RESTORING A DEGRADED RANGELAND: USING FIRE AND HERBIVORY TO CONTROL *OPUNTIA* CACTI ENCROACHMENT

A Thesis

by

GABRIELA SOSA

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

MASTER OF SCIENCE

December 2009

Major Subject: Rangeland Ecology and Management

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Approved by:

Chair of Committee,	William E. Rogers
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ABSTRACT

Restoring a Degraded Rangeland: Using Fire and Herbivory to Control *Opuntia* Cacti Encroachment. (December 2009)

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Chair of Advisory Committee: Dr. William E. Rogers

Innovative restoration strategies are critically needed in the South Texas Plains for controlling increased *Opuntia* cacti invasions. Using a replicated and randomized experimental study, I have examined the effects of fire seasonality and herbivory on the dominant cacti and herbaceous plant species in this semi-arid ecosystem. Results from this study demonstrate that the combination of fire and wildlife herbivory significantly reduces *Opuntia* cactus cover. I was able to empirically demonstrate that prescribed fire decreases prickly pear cactus cover. Moreover, this decrease is further exacerbated by the effects of large mammalian herbivores consuming and/or disturbing recently burned mottes. In the absence of fire, both mottes with and without herbivore exclosures increased in size. The ecological insights gained from this study will contribute to the development of management strategies of *Opuntia* cacti, while promoting the restoration and long-term sustainability of Texas rangelands.

DEDICATION

To my family, they inspire and motivate me to reach for my goals.

ACKNOWLEDGEMENTS

I wish to extend my sincere appreciation to my major advisor, Dr. William Rogers, for his guidance, assistance and for believing in me. Thanks are also expressed to Dr. Fred E. Smeins and Dr. Charles W. Lafon for their suggestions and unconditional encouragement.

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Financial support provided by the Texas Natural Resources Conservation Service is greatly acknowledged. I would also like to thank the Office of Graduate Studies at Texas A&M University for awarding me a two year fellowship that allowed me to complete my program of study.

A most special recognition goes to my family, for their help in collecting field data and assisting me in administering experimental treatments. Without their encouragement and support this study would not have been possible.

NOMENCLATURE

ANOVA	Analysis of Variance
CAM	Crassulacean Acid Metabolism
LSD	Fisher's Least Significant Difference
SPSS	Statistical Package for the Social Sciences

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CHAPTER I

INTRODUCTION

In recent history the vegetative composition of Texas rangelands has been altered as a result of land use changes (Archer 1995;Van Auken 2000). Woody species and succulents have increased in density and cover. *Opuntia* cacti, a native succulent, is of particular interest to land managers and landowners in Texas rangelands who are attempting to stall the encroachment of woody and succulent species into these grassland savannas (Bunting*, et al.* 1980). The increase in *Opuntia* cacti density is technically referred to as cacti encroachment and not invasion because this species has been present in this landscape at lower densities for hundreds of years (Amos and Gehlbach 1988;Chavez-Ramirez*, et al.* 1997). Nevertheless, the terms encroachment and invasion are often used interchangeably by various stakeholders. *Opuntia* is a native succulent that has increased in density as a result of recent land management practices that have in turn led to changes in local abiotic or abiotic conditions (Sprugel 1991).

The factors that initiated changes in woody and succulent density in rangelands have been difficult to determine. There are several environmental and social factors working in conjunction at different spatial and temporal scales that contribute to shifting this predominantly open grassland savanna into a dense woodland (Van Auken 2000). The mismanagement of resources (e.g., overgrazing, fire suppression) is perhaps the most significant cause contributing to changes in species composition and subsequent land degradation in this landscape.

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This thesis follows the style of the journal *Ecological Management & Restoration*.

Intensive grazing often causes soil disturbances favor the establishment and competitive success of *Opuntia* cacti and other woody compared to herbaceous species (Engle*, et al.* 1993). Additionally, human suppression of fire disturbance has contributed to the current increase in the number of woody and succulent plants, as well as, other invasive species on Texas rangelands (Ansley*, et al.* 1998). Prescribed burning is an important rangeland management tool that can affect plant community and ecosystem processes and result in increased biodiversity. The use of fire as a restoration tool has been suggested as an optimal mechanism for stalling current vegetative successional trends that have led to degradation (Hobbs and Huenneke 1992). For instance, in an area being converted into a mesquite dominated woodland the use of prescribed fire can successfully kill some of the susceptible woody seedlings and open habitat patches for establishment of more desirable grassland species (Ansley and Jacoby 1998).

Fire suppression and overgrazing have decreased grass species and allowed the widespread proliferation of cacti. Currently, there is limited knowledge on the physiological response of *Opuntia* cactus mottes to fire. This lack of ecological understanding limits the potential effectiveness of current management recommendations. This study will focus on the effects of fire season and herbivory on *Opuntia* survival and expansion. The findings from this study are expected to assist and improve management strategies available to landowners with rangelands that have been degraded by an elevated presence of *Opuntia* cacti.

Problem Statement

The suppression of fire, in conjunction with overgrazing, has led to an increase in *Opuntia* cacti cover on the Edwards Plateau of Central Texas. This has led to a decline in perennial grass cover and quality of wildlife habitat (Cable 1967). Ranchers have found it difficult to implement effective management strategies for suppressing *Opuntia* encroachment. Resources are invested in *Opuntia* cacti removal and management, but most often the problem continues to persist. In order to effectively restore these degraded rangelands more knowledge is needed about ecological and systematic responses to of *Opuntia* cacti to disturbances and alternative control strategies in this degraded ecosystem.

Objectives and Hypotheses

The overall objective of this study is to improve recommendations for the management of *Opuntia* cacti encroachment on Texas rangelands. It will examine the effectiveness of summer fires at suppressing *Opuntia* cacti encroachment and the effect of wildlife herbivory on recently burned cactus mottes. This study will be the first to take into account the effects of wildlife herbivory on recently burned cactus mottes. No previous study has concurrently examined the effects of fire seasonality and wildlife herbivory as a management tool for *Opuntia* (Ansley and Castellano 2007;Everitt and Drawe 1974;van Langevelde*, et al.* 2003). Key hypotheses that will be tested:

1. Summer fires are more effective at reducing cover and encroachment of *Opuntia* cacti than winter fires.

2. Wildlife herbivory following summer fires is higher in burned mottes and contributes to cacti suppression and mortality.
3. By maintaining heat intensity, variation in seasonal plant physiology will affect mortality and cactus cover.
4. Variability in tissue moisture content may influence susceptibility to wildlife herbivory post-fire.

CHAPTER II

LITERATURE REVIEW

Past Management Practices on Texas Rangelands

Rangelands have been exploited and significantly affected by anthropogenic activities in recent history. Prior to European settlement these vast landscapes and plant communities were maintained by cyclic intervals of fire and grazing that resulted in elevated levels of grass and forbs production and diversity (Sauer 1950). Introduction of livestock at high densities on these rangelands and the suppression of fire decreased production and availability of desirable forage and browse vegetation. For many decades Texas ranchers operated their lands without a comprehensive land management plan which resulted in an increase of undesirable plant species, such as honey mesquite (*Prosopis glandulosa*), ash juniper (*Juniperus ashei*), and prickly pear (*Opuntia* spp.) cacti (Archer 1995). The encroachment of woody and succulent species diminished carrying capacity for livestock and wildlife. In the Edwards Plateau region of south-central Texas the increase of undesirable woody plants and cacti has initiated a negative degradation feedback, as undesirables increased across the landscape, the cover by desirable grasses and forbs decreases in abundance (Hodgkinson 1991).

Not all landowners consider *Opuntia* cactus an undesirable species. Some ranchers appreciate having these succulents distributed sporadically across their rangelands because of its ability of providing emergency forage for livestock in times of drought (Everitt*, et al.* 1981;McMillan*, et al.* 2002). When the herbaceous cover is limited, prickly pear mottes can be scorched using a hand held propane burner to remove the spines from the cladodes and permit livestock to forage (Rakowitz 1997). In times of drought there is limited resources available and *Opuntia* is a viable solution for desperate ranchers in the West (Hanselka and Paschal 1991). This burning practice is very different of that of natural fires in rangelands; the use of fire was limited to specific mottes. In contrast, natural fires move along a landscape and remove litter that limits herbaceous plant establishment. These natural fires often result in a shift in plant community composition. Conversely, targeted fires that only remove the outer band of *Opuntia* tissue and leaves the herbaceous vegetation surrounding the motte mostly intact (Myster 2001). Even when cactus is used as forage during drought, ranchers still understood that needed to be managed in instances where it increased dramatically in landscape cover. As this succulent expands across the landscape it competes for space and resources with grasses and forbs. Increased cacti abundance corresponds with reductions in forage production during years of normal and elevated precipitation (Briske, *et al.* 2005).

Mechanical and herbicide treatments of prickly pear have largely been limited by their costs, and are therefore not effective management strategies for current landowners. Mechanical removal of woody species with the use of anchor chains may increase *Opuntia* cover following the treatment if it is not immediately followed by a prescribed fire (Hanselka and Paschal 1991). The disturbance caused by machinery crushes and separates mottes which allows individual pieces of crushed cladodes (i.e., cactus pads) to self-propagate and leads to increases in *Opuntia* establishment across the landscape

(Mondragón-Jacobo, *et al.* 2001). Following this type of disturbance, cactus encroachment can be so vast that it takes over all open patches and rapidly leads to habitat degradation. For instance, the lands associated with dense prickly pear have been shown to have higher rates of soil erosion (van Langevelde, *et al.* 2003). Disrupting the established root system of *Opuntia* mottes and other woody species can lead to extensive soil erosion in areas surrounding cacti that have little or no herbaceous cover. The stability of the soil and the addition of water are the two fundamental factors that dictate the current and future plant communities (Glantz 1977). The establishment of *Opuntia* in this resource limited ecosystem inhibits the establishment of grasses and restricts floral biodiversity as it competes with surrounding vegetation (Guthery, *et al.* 1987).

The ecological function of disturbed systems is decreased as encroachment by a single species limits desirable herbaceous species diversity and abundance (Walter 2008). Land stewards have used a combination of techniques to remove cacti from their lands but have faced many obstacles in their efforts. The cost and manpower necessary to remove undesirable species is one of the most significant limitations (Mack, *et al.* 2000). As more grassland savannas disappear, ecologists and landowners realize that they play an integral part in the future, as the sole habitat for some wildlife and flora. The maintenance and restoration of degraded rangelands is an investment that improves ecological services.

Life History Characteristics of *Opuntia* Cacti

Prickly pear cactus (*Opuntia* spp.) is a rapid growing, drought tolerant succulent plant that can grow in extreme climates (Rebman and Pinkava 2001). This perennial cactus produces cladodes, commonly referred to as cactus pads, that are covered with spines and glochids that are joined in chains rising from the stem (Buxbaum 1950;Higgins 1946). Glochids are tiny, finely barbed spines found at the base of the areoles of cactus pads. The group of pads that make up a single cactus plant is referred to as a motte. Prickly pear cacti have the capability to sexually reproduce from seed or vegetatively reproduce from existing pads that become fragmented and produce roots (Lamb and Lamb 1955). The pad of an *Opuntia* cactus can take root and establish in disturbed soil if it becomes detached from the main plant (Preston-Mafham 1994). For instance, livestock and wildlife can disperse pads, thereby facilitating vegetative establishment in new locations. Attached pads in direct contact with soil have also been documented to separate and become established as a new individual (Chavez-Ramirez, *et al.* 1997).

The morphological and physiological adaptations that characterize succulent species, allow *Opuntia* cacti to store water in its pad tissues and thus allows it to survive in arid environments (Barcikowski and Nobel 1984). Prickly pear pads are modified branches that store water and like many other succulents carries out a distinctive type of photosynthesis called Crassulacean Acid Metabolism (CAM) (Spoehr 1919). CAM plants differ from conventional photosynthetic pathways. Typically plants open their stomata during the day to allow it to produce sugars and oxygen from the bonding of carbon dioxide and water with the use of light energy (MacDougal and Spalding 1910). Instead CAM plants, in an effort to save water, close their stomata during the day and open them during the night when tissue moisture loss due to evaporation is lower. The carbon dioxide collected during the night is then stored as an acid and is released during the day after it has been metabolized to produce the sugars the plant needs to carry out growth and development functions (Higgins 1946;Richards 1915). This adaptation allows *Opuntia* to live and persist in harsh environments where water is scarce.

Opuntia Cacti: A Problematic Species

Prickly pear cactus is a native succulent that has significantly increased in cover during the past century (McGinty, *et al.* 2001). Historically, it has been sparsely dispersed across the landscape similar to tree densities in savanna ecosystems (Everitt and Drawe 1974). However, today it has increased in density to the point of being considered a problematic pest-like species. It is a hardy plant that can adapt to extreme environments, hot and dry summers and cold winters. Although it is an evergreen species that remains physiologically active year round, it is characterized by having a slow metabolism. There is limited information available on the role prescribed fire has in limiting and reducing prickly pear encroachment, but one recent study suggests that summer prescribed burning decreases cacti cover while improve rangeland condition (Ansley and Castellano 2007).

Management Strategies

Herbicides and Mechanical

Herbicides have been used to control *Opuntia* encroachment, however, this tool has been found to be extremely laborious and economically expensive (Kreuter, *et al.* 2008). The time that it takes to see visible results can be as much as five years (McGinty and Texas Cooperative Extension. 2005). The herbicide recommended for controlling prickly pear are picloram and surmount (Aldridge and Texas Agricultural Experiment Station. 1983), however, this control method is considered to be too costly for most ranchers and land managers. One advantage of herbicides is that they can be highly effective in causing motte mortality if applied consistently at the right time of the year. Herbicide treatments can potentially be applied to a large scale across the landscape or they can be applied to treat mottes individually (Wicks, *et al.* 1969). For herbicides to be effective, management plans require that they be applied repeatedly during the flowering season (McGinty, *et al.* 2005). While it may be possible to reduce undesirable *Opuntia* cacti with herbicides while promoting and maintaining desired herbaceous vegetation for livestock and wildlife there are numerous disadvantages to using herbicides, such as the unintended mortality and reduction in diversity of grasses and density of forbs (McGinty and Texas Cooperative Extension. 2005).

Opuntia cacti have also been difficult to control using traditional mechanical removal methods (Aldridge and Texas Agricultural Experiment Station. 1983). For example, if the stem of the cactus mottes is not completely pulled out the succulent has an opportunity to reestablish by re-sprouting new pad growth on existing tissue. As previously mentioned, prickly pear can easily anchor new roots from pads scattered by machinery (Hanselka and Paschal 1991). In the past, mechanical brush control efforts have unintentionally done much to spread and intensify cactus densities across rangelands (Aldridge and Texas Agricultural Experiment Station. 1983). Mechanical removal with the use of a chain is vastly ineffective without the use of fire immediately following the removal. Without further management, broken cladode pieces dispersed by mechanical chaining will re-root and likely establish at a higher densities than before mechanical control treatments were implemented (van Langevelde, *et al.* 2003).

Herbivores

In general, forage quality is lower for both domesticated and wildlife species in areas with a high abundance of cacti and woody plants (Anderson, *et al.* 2007). Nevertheless, there are some advantages to having cacti present in the landscape. Prickly pear becomes an important source of live plant tissue for livestock and wildlife when other sources of food are scarce, particularly during periods of drought. *Opuntia* cacti can provide a source of moist live plant tissue when most other plants are dormant or water stressed (North and Nobel 1998). White-tailed deer especially utilize cacti to supplement their diets during drought. One study found that cacti accounts for up to 20% of the annual forage for deer (Everitt and Drawe 1974). White-tailed deer also have been documented to rely heavily on cacti during the late fall through the early winter period when the availability of browse and forbs are limited (Chavez-Ramirez, *et al.* 1997). The prickly pear pads consumed by browsing deer are high in sugars, starch, ether extract, crude protein, amino acids, and fiber (Nobel, *et al.* 1987). The fluctuation in foraging patterns of prickly pear is influenced by rainfall patterns and by seasonality. In southern parts of Texas, *Opuntia* has been shown to comprise as much as 61% of the diet by volume and approximately 55% of the total diet of white-tailed deer (Everitt and Gonzalez 1979). The variability in diets of deer from one region to another has made it difficult to predict the exact diet requirements for this species. A study documenting deer in the semi-arid areas of the Edwards Plateau found that they are primarily browsers except for the spring time when grasses and forbs become an increased portion of their diets (Everitt and Drawe 1974). In contrast, other studies that show prickly pear as being an integral part of deer diet that same study documented that in a year it only accounted for 15.4% of the diet. A number of other wildlife species in the Edwards Plateau depend on *Opuntia* cacti for nourishment, water, and cover. The need to understand dietary requirements of wildlife is becoming increasingly important in states like Texas as the economic benefits that landowners receive from hunting leases surpasses livestock husbandry (Everitt and Drawe 1974).

The benefits and negative consequences of having prickly pear on grazing lands are notable. Although *Opuntia* cactus competes with herbaceous forage it is sometimes used as emergency feed during drought. Because of the presence of spines, livestock generally avoid eating prickly pear when other forage is available. When it is necessary that cacti be used as forage for cattle ranchers will first scorch pads with a propane burner to remove the spines (McMillan, *et al.* 2002). Prickly pear without spines is highly favored by cattle (Mondragón-Jacobo, *et al.* 2001). If present, the spines from prickly pear can cause physical injury to the lips, mouth, as well as the upper gastrointestinal tract (McGinty, *et al.* 1983). In Texas it is estimated that approximately one fifth of the ranchers burn and feed prickly pear as an emergency feed for their cattle. In the late 1980s the cost associated with this practice amounted to an average cost of $.22/head/day (Hanselka and Paschal 1991). Today the cost is comparable, however, it has become more challenging to reach heavily encroached areas because they limit human and animal movement across the landscape (Van Auken 2000).

