in grasslands using two different restoration methods. The Grand River Grasslands has been identified as one of the most promising areas to restore a functioning tallgrass prairie ecosystem due to the presence of remnant prairies which are
sources of local genetics, and the high percentage of grassland vs cropland in the area (Missouri Department of Conservation 2005; Davit 2008). All study sites were part of a long-term, ongoing project designed to develop adaptive management practices that increase bird and insect diversity in grasslands dominated by tall fescue. Study sites were located in ecoregions characterized by gently undulating hills with dark, fertile loess soils over glacial till (Chapman et al. 2002).

Vegetation in our study sites were dominated by exotic C_3 grasses, including tall fescue (Schedonorus arundinaceus Schreb.) and smooth bromegrass (Bromus inermis Leyss), exotic legumes including birdsfoot trefoil (Lotus corniculatus L.) and clovers (Trifolium spp.), and C_4 native tallgrasses including big bluestem (Andropogon gerardii Vitman), switchgrass (Panicum virgatum L.), and Indiangrass (Sorghastrum nutans L.).

The 30-year average annual precipitation of the region is 1025 mm, 71% occurring from April-September (IEM 2018). Mean annual temperatures for the region are −6°C in January and 24°C in July (IEM 2016). Soils are dominated by Gara loam (fine-loamy, mixed superactive, mesic Mollic Hapludalfs) and Armstrong loam (fine smectitic, mesic Aquertic Hapludalfs) with slopes ranging from 5 to 14% and 9 to 25%, respectively (USDA-NRCS 2014).

**Treatments**

For the objective of this study we selected four sites within the GRG experimental landscape. Two sites had been degraded pasture and were restored using the BEF perspective. In preparation for seeding, one BEF site had been planted to soybeans for several years. In the spring of 2009, a diverse mixture of southern Iowa variety grasses
and forbs was seeded into the soybean stubble using a seed drill. Dominant species in the seed mix included little bluestem (*Schizachyrium scoparium* (Michx.)), Indiangrass, and sideoats grama (*Bouteloua curtipendula* (Michx.)). The degraded pasture on the other BEF site was sprayed with glyphosate at 4.3 l/ha using a tractor and broadcast sprayer in the late summer of 2002, and seeded to the same diverse mixture the following spring. Following seeding, the sites were burned at 3- to 4-year intervals in early spring (March or April) to control woody encroachment. The sites were not grazed by livestock. In 2014, dominant species included big bluestem, little bluestem, switchgrass, and Indiangrass. Common forbs included ironweed (*Vernonia* spp.), purple prairie-clover (*Dalea purpurea* Vent.), blazing star (*Liatris* spp.), black-eyed susan (*Rudbeckia hirta* L.), and coneflowers (*Echinacea* spp.). The other two sites (mean of 27.6 ha) were restored using the RPP perspective. Prior to treatment application, one RPP site was grazed up to 15 AUM ha$^{-1}$ during the growing season each year, while the other site had no record of being grazed for the five years prior to the initiation of this study (see McGranahan et al. 2014). In 2007, each RPP site was fenced along its perimeter and divided into three patches of equal size by mowing burn lines. Each patch was burned at a three-year interval on a rotating basis to create a landscape with three patches, each with a different time since fire. Patches were burned in mid-March to early-April as weather and burn conditions permitted. Black Angus cattle grazed the two sites from early April to early October with a stocking rate of 2.5 AUM ha$^{-1}$. Dominant species included the invasive cool-season grass tall fescue as well as other exotic species.
including Kentucky bluegrass (*Poa pratensis* L.), smooth bromegrass, birdsfoot trefoil (*Lotus corniculatus* L.) and clover species (*Trifolium* spp. L.).

**Data collection**

Vegetation surveys were conducted in late May-early June, and again in August of 2014 and 2015. Within each BEF site, and within each of patch of each RPP site, we sampled along six permanently-marked, 300-m transects. One 300-m transect was permanently placed in each BEF site, and within each burn patch of each RPP site. Samples were taken every 3 m using a 0.25-m x 0.5-m quadrat frame. This resulted in 100 samples taken in each BEF site, and 300 samples (100 per patch) taken in the RPP sites. Percentage canopy cover of total live, cool-season grasses, warm-season grasses, forbs, and standing dead and percentage cover of litter and bare ground at each quadrat placement was estimated and recorded. Cover measurements were recorded using the mid-value of the following cover classes: 0 – 5%, 5 – 25%, 25 – 50%, 50 – 75%, 75 – 95%, 95 – 100% (Daubenmire 1959). Vegetation height was measured to the nearest half cm at three randomly-located points within each quadrat and then averaged. Visual obstruction readings (VOR; Robel et al. 1970) were recorded within each quadrat by recording the highest half dm that vegetation obscured the Robel pole. At each quadrat VOR was recorded in each of the four cardinal directions and then averaged.

**Data Analysis**

To examine how each vegetation measurement contributed to spatial heterogeneity we calculated the standard deviations for the following spatial scales: (i) point scale which accounted for the data from the 100 quadrat placements along each 100-m transect, (ii)
patch scale, which accounted for the data from the BEF treatment (n=1), and the patches in the RPP treatment (n=3), and (iii) pasture scale which accounted for the data from the two pastures in each treatment. This was done for the composition (functional group cover, litter and bare ground cover) and structure (plant height and VOR) data.

We used NDMS with Bray-Curtis distances (Beals, 1984) to visualize temporal heterogeneity in plant community composition among the two restoration treatments. VOR readings, functional group cover, and litter and bare ground cover were subjected to NMDS, using the vegan package in R (Oksanen et al. 2013). We plotted ellipses for standard errors for each treatment at the four sampling periods (June 2014, August 2014, June 2015, and August 2015) to visualize how the plant community changed through time in each restoration treatment. To further visualize how patch-scale heterogeneity changed throughout the course of the study, we calculated heterogeneity (standard deviation) for plant composition and structure measurements across our four sampling periods.

RESULTS

Temporal heterogeneity

The structure and composition of BEF and RPP treatments exhibited low temporal variability over the course of this study. NMDS ordination showed that for both treatments, data from all sampling periods occupied much of the same ordination space (Figure 1-2). Structural and compositional metrics were similar within each sampling period for both treatments, as indicated by the high overlap of ellipses; and no directional shift in data was observed within the temporal extent of this study which is indicative of a
landscape with little temporal variance. Likewise, patch-scale heterogeneity showed no directional shift in standard deviations (Figure 1-3). Standard deviation did not change throughout time except in litter and bare ground cover. This change did not appear to have a directional change.

