

IMPLICATIONS OF PYRIC-HERBIVORY ON  
CENTRAL NORTH AMERICAN GRASSLAND  
ECOLOGY, MANAGEMENT AND PRODUCTION

By

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*Proverbs 16:3 – “Commit your work to the Lord, and your plans will be established.”*

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Title of Study: IMPLICATIONS OF PYRIC-HERBIVORY ON CENTRAL NORTH AMERICAN GRASSLAND ECOLOGY, MANAGEMENT AND PRODUCTION

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Abstract: The interaction of fire and grazing is an ecological process regulating fire-dependent ecosystems. Prior to European settlement, grasslands were regulated by fires and focal grazing by herbivores (pyric-herbivory), a disturbance pattern largely removed from the landscape. Pyric-herbivory, applied as patch-burn grazing, can sustain cattle production by reducing input costs and maintaining herbaceous plant communities for forage.

Management for heterogeneity with interactive fire and grazing has been effective in many ecosystems, but its efficacy has been variable in fragmented and invaded grasslands. We assessed factors constraining the fire-grazing interaction in Iowa, USA from 2007 - 2013. The most informative model included stocking rate, burn completion and precipitation. The lightest stocking rate did not establish low vegetative structure in the burn patch and the heaviest stocking rate did not maintain low vegetative structure in the burn patch. The intermediate stocking rate resulted in the lowest vegetative structure in the burn patch and the greatest heterogeneity.

We compared the influence of patch-burn grazing to traditional range management on the most economically injurious fly parasites of cattle in Oklahoma and Iowa in 2012 and 2013. Horn flies and face flies were below economic thresholds with patch-burn grazing but at or above economic thresholds in unburned pastures in Iowa. Pastures that burned completely had fewer horn flies but did not have fewer face flies when compared to no burning in Iowa. Stable flies on both treatments were below economic thresholds suggesting that regular fire can help maintain low levels of infestation.

We assessed how *Symphoricarpos orbiculatus* (buckbrush), the dominant shrub of tallgrass prairie, was affected by patch-burn grazing, complete pasture fires and grazing or complete fire and grazing exclusion in Iowa from 2011 - 2013. Height in burned plots was lower than unburned plots but *S. orbiculatus* reached ~ 84% of pre-burn height 120 days after fire. Stems per ramet were 2x greater in the most recently burned plots. Burned pastures had marginally lower densities than plots excluded from fire ( $P = 0.07$ ). Fire triggered new layering stems. Dormant season fires did not result in mortality, but reduced structural dominance, and maintained lower densities.

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## CHAPTER I

Restoring the fire-grazing interaction sustains cattle production in fire-dependent ecosystems: review and synthesis

**Restoring the fire-grazing interaction sustains cattle production in fire-dependent ecosystems: review and synthesis**

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## HIGHLIGHTS

- Fire and grazing interact ecologically to regulate fire-dependent ecosystems.
- We synthesize benefits of interactive fire and grazing for cattle production.
- Interactive fire and grazing maintain grassland vegetation critical for forage.
- Input costs for feed, parasites, and brush control are reduced with regular fire.
- The fire-grazing interaction is critical to conserve native flora and fauna.

## ABSTRACT

The interaction of fire and grazing is an ecological process regulating fire-dependent ecosystems globally. Prior to European settlement in North America, grasslands, savannahs and shrublands were regulated by fires and focal grazing by large herbivores (pyric-herbivory or fire driven grazing), a disturbance pattern that has largely been removed from the landscape. Ecologists have been attempting to re-couple fire and grazing for the conservation of biodiversity with pyric-herbivory, by burning spatially and temporally discrete patches and allowing livestock to choose where and when to graze. Considering that the primary intent of restoring pyric-herbivory on fire-dependent ecosystems has been for the conservation of biodiversity, we reviewed the literature to assess potential benefits of pyric-herbivory for cattle production. Our review focused on three areas: 1) minimizing or reducing inputs at the animal and ranch level, 2) individual animal and herd performance, and 3) maintaining or improving grassland function and biodiversity. Our review found 68 studies that quantify effects in these three areas. Pyric-herbivory can sustain and/or optimize cattle production and reduce or offset input costs such as supplemental feed, insecticides, herbicides, mechanical brush control and

cross fencing. Pyric-herbivory also can improve animal welfare. Grazing animals make resource selection decisions without the use of force which optimizes thermal regulation, diet diversity, space, reducing disease and physical dermatitis. Lastly, pyric-herbivory has the potential to maintain native herbaceous plant communities that are the resource base for cattle grazing enterprises. Applying regular fire coupled with ungulate grazing reduces woody plant encroachment, stimulating above-ground and below-ground biomass of native perennial grasses, enhancing nutrient cycling, and optimizing plant diversity. Pyric-herbivory shifting through space and time creates a mosaic of habitat composition and structure critical for all trophic levels of wildlife and are critical for threatened and endangered invertebrates and grassland birds. Subsequently, pyric-herbivory could be valuable for the diversification of enterprises for landowners. Fundamentally, pyric-herbivory is a bottom-up approach to grazing management that is based on historical ecological processes and has low-input costs. Comparatively, other grazing strategies are often top-down approaches that impose command-and-control with high-input costs. Further research is needed on the application of pyric-herbivory in ecosystems with arid and semi-arid climate, constraints limiting effective application of pyric-herbivory in degraded areas, economics of pyric-herbivory, effects of fire on gastrointestinal parasites, and other metrics of cattle production.

Keywords:

beef; biodiversity; input costs; sustainability; patch burning; pyric-herbivory

## 1. INTRODUCTION

Many of the world's naturally occurring ecosystems, such as grasslands, savannahs and shrublands are considered fire-dependent (Bond and Keeley 2005) and are important for livestock production. Anthropogenic and lightning fires removed rank and unpalatable vegetation, attracting large herbivores to the nutritious regrowth of recently burned areas (Yadava 1990; Vinton et al. 1993; Kramer et al. 2003; Archibald et al. 2005; Anderson 2006; Murphy and Bowman 2007). This ecological interaction of fire driven grazing, termed pyric-herbivory, results in a variable mosaic of landscape patterns which increases broad-scale heterogeneity (Fuhlendorf et al. 2009). The fire regime and the spatio-temporally variable disturbance pattern maintained grassland by stimulating perennial grasses and preventing woody plant encroachment. For these reasons, the coupled interaction of fire and grazing has been suggested as the most important driver of central North American grasslands other than climate (Anderson 2006).

In North America, settlement patterns by non-indigenous people led to the suppression of fire and extirpation of bison, effectively removing these disturbances from the landscape (Pyne 1997). Settlers were drawn to the vast expanses of productive forages that could be the foundation of a burgeoning livestock industry in the western USA. Conventional livestock production in these fire-dependent ecosystems has replaced bison with cattle and sought for uniformity in grazing patterns and plant communities. Incidentally, suppressing fire and managing for uniform domestic cattle grazing has been to the detriment of many wildlife species, especially grassland birds as a result of the

homogenization of vegetation structure and composition across the landscape (Fuhlendorf et al. 2006).

Over the last decade, ecologists have tried to restore the interaction of fire and grazing as a conservation strategy (Figure 1). Prescribed burning of a patch within a fenced pasture and free access grazing allows cattle free access to choose burned or unburned areas.

This fire-driven grazing has been termed pyric-herbivory, with patch-burn grazing as the application of pyric-herbivory (Fuhlendorf et al. 2001; Hamilton 2007). Pyric-herbivory moves fire and grazing disturbances around the landscape and causes vegetation patterns to shift through space and time (Vermeire et al. 2004; Fuhlendorf et al. 2009).

Depending upon the elapsed time-since-fire of a given patch, the probability of grazing or burning of that patch varies due to the resulting vegetative structure. Re-coupling fire and grazing interactively restores the developmental ecological process, other than climate, driving vegetation patterns (Fuhlendorf and Engle 2004). Pyric-herbivory has been proposed as an approach to restoring landscape heterogeneity and conserving biodiversity using cattle and fire as a means to accomplish those goals (Fuhlendorf and Engle 2001; Wiens 2000). Moreover, pyric-herbivory is different from conventional approaches to grazing management because it integrates conservation and production which is becoming increasingly important in many rangeland landscapes. The process based design to pyric-herbivory is a bottom-up, low-input approach that is diametrically opposite of top-down intensive grazing that uses high-inputs of fencing, labor and other inputs (Holling and Meffe 1996).

The majority of the research on pyric-herbivory to date has been on natural resource conservation, with a major focus on wildlife population ecology, native plant conservation, and soil processes, etc. More recently though, implications for sustaining beef cattle production with pyric-herbivory have been emerging in the peer-review and non-technical literature. Our objectives are to examine the literature for beef cattle production implications in three areas: 1) minimizing or reducing inputs at the animal and ranch level, 2) individual animal and herd welfare, and 3) maintaining or improving ecosystem function and biodiversity. We place this information within the context of the North American Great Plains, but the fundamental ecology of the fire-grazing interaction spans many continents, vegetation types, and organisms (Yadava 1990; Kramer et al. 2003; Archibald et al. 2005; Anderson 2006; Murphy and Bowman 2007). We also identify gaps in the knowledge base and recommend areas for additional study.

## 2. REDUCE INPUT COSTS

### *2.1 Feed costs*

The largest input cost of cattle production is supplemental feed, which exceeds more than half of the direct cost in cow-calf operations (Short 2001). Feeding strategies attempt to overcome seasonal periods of inadequate forage quality such as the winter in perennial C4 grasslands of North America and/or periods of inadequate forage quantity such as periods of drought (Waterman et al. 2012). Reports on the value of patchy fires for cattle production in native fire-dependent ecosystems date back to the 1960's. A study in native longleaf pine – bluestem rangeland reported that patchy fires every three years increased forage palatability, nutritive value, herbaceous plant dominance, and cow and

calf weight gains (Duvall and Whitaker 1964). Patchy fires have been shown to increase cattle gains, crude protein content of forage plants, and grazing of wiregrasses (*Aristida* spp.) (Hilmon and Hughes 1965). A recent study in tallgrass prairie reported that pyric-herbivory increased forage quality in burned patches by a factor of four when compared to unburned patches, 18% and 4% crude protein respectively (Allred et al. 2011).

Accordingly, cattle use of the recently burned patch is greatly disproportionate to the area of the patch, for example, 75% of grazing time in the most recently burned patch in tallgrass prairie (Fuhlendorf and Engle 2004). Secondly, patch-burning and pyric-herbivory maximizes forage quantity in patches that have not been burned for an extended period of time—and subsequently have not been grazed—and have accumulated forage that could be considered as stockpiled forage or standing hay. As a result, pyric-herbivory optimizes forage quality and quantity potentially mediating feed costs by providing both high quality forage (low quantity) and high quantity forage (low quality).

Cattle production studies in the southern Great Plains of the USA of both cow-calf and stocker cattle enterprises have reported that pyric-herbivory did not decrease production and at times maximized production over multiple years, compared to continuous grazing (Limb et al. 2011b). Heavier weaning weights and greater body condition of cows has also been reported in the northern Great Plains as a result of pyric-herbivory (Baumann 2013). Another key benefit to production is that winter supplemental feeding can be delayed due to the extension of higher forage quality in the fall in pastures managed with pyric-herbivory (Weir et al. 2013). Lastly, a recent multi-year study compared pyric-herbivory to the practice of annually burning the entire pasture and seasonally grazing



stocker cattle, a common practice in the Flint Hills region of the USA. This study reported that pyric-herbivory minimized losses in individual animal gains during dry years providing a risk management strategy against drought (Allred et al. 2014). This study strengthens reports from ranchers in the Flint Hills region of Kansas USA that reported similar results during the drought of 2012 (Personal interview, unpublished).

## 2.2 Parasites and insecticides

Parasites constitute another major source of potential economic loss and input costs for cattle enterprises accounting for > \$2.2 Billion in domestic losses annually (Byford et al. 1992). Individual animal performance can be inhibited by heavy parasite loads due to blood loss, annoyance, decreasing grazing time, decreased milk production, and exposure to disease. Two of the most economically injurious parasites in the USA are flies and ticks (Byford et al. 1992). Estimated annual economic losses from flies and ticks in the USA alone exceed \$1.5 Billion (Drummond 1987; Kunz et al. 1991). The most injurious fly, the horn fly (*Haematobia irritans*), is a blood feeding fly that relies on cattle for nutrition and fecal resources for reproduction (Byford et al. 1992). In the USA Great Plains, horn flies overwinter as dormant pupae in cattle fecal pats. Ticks, especially the lonestar tick (*Amblyomma americanum*), cause similar economic loss due to blood consumption (Polito et al. 2013). Both parasites, along with other similar ectoparasites, serve as vector for diseases that can result in additional input costs for medicine and veterinary services (Birkett et al. 2004; Jongejan and Uilenberg 2004).

Conventional parasite management relies on chemical insecticides which are costly, variable in efficacy, and at times ineffective as the rapid biological cycles of these parasites leads to rapid development of genetic resistance (de la Fuente et al. 2007; Oyarzún et al. 2008). A four year study comparing pyric-herbivory to traditional management did not result in a significant reduction in pasture tick numbers but did result in a significant reduction in ticks physically present on both cows and calves, regardless if the control pastures were completely burned or not burned at all (Polito et al. 2013). A similar study found pyric-herbivory resulted in a 41% reduction in horn flies compared to management with no burning, reducing fly levels below the economic threshold for insecticidal treatments (Scasta et al. 2012). Although no studies have reported the effects of fire on cattle gastro-intestinal parasites, Stone's sheep (*Ovis dalli stonei*) with access to burned areas had up to ten times lower lungworm (*Protostrongylus* spp.) loads (Seip and Bunnell 1985). Thus, pyric-herbivory reduces ectoparasites on cattle along with the potential to reduce endoparasites, and lowers overall insecticide applications, input costs and associated losses in production.

### *2.3 Herbicides for invasive weed management*

Another threat to sustainable livestock enterprises is the encroachment of exotic plants that are often combatted with herbicides, an additional input cost. In the southern Great Plains and Midwestern USA, an exotic legume, sericea lespedeza or Chinese bushclover (*Lespedeza cuneata* (Dum.Cours.) G.Don), is presenting a threat and management challenge to cattle ranches. As *L. cuneata* invades it creates monocultures that displace native grasses, alters structure and composition of plant communities, and decreases the

overall grazable forage (Price and Weltzin 2003). A primary mechanism facilitating *L. cuneata* invasion and dominance over native plant communities is the high level of tannins that deter grazing (Allred et al. 2010).

Large ranches and conservation organizations have reported that *L. cuneata* is a major threat and have allocated a substantial portion of their operating budget spraying for *L. cuneata*, often with only marginal success (Palmer 1999; Cook and Hickman 2012). The application of pyric-herbivory overcomes the tannin grazing deterrent and results in increased herbivory that slows the rate of invasion – three times slower than in traditionally managed pastures (Cummings et al. 2007). Functionally, pyric-herbivory drives grazing before plants mature and become unpalatable, and the continued focal grazing in the recently burned patch perpetuates the earlier phenological plant stage. Hence, pyric-herbivory has the potential to slow exotic plant invasion, reduce herbicide application costs, and minimize losses to the grazable forage base.

#### *2.4 Mechanical tree and brush control management*

Woody plant encroachment is another threat because species such as eastern redcedar (*Juniperus virginiana* L.) convert open grassland to closed woodland in as little as 40 years (Briggs et al. 2002). Historically, fires relegated these non-sprouting and fire sensitive trees to shallow soils and topography where fire was unlikely to spread. The threat to livestock production is the low growing canopy of *J. virginiana* that reduces herbaceous plant production and grazing capacity (Engle et al. 1987; Limb et al. 2010).

Other *Juniperus* specie, such as *J. ashei* and *J. pinchotii* are similarly problematic in other regions of the USA (Ansley et al. 2005).

Ranchers have applied a variety of costly and temporary mechanical brush control practices including mowing, hand cutting, bulldozing and others that are two to five times more expensive than burning, depending on land area and plant density (Bidwell et al. 2002). Pyric-herbivory offers a practical framework for applying regular fire in a manner that would reduce the need for costly mechanical brush control costs. The interaction of fire with grazing facilitates fuel accumulation by drawing grazing animals from areas that then accumulate adequate fuel for the next successful fire and creates fire breaks by focusing grazing and removing fine fuels in other areas (Kerby et al. 2007). This pattern of fuel accumulation driven by fire-grazing patterns enhances the potential success of prescribed fires that target *J. virginiana* (Weir et al. 2013).

Encroachment by resprouting shrubs is also a concern in fire-dependent ecosystems. Exacerbating the problem, many shrub species are able to resprout basally and/or epicormatically, and are not killed by fire. Fire, however, can alter the structure of these shrubs benefitting the herbaceous plant community important for cattle grazing (Heisler et al. 2004). Pyric-herbivory with summer fires reduced cover of honey mesquite (*Prosopis glandulosa* Torr.) and other resprouting shrubs facilitating herbaceous plant recovery (Teague et al. 2008). Therefore, regular fire has the potential to slow the invasion of undesirable plants that can reduce forage available for cattle and offset the need for expensive and temporary mechanical brush control costs.

## *2.5 Nitrogen additions*

Net primary productivity of most terrestrial ecosystems is nitrogen limited and this leads to additional input costs for livestock production (LeBauer and Treseder 2008).

Functionally, nitrogen is critical for plant growth and microbial breakdown of cellulosic material in the rumen of cattle (Belasco 1954). In tallgrass prairie, pyric-herbivory enhances nitrogen availability by interactively cycling nutrients rapidly with fire followed by focal grazing (Anderson et al. 2006). The authors explicitly stated that this interaction between fire and grazing and the concomitant increase in plant available nitrogen may offer a strategic management approach that could sustain livestock production.

Furthermore, the disturbance of fire in tallgrass prairie removes detritus, increasing productivity, nutrient cycling and plant available nitrogen (Knapp and Seastedt 1986; Blair 1997). Considering the different inputs managers use in the attempt to distribute/increase nitrogen across the landscape (supplemental feed high in nitrogen content, fertilizer, establish exotic legumes, etc.), the accelerated nutrient cycling associated with pyric-herbivory could reduce these inputs.

## *2.6 Cross-fencing and water development to manipulate grazing distribution*

Grazing distribution continues to be a major challenge for livestock production in North America (Holechek et al. 1995). Managers have used a variety of inputs to manipulate grazing distribution across the landscape, including cross fencing, mobile feeders, water, and more. Cross fencing, in particular, is expensive for the initial construction and the required maintenance. A 2011 study estimated the cost of construction to exceed \$8,000

per mile, with 8% of the initial cost needed annually for maintenance (Knight et al. 2011). Pyric-herbivory distributes grazing by manipulating forage quality with fire as opposed to cross fencing, developing water, moving feeds, etc. The attraction to the recently burned areas tends to override topography, distance to water or shade, although cattle showed an affinity for woody plant cover shade and bison avoided woody plant cover instead selecting for elevation (Allred et al. 2011).

A three year study reported economic returns from pyric-herbivory on tallgrass prairie could exceed those of management intensive grazing (MIG) on endophyte infected tall fescue (*Schedonorus arundinaceus* (Schreb.) Dumort., nom. cons.) pasture due to almost ten times greater input cost primarily from fencing and water development (Jamison and Underwood 2008; Davit and Alleger 2008). This study suggested that endophyte free *S. arundinaceus* pastures managed with MIG could produce greater economic returns, although stocking rates were three times higher than patch-burned pastures and it is unknown if endophyte free *S. arundinaceus* could persist over time with such intensive grazing. Interestingly, gains per animal (yearling cattle) averaged 1.5 lbs per head per day for pyric-herbivory, and 1.6 and 1.0 lbs per head for MIG endophyte free and endophyte infected *S. arundinaceus* pastures respectively. A primary difference between the patch-burned pastures and MIG pastures in this study was the fire dependency of the plant community and the associated implications of integrating production and conservation in fire dependent plant communities. Furthermore, *S. arundinaceus* requires high inputs, has the potential to transform ecosystems by reducing biodiversity, and the

fungal endophyte can have negative effects in mammals and invertebrates (Barnes et al. 1995; Rudgers and Clay 2007).

While construction of cross fences may be subsidized by the federal government in the USA, the land owner is burdened with the long-term maintenance cost, substantially increasing overhead. A recent assessment of the economics of cross fencing, it was concluded that stocking rate would have to increase 9 to 16% (subsidized and unsubsidized) to simply break-even. This study concluded that the tradeoff of cross fencing is short-term economic gain and potential long-term negative effects on wildlife habitat and biodiversity (Knight et al. 2011). Cross fencing increases perches for birds and serves as a recruitment pathway for bird-dispersed seeds of woody plants especially *J. virginiana*, a major threat to North American grasslands (McDonnell 1986; Coppedge et al. 2001). Cross fencing rangelands can also have deleterious effects on the movement of wildlife including grassland birds such as the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) and Greater Sage-Grouse (*Centrocercus urophasianus*) due to collisions (Stevens et al. 2012) and migrating ungulates such as pronghorn antelope (*Antilocarpa americana*), which typically go through fences as opposed to jumping them (Scott 1992). The use of spatially and temporally discrete fires could serve as a proxy for cross fencing to influence grazing distribution that does not sacrifice conservation in the name of production, but rather integrating the two while reducing overhead, financial risk, and ecological risks associated with woody plant encroachment and wildlife movements.

### 3. OPTIMIZE ANIMAL PERFORMANCE

#### *3.1 Resource selection and adapting to climate change*

Pyric-herbivory allows grazing animals to make resource selection decisions without the use of force that is applied in other types of grazing management such as cross fencing that forces high levels of forage utilization. The use of patchy fires increases higher levels of forage utilization in burn patches compared to unburned areas but still allows animals to select locations for optimal thermal regulation without restricting animals to a fenced paddock. As climate change studies are predicting warming temperatures, this has implications for cattle herds that are increasingly black in hide color. Dark hided cattle display higher respiration rates, panting scores, surface temperatures, and stress behavior than the lighter color breeds under heat stress (Brandl et al. 2006; Garcia et al. 2008). If cattle are restricted in their ability to use the landscape to select optimal thermal cover it ultimately could result in death from heat stroke (Blackshaw and Blackshaw 1994). Ultimately, heterogeneity of landscape features is an important feature that will allow cattle to adapt to climate change.

#### *3.2 Diet diversity and inter-animal competition*

Dietary diversity has positive associative effects for herbivores but constructing species mixtures that complement one another in nutrient content and secondary compounds is not well understood (Provenza et al. 2007). Considering that pyric-herbivory hinges on the mechanism of cattle responding to burned patches and shifts the grazing decision from the plant scale to the patch scale, consumption of a greater variety plants is expected. This change in dietary selection is supported by studies reporting pyric-



herbivory resulted in cattle grazing plant species that they typically avoid without fire (Coppedge et al. 1998; Helzer and Steuter 2005; Cummings et al. 2007). Furthermore, the absence of cross fences maximizes space and minimizes inter-animal competition, such as high stock density imposed by cross fencing, which can negatively reduce individual foraging efficiency, body condition, and performance (Wyffels 2009).

### *3.3 Diseases, physical irritants and reproductive efficiency*

Because animal health related costs account for 7 to 13% of operating costs (Short 2001), reducing ecto-parasite pressure with pyric-herbivory will lead to a reduction in animal health costs by reducing exposure to diseases (Polito et al. 2013; Scasta et al. 2012). Ticks serve as vectors for bacterial, viral, and protozoal disease agents that can also lead to paralysis, toxicosis, irritation and allergy (Jongejan and Uilenberg. 2004). Horn flies have been implicated in the transmission of bovine leukosis virus, helminths of the skin and more (Buxton et al. 1985). Furthermore, the lack of fire leads to the encroachment of *J. virginiana* that is positively correlated with *Culex tarsalis*, a mosquito vectoring West Nile virus, a threat to animals and humans (O'brien and Reiskind 2013). Lastly, many rangeland plants have physical defense mechanisms to deter grazing including thorns and pointed leaves that can injure upon contact (dos Reis et al. 2010). A well-known example is prickly pear cactus (*Opuntia* spp.) that has spines that can reduce forage consumption, cause physical damage to the mouth and upper GI tract of sheep, goats and cattle (Migaki et al. 1969; McMillian et al. 2002). Fire can offer a practical and economical strategy to remove the spines and reduce the contact dermatitis (McMillian et al. 2002).

