

THE PROSPECTS FOR SPREAD AND IMPACTS OF REMOVAL  
OF *ERAGROSTIS LEHMANNIANA* NEES

by

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A Dissertation Submitted to the Faculty of the

SCHOOL OF NATURAL RESOURCES

In Partial Fulfillment of the Requirements  
For the Degree of

DOCTOR OF PHILOSOPHY  
WITH A MAJOR IN RENEWABLE NATURAL RESOURCES

In the Graduate College

THE UNIVERSITY OF ARIZONA

2005

THE UNIVERSITY OF ARIZONA  
GRADUATE COLLEGE

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entitled The Prospects for Spread and Impacts of Removal of *Eragrostis lehmanniana* Nees

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.

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## ACKNOWLEDGEMENTS

A great deal of credit goes first to my fabulous husband, Michael Crimmins, for providing the love and support I needed to complete this degree. He provided a wonderful sounding board for my thoughts and had major positive influence over this document's content. Great thanks also are in order for my parents (both sets!), my sisters, and my friends for their encouragement and listening ears.

Many thanks are in order for my committee, Drs. Randy Gimblett, Steve Archer, Andrew Comrie, John Kupfer, and especially my advisor, Dr. Guy McPherson. Their input and guidance at various times throughout my career at the University of Arizona helped to shape this study and will have lasting impacts.

I was fortunate to perform my field experiment at three locations in southeastern Arizona and several kind individuals made this possible. Thanks to Coronado National Memorial staff and Chief of Resources Barbara Alberti for their on-site support of my study. Mark Heitlinger and Dr. Mitch McClaran made it possible for me to replicate my study at the Santa Rita Experimental Range. Finally, Dave Harris and Barbara Clark of The Nature Conservancy considerately allowed the experiment to take place on the Three Links Farm. Additionally, Arturo Baez and Mark Carson of the Campus Agricultural Center, provided facilities support of the greenhouse portion of the study.

Many individuals graciously donated their time to assist with field data collection, including Barbara Alberti, Jeff Balmat, Kristen Beaupre, Mike Crimmins, Andy Hubbard, Sara Jensen, John Kupfer, Melissa Mauzy, Jeff McGovern, Guy McPherson, Sheila Merrigan, Katie Nasser, Meg Quinn, Sarah Studd, Amy Tendick, Jason Welborn, Marcela Yopez, and several volunteers from Coronado National Memorial. Meg Quinn provided plant identification expertise. Very special recognition is order for the generous members of Majestic Management: Dennis Crimmins, Jim Nunnold, John Connors, Steve Britz, Gordon Ruttan. These individuals repeatedly traveled from Michigan to Arizona, on their own time and money, to assist with fieldwork. I owe them beer wages for decades to come!

I am especially grateful to my wonderful co-workers at the Sonoran Desert Network Inventory & Monitoring office. Kristen Beaupre and Debbie Angell provided invaluable data management support and Melissa Mauzy played a very important role in field and greenhouse data collection. Andy Hubbard served as a second mentor to me, reading multiple drafts and providing priceless guidance on data analysis and reporting techniques. Andy also provided plenty of comic relief.

Several friends offered great intellectual contributions, especially Erika Geiger and Heather Schussman. Our collaboration will continue far beyond this document.

Administrative support was provided by Valery Catt, Cheryl Craddock, Anne Hartley, Dee Simons, and Cecily Westphal.

This research was funded in part by the University of Arizona Space Grant Fellowship Program, Center for Invasive Plant Management Award Number ESA-000011, and a grant from T&E, Inc.

Theresa Mau-Crimmins

## DEDICATION

*To Mike, who provided the love and support to make this possible, and to the wonderful members of Majestic Management: Dennis Crimmins, Jim Nunnold, John Connors, Steve Britz, and Gordon Ruttan.*

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## ABSTRACT

Non-indigenous invasive species are a major threat to native species diversity and ecosystem function and have been called the single worst threat of natural disaster of this century. *Eragrostis lehmanniana* Nees (Lehmann lovegrass), a tufted perennial bunchgrass native to southern Africa, is one such problematic species in Arizona, USA. This dissertation research is a mix of predictive modeling and field experiments designed to inform management decisions based on greater understanding of this nonnative species, with emphasis on the potential for spread and the impacts of removal.

The modeling studies in this dissertation aimed to predict the potential distribution of *E. lehmanniana* in the southwestern United States under current and potential future climate conditions. The first portion of study addressed a common assumption in predictive modeling of nonnative species: data from the species' native range are necessary to accurately predict the potential distribution in the invaded range. The second portion of this study predicted the distribution of *E. lehmanniana* under 28 different climate change scenarios. Results showed the distribution of *E. lehmanniana* progressively shrinking in the southeastern and northwestern portions of the state and increasing in the northeastern portion of the state with increasing temperatures and precipitation. Key shifts occurred under scenarios with increases in summer and winter precipitation of 30% or more, and increases in summer maximum and winter minimum temperatures of at least 2°C.

The field experiment served as a pre-eradication assessment for *E. lehmanniana* and indicates how semi-desert grassland communities in southeastern Arizona may

respond to the removal of this species. This study suggested that plant community response to removal of an introduced species is mediated by precipitation variability (timing and amount), local site history, and edaphic conditions. The response observed on a site previously farmed for decades was to subsequently become dominated by other nonnative annual species. However, the two other sites with histories of livestock grazing responded more predictably to the removal, with an increase in annual ruderal species (2 to 10 times the amount of annual cover recorded on control plots).

## CHAPTER 1. INTRODUCTION

### **Explanation of the Problem**

Exotic species have been called the “single most formidable threat of natural disaster of the 21<sup>st</sup> century” (Schnase et al. 2002), causing economic impacts estimated at more than \$100 billion annually (Pimentel et al. 1999). Non-indigenous invasive species are a major threat to native species diversity and ecosystem function and can impact native species and ecosystems in potentially irreversible ways (Chapin et al. 1996, Mack and D’Antonio 1998, Wilcove et al. 1998). The continued introduction of nonnatives is expected to increase with increases in international trade (Office of Technology Assessment 1993).

Anticipating the impacts of introduced species is difficult, as species’ distributions are expected to change under predicted climate change (Watson et al. 1996). Climate plays a large role in determining the distribution of plant species and communities (Huntley and Webb 1988, Wright et al. 1993). Significant increases in precipitation and temperature as well as shifts in precipitation seasonality are expected for the southwestern United States in the coming decades (IPCC 2001), suggesting major shifts in community and species distributions. The structure and diversity of ecosystems are expected to undergo considerable changes (IGBP 1988, Watson et al. 1996), potentially having detrimental impacts on ecosystem stability (Mooney 1997). Such reshuffling could favor nonindigenous species, especially those with the capacity to disperse rapidly and compete strongly for resources.

Managing nonnative species is resource-intensive, requiring a long-term commitment (Hiebert 1997). Effective management strategies must be based on thorough knowledge of introduced species' modes and rates of spread, potential and known effects, and control methods. Byers et al. (2002) identify a disconnect between science and management, and managers are not receiving the information they need to make informed decisions. Scientists can help managers make sound decisions by providing them answers to questions such as:

- Are nonnative species still spreading to new regions?
- Will spread of nonnative species continue at the same rate under an altered climate?
- What events follow the control or eradication of a nonnative species?

This study attempts to address this research gap by exploring these questions for a nonnative perennial grass in southern Arizona, *Eragrostis lehmanniana* Nees (Lehmann lovegrass).

## **Approach**

This dissertation research is a mix of predictive modeling and field experiments designed to inform management decisions based on greater understanding of nonnative species, with emphasis on the potential for spread and the impacts of removal. The target species for these studies is *Eragrostis lehmanniana* Nees, a tufted perennial bunchgrass native to southern Africa that was brought to Arizona, USA in the 1930s to counteract low plant cover and highly eroded soils resulting from decades of overgrazing and

drought. As part of a far-reaching search for drought-tolerant plants, several accessions of *E. lehmanniana* were brought to Arizona (Crider 1945). In Arizona, *E. lehmanniana* has been associated with decreased plant and animal species richness (Cable 1971, Bock et al. 1986) and plant species diversity (Geiger and McPherson 2004). This apomictic grass has also been linked to alteration of ecosystem processes (Cable 1971, Williams and Baruch 2000). The modeling studies in this dissertation aim to predict the potential distribution of *E. lehmanniana* in the southwestern United States, under current and potential future climate conditions. The field experiment serves as a pre-eradication assessment for *E. lehmanniana* and indicates how semi-desert grassland communities in southeastern Arizona may respond to the removal of this species. A second objective of the field study was to characterize the seed banks at these sites; this was accomplished through a greenhouse study of seed bank samples.

### **Organization of the Dissertation**

The research presented in this dissertation consists of three separate, but related, studies. Each study is presented as a separate paper in the appendix and is ready for submission to a journal for consideration of publication. Literature reviews for each study are found within respective papers.

Appendix A, titled, “Can an invading species’ distribution be predicted using data from its invaded range? Lehmann lovegrass (*Eragrostis lehmanniana*) in the southwestern United States,” was co-authored with Heather Schussman and Erika Geiger and has been submitted to *Ecological Modelling*. Schussman and Geiger assisted with

original idea formulation and provided extensive assistance in reviewing and revising drafts of this paper. This study addressed a common assumption in predictive modeling of nonnative species: data from the species' native range are necessary to accurately predict the potential distribution in the invaded range. The purpose of this study was to explore differences in distribution predicted from two different sets of input data.

Appendix B, titled, "Modeling future potential distributions of *Eragrostis lehmanniana* (Lehmann lovegrass) in Arizona, USA" was prepared for submission to *Diversity and Distributions*. In this study, I explored the potential effects of climate change on the distribution of *E. lehmanniana* in the southwestern United States using ecological niche modeling. The Genetic Algorithm for Rule-set Prediction, a well-tested ecological niche modeling tool (Stockwell and Peters 1999, Peterson et al. 2001, Peterson et al. 2002, Oberhauser and Peterson 2003, Peterson and Shaw 2003), was used to predict the distribution of *E. lehmanniana* under 28 climate change scenarios. I will be sole author of this manuscript.

Appendix C, titled, "Community-level and seed bank response to the removal of *Eragrostis lehmanniana* (Lehmann lovegrass) at three sites in southeastern Arizona," was prepared for submission to *Ecological Monographs*. This study serves as a pre-eradication assessment for *E. lehmanniana* and indicates how semi-desert grassland communities in southeastern Arizona may respond to the removal of this species. A second objective of this study was to characterize the seed banks at these sites, which was accomplished through a greenhouse study of seed bank samples. This study will be co-

authored by Dr. Guy McPherson, who played a large role in research question formulation and study design.

## CHAPTER 2. PRESENT STUDY

The methods, results, and conclusions of this dissertation are distributed in the appended papers. Together, the three studies address gaps in our understanding of nonnative plant species, specifically regarding the potential for spread and impacts of their removal. This applied research is directly applicable for land management decision-making.

Appendix A – “Can an invading species’ distribution be predicted using data from its invaded range? Lehmann lovegrass (*Eragrostis lehmanniana*) in the southwestern United States”

Ecological niche modeling and climate-matching have gained momentum recently for predicting potential invasions (Hoffman 2001, Peterson and Vieglais 2001, Welk et al. 2002, Peterson 2003). These methods are based on the assumption that a species’ ecological niche can be described as the  $n$ -dimensional hypervolume of environmental conditions under which it is able to maintain populations without immigration (Grinnell 1917). Almost exclusively, species’ invasions outside of their native ranges have been predicted with this method using locations where it is confirmed to exist, or known presence points, from their native ranges. However, using locations from the native range assumes the same factors determine the distribution of the species in the invaded range. Depending on the species’ introduction history, this assumption may not be appropriate. In addition, acquiring data from native ranges is often very expensive and time-

consuming and is not always feasible. Finally, the scale at which species' potential invaded-range distributions can be modeled using native-range data is often too coarse for specific management decisions. The purpose of this study was to investigate whether invaded-range models could work as well or better than native-range models in the case of a purposely-introduced species.

We used confirmed presence points from the native range, southern Africa, and the invaded range, the southwestern United States, to predict the potential distribution of the perennial bunchgrass *Eragrostis lehmanniana* Nees (Lehmann lovegrass), in its invaded range in the U.S. The two models showed strong agreement for the area encompassed by the presence points in the invaded range, and offered insight into the overlapping but slightly different ecological niche occupied by the introduced grass in the invaded range. Regions outside of the scope of inference showed less agreement between the two models. *Eragrostis lehmanniana* was selected via seeding trials before being planted in the United States and therefore represents an isolated genotype from the native-range population. The results of this study demonstrate that geographic distributions of invading species built on points occupied in the invaded range may perform as well or better than those developed from the native range, at least for the region encompassed by confirmed presence points in the invaded range. In addition, predictions based on invaded-range points can offer insight into the environmental conditions tolerated by the invader and inconsistencies in the ecological niche between native to invaded ranges. Models created from locations in both the invaded and native

ranges can lead to a more complete understanding of an introduced species' potential for spread, especially in the case of anthropogenic selection.

Appendix B – “Modeling future potential distributions of *Eragrostis lehmanniana* (Lehmann lovegrass) in Arizona, USA”

Climate plays a large role in determining the distribution of plant species and communities (Huntley and Webb 1988, Wright et al. 1993). Significant increases in precipitation and temperature as well as shifts in the seasonality of precipitation are expected for the southwestern United States in the coming decades (IPCC 2001), suggesting major shifts in community and species distributions. The structure and diversity of ecosystems are expected to undergo considerable changes (IGBP 1988, Watson et al. 1996), potentially having detrimental impacts on ecosystem stability (Mooney 1997). Such reshuffling could favor nonindigenous species, especially those with the capacity to disperse rapidly and compete strongly for resources.

Because *E. lehmanniana* has been observed to invade native communities in southern Arizona and disperse widely without the aid of disturbance (Cable 1971, Anable et al. 1992), this species can be expected to spread into new areas with a changing climate. Future spread predictions can facilitate early detection and control measures, thereby keeping recently established populations in check. In this study I explored the potential effects of climate change on the distribution of *E. lehmanniana* in Arizona using ecological niche modeling. In addition to the prediction maps, one benefit of this

approach was that model parameters were compared directly with key limiting ecological parameters known to affect populations of the species in question.

Based on predictions of popular global-scale general circulation models, 28 climate-change scenarios were created for this study by modifying existing long-term averages of climatic variables. Using the Genetic Algorithm for Rule-set Prediction model (GARP; Stockwell and Peters 1999), I modeled the ecological niche for *E. lehmanniana*. This niche, characterized by a set of rules, was then projected onto each of the 28 climate change scenarios to represent potential habitat under potential future conditions. Future scenarios show the distribution of *E. lehmanniana* progressively shrinking in the southeastern and northwestern portions of the state and increasing in the northeastern portion of the state with increasing temperatures and precipitation. Key shifts occur under scenarios with increases in summer and winter precipitation of 30% or more, and increases in summer maximum and winter minimum temperatures of at least 2°C. Spread to new environments will be limited by the ability of viable *E. lehmanniana* seed to reach new habitats.

Appendix C – “Community-level and seed bank response to the removal of *Eragrostis lehmanniana* (Lehmann lovegrass) at three sites in southeastern Arizona”

Often, the response to the discovery of an exotic species with detrimental impacts is control or eradication, based in part on the success of other large-scale eradication efforts (Myers et al. 2000). However, eradication may not lead to the recovery of the affected system, as some species alter systems so greatly that they are shifted to a

different stable state (Westoby et al. 1989, Zavaleta et al. 2001). Alternatively, the effect of such a management action could actually exacerbate the problem. For example, efforts to control and reduce a nonnative plant species could initiate unexpected and undesirable feedbacks, such as favoring other nonnative species or drastically reducing plant cover to the detriment of wildlife and soil resources.

Zavaleta et al. (2001) argue for pre-eradication assessments to ascertain that a removal will yield the expected results and minimize unwanted effects. Assessments can help determine a community's response to the removal of a nonnative species, especially when the nonnative species is dominant. Such assessments should address direct and indirect effects of removing the nonnative species, including response of both plants and animals in the system. A second component of a pre-eradication assessment is an assessment of the potential for reestablishment by members of the native community. Seed bank studies provide some insight into a site's potential for recovery when the exotic species being removed is a plant. The response of animals to the removal of *E. lehmanniana* was beyond the scope of this study, and not included.

This study was a pre-eradication assessment of *Eragrostis lehmanniana* Nees (Lehmann lovegrass), a perennial bunchgrass that has been associated with decreased plant and animal species richness (i.e., Cable 1971, Bock et al. 1986) and plant species diversity (Geiger and McPherson 2004). In addition to decreased species richness, *E. lehmanniana* has been associated with the alteration of ecosystem processes (Cable 1971, Bock et al. 1986, Williams and Baruch 2000), modification of community composition

(Anable et al. 1992), and changes in fire regimes (Ruyle et al. 1988, Burquez and Quintana 1994, Biedenbender and Roundy 1996).

The results of this study indicate how semi-desert grassland communities in southeastern Arizona may respond to the removal of this species. This was addressed through a removal experiment of *E. lehmanniana* at three sites dominated by the nonnative grass. Field studies offer the best representation of the effects of a wide-scale eradication effort, as study sites are subject to natural variations in temperature and precipitation and reflect its disturbance history. Because seed banks represent, in part, a site's potential for recovery following removal of aboveground vegetation, a second objective of this study was to characterize the seed banks at these sites. This was accomplished through a greenhouse study of seed bank samples.

The results of this study suggest that the response of a site to the removal of a dominant nonnative grass varies between sites. In this study, a site with a history of intensive agriculture showed no strong response to the removal of a dominant nonnative species. Two other sites with a history of livestock grazing demonstrated similar strong responses to the removal, with large increases in native plant cover, increases in species richness and no evidence of "new" nonnative species replacing removed species. The findings from the latter two sites are consistent with other experiments that removed dominant nonnative plants (Farnsworth and Meyerson 1999, Morrison 2002). The seed banks of these three sites indicate that the potential for the nonnative plant to recover from seed is limited, as the seed bank declines dramatically without the input of seed rain.

Community composition of the treated plots at the three sites varied considerably, and reflected common species near each site. Seed-bank studies revealed a small number of additional species not observed in the aboveground vegetation for each site. These patterns suggest that removing the nonnative plant from a site would result in the site's conversion to an ecosystem dominated by native plants. However, if the goal is restoration of the site to a pre-invasion grassland, it may be advisable to undertake restoration measures in conjunction with removal efforts. Seeds of native perennial species may promote transition from an annual-dominated site to a more diverse, perennial-dominated community.

