

PRESCRIBED FIRE AS THE CATALYST TO CONTROL
PRICKLY PEAR CACTUS ENCROACHMENT AND RESTORE
THE ECOLOGICAL INTEGRITY OF TEXAS RANGELANDS

A Dissertation

by

GABRIELA SOSA

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

DOCTOR OF PHILOSOPHY

Chair of Committee,
Committee Members,

Interim Head of
Department,

William E. Rogers
Bret A. Collier
Steve G. Whisenant
Fred E. Smeins
G. Cliff Lamb

May 2019

Major Subject: Ecosystem Science and Management

Copyright 2019 Gabriela Sosa

ABSTRACT

There is a pressing need to assist resource managers and ranchers with the recovery of degraded rangelands in the Edwards Plateau region of Texas. In the last century, the plant community in this rangeland savanna ecosystem has experienced a significant shift in vegetation structure and composition, as well as a considerable decline in ecological function and productivity. The widely observed increase in *Opuntia* spp. (prickly pear cactus) encroachment is of economic and ecological concern for rangeland producers and managers. Prickly pear is a hardy succulent with an aggressive competitive nature, which allows it to rapidly establish dominance in recently disturbed areas in the absence of effective brush management control. The field-based studies presented in this dissertation aim to assess innovative management strategies that may better prevent or hinder the progressive expansion of this problematic spiny succulent in these increasingly imperiled ecosystems. In particular, we examine the viability of prescribed fire as a catalyst to restore the ecological integrity of degraded rangeland ecosystems. The insights gained from this research should also improve our understanding of the successional dynamics and complex ecological processes that occur in these fire-dependent plant communities.

DEDICATION

I wish to dedicate this dissertation to my wonderful parents, Juan Manuel and Rosa Teresa Sosa, sister, Daniela Sosa, and my wonderful husband, Hasan Khalil. Your support, patience, understanding and love were instrumental in the completion of this study.

ACKNOWLEDGEMENTS

I would like to express my sincere appreciation to Dr. William E. Rogers for his encouragement, guidance and patience throughout the course of my graduate program at Texas A&M University. The mentorship and advice of Mr. Wayne Hamilton, Dr. Manuel Piña Jr., Dr. Charles A. Taylor, and Dr. X. Ben Wu are gratefully acknowledged. I also extend my thanks to my committee members, Dr. Fred E. Smeins, Dr. Steve G. Whisenant, and Dr. Bret A. Collier for their valuable input and support throughout my graduate program.

A special acknowledgment is due to the staff at the Texas A&M AgriLife Research Station, for allowing me to use of the facilities at Sonora, Texas and Barnhart, Texas, without which this dissertation would not have been possible.

I thank my friends Dr. Denise Robledo, Dr. Christopher Cheleuitte-Nieves, Dr. Alejandra Maldonado, Beverly Saunders, Dr. Maura Palacios, Dr. Zaria Torres, Matt Sifuentes and Dr. Julie Ton for their support. I would also like to thank my husband, Hasan Khalil for his love, kindness, encouragement, and his fearlessness to share a life full of joy and adventure.

I will be forever grateful to the Alfred P. Sloan Foundation for funding a significant portion of this research. Finally, a most special recognition and my deepest gratitude goes to my family for their unrelenting encouragement and personal sacrifice as I completed this dissertation.

CONTRIBUTORS AND FUNDING SOURCES

Contributors

All work for the dissertation was completed by the student, under the supervision of Professor William E. Rogers of the Department of Ecosystem Science and Management and the dissertation committee. The committee consisted of Professor Fred E. Smeins and Professor Steve G. Whisenant of the Department of Ecosystem Science and Management, and Dr. Bret A. Collier in the School of Renewable Natural Resources at Louisiana State University. A portion of this research was conducted on a shared field site with a peer graduate student under the supervision of Dr. Rogers and Dr. Dirac Twidwell.

Funding Sources

These research studies were made possible in part by a fellowship from Texas A&M University, the Harry Wayne Springfield Research Award, a doctoral scholarship from Alfred P. Sloan Foundation, and by the Texas Natural Resource Conservation Service grant CIG# 68-7442-7-481 and the USDA Natural Resource Conservation Service grant CIG# 68-3A75-5-180.

TABLE OF CONTENTS

	Page
ABSTRACT.....	ii
DEDICATION.....	iii
ACKNOWLEDGEMENTS.....	iv
CONTRIBUTORS AND FUNDING SOURCES.....	v
TABLE OF CONTENTS.....	vi
LIST OF FIGURES.....	ix
LIST OF TABLES.....	xv
CHAPTER I INTRODUCTION.....	1
Literature Review.....	4
Fleshy Joint Stems.....	5
Crassulacean Acid Metabolism Photosynthesis.....	6
Thick Waxy Cuticle.....	7
Mechanical Defenses.....	7
Fibrous Root System.....	8
Reproductive Characteristics.....	9
Traditional Control Strategies.....	11
Mechanical.....	11
Chemical.....	12
Biological.....	13
Prescribed Fire.....	14
Impediments to Current Management Efforts.....	15
CHAPTER II REGIONAL OVERVIEW OF RESEARCH SITES.....	16
Description and Characteristics of the Edwards Plateau.....	16
Geomorphology and Soils.....	17
Regional Climate.....	18
Vegetation and Regional Ecology.....	20
Land Management.....	22
Texas AgriLife Research Station near Sonora, Texas.....	23
Texas AgriLife Range Station near Barnhart, Texas.....	28

CHAPTER III RESEARCH OBJECTIVES.....	32
CHAPTER IV RECLAMATION PRESCRIBED FIRE AS THE CATALYST TO RESTORE A PRICKLY PEAR ENCROACHED RANGELAND.....	34
Introduction.....	34
Methods.....	37
Study Site.....	37
Experimental Design.....	38
Prescribed Fire Treatments.....	40
Vegetation Assessment and Fuel Characteristics.....	42
Statistical Analysis and Procedures.....	43
Results.....	45
Vegetation Response to Fire.....	46
Prickly Pear Cactus Cover.....	47
The Combustion of the <i>Opuntia</i> Cladodes.....	48
Herbaceous Vegetation Layer.....	49
Bare Ground Cover.....	52
Discussion.....	56
Prickly Pear in Response to Fire.....	56
Prickly Pear’s Response in the Absence of Fire.....	58
Recovery of Herbaceous Layer.....	62
Herbaceous Layer in the Absence of Fire.....	63
Broader Implication for Rangeland Ecology and Management.....	64
Adaptive Management.....	65
CHAPTER V THE SUSCEPTIBILITY OF DROUGHT-STRICKEN CACTUS TO PRESCRIBED FIRE: A FIELD STUDY.....	67
Introduction.....	67
Methods.....	70
Experimental Design.....	71
Vegetation Assessments and Fuel Characteristic.....	71
<i>In situ</i> Field Treatments.....	72
Drought Simulation.....	72
Prescribed Fire.....	73
Tissue Harvesting Technique.....	76
Statistical Analysis and Procedures.....	77
Results.....	79
Recorded Temperature of Prescribed Fires.....	79
Vegetation Response to Drought and Fire.....	80
Prickly Pear Cactus Cover.....	80
Moisture Content of Harvested Stems.....	82
Herbaceous Vegetation Layer.....	84

Bare Ground Cover.....	86
Discussion.....	89
Prickly Pear in Response to Fire and Drought.....	89
Prickly Pear’s Response to Drought in the Absence of Fire.....	94
Recovery of Herbaceous Layer.....	96
Broader Implications for Rangeland Ecology and Management.....	97
CHAPTER VI INTEGRATED RESTORATION STRATEGIES TO CONTROL PRICKLY PEAR ENCROACHMENT: EXPERIMENT ASSESSING PRESCRIBED FIRE AND A NON-RESTRICTED HERBICIDE.....	99
Introduction.....	99
Methods.....	106
Study Site.....	106
Experimental Design.....	107
Prescribed Fire Treatments.....	108
Herbicide Treatments.....	109
Vegetation Assessment and Fuel Characteristics.....	112
Statistical Analysis and Procedures.....	112
Results.....	114
Vegetation Response to Fire and Herbicides.....	114
Prickly Pear Cactus Cover.....	114
Herbaceous Vegetation Layer.....	117
Bare Ground Cover.....	120
Discussion.....	125
Prickly Pear in Response to Herbicides and Fire.....	125
Prickly Pear’s Response to Herbicides in the Absence of Fire.....	127
Recovery of Herbaceous Layer.....	129
Broader Implications for Rangeland Ecology and Management.....	132
CHAPTER VII SUMMARY AND CONCLUSION.....	134
Land Management Recommendations.....	137
Significance and Future Research Directions.....	138
LITERATURE CITED.....	141
APPENDIX A.....	187
APPENDIX B.....	191
APPENDIX C.....	195

LIST OF FIGURES

	Page
Figure 1. A picture of a low and wide-spreading prickly pear cactus mottle found in the vicinity of the Edwards Plateau region of Texas.....	5
Figure 2. Prickly pear is the official state plant of Texas; its stem joint segments are covered with sharp, needle-like spines.....	8
Figure 3. The prickly pear pads produce fleshy fruits that are commonly referred to as ‘tuna’ ‘cactus fig’ or ‘pear apples’.....	10
Figure 4. The geographic location of the research stations where ecological field research studies were conducted.....	16
Figure 5. The Texas AgriLife Range Station near Barnhart, Texas and the Texas AgriLife Research Station near Sonora, Texas are located over the Edward Plateau ecological resource area.....	17
Figure 6. Ecological research studies were conducted on sites typified by rolling stony hill topography. The geology corresponding to the 93,000 km ² Edwards Plateau is underlain by Cretaceous carbonate bedrock.....	18
Figure 7. Average annual precipitation for the state of Texas varies from less than 254 mm in the west to over 1524 mm in the east (1990-2009). This figure indicates the location of Texas AgriLife Range Station and the Texas AgriLife Research Station.....	19
Figure 8. Monthly mean temperature and precipitation for the Texas AgriLife Research Station near Sonora, Texas. Annual precipitation is bimodially distributed, with the wettest months occurring in the spring (May/June) and fall (September/October).....	24
Figure 9. Prickly pear cactus is moderately thick at the Texas AgriLife Research Station near Sonora, Texas. Following a survey in 2008, we calculated an average prickly pear density of <i>c.</i> 341 cactus plants (i.e. mottes) per hectare on sites corresponding to this dissertation research.....	25
Figure 10. Monthly mean temperature and precipitation for the Texas AgriLife Range Station near Barnhart, Texas. The station receives an average annual precipitation of 480.3 mm; it follows a bimodal precipitation pattern with most rainfall occurring during spring (May) and fall (October) peaks.....	29

Figure 11. Prickly pear cactus mottes on these rangelands at the Texas AgriLife Range Station near Barnhart, Texas, form entangled thickets; we calculated $c.747$ cactus plants per hectare.....	31
Figure 12. Schematic representation of the independent permanent plots established at the Texas A&M AgriLife Research Station near Sonora, Texas to examine the use of prescribed fire on a prickly pear encroached rangeland.....	39
Figure 13. Ground view of prickly pear mottes scattered throughout at rangeland at the Texas A&M AgriLife Research Station near Sonora, Texas.....	43
Figure 14. A comparison of the mean (\pm S.E.) fireline intensities of the prescribed fire treatments conducted on the experimental plots. A significant difference ($P < 0.05$) between treatments is indicated by different letters.....	46
Figure 15. A ground view of the study area at the Texas A&M AgriLife Research Station near Sonora, Texas, immediately following the reclamation prescribed fire treatments (August 2008).....	47
Figure 16. An assessment of the percent change in prickly pear canopy cover (m^2) in response to the prescribed fire treatments. All results are presented as mean (\pm S.E.) and any significant difference ($P < 0.05$) between the treatments is indicated by different letters.....	48
Figure 17. This image was captured immediately after the fire. The photosynthetic tissue of the cactus pads was spongy and blistering with melted waxes, and the internal tissue, where the mucilaginous content is found, remained exposed.....	49
Figure 18. Percent standing herbaceous cover measured at the 2.5 m scale before and after the prescribed fire treatments. All results are presented as mean (\pm S.E.) and any significant difference ($P < 0.05$) between treatments is indicated by an asterisk.....	50
Figure 19. Percent change in standing herbaceous cover measured at the 2.5 m scale. These findings are based on data collected from 2007-2012. All results are presented as mean (\pm S.E.) and any significant difference ($P < 0.05$) between treatments is indicated by different letters.....	52
Figure 20. Percent change in bare ground measured at the 2.5 m scale. These findings are based on data collected from 2007-2012. All results are presented as mean (\pm S.E.) and any significant difference ($P < 0.05$) between treatments is indicated by different letters.....	54

Figure 21. The mean percent of bare ground surrounding the cactus mottes was measured at the 2.5 m scale. All results are presented as mean (\pm S.E.) and an asterisk indicates any significant difference ($P < 0.05$) between treatments.....	55
Figure 22. A regional-scale drought representation in the rangelands of Texas obtained from the U.S. Drought Monitor for the 2009 growing season (April, July, and September) following the application of ‘reclamation’ prescribed fire treatments (August 2008). The star on the maps represents the location of the Texas AgriLife Research Station near Sonora, Texas.....	59
Figure 23. A regional-scale drought representation in the rangelands of Texas obtained from the U.S. Drought Monitor for the 2011 and 2012 growing season (April and September). In November 2010, the plots that were previously burned with ‘reclamation’ prescribed fires were once again burned with a ‘maintenance’ prescribed fire treatment. The star on the maps represents the location of the Texas AgriLife Research Station near Sonora, Texas.....	61
Figure 24. Aerial view of the study area at the Texas A&M AgriLife Research Station near Sonora, Texas.....	70
Figure 25. A) An illustration of the open-sided, open-ended, rainout shelter, and B) ground view of a prickly pear motte covered by SUNTUF® polycarbonate roofing panels at our field site at the Texas AgriLife Research Station.	72
Figure 26. A) A diagram that references the height, depth and width of the portable burn compartment, and B) a photograph of the metal compartment.....	74
Figure 27. A schematic representation of a headfire spreading through a 4m ² plot with a prickly pear motte and an OMEGA™ thermocouple connected to a commercially available electronic data logger.....	75
Figure 28. A view of a smoldering prickly pear cactus inside the burn compartment. The maximum fire temperature was measured with an OMEGA™ thermocouple sensor as the flames progressed through the plot consuming the succulent’s photosynthetic tissue in a manner similar to that observed in Chapter IV.....	76
Figure 29. inner mucilaginous tissue of a harvested sample, and B) a stem segment that has been perforated with a cork borer.....	77

Figure 30. A comparison of the mean (\pm S.E.) maximum instantaneous fire temperature ($^{\circ}$ C) for the prescribed fires treatments administered late-September (2012) on the experimental plots with the rainout shelter and those left under ambient (control) conditions. A significant difference ($P < 0.05$) between the treatments is indicated by different letters.....80

Figure 31. An assessment of the percent change in prickly pear cactus motte cover (m^2) in response to the prescribed fire treatments under plots with a rainout shelter compared to plots under ambient (control) conditions ($P=0.595$). All results are presented as a mean value (\pm S.E.).....81

Figure 32. An image of a harvested prickly pear cactus stem from a motte that was found under a rainout shelter.....82

Figure 33. The average wet weight (g) of the harvested prickly pear cactus stem tissue samples. Results are presented as a mean value (\pm S.E.) and any significant difference ($P < 0.05$) between the treatments is indicated by different letters.....83

Figure 34. A comparison of the mean (\pm S.E.) percent standing herbaceous vegetation cover on the plots prior to the prescribed fire and drought simulation treatments in 2010 ($P=0.162$).....84

Figure 35. An assessment of the percent change in standing herbaceous vegetation cover in response to the prescribed fire treatments under plots with a rainout shelter compared to plots under ambient (control) conditions. All results are presented as a mean value (\pm S.E.).....85

Figure 36. A comparison of the percent bare ground between the plots with and without a rainout shelter prior to the prescribed fire treatments (2010) and post-treatment (2013). All results are presented as a mean (\pm S.E.) and any significant difference ($P < 0.05$) in response to the fire treatments is indicated by different letters.....87

Figure 37. A post-treatment (2013) comparison of the percent bare ground by fire treatments between the plots with and without a rainout shelter. All results are presented as a mean (\pm S.E.) and an asterisk indicates any significant difference ($P < 0.05$) between treatments.....88

Figure 38. A regional-scale drought representation in the rangelands of Texas obtained from the U.S. Drought Monitor for the 2010, 2011, and 2012 growing seasons (April, July, and September) immediately prior to and following the establishment of the *in situ* drought simulation treatments, using the fixed-location rainout shelter technique (June 2010). The star on the maps represents the location of the Texas AgriLife Research Station near Sonora, Texas.....91

Figure 39. A regional-scale drought representation in the rangelands of Texas obtained from the U.S. Drought Monitor for the 2011 growing season (April, July, and September) following the prescribed fire treatments administered April 9, 2011. The star on the maps represents the location of the Texas AgriLife Research Station near Sonora, Texas.....	93
Figure 40. A regional-scale drought representation in the rangelands of Texas obtained from the U.S. Drought Monitor for late 2012 and early 2013, following the application of prescribed fire treatments (September 24, 2012). The star on the maps represents the location of the Texas AgriLife Research Station near Sonora, Texas.....	95
Figure 41. A ground view of a recently burned site found at the Edwards Plateau of Texas, where prickly pear form entangled thickets with weed-like characteristics (ca. 747 cactus plants per hectare).....	100
Figure 42. A laborer spraying prickly pear cactus with a ground applicator on a woody brush and succulent infested rangeland in Texas in the 1930s.....	101
Figure 43. Schematic representation of the split-plot experimental design used at the Texas Range Station near Barnhart, Texas to assess the interactions between prescribed fire and herbicide treatments.....	108
Figure 44. The 2-D chemical structure of floxypyr.....	110
Figure 45. The 2-D chemical structure of picloram.....	110
Figure 46. A comparison of the percent change in prickly pear cactus motte cover (m ²) in response to the prescribed fire and herbicide treatments (P=0.0001). All results are presented as a mean value (\pm S.E.).....	115
Figure 47. A partially burned prickly pear cactus motte. The peripheral stem segments were scorched by the fire, whereas those found near the center and apex remained intact.....	116
Figure 48. A prickly pear cactus motte treated with a selective herbicide. These phytotoxic chemicals resulted in malformation and decomposition of the stem segments.....	117
Figure 49. A comparison of the mean (\pm S.E.) percent standing herbaceous vegetation cover on the plots measured at the 2.5 m scale prior to the prescribed fire and herbicide treatments (P=0.078).....	118

Figure 50. An assessment of the percent change in standing herbaceous vegetation cover in response to the prescribed fire and herbicide treatments ($P= 0.147$). All results are presented as a mean value (\pm S.E.).....119

Figure 51. A comparison of the percent bare ground between the plots prior to the prescribed fire and herbicide treatments (2011) and post-treatment (2013). All results are presented as a mean (\pm S.E.) and any significant difference ($P < 0.05$) in response to the fire and herbicide treatments is indicated by different letters.....121

Figure 52. A ground view of a burned plot at the Texas A&M AgriLife Range Station near Barnhart, Texas (February 07, 2012).....123

Figure 53. A post-treatment (2013) comparison of the percent bare ground measured at the 2.5 m scale by herbicide treatments between the plots with and without a prescribed fire. All results are presented as a mean (\pm S.E.) and an asterisk indicates any significant difference ($P < 0.05$) between treatments.....124

Figure 54. A regional-scale drought representation in the rangelands of Texas obtained from the U.S. Drought Monitor following the herbicides treatment application administered early fall (November 13, 2012). The star on the maps represents the location of the Texas AgriLife Range Station near Barnhart, Texas.....128

Figure 55. A regional-scale drought representation in the rangelands of Texas obtained from the U.S. Drought Monitor for the 2012 growing season (April, July, and September) following the application of the prescribed fire treatments (February 7, 2012). The star on the maps represents the location of the Texas AgriLife Range Station near Barnhart, Texas.....131

LIST OF TABLES

	Page
Table 1. Descriptive statistics of the fireline intensities (kW/m) between the prescribed burn treatments.....	187
Table 2. Independent-samples t-test comparing the fireline intensities (kW/m) for the reclamation and maintenance prescribed fire treatments.....	187
Table 3. A comparison of the percent area burned for the fire treatments conducted on the experimental plots.....	187
Table 4. Descriptive statistics of the percent change in prickly pear canopy cover in response to the prescribed fire treatments.....	187
Table 5. Analysis of variance for the percent change in prickly pear canopy cover in response to the prescribed fire treatments.....	188
Table 6. Descriptive statistics comparing the percent change of cactus cover in response to the different prescribed fire treatments.....	188
Table 7. Independent-samples t-test comparing the percent change of cactus cover in response to the different prescribed fire treatments.....	188
Table 8. Descriptive statistics of the percent standing herbaceous cover collected before (July 2007) and after (December 2012) the prescribed fire treatments.....	188
Table 9. Descriptive statistics of the percent change in standing herbaceous cover in response to the prescribed fire treatments.....	188
Table 10. Independent-samples t-test comparing the change in percent standing herbaceous cover between the prescribed fire treatments.....	189
Table 11. Descriptive statistics of the percent bare ground cover collected before (July 2007) and after (December 2012) the prescribed fire treatments.....	189
Table 12. Descriptive statistics of the percent change in bare ground cover in response to the prescribed fire treatments.....	189
Table 13. Analysis of variance for the percent change in bare ground in response to the prescribed fire treatments.....	189

Table 14. Independent-samples t-test comparing the change in percent bare ground cover between the prescribed fire treatments.....	190
Table 15. Descriptive statistics of the mean maximum instantaneous fire temperature (degrees Celsius) of the plots under different hydration treatments.....	191
Table 16. Independent-samples t-test comparing the mean maximum instantaneous fire temperature (degrees Celsius) of the plots under different hydration treatments...	191
Table 17. Descriptive statistics of the percent change in prickly pear canopy cover in response to the hydration and prescribed fire treatments.....	191
Table 18. Analysis of variance for the percent change in prickly pear cover in response to the hydration and prescribed fire treatments.....	191
Table 19. Independent-samples t-test comparing the change in percent prickly pear canopy cover in response to the hydration and prescribed fire treatments.....	192
Table 20. Descriptive statistics of the mean wet weight (g) of the harvested cactus stem tissue samples.....	192
Table 21. Independent-samples t-test comparing the mean weight (g) of the harvested prickly pear cactus stems under different hydration treatments.....	192
Table 22. Descriptive statistics of the mean standing herbaceous vegetation cover present on the plots before (June 2010) the establishment of the hydration and prescribed fire treatments.....	192
Table 23. Analysis of variance for the mean standing herbaceous vegetation cover present on the plots before (June 2010) the establishment of the hydration and prescribed fire treatments.....	193
Table 24. Descriptive statistics of the mean standing herbaceous vegetation cover present on the plots after (March 2013) the establishment of the hydration and prescribed fire treatments.....	193
Table 25. Analysis of variance for the mean standing herbaceous vegetation cover present on the plots after (March 2013) the establishment of the hydration and prescribed fire treatments.....	193
Table 26. Independent-samples t-test comparing the change in percent standing herbaceous vegetation cover in response to the hydration and prescribed fire treatments.....	193

Table 27. Descriptive statistics of the mean percent bare ground cover on the plots before (June 2010) the establishment of the hydration and prescribed fire treatments.....	194
Table 28. Analysis of variance for the mean percent bare ground cover on the plots before (June 2010) the establishment of the hydration and prescribed fire treatments.....	194
Table 29. Descriptive statistics of the mean percent bare ground cover on the plots after (March 2013) the establishment of the hydration and prescribed fire treatments.....	194
Table 30. Independent-samples t-test comparing the change in percent bare ground cover in response to the hydration and prescribed fire treatments.....	194
Table 31. Descriptive statistics of the percent change in prickly pear canopy cover in response to the application of herbicide and prescribed fire treatments.....	195
Table 32. Analysis of variance for the percent change in prickly pear canopy cover in response to the application of herbicide and prescribed fire treatments.....	195
Table 33. Independent-samples t-test comparing the percent change in prickly pear canopy cover in response to the application of herbicide and prescribed fire treatments.....	195
Table 34. Independent-samples t-test comparing the percent change in prickly pear canopy in response to the application of herbicide treatments in combination with prescribed fire treatments administered February 2012.....	196
Table 35. Independent-samples t-test comparing the percent change in prickly pear canopy cover in response to the application of herbicide treatments in the absence of prescribed fire.....	196
Table 36. Descriptive statistics of the mean standing herbaceous vegetation cover present on the plots before (July 2011) the establishment of the herbicide and prescribed fire treatments.....	196
Table 37. Analysis of variance for the mean standing herbaceous vegetation cover present on the plots before (July 2011) the establishment of the herbicide and prescribed fire treatments.....	196
Table 38. Descriptive statistics of the percent change in herbaceous cover in response to the application of herbicide and prescribed fire treatments.....	197

Table 39. Analysis of variance for the percent change in herbaceous cover in response to the application of herbicide and prescribed fire treatments.....	197
Table 40. Independent-samples t-test comparing the percent change in standing herbaceous vegetation cover in response to the application of herbicide and prescribed fire treatments.....	197
Table 41. Independent-samples t-test comparing the percent change in standing herbaceous cover in response to the application of herbicide and prescribed fire treatments in early-February 2012.....	197
Table 42. Independent-samples t-test comparing the percent change in standing herbaceous cover in response to the application of herbicide treatments in the absence of prescribed fire.....	198
Table 43. Descriptive statistics of the mean percent bare ground cover on the plots before (July 2011) the application of the herbicide and prescribed fire treatments.....	198
Table 44. Analysis of variance for the mean percent bare ground cover on the plots before (July 2011) the application of the herbicide and prescribed fire treatments.....	198
Table 45. Descriptive statistics of the mean percent bare ground cover on the plots after the application of the herbicide treatments in the absence of prescribed fire (March 2013).....	198
Table 46. Independent-samples t-test comparing the man percent bare ground cover in response to the application of herbicide treatments in the absence of prescribed fire (March 2013).....	199
Table 47. Descriptive statistics of the mean percent bare ground cover on the plots in response to the application of herbicide and prescribed fire treatments (March 2013).....	199
Table 48. Independent-samples t-test comparing the mean percent bare ground cover on the plots in response to the application of herbicide and prescribed fire treatments (March 2013).....	199
Table 49. Descriptive statistics comparing the mean percent bare ground cover the plots with different prescribed fire treatments in response to the application of herbicides (March 2013).....	199
Table 50. Analysis of variance for the mean percent bare ground cover on the plots with different prescribed fire treatments in response to the application of herbicides (March 2013).....	200

Table 51. Independent-samples t-test comparing the mean percent bare ground cover on the plots with different prescribed fire treatments in response to the application of the herbicides (March 2013).....200

CHAPTER I

INTRODUCTION

In the last century, the widely observed encroachment of prickly pear cactus (*Opuntia* spp.; hereafter, prickly pear) throughout its native range is of particular concern for rangeland producers and landowners in the Edwards Plateau region of west-central Texas. The prolific expansion of this indigenous succulent has caused a reduction in productivity in these semi-arid rangeland savannas (i.e. decline in herbaceous forage availability) (Archer, et al. 1995; Blomquist 1990; Foster 1917, Fuhlendorf 1992; Hamilton and Ueckert 2004; Lundgren, et al. 1981; Mayeux and Johnson 1989; Scifres 1980; Scholes and Archer 1997; Smeins and Merrill 1988; Taylor 2007; Ueckert, et al. 1988). Prickly pear is a plant that outcompetes and restricts the growth of desirable high quality native perennial grasses and forbs (Ansley and Castellano 2007*b*; Dodd 1940; Fuhlendorf and Smeins 1997; Merrill, et al. 1980; Scifres and Hamilton 1993; Scifres 1980; Ueckert, et al. 1988; Walker 1993; Weaver and Clements 1929). An increase in density and dominance by this succulent impairs the movement and handling of grazing animals (Bunting, et al. 1980; Taylor, et al. 1980). A poor distribution of grazing animals is problematic to ranchers and producers because it increases the grazing pressure on the remaining palatable herbaceous forage and this reduces the carrying capacity of these rangelands which ultimately impedes profitable ranching (Ansley and Castellano 2007*a*; Dodd 1940; Scifres 1980; Ueckert, et al. 1988; Walker 1993).

Historically, the onset of unsustainable year-long grazing management systems (i.e. high forage consumption) to support the demands of the livestock industry and a long history of anthropogenic fire suppression by early Euro-American settlers have been identified as the main drivers of this increase in prickly pear (Ansley and Taylor 2004; Lundgren, et al. 1981; Scifres and Hamilton 1993; Van Auken 2009). These regional unsustainable agricultural practices transformed what was once an open grassland savanna to its current dense shrubland state (du Toit 2011; Frank, et al. 1998; Scholes and Archer 1997; Stoddart and Smith 1943, Teague, et al. 2008). The consequence of altering the desirable brush-to-grass ratio in this landscape has also reduced water infiltration rates given that these brush encroached rangelands are not as efficient at anchoring and protecting the soils from potential erosion (McCalla, et al. 1984; Schlesinger, et al. 1999; Whisenant 1995). Land managers and ranchers need to manage and control its density in this plant community to prevent a considerable decline in wildlife habitat and ecological function (i.e. site stability and integrity) (Arnold and Drawe 1979; Chavez-Ramirez, et al. 1997; Everitt, et al. 1981; Fontenot, et al. 1991; Rakowitz 1997; Scifres 1980; Taylor, et al. 1980; Taylor 2007; Ueckert, et al. 1988; Ueckert, et al. 1990).

In this dissertation we conducted a series of ecological field research studies to examine the viability of alternative control strategies to suppress prickly pear encroachment. Specifically, we investigated the susceptibility of prickly pear to prescribed fire during environmentally stressful conditions (i.e. drought and extreme-hot summers).

An additional aspect of this research was to examine this succulent's physiological response to a federally non-restricted herbicide with no soil residual activity.

LITERATURE REVIEW

North American prickly pear is a member of the Cactaceae family that evolved from Central Mexico and is capable of growing in extreme conditions, such as hot, dry summers and cold winters (Rebman and Pinkava 2001). This succulent was originally confined to arid and semi-arid ecosystems of the southwestern United States and northern Mexico, but in the last century it has become a common floristic component throughout most of the United States, and arid, semi-arid and Mediterranean regions throughout the world (Chavez-Ramirez, et al. 1997; Rebman and Pinkava 2001). In particular, prickly pear is a member of the *Opuntia* genus that includes over 181 species and are distinguished by having flattened oblong shaped stem joints that are commonly referred to as cladodes, pads, cladophylls, or phyloclads (Labra, et al. 2003). Morphologically, a discernible cluster of connected stem joints (i.e. ramets) forms a cohort that is known as a prickly pear motte (Buxbaum 1950; Higgins 1946) (Figure 1). The most common species of prickly pear in the rangelands associated with the Edwards Plateau region are *Opuntia engelmannii*, *Opuntia lindheimeri* and *Opuntia edwardsii* (Ueckert, et al. 1997).

Prickly pear is a persistent evergreen succulent and a drought-tolerant species that remains physiologically active year-round even when soil water availability is exceptionally low (Burger and Louda 1995; Nobel 1988). It is characterized by having a series of ecological adaptations that provide it with the hardiness it needs to survive and thrive in xerophitic (i.e. water-limited) environments (i.e. fleshy stem joints with a high water-retaining capacity, a carbon fixation pathway that minimizes water loss, a thick

cuticle, mechanical defenses that protect the plant's photosynthetic material, an extensive root system, and prolific reproduction) (Nobel 1991). In particular, this multi-stemmed plant possesses morphological plasticity, meaning it has the ability to alter its form and structure in response to physiological cues triggered by changes in environmental conditions (e.g., light, water availability) (Cushman and Bohnert 1999; Taiz and Zeiger 1998). These plants are commonly used as ornamentals for low-maintenance landscaping (Chance 2016).



Figure 1. A picture of a low and wide-spreading prickly pear cactus motte found in the vicinity of the Edwards Plateau region of Texas.

Fleshy Joint Stems

The inner tissue of stem joints serves as a moisture reservoir giving this succulent an innate physiological tolerance to drought (Trachtenberg and Mayer 1980). Field research has demonstrated that 80 to 95 percent of its weight is water in a well-hydrated stem joint (Sosa 2009). The rainfall that is absorbed into these fleshy stems is converted

into mucilage, a slimy, viscous-like substance that can effectively improve the plants water-retaining capacity (Trachtenberg and Mayer 1980). The large amounts of mucilage in the stem joints provide them the ability to expand and contract as water availability changes (Rebman and Pinkava 2001). For example, with adequate water absorption the stem joints appear turgid (Barcikowski and Nobel 1984). Additionally, this mucilaginous substance, unique to the photosynthetic material of succulents, does not evaporate as readily as water (Szarek, et al. 1973). It provides them with a high relative tissue water content and high water potential even when it is exposed to harsh environmental conditions, extreme temperatures and low relative humidity (Hinckley, et al. 1980; Oppenheimer 1960; Gibson and Nobel 1986).

Crassulacean Acid Metabolism Photosynthesis

Prickly pear is uniquely characterized by having a slow metabolism and a high water-use efficiency (WUE) (Burger and Louda 1995; Chavez-Ramirez, et al. 1997; Nobel 1988). In contrast to C₃ and C₄ plants that typically conduct photosynthesis during the day when evapotranspiration rates are high and the likelihood of water loss is greatest, this xerophyte has evolved to conduct crassulacean acid metabolism (CAM) photosynthesis (Kluge and Ting 2012). The adaptation of this carbon fixation pathway allows this perennial angiosperm (i.e. flowering plant) to close its stomata during the day to reduce evapotranspiration and carbon dioxide (CO₂) leakage and to open at night to collect CO₂ (Gibson and Nobel 1986). This distinctive type of photosynthesis provides a three-to-five fold higher WUE compared to C₃ or C₄ plants (Graham and Nobel 1996; Nobel 1999). CAM photosynthesis has not only provided this succulent with the ability

to survive but has also allowed the plant to thrive in these drought-prone and arid environments, giving it the ability to be a dominant species within plant communities characterized by extreme aridity and other harsh environmental conditions (Burger and Louda 1994).

Thick Waxy Cuticle

Modified branches, or stem joints, of the prickly pear are covered by a thick and continuous waxy cuticle that protects the photosynthetic material (e.g., epidermis) (Feugang, et al. 2006; Dimmitt 2000). This cuticle is primarily known for its hydrophobic properties (Pechook and Pokroy 2012). While providing insulation, this mechanism sacrifices surface water absorption to prevent excessive water loss, which allows it to thrive in full sunlight and arid conditions (Shedbalkar, et al. 2010). The cuticle of the basal stem of the prickly pear mottes undergoes a process similar to lignification in woody species (Chow, et al. 1966a). This lignified area of cuticle becomes surrounded by a thick cork layer that provides additional insulation to the plant tissue (Ramírez-Tobías, et al. 2012).

Mechanical Defenses

Prickly pear evolved structural features, stem joints that are covered with spines, which are modified leaves and glochids, sharp bristle-like barbs (Theimer and Bateman 1992) (Figure 2). These features provide this succulent plant with mechanical defensive capabilities to protect the photosynthetic tissue from wild and domesticated herbivores (Hanley, et al. 2007). Reptiles, small mammals and ground birds benefit from these mechanical defenses, the cactus plants provide them with protection from predators and

suitable nesting sites (Hernández, et al. 2003). The sharp spines stick easily to the flesh of predators and are difficult to remove (DeFelice 2004). Prickly pear is considered a nuisance to humans and livestock, as their spines and glochids greatly reduce digestibility and can cause skin irritations, wounds and infections (Hanselka and Paschal 1991). In addition, because these needle-like protrusions are not photosynthetic and significantly smaller than leaves, they reduce evapotranspiration (Keddy 2017). The spines also minimize the direct effects of drought by providing shade and reducing heat loading (Drezner 2011; Keddy 2007).



Figure 2. Prickly pear is the official state plant of Texas; its stem joint segments are covered with sharp, needle-like spines.

Fibrous Root System

Another ecological adaptation by prickly pear is the ability to laterally spread its fibrous roots within the top 10 cm of the soil surface (Rebman and Pinkava 2001). This

shallow-rooted succulent lives and persists in harsh environments where water availability is scarce (Turner and Costello 1942). Compared to grass, prickly pear is a succulent with an extremely superficial, extensive root system that allows it to thrive in shallow gravel or clefts in rocks (Oppenheimer 1960) and efficiently utilize moisture from rainfall (Burger and Louda 1994). In times of drought, a lack of precipitation results in the shrinkage of existing roots which helps prevent water from escaping back to the soil (Nobel 1997). Whereas, an exceptional period of precipitation may stimulate the expansion and thickening of existing roots, as well as the production of additional rain roots to rapidly absorb water from a large area (Burger and Louda 1994; Nobel 1988; Oppenheimer 1960).

Reproductive Characteristics

Prickly pear also has the capacity to rapidly and easily propagate (Griffith 2004; Rebman and Pinkava 2001). Like most plants, prickly pear can reproduce sexually. Insect pollinated flowers develop into sweet, fleshy fruits that are a source of carbohydrates, starch, ether extract, crude protein, amino acids, and fiber for foraging wildlife and livestock (Nerd and Mizrahi 1997; Russell and Felker 1987). The insects that are commonly found on prickly pear are the North American cactus moth (*Melitara dentate*) (i.e. blue cactus borers), snout moth (*Melitara subumbrella*) (i.e. banded cactus borers), cochineals (*Dactylopius confusus* and *D. opuntiae*), cactus bugs (*Chelinidea vittiger*), and red spider mites (*Tetranychus opuntiae*) (Bugbee and Reigel 1945; Bunting, et al. 1980; Burger and Louda 1995; Dodd 1940; Cook 1942; Gilreath and Smith 1988; Sickerman and Wangberg 1983; Watts, et al. 1989). Additionally, livestock

and wildlife also facilitate the dispersal of prickly pear cactus seeds throughout the landscape (Fontenot, et al. 1991; Potter, et al. 1986; Taylor, et al.1980) (Figure 3).



Figure 3. The prickly pear pads produce fleshy fruits that are commonly referred to as ‘tuna’ ‘cactus fig’ or ‘pear apples.’

This succulent can also reproduce vegetatively from an existing tissue segment (i.e. vegetative cuttings) (Reyes-Agüero, et al. 2006). Vegetative replication is a form of asexual reproduction. When a detached individual stem joint is pressed into moist soil, it has the ability to take root and establish a basal stem to anchor a new plant that is a clone of the parent plant (Chavez-Ramirez, et al. 1997). These reproductive characteristics can drastically increase the prickly pear stand density especially on landscapes with recent soil disturbance (Burger and Louda 1995; Preston-Mafham, K. 1994; Turner and Costello 1942). Prickly pear thrives in these highly disturbed landscapes and relies on vegetative replication as its primary mean of reproduction (Freeman 1992; Taylor, et al.

1980). Domesticated and wild herbivores cause disturbances to the soil and they inadvertently scatter the stem joints when they forage (Nobel 1988). The dispersed stem joint segments that make contact with the soil surface can rapidly take root (Turner and Costello 1942; Warming 1925). These new roots will emerge from aereols (i.e. modified axillary buds) or from the attachment node, where the stem joint originally broke from the parent plant (Hanselka and Paschal 1991).

Traditional Control Strategies

Since the 1930's, ranchers and land managers have sought out strategies to mitigate prickly pear's aggressive competitive nature (Dameron and Smith 1939; Hyder, et al. 1975; McGinty 2001). Unfortunately, the strategies traditionally available to control this succulent (i.e. mechanical, chemical, biological, and judicious use of low-intensity prescribed fire) are widely regarded as ineffective (Aldridge, et al. 1983; Taylor 2008). Prickly pear's ease of establishment is a major impediment for profitable and sustainable ranching on these deteriorated rangelands (Ansley and Castellano 2007*b*; Dodd 1940; Lundgren, et al. 1981; McCalla, et al. 1984; Scholes and Archer 1997; Scifres 1980; Stoddart and Smith 1943; Teague, et al. 2008; Ueckert, et al. 1988; Van Auken 2009; Walker 1993). In the following section, an overview of the strategies that have been developed to prevent prickly pear encroachment is presented.

Mechanical

The selective physical removal of problematic and undesirable species by hand or with heavy machinery is an effective approach in easily accessible areas with a relatively low density of prickly pear (Costello 1941; Dameron and Smith 1939; Dodd

1968; Holechek, et al. 1989). However, this strategy is comparably expensive in these low-production areas, characterized by having low economic returns, as the initial investment is high (Gaylord 1982; Holechek and Hess 1994; Ueckert, et al. 1988). The two main concerns regarding this mechanical approach are its inability to be used on rough terrain (i.e. hills, rocky areas) and its potential to increase the density of cactus (Hanselka and Paschal 1991). The crushed prickly pear pads left on the disturbed soil surface have the ability to propagate and eventually increase the relative dominance of this problematic succulent (Ansley and Castellano 2007*b*).

Chemical

The use of herbicides on undesirable prickly pear is an effective way to halt its encroachment in areas with a relatively low density of cactus (McGinty and Ueckert 2005). The phytotoxic compounds in herbicides will cause the death of the plant tissue. However, the efficacy of this strategy is often limited by multiple factors. First, there are environmental factors including soil moisture availability and seasonality that limit the performance of herbicides (Fletcher and Kirkwood 1982). Second, the application of herbicides is also cost-prohibitive to most ranchers (McMillan, et al. 2002). Lastly, a special chemical applicators license for restricted herbicides is needed to comply with federal and state environmental regulations (Martinelli, et al. 1982). These regulations have been set to limit the adverse environmental impacts on the surrounding vegetation, and in particular to fragile aquatic ecosystems (Cobb, et al. 1992).

Biological

The use of natural herbivores (i.e. insects, ungulates) can be a comparatively inexpensive strategy to exert environmental stress to reduce the dominance of the undesirable vegetation (Campbell and Taylor 2006; Hajek 2004; Wilson and McCaffrey 1999). However, it is often not a precise or targeted form of weed and brush control, and it can inadvertently cause greater ecological problems (i.e. eradication of valuable species, overgrazing) if it is not managed with extreme care (Pearson and Callaway 2005; Simberloff and Stiling 1996; Smith 1899). Unfortunately, there is no consensus of the short-term and long-term effects of biological brush control strategies to control prickly pear encroachment in the Edwards Plateau region of Texas (Russell and Felker 1987; Stiling 2002). Specifically, this method has the following two adverse consequences. First, the use of insects as a biological control is especially problematic for ranchers, because it could potentially lead to the elimination of other desirable (i.e. profitable) succulent crops (Hanselka and Paschal 1991; Pimienta-Barrios 1994; Russell and Felker 1987). Second, the complete eradication of prickly pear is not ideal, because ranchers rely on prickly pear as an emergency source of supplemental feed for wildlife and domestic livestock during extreme drought when other forage sources are depleted or dormant (Ansley and Castellano 2007a; Bement 1968; Chamrad and Box 1965; Chavez-Ramirez, et al. 1997; Griffiths 1905; Hernández 1999; Taylor, et al. 1980; Ueckert, et al. 1988). The consumption of the prickly pear stems joints by mammalian herbivores is particularly dependent upon fire first removing the spines (Reynolds and Bohning 1956; Ueckert, et al. 1990). Once scorched, the succulent stem tissue

commonly referred to as “chumascado” by ranchers in South Texas, is especially palatable to herbivores (Thomas 1991).

Prescribed Fire

During the Pre-Columbian era, fire was a commonly used brush control strategy adopted by indigenous cultures in an effort to increase high quality forage density (Scholes and Archer 1997; Stoddart and Smith 1943; Teague, et al. 2008; Van Auken 2009). This practice has now been recognized as a potential brush management strategy to control undesirable prickly pear encroachment (Bailey 1988; Cable 1967; Fuhlendorf, et al. 2009; Scifres, et al. 1985). Fire can be judiciously applied in a variety of terrestrial ecosystems as long as the environmental conditions are adequate and there is sufficient fuel to carry the fire across the landscape (Ansley and Taylor 2004; Bowman, et al. 2009; Lundgren, et al. 1981; Scifres and Hamilton 1993; Van Auken 2009; Weir 2009; Wright and Bailey 1982). Prescribed fire (i.e. controlled burning) is also comparatively less expensive than other brush control strategies (i.e. mechanical and chemical). However, careful planning by fire-management experts is necessary to prevent wildfires (Bova and Dickinson 2005; Limb, et al. 2016). Close attention is especially required for sites with a history of fire suppression now experiencing an accumulation of highly volatile fuels (Pyke, et al. 2010).

