

THE ROLE OF FIRE AND A NONNATIVE GRASS AS DISTURBANCES
IN SEMI-DESERT GRASSLANDS OF SOUTHEASTERN ARIZONA

by

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DEDICATION

To Eric Albrecht who is graduating along with each of us.

To Elizabeth and Zachary who are his life.

&

To Jane and Carl who brought me to Arizona.

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ABSTRACT

Disturbances are key processes that alter environmental conditions which have consequences for species interactions; therefore, disturbances are important to maintenance of biological diversity. Climate, fire, livestock grazing, introduction of nonnative species, and humans all influence semi-desert grasslands of the southwestern United States. In southeast Arizona, a nonnative perennial grass, Lehmann lovegrass (*Eragrostis lehmanniana*), was introduced in the 1930s in an effort to restore degraded rangelands. I quantified annual fluctuations of Lehmann lovegrass and the response of native plants along a gradient of dominance by this nonnative grass. Biomass and richness of native plants declined with increasing dominance by Lehmann lovegrass. Substantial increases in biomass by Lehmann lovegrass in response to above-average rainfall did not result in decreases in native plants. Fire is an important disturbance in semi-desert grasslands. Herbaceous plants are favored over trees and shrubs in areas with frequent fires, therefore fire maintains grassland physiognomy. Humans have manipulated natural fire regimes however, by altering their frequency, season, and spatial extent. I experimentally investigated the possibility of a positive feedback cycle in grasslands invaded by Lehmann lovegrass by assessing whether the presence of Lehmann lovegrass was enhanced by fire to the detriment of native plants. In the two years post-fire, the proportion of Lehmann lovegrass on burned sites did not increase compared to unburned sites or to pre-fire conditions. I also detected no changes in species richness,

diversity, or biomass of native plants in response to fire for 2-3 years after fires. Changes in biomass of all plants varied among years, especially due to exceptionally wet conditions during spring 2001, and varied if fires were set in spring versus summer. Lastly, I investigated the response of *Agave palmeri* to fire, a species that provides forage for a migratory bat that is federally endangered. Survival of agave varied with soil type, fire season, and size of the plant. In general, agave can tolerate up to 85% damage before mortality. Germination of agave seed was decreased by fire. Based on my research, I recommend setting fire at natural frequency and season for the maintenance of semi-desert grasslands.

CHAPTER 1. INTRODUCTION

Disturbances are key ecological processes that alter environmental conditions and species interactions and therefore are important to maintenance of biological diversity (Whittaker 1975, Huston 1994). Disturbances may positively affect diversity by releasing resources such as space or nutrients (Connell 1978, Petraitis et al. 1989) and by creating structural mosaics on the landscape (Turner et al. 1993). Additionally, disturbances act as drivers of evolutionary change (Hoffman and Parson 1991, Ackerly 2003, Gutschick and BassiRad 2003). Disturbances may be characterized by their frequency, intensity, timing, and extent (White and Pickett 1985, van der Maarel 1993) and community composition may vary in response to the relative magnitude of each characteristic (Hobbs and Huenneke 1992). Substantial modification of existing disturbance regimes may result in undesirable or unpredictable changes to ecosystems (Mack and D'Antonio 1998). Humans have influenced disturbance regimes via suppression (e.g., fire), escalation (e.g., flooding due to increased runoff), and introduction (e.g., nonnative species).

Fire regimes (both anthropogenic and naturally-ignited) and the human-caused introduction of nonnative species are among the most influential drivers of ecological change. Fire, under its natural regime, is thought to be important in maintaining grassland physiognomy and diversity by limiting recruitment and spread of woody plants (McPherson 1997). One of a variety of ways that nonnative species often reduce diversity by occupying niches once held by native species (Shea and Chesson 2002). These two

disturbances can interact in complex and unexpected ways. Disturbance may facilitate invasion by nonnative species (Ewel 1986, Hobbs 1989, 1991, Rejmanek 1989), for example, invasion varied with fire season (Hobbs and Atkins 1990). Thus, in a system where fires naturally occurred at a particular frequency and time of year, and thereby maintained a certain plant community, a critical question for conservation biologists is: How do human alterations to the fire regime and the introduction of nonnative species affect community structure?

In grasslands of the southwestern United States, plant communities have been altered significantly by the lack of fire and introduction of various nonnative species (particularly African grasses) that have interacted to change structure of the plant community (McPherson and Weltzin 2000). A lack of fire along with grazing, another major anthropogenic disturbance in these ecosystems, has allowed the abundance of woody plants, such as mesquite species to increase (Archer 1989). Diminished herbaceous cover and reduced fire occurrence, intensity, and spread have created a positive feedback by reducing competition by grasses for water and nutrients and enhancing colonization and establishment of seedlings of woody plants (Archer 1989). At the same time, introduction of nonnative grasses has increased abundance of herbaceous biomass, which may have reduced richness of native species. Additionally, fire may enhance the dominance and spread of these species over native species (Bock et al. 1986, D'Antonio and Vitousek 1992). As conservation practitioners attempt to maintain diversity in these systems, they are faced with the dilemma of restoring ecologically

important processes such as fire at the appropriate season while reducing the impact of nonnative grasses.

The impetus for this project was provided by land managers faced with the challenge of restoring desired physiognomy and disturbance regimes while minimizing the impact of nonnative grasses in semi-desert grasslands in southern Arizona. A century of overgrazing, fire suppression, and introduction of nonnative grasses had modified these ecosystems. Notably, Lehmann lovegrass (*E. lehmanniana*) was brought in by the Soil Conservation Service in the 1930s to stabilize soils on degraded rangeland (Crider1945). The grass has subsequently spread to undisturbed native grasslands and replaced native species as the dominant cover.

In addition to changes in grassland diversity associated with Lehmann lovegrass, woody plant cover has increased and contributed to decreased cover of herbaceous species during the last 130 years. Thus, conservation practitioners wanted to reintroduce fire as a natural process to aid suppression of woody plants and restore ecosystems to dominance by native grasses. However, at least two conflicts have arisen in conjunction with reintroducing fire: (1) lack of knowledge about the response of plant communities and plant species to altered fire occurrence and season and (2) the threat of encouraging spread of Lehmann lovegrass, a species that evolved in a fire-prone system.

The goal of this research was to investigate how these disturbances affect grassland plant communities. To meet this goal I investigated how fire season and abundance of a nonnative grass acted as drivers of change in plant communities in semi-

desert grasslands. My objectives were to (1) describe the dynamics of Lehmann lovegrass over time and the resulting effects on native plant community structure, (2) investigate potential interactions between Lehmann lovegrass and fire season and the influence on native plant communities, and (3) determine the influence of fire on survival of a locally important species, Palmer agave, *Agave palmeri*, at various life-stages. For each of these objectives I attempt to provide potential management recommendations given presence of a nonnative grass and protected species.

Chapter 2 provides an overview of the approaches used in the study and its most important findings. The methods, results, and conclusions of this study are presented in the papers appended to this dissertation: Chapter 3 focuses on the first objective, Chapter 4 focuses on the second objective, and Chapter 5 focuses on the third objective.

CHAPTER 2. PRESENT STUDY

In the papers appended to this dissertation I describe the methods, results, and conclusions of my research. As a whole, these three studies address the roles of fire and invasion by a nonnative grass as disturbances by measuring their effects on native plant species and communities. My goals are to contribute to the existing body of ecological theory and to provide guidance for practical applications to land management.

Appendix A – “Effects of invasion by a nonnative grass on native plant species and communities”

Nonnative species have been linked to declines in diversity of native species in virtually all ecosystems (Vitousek et al. 1997, Wilcove et al. 1998). Climate may be critical to the spread and establishment of introduced species, especially in semi-arid areas. In these systems, germination and growth are episodic, as rainfall is both limiting and sporadic. In grasslands of the southwestern U.S., for example, Lehmann lovegrass (*Eragrostis lehmanniana*), a perennial grass from South Africa, has been associated with low native biodiversity (Cable 1971, Bock et al. 1986). I quantified variability in presence and abundance of native grasses and herbaceous dicots as they related to changes in biomass of Lehmann lovegrass over a five-year period. I sampled during two seasons, in spring (April) to capture the growth of plants that respond primarily to winter

rainfall and during fall (September) to measure peak standing biomass of plants that grow in response to summer rainfall. I selected three sites in each of three plant community types: native (< 20% biomass of *E. lehmanniana*), mixed (40-60% biomass of *E. lehmanniana*), and nonnative (>60% biomass of *E. lehmanniana*). I compared community structure to variation in precipitation during the study.

Increased dominance of Lehmann lovegrass was always associated with a reduction in richness and diversity of native plants. Transient species—those present only during 1-2 years of the study—were important contributors to grassland diversity and were uncommon on plots dominated by Lehmann lovegrass compared to those dominated by native grasses. Although biomass of Lehmann lovegrass increased substantially in 2001, biomass of native species also increased, which suggests they were able to access resources despite dominance by this nonnative grass. Patterns in growth of native and nonnative grasses suggest a difference in the use of seasonal precipitation. Biomass of native grasses increased substantially after early-summer precipitation in 2000 but then was reduced, presumably by interference, when native herbaceous dicots responded in 2001 to abundant winter and spring rainfall. In contrast, Lehmann lovegrass responded little to length of the extended summer rains but instead increased in response to the same cool-season rains that favored herbaceous dicots. Lehmann lovegrass was more common on clayey soils compared to loamy soils found in floodplains or on slopes of limestone parent material where native plants were more common. I observed Lehmann lovegrass spreading to areas where the grass had not been present at the start of the study.

Appendix B - “The role of fire and a nonnative plant as disturbances in semi-desert grasslands”

Fire is one of several ecological processes important in maintaining grassland physiognomy by favoring survival of grasses over woody plants. Although fire helps maintain structure of grasslands, the presence of nonnative grasses may alter fire regimes and alter the structure of the existing plant community. Nonnative grasses may contribute to a positive feedback cycle that alters the extent, frequency, or intensity of fire and that favors nonnative over native plants. Humans contribute to alterations to fire regimes and alter the timing of fires compared to timing of natural fires. In southeastern Arizona, the threat of Lehmann lovegrass contributing to a positive feedback cycle complicates the reintroduction of fire as an ecological process in these systems.

I quantified changes to biomass, species richness, and diversity of native plant communities to dominance of *E. lehmanniana* in the presence of prescribed fire using a large-scale experiment. I selected sites along a gradient of dominance by Lehmann lovegrass that were burned in either spring or summer or left unburned. I investigated the importance of year by conducting the experiment in 2001 and in 2002. The response of plant communities depended on the interaction between year and fire season, perhaps because intensity of fire varied with conditions at the time of fire such as moisture availability in the months preceding and following the fires. Two years post-fire, biomass

on burned and unburned plots were similar because biomass on unburned plots had declined over time due to drought. In contrast to studies that report positive feedbacks between fire and nonnative grasses (e.g., D'Antonio and Vitousek 1992), I found that fire did not influence abundance or dominance by Lehmann lovegrass at least during the course of this study. Lehmann lovegrass did increase on some plots, however, regardless of fire treatment suggesting that spread of this species has not ceased.

Appendix C – “Does fire affect germination and survival of *Agave palmeri*?”

Management of ecosystems can be a complex task and practical constraints may force managers to apply fire in a way that differs from the frequency, timing, or extent of natural fires that typically occurred during a hot, dry period between May and June. Plants can survive fire either through tolerance (e.g., protective tissue, enhanced seed germination, ability to re-sprout) or avoidance (e.g., inhabit areas unlikely to burn, complete reproductive cycle faster than fire frequency). Persistence of many species in these systems may be reduced when the fire regime with which they evolved is altered. Palmer agave (*Agave palmeri*) is thought intolerant of fire because it does not have protective tissue such as thick bark nor does it re-sprout after fire or reproduce vegetatively. Palmer's agave is an important species because it is a primary food source for the federally endangered lesser long-nose bat (*Leptonycteris curasoae yerbabuena*) and is part of the 'nectar corridor' used by some animals during migration (Nabhan 2004).

To assess the effects of fire on agave I monitored survival and germination of agave before and 1-2 years after prescribed fires and on control plots in spring and summer. Fires affected agave directly by destroying tissue and potentially indirectly by altering microclimate on two distinct soil surfaces that agave inhabit and making conditions unfavorable to survival. Agave survived up to 85% damage to leaves before dying regardless of plant height, fire season, or soil surface. The probability of survival increased with plant size. The influence of fire on survival of plants taller than 30 cm was minimal (provided the plants had less than 85% damage). Survival of agave shorter than 30 cm on burned plots generally was reduced by 50% compared to survival on unburned plot however, survival of agave burned in summer on Carbine soils was 75%.

Germination of agave seeds was lower on burned compared to unburned plots, higher on soils with more clay content, and was higher in 2004 than 2003 probably because of more available moisture in the soil for all three factors. Fires, particularly in spring, may affect germination and survival of agaves. Because many small agave survive in areas that are burned by avoiding fire or tolerating fire damage, fires lit during seasons and at frequencies of the natural fire regime are not likely to negatively impact agave across the landscape.

Summary

Ecosystems contain unique assemblages of species with a shared evolutionary history. Disruptions to abiotic and biotic components of an ecosystem may have profound

consequences to ecosystem structure and processes if they represent a force outside of that evolutionary history (Mooney and Cleland 2001, Callaway et al. 2004). In semi-desert grasslands, introduction of Lehmann lovegrass produces novel interactions for native plants including alterations to fire regime that may represent disturbances that are beyond the physiological limits of some plants. The main conclusions of my dissertation research about fire and a nonnative grass in semi-desert grasslands are:

- Increased dominance by Lehmann lovegrass was associated with declines in species richness and abundance of native plants, although annual fluctuations in biomass of Lehmann lovegrass did not affect the relative proportions of total biomass nor did it limit increases in native dicots responding to above-average rainfall.
- There was no evidence of a positive feedback cycle between fire and Lehmann lovegrass in these grasslands 2-3 years post-fire. Fire reduced biomass for at least 3 seasons post-fire but only influenced richness and diversity of native plants one season post-fire.
- Fire reduced survival of agave <30 cm and the germination of agave seeds. Fires in spring had a greater impact on germination and survival on some soils than summer fires, perhaps due to the extended time soils were exposed before the arrival of summer rains.

The future distribution of Lehmann lovegrass in semi-desert grasslands will be a result of interactions among the environment, native species, and human activities (Mau-

Crimmins et al. 2006, Schussman et al. 2006). Fire has been a natural force shaping the plant communities in semi-desert grasslands and can continue to act as a disturbance important to biological diversity (McPherson 1995).

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APPENDIX A

**EFFECTS OF INVASION BY A NONNATIVE GRASS ON NATIVE PLANT
SPECIES AND COMMUNITIES IN SEMI-DESERT GRASSLANDS**

ERIKA L. GEIGER

(To be submitted to Biological Invasions)

Abstract

Nonnative species have been linked to declines in diversity of native species in virtually all ecosystems. Climate may be critical to the spread and establishment of introduced species, especially in semi-arid areas. In these systems, germination and growth are episodic, as rainfall is both limiting and sporadic. In grasslands of the southwestern U.S., for example, Lehmann lovegrass (*Eragrostis lehmanniana*), a perennial grass from South Africa, has been associated with low native biodiversity. I quantified variability in presence and abundance of native grasses and herbaceous dicots as they related to changes in biomass of Lehmann lovegrass over a five-year period. I predicted that annual fluctuations of Lehmann lovegrass biomass would drive changes in richness, diversity and biomass of native plant species. Increased dominance of Lehmann lovegrass was always associated with a reduction in richness and diversity of native plants. Transient species—those present only during 1-2 years of the study—were important contributors to grassland diversity and were uncommon on plots dominated by Lehmann lovegrass compared to those dominated by native grasses. Although biomass of Lehmann lovegrass increased substantially in 2001, biomass of native plant species also increased, which suggests they were able to access resources despite dominance by this nonnative grass. Patterns in growth of native and nonnative grasses suggest a difference in the use of seasonal precipitation. Shifts in relative proportion of Lehmann lovegrass were site-specific and were not linked to any measured factor.

Introduction

Invasion and dominance by nonnative organisms often results in reduced species diversity and richness and subsequent alteration of ecological processes (D'Antonio and Vitousek 1992). Areas of high diversity tend to support uncommon species that may have important roles (Lyons et al. 2005) such as acting as keystone species or buffers to disturbance and climate (e.g., Yachi and Loreau 1999). Consequently, community heterogeneity across a landscape may be dampened by reducing variability linked to soil types, climatic fluctuations, and large-scale disturbances such as grazing and fire. The influence of dominant species on species diversity and productivity has been studied intensely in mesic grasslands (e.g., Tilman et al. 1996, Aarssen 1997, Hooper and Vitousek 1997, Tilman 1997). In those systems, areas dominated by a few species have high year-to-year variation in total aboveground biomass of plant communities (Tilman 1996). However, annual variation of species abundances is not stabilized by richness, which highlights the importance of species composition in plant communities (Tilman 1996, 1999). Although the cause of the diversity-stability relationship may be explained as a statistical artifact more than a result of competition or other factors (Doak et al. 1998), the effects of temporal variability on community structure and processes are still being explored.

In savannas of the southwestern United States, a nonnative perennial grass from South Africa, Lehmann lovegrass (*Eragrostis lehmanniana*), was introduced in the 1930s to restore rangelands that had lost perennial grass cover (Cox and Ruyle 1986).

Contemporary scientific consensus suggests that the presence of Lehmann lovegrass exerts considerable control over structure, function, and variability in many of these rangeland systems. For example, dominance by Lehmann lovegrass is associated with declines in native plants and animals (Cable 1976, Bock et al. 1986). Lehmann lovegrass produced about four times as much green biomass as native species (Cox et al. 1990). Additionally, Lehmann lovegrass maintained a maximum relative growth rate under drought conditions and produced twice the biomass in one quarter the time compared to native grasses under well-watered conditions (Fernandez and Reynolds 2000). Unlike native perennial grasses that respond primarily to summer rains (Cable 1969), Lehmann lovegrass remains photosynthetically active all year (Bridges 1941, Cox 1984) and because of its high lignin content (C:N ratio), leaf litter decomposes slowly (Cox et al. 1990). Lehmann lovegrass also may receive indirect advantages of many native species through its differential responses to disturbance and human activities. For example, livestock have been observed to selectively graze native grasses over Lehmann lovegrass favoring increased dominance and reduced diversity (Cable 1971). While many studies of Lehmann lovegrass invasion have explored grassland composition at a single point in time, few studies have described the interactions of native species and Lehmann lovegrass over time to reveal potential shifts in year-to-year variability.

In a paper titled “Why ecology fails at application: should we consider variability more than regularity?” Hansson (2003) argues that ecologists should embrace the diversity of ecological outcomes and seek to reveal possible distinctive states or locations

in habitat, climatic, or geographical gradients. However, most ecological research is constrained by lack of knowledge about the range of variability within a community or population. Additionally, variability is specific to the metric of interest and sensitive to temporal and spatial scales (Collins 2000). Baseline information about inherent variability of the system is required to determine whether response to a treatment is consequential. Knowing the background variability of plant community responses to seasonal fluctuations or frequent perturbations may highlight changes outside the range of variability that may indicate distinct transitions, states, and thresholds (*sensu* Archer 1989, Westoby et al. 1989, Lockwood and Lockwood 1993, Schroeder et al. 2005). Ideally a measure of variability is encompassed by data collected over several decades to reveal extremes, perhaps enabling the researcher to determine when and where these thresholds or unique states occur.

The purpose of this paper is to describe the variability of species diversity and abundance in southern Arizona savannas over a period of five years. I assessed this variability across a gradient of dominance by Lehmann lovegrass (community type) to determine if average total biomass, biomass of functional groups, richness, or diversity was also distinct among community types or if it moved in response to the proportion of Lehmann lovegrass. I predicted that annual fluctuations of Lehmann lovegrass biomass would drive changes in richness, diversity and biomass of native plant species.

Methods

Study sites

I monitored plant communities in the grasslands and mesquite (*Prosopis velutina* Woot.) savannas flanking the northern and eastern base of the Huachuca Mountains (31° 34' N, 110° 26' W) of southern Arizona (Figure A.1). Elevations range from 1420 to 1645 meters. Average annual precipitation between 1998 and 2003 was 347 mm; the long-term average is 379 mm (Fort Huachuca Military Reservation climate records). About two-thirds of the total annual rain arrives between May and September in intense local events known as “monsoons” and one-third falls between October and April. The region is characterized by a hot, dry period in May and June prior to the onset of the monsoons when natural fires occur.

I selected sites on Fort Huachuca Military Reservation (FHMR), an active installation of the U.S. Army characterized by the absence of livestock and frequency of fires similar to pre-Anglo settlement (McPherson 1995). Few livestock have grazed at FHMR since the late 1800s, and livestock have been excluded completely since 1950. Therefore, in conjunction with regular ignition sources from military training activities, adequate fine fuels allowed for a fire frequency higher than on surrounding areas. This land use history probably contributes to a greater abundance of perennial grasses and fewer woody species at FHMR than surrounding lands, which were subject to decades of livestock grazing and fire suppression.