At The Nature Conservancy's Tallgrass Prairie Preserve in Osage County, Oklahoma, USA, fire and grazing have been recoupled at the landscape scale. They have allowed fire and bison grazing to freely interact, resulting in high bison reproductive rates without nutritional supplementation (Fuhlendorf and Engle 2001). The direct benefits to animal welfare may be the least understood benefit of pyric-herbivory. However, evidence suggests that patchy fires can optimize thermal regulation, optimize individual animal space and competition for space and subsequent performance, reduce disease exposure, and reduce physical dermatitis from vegetation.

#### 4. ENHANCE ECOSYSTEM STRUCTURE AND FUNCTION

##### *4.1 Plant composition*

The most common approaches to cattle production either completely exclude fire or burn everything, with the former being most predominant in North America with a few exceptions such as the Flint Hills in Kansas and Oklahoma USA. These two common approaches may only benefit certain segments of the plant community. For example, the interaction of fire and grazing in pyric-herbivory stimulates below ground and above ground biomass of one of the most common perennial C4 grasses in mixed and tallgrass prairies, little bluestem (*Schizachrium scoparium* (Michx.) Nash) (Limb et al. 2011a).

The interaction of fire and grazing can also improve plant root tissue quality and initiate faster cycling of nitrogen (Johnson and Matchett 2001). In tallgrass prairie, the interactive disturbance of fire and grazing increases plant diversity due to the release of

flowering plants that are often inhibited by the structurally dominating tallgrass species. (Coppedge et al. 1998; Vermeire et al. 2004; Helzer and Steuter 2005). Thus pyric-herbivory integrates fire and grazing disturbances that optimize warm-season grasses that are critical for ruminant livestock and can increase floristic diversity of fire-dependent ecosystems.

#### *4.2 Vegetation structure*

The primary intent of pyric-herbivory has been to restore patterns of landscape heterogeneity because heterogeneity is the root of biological diversity at all levels of ecological organization and scales (Wiens 1974; Ostfeld et al. 1997; Fuhlendorf and Engle 2001). Many studies have reported that pyric-herbivory increased heterogeneity of vegetation visual obstruction, or contrast between patches, at the patch scale in contrast to methods that promote homogeneity through annual burning and grazing or not burning at all (Fuhlendorf et al. 2004; Winter et al. 2012; Leis et al. 2013). In ecosystems with a dominant shrub component, such as sand sagebrush (*Artemisia filifolia*), pyric-herbivory restored heterogeneous vegetation patterns and maintained herbaceous plant dominance and plant succession (Winter et al. 2012).

However, not all studies have resulted in the desired level of heterogeneity. Potential constraints to heterogeneity management include overgrazing prior to attempting to burn and exotic species (McGranahan et al. 2012). These constraints are hypothesized to modify the fuel bed and limit fire spread. Furthermore, the interactive effects of fire and grazing on structural heterogeneity are scale dependent and in some areas may also be

constrained by topography (Collins and Smith 2006; Augustine and Derner 2012). The lack of structural heterogeneity in highly disturbed and/or semi-arid environments is a major gap in the literature at this time.

#### 4.3 Invertebrates

The subsequent effects of the interaction of fire and grazing span many trophic levels of wildlife, including invertebrates. A mesic prairie study reported 50% greater total invertebrate biomass and greater abundance of multiple invertebrate orders in the patch that was burned and focally grazed the previous year compared to traditionally managed pastures (Engle et al. 2008). A similar study in semi-arid sagebrush communities reported that Araneae needs unburned areas, Hemiptera needs burned areas, and Orthoptera equally use areas that are both burned and unburned (Doxon et al. 2011).

Pollinators may also benefit from pyric-herbivory as Monarch butterflies (*Danaus plexippus*) increased concurrently with increases in the host plant green antelopehorn milkweed (*Asclepias viridis* Walter) in patch-burned pastures that used summer fires (Baum and Sharber 2012). Other butterfly studies have reported variable responses to fire and grazing with different species having different sensitivities to elapsed time since fire and grazing (Moranz 2010; Moranz et al. 2012). However, it is evident from these studies that butterflies are sensitive to changes in the herbaceous plant community and the risk of not burning at all is a potential shift to a woodland state and alternatively, burning entire patches can reduce larvae and potentially eliminate populations that inhabit isolated grassland fragments (Vogel et al. 2007). Thus, pyric-herbivory provides

an alternative to paradigms that promote homogeneity on rangelands or the idea of managing towards the middle which are common practices across most rangelands in North America (Fuhlendorf and Engle 2004; Holocheck et al. 2004).

Furthermore, many of the native nectar plants that pollinators depend on are forbs which increase with pyric-herbivory (Coppedge et al. 1998; Vermeire et al. 2004). It has also been shown that the maintenance of native vegetation by combatting the encroachment of cedar (*Juniperus* spp.) is critical for conserving the federally endangered American Burying Beetle (*Nicrophorus americanus*) and other grassland obligate detritivores (Walker and Hoback 2007). Clearly, the spatio-temporal interaction of fire and grazing has important implications for invertebrate biodiversity.

#### 4.4 Grassland birds

Pyric-herbivory restores structural and compositional heterogeneity that can benefit imperiled grassland bird species (Wiens et al. 1974; Fuhlendorf et al. 2006; Powell 2006; Pillsbury et al. 2011). Increased landscape heterogeneity from pyric-herbivory creates greater variability in the grassland bird community associated with greater diversity and richness of grassland obligate bird species (Fuhlendorf et al. 2006; Coppedge et al. 2008). Species reported to be declining across their historical range tend to occur at the extreme ends of the spectrum of vegetation structure; such as Upland sandpipers (*Bartramia longicauda*) prefer recently burned and heavily grazed patches while Henslow's sparrows (*Ammodramus henslowii*) require patches not recently burned or grazed. Similar research reported increased bird species richness and greater abundance of imperiled Greater

Prairie-Chickens (*Tympanuchus cupido*) and Horned Larks (*Eremophila alpestris*) in patch-burned pastures in comparison to control pastures (Jamison and Underwood 2008). Additionally, bird demographic studies reported increased nest survival for Dickcissels (*Spiza americana*) and Grasshopper Sparrows (*Ammodramus savannarum*) in patch-burned pastures compared to pastures with homogenous vegetative structure (Churchwell et al. 2008; Hovick et al. 2012).

A long-term assessment of grassland birds over two decades suggests that fire and grazing must be variable in intensity of disturbance and restore heterogeneity if grassland birds are to be conserved (Powell 2006). In the western USA, Mountain plovers (*Charadrius montanus*) are also tightly coupled with the fire-grazing disturbance that creates low statured and bare ground habitat they require (Augustine and Derner 2012). Patchy fires are also required by Northern Bobwhite quail (*Colinus virginianus*) to provide the suite of vegetation structure needed for all life phases and pyric-herbivory has been suggested as the best strategy for providing this habitat mosaic (Hernández and Guthery 1986; Bidwell et al. 2004). Finally, a patchy application of disturbance to tallgrass prairie has consistently been recommended to prevent the continued decline of Greater Prairie-Chickens throughout the Flint Hills of Kansas and Oklahoma, USA (Robbins et al. 2002; McNew et al. 2012). These results support the role of pyric-herbivory in integrating grazing and biological conservation by restoring critical disturbance processes that shape grassland environments for birds obligated to this type of habitat.

#### *4.5 Soil and water resources*

The shifting mosaic of vegetation patterns and attraction of animals to recently burned areas overrides other resource selection criteria for cattle and has been hypothesized to potentially reduce animal preference for riparian areas. A study in semi-arid rangeland reported pyric-herbivory led cattle to select riparian areas five times less than cattle in traditionally managed pastures, effectively increasing the temporal and spatial heterogeneity of riparian area disturbance due to grazing (Hiatt, 2014). Given the preference of cattle for both shade and water, along with predictions for a warming climate, pyric-herbivory can strategically mitigate the risk to riparian areas being overutilized and degraded (Allred et al. 2013). Pyric-herbivory also creates a shifting pattern of vegetation structures that varies through space and time and reduces or eliminates 'sacrifice' areas where animals congregate resulting in degradation (Teague et al. 2008).

A study on pyric-herbivory in coarse textured soils found an increased rate of erosion on burned patches but no drifting or blowouts were observed in burned patches. In the same study, when spring weather promoted early plant growth erosion was similar between burned and unburned patches (Vermeire et al. 2005). Furthermore, this study found that soil water content and plant productivity were unaffected by pyric-herbivory but soils in burned patches were 1° to 3° C warmer than unburned plots based on mid-day measurements (a characteristic of pyric-herbivory generally associated with earlier green up in the spring). The impact of pyric-herbivory on soil and water resources is one of the least studied aspects and is an area that that should receive more focus.

#### 4.6 Mammals

Small and large mammals also respond to the interaction of fire and grazing. Small mammals mirror the response of other taxa with variable species responses at the changing levels of recovery post-disturbance. For example, deer mouse (*Peromyscus maniculatus*) were ten times more abundant on burned patches, but hispid pocket mouse (*Chaetodipus hispidus*) were ten times more abundant on intermediate patches. Hispid cotton rat (*Sigmodon hispidus*), prairie vole (*Microtus ochrogaster*), and fulvous harvest mouse (*Reithrodontomys fulvescens*) all dominated patches not burned in > 2 years (Fuhlendorf et al. 2010). Additionally, black-tailed prairie dog (*Cynomys ludovicianus*) colonies expanded two times faster into burned areas compared to unburned areas in short grass steppe (Augustine et al. 2007; Breland 2010).

White-tailed deer (*Odocoileus virginianus*) responded to areas burned in the summer with peak use occurring within the first two months after fire (Meek et al. 2008). Elk (*Cervus canadensis*) responded to patchy fires in sagebrush communities resulting in greater herbivory of burn patches the first two years after fire and an increase in grass and forb diversity (Dyke and Darragh 2007). Similar long-term effects were reported for the winter nutritional plane of *C. canadensis* and mule deer (*O. hemionus*) with positive associative effects lasting up to two years (Hobbs and Spowart 1984). The value of burned areas may be increasingly important for winter habitat and nutrition as elk and bison used burned areas more than expected especially during mid to late winter (Pearson et al. 1995). From a conservation standpoint, the use of patchy fire has also been



suggested as a habitat restoration tool for bighorn sheep (*Ovis canadensis*) (Bleich et al. 2008; Holl et al. 2012). Stone's sheep (*Ovis dali stonei*) in sub-alpine and alpine ranges also benefit from patch fires due to greater forage quantity on burned range that resulted in lower internal parasite loads and greater lamb crops than sheep on unburned range (Seip and Bunnell 1985).

Although, all of the studies presented do not use domestic livestock, they do all investigate the response of large ungulates and their response to patchy fires. Some of these studies do not necessarily test the response of the wildlife species to the interaction of fire and domestic livestock grazing, but rather test the interaction of fire and wild herbivore grazing. Nonetheless, all sizes of wild mammals respond to patchy fires and the restoration of the historic fire regime that allows animals to freely interact has positive benefits for biodiversity. While the strength of response to burned areas can be determined by body size (Sensenig et al. 2010), evidence from North America suggests that most, if not all native wildlife species respond to fire in some way.

#### *4.7 Wildfire risk mitigation*

Pyric-herbivory also minimizes wildfire risks by reducing wildfire spread and fire intensity (Kerby et al. 2007). According to percolation theory, the connectivity of cells regulates movement with critical thresholds that has been applied to wildfire (Nahmias et al. 2000). The heterogeneous pattern created by cattle responding to patchy fires alters fuel continuity by creating patches that vary in ignition probability and fire spread characteristics (Kerby et al. 2007). Furthermore, as the spatial scale is reduced, the

variance of areas burned by fire types changes as more area is burned by backing or flanking fires rather than headfires (Kerby et al. 2007). Consequently, pyric-herbivory could be applied as a technique to minimize the risk of extreme wildfires that could have a negative effect on forage supply depending on season of the year such as burning the entire ranch in the fall with little re-growth occurring until the spring. Recently burned and grazed patches could also provide refuge for cattle from fast moving wildfires that threaten life and property.

## 5. DISCUSSION

This review has examined fire-grazing interaction research from North America and has assessed studies that span temperature and precipitation gradients (Figure 2). While this review has been restricted to a single continent, the interaction of fire and grazing is a global process with global implications for livestock production, biodiversity loss, and ecosystem function and services (Yadava 1990; Kramer et al. 2003; Archibald et al. 2005; Anderson 2006; Murphy and Bowman 2007). Pyric-herbivory attempts to restore the ecological interaction of fire and grazing in a way that restores broad-scale heterogeneity through a shifting grassland mosaic (Fuhlendorf and Engle 2004). The implications for cattle production in grasslands, rangelands, shrublands and prairies of North America include direct animal benefits and indirect production benefits (Table 1). The literature supports the potential for pyric-herbivory to sustain production by sustaining or optimizing cattle gains, optimizing forage quality and quantity, mitigating the negative effects of drought, reducing parasite pressure and insecticide treatments, reducing chemical and mechanical weed and brush control inputs, reducing nitrogen

additions, and offering an alternative to expensive cross fencing and water development to overcome grazing distribution constraints (Table 1). Globally, low-input pasture based livestock production systems are essential for meeting societal demands for goods and services but additional strategies that mitigate climate and market fluctuations will enhance sustainability (Bernués et al. 2011). The potential reduction in input costs and stability during droughts is evidence that pyric-herbivory moves in the direction of more sustainable cattle production in fire-prone ecosystems of North America.

Furthermore, pyric-herbivory has the potential to enhance production by allowing resource selection decisions to be made by the animal rather than the manager. Given the predictions for a warming climate and increased climatic uncertainty it is critical that livestock systems improve the ability of individual animals to cope with environmental stress (Nardone et al. 2010). Pyric-herbivory optimizes thermal regulation of individual animals by maximizing space and resources, along with manipulating forage selectivity that will increase in importance as cattle cope with increasing thermal extremes. Animal health is also enhanced by reducing exposure to insects vectoring disease, changing the physical structure of vegetation that can irritate the face of cattle, optimizing individual animal space, etc. Furthermore, patchy fires can overcome vegetative, topography, distance to water and shade constraints that typically drive feeding site selection of cattle in complex landscapes (Diaz Falu et al. 2013).

A critical benefit of the process driven approach that pyric-herbivory offers is the ability to integrate livestock production and natural resource conservation in working landscapes

by restoring critical ecological functions (Miller et al. 2012) (Table 2). Land managers should not have to choose one over the other but rather should be able to integrate the two in a complementary approach (Ferreira et al. 2013). Many of the native insects, birds and mammals are dependent on fire-grazing processes to increase suitability for breeding habitats, thermal regulation, and foraging opportunities (Churchwell et al. 2008; Moranz et al. 2012; Fuhlendorf et al. 2010). The resulting patterns and vegetative succession optimize the variable habitat and foraging needs of a wide spectrum of species (Wiens 1974). Furthermore, native plant species and communities are maintained and woody plant encroachment is minimized. Native wildlife species that are of concern can be managed in concert with cattle production and potentially enhanced (Derner et al. 2009). This could be increasingly important for landowners to diversify economic enterprises by offering other recreational opportunities for the general public. This approach to integrating wildlife conservation with production could qualify landowners for incentive type of programs.

## 6. FUTURE RESEARCH CONSIDERATIONS

The application of pyric-herbivory is not without limitations or knowledge gaps. Some ecosystems may be so constrained by moisture that fire did not occur very often and large ungulate grazing was not a prevalent disturbance (for example, some deserts, and some ecosystems, such as the Palouse prairie) (Holechek et al. 1995) (Figure 2). Some ecosystems have fire sensitive species that are critical to conservation, such as big sagebrush communities (*Artemisia tridentata*) and patchy fires may need to be reconsidered and modified in terms of spatial and/or temporal scales (Beck et al. 2011).

However, sagebrush communities are threatened not only by the encroachment of woody shrubs such as *Juniperus* spp. and *Pinus* spp. that are thought to have been regulated by fire, but they are also threatened by wildfire (Shindler et al. 2011). Thus, additional research is needed on how patchy fires can be applied in a sustainable manner to optimize non-sprouting *Artemisia* spp. and minimize woody plant encroachment and wildfire threats. Regarding semi-arid rangelands, a recent study using a four year fire return interval reported grazing preference for the most recently burn patch, however, the preference was lower than the reports from mesic ecosystems (Augustine and Derner 2013). Therefore, we suggest additional research is needed on the controls of the strength and timing of the fire-grazing interaction in more arid ecosystems. This type of information will broaden our understanding of how herbivores respond to fire across a precipitation gradient and assist managers in tailoring the spatial and temporal prescription for fire-grazing interactions accordingly. Further research is also needed on appropriate stocking rate (Helzer and Steuter 2005), the optimum level of heterogeneity, additional cost-benefit analyses of diet optimization, optimum fire-return interval within context of climate and vegetation constraints, the application of fire at different seasons of the year, and potential effects on gastrointestinal parasites of livestock. Lastly, not all studies have resulted in the desired level of structural heterogeneity and the potential constraints need to be empirically examined (McGranahan et al. 2012).

## 7. CONCLUSIONS

Ultimately, the robust data from numerous studies that we have presented are clear evidence that restoring the interaction of fire and grazing can benefit cattle production,

ecosystem function, and rural citizens over the long-term. The broad geographical range of studies in North America indicate that the attraction of herbivores to recently burned patches spans both precipitation and temperature gradients (Figure 2). Some of the studies discussed here are not strictly about pyric-herbivory, but about the need for fire and woody plant control. Consequently, fire is critical and pyric-herbivory is a method that re-incorporates fire while integrating grazing. Pyric-herbivory is a bottom-up approach to grazing management that is ecologically process based and low-input allowing animals to behave and respond to heterogeneity. Conversely, most other grazing strategies, such as rotational grazing, are top-down approaches that impose command-and-control and are high-input (Holling and Meffe 1996). High-input command-and-control approaches do not always result in increases in production and often result in lower animal performance and lower long-term sustainability (Derner et al. 2008; Briske et al. 2008; Knight et. Al. 2011).

The greatest importance of pyric-herbivory to livestock production and fire management is using patchy fires to drive grazing and vegetation patterns helps to overcome the forage vs. fuel paradox in a fenced off landscape. In other words, when entire pastures are burned, all forage was consumed as fuel by fire and livestock have low forage availability until adequate moisture is available (Allred et al. 2014). Pyric-herbivory overcomes that relationship by optimizing fuel accumulation in unburned patches to increase fire intensity and mortality on woody plants or serve as a forage reserve during drought. Pyric-herbivory integrates fire and grazing without having to sacrifice one or the other; deferring grazing to accumulate enough fuel to burn and to woody plant invasion or grazing and not being able to burn at all.

Fundamentally, this restoration of fire and grazing embraces variation through space and time, a diametric opposite to the utilitarian model of uniform utilization promoted by conventional management (Fuhlendorf et al. 2012). Embracing variation and disturbances has been suggested to increase resilience and sustainability of livestock production systems (Ten Napel et al. 2011). The value of the fire-grazing interaction for sustaining ecosystem goods and services is clearly evident in the studies evaluated in this review and is driving its application beyond the core area of the Great Plains where the majority of research has been conducted (Winter et al. 2013). As landscape patterns change, fragmentation escalates and woody plant encroachment changes herbaceous plant communities, agricultural production and biodiversity suffer (Coppedge et al. 2001) and restoration of the interaction of fire and grazing has the potential to mitigate these negative changes, especially in fire-dependent and/or fire-prone plant communities.

#### CONFLICT OF INTEREST STATEMENT

There is no conflict of interest.

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## Tables

Table 1. Summary of potential benefits of the interaction of fire and grazing to animal production

<b>Benefit</b>	<b>Effect</b>	<b>Source</b>
<b>DIRECT PRODUCTION BENEFITS</b>		
Feed costs	Optimize both forage quality and quantity	Allred et al. 2011
Cow-calf production	Sustained cow body condition and calf gains	Limb et al. 2011b
Stocker cattle production	Sustained or increased gains of stocker cattle	Limb et al. 2011b
Optimize reproduction	High bison reproductive rates w/o supplement	Fuhlendorf et al. 2001
Drought losses	Stabilized gains versus burn everything	Allred et al. 2014
Parasites	41% horn fly reduction vs. no fire	Scasta et al. 2012
	57% tick reduction vs. burn all or no fire	Polito et al. 2013
	4x-10x lower GI parasites in Stone's sheep	Seip and Bunnell 1985
Disease exposure	Reduces exposure to disease vectoring insects	(see parasites above)
Thermal regulation	Optimizes options for thermal regulation	Allred et al. 2013
Physical dermatitis	Fire can reduce structures damaging mouth	McMillian et al. 2002; Migaki, G. et al. 1969
<b>INDIRECT PRODUCTION BENEFITS</b>		
Herbicide inputs	3x slower invasion <i>Sericea lespedeza</i> vs. no fire	Cummings et al. 2007
	Reduced cover of resprouting shrubs	Teague et al. 2008
Mechanical brush control	Mechanical 2x-5x more expensive for <i>Juniperus</i>	Bidwell et al. 2002
Nitrogen inputs	Enhances N availability in burn patch	Anderson et al. 2006
Cross fencing costs	Overcomes distribution constraints w/o fence	Davit and Alleger 2008

Table 2. Summary of potential ecological benefits associated with the interaction of fire and grazing

<b>Ecological Benefit</b>	<b>Sources</b>
<b>PLANT COMPOSITION AND STRUCTURE</b>	
Regulate woody plant encroachment/dominance	Bidwell et al. 2002; Kerby et al. 2007; Teague et al. 2008; Winter et al. 2012; Weir et al. 2013
Increase plant diversity	Vermeire et al. 2004; Coppedge et al. 1998
Optimize vegetation heterogeneity	Fuhlendorf et al. 2004; Winter et al. 2012; Leis et al. 2013
Stimulates above/below ground biomass C4 grasses	Limb et al. 2011a
Increased plant root tissue quality and nutrient cycling	Johnson and Matchett 2001
Removes detritus increasing productivity	Knapp and Seastedt 1986; Anderson et al. 2006
<b>SOIL WATER RESOURCES</b>	
Reduces animal preference/use of riparian areas	Allred et al. 2013
Reduces degradation of sacrifice areas	Teague et al. 2008
<b>WILDFIRE RISK</b>	
Minimize the spread of wildfires and potentially increase ability to absorb wildfires to protect fire-sensitive areas from catastrophic fires	Kerby et al. 2007
<b>INVERTEBRATES</b>	
Increase invertebrate diversity and abundance	Engle et al. 2008; Doxon et al. 2011
Benefit pollinators	Vogel et al. 2007; Baum and Sharber 2012
Benefit detritivores	Walker and Hoback 2007
<b>GRASSLAND BIRDS</b>	
Mosquitoes vectoring West Nile virus (a threat to some species) prefer woody invaded areas	O'brien and Reiskind 2013
Increased diversity and survival	Fuhlendorf et al. 2006; Powell 2006; Jamison and Underwood 2008; Coppedge et al. 2008; Augustine and Derner 2012 Chrchwell et al. 2008, Hovick et al. 2012
<b>SMALL MAMMALS</b>	
Optimize habitat benefitting composition	Fuhlendorf et al. 2010
Prairie dogs expand more rapidly in burned areas	Augustine et al. 2007; Breland 2010
<b>LARGE MAMMALS</b>	
White-tailed deer increased use 2 months after fire	Meek et al. 2008
White-tailed and mule deer winter nutrition improved	Hobbs and Spowart 1985
Elk increased use for up to 2 years after fire	Pearson et al. 2005; Dyke and Darragh 2007
May be used to restore bighorn sheep habitat	Bleich et al. 2008; Holl et al. 2012
Increased lamb crop of Stone's sheep	Seip and Bunnell 1985

## Figures

Figure 1. Functional diagram of pyric-herbivory using a three-year fire return interval (it does not have to be three-years and would likely to be variable depending on site productivity and vegetation). Note the movement of fire and grazing through space and time as cattle follow fire to the most recently burned patches.

Figure 2. Study locations assessing the interaction of fire and grazing in North America.

- Symbols represent studies that explicitly test the response of cattle or bison to patchy fires.
- ▲ Symbols represent studies that test other combinations of fire and grazing or the response of native wildlife species to patchy fires without domestic livestock grazing or bison with a perimeter fence.

Figure 3. Potential plant successional trends through space and time and cost/benefit assesment associated with various management schemes. Benefits to livestock production and conservation of biodiversity are estimated through time. Negative estimates to livestock production and conservation are attributed to loss of forage and habitat due to woody plant encroachment or lack of structural heterogeneity for benefit a broad spectrum of species. Financial and ecological costs are estimated for implementation, maintenance, and potential negative effects for wildlife movements or woody plant encroachment.