### **Summary**

Nonnative species introductions have been taking place as long as humans have inhabited the planet (Mack 2001), some with devastating impacts. Some of the most problematic and widespread plant introductions have been grasses in ecosystems worldwide (Whisenant 1990, D'Antonio and Vitousek 1992, Weber 1997, White et al. 1997, D'Antonio et al. 1998). Introduced grasses directly affect resource availability (Gordon et al. 1989, Williams and Hobbs 1989), alter fire frequency (D'Antonio and Vitousek 1992, Brooks et al. 2004), and impact nitrogen and carbon cycling (Wedin and Tilman 1990, Fisher et al. 1994, Johnson and Wedin 1997). The findings of these three studies have specific implications for communities already invaded or expressing the potential for invasion by *Eragrostis lehmanniana*, but also demonstrate important

findings that are generalizable to grasslands worldwide. Overall, the main findings can be summarized in the following points:

- Geographic distributions of *Eragrostis lehmanniana* built on points occupied in the invaded range may perform as well or better than those developed from the native range, at least for the region encompassed by confirmed presence points in the invaded range.
- *Eragrostis lehmanniana* is not likely to disappear under a changing climate. This plant apparently is still spreading to available habitat, and likely will continue to expand its range as long as seed dispersal vectors facilitate its spread to new habitats. However, major range shifts are not predicted to occur until average summer maximum and winter minimum temperatures increase by at least two degrees and summer and winter precipitation increase by at least 30%.
- The response of a site to the removal of a dominant nonnative grass varies between sites, based on land use history, edaphic conditions, and seasonal precipitation patterns. A site with a history of intensive agriculture responded little to the removal of *E. lehmanniana*, but two other sites with similar histories of livestock grazing shifted to communities dominated by native species.

The three studies presented herein underscore the complexities of nonnative species introductions. Effective management solutions require a thorough understanding of invading species' impacts and likelihood of persistence. These studies demonstrate the tremendous need for improved awareness and attention to nonindigenous species, as the

rate of introductions is predicted to increase into the future (National Research Council 2002).

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**APPENDIX A**

**CAN AN INVADING SPECIES' DISTRIBUTION BE PREDICTED USING DATA  
FROM ITS INVADED RANGE? LEHMANN LOVEGRASS (*ERAGROSTIS  
LEHMANNIANA*) IN THE SOUTHWESTERN UNITED STATES**

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*(In review at Ecological Modelling)*

## Abstract

Predictions of species invasions are often made using information from their native ranges. Acquisition of native range information can be very costly and time-consuming and in some cases may not reflect conditions in the invaded range. Using information from the invaded range can enable models to be built more rapidly and at finer geographic resolutions than using information from a species' native range. We used confirmed presence points of the perennial bunchgrass *Eragrostis lehmanniana* Nees, (Lehmann lovegrass) from its native range in southern Africa, and its invaded range, the southwestern United States, to predict the potential distribution, in its invaded range in the U.S. The two models showed strong agreement for the area encompassed by the presence points in the invaded range and offered insight into niche differentiation in the invaded range. Regions outside of Arizona showed less agreement between the two models. *Eragrostis lehmanniana* was selected via seeding trials before being planted in the United States and therefore represents an isolated genotype from the native population. Models built using confirmed presence points from the invaded range can provide insight into how the selected genotype is expressed on the landscape and considers influences not present in the native range. Models created from locations in both the invaded and native ranges can lead to a more complete understanding of the introduced species' potential for spread, especially in the case of anthropogenic selection.

**Keywords:** Genetic Algorithm for Rule-set Prediction; distribution modeling, *Eragrostis lehmanniana*; Invasive plants; Invaded-range models.

## 1. Introduction

Non-indigenous invasive species are a major threat to native species diversity and ecosystem function, causing economic impacts estimated at more than \$100 billion annually (Pimentel et al. 1999). Invasive species have been called the “single most formidable natural disaster threat of the 21<sup>st</sup> century” (Schnase et al. 2002). Early detection of invaders is critical: predictive models can enable early detection by focusing research efforts on areas most likely to be impacted.

Ecological niche modeling and climate-matching has gained momentum recently for predicting potential invasions (Hoffman 2001, Peterson and Vieglais 2001, Welk et al. 2002, Peterson 2003). These approaches are based on the assumption that a species’ ecological niche can be described as the  $n$ -dimensional hypervolume of environmental conditions under which it is able to maintain populations without immigration (Grinnell 1917). Almost exclusively, species’ invasions outside of their native ranges have been predicted with this method using locations where it is confirmed to exist (known presence points) from their native ranges. However, using locations from the native range assumes the same factors will determine the distribution range of the species from the invaded locations. Depending on the species’ introduction history, this assumption may not be

appropriate (Hierro et al. 2005). In addition, acquiring data from native ranges is often very expensive and time-consuming and not always feasible. Finally, the scale at which species' potential invaded-range distributions can be modeled using native-range data is often too coarse for specific management decisions.

Because of the drawbacks associated with making predictions for an invasion using native range information, the question of whether confirmed presences in a species' invaded range can be used to successfully predict its eventual distribution is fertile ground for research. A recent study tested whether the invaded-range distribution of *Lythrum salicaria* (Purple loosestrife) in North America could be predicted accurately from known presence points in the invaded range (Welk 2004). The results of this study suggested that such an approach could be successfully implemented only 100-150 years post-introduction, arguing that this amount of time was necessary to amass confirmed presence locations representing the full range of climatic values to which the invader was adapted (Welk 2004). The purpose of the present study was to investigate whether invaded-range models could work as well or better than native-range models in the case of a purposely-introduced species.

To explore this idea, we selected *Eragrostis lehmanniana*, a perennial bunchgrass with a unique introduction history to the southwestern United States. In the 1930s, several accessions of *E. lehmanniana* were brought from southern Africa to Arizona to counteract low plant cover and highly eroded soils resulting from decades of overgrazing

and drought (Crider 1945). Seed from a single cultivar (A-68), selected for its drought-tolerance and high seed production, was produced and distributed widely in Arizona and neighboring states from the 1930s through the 1980s (Cox and Ruyle 1986). Geographic range predictions for *E. lehmanniana* made using invaded-range points may be superior to those using native-range points because *E. lehmanniana* populations in the U.S. represent a subset of genetic variation present in African populations (Schussman 2002). Further, very little genetic change is expected because the individuals brought to Arizona and used to produce seed for erosion control were apomictic (Burson and Voigt 1996). Apomictic reproduction allows for the production of seeds that are genetically identical to the maternal plant. Given its introduction history and reproductive biology, we believe that *E. lehmanniana* represents an ideal candidate for investigating the variability in models predicted using native and invaded-range information for species with little genetic variability.

We built two models to predict the range of *E. lehmanniana* to explore differences in distribution predicted using two different sets of input data. The first model predicted the potential distribution of *E. lehmanniana* in the United States using the ecological niche predicted from its native range in South Africa; the second model predicted the potential distribution of *E. lehmanniana* in the U.S. using the ecological niche predicted using environmental data from areas known to be invaded within the United States. The results of these models were then compared to independent test points in the invaded range.

## 2. Materials and methods

### 2.1 Distribution data

We collected 350 point locations of *E. lehmanniana* within South Africa, Namibia, Botswana, and Lesotho from the Southern African Botanical Diversity Network's PRECIS database, the Natal Herbarium, the C.E. Moss Herbarium, and Kruger National Park. To minimize spatial autocorrelation, we randomly selected a subset of 200 well-distributed points. The native-range study area for predictions and sensitivity analysis was restricted to a rectangular grid containing southern Africa, from 16°S to 36°S and 11°E to 38°E.

We obtained over 1,000 localities of species' occurrences within Arizona and New Mexico from several sources including the Santa Rita Experimental Range, Bureau of Land Management, The Nature Conservancy, U.S. Department of Defense, U.S. Fish and Wildlife Service, U.S. Forest Service, U.S. Geological Survey, and the U.S. National Park Service. We randomly selected 100 of the 1000 tightly-clustered presence points to minimize spatial autocorrelation. The invaded range study area was restricted to the southwestern United States, from 23° N to 51° N and 66° W to 126° W, then subsetted to the region roughly bounded by the state of Arizona, from 106° W to 115° W and 31° N to 37° N.

### 2.2 Environmental data

The base environmental data consisted of 19 global geographic coverages. Elevation, slope, aspect, flow direction, flow accumulation, and topographic index (U.S. Geological Survey 2001) were generalized to 0.1-degree resolution from 0.01-degree datasets. Climate data averaged for the period 1961-1990 were resampled from 0.5-degree datasets to 0.1-degree datasets; these data included mean annual precipitation; maximum, minimum, and mean annual temperatures; wet days; vapor pressure; solar radiation; and frost days (International Panel on Climate Change 2004). We created grids representing seasonal precipitation by summing monthly precipitation averages for the period 1961-1990 (IPCC 2004). Seasons were defined as winter (DJFM), spring (AMJ), summer (JAS), and autumn (ON) in the U.S. and winter (JAS), spring (ON), summer (DJFM), and autumn (AMJ) in southern Africa (Cox et al. 1988). Season definitions differ from the convention of even three-month seasons to capture the unique seasonality of precipitation and temperature in Arizona and southern Africa. Datasets representing soil texture in the upper soil horizon (top 1-m) were downloaded from the Oak Ridge National Laboratory Distributed Active Archive Center (Post and Zobler 2000) and resampled from 0.5-degree to 0.1-degree datasets.

### 2.3 Modeling

The Genetic Algorithm for Rule-Set Prediction (Stockwell and Noble 1992, Stockwell and Peters 1999) is a niche-based model receiving wide application. GARP is an iterative artificial intelligence-based approach that includes several inferential tools. This model has proven successful at predicting species' potential distributions under a wide variety of

conditions (Peterson and Cohoon 1999, Peterson et al. 1999, Peterson et al. 2001, Peterson et al. 2002a, Peterson et al. 2002b, Peterson et al. 2002c, Godown and Peterson 2000, Sánchez-Cordero and Martínez-Meyer 2000, Peterson 2001, Feria and Peterson 2002, Stockwell and Peterson 2002a, Peterson 2002b).

The GARP model predicts species' environmental niches by identifying non-random relationships between environmental characteristics of known presence localities in comparison with the entire study region. Known presence points are divided into training and test data sets. GARP works in an iterative process of rule selection, evaluation, testing, and incorporation or rejection to create a rule-set that best represents the environmental conditions under which the species is found (Peterson et al. 1999). First, GARP chooses a method from a set of possibilities (e.g. logistic regression, bioclimatic rules) and applies it to the data. Then, a rule is generated and its accuracy is evaluated via test points intrinsically re-sampled from both the known study region and from the study region as a whole. The change in predictive accuracy from one iteration to the next is used to select among rules for the final model. Rules may change in ways similar to the ways DNA mutates, hence, the name "genetic algorithm." As implemented here, the algorithm runs either for 1,000 iterations or until convergence. The final rule-set, or ecological niche model, is then projected onto a digital map as the species' potential geographic distribution and imported into ArcView 3.2 (ESRI 1999) using the Spatial Analyst extension for visualization.

## 2.4 Native and Invaded Range Modeling

The general steps for the modeling were:

1. Build models using native-range (southern African) datasets, select subset of 10 best models
2. Project rules onto native range (southern Africa) and invaded range (southwestern U.S.)
3. Build models using invaded-range (southwestern U.S.) datasets, select subset of 10 best models
4. Project rules onto invaded range (southwestern U.S.) and native range (southern Africa)

Specifically, we produced 300 replicate models of *E. lehmanniana*'s ecological niche using the subset of training points for southern Africa (native range). For each model, points were randomly split into two equally sized training and testing datasets of available occurrence points. To choose the best subset of the 300 native range models, we adopted a best-subsets selection procedure (Anderson et al. 2003, Peterson et al. 2003). Following this method, we selected the best subset of models by eliminating all models that had non-zero omission error based on independent test points, calculated the median area predicted present among these zero-omission points, and then identified the ten models closest to the overall median area predicted. These ten models were summed to create a final output grid of model agreement, ranging from 0 (areas not predicted present by any of the ten models) to 10 (areas predicted present by all ten models). The rule sets

from these ten models were projected onto the same environmental grids for the United States (invaded range) to generate predictions of *E. lehmanniana* distribution. This procedure was repeated using the environmental base layers and unique presence points collected within the southwestern U.S. and then projected onto both the South African and U.S environmental grids to determine how well GARP could predict *E. lehmanniana*'s ecological niche within southern Africa and the southwestern United States and Mexico.

## 2.5 Model Testing and Visualization

We tested the predictive power of the models by overlaying extrinsic test data and tallying observed correct predictions. The proportion of the total study extent predicted as present (occupied by the species) multiplied by the number of extrinsic test data points is used as a random expectation of successful prediction points if no non-random association existed between prediction and test points (Peterson and Shaw 2003). Following Peterson and Shaw (2003), we implemented a chi-squared test (1 df) to test the significance of the departure from random expectations. We used 147 randomly selected extrinsic points to test the native range models, and 183 randomly selected extrinsic points to test the invaded range models.

To identify environmental dimensions important for defining *E. lehmanniana*'s geographic potential, we used a series of sequential jackknife manipulations in which all possible combinations of a reduced set (e.g.,  $N-1$ ) of  $N$  environmental coverages were

used to generate native range models. We assessed model quality by exploring correlation between variable inclusion and omission error (Peterson and Cohoon 1999). Variables that were positively correlated with improvement in avoiding omission error were considered to be most important in defining *E. lehmanniana*'s environmental niche.

Using the subsets of known presence points in Arizona and South Africa selected for the models, a correlation-based principal components analysis (PCA) was performed on the environmental variables associated with the points using PRIMER v5 (PRIMER-E Ltd. 2001). Prior to analysis, skewed variables were transformed using the log or square-root transformation.

### **3. Results**

#### **3.1 Model Predictivity and Influential Variables**

Ecological niche models developed in this study were highly predictive of the distribution of *E. lehmanniana* based on random subsets. All of the best-subsets models were statistically significant when compared with random expectations ( $\chi^2$  tests,  $df = 1$ , all best-subsets models  $P < 0.001$ ).

Jackknife manipulations of the different environmental coverages (Peterson and Cohoon 1999) suggested that the following variables were critical in constituting the ecological niche of *E. lehmanniana* in its native range: spring, summer, and fall precipitation; radiation; silt; annual minimum temperature; annual number of freezing days; and

elevation. In the invaded range, slope, aspect, fall precipitation, and elevation appeared to be influential in defining the plant's niche.

### 3.2 Model Output Comparison and Visualization

The two approaches used to predict the geographic distribution of *E. lehmanniana* in the United States produced results with rather dissimilar patterns, except for the region surrounding the known presence points (Figure 1). The results of the two methods had strongest agreement for the region surrounding the known presence points in the U.S., centered on Arizona. The strongest disagreements occurred in Texas, California, and Mexico, regions not represented by invaded range points. Models generated from native-range points predict much greater distributions for these areas than models created using invaded-range points. Areas in the northeastern and southwestern portions of Arizona were more strongly predicted by the native-range model (i.e., possessing higher values on the final model output grid), and the central portion of the state was more strongly predicted by the invaded-range model. The two models also showed strong disagreement for portions of Mexico.

Using the invaded range rules to predict *E. lehmanniana*'s distribution in its native range provides insight into the different rules being formulated in the two regions. When rules generated from invaded range points are projected onto the native range, a very small set of the known distribution is predicted. The area predicted appears in the south-central portion of South Africa, characterized by relatively warm, dry conditions similar to

Arizona. Figure 2 displays the area predicted occupied by *E. lehmanniana* using points from the native range (top) and from the invaded range (bottom).

The first four components from the PCA of environmental variables for confirmed presence points in the native and invaded ranges accounted for 80.9% of the variance (36.4%, 20.7%, 15.4%, and 8.5%, respectively; Table 1). Component 1 loaded most highly on temperature variables. Precipitation variables contributed the highest loadings to Component 2. Components 3 and 4 are a mix of soil variables, radiation, and precipitation variables. Separation of known presence points in Arizona from known presence points in southern Africa occur primarily along the second axis (Figure 3).

#### **4. Discussion**

Predictions of species invasions are most commonly made using information from their native ranges (Hoffman 2001, Peterson and Vieglais 2001, Welk et al. 2002, Peterson et al. 2003, Peterson et al. 2004). Acquisition of native range information can be very costly and time-consuming, and in some cases infeasible, involving extensive literature searches of sources in different languages. Records must be geographically referenced, which is rare for many herbaria. Peterson et al. (2003) reported spending 2 months obtaining native-range records, versus 1 hour obtaining invaded-range records for a study similar to this one.

Another advantage of invaded-range models is that they usually can be built using finer-scale input data layers. To build models in the native range and project the resulting rules onto the invaded range requires the same environmental layers for the two regions. Currently, most environmental layers available on a global scale are coarse, on the order of 0.1-degree to 1-degree cells. Limiting models to only one continent enables finer-scale datasets specific to that region to be included in the models.

Few studies have explored the performance of invaded- versus native-range datasets for predicting invaded-range distributions. Those that have, suggested that species will occupy an overlapping but different set of environmental conditions in an invaded range than in their native range (Malanson et al. 1992). Kriticos and Randall (2001) suggested that a species' invaded range is predicted best using information from a second invaded range; they reasoned that in invaded ranges the fundamental niche may be more fully realized than in the native range where the species is constrained by competition and dispersal barriers. Welk (2004) tested the use of invaded range points to predict the distribution of the invasive *Lythrum salicaria* in North America and suggested a method combining the use of invaded and native range information would be most insightful.

*E. lehmanniana* constitutes a special case for invasion prediction, given its unusual introduction scenario. Seed traceable to a limited number of apomictic individuals was widely distributed and planted in the southwestern U.S., leading to an invading population with low genetic variability and few mechanisms to evolve. For these reasons,

it seems logical to build predictive models using both native and invaded range points to explore the potential distribution of *E. lehmanniana*. Building models from the species' introduced range, or a combination of both native and introduced ranges, may be the most appropriate approach for purposely-introduced plants. This is especially suitable when specific traits were selected for during the introduction, for plants with limited genetic variation due to asexual reproduction, or for plants where a limited number of individuals were introduced.

#### 4.1 Model visualization and interpretation

Predictions made of the distribution of *E. lehmanniana* in the U.S. show similar patterns for Arizona and the region surrounding known presence points in the U.S.; the largest differences occur in Texas, California, and New Mexico as well as Mexico. Models created using native range points predict much greater distributions for these areas than models created using invaded range points. Spatial coverage of known presence points used in this study come from sites in Arizona, where confirmed presence points are most readily available. Because of the extent of the known presence points used to build and test the models, inference is approximately limited to the state of Arizona. Currently, Arizona is the state in the U.S. most heavily impacted by *E. lehmanniana*. Within Arizona, areas in the northeastern and southwestern portions of the state are more strongly predicted (i.e., possessing higher values on the final model output grid) by the native range model, and the central portion of the state is more strongly predicted by the invaded range model.

The disagreement in the two models' output could be due to a paucity of points in the invaded range, as known presence points used in this study represent only Arizona, where confirmed presence points are most readily available. However, the disagreement in the two models' output is more likely due to differences in the ecological niches realized by the native-range populations and U.S. populations of *E. lehmanniana*. The results of the PCA depict the range of environmental conditions occupied by *E. lehmanniana* in both its native and invaded ranges. Points in Arizona occupy an overlapping but slightly different location in multivariate space than those in *E. lehmanniana*'s native range (Figure 3), which coincides with the slight disagreement in the two models for Arizona. This suggests that the niche occupied by *E. lehmanniana* in Arizona is narrower and slightly different than that occupied in its native range. This conclusion is supported by the projection of invaded range niche rules onto the native range. Using invaded-range rules, only a small portion of the entire distribution is represented, presumably representing only a portion of the ecological niche available in its native range (Figure 2).

The invaded-range model predicts occupation under conditions of higher temperature and lower total precipitation as well as lower precipitation in all seasons than the native-range model, which argues against *E. lehmanniana*'s occupation of Texas and California.