Feeding prickly pear can present several disadvantages in the long-term. It has been observed that livestock continue feeding on cactus, even after all of the scorched spineless pads are gone. If continued those livestock that persist consuming prickly pear even after alternative forage is available, they are at risk of developing health problems (Hanselka and Paschal 1991). A recent study near the Edwards Plateau found that livestock were negatively affected by consuming prickly pear. Observation of the feeding habits showed that they persist consuming tunas, the fleshy fruit produced by prickly pear (McMillan, *et al.* 2002). These fruits from *Opuntia* appear in late spring and persist on the plant for most of the summer, until late summer when they ripen. Consuming tunas in excess leads to injuries the oral cavities, the spines irritate the lips and tongue. When sheep show visible symptoms of lesions it is recognized as "pear mouth" by ranchers. What is even more alarming is the effects tuna seed can have on the animal, sheep cannot easily digest the seeds found within tunas. Often the seeds become compacted in a segment of the rumen and can cause blockages that may lead to premature death (Hanselka and Paschal 1991). Moreover, the amount of nutrients found in *Opuntia* cacti for ruminant animals cannot be attained solely on this grazing source.

Fire & Rangeland Restoration

An alternative restoration strategy for managing degraded rangelands is the use of prescribed fire. Fires consume accumulated plant litter, while improving access and visibility in areas previously consisting of dense vegetation where few herbaceous species could establish. Fire disturbance causes a shift in the plant community composition by stimulating herbaceous plant productivity while decreasing the density of other species (Grubb 1977;Hobbs and Huenneke 1992). On Texas rangelands prior to European settlement fire was a natural ecological factor that played an important role in this ecosystem and was a vital part of ecosystem function (Denevan 1992). Since fire was a natural phenomenon on these rangelands the majority of plant species were well adapted to frequent burning (Castellano and Ansley 2007). Historically, lightning in the warm season would start fires that would consume grasses and suppress woody plants from encroaching in to the open grassland savannas (Amos and Gehlbach 1988;Ansley and Jacoby 1998;Jacoby*, et al.* 1992). Nowadays the use of fire as a management tool has predominantly been conducted during the winter season. These fires are referred to as cool season fire ane are administered during the winter months after the passing of a cold front when the temperatures decrease and the amount of humidity has fallen (Ansley*, et al.* 1998;Whisenant*, et al.* 1984). They are prescribed fires administered with the intent of increasing grass and forb vegetative production and suppressing undesirable species such as *Opuntia* and Juniper. Recent studies have observed that these fires are ineffective at controlling the encroachment of undesirable species like *Opuntia* and other woody species. It has been suggested that areas with dense cover of undesired species require extreme summer fires to effectively control problematic woody and succulent species (Ansley and Castellano 2007).

For landowners already spending a significant amount of their budget on *Opuntia* encroachment management the application of prescribed fires may be a viable alternative (Bond and Keeley 2005). Prescribed burning is the application of fire on a designated area in order to accomplish specific management and ecological objectives. Each management and ecological objective requires a particular set of conditions for burning, as well as, a specific type of fire to achieve the desired response. All objectives should be thoroughly evaluated in order to create a fire plan that achieves the management goals. In contrast to wildfires, prescribed burns are conducted under predetermined weather conditions. Prescribed fire is recognized as an effective management tool that requires careful and informed planning (Engle, *et al.* 1993). With prescribed burning, conditions such as temperature, humidity, wind speed, fuel moisture and condition of vegetation are carefully selected to ensure a safe and effective burn plan designed to maximize desired effect (Ansley, *et al.* 1998).

Prescribed burning should be of great interest to landowners since it is a relatively inexpensive method for managing woody and succulent encroachment. Although fire is effective at changing plant composition, there continues to be uncertainty about the role that season, fuel loads and fire behavior have on specific vegetation. In the case of fire effects on *Opuntia* cacti, a few studies that have assessed the role of seasonality and herbivory, but their effects have never been combined (Ansley and Castellano 2007;Everitt and Drawe 1974;van Langevelde, *et al.* 2003).

Extreme fires occur predominantly during the summer months when temperatures are high, humidity is low and plant tissues are drought stressed and highly flammable. These warm season fires are characterized by intense temperatures that increase the probability of mortality for undesirable species that densely dominate the landscape (Engle, *et al.* 1993). Many land managers regard prescribed summer fires as a risky practice. However, recent studies haves suggested prescribed fire is a proven tool in managing habitat for livestock and wildlife (Ansley and Jacoby 1998). In contrast to scorching individual mottes or plants using a propane burner, it can swiftly consume vegetation found in dense stands of brush and open up landscapes for colonization and establishment of desirable herbaceous plant species. Prescribed burning should be of great interest to ranchers because it a relatively inexpensive method of encroachment control compared to alternative mechanical or chemical treatments. When integrated with other practices, fire can be used to maintain the long-term sustainability of Texas rangelands(Glantz 1977;Nath 1998). Fire can be a valuable restoration tool to alter the progressive encroachment of woody plants and cacti in Texas rangelands and help maintain ecologically and economically advantageous vegetation composition and structure (Amos and Gehlbach 1988;Teague, *et al.* 2009;van Langevelde, *et al.* 2003).

CHAPTER III

STUDY AREA

The study was conducted at the Texas A&M University Sonora AgriLife Research Station (30^o N, 100^o W). The 1430 hectare station is located in Sutton and Edwards counties over the Edwards Plateau Land Resource Area (Bryant*, et al.* 1981). The landscape contains limestone fragments, stones and gravel, and is underlain by limestone bedrock.

The station is approximately 763 m in elevation with an average growing season of 240 days. The climate in of this part of the Edwards Plateau is semi-arid with an average annual precipitation of approximately 57.5 cm. The maximum recorded annual rainfall at that station was 105.4 cm in 1937 and the lowest was 16 cm in 1951. Seasonal and annual droughts are common, as are above-normal rainfall events that result from intense, short duration thunderstorms (Amos and Gehlbach 1988). Annual precipitation is bimodal with peaks occurring in the spring and fall. Temperatures average 30 ^{o}C in July and 9 ^{o}C in January (Fuhlendorf*, et al.* 2001).

Although historically characterized as semi-arid grassland savannah, many areas on the site, and quite characteristic of this region in general, are severely degraded as a result of encroachment by woody species such as mesquite and juniper. The majority of these areas are experiencing additional degradation as a result of aggressive *Opuntia* cacti invasions. Woody plants include live oak (*Quercus fusiformis*), scrub oak (*Q. pungens*), Ashe juniper (*Juniperus ahei*), redberry juniper (*J. pinchotti*), and Texas persimmon (*Diospyros texana*). The open areas are dominated by herbaceous plants that include common curlymesquite (*Hilaria belangeri*), threeawns (*Aristida* spp.), sideoats grama (*Bouteloua curtipendula*), cane bluestem (*Bothriochloa barbindis*), red grama (*Baouteloua trifida*), Texas cupgrass (*Eriochloa sericea*), Texas wintergrass (Stipa leucotricha), and hairy grama (Bouteloua hirsuta). Perennial forbs such as scurfpea (*Psoralidium lanceolatum)*, bushsunflower (*Simsia calva)*, Mexican sagewort (*Artemisia ludoviciana*), Engelmann daisy (*Engelmannia peristenia*), and menodora (*Menodora spp.) are found on* the site.

The study area was located over two gentle sloping soil series; (refer to map in Figure 1). The dominant soil in the study area was the Valera clay soil which is moderately alkaline and up to 35 cm deep. These soils have slopes of 0 to 2%, are well drained and have a low capacity to store water (Gabriel and Loomis 2000). The parent material for these soils comes from slope alluvium derived from limestone. Prade-Eckrant complex soils also occupy portions of the area. These soils are composed mainly of silt and clay; they also contain many cobbles and are 20 to 38 cm deep. These soils have slopes of 0 to 3%, are also well drained and a very low capacity to store water. The parent material for these soils comes from residuum weathered from limestone bedrock (Gabriel and Loomis 2000).

From the mid-1800s until approximately the mid-twentieth century, the land now associated with the station was heavily grazed by cattle, sheep and goats (Amos and Gehlbach 1988;McCalla*, et al.* 1984). This exploitation of natural resources degraded the rangelands and decreased the health of livestock (Archer 1995). In 1916, in order to effectively investigate and provide solutions to affected ranchers and landowners, the station was established (Amos and Gehlbach 1988). Researchers at the station studied animal diseases as well as the management and breeding of cattle, sheep, and goats in order to improve range conditions and animal health and production. As a result of confined, continuous grazing and fire suppression the natural plant community changed significantly and became dominated by shortgrasses, less palatable annual and perennial forbs, woody plants such as Ashe juniper (*Juniperus ahei*), and succulents like prickly pear cactus (Hanselka and Paschal 1991). Presently the station is grazed moderately, while the approximately 5 hectare area associated with this study was not grazed by cattle, sheep, or goats for a continuous yearlong basis; (refer to Figure 1 for a map of the study site).

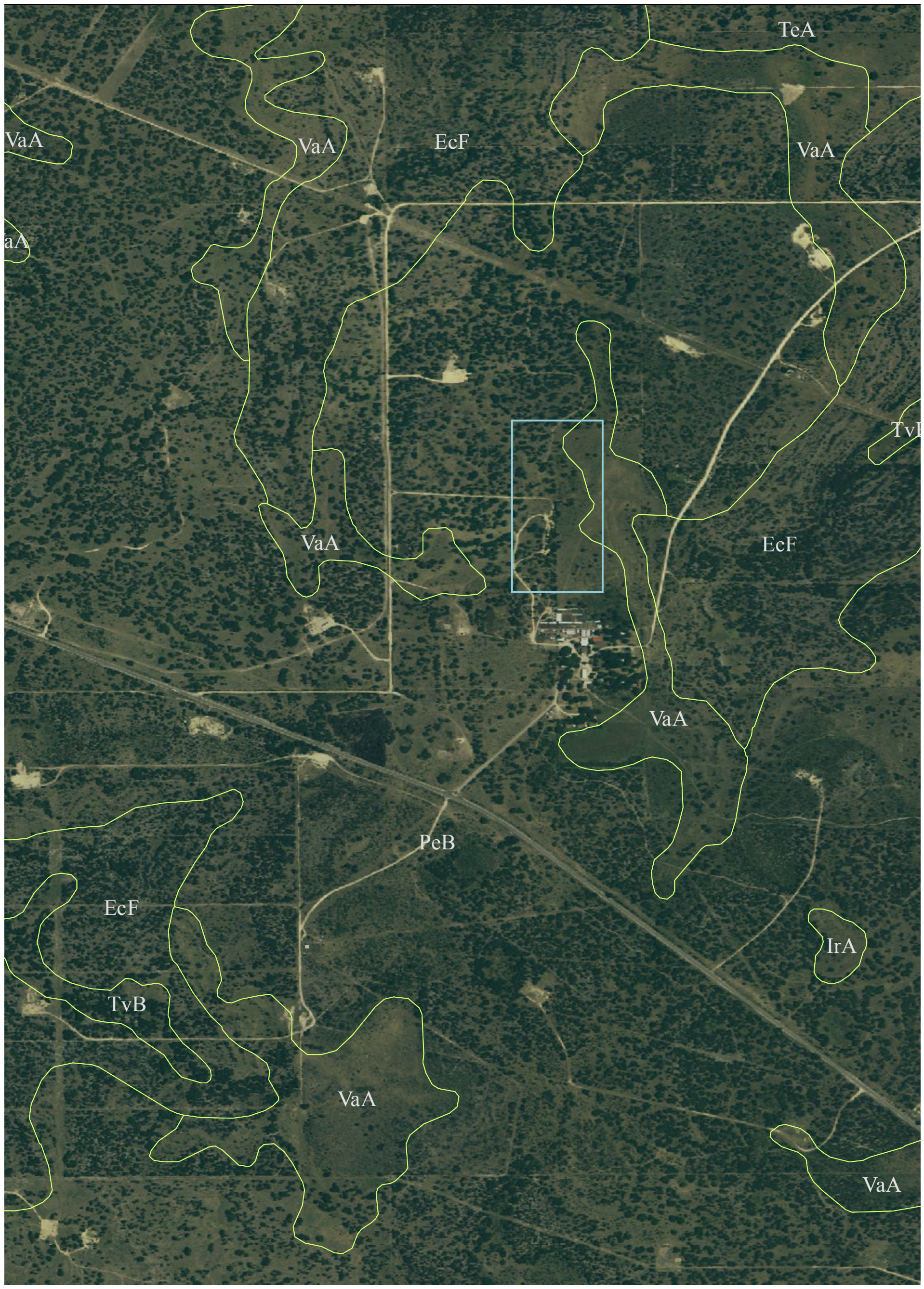

Figure 1. Map of study site within the Sonora Texas AgriLife Research Station. An aerial photography of the station that has been superimposed over a layer that contains the soils, the data was provided by the National Cooperative Soil Survey (Gabriel and Loomis 2000). The region outlined in blue is the area associated with the experiments for this study.

CHAPTER IV

METHODS

Study Design

To assess the interactive effects of fire season and wildlife herbivory on *Opuntia* cacti growth and survival, we burned cactus mottes during two different time periods in a study that took place from January 2008 through December 2008. We established a completely randomized, multi-factorial experimental design in a landscape with significant prickly pear cactus encroachment. The cactus mottes used for this study were selected from a 1-ha site with a similar grazing and management history.

We located 60 cactus mottes in mid-January 2008 within an area of high prickly pear density (Fig. A-1). Livestock were excluded from the area, but deer and other wildlife had easy accessibility. Mottes were selected with diameters that ranged from 0.5 m to 1.5 m to keep sizes constant. Each motte was tagged and its spatial location was established using a Global Positioning Systems (GPS) unit with sub-meter accuracy (Figures 2 and A-2). We measured in meters the length and width of each motte using cardinal directions and measured its height from the ground to top of the tallest cladode with a meter stick. The dimensions and characteristics of each and every cladode found within the 60 cactus mottes were collected, this included characteristics such as percent mortality, live tissue, and herbivory present at the moment of sampling.

The plant community structure and fuel characteristics of the surrounding bulk vegetation was also measured and recorded at the time of data collection. The height and percent density of herbaceous cover was measured in meters. The fine fuels data may allow for the correlation of fire behavior and effects on cactus mottes damage and overall mortality. We calculated the percent cactus cover, as well as, the cover of surrounding litter, fuel, and vegetation at three distinct spatial scales with a radius of 0.50 m, 1.0m, and 2.5 m. To calculate the percentages of prickly pear cover, woody cover, herbaceous cover, herbaceous litter, juniper litter, oak litter, 1 hour fuels, 10 hour fuels, 100 hour fuels, and bare ground a 2.5 m pole was placed directly at the center of the cactus motte where estimates at the three scales were recorded. The 1, 10 and 100 hour fuels are dead fuels that are critical in determining fire potential given that their size relates to how fast it will react to gains or losses in moisture due to changes in its environment.

Each motte was randomly assigned an experimental treatment combination that included fire (dormant season head fire, dormant season compartment fire, growing season compartment fire, or no fire/control) and wildlife herbivory (exclosure fence or control). This design provides 10 replicates of the dormant season head fire, 10 replicates of the no fire control, 5 replicates of the dormant fires using the burn compartment, and 5 replicates of the growing season fires using the burn compartment all with and without wildlife herbivory exclosures. The mottes assigned wildlife herbivory exclosures were enclosed using aluminum wire mesh anchored by four 1.2 m steel rebar posts (Fig. A-3). The structures resulted in motte enclosures that protected it from large herbivores. The diameter of the exclosures varied depending on the existing mottes dimensions; however the height was consistent at 1.2 m.

To limit the seasonal variability of vegetative combustible fuel and to contain the individual motte fires we designed a self-contained burning compartment constructed from angle iron and sheet metal panels (refer to Figures B-1 and B-2). This $2m^3$ "burn-box" created a constant burn area with equivalent amounts of fuel that allowed us to conduct fires of similar intensity in different growing seasons. All fires conducted within the compartment received an additional amount of dry hay to allow the fuel loads to be unvarying regardless of seasonal differences. By regulating and equilibrating fire intensity we were able to independently assess prescribed fire effects on cactus plants with different physiological states. These factors are typically confounded by seasonal conditions. The compartment entirely surrounded each motte and allowed us to ignite a self-contained head fire for across each motte. Confining the fire also permitted us to monitor and quantify the temperature of the fires within each burn compartment, using a protected electronic OMEGA™ temperature data logger (Fig. B-3).

The first set of prescribed fires were administered during the winter in mid-March 2008. A total of twenty cactus mottes were burned with a head fire that consumed most of the vegetative patches throughout an area that extended approximately one hectare. The fire moved rapidly across the landscape, fueled by accumulated dry litter and strong winds. The cactus mottes burned with the head fire served as a basis for comparing the motte-specific prescribed burns conducted within the burn compartment that same day. The ten cactus mottes burned in the burn compartment received 4.5 kilograms of supplemental dry fuel to equalize the fuel loads and create similar fire intensities. The dry hay was spread out evenly across the $2m^2$ area prior to placing the compartment over the designated burn area. The vegetation surrounding the compartment was wetted with a mixture of water and fire retardant. The OMEGA™ temperature probe was inserted on the ground inside the burn compartment to obtain detailed time series temperature data for each fire. All of the fires were started from the southern end of the compartment using of a drip torch. Each fire was timed and allowed to completely extinguish before removing the compartment. During this time the temperature data logger took readings at 1-second intervals. The wildlife herbivory exclosures were not removed to conduct the burns. We conducted the growing season prescribed burns on the remaining 10 cactus mottes in early October 2008. The mottes were burned within the burn compartment using the same procedure as the fires conducted during March.