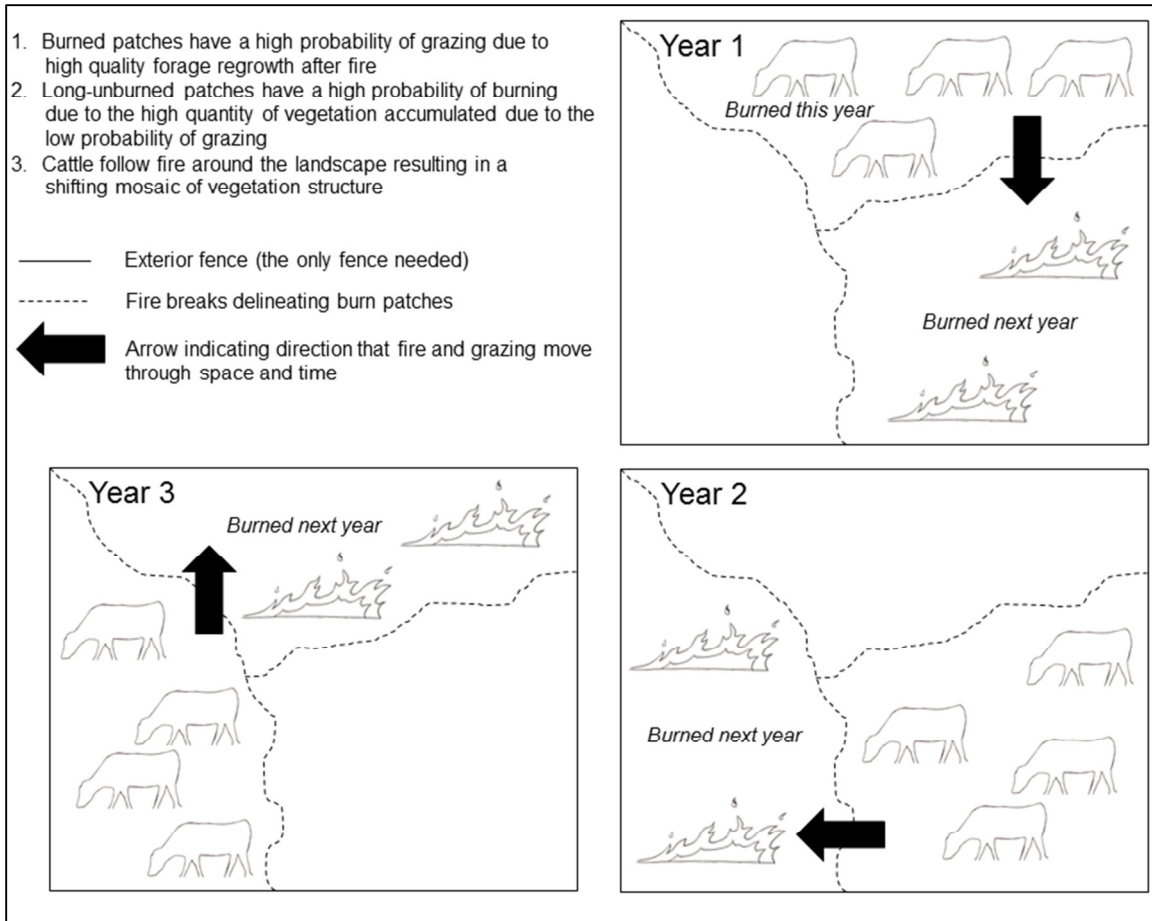


Figure 1.

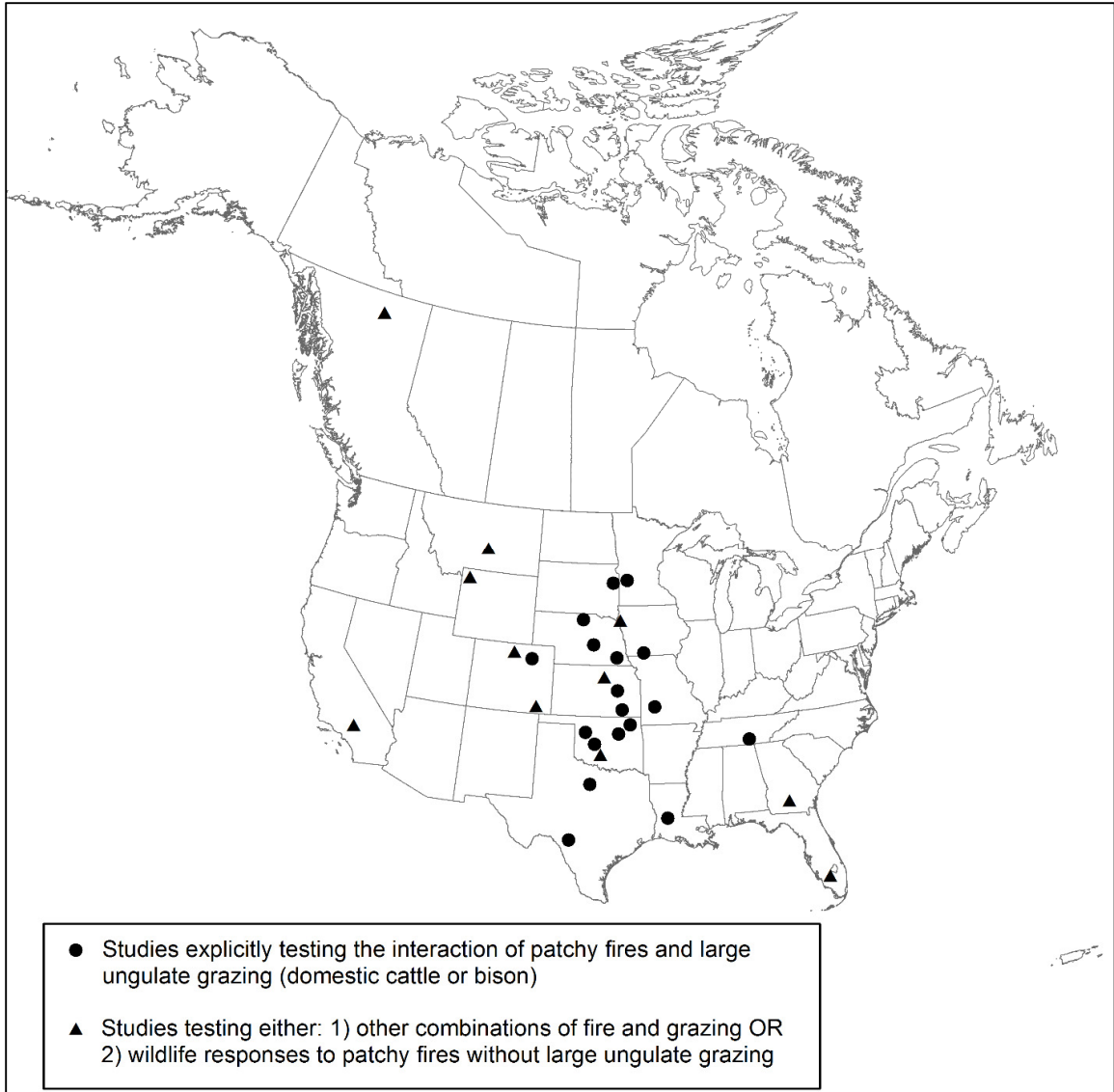


Figure 2.

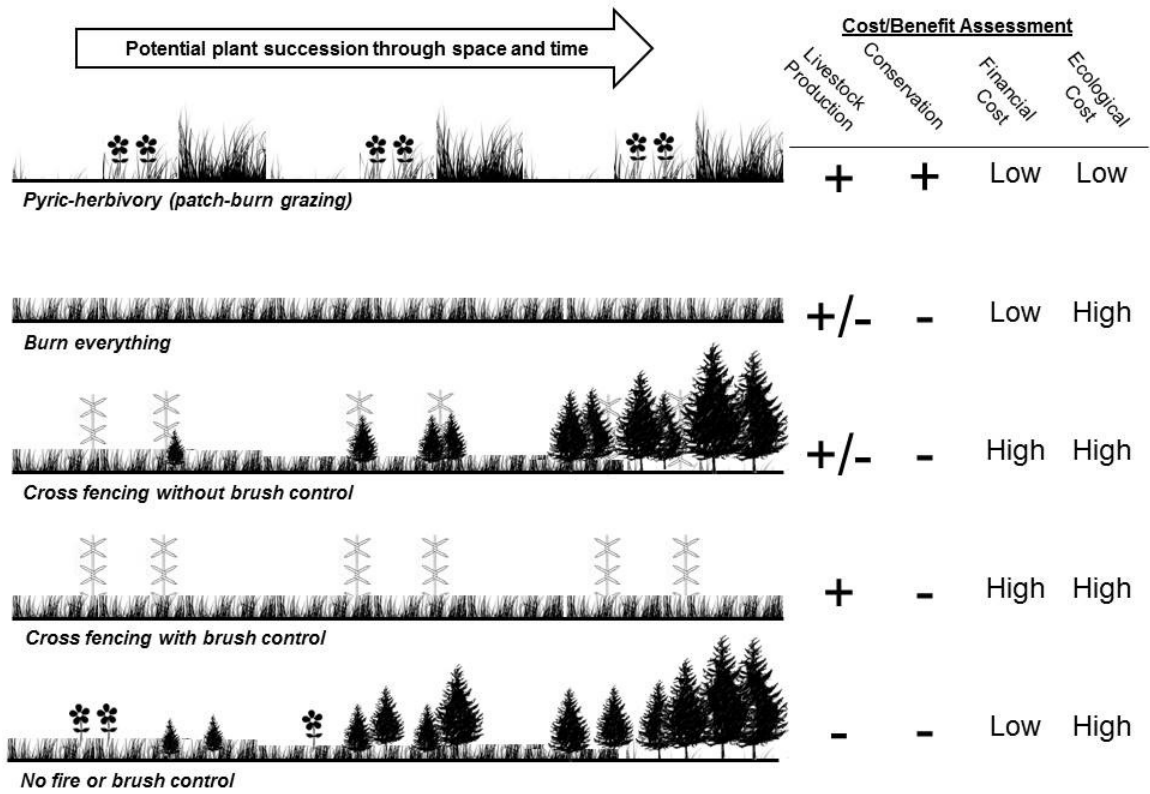


Figure 3.

## CHAPTER II

Grazing decisions constrain fire-grazing based heterogeneity management

## **Grazing decisions constrain fire-grazing based heterogeneity management**

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## ABSTRACT

Management for heterogeneity with interactive fire and grazing has been effective in many ecosystems, but its efficacy has been variable in fragmented and invaded grasslands. Using an information-theoretic approach, we assessed factors constraining the fire-grazing interaction in tallgrass prairies in Iowa, USA from 2007 to 2013. We assessed how livestock management, fire management, and biotic and abiotic landscape features influenced the establishment and maintenance of low vegetative structure in burned patches, the positive feedback driving the fire-grazing interaction. We hypothesized that the exotic C3 grass tall fescue (*Schedonorus arundinaceus* (Schreb.) Dumort., nom. cons.), lag-time between burning and stocking cattle, and burn date would be the constraining factors. However, the most informative model included stocking rate, burn completion and precipitation and no other model was competitive. The lightest stocking rate of 1.5 AUM ha<sup>-1</sup> was ineffective because cattle did not establish low vegetative structure in the burn patch and resulted in the lowest heterogeneity among patches. The heaviest stocking rate of 3.2 AUM ha<sup>-1</sup> initially established but did not maintain low vegetative structure in the burn patch. Completeness of prescribed fires was lowest at the heaviest stocking rates and the constraint on fire efficacy lagged one year behind stocking rate adjustments. The intermediate stocking rate of 2.4 AUM ha<sup>-1</sup> resulted in the lowest vegetative structure in the burn patch and the greatest heterogeneity among patches. The relationship of stocking rate to burn patch vegetative structure and heterogeneity was quadratic and both were optimized at intermediate levels of stocking. Appropriate stocking rates can overcome the fire behavior constraint associated with

exotic species invasion and render fire as the effective driver of grazing patterns and vegetation structure.

Keywords:

conservation; grassland; invasion; production; rangeland; *Schedonorus arundinaceus*

## INTRODUCTION

The spatial variation of landscape features, or heterogeneity, has been suggested as the most important factor influencing species habitats and biodiversity (Fuhlendorf and Engle 2001; Tews 2004). Patterns of landscape heterogeneity are influenced by topographic features but are also regulated by ecological processes including disturbances functioning variably in frequency, severity and type (Levin 1992; Turner 1989). Changes in important ecological processes and landscape heterogeneity impact wildlife species at various spatial and temporal scales (Wiens 1989).

In the grasslands of central North America, the primary regulators of vegetative composition, structure and heterogeneity have been disturbances, mainly fire, grazing and climate (Anderson 2006). Prior to European settlement, the disturbance pattern was largely driven by lightning and anthropogenic fires that stimulated palatable regrowth that was attractive to large herbivores (Fuhlendorf et al. 2009). The interaction of fire and grazing was driven by a series of positive and negative feedbacks (Allred et al. 2011). The positive feedback, considered to be the primary effect, was recently burned

areas that drew and retained focal grazing by large herbivores due to palatable post-fire vegetative regrowth (Archibald et al. 2005). Consequently, the negative feedback, considered to be the secondary effect, was unburned areas not as likely to be grazed due to accumulated detritus deterring grazing and increasing burn potential (Coppedge and Shaw 1998; Fuhlendorf and Engle 2004).

Research suggests that the fire-grazing interaction positively impacts landscape heterogeneity, biodiversity and function in fire dependent grasslands (Fuhlendorf et al. 2009). Landscape fragmentation, domestic livestock grazing and fire suppression have largely resulted in the removal of the fire-grazing interaction from North America (Briggs et al. 2002; Fuhlendorf et al. 2012). Though the results of experiments restoring the fire-grazing interaction with patch-burn grazing have been encouraging, they have not always increased landscape heterogeneity (McGranahan et al. 2012b). Furthermore, the practical application is limited as the majority of studies have been conducted in contiguous areas of undisturbed C4 grasslands (Fuhlendorf and Engle 2004; Vermeire et al. 2004; McGranahan et al. 2012b; Leis et al 2013).

In light of the potential positive ecological outcomes of the fire-grazing interaction and the mixed results in altered grassland systems, we examined factors potentially constraining the efficacy of patch-burn grazing. Using an information-theoretic approach, we modeled potential constraints to creating the primary positive feedback that drives heterogeneity management with fire and grazing: the establishment and maintenance of low vegetative structure in the most recently burned patch (Archibald et al. 2005; Allred et al. 2011). We assessed abiotic factors such as precipitation, slope, and bare ground, as well as the biotic effects of the invasive C3 graminoid tall fescue

(*Schedonorus arundinaceus* (Schreb.) Dumort., nom. cons.), C4 grasses, and litter. We also assessed how grazing and fire management decisions potentially constrain or enhance efficacy. Our objectives for this study were to: 1) determine constraints limiting the creation of a grazing lawn in the burn patch, the positive feedback of the fire-grazing interaction; 2) understand if constraints were biotic, abiotic, management or some related combination; and 3) develop recommendations for the implementation of the fire-grazing interaction in areas that are degraded, invaded and fragmented to guide management. Two differences between our study location and other study locations are the dominance of the exotic C3 grass tall fescue and the ‘lag time’ between burning and stocking cattle on pastures. Thus, we hypothesized that tall fescue, lag-time, and burn date (potentially constrained by the tall fescue) are the primary constraints in the fragmented and invaded prairies we studied and are greater inhibitors than other livestock, fire, biotic or abiotic features.

## MATERIALS AND METHODS

### *Study Area and Design*

An experiment was initiated in the Grand River Grasslands of southern Iowa, USA and northern Missouri, USA to examine the effects of the fire-grazing interaction compared with more traditional forms of land management. The Grand River Grasslands has been identified as one of the most promising areas in the region to restore a functioning tallgrass prairie ecosystem (Missouri Department of Conservation 2005). Pastures ranged from 23 to 32 ha ( $\bar{x}$  = 28 ha) with seasonal grazing of domestic cattle.

Four patch-burned pastures were divided into three patches with only a perimeter fence. In each pasture, one patch was burned annually for a fire return interval of three years. Prescribed fires were conducted in the dormant season from mid-March to early April as snow melt allowed. Cattle were mature angus-base cows grazed seasonally from May to October (~ 150 days) with full access to the pasture. Stocking rates ranged from light to heavy (1.08 to 4.44 AUM ha<sup>-1</sup>).

### *Data Collection*

Vegetation structure in the all patches was measured in mid-July from 2007 to 2013 using a non-destructive method of visual obstruction. Robel poles delineated at 1 dm intervals were observed from 4 m distance at each of the cardinal directions (Robel et al. 1970; Vermeire and Gillen 2001). Vegetation structural measurements were used to assess visual obstruction in the burn patch and heterogeneity among patches. Post-grazing forage residue was sampled in the fall by measuring vegetation visual obstruction at 10 points in each patch, 30 total points per pasture, on a transect oriented on the long axis of each pasture. Visual obstruction was calibrated with herbage mass clipped in 10, 0.1 m<sup>2</sup> quadrats (Vermeire and Gillen 2001). Post grazing forage residue served as the basis for adjusting stocking rate to attain the goal of low visual obstruction in the burn patch.

Abundance of warm-season grass, litter, bare ground, and tall fescue was sampled by estimating canopy cover of 0.5 m<sup>2</sup> quadrats at each point vegetation structure was measured using the Daubenmire scale of cover classes: 0, <1%, 1-5%, 6-25%, 51-75%,

76-95% and 96-100% respectively categorized as 0, 1, 3, 16, 38, 63, 86, and 98 (Daubenmire 1959). Canopy cover totals were allowed to exceed 100% to account for overlapping vegetation layers. Measurements were along permanent line transects positioned perpendicular to the long axis of each patch with equally spaced observation points positioned 25 m on both sides of the line. Each patch had two transects, except one that had three due to irregular shape and orientation, with 30 total observation points per patch assessed annually in mid-July. We calculated the average slope difference of each pasture using a 1m resolution digital elevation model (DEM) of Ringgold County, Iowa, (Iowa NRGIS 2013) and calculating slope using the Spatial Analyst function in ArcGIS 10 (ESRI 2011). Precipitation data was acquired from the Mt. Ayr, IA, USA mesonet station (Iowa Environmental Mesonet 2014).

Stocking rates were manipulated in three phases of the project to ascertain the rate at which heterogeneity between patches is optimized. Stocking rate was heaviest ( $3.2 \pm 0.2$  AUM ha<sup>-1</sup>) in Phase 1 (2007 – 2009) due to pre-existing contract between public land managers and landowners. Additionally, no vegetative production data was available for the study sites initially during this initial phase. In Phase 2 (2010 – 2011), stocking rate was reduced to the lightest levels in the study ( $1.5 \pm 0.1$  AUM ha<sup>-1</sup>). To address the issue of no vegetative production data we began sampling post-grazing forage residue (described above) to adaptively manage stocking rate in 2011 through 2013. In Phase 3 (2012 – 2013), stocking rate was moderated ( $2.4 \pm 0.2$  AUM ha<sup>-1</sup>). These stocking rate adjustments are informative because other researchers have identified grazing management decisions as a gap in fire-grazing based heterogeneity management (Fuhlendorf and Engle 2004; Helzer and Steuter 2005).

### *Identifying Potential Constraints*

We identified potential constraining variables *a priori* based on observations and peer-reviewed literature (Table 1). Grazing management was quantified with three variables: stocking rate, stocking date and lag-time. Stocking rate has been proposed as the key grazing management decision that is more important than grazing system (Holecheck et al. 2001; Briske et al. 2011). Stocking date could influence the strength of the interaction between grazing and plant phenology because forage quality declines quadratically after fire (Allred et al. 2011). Mean stocking date was 124 d (May 4th) and ranged from 106 d (April 16th) to 140 d (May 20th). We recorded “lag-time” between fire and grazing as the elapsed number of days after a fire is conducted and before cattle are stocked on a pasture. Related to stocking date and when fires are conducted, lag-time has been proposed as a critical resource parameter for utilization in fire-prone ecosystems (Klop et al. 2007; Allred et al. 2011).

Fire management was quantified with two variables: burn completeness and burn date. Both of these variables can be strongly affected by tall fescue abundance, live fuel moisture and plant phenology relative to greenup in the spring (McGranahan et al. 2012a; McGranahan et al. 2012b; McGranahan et al. 2013). Burn completeness was considered a measure of prescribed fire efficacy and was based on a composite estimate by multiple observers immediately post-fire of the proportion of the patch that was burned. Mean burn date was 83 d (March 24) and ranged from 65 d (March 6<sup>th</sup>) to 112 d (April 22).

Biotic features were the canopy cover of the dominant vegetation types including tall fescue, warm-season (C4) grass and herbaceous litter. Tall fescue specifically can reduce fire spread and herbivory, the two key features of the fire-grazing interaction (McGranahan et al. 2012a; McGranahan et al. 2012b; McGranahan et al. 2013). Warm-season grass cover and litter cover both influence fire potential as litter represents dormant fuels and the low digestibility of dormant vegetation also influences herbivory (Fuhlendorf and Engle 2004; McGranahan et al. 2012b).

Abiotic features were topography, bare ground and precipitation. First, topography of a site, specifically slope, limits cattle distribution because foraging by cattle declines as slope increases (Bailey et al. 1996; Vermeire et al. 2004; Allred et al. 2011). Secondly, bare ground is an indication of fuel continuity and fire spread (Knapp and Keeley 2006). Lastly, precipitation for the critical period of herbaceous biomass accumulation in the spring and summer can also influence fire and herbivory (Fay et al. 2000). Thus, we defined effective precipitation as the total accumulated precipitation from January 1<sup>st</sup> to June 30<sup>th</sup> (henceforth effective precipitation). Mean effective precipitation was 582 mm and deviated -130 mm (2012) to +198 mm (2010) from the seven year mean.

## STATISTICAL ANALYSES

We considered the burn patch as the experimental unit ( $n = 28$ ). All analyses were conducted in SAS 9.2 (SAS Institute 2011). We used stocking rate, stocking date, lag-time between fire and stocking pastures with cows, percent burn completeness, burn



date, percent warm-season grass cover, percent herbaceous litter cover, percent tall fescue cover, effective precipitation, percent bare ground and slope as independent variables. Stocking rate was relativized to a three year mean of annual primary productivity for each pasture for analyses to account for intra-pasture variation (Scarnecchia and Kothmann 1982). The three year mean annual primary productivity of each pasture was based on post-grazing forage residue samples taken in 2010, 2011 and 2012 plus the amount of forage grazed during the grazing season based on animal demand. These three years included the wettest and driest years during the study. To meet assumptions of normality we log transformed stocking rate, burn completeness, litter, bare ground and precipitation.

We modeled cumulative effects on patch visual obstruction and determined the top predictive models using Akaike's Information Criterion corrected for small sample sizes (AICc) using proc glimmix in SAS 9.3 (Burnham and Anderson 2002; SAS Institute 2011). Modeling was based on identified explanatory variables *a priori* and allowed us to select the most parsimonious model (Burnham and Anderson 2002). At each step, AICc values were scaled relative to the top model (considered the model with the lowest AICc), thus the top model AICc was zero. Within each step, models with  $\Delta\text{AICc}$  values  $\leq 2$  were considered to be in the top set (Burnham and Anderson 1998). Difference between models ( $\Delta\text{AICc}$ ) was calculated and used to rank models. Akaike weights ( $\omega_i$ ) were calculated to assist in determining the top model as  $\omega_i$  values indicate the relative likelihood of candidate models (Wagenmakers and Farrell 2004). We first assessed categories of models separately: livestock, fire, biotic, abiotic factors. This approach allowed us to compare different metrics within each category, and then begin to build

more complex models regardless of order. After we completed the categorical modeling steps we then used the top models from each category to assess models across all categories, again based on  $\Delta\text{AICc}$  values  $\leq 2$  and also compared these to the null model and global model. We assessed Pearson correlation coefficients to ensure final candidate models did not include autocorrelated explanatory variables ( $r > 0.7$ ) (Ribic and Sample 2001; Coppedge et al. 2008; Dzialak et al. 2013). Then 95% confidence intervals were calculated to identify uninformative parameters (Arnold 2010).