I established 18 1-ha plots within 3 types of grassland communities, representing a gradient of plant invasion. “Nonnative” sites were grasslands dominated by Lehmann lovegrass (*Eragrostis lehmanniana* Nees). “Native” sites were grasslands dominated by native perennial caespitose grasses including *Aristida* spp., *Bothriochloa barbinodis* (Lag.) Herter, *Bouteloua* spp., *Digitaria californica* (Bentham) Henrickson, *Eragrostis intermedia* A. S. Hitchc., and *Panicum* spp. “Mixed” sites were grasslands composed of a mix of nonnative and native species. I classified sites based on visual surveys *a priori* and generally these designations were accurate for the duration of the study. One plot was burned by a wildfire in the summer of 2002 and I replaced it with a new plot 300 m away that had a lower proportion of Lehmann lovegrass than the original plot. I focused exclusively on grassland composition and did not attempt to control for land-use history, except that, I avoided locating plots an area burned in 1998. No plot had burned for at least 9 years before the start of the present study.

Plots were located on 4 classes of range sites: limy slopes, loamy bottom swales, sandy loam uplands, loamy uplands. A range site is a description of land based on soil, relief, climate, and a distinct plant community (Natural Resources Conservation Service 2000, p. 324). Limy slopes are loamy, mixed, superactive, thermic, shallow Petrocalcic Calciustolls (NRCS 2000, p. 47) found on 3-30% hill slopes. Soils are shallow to moderately deep (13-50 cm), covered with 20-45% gravel and/or cobble, are well-drained with moderately rapid permeability, runoff potential is medium to very high, available water holding capacity (AWHC) is very low. Loamy bottom swales are located in

floodplains that grade into uplands. Slopes generally are less than 5% and sites accumulate water and sediment runoff from surrounding uplands. Soils are a complex of fine-loamy, mixed, superactive, thermic Aridic Haplustalfs and coarse-loamy, mixed, superactive, thermic Pachic Halpustolls (NRCS 2000, pp. 101-2). Soils are deep (1.5 m or more) and well-drained, have moderately slow permeability, moderate or high AWHC. Plots located on fan terraces are classified as loamy upland or sandy loam upland sites. These range sites have deep (1.5 m or more), well-drained soils and are distinguished by their soil surface layer, which will not exceed 10 cm on loamy uplands but are 10-30 cm on sandy loam uplands. The range sites are composed of fine, mixed, superactive, thermic Aridic Paleustalfs on slopes of 0-45% and fine, mixed, superactive, thermic Ustic Haplargids on slopes of 1-30% (NRCS 2000, pp. 173-6, 184-5). These soils are well-drained, have moderate to high AWHC, slow permeability, and runoff potential is variable due to the range of slopes. Some range sites are characterized by 5-30% cobble and/or gravel on the soil surface. Lehmann lovegrass often dominates these two range sites.

I collected aboveground biomass in September, after the summer rains when a majority of plants achieve peak standing biomass. I clipped plants rooted in 25, 1-m x 0.5- m quadrats randomly located in 1-ha plots from 1999 to 2003. I did not sample locations if they coincided with previously clipped quadrats or were inaccessible because they were beneath dense tree canopies. I harvested by species at 2.5 cm above the ground for perennial grasses and at ground level for all other vegetation. Also, I collected litter,

which I defined as plant biomass that was detached and lying on the ground. Samples were oven-dried at 65 °C for 48 hours and weighed to the nearest 0.1 g.

To assess changes in plant community composition before the current study I obtained unpublished data collected on Fort Huachuca in 1985 (n = 9) and 1991 (n = 24) from the Natural Resources Conservation Service (NRCS). Only two sampling sites directly overlapped our plots although many were located within 500 m of our plots and all were within the same four range sites listed above. The data are not directly comparable because our biomass samples were oven-dried and NRCS samples were air-dried. However, based on a comparison of grassland samples air-dried and oven-dried (65 °C for 24 hours); samples lost an additional 4.2% of total air-dried weight (unpublished data). Also, sampling units were not the same size so I determined a relative value for each species (i.e., the relative contribution of that species' weight to total weight of the sampling area).

Analysis

I used PCA of the variance-covariance matrix to explore trends in plant communities over the 5-year sampling period and, compared these assemblages to NRCS assessments from 1985 and 1991. Additionally, I calculated community metrics for each plot: average biomass of plant lifeform (nonnative grass, native grass, and herbaceous dicot), richness (number of unique species), diversity (Simpson's c and Shannon's H), and proportion of Lehmann lovegrass to total biomass for each of the 5 sampling years.

Because I was unable to determine species-specific sources of litter, it was not included in calculation of total biomass. Simpson's (c) and Shannon's (H) Indices were correlated ($r^2=0.98$, $p<0.0001$) therefore I report only Simpson's index. I analyzed data using repeated-measures analysis of variance with community metrics as the response variables and plant community type (nonnative, mixed, native) as the explanatory variable. I transformed biomass of functional type values using the square root, biomass of Lehmann lovegrass using natural log, and proportion of Lehmann lovegrass using arcsine square root. Results are presented with raw means and standard errors. I used a repeated-measures mixed model analysis of variance with an autoregressive 1 covariance matrix structure with community type as a random variable and all others as fixed. I excluded data from 1999 from analysis because of a difference in sampling dates, however these data are shown in figures.

Results

Composition of native plant communities was similar over time; plots exhibited small changes between 1999 and 2003 based on component scores from Principal Components Analysis on the correlation matrix. Additionally, dominance by Lehmann lovegrass changed little on plots over time based on PCA on the variance-covariance matrix (Figure A.2). The first axis explained 58% of the variation on plots between 1999-2003; plots primarily ordinated along the first axis according to amount of Lehmann lovegrass. The second axis only explained only an additional 8.4% of the variation but

shows a clear separation of high-biomass and low-biomass native plots with distinct plant assemblages. Additionally, current composition of plant communities and dominance by Lehmann lovegrass did not differ from composition in 1985 or 1991 based on a comparison with data collected by the NRCS (see dispersion of gray circles in Figure A.2)

Total Biomass of plant communities

Average total biomass was lowest on native plots ($230.1 \pm 55.7 \text{ gm}^{-2}$), intermediate on mixed plots ($289.0 \pm 80.5 \text{ gm}^{-2}$), and highest on nonnative plots ($356.1 \pm 91.9 \text{ gm}^{-2}$) ($F_{2,15} = 7.48$, $P=0.0056$) (Figure A.3). Average total biomass varied over time ($F_{3,45} = 17.15$, $P < 0.0001$) although all community type responded similarly to annual variation ($F_{6,45} = 1.86$, $P = 0.11$). Biomass of all community types increased during the first 2 years of the study (2000: 265.6 ± 73.5 , 2001: 345.6 ± 91.8) and declined after 2001 (2002: 307.8 ± 90.5 , 2003: 247.8 ± 85.3) ($F_{2,15} = 16.94$, $P < 0.0001$) (Figure A.3, A.4a).

Biomass by Functional type

Although communities responded similarly to changes in precipitation, the functional types (annual grasses, dicots, native grasses, and Lehmann lovegrass) contributing to these changes varied across community type over time ($F_{24,221} = 1.92$, $P=0.008$) (Figure A.3). In 2001, herbaceous dicots contributed significantly to increases in biomass on native plots and to a lesser degree on mixed plots whereas Lehmann

lovegrass was the primary contributor to increases in biomass on nonnative plots.

Deviation of average biomass from the 5-year average was greater on nonnative and mixed plots than native plots (Figure A.4a).

Lehmann lovegrass

On most plots, the biomass of Lehmann lovegrass did not increase or decrease over the course of the study; the only significant change in biomass was an increase on native plots during the final year of the study. Lehmann lovegrass consistently drove a gradient of high biomass on nonnative plots ($276.6 \pm 85.7 \text{ g m}^{-2}$) to intermediate biomass on mixed plots ($157.8 \pm 94.5 \text{ g m}^{-2}$) and low biomass on native plots ($12.4 \pm 10.6 \text{ g m}^{-2}$) ($F_{2,15} = 80.06$, $P < 0.0001$, Figure A.3). However, biomass on mixed plots was not significantly different from nonnative plots and there was large variability within nonnative and mixed community types (Figure A.4b).

Native Grasses

Native grass biomass differed across community types but did not differ across years (Figures A.3, A.4c). Plots dominated by native grasses were located on two range sites (Figures A.1 and A.2) and over the 5-year study, biomass on limy slopes averaged $79 \pm 6 \text{ g m}^{-2}$ whereas biomass on loamy bottoms averaged $149 \pm 15 \text{ g m}^{-2}$. Additionally, loamy bottom swales differed from the mean by nearly 50 g m^{-2} (140 ± 8 vs. $93 \pm 10 \text{ g m}^{-2}$) in 2000.

Herbaceous Dicots

Biomass of herbaceous dicots was greater on native plots than mixed and nonnative plots and increased substantially on all plots in 2001 through 2002 compared to 2000 and 2003 (Figure A.3). Dicots show a distinct deviation from the 5-year mean on all plots in 2001 (above average) and deviated on native plots in 2000 (below average) (Figure A.4d).

Percent of Lehmann lovegrass

Biomass of Lehmann lovegrass was highly correlated with proportion up to about 70% where the biomass can fluctuate widely for a given proportion. Percent Lehmann lovegrass biomass of total biomass did not differ significantly over time within community types, but proportion did differ across community types (Figure A.5). Proportion over the five-year period averaged $76.8 \pm 11.2\%$ (mean \pm SE) on nonnative plots, $51.3 \pm 19.7\%$ on mixed plots and $3.8 \pm 4.7\%$ on native plots ($F_{2,15}=72.12$, $P<0.0001$). However, proportion varied greatly across plots within a given year (Figure A.5b); variability was greatest in mixed plots, except in 2001.

Richness and Diversity

Richness and diversity declined with increasing proportion of Lehmann lovegrass (Figure A.6). Richness was highest on native plots (7.6 ± 1.6), intermediate on mixed

plots (6.1 ± 1.7), and lowest on nonnative plots (5.0 ± 1.7) ($F_{2,15} = 13.89$, $P = 0.0004$) (Figure A.7a). Average richness per plot varied among years; richness was greater in years 2001 and 2002 (7.4 ± 1.0 ; 6.7 ± 2.2) than years 2000 and 2003 (5.4 ± 2.0 ; 5.0 ± 1.7) ($F_{3,45} = 11.66$, $P < 0.0001$). There was evidence of an interaction between year and community type: in 2002, richness on native plots was 9.0 ± 0.9 compared to 6.3 ± 1.2 on mixed and 4.8 ± 1.9 on nonnative plots; in 2003 richness on nonnative plots (3.2 ± 0.6) dropped far below mixed (5.5 ± 1.5) and native (6.3 ± 0.8) plots ($F_{6,45} = 2.05$, $P = 0.0787$).

Diversity (1-c) varied by year ($F_{3,45}=17.87$, $P < 0.0001$) and by community type ($F_{2,15}=32.32$, $P < 0.0001$) (Figure A.7b). Diversity increased from 0.35 ± 0.13 in 2000 to 0.45 ± 0.12 in 2001, dropped slightly in 2002 to 0.41 ± 0.15 and returned to initial levels at 0.34 ± 0.12 in 2003. Diversity was highest on native plots (0.51 ± 0.07), intermediate on mixed plots (0.39 ± 0.10), and lowest on nonnative plots (0.25 ± 0.08).

Discussion

Changes in plant community richness, diversity, average total biomass, and individual species responses varied with the proportion of Lehmann lovegrass on a plot and year. Despite distinct differences in community-level metrics across community types (native, mixed, nonnative), all community-level metrics showed similar increases in 2001. Variability of nonnative grasses, native grasses, and herbaceous dicots was associated with their relative abundance on plots and this relationship also influenced

variability of average total biomass. The most distinct occurrences over the course of the study were the increase of native grasses in response to an unusual pattern of summer rainfall in 2000 and the increase of Lehmann lovegrass grass on mixed and nonnative plots and native herbaceous dicots on all plots in fall 2001 after an above-average winter rainfall. Comparisons of native- and nonnative-dominated communities are inextricably confounded by soils. Lehmann lovegrass tends to spread and dominate on sandy or sandy loam soils (Cox and Ruyle 1986). In the area where I carried out my research, presence of Lehmann lovegrass was linked tightly to range site. Lehmann lovegrass was found almost exclusively on sandy loam uplands and loamy uplands whereas native plants dominate on loamy bottoms and limy slopes (range sites are described in methods section).

Changes in richness and diversity closely tracked with changes in total biomass and proportion of Lehmann lovegrass. The increase in richness and diversity in 2001 primarily resulted from the appearance of new species (especially species in the composite family) and secondarily resulted from increased frequency and abundance of existing species. Richness continued to increase in 2002 (mostly herbaceous dicots), however, these species contributed very little biomass relative to other more common species thus diversity declined in 2002. Species that appeared in 2001 tended to persist only one year and those that persisted for two years exhibited reduced frequency and abundance during the subsequent year. The lowest variability in richness occurred in 2001 and plots were more variable across years than communities.

While there were increases in the richness and diversity in 2001 relative to previous years on nonnative plots there was also a consistent trend maintained over the five-year period that plots with more Lehmann lovegrass contain fewer species than plots without Lehmann lovegrass. This trend has been noted since the 1970s (Cable 1971, Bock et al. 1986) although it is not known whether the grass invades communities of low diversity or drives out species from high diversity areas. There is only anecdotal evidence that sites invaded by Lehmann lovegrass probably did not differ greatly in their species diversity compared to sites not invaded (D. Robinett, unpublished data).

A few species, *Viguiera annua* and *Macarantthera tagetina*, were unusual compared to most native species in that they were more common on mixed and nonnative plots than native plots and contributed abundant biomass compared to other uncommon species. These species tend to grow on sites with soils of high clay content such as the loamy upland and sandy loam upland where Lehmann lovegrass dominates.

Grasslands in this study show large variability across years and community types. The unusual distribution of summer precipitation led to sharp increases in biomass on native plots in loamy bottom sites in 2000 and above-average rainfall that autumn contributed to significant increases in biomass of Lehmann lovegrass and biomass and richness of herbaceous dicots in the autumn of 2001. Native grass biomass and proportion actually declined on native plots, perhaps because of interference from native dicots or distribution of summer rains. Native plots located on loamy bottom swales supported abundant native annual grasses (primarily *Aristida adscensionis*, *Bracharia arizonica*,

Eriochloa acuminata, and *Panicum hirticaule*) in 2000 but most of these species disappeared in 2001. In addition to these annual grasses, a few of the robust native perennial grasses declined and were replaced by a suite of herbaceous dicots including high-biomass species of the sunflower family such as the *Conyza canadensis*, *Helianthus petiolaris*, *Heterotheca subaxillaris*, and many small species in the *Gnaphalium* and *Erigeron* genera. These and other herbaceous dicots such as *Eriogonum polyclaydon*, *Evovulus arizonica*, *Monarda citradora*, *Oenothera lacineata*, and *Plantago patagonica* germinated or resumed growth in the spring by utilizing moist soil conditions following the abundant winter rains. When the time arrived in summer for the annual and perennial grasses to either germinate or resume growth, the herbaceous dicots may have exploited soil water and thereby precluded use by grasses or filled in open spaces. In subsequent years, precipitation fell below average; herbaceous dicot biomass decreased, native-grass biomass remained low, and native annual grasses still were absent.

The pattern of temporal variability in plant community structure is useful to assess stability (Tilman 1996, Collins 2000) and may guide adaptive management. Plots dominated by a single dominant species may differ in their resistance to perturbation both in their amplitude and their elasticity or resilience (Orians 1974) compared to diverse communities (Tilman 1996). Plots dominated by Lehmann lovegrass tended to have higher biomass (Figure A.3) and lower species diversity (Figure A.7b). Thus, in addition to plasticity in growth and reproduction I expect that a site dominated by Lehmann lovegrass would likely exhibit greater temporal variability than native-dominated plots

(Figure A.4). In agreement with this, plots dominated by Lehmann lovegrass exhibited larger year-to-year deviations from average biomass than did native plots. Alternatively, native plots show the importance of a diversity of species' responses to climatic fluctuations. Diverse communities may resist invasion by nonnative species (Tilman 1999) or buffer against increased herbivory (Walker et al. 1999) or environmental stochasticity (Yachi and Loreau 1999).

Diversity is not the only factor influencing ecosystem processes, species composition also affects ecosystem function (Tilman 1997). Nonnative grasses in savannas often have characteristics distinct from native species that have led to altered ecosystem processes (D'Antonio and Vitousek 1992). In this study, temporal variation of native versus nonnative species suggests that they use seasonal precipitation differently. Lehmann lovegrass uses winter rainfall (Cable 1976) as it photosynthesizes and reproduces during the winter months (Fraiser and Cox 1994). Plant biomass across community type increased significantly in response to abundant winter rainfall and average summer rainfall in 2001, especially on mixed and nonnative plots. Much of this increase can be attributed to Lehmann lovegrass and herbaceous dicots. Despite most perennial plant species existing in a dormant stage from October through May, winter rainfall is an important contributor to growth of perennial grasses in the subsequent growing season (Weltzin and McPherson 1997).

In contrast to Lehmann lovegrass, native grasses changed little in response to amount of winter precipitation. Rather, biomass increased by nearly 50 gm^{-2} on native

plots on loamy bottom sites in response to early arrival of summer rainfall in 2000.

Native herbaceous dicots seemed to have an important interaction with native grasses: in a year with very low biomass of herbaceous dicots, native grass biomass was high whereas in a year of abundant dicot biomass, native grass biomass declined. In a previous study in the same area between 1993 and 1997, native grasses declined substantially coincident with an increase of herbaceous dicots (McPherson and Weltzin 1998).

Plots dominated by Lehmann lovegrass had few herbaceous dicots and thus had the effect of dampening temporal variability of this group in these communities. This response to seasonal precipitation suggests that Lehmann lovegrass may be able supplant native species by competing with native dicots for access to winter precipitation. As I noted, native grasses seem to have a transient negative association with herbaceous dicots. Thus if dicots were excluded by Lehmann lovegrass because of overlapping resource needs, eventually it could lead to declines in native grasses once the nonnative grass becomes established. The difference in seasonal water use by Lehmann lovegrass, herbaceous dicots, and native grasses has implications for hydrologic cycling and consequences for community composition exist if seasonality of precipitation shifts under global climate change.

In many semi-arid systems, soil water typically limits productivity and diversity (Noy-Meir 1973). I anticipated that temporal increases in Lehmann lovegrass would be associated with declines in native species biomass because of the pattern I saw of decreased diversity with increased Lehmann lovegrass across community type. In 2001,

however, substantial increases in Lehmann lovegrass were not associated with declines in native grass or herbaceous dicots. This single species can maintain a faster growth rate and can produce more biomass than many native grasses under drought or well-watered conditions (Cox et al. 1990, Fernandez and Reynolds 2000). During years of above-average precipitation, however, dominance by Lehmann lovegrass may ameliorate water relations and shift the drivers of these systems to light and nutrients. Active growth of Lehmann lovegrass coupled with high lignin content may result in accumulation of dead standing biomass particularly when summers are dry and termites (*Gnathamitermes perplexus*) are relatively inactive (Cox 1984), thus available light may be diminished compared to native grasslands. Additionally, high C:N ratios of lignin prevents biomass from readily breaking down and keeps nutrients tied up in biomass. Likewise, once tissue with high C:N is broken down, less nitrogen is available than would be if the plant contained low C:N ratios. In tallgrass prairie, accumulation of litter led to internally generated dynamics of feedback of litter on production and impacted plant population dynamics (Molofsky et al. 2000). These effects may be especially noticeable in conjunction with disturbances such as drought, fire, and herbivory. For example, 2-year oscillations in annual net primary productivity were unrelated to climatic conditions that followed a severe drought (Briggs and Knapp 1995, Haddad et al. 2002). On some mixed plots in particular there were oscillations in the proportion of Lehmann lovegrass to total biomass on a plot-by-plot basis that may indicate a feedback within those communities.

Not all plots experienced oscillations, however, and the change in proportion did not necessarily follow the same trend as changes in biomass.

On average there was no dramatic increase in the proportion of Lehmann lovegrass across community types and even those plots most heavily dominated by Lehmann lovegrass showed at least some increase or persistence of native species in years of abundant rainfall. However, there were 5 of 18 plots in which proportion of Lehmann lovegrass showed a nearly constant increase each year over the 5-year study (native plot 5-14% (7-17 gm⁻²); mixed plots 24-50% (24-52 gm⁻², 29-71 gm⁻²); nonnative plot 69-91% (65-197 gm⁻²) or appeared suddenly and with great magnitude (native 0-20%, 0-24 gm⁻²). These increases were not exclusive to one type of range site nor were they linked to any associated trend in richness, diversity, or total biomass.