**Spatial heterogeneity**

**Point-scale**

Heterogeneity was the highest at the point-scale compared to patch and pasture-scales for both treatments, and each treatment affected point-scale heterogeneity differently for each structure and composition metric. BEF had greater point-scale heterogeneity for plant height, and total live, warm-season grasses, forbs, and standing dead (Figure 1). Point-scale heterogeneity of cool-season grasses, litter, and bare ground, was greater in the RPP treatment than the BEF treatment. Point-scale heterogeneity of visual obstruction of each treatment was within one standard deviation of each other (Figure 1).

**Patch-scale**

Patch-scale heterogeneity for all plant functional groups and structure measurements was greater in RPP than in BEF. In the RPP treatment, heterogeneity (standard deviation) was below five for all plant measurements except litter and bare ground cover which were 25 and 23, respectively.

**Pasture-scale:**

Pasture-scale heterogeneity of total live herbaceous, cool-season grasses, height, and VOR were similar (within 1 SD) between treatments. Heterogeneity of warm-season grasses, forbs, and standing dead cover was greater in the BEF treatment than in the RPP
treatment. Pasture-scale heterogeneity of litter and bare ground was greater in RPP treatments. This is indicative of homogeneous treatment sites that did not differ from each other in terms of composition and structural measurements.

**DISCUSSION**

As expected in an exotic-dominated grassland, prioritizing a single restoration ideology of composition without pattern-process (BEF) or restoration of pattern-process without composition (RPP) did not result in sufficient spatial complexity known to be important for multiple taxa in tallgrass prairie. BEF sites were dominated with native tallgrass species, but did not include feedbacks capable of creating patch-level heterogeneity. As a result, BEF sites were virtually one homogeneous patch, resulting in no patch-level heterogeneity for all plant measurements. In contrast, patch-scale heterogeneity was constrained without the removal of tall fescue and re-establishment of native species in RPP treatments. In native tallgrass prairie, fire and grazing have created a structurally heterogeneous environment and the occurrence of some exotic invasive species, such as sericea lespedeza, have not constrained heterogeneity to the extent observed in this study (Fuhlendorf et al. 2004). Patch-burning in the RPP treatment increased patch-level heterogeneity for the functional groups of litter and bare ground, but did not increase heterogeneity in living plant structure or functional groups in this invaded fescue-dominated prairie.

Point-scale heterogeneity in plant communities is influenced by interactions of plant species that are influenced by the same disturbances, and compete for light and nutrients (Grace and Tilman 1990). Greater heterogeneity was observed at local, point-scales than
at landscape levels for both BEF and RPP treatments. Small-scale heterogeneity in this
study was associated with abundance of the plant functional groups in each treatment.
Heterogeneity on BEF sites manifested at small scales in functional groups that were
most abundant. In the BEF treatment, heterogeneity was greater for the dominant
functional groups in these pastures: native warm-season grasses, forbs, and standing dead
(Table 1). Contrastingly, heterogeneity of cool-season grasses was low in BEF sites
where the abundance of this functional group was low. In RPP sites, cool-season grasses
and forbs were common, and small-scale heterogeneity was greater for these two
functional groups. The forbs on BEF sites were exotic legumes including birdsfoot trefoil
and white and red clover. These exotic legumes compete with tall fescue (Dirihan et al.
2015; Hill and Hoveland 1993; Haynes 1980), and small-scale heterogeneity was high as
forbs coexisted with tall fescue creating small scale variability in these two functional
groups. Additionally, consistent with expectations for a spatially homogeneous, invaded
landscape, the greatest amount of temporal heterogeneity was exhibited as a result of
seasonal changes than spatial complexity (Figure 1-2).

Under the RPP perspective, restoring the fire-grazing interaction through patch-
burning has been successful at increasing patch-level heterogeneity in grasslands
dominated by native species (Fuhlendorf and Engle 2001). In native dominated
grasslands of Oklahoma, Fuhlendorf et al. (2004) found that patch-burning created more
heterogeneity in litter, bare ground, and plant structure (as estimated using the angle of
obstruction) than in the unburned grasslands. Additionally, Winter et al. (2011) found
that in an Artemisia filifolia shrubland, patch-burning increased patch-scale heterogeneity
of height, VOR, bare ground, litter, standing dead, and live and dead functional groups.

Patch-burning also increased patch-level heterogeneity in tallgrass prairie vegetation measurements including of warm-season grasses, litter and bare ground cover, VOR, and plant height compared to traditionally grazed treatments (Engle et al. 2008; Fuhlendorf et al. 2006; Hovick et al. 2014; Smith 2014).

Previous studies examining the response of bird and insect taxa to RPP treatments indicated that diversity and abundance of bird and insect taxa on tall-fescue dominated sites were not greater than homogeneously-managed grasslands (i.e., BEF treatments or grazing with burning of the entire unit every three years; Debinski et al. 2011, Moranz et al. 2012, Delaney et al. 2016, Smith et al. 2016). Alternatively, diversity of obligate grassland birds was greater in RPP sites compared to BEF treatments in two years of a seven-year study (Duchart et al. 2016). This lack of consistent response of birds and insects to RPP treatments supports the conclusion that prioritizing one restoration practice over another under the parameters of this study did not increase the heterogeneity that promotes diversity of higher taxa (i.e., patch-level heterogeneity).

Management implications:

Restoring invaded landscapes is a widespread challenge in restoration ecology. Invasive plant species have the potential to disrupt ecosystem processes (D’Antonio and Vitousek 1992; Levine et al. 2003), decrease native biodiversity (Heywood 1989), and alter ecosystem structure and function (Chapin et al. 2000). Additionally, controlling invasive species is often costly and time consuming (Mack et al 2000; Pimentel et al. 2000). It is important to determine if an invaded area can benefit from restoring native
Identifying specific restoration goals and characteristics of a site are critical in determining which restoration methods will be successful (McGranahan et al. 2013). Plant composition and process restoration commonly respond favorably to RPP methods (e.g., prescribed fire and grazing) without seed and herbicides in tallgrass prairie or pasture invaded by Kentucky bluegrass or smooth bromegrass (Hanson et al. 2010; Towne and Kemp 2008). Alternatively, BEF methods can be appropriate for converting old farm land to reconstructed prairies that support higher taxa such as invertebrate communities similar to those found in remnant grasslands (Orlofske et al. 2011). However, when a landscape contains an invasive species that causes substantial changes in ecosystem structure and function, restoration of both native species and processes likely are needed.

