

FROM THEORY TO APPLICATION: EXTREME FIRE, RESILIENCE,
RESTORATION, AND EDUCATION IN SOCIAL-ECOLOGICAL DISCIPLINES

A Dissertation

by

DIRAC LARS TWIDWELL JR.

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

DOCTOR OF PHILOSOPHY

May 2012

Major Subject: Rangeland Ecology and Management

From Theory to Application:

Extreme Fire, Resilience, Restoration, and Education in Social-Ecological Disciplines

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ABSTRACT

From Theory to Application: Extreme Fire, Resilience, Restoration, and Education in
Social-Ecological Disciplines. (May 2012)

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Conceptual and theoretical advancements have been developed in recent years to break down the assumptions and traditional boundaries that establish seemingly independent disciplines, and the research outlined in this dissertation aspires to build on these advancements to provide innovative solutions to a broad array of modern problems in social-ecological. I used a variety of techniques to address challenges ranging from disconnections between theory and application, perceived versus realized roles of prescribed fire in resprouting shrublands, and the need for broader participation in research as part of undergraduate education.

The chapters in this dissertation serve as a case-study approach across multiple scientific disciplines that overcome the traditions and assumptions that conflict with our ability to develop innovative solutions to modern social-ecological problems. First, I bridge theoretical and applied concepts by showing how recent theoretical advancements in resilience can be integrated into a predictive framework for environmental managers. Second, experimental data from multiple experiments were collected in two ecological

regions of Texas to assess the potential for using extreme fire, in isolation and in combination with herbicide, as a novel intervention approach in resprouting shrublands of the southern Great Plains. The findings from these experiments demonstrate the importance of moving past traditional assumptions of when prescribed fire should be applied to demonstrate new patterns of woody plant responses to the applications of “more extreme” prescribed fires while not causing undesirable invasions by exotic grasses and exotic insects. Finally, I initiated a PhD instructed course on undergraduate research that sought to increase undergraduate participation while lowering the costs of conducting research. This chapter shows how traditional approaches of supporting undergraduate research are incapable of meeting the broader goals established by society and reveal a novel approach that can provide an additional pathway for supporting undergraduate student participation at large, research-based universities. Ultimately, this research suggests that our capacity to enhance services in social-ecological systems ultimately hinges upon the integration of theoretical and applied concepts that drive policy and governance and overcoming the assumptions and traditions that limit their integration.

DEDICATION

to
Kristin and Marin
(and Jake)

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CHAPTER I

INTRODUCTION:

TRADITIONS AND DUALISMS IN SCIENTIFIC DISCIPLINES AND THEIR CONFLICTS WITH INNOVATIVE SOLUTIONS TO MODERN PROBLEMS

Science versus management, theory versus application, social versus ecological systems, restoration versus conservation, prescribed fire versus wildfire - all classification schemes of human origin that establish discrete disciplinary boundaries yet represent false delineations in an interconnected world. Scientists study the natural world, and managers manage it; theoretical developments in basic research lead to applied hypotheses; scientific theories drive management applications. Yet, these traditional approaches are failing to provide solutions in an era where there are growing gaps between scientists and managers, basic and applied researchers, and those that develop theories from those that apply them. Even the pursuit for knowledge has led to fragmented scientific disciplines that further reinforce disciplinary boundaries and prevent the flow of information across areas of science. As an example, most scientists study social systems and ecological systems in isolation even though it is clear that modern problems require interdisciplinary solutions that couple social-ecological dynamics. Developing interdisciplinary solutions, however, requires us to overcome long-held cultural practices and attitudes that reinforce disparate viewpoints. Not only

This dissertation follows the style of Restoration Ecology.

must scientists be fluent as managers (and vice versa), but our view of pattern and process in nature must not be biased by our heritage or by internal pressures from society. Consider something as simple as prescribed fire versus wildfire. Prescribed fire can be controlled. Wildfire cannot. This dichotomy has framed how Western scientists have approached the study of fire, its value in modern society, its use in environmental management, and its view as a destructive wildland force in human systems. Other cultures do not share the same beliefs. Fire is viewed in a universal context, and the distinctions of prescribed fire versus wildfire do not exist.

Overcoming traditional disciplinary boundaries to develop innovative solutions for modern social-ecological problems represents a great challenge. Demand is growing for more efficient utilization and management of environmental services. The ability to provide these services ultimately hinges upon the integration of theoretical and applied concepts that drive ecosystem governance. Such an approach requires interdisciplinary thinking that couples social-ecological dynamics and develops an understanding of how physical, chemical, ecological, social, and cultural processes interact. Developing this type of interdisciplinary approach demands that future generations of social-ecological stewards are developed under an education framework that differs from current and past educational curricula, which reinforced disparate disciplines and inhibited creative, multifaceted solutions.

Conceptual and theoretical advancements have been developed in recent years to break down the traditional boundaries that establish seemingly independent disciplines. Social versus ecological systems or the view and study of humans as distinct from nature

has been integrated into coupled social-ecological systems and described as a panarchy (Gunderson and Holling 2002). Restoration and conservation have been integrated as unified ecological objectives under the basic principles of intervention ecology (Hobbs et al. 2011). Conventional distinctions of prescribed fire versus wildfire has been blurred and proposed to be constructs of human thought rather than distinct physical processes by Taylor (2011) in “Taking the Wild out of Fire.” Finally, the theoretical foundations that drive the techniques used for learning, teaching, and education are sought to be guided by integrating multiple cognitive elements, as represented in the Theory of Successful Intelligence (Sternberg 1999), instead of focusing solely on rote memorization.

The aforementioned approaches drove my thinking and approach to research during my PhD and are important features in this dissertation. The research activities outlined in my dissertation aspire to span traditional boundaries and to provide innovative solutions to modern problems in social-ecological systems of Texas. It is obviously impossible to accomplish this goal for all social-ecological issues in the time frame of a single dissertation. Even so, the chapters provide unique directions across an array of “independent” disciplines, seeking to span theoretical and applied dimensions of ecosystem science, management, and education. Each chapter therefore serves as a case-study to meet this overarching theme.

Chapter 2, *Forecasting collapse and restoration of social-ecological systems using a quantitative resilience framework*, seeks to expand upon current conceptual and theoretical approaches for quantifying transformations of social-ecological systems, their

resilience, the approaches needed to overcome the thresholds that reinforce desirable and undesirable properties of a system, and how resilience-based frameworks can provide a predictive basis for restoration activities.

The remaining chapters showcase examples that link theoretical and applied concepts in science and education. Chapter 3-6 feature empirical studies that test key aspects of the conceptual and theoretical ideas introduced in chapter two and are among the first experimental manipulations in the Great Plains to design, ignite, and control prescribed fires in experimental plots under conditions that typify wildfires. In chapter 3, *Long-term effects of fire, livestock herbivory removal, and climatic variability in Texas semiarid savanna*, I examined 12 years of data from an ongoing, long-term study on the Edwards Plateau ecological region of Texas that reintroduced the frequency and intensity of the historic fire regime (high intensity, 4-6 year frequency) in different seasons (i.e. repeat summer versus repeat winter burn treatments). An important contribution of this chapter is that I use relatively recent advancements in statistical techniques to test for significant differences among treatments in a data set with minimal replication (e.g., $N = 2$) rather than relying on pseudoreplication and potentially producing unreliable results.

Chapter 4, *Prescribed extreme fire effects on species richness and invasion in coastal prairie*, compares native and exotic herbaceous species richness and aboveground herbaceous biomass one year following the application of high intensity fires in Texas coastal prairie. Findings from this experiment counter widely-held, unsubstantiated assumptions in coastal tallgrass prairies that prescribed extreme fire will

decrease native herbaceous species richness and lead to rapid invasions by KR bluestem and other alien species.

Chapter 5, *Does prescribed fire facilitate fire ant invasions in coastal prairies or aid management by improving mound search efforts?*, uses the high intensity prescribed fire experiment discussed in Chapter 4 to assess (1) the efficacy of individual mound-based fire ant chemical control strategies, based on the proportion of mounds that are likely to be found in prairie, and (2) to track changes in the densities of fire ant and native red harvester ant mounds in response to prescribed fire. The findings from this experiment suggests that using chemical control methods in combination with fire, which increases the capacity to locate fire ant mounds, may improve fire ant control.

Chapter 6, *Intervention with extreme prescribed fire and herbicide in resprouting shrublands of the southern Great Plains*, introduces a replicated study that was established across two ecological regions of Texas to determine the potential for grassland and savanna restoration from a heavily invaded mesquite woodland state.

Chapter 7, *PhD student instructed undergraduate research: more than an undergraduate education and doctoral dissertation*, introduces a new approach that has the potential to provide a stable, long-term environment for undergraduate research in academia. I compared this framework to traditional approaches of funding undergraduate research (e.g. NSF REU) using data from 8 undergraduate students that have conducted mentored, autonomous research over the past two years in an undergraduate research program that I initiated in the Department of Ecosystem Science and Management.

CHAPTER II
FORECASTING COLLAPSE AND RESTORATION OF SOCIAL-ECOLOGICAL
SYSTEMS USING A QUANTITATIVE RESILIENCE FRAMEWORK

Introduction

Successful restoration of ecological phases or states hinges upon our ability to shift resilience mechanisms from those that maintain a degraded phase to those that support large amounts of environmental services (Carpenter and Cottingham 1997, Gunderson and Holling 2002). Collapsing a degraded phase is often difficult. Sufficient changes in biotic and abiotic factors from the previous phase can reinforce the resilience of a degraded phase, making it resistant to restoration efforts (Bakker and Berendse 1999). For restoration to occur, the mechanisms that maintain the degraded phase must be overcome to promote a new set of stabilizing feedbacks (Carpenter and Cottingham 1997). Yet in most restoration efforts the driving feedbacks are reintroduced in a manner consistent with how they stabilized the previous, more productive phase and are typically incapable of collapsing the current, degraded phase (Scheffer et al. 2001).

The inability to consistently promote or to mitigate for the collapse of ecological phases demonstrates the need for resilience concepts to be more quantitatively linked with restoration and management techniques. Perhaps the greatest promise of the resilience concept is its potential to be used as a measure of whether an ecological phase will persist or collapse in response to complex ecosystem drivers. The definition of the term, resilience, was initially introduced as a measure of the amount of change a phase

can withstand and continue to persist (Holling 1973). The most important part of this definition is that resilience is “a measure of the amount of change”, and therefore, can be quantified or estimated for all ecological phases. Instead, the term has evolved into a more general “buzz word” with multiple ecological meanings and without a specific quantitative framework (Carpenter et al. 2001, Walker et al. 2004). A conceptual, qualitative understanding of resilience is further reinforced by the abundance of research searching for generalities in the pattern of resilience related relationships, which greatly hinders our ability to test traditional models of resilience with data or to apply those models in management. For example, much of the work on phase stability and resilience has focused on species-level interactions, which in general are not the primary drivers of phase shifts (Ives and Carpenter 2007), and less attention has been attributed to pulse events such as disturbance. Considerably less research is available that pursued quantitative resilience relationships in ecological systems (but see Peterson 2002). Of those that have been performed, models that investigate resilience with respect to the adaptive capacity of coupled social-ecological systems (e.g. Carpenter and Brock 2008) appear to be of greatest appeal to policy makers and land managers (Berkes and Folke 1998, Carpenter and Gunderson 2001).

The adaptive capacity of social-ecological systems refers to the capacity to adjust to changes in the intrinsic and extrinsic properties that exhibit force on the system. Building adaptive capacity therefore requires an understanding of how drivers in both ecological and social systems interact to impact desirable environmental goods and services (Adger 2000, Folke et al. 2005). The resilience concept provides the foundation

to analyze the dynamics of social-ecological systems (Folke 2006) but there continues to be a lack of an approach that directly tests and links ecological relationships to social perceptions, policies, and practices. To link these concepts and make them more practical for application by governing officials and land managers, resilience may need to be structured within more of a predictive or forecasting framework (Thrush et al. 2009).

The purpose of this paper is to apply the resilience concept within a framework that provides a predictive platform for the management and restoration of desired resources within a coupled social-ecological system. While the concepts introduced in this paper are applicable to a diverse set of ecological and social drivers, we use prescribed fire to introduce this resilience framework because the application or removal of fire can drive phase shifts, yet fire is perceived in social systems to be of great risk to life and property while providing and of little benefit. Here we focus on integrating social and ecological constraints pertaining to fire by showing how (1) the use of prescribed extreme fire can overcome ecological resilience within a post-grassland, juniper woodland, (2) quantifying aspects of resilience over time can benefit restoration efforts, and (3) the development of public, cooperative networks can overcome social resilience to the use of prescribed extreme fire.

Overcoming ecological resilience: case study

The loss of grassland and savanna to juniper woodland is a classic example of a phase transition that is difficult to restore (Fuhlendorf et al. 1996, Briggs et al. 2005).

The removal of fire in grasslands is largely responsible for this conversion. Non-resprouting, fire sensitive trees, such as Eastern redcedar (*Juniperus virginiana*) and Ashe juniper (*Juniperus ashei*), particularly benefited and are now among two of the most widespread native woody plant invaders throughout the continent (Van Haverbeke and Read 1976, Little 1979). Once dominant, juniper woodlands are highly stable ecological phases resilient to the reintroduction of fire. Although traditional prescribed fires of low intensity are capable of maintaining grasslands and savannas (Bragg and Hulbert 1976, Briggs et al. 2002), the same fires are wholly ineffective at restoring grasslands after conversion to juniper woodland has occurred. No study has shown that reintroducing prescribed fire can force the collapse of a post-grassland, mature juniper woodland, irrespective of their frequency or seasonal application (Table 1).

The ineffectiveness of fire is linked to the emergence of a new set of feedbacks that promote juniper woodland resilience. As juniper increases in size, density, and distribution, the productivity (fine fuel load) and continuity of dominant grasses are reduced, thereby lowering fire intensity and juniper mortality from fire (Engle et al. 1987, Briggs et al. 2002). It has often been suggested that fires conducted in more extreme conditions could increase woody plant mortality (Fuhlendorf et al. 1996, Briggs et al. 2005), but experimental data from such fires are limited since most fire practitioners are unwilling or unable to burn in conditions that generate intense fires.

We designed a study at the Texas A&M Agrilife Research Center located near Sonora, TX, USA, so that prescribed fires could be safely conducted in environmental conditions that typically produce wildfires in order to determine if fire can overcome the

resilience of a mature juniper woodland; we compared the effects of prescribed extreme fire (i.e. high intensity fires) with traditional, low intensity fires. Historically, this site was characterized as grassland, with total woody canopy coverage of less than 5% (Fuhlendorf and Smeins 1997). Due to extensive juniper invasion and maturation, total woody cover now exceeds 40%, at which point, regional management agencies states that fire alone is ineffective as a restoration strategy (e.g. USDA, NRCS 2004).

Unlike traditional applications of prescribed fire, prescribed extreme fire has the potential to overcome the resilience of woodland ecosystems to restore grasslands and savannas. Our experiment showed the resilience of an entire ashe juniper woodland community was overcome (i.e. all juniper trees were killed) using prescribed extreme fire (Fig. 1), regardless of variation in fine fuel load or differences in tree height (Twidwell et al. 2009), leading to the emergence of a herbaceous dominated ecosystem. Such findings, however, were observed only for prescribed fires ignited in low herbaceous fuel moistures, resulting from an extended period of drought, which prompted the types of fire intensities observed in severe wildfires. When fires were ignited in more traditional, mild fire conditions, approximately 80% of juniper trees survived and the system remained in a juniper dominated phase (Fig. 1).

Quantifying aspects of resilience

Finding that prescribed extreme fire can overcome the resilience of non-resprouting juniper woodlands reveals a useful set of information for understanding resilience within the adaptive cycle of grassland and juniper woodland phases. The

theory of the adaptive cycle states four characteristic trends exist to describe ecosystem dynamics; they are rapid growth and exploitation (r), conservation or maintenance (K), collapse or release (Ω), and renewal or reorganization (α) (Gunderson et al. 1995, Gunderson and Holling 2002). We focus on two of these areas, maintenance (K) and collapse (Ω), to provide a framework for quantifying resistance and persistence, two important features of resilience. Other characteristic features of the adaptive cycle (i.e., α , r) could also be incorporated into the featured framework but fall outside the context of resilience for the purposes of this paper. Our approach aims to provide a more quantitative depiction of resilience and should be viewed as a point of departure that complements more traditional, qualitative characterizations (e.g., resilience is the width or size of the basin in the ball and cup model, Fig. 2). While grassland and non-resprouting juniper woodlands are simple examples of fire dependent and post-fire dependent phases, they provide a foundation for the advancement of resilience management and for predicting the impacts of restoration. Moreover, the Texas A&M Agrilife Research Center is an ideal model system to test aspects of resilience within the adaptive cycle because the system lacks exotic, invasive herbaceous or woody plants that rapidly invade following disturbance, the species of concern is a non-resprouting fire sensitive tree, and the system is a simple fire-driven cycle between two plant communities, grassland and juniper-dominated woodland. The ability to quantify aspects of resilience within this system can, therefore, provide a solid foundation for characterizing resilience within more complex post-fire dependent phases as well as other ecosystems driven by alternate pulse perturbation events.

To calculate phase resistance and phase persistence, grassland (G) and juniper woodland (W) from the case study were plotted over time in terms of the minimum amount of fire intensity required to maintain each phase (I_K) relative to the minimum amount associated with their collapse (I_Ω) (Fig. 3). Phase resistance (R) is defined as the maximum amount of change a phase can absorb before its collapse. The simplest way to calculate ecological resistance is to take the difference of the amount required for phase maintenance from the amount associated with phase collapse (i.e., $R = \Omega - K$). Since juniper woodland does not require fire to maintain itself (i.e., $I_{K,W} = 0$) its resistance to fire is therefore the amount required for its collapse (i.e., $R_W = I_{\Omega,W}$; $\text{kJ m}^{-1} \text{s}^{-1}$). This intensity, or threshold, lies somewhere between the two fire events observed in this case study and could be derived through further experimentation. In contrast, the resistance of this grassland to the removal or reduction of fire is, or approaches, zero (i.e., $R_G \sim I_{\Omega,G} \sim I_{K,G}$; $\text{kJ m}^{-1} \text{s}^{-1}$). This should be consistent for other fire dependent phases. Fire is an integral part of the feedbacks that make fire dependent phases resilient to other forces of change and the lack of any resistance to cope with the reduction or removal of fire should be intuitively obvious. Such phases require some amount of fire to persist (or else they would not be fire dependent) and simply removing or reducing this amount results in their collapse.

The persistence (ϕ) of each phase is defined here as the length of time an ecological phase continues to persist after the conditions required to collapse that phase have been surpassed (i.e., $\phi = t_{f,\Omega} - t_{O,\Omega}$; s/days/mo/yr). Although phase persistence was not specifically tracked in our study, we can use others' findings from these ecosystems

to infer the relative persistence of grassland and juniper woodland. As defined here, phase persistence is extremely low for non-resprouting juniper woodlands; their collapse occurs almost simultaneously with the input of fires at intensities above the collapse threshold. At that point the system enters into a period of reorganization. As shown in the case study, all juniper trees were completely consumed by prescribed extreme fires, resulting in the immediate collapse of the juniper woodland ecosystem and the emergence of a grassland dominated ecosystem (Fig. 1). On the other hand, this grassland ecosystem exhibits high persistence. It may take over 20 years for grassland to collapse after the removal of fire from this ecosystem (i.e., $\phi \sim 20$ years) (Fuhlendorf et al. 1996).

Resilience, restoration, and forecasting

Forecasting techniques provide a sound basis for integrating theoretical concepts of resilience into on-the-ground restoration objectives. Forecasting is used to support the application of a decision or management strategy or to test a scientific hypothesis (Botkin et al. 2007). Policy-makers and resource managers often rely on forecasting techniques to predict and plan for changes in desirable ecosystem services (Clark et al. 2001).

In ecology, forecasting has been broadly applied. Forecasting techniques have been used to project global losses in biodiversity in response to global change (Sala et al. 2000), human facilitation of biological invasions (Levine and D'Antonio 2003), the impacts of agricultural expansion (Tilman et al. 2001), among others, but its primary

application is to project the impacts of climate change (IPCC 2001, Meehl and Tebaldi 2004). While models produced from forecasting techniques are limited, they are useful in situations where the pre-existing conditions, assumptions, and uncertainties of the model are well defined and understood (Clark et al. 2001, Botkin et al. 2007).

A quantitative framework that directly integrates forecasting into a resilience framework can greatly enhance attempts to manage and restore desirable ecosystem services. The lack of conceptual frameworks, much less quantitative ones, continues to limit restoration practices (Allen et al. 1997). By depicting the maintenance and collapse of ecological phases over time, a natural resource manager is able to project the magnitude of change required to maintain or achieve a desired phase relative to the magnitude required to maintain current and previous phases. Such an approach is greatly needed for restoration ecology to continue to move past the “artistry” stage and develop into an applied scientific discipline founded on quantitative, theoretical concepts (Brown 1994, Hobbs and Norton 1996). Managers can weigh costs associated with collapsing a “degraded” phase versus the benefits and costs of maintaining the projected desired phase, and compare those to the costs, risks, and benefits of partial effort or inaction. Further experimentation and data accumulation by researchers will then enable resource professionals to evaluate the potential success of management and restoration strategies prior to their implementation (*sensu* Hobbs and Harris 2001). As more information becomes available, the uncertainty associated with the impacts of various management strategies will become more evident and expectations associated with restoration results will become clearer.

Ecological phases and resilience are dynamic

Advancements in theoretical and applied concepts in restoration may improve our ability to manage ecosystem services but a constant, growing demand of society is to manage and restore ecosystems in the face of environmental change. One of the most common applications of ecological forecasting is to predict how climate and disturbance will impact the composition and distribution of ecological phases over time, rendering it possible for direct integration with the quantified model presented here. Using this model, we illustrate how changes in other ecological drivers can alter the resilience of grassland and juniper woodland resilience in this system (Fig. 4).

The cycle of maintenance and collapse between grassland and juniper woodland (Fig. 3) can, in theory, perpetually repeat itself as long as the current factors driving phase transitions remain constant. Fire (including its removal) is currently the primary driver of phase transitions in this system but changes in other drivers or the emergence of new ones can disrupt the cyclic capacity of this system. Changes in climate, the introduction and rapid expansion of invasive species, and interactions with other disturbances (e.g., herbivory) all have the potential to impact fire regimes and alter the magnitude of fire required to shift from one phase to another (D'Antonio and Vitousek 1992, Mack and D'Antonio 1999, Brooks et al. 2004).

It is therefore critical to recognize that the maintenance, collapse, and corresponding resilience of ecological phases are not static and will change over time (Scheffer and Carpenter 2003). For example, current climatic conditions favor juniper

woodland when fire is removed from our site in Central Texas, but climate changes could further enhance or degrade grassland resilience. Climate changes that bring about increased rainfall might be perceived by many to be a benefit to grasslands because of increased primary production, but the opposite conclusion may be derived when viewing the system over time within the resilience framework. Larger quantities of rainfall can increase the invasive potential of woody plants as germination, photosynthesis, and seed production are enhanced (Brown et al. 1997, Davis et al. 1999). In this case, a shorter fire return interval is needed to maintain grassland because the amount of time before grassland collapses is decreased if fire is removed (i.e. phase persistence) (Fig. 4A) (Fuhlendorf et al. 2008). By contrast, if rainfall is reduced in this system, the invasive potential of juniper woodland decreases, thereby reducing the fire return interval needed for phase maintenance and increasing grassland persistence. At some point, fire may be unnecessary for maintenance because conditions are insufficient to support the establishment and occurrence of mature juniper woodland. For example, 90% mortality of mature juniper had been observed during a severe drought at Sonora Agrilife Research Center (Merrill and Young 1959). The emergence of a long-term change in the magnitude of precipitation, in a manner consistent with short-term drought events, could ultimately result in a transition from the current fire driven adaptive cycle to an alternate adaptive cycle driven by a different ecological process, such as herbivory (Fig. 4B) (e.g. shortgrass steppe ecoregion; Milchunas et al. 1988).

It is important to clarify that the above examples are not to be viewed as highly probabilistic forecasts of expected change in this case study system; nor are we implying

that phase shifts are always deterministic events. Emergent forces acting upon the system could introduce a new set of selective pressures that result in an entirely novel ecosystem (Chapin and Starfield 1997, Hobbs et al. 2006). The key is that phase resilience can be quantified with respect to an ecological driver, but variability in that or other co-drivers can influence aspects of resilience, as shown here with precipitation. Resilience is therefore a dynamic, changing quantity that corresponds to the response of ecological phases to fluctuations in environmental conditions. Actual calculations of resilience will subsequently fluctuate as a result of the interactions of multiple drivers operating across various spatial and temporal scales that alter the conditions needed to maintain and collapse ecological phases (*sensu* Levin 1999). Our capacity to understand those interactions will determine the potential for stochasticities, probabilities, and levels of uncertainty to be integrated into the resilience framework to provide more efficient forecasts of phase shifts. Such an approach is a daunting task for ecological researchers, but it opens the opportunity to build adaptive capacity by opening dialogue between scientists, policy makers, land managers, and the general public (e.g. Sandker et al. 2007).

Overcoming social resilience

While quantifying ecological resilience can improve our understanding of ecological dynamics, this knowledge will not lead to widespread application of such knowledge unless we consider the properties and processes within social systems that promote or suppress ecological dynamics. Indeed, ecological and social systems are

inherently linked (Adger 2000). Social systems depend on the goods and services of ecological systems for individuals and communities to maintain livelihoods, economic stability, and social order, and in turn, social systems are organized by numerous institutions, each with formal structures or policies engrained in law and/or governance, which by promoting the maximization of resource production for societal use exert massive pressure on ecological systems (Machlis et al. 1990). The degree to which institutional policies act to support the production and sustainability of ecological services is often debated. Some contest such policies are in place only to support alternate social practices, lack the robustness to be effective during periods of environmental change, or put a greater emphasis on maximizing short-term production at the expense of long-term sustainability (Adger 2000). Regardless, the capacity for policy to most effectively manage and restore ecosystems will continue to be broadly debated as long as ecological and social dynamics are treated as independent disciplines (Hobbs and Norton 1996, Westley et al. 2002) rather than a coupled social-ecological system (Berkes and Folke 1998). By understanding the processes operating within a social system, and integrating those with a quantifiable, ecologically derived resilience model (e.g. Fig. 3), we can better understand how social practices promote or suppress dynamics of ecological systems. Such an approach may enable policies to be altered more rapidly so that ecosystems can be managed more effectively in the future. Here we discuss the social practices from the case study system that constrain the use of prescribed extreme fire and then present ways to overcome those constraints by directly

integrating them with aspects of resilience from the ecological system using a coupled social-ecological framework.

Although fire is such an important driver in the conservation and restoration of a diverse set of fire dependent systems, its use is regulated largely by social constraints (Yoder et al. 2004; Kreuter et al. 2008). The most dominant social constraint limiting prescribed fire is associated with the risk of fire escape (i.e. prescribed fire becoming wildfire). As a result, prescribed fire is often not applied at all and when it is applied it is normally designed to occur within a narrow range of mild, safe fire conditions to ensure safety and containment. A cautionary approach to prescribed fire may mitigate risks but it diametrically opposes the conditions required to maximize fire effects for restoration. Since society values conservation of diverse ecosystems as well as public safety, a reassessment of how fire is applied may be in order. For example, prescribed fire is most commonly approached with the following question, “Are we within the range of conditions needed to prevent spot-fires (i.e., to prevent unwanted fire ignitions outside the intended burn unit) and ensure containment?” However, if we are to integrate societal and ecological needs, future questions should be, “What conditions do we need to burn in to maintain or restore a fire-dependent phase (i.e. meet the ecological objectives of the fire), and given those conditions, how do we design the area to be burned so that containment is ensured (i.e. meet the social objectives of the fire)?” Such an approach is the key to designing restoration plans that can be successful, both ecologically and socially.

Approaching the application of fire from a social-ecological perspective can empower resource managers to mitigate risk while meeting restoration objectives. Such is the case for the Edward's Plateau Prescribed Burn Association (EPPBA, Table 2), a private organization in Texas focused on introducing prescribed extreme fire to restore fire dependent grasslands and savannas over broad spatial scales (Taylor 2005). Like most places, a negative perception of prescribed fire dominated the region at the time the EPPBA was founded, but since landowners were determined to use fire as a management tool, the risk of implementing prescribed extreme fire was the chief barrier facing the EPPBA. To minimize risk, a fire cooperative was established where neighbors assisted each other by pooling experience and fire equipment. A decade after its inception, the EPPBA has grown from 30 members to more than 500 with over one million acres enrolled in the organization (Table 2).