Although the ecological debate over the degree of influence that diversity has on ecosystem processes continues, scientists point out that uncommon species may play important roles (Lyons et al. 2005). The appearance of these transient species (*sensu* Grime 1998), which are able to coexist in space by shifting their existence in time, is important to maintenance of community diversity (Thompson and Grime 1979). The function of some species may be revealed only across relatively long temporal scales. Diversity may have filter and/or founder effects on communities (Grime 1998). Diversity and richness were higher on native than nonnative plots and biomass of dicots on nonnative plots was half that on native plots probably because of lack of space for these species to occupy or may be an artifact of having only one dominant grass species. Plots

dominated by native species had lower biomass than nonnative plots, even in loamy bottom swales that receive substantial runoff and support native perennial grasses with high biomass (173 gm^{-2} and 264 gm^{-2} compared to 339 gm^{-2}). Because Lehmann lovegrass already dominates loamy upland and sandy loam uplands, of greater concern is the potential for this nonnative to occupy open spaces in these grasslands thereby reducing diversity and biomass of uncommon species. One of our native sites in a loamy bottom swale did contain 33% Lehmann lovegrass suggesting that although it does not currently dominate these sites it has the potential to replace native species there. Unfortunately it is doubtful that in areas dominated by Lehmann lovegrass native perennial grasses would return without continued removal of Lehmann lovegrass. In some areas native species coexist, however, the proportion of Lehmann lovegrass does not appear to be stable and may increase to dominant proportions under ideal environmental conditions. Our research shows that transient species are important contributors to diversity, especially during wet years, and may be the first species excluded once Lehmann lovegrass occupies a site.

Summary

I investigated the variability of plant communities in semi-desert grasslands in southern Arizona across a gradient of invasion by a dominant, nonnative grass. Native and nonnative perennial grasses contributed most of the biomass to a site (compared to dicots and annual grasses), occupied different soil types, had distinct responses to

seasonal precipitation and varied in their influence on native herbaceous dicots. Our results contribute to long-term patterns of temporal dynamics and elucidate potential changes to these trends in communities invaded by a nonnative perennial grass, particularly in response to climatic fluctuations. The results also provide baseline information on temporal variability from which we can assess differences in resilience of communities across a gradient of invasion to disturbances such as fire or extreme climatic events.

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Figure A.1 Study sites at Fort Huachuca Military Reservation, Arizona, USA, classified into 3 community types: nonnative (triangles), mixed (squares), or native (circles) based on proportion of Lehmann lovegrass from high to low, respectively.

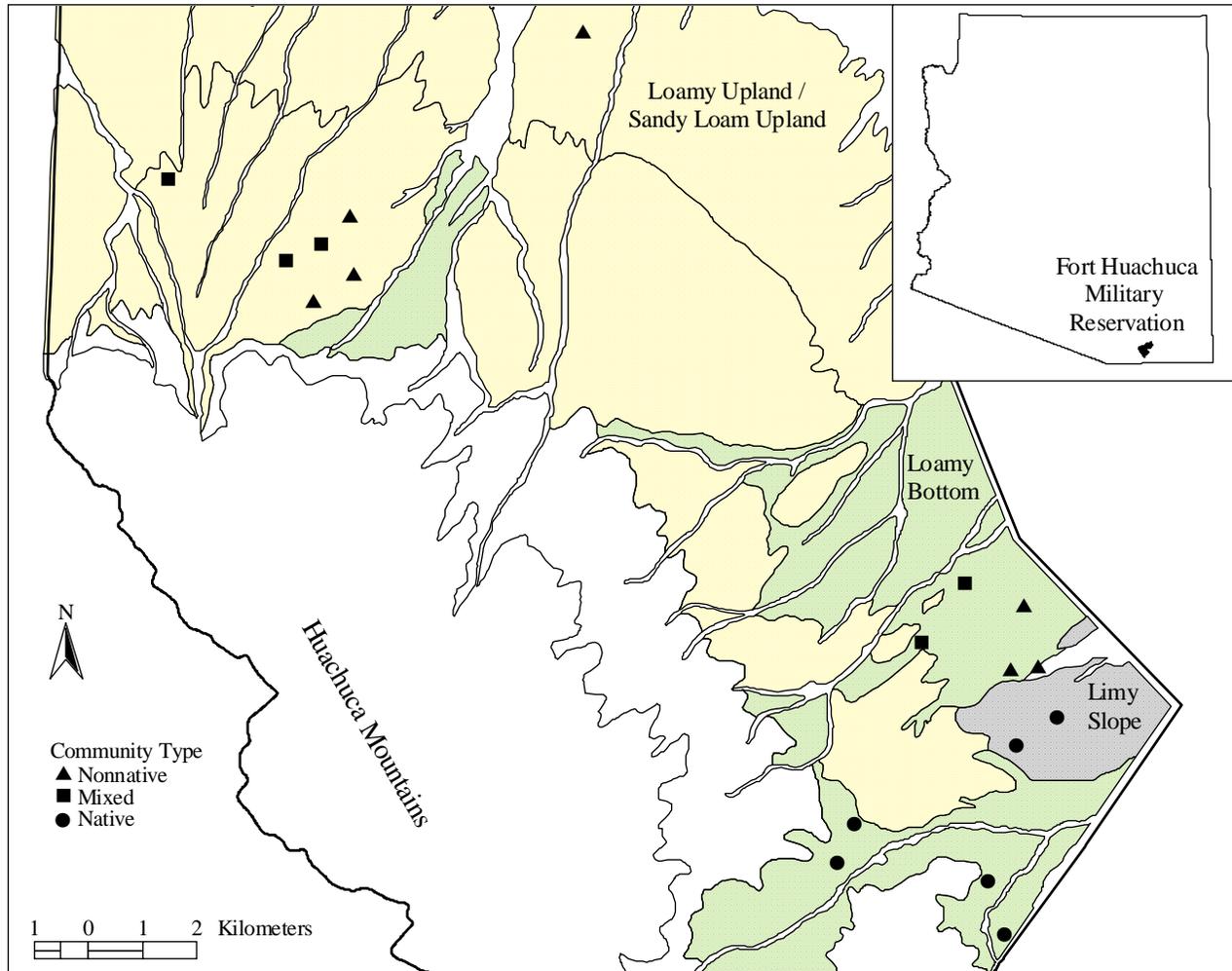


Figure A.2. Principal components analysis on the Variance-Covariance matrix. Plot scores for each year sampled in this study (1999-2003) are open triangles and plots from NRCS data shown as filled circles. Plots ordinated according to proportion of Lehmann lovegrass (shown with graduated symbols) on first axis and by distinct native plant communities on the second axis.

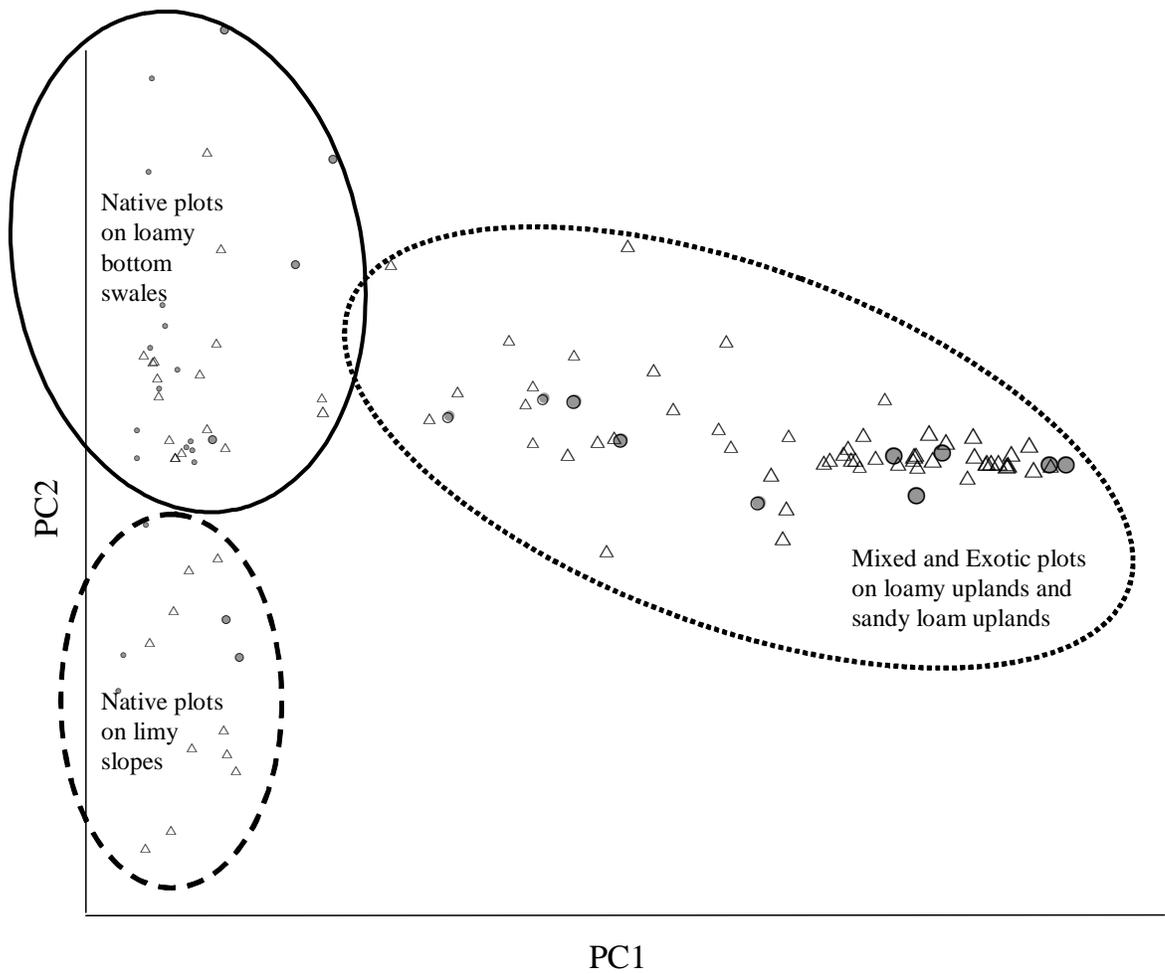


Figure A.3. Total aboveground biomass (g m^{-2}) of Lehmann lovegrass (dark gray), native grasses (light gray), and herbaceous dicots (black) in native-dominated, mixed, and nonnative-dominated grasslands sampled in fall at Fort Huachuca Military Reservation, Arizona, USA over a 5-year period ($n = 9$ in 1999, $n = 18$ from 2000 to 2003).

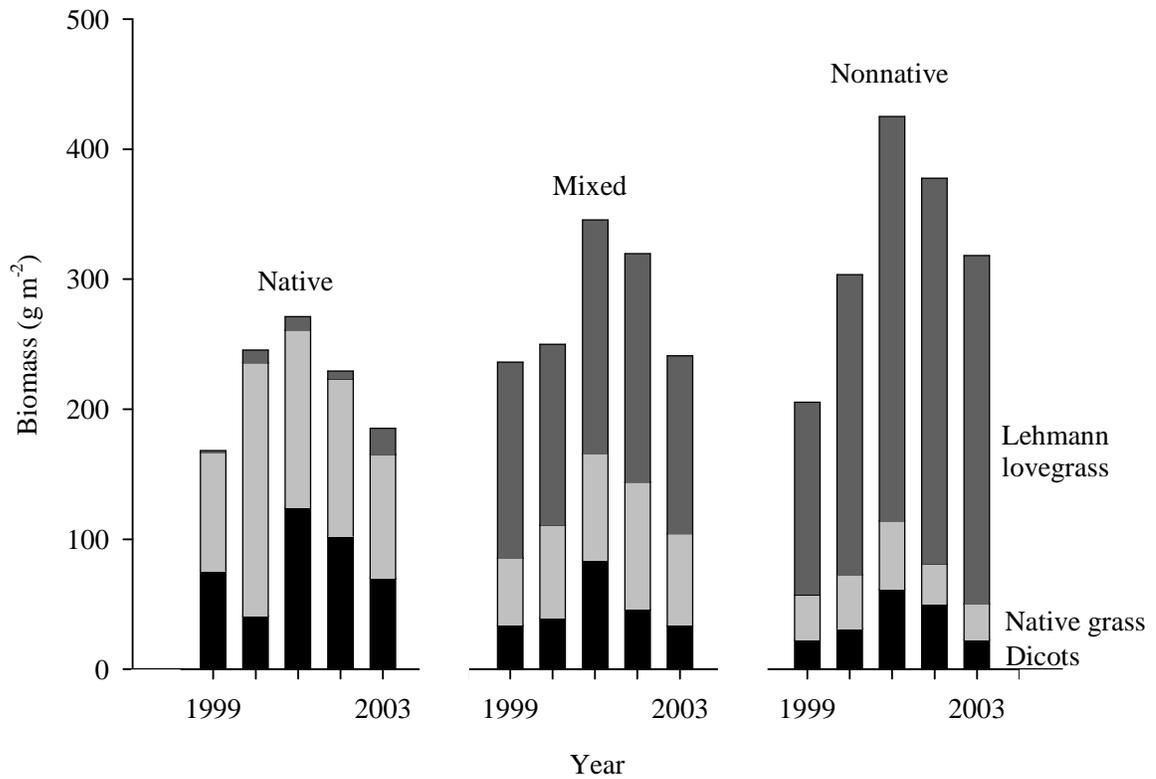


Figure A.4. Deviation of (a) average total biomass, (b) average biomass of Lehmann lovegrass, (c) average biomass of native grasses, and (d) average biomass of herbaceous dicots from 5-year average in native-dominated (open circles), nonnative-dominated (black circles), and mixed (gray circles) grasslands at Fort Huachuca Military Reservation, Arizona, USA.

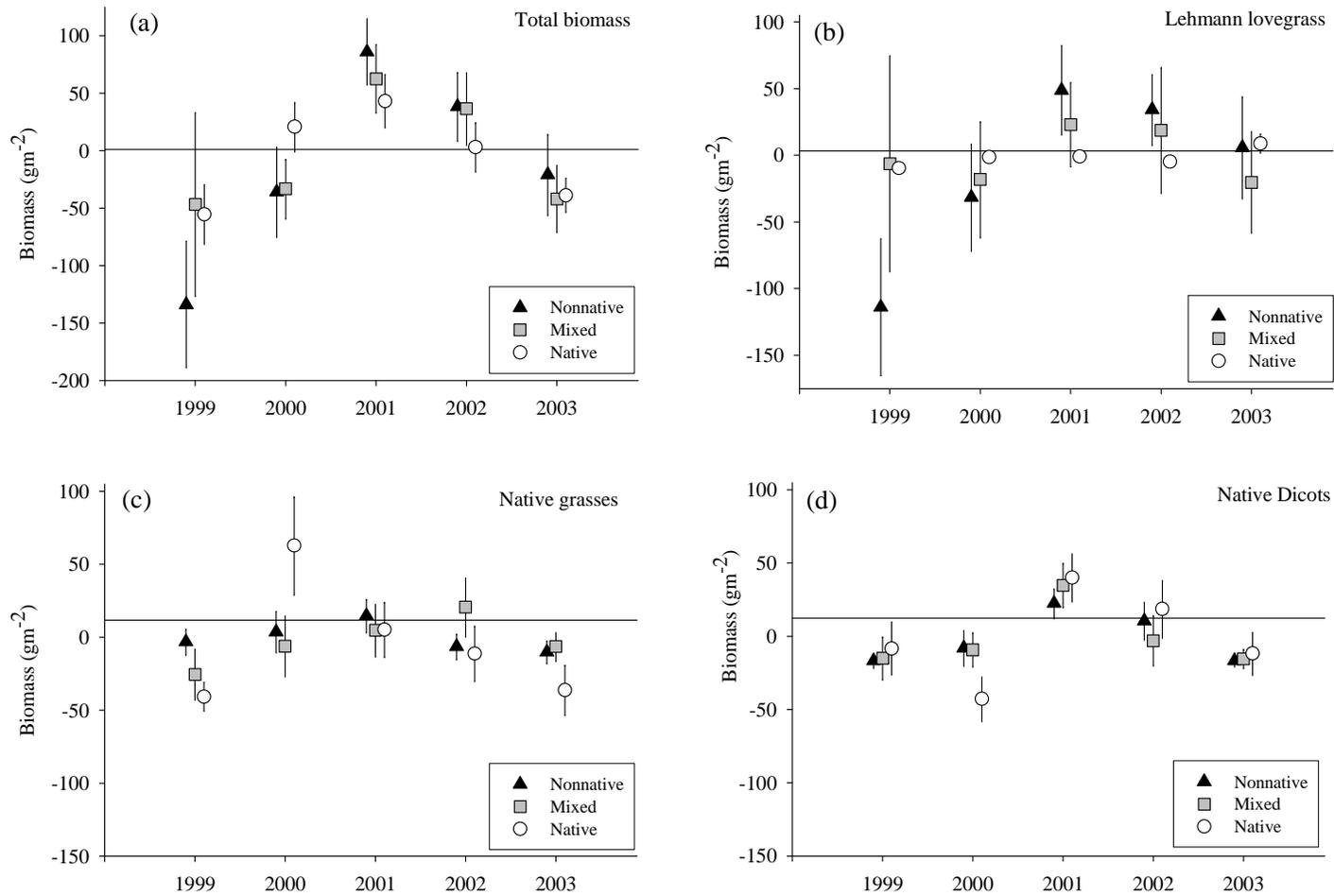


Figure A.5. Percent Lehmann lovegrass biomass of total biomass (a) and deviation of percent (b) in native-dominated (open circles), nonnative-dominated (black triangles), and mixed (gray squares) grasslands at Fort Huachuca Military Reservation, Arizona, USA.

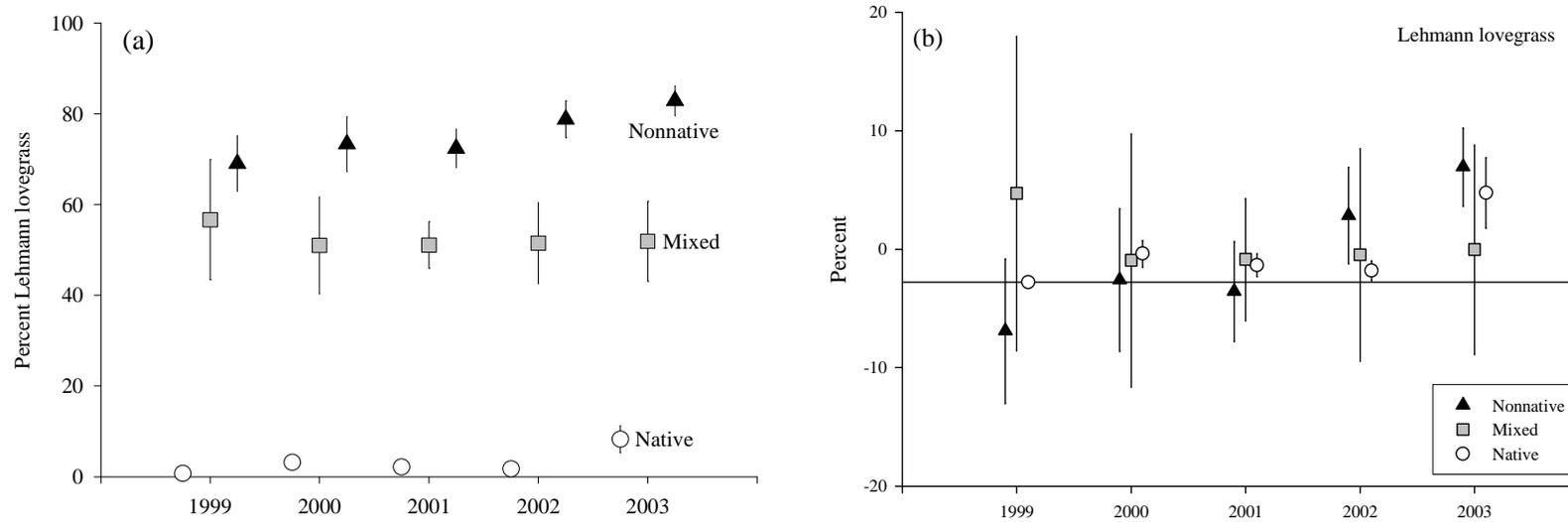


Figure A.6. Relationship between richness (left axis, crosses) or Simpson's diversity (right axis, circles) and proportion of Lehmann lovegrass at Fort Huachuca Military Reservation, Arizona, USA over a 5-year period.