Post-fire data was collected during mid-June and mid-December 2008 . In addition to repeating the pre-treatment measurements taken earlier, measurements of all the new growth were recorded for all cactus mottes in the study (n = 60). These measurements allowed us to assess the herbivory and fire damage on existing and new cactus cladodes. For the duration of this study environmental variables, such as precipitation and temperature were monitored.

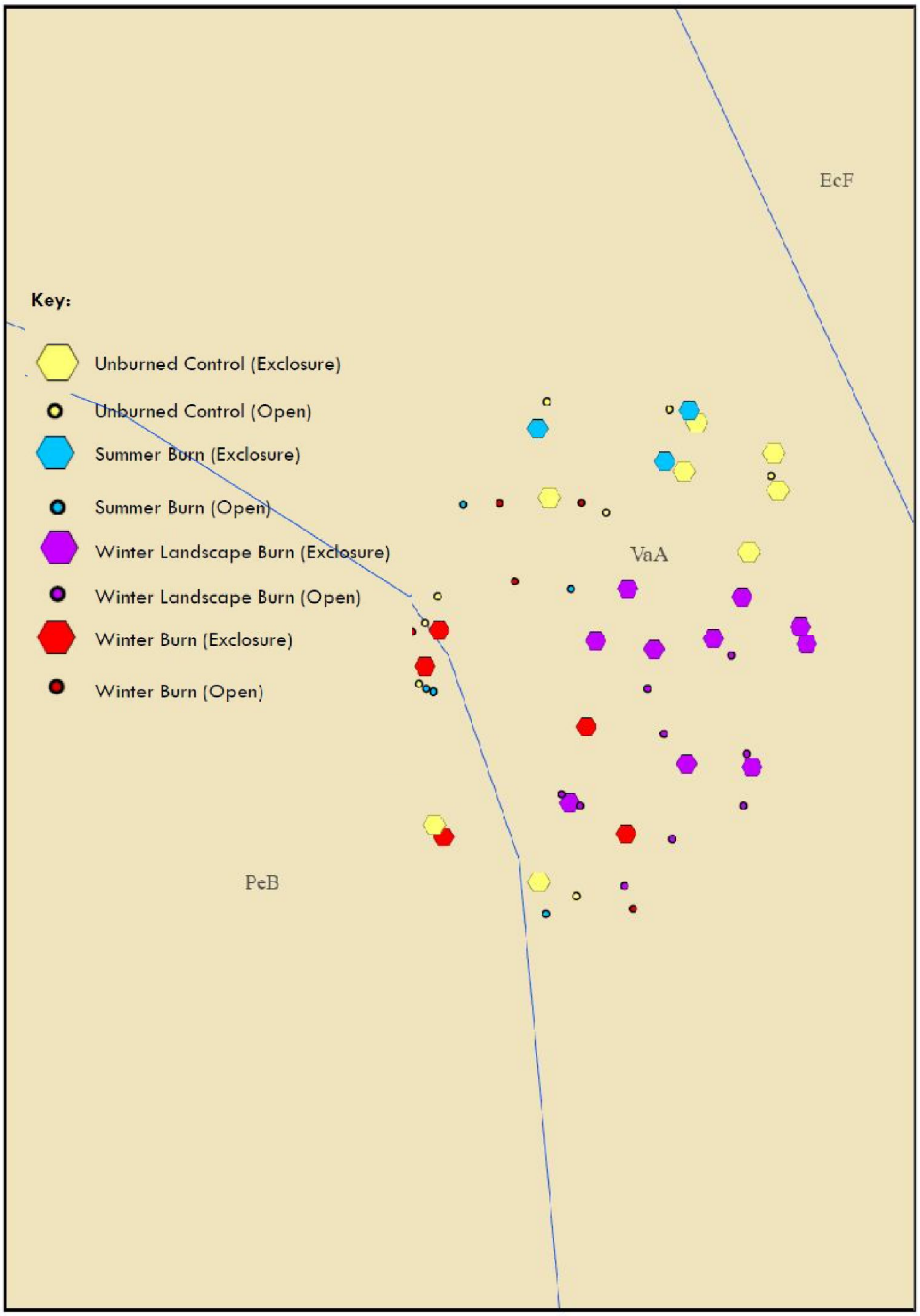

Figure 2. Cactus motte distribution within study site. Map shows the cactus motte distribution, note that they are found over two distinct soil types.

Sub-Experiment: Tissue Moisture Variability

To determine if cacti cladode tissue moisture varies by season and, if this in turn affects prickly pear cacti mortality during a prescribed fire, we quantified the tissue water content of *Opuntia* cladodes. We collected plant tissue for a total of 60 cactus mottes found in an adjacent field close to the main study site with a similar grazing and management history. We selected mottes that were between 0.5 m and 1.5 m in diameter that contained at least two chains with at least four cladodes (cactus pads). The mottes were tagged and demographic data similar to the experiment above was measured. We destructively harvested 30 cactus mottes on the same day the burns were conducted in mid-March and early-October 2008, respectively. A total of eight cladodes were collected from each motte. In each instance, 30 mottes were harvested by separating four cladodes from each chain and having each cladode placed in an individually marked paper bags with their designated relative location within the motte, (Fig. 3). In total, 240 cladodes in each growing season resulting in 480 cladodes collected by the end of the study. The weight of each cladode and its demographic measurements were recorded immediately after harvesting. The moist cladode tissues were transferred to a drying oven for approximately two weeks until the samples were completely dehydrated. The dry weight of each cladode was allowing us to calculate the amount of moisture present in each at the time of burn, as well as, assess the moisture distribution among cladodes within the cactus.

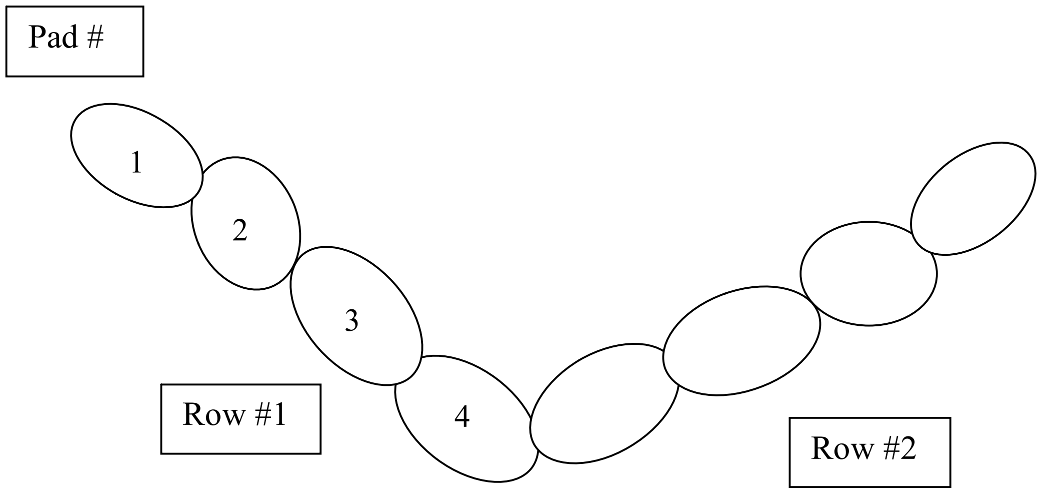

Figure 3. Cladode Harvesting Design. Harvesting design for sub-experiment required that all cacti cladodes were collected using this pre-established scheme.

Statistical Methods

For all analyses in this study the significance level is α=0.05 for general cases and α=0.10 for interaction effects tests. A one-way analysis of variance (one-way-ANOVA) was used to determine if there was a seasonal (winter vs. summer) difference in the maximum temperatures reached within the fire compartment.

Pre-treatment and post-treatment data were compared for the various experimental manipulations using one-way-ANOVAs. We analyzed the length, width, and the calculated motte cover area (length*width) of each cactus motte. Four post-treatment ANOVA comparisons were performed at distinct response times. These include 3 and 9 months post-fire treatment with each requiring the use of different post-data collection dates since there was a seasonal lag for the treatments. We also analyzed the post-treatment data at 12 and 18 months from the beginning of the study. The comparison at different times post-disturbance may provide insight into the response by assessing the effectiveness of the treatments on *Opuntia* cacti mottes. Each of these comparisons the percent difference in cactus motte cover area was calculated using the following formula:

$$\text{Change in Motte Cover Area} = \frac{\text{(Post-Treatment Area – Pre-Treatment Area)}}{\text{(Pre-Treatment Area)}} * 100$$

It was often difficult to discern whether cactus tissues were dormant or dead. As a result, we conservatively assumed that all intact, non-decomposed or non-combusted tissues were alive and incorporated them into our cover estimates. This may have led to overestimates of total motte cover in some instances, particularly in the early months following the fires before dead tissues began decomposing. Nevertheless, seemingly dead tissues were frequently observed to “green-up” or establish new sprouts, thus demonstrating they were merely dormant, and necessitating the more inclusive cover estimates. This methodology also contributes to an apparent discrepancy in our estimates of motte survival. If after 18 months from the beginning of the study there was no new or visible green growth on a motte we classified it as dead in our mortality calculation. This is despite the possibility that the same motte that was classified as dead may have received a cover estimate at the same time.

The values calculated were analyzed separately with the SPSS Statistical Package. For all these comparisons the goal was to determine if the fire and herbivory treatments has a significant interaction, if it was determined that they did, then it was possible to compare within treatments. We used Fisher's Least Significant Difference (LSD) procedure to test all possible pair-wise comparisons.

Sub-Experiment Analysis

Differences in cladode moisture content by season among cacti and differences in moisture distribution among cladodes within a single cactus were assessed by one-way ANOVAs. The moisture content of each cladode was analyzed at multiple locations and at two distinct harvesting seasons, winter and summer. A Fisher's LSD statistical test was used to examine all possible pair-wise comparisons.

CHAPTER V

RESULTS

Maximum Fire Temperature at Different Seasons

As the prescribed fires consumed the vegetation within the burn compartment in during both the winter and summer seasonal treatments, the fire temperature was digitally recorded every second with the use of an external thermocouple attached to an OMEGA data logger, model HH806AU (Fig. B-3). No significant difference ($p = 0.425$) was found in the maximum temperatures reached between the winter and summer prescribed fires (Tables 1-3). The average maximum temperatures recorded were very similar regardless of season in which the prescribed fires were conducted (Figure 4). The average maximum temperature recorded during the winter prescribed burns was of 389.8 ± 33.22 ^{o}C, slightly a few degrees lower than the maximum temperature recorded in the summer of 422.3 ± 23.03 ^{o}C (Fig. 4). The range of temperatures recorded was 201.6-514.7 ^{o}C for the winter fires and 301.4-501.7 ^{o}C for the summer fires (Table 1).

Table 1. Seasonal comparison of maximum fire temperatures. The mean, standard deviation, standard error, and 95% confidence interval of the maximum fire temperature reached during the winter prescribed burn, conducted March 2008, and summer prescribed burn, conducted October 2008.

Seasonal Comparison of Maximum Fire Temperatures

Maximum Temperature

					95% Confidence Interval for			
	N	Mean	Std. Deviation	Std. Error	Lower Bound	Upper Bound	Minimum	Maximum
Winter Burn	9	389.8222	99.67659	33.22553	313.2040	466.4404	201.60	514.70
Summer Burn	10	422.3300	72.81862	23.02727	370.2387	474.4213	301.40	501.70
Total	**19**	**406.9316**	**85.70363**	**19.66176**	**365.6238**	**448.2394**	**201.60**	**514.70**

Table 2. Analysis of maximum fire temperatures. The maximum fire temperature reached during the winter prescribed burn, conducted March 2008, and summer prescribed burn, conducted October 2008 were not significantly differ at the 0.05 level of probability.

Analysis of Maximum Fire Temperatures

Maximum Temperature

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	5,005.684	1	5,005.684	0.669	**0.425**
Within Groups	127,206.337	17	7,482.726		
Total	132,212.021	18			

Table 3. Recorded maximum fire temperatures. A total of 19 maximum temperatures were recorded during the winter prescribed burn, conducted March 2008, and summer prescribed burn, conducted October 2008

Recorded Maximum Fire Temperatures	
Temperature ^{o}C	**Precribed Fire Treatment**
502.7	Winter Prescribed Burn
321.7	Winter Prescribed Burn
201.6	Winter Prescribed Burn
335.8	Winter Prescribed Burn
358.7	Winter Prescribed Burn
396.9	Winter Prescribed Burn
403	Winter Prescribed Burn
514.7	Winter Prescribed Burn
473.3	Winter Prescribed Burn
486.5	Summer Prescribed Burn
331.6	Summer Prescribed Burn
301.4	Summer Prescribed Burn
361	Summer Prescribed Burn
496.7	Summer Prescribed Burn
471.3	Summer Prescribed Burn
501.7	Summer Prescribed Burn
396.4	Summer Prescribed Burn
466.4	Summer Prescribed Burn
410.3	Summer Prescribed Burn

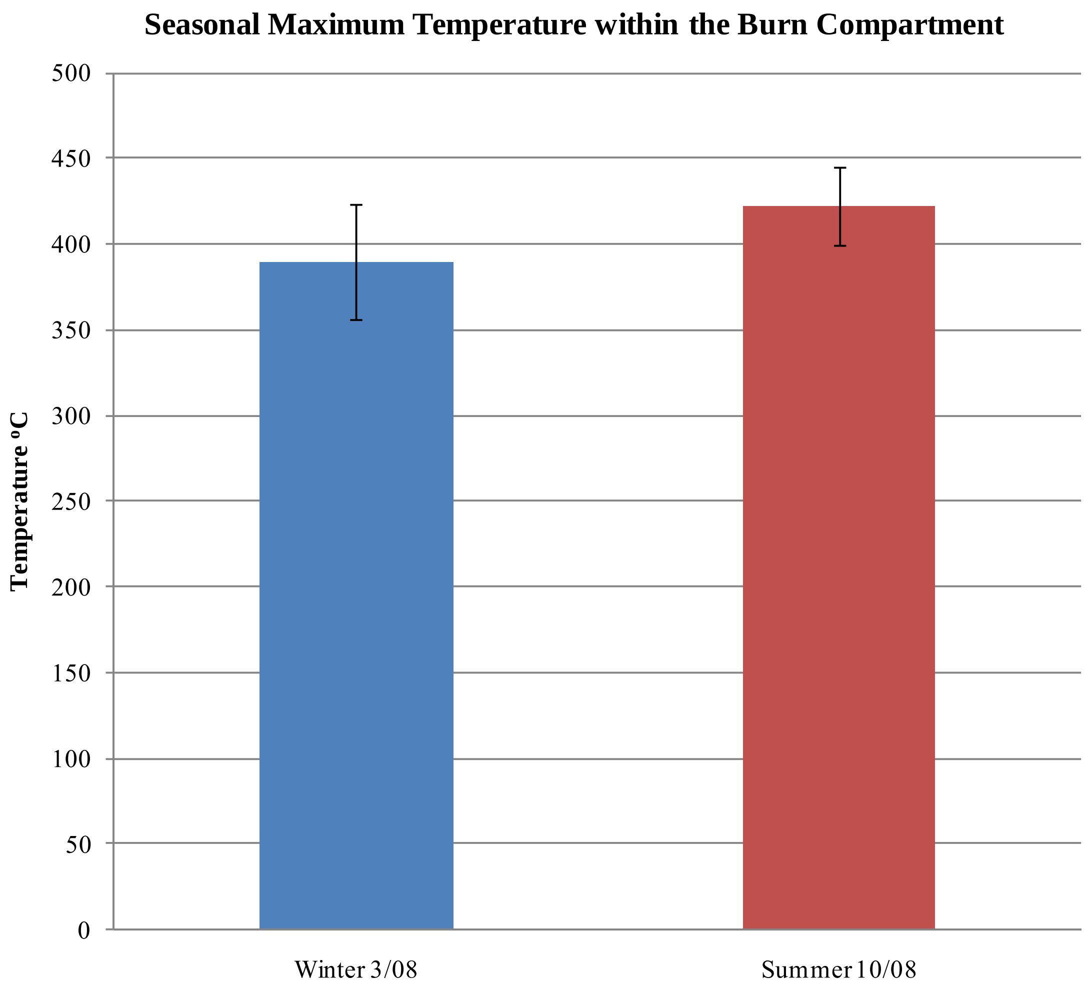

Figure 4. Seasonal maximum temperature within the burn compartment. There is no significant difference in the maximum fire temperature reached during the winter prescribed burn, conducted March 2008, and summer prescribed burn, conducted October 2008.

Interactive Effects of Fire and Wildlife Herbivory

Pre-treatment analyses of cactus motte length, width, and cover, in the multi-factorial fire and herbivory experiment show no significant differences among treatments (Tables 4-6). Three months post-fire indicates that cactus motte cover had decreased by 84.74% in plots exposed to summer fire and wildlife herbivory (Table 8).

