

EVALUATING THE INTERACTIVE EFFECTS OF SEASONAL PRESCRIBED FIRE
AND GRAZING ON INVASIVE GRASS ABUNDANCE AND WOODY BRUSH
ENCROACHMENT

A Thesis

by

MICHELE DIANE CLARK

Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Chair of Committee,	William E. Rogers
Co-Chair of Committee,	Urs P. Kreuter
Committee Member,	Charles W. Lafon
Head of Department,	Kathleen Kavanagh

December 2014

Major Subject: Ecosystem Science and Management

Copyright 2014 Michele Diane Clark

ABSTRACT

Developing effective restoration techniques for encroached and invaded grasslands requires an understanding of two fundamental ecological processes: fire and grazing. Prescribed fire and grazing are suggested management techniques for preventing shrub encroachment and suppressing non-native species, especially in areas with functionally distinct native and exotic grasses. This study evaluates the effects on two encroached grasslands in South Africa and south Texas. In south Texas, native prairies are undergoing woody brush encroachment and exotic plant invasion concurrently. The exotic C4 grass species (*Bothriochloa ischaemum* and *Dichanthium sericeum*) are not physiologically distinct from the native C4 species they displace; therefore, the native and invading species may respond similarly to treatment techniques thus decreasing targeted management options. I established a full-factorial, completely randomized experiment to examine the interactive effects of seasonal prescribed fire and grazing on invasive grass abundance and woody brush density. Thirty-six 10m x 10m plots were assigned six treatments including: i.) summer burned-fenced ii.) summer burned-unfenced iii.) winter burned-fenced iv.) winter burned-unfenced v.) unburned-fenced vi.) unburned-unfenced. Prescribed fires were conducted in August 2013 and February 2014. Each season of burn treatment was followed by a grazing treatment.

Shrub height and cover significantly decreased across all shrub species in response to fire. Fire seasonality had no effect on invasive grass abundance but grazing reduced foliar cover ($p=0.02$) of the dominant invader (*D. sericeum*). Both treatments

increased total species diversity. These results indicate that both seasonal fire and grazing can be used together to decrease shrub and invasive grass cover and maintain diversity.

This experiment complements another similarly designed study in South Africa, which determines the response of the encroaching shrub, *Seriphium plumosum*, to single season (winter) prescribed fire and grazing. Results indicate that fire can reduce shrub stature and canopy cover ($p < 0.01$). Both treatments had no effect on herbaceous community composition ($p = 0.66$). Comparing differential plant community responses to prescribed burn season in combination with grazing will provide important insights into the factors influencing woody vegetation dynamics and invasive grass growth and survival. This study provides a baseline of information to assist with the development of management techniques for multiple rangeland objectives.

DEDICATION

To my aunts Valerie Varzos and Mary Ramirez

ACKNOWLEDGMENTS

I would like to thank the Welder Wildlife Foundation, which provided the financial support and materials for the south Texas research project. The director, Dr. Terry Blankenship, was immensely helpful throughout my time at the Welder Wildlife Refuge. I appreciate all of the edits and input from my committee members and guidance from my professors. I would also like to extend my gratitude to my friends and colleagues at Texas A&M University, especially Carissa Wonkka, who helped perform fieldwork and assisted with various components of my research.

I would like to thank my mother, father, and sister for always encouraging and supporting me. I'm also very thankful for Travis Nielsen's contribution to my research and fieldwork and for his constant love and support throughout this entire process.

Finally, I would be remiss if I didn't mention Dr. James A. Young, my first mentor and the person who introduced me to the field of rangeland ecology and management.

TABLE OF CONTENTS

	Page
ABSTRACT	ii
DEDICATION	iv
ACKNOWLEDGMENTS.....	v
TABLE OF CONTENTS	vi
LIST OF FIGURES.....	ix
LIST OF TABLES	xi
CHAPTER I INTRODUCTION	1
CHAPTER II EVALUATING THE INTERACTIVE EFFECTS OF SEASONAL PRESCRIBED FIRE AND GRAZING ON <i>DICHANTHIUM SERICEUM</i> AND <i>BOTHRIOCHLOA ISCHAEMUM</i> ABUNDANCE	4
Introduction	4
Old world bluestem grasses.....	8
Ecology and distribution	10
Management	12
Herbicide application	13
Mechanical treatment application	13
Prescribed fire.....	14
Grazing	15
Methods.....	18
Study site	18
Experimental design	21
Data collection and treatment application	22
Prescribed fire.....	23
Grazing rotation.....	25
Percent utilization.....	25
Species diversity and richness.....	26
Statistical analysis of focal species	27
Fire frequency model.....	28
Results	29
Fire treatment	30
Grazing treatment	30

Species diversity and richness	31
Focal species response.....	33
Fire frequency model.....	39
Discussion	40
C3 vs C4 grass response	41
Species diversity and richness.....	42
Total grass response	45
Fire frequency.....	45
Focal species response.....	46
CHAPTER III AN EXPERIMENTAL ASSESSMENT OF SEASONAL PRESCRIBED FIRE AND GRAZING ON WOODY BRUSH ENCROACHMENT IN A SOUTH TEXAS COASTAL PRAIRIE.....	49
Introduction	49
Methods.....	55
Study site	55
Experimental design	56
Prescribed fires	57
Grazing	58
Statistical analyses.....	58
Results	59
Fuel load and fire descriptions	59
Species richness.....	60
Focal woody species response.....	61
Discussion	66
Seasonal fire	66
Grazing	67
Herbaceous and woody shrub response.....	68
Fire frequency.....	68
CHAPTER IV DETERMINING THE EFFECT OF SINGLE SEASON PRESCRIBED FIRE AND GRAZING ON <i>SERIPHIMUM PLUMOSUM</i> IN A SOUTH AFRICAN SOUR BUSHVELD	70
Introduction	70
Distribution.....	72
Ecology.....	75
Management	76
Methods.....	79
Study site	79
Statistical analyses.....	82
Results	85
Discussion	90

Herbaceous community response	93
CHAPTER V CONCLUSION	97
Managing for multiple objectives.....	97
Ecological generalizations.....	99
REFERENCES	101
APPENDIX	120

LIST OF FIGURES

	Page
Figure 2. 1 Average precipitation rate and monthly precipitation for 2013 and 2014 at the Welder Wildlife Refuge.	20
Figure 2. 2 Aerial view of plot locations within the pasture.	20
Figure 2. 3 Timeline of treatment implementation and data collection	23
Figure 2. 4 Herbaceous species percent cover following summer burn and grazing treatments	35
Figure 2. 5 Herbaceous species percent cover following winter burn and grazing treatments	36
Figure 2. 6 <i>Bothriochloa ischaemum</i> (BOIS % cover) response to summer and winter burn and grazing treatments	37
Figure 3. 1 Means of shrub characteristics following summer burn and grazing treatments	62
Figure 3. 2 Means of shrub characteristics following winter burn and grazing treatments	63
Figure 3. 3 Species percent cover following summer burn and grazing treatments	64
Figure 3. 4 Species percent cover following winter burn and grazing treatments	65
Figure 4. 1 Map of <i>Seriphium plumosum</i> distribution in South Africa	74
Figure 4. 2 Image of <i>S. plumosum</i> entire shrub and seed head	74
Figure 4. 3 Study site location in South Africa and location within Ukulima research station	80
Figure 4. 4 Mean annual precipitation (cm) in the Waterburg district, Limpopo province, South Africa	81
Figure 4. 5 NMDS ordination based on two axes.	84

Figure 4. 6 Species accumulation curve calculated from random starting configurations.....	84
Figure 4. 7 <i>S.plumosum</i> characteristics and total cover by functional group.....	87
Figure 4. 8 Scree plot used to determine minimum stress	89

LIST OF TABLES

	Page
Table 2. 1 Species diversity of grasses and forbs for summer burned and winter burned plots	32
Table 2. 2 Grass species richness following summer and winter burning and grazing treatments.	32
Table 2. 3 Analysis of variance of multiple cover types	34
Table 2. 4 Response of cover types to summer vs winter burning and grazing treatments	39
Table 3. 1 Shrub species richness post-fire and grazing treatments.....	60
Table 3. 2. Analysis of variance of multiple shrub characteristics	60
Table 4. 1 Analysis of variance of shrub characteristics and cover types.....	86
Table 4. 2 Percent change from pretreatment to two year post treatment data for certain dominant grasses	88
Table 4. 3 ANOVA herbaceous biomass two years post treatment	89
Table 4. 4 Shannon diversity index post treatment for all species	90
Table 4. 5 List of common grass species in the study site	94

CHAPTER I

INTRODUCTION

Historically, fire has been an important factor in maintaining grasslands (Govender et al. 2006). Periodic fires play a vital role in nutrient recycling and maintaining herbaceous community composition (Bond and Van Wilgen 1996). Exclusion of fire and improper stocking rates lead to a reduction in fine fuel accumulation and reduced fire frequency (Briggs et al. 2005). As a result, native shrubs have increased in density and distribution globally across rangelands. Increased shrub density can alter fuel loads, decrease herbaceous production (Van Auken 2009), reduce species richness in grasslands (Ratajczak et al. 2012) and diminish ecosystem services (Van Wilgen et al. 1996). In addition to shrub encroachment, many grasslands are undergoing simultaneous invasion by non-native aggressive herbaceous species.

South Texas rangelands are being degraded as a result of shrub encroachment and non-native C4 grass invasion. The dominant non-native invading grass species are referred to as old world bluestem grasses (OWBGs). These grasses are known for their rapid colonization and establishment into native C4 tallgrass prairies and for their ability to significantly decrease species richness and diversity (Gabbard and Fowler 2007). Further adding to the complexity of the issue, the non-native invading species are physiologically similar to the surrounding native C4 species. Applying management techniques to control undesirable species is more difficult when the non-target species response is similar to the target species. Studies have shown that certain seasons of

prescribed fire application can promote OWBGs (Pase 1971, Simmons et al. 2007). For this reason, land managers are concerned that prescribed fires targeted at controlling woody brush could exacerbate the understory invasive grass issue (Fulbright 1991). Management plans are often targeted at controlling woody brush in order to increase desirable grass community composition and production (Fulbright 1991); however, invasive grasses can act as an obstacle towards successful regeneration of native plant communities (Menke 1992) following woody brush control measures. Therefore, it is necessary to evaluate both the herbaceous community response to seasonal fire application and the response of the encroaching shrub species, so that one problem (encroaching shrubs) is not replaced by another (invading herbaceous species) following fire application.

Targeted grazing following prescribed fire is another potential management technique to control invasive herbaceous species. If the non-native grass species are selectively preferred over the native species, then targeted grazing rotations could reduce invasive grass abundance while maintaining the native herbaceous community. Moreover, the palatability of re-growing shrub stems is often much higher following fire (Schindler et al. 2004) and as such, grazing applications post-fire could potentially reduce woody shrub species abundance as well.

The research outlined in this thesis is designed to evaluate the interactive effects of livestock grazing and prescribed fire on several species of woody vegetation encroaching into coastal grasslands of southern Texas and the sour bushveld of South Africa. These studies will provide important insights into the factors influencing woody

vegetation growth and survival and will assist with the development of management efforts that attempt to prevent further encroachment into grasslands. Additionally, the experimental studies established in Texas will contribute a better understanding of the population dynamics and potential management strategies used to alter the abundance of non-native old world bluestem grass species that have begun to invade and degrade this ecosystem. An understanding of the plant community responses of native and invasive grasses with similar plant functional traits to the seasonality of prescribed fire and grazing will help to inform invasive species management decisions in the future. The first two chapters of the thesis will be directly applicable to the management of woody species and invasive grasses within the Weller Wildlife Refuge and the coastal grasslands of Texas. The final chapter focuses on a South African grassland. This study evaluates the effects of prescribed fire and grazing on a native woody encroacher referred to locally as 'bankrupt bush' (*Seriphium plumosum*). The species was given the name 'bankrupt bush' for its ability to establish dense monocultures of shrublands which can reduce livestock grazing capacity and severely diminish land value. This study will provide insights into the ecology of the encroaching shrub species and evaluate fire and grazing as a management technique.

Comparisons from these two study sites, allows for a broader, cross-continental analysis that attempts to generalize ecological traits between two semi-arid ecosystems. Additional information on the effects of fire and grazing on the shrub species will be essential for maintaining ecosystem integrity and informing landowners and stakeholders about brush management options.

CHAPTER II
EVALUATING THE INTERACTIVE EFFECTS OF SEASONAL PRESCRIBED FIRE
AND GRAZING ON *DICHANTHIUM SERICEUM* AND *BOTHRIOCHLOA*
ISCHAEMUM ABUNDANCE

Introduction

Grasslands are considered one of the most vulnerable ecosystems in the world with more than fifty-five grassland species currently listed as threatened or endangered in the United States alone (Samson and Knopf 1994). Grasslands have been altered by livestock over-grazing, residential development, woody brush encroachment, non-native species invasions, cultivation, or conversion related to other agricultural practices (Briggs et al. 2005). It has been estimated that greater than 70% of grasslands have already been converted as a result of land use changes (Goldewijk 2001, Foley et al. 2005, Hickman et al. 2006).

Within the state of Texas, the historic distribution of tallgrass and mixed-grass prairie has declined by 90% and 30%, respectively (Samson and Knopf 1994). Less than one percent of the original 3.7 million hectares of coastal prairie stretching from central Louisiana to southern Texas remains in pristine condition (Smeins et al. 1992). As one of the major ecosystem types in North America, the loss of these grassland communities is resulting in significant decreases in biological diversity, particularly in desirable wildlife species, reduced forage production (and consequently reductions in animal grazing capacity), and diminished critical ecosystem services such as groundwater

recharge, carbon sequestration, and pollinator habitat. Knopf (1994) found that grassland bird species have the highest rate of decline when compared to all other North American bird groups. Habitats within the coastal prairie are exclusive to several critically imperiled grassland birds, such as the endangered Attwater's prairie chicken (*Tympanuchus cupido attwateri*) (Cogar et al. 1977) and Whooping Crane (*Grus americana*) (Grace 1998). Grasslands are necessary for food production, the hydrological system, and function as critical habitat for endemic and endangered wildlife species. As a result, grassland degradation is of major importance to conservation.

One of the primary threats to native grassland diversity, second only to habitat conversion, is the invasion of exotic herbaceous species (Westbrooks 1998, Grace et al. 2000). Invasions by exotic plant species can result in alterations to ecosystem function and processes (Westbrooks 1998) most notably in relation to biogeochemical cycling (Evans et al. 2001, Asner and Vitousek 2005), litter decomposition dynamics (Mack and D'Antonio 2003), nutrient cycling (Evans et al. 2001), hydrologic processes (Vitousek et al. 1987, Ehrenfeld 2003) and microbial community properties (Hawkes et al. 2006). Aggressive invasions by highly competitive exotic plant species can cause widespread alterations to the ecology of an ecosystem. For instance, invasion of the exotic annual grass, *Bromus tectorum*, in the intermountain west has led to reductions in species diversity as the native perennial sagebrush-steppe community transitions to monocultures of the exotic annual (Young et al. 1987, Monaco et al. 2003). *B. tectorum* invasions can lead to accumulation of flammable fuel and increased fire frequency which further promotes invasion and suppresses native vegetation (D'Antonio and

Vitousek 1992, Billings 1994, Ziska et al. 2005). Another example is the non-native perennial C3 grass, smooth brome, *Bromus inermis*, which invades remnant native prairie and is capable of forming dense monocultures and markedly altering ecosystem properties and decreasing species diversity (Sather 1987, Blankespoor and May 1996, Bahm et al. 2011). These dramatic shifts in community composition can lead to soil erosion, ecosystem degradation, reductions in biodiversity and a loss of a multitude of ecosystem services (D'Antonio and Vitousek 1992, D'Antonio and Meyerson 2002).

Altered ecosystem processes resulting from invasive plant species can have irreversible effects on the stability and function of an ecosystem (Ehrenfeld 2003). For this reason, invasive plant management techniques are being investigated to better devise control efforts of non-native species populations in order to prevent further ecosystem degradation. Management techniques such as mechanical, chemical, and biological control can be expensive, have limited success, disturb the soil matrix, have unintended negative consequences, and/or oftentimes provide only marginal long-term solutions to invasion (Dahlsten 1986, Simmons 2005).

Prescribed burning is an important management technique for restoring ecological processes and suppressing non-native species invasion. In systems where the invading species has distinct physiology from the native species, targeted management techniques, like prescribed fire, can be applied effectively. Targeted prescribed fires in tallgrass prairie regions were able to promote native warm-season grass establishment while decreasing non-native perennial cool-season grass abundance (Robocker and Miller 1955, DiTomaso et al. 2009). In this region, the application of prescribed fires to

reduce non-native grasses was successful because the invading exotic plant species (C3 photosynthetic pathway) were functionally distinct from the native species (C4 pathway) they displace (DiTomaso et al. 2009). Conversely, prescribed burning can increase non-native species establishment and growth if the invader creates conditions that significantly alter the historical fire regime (D'Antonio and Vitousek 1992, D'Antonio 2000). Studies in the intermountain west have shown that fire significantly increases cover of the invasive annual grass *Bromus tectorum* and the weedy native forb *Gutierrezia sarothrae* (Young and Evans 1978, Towne and Owensby 1983, Chambers et al. 2007). The variable and unpredictable influence of fire on plant community dynamics where non-native species invasions have occurred highlight the complexities of using prescribed burning as part of a management strategy and emphasize the importance of properly timing prescribed fire applications in order to suppress specific species and achieve particular outcomes.

In addition to prescribed fire, targeted grazing rotations can be used to achieve range management objectives related to invasive species control (Popay and Field 1996). Understanding differences in cattle foraging preferences can be useful when attempting to apply a prescriptive grazing rotation that targets the undesirable species, especially if the non-native species is more palatable than the surrounding native species (Frost and Launchbaugh 2003). Studies have shown that targeted grazing during periods when the non-native plant is more susceptible to defoliation and therefore at a competitive disadvantage relative to the native community can be successful in controlling non-native herbaceous species (Myers and Squires 1970, Frost and Launchbaugh 2003).

Although prescription grazing can be a useful tool in invasive species management, inappropriate stocking densities and poorly timed grazing rotations could promote invasion (Brooks and Pyke 2000). Studies have shown that many areas with a history of high cattle stocking rates are more sensitive to invasion and have higher non-native plant densities when compared to ungrazed areas (Webb and Stielstra 1979, Brooks 1995). Given the complexity of potential outcomes of fire and herbivory on plant communities, an understanding of species specific plant-fire-grazing interactions is necessary before land managers can create targeted goals that aim to manipulate plant community composition. Both fire and grazing can be successful management techniques used to alter community composition when applied appropriately. For this reason, seasonality of fire and grazing intensity and stocking rate in relation to the specified target species and the potential response of the native community should be evaluated prior to landscape scale application.

Old world bluestem grasses

Coastal prairie, tall and mid-grass prairies of the Great Plains, and central U.S. grasslands are subject to invasion by a category of non-native grasses known as old world bluestem grasses (Sims and Dewald 1982). This classification of grasses predominately consists of C4 exotic, perennial bunchgrasses from the genera *Bothriochloa* and *Dichanthium* (Ruffner et al. 2012). In addition to this invasion by non-native grass species, a large portion of these grasslands have been degraded by encroaching native woody plant species and many have been fully converted to become shrub dominated ecosystems (Archer 1989, Knapp et al. 2008). The low light availability

beneath the shrub canopy and competitive dominance of the shrub species creates an environment further conducive for shade tolerant, non-native understory herbaceous species to invade (Ravi et al. 2009). Land management options for controlling shrub species can be costly, ineffective (Burgess 1989), and may exacerbate the understory invasive species issue (Rinella et al. 2009).

During the late 1800s and early 1900s, old world bluestem grasses (hereafter referred to as OWBGs) were introduced into North America from Eurasia, Africa and Australia due to their assumed superior forage characteristics relative to native North American bluestems (Eck and Sims 1984, Coyne and Bradford 1985b, Dewald et al. 1985). OWBGs have high grazing tolerance and can rapidly grow and establish (Celarier and Harlan 1955) allowing for higher competitive dominance compared to native grass species. During the initial introduction of OWBGs, there were a variety of range management practices and programs that determined the best methods of establishing monocultures of OWBGs in the southern Great Plains, Texas, and Oklahoma (McCoy et al. 1992, Dalrymple 2001). OWBGs are known for their ability to persist under grazing and for their high forage yield relative to native bluestems (*Andropogon spp.*) (Dabo et al. 1988). The grasses ability to withstand repeated grazing and produce higher subsequent yields compared to favored range species like bermudagrass (*Cynodon dactylon*) and weeping lovegrass (*Eragrostis curvula*), encouraged land managers to seed millions of hectares of OWBGs to increase rangeland productivity (Coleman and Forbes 1998). Additionally, the high rates of growth and establishment encouraged soil conservationists to prescribe seeding of OWBGs in areas susceptible to heavy soil

erosion (Gould 1975, Coyne and Bradford 1985b, Berg 1993, Gabbard and Fowler 2007). It is assumed that the species escaped cultivation in the 1940's (Gabbard 2003); as a result, many roadsides and pasturelands throughout Texas and Oklahoma are dominated by the species. OWBGs were considered the primary grass to be planted for the intent of improving pasturelands in Texas and Oklahoma in the 1990's (Berg 1993). Widespread introduction of the grasses and their apparent superiority over native species allowed them an opportunity to invade native prairies, roadsides, and agricultural lands. OWBGs are still planted or seeded currently, as erosion control or in rangeland improvement efforts (Gabbard and Fowler 2007), despite their general negative association as an invasive weed species. While OWBGs were originally considered desirable rangeland species from a forage yield perspective, studies have shown that they have a negative impact on native species diversity and richness and adversely affect numerous desirable ecosystem functions. OWBGs aggressively invade abandoned farmlands, heavily disturbed areas, roadsides, and pastures.

Ecology and distribution

Since their introduction, OWBGs have established in a broad range of geographic areas in the United States. OWBGs are adapted to a variety of soil types but are most often found on finer-textured soils such as clays, loams, and silt loams. The species silky bluestem [*Dichanthium sericeum* (R.br.) A. Camus], is an invasive C4 OWBG originally from Australia and Papua New Guinea that has established in Texas, Mississippi, Florida (USDA 2014) and Arizona (Felger et al. 2005). *D. sericeum* is specifically restricted to vertisol soils (heavy black clays) in subtropical climates

(Jacobsen 1981). Vertisol clay soils often undergo episodic wetting and drying periods (shrink-swell) which may prevent or delay native seed germination during periods of drought. One characteristic of *D. sericeum* that adds to the invasiveness of the species, is its ability to exhibit hydropedesis (Watt 1978, 1982). Hydropedesis is a phenomenon that allows the imbibed seed to re-enter a stage of dormancy during periods of immediate water stress and then complete the germination process once water resources are available again (Silcock and Johnston 1993, Paterson 2011). Since *D. sericeum* is capable of germinating immediately following desiccation (Watt 1982), this might explain its establishment on vertisol soils. This drought adaptation could allow the species to effectively outcompete native seedlings susceptible to cyclical water stress events. *D. sericeum* is valued for its high forage quality and palatability in territories of Australia (Fensham et al. 1999).

The OWBG variety, yellow bluestem (also known as King Ranch bluestem [*Bothriochloa ischaemum* (L.) Keng]), originates from Europe, Asia and North Africa (Bailey et al. 1976) and can occur on a wide range of soil types (McCoy et al. 1992). King Ranch bluestem reproduces from June to October and is known for its winter hardiness (Harlan et al. 1961, Harlan 1963). The species establishes on sandy, loam, or clay soils (McCoy et al. 1992) and is considered highly drought tolerant but may be intolerant of flooding (Moser et al. 2004). In general, OWBGs fail to establish or grow on sandy soil types or soils with high salinity or high soil pH (alkalinity). OWBGs are tolerant of drought and heavy grazing pressure and are able to reproduce both

vegetatively (through stolons and rhizomes) and by seed (Celarier and Harlan 1955, Schmidt and Hickman 2006).

Exotic grass species have been shown to strongly compete with native prairie grasses especially at the seedling stage where they are capable of faster growth rates compared to native grass species (McKenna et al. 1991, Potvin 1993). A greenhouse study by Coyne and Bradford (1985a) found that seedlings of two OWBGs ('Yellow' bluestem *B. ischaemum* and 'caucasian' bluestem *B. bladhii*) produced more tillers, leaves per tiller, and greater biomass compared to native prairie grasses (*Andropogon spp.* and *Panicum spp.*). One study found that the presence of the species *B. ischaemum* on any habitat type (types are related to previous grazing or burning history, woody cover, slope, or absence/presence of roads) results in decreased native species richness and diversity (Gabbard and Fowler 2007).

Management

Management techniques related to chemical, mechanical, grazing, and prescribed fire treatments have been studied to determine possible management applications that will reduce invasive C4 grass dominance and allow for increased establishment of native grass species. The majority of studies focus primarily on King Ranch Bluestem (*B. ischaemum var. songarica*) since this variety was intentionally hybridized and created for its high biomass production. *B. ischaemum* has the largest distribution across the state of Texas (Shaw 2011) and much of the Southern Great Plains compared to other invasive OWBGs (Wilsey and Polley 2003, USDA 2014). Additionally, other OWBG species such as, *Dichanthium sericeum* (silky bluestem) and *Dichanthium annulatum*

(Kleberg's bluestem), are invading southern Texas, the coastal prairie, Louisiana, and have become a species of concern in Arizona (Felger et al. 2005, USDA 2014).

Herbicide application

Mittelhauser et al. (2011) found that, regardless of rigorous site preparation techniques and application of the pre-emergent herbicide, imazapic, and a general herbicide, glyphosphate, there was no significant effect of herbicide on the establishment of two OWBGs (*D. sericeum* and *B. ischaemum*). Another study by Harmoney et al. (2009) found that five of the nine herbicides evaluated were capable of reducing biomass or tiller production of OWBGs for the first year after a single herbicide application. However, this was a short-term study that did not examine the potential negative effects of herbicide application on the surrounding native grasses or the likelihood of OBWG dominance rapidly reestablishing in the surrounding plant community (Harmoney et al 2009).