Traditionally low-intensity fires, referred to as ‘maintenance’ prescribed burns, were applied as surface fires in the winter months under mild environmental conditions (i.e. low air temperature, high relative humidity, consistently low wind speed). However, ecological state shifts on landscapes with significant prickly pear and brush

encroachment are difficult to reverse with the application of a low-intensity prescribed fire (Ansley and Taylor 2004; Suding, et al. 2004) .

Impediments to Current Management Efforts

Unfortunately, the control strategies that are currently available (i.e. mechanical, chemical, biological, and judicious use of low-intensity prescribed fire) have not kept pace with the present rate of prickly pear encroachment (Taylor, et al. 1993). These management efforts are not well-adapted because they are not efficient at mitigating this succulents' expansion. Landscapes with substantial prickly pear expansion are challenging and costly to restore with traditional strategies, and they do not provide a suitable economic return to agricultural producers and land managers tasked with maintaining sustainable rangeland ecosystems (Gaylord 1982; Holechek and Hess 1994; Lundgren, et al. 1981; Weltz, et al. 2003).

CHAPTER II

REGIONAL OVERVIEW OF RESEARCH SITES

DESCRIPTION AND CHARACTERISTICS OF THE EDWARDS PLATEAU

The field experiments associated with this dissertation were established on rangeland sites located within the Edwards Plateau ecological resource area (Figure 4).

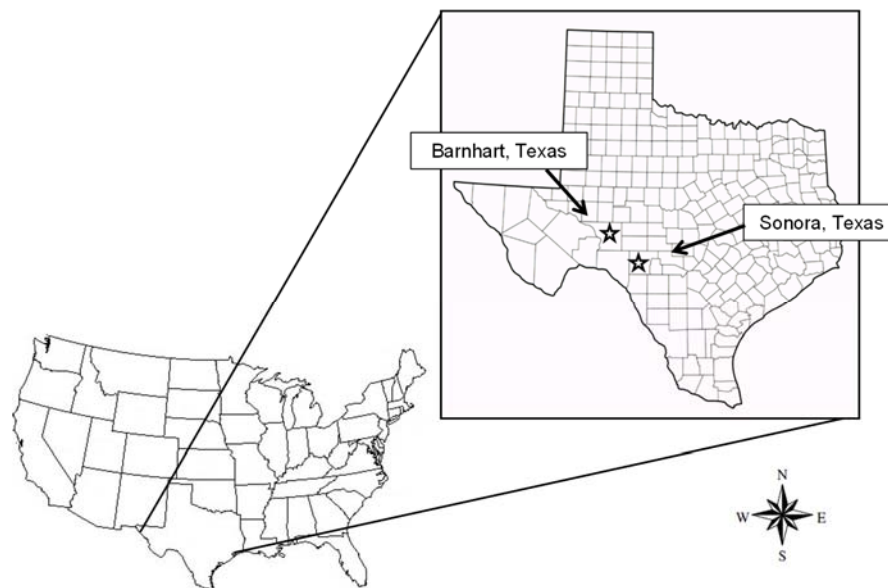


Figure 4. The geographic location of the research stations where ecological field research studies were conducted.

The Edwards Plateau ecological region is located in west central Texas. This semi-arid plateau is part of the vast grassland ecosystem that comprises the Great Plains of North America. It is a patchwork of vegetation and soil types that occupies approximately 9.7 million hectares (Huston, et al. 1981). Historically, the potential vegetation present on these rocky plateaus was characterized as a tall grassland savanna

(Küchler 1964). The Edwards Plateau ecological resource area is bordered by the Chihuahuan Desert on the west, the High Plains on the northwest, the Southwestern Tablelands, the Central Great Plains, and the Cross Timbers on the north, and the Southern Texas Plains on the South (Omernik 1987) (Figure 5).

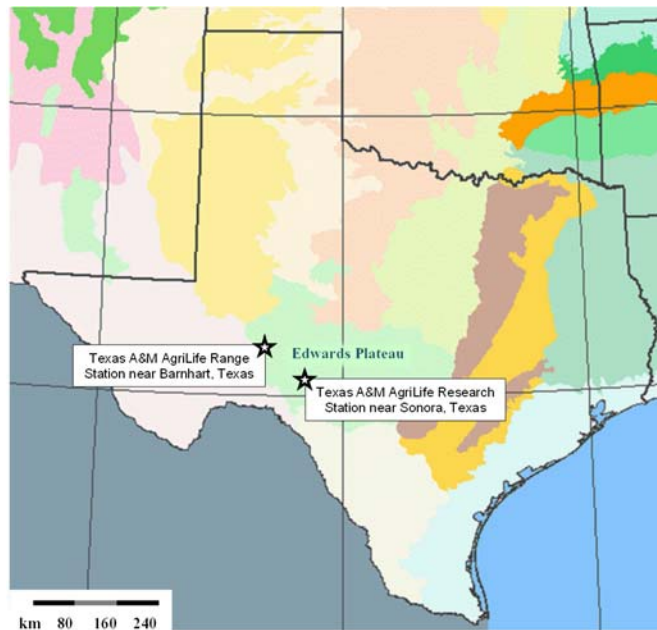


Figure 5. The Texas AgriLife Range Station near Barnhart, Texas and the Texas AgriLife Research Station near Sonora, Texas are located over the Edwards Plateau ecological resource area (Omernik 1995; U.S. Geological Service 2014a).

Geomorphology and Soils

The Edwards Plateau is referred to as the “hill country” of Texas. The underlying material is limestone bedrock (Toomey, et al. 1993) (Figure 6). The karst topography of these dissected plateaus is rugged and it is characterized by rocky outcrops (Taylor 2005). The landscape contains limestone fragments, stones and gravel. The soils

corresponding to this ecological resource area are moderately shallow, and they have a very low to low total available water holding capacity (Heilman, et al. 2009). The soil parent material comes from residuum weathered from limestone (Rabenhorst and Wilding 1986a).

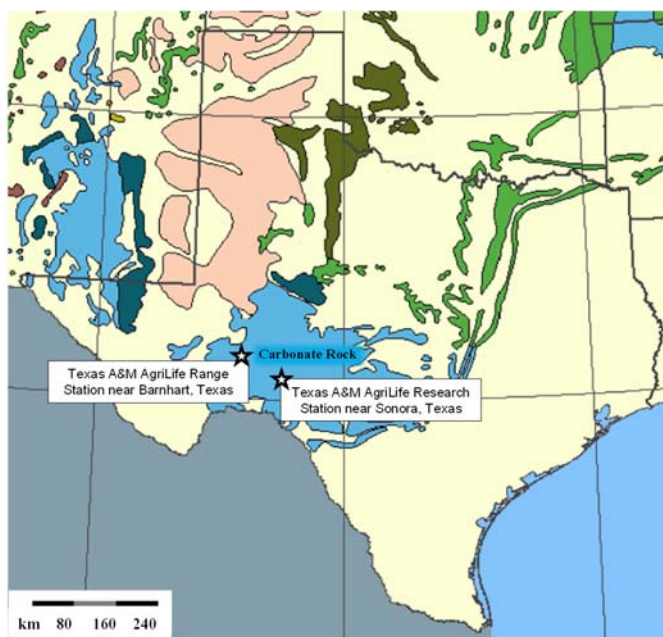


Figure 6. Ecological research studies were conducted on sites typified by rolling stony hill topography. The geology corresponding to the 93,000 km² Edwards Plateau is underlain by Cretaceous carbonate bedrock (Rabenhorst and Wilding 1986c; Schwinning 2008; U.S. Geological Service 2014b).

Regional Climate

The Texas Edwards Plateau is a region that experiences moderate seasonal and annual drought (Fuhlendorf and Smeins 1997) (Figure 7). The climate is characterized as semi-arid, it is hostile and precipitation is unpredictable and highly variable (Taylor, et al. 1993). The summer months are moderately warm and dry and winters are relatively

mild (Toomey, et al. 1993). The average growing season is approximately 240 days (Thurow, et al. 1986). The regional frost-free period extends from mid-March through mid-November and annual precipitation is bimodal with rainfall concentrated in the spring and fall (Huston, et al. 1981). The majority of precipitation events are described as brief and intense resulting from convective storms that develop during warm and humid atmospheric conditions (Amos and Gehlbach 1988). Frontal storms in the cool-season months are characterized by slow, steady rainfall. These rainfall events range from October through April.

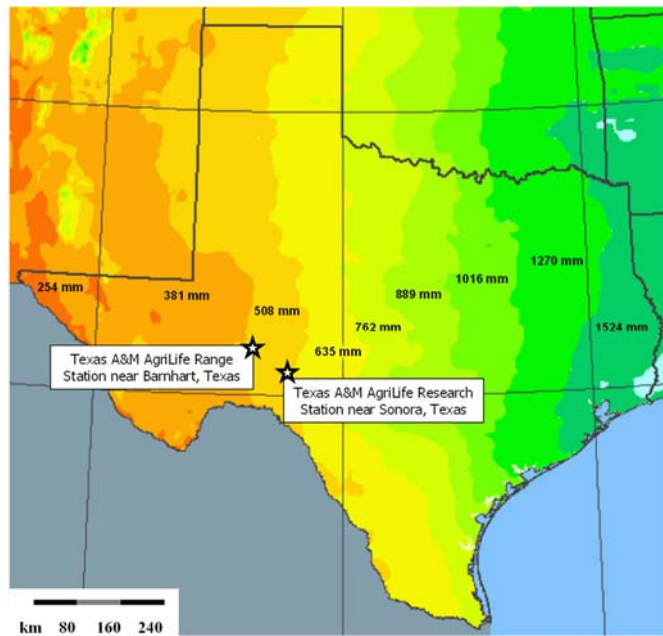


Figure 7. Average annual precipitation for the state of Texas varies from less than 254 mm in the west to over 1524 mm in the east (1990-2009) (NOAA 2014). This figure indicates the location of Texas AgriLife Range Station and the Texas AgriLife Research Station.

Vegetation and Regional Ecology

Climate, topography, geomorphology, pyric succession and management practices are controlling factors in vegetation and soil development. The Edwards Plateau resource area is characterized by vegetation that has a high tolerance to dry conditions and a relative low per unit area productivity (Fowler and Dunlap 1986; Taylor, et al. 1993). The majority of the annual growth occurs during March, April, May, and July, as a result of spring and early summer rains, when growing conditions are favorable (Bryant, et al. 1979). This region has the potential to support a heterogeneous mixture of grasses, trees and shrubs (Taylor, et al. 1993).

Prior to European settlement, historical accounts describe the Texas Edwards Plateau as a short and mid grass dominated landscape (Smeins 1980; Taylor 2007; Toomey, et al. 1993). This ecosystem evolved under a regime of naturally occurring fires and a constant low grazing pressure (Fowler and Dunlap 1986). The ecological structure of the flora was characterized as extensive grasslands punctuated by occasional trees and shrubs that were scattered or widely spaced (Smeins 1980; Smeins, et al. 1997). However, today, as a result of euro-centric land management practices, these highly desirable native perennial mid grasses have been replaced by less palatable and less desirable woody (i.e. mesquite, juniper) and succulent species (Beever et al. 2003; Fuhlendorf, et al. 1997; Lundgren, et al. 1981).

A policy of fire suppression and a history of heavy continuous livestock grazing have altered the fire regime (Archer 1989; Frost 1998). Most notably, excessive stocking rates have uniformly reduced the standing crop biomass (i.e. fuel loads) which has led to

feedbacks that further reduce the probability of natural fires (Fuhlendorf, et al. 1996). The establishment of the cattle industry at the beginning of the late nineteenth century progressively reduced the density and production of desirable palatable forage species, this change has altered the species composition, structure, and ecological function of this rangeland ecosystem (Archer, et al. 1995, Holechek 2002; Noble and Slatyer 1980).

Today, woody brush infestation has suppressed herbaceous production. This semi-arid plant community is dominated by a high density of trees of woody shrub species, short grasses, less palatable annual and perennial forbs, and succulents (Hanselka and Paschal 1991; Taylor 2007). A reduction in fire frequency and extent is recognized as a driving factor in the ecological degradation of this fire-prone ecosystem (Frost and Robertson 1987; Fuhlendorf, et al. 2012; McGranahan, et al. 2012; Stronach and McNaughton 1989). Conditions now favor woody and succulent plants (Mayheux, et al. 1991; Van Auken 2000). These savanna landscapes have been converted to dense brushlands and thickets that interfere with the handling and movement of livestock (Dameron and Smith 1939; Hanselka and Falconer 1994; Lundgren, et al. 1981; Stoddart and Smith 1943; Taylor 2008). An increase in prickly pear cactus abundance has resulted in an economic loss to ranchers, it has severely reduced forage quality and quantity, and it has degraded range and wildlife habitat (Ansley and Castellano 2007b; Augustine and Milchunas 2009; Holechek 2007; Maczko, et al. 2011; Teague, et al. 2008).

Land Management

This vast region provides ideal wildlife habitat for whitetail deer (*Odocoileus virginianus*), wild turkey (*Meleagris gallopavo*), javelina (*Tayassu tajacu*), White-winged Doves (*Zenaida asiatica*), scaled quail (*Callipepla squamata*), common gray fox (*Urocyon cinereoargenteus*), raccoon (*Procyon lotor*), western spotted skunk (*Spilogale gracilis*), opossum (*Didelphis virginiana*), armadillo (*Dasypus novemcinctus*), eastern cottontail (*Sylvilagus floridanus*), black-tailed jack rabbit (*Lepus californicus*), rock squirrel (*Spermophilus variegatus*), Mexican free-tailed bats (*Tadarida brasiliensis*), numerous rodents, coyote (*Canis latrans*), bobcat (*Lynx rufus*), along with an occasional mountain lion (*Felis concolor*) (Chavez-Ramirez and Slack 1993; Clark 1951; Hernández, et al. 1997; Huston, et al. 1981; Small, et al. 2010; Toweill and Teer 1977). The xeric environment and rugged terrain that typifies this region is predominantly grazed by sheep and goats, it is not ideal for crop cultivation (Chambers 1932; Gaxiola, et al. 2010).

Today, ranchers on the Edwards Plateau are pursuing a multiple-use approach to land management (e.g., ranching, hunting leases, and recreation) (Brown, et al. 2008; Bryant 1991; Anderson and McCuistion 2008). This approach allows them to diversify sources of potential income (Costanza, et al. 1997; Galt, et al. 2000). Ranchers have realized that the economic value of hunting leases can often equal to or exceeds the net income derived from livestock production (Berger 1973; Richards and George 1996).

TEXAS AGRILIFE RESEARCH STATION NEAR SONORA, TEXAS

Ecological research studies were conducted at the Texas AgriLife Research Station located approximately 56 km southeast of Sonora, Texas, USA (30° N, 100° W) (Thurrow, et al. 1986). This 1,404 hectare research station lies on the boundary separating Sutton and Edwards counties, it is located on the Edwards Plateau Major Land Resource Area (81B-*Edwards Plateau, Central Part*) (Bryant, et al. 1981; McGinty, et al. 1979; Taylor and Ralphs 1992). The research station was established early in the twentieth-century with the goal of providing Texas ranchers and landowners with improved management strategies that would benefit rangeland conditions and animal health (Thurrow and Taylor 1999). Throughout its c.100 year history, researchers affiliated with the station have pursued wide-ranging areas of inquiry including grazing management and ecology, brush management, livestock health and production, wildlife management, plant ecology, restoration ecology, and ecohydrology (Amos and Gehlbach 1988; Fuhlendorf, et al. 1997).

The topography of this region is generally typified as dissected limestone plateaus. The station is primarily composed of the low stony hill range sites; it has an elevation of approximately 763 m (Kastning 1983; Fuhlendorf, et al. 1997). The climate in this part of the Edwards Plateau is temperate (mean annual temperature 17.9°C), air temperatures average 28°C in July and 7°C in January (NOAA 2014; Figure 8). This semi-arid region receives an average annual precipitation of approximately 586.4 mm. Of this, the station receives an average of 470.1 mm, or 80.2 percent, falls in March through October. The prevailing wind is from the southeast.

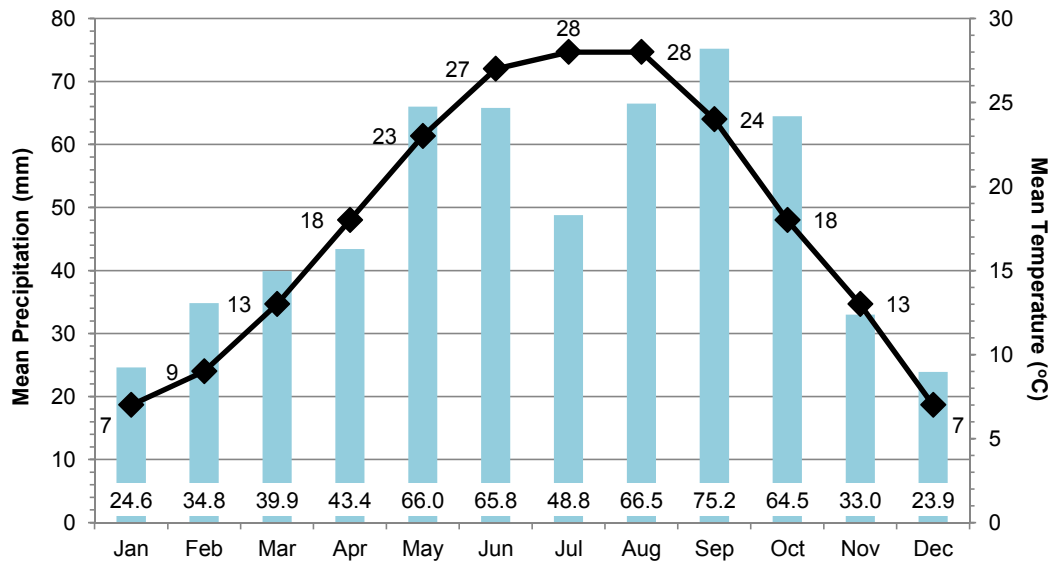


Figure 8. Monthly mean temperature and precipitation for the Texas AgriLife Research Station near Sonora, Texas. Annual precipitation is bimodally distributed, with the wettest months occurring in the spring (May/June) and fall (September/October) (NOAA 2014).

The soils associated with the experiments at the research station are typical of the central part of the Edwards Plateau. The soil series present on the research sites include the Eckrant-Rock outcrop complex soil (EcF), Prade-Eckrant complex soil (PeB) and the Valera Clay complex soil (VaA). EcF and PeB soils are derived from residuum weathered limestone bedrock (Rabenhorst and Wilding 1986*b*). These moderately alkaline and calcareous soils are very shallow and well drained; they are characterized by having a very low to low available water holding capacity (USDA-NRCS 2017). EcF soils correspond to the taxonomic class, Clayey-skeletal, smectitic, thermic Lithic Haplustolls, and they have a slope of 1 to 20 percent. PeB soils are composed mainly of silt and clay, and correspond to the taxonomic class, Clayey-skeletal, smectitic, thermic Petrocalcic Calciustolls, these soils have 0 to 3 percent slopes (USDA-NRCS 2017). In

contrast, Valera Clay complex soils (VaA) have 0 to 2 percent slopes and high moisture holding capacity. These clay soils correspond to the taxonomic class, fine, smectitic, thermic Petrocalcic Calciustolls (USDA-NRCS 2017).

Although previously characterized as semi-arid grassland savanna, nowadays sites corresponding to the research station near Sonora, Texas are degraded as a result of a history of chronic high levels of livestock grazing and fire suppression (Smeins, et al. 1976). The historic climax plant community (i.e. C4 grasses, desirable forbs) have been replaced by short grasses, woody shrubs and prickly pear (McCarron and Knapp 2001) (Figure 9). The co-occurrence of woody brush encroachment (i.e. mesquite, juniper) with increased prickly pear density has significantly altered the vegetation structure and the ecological condition of these rangelands (Gleason 1951; Van Auken 2009).



Figure 9. Prickly pear cactus is moderately thick at the Texas AgriLife Research Station near Sonora, Texas. Following a survey in 2008, we calculated an average prickly pear density of *c.* 341 cactus plants (i.e. mottes) per hectare on sites corresponding to this dissertation research.

The dominant woody plants and shrub species present at the station include live oak (*Quercus virginiana*), scrub oak (*Quercus pungens*), Vasey shin oak (*Quercus pungens* var. *vaseyana*), Plateau oak (*Quercus virginiana* var. *fusiformis*), honey mesquite (*Prosopis glandulosa* var. *glandulosa*), ashe juniper (*Juniperus asheii*), redberry juniper (*Juniperus pinchotii*), Texas persimmon (*Diospyros texana*), and prickly pear (*Opuntia* spp.) (Fuhlendorf and Smeins 1998, Taylor and Ralphs 1992, Taylor 2007, Taylor, et al. 1993). The most abundant forb species present include scurfpea (*Psoralidium lanceolatum*), bushsunflower (*Simsia calva*), Mexican sagewort (*Artemisia ludoviciana*), Engelmann daisy (*Engelmannia peristenia*), Texas bluebonnet (*Lupinus texensis*), common horehound (*Marrubium vulgare*), Western bitterweed (*Hymenoxys odorata*), spreading sida (*Sida filicaulis*), and doze daisy (*Aphanostephus ramossissimus*) (Taylor, et al. 1980).

The short grasses found on this research site include, common curly-mesquite (*Hilaria belangeri*), hairy grama (*Bouteloua hirsuta*), buffalograss (*Bouteloua dactyloides*), Texas wintergrass (*Stipa leucotricha*), hairy tridens (*Erioneuron pilosum*), red grama (*Bouteloua trifida*), rescue grass (*Bromus unioloides*), threeawns (Wright threeawn (*Artistida wrightii*) and purple threeawn (*A. purpurea*) (Fuhlendorf and Smeins 1997; McCalla, et al. 1984). The aforementioned grasses have replaced higher successional grasses including, sideoats grama (*Bouteloua curtipendula*), Texas cupgrass (*Eriochloa sericea*), little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardi*), Indiangrass (*Sorghastrum nutans*), cane bluestem (*Bothriochloa barbendis*), switchgrass (*Panicum virgatum*), fall witchgrass (*Digitaria cognata*), Merrill

bluestem (*Bothriochloa edwardsiuna*), and vine mesquite (*Panicum obtusum*) (Fuhlendorf and Smeins 1997; Taylor and Ralphs 1992; Taylor, et al. 1993; Taylor, et al. 1980; Taylor 2007). Early in the twentieth century, these midgrasses were rigorously defoliated by domestic herbivores (i.e. cattle, sheep, goats), stocking rates at the station were recorded to be as high as c. 2.7 ha/auy (Fuhlendorf and Smeins 1997; Smeins, et al. 1976; Taylor and Ralphs 1992; Thurow and Taylor 1999). In its current condition, the herbaceous production for the research sites at the station can range from 1,128 to 5,078 kilograms/hectare (i.e. total dry-weight production) (USDA-NRCS 2017). A conservative stocking rate for this semi-arid rangeland requires the use of about 35% of the forage resources (Holechek, et al. 1999).

TEXAS AGRILIFE RANGE STATION NEAR BARNHART, TEXAS

A research study was conducted in the northwestern portion of the Edwards Plateau on the Texas AgriLife Range Station located along Texas State Highway 163 between Ozona and Barnhart, Texas, USA (31° N, -101° W) (Huss and Allen 1969). This 1,279 hectare station is located in Crockett county on the western edge of the Edwards Plateau Major Land Resource Area (81A—*Edwards Plateau, Western Part*) (Bryant, et al. 1981). The range station was established in 1938 on land that is used for grazing of livestock and wildlife habitat (Thomas and Young 1954).

The climate in this northwestern part of the Edwards Plateau is temperate (mean annual temperature 18°C) with an average growing season equal to or greater than 209 days (USDA-NRCS 2017). Mean monthly air temperatures range from 28°C in July and 7°C in January (NOAA 2014; Figure 10). Drought is common; there is a large variability in annual and seasonal rainfall. This region receives a mean annual precipitation of approximately 480.3 mm; it follows a bimodal pattern, with peaks in May and October. Of this, the station receives an average of 389.3 mm, or 81.1 percent, falls in March through October (NOAA 2014). The prevailing wind is from the south.

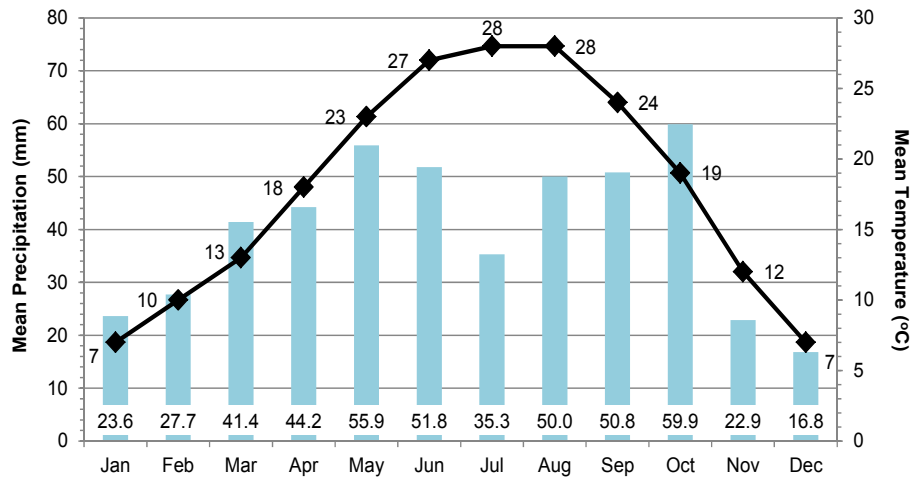


Figure 10. Monthly mean temperature and precipitation for the Texas AgriLife Range Station near Barnhart, Texas. The station receives an average annual precipitation of 480.3 mm; it follows a bimodal precipitation pattern with most rainfall occurring during spring (May) and fall (October) peaks.

The Texas AgriLife Range Station has an elevation of approximately 800 m; the regional topography is generally typified as dissected limestone plateaus. The terrain of the station is gently to moderately sloping, the landscape consists of broad valleys and flat divides that are primarily characterized by scattered shallow depressions derived from ancient dry playa lake beds (Taylor and Ralphs 1992; USDA-NRCS 2017). Texon-Ozona complex soil (ToB) is the dominant soil present in the study area. ToB is composed of calcareous clayey materials that are characterized as moderately alkaline silt loam, and the sub-soil is composed of moderately alkaline silty clay (USDA-NRCS 2017). The Texon series soils are fine, smectitic, thermic Torrertic Calciustolls. The Ozona series soils are loamy mixed, superactive, thermic, shallow Petrocalcic Calciustolls. The parent material for these soils comes from slope alluvium derived from weathered limestone bedrock. ToB soil has slopes of 0 to 3 percent, it is well drained

and it has a high moisture holding capacity. Intense rainfall events can result in soil surface runoff if these rangelands are lacking herbaceous vegetation cover (Soto and Díaz-Fierros 1998; USDA-NRCS 2017).

The historic climax plant community for this semi-arid site was described as an open savanna dominated by mid- and short-grasses with scattered woody shrub and succulent species (Taylor and Ralphs 1992; USDA-NRCS 2017). The palatable mid grasses present included sideoats grama (*Bouteloua curtipendula*), cane bluestem (*Bothriochloa barbendis*), vine mesquite (*Panicum obtusum*), Arizona cottontop (*Digitaria californica*), plains bristlegrass (*Setaria vulpiseta*), black grama (*Bouteloua eriopoda*) (Petersen, et al. 1987). In the past century, further range degradation occurred under continuous heavy grazing by sheep and goats (McGinty, et al. 1979; van de Koppel, et al. 1997). The aforementioned later successional mid grasses were replaced by tobosagrass (*Hilaria mutica*), buffalograss (*Bouteloua dactyloides*), curly-mesquite (*Hilaria belangeri*), slim tridens (*Tridens muticus*), Texas cupgrass (*Eriochloa sericea*), other undesirable stoloniferous short grasses, weedy annuals, mesquite (*Prosopis glandulosa*), prickly pear (*Opuntia* spp.), and annual forbs, such as broomweed (*Amphiachyris drancunculoides*) (Taylor and Ralphs 1992; USDA-NRCS 2017).



Figure 11. Prickly pear cactus mottes on these rangelands at the Texas AgriLife Range Station near Barnhart, Texas, form entangled thickets; we calculated *c.* 747 cactus plants per hectare.

Today, these lands are dominated by thick stands of prickly pear with an overstory of woody brush, while the herbaceous plant community has experienced a significant decline in cover (Figure 11). In its present condition, herbaceous production on Texon-Ozona complex soil (ToB) within the western Edwards Plateau can range from 1,120 to 2,914 kilograms/hectare (i.e. total dry-weight production) and it is moderately grazed by sheep and goats (USDA-NRCS 2017). The herbaceous plant community consists of almost pure stands of tobosagrass, a C4 rhizomatous perennial bunch grass that produces large amounts of dry standing biomass, and high density of broomweed, an annual warm-season native plant (Taylor and Ralphs 1992).

CHAPTER III

RESEARCH OBJECTIVES

In this dissertation we conducted three quantitative ecological studies in a field setting to assess whether management strategies that differ from traditional approaches are better suited to improve the rangeland productivity and promote the conservation and ecological integrity of brush encroached rangeland ecosystems in the Edwards Plateau of Texas. Herein, the specific research objectives are described:

The first study is presented in Chapter IV, and it was designed to evaluate the response of prickly pear to high-intensity prescribed fires (commonly referred to as ‘reclamation’ fires) in combination with the subsequent application of a low-intensity prescribed ‘maintenance’ fire. The particular aim of this research experiment was to determine if this combination of distinct prescribed fire treatments (i.e. reclamation, maintenance fires) would be a favorable management strategy to reduce problematic succulent encroachment.

The second study is presented in Chapter V, and the fundamental purpose of this research was to examine the susceptibility of a drought-stricken succulent to a low-intensity prescribed ‘maintenance’ fire. Specifically, we compared the response of induced, drought-stricken succulents versus succulents under natural field conditions. This experiment was designed to assess the correlative effects of drought and fire on a succulent’s thermo-physiological tolerance.

Lastly, the objective of the third study was to evaluate the integration of more than one brush control management strategy. In particular, the intent of Chapter VI of this experiment was to determine the reduction in prickly pear cover from a ‘maintenance’ prescribed fire in combination with a follow-up application of a federally non-restricted (i.e. Vista®) or federally restricted-use (i.e. Surmount™) herbicide brush control treatment. This field study was also designed to compare the effectiveness of the non-restricted versus restricted herbicide on this succulent.

CHAPTER IV
RECLAMATION PRESCRIBED FIRE AS THE CATALYST TO
RESTORE A PRICKLY PEAR ENCROACHED RANGELAND

INTRODUCTION

Ecological state shifts on landscapes with significant degradation are difficult to reverse with traditional management practices because there are numerous biotic and abiotic variables that influence ecological processes and enhance ecosystem resilience (Gunderson 2000; Scheffer and Carpenter 2003). Degradation will cause a transition of plant communities into new, non-historical configurations of species composition and assemblages (Hobbs et al. 2013; Seastedt, et al. 2008). Because it alters the intra- and interspecific vegetation dynamics and soil processes, degradation can negatively influence the productivity and sustainability of these ecosystems, leaving them in a state of lower ecological order (Pickett, et al. 2009; van de Koppel, et al. 1997; Weltz, et al. 2003). The properties or functions of these communities lie outside their historic ranges of variability, resulting in no-analog, novel, or emerging ecosystems (Hobbs, et al. 2006; Hobbs et al. 2009; Weixelman, et al. 1997). In order to restore ecological communities and enhance ecosystem sustainability, it is critical to understand the response of these degraded ecosystems to intervention strategies (i.e. managerial inputs) and better predict how they might respond to other natural disturbances (i.e. drought, overgrazing) (Allen 1995; Anderson and Brown 1986; Chapin III, et al. 2009; Folke, et al. 2004; Hobbs and Harris 2001; Huston 2004; Ruiz-Jaen and Mitchell Aide 2005; Weltz, et al. 2003).

Prickly pear is a hardy succulent with an aggressive competitive nature which presents a significant impediment for land managers committed to maintaining profitable and sustainable rangelands (Taylor, et al. 2012). Specifically, it has encroached in rangeland ecosystems of the Edward Plateau in Texas with a history of fire suppression and overgrazing (Taylor 2007). This encroachment has contributed to a change in the plant community in Texas rangelands which provides an ideal case study opportunity to examine ecological state shifts. In the absence of effective brush management control prickly pear will rapidly establish its dominance in these rangelands, as it will reduce forage availability and limit management activities (i.e. livestock movement and accessibility) (Amos and Gehlbach 1988; Chavez-Ramirez, et al. 1997; McGinty 2001; Taylor, et al. 1993).

The removal of prickly pear encroachment is difficult to achieve with only a traditional mild prescribed fire or with just one brush control treatment (Lundgren, et al. 1981). Researchers who have conducted studies on Texas rangelands have reported that during the growing season, prickly pear tissue is physiologically active and appears to be more susceptible to fire damage (Ansley and Castellano 2007*b*; Benson and Walkington 1965; Brown and Minnich 1986; Daubenmire 1968; McPherson 1995; Humphrey and Everson 1951; O'Leary and Minnich 1981). Even though prior evidence suggests that cacti susceptibility to fire differs seasonally, there is limited information available about the ecological response of cactus dominated rangeland savannas to high intensity 'reclamation' fire. In particular, there is a need to examine the effectiveness of these specific fires at controlling prickly pear encroachment.

A field study was designed to empirically evaluate the response of prickly pear to the application of a high-intensity ‘reclamation’ prescribed fire in combination with the subsequent application of a low-intensity ‘maintenance’ prescribed fire. These ‘reclamation’ or so-called extreme prescribed fires are typically applied during the summer months when the environmental conditions are characterized by exceptionally hot temperatures and a relatively low humidity (Hamilton and Ueckert 2004; Taylor 2003). In addition to these distinct environmental conditions, the intensity of the ‘reclamation’ fires is dependent on an abundance of flammable fuel loads (Cable 1972; Hamilton and Ueckert 2004; Kerby, et al. 2007; Whelan 1995). In contrast, ‘maintenance’ fires are applied under mild environmental conditions (i.e. low air temperature, high relative humidity) in the late-fall and throughout the winter months (Ansley and Jacoby 1998; Hodgkinson 1991; Peterson and Reich 2001; Whisenant, et al. 1984).

We hypothesize that ‘reclamation’ fires are the catalyst that will induce a change in the ecological succession in this degraded plant community. To further this hypothesis, we also submit that the application of a ‘maintenance’ prescribed fire treatment following a ‘reclamation’ fire will inhibit additional prickly pear establishment. The findings from this research will be of keen interest to land managers looking for an effective approach to reduce the chronic expansion of prickly pear in an effort to increase desirable forage cover and restore the ecological integrity of these rangelands.

METHODS

Study Site

In June 2007, a field-based ecological research study was established in the southwestern portion of the Edwards Plateau Major Land Resource Area (81B-*Edwards Plateau, Central Part*) at the Texas AgriLife Research Station (Bryant, et al. 1981; Taylor and Ralphs 1992). Historically, the vegetation present on these rocky plateaus was characterized as mid-short grassland savannah (Gleason 1951; USDA-NRCS 2017). Presently, the vegetation at the station has transitioned into a woody brush and prickly pear dominated rangeland (c. 341 cactus mottes per hectare). The 1,401 hectare station is located along Texas State Highway 55 between Rocksprings and Sonora, Texas (30° N, -100° W; elevation of approximately 763), and it lies on the boundary separating Sutton County and Edwards County. This temperate semi-arid site experiences a growing season spanning 235 days, a mean annual temperature of 17.9°C and it receives a mean annual precipitation of approximately 586.4 mm (Bryant, et al. 1980; NOAA 2014; USDA-NRCS 2017). The station has a topography that is generally typified as dissected limestone plateaus with moderately shallow soils that have a very low to low total available water holding capacity. According to the USDA-NRCS (2017), the dominant soil series present at the station include the Eckrant-Rock outcrop complex soil (EcF), Prade-Eckrant complex soil (PeB) and the Valera Clay complex soil (VaA). In 1916, the station was established to assist the local livestock industry with ranch management problems, and its current purpose is to facilitate research in wide-ranging areas of inquiry including grazing and brush management, livestock health and

production, wildlife management, plant ecology, restoration ecology, and ecohydrology (Fuhlendorf, et al. 1996). For the duration of this experiment, all domestic ungulate grazing was deferred from the pastures associated with our research site to prevent domestic livestock (i.e. cattle, sheep, or goats) trampling of the mottes; however, these pastures were accessible to wildlife (e.g., white-tailed deer, rabbits, rodents).

Experimental Design

We employed a completely randomized balanced research design to examine the *in situ* response of prickly pear to prescribed fire treatments. Each experimental plot was randomly assigned to one of the following treatments: [reclamation prescribed fire], reclamation prescribed fire + follow-up, maintenance fire], and [no fire (control)] (Figure 12).

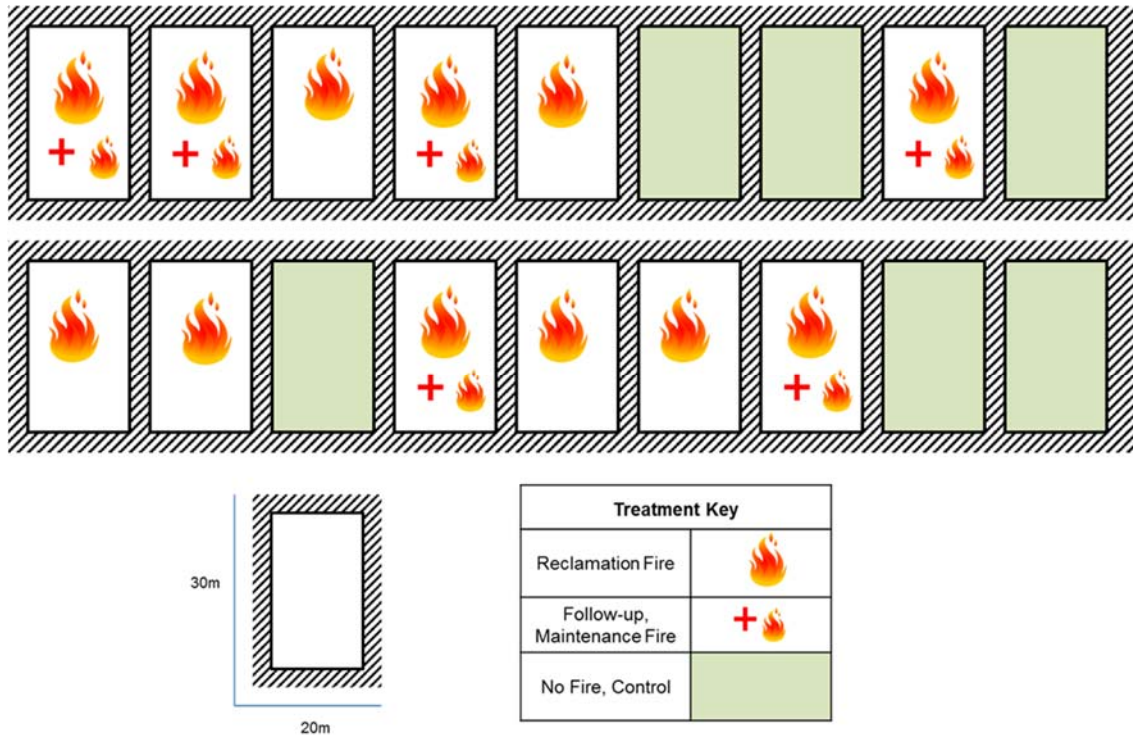


Figure 12. Schematic representation of the independent permanent plots established at the Texas A&M AgriLife Research Station near Sonora, Texas to examine the use of prescribed fire on a prickly pear encroached rangeland.

We delineated eighteen rectangular (20 by 30 m) plots on a one-hectare site with a similar grazing and land management history. The vegetation on these pastures was primarily composed of grasses, trees, succulents and forbs. The most common grasses are curly-mesquite (*Hilaria belangeri*), hairy grama (*Bouteloua hirsuta*), buffalograss (*Bouteloua dactyloides*), Texas wintergrass (*Stipa leucotricha*), hairy tridens (*Erioneuron pilosum*), red grama (*Bouteloua trifida*), rescue grass (*Bromus unioloides*), threeawns (Wright threeawn (*Artistida wrightii*), and purple threeawn (*A. purpurea*). The most common trees are live oak (*Quercus virginiana*), scrub oak (*Quercus pungens*), Vasey shin oak (*Quercus pungens* var. *vaseyana*), Plateau oak (*Quercus*

virginiana var. *fusiformis*), honey mesquite (*Prosopis glandulosa* var. *glandulosa*), ashe juniper (*Juniperus asheii*), redberry juniper (*Juniperus pinchotii*), and Texas persimmon (*Diospyros texana*). The common succulent is prickly pear (*Opuntia* spp.), and the most common annual forbs found in this region are scurfpea (*Psoraleidium lanceolatum*), bushsunflower (*Simsia calva*), Mexican sagewort (*Artemisia ludoviciana*), Engelmann daisy (*Engelmannia peristenia*), Texas bluebonnet (*Lupinus texensis*), common horehound (*Marrubium vulgare*), Western bitterweed (*Hymenoxys odorata*), spreading sida (*Sida filicaulis*), and doze daisy (*Aphanostephus ramossissimus*) (Fuhlendorf and Smeins 1997; Fuhlendorf and Smeins 1998; Taylor, et al. 1980; Taylor and Ralphs 1992; Taylor 2007; Taylor, et al. 1993).

To prevent the accidental burning of vegetation outside of the plots, backfires were established downwind of the plot edges prior to the burning of the individual plots. Each plot was separated by a 15 m-wide firebreak that was cleared of vegetation to prevent firebrands from starting unintentional fires outside their respective individual burn units. This research design provided six replications of each experimental treatment with an average number of prickly pear mottes, which allowed us to have repeated measures of multiple cacti, as well as the surrounding woody brush and herbaceous vegetation (Twidwell, et al. 2016). Each plot unit was ignited independently and served as a true replicate of the prescribed fire treatments.

Prescribed Fire Treatments

Initially, twelve plots were subjected to a single reclamation prescribed fire treatment, while the remaining six experimental plots were left unburned as controls

(reference research design; Figure 12). On August 4-5, 2008, a prescribed burn manager supervised the application of fires conducted with special exemptions during periods of government-imposed burning restrictions. As an additional precaution, a crew with the proper equipment was also present at all times to guard against accidental spotfires. The plots were burned during a state-imposed burn ban with high-intensity headfires that were applied in the afternoon hours, under relatively extreme fire weather conditions (i.e. low fine-fuel moisture, high temperature, and low relative humidity) with an average air temperature of 37 °C, southerly winds of 14.8 kph, and 25% relative humidity. Half of the plot replicates that were burned with a reclamation prescribed fire treatment received a second follow-up, low-intensity, maintenance fire treatment on November 5, 2010. In this follow-up treatment, six plots were burned with low-intensity headfires that were applied in the afternoon hours, under mild fire weather conditions with an average air temperature of 20 °C, southerly winds of 12.9 kph, and 18% relative humidity. All of the prescribed fire treatments in this study were started with a torch containing a mixture of gasoline and diesel oil (1:3).

Wind direction and speed, air temperature, barometric pressure, relative humidity and rainfall were monitored with a Kestrel weather meter and a nearby rain gauge. The methodology outlined in Rothermel and Deeming (1980) was used to quantify fire intensity. The mean and maximum flame lengths were recorded based on ocular estimates. We estimated the amount of energy released during the prescribed fires using Byram's intensity equation [$I = HWR$] (1959). In this equation, I is the fireline intensity (kW/m), H is the heat yield (kJ/kg), W is the amount of fuel consumed (kg/m²), and R is

the rate of spread (m/sec). In addition, in each plot, nine ceramic tiles with thermo-color pyrometers were distributed to measure the maximum instantaneous surface temperatures during the prescribed fire plot treatments (Jacoby, et al. 1992; Kennard 2013). The ceramic tiles were painted with 25 temperature-indicating lacquers that measure up to 1038 °C (Twidwell 2012).