*Eragrostis lehmanniana* was originally planted in portions of Texas and New Mexico with the A-68 accession, but disappeared within five years of planting (Cox and Ruyle 1986). Experts in Texas, New Mexico, and California all report that though *E.*

*lehmanniana* has been observed—and in some cases is intentionally planted—in these states, it does not appear to substantially encroach on native grasslands relative to other species (B. Carr and J. Bergan, The Nature Conservancy, Texas Chapter; F. Miller, New Mexico State Weed Coordinator; B. Rice, The Nature Conservancy Wildland Invasive Species Team; J. DiTomaso, University of California-Davis; D. Johnson, California Invasive Plant Council, pers. comms.; Barkworth and Capels 2004). These observations suggest that northern New Mexico, California, and Texas are on the edge of the ecological niche that the A-68 *E. lehmanniana* accession occupies, and that the potential distribution map created using the invaded-range model is most plausible. No information was available regarding the status of *E. lehmanniana* in Mexico.

The second axis of the PCA is dominated by precipitation variables including summer precipitation, spring precipitation, and annual precipitation, all decreasing up the axis. Based on the partial overlap for the two sets of points along the second axis, it appears that both temperature and precipitation, particularly seasonality of precipitation, is a key variable in determining the distribution of U.S. *E. lehmanniana* populations. Because the A-68 accession was selected to be especially drought-tolerant, the U.S. *E. lehmanniana* may not compete as well under more mesic conditions, as in western Texas and California. However, the potential for *E. lehmanniana* to dominate grasslands in these areas may exist if the conditions in Texas and California grasslands were to become drier.

Based on field observations by experts, it appears that the model constructed using invaded-range points more accurately represents the potential distribution for *E. lehmanniana* in Arizona. In addition, building two separate models suggests some difference in environmental niches occupied by the same species in the two locations, suggesting genetic variations in the two populations. The results of this study suggest that models built using both native- and invaded-range points can provide insight into how the selected genotype is expressed on the landscape. In addition, this study demonstrates that invaded-range models may work as well or better than native-range models, especially in the case of a purposely-introduced species. Therefore, species with little genetic variation and well-known introduction histories may be best modeled with invaded range points, minimizing the costs and time involved, as well as increasing model accuracy.

Experiments are the best way to test predictions made by models. Predictive models can offer insight into the potential spread of invasive species, but do not consider factors affecting species distributions such as biotic interactions. Mechanistic studies addressing these factors are necessary to augment the predictions made by correlative models. In addition, incorporation of predictive model output with invasibility models (Shea and Chesson 2002) could offer insight into areas within the predicted habitat that are most threatened by invasion.

## **5. Conclusions**

The results of this study demonstrate that geographic distributions of invading species built on points occupied in the invaded range may perform as well or better than those developed from the native range, at least for the region encompassed by confirmed presence points in the invaded range. In addition, predictions made using invaded-range points can offer insight into the environmental conditions tolerated by the invader and inconsistencies in the ecological niche between native to invaded ranges. The sole use of invaded-range points to make invaded-range predictions may be the most appropriate method for modeling distributions of intentionally introduced plants, especially when the introduction involved intense selection of the plant, as in the case of *Eragrostis lehmanniana*. Intense selection, asexual reproduction, and limited introduction numbers all function to create a nonnative population with an environmental niche that represents a subset of the native range niche. Since not all invaders can be predicted to represent a subset of the native range and most likely occupy an overlapping but different niche in the invaded range, it is likely best to use information from the plants' native and invaded ranges.

## **6. Acknowledgments**

This research was supported by the Center for Invasive Plant Management grant ESA 000011, T&E, Inc, and the University of Arizona/NASA Space Grant. The South African National Biodiversity Institute is thanked for the use of data from the National Herbarium, Pretoria (PRE) Computerized Information System (PRECIS). Kruger National Park, Natal Herbarium, and C.E. Moss Herbarium also kindly provided South African data. The authors thank the following organizations for providing United States data: Santa Rita Experimental Range; The Nature

Conservancy, Arizona Chapter; U.S. National Park Service; U.S. Bureau of Land Management; U.S. Department of Defense; U.S. Fish and Wildlife Service; U.S. Forest Service; and the U.S. Geological Survey. M. Crimmins, R. Gimblett, A. Hubbard, and G. McPherson provided useful suggestions on the manuscript.

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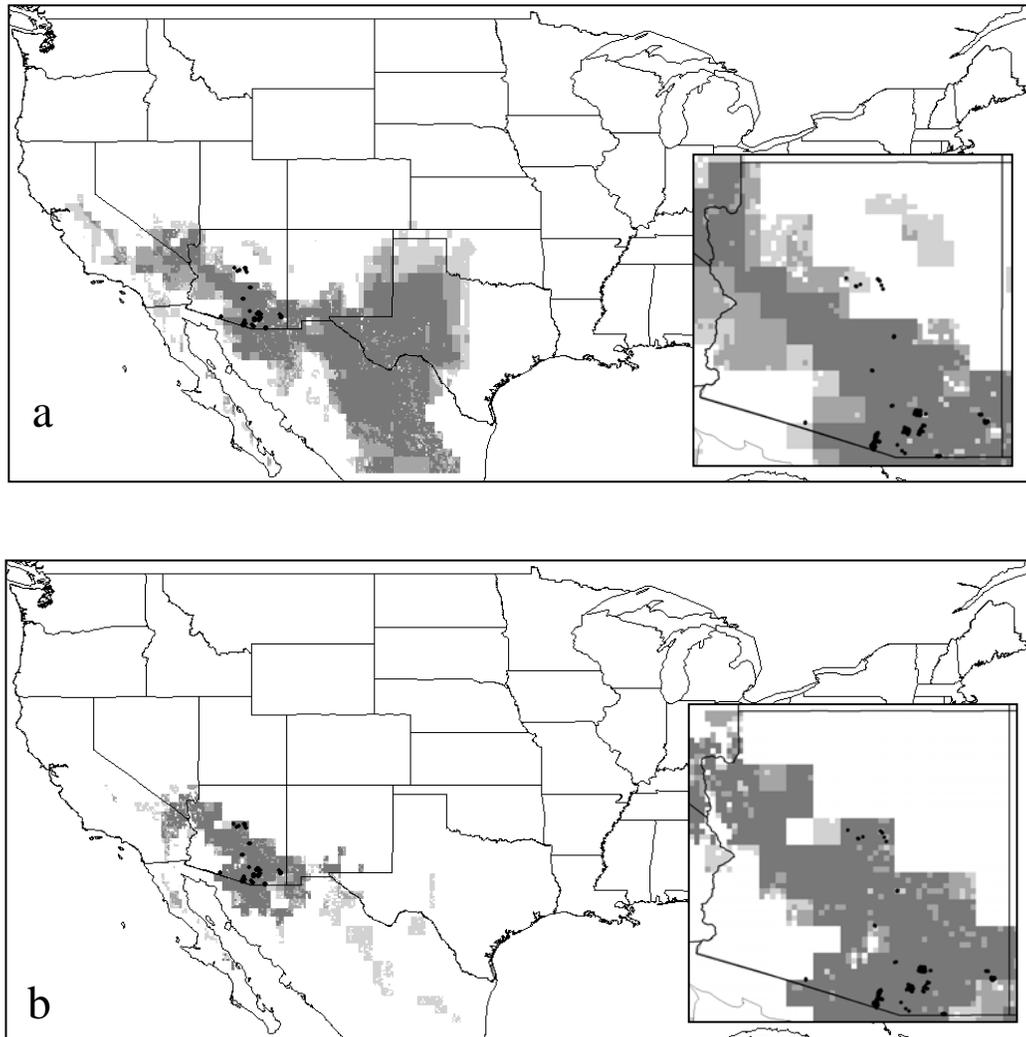
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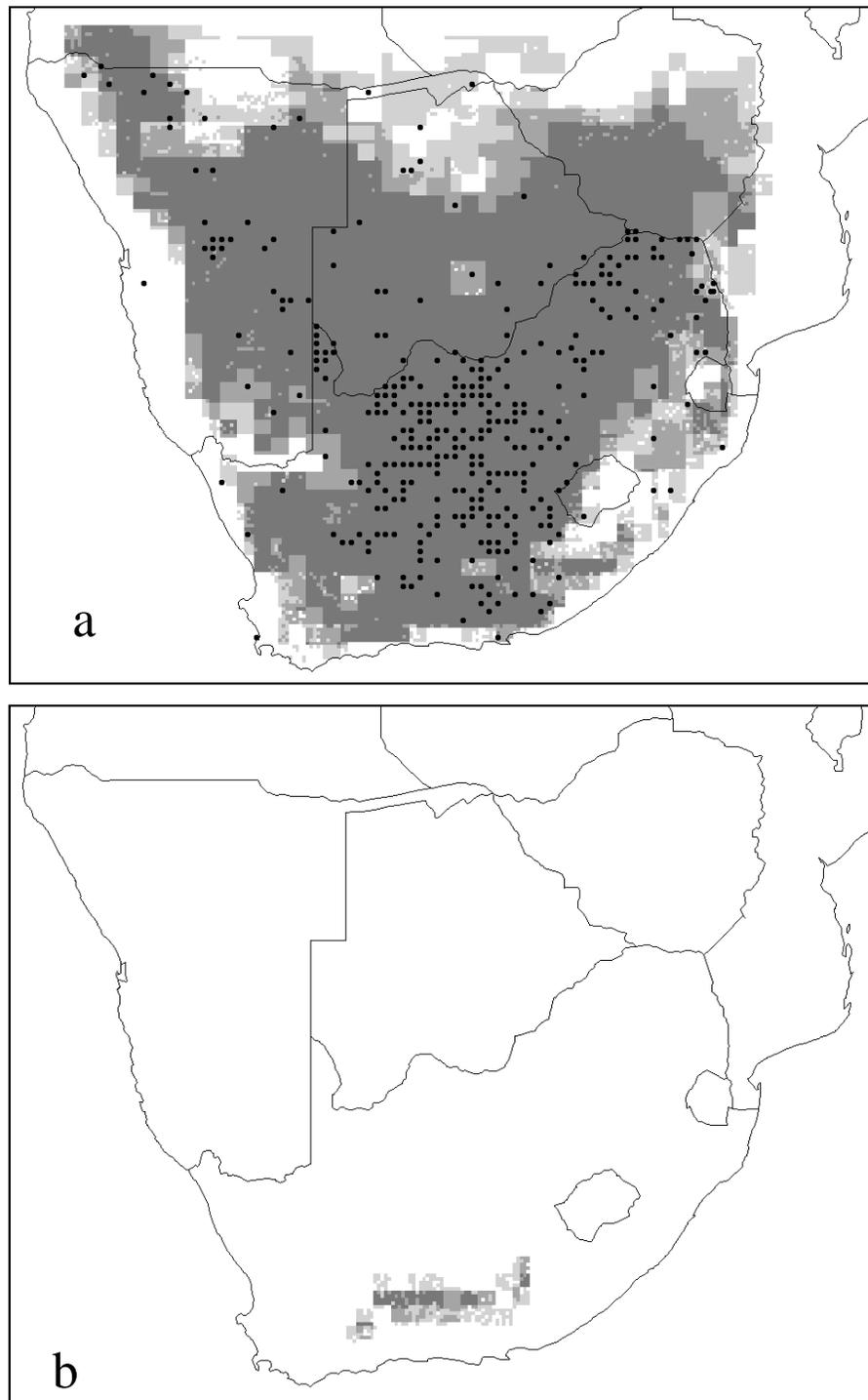
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**Table 1.** Four-component solution generated by principal components analysis for predicting distribution of *Eragrostis lehmanniana* in Arizona, USA.

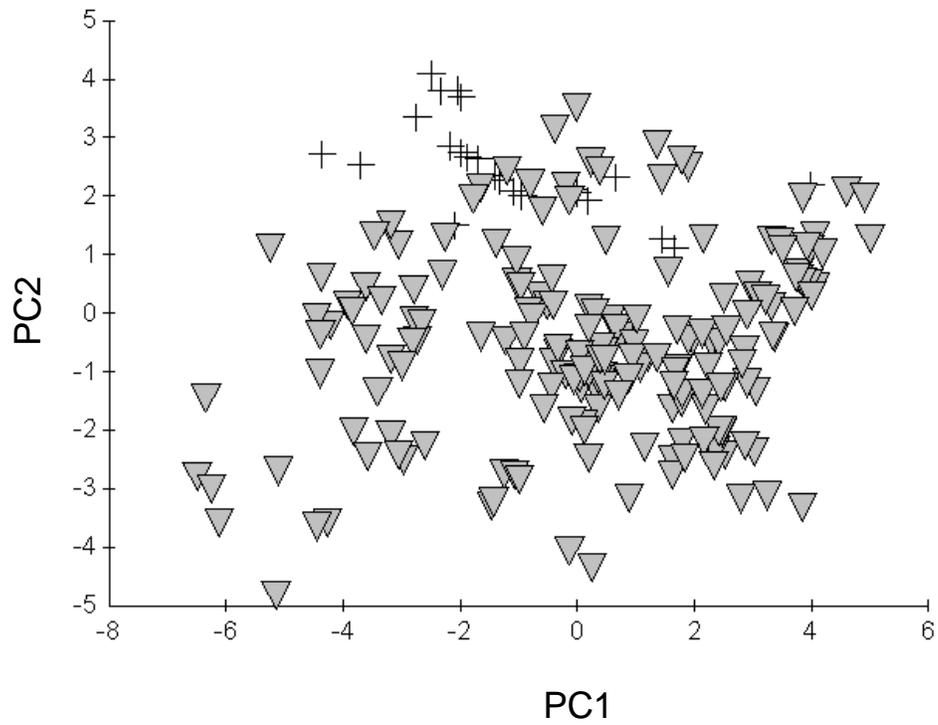
Variable	PC1	PC2	PC3	PC4
Max annual temperature	0.351	-0.086	0.131	-0.175
Annual temperature	0.332	-0.205	0.214	-0.101
Min annual temperature	0.272	-0.298	0.269	-0.014
Summer precipitation	-0.145	-0.469	-0.112	-0.011
Frost days	-0.211	0.266	-0.354	0.047
Fall precipitation	-0.213	-0.256	-0.227	0.365
Elevation	-0.173	0.126	-0.321	-0.023
Aspect	-0.006	-0.025	-0.012	0.042
Winter precipitation	-0.252	0.236	0.150	-0.371
Wet days	-0.314	-0.272	-0.031	-0.124
Spring precipitation	-0.246	-0.384	-0.002	-0.166
Slope	-0.214	0.162	0.208	-0.132
Silt	-0.229	0.209	0.393	0.121
Sand	0.241	-0.094	-0.417	-0.280
Radiation	0.259	0.005	-0.310	0.364
Annual precipitation	-0.276	-0.327	-0.023	-0.277
Clay	-0.170	-0.163	0.283	0.566
Eigenvalue	6.19	3.51	2.62	1.44
Explained variance (%)	36.4	20.7	15.4	8.5
Cumulative variance explained (%)	36.4	57.1	72.5	80.9



**Figure 1.** *Eragrostis lehmanniana* potential distribution using native range data (a) and introduced range data (b). Known presence points are black dots. Increasingly dark shades of gray indicate greater model agreement.



**Figure 2.** *Eragrostis lehmanniana* potential distribution using native range data (a) and introduced range data (b). Known presence points are black dots. Increasingly dark shades of gray indicate greater model agreement.



**Figure 3.** Principal components analysis plot of environmental conditions associated with known *Eragrostis lehmanniana* presence points in Arizona, USA and southern Africa. Triangles represent known points in Africa; crosses represent known points in Arizona.

**APPENDIX B**

**MODELING FUTURE POTENTIAL DISTRIBUTIONS OF *ERAGROSTIS*  
*LEHMANNIANA* (LEHMANN LOVEGRASS) IN ARIZONA, USA**

THERESA M. MAU-CRIMMINS

*(To be submitted to Diversity and Distributions)*

## Abstract

Climate plays a large role in determining the distribution of plant species and communities (Huntley and Webb 1988). Significant increases in precipitation and temperature as well as shifts in the seasonality of precipitation are expected for the southwestern United States in the coming decades, suggesting major shifts in community and species distributions. The structure and diversity of ecosystems are expected to undergo considerable changes (IGBP 1988, Watson et al. 1996), potentially having detrimental impacts on ecosystem stability (Mooney 1997). Such reshuffling could favor nonindigenous species, especially those with the capacity to disperse rapidly and compete strongly for resources. In this study I explored the potential effects of climate change on the distribution of *Eragrostis lehmanniana* (Lehmann lovegrass), a perennial warm-season bunchgrass, in the southwestern U.S. using ecological niche modeling.

Based on predictions of popular global-scale general circulation models, 28 climate-change scenarios were created by modifying existing long-term averages of climatic variables in Arizona and western New Mexico. Using the Genetic Algorithm for Rule-set Prediction model (GARP; Stockwell and Peters 1999), I modeled the ecological niche for *E. lehmanniana*. This niche, characterized by a set of rules, was then projected onto each of the 28 climate change scenarios to represent potential habitat within Arizona under potential future conditions. Future scenarios show the distribution of *E. lehmanniana* progressively shrinking in the southeastern and northwestern portions of Arizona and increasing in the northeastern portion of the state with increasing temperatures and precipitation. Key shifts occurred under scenarios with increases in

summer and winter precipitation of 30% or more, and increases in summer maximum and winter minimum temperatures of at least 2°C. Spread to new environments will be limited by the ability of viable *E. lehmanniana* seed to reach new habitats.

## **Introduction**

*Eragrostis lehmanniana*, a tufted perennial bunchgrass native to southern Africa, was brought to Arizona, USA in the 1930s to counteract low plant cover and highly eroded soils resulting from decades of overgrazing and drought. This plant is now one of the most dominant and problematic nonnative species in the southwestern U.S. Following intentional seeding to 69,000 ha in Arizona, *E. lehmanniana* spread to an additional 79,000 ha, invading recently cleared lands and undisturbed native grasslands alike (Cox and Ruyle 1986, McClaran and Anable 1992). The ability to produce copious drought-tolerant seed and to survive long dry periods makes this grass an effective competitor (Sumrall et al. 1991, Abbott and Roundy 2003). *E. lehmanniana* also produces abundant lignin-rich biomass, and may be associated with changes in fire regime and nutrient cycling (Cable 1971, Biedenbender and Roundy 1996, Williams and Baruch 2000). Accordingly, sharp declines in animal species richness have been associated with *E. lehmanniana*-dominated plots (Cable 1971, Bock et al. 1986, Medina 1988). It is unclear whether this plant is still spreading to new locations in the U.S. (Cox et al. 1988).

Climate plays a large role in determining the distribution of plant species and communities (Huntley and Webb 1988). Significant increases in precipitation and temperature are expected for the southwestern United States in the coming decades

(IPCC 2001), potentially altering ecosystem stability by causing major shifts in community and species distributions and hence, the structure and diversity (IGBP 1988, Watson et al. 1996, Mooney 1997). Increases in annual average temperature have been documented at 1°-2° C in the western United States since the late 1940s (Dettinger et al. 1995), concurrent with earlier onset of phenological events (Cayan et al. 2001). Additionally, documented increases in carbon dioxide concentrations and availability of nitrogen and other nutrients directly affect photosynthesis and elicit a variety of responses in plants (Holland et al. 1999). Such changes could favor nonindigenous species (Dukes and Mooney 1999, Smith et al. 2000), especially those with the capacity to disperse rapidly and compete strongly for resources.