Mechanical treatment application

There are several mechanical techniques available when attempting to control invasive grass species ranging from: hand-pulling, disc harrowing, mowing, tilling, and chaining (DiTomaso 2009). Successful mowing applications are often based on correct timing, since poorly selected mowing times have been shown to increase seed production and dispersal (Venner 2006). In relation to controlling exotic grasses, mowing is a widely studied mechanical control technique since it is relatively less expensive than herbicide application and can be applied to dense infestations or along invaded roadsides. A significant financial expense is incurred by continuous mowing of

OWBG dominated roadsides for aesthetic purposes and roadside safety (Venner 2006); consequently, exploring the effectiveness of mowing applications is of interest from an economic standpoint. Simmons et al. (2007) found that a single and double application of mowing during the early and late growing season of OWBGs had a neutral effect on the frequency of *B. ischaemum*, suggesting that mowing is ineffective at reducing *B. ischaemum* (the dominate invasive grass on the two sites observed).

Prescribed fire

Studies documenting the effectiveness of prescribed fire on OWBGs have been contradictory in regards to the optimal timing, intensity, and interval of prescribed fire application necessary to decrease OWBG abundance. Most studies tend to suggest that winter burn applications of prescribed fire increases KR bluestem (*B. ischaemum*) production while summer prescribed fires decrease or have a neutral effect on the species. A study by Simmons et al. (2007) found that application of early and late growing season prescribed fire had a neutral effect on two OWBGs, silky bluestem (*D. sericeum*) and Kleberg's bluestem [*Dichanthium annulatum* (Forssk.) Stapf], however this may be due to small sample size. Unlike these two species, percent foliar cover of *B. ischaemum* was significantly reduced by early and late growing-season prescribed fire, suggesting growing season prescribed fire as a potential control technique (Simmons et al. 2007). A dormant season prescribed fire study by Pase (1971) found that *B. ischaemum* production increased by 16% by the end of the first post-burn growing season and was found to be significantly more abundant and more robust (greater number of tillers and height of seed stalks increased) when compared to unburned

controls. Twidwell et al. (2012) found no significant increases in *B. ischaemum* production after extreme prescribed summer fire applications. Gabbard and Fowler (2007) suggest that *B. ischaemum* is highly tolerant of dormant season prescribed fire since it was found to occur on both unburned and repeatedly winter burned sites. Few studies have evaluated whether all OWBG species respond the same to fire or if there are species level differences in response.

Grazing

Most studies related to grazing applications on OWBGs are focused on optimal grazing timing and strategies to increase or maintain production and forage quality of the grasses (McCoy et al. 1992, Hodges and Bidwell 1993, Dalrymple 2001, Philipp et al. 2005). Studies attempting to quantify differences in production, percent cover, or frequency of OWBGs in grazed versus ungrazed plots are lacking. It has been proposed that *B. ischaemum* has decent palatability and is a preferred species for steers grazing among other native and non-native species (Dwyer et al. 1964, McCoy et al. 1992). If non-native species are preferentially selected over native species, then there is potential for ungulate grazers to decrease non-native species densities and allow for competitive release of the suppressed native species. Ungulate grazing also allows for manipulation of plant communities that can't be offered by broad aerial applications of herbicide or large scale applications of mechanical treatments.

A greater understanding of the ecology of both the native and invading grass species can provide deeper insights into potential selective management techniques. Unfortunately, there is little information that directly compares the response of native

grasses and invasive OWBGs to various management treatments. Most studies documenting the effectiveness of management techniques often focus on a single variety of OWBG (*B. ischaemum*) and rarely capture the effects on less abundant invasive OWBGs such as *D. sericeum* or *D. annulatum*. The majority of OWBG studies compare independent treatment events or repeated applications of the same treatment, but few studies concurrently examine the interactive effects of treatments, specifically prescribed fire and grazing. Studies have shown that prescription grazing has the potential to put selective pressure on the non-native species (Frost and Launchbaugh 2003) and growing season prescribed fire may reduce cover of at least one variety of OWBG. This justifies a study that further investigates the interactive effects of both prescribed fire in combination with grazing as a potential OWBG management technique.

In our study region, coastal tallgrass prairie, the native C4 community has been invaded by exotic C4 species with similar functional traits. This may alter the potential effectiveness of prescribed fire as an invasive species management tool since it may be more difficult to selectively target the non-native species at a time when they are more vulnerable to fire than the native species. The coastal tallgrass prairie is highly fertile and productive allowing for a higher grazing capacity. Various grazing regimes (altered frequency, timing, and intensity) have the potential to shift plant communities. Consequently, it is important to also understand the influence of grazing post fire disturbance on these C4 grass communities. Given the complexity of plant responses to variable treatments, a more complete understanding of the effects of seasonal (winter vs.

summer) prescribed fire and grazing is necessary in order to identify potential management techniques.

This study assesses the response of invasive OWBGs to different seasonal fire applications followed by ungulate grazing. It explores the effectiveness of both winter and summer prescribed fire on reducing the abundance of *Dichanthium sericeum* and *Bothriochloa ischaemum* in an infested coastal prairie. The study evaluates the effects of treatments on plant community composition over a six month period and identifies fire seasons (winter or summer) that are beneficial or harmful in altering herbaceous community composition and woody shrub density. Multiple species of OWBGs are highly fire tolerant as shown by their accelerated rate of production following fire (Grace et al. 2000, Towne et al. 2005). In addition, native C4 grasses from the coastal tallgrass prairie evolved with fire and typically respond positively to fire application in the dormant season (Hansmire et al. 1988, Grace 1998), though other studies have shown that plant responses to fire are species specific (Mayeux Jr and Hamilton 1988, Howe 1994). I predict both the invasive and native grasses will respond positively to the dormant season prescribed fire. This is because fire is less likely to damage grasses and nutrient reserves during the dormant season and more likely to disrupt grass growth during the growing season (Daubenmire 1968, Howe 1994). While both native and non-native C4 grasses may respond positively to fire, the rapid growth rate of the non-native species may give them a competitive advantage over the native species. The native and invasive grasses may have distinct responses to grazing treatments since cattle are likely to exhibit selective preference for more palatable grass species (Ganskopp et al. 1997).

D. sericeum has high forage quality and is often the preferred forage type in its native region of Australia (Jacobsen 1981); therefore, I would expect *D. sericeum* to be selectively targeted by grazers.

Methods

Study site

Research was conducted on the Rob and Bessie Welder Wildlife Foundation, in San Patricio County, Texas, approximately 13 km northeast of Sinton, on U.S. Highway 77. The study site is located on a 450 acre pasture, locally known as Coyote pasture. The herbaceous community is dominated by a native C3 and non-native C4 grass species: Texas winter grass [*Nassella leucotricha* (Trin. & Rupr.) Pohl] and silky bluestem [*Dichanthium sericeum* (R. Br.) A. Camus] respectively. Coyote pasture has been subjected to a constant rate of stocking prior to the initiation of this study. Co-dominant grass species include *Panicum obtusum* [(Kunth)], *Bouteloua dactyloides* [(Nutt.) J.T. Columbus], *Aristida diffusa* [(Trin)], *Bothriochloa ischaemum* [(L.) Keng], *Panicum halli* [(Vasey)], and other species of *Setaria* sp., *Andropogon* sp., *Eragrostis* sp., and *Sporobolus* sp. The site also consists of a variety of woody shrub and forb species. The dominant woody species are mainly spinescent, re-sprouting, leguminous shrubs such as, honey mesquite [*Prosopis glandulosa* Torr.], twisted acacia [*Acacia farnesiana* (L.) Willd], spiny hackberry [*Celtis ehrenbergiana* (Klotzsch) Liebm.], lime prickly ash [*Zanthoxylum fagara* (L.) Sarg] and agarita [*Mahonia trifoliolata* (Moric.) Fedde]. Shrubs make up less than 20% of the estimated foliar cover. Further details on the shrub component will be introduced in Chapter 2. Additionally, there is a minor forb

component that makes up less than 10% of the percent foliar cover. Dominant forb species vary by season but generally consist of various euphorbs, legumes and forbs from the genera *Croton* sp. *Cirsium* sp., *Solanum* sp, *Oxalis* sp., and *Lesquerella* sp.

Soils within the study site are characterized as Victoria clay soils. The mollic epipedon is a clay and below the clay is a very indurate duripan. Dry weather conditions from July to September result in decreased soil moisture; as a result, fissures in the soil surface ranging from 10 to 76mm in width occur throughout the dry season. Soils are mostly level with gentle slopes from 0 to 3 percent (National Cooperative Soil Survey). Victoria soils are characteristically deep, well drained soils that are calcareous throughout the horizons (except the A horizon). Most areas are used for forage production for livestock grazing.

Average yearly summer temperature is approximately 30°C with a yearly rainfall total of 74 cm (Guckian and Garcia 1979). Yearly rainfall totals were slightly below average for the 2013 and 2014 sampling year (Fig. 2.1).

Figure 2. 1 Average precipitation rate and monthly precipitation for 2013 and 2014 at the Welder Wildlife Refuge. Data are from the National Oceanic and Atmospheric Administration (NOAA).

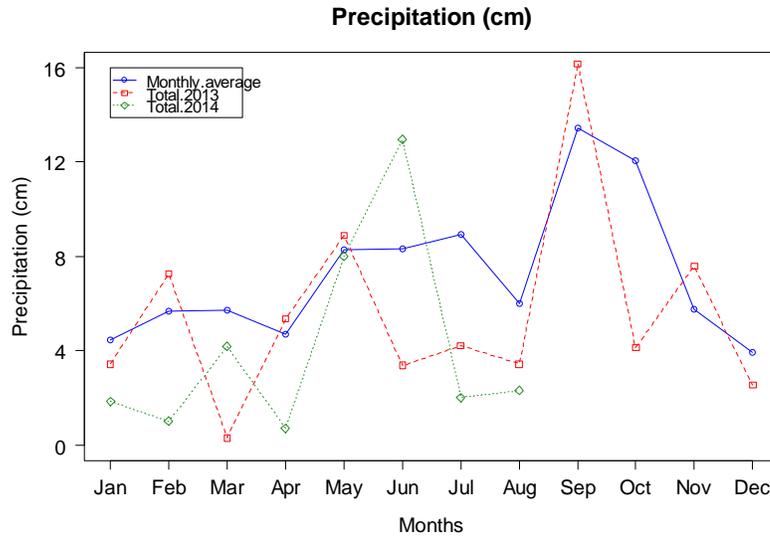
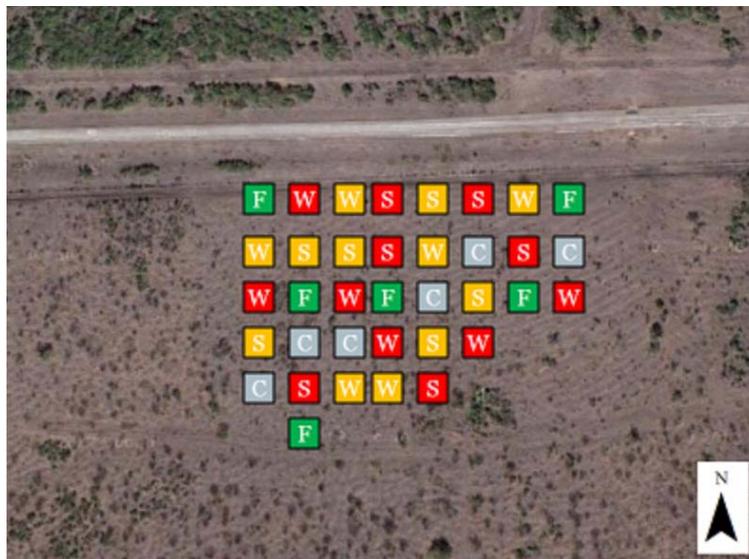


Figure 2. 2 Aerial view of plot locations within the pasture. Plot spacing is approximately 8-10 meters. Each color and letter combination represents a different treatment type within the plots (six treatments with six replications each). Letters identify burn or fence treatment types: Summer (S), Winter (W), Fenced-no burn (F), Control unfenced-no burn (C).



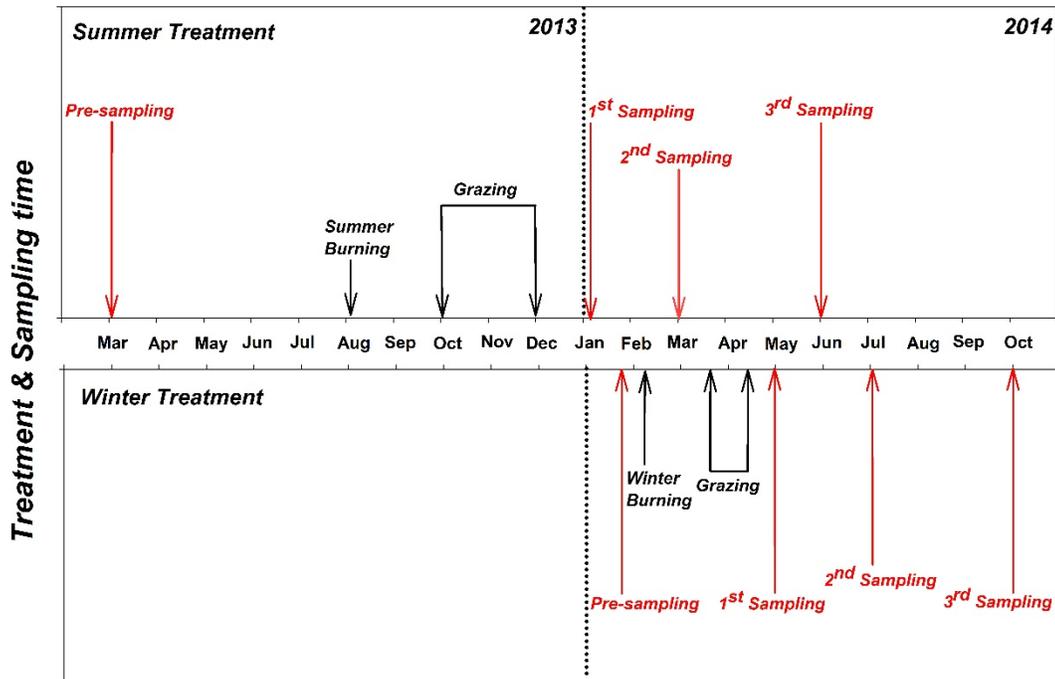
Experimental design

I established thirty-six 10 x 10m plots located on the cattle allotment to measure seasonal prescribed fire and grazing influences on woody shrubs and herbaceous community. Treatments consisted of two grazing treatments (grazed/ungrazed) and three fire treatments (summer, winter, and no fire) in a full factorial design. The six treatment combinations are winter (dormant season) burn only, summer (growing season) burn only, winter burn and fence, summer burn and fence, fence only (no burn), and an unfenced unburned control. I randomly assigned six treatments to six plots for a total of 36 plots (Fig. 2.2). In total, there are 720 meters of four-strand barbed-wire fencing that surrounds 18 study plots (6 fenced and winter burned, 6 fenced only, 6 fenced and summer burn). The other unfenced control and burn only plots are demarcated by four steel T-posts at each corner of the study plots, but otherwise do not inhibit access to grazing cattle. Plots are spaced approximately 10m apart in order to allow adequate space for mowing and disc harrowing equipment to create fire breaks.

Data collection and treatment application

Within each plot I collected plant community data, to assess whole plot vegetation cover to species. Aerial cover of each species was estimated using 5% cover classes. Each plot was partitioned into four 5 x 5m quadrats in order to fully sample the entire plot. Species cover was averaged by plot. Visual estimations of percent bare ground and litter cover were recorded. Plant community cover data were collected prior to initiating treatments in April 2013 for the summer fire treatment and January 2014 for the winter fire treatment group. During August 2013, I implemented pre-assigned independent early-season summer prescribed burns in 12 of the 36 plots. For the winter fires, pre-assigned independent prescribed fires were set in 12 plots during February 2014. The remaining 12 plots served as unburned controls that could be used to compare both summer and winter fire treatments. Post-treatment data was collected at one, three, and six month intervals following the completion of both the prescribed fire and grazing treatments (Fig. 2.3) using the same data collection methods described above to identify changes in invasive grass abundance and herbaceous community diversity. Dates of post-treatment data collection for the summer fire and grazing treatments are January, March, and June 2014 (Fig. 2.3). Dates of data collection for the winter fire and grazing treatment are May, July, and October 2014 (Fig. 2.3).

Figure 2. 3 Timeline of treatment implementation and data collection. Each red arrow indicates a sampling time and each black arrow represents a fire or grazing treatment. All sampling times related to the summer fire or grazing treatments are at the top of the figure and all sampling times related to winter fire or grazing treatments are at the bottom.



Prescribed fire

Summer (growing season) prescribed fires were applied in mid-August 2013. Individual ring fires were set starting at the northwest corner of each summer burn plot based on the prevailing winds. Fires were set in the morning to avoid high ambient temperatures. Wind speeds during the burns ranged from 5 to 11 mph, average relative humidity was 56%, and average temperature was 94F. Timing of complete combustion of individual plots averaged two minutes. I assessed the maximum temperature of each individual fire by averaging three randomly placed temperature indicating tiles within

each plot. Temperature tiles were created by applying a coat of temperature indicating lacquer OMEGALAQ® at nine different degrees (79°C, 135°C, 177°C, 204°C, 246°C, 302°C, 343°C, 299°C, and 427°C) onto ceramic tiles. Tiles were evaluated immediately following the fire.

Winter prescribed fires applied in early February 2014 followed the same burning protocol. Standing dead biomass in the winter plots was significantly lower than the summer, since plots only received a four month rest period from grazing prior to igniting the fires. For this reason, fuel loads were artificially homogenized in order to achieve complete and consistent combustion. I applied approximately 6.8 kg, or ½ square bales, of cured coastal Bermuda grass to each winter burn plot in order to effectively normalize the fuels. Temperature tiles were randomly placed throughout the winter burn plots.

Winter fires were also set in the morning and had slightly lower wind speeds and relative humidity compared to summer fires. Wind speeds ranged from 2 to 9 mph, relative humidity was 45% on average, ambient temperature was 70°F, and time until complete combustion of individual plots averaged 2.5 minutes. I compared winter burn and summer burn maximum temperatures in order to determine differences in fire temperature due to altered fuel loads and varied weather conditions.

Prior to initiating burns, I visually estimated percent cover of cured herbaceous fuel and depth of cured fuel at two random 1x1m quadrat locations within each burn plot. Within the quadrats, fine and coarse woody fuel were assessed for each fuel class (1hour: up to ¼”, 10 hour: ¼ to 1”, 100 hour: 1-3”, and 1000 hour:3-8”) to determine

the fuel load (Fosberg and Schroeder 1971). I averaged dead herbaceous cover, height, and biomass to calculate fuel load using the following equation:

$$\text{Fuel load (kg/m}^3\text{)} = \text{Height (m)} * \text{Percent cover (\%)} * \text{Dry biomass (kg/m}^3\text{)}$$

Grazing rotation

Available vegetation within the pasture determined the timing and duration of the grazing rotations. Since grazing duration is affected by available palatable forage for cattle, I expected the grazing rotation following the winter burn to be significantly shorter than the grazing rotation following the summer burn. I assessed differences between the two distinct seasonal grazing rotations by comparing percent utilization from the dry biomass of each summer and winter burn plot to ensure that the cattle were evenly applying a grazing treatment. Actual stocking density was determined by the land manager in order to adhere to realistic land management decisions. I assessed total animal units and available forage to ensure that stocking rates were sustainable during the duration of the study.

Percent utilization

The study site occupies approximately 3 acres of a 450 acre pasture. In order to determine if the cattle truly grazed the study site during the grazing rotation, I created two utilization cages per 'unfenced' plot. Utilization cages were constructed from 10 cm galvanized steel fencing to a height of 1.2m with the top covered in a single layer of chicken wire to prevent grazing and minimize microsite effects. Two utilization cages were randomly placed in each plot for the duration of the grazing rotation and each cage surrounded a 0.5m² quadrat. Cages were placed in areas that avoided shrub clusters or

woody brush, since the intent was to measure herbaceous biomass utilization. A total of four quadrats (two caged and two uncaged) were destructively harvested for herbaceous biomass at the end of each grazing rotation (one following each burn season).

Herbaceous material was dried at 79° C for 48 or 72 hours dependent upon the time required for the dry weight measurement of the clippings to equilibrate. Percent utilization per plot was calculated as the difference between total caged and uncaged dry biomass weights divided by the total caged weight. Statistical comparisons of burned and unburned utilization samples were compared using a Student's t-test; p-values less than 0.05 were considered statistically significant.

Equation for percent utilization:

$$\left[\frac{\text{Protected quadrat weight (g)} - \text{Unprotected quadrat weight (g)}}{\text{Protected quadrat weight (g)}} \right] * 100$$

Species diversity and richness

This experiment is also designed to assess shifts in community composition due to treatment effects. I used the Shannon-Wiener index to assess herbaceous species diversity after burning and grazing treatments. Percent cover estimates for each species were used to calculate richness and diversity indices across treatments. P_i , the cover of species 'i' divided by the total cover of all herbaceous grass species in the plots, was calculated for each species in each plot. I then calculated Shannon's diversity index, $(H) = -\sum P_i(\ln P_i)$ (Preston 1948). I used analysis of variance to determine if species diversity indices were significantly different between treatments. This analysis was completed for grass species and perennial and annual forb species separately, in order to determine if differences in diversity occurred within these particular functional groups

following grazing and fire treatments. Estimations of species richness were averaged for all plots and compared between treatment types using analysis of variance. Species richness and diversity analyses were completed on the most recent post-treatment data collection July 2014 for summer burn treatments and June 2014 for the winter burn treatments. No comparisons were made between preliminary and post-treatment data since the experiment has adequate controls (unburned-grazed and unburned-ungrazed treatments).

Statistical analysis of focal species

Since data from each summer and winter burn treatment were collected at multiple time intervals and the points of data collected are not independent, I used repeated measures ANOVA to analyze the data sets. Data for the response variables (herbaceous species and bare ground cover) were summarized as estimates of the means for each plot, which were then used to estimate the least square means and variance for each of the six treatment types. I analyzed the following herbaceous species separately: *N. leucotricha*, *D. sericeum*, and *B. ischaemum*. I also estimated mean response of total grass, total C4 grass, total C3 grass, native C4 grass, and bare ground cover. *N. leucotricha* is the only C3 grass species in the study site; therefore, C3 and C4 grass comparisons will be made between *N. leucotricha* and C4 grass cover analyses. Repeated measures ANOVA, with time of data collection as the repeated measure, was used to evaluate time and treatment effects of fire and grazing. I used a probability level of 0.05 to determine significant differences. If there were no significant interactions between fire and grazing treatments then I only examined the main effects of fire and

grazing on species cover. I tested analysis of variance assumptions of normality and homoscedasticity using normal quantile plots and Levene's or Bartlett's test (depending on the distribution). Species cover data that did not satisfy the assumptions were log transformed. *B. ischaemum* was typically less than 5% of the plot cover, so I log transformed all *B. ischaemum* data, however the dataset still displayed unequal variances and non-normal distribution. For this reason, conclusions from *B. ischaemum* data analyses may not be reliable. All analyses were completed using R version 3.1.1 (The R Foundation for Statistical Computing 2014).

Fire frequency model

In order to estimate the effects of repeated fires on native and herbaceous community abundance I created a fire frequency model based on herbaceous data collected one month following both summer and winter fire and grazing treatments. This model could be integrated with a similarly designed shrub community model to estimate the effects of fire frequency and grazing on total community composition. The conceptual model for identifying native and invasive grass abundance consists of four state variables. Two state variables represent stages of native grass abundance and two represent stages of invasive grass abundance. The description of each material transfer and state variable is the same for invasive and native grasses (descriptions of each state variable and material transfer is provided in APPENDIX A.1). The model is based on multiple assumptions of herbivory and growth. I assume additional nutrient inputs from cattle manure will be insignificant in altering monthly aboveground biomass (although I recognize that significant inputs can increase above and belowground plant biomass). I

recognize that un-even fuel load distributions across the pasture can affect grazing patterns and fire spread, however I assume homogenized fuel loads to simplify the model.

The model (APPENDIX A.1) is quantitatively represented through rates and difference equations ($\Delta t = 1$ month) (Grant and Swannack 2008). The amount of senesced biomass accumulated in the pasture determines fire fuel loads. The season of fire influences the rate of growth during the growing season months on each “live grass abundance” state variable. All “dead fuel” is either consumed or is removed from the system (determined by a monthly constant of decay). As recommended by Grant and Swannack (2008), the model is first evaluated against a baseline (reference model with no treatments), then the frequent fire component is included, followed by the grazing treatment. All model components (conceptual and quantitative) were created using Stella II (vs. 7.0.3).

Results

In the following analyses, the focal datasets (summer burned vs winter burned treatments) were collected at different time intervals within the 2013 to 2014 calendar years. Each dataset was collected at one, three and six month intervals after completion of the grazing rotation following both the summer and winter prescribed fires. For this reason, the summer burn dataset is complete (fully sampled to the sixth month) while the winter burn dataset is lacking one sample period (the six month data collection). Therefore, winter burn datasets were analyzed using the available pre-treatment and

post-treatment (one and three month) data collections. The six month winter burn dataset will be collected in October 2014 and subsequently analyzed.

Fire treatment

Temperature tile analyses indicate that summer fire temperatures ranged from 79 to 246°C and winter fire temperatures ranged from 79 to 135°C. Lower temperature in the winter fires was likely attributed to differences in weather conditions at the time of ignition. Average fuel loads calculated for the summer fires were 7.44 kg per plot, approximately 2976 kg per acre. Fuel loads calculated for the winter fires included the available fuel plus the hay addition (6.8 kg of cured grass per plot) and averaged 3100 kg per acre. Summer and winter fuel loads were within the typical range of North American grassland fuel loads (Grace et al. 2005) and were considered moderate to heavy for a coastal tallgrass prairie with light shrub cover.

Grazing treatment

Percent herbaceous utilization did not significantly differ between burned (61%) and unburned (64%) plots following the summer fire treatments. However, herbaceous utilization did significantly differ between burned (37%) and unburned (67%) plots following the winter fire treatments (p -value < 0.05). This is surprising considering C3 grass production increased following the winter burns at a time when all C4 grasses were dormant, therefore it would have provided additional available green forage during the grazing rotation. Since the dominant C3 grass was *Nassella leucotricha*, a grass with lower palatability and quality compared to the adjacent vegetation, the cattle may have avoided the winter burned plots and selectively grazed the unburned areas. It has also

been suggested that winter fire in these regions stimulates forb growth and diversity (Hansmire et al. 1988), so an increase in forb production immediately following the fires may have deterred grazers. Winter fires stimulated forb production but the dominant forbs following the winter fires were *Croton spp.* and *Solanum triquetrum*, two highly unpalatable forbs that are seldom grazed by livestock (USDA 2014). Cattle likely decreased forage utilization in winter burn plots for this reason.