In the first modeling step, we assessed the null model with no covariates. In the attempt to account for variation through space and time, we then used a mixed effects modeling approach and tested the potential random effects of Patch, Pasture and Year. Patch, Pasture and all possible combinations of Patch, Pasture or Year did not improve the AICc but Year singularly did and thus, was included as a random effect in all subsequent modeling steps (Null without Year as random AICc = 91.60 and Null with Year as random AICc = 84.60). In the second modeling step, we assessed basic livestock management decisions using three variables including stocking rate, stocking date and the elapsed time between burning and stocking cattle (lag-time). We then assessed the combined livestock management model (stocking rate + stocking date + lag-time). In the third modeling step, we assessed indications of fire management with two variables; burn completeness and burn date. We then assessed the combined fire management model (burn completeness + burn date). In the fourth modeling step, we incorporated potential biotic features that could influence the fire-grazing interaction including warm-season grass cover, litter cover and tall fescue cover. We then assessed the combined biotic model (warm-season grass + litter cover + tall fescue cover). In the fifth modeling step,

we examined abiotic features that could constrain the fire-grazing interaction including slope difference, bare ground and effective precipitation. We then assessed the combined abiotic model (slope difference + bare ground + effective precipitation). In the sixth modeling step, we added the top models from each of the four categories to the top univariate model. We then tested all additive and multiplicative combinations of the top models. After comparing all models, only models with  $\Delta\text{AICc}$  values  $\leq 2$  were considered to be in the top set of candidate models (Burnham and Anderson 1998).

Based on the results of our modeling, we then sought to visually compare the top candidate models to hypothetical and observed vegetation responses by graphing the mean visual obstruction of all patches through time. Hypothetical vegetation responses were postulated based on published literature (described in results) (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2006; Leis et al. 2013). Heterogeneity between patches, measured as the standard deviation between the mean visual obstruction of the most recently burned patch, the patch that had not been burned for over two years, and the intermediate patch burned the previous year (Fuhlendorf et al. 2006), was also calculated and graphed through time. Mean of burn completeness was graphed through time and analyzed with ordinary least squares linear regression and ANOVA ( $P \leq 0.05$ ).

## RESULTS

For the livestock models, the top model was stocking rate; stocking date and lag-time models were not competitive (Table 2). Akaike weights ( $\omega_i$ ) suggest stocking rate (0.98) was 98 times more influential for visual obstruction than stocking date (0.01) or lag-time ( $<0.01$ ). The top fire model was burn completeness; the burn-date model was

not competitive (Table 2). Akaike weights suggest burn completeness (0.94) was 94 times more influential for burn patch visual obstruction than burn date ( $<0.01$ ).

Litter was the top biotic model; warm-season grass and tall fescue were not competitive (Table 2). Akaike weights suggest litter (0.91) was 15 times more influential for visual obstruction than warm-season grass (0.06) or tall fescue (0.03). Effective precipitation was the top abiotic model; bare ground and slope were not competitive (Table 2). Akaike weights suggest effective precipitation (0.83) was 5 times more influential than bare ground (0.17) or 83 times more influential than slope ( $<0.01$ ) for visual obstruction.

Two models were in the top set of predictive candidate models for burn patch visual obstruction (Table 2). Both included burn completeness, stocking rate and effective precipitation. The top model also included litter canopy cover. The parameter estimate for stocking rate was positive indicating that as the relative proportion of biomass allocated per animal unit increased (or stocking rate was reduced) burn patch visual obstruction increased. The parameter estimate for litter was also positive indicating that as litter canopy cover increased so did burn patch visual obstruction. Parameter estimates for burn completeness and effective precipitation displayed an inverse relationship indicating that as the proportion of a patch that is burned increased and effective precipitation increased, burn patch visual obstruction decreased (Table 3). The 95% confidence intervals of these four parameter estimates indicate that stocking rate, burn completeness and effective precipitation regulated burn patch visual obstruction establishment and maintenance, but litter canopy cover was not informative as its 95% CI overlap zero (Arnold 2010). Thus, we conclude that the primary constraint

to establishing and maintaining a grazing lawn in the burn patch in the Grand River Grasslands is attributed to grazing management decisions, ability to conduct effective prescribed fires and climate.

Based on published studies, we hypothesized that vegetative structural response to patch-burn grazing in the burn patch would have the lowest visual obstruction of vegetation, the patch that had not been burned for over two years would have the highest visual obstruction of vegetation and the intermediate patch would have an intermediate height of vegetation visual obstruction, and inter-annual climatic variation may result in slight but non-significant differences between years (Fig.1a) (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2006; Leis et al. 2013). The actual response from 2007 to 2011 however did not follow our hypothesized pattern in the early stages of the project (Fig. 1b). In 2008 and 2009, a grazing lawn in the burn patch was established but not maintained. Furthermore, there was no separation between the intermediate patch and the long unburned patch, potentially because the heaviest stocking rate does establish a grazing lawn but cattle need to move into other patches to satisfy forage intake requirements. Thus, burning spatially and temporally discrete patches with a heavy stocking rate established the positive feedback but too many cattle minimized the negative feedback of accumulated detritus in the unburned patches. In 2010 and 2011, there was no establishment of a grazing lawn in the burn patch with very little separation between patches, especially in 2010. We hypothesize that stocking rate was too light and cattle were unable to keep up with post-fire vegetative regrowth in the burn patch. However, in 2012 and 2013 we began to see the actual response match the hypothetical response (Fig.1c). Cattle were able to both establish and maintain a grazing lawn and we

began to see separation between the patches, especially in 2013. This is attributed to the intermediate stocking rate based on our model selection and the actual response observed in Fig. 1c.

The results in Fig. 1b and Fig. 1c indicate that the relationship between stocking rate and burn patch visual obstruction and heterogeneity was non-linear. Rather, burn patch visual obstruction was lowest and heterogeneity was highest at intermediate levels of animal demand. In comparison, at lower and higher levels of animal demand, burn patch visual obstruction was higher and heterogeneity was lower than at intermediate levels.

To assess heterogeneity of vegetation structure in our experiment, we used the mean of visual obstruction among patches (Fig. 1b) to calculate the standard deviation as the indices of heterogeneity (Fig. 1c) (Fuhlendorf et al. 2006). From 2008 to 2009, the standard deviation was 0.5, from 2010 to 2011 the standard deviation was 0.3 and from 2012 to 2013 the standard deviation was 0.7. Thus, heterogeneity was 1.4 times to 2.3 times greater in 2012 and 2013 compared to the previous two year cycles

When this experiment was initially established, it was difficult to conduct complete prescribed burns (Fig. 2). However, through the course of this study, the completeness of prescribed fires increased. Heavy stocking rates in 2008 and 2009 may explain, at least in part, the poor ability to conduct complete prescribed fires if cattle moved away from the burn patch and began grazing in the long unburned patch. However, the focal grazing in the burn patch was optimized at intermediate stocking rates

which enhanced fuel accumulation and continuity in the long-unburned patch (Kerby et al. 2007).

## DISCUSSION

The primary constraints of fire-grazing based heterogeneity management in the fragmented and invaded landscapes we studied are grazing management, fire management and climate. Surprisingly, our initial hypothesis that the exotic C3 grass tall fescue, lag-time between burning and stocking cattle, and burn date as the primary constraining factors was incorrect. Other assertions of initial failure at this location have been primarily associated with overgrazing prior to the start of the experiment and the exotic C3 graminoid tall fescue (McGranahan et al. 2012a). However, tall fescue abundance was not correlated with burn completeness ( $r = 0.09$ ,  $P = 0.62$ ) and did not constrain burn completeness.

This lack of constraint by tall fescue is important as it suggests the fire-grazing interaction can override constraints of exotic species with secondary compounds that deter grazing. For tall fescue this is relevant given the defensive mutualism of the fungal endophyte and host and similar grazing deterrence of tannins in *Lespedeza cuneata* that was altered by the interaction of fire and grazing (Clay 1988; Cummings et al. 2007). Because focal grazing in the burn patch should maintain earlier phenological stages for longer periods of time, fungal endophyte development on an individual plant is likewise impeded (Rottinghaus et al. 1991; Hall et al. 2014). The fire-grazing interaction can also override the high moisture content and altered fuelbed characteristics associated with tall

fescue invasion that can inhibit fire spread by allowing for increasing dead fuel accumulation in patches that have not been burned in the current growing season (Kerby et al. 2007; McGranahan et al. 2012a; McGranahan et al. 2013).

Heavy grazing reduces fuel continuity due to greater plant interspaces and reduced fuel loads causing the inverse relationship between stocking rate and the ability to conduct prescribed fires demonstrated in our results (Derner and Whitman 2009; Davies et al. 2010; Leonard et al. 2010). However, once stocking rate was moderated in 2010, burn completeness improved although there was a one year lag after grazing adjustments were applied (Fig. 2). The reduction in stocking rate in 2010 may have also had a rest or deferment effect and been necessary to reinstate effective prescribed fires after heavy stocking in the earlier years (McGranahan et al. 2012b). Establishing fire-driven grazing patterns can also improve the ability to burn after drought years because burn completeness was highest in 2013, the year after the lowest year of effective precipitation in our study (448 mm).

Our study indicates that the successful application of the fire-grazing interaction must rely on basic grazing management decisions; insight addressing a critical knowledge gap (Fuhlendorf and Engle 2004; Helzer and Steuter 2005). This information corresponds with the fundamental rangeland management principle that stocking rate is the key grazing management decision and more important than grazing system (Holechek et al. 2001; Hickman et al. 2004; Briske et al. 2011). For these reasons, determining the effective stocking rate will be critical for the successful application of patch-burning on fragmented landscapes and for the realization of benefits to biodiversity (Fuhlendorf et al. 2006; Coppedge et al. 2008; Davit and Alleger 2008).



However, stocking rates are difficult to interpret and compare in the context of variable annual primary productivity across pastures and regions. For example, previous studies noted that stocking rate in 2007 to 2010 at our study location (3.1 AUM ha<sup>-1</sup>) was ‘heavy’ compared to four other studies (0.8 to 4.3 AUM ha<sup>-1</sup> noted to vary from light to moderate) (McGranahan et al. 2012b). However, when stocking rate is relativized to annual primary productivity for the five locations, the stocking rate was the lightest at our study location during that time period (McGranahan et al. 2012b). Furthermore, our study sites had a history of abuse, overgrazing and were highly invaded by C3 exotic plants and responses may not be comparable to C4 dominated prairies due to asynchronous growing and burning patterns (Ode et al. 1980).

In our study, the intermediate level of stocking (equivalent to a stocking rate of 2.4 AUM ha<sup>-1</sup>) resulted in the greatest levels of heterogeneity. Other North American fire-grazing interaction studies, across a broad precipitation gradient, reported stocking rates ranging from 0.5 AUM ha<sup>-1</sup> to 4.3 AUM ha<sup>-1</sup>) (Jamison and Underwood 2008; McGranahan et al. 2012b; Smith 2014; Augustine and Derner 2014; Allred et al. 2014). Other studies of seasonal continuous and rotational grazing systems in tallgrass prairie have reported stocking rates ranging from 3.1 AUM ha<sup>-1</sup> to 7.0 AUM ha<sup>-1</sup> (Hickman et al. 2004; Towne et al. 2005).

The inverse relationship of precipitation with visual obstruction indicates that precipitation is related to the strength of the fire-grazing interaction. In other words, precipitation is needed to maintain a grazing lawn. If precipitation is too low, early vegetative growth slows or stops and animals leave the patch to satisfy forage intake requirements. The importance to our overall top model corresponds with research from

mixed grass prairie that suggests precipitation explained half of the variation of peak standing crop, as much as stocking rate (Derner and Hart 2007).

The effective application of heterogeneity management with fire and grazing in the mesic prairies of the Grand River Grasslands appears to be primarily constrained by anthropogenic management, specifically fire and grazing management. Optimizing stocking rate will allow managers to realize successful establishment of vegetation structural heterogeneity with the ecological interaction of fire and grazing and potentially reversing homogenization of grassland habitat and declines of grassland bird populations (Herket 1994; Brennan and Kuvlesky 2005; Fuhlendorf et al. 2006; Sauer et al. 2012). Although the application of the fire-grazing interaction is fundamentally different than the utilitarian paradigm of more traditional rangeland management, basic stocking rate decisions are still critical (Briggs et al. 2002; Fuhlendorf et al. 2012).

## IMPLICATIONS

Based on our data and the non-linear relationship between stocking rate and burn patch visual obstruction and heterogeneity, we propose a universal model to guide grazing decisions within fire-driven management schemes. In this model, the appropriately applied intermediate stocking rate is critical for establishing and maintaining a grazing lawn in the burn patch and optimizing heterogeneity (Fig. 4). This universal model is based on the relationship between stocking rate, burn patch vegetation structure and heterogeneity that is non-linear. Intermediate stocking rates minimize the low structure by establishing and maintaining a grazing lawn in the burn patch and

maximize the structural heterogeneity or contrast between patches. When stocking rates are too light, herbivores cannot establish a grazing lawn in the burn patch and when stocking rates are too heavy they cannot maintain the grazing lawn in the burn patch (Fig. 4). At too light of stocking rates, no burn patch is established (Fig. 5a). At intermediate stocking rates, the burn patch is established and maintained and biomass accumulation is maximized in the long-unburned patch (Fig. 5b). At heavy stocking rates, the burn patch is established but not maintained and as cattle move to other patches to satisfy intake requirements, biomass accumulation is reduced and fuel continuity is negatively altered (Fig. 5c).

Understanding how stocking rates affect the fire-grazing interaction has been a knowledge gap limiting its use and effective application (Fuhlendorf and Engle 2004; Helzer and Steuter 2005). The reason determining stocking rates is complicated in fire-driven grazing systems is the paradox of herbaceous plants as either fuel for fire, forage for livestock, or both. It is also difficult to replicate the pre-settlement patterns of free-ranging native herbivores and highly variable fires that occurred across broad scales within small fenced pastures.

Research has shown that managing rangeland with interactive fire and grazing can sustain cattle production while optimizing wildlife habitat (Fuhlendorf et al. 2006; Limb et al. 2011; Scasta et al. 2012; Polito et al. 2013; Allred et al. 2014). Even though this approach to managing rangelands is novel and integrates conservation and production goals, basic rangeland management principles such as stocking rate are still essential (Fuhlendorf et al. 2012). Our study also indicates that prior overgrazing, exotic species and other biotic and abiotic features may impede the interaction of fire and grazing, but

the efficacy of restoring fire-grazing processes and vegetation structural patterns is still regulated by fire, grazing and climate (Anderson 2006). Furthermore, stocking rate continues to be the key grazing management decision that is more important than the grazing system, even fire-driven grazing systems and corresponds to the efficacy of prescribed fires (Holecheck et al. 2001; Briske et al. 2011).

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## Tables

Table 1. Justification of including candidate variables in assessing the potential constraining factors to establish and maintain a grazing lawn in the burn-patch in patch-burn grazed pastures.

The study location is the Grand River Grasslands of Iowa, USA from 2007 to 2013

Candidate variables	Justification for inclusion <sup>a</sup>
Stocking rate	key grazing management decision (3, 7)
Stocking date	forage quality declines quadratically after fire (1)
Lag-time	influential parameter for herbage utilization (1, 8)
Burn completeness	inhibited by vegetation patterns (4, 10 - 12)
Burn date	inhibited by live-fuel moisture (10 - 12)
Tall fescue cover <sup>b</sup>	reduces fire spread and herbivory (10 - 12)
Warm-season grass cover	important for fire success and herbivory (11)
Litter cover	increases fire potential and herbivory (6)
Slope difference	constrains herbivore distribution (1, 2)
Bare ground	indicator of fuel continuity and burn completeness (9)
Effective precipitation	temporal variation relative to critical growth periods could impede grazing effects (5)

<sup>a</sup>Numbers refer to the literature source justifying inclusion of a specific variable (1 - Allred et al. 2011; 2 - Bailey et al. 1996; 3 - Briske et al. 2011; 4 - Davies et al. 2010; 5 - Fay et al. 2000; 6 - Fuhlendorf and Engle 2004; 7 - Holecheck et al. 2001; 8 - Klop et al. 2007; 9 - Knapp and Keeley 2006; 10 - McGranahan et al. 2012a; 11 - McGranahan et al. 2012b; 12 - McGranahan et al. 2013)

<sup>b</sup>*Schedonorus arundinaceus*

Table 2. Livestock, fire, biotic and abiotic models assessed for potential constraints on visual obstruction of burn patches in patch-burn grazed pastures in the Grand River Grasslands of Iowa, USA from 2007 to 2013.

Model	$K^a$	AICc <sup>b</sup>	$\Delta$ AICc	$\omega_i$
<i>Livestock models</i>				
Stocking rate (stck_rate)	2	81.00	0.00	0.98
Stocking date	2	89.99	8.99	0.01
Lag-time between fire and grazing	2	91.49	10.49	<0.01
All livestock covariates	4	92.06	11.06	<0.01
<i>Fire models</i>				
Burn completeness (burn_com)	2	78.82	0.00	0.94
Burn date	2	91.09	12.27	<0.01
All fire covariates	3	84.42	5.60	0.06
<i>Biotic models</i>				
Litter (litt)	2	84.12	0.00	0.91
Warm-season grass	2	89.74	5.62	0.06
Tall fescue ( <i>S. arundinaceus</i> )	2	91.00	6.88	0.03
All biotic covariates	4	95.34	11.22	<0.01
<i>Abiotic models</i>				
Effective precipitation (precp)	2	80.66	0.00	0.83
Bare ground	2	83.86	2.97	0.17
Slope	2	99.36	18.70	<0.01
All abiotic variables	4	94.69	14.03	<0.01
<i>Best models<sup>d</sup></i>				
burn_com + stck_rate + precp + litt	5	67.23	0.00	0.57
burn_com + stck_rate + precp	4	68.27	1.04	0.34
Null (intercept with year as random)	1	84.60	17.37	<0.01
Global model with all covariates	12	99.73	32.50	<0.01

<sup>a</sup> Number of parameters in the model

<sup>b</sup> Akaike's information criterion corrected for small sample sizes. Values are based on differences from the best model within each stage.

<sup>c</sup> Model weight.

<sup>d</sup> The next best model had a  $\Delta$ AICc > 6 and all other models had  $\omega_i \leq 0.02$  and are not presented in this table.

Table 3. Top candidate model coefficient estimates, standard error and 95% confidence intervals (CI) for potential constraints of vegetation visual obstruction within burn patches established by the fire-grazing interaction in the Grand River Grasslands of Iowa, USA, 2007 to 2013.

Parameter	Estimate	SE	95% CI
Intercept	711.33	207.56	280.88 to 1141.78
Stocking rate	2.49	1.20	0.10 to 4.87
Burn completeness	-3.40	1.55	-6.61 to -0.18
Litter	0.42	0.42	-0.45 to 1.28
Effective precipitation	-5.31	2.54	-10.57 to -0.05



## Figures

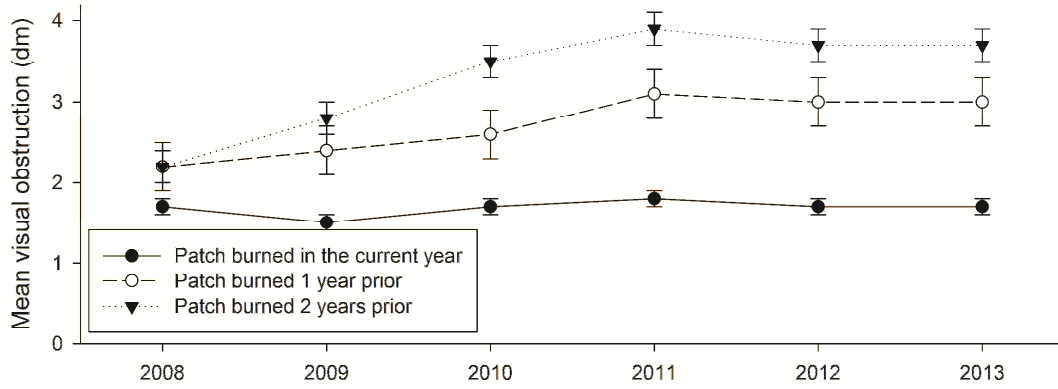
Figure 1. A) Hypothetical response and B) Actual response of vegetation structure to patch-burning in the Grand River Grasslands of Iowa USA from 2008 to 2013. C) Development of heterogeneity or contrast between patches as quantified by the standard deviation of the three corresponding mean visual obstruction values of vegetation structure for each patch by year. Heterogeneity was greatest ( $\square$  SD = 0.7) in 2012 and 2013 when stocking rate was moderate, lag-time between fire and grazing was shortest and completeness of patch burns was greatest.

Figure 2. Completeness of patch burns conducted in the Grand River Grasslands of Iowa USA from 2007 to 2013. Completeness is a visual estimate of >2 individuals. Percent of patch burned increased through time. Note the low completeness ~ 60% in 2007 and 2010, years after the highest stocking rates (3.92 AUM ha<sup>-1</sup> and 3.27 AUM ha<sup>-1</sup> respectively) compared to high-level completeness ~ 98% in 2011 and 2013, years after low to moderate stocking rates (1.45 AUM ha<sup>-1</sup> and 2.41 AUM ha<sup>-1</sup> respectively). Means and Standard Errors bars represent the mean of the four patches burned in four patch-burned pastures ( $n = 4$ ).

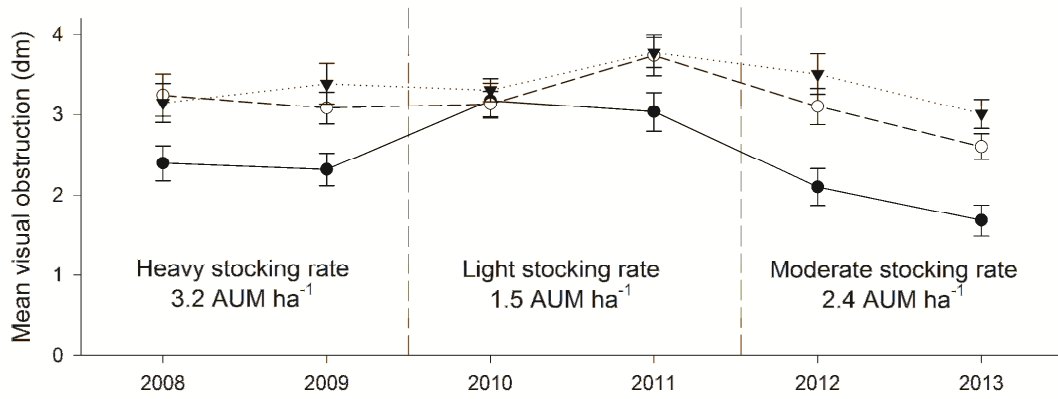
Figure 3. Effect of stocking rate on effectively applying heterogeneity management with fire-driven grazing and establishing a shifting mosaic of vegetation structure. Moderate stocking rates minimize the low structure by establishing and maintaining a grazing lawn in the burn patch and maximize the structural heterogeneity or contrast between patches.

Figure 4. Vegetative structure established by three levels of grazing intensity and the interaction with spatially and temporally discrete fires. Patch elapsed time since fire indicates patches that were burned in the current year (0 years), burned one year before (1 years) and burned two years before (2 years). **a)** Light stocking rate may be ineffective because cattle are unable to establish low vegetative structure in the burn patch and results in low levels of heterogeneity across patches. **b)** Moderate stocking rate) is most effective because it resulted in the lowest vegetative structure in the burn patch and the highest levels of heterogeneity among patches. **c)** Heavy stocking rate may also be ineffective because cattle established but did not maintain low vegetative structure in the burn patch because cattle moved into other patches to satisfy forage intake requirements. Consequently, cattle modify fuel continuity, fuel load and fire behavior in unburned patches making it difficult to conduct complete prescribed fires.