Tall fescue has a deep root system and persistent vegetation cover which allows it to tolerate a wide array climatic conditions and soil types (Hannaway et al. 2009, Belesky and West 2009), and to persist under high grazing pressure (Roberts et al. 2009). Heavy grazing, especially when followed by a rest period, commonly stimulates rhizome development and increases tiller density of tall fescue (Fribourg and Milne 2009); therefore, heavily-grazed pastures in tall fescue invaded areas tend to become dominated by dense, uniformly-short stands of tall fescue. Because of these characteristics and others of tall fescue pasture, creating patch-level heterogeneity in tall fescue grasslands presents a challenge (McGranahan et al. 2013). In our study, patch-burn grazing as an RPP method on tall fescue grassland did not increase patch-level heterogeneity in plant structure or plant functional group composition as compared to native tallgrass prairie
ecosystems (Engle et al. 2008; Fuhlendorf et al. 2004; Fuhlendorf et al. 2006; Smith 2014). However, restoring degraded pasture in the tallgrass prairie region by a BEF method without concern of restoring grassland processes appears inadequate in restoring grassland heterogeneity. Results suggest that applying the fire-grazing interaction on existing BEF restored grasslands (i.e., CRP) could be an appropriate approach of increasing heterogeneity in existing reseeded grasslands. In RPP restored grasslands still dominated by tall fescue, more research should be conducted on how to increase heterogeneity meaningful to management goals, through such practices as altering the timing and intensity of grazing and fire.
Table 1-1. A comparison of possible management goals, and guidelines for two different restoration processes. Each column represents the restoration method: Restoration of Pattern and Process (RPP) and Restoration of Biodiversity and Ecosystem Function (BEF), and how these methods were used in fescue dominated sites.

<table>
<thead>
<tr>
<th>Management goals:</th>
<th>RPP</th>
<th>BEF</th>
<th>RPP on tall fescue dominated sites</th>
<th>BEF on tall fescue dominated sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Increase diversity of species at all trophic levels.</td>
<td>Restore dominant plant species known to be important for the ecosystem's function.</td>
<td>Restore fire-grazing interaction on grassland ecosystem.</td>
<td>Restore native tallgrass plant community.</td>
<td></td>
</tr>
<tr>
<td>Reintroduction of principal processes including fire, grazing, water regimes which help promote native diversity of the ecosystem.</td>
<td>Removal of undesirable species through herbicide treatment, farming, burning, disking, and mowing, followed by seeding to native seed mixture.</td>
<td>Burning one third of each site, each year on a rotating basis; grazing with cattle from April-October at 2.5 AUM ha⁻¹.</td>
<td>Farming followed by seeding with tallgrass prairie high diversity seed mixture.</td>
<td></td>
</tr>
<tr>
<td>Several years, with continued management of disturbances.</td>
<td>Several years with minimal continuous input.</td>
<td>2006-present</td>
<td>2009-present</td>
<td></td>
</tr>
<tr>
<td>Increased heterogeneity in plant structure and composition, and increase in diversity of animal taxa.</td>
<td>Established a target native plant community with a diversity of higher taxa.</td>
<td>Heterogeneity (SD) in plant structure and composition, and diversity of higher taxa.</td>
<td>Native tallgrass prairie species dominance, increased diversity of higher taxa.</td>
<td></td>
</tr>
<tr>
<td>Continual disturbance application to promote heterogeneity on the landscape.</td>
<td>Use disturbances such as fire and mowing to keep plant community from losing desired species.</td>
<td>Continuous application of patch-burning each growing season.</td>
<td>Burn every 3-4 years to prevent woody encroachment.</td>
<td></td>
</tr>
</tbody>
</table>
Table 1-2. Mean plant height, VOR (visual obstruction reading, and functional group percent cover of Grand River Grasslands in Restoration of Pattern and Process (RPP) and Restoration of Biodiversity and Ecosystem Function (BEF) restoration treatments.

<table>
<thead>
<tr>
<th>Treatment:</th>
<th>BEF</th>
<th>RPP 0</th>
<th>RPP 1</th>
<th>RPP 2</th>
<th>total</th>
</tr>
</thead>
<tbody>
<tr>
<td>VOR (dm)</td>
<td>2.4</td>
<td>0.9</td>
<td>1.2</td>
<td>1.3</td>
<td>1.1</td>
</tr>
<tr>
<td>Height (cm)</td>
<td>18.1</td>
<td>5.8</td>
<td>7.9</td>
<td>7.7</td>
<td>7.1</td>
</tr>
<tr>
<td>Total live herbaceous (%)</td>
<td>75.0</td>
<td>83.6</td>
<td>82.3</td>
<td>81.1</td>
<td>82.3</td>
</tr>
<tr>
<td>Warm-season grasses (%)</td>
<td>41.5</td>
<td>8.9</td>
<td>9.1</td>
<td>8.1</td>
<td>8.7</td>
</tr>
<tr>
<td>Cool-season grasses (%)</td>
<td>9.3</td>
<td>43.6</td>
<td>49.5</td>
<td>47.0</td>
<td>46.7</td>
</tr>
<tr>
<td>Forbs (%)</td>
<td>28.9</td>
<td>37.9</td>
<td>30.9</td>
<td>31.2</td>
<td>33.3</td>
</tr>
<tr>
<td>Standing dead (%)</td>
<td>21.5</td>
<td>4.6</td>
<td>11.1</td>
<td>12.8</td>
<td>9.5</td>
</tr>
<tr>
<td>Litter (%)</td>
<td>78.0</td>
<td>27.5</td>
<td>60.3</td>
<td>74.6</td>
<td>54.2</td>
</tr>
<tr>
<td>Bare ground (%)</td>
<td>10.0</td>
<td>54.4</td>
<td>21.5</td>
<td>11.3</td>
<td>29.0</td>
</tr>
</tbody>
</table>
Figure 1-1a: Standard deviation of percentage cover contributed by spatial scales (point, patch, and pasture) for plant functional group in Restoration of Pattern and Process (RPP; open circles) and Restoration of Biodiversity and Ecosystem Function (BEF; closed circles) treatments.
Figure 1-1b: Standard deviation of height (cm) and visual obstruction readings (VOR; dm) contributed by spatial scales (point, patch, and pasture) in Restoration of Pattern and Process (RPP; open) and Restoration of Biodiversity and Ecosystem Function (BEF; closed circles) treatments.
Figure 1-2: Nonmetric multidimensional scaling of vegetation functional group and structure measurements in two tallgrass prairie restoration treatments, Restoration of Pattern and Process (RPP) and Restoration of Biodiversity and Ecosystem Function (BEF). Treatments and sampling periods are coded as follows. Color represents restoration treatments of RPP (blue) and BEF (yellow). Shade of points represent sampling period from June 2014 (lightest shade) to August 2015 (darkest shade). Ellipses represent how the community of each treatment changed with sampling period. Shade of ellipses indicates sampling period.
Figure 1-3 Patch-scale heterogeneity (standard deviation) across time for plant functional group percentage cover, and plant structural measurements in Restoration of Pattern and Process (RPP; open circles) and Restoration of Biodiversity and Ecosystem Function (BEF; closed circles) treatments.
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CHAPTER II