While the EPPBA has overcome risk to burn in more extreme conditions, application of fire within the group continues to be limited as a result of an alternate social constraint. The social barrier this time, however, pertains to limitations in understanding of the ecological system, or more specifically, the conditions necessary to achieve mortality on juniper (i.e. what is $I_{Q,W}$? – Fig. 3). The EPPBA was founded to burn in extreme fire conditions for restoration purposes, and subsequently, fires are only ignited when members are certain sufficient fire intensity will be produced to meet restoration objectives. As a result, numerous planned fires are cancelled because members are uncertain whether the desired effects will be achieved, even though conditions may be fully capable of producing the desired outcome.

The constraints limiting the EPPBA, as well as other social groups, can be resolved by integrating social thresholds with quantitative aspects of resilience. Limitations in ecological understanding correspond directly to the intensity required to overcome juniper woodland resistance ($R_w = I_{\Omega, W}$). Research can quantify the intensity of this threshold, and in addition, identify various combinations of fuel and weather conditions that correspond with that intensity level. Once this is accomplished, a multi-faceted threshold model can be produced that identifies how social and ecological factors interact to drive system dynamics (Fig. 5). In this depiction, the minimum conditions needed to achieve juniper mortality are shown by the dashed line and any combination of conditions above this line result in juniper mortality. Most prescribed fire practitioners traditionally apply fire under conditions that fall underneath the risk threshold, due to the risk aversion of most land managers. Under these conditions, the mortality of juniper is relatively low. In contrast, the EPPBA ignites fires almost exclusively under conditions that result in extremely intense fire and high juniper mortality. However, these members are not taking advantage of all the conditions that result in juniper mortality because of a lack of ecological understanding of multiple ecological drivers that lead to juniper mortality. Fires conducted within traditional fire prescriptions can lead to juniper mortality if enough fine fuel is available (Briggs et al. 2005, Twidwell et al. 2009), but since the amount required for mortality is unknown to most landowners, they only target fires in more extreme conditions to meet their goals.

While the framework described above focuses on the two social thresholds that constrain the use of fire in juniper woodlands, the concept can be similarly applied to

alternate, quantifiable ecological and social relationships to provide a greater understanding of the specific problems associated with the application and effectiveness of various resource management activities. For example, this framework is relevant to any invasive plant species with properly described mortality threshold parameters and can be coupled with the multitude of social drivers that interact at various spatial and temporal scales to determine how to structure policies to mitigate its invasion. However, social drivers vary across international, national, regional, and local levels, and even among social groups within the same level, and this variability will impact the restoration and management strategies applied in those systems. Many systems will therefore require more complex solutions than those needed to overcome ecological and social resilience in the case study presented here. The key to developing integrated social-ecological solutions will ultimately depend on our ability to quantify aspects of resilience in ecological phases, characterize the different social groups and different social constraints that support or suppress the maintenance and collapse of ecological phases, and the ability to adapt to changes in the environmental or social conditions acting upon the social-ecological system.

Conclusions

Demand is growing for more efficient utilization and management of environmental services. The ability to manage and restore these services ultimately hinges upon the integration of theoretical and applied concepts that drive ecosystem governance. Here we show how the development of a quantitative resilience model,

based on the maintenance and collapse of ecological phases, can be used to overcome resilience in a social-ecological system. Natural resource professionals and policy makers can then assess the risks and benefits associated with the application of different management strategies. To illustrate, we have shown fire can be successful in overcoming phase resistance in post-grassland juniper woodland if conditions permit sufficient fire intensity. However, current policies deter managers from burning in these conditions since they are beyond traditional safety recommendations (e.g. Wright and Bailey 1982). Unless policies change so that burns can be conducted in ‘more extreme’ conditions, social constraints such as perceived risks and a lack of ecological understanding will continue to cause fire to be largely unsuccessful as a management or restoration tool in fire dependent ecosystems.

Directly integrating social and ecological dynamics will become even more important in the future. An increasingly complex dilemma for modern society is to understand how best to adapt to increased limitations in environmental resources. Increasing human population size and resource consumption, fluctuating human values and economies, changes in biophysical processes at a global scale, and large-scale pulse disturbance events or surprises are merely a subset of challenges facing modern and future natural resource professionals and policy makers. Quantifying resilience within a forecasting framework can help provide a testable, decision support model for social and ecological planners, potentially leading to more effective utilization of current resources while lessening the impact of modern practices on future generations. Nevertheless, this framework can only help provide solutions to these challenges. The magnitudes and

rates with which society integrates those solutions into governing laws and principles will determine the actual impact of modern society on future social-ecological systems.

CHAPTER III
LONG-TERM EFFECTS OF FIRE, LIVESTOCK HERBIVORY REMOVAL, AND
WEATHER VARIABILITY IN TEXAS SEMIARID SAVANNA

Introduction

Semiarid savannas once covered more than 10% of the global land surface (Scholes and Walker 1993) but many are transitioning away from the grass-tree co-dominance that long characterized these ecosystems toward economically and aesthetically less desirable shrub-dominated woodlands (Hobbs and Mooney 1986; Trollope et al. 1989; Archer 1995; Silva et al. 2001; Brook and Bowman 2006). Such changes have been linked to problematic or invasive plant species, climate change, and human-induced alteration of top-down (e.g., fire, herbivory) and bottom-up (e.g., water, nutrients) controls (Johnson 1993; Scholes and Archer 1997; Bachelet et al. 2001; Bond and Midgley 2001; Bond 2008). Understanding the relative contributions and interactions among these causal drivers is therefore essential if rangeland managers are to maintain the desired proportion of grasses and trees that are essential to rangeland enterprises, livestock operations, and a variety of unique plant and animal species in semiarid environments.

Fire is an important top-down determinant of woody plant densities in many semiarid savannas (Scholes and Archer 1997; Bond et al. 2003; Sakranan 2004; Sakranan 2005; Higgins et al. 2007), but human induced alteration of other top-down controls has resulted in extensive changes to fire regimes in semiarid regions (Scholes

and Archer 1997). In particular, the global expansion of the cattle industry has led to unfavorable changes in fire-related feedbacks that maintain savanna (van Vegten 1983). Overstocking with cattle over long periods has enabled problematic woody plant species to invade by reducing fine fuel load, fire intensity, and fire effects on woody plant species (Scholes and Archer 1997; Roques et al. 2001; van Langevelde et al. 2003, Archibald et al. 2005). Moreover, expansion of the cattle industry to new regions has led to widespread displacement of domestic and native browsers (e.g. goats) that are remarkably effective at maintaining the density and structure of semiarid savanna when used in combination with fire (Trollope 1974; Higgins et al. 2000; Staver et al. 2009). As a result of the widespread reductions in grassland fuel loading, continuity, and fire intensity, heavy grazing with cattle has been implicated as the primary facilitating driver of woody plant encroachment in grassland and increased densities in savannas (Van Langevelde et al. 2003; Briggs et al. 2005).

Numerous woody plants are invading or causing other problems on the Edwards Plateau region of Texas, USA. Sacahuista (*Nolina texana* S. Watson), while not particularly invasive, is a toxic subshrub that can be life-threatening to cattle, sheep, and especially goats (Merrill and Schuster 1978; Taylor and Ralphs 1992). Prickly pear cactus (*Opuntia* spp.) can form dense thickets, limiting livestock movement, reducing herbaceous production, and displacing native grasses (Freeman 1992; Lotter and Hoffman 1998). Ashe juniper (*Juniperus ashei* J. Buchholz), Pinchot's juniper (*J. pinchotii* Sudw.), and honey mesquite (*Prosopis glandulosa* Torr.) are notorious for their

ability to rapidly invade grasslands and savannas in the absence of fire (Archer et al. 1988; Van Auken 2000).

This paper presents the findings from an ongoing, long-term comparison of the effects of fire in different seasons on semiarid savanna vegetation in the Edwards Plateau. Fire treatments were ignited in fire weather and fuel conditions that maximized fire intensity. Fires were conducted in the summer and winter every 6 years, on average, to match the estimated historical fire frequency of the region (Frost 1998) and to allow maximum fine fuel accumulation. Fire season is used as a proxy for fire intensity in this study since summer fires were specifically conducted in drought conditions to promote high intensity fires and maximize mortality of non-resprouting woody plants. Our objective is to determine if conducting fires during droughts in the growing season creates a different savanna community when livestock herbivory is excluded than burning in the winter or not burning.

Methods

Study area

This research was conducted in the Edwards Plateau ecological region on the Texas AgriLife Research Station (31°N; 100°W) located 56 km south of Sonora, Texas. This site features gently rolling topography on soils of the Tarrant silty clay series, which are members of the clayey-skeletal, montmorillonitic, thermic family of Lithic Haplustalls (Wiedenfeld and McAndrew 1968). The elevation of the station is 730 m. The mean frost free period is 240 days. Precipitation is highly variable within and

among years (median annual precipitation = 557 mm, range = 156 to 1,054 mm; station data records from 1919 - 2007). Precipitation is bimodal, usually occurring from intense, short-duration thunderstorms in the spring and autumn, interspersed with frequent, prolonged drought events. Plant communities include oak savanna, dominated by small clusters of live oak (*Quercus virginiana* Mill.) and pungent oak (*Q. pungens* Liebm.), and closed-canopy juniper woodland consisting of Ashe juniper and Pinchot's juniper, depending on management history (Kuchler 1964, Hatch et al. 1990, Fuhlendorf and Smeins 1998). Herbaceous vegetation is dominated by common curly mesquite (*Hilaria belangeri* (Steud.) Nash), Wright's threeawn (*Aristida wrightii* Nash), sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), hairy grama (*Bouteloua hirsuta* Lag.), Texas wintergrass (*Nassella leucotricha* (Trin. & Rupr.) Pohl), Texas cupgrass (*Eriochloa sericea* (Scheele) Munro ex Vasey), and to a lesser extent, little bluestem (*Schizachyrium scoparium* (Michx.) Nash).

A 12-ha portion of the station was fenced in 1994 to implement a long-term fire study. This section was chosen because it was one of the most homogenous units on the station. The area was characterized by similar soils, flat topography, consistent grazing and brush management history, and similar vegetation patterns (i.e., oak savanna). Sheep, goats, and cattle were removed from the unit prior to this experiment and all livestock were excluded for the duration of this study.

Six experimental units of equal area (2-ha) were established in the 12-ha section. Each unit was randomly assigned a long-term seasonal burn treatment of repeated summer burn, repeated winter burn, or non-burned control. Fire treatments were

repeated every 6 yr, on average, to match the estimated historical mean fire frequency of this region (Frost 1998) while allowing enough flexibility to conduct high-intensity fires by skipping burns scheduled during seasons of high precipitation or to burn sooner than scheduled if ideal conditions became available. Summer burn units were burned in August 1994, July 2000, and July 2006. Winter burn units were burned in January 1996, January 2000, and February 2006. Each unit was burned independently.

Fire treatments were conducted during periods of below-average precipitation. Mean annual precipitation was 611 ± 93 mm from 1994 to 2006; maximum and minimum annual precipitation were 837 mm in 2004 and 524 in 1999, respectively. Total precipitation for the second summer burn was approximately 18 mm during July - September 2000, 90% less than the long-term average of 187 mm and marking the second most severe drought (according to Palmer Drought Severity Index, Palmer 1965) since the establishment of the Sonora Research Station (ca. 1919). Total precipitation was 114 mm and 187 mm in July - September for the other two summer burns conducted in 1994 and 2006. Total precipitation was also less than the long-term average of 79 mm when the winter burn treatments were conducted. Precipitation levels during the months of December - February were 13%, 26%, and 84% of the long-term average for the 1996, 2000, and 2006 winter burns, respectively.

Vegetation sampling

The frequency of occurrence of graminoid species, woody plant species, and prickly pear cactus were sampled in each experimental unit along 10 randomly

established and permanently marked 50-m transects. Prior to fire treatment in 1994, and again in 2006, a 0.25 m² quadrat was placed at 2-m increments along each transect to record the three most abundant graminoid species according to canopy cover.

Frequencies of occurrence of each woody plant species and prickly pear cactus were measured along the transects in the overstory (≥ 1.5 m) and understory (< 1.5 m). In 2006, total woody canopy cover was measured using the line intercept method (Floyd and Anderson 1987). A value of 0.10-m was established *a priori* as the minimum amount of cover needed for an individual to count toward the frequency data and cover estimates. Gaps < 0.10 m in the canopy were ignored. Pre-treatment woody plant canopy cover was not available for each transect; however, aerial photography showed total woody cover did not differ across the study site prior to this experiment.

Data analysis

To test for differences in the overall plant community, data were analyzed using permutational multivariate analysis of variance (PERMANOVA; Anderson 2005).

PERMANOVA is a useful tool that uses permutations to test hypotheses and calculate *P*-values in data from experimental designs that do not conform to assumptions of traditional one-way ANOVA or parametric MANOVA. A key difference between these statistical techniques is that PERMANOVA only assumes that the observation units are exchangeable (i.e. observation units are independent) whereas ANOVA and MANOVA assume independent observations, normally distributed residuals, equality of variances and additive treatment effects (Anderson 2001, Hinkelmann and Kempthorne 2008).

PERMANOVA is designed to analyze ecological data, which commonly fail to conform to assumptions of normality; in addition, it avoids pseudo-replication in ecological designs with low replications (Anderson 2001, McArdle and Anderson 2001), such as this one ($n=2$). In this study, PERMANOVA was performed on Bray-Curtis distances of $\ln(x+1)$ transformed frequency data. Data were analyzed using burn treatment (repeat summer burns, repeat winter burns, and control) and height (< 1.5 m and > 1.5 m, representing understory and overstory vegetation, respectively) as fixed factors. Data from 1994 and 2006 were analyzed separately because PERMANOVA should not be used to test for treatment x time interactions since data are autocorrelated in permanent plots that are repeatedly measured over time. Such was the case in this study. There are ways to account for autocorrelation to test for treatment x time interactions (e.g. Fule et al. 2005) but we did not use such techniques in this analysis due to the low replication of this design. *P*-values are based on Monte Carlo asymptotic permutation using 4999 runs; a Monte Carlo approach is appropriate when the experimental design lacks the number of observational units needed to obtain a reasonable number of permutations (Anderson and Robinson 2001, Anderson and Robinson 2003). Terms and interactions found to be significant in the full model were investigated using pair-wise comparisons where appropriate.

After testing for differences in the overall plant community, we separated the community data into grasses and woody plants to test hypotheses related to each functional group. Both groups were tested for pre-existing differences among assigned treatments in 1994 and for differences in 2006 resulting from burn treatments. In

addition, the total canopy cover of woody plants in 2006 was tested for differences among burn treatments. Significant terms were evaluated using pair-wise comparisons where appropriate.

We performed canonical analysis of principal coordinates (CAP; Anderson and Willis 2003) to visualize differences in the plant community among treatments over time. CAP is a constrained ordination technique that accounts for the correlation structure among species, making it more appropriate than PERMANOVA or unconstrained ordination techniques (e.g. non-metric multidimensional scaling, NMS) when treatment groups differ in a direction of the multivariate space that is not strictly parallel with the direction of greatest overall variation (Anderson and Robinson 2003; Anderson and Willis 2003). Plant species that occurred in < 5% of all samples for both years were omitted to limit the effect of rare species and increase the ability to detect relationships between experimental treatments/environmental factors and changes in the plant community (McCune and Grace 2002).

Results

Plant community

Burn treatments altered the trajectory of the plant community from 1994 to 2006 relative to the control (Table 3). Repeatedly burning in the summer resulted in a woody plant community that differed from the control in 2006 while maintaining a similar grass community (Table 4). The winter burn treatment produced an overstory woody plant community that was similar to the overstory of the summer burn treatment, an

understory woody plant community that was similar to the control, and a unique grass community (Table 4). Overall, burn treatments had the greatest effect on the overstory woody plant community, which changed more from 1994 to 2006 than woody plants and grasses in the understory (Fig. 6a, Axis 2). Understory woody plant communities did not differ among treatments in 2006 (Table 4), but increases in the frequency of Ashe juniper and other species commonly associated with the overstory plant community (e.g., Pinchot's juniper, honey mesquite) caused the understory of the control treatment to shift away from pre-treatment levels (Fig. 6, Axis 1).

The only difference prior to treatment in 1994 was the presence of distinct plant communities in the overstory and the understory (Table 3). Differences between understory and overstory layers continued in 2006 (Table 3) and explained the greatest amount of variation in this plant community (Fig. 6a, Axis 1). Such a finding was expected since savanna ecosystems typically feature a codominance of unique understory and overstory plant species. In general, live oak and Ashe juniper dominated the overstory, whereas Texas persimmon (*Diospyros texana* Scheele), prickly pear cactus, sacahuista, and algerita (*Mahonia trifoliolata* (Moric.) Fedde) were almost exclusively understory species (Fig. 6, Axis 1). Pinchot's juniper and honey mesquite occurred in relatively similar proportions in the overstory and understory (Fig. 6, Axis 1).

Woody plants (and cactus)

Woody plants and cactus increased from 1994 to 2006 in the overstory and understory of the control treatment. Live oak increased in the overstory of the control more than any other woody plant species (Table 5). Ashe juniper was approximately six times more frequent in the understory and overstory of the control in 2006 than in 1994 (Table 5). Pinchot's juniper, which was not found in control units in 1994, was present in the understory and overstory in 2006 (Table 5). Mesquite was also found in the overstory in 2006 after being absent from the overstory prior to treatment (Table 5). As a result, the overstory plant community of the control was converted from a live oak dominated overstory to a live oak – Ashe juniper dominated overstory interspersed with Pinchot's juniper and mesquite (Fig. 7). Similar trends were observed in the understory of the control. All species except algerita increased in the understory (Table 5).

Repeatedly burning in the summer maintained the overall frequency of individuals and changed the presence of species in the woody plant community (Table 5), creating overstory and understory woody plant communities that differed from the control in 2006 (Fig. 7a,b). Sacahuista and Ashe juniper were no longer present in the understory of the summer burn treatment in 2006 (Table 5; Fig. 7d). The overstory (Fig. 7a) consisted almost exclusively of live oak in 2006 due to the complete removal of Ashe juniper and the conversion of other overstory woody plants to the understory (Table 5; Fig. 7). Honey mesquite was the only other woody plant species that remained in the overstory in 2006 and it remained at low frequencies (Table 5).

The winter burn treatment generally maintained the number of species present in the understory and overstory but not the frequency of individuals. Burning in the winter maintained a live oak dominated overstory plant community over time (Fig. 7a) by preventing Ashe juniper from becoming a dominant component of the overstory (Fig. 7c; Table 5). However, unlike the summer burn treatment, repeatedly burning in the winter did not maintain the overall frequency of woody plants in the overstory due to large increases in live oak (Table 5). In contrast to the overstory plant community, the understory community of the winter burn treatment was more similar to the control than the summer burn treatment (Fig. 7b, Axis 1). Like the control, the overall frequency of woody plant individuals increased over time in the understory of the winter burn treatment (Table 5). Species that increased most in the winter burn and control treatments were live oak, prickly pear cactus, and sacahuista (Table 5). The primary differences between the two understory plant communities was that Ashe juniper increased in the control treatment whereas it was essentially removed in the winter burn treatment, live oak increased considerably more in the winter burn treatment, and prickly pear cactus increased considerably more in the control (Table 5).

Changes in the frequency of individual woody plants in the understory and overstory led to differences in the total cover of woody plants among treatments in 2006 (Table 6). Total woody cover was $18.2 \pm 1.3\%$ of the transect length in the summer burn treatment and was significantly less than the $44.0 \pm 1.2\%$ cover in the control; woody cover in the winter burn treatment was $38.2 \pm 0.7\%$ and did not differ from summer burn or control treatments.

Grasses

The frequencies of occurrence of the most abundant grasses were primarily influenced by changes occurring over time (Fig. 8a, axis 1) and pre-existing variation within and among treatment units (Fig. 8a, axis 2). Consequently, fire was not the primary driver of the observed differences in the grass community among treatments in 2006. Each grass species, except little bluestem, responded consistently across all treatments (Table 7). Grass species that increased from 1994 to 2006 (Table 7) were negatively correlated with CAP axis 1 across treatments (Fig. 8b), whereas grass species correlated positively with axis 1 (Fig. 8b) decreased over time (Table 7). Little bluestem was weakly correlated with axis 1 ($r = 0.04$), increased in the winter burn treatment, remained fairly constant in the summer burn treatment, and decreased in the control (Table 7). Moreover, species that occurred the most in a given treatment at the beginning of the study continued to occur with greatest frequency in the same treatment in 2006 (e.g. the frequency of little bluestem occurrence was the most in the winter burn treatment in 1994 and 2006). This legacy effect is shown by CAP axis 2 (Fig. 8). Grass species strongly and positively correlated with axis 2 (Fig. 8b) occurred more frequently in 1994 and 2006 in the winter burn treatment than in the summer burn or control (Fig. 8a). Species negatively correlated with axis 2 (Fig. 8b) occurred more frequently in the summer burn treatment in 1994 than in the winter burn or control (Fig. 8a). Only common curly mesquite broke this pattern in 2006, becoming more frequent in the

control (Table 7). Other grass species continued to occur more frequently in the summer burn treatment.

Discussion

Woody plant (and cactus) community

Burning in the summer was the only treatment with less woody plant cover than the control and maintained the overall frequency of woody plants from 1994 to 2006, suggesting high intensity fires are needed to maintain semiarid live oak savanna. One potential consequence of applying high intensity fires is that overstory woody plants will be eliminated, causing the savanna to transition to grassland (Higgins et al. 2000) or to an understory-dominant community featuring resprouting woody plants. The propensity for some individuals in this live oak savanna to escape or limit fire-induced damage is likely associated with the Oskar-Gulliver hypothesis and spatial variation in fire intensity. The Oskar-Gulliver hypothesis (Bond and van Wilgen 1996; Higgins et al. 2007) states that some individuals in savanna are old but kept small by fire (Oskar syndrome) and others have the potential to become giants once they escape fire (Gulliver syndrome). Live oak, the tallest tree at this site, was the primary species to have some individuals escape fires and become “giants”, whereas other individuals of live oak, as well as Texas persimmon, Pinchot’s juniper and honey mesquite, were kept small or reduced from overstory to understory plants.

An individual occurring as an overstory versus understory plant in this system is expected to be primarily a function of spatial variation in fire intensity. Fine-scale

variation in grass fuels has been shown to drive spatial variation in fire intensity and lead to differential responses of individual woody plants in this system (Twidwell et al. 2009). Spatial variation in fire intensity and fire effects can result from localized variability in grass moisture content (Knapp and Keeley 2006), fine fuel load (Thaxton and Platt 2006; Twidwell et al. 2009), and tree-grass interactions (Slocum et al. 2003), among other factors. The combination of live oak being the tallest tree and influencing surrounding surface fuels likely explains why live oak was able to escape or limit the negative effects of fire more than other species.

While an increase in live oak is generally viewed positively due to its high preference as browse forage by goats in this region (Taylor and Kothmann 1990) and aesthetic appeal (Kreuter et al. 2004), large populations of live oak are currently being crippled in Texas by *Ceratocystis fagacearum*, a fungal pathogen that causes oak wilt (Appel 1995; Koch et al. 2010). An increase in the density and regeneration of live oak has led to highly interconnected root systems that facilitate the spread of oak wilt through common root systems and root grafts (Juzwik et al. 2008; Koch et al. 2010). Reducing current live oak densities or maintaining densities at pre-settlement levels is therefore a high priority (Koch et al. 2010). However, fire is not currently listed as a preventative strategy for oak wilt management. Combining the findings of this study with those conducted in savannas elsewhere (Trollope 1974; Holdo et al. 2009; Staver et al. 2009) suggests a combination of high-intensity fires and livestock browsing is more likely to provide an effective means of maintaining overstory and understory densities at desired levels.

The exclusion of fire has led to encroachment of overstory-dominant plants in the understory of the control and reveals this system is on the verge of a regime shift from live oak savanna to live oak-juniper dominated woodland after only 12 yr. This result supports earlier simulations of the Edwards Plateau region (Fuhlendorf et al. 1996) that suggests grass-tree codominance will be lost after 20 yr of fire exclusion. The continued absence of fire eventually produces a closed canopy Ashe juniper woodland interspersed with dense clusters of prickly pear cactus and little to no herbaceous surface fuels (Van Auken 2000) within 75 yr (Fuhlendorf et al. 1996). Such ecosystems are extraordinarily resilient to fire (Van Auken 2000), but restoration may be possible if high intensity fires are conducted during periods of drought (Twidwell et al. 2009).

Grass community

In contrast to the woody plant response, fire treatments did not explain the observed variability of the most frequently occurring grasses in this study. The greatest amounts of variation in these data were explained by changes occurring over time and legacy effects resulting from pre-existing variability. As a result, changes from 1994 to 2006 were consistent across treatments for all grass species except little bluestem. Similar to our findings, a previous livestock enclosure experiment at the Sonora Research Station showed sideoats grama and Texas cupgrass increased in basal area and dominance after a severe drought in the 1950s whereas common curly mesquite and Wright's threeawn sharply decreased in basal area and dominance (Smeins et al. 1976). Livestock herbivory and precipitation variability, including the occurrence of the second

most severe, prolonged drought in the history of the research station (Palmer Drought Severity Index ≤ -4 , 2000; Station Records 1919-2006), therefore played a larger role in shaping the grass community over this time period than whether sites were burned repeatedly in the summer, winter, or excluded from fire.

Researchers conducting grazing studies have long been aware that interannual variability in rainfall can mask the influence of grazing on the direction of vegetation change (Westoby 1980; O'Connor and Roux 1995) and have subsequently emphasized the use of long-term data sets (e.g., Milchunas et al. 1989; O'Connor 1994; Allen et al. 1995; O'Connor and Roux 1995; Fuhlendorf et al. 1997; Biondini et al. 1998; Fuhlendorf et al. 2001) and technology (e.g., remote sensing) to determine whether grazing or drought is a more dominant driver of long-term vegetation change (Walker 1988; Fuhlendorf et al. 2008). A 40+ yr grazing manipulation in this live oak savanna showed grazing intensity drove the long-term direction of herbaceous vegetation change whereas annual variability in precipitation explained the short-term rate and direction of change (Fuhlendorf and Smeins 1997; Fuhlendorf et al. 2001). As a result of the 12-yr sampling interval and duration of this study, we were unable to detect if short-term oscillations occurred or if drought masked a long-term, fire-driven influence on the grass community. Few other long-term semiarid experiments have established the contributions of fire relative to grazing and climatic variability or their influence on short-term versus long-term change. For those that exist, grazing has been shown to be a more dominant long-term driver than fire (Belsky 1992) and climatic variability has been shown to be more dominant than fire and grazing (Savadogo et al. 2008). We are

unaware of a single long-term study that shows fire, not grazing or climatic variability, is a more dominant source of long-term change of grasses in native, semiarid rangelands. The limited number of long-term studies investigating this topic makes it difficult to determine how fire, herbivory, and climate interact to influence herbaceous vegetation change in semiarid environments over various temporal scales.

Management implications

Managers and scientists have long questioned the merits of burning in rangelands. A couple unresolved ecological issues have been at the forefront of managerial concerns in semiarid live oak savanna and were addressed in this experiment. One of the prevailing concerns historically is that fire will kill grass and degrade rangelands over time (e.g. Wright and Klemmedson 1965). This long-term fire experiment provides evidence to suggest that conducting high intensity fires in the summer during periods of below-average precipitation, when C4 grasses desired by managers are stressed, can reduce or eliminate woody plant species that threaten the stability of live oak savannas while having little long-term effect on the occurrence of the most abundant grasses. However, many managers want to protect mature live oak trees and are concerned that high intensity fires will top-kill those individuals (Olenick et al. 2004). The downside of not burning or only burning in milder fuel and fire weather conditions is that the number of live oak trees will increase, which may make the population more susceptible to oak wilt. Only high intensity fires conducted in the summer maintained the frequency of woody plants in this study after 12 yr and slowed

the increasing numbers of live oak compared to the control. While some individual trees were top-killed with high intensity fires, many trees escaped fire and maintained the aesthetic appeal of an overstory live oak savanna.