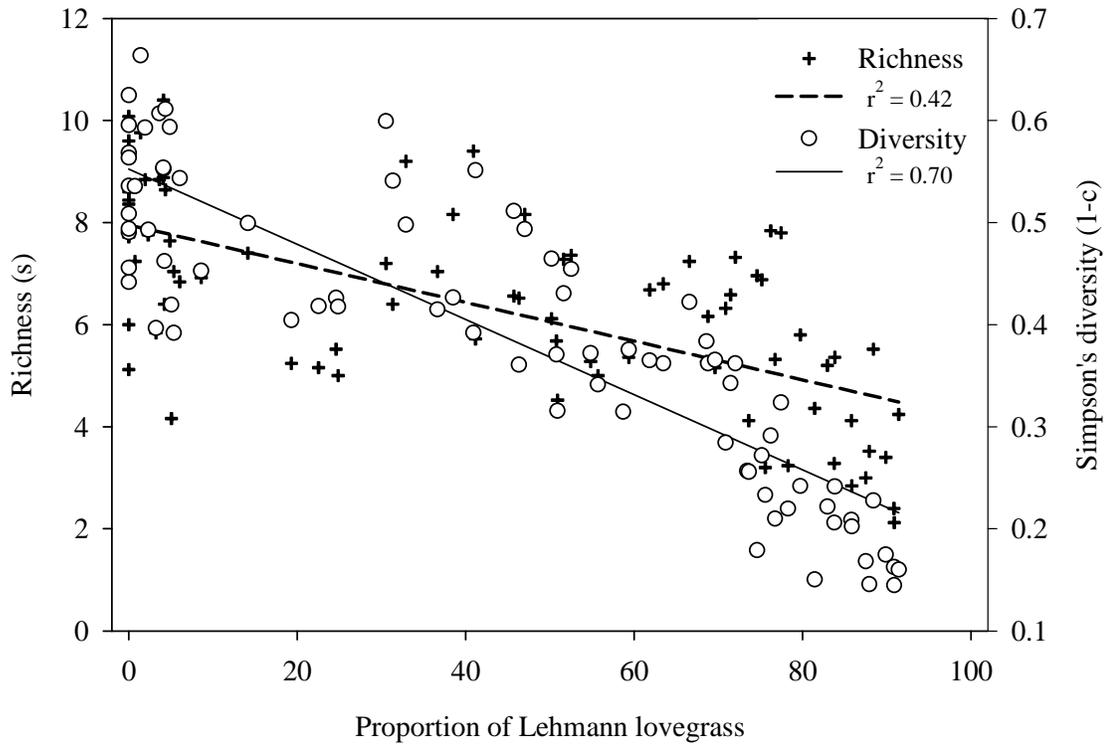


Figure A.7. (a) Richness (mean \pm SE) and (b) Simpson's diversity (mean \pm SE) in 0.5-m x 1-m quadrats in native-dominated (open circles), nonnative-dominated (black triangles), and mixed (gray squares) grasslands at Fort Huachuca Military Reservation, Arizona, USA.

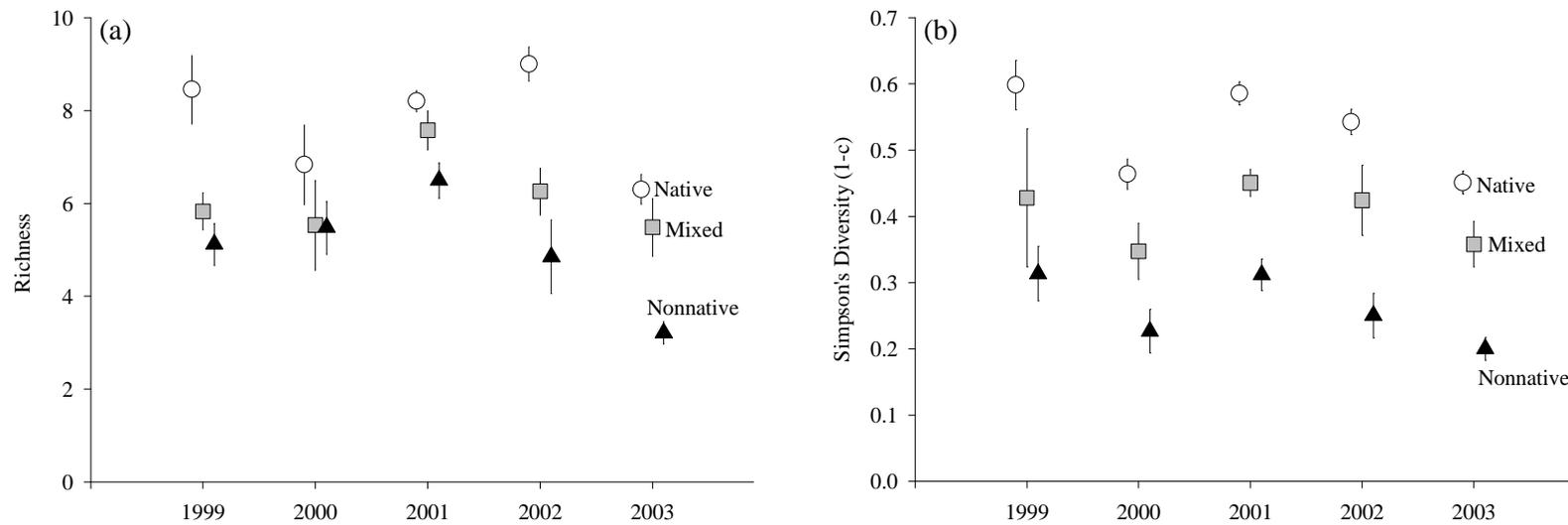
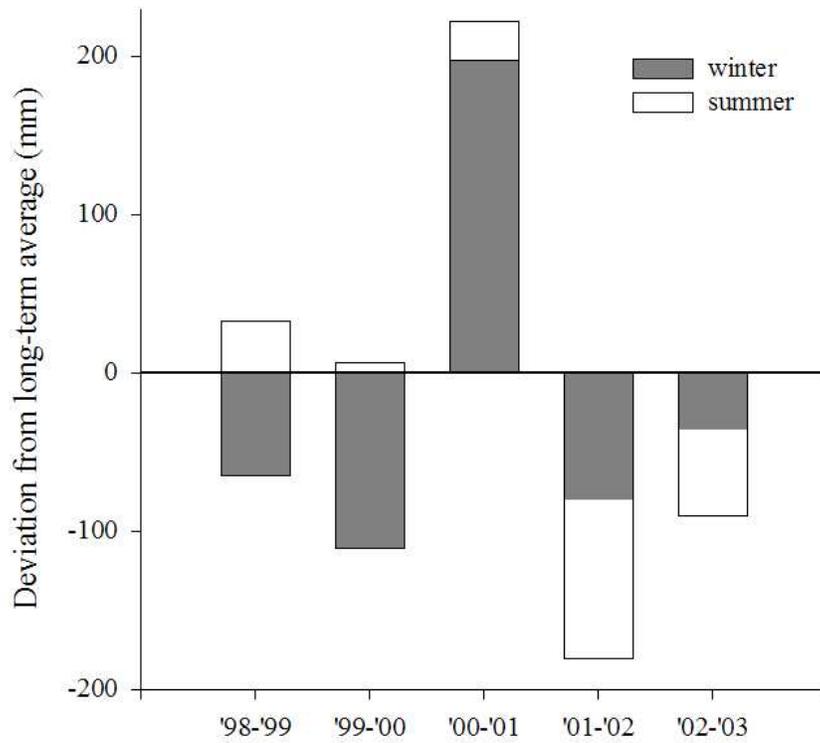


Figure A.8. Summer (May – September) and winter (October – April) rainfall deviation from long-term mean at Fort Huachuca Military Reservation, Arizona, USA over a 5-year period.



APPENDIX B

**THE ROLE OF FIRE AND A NONNATIVE PLANT AS DISTURBANCES IN
SEMI-DESERT GRASSLANDS**

ERIKA L. GEIGER

(To be submitted to Ecological Applications)

Abstract

Fire is one of several ecological processes important in maintaining grassland physiognomy by favoring survival of grasses over woody plants. Although fire helps maintain structure of grasslands, the presence of nonnative grasses may alter fire regimes and alter the structure of the existing plant community. Nonnative grasses may contribute to a positive feedback cycle that alters the extent, frequency, or intensity of fire and that favors nonnative over native plants. Humans contribute to alterations to fire regimes and alter the timing of fires compared to timing of natural fires. In southeastern Arizona the threat of Lehmann lovegrass, a nonnative perennial grass, contributing to a positive feedback cycle complicates the reintroduction of fire as an ecological process in these systems. I quantified changes to biomass, species richness, and diversity of native plant communities to dominance of *E. lehmanniana* in the presence of prescribed fire using a large-scale experiment. I selected sites along a gradient of dominance by Lehmann lovegrass that were burned in either spring or summer or left unburned. The response of plant communities depended on the interaction between year and fire season, perhaps because intensity of fire varied with conditions at the time of fire such as moisture availability in the months preceding and following the fires. Two years post-fire, biomass on burned and unburned plots were similar because biomass on unburned plots had declined over time due to drought. In contrast to studies that report positive feedbacks between fire and nonnative grasses, I found that fire did not influence abundance or dominance by Lehmann lovegrass at least during the course of this study. Lehmann

lovegrass did increase on some plots, however, regardless of fire treatment suggesting that spread of this species has not ceased.

Introduction

Variations in the magnitude, frequency, and timing of disturbances can have significant consequences for plant communities (Osman 1977, Connell 1978, Levin and Paine 1974, Denslow 1980, Miller 1982). Altered fire regimes potentially influence the degree to which certain species are affected and which species have access to post-fire release of resources. For example, fires that occur in a season dissimilar to the natural regime may affect resource use by plant: physiologically active plants have carbohydrates stored in aboveground rather than belowground parts and thus are susceptible to damage if they are growing at the time of a fire (Towne and Owensby 1984), which can delay post-fire recovery (Pate et al. 1990). Additionally, seeds that germinate in response to fire (Keeley 1991, Herranz et al. 1998, Tieu et al. 2001, Hanley et al. 2003) may break dormancy at a time that is less conducive to survival. Fires that occur more frequently than historical regimes may force plants recovering from fire to exhaust resources, stressing plants and increasing susceptibility to pathogens, herbivory, or competition. Altering fire regimes may sway competitive interactions in favor of certain species or life forms because disturbance influences competitive interactions (Connell 1978, Drury and Nisbet 1973). For example, in tallgrass prairie, warm-season species are facilitated and cool-season species are hindered by dormant-season fires (Owensby and Anderson 1967,

Hover and Bragg 1981, Hulbert 1988, Howe 1994), however, fires during the growing season produce the opposite response (Hover and Bragg 1981, Biondini et al. 1989, Howe 1994).

Wildfire in western North America is strongly seasonal (Westerling et al. 2003) and is determined by characteristics of winter rains, arid spring, and summer “monsoon” (Swetnam 1990). In southern Arizona, the occurrence of wildfire peaks during May and June during the hot dry early summer when lightning strikes ignite desiccated fine fuels prior to rain in July and August. Fire severity often is enhanced by moisture conditions one to two years before the fire season that increase fuel loads (Rogers and Vint 1987, Swetnam and Betancourt 1998, Westerling et al. 2003, Crimmins and Comrie 2004). When these conditions are followed by a drought year the fire season may be explosive. Before 1800, fires tended to occur late in the season probably as a consequence of lower summer rainfall and more frequent El Nino events, compared to post-1800 El Nino events that produced abundant winter precipitation, which in turn produced abundant fine fuels. Changing rainfall patterns associated with global change may continue to stimulate changes in regional to continental-scale fire activity (Grissino-Mayer and Swetnam 2000).

In addition to large-scale patterns influencing fire, fire regimes often are regulated by humans at regional to local scales. Historically, extent, frequency, season and intensity of wildfires were determined by climate, fuel characteristics and topography (Wright and Bailey 1982). Over the past century, however, humans have altered fire regimes primarily

by suppression, therefore when fires do occur they burn at relatively high intensities because fuels have been accumulating for decades (Covington and Moore 1994). Other anthropogenic changes in fire regimes are caused by supplying ignition sources at a time of year when lightning does not occur and forcing fire within unnatural boundaries (e.g. roads). More often than not, prescribed fires are set outside of the historical regime during cool seasons when they are easier to manage. Changes to historical fire regimes have implications for plant community structure and processes. Slight shifts in the drivers of plant community structure become especially important in ecotonal communities such as savannas (Risser 1990, Neilson 1993).

Prior to Anglo settlement, fire in semi-arid savannas affected hundreds of square miles during June and July occurring with a frequency of about 2.5 to 10 years (Bahre 1985, McPherson 1995, Kaib et al. 1996). Unlike mesic grasslands, semi-arid savannas are constrained by erratic precipitation and patchy fine fuel arrangement with relatively low overall biomass. In many places, severe overgrazing has led to loss of topsoil and encroachment by woody plants and thus limited colonization by grasses. At a local-level, land managers are becoming increasingly interested in reintroducing fire for a variety of reasons including the desire to restore natural processes to these ecosystems, to alter current savanna physiognomy with the hope of shifting the grass-tree ratio to favor herbaceous species, to reduce litter, and to stimulate new plant growth. Nationally the mandate to restore fire-adapted systems and development of the LANDFIRE program also is leading land managers to reintroduce fires. In the southwestern United States,

some land managers are hesitant to reintroduce fire because they fear it may hasten invasion by a nonnative perennial grass, Lehmann lovegrass (*Eragrostis lehmanniana*), while others hope to reduce its dominance in grasslands.

Lehmann lovegrass was introduced to Arizona in the 1930s for livestock forage and erosion control. Lehmann lovegrass originated in a fire-dominated system in South Africa and its growth characteristics may influence fire regimes. Lehmann lovegrass differs from native perennial grasses in its extended period of growth (spring through fall). During drought, Lehmann lovegrass produces about four times as much green biomass as native species (Cox et al. 1983) and maintains its maximum relative growth rate (Fernandez and Reynolds 2000); under well-watered conditions this nonnative grass can double its biomass in less than one week, up to four times as fast as native grasses (Fernandez and Reynolds 2000). This abundant biomass tends to decompose more slowly than biomass from most native grasses because of its high carbon-to-nitrogen ratio. Accumulation of old-dead standing biomass may be significant when summers are dry and termites (e.g., *Gnathamitermes perplexus*) are relatively inactive (Cox 1984). Upland sites with shallow soils appear to be heavily dominated by Lehmann lovegrass whereas bottomlands are occupied by native species with higher biomass (pers. obs.). As a result, Lehmann lovegrass is expected to have a greater influence on fire frequency and intensity on uplands than on bottomland sites. In addition to its expected influence on fires, germination of Lehmann lovegrass is enhanced by fire (Cable 1965, 1971, Ruyle et al. 1988, Sumrall et al. 1991, Robinett 1992, Biedenbender and Roundy 1996). Thus,

Lehmann lovegrass and fire appear to be part of a positive feedback cycle whereby large amounts of biomass contribute to a fine fuel source that promotes fire, and rapid germination and recovery following fire encourages rapid fire-return intervals (D'Antonio and Vitousek 1992).

Using a large-scale experiment I investigated the response of semi-desert grassland communities to combined effects of nonnative grass and fire regime. Specifically, I was interested in determining if Lehmann lovegrass mediates native plant response to altered fire regimes. For example, does the interaction between fire season and increasing proportion of Lehmann lovegrass lead to positive feedbacks in abundance of this nonnative grass and therefore fine fuels or negative feedbacks in richness or abundance of native species. Further, could responses lead to potential changes to vegetation states?

Methods

Study sites

I studied plant communities in the grasslands and mesquite (*Prosopis velutina* Woot.) savannas flanking the northern and eastern base of the Huachuca Mountains (31° 34' N, 110° 26' W) of southern Arizona (Figure B.1). Elevations range from 1420 to 1645 meters. Average annual precipitation between 1998 and 2003 was 347 mm (data from 5 stations across Fort Huachuca); the long-term average is 379 mm (based on averages of 2 stations at Fort Huachuca; 1900 to 1917, 1955 to 1981, 1955 to 1998).

About two-thirds of annual rain arrives between May and September in intense local storms and one-third falls between October and April. The region is characterized by a hot, dry period in May and June prior to the onset of the monsoons when natural fires occur.

I selected sites on Fort Huachuca Military Reservation (FHMR), an active installation of the U.S. Army characterized by the absence of livestock and frequency of fires similar to pre-Anglo settlement (see McPherson 1995). Perennial grasses are more abundant and woody species are fewer at FHMR than surrounding lands, probably because few livestock have grazed at FHMR since the late 1800s, and livestock have been excluded completely since 1950. Therefore, in conjunction with regular ignition sources from military training activities, adequate fine fuels allowed for a fire regime similar to historical regimes. The most recent fires at the study sites occurred 9 to 24 years before the present study.

I set up an experiment with a split-plot design with plant community type as the whole-plot factor and fire treatment as the split-plot factor. I selected 18 sites at FHMR and classified the sites into 3 plant community types based on degree of dominance by Lehmann lovegrass. Nonnative sites were grasslands dominated by Lehmann lovegrass. Native sites were dominated by native perennial caespitose grasses including *Aristida* spp., *Bothriochloa barbinodis* (Lag.) Herter, *Bouteloua* spp., *Digitaria californica* (Bentham) Henrickson, *Eragrostis intermedia* A. S. Hitchc., and *Panicum* spp. and Mixed sites were composed of a mix of nonnative and native species. I classified sites

based on visual surveys *a priori* and generally these designations were accurate for the duration of the study. At each site established three permanent square 1-ha plots with a minimum buffer of 50 m between plots. I randomly assigned each plot to one of three prescribed-fire treatments: no fire, spring fire, summer fire. I treated nine sites in 2001 and monitored from fall 1999 to 2003 and an additional nine sites which I treated in 2002 and monitored from fall 2000 to 2003. The design yielded 3 replicates per community type ($n = 3$) per treatment ($n = 3$) in a given year ($n = 2$). During the study, one plot was burned by a wildfire in the summer of 2002 and I replaced it with a new plot 300 m away. The replacement plot had a lower proportion of Lehmann lovegrass than the original plot.

Plots were located on 4 classes of range sites: limy slopes, loamy bottom swales, sandy loam uplands, loamy uplands. A range site is a description of land based on soil, relief, climate, and a distinct plant community (Natural Resources Conservation Service 2000, p. 324). Limy slopes are loamy, mixed, superactive, thermic, shallow Petrocalcic Calciustolls (NRCS 2000, p. 47) found on 3-30% hill slopes. The soils are shallow to moderately deep (13-50 cm), covered with 20-45% gravel and/or cobble, are well-drained with moderately rapid permeability, runoff potential is medium to very high, available water holding capacity (AWHC) is very low. Loamy bottom swales are located in floodplains that grade into uplands. Slopes generally are less than 5% and sites accumulate water and sediment runoff from surrounding uplands. These range sites are a complex of fine-loamy, mixed, superactive, thermic Aridic Haplustalfs and coarse-loamy, mixed, superactive, thermic Pachic Halpustolls (NRCS 2000, pp. 101-2). Soils are deep

(1.5 m or more) and well drained, have moderately slow permeability, moderate or high AWHC. The remaining plots are located on fan terraces and are loamy upland or sandy loam upland sites. These range sites have deep (1.5 m or more), well-drained soils and are distinguished by their soil surface layer, which will not exceed 10 cm on loamy uplands but are 10-30 cm on sandy loam uplands. These range sites are composed of fine, mixed, superactive, thermic Aridic Paleustalfs on slopes of 0-45% and fine, mixed, superactive, thermic Ustic Haplargids on slopes of 1-30% (NRCS 2000, pp. 173-6, 184-5). These soils are well drained, have moderate to high AWHC, slow permeability, and runoff potential is variable due to the range of slopes. Some range sites are characterized by 5-30% cobble and/or gravel on the soil surface. Lehmann lovegrass often dominates these range sites as it did on our plots.

I collected aboveground biomass in spring (April) to capture the response of plants to winter rainfall and in fall (September) after the summer rains when a majority of plants achieve peak standing biomass. I clipped plants rooted in 25, 1-m x 0.5-m quadrats randomly located in 1-ha plots from 1999 to 2003. I did not sample locations if they coincided with previously clipped quadrats or were inaccessible because they were beneath dense tree canopies. I harvested by species at 2.5 cm above the ground for perennial grasses and at ground level for all other vegetation. Also, I collected litter, which I defined as plant biomass that was detached from a plant or the ground. Samples were oven-dried at 65 °C for 48 hours and weighed to the nearest 0.1 g.

Experimental Design and Analysis

I calculated community metrics for each plot: average biomass of plant lifeform (nonnative grass, native grass, and herbaceous dicot), richness (number of unique species), diversity (Simpson's c and Shannon's H), and proportion of Lehmann lovegrass to total biomass for each of the 5 sampling years. Because I was unable to determine species-specific sources of litter, it was not included in calculation of total biomass. H and c were correlated ($r^2 = 0.98$, $p < 0.0001$), therefore I report only c .

I analyzed data using repeated-measures mixed model analysis of variance with community metrics as the response variables and plant community type (nonnative, mixed, native) and fire treatment (no fire, spring fire, summer fire) as the explanatory variables. I modeled community type as a random effect and fire treatment as a fixed effect and used an autoregressive 1 covariance matrix structure. I transformed biomass of functional type values using the square root, biomass of Lehmann lovegrass using the log, and proportion of Lehmann lovegrass using arcsine square root. Results are presented as untransformed means \pm 1 standard error.

Results

Generally, spring data were highly correlated with data from the prior fall (biomass: $r^2 = 0.77$, proportion: $r^2 = 0.91$, diversity: $r^2 = 0.81$), responding similarly to treatments over time. Some differences between season were due to sampling immediately after fire on plots burned in spring and because of rare species present in

only one year (richness: $r^2 = 0.57$) . Therefore, I restrict my presentation of results to the fall sampling season because of the similarity of most responses between seasons, but I incorporate some discussion of spring data where applicable.