Heterogeneity following fire and grazing in tall fescue invaded Tallgrass prairie

ABSTRACT

Grasslands are complex ecosystems which are maintained by an interplay of abiotic and biotic factors. These factors work at different spatial and temporal scales to create heterogeneity in plant community structure and composition. Patch burn grazing is used to create a fire-grazing interaction as grazers preferentially graze on patches of the landscape that have been recently burned. This type of management can increase heterogeneity within managed grasslands at certain scales, but does not always produce the desired heterogeneity at the patch-burn level. In this study, conducted in Iowa’s Grand River Grasslands, we quantified structural heterogeneity at two scales: (a) between burn patches, and (b) within burn patches in tallgrass pastures invaded by tall fescue (Schedonorus arundinaceus). We quantified structural heterogeneity in exotic dominated landscapes managed with patch-burn grazing under two different grazing strategies. The grazing strategies we compared were 1) season-long stocking (April – September) and 2) intensive early stocking (April – July). Data were collected early, late, and after the growing season in 2014 and 2015 to determine how heterogeneity changed throughout the year. We measured visual obstruction, plant height, and canopy cover of vegetation every 3-m on 300-m long transects permanently located in each patch of each pasture. We used a permutational multivariate analysis of variance to compare plant structure and functional group composition between patches, and a principal component analysis to visualize spread of data. To compare within-patch heterogeneity we created semivariograms of plant functional groups and compared sill and range values to determine the amount of within-patch heterogeneity and what spatial scale it occurred. Results from semivariograms showed a mixed response of functional groups to grazing treatment and YSF. IES did not increase patch-level heterogeneity in this study, and within-patch heterogeneity was influenced by grazing treatment with higher sill and range values for some functional groups in IES compared to SLS. Several factors influence the efficacy of patch-burn grazing to create spatial heterogeneity on grasslands. Reasons for lack of patch-level heterogeneity could be due to 1. lack of forage quality differences between burned patches due to the low amount of standing dead in less recently burned patches and 2. low stocking rates. Our findings highlight how changing the grazing strategy in the fire-grazing interaction can influence heterogeneity of exotic dominated landscapes, and the scale at which heterogeneity occurs.
Grassland ecosystems are inherently heterogeneous in space and time. Heterogeneity in grassland ecosystems is defined as spatial and temporal variability in vegetation stature, composition, biomass, and density across the landscape (Fuhlendorf and Engle, 2001). Heterogeneity is influenced by a multitude of abiotic and biotic factors including topoedaphic features, climate, and disturbances working at different spatial and temporal scales (Turner 1989; Fuhlendorf and Smeins 1999). However, many grasslands are managed under a utilitarian paradigm that prioritizes livestock production and soil stability and constrains factors that create heterogeneity (Fuhlendorf and Engle 2001; Vallentine 1990; Wilson 1986; Holechek et al. 2003).

Recently, development and implementation of management tools that promote heterogeneity have become the foci in conservation biology. Understanding the patterns and spatial scale of heterogeneity occurring in plant communities across landscapes is critical to understanding how management practices meet specific management goals. Spatial tools have been developed recently to examine the patterns and spatial scale of vegetation data occurring on a landscape (Turner 2001). One tool used in landscape ecology to examine spatial data is the semivariogram. Semivariograms are useful geostatistical tools that show spatial correlation in data measured at known locations. Distance between data points must be known when creating semivariograms, and data are often collected at set intervals along a transect.

Semivariograms are used to illustrate the amount of variability (semivariance) occurring on a landscape, and the spatial size (lag) at which variability is occurring.
Semivariograms are a useful tool because they quantify heterogeneity in data, and identify the spatial scale at which the given amount of heterogeneity is occurring. Semivariograms often illustrate semivariance increasing as lag distance increases until a leveling-off point is reached (Figure 1a). The sill is the semivariance, and the range is the lag distance at which this leveling off occurs, and indicates where data points are spatially correlated. Sill and range values indicate the variability and spatial scale that heterogeneity is occurring across an area. Semivariograms exhibit a level of semivariance at a lag distance of zero, which is called the nugget effect and is often attributed to variability due to measurement error. Conservation biologists are concerned with increasing variability at the spatial scales that will create conditions to meet management objectives. In semivariograms this translates to an increase in sill and range values where landscapes with more heterogeneity at large scales have high sill and range values, while homogeneous landscapes have low sill and range values (Figure 1b).

Several management tools were developed to promote plant community heterogeneity at large scales to replace homogeneous utilitarian management practices. Fuhlendorf and Engle (2001) proposed a management model that uses the interactive effects of fire and grazing to promote heterogeneity on grasslands. This fire-grazing interaction is an ecological process described as grazing driven by fire (Fuhlendorf et al. 2009). When applied as a management practice (known as patch-burn grazing), the fire-grazing interaction can increase heterogeneity on landscapes as grazers preferentially graze recently burned patches over those with greater time since fire (Fuhlendorf and Engle 2004; Allred et al. 2011).
Patch-burn grazing includes burning different spatially discrete areas within a management unit each year, and allowing grazers free access to the entire management unit. Herbivores will then preferentially select recently burned patches over those with greater time since fire (Fuhlendorf and Engle 2004; Allred et al. 2011), creating patches of vegetation communities that differ in structure and composition. Patch contrast (the degree of difference of plant structure and composition between patches [Kotliar and Wiens 1990]) can be used to describe the diversity of habitat types created through patch-burn grazing by quantifying the difference in plant communities between patches burned at different times. Patch contrast is created when grazing pressure is concentrated on recently burned patches, while grazing pressure is much lower on neighboring patches that have not been burned recently. Differences in grazing pressure creates patches ranging from relatively short “grazing lawns” with low litter and high bare ground, to relatively tall and densely vegetated patches that have high amounts of dead plant material (Fuhlendorf and Engle 2004).

Compared to areas with homogeneous-based management practices (i.e., areas where fire and grazing are applied uniformly to the landscape), heterogeneity created with patch-burn grazing can positively influence bird (Fuhlendorf et al. 2006; Coppedge et al. 2008; Bouwman and Hoffman 2007), invertebrate (Engle et al. 2008; Debinski et al. 2011; Doxon et al. 2011), and mammal (Fuhlendorf et al. 2010) diversity. Patch-burn grazing also improves forage quality for livestock (Allred et al. 2011; McGranahan et al. 2014), maintains cattle gains (Limb et al. 2011), increases forage utilization by wildlife (Augustine and Derner 2015), and can assist in controlling pest insects (Polito et al. 2013;
Scasta et al. 2012) and non-native plants (Fuhlendorf and Engle 2004; Cummings et al. 2007). Although successful in large grassland tracts (Fuhlendorf et al. 2006; Coppedge et al. 2008), patch-burn grazing does not universally produce desired structural or compositional heterogeneity in plant communities (McGranahan et al. 2012b). Several factors can influence the efficacy of patch burning to create patch contrast including grazing pressure, completeness of burn, climate, and the presence of non-native forage species (McGranahan et al. 2012b; Scasta et al. 2014).