It is important for rangeland managers to be aware of the knowledge gaps that still need to be addressed by further scientific research. The 12 yr time span between sampling dates does not allow us to provide information on whether most of the change in the woody plant community occurs after the first high intensity fire or subsequent fires. The specific fire intensity required to kill non-resprouting trees or alter the structure of resprouting species is unknown. It is also unclear how the treatments imposed in this study influence total herbaceous biomass, the productivity of individual grass species, herbaceous species diversity, and important minor grass species. Answers to these knowledge gaps will help rangeland managers more flexibly use high intensity fires in drought conditions to target problematic woody plant species while understanding the short-term and long-term impacts on the herbaceous community.

CHAPTER IV
PRESCRIBED EXTREME FIRE EFFECTS ON SPECIES RICHNESS AND
INVASION IN COASTAL PRAIRIE

Introduction

Introductions of herbaceous species to new continents are occurring at an unprecedented rate (Mooney et al. 2005) and pose a serious threat to the biodiversity, productivity, and economic profitability of the world's grasslands (DiTomaso 2000; Mack et al. 2000; Pimentel et al. 2005). Hence, understanding the reasons for invasion of exotic herbaceous plants is of considerable importance to scientists and managers. One of the more alarming recent global trends is the capacity for exotic plants to rapidly colonize and invade grasslands following fire (D'Antonio and Vitousek 1992; Keeley 2001). The more notorious exotic invaders of recently burned grasslands are cheatgrass (*Bromus tectorum* L.) in the northwestern U.S. (Harnis and Murray 1973; Mack 1981), gamba grass (*Andropogon gayanus* Kunth) in Australia (Rossiter et al. 2003), and buffelgrass (*Pennisetum ciliare* (L.) Link) in Australia (Butler and Fairfax 2003) and Mexico (Franklin et al. 2006). Invasions by these species have led to widespread detrimental impacts to native ecosystems that include severe losses in native diversity (Knapp 1996; Fairfax and Fensham 2000; Clarke et al. 2005; Sands et al. 2009), lower forage quality and quantity for livestock (McHenry and Murphy 1985), and drastically modified fire regimes (D'Antonio and Vitousek 1992; Martin et al. 1999; Rossiter et al. 2003). Such undesirable effects have created a management dilemma in grasslands.

Fire is considered to be a critical factor in the conservation and management of the world's grasslands (Bond 2008). Yet, the catastrophic examples of fire triggering widespread invasion of exotic plants may prevent managers from using fire for the conservation of other grassland ecosystems where invasive herbaceous species are present (Keeley 2006).

The conservation-invasion fire dilemma is a pressing management concern in the coastal tallgrass prairie ecological region located along the Gulf of Mexico (USA). The coastal tallgrass prairie represents one of the rarest and most diverse plant community types in North America (Grace 1998). Coastal prairie is estimated to have once occupied between 3.4 – 8.0 million ha in the U.S. along the Gulf of Mexico (Diamond and Smeins 1988; Smeins et al. 1991). Today, less than 1% of this ecosystem remains in a non-agricultural or non-urban state, and rapid shrub encroachment threatens to convert the coastal prairie remnants to shrubland (Scifres et al. 1982; Bruce et al. 1995).

Conservation organizations and scientists recognize that such widespread transitions jeopardize the high biodiversity of the ecoregion and threaten endangered animal species that depend on coastal tallgrass prairie for habitat, such as the whooping crane (*Grus americana*) and Attwater's greater prairie chicken (*Tympanuchus cupido attwateri*) (Grossman et al. 1994; Grace 1998). Fire was historically critical to the maintenance of coastal prairies (Grace 1998) and is often used to kill small woody plants, decrease the canopy cover of mature shrubs, and limit further grassland degradation by preventing the establishment of new woody individuals (Van Auken 2000; Bond 2008). However, the

emergence of numerous alien invasive grass and forb species has many conservation managers concerned that fire may facilitate their invasion (Grace et al. 2001).

One of the major invasive threats in Gulf coastal prairie is King Ranch (KR) bluestem (*Bothriochloa ischaemum* (L.) Keng) (Grace et al. 2001), an invasive C₄ grass introduced in the 1920s and 1930s from Europe and Asia as a forage species (Gould 1975). KR bluestem has led to declines in the richness of plant, avian, and arthropod species in areas it has invaded (Hickman et al. 2006; Johnson et al. 2008). It is therefore important to determine whether the use of fire for the conservation of coastal prairie will inadvertently trigger rapid KR bluestem invasion. Experimental studies in other ecosystems have shown KR bluestem responds favorably to fires applied during dormant periods of plant growth (Gabbard and Fowler 2006), whereas fires conducted during the growing season have reduced KR bluestem (Simmons et al. 2007; Ruckman et al. 2011) with the greatest reductions occurring during periods of drought (Simmons et al. 2007). Growing season fires may therefore present a favorable management option for coastal prairie conservationists. However, much of our knowledge on how herbaceous species respond to fire is limited to the dormant season, which is consistent with conventional fire management practices in tallgrass coastal prairie (Hansmire et al. 1988) and elsewhere in the Great Plains (Howe 1994; Pavlovic et al. 2011). As a result, numerous uncertainties regarding post-fire plant species changes limit the use of growing season fires in restoration and management of Gulf coastal prairies. The two primary concerns are that fire will decrease native herbaceous species richness (e.g. Abrams 1987) and facilitate invasions of alien invasive grass and forb species (Grace et al. 2001).

The objective of our experiment was to compare the rapid responses of native and exotic herbaceous species in burned and unburned treatments in a coastal tallgrass prairie with high levels of shrub encroachment. In this study, prescribed fires were conducted in the growing season during a severe, prolonged drought that caused considerable grass curing (for details on grass curing see Luke and McArthur 1979, Cheney and Sullivan 1997, Wittich 2011) and the potential for high fire intensities (hereafter these fires are referred to as prescribed extreme fires). Our study is designed to test hypotheses associated with previously unsubstantiated assumptions in coastal tallgrass prairies that (1) prescribed extreme fire will decrease native herbaceous species richness and (2) prescribed extreme fire will trigger rapid increases in alien species.

Methods

Study site

The experiment was established at the Rob and Bessie Welder Wildlife Refuge, located approximately 11 km north of Sinton, Texas. The 3150 ha Welder Wildlife Refuge functions as a working ranch and wildlife reserve (<http://www.welderwildlife.org>). Traditional grassland management practices, such as fire and cattle grazing, play an integral role in conserving the numerous plant and animal species on the refuge. Prescribed fire is used to maintain grassland dominance and productivity and to control woody plant encroachment. Cattle are rotated among the fenced pastures on the refuge, consistent with the long-term grazing practices of the region. Average annual rainfall at the site is 900 mm, with peak rainfall occurring in the

months of May through June and September (Janecka et al. 2007). Soils are mainly Victoria clays, a deep, well-drained, and relatively hydrophobic soil and range from 0-1% in slope (Hansmire et al. 1988).

The upland areas of the Welder Wildlife Refuge were characterized historically as coastal tallgrass prairie, but lack of fire in some areas has increased woody vegetation cover to its current condition of a high density, thorn-scrub woodland (Scifres et al. 1982). We selected a 60 ha section of the refuge dominated by honey mesquite (*Prosopis glandulosa* Torr.) and huisache (*Acacia farnesiana* (L.) Willd.), interspersed with shrub clusters of lime prickly ash (*Zanthoxylum fagara* (L.) Sarg.), spiny hackberry (*Celtis ehrenbergiana* (Klotzsch) Liebm.), and Brazilian bluewood (*Condalia hookeri* M.C. Johnst.) (Box 1961). Primary native perennial grasses include vine mesquite (*Panicum obtusum* Kunth), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), buffalograss (*Bouteloua dactyloides* (Nutt.) J.T. Columbus), bristle grass (*Setaria* spp.) among others. Common native forbs include noseburn (*Tragia* spp.), limestone wild petunia (*Ruellia strepens* L.), yellow puff (*Neptunia lutea* (Leavenworth) Benth.), trailing krameria (*Krameria lanceolata* Torr.), and blue mist flower (*Eupatorium coelestinum* (L.) DC.). Introduced noxious plants include bindweed (*Convolvulus arvensis* L.), woodsorrel (*Oxalis* spp.), and KR bluestem. Cattle were removed prior to initiation of this experiment and were excluded for its duration.

Experimental design and treatments

Prescribed fire and herbicide treatments were applied in eighteen plots, each 30 m x 20 m, using a split-plot experimental design (Fig. 9). Burned and unburned plots were randomly assigned at the whole plot level. Three herbicide treatments were randomly assigned to one of three subplots within each whole plot to treat woody plants (Fig. 9). Each subplot was 20 m x 10 m. Herbicide treatments included (1) herbicide in 2007, which was timed to occur one year prior to conducting the burn treatment, (2) herbicide in 2009, which was timed to occur when resprouting stems from burned mesquite trees were approximately 0.5-m in length, and (3) no herbicide, which served as a control.

At the time of these analyses, the experimental design consisted of 12 replicate burned plots and 6 replicate unburned plots. There were 12 replicate plots in the burned treatment to allow half the burned plots to be assigned different fire frequency treatments in the future. This resulted in an unbalanced design for the present analyses. A blocked experimental design was not used in this study because plots were located on a relatively homogeneous upland site on the refuge. Every whole plot was surrounded by at least a 15-m wide bare ground firebreak. Each burned plot was therefore ignited independently of other burned plots and served as true replicates.

Herbicide was applied to all woody plants by spraying a 75% diesel – 25% Remedy Ultra mix (triclopyr, Dow Agrosiences) at the base of their stems. Herbicide was not directly sprayed on herbaceous vegetation. At the time of establishing this experiment, basal application of this herbicide mixture was regarded as the best

approach for killing mesquite (McGinty and Ueckert 1997; McGinty et al. 2000) and other invasive woody plants (McGinty et al. 2000) and has been widely adopted by Texas landowners as a preferred management practice for controlling shrub encroachment (Kreuter et al. 2001).

Plots were burned with headfires in the direction of a large buffer area that was burned in mild fuel and fire weather conditions (i.e., high fine fuel moisture, low temperature, high relative humidity, low wind speed) prior to conducting the extreme fire treatment (Fig. 9). The purpose of the buffer area was to remove surface fuels and provide sufficient space to prevent firebrands from starting spot-fires outside the burn unit. The size of the buffer area was determined using rules-of-thumb established for rangelands by Wright (1974) and comparing those guidelines to quantitative predictions of spot-fire distance in flat terrain using Albini (1979, 1981).

Fireline intensity and fire temperatures were measured in each subplot. Ocular estimates of mean and maximum flame length were recorded in each subplot, and fireline intensities were calculated for each subplot using the methodology outlined in Rothermel and Deeming (1980). Maximum fire temperatures were recorded using ceramic tile pyrometers. Tiles were painted with 25 temperature-indicating lacquers (OMEGALAQ[®] Liquid Temperature Lacquers; Omega, Inc.) that melted from 79°C to 1038°C. A temperature of 1038°C represents the second highest temperature-indicating lacquer sold by Omega, Inc. The highest temperature, 1093°C, was not available in sufficient quantities at the time of purchase. Lacquers were chosen at approximately 50°C to 100°C increments, depending on the products available, to achieve a relatively

even distribution of temperature indicators. Tile pyrometers were located at the base of a large tree (> 1.5-m). Three trees were randomly selected in each subplot. At the base of each tree, a tile pyrometer was placed on the ground (0-cm height) and another at a height of 150-cm by affixing the tile to a piece of metal conduit that was pounded into the ground. This protocol was established for research objectives that are beyond the purview of this analysis; however, the fire temperature data are useful in characterizing the fire temperatures produced in this experiment and in making comparisons to temperatures reported in other studies. A total of 216 tile pyrometers were used in this study [2 tiles per location/tree (1 tile at 0-cm + 1 tile at 150-cm) x 3 locations per subplot x 3 subplots per plot x 12 burned plots]. The side of the tile with lacquers was oriented upwards, which may have resulted in an insulating effect since ceramic tiles were used (Kennard et al. 2005). Pyrometers at a height of 150 cm may therefore have underestimated the actual fire temperatures produced in this study, which should be taken into account when comparing fire temperatures produced in other studies.

Due to the number of burned plots, the amount of preparation required to set up pyrometers prior to burning each plot, the time required to burn each plot individually, and the amount of monitoring associated with conducting fires during burn bans, it took three days to burn 12 plots. Fires were conducted June 17-19, 2008. Minimum and maximum temperature, relative humidity, and wind speed at the time of conducting fires were 35.0°C and 38.3°C, 28.9% and 43.3%, and 1.1 km h⁻¹ and 14.6 km h⁻¹, respectively.

Vegetation sampling

Vegetation sampling was conducted one year after the prescribed fires by clipping all the herbaceous material within three randomly located 0.25 m² quadrats in each subplot. A total of 162 quadrats were sampled. Each live herbaceous individual was identified to species, with the exception species of *Carex*, *Eragrostis*, *Oxalis*, *Croton*, *Tragia*, *Setaria* and *Paspalum*, which could only be identified to genus because they did not exhibit necessary vegetation characteristics for more detailed identification and were generally in low abundance. After species identification, samples were dried (70°C, 48 h) to measure aboveground productivity and compare differences among treatments.

Data analysis

Testing for differences in herbaceous species richness and aboveground herbaceous biomass as a result of the application of herbicide on woody plants using non-balanced split-plot ANOVA revealed no significant differences among subplot treatments ($F = 1.75$, $P = 0.18$). Therefore, data from the herbicide-treated subplots were pooled in each whole plot (i.e. 3 quadrats per subplot x 3 subplots = 9 quadrats per whole plot) to test for differences between burned and unburned treatments. Species richness (number of species per 0.25 m² quadrat) data were averaged for all quadrats in a plot, and the averaged values were analyzed using an independent samples t-test with unequal sample sizes of equal variance and normal distribution. Data for herbaceous biomass were square-root transformed to meet assumptions of normality. Levene's test

indicated unequal variances for the herbaceous biomass data ($F = 9.88$; $P = 0.006$), so these data were analyzed using an independent samples t-test that did not assume homogeneity of variances. Non-metric multidimensional scaling (NMS) was used to visualize differences in the herbaceous plant community between burn treatments. NMS ordinations were produced with PC-ORD (McCune and Mefford 1999) using Bray-Curtis distances with random starting configurations, three dimensions, 100 runs of real data with 500 iterations per run, and a stability criterion of 0.00001. Individual species were not included in the NMS if they occurred in less than 5% of all treatment units, following the recommendations by McCune and Grace (2002). Statistical analyses assumed plots were not different prior to treatment because pre-treatment data were not collected due to the presence of adequate controls, the assignment of completely randomized treatments, and a relatively homogeneous study area (visual observation). Multiple pair-wise comparisons were performed using Tukey HSD to test for differences in fire temperatures as a result of the herbicide treatments applied to each subplot.

Results and discussion

Weather and fire intensity

Prescribed fires were conducted in environmental conditions that led to remarkably high fire intensities for this ecosystem. The research site had been in an extended drought for nearly five months at the time of burning in June 2008 (Welder Wildlife Refuge station records). Total precipitation was less than the long-term monthly average from February through June (Fig. 10a). When fires were conducted,

the site had not received a substantial rain event for 46 days (Fig. 10b) and total precipitation in June was only 0.41 cm, which was 96% below the long-term monthly average. The shortage of rainfall resulted in nearly complete grass curing (personal observation; Luke and McArthur 1979, Cheney and Sullivan 1997, Wittich 2011) and contributed to high fire temperatures and intensity levels. Fire temperatures averaged 886°C at ground level and 461°C at a height of 150 cm. The temperature of the highest indicating lacquer (1038°C) was reached on 88% of pyrometers at ground level (95 of 108). As a result, the tile pyrometers likely underestimated the actual mean fire temperatures produced at ground level in these fires. Mean fireline intensity across all burned plots was $897 \pm 124 \text{ kJ m}^{-1} \text{ s}^{-1}$; however, maximum flame lengths observed in this study were 5 m, producing fireline intensities of approximately $8500 \text{ kJ m}^{-1} \text{ s}^{-1}$ in localized areas of multiple plots.

The fire temperatures recorded in this study are far above values typically observed in other fire studies in Gulf coastal prairie. Few studies have directly measured and reported fire temperature or intensity data in Gulf coastal prairie ecosystems. An earlier study at the Welder Wildlife Refuge observed maximum fire temperatures ranging from 330°C to 460°C at ground level in a plant community similar to this experiment (i.e. thorn-scrub woodland) and 689°C to 820°C at ground level in a bunchgrass-dominated area where herbaceous fuel load was higher (Scifres et al. 1988). Maximum fire temperatures averaged 235°C and 280°C for fires conducted in two different years in Texas coastal tallgrass prairie (range was 110-300°C for fires in both years; Hartley et al. 2007). In other studies, peak fire temperatures ranged between

150°C to 500°C for a single fire in Texas coastal prairie (values approximated from figure; Grace et al. 2005) and 116°C to 525°C in Louisiana coastal marsh (Owens et al. 2007).

Applying herbicide on woody plants one year before conducting fires in 2008 did not result in greater fire temperatures or fireline intensities than other subplots (Tukey's HSD, $P = 0.99$ and $P = 0.14$ for temperatures in herbicide after fire and no herbicide treatments, respectively; $P = 1.00$ and $P = 1.00$ for fireline intensities in herbicide after fire and no herbicide treatments). Mean fire temperatures were 846°C, 863°C, and 949°C in herbicide before fire (2007), herbicide after fire (2009), and no herbicide subplots respectively. Mean fireline intensities were 913 $\text{kJ m}^{-1} \text{s}^{-1}$, 870 $\text{kJ m}^{-1} \text{s}^{-1}$, and 909 $\text{kJ m}^{-1} \text{s}^{-1}$ in herbicide before fire (2007), herbicide after fire (2009), and no herbicide subplots respectively.

Coastal prairie species composition

Overall this herbaceous plant community was dominated by relatively few species (Table 8). Perennial grasses comprised the majority of plant species. Of these, KR bluestem and vine mesquite were the most frequently observed plants in both the burned and unburned treatments. Texas wintergrass, a perennial C3 grass, ranked third in frequency of occurrence. Only one annual grass, prairie threeawn, was found and only with infrequent occurrences in the burned treatment. The dominant forbs were yellow puff, noseburn, blue mistflower, and trailing krameria. Two introduced forbs, field bindweed and wood sorrel, occurred infrequently in the plots.

The number of species was low in this coastal tallgrass prairie relative to its potential richness. Over 900 plant species have been documented throughout the coastal tallgrass prairie range, with a large proportion of its diversity owed to a high number of forb species (Grace 1998). In contrast, coastal prairie in our study area was dominated by a few perennial grasses species, particularly in the unburned control, and had only one annual grass species. Perennial species dominance commonly reduces the number of annuals (Pickett 1982). In addition, many coastal prairie ecosystems are undergoing a regime shift to shrub forest or woodland, leading to extensive species displacement (Bruce et al. 1995; Grace et al. 2000). These factors are leading to widespread shifts in species composition and losses in species richness throughout prairie ecosystems (Howe 1994; Leach and Givnish 1996; Sluis 2002) and likely explain why only 19 native species were observed in unburned coastal prairie in this study.

Fire effects on herbaceous species

Contrary to widely held assumptions and the prediction of our first hypothesis, conducting prescribed extreme fires in the growing season did not decrease native species richness (Fig. 11). Rather, native forb species richness was greater in burned areas compared to unburned areas ($t = 2.65$, $df = 16$, $P = 0.02$; Fig. 11b) and the richness of native grass species did not differ between treatments ($t = -0.35$, $df = 16$, $P = 0.73$; Fig. 11b). Total species richness did not differ between burned and unburned treatments ($t = 1.91$, $df = 16$, $P = 0.07$; Fig. 11a), and no other native or introduced functional group differed between treatments ($P > 0.10$; Fig. 11b, 11c). Aboveground herbaceous

biomass was significantly lower in the burned treatment after one year ($t = -3.17$, $df = 6$, $P = 0.02$; Fig. 12).

Forb-driven increases in species richness is often observed following growing season burns in other prairies (Biondini et al. 1989; DiTomaso et al. 1999; Copeland et al. 2002; Towne and Kemp 2008); however, the number of species can vary considerably following fire (Suding and Gross 2006) so no universal pattern between fire and species richness has emerged. Regardless, a fire-stimulated increase in richness is typically short-lived and decreases with time since fire (Gibson and Hulbert 1987; Kyser and DiTomaso 2002), often as a result of long-term accumulation of grass litter (Hobbs and Huenneke 1992; Tilman 1993; Shay et al. 2001). Managers will therefore need to consider the frequency with which fires are to be reapplied in prairie ecosystems if fire management programs are to successfully maintain high levels of species richness.

Although the richness of native forbs was the only functional group to differ between burned and unburned treatments (Fig. 11b, 11c), many herbaceous species within a functional group differed in their response to fire. Differential responses among species were shown by NMS ordination, which generally separated unburned and burned treatment units along NMS axis 1 (Fig. 13). Total species richness and native forb species richness were positively correlated in the direction of burned plots along axis 1 ($r = 0.48$ and 0.64 , respectively). The dominant native forbs that accounted for this trend were noseburn, yellow puff, and trailing krameria. Such species were found in considerably greater abundances in burned areas than in unburned areas and were highly correlated with NMS axis 1 (Table 8; Fig. 13). In contrast, blue mistflower was

negatively associated with burned sites and NMS axis 1 (Table 8; Fig. 13). KR bluestem was positively associated with the direction of burned plots, whereas the dominant native species, vine mesquite and Texas wintergrass, along with shortspike windmill grass, were negatively associated with axis 1 (Table 8; Fig. 13). Buffalograss, bristlegrass, and gaping grass were positively associated with axis 1 (Table 8; Fig. 13).

Introduced plant species did not differ significantly between burned and unburned treatments after one year, which counters our second hypothesis and challenges the widely held concern that prescribed extreme fires will promote rapid invasion by undesirable exotic grasses and forbs. The richness of introduced forbs did not differ significantly between burned and unburned treatments ($t = 0.00$, $df = 16$, $P = 1.00$; Fig. 11c). The occurrence of KR bluestem, the only introduced grass species observed in this study, did not differ significantly between burned and unburned treatments after one year ($t = 0.32$, $df = 16$, $P = 0.32$; Fig. 11c) but was positively associated with the direction of burned plots in NMS ordination (Fig. 13, Table 8). Two separate studies support our findings that KR bluestem does not rapidly invade prairies burned by prescribed extreme fires (Simmons et al. 2007; Ruckman et al. 2011). KR bluestem has been reduced by fires conducted early in the growing season, when the phenological development of the plant is less advanced (Ruckman et al. 2011), and the greatest reductions have occurred when growing season fires are conducted during drought (Simmons et al. 2007). In contrast, KR bluestem has responded favorably to fires conducted in milder conditions during dormant periods of plant growth (Pase 1971; Gabbard and Fowler 2006). However, this experiment and all the aforementioned

studies characterize the short-term effect of fire on KR bluestem and research has yet to establish its response over longer time intervals in a post-fire environment.

Summary and conservation implications

The potential to use prescribed extreme fire to increase native forb species richness while not increasing KR bluestem suggests that prescribed fires conducted during droughts in the growing season may be more effective than dormant season fires at meeting native coastal prairie conservation goals. This counters the majority of fire management practices in tallgrass prairie (Howe 1994; Pavlovic et al. 2011). Most prescribed fires in coastal prairie are ignited in December through February when plants are dormant (Hansmire et al. 1988), often with the intent of increasing forbs for wildlife species (Chamrad and Box 1968; Lehman 1984). Such a strategy is likely to produce the opposite effect in coastal prairies invaded by KR bluestem. Burning during the dormant season is more likely to facilitate KR bluestem invasion (Pase 1971; Gabbard and Fowler 2006; Ruckman et al. 2011), which can lead to decreases in the composition and richness of plants and animals across multiple trophic levels (Hickman et al. 2006; Johnson et al. 2008). In contrast, burning during drought periods in the growing season increased forb richness and did not significantly increase KR bluestem occurrence in this study and decreased KR bluestem in previous research (Simmons et al. 2007; Ruckman et al. 2011). This information, coupled with research showing prescribed fire can reduce woody plant dominance in coastal prairie (Grace 1998; Allain and Grace 2001; Twidwell 2012) and cause high levels of woody plant mortality in other ecosystems

(Twidwell et al. 2009; Taylor et al. 2012), provides preliminary evidence that prescribed extreme fires conducted in the growing season can be a viable management strategy in coastal prairies.

CHAPTER V
DOES PRESCRIBED FIRE FACILITATE FIRE ANT INVASIONS IN COASTAL
PRAIRIES OR AID MANAGEMENT BY IMPROVING MOUND SEARCH
EFFORTS?

Introduction

Coastal prairies once covered approximately 3 - 8 million ha along the US Gulf Coast, but less than 1% of this ecoregion exists today (Diamond and Smeins 1988; Smeins et al. 1991). Many coastal prairies have been converted to agriculture or urban areas and changes in the fire regime have led to widespread shrub encroachment in undeveloped remnants, resulting in greatly reduced forage availability, livestock productivity, and species diversity (Grace 1998). Conversion of coastal grasslands to shrublands also threatens endangered species, such as the Attwater's prairie chicken (*Tympanuchus cupido attwateri*) and Whooping crane (*Grus americana* Linnaeus), which depend on coastal prairie habitat for all or part of their life cycle (Grace 1998; Grossman et al. 1994).

Since fire was critical to the maintenance of coastal prairies historically (Grace 1998), it is being reintroduced as one of the preferred restoration and management strategies of landowners and conservationists seeking to reduce further degradation of these grassland ecosystems (Van Auken 2000). However, many land managers are concerned it will have unforeseen, potentially negative, consequences (Kreuter et al. 2008). Of foremost concern is that fire will promote invasions and increase the density

of the red imported fire ant (*Solenopsis invicta* Buren), which poses a serious threat to the economic profitability and biodiversity of coastal prairies. Fire ants are one of the most economically important non-native species in the United States (Pimentel et al. 2000) and are estimated to be responsible for 5 million (US\$) per year in livestock losses, 16 million (US\$) per year in control costs, and 75 million (US\$) per year in damages in Texas agricultural areas (Lard et al. 2002). Such expenses are a major concern for conservation and wildlife programs because their economic and ecological impact is extensive. Fire ants are associated with declines in the diversity, abundance, and fitness of species from nearly every faunal guild (Allen et al. 1994, Eubanks 2001, Porter and Savignano 1990, Stuble et al. 2009) and are implicated as a threat to the conservation of multiple endangered species in coastal prairie, including the Attwater's prairie chicken (Wilson and Silvy 1988) and Texas horned lizard (*Phrynosoma cornutum*) (Donaldson et al. 1994).

Understanding the factors that make fire ants successful invaders is an important issue that may influence the decisions of coastal prairie managers. Two prevailing hypotheses that seek to explain the successful invasion of fire ants in coastal prairies include the superior aggressor/competitor hypothesis and the ecosystem transition/disturbance hypothesis. The superior aggressor/competitor hypothesis states fire ants are superior competitors to native ant species and exhibit more aggressive behavior toward other organisms, leading to the rise of fire ant dominance and a corresponding decline of native species abundances (Porter and Savignano 1990, Wojcik 1994). Alternatively, the ecosystem transition/disturbance hypothesis proposes that fire

ants and native species are primarily passengers that increase and decrease as a result of contemporary disturbance regimes and widespread shifts in plant community composition and structure (King and Porter 2007; King and Tschinkel 2006; King and Tschinkel 2008; MacDougall and Turkington 2005). This is a plausible hypothesis in coastal prairies as increases in fire ants and decreases in native species have coincided with a shift from prairie to shrubland throughout the ecoregion. However, this hypothesis does not explicitly differentiate between responses associated with ecosystem transitions versus those associated with disturbance. For example, it is currently not known how fire ants respond to restoration activities that use fire as a disturbance. Will using fire in restoration activities decrease fire ants and increase native species as a result of changing the trajectory of the system from shrubland back toward prairie (i.e. passengers of ecosystem transitions hypothesis)? Or, will using prescribed fire in coastal prairie increase fire ants because fire is a disturbance (i.e. disturbance mediated invasion hypothesis)? Both questions are of foremost interest to managers, but the latter has the potential to force managers to choose between using fire to control woody encroachment while exacerbating the fire ant problem or excluding the application of fire in an ecosystem dependent upon it.