Biomass

On unburned mixed and nonnative plots biomass increased dramatically in response to abundant winter rainfall whereas biomass on unburned native plots did not vary over time (Figure B.2, Table B.1). Thus, because of fuel load differences, fire treatments had the largest immediate impacts on nonnative then mixed then native plots (Table B.2). Fires in spring 2001 occurred under cooler, wetter conditions associated with the above-average winter rainfall and resulted in no change from pre-burn biomass values (Figure B.2, left panel). Post-fire biomass on plots treated in 2001 was distinctly different for all fire treatments on nonnative plots for three seasons post fire, on mixed plots for two seasons post fire and on native plots for one season post fire (Figure B.2, left panel). For native and mixed plots, congruence of biomass values in 2001 was not due to an increase in biomass on burned plots but rather a decline in biomass on unburned plots (Figure B.2, left panel). Across community types, biomass on most plots burned in spring and summer of 2002 was lower than biomass on unburned plots for two seasons post fire (Figure B.2, right panel). One exception was on mixed plots treated in 2002, which show an increase in biomass two growing seasons post-fire that was not seen on native or nonnative plots (Figure B.2, right panel).

Relative proportion of Lehmann lovegrass

Although plots varied considerably from year to year, the relative proportion of Lehmann lovegrass generally was consistent over time and thus fire caused no change in community type for the duration of the study (Figure B.3, Table B.3). There was an increase in proportion over time (0.65 to 0.83) on some unburned plots dominated by Lehmann lovegrass and on an unburned plot dominated by native species, due primarily to one plot with two of 25 subsamples dominated by Lehmann lovegrass (114 g and 372 g in a 1-m x 0.5-m quadrat) where Lehmann lovegrass had not occurred in prior years. The relative proportion on burned plots showed a similar trajectory to biomass (Figures B.2, B.3). The relative proportion declined on all treated plots except spring 2001, but the decrease persisted only 1-2 growing seasons post-fire (Figure B.3, left panel). Differences among fire treatments were more distinct on nonnative plots than other community types (Figure B.3).

Richness and Diversity

Richness and diversity declined with increasing proportion of Lehmann lovegrass (Figure B.4) and generally were highest in 2001 and lowest in 2003 (fall) and 2004 (spring) (Figures B.5, B.6, B.7). Differences in diversity were dependent on community type and year and increased slightly in response to temporary declines in proportion of Lehmann lovegrass post-fire (Figure B.5, Table B.4). Plant species richness in fall varied

by the interaction of community type and year but not by fire treatment (Figure B.6, Table B.5).

Discussion

Recently, the main premise guiding fire management in semi-arid communities has been the presumption that nonnative species present in these communities will enter into a positive feedback relationship with fire, which will alter fire regimes and thus community properties (D'Antonio and Vitousek 1992). I found that fire did not influence the proportion of a nonnative grass, Lehmann lovegrass, in semi-arid grasslands in southeastern Arizona (Figure B.2). Our results do not support findings of other studies of nonnative grasses or predictions about the response of Lehmann lovegrass based on known germination responses to fire and growth characteristics compared to native grasses.

Previous research has described the ability of Lehmann lovegrass to produce copious amounts of seed, spread out its timing of germination to guarantee success of at least a portion of the seed bank (Abbott et al. 1995) and germinate readily following canopy removal (Sumrall et al. 1991). These characteristics, along with the plant's ability to produce biomass more rapidly than natives even under drought conditions (Fernandez and Reynolds 2000), suggests that Lehmann lovegrass may replace native species following disturbance. Based on the species' characteristics I expected to see an increase in the proportion of Lehmann lovegrass if the species outcompetes natives or is given a

foothold after fire. Thus, lack of a response indicates that other factors, beyond removal of native vegetation following disturbance, may contribute to Lehmann lovegrass replacing native species as dominant.

I expected proportion to change marginally on native and nonnative plots, but substantially on mixed plots. Many native plots had no Lehmann lovegrass or such a low proportion that increases would be expected to be incremental either by dominance in a small area or an increased frequency at low abundance. The only increases were restricted to particular plots and were not related to fire. For example, one site treated in 2002 experienced a very small change after a spring burn (19% pre- to 22% post-fire), an intermediate change after a summer burn (10.5% pre- to 26% post-fire), and a large change on the unburned plot (0% to 20%) that was the result of unusually high Lehmann lovegrass biomass for a native site in two subsamples. The greatest increase on these plots over the 4-year period occurred in 2003, the second consecutive year of below-average winter and summer precipitation. This trend was only noted on one of six native sites included in the study and thus I emphasize the importance of the match between a nonnative species and the location and timing of invasion rather than characterizing a species as 'invasive' or a community as 'invasible' in a general sense (Kolar and Lodge 2001, Shea and Chesson 2002).

Alternatively, plots dominated by Lehmann lovegrass have low diversity (Figure B.5) and thus I expected this species would maintain its dominance at these locations. I did observe a transient decline in the proportion of Lehmann lovegrass on plots burned in

summer 2001 but not on plots treated in 2002 (Figure B.2). Also, on half of the nonnative unburned plots, Lehmann lovegrass achieved proportions greater than 0.88 in 2003, the highest proportion at those sites during the period of study. Germination of seeds, even those of Lehmann lovegrass, is unlikely when dead-standing biomass is present (Sumrall et al. 1991) and reducing the proportion of Lehmann lovegrass at these sites to enhance native species likely will require direct management.

In between native and nonnative plots, mixed plots contain 30-60% biomass of Lehmann lovegrass with well-established plants. However, many native species have maintained a strong presence on these plots. If Lehmann lovegrass is able to supplant native species following disturbance we should see the largest increases in proportion on these plots. Fire regime did not influence the proportion of Lehmann lovegrass on these plots for two years after fire (Figure B.2). Most plots maintained a proportion of Lehmann lovegrass over time that differed by about 0.30 suggesting that this mix of native grasses and Lehmann lovegrass is stable perhaps due to abiotic constraints on dominance by the nonnative grass or the ability for natives on these sites to effectively compete with Lehmann lovegrass. Alternatively, perhaps proportion of Lehmann lovegrass could be considered a stable state until a particular combination of disturbances would force the community to a new state of higher proportion, such as exemplified by the nonnative sites in this study (Archer 1989, Westoby et al. 1989).

Recent concerns over the possibility of Lehmann lovegrass spreading as a result of fire have left managers with difficult decisions about maintaining grasslands. Plant

characteristics suggest that the species will increase after fire but our results show that the proportion of Lehmann lovegrass did not increase 2-3 growing seasons post fire (Figure B.3). Although scientists do not know long-term consequences of fire in these systems, it is likely that a shift in proportion of Lehmann lovegrass will not be explained generally by fire alone. Excluding fire probably is not feasible and may contribute to the extirpation of native species adapted to fire in grassland ecosystems. If fire is believed to create an opening for Lehmann lovegrass, then drought may pose a similar problem. Biomass on unburned native and mixed plots dropped to levels similar to plots burned under dry conditions (Figure B.2). Likewise, grazing is another factor that reduces biomass of native grasses thus leaving open spaces where Lehmann lovegrass could invade. Low plant cover, regardless of disturbance, provides the opportunity for spread (Crawley 1986, 1987) and Lehmann lovegrass may spread in absence of some disturbances (McClaran and Anable 1992). It is unclear which disturbances if any may facilitate invasion by Lehmann lovegrass to native-dominated communities; fire does not appear to influence invasion.

Another assumption about the effects of Lehmann lovegrass on semi-arid grasslands is that areas dominated by the species have much more biomass than areas dominated by native species (Fernandez and Reynolds 2000, Cox et al. 1983) and thus may alter fire regimes. Researchers also have expressed concern about the potential of nonnative grasses to alter fire regime such as frequency, intensity, or spread once it dominates a site (D'Antonio and Vitousek 1992). Lehmann lovegrass does appear to alter

the abundance of fine fuels both spatially and temporally. However, these differences are apparent on unburned plots and the trends do not hold for burned plots. Despite claims that Lehmann lovegrass can produce more biomass in drought years compared to native grasses, there was no difference in biomass recovery on burned plots across community types during the 1-2 years post-fire. In contrast, nonnative plots tended to maintain higher biomass to a greater extent than native plots on unburned plots relative to burned plots. During dry years when production was low, native plots tended to lose biomass more rapidly than nonnative plots: highly lignified biomass of Lehmann lovegrass degrades slowly and remains attached to the plant whereas native grass biomass tends to break away from the plant and decomposes more readily. Thus, fire would be more likely to spread across sites dominated by Lehmann lovegrass if high biomass is maintained.

While biomass on unburned plots differed consistently across community types post-treatment, biomass for most burn treatments was remarkably similar: on plots burned during summer 2001, biomass averaged 100 g/m^2 (Figure B.2, left panel). Biomass was $50\text{-}100 \text{ g/m}^2$ on plots burned in 2002, a drier year than 2001 (Figure B.2, right panel). Plots burned during spring 2001 had less damage to existing plants due to wet conditions and thus less severe fires, yet biomass was similar across community type. Thus, regardless of initial biomass and differences across unburned plots of the three communities, biomass was approximately equal for burned plots, and the minimum biomass return on these plots was 50 g/m^2 . Plots with the lowest biomass post-fire tended to be the plots with the highest biomass pre-fire, suggesting that Lehmann lovegrass may

contribute to high-intensity fires that kill plants. The change in fire intensity in these cases would have a greater effect on the nonnative grass than native plant communities and thus would affect fewer species in these low-diversity areas. One possible negative consequence of increased intensity at sites dominated by Lehmann lovegrass is the potential for wind erosion if more plants are killed and recovery time is slow.

In burned areas I expected that plots dominated by Lehmann lovegrass would increase biomass more rapidly than native-dominated plots because of its reported growth abilities under wet and dry conditions (Fernandez and Reynolds 2000). Lehmann lovegrass maintained low levels of biomass, similar to native and mixed plots for 2-3 growing seasons post fire. Recovery is 1-2 growing seasons under average conditions (Cable 1975, Wright 1980, Martin 1983, Bock and Bock 1992, Gosz and Gosz 1996) or 3-4 growing seasons post-fire under drought conditions. (Reynolds and Bohning 1956, Cable 1965, Wright 1980, Valone and Kelt 1999). On some native plots, burned plots converged with unburned plots in amount of biomass two growing seasons after fire. However, burned plots did not recover, rather unburned plots lost biomass. This trend was evident for mixed and nonnative plots although the degree of convergence decreased with increasing proportion of Lehmann lovegrass. Only a subset of plots (T02 mixed plots) exhibited a trend toward biomass recovery on burned plots. Although Lehmann lovegrass is said to grow better than native grasses under drought conditions (Cox et al. 1990, Reynolds and Fernandez 2000) it appears that this growth may be minimal and that years of abundant rainfall are more important for high levels of biomass, which does not

decline as rapidly as on native plots. Thus I doubt that Lehmann lovegrass has much effect on fire frequency except in successive years or perhaps decades of above-average precipitation (see Crimmins and Comrie 2004).

Precipitation not only affects plant recovery post-fire but also has important consequences for fire behavior and intensity and thus likely will produce differences in plant community response to fire. High precipitation in early winter 2000 (Figure B.8) altered the response of plant communities to spring fires and contributed to dramatic increases in biomass, particularly on nonnative and mixed plots sampled in fall 2001. This response of Lehmann lovegrass to winter precipitation has been noted for many years (Cable 1976). Plots burned in spring 2001 did not change in biomass from previous years while unburned plots experienced spikes in biomass. Presumably relatively few plants were damaged by fires during spring 2001 because of high antecedent winter precipitation and available water from recent precipitation events gave burned plants the opportunity to recover. Alternatively, plots burned in summer 2001 and spring and summer 2002 were treated under dry conditions.

One factor that may become more important for management of plant communities is antecedent climatic condition. Fires occurring during dry years may produce profound differences compared to wet years. Transient species—those present only during 1-2 years of the study during a year of above-average rainfall—were important contributors to grassland diversity and were uncommon on plots dominated by Lehmann lovegrass compared to those dominated by native grasses (Appendix A, this

volume). If a management goal is to enhance plant species diversity, fires in these years could negatively impact the populations of these species. For example, annual goldeneye (*Vigueira annua*) appeared in 2001 and persisted through 2002. It was one of the few species that was abundant on plots dominated by Lehmann lovegrass (mixed and nonnative plots), probably in association with soils of higher clay content compared to other plots. On burned plots, biomass and frequency of annual goldeneye dropped between 50 and 100% compared to unburned plots. It is possible that these declines reduced the seed bank for future generations of this species. Alternatively, similar to perennial grasses, a common perennial dicot, *Evolvulus arizonica*, remained stable or increased after fire.

The ability of land managers to suppress wildfires is declining as climate change drives increasingly extreme events (Neilson 1993, Solomon and Kirilenko 1997, Holt 2003). For example, the 'Ryan Fire' burned more than 15,000 ha in southeastern Arizona in 2002 and easily burned across grazed and ungrazed lands alike (Figure 2 in Kupfer and Miller 2005). It was the fourth largest fire in Arizona, with the largest occurring just six years earlier in central Arizona. I argue that fire will not cause an increase in Lehmann lovegrass any more than other disturbances such as drought or livestock grazing. There do not appear to be different responses to fire based on season for plant communities. Some negative effects on transient spring-germinants may not become apparent for many years. Also, since there is little documentation about fire season effects for other organisms in these communities I argue that prescribed fires should mimic the historical

regime of summer fires with which these communities evolved. Reproduction and development of many species is linked to seasonal environmental cues; therefore disruptions to these evolutionary cycles likely would have negative impacts to populations with potential cascading effects to the system. Additionally, if land managers are attempting to reduce woody plant cover, summer fires are more likely to kill woody plants as summer fires burn at higher intensities than fires during other seasons and the plants are more vulnerable than other seasons when they are dormant. Movements toward whole-system management argue for site-specific management efforts: attempting to make broad generalizations about fire effects leads to over-simplification of the natural patterns (Glenn-Lewin et al. 1990).

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Table B.1 Results from repeated-measures analysis of variance with biomass as the response variable and treatment, type (random effect), and year (time) as explanatory variables. The columns on the left are for plots treated in 2001, the columns on the right are for plots treated in 2002.

Effect	2001			2002		
	df	F	p	df	F	p
Type	2, 18	1.92	0.176	2, 18	15.18	0.0001
Year	4, 72	5.29	0.001	3, 54	162.27	<0.0001
Treatment	2, 72	6.14	0.003	2, 54	26.49	<0.0001
Year*Type	8, 72	0.46	0.882	6, 54	9.08	<0.0001
Type*Treatment	4, 72	0.51	0.729	4, 54	1.69	0.166
Year*Treatment	8, 72	10.66	<0.0001	6, 54	27.75	<0.0001
Year*Type*Treatment	16, 72	1.11	0.360	12, 54	3.01	0.003

Table B.2. Percent change of biomass from one growing season pre-fire to one growing season post-fire. Nonnative plots exhibited the largest decrease in biomass from pre-burn to post-burn and losses were greater across all community types in 2002 than 2001. At the time of burning, communities were in an upward trend in 2001 and a downward trend in 2002.

Biomass	non01	spr01	sum01	non02	spr02	sum02
Native	17.8	-27.9	-50.6	-18.9	-62.3	-70.5
Mixed	30.9	-8.5	-57.5	-6.2	-75.8	-76.3
Nonnative	69.1	-16.5	-62.4	-3.6	-78.9	-89.3

Table B.3. Results from repeated-measures analysis of variance with proportion of Lehmann lovegrass biomass of total biomass as the response variable and treatment, type (random effect), and year (time) as explanatory variables.

Effect	2001			2002		
	df	F	p	df	F	p
Type	2, 18	96.51	<0.0001	2, 18	56.09	<0.0001
Year	4, 72	4.92	0.002	3, 54	11.90	<0.0001
Treatment	2, 72	1.78	0.176	2, 54	0.18	0.840
Year*Type	8, 72	1.66	0.124	6, 54	2.98	0.014
Type*Treatment	4, 72	1.26	0.294	4, 54	1.26	0.298
Year*Treatment	8, 72	3.43	0.002	6, 54	2.25	0.052
Year*Type*Treatment	16, 72	1.17	0.316	12, 54	1.52	0.147

Table B.4. Results from repeated-measures analysis of variance with diversity as the response variable and treatment, type (random effect), and year (time) as explanatory variables.

Effect	2001			2002		
	df	F	p	df	F	p
Type	2, 18	39.25	<0.0001	2, 18	52.85	<0.0001
Year	4, 72	20.35	<0.0001	3, 54	20.98	<0.0001
Treatment	2, 72	1.29	0.264	2, 54	0.25	0.958
Year*Type	8, 72	1.64	0.201	6, 54	0.69	0.506
Type*Treatment	4, 72	0.89	0.472	4, 54	0.46	0.762
Year*Treatment	8, 72	0.84	0.574	6, 54	0.95	0.470
Year*Type*Treatment	16, 72	0.90	0.575	12, 54	0.25	0.994

Table B.5. Results from repeated-measures analysis of variance with richness as the response variable and treatment, type (random effect), and year (time) as explanatory variables.

Effect	2001			2002		
	df	F	p	df	F	p
Type	2, 18	39.67	<0.0001	2, 18	16.78	<0.0001
Year	4, 72	18.43	<0.0001	3, 54	16.66	<0.0001
Treatment	2, 72	2.66	0.013	2, 54	2.99	0.014
Year*Type	8, 72	0.32	0.730	6, 54	0.30	0.745
Type*Treatment	4, 72	0.54	0.704	4, 54	0.07	0.990
Year*Treatment	8, 72	0.96	0.475	6, 54	1.02	0.419
Year*Type*Treatment	16, 72	0.30	0.996	12, 54	0.16	0.999

Figure B.1 Eighteen study sites at Fort Huachuca Military Reservation, Arizona, USA, classified into 3 community types: nonnative (L), mixed (M), or native (N) based on the proportion of Lehmann lovegrass from high to low, respectively. At each site, 1-ha plots were randomly assigned a treatment: no fire, spring fire, or summer fire.

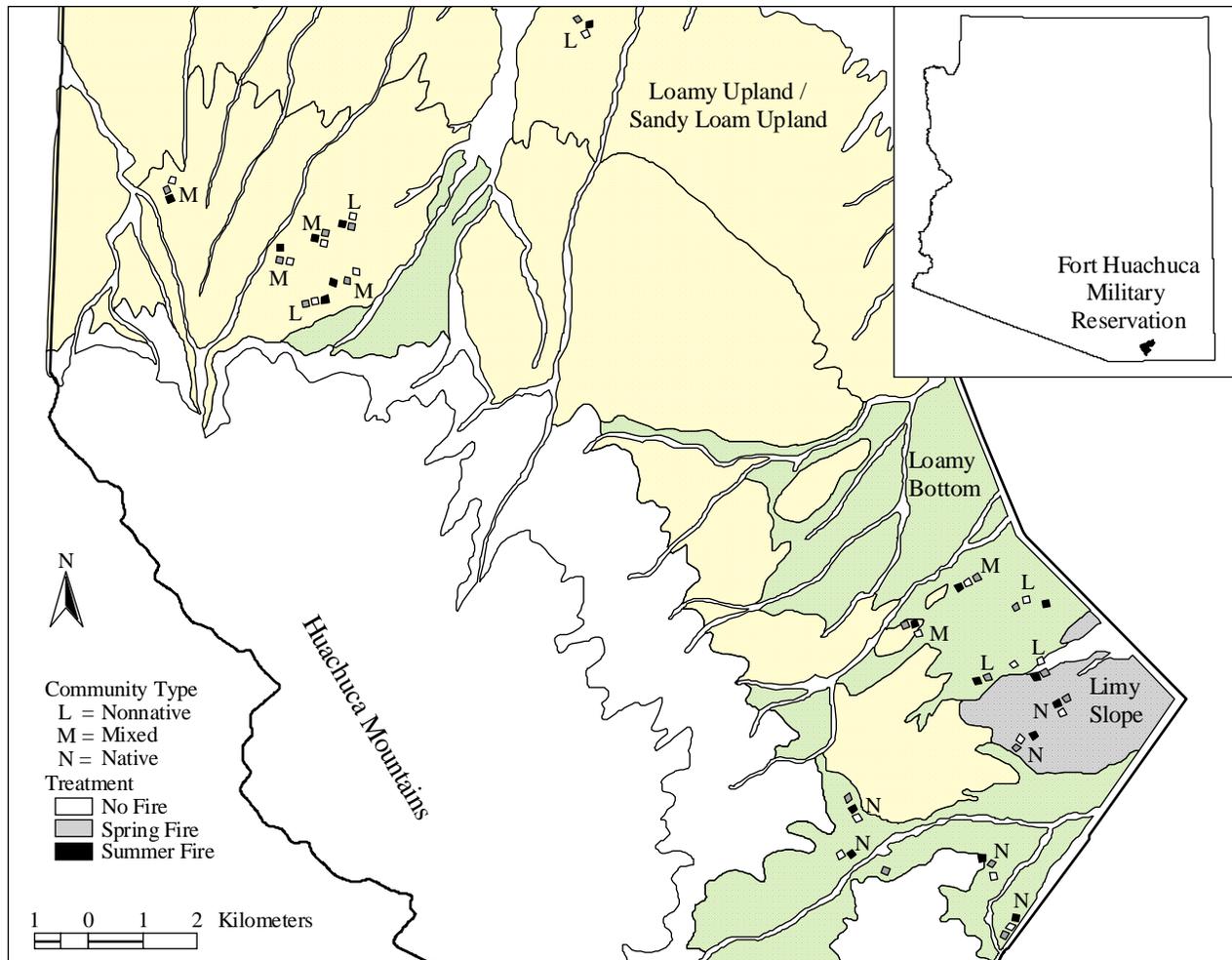


Figure B.2 Total biomass ($\text{g}\cdot\text{m}^{-2}$) sampled in fall at FHMR from 1999-2003 (left panel) and from 2000-2003 (right panel) on native (circles), mixed (squares), and nonnative (triangles) sites for plots treated with no fire (white), spring fire (gray), and summer fire (black).