Because *E. lehmanniana* has been observed to encroach into native communities in southern Arizona and disperses seed widely via wind and water, this species can be expected to spread into new areas with a changing climate. Future spread predictions can facilitate early detection and control measures, thereby keeping newly established populations in check. Here I explore the potential effects of climate change on the distribution of *E. lehmanniana* in the southwestern U.S. using ecological niche modeling. In addition to the prediction maps, one benefit of this approach is that model parameters can be compared directly with key limiting ecological parameters known to affect populations of the species in question.

## Methods

Niche-based modeling is one approach for predicting species' invasion potential that has recently gained popularity (Hoffman 2001, Peterson and Vieglais 2001, Welk et al. 2002, Peterson 2003). This method is based on the belief that a species' ecological niche can be described as the  $n$ -dimensional hypervolume of environmental conditions under which it is able to maintain populations without immigration (Hutchinson 1957). One example of a model applying this concept is the Genetic Algorithm for Rule-set Prediction (GARP). The GARP model has been applied to predict changes in species' distributions following climate change in several cases (Peterson et al. 2001, Peterson et al. 2002, Oberhauser and Peterson 2003, Peterson and Shaw 2003). Advantages of this model over other approaches are its use of several inferential tools, theoretically increasing its predictive ability over any one method independently (Stockwell and Peters 1999); the ability to incorporate information from both categorical and continuous variables (Stockwell and Peterson 2002); and its ability to work with relatively small sample sizes (Stockwell and Peterson 2002).

## Input Data

*Eragrostis lehmanniana* seeded throughout Arizona, New Mexico, and Texas can be traced to a single plant introduced from South Africa (Crider 1945). Recent research has shown that genetic variation in U.S. *E. lehmanniana* populations does exist, though it is unknown whether this variation is the result of the U.S. population undergoing mutation and genetic drift or due to genotypic variability present in the introduced

individual (Schussman 2002). Regardless, the U.S. population may occupy a slightly different environmental niche than populations in its native range due to this isolation (Mau-Crimmins et al. submitted). Accordingly, predictions about future *E. lehmanniana* distributions were made in this study using known presence points in the U.S., a departure from convention (Peterson and Vieglais 2001, Peterson 2003, Peterson et al. 2003). Traditionally, species' potential distributions outside of their native ranges are predicted using data from the species' native ranges (Hoffman 2001, Peterson and Vieglais 2001, Welk et al. 2002, Peterson 2003). This study relies on invaded-range data to make future distribution predictions, which could potentially misrepresent the species' environmental niche.

Unique localities of species' occurrences within Arizona and western New Mexico were obtained from several sources including the Santa Rita Experimental Range, Bureau of Land Management, The Nature Conservancy, U.S. Department of Defense, U.S. Fish and Wildlife Service, U.S. Forest Service, U.S. Geological Survey, and the U.S. National Park Service, resulting in nearly 500 localities. Due to tight clustering of presence points and the potential for spatial autocorrelation between them, a subset of 100 evenly distributed points was randomly selected. The remainder of the points was retained for extrinsic model testing.

The base environmental data consisted of 13 geographic coverages obtained at 1-km resolution covering Arizona and western New Mexico. Elevation was obtained from the U.S. Geological Survey (2001); slope and cosine of aspect were derived from this grid. Additional coverages included aspects of climate averaged for the period 1980 to

1997 encompassing mean monthly precipitation, solar radiation, and average maximum and minimum annual temperatures (DayMet grids; Thornton et al. 1997, Thornton et al. 2000); and soil characteristic data and depth to bedrock (Miller and White 1998). From the monthly precipitation data, I calculated grids representing mean summer precipitation (June, July August) and mean winter precipitation (December, January, February, March). Season definitions were designed to capture the unique seasonality of precipitation in Arizona. Soil characteristic data were averaged across the soil layers up to 1 m in depth to estimate the percent sand, clay, and silt in the soil profile.

### Niche Modeling

All modeling in this study was carried out on a desktop implementation of GARP (<http://www.lifemapper.org/desktopgarp>). The Genetic Algorithm for Rule-set Prediction models species' environmental niche by identifying non-random relationships between environmental characteristics of known presence localities versus those within the overall study region. Occurrence points are divided evenly into training and test data sets. GARP is designed to work based on presence-only data; absence information is included in the modeling via sampling of pseudoabsence points from the set of pixels where the species has not been detected. GARP works in an iterative process of rule selection, evaluation, testing, and incorporation or rejection to produce a heterogeneous rule-set characterizing the species' ecological requirements (Peterson et al. 1999). First, a method is chosen from a set of possibilities (e.g. logistic regression, bioclimatic rules), and it is applied to the data. Then, a rule is developed and predictive accuracy (sensu Stockwell and Peters

1999) is evaluated via training points intrinsically re-sampled from both the known study region and from the study region as a whole. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model (rule-set). Rules may evolve by a number of means that mimic DNA evolution: point mutations, deletions, and crossing over. As implemented here, the algorithm runs either for 1,000 iterations or until convergence. The final rule-set, or ecological niche model, is then projected onto a digital map as the species' potential geographic distribution and imported into ArcView 3.2 (ESRI 1999) using the Spatial Analyst extension for visualization.

To reduce environmental layers to just those that provide the highest predictive accuracy, I used a jackknife manipulation (Tukey 1958). I ran multiple iterations of models, omitting each data layer systematically. I then calculated correlations between inclusion of each data layer in the model (coded binarily) and omission error (percentage of extrinsic test presence data not predicted as present) to detect data layers that contribute negatively to model performance when evaluated based on independent test data. Correlations of  $r > 0.05$  have been suggested to be indicative of data layers that detract from model quality (Peterson et al. 2003); no data layers were correlated at this level. Therefore all layers were retained for further analyses.

Using the subset of 100 unique species occurrence points for Arizona and New Mexico, I produced 300 replicate models of *Eragrostis lehmanniana*'s ecological niche based on random 50-50 splits of available occurrence points. To choose the best subset of native range models, I adopted a best-subsets selection procedure (Anderson et al. 2003,

Peterson et al. 2003a). Following this method, I selected the best subset of models by eliminating all models that had non-zero omission error based on independent test points, calculated the median area predicted present among these zero-omission points, and then identified the ten models closest to the overall median area predicted. These ten models were summed to create a final output grid, ranging from 0 (areas not predicted present by any of the ten models) to 10 (areas predicted present by all ten models). For area calculations, pixels predicted by at least 9 of the best-subsets models were used.

### Climate Change Projections

General circulation models (GCMs) predict changes in temperatures from  $-0.5$  to  $+3^{\circ}\text{C}$  and increases in precipitation  $-0.5$  to  $+3$  mm/day by 2020 for the southwestern U.S. (IPCC 2001). However, Arizona's summer monsoon season is not well captured by these models, introducing uncertainty in regional precipitation predictions (Southwest Regional Assessment Group 2000.). In addition, the spatial resolution of GCMs is very coarse in comparison to the scale of this study, resulting in unrealistic "jumps" in neighboring pixel values when GCM predictions are applied to current conditions. Because of these limitations, I created 28 climate-change scenarios within the range suggested by GCMs for the southwestern United States (Table 1). Precipitation increases were represented as a percent of the current value, to represent increases with greater precision than GCM predictions. The local fine-scale climate datasets were modified to reflect each of these scenarios, resulting in smoother, more realistic future scenarios than that from GCMs.

Ecological niche models developed with GARP can be projected onto modeled future landscapes to predict potential distributions. Once the current distribution map was completed, the ordered series of if-then statements comprising this model were applied to each of the future climate scenarios to generate a series of future distribution predictions.

### Testing Predictive Power of Ecological Niche Models

Tests of model predictive power can be accomplished by overlaying extrinsic test data and tallying observed correct predictions. The proportion of the total study extent predicted as present (occupied by the species) multiplied by the number of extrinsic test data points is used as a random expectation of successful prediction points if no non-random association existed between prediction and test points (Peterson and Shaw 2003). Following Peterson and Shaw (2003) and using the 316 extrinsic test points held out from the model, I implemented a chi-squared test (1 df) to test the significance of the departure from random expectations.

To identify environmental dimensions important for defining *E. lehmanniana*'s geographic potential, I conducted a series of sequential jackknife manipulations in which all possible combinations of a reduced set (i.e.,  $N-1$ ) of  $N$  environmental coverages were used to generate native-range models. I assessed model quality by exploring correlations between variable inclusion and omission error (Peterson and Cohoon 1999). Variables that were positively correlated were considered to be most important in defining *E. lehmanniana*'s environmental niche.

## Model Output Visualization

### *Current Distribution Prediction*

To explore relationships between known presence points and predicted presence points in multivariate space, a correlation-based principal components analysis (PCA) was performed on the environmental variables associated with the known presence points and pixels within the study area using PRIMER v5 (PRIMER-E Ltd. 2001). Prior to analysis, variables were transformed using the log or square-root transformation if distributions were skewed.

## **Results**

### Tests of Model Predictivity

Ecological niche models developed in this study were highly predictive of distributional phenomena based on random subsets. All of the best-subsets models were highly statistically significant in comparison with random expectations ( $X^2$  tests,  $df = 1$ , all best-subsets models  $P < 0.001$ ).

Jackknife manipulations of the different environmental coverages (Peterson and Cohoon 1999) suggested summer precipitation, winter minimum temperature, elevation, summer maximum temperature, solar radiation, and clay content were the critical variables, in decreasing magnitude, constituting the ecological niche of *E. lehmanniana*. These variables correlated positively with improvement in avoiding omission error (Peterson and Cohoon 1999, Oberhauser and Peterson 2003).

## Model Output and Visualization

### *Current Distribution Prediction*

Approximately 110,200 km<sup>2</sup> are predicted as ‘present,’ or highly likely to host *E. lehmanniana* under current conditions (predicted present by at least 9 out of 10 best-subset models). Models of current *E. lehmanniana* distribution consistently strongly predict presence across the southeastern portion of the state and up into the northwest portion of the state (Figure 1).

PCA on the environmental variables for confirmed presence points in the native and invaded ranges yielded a 4-component solution accounting for 81.4% of the variance in the raw dataset (Table 2; Figure 3). Component 1 loads highly on elevation, total precipitation, summer precipitation, summer maximum temperature, and winter minimum temperature. The highest loadings for component 2 were winter precipitation, radiation, sand, and winter minimum temperature. Component 3 loads highly on silt, clay, and slope; component 4 loads most highly on sand and rock depth.

### *Future Climate Change Predictions*

Understanding both the location and amount of area predicted to be invaded by an invasive species is important for planning and management decisions. It is key to know both whether *E. lehmanniana* is expected to spread to new areas as well as whether it will expand or shrink in distribution.

Future scenarios show *E. lehmanniana*’s distribution progressively shrinking in the southeastern and northwestern portions of the state and increasing in the northeastern

portion of the state with increasing temperatures and precipitation (Figure 2). The amount of land area predicted to be potential habitat for *E. lehmanniana* does not increase drastically under the different scenarios, but does change spatially (Table 3). For scenarios 1-20, the change in total area predicted present by at least 9 of the 10 best subsets models increases up to 10.7% (117.4 ha) from the predicted current distribution. Key shifts occur under scenarios 21-28 (Figure 4), where overlap with the current predicted distribution drops sharply from near 80% down to 30%. These scenarios are characterized by increases in summer and winter precipitation of 30% or more and increases in summer maximum and winter minimum temperatures of at least 2°C.

## **Discussion**

Byers et al. (2002) call for a prioritized approach to invasive species control, recognizing limited resources available to land managers. *E. lehmanniana* is widely recognized in Arizona and New Mexico as a problem plant, nullifying the need for prioritization. Instead, emphasis should be placed on understanding regions most vulnerable to new infestations under current and future conditions. Predictions can facilitate early detection and control measures, thereby keeping new infestations in check (Moody and Mack 1988).

### Current Distribution Prediction

Studies of *E. lehmanniana* in the southwestern U.S. have suggested that elevation, summer precipitation, winter minimum temperature, and soil texture play key roles in

the distribution of this species (Anderson et al. 1957, Cable 1971, Cox and Martin 1984, Cox and Ruyle 1986, Cox et al. 1988, Anable 1990). My model projections support these findings. Based on the jackknife of the environmental layers, summer maximum and winter minimum temperatures, summer precipitation, elevation, incoming solar radiation, and clay in the upper horizons have the greatest influence on predicting the distribution of *E. lehmanniana*. However, winter precipitation, slope, aspect, average annual precipitation, and depth to bedrock also play a role in *E. lehmanniana*'s presence.

The current potential distribution for *E. lehmanniana* depicts the influence of elevation in the model; mountaintops were excluded from predictions. The northeastern and southwestern corners of the state are not predicted to fall within the ecological niche of *E. lehmanniana*. The southwestern portion of the state is characterized by higher winter minimum and summer maximum temperatures and lower precipitation values than the ranges of these variables predicted to be present by the model. The northeastern portion of the state appears to be predicted as inappropriate habitat primarily due to low winter minimum temperatures. In this prediction, approximately 110,200 km<sup>2</sup> are predicted as 'present,' or highly likely to host *E. lehmanniana* under current conditions. This figure is nearly 75 times as great as that proposed by Cox and Ruyle (1986), who stated that *E. lehmanniana* appeared to have expanded as far as possible within Arizona. My model predicts areas much farther north and west than Cox and Ruyle (1986) predicted, in areas both colder, wetter, and drier than expected in their study.

Because several environmental variables together shape the presence and distribution of *E. lehmanniana*, it is perhaps best to interpret its niche in multivariate

space. The first axis of the PCA on the environmental variables for confirmed and predicted presence points is that of decreasing values (from left to right) for winter minimum temperature and summer maximum temperature, roughly equally weighted, and elevation, total precipitation, and summer precipitation, roughly equally weighted, with the opposite trend. The second axis is dominated by sand and radiation, increasing up the PC2 axis, and winter minimum temperature and winter precipitation decreasing up the axis. Of the environmental conditions represented within the study area, *E. lehmanniana* is known and predicted to occupy regions characterized by lower winter minimum and summer maximum temperatures and winter precipitation as well as higher elevation, summer precipitation, total precipitation, and sandier soils (Figure 3).

The multivariate plot also offers insight into model performance. From this plot, it is possible to see that the model does not predict conditions far outside of the set of conditions known to be occupied by *E. lehmanniana* currently. Therefore, regions predicted as current habitat but not yet occupied by *E. lehmanniana* are the regions most likely to host *E. lehmanniana*.

### Climate Change Predictions

For scenarios 1-20, the amount of area predicted to host *E. lehmanniana* does not increase a great deal; in addition, the predicted distribution continues to overlap by at least 80% for all of these scenarios. This suggests that changes of a magnitude of 1°C and +25% precipitation are unlikely to have dramatic impacts on the distribution of *E. lehmanniana* in Arizona.

Large changes in the predicted distribution of *E. lehmanniana* occur under scenarios 20-28, where changes in summer and winter temperatures range from 0.5 to 3°C and changes in summer and winter precipitation range from 0 to 125% (Figure 2). However, the distributions predicted by scenarios 24-28 do not vary considerably, and the amount of area predicted as likely habitat by these models is actually less than that predicted by the current model. *E. lehmanniana* is predicted to move further upslope and to increasing latitudes under warmer and wetter conditions. Areas predicted as potential habitat under the current distribution model, in the southeastern and northwestern portions of the state, become too warm to fall within the environmental niche predicted for *E. lehmanniana* by this model. Expanding the extent of the study area may show that *E. lehmanniana* has the potential to greatly expand its range into neighboring states under these possible future conditions.

#### Limitations of the Study

Three important limitations of niche-based models are the lack of accounting for biotic interactions, dispersal, and evolutionary change (Pearson and Dawson 2003). I now address each of these potential shortcomings with the present model of *E. lehmanniana*.

#### *Biotic interactions*

Correlative models such as niche-based or bioclimatic envelope models have been criticized for not capturing species interactions (Davis et al. 1998). Competitive

interactions can limit the geographic distribution realized by a species; models built on known presence points under these conditions can underestimate the environmental niche that the target species has the ability to occupy (Peterson et al. 2002). Projecting this underestimated niche onto future climate scenarios would compound underprediction. Conversely, several studies have shown complex relationships between species, whereby removal of one member has rippling, unpredicted effects through the ecosystem (e.g., Silander and Antonovics 1982). Environmental niche models that do not account for these relationships can lead to incorrect predictions of future species distributions (Pearson and Dawson 2003).

Current knowledge of *E. lehmanniana* in the U.S. suggests that this plant is minimally constrained by interactions with other species. Instead, it has been observed to spread aggressively into native grasslands and shrublands from seeded areas, independent of disturbance (Anable et al. 1992). Cable (1971) predicted the spread of *E. lehmanniana* into appropriate habitat would be limited only by the ability of viable seed. Biotic interactions operate at a local scale, on the order of meters to kilometers (Willis and Whittaker 2002, Pearson and Dawson 2003), the scale of the model presented in this paper. However, because *E. lehmanniana* apparently moves across the landscape independently of other species, this criticism of correlative models does not pertain to the present model.

### *Dispersal*

Niche-based models assume the ability of species to follow their habitat across the landscape under a changing climate. Whether *E. lehmanniana* will move to new locations under increases in temperature and precipitation will depend primarily on whether viable seed is spread to these regions. Previous studies have estimated spread of *E. lehmanniana* at 6-10 m/yr and up to 175 m/yr (Kincaid et al. 1959, McClaran and Anable 1992), citing its ability to produce copious wind- and water-dispersed seed.

*E. lehmanniana* is widespread across the southwestern portion of Arizona and seems to still be spreading north and west across the state (D. Robinett, pers. comm. 2001), actively occupying native stands as well as areas cleared by grazing, fire, or drought (Sumrall et al. 1991, Anable et al. 1992). Therefore, it is likely that *E. lehmanniana* will be able to spread with a changing climate, moving to new locations at higher elevation and latitude. Areas receiving frequent seed introductions and near roads and trails are most likely to become invaded first, with populations spreading from these loci (Moody and Mack 1988). Remote locations, far from existing *E. lehmanniana* populations and from roads and trails, are least likely to become populated due to lower probability of seed introduction. In addition, locations separated from existing invasions by barriers, such as the region to the north of the Grand Canyon, are also less likely to become quickly invaded.

### *Evolutionary change*

Under the pressures of climate change, some species evolve rapidly, selecting traits enabling their survival (Woodward 1990, Thomas et al. 2001). The ability of some species to quickly evolve is an important factor impacting species' distributions not addressed by niche models. The introduction history of *E. lehmanniana* to the U.S. is well known; seed planted across Arizona can be traced to a single plant (Crider 1945). Recent research has shown that genetic variation in U.S. populations does exist, though it is unclear whether this variation is the result of genetic mutations following introduction or due to genotypic plasticity in the original maternal plant (Schussman 2002). Regardless, these findings demonstrate that *E. lehmanniana* may possess the ability to adapt to new environments quickly. The future distributions presented in this paper may therefore be conservative.