**A) Hypothetical response**



**B) Actual response**



**C) Development of heterogeneity**

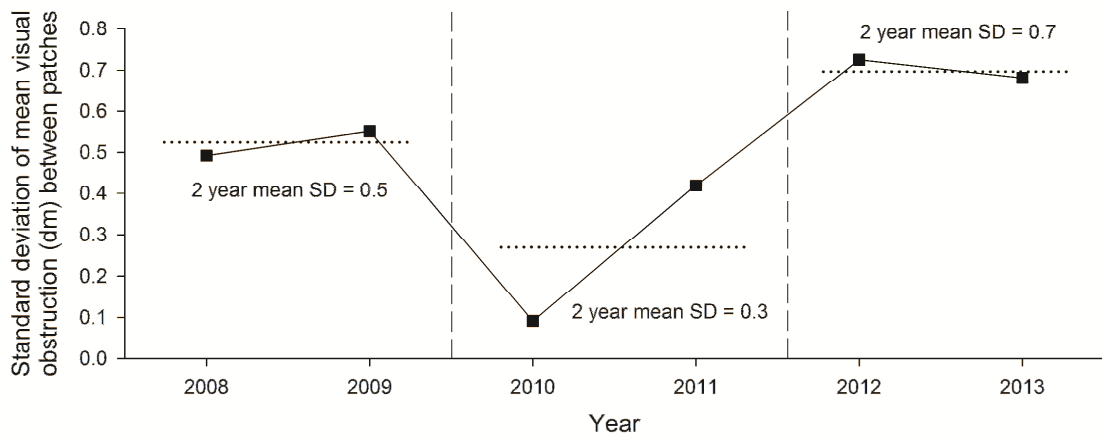


Figure 1

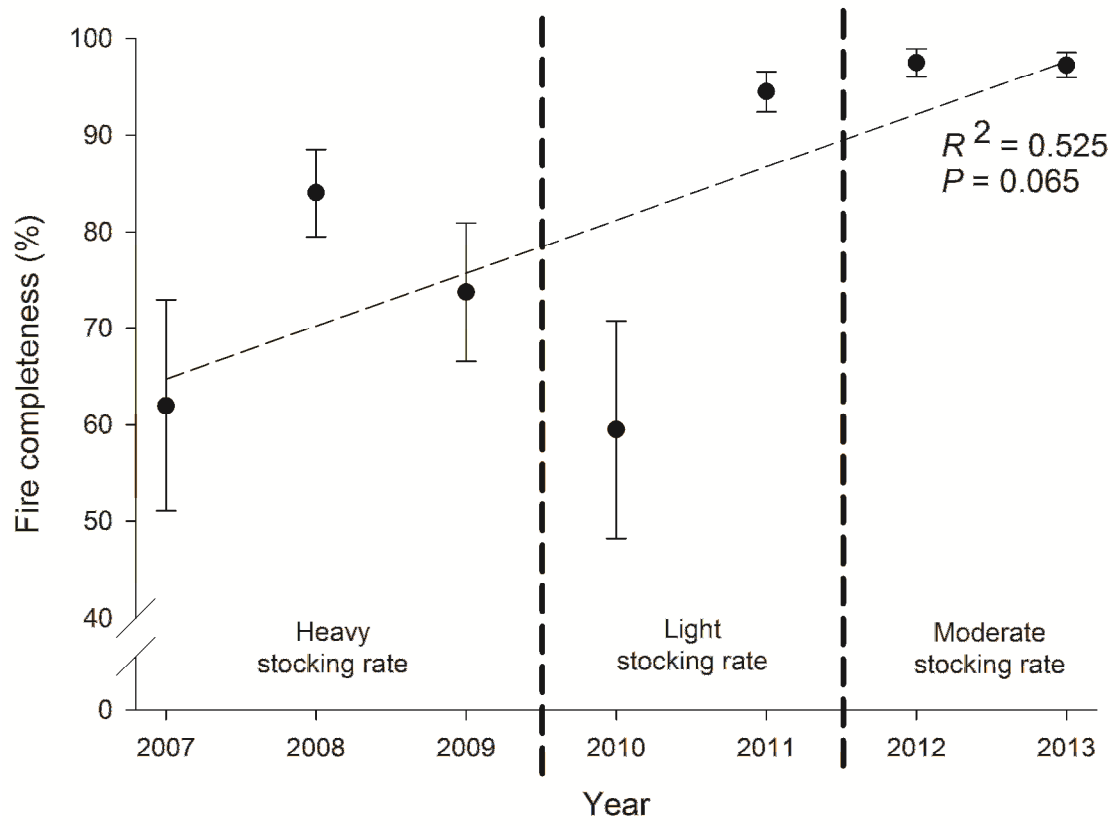


Figure 2

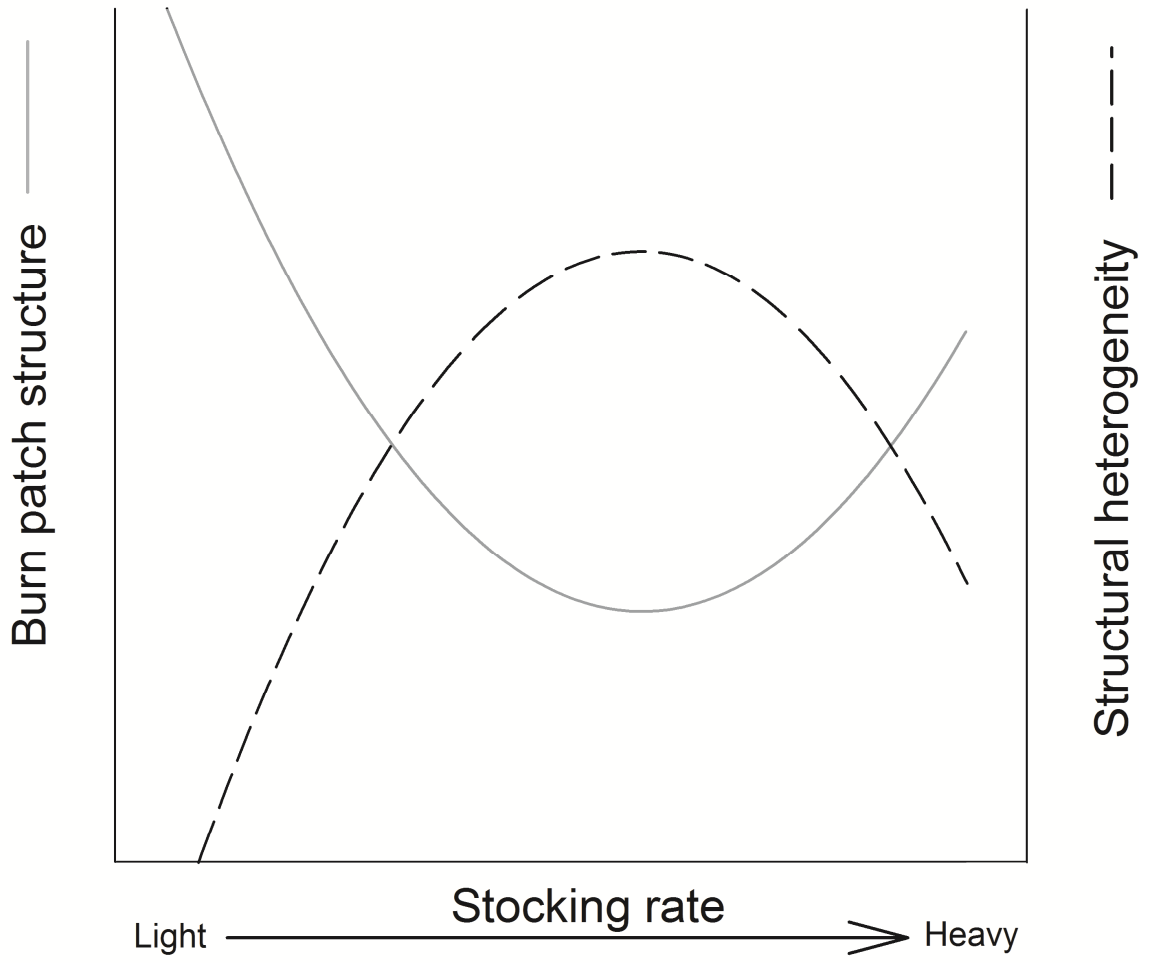


Figure 3

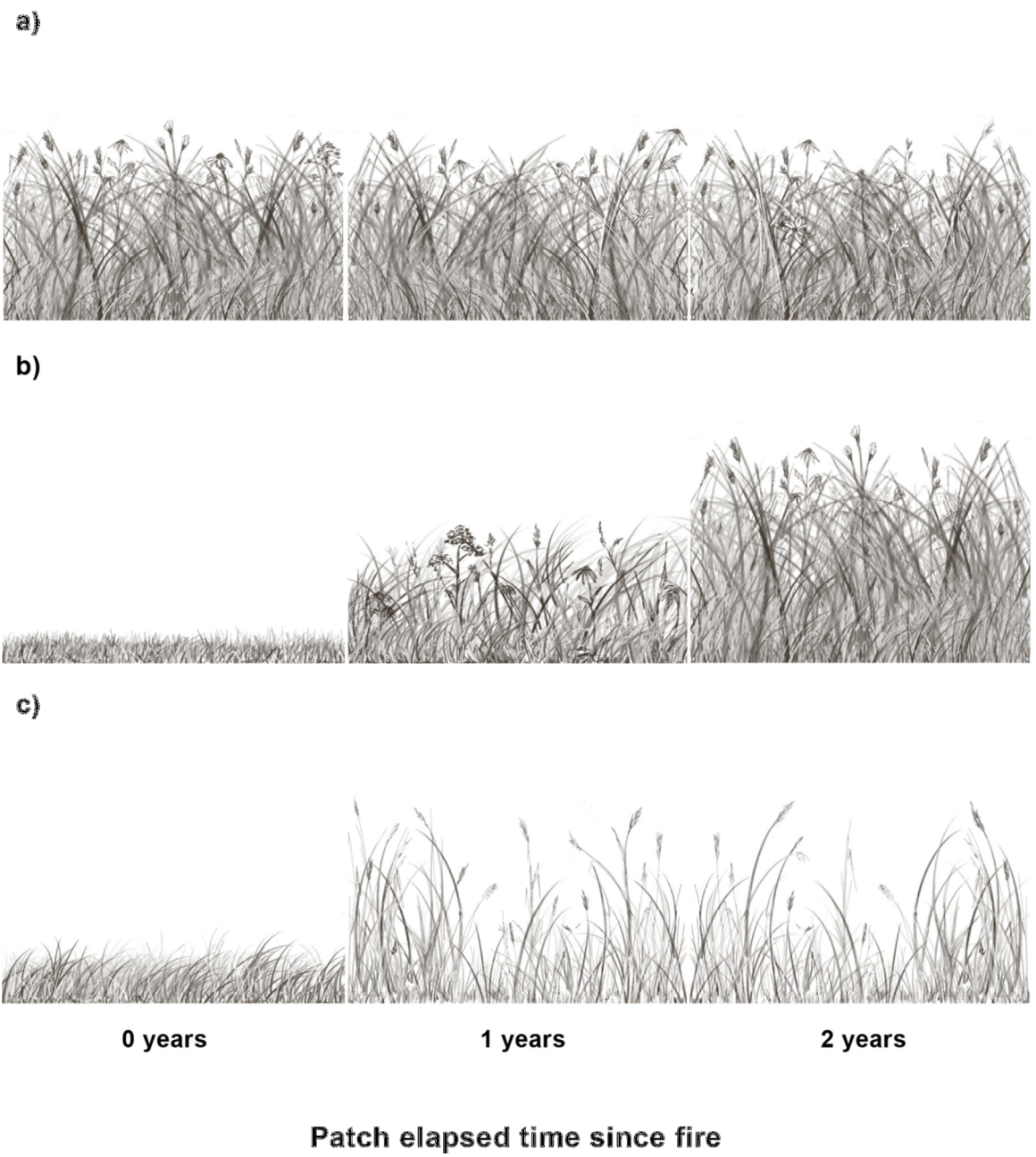


Figure 4

## CHAPTER III

Restoring interactive fire and grazing processes to mitigate parasitic flies of cattle

## **Restoring interactive fire and grazing processes to mitigate parasitic flies of cattle**

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## ABSTRACT

We compared the influence of patch-burn grazing to traditional range management practices on season-long numbers of the most economically injurious fly parasites of cattle. Horn flies (*Haematobia irritans*), face flies (*Musca autumnalis*), stable flies (*Stomoxys calcitrans*), and horse flies (*Tabanus spp.*) were assessed in Oklahoma and Iowa, USA in 2012 and 2013. Experiments at both locations were spatially replicated three times on rangeland grazed by mature Angus-base cows. Grazing was year-long in Oklahoma and seasonal in Iowa from May to September. One-third of patch-burn pastures were burned annually and traditionally managed pastures were burned completely in 2012 but not at all in 2013. Because of significant location effects, we analyzed locations separately with a mixed effects model. Horn flies and face flies were below economic thresholds with patch-burn grazing but at or above economic thresholds in unburned pastures in Iowa. Pastures that burned completely had fewer horn flies but did not have fewer face flies when compared to no burning in Iowa. There was no difference among treatments in horn fly or face fly abundance in Oklahoma pastures. Stable flies on both treatments at both locations were below economic thresholds suggesting that burning patches annually or burning entire pastures every few years may help maintain low levels of infestation. Horse flies at both locations, and face flies in Oklahoma were in such low abundance that it was difficult to detect or explain treatment differences. The lack of a treatment effect in Oklahoma and variable year effects, is the result of a drought year followed by a wet year, reducing the strength of feedbacks driving grazing behavior on pastures burned with patchy fires. Patch-burning or periodically burning entire pastures in mesic grasslands can be a viable cultural method

for managing parasitic flies and integrating natural resource conservation and livestock production objectives.

Keywords:

ecology; patch-burning; pest management; production; pyric-herbivory; rangeland

## INTRODUCTION

External parasites of beef cattle cause substantial financial losses, exceeding \$2 billion annually in the US (Byford et al. 1992). Parasitic flies of the order Diptera are some of the most damaging arthropods affecting grazing livestock (Huddleston et al. 1974). Production losses associated with fly parasites are directly attributed to blood loss, annoyance, disease exposure, reduced foraging time and reduced gains (Harvey and Launchbaugh 1982; Buxton et al. 1985; Boland et al. 2008). Considering that approximately 50% of the US beef cattle herd relies on the forage base of central North American grasslands, the ecology and management of these grasslands may have meaningful implications for fly parasite mitigation and profitability of beef enterprises (USDA 2012).

Before European settlement, central North American grasslands burned regularly due to natural and anthropogenic ignitions followed by ungulate focal grazing on recently burned areas (Anderson 2006). Over the last two centuries, settlement patterns and domestic livestock grazing have largely resulted in the removal of these fire and grazing disturbances in favor of a more utilitarian approach to rangeland management (Pyne 1997). These changes have included the removal of bison and replacement with domestic

livestock, broad fire suppression, and managing for moderate forage utilization across the landscape. Rangeland ecologists have recently suggested a different management paradigm is needed for the conservation of patterns and processes essential to conserving biodiversity in these fire-dependent grasslands (Fuhlendorf and Engle 2012). Rather than complete fire suppression and moderate utilization of forage across the landscape associated with traditional rangeland management, they suggest that fire and grazing should be allowed to interact through space and time across the landscape (Fuhlendorf et al. 2001). The primary method of restoring the fire-grazing interaction has been called patch-burn grazing. Functionally, it is applied by burning spatially discrete patches of a pasture and allowing cattle to select where they want to graze. Patch-burn grazing results in a mosaic of patches with variable probabilities of igniting or being grazed that shifts through space and time (Fuhlendorf and Engle 2004).

The interaction of fire and grazing creates structural heterogeneity of the vegetation structure benefitting many trophic levels of wildlife (Fuhlendorf and Engle 2004; Leis et al. 2013). Consequently, this regular application of fire also mitigates invasive plant encroachment and maintains native herbaceous plant dominance in grasslands (Cummings et al. 2007). While the benefits to biodiversity are well-understood, researchers have recently reported benefits to livestock production. Patch-burn grazing can sustain cow-calf and stocker cattle production compared to traditional management and can stabilize losses associated with climate variability (Limb et al. 2011; Allred et al. 2014).

Patch-burn grazing also can reduce external parasites on cattle. Horn flies (*Haematobia irritans*) on cows during peak periods of activity were reduced on patch-

burned pastures compared to pastures not burned at all (Scasta et al. 2012). Season-long tick burdens on cows and calves were also reduced with patch-burn grazing compared to not burning or burning the entire pasture (Polito et al. 2013). These results are novel because no other cultural livestock parasite management practice has been developed that could be logistically applied across large landscapes. Furthermore, the rapid biological cycles of external parasites leading to development of resistance to insecticides and off-target effects of insecticides used for livestock parasite control are becoming major concerns. These concerns drive the need to understand novel cultural methods that could be integrated with technology and/or minimize applications of insecticides (Spratt 1997; Wardhaugh 2005; Oyarzún et al. 2008).

A recent study reported parasitic fly response to fire and grazing (Scasta et al. 2012), but the study reported only a single fly species, assessed only peak periods of activity, and compared only patch-burn grazing to no burning. Therefore, we sought to expand on that previous work to understand how fire and grazing interactively affect season-long numbers of the most injurious parasitic flies of beef cattle on central North American grasslands. Our objective for this study was to assess four species of flies (horn flies (*Haematobia irritans*), face flies (*Musca autumnalis*), stable flies (*Stomoxys calcitrans*), and horse flies (*Tabanus spp.*)) on beef cows grazing pastures managed with patch-burning and pastures managed with traditional management, and determine the efficacy of different applications of fire as a potential management strategy.

## MATERIALS AND METHODS

In 2012 and 2013, we examined patch-burn grazing experiments in Oklahoma and Iowa, USA that were established in 1999 and 2006, respectively. Parasitism of cattle by four species of parasitic flies was assessed on pastures managed with patch-burn grazing (PBG) and compared to more traditional types of management. The traditional management approach was considered as our control and included burning a pasture completely and no burning the following two years, henceforth grazing and burning (GAB). Experiments at both locations were spatially replicated three times with three patch-burn grazed pastures and three control pastures. All cattle were mature beef cows (*Bos taurus*) of the Angus breed. Mean pasture size was 55 ha in Oklahoma and 27 ha in Iowa. The Oklahoma experiment used year-long grazing and stocking rate was  $2.6 \pm 0.1$  AUM ha<sup>-1</sup> in 2012 and was reduced to  $1.8 \pm 0.1$  AUM ha<sup>-1</sup> in 2013 due to drought in 2011 and 2012. The Iowa experiment used seasonal grazing (May to September) and stocking rate was  $2.6 \pm 0.3$  AUM ha<sup>-1</sup> in 2012 and  $2.4 \pm 0.4$  AUM ha<sup>-1</sup> in 2013.

Patch-burn pastures at both locations used a three-year fire-return interval by burning a different third of the pasture each year. In Oklahoma, 1/6 of the pasture was burned with a spring burn (March or early April) and 1/6 with a growing season burn (July thru October depending on burn bans and fire weather) (burning 1/3 of the pasture in total annually) and in Iowa 1/3 of the pasture was burned with a spring burn (March or early April) (i.e., the patch-burn). Traditional control pastures had last been burned in 2009 and were burned completely in the spring of 2012 but not burned in 2013. Pastures and patches were burned by lighting back-fires and flank-fires to build sufficient fire breaks before igniting headfires in a ring fire technique (Weir 2009). The dominant

vegetation in Oklahoma was characterized by perennial C4 tallgrass species such as big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), and indiagrass, (*Sorghastrum nutans* (L.) Nash). The dominant vegetation in Iowa was co-dominated by the aforementioned species and the exotic C3 grass tall fescue (*Schedonorus arundinaceus* (Schreb.) Dumort., nom. cons.)

We assessed the same four species of parasitic flies at both locations: horn flies (*Haematobia irritans* L.), face flies (*Musca autumnalis* De Geer), stable flies (*Stomoxys calcitrans* L.), and horse flies (*Tabanus spp.*). Sixty-four tabanid species have been identified in Oklahoma (Wright et al. 1986), but for this study, we identified tabanids only to genus. The most common tabanid species was *Tabanus abactor*, but several other species including *T. sulcifrons* were observed in our samples. Flies were assessed weekly from May to October in Oklahoma and May to August in Iowa. We used digital photographs of four different cows in each pasture at each sampling date taken between 0700 am and 1100 am (Lima et al. 2002; Boland et al. 2008). Images were collected from a distance of < 30 m and included the single side of each cow. To assess face flies, we limited images to those in which cows were standing broadside to the camera with the head turned facing the camera so eyes and nostrils were visible. Images were then systematically evaluated in the laboratory by the same trained technician for the duration of the project. The technician overlaid a digital grid on each image and used digital zoom to count the number of each fly species per cow. None of the herds received conventional insecticides for fly parasites during the study.

Monthly precipitation and monthly mean temperature data from both state automated weather observation networks were collected from the Mt. Ayr, Iowa and

Marena, Oklahoma stations and summarized (Iowa Environmental Mesonet 2014; Oklahoma Mesonet 2014). Precipitation was summarized based on the accumulating monthly records for 2012 and 2013 and plotted with the long-term mean. Monthly mean temperature was summarized on a monthly basis and also plotted with the long-term mean. Long-term means for the stations were calculated differently -- 1893 to present for Mt. Ayr, Iowa and 1999 to 2013 (the period of record) for Marena, Oklahoma.

## STATISTICAL ANALYSES

We aggregated fly abundance data from the sampling unit, the individual cow, into herd averages by fly species for each weekly sampling period. Fly counts were first analyzed with an ANOVA for each species to determine if abundance differed between treatments (PBG and GAB), years and locations and to estimate residual covariance (Table 1). After the initial analyses described above, significant location effects were observed for all four species ( $P < 0.0001$ ) and significant year effects were observed for horn flies and face flies ( $P < 0.05$ ). To better understand the role of inter-annual variation, we then assessed each location separately for year effects for all four species.

Due to significant location effects and variable year effects within locations (Table 1), we then analyzed locations separately with a mixed effects model (PROC MIXED) using the residual maximum likelihood estimation method. The main fixed effect was a combination of treatment and year (PBG '12, PBG '13, GAB '12, GAB '13) and year was used as a random effect only for the instances where a significant year effect was identified. The season-long mean abundance for each of the four species of flies was used as response variables in each analyses. Covariance parameter estimates for

residual and random effects were calculated and type III tests assessed fixed effects for significance. To further understand if the driving mechanism of reductions were associated with 1) how fire was applied (patchy versus complete pasture) or 2) whether or not fire was applied, we then conducted a final series of analyses using treatments pooled across years and fire presence/absence pooled across years as separate fixed effects with year assigned as a random effect where previously identified as significant. The three herds/pastures per treatment at each location were used as replicates and the weekly sampling replicants were considered repeated measures in all analyses (Polito et al. 2013). Significance of ANOVA models was set at  $P \leq 0.05$  (Littell 2006; SAS Institute 2011).

## RESULTS

### *Horn Fly (H. irritans)*

Oklahoma cows had 4 times more horn flies than cows in Iowa ( $F=117.42$ ,  $df=1,391$ ,  $P<0.0001$ ) (Table 1). Year was not significant for horn flies in Iowa ( $F=0.11$ ,  $df=1,135$ ,  $P=0.7447$ ). However, in Oklahoma more horn flies were observed in 2012 (mean  $\pm$  SE,  $275 \pm 15$ ) than in 2013 ( $201 \pm 17$ ) ( $F=10.88$ ,  $df=1, 256$ ,  $P=0.0011$ ). In Iowa, cows in patch-burned pastures both years ( $61 \pm 8$  and  $41 \pm 8$ ) had fewer horn flies than cows in traditionally managed pastures when it was burned ( $71 \pm 8$ ) and not burned ( $96 \pm 8$ ) ( $F=9.30$ ,  $df=3, 133$ ,  $P<0.0001$ ) (Fig. 1a). The driving mechanism of the reduction in Iowa is a function of both treatment and fire presence/absence as cows in patch-burned pastures had fewer horn flies than traditionally managed pastures ( $F=4.21$ ,  $df=1, 134$ ,  $P=0.0421$ ) and the cows on traditionally managed pastures the unburned year



had more horn flies ( $86 \pm 9$ ) than pastures with patchy or complete pasture fires ( $61 \pm 5$ ) ( $F=5.37$ ,  $df=1,135$ ,  $P=0.0219$ ). Furthermore, in burned pastures, horn flies were always below the economic threshold of 100 flies per cow side but without any fire horn flies were at the threshold. Burning reduced horn flies in Iowa, but in Oklahoma there was no apparent treatment effect due to the significant year effect (Fig. 1a). Horn flies did not differ by treatment ( $F=0.24$ ,  $df=1,254$ ,  $P=0.6228$ ) or fire presence/absence ( $F=0.027$ ,  $df=1, 254$ ,  $P=0.6023$ ). Horn flies in Oklahoma exceeded 200 per cow side in all treatments, which was much greater than the economic threshold (Fig. 1a).