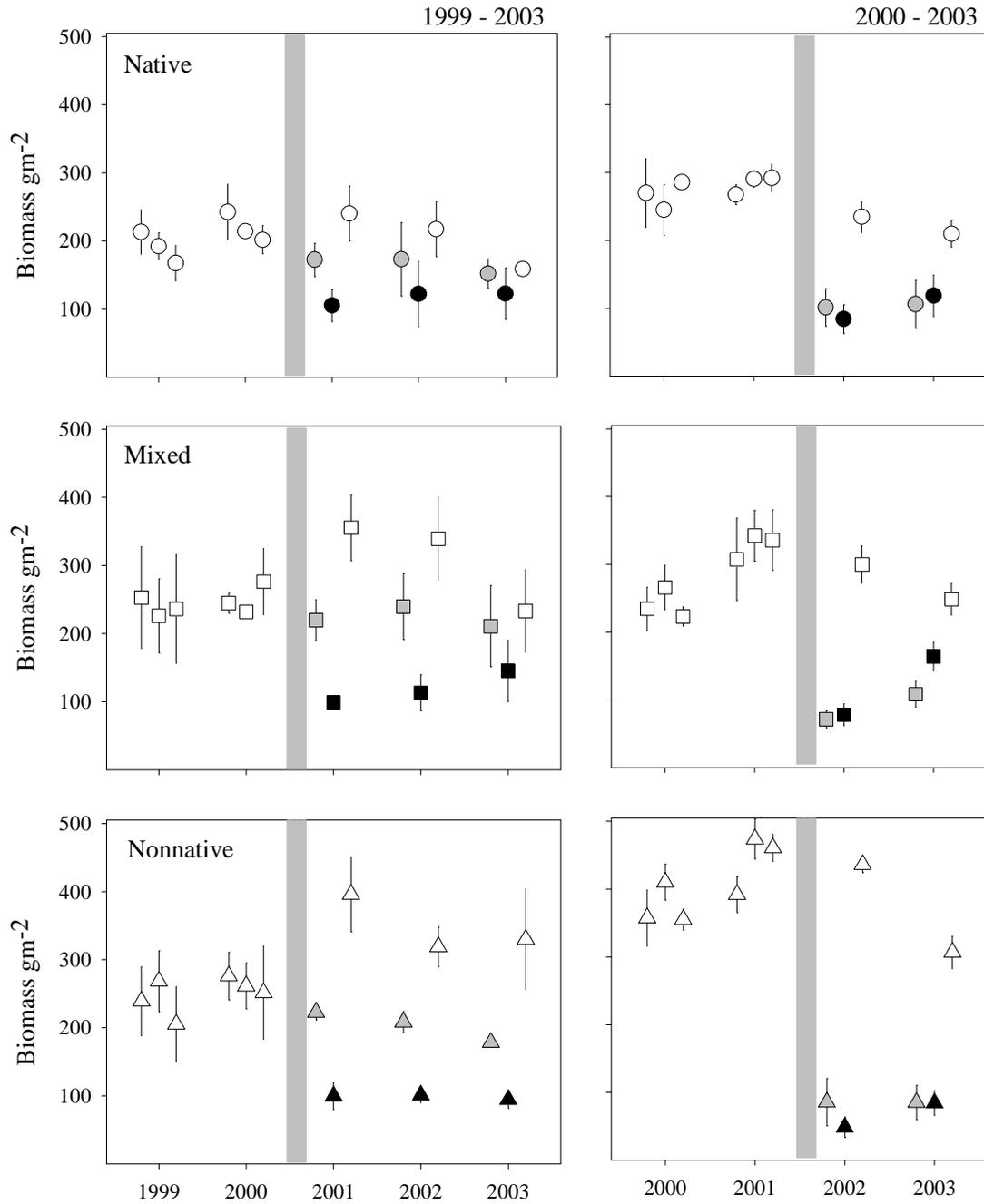


Figure B.3. Proportion of Lehmann lovegrass of total biomass sampled in fall at FHMR from 1999-2003 (left panel) and from 2000-2003 (right panel) on native (circles), mixed (squares), and nonnative (triangles) sites for plots treated with no fire (open symbols), spring fire (gray), and summer fire (black).

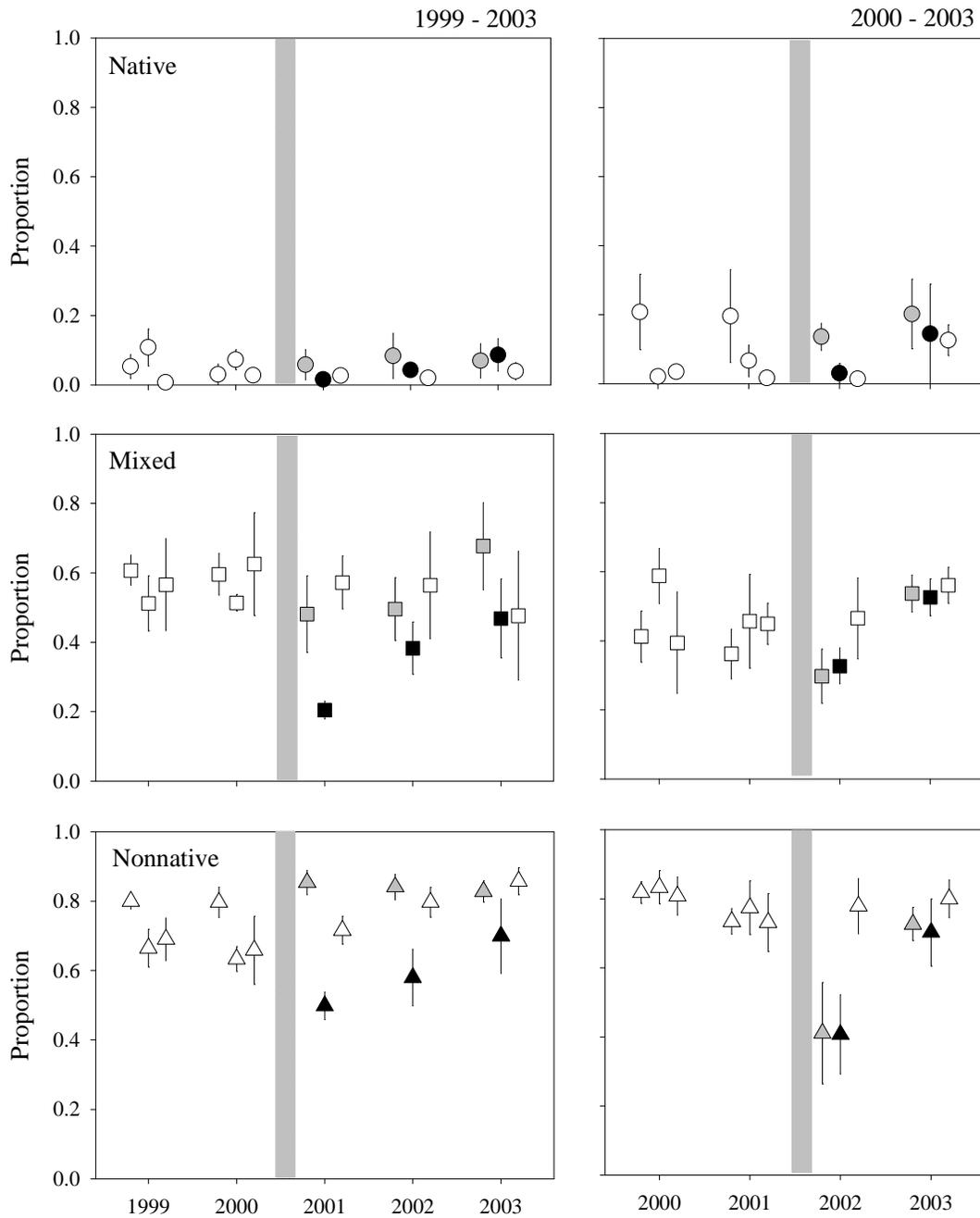


Figure B.4. Relationship between diversity (Simpson's Index, 1-c) and proportion of Lehmann lovegrass on plots sampled in fall at FHMR from 1999-2003. Open symbols represent unburned plots, gray symbols represent plots burned in spring, black symbols represent plots burned in summer. Native plots are represented by circles, mixed plots by squares, and nonnative plots by triangles.

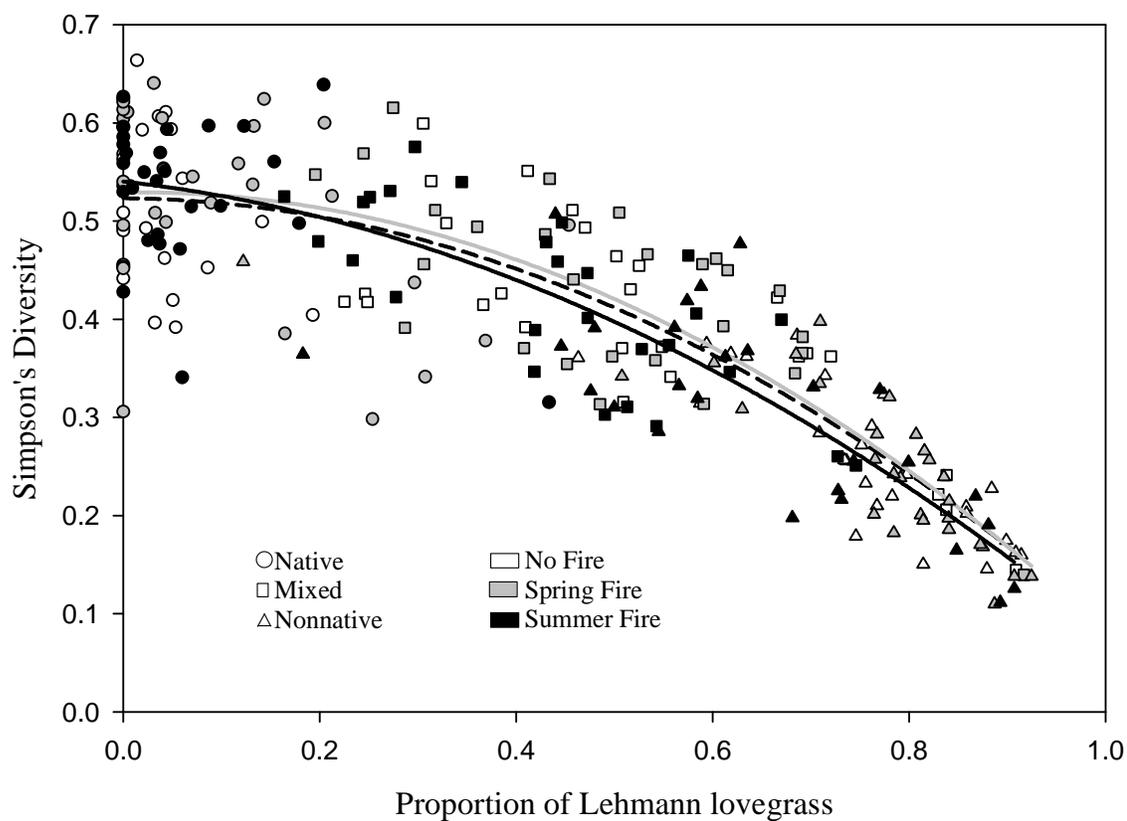


Figure B.5. Simpson's Diversity (1-c) sampled in fall at FHMR from 1999-2003 (left panel) and from 2000-2003 (right panel) on native (circles), mixed (squares), and nonnative (triangles) sites for plots treated with no fire (open symbols), spring fire (gray), and summer fire (black).

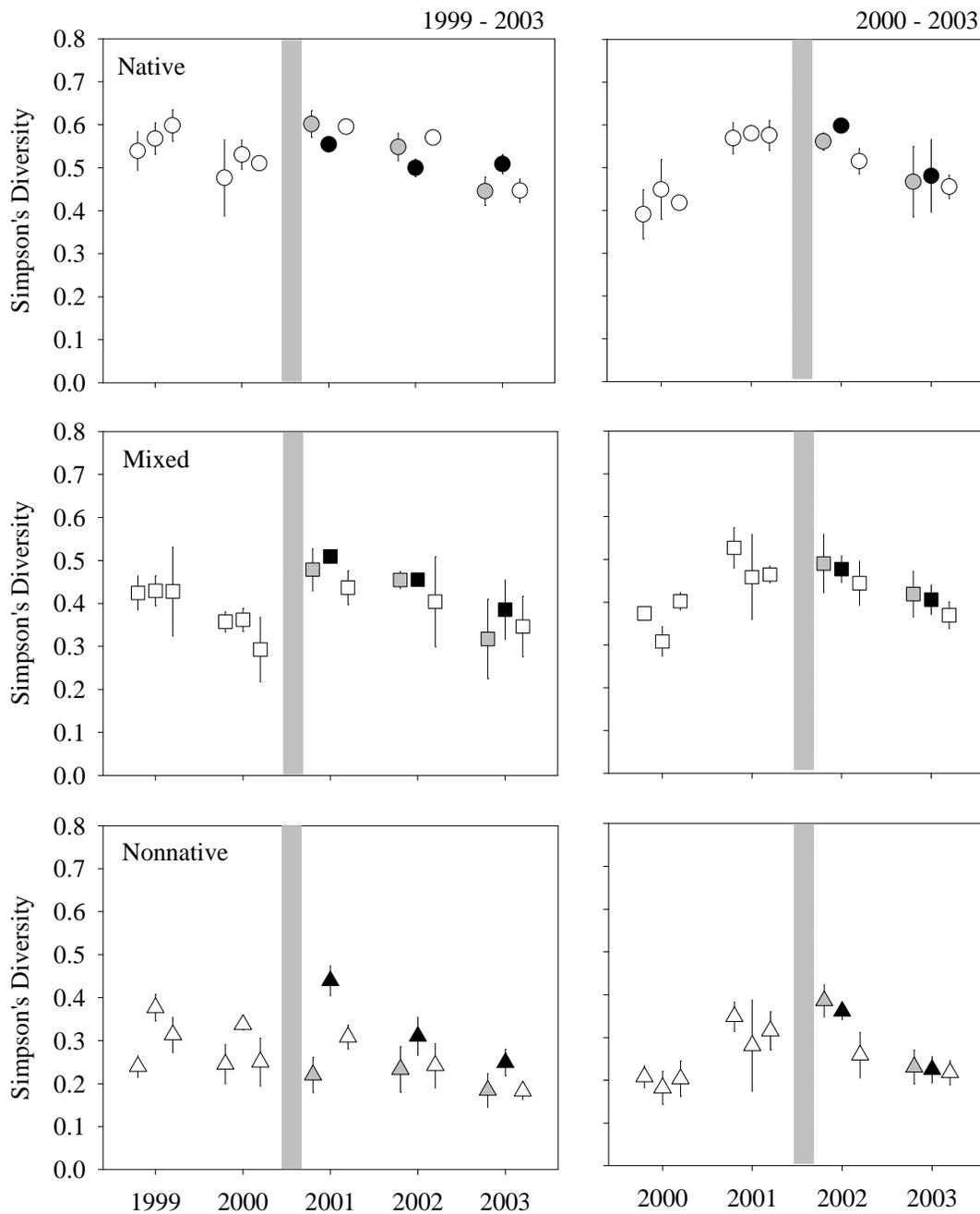


Figure B.6. Richness sampled in fall at FHMR from 1999-2003 (left panel) and from 2000-2003 (right panel) on native (circles), mixed (squares), and nonnative (triangles) sites for plots treated with no fire (open symbols), spring fire (gray), and summer fire (black).

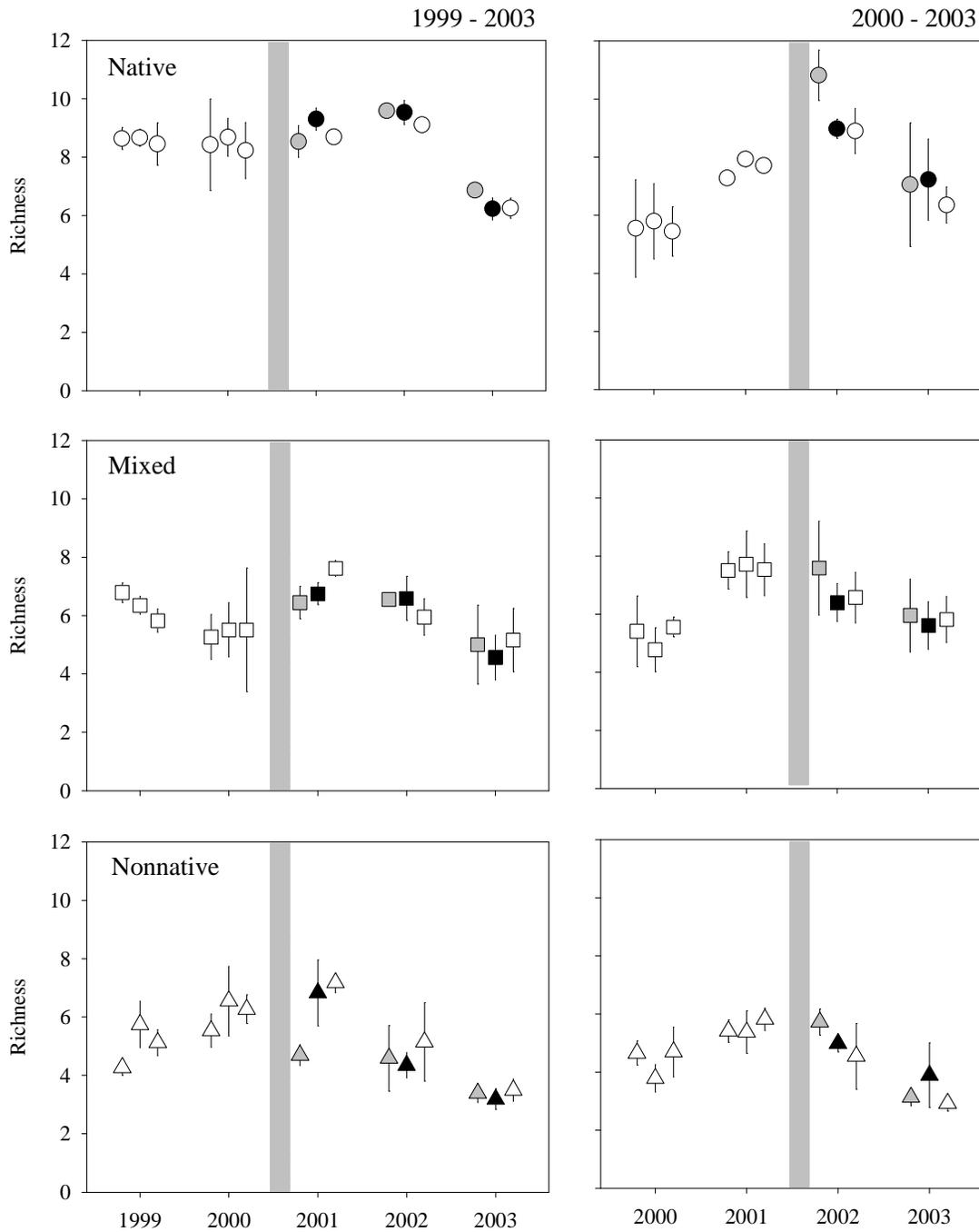


Figure B.7. Richness sampled in spring at FHMR from 2000-2004 (left panel) and from 2001-2004 (right panel) on native (circles), mixed (squares), and nonnative (triangles) sites for plots treated with no fire (open symbols), spring fire (gray), and summer fire (black).