Tall fescue (*Schedonorus arundinaceus* (Schreb.)) is an invasive forage grass found in approximately 5.7 million ha of the eastern half of the USA (Fribourg et al. 1991). Tall fescue limits structural and compositional heterogeneity in grasslands because it homogenizes plant communities by decreasing total and native species richness, and forms dense mats in response to grazing, (Barnes et al. 1995, Cid and Brizuela 1998, McGranahan et al. 2012a). In landscapes invaded by tall fescue, patch-burn grazing creates patch contrast in bare ground and litter cover, but not in vegetation structure or functional group composition (McGranahan et al. 2013). Subsequent studies on these areas showed a mixed response in bird and invertebrate species to patch-burn grazing treatments. For example, patch-burn grazing had no effect on abundance, richness, or diversity measures of several invertebrate taxa (Debinski et al. 2011; Moranz et al. 2012); and bird diversity did not increase under patch-burn grazing treatments, although avian community structure on these sites differed from other grazing and burn treatments (Pillsbury et al. 2011). Further, a study by Scasta et al. (2014) showed that grazing pressure was a major determinant of the efficacy of patch burning to create heterogeneity
on these landscapes. Light stocking rates are ineffective at increasing heterogeneity because grazing pressure is not high enough to establish a “grazing lawn”; whereas, heavy stocking rates can create gaps in the fuel bed, prevent biomass accumulation needed for future fires, and result in cattle grazing all burn patches, regardless of time since fire (McGranahan et al. 2012b, Scasta et al. 2014).

Research on patch-burn sites dominated by tall fescue has primarily compared heterogeneity in patch-burn grazing treatments to homogeneous management practices (entire pasture is burned every three years, with or without grazing; Debinski et al. 2011; Pillsbury et al. 2011; Moranz et al. 2012, McGranahan et al. 2012b). However, no studies have been conducted on how grazing strategy effects spatial and temporal heterogeneity within patch-burn areas. Patch-burn grazing in the Great Plains is associated with season-long continuous stocking (SLS) in a 5- to 6-month grazing season. Intensive-early stocking (IES) is a grazing strategy that reduces grazing season length in season-long continuous stocking by as much as 50% (Smith and Owensby 1978). With IES, cattle numbers generally are doubled with cattle grazing a pasture for the first half of the grazing season only. IES appears to be a good match with patch-burn grazing for two main reasons. First, the high early-season grazing pressure associated with IES increases the likelihood of creating a “grazing lawn” on the recently burned patch, thus creating greater contrasts in vegetation structure among the patches. Second, removing cattle in mid-season (early July) allows vegetation to recover and accumulate end-of-season aboveground biomass needed for subsequent fires (Owensby et al. 1988); this is
especially true for pastures with warm-season tallgrasses that are actively growing in mid-season.

We established this study to determine whether manipulating grazing pressure and timing could increase heterogeneity in landscapes dominated by an invasive cool-season grass and managed with patch-burn grazing. We used IES and SLS on patch-burn grazed pastures to create different grazing pressure and timing. A priori expectations were that IES would increase heterogeneity, but the scale of increased heterogeneity would be (i) among patches, as typically shown in tallgrass prairie landscapes that are dominated by warm-season grasses, or (ii) limited to localized areas in burn patches, which has been shown in other studies when abiotic or biotic controls impose bounds on the amount of heterogeneity that can be created with patch burning.

Because grazing pressure is low in SLS pastures in the study area, I hypothesized that:

1. IES would increase among-patch heterogeneity compared to SLS and
2. IES would decrease within patch heterogeneity compared to SLS. To test the first hypothesis, a multivariate approach was used to compare patch level heterogeneity using plant structure and functional group composition measurements. To test the second hypothesis, semivariograms were used to compare sill and range values (indicating the amount of heterogeneity and the spatial scale at which the heterogeneity occurred within burn patches) between grazing treatments.

METHODS

Study Area
The study was conducted on grasslands managed by the Iowa Department of Natural Resources in the Grand River Grasslands (GRG) region of southern Iowa, USA (40°42’ N, 94°5’ W; See Figure 5). Mean annual temperature for the site is 10°C, ranging from -5°C in January to 24°C in July (IEM, 2016). Mean annual precipitation of the region is 940 mm with 58.5% occurring from April through September (IEM, 2016). Soils of the GRG belong to the Gara-Armstrong-Pershing association and dominant soil types within our study sites were Armstrong loam (fine, smectitic, mesic Aquertic Hapludalfs) and Gara loam (fine-loamy, mixed, superactive, mesic Mollic Hapludalfs) with slopes ranging from 5 to 14% and 9 to 25%, respectively (USDA-NRCS 2014).

Vegetation within the study area is tallgrass prairie that has been invaded to varying degrees by non-native C₃ grasses tall fescue, smooth brome grass (Bromus inermis Leyss.), and Kentucky bluegrass (Poa pratensis L.) and nonnative, herbaceous legumes including birdsfoot trefoil (Lotus corniculatus L.), red clover (Trifolium pretense L.) and white clover (Trifolium repens L.). Native tall grasses include little bluestem (Schizachyrium scoparium Michx.), big bluestem (Andropogon gerardii Vitman.), and indiangrass (Sorghastrum nutans L.). Native forbs include Canada goldenrod (Solidago altissima L.), prairie ironweed (Vernonia fasciculate Michx.), wild bergamont (Monarda fistulosa L.), and black-eyed Susan (Rudbeckia hirta L.). Woody plants such as osage orange (Maclura pomifera Rafin.), black raspberry (Rubus occidentalis L.), mulberry (Morus rubra L.), wild rose (Rosa carolina L.), eastern redcedar (Juniperus virginiana Larg.), and oak (Quercus spp.) are commonly found in fence rows and bottomlands.

Experimental Design
This study was conducted on four patch-burn pastures ranging in size from 23 to 32 ha. Each pasture was divided into thirds and each third (i.e., a patch) was burned once in 3 years in mid-March to early April since 2006. The pastures were assigned to one of two grazing treatments: (1) SLS with the pastures stocked from early April through mid-September and (2) IES with pastures stocked from early April through early July. Each pasture was stocked with cross-bred Black Angus cows or heifers at rates based on forage availability. To maintain comparable grazing pressure among pastures, stocking rates were set to arrive at similar end-of-season forage mass for all pastures. The target for end-of-season forage mass was 5000 kg/ha which was estimated to be the amount of fine fuel needed for a spatially even fire in the subsequent year (Hillhouse unpublished data).