*Face Fly (M. autumnalis)*

Iowa cows had 4 times more face flies than cows in Oklahoma ( $F=130.17$ ,  $df=1,391$ ,  $P<0.0001$ ) (Table 1). Year was not significant for face flies in Iowa ( $F=0.97$ ,  $df=1,135$ ,  $P=0.3269$ ). However, in Oklahoma more face flies were observed in 2012 (mean  $\pm$  SE,  $2 \pm 0.3$ ) than in 2013 ( $1 \pm 0.3$ ) ( $F=5.45$ ,  $df=1, 256$ ,  $P=0.0203$ ). Face flies were at or below the economic threshold of 5 flies per cow face in Iowa in patch-burned pastures both years and lower than cows on traditionally managed pastures regardless if they were burned completely ( $10 \pm 1$ ) or not burned at all ( $9 \pm 1$ ) ( $F=7.12$ ,  $df=3,133$ ,  $P=0.0002$ ) (Fig. 1b). The driving mechanism of the face fly reduction in Iowa is attributed to how fire was applied rather than simply fire presence/absence because fire presence was not significant ( $F=0.74$ ,  $df=1,134$ ,  $P=0.3914$ ) but treatment was ( $F=16.91$ ,  $df=1,134$ ,  $P<0.0001$ ). In Oklahoma, the year effect washed out any differences between treatments ( $F=1.98$ ,  $df=1,254$ ,  $P=0.1604$ ) or fire presence/absence ( $F=2.00$ ,  $df=1,254$ ,

$P=0.1585$ ) (Fig. 1b). Face flies in Oklahoma were below the economic threshold all years for all treatments (Fig. 1b).

*Stable Fly (S. calcitrans) and Horse Fly (Tabanus spp.)*

Stable flies and horse flies were in lower abundance compared to other species across locations and treatments. Oklahoma cows had 13 times more stable flies than cows in Iowa ( $F=16.38$ ,  $df=1,391$ ,  $P<0.0001$ ) (Table 1). Year was significant in Iowa as cows had more stable flies in 2012 ( $0.14 \pm 0.05$ ) than 2013 ( $<0.01 \pm 0.05$ ) ( $F=4.28$ ,  $df=1,135$ ,  $P=0.0405$ ) but year was not significant in Oklahoma ( $F=0.03$ ,  $df=1,256$ ,  $P=0.8743$ ). Stable flies were well below the economic threshold of 3 flies per leg regardless of location or treatment (Fig. 1c). In Iowa, stable flies were in low abundance, occurring on ~1% of the observed cows but in Oklahoma stable flies occurred on ~11% of the observed cows. In Iowa, there were no differences among treatment and year ( $F=0.86$ ,  $df=3,133$ ,  $P=0.4647$ ), treatments pooled by year ( $F=0.18$ ,  $df=1,133$ ,  $P=0.6724$ ) or fire presence/absence ( $F=0.36$ ,  $df=1,133$ ,  $P=0.5501$ ). In Oklahoma, there were no differences among treatment and year ( $F=0.35$ ,  $df=3,133$ ,  $P=0.7862$ ), treatments pooled by year ( $F=0.77$ ,  $df=1,255$ ,  $P=0.3799$ ) or fire presence/absence ( $F=0.01$ ,  $df=1,255$ ,  $P=0.9159$ ).

Horse flies at both locations were also in very low abundance with less than 1 horse fly per cow side regardless of location. Oklahoma cows had 2.5 times more horse flies than cows in Iowa ( $F=23.40$ ,  $df=1,391$ ,  $P<0.0001$ ) (Table 1). Year was significant in Iowa as cows had more horse flies in 2012 ( $0.6 \pm 0.01$ ) than 2013 ( $0.3 \pm 0.01$ ) ( $F=5.82$ ,  $df=1,135$ ,  $P=0.0172$ ) but year was not significant in Oklahoma ( $F=0.20$ ,  $df=1,256$ ,

$P=0.6561$ ). Horse flies occurred on ~10% of the cows observed in Iowa and ~28% of the cows observed in Oklahoma. In Iowa, in a mixed effects model with year as the random effect, yearly differences washed out differences among treatments and years ( $F=1.51$ ,  $df=3,133$ ;  $P=0.2136$ ) (Fig. 1d). However, in Iowa when comparing only the treatment mean pooled across years, cows on patch-burned pastures had 2.5 times fewer horse flies ( $0.2 \pm 0.1$ ) than cows on traditionally managed pastures ( $0.5 \pm 0.1$ ) ( $F=6.05$ ,  $df=1, 133$ ,  $P=0.0152$ ). In Iowa there was no difference between fire presence/absence ( $F=2.94$ ,  $df=1,133$ ,  $P=0.0887$ ). In Oklahoma, mean horse flies per cow ranged from  $0.9 \pm 0.2$  to  $1.1 \pm 0.1$  across all treatments and there were no differences among treatments and years ( $F=0.76$ ,  $df=3,254$ ,  $P=0.5160$ ), treatments pooled by year ( $F=0.36$ ,  $df=1,255$ ,  $P=0.5501$ ) or fire presence/absence ( $F=0.19$ ,  $df=1,255$ ,  $P=0.663$ ) (Fig. 1d).

## DISCUSSION

The recoupling of fire and grazing is known to be important for maintaining biodiversity in fire-dependent ecosystems but the results from our study indicate interactive fire and grazing directly benefits parasite management of livestock on rangelands (Fuhlendorf and Engle 2012). This study assessed four of the most injurious and economically detrimental parasitic flies in North America and quantified reductions of some species when drought was not constraining the effective application of fire and grazing. Furthermore, the application of spatially and temporally distinct fires and livestock grazing is a novel approach to culturally managing livestock parasites at the landscape scale. These results are relevant to science and management because effective livestock parasite management has been hindered by the development of chemical

resistance, the expense of insecticides, and the labor required for conventional parasite management programs (Spratt 1997; Wardhaugh 2005; Oyarzún et al. 2008).

The lack of an effect on horn flies in Oklahoma compared to previous studies, and the significant year effect for other species and locations may be attributed to climatic variation. The drought year of 2012 followed by the wet year of 2013 (Fig. 2a) likely reduced the strength of positive and negative feedbacks driving grazing behavior on pastures burned with patchy fires. The drought of 2012 was one of the most severe on record and caused us to reduce stocking rates. Furthermore, inter-annual climate variation was also characterized by earlier warming in 2012 than average, later warming in 2013 than average, and greater heat peaks at both locations compared to long-term means (Fig. 2b). The combined effects of below average precipitation and above average temperatures may also have reduced fuel continuity, burn completeness and the contrast between burned areas and unburned areas. The combination of reduced burn efficacy reduces the ability to alter parasite habitat and attract livestock to recently burned areas, ultimately reducing the strength of the fire-grazing interaction.

Two other differences between our study locations could explain, at least in part, the significant location effect. First, seasonal grazing was used at the Iowa location and year-long grazing at the Oklahoma location. In Iowa, the movement of the privately owned cattle to the research property typically occurred in May after flies had become active. A large-scale study in Texas reported lower horn flies following movement of cattle to pastures 11 km and 19 km away in July and September, respectively (Pruett et al. 2003). The maximum distance from a private cattleman's headquarters and a research pasture in our Iowa study location was 15 km. Secondly, the pastures in Iowa have a

large component of tall fescue, an exotic C3 grass that harbors a toxic endophyte (*Acremonium coenophialum*). Specific alkaloids associated with this endophyte can cause toxicity to mammals and invertebrates. In particular, loline alkaloids have been implicated in invertebrate toxicity. Entomological studies have reported that both horn flies and face flies have lower pupation and pupal liveweights in feces from cattle fed endophyte infected fescue due to loline exposure (Dougherty and Knapp 1994; Dougherty et al. 1998; Dougherty et al. 1999; Parra et al. 2013). At the Iowa site, herbivory of *S. arundinaceus*, and subsequent consumption of lolines, could potentially be increased in the most recently burned patch as previous studies have shown that fire can overcome cattle aversion to plants containing secondary compounds, such as tannins in *Lespedeza cuneata* (Cummings et al. 2007).

Our study confirms that differences in life histories and habitat requirements among these parasitic flies can explain most of the results of our experiment. Each of the fly species assessed in our study has a unique biological cycle so that mechanisms of coping with fire may be species specific. Horn flies are obligate blood sucking parasites that only leave cows to deposit eggs in fresh manure and pupae overwinter in fecal pats (Foil and Hogsette 1994). The drying of feces between ovipositing and the spring burning season in the Great Plains is suspected to be the primary causal effects for horn fly reduction following burning of pastures (Scasta et al. 2014). Comparatively, horse flies are one of the most livestock independent species that need very few blood meals and larval habitats are independent of livestock (Foil and Hogsette 1994). Eggs are generally deposited in vegetation that is in or over water and larvae drop into the water after hatching (Huddleston et al. 1974). Other studies have reported that tabanid

distribution is associated with landscape structure. Biting activity is not associated with landscape structure but instead is rather a function of attractiveness to herds, dispersal ability of tabanids, and weather (Baldacchino et al. 2014). Consequently, the effects of patch-burning on horse flies in Iowa are difficult to interpret considering the low population of horseflies coupled with the absence of a clear influence of burning on the habitat or life cycle of the horse fly. The lower number of horse flies in Iowa, when pooled by treatment across years, could be attributed to fescue toxicity and attracting cattle away from riparian areas.

Stable flies are also much less dependent on livestock than horn flies. They require blood for survival and reproduction but spend a relatively small amount of time with the host. Stable flies lay eggs in feces and other substrates such as decaying vegetation, particularly accumulated wasted hay around hay feeding sites (Talley et al. 2009). Thus, a potential reduction mechanism for stable flies, and potential explanation for the difference in stable fly abundance between locations, could be attributed to hay feeding practices. In Iowa, the seasonal-grazing management does not require any hay feeding on the treatment pastures, whereas in Oklahoma, year-long grazing requires some hay feeding during extreme winter weather. Therefore, the lack of hay feeding may partially explain the lower abundance and occurrence of stable flies in Iowa. Furthermore, the application of fire in general may help maintain stable fly numbers below economic thresholds as all of our locations were burned at least once during the two-year study period.

Lastly, face flies do not rely on blood from bites they initiate, but rather from mucus secretions from the eyes and nose. Face flies also overwinter in feces and have an

affinity for woody plants for thermal regulation (Krafsur and Moon 2008). Thus, reduction of shrubs and trees and combustion of fecal pats with fire may reduce face fly habitat. Although we did not detect a fire effect, differences in fire completeness among treatments may have hindered our ability to detect a difference (Kerby et al. 2007). The lack of grazing in long-unburned patches results in rapid fuel accumulation and greater fire intensity will result in greater scorch and mortality of woody plants (Van Wagner 1973). Furthermore, the Oklahoma sites are near the range limits for face flies and due to the sampling method flies could have been confused with house flies (*Musca domestica* L.) (Krafsur and Moon 2008). Face flies do occur in Oklahoma and have recently been detected northeast of our study site. However, they were in low abundance during our study and are rarely a problem (Krafsur and Moon 2008; Talley 2012).

The origin and developmental adaptation to fire-grazing disturbances of each of these species may also explain reductions realized with patch-burn grazing. Horn flies and face flies are considered to be non-indigenous to North America as they were both introduced from Europe (Huddleston et al. 1974; Fincher et al. 1990). The origin of stable flies has been debated, but it is generally accepted that they are non-indigenous to North America as well (Colautti et al. 2006). These non-indigenous flies were brought to North America with the introduction of cattle. The *Tabanus* species assessed at our study sites, however, are considered to be indigenous to North America (Goodwin 1994). Thus, the non-indigenous species for which we observed a reduction after burning may not be adapted to the fire-grazing disturbance.

## IMPLICATIONS

Reducing flies has the potential to result in production benefits (Kunz et al. 1984). Specifically, increases in weight gains can be associated with a reduced loss of blood, reduced levels of annoyance, reduced annoyance behavior such as stomping or shaking, and more time spent grazing (Harvey and Launchbaugh 1982). The reduction of flies also has the potential to reduce livestock, wildlife, and potentially human, exposure to diseases as all four species vector numerous diseases and may be pestiferous of livestock, wildlife and humans. Horn flies are a well-known vector of mastitis (McDougall et al. 2009). Face flies serve as vectors of bovine keratoconjunctivitis (pinkeye) and nematode eyeworms (Hall 1984; O'Hara and Kennedy 1991). Stable flies transmit *Bacillus anthracis* (anthrax), an epizootic disease that occurs globally (Turell and Knudson 1987). Horse flies are known to vector at least thirty viral, bacterial, protozoal and helminth disorders including vesicular stomatitis, hog cholera, and tick-borne encephalitis (Krinsky 1976). Horse flies are also considered one of the main mechanical vectors of anaplasmosis (Hawkins et al. 1982). Stable flies, horn flies and Tabanids have all been implicated as vectors of bovine leukosis (Buxton et al. 1985). Lastly, in an Iowa control pasture the year it was not burned, cows and calves had high levels of face flies (Fig. 3a) with animals developing white discoloration of the cornea, an initial symptom of pink eye (Fig. 3b). The treatment of many of these diseases tends to be reactive but the application of fire could be a more proactive and preventative approach that alters fly habitat.

The scale of fly dispersion and ability to detect a host is also relevant to the effective application of cultural approaches of parasite management. Face flies emerging from fecal pats can disperse up to 600 m and mature horn flies and face flies have been



noted to disperse as far as 8 km (Byford et al. 1987; Walsh et al. 2010; Peck et al. 2014). Not surprisingly, moving cattle at a smaller scale did not reduce horn flies in a study that compared various paddock sizes (1.3 ha to 3.2 ha) and stocking rates in a 7-d rotational grazing program compared to continuous grazing (Steelman et al. 2003). At our Iowa sites where horn flies and face flies were both lower in patch-burn grazed pastures, the distance between a burn patch in 2012 and a burn patch in 2013, center to center, ranged from 230 m to 565 m. Considering dispersal ability, cultural methods must manage at an effective landscape scale and patch-burn grazing mimics a large disturbance and movement pattern.

We hypothesize patch-burn grazing reduces parasitic flies on cattle via five mechanisms. First, fire combusts or reduces overwintering fecal habitat that contains puparium (Scasta et al. 2014). Secondly, spatially discrete burned patches attract animals to the patches where overwintering fecal habitat has been reduced, a potentially parasite free area due to fire (Allred et al. 2011). Third, fire mitigates woody plant encroachment and consumes plant litter thus reducing habitat needs of some species (Bragg and Hulbert 1976; Fuhlendorf et al. 2004). Fourth, moving fire and preferentially grazed areas around the landscape through space and time moves the disturbance of habitat around the landscape (Vermeire et al. 2004). Last, creating livestock movements and fire/grazing disturbances at an effective landscape scale disrupts the biological cycle as new generations emerge and may not effectively disperse to new hosts (Allred et al. 2013).

Other than when fly populations are below the economic threshold or drought constrains the strength of the interaction of fire and grazing, patch-burn grazing can be a viable cultural method for managing a broad suite of parasitic flies on grazing cattle in

central North American grasslands. Additional research is needed to understand how patchy fires could be integrated with other chemical and biological control strategies. Ultimately, the interaction of fire and grazing on central North American grasslands, and subsequent effects on parasites of cattle, links natural resource conservation (Fuhlendorf and Engle 2001; Allred et al. 2014) and livestock production (Limb et al. 2011; Alred et al.) as the fire-grazing interaction can sustain dominance of desirable herbaceous plants while reducing parasite pressure.

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## Tables

Table 1. Summary from initial ANOVA for location, year and treatment effects for four species of flies that parasitize cattle in 2012 to 2013 on studies in Iowa and Oklahoma, USA.

Species	<i>P</i> -value			Residual covariance parameter estimate
	Location	Year	Treatment	
Horn fly ( <i>Haematobia irritans</i> )	< <b>0.0001</b>	<b>0.0018</b>	0.5557	22,123
Face fly ( <i>Musca autumnalis</i> )	< <b>0.0001</b>	<b>0.0315</b>	< <b>0.0001</b>	21.480
Stable fly ( <i>Stomoxys calcitrans</i> )	< <b>0.0001</b>	0.9257	0.3338	4.0119
Horse fly ( <i>Tabanus spp.</i> )	< <b>0.0001</b>	0.7509	0.6940	1.4702

## Figures

Figure 1. Fly responses to treatments in 2012 and 2013 using a mixed effects model with a combination of treatment and year (PBG '12, PBG '13, GAB '12, GAB '13) as the fixed effect and year as a random effect in cases where year was significant. Treatment notation is PBG (patch-burn grazing) and GAB (traditional management where pastures are burned completely every third year). Each bar represents three herds/pastures at that location, year and for that treatment ( $n = 3$ ). Dashed lines indicate that no fire was applied in that treatment that year. See text for treatment descriptions. P-values for fixed effects are considered significant at  $P \leq 0.05$ . Iowa is in the left column and Oklahoma in the right column. A) Horn flies per cow side, B) Face flies per cow, C) Stable flies per cow side, and D) Horse flies per cow side. Economic threshold is indicated with a dashed, horizontal line.

Figure 2. A) Annual accumulated precipitation (mm) and B) monthly temperature ( $^{\circ}\text{C}$ ) for experiment locations in Mt. Ayr, Iowa, USA and Marena, Oklahoma, USA during 2012 and 2013, and the long-term mean from each respective location. 1) Oklahoma experienced one of the most severe droughts in recorded history in 2011 and 2012 with the Stillwater mesonet station reporting only 68% of the long-term mean annual precipitation in 2012. 2) Both locations reported earlier warming trends and 3) higher peak temperatures in 2012 compared to 2013 and the long-term mean.

Figure 3. Examples of cattle on unburned pastures from the Iowa experiment in 2013. A) Cow is on unburned pasture with  $>3$  times the economic threshold of horn flies

(*Haematobia irritans*) and face flies (*Musca autumnalis*) (thresholds are 100 horn flies per side and 5 face flies per cow, respectively). B) Calf in picture is from 2013 on unburned pasture. Face flies vector infectious bovine keratoconjunctivitis or pinkeye. Note the large number of face flies (>3 times the economic threshold) and white discoloration of the cornea, an early stage of pinkeye. Photographs by J.D. Scasta.

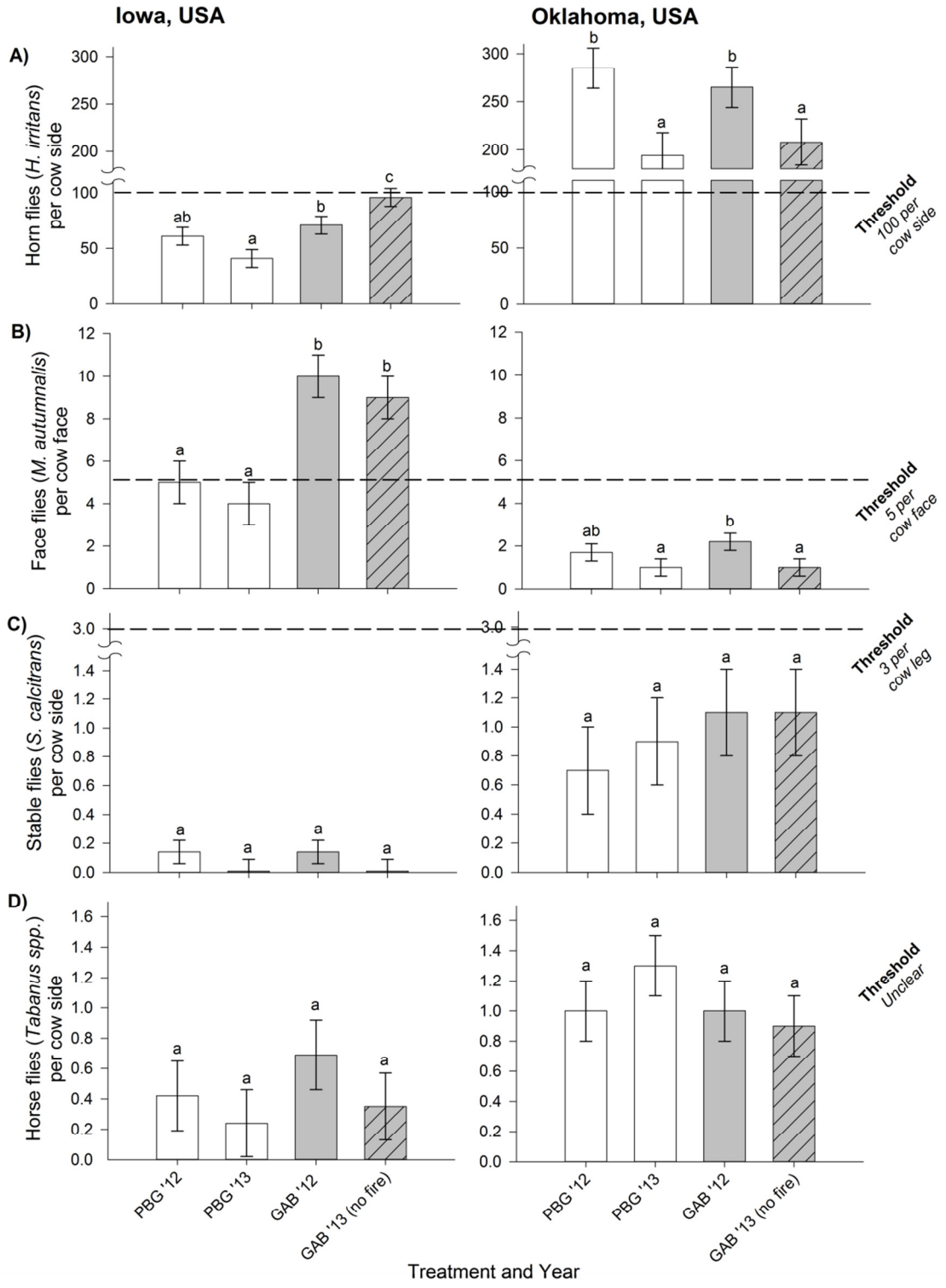


Figure 1

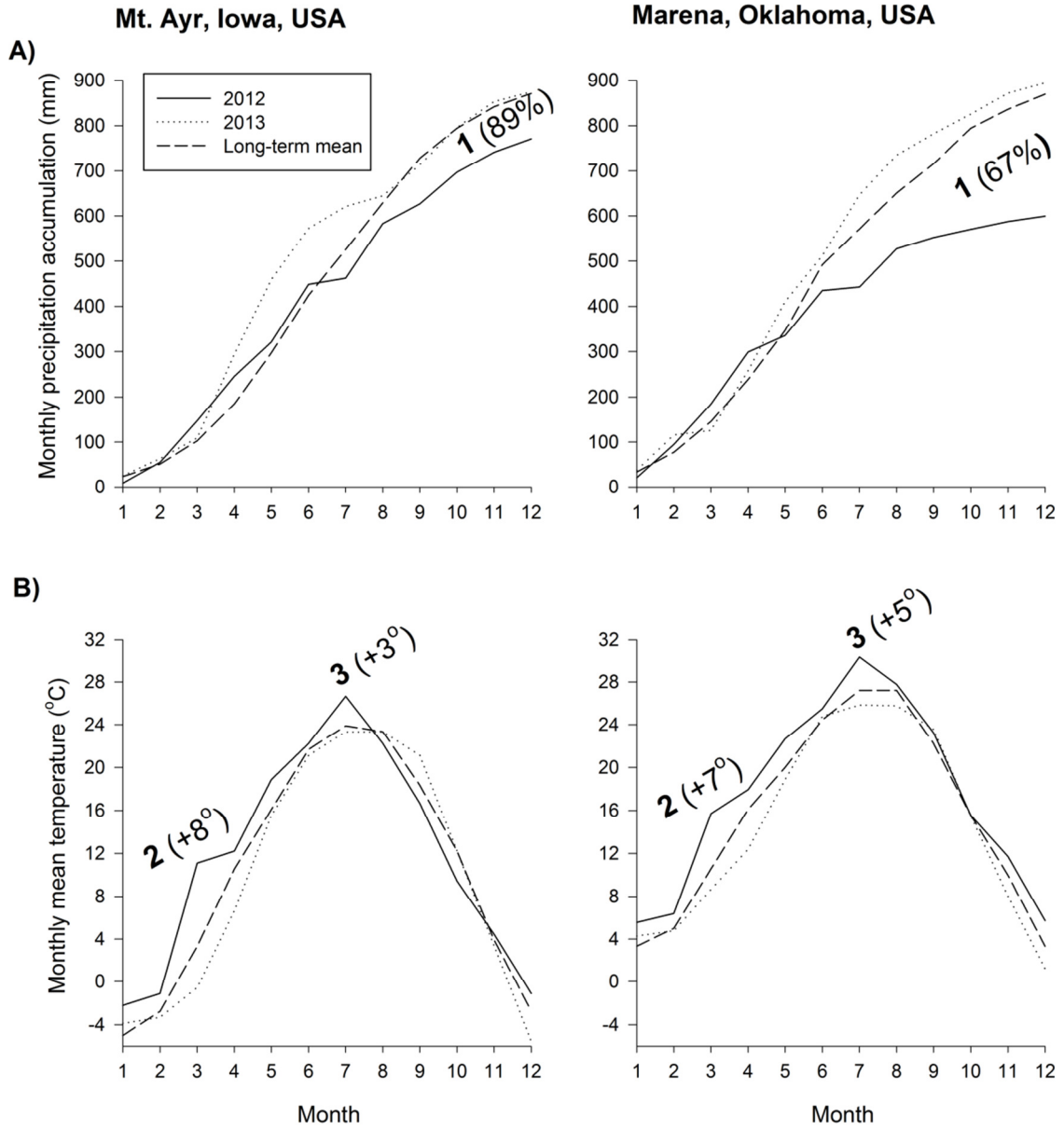


Figure 2

a)



b)



Figure 3



## CHAPTER IV

Fire induced regeneration mechanisms of a *Symphoricarpos* (Caprifoliaceae) shrub

**Fire induced regeneration mechanisms of a *Symphoricarpos* (Caprifoliaceae) shrub**

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## ABSTRACT

*Symphoricarpos orbiculatus* (buckbrush) is the dominant shrub of tallgrass prairie, often forming large colonies. Perceived competition with herbaceous plants has led to control recommendations. However, restoring a functioning fire-regime could mediate invasion while sustaining this shrub for wildlife. In 2011 we conducted a shrub species inventory in the Grand River Grasslands, Iowa, USA at four spatial scales (0.5 m<sup>2</sup> to 500 m<sup>2</sup>). Then from 2011 to 2013, we assessed how *S. orbiculatus* basal resprouting and layering stems were affected by patchy fires, complete pasture fires or fire exclusion. We measured ramet height, ramet canopy diameter, stems per ramet, ramets per 100 m<sup>2</sup>, and probability of new layering stems 120 days after fire. *S. orbiculatus* was the most common shrub in our research sites regardless of spatial scale. Height in burned plots was lower than unburned plots but *S. orbiculatus* reached ~ 84% of pre-burn height 120 days after fire. Stems per ramet were 2x greater in the most recently burned plots due to basal resprouting. Canopy diameter and density of ramets was not affected by time since fire, but burned pastures had marginally lower densities than plots excluded from fire ( $P = 0.07$ ). Fire triggered new layering stems and no new layering stems were found in plots excluded from fire. This suggests *S. orbiculatus* is fire tolerant because the species possesses several regeneration mechanisms following fire. Dormant season fires did not result in mortality, but reduced *S. orbiculatus* structural dominance, invigorated decadent stands, and maintained lower densities.