Vegetation Assessment and Fuel Characteristics

A complete census of the prickly pear cactus, herbaceous and woody shrub community in each of the plots was collected July 2007 (i.e. pre-treatment), August 2009, March 2011, and November 2012 (Figure 13). To examine average sized cactus and to eliminate potential outliers, the cactus mottes selected for this study had a diameter range between 0.5 m to 1.5 m. The cactus mottes were permanently marked with a tag for identification purposes, and the spatial location of each plant was recorded with a Global Positioning Systems (GPS) unit with sub-meter accuracy. We also calculated the canopy cover area (m²) of each prickly pear motte using cardinal directions to measure the length and width, as well as its height from the ground to the top of the tallest cladode. Furthermore, the vegetation surrounding each prickly pear was assessed using a circular frame with a 2.5 m radius. Visual estimates of herbaceous vegetation cover (i.e. grass and forbs), woody brush, herbaceous litter, juniper litter, oak litter, dead woody fuels, and patches of bare ground were calculated at the nearest five percent, and the characteristics of the dead woody fuels were grouped into three time lag classes: 1-hour fuels, 10-hour fuels, and 100-hour fuels (Pyne 1984). The following

equation was used to calculate the percentage of change in cactus canopy cover (fixed factor) from pre-treatment to post-treatment:

$$\% \text{ Change in Prickly Pear Canopy Cover (m}^2\text{)} = \left(\frac{\text{Pre} - \text{Post}}{\text{Pre}} \right) \times (100) \times (-1)$$



Figure 13. Ground view of prickly pear mottes scattered throughout at rangeland at the Texas A&M AgriLife Research Station near Sonora, Texas, USA.

Statistical Analysis and Procedures

We used group comparison statistical procedures (e.g., analysis of variance [ANOVA], *t*-test) to compare the differences among the treatments. A paired Student's *t*-test was used to compare the differences in fireline intensity (calculated using the Byram's intensity equation) difference between the fire treatments. To compare the

variables following the application of different experimental treatments we used a combined ANOVA to evaluate the cover area of each prickly pear motte, the vegetation and the amount of bare ground surrounding each motte. If there was a difference between treatments, the Fisher's Least Significant Difference (LSD) method was used to compare the treatment group means. All the statistical analyses were performed using SPSS statistical software (IBM Corp. 2013), and the significance levels for all tests conducted using group comparison statistical procedures were set at $\alpha = 0.05$.

RESULTS

Based on the criteria set in the methods we located a total of 367 cactus mottes and tracked them over a five year study period (July 2007 through November 2012). The plots were last inspected November 2012, 4 years 2 months after the first set of reclamation prescribed fire treatments were administered. This field-based research design allowed us to monitor fireline intensity, the rate at which a fire produces thermal energy (Twidwell 2012). There was a significant difference in fire intensity between burn treatments ($P=0.004$) (Figure 14). The mean fireline intensity for these reclamation fires (August 2008) was 1,270.60 kW/m (± 169.3). In contrast, the plots that were burned with follow-up, maintenance prescribed fires (November 2010) had a mean fireline intensity of 419.61 kW/m (± 63.3). Reference Appendix A for the descriptive data and statistical analysis (Tables 1, 2).

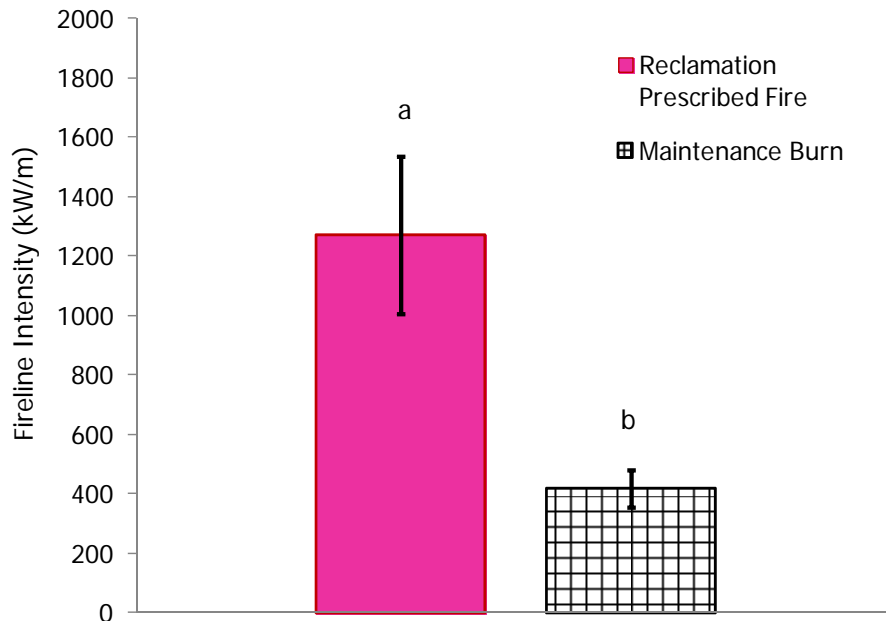


Figure 14. A comparison of the mean (\pm S.E.) fireline intensities of the prescribed fire treatments conducted on the experimental plots. A significant difference ($P < 0.05$) between treatments is indicated by different letters.

Vegetation Response to Fire

After the reclamation fire (August 2008), 99.5 (\pm 0.5) percent of the area was burned (Figure 15), and 100 (\pm 0) percent of the area burned after the follow-up, maintenance prescribed fires (November 2010). Reference Appendix A for the comparison of the percent area burned for the fire treatments conducted on the experimental plots (Table 3).



Figure 15. A ground view of the study area at the Texas A&M AgriLife Research Station near Sonora, Texas, immediately following the reclamation prescribed fire treatments (August 2008).

Prickly Pear Cactus Cover

There was a significant difference in the change in prickly pear canopy cover (m^2) between the prescribed fire treatments (Figure 16). The research plots that were burned with a reclamation prescribed fire (August 2008) had a mean reduction of 95.07 (± 1.71) percent in prickly pear canopy cover, whereas those plots that were burned with a follow-up maintenance fire treatment (November 2010) had a mean reduction of 99.57 (± 0.26) percent. The prickly pear mottes that experienced two prescribed burn treatments (i.e. an initial reclamation fire followed by a maintenance prescribed fire) yielded a slightly larger but significant negative percent change when compared to plots that were burned with only a reclamation prescribed burn ($P=0.004$). In contrast, the prickly pear mottes found in the unburned control plots experienced a mean cover reduction of 29.44 (± 14.73) percent. Reference Appendix A for the descriptive data and statistical analyses (Tables 4, 5, 6, 7).

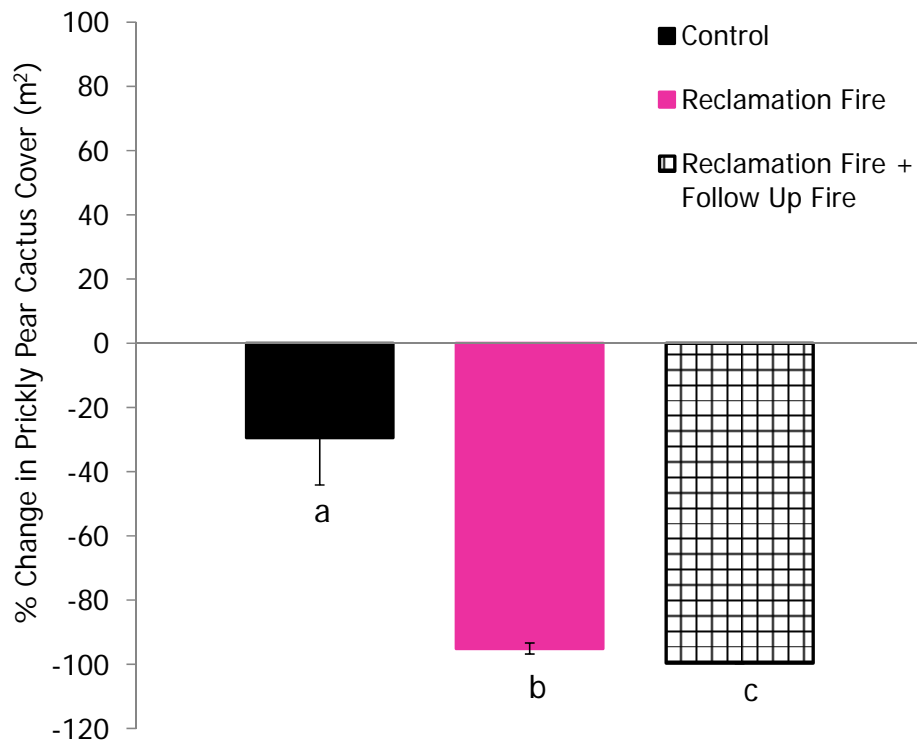


Figure 16. An assessment of the percent change in prickly pear canopy cover (m²) in response to the prescribed fire treatments. All results are presented as mean (\pm S.E) and any significant difference ($P < 0.05$) between the treatments is indicated by different letters. A comparison of data collected at the start (July 2007) and conclusion (November 2012) of the field study

The Combustion of the Opuntia Cladodes

Prickly pear pad tissue was observed to be very susceptible to reclamation prescribed fires. As the high-intensity fires progressed through the plot, the moisture in the cacti stems was heated and the prickly pear pads ‘cladodes’ reached a point of

expansion that resulted in the split of the pad epidermis and the removal of the wax layer on the pads. The cladodes exploded and “pop” sounds were heard, this observation was noted. The split exposed the internal plant tissue to the environment (Figure 17).



Figure 17. This image was captured immediately after the fire. The photosynthetic tissue of the cactus pads was spongy and blistering with melted waxes, and the internal tissue, where the mucilaginous content is found, remained exposed.

In addition, some of the succulent plant tissue was scorched during the combustion process. The spines were burned from the cacti. Within a few days of the fire, the cacti developed a tough scar tissue, and the damaged epidermis appeared desiccated.

Herbaceous Vegetation Layer

In December 2012, following the application of the prescribed fire treatments, the plots that were burned with a reclamation prescribed fire had a mean of 9.92 (\pm 1.07) percent standing herbaceous cover in comparison to the 65.04 (\pm 2.00) percent cover that was recorded prior to any treatment. On the other hand, the plots that were burned again with a follow-up maintenance fire had a mean of 9.47 (\pm 0.94) percent standing herbaceous cover in comparison to the 65.03 (\pm 1.74) percent cover that was recorded

prior to any treatment. As for the unburned control plots, the mean standing herbaceous cover at the conclusion of the study was approximately two times greater, experiencing a mean of 20.26 (± 1.92) percent standing herbaceous cover compared to the 69.95 (± 2.30) percent cover that was recorded during the initial reconnaissance of the study site (Figure 18). Reference Appendix A for the descriptive data (Table 8).

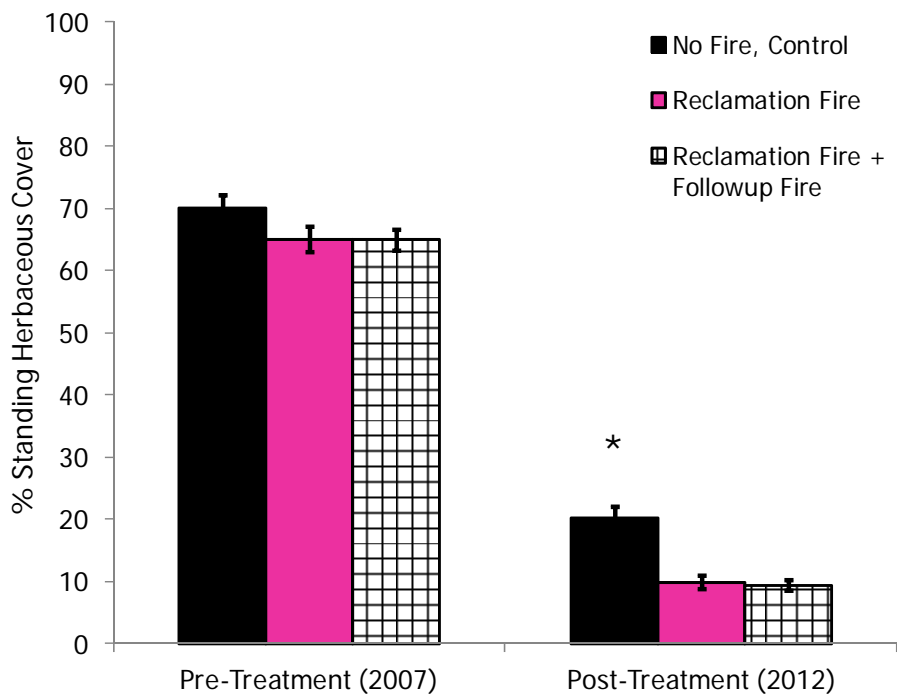


Figure 18. Percent standing herbaceous cover measured at the 2.5 m scale before and after the prescribed fire treatments. All results are presented as mean (\pm S.E.) and any significant difference ($P < 0.05$) between treatments is indicated by an asterisk. A comparison of data collected at the start (July 2007) and conclusion (November 2012) of the field study

Based on these initial and final measurements, we calculated the percent change in standing herbaceous cover for the three different types of plots (Figure 19). The plots

that were burned once with a reclamation prescribed fire had a negative mean change of 79.60 (± 2.56) percent. The plots that were burned with both a reclamation prescribed fire and a follow-up maintenance fire had a negative mean change of 81.56 (± 2.95) percent. In comparison, the unburned control plots had a negative mean change of 69.73 (± 3.01) percent.

The visual estimate of the plant community structure surrounding each cactus motte before and after the prescribed fire treatments allowed us to conduct statistical analysis on this data (i.e. combined ANOVA). This analysis showed that there was not a statistically significant change in the percent standing herbaceous cover between the plots that experienced two prescribed burn treatments (i.e. an initial reclamation fire followed by a maintenance prescribed fire) and those that were burned with only a reclamation prescribed burn ($P=0.625$). In contrast, the change in percent standing herbaceous cover found in the unburned control plots compared to the plots that experienced two prescribed burn treatments was significant ($P=0.008$). The change in percent standing herbaceous cover found in the unburned control plots compared to the plots that received a single reclamation burn treatment was also significant ($P=0.013$). Reference Appendix A for the descriptive data and statistical analysis (Tables 9, 10).

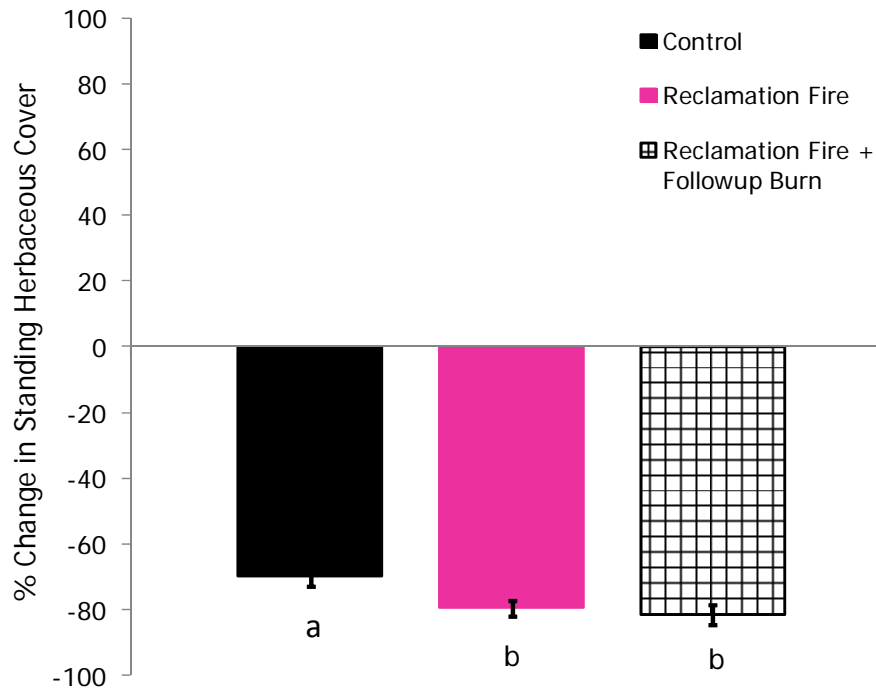


Figure 19. Percent change in standing herbaceous cover measured at the 2.5 m scale. These findings are based on data collected from 2007-2012. All results are presented as mean (\pm S.E.) and any significant difference ($P < 0.05$) between treatments is indicated by different letters. A comparison of data collected at the start (July 2007) and conclusion (November 2012) of the field study

Bare Ground Cover

The percent of bare ground was recorded periodically throughout this study. The plots burned with a reclamation prescribed fire had a mean of 66.74 (± 2.74) percent bare ground cover in comparison to the 3.47 (± 0.73) mean percent cover that was recorded prior to any treatment. On the other hand, the plots that were burned again with a follow-up maintenance fire had a mean of 68.07 (± 2.70) percent bare ground cover in comparison to the 8.47 (± 0.84) mean percent cover that was recorded prior to any treatment. As for the unburned control plots, they experienced a mean of 43.81 (± 3.87)

percent bare ground cover compared to the 8.97 (\pm 1.42) percent cover that was recorded during the initial reconnaissance of the study site.

Based on these initial and final measurements, we calculated the percent change in bare ground for the three different types of plots, which is presented below in Figure 20. The plots that were burned once with a reclamation prescribed fire had a positive mean change of 63.26 (\pm 2.78) percent. The plots that were burned with both a reclamation prescribed fire and a follow-up maintenance fire had a positive mean change of 59.60 (\pm 2.72) percent. In comparison, the unburned control plots had a positive mean change of 34.39 (\pm 3.39) percent. Reference Appendix A for the descriptive data and statistical analyses (Tables 11, 12, 13).

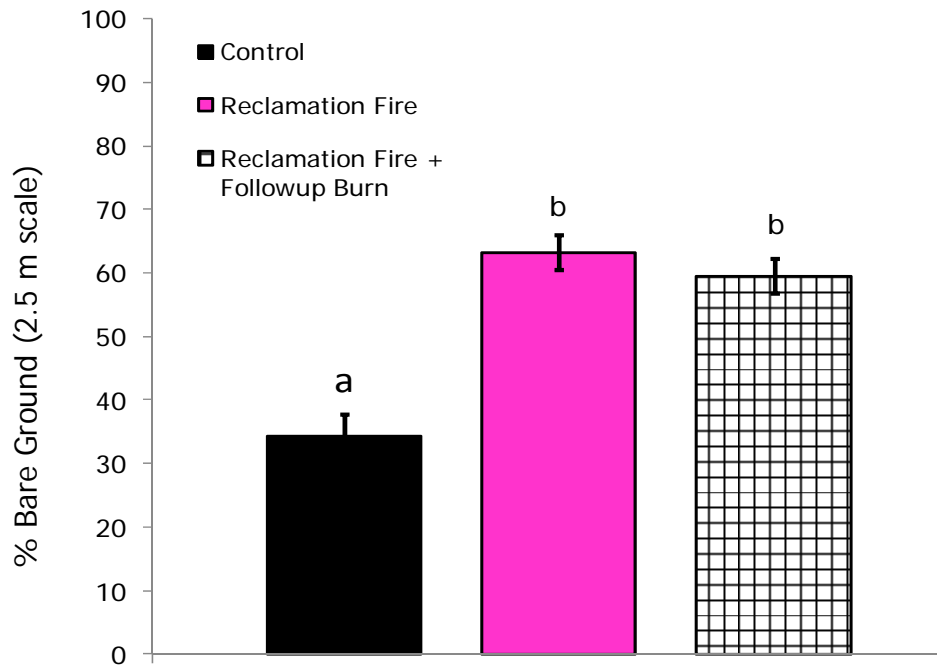


Figure 20. Percent change in bare ground measured at the 2.5 m scale. These findings are based on data collected from 2007-2012. All results are presented as mean (\pm S.E.) and any significant difference ($P < 0.05$) between treatments is indicated by different letters. A comparison of data collected at the start (July 2007) and conclusion (November 2012) of the field study

The statistical analysis of the denude soil cover surrounding each cactus motte before and after the prescribed fire treatments was conducted using a combined ANOVA. This analysis, presented below in Figure 21, showed that there was not a statistically significant change in the percent bare ground cover between the plots that experienced two prescribed burn treatments (i.e. an initial reclamation fire followed by a maintenance prescribed fire) and those that were burned with only a reclamation prescribed burn ($P=0.357$). In contrast, the change in percent bare ground cover found in the unburned control plots compared to the plots that experienced two prescribed burn

treatments was significant ($P=0.00$). Similarly, the change in percent bare ground cover found in the unburned control plots compared to the plots that received a single reclamation burn treatment was also significant ($P=0.000$). Reference Appendix A for the statistical analyses (Table 14).

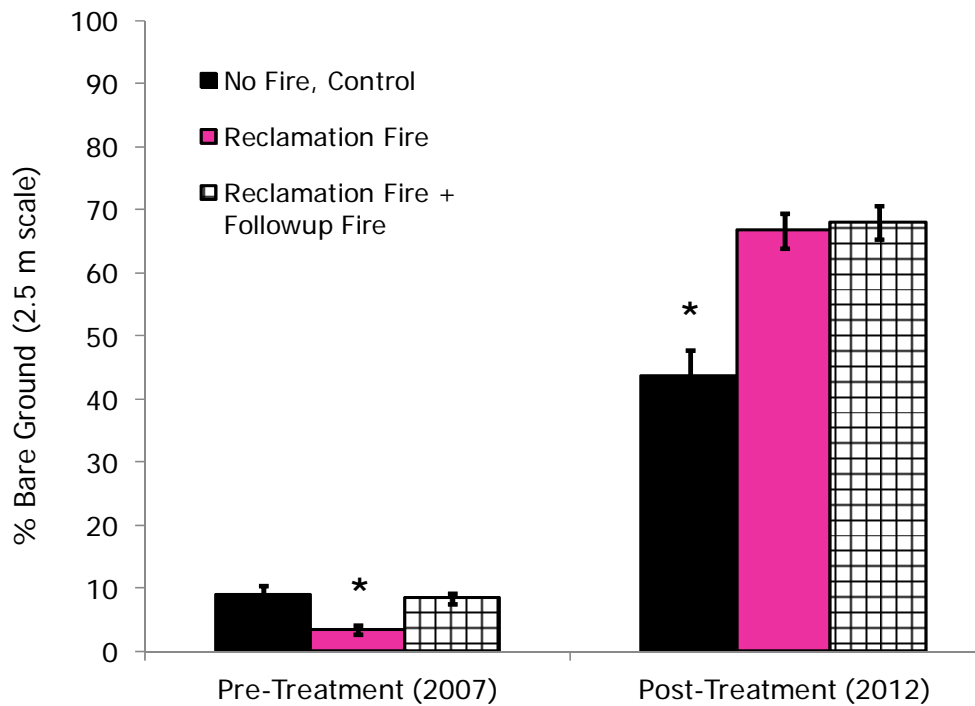


Figure 21. The mean percent of bare ground surrounding the cactus mottes was measured at the 2.5 m scale. All results are presented as mean (\pm S.E.) and an asterisk indicates any significant difference ($P < 0.05$) between treatments. A comparison of data collected at the start (July 2007) and conclusion (November 2012) of the field study

DISCUSSION

Over the last century, an increase in prickly pear cactus encroachment has further altered the ecological integrity of semi-arid rangeland ecosystems the Edwards Plateau region of central Texas (Ansley and Castellano 2007*b*; Brown, et al. 1997; DiTomaso 2000; Fuhlendorf, et al. 2012; Westoby, et al. 1989). The use of a high-intensity ‘reclamation’ prescribed fire followed by low-intensity ‘maintenance’ prescribed fires at frequent fire-return intervals has been proposed as a viable brush control strategy to reduce prickly pear coverage (Ueckert, et al. 1988). However, despite the ecological and economic significance of this encroachment, the factors that control the management and suppression of this problematic succulent using prescribed fire remains poorly understood. In particular, it would be beneficial to have a better understanding of prickly pear response to burns conducted at increased frequency and intensities.

Prickly Pear in Response to Fire

In this study, the application of a ‘maintenance’ prescribed fire on plots that were previously burned with ‘reclamation’ fires resulted in a 99.57 percent reduction in prickly pear cactus coverage, whereas those plots that were burned with a single ‘reclamation’ prescribed fire resulted in slightly (yet significantly) lower reduction in prickly pear cactus coverage of 95.07 percent. The findings indicate that the combination of increased fire frequency and intensity led to a statistically significant greater reduction in prickly pear cactus coverage. These results yield a strong support for our hypothesis that the application of a low-intensity ‘maintenance’ prescribed fire subsequent to a

high-intensity 'reclamation' prescribed fire is an effective strategy to suppress prickly pear cactus.

The significant decrease in prickly pear coverage reported in this chapter is in line with those of previous studies that suggest the use of prescribed fire can be an effective and necessary management tool to maintain productive and sustainable rangelands (Bunting, et al. 1980; Simanton 1991; Ueckert, et al. 1988). There are similarities between this study and the findings described by Taylor (2001) and Ansley and Castellano (2007*b*) who conducted studies in Texas rangelands and found that an application of a high-intensity fire reduced 97 percent and 86 percent prickly pear density, respectively. These findings also corroborate the ideas of Thomas (1991), O'Leary and Minnich (1981), and Brown and Minnich (1986) who have speculated that the successful suppression of succulents using prescribed fire is dependent upon intensity of the burns.

In addition, these results reflect those of numerous studies that have indicated this succulent's limited tolerance to a harsher fire regime (i.e. frequency of repeated fire treatments) (Ansley and Castellano 2007*b*; Bunting et al. 1980; Humphery and Everson 1951; Taylor 2001). These findings also agree with studies that have recommended an increase in fire frequency as an effective strategy to reduce prickly pear cactus dominance in brush infested semi-arid ecosystems (Davis and Moritz 2001; Duncan 2003; Simanton 1991; Westoby, et al. 1989). Consistent with the literature, the results from this study support the observation that the prickly pear cacti stems that remain alive

and standing after a fire are more susceptible to other disturbances, including herbivory, during the post-fire recovery period (Ansley and Jacoby 1998; Ansley and Taylor 2004).

Prickly Pear's Response in the Absence of Fire

Contrary to expectations, our results show that prickly pear cactus coverage in the unburned control plots was also reduced by 29.44 percent. This outcome differs from that of Ueckert, et al. (1988) and Petersen, et al. (1988) who found that there was a 38 percent and 47 percent increase in live prickly pear cactus cover in the untreated plots, respectively. Similarly, Ansley and Castellano (2007b) reported an increase of 135 percent in the number of prickly pear cladodes in the small cactus mottes assigned to a no-fire (control) treatment. These findings are also contrary to those of a study published in 1957 that reported an increase of 200 percent prickly pear cactus in density over a 19-year period in the Edwards Plateau region of Texas (Gonzalez 1957). A possible explanation for these results may be related to the extended drought that affected the region following the prescribed fire treatments (Twidwell et al. 2014).

According to the National Drought Mitigation Center, following the 'reclamation' fires (August 2008), the growing season in 2009 was classified as 'abnormally dry' and assigned a Palmers Drought Severity Index (PDSI) of -1.0 to -1.9 (National Centers for Environmental Information, NOAA 2015). Reference Figure 22 for the U.S. Drought Monitor Maps from April 2009, July 2009, and September 2009.

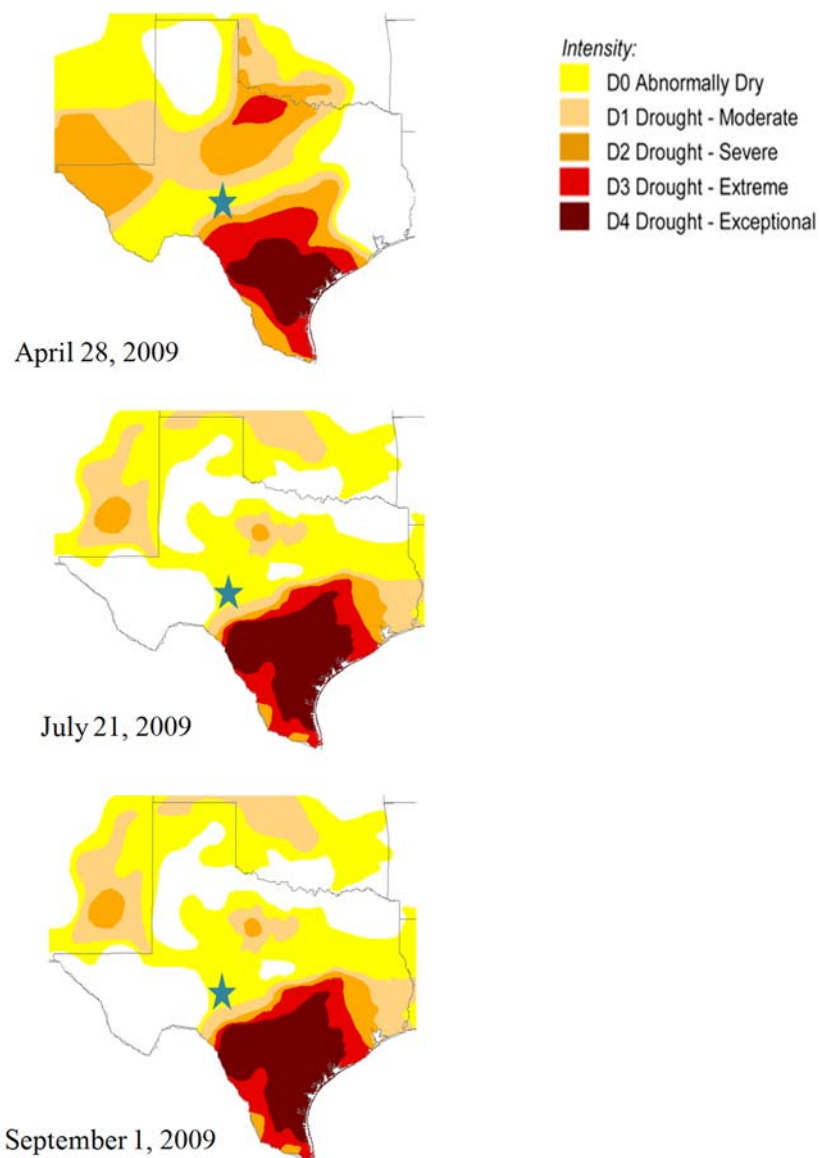


Figure 22. A regional-scale drought representation in the rangelands of Texas obtained from the U.S. Drought Monitor for the 2009 growing season (April, July, and September) following the application of ‘reclamation’ prescribed fire treatments (August 2008). The star on the maps represents the location of the Texas AgriLife Research Station near Sonora, Texas (National Centers for Environmental Information, NOAA 2015).

During this study, the regional-scale drought conditions also did not improve following the application of the follow-up ‘maintenance’ prescribed fire treatments (November 2010) on plots that were previously burned with ‘reclamation’ prescribed fires. The early growing season in 2011 corresponding to the post-fire recovery period was classified as an ‘extreme drought’ and assigned a PDSI of -4.0 to -4.9. In comparison, the late growing season was classified as an ‘exceptional drought’ and assigned a PDSI of -5.0 or less (National Centers for Environmental Information, NOAA 2015, Twidwell, et al. 2016). Reference Figure 23 for the U.S. Drought Monitor Maps from April 2011 and September 2011.

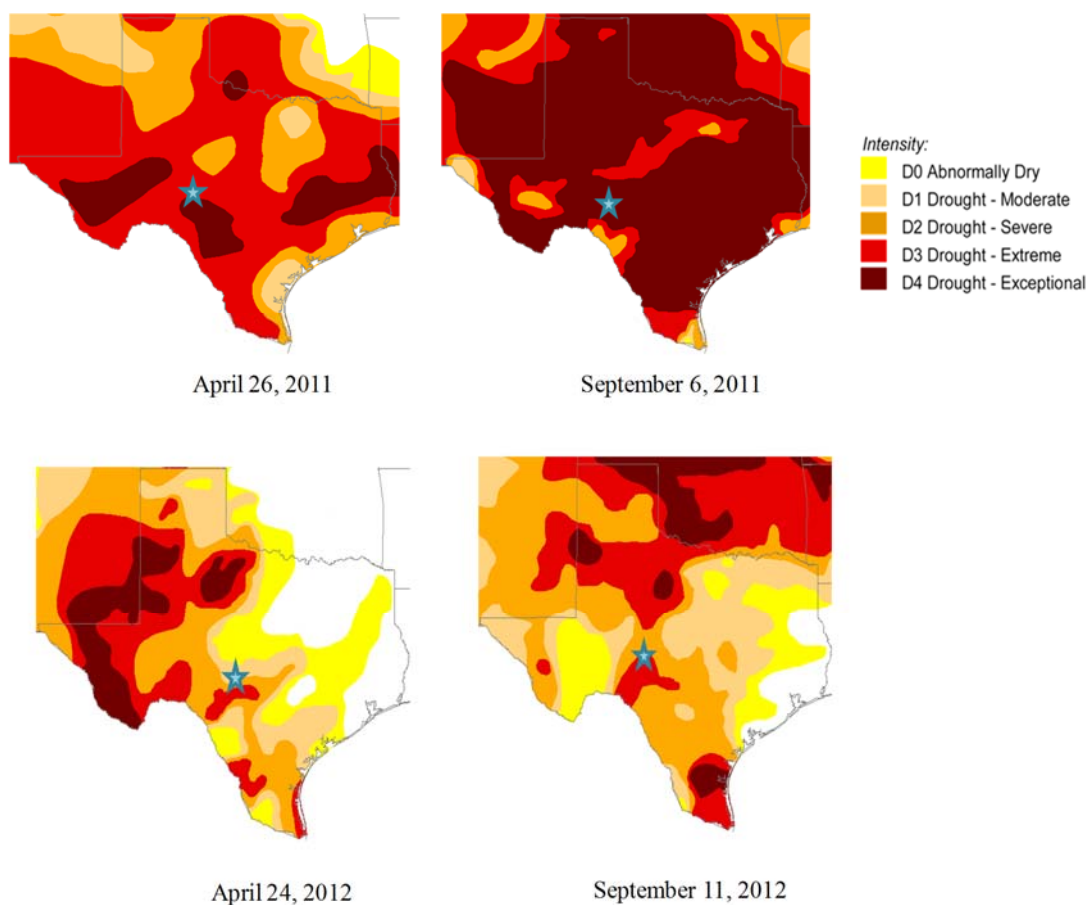


Figure 23. A regional-scale drought representation in the rangelands of Texas obtained from the U.S. Drought Monitor for the 2011 and 2012 growing season (April and September). In November 2010, the plots that were previously burned with ‘reclamation’ prescribed fires were once again burned with a ‘maintenance’ prescribed fire treatment. The star on the maps represents the location of the Texas AgriLife Research Station near Sonora, Texas (National Centers for Environmental Information, NOAA 2015).

Even though cacti are characterized as drought-hardy species, they can be adversely affected by periods of abnormally low precipitation (McDowell, et al. 2008). During periods of extended drought the cactus loses its natural water-harvesting function and it can undergo a metabolic modification referred to as ‘CAM idling’ which results in no net CO₂ assimilation (Drennan and Nobel 2000; Rietkerk and van de Koppel 1997).

In line with our findings, in 1956, after a period of exceptional drought, it was reported that many of the older prickly pear cactus plants died (Young 1956). The decline in prickly pear coverage in the unburned control plots in this chapter is also consistent with studies that have monitored drought-induced mortality in shrubs and woody species (Franklin, et al. 1987; Owens, et al. 1998; Roques, et al. 2001; Van Auken 2009). Breshears, et al. (2005) and Westoby, et al. (1989) have reported that large-scale drought in rangelands has been attributed to wide-spread die offs of piñon pine (*Pinus edulis*) and bladder saltbush (*Altriplex vesicaria*), respectively.

Recovery of Herbaceous Layer

Contrary to expectations, a decrease in prickly pear cactus dominance did not promote the establishment of standing herbaceous cover. In this study, the results do not show any significant difference in the standing herbaceous cover between the plots burned with the different prescribed fire treatments; the plots that were burned with a reclamation prescribed fire and the plots that were burned again with a follow-up maintenance fire had a mean percent standing herbaceous cover of 9.92 and 9.47, respectively. Our findings do not support the hypothesis that an increase in fire intensity and frequency would induce changes and alter fundamental ecosystem process (i.e. succession) that would shift the cacti and brush infested rangelands to an open landscape dominated by standing herbaceous cover. These results are contrary to previous studies that have determined that prescribed fires are an effective strategy that can be used to modify rangeland vegetation dynamics in favor of herbaceous forage species (DiTomaso

2000; Ewing and Engle 1988; Fuhlendorf, et al. 2012; Ravi, et al. 2010*b*; Taylor 2007; Whisenant, et al. 1984).

It is likely that the severe drought following the prescribed fire treatments could have also inhibited the establishment of the standing herbaceous cover. These results are consistent with those of multiple studies conducted in semi-arid and arid regions who reported that herbaceous species were negatively impacted, and unable to recover, if the prescribed fires were followed by periods of limited rainfall (Bond and Keeley 2005; Fuhlendorf, et al. 2012; Wright 1974). Post-fire colonization in semi-arid regions is an extremely slow process that depends in large measure on the extent and timing of soil moisture availability (Chamrad and Box 1965; Hobbs 1996; Simanton 1991).

Herbaceous Layer in the Absence of Fire

The severe drought was also likely a limiting factor that resulted in a marked reduction in the standing herbaceous cover in the unburned control plots. Our results show that at the conclusion of this study, the unburned plots had a mean standing herbaceous cover of 20.26 percent in 2012, compared to the 69.95 percent cover that was recorded during the initial reconnaissance of the study site in 2007. These results reflect those of Young (1956) and Ansley, et al. (2006*b*) who found that if the physiological needs of the herbaceous vegetation are not met, they will experience drought induced mortality (Chamrad and Box 1965; Rietkerk and van de Koppel 1997; Thurow and Taylor 1999). The vegetation (i.e. grasses, forbs) must have suitable physiological and morphological characteristics to resprout and survive during periods of limited moisture availability (Hobbs 1996).

The establishment of adequate coverage is particularly critical because a failure to stabilize the soils increases the potential for accelerated erosion and it could further degrade the functional integrity of these rangelands (Benavides-Solorio and McDonald 2001; Johansen et al. 2001; Ludwig et al. 2004; Neary, et al. 1999; Schlesinger, et al. 1999; Soto and Díaz-Fierros 1998). In this study, the amount of bare ground cover on the plots following the application of the prescribed fire treatments was inversely related to the amount of standing herbaceous cover. On one hand, the bare ground cover on plots burned with a reclamation prescribed fire and those burned again with a follow-up ‘maintenance’ fire was 68.97 and 66.77 percent, respectively, and they did not show any significant difference. On the other hand, our results show that the unburned control plots also experienced an increase in bare ground cover; at the conclusion of the study, the plots had ground cover of 43.88 percent.

Broader Implication for Rangeland Ecology and Management

Based on these findings, ranchers and land managers interested in restoring the vegetation dynamics in prickly pear infested rangelands should consider prescribed fires as a viable strategy. In particular, the combination of a high-intensity ‘reclamation’ prescribed fire and a follow-up low-intensity ‘maintenance’ prescribed fire could be used to reduce prickly pear dominance on these lands. The ‘reclamation’ fire functions as the catalyst that forces the system along an alternate ecological trajectory (Twidwell, et al. 2016). This abrupt physio-chemical disturbance initiates the transition from a dense cactus and woody brush-infested landscape to an exposed scorched site characterized by unvegetated (i.e. denude) soil that could promote the development and establishment of

a grassland savanna. Whereas, the increase in fire frequency with the follow-up ‘maintenance’ fire suppresses future prickly pear encroachment, it specifically targets the succulents that survived the earlier brush control treatments (i.e. ‘reclamation’ prescribed fires). Despite these promising results, there is ample ground for continued research that can provide us with a better insight into the long-term recovery of the overall plant community following the aforementioned prescribed fire treatments. It stands to reason that the removal of undesirable species does not necessarily ensure a more desirable species will be replaced (Ravi 2010*b*). In particular, researchers should evaluate how these brush infested lands respond to fire in terms of desirable forage quantity and quality during periods of prolonged drought.

Adaptive Management

The findings from this work can be used by natural resource professionals in developing land management plans to help reduced the chronic expansion of prickly pear cactus. However, any management plan should take into consideration that drought is an inevitable occurrence that influences fundamental processes and dynamics in these semi-arid rangeland ecosystems (Herrick, et al. 2012; Thurow and Taylor 1999). Given these circumstances, an adaptive management approach should be adopted. This strategy may provide ranchers and land managers with the flexibility to respond to drought and achieve the restoration of these degraded lands (Ash, et al. 2012; Bradshaw 1996; Ehrenfeld 2000; Monaco, et al. 2012). In addition to monitoring the post-fire vegetation recovery, evaluating the erosion potential of the sites is necessary to develop effective adaptive management plans (Soto and Díaz-Fierros 1998). Having an adequate recovery

of standing herbaceous cover is integral to the stability of rangelands (Adler, et al. 2001; Call and Roundy 1991). A lack of a suitable herbaceous layer community (i.e. continuous stands of fine fuel) following a fire can result in an increased potential for accelerated soil erosion, and it can also impede or temporally delay the application of prescribed fire treatment at the desired fire-return intervals (Duncan 2003; Fuhlendorf, et al. 2012).

CHAPTER V
THE SUSCEPTIBILITY OF DROUGHT-STRICKEN
CACTUS TO PRESCRIBED FIRE: A FIELD STUDY

INTRODUCTION

Drought events are expected to happen more frequently and with greater intensity in the southwestern United States due to global climate change and cyclical weather patterns (Archer and Predick 2008; Dai 2011; National Centers for Environmental Information, NOAA 2015; Ojima, et al. 1991). Models predict that climate change when combined with overgrazing by domestic and wild herbivores could have a particularly detrimental impact on the integrity and sustainability of Texas rangelands (Archer 1989; EPA 2017; Gillson and Hoffman 2007; Seager, et al. 2007).

Prickly pear cactus (*Opuntia* spp.) is a hardy succulent that thrives under water-limiting environmental conditions and the absence of effective land management and brush control strategies (Bement 1968; Bugbee and Reigel 1945; Hoffman et al. 1955; McDowell 2011; Turner and Costello 1942). Notably, prolonged drought has been identified as a critical factor that leads to prickly pear growth at the expense of more ecologically desirable species. Indeed, over a 19-year drought-stressed period, Gonzalez (1957) recorded a 200% increase in prickly pear cover on a site located in the western edge of the Edwards Plateau near Barnhart, Texas.

Encroachment by prickly pear reduces livestock carrying capacity and transitions the plant community into a structurally and compositionally altered state of lower

productivity (Van Auken 2009). It displaces desirable herbaceous warm-season perennial grasses and contributes to a depletion of annual herbaceous species in the soil seed bank (Ravi, et al. 2010a; Turner and Costello 1942). Past management of prickly pear encroachment has utilized a variety of brush control techniques (i.e. chemical, mechanical, and prescribed fire). Of these options, fire is increasingly being recognized as an effective strategy to suppress undesirable woody brush and prickly pear plant encroachment in these ecosystems (Kreuter et al. 2001) due to its relatively inexpensive, yet highly effective, cost-to-benefit return compared to other brush control strategies (Bailey 1988; Taylor 2003; Teague et al. 2008). However, the effectiveness of prescribed fire under environmental conditions in which prickly pear thrives (i.e. prolonged drought) has not been adequately assessed.

Physiological condition and phenological state of development influence the resilience of a plant to immediate and long-term environmental stressors such as drought and other disturbances like fire and herbivory (Whisenant 1982). Generally a plant's ability to withstand fire significantly decreases when its tissue is experiencing prolonged drought conditions (Wright 1974). Physiologically-stressed plants are deprived of necessary resources such as stored carbohydrates and hydration, and therefore they will endure greater tissue damage and mortality when they experience a fire (Breshears, et al. 2005; Breshears, et al. 2009; McDowell 2011; Skov, et al. 2004). Plant tissue that has a low amount of moisture content relative to its dry weight typically has a considerably lower heat threshold (Winter and Smith 1996). Therefore, less energy is needed to increase the temperature of physiologically-stressed plant tissue (Thomas 1991; Wright

1974). Based on this information, even though prickly pear is a drought tolerant CAM plant with considerable morphological and physiological plasticity (Cushman and Bohnert 1999; Winter and Smith 1996), prolonged drought could magnify the negative impacts a prescribed fire has on this succulent species. In this study, we hypothesized that drought-stressed prickly pear cactus would be more susceptible to fire-induced tissue damage than non-drought stressed individuals. Consequently, we predict this would thereby lead to greater incidences of mortality in plants experiencing both drought and prescribed fire.