Table 4. Pre-treatment: Differences in length of cacti mottes. The cactus motte length at the time initial point of collection, prior to beginning the study was not significantly different between treatments.

Pre-Treatment: Differences in Length of Cacti Mottes					
ANOVA					
	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	0.413	7	0.059	1.042	**0.414**
Within Groups	2.942	52	0.057		
Total	3.354	59			

Table 5. Pre-treatment: Differences in width of cacti mottes. The cactus motte width at the time initial point of collection, prior to beginning the study was not significantly different between treatments.

Pre-Treatment: Differences in Width of Cacti Mottes					
ANOVA					
	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	0.262	7	0.037	0.669	**0.697**
Within Groups	2.915	52	0.056		
Total	3.177	59			

Table 6. Pre-treatment: Differences in cover of cacti mottes. The cactus motte cover area at the time initial point of collection, prior to beginning the study was not significantly different between treatments.

Pre-Treatment: Differences in Cover of Cacti Mottes					
ANOVA					
	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	1.284	7	0.183	1.286	**0.276**
Within Groups	7.420	52	0.143		
Total	8.704	59			

Mottes with accessibility to large mammalian herbivores and that received either prescribed winter burn compartment fires or winter landscape fires saw a cactus motte area cover decrease of 69.81% and 42.90%, respectively (Fig. 5). In comparison, fire treatments that were combined with herbivore exclosures showed a decrease of 30.64% for the prescribed summer burn compartment fire treatment, a lesser 4.54% decrease for the prescribed winter burn compartment fire treatment and only a 2.03% increase for the winter landscape burn treatment (Fig. 5).

Table 7. Descriptive statistics 3 months post-fire treatment. Means and standard deviations of cactus motte cover in response to fire and herbivory treatments at three months post-fire.

Descriptive Statistics 3 Months Post-Fire Treatment				
Dependent Variable: 3 Months Post- Fire Treatment				
Prescribed Fire Treatment	Herbivory Treatment	Mean	Std. Deviation	N
Summer Burn	Open	84.7400	8.42543	5
	Enclosed	30.6460	12.75557	5
Winter Burn	Open	69.8160	16.42885	5
	Enclosed	4.5400	12.95880	5
Winter Lanscape Burn	Open	42.9060	27.52715	10
	Enclosed	-2.0380	13.69999	10
Control	Open	-6.1930	39.38281	10
	Enclosed	-11.7900	15.43812	10

Unburned treatments with and without herbivory experienced an increase in cactus motte cover area (Fig. 5). Mottes that were accessible to herbivores experienced an increase of 6.19%, while the mottes with no herbivory had an increase of 11.79% (Table 7, Fig. 5). Statistical analysis of cactus motte cover three months post-fire revealed a significant interaction of fire and herbivory treatments ($p = 0.004$, Table 8).

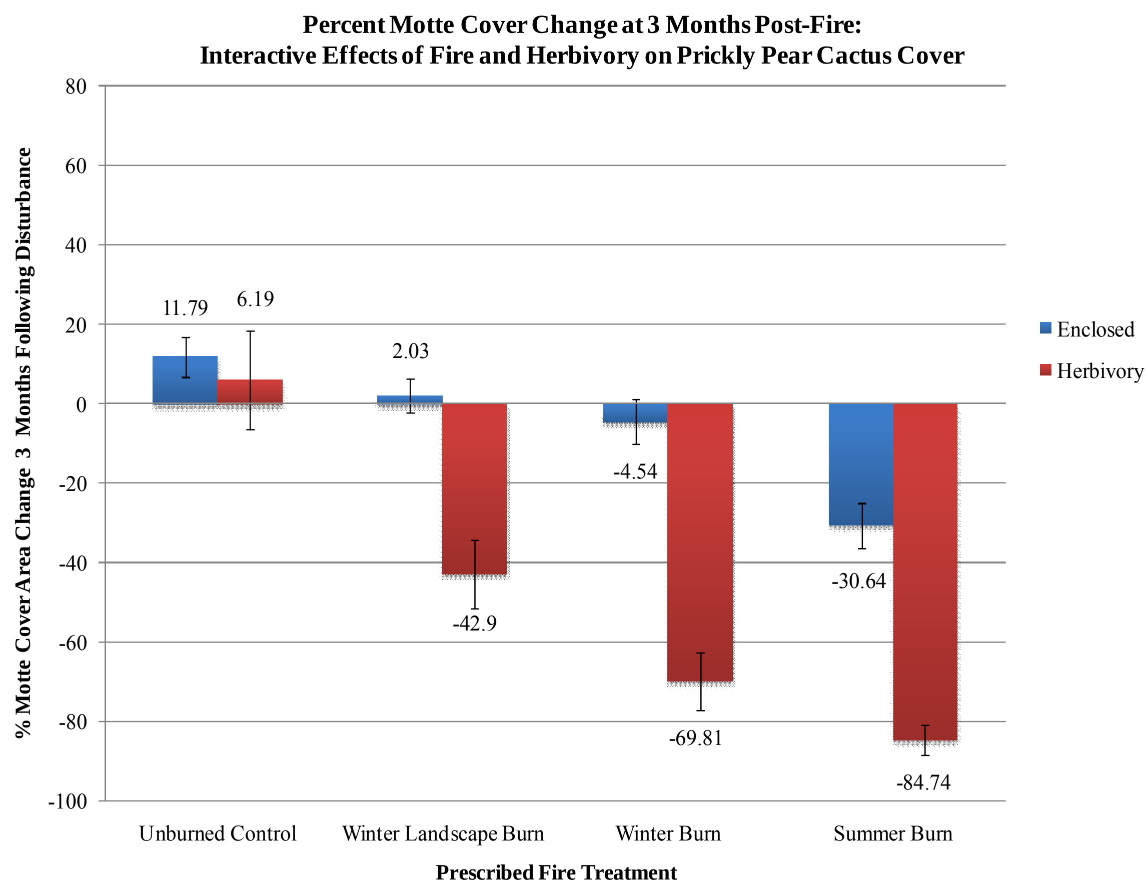

Figure 5. Percent motte cover change at 3 months post-fire. Mean (±1SE) percent motte cover change for prescribed fire and herbivory treatments at three months post-fire treatment.

Table 8. ANOVA for cactus motte cover in 3 months post-fire. ANOVA for cactus motte cover in response to fire and herbivory treatments at three months post-fire treatment (significance level determined at α=0.05).

ANOVA for Cactus Motte Cover in 3 Months Post-Fire					
Tests of Between-Subjects Effects					
Dependent Variable: 3 Months Post-Treatment					
Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Prescribed Fire Treatment	33,963.975	3	11,321.325	21.565	0.000
Herbivory Treatment	24,058.123	1	24,058.123	45.827	0.000
Prescribed Fire Treatment * Herbivory Treatment	7,974.622	3	2,658.207	5.063	**0.004**
Error	27,299.097	52	524.983		
Total	112,598.105	60			
Corrected Total	89,487.312	59			
a. R Squared = .695 (Adjusted R Squared = .654)					

Table 9. Fisher's LSD comparison of treatments 3 months post-fire. Fisher's LSD means contrasts of cactus motte cover for fire and wildlife herbivory treatments through a pair-wise comparison at three months post-fire.

Fisher's LSD Comparison of Treatments 3 Months Post-Fire				
Dependent Variable: 3 Months Post-Treatment				
(I) Treatment	(J) Treatment	Mean Difference (I-J)	Std. Error	Sig.
SummerBurn Enclosure	SummerBurn Herbivory	-54.0940(*)	14.49114	0.000
	WinterBurn Enclosure	26.1060	14.49114	0.077
	Winter LandscapeBurn Enclosure	32.6840(*)	12.54969	0.012
	Control Enclosure	42.4360(*)	12.54969	0.001
SummerBurn Herbivory	SummerBurn Enclosure	54.0940(*)	14.49114	0.000
	WinterBurn Herbivory	14.9240	14.49114	**0.308**
	Winter LandscapeBurn Herbivory	41.8340(*)	12.54969	0.002
	Control Herbivory	90.9330(*)	12.54969	0.000
WinterBurn Enclosure	SummerBurn Enclosure	-26.1060	14.49114	0.077
	WinterBurn Herbivory	-65.2760(*)	14.49114	0.000
	Winter LandscapeBurn Enclosure	6.5780	12.54969	**0.602**
	Control Enclosure	16.3300	12.54969	**0.199**
WinterBurn Herbivory	SummerBurn Herbivory	-14.9240	14.49114	**0.308**
	WinterBurn Enclosure	65.2760(*)	14.49114	0.000
	Winter LandscapeBurn Herbivory	26.9100(*)	12.54969	0.037
	Control Herbivory	76.0090(*)	12.54969	0.000
Winter LandscapeBurn Enclosure	SummerBurn Enclosure	-32.6840(*)	12.54969	0.012
	WinterBurn Enclosure	-6.5780	12.54969	**0.602**
	Winter LandscapeBurn Herbivory	-44.9440(*)	10.24678	0.000
	Control Enclosure	9.7520	10.24678	**0.346**
Winter LandscapeBurn Herbivory	SummerBurn Herbivory	-41.8340(*)	12.54969	0.002
	WinterBurn Herbivory	-26.9100(*)	12.54969	0.037
	Winter LandscapeBurn Enclosure	44.9440(*)	10.24678	0.000
	Control Herbivory	49.0990(*)	10.24678	0.000
Control Enclosure	SummerBurn Enclosure	-42.4360(*)	12.54969	0.001
	WinterBurn Enclosure	-16.3300	12.54969	**0.199**
	Winter LandscapeBurn Enclosure	-9.7520	10.24678	**0.346**
	Control Herbivory	-5.5970	10.24678	**0.587**
Control Herbivory	SummerBurn Herbivory	-90.9330(*)	12.54969	0.000
	WinterBurn Herbivory	-76.0090(*)	12.54969	0.000
	Winter LandscapeBurn Herbivory	-49.0990(*)	10.24678	0.000
	Control Enclosure	5.5970	10.24678	**0.587**
Based on observed means.				
*. The mean difference is significant at the .05 level.				

Three months post-fire indicates that cactus motte cover had decreased by 93.34% in treatments experiencing a combination of prescribed summer fire and herbivory (Table 10, Fig. A-4). The mottes that had access by large mammalian herbivores and received either prescribed winter burn compartment fires and a winter landscape fire had decreases of 73.98% and 40.89% in cactus motte cover, respectively.

In comparison, fire treatments that were combined with no herbivory by large mammals showed a decrease of 34.70% for the prescribed summer burn compartment fire treatment, a 24.14% decrease for the prescribed winter burn compartment fire treatment and only a 3.98% decrease for the winter landscape burn treatment. Unburned treatments with and without herbivory experienced an increase in cactus motte cover area. Mottes that were accessible to herbivores experienced an increase of 43.47%, while mottes with no herbivory had an increase of 44.28% (Table 10, Fig. 8). Statistical analysis of cactus motte cover nine months post-fire revealed a marginally non-significant interaction of fire and herbivory treatments ($p = 0.106$, Table 11), but revealed strong visual trends similar to the patterns observed for the three-month post-fire data (Table 12).

Table 10. Descriptive statistics 9 months post-fire treatment. Means and standard deviations of cactus motte cover in response to fire and herbivory treatments at nine months post-fire.

Descriptive Statistics 9 Months Post-Fire Treatment				
Dependent Variable: 9 Months Post-Fire Treatment				
Prescribed Fire Treatment	Herbivory Treatment	Mean	Std. Deviation	N
Summer Burn	Open	93.3480	6.41309	5
	Enclosed	34.7060	33.26506	5
Winter Burn	Open	73.9860	13.56558	5
	Enclosed	24.1520	10.88849	5
Winter Lanscape Burn	Open	40.8900	24.51437	10
	Enclosed	3.9810	15.57830	10
Control	Open	-43.4780	64.35486	10
	Enclosed	-44.2880	33.74444	10

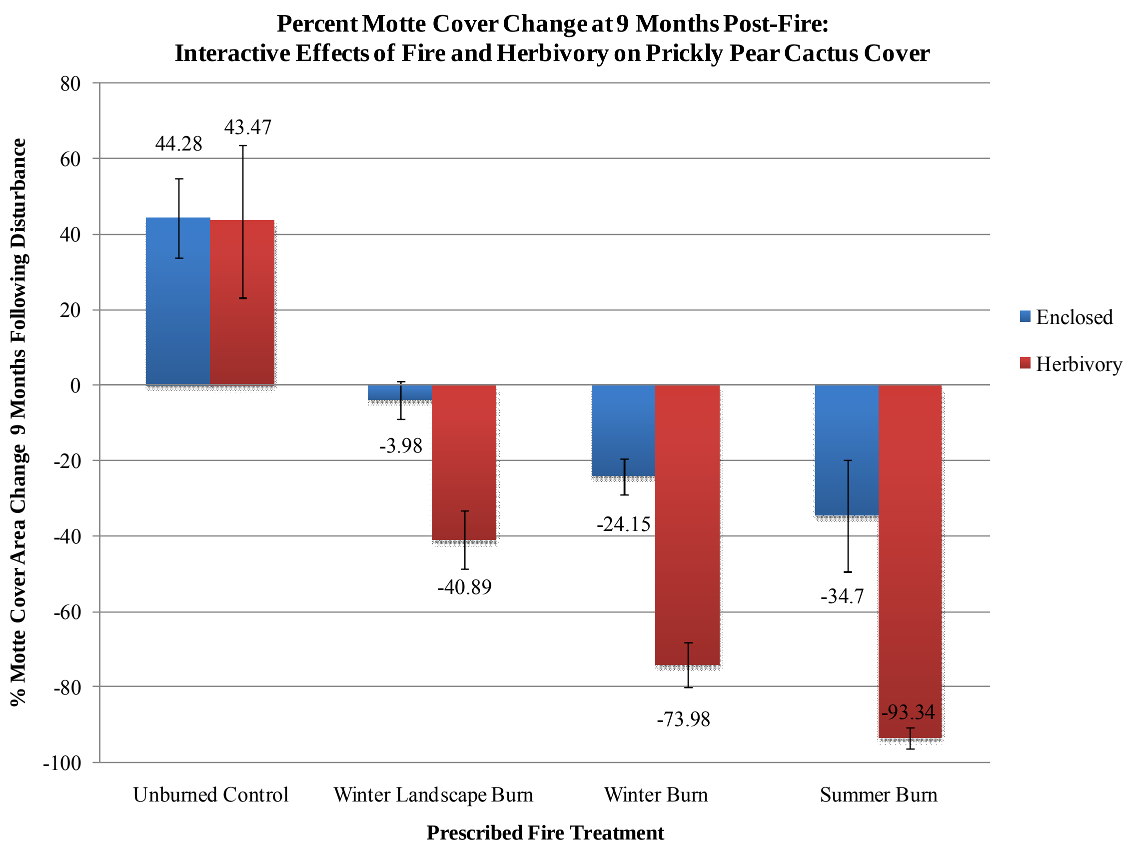

Figure 6. Percent motte cover change at 9 months post-fire. Mean (±1SE) percent motte cover change for prescribed fire and herbivory treatments at nine months post-fire treatment.

Table 11. ANOVA for cactus motte cover in 9 months post-fire. ANOVA for cactus motte cover in response to fire and herbivory treatments at nine months post-fire treatment (significance level determined at α=0.05).

ANOVA for Cactus Motte Cover in 9 Months Post-Fire					
Tests of Between-Subjects Effects					
Dependent Variable: 9 Months Post-Treatment					
Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Prescribed Fire Treatment	105,439.988	3	35,146.663	30.002	0.000
Herbivory Treatment	17,810.815	1	17,810.815	15.204	0.000
Prescribed Fire Treatment * Herbivory Treatment	7,526.948	3	2,508.983	2.142	**0.106**
Error	60,915.954	52	1,171.461		
Total	196,190.008	60			
Corrected Total	187,976.373	59			
a. R Squared = .676 (Adjusted R Squared = .632)					

Table 12. Fisher's LSD comparison of treatments 9 months post-fire. Fisher's LSD means contrasts of cactus motte cover for fire and wildlife herbivory treatments through a pair-wise comparison at nine months post-fire treatment.