### Keywords:

disturbance; ecology; prairie; rangeland; resprout; restoration; woody plant

## INTRODUCTION

Global vegetation distribution patterns are largely driven by climatic constraints and disturbance regimes (Clark 1991; Collins 2000). Grasslands on several continents were regulated by the developmental disturbances of fire, large ungulate grazing, and the synergistic interaction of the two (Fuhlendorf and Engle 2001). The vegetation composition of these fire prone grasslands includes shrubby angiosperm species that persist after fire due to vegetative regeneration mechanisms rather than recruitment (Bond and Midgley 2001).

The resprouting life strategy results in tradeoffs between growth and reproduction as resprouting shrubs often have smaller seeds, poor reproduction from seeds, and short-lived seed banks (Bond and Wilgen 1996; Kruger et al. 1997). The cost of energy allocation belowground to survive fire also reduces growth rate (Bond and van Wilgen 1996). Subsequently, form follows function, and resprouting species typical of disturbance prone ecosystems are multi-stemmed and short statured to optimize rapid recovery. In contrast, recruiting species are typically single-stemmed and taller, an advantage for the competition for light and dispersion of seed (Bellingham and Sparrow 2000; Bond and Midgley 2003). Researchers have suggested that scientific inquiry has focused more on seedling ecology than resprouting mechanisms as a plant life history trait, although neither regeneration strategy is mutually exclusive (Olson and Platt 1995; Higgins et al. 2000; Bond and Midgley 2001). Furthermore, basal resprouting mechanisms are not uniform within a functional group type (i.e., not all shrubs resprout basally or epicormically) or even within Genera (Enright and Goldblum 1999; Bellingham and Sparrow 2000; Ansley and Rasmussen 2005; Winter et al. 2011).

In North America, *Symphoricarpos* is one of the most broadly distributed shrub Genera, ranging in latitude from northern Mexico to Canada and in longitude from California to Maine (USDA Plant Database 2013). A member of the Caprifoliaceae family, *Symphoricarpos* consists of about 16 species of clonal deciduous shrubs that spread sexually and asexually. Members of this genus are found on rangelands, prairies and woodlands and include *S. albus* (common snowberry), *S. occidentalis* (western snowberry), *S. orbiculatus* (buckbrush), and *S. oreophilus* (mountain snowberry). Asexual spread is from rhizomes and rooting of aerial stems (henceforth layering) (Pelton 1953; Hullick and Maske 2006; Nesmith et al. 2006). Layering occurs when vertical stems droop horizontally and produce adventitious roots when they come into contact with the soil. While the layering mechanism has been studied from a horticultural propagation standpoint, it has been largely neglected in the native plant ecology literature (Hartmann and Kester 1975; Deb and Pogener 2012).

*S. orbiculatus* has been described as the dominant shrub of the tallgrass prairie and occurs across the eastern half of North America (Holecheck et al. 2001; USDA Plant Database 2013). The conversion of prairies to cropland and the suppression of fire has relegated tallgrass prairie in North America as one of the most threatened ecosystems globally with > 99% extirpated (Sampson and Knopf 1994). These threatened prairies are increasingly important for biological conservation and it is increasingly important that we understand the organismal communities and ecological drivers (Samson 2004). Prior to European settlement, tallgrass prairie was prone to burning every three to five years (Collins 2000). The exclusion of regular fire in tallgrass prairie alters plant succession

toward a shrub dominated community, of which a major component is *S. orbiculatus* (Collins and Adams 1983; Collins 1992).

In eastern tallgrass prairie, the most common shrub *S. orbiculatus* has been characterized as a major invader of unburned prairie and classified as a weedy species (Bragg and Hulbert 1974; Stubbendieck et al. 2003). These designations coupled with allelopathic and encroachment potential has led to broad applications of herbicides in the name of conservation biology or livestock production (Smith 1977). Finally, a paucity of research exists on the fire ecology of *S. orbiculatus* compared to other *Symphoricarpos* species, specifically *S. albus*, *S. occidentalis*, *S. oreophilus*, *S. longiflorus*, and *S. mollis* (Snyder 1991; Aleksoff 1999; McWilliams 2000; McWilliams 2005; Hauser 2007).

Quantifying *S. orbiculatus* reproductive mechanisms after fire will yield basic biological insights to assist managers in appropriately applying disturbance regimes. Our objectives were to assess how *S. orbiculatus* vegetative regeneration is affected by late dormant-season fire, the fire season most common in North American grasslands. We hypothesized that basal resprouting and layering would be dependent on elapsing time since fire. To test our hypothesis we quantified vegetative response to prescribed fire by measuring ramet height, ramet canopy diameter, stems per ramet, ramets per 100 m<sup>2</sup>, and probability of new layering stems.

## MATERIALS AND METHODS

### *Study location and design*

The study was conducted from 2011-2013 in tallgrass prairie in Ringgold County, Iowa in the Grand River Grasslands (GRG) of Iowa, USA (40°34'N, 94°10'W). The

GRG is in the glaciated plains of the Central Tallgrass Prairie Ecoregion and has been described as one of the premier places to restore a functioning tallgrass prairie ecosystem (Missouri Department of Conservation 2005). Annual precipitation was 968 mm in 2011 (+ 97 mm above long-term mean), 798 mm in 2012 (- 73 mm below long-term mean), 874 mm in 2013 (+ 3 mm above long-term mean and averaged 870 mm during the three year study (+1 mm above long-term mean) (Iowa Environmental Mesonet 2014). Soils are loess hills with glacial till side slopes with slopes in some areas exceeding 9 percent. Subsoils have high clay content ranging from 42 to 48% and native vegetation was tallgrass prairie (USDA NRCS 2013). Herbaceous vegetation across all study pastures was dominated by perennial C4 graminoids (*Andropogon gerardii* (big bluestem), *Schizocyrium scoparium* (little bluestem), and *Sorghastrum nutans* (indian grass) with a component of exotic C3 graminoids and legumes (*Schedonorus arundinacea* (tall fescue), *Bromus inermis* (smooth brome), *Lotus corniculatus* (birdsfoot trefoil), and *Trifolium spp.* (clover).

#### *Experiment 1: Shrub Inventory Sampling*

To corroborate the claims of *S. orbiculatus* as the dominant shrub in tallgrass prairie, we conducted a shrub inventory of six common shrubs in the spring of 2011. Species assessed were *Cornus drummondii* (dogwood), *Prunus spp.* (plum), *Rhus glabra* (smooth sumac), *Rosa multiflora* (multiflora rose), *Rubus spp.* (raspberry), and *S. orbiculatus*. To account for spatial variation among these shrub species, presence/absence was evaluated in permanent modified Whitaker plots designed with multiple spatial scales nested within a 500 m<sup>2</sup> (25-m x 20-m) plot (Stohlgren et al. 1998;

McKell 2012). Only the six pastures that were burned and assessed in experiment 2 (see below) were used for the shrub inventory and included six modified Whitaker plots per pasture controlling for catena and soil type (Debinski et al. 2011). Within each modified Whitaker plot there were 10 – 0.5 m<sup>2</sup> quadrats and 2 - 2.5 m<sup>2</sup> quadrats nested within 1 - 100 m<sup>2</sup> quadrat that was nested within a 500 m<sup>2</sup> quadrat (Figure 1).

### *Experiment 2: Fire Effects Sampling*

Three treatments were applied and assessed: 1) Patch-burn grazing (PBG) or burning one-third of a pasture annually (the patch) with cattle having full access to the pasture, 2) Graze and burn (GAB) or burning pastures completely every three years with cattle having full access to the pasture, and 3) Unburned or no fire for over three years (Figure 2). Grazing was seasonal from late-April to October with mature angus-base cows. Mean ( $\pm$  SE) size of each pasture was  $27 \pm 3$  ha and mean ( $\pm$  SE) stocking rate was  $2.3 \pm 0.2$  AUM ha<sup>-1</sup>. All prescribed fires were conducted in the late dormant season (March 8 to April 4) prior to the emergence of *S. orbiculatus* leaves. The fire and grazing treatments were in place prior to the initiation of sampling in 2011, so all patches and pastures had a consistent elapsed time since fire (0.3, 1, 2 years since fire) (Figure 2). The designation of 0.3 years since fire indicates that samples were measured four months after fire. We had less control over the unburned treatments and elapsed time since fire for those pastures was more than three years but the exact number of years is unknown. When we returned in 2013 to conduct a second assessment of unburned pastures, they had all either been burned or mowed so no follow up measurements were possible.



Fire effects measurements in Experiment 2 were conducted from 2011 to 2013 and included the same six pastures from the shrub inventory but only plots with *S. orbiculatus* present (32 of 36). If *S. orbiculatus* was not present within a permanent plot, we assessed 25 m north or south of the permanent marking pins for *S. orbiculatus* presence, allowing us to evaluate fire effects in 3 additional plots. Three additional pastures that had not been burned in more than three years were included for fire effects measurements and had three plots per pasture ( $n = 9$ ). Plots were all permanent and ranged from 16 m<sup>2</sup> (16 m x 1 m) to 350 m<sup>2</sup> (25 m x 14 m). Plots were variable in size due to the variable density of *S. orbiculatus* ramets. Thus, to ensure adequate sample size and in the sake of time, we sampled plots for a minimum of ten ramets to a maximum of fifty ramets in each plot. Given the clonal nature of *S. orbiculatus*, we conducted measurements at the ramet level. We define ramets as individual plants or clonal fragments in the colony that are rooted and may have originated from either seed or rooted nodes from aerial layering stems that may or may not be connected to other ramets (Nesmith et al. 2006) (Figure 3). Individual ramets were identified by spatial independence based on vertical stems arising from the same root crown. Ramet measurements were conducted approximately 120 days after fire. Maximum height of the ramet was measured as the tallest individual stem of a ramet. Maximum canopy diameter was measured as the longest horizontal axis of a ramet. Stems per ramet was measured as the total number of vertical live stems arising from the same root crown and is a reflection of the regeneration from basal resprouts. Ramets per 100 m<sup>2</sup> was measured by noting the total number of ramets in a plot and then converting that to 100 m<sup>2</sup> and reflects alterations to ramet density from fire-induced mortality. New aerial layering

stems were measured as vertical stems arising from the root crown but having a horizontal orientation but not yet rooting at the tip (Figure 3). All measurements for fire effects were conducted in 2011, 2012 and 2013 except presence/absence of new layering stems. New layering stems were only identified in 2011 and 2013 in the PBG pastures and in unburned pastures in 2011 only.

## STATISTICAL ANALYSES

In experiment 1, we summarized shrub species presence at the four nested spatial sampling scales. At each spatial scale we summarized the percent of quadrats with that species present. In experiment 2, to assess the response of *S. orbiculatus* to prescribed fires we used maximum ramet height, maximum ramet canopy diameter and number of live stems per ramet, and density of ramets per 100 m<sup>2</sup> as response variables. We aggregated data from the sampling unit, the individual *S. orbiculatus* ramet, into plot means as the experimental unit. We used mixed effects models (proc mixed) using the residual maximum likelihood estimation method with treatment, elapsed time since fire and the interaction between treatment and elapsed time since fire as fixed effects (SAS Institute 2011). To account for variation associated with topoedaphic features, disturbance history and spring precipitation, we used plot and year as random effects. Covariance parameter estimates for each random effect were calculated and fixed effects assessed for significance ( $\alpha$  0.05). We then conducted post hoc least squares test for all pairwise comparisons of all combinations for fixed effects at the 95% confidence level. Binary presence/absence data of horizontal layering stems data were used to determine odds ratios (odds =  $e^{\beta x}$ ) for the presence/absence probability of layering stems related to

elapsed time since fire. The logit function in proc genmod was used to model probability, assess goodness of fit and determine parameter estimate for time since fire (SAS Institute 2011).

## RESULTS

### *Experiment 1: Shrub Inventory Results*

According to our shrub inventory, *S. orbiculatus* was the most common shrub in our research sites regardless of the spatial scale of assessment. At the finest spatial scales (0.5 m<sup>2</sup> and 2.5 m<sup>2</sup>), *S. orbiculatus* occurred 8 times and 23 times more often than any other shrub species respectively. No other shrub species occurred more than 2% of the time at the finest spatial scales. At the 100 m<sup>2</sup> spatial scale, *S. orbiculatus* occurred 4 to 10 times more often than any other shrub species. At the broadest scale (500 m<sup>2</sup>), *S. orbiculatus* occurred 2 to 6 times more often than any other shrub species. *R. glabra*, a common shrub in tallgrass prairie, is present in this region but was not detected in any of our plots. The exotic shrub, *R. multiflora*, was the next most abundant shrub but was not detected at the finest spatial scales. The other native shrubs assessed, *C. drummondii*, *Prunus spp.* and *Rubus spp.*, did not occur in more than a third of the plots even at the broadest spatial scale (Table 1).

### *Experiment 2: Fire Effects Results*

Ramet height on burned pastures, regardless of how fire was applied (henceforth, whether fire was a patch burn of one-third of the pasture annually (PBG) or a complete pasture burn every third year (GAB)), was significantly lower ( $F_{2,66} = 5.47$ ;  $P < 0.01$ )

than pastures managed without fire. Ultimately, the lower ramet height on burned pastures is largely a function of elapsed time since fire rather than how fire was applied because time since fire was positively correlated with ramet height ( $F_{3,64} = 23.66$ ;  $P < 0.01$ ) and the two burned treatments did not differ ( $P = 0.32$ ) (Fig. 4A). The tallest *S. orbiculatus* ramets measured were 114 cm and were found in unburned pastures or GAB pastures 2 years after fire. Four months after fire, ramet height had reached ~ 84% of its pre-fire height, regardless of how fire was applied.

Ramet canopy diameter did not differ between the three treatments ( $F_{2,66} = 0.09$ ;  $P = 0.92$ ) (Fig. 4B). However, the interaction between treatment and elapsed time since fire was significant ( $F_{6,62} = 4.74$ ;  $P < 0.01$ ) as canopy diameter within PBG and GAB treatments, respectively, was lower at 0.3 years after fire than 1 or 2 years after fire (Fig. 2B). The greatest ramet canopy diameter measured was 143 cm and was in a GAB pasture 2 years after fire.

Ramets in the most recently burned patches in PBG pastures had 2.6 times more stems, and ramets in GAB pastures the year it was burned had 2.2 times more stems than pastures not burned in over 3 years. The number of stems per ramet on burned pastures, regardless of how fire was applied, was significantly higher ( $F_{2,66} = 6.39$ ;  $P < 0.01$ ) than pastures not burned in over 3 years (Fig. 4C). Elapsed time since fire was negatively correlated with stems per ramet ( $F_{3,64} = 17.79$ ;  $P < 0.01$ ) and the two burned treatments did not differ ( $P = 0.30$ ) (Fig. 4C). Thus, the relationship between number of stems per ramet and fire is largely a function of elapsed time since fire rather than how fire was applied.

Ramets per 100 m<sup>2</sup> did not differ between the three treatments ( $F_{2,66} = 0.03$ ;  $P = 0.30$ ). However, the interaction between treatment and elapsed time since fire was marginally significant ( $F_{6,62} = 2.04$ ;  $P = 0.07$ ) with PBG and GAB treatments displaying consistently lower densities than unburned pastures (Fig. 4D). There was no apparent mortality in recently burned PBG patches or when complete GAB pastures were burned (Fig. 4D).

Using logistic regression of the binomial presence/absence of new layering stems, the parameter estimate for elapsed time since fire was -1.3 and was significant ( $P < 0.01$ ) (Table 2). Based on the exponentiation of the parameter estimate, the odds of having a layering stem present in a plot improve 3.77 times for every year closer to the burn year. Hence, 83% of the most recently burned patches had layering stems present with a steady decrease as time since fire elapsed. Pastures not burned in over 3 years had no new layering stems ( $P < 0.01$ ) (Fig. 5A). In a similar fashion, as time since fire elapsed, the density of layering stems per 100 m<sup>2</sup> declines ( $P < 0.01$ ) (Fig. 5B).

## DISCUSSION

The results of our shrub inventory of tallgrass prairie sites in the Grand River Grasslands of Iowa, USA confirms that *S. orbiculatus* is the most common shrub (Holechek et al. 2001). Furthermore, the assessment of shrub presence at different spatial scales suggests that *S. orbiculatus* is more readily detectable at a finer scale than the other shrubs (McKell 2012). However, regardless of the scale of assessment, *S. orbiculatus* is the dominant shrub. Considering the dominance and regeneration capabilities of *S. orbiculatus*, this species presents a threat to mesic grasslands because of its potential for

encroachment and the transition of grassland towards a shrubland state (Müller et al. 2007).

Our study examining the regeneration of *S. orbiculatus* after fire indicates that this shrub is very tolerant of low-intensity prescribed fires conducted in the early spring prior to emergence of leaves. *S. orbiculatus* was able to rapidly regenerate from basal resprouts, recovering to ~ 84% of its pre-fire height 120 days after fire with no apparent mortality. *S. orbiculatus* also uses aerial layering as a regeneration strategy to recover after the disturbance of fire. Ramet height increased with time since fire, but stems per ramet and aerial layering probability decreased with time since fire. Fire initially created a physical alteration of shrub structure as measured by ramet height and stems per ramet. However, the initial structural change was only temporary as the trend indicates that as time elapses past four years, physical shrub structure became more similar to unburned pastures, similar to *Artemisia filifolia* (sand sagebrush) (Winter et al. 2011).

The rapid structural regeneration of *S. orbiculatus* within the burn-year growing season is similar to other species that display rapid regrowth the first year with a declining rate of growth in the next three to four years (Gratani and Amadori 1991). The rate of recovery for *S. orbiculatus* was slower than *Prosopis glandulosa* (mesquite) that recovered to pre-burn heights within one year after fire (Drewa 2003). A similar study in tallgrass prairie suggested that *R. glabra* can rapidly recover to its pre-burn height and fire can result in greater plant heights than in unburned areas for both *P. glandulosa* and *R. glabra* (Drewa 2003; Hajny et al. 2011). However, fire did not appear to increase *S. orbiculatus* in our study. In more arid environments with coarse sandy soils, within the first year of a burn, *A. filifolia* and *Quercus havardii* (sand shinnery oak) recovered to

only ~ 55% of pre-burn height (Harrell et al. 2001; Winter et al. 2011). However, *S. orbiculatus* is similar to *A. filifolia* and *Q. havardii* because it took three years or more for all three species to recover to pre-burn heights. Considering these variable responses, fire only altered the physical structure of these fire-tolerant shrubs for a relatively short period, typically less than four years, and these shrubs regenerated at different rates depending on climate and soil limitations (Olson and Platt 1995; Iwasa and Kubo 1997).

Given that the seeds of *S. orbiculatus* have little to no potential to form a long lived soil seed bank (Hidayata et al. 2001) and the rapid regeneration after fire reported herein, vegetative regeneration appears to be the primary recovery mechanism of *S. orbiculatus*. In context, the tallgrass prairie is a disturbance driven ecosystem that historically had a fire return interval of three to five years (Collins 2000). The life history tradeoff between resprouting and seedling recruitment is largely determined by disturbance regimes and tallgrass prairie was historically disturbed by fire regularly (Wells 1969; Bellingham and Sparrow 2000; Collins 2000). Episodic resprouting events triggered by fire are followed by extended periods of self-thinning as indicated by the relationship with elapsing time since fire and declining stems per ramet in our study (Clark 1991; Hodgkinson 1998).

The low growing and multi-stemmed architecture of *S. orbiculatus* is also reflective of the disturbance regime of tallgrass prairie and its ability to rapidly recover post fire (Midgley 1996; Bellingham and Sparrow 2000). However, vegetative regeneration of *S. orbiculatus* after fire is not limited to basal resprouting but also appears to include aerial layering. The initiation of aerial layering has also been reported to be triggered by physical disturbances for *Rubus trivialis* (dewberries) from grazing and

*Oplopiana horridus* (devil's club) from recent logging activity (Abrahamson 1975; Lantz and Antos 2002). The absence of cattle grazing activity in the unburned pastures could also help explain the lack of new *S. orbiculatus* layering stems (Abrahamson 1975). In the Douglas-Fir forests of Oregon, USA, burning did not increase aerial layering but did increase basal resprouting of *Acer circinatum* (vine maple) while the physical disturbance of thinning and falling branches stimulated layering (Odea et al. 1995). However, in this old growth forest ecosystem the historic fire return interval is estimated to be 230 years compared to our study area that burned every three to five years (Agee 1993).

Our results quantifying the ability of *S. orbiculatus* to regenerate after low-intensity prescribed fires conducted in the early spring is similar to other *Symphoricarpos* species, although not every species is noted to be tolerant of fire. *S. occidentalis* (western snowberry) and *S. albus* (common snowberry) are highly tolerant to fire due to vegetative regeneration mechanisms (McClean 1969; Anderson and Bailey 1979; Morgan and Neuenschwander 1988; Romo et al. 1993; Youngblood et al. 2006). In contrast, *S. oreophilus* (mountain snowberry), *S. longiflorus* (longflower snowberry), and *S. mollis* (creeping snowberry) have been reported to be only low to moderately resistant to fire (Bartos and Mueggler 1981; Snyder 1991; Aleksoff 1999; McWilliams 2000; McWilliams 2005; Knapp et al. 2006; Rocca 2009). Interestingly, even if a species is not highly tolerant of fire, it still may be fire dependent as *S. oreophilus* occurred only on burned sites (Poreda and Willstein 1994). This variable response to fire within the genus is attributed to species distributions and biogeographic disturbance patterns because disturbance frequency is a major determinant of resprouting strength (Westman and O'Leary 1986; USDA Plant Database 2013).