To test these predictions, we conducted a multi-year field study to empirically evaluate the ecological response and susceptibility of drought-stressed prickly pear to the application of low-intensity prescribed fire treatments administered in the early-spring and early-fall season using a completely randomized experimental design. Prior to the application of the prescribed fire treatments, *in situ* water exclusion treatments were randomly assigned to a set of the prickly pear plants (i.e. cactus mottes) in order to experimentally manipulate their hydration status. In addition to better elucidating the ecological mechanisms that enhance prickly pear resilience and promote its encroachment into semi-arid ecosystems at the expense of other ecologically desirable herbaceous species, the findings from this study will be of particular interest to land managers seeking more effective rangeland restoration efforts and better control strategies for problematic plant species.

METHODS

During June 2010, we located forty-eight prickly pear cactus mottes in a 3 ha rangeland site at the Texas A&M AgriLife Research Station near Sonora, Texas (Figure 24). The cactus mottes selected for this experiment were tagged and their spatial location recorded with a Global Positioning Systems (GPS) unit with sub-meter accuracy. The cactus mottes had a diameter range between 0.25 m to 1.5 m and were randomly distributed across a brush encroached, semi-arid savanna landscape. For the duration of this study, all domestic ungulate grazing was deferred from the site to prevent livestock trampling of the mottes, however, the area was accessible to wildlife (e.g., white-tailed deer, rabbits, rodents) (Site Description, Chapter IV).



Figure 24. Aerial view of the study area at the Texas A&M AgriLife Research Station near Sonora, Texas.

Experimental Design

In this study, we established a 3×2 full-factorial experimental design manipulating fire season and precipitation. Each experimental unit (i.e. cactus motte) was randomly assigned one of the following six treatment combinations: [early-spring season fire \times rainout shelter], [early-spring season fire \times ambient conditions (control)], [early-fall season fire \times rainout shelter], [early-fall season fire \times ambient conditions (control)], [no fire (control) \times rainout shelter], and [no fire (control) \times ambient conditions (control)]. Each experimental treatment combination was replicated eight times for a total of 48 plots centered on an individual prickly pear motte.

Vegetation Assessments and Fuel Characteristic

The baseline vegetation and fuel characteristics data were recorded June 2010 (i.e. pre-treatment), and additional sets of data were collected early spring (March 2011), early fall (September 2012), and early spring (March 2013). We calculated the cover area (m^2) of each prickly pear motte using cardinal directions to measure the length and width. Vegetation surrounding each prickly pear was assessed using a circular frame with a 2.5 m radius. Visual estimates of herbaceous vegetation cover (i.e. grass and forbs), woody brush, herbaceous litter, juniper litter, oak litter, dead woody fuels, and patches of bare ground were calculated at the nearest five percent. Additionally, the characteristics of the dead woody fuels were grouped into three time lag classes: 1-hour fuels, 10-hour fuels, and 100-hour fuels (Pyne 1984).

***In situ* Field Treatments**

Drought Simulation

Twenty-four prickly pear mottes were randomly selected to undergo the drought simulation treatment and were placed under a fixed-location shelter using protocols similar to those established by Yahdjian and Sala (2002) (Figure 25). On June 04, 2010, the rainout shelters were assembled and placed over the cactus mottes with a west-east orientation, with the tallest side to the west. These shelters were designed to block rainfall from reaching a 4m² area, while causing minimal modifications to the landscape and allowing other microclimate and environmental variables (i.e. wind speed, air and soil temperature, relative humidity, and sunlight availability) to remain largely unchanged (English, et al. 2005).

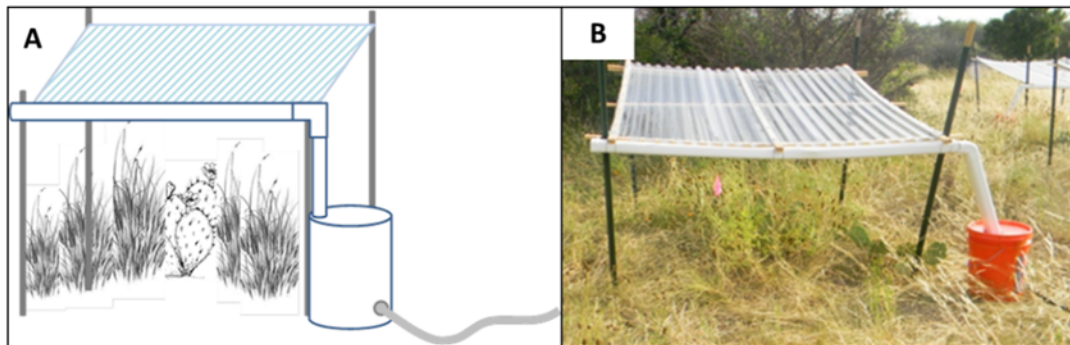


Figure 25. A) An illustration of the open-sided, open-ended, rainout shelter, and B) ground view of a prickly pear motte covered by SUNTUF® polycarbonate roofing panels at our field site at the Texas AgriLife Research Station.

The shelters were constructed using four 1.8 m steel fence t-post, SUNTUF® corrugated polycarbonate roofing paneling, pine wood boards (1 in. x 2 in. x 8 ft.), hex

nuts, bolts and metal ties, heavy duty vinyl gutter, a 18.92 liter storage tank with an escape valve, and a garden hose. A 2 m x 2 m roof was built with lightweight, highly resistant SUNTUF® polycarbonate roofing panels (2.81 kg) that were anchored to a pine wood frame for stability and support (reference Figure 25-B). The panels were made from a material that allows over 90% of the sunlight radiation to penetrate. To establish a foundation that could withstand adverse weather conditions (e.g., high winds), the four steel fence t-post were driven 0.4 m into the ground. The maximum height of the shelter was at 1.2 m and the roofing frames were firmly attached with metal wires to the t-post and placed at a 20° inclination. This design also included a heavy duty vinyl gutter that was installed to divert the intercepted rainwater into a storage tank. The tank had a capacity to hold 18.92 liters and it was modified to include an escape valve at its base. The valve was connected to a lengthy garden hose (4 m) to drain the captured water away from the shelter and to prevent an overflow of the storage tank. We did not modify the natural ambient conditions of the remaining twenty four mottes without rainout shelters.

Prescribed Fire

Thirty-two prickly pear mottes were burned *in situ* within a specially designed portable burn compartment that confined the size of the fire to a 4m² area (Figure 26; Sosa 2009). The use of this *in situ* field technique made it possible for us to conduct numerous small-scale prescribed fire treatments (Britton and Wright 1979; Korfmacher, et al. 2003). The first set of sixteen prescribed fire treatments were conducted early spring season (April 09, 2011), followed by another sixteen prescribed fires in the early

fall season (September 24, 2012). To examine if a lack of moisture during the burn impacted the cactus mottes, the rainout shelters were dismantled from any motte that was assigned to receive a prescribed fire treatment. The rainout shelters on the eight cactus mottes that were selected as unburned (control) treatments were removed March 05, 2013, until we completed the final, post-treatment, vegetation assessment

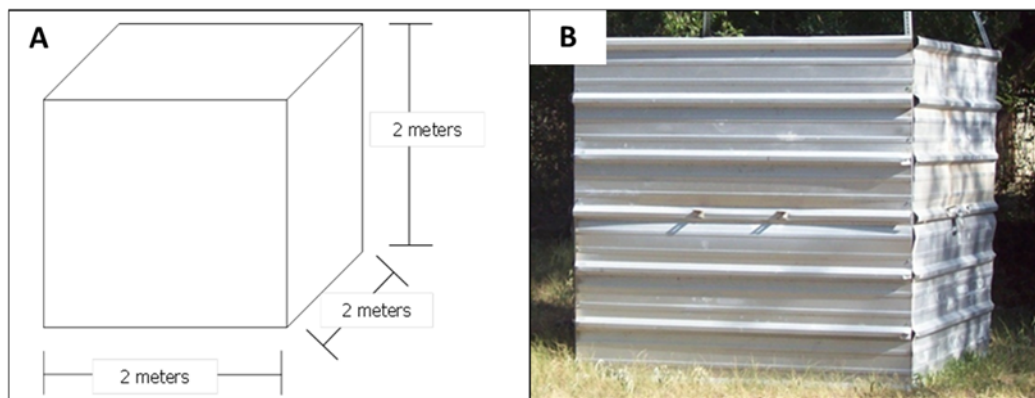


Figure 26. A) A diagram that references the height, depth and width of the portable burn compartment, and B) a photograph of the metal compartment.

The portable burn compartment was constructed using the following highly heat resistant materials: corrugated, galvanized sheet metal panels, angle iron, four heavy-duty metal handles, hex nuts and bolts. The sheet metal panels were firmly fastened with hex nuts and bolts to the sides of the sturdy angle iron frame. For ease of transport, heavy-duty handles were installed to each side of the compartment. The cactus motte and its surrounding vegetation were placed at the center of the burn compartment, and an OMEGA™ thermocouple was positioned in the intended path of the headfire to measure the maximum instantaneous temperatures of the fire (Jacoby, et al. 1992; Figure 27).

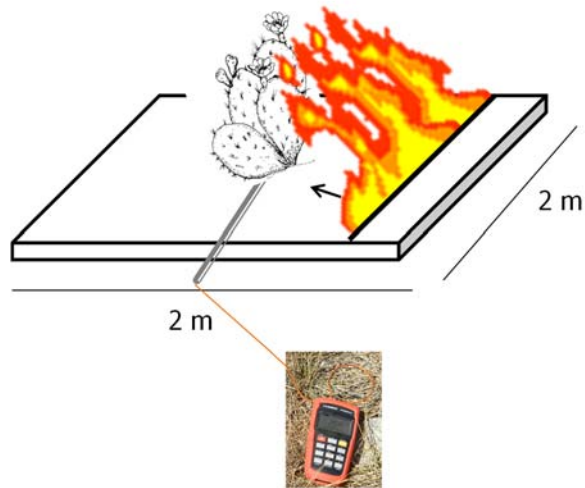


Figure 27. A schematic representation of a headfire spreading through a 4m² plot with a prickly pear cactus and an OMEGA™ thermocouple connected to a commercially available electronic data logger.

Vegetation adjacent to the burn compartment was mechanically cleared and safety equipment was on hand (e.g., water truck, radio, fence pliers, shovels and rakes). A Kestrel weather meter was used to monitor the atmospheric conditions at the field site during the prescribed burns (i.e. air temperature, wind direction and speed, barometric pressure, and relative humidity). The fires were ignited with a sealed aluminum drip torch containing a mixture of gasoline and diesel oil (1:3). We left the compartment and the thermocouple in place for five minutes after the fires were completely extinguished to limit the residual heat accumulated within the metal frame (Korfmacher, et al. 2003) (Figure 28).



Figure 28. A view of a smoldering prickly pear cactus inside the burn compartment. The maximum fire temperature was measured with an OMEGA™ thermocouple sensor as the flames progressed through the plot consuming the succulent's photosynthetic tissue in a manner similar to that observed in Chapter IV.

Tissue Harvesting Technique

We analyzed the moisture content of thirty-two prickly pear mottes (i.e. sixteen mottes with the drought simulation treatment, and another set of sixteen mottes that were left to reflect ambient conditions) to determine if the drought simulation treatment had effectively contributed to the dehydration of the tissue. Two samples were harvested from each cactus motte on the day we administered the early fall season prescribed fire treatments (September 24, 2012). We used a destructive harvesting technique to collect a total of sixty-four tissue samples from individual terminal stem segments (i.e. cladodes) (Graham and Nobel 1996). The randomly selected stem segments were perforated with a cork borer with a 2.5 cm diameter and each sample was stored in a heavy duty paper bag to prevent desiccation (Figure 29). The tissue samples were returned to the laboratory on

the day the prescribed fires were administered and the weight of each sample was recorded.

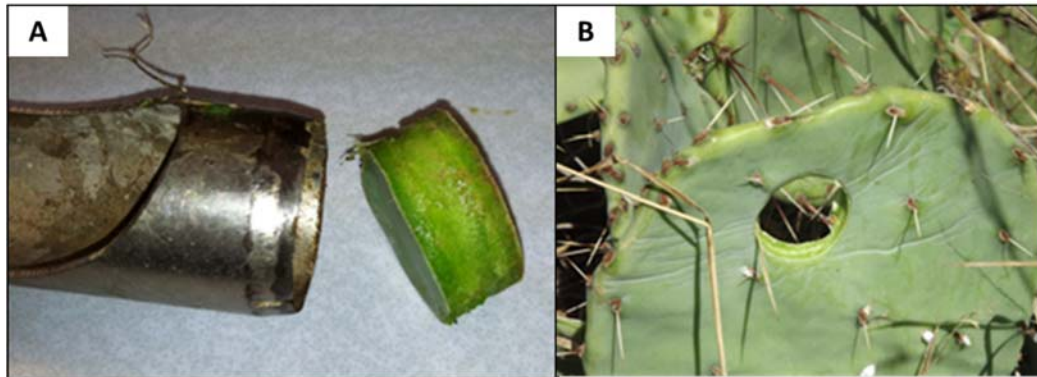


Figure 29. A) The inner mucilaginous tissue of a harvested sample, and B) a stem segment that has been perforated with a cork borer.

Statistical Analysis and Procedures

We used group comparison statistical procedures (e.g., analysis of variance [ANOVA], *t*-test) to compare the differences among the treatments and treatment combinations. The maximum instantaneous fire temperature data recorded was analyzed using a paired Student's *t*-test to determine if there was a difference between the fires conducted on the cactus mottes undergoing drought simulation treatments and those that were left to reflect ambient conditions. A paired Student's *t*-test was also used to examine the differences in moisture content of the harvested tissue samples that were collected from cactus mottes undergoing different treatment combinations. To compare the variables following the application of different experimental treatments we used a combined ANOVA to evaluate the cover area of each prickly pear motte and the

vegetation surrounding each motte. If there was a difference between treatments, the Fisher's Least Significant Difference (LSD) method was used to compare the treatment group means. All the statistical analyses were performed using SPSS statistical software (IBM Corp. 2013), and the significance levels for all tests conducted using group comparison statistical procedures were set at $\alpha = 0.05$ for general cases and $\alpha = 0.10$ for interaction effect.

RESULTS

Based on the criteria set in the methods we located a total of 48 cactus mottes and tracked them over a three year period (June 2010 through March 2013). The plots were last inspected March 05, 2013, 2 years 1 month after the early-April 2011 fire treatments and 6 months after the early-September 2012 fire treatments.

Recorded Temperature of Prescribed Fires

The mean maximum instantaneous fire temperature of the plots with a rainout shelter reached a temperature of 183.8 °C (\pm 31.02); whereas, those left under ambient (control) conditions reached a temperature of 92.3 °C (\pm 17.28) producing a statistically significant difference in the maximum instantaneous fire temperature recorded between the plots that underwent the drought simulation treatments and those left under ambient conditions (P=0.022) (Figure 30). Reference Appendix B for the descriptive data and statistical analysis (Tables 15, 16).

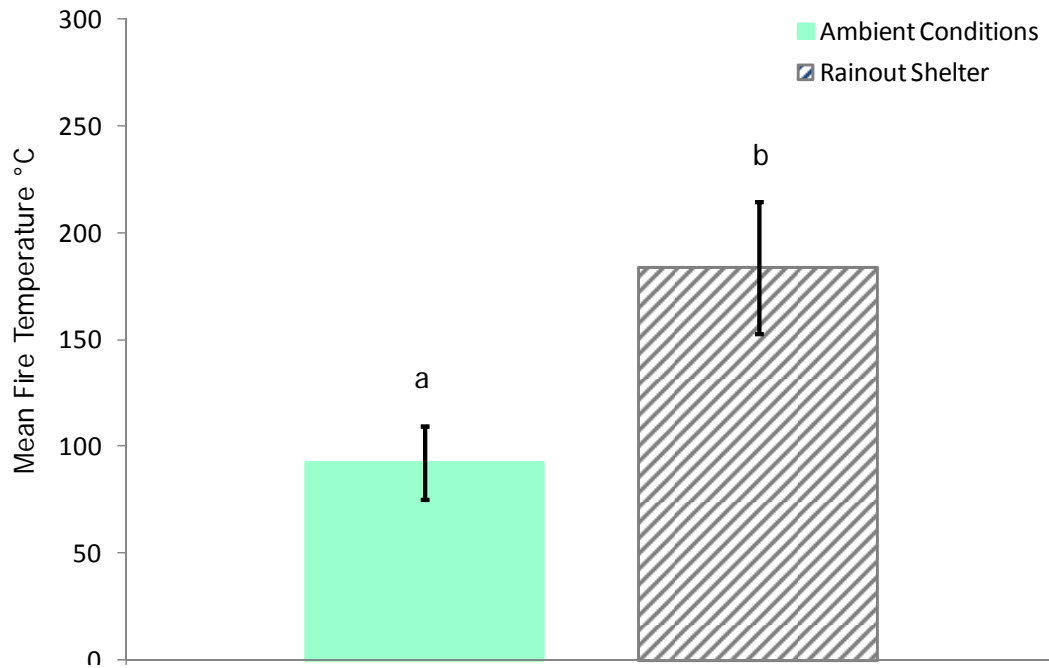


Figure 30. A comparison of the mean (\pm S.E.) maximum instantaneous fire temperature ($^{\circ}$ C) for the prescribed fires treatments administered late-September (2012) on the experimental plots with the rainout shelter and those left under ambient (control) conditions. A significant difference ($P < 0.05$) between the treatments is indicated by different letters.

Vegetation Response to Drought and Fire

Prickly Pear Cactus Cover

The prescribed fire treatments shown in Figure 28 did not result in a statistically significant change in motte cover area (m^2) between the plots with and without a rainout shelter ($P=0.595$) (Figure 31). Prescribed fires administered in early-April 2011 caused a 34.72 (\pm 11.27) percent reduction of prickly pear cover in the plots with a rainout shelter compared to a 4.34 (\pm 30.04) percent reduction of prickly pear in the plots under ambient (control) conditions, however, the difference was not statistically significant ($P=0.360$). Prescribed fires administered in late-September 2012 resulted in a 15.98 (\pm 36.43)

percent reduction of prickly pear cover in the plots with a rainout shelter compared to a 16.98 (\pm 23.01) percent increase of prickly pear in the plots under ambient conditions although this difference was not statistically significant either ($P=0.457$). In the absence of prescribed fire, there was a 3.35 (\pm 13.41) percent reduction of prickly pear in the plots with a rainout shelter compared to a 17.06 (\pm 10.65) percent increase of prickly pear in the plots under ambient conditions. Yet again, this difference was not statistically significant ($P=0.253$). Reference Appendix B for the descriptive data and statistical analyses (Tables 17, 18, 19).

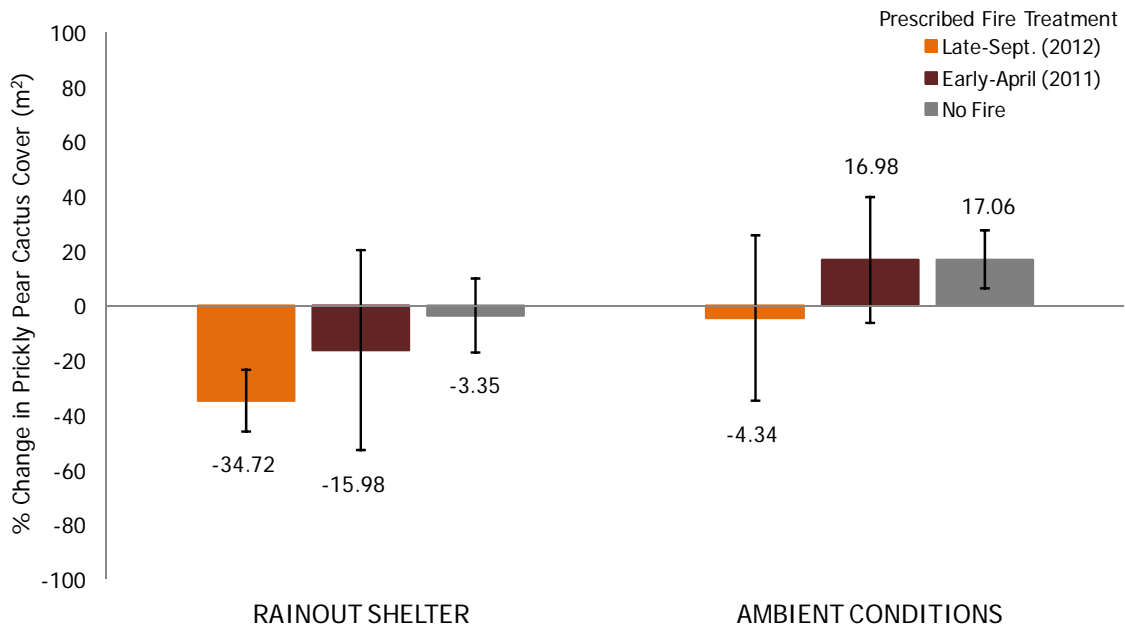


Figure 31. An assessment of the percent change in prickly pear cactus cover (m^2) in response to the prescribed fire treatments under plots with a rainout shelter compared to plots under ambient (control) conditions ($P=0.595$). All results are presented as a mean value (\pm S.E.). A comparison of data collected at the start (June 2010) and conclusion (March 2013) of the field study

Moisture Content of Harvested Stems

The *in situ* drought simulation treatments, using the fixed-location rainout shelter technique, allowed us to alter the water availability and manipulate the tissue moisture content of the prickly pear cactus stems. Despite the high water-use efficiency of this shallow-rooted succulent (Ogburn and Edwards 2010), we observed tissue withering and partial desiccation of the cactus stem under the shelters. The tissue wilted as the mucilaginous content in the stems contracted due to a lack of water availability (Figure 32). These results are consistent with numerous vegetation ecology studies that have used ‘rainout shelters’ in semi-arid regions to induced localized drought-stress (Koerner and Collins 2014; Reynolds, et al. 1999; Yahdjian and Sala 2002).



Figure 32. An image of a harvested prickly pear cactus stem from a motte that was found under a rainout shelter.

In comparison, the cactus stems found under ambient (control) conditions appeared to be upright and firm, an indication that the plant cells were saturated with

moisture. The mean wet weight of the harvested prickly pear cactus stem tissue samples for the cactus mottes found in the plots with a rainout shelter and for those found in ambient conditions were 3.63 g (\pm 0.22) and 5.48 g (\pm 0.19), respectively. As noted from the Student's t-test, there was a significant difference in tissue moisture content between those prickly pear cactus that underwent the drought simulation treatments and those left under ambient conditions ($P=0.0001$) (Figure 33). Reference Appendix B for the descriptive data and statistical analysis (Tables 20, 21).

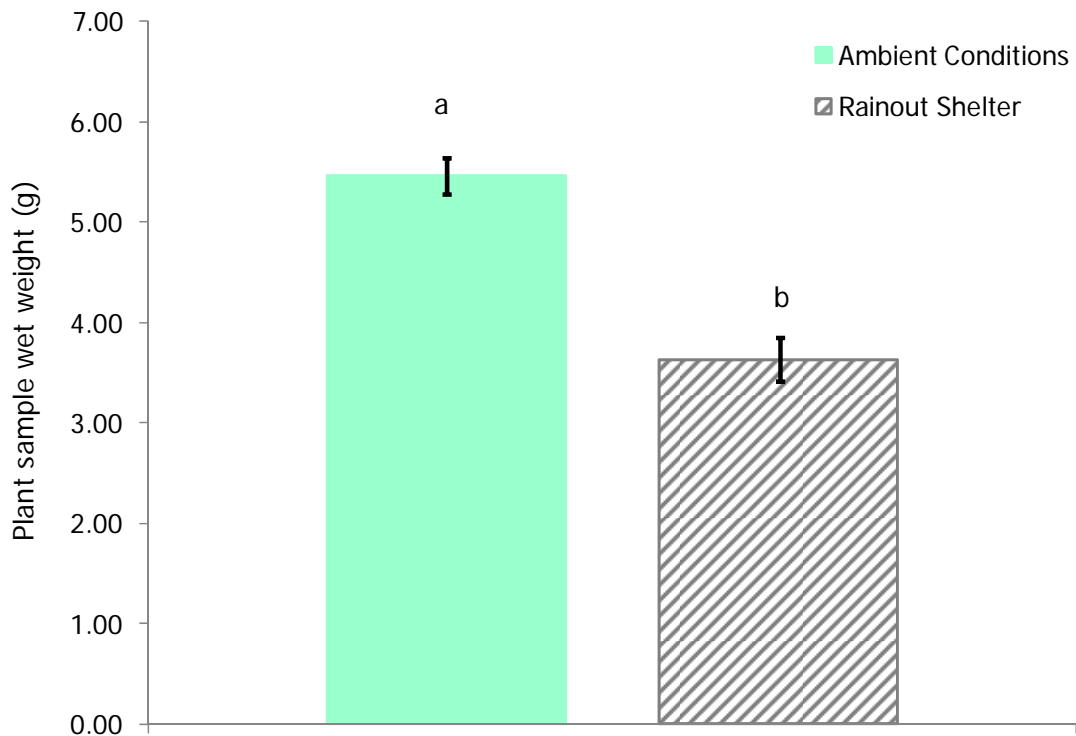


Figure 33. The average wet weight (g) of the harvested prickly pear cactus stem tissue samples. Results are presented as a mean value (\pm S.E) and any significant difference ($P < 0.05$) between the treatments is indicated by different letters.

Herbaceous Vegetation Layer

In June 2010, before the establishment of the rainout shelters and the application prescribed fire treatments, the plots had a mean standing herbaceous vegetation cover of 64.38 (\pm 2.47) percent (Figure 34). There was not a significant difference between the plot treatments ($P=0.162$). Reference Appendix B for the descriptive data and statistical analysis (Tables 22, 23).

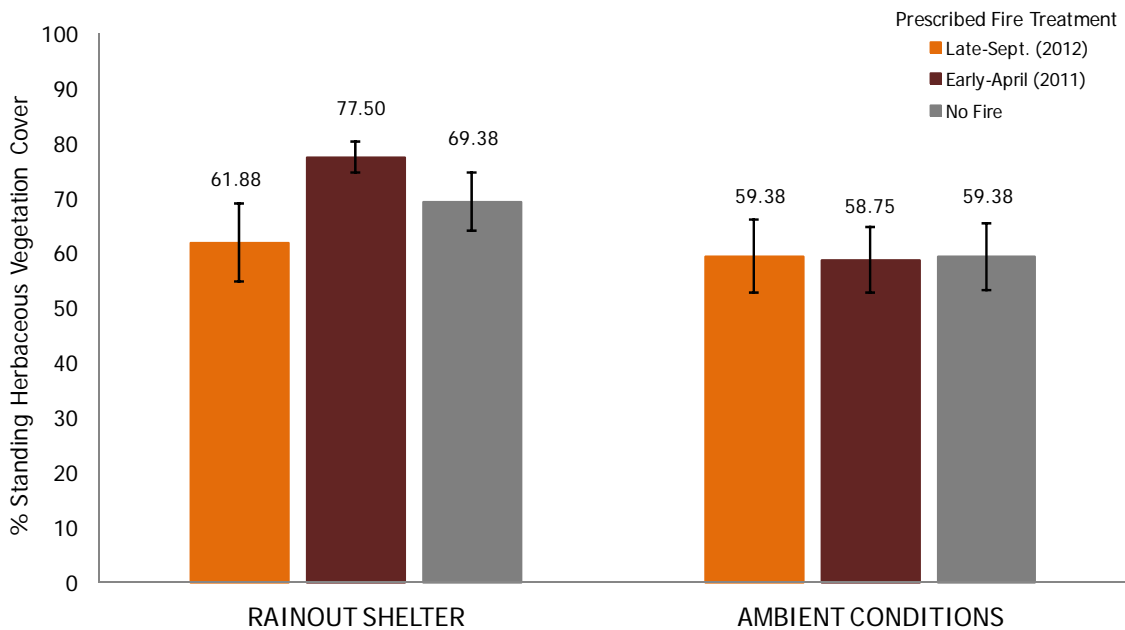


Figure 34. A comparison of the mean (\pm S.E.) percent standing herbaceous vegetation cover on the plots prior to the prescribed fire and drought simulation treatments in 2010 ($P=0.162$). Data for this analysis was collected at the start (June 2010) and conclusion (March 2013) of the field study

The prescribed fire treatments resulted in a statistically significant change in the percent standing herbaceous vegetation cover between the plots with and without a

rainout shelter ($P=0.0001$) (Figure 35). Reference Appendix B for the descriptive data and statistical analysis (Tables 24, 25).

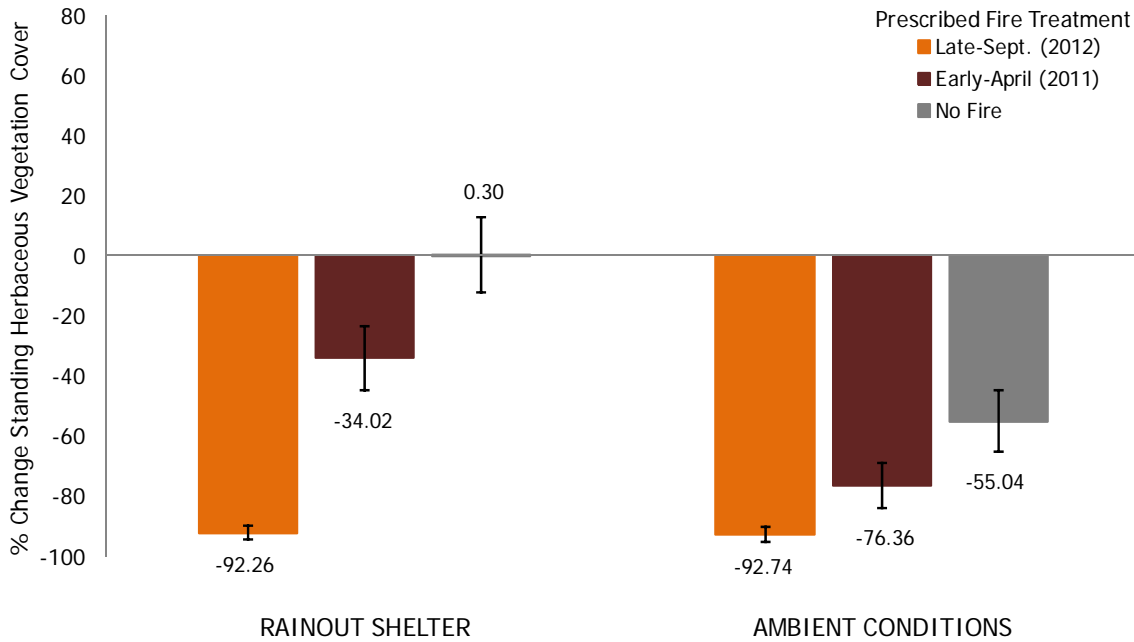


Figure 35. An assessment of the percent change in standing herbaceous vegetation cover in response to the prescribed fire treatments under plots with a rainout shelter compared to plots under ambient (control) conditions. All results are presented as a mean value (\pm S.E.). A comparison of data collected at the start (June 2010) and conclusion (March 2013) of the field study

For the prescribed fires administered early-April 2011, the plots with a rainout shelter experienced a significantly greater reduction in herbaceous cover ($P=0.006$). There was a $34.02 (\pm 10.63)$ percent reduction of herbaceous cover in the plots with a rainout shelter, whereas the plots under ambient (control) conditions had a $76.36 (\pm 7.50)$ percent reduction of herbaceous cover. In contrast, there was not a statistically significant difference in the percent change of herbaceous cover between the burned

plots with and without a rainout shelter for the fire treatments that were administered late-September 2012 ($P=0.887$). There was a 92.26 (± 2.30) percent reduction of herbaceous cover in the plots with a rainout shelter and a 92.74 (± 2.38) percent reduction of herbaceous cover in the plots under ambient (control) conditions. In the absence of prescribed fire, there was a 0.30 (± 12.51) percent increase of standing herbaceous cover in the plots with a rainout shelter compared to a 55.04 (± 10.03) percent decrease in herbaceous cover in the plots under ambient conditions; a statistically significant difference ($P=0.004$). Reference Appendix B for the descriptive data and statistical analyses (Table 26).

Bare Ground Cover

In June 2010, prior to the establishment of the rainout shelters and the application of the prescribed fire treatments there was a mean percent bare ground cover of 12.08 (± 1.41) ($P=0.545$) in the plots (Figure 36). In 2013, the plots with a rainout shelter that were left as unburned (control) treatments had a mean of 5.63 (± 1.48) percent bare ground cover; whereas, those burned during late-September (2012) and early-April (2011) had a mean bare ground cover of 81.25 (± 5.32) and 26.25 (± 6.53) percent, respectively. The plots without a rainout shelter that were left unburned had a mean of 35.00 (± 5.09) percent bare ground cover. In comparison, those burned during late-September (2012) and early-April (2011) had a mean bare ground cover of 63.75 (± 7.43) and 43.75 (± 5.49) percent, respectively. Reference Appendix B for the descriptive data and statistical analysis (Tables 27, 28).

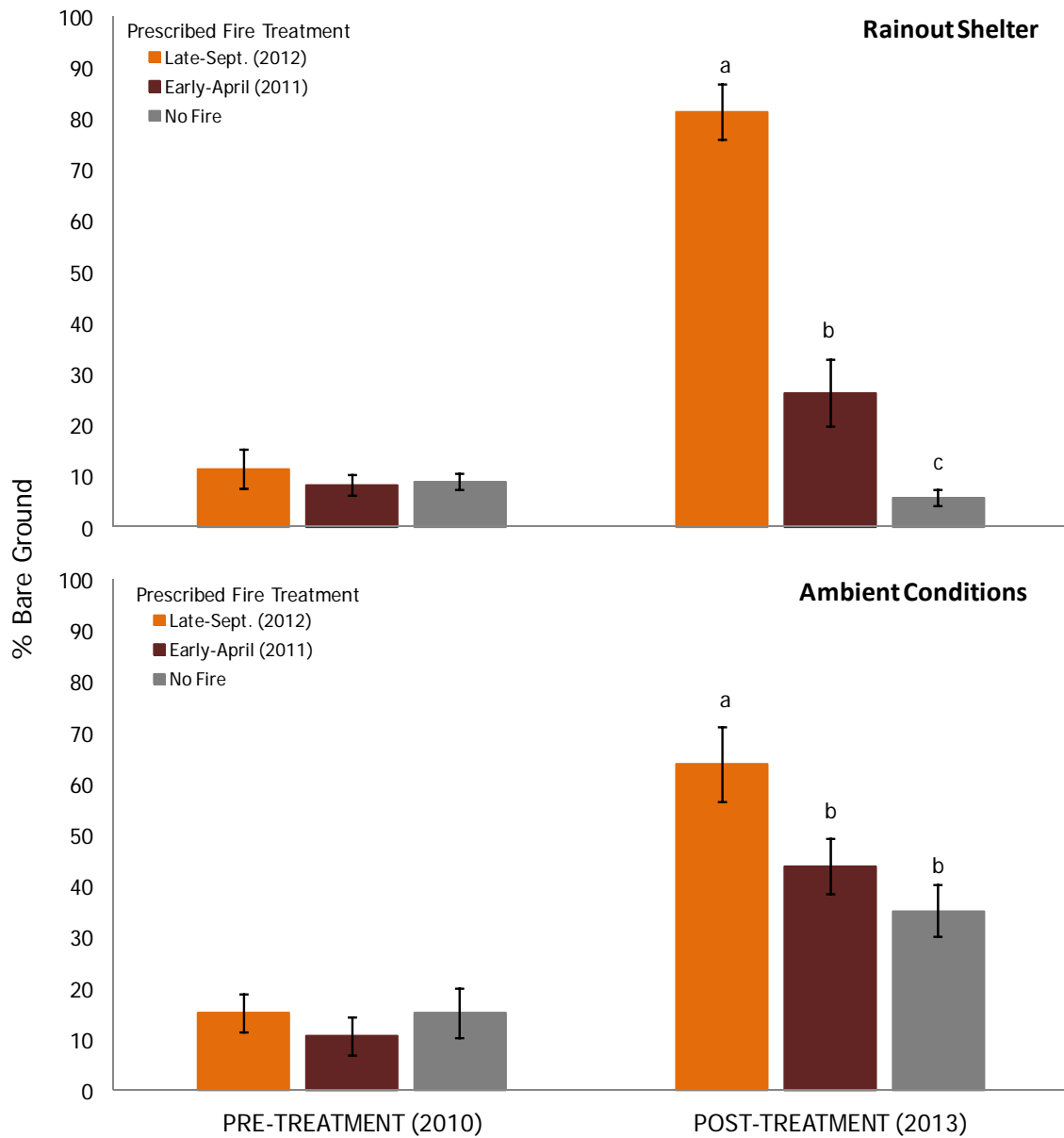


Figure 36. A comparison of the percent bare ground between the plots with and without a rainout shelter prior to the prescribed fire treatments (2010) and post-treatment (2013). All results are presented as a mean (\pm S.E.) and any significant difference ($P < 0.05$) in response to the fire treatments is indicated by different letters. Data for this analysis was collected at the start (June 2010) and conclusion (March 2013) of the field study

The late-September (2012) prescribed fire treatments did not result in a statistically significant difference in the percent bare ground cover between the plots with and without a rainout shelter ($P=0.076$) (Figure 37). Similarly, the percent bare ground cover in the plots with and without a rainout shelter was not statistically significant for the plots that were burned early-April 2011 ($P=0.059$). In contrast, there was a statistically significant difference in the percent bare ground cover between the plots with and without a rainout shelter in the absence of a prescribed fire treatment ($P=0.00007$). Reference Appendix B for the descriptive data and statistical analyses (Tables 29, 30).

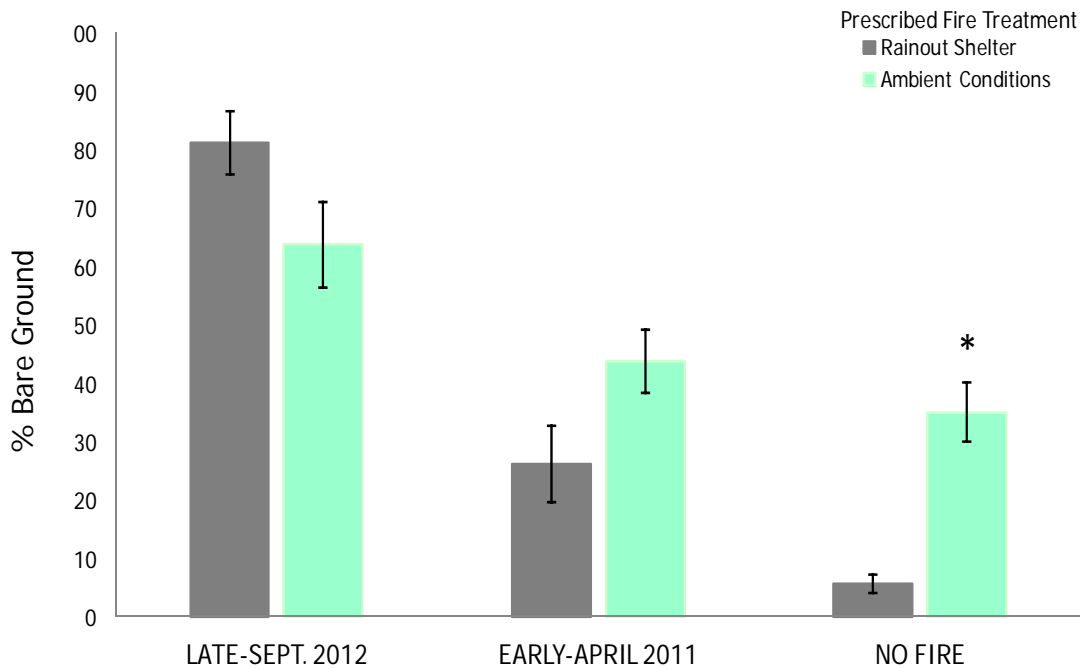


Figure 37. A post-treatment (2013) comparison of the percent bare ground by fire treatments between the plots with and without a rainout shelter. All results are presented as a mean (\pm S.E.) and an asterisk indicates any significant difference ($P < 0.05$) between treatments. Data was collected at the conclusion (March 2013) of the field study

DISCUSSION

The management and control of prickly pear cactus encroachment in rangelands is more difficult and prohibitively expensive to achieve once it establishes as the dominant species (Ansley and Castellano 2007*a*; Petersen, et al. 1988; Uecker, et al. 1988). The application of prescribed fire treatments following a period of prolonged-drought has been proposed as a favorable strategy to suppress the expansion of this problematic succulent. However, to date, despite the ecologic and economic significance of prickly pear encroachment in these rangeland ecosystems, the thermo-tolerance of drought-stressed succulent plants to prescribed fire treatments remains poorly understood. Land managers would benefit from having greater insight into the impact of fire on drought-stricken prickly pear cactus, in particular, if this combination could lead to a *de facto* increase in fire severity that is independent of fire intensity.

Prickly Pear in Response to Fire and Drought

The prescribed fires on the plots with a rainout shelter were able to reach a significantly higher maximum instantaneous fire temperature when compared to the plots that were left under ambient conditions. It is probable that the drought-stricken prickly pear cactus stems under the shelters were more prone to smoldering combustion (Bond and Keeley 2005; Humphery and Everson 1951; Thomas 1991; van Mantgem, et al. 2013; Wright 1974). However, contrary to expectations, a simulated drought did not decrease this succulents' thermo-tolerance to the prescribed fire treatments. In this study, the application of prescribed fires in early-April 2011 resulted in a greater prickly pear cactus coverage reduction on the plots with a rainout shelter compared to those left

under ambient conditions. Yet, despite the slight trend indicating greater prickly pear cover reduction; this difference was not statistically significant. These findings do not support our hypothesis that prickly pear cactus will be more negatively impacted by a prescribed fire when it is drought-stressed. This outcome is contrary to that of Wright (1974) and van Mantgem, et al. (2013) who have suggested that a plants ability to withstand fire significantly decreases when its tissue is experiencing prolonged drought. It is also differs from the findings by Roques et al. (2001) who found that fire and drought can act in concert, amplifying the effects of the burns, yielding a greater reduction to brush encroachment in a savanna ecosystem. It is also possible that the prolonged drought that impacted the region following the application of the April 9, 2011 prescribed fire treatments could have reduced some of the contrast between the drought simulation treatments (i.e. shelter, no shelter). According to the National Drought Mitigation Center, the growing season in 2011 was classified as an ‘extreme’ and ‘exceptional’ drought with a Palmers Drought Severity Index (PDSI) of -4.0 to -4.9 and -5.0 or less, respectively (National Centers for Environmental Information, NOAA 2015). Reference Figure 38 for the U.S. Drought Monitor Maps from April 2011, July 2011, and September 2011.