Based on the superior aggressor/competitor and disturbance mediated invasion hypotheses, fire ant management strategies would ideally involve direct control treatments applied over large acreages, typically with broadcast baits or individual mound-based insecticides. In non-urban areas in Texas, the current management recommendation is to apply broadcast bait first and follow with chemical treatment of

individual mounds (Drees et al. 1998, 2008) while also encouraging population growth of native ant species with the hope of further suppressing fire ant numbers through competition (Drees et al. 1998, 2000). However, applying broadcast baits is unfeasible in areas heavily invaded by woody plants because many locations are inaccessible. This places a premium on the efficacy of individual mound-based treatments in ecosystems like the shrubland dominated coastal prairie. Yet, applying such treatments can be difficult due to the arduous task of locating fire ant mounds over large areas with high amounts of vegetative biomass and cover (Vogt and Walleet 2008). This is an important difference between mowed, well-groomed urban areas and wildland areas, such as prairies, savannas and shrublands, that can potentially cause insecticide applicators to fail to locate numerous fire ant mounds when conducting individual mound-based treatments.

We used an experimental fire manipulation aimed at restoring coastal prairie from shrubland to test management issues related to fire ant invasion. First, if chemical control is to be successful in coastal prairie using individual mound based treatments, we would predict that applicators will find (and treat) nearly all fire ant mounds in a given area. A prescribed fire experiment is an ideal design to test this prediction because it enables us to estimate the rate at which fire ant mounds are not located (and therefore not treated) by comparing the number of mounds located in an unburned, dense vegetation unit relative to the numbers found in a burned area where the herbaceous material that potentially “hides” fire ant mounds has been completely removed. Second, in contrast to the other prevailing hypotheses, the passengers of ecosystem transitions

hypothesis would cause managers to place greater emphasis on the restoration of the plant communities and disturbance dynamics that occurred prior to fire ant invasion than chemical control techniques. If the passengers of ecosystem transitions hypothesis explains fire ant invasion and is to drive management decisions, then fire ant mound densities should decrease in this experiment and native ants mounds, such as harvester ants (*Pogonomyrmex barbatus* Smith), should increase as a result of restoration. In contrast, if the disturbance mediated invasion hypothesis is to drive management, fire ant mound densities should increase and mound densities of native harvester ants, which have a long history of thriving in an environment with frequent fire (Zimmer and Parmenter 1998), should either remain constant or increase in abundance.

Study area

This study was conducted on the Coastal Bend ecoregion at the Rob and Bessie Welder Wildlife Refuge. Welder Wildlife Refuge (28° 06' 47.75"N 97° 25' 01.0"W) is a 3160 ha wildlife reserve located 71 km north of Corpus Christi, TX (Hirth 1977). Vegetation at the Welder Wildlife Refuge is consistent with the composition, structure, and long-term patterns of change of the non-agricultural plant communities in the region. Historically, the vegetation at Welder and in the southern portion of the Coastal Bend ecoregion consisted of an interspersion of tallgrass prairie and oak woodland (Drawe et al. 1978). Over time, prairie sites have transitioned to a thorn-scrub shrubland with high densities of honey mesquite (*Prosopis glandulosa* Torr.), huisache (*Acacia farnesiana* (L.) Willd.), and other invasive woody plants (Drawe et al. 1978). Mean annual

precipitation at the site is 915 mm (Refuge Records, 1956-2010), with a sporadic rainfall pattern and hurricane season in August and September leading to variable precipitation in any month (Hirth 1977). There are approximately 300 frost free days (Fafarman and DeYoung 1986) with minimum and maximum monthly temperatures normally ranging from 23.9°C – 34.2°C in the summer months (mean = 29.1°C in August) to 8.2°C – 19.2°C (mean = 13.7°C in January) (data summarized from NOAA Corpus Christ Weather Station, 27.79° N 97.40° W, 1971-2000) . Elevation is 12 m with flat and gently sloping topography. Soils are Haplustert of the Victoria clay series (USDA, NRCS Soil Survey), with dense clay to clay-loam soils in the bottomland and well drained sandy soils in the upland.

Methods

We initiated an experiment aimed at restoring grassland dominance using combinations of fire and herbicide. Eighteen plots, each 30 m x 20 m, were established at the Welder Wildlife Refuge within a 60 ha area dominated by honey mesquite and huisache. Plots were randomly assigned fire treatments of burned once, burned repeatedly or unburned with six replicates of each. Initial prescribed fire treatments were conducted in June, 2008 and the second fires were conducted in the burned repeatedly treatment in August, 2009. Three 20 m x 10 m subplots within each plot were randomly assigned an herbicide treatment. The following herbicide treatments were assigned: herbicide all woody plants before the first fire, herbicide all woody plants

after the first fire, or no herbicide applications. Livestock grazing was excluded from all plots for the duration of this experiment.

A systematic sampling approach was designed to estimate the number of fire ant mounds in each plot and to limit inconsistencies associated with observer bias and sampling effort. Nine parallel belt-transects (3 per subplot) were established at equidistant intervals of 3 m to provide systematic detection and tallying of fire ant mounds in each plot (Fig. 14). Sampling was performed by visually inspecting for fire ant mounds within each belt transect, and upon detection, each mound was lightly agitated to differentiate between active and inactive mounds. Only active fire ant mounds were included in this analysis. To estimate the number of fire ant mounds that were not located in unburned plots at the beginning of the study, burned ($n = 12$) and unburned ($n = 6$) plots were sampled within 24 hours of conducting the initial burn treatments in 2008. Data were analyzed using an independent samples t-test with unequal sample sizes and met assumptions of equal variance and normal distribution. To test for differences in the number of fire ant and harvester ant mounds among treatments over time, transects were sampled within 24 hours of burning in 2008 and 2009, and all plots were sampled on the same day in 2010. In plots that were not burned, data were adjusted to represent the number of fire ant mounds that were predicted to have occurred in the field after correcting for sampling errors associated with visually obstructed mounds that were not located in searches of the unburned plots relative to burned plots at the beginning of the study. Data were analyzed using a two-factor

ANOVA and $\log(x)$ transformed to meet assumptions of equal variance and normal distribution. Post-hoc comparisons were made with Tukey's HSD test.

Results

Testing for differences in the number of fire ant and harvester ant mounds as a result of the application of herbicide on woody plants showed no significant differences among treatment groups so data were pooled to test for differences occurring solely as a function of the burned treatments.

Locating fire ant mounds

The likelihood of overlooking fire ant mounds is significant in prairie environments ($t = 4.06$, $df = 16$, $P = 0.001$). Data comparing burned and unburned areas within 24 hours of treatment showed 48% of the fire ant mounds were unaccounted for in unburned areas at the Welder Wildlife Refuge (Fig. 15), despite our systematic sampling efforts. Our inability to locate many fire ant mounds was most likely due to the presence of numerous small mounds that were well hidden in unburned coastal prairie (Fig. 16a). In general, such mounds became visible only after burning removed all herbaceous vegetation (Fig. 16b), whereas large fire ant mounds were easier to detect within dense vegetation in unburned areas (Fig. 16c).

Failing to correct for the proportion of mounds that were not located in unburned environments would considerably alter the observed responses of fire ants to burn treatments. Under the assumption that sampling error was equal among burned and

unburned treatments, we would have incorrectly concluded that fire ants significantly differed among treatments over time ($F_{4,53} = 19.0$, $P = 0.006$) and that fire ant mounds nearly doubled in burned repeatedly and burned once plots within 24 hours of burning in 2008 ($P = 0.01$ and 0.01 , respectively compared to unburned treatment; Fig. 17). In contrast, correcting for sampling error showed fire ant mounds significantly differed over time ($F_{2,53} = 41.8$, $P < 0.001$) but not as a function of the treatments ($F_{2,53} = 1.2$, $P = 0.30$) or their interaction ($F_{4,53} = 1.5$, $P = 0.22$).

Fire ant and harvester ant response

Correcting for our inability to locate fire ant mounds in unburned prairie showed fire ant mounds did not significantly differ among burned repeatedly, burned once, and unburned treatments in any year ($P > 0.05$ for all pairwise comparisons; Fig. 17). However, fire ant mound densities were highly variable among years. The number of fire ant mounds decreased significantly from 2008 to 2009 ($P < 0.001$), but numbers rebounded and did not differ from pre-treatment levels in 2010 ($P = 0.15$). Similarly, harvester ant numbers did not differ among burned and unburned treatments ($F_{2,53} = 3.1$, $P = 0.06$; Fig. 18). However, harvester ant mounds were relatively constant and did not change over the timeline of this study ($F_{2,53} = 0.2$, $P = 0.79$; Fig. 18). The number of harvester mounds did double two years following the fire treatment in plots that were burned once (Fig. 18); however, this change was not significantly different from the burned repeatedly ($P = 0.73$) or unburned treatments ($P = 0.31$).

Discussion

Failing to locate nearly one-half of fire ant mounds in unburned areas has important implications for the control and management of fire ants in coastal prairie. Insecticides are the most common means of treating fire ant infestations (Williams 1994; Drees et al. 1998; Myers et al. 1998) but their efficacy on fire ant populations in non-urban areas where broadcast bait applications are restricted is largely dependent on the ability of an individual to locate and treat individual fire ant mounds. Clearly the ability to successfully locate and treat individual mounds is reduced in prairie environments with high levels of woody and herbaceous plant canopy cover (Fig. 15; Fig. 16). Given these search limitations, one would not expect mound-based fire ant chemical applications to completely eradicate fire ant populations in unburned coastal grasslands. These circumstances may help explain the increased density and distribution of fire ants in non-urban areas even when insecticides are widely used as part of a control plan (Kemp et al. 2000). A novel approach that may improve mound search efforts and the effectiveness of fire ant control in areas like the coastal prairie is for insecticide applicators to apply individual mound-based treatments shortly after prescribed fire when dense herbaceous vegetation has been completely removed.

Our results do not support the disturbance mediated invasion hypothesis and therefore suggests that the use of prescribed fire does not contribute to increasing fire ant abundances in coastal prairie ecosystems. This suggests that fire ants respond differently to fire than many other ecological perturbations. Fire ants have been shown to increase in areas disturbed by mowing (King and Tshinkel 2008), plowing (King and Tshinkel

2008), grazing (Hill et al. 2008; Tucker et al. 2010), and other human-driven activities (Forys et al. 2002, King et al. 2009; Stiles and Jones 1998; Todd et al. 2008). Like fire, these disturbances remove or reduce herbaceous vegetation. Fire ant abundances are typically higher in areas with less vegetation cover because fire ants prefer sites with sufficient sunlight to allow brood thermoregulation (Plowes et al. 2007; Porter and Tschinkel 1993; Sternberg et al. 2006). The differential responses of fire ants to fire relative to other disturbances suggests the disturbance mediated invasion hypothesis should be refined to account for differences in the intensity, duration, frequency, or severity of different disturbances. Such a distinction is important because mechanical equipment used to manage woody plants in coastal prairie creates a disturbance similar to plowing or mowing and is likely to cause similar increases in fire ant abundances. Fire may therefore be the best option available for preventing the establishment of woody plants in coastal prairies invaded by fire ants.

It is unclear whether our findings translate to more traditional, low intensity prescribed fires that are conducted during periods of average or above-average precipitation. Fires in this study were conducted during periods of severe drought, leading to considerable grass curing, low fine fuel moistures, and high fire intensities (e.g. Taylor et al. 2012; Twidwell et al. 2009). Multiple authors have suggested fire ants are negatively affected by drought (Hung and Vinson 1978; Kidd and Apperson 1984; Stuble et al. 2009) and fire mediated responses of dominant ant species have been shown to be specific to the timing, seasonality, and intensity of fires (Andersen et al. 2007).

Consequently, the reason fire ants did not increase as a result of burning in this study may be because the timing of our fire treatments coincided with drought episodes.

The number of fire ant and harvester ant mounds did not respond to our experimental restoration treatments and therefore our data do not support the passengers of ecosystem transitions hypothesis. It is important to acknowledge, however, that the time frame of this study is likely insufficient to document colony turnover and displacement dynamics. In addition, even though our fire and herbicide treatments have dramatically altered the composition and structure of the woody plant community (Twidwell 2012), the ecosystem has not been fully restored to coastal tallgrass prairie. As a result, it is likely too early to determine whether restoration treatments are having a long-term effect on fire ant and harvester ant abundances. Moreover, using alternate sampling techniques, such as pitfall traps, would provide a more precise measure of how populations of fire ants and harvester ants are responding to the initial restoration treatments (Schlick-Steiner et al. 2006).

CHAPTER VI
INTERVENTION WITH EXTREME PRESCRIBED FIRE AND HERBICIDE IN
RESPROUTING SHRUBLANDS OF THE SOUTHERN GREAT PLAINS

Introduction

Intervention in novel ecosystems requires the creation and application of novel resource management strategies that push the boundaries of conventional management practices. In a non-analog world (Williams and Jackson 2007), where climate change, the presence of invasive species, alterations in disturbance regimes, and human-aided global dispersal processes have altered successional processes from their perceived historical contexts, conventional restoration and conservation approaches have offered false promise and have often failed to meet the expectations of ecological managers (Hobbs et al. 2011). Worse yet, conventional management practices have led to accidental, catastrophic ecological regime shifts and the loss of desired ecosystem dynamics in some cases (Folke et al. 2004). As a result, a relatively recent conceptual shift has been proposed (termed intervention ecology) that focuses on enhancing environmental services in the present and future with the expectation for future environmental change rather than seeking to restore ecosystem services in potentially unattainable past ecological states (Hobbs and Cramer 2008; Hobbs et al. 2011). Intervention ecology therefore challenges scientists and managers to recognize and move beyond the myths and dogmas of many conventional practices that have become engrained in human thinking.

The effects of fire in resprouting shrublands are well-established, yet our understanding of the role of fire in shrublands may benefit from viewing fire in an intervention approach. Based on conventional norms, prescribed fire is a useful practice for the conservation of grasslands and savannas but has failed as a restoration technique once resprouting shrublands dominate a site. This is supported by numerous experimental manipulations throughout the world that shows prescribed fire can limit woody recruitment in grasslands and savannas (Bragg and Hulbert 1976, Collins and Wallace 1990, Andersen 1990, Briggs and Gibson 1992, Scifres and Hamilton 1993, Leach and Givnish 1996, Scholes and Archer 1997, Hartnett and Fay 1998, Briggs et al. 2002, Heisler et al. 2003, Fuhlendorf and Engle 2004, Ansley and Rasmussen 2005), but it has also been reported that fire only alters the structure of woody plants once they establish and not their density (Briggs et al. 2002, 2005, Ansley and Rasmussen 2005, Higgins et al. 2007). However, most prescribed fires are limited to the “milder” end of the fire spectrum to ensure safety and containment, which may be driving our understanding of the role of fire as an agent of change in both non-analog and historically referenced ecosystems.

The inability of fire to restore grasslands and savannas after conversion to shrubland has limited its application by grassland managers. Managers have instead turned to more expensive alternatives that are more effective at killing woody plants. Mechanical equipment and herbicides are most commonly used in post-grassland and post-savanna environments to “set back” succession, but there are economic and ecological limitations to these strategies as well (Teague et al. 2001, Olenick et al. 2005,

Kreuter et al. 2005, Noel and Fowler 2007, Ansley and Wiedemann 2008). Herbicide and mechanical treatments are expensive, can cause unintended damage to soils and non-target species, often have limited effectiveness in controlling invasive species, and have triggered catastrophic increases in undesirable woody species in some instances (Scifres 1980, Hamilton et al. 2004).

We test two novel interventionist approaches that aim to halt shrub encroachment, increase mortality levels of resprouting shrubs in excess of levels observed in conventional management practices, and alter the ecological trajectory of the system by decreasing the densities of existing shrubs. First, we established an experiment to determine whether fire can be a useful reactive intervention approach by designing an experiment to ignite, control, and study the effects of extreme prescribed fires in degraded grasslands heavily encroached by woody plants. For extreme prescribed fire to be useful in intervention, it needs to be more effective than conventional applications of prescribed fire, reduce the densities of existing shrubs, and limit recruitment of new shrubs relative to areas that are not burned. As a second intervention approach, we used herbicide in combination with extreme fire to determine whether their use in combination could be more effective than the conventional approach of using herbicide alone. For this to occur, mortality rates from fire and herbicide combinations need to exceed mortality levels that result from the sole use of herbicide.

Methods

Study sites and experimental design

We established this experiment in two different ecological regions heavily encroached by shrubs to determine the potential for broader application of the proposed intervention strategies. The two sites included (1) the Rob and Bessie Welder Wildlife Refuge, a subhumid site located near Sinton, Texas, and (2) Texas A&M Agrilife Research Center, a semiarid site located near Sonora. Eighteen plots, each 30 m x 20 m, were established at each site and randomly assigned prescribed fire and herbicide treatments using a split-plot experimental design. Prescribed fire treatments were randomly assigned to whole plots. At each site, six plots were burned with a single extreme prescribed fire, six other plots were burned twice, and six were not burned and served as controls. Every plot was surrounded by at least a 15-m wide bare ground fire break. Plots were ignited independently and served as true replicates. The first set of fire treatments were conducted in June 2008 at Welder and August 2008 at Sonora. Twelve plots were burned at each site at that time. In the burned twice treatment, six plots were burned again in July 2009 at Welder and six were burned again in September 2010 at Sonora. Fire treatments could not be conducted in 2009 at both sites because the plots at Sonora did not accumulate sufficient herbaceous fuel load and continuity one year following fires in 2008.

Each whole plot was divided into three subplots of equal area (20 m x 10 m) to apply different herbicide treatments (Fig. 9). Herbicide treatments included (1) herbicide in 2007, which was timed to occur one year prior to conducting the burn

treatment, (2) herbicide in 2009, which was timed to occur when resprouting stems from burned mesquite trees were approximately 0.5-m in length, and (3) no herbicide, which served as a control. Herbicide was applied to all woody plants by spraying a 75% diesel – 25% Remedy Ultra mix (triclopyr, Dow Agrosiences) at the base of their stems.

Extreme prescribed fire design

All fire treatments were conducted with special exemptions during periods of government-imposed burning restrictions. To ensure containment of extreme prescribed fires and to prevent wildfires, a large “buffer area” with little to no surface fuel was established at each site to provide sufficient space to prevent firebrands originating from the extreme fire treatments from starting spot-fires and the potential for “prescribed fire turned wildfire.” The buffer area was established down-wind of the plots in the direction of the prevailing wind. Plots were oriented next to the buffer area in a horizontal configuration so that each plot could be burned with a headfire (Fig. 9). Surface fuels were removed in the buffer area by burning it in mild fuel and fire weather conditions (i.e., high fine fuel moisture, low temperature, high relative humidity, low wind speed) prior to conducting the extreme fire treatment. The size of the buffer area was determined using rules-of-thumb established for rangelands by Wright (1974) and comparing those guidelines to quantitative predictions of spot-fire distance in flat terrain using Albini (1979, 1981).

Woody vegetation measurements

Prior to applying the initial fire and herbicide treatments, every individual woody plant ≥ 100 cm tall was identified, measured, and tagged to track how each individual responded to treatment combinations of fire and herbicide. This resulted in a total of 4,203 shrubs being sampled in 2006 ($n = 1,634$ at Welder; $n = 2,569$ at Sonora).

For each individual shrub, measurements included shrub height (m), number of stems, and crown diameters (m) in north-south and east-west directions. Measures of crown diameters were used to calculate the area of the crown (m^2) for each individual shrub using the equation for an ellipse. Because fires were designed to maximize fire severity and consume aboveground portions of the plant, shrubs in burned treatments were tagged by placing a metal flag with a aluminum tag hanging from it next to the northern-most base of each individual. The only exception to this rule occurred when multiple individual shrubs were located in a single cluster or “motte” at which point flags were placed next to the base of each individual, irrespective of direction. These tags were used to re-identify each individual when shrubs were resampled in 2011 after all experimental treatments were finalized. At that time, all detailed measurements were retaken for each tagged shrub, and every tagged shrub was assessed for mortality.

This sampling protocol enabled us to identify and measure the recruitment of new juvenile individuals in 2011. Juvenile recruits were those individuals that were ≥ 100 cm tall in 2011 but were not measured in 2006 because they were either too small (i.e. < 100 cm) or were not present. The same measurements for tagged shrubs were conducted for new recruits. Shrub height (m), number of stems, and crown diameters

(m) in north-south and east-west directions were measured for each new individual recruit.

Data analysis

To determine how the density of shrubs changed in response to the treatments, percent change was calculated by comparing the number of individuals in 2006 (denoted by the number of tagged individuals) to the number of individuals in 2011 (denoted by the number of tagged individuals plus new recruits) for each subplot. A split-plot ANOVA was used to test for differences in the percent change in the density of shrubs. Pairwise comparisons were made for each treatment combination using student's t-test. This test was repeated at the species level to determine if treatments caused differential effects among the dominant species within a site or differential effects between sites for a given species. Mesquite and huisache were included in this test for Welder and mesquite and Pinchot's juniper were included for Sonora. Differences in the density of new recruits among subplots were tested using split-plot ANOVA. The hypothesis associated with this test was established after the initiation of the study, so pairwise comparisons between treatments were made using Tukey's HSD.

To determine how individual shrubs responded to the treatments, measurements from only the tagged shrubs were used to calculate percent mortality and percent changes in shrub height, number of stems, and crown area for each individual from 2006 to 2011. Percent mortality was calculated for each subplot by dividing the number of tagged shrubs that died in a given subplot in 2011 to the number of tagged shrubs that

were alive in a given subplot at the beginning of the study in 2006. Values of percent change were averaged for all live and dead tagged individuals within a subplot. Note that percent change of a dead shrub is -100% for all demographic measurements. The mean for each subplot was then used to test for differences in the percentage changes in shrub height, number of stems, and area among treatments using split-plot ANOVA. Pairwise comparisons were made for each treatment combination using student's t-tests since these hypotheses were established *a priori*.

Results

Extreme fire effects (no herbicide)

Extreme fire treatments resulted in consistent, significant changes to the density and structure of the woody plant community in both ecological regions. Shrub densities in the burned twice and burned once treatments were significantly lower at both sites than in control treatments that were not burned (Table 9) and the magnitudes of change were remarkably consistent at both sites (Fig. 19a, Fig. 19b). The height and crown area of shrubs were significantly lower in burning treatments at both sites compared to the control (Fig. 20a, Fig. 20b; Table 9) whereas the number of stems was significantly greater in burned plots at both sites (Fig. 20a, Fig. 20b; Table 9). On the Edwards Plateau, burning twice significantly decreased shrub height and crown area compared to burning once but did not differ significantly in the number of stems (Fig. 20; Table 9). Shrub height and area of crowns did not differ between burned twice and burned once treatments on the Coastal Bend (Fig. 20b; Table 9).

Significantly lower shrub densities in the burned treatments compared to the control reflect differences in rates of mortality of established individuals relative to rates of recruitment of new individuals. At both sites, burning treatments resulted in greater rates of mortality than rates of newly established juveniles. In burned twice treatments, mortality of individual shrubs averaged 13.5 ± 4.5 on the Edwards Plateau and 6.5 ± 2.9 on the Coastal Bend. Recruitment in burned twice treatments averaged 1.2 ± 0.7 and 2.7 ± 0.9 on the Edwards Plateau and Coastal Bend, respectively. In burned once treatments, mortality of individual shrubs averaged 8.5 ± 2.5 on the Edwards Plateau and 4.2 ± 0.9 on the Coastal Bend, and mean recruitment was 2 ± 0.7 and 6.5 ± 1.8 on the Edwards Plateau and Coastal Bend, respectively. In contrast, recruitment exceeded mortality in control plots that were not burned at both sites. Recruitment and mortality averaged 12.2 ± 5.2 and 2.7 ± 0.7 , respectively, in control plots on the Edwards Plateau and 9.8 ± 2.2 and 1.8 ± 0.7 , respectively, in control plots on the Coastal Bend.

On the Coastal Bend, we observed significant decreases in the density of huisache (Fig. 21a; $F_{2,15} = 5.64$, $P = 0.0149$) due to significantly different rates of recruitment (Fig. 21b) and mortality (Fig. 21c) among burned treatments. Huisache mortality was greater than any other woody species in plots that were burned (Table 10). In plots that were not burned, huisache recruitment was greater than any other woody species (Table 10). Rates of huisache mortality exceeded rates of huisache recruitment (mean mortality in Fig. 21b versus mean recruitment in Fig. 21c), whereas recruitment exceeded mortality in plots that were not burned (Fig. 21b vs. Fig. 21c). Differences in mortality relative to recruitment led to huisache densities that were 91% and 78% lower,

on average, in plots burned twice and burned once, respectively, than in plots that were not burned (Fig. 21a).

Other dominant species did not differ among burned treatments. Changes in the density of mesquite did not significantly differ among burn treatments at either site ($F_{2,15} = 0.42$, $P = 0.6662$ at Edwards Plateau site; $F_{2,15} = 0.82$, $P = 0.4612$ at Coastal Bend site). Pinchot's juniper, the other dominant resprouting shrub encroaching on the Edwards Plateau, also did not differ in density among burn treatments ($F_{2,15} = 2.18$, $P = 0.1473$).

Herbicide effects (no fire)

All demographic characteristics differed significantly among herbicide treatments (Table 9) and were significantly lower in herbicide treatments that were not burned than in the control that was not burned or sprayed with herbicide (Fig. 19, Fig. 20). Such trends were consistent across both sites (Fig. 19, Fig. 20). Herbicides applied in 2007 did not significantly differ from herbicide applications in 2008 for any response variable (Fig. 19, Fig. 20).

Effects of fire and herbicide in combination

We observed significant fire and herbicide interactions for most demographic variables (Table 9); however, this statistical effect was driven by the herbicide treatment and does not reflect an ecologically meaningful interaction in most cases. Fire and herbicide combinations did not significantly reduce densities of shrubs compared to

herbicide alone at either site (Fig. 19). Similar non-significant patterns were observed for most other demographic patterns (Fig. 20). The primary exception was that fire and herbicide significantly reduced shrub height in both burned treatments on the Edwards Plateau (Fig. 20a), but shrub height did not differ between fire-herbicide combinations and the herbicide alone treatments on the Coastal Bend (Fig. 20b).

Discussion

Moving beyond long-held dogmas associated with conventional management and restoration practices is critical if novel intervention strategies are to be successful. Dogmas can result from a variety of practices. Long-term untested experimental assumptions, oversimplification of physical, ecological and social dynamics, or even social thresholds that constrain the conditions we can conduct experimental manipulations in nature are dominant factors that need to be considered as intervention strategies are being developed. The latter likely explains the long-held dogma regarding the inability for fire to significantly decrease resprouting shrub densities. So many fire experiments have been conducted within socially acceptable experimental conditions, and thereby failed to decrease shrub densities, that fire alone has been deemed incapable of decreasing woodland dominance, even in mature stands of non-resprouting juniper species (e.g. Van Auken 2000). Progressing beyond such dogmas requires researchers to question long-held ecological assumptions, something that is not often done in fire ecology research (Johnson and Miyanishi 2001), and to identify the specific environmental conditions that bind experimental findings. A key step for future research

is to identify *how* high intensity fires conducted in the growing season during drought caused mortality in resprouting shrubs (rather than simply showing *that* mortality is possible, as done in this study). This requires researchers to seek to quantify thresholds connected with interactions among heat transfer, combustion, and how they relate to physiological processes associated with burning during periods of water deficit. If such thresholds are quantified and linked to the fire weather and fuel conditions driving fire behavior, researchers can provide managers with much more realistic expectations of how and when fire can be used for intervention.

Establishing realistic expectations is a central tenant of intervention ecology (Hobbs and Cramer 2008; Hobbs et al. 2011), and we do not want to add to the myths of what fire can or cannot do. While extreme prescribed fires met the baseline requirements we established to determine whether it has the potential to be a useful intervention approach in resprouting shrublands, it is equally important to recognize the limitations and uncertainties surrounding its use. Most importantly, extreme prescribed fire is a qualitative term that is relative to a specific ecosystem and observer. Managers are very likely to be disappointed if they burn beyond conventional prescriptions, yet are still burning in conditions that are well below those required to exceed fire induced woody plant mortality thresholds. That said, in the right conditions extreme prescribed fire can be expected to decrease shrub densities compared to not burning. However, it is not a “silver bullet” or “one off” intervention practice that kills all undesirable resprouting woody plants and recreates an idealized historic grassland or savanna state. Extreme prescribed fire should be included as part of an intervention regime that

increases the probability of killing established shrubs while decreasing the probability of encroachment by newly established individuals. As a result, changes in the density of the woody plant community are likely to be subtle, whereas structural changes are readily evident. Ultimately, the goal of using extreme prescribed fire for reactive intervention is to enhance the services provided by the ecosystem. It is currently unclear how far extreme prescribed fires can shift woody plant dominance in non-analog ecosystems, and it is too early to determine the potential benefits (e.g. increased biomass, increased biodiversity) or the potential trade-offs (decreased biomass, decreased biodiversity, increased invasion) of its use. What is known is that high intensity fires conducted during droughts in the growing season can decrease densities of woody plants and alter the trajectory of the ecosystem, something thought to be impossible with conventional applications of prescribed fire.