**Field methods**

**Plant community**

To examine how the grazing treatments affected spatial heterogeneity in the plant community, vegetation structure and plant functional group measurements were collected in June, August, and November of 2014 and 2015. One 300-m transect was permanently established in each patch of each pasture. Transect locations were chosen to span all topographic positions (hill top, slope, bottom) present within each patch. Vegetation measurements were taken within a 25 x 50-cm quadrat that was placed at 3-m intervals along each transect (100 quadrats patch⁻¹).

Vegetation visual obstruction readings (VOR) were recorded at each quadrat, with the Robel pole placed at the center of the quadrat. One reading was taken in each cardinal direction at a 4-m distance from the Robel pole and a 1-m height on the reading pole.
(Robel et al. 1970). Measurements of litter depth were taken at three points within each quadrat. Estimates of percentage cover of bare ground and litter cover and canopy cover of plant functional groups were estimated within each quadrat. Plant functional groups included total live herbaceous, total grass, warm-season grasses, cool-season grasses, forbs, woody plants, and standing dead. Cover measurements used the following cover classes: 0 – 5%, 5 – 25%, 25 – 50%, 50 – 75%, 75 – 95%, 95 – 100% (Daubenmire 1959). Center points of each cover class were then used in analysis.

Data analysis

To test for differences in the overall plant community at the burn-patch scale, VOR, litter depth, bare ground and litter cover, and plant functional group cover data were analyzed using a permutational multivariate analysis of variance (PERMANOVA). PERMANOVA is a useful tool when analyzing ecological data with low replications. In this study, PERMANOVA was performed using a Bray-Curtis distance of ln(x + 1) transformation. Data were analyzed using grazing treatment (IES and SLS) and sampling period (June 2014-November 2015) as fixed factors. Principal component analysis (PCA) on VOR, litter depth, and percentage cover of plant functional groups, standing dead, bare ground, and litter was used to investigate the relationship of plant community composition between grazing treatments and among burn patches.

Semivariograms show the spatial correlation in data measured at known locations. Semivariograms for each patch of each pasture were created for each sampling period to examine how grazing treatment affected within-patch heterogeneity (sill and range values) throughout the duration of the study. Data collected along the permanently
established transects and used in this portion of analysis were percentage cover of warm-season grasses, cool-season grasses, forbs, standing dead, bare ground, and litter cover. Woody plants made up less than 5% of total percentage cover and were left out of the analysis. Because hundreds of semivariograms were produced, semivariograms were compiled into a single figure to more easily illustrate what the sill and range values of each plant structural measurement were throughout the study. Each figure includes grazing treatments, year-since-fire (YSF), and sampling period.

RESULTS

Testing Hypothesis 1

The results of the PERMANOVA showed that plant structure measurements differed as a result of grazing treatment and YSF (Table 1). No significant treatment x YSF interaction was observed. PCA ordination provided additional indication of differences in patches between treatments and YSF. The first two axes of the PCA accounted for 56% of the variance in the data (Figure 2-2). The order of importance of plant structure and functional group measurements on PCA axis 1 was litter depth, warm-season grasses, standing dead, bare ground, litter cover, forbs, and cool-season grasses. Litter depth, litter cover, standing dead, and cool-season grasses had highly positive coefficients for PC axis-1 and bare ground, forbs and warm-season grasses had highly negative coefficients for PC axis-1. The order of importance of plant structure and functional group measurements on PCA axis 2 was warm-season grasses, litter depth, bare ground, litter cover, VOR, and cool-season grasses. Warm-season grasses, litter depth, litter cover, and VOR had highly positive coefficients for PC axis-2, while bare ground, and cool season
Grasses had highly negative coefficients for PC axis-2. Total live herbaceous cover and total grass appear to contribute very little to differences in the plant community between grazing treatments or among patches. A slight separation occurred orthogonally between grazing treatments, and appeared to be driven by warm-season grasses and cool-season grasses. A separation occurred between different patches along PC axis-1, and appears to be driven by warm-season grasses, bare ground, forbs, litter depth, litter cover, standing dead and cool season grasses.

**Testing Hypothesis 2**

Figure 2-3a displays sill and range values of 216 semivariograms created for this study. Distance from the center of the circle indicates sill (variance) values, and the size of each point corresponds to range values. A lag distance of 10 indicates that information at one sampling location within that burn patch can be used to predict vegetation within 10 sampling locations and can be used to indicate the size of small-scale heterogeneity occurring within a burn patch. Within-patch heterogeneity of each plant structural measurement responded differently and few long-term patterns emerged in sill and range values.

**Warm-Season Grasses.** In all SLS burn patches the sill was low and the range was zero throughout the duration of the study. In August 2014 and 2015, two IES patches had higher sill values than SLS. In June and August of 2014, one IES patch (2 YSF) had a higher sill and a higher range value than the 2 YSF SLS patch. No other increases in sill and/or range values occurred throughout the study.
Cool-Season Grasses. Sill and range values of cool-season grasses remained relatively high throughout the duration of this study. In the 2 YSF patches, IES had higher range and sill values than SLS in August of both years. There were no other long-term patterns in the sill and range values although IES pastures had higher range values than SLS pastures overall.

Forbs. All SLS patches had a range of zero throughout the study. No long-term increases in range values occurred in either treatment. However, in August and November 2014, IES had higher sill and range values in the 0 and 1 YSF patches, which did not carry over to the following year. IES patches typically had higher sill than SLS patches in August of both years, but range values did not differ between treatments.

Bare Ground. In the most recently burned patch, SLS had higher sill and range values than IES in June of both years. No long-term patterns in sill and range values were seen in either grazing treatments in the 1 YSF patches. In the 2 YSF patches, IES had a higher sill during all sampling periods but range values were not higher in all but two sampling periods.

Litter. Grazing treatment did not appear to affect either sill or range values of litter cover. However, in June of both years, IES sill values were low in the most recently burned patch and high in the 1 and 2 YSF patches. In June of both years, SLS sill values decreased with increased YSF, and range values were higher in 2 YSF patches than in IES 2 YSF patches. In the most recently burned patches, SLS had higher sill values than IES in June of both years. In June and August of both years IES 2 YSF patches had higher sill values than SLS 2 YSF patches.
Standing Dead. The sill and range of standing dead were low for both treatments in June and August of both years. The sill and range increased in 2 and 3 YSF patches and 1 and 2 YSF patches of IES pastures in November of 2014 and 2015, respectively.