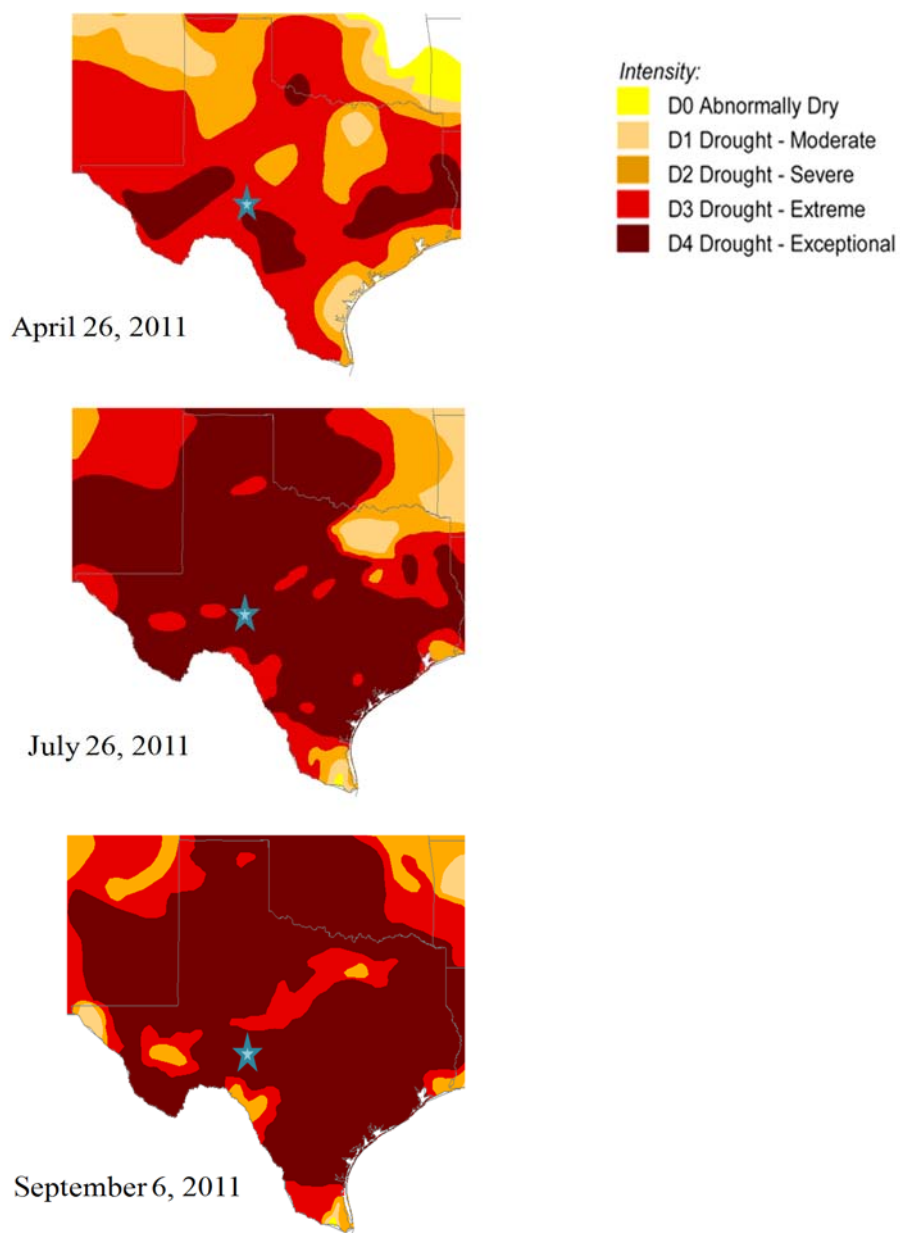


Figure 38. A regional-scale drought representation in the rangelands of Texas obtained from the U.S. Drought Monitor for the 2011 growing season (April, July, and September) following the prescribed fire treatments administered April 9, 2011. The star on the maps represents the location of the Texas AgriLife Research Station near Sonora, Texas (National Centers for Environmental Information, NOAA 2015).

Similarly, the application of prescribed fires in late-September 2012 did not result in statistically significant differences between precipitation treatments; the plots with a rainout shelter had a reduction in prickly pear cactus coverage compared to those left under ambient conditions that experienced an increase. Again, these findings do not support our hypothesis that drought-stressed prickly pear cactus is more susceptible to fire-induced damage and mortality than non-drought individuals. Furthermore, contrary to expectation this research does not support previous studies that have suggested that prickly pear cacti's response to fire varies seasonally (Ansley and Castellano 2007*b*). This outcome differs from previous studies that have suggested that prescribed fires conducted toward the end of the growing season (i.e. August, September) will be particularly damaging since it corresponds to a period when the plants are most dehydrated (Brockway, et al. 2002; Humphrey and Everson 1951). In particular, an increase in prickly pear cactus cover in the plots that were left under ambient conditions was a finding that was more in line with that of Daubenmire (1968), Duncan (2003) and Trollope (1984) who suggests that plants are more tolerant to fires when they are physiologically inactive (i.e. dormant). The extended regional drought that affected the region following the September 24, 2012 prescribed fire treatments also could be a possible explanation for these results. The months following the fire were classified as 'severe' and 'extreme' drought with a PDSI of -3.0 to 3.9 and -4.0 to -4.9, respectively (National Centers for Environmental Information, NOAA 2015). Reference Figure 39 for the U.S. Drought Monitor Maps from October 2012, November 2012, and March 2013.

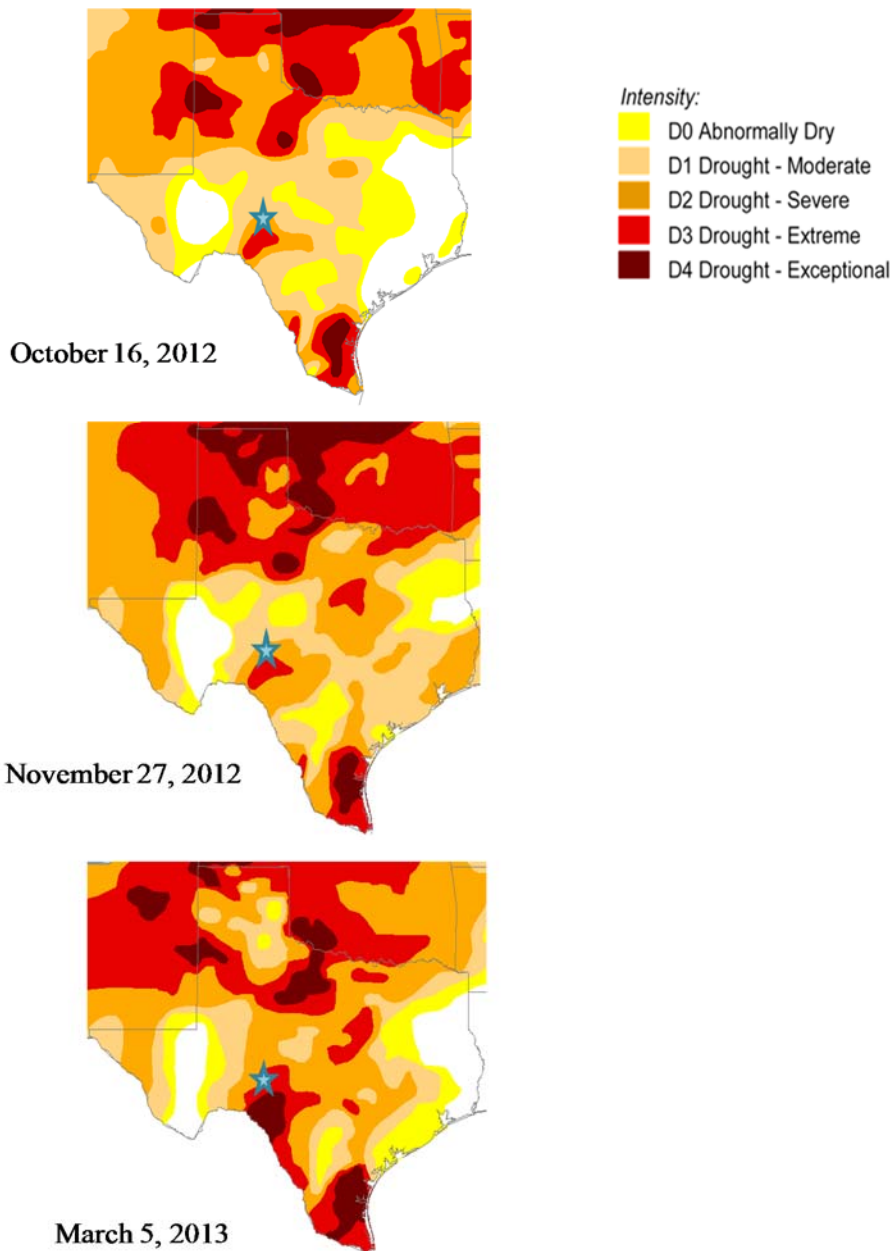


Figure 39. A regional-scale drought representation in the rangelands of Texas obtained from the U.S. Drought Monitor for late 2012 and early 2013, following the application of prescribed fire treatments (September 24, 2012). The star on the maps represents the location of the Texas AgriLife Research Station near Sonora, Texas (National Centers for Environmental Information, NOAA 2015).

Prickly Pear's Response to Drought in the Absence of Fire

The unburned plots with a rainout shelter had a slight reduction in prickly pear cactus coverage (3.35 percent). The decline in prickly pear cactus coverage in the plots with the drought simulation treatments is in line with studies that examined drought-induced mortality of rangeland savanna plants (Roques, et al. 2001; Van Auken 2009). Young (1956) reported that many of the prickly pear cacti died after a period of exceptional drought. However, contrary to expectations, in the absence of prescribed fire, there was no statistically significant difference in prickly pear cover between the drought-simulation and ambient control (no shelter) treatments. It is also likely that the aforementioned drought could have reduced some of the contrast between the treatment combinations and rendered the ambient conditions (i.e. no shelter) null as a control group. The two years that followed the establishment of the *in situ* drought simulation treatments (June 2010) were followed by growing seasons experiencing prolonged drought conditions. The National Drought Mitigation Center classified the 2011 growing season as an 'extreme' and 'exceptional' drought with a Palmers Drought Severity Index (PDSI) of -4.0 to -4.9 and -5.0 or less, respectively. Similarly, the 2012 growing season was classified as a 'severe' and 'extreme' drought with a PDSI of -3.0 to 3.9 and -4.0 to -4.9, respectively (National Centers for Environmental Information, NOAA 2015). Reference Figure 40 for the U.S. Drought Monitor Maps from April, July, September (2010, 2011, and 2012).

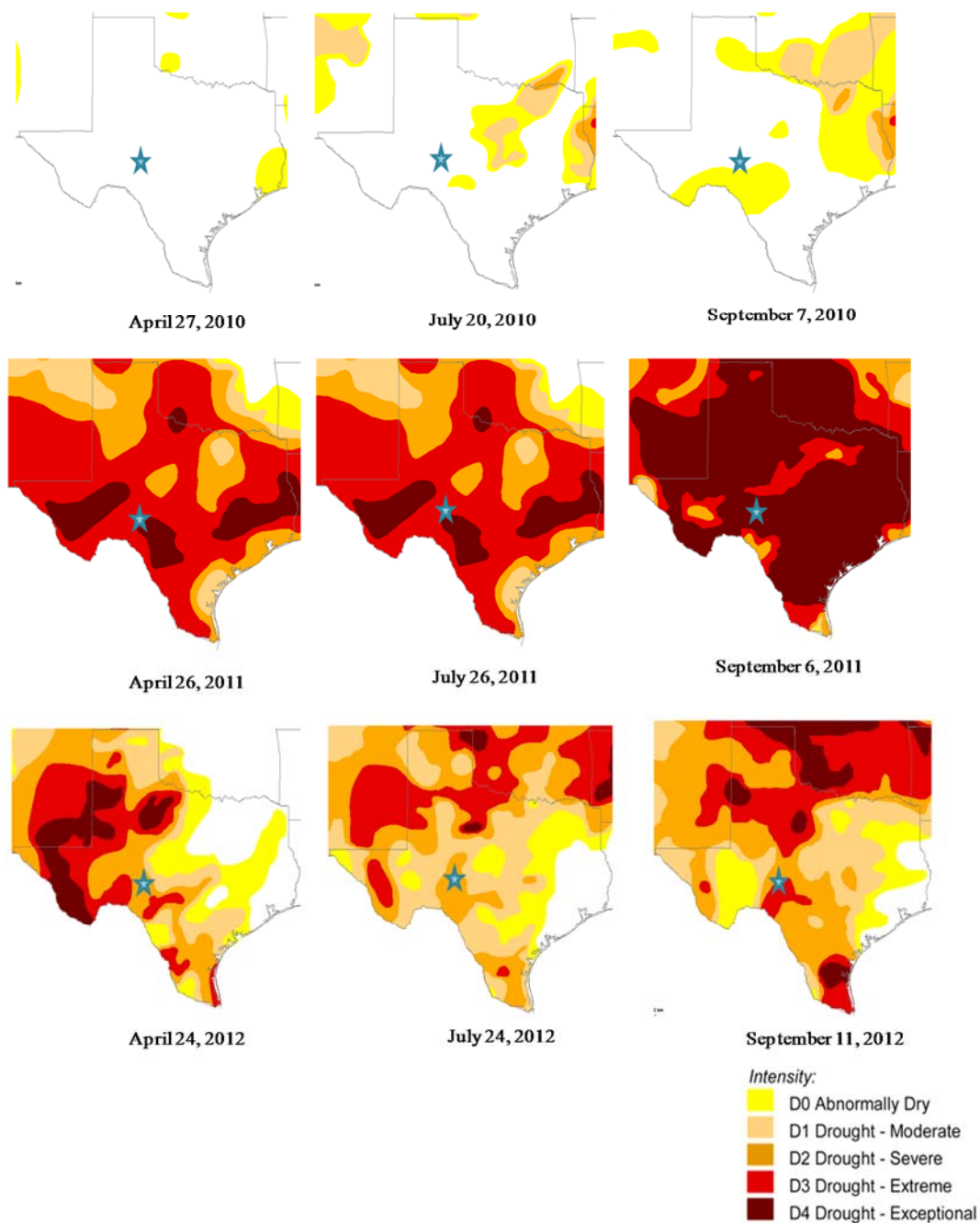


Figure 40. A regional-scale drought representation in the rangelands of Texas obtained from the U.S. Drought Monitor for the 2010, 2011, and 2012 growing seasons (April, July, and September) immediately prior to and following the establishment of the *in situ* drought simulation treatments, using the fixed-location rainout shelter technique (June 2010). The star on the maps represents the location of the Texas AgriLife Research Station near Sonora, Texas (National Centers for Environmental Information, NOAA 2015).

The unburned plots without the shelter experienced an increase in prickly pear cactus coverage of 17.06 percent, but it was not significantly different from the unburned plots with the rainout shelter. This expansion of prickly pear in the absence of control strategies is consistent with studies by Ueckert, et al. (1988) and Petersen, et al. (1988) who found that there was a 38 percent and 47 percent increase in live prickly pear cactus cover in the untreated plots, respectively.

Recovery of Herbaceous Layer

In this study, the application of prescribed burns in early-April 2011 resulted in a significant difference in standing herbaceous cover between the hydration treatments; the plots left under ambient precipitation had a greater reduction in standing herbaceous coverage compared to those under a rainout shelter. Similarly, the unburned plots with a rainout shelter and those left under ambient conditions also had a difference in standing herbaceous cover that was statistically significant. The unburned plots with a rainout shelter experienced a slight increase in standing herbaceous cover whereas those left under ambient precipitation conditions experienced a decrease. These results are consistent with those of Bates et al. (2006) who found that control (no shelter) treatment had less herbaceous litter cover than *in situ* rainout shelter treatments. In contrast, the application of prescribed fires in late-September 2012 did not result in statistically significant differences in standing herbaceous cover between precipitation treatments; the plots with a rainout shelter and those left under ambient conditions experienced a comparable reduction in standing herbaceous cover.

The amount of bare ground cover on the plots with different precipitation and prescribed fire treatments was inversely related to the amount of standing herbaceous cover. The plots that were burned in early-April 2011 and those that were left as unburned treatments had less bare ground on the plots with a rainout shelter. The application of prescribed fires in early-April 2011 resulted in greater bare ground cover on the plots without a shelter compared to those with a rainout shelter. Yet, despite the slight trend indicating greater bare ground cover for those left under ambient conditions; this difference was not statistically significant. Similarly, the plots that were burned in late-September 2012 also did not have a statistically significant difference between the treatments with a rainout shelter and those without a shelter. However, these treatments had a greater amount of bare ground cover on the plots with a rainout shelter compared to those left under ambient conditions. In contrast, the unburned control treatments had a statistically significant greater amount of bare ground on plots with a rainout shelter compared to those with a without a rainout shelter. Presumably, the prolonged regional drought and the fire treatments did not allow for the prompt establishment of herbaceous cover on these bare ground plots (Chamrad and Box 1965; Koerner and Collins 2014; Marshall 1973).

Broader Implications for Rangeland Ecology and Management

Ranchers and land managers interested in adopting intervention brush control strategies aimed at reducing the continual expansion of prickly pear cactus in Texas rangelands will be able gain insight from this field study. Based on the results from the prescribed fires that were administered in late-September, we can recommend the use of

prescribed burning on sites with an adequate fuel load as soon as prickly pear becomes a problem, because this strategy will still cause tissue damage (i.e. scorch, mortality) regardless of this succulent's drought-stressed status (Heirman and Wright 1973). The simulated drought conditions (i.e. hydration status treatments) did not alter this problematic succulent's thermo-physiological tolerance to fire. Despite these findings, there is ample ground for continued research that addressed the management of rangelands when confronted with the projected increases in temperature and drought due to climate change and rising atmospheric CO₂ concentrations (Brown and Thorpe 2008; Garcia de Cortázar and Nobel 1990; Gillson, et al. 2013; Graham and Nobel 1996; Kattenberg, et al. 1996; McCarthy, et al. 2001; Mouillot, et al. 2013; Staudt, et al. 2008; Zavaleta, et al. 2003).

CHAPTER VI
INTEGRATED RESTORATION STRATEGIES TO
CONTROL PRICKLY PEAR ENCROACHMENT: EXPERIMENT ASSESSING
PRESCRIBED FIRE AND A NON-RESTRICTED HERBICIDE

INTRODUCTION

In the absence of effective brush control, Texas rangelands experience significant prickly pear cactus (*Opuntia* spp.) encroachment. The encroachment of this spiny succulent is a problem that degrades the ecological integrity and economic value of the land (Fuhlendorf, et al. 2001; Van Auken 2000; Young, et al. 1948). Increased prickly pear density decreases the productivity of the range (i.e. carrying capacity) because it interferes with and limits the movement and handling of livestock (Bentley 1898; Sosa 2009). In 1980, prickly pear was estimated to inhabit 103 million ha of Texas rangelands, which is ca. 25% of all rangeland in the state (Hanselka, 1981). Today, prickly pear encroachment is more severe in some areas than others, depending on the land management legacy of the ecosystem (i.e. grazing history) as well as environmental factors (i.e. climate, topography) (Hanselka and Falconer 1994). There are rangeland sites in west and central Texas where prickly pear covers over ca. 70% of the landscape (Figure 41). Herbicides and prescribed fire are frequently used strategies by rangeland managers to suppress undesirable vegetation in these semi-arid ecosystems (DiTomaso 2000; Kreuter et al. 2008; Young, et al. 1950).



Figure 41. A ground view of a recently burned site found at the Edwards Plateau of Texas, where prickly pear form entangled thickets with weed-like characteristics (ca. 747 cactus plants per hectare).

Since the 1930s, the use of herbicides (i.e. pesticides targeting plants) in the United States has been a common practice to suppress the spread of undesirable vegetation (Dameron and Smith 1939). In 1997, for example, over 100 million ha of rangelands (which account for ca. 25% of all rangelands in the United States) were treated with these chemicals (Bussan and Dyer 1999). The phytotoxic compounds in herbicides disrupt multiple metabolic processes, inhibiting protein synthesis and normal cell division, resulting in the death of the vegetative tissue (Reade and Cobb 2002). Herbicides are readily available to land managers and can be applied to undesirable woody brush and succulent species in range and pasture lands using a number of techniques, including aerial and ground applicators (i.e. aircraft, backpack sprayers) (Bovey 1987, 1995; Scifres 1980; Young, et al. 1950).

The use of chemical treatments as a suppression strategy to control prickly pear encroachment is effective on sites where prickly pear covers limited portions of the

landscape because they are accessible for treatment and it is typically not cost-prohibitive (Gaylord 1982; Vallentine 2004; Young, et al. 1948). However, on sites experiencing a high density of prickly pear, the accessibility and cost (e.g., labor, lease and purchase of specialized equipment, state-issued applicators license) are serious impediments to ranchers and land managers who attempt to apply herbicides to suppress prickly pear encroachment (Figure 42) (Bussan and Dyer 1999; McMillan, et al. 2002).



Figure 42. A laborer spraying prickly pear cactus with a ground applicator on a woody brush and succulent infested rangeland in Texas in the 1930s (Dameron and Smith 1939).

Unfortunately, these economic and logistical constraints limit the effectiveness of herbicide use as a single-treatment land management approach. Because of these constraints, the long-term control of prickly pear cactus has been largely ineffective (McGinty and Ueckert 2005; Slater, et al. 2001). These limitations have contributed to today's chronic rate of cactus encroachment, which is so significant, that it calls for

action from local, state and federal stakeholders and researchers (DeFelice 2004; Ueckert and McGinty 1997). Additionally, there are adverse environmental consequences with applying traditionally and commonly used federally restricted-use herbicides (i.e. Surmount™, Tordon® 22K) (EPA 2017). These restricted-use herbicides are composed of chemicals that can potentially have greater environmental harm (e.g., risk to on- and off-site endangered terrestrial, semiaquatic, and aquatic plant species, adverse effects on other on and off-site non-target plants, and potential for further groundwater contamination) and it can only be purchased, handled and applied by an individual holding a state-issued applicator's license (Hunt and Thompson 1992; EPA 2017).

In the last few decades, there have been advances in foliage applied herbicide formulations with active ingredients that are considered to be significantly less harmful to human health and to the environment. Unlike federally restricted-use herbicides, less environmentally harmful herbicides are classified as federally non-restricted use, which do not require a license and are readily available to the general public in the United States (Kochenderfer, et al. 2012). These non-restricted use herbicides are also more likely to be adopted by ranchers and landowners who are concerned about the potential adverse environmental impacts that are associated with federally restricted-use herbicides (Bauder, et al. 2010).

The use of prescribed fire as a means of controlling brush and undesirable succulent encroachment has also increased in the past few decades (Kreuter et al. 2008). Rangeland managers in Texas are increasingly selecting prescribed fire as an alternative

to other strategies (i.e. mechanical, chemical) (Teague, et al. 1997). Prescribed fire is relatively inexpensive and effective at suppressing undesirable woody brush and succulent plant encroachment in these rangeland ecosystems (Ruthven III, et al. 2003; Taylor 2003; Teague et al. 2008). However, the use of herbicides or prescribed fire does not have to be exclusive in addressing the current prickly pear encroachment problem. Insights into ways these strategies can be used in combination to produce a ‘synergistic’ brush management response may produce markedly enhanced effects that maximize ecological objectives while reducing economic costs (Hamilton and Ueckert 2004).

In the past, there has been considerable success with integrating more than one brush control strategy (i.e. mechanical, chemical, prescribed fire, biological) to halt the expansion of undesirable rangeland vegetation (Masters and Sheley 2001). Considering that the prickly pear tissues are covered by a thick waxy cuticle layer that serves as a protection mechanism for the plant (Gibson and Nobel 1986), burning the stems with a prescribed fire could increase the plants physiological susceptibility to a follow-up application of an herbicide treatment. In a notable study by Ueckert et al. (1988), rangeland researchers combined prescribed fire and the mixture of two federally restricted-use herbicides 2,4,5-T and picloram (i.e. Tordon® 22K) to effectively reduce 98% of prickly pear coverage on a site in central Texas with a history of woody brush and succulent encroachment. Although, this combination brush control strategy was effective, it disregards the effects these federally restricted-use herbicide have on the environment.

Vista® (i.e. fluroxypyr) is a federally non-restricted use foliage applied herbicide that is a trademark of The Dow Chemical Company (Dow AgroSciences 2017*b*). This non-restricted herbicide has the potential to be an alternative to widely-used federally restricted-use herbicides (i.e. Surmount™, Tordon® 22K). Despite the readily-available access to fluroxypyr by the general public, there has yet to be an attempt to assess the efficacy of this non-restricted herbicide in combination with prescribed fire as a potential strategy to suppress the expansion of prickly pear encroachment. There is limited insight of the ecological response of prickly pear when it receives a combination of brush control treatments. Due to this lack of controlled efficacy assessments there is currently no land management recommendation for the use of fluroxypyr and prescribed fire on sites experiencing succulent encroachment.

Using a randomized and replicated split-plot research design, we conducted a field research study that allowed us to assess the immediate response of prickly pear to the application of two distinct brush control strategies. Prescribed fire and both a federally restricted-use and a non-restricted foliage applied herbicide were sequentially integrated with aim of suppressing prickly pear cactus encroachment in degraded rangelands. This design also allowed us to test the effectiveness of a non-restricted herbicide, fluroxypyr, at reducing prickly pear cactus coverage in comparison to the widely-used, federally restricted-use herbicide Surmount™ (i.e. picloram) a trademark of The Dow Chemical Company (Dow AgroSciences 2017*a*).

We predict that the combination of a prescribed fire and Vista® is a viable restoration strategy to control prickly pear encroachment in Texas rangelands that is

superior to either management treatment by itself. The sequential integration of a prescribed fire, followed by the judicious application of a fluroxypyr, will operate synergistically and result in a positive interaction that will exceed the expected sum of reduction of prickly pear coverage over that of either treatment applied alone. In this study, we also submit that the prescribed fire scorches the epidermis covering the prickly pear stem tissue, as noted in Chapter IV, allowing fluroxypyr to be comparably as effective as the conventional, federally-restricted herbicide at reducing prickly pear coverage.

METHODS

Study Site

In July 2011, a field-based study using a randomized and replicated split-plot research design was established in the northwestern portion of the Edwards Plateau at the Texas AgriLife Range Station. The historic climax plant community for this semi-arid site was described as an open savanna dominated by mid and short grasses with scattered woody shrub and succulent species (Taylor and Ralphs 1992; USDA-NRCS 2017). Today, the vegetation on these rangelands has transitioned into a prickly pear dominated brushland (*c.* 747 cactus mottes per hectare). This encroachment has suppressed the quantity and quality of desirable herbaceous forage vegetation (Hanselka and Paschal 1991; Lundgren, et al. 1981; Taylor 2007; Teague, et al. 2008). The 1,279 hectare station is located along Texas State Highway 163 between Ozona and Barnhart, Texas, USA (31° N, -101° W) and has an elevation of approximately 800 m. This temperate semi-arid site has a growing season spanning 209 days, a mean annual temperature of 18°C and it receives a mean annual precipitation of approximately 480.3 mm (NOAA 2014; USDA-NRCS 2017). The dominant soil present at the station is Texon-Ozona complex (ToB). ToB has a high moisture holding capacity, it is composed of calcareous clayey materials that are characterized as moderately alkaline silt loam, and the sub-soil is composed of moderately alkaline silty clay (USDA-NRCS 2017). Established in 1938, the station was used for grazing of livestock (e.g., sheep and goats). However, for the duration of this study, the pastures associated with our research site

were only accessible to wildlife (e.g., white-tailed deer, rabbits, rodents), all domestic ungulate grazing was deferred from the area to prevent livestock trampling of the mottes.

Experimental Design

A split-plot experimental design was used to examine the *in situ* response of prickly pear to interactive effects of prescribed fire and herbicide application treatments. Each experimental plot was randomly assigned one of the following treatment combinations: [late-winter season fire × fluroxypyr herbicide], [late-winter season fire × picloram herbicide], [late-winter season fire × no herbicide (control)], [no fire (control) × fluroxypyr herbicide], [no fire (control) × picloram herbicide], and [no fire (control) × no herbicide (control)]. We delineated ten rectangular (15 by 45 m) plots over a 4 ha site containing the ToB complex soil series, in a range area characterized by a similar grazing and land management history. The vegetation on these pastures was primarily composed of tobosagrass (*Hilaria mutica*), buffalograss (*Bouteloua dactyloides*), curly-mesquite (*Hilaria belangeri*), slim tridens (*Tridens muticus*), Texas cupgrass (*Eriochloa sericea*), other stoloniferous short grasses, weedy annuals, mesquite (*Prosopis glandulosa*), prickly pear (*Opuntia* spp.), and annual forbs, such as broomweed (*Amphichyris drancunculoides*) (Taylor and Ralphs 1992; USDA-NRCS 2017). Each plot was separated by 4 m-wide buffer zones that were mechanically cleared of vegetation to remove all flammable surface materials (i.e. fuels). This balanced design provided five replications of each treatment combination (Figure 43).

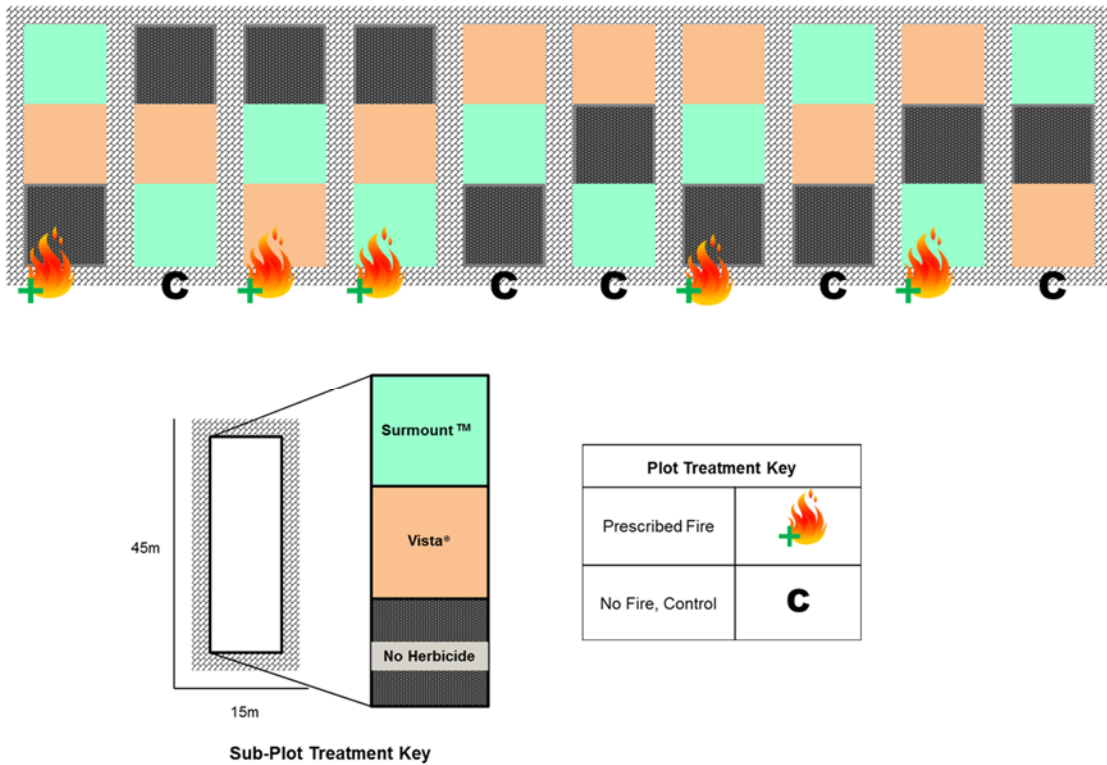


Figure 43. Schematic representation of the split-plot experimental design used at the Texas Range Station near Barnhart, Texas to assess the interactions between prescribed fire and herbicide treatments.

Prescribed Fire Treatments

Five plots were subjected to a single late-winter prescribed fire treatment, while the remaining five experimental plots were left unburned. On February 7, 2012, a prescribed burn manager supervised the application of these independent experimental fire treatments that were characterized as the ‘full-plot effect’ (reference research design; Figure 43). The plots were burned with low-intensity headfires that were applied in the afternoon hours, under the mild fire weather conditions with an average air temperature of 12.7°C, southerly winds of 11.3 kph, and 41% relative humidity. To prevent the start

of accidental new fires by the spread of embers outside the delineated buffer zones and into adjacent plots, the flames from the headfire were fanned within the plot in the direction of the prevailing wind until they reached the fire line from a backfire that was simultaneously set downwind of each plot (Jacoby, et al. 1992; Wright 1974). As an additional safety precaution to contain the fires, a mobile water supply, radio, fence pliers, shovels and rakes were strategically located near the prescribed burn area, and a Kestrel weather meter monitored the air temperature, wind direction and speed, barometric pressure, and relative humidity at the field site undergoing the fire treatments.

Herbicide Treatments

Prickly pear foliage herbicide treatments were applied as a follow-up to the prescribed fires (reference design; Figure 43). The 10 plots were equally divided into three sub-plots (15 by 15 m), and each sub-plot was randomly assigned to one of the following herbicide treatments: (i) fluroxypyr (a non-restricted use selective herbicide), (ii) picloram (a restricted use selective herbicide), and (iii) no herbicide (control).

Vista® is a trademark of The Dow Chemical Company. This is a non-restricted use herbicide, which does not require a license to purchase, handle, or apply (Dow AgroSciences 2017*b*). The active ingredient in this non-petroleum based solvent is fluroxypyr with the common name of 1-methylheptyl ester [(4-amino-3,5-dichloro-6-fluoropyridin-2-yl)oxy]acetic acid (Figure 44).

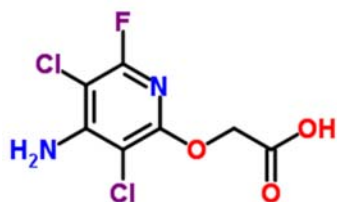


Figure 44. The 2-D chemical structure of fluroxypyr.

Surmount™ is a trademark of The Dow Chemical Company, and it is a federally restricted herbicide can only be purchased, handled, and applied by an individual holding the proper certification (Dow AgroSciences 2017a; Martinelli, et al. 1982). The active ingredients in this herbicide are a combination of fluroxypyr and picloram. The common name for picloram is 4-amino-3,5,6-trichloropicolinic acid triisopropanolamine salt (Figure 45).

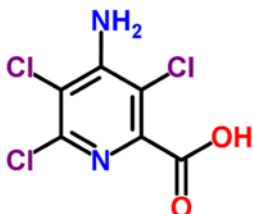


Figure 45. The 2-D chemical structure of picloram.

Fluroxypyr and picloram were diluted in water and applied at the recommended 1% concentration (McGinty and Ueckert 2005). A non-ionic commercial surfactant at a 0.25% concentration was added to each solution to reduce surface tension and improve the plants' absorption and retention of the herbicide (De Ruiter, et al. 1990). This

mixture was combined with Turf Mark Blue®, a temporary non-toxic blue dye, at a 0.25% concentration to ensure that the prickly pear stems were thoroughly covered with an herbicide coating. During the *in situ* application, the colorant prevented us from inadvertently wasting chemicals and visually enhanced where the plants intercepted the herbicide treatments.

To reduce drift potential into adjacent plots, we avoided spraying herbicides during windy conditions. Additionally, the effectiveness of the herbicides was improved by limiting the application to periods when the exterior of the mottes were wet (McGinty and Ueckert 2005). The herbicide treatments were applied November 13, 2012, 9-months after the application of the prescribed fires on a mild, clear afternoon with a 41% relative humidity, with southerly winds at 11.3 kph and an average air temperature of 12.7°C.

The prickly pear mottes within the plots were sprayed with distinct herbicide treatments using the individual plant treatment (IPT) technique (Cobb 1992). These early-fall season herbicide treatments were applied with a hand operated backpack sprayer that allowed us to target dense, hard to reach prickly pear mottes found in rough terrain. To ensure adequate herbicide coverage of the prickly pear stems, the sprayer's adjustable nozzle was set to release coarse droplets during our targeted ground broadcast applications. As a reference to compare the effectiveness of the fluroxypyr and picloram, the cactus mottes found in the no herbicide (control) sub-plot were sprayed with a fine mist of water. In order to ensure the compliance with all federal and state regulations, the application of picloram (restricted herbicide) was supervised by a

certified pesticide applicator affiliated with Texas A&M AgriLife Research & Extension.

Vegetation Assessment and Fuel Characteristics

A complete census of the prickly pear cactus, herbaceous and woody shrub community in each of the plots was collected July 2011 (i.e. pre-treatment), November 2012, and March 2013. The cactus mottes selected for this study a diameter average of 1.45 m, and they were randomly distributed within the plots. The cactus mottes were permanently marked with a tag for identification purposes, and the spatial location of each plant was recorded with a Global Positioning Systems (GPS) unit with sub-meter accuracy. We also calculated the cover area (m²) of each prickly pear motte using cardinal directions to measure the length and width, as well as its height from the ground to the top of the tallest cladode. Furthermore, the vegetation surrounding each prickly pear was assessed using a circular frame with a 2.5 m radius. Visual estimates of herbaceous vegetation cover (i.e. grass and forbs), woody brush, herbaceous litter, juniper litter, oak litter, dead woody fuels, and patches of bare ground were calculated at the nearest five percent, and the characteristics of the dead woody fuels were grouped into three time lag classes: 1-hour fuels, 10-hour fuels, and 100-hour fuels (Pyne 1984).

Statistical Analysis and Procedures

A combined analysis of variance (ANOVA) was used to evaluate the experimental treatments applied in this split-plot design. This group comparison statistical procedure allowed us to compare the differences among the treatments and treatment combinations. We assessed the effects our prescribed fire and herbicide

treatments had on prickly pear and herbaceous vegetation cover. We also analyzed the amount of bare ground (i.e. exposed soil) surrounding each cactus motte. If there was a difference between treatments, the Fisher's Least Significant Difference (LSD) method was used to compare the treatment group means. All the statistical analyses were performed using SPSS statistical software (IBM Corp. 2013), and the significance levels for our analysis using ANOVA's was set at $\alpha = 0.05$ for general cases and $\alpha = 0.10$ for interaction effect.

RESULTS

A total of 512 prickly pear cactus mottes and tracked them from July 2011 through March 2013. The plots were last inspected March 10, 2013, 1 year 1 month after the early-February 2012 fire treatments and 4 months after the early-November herbicide treatments.

Vegetation Response to Herbicides and Fire

Prickly Pear Cactus Cover

The prescribed fire treatments resulted in a statistically significant decrease in prickly pear cactus motte cover area (m²) between the plots with different herbicide treatments (P=0.0001). The plots that were sprayed with fluroxypyr (non-restricted) herbicide and left as unburned treatments had a mean of 32.77 (\pm 7.60) percent increase of prickly pear cover; whereas those that were burned in early-February (2012) had a 20.91 (\pm 4.93) percent reduction of prickly pear, and the difference was statistically significant (P=0.0001). The plots that were sprayed with picloram (restricted) herbicide, there was a 43.04 (\pm 8.45) percent increase of prickly pear cover in the plots that were left as unburned treatments compared to a 35.05 (\pm 5.57) percent reduction of prickly pear in the plots that were burned in early-February (2012), and similarly, this difference was statistically significant (P=0.0001). In the absence of an herbicide treatment, there was a 33.57 (\pm 5.47) percent increase of prickly pear cover in the plots that were left as unburned treatments compared to a 20.64 (\pm 5.48) percent reduction in the plots that were burned during early-February (2012), and the difference was also statistically

significant ($P=0.0001$). Reference Appendix C for the descriptive data and statistical analyses (Tables 31, 32, 33).

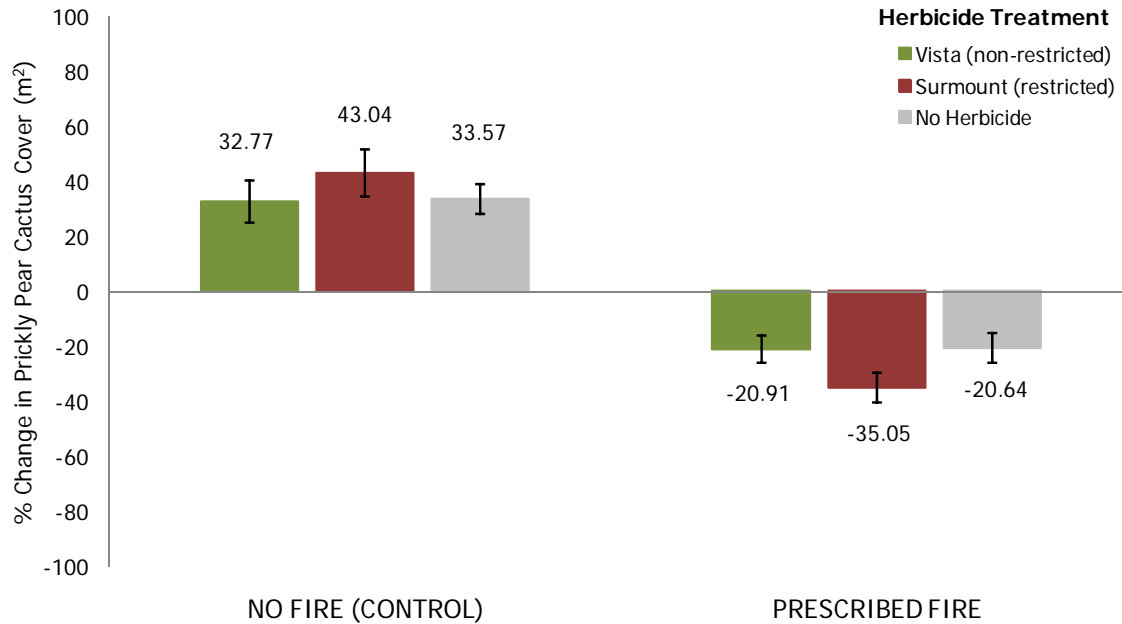


Figure 46. A comparison of the percent change in prickly pear cactus cover (m²) in response to the prescribed fire and herbicide treatments ($P=0.0001$). All results are presented as a mean value (\pm S.E.). A comparison of data collected at the start (July 2011) and conclusion (March 2013) of the field study

For the plots that were burned in early-February (2012), the percent change of prickly pear cactus cover in the plots that were sprayed with fluroxypyr (non-restricted) compared those that were sprayed with picloram (restricted) was not statistically significant ($P=0.060$). Likewise, the percent change of prickly pear cover in the plots that were left as a no herbicide treatment compared to the plots that were sprayed with fluroxypyr (non-restricted) or picloram (restricted) did not differ significantly, ($P=0.971$) and ($P=0.070$), respectively. On the other hand, in the absence of prescribed fire, the

percent change of prickly pear cover in the plots that were sprayed with fluroxypyr (non-restricted) compared to those that were sprayed with picloram (restricted) was also not statistically significant ($P=0.397$). Similarly, the percent change of prickly pear cover in the plots that were left as a no herbicide treatment compared to the plots that were sprayed with fluroxypyr (non-restricted) or picloram (restricted) resulted in a difference that was also not statistically significant, ($P=0.930$) and ($P=0.354$), respectively.

Reference Appendix C for the statistical analyses (Tables 34, 35).



Figure 47. A partially burned prickly pear cactus motte. The peripheral stem segments were scorched by the fire, whereas those found near the center and apex remained intact.



Figure 48. A prickly pear cactus motte treated with a selective herbicide. These phytotoxic chemicals resulted in malformation and decomposition of the stem segments.

Herbaceous Vegetation Layer

In July 2011, before the application of prescribed fire and herbicide treatments, the plots had a mean standing herbaceous vegetation cover of 65.59 (± 1.04) percent (Figure 49). There was not a significant difference between the plot treatments ($P=0.078$). The herbaceous vegetation on this site consisted of almost pure stands of tobosagrass (*Hilaria mutica*) and annual broomweed (*Xanthocephelum dracunculoides*). Reference Appendix C for the descriptive data and statistical analysis (Tables 36, 37).

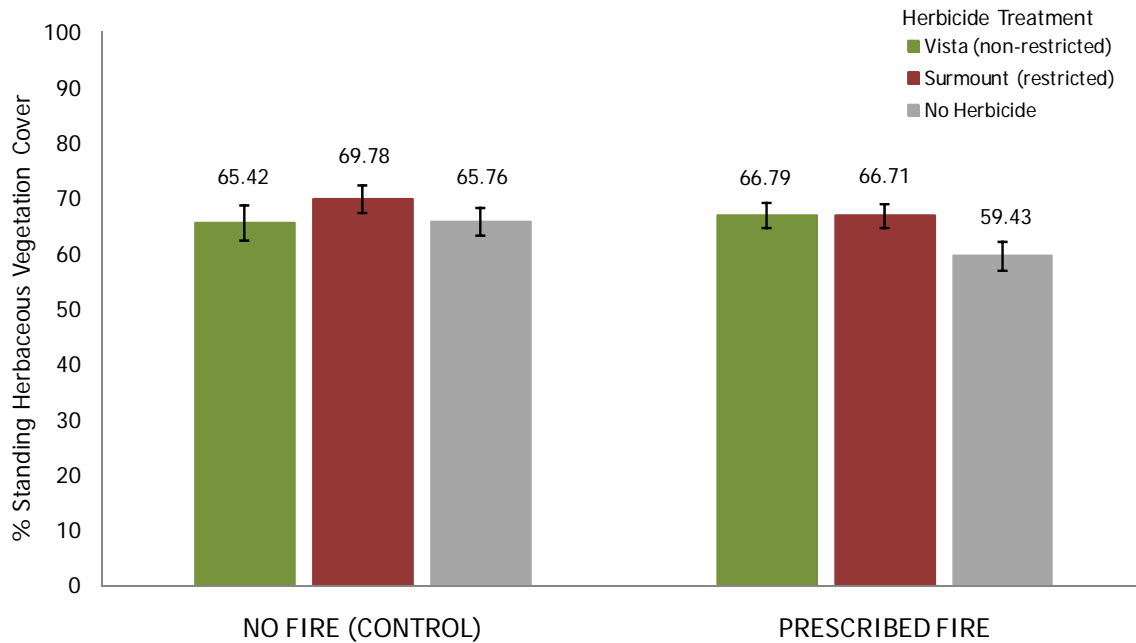


Figure 49. A comparison of the mean (\pm S.E.) percent standing herbaceous vegetation cover on the plots measured at the 2.5 m scale prior to the prescribed fire and herbicide treatments ($P=0.078$). The data for this analysis was collected at the start (July 2011) and conclusion (March 2013) of the field study

The prescribed fire treatments did not result in a statistically significant change in the percent standing herbaceous vegetation cover between the plots with different herbicide treatments ($P=0.147$) (Figure 50). For the plots that were sprayed with fluroxypyr (non-restricted), there was a 43.28 (\pm 4.22) and 29.84 (\pm 11.59) percent reduction of herbaceous cover in the plots that were burned early-February (2012) and those left as unburned treatments, respectively, and this difference was not statistically significant ($P=0.194$). Likewise, for the plots that were sprayed with picloram (restricted), there was a 32.69 (\pm 4.05) and a 3.97 (\pm 21.30) percent reduction of herbaceous cover in the plots that were burned in early-February (2012) and those left as

unburned treatments, respectively, and this difference was also not statistically significant ($P=0.221$). The plots that were left as a no herbicide treatment had a $28.11 (\pm 6.77)$ and $30.74 (\pm 3.96)$ percent reduction of herbaceous cover in the plots that were burned early-February (2012) and those left as unburned treatments, respectively, and this difference was also not statistically significant ($P=0.745$). Reference Appendix C for the descriptive data and statistical analyses (Tables 38, 39, 40).