Based on the findings from this study, researchers and managers may be quick to point out that mortality levels were much lower with extreme fire than with herbicide and the combination of fire and herbicide did not increase mortality levels over herbicide alone. Some may take these outcomes as justification for using herbicide over extreme fire. If killing resprouting shrubs is the managerial objective, and other considerations are unimportant, then we would agree with this line of reasoning. Herbicides are clearly renowned for their ability to kill resprouting shrubs (DiTomaso 2000; Ansley and Castellano 2006), and the herbicide used in this experiment was specifically selected because it is recognized as an effective method for killing numerous resprouting shrub species in Texas (Hanselka and Lyons 2004; McGinty and Ueckert 2005). Our intent,

however, is not to direct the practices of individual managers. Rather, our findings bring to light that fire, which has been globally discounted as a potential intervention approach in resprouting shrublands, is a viable option that can kill a significant proportion of resprouting shrubs and may produce the desired ecosystem services for some land managers. In the end, the decision to use either extreme fire or herbicide will likely depend on a suite of ecological or social factors that go beyond shrub mortality.

Reactive intervention often poses the most challenging ethical dilemmas for scientists, managers and the general public (Hobbs et al. 2011), and the use of extreme fire for reactive intervention in resprouting shrublands is no different. On one hand, humans can manipulate and control fire on the landscape during conditions that are most likely to meet their objectives of shifting shrubland dominance. On the other, such fires are conducted when uncontrolled wildfires are in widespread occurrence or when the threat of wildfires is high. When extreme prescribed fire for intervention is likely to work, federal agencies are frequently spending more than one billion (\$US) per year in the United States to suppress fire (Dombeck et al. 2004). The future of extreme prescribed fire in this system depends on the future transformation of the legislation and regulatory policies that dictate its application and effectiveness. Can more flexible regulations be created that manage risks associated with wildfires while allowing environmentally-based organizations to meet their goals and objectives? In other regions of the world, some organizations and individuals are able acquire permits to burn in burn bans for ecological purposes (e.g. Mali, West Africa; Bassett and Zuéli 2000, Goldammer and de Ronde 2004). Can similar legislation work elsewhere, thereby

allowing extreme prescribed fire to be purposefully reinstated on the landscape after more than a century of extreme fire prevention and suppression? At present, policies in the United States have been aimed at suppressing fires, reducing fuels, and lowering fire intensities, but the high costs and ineffectiveness of this approach have led to heavy scrutiny (Busenberg 2004, Stephens and Ruth 2005). Do policies and legislation permitting the application of extreme prescribed fire put human life and property at risk? It is often assumed that extreme fire behavior and crown fires pose a direct threat to human communities (Allen et al. 2002, Van Auken 2008). Or, does the ability of an individual or an organization to plan, design, ignite, and control extreme fire on the landscape show the need to distinguish between uncontrollable wildfires and prescribed fires that exhibit wildfire-type intensities? These questions will likely be debated among scientists, resource professionals, politicians, and the general public for the foreseeable future. Yet, the decisions derived from this debate will undoubtedly result in governing regulations that have profound impacts in fire-dependent ecosystems.

CHAPTER VII

PH.D. STUDENT INSTRUCTED UNDERGRADUATE RESEARCH: MORE THAN AN UNDERGRADUATE EDUCATION AND DOCTORAL DISSERTATION

Introduction

The benefits of conducting undergraduate research have caused academic institutions to restructure education and curriculum in an effort to provide research experiences to more undergraduate students. Students conducting research are actively engaged in their own learning and benefit from enhanced analytical reasoning, critical thinking and creativity, greater knowledge acquisition and retention, and increased confidence to conduct research and contribute to science (Landrum and Nelsen 2002; Seymour et al. 2004; DeHaan 2005; Hunter et al. 2007; Russell et al. 2007). Such benefits transfer beyond academia. Undergraduate researchers report to be better prepared for employment, display improved technical skills, and exhibit increased interest in careers related to science, technology, engineering, and mathematics (STEM) (Seymour et al. 2004; Landrum and Nelsen 2002; Hunter et al. 2007; Russell et al. 2007). As a result, most colleges and universities have incorporated faculty-mentored research programs into undergraduate curriculum, and numerous funding sources have arisen to support the costs of conducting undergraduate research (e.g. NSF, NIH, EPA, NASA). Nevertheless, mentoring constraints and insufficient funds continue to be the two dominant issues limiting broader participation in undergraduate research (Russell

2006) and preventing academic institutions from meeting their goal of providing the majority of undergraduate students with authentic research experiences (DeHaan 2005).

Issues preventing broader participation in research are partly the result of how undergraduate research has traditionally been supported. The standard approach to undergraduate research has followed the faculty-mentored graduate student model, imposing high costs and high mentoring demands. Undergraduates often work on stipends, require laboratory or office space, demand equipment and supplies, and command attention and time from professors (DeHaan 2005). Funding from agencies, while helping to offset costs for a limited number of students, can actually reinforce the cost-prohibitive perception of undergraduate research by setting the bar at thousands to tens-of-thousands (\$US) per student (Table 11). If this is the cost per student, how are academic departments to financially support undergraduate research for a vast majority of undergraduate students? Moreover, such financial support provides little for faculty mentors who are directly responsible for advising undergraduate research. Faculty mentors of undergraduate research programs are therefore presented with a trade-off between academic service and productivity, especially for those at large research universities (Dolan and Johnson 2010) where increasing the number of undergraduate students in the research lab reduces the mentoring time and money available for more productive graduate and post-doctoral students (Zydney et al. 2002; Dolan and Johnson 2009). This is often why many faculty researchers view undergraduate research as a service to the student rather than a worthwhile research exercise that also benefits the faculty mentor (Dolan and Johnson 2010).

Innovative approaches are needed to overcome the dominant constraints limiting broader participation in undergraduate research. Many departments at Texas A&M University, like other institutions with large numbers of graduate student researchers, have not been able to offer genuine research opportunities to the majority of undergraduate students. Because funding and mentoring constraints are the critical issues limiting broader participation, we developed a new course on undergraduate research in the College of Agriculture and Life Sciences wherein a PhD student served as the instructor of record and interested undergraduate students interviewed to enroll in the course to conduct mentored, independent research projects. A key objective of the course was to evaluate whether a PhD student instructed course could be designed so that no funds were needed from the university or external funding sources while simultaneously increasing the number of research opportunities available to undergraduates. In this paper, we discuss expenditures and income from the PhD-student instructed course on undergraduate research, the challenges and potential pitfalls in its implementation, and its potential benefits to academic and scientific endeavors.

Ph.D.-student instructed undergraduate research

Course description and participation

Our aim in offering a PhD student taught course on undergraduate research was to directly integrate graduate and faculty research activities into the academic curriculum of undergraduates in a manner that lowers the cost of conducting research while simultaneously extending the number of research opportunities available. Various

learning strategies could be implemented in a course to achieve such a result. Since our specific intent was to provide undergraduate students with the training needed to succeed as researchers, we considered including elements that introduced them to foundational scientific principles, hypothesis testing, experimental design, sampling or measurement, statistical analysis and interpretation, technical writing, literature review, and publication. In the end, the course was designed to provide undergraduates experience in communicating their research by writing a paper in the form of a peer-reviewed scientific article and to provide the PhD instructor with experience in mentoring students that are conducting research and going through the process of writing manuscripts for peer-review. One PhD student, the lead author of this paper, designed and taught this course from 2008-2010. A total of eight undergraduate students were selected from interviews and enrolled in this one semester course over those two years.

Undergraduate students who enrolled in the course conducted mentored, autonomous research on a project related to the PhD student's dissertation research. The PhD's dissertation was in the domain of ecology with specific emphasis on ecological restoration, fire ecology, and the resilience of social-ecological systems. Each undergraduate student was able to pursue any research question that was broadly related to the PhD's project and could be carried out over a reasonable timeline. Over the two years, undergraduate projects ranged from *in situ* experimental manipulations within the PhD's field experiment (4 of 8 students), such as plant-animal invasions following wildfire, to formal literature reviews (2 of 8 students) on fire and environmental policy, to the use of pre-existing data sets (2 of 8 students) for mechanistic analyses of spatial

fire data and long-term evaluations of seasonal fire applications in semiarid *Quercus* savanna. Regardless of the project of each individual, students met as a group weekly in the classroom to discuss general scientific principles, the scientific literature, their research projects, and the obstacles limiting their advancement. Students met as a group so that each student could benefit from the experiences of others and to increase their tolerance to the struggles that occur throughout the research process by observing other students in similar situations. Upon successful completion of the course, undergraduates were prepared to conduct an international search for relevant scientific literature, develop an independent series of testable questions and ideas, critically assess and interpret research findings, write and format a scientific paper in the form of a peer-reviewed scientific journal, and present findings to regional, national, and international conferences. A manuscript was submitted at the end of the course and was evaluated by the PhD instructor using a rubric modified from Reynolds et al. (2009).

Economic assessment

The design of the course and the culture it established at the undergraduate level enabled research projects to be conducted without the high expense of graduate and undergraduate salaries. The PhD student served as an instructor of record as part of his academic training and did not require a salary beyond his grant-funded graduate stipend. Similarly, all undergraduates viewed the course as part of their scholastic training and received course credits rather than salaries.

Coupling undergraduate projects to the PhD's research allowed undergraduates to conduct a major research project without internal or external funding beyond the grant supporting the PhD's dissertation research (Table 12). Four of eight students conducted formal reviews or used pre-existing data, so no funding was needed to complete their research. The other four undergraduates worked *in situ*, but those expenditures were offset by *piggy-backing* on the PhD's research project and driving to research sites as a group, sharing accommodations, and pooling equipment. In effect, a sustainable research environment was created because undergraduates worked with the PhD as part of a cohesive research team. The only additive costs incurred in the course were the result of offering undergraduates the opportunity to present their research with the PhD student at major, internationally-themed scientific conferences (Table 12), which was paid for by small internal grants secured by the PhD student. Ultimately, our PhD instructed undergraduate research course produced greater income via student enrollment than the total expenses accrued over a two year period (Table 12).

Challenges and potential pitfalls

In a PhD instructed course, undergraduates and PhDs must function as part of a team with the intent of maximizing research productivity, but a number of potential pitfalls can reduce the efficiency of undergraduates and graduates in the research lab (Chmielewski and Stapleton 2009; Dolan and Johnson 2010). First, a PhD student instructed course on undergraduate research follows the mentor-advisee model and therefore necessitates a strong graduate-undergraduate relationship if projects are to be

completed on time. Without sufficient PhD input, undergraduates are likely to become frustrated, lose interest in the research process, and become little more than data collectors. Without sufficient undergraduate effort and ability, PhDs are likely to spend too much time mentoring and not enough time on their own research or publishing.

Second, *piggy-backing* on the PhD's research project may not be feasible for all scientific domains or fit within the ideology of certain research labs and therefore our ability to create a cost-effective undergraduate research environment may not be widely transferrable. A couple potential solutions would be to charge a small class fee, obtain small grants, or withdraw funds from the primary grant backing the project, if deemed appropriate by the faculty advisor overseeing the grant. Further experimentation of this course and the development of creative solutions that seek to admonish the high cost nature of undergraduate research are needed in other academic domains to determine the level of applicability of the PhD instructed undergraduate research model.

Third, this course shifts the burden of responsibility of mentoring undergraduate researchers from professors to the PhD level. This could be viewed positively because nearly all professors directly mentoring and paying for undergraduate research indicate that they cannot support additional students (Zydney et al. 2002); however, it does pose a considerable challenge to PhDs since they too have an extensive work load, limited time for additional responsibilities, and no training available that specifically develops PhD instructors for undergraduate research. Even with such challenges, many PhD students welcome this shift because it offers them the opportunity to increase their productivity (Dolan and Johnson 2010) and gain skills that are not typically acquired

during their doctoral training and education (e.g. mentoring, managing and organizing a team, effectively communicating how to overcome obstacles that occur throughout the research process; Nyquist et al. 1999; Austin 2002; Melin and Janson 2006; Trautmann and Krasny 2006). While PhD students may be less experienced than professors at guiding research activities, undergraduates have remarked that PhDs provide unique mentoring experiences because they are more approachable, have fewer competing responsibilities, and more flexible schedules than professors (Dolan and Johnson 2010), more easily relate to problems at the undergraduate level (Liang et al. 2002; Dutton and Raggins 2006), and are an additional connection to other experts in the field (Tenenbaum et al. 2001). Undergraduate students also get the impression that their work is more meaningful because it is directly contributing to the success of the PhD's research project (Dolan and Johnson 2010).

Fourth, the success of undergraduate students, and the quality of training they receive, is entirely dependent upon the talents and mentorship provided by the PhD student. PhDs should therefore serve in a capacity that matches their level of mastery in their domain of study. To effectively instruct the course outlined previously without significant professor input, one will need to have mastered all the elements taught in the course – conducting and interpreting research, experimental design, statistical analysis, technical writing, and publication. This is a considerable challenge to PhD students since nearly all are developing such skills themselves but some individuals are clearly capable of undertaking this challenge and succeeding. Many PhDs serve as teaching assistants, lecturers, instructors, collaborators on major grants, and publish findings from

their PhD or Masters studies, so why do so few opportunities exist for professors-to-be to develop skills in mentoring and leading a research lab? Given the opportunity, nearly everyone would choose to acquire experience in these areas prior to making the career jump to professor and being forced to learn on-the-job (Pfund et al. 2006).

Developing successful Ph.D. instructors of undergraduate research

Universities can help PhDs avoid the potential pitfalls associated with teaching research and mentoring undergraduates. Universities can create programs that provide training, information, and successful models of instruction for PhDs to follow. Such programs also foster the professional development of PhDs and better prepare them for future mentoring roles as a faculty member or director of a research lab. In addition, the course can be modified so that the PhD instructor is evaluated by professors. Some academic departments may even choose to design the course so that the PhD students/instructors also enroll in the class and are evaluated by professors based on their development as a research mentor. Furthermore, the PhD's faculty advisor can help guide the student by providing short-term and long-term research directions, fostering a research culture, helping to regulate expenditures, and approving or vetoing proposed projects or changes to the experimental protocol and research approach.

A final way to help secure success of a PhD instructed course on undergraduate research is for all invested parties to set the bar at a manageable level. The goal is for students to develop into expert researchers and expert mentors while maintaining or increasing the overall productivity of the lab. Each individual must therefore

compensate for the limitations of individuals at lower levels and rely on the strengths of individuals at higher levels. To illustrate, PhDs may need to conduct statistical analyses since few undergraduates have adequate training in statistics. At the same time, PhDs may need to rely on the experience of their professors to help provide short-term and long-term research directions and project timelines. Undergraduates are unlikely to consistently produce if their research projects match the breadth and timeline of a PhD's – something short-term coupled to a long-term project may prove to result in publication with greater regularity. Other strategies could also result in productive output for the undergraduate but may be less meaningful to others. For example, journals are now widely available that publish undergraduate-only research, but such journals do not count as productive output for most professors (Ferrari 2002). Furthermore, while undergraduate-only publications can be beneficial to those applying to graduate school, it may leave negative impressions on undergraduates as they question whether their contributions were meaningful to the field (Ferrari 2002).

Benefits of Ph.D. instructed undergraduate research

To students and faculty

Numerous benefits emerge in a PhD instructed course on undergraduate research. For professors, the course removes the burden of mentoring that can reduce their productivity and shifts this responsibility to the PhD level. In turn, PhDs gain experience teaching, providing technical support, editing and revising manuscripts as the primary team leader, mentoring multiple students, running a research lab, and attempting

to increase their overall publication output. Essentially, they are proving themselves as principal research investigators and graduate advisors at the next level. This helps to facilitate a strong productivity-based culture at the graduate level, while establishing an active learning – research culture at the undergraduate level.

Creating an economically sustainable undergraduate research environment (e.g. Table 12) and reducing mentoring demands on professors also affords the opportunity for students other than the few “undergraduate academic elite” to participate in research activities. In contrast, for those professors directly mentoring and paying for undergraduate research, nearly all suggest they cannot support additional students (Zydney et al. 2002). Without major funding, such students often operate more like undergraduate technicians than researchers, serving in a lab to do the bidding of graduate students or professors. While worthwhile, this lessens the value of research at the undergraduate level (Karsai and Kampis 2010) and fails to develop critical components of intelligence in students – namely aspects of analytical, creative, and practical intelligence (Sternberg 1999).

To science and society

Improved research experiences at lower levels of education may provide even greater benefits to the general public and scientific community. Many technology-dependent countries, such as the US, face a future crisis in the work-force due to shortcomings in the training and expertise of individuals in science and engineering (Jackson 2003). This increased demand requires more and better trained individuals in

science and technology at lower levels. Even more problematic is that all facets of the general public are in need of better education on the principles and aims of scientific research. Is it any wonder then that researchers are struggling to bridge the gap between science and society (Agre and Leshner 2010)? A formal education in scientific research is largely an exclusive club for those in graduate schools or beyond. In the US, only 38% of employed college graduates attained a degree higher than a bachelor's, and 74%, 70%, and 43% of respective individuals with bachelor's, master's, or doctorate degrees were employed in non-science and non-engineering fields (NSF 2005). Using a PhD-instructed course adds a novel approach to undergraduate research that has the potential to overcome mentoring and cost constraints and moves STEM disciplines one step in the direction of formally introducing a larger proportion of the general public into the field of science.

Summary

For undergraduate research to be worthwhile to PhD students and appealing to their faculty advisors, it should be more than a service to undergraduate students. The aim of PhD instructed undergraduate research is to increase the research productivity of the lab while simultaneously enhancing the professional development of graduate and undergraduate students. This approach therefore raises the bar. The course requires undergraduates to do more than is traditionally asked in their education and PhD students to do more than is traditionally asked of doctoral dissertations. Undergraduates must to go to class, get good grades *and* conduct research and publish. Similarly, PhDs

must go to class, get good grades, conduct research, publish *and* mentor undergraduates and run a research lab. Moreover, undergraduates and PhDs must function as part of a team with the intent of maximizing research productivity and publication output. A number of potential pitfalls can prevent PhDs and undergraduates from meeting their research goals and developing as expert mentors and researchers, but university training programs, reasonable expectations among students and faculty, and feedback from professors may help students meet the challenges of conducting PhD instructed undergraduate research and provide a more beneficial research and mentoring experience to undergraduate and doctoral students.

CHAPTER VIII

SUMMARY

The foundation of this dissertation is that our capacity to enhance services in social-ecological systems ultimately hinges upon the integration of theoretical and applied concepts that drive policy and governance and overcoming the assumptions and traditions that limit their integration. I have shown numerous examples of how this approach is beneficial. I show how we can use quantitative measures of resilience to forecast the effects of restoration strategies in social-ecological systems (Chapter 2). I demonstrate the importance of moving past traditional assumptions of when prescribed fire should be applied to demonstrate new patterns of woody plant responses to the applications of “more extreme” prescribed fires (Chapters 2, 3, and 6) while not causing undesirable invasions by exotic grasses (Chapter 4) and exotic insects (Chapter 5). Finally, I have shown how traditional approaches of supporting undergraduate research are incapable of meeting the broader goals established by society and reveal a novel approach that can increase undergraduate participation at large, research-based universities. These chapters provide case-study examples of how we can overcome traditions and assumptions in scientific disciplines to develop innovative solutions to modern problems. These case studies are summarized in greater detail below.

In Chapter 2, we use a fire case study to introduce a quantitative resilience framework, based on aspects of the adaptive cycle, to quantify components of resilience. Resilience was initially defined as a measure of the amount of disturbance an ecosystem

can withstand and continue to persist. While this definition has promising quantitative potential, the resilience concept has transitioned to multiple, more general definitions and continues to lack a specific quantitative framework. Using resilience within this context may promote new ideas and facilitate management and restoration efforts, but it also leads to contradictory interpretations and applications of the resilience concept. A key feature of the framework proposed here is that forecasting techniques can be directly linked with quantitative aspects of resilience to provide a testable decision support model for social-ecological planners. We then show how quantitative aspects of resilience can be directly integrated with social constraints to more efficiently manage and restore desirable environmental services.

In Chapter 3, we examined how the occurrence and structure of grasses and woody plants changed after 12 years of a fire season manipulation and removal of livestock herbivores. Applying high intensity fires in the summer preserved the structural integrity of this semiarid live oak (*Quercus virginiana* Mill.) savanna while decreasing or eliminating numerous problematic plants in the understory and overstory, such as prickly pear cactus (*Opuntia* spp.), sacahuista (*Nolina texana* S. Watson), Ashe juniper (*Juniperus ashei* J. Buchholz), Pinchot's juniper (*J. pinchotii* Sudw.), and honey mesquite (*Prosopis glandulosa* Torr.). In the less intense repeat winter burning treatments, undesirable woody plants were generally maintained at pre-treatment levels in the overstory but all woody plants except Ashe juniper increased in the understory. Alternatively, areas excluded from fire in the control treatment rapidly transitioned from a grass-tree co-dominated savanna environment to one that is heavily dominated by

woody plants. In the grass community, the most frequently occurring grass species in the winter burn treatment differed from summer burn and control treatments, whereas the summer burn treatment was not different from the control. Of the herbaceous plants, only little bluestem (*Schizachyrium scoparium* (Michx.) Nash) responded to fire treatments. Little bluestem increased in the winter burn treatment, remained fairly constant in the summer burn treatment, and decreased in the control. Other grasses varied largely as a function of annual weather variability, the removal of livestock, and legacy effects resulting from pre-existing variability. These findings suggest that fire can reduce or eliminate woody plant species that threaten the stability of live oak savannas while having little long-term effect on grasses desired by rangeland managers.

We established a more recent experiment (Chapter 4) to expand upon the findings in Chapter 3 and determine if high intensity fires in an alternate ecosystem, Texas coastal prairie, were detrimental to native herbaceous species and facilitate invasion by exotic species. The most problematic invasive herbaceous species in this ecosystem is KR bluestem. KR bluestem is an invasive C4 grass introduced from Europe and Asia that has led to declines in the richness of plant, avian, and arthropod species in prairie ecosystems. Managers in Texas Gulf coastal prairies are concerned that using fire to manage woody plant encroachment will trigger rapid invasion by KR bluestem and decrease native herbaceous species richness. In this study, prescribed fires were conducted in the growing season with special permission during a county mandated burn ban initiated by a severe, prolonged drought. Our results counter previously unsubstantiated assumptions in coastal tallgrass prairies and show that prescribed

extreme fire increased native forb species richness while maintaining the richness of native grasses and not increasing King Ranch bluestem significantly. Since other research has shown burning in the dormant season is more likely to facilitate rapid invasion by KR bluestem, prescribed extreme fires in the growing season may be more effective at maintaining herbaceous species richness in coastal prairies prone to KR bluestem invasion.

In Chapter 5, we continued our evaluation of whether prescribed extreme fire facilitates invasion by exotic species. The target species in this chapter was the red imported fire ant, an invader that poses a serious threat to species in multiple trophic levels and is one of the most expensive non-native species in the United States. The objective of this study was to determine (1) the efficacy of individual mound-based fire ant chemical control strategies, based on the proportion of mounds that are likely to be found in prairie, and (2) to track changes in the densities of fire ant and native red harvester ant mounds in response to prescribed extreme fire. Our data suggest insecticide applicators are likely to miss 48% of fire ant mounds when applying individual mound treatments in shrub-infested prairie. This finding, coupled with evidence that prescribed fire did not increase fire ants or decrease harvester ants, suggests that using chemical control methods in combination with fire, which increases the capacity to locate fire ant mounds, may improve fire ant control.

Chapters 3-5 suggest extreme prescribed fire does not result in undesirable trade-offs, but the real potential of prescribed extreme fire is its use as an intervention strategy in resprouting shrub-dominated grasslands and savannas (Chapter 6). We established an

experiment to test whether extreme prescribed fire could reduce shrub densities in a semiarid savanna and a subhumid grassland. Both sites were heavily invaded by resprouting shrubs. Our findings counter long-held assumptions that prescribed fire cannot reduce the density of shrubs in post-grassland and post-savanna environments. Even more, huisache, considered to be the most problematic woody plant in the southern portion of the Coastal Bend ecological region, experienced the greatest reductions in density as a result of extreme prescribed fire. . However, many knowledge gaps exist with respect to prescribed extreme fire and managers should not expect it to be a “silver bullet” or “one off” intervention practice that kills all undesirable resprouting woody plants and recreates an idealized historic grassland or savanna state. What is known is that high intensity fires conducted during droughts in the growing season can decrease densities of woody plants and alter the trajectory of the ecosystem, something thought to be impossible with conventional applications of prescribed fire.

Chapter 7 moves away from our testing of prescribed extreme fire as a novel intervention strategy to the introduction of a novel approach in the education of undergraduate students in academia. Universities and funding agencies have developed numerous programs in recent years to support the overarching goal of providing the majority of undergraduate students with authentic research experiences. Yet, this goal is far from being realized, especially at research-based universities with large populations of graduate and post-doctoral students. In this chapter, we introduce a cost-effective approach to undergraduate research by integrating undergraduate and graduate research with departmental curriculum and having a qualified PhD student formally instruct and

mentor undergraduates as part of their professional development. One PhD student designed, instructed, and mentored eight undergraduates in this course from 2008-2010. The structure of the course enabled research to be conducted without paying students salaries or securing additional funding beyond the grant supporting the PhD. In this paper, we discuss the costs and income from the PhD-student instructed course on undergraduate research, the challenges and potential pitfalls in its implementation, and its potential benefits.

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APPENDIX A

Table 1. A review of the impact of fire on non-resprouting juniper in post-grassland ecosystems. Note the general lack of control and mortality of mature juniper (> 1.8 m tall).

Reference	Tree height (m)	% control*	% mortality
Dalrymple 1969	< 0.6		100
	0.6 – 1.8		77
	> 1.8		27
Buehring et al. 1971 [§]	< 0.45	100 (Site 1) 92 (Site 2)	100 (Site 1) 98 (Site 2)
	0.45 – 0.9	90 (Site 1) 75 (Site 2)	90 (Site 1) 85 (Site 2)
	0.9 – 1.8	70 (Site 1) 55 (Site 2)	60 (Site 1) 70 (Site 2)
	> 1.8		
Owensby et al. 1973	< 0.6	89	72
	0.6 – 1.8	83	48
	> 1.8	39	20
Wink and Wright 1973	< 1.8		99
Engle and Stritzke 1995	< 1.5	71 (Summer) 92 (Winter)	52 (Summer) 87 (Winter)
	1.5 – 2.5	54 (Summer) 81 (Winter)	41 (Summer) 62 (Winter)
	2.5 – 5.0	39 (Summer) 30 (Winter)	27 (Summer) 0 (Winter)
	< 1.0		88
	1.0 – 2.0		60
	2.0 – 3.0		35
Ortmann et al. 1998	> 3.0		10
	< 1.5		50 (grazed) 100 (ungrazed)
	1.5 – 2.5		20 (grazed) 90 (ungrazed)

2.5 – 3.0	10 (grazed) 85 (ungrazed)
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Table 1 Continued

Note: *% control is defined as the percentage of trees that exhibit obvious effects from treatment (e.g. scorch, dead branches) (definition adapted from Owensby et al 1973).

§values are approximated from a figure in the publication; In Buehring et al. (1971), percent control represents trees exhibiting scorch within one month of each burn; percent mortality represents effects one year after burn.

Table 2. Fact sheet for the Edwards Plateau Prescribed Burn Association, Inc. (EPPBA).

Established: 1997

Legal status: 501 c3 non-profit

Mission:

To restore the productivity and ecological stability of Edwards Plateau, Texas, rangelands using a neighbor-help-neighbor prescribed fire cooperative.

Constituents:

Over 500 ranchers, agency employees, and members of the general public representing greater than one million acres of rangeland across 20 counties of Texas.

Goals:

To empower and equip ranchers to manage rangelands by sharing prescribed fire equipment and labor among constituents; to train constituents in proper, effective, and safe application of prescribed fire; to foster good relations within local and regional communities on the use and benefits of prescribed fire.

Bylaws (at a glance):

A membership fee of \$25 per year is required for the purchasing of prescribed fire related equipment, administrative costs (e.g. correspondence, newsletters, educational material), and prescribed fire training.

Landowners must cooperate on at least one prescribed burn before landowners can schedule a burn on their own property.

A burn plan must be submitted and approved prior to scheduling of the burn.