Fisher's LSD Comparison of Treatments 9 Months Post-Fire				
Dependent Variable: 9 Months Post-Treatment				
(I) Treatment	(J) Treatment	Mean Difference (I-J)	Std. Error	Sig.
Summer Burn Enclosure	Summer Burn Herbivory	-58.6420(*)	21.64681	0.009
	Winter Burn Enclosure	10.5540	21.64681	**0.628**
	Winter Landscape Burn Enclosure	30.7250	18.74669	0.107
	Control Enclosure	78.9940(*)	18.74669	0.000
Summer Burn Herbivory	Summer Burn Enclosure	58.6420(*)	21.64681	0.009
	Winter Burn Herbivory	19.3620	21.64681	**0.375**
	Winter Landscape Burn Herbivory	52.4580(*)	18.74669	0.007
	Control Herbivory	136.8260(*)	18.74669	0.000
Winter Burn Enclosure	Summer Burn Enclosure	-10.5540	21.64681	**0.628**
	Winter Burn Herbivory	-49.8340(*)	21.64681	0.025
	Winter Landscape Burn Enclosure	20.1710	18.74669	**0.287**
	Control Enclosure	68.4400(*)	18.74669	0.001
Winter Burn Herbivory	Summer Burn Herbivory	-19.3620	21.64681	**0.375**
	Winter Burn Enclosure	49.8340(*)	21.64681	0.025
	Winter Landscape Burn Herbivory	33.0960	18.74669	0.083
	Control Herbivory	117.4640(*)	18.74669	0.000
Winter LandscapeBurn Enclosure	Summer Burn Enclosure	-30.7250	18.74669	0.107
	Winter Burn Enclosure	-20.1710	18.74669	**0.287**
	Winter Landscape Burn Herbivory	-36.9090(*)	15.30660	0.019
	Control Enclosure	48.2690(*)	15.30660	0.003
Winter Landscape Burn Herbivory	Summer Burn Herbivory	-52.4580(*)	18.74669	0.007
	Winter Burn Herbivory	-33.0960	18.74669	0.083
	Winter Landscape Burn Enclosure	36.9090(*)	15.30660	0.019
	Control Herbivory	84.3680(*)	15.30660	0.000
Control Enclosure	Summer Burn Enclosure	-78.9940(*)	18.74669	0.000
	Winter Burn Enclosure	-68.4400(*)	18.74669	0.001
	Winter Landscape Burn Enclosure	-48.2690(*)	15.30660	0.003
	Control Herbivory	-0.8100	15.30660	**0.958**
Control Herbivory	Summer Burn Herbivory	-136.8260(*)	18.74669	0.000
	Winter Burn Herbivory	-117.4640(*)	18.74669	0.000
	Winter Landscape Burn Herbivory	-84.3680(*)	15.30660	0.000
	Control Enclosure	0.8100	15.30660	**0.958**
Based on observed means.				
*. The mean difference is significant at the .05 level.				

At 12 months from the beginning of the study (January 2008-2009), an analysis of fire and herbivory effects indicate that the largest decrease in cactus motte cover (80.72%) occurred in treatements experiencing prescribed summer burn compartment fires and large mammalian herbivory (Table 13). Cactus mottes that were accessible to large mammalian herbivores and received prescribed winter burn compartment fires or a winter landscape saw a cactus motte area cover decrease of 73.98% and 40.89%, respectively (Table 13, Fig. A-5). In comparison, fire treatments with herbivore exclosures showed a decrease of 6.73% for the prescribed summer burn compartment fire treatment, a 24.15% decrease for the prescribed winter burn compartment fire treatment and a 3.98% decrease for the winter landscape burn treatment (Table 13). Unburned treatments with and without herbivory experienced an increase in cactus motte cover area. Mottes that were accessible to herbivores experienced an increase of 6.197%, while mottes with no herbivory had an increase of 11.79% (Fig. 7, Table 13). Statistical analysis of cactus motte cover at 12 months from the beginning of the study revealed a significant interaction of fire and herbivory treatments ($p = 0.002$, Table 14 and 15).

Table 13. Descriptive statistics 12 months from beginning of study. Means and standard deviations of cactus motte cover in response to fire and herbivory treatments at 12 months from the beginning of the study.

Descriptive Statistics 12 Months from Beginning of Study				
Dependent Variable: 12 Months from Beginning of Study				
Prescribed Fire Treatment	Herbivory Treatment	Mean	Std. Deviation	N
Summer Burn	Open	80.7200	10.53074	5
	Enclosed	6.7300	14.96631	5
Winter Burn	Open	73.9860	13.56558	5
	Enclosed	24.1520	10.88849	5
Winter Lanscape Burn	Open	40.8900	24.51437	10
	Enclosed	3.9810	15.57830	10
Control	Open	-6.1930	39.38281	10
	Enclosed	-11.7900	15.43812	10

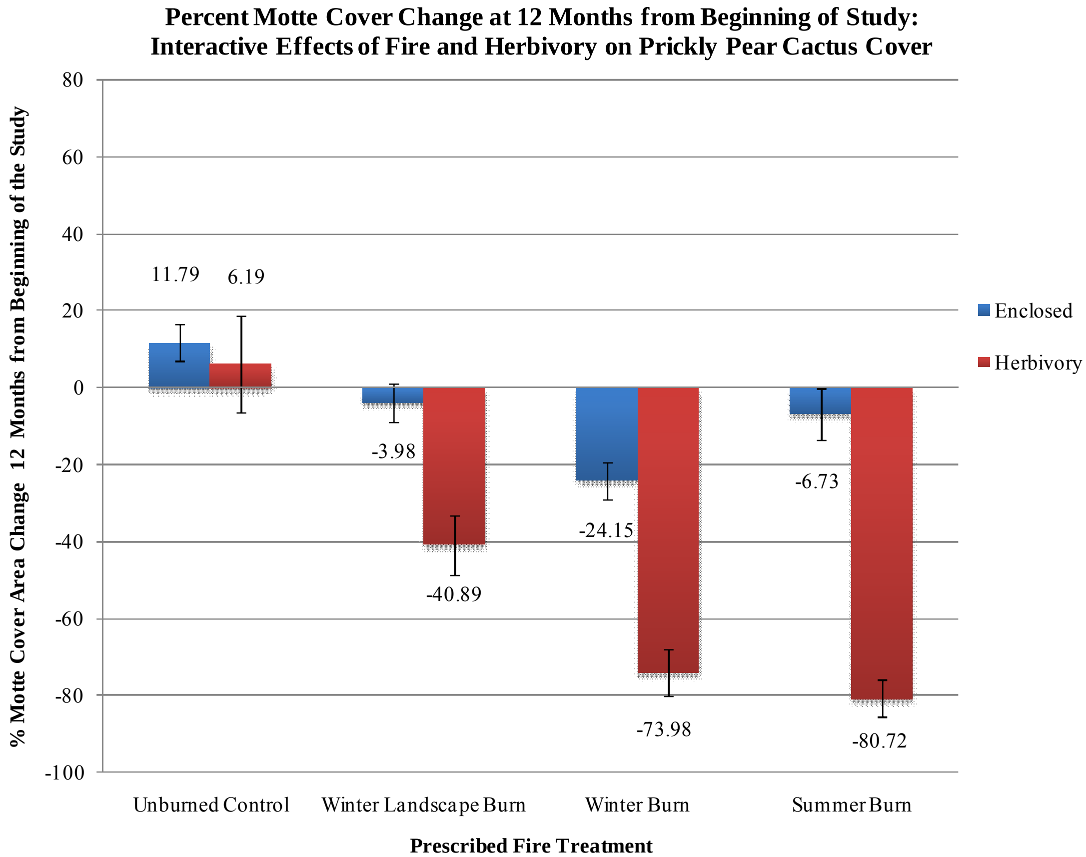

Figure 7. Percent motte cover change at 12 months from beginning of study. Mean (±1SE) percent motte cover change for prescribed fire and herbivory treatments at 12 months from the beginning of the study.

Table 14. ANOVA for cactus motte cover in 12 months from beginning of study. ANOVA for cactus motte cover in response to fire and herbivory treatments at 12 months from the beginning of the study (significance level determined at α=0.05).

ANOVA for Cactus Motte Cover in 12 Months from Beginning of Study					
Tests of Between-Subjects Effects					
Dependent Variable: 12 Months from Beginning of Study					
Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Prescribed Fire Treatment	31,007.430	3	10,335.810	20.477	0.000
Herbivory Treatment	23,054.724	1	23,054.724	45.676	0.000
Prescribed Fire Treatment * Herbivory Treatment	8,691.008	3	2,897.003	5.740	**0.002**
Error	26,246.698	52	504.744		
Total	107,989.969	60			
Corrected Total	84,117.001	59			
a. R Squared = .688 (Adjusted R Squared = .646)					

Table 15. Fisher's LSD comparison of treatments 12 months from beginning of study. Fisher's LSD means contrasts of cactus motte cover for fire and wildlife herbivory treatments through a pair-wise comparison at 12 months from the beginning of the study.

Fisher's LSD Comparison of Treatments 12 Months from Beginning of Study				
Dependent Variable: 12 Months from Beginning of Study				
(I) Treatment	(J) Treatment	Mean Difference (I-J)	Std. Error	Sig.
Summer Burn Enclosure	Summer Burn Herbivory	-73.9900(*)	14.20907	0.000
	Winter Burn Enclosure	-17.4220	14.20907	**0.226**
	Winter Landscape Burn Enclosure	2.7490	12.30542	**0.824**
	Control Enclosure	18.5200	12.30542	**0.138**
Summer Burn Herbivory	Summer Burn Enclosure	73.9900(*)	14.20907	0.000
	Winter Burn Herbivory	6.7340	14.20907	**0.638**
	Winter Landscape Burn Herbivory	39.8300(*)	12.30542	0.002
	Control Herbivory	86.9130(*)	12.30542	0.000
Winter Burn Enclosure	Summer Burn Enclosure	17.4220	14.20907	**0.226**
	Winter Burn Herbivory	-49.8340(*)	14.20907	0.001
	Winter Landscape Burn Enclosure	20.1710	12.30542	0.107
	Control Enclosure	35.9420(*)	12.30542	0.005
Winter Burn Herbivory	Summer Burn Herbivory	-6.7340	14.20907	**0.638**
	Winter Burn Enclosure	49.8340(*)	14.20907	0.001
	Winter Landscape Burn Herbivory	33.0960(*)	12.30542	0.010
	Control Herbivory	80.1790(*)	12.30542	0.000
Winter Landscape Burn Enclosure	Summer Burn Enclosure	-2.7490	12.30542	**0.824**
	Winter Burn Enclosure	-20.1710	12.30542	**0.107**
	Winter Landscape Burn Herbivory	-36.9090(*)	10.04733	0.001
	Control Enclosure	15.7710	10.04733	**0.123**
Winter Landscape Burn Herbivory	Summer Burn Herbivory	-39.8300(*)	12.30542	0.002
	Winter Burn Herbivory	-33.0960(*)	12.30542	0.010
	Winter Landscape Burn Enclosure	36.9090(*)	10.04733	0.001
	Control Herbivory	47.0830(*)	10.04733	0.000
Control Enclosure	Summer Burn Enclosure	-18.5200	12.30542	**0.138**
	Winter Burn Enclosure	-35.9420(*)	12.30542	0.005
	Winter Landscape Burn Enclosure	-15.7710	10.04733	**0.123**
	Control Herbivory	-5.5970	10.04733	**0.580**
Control Herbivory	Summer Burn Herbivory	-86.9130(*)	12.30542	0.000
	Winter Burn Herbivory	-80.1790(*)	12.30542	0.000
	Winter Landscape Burn Herbivory	-47.0830(*)	10.04733	0.000
	Control Enclosure	5.5970	10.04733	**0.580**
Based on observed means.				
*. The mean difference is significant at the .05 level.				

At 18 months from the beginning of the study (January 2008- July 2009), an analysis of fire and herbivory effects indicate that the largest decrease in cactus motte cover (91.53%) occurred in treatments experiencing prescribed summer burn compartment fires and large mammalian (Table 16). Cactus mottes that were accessible to large mammalian herbivores and received prescribed winter burn compartment fires or a winter landscape saw a cactus motte area cover decrease of 80.25% and 64.01%, respectively (Table 16). In comparison, fire treatments with herbivore exclosures showed a decrease of 25.82% for the prescribed summer burn compartment fire treatment, a 30.29% decrease for the prescribed winter burn compartment fire treatment and a 14.91% decrease for the winter landscape burn treatment (Table 16). Unburned treatments with and without herbivory experienced an increase in cactus motte cover area. Mottes that were accessible to herbivores experienced an increase of 43.47%, while mottes with no herbivory had an increase of 44.28% (Fig. 8, Table 16). Statistical analysis of cactus motte cover at 12 months from the beginning of the study revealed a significant interaction of fire and herbivory treatments ($p = 0.053$, Table 17 and 18).

Table 16. Descriptive statistics 18 months from beginning of study. Means and standard deviations of cactus motte cover in response to fire and herbivory treatments at 18 months from the beginning of the study.

Descriptive Statistics 18 Months from Beginning of Study				
Dependent Variable: 18 Months from Beginning of Study				
Prescribed Fire Treatment	Herbivory Treatment	Mean	Std. Deviation	N
Summer Burn	Open	91.5320	7.73716	5
	Enclosed	25.8200	34.82130	5
Winter Burn	Open	80.2520	22.72679	5
	Enclosed	30.2900	17.67113	5
Winter Lanscape Burn	Open	64.0160	10.44743	10
	Enclosed	14.9180	23.39450	10
Control	Open	-43.4780	64.35486	10
	Enclosed	-44.2880	33.74444	10

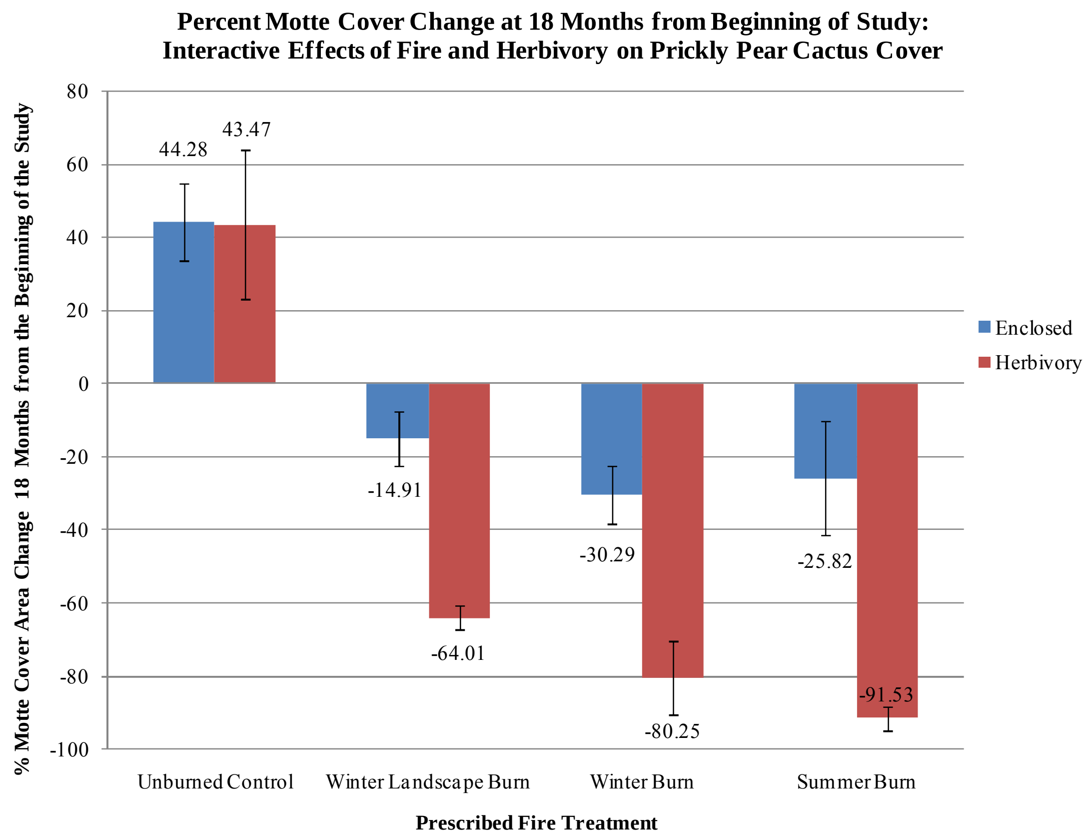

Figure 8. Percent motte cover change at 18 months from beginning of study. Mean (±1SE) percent motte cover change for prescribed fire and herbivory treatments at 18 months from the beginning of the study.

Table 17. ANOVA for cactus motte cover in 18 months from beginning of study. ANOVA for cactus motte cover in response to fire and herbivory treatments at 18 months from the beginning of the study (significance level determined at α=0.05).

ANOVA for Cactus Motte Cover in 18 Months from Beginning of Study					
Tests of Between-Subjects Effects					
Dependent Variable: 18 Months from Beginning of Study					
Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Prescribed Fire Treatment	116,229.528	3	38,743.176	32.581	0.000
Herbivory Treatment	22,847.832	1	22,847.832	19.214	0.000
Prescribed Fire Treatment * Herbivory Treatment	9,743.711	3	3,247.904	2.731	**0.053**
Error	61,834.823	52	1,189.131		
Total	225,571.643	60			
Corrected Total	207,156.370	59			
a. R Squared = .702 (Adjusted R Squared = .661)					

Table 18. Fisher's LSD comparison of treatments 18 months from beginning of study. Fisher's LSD means contrasts of cactus motte cover for fire and wildlife herbivory treatments through a pair-wise comparison at 18 months from the beginning of the study.