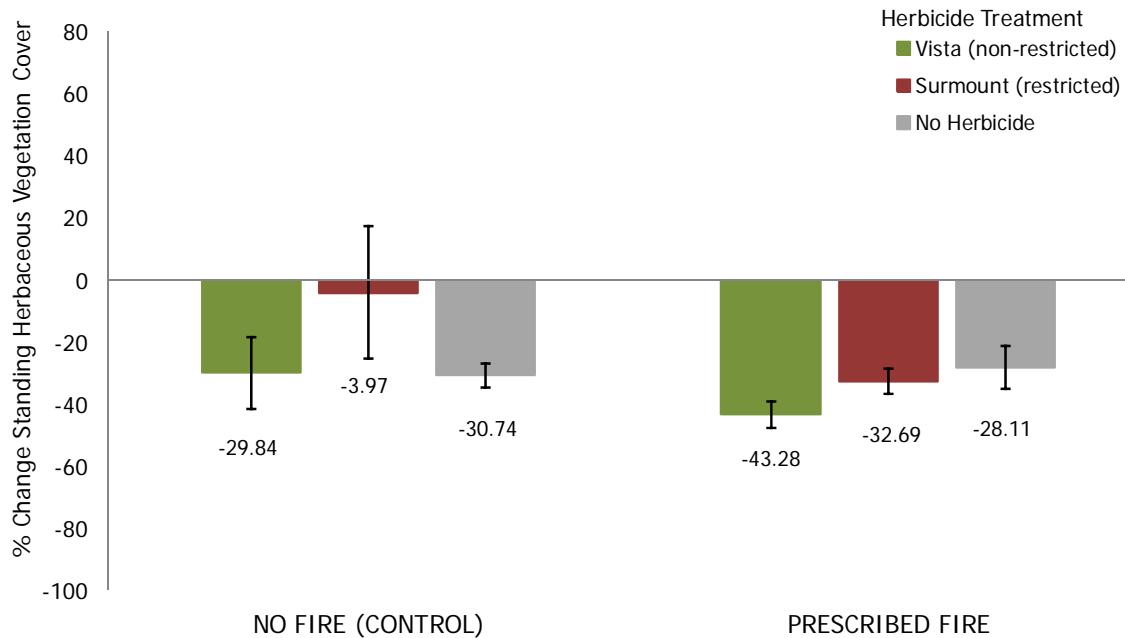


Figure 50. An assessment of the percent change in standing herbaceous vegetation cover in response to the prescribed fire and herbicide treatments ($P= 0.147$). All results are presented as a mean value (\pm S.E.). A comparison of data collected at the start (July 2011) and conclusion (March 2013) of the field study

For the plots that were burned in early-February (2012), the percent change of herbaceous cover in the plots that were sprayed with fluroxypyr (non-restricted) compared those that were sprayed with picloram (restricted) was not statistically

significant ($P=0.082$). Similarly, the percent change of herbaceous standing cover in the plots that were left as a no herbicide treatment and sprayed with fluroxypyr (non-restricted) or picloram (restricted) did not differ significantly, ($P=0.054$) and ($P=0.588$), respectively. In comparison, the plots that were left as unburned treatments, the percent change of herbaceous standing cover in the plots that were sprayed with fluroxypyr (non-restricted) compared those that were sprayed with picloram (restricted) was not statistically significant ($P=0.354$). Likewise, the percent change of herbaceous standing cover in the plots that were left as a no herbicide treatment and sprayed with fluroxypyr (non-restricted) or picloram (restricted) did not differ significantly, ($P=0.933$) and ($P=0.226$), respectively. Reference Appendix C for the statistical analyses (Tables 41, 42).

Bare Ground Cover

In July 2011, prior to the application of the prescribed fire and herbicide treatments there was a mean percent bare ground cover of 4.87 (± 0.26) ($P=0.052$) in the plots measured at the 2.5 m scale (Figure 51). Reference Appendix C for the descriptive data and statistical analysis (Table 43, 44).

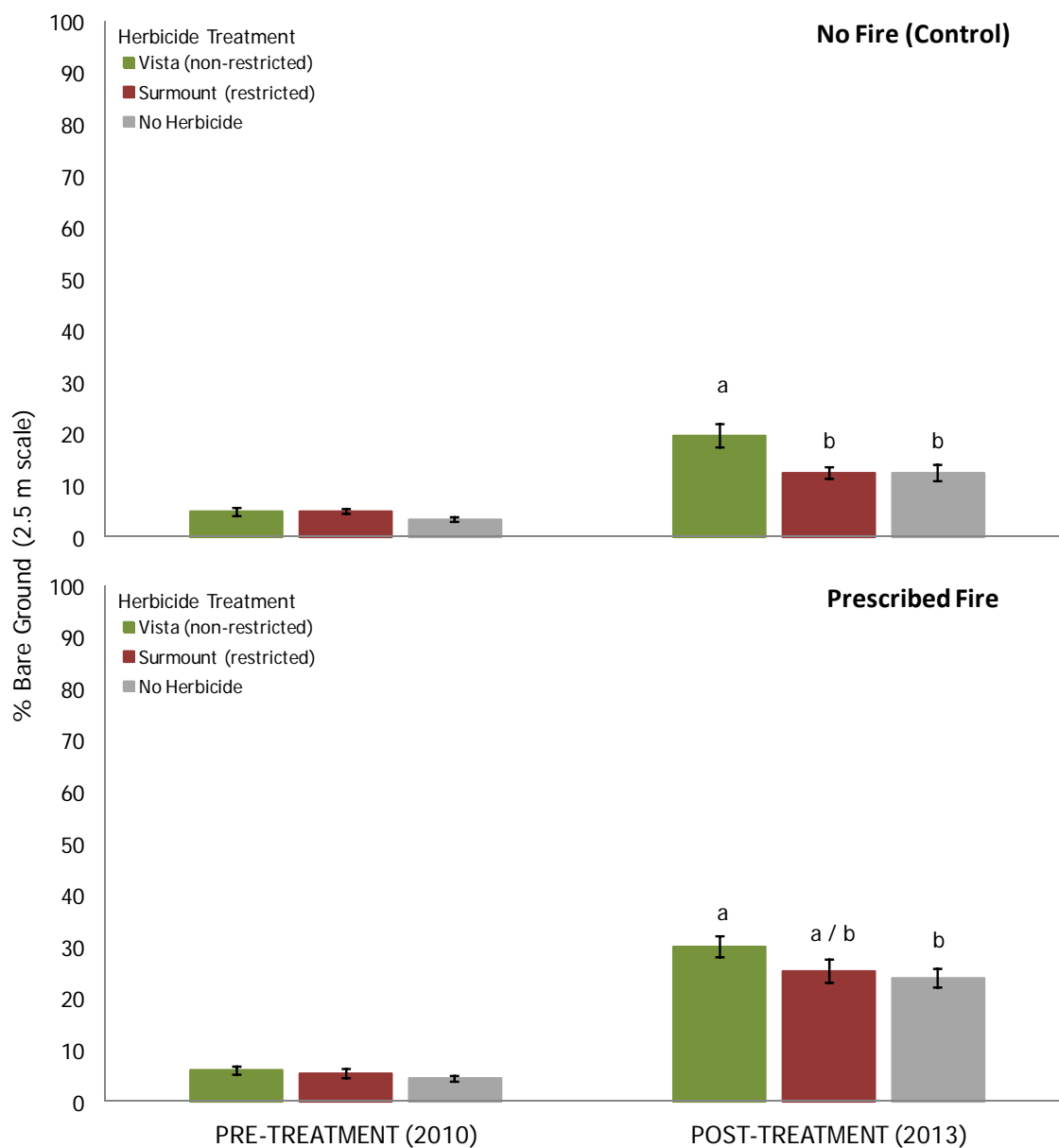


Figure 51. A comparison of the percent bare ground between the plots prior to the prescribed fire and herbicide treatments (2011) and post-treatment (2013). All results are presented as a mean (\pm S.E.) and any significant difference ($P < 0.05$) in response to the fire and herbicide treatments is indicated by different letters.

In March 2013, the plots that were left as unburned treatments and applied fluroxypyr (non-restricted) had a mean of 19.66 (\pm 2.28) percent bare ground cover; whereas, those applied picloram (restricted) or left as no herbicide treatments had a mean bare ground cover of 12.36 (\pm 1.19) and 12.44 (\pm 1.57) percent, respectively. There was a statistically significant difference in the percent change of ground cover in the plots that were applied fluroxypyr (non-restricted) compared those that were applied picloram (restricted) or those left as a no herbicide treatment, ($P=0.002$) and ($P=0.008$), respectively. However, the percent change of ground cover between the plots that were sprayed with picloram (restricted) and those left as a no herbicide treatment did not differ statistically ($P=0.967$). Reference Appendix C for the descriptive data and statistical analysis (Tables 45, 46).

In contrast, the plots that were burned in early-February (2012) and applied fluroxypyr (non-restricted) had a mean of 29.95 (\pm 2.05) percent bare ground cover, in comparison to the 25.20 (\pm 2.24) and 23.91 (\pm 1.89) percent mean bare ground cover for the plots applied picloram (restricted) or left as a no herbicide treatment, respectively. There was not a statistically significant difference in the percent change of ground cover in the plots that were applied fluroxypyr (non-restricted) compared those that were applied picloram (restricted) ($P=0.125$). Similarly, there was not a statistically significant difference in the percent change of ground cover in the plots that were applied picloram (restricted) compared those left as a no herbicide treatment ($P=0.658$). On the other hand, the percent change of ground cover between the plots that were applied fluroxypyr (non-restricted) compared to those left as a no herbicide treatment

was statistically significant ($P=0.033$). Reference Appendix C for the descriptive data and statistical analyses (Tables 47, 48).



Figure 52. A ground view of a burned plot at the Texas A&M AgriLife Range Station near Barnhart, Texas (February 07, 2012).

The prescribed fire treatments resulted in a statistically significant increase in the percent bare ground cover between the plots applied the different herbicide treatments ($P=0.0001$) (Figure 53). The increase in percent bare ground cover on the plots that were sprayed with fluroxypyr (non-restricted) or picloram (restricted) was statistically significant when we compared the plots that were burned and those left as unburned treatments, ($P=0.002$) and ($P=0.0001$), respectively. In the absence of an herbicide application treatment, there was also a statistically significant differential response in the percent bare ground cover between the plots that were burned and those left as unburned treatments ($P=0.0001$). Reference Appendix C for the descriptive data and statistical analyses (Tables 49, 50, 51).

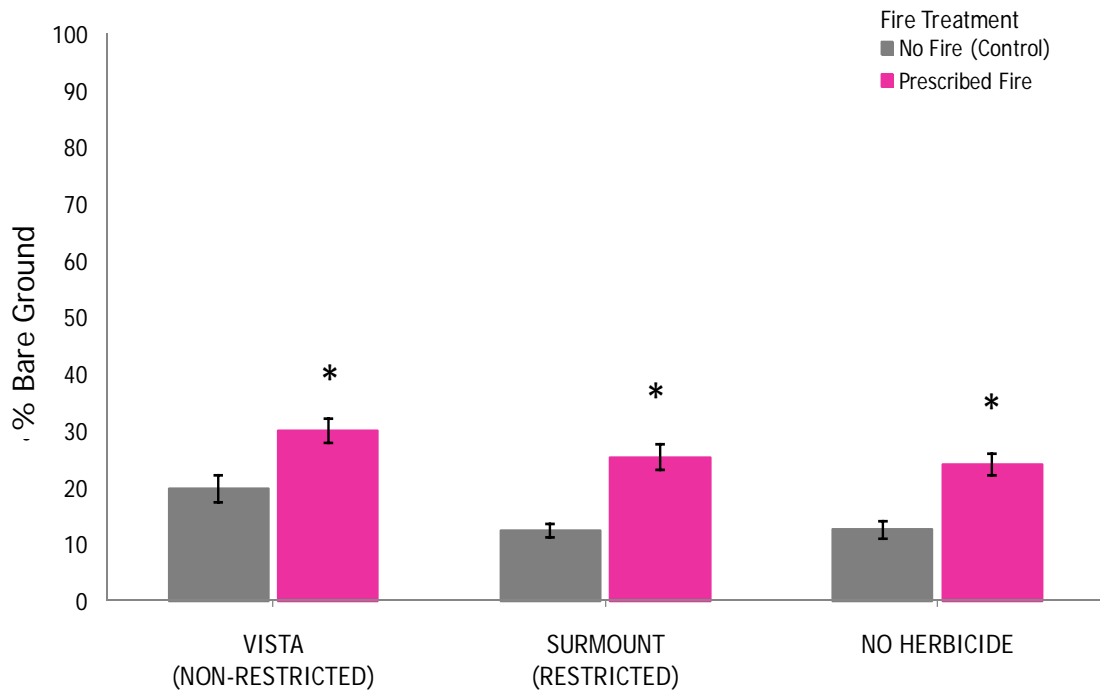


Figure 53. A post-treatment (2013) comparison of the percent bare ground measured at the 2.5 m scale by herbicide treatments between the plots with and without a prescribed fire. All results are presented as a mean (\pm S.E.) and an asterisk indicates any significant difference ($P < 0.05$) between treatments. Data was collected at the conclusion (March 2013) of the field study

DISCUSSION

Despite the ecologic and economic impacts prickly pear cactus encroachment has on the integrity and productivity of rangelands, ranchers and land managers have not been able to make significant progress at suppressing this problematic succulent using traditional brush control strategies. The use of prescribed fire followed by the application of Vista® a federally non-restricted herbicide (i.e. fluroxypyr) has been proposed as a viable approach to accelerate the restoration of these prickly pear dominated rangelands. This integrated management approach has the potential for complementary or synergistic interactions that augment phytotoxicity of the herbicides and result in greater damage to the cactus plants (Hanselka, et al. 1996). It would be beneficial to determine if the combined effect of these strategies would produce an outcome that is greater than the sum of their separate effects. In this study, quantifying the efficacy of a federally non-restricted herbicide was also of particular interest because of its reduced potential for adverse effects on the environment.

Prickly Pear in Response to Herbicides and Fire

In contrast to what we expected, the findings indicate that the combination of prescribed fire and herbicide treatments was an ineffective strategy that was not additive because it did not result in statistically greater reduction in prickly pear cactus coverage. The herbicide treatments of fluroxypyr (non-restricted) and picloram (restricted) were equally ineffective at reducing prickly pear cactus, whereas prescribed fire was the driving force that achieved greater prickly pear cactus suppression. For the plots that were burned in early-February (2012), there was no statistically significant difference in

cactus cover between any of the herbicide treatments. These findings do not yield support for our hypothesis that the use of prescribed fire and herbicides would produce a synergistic interaction between the brush control strategies. The reduction in prickly pear cactus coverage with these treatment combinations was not greater than the sum of their separate effects.

The outcomes reported in this study are contrary to that of Ueckert and Whisenant (1980) and Ueckert et al. (1988) who have found that the integration of prescribed burning with a restricted herbicide (i.e. picloram) significantly increases the control of prickly pear cactus on Texas rangelands. Ueckert and Whisenant (1980) reported that burning alone reduced the prickly pear canopies by 42 percent after one growing season, while the combination of fire and herbicides reduced the prickly pear canopies by 76 percent over the same period. A possible explanation for our results could be attributed to the timing of the herbicide applications after the prescribed fire treatments; in their study, the burns were conducted late-March and the herbicides were applied one month later in late-April. In contrast, the period of time between our sequential applications of prescribed fire and herbicide treatments was considerably greater; the fires were ignited early-February (2012) and the foliar herbicides sprays were applied nine months later in early-November (2012). The decision to apply the chemical treatments at a later date was made based on guidance that it is easier to control perennials and shrubs with autumn/fall applied herbicides (DiTomaso 2000; McGinty et al. 2005). Even though the prescribed fire scorched the cactus stem tissue, these succulent species exhibit a variety of fire-adaptive traits and mechanism by which they

are able to recover from a fire and limit their susceptibility to herbicide exposure and other disturbances (Keeley, et al. 2011; Masters and Sheley 2001; Thomas 1991).

Considering this information, it is likely that the time allotted between our treatments negated the phytotoxicity of the herbicides.

Prickly Pear's Response to Herbicides in the Absence of Fire

In this study, in the absence of fire, the foliage applied herbicides fluroxypyr (non-restricted) and picloram (restricted) were equally ineffective at reducing prickly pear cactus encroachment. Our assessment of the sites four months after the early-November herbicide treatments indicates that all of the treatments experienced an increase in prickly pear coverage. Contrary to expectations, the cactus plants that were left as unburned and applied fluroxypyr (non-restricted) or picloram (restricted) did not experience a significantly greater reduction than those that were left as no herbicide (control) treatments. However, these results are not in line with those of numerous rangeland studies that have found that herbicides are a highly effective at controlling prickly pear cactus, albeit cost prohibitive for most landowners (Kreuter et al. 2005; Ueckert, et al. 1988).

A possible explanation for our findings may be related to the extended regional drought that affected the region following application of the fluroxypyr (non-restricted) and picloram (restricted) herbicide treatments. According to the National Drought Mitigation Center, the herbicide treatments were applied during a period that was classified as 'moderate' drought with a Palmers Drought Severity Index (PDSI) of -2.0 to -2.9; the months following this chemical treatment were also impacted by

moderate drought (National Centers for Environmental Information, NOAA 2015).

Reference Figure 54 for the U.S. Drought Monitor Maps from November 2012,

December 2012, February 2013, and March 2013.

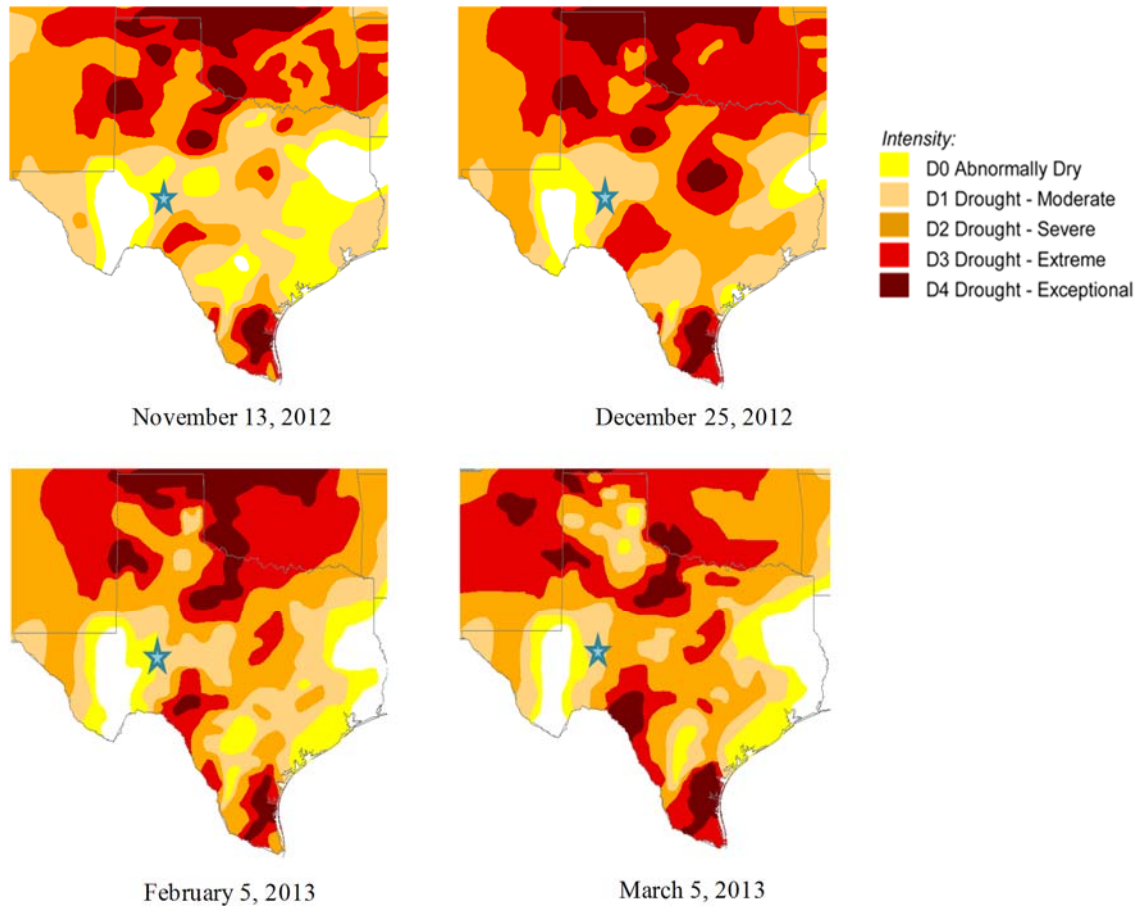


Figure 54. A regional-scale drought representation in the rangelands of Texas obtained from the U.S. Drought Monitor following the herbicides treatment applications administered early fall (November 13, 2012). The star on the maps represents the location of the Texas AgriLife Range Station near Barnhart, Texas (National Centers for Environmental Information, NOAA 2015).

During periods of extended drought, the photosynthates that move the herbicides throughout these succulent plants are not adequately replenished (Masters and Sheley 2001; Chow et al. 1996*b*; Ueckert, et al. 1988). Consequently, this drought could have limited the absorption and translocation of the herbicides into the prickly pear roots, crowns, and stub-terminal stems. Furthermore, according to Ueckert et al. 1988, when herbicides are used as a single management strategy, they seldom provide prompt control of prickly pear. Furthermore, when used according to their chemical label, the cactus stems remain standing as they slowly decompose in these semi-arid environments; it may take up to two to three years for the impacts of the herbicide to be fully manifested (Dow AgroSciences 2017*a*).

Recovery of Herbaceous Layer

The application of prescribed fire and herbicide treatments did not result in a significant difference in standing herbaceous cover between the different treatment combinations. The results show that there was a decrease in standing herbaceous cover for all of the plots that were burned and subsequently applied an herbicide treatment. This outcome differs from that of Wright (1972) and Ansley et al. (2008) who conducted research in this region and found that the live yield of tobosagrass increases after a fire.

However, it is likely that the regional-drought conditions that followed the prescribed fire treatments (February 2012) could have contributed to the limited growth and recovery of the herbaceous layer in these rangelands (Hamilton and Scifres 1982; Westoby, et al. 1989; Young 1956). According to the National Drought Mitigation Center classified the 2012 growing season as a ‘severe’ and ‘moderate’ drought with a Palmers Drought Severity Index (PDSI) of -3.0 to -3.9 and -2.0 to -2.9, respectively (National Centers for Environmental Information, NOAA 2015). Reference Figure 55 for the U.S. Drought Monitor Maps from April 2012, July 2012, and September 2012.

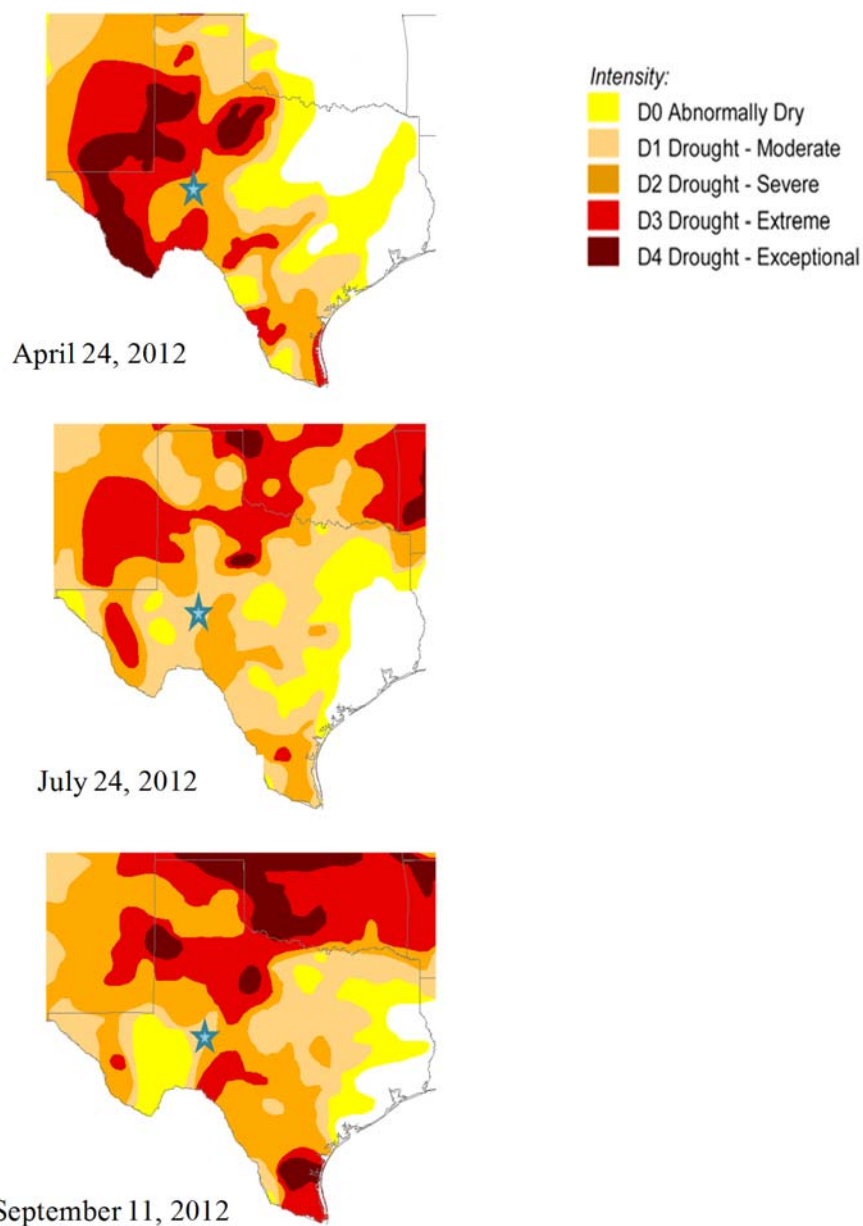


Figure 55. A regional-scale drought representation in the rangelands of Texas obtained from the U.S. Drought Monitor for the 2012 growing season (April, July, and September) following the application of the prescribed fire treatments (February 7, 2012). The star on the maps represents the location of the Texas AgriLife Range Station near Barnhart, Texas (National Centers for Environmental Information, NOAA 2015).

In the absence of prescribed fire, our results show that the plots that were applied an herbicide treatment also experienced a similar reduction in standing herbaceous cover; the differences between fluroxypyr (non-restricted), picloram (restricted) and those that were left as no herbicide (control) were not statistically significant. These findings are contrary to what we expected. Neary et al. (2000) and Vallentine (1983) have suggested that the use of selective herbicides can be a preferable management tool if the aim is to remove undesirable plants in a highly targeted manner, while simultaneously benefiting (i.e. protecting) desirable herbaceous species and preventing soil erosion. However, it is likely that the aforementioned drought also contributed to this reduction in standing herbaceous cover in the unburned plots. These results are consistent with those of multiple studies conducted in semi-arid and arid regions who reported that herbaceous species were negatively impacted by drought (Greene et al. 1990; Rietkerk and van de Koppel 1997). If the physiological needs of the herbaceous vegetation are not met during periods of limited rainfall, they will experience drought-induced mortality (Chamrad and Box 1965; Fay, et al. 2003; Thurow and Taylor 1999).

Broader Implications for Rangeland Ecology and Management

Based on the findings from this research, the use of prescribed fire should be considered as a viable strategy to suppress problematic prickly pear encroachment. However, given that the herbicide treatments of fluroxypyr (non-restricted) and picloram (restricted) were equally ineffective at suppressing this succulent within the time frame of this field study, we do not recommend the combination of prescribed fire and herbicide treatments as a practical restoration strategy. This information can be used by

extension agents at the regional level to inform land managers and ranchers interested in developing range management plans using science-based decision making (Peters, et al. 2012). However, there is still ample ground for continued research that can provide information to apprehensive ranchers and landowners who are interested in applying herbicides but are concerned about the adverse effects such synthetic chemicals have on the environment. In the future, more research is needed to quantify the long-term ecosystem effects federally non-restricted herbicides have on the rangeland plant community composition and structure. Moreover, any mention of trademarks or product names in this chapter does not imply endorsement by the author or the Texas A&M University System, it also does not constitute an approval of those products to the exclusion of others that also may be suitable.

CHAPTER VII

SUMMARY AND CONCLUSION

In this dissertation, three completely independent, yet complementary studies were conducted to assess whether management strategies that differ from traditional approaches are better suited for improving the ecological integrity of rangeland ecosystems in the Edwards Plateau of Texas. These studies had two overarching goals. One goal was to improve our understanding of the vegetation dynamics in these succulent infested, semi-arid rangelands, and the other was to examine the use of alternative brush control strategies to suppress prickly pear encroachment.

Prickly pear infestations degrade rangeland ecosystems by displacing herbaceous forage (Taylor, et al. 2012). There is an increase in soil erosion and desertification as a result of this succulent infestation (McCalla, et al. 1984; Le Houérou 1996; Lundgren, et al. 1981). Consequently, these denuded rangelands are more likely to transition into an ecological state of degradation (i.e. retrogression) (Ansley and Castellano 2007a; Dodd 1940; Grubb 1977; Scholes and Archer 1997; Stoddart and Smith 1943; Schlesinger, et al. 1999; Scifres 1980; Teague, et al. 2008; Ueckert, et al. 1988; Walker 1993). From a livestock grazing standpoint, a reduction in high quality herbaceous forage is a significant impediment for ranchers committed to maintaining a profitable and sustainable livestock enterprise (Merrill, et al. 1980; Ueckert 1980). Additionally, from a wildlife habitat management standpoint, the loss of herbaceous cover decreases the quality and function of this ecosystem (Kiel 1980).

Unfortunately, there is a lack of empirical evidence on how ranchers and land managers can control the expansion of prickly pear. Furthermore, it is unknown how this succulent responds to a combination of brush control strategies under distinct environmental conditions. This deficit of scholarship on cactus ecology in these rangelands is what primarily motivates the research presented in the previous chapters (IV, V, and VI).

The first study evaluated the response of prickly pear to a high-intensity ‘reclamation’ prescribed fire in combination with the subsequent application of a low-intensity prescribed ‘maintenance’ fire. The results presented in Chapter IV demonstrate that a combination of these two fire treatments was a highly effective succulent control strategy. There was a statistically significant greater reduction in prickly pear within the plots that received a high-intensity ‘reclamation’ prescribed fire in combination with a low-intensity prescribed ‘maintenance’ fire.

The second study examined the susceptibility of an experimentally drought-stricken succulent to low-intensity ‘maintenance’ fire treatments administered in the early-spring and early-fall season. The results presented in Chapter V confirm that the use of the drought simulation ‘rainout shelter’ technique allowed us to manipulate the hydration status of the plant. There was statistically significant lower tissue moisture content in the succulents found under the rainout shelters when compared to those succulents found in the control treatment (i.e. ambient field conditions). Despite the slight trend indicating greater prickly pear cover reduction from prescribed fire for plants under the ‘rainout shelter’ when compared to the control treatment, this difference was

not statistically significant. The simulated drought conditions did not alter this succulent's thermo-physiological tolerance to fire as survival rates were indistinguishable between the treatments.

The results presented in Chapter VI show that the combined effect of a 'maintenance' prescribed fire and herbicide treatments was not greater than the sum of their separate effects. The burned cactus did not experience an increased susceptibility to the herbicide treatments (i.e. tissue damage, mortality). Therefore, unlike the combination of a 'reclamation' and 'maintenance' prescribed fire, the integration of these treatments was not additive at mitigating prickly pear cover encroachment. Furthermore, an assessment of the efficacy of the non-restricted and restricted herbicides indicated that the difference between these treatments was not statistically significant. In this field study, 'maintenance' fire was the driving factor that influenced and achieved a greater suppression of prickly pear cover.

LAND MANAGEMENT RECOMMENDATIONS

Based on the findings from Chapter VI, the combination of prescribed fire and herbicide treatments did not improve the effectiveness of prickly pear suppression. We do not recommend this combination as a means to control prickly pear. However, the study in Chapter IV found that the combination of ‘reclamation’ and a follow-up ‘maintenance’ fire as a brush control strategy was effective at controlling prickly pear. If this trend holds in the future, those trying to control prickly pear should consider the use of a high-intensity fire and a follow-up prescribed ‘maintenance’ fire to achieve greater control. Furthermore, based on the findings from Chapter V, we can also recommend the use of prescribed burning on sites with an adequate fuel load as soon as prickly pear becomes a problem, because this strategy will still cause tissue damage (i.e. scorch, mortality) regardless of this succulent’s drought-stressed status.

SIGNIFICANCE AND FUTURE RESEARCH DIRECTIONS

The future use and sustainability of rangelands in the Edwards Plateau region of Texas depends on the ability of resource managers and ranchers to successfully intervene before there is wide-spread prickly pear encroachment. Despite the above mentioned contributions this dissertation has made through examining the use of fire as a catalyst for rangeland restoration, certain questions remain unanswered, and they must be addressed because these unknown factors can limit the effective implementation of restoration and conservation efforts (Ehrenfeld 2000; Monaco, et al. 2012; Ruiz-Jaen and Mitchell Aide 2005). The following research areas warrant further consideration by researchers: climate change, the long-term efficacy of prickly pear control treatments, and the financial limitations associated with the application of these ecological strategies to suppress prickly pear encroachment, and the potential arrival of *Cactoblastis cactorum* moth from Caribbean moth populations (Marsico, et al. 2011).

To determine the extent that climate change is contributing to an increase in prickly pear growth and encroachment, there is a need to quantify and correlate the relationship between brush encroachment and a rise in atmospheric CO₂ (Leakey and Lau 2012; Tyree and Alexander 1993). It is necessary to examine how prolonged and extreme weather events (i.e. drought) and the carbon fertilization effect are impacting prickly pear particularly given its unique CAM photosynthesis strategy relative to plants utilizing C₃ and C₄ photosynthesis pathways. Additionally, the field studies presented in this research examine the use of prescribed fire and herbicides in the short-term, and they only consider the immediate impacts of these treatments. However, to ensure we

conduct well-informed land management, it is critically important to understand how the ecological successional trajectory is impacted by previously defined environmental stressors (Chapin III, et al. 2010; Clements 1916; Knutson and Haigh 2013). Therefore, future studies should comprehensively evaluate the long-term transition of these terrestrial ecosystems from one ecological state to another (i.e. thresholds). Because this dissertation only examined the ecological response and did not consider the financial limitations associated with the application of these control strategies, there is a need for professionals in applied social science fields (i.e. agricultural economics, environmental economics) to conduct an economic assessment of the viability of prickly pear control and restoration strategies (Holechek and Hess 1994). Lastly, future studies should also be conducted to evaluate the potential ecological risks and impacts of the unintentional introduction and spread of *Cactoblastis cactorum* moth into the southwestern United States and northern Mexico. A preemptive management plan should be developed to control the expansion of this invasive insect and to protect native *Opuntia* cactus populations and a wide-spread loss of the ecosystems it supports. The ideal prickly pear density for each site is distinct because each ecoregion has different range and wildlife management objectives (Stiling 2002).

The information gathered from this and future studies can be integrated to enhance modeling frameworks (i.e. alternative steady state or state-and-transition models) and to develop modern and sustainable land management practices that can be used to limit prickly pear encroachment (Bestelmeyer, et al. 2003; Briske, et al. 2005; Briske, et al. 2008; Didham and Norton 2007; Stringham, et al. 2003). The results from

these studies are valuable to ranchers and land managers alike, as they can also help guide the development of future natural resource public policy and regulations that support the successful restoration and conservation of these rangelands. Timely action by researchers in the fields of rangeland ecology and restoration ecology is needed to prevent the economic strain and potential economic downfall of rural communities that depend on the agricultural productivity of these lands (Weltz, et al. 2003).

LITERATURE CITED

- Adler, P., Raff, D. & Lauenroth, W. (2001) The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia*, **128**, 465-479.
- Aldridge, V. R., Jacoby, P. W., Steger, R. E. & Hartmann, F. S. (1983) Short-term responses of pricklypear (*Opuntia lindheimeri*) to foliar-and soil-applied picloram in the southern rolling plains. *Texas Agricultural Experiment Station*. Progress Report (4127), College Station, Texas.
- Allen, E. B. (1995) Restoration ecology: limits and possibilities in arid and semiarid lands. Pages 7-15. In: Roundy, B. A., McArthur, E. D., Haley, J. S. & Mann, D. K. (Editors). *Proceedings of the wild land shrub and arid land restoration symposium*. October 19-21, 1993. Las Vegas, Nevada.
- Amos, B. & Gehlbach, F. R. (1988) *Edwards Plateau vegetation: plant ecological studies in central Texas*. Baylor University Press, Waco, Texas.
- Anderson, A. & McCuiston, K. C. (2008) Evaluating strategies for ranching in the 21st century: successfully managing rangeland for wildlife and livestock. *Rangelands*, **30**, 8-14.
- Anderson, R. C. & Brown, L. E. (1986) Stability and instability in plant communities following fire. *American Journal of Botany*, **73**, 364-368.

- Ansley, R. J. & Taylor, C. A. (2004) The future of fire as a tool for managing brush. Pages 200-210. In: Hamilton, W. T., McGinty, A., Ueckert, D. N., Hanselka, C. W. & Lee, M. R. (Editors). *Brush Management: Past, Present and Future*. Texas A&M University Press, College Station, Texas.
- Ansley, R. J., Castellano, M. J. & Pinchak, W. E. (2006b) Sideoats grama growth responses to seasonal fires and clipping. *Rangeland Ecology & Management*, **59**, 258-266.
- Ansley, R. J. & Castellano, M. J. (2007a) Effects of summer fires on woody, succulent, and graminoid vegetation in southern mixed-prairie ecosystems: a review. In: *Fire in Grassland and Shrubland Ecosystems. Tall Timbers fire ecology conference proceedings*, **23**, 63-70.
- Ansley, R. J. & Castellano, M. J. (2007b) Prickly pear cactus responses to summer and winter fires. *Rangeland Ecology & Management*, **60**, 244-252.
- Ansley, R. J. & Jacoby, P. W. (1998) Manipulation of fire intensity to achieve mesquite management goals in north Texas. In: *Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers fire ecology conference proceedings*, **20**, 195-204.
- Ansley, R. J., Pinchak, W. E. & Jones, D. L. (2008) Mesquite, tobosagrass, and common broomweed responses to fire season and intensity. *Rangeland Ecology & Management*, **61**, 588-597.
- Archer, S. (1989) Have southern Texas savannas been converted to woodlands in recent history? *The American Naturalist*, **134**, 545-561.

- Archer, S., Schimel, D. S. & Holland, E. A. (1995) Mechanisms of shrubland expansion: land use, climate or CO₂? *Climatic Change*, **29**, 91-99.
- Archer, S. R. & Predick, K. I. (2008) Climate change and ecosystems of the Southwestern United States. *Rangelands*, **30**, 23-28.
- Arnold, L. A. & Drawe, D. L. (1979) Seasonal food habits of white-tailed deer in the South Texas Plains. *Journal of Range Management*, **32**, 175-178.
- Ash, A., Thornton, P., Stokes, C. & Togtohyn, C. (2012) Is proactive adaptation to climate change necessary in grazed rangelands? *Rangeland Ecology & Management*, **65**, 563-568.
- Augustine, D. J. & Milchunas, D. G. (2009) Vegetation responses to prescribed burning of grazed shortgrass steppe. *Rangeland Ecology & Management*, **62**, 89-97.
- Bailey, A. W. (1988) Understanding fire ecology for range management. Pages 527-557. In: Tueller, P. T., (Editor). *Vegetation science applications for rangeland analysis and management*. Kluwer Academic Publisher, Boston, Massachusetts.
- Barcikowski, W. & Nobel, P. S. (1984) Water relations of cacti during desiccation: distribution of water in tissues. *Botanical Gazette*, **145**, 110-115.
- Bates, J. D., Svejcar, T., Miller, R. F. & Angell, R. A. (2006) The effects of precipitation timing on sagebrush steppe vegetation. *Journal of Arid Environments*, **64**, 670-697.
- Bauder, T., Waskom, R. & Pearson, R. (2010) Best management practices for agricultural pesticide use to protect water quality. *Cooperative Extension Service*. Bulletin (XCM-177), Fort Collins, Colorado.

- Beever, E. A., Tausch, R. J. & Brussard, P. F. (2003) Characterizing grazing disturbance in semiarid ecosystems across broad scales, using diverse indices. *Ecological Applications*, **13**, 119-136.
- Bement, R. E. (1968) Plains pricklypear: relation to grazing intensity and blue grama yield on central Great Plains. *Journal of Range Management*, 83-86.
- Benavides-Solorio, J. & MacDonald, L. H. (2001) Post-fire runoff and erosion from simulated rainfall on small plots, Colorado Front Range. *Hydrological Processes*, **15**, 2931-2952.
- Bentley, H. L. (1898) *Cattle ranges of the Southwest: a history of the exhaustion of the pasturage and suggestions for its restoration*. U.S. Dept. Agriculture, Volume 72. Washington, District of Columbia.
- Berger, M. E. (1973) Recreation potential of Texas rangelands. *Journal of Range Management*, **26**, 92-93.
- Bestelmeyer, B., T., Brown, J. R., Havstad, K. M., Alexander, R., Chavez, G. & Herrick, J. E. (2003) Development and use of state-and-transition models for rangelands. *Journal of Range Management*, **56**, 114-126.
- Blomquist, K. W. (1990) *Selected life history and synecological characteristics of Ashe juniper on the Edwards Plateau of Texas* (Doctoral dissertation, Texas A&M University).
- Bond, W. J. & Keeley, J. E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, **20**, 387-394.

- Bova, A. S. & Dickinson, M. B. (2005) Linking surface-fire behavior, stem heating, and tissue necrosis. *Canadian Journal of Forest Research*, **35**, 814-822.
- Bovey, R. W. (1987) Weed control problems, approaches, and opportunities in rangeland. *Reviews of Weed Science*, **3**, 57-91.
- Bovey, R. W. (1995) Weed management systems for rangelands. Pages 519-552. In: Smith, A. E. (Editor). *Handbook of weed management systems*. Marcel Dekker, Inc. New York, New York.
- Bowman, D. M. J. S., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., D'Antonio, C. M., DeFries, R. S., Doyle, J. C., Harrison, S. P., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Marston, J. B., Moritz, M. A., Prentice, I. C., Roos, C. I., Scott, A. C., Swetnam, T. W., van der Werf, G. R. & Pyne, S. J. (2009) Fire in the earth system. *Science*, **324**, 481-484.
- Bradshaw, A. D. (1996) Underlying principles of restoration. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 3-9.
- Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., Romme, W. H., Kastens, J. H., Floyd, M. L., Belnap, J., Anderson, J. J., Myers, O. B. & Meyer, C. W. (2005) Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 15144-15148.