### Caveats

It is important to interpret the future-distribution scenarios presented here as first approximations and not precise simulations of *E. lehmanniana*'s future distribution for several reasons. First, two key assumptions are made with environmental niche models that, if not met, can drastically impact the results. One assumption is that the species is in equilibrium with its environment and that the presence points used to build the model accurately capture the species' niche. Next, it is assumed that the environmental variables used to build the model are the parameters that have primary influence on the species' distribution. Additionally, this model does not account for biotic interactions, which

could have great influence on the species' future distribution. Finally, the climate change models employed in this study are not necessarily representative of future conditions; large uncertainty surrounds future climate conditions. Therefore, the current and future predictions are "best guesses" for where *E. lehmanniana* could likely remain and spread but should not be interpreted literally.

Consideration of additional variables, such as land use and land cover, could improve model predictions. In addition, incorporation of disturbance regimes could highlight regions expected to become invaded most quickly under future climate conditions.

## **Conclusion**

*Eragrostis lehmanniana*, a troublesome perennial grass occupying continuous, dense stands in the southwestern U.S., is not likely to disappear under a changing climate. Predicted to potentially occupy over 110,000 km<sup>2</sup> in Arizona, this plant apparently is still spreading to available habitat. It likely will continue to expand as long as seed dispersal vectors facilitate its spread to new habitats. Under changing climatic conditions, *E. lehmanniana* is expected to expand its range to the north and upslope. Its projected future range will contract in the southern and central portions of the state as conditions become too warm. However, major range shifts are not predicted to occur until average summer maximum and winter minimum temperatures increase by at least 2°C and summer and winter precipitation increases by at least 30%.

The current model does not account for *E. lehmanniana*'s ability to adapt to new environmental conditions, which could allow *E. lehmanniana* to occupy more area than predicted here. In addition, biotic interactions are not considered; these can have profound impacts on species' distributions. Therefore, predictions presented in this paper should be considered "best guesses," but not interpreted literally.

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**Table 1.** Future climate scenarios used to predict potential distribution of *Eragrostis lehmanniana* in Arizona, USA. Negative values represent a decrease; positive values represent an increase.

Scenario	Change in Summer Precipitation (%)	Change in Winter Precip (%)	Change in Summer Maximum Temperature (°C)	Change in Winter Minimum Temperature (°C)
1	-10	-10	0.5	0.5
2	-10	-10	1	1
3	-5	-5	0.5	0.5
4	-5	-5	1	1
5	0	0	0.5	0.5
6	0	10	0.5	1
7	0	25	0.5	1
8	0	0	1	1
9	0	25	1	0.5
10	5	5	0.5	0.5
11	5	5	1	1
12	10	10	0.5	0.5
13	10	0	0.5	1
14	10	10	1	1
15	10	0	1	0.5
16	10	10	1.5	1.5
17	10	10	2	2
18	20	20	1.5	1.5
19	25	0	0.5	1
20	25	0	1	0.5
21	30	30	2	2
22	30	30	3	3
23	50	50	2	2
24	75	75	2	2
25	75	75	3	3
26	100	100	2	2
27	100	100	3	3
28	125	125	3	3

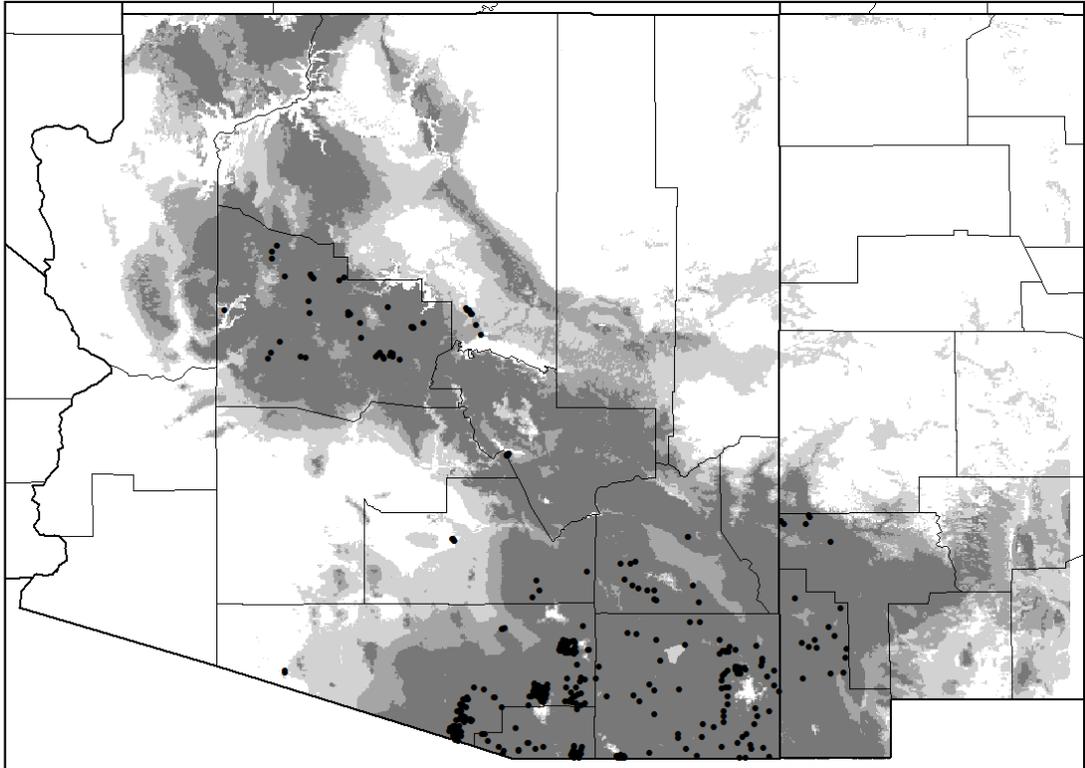
**Table 2.** Four-component solution generated by principal components analysis for predicting distribution of *Eragrostis lehmanniana* in Arizona, USA.

Variable	PC1	PC2	PC3	PC4	PC5
Winter minimum temperature	0.367	-0.332	0.091	0.149	0.079
Silt	-0.076	-0.243	0.483	0.022	-0.222
Sand	0.100	0.349	-0.125	0.562	-0.025
Elevation	-0.415	0.255	-0.095	-0.066	-0.045
Cosine of Aspect	0.004	-0.041	-0.183	0.013	-0.942
Clay	-0.125	-0.268	0.447	-0.330	-0.062
Winter precipitation	-0.227	-0.468	-0.069	0.379	0.056
Total precipitation	-0.405	-0.228	0.029	0.293	0.029
Summer precipitation	-0.406	-0.074	0.144	0.223	0.008
Summer maximum temperature	0.432	-0.200	0.075	0.037	0.048
Slope	-0.187	-0.272	-0.406	-0.040	0.186
Rock depth	0.147	0.163	0.384	0.506	-0.040
Radiation	-0.194	0.392	0.395	-0.097	0.094
Eigenvalue	4.61	2.19	1.62	1.13	1.02
Explained variance (%)	35.5	16.9	12.5	8.7	7.9
Cumulative variance explained (%)	35.5	52.3	64.8	73.5	81.4

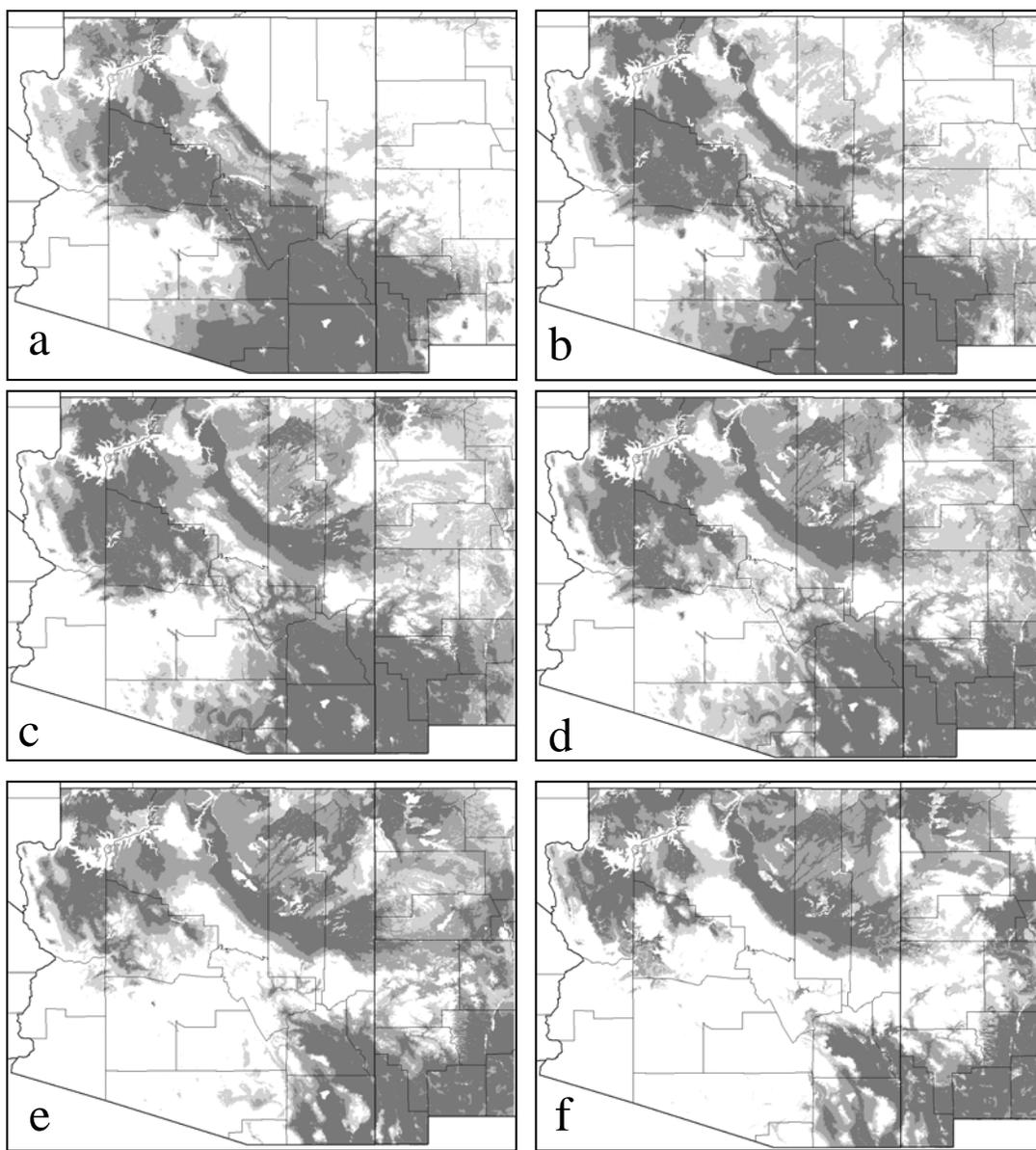
**Table 3.** Area occupied and spread of *Eragrostis lehmanniana* under climate change scenarios (Table 1) in Arizona, USA.

Scenario	Area predicted (km <sup>2</sup> )	Change Relative to Current Prediction		Overlap with Current Prediction	
		km <sup>2</sup>	%	km <sup>2</sup>	%
1	106,186	-4,004	-3.6	98,491	89.4
2	114,880	4,690	4.3	94,033	85.3
3	109,787	-403	-0.4	102,759	93.3
4	107,649	-2,541	-2.3	88,963	80.7
5	111,914	1,724	1.6	105,953	96.2
6	115,682	5,492	5.0	96,220	87.3
7	117,297	7,107	6.4	95,892	87.0
8	112,316	2,126	1.9	92,728	84.2
9	107,257	-2,933	-2.7	95,245	86.4
10	114,606	4,416	4.0	104,443	94.8
11	117,897	7,707	7.0	95,778	86.9
12	118,778	8,588	7.8	100,694	91.4
13	117,672	7,482	6.8	97,921	88.9
14	119,561	9,371	8.5	98,936	89.8
15	108,073	-2,117	-1.9	97,179	88.2
16	122,204	12,014	10.9	94,578	85.8
17	122,250	12,060	10.9	91,111	82.7
18	121,619	11,429	10.4	91,548	83.1
19	121,932	11,742	10.7	99,636	90.4
20	112,487	2,297	2.1	99,019	89.9
21	123,864	13,674	12.4	81,878	74.3
22	128,213	18,023	16.4	77,098	70.0
23	114,574	4,384	4.0	64,758	58.8
24	112,049	1,859	1.7	55,300	50.2
25	109,645	-545	-0.5	42,766	38.8
26	98,133	-12,057	-10.9	38,017	34.5
27	102,458	-7,732	-7.0	33,875	30.7
28	98,813	-11,377	-10.3	33,555	30.5

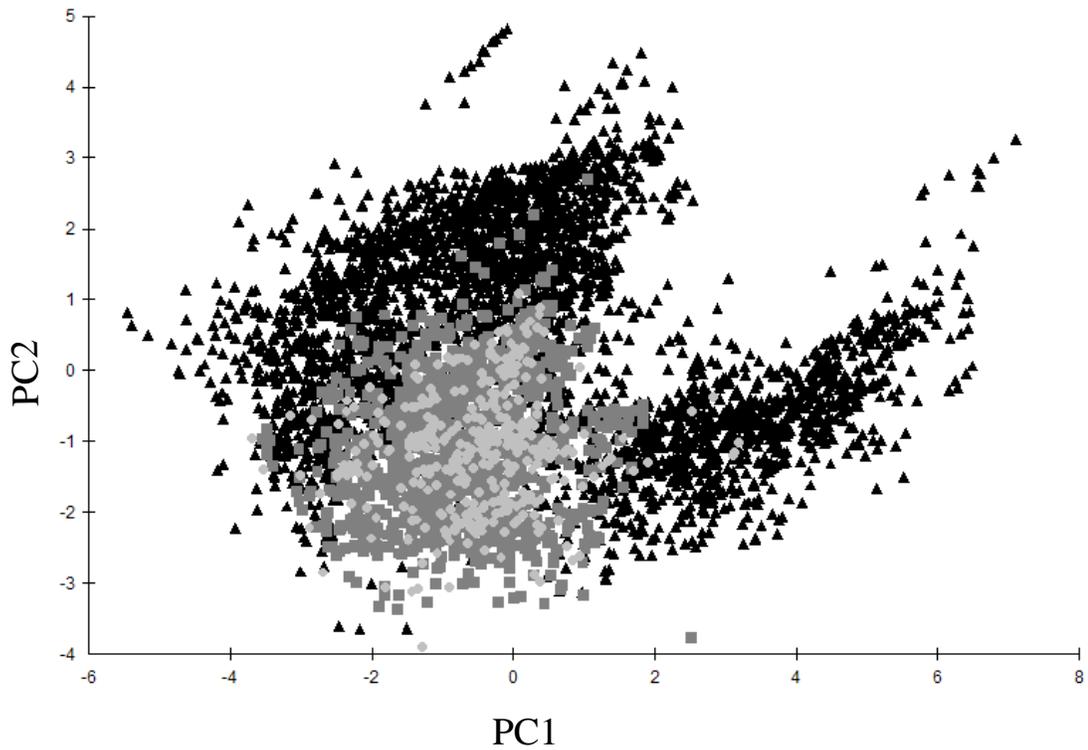
**Figure 1.** Predicted current distribution of *Eragrostis lehmanniana* in Arizona and western New Mexico using ten best models. Pixels shaded dark grey are predicted present by at least 9 out of 10 models; medium grey is predicted present by 6-8 models; light grey is predicted present by 3-5 models. Black dots represent known presence locations.



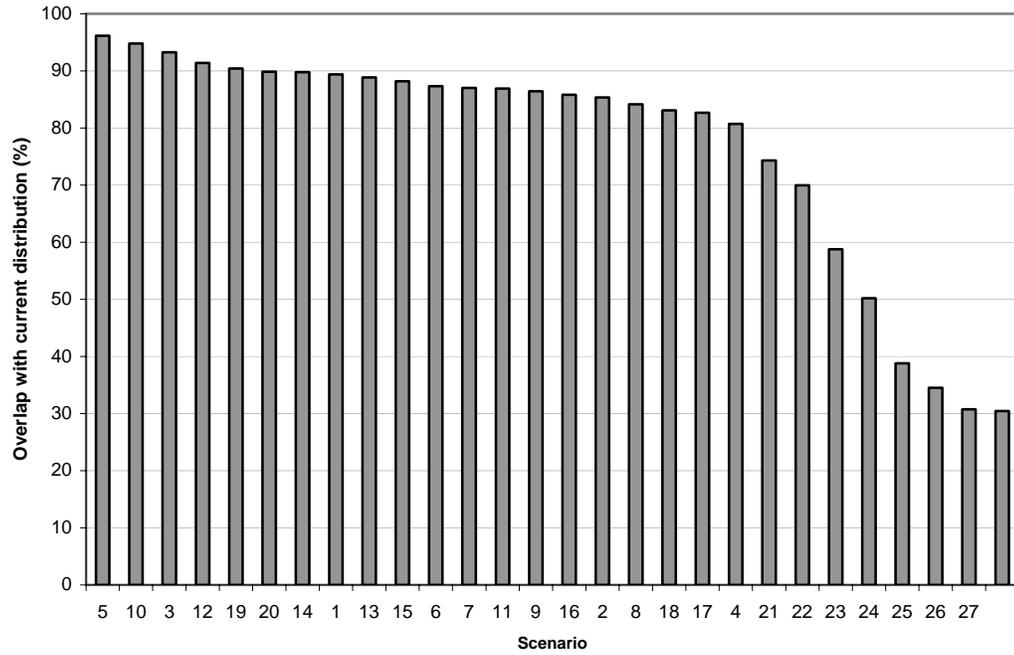
**Figure 2.** Predicted *E. lehmanniana* under various climate change scenarios. 2a displays prediction for scenario 1 (10% decrease in precipitation; 0.5°C increase in temperature); 2b displays scenario 14 (10% increase in precipitation; 1°C increase in temperatures); 2c displays scenario 21 (30% increase in precipitation; 2°C increase in temperatures); 2d displays scenario 23 (50% increase in precipitation; 2°C increase in temperatures); 2e displays scenario 25 (75% increase in precipitation; 3°C increase in temperatures); 2f displays scenario 28 (125% increase in precipitation; 3°C increase in temperatures). Darker shades of grey indicate greater model coincidence in predicting presence for *E. lehmanniana*.



**Figure 3.** Principal components analysis for predicting distribution of *Eragrostis lehmanniana* in Arizona. Black triangles represent all conditions available in study area. Dark grey squares are pixels predicted present by the model. Light grey circles are known presence points.



**Figure 4.** Spatial overlap of predicted future distributions of *Eragrostis lehmanniana* with predicted current distribution in Arizona, USA.



**APPENDIX C**

**COMMUNITY-LEVEL AND SEED BANK RESPONSE TO THE REMOVAL OF  
A NONNATIVE PERENNIAL GRASS AT THREE SITES IN SOUTHEASTERN  
ARIZONA**

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*(To be submitted to Ecological Monographs)*

**Abstract**

An understanding of ecosystem response to the removal of a dominant nonnative species is critical for planning control or eradication efforts. The objective of this study was to evaluate the response of herbaceous plants to the removal of *Eragrostis lehmanniana*, a dominant perennial bunchgrass, in semi-desert grasslands. *E. lehmanniana* was removed from 5 m x 5 m plots at three sites in southeastern Arizona. Because seed banks represent, in part, a site's potential for recovery following removal of aboveground vegetation, a second objective of this study was to characterize the seed banks at these sites.