DISCUSSION

Patch-burn grazing has been introduced as a method for increasing spatial heterogeneity and biodiversity in grasslands, but has had limited success in landscapes invaded with tall fescue (Fuhlendorf and Engle 2001; McGranahan et al. 2012b; Scasta et al. 2016). Grazing pressure influences vegetation heterogeneity in rangeland ecosystems, and is one of the most important factors influencing the efficacy of patch-burning (Scasta et al. 2016; Fuhlendorf et al. 2006). Because stocking rates are relatively low on patch-burn pastures in the GRG, IES was applied to increase grazing pressure during the early growing season, while maintaining stocking rates at a comparable level over the study area. Few studies have shown how altering the intensity and timing of grazing pressure can affect heterogeneity in patch-burn landscapes (but see Scasta et al. 2016). The results of this study showed that increasing grazing pressure at the beginning of the growing season influences heterogeneity on invaded landscapes managed with patch-burning, but not at the scales expected.

Hypothesis I

Intensive-early stocking did not increase patch-level heterogeneity in this study. Plant community structure and functional group composition were influenced by grazing treatment and YSF (Table 1). McGranahan et al. (2013) found that among-patch heterogeneity in SLS pastures occurred in bare ground and litter measurements, but not in
plant structure or functional group composition. Our study showed that the most important factors contributing to the spread of patches in ordination space were litter depth, warm-season grasses, standing dead, bare ground, and litter. Litter measurements, and standing dead, are positively correlated with YSF, and bare ground is negatively correlated with YSF (Fuhlendorf and Engle 2004). Grasses typically decrease in dominance right after a fire, and eventually reach pre-fire levels after 2 years or more (Fuhlendorf and Engle 2004). The spread in warm-season grass cover among burn patches in ordination space did not appear to follow this pattern in our pastures. Patch contrast in warm-season grasses appeared to be associated with two sampling periods (June 2015 and August 2015; Figure 4) when warm-season grasses were negatively correlated with YSF on IES pastures.

Among-patch heterogeneity was driven by time since fire, and IES did not increase heterogeneity at this scale compared to SLS (Figure 2-2). Patch contrast was similar in IES and SLS pastures, with the contrasts caused by differences in the mean values of bare ground, standing dead, forbs, litter cover, and litter depth, all of which were influenced by time since fire (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2006). Grazing treatment influenced the plant community in this study (Table 1). Differences in plant communities between grazing treatments were driven by warm-season and cool-season grasses. Previous research found that IES promotes regrowth and end-of-season standing crop of perennial warm-season grasses, and disfavors certain exotic cool-season grasses compared to SLS (Owensby et al. 1977; McCollum et al. 1990; Jameson 1991). In this study, IES pastures tended to have greater percentage cover of warm-season grasses in all
patches compared to SLS pastures (Figure 4). Additionally, IES patches had lower cover of cool-season grasses in the current-year burn patches throughout the study, and less cool-season grasses in the 1 YSF patches in 2015. Results suggest that IES decreased cover of cool-season grasses on the current-year burn patch, and this decrease carried over to the subsequent year.

Hypothesis II

Intensive early stocking increased within-patch heterogeneity compared to SLS treatments. Overall, the sill values were higher in IES for most variables, and range values were greater more often in IES pastures than SLS pastures. However, increases in sill and range values were not maintained throughout the length of the study, and results from semivariograms illustrate the mixed responses of functional groups to grazing treatment and YSF (Figure 3a). In June and November 2014 and 2015, grazing treatment and YSF appear to have little effects on range and sill values of all functional groups. In August of both years, however, IES increased or maintained sill and range values compared to SLS after cattle had been removed from IES pastures. This indicates that IES positively influenced within-patch heterogeneity.

IES increases grazing pressure on grazing lands at the beginning of the growing season (Owensby et al. 1977). In this study, IES treatments increased within-patch heterogeneity regardless of YSF (Figure 3a), indicating that cattle grazing was patchy in all burn patches. The higher grazing pressure in the IES pastures created more small scale heterogeneity than the lower grazing pressure did in the SLS pastures. The increased grazing pressure in IES pastures appeared to result in more heavy and even use of tall
fescue at the beginning of the growing season, thus decreasing tall fescue at small scales and decreasing within-patch heterogeneity. However, the unevenly-distributed warm-season grasses, which initiated growth later, appeared to be favored by the early, heavy use of the tall fescue and created greater within-patch heterogeneity. Heterogeneity in soil type, precipitation, slope, and aspect create inherent spatial and temporal heterogeneity in grassland ecosystems (Burke et al. 1998, 1999). Inconsistent response to range and sill values of plant functional groups (warm-season grasses, cool-season grasses, and forbs) between years, could be the result of inter-annual heterogeneity in plant communities driven by abiotic factors interacting with fire and grazing treatment to create small scale heterogeneity. Small scale heterogeneity seemed to be particularly responsive to IES treatments in 2015, suggesting that IES may continue to increase small scale heterogeneity as the study continues.

**General Discussion:**

Several factors influence the efficacy of patch-burn grazing to create spatial heterogeneity on grasslands. First, fire must be the primary driver of grazing selection (Allred et al. 2011). In native tallgrass and mixed grass prairies, grazers preferentially graze the most recently burned patches, which creates among-patch heterogeneity (Knapp et al. 1999; Fuhlendorf and Engle 2004; Fuhlendorf et al. 2006; Allred et al. 2011).

Preferential use of the current-year burn patches by grazers is often associated with higher forage quality relative to unburned patches (Sensenig et al. 2010; Allred et al. 2011). In fact, previous studies show that crude protein in recently burned grassland areas can be 1 to 5 times greater than in areas with longer times since fire (Augustine and
Milchunas 2009; Allred et al. 2011, Sensenig et al. 2010). However, the primary driver of declining crude protein content of standing plant biomass in patches is likely due to the standing dead accumulation as time since fire increases. The standing dead biomass is not only lower in forage quality but it also interferes with the grazing animal’s access to new plant growth. In warm-season dominated grasslands, grazers are attracted to recently burned areas because forage in these areas have higher nutritive quality, leaf:stem ratios, live:dead tissue ratios, and dry matter digestibility (Stuth 1991; Mitchell and Villalobos 1999; Van De Vijver et al. 1999; Anderson et al. 2007).