- Breshears, D. D., Myers, O. B., Meyer, C. W., Barnes, F. J., Zou, C. B., Allen, C. D., McDowell, N. G. & Pockman, W. T. (2009) Tree die-off in response to global change-type drought: Mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment*, **7**, 185-189.
- Briske, D. D., Bestelmeyer, B. T., Stringham, T. K. & Shaver, P. L. (2008) Recommendations for development of resilience-based state-and-transition models. *Rangeland Ecology & Management*, **61**, 359-367.
- Briske, D. D., Fuhlendorf, S. D. & Smeins, F. E. (2005) State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology & Management*, **58**, 1-10.
- Britton, C. M. & Wright, H. A. (1979) A portable burner for evaluating effects of fire on plants. *Journal of Range Management*, **32**, 475-476.
- Brown, D. E. & Minnich, R. A. (1986) Fire and changes in creosote bush scrub of the western Sonoran Desert, California. *American Midland Naturalist*, **116**, 411-422.
- Brown, J. H., Valone, T. J. & Curtin, C. G. (1997) Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Sciences*, **94**, 9729-9733.
- Brown, J. R., Bestelmeyer, B. T. & Havstad, K. M. (2008) Rangeland ecology and management in a changing world. Volume 1, Pages 41-43. In: *Multifunction Grassland in a Changing World*. Guangdong People's Publishing House. Guangzhou, China.

- Brown, J. R. & Thorpe, J. (2008) Rangelands and climate change: a synthesis and challenges. *Rangelands*, **30**, 52-53.
- Bryant, F. C., Kothmann, M. M. & Merrill, L. B. (1979) Diets of sheep, Angora goats, Spanish goats and white-tailed deer under excellent range conditions. *Journal of Range Management*, **32**, 412-417.
- Bryant, F. C., Taylor, C. A. & Merrill, L. B. (1981) White-tailed deer diets from pastures in excellent and poor range condition. *Journal of Range Management*, **34**, 193-200.
- Bryant, F. C. (1991) Managed habitats for deer in juniper woodlands of west Texas. Pages 59-75. In: Rodiek, J. E. & Bolen, E. G. (Editors). *Wildlife and habitats in managed landscapes*. Island Press, Washington, District of Columbia.
- Bugbee, R. E. & Reigel, A. (1945) The Cactus Moth, *Melitara dentata* (Grote), and its effect on *Opuntia macrorrhiza* in western Kansas. *The American Midland Naturalist*, **33**, 117-127.
- Bunting, S. C., Wright, H. A. & 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.
- Burger, J. C. & Louda, S. M. (1994) Indirect versus direct effects of grasses on growth of a cactus (*Opuntia fragilis*): insect herbivory versus competition. *Oecologia*, **99**, 79-87.
- Burger, J. C. & Louda, S. M. (1995) Interaction of diffuse competition and insect herbivory in limiting brittle prickly pear cactus, *Opuntia fragilis* (Cactaceae). *American Journal of Botany*, **82**, 1558-1566.

- Bussan, A. J. & Dyer, W. E. (1999) Herbicides and rangeland. Pages 116-132. In: Sheley, R. L. & Petroff, J. K. (Editors). *Biology and management of noxious rangeland weeds*. Oregon State University Press, Corvallis, Oregon.
- Buxbaum, F. (1950) *Morphology of cacti*. Abbey Garden Press, Pasadena, California.
- Byram, G. M. (1959) Combustion of forest fuels. In: Davis, K. P., (Editor). *Forest fire control and use*. McGraw-Hill, New York, New York.
- Cable, D. R. (1967) Fire effects on semidesert grasses and shrubs. *Journal of Range Management*, **20**, 170-176.
- Cable, D. R. (1972) Fire effects in southwestern semidesert grass-shrub communities. *Tall Timbers fire ecology conference proceedings*, **12**, 109-127.
- Call, C. A. & Roundy, B. A. (1991) Perspectives and Processes in Revegetation of Arid and Semiarid Rangelands. *Journal of Range Management*, **44**, 543-549.
- Campbell, E. & Taylor, C. A. (2006) Targeted grazing to manage weedy brush and trees. Pages 77-88. In: Launchbaugh, K. *Targeted Grazing: a natural approach to vegetation management and landscape enhancement*. American Sheep Industry Association. Cottrell Printing, Centennial, Colorado.
- Chambers, W. T. (1932) Edwards Plateau, a combination ranching region. *Economic Geography*, **8**, 67-80.
- Chamrad, A. D. & Box, T. W. (1965) Drought-associated mortality of range grasses in South Texas. *Ecology*, **46**, 780-785.
- Chamrad, A. D. & Box, T. W. (1968) Food habits of white-tailed deer in South Texas. *Journal of Range Management*, **21**, 158-164.

- Chance, L. (2016) Pushing the limits landscaping with cacti and succulents in cold climates. *Cactus and Succulent Journal*, **88**, 234-341.
- Chapin III, F. S., Carpenter, S. R., Kofinas, G. P., Folke, C., Abel, N., Clark, W. C., Olsson, P., Smith, D. M. S., Walker, B., Young, O. R. & Berkes, F. (2010) Ecosystem stewardship: sustainability strategies for a rapidly changing planet. *Trends in Ecology & Evolution*, **25**, 241-249.
- Chapin III, F. S., Kofinas, G. P. & Folke, C. (Editors) (2009) *Principles of ecosystem stewardship: resilience-based natural resource management in a changing world*. Springer Science & Business Media. New York, New York.
- Chavez-Ramirez, F. & Slack, R. D. (1993) Carnivore fruit-use and seed dispersal of two selected plant species of the Edwards Plateau, Texas. *The Southwestern Naturalist*, **38**, 141-145.
- Chavez-Ramirez, F., Wang, X., Jones, K., Hewitt, D. & 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**, 9-1.
- Chow, P. N., Burnside, O. C. & Lavy, T. L. (1966a) Physiological studies with prickly pear. *Weeds*, **14**, 58-62.
- Chow, P. N., Burnside, O. C., Lavy, T. L. & Knoche, H. W. (1966b) Absorption, translocation, and metabolism of Silvex in prickly pear. *Weeds*, **14**, 38-41.
- Clark, W. K. (1951) Ecological life history of the armadillo in the eastern Edwards Plateau region. *American Midland Naturalist*, **46**, 337-358.

- Clements, F. E. (1916) *Plant succession: an analysis of the development of vegetation*. Carnegie Institution of Washington. Washington, District of Columbia.
- Cobb, A. (1992) *Herbicides and plant physiology*. Chapman & Hall. London, United Kingdom.
- Cook, C. W. (1942) Insects and weather as they influence growth of cactus on the central Great Plains. *Ecology*, **23**, 209-214.
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P. & van den Belt, M. (1997) The value of the world's ecosystem services and natural capital. *Nature*, **387**, 253-260.
- Costello, D. F. (1941) Pricklypear control on short grass range in the central Great Plains. U.S. Dept. Agriculture, Leaflet 210. Washington, District of Columbia.
- Cushman, J. C. & Bohnert, H. J. (1999) Crassulacean acid metabolism: molecular genetics. *Annual Review of Plant Biology*, **50**, 305-332.
- Dai, A. (2011) Drought under global warming: a review. *Wiley Interdisciplinary Reviews: Climate Change*, **2**, 45-65.
- Dameron, W. H. & Smith, H. P. (1939). Prickly pear eradication and control. *Texas Agricultural Experiment Station. Bulletin (575)*, College Station, Texas.
- Daubenmire, R. (1968) Ecology of fire in grasslands. *Advances in ecological research*, **5**, 209-266.

- Davis, F. W. & Moritz, M. (2001) Mechanisms of disturbance. Volume 2, Pages 153-160. In: Levin, S. A., (Editor). *Encyclopedia of biodiversity*. Academic Press, San Diego, California.
- De Ruiter, H., Uffing, A. J., Meinen, E. & Prins, A. (1990) Influence of surfactants and plant species on leaf retention of spray solutions. *Weed Science*, **38**, 567-572.
- DeFelice, M. S. (2004) Prickly pear cactus, *Opuntia* spp.—a spine-tingling tale. *Weed Technology*, **18**, 869-877.
- Didham, R. K. & Norton, D. A. (2007) Alternative logical states. *Oikos*, **116**, 358-360.
- Dimmitt, M. A. (2000) Plant ecology of the Sonoran Desert region. *A Natural History of the Sonoran Desert*. Arizona-Sonoran Desert Museum Press, Tucson, Arizona and University of California Press, Berkeley, California.
- DiTomaso, J. M. (2000) Invasive weeds in rangelands: species, impacts, and management. *Weed Science*, **48**, 255-265.
- Dodd, A. P. (1940). *The biological campaign against prickly-pear*. Commonwealth Prickly Pear Board, Government Printer, Brisbane, Australia.
- Dodd, J. D. (1968) Mechanical control of pricklypear and other woody species on the Rio Grande Plains. *Journal of Range Management*, **21**, 366-370.
- Dow AgroSciences (2017a) Surmount specimen label. Dow AgroSciences LLC, Indianapolis, Indiana.
- Dow AgroSciences (2017b) Vista XRT specimen label. Dow AgroSciences LLC, Indianapolis, Indiana.

- Drennan, P. M. & Nobel, P. S. (2000) Responses of CAM species to increasing atmospheric CO₂ concentrations. *Plant, Cell & Environment*, **23**, 767-781.
- Drezner, T. D. (2011) Cactus surface temperatures are impacted by seasonality, spines and height on plant. *Environmental and experimental botany*, **74**, 17-21.
- du Toit, J. T. (2011) Coexisting with cattle. *Science*, **333**, 1710-1711.
- Duncan, K. W. (2003) Considerations for prescribed burning. *Cooperative Extension Service, College of Agriculture and Home Economics, New Mexico State University*. Circular (522), Las Cruces, New Mexico.
- Ehrenfeld, J. G. (2000) Defining the limits of restoration: the need for realistic goals. *Restoration Ecology*, **8**, 2-9.
- English, N. B., Weltzin, J. F., Fravolini, A., Thomas, L. & Williams, D. G. (2005) The influence of soil texture and vegetation on soil moisture under rainout shelters in a semi-desert grassland. *Journal of Arid Environments*, **63**, 324-343.
- EPA (2017) Restricted use products report. U.S. Environmental Protection Agency. Retrieved from <https://www.epa.gov/pesticide-worker-safety/restricted-use-products-rup-report>
- Everitt, J. H., Gonzalez, C. L., Scott, G. & Dahl, B. E. (1981) Seasonal food preferences of cattle on native range in the South Texas Plains. *Journal of Range Management*, **34**, 384-388.
- Ewing, A. L. & Engle, D. M. (1988) Effects of late summer fire on tallgrass prairie microclimate and community composition. *American Midland Naturalist*, **120**, 212-223.

- Fay, P. A., Carlisle, J. D., Knapp, A. K., Blair, J. M. & Collins, S. L. (2003) Productivity responses to altered rainfall patterns in a C₄-dominated grassland. *Oecologia*, **132**, 245-251.
- Feugang, J. M., Konarski, P., Zou, D., Stintzing, F. C. & Zou, C. (2006) Nutritional and medicinal use of cactus pear (*Opuntia* spp.) cladodes and fruits. *Front Biosci*, **11**, 2574-2589.
- Fletcher, W. W. & Kirkwood, R. C. (1982) *Herbicides and Plant Growth Regulators*. Taylor & Francis. St. Albans, United Kingdom.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C. S. (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 557–581.
- Fontenot, N. J., Engdahl, G. R., Holland, G. L. & Schacht, W. H. (1991) Seasonal diet selection of white-tailed deer (*Odocoileus virginianus*) in relation to forage availability in west central Texas. *Instruction and Research (MIR) Center, San Angelo State University*. Progress Report (R-5:8-9), San Angelo, Texas.
- Foster, J. H. (1917) The spread of timbered areas in central Texas. *Journal of Forestry*, **15**, 442-445.
- Fowler, N. L. & Dunlap, D. W. (1986) Grassland vegetation of the eastern Edwards Plateau. *American Midland Naturalist*, **115**, 146-155.
- Frank, D. A., McNaughton, S. J. & Tracy, B. F. (1998) The ecology of the earth's grazing ecosystems. *BioScience*, **48**, 513.

- Franklin, J. F., Shugart, H. H. & Harmon, M. E. (1987) Tree death as an ecological process. *BioScience*, **37**, 550-556.
- Freeman, D. B. (1992) Prickly pear menace in Eastern Australia 1880-1940. *Geographical Review*, **82**, 413-429.
- Frost, C. C. (1998) Presettlement fire frequency regimes of the United States: a first approximation. In: *Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers fire ecology conference proceedings*, **20**, 70-81.
- Frost, P. G. M. & Robertson, F. (1987) Ecological effects of fire in savannas. Pages 93-140. In: Walker, B. H., (Editor). *Determinants of tropical savannas*, pp. 93-140. IUBS Monograph Series No. 3. IRL Press, Oxford, United Kingdom.
- Fuhlendorf, S. D. (1992) *Influence of age/size and grazing history on understory relationships of Ashe juniper*. Doctoral dissertation, Texas A&M University.
- Fuhlendorf, S. D., Briske, D. D. & 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.
- Fuhlendorf, S. D., Limb, R. F., Engle, D. M. & Miller, R. F. (2012) Assessment of prescribed fire as a conservation practice. Pages 75-104. In: Briske, D. D., (Editor). *Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps*. USDA Natural Resources Conservation Service. Allen Press, Inc. Lawrence, Kansas.

- Fuhlendorf, S. D. & Smeins, F. E. (1997) Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus-Quercus* savanna. *Journal of Vegetation Science*, **8**, 819-828.
- Fuhlendorf, S. D. & Smeins, F. E. (1998) The influence of soil depth on plant species response to grazing within a semi-arid savanna. *Plant Ecology*, **138**, 89-96.
- Fuhlendorf, S. D., Smeins, F. E. & Grant, W. E. (1996) Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. *Ecological Modelling*, **90**, 245-255.
- Fuhlendorf, S. D., Smeins, F. E. & Taylor, C. A. (1997) Browsing and tree size influences on Ashe juniper understory. *Journal of Range Management*, **50**, 507-512.
- Fuhlendorf, S. D., Engle, D. M., Kerby, J. A. Y. & Hamilton, R. (2009) Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology*, **23**, 588-598.
- Galt, D., Molinar, F., Navarro, J., Joseph, J. & Holechek, J. (2000) Grazing capacity and stocking rate. *Rangelands*, **22**, 7-11.
- Garcia de Cortázar, V. & Nobel, P. S. (1990) Worldwide environmental productivity indices and yield predictions for a CAM plant, *Opuntia ficus-indica*, including effects of doubled CO₂ levels. *Agricultural and Forest Meteorology*, **49**, 261-279.

- Gaxiola, A., McNeill, S. M. & Coomes, D. A. (2010) What drives retrogressive succession? Plant strategies to tolerate infertile and poorly drained soils. *Functional ecology*, **24**, 714-722.
- Gaylord, R. A. (1982) Evaluating the economics of brush control. *Rangelands*, **4**, 151-153.
- Gibson, A. C. & Nobel, P. S. (1986) *The cactus primer*. Harvard University Press, Cambridge, Massachusetts.
- Gillson, L., Dawson, T. P., Jack, S. & McGeoch, M. A. (2013) Accommodating climate change contingencies in conservation strategy. *Trends in Ecology & Evolution*, **28**, 135-142.
- Gillson, L. & Hoffman, M. T. (2007) Rangeland ecology in a changing world. *Science*, **315**, 53-54.
- Gilreath, M. E. & Smith, J. W. (1988) Natural enemies of *Dactylopius confusus* (Homoptera: Dactylopiidae): exclusion and subsequent impact on *Opuntia* (Cactaceae). *Environmental Entomology*, **17**, 730-738.
- Gleason, L. S. (1951) *The effectiveness of chemical herbicides for the control of prickly pear cactus (Opuntia spp.) in the vicinity of the Sonora Ranch Experiment Station*. Doctoral dissertation, Texas A&M University.
- Gonzalez, M. H. (1957) Grazing value and management of tobosa grass (*Hilaria mutica* (Buckl.) Benth.) on the Texas Range Station near Barnhart (M. S. Thesis, Texas A&M University).

- Graham, E. A. & Nobel, P. S. (1996) Long-term effects of a doubled atmospheric CO₂ concentration on the CAM species *Agave deserti*. *Journal of Experimental Botany*, **47**, 61-69.
- Greene, R. S. B., Chartres, C. J. & Hodgkinson, K. C. (1990) The effects of fire on the soil in a degraded semiarid woodland. I. Cryptogam cover and physical and micromorphological properties. *Soil Research*, **28**, 755-777.
- Griffiths, D. (1905) *The prickly pear and other cacti as food for stock* (Vol. 74). U.S. Department of Agriculture. Government Printing Office. Washington, District of Columbia.
- Griffith, M. P. (2004) The origins of an important cactus crop, *Opuntia ficus-indica* (Cactaceae): new molecular evidence. *American Journal of Botany*, **91**, 1915-1921.
- Grubb, P. J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological reviews*, **52**, 107-145.
- Gunderson, L. H. (2000) Ecological resilience—in theory and application. *Annual review of ecology and systematics*, **31**, 425-439.
- Hajek, A. E. (2004) *Natural enemies: an introduction to biological control*. Cambridge University Press, Cambridge, United Kingdom.
- Hamilton, W. T. & Scifres, C. J. (1982) Prescribed burning during winter for maintenance of buffelgrass. *Journal of range management*, **35**, 9-12.

- Hamilton, W. T. & Ueckert, D. N. (2004) Rangeland woody plant and weed management—past, present, and future. Pages 3-13. In: Hamilton, W. T., McGinty, A., Ueckert, D. N., Hanselka, C. W. & Lee, M. R. (Editors). *Brush Management: Past, Present and Future*. Texas A&M University Press, College Station, Texas.
- Hanley, M. E., Lamont, B. B., Fairbanks, M. M. & Rafferty, C. M. (2007) Plant structural traits and their role in anti-herbivore defense. *Perspectives in Plant Ecology, Evolution and Systematics*, **8**, 157-178.
- Hanselka, C. W. & Falconer, L. L. (1994) Pricklypear management in South Texas. *Rangelands*, **16**, 102-106.
- Hanselka, C. W., Hamilton, W. T., & Conner, J. R. (1996) Integrated brush management systems for Texas: strategies and economics. *Texas Agricultural Extension Service*. Leaflet L-5146, College Station, Texas.
- Hanselka, C. W. & Paschal, J. C. (1991) Prickly pear cactus: a Texas rangeland enigma. *Rangelands*, **13**, 109-111.
- Heilman, J. L., McInnes, K. J., Kjelgaard, J. F., Owens, M. K. & Schwinning, S. (2009) Energy balance and water use in a subtropical karst woodland on the Edwards Plateau, Texas. *Journal of Hydrology*, **373**, 426-435.
- Heirman, A. L. & Wright, H. A. (1973) Fire in medium fuels of west Texas. *Journal of Range Management*, **26**, 331-335.
- Hernández, F. (1999) *The value of prickly pear cactus as nesting cover for northern bobwhite*. Dissertation, Texas A&M University-Kingsville, Kingsville, Texas.

- Hernández, F., Henke, S. E., Silvy, N. J. & Rollins, D. (2003) The use of prickly pear cactus as nesting cover by northern bobwhites. *The Journal of Wildlife Management*, **67**, 417-423.
- Hernández, F., Rollins, D. & Cantu, R. (1997) Evaluating evidence to identify ground-nest predators in west Texas. *Wildlife Society Bulletin*, **25**, 826-831.
- Herrick, J. E., Duniway, M. C., Pyke, D. A., Bestelmeyer, B. T., Wills, S. A., Brown, J. R., Karl, J. W. & Havstad, K. M. (2012) A holistic strategy for adaptive land management. *Journal of Soil and Water Conservation*, **67**, 105A-113A.
- Higgins, V. (1946) *The study of cacti*. Blandford Press, Ltd. London, United Kingdom.
- Hinckley, T. M., Duhme, F., Hinckley, A. R. & Richter, H. (1980) Water relations of drought hardy shrubs: osmotic potential and stomatal reactivity. *Plant, Cell & Environment*, **3**, 131-140.
- Hobbs, N. T. (1996) Modification of ecosystems by ungulates. *The Journal of Wildlife Management*, **60**, 695-713.
- Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., Epstein, P. R., Ewel, J. J., Klink, C. A., Lugo, A. E. & Norton, D. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global ecology and biogeography*, **15**, 1-7.
- Hobbs, R. J. & Harris, J. A. (2001) Restoration ecology: repairing the earth's ecosystems in the new millennium. *Restoration Ecology*, **9**, 239-246.
- Hobbs, R. J., Higgs, E. & Harris, J. A. (2009) Novel ecosystems: implications for conservation and restoration. *Trends in ecology & evolution*, **24**, 599-605.

- Hobbs, R. J., Higgs, E. S. & Hall, C. (2013) *Novel ecosystems: intervening in the new ecological world order*. John Wiley & Sons. Oxford, United Kingdom.
- Hodgkinson, K. C. (1991) Shrub recruitment response to intensity and season of fire in a semi-arid woodland. *Journal of Applied Ecology*, **28**, 60-70.
- Hoffman, G. O., Walker, A. H. & Darrow, R. A. (1955) Pricklypear, good or bad. *Texas Agricultural Extension Service*. Bulletin (806), College Station, Texas.
- Holechek, J. L., Pieper, R. D. & Herbel, C. H. (1989) *Range management. Principles and practices*. Prentice-Hall. Englewood Cliffs, New Jersey.
- Holechek, J. L. (2002) Do most livestock losses to poisonous plants result from "poor" range management? *Journal of Range Management*, **55**, 270-276.
- Holechek, J. L. (2007) National security and rangelands. *Rangelands*, **29**, 33-38.
- Holechek, J. L. & Hess, K. (1994) Brush control considerations: a financial perspective. *Rangelands*, **16**, 193-196.
- Holechek, J. L., Hilton, G., Molinar, F. & Galt, D. (1999) Grazing studies: what we've learned. *Rangelands*, **21**, 12-16.
- Humphrey, R. R. & Everson, A. C. (1951) Effect of fire on a mixed grass-shrub range in southern Arizona. *Journal of Range Management*, **4**, 264-266.
- Hunt, T. E. & Thompson, S. E. (1992) Civil and criminal environmental enforcement in Texas. *Texas Environmental Law Journal*, **23**, 131.
- Huss, D. L. & Allen, J. V. (1969) Livestock production and profitability comparisons of various grazing systems. *Texas Agricultural Experiment Station*. Bulletin (1089), College Station, Texas.

- Huston, J. E., Rector, B. S., Merrill, L. B. & Engdahl, B. S. (1981) Nutritional value of range plants in the Edwards plateau region of Texas. *Texas Agricultural Experimental Station. Bulletin* (1357), College Station, Texas.
- Huston, M. A. (2004) Management strategies for plant invasions: manipulating productivity, disturbance, and competition. *Diversity and Distributions*, **10**, 167-178.
- Hyder, D. N., Bement, R. E., Remmenga, E. E. & Hervey, D. F. (1975) Ecological responses of native plants and guidelines for management of shortgrass range. *U.S. Department of Agriculture, Agricultural Research Service. Technical Bulletin* (1503), Washington, District of Columbia.
- IBM Corp. (2013) IBM SPSS statistics for Windows, version 22.0. Armonk, New York.
- Jacoby, P. W., Ansley, R. J. & Trevino, B. A. (1992) An improved method for measuring temperatures during range fires. *Journal of Range Management*, **45**, 216-220.
- Johansen, M. P. Hakonson, T. E. & Breshears, D. D. (2001) Post-fire runoff and erosion from rainfall simulation: contrasting forests with shrublands and grasslands. *Hydrological processes*, **15**, 2953-2965.
- Kastning, E. H. (1983) Relict caves as evidence of landscape and aquifer evolution in a deeply dissected carbonate terrain: southwest Edwards Plateau, Texas, USA. *Journal of Hydrology*, **61**, 89-112.

- Kattenberg, A., Giorgi, F., Grassl, H., Meehl, G. A., Mitchell, J. F. B., Stouffer, R. J., Tokioka, T., Weaver, A. J. & Wigley, T. M. (1996) Climate models—projections of future climate. Pages 285-357. In: Houghton, J. T., Meira Filho, L. G., Callender, B. A., Harris, N., Kattenberg, A. & Maskell, K. *Climate Change 1995: The Science of Climate Change. Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom.
- Keddy, P. (2007) *Plants and vegetation: origins, processes, consequences*. Cambridge University Press, Cambridge, United Kingdom.
- Keddy, P. (2017) *Plant ecology: origins, processes, consequences. Second Edition*. Cambridge University Press. Cambridge, United Kingdom.
- Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J. & Bradstock, R. A. (2011) Fire as an evolutionary pressure shaping plant traits. *Trends in plant science*, **16**, 406-411.
- Kennard, D. K. (2013) Fireline Intensity. *Forest Encyclopedia*. Retrieved from <http://www.forestencyclopedia.net>
- Kerby, J. D., Fuhlendorf, S. D. & Engle, D. M. (2007) Landscape heterogeneity and fire behavior: scale-dependent feedback between fire and grazing processes. *Landscape Ecology*, **22**, 507-516.

- Kiel, B. (1980) Range burning and wildlife habitat. Pages 72-76. In: Hanselka, C. W., (Editor). *Prescribed range burning in the Coastal Prairie and Eastern Rio Grande Plains of Texas*. Texas Agricultural Experiment Station. College Station, Texas.
- Kluge, M. & Ting, I. P. (2012) *Crassulacean acid metabolism: analysis of an ecological adaptation* (Vol. 30). Springer Science & Business Media. Berlin, Germany.
- Knutson, C. & Haigh, T. (2013) A drought-planning methodology for ranchers in the Great Plains. *Rangelands*, **35**, 27-33.
- Kochenderfer, J. D., Kochenderfer, J. N. & Miller, G. W. (2012) *Manual herbicide application methods for managing vegetation in Appalachian hardwood forests*. U.S. Department of Agriculture, Forest Service, Northern Research Station. General Technical Report (NRS-96). Newtown Square, Pennsylvania.
- Koerner, S. E. & Collins, S. L. (2014) Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. *Ecology*, **95**, 98-109.
- Korfmacher, J. L., Chambers, J. C., Tausch, R. J., Roundy, B. A., Meyer, S. E. & Kitchen, S. (2003) Technical note: a technique for conducting small-plot burn treatments. *Journal of Range Management*, **56**, 251-254.
- Kreuter, U. P., Amestoy, H. E., Ueckert, D. N. & McGinty, W. A. (2001) Adoption of brush busters: results of Texas county extension survey. *Journal of Range Management*, **54**, 630-639.

- Kreuter, U. P., Amestoy, H. E., Kothmann, M. M., Ueckert, D. N., McGinty, W. A. & Cummings, S. R. (2005) The use of brush management methods: a Texas landowner survey. *Rangeland Ecology & Management*, **58**, 284-291.
- Kreuter, U. P., Woodard, J. B., Taylor, C. A. & Teague, W. R. (2008) Perceptions of Texas landowners regarding fire and its use. *Rangeland Ecology & Management*, **61**, 456-464.
- Küchler, A. W. (1964) *Potential natural vegetation of the conterminous United States* (Vol. 36). American Geographical Society. New York, New York.
- Labra, M., Grassi, F., Bardini, M., Imazio, S., Guiggi, A., Citterio, S., Banfi, E. & Sgorbati, S. (2003) Genetic relationships in *Opuntia* Mill. genus (Cactaceae) detected by molecular marker. *Plant Science*, **165**, 1129-1136.
- Leakey, A. D. B. & Lau, J. A. (2012) Evolutionary context for understanding and manipulating plant responses to past, present and future atmospheric [CO₂]. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 613-629.
- Le Houérou, H. N. (1996) Climate change, drought and desertification. *Journal of Arid Environments*, **34**, 133-185.
- Limb, R. F., Fuhlendorf, S. D., Engle, D. M. & Miller, R. F. (2016) Synthesis paper: assessment of research on rangeland fire as a management practice. *Rangeland ecology & management*, **69**, 415-422.

- Ludwig, J. A., Tongway, D. J., Bastin, G. N. & James, C. D. (2004) Monitoring ecological indicators of rangeland functional integrity and their relation to biodiversity at local to regional scales. *Austral ecology*, **29**, 108-120.
- Lundgren, G. K., Whitson, R. E., Ueckert, D. E., Gilstrap, F. E. & Livingston, C. W. (1981) Assessment of the prickly pear problem on Texas rangeland. *Texas Agricultural Experiment Station*. Misc. Publication (1483), College Station, Texas, 22.
- Maczko, K., Tanaka, J. A., Breckenridge, R., Hidinger, L., Heintz, H. T., Fox, W. E., Kreuter, U. P., Duke, C. S., Mitchell, J. E. & McCollum, D. W. (2011) Rangeland ecosystem goods and services: values and evaluation of opportunities for ranchers and land managers. *Rangelands*, **33**, 30-36.
- Marsico, T. D., Wallace, L. E., Ervin, G. N., Brooks, C. P., McClure, J. E. & Welch, M. E. (2011) Geographic patterns of genetic diversity from the native range of *Cactoblastis cactorum* (Berg) support the documented history of invasion and multiple introductions for invasive populations. *Biological Invasions*, **13**, 857-868.
- Marshall, J. K. (1973) Drought, land use and soil erosion. Pages 55-77. In: Lovett, J. V., (Editor). *The environmental, economic and social significance of drought*. Angus and Robertson Publishing, Sydney, Australia.
- Martinelli, P. C., Young, J. A. & Evans, R. A. (1982) Pesticide certification and range managers. *Rangelands*, **4**, 153 -154.

- Masters, R. A. & Sheley, R. L. (2001) Principles and practices for managing rangeland invasive plants. *Journal of Range Management*, **54**, 502-517.
- Mayeux, H. S. & Johnson, H. B. (1989) Absorption and translocation of picloram by Lindheimer pricklypear (*Opuntia lindheimeri*). *Weed Science*, **37**, 161-166.
- Mayheux, H. W., Johnson, H. B. & Polley, W. H. (1991) Global change and vegetation dynamics. Pages 62-74. In: James, L. F., (Editor). *Noxious range weeds*. Westview Press, Boulder, Colorado.
- McCalla, G. R., Blackburn, W. H. & Merrill, L. B. (1984) Effects of live- stock grazing on infiltration rates, Edwards Plateau of Texas. *Journal of Range Management*, **37**, 265-269.
- McCarron, J. K. & Knapp, A. K. (2001) C3 woody plant expansion in a C4 grassland: are grasses and shrubs functionally distinct? *American Journal of Botany*, **88**, 1818-1823.
- McCarthy, J. J., Canziani, O. F., Leary, N. A., Dokken, D. J. & White, K. S. (Editors) (2001) *Climate change 2001: impacts, adaptation, and vulnerability: contribution of Working Group II to the third assessment report of the Intergovernmental Panel on Climate Change (Vol. 2)*. Cambridge University Press, Cambridge, United Kingdom.
- McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G. & Yezzer, E. A. (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, **178**, 719-739.

- McDowell, N. G. (2011) Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology*, **155**, 1051-1059.
- McGinty, W. A., Smeins, F. E. & Merrill, L. B. (1979) Influence of soil, vegetation, and grazing management on infiltration rate and sediment production of Edwards Plateau rangeland. *Journal of Range Management*, **32**, 33-37.
- McGinty, A. (2001) How to take care of pricklypear and other cacti. *Texas Agricultural Extension Service*. Leaflet (5171), College Station, Texas.
- McGinty, A., Ansley, J., Cadenhead, J. F., Hamilton, W. T., Hanselka, C. W., Hart, C. R. & Ueckert, D. (2005) Chemical Weed and Brush Control: Suggestions for Rangeland. *Texas AgriLife Extension*. Bulletin (1466), College Station, Texas.
- McGinty, A. & Ueckert D. (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*. Leaflet (5171), College Station, Texas.
- McGranahan, D. A., Engle, D. M., Fuhlendorf, S. D., Winter, S. J., Miller, J. R. & Debinski, D. M. (2012) Spatial heterogeneity across five rangelands managed with pyric-herbivory. *Journal of Applied Ecology*, **49**, 903-910.
- McMillan, Z., Scott, C. B., Taylor, C. A. & Huston, J. E. (2002) Nutritional value and intake of prickly pear by goats. *Journal of Range Management*, **55**, 139-143.
- McPherson, G. R. (1995) The role of fire in desert grasslands. Pages 130-151. In: McClaran, M. P. & Van Devender, T. R. *The desert grassland*. University of Arizona Press, Tucson, Arizona.

- Merrill, L. B., Taylor, C. A., Dusek, R. & Livingston, C. W. (1980) Sheep losses from range with heavy prickly pear infestation. In: Ueckert, D. N. & Huston, J. E. (Editors). *Rangeland resources research. Texas Agricultural Experiment Station. Consolidated Progress Report (3665)*, San Angelo, Texas.
- Monaco, T. A., Jones, T. A. & Thurow, T. L. (2012) Identifying rangeland restoration targets: an appraisal of challenges and opportunities. *Rangeland Ecology & Management*, **65**, 599-605.
- Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H. & Bellwood, D. R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, **28**, 167-177.
- National Centers for Environmental Information, NOAA (2015) *United States Drought Monitor*. U.S. Department of Commerce, National Oceanic and Atmospheric Administration. Washington, District of Columbia.
- Neary, D. G., Klopatek, C. C., DeBano, L. F. & Ffolliott, P. F. (1999) Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management*, **122**, 51-71.
- Neary, D. G., DeBano, L. F. & Ffolliott, P. F. (2000) Fire impacts on forest soils: a comparison to mechanical and chemical site preparation. *Tall Timbers fire ecology conference proceedings* **21**, 85-94.
- Nerd, A., & Mizrahi, Y. (1997). Reproductive biology of cactus fruit crops. *Horticultural Reviews*, **18**, 321-346.

- NOAA (2014) United States divisional and station climatic data. U.S. Department of Commerce, National Oceanic and Atmospheric Administration. Washington, District of Columbia.
- Noble, I. R. & Slatyer, R. O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, **43**, 5-21.
- Nobel P. S. (1988) *Environmental Biology of Agaves and Cacti*. Cambridge University Press, Cambridge, United Kingdom.
- Nobel, P. S. (1991) Achievable productivities of certain CAM plants: basis for high values compared with C3 and C4 plants. *New phytologist*, **119**, 183-205.
- Nobel, P. S. (1997) Recent ecophysiological findings for *Opuntia ficus-indica*. *Journal of the Professional Association for Cactus Development*, **2**, 89-96.
- Nobel, P. S. (1999) *Physicochemical & Environmental Plant Physiology*. Academic Press, San Diego, California.
- Ogburn, R. M. & Edwards, E. J. (2010) The ecological water-use strategies of succulent plants. Pages 179-225. In: Jean-Claude Kader, J. & Delseny, M. (Editors). *Advances in botanical research*. Academic Press, London, United Kingdom.
- Ojima, D. S., Kittel, T. G. F., Rosswall, T. & Walker, B. H. (1991) Critical issues for understanding global change effects on terrestrial ecosystems. *Ecological Applications*, **1**, 316-325.
- O'Leary, J. F. & Minnich, R. A. (1981) Postfire recovery of creosote bush scrub vegetation in the western Colorado Desert. *Madroño*, **28**, 61-66.

- Omernik, J. M. (1987) Ecoregions of the conterminous United States. *Annals of the Association of American geographers*, **77**, 118-125.
- Omernik, J. M. (1995) *Level III ecoregions of the continental United States*. Corvallis Environmental Research Laboratory, U.S. Environmental Protection Agency. Washington, District of Columbia.
- Oppenheimer, H. R. (1960) Adaptation to drought: xerophytism. *Plant-Water Relationships in Arid and Semi-Arid Conditions*. Reviews of Research. UNESCO, Paris **15**, 105-138.
- Owens, M. K., Lin, C. D., Taylor, C. A. & Whisenant, S. (1998) Seasonal patterns of plant flammability and monoterpenoid content in *Juniperus ashei*. *Journal of Chemical Ecology*, **24**, 2115-2129.
- Pearson, D. E. & Callaway, R. M. (2005) Indirect nontarget effects of host-specific biological control agents: implications for biological control. *Biological Control*, **35**, 288-298.
- Pechook, S. & Pokroy, B. (2012) Self-assembling, bioinspired wax crystalline surfaces with time-dependent wettability. *Advanced Functional Materials*, **22**, 745-750.
- Peters, D. P. C., Belnap, J., Ludwig, J. A., Collins, S. L., Paruelo, J., Hoffman, M. T. & Havstad, K. M. (2012) How can science be general, yet specific? The conundrum of rangeland science in the 21st century. *Rangeland Ecology & Management*, **65**, 613-622.

- Petersen, J. L., Ueckert, D. N., Potter, R. L. & Huston, J. E. (1987) Ecotypic variation in selected fourwing saltbush populations in western Texas. *Journal of Range Management*, **40**, 361-366.
- Petersen, J. L., Ueckert, D. N. & Potter, R. L. (1988) Herbicidal control of pricklypear cactus in western Texas. *Journal of Range Management*, **41**, 313-316.
- Peterson, D. W. & Reich, P. B. (2001) Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecological Applications*, **11**, 914-927.
- Pickett, S., Cadenasso, M. L. & Meiners, S. J. (2009) Ever since Clements: from succession to vegetation dynamics and understanding to intervention. *Applied Vegetation Science*, **12**, 9-21.
- Pimienta-Barrios, E. (1994) Prickly pear (*Opuntia* spp.): a valuable fruit crop for the semi-arid lands of Mexico. *Journal of Arid Environments*, **28**, 1-11.
- Potter, R. L., Petersen, J. L. & Ueckert, D. N. (1986) Seasonal trends of total nonstructural carbohydrates in Lindheimer pricklypear (*Opuntia lindheimeri*). *Weed Science*, **34**, 361-365.
- Preston-Mafham, K. (1994) *Cacti and succulents in habitat*. Cassell. London, United Kingdom.
- Pyke, D. A., Brooks, M. L. & D'Antonio, C. (2010) Fire as a restoration tool: a decision framework for predicting the control or enhancement of plants using fire. *Restoration Ecology*, **18**, 274-284.
- Pyne, S. J. (1984) *Introduction to wildland fire. Fire management in the United States*. John Wiley & Sons, Inc. New York, New York.

- Rabenhorst, M. C. & Wilding, L. P. (1986a) Pedogenesis on the Edwards Plateau, Texas: I. Nature and continuity of parent material. *Soil Science Society of America Journal*, **50**, 678-687.
- Rabenhorst, M. C. & Wilding, L. P. (1986b) Pedogenesis on the Edwards Plateau, Texas: II. Formation and occurrence of diagnostic subsurface horizons in a climosequence. *Soil Science Society of America Journal*, **50**, 687-692.
- Rabenhorst, M. C. & Wilding, L. P. (1986c) Pedogenesis on the Edwards Plateau, Texas: III. New model for the formation of petrocalcic horizons. *Soil Science Society of America Journal*, **50**, 693-699.
- Rakowitz, L. (1997) The significance of prickly pear on south Texas rangelands. *Rangeland Archives*, **19**, 15-17.
- Ramírez-Tobías, H. M., López-Palacios, C., Aguirre-Rivera, J. R. & Reyes-Agüero, J. A. (2012) Hydroponic cactus pear production, productivity and quality of nopalito and fodder. In: Asao, T., (Editor). *Hydroponics. A Standard methodology for plant biological researches*. InTech. Rijeka, Croatia.
- Ravi, S., Breshears, D. D., Huxman, T. E. & D'Odorico, P. (2010a) Land degradation in drylands: interactions among hydrologic–aeolian erosion and vegetation dynamics. *Geomorphology*, **116**, 236-245.
- Ravi, S., D'Odorico, P., Huxman, T. E. & Collins, S. L. (2010b) Interactions between soil erosion processes and fires: implications for the dynamics of fertility islands. *Rangeland Ecology & Management*, **63**, 267-274.

- Reade, J. P. & Cobb, A. H. (2002) Herbicides: modes of action and metabolism. In: Naylor, R., (Editor). *Weed Management Handbook, 9th Edition*. Blackwell Science. Oxford, United Kingdom.
- Rebman, J. P. & Pinkava, D. J. (2001) *Opuntia* cacti of North America: an overview. *Florida Entomologist*, **84**, 474-483.
- Reyes-Agüero, J. A., Aguirre, J. R. & Valiente-Banuet, A. (2006) Reproductive biology of *Opuntia*: a review. *Journal of arid environments*, **64**, 549-585.
- Reynolds, H. & Bohning, J. (1956) Effects of burning on a desert grass-shrub range in Southern Arizona. *Ecology*, **37**, 769-777.
- Reynolds, J. F., Virginia, R. A., Kemp, P. R., De Soyza, A. G. & Tremmel, D. C. (1999) Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecological Monographs*, **69**, 69-106.
- Richards, R. T. & George, M. R. (1996) Evaluating changes in ranch management practices through extension education. *Journal of Range Management*, **49**, 76-80.
- Rietkerk, M. & van de Koppel, J. (1997) Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos*, **79**, 69-76.
- Roques, K. G., O'Connor, T. G. & Watkinson, A. R. (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*, **38**, 268-280.

- Rothermel, R. C. & Deeming, J. E. (1980) *Measuring and interpreting fire behavior for correlation with fire effects*. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. General Technical Report (INT-93). Missoula, Montana.
- Ruiz-Jaen, M. C. & Mitchell Aide, T. (2005) Restoration success: how is it being measured? *Restoration Ecology*, **13**, 569-577.
- Russell, C. E. & Felker, P. (1987) The prickly-pears (*Opuntia* spp., Cactaceae): a source of human and animal food in semiarid regions. *Economic Botany*, **41**, 433-445.
- Ruthven III, D. C., Braden, A. W., Knutson, H. J., Gallagher, J. F. & Synatzske, D. R. (2003) Woody vegetation response to various burning regimes in South Texas. *Journal of Range Management*, **56**, 159-166.
- Scheffer, M. & Carpenter, S. R. (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in ecology & evolution*, **18**, 648-656.
- Schlesinger, W. H., Abrahams, A. D., Parsons, A. J. & Wainwright, J. (1999) Nutrient losses in runoff from grassland and shrubland habitats in Southern New Mexico: I. Rainfall simulation experiments. *Biogeochemistry*, **45**, 21-34.
- Schwinning, S. (2008) The water relations of two evergreen tree species in a karst savanna. *Oecologia*, **158**, 373-383.
- Scifres, C. J. (1980) *Brush management: principles and practices for Texas and the Southwest*. Texas A&M University Press, College Station, Texas.

- Scifres, C. J., Rasmussen, G. A., Hamilton, W. T., Smith, R. P., Conner, J. R., Stuth, J. W., Inglis, J. M. & Welch, T. G. (1985) Integrated brush management systems for South Texas: development and implementation. *Texas Agricultural Experiment Station. Bulletin* (1943), College Station, Texas.
- Scifres, C. J. & Hamilton, W. T. (1993) Prescribed burning for brushland management: the south Texas example. Texas A&M University Press, College Station, Texas.
- Scholes, R. J. & Archer, S. R. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology & Systematics*, **28**, 517.
- Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H. P., Harnik, N., Leetmaa, A., Lau, N.C. & Li, C. (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. *Science*, **316**, 1181-1184.
- Seastedt, T. R., Hobbs, R. J. & Suding, K. N. (2008) Management of novel ecosystems: are novel approaches required? *Frontiers in Ecology and the Environment*, **6**, 547-553.
- Selleck, G. W. (1960) The climax concept. *The Botanical Review*, **26**, 534-545.
- Shedbalkar, U. U., Adki, V. S., Jadhav, J. P. & Bapat, V. A. (2010) *Opuntia* and other cacti: applications and biotechnological insights. *Tropical Plant Biology*, **3**, 136-150.
- Sickerman, S. L. & Wangberg, J. K. (1983) Behavioral responses of the cactus bug, *Chelinidea vittiger* Uhler, to fire damaged host plants. *Southwestern Entomologist*, **8**, 263-267.