Species diversity and richness

Grass species and forb species diversity were calculated separately. There were no significant interactions from grazing and burning treatments on species diversity, therefore all species diversity results are based on main effects. Grass species diversity was significantly lower in unburned plots compared to summer burned plots (Table 2.1). Grazing plots following summer fire application had no significant effect on grass species diversity. Winter burning had no significant effects, however grazing during the winter season increased grass species diversity ($p < 0.05$). Grass species richness was not significantly influenced by any of the burn or grazing treatments (Table 2.2) although the winter burns had slightly greater richness compared to unburned plots ($p = 0.06$).

Forb species diversity was not affected by the summer burn or grazing treatments (Table 2.1). Forb diversity was higher following the winter burn treatments but not significantly (Table 2.1). Grazing following the winter burns did significantly increase the forb diversity index from 0.53 to 0.81 ($p\text{-value} < 0.01$). In general, forb species diversity was lower than grass species diversity on the study site.

Table 2. 1 Species diversity of grasses and forbs for summer burned and winter burned plots. Analyses for winter burned plots are on 3 month post treatment (July 2014) data and summer burned plots are 6 month post-treatment (June 2014) data.

<i>Grass species only</i>	Shannon diversity index (H')	
Summer burned	1.52	*
Unburned	1.25	*
Grazed	1.44	ns
Ungrazed	1.32	ns
Winter burned	1.73	ns
Unburned	1.59	ns
Grazed	1.73	*
Ungrazed	1.55	*
<i>Forb species only</i>		
Summer burned	0.86	ns
Unburned	0.81	ns
Grazed	0.82	ns
Ungrazed	0.85	ns
Winter burned	0.72	ns
Unburned	0.62	ns
Grazed	0.81	**
Ungrazed	0.53	**

* significant at 0.05

** significant at 0.01

Table 2. 2 Grass species richness following summer and winter burning and grazing treatments.

<i>Grass species only</i>	Species richness	p-value
Summer burned	0.87	0.71
Unburned	0.90	
Grazed	0.91	
Ungrazed	0.86	
Winter burned	1.05	0.06
Unburned	0.97	
Grazed	1.01	
Ungrazed	1.01	

Focal species response

I analyzed winter burn and summer burn data separately and compared each to their respective ungrazed-unburned and grazed-unburned controls. Time was evaluated as the repeated measure to ensure that the timing of data collection was accounted for in the analysis. I evaluated the total grass species (dominant and co-dominant combined) and separately analyzed the dominant C3 native and two C4 non-native grass species: *Nassella leucotricha*, *Dichanthium sericeum* and *Bothriochloa ischaemum* respectively. In this study region, *B. ischaemum* is not the dominant invader nor is it a dominant species, however I chose to analyze it separately from the other grass species to compare the response to the dominant OWBG and invader in this region, *D. sericeum*. I used least square means of the percent cover for each treatment type and plotted the data against the time of data collection.

Total grass cover was significantly reduced by the summer fire and grazing treatments (Fig. 2.3, Table 2.3). Summer burning significantly reduced *N. leucotricha* while grazing did not significantly influence the cover. The grazing treatment reduced *D. sericeum* cover while the ungrazed plots exhibited significantly higher *D. sericeum* cover compared to the controls (Fig. 2.4). *B. ischaemum* cover responded positively to summer burning and grazing. Summer fire treatments had significantly higher total forb production compared to the unburned controls. The summer grazing rotation did not alter forb production. Bare ground cover increased by 11% in the grazing treatments and 20% following the summer burn treatments.

Table 2. 3 Analysis of variance of multiple cover types

Cover type	Treatment	Summer burned				Winter burned			
		MSE	F ratio	P-value		MSE	F ratio	P-value	
Total grass	Fire	2981.51	39.16	0.001	*	0.19	85.33	0.001	*
	Graze	1406.89	18.47	0.001	*	0.05	23.76	0.001	*
	Time of collection	2188.13	28.74	0.001	*	0.09	41.76	0.001	*
<i>Nassella leucotricha</i> C3 only	Fire	2457.18	6.57	0.01	*	660.1	1.88	0.18	
	Graze	41.02	0.101	0.74		25.1	0.07	0.79	
	Time of collection	1829	4.89	0.003	*	5092.3	14.5	0.001	*
<i>Dichanthium sericeum</i>	Fire	14.26	0.05	0.83		356.67	1.28	0.26	
	Graze	2085.77	6.79	0.01	*	1565.7	5.63	0.02	*
	Time of collection	39.85	0.13	0.94		1922.55	6.91	0.001	*
Total C4 grass species	Fire	25.27	0.07	0.79		1735.61	5.29	0.02	*
	Graze	1928.29	5.07	0.03	*	1544.81	4.71	0.03	*
	Time of collection	1398.27	3.67	0.02	*	8375.4	25.54	0.001	*
Native C4 grass species only	Fire	1.56	0.01	0.92		518.69	3.46	0.07	
	Graze	3.1	0.02	0.89		0.07	0.001	0.98	
	Time of collection	1267.43	8.41	0.001	*	2545.52	16.99	0.001	*
Total forb	Fire	118.15	0.13	0.02	*	0.843	15.7	0.001	*
	Graze	30.94	5.26	0.24		0.477	8.88	0.004	*
	Time of collection	396.92	1.38	0.001	*	0.317	5.91	0.004	*
Bare ground	Fire	2035.04	77.72	0.001	*	6.23	113.86	0.001	*
	Graze	805.04	30.74	0.001	*	1.5	27.42	0.001	*
	Time of collection	474.44	18.11	0.001	*	0.25	4.53	0.014	*
<i>Bothriochloa ischaemum</i>	Fire	1.04	5.49	0.02	*	0.54	5.61	0.02	*
	Graze	0.37	1.97	0.16		0.08	0.87	0.35	
	Fire*Graze*Time	0.45	2.41	0.07		0.38	3.93	0.024	*
	Time of collection	0.54	2.91	0.03		0.46	0.23	0.09	

*p-values <0.05

Figure 2.4 Herbaceous species percent cover following summer burn and grazing treatments. Points are least-square means of each treatment type. Only main effects are displayed because interactions are insignificant. Grass species are represented by a four letter code: DISE= *D. sericeum* and NALE= *N. leucotricha*.

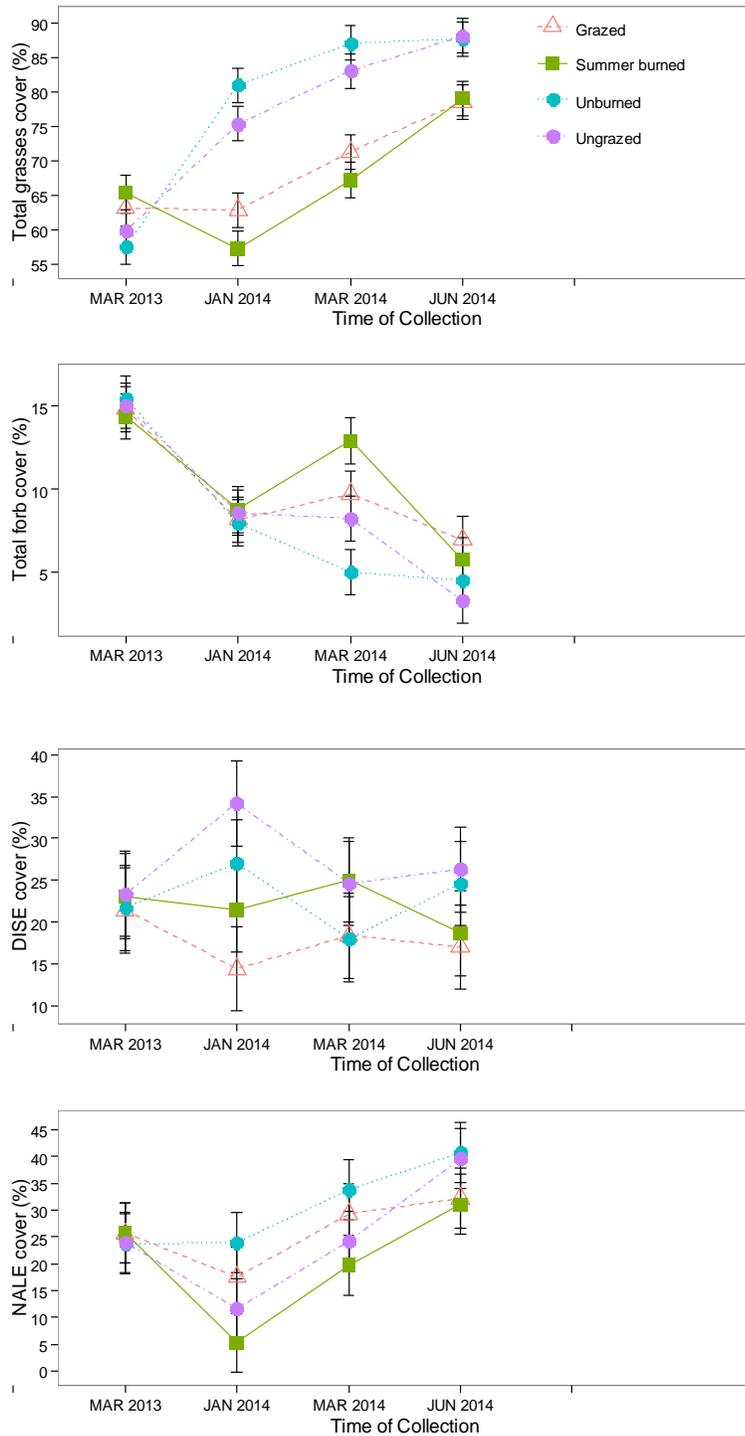


Figure 2. 5 Herbaceous species percent cover following winter burn and grazing treatments. Points are least-square means of each treatment type. Only main effects are displayed because interactions are insignificant. Vertical lines are one standard error.

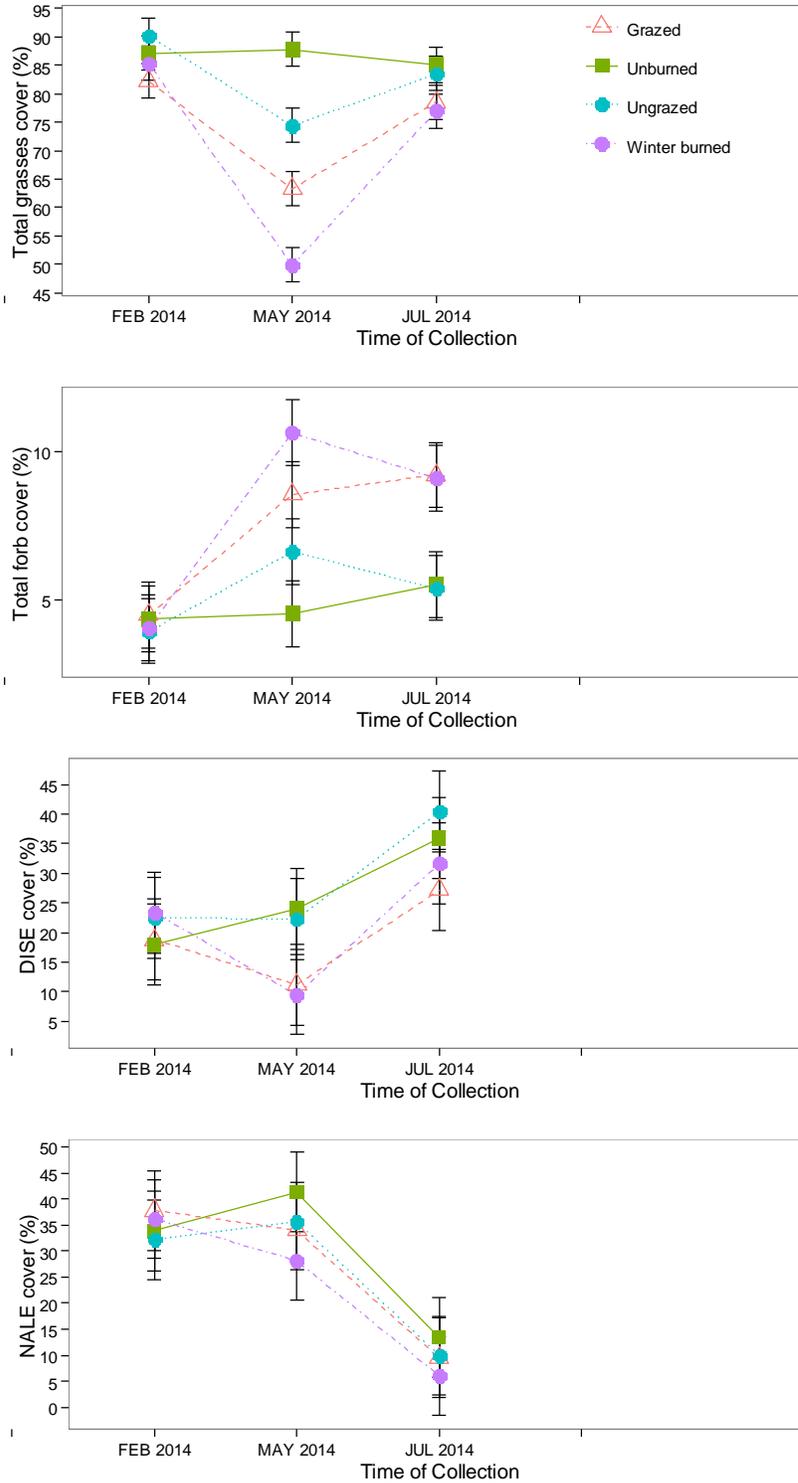
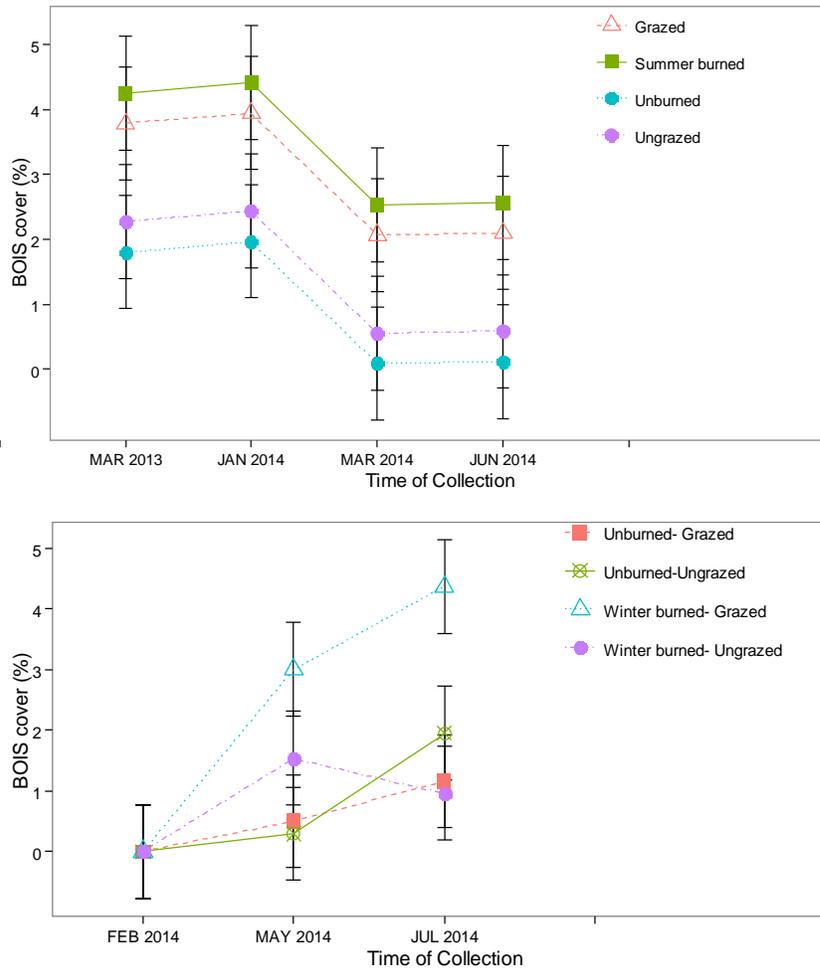


Figure 2. 6 *Bothriochloa ischaemum* (BOIS % cover) response to summer and winter burn and grazing treatments. Points are least-square means of each treatment type. Significant interactions are displayed for the winter burn treatment dataset. Main effects are displayed for the summer burn dataset.



Winter burning and grazing treatments significantly decreased total grass cover but stimulated forb production and increased total forb cover (Fig. 2.5). The dominant invasive grass *D. sericeum* was significantly reduced by grazing during the dormant season however winter burning did not have a strong negative effect on cover. There was

a significant interaction between winter burning and grazing treatments on *B. ischaemum* cover. *B. ischaemum* significantly increased following winter burned and grazed treatments (Fig. 2.6), but this could be attributed to the non-normal distribution and small sample size. Bare ground cover was also significantly increased by both grazing and dormant season fire application.

Total C4 grasses were significantly influenced by the grazing and winter burn treatments but did not respond to summer burn treatments (Table 2.3). Winter burned and grazed treatments had lower percent cover compared to the unburned and ungrazed treatments. C3 grasses were not affected by the winter burn and grazing treatments. C4 grasses responded negatively to winter burns and graze treatments while C3 grasses only responded negatively to the summer burn treatments (Table 2.3).

D. sericeum and *B. ischaemum* were removed from the total C4 grass cover to identify differences in native C4 grass abundance and non-native (*D. sericeum*) C4 grass abundance following fire and grazing treatments. Native C4 grasses were not significantly influenced by any of the fire or grazing treatments (Table 2.3) while grazing treatments significantly influenced the dominant non-native species.

In general, total grass, forb, *D. sericeum* and *N. leucotricha* cover responded similarly to the summer and winter burn treatments (Table 2.4). The only cover types that responded distinctly to summer versus winter fire and grazing treatments were *N. leucotricha* and total forb cover. Total forb cover significantly increased following the winter grazing rotation but summer grazing had a neutral effect on forb production. *N. leucotricha* responded negatively to summer burning however winter burning had a

neutral effect. Notably, the dominant invader, *D. sericeum*, responded neutrally to summer and winter prescribed fire treatments, but was significantly reduced by subsequent grazing treatments.

Table 2. 4 Response of cover types to summer vs winter burning and grazing treatments.

Cover type	Summer		Winter	
	Burning	Grazing	Burning	Grazing
Total grass	decrease	decrease	decrease	decrease
Total forb	increase	neutral	increase	increase
<i>N. leucotricha</i>	decrease	neutral	neutral	neutral
<i>D. sericeum</i>	neutral	decrease	neutral	decrease

Fire frequency model

The model was evaluated by comparing it to a baseline model (no treatment effects) over a 120 month period with the initial biomass at the beginning of each growing season (month=2) equal to biomass in the final month of the previous growing season (month=9). The baseline simulation is similar to observed data from the un-burned/grazed treatment (control treatment of the experiment). The cattle could graze during peak biomass months but then must be removed during the dormant season (this is to be expected since there is no longer any accumulation of live green biomass during the dormant season). This simulation assumes all grasses respond similarly and there is no summer or winter prescribed fire application.

The next simulation incorporated the effect of seasonal prescribed frequent fire on the increase in invasive and native biomass abundance. I found that both repeated winter and summer fires are able to reduce invasive grass abundance below 80% of its original biomass. The simulation shows that summer fire is capable of reducing invasive biomass after month 18 (two fire treatments) and winter fire was able to decrease invasive grass abundance after month 24 (two fire treatments).

Finally, I simulated the sustainable grazing (cattle were “removed” from the simulation if forage levels were too low to maintain livestock grazing) treatment. In this instance, grazing following both summer and winter fire was capable of greatly reducing invasive grass biomass (<80% of its original biomass) after month 8 and month 9 respectively. Winter fire has a more neutral (slightly less negative) effect on growth rate compared to the summer fire application; however, both are feasible options for invasive grass removal.

Discussion

Native C4 grasses responded neutrally to all treatment types. *D. sericeum* significantly decreased in cover following grazing treatments but not fire treatments. Results from this study suggest that grazing treatments can effectively reduce *D. sericeum* abundance while maintaining the native C4 grass community. Seasonal fire and grazing had variable effects on total C3 and C4 grass cover. C4 grasses were affected by grazing treatments and winter fire treatments while C3 grasses were only affected by the summer fire treatments. Total C3 grasses were only represented by one grass, *N. leucotricha* a species known to exhibit variable growing seasons. Grass species

diversity significantly increased following the summer burn and grazing treatments and forb species diversity positively responded to grazing treatments. These findings suggest that fire and grazing could be useful tools in decreasing non-native grass abundance and shifting plant community composition towards more desirable grass species with greater forb diversity.

C3 vs C4 grass response

The prairie is mainly dominated by C4 grass species, which can be especially susceptible to fire during the growing season. During the summer burns, C4 grasses are undergoing a demanding growth stage where meristematic tissue is more exposed and soil water content is deficient, causing the plant to undergo additional water stress (Risser et al. 1981, Ewing and Engle 1988). For this reason, we would expect C4 grasses to respond negatively to summer fire. However, in this study, C4 grasses responded neutrally to summer burns but were significantly reduced by the grazing and winter burn treatments (Table 2.3) while C3 grasses responded negatively to the summer burn treatments (Fig. 2.4). The C4 grasses only responded negatively to winter burns immediately following the fires (one month post-treatment). C4 grass responses to winter burns during the growing season data collections (July-summer) showed no significant differences between burned (71 ± 5.6 % mean cover) and unburned (70 ± 5.6 % mean cover) treatments. The negative C3 grass response to summer burning was unexpected, since we would anticipate C3 grasses to be neutrally affected by a fire applied while the grass is dormant. Unlike other C3 grasses, *N. leucotricha* has a variable growing season that can occur throughout the year (Ansley and Castellano

2007). Therefore, *N. leucotricha* may not be a good indicator of typical C3 grass responses to fire and grazing.

C4 grasses responded negatively to grazing treatments while C3 grasses were not significantly altered. C4 grasses on the prairie are typically more palatable than the available C3 grass species (*N. leucotricha*) so they were likely selectively grazed. Additionally, *N. leucotricha* is tolerant of grazing and is known for its ability to increase in abundance as a response to herbivory (Anderson and Briske 1995). Therefore a combination of herbivore selectivity of C4 grasses and C3 grass tolerance to grazing likely drive C3 and C4 grass responses in this study.

Species diversity and richness

Fire can create newly exposed bare soils that allow ruderal or weedy disturbance-prone species to establish. This could potentially alter the competitive success of certain species leading to reduced abundance of subordinate species, and altered species diversity and richness (Abrams and Hulbert 1987, Collins 1987, Collins and Gibson 1990). Both fire and grazing are considered large scale disturbances (Collins and Barber 1986) that can influence species diversity. Responses of plant community species richness and diversity following fire application in grassland ecosystems are inconsistent. Many studies have observed varied results suggesting complex responses to fire. Blankespoor (1987) and Collins (1987) observed increases in species diversity following fire while Adams et al. (1982) found significantly reduced species richness as a result of fire in a tallgrass prairie. Another study suggests species richness is not influenced by fire (Abrams and Hulbert 1987). These variable responses are likely due to

differences in season of fire application, intensity, or land management history. Similar to the inconsistency of responses found in other studies, this study demonstrates that summer burning increases grass species diversity while winter burning has a neutral effect (Table 2.4).

Grazing could also alter species diversity since grazing animals can increase bare ground exposure, allowing for improved production or germination of ruderal species (Weaver 1968, Hartnett et al. 1996). Increases in grass diversity following grazing are not surprising, since it has often been observed that certain grasses can be tolerant of grazing while others are not; thus, herbivory from ungulate grazers can alter productivity and community composition in grasslands (Hobbs and Huenneke 1992). Although grass diversity increased, total grass cover was significantly reduced by summer burning. This reduction in cover may have allowed more diverse grass species to compete with the dominant grasses for light and nutrients, thereby increasing grass species diversity. Since our study site has similar land management history to the surrounding coastal tallgrass prairie, findings from this study are directly applicable to coastal tallgrass prairie management. Assessments of species diversity disparities as a result of seasonal fire and grazing interactions can allow land managers to gain a better understanding of the potential consequences of variable land management techniques in coastal tallgrass prairies invaded by OWBGs.

Forb diversity was not influenced by winter or summer fire, but was significantly increased by grazing. The stimulation in forb production following grazing could be attributed to the hoof impact of livestock on the soil, which exposes bare ground and can

increase ruderal forb establishment (Weaver 1968, Hartnett et al. 1996). Declines in total grass cover could also be attributed to preferential grazing of palatable grasses. The reduction in the dominant grass species leads to a simultaneous competitive release of suppressed forb or grass species (Weaver 1968), and allows for increased colonization and establishment of forbs. Previous studies have shown that grass yield is highest in response to late winter fire applications while forb yield is lowest (Hansmire et al. 1988). Winter fires were applied late in the season, February 2014, in accordance with the normal timing of prescribed burning in the Texas coastal prairie (Hansmire et al. 1988). In this region, fire is often applied in the early winter to stimulate forb yield for wildlife habitat and forage. Our study applied winter fire later in the season based on these assumptions related to increased grass production. Findings from our study suggest that forb cover significantly increased following both summer and winter fires while forb diversity was maintained.

Increased forb growth and establishment is an often sought after land management objective since forbs offer valuable wildlife forage and can improve habitat quality (Harper 2009). These overall increases in diversity following both fire seasons and grazing are an indication that summer and winter prescribed fire and grazing can have a positive effect on species diversity and are capable of affecting plant community composition. Prescribed grazing techniques could then be applied to decrease non-native grass cover while improving wildlife habitat or forage production (Holechek et al. 1982). This would be especially useful for land managers who have multiple objectives to improve wildlife forage and livestock production concomitantly.