This study suggests that plant community response to removal of an introduced species is mediated by precipitation variability (timing and amount), local site history, and edaphic conditions. The response observed on a site previously farmed for decades was to subsequently become dominated by other nonnative annual species. However, the two other sites with histories of livestock grazing responded more predictably to the removal, with an increase in annual ruderal species (2 to 10 times the amount of annual cover recorded on control plots). Treated plots at these two sites also exhibited increases in percent native cover (1.5 to 4 times native plant cover than in control plots) and forb cover (3 to 25 times the amount of forb cover recorded on control plots). The findings suggest that changes may continue on these sites if *E. lehmanniana* were to continue to be excluded from treatment plots, resulting in the eventual establishment of native perennial species.

The seed banks of all three sites hosted several species not observed in aboveground vegetation. However, the seed banks also indicated that the potential for the *E. lehmanniana* to recover from seed is limited; the *E. lehmanniana* seed bank tapered off noticeably (up to 25% less than in control plots) without the input of seed rain from above-ground plants.

## **Introduction**

Nonnative species introductions have been taking place as long as humans have inhabited the planet (Mack 2001), some with devastating impacts. It is estimated that approximately 10% of species introduced to a new environment become truly problematic (Williamson 1996), having impacts ranging from the displacement or replacement of native species to the complete reorganization of biotic communities.

Some of the most problematic and widespread plant introductions have been grasses, affecting ecosystems worldwide (Whisenant 1990, D'Antonio and Vitousek 1992, Weber 1997, White et al. 1997, D'Antonio et al. 1998). Introduced grasses directly affect resource availability (Gordon et al. 1989, Williams and Hobbs 1989), alter fire frequency (D'Antonio and Vitousek 1992, Billings 1994, Peters and Bunting 1994), and impact nitrogen and carbon cycling (Wedin and Tilman 1990, Fisher et al. 1994, Johnson and Wedin 1997).

Often, the response to the discovery of an exotic species with detrimental impacts is control or eradication, based in part on the success of other large-scale eradication efforts (Myers et al. 2000). However, eradication may not lead to the recovery of the

affected system, as some species alter systems so greatly that they are shifted to a different stable state (Westoby et al. 1989, Zavaleta et al. 2001). Alternatively, the effect of such a management action could actually exacerbate the problem. For example, efforts to control and reduce a nonnative plant species could initiate unexpected and undesirable feedbacks, such as favoring other nonnative species or drastically reducing plant cover to the detriment of wildlife and soil resources.

Zavaleta et al. (2001) argue for pre-eradication assessments to ascertain that a removal will yield the expected results and minimize unwanted effects. Such assessments can help determine a community's potential response to the removal of a nonnative species, especially when the nonnative is dominant. Ideally, such assessments should address direct and indirect effects of removing the nonnative species, including response of both plants and animals in the system. A second component of a pre-eradication assessment is an assessment of the potential for reestablishment by members of the native community. Seed bank studies provide some insight into a site's potential for recovery when the exotic species being removed is a plant (Rice 1989). Seeds of many perennial grasses are short-lived, requiring seed additions to restore vegetation.

This study is a pre-eradication assessment for *Eragrostis lehmanniana* Nees (Lehmann lovegrass), a perennial bunchgrass that has been associated with decreased plant and animal species richness (i.e., Cable 1971, Bock et al. 1986) and plant species diversity (Geiger and McPherson 2004). In addition to decreased species richness, *E. lehmanniana* has been associated with the alteration of ecosystem processes (Cable 1971, Bock et al. 1986, Williams and Baruch 2000), modification of community composition

(Anable et al. 1992), and changes in fire regimes (Ruyle et al. 1988, Burquez and Quintana 1994, Biedenbender and Roundy 1996).

The results of this study sought to address how semi-desert communities in southeastern Arizona would respond to the removal of this species. This was addressed through a removal experiment of *E. lehmanniana* at three sites dominated by this plant. Field studies offer the best representation of the effects of a wide-scale eradication effort, as study sites are subject to natural variations in temperature and precipitation and reflect its disturbance history. Because seed banks represent, in part, a site's potential for recovery following removal of aboveground vegetation, a second objective of this study was to characterize the seed banks at these sites in a greenhouse study.

## **Methods**

### *Species information*

*Eragrostis lehmanniana* was introduced from Africa and officially released by the U.S. Soil Conservation Service (currently the NRCS) to stabilize soils and provide cattle forage (Cox et al. 1984). This species spreads aggressively to dominate perennial grass composition, establishes in new areas without disturbance, and produces copious amounts of seed that disperse by wind and water (Anable et al. 1992). In the 50 years following its introduction, this grass occupied twice the area to which it was originally sown (Cox and Ruyle 1986), and is predicted to spread to areas far beyond its current range (Mau-Crimmins et al. submitted). *E. lehmanniana* seed planted throughout Arizona, New Mexico, and Texas can be traced to a single plant (Crider 1945). Recent research has

shown that genetic variation in U.S. *E. lehmanniana* populations does exist, though it is unknown whether this variation is the result of the U.S. population undergoing mutation and genetic drift or due to genotypic variability present in the introduced individual (Schussman 2002).

### *Site descriptions*

This experiment was conducted at three locations in southeastern Arizona: the Santa Rita Experimental Range (SRER), Coronado National Memorial (CORO), and the Three Links Farm (TLF, Figure 1). At all study locations, *E. lehmanniana* was the dominant plant species.

The Santa Rita Experimental Range is 40 km southeast of Tucson, AZ (31.80°N, 110.83°W; elevation 1,200 m). The pasture selected for this study, the “airstrip” enclosure in pasture 34, has been excluded from cattle grazing for nearly 25 years (M. Heitlinger, pers. comm. 2005), and an arson fire burned the site in June of 1994 (Biedenbender and Roundy 1996). The soil is a Comoro sandy loam (thermic Typic Torrifluent), comprised of recent alluvium weathered from granitic rocks. The soil varies in depth to 60 cm with a moderately acid pH of 6.2-6.9 (Hendricks 1985, USDA NRCS 2004). Annual precipitation is 56.5 cm (Western Regional Climate Center 2005). Average daytime temperatures are 18°C and often reach 42°C in June and July. Average winter minimum temperatures are 3°C in January and February (WRCC 2005).

The second study site was located within the Montezuma Allotment at Coronado National Memorial near Hereford, Arizona (31.33°N, 110.23°W; elevation 1,500 m).

Cattle grazed this allotment from at least 1929 until 1990 (University of Arizona Student Chapter, Society for Range Management 1995). The soil at this site is a Lanque sandy loam (thermic Pachic Haplustoll), with a slightly acid to slightly alkaline pH (6.1-7.8) and a depth of greater than 150 cm (Denny and Peacock 2000). The soils are alluvium derived from granite (Denny and Peacock 2000). Annual precipitation at Coronado NM is 52.5 cm (WRCC 2005). Average daytime temperatures are 16°C. Maximum temperatures reach 32°C in June and July, and winter minimum temperatures reach approximately 0°C in January and February (WRCC 2005).

The third study site was located on the Three Links Farms (TLF) near Cascabel, Arizona (32.11°N, 110.31°W; elevation 1,060 m), on agricultural fields farmed for 30-40 years then abandoned in 1999 and invaded by *E. lehmanniana* (B. Clark, pers. comm. 2003). The soil is a saline-sodic Hantz silty clay loam (thermic Vertic Torrifuvent) with a pH of 7.9 to 8.4 (Svetlik unpublished data). At nearby Cascabel, AZ, annual precipitation is 35.1 cm (WRCC 2005). Average daily temperatures are 18°C, with June and July maximum temperatures reaching 37°C. Wintertime low temperatures drop to -1°C in December and January (WRCC 2005).

The three study sites are dominated by *E. lehmanniana*, but they exhibit considerable variation in annual precipitation, edaphic characteristics, and land use history. Replicating the experiment at three different locations potentially expands the generality of the results in addition to the site-specific findings (Willems et al. 1993, Gurevitch and Collins 1994).

### *Field methods*

The experiment used a randomized block design. Twelve experimental plots 5 m x 5 m in size were established at TLF; fourteen plots were established at CORO in anticipation that one or two plots might have needed to be abandoned due to high foot traffic in this area on the US-Mexico border. Twenty-four plots were established at SRER with the original intention of a second experimental treatment. Plot locations were selected to maximize cover by *E. lehmanniana* and minimize presence of other species. A buffer of at least 1 m separated plots. At each site, one-half of the plots were randomly assigned the ‘removal’ treatment; the remaining plots were untreated.

In the spring (April and May) of 2003, plant cover was estimated in all plots using the point-intercept method (Greig-Smith 1983). Five parallel transects spaced 1 m apart were placed in each plot. Aerial cover was recorded every 10 cm along each transect, resulting in 250 points per plot. In addition, all species observed in a plot but not encountered using the point-intercept method also were recorded. Species were identified and assigned native or nonnative status; annual, biennial, or perennial habit; and graminoid, forb/herb, shrub, tree, or vine growth form according to the PLANTS database (<http://plants.usda.gov>). A few species had insufficient characteristics for identification but were clearly distinct from other species in the plots and were labeled as morphospecies. Plant names follow the Integrated Taxonomic Information System (ITIS) convention (<http://www.itis.usda.gov>).

Immediately following the plot inventories, the non-selective herbicide glyphosate (RoundUp) was applied to the “treatment” plots to remove *E. lehmanniana*.

Prior to treatment, all non-target forbs and grasses were identified and shielded from treatment by covering with plastic bags. The glyphosate was applied in a low-volume broadcast application using hand-held spray equipment at a rate of 45 ml/ha. Dead *E. lehmanniana* litter was not removed, as a previous study suggested *E. lehmanniana* does not replace itself on herbicide-treated plots with the canopy left intact (Sumrall et al. 1991). Follow-up treatments to kill *E. lehmanniana* plants which subsequently established in the “treatment” plots were applied in July and August of 2003 and again in May and July of 2004. Plots were again sampled in the fall (August-September) of 2003, and again in the spring and fall of 2004. From this point forward, spring seasons are referred to as SP03 and SP04, and fall seasons are named FA03 and FA04.

In addition to measures of species cover, standing live and dead biomass and surface litter was measured in areas adjacent to the study plots. At each site, 20 1.0 m x 0.5 m quadrats were placed in random locations within 1 m of study plots. The samples were sorted into standing biomass by species and litter. The samples were dried for 48 hours at 68°C and weighed to the nearest 0.1 g. Biomass samples were collected in FA02, SP03, FA03, SP04, and FA04.

Seed banks were sampled in May, July, and September of 2003 and 2004 (denoted SP03, SU03, FA03 and SP04, SU04, and FA04) in an attempt to capture peaks in seed abundance. The emergence technique (Brown 1992) was used to assess the composition of the soil seed banks. Four cores measuring 7 cm in diameter and 3 cm deep were randomly located and sampled from each of the study plots. Samples were combined by plot in a single labeled paper bag. Soil samples were stored in paper bags

until air dry. Each sample was sieved through a #10 mesh to remove rocks and other debris and spread approximately 1 cm thick onto sterilized potting soil in four 100 cm<sup>2</sup> pots. Seedling trays were kept in a greenhouse and watered daily. The greenhouse was cooled in summer and heated in winter, but experienced considerable daily and seasonal variation in temperature. To ensure conditions were appropriate for native species we expected to see, seed of three common grasses (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths, *Bouteloua curtipendula* (Michx.) Torr., *Digitaria californica* (Benth.) Henr.) were added to pots containing only the sterilized growing medium.

When seedlings could be identified, they were counted and pulled to minimize competition within pots. The top layer of the soil samples was stirred approximately four weeks following initiation to encourage further germination. Seed bank samples were maintained in the greenhouse until emergence ceased, typically after six months or less. Seedlings recorded for the four pots per plot were combined for further analysis.

To characterize basic soil properties for the three sites, soil samples consisting of six cores 7 cm in diameter and 5 cm depth were collected across each of the three study sites, outside of plots in July 2004. Two such samples were collected each at CORO and SRER; one sample was taken at TLF due to the homogeneity observed at the previously tilled site. The samples taken from each site were combined and air-dried in paper bags. The Soil, Water, and Plant Analysis Laboratory (Tucson, AZ) analyzed the samples for pH, cation exchange capacity, phosphorus, potassium, total organic carbon, and texture.

### *Precipitation data*

Daily precipitation data for the three study sites were downloaded from the National Climatic Data Center (NOAA 2005). Stations for CORO and SRER were located within three km of the respective study plots. However, the closest station to TLF was located in Cascabel, AZ, approximately 15 km northwest of the study plots at TLF. Precipitation was totaled for each site for winter months (December-January) and summer months (June-September) of 2003 and 2004 to capture the bimodal precipitation pattern evident in southern Arizona. Precipitation patterns at CORO and SRER were similar over the study period; precipitation for each winter and summer month was compared between these two sites using a non-parametric Wilcoxon/Kruskal-Wallis (rank sums) test to detect differences in the temporal distribution of seasonal precipitation.

### *Statistical analyses: Aboveground vegetation*

To test whether there was a significant treatment or site effect on the plant communities of the study plots, I performed several multivariate analysis of variance (MANOVA) tests with each sampling date treated as a different dependent variable. Dependent variables included percent plant cover, relative percent native cover, relative percent nonnative cover, relative percent grass cover, relative percent forb cover, relative percent annual cover, relative percent perennial cover, and species richness, each treated individually. Independent variables included site, treatment, and the site\*treatment interaction. Repeated-measures data were analyzed with MANOVA due to potential

autocorrelation between consecutive sampling dates. Data were transformed with the arcsine square-root transformation prior to analysis to increase homogeneity of variances (Sokal and Rohlf 1995). To minimize spatial autocorrelation, the Greenhouse-Geisser adjustment was applied to “within-subjects” effects (Greenhouse and Geisser 1959, Littell et al. 1992). MANOVA analyses were performed using SAS v8.02 (SAS Institute 2001). Because FA04 samples were not allowed to completely germinate, these data were excluded from analyses.

#### *Aboveground community analyses*

Following the removal of rare species (contributing <5%), Bray-Curtis similarity coefficients (Bray and Curtis 1957) were calculated for aboveground abundance data using a square-root transformation to balance the influence of dominant and rare species (Clarke and Warwick 2001). Analysis of similarity (ANOSIM) was then used to test for changes in community composition following experimental treatments. Within a particular season, communities of treated plots at a site were compared to control plots at the same site. ANOSIM was also used to test for differences from season to season within each site and treatment combination. ANOSIM is a non-parametric permutation procedure based on the ranking coefficients derived from similarity matrices. ANOSIM calculates a test statistic (R) typically ranging from 0 to 1, where R=0 when there is an equivalent degree of similarity between and within groups, and where R=1 when all replicates within groups are more similar than any replicates from different groups

(Clarke and Warwick 2001). The statistic was recomputed 5,000 times/test using a Monte Carlo permutation (Clarke and Warwick 2001).

When differences in species assemblages were detected using ANOSIM, the particular species responsible for differences in overall community composition were determined using the ‘Similarity Percentages’ (SIMPER) routine. SIMPER is a technique that identifies the species responsible for particular aspects of a multivariate plot by considering the contribution of species to both the average similarity within groups as well as the average dissimilarity between groups (Clarke and Warwick 2001). All community analyses were performed using PRIMER software v5.2.8 (PRIMER-E Ltd. 2001).

#### *Seed bank abundance*

To test whether there was a significant treatment or site effect on the abundances of germinable seedlings in the seed bank of the study plots, I performed MANOVA with each sampling date treated as a different dependent variable. Dependent variables included total seeds germinated, percent native seedlings, percent graminoid seedlings, and percent perennial seedlings. Independent variables included site, treatment, and the site\*treatment interaction. Repeated-measures data were analyzed with MANOVA due to potential correlation between consecutive sampling dates. “Total number of seedlings” was transformed with a square-root transformation prior to analysis and all other variables were transformed using the arcsine square-root transformation to increase homogeneity of variances. To minimize spatial autocorrelation, the Greenhouse-Geisser

adjustment was applied to “within-subjects” effects (Greenhouse and Geisser 1959, Littell et al. 1992). To test whether site or treatment had an effect on the percent of seedlings that were *E. lehmanniana*, I used MANOVA. Percent of seedlings that were *E. lehmanniana* was the dependent variable and independent variables included site, treatment, and the site\*treatment interaction.

#### *Seed bank community analyses*

Seedlings counted were totaled for each plot and sampling event. The percent of the total seedlings for each plot and sampling event was then calculated by species. Following the removal of rare species (contributing <5%), Bray-Curtis similarity coefficients were calculated for seed bank data using a square-root transformation to balance the influence of dominant and rare species. ANOSIM was then used to test for changes in community composition following experimental treatments. Within a particular season, communities of treated plots at a site were compared to control plots at the same site. ANOSIM was also implemented to test for differences from season to season within each site and treatment combination. When differences in species assemblages were detected using ANOSIM, the particular species underlying differences in overall community composition were determined using SIMPER.

#### *Comparison of abundance and soil seed bank datasets*

To compare the composition of species represented in both the seed bank and the vegetation survey, the data were combined into one matrix and analyzed using non-

metric multi-dimensional scaling (NMS) based on Bray-Curtis similarity values. Rare (contributing <5%) species were removed and similarity values were calculated for data using a square-root transformation. NMS is a non-parametric ordination technique that constructs a configuration of the sample data such that similar samples are located in close proximity in ordination space (Clarke and Warwick 2001).

### *Biomass data*

Analysis of variance (ANOVA) was used to determine whether site had an effect on the biomass of *E. lehmanniana* within a single season. Abundance in kilograms per hectare of *E. lehmanniana* was the dependent variable and site was the independent variable. The Tukey-Kramer HSD test for multiple comparisons was used to control the overall error rate. A visual estimation of residual plots indicated that distributions were not substantially skewed. Therefore, analyses were performed on untransformed data.

## **Results**

### *Aboveground vegetation statistical analyses*

Over the course of the study, 65 different species were recorded within study plots at TLF, 79 species were recorded at SRER, and 80 species were recorded at CORO. CORO and SRER shared 33 species in common, SRER and TLF shared 22 species in common, and only 14 species were found at both CORO and TLF. For two of the dependent variables tested (relative percent perennial cover and species richness), there was a significant relationship three-way interaction between site, treatment, and sampling

season ( $p \# 0.038$ ). The two-way interaction between treatment and sampling season was significant for every other variable tested ( $p \# 0.0012$ ; Table 1). Finally, the two-way interaction between site and sampling season was significant for total percent plant cover, relative percent forb cover, relative percent grass cover, and relative percent annual cover ( $p \# 0.015$ ; Table 1). The interactive effects of both site and treatment with sampling season were significant for total plant cover; relative percent forb cover, relative percent grass cover, and relative percent annual cover ( $p \# 0.015$ ; Table 1).