- Simanton, J. R. (1991) Revegetation of semiarid rangelands: problems, procedures, and probabilities. *Rangelands*, **13**, 129-132.
- Simberloff, D. & Stiling, P. (1996) How risky is biological control? *Ecology*, **77**, 1965-1974.
- Skov, K. R., Kolb, T. E. & Wallin, K. F. (2004) Tree size and drought affect ponderosa pine physiological response to thinning and burning treatments. *Forest Science*, **50**, 81-91.
- Slater, S. C., Rollins, D., Dowler, R. C. & Scott, C. B. (2001) *Opuntia*: a "prickly paradigm" for quail management in West-Central Texas. *Wildlife Society Bulletin*, **29**, 713-719.
- Smeins, F. E., Taylor, T. W. & Merrill, L. B. (1976) Vegetation of a 25-year enclosure on the Edwards Plateau, Texas. *Journal of Range Management*, **29**, 24-29.
- Smeins, F. E. (1980) Natural role of fire on the Edwards Plateau. In: White, L. D., (Editor). *Prescribed burning of the Edwards Plateau of Texas*. Texas Agricultural Extension Service, College Station, Texas.
- Smeins, F. E., Fuhlendorf, S. & Taylor, C. A. (1997) Environmental and land use changes: a long-term perspective. Pages 1-21. In: Taylor, C. A., (Editor). *Juniper symposium proceedings*. Texas Agriculture Experiment Station. Technical Report (97-1), San Angelo, Texas.
- Smeins, F. E. & Merrill, L. B. (1988) Long-term change in a semi-arid grassland. Pages 101-114. In: Amos, B. & Gehlbach, F. R. (Editors). *Edwards Plateau vegetation plant ecological studies in Central Texas*. Baylor University Press, Waco, Texas.

- Smith, J. G. (1899) *Grazing problems in the Southwest and how to meet them*. Pages 7-8. Bulletin No. 16. U.S. Department of Agriculture, Division of Agrostology. Government Printing Office. Washington, District of Columbia.
- Sosa, G. (2009) *Restoring a degraded rangeland: using fire and herbivory to control *Opuntia cacti* encroachment* (Thesis, Texas A & M University).
- Soto, B. & Díaz-Fierros, F. (1998) Runoff and soil erosion from areas of burnt scrub: comparison of experimental results with those predicted by the WEPP model. *Catena*, **31**, 257-270.
- Staudt, A., Huddleston, N. & Kraucunas, I. (2008) *Understanding and Responding to Climate Change: Highlights of National Academies Reports*. National Academy Press, Washington, District of Colombia.
- Stiling, P. (2002) Potential non-target effects of a biological control agent, prickly pear moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), in North America, and possible management actions. *Biological invasions*, **4**, 273-281.
- Stoddart, L. A. & Smith, A. D. (1943) *Range management*. McGraw-Hill, New York, New York.
- Stringham, T. K., Krueger, W. C. & Shaver, P. L. (2003) State and transition modeling: an ecological process approach. *Journal of Range Management*, **56**, 106-113.
- Stronach, N. R. & McNaughton, S. J. (1989) Grassland fire dynamics in the Serengeti ecosystem, and a potential method of retrospectively estimating fire energy. *Journal of Applied Ecology*, **26**, 1025-1033.

- Suding, K. N., Gross, K. L. & Houseman, G. R. (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, **19**, 46-53.
- Szarek, S. R., Johnson, H. B. & Ting, I. P. (1973) Drought adaptation in *Opuntia basilaris* significance of recycling carbon through crassulacean acid metabolism. *Plant Physiology*, **52**, 539-541.
- Taiz, L. & Zeiger, E. (1998) *Plant Physiology*. Sinauer Associates, Inc. Sunderland, Massachusetts.
- Taylor, C. A. (2001) Summer fire for the western region of the Edwards Plateau: a case study. *Texas Agricultural Experiment Station*. Technical Report (01-2), College Station, Texas.
- Taylor, C. A. (2003) Rangeland monitoring and fire: wildfires and prescribed burning, nutrient cycling, and plant succession. *Arid Land Research and Management*, **17**, 429-438.
- Taylor, C. A., Garza, N. E. & Brooks, T. D. (1993) Grazing systems on the Edwards Plateau of Texas: are they worth the trouble? I. Soil and vegetation response. *Rangelands*, **15**, 53-57.
- Taylor, C. A., Kothmann, M. M., Merrill, L. B. & Elledge, D. (1980) Diet selection by cattle under high-intensity low-frequency, short duration, and Merrill grazing systems. *Journal of Range Management*, **33**, 428-434.
- Taylor, C. A. (2005) Prescribed burning cooperatives: empowering and equipping ranchers to manage rangelands. *Rangelands*, **27**, 18-23.

- Taylor, C. A. (2007) Role of summer prescribed fire to manage shrub-invaded grasslands. Pages 52-55. In: Sosebee, R. E., Wester, D. B., Britton, C. M., McArthur, E. D. & Kitchen, S. G. (Editors). *Proceedings: shrubland dynamics—fire and water*. August 10-12, 2004. Lubbock, Texas. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. General Technical Report (RMRS-P-47). Fort Collins, Colorado.
- Taylor, C. A. (2008) Ecological consequences of using prescribed fire and herbivory to manage *Juniperus* encroachment. Pages 239-252. In: *Western North American Juniperus Communities*. Springer-Verlag. New York, New York.
- Taylor, C. A., Twidwell, D., Garza, N. E., Rosser, C., Hoffman, J. K. & Brooks, T. D. (2012) Long-term effects of fire, livestock herbivory removal, and weather variability in Texas semiarid savanna. *Rangeland Ecology & Management*, **65**, 21-30.
- Taylor, C. A. & Ralphs, M. H. (1992) Reducing livestock losses from poisonous plants through grazing management. *Journal of Range Management*, **45**, 9-12.
- Teague, R., Borchardt, R., Ansley, J., Pinchak, B., Cox, J., Foy, J. K. & McGrann, J. (1997) Sustainable management strategies for mesquite rangeland: the Waggoner Kite Project. *Rangelands*, **19**, 4-8.
- Teague, W. R., Grant, W. E., Kreuter, U. P., Diaz-Solis, H., Dube, S., Kothmann, M. M., Pinchak, W. E. & Ansley, R. J. (2008) An ecological economic simulation model for assessing fire and grazing management effects on mesquite rangelands in Texas. *Ecological Economics*, **64**, 611-624.

- Theimer, T. C. & Bateman, G. C. (1992) Patterns of prickly-pear herbivory by collared peccaries. *The Journal of Wildlife Management*, **56**, 234-240.
- Thomas, P. A. (1991) Response of succulents to fire: a review. *International Journal of Wildland Fire*, **1**, 11-22.
- Thomas, G. W. & Young, V. A. (1954) Relation of soils, rainfall and grazing management to vegetation, Western Edwards Plateau of Texas. *Texas Agricultural Experiment Station. Bulletin* (786), College Station, Texas.
- Thurrow, T. L., Blackburn, W. H. & Taylor, C. A. (1986) Hydrologic characteristics of vegetation types as affected by livestock grazing systems, Edwards Plateau, Texas. *Journal of Range Management*, **39**, 505-509.
- Thurrow, T. L. & Taylor, C. A. (1999) Viewpoint: the role of drought in range management. *Journal of Range Management*, **52**, 413-419.
- Toomey, R. S., Blum, M. D. & Valastro, S. (1993) Late quaternary climates and environments of the Edwards Plateau, Texas. *Global and Planetary Change*, **7**, 299-320.
- Toweill, D. E. & Teer, J. G. (1977) Food habits of ringtails in the Edwards Plateau region of Texas. *Journal of Mammalogy*, **58**, 660-663.
- Trachtenberg, S. & Mayer, A. M. (1980) Biophysical properties of *Opuntia ficus-indica* mucilage. *Phytochemistry*, **21**, 2835-2843.
- Trollope, W. S. W. (1984) Fire behaviour. In: *Ecological effects of fire in South African ecosystems*. Springer. Berlin, Heidelberg, Germany.

- Turner, G. T. & Costello, D. F. (1942) Ecological aspects of the pricklypear problem in eastern Colorado and Wyoming. *Ecology*, **23**, 419-426.
- Twidwell, D. L. (2012) *From theory to application: extreme fire, resilience, restoration, and education in social-ecological disciplines*. Dissertation, Texas A&M University.
- Twidwell, D., Wonkka, C. L., Taylor, C. A., Zou, C. B., Twidwell, J. J. & Rogers, W. E. (2014) Drought-induced woody plant mortality in an encroached semi-arid savanna depends on topographic factors and land management. *Applied Vegetation Science*, **17**, 42-52.
- Twidwell, D., Rogers, W. E., Wonkka, C. L., Taylor, C. A. & Kreuter, U. P. (2016) Extreme prescribed fire during drought reduces survival and density of woody resprouters. *Journal of applied ecology*, **53**, 1585-1596.
- Tyree, M. T. & Alexander, J. D. (1993) Plant water relations and the effects of elevated CO₂: a review and suggestions for future research. *Vegetatio*, **104/105**, 46-62.
- Ueckert, D. N., Livingston, C.W., Huston, J.E., Menzies, C.S., Dusek, R. K., Petersen, J.L. & Lawrence, B.K. (1990) Range and sheep management for reducing pearmouth and other pricklypear-related health problems in sheep flocks. Pages 40-41. *Texas Agricultural Experimental Station*. Program Report (4782), College Station, Texas.
- Ueckert, D. N. & McGinty, W. A. (1997) Brush Busters-how to take care of pricklypear and other cacti. *Texas Agricultural Research and Extension Center*. Leaflet (L-5171), San Angelo, Texas.

- Ueckert, D. N., Petersen, J. L., Potter, R. L., Whipple, J. D. & Wagner, M. W. (1988) Managing pricklypear with herbicides and fire. Pages 10-15. *Texas Agricultural Experiment Station*. Report (4570), College Station, Texas.
- Ueckert, D. N., Rollins, D. & Brown, C. G. (1997) Prickly pear ecology. In: *Brush Sculptors*. Texas Agriculture Extension Service. San Angelo, Texas.
- Ueckert, D. N. & Whisenant, S. G. (1980) Susceptibility of honey mesquite and prickly pear to a burning/herbicide control system. Page 26. In: *Rangeland Resources Research*. Texas Agricultural Experiment Station. Consolidated Progress Report (3665), College Station, Texas.
- USDA-NRCS (2017) Soil Survey of Edwards and Real Counties. United States Department of Agriculture (USDA), Natural Resource Conservation Service (NRCS), National Soil Survey Center. Washington, District of Columbia.
- U.S. Geological Survey (2014a) Ecological Resource Areas, Texas [map]. United States Department of the Interior. Reston, Virginia.
- U.S. Geological Survey (2014b) Topography of the Edwards Plateau, Texas [map]. United States Department of the Interior. Reston, Virginia.
- Vallentine, J. F. (1983) The application and use of herbicides for range plant control. Pages 39-48. In: Monsen, S. B., Stevens, R. & Shaw, N. L. (Editors). *Range management, weed control*. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. General Technical Report (INT-157). Ogden, Utah.

- Vallentine, J. F. (2004) Herbicides for plant control. Pages 89-100. In: Monsen, S. B., Stevens, R. & Shaw, N. L. (Editors). *Restoring western ranges and wildlands*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. General Technical Report (RMRS-GTR-136). Fort Collins, Colorado.
- Van Auken, O. W. (2000) Shrub invasions of North American semiarid grasslands. *Annual review of ecology and systematics*, **31**, 197-215.
- Van Auken, O. W. (2009) Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management*, **90**, 2931-2942.
- van de Koppel, J., Rietkerk, M. & Weissing, F. J. (1997) Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends in Ecology & Evolution*, **12**, 352-356.
- van Mantgem, P. J., Nensmith, J. C., Keifer, M., Knapp, E. E., Flint, A. & Flint, L. (2013) Climatic stress increases forest fire severity across the western United States. *Ecology Letters*, **16**, 1151-1156.
- Wali, M. (1999) Ecological succession and the rehabilitation of disturbed terrestrial ecosystems. *Plant and Soil*, **213**, 195-220.
- Walker, B. H. (1993) Rangeland ecology: understanding and managing change. *Ambio*, **22**, 80-87.
- Warming, E. (1925) *Oecology of plants: an introduction to the study of plant-communities*. Oxford University Press, London, United Kingdom.

- Watts, J. G., Hewitt, G. B. Huddleston, E. W., Kinzer, H. G., Lavigne, R. J. & Ueckert, D. N. (1989) *Rangeland Entomology. Second Edition*. Society for Range Management, Denver, Colorado.
- Weaver, J. E. & Clements, F. E. (1929) *Plant ecology*. McGraw-Hill Book Co., Inc., New York, New York.
- Weir, J. R. (2009) *Conducting Prescribed Fires: A Comprehensive Manual*. Texas A&M University Press, College Station, Texas.
- Weixelman, D. A., Zamudio, D. C., Zamudio, K. A. & Tausch, R. J. (1997) Classifying ecological types and evaluating site degradation. *Journal of Range Management*, **50**, 315-321.
- Weltz, M. A., Dunn, G., Reeder, J. & Frasier, G. (2003) Ecological sustainability of rangelands. *Arid Land Research and Management*, **17**, 369-388.
- Westoby, M., Walker, B. & Noy-Meir, I. (1989) Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, **42**, 266-274.
- Whelan, R. J. (1995) *The ecology of fire*. Cambridge University Press, Cambridge, United Kingdom.
- Whisenant, S. G. (1982) Ecological effects of fire on Texas wintergrass. Doctoral dissertation, Texas A&M University.
- Whisenant, S. G. (1995) Landscape dynamics and arid land restoration. Pages 26-34. In: Roundy, B. A., McArthur, E. D., Haley, J. S. & Mann, D. K. (Editors). *Proceedings of the wild land shrub and arid land restoration symposium*. October 19-21, 1993. Las Vegas, Nevada.

- Whisenant, S. G., Ueckert, D. N. & Scifres, C. J. (1984) Effects of fire on Texas wintergrass communities. *Journal of Range Management*, **37**, 387-391.
- Wilson, L. M. & McCaffrey, J. P. (1999) Biological control of noxious rangeland weeds. Pages 97-115. In: *Biology and management of noxious rangeland weeds*. Oregon State University Press, Corvallis, Oregon.
- Winter, K. & Smith, J. A. C. (1996) An introduction to crassulacean acid metabolism. Biochemical principles and ecological diversity. In: *Crassulacean acid metabolism*. Springer. Berlin, Heidelberg, Germany.
- Wright, H. A. (1972) Fire as a tool to manage tobosa grasslands. *Tall Timbers fire ecology conference proceedings*, **12**, 195-204.
- Wright, H. A. (1974) Range Burning. *Journal of Range Management Archives*, **27**, 1-11.
- Wright, H. A. & Bailey, A. W. (1982) *Fire ecology: United States and Southern Canada*. John Wiley & Sons. New, York, New York.
- Yahdjian, L. & Sala, O. (2002) A rainout shelter design for intercepting different amounts of rainfall. *Oecologia*, **133**, 95-101.
- Young, V. A. (1956) The effects of the 1949-1954 drought on the ranges of Texas. *Journal of Range Management*, **9**, 139-142.
- Young, V. A., Anderwald, F. R. & McCully, W. G. (1948) Brush problems on Texas ranges. Pages 1-19. *Texas Agricultural Experiment Station*. Misc. Publication (21), College Station, Texas.

- Young, V. A., Fisher, C., Darrow, R., McGully, W. & Young, D. (1950) Recent developments in the chemical control of brush on Texas ranges. *Texas Agricultural Experiment Station. Bulletin (721)*, College Station, Texas.
- Zavaleta, E. S., Shaw, M. R., Chiariello, N. R., Mooney, H. A. & Field, C. B. (2003) Additive effects of simulated climate changes, elevated CO₂, and nitrogen deposition on grassland diversity. *Proceedings of the National Academy of Sciences*, **100**, 7650-7654.

APPENDIX A

CHAPTER IV SUPPORTING TABLES

Table 1. Descriptive statistics of the fireline intensities (kW/m) between the prescribed burn treatments.

	Fire Treatment	N	Mean	Std. Deviation	Std. Error Mean
Fireline Intensity	Reclamation Fire	18	1270.60	1130.60	266.49
	Maintenance Fire	18	419.61	268.59	63.31

Table 2. Independent-samples t-test comparing the fireline intensities (kW/m) for the reclamation and maintenance prescribed fire treatments.

		t-test for Equality of Means					95% Confidence Interval of the Difference	
		t	df	P-value	Mean Difference	Std. Error Difference	Lower	Upper
Fireline Intensity	Equal variances assumed	3.107	34	.004	850.99	273.90	294.36	1407.63

Table 3. A comparison of the percent area burned for the fire treatments conducted on the experimental plots.

Year	Fire Treatment	Area burned (%)
Mean (\pm S.E.)		
2008	Reclamation Prescribed Fire	99.5 \pm 0.5
2010	Maintenance Prescribed Fire	100 \pm 0

Table 4. Descriptive statistics of the percent change in prickly pear canopy cover in response to the prescribed fire treatments.

Fire Treatment	N	Mean	Std. Deviation	Std. Error
Reclamation Fire	121	-95.07	18.82	1.71
Reclamation + Maintenance Fire	150	-99.59	3.16	.26
No Prescribed Fire	96	-29.44	144.34	14.73
Total	367	-79.75	80.19	4.19

Table 5. Analysis of variance for the percent change in prickly pear canopy cover in response to the prescribed fire treatments.

	Sum of Squares	df	Mean Square	F	P-value
Between Groups	330377.140	2	165188.570	29.721	.000
Within Groups	2023120.851	364	5558.024		
Total	2353497.991	366			

Table 6. Descriptive statistics comparing the percent change of cactus cover in response to the different prescribed fire treatments.

	Fire Treatment	N	Mean	Std. Deviation	Std. Error Mean
Percent Change Cactus Cover	Reclamation + Maintenance Fire	150	-99.59	3.16	.26
	Reclamation Fire	121	-95.07	18.82	1.71

Table 7. Independent-samples t-test comparing the percent change of cactus cover in response to the different prescribed fire treatments.

		t-test for Equality of Means						
		t	df	P-value	Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference	
							Lower	Upper
Percent Change Cactus Cover	Equal variances assumed	-2.892	269	.004	-4.52	1.56	-7.59	-1.44

Table 8. Descriptive statistics of the percent standing herbaceous cover collected before (July 2007) and after (December 2012) the prescribed fire treatments.

	Fire Treatment	N	Mean	Std. Deviation	Std. Error
July 2007	Reclamation Fire	121	65.04	22.04	2.00
	Reclamation + Maintenance Fire	150	65.03	21.32	1.74
	No Prescribed Fire	97	69.95	22.67	2.30
	Total	368	66.33	21.96	1.14
December 2012	Reclamation Fire	121	9.92	11.81	1.07
	Reclamation + Maintenance Fire	150	9.47	11.49	.94
	No Prescribed Fire	97	20.26	18.92	1.92
	Total	368	12.46	14.65	.76

Table 9. Descriptive statistics of the percent change in standing herbaceous cover in response to the prescribed fire treatments.

Fire Treatment	N	Mean	Std. Deviation	Std. Error
Reclamation Fire	121	-79.598	28.19	2.56
Reclamation + Maintenance Fire	150	-81.561	36.15	2.95
No Prescribed Fire	97	-69.727	29.65	3.01
Total	368	-77.796	32.32	1.68

Table 10. Independent-samples t-test comparing the change in percent standing herbaceous cover between the prescribed fire treatments.^b

	Fire Treatment	N	Mean	Std. Deviation	Std. Error Mean	df	t	P-value
Percent Change Herbaceous Cover	Reclamation Fire	121	-79.60	28.19	2.56	269	.489	.625
	Reclamation + Maintenance Fire	150	-81.56	36.15	2.95			
	Reclamation + Maintenance Fire	150	-81.56	36.15	2.95	245	2.69	.008
	No Prescribed Fire	97	-69.73	29.65	3.01			
	Reclamation Fire	121	-79.60	28.19	2.56	216	2.51	.013
	No Prescribed Fire	97	-69.73	29.65	3.01			

b. Equality of variances assumed

Table 11. Descriptive statistics of the percent bare ground cover collected before (July 2007) and after (December 2012) the prescribed fire treatments.

	Fire Treatment	N	Mean	Std. Deviation	Std. Error
July 2007	Reclamation Fire	121	3.47	8.01	.73
	Reclamation + Maintenance Fire	150	8.47	10.31	.84
	No Prescribed Fire	97	8.97	14.01	1.42
	Total	368	6.96	11.02	.57
December 2012	Reclamation Fire	121	66.74	30.12	2.74
	Reclamation + Maintenance Fire	150	68.07	33.05	2.70
	No Prescribed Fire	97	43.81	38.08	3.87
	Total	368	61.24	35.05	1.83

Table 12. Descriptive statistics of the percent change in bare ground cover in response to the prescribed fire treatments.

Fire Treatment	N	Mean	Std. Deviation	Std. Error
Reclamation Fire	121	63.26	30.53	2.78
Reclamation + Maintenance Fire	150	59.60	33.30	2.72
No Prescribed Fire	97	34.48	33.76	3.43
Total	369	54.11	34.55	1.80

Table 13. Analysis of variance for the percent change in bare ground cover in response to the prescribed fire treatments.

	Sum of Squares	df	Mean Square	F	P-value
Between Groups	52019.671	2	26009.835	24.564	.000
Within Groups	386485.764	365	1058.865		
Total	438505.435	367			

Table 14. Independent-samples t-test comparing the change in percent bare ground cover between the prescribed fire treatments.^b

	Fire Treatment	N	Mean	Std. Deviation	Std. Error Mean	df	t	P-value
Percent Change Ground Cover	Reclamation Fire	121	63.26	30.53	2.78	269	.934	.351
	Reclamation Fire + Maintenance Fire	150	59.60	33.30	2.72			
	Reclamation Fire + Maintenance Fire	150	59.60	33.30	2.72	245	5.76	.000
	No Prescribed Fire	97	34.48	33.76	3.43			
	Reclamation Fire	121	63.26	30.53	2.78	216	6.60	.000
	No Prescribed Fire	97	34.48	33.76	3.43			

b. Equality of variances assumed

APPENDIX B

CHAPTER V SUPPORTING TABLES

Table 15. Descriptive statistics of the mean maximum instantaneous fire temperature (degrees Celsius) of the plots under different hydration treatments.

	Treatment	N	Mean	Std. Deviation	Std. Error Mean
Max. Instantaneous Temperature	Rainout Shelter	8	183.80	87.73	31.02
	Ambient Conditions	8	92.30	48.87	17.28

Table 16. Independent-samples t-test comparing the mean maximum instantaneous fire temperature (degrees Celsius) of the plots under different hydration treatments.

		t-test for Equality of Means						
	Equal variances assumed	t	df	P-value	Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference	
							Lower	Upper
Max. Instantaneous Temperature		-2.577	14	.022	-91.50	35.50	-167.65	-15.35

Table 17. Descriptive statistics of the percent change in prickly pear canopy cover in response to the hydration and prescribed fire treatments.

Treatment Combination	N	Mean	Std. Deviation	Std. Error
Rainout Shelter, Fire (April 2011)	8	-34.72	31.88	11.27
Ambient Conditions, Fire (April 2011)	8	-4.34	84.97	30.04
Rainout Shelter, Fire (Sept. 2012)	8	-15.98	103.04	36.43
Ambient Conditions, Fire (Sept. 2012)	8	16.98	65.08	23.01
Rainout Shelter, No Prescribed Fire	8	-3.35	37.92	13.41
Ambient Conditions, No Prescribed Fire	8	17.06	30.11	10.65
Total	48	-4.06	64.21	9.27

Table 18. Analysis of variance for the percent change in prickly pear cover in response to the hydration and prescribed fire treatments.

	Sum of Squares	df	Mean Square	F	P-value
Between Groups	15771.432	5	3154.286	.744	.595
Within Groups	178034.022	42	4238.905		
Total	193805.454	47			

Table 19. Independent-samples t-test comparing the change in percent prickly pear canopy cover in response to the hydration and prescribed fire treatments.^b

	Treatment Combination	N	Mean	Std. Deviation	Std. Error Mean	df	t	P-value
Percent Change Cactus Cover	Rainout Shelter, Fire (April 2011)	8	-34.72	31.88	11.27	14	-.947	.360
	Ambient Conditions, Fire (April 2011)	8	-4.34	84.97	30.04			
	Rainout Shelter, Fire (Sept. 2012)	8	-15.98	103.04	36.43	14	-.765	.457
	Ambient Conditions, Fire (Sept. 2012)	8	16.98	65.08	23.01			
	Rainout Shelter, No Prescribed Fire	8	-3.35	37.92	13.41	14	-1.192	.253
	Ambient Conditions, No Prescribed Fire	8	17.06	30.11	10.65			

b. Equality of variances assumed

Table 20. Descriptive statistics of the mean wet weight (g) of the harvested cactus stem tissue samples.

Hydration Treatment	N	Mean	Std. Deviation	Std. Error
Rainout Shelter	32	3.62	1.22	.22
Ambient Conditions	32	5.48	1.06	.19
Total	64	4.55	1.47	.18

Table 21. Independent-samples t-test comparing the mean weight (g) of the harvested prickly pear cactus stems under different hydration treatments.

		t-test for Equality of Means						
		t	df	P-value	Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference	
							Lower	Upper
Wet Weight (g)	Equal variances assumed	6.496	62	.000	1.85	.29	1.28	2.42

Table 22. Descriptive statistics of the mean standing herbaceous vegetation cover present on the plots before (June 2010) the establishment of the hydration and prescribed fire treatments.

Treatment Combination	N	Mean	Std. Deviation	Std. Error
Rainout Shelter, Fire (Sept. 2012)	8	61.88	20.17	7.13
Ambient Conditions, Fire (Sept. 2012)	8	59.38	18.79	6.64
Rainout Shelter, Fire (April 2011)	8	77.50	8.02	2.83
Ambient Conditions, Fire (April 2011)	8	58.75	16.85	5.96
Rainout Shelter, No Prescribed Fire	8	69.38	15.22	5.38
Ambient Conditions, No Prescribed Fire	8	59.38	17.20	6.08
Total	48	64.38	17.09	2.47

Table 23. Analysis of variance for the mean standing herbaceous vegetation cover present on the plots before (June 2010) the establishment of the hydration and prescribed fire treatments.

	Sum of Squares	df	Mean Square	F	P-value
Between Groups	2281.250	5	456.250	1.674	.162
Within Groups	11450.000	42	272.619		
Total	13731.250	47			

Table 24. Descriptive statistics of the mean standing herbaceous vegetation cover present on the plots after (March 2013) the establishment of the hydration and prescribed fire treatments.

Treatment Combination	N	Mean	Std. Deviation	Std. Error
Rainout Shelter, Fire (Sept. 2012)	8	-92.26	6.50	2.30
Ambient Conditions, Fire (Sept. 2012)	8	-92.74	6.73	2.38
Rainout Shelter, Fire (April 2011)	8	-34.02	30.08	10.63
Ambient Conditions, Fire (April 2011)	8	-76.36	21.20	7.49
Rainout Shelter, No Prescribed Fire	8	.30	35.39	12.51
Ambient Conditions, No Prescribed Fire	8	-55.04	28.36	10.03
Total	48	-58.35	40.76	5.88

Table 25. Analysis of variance for the mean standing herbaceous vegetation cover present on the plots after (March 2013) the establishment of the hydration and prescribed fire treatments.

	Sum of Squares	df	Mean Square	F	P-value
Between Groups	53593.194	5	10718.639	18.385	.000
Within Groups	24486.388	42	583.009		
Total	78079.582	47			

Table 26. Independent-samples t-test comparing the change in percent standing herbaceous vegetation cover in response to the hydration and prescribed fire treatments.^b

	Treatment Combination	N	Mean	Std. Deviation	Std. Error Mean	df	t	P-value
Percent Change Herbaceous Cover	Rainout Shelter, Fire (April 2011)	8	-34.02	30.08	10.63	14	-3.255	.006
	Ambient Conditions, Fire (April 2011)	8	-76.36	21.20	7.50			
	Rainout Shelter, Fire (Sept. 2012)	8	-92.26	6.50	2.30	14	-.144	.887
	Ambient Conditions, Fire (Sept. 2012)	8	-92.74	6.73	2.38			
	Rainout Shelter, No Prescribed Fire	8	.30	35.39	12.51	14	-3.451	.004
	Ambient Conditions, No Prescribed Fire	8	-55.04	28.36	10.03			

b. Equality of variances assumed

Table 27. Descriptive statistics of the mean percent bare ground cover on the plots before (June 2010) the establishment of the hydration and prescribed fire treatments.

Treatment Combination	N	Mean	Std. Deviation	Std. Error
Rainout Shelter, Fire (Sept. 2012)	8	11.25	10.94	3.87
Ambient Conditions, Fire (Sept. 2012)	8	15.00	10.69	3.78
Rainout Shelter, Fire (April 2011)	8	8.13	5.94	2.10
Ambient Conditions, Fire (April 2011)	8	14.38	10.50	3.71
Rainout Shelter, No Prescribed Fire	8	8.75	4.43	1.57
Ambient Conditions, No Prescribed Fire	8	15.00	13.63	4.82
Total	48	12.08	9.78	1.41

Table 28. Analysis of variance for the mean percent bare ground cover on the plots before (June 2010) the establishment of the hydration and prescribed fire treatments.

	Sum of Squares	df	Mean Square	F	P-value
Between Groups	397.917	5	79.583	.816	.545
Within Groups	4093.750	42	97.470		
Total	4491.667	47			

Table 29. Descriptive statistics of the mean percent bare ground cover on the plots after (March 2013) the establishment of the hydration and prescribed fire treatments.

Treatment Combination	N	Mean	Std. Deviation	Std. Error
Rainout Shelter, No Prescribed Fire	8	5.63	4.17	1.48
Rainout Shelter, Fire (Sept. 2012)	8	81.25	15.06	5.32
Rainout Shelter, Fire (April 2011)	8	26.25	18.47	6.53
Ambient Conditions, No Prescribed Fire	8	35.00	14.39	5.09
Ambient Conditions, Fire (Sept. 2012)	8	63.75	21.00	7.43
Ambient Conditions, Fire (April 2011)	8	43.75	15.53	5.49
Total	48	42.60	28.95	4.18

Table 30. Independent-samples t-test comparing the change in percent bare ground cover in response to the hydration and prescribed fire treatments.^b

Treatment Combination		N	Mean	Std. Deviation	Std. Error Mean	df	t	P-value
Percent Bare Ground Cover	Rainout Shelter, Fire (Sept. 2012)	8	81.25	15.06	5.32	14	-1.92	.076
	Ambient Conditions, Fire (Sept. 2012)	8	63.75	21.00	7.43			
	Rainout Shelter, Fire (April 2011)	8	26.25	18.47	6.53	14	2.051	.059
	Ambient Conditions, Fire (April 2011)	8	43.75	15.53	5.49			
	Rainout Shelter, No Prescribed Fire	8	5.63	4.17	1.48	14	5.545	.000
	Ambient Conditions, No Prescribed Fire	8	35.00	14.39	5.09			

b. Equality of variances assumed

APPENDIX C

CHAPTER VI SUPPORTING TABLES

Table 31. Descriptive statistics of the percent change in prickly pear canopy cover in response to the application of herbicide and prescribed fire treatments.

Treatment Combination	N	Mean	Std. Deviation	Std. Error
Vista, No Prescribed Fire	59	32.77	58.39	7.60
Vista, Fire (Feb. 2012)	104	-20.91	50.24	4.93
Surmount, No Prescribed Fire	86	43.04	79.17	8.54
Surmount, Fire (Feb. 2012)	76	-35.05	48.59	5.57
No Herbicide, No Prescribed Fire	84	33.57	50.09	5.47
No Herbicide, Fire (Feb. 2012)	95	-20.64	53.38	5.48
Total	504	3.29	65.15	2.90

Table 32. Analysis of variance for the percent change in prickly pear canopy cover in response to the application of herbicide and prescribed fire treatments.

	Sum of Squares	df	Mean Square	F	P-value
Between Groups	491200.309	5	98240.062	29.763	.000
Within Groups	1643743.644	498	3300.690		
Total	2134943.953	503			

Table 33. Independent-samples t-test comparing the percent change in prickly pear canopy cover in response to the application of herbicide and prescribed fire treatments.^b

	Treatment Combination	N	Mean	Std. Deviation	Std. Error Mean	df	t	P-value
Percent Change Cactus Cover	Vista, No Prescribed Fire	59	32.77	58.39	7.60	161	-6.18	.000
	Vista, Fire (Feb. 2012)	104	-20.91	50.24	4.93			
	Surmount, No Prescribed Fire	86	43.04	79.17	8.54	160	-7.45	.000
	Surmount, Fire (Feb. 2012)	76	-35.05	48.59	5.57			
	No Herbicide, No Prescribed Fire	84	33.57	50.09	5.47	177	-6.98	.000
	No Herbicide, Fire (Feb. 2012)	95	-20.64	53.38	5.48			

b. Equality of variances assumed

Table 34. Independent-samples t-test comparing the percent change in prickly pear canopy cover in response to the application of herbicide treatments in combination with prescribed fire treatments administered February 2012.^b

	Treatment Combination	N	Mean	Std. Deviation	Std. Error Mean	df	t	P-value
Percent Change	Vista, Fire (Feb. 2012)	104	-20.91	50.24	4.93	178	1.89	.060
Cactus Cover	Surmount, Fire (Feb. 2012)	76	-35.05	48.59	5.57			
	No Herbicide, Fire (Feb. 2012)	95	-20.64	53.38	5.48	197	.036	.971
	Vista, Fire (Feb. 2012)	104	-20.91	50.24	4.93			
	No Herbicide, Fire (Feb. 2012)	95	-20.64	53.38	5.48	169	1.82	.070
	Surmount, Fire (Feb. 2012)	76	-35.05	48.59	5.57			

b. Equality of variances assumed

Table 35. Independent-samples t-test comparing the percent change in prickly pear canopy cover in response to the application of herbicide treatments in the absence of prescribed fire.^b

	Treatment Combination	N	Mean	Std. Deviation	Std. Error Mean	df	t	P-value
Percent Change	Vista, No Prescribed Fire	59	32.77	58.39	7.60	143	-.850	.397
Cactus Cover	Surmount, No Prescribed Fire	86	43.04	79.17	8.54			
	No Herbicide, No Prescribed Fire	84	33.57	50.09	5.47	141	.088	.930
	Vista, No Prescribed Fire	59	32.77	58.39	7.60			
	No Herbicide, No Prescribed Fire	84	33.57	50.09	5.47	168	-.929	.354
	Surmount, No Prescribed Fire	86	43.04	79.17	8.54			

b. Equality of variances assumed

Table 36. Descriptive statistics of the mean standing herbaceous vegetation cover present on the plots before (July 2011) the establishment of the herbicide and prescribed fire treatments.

Treatment Combination	N	Mean	Std. Deviation	Std. Error
Vista, No Prescribed Fire	59	65.42	23.77	3.09
Surmount, No Prescribed Fire	89	69.78	23.51	2.49
No Herbicide, No Prescribed Fire	86	65.76	23.12	2.49
Vista, Fire (Feb. 2012)	106	66.79	22.88	2.22
Surmount, Fire (Feb. 2012)	76	66.71	19.38	2.22
No Herbicide, Fire (Feb. 2012)	96	59.43	26.50	2.70
Total	512	65.59	23.50	1.04

Table 37. Analysis of variance for the mean standing herbaceous vegetation cover present on the plots before (July 2011) the establishment of the herbicide and prescribed fire treatments.

	Sum of Squares	df	Mean Square	F	P-value
Between Groups	5457.879	5	1091.576	1.996	.078
Within Groups	276666.340	506	546.771		
Total	282124.219	511			

Table 38. Descriptive statistics of the percent change in herbaceous cover in response to the application of herbicide and prescribed fire treatments.

Treatment Combination	N	Mean	Std. Deviation	Std. Error
Vista, Fire (Feb. 2012)	106	-43.28	43.48	4.22
Vista, No Prescribed Fire	59	-29.84	89.03	11.59
Surmount, Fire (Feb. 2012)	76	-32.69	35.33	4.05
Surmount, No Prescribed Fire	89	-3.97	200.96	21.30
No Herbicide, Fire (Feb. 2012)	96	-28.11	66.32	6.77
No Herbicide, No Prescribed Fire	86	-30.74	36.75	3.96
Total	512	-28.38	98.09	4.34

Table 39. Analysis of variance for the percent change in herbaceous cover in response to the application of herbicide and prescribed fire treatments.

	Sum of Squares	df	Mean Square	F	P-value
Between Groups	78578.166	5	15715.633	1.644	.147
Within Groups	4838263.229	506	9561.785		
Total	4916841.395	511			

Table 40. Independent-samples t-test comparing the percent change in standing herbaceous vegetation cover in response to the application of herbicide and prescribed fire treatments.^b

	Treatment Combination	N	Mean	Std. Deviation	Std. Error Mean	df	t	P-value
Percent Change Herbaceous Cover	Vista, Fire (Feb. 2012)	106	-43.28	43.48	4.22	163	-1.30	.194
	Vista, No Prescribed Fire	59	-29.84	89.03	11.59			
	Surmount, Fire (Feb. 2012)	76	-32.69	35.33	4.05	163	-1.23	.221
	Surmount, No Prescribed Fire	89	-3.97	200.96	21.30			
	No Herbicide, Fire (Feb. 2012)	96	-28.11	66.32	6.77	180	.326	.745
	No Herbicide, No Prescribed Fire	86	-30.74	36.75	3.96			

b. Equality of variances assumed

Table 41. Independent-samples t-test comparing the percent change in standing herbaceous cover in response to the application of herbicide and prescribed fire treatments in early-February 2012.^b

	Treatment Combination	N	Mean	Std. Deviation	Std. Error Mean	df	t	P-value
Percent Change Herbaceous Cover	Vista, Fire (Feb. 2012)	106	-43.28	43.48	4.22	180	-1.75	.082
	Surmount, Fire (Feb. 2012)	76	-32.69	35.33	4.05			
	No Herbicide, Fire (Feb. 2012)	96	-28.11	66.32	6.77	200	1.940	.054
	Vista, Fire (Feb. 2012)	106	-43.28	43.48	4.22			
	No Herbicide, Fire (Feb. 2012)	96	-28.11	66.32	6.77	170	.543	.588
	Surmount, Fire (Feb. 2012)	76	-32.69	35.33	4.05			

b. Equality of variances assumed

Table 42. Independent-samples t-test comparing the percent change in standing herbaceous cover in response to the application of herbicide treatments in the absence of prescribed fire.^b

	Treatment Combination	N	Mean	Std. Deviation	Std. Error Mean	df	t	P-value
Percent Change Herbaceous Cover	Vista, No Prescribed Fire	59	-29.84	89.03	11.59	146	-.929	.354
	Surmount, No Prescribed Fire	89	-3.97	200.96	21.30			
	No Herbicide, No Prescribed Fire	86	-30.74	36.75	3.96	143	-.085	.933
	Vista, No Prescribed Fire	59	-29.84	89.03	11.59			
	No Herbicide, No Prescribed Fire	86	-30.74	36.75	3.96	173	-1.22	.226
	Surmount, No Prescribed Fire	89	-3.97	200.96	21.30			

b. Equality of variances assumed

Table 43. Descriptive statistics of the mean percent bare ground cover on the plots before (July 2011) the application of the herbicide and prescribed fire treatments.

Treatment Combination	N	Mean	Std. Deviation	Std. Error
Vista, No Prescribed Fire	59	4.92	6.05	.79
Surmount, No Prescribed Fire	89	4.94	4.09	.43
No Herbicide, No Prescribed Fire	86	3.37	3.79	.41
Vista, Fire (Feb. 2012)	106	6.04	7.71	.75
Surmount, Fire (Feb. 2012)	76	5.39	7.11	.82
No Herbicide, Fire (Feb. 2012)	96	4.43	5.07	.52
Total	512	4.87	5.88	.26

Table 44. Analysis of variance for the mean percent bare ground cover on the plots before (July 2011) the application of the herbicide and prescribed fire treatments.

	Sum of Squares	df	Mean Square	F	P-value
Between Groups	377.863	5	75.573	2.212	.052
Within Groups	17288.885	506	34.168		
Total	17666.748	511			

Table 45. Descriptive statistics of the mean percent bare ground cover on the plots after the application of the herbicide treatments in the absence of prescribed fire (March 2013).

Treatment Combination	N	Mean	Std. Deviation	Std. Error
Vista, No Prescribed Fire	59	19.66	17.54	2.28
Surmount, No Prescribed Fire	89	12.36	11.18	1.19
No Herbicide, No Prescribed Fire	86	12.44	14.59	1.57

Table 46. Independent-samples t-test comparing the mean percent bare ground cover in response to the application of herbicide treatments in the absence of prescribed fire (March 2013).^b

	Treatment Combination	N	Mean	Std.	Std. Error	df	t	P-value
				Deviation	Mean			
Percent Bare Ground Cover	Vista, No Prescribed Fire	59	19.66	17.54	2.28	146	3.09	.002
	Surmount, No Prescribed Fire	89	12.36	11.18	1.19			
	Vista, No Prescribed Fire	59	19.66	17.54	2.28	143	2.69	.008
	No Herbicide, No Prescribed Fire	86	12.44	14.59	1.57			
	Surmount, No Prescribed Fire	89	12.36	11.18	1.19	173	-.042	.967
	No Herbicide, No Prescribed Fire	86	12.44	14.59	1.57			

b. Equality of variances assumed

Table 47. Descriptive statistics of the mean percent bare ground cover on the plots in response to the application of herbicide and prescribed fire treatments (March 2013).

Treatment Combination	N	Mean	Std. Deviation	Std. Error
Vista, Fire (Feb. 2012)	106	29.95	21.15	2.05
Surmount, Fire (Feb. 2012)	76	25.20	19.55	2.24
No Herbicides, Fire (Feb. 2012)	96	23.91	18.51	1.89

Table 48. Independent-samples t-test comparing the mean percent bare ground cover on the plots in response to the application of herbicide and prescribed fire treatments (March 2013).^b

	Treatment Combination	N	Mean	Std.	Std. Error	df	t	P-value
				Deviation	Mean			
Percent Bare Ground Cover	Vista, Fire (Feb. 2012)	106	29.95	21.15	2.05	180	1.543	.125
	Surmount, Fire (Feb. 2012)	76	25.20	19.55	2.24			
	Surmount, Fire (Feb. 2012)	76	25.20	19.55	2.24	170	.443	.658
	No Herbicide, Fire (Feb. 2012)	96	23.91	18.51	1.89			
	Vista, Fire (Feb. 2012)	106	29.95	21.15	2.05	200	2.152	.033
	No Herbicide, Fire (Feb. 2012)	96	23.91	18.51	1.89			

b. Equality of variances assumed

Table 49. Descriptive statistics comparing the mean percent bare ground cover on the plots with different prescribed fire treatments in response to the application of herbicides (March 2013).

Treatment Combination	N	Mean	Std. Deviation	Std. Error
Vista, No Prescribed Fire	59	19.66	17.54	2.28
Surmount, No Prescribed Fire	89	12.36	11.18	1.19
No Herbicide, No Prescribed Fire	86	12.44	14.59	1.57
Vista, Fire (Feb. 2012)	106	29.95	21.15	2.05
Surmount, Fire (Feb. 2012)	76	25.20	19.55	2.24
No Herbicide, Fire (Feb. 2012)	96	23.91	18.51	1.89
Total	512	20.93	18.71	.83

Table 50. Analysis of variance for the mean percent bare ground cover on the plots with different prescribed fire treatments in response to the application of herbicides (March 2013).

	Sum of Squares	df	Mean Square	F	P-value
Between Groups	23692.442	5	4738.488	15.455	.000
Within Groups	155141.884	506	306.605		
Total	178834.326	511			

Table 51. Independent-samples t-test comparing the mean percent bare ground cover on the plots with different prescribed fire treatments in response to the application of the herbicide (March 2013).^b

	Treatment Combination	N	Mean	Std. Deviation	Std. Error Mean	df	t	P-value
Percent Bare Ground Cover	Vista, No Prescribed Fire	59	19.66	17.54	2.28	163	3.18	.002
	Vista, Fire (Feb. 2012)	106	29.95	21.15	2.05			
	Surmount, No Prescribed Fire	89	12.36	11.18	1.19	163	5.27	.000
	Surmount, Fire (Feb. 2012)	76	25.20	19.55	2.24			
	No Herbicide, No Prescribed Fire	86	12.44	14.59	1.57	180	-4.6	.000
	No Herbicide, Fire (Feb. 2012)	96	23.91	18.51	1.89			

b. Equality of variances assumed