Only landowners and members of the general public can serve on the EPPBA advisory board. Those affiliated with government agencies or academic institutions can be members only.

Dealing with risk:

Experience, equipment, and money is pooled within the burn cooperative to provide education and training, to mitigate risk, and to establish a regional fire culture by fostering good relations among neighbors within the local community. Many counties now allow EPPBA members to burn during burn bans to meet restoration objectives as a result of their long-established safety record.

Challenges to continued success:

Continued success hinges upon the ability of EPPBA to conduct prescribed fires in a variety of conditions, both mild and extreme. Long-term, inflexible burn bans, emergency declarations, and a lack of education within the general public regarding the importance of fire can greatly disrupt EPPBA operations.

Table 3. PERMANOVA results of tests for differences in the frequency of woody plants and grasses among burn treatments, between sampling heights, and for their interaction for each plant community functional group in 1994 and 2006.

Source	df	1994			2006		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
<i>All plants</i>							
Treatment (T)	2	672	2.48	0.1262	1230	12.38	0.0016
Height (H)	1	18391	67.93	0.0002	17465	175.89	0.0002
T X H	2	129	0.48	0.6900	209	2.10	0.1614
Residual	6	271			99		
Total	11						
<i>Woody plants</i>							
Treatment (T)	2	1032	2.05	0.1490	1779	8.66	0.0014
Height (H)	1	6898	13.69	0.0014	6265	30.50	0.0002
T X H	2	142	0.28	0.8848	207	1.01	0.4324
Residual	6	504			205		
Total	11						
<i>Grasses</i>							
Treatment (T)	2	91	4.38	0.0618	6719	322.91	0.0002
Residual	3	21			21		
Total	5						

Notes: Bold *P*-values indicate statistically significant results ($P < 0.05$).

Table 4. Pair-wise comparisons of differences in the frequency of species in each functional group between summer burn (SB), winter burn (WB), and control (C) treatments in 2006.

Source	Statistic	SB versus WB	SB versus C	WB versus C
<i>All plants</i>				
Understory	<i>t</i>	1.93	2.01	1.88
	<i>P</i>	0.1152	0.1042	0.1074
Overstory	<i>t</i>	1.62	3.96	2.84
	<i>P</i>	0.1864	0.0308	0.0480
<i>Woody plants</i>	<i>t</i>	0.92	2.14	1.21
	<i>P</i>	0.4420	0.0296	0.3438
<i>Grasses</i>	<i>t</i>	18.06	2.47	124.55
	<i>P</i>	0.0018	0.0864	0.0004

Notes: Bold *P*-values indicate statistically significant results ($P < 0.05$).

Table 5. Frequency of occurrence of each woody plant and cactus species in the understory (U) and overstory (O) of repeat summer burn (SB), repeat winter burn (WB), and control (C) treatments in 2006. Values are means \pm SE (and mean change from 1994 to 2006).

Woody species	Acronym	<u>SB</u>		<u>WB</u>		<u>C</u>	
		U	O	U	O	U	O
Live oak	QUVI	28 \pm 12 (+ 18)	44 \pm 2 (+ 14)	68 \pm 9 (+ 41)	28 \pm 2 (+ 24)	26 \pm 5 (+ 12)	69 \pm 8 (+ 47)
Texas persimmon	DITE	5 \pm 1 (+ 5)	0 (- 2)	0 (- 3)	6 \pm 2 (+ 1)	3 \pm 2 (+ 1)	1 \pm 1 (- 1)
Ashe juniper	JUAS	0 (- 3)	0 (- 7)	1 \pm 1 (- 3)	1 \pm 1 (- 2)	9 \pm 3 (+ 8)	23 \pm 6 (+ 19)
Pinchot's juniper	JUPI	3 \pm 2 (- 1)	0 (- 4)	0 (- 1)	2 \pm 1 (+ 2)	4 \pm 2 (+ 4)	6 \pm 2 (+ 6)
Honey mesquite	PRGL	3 \pm 3 (0)	1 \pm 1 (- 3)	1 \pm 1 (+ 1)	1 \pm 1 (+ 1)	4 \pm 1 (+ 2)	4 \pm 2 (+ 4)
Prickly pear	OPSP	5 \pm 3 (- 5)	0 (- 4)	0 (0)	15 \pm 3 (+ 6)	32 \pm 6 (+ 20)	0 (0)
Sacahuista	NOTE	0 (- 11)	0 (- 2)	0 (0)	22 \pm 16 (+ 6)	21 \pm 10 (+ 11)	0 (0)
Algerita	MATR	1 \pm 1 (- 1)	0 (- 1)	0 (- 1)	6 \pm 4 (0)	4 \pm 1 (- 1)	3 \pm 3 (+ 3)
Total mean change		+ 4	- 7	+ 35	+ 37	+ 56	+ 77

Table 6. PERMANOVA investigating differences in the total cover of woody plants among fire treatments in 2006 and the subsequent pair-wise comparisons between summer burn (SB), winter burn (WB), and control (C) treatments.

Source	df	MS	<i>F</i>	<i>P</i>
Treatment	2	91	11.98	0.0268
Residual	3	7		
Total	5			
*Pair-wise comparisons			<i>t</i>	<i>P</i>
SB vs WB			1.83	0.1582
SB vs C			4.02	0.0420
WB vs C			2.66	0.0838

Notes: Bold *P*-values indicate statistically significant results ($P < 0.05$).

Table 7. Frequency each grass species was one of the three most abundant grasses in a sample in repeat summer burn (SB), repeat winter burn (WB), and control (C) treatments in 2006. Values are percent means \pm SE (and percent mean change from 1994 to 2006).

Grass species	Acronym	SB	WB	C
Sideoats grama	BOCU	35 \pm 6 (+ 7)	35 \pm 1 (+ 12)	16 \pm 3 (+ 7)
Sedge spp.	CASP	17 \pm 2 (+ 5)	26 \pm 1 (+ 8)	26 \pm 7 (+ 11)
Texas cupgrass	ERSE	3 \pm 3 (+ 2)	1 \pm 0 (+ 1)	1 \pm 0 (+ 1)
Texas wintergrass	NALE	56 \pm 4 (+ 15)	46 \pm 3 (+ 14)	50 \pm 2 (+ 13)
Wright's threeawn	ARWR	8 \pm 2 (- 22)	26 \pm 2 (- 4)	20 \pm 3 (- 18)
Hairy grama	BOHI	3 \pm 0 (- 11)	23 \pm 1 (- 21)	8 \pm 2 (- 11)
Common curly mesquite	HIBE	52 \pm 3 (- 16)	46 \pm 4 (- 8)	56 \pm 4 (- 4)
Little bluestem	SCSC	1 \pm 1 (+ 1)	11 \pm 0 (+ 4)	1 \pm 1 (- 3)

Table 8. List of species observed in this experiment at the Welder Wildlife Refuge, their growth characteristics, and the frequencies (% of quadrats) and Pearson correlations (r) with NMS axis 1 of each plant species in burned (n = 12) and unburned (n = 6) treatments.

Scientific species name	Common name	Acronym	Provenance	Growth form	Periodicity	Frequency (%)		r
						Burned	Unburned	
<i>Bothriochloa ischaemum</i>	King Ranch bluestem	BOIS	I [†]	G	P	20.37	16.67	0.53
<i>Convolvulus arvensis</i>	field bindweed	COAR4	I [†]	F	P	0.31	0.62	-
<i>Oxalis</i> spp.	woodsorrel	OXCO	I	F	P	0.31	0	-
<i>Bothriochloa laguroides</i>	silver beardgrass	BOLA	N	G	P	0	1.23	-
<i>Buchloe dactyloides</i>	buffalograss	BODA2	N	G	P	2.47	1.85	0.39
<i>Chloris x subdolichostachya</i>	shortspike windmill grass	CHSU3	N	G	P	1.54	3.09	- 0.59
<i>Coelorachis cylindrica</i>	cylinder jointtail grass	COCY	N	G	P	0	0.62	-
<i>Dichanthelium oligosanthes</i>	rosette grass	DIOL	N	G	P	0.31	0	-
<i>Eragrostis intermedia</i>	plains lovegrass	ERIN	N	G	P	0.31	0	-
<i>Hilaria belangeri</i>	curly mesquite	HIBE	N	G	P	0.31	0	-
<i>Nassella leucotricha</i>	Texas wintergrass	NALE3	N	G	P	1.85	5.56	- 0.34
<i>Panicum obtusum</i>	vine mesquite	PAOB	N	G	P	9.88	12.35	- 0.55
<i>Panicum hians</i>	gaping grass	STHI3	N	G	P	3.70	1.23	0.38
<i>Paspalum</i> spp.	paspalum	PASE	N	G	P	1.23	0	-

Table 8 Continued

Scientific species name	Common name	Acronym	Provenance	Growth form	Periodicity	Frequency (%)		<i>r</i>
						Burned	Burned	
<i>Schizachyrium scoparium</i>	little bluestem	SCSC	N	G	P	1.23	0	-
<i>Setaria</i> spp.	bristlegrass	SETAR	N	G	P	3.09	1.85	0.33
<i>Tridens albescens</i>	white tridens	TRAL2	N	G	P	0.93	0.62	-
<i>Aristida oligantha</i>	prairie threeawn	AROL	N	G	A	0.31	0	-
<i>Ambrosia psilostachya</i>	Cuman ragweed	AMPS	N	F	A/P	0	0.62	-
<i>Eupatorium coelestinum</i>	blue mistflower	COCO13	N	F	P	4.01	6.79	-0.41
<i>Krameria lanceolata</i>	trailing krameria	KRLA	N	F	P	5.25	3.70	0.43
<i>Neptunia lutea</i>	yellow puff	NELU2	N	F	P	12.35	6.17	0.60
<i>Ruellia strepens</i>	limestone wild petunia	RUST2	N	F	P	0.93	0	-
<i>Rubus trivialis</i>	dewberry	RUTR	N	F	P	0	0.62	-
<i>Solanum elaeagnifolium</i>	silverleaf nightshade	SOEL	N	F	P	0.93	0.62	-
<i>Tragia</i> spp.	noseburn	TRAGI	N	F	P	14.51	3.09	0.50

† Listed as noxious plants in Texas (USDA, NRCS 2011). Abbreviations are: I = Introduced; N = Native; G = Graminoid; F = Forb; A = Annual; P = Perennial. Acronyms are from PLANTS database (USDA, NRCS 2011). Species without correlations (shown by a dash) were present in less than 5% of all plots and were excluded from the ordination. Only correlations with NMS axis 1 are shown since other axes did not separate groups according to differences between treatments.

Table 9. Results of the split-plot ANOVA for the effects of fire and herbicide on the density of shrubs, shrub height, stem number, and crown area on the Edwards Plateau and Coastal Bend ecological regions of Texas.

Ecological region	Response variable	Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Edwards Plateau	Density	Fire treatment	2, 15	2016	4.92	0.0227
		Herbicide treatment	2, 30	26850	75.99	<.0001
		Fire x Herb	4, 30	1159	2.76	0.0458
	Shrub height	Fire treatment	2, 15	4234	60.62	<.0001
		Herbicide treatment	2, 30	6842	80.17	<.0001
		Fire x Herb	4, 30	887	10.40	<.0001
	Stem number	Fire treatment	2, 15	24378	2.89	0.0863
		Herbicide treatment	2, 30	218282	59.73	<.0001
		Fire x Herb	4, 30	2860	0.78	0.5453
	Crown area	Fire treatment	2, 15	8698	22.21	<.0001
		Herbicide treatment	2, 30	14294	60.74	<.0001
		Fire x Herb	4, 30	2646	11.24	<.0001
Coastal Bend	Density	Fire treatment	2, 15	1004	2.50	0.1151
		Herbicide treatment	2, 30	31871	75.93	<.0001
		Fire x Herb	4, 30	1158	2.76	0.0458

Table 9 Continued

Ecological region	Response variable	Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
	Shrub height	Fire treatment	2, 15	2438	5.98	0.0123
		Herbicide treatment	2, 30	19642	41.34	<.0001
		Fire x Herb	4, 30	1086	2.28	0.0833
	Stem number	Fire treatment	2, 15	6796	3.07	0.0760
		Herbicide treatment	2, 30	128051	46.12	<.0001
		Fire x Herb	4, 30	3630	1.30	0.2895
	Crown area	Fire treatment	2, 15	11016	17.31	0.0001
		Herbicide treatment	2, 30	636	45.91	<.0001
		Fire x Herb	4, 30	3539	3.42	0.0203

Note: Bold p-values are significant at $P < 0.05$.

Table 10. Total number of individuals sampled prior to treatment in areas that were part of burn treatments but were not sprayed with herbicide (total sampled in 2006), total number of new individuals in 2011 (total recruits in 2011), and the relative rates of mortality in 2011 (%_m) observed for each shrub species in extreme fire experiments conducted in the Coastal Bend (CB) and Edwards Plateau (EP) ecological regions of Texas. A total of 1,380 individual shrubs were sampled in plots burned twice (B2), burned once (B1), and not burned (NB) in 2006 across the two sites and were resampled again in 2011 to assess mortality (a total of 4,203 individual shrubs occurred in both the fire and herbicide treatments).

Shrub species	Ecological region	Burn treatment	Total sampled in 2006	% _m	Total recruits in 2011
Larger shrubs					
<i>Acacia farnesiana</i> (L.) Willd.	CB	B2	38	53.6	5
		B1	29	41.4	9
		NB	55	3.6	16
<i>Prosopis glandulosa</i> Torr.	CB	B2	38	7.9	1
		B1	25	8.0	3
		NB	37	13.5	5
	EP	B2	121	16.5	2
		B1	118	16.1	1
		NB	76	11.8	1
<i>Juniperus pinchotii</i> Sudw.	EP	B2	12	66.7	0
		B1	4	25.0	1
		NB	8	0.0	1
<i>Diospyros texana</i> Scheele	CB	B2	25	16.0	2
		B1	18	5.6	8
		NB	25	0	2

Table 10 Continued

Shrub species	Ecological region	Burn treatment	Total sampled in 2006	% _m	Total recruits in 2011
<i>Acacia rigidula</i> Benth.	EP	B2	33	39.4	2
		B1	26	15.4	0
		NB	30	20.0	0
	CB	B2	24	16.7	2
		B1	15	6.7	4
		NB	22	4.5	10
<i>Condalia hookeri</i> M.C. Johnst. var. <i>hookeri</i>	CB	B2	11	9.1	0
		B1	11	0.0	3
		NB	14	7.1	2
<i>Celtis ehrenbergiana</i> (Klotzsch) Liebm.	CB	B2	12	0.0	1
		B1	11	0.0	1
		NB	13	0.0	2
Smaller shrubs					
<i>Mahonia trifoliolata</i> (Moric.) Fedde	CB	B2	22	18.2	0
		B1	26	15.4	1
		NB	15	0.0	1
	EP	B2	33	39.4	0
		B1	26	15.4	0
		NB	30	20.0	3
<i>Aloysia gratissima</i> (Gillies & Hook.) Troncoso	EP	B2	60	18.3	3
		B1	83	15.7	10
		NB	18	5.6	39

Table 11. A summary of the costs associated with supporting undergraduate research by major funding programs.

Funding program	Estimated annual expense per undergraduate student	Anticipated no. students supported in 2010	Award length
NSF REU	\$23,400*	~4,500 ^δ	Varies*
NIH UGSP	up to \$20,000 [†]	15	1 year [¥]
EPA GRO	up to \$17,000 education expenses up to \$ 7,500 summer internship support	30	2 years
NASA ASP	\$15,000 education expenses \$10,000 summer internship support	20	2 years

Notes: *Projected annual expense based on a typical 10-week summer stipend; estimate

derived from multiple, selected REU sites funded in 2009 in Biology and Earth

Sciences; costs associated with conducting research were paid for by corresponding

REU grants ranging from \$125,000 - \$850,000 in NSF Biology and Earth Sciences.

^δValue is a coarse estimate based on annually funded projects for 170 REU sites and 1650 REU supplements; estimate derived by randomly subsampling 2010 REU sites, which revealed an average participation of 10.5 students per REU site per year whereas REU supplements support 1 to 2 students per year (S5).

[†]Does not cover any costs associated with conducting research.

[¥]Renewable up to 4 years.

Table 12. The undergraduate research course taught by the lead author demonstrates the potential to create a sustainable, cost-effective undergraduate research program.

Activity	Total Expense for 8 Students	Total Income from 8 Students
Conducting research	\$0*	
Instructor salary	\$0	
Presenting at major scientific conferences (10 total)	\$2,575 ^δ	
Publication charges	Forthcoming	
Enrollment		\$4237.20 [†]
Course fees		\$0

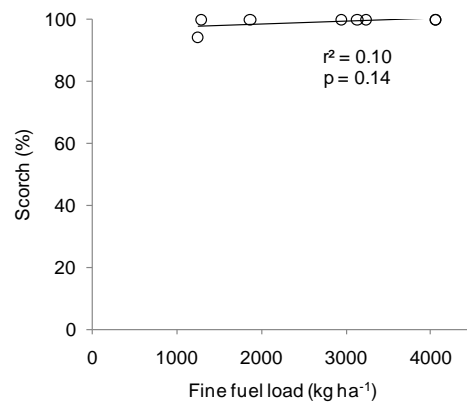
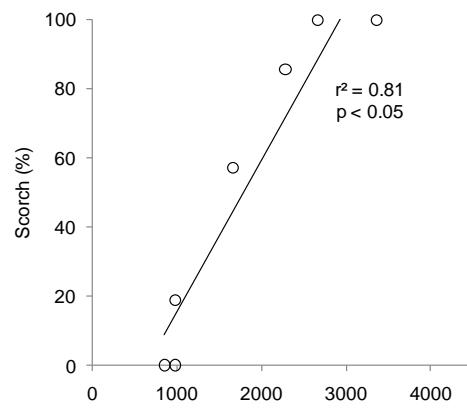
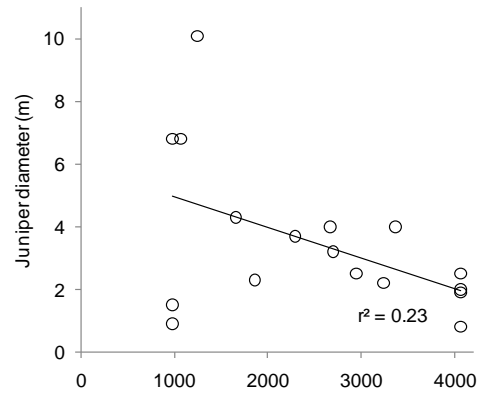
Notes: *Travel and field sampling/research costs, were respectively covered by travel grants and the primary grant of the PhD project and incurred no additional costs.

^δAdditive costs for undergraduate attendance at scientific conferences included registration fees and some lodging. Expenses for presenting at scientific conferences were paid through small internal grants acquired from College of Agriculture and Life Sciences and Department of Ecosystem Science and Management at Texas A&M University. Undergraduates presented at the following internationally-based scientific conferences: (1) 62nd Annual Meeting of the Society of Range Management.

Albuquerque, NM, February 8-12, 2009; (2) 94th Ecological Society of America Annual Meeting, Albuquerque, NM, August 2-7, 2009; (3) 16th International Symposium on Society and Resource Management. Corpus Christi, TX, June 2-6, 2010.

[†]Based on total enrollment and \$176.55 per credit hour for resident undergrad in 2010; does not include associated fees.

Figure 1. Ecological resilience of a post-grassland, woodland phase can be overcome but fire must be applied at much greater intensities than were needed to maintain the original grassland. Juniper trees from 1 m to 10 m in diameter were present on this site and had varying impacts on fine fuel load beneath individual juniper crowns (Picture 1). Note that fires conducted in mild conditions were able to overcome feedbacks in localized areas but only when a sufficient amount of fine fuel was available underneath individual juniper trees (Picture 2). In contrast, the resilience of the entire juniper woodland was overcome when fires were conducted in extreme fire conditions, irrespective of the amount and distribution of fine fuel load (Picture 3).



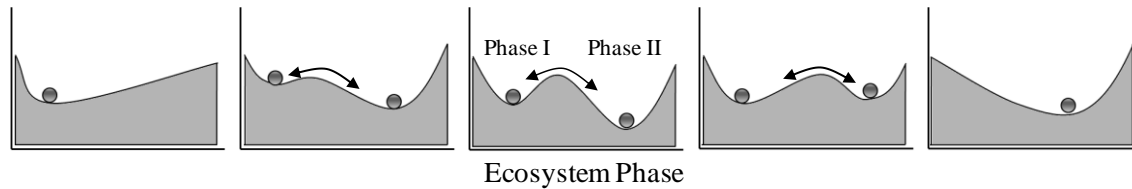


Figure 2. Traditional, qualitative representation of resilience and phase shifts using the ball-and-cup model. In this representation, the system (shown as the ball) can shift from one phase to another (shown as cups or basins) as a function of changes in biotic or abiotic conditions. To shift from one phase to another, the system must overcome the threshold separating phases. It may take a long time to overcome the threshold and shift to a new phase, or the phase shift can be sudden and catastrophic (Scheffer et al. 2001). This is partially determined by the resilience, depicted as the width of the cup, of the current phase. While this model is a benchmark for the advancement of ecological theory and management, there is growing demand for a more robust framework that can directly integrate multiple drivers operating across multiple spatial and temporal scales to influence social-ecological systems.

Figure 3. A simple depiction of a quantifiable, predictive model of resilience to fire based on the maintenance (K) and collapse (Ω) of grassland and juniper woodland phases over time. Two features of resilience are characterized here. Phase resistance (R) is the maximum amount of change a phase can absorb before its collapse ($I_K - I_\Omega$). Phase persistence (ϕ) is the length of time an ecological phase continues to persist after the conditions required to collapse that phase have been surpassed ($t_{f-\Omega} - t_{O-\Omega}$). Upon the collapse of each phase, the system goes into a phase of reorganization (α). Here the cycle of grassland and juniper woodland continues, but a new ecosystem could emerge during reorganization, one maintained by alternate drivers (i.e. other than fire) that could lead to the emergence of a new cyclic system.

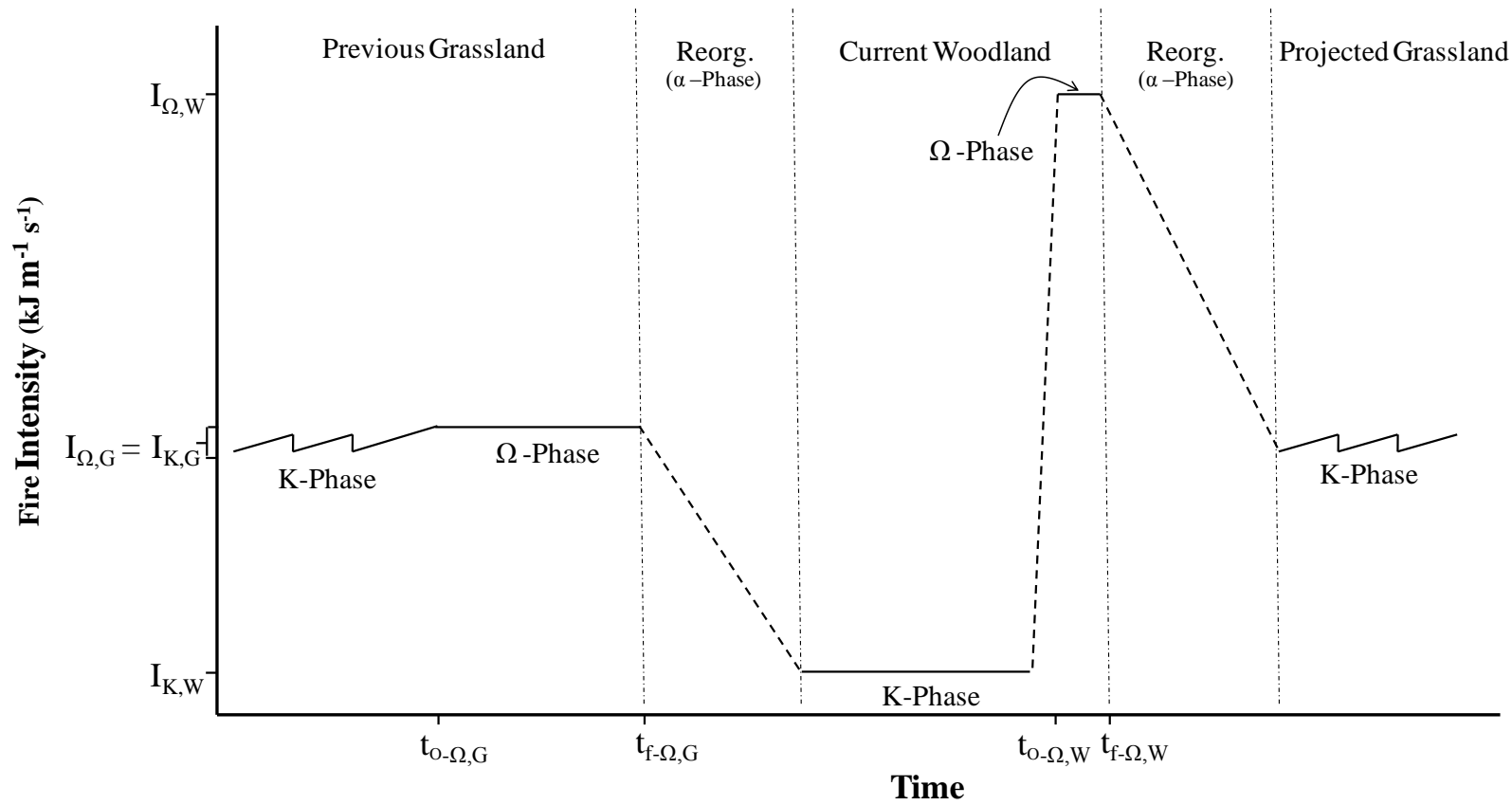
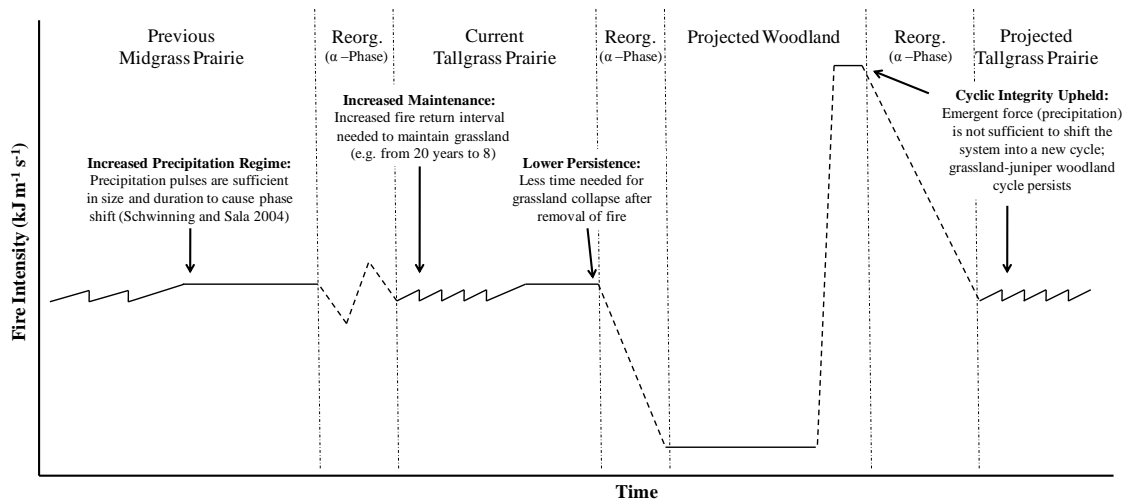


Figure 4. The maintenance, collapse, and corresponding resistance and persistence of ecological phases are not static and will change over time as a function of changes in environmental drivers. Here we show a grassland phase going through a period of reorganization due to changes in precipitation. Sufficient changes in precipitation can alter phase persistence and the magnitude of fire required to maintain grassland due to changes in the invasive potential of juniper woodland. These changes may simply alter the current grassland-juniper woodland cycle (e.g. transition to Tallgrass Prairie of Kansas, **A**) or they may be sufficient enough to promote the emergence of a system that is seemingly independent of fire (e.g. transition to Shortgrass Steppe of Colorado, **B**) and a cycle driven by alternate drivers, such as precipitation.