For total plant cover, control plots exhibited 1.5 to 3 times the percent plant cover as treated plots (Figure 2). The site exhibiting the highest percent cover fluctuated by season. Following treatment, total percent cover dropped sharply on treated plots across all three sites for two seasons (FA03-SP04). Total percent cover began to rebound in FA04 (Figure 2). Treated plots hosted from 3 to 25 times the amount of forb cover as control plots. SRER consistently produced greater forb cover than CORO; TLF exhibited high forb cover in both seasons in 2004 (Figure 3). Relative percent forb cover showed a dramatic increase following treatment. The two fall seasons post-treatment exhibited higher forb cover than the post-treatment spring season (Figure 3). Control plots exhibited nearly double the relative grass cover than treated plots. Relative grass cover at SRER and CORO fluctuated seasonally in a similar fashion; grass cover dropped off sharply one year post-treatment at TLF. Finally, treated plots exhibited between 2 and 10 times the amount of relative cover by annual species than control plots (Figure 4). The three sites showed a consistent pattern over the three post-treatment sampling seasons, with TLF hosting the greatest proportion of annuals by cover and CORO consistently

hosting the least. Relative percent annual cover showed dramatic increases following treatment across the three sites, with the greatest amounts appearing in the two fall sampling seasons (Figure 4).

The interaction of treatment and sampling season had a significant “within subjects” effect on relative percent native cover ( $p = 0.004$ ; Table 1), with treated plots exhibiting 1.5 to 4 times the native plant cover than control plots (Figure 5). Percent native cover was higher in both fall seasons sampled than the spring sampling event. Control plots exhibited rather consistent relative percent native cover, whereas treated plots fluctuated between 35% and 65% relative native cover.

The three-way interaction between site, treatment, and sampling season was significant for relative percent perennial cover ( $p = 0.038$ ; Table 1). In FA03 and FA04, control plots at CORO and SRER were not significantly different from each other, but exhibited significantly higher relative percent perennial cover than all other site and treatment combinations (Figure 6). In SP04, control plots at CORO and SRER again were not significantly different from each other, but the differentiation between these plots and treated plots at these same sites was not as clear (Figure 6).

The three-way interaction between site, treatment, and sampling date was significant for species richness ( $p = 0.014$ ; Table 1). In both FA03 and FA04, treated plots at both SRER and CORO showed significantly higher richness values than control plots at these sites (Figure 7). In SP04, treated plots had significantly higher species richness than control plots at SRER, but this was not true at CORO. No significant

pattern could be detected in any season for TLF. Overall, species richness increased slightly over the course of the study (Figure 7).

#### *Aboveground vegetation – community analyses*

In the pre-treatment season (SP03), composition on control plots was not significantly different from treatment plots within any site (Table 2). Within FA03, the first post-treatment sampling period, treated and control plots were significantly different at both CORO and SRER. The same pattern held through SP04 and FA04. However, treated and control plots were not differentiated during any season at TLF (Table 2).

Results of SIMPER analyses indicate that the differences between treated and control plots at CORO in all post-treatment seasons were due mainly to the lack of *E. lehmanniana* in treated plots, as well as increases in *Mollugo verticillata* L., and *Calliandra eriophylla* Benth. (Table 2). The differences between treated and control plots at SRER can also be mainly attributed to the removal of *E. lehmanniana*; treated plots saw increases in *Mollugo verticillata*, *Urochloa arizonica* (Scribn. & Merr.) O. Morrone & F. Zuloaga, and *Kallstroemia grandiflora* Torr. ex Gray in the two fall sampling seasons and *Ambrosia confertiflora* DC. and *Spermolepis echinata* (Nutt. ex DC.) Heller in SP04 (Table 2). All of these species are native to Arizona; most are annuals. However, *Calliandra eriophylla* is a short-statured, perennial woody plant.

No pattern was detectable within the CORO control plots, and the only significant difference in successive seasons in treated plots at CORO occurred between the first two seasons sampled (SP03-FA03;  $p < 0.001$ ; Table 3), due to the removal of *E.*

*lehmanniana*. Aside from the effect of the removal treatment, SIMPER analyses indicated increases in *Mollugo verticillata*, *Nissolia wislizeni* (Gray) Gray, and *Calliandra eriophylla*, all native species, from SP03 to FA03. Also attributable to the removal of *E. lehmanniana*, treated plots at CORO were significantly different from SP03 to SP04. SIMPER indicated increases in *Calliandra eriophylla* as the other major contributing species (Table 3).

All seasons were significantly different ( $p < 0.001$ ) for both control and treated plots at SRER (Table 3). From SP03 to FA03, *E. lehmanniana* cover increased on control plots by 20%; in addition, *Mollugo verticillata* increased by 3%. In SP04, *Mollugo verticillata* was no longer present, a 15% decrease in *E. lehmanniana* was observed, and several species appeared in small amounts (<1% cover), including *Gilia scopulorum* M.E. Jones, *Spermolepis echinata*, *Boerhavia coccinea* P. Mill., and *Ambrosia confertiflora*. FA04 was characterized by the disappearance of *Gilia scopulorum*, which is a spring annual forb, and the reappearance of a small amount of *Mollugo verticillata* and *Urochloa arizonica* (1% and 0.5%, respectively). Every one of these species is considered native to Arizona.

Treated plots at SRER exhibited different community assemblages from control plots, and each season was consistently different from the previous. Following removal of *E. lehmanniana*, treated plots saw a dramatic increase in *Mollugo verticillata* (27%), *Kallstroemia grandiflora* (4%), and *Urochloa arizonica* (4%) in FA03. In SP04, none of these annual species were observed; *Ambrosia confertiflora* and *Spermolepis echinata*

became more prevalent. Finally, FA04 saw resurgences in *Mollugo verticillata* and *Urochloa arizonica*.

The spring-to-spring and fall-to-fall differences observed for both SRER control and treated plots are consistent across the treatments. SP03 was characterized by *Erigeron divergens* Torr. & Gray, *Lotus greenei* Ottley ex Kearney & Peebles, and *Ambrosia confertiflora*. SP04 exhibited *Ambrosia confertiflora* in greater amounts, as well as *Gilia scropulorum*, *Solanum elaeagnifolium* Cav., and *Spermolepis echinata*. The common species were rather consistent across the two falls sampled; *Mollugo verticillata*, *Kallstroemia grandiflora*, and *Urochloa arizonica* were recorded in higher amounts in FA03. FA04 also saw the proliferation of *Boerhavia coccinea* (Table 3).

The within-site/treatment ANOSIM tests show on-going changes in community composition at TLF. For both control and treated plots, all seasons were different from all others tested (Table 3). SIMPER results show a shift in both control and treated plots from an *E. lehmanniana*-dominated community in SP03 to much more bare ground and cover of *Eragrostis cilianensis* (All.) Vign. ex Janchen and *Sporobolus cryptandrus* (Torr.) Gray in FA03. Control plots shifted from 59% *E. lehmanniana* cover in SP03 to 3% *E. lehmanniana* cover in FA03; treated plots shifted from 62% to 5% *E. lehmanniana* cover in the same time. SP04 saw increases in *Salsola kali* L., and *Sisymbrium irio* L. with concurrent declines in *Eragrostis cilianensis* and *Sporobolus cryptandrus*. Finally, in FA04, a surge in *Salsola kali* (37% and 40% increases on treated and control plots, respectively) and increases in *Eragrostis cilianensis* and *Bouteloua aristidoides* (Kunth) Griseb. occurred. With the exception of *Sporobolus cryptandrus*, all of the dominant

species at TLF were annual species. Additionally, all were nonnative except *Sporobolus cryptandrus* and *Bouteloua aristidoides*, a perennial grass and a short-lived summer grass, respectively.

The spring-to-spring differences observed in control and treated plots at TLF (Table 3) can be attributed mainly to the sharp decrease in *E. lehmanniana* following SP03. The fall-to-fall differences are mainly due to the proliferation of *Salsola kali* in FA04.

#### *Seed bank statistical analyses*

Over 22,000 seedlings germinated over the course of the study period. Of these, more than 36% (8,152) were *E. lehmanniana* seedlings. Table 4 summarizes total numbers of seedlings counted by sampling season. Fifty-nine species were recorded for SRER seed bank samples. For TLF, 38 species were identified, and 32 species were recorded for CORO. All three native grasses seeded to sterilized growing medium (*Bouteloua gracilis*, *Bouteloua curtipendula*, and *Digitaria californica*) germinated, demonstrating that conditions within the greenhouse were appropriate for these grass species.

There were no significant three-way interactions between site, treatment, and sampling date ( $p < 0.05$ ) for total seeds germinated, percent graminoid seedlings, or seed bank species richness (Table 5). The two-way interaction between site and sampling date had a significant “within subjects” effect on both total seeds germinated and seed bank species richness ( $p < 0.0001$ ; Table 5). SRER germinated 3 to 8 times as many seeds as

CORO throughout the course of the study. TLF showed very high germination rates in the first two sampling seasons, but then germination rates dropped off markedly (Figure 8). Samples from CORO consistently exhibited the lowest species richness (Table 5). Richness values for all study sites fluctuated between approximately three and nine (Figure 9).

The two-way interaction between site and sampling season was significant for percent graminoid seedlings ( $p = 0.02$ ; Table 5); similarly, the two-way interaction between treatment and sampling season was significant for percent graminoid seedlings ( $p = 0.0009$ ; Table 5). Samples taken from treated plots had lower percentages of graminoid seeds for all sample dates. TLF consistently exhibited the highest percentage of graminoid seedlings, and SRER consistently germinated the fewest grass seedlings (Figure 10).

The three-way interaction between site, treatment, and sampling date was significant for percent perennial seedlings ( $p = 0.029$ ; Table 5). Control plots at CORO and SRER consistently exhibited higher percentages of perennial seedlings than treated plots at these sites, but the response was mixed for TLF (Figure 11). Similarly, the three-way interaction between site, treatment, and sampling date was also significant for percent native seedlings ( $p = 0.002$ ; Table 5). Control plots at CORO had consistently lower proportions of native seeds than treated plots at CORO, but this pattern was not as clear for the other sites (Figure 12).

The three-way interaction between site, treatment, and sampling date was also significant for the percent of the seedlings that were *E. lehmanniana* ( $p = 0.003$ ; Table 5).

Patterns within parks were quite consistent, with treated plots at both CORO and SRER germinating lower percentages of *E. lehmanniana* than control plots on the same sites in every season sampled (Figure 13). The response was more mixed for TLF, but the temporal pattern was consistent between treatments.

#### *Seed bank community composition*

Within control plots at all three sites, most seasons were significantly different from their predecessor with respect to community composition (Table 6). Likewise, within treated plots at all three sites, most seasons were significantly different from their predecessors. However, the pattern of seasons that were different was not consistent within sites (Table 6).

SIMPER analyses indicate the main differences between seed bank sampling seasons for control plots at CORO to be attributed to fluctuations in the abundances of *E. lehmanniana*, *Pseudognaphalium arizonicum* (Gray) A. Anderb., *Gnaphalium palustre* Nutt., *Mollugo verticillata*, and *Oxalis corniculata* L., all native annual forb species with the exception of *E. lehmanniana*. Seed bank samples from treated plots at CORO varied slightly in composition of the same species as for control plots, as well as *Erigeron divergens* (Table 6). Differences in seed bank composition between seasons in both control and treated plots at SRER were mainly due to fluctuations in *E. lehmanniana*, *Pseudognaphalium arizonicum*, *Mollugo verticillata*, *Androsace occidentalis* Pursh., and *Crassula connata* (Ruiz & Pavón) Berger (Table 6), also all annual forb species. Differences between seasons in both treated and control plots at TLF were mainly

characterized by fluctuations in the abundances of *E. lehmanniana*, *E. cilianensis*, *Oxalis corniculata*, *Panicum sp.*, *Sporobolus cryptandrus*, and *Sisymbrium irio* (Table 6). These species are a mix of native and nonnative species, as well as grass and forb species.

The seed banks of treated and untreated plots were not significantly different at TLF within any season sampled, and only differed at CORO for the SU04 sampling period (Table 7). SIMPER results indicated differences in the abundances of *Mollugo verticillata*, *Oxalis corniculata*, *Erigeron divergens*, *Pseudognaphalium arizonicum*, and *Eragrostis intermedia* A.S. Hitchc. to account for the significant differences between samples taken from control and treated plots in SU04 at CORO (Table 7). In addition to differences in these species, the percent of germinating seeds that were *E. lehmanniana* was markedly different between the two treatments (79% for samples from control plots; 44% for samples from treated plots).

The seed banks of treated and control plots were significantly different at SRER in SP04, SU04, and FA04 (Table 7). In all three cases, the percent of germinating seedlings that were *E. lehmanniana* was dramatically lower in treated plots than in control plots (53% in control plots vs. 32% in treated plots in SP04; 54% in control plots vs. 17% in treated plots in SU04; 8% from control plots vs. 3% from treated plots in FA04). Other major differences in the seed bank composition were attributable to *Mollugo verticillata* (64% of seeds from treated plots vs. 32% of seeds from control plots in SP04; 66% of seeds from treated plots vs. 33% of seeds from control plots in SP04), *Oxalis corniculata*, *Pseudognaphalium arizonicum*, *Androsace occidentalis* and *Crassula connata* (Table 7).

*Comparison of abundance and soil seed bank datasets*

The non-metric multi-dimensional scaling ordination illustrates significant compositional dissimilarities between the seed bank and aboveground plant communities at each site. Within each site, seed bank sample communities and aboveground communities are very clustered, with very little overlap (Figure 14). This suggests that despite the season sampled, communities germinating from seed bank samples do not represent the aboveground communities. These plots include all sampling seasons together; this demonstrates that there is no substantial relationship between seed bank and aboveground plant abundances in any of the seasons sampled and no evidence that a lag relationship exists.

At CORO, of the 80 species observed in the aboveground vegetation, 16 were germinated from seed bank samples. An additional sixteen species were germinated from soil samples that were not observed in aboveground vegetation. Of the species residing in the seed bank not expressed in aboveground vegetation, all but 3 species were natives, and all but 2 species were annuals. Five species were graminoids; the rest were forb species.

Of the 79 species recorded in aboveground vegetation at SRER, 13 appeared in seed bank samples. Twenty-four other species were recorded in the seed bank samples taken from SRER. Of these, only three are known to be nonnatives. Most species recorded were annual species; about half were graminoids and half were forb species.

At TLF, of the 65 species recorded in aboveground vegetation at study plots, 19 appeared in seed bank samples. Nineteen other species were recorded in TLF seed bank samples. Of these, all but two species were natives, and only one species was perennial. Six of the 19 species were graminoids.

#### *Aboveground biomass from field sites*

Biomass of *E. lehmanniana* was much greater at CORO and SRER than at TLF throughout the course of the study (Figure 15). Abundance of *E. lehmanniana* at TLF dropped off markedly following SP03. Conversely, *E. lehmanniana* abundance increased ( $p = 0.022$ ) at SRER and remained the same at CORO following SP03 (Figure 15).

Other species which were abundant at CORO included *Calliandra eriophylla* (338 kg/ha; 95% CI: 176 to 498 kg/ha averaged over 5 sampling periods) and *Bouteloua eripoda* (Torr.) Torr. (8 kg/ha; 95% CI: 0 to 18 kg/ha). Aside from ERLE, abundant species at SRER were *Solanum elaeagnifolium* (16 kg/ha; 95% CI: 0 to 30 kg/ha), *Kallstroemia grandiflora* (10 kg/ha; 95% CI 0 to 24 kg/ha), and *Mollugo verticillata* (8 kg/ha; 95% CI: 0.8 to 14.8 kg/ha). The most common species at TLF were *Salsola kali* (620 kg/ha; 95% CI: 246 to 744 kg/ha), *Sporobolus cryptandrus* (74 kg/ha; 95% CI: 26 to 104 kg/ha), and *Cynodon dactylon* (L.) Pers. (90 kg/ha; 95% CI: 36 to 128 kg/ha).

#### *Soils properties*

Soil pH fell within the expected range of 6.2 to 6.9 at SRER (Table 8). Soil pH measurements for CORO were slightly lower than expected based on soil survey

information, and the pH measured at TLF was lower than predicted by the soil survey (Svetlik unpublished data). Additionally, texture analysis suggested TLF was characterized as a sand with 4.5% clay, much different from the silty clay loam suggested by the soil survey (Svetlik unpublished data). Soil electrical conductivity (EC), total organic carbon, and potassium were highest at TLF (Table 8). Soil pH was on average approximately 0.5 unit lower at CORO than at SRER, which equates to approximately three times the acidity. Values for other soil characteristics did not vary perceptibly between SRER and CORO.

#### *Precipitation data*

Total precipitation over the study period was much less at TLF than at the other two sites (Figure 16); CORO and SRER followed similar patterns over this period. At TLF, seasonal precipitation totals were much lower than at CORO and SRER. SP03 precipitation measured just less than 10 cm, and FA03 precipitation was even lower, at 9.4 cm. SP04 totaled 9.5 cm and FA04 measured just over 17.8 cm. Because precipitation was so different at TLF than at the other two sites, it was treated separately for further analyses.

For SRER, precipitation was much more evenly distributed across winter months in 2004 than in 2003 (Figure 17a). The same pattern was generally true for CORO, but precipitation was not as evenly distributed across winter months in 2004 for CORO as for SRER. Within the monsoon season (June-September), moisture was more evenly distributed across the months at CORO than at SRER, especially in 2004 (Figure 17b).

December precipitation differed in event size and frequency at CORO in 2002 and 2003 (one-sided  $p$ -value = .003, from the rank-sum test). In addition, January precipitation differed at CORO between 2003 and 2004 (one-sided  $p$ -value = .013, from the rank-sum test). There was not strong evidence of a difference between the two years for either February (one-sided  $p$ -value = .462, from the rank-sum test) or March (one-sided  $p$ -value = .494, from the rank-sum test) between the two years.

At SRER, there was suggestive but inconclusive evidence of a difference between 2003 and 2004 January precipitation (one-sided  $p$ -value = .096, from the rank-sum test). Differences between 2002 and 2003 precipitation at SRER were even less suggestive (one-sided  $p$ -value = .125, from the rank-sum test). Precipitation did not differ between 2003 and 2004 for the months of February (one-sided  $p$ -value = .278, from the rank-sum test) or March (one-sided  $p$ -value = .780, from the rank-sum test) at SRER.

June precipitation differed in event size and frequency at SRER in 2003 and 2004 (one-sided  $p$ -value = .078, from the rank-sum test). August precipitation differed at SRER in 2003 and 2004 (one-sided  $p$ -value = .059, from the rank-sum test). However, there was little evidence of a difference between years at SRER for July (one-sided  $p$ -value = .970, from the rank-sum test) or September (one-sided  $p$ -value = .416, from the rank-sum test).

There was little evidence of differences in precipitation in the month of June between 2003 and 2004 at CORO (one-sided  $p$ -value = .394, from the rank-sum test). Also, there was not strong evidence for a difference between the two years for July (one-

sided  $p$ -value = .451, from the rank-sum test), August (one-sided  $p$ -value = .122, from the rank-sum test), or September (one-sided  $p$ -value = .400, from the rank-sum test).

## **Discussion**

This study suggests that the post-treatment effects of removing an introduced species are mediated by both precipitation variability (timing and amount) and local site history and edaphic conditions. The net result of these complex interactions are aboveground plant communities dominated in the short-term by several native species that bear little resemblance to the membership of their corresponding seed bank.

### *Treatment Effect*

All three study sites showed immediate responses to the removal of a dominant nonnative species, but the magnitude and composition of the responses varied by location. First, as expected, removing *E. lehmanniana* resulted in significant drops in total plant cover in treated plots, which rebounded following the initial post-treatment reduction. The removal also resulted in significant increases in species richness at CORO and SRER that were sustained for the duration of the experiment. This finding is consistent with several other removal experiments where removal of a dominant species resulted in increases in species richness (Abul-Fatih and Bazzaz 1979, Hils and Vankant 1982, Armesto and Pickett 1985, Farnsworth and Meyerson 1999). Responses to the complete removal of *E. lehmanniana* could potentially be stronger than those observed in

this study; treatment plots were surrounded by thick stands of *E. lehmanniana*, providing ample seed source and the opportunity for the plant to vegetatively encroach.