Total grass response

Total grass cover significantly decreased in grazed and burned plots, regardless of season of fire and grazing application. Despite these general reductions in cover, grass species diversity increased significantly in summer burned and grazed plots and was maintained in winter burn plots. Reductions in total grass cover in the grazed plots and a subsequent increase in forb cover was expected since grasses are typically preferred by cattle over forbs. These disparities in forb and grass species abundances following herbivory are typical in tallgrass prairie systems that have been grazed by bison or cattle (Voigt and Weaver 1951, Dyksterhuis 1958).

Fire frequency

Studies have shown significant decreases in species richness and increases in non-native species establishment following frequent fire applications (Whisenant 1990, D'Antonio and Vitousek 1992). However, Smith and Knapp (1999) found frequent fire in tallgrass prairies maintains productivity and reduces invasibility. It has been suggested that a class of old world grass invaders are especially capable of benefiting from and enhancing fire frequency at the detriment of the surrounding native grasses (D'Antonio and Vitousek 1992, Simberloff and Von Holle 1999, Brooks et al. 2004). Additional empirical evidence and community models that evaluate the responses of plant populations to repeated fire could be further assessed to verify whether recurrent seasonal fires are capable of achieving multiple management objectives. I created a model to evaluate the effects based on known species-specific responses to fire and grazing. Though the model assumptions are broad (assumptions: non-preferential

grazing, precipitation regimes consistent with the yearly averages, homogenous fuel loads, and predictable forage removal by cattle), it is structured to provide a baseline of information regarding herbaceous species responses to fire. The current herbaceous conceptual model was quantified using one-month post-treatment native and invasive herbaceous responses then simulated based on these response variables. Initial model simulations revealed that proactive grazing management practices would need to be put in place, but non-native grasses could be reduced to manageable levels (less than 80% of the original cover) within two years of repeated fire application regardless of season (APPENDIX A.1. Description of conceptual diagram). Model simulations can contribute to a better understanding of the potential consequences of seasonal fire and grazing application when managing for multiple objectives. Increasing the interval of fire application and monitoring the effects on both the invasive herbaceous and the woody encroaching species should be explored in the future.

Focal species response

While a general understanding of the effects of fire and grazing on grass and forb production and diversity are valuable from a management perspective, this study aims to more specifically identify the season of prescribed fire and grazing most effective at reducing invasive OWBGs while simultaneously maintaining native species diversity and cover. Findings from this study suggest that both dormant and growing season prescribed fire have a neutral effect on *D. sericeum* cover. Meanwhile, the grazing treatment proved capable of significantly reducing *D. sericeum*. This likely occurred

because the grass species is considered highly palatable by grazers (Fensham et al. 1999) and consequently was preferentially selected by livestock during the grazing period.

Additionally, analyses of only the native C4 cover demonstrated that native C4 species were not influenced significantly by any of the fire or grazing treatments. This suggests that grazing treatments, like those found in this study, can reduce undesirable non-native grass cover while concurrently maintaining the native C4 grass community. The grazing treatments also allowed for increased forb production and species diversity. Grazing treatments could then be considered desirable management practices, since land management objectives were met while maintaining livestock grazing capacity.

Seasonal fire application had a neutral effect on *D. sericeum*, suggesting that fire application at any season will not exacerbate the invasive species problem when applied to prairies infested with this species. In contrast, studies that evaluated seasonal fire on *B. ischaemum* suggest certain periods of fire application could further increase its growth and establishment. In this study, *B. ischaemum* responded positively to winter and summer burn season. These results are in accordance with a study by Pase (1971) which found growing season fires promote *B. ischaemum* growth and establishment. In contrast to reports from Simmons et al. (2007), our study found dormant season fire also stimulates *B. ischaemum* cover.

Differential responses of two OWBGs, *B. ischaemum* and *D. sericeum*, to fire and grazing treatments suggest land management techniques for controlling OWBGs need to consider species-specific treatment responses. Evaluations of management techniques to control OWBGs do not account for the variability in responses at the

species level; instead, the majority of studies focus purely on *B. ischaemum* and rarely capture treatment influences on less dominant OWBG invaders such as *D. sericeum* and *D. annulatum*. These differences in species level responses could further complicate issues with invasive species control especially in prairies co-dominated by multiple genera of OWBGs. Collecting additional empirical evidence on the interactive effects of seasonal prescribed fire and grazing at the species level could have important implications for range management and maintenance of grassland diversity. Subsequently, various levels of seasonal fire and grazing applications should be evaluated for each OWBG species.

Invasive plant responses to prescribed fire and grazing are species specific. Inferences from this study suggest that if *D. sericeum* is the dominant non-native invading grass, then grazing appears to be the most suitable method of control. Grazing decreased non-native grass establishment while effectively increasing forb production and simultaneously maintaining the native C4 grass community. Grazing in combination with prescribed fire does not appear to significantly influence *D. sericeum* abundance because it responded neutrally to both dormant and growing season fire. This study clearly indicates that grazing can have a positive effect on maintaining species diversity and reducing non-native grass cover. Nonetheless, timing and intensity of grazing should also be evaluated in order to sustain appropriate levels of livestock on the pasture.

CHAPTER III
AN EXPERIMENTAL ASSESSMENT OF SEASONAL PRESCRIBED FIRE AND
GRAZING ON WOODY BRUSH ENCROACHMENT IN A SOUTH TEXAS
COASTAL PRAIRIE

Introduction

Woody shrubs are rapidly displacing grasslands due to changes in land use, fire suppression, and global climate change (Scholes and Archer 1997, Van Auken 2009). Shrub species have expanded into over 330 million hectares of non-forested land in the United States alone (Knapp et al. 2008). This phenomenon of increased cover, density, and biomass of indigenous woody shrub species, referred to as woody brush encroachment (Van Auken 2000), is believed to largely be a result of decades of fire suppression (Bond and Keeley 2005). The important role that fire plays in managing woody brush encroachment in tallgrass prairie has long been recognized and documented (Adams and Anderson 1978, Adams et al. 1982, Collins and Gibson 1990, Collins and Wallace 1990). Historically, fire has been common throughout most grasslands (Anderson 1990). However, since European settlement in North America, fire frequency has decreased as a result of active fire suppression (Tilman et al. 2000). Fire-free intervals provide an opportunity for new seedlings of woody species to grow and establish on the site, and continuous fire suppression allows for those woody species to displace herbaceous vegetation and dominate grassland plant communities (Scholes and

Archer 1997, Bond and Keeley 2005). For this reason, fire is a necessary ecological process used to control and prevent woody encroachment into grasslands.

Additionally, increased woody brush establishment has been attributed to atmospheric CO₂ enrichment and over-grazing by livestock (Archer et al. 1995, Scholes and Archer 1997). Elevated CO₂ concentrations favor C₃ woody plant biomass accumulation and establishment (Bond and Midgley 2000, Van Auken 2009). Heavy grazing changes the competitive interaction between grasses and shrubs/trees, thereby providing an opportunity for woody plants to invade (Asner et al. 2004). Furthermore, high grazing intensity reduces fuel load accumulation, which can prevent natural fires from occurring (Anderson 1990). Fire-free intervals, increased grazing, and altered atmospheric CO₂ all contribute to increased woody brush establishment in grasslands (Scholes and Archer 1997).

The long-term establishment of woody shrubs into grasslands leads to substantial and potentially irreversible alterations in community structure and function (Van Auken 2009). Woody vegetation invasion results in significant declines in overall species richness in grasslands (Ratajczak et al. 2012). Alterations to community composition can also have additional implications for carbon and nitrogen dynamics and above or below-ground nutrient pools and fluxes in grasslands (Archer et al. 2001, Wheeler et al. 2007). Changes in nutrient dynamics are especially noticeable in areas invaded by leguminous nitrogen fixing shrubs, which have the capacity to increase the nitrogen pool size (Wheeler et al. 2007).

One of the concerns regarding woody encroachment is that it decreases the productivity of grasslands by converting them to shrublands (Van Auken 2009), which leads to a reduction in ungulate grazing capacity. This also has negative implications for wildlife and results in alterations in the hydrology of the site (which is especially important in regards to waterfowl in more hydric grasslands). Shifts in avian communities (Lloyd et al. 1998) and the diversity and abundance of arthropod communities (Warren et al. 1987, Rieske et al. 2002, Hartley et al. 2007) have occurred as a result of changes in vegetation structure and composition of grasslands as they convert to shrublands. Shrub expansion is capable of producing widespread ecological changes to diversity, biogeochemical cycling and community composition. For this reason, management and prevention techniques are being explored to remove brush and restore grassland communities. Restoring historic fire regimes to the encroached systems and adjusting grazing intensities are among some of the management approaches being evaluated for shrub control.

Once these shrubs are established, they are not easily eliminated, even after the re-introduction of fire as a management tool (Scholes and Archer 1997, Briggs et al. 2005). As a result, landowners and managers who seek to reestablish the goods and services provided by grassland and savanna ecosystems are required to seek alternative restoration strategies. Other possible management techniques include changes in grazing intensity and mechanical or chemical brush treatments. Mechanical or chemical removal of newly encroached areas can be expensive and often provides only temporary benefits since many woody shrubs aggressively re-sprout new stems from belowground

meristematic tissues and perennating organs (Wilson et al. 1975, Enright et al. 1998, Klimeš 2007). Moreover, these management strategies do not kill the seed banks of these woody species and new recruitment may persist for prolonged periods of time (Berger 1993, Hamilton 2004, Paynter and Flanagan 2004).

Restoring the ecological process of fire to the ecosystem is important in maintaining grassland diversity and production of herbaceous species (Brockway et al. 2002). Prescribed fire as a management approach for controlling woody species depends on a variety of factors including fire season, intensity and frequency (Ansley and Jacoby 1998). Additionally, the species of encroaching shrub can alter the success of prescribed fire practices since fire tolerant species can respond neutrally or positively to fire application especially if seedling germination is promoted (Moreno and Oechel 1991). Nonetheless, fire is an important component of the ecosystem and is capable of shifting community composition, decreasing shrub establishment, and increasing production and diversity, especially in the herbaceous community (Uys et al. 2004). While certain seasons of prescribed fire treatments may reduce woody brush establishment, it could also have deleterious effects on the herbaceous community if the community consists of aggressive invading species. Certain seasons of prescribed fire can promote invasive grass growth and establishment (D'Antonio and Vitousek 1992, Simmons et al. 2007). The coastal tallgrass prairie has been invaded by old world bluestem grasses, which may increase after seasonal fire application (Simmons et al. 2007). For this reason, it is necessary to identify the effects of fire on both the woody shrub community and the invasive herbaceous vegetation.

One of the primary reasons for reducing woody brush abundance is to create an opportunity for the herbaceous community to re-establish with the goal of increasing grassland diversity and ungulate grazing capacity (Scholes and Archer 1997). Historically, grazing has been of major importance in maintaining tallgrass prairies (Axelrod 1985, Knapp and Seastedt 1998, Briggs et al. 2002), therefore, integrating sustainable livestock grazing practices into encroached grasslands should be evaluated. Management options to prevent shrub invasion and maintain grassland diversity and productivity need to be explored, especially in areas susceptible to dense brush conversion and non-native grass invasion.

Native coastal tallgrass prairies in south Texas are undergoing encroachment and invasion from both the surrounding native C3 woody shrub species and non-native C4 old world bluestem grasses. Invasive grasses can act as an obstacle towards successful regeneration of native plant communities (Menke 1992) following woody brush control measures; thus, land managers are concerned techniques targeted at controlling woody brush will exacerbate the invasive weed issues or vice versa (Fulbright 1991). Management plans are often targeted at controlling woody brush in order to increase desirable grass community composition and production (Fulbright 1991). For this reason, it is necessary to evaluate both the herbaceous community response to seasonal fire application and the response of the encroaching shrub species, so that one problem (encroaching shrubs) is not replaced by another (invading herbaceous species) following fire and grazing events. This study aims to assess what combination of seasonal fire and grazing is most capable of reducing shrub coverage and controlling or maintaining the

aggressive invading herbaceous species. The potential large-scale, broad ecological generalities of these management treatments on herbaceous and woody shrub abundance across ecosystems and continents will be evaluated in a later chapter.

Certain predictions of the responses of woody brush to treatments can be formulated based on expectations of fire seasonality and herbivore preferences. Selecting the appropriate fire that most negatively affects shrub density and recruitment may depend on fire season and fire intensity. The dominant woody species, honey mesquite (*P. glandulosa*) and twisted acacia (*A. farnesiana*), are dormant in the cooler months (spring and winter) and actively grow in summer months from April to October (Ansley et al. 1991, Ansley and Jacoby 1998). Implementing fires, while the shrubs are physiologically active, could potentially result in increased shrub mortality and reduced canopy cover (Ansley and Jacoby 1998). Summer fires can target the shrub species during their growing season when photosynthetic activity and processes related to biomass accumulation are more demanding on nutrient reserves. Therefore, I expect summer fires to have a more negative effect on the re-sprouting shrub species compared to the dormant season winter fires.

I expect cattle grazing alone (without prescribed fire) will not be effective at reducing shrub cover since shrub spinescence will deter herbivory. Prescribed fire has been suggested to increase shrub nutrient content (specifically digestible proteins in leaf matter of *P. glandulosa*) and temporarily decrease spinescence and other physical defense mechanisms (Schindler et al. 2004) against herbivory. Therefore, I hypothesize that the cumulative effect of the grazing and fire treatment will significantly decrease

shrub cover and result in a more effective management strategy for controlling problematic woody plant encroachment in coastal grasslands.

Methods

Study site

Research was conducted on the Rob and Bessie Welder Wildlife Foundation, in San Patricio County, Texas, approximately 13 km northeast of Sinton, on U.S. Highway 77. The study site is located on a 450 acre pasture, locally known as Coyote pasture. The herbaceous community is dominated by a native C3 and non-native C4 grass species: Texas winter grass [*Nassella leucotricha* (Trin. & Rupr.) Pohl] and silky bluestem [*Dichanthium sericeum* (R. Br.) A. Camus] respectively. Coyote pasture has been subjected to a constant rate of stocking prior to the initiation of this study. Co-dominant grass species include *Panicum obtusum* [(Kunth)], *Bouteloua dactyloides* [(Nutt.) J.T. Columbus], *Aristida diffusa* [(Trin)], *Bothriochloa ischaemum* [(L.) Keng], *Panicum halli* [(Vasey)], and other species of *Setaria* sp., *Andropogon* sp., *Eragrostis* sp., and *Sporobolus* sp. The site also consists of a variety of woody shrub and forb species. The dominant woody species are mainly spinescent, re-sprouting, leguminous shrubs such as, honey mesquite [*Prosopis glandulosa* Torr.], twisted acacia [*Acacia farnesiana* (L.) Willd], spiny hackberry [*Celtis ehrenbergiana* (Klotzsch) Liebm.], lime prickly ash [*Zanthoxylum fagara* (L.) Sarg] and agarita [*Mahonia trifoliolata* (Moric.) Fedde]. The study site contains 11 shrub species, two of which, honey mesquite and twisted acacia, dominate (>85% of the total shrub coverage). Shrubs make up less than 20% of the estimated foliar cover. Additionally, there is a minor forb component that makes up less

than 10% of the percent foliar cover. Dominant forb species vary by season but generally consist of various euphorbs, legumes and forbs from the genera *Croton* sp. *Cirsium* sp., *Solanum* sp, *Oxalis* sp., and *Lesquerella* sp (Jones 1975, Lehman et al. 2009).

Experimental design

I established thirty-six 10 x 10m plots located on the Coyote pasture cattle allotment to measure seasonal prescribed fire and grazing influences on woody shrub encroachment. Treatments consisted of two grazing treatments (grazed/ungrazed) and three fire treatments (summer, winter, and no fire) in a full factorial design. The six treatment combinations are winter (dormant season) burn only, summer (growing season) burn only, winter burn and fence, summer burn and fence, fence only (no burn), and an unfenced unburned control. I randomly assigned six treatments to six plots for a total of 36 plots. In order to assess the effects of fire and grazing on the shrub community, I collected percent cover of the shrub species within each plot prior to any treatment applications. I then demarcated 10 haphazardly selected shrubs of any species taller than 20 cm within each plot to evaluate height, shrub canopy area, and stem number. All data were collected at one month, three month, and six month intervals following the completion of both summer and winter prescribed fire and grazing applications. I also recorded observations of shrub herbivory, flowering, coppicing, and/or senescence. I measured the length and width of the total canopy area of each demarcated shrub per plot, and then used the measurements to calculate the area of an ellipse to determine total canopy area of each individual.

Prescribed fires

Summer (growing season) prescribed fires were applied in mid-August 2013. Individual ring fires were set starting at the northwest corner of each summer burn plot based on the prevailing winds. Wind speed during the burns ranged from 5 to 11 mph, average relative humidity was 56%, and average temperature was 94F. Timing of complete combustion of individual plots averaged two minutes.

Winter prescribed fires followed the same burning protocol. Wind speed ranged from 2 to 9 mph, relative humidity was 45% on average, ambient temperature was 70F, and time until complete combustion of individual plots averaged 2.5 minutes. Standing dead biomass in the winter plots was significantly lower than the summer, since plots only received a four month rest period from grazing prior to igniting the fires. For this reason, fuel loads were artificially homogenized in order to achieve complete and consistent combustion. I applied approximately 6.8 kg, or ½ square bales, of cured coastal Bermuda grass to each winter burn plot in order to effectively normalize the fuels. Temperature tiles were randomly placed throughout the winter burn plots.

Temperature tile analyses indicate that summer fire temperatures ranged from 79 to 246C and winter fire temperatures ranged from 79 to 135C. I recorded the percent cover of scorch marks for each plot following summer and winter fire. Scorch was defined as areas that were visibly charred or otherwise discolored due to the fire. Percent cover of scorch for each plot was compared to summer and winter fires to determine consistency of fuel combustion across the plots.

Grazing

I monitored percent utilization to determine if each plot experienced a grazing treatment but only from an herbaceous utilization perspective. I did not clip biomass from woody shrubs to determine shrub utilization, instead each shrub was evaluated for signs of herbivory on the re-sprouting stems. Utilization information was used to evaluate if the cattle actively visited the grazed treatments. Percent utilization was assessed by placing two utilization cages in each plot for the duration of the grazing rotation. Cages were placed in areas that avoided shrub clusters or woody brush, since the intent was to measure herbaceous biomass utilization. A total of four 0.25m² quadrats (two caged and two uncaged) were destructively harvested for herbaceous biomass at the end of each grazing rotation (one following each burn season). Percent utilization per plot was calculated as the difference between total caged and uncaged dry biomass weights divided by the total caged weight. Statistical comparisons of burned and unburned utilization samples were compared using a Student's t-test; p-values less than 0.05 were considered statistically significant.

Statistical analyses

I analyzed treatment effects of winter and summer fire and grazing on percent cover of total shrubs and two focal species, honey mesquite (*P. glandulosa*) and twisted acacia (*A. farnesiana*), using repeated measures ANOVA. Time was used as the repeated measure in order to evaluate the effect of time of data collection on measured shrub characteristics and cover. I also evaluated treatment effects on shrub height, canopy area and total stem count. I used diagnostic plots and Levene's or Bartlett's test for

homogeneity of variances to evaluate whether the assumptions of normality and homoscedasticity were satisfied. Data that did not satisfy the assumptions were log transformed. If interactions were not significant they were removed from the model and main effects were presented. All analyses were completed using R version 3.1.1 (The R Foundation for Statistical Computing 2014).

Results

The following analyses are based on a complete (pre-treatment, one, three, and sixth month post-treatment data) summer burn and grazing dataset and a partially complete (pre-treatment, one and three month post-treatment) winter burn and grazing dataset. Therefore, all winter burn tables and figures will exclude the six month post-treatment dataset. Final sixth month winter burn data will be collected in October 2014 and subsequently analyzed.

Fuel load and fire descriptions

Percent of plot scorch averaged 72% for summer fires and 95% for winter fires. Summer burn plots had a less consistent fuel load compared to the winter burn plots and had greater green herbaceous material mostly from forbs (mean percent cover total forbs summer= $14 \pm 2.1\%$, winter= $5 \pm 1.1\%$ prior to burns). The formation of uplifted areas following precipitation events on the shrink-swell clay soils created micro-topographic regions of suitable habitat for increased forb production. In these areas, forbs, predominantly *Croton spp.* and *Solanum spp.*, provided inconsistent green fuel, which led to un-scorched areas of the summer burn plots.

Species richness

No shrub recruitment or shrub mortality occurred in any of the grazed or burn treatments; therefore, average shrub richness by treatment type remained the same throughout the duration of the study. Shrub species richness was not affected by any of the fire or grazing treatments (Table 3.1).

Table 3. 1 Shrub species richness post-fire and grazing treatments

Treatment	Shrub richness
Unburned-Ungrazed	2.5
Unburned-Grazed	2.5
Winter burned- Ungrazed	2.2
Winter burned- Grazed	3.6
Summer burned- Ungrazed	4.0
Summer burned-Grazed	2.8

Table 3. 2. Analysis of variance of multiple shrub characteristics

Cover type	Treatment	Summer burned		*	Winter burned		*
		F ratio	P-value		F ratio	P-value	
Total shrub	Fire	12.06	0.01	*	7.4	0.01	*
	Graze	0.52	0.47		0.001	0.96	
	Time of collection	10.13	<0.001	*	17.91	<0.001	*
Twisted acacia	Fire	7.42	0.01	*	0.34	0.56	
	Graze	0.53	0.47		<0.001	0.99	
	Time of collection	2.54	0.06	*	9.75	<0.001	*
Honey mesquite	Fire	12.98	<0.001	*	11.98	0.002	*
	Graze	0.09	0.75		28.37	0.71	
	Time of collection	27.53	<0.001	*	0.15	<0.001	*
Shrub characteristic							
Average height	Fire	72.74	<0.001	*	40.88	<0.001	*
	Graze	1.46	0.24		2.11	0.16	
	Time of collection	34.45	<0.001	*	39.44	<0.001	*
Average canopy area	Fire	33.57	<0.001	*	34.14	<0.001	*
	Graze	1.71	0.205		1.45	0.24	
	Time of collection	69.81	<0.001	*	5.47	0.007	*
Total stem count	Fire	3.32	0.08		6.18	0.02	*
	Graze	0.21	0.65		0.16	0.69	
	Time of collection	31.01	<0.001	*	20.53	<0.001	*

*p-values <0.05

Focal woody species response

In general, the shrub characteristics height, canopy area, and stem count, were all significantly affected by summer and winter burning treatments (Fig. 3.1, 3.2). Shrub height and canopy area were reduced by summer and winter burn treatments ($p < 0.001$) but neither were influenced by grazing treatments (Table 3.2). Shrub total stem counts decreased following winter fire ($p = 0.02$) but were not significantly altered by summer burning ($p = 0.08$) (Fig. 3.1).

Percent foliar cover of total woody species and the two focal woody species, honey mesquite and twisted acacia, decreased in both the summer and winter burn treatments, but none of the woody plants were eliminated following summer or winter fire (Fig. 3.3, Fig. 3.4). Cattle did not noticeably browse the shrub species (even those that experienced a burn) therefore grazing treatments never had a significant effect on percent cover of individual or total woody shrubs (Table 3.2).

Figure 3. 1 Means of shrub characteristics following summer burn and grazing treatments. Points are least-square means of each treatment type and vertical lines are standard error bars. Interactions are insignificant so only main effects are displayed.

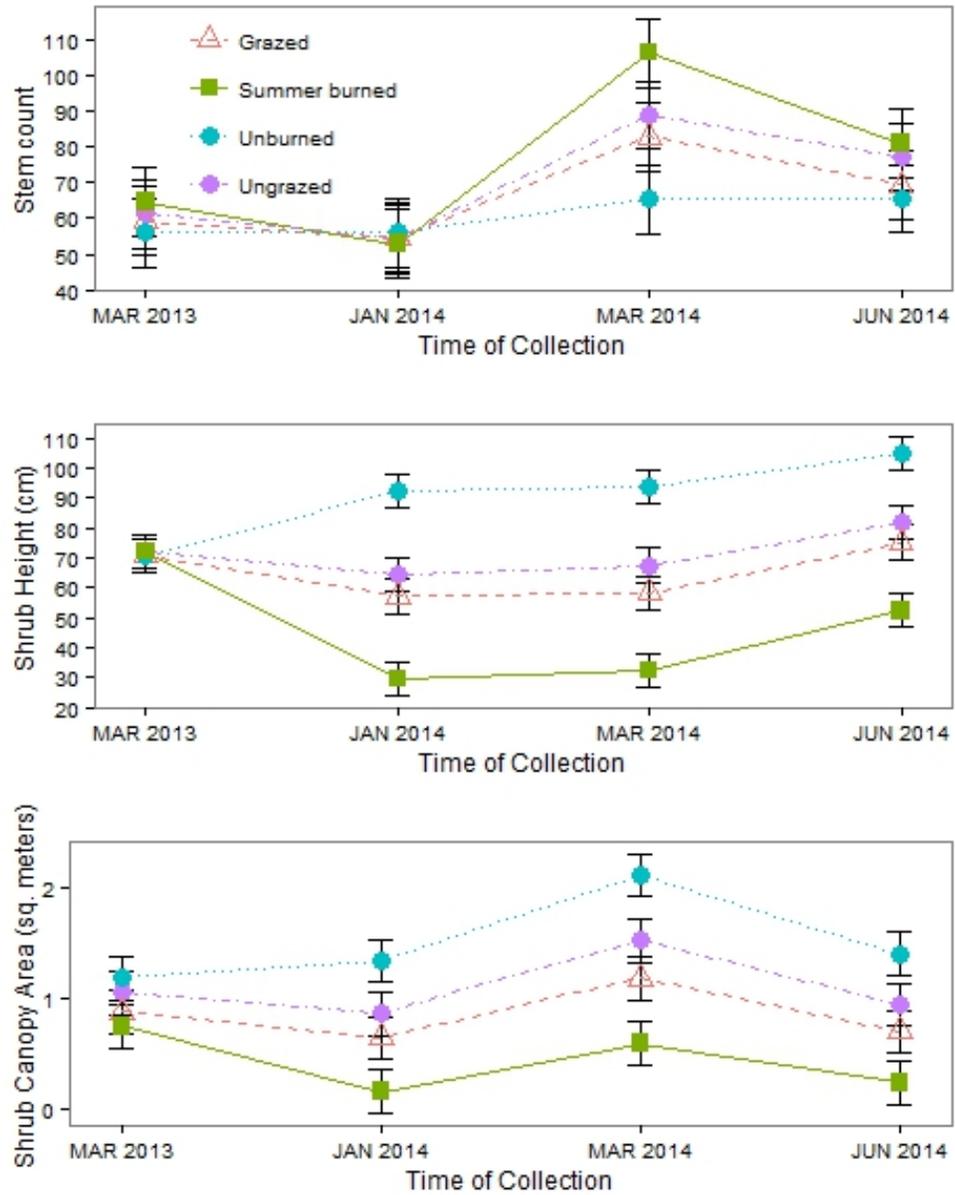


Figure 3. 2 Means of shrub characteristics following winter burn and grazing treatments. Points are least-square means of each treatment type and vertical lines are standard error bars. Interactions are insignificant so only main effects are displayed.