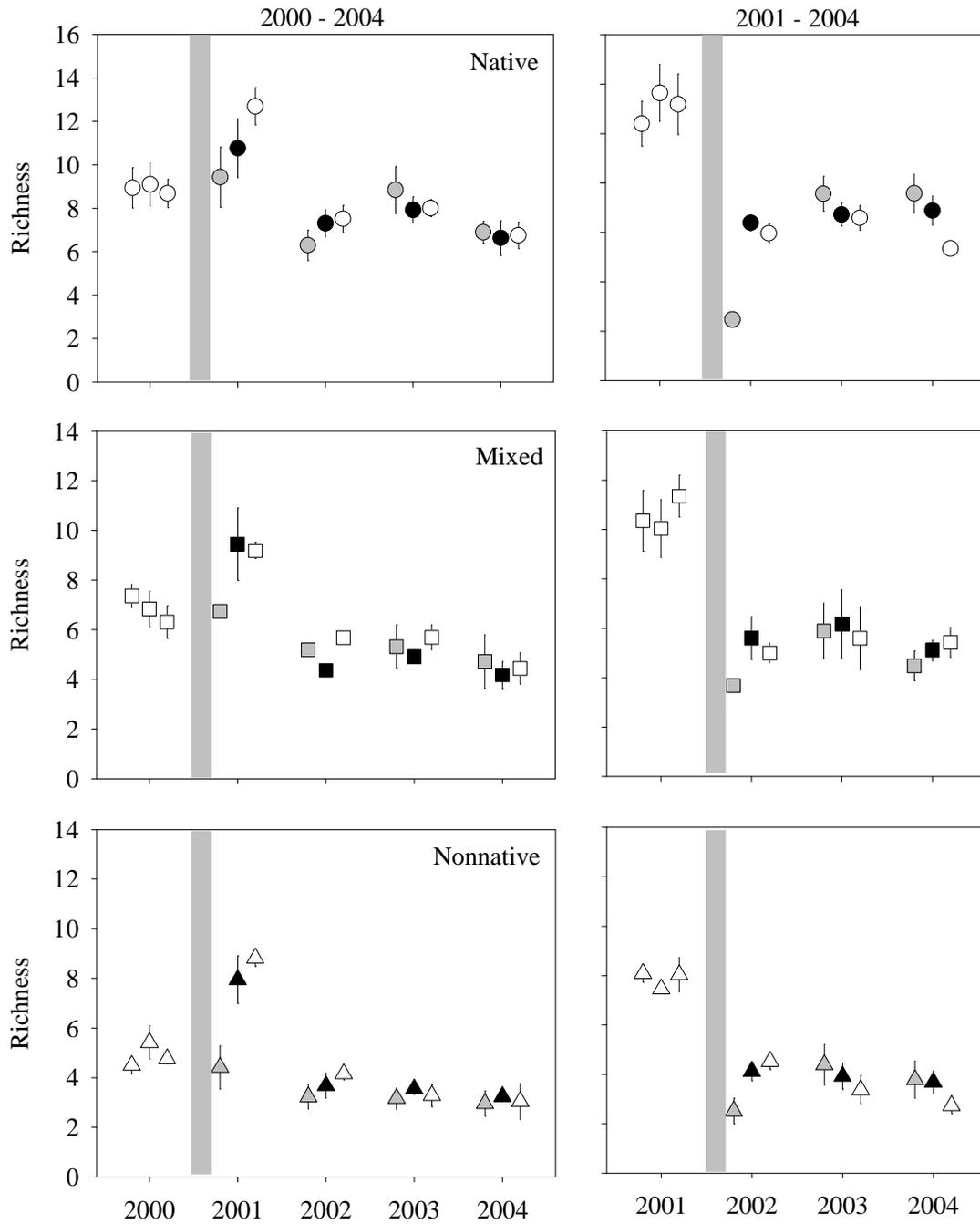
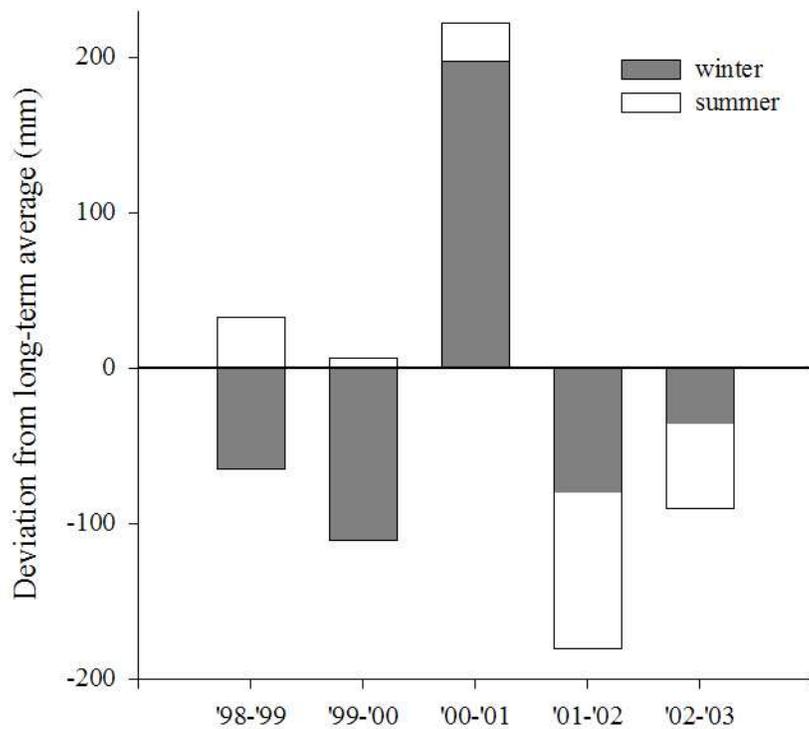


Figure B.8. Summer (May – September) and winter (October – April) rainfall deviation from long-term mean (379 mm) at Fort Huachuca Military Reservation, Arizona, USA over a 5-year period.



APPENDIX C

**DOES FIRE AFFECT GERMINATION AND SURVIVAL OF *AGAVE PALMERI*
IN SEMI-DESERT GRASSLANDS?**

ERIKA L. GEIGER

(To be submitted to International Journal of Wildland Fire)

Abstract

Management of ecosystems can be a complex task and practical constraints may force managers to apply fire in a way that differs from the frequency, timing, or extent of natural fires. Plants can survive fire either through tolerance or avoidance, however, persistence of many species may be reduced when the fire regime with which they evolved is altered. In grasslands in southern Arizona, fire may threaten *Agave palmeri*, a primary food source for the federally endangered lesser long-nose bat (*Leptonycteris curasoae yerbabuena*). To assess the effects of fire on agave I monitored survival and germination of agave on two soil types before and 1-2 years after prescribed fires and on control plots in spring and summer. Fires affected agave directly by destroying tissue and potentially indirectly by altering microclimate. Agave survived up to 85% damage to leaves before dying regardless of plant height, fire season, or soil surface. The probability of survival increased with plant size. Survival of small agave and germination of agave seed was reduced on burned plots compared to unburned plots, however, many small agave survived in areas that burned by avoiding fire or tolerating fire damage. Results from this study suggest that fires lit during seasons and at frequencies of the natural fire regime are not likely to negatively impact agave across the landscape.

Introduction

Succulents such as agave, yucca, and cactus are not typically characterized as fire-adapted species because they do not have protective outer bark and many do not resprout

after fire (Thomas and Goodson 1992), in contrast to many woody plants in fire-prone systems. Thus, after fire, mortality of succulents may be quite high (Humphrey and Everson 1951, Reynolds and Bohning 1956, White 1969, Humphrey 1963, O'Leary and Minnich 1981, Ahlstrand 1982, McLaughlin and Bowers 1982, Cave and Patten 1984, Brown and Minnich 1986, Thomas and Goodson 1992, Thomas 2006).

Despite apparent intolerance of fire, many succulents inhabit ecosystems where abundant, continuous fuels historically supported frequent fires (Wright and Bailey 1982). Their ability to persist in such environments is likely a result of two factors. First, fire frequency is heterogeneous across the landscape, especially where grass cover is sparse, probably allowing some individuals to escape fire until their life cycle was complete (Thomas 1991, McLaughlin and Bowers 1982). Second, succulents may tolerate fire (Thomas and Goodson 1992) depending on the life-stage or size of the plant. On large plants, meristematic tissue may be above flame height, and although tissue may be damaged, the plant continues to grow. Few studies document the effects of fire on *Agave* species and available data focus primarily on mortality of adult plants (Thomas and Goodson 1992). For example, an experimental burn resulted in the mortality of 18% of 41 individual *Agave palmeri* Engelm. (Agavaceae); of the remaining individuals, 83% survived by apical regrowth and 17% by evasion of fire in refugia (Thomas and Goodson 1992). The distribution and abundance of agave may have increased during the past century as an artifact of human-induced changes to fire regime: reduced fire frequency and intensity could have resulted in human-made and maintained refugia that supported

high numbers of agave individuals (Thomas 1991).

Reintroduction of fire into these ecosystems may alter the ability of agave to persist not only because fire has been absent but also because reintroduction likely will occur at different frequency, intensity, and seasonality than historic regimes. Wildfires in Arizona occurred during May and June when dry lightning strikes ignited desiccated fine fuels (Barrows 1978, Swetnam 1990). In contrast, prescribed fires often are set during cool or wet periods (October - March) to reduce the risk of the fire escaping. In addition the location and extent of fire is altered as ignitions and boundaries are forced rather than the result of vegetation characteristics (fuel distribution, moisture, or combustibility) and weather conditions (ignition season, humidity, or temperature). Prescribed fires might increase the probability of a site burning, especially if managers increase fire frequency, thereby limiting the ability of agave to “avoid” the effects of fire. Finally, fires may change grassland composition and thus alter the availability of fine fuels.

Setting fires in a season dissimilar to the natural regime may modify the resource use by plants. However, in one study comparing burned and unburned plants at three sites, fires were not found to affect nectar production, fruit or seed set of *A. palmeri* (Slauson 2002). Despite copious seed production, fires might influence dispersal distance and availability and quality of sites or likelihood of seed predation. For example, in an intact community, Nobel (1977) reported that rodents took 84% of seeds produced by another species of agave (*Agave deserti*). Fires alter microsite conditions such as temperature and available moisture (Daubenmire 1968). No research exists on the

germination of agave seeds after fire.

A conspicuous species in these grasslands, *Agave palmeri*, is a primary food source for the federally endangered lesser long-nosed bat (*Leptonycteris curasoae yerbabuena* Martinez and Villa). Despite documentation of the overabundance of nectar available to the bats (Ober 2000), managers consider agave to be fire-sensitive plants and are concerned that reintroducing fire will impact agave negatively and thereby reduce food resources for the lesser long-nosed bat. Many populations of *A. palmeri* are non-suckering (Gentry 1972) and thus would rely on regeneration from seed or the apical meristem if not damaged by fire. *A. palmeri* is a monocarpic perennial that must survive for several decades before a single reproductive effort produces 1300-2200 flowers and thousands of seeds (Gentry 1972, Howell and Roth 1981, Slauson 2000). This type of reproduction may represent 59% of measurable energy in biomass of the plant (Howell and Roth 1981).

Once seeds germinate they are still vulnerable to predation, mortality due to desiccation, and competition. Unless they are well protected, seeds and seedlings undoubtedly would suffer mortality from fire. Only about one in 2×10^9 seeds survives to the stage of reproduction (Gentry 1972). With adequate precipitation, seeds dispersed into recently burned areas would have greater access to available nitrogen, water, and space than in unburned areas (Wright and Bailey 1982). No data describe survival of fire by plants based on life stage. Assessment of fire effects on seedlings may be difficult because plants less than 3 years old are inconspicuous in the field (Gentry 1972).

Although dependent on characteristics of the fire, if fire occurred on average every 10 years (perhaps more than 10 years on sparsely vegetated sites), and some agave reach maturity within a decade, the species could easily persist in a fire-prone system.

Decreases in agave populations may result from mortality of extant plants, altered reproduction, and reduced germination following altered fire regimes. The objectives of this research are to quantify the effects of fire on survival and germination of *A. palmeri*. In addition, to investigate other potential factors influencing presence and survival of *A. palmeri*, I determined the potential for seed germination of *A. palmeri* on three soil types.

Methods

Study sites

The experiment was conducted in grasslands and mesquite (*Prosopis velutina* Woot.) savannas at the base of the Huachuca Mountains (31° 34' N, 110° 26' W) of southern Arizona. Elevations range from 1420 to 1645 meters and about two-thirds of the average annual precipitation of 440 mm falls between July-October and 20% falls between December-March (Fort Huachuca Military Reservation climate records). The region is characterized by a hot, dry period between late March and early July prior to the onset of seasonal “monsoon” rain. The most recent fires at the sites prior to treatment occurred 11 to 24 years ago. Few livestock have grazed at Fort Huachuca Military Reservation (FHMR) since the late 1800s, and livestock have been excluded since 1950.

Survival

I monitored 993 agave ≥ 30 cm on 15 1-ha plots at FHMR and 525 agave < 30 cm on 13, 20 m x 20 m subplots within the 1-ha plots. Each 1-ha plot was assigned to 1 of 3 prescribed-fire treatments: no fire, spring fire, summer fire (Figure C.1) and treated in 2001 (n = 9) or 2002 (n = 6). For each individual agave I measured height, diameter, and number of whorls (a whorl is a set of leaves produced each year) as an indicator of age (Howell 1996). Height was highly correlated among years (0.92-0.96) and was correlated with width within year (0.93-0.94). I selected height as the response metric for analyses because it is less likely to vary after fire treatment. I visually estimated and recorded percent fuel (woody and herbaceous biomass) surrounding the agave prior to fire. Additionally I estimated percent damaged after fire based as the number of whorls with greater than 25% of the leaves burned divided by the total number of whorls on the plant. Also, I noted whether the agave plant had bolted (production of inflorescence resulting in death) and whether the inflorescence was browsed.

I analyzed the effect of fuel, fire, and damage to plant on survival of small and large agave one and two years post-fire using logistic regression. I investigated survival at two levels: (1) a 1-ha plot as the experimental unit receiving one of three fire treatments and (2) individual agave plants as the experimental unit exposed to fire treatments. The latter analysis is a result of the inherent patchiness of fires, particularly those set in cool, wet conditions: some plants on burned plots were not damaged by fire and thus were considered “unburned.” Model outcome was similar for both levels and

only the data of effects on individual agave are presented here; any differences between the models and their implications are addressed in the discussion. Inclusion of fuel in the model reduced the total sample number because of incomplete data.

Germination and Fire

I selected a study site on soils of the Terrarosa complex (fine, mixed, superactive, thermic Aridic Paleustalfs) at FHMR. These soils support large populations of *A. palmeri* Engelm. and are dominated by a nonnative grass, *Eragrostis lehmanniana* Nees. In 2003, I established 30, 5-m by 5-m plots separated by a 2-m buffer. I assigned randomly one of three fire treatments to each plot: no fire, spring fire, summer fire. After fire treatment in center of each plot I placed a 1-m by 1-m fiberglass bags filled with 20 seeds. Half of the plots received supplemental watering treatments when the seeds were placed in the field. These 15 plots received water equivalent to a 20-mm precipitation event once weekly for one month. I had collected seed from agave fruits that had germinated the year prior and were tested in the lab for viability. At the end of the growing season (November) I collected the bags from the field and in the lab I placed seeds in petri dishes on Whatman #3 filter papers to allow germination; papers were treated with fungicide. I placed Petri dishes in an open well-lit lab and exposed them to 10 hours of light and 14 hours of dark for each 24-hour period. The number of seeds germinated (defined as radicle emergence) was recorded after 12 days; no seeds germinated after 12 days. To determine if the seed had germinated in the field or if it was not viable I cut open seeds that did not germinate

in the lab. I repeated the experiment in 2004.

I analyzed data on the number of seeds germinated in the field using logistic regression for binomial counts. The explanatory variables included fire treatment, plant date, and watering treatment. I analyzed the main effects and the 2-way interactions of these effects to determine which combinations of variables were significant indicators of germination success over time. Likely because of abundant rainfall during the summer monsoon both years, there was no effect of watering treatment and I excluded this variable and pooled data for the final model.

Germination and Soils

I tested germination of agave seed on 3 different soil surfaces based on soil series found on FHMR where agave are observed in varying abundance (Figure C.1): Terrarosa-Blacktail-Pyeatt Complex (Fine, mixed, superactive, thermic Aridic Paleustalfs – Fine, mixed, superactive, thermic Calcic Argiustolls – Coarse-loamy, mixed, superactive, thermic Aridic Calciustolls), Terrarosa Complex, and Carbine Very Gravelly Loam (Loamy, mixed, superactive, thermic, shallow Petrocalcic Calciustolls). At each site, I placed 8 fiberglass-mesh bags that contained 20 seeds at a depth of 1.5 cm. I harvested seed bags at 2, 4, 8, and 12 weeks, and 8, 9, 10, and 12 months. I counted the number of seeds that germinated in the field. For seeds that had not germinated in the field I tested germination in the laboratory to assess viability of seeds. I repeated the entire experiment in 2004.

Results

Survival

Fuel did not explain a significant portion of the variability in the models, therefore this variable was removed to allow for inclusion of more plants in the final model.

Survival of individual agave one and two years after treatment application varied with soil, height of agave, and fire treatment (Table C.1). Survival of large agave plants (≥ 30 cm) was slightly lower on Carbine soils ($82 \pm 2\%$) than Terrarosa soils ($91 \pm 1\%$) one year post-treatment and this difference increased in the second year (62% compared to 88%, respectively). In general, survival of large agave plants was not affected by fire except for slight evidence of a decrease in survival ($55 \pm 4\%$) two years after summer fire on Carbine sites compared to other sites (Figure C.2). Alternatively, for small agave survival was lower after fire, with reductions in survival as high as 50% two years post-fire compared to unburned plants. On Terrarosa sites, survival was 54-58% lower one year post-treatment and 38-50% lower two years post-treatment on burned plots, but response did not differ among fire seasons (Figure C.2). On Carbine sites, survival of small agave plants one year post-treatment varied with season, with agave exposed to summer fires resulting in survival 22% lower and spring fires 49% lower than survival of agave not exposed to fire. Two years post-treatment, survival was 38% lower for small agave plants exposed to spring fire but only 9% lower for those exposed to summer fire. Reduced survival due to factors other than fire (i.e., unburned agave) after two years was $73 \pm 4\%$ on Carbine soils and $84 \pm 5\%$ Terrarosa soils for small agave and $69 \pm 6\%$ on

Carbine soils and $92 \pm 3\%$ Terrarosa soils for large agave (Figure C.2).

Damage

Degree of fire damage to individual plants varied by fire season, soil type, and size (Table C.2). Individual agave plants suffered more damage from spring fires ($71 \pm 1\%$) than summer fires ($61 \pm 1\%$). Damage was 5% higher on Carbine than Terrarosa soils and small agave plants had 20% more damage than large plants agave. However, survival across fire season, soils, and size decreased only if 85% of the plant was damaged ($85 \pm 6\%$) and only $8 \pm 2\%$ plants survived with damage greater than 95%. Thus, agave plants had high tolerance to damage and survived as long as the center leaves remained unburned (Figure C.3).

Germination and fire

The proportion of agave seeds germinating in the field was influenced by two-way interactions between burn treatment and year, year and plant date, and burn treatment and plant date (Figure C.4) (Table C.3). Germination always was higher on unburned plots than burned plots although the magnitude of the difference varied by plant date and year. Seed germination was higher in 2004 ($49 \pm 4\%$) than to 2003 ($15 \pm 2\%$). In 2003, seeds on plots burned in summer had half the germination as those on plots burned in spring whereas in 2004, seed germination on plots burned in summer was 1.5 times higher than those burned in spring. Seed germination was about 25% on plots burned in

spring regardless of plant date whereas seed germination on unburned plots was 1.3 times higher for seeds planted in summer than seeds planted in spring. Seed on plots burned in summer were planted only in summer and germination was only 1.2 times higher than those planted in spring. In 2003, seeds planted in spring had twice the germination as seeds planted in summer whereas in 2004, seeds planted in summer had 1.4 times higher germination than those planted in spring.

Germination and soils

Germination occurred after the arrival of the summer rains in July and August. Seeds planted on Terrarosa complex or Terrarosa-Blacktail-Pyeatt complex soils had higher germination than seeds planted on Carbine gravelly loam after one year (Figure C.5). These differences increased (as did variability across Terrarosa soils) after two years in the field (Figure C.5) (Table C.4).

Discussion

Survival and soils

While the main focus of this study centered on effects of fire on *Agave palmeri*, I begin with a summary of the differences in agave demography and survival on two soil types as they provide the broadest explanation of our results and the other important factors tempering agave survival are contingent upon this resource. The relationship between soils and agave on our study sites is complex and varied. As I will describe in

subsequent paragraphs, effects of fire depend on size of agave and thus survival, as mediated by soil surfaces. The Methods section contains detailed information about the two soil surfaces included in this study: Carbine and Terrarosa. The former soils consist of very gravelly loam soils, are covered by cobbles, and occur on hillsides whereas Terrarosa sites contain more clay, are covered by cobbles, and occur primarily on flat surfaces.

Terrarosa sites supported 3 times the number of large agave plants (≥ 30 cm) as Carbine sites. Carbine sites seemed to favor the survival of small agave plants (< 30 cm) with approximately twice the number of small as large agave plants. This demography is perplexing when compared to Terrarosa sites that had nearly 2-3 times more large than small agave plants. Large agave plants may have been affected by historic fires but current numbers of small agave on the two soil surfaces is unlikely to have been directly influenced by fire as none of our study sites burned within the last 11-24 years. Survival of agave plants not exposed to fire for both years of the study was higher on Terrarosa sites than Carbine sites regardless of size of the plant. Our germination data suggest that conditions for survival of small agave plants should have been favored on Terrarosa sites because germination was higher than on Carbine sites. The combination of fine soil and large cobbles may help retain soil water on Terrarosa sites. In the Sonoran Desert the seedlings of saguaro, large columnar cacti, tend to grow adjacent to rocks on rocky soils perhaps because of slightly higher soil moisture than areas away from rocks (Turner et al. 1966). Microsite influences are critical for germination and establishment of many other

species as well. For example, surfaces with little soil development at Mount St. Helens, seedling establishment was higher on microsites with uneven terrain than flat surfaces (Shiro et al. 1997). Additional characteristics differ between the two surfaces and these may influence survival of agave include, available water holding capacity, albedo, specific heat, and available nutrients. Finally, distinct plant communities occupy these two surfaces: Carbine sites have more soil exposure and less vegetation biomass than Terrarosa sites.