Grazing location by cattle is often determined by tradeoffs between quality and quantity of forage (Demment and van Soest 1985; Senft et al. 1987). In our study, percentage cover of standing dead on the current-year burned patches appeared to be similar to patches with greater times since fire, thus limiting the change in live:dead tissue ratios needed to attract grazers (Stuth 1991; Mitchell and Villalobos 1999; Anderson et al. 2007). At the beginning of the growing seasons in 2014 and 2015, the current-year burned patches of our sites had 3-8% standing dead canopy cover. On 1 and 2 YSF patches standing dead made up 9-15% of canopy cover (Figure 4). Winter et al. (2015) found that in grazed tallgrass prairie in Oklahoma recently burned areas had 7.25% cover of dead vegetation, while areas that had been burned two or three years previously had 39.67% cover dead vegetation. IES did not increase patch-level heterogeneity in this study, possibly because the mechanisms that drive grazer selection on native grasslands are not present in tall fescue dominated landscapes. Instead of
selectively grazing current-year burned patches as typically seen in native tallgrass prairie, grazers in tall fescue dominated grasslands may instead graze in all burned areas. A second important factor influencing the efficacy of patch-burning is stocking rate. Stocking rates must be set in order to match grazing pressure to forage supply within the most recently burned patch (McGranahan et al. 2012b; Scasta et al. 2016). Overstocking results in lower among-patch heterogeneity because cattle graze all patches to satisfy intake requirements (McGranahan et al. 2012b). Understocking results in grazing pressures which do not match forage supply on the current-year burned patches and results in low levels of heterogeneity among burn patches, but higher amounts of heterogeneity within patches due to grazers selectively grazing in all burn patches (Arterburn et al. 2016). At low grazing pressures, grazers selectively graze the landscape and create small-scale (within patch) heterogeneity within burn patches (Fuhlendorf and Engle 2001; Fuhlendorf et al. 2009). We set our stocking rates to leave the amount of fine fuel needed for a subsequent fire to burn the vegetation cover of a patch evenly and completely. Cattle were stocked an average of 2.5 AUM ha\(^{-1}\) which is approximately half of the normal stocking rate for the area (Josh Rusk, personal communication). Our results suggest that stocking rates were set too low to create patch-level heterogeneity in these sites.

IES increased within-patch heterogeneity compared to SLS. Cid and Brizuela (1998) reported that cattle selectively grazed areas in tall fescue dominated pastures, and that these grazed areas were repeatedly utilized because the grazed plants maintained higher crude protein levels than ungrazed portions of the pastures. In our study, cattle in both
grazing treatments grazed selectively and created within-patch heterogeneity in all patches. However, higher grazing pressure in IES created more small-scale heterogeneity by creating more heavily utilized patches throughout the beginning of the growing season, and allowing warm-season grasses a competitive advantage later in the growing season when they were at their peak growth rate (Owensby et al. 1977; McCollum et al. 1990; Jameson 1991; Cid and Brizuela 1998).

Pyric herbivory is known to be a critical component of spatial and temporal heterogeneity in grassland ecosystems (Fuhlendorf and Engle, 2001); however, the effects of patch-burning on grassland heterogeneity are usually studied at a single spatial (patch) and temporal (growing season) scale (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2010, McGranahan et al. 2012b). Recent studies (Bielski et al. 2018, Arterburn et al. 2016) show that factors such as drought and grazing pressure can shift the spatial and temporal heterogeneity observed on patch-burned areas. These studies along with our study illustrate the importance of studying heterogeneity at multiple spatial and temporal scales to better understand how heterogeneity manifests on a landscape (Bielski et al. 2018). Examining tall fescue dominated grasslands at several spatial scales allowed us to see emergent heterogeneity that would have been overlooked had we examined the patch-scale only. Examining heterogeneity at multiple scales will allow researchers to gain insights into how heterogeneity of plant communities affect diversity of higher taxa.

The importance of understanding the ecological consequences of the fire-grazing interaction on invaded landscapes is essential to provide a sound basis for managing these lands for short- and long-term goals. Our findings highlight how an exotic cool-season
grass can alter the efficacy of patch burning, and influence the scale at which heterogeneity occurs. Even by doubling the stocking rate in the first half of the grazing season, the increased grazing pressure of IES did not increase among-patch contrast as would be expected, but did show a weak increase in within-patch heterogeneity. In other grassland systems, exotic species have altered natural processes resulting in the need for alternative management practices to reach new or existing management goals (McGranahan et al. 2012a; Smith and Tunison 1992; Whisenant 1990). Patch burning has increased heterogeneity in grasslands compared to management practices which apply fire and grazing uniformly to the landscape (Fuhlendorf et al. 2006; Bouwman and Hoffman 2007; Coppedge et al. 2008; Engle et al. 2008; Debinski et al. 2011; McGranahan et al. 2012b; Doxon et al. 2011; Scasta et al. 2014). However, IES did not increase patch-level heterogeneity on these landscapes compared to SLS. Further research is needed in these areas to identify how grazing method and fire interact to create heterogeneity in invaded landscapes.
Table 2-1. Results of permutational multivariate analysis of variance of vegetation structure at the landscape scale (based on the percentage cover of plant functional groups, visual obstruction readings (VOR), bare ground, litter cover, and litter depth between grazing treatments, among year since fire (YSF) patches, and for a grazing treatment x YSF interaction).

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Figure 2-1. (a) Semivariograms with different sill and range values and (b) raw data associated with variograms in (a). Grey data points correspond to higher range and sill values, black data points correspond to lower range and sill values, and green data points correspond to very low range and sill values. (c) Illustration of a landscape with different sill (variance) and range (patch size) values (1) Low sill and range values, (2) high sill and range values, and (3) medium sill and range values.
Figure 2-2. Ordination of principal components. Symbols are as follows: shapes represent grazing treatments of intensive-early stocking (IES; circles) and season-long stocking (SLS; triangles); colors represent years since fire (YSF) of current year burn (pink), one YSF (green), and two YSF (blue).
Figure 2-3a. Semivariogram results from six functional groups. Distance from center corresponds to sill values, and size of the symbols indicate lag distance or the size of patches occurring within each patch. Shapes represent grazing treatments of intensive-early stocking (IES; circles) and season-long stocking (SLS; triangles).
Figure 2-3b. Semivariograms and corresponding raw data of warm-season grasses and cool-season grasses in intensive-early stocking (IES) pastures in June 2014.
Figure 2-4. Mean and standard error of vegetation structure (height, litter depth, bare ground and litter cover, and visual obstruction) and functional group metrics (total live, total grasses, warm-season grasses, cool-season grasses, and forb cover) collected over six sampling periods in tallgrass prairie invaded by tall fescue and managed with patch-burning. Green = 0-1 year since fire (YSF), blue = 1-2 YSF, and black = >2 YSF. Semi-transparent bars = intensive-early stocking (IES) treatment, and solid bars = season-long stocking (SLS) treatment.
Figure 5. Map of the Grand River Grasslands. Black polygons represent areas under the management of the Iowa Department of Natural Resources. Stars indicate pasture locations.
LITERATURE CITED