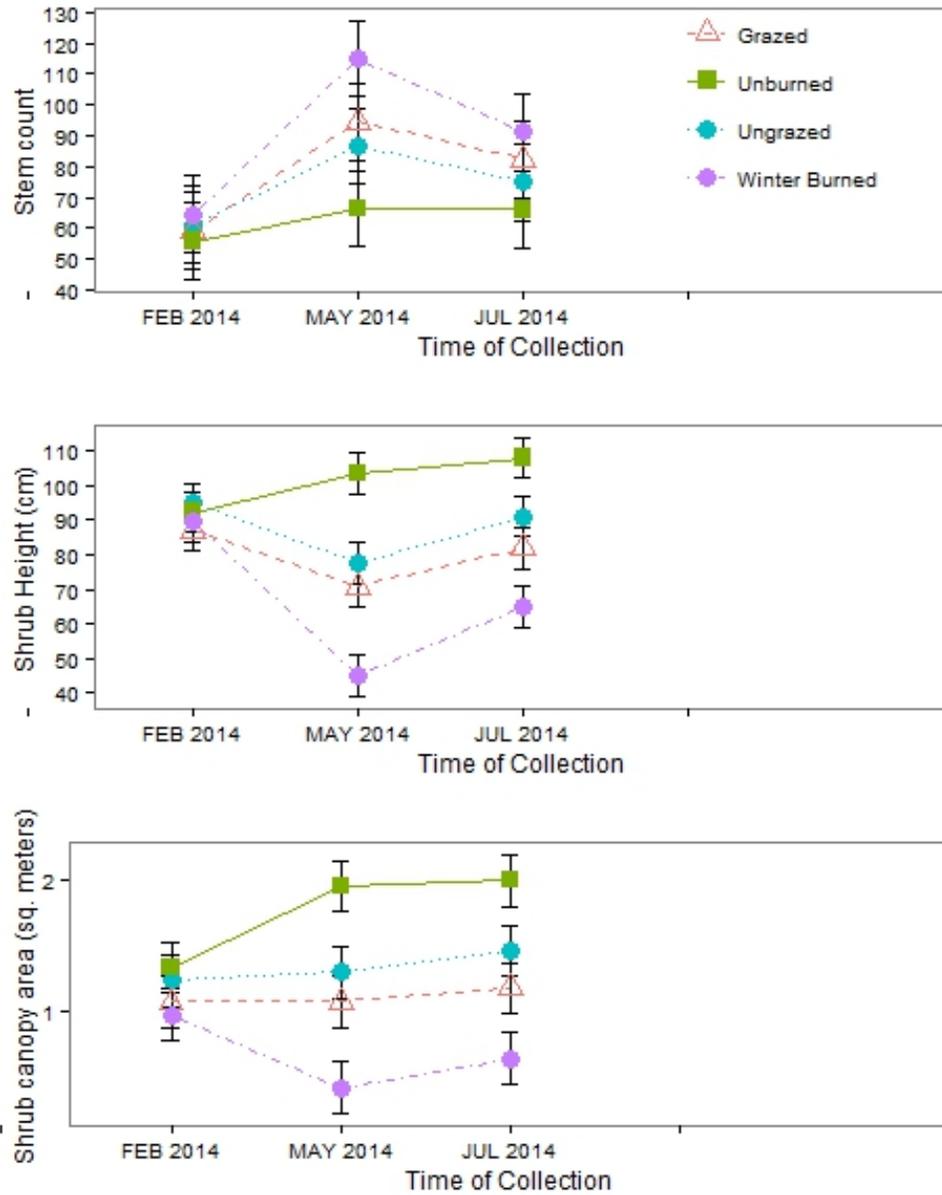


Figure 3. 3 Species percent cover following summer burn and grazing treatments. Points are least-square means of each treatment type and vertical lines are standard error bars. Interactions are insignificant so only main effects are displayed.

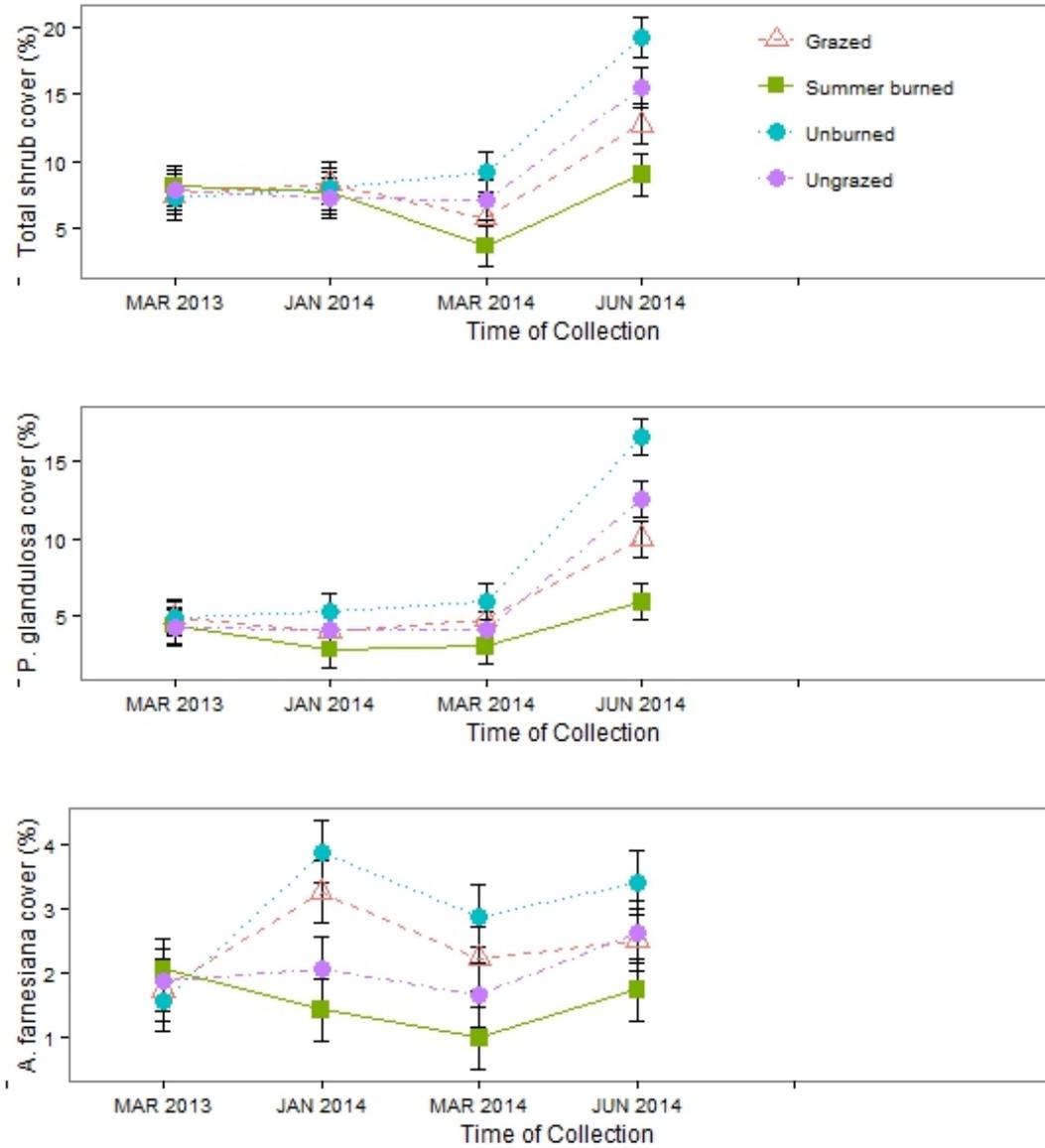
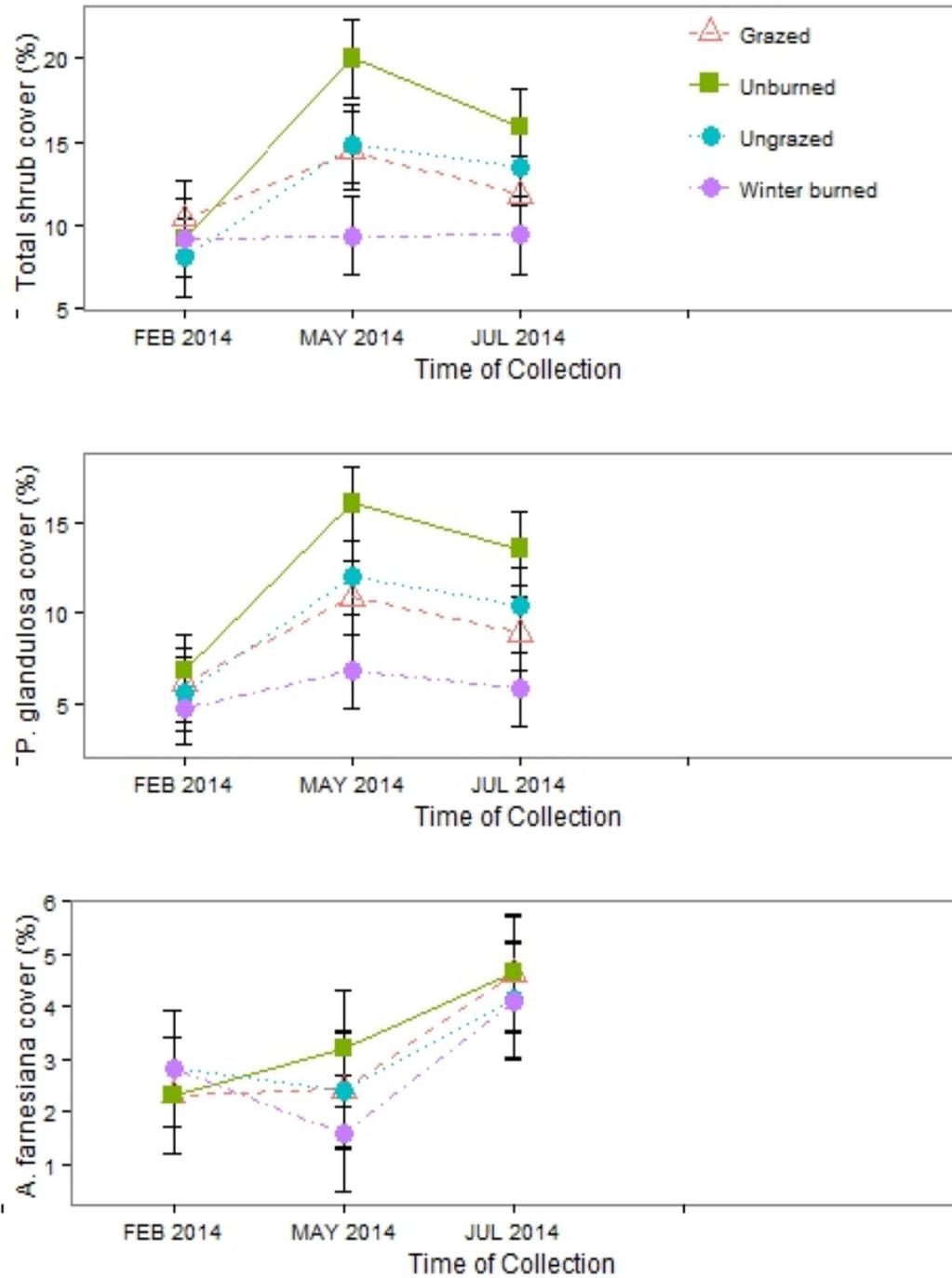


Figure 3. 4 Species percent cover following winter burn and grazing treatments. Points are least-square means of each treatment type and vertical lines are standard error bars. Interactions are insignificant so only main effects are displayed.



Discussion

Variability in the successful application of fire can depend on fire frequency, season and intensity. Distinct seasons of fire application could potentially promote grass production, decrease woody brush establishment, and shift community composition; therefore, prescribed fire application should be strategically and properly timed to achieve management goals. In general, various shrub species can exhibit wide-ranging responses to seasonal fire (Wright et al. 1976, Adams et al. 1982). Results from this study suggest prescribed fire application, regardless of winter or summer season, is capable of significantly decreasing total woody shrub cover, height and canopy area. Increased herbivory on the re-growing stems following fire was not demonstrated. Grazing without fire had no effect on shrub stature or cover.

Seasonal fire

Results from this study suggest that both fires conducted in the summer during the growing season as well as those conducted in the winter during the dormant season were capable of reducing shrub cover, canopy area and height. In contrast, a study by Owens et al. (2002), found that summer and winter prescribed fires were both equally ineffective at reducing the cover of the woody shrub honey mesquite (*Prosopis glandulosa*). However, they did observe that shrubs less than 50cm in height decreased in cover with both summer and winter prescribed fires (Owens et al. 2002). Perhaps the decrease in shrub cover following both seasons of fire application in our experiment could be attributed to shrub stature, considering the majority of shrubs in this study are less than 1m in height.

Adams et al. (1982) found that late winter fire was more likely to decrease native brush cover than summer fire, though this did not occur for the fire-adapted re-sprouting shrub species. Since the focal species, honey mesquite and twisted acacia, in this study are fire adapted, reductions in shrub cover may only be a temporary response to fire. Nevertheless, initial trends suggest both winter and summer fire have a pronounced effect on shrub cover, height, and canopy area. These initial reductions might allow an opportunity for the herbaceous species to capitalize on the increased light availability and immediate release of nutrients following fire, potentially allowing them to out-compete the shrubs for nutrients, even if only temporarily. Subsequent prescribed fire applications could then be applied to lower the competitive interaction between the shrub species and the understory herbaceous species (Bond and Van Wilgen 1996, Higgins et al. 2000).

Grazing

Percent utilization analyses suggest that cattle visited and grazed the burned and un-fenced plots following summer burns (61% utilization) and winter burns (37% utilization). Few shrubs experienced herbivory on the new re-sprouting stems, despite expectations that cattle would graze the tender re-growing stems after spinescence decreased following fire. In the burn treatments, shrubs experienced visible trampling from the cattle. Shrubs within the fire and grazing treatments experienced more trampling since cattle visited these plots more heavily and the brittle burned shrub stems were more vulnerable to fracture. Nonetheless, these effects did not contribute to lowered shrub densities or cover. Although grazing had no apparent effect on shrub

cover or abundance, studies have shown exclusion of grazing and browsing ungulates could lead to lowered species diversity (Rambo and Faeth 1999). While ungulate browsers did not play a dominant role in decreasing shrub cover in this study, continued grazing of the pasture may help to reduce shrub dominance and maintain diversity.

Herbaceous and woody shrub response

The combined herbaceous and woody brush studies suggest seasonal fire and grazing could be used to manipulate non-native species and woody brush separately, without exacerbating either of the problems. Winter and summer fire had no effect on the non-native herbaceous community (Table 2.3) but both seasonal fires significantly decreased woody brush cover. Ungulate grazing had no effect on woody brush density or cover, but significantly decreased the dominant non-native grass species. These results suggest that both summer and winter prescribed fire used in conjunction with grazing can achieve multiple land management objectives to decrease woody shrub and non-native grass cover.

Fire frequency

Frequent summer or winter fire application may be beneficial in reaching one land management objective, reducing shrub cover, but could have deleterious effects on the herbaceous community if non-native aggressive forbs or grasses are present. Incorporating additional empirical evidence from the woody brush component of this study to the herbaceous model (APPENDIX A.1) could create an integrated shrub and herbaceous community model used to evaluate assumptions of the entire plant community response to seasonal repeated fire and grazing. Although this study only

determined the effects of single fire applications, empirical evidence from other studies have shown decreased shrub dominance and increased herbaceous vegetation following frequent fires (Pekin et al. 2014). A 15-year study on altering fire frequency found that frequent (annual) fire application effectively suppressed shrub establishment (Briggs et al. 2002). Annual burning of tallgrass prairie can greatly decrease woody brush density in most native grasslands (Bragg and Hulbert 1976, Briggs and Gibson 1992). It has been suggested that applying more frequent fires (every four years on average) could potentially decrease shrub cover and seedling recruitment, though it may have no effect on mortality of established re-sprouting shrubs (Roques et al. 2001). Ecological model simulations can contribute to a better understanding of the potential consequences of treatment application when managing for multiple objectives. Empirical evidence of the effects of increased fire application on both the invasive herbaceous and the woody encroaching species could be used to construct practical ecological models.

Additional research could help to eliminate uncertainties related to the use of prescribed fire and grazing as management practices. Management practices targeted at achieving shrub management goals to increase native herbaceous production or diversity should be investigated for potential implications on invasive species abundance (Zouhar et al. 2008).

CHAPTER IV
DETERMINING THE EFFECT OF SINGLE SEASON PRESCRIBED FIRE AND
GRAZING ON *SERIPHIMUM PLUMOSUM* IN A SOUTH AFRICAN SOUR
BUSHVELD

Introduction

Encroachment by woody shrubs is a global issue that has been documented on nearly every continent (Roques et al. 2001). In southern Africa, an estimated 13 million hectares of savanna have undergone some level of shrub encroachment (Trollope et al. 1989). Consequences of shrub encroachment range from reduced land value, decreased total production and grazing capacity (Van Auken 2009), altered nutrient cycling (Knapp et al. 2008), and decreased biological richness and diversity (Ratajczak et al. 2012). Causes of shrub encroachment have been attributed to a combination of factors including fire suppression, poor land management practices like over-grazing by livestock (Scholes and Archer 1997), exotic plant invasions (Archer 2010), and increased atmospheric CO² (Knapp et al. 2008). Consensus on adequate brush management techniques to control the proliferating shrub species is lacking. Typically, management practices and policies are based on the premise that reintegration of the removed or altered processes and mechanisms thought to drive woody brush encroachment should reverse the problem (Roques et al. 2001). However, researchers have questioned whether reintegration of ecological processes, such as fire, will be able to restore shrub encroached grasslands or savannas (Walker et al. 1981, Dublin et al. 1990, Suding et al. 2004). Van Auken (2009) suggests that reversing shrub encroachment by reintegrating

fire or sustainable rangeland management practices may not be enough to overcome woody brush resilience. Therefore, a better understanding of the ecological mechanisms driving shrub encroachment and the species-specific responses to management techniques are necessary for the development of effective land management practices.

One of the dominant invading shrubs degrading grassland and savanna ecosystems in South Africa is *Seriphium plumosum* (L.) (syn. *Stoebe plumosa* (L.) Thunb.). *S. plumosum* is a native encroaching shrub that poses a serious threat to both the ecological and economic integrity of South African rangelands. *S. plumosum* establishment is associated with increased soil erosion (Daemane et al. 2012) and reduced species diversity (CARA 1983). Other studies have found that shrub encroachment can significantly decrease species diversity (Ratajczak et al. 2012) and diminish ecosystem services such as available water resources and water quality (Van Wilgen et al. 1996). Encroachment by *S. plumosum*, can decrease grazing capacity and total production potential of the grassland (Du Toit and Sekwadi 2012) since shrub canopies reduce shade intolerant grass species. Its ability to proliferate and form dense impenetrable shrub mats makes it difficult to remove using mechanical or hand-plowing methods (Krupko and Davidson 1961). Once grasslands have become severely encroached by the shrub, complete eradication is almost impossible, reducing grassland productivity and rendering the land unusable for agricultural activities (Snyman 2010). As a result of this ecological degradation that results in diminished economic returns, *S. plumosum* is colloquially referred to as “bankrupt bush”.

Distribution

S. plumosum is indigenous to South Africa, but also occurs in Namibia, Mozambique, Zimbabwe (Germishuizen and Meyer 2003) and Madagascar (Schmidt et al. 2002, Badenhorst 2009). The species has been documented in Angola in an area with high rainfall (1400mm), well-drained soils, and a surrounding fire-prone shrub community maintained by anthropogenic fire (Mills et al. 2011). The shrub has been sold commercially to the United States for ornamental horticulture (Tropicals 2014). Documentation of shrub encroachment in general in southern Africa began in the early 1920s (Wepener 2007), however the specific timing and extent of the expansion of *S. plumosum* was not recorded. In South Africa, *S. plumosum* is predominately distributed across the Western Cape, Eastern Cape, Free State, and occurs heavily in the North West and lower Limpopo province (Fig. 4.1).

Aggressive proliferation of *S. plumosum* has been observed on over-grazed or improperly managed agricultural lands (Walker and Noy-Meir 1982). *S. plumosum* seems to prefer sandy, well-drained, infertile soils (Walker and Noy-Meir 1982), or acidic soils with a mean annual rainfall of 630 mm (Snyman 2012) and it avoids clay or wetter soils with high soil water tables (Snyman 2012). Though the issue is pervasive and the consequences severe, little is known about the causes of *S. plumosum* encroachment. Few studies have examined the original distribution of *S. plumosum* compared to the current distribution, thereby making it difficult to understand the underlying patterns of or reasons for its expansion, although several studies suggest that low soil fertility and poor land management practices are the leading drivers for its expansion (Hattingh 1953, Krupko and Davidson 1961, Snyman 2011). Due to its proliferation, *S. plumosum* has been classified as an encroacher species according to the Conservation of Agriculture Resources Act (CARA). Once a species is officially proclaimed as an encroacher, land owners are obligated to regulate it on their property (Jordaan 2007, Snyman 2009b). The three prescribed measures recognized by CARA to administer to encroached lands are: uprooting or cutting the shrubs, applying registered herbicides, or reducing livestock utilization (CARA 1983). Consequently, controlling the proliferation of *S. plumosum* has become a significant financial burden for land managers (Snyman 2012).

Figure 4. 1 Map of *Seriphium plumosum* distribution in South Africa. Data from Acocks, image re-formatted from (Du Toit 2012) *.

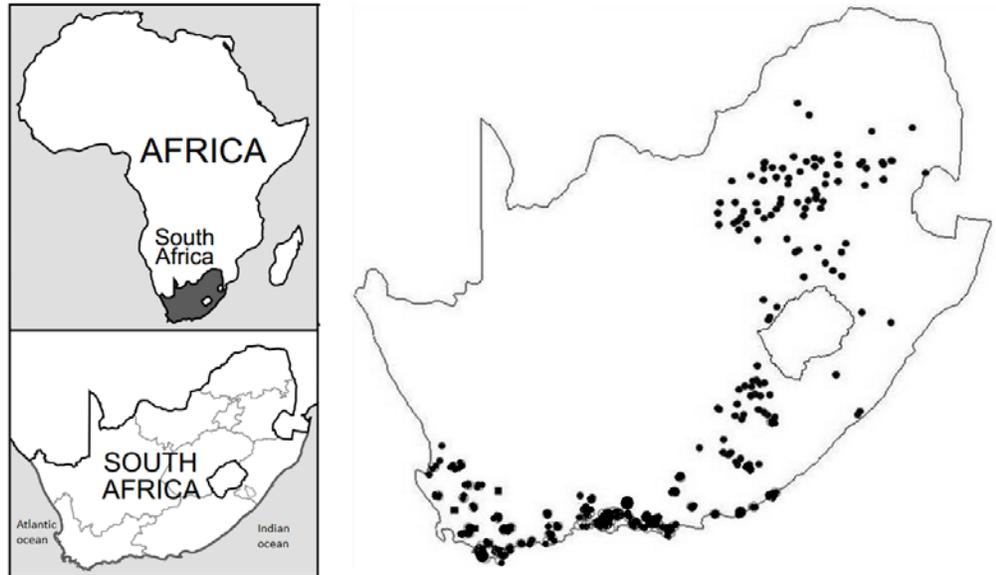
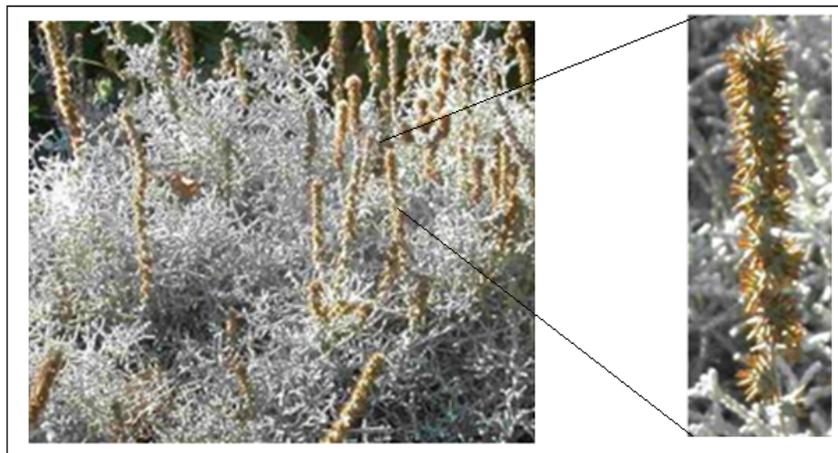


Figure 4. 2 Image of *S. plumosum* entire shrub and seed head. Photo by Louise Badenhorst.



* Reprinted with permission from “Problems with using the herbicide tebuthron for controlling *Seriphium plumosum*” by J.C. Du Toit, 2012. Grootfontein Agricultural Development Institute, 12: 1-30, Copyright [2012] GADI.