Fisher's LSD Comparison of Treatments 18 Months from Beginning of Study				
Dependent Variable: 18 Months from Beginning of Study				
(I) Treatment	(J) Treatment	Mean Difference (I-J)	Std. Error	Sig.
Summer Burn Enclosed	Summer Burn Herbivory	-65.7120(*)	21.80946	0.004
	Winter Burn Enclosed	-4.4700	21.80946	**0.838**
	Winter Landscape Burn Enclosed	10.9020	18.88755	**0.566**
	Control Enclosed	70.1080(*)	18.88755	0.001
Summer Burn Herbivory	Summer Burn Enclosed	65.7120(*)	21.80946	0.004
	Winter Burn Herbivory	11.2800	21.80946	**0.607**
	Winter Landscape Burn Herbivory	27.5160	18.88755	**0.151**
	Control Herbivory	135.0100(*)	18.88755	0.000
Winter Burn Enclosed	Summer Burn Enclosed	4.4700	21.80946	**0.838**
	Winter Burn Herbivory	-49.9620(*)	21.80946	0.026
	Winter Landscape Burn Enclosed	15.3720	18.88755	**0.419**
	Control Enclosed	74.5780(*)	18.88755	0.000
Winter Burn Herbivory	Summer Burn Herbivory	-11.2800	21.80946	**0.607**
	Winter Burn Enclosed	49.9620(*)	21.80946	0.026
	Winter Landscape Burn Herbivory	16.2360	18.88755	**0.394**
	Control Herbivory	123.7300(*)	18.88755	0.000
Winter Landscape Burn Enclosed	Summer Burn Enclosed	-10.9020	18.88755	**0.566**
	Winter Burn Enclosed	-15.3720	18.88755	**0.419**
	Winter Landscape Burn Herbivory	-49.0980(*)	15.42162	0.002
	Control Enclosed	59.2060(*)	15.42162	0.000
Winter Landscape Burn Herbivory	Summer Burn Herbivory	-27.5160	18.88755	**0.151**
	Winter Burn Herbivory	-16.2360	18.88755	**0.394**
	Winter Landscape Burn Enclosed	49.0980(*)	15.42162	0.002
	Control Herbivory	107.4940(*)	15.42162	0.000
Control Enclosed	Summer Burn Enclosed	-70.1080(*)	18.88755	0.001
	Winter Burn Enclosed	-74.5780(*)	18.88755	0.000
	Winter Landscape Burn Enclosed	-59.2060(*)	15.42162	0.000
	Control Herbivory	-0.8100	15.42162	**0.958**
Control Herbivory	Summer Burn Herbivory	-135.0100(*)	18.88755	0.000
	Winter Burn Herbivory	-123.7300(*)	18.88755	0.000
	Winter Landscape Burn Herbivory	-107.4940(*)	15.42162	0.000
	Control Enclosed	0.8100	15.42162	**0.958**
Based on observed means.				
*. The mean difference is significant at the .05 level.				

Cactus Motte Mortality

After 18 months from the start of the study we found that unburned mottes had a 100% survival rate, regardless of the presence of herbivores (Table 19). Three out of twenty cactus mottes in the landscape burn treatment (two in herbivore exclosures) had no live visible growth after 18 months and appeared to have died (Table 19). Half of all the prescribed summer fires conducted in the burn compartment experienced complete mortality and had no live tissue visible after 18 months from the start of the study (Table 19). Interestingly, all of these dead mottes were located in fenced exclosures and, thereby, inaccessible to wildlife herbivores. Overall, throughout the duration of the study, a total nine mottes out of the sixty present experienced visible mortality (Table 19).

Table 19. Cactus motte mortality at 18 months from the beginning of the study. Cactus motte mortality (no visible live tissue) in response to the experimental fire and herbivory treatments at the conclusion of the 18 month study.

Cactus Motte Mortality at 18 Months from the Beginning of the Study	
Treatment	**% Mortality**
Unburned Control - Enclosed	0% (0/10)
Unburned Control - Open to Large Mamaliam Herbivores	0% (0/10)
Winter LandscapeBurn - Enclosed	20% (2/10)
Winter LandscapeBurn - Open to Large Mamaliam Herbivores	10% (1/10)
WinterBurn - Enclosed	0% (0/5)
WinterBurn - Open to Large Mamaliam Herbivores	20% (1/5)
SummerBurn - Enclosed	**100% (5/5)**
SummerBurn - Open to Large Mamaliam Herbivores	0% (0/5)

Sub-Experiment: Seasonal Moisture Variation

Analysis of the cladode tissue moisture content showed a significant interaction between harvesting season and the cladodes relative location within the cactus motte ($p = 0.016$, Table 20). There was a marked trend for tissue moisture content to decrease from the base cladodes to the distant cladodes and the end of cactus chains (Table 21).

The lowest amount of moisture was found in cladodes furthest away from the base of the cactus motte (location 1, see Fig. 3). Cladodes in the outer-most portion of the motte had an average moisture content of 53.46 g and 84.10 g, in the winter and summer, respectively (Fig. 9). Accordingly, cladodes with the highest moisture content were those at the base (location 4, see Fig. 3). Average moisture content of cladodes harvested in the winter and summer were 111.88 g and 189.45 g, respectively (Fig. 9).

Table 20. ANOVA of the interaction effect between season & cladode location. The analysis of variance demonstrated that there was an interaction effect between season and the cladodes location within the cactus motte.

ANOVA of the Interaction Effect between Season & Cladode Location					
Tests of Between-Subjects Effects					
Dependent Variable: Cladode Moisture Content					
Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Location	461,412.069	3	153,804.023	41.081	0.000
Season	389,433.248	1	389,433.248	104.018	0.000
Location * Season	39,019.589	3	13,006.530	3.474	**0.016**
Error	1,767,121.856	472	3,743.902		
Total	9,255,751.102	480			
Corrected Total	2,656,986.762	479			
a. R Squared = .335 (Adjusted R Squared = .325)					

Table 21. Fisher's LSD comparison of cladode moisture content. A comparison of the cladode moisture content along the plant cactus motte was determined through Fisher's LSD.

Fisher's LSD Comparison of Cladode Moisture Content				
Dependent Variable: Cladode Moisture Content				
(I) Location	(J) Location	Mean Difference (I-J)	Std. Error	Sig.
1.00	2.00	-44.4675(*)	7.89926	0.000
	3.00	-67.5240(*)	7.89926	0.000
	4.00	-81.8868(*)	7.89926	0.000
2.00	1.00	44.4675(*)	7.89926	0.000
	3.00	-23.0565(*)	7.89926	0.004
	4.00	-37.4193(*)	7.89926	0.000
3.00	1.00	67.5240(*)	7.89926	0.000
	2.00	23.0565(*)	7.89926	0.004
	4.00	-14.3628	7.89926	**0.070**
4.00	1.00	81.8868(*)	7.89926	0.000
	2.00	37.4193(*)	7.89926	0.000
	3.00	14.3628	7.89926	**0.070**
Based on observed means.				
*. The mean difference is significant at the .05 level.				

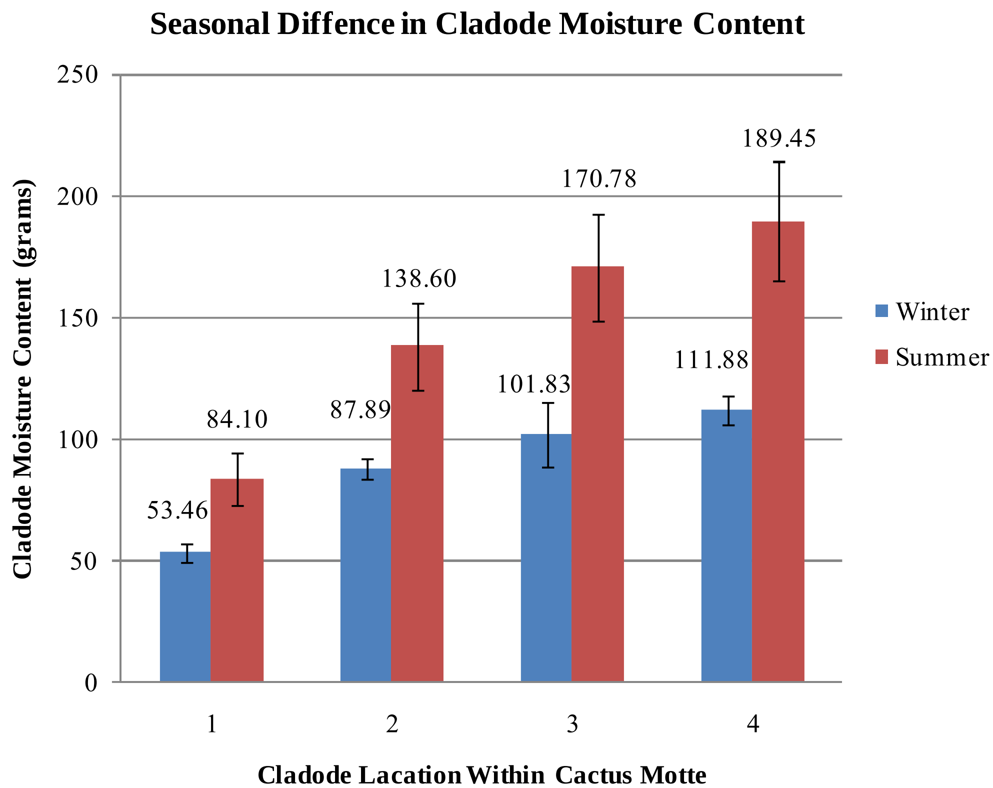

Figure 9. Seasonal difference in cladode moisture content. The amount of moisture increases as the cladode is positioned closer to the base.

Precipitation records from the research station for the last three years were analyzed and compared to the 30-year average precipitation (Figure 10). The summer of 2007, a few months prior to beginning this, study there was an abnormal amount of rainfall followed by a period of below average precipitation (Figure 11). However, it was only a one-time event because for the remaining duration of the study, the amount precipitation received in the area was below average (Figures 12 & 13).

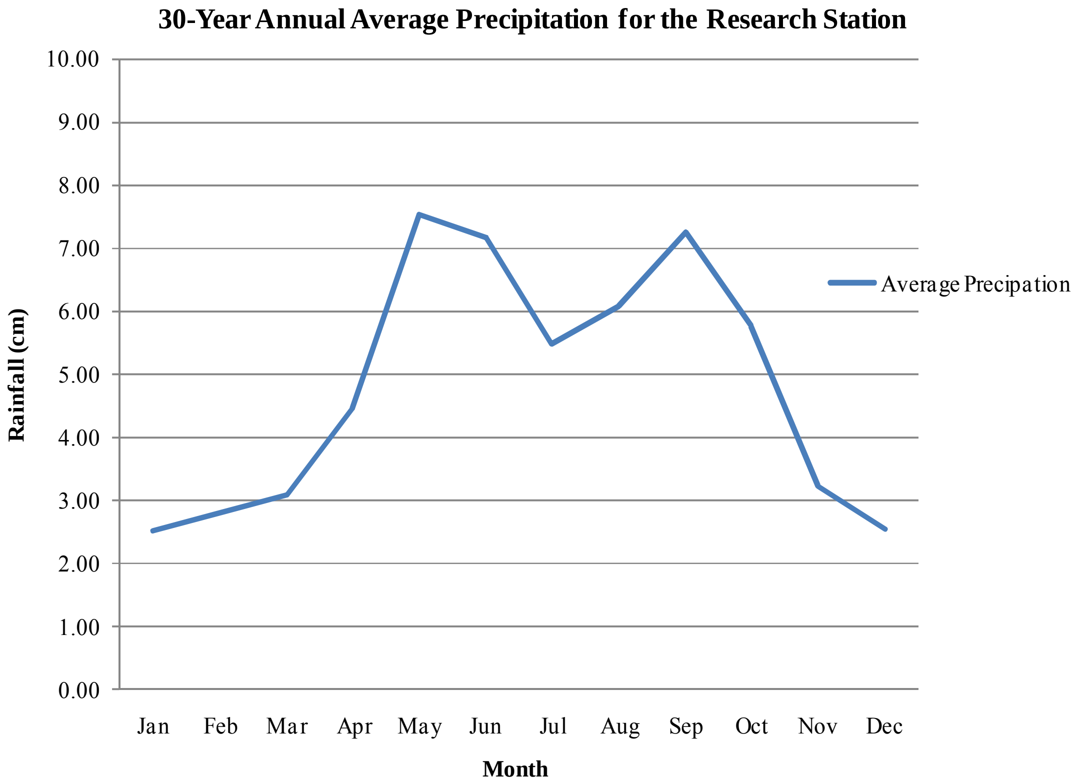

Figure 10. 30-year annual average precipitation for the research station. Depicts the bimodal annual distribution of precipitation experience at in the Western Edwards Plateau region, where there are peaks in rainfall in May and October.

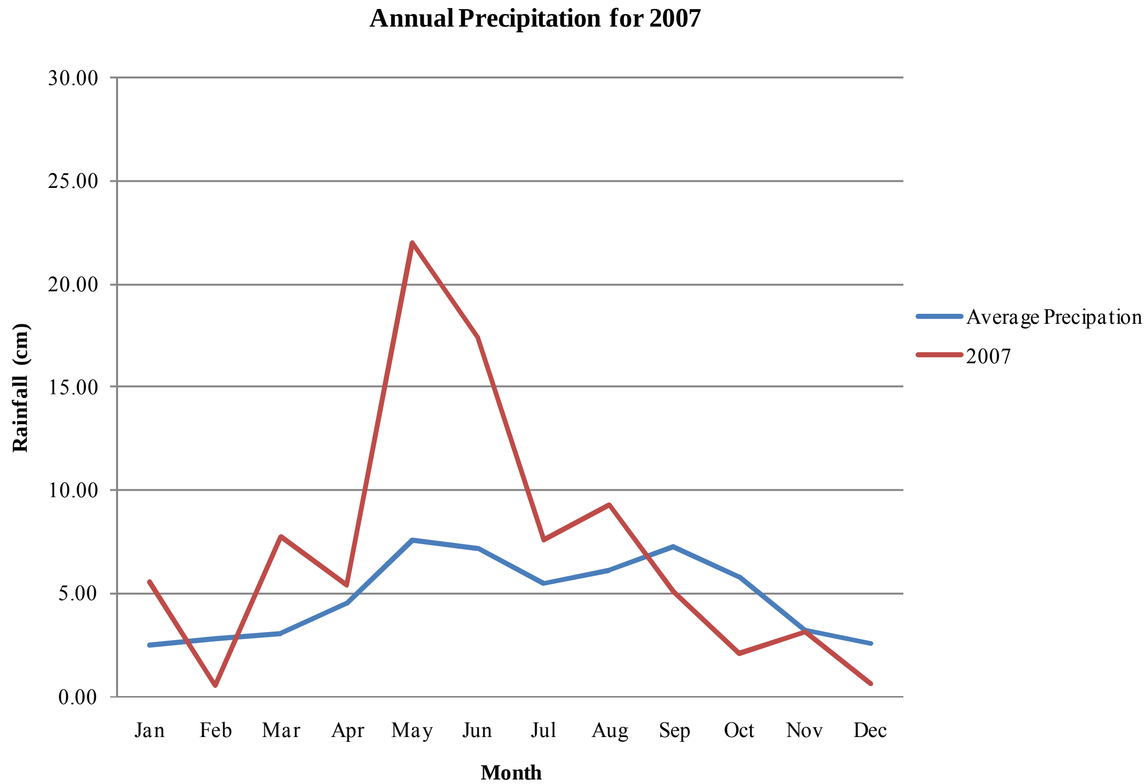

Figure 11. Annual precipitation for 2007. In 2007 the area received an abnormal amount of precipitation for the months of May, June and July.

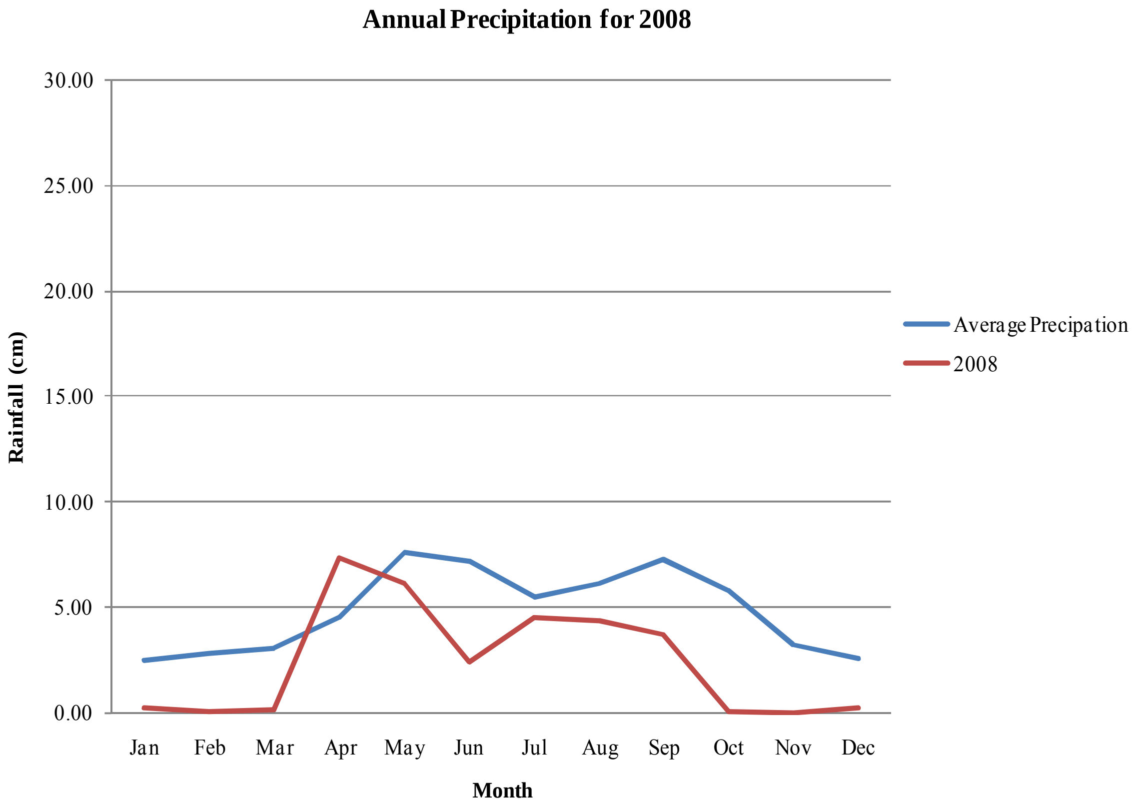

Figure 12. Annual precipitation for 2008. 2008 was the year the treatments for this study were conducted. The amount of rainfall was below average.