A



B

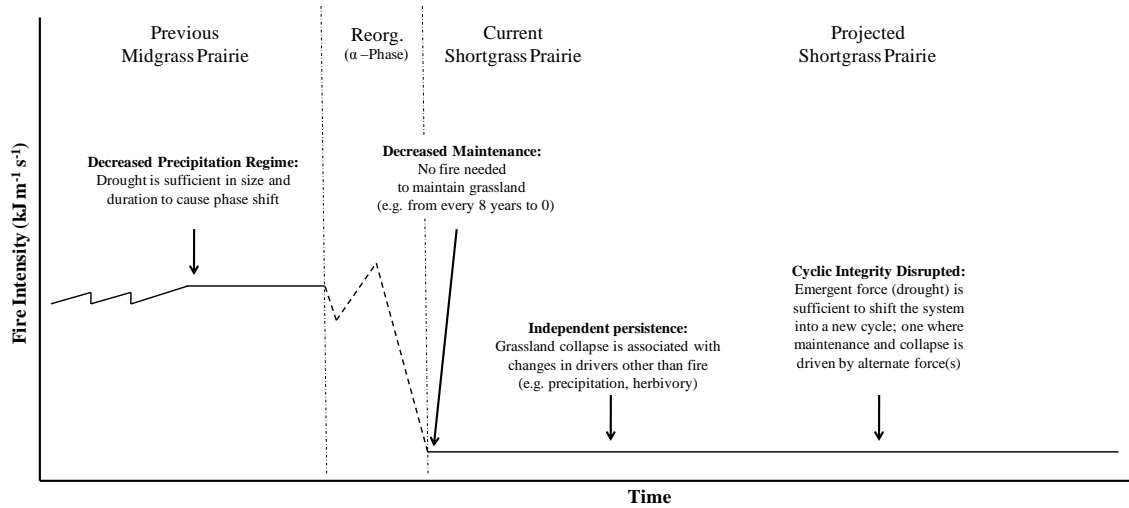


Figure 5. A multifaceted framework that integrates the ecological and social constraints that drive the application and effectiveness of fire in this social-ecological system. The area above the juniper mortality threshold represents the combination of conditions that result in sufficient fire intensity to collapse juniper woodland, whereas juniper woodland will persist if fires are ignited in conditions below the threshold. The ultimate goal using this conceptual framework is to maximize the amount of space above the mortality threshold. Traditional burning conditions rarely, if ever, suffice to overcome the mortality thresholds and risks associated with the use of fire prevent burning in more extreme conditions. While the framework of the EPPBA was established to overcome such “socially unacceptable” risks, limitations in the ecological understanding of the conditions needed to achieve juniper mortality continue to prevent widespread application of fire from this social group. Ultimately, the adaptive capacity of the social-ecological system can shift these constraints (represented by arrows) to the benefit (toward the desired social group position) or detriment (away from the desired position) of each social group as a result of emergent ecological, economic, or social pressures. The ability to shift such social constraints to achieve the “desired social group position” will depend upon the ability of researchers to explain ecological dynamics (e.g. to overcome limitations in ecological understanding) and the degree with which society values the functioning of ecological systems (e.g. to overcome risk).

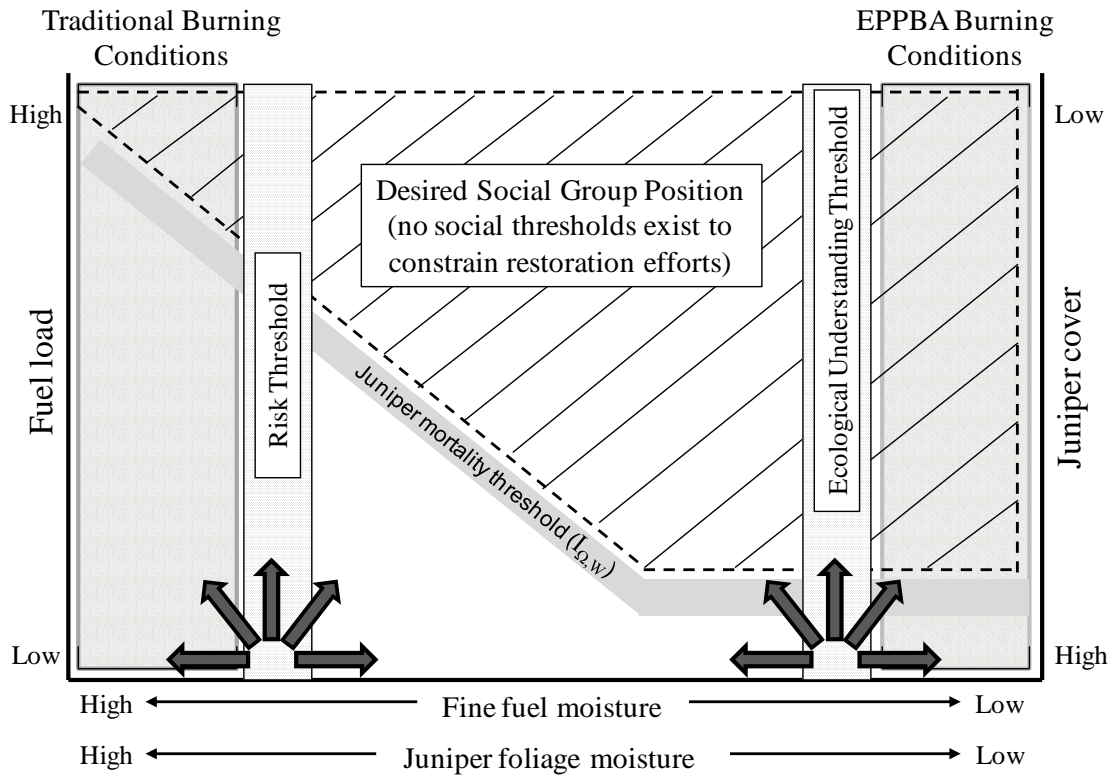
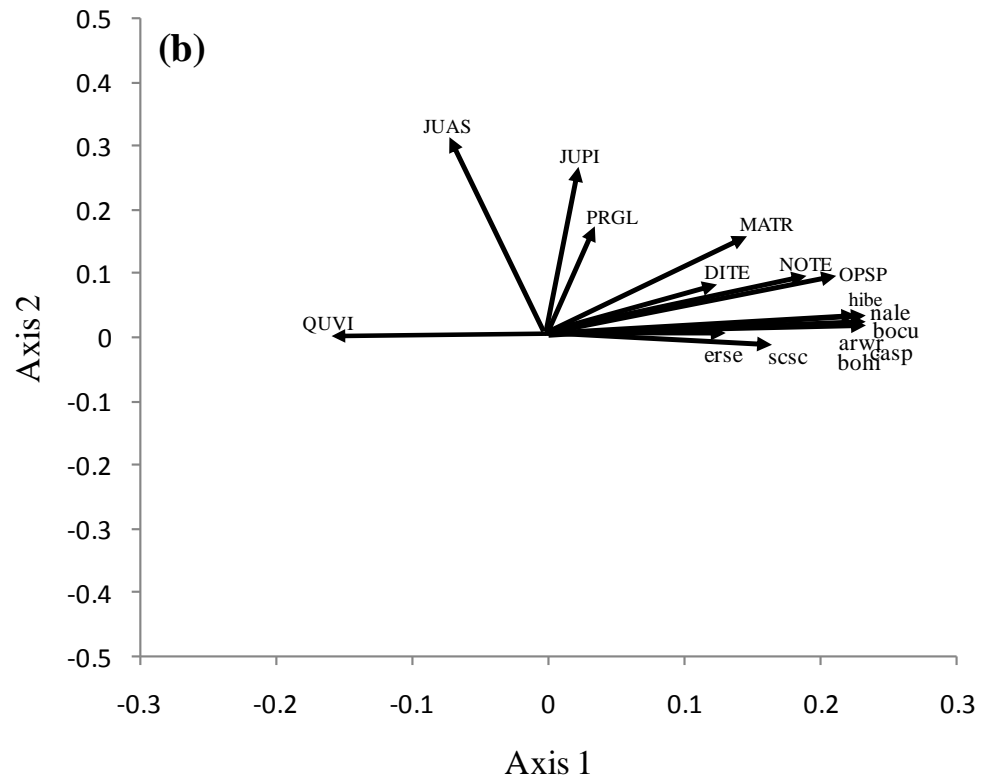
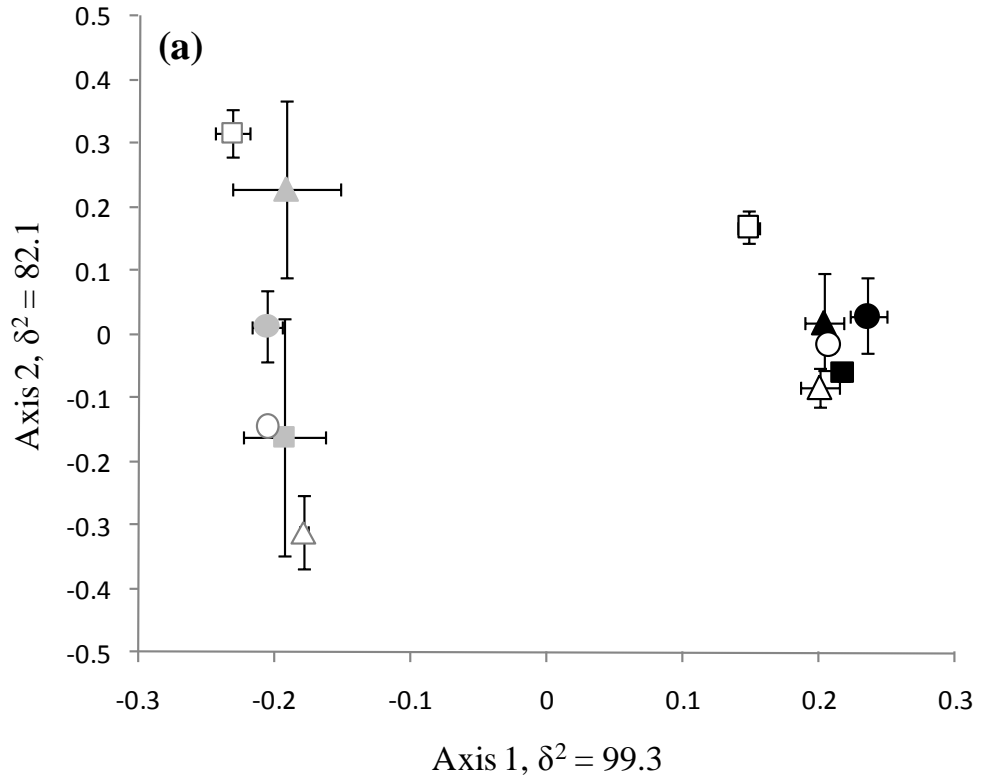


Figure 6. Canonical analysis of principal coordinates (**a**) of the plant community showing each combination of treatment, sampling height, and sampling year and the corresponding biplot (**b**) of all understory and overstory plant species. Symbols are as follows: shapes represent burn treatments of repeat summer burn (triangles), repeat winter burn (circles), and control (squares); colors represent sampling heights of < 1.5 m (black) and ≥ 1.5 m (gray); filled/open shapes represent sampling years of pre-treatment in 1994 (filled) and post-treatment in 2006 (open). Data from CAP output were pooled for each replicate and shown here as means \pm SE. The biplot (**b**) shows woody species (capitalized) and grass species (lower case); species acronyms are listed in Tables 3 and 5.



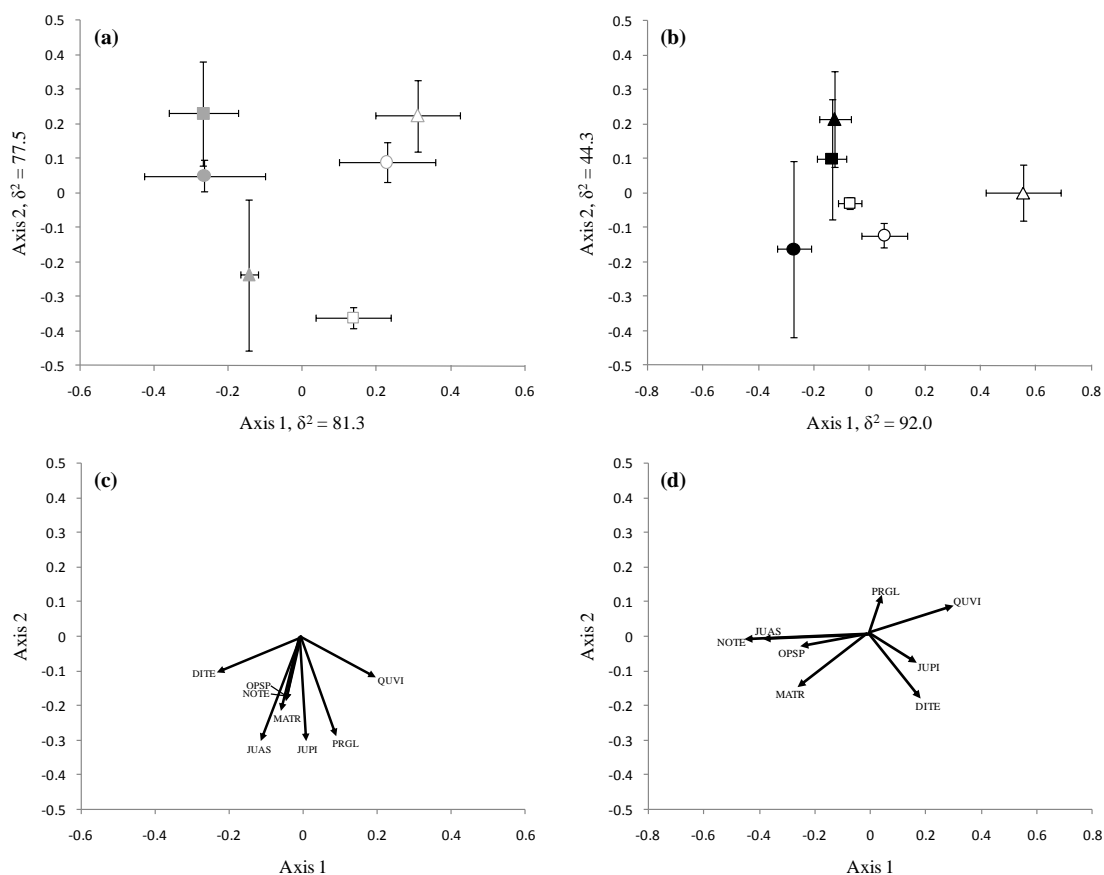
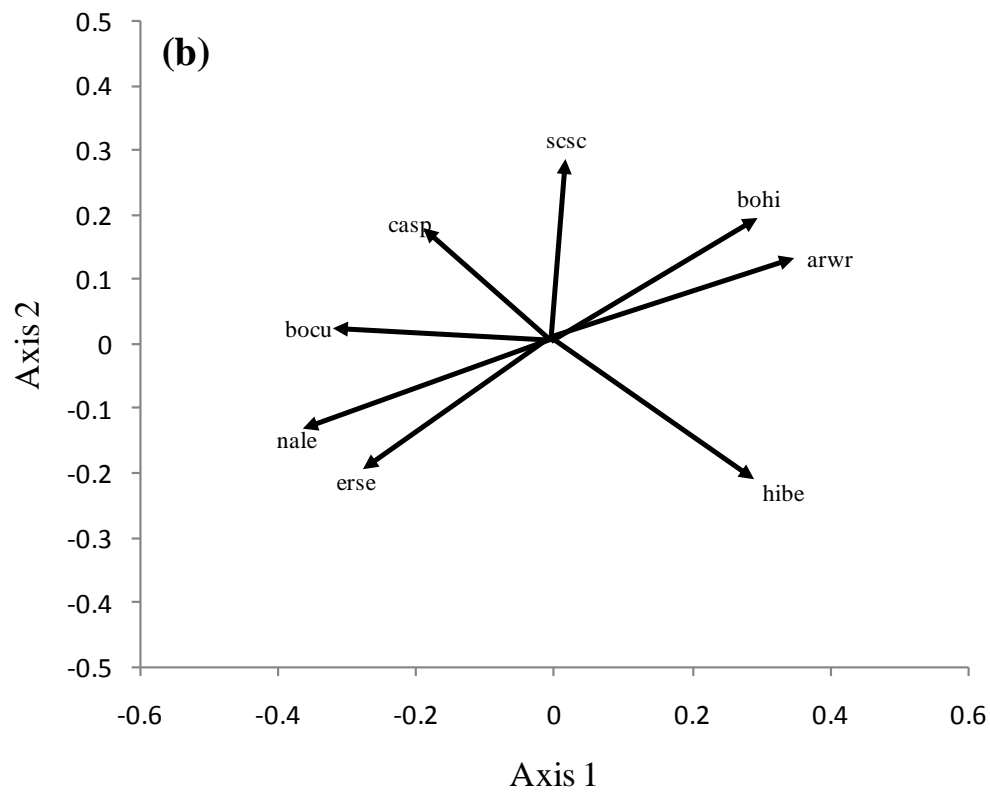
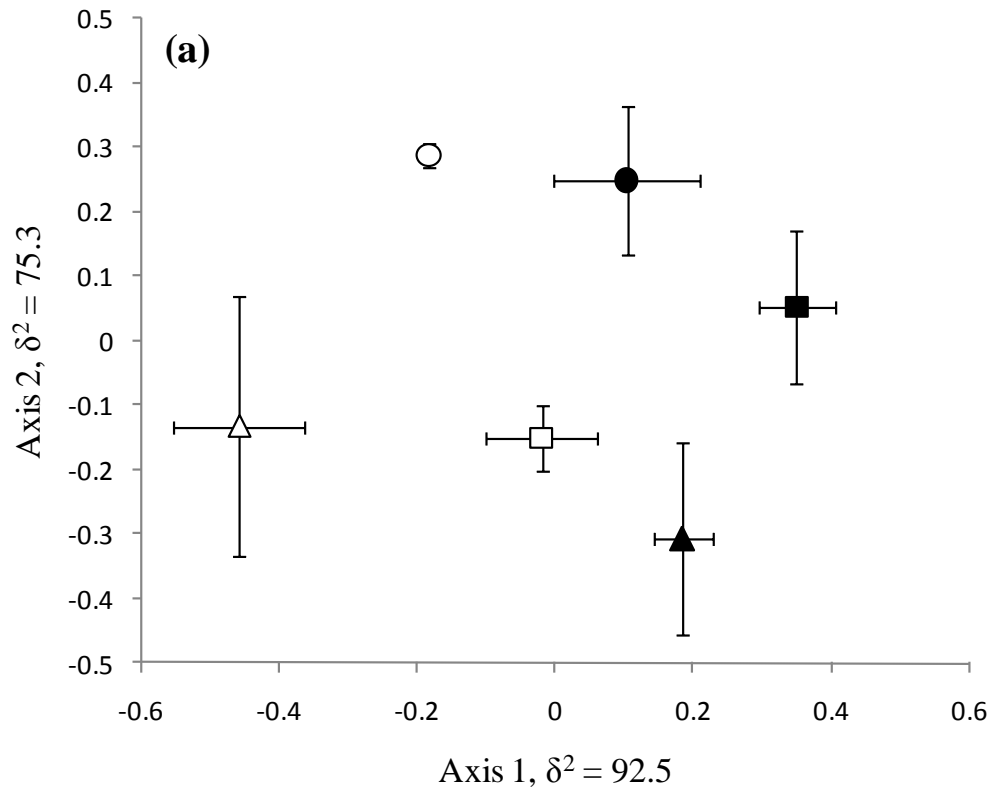


Figure 7. Canonical analysis of principal coordinates **(a)** of the overstory woody plant and **(b)** understory woody plant communities showing each combination of treatment and sampling year and the corresponding biplots of **(c)** overstory and **(d)** understory species. Symbols are as follows: shapes represent burn treatments of repeat summer burn (triangles), repeat winter burn (circles), and control (squares); filled/open shapes represent sampling years of pre-treatment in 1994 (filled) and post-treatment in 2006 (open). Data from CAP output were pooled for each replicate and shown here as means + SE. Species acronyms are listed in Table 5.

Figure 8. Canonical analysis of principal coordinates **(a)** of the grass community showing each combination of treatment and sampling year and the corresponding biplot **(b)** of grass species. Symbols are as follows: shapes represent burn treatments of repeat summer burn (triangles), repeat winter burn (circles), and control (squares); filled/unfilled shapes represent sampling years of pre-treatment in 1994 (filled) and post-treatment in 2006 (hollow). Data from CAP output were pooled for each replicate and shown here as means + SE. Species acronyms are listed in Table 7.



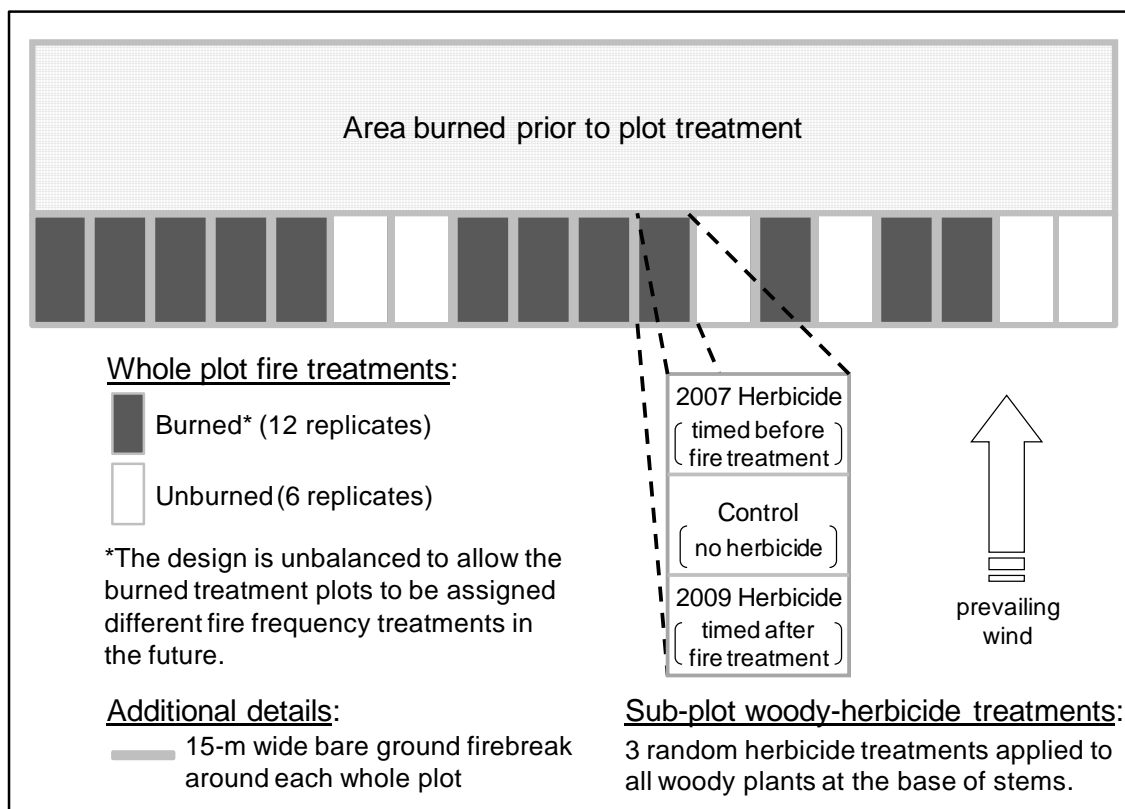


Figure 9. Illustration showing the conceptual framework for the split-plot experimental design and layout of 18 plots at the Welder Wildlife Refuge.

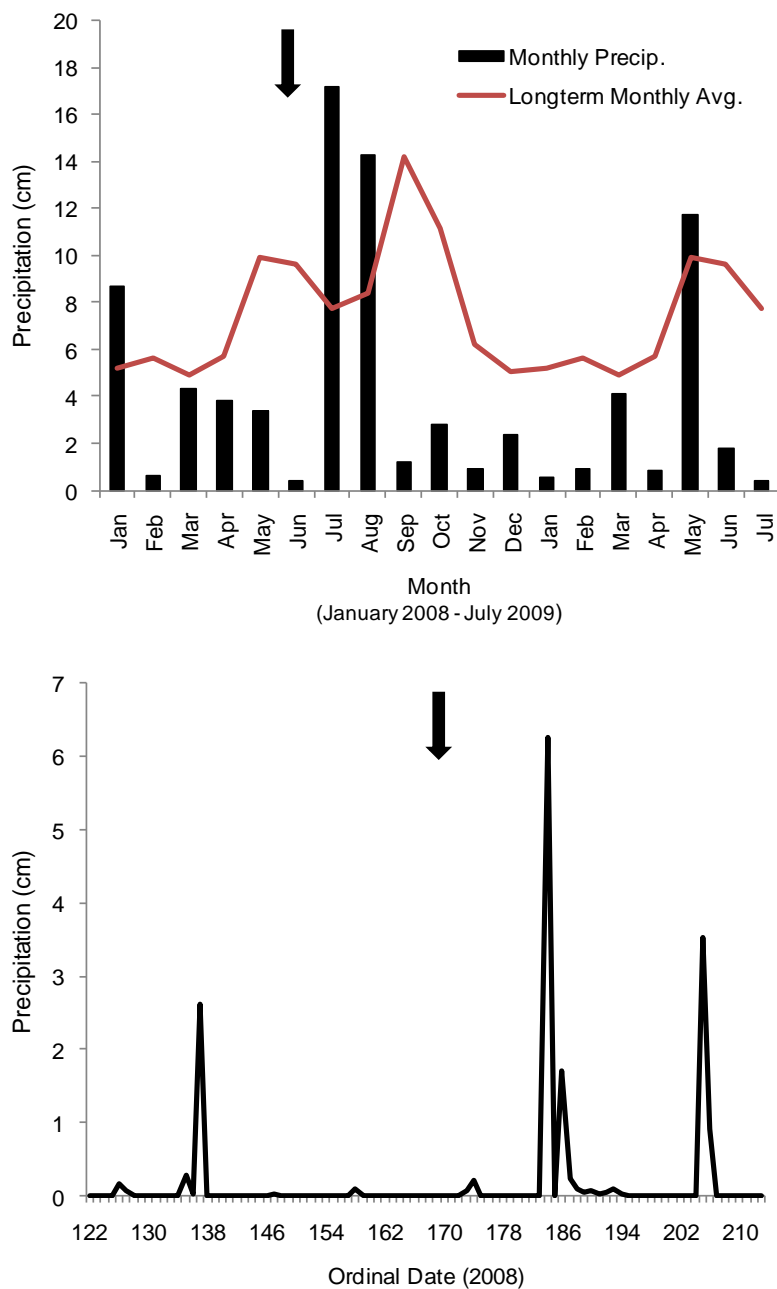
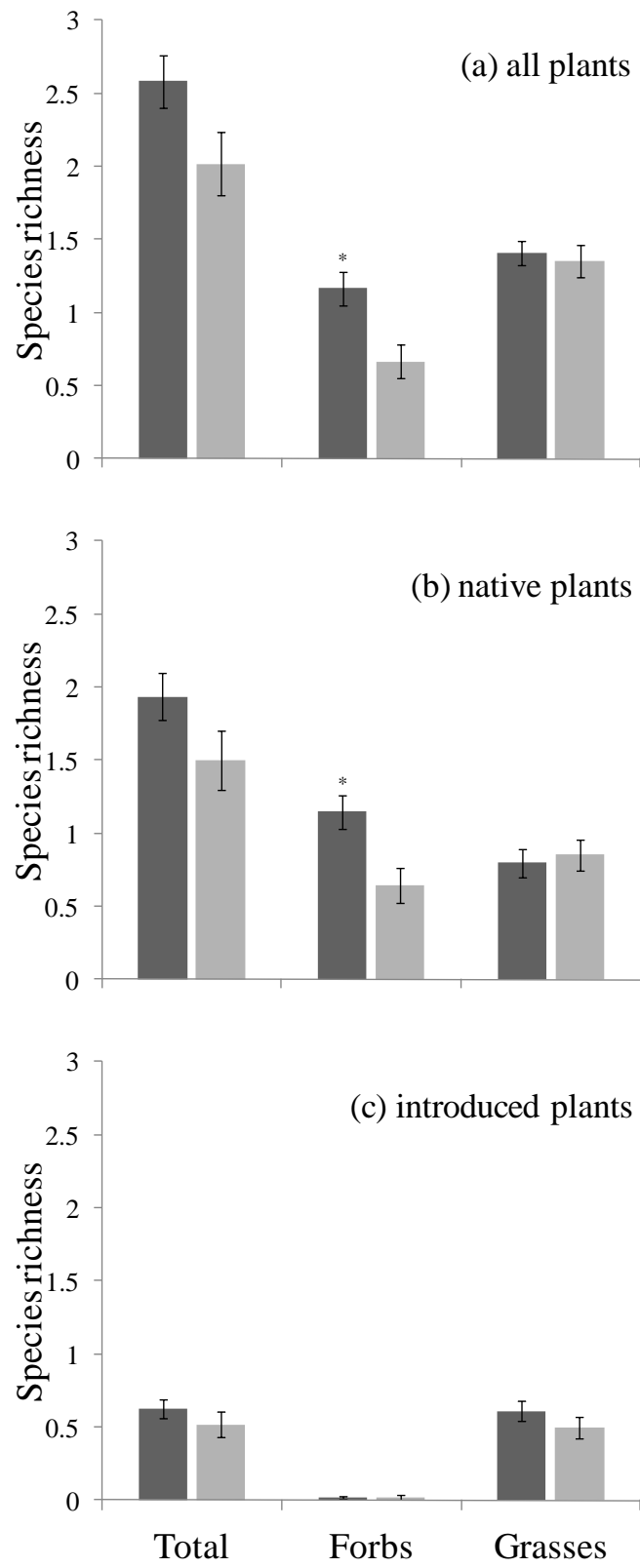


Figure 10. Monthly and long-term average precipitation (a) and daily precipitation before and after fires were conducted (b) at Welder Wildlife Refuge from January 2008 to July 2009. Arrows show dates prescribed fires were conducted (June 17-19, 2008). Samples were collected in July 2009.