Ecology

S. plumosum has small, light silver-grey leaves with a wooly covering of fine white hairs (Hattingh 1953) (Fig. 4.2). The genus *Stoebe* (or *Seriphium*) is known for its production of secondary chemicals (Scott et al. 2004). The shrub secretes volatile oils that increase flammability during fires and decrease palatability. It is not heavily browsed by herbivores for this reason. *S. plumosum* is considered a dwarf shrub since it typically does not exceed 1.5 meters in height at maturity (Schmidt et al. 2002). The shrub can extend its canopy up to three meters in diameter. *S. plumosum* is compact in form with slender branches that form tangled mats of dense wiry stems. The shrub is a member of the Asteraceae family, known for its distinct composite florets that appear as one single flower but are actually made up of multiple ray flowers and florets (Koch 1930). The stems of the shrub are durable and dense but are often predated upon by a specific species of arthropod, *Stoebea barbertonensis* (Schuh 1974), which acquires nutrients from the shrub stems. Predation does not result in shrub mortality; instead, it forms a tumorous like growth in the plant tissue called a gall (Raman et al. 2005). This is fairly common among shrub species in the aster family. The shrub has not been known to reproduce vegetatively, instead it relies on propagation through an abundant annual production of seeds (Hattingh 1953). The seeds are light weight and typically wind dispersed. A single *S. plumosum* plant is capable of producing millions of tiny, seeds annually (Snyman 2009a, 2010), resulting in a fine layer of seeds surrounding each plant.

Management

It has been documented that as grazing pressure increases in South African rangelands, palatable grasses decrease and dwarf shrubs subsequently increase (Evans et al. 1997). From an agricultural land use perspective, *S. plumosum* is a major competitor with herbaceous species since its dense canopy of branches reduces shade intolerant grass species and strongly competes with herbaceous species for available nutrients and water; as *S. plumosum* increases in density (shrubs/ha), grass phytomass production significantly decreases leading to lowered forage availability (Snyman 2009a, 2012) and therefore decreased grazing capacity. The competitive dominance of this shrub leads to reduced herbaceous productivity, lowered forage availability (Snyman 2009a) and therefore decreased grazing capacity.

A variety of shrub control techniques have been attempted to reduce total density and allow for more desirable grass species to establish. One technique for manipulating shrub and herbaceous density is to apply selective herbicides; however this may only temporarily reduce *S. plumosum* density (Krupko and Davidson 1961). Certain herbicide applications have proved ineffective or variable in success. Success of the application of herbicides may depend on factors such as the length of time the treatment persists in the soil or the weather conditions following the herbicide application, specifically for herbicides containing tebuthiuron which requires water to release the active ingredient (Jordaan and Province 2009). In addition, applying non-selective herbicides, such as tebuthiuron, has the potential for non-target effects that inhibit desirable native seedling recruitment (Du Toit 2012).

A study by Snyman (2011) suggests that *S. plumosum* germination can significantly increase following a fire; however, the increase in seedling emergence may be attributed to the increase in light availability following the fire. Native browsers avoid the shrub since the leaves contain volatile oils, making it fairly unpalatable and also highly flammable. Therefore, most management methods have suggested that fire and grazing are not suitable treatment options for reducing shrub cover or encouraging mortality. Conversely, a recent observation by Du Toit (2013) suggests that cattle may graze *S. plumosum* in areas that have previously burned and are utilized during a time of low forage availability. While this theory needs further empirical evidence and explanation, it warrants a study that determines the interactive effects of prescribed fire in combination with grazing as management options for shrub control.

Few studies have identified control mechanisms that successfully reduce *S. plumosum* density. The main goal of this study is to identify the effects of fire and grazing treatments on *S. plumosum* abundance in order to gain a better understanding of the ecology of the species and to determine the effectiveness of these treatments as potential management strategies. Studies have shown that fire can stimulate new vegetative growth, increase nutrient content, and therefore palatability of shrubs to grazers (Schindler et al. 2004), which could temporarily increase grazing pressure resulting in decreased shrub cover and density. Prescribed fire has also been known to increase nutritive content of herbaceous regrowth (Van de Vijver et al. 1999) and allow for increased plant growth and establishment (Collins and Wallace 1990) while grazing could decrease aboveground herbaceous production (Milchunas and Lauenroth 1993) or

alter species composition through selective grazing of more palatable species (Augustine and McNaughton 1998). Therefore, we also need to evaluate the effects of fire and grazing on the surrounding herbaceous community.

The overall aim of this study is to evaluate whether species diversity and community structure differ between the burned and grazed treatments. I predict prescribed fire will negatively influence shrub foliar cover. Since the shrubs are highly flammable, fire intensity may be high enough to increase shrub mortality. Grazing alone, without a prescribed fire treatment, will likely have no effect on the shrub species but may alter herbaceous community composition as cattle selectively graze preferred species. I expect the combined effects of prescribed fire followed by grazing will increase shrub palatability in re-growing stems and encourage livestock to browse the shrubs.

Methods

Study site

This study was conducted at the Ukulima Farm Research Center in the Limpopo province of South Africa (Fig. 4.3). The research center maintains a 9200-acre tract of land located in the northern Waterburg District approximately 7 km from the town of Alma (Lat: -24.549472°, Long: 28.105861°). Historically, this region is a mosaic of savannas and prairies referred to as sour bushveld. The study site resides on a pasture consisting of sandy, infertile soils. The general plant community is predominately composed of grasses and some shrubs with less than 5% foliar cover of forbs. Vegetation in this district is considered sour bushveld (Acocks 1988), which consists of an open savanna with moderately nutritious grasses that decline in quality during the winter months and low growing woody plants. Dominant grass species include: *Eragrostis curvula* [(Schrad.) Nees], *Pogonarthria squarrosa* [(Roem. & Schult.) Pilg.], *Aristida congesta* [Roem. & Schult], *Perotis patens* [Gand.], and *Schizachyrium jeffreysii* [(Hack.) Stapf.]. The shrub community is almost entirely composed of *S. plumosum*. Annual rainfall in the Waterburg district ranges from 500 to 700 mm and typically occurs in the summer months (November to March) (Fig. 4.4). Low and variable rainfall in this region usually promotes dry land crop production and land use generally consists of irrigated farming or livestock grazing.

Figure 4. 3 Study site location in South Africa and location within Ukulima research station. Experimental design: each square represents a different plot and each color represents one of the four treatment types: unburned-ungrazed (dark red), burned-ungrazed (light red), unburned-grazed (blue), burned-grazed (black). Ukulima research station plot image and Waterburg District map reformatted from (Baker 2011). Map of South Africa biomes from (Bredenkamp et al. 1996, Rutherford et al. 2004).

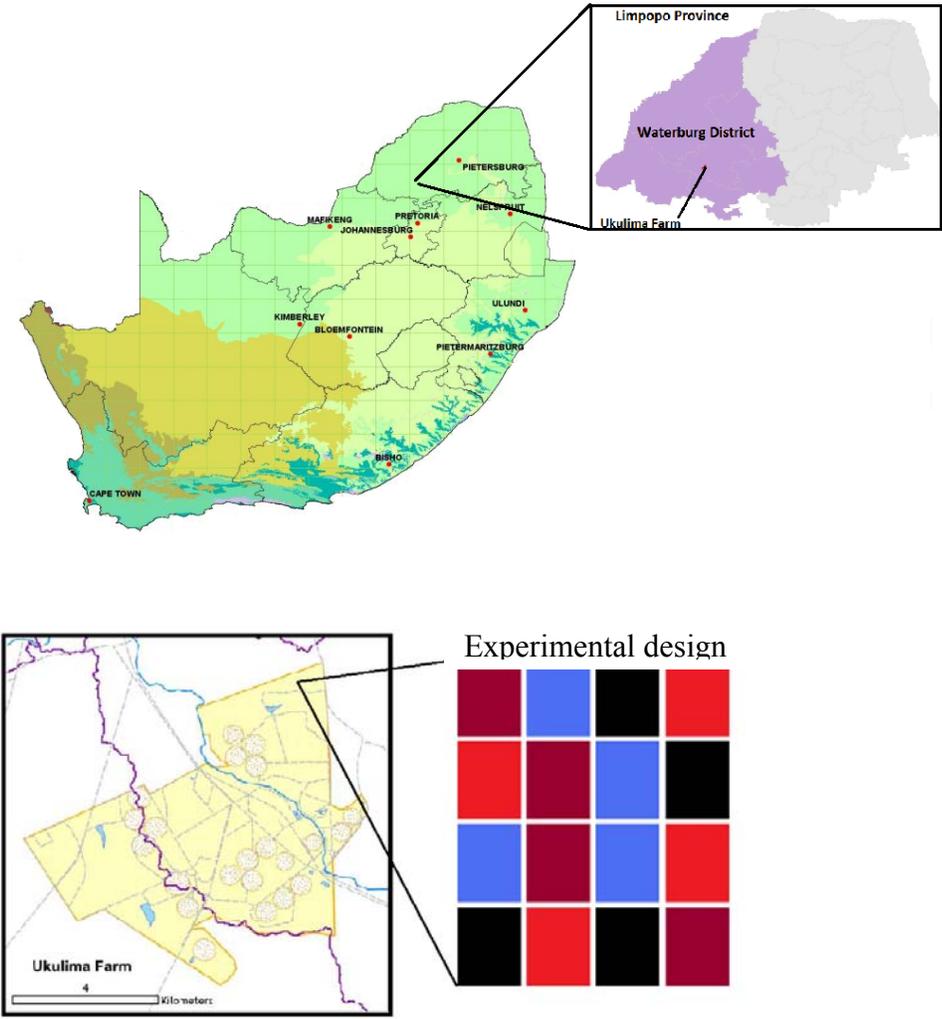
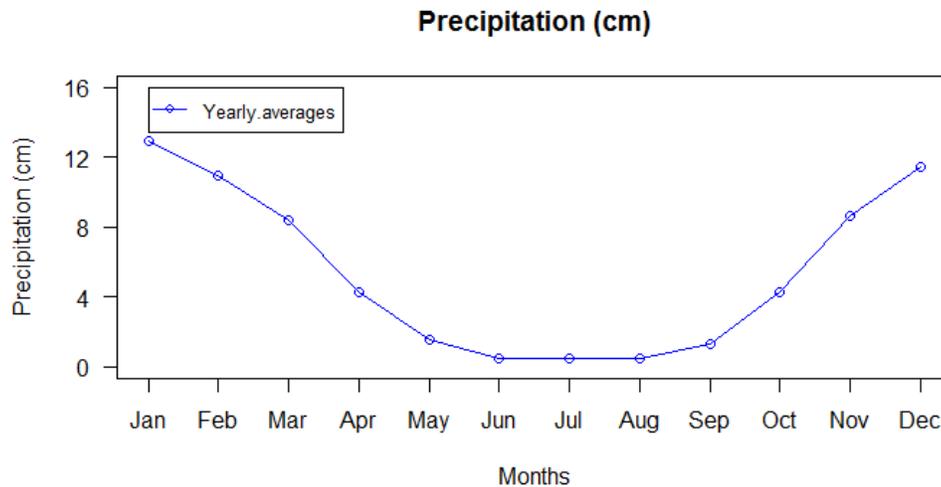


Figure 4. 4 Mean annual precipitation (cm) in the Waterburg district, Limpopo province, South Africa.



I established a full-factorial, completely randomized experiment to examine the interactive effects of prescribed fire and ungulate grazing on *Seriphium* and herbaceous community structure. The experiment was located on a pasture with 118 cow/calf pair of Bonsmara cattle. Sixteen 10x10m plots were randomly assigned one of four treatment combinations. Treatments include i) burned and fenced, ii) burned, not fenced, iii) fenced, not burned, and iv) unburned, unfenced. The plots were aggregated within a parcel of the pasture (approximately 0.5 ha in size) with 45-75% *Seriphium* cover. Unfenced plots were demarcated with a rebar post at each corner. Cattle grazing exclosures were constructed using 4-strands of evenly spaced barbed wire fence to a height of 2m. *S. plumosum* demography and plant community cover and composition data were collected prior to initiating any grazing or fire treatments. Each plot was fully sampled in June 2012 to estimate percent cover of herbaceous and woody plant species.

Permanently located markers were set at the base of ten randomly selected *S. plumosum* shrubs in each plot to assess shrub height, canopy area, and stem number over the study period. Immature shrubs, less than 20cm tall, were not selected for the study.

Independent prescribed fires were conducted for each burn plot on July 12, 2012 using a ring fire technique. After the plots were burned, cattle were immediately allowed to resume grazing in all of the unfenced plots in the pasture. Cattle were periodically rotated out of the pasture based on the amount of available forage. They were allowed to graze during the growing season months of December, February, and May of 2013 and 2014. The length of each rotation was typically 14 days. Post-treatment shrub demography and community cover data were collected six months (January 2013) and two years (June 2014) following the application of the fire treatment.

Statistical analyses

Shrub characteristic and community cover data were collected at multiple time intervals and therefore are not independent. I used repeated measures ANOVA to evaluate effects of burning, grazing, the timing of the data collection, and any treatment interactions for the shrub characteristics and herbaceous cover data. In order to determine shrub mortality or recruitment as a result of fire and grazing treatments, I calculated percent change differences in total number of individual shrubs per plot from pre-treatment to two years post treatment.

To identify differences in herbaceous community composition, I calculated percent change of three dominant grass species: *Eragrostis curvula*, *Aristida congesta*, and *Pogonarthria squarrosa*. These grass species were selected because they were

typically the most abundant before or after the fire applications. I also evaluated percent change of herbaceous biomass to determine effects of treatments on grass production. Percent change data was analyzed with a two-way ANOVA to identify interactive effects or treatment differences on community cover. Tukey's HSD test and t-tests were used to determine significance at $p < 0.05$. Percent change differences were calculated between the pre-treatment and two post-treatment data sets.

Equation for percent change:

$$[(\text{Post trt mean \% cover} - \text{Pre trt mean \% cover}) / \text{Pre trt mean \% cover}] * 100$$

To illustrate effects on herbaceous community composition, I used non-metric multidimensional scaling (NMDS) to visually display changes in species composition in each of the four treatment types. Ordinations were produced using a Bray-Curtis dissimilarity matrix with random starting configurations, two dimensions, and 100 runs of real data with 500 iterations per run. I extracted the lowest stress configuration using the two dimensional axes and plotted the ordination, then created polygons around observations from the same treatment types. The polygons are minimum area ellipses that contain all points of a given treatment level. Therefore, each outlined polygon relates to a different treatment type (Fig. 4.5). Polygons that overlap greatly indicate similar community composition. Species that occurred in less than 5% of all of the plots were removed from the data set (McCune et al. 2002). I used Multi Response Permutation Procedure (MRPP) to determine whether the species composition differed between treatment types. MRPP was calculated using the Bray-Curtis dissimilarity matrix to be consistent with the NMDS. In order to determine if the community was

adequately sampled, I created a species accumulation curve (Fig. 4.6). All ordination analyses were completed using the ‘vegan’ package in R version 3.1.1 (The R Foundation for Statistical Computing 2014).

Figure 4. 5 NMDS ordination based on two axes. Outlined polygons represent plots with the same treatment type. Colors of numbered points represent treatment types.

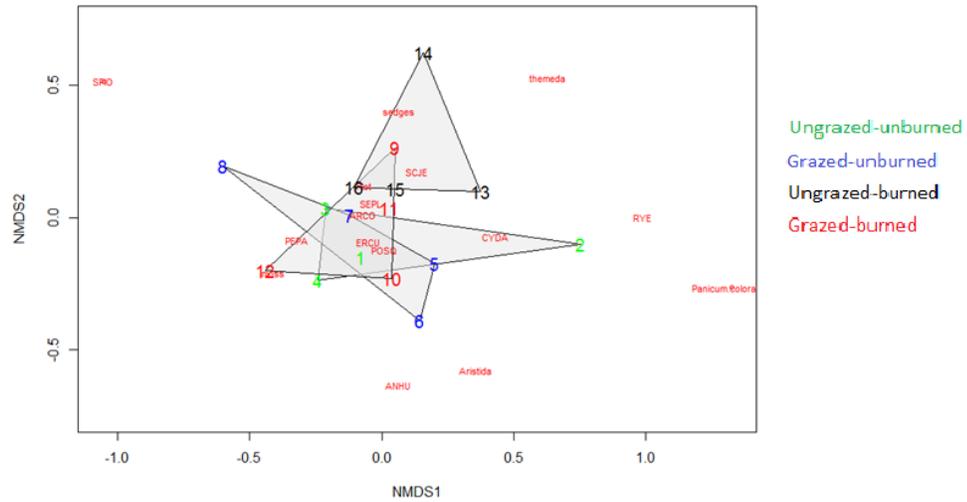
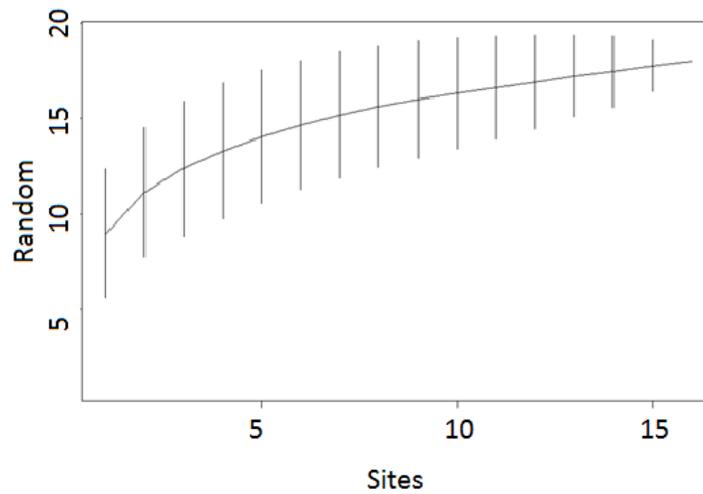


Figure 4. 6 Species accumulation curve calculated from random starting configurations.



Species diversity was determined using Shannon's diversity index (Preston 1948) based on percent cover of each species within the plots. All forbs were excluded from the diversity index calculation because they comprised less than 5% of each plot. Understanding diversity differences between treatments could further explain treatment effects on overall community composition in the study site.

Results

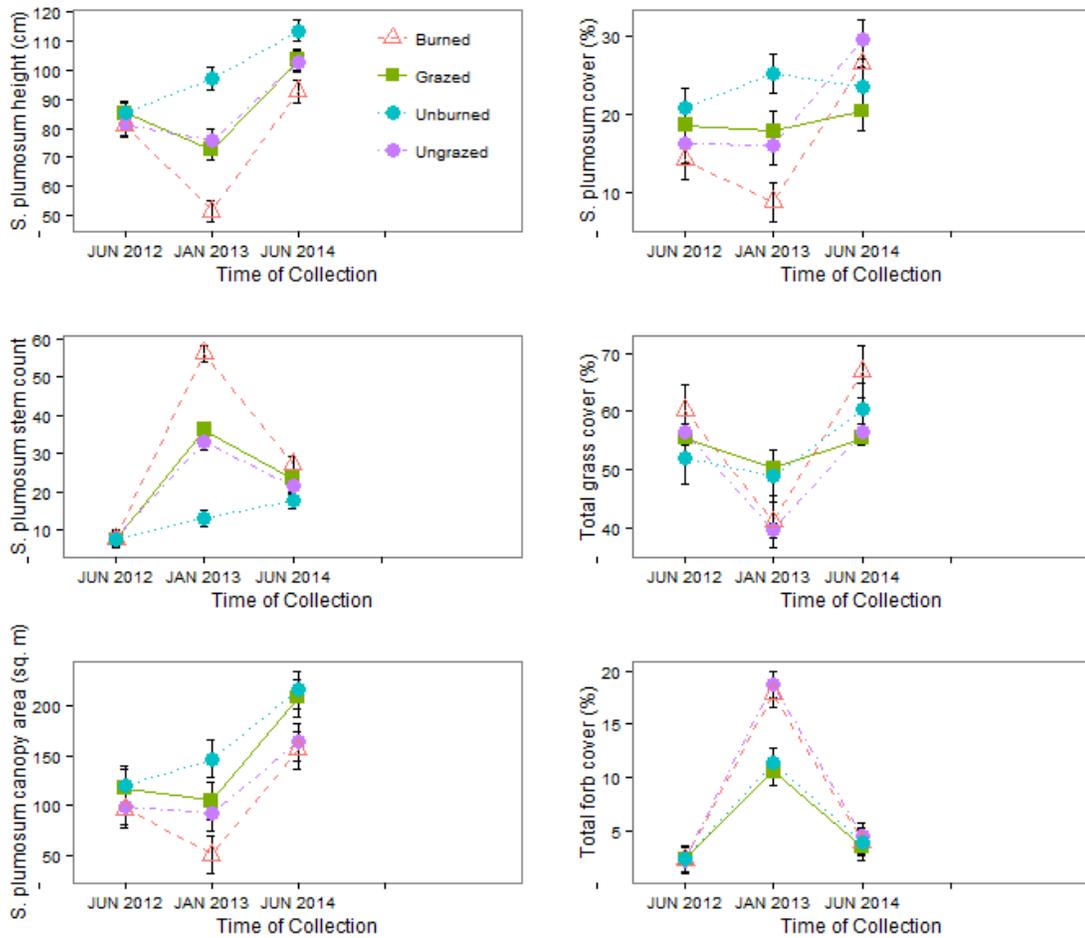
All of the measured shrub characteristics (height, canopy area, and stem count) were significantly influenced by the fire treatments. There were no significant interactions between fire and grazing treatments, so the interaction was removed from the model and only main effects are displayed (Fig. 4.7). Shrub canopy area and height were both significantly decreased by the fire treatments (Table 4.1). The fire treatment initially stimulated stem production during the six month post-treatment data collection, but by two years after the fire, the mean stem counts did not differ greatly (Fig. 4.7). Total *S. plumosum* cover was significantly influenced by fire treatments ($p=0.002$) but not grazing ($p=0.414$). In addition, total forb cover was influenced by grazing and fire treatments initially (six month post treatment), but this trend did not continue into the two year post treatment sampling period (Fig. 4.7). Total grass cover was not significantly influenced by either the fire or grazing treatments.

Table 4. 1 Analysis of variance of shrub characteristics and cover types

Shrub characteristic	Treatment	MSE	F ratio	P-value	
Height	Fire	6719.70	59.77	<0.001	*
	Graze	2.30	0.02	0.88	
	Time of collection	3476.60	30.92	<0.001	*
Canopy area (m)	Fire	426695295	5.07	<0.001	*
	Graze	71955359	2.54	0.12	
	Time of collection	722856320	12.77	<0.001	*
Stem count	Fire	3671.30	101.24	<0.001	*
	Graze	28.50	0.78	0.38	
	Time of collection	2890.50	79.71	<0.001	*
Cover types					
<i>S. plumosum</i>	Fire	524.04	10.26	0.002	*
	Graze	34.85	0.68	0.414	
	Time of collection	324.21	6.35	0.004	*
Total grass	Fire	65.57	0.42	0.5204	
	Graze	0.03	0.00	0.989	
	Time of collection	1395.12	8.96	<0.001	*
Total forb	Fire	55.04	4.36	0.04	*
	Graze	108.00	8.56	0.005	*
	Time of collection	711.93	56.43	<0.001	*

*p-values <0.05

Figure 4. 7 *S.plumosum* characteristics and total cover by functional group



Dominant grasses were selected to evaluate percent change differences following fire and grazing treatments. *E. curvula* significantly decreased following the fire treatment but was not affected by the grazing treatment. *P. squarrosa* was not influenced by either the fire or the grazing treatment while *A. congesta* significantly increased in the ungrazed plots (Table 4.2). Herbaceous biomass data were evaluated to determine differences in grass production between treatments. Burned plots did not have

significantly different biomass from the unburned plots, but grazed plots had significantly reduced biomass compared to the ungrazed plots (Table 4.3).

NMDS was selected as an ordination technique because it is robust to typical characteristics of community data, such as non-linearity. The data are represented in distance space and are non-metric so that rank order of each treatment observation is preserved. In order to determine the best number of axes for the ordination I generated a scree plot using random starting configurations. At two axes, the stress level rapidly decreases and has minor variation (Fig. 4.8). For this reason, I selected a two dimensional axis for the purposes of this ordination. Species accumulation curves were created to identify how well our sample represents the community. The curve doesn't level off before the number of observations indicating that the community was not sufficiently sampled (Fig. 4.8); this implies that inferences from this dataset may be inaccurate.

Table 4. 2 Percent change from pretreatment to two year post treatment data for certain dominant grasses.

Cover types	Treatment	Percent change	SE	P-value
<i>E. curvula</i>	Grazed	-0.04	0.18	0.987
	Ungrazed	-0.04	0.18	
	Burned	-0.39	0.18	0.018 *
	Unburned	0.31	0.18	
<i>P. squarrosa</i>	Grazed	7.84	4.40	0.858
	Ungrazed	6.71	4.40	
	Burned	7.91	4.40	0.842
	Unburned	6.65	4.40	
<i>A. congesta</i>	Grazed	10.38	9.06	0.081 *
	Ungrazed	34.56	9.06	
	Burned	38.46	9.06	0.026
	Unburned	6.47	9.06	

*p-values <0.05

Figure 4. 8 Scree plot used to determine minimum stress

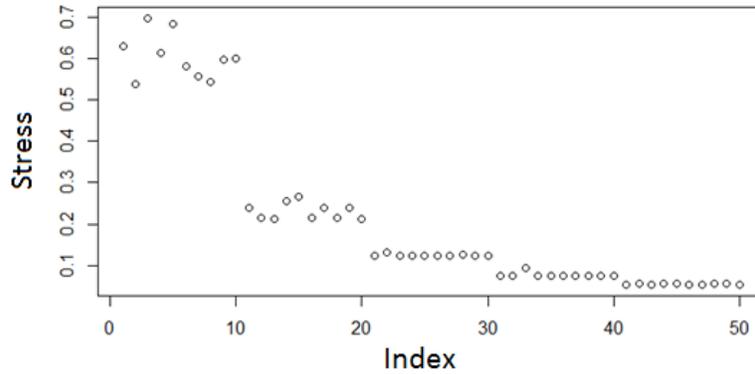


Table 4. 3 ANOVA herbaceous biomass two years post treatment

Treatment	Mean (g)	SE	MSQ error	F ratio	P-value
Burned	45.21	6.22	396.3	1.28	0.279
Unburned	35.25	6.22			
Grazed	20.65	6.22	6137.4	19.84	<0.001
Ungrazed	59.82	6.22			

*

Visual observations from the ordination (Fig. 4.5) suggest that the ungrazed-burned plots are distinct from all other treatment types. The remaining treatment combinations overlap and therefore have similar community composition. Multivariate tests can explain differences in community composition between the treatment types. I used both MRPP and analysis of similarities to determine if statistically significant differences exist. MRPP did not reveal significant differences in species composition between treatments from two year post treatment data ($A=0.418$; $p= 0.665$). The analysis of similarities statistic was also insignificant ($p=0.435$). Since the two

multivariate analyses did not indicate differences in community composition I did not perform an indicator species analysis to identify which species differ between the treatment types, since these interpretations could lead to inaccurate conclusions about the dataset. Evaluation of the diversity index for each plot also found no significant differences between treatment types, although grazed and burned plots typically had lower diversity compared to their treatment counterparts. The diversity index (H') ranged from 1.49 to 1.73 (Table 4.4).