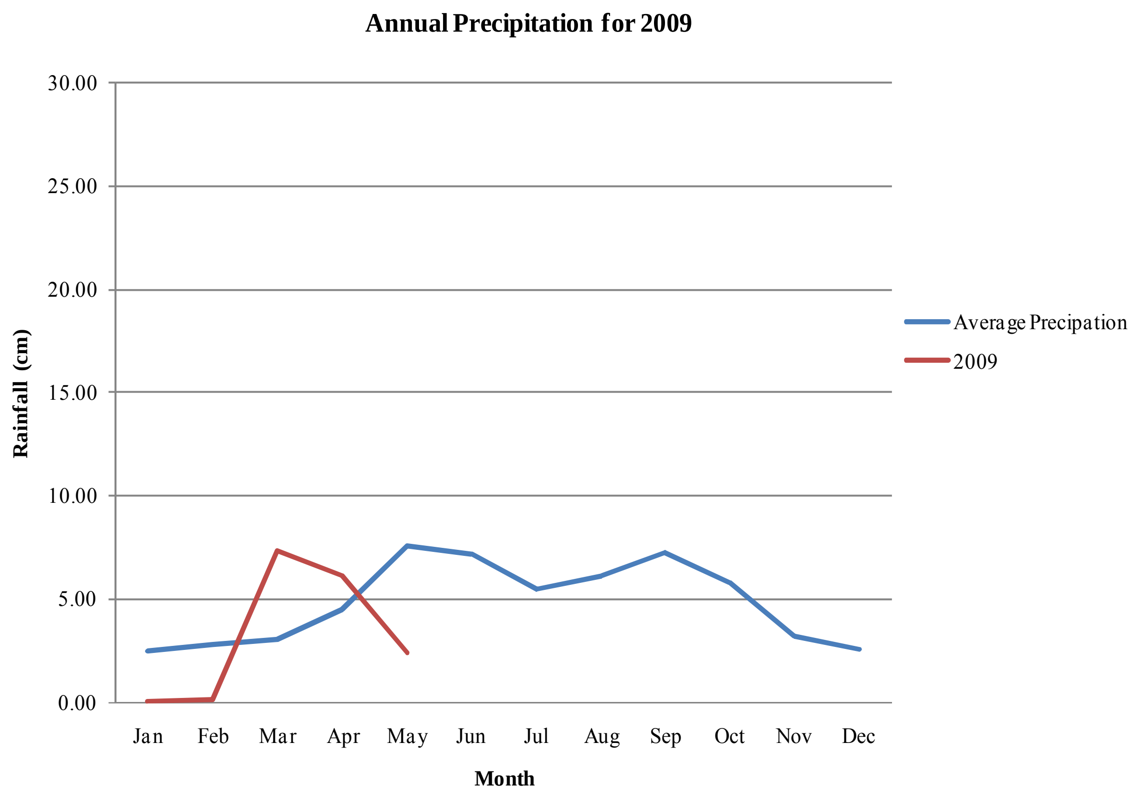

Figure 13. Annual precipitation for 2009. The drought experienced the months of January and February in the early part of 2009 is followed by an abnormal peak in precipitation in March.

On the two occasions the prescribed fire treatments were administered, there was no precipitation and the temperatures ranged from mid-50s to low-60s at pre-dawn, with higher temperatures being in the middle of the day of up to the low-90s (Table 23).

Table 22. Meteorological data for days corresponding to prescribed burns. Meteorological data extracted from the stations records; it shows the temperature and precipitation experienced the days of the prescribed fires.

Meteorological Data for Days Corresponding to Prescribed Burns			
Prescribed Burning Date	Low Temperature	High Temperature	Precipiation
Winter Burns: 15-Mar-2008	12.2^{o}C	32.8^{o}C	0 cm
Summer Burns: 3-Oct-2008	15.5^{o}C	33.3^{o}C	0 cm

CHAPTER VI

DISCUSSION

The results from this study are comparable to what has been observed in rangelands when *Opuntia* is burned during the summer. However, this investigation has demonstrated that herbivory by wildlife following fire results in significant additional reductions in *Opuntia* cacti cover and abundance. Previous studies using fire as a means to control *Opuntia* in Central Texas determined that summer fires could decrease *Opuntia* as much as 96% across a landscape (Taylor 2007). However, this previous study did not quantify the role of wildlife herbivory. An additional strength of our investigation is that we were able to maintain consistent fire intensities for both winter and summer seasons. This allowed us to directly assess the effect of prescribed burning on cactus growth and survival in a manner that was independent of seasonal and environmental influences on fire behavior. Consequently, our results showing greater decreases in cactus motte cover are directly attributable to the effects of fire and herbivory on variation in plant physiological and phenological status that occurs with different seasonal and environmental conditions. These results are not confounded by greater fire intensities being achieved during summer fires. Moreover, the large variability in cladode moisture content by season potentially explains these results. The higher cladode moisture content measured in *Opuntia* during the summer sampling period may have contributed to greater catastrophic effects of fire on individual pads (e.g., exploding cladodes) and greater physiological costs (e.g., losses of stored resources) to individual plants. As a result, this information on fire effects and plant physiological status should prove useful when designing future management strategies for controlling problematic prickly pear cactus invasions that are degrading Texas rangelands.

Manipulating Fire Temperature

A factor limiting the interpretation of past studies was inability to control fire intensity at different burning seasons. The difference in the intensity of a prescribed fire affects the future structure and function of the plant community (Hodgkinson 1991;Taylor 2007). Earlier studies on *Opuntia* have demonstrated that summer fires are more intense, and subsequently hotter, than winter fires. The higher temperature in combination with elevated ambient temperature and lower relative humidity causes greater mortality and leads to an overall greater reduction of *Opuntia* cacti in rangelands (Ansley and Castellano 2007). However, with the addition of dry herbaceous fuels in our study and the manipulation of the burn area within the burn compartment, we were able to control the maximum fire temperatures in both the summer and winter burns. This allowed us to remove the variability in fuel loads that typically occurs in prescribed landscape fires (Rowe 1983). In addition, it allowed us to minimize seasonal differences in fire intensity to clarify fires effect on different physiological conditions exhibited by *Opuntia* in different seasons. It also provided the opportunity to further understand if there are physiological and morphological differences within the cactus mottes during the winter and summer seasons that cause it to be more susceptible to subsequent wildlife herbivory and mortality (Hehman and Fulbright 1997;North and Nobel 1998).

Effects of Fire Season & Wildlife Herbivory on Reducing *Opuntia* Cacti Cover

Research on white-tailed deer, which make up a significant portion of the large mammalian herbivores in Central Texas, has found that in some regions of Texas *Opuntia* cacti tissue accounts for up to 61.1% of their diet, even when the cacti tissue is unburned (Bryant*, et al.* 1981;Everitt and Gonzalez 1979;Hehman and Fulbright 1997). While there is a tremendous scientific literature on the interactive effects of fire and herbivory (Anderson*, et al.* 2007;van Langevelde*, et al.* 2003) and white-tail deer effects on vegetation have been extensively studied (Russell*, et al.* 2001) little is known regarding the effects of fire and deer herbivory on *Opuntia* cacti. Our results demonstrate that while fire significantly reduces cactus motte cover, it is mottes that are exposed to both the effects of fire and wildlife herbivory that experienced the largest cover decreases. At the conclusion of this study, burned mottes not protected by herbivore exclosures experienced a 91.53% and 80.25% decrease when they received a prescribed summer and winter fire within the burn compartment, respectively, and a 64.01% decrease when they underwent a prescribed winter fire at the landscape level. Interestingly, the effects of herbivory in the absence of fire were negligible and the cover of all unburned cactus mottes increased markedly throughout the study.

Our findings suggest that the use of fire alone is not sufficiently effective to rapidly reduce *Opuntia* cover. Instead, the interaction of fire with wildlife herbivory is synergistically responsible for reducing cactus cover. The fire treatments where mottes were protected from wildlife herbivores experienced a fraction of the reduction in *Opuntia* cover. The motte area cover decreased by 25.82%, 30.29%, and 14.91% for the prescribed summer and winter fire within the burn compartment and the winter fire at the landscape level, correspondingly. These data support our prediction that wildlife herbivory following prescribed fire, particularly summer fires, is higher in burned mottes and contributes to cacti suppression.

The results from this study also suggest that if left unmanaged *Opuntia* can aggressively expand across the landscape. A significant increase in the size and cover of *Opuntia* mottes occurred if the fire treatments were not applied. For example, the control treatments showed an overall 44.48% and 43.47% increase in cover for the no herbivory and herbivory treatments, respectively. For the 18 month duration of this research those mottes left undisturbed increased and expanded to what we presume are comparable expansion rates for mottes across similar Texas rangelands. This confirms the importance of historical disturbances like fire and explains the recent plant community shifts in Central Texas toward an increase in woody and succulents species (Van Auken 2000).

It could be argued that fires in the burn compartment were an atypical method to conduct a prescribed fire, however, our findings suggest otherwise. When we compare the percent *Opuntia* cover reduced after the fire treatments for the winter landscape fire and the winter fire within burn compartment, at three months post-fire treatment, the two winter fire applications were significantly different. However, by the end of this 18-

month study they were no longer significantly different. The method of applying fire was different, but the outcome this disturbance was controlled by the same environmental and ecological factors.

Effects of Fire Season & Wildlife Herbivory on *Opuntia* Cacti Mortality

Although post-fire wildlife herbivory decreased cactus motte cover, it did not correspondingly increase motte mortality. An unexpected result of our study showed that the highest level of mortality was in mottes that received a summer fire treatment and were protected from herbivores. Our data show that summer burned mottes inside herbivore exclosures experienced 100% mortality, whereas, the summer burned mottes that were exposed to herbivory only had zero percent mortality. This was surprising given the general observation in our study that cactus motte cover decreased by greater percentages when both burned and subjected to herbivory. Recall that after 18 months from the beginning of the study we observed mottes receiving summer fire with wildlife herbivory experience a reduction motte area of reduction of 91.51% while similarly burned mottes without wildlife herbivory decreased in cover only 25.82%. Even though there was a significantly greater reduction in cover for the summer fire treatment with herbivory this did not translate to higher rates of motte mortality. These results were not expected, particularly given past studies on *Opuntia* cacti showing 80-100% mortality for all plants experiencing summer fire (Ansley and Castellano 2007). It should be noted however that this study did not experimentally isolate the effects of fire and herbivory.

Field observations of greater survival in summer burned mottes exposed to herbivores suggests that it was mostly new plant tissue growth that accounted for live status of the cactus motte. It is possible that disturbance caused by animal activities in burned mottes may have triggered establishment of new plant tissue or created establishment sites for the germination of new cacti. The combination of the fire and herbivory disturbance might be producing the specific growth requirements for new cladode propagules to sprout within the animal disturbed mottes (Grubb 1977). Research examining the effect of grazing on seedling establishment concluded that disturbance caused by grazing creates safe-sites where new plants can establish, it appears likely that a similar phenomena occurred within our mottes (Oesterheld and Sala 1990).

Finally, it should be noted that after 18 months the unburned mottes had a 100% survival rate, regardless of the presence of herbivores. All of the other fire treatments experience some level of mortality, but unburned mottes exhibited both high survival and rapid cover expansion.

Seasonal Variability in Tissue Moisture Content of Cactus Mottes

It was determined that during the summer and winter fire treatments the cladode moisture content was significantly higher for samples collected in the summer. Within the mottes, the moisture content in cladodes increased the closer they were to the base of the plant. The incremental gradient is likely an adaptation to arid environments where water is kept closer to the base where the soil resources are more readily available (North and Nobel 1994;North and Nobel 1998).

Variability in the amount of precipitation may be the cause for the marked seasonal differences in tissue moisture. An assessment of the precipitation data for the area revealed that there was a period of prolonged drought three months prior to the winter fires. A drought period can affect the thermo-tolerance and physiological responses by the *Opuntia* mottes to the distinct fire treatments and subsequent herbivory disturbance, as well as its response to changes in the tissue lethal threshold (Kozlowski 2002). Overall the area only received 0.89 cm of rainfall for the months of December, January and February. This was not the case prior to the execution of the summer burns, when the site experienced precipitation comparable to the historic patterns and quantities. Environmental conditions changed again four months following the summer burns when the research site experienced an extreme drought. For an extended period of time the station recorded traces of rainfall that only accounted for a total of 0.39 cm. A drought immediately following a major disturbance like prescribed fire can affect the immediate and long-term response of the *Opuntia* cacti mottes and its surrounding plant community. The drought period that followed the summer fires could have potentially led to an increase in wildlife herbivory pressure as the scarcity of other foraging resources increased by the subsequent limited plant productivity (Everitt and Gonzalez 1979). Additionally, the higher cladode moisture content during the summer may potentially explain the higher mortality levels and greater motte cover reduction observed for summer fires. It is possible that fully hydrated cladodes results in greater catastrophic effects of fire (e.g., exploding cladodes were frequently observed) and greater physiological costs (e.g., higher losses of aboveground stored resources and water) to individual plants. Future studies should observe the seasonal effects of fire on cactus mottes while experimentally manipulating water availability across seasons.

CHAPTER VII

CONCLUSION

Overall, this study suggest that herbivory by large mammalian wildlife on recently burned *Opuntia* cactus mottes can be a viable solution for the reduction and management of problematic cactus invasions within Texas rangelands. It is important to note that if *Opuntia* encroachment is left unaddressed the cover by cactus mottes will likely continue to significantly increase across the landscape, thereby, leading to further ecosystem degradation. In the absence of fire cactus motte cover expanded an average of 44% in 18 months. This is a significant increase over a short period of time. It is
for Cactus Motte Cover in 9 Months Post-Fire. ANOVA for cactus motte cover in
onse to fire and herbivory treatments at nine months post-fire (significance level

Our results clearly demonstrate that the combination of fire and wildlife herbivory significantly reduces *Opuntia* cactus cover. Despite the artificial conditions established by our experimental design, we were able to empirically demonstrate that prescribed fire decreases prickly pear cactus cover. Moreover, this decrease is further exacerbated by the effects of large mammalian herbivores consuming and/or disturbing recently burned mottes. In the absence of fire, both mottes with and without herbivore exclosures increased in size.

Studies examining the effects of fire in different seasons are often confounded by increased fire intensities during hotter, drier periods and changing plant physiological and phenological status with seasonal and environmental conditions. By maintaining fire intensity in both the winter and summer seasons, we were able to examine the role of fire on cactus growth and survival in a manner that is independent of seasonal effects on fire behavior and solely examine plant responses to equivalent prescribed burns at distinctly different times of the year. Seasonal moisture variability within cactus mottes likely affected the mottes response to the prescribed fires. The plants thermo-tolerance may have been lower during the winter fires when the environmental conditions were more extreme.

The interactive effects of prescribed fire and wildlife herbivory causing significant reductions in prickly pear cactus cover were encouraging. If the abundance of *Opuntia* in degraded Texas rangelands can effectively be eliminated and/or significantly reduced, while concomitantly increasing the density of native grasses and forbs, the ecological integrity of the land will be increased and higher rates of wildlife and livestock production can be achieved. While there are realistically many possible treatment combinations that could potentially restore sites like this one, our study prescribed fire in areas of modest wildlife densities can be and inexpensive, yet highly effective control strategy Future studies should examine if this treatment is applicable at an extensive landscape scale from both an ecological and an economic/management perspective. Other critical areas of inquiry include the role variable weather conditions (e.g., drought) may play in fire and herbivory effects on cactus encroachment and whether the introduction of livestock to recently burned areas provides comparable to the results to those observed for wildlife herbivory.

REFERENCES

Aldridge V. R. and Texas Agricultural Experiment Station. (1983) *Short-term responses of pricklypear (Opuntia Lindheimeri) to foliar- and soil-applied picloram in the southern rolling plains.* Texas Agricultural Experiment Station, Texas A&M University System, College Station, TX.

Amos B. and Gehlbach F. R. (1988) *Edwards Plateau vegetation: Plant ecological studies in central Texas*. Baylor University Press, Waco, TX.

Anderson T. M., Ritchie M. E., Mayemba E., Eby S., Grace J. B. and McNaughton S. J. (2007) Forage nutritive quality in the Serengeti ecosystem: The roles of fire and herbivory. *American Naturalist* **170**, 343-357.

Ansley R. J. and Castellano M. J. (2007) Prickly pear cactus responses to summer and winter fires. *Rangeland Ecology & Management* **60**, 244-252.

Ansley R. J. and Jacoby P. W. (1998) *Manipulation of fire intensity to achieve mesquite management goals in north Texas.* Tall Timbers Fire Ecology Conference Proceedings, Tall Timbers Research Station, Tallahassee, FL.

Ansley R. J., Jones D. L., Tunnell T. R., Kramp B. A. and Jacoby P. W. (1998) Honey mesquite canopy responses to single winter fires: Relation to herbaceous fuel, weather and fire temperature. *International Journal of Wildland Fire* **8**, 241-252.

Archer S. (1995) Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland - reconstructing the past and predicting the future. *Ecoscience* **2**, 83-99.

Barcikowski W. and Nobel P. S. (1984) Water relations of cacti during desiccation: Distribution of water in tissues. *Botanical Gazette* **145**, 110-115.

Bond W. J. and Keeley J. E. (2005) Fire as a global 'herbivore': The ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* **20**, 387-394.