In contrast to our study, other studies have reported reductions in *S. orbiculatus* with fire. Late spring burning in tallgrass prairie reduced *S. orbiculatus* due to lower carbohydrate reserves because plants had already leafed out (Hulbert 1986) which is different than our early spring burns and no apparent reductions. Furthermore, two successive years of spring burning in April in a forested corridor of Kansas reduced *S. orbiculatus* canopy cover from 40% to 9% but did not alter shrub species richness (Abrams 1988). Thus, burning later in the season or burning a site repeatedly for successive years may result in reductions of *S. orbiculatus*. However, at our research sites, most burning is done in the early spring and may not be possible in late spring due to tall fescue *Schedonorus arundinaceus* (tall fescue) greenup and alteration of fire behavior (McGranahan et al. 2012). Furthermore, it can be difficult to graze and burn complete pastures for successive years.

The spread of *S. orbiculatus* and the allelopathic competition with forbs and grasses has driven research on herbicide options for control (Smith 1977; Stubbendieck et al. 2003). Recommendations have included two successive years of foliar herbicide applications (Defelice 1991). However, the historic regulation of woody plant encroachment in grasslands was driven by fire which has largely been removed from the landscape (Pyne 1997; Briggs et al. 2005). Restoring a functioning fire regime may mediate *S. orbiculatus* encroachment while preserving the role it serves for wildlife. Our study suggests that a three-year fire return interval using dormant season prescribed fires can result in altered physical structure and could maintain lower densities of *S. orbiculatus*. While our study did not document mortality, this is a common result for resprouting shrubs (Canadell et al. 1991; Olson and Platt 1995). However, we did

document a trend of lower densities on pastures managed with regular fire compared to higher densities on pastures managed with long-term fire exclusion. Unlike other shrub species such as *R. glabra* that may increase with fire, *S. orbiculatus* density and expansion appears to be mediated by regular fire (Hajny et al. 2011).

Our study also included the spatio-temporal application of patchy fires (PBG) and cattle grazing, an attempt to recouple pre-settlement fire and grazing processes (Fuhlendorf and Engle 2001). The attraction to recently burned patches alters grazing patterns and results in fuel accumulation in long-unburned patches and potentially enhances fire behavior (Kerby et al. 2007). However, when compared to attempting to burn a pasture completely, we did not observe different vegetative responses associated with fire intensity or herbivory. This is not surprising because *S. orbiculatus* is an extremely effective resprouter after fire and cattle do not graze *S. orbiculatus* (Stubbendieck et al. 2003).

*S. orbiculatus* is an important native plant for a wide range of wildlife species and is the dominant shrub of mesic tallgrass prairie. As the common name buckbrush implies, this species is a desirable browse plant for whitetail deer. In the spring, *S. orbiculatus* browse is greater than 13% crude protein and *S. orbiculatus* can make up about 10% of deer diet by volume (Korschgen 1962; Soper et al. 1993). A functioning shrub component is also critical for other wildlife species such as quail and regular fire could be important for maintaining or optimizing density and structure of *S. orbiculatus* in tallgrass prairie (Guthrey 1980). This may be important also because our research sites do not have the richness of shrub species like the southwestern US and have experienced a decline in quail (Brennan 1991; Harrell et al. 2001; Stubbendieck et al. 2003).

## CONCLUSIONS

Our documentation of fire triggering aerial layering of *S. orbiculatus* is the first in the literature for this species. While other studies have documented physical stimulation of aerial layering for other species in less fire-prone ecosystems or for horticultural purposes (Hartmann and Kester 1975; O’Dea et al. 1995; Lantz and Antos 2002; Deb and Pogener 2012), our study has developed basic ecological information that is relevant to fire-prone mesic grasslands. As woody plants continue to encroach and transition these critical areas for conservation from grasslands to shrublands, it is increasingly critical that we continue to understand the organismal communities and ecological drivers (Samson 2004; Briggs et al. 2005). We suggest that aerial layering be considered as an adaptation to fire disturbances and that additional research is warranted. Areas for additional inquiry include how aerial layering and seed production of *S. orbiculatus* fluctuate along a gradient of disturbance and how fire intensity and fire return interval affect belowground carbohydrate reserves because anthropogenic fire regimes may not replicate a natural lightning-ignited fire regime (Kennedy and Potgieter 1993). Finally, it is also important to understand how this basic plant ecology information applies to other resprouting shrub species that use a layering mechanism and how it applies to land management and conservation (Hodgkinson 1998).

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## Tables

Table 1 Shrub occurrence at four nested spatial scales in tallgrass prairie of the Grand River Grasslands of Iowa, USA in 2011. Within each 500 m<sup>2</sup> quadrat there were 10 – 0.5 m<sup>2</sup> quadrats and 2 - 2.5 m<sup>2</sup> quadrats nested within 1 - 100 m<sup>2</sup> quadrat nested within the 500 m<sup>2</sup> quadrat.

Species	Percent occurrence at four spatial scales			
	0.5 m <sup>2</sup>	2.5 m <sup>2</sup>	100 m <sup>2</sup>	500 m <sup>2</sup>
<i>Cornus drummondii</i>	1%	1%	14%	33%
<i>Prunus spp.</i>	2%	< 1%	19%	31%
<i>Rhus glabra</i>	0%	0%	0%	0%
<i>Rosa multiflora</i>	0%	0%	11%	56%
<i>Rubus spp.</i>	< 1%	1%	8%	14%
<i>Symphoricarpos orbiculatus</i>	14%	32%	83%	86%

Table 2 Maximum likelihood parameter estimates for time since fire and probability of the presence of new aerial layering stems based on the logit function (proc genmod) and binomial presence/absence data. Based on the exponentiation of the parameter estimate, the odds of having a layering stem present improve 3.77x for every year closer to the burn year.

Parameter	Estimate	Standard Error	Likelihood Ratio 95% Confidence Limits		P value
Intercept	3.420	1.077	1.537	5.858	0.002
Time Since Fire	-1.330	0.403	-2.235	-0.622	<b>0.001</b>

## Figures

Fig. 1. Diagram of quadrats for experiment 1: shrub inventory at multiple spatial scales and experiment 2: fire effects on *S. orbiculatus*.

Fig. 2. Diagram of fire treatments in the Grand River Grasslands of Iowa, USA, 2011-2013. Treatments are 1) Patch-burn grazing (PBG) where one-third of a pasture (the patch) is burned and cattle have full access to the pasture, 2) Graze and burn (GAB) where the entire pasture is burned every third year (2012 was the burn year) and cattle have full access to the pasture, 3) Not burned for more than three years with no grazing. Treatments were in place before sampling in 2011 so all patches and pastures had a consistent elapsed time since fire (0.3, 1, 2 years since fire). We had less control over the unburned treatment and elapsed time since fire for those pastures was > 3 years. When we returned in 2013 to conduct a second assessment of unburned pastures, they had all either been burned or mowed.

Fig. 3. Diagram of fire effects measurements given the clonal nature of *S. orbiculatus*. We conducted measurements at the ramet level and define ramets as individual plants or clonal fragments in the colony that are rooted and may or may not be connected to other ramets by rhizomes or rooted aerial layering stems. Individual ramets were identified by spatial independence based on vertical stems arising from the same root crown. New aerial layering stems were measured as vertical stems arising from the root crown, having a horizontal orientation, and not yet rooting at the tip

Fig. 4 Mean  $\pm$  SE of ramet height (**a**), ramet canopy diameter (**b**), stems per ramet (**c**), and ramets per 100 m<sup>2</sup> (**d**) for *Symphoricarpos orbiculatus* plants exposed to three fire

treatments in the Grand River Grasslands of Iowa, USA, 2011-2013. Treatments are 1) Patch-burn grazing (PBG) where one-third of a pasture (the patch) is burned and cattle have full access to the pasture, 2) Graze and burn (GAB) where the entire pasture is burned every third year (2012 was the burn year) and cattle have full access to the pasture, 3) Unburned for greater than three years with no grazing. The *asterisk* indicates if the unburned treatment is significantly different ( $P \leq 0.05$ ) than the burned treatments and all elapsed time since fire categories (0.3, 1 or 2 years after fire. Letters indicate significant differences within a treatment ( $P \leq 0.05$ ) (lower case for PBG and capitalized for GAB) based on a mixed effects model.

Fig. 5 Effect of elapsed time since fire on new *Symphoricarpos orbiculatus* horizontal layering stems based on percent of plots with new layering stems (**a**), and new layering stem density (**b**) in the unburned pastures and the Patch-burn grazed (PBG) pastures in in the Grand River Grasslands of Iowa, USA, 2011 and 2013. Letters indicate differences ( $P \leq 0.05$ ) based on a mixed effects model.



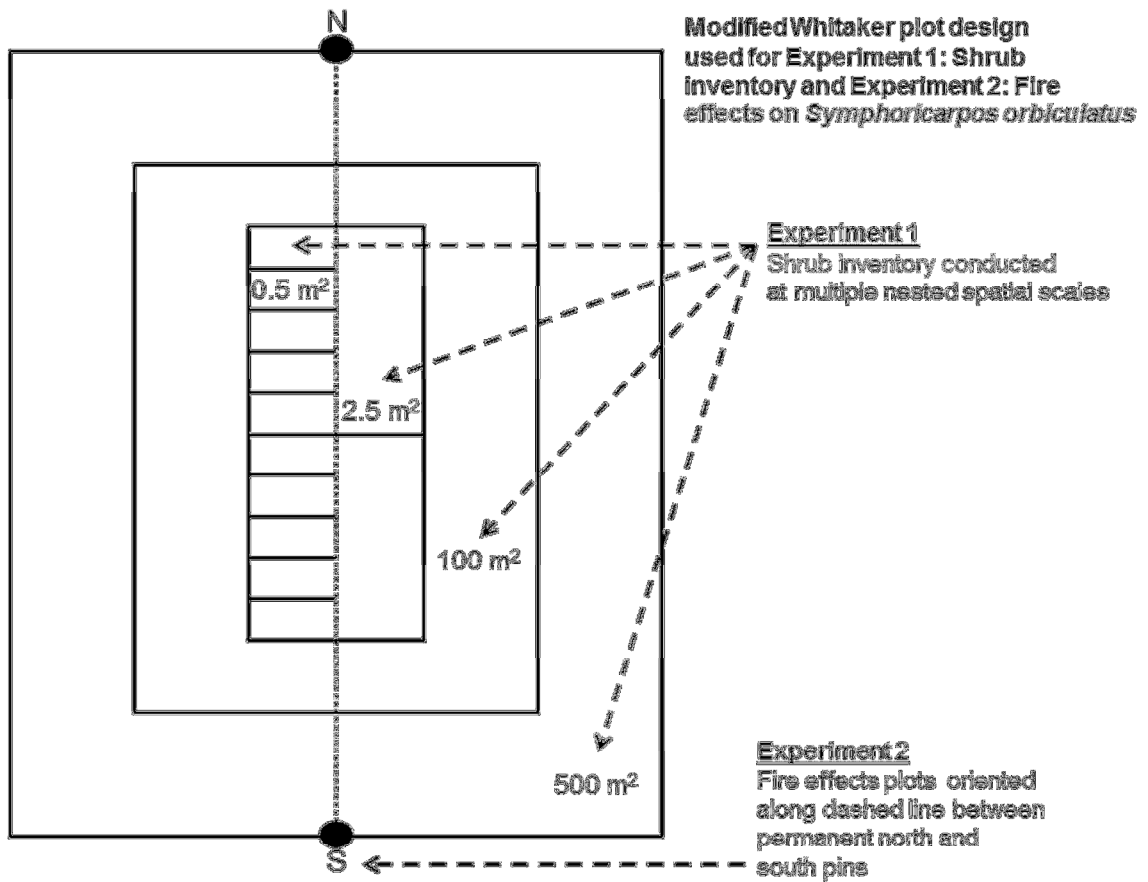
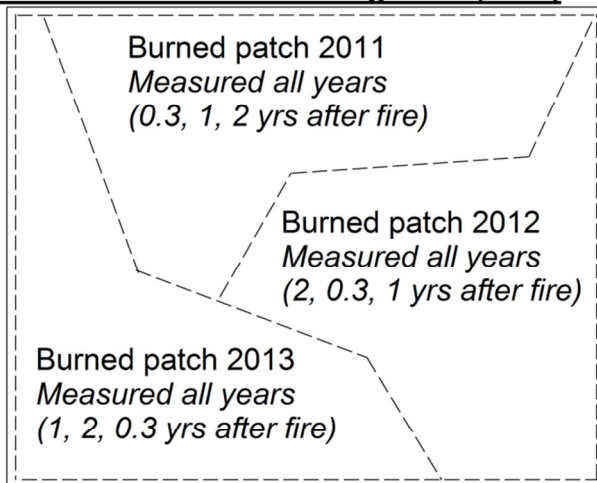
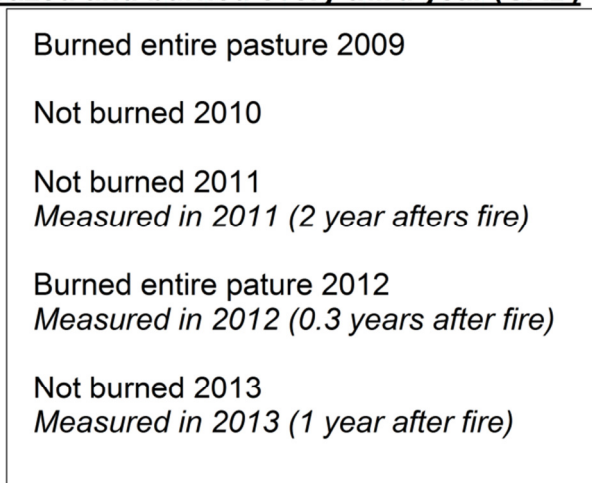


Figure 1

**Patch-burn 1/3 annual and grazed (PBG)**



**Grazed and burned every third year (GAB)**



**Unburned > 3 years with no grazing**

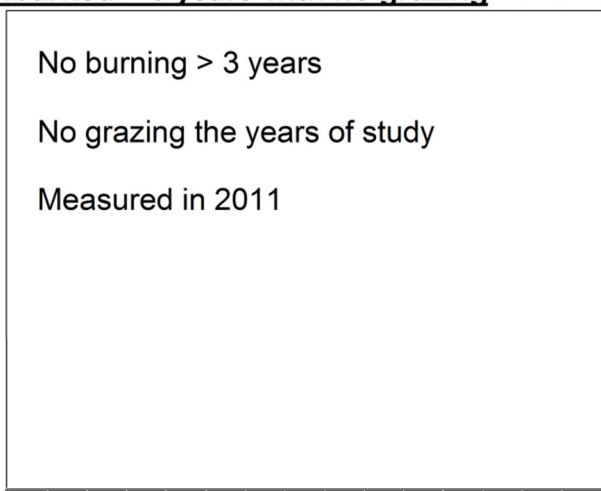


Figure 2

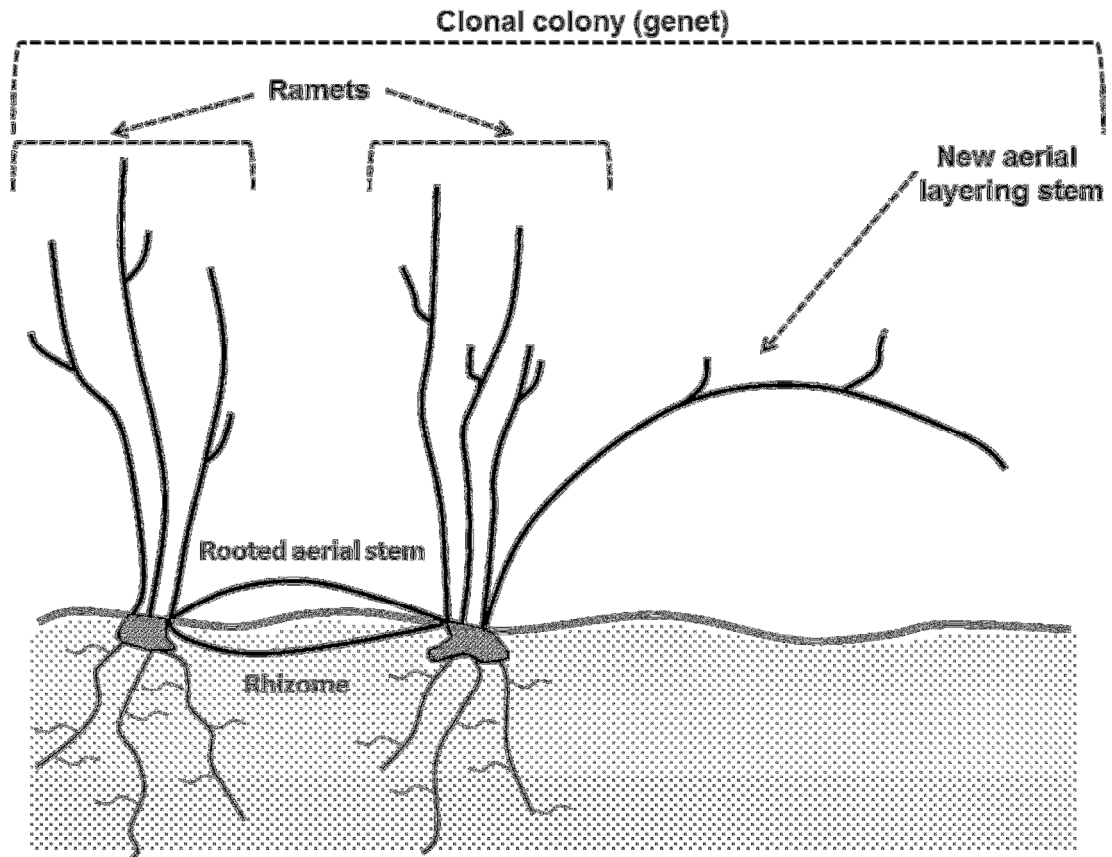


Figure 3

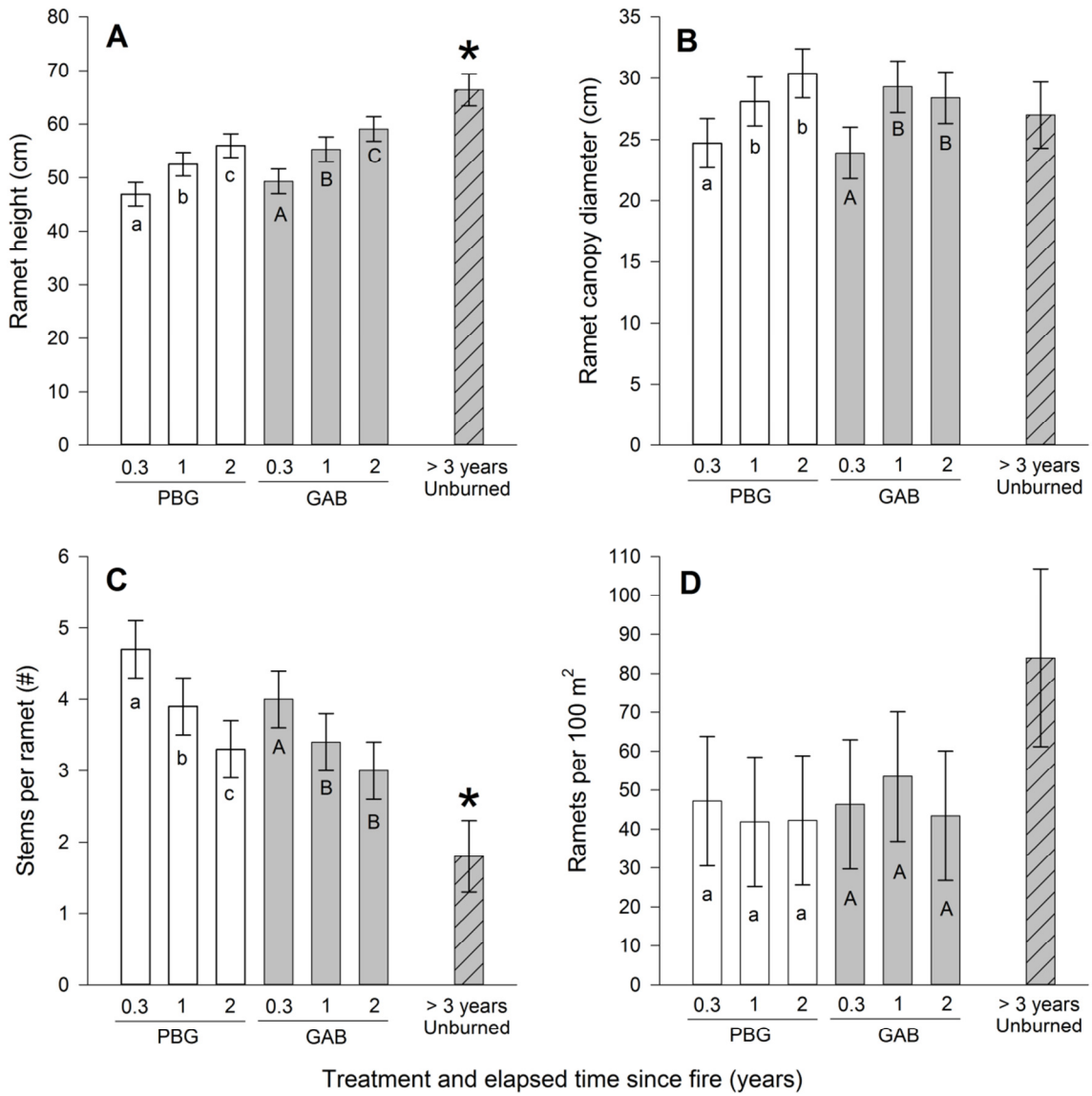
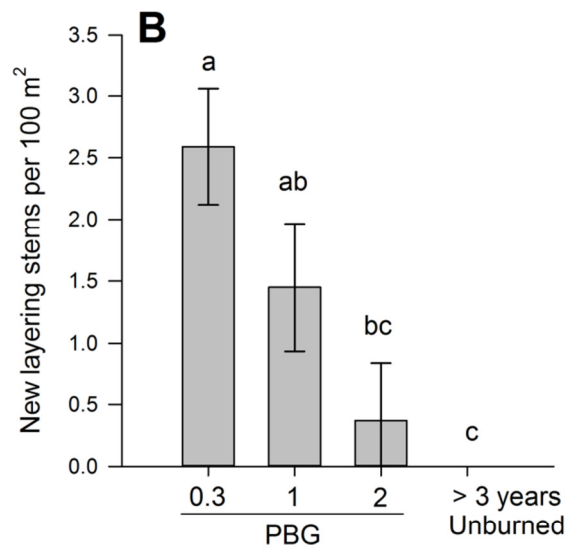
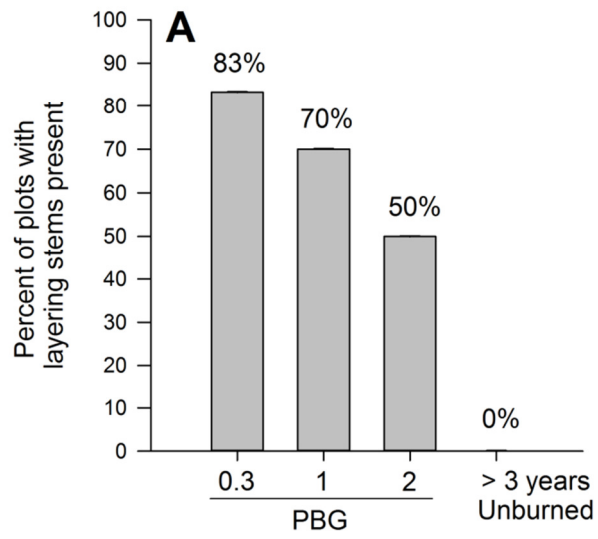


Figure 4



Treatment and elapsed time since fire (years)

Figure 5

VITA

John Derek Scasta

Candidate for the Degree of

Doctor of Philosophy

Thesis: IMPLICATIONS OF PYRIC-HERBIVORY ON CENTRAL NORTH  
AMERICAN GRASSLAND ECOLOGY, MANAGEMENT AND  
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