Figure 11. Mean (+ SE) species richness (# species/0.25m²) of forbs and perennial grasses in burned (dark gray) and unburned (light gray) treatments for (a) all plants, (b) native plants, and (c) introduced plants. * indicates significant differences at $P < 0.05$, compared to the unburned controls of each functional group.



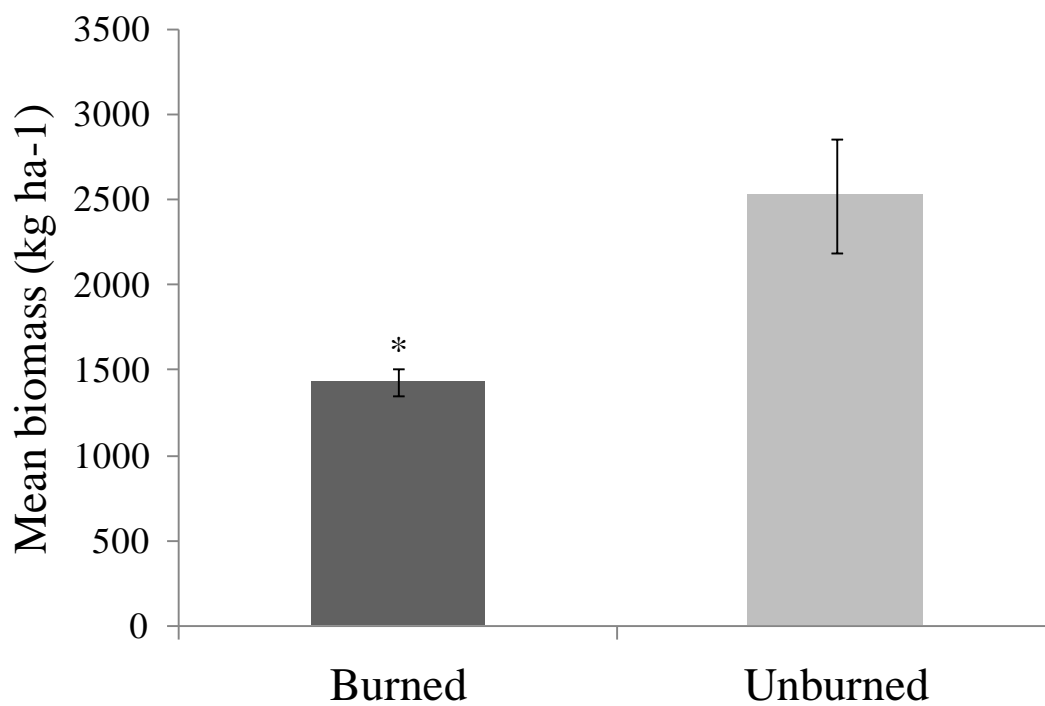


Figure 12. Mean (+ SE) aboveground herbaceous biomass in burned and unburned treatments (* indicates statistically significant difference at $P < 0.05$ compared to unburned control).

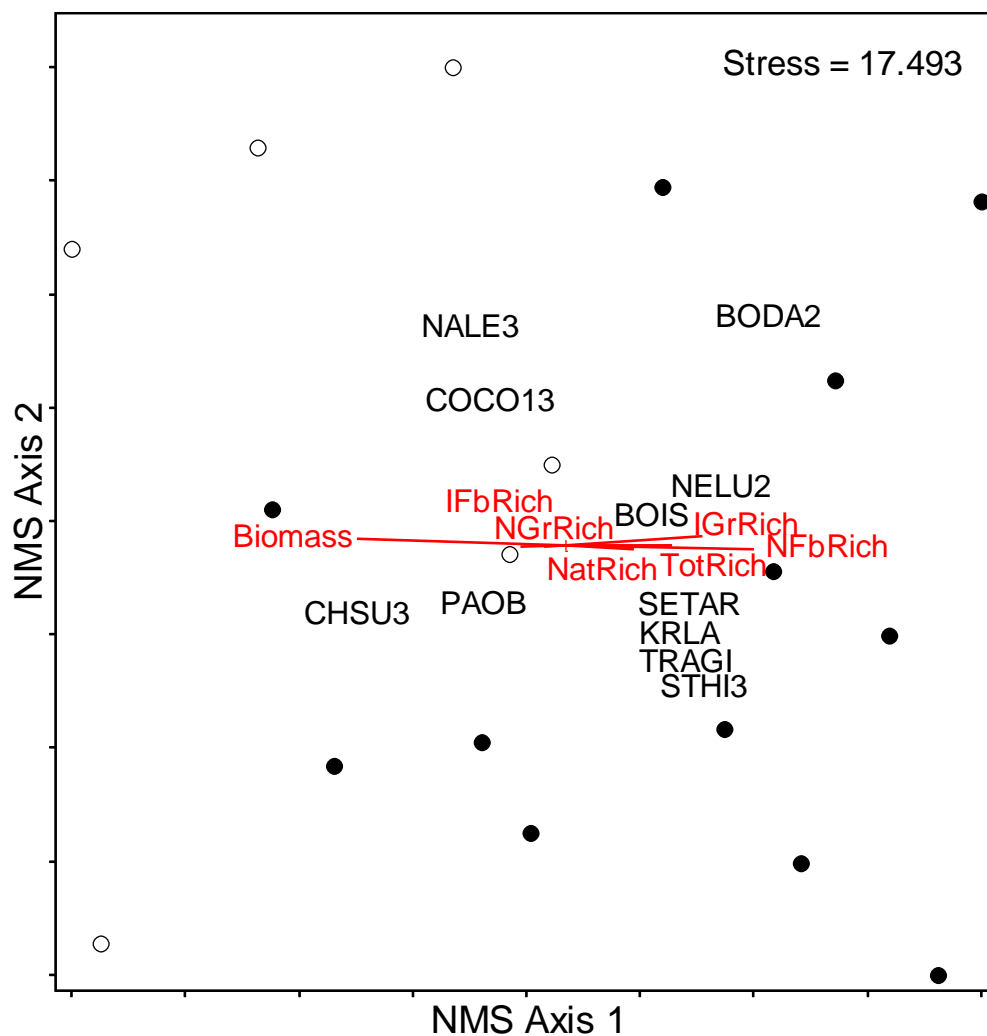


Figure 13. NMS ordination showing the differences in the distribution of the herbaceous plant community in burned (filled circles) and unburned (hollow circles) treatments. NMS ordinations were rotated in the direction of total richness. Biplots show the direction and strength of relationships between ordination scores and total richness (TotRich), native richness (NatRich), native grass richness (NGrRich), native forb richness (NFbRich), introduced grass richness (IGrRich), and introduced forb richness (IFbRich). Species are plotted by their acronyms; full names for species acronyms are given in Table 8.

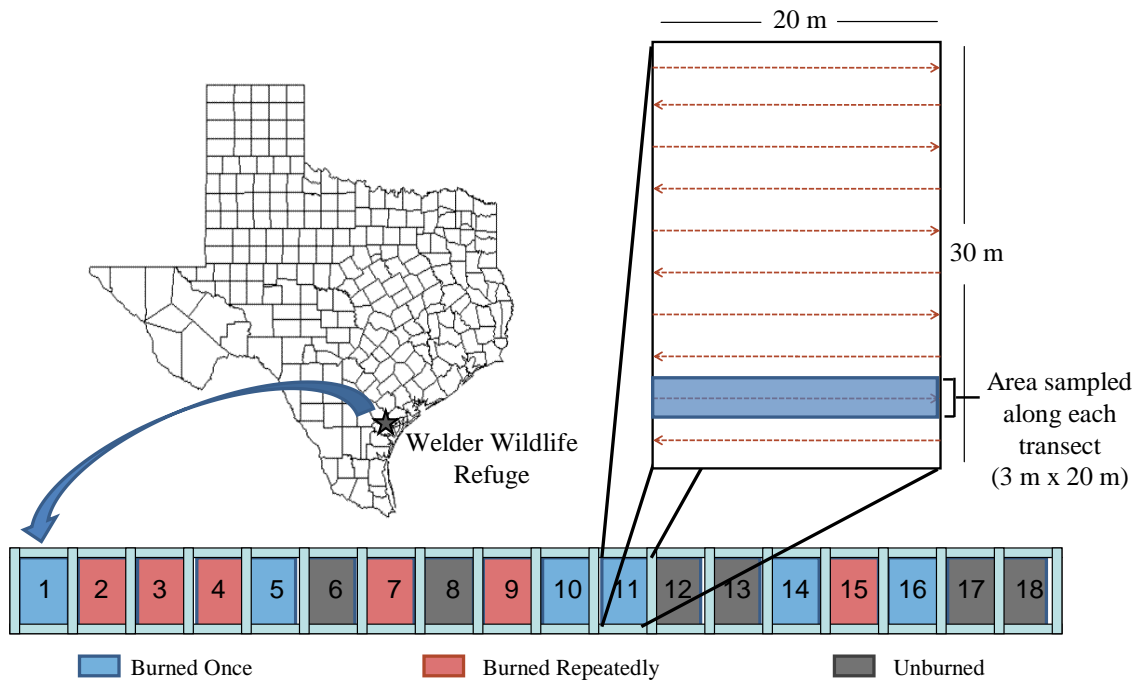


Figure 14. Illustration showing the location, experimental design, and systematic sampling design used to sample fire ants and harvester ants at the Welder Wildlife Refuge. Within each plot, 9 parallel belt transects were established (represented as dashed arrows) at equidistant intervals to search the entire plot for fire ant mounds.

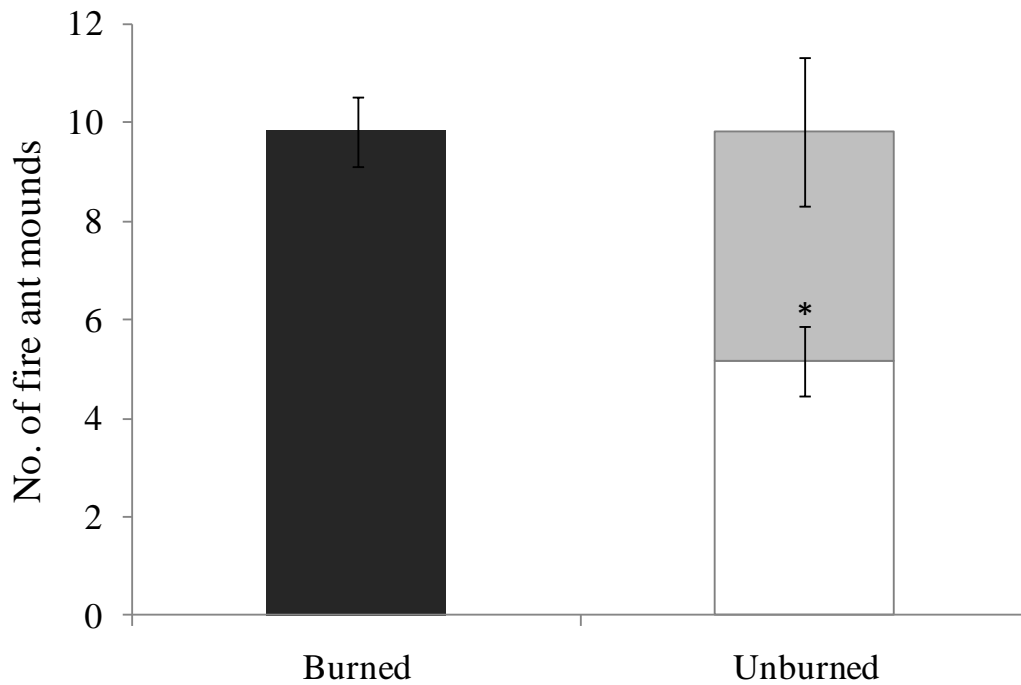


Figure 15. The number of fire ant mounds (mean \pm SE) found in burned (black) and unburned plots within 24 hours of conducting the initial burn treatments. Data were collected to estimate the number of mounds that were not located in unburned areas. The stacked columns in the unburned treatment represent the number of fire ant mounds found in the field (white) and the number of mounds that were predicted to have occurred in the field after correcting for sampling error in unburned plots relative to burned plots (light grey). * indicates significant difference at $P < 0.05$ compared to the burned treatments.



Figure 16. Pictures illustrating how herbaceous vegetation can make it difficult to locate fire ant mounds in unburned coastal tallgrass prairie. Many small fire ant mounds were completely concealed by herbaceous vegetation in unburned plots (a), causing a large proportion of fire ant mounds to go undetected in unburned areas compared to burned plots (b). However, herbaceous vegetation is unable to conceal most large mounds, making them readily detectable in both burned (c) and unburned (d) areas in this study.

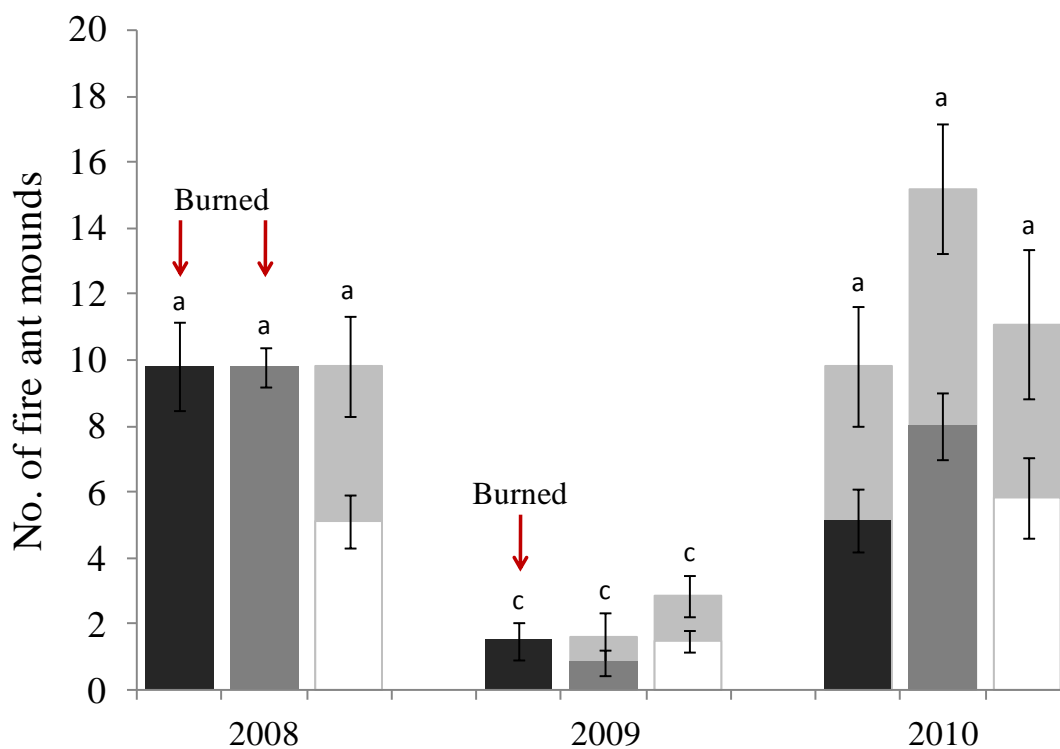


Figure 17. The number of fire ant mounds (mean \pm SE) found in burned repeatedly (black), burned once (dark grey), and unburned (white) treatments. The stacked columns represent the number of fire ant mounds that were predicted to have occurred in the field (light grey) after correcting for sampling error in unburned plots relative to burned plots at the beginning of the study (Fig. 15); uncorrected data are shown but were not incorporated into the statistical model. Different letters indicate significant differences between treatments ($P < 0.05$).

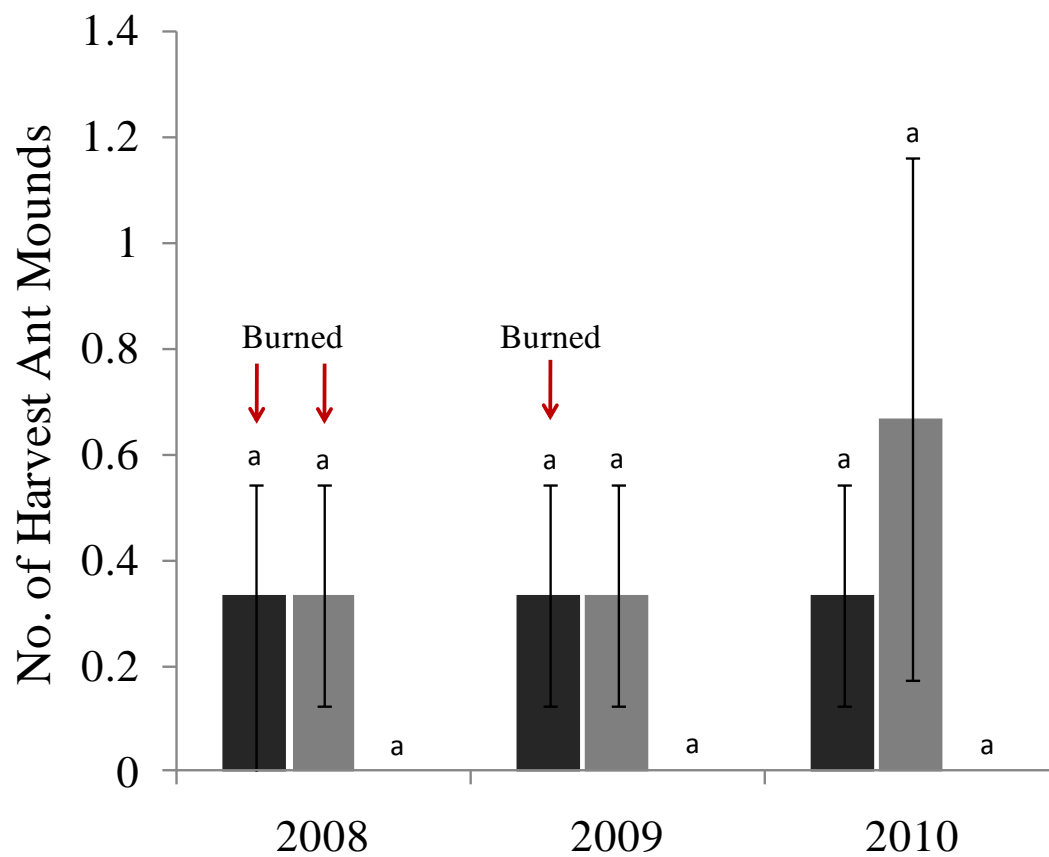


Figure 18. The number of harvester ant mounds (mean \pm SE) found in burned repeatedly (black), burned once (dark grey), and unburned (white) treatments. No harvester ant mounds were located in the unburned treatment in any year. Different letters indicate significant differences between treatments ($P < 0.05$).

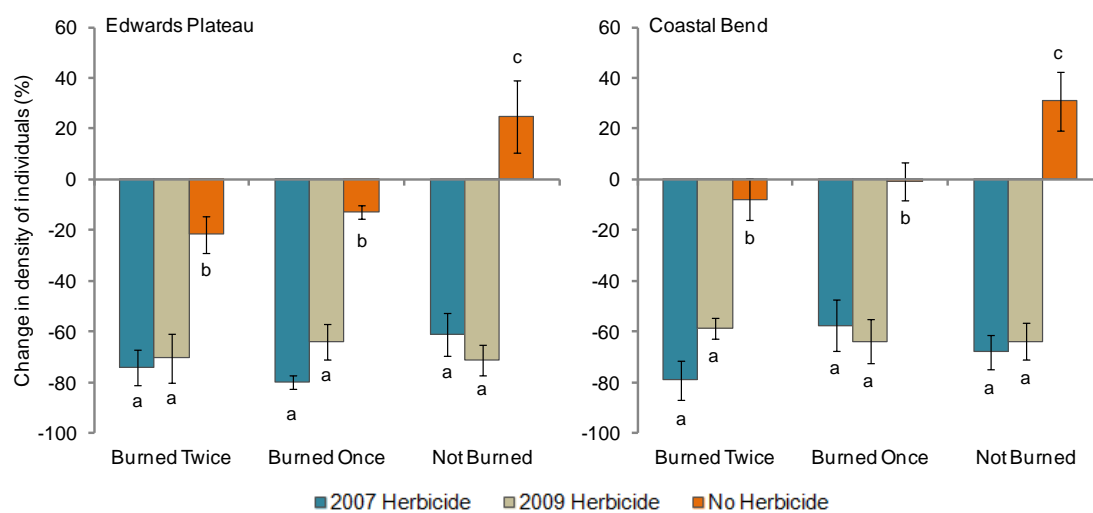


Figure 19. Mean (\pm SE) percent change in the density of shrubs after applications of extreme prescribed fire and herbicide treatments in the Edwards Plateau and Gulf Coastal Bend ecological regions of Texas.

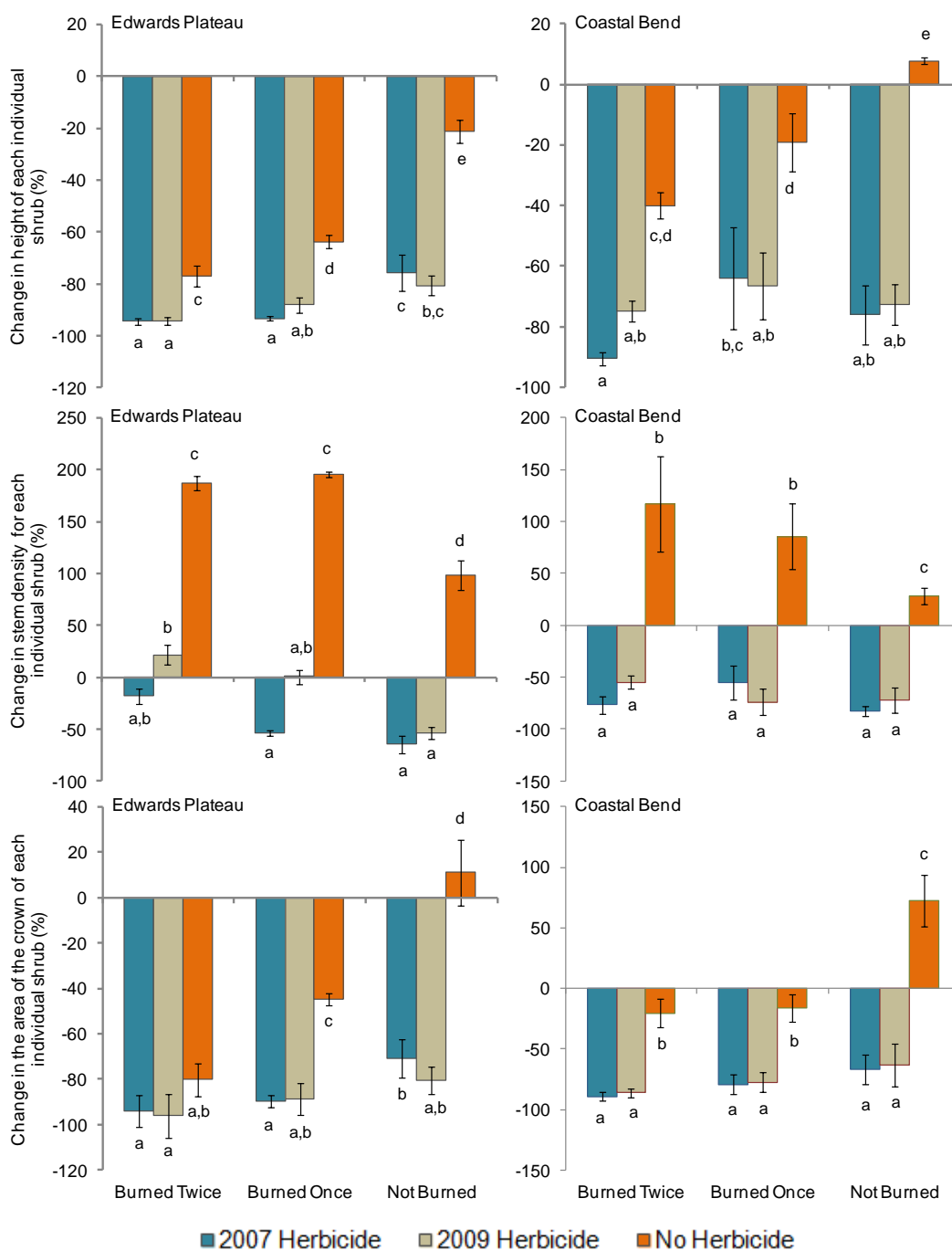


Figure 20. Changes (percent mean \pm SE) in the height, number of stems, and crown area of individual shrubs after applications of extreme prescribed fire and herbicide treatments in the Edwards Plateau and Gulf Coastal Bend ecological regions of Texas.

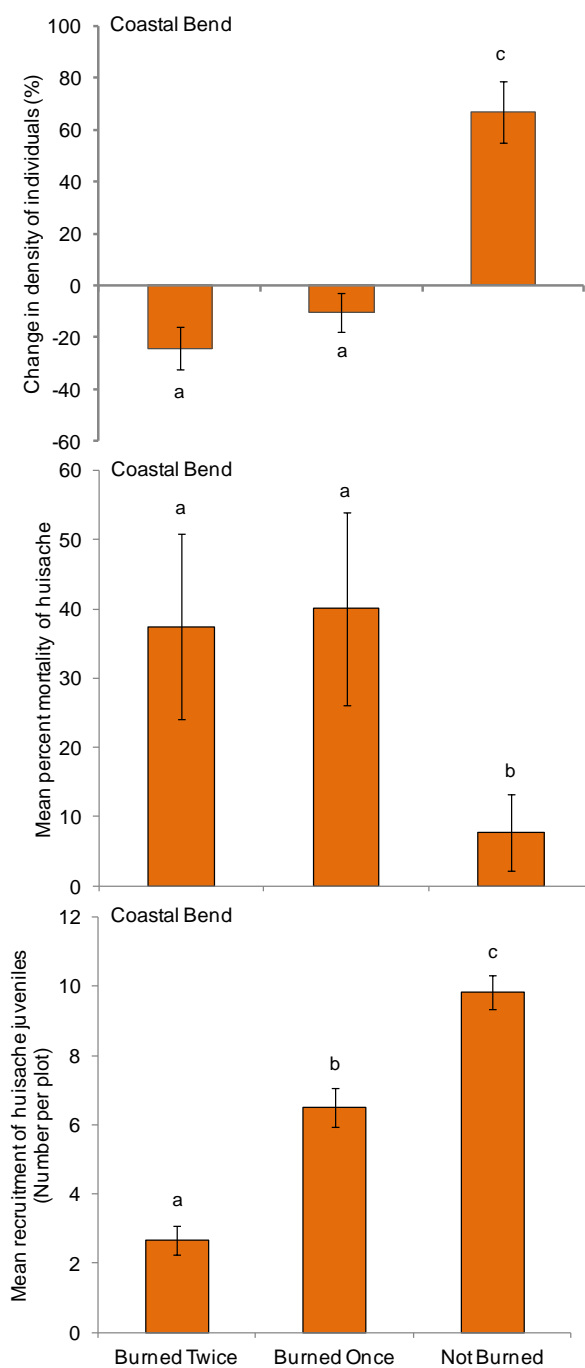


Figure 21. Percent changes in the density, percent mortality, and mean recruitment of huisache in extreme prescribed fire treatments in the Gulf Coastal Bend and Edwards Plateau ecological regions of Texas.

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