Table 4. 4 Shannon diversity index post treatment for all species

Treatment	H' Diversity index	SE	F-ratio	P-value
Burned	1.49	0.12	2.52	0.136
Unburned	1.73	0.12		
Grazed	1.52	0.12	1.21	0.290
Ungrazed	1.69	0.12		

Discussion

The sour bushveld of northern South Africa is being predominately invaded by one species of woody encroacher, *S. plumosum*. Like many South African shrubs prone to fire, this species likely evolved adaptations, such as re-sprouting, to persist following fire (Bond and Midgley 2001). Studies have shown that *S. plumosum* can respond favorably to fire application through post-fire regeneration by seedling recruitment, increased germination potential, or basal re-sprouting (Wepener 2007, Snyman 2011).

The few studies that have explored the response of *S. plumosum* to fire have indicated variable effectiveness of fire application as a control technique for this species. One recent study reported that fire applied in July (dry winter month) increased post-fire plant densities and seedling emergence and reduced percent cover of *S. plumosum* (Wepener 2007). Our July fire treatment resulted in significantly reduced total canopy area, cover, and height. Initially, shrub stem counts increased significantly but this response did not persist two years after the fire treatment. There were no significant differences in shrub density for fire ($F=0.11$, $p=0.75$) or grazing ($F=0.01$, $p=0.92$) treatments, indicating that there was little shrub mortality or recruitment.

Even though shrub canopy area and cover decreased during fire treatments, shrub density remained the same due to regeneration and coppicing of the burned shrubs. None of the shrub characteristics were significantly affected by grazing treatments indicating that palatability is still fairly low following fire or perhaps browsing has little effect on shrub stature or mortality. Observations by Du Toit (2013) suggest that cattle may begin to browse *S. plumosum* if the quality of the surrounding forage is low. The herbaceous vegetation on this study site ranges from low to high palatability and all of the dominant grass species exhibit moderate to low palatability. Perhaps as community composition shifts towards lower palatable vegetation, there is a potential to reduce shrub height and canopy area as shrubs may be selectively grazed. In areas with extremely high shrub density and low available herbaceous vegetation, browsing of *S. plumosum* could be a beneficial and cost-effective treatment option. Nutritive value, proper grazing management techniques, and the potential negative consequences of grazing severely

degraded rangelands would need to be evaluated prior to using grazing as a restoration tool. Additional research experiments that focus on the potential for cattle grazing of *S. plumosum* should be considered in the future.

Early research on *S. plumosum* suggests that fire is not a viable management option to control the shrub once it has already established (Cohen 1935, 1940). Later studies suggest that only certain seasons of burning (spring and summer) were capable of reducing *S. plumosum* seedling establishment but did not report any mortality of established shrubs (Hattingh 1953). In contrast, an additional study found that fire in combination with heavy grazing was capable of eliminating the shrub from rangelands (Krupko and Davidson 1961). Since these early studies, little additional research has been dedicated to evaluating seasons or frequencies of prescribed fire or grazing that could control *S. plumosum*. Indeed, the majority of research on the species during the past 20 years has focused on various labor-intensive individual herbicide treatments to control the species. Du Toit (2012) indicated that herbicide application may be the primary treatment technique used by land managers despite its potential deleterious effects on native desirable plant growth and establishment. In other grassland ecosystems, prescribed burn applications have proved beneficial in inhibiting woody species encroachment (Adams et al. 1982) but may not be capable of reversing encroachment of already established woody species (Van Auken 2000). In this study, a single prescribed fire did not result in *S. plumosum* mortality but did decrease shrub cover, canopy area, and height. Fire application could be a beneficial, low cost treatment technique to alter shrub stature.

Herbaceous community response

Herbaceous biomass production was not affected following the fires (two year post treatment analysis) but was significantly increased by the exclusion of grazing (Table 4.3). Grass cover was not significantly affected by the burn treatments at any time during the post-treatment surveys (six month or two year data collections). It is expected that certain less palatable species would dominate the veld following the grazing treatment since they would have a competitive advantage over the preferred species. *Aristida congesta* was significantly lower in the grazed plots compared to the ungrazed plots (Table 4.2). This grass species is of fairly low palatability unless it is particularly young, so perhaps it was sensitive to increased trampling in the grazed plots. *E. curvula* significantly decreased in the burned plots versus the unburned plots. However, the actual percent change between the treatments is small (Table 4.2). Analysis of the two year post treatment percent cover of *E. curvula* data shows that there are no significant differences between fire ($F=1.61$, $p= 0.22$) and grazing ($F=0.71$, $p= 0.42$) treatments. *E. curvula* typically responds positively to fire and is found to occur at higher frequencies in burned sites compared to unburned sites in South Africa (Snyman 2004, Gucker 2009). This grass species is highly palatable to grazers before it reaches maturity and has been introduced in other rangelands for its ability to decrease soil erosion and increase available forage. The four dominant grass species following all treatment types have variable palatability (Table 4.5). Most of the dominant grasses are considered ‘increaser’ species which suggests that the study site location has been mismanaged (Bosch and vanRensburg 1987) and is becoming highly degraded (Smet and Ward 2005).

Table 4. 5 List of common grass species in the study site. Dominant grass species (mean cover greater than 10%) are highlighted in bold. Grass descriptions and ecological status from (Chippindall and Meredith 1955, Oudtshoorn 2002).

Scientific name	Life form	Palatability	Ecological status	
<i>Aristida congesta</i>	P*	Low	increaser	+
<i>Eragrostis curvula</i>	P	High	increaser	+
<i>Perotis patens</i>	P*	High		
<i>Pogonarthria squarrosa</i>	P	Low	increaser	+
<i>Schizachyrium jeffreysii</i>	P	High		
<i>Cynodon dactylon</i>	P	High	increaser	+
<i>Sporobolus ioclados</i>	P		increaser	
<i>Aristida diffusa</i>	P		increaser	
<i>Melinis repens</i>	P	Low	increaser	+
<i>Anthephora pubescens</i>	P			
<i>Imperata cylindrica</i>	P	High	decreaser	
<i>Aristida diffusa</i>	P		increaser	
<i>Andropogon huillensis</i>	P	High		
<i>Digitaria spp.</i>	P			
<i>Carex spp.</i>	P			

* classified as short lived perennial

(+) known to colonize disturbed areas or is considered invasive in other regions

Total plant species diversity was not influenced by either of the treatments. Diversity was slightly lower in burned and grazed plots but not significantly. According to the visual display of species overlap in the ordination (Fig. 4.5), only the burned-ungrazed plots had slightly different community composition compared to all other treatment types. However, the Multi Response Permutation Procedure test revealed no significant differences in community composition between treatment types (p=0.66).

Therefore, there was likely little difference in overall species community composition following treatments.

The neutral response of species composition to both grazing and burn treatments could be a result of two factors; low soil fertility and low potential for diverse seedling recruitment. The study site is located on sandy, infertile soils with a history of heavy grazing. The pre-treatment grass community consisted of species often associated with colonizing disturbed or low fertility grasslands (Table 4.5). Poor soil quality and low fertility can inhibit colonization and lower productivity (Olf and Ritchie 1998). In addition, the low quality of grass species and previous poor range management practices may have eradicated desirable native herbaceous vegetation or palatable grass species. This could deplete the soil seed bank and reduce the potential for seedling recruitment. Additionally, sandy poor quality soils may require more time to respond to grazing exclusion than highly fertile soils. Yong-Zhong et al. (2005) reported after five and ten years of grazing exclusion on unfertile sandy soils, grasslands can begin to recover vegetation and accumulate litter. Xu (1998) found that severely degraded and over-grazed grasslands have a much longer recovery time on infertile soils. While our study site is not severely degraded, it is dominated by indicator species of degradation (*E. curvula*, *A. congesta*, *P. squarrosa*). Therefore, a two year grazing deferment may not have been adequate to allow ungrazed pastures to recover desirable native vegetation, especially if the soil seed bank has been depleted. Excluding grazing and applying fire were not sufficient to recover species lost to over-grazing and woody brush encroachment in other studies as well (Noy-Meir 1975, Van Auken 2000). This could be

due to a loss of native species pools, indicating additional re-seeding treatments may be necessary to re-establish the native vegetation.

Our study indicates that neither burning nor grazing had a pronounced effect on community composition, but did negatively affect *S. plumosum* canopy area, cover and height. Although shrub cover decreased, there was no apparent mortality of individual shrub species. This reduction in cover did not lead to greater grass cover or alterations to total species diversity. Many factors, such as season and intensity of fire, pretreatment community composition, precipitation, and available seed bank, could directly affect species recovery and composition following fire and grazing treatments. Results from this study suggest the need to consider multiple factors (soil, surrounding vegetation, grazing intensity, fire seasonality and intensity) when analyzing the effect of fire and grazing as management techniques for *S. plumosum*. Possible future studies should explore combined management approaches, such as mowing treatments that are followed by targeted herbicides or repeated prescribed fire and data collections should be conducted over longer time intervals due to the potentially slow response of vegetation treatments in these sandy infertile soils.

CHAPTER V

CONCLUSION

Managing for multiple objectives

Managing for multiple land management objectives requires an understanding of complex species level interactions and their responses to treatments and techniques. Exclusion of woody plants and eradication of non-native species may not be possible, but finding control techniques that maintain productive and functioning prairies can be essential for maintaining productivity, land value, and other ecosystem services (DiTomaso 2009).

Blanket management applications to control for a variety of herbaceous invading and woody encroaching species are unlikely to be successful. For this reason, studies that evaluate the response of multiple species to multiple treatment factors are better able to identify integrated rangeland maintenance strategies that preserve the native species as natural biological agents of regeneration while selectively targeting the non-native species. Broad scale, non-target management techniques, like herbicide application and mechanical mowing or disc harrowing, provide little opportunity to put selective pressure on target species without indirectly disrupting the non-target native species (Crone et al. 2009). Non-selective herbicide eradication of invasive plants could lead to vacant niches that are then exploited by other invasive or encroaching plant species (Masters and Sheley 2001). This can occur if there is no desirable surrounding native plant community available to successfully re-colonize the vacant niche. In many

instances rangelands have degraded to the point that serious pro-active restoration techniques need to be implemented in order to restore the rangeland. Other areas that still have desirable native species present with dominant or co-dominant invading species need to be carefully managed so that the native species can be maintained and the non-native species reduced (Wittenberg and Cock 2001).

Selective management approaches, such as livestock grazing, which can target preferential species, prescribed fire or labor-intensive hand-pulling of target species can be applied seasonally with varying intensities to reduce undesirable species and potentially benefit or neutrally affect the native species. The combined herbaceous invader and woody shrub encroaching studies aim to determine management techniques that can maintain the integrity of the current ecological community while decreasing the invading woody brush or invasive species. While severely degraded rangelands may need intense active management procedures to restore ecological processes and functions, systems that are newly encroached or have lowered levels of invasion should not be ignored, since these communities are likely to benefit from less intensive or less costly restoration or maintenance activities (DiTomaso 2009).

Integrated results from chapter one and two, a combined study on the interactive effects of prescribed fire and grazing on woody brush encroachment and invasive grass abundance, suggest that multiple land management goals could be achieved with seasonal fire application and grazing. Both summer and winter fire were successful in reducing or maintaining shrub cover and height, but neither had a negative effect on abundance of the dominant invading grass, *Dichanthium sericeum*. Instead, grazing

significantly lowered *D. sericeum* production and cover while promoting forb and grass diversity and maintaining the native C4 grass community. These findings suggest that multiple management objectives, reducing shrub cover and decreasing invasive grass cover, could be achieved if both fire and grazing are applied to the infested prairie. Invading herbaceous species should be surveyed prior to management applications so that strategic management applications can be applied to specifically target the invaders.

Ecological generalizations

Another objective of this thesis is to determine if we can develop broad ecological generalizations about the effectiveness of fire and grazing as management treatments to reduce shrub encroachment across continents. The coastal prairie experiment has a parallel experimental design to the South African woody brush study. Both studies explore similar questions related to woody brush encroachment. For this reason, it provides an opportunity to assess cross-continental similarities in shrub and herbaceous community response to prescribed fire and grazing. Analysis of the data indicates fairly consistent effects of fire and grazing on herbaceous plant species and woody brush abundance on both continents. Both studies found that woody brush cover, canopy area, and height decrease following prescribed fire. Grazing had negligible effects on shrub cover, refuting both hypotheses of increased palatability and utilization following fire applications. Seasonal fire application also significantly decreased total grass cover but increased total forb cover on both study sites. Responses of species richness and diversity between South African and Texas grasslands were inconsistent. Other studies have shown that species diversity is highly variable and unpredictable

following fire and grazing treatments (Abrams and Hulbert 1987, Blankespoor 1987, Collins 1987). Species diversity was not altered by fire and grazing treatments in South African grasslands; however, species diversity increased after both treatments in the Texas coastal prairie. This could be explained by a variety of factors including soil fertility, precipitation, available seed bank, previous land management and soil type.

Understanding species specific responses to grazing and fire treatments is important for the development of targeted management practices. Nonetheless, reports from multiple species can assist in the development of broad ecological generalities across biomes and genera. Results from this study suggest that multiple re-sprouting fire-prone species in different environments respond similarly to fire and grazing treatments. These analyses would be beneficial in formulating research questions to test ecological hypotheses across ecosystems. Further studies that test ecological generalities across ecosystems will require longer term and multi-scale ecological experiments (Knapp et al. 2004). Though this study only evaluated the short-term response to treatments, it nevertheless adds to the pool of information that attempts to form ecological conclusions across multiple species and ecosystems. A general understanding of these responses could further develop large scale land management practices targeted at restoring encroached and invaded rangelands.

REFERENCES

- Abrams, M. D., and L. C. Hulbert. 1987. Effect of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. *American Midland Naturalist* 117:442-445.
- Acocks, J. P. H. 1975. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa*, No. 40, 2nd edition. National Botanical Institute, Kirstenbosch.
- Adams, D. E., and R. C. Anderson. 1978. The response of a central Oklahoma grassland to burning. *The Southwestern Naturalist* 23:623-631.
- Adams, D. E., R. C. Anderson, and S. L. Collins. 1982. Differential response of woody and herbaceous species to summer and winter burning in an Oklahoma grassland. *The Southwestern Naturalist* 27:55-61.
- Anderson, R. C. 1990. The historic role of fire in the North American grassland. In *Fire in North American Tallgrass Prairies*, ed. S.L. Collins, LL. Wallace. University of Oklahoma Press, Norman:8-18.
- Anderson, V. J., and D. D. Briske. 1995. Herbivore-induced species replacement in grasslands: is it driven by herbivory tolerance or avoidance? *Ecological Applications* 5:1014-1024.
- Ansley, R., and P. Jacoby. 1998. Manipulation of fire intensity to achieve mesquite management goals in north Texas. *Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers Fire Ecology Conference Proceedings*: 195-204.
- Ansley, R., P. Jacoby, and R. Hicks. 1991. Leaf and whole plant transpiration in honey mesquite following severing of lateral roots. *Journal of Range Management* 44:577-583.
- Ansley, R. J., and M. J. Castellano. 2007. Texas wintergrass and buffalograss response to seasonal fires and clipping. *Rangeland Ecology & Management* 60:154-164.
- Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? *American Naturalist* 134:545-561.
- Archer, S., T. W. Boutton, and K. A. Hibbard. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In *Global biogeochemical cycles in the climate system*, ed. E.D. Schulze, M. Heimann, S.

- Harrison, E. Holland, J. Lloyd, I.C. Prentice, and D. Schimel. Academic Press, Durham: 115-138
- Archer, S., D. S. Schimel, and E. A. Holland. 1995. Mechanisms of shrubland expansion: land use, climate or CO₂? *Climatic Change* 29:91-99.
- Archer, S. R. 2010. Rangeland Conservation and Shrub Encroachment: New Perspectives on an Old Problem. *Wild rangelands: Conserving wildlife while maintaining livestock in semi-arid ecosystems* 6:53.
- Asner, G. P., A. J. Elmore, L. P. Olander, R. E. Martin, and A. T. Harris. 2004. Grazing systems, ecosystem responses, and global change. *Annual Review Environmental Resources* 29:261-299.
- Asner, G. P., and P. M. Vitousek. 2005. Remote analysis of biological invasion and biogeochemical change. *Proceedings of the National Academy of Sciences of the United States of America* 102:4383-4386.
- Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *The Journal of wildlife management* 62:1165-1183.
- Axelrod, D. I. 1985. Rise of the grassland biome, central North America. *The Botanical Review* 51:163-201.
- Badenhorst, L. 2009. *Seriphium plumosum*. South African National Biodiversity Institute. Retrieved from PlantZAfrica.com.
- Bahm, M. A., T. G. Barnes, and K. C. Jensen. 2011. Herbicide and fire effects on smooth brome (*Bromus inermis*) and Kentucky bluegrass (*Poa pratensis*) in invaded prairie remnants. *Invasive Plant Science and Management* 4:189-197.
- Bailey, L. H., E. Z. Bailey, L. H. B. Hortorium, and N. Ithaca. 1976. *Hortus third: A concise dictionary of plants cultivated in the United States and Canada*. Macmillan, New York.
- Baker, T. J. 2011. *Ukulima Farm: Agriculture, Conservation, and Water Resources Research*. Texas Agrilife extension, College Station, Texas. Retrieved from http://borlaug.tamu.edu/files/2011/03/Baker_UkulimaFarm.pdf.
- Berg, W. A. 1993. Old world bluestem response to fire and nitrogen fertilizers. *Journal of Range Management* 46:421-425.

- Berger, J. J. 1993. Ecological restoration and nonindigenous plant species: a review. *Restoration Ecology* 1:74-82.
- Billings, W. 1994. Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. *Proceedings- Ecology and Management of Annual Rangelands*, ed., S.B. Monsen and S.G. Kitchen. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Boise:22-30.
- Blankespoor, G., and J. May. 1996. Alien smooth brome (*Bromus inermis* Leys.) in a tallgrass prairie remnant: seed bank, seedling establishment, and growth dynamics. *Natural Areas Journal* 16:289-294.
- Blankespoor, G. W. 1987. The effects of prescribed burning on a tall-grass prairie remnant in eastern South Dakota. *Prairie Naturalist* 19:177-188.
- Bond, W., and B. Van Wilgen. 1996. *Fire and Plants (Population and Community Biology Series 14)*. Fire and plants-population and community biology series 141996. Chapman and Hall, London.
- Bond, W. J., and J. E. Keeley. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* 20:387-394.
- Bond, W. J., and G. F. Midgley. 2000. A proposed CO₂-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* 6:865-869.
- Bond, W. J., and J. J. Midgley. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution* 16:45-51.
- Bosch, O., and F. J. vanRensburg. 1987. Ecological status of species on grazing gradients on the shallow soils of the western grassland biome in South Africa. *Journal of the Grassland Society of southern Africa* 4:143-147.
- Bragg, T. B., and L. C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. *Journal of Range Management* 29:19-24.
- Bredenkamp, G., N. Van Rooyen, A. Low, and A. Rebelo. 1996. Rocky highveld grassland. In *Vegetation of South Africa, Lesotho and Swaziland*, ed. A. Low and Rebelo. Department of Environmental Affairs and Tourism, Pretoria:39.
- Briggs, J. M., and D. J. Gibson. 1992. Effect of fire on tree spatial patterns in a tallgrass prairie landscape. *Bulletin of the Torrey Botanical Club*:300-307.

- Briggs, J. M., A. K. Knapp, J. M. Blair, J. L. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* 55:243-254.
- Briggs, J. M., A. K. Knapp, and B. L. Brock. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. *The American Midland Naturalist* 147:287-294.
- Brockway, D. G., R. G. Gatewood, and R. B. Paris. 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. *Journal of Environmental Management* 65:135-152.
- Brooks, M. L. 1995. Benefits of protective fencing to plant and rodent communities of the western Mojave Desert, California. *Environmental Management* 19:65-74.
- Brooks, M. L., C. M. D'antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54:677-688.
- Brooks, M. L., and D. A. Pyke. 2000. Invasive plants and fire in the deserts of North America. *Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species* 1:14.
- Burgess, D. 1989. economic perspective on chemicals for shrub control in the western division. New South Wales Department of Agriculture and Fisheries, Farm Business Notes No. 48.
- CARA. 1983. Conservation of Agricultural Resources Act (43). Notice No. 883.
- Celazier, R. P., and J. R. Harlan. 1955. Studies on Old World bluestems. Technical Bulletin, T-58 Oklahoma Agricultural Experimental Station.
- Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs* 77:117-145.
- Chippindall, L. K., and D. Meredith. 1955. The grasses and pastures of South Africa. Part 1. A guide to the identification of grasses in South Africa. Central News Agency, Cape Town: 1-771.
- Cohen, C. 1935. *Stoebe* sp. A contribution to its ecology. *Journal of South African Botany* 1:171-175.

- Cohen, C. 1940. *Stoebe vulgaris*, a study of an ecological problem. *Journal of South African Botany* 6:79-110.
- Coleman, S. W., and T. Forbes. 1998. Herbage characteristics and performance of steers grazing old world bluestem. *Journal of Range Management* 51:399-407.
- Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. *Ecology* 68:1243-1250.
- Collins, S. L., and S. C. Barber. 1986. Effects of disturbance on diversity in mixed-grass prairie. *Vegetation* 64:87-94.
- Collins, S. L., and D. J. Gibson. 1990. Effects of fire on community structure in tallgrass and mixed-grass prairie. In *Fire in North American tallgrass prairies*, ed. S.L. Collins, L.L. Wallace. University of Oklahoma Press, Norman:81-98.
- Collins, S. L., and L. L. Wallace. 1990. *Fire in North American tallgrass prairies*. University of Oklahoma Press, Norman.
- Coyne, P., and J. Bradford. 1985a. Morphology and growth in seedlings of several C₄, perennial grasses. *Journal of Range Management* 38:504-512.
- Coyne, P., and J. Bradford. 1985b. Some growth characteristics of four Old World bluestems. *Journal of Range Management* 38:27-33.
- Crone, E. E., M. Marler, and D. E. Pearson. 2009. Non-target effects of broadleaf herbicide on a native perennial forb: a demographic framework for assessing and minimizing impacts. *Journal of Applied Ecology* 46:673-682.
- D'Antonio, C., and L. A. Meyerson. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restoration Ecology* 10:703-713.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual review of Ecology and Systematics* 23:63-87.
- D'Antonio, C. M. 2000. Fire, plant invasions, and global changes. *Invasive species in a changing world*. Island Press, Washington, D.C.:65-93.
- Dabo, S., C. Taliaferro, S. Coleman, F. Horn, and P. Claypool. 1988. Chemical composition of old world bluestem grasses as affected by cultivar and maturity. *Journal of Range Management* 41:40-48.

- Daemane, M. E., S. S. Cilliers, and H. Bezuidenhout. 2012. Classification and description of the vegetation in the Spitskop area in the proposed Highveld National Park, North West Province, South Africa. *Koedoe* 54:1-7.
- Dahlsten, D. L. 1986. Control of invaders. Ecology of biological invasions of North America and Hawaii. Springer, New York.
- Dalrymple, R. L. 2001. Old World Bluestem: planting, stand establishment, and early stand production management, with considerations for other grasses. Agricultural division: The Samuel Roberts Noble Foundation, Inc. NF-FO-01-02.
- Daubenmire, R. 1968. Plant communities. A textbook of plant synecology. Harper and Row, New York.
- Dewald, C. L., W. A. Berg, and P. L. Sims. 1985. New seed technology for old farmland. *Journal of Soil and Water Conservation* 40:277-279.
- DiTomaso, J. M. 2009. Invasive weeds in rangelands: species, impacts, and management. *Weed Science* 48: 255-265.
- DiTomaso, J. M., M. L. Brooks, E. B. Allen, R. Minnich, P. M. Rice, and G. B. Kyser. 2009. Control of Invasive Weeds with Prescribed Burning. *Weed Technology* 20:535-548.
- Du Toit, J. C. 2012. Problems with using the herbicide tebuthiuron for controlling *Seriphium plumosum*. *Grootfontein Agricultural Development Institute* 12:1-30.
- Du Toit, J. C., Cronje, W.B., Trollope, W. 2013. Towards low-input control of Slangbos (*Seriphium plumosum*)-Quality and grazing interaction hypothesis. *Grootfontein Agricultural Development Institute* 13:1.
- Du Toit, J. C., and K. P. Sekwadi. 2012. Tebuthiuron residues remain active in soil for at least eight years in a semi-arid grassland, South Africa. *African Journal of Range & Forage Science* 29:85-90.
- Dublin, H. T., A. Sinclair, and J. McGlade. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *The Journal of Animal Ecology* 59:1147-1164.
- Dwyer, D. D., P. L. Sims, and L. Pope. 1964. Preferences of steers for certain native and introduced forage plants. *Journal of Range Management* 17:83-85.
- Dyksterhuis, E. 1958. Ecological principles in range evaluation. *The Botanical Review* 24:253-272.