Survival and fire

“In nearly every influence of burning, the time of the year, or even the time of day, when the fire occurs is almost as important as the occurrence of the fire itself” (Daubenmire 1968). Fire was less important to survival of large agave plants than soil type. However, survival of small agave plants was influenced by fire and the effect of season was contingent upon soil type. I do not know the mechanism by which season of fire had a differential affect on survival of small agave plants. The treatments could have affected vegetation differently because of antecedent climate conditions, fire characteristics, and conditions after fire. Survival of agave might be influenced by fire season because of differences in fire intensity determined by weather conditions prior to and at the time of fire (e.g., wind velocity), which determine the fuel and soil moisture and the additional heat required for fuel to combust (Daubenmire 1968). On average, fuel moisture immediately prior to summer fires was slightly higher than for spring fires,

which may have reduced the intensity of the former fires. On Carbine sites, spring fires were patchy (78% burned area) but summer fires burned completely (99%). On Terrarosa sites after spring and summer fires the amount of burned area was similar (88% and 92% respectively).

In general, large agave plants were favored on Terrarosa sites compared to Carbine sites, with survival at least 20% greater across treatments after two years. However, survival of large agave plants on Carbine sites burned in summer was lower than survival on spring-burned or unburned sites. I observed many large, healthy-looking agave plants that were uprooted, perhaps a result of herbivory by the Collared peccary (*Tayassu tajacu*) or pocket gophers (*Thomomys bottae*, *T. umbrinus*), whose patterns may have been altered by available herbaceous vegetation on sites burned during different seasons. Lower survival might have resulted from summer fires being more complete, although the effect of fire season was opposite from expected for small agave plants.

Survival of small agave plants was reduced by more than 50% when exposed to fire on Terrarosa soils regardless of fire season, and most of the mortality was evident within the first year after fire. Survival of unburned agave plants declined by 16% indicates background mortality less substantial than mortality caused by fire. Survival of small agave plants on Carbine sites also was reduced by 50% but only for agave plants exposed to spring fire. Survival of small agave plants on Carbine sites after summer fire dropped by 22% within the first year. Mortality of small agave plants on some sites that have not burned can be quite high, equaling the effect of fire, particularly if some plants

survive fire via tolerance or avoidance (Thomas 1991). Unburned agave dropped by 20% in the second year but two-thirds of the plants that died were located on burned plots but were not damaged by fire. This pattern suggests that survival may depend not only on direct effects of fire but also on indirect effects such as decreased plant cover.

Damage

Although mortality could be inferred by degree of damage to a plant (i.e., plants that did not survive averaged >95% damage), degree of damage was not as clearly related to season of fire, size of plant, or soil as might be expected. I assumed damage would be greater for plants exposed to summer fire because fuels are drier and temperatures hotter compared to spring fires. Additionally, I expected damage to be greater on Terrarosa sites because biomass is about 1.5 times greater than on Carbine sites (Chapter 3, this volume). Finally, I expected that smaller agave plants would be damaged more than large plants because it is more likely that heat and flames would reach the central tip of the former plants, especially if they were growing beneath vegetation. *Agave deserti* was commonly found growing beneath the grass *Hilaria rigida*, which provided more than a 20° C difference in temperature, helped to retain soil moisture and extended the growing season (Jordan and Nobel 1979). While herbs might act as nurse plants, agave plants growing beneath herbaceous plants may be at high risk of being exposed to fire.

Unexpectedly, agave experienced high mortality when exposed to spring fires and amount of fuel surrounding the plant did not influence damage or survival. Perhaps the

indirect effect of fire on vegetation and thus local changes to microclimate has a more profound effect on agave populations than flames damaging individual plants. If vegetation influenced high soil moisture, fire intensity and severity might be low. Although spring fires might burn at lower intensities than summer fires, spring fires also are followed by an extended period during which soils are exposed to solar radiation, thus temperatures are increased and soil moisture reduced. Summer fires, although more intense than spring fires, are immediately followed by rainfall and thus may stress the agave plants for a shorter period of time than fires during the spring. Shreve (1931) found that summer rains cooled soils to a depth of 7.5 cm. Perhaps other factors influencing fire behavior such as quality of litter, duration of fire, or climatic conditions such as drought may be better indicators of how fire will impact agave. Finally, fire seemed to have less of an effect on larger agave plants than smaller plants, perhaps both because the meristematic tissue has a better chance of surviving if further away from flames and also because large plants have large water-storage capacity compared to small plants that would allow them to survive xeric conditions after fire.

Germination and Fire

Agave germination in this study was lower on burned than unburned sites. For germinating seeds, fire likely has greater indirect than direct effects. Grassland seeds typically survive wildland fires and germination may be enhanced after fire (Daubenmire 1968, Wright and Bailey 1982). However, removal of vegetation reduces soil moisture

and increases soil surface temperature, thereby creating drought-like conditions in many grasslands (Phillips 1919, Scott 1934, Aldous 1934, Hanks and Anderson 1957, Anderson 1964, Cook 1939, McMurphy and Anderson 1965, West 1965). In drought years, biomass does not recover for several years (Reynolds and Bohning 1956, Cable 1965, Daubenmire 1968, Wright 1980, Wright and Bailey 1982, Valone and Kelt 1999, Appendix B, this volume) and in drier climates, there is an increase in the degree of drought in burned areas (West 1965). If soils were dry because a fire in spring left ground exposed for several months, these areas may require more precipitation than unburned areas to allow for germination. The substantial increase in germination of agave seeds between 2003 and 2004 may be a result of abundant rainfall in April 2004 after the spring fires, and this rainfall may have maintained soil moisture and reduced stress to seeds. An alternative explanation is the early start (June) of summer rains that prolonged the summer growing season that same year.

Germination and Soils

Seed germination trials on two soil surfaces revealed that seeds germinated in response to the summer rains, not all seeds germinated within the first year, and germination was higher on Terrarosa than Carbine surfaces. These two soil surfaces are characterized by distinct microsites based on their different soil textures, topography, albedo, and associated vegetation that are particularly important in influencing soil moisture. Establishment of *A. deserti* was limited by drought to only one year in 17,

suggesting that water stress in the seedling stage is a critical factor affecting establishment (Jordan and Nobel 1979). Indeed, despite large reproductive efforts, mortality of succulents may be quite high (Shreve 1917, Gentry 1972). Number of germinating seeds did not conform to demography of agave on the sites I sampled, perhaps because conditions for germination do not match requirements for survival. For example, while shade increased germination of saguaro seedlings, survival of unshaded plants was higher than shaded plants because of associated increased insect injuries (Turner et al. 1966).

Management Implications

While I recognize the socio-political constraints to land managers' setting fire at the historically appropriate season, altered disturbance regimes may not produced the desired state of an ecosystem (*sensu* Westoby et al. 1989). Many species may be adapted to fires occurring immediately prior to the arrival of the summer rains whereas fires occurring at other times of year leave the soils exposed for a long period. Unlike the rapid response of vegetation after early summer fires, most plants are dormant during other seasons and thus a fire at these times would leave soils exposed to increased solar radiation, erosion by wind and water, and increased evaporation of water.

Altered fire regimes may not be the only threat to succulent species; plant communities have transformed from open grasslands dominated by native grasses to savannas dominated by woody plants and nonnative grasses. Semi-arid grasslands were

characterized by caespitose (“bunch”) grasses with intervening bare ground (Brown 1994) that may have resulted in patchy fires; this physiognomy differs from the continuous cover resulting from the introduction and dominance of *Eragrostis lehmanniana* Nees. This perennial grass from South Africa produces more biomass than native grasses even during drought, and tends to decompose slowly because of its high carbon-to-nitrogen ratio (Cox et al. 1990; Appendix B, this volume). *Agave palmeri* plants at Fort Huachuca typically are found on surfaces with abundant cobbles where the associated vegetation is widely spaced. The presence of *E. lehmanniana* may negatively affect populations of Palmer agave by filling in open spaces, thus competing for resources and increasing the probability of fire exposure by providing a continuous cover of fine fuels. These changes in plant community structure and fire regime might alter the ability of individual agave to “avoid” or tolerate fires either as large plants, seedlings, or seeds waiting to germinate.

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Table C.1 Importance of agave height, fire treatment (no fire, spring fire, summer fire) and soil series (Carbine or Terrarosa) on percent survival of individual agave one and two years post-treatment based on logistic regression for binary counts (n=1518).

Effect	Year 1			Year 2		
	df	X²	p	df	X²	p
Height	1	55.83	<0.0001	1	30.35	<0.0001
Fire	2	87.13	<0.0001	2	52.63	<0.0001
Soil	1	7.18	0.007	1	49.13	<0.0001

Table C.2 Influence of soil, agave height, and fire season (spring or summer) on percent damage to individual agave based on analysis of variance.

Effect	df	SS	MS	F	p
Soil	1	2,672	9,556	9.89	0.016
Height	1	65,879	1,432	1.48	<0.0001
Fire season	1	3,940	8,822	9.13	0.003
Error	1018	462,486	454		

Table C.3 Importance of fire, year, and plant date for germination of *Agave palmeri* seeds based on logistic regression for binary counts.

Effect	df	X²	p
Fire	2	28.91	<0.0001
Year	1	88.18	<0.0001
Plant date	1	1.41	0.24
Fire x Year	2	9.45	0.01
Year x plant date	1	7.51	0.01
Fire x plant date	1	6.41	0.01
Fire x year x plant date	1	0.86	0.35

Table C.4 Importance of soil series (Carbine very gravelly loam, Terrarosa Complex, Terrarosa-Blacktail-Pyeatt Complex) and year (one and two years after planting) on germination of *Agave palmeri* seeds based on logistic regression for binary counts.

Effect	df	X²	p
Year	1	68.35	<0.0001
Soil	2	15.24	0.0005
Year x soil	2	15.25	0.0005

Figure C.1 Location of sites for agave seed germinations on three soil types (flags) and for monitoring of small and large agave on experimental fire plots (black circles, squares, triangles) at Fort Huachuca Military Reservation, Arizona, USA.

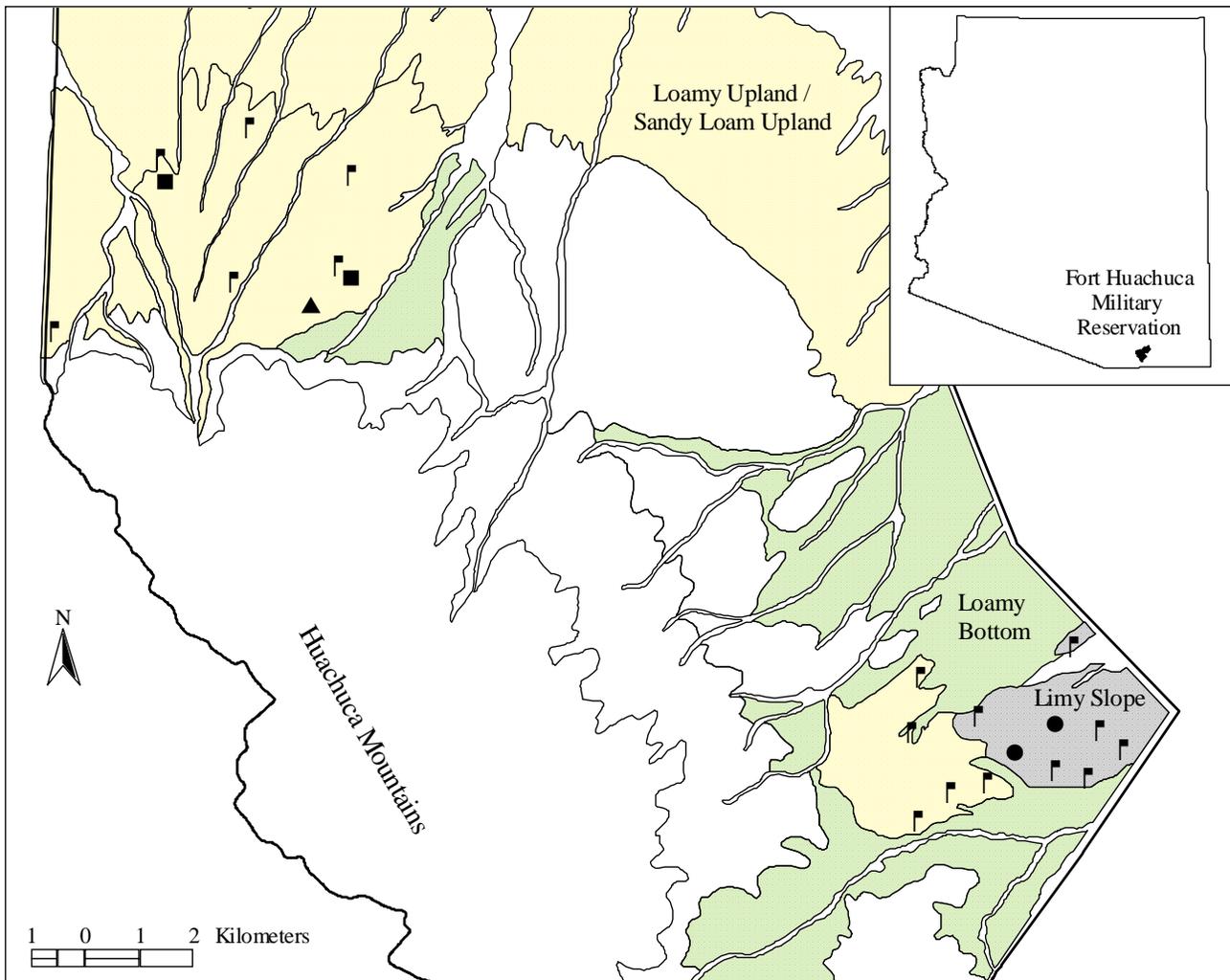


Figure C.2 Survival of individual small and large agave exposed to spring (light gray bars), summer (dark gray bars), or no fire (white bars) on Carbine and Terrarosa sites one (solid bars) and two years (bars with lines) after prescribed fire at Fort Huachuca Military Reservation, Arizona.

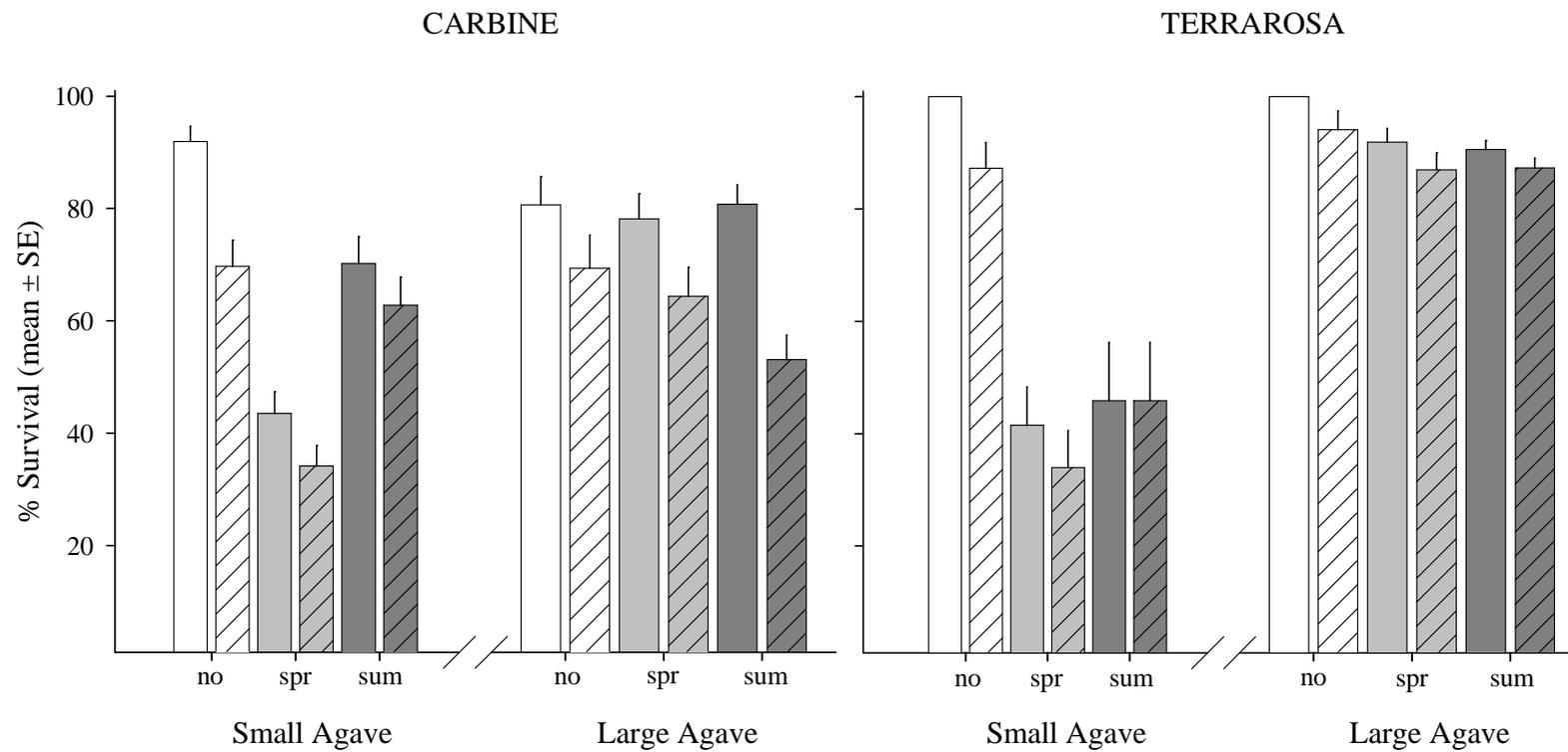


Figure C.3. Large agave (>30 CM) with 50% damage to leaves and center tip unburned one year after prescribed fire at Fort Huachuca Military Reservation, Arizona, USA.



Figure C.4. Percent seed germination of *Agave palmeri* (mean \pm SE) in the field after fire treatment (no fire, spring fire, summer fire) and by plant date (May or June) in 2003 (solid bars) and 2004 (striped bars) at Fort Huachuca Military Reservation, Arizona, USA.

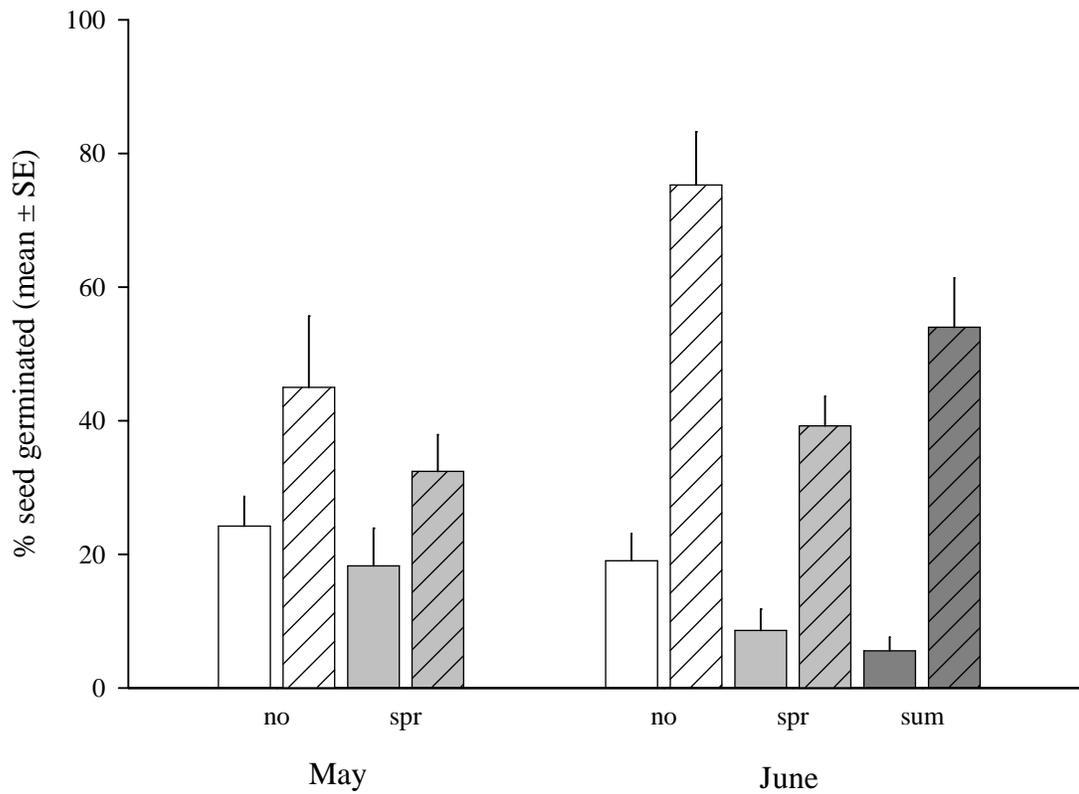


Figure C.5 Percent seed germination of *Agave palmeri* (mean \pm SE) in the field one year (solid bars) and two years (striped bars) after planting on three soil series: Carbine very gravelly loam, Terrarosa Complex, Terrarosa-Blacktail-Pyeatt Complex, at Fort Huachuca Military Reservation, Arizona, USA.