Briske D. D., Fuhlendor S. D. and Smeins E. E. (2005) State-and-transition models, thresholds, and rangeland health: A synthesis of ecological concepts and perspectives. *Rangeland Ecology & Management* **58**, 1-10.

Bryant F. C., Taylor C. A. and Merrill L. B. (1981) White-tailed deer diets from pastures in excellent and poor range condition. *Journal of Range Management* **34**, 193-200.

Bunting S. C., Wright H. A. and Leon F. N. (1980) Long-term effects of fire on cactus in the southern mixed prairie of Texas. *Journal of Range Management* **33**, 85-88.

Buxbaum F. (1950) *Morphology of cacti*. Abbey Garden Press, Pasadena, CA.

Cable D. R. (1967) Fire effects on semidesert grasses and shrubs. *Journal of Range Management* **20**, 170-176.

Castellano M. J. and Ansley R. J. (2007) Fire season and simulated grazing differentially affect the stability and drought resilience of a C-4 bunchgrass, C-3 bunchgrass and C-4 lawngrass. *Journal of Arid Environments* **69**, 375-384.

Chavez-Ramirez F., Wang X. G., Jones K., Hewitt D. and Felker P. (1997) Ecological characterization of *Opuntia* clones in South Texas: Implications for wildlife herbivory and frugivory. *Journal of the Professional Association for Cactus Development* **2**, 9-19.

Denevan W. M. (1992) The pristine myth - the landscape of the Americas in 1492. *Annals of the Association of American Geographers* **82**, 369-385.

Engle D. M., Stritzke J. F., Bidwell T. G. and Claypool P. L. (1993) Late-summer fire and follow-up herbicide treatments in tallgrass prairie. *Journal of Range Management* **46**, 542-547.

Everitt J. H. and Drawe D. L. (1974) Spring food habits of white-tailed deer in the South Texas Plains. *Journal of Range Management* **27**, 15-20.

Everitt J. H. and Gonzalez C. L. (1979) Botanical composition and nutrient content of fall and early winter diets of white-tailed deer in South Texas. *The Southwestern Naturalist* **24**, 297-310.

Everitt J. H., Gonzalez C. L., Scott G. and Dahl B. E. (1981) Seasonal food preferences of cattle on native range in the South Texas Plains. *Journal of Range Management* **34**, 384-388.

Fuhlendorf S. D., Briske D. D. and Smeins F. E. (2001) Herbaceous vegetation change in variable rangeland environments: The relative contribution of grazing and climatic variability. *Applied Vegetation Science* **4**, 177-188.

Gabriel W. J. and Loomis L. W. (2000) Soil Survey of Edwards and Real Counties, Texas. In: National Cooperative Soil Survey, Washington, DC.

Glantz M. H. (1977) *Desertification: Environmental degradation in and around arid lands*. Westview Press, Boulder, CO.

Grubb P. J. (1977) Maintenance of species-richness in plant communities: The importance of regeneration niche. *Biological Reviews of the Cambridge Philosophical Society* **52**, 107-145.

Guthery F. S., Shupe T. E., Bareiss L. J. and Russell C. E. (1987) Responses of selected plants to herbicide treatment of disturbed soil. *Wildlife Society Bulletin* **15**, 247-251.

Hanselka C. W. and Paschal J. C. (1991) Prickly pear cactus: A Texas rangeland enigma. *Rangelands* **13**, 109-111.

Hehman M. W. and Fulbright T. E. (1997) Use of warm-season food plots by white-tailed deer. *The Journal of Wildlife Management* **61**, 1108-1115.

Higgins V. (1946) *The study of cacti*. Blandford Press, London.

Hobbs R. J. and Huenneke L. F. (1992) Disturbance, diversity, and invasion: Implications for conservation. *Conservation Biology* **6**, 324-337.

Hodgkinson K. C. (1991) Shrub recruitment response to intensity and season of fire in a semiarid woodland. *Journal of Applied Ecology* **28**, 60-70.

Jacoby P. W., Ansley R. J. and Trevino B. A. (1992) An improved method for measuring temperatures during range fires. *Journal of Range Management* **45**, 216-220.

Kozlowski T. T. (2002) Acclimation and adaptive responses of woody plants to environmental stresses. *The Botanical Review* **68**, 270-334.

Kreuter U. P., Woodard J. B., Taylor C. A. and Teague W. R. (2008) Perceptions of Texas landowners regarding fire and its use. *Rangeland Ecology & Management* **61**, 456-464.

Lamb E. and Lamb B. M. (1955) *The illustrated reference on cacti & other succulents*. Blandford P., London.

MacDougal D. T. and Spalding E. S. (1910) *The water-balance of succulent plants*. Carnegie Institution of Washington, Washington, DC.

Mack R. N., Simberloff D., Lonsdale W. M., Evans H., Clout M. and Bazzaz F. A. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* **10**, 689-710.

McCalla G. R., II, Blackburn W. H. and Merrill L. B. (1984) Effects of livestock grazing on sediment production, Edwards Plateau of Texas. *Journal of Range Management* **37**, 291-294.

McGinty A., Smeins F. E. and Merrill L. B. (1983) Influence of spring burning on cattle diets and performance on the Edwards Plateau. *Journal of Range Management* **36**, 175-178.

McGinty A., Texas Agricultural Extension Service and Texas Agricultural Experiment Station (2001) *How to take care of pricklypear and other cacti*. Texas Agricultural Extension Service: Texas Agricultural Experiment Station, Texas A&M University System.

McGinty A. and Texas Cooperative Extension. (2005) *Chemical weed and brush control suggestions for rangeland*. Texas Cooperative Extension, Texas A&M University System.

McGinty A., Ueckert D., Texas Cooperative Extension and Texas Agricultural Experiment Station (2005) *How to take care of pricklypear and other cacti: A safe and effective three-step way to control pricklypear, tasajillo (pencil cholla), tree cholla, dog cactus and other cacti on small or large acreages*. Texas Cooperative Extension, Texas Agricultural Experiment Station, Texas A&M University System.

McMillan Z., Scott C. B., Taylor C. A., Jr. and Huston J. E. (2002) Nutritional value and intake of prickly pear by goats. *Journal of Range Management* **55**, 139-143.

Mondragón-Jacobo C., Pérez-González S. and Food and Agriculture Organization of the United Nations. (2001) *Cactus (*Opuntia *spp.) as forage*. Food and Agriculture Organization of the United Nations, Rome.

Myster R. W. (2001) Mechanisms of plant response to gradients and after distrubances. *Botanical Review* **67**, 441-452.

Nath B. (1998) *Environmental management in practice*. Routledge, London.

Nobel P. S., Russell C. E., Felker P., Medina J. G. and Acuna E. (1987) Nutrient relations and productivity of prickly pear cacti. *Agronomy Journal* **79**, 550-555.

North G. B. and Nobel P. S. (1994) Changes in root hydraulic conductivity for two tropical epiphytic cacti as soil moisture varies. *American Journal of Botany* **81**, 46-53.

North G. B. and Nobel P. S. (1998) Water uptake and structural plasticity along roots of a desert succulent during prolonged drought. *Plant Cell and Environment* **21**, 705-713.

Oesterheld M. and Sala O. E. (1990) Effects of grazing on seedling establishment: The role of seed and safe-site availability. *Journal of Vegetation Science* **1**, 353-358.

Preston-Mafham K. (1994) *Cacti and succulents in habitat*. Cassell, New York.

Rakowitz L. (1997) The significance of prickly pear on south Texas rangelands. *Rangelands* **19**, 15-17.

Rebman J. P. and Pinkava D. J. (2001) *Opuntia* cacti of North America: An overview. *The Florida Entomologist* **84**, 474-483.

Richards H. M. (1915) *Acidity and gas interchange in cacti*. Carnegie Institution of Washington, Washington, DC.

Rowe J. S. (1983) *Concepts of fire effects on plant individuals and species*. John Wiley & Sons, New York.

Russell F. L., Zippin D. B. and Fowler N. L. (2001) Effects of white-tailed deer (Odocoileus virginianus) on plants, plant populations and communities: A review. *American Midland Naturalist* **146**, 1-26.

Sauer C. O. (1950) Grassland climax, fire, and man. *Journal of Range Management* **3**, 16-21.

Spoehr H. A. (1919) *The carbohydrate economy of cacti*. Carnegie Institution of Washington, Washington, DC.

Sprugel D. G. (1991) Disturbance, equilibrium, and environmental variability: What is natural vegetation in a changing environment? *Biological Conservation* **58**, 1-18.

Taylor C. A. (2007) Role of summer prescribed fire to manage shrub-invaded grasslands. In: *Shrubland dynamics - fire and water* eds R. E. Sosebee, D. B. Wester, C. M. Britton, E. D. McArthur and S. G. Kitchens) pp. 52-55. US Department of Agriculture, Forest Service, Lubbock, TX.

Teague W. R., Kreuter U. P., Grant W. E., Diaz-Solis H. and Kothmann M. M. (2009) Economic implications of maintaining rangeland ecosystem health in a semi-arid savanna. *Ecological Economics* **68**, 1417-1429.

Van Auken O. W. (2000) Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* **31**, 197-215.

van Langevelde F., van de Vijver C. A. D. M., Kumar L., van de Koppel J., de Ridder N., van Andel J., Skidmore A. K., Hearne J. W., Stroosnijder L., Bond W. J., Prins H. H. T. and Rietkerk M. (2003) Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**, 337-350.

Walter G. H. (2008) Individuals, populations and the balance of nature: The question of persistence in ecology. *Biology & Philosophy* **23**, 417-438.

Whisenant S. G., Ueckert D. N. and Scifres C. J. (1984) Effects of fire on Texas wintergrass communities. *Journal of Range Management* **37**, 387-391.

Wicks G. A., Fenster C. R. and Burnside O. C. (1969) Selective control of plains pricklypear in rangeland with herbicides. *Weed Science* **17**, 408-411.

APPENDIX A

Figure A-1. Image of vegetation present at study site. The landscape is has significant presence of *Opuntia* cacti.

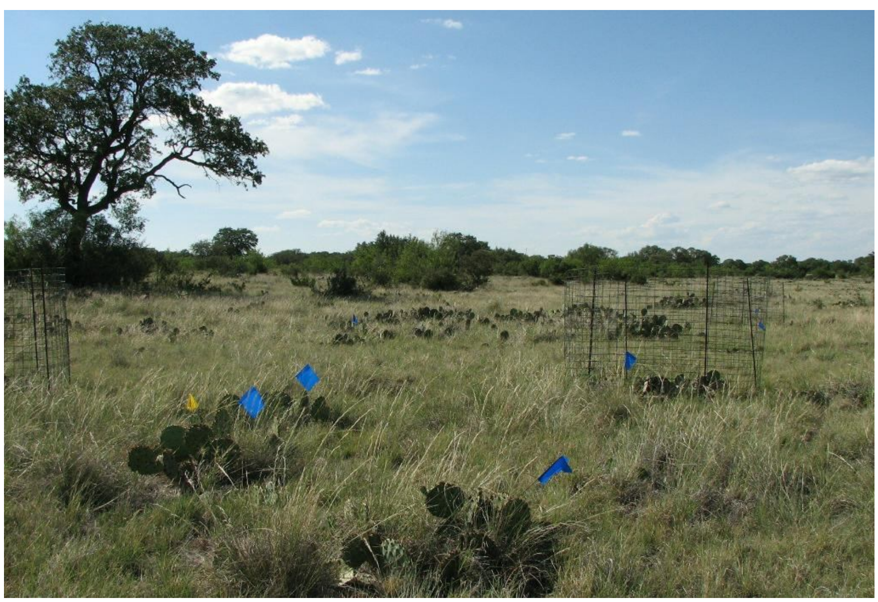

Figure A-2. Image of study site where the flags indicate the location of an experimental treatment on the cactus motte

Figure A-3. Image of a motte exclosed from large wildlife herbivores, the structure is made out of re-bar and wire mesh.

Figure A-4. Image of disturbed cactus motte.

Figure A-5. Image of study site, mottes treated during this investigation had a blue flag.

APPENDIX B

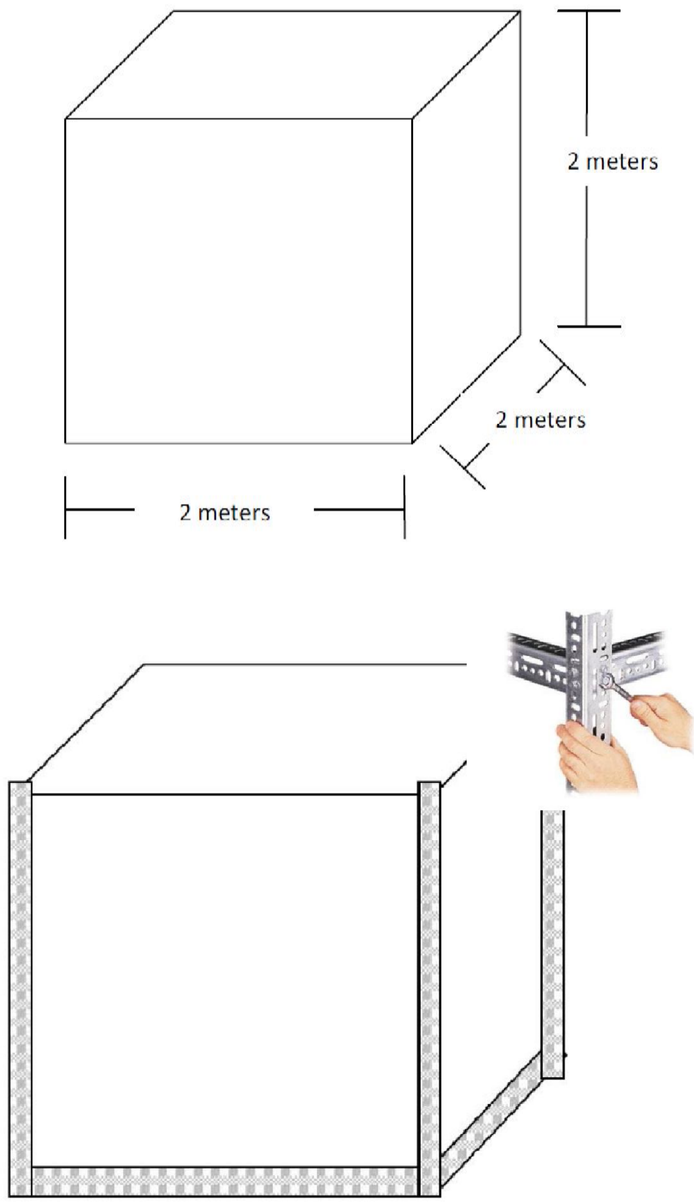

Figure B-1. Original blue-prints for the burn compartment, “burn-box” created for this study.

Figure B-2. Burn compartment created for this study, the final product was light-weight and easily transferable within burn treatments.

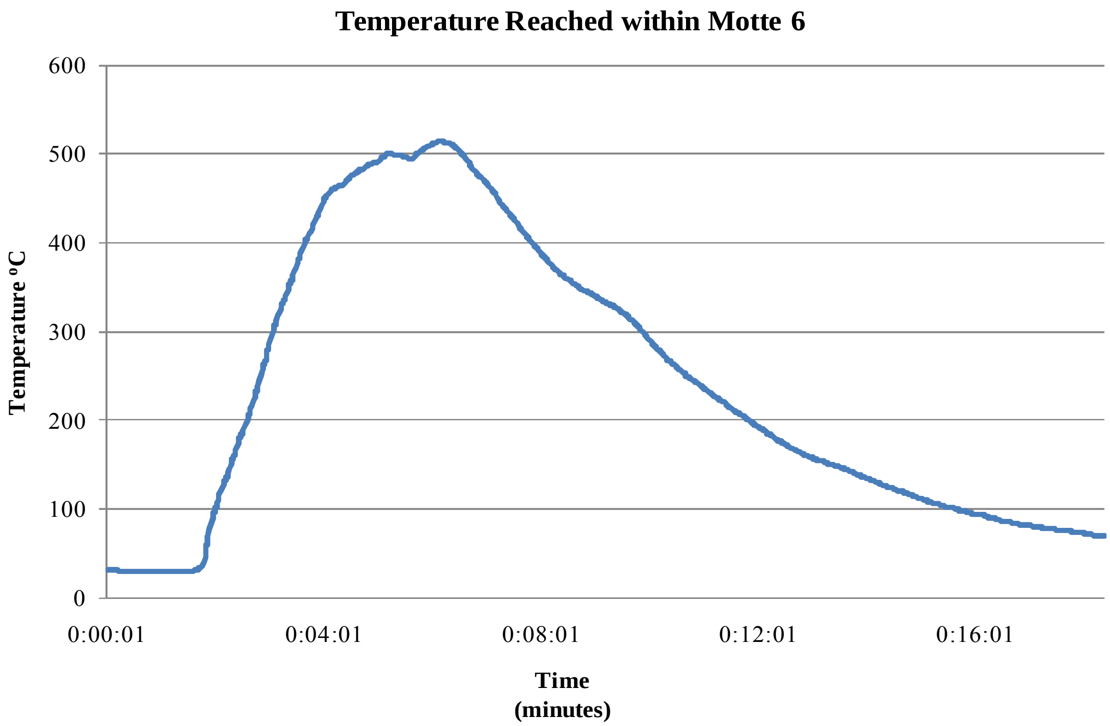

Figure B-3. The temperature graph is an example of how data is recorded by the OMEGA probe is interpreted.

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