- Eck, H., and P. Sims. 1984. Grass species adaptability in the Southern High Plains: a 36-year assessment. *Journal of Range Management* 37:211-217.
- Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503-523.
- Enright, N. J., R. Marsula, B. B. Lamont, and C. Wissel. 1998. The ecological significance of canopy seed storage in fire-prone environments: a model for resprouting shrubs. *Journal of Ecology* 86:960-973.
- Evans, N., A. Avis, and A. Palmer. 1997. Changes to the vegetation of the mid-Fish River valley, Eastern Cape, South Africa, in response to land-use, as revealed by a direct gradient analysis. *African Journal of Range & Forage Science* 14:68-74.
- Evans, R., R. Rimer, L. Sperry, and J. Belnap. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications* 11:1301-1310.
- Ewing, A., and D. Engle. 1988. Effects of late summer fire on tallgrass prairie microclimate and community composition. *American Midland Naturalist* 120:212-223.
- Felger, R., T. L. Burgess, S. Dorsi, J. R. Reeder, and T. R. Van Devender. 2005. *Dichanthium* (Poaceae) new to Arizona: open door for a potentially invasive species. *SIDA, Contributions to Botany* 21:1905-1908.
- Fensham, R., J. Holman, and M. Cox. 1999. Plant species responses along a grazing disturbance gradient in Australian grassland. *Journal of Vegetation Science* 10:77-86.
- Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, and H. K. Gibbs. 2005. Global consequences of land use. *science* 309:570-574.
- Fosberg, M. A., and M. J. Schroeder. 1971. Fine herbaceous fuels in fire-danger rating. Rocky Mountain Forest and Range Experiment Station, Forest Service, US Dept. of Agriculture, Washington D.C.:185.
- Frost, R. A., and K. L. Launchbaugh. 2003. Prescription grazing for rangeland weed management: A new look at an old tool. *Rangelands* 25:43-47.
- Fulbright, T. E. 1991. Why does brush increase? Proceedings of brush management symposium 1:6-15.

- Gabbard, B. L. 2003. The population dynamics and distribution of the exotic grass *Bothriochloa ischaemum*. Ph.D. dissertation, The University of Texas, Austin.
- Gabbard, B. L., and N. L. Fowler. 2007. Wide ecological amplitude of a diversity-reducing invasive grass. *Biological Invasions* 9:149-160.
- Ganskopp, D., B. Myers, S. Lambert, and R. Cruz. 1997. Preferences and behavior of cattle grazing eight varieties of grasses. *Journal of Range Management* 50:578-586.
- Germishuizen, G., and N. Meyer. 2003. Plants of southern Africa: an annotated checklist. National Botanical Institute, Pretoria:1231
- Goldewijk, K. K. 2001. Estimating global land use change over the past 300 years: the HYDE database. *Global Biogeochemical Cycles* 15:417-433.
- Gould, F. W. 1975. The grasses of Texas. Texas A&M University Press, College Station.
- Govender, N., W. S. Trollope, and B. W. Van Wilgen. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* 43:748-758.
- Grace, J. B. 1998. Can prescribed fire save the endangered coastal prairie ecosystem from Chinese tallow invasion. *Endangered Species Update* 15:70-76.
- Grace, J. B., L. K. Allain, H. Q. Baldwin, A. G. Billock, W. R. Eddleman, A. M. Given, C. W. Jeske, and R. Moss. 2005. Effects of prescribed fire in the coastal prairies of Texas. USGS Open File Report:1287.
- Grace, J. B., M. D. Smith, S. L. Grace, S. L. Collins, and T. J. Stohlgren. 2000. Interactions between fire and invasive plants in temperate grasslands of North America. Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species. Tall Timbers Research Station, Tallahassee, Florida: 40-65.
- Grant, W. E., and T. M. Swannack. 2008. Ecological modeling: A common-sense approach to theory and practice. Cambridge University Press, Cambridge.
- Gucker, C. L. 2009. *Eragrostis curvula*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.

- Guckian, W. J., and R. N. Garcia. 1979. Soil survey of San Patricio and Aransas counties, Texas. U.S. Department of Agriculture, NRCS, Washington D.C.
- Hamilton, W. T. 2004. Brush management: past, present, future. Texas A&M University Press, College Station.
- Hansmire, J. A., D. L. Drawe, D. B. Wester, and C. M. Britton. 1988. Effect of winter burns on forbs and grasses of the Texas Coastal Prairie. *The Southwestern Naturalist* 33:333-338.
- Harlan, J. R. 1963. Natural introgression between *Bothriochloa ischaemum* and *B. intermedia* in West Pakistan. *Botanical Gazette* 124:294-300.
- Harlan, J. R., J. De Wet, W. Richardson, and H. Chheda. 1961. Studies on old world bluestems III. Technical Bulletin. Oklahoma Agricultural Experiment Station 92.
- Harmony, K. R., P. W. Stahlman, and K. R. Hickman. 2009. Herbicide Effects on Established Yellow Old World Bluestem (*Bothriochloa ischaemum*). *Weed Technology* 18:545-550.
- Harper, C. A. 2009. Strategies for managing early succession habitat for wildlife. *Weed Technology* 21:932-937.
- Hartley, M. K., W. E. Rogers, E. Siemann, and J. Grace. 2007. Responses of prairie arthropod communities to fire and fertilizer: balancing plant and arthropod conservation. *The American Midland Naturalist* 157:92-105.
- Hartnett, D. C., K. R. Hickman, and L. E. F. Walter. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Journal of Range Management* 49:413-420.
- Hattingh, E. 1953. Observations on the ecology of *Stoebe vulgaris* Levyns. *Empire Journal of Experimental Agriculture* 21:309-313.
- Hawkes, C. V., J. Belnap, C. D'Antonio, and M. K. Firestone. 2006. Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. *Plant and Soil* 281:369-380.
- Hickman, K. R., G. H. Farley, R. Channell, J. E. Steier, and C. Lauver. 2006. Effects of old world bluestem (*Bothriochloa ischaemum*) on food availability and avian community composition within the mixed-grass prairie. *The Southwestern Naturalist* 51:524-530.

- Higgins, S. I., W. J. Bond, and W. S. Trollope. 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology* 88:213-229.
- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation biology* 6:324-337.
- Hodges, M., and T. Bidwell. 1993. Production and management of old world bluestems. OSU extension facts. Oklahoma State Univeristy, Stillwater.
- Holechek, J. L., R. Valdez, S. D. Schemnitz, R. D. Pieper, and C. A. Davis. 1982. Manipulation of grazing to improve or maintain wildlife habitat. *Wildlife Society Bulletin* 10:204-210.
- Howe, H. F. 1994. Response of early-and late-flowering plants to fire season in experimental prairies. *Ecological Applications* 4:121-133.
- Jacobsen, C. 1981. Review of the species of *Dichanthium* native to Australia with special reference to their occurrence in Queensland. *Tropical grasslands* 15: 85-94.
- Jones, F. B. 1975. Flora of the Texas coastal bend. Welder Wildlife Foundation, Sinton.
- Jordaan, D., and N. W. Province. 2009. Bankruptbush (Slangbos)—A silent threat to grasslands? *Grassroots* 9:40-42.
- Jordaan, D. J. a. F. P. 2007. Probleem-plant in die Suidwes-gebied. *One Eie* 42.
- Klimeš, L. 2007. Bud banks and their role in vegetative regeneration—a literature review and proposal for simple classification and assessment. *Perspectives in Plant Ecology, Evolution and Systematics* 8:115-129.
- Knapp, A., and T. Seastedt. 1998. Grasslands, Konza Prairie, and long-term ecological research. *Grassland dynamics: longterm ecological research in tallgrass prairie*. Oxford University Press, New York.
- Knapp, A. K., J. M. Briggs, S. L. Collins, S. R. Archer, M. S. Bret-Harte, B. E. Ewers, D. P. Peters, D. R. Young, G. R. Shaver, and E. Pendall. 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology* 14:615-623.
- Knapp, A. K., M. D. Smith, S. L. Collins, N. Zambatis, M. Peel, S. Emery, J. Wojdak, M. C. Horner-Devine, H. Biggs, and J. Kruger. 2004. Generality in ecology:

- testing North American grassland rules in South African savannas. *Frontiers in Ecology and the Environment* 2:483-491.
- Koch, M. F. 1930. Studies in the Anatomy and Morphology of the Composite Flower I. The Corolla. *American Journal of Botany* 17:938-952.
- Krupko, I., and R. Davidson. 1961. An experimental study of *Stoebe vulgaris* in relation to grazing and burning. *Empire Journal of Experimental Agriculture* 29:175.
- Lehman, R. L., R. O'Brien, and T. White. 2009. *Plants of the Texas coastal bend*. Texas A&M University Press, College Station.
- Lloyd, J., R. Mannan, S. Destefano, and C. Kirkpatrick. 1998. The effects of mesquite invasion on a southeastern Arizona grassland bird community. *The Wilson Bulletin* 110:403-408.
- Mack, M. C., and C. M. D'Antonio. 2003. Exotic grasses alter controls over soil nitrogen dynamics in a Hawaiian woodland. *Ecological Applications* 13:154-166.
- Masters, R. A., and R. L. Sheley. 2001. Principles and practices for managing rangeland invasive plants. *Journal of Range Management* 54:502-517.
- Mayeux Jr, H. S., and W. T. Hamilton. 1988. Response of false broomweed and associated herbaceous species to fire. *Journal of Range Management* 41:2-6.
- McCoy, S. D., J. C. Mosley, and D. M. Engle. 1992. Old World bluestem seedlings in western Oklahoma. *Rangelands Archives* 14:41-44.
- McCune, B., J. B. Grace, and D. L. Urban. 2002. *Analysis of ecological communities. MjM software design* Gleneden Beach, Oregon.
- McKenna, J., D. Wolf, and M. Lentner. 1991. No-till warm-season grass establishment as affected by atrazine and carbofuran. *Agronomy journal* 83:311-316.
- Menke, J. W. 1992. Grazing and fire management for native perennial grass restoration in California grasslands. *Fremontia* 20:22-25.
- Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63:327-366.
- Mills, M. S. L., F. Mills, M. Olmos, and Dean. 2011. Mount Moco: its importance to the conservation of Swierstra's Francolin *Pternistis swierstrai* and the Afromontane avifauna of Angola. *Bird conservation international* 21:119-133.

- Mittelhauser, J. R., P. W. Barnes, and T. G. Barnes. 2011. The effect of herbicide on the re-establishment of native grasses in the Blackland prairie. *Natural Areas Journal* 31:226-233.
- Monaco, T. A., B. L. Waldron, R. L. Newhall, and W. H. Horton. 2003. Re-establishing perennial vegetation in cheatgrass monocultures. *Rangelands* 25:26-29.
- Moreno, J. M., and W. C. Oechel. 1991. Fire intensity effects on germination of shrubs and herbs in southern California chaparral. *Ecology* 72:1993-2004.
- Moser, L. E., B. L. Burson, and L. E. Sollenberger. 2004. *Old World Bluestems*. American Society of Agronomy Monographs No. 45. American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America Publishers, Madison, Wisconsin.
- Myers, L., and V. Squires. 1970. Control of barley grass (*Hordeum leporinum*) by grazing management in irrigated pastures. *Animal Production Science* 10:151-155.
- Noy-Meir, I. 1975. Stability of grazing systems: an application of predator-prey graphs. *The Journal of Ecology* 63:459-481.
- Olf, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution* 13:261-265.
- Oudtshoorn, F. V. 2002. *Guide to grasses of Southern Africa*. Briza Publications, Pretoria.
- Owens, M. K., J. Mackley, and C. Carroll. 2002. Vegetation dynamics following seasonal fires in mixed mesquite/acacia savannas. *Journal of Range Management* 55:509-516.
- Pase, C. P. 1971. Effect of a February burn on Lehmann lovegrass. *Journal of Range Management Archives* 24:454-456.
- Paterson, M. F. 2011. The development of grass establishment mats for use in revegetation: Implications of seed biology and water uptake mechanisms. Ph.D. dissertation, The University of Queensland, Australia.
- Paynter, Q., and G. J. Flanagan. 2004. Integrating herbicide and mechanical control treatments with fire and biological control to manage an invasive wetland shrub, *Mimosa pigra*. *Journal of Applied Ecology* 41:615-629.

- Pekin, B. K., M. J. Wisdom, B. A. Endress, B. J. Naylor, and C. G. Parks. 2014. Ungulate Browsing Maintains Shrub Diversity in the Absence of Episodic Disturbance in Seasonally-Arid Conifer Forest. *PloS one* 9:e86288.
- Philipp, D., V. Allen, R. Mitchell, C. Brown, and D. Wester. 2005. Forage nutritive value and morphology of three Old World bluestems under a range of irrigation levels. *Crop science* 45:2258-2268.
- Popay, I., and R. Field. 1996. Grazing animals as weed control agents. *Weed Technology* 10:217-231.
- Potvin, M. A. 1993. Establishment of native grass seedlings along a topographic/moisture gradient in the Nebraska Sandhills. *American Midland Naturalist* 130:248-261.
- Preston, F. W. 1948. The commonness, and rarity, of species. *Ecology* 29:254-283.
- Raman, A., C. Schaefer, T. Withers, A. Raman, C. Schaefer, and T. Withers. 2005. Galls and gall-inducing arthropods: an overview of their biology, ecology and evolution. In *Biology, Ecology, and Evolution of Gall-inducing Arthropods*. Science Publishers, Inc., Enfield, New Hampshire:1-33.
- Rambo, J. L., and S. H. Faeth. 1999. Effect of vertebrate grazing on plant and insect community structure. *Conservation biology* 13:1047-1054.
- Ratajczak, Z., J. B. Nippert, and S. L. Collins. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology* 93:697-703.
- Ravi, S., P. D'Odorico, S. L. Collins, and T. E. Huxman. 2009. Can biological invasions induce desertification? *New Phytologist* 181:512-515.
- Rieske, L., H. Housman, and M. Arthur. 2002. Effects of prescribed fire on canopy foliar chemistry and suitability for an insect herbivore. *Forest ecology and management* 160:177-187.
- Rinella, M. J., B. D. Maxwell, P. K. Fay, T. Weaver, and R. L. Sheley. 2009. Control effort exacerbates invasive-species problem. *Ecological Applications* 19:155-162.
- Risser, P. G., E. Birney, H. Blocker, S. May, W. a. Parton, and J. Wiens. 1981. The true prairie ecosystem. Hutchinson Ross Publishing Company, Stroudsburg.

- Robocker, W., and B. J. Miller. 1955. Effects of clipping, burning and competition on establishment and survival of some native grasses in Wisconsin. *Journal of Range Management* 8:117-120.
- Roques, K., T. O'Connor, and A. Watkinson. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* 38:268-280.
- Ruffner, M. E., R. L. McCulley, J. A. Nelson, and T. G. Barnes. 2012. Ecosystem function differs between Old World bluestem invaded and native coastal prairie in South Texas. *Biological Invasions* 14:1483-1500.
- Rutherford, R., R. M. Cowling, D. M. Richardson, and S. M. Pierce. 2004. *Vegetation of southern Africa*. Cambridge University Press, Cambridge.
- Samson, F., and F. Knopf. 1994. *Prairie conservation in north america*. BioScience 44:418-421.
- Sather, N. 1987. Element Stewardship Abstract for *Bromus inermis* Awnless Brome, Smooth Brome. The Nature Conservancy, Arlington.
- Schindler, J. R., T. E. Fulbright, and T. Forbes. 2004. Shrub regrowth, antiherbivore defenses, and nutritional value following fire. *Rangeland Ecology & Management* 57:178-186.
- Schmidt, C. D., and K. R. Hickman. 2006. Stolon production by Caucasian bluestem (*Bothriochloa bladhii*). *Transactions of the Kansas Academy of Science* 109:74-76.
- Schmidt, E., M. Lotter, and W. McClelland. 2002. *Trees and shrubs of Mpumalanga and Kruger National Park*. Jacana Media, Johannesburg.
- Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. *Annual review of Ecology and Systematics* 28:517-544.
- Schuh, R. T. 1974. The Orthotylinae and Phylinae (Hemiptera: Miridae) of South Africa with a phylogenetic analysis of the ant-mimetic tribes of the two subfamilies of the world. *Entomologica Americana* 47:1-332.
- Scott, G., E. Springfield, and N. Coldrey. 2004. A pharmacognostical study of 26 South African plant species used as traditional medicines. *Pharmaceutical Biology* 42:186-213.

- Shaw, R. B. 2011. Guide to Texas grasses. Texas A&M University Press, College Station.
- Silcock, R., and P. Johnston. 1993. Tropical pasture establishment. 9. Establishing new pastures in difficult tropical environments—do we expect too much. *Tropical grasslands* 27:349-358.
- Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1:21-32.
- Simmons, M. T. 2005. Bullying the bullies: the selective control of an exotic, invasive annual (*Rapistrum rugosum*) by oversowing with a competitive native species (*Gaillardia pulchella*). *Restoration Ecology* 13:609-615.
- Simmons, M. T., S. Windhager, P. Power, J. Lott, R. K. Lyons, and C. Schwope. 2007. Selective and Non-Selective Control of Invasive Plants: The Short-Term Effects of Growing-Season Prescribed Fire, Herbicide, and Mowing in Two Texas Prairies. *Restoration Ecology* 15:662-669.
- Sims, P. L., and C. L. Dewald. 1982. Old World bluestems and their forage potential for the Southern Great Plains--a review of early studies. *Agricultural reviews and manuals*. ARM-S-United States, Dept. of Agriculture, Agricultural Research Service, Southern Region. New Orleans, Louisiana.
- Smeins, F., D. Diamond, and C. Hanselka. 1992. Coastal prairie. *Ecosystems of the world* 8:269-290.
- Smet, M., and D. Ward. 2005. A comparison of the effects of different rangeland management systems on plant species composition, diversity and vegetation structure in a semi-arid savanna. *African Journal of Range and Forage Science* 22:59-71.
- Smith, M. D., and A. K. Knapp. 1999. Exotic plant species in a C4-dominated grassland: invasibility, disturbance, and community structure. *Oecologia* 120:605-612.
- Snyman, H. 2004. Short-term influence of fire on seedling establishment in a semi-arid grassland of South Africa. *South African Journal of Botany* 70:215-226.
- Snyman, H. 2009a. Germination potential of *Seriphium plumosum* (bankrupt bush, slangbos or vaalbos). *Grassroots* 9:43-48.
- Snyman, H. 2009b. A philosophical approach to the distribution and spread of *Seriphium plumosum*. *Grassroots* 9:29-37.

- Snyman, H. 2010. Allelopathic potential, seed ecology and germination of the encroacher shrub *Seriphium plumosum*. *African Journal of Range & Forage Science* 27:29-37.
- Snyman, H. 2011. Short-term response of the encroacher shrub *Seriphium plumosum* to fire. *African Journal of Range & Forage Science* 28:65-77.
- Snyman, H. 2012. Habitat preferences of the encroacher shrub, *Seriphium plumosum*. *South African Journal of Botany* 81:34-39.
- Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution* 19:46-53.
- Survey, N. C. S. 2014. National Cooperative Soil Characterization Database. United States Department of Agriculture, Natural Resource Conservation Service. Washington D.C., USA. Retrieved from <http://ncsslabdatamart.sc.egov.usda.gov/>
- Tilman, D., P. Reich, H. Phillips, M. Menton, A. Patel, E. Vos, D. Peterson, and J. Knops. 2000. Fire suppression and ecosystem carbon storage. *Ecology* 81:2680-2685.
- Towne, E. G., D. C. Hartnett, and R. C. Cochran. 2005. Vegetation trends in tallgrass prairie from bison and cattle grazing. *Ecological Applications* 15:1550-1559.
- Towne, G., and C. Owensby. 1983. Annual broomweed (*Gutierrezia dracunculoides* (DC.) Blake) response to burning and mulch addition. *Journal of Range Management Archives* 36:711-712.
- Trollope, W., A. Potgieter, and N. Zambatis. 1989. Assessing veld condition in the Kruger National Park using key grass species. *Koedoe* 32:67-93.
- Tropicals, T. 2014. Catalog of rare and tropical plants for home and garden. Retrieved from http://toptropicals.com/cgi-bin/garden_catalog/cat.cgi?find=seriphium&search_op=and&keyword_op=and&language=e&number=10&no_change_lang=1&v1=sss&user=tt&sale=1&first=1.
- Twidwell, D., W. E. Rogers, E. A. McMahon, B. R. Thomas, U. P. Kreuter, and T. L. Blankenship. 2012. Prescribed extreme fire effects on richness and invasion in coastal prairie. *Invasive Plant Science and Management* 5:330-340.
- USDA, N. 2014. The Plants database. National Plant Data Team, Greensboro, North Carolina, USA.

- Uys, R. G., W. J. Bond, and T. M. Everson. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. *Biological Conservation* 118:489-499.
- Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annual review of Ecology and Systematics* 31:197-215.
- Van Auken, O. W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management* 90:2931-2942.
- Van de Vijver, C., P. Poot, and H. Prins. 1999. Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. *Plant and Soil* 214:173-185.
- Van Wilgen, B. W., R. M. Cowling, and C. J. Burgers. 1996. Valuation of ecosystem services. *BioScience* 46:184-189.
- Venner, M. 2006. Control of invasive species: a synthesis of highway practice. Transportation Research Board, Washington D.C., 1st, edition.
- Vitousek, P. M., L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois, and P. A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238:802-804.
- Voigt, J. W., and J. Weaver. 1951. Range condition classes of native midwestern pasture: an ecological analysis. *Ecological Monographs* 21:39-60.
- Walker, B. H., D. Ludwig, C. S. Holling, and R. M. Peterman. 1981. Stability of semi-arid savanna grazing systems. *The Journal of Ecology* 69:473-498.
- Walker, B. H., and I. Noy-Meir. 1982. Aspects of the stability and resilience of savanna ecosystems. In *Ecology of tropical savannas*. Springer, Berlin, Heidelberg.
- Warren, S., C. Scifres, and P. Teel. 1987. Response of grassland arthropods to burning: a review. *Agriculture, ecosystems & environment* 19:105-130.
- Watt, L. 1978. Some characteristics of the germination of Queensland blue grass on cracking black earths. *Crop and Pasture Science* 29:1147-1155.
- Watt, L. 1982. Germination characteristics of several grass species as affected by limiting water potentials imposed through a cracking black clay soil. *Crop and Pasture Science* 33:223-231.

- Weaver, J. E. 1968. *Prairie plants and their environment. A fifty-year study in the midwest.* University of Nebraska Press, Lincoln.
- Webb, R. H., and S. S. Stielstra. 1979. Sheep grazing effects on Mojave Desert vegetation and soils. *Environmental Management* 3:517-529.
- Wepener, J.-P. 2007. *The control of Stoebe vulgaris encroachment in the Hartbeesfontein area of the North West Province/JP Wepener.* Ph.D. dissertation, North-West University.
- Westbrooks, R. G. 1998. *Invasive plants: changing the landscape of America.* US Government Documents Utah Regional Depository:490.
- Wheeler, C. W., S. R. Archer, G. P. Asner, and C. R. McMurtry. 2007. Climatic/edaphic controls on soil carbon/nitrogen response to shrub encroachment in desert grassland. *Ecological Applications* 17:1911-1928.
- Whisenant, S. G. 1990. *Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications.* General Technical Report INT - U.S. Department of Agriculture, Forest Service, Intermountain Research Station Ogden, Utah.
- Wilsey, B. J., and H. W. Polley. 2003. Effects of seed additions and grazing history on diversity and productivity of subhumid grasslands. *Ecology* 84:920-931.
- Wilson, R. T., B. E. Dahl, and D. R. Krieg. 1975. Carbohydrate concentrations in honey mesquite roots in relation to phenological development and reproductive condition. *Journal of Range Management* 52:286-289.
- Wittenberg, R., and M. J. Cock. 2001. *Invasive alien species: a toolkit of best prevention and management practices.* CAB International. Wallingford, United Kingdom.
- Wright, H. A., S. C. Bunting, and L. F. Neuenschwander. 1976. Effect of fire on honey mesquite. *Journal of Range Management* 29:467-471.
- Xu, B., Zhao, H.L., Liu, X.M., Nemoto, M., Ohkuro, T. 1998. An experimental study on the differential characteristics of the plant communities under the different grazing gradation and the mechanism of desertification in the natural sandy rangeland. *J. Lanzhou University* 30:137 - 142.
- Yong-Zhong, S., L. Yu-Lin, C. Jian-Yuan, and Z. Wen-Zhi. 2005. Influences of continuous grazing and livestock exclusion on soil properties in a degraded sandy grassland, Inner Mongolia, northern China. *Catena* 59:267-278.

- Young, J. A., and R. A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. *Journal of Range Management* 31:283-289.
- Young, J. A., R. A. Evans, R. E. Eckert Jr, and B. L. Kay. 1987. Cheatgrass. *Rangelands* 9:266-270.
- Ziska, L., J. Reeves, and B. Blank. 2005. The impact of recent increases in atmospheric CO₂ on biomass production and vegetative retention of Cheatgrass (*Bromus tectorum*): implications for fire disturbance. *Global Change Biology* 11:1325-1332.
- Zouhar, K., J. K. Smith, S. Sutherland, and M. L. Brooks. 2008. Wildland fire in ecosystems: fire and nonnative invasive plants. General Technical Report 42:6. USDA Forest Service, Rocky Mountain Research Station Ogden, Utah, USA.

APPENDIX

A.1 DESCRIPTION OF MODEL: Conceptual framework of the model is based on state variables (square boxes) and the transfer of materials or information to the main variables (arrowed circular figures). Each variable and transfer of the conceptual model is described below.

State variables (S)

“Live invasive/or native grass abundance”: this is the aboveground abundance (kg biomass per month) of live or photosynthetically active vegetation. This variable is altered by seasonal (dormant vs. growing) rates of growth.

“Dead fuel invasive/or native grass abundance”: this represents the aboveground abundance (kg biomass per month) of “dead” standing grass that is considered available fine fuel for the fire and not for cattle consumption. This variable is driven by the amount of live green grass that senesces and becomes photosynthetically inactive vegetation during the dormant season (winter for this particular species).

Material transfers (and information transfers) describing the native and invasive grass component of the model

“Gain invasive/or native”: live green vegetative gain to the system as a result of the variables month and fire season (assuming certain seasons of prescribed fire application will have positive or negative consequences for foliar biomass).

“Transition to senescence invasive/or native”: contributes to standing ‘dead’ fuel loads. Live green biomass transitions to ‘dead’ standing fuel depending on the season (month). “Dead” in this scenario signifies that the aboveground foliage has senesced (the grass is dormant and is no longer actively photosynthesizing and producing green foliage). “Senescence loss: invasive/or native”: this material transfer pertains to the dead plant material that is no longer photosynthetically active and is completely detached from the plant (litter). This component only contributes information to the rate of fire spread or intensity.

“Invasive/or native dead loss due to fire”: attached senesced grass that becomes fuel for the fire.

“Invasive/ or native loss due to cattle”: the amount of biomass lost due to ungulate herbivory. I assume that the cattle are only consuming green vegetation. This material transfer is influenced by the forage requirements of the herd and the relative amount of available vegetation.

“Invasive/ or native loss due to fire”: the amount of dead standing fuel that is consumed in the fire.