Following removal of the dominant nonnative species, substantial increases in the cover of annual species, forb species, and native species were observed. These increases are not attributable to the increase in one or two species, but rather to broader shifts in community composition. At SRER, increases in the cover of *Mollugo verticillata*, *Kallstroemia grandiflora*, and *Ambrosia* spp. comprised the main differences between treated and untreated plots in FA03 and FA04 (Table 2). These species are all native annual forbs. However, *Urochloa arizonica*, a native annual graminoid, and *Solanum elaeagnifolium* and *Boerhavia coccinea*, both native perennial forbs, also contributed to these compositional changes. At CORO, species demonstrating the greatest increases on treated plots were *Mollugo verticillata*, *Nissolia wislizeni*, *Evolvulus nuttallianus* J.A. Schultes, and *Calliandra eriophylla* (Table 2). *Calliandra eriophylla* is a native perennial shrub. Both *Nissolia wislizeni* and *Evolvulus nuttallianus* are native perennial forb species. Similarly, other community-level studies have demonstrated an increase in less common species following removal of the dominant species (Hils and Vankat 1982, Silander and Antonovics 1982, Farnsworth and Meyerson 1999). The control and treated communities were not significantly different at TLF.

The removal treatment had moderate to strong positive impacts on the proportion of the seed banks of the three sites that were *E. lehmanniana*, suggesting the potential for site restoration. The percent of seeds that were graminoids, the percent that were perennial species, and the percent that were native species differed by both site and

treatment. The difference between treatments reflects reduced number of *E. lehmanniana* seeds in the seed banks of treated plots. Removing the aboveground *E. lehmanniana* from treated plots resulted in a substantial decrease in *E. lehmanniana* seeds germinating in soil samples from these plots. This phenomenon is critical from a site restoration perspective: Removing the aboveground *E. lehmanniana* permanently has a large impact on the *E. lehmanniana* seed bank. This is in opposition to several other removal studies of exotic species, where these exotics were observed to restore dominance of above-ground vegetation from the seed bank following a disturbance (Major and Pyott 1966, Pyke 1990, Kyser and DiTomaso 2002). This may be due to particular life history traits of *E. lehmanniana* and edaphic factors of semi-desert grasslands.

#### *Influence of land use history*

Overall TLF, a site with a very different land use history than the other two study sites, showed very different responses from SRER and CORO for many of the variables tested in this study, indicating that TLF is responding differently than the other two sites. Because *E. lehmanniana* individuals in southeastern Arizona can be traced to seed grown from a single accession (Crider 1945), it can be concluded that differences observed among the study sites is not attributable to genetic differences.

At the outset of this study, TLF was dominated by *E. lehmanniana* (nearly 60% absolute cover in December 2002, T. Mau-Crimmins, unpublished data), though the plants were reduced in size compared with CORO and SRER. The small plant size is evident in the biomass measures (Figure 15). However, following SP03, *E. lehmanniana*

nearly vanished from the site regardless of treatment. Total plant cover dropped sharply in FA03, and the plants observed in this season were primarily *E. lehmanniana* and *E. cilianensis*. This is likely the result of very low total precipitation measured for FA03 at this site. SP04 saw a dramatic increase in plant cover, specifically annual forbs – primarily *Sisymbrium irio*. The same pattern held in FA04, primarily due to a large increase in *Salsola kali* (Table 3). Both of these species are nonnative annual forb species. *Sisymbrium irio* is considered an invasive species by both the Western Society of Weed Science and the Southern Weed Science Society (Whitson et al. 1996, Southern Weed Science Society 1998). *Salsola kali* is considered invasive in several states (NRCS PLANTS database 2005). However, it is worth noting that the cover of *Sporobolus cryptandrus*, a native perennial bunchgrass, increased from 0.2% (95% CI: 0 to 0.4%) to an average of 7% (95% CI: 3.3 to 10.5%) over the course of the study in both control and treated plots at TLF, with 21% cover in one plot in FA04. *Sporobolus cryptandrus* is one of the few native perennial grasses that is persistent in seed banks (Coffin and Laurenroth 1989). No forb species showed such patterns at TLF.

There were no discernible differences between control and treated plots for total plant cover, species richness, percent relative native cover, percent relative forb or grass cover, or percent relative annual or perennial cover at TLF. In addition, treated and control plots were not significantly different on a community basis. The absence of difference between control and treated plots at TLF for any of the dependent variables tested as well as the community-level analyses suggests that TLF is not responding to the removal of *E. lehmanniana*. Rather, TLF seems to be hosting one opportunistic weedy

species after another, responding to fluctuations in seasonal precipitation. This response could be in large part due to the disturbance history of the site – the fields were intensively farmed for decades prior to this study. The soil is very sandy and it appears to lack aggregates and structure, which are important for soil moisture retention (Brady and Weil 2002). In desert and semi-desert ecosystems, precipitation is the dominant controlling factor, constraining plant growth and survivorship as well as other ecological processes such as carbon and nitrogen fixation (Noy-Meir 1973, Cui and Caldwell 1997, Schwinning et al. 2003, Belnap et al. 2004). In such a water-limited system, the ability for soils to retain plant-available moisture is critical.

Electrical conductivity was at least two times higher at TLF than the other samples. Though the salinity measurement from this site is not considered high enough to injure plants, it is considered to be “medium salinity” and can impact the composition of plants occupying the site (Silvertooth 2001, Bauder 2005). Soil salinity affects plants’ ability to maintain osmotic balance; the more saline the soils, the stronger the pull of water from plants (Brady and Weil 2002). The presence of soil salts at TLF, in conjunction with sandy texture lacking aggregates, may yield much lower plant-available water than at the other two sites, even under adequate precipitation amounts.

One interesting and potentially encouraging pattern observed at TLF is the steadily increasing species richness over the course of this study. Over this period, average species richness for both control and treated plots at TLF increased from just over 5 (95% CI: 4.5 to 6.5) to over 13 species per plot (95% CI: 12.2 to 14.3). This may suggest a slow improvement in conditions, from a site dominated by one nonnative

species to a more diverse community. This pattern also may be due to the dramatic increase in precipitation recorded in FA04 from FA03. Either way, these results suggest that even in a semi-arid environment on a heavily impacted site, progression toward a stable, native community may be possible and may be occurring at TLF.

It is also interesting to note that the increase in aboveground species richness was not matched by a concomitant increase in seed bank species richness. The seed bank at TLF, similar to the aboveground vegetation, appears to be undergoing major shifts. The first two sampling periods germinated large quantities of seeds, the majority of which were *E. lehmanniana* seedlings. The *E. lehmanniana* proportion of the seed bank tapered off dramatically over the course of the study, concurrent with the drop-off in aboveground *E. lehmanniana*. The relative paucity of *E. lehmanniana* seeds in later seed bank samples can be explained by the lack of seed rain inputs. Later seed bank samples exhibited relatively large increases in the abundance of *Sporobolus cryptandrus* and *Panicum* sp. seedlings; both grass species and likely both native as there are no known nonnative *Panicum* species in the area. The discrepancies between species richness of aboveground vegetation and the seed bank suggests that many of the species observed in aboveground vegetation arrived from off-site, rather than as a result of viable seeds remaining latent in the seed bank. The species exhibiting the greatest consistencies between aboveground vegetation and seed bank were *Sporobolus cryptandrus*, *E. lehmanniana*, and *E. cilianensis*, all grass species. These similarities may explain the slight overlap observed in aboveground vegetation and seed bank samples in the NMS plot (Figure 14).

*Eragrostis lehmanniana* produces abundant seed (Allison 1998). Therefore, the relative rarity of *E. lehmanniana* seeds in later seed bank samples from TLF implies a decrease in *E. lehmanniana* seeds in these seed bank samples. However, *E. lehmanniana* seeds require approximately six to nine months of afterripening, but can remain dormant for much longer (Weaver and Jordan 1986, Voigt et al. 1996). One study reported only 10% germination after 88 weeks post-harvest (Hardegree and Emmerich 1993), suggesting that a large number of viable *E. lehmanniana* seeds may have still remained in the soil samples but had not yet broken dormancy. To address this unanswered question, subsequent longer-term seed bank studies should be undertaken.

Species that were observed in the seed bank but not in aboveground vegetation can offer some additional clues to the site's potential for restoration. Several species appeared in very small quantities (one or two seedlings), but the abundance of a few key native grasses suggest a viable seed bank. Over the course of the six sampling seasons, 402 *Panicum* sp. seedlings were recorded and 41 *Leptochloa panicea* (Retz.) Ohwi ssp. *brachiata* (Steudl.) N. Snow seedlings were counted. *Leptochloa panicea* is a native perennial graminoid, and *Panicum* sp. is a graminoid, likely native due to the lack of nonnative *Panicum* species in the area. The next three most commonly germinating species in this group were also native species, *Chamaesyche micromera* (Boiss. ex Engelm.) Woot. & Standl., *Eriochloa acuminata* (J. Presl) Kunth, and *Erigeron divergens*. Two of the most common species germinating in the seed bank that were also observed in the aboveground vegetation were native perennial grasses, *Sporobolus cryptandrus* and *Eragrostis intermedia*. However, these seed numbers are swamped by

the nonnative grasses observed at the site; 4,005 *E. lehmanniana* seedlings were counted over the seed bank study and 2,382 *E. cilianensis* seeds were recorded. These facts suggest that though some native species are increasing in numbers and cover, the study sites harbor many abundant nonnative species providing plenty of competition for limited nutrients at this site.

*Similarities and differences between two study sites with similar land use histories*

Removal effects on plant communities and seasonal dynamics

Overall, the communities sampled at CORO and SRER responded similarly over the course of this study. *E. lehmanniana* biomass followed the same seasonal patterns (Figure 15), exhibiting peaks in the fall seasons sampled. Treated plots at both sites exhibited increases in relative native cover following treatments. In addition, both study sites experienced similar increases in relative forb and annual cover in the two post-treatment fall seasons. For several of the variables tested, differences between the two study sites were not significant.

The results of the within-site/treatment ANOSIM tests reveal interesting patterns that suggest that SRER and CORO, though similar in some ways, are responding differently to the removal of *E. lehmanniana*. On control plots at CORO, each successive season was not significantly different from the previous, indicating a stable, *E. lehmanniana*-dominated community. However, each successive season is significantly different from the previous on control plots at SRER, suggesting fluctuations in the non-*E. lehmanniana* portion of the community. Indeed, the non-*E. lehmanniana* portion of

these communities showed little overlap through the four seasons (Table 2). Nearly all of the species observed in all of these seasons were native annual species, primarily forbs. The exception is *E. curvula*, a nonnative perennial grass related to *E. lehmanniana* and introduced from South Africa at the same time (Crider 1945).

Every successive season was significantly different from the previous on treated plots at SRER from a community perspective, suggesting considerable changes in community composition from one season to the next. The shifts in community composition in treated plots are caused by many of the same species listed for control plots at SRER above; however, in treated plots, they typically occurred in much greater amounts.

From a community perspective, only one successive season was significantly different from the previous on treated plots at CORO: FA03 differed from the previous spring. This difference is explained by the removal of *E. lehmanniana* from these plots. The lack of other significant changes from one season to the next indicates consistent community composition in treated plots. Every one of the most common species recorded is native to Arizona.

#### Climate and soil influences on the effects of removal

Monthly precipitation values during the monsoon seasons of 2003 and 2004 differed in both June and August at SRER, but no such differences were detectable at CORO (Figure 17). The more consistent rainfall at CORO during this wet period may explain the similar communities observed at CORO in FA03 and FA04. The sporadic

rainfall observed at SRER, especially in the summer of 2004, may explain the differences in community composition and cover values in both treated and untreated plots at SRER. Much of the 2004 monsoon season rainfall recorded at SRER occurred in July, specifically in a few large events. Recent greenhouse and field studies have demonstrated the sensitivity of native species to variable rainfall patterns (Frasier et al. 1985, Frasier 1989, Abbott et al. 1995, Abbott and Roundy 2003). High and rapid germination rates of native species are common following initial rainfall events. However, without consistent rainfall following germination, these species are susceptible to desiccation (Abbott and Roundy 2003). The 2004 monsoon season rainfall at SRER exhibits the pattern of rapid bursts of precipitation followed by long dry periods that could have impacted native species negatively. The presence of *Kallstroemia granidiflora* at SRER in large quantities in FA03 but not in FA04 supports this hypothesis. *Kallstroemia granidiflora* is a summer annual that responds strongly to summer rains (Dimmitt 2000).

Between CORO and SRER, one notable difference in the soil characteristics measured was pH, which was on average approximately three times more acidic at CORO than at SRER. Soil pH has a large influence on root uptake of nutrients as well as the formation of aggregate structure (Brady and Weil 2002). In addition, pH is a major determinant of the species which can grow at a site (Brady and Weil 2002). The other notable difference in the soil characteristics measured at the two sites was potassium, which was slightly higher in both samples at SRER than at CORO. The values for both sites are considered to be in the low range for dryland ecosystems (Soltanpour and Follett 1999). Potassium is the third most likely nutrient to limit plant growth, after nitrogen and

phosphorus, and plays an important role in plants' drought tolerance and disease resistance (Brady and Weil 2002). However, potassium levels apparently are not highly correlated with grassland organization or composition (Curtis 1955, Aerts et al. 1990, Piper 1994). It appears that at least for the edaphic characteristics measured, soils are not responsible for the differences observed between CORO and SRER in this study. Rather, differences in the timing and amount of precipitation appear to be important mediating factors.

#### Seasonal and removal effects on seed bank

As with aboveground communities, seed bank samples from CORO and SRER also exhibit strong similarities. Fluctuations in the proportion of samples that were *E. lehmanniana* seeds were very consistent across the two sites, suggesting stable, well-established communities at each site responding similarly to seasonal cues. Untreated plots at both sites germinated much higher proportions of *E. lehmanniana* seeds than treated plots, responding to the consistent aboveground inputs of these plots. The two sites also exhibited similar seasonal patterns in total seeds germinated and species richness, though the magnitude of the fluctuations was greater at SRER.

On a community basis, seed bank samples from treated plots were significantly different from control plots at SRER on three occasions and once at CORO in the second year of the study (Table 6). These differences were in part due to the smaller numbers of *E. lehmanniana* seeds germinating in samples from treated plots at these sites, but in most cases, other species, typically native species, were responsible for more of the

dissimilarity than *E. lehmanniana*. This demonstrates the potential for a strong response on behalf of native species residing in the seed bank to the removal of *E. lehmanniana* on these sites.

#### Correspondence between plant communities and seed banks

Species that appeared in the seed banks at SRER but not in aboveground vegetation were mainly annual species, many of which occurred in very small numbers. The most abundant seed bank species, by far, was *Crassula connata*, a mat-forming succulent annual, with more than 3,500 individuals germinating. Also abundant were *Androsace occidentalis*, *Oxalis corniculata*, and *Gnaphalium palustre*, with 445, 394, and 112 seedlings, respectively. Each of these species is a native annual forb. Several other native annual forbs were abundant in both the seed bank and the aboveground vegetation; these included *Mollugo verticillata*, *Pseudognaphalium arizonicum*, *Eriastrum diffusum* (Gray) Mason, *Erigeron divergens*, and *Spermolepis echinata*. Seeds of native grasses generally do not have persistent seed banks (Rabinowitz 1981, Coffin and Laurenroth 1989, Kinucan and Smeins 1992), so it is not surprising that their seeds did not appear in the seed bank. The presence of native annuals is encouraging, as these species could mitigate erosion and provide a safe site for native perennial establishment following nonnative removal.

At CORO, the most common species germinating in the seed bank but not appearing in aboveground vegetation was *Pseudognaphalium arizonicum*. *Oxalis corniculata*, *Sisymbrium irio*, and *Veronica peregrina* L. were also common. All of these

are native annual forbs, with the exception of *Sisymbrium irio*, which is not native to the continent. The most abundant species in the seed bank that also appeared in the aboveground vegetation at CORO included *Muhlenbergia* sp., *Pseudognaphalium arizonicum*, and *Oxalis corniculata*. Similar to at SRER, the lack of perennial grass species is not surprising, but the presence of native annual species is heartening.

Inconsistencies between aboveground vegetation and seed banks are often observed (Thompson and Grime 1979, Rabinowitz 1981, Hills and Morris 1992, Warr et al. 1993, Arkle et al. 2002). It has been suggested that species observed in seed banks but not expressed in aboveground vegetation are a “memory” of past ecological conditions at the site and may germinate if these conditions reappear (Templeton and Levin 1979, Rabinowitz 1981). Another viable explanation for seed bank species not appearing in aboveground vegetation is lack of necessary soil moisture in the field, which is one of the most important site characteristics for germination (Winkel et al. 1991). Regardless, these species offer insight into the possible trajectory of the site following a large-scale removal of *E. lehmanniana*. The results of the *E. lehmanniana* removal experiment and the seed bank study suggest that upon removal of *E. lehmanniana* at both CORO and SRER, the native species latent in the seed bank begin to appear in aboveground vegetation. *E. lehmanniana* also continues to reappear from seed as expected due to its high degree of dormancy (Weaver and Jordan 1986, Voigt et al. 1996). However, the numbers of *E. lehmanniana* are reduced considerably when the aboveground *E. lehmanniana* seed inputs are removed.

Native species observed in both seed banks and aboveground vegetation were in large part annual species. Removing *E. lehmanniana* from sites heavily dominated by this species resulted in the removal of nearly all plant cover on treatment plots at CORO and SRER. The proliferation of annual species following this disturbance could be the natural response of plants in this area. It may be possible to expect change to continue on sites if *E. lehmanniana* were to continue to be excluded from treatment plots, and result in the eventual establishment of native perennial species. Further studies are necessary to determine whether such a pattern would occur.

### *Conclusion*

Although the negative impacts of introduced species are widely recognized (Chapin et al. 1996, Mack and D'Antonio 1998, Wilcove et al. 1998), few studies are undertaken to examine the response of a site following a large-scale eradication effort. Eradication or control is often the preferred response to an invasion by a particularly problematic species, but as Zavaleta et al. (2001) propose, pre-eradication assessments are necessary to determine whether a removal will result as expected and not augment the problem. The results of this study suggest that the response of a site to the removal of a dominant nonnative grass varies between sites. In this study, a site with a history of intensive agriculture showed no strong response to the removal of a dominant nonnative species. Two other sites with a history of livestock grazing demonstrated similar strong responses to the removal, with large increases in native plant cover, increases in species richness and no evidence of “new” nonnative species replacing removed species. The

findings from the second two sites are consistent with other experiments removing dominant nonnative species (Farnsworth and Meyerson 1999, Morrison 2002).

Community composition of the treated plots at the three sites varied considerably, and reflected common species near each site. Seed bank studies revealed a small number of additional species not observed in the aboveground vegetation for each site. These patterns suggest that removing the nonnative from a site would result in the site's conversion to an ecosystem dominated by native plants. However, if the goal is restoration of the site to a pre-invasion grassland, it may be advisable to undertake restoration measures in conjunction with removal efforts. Seeds of native perennial species may promote transition from an annual-dominated site to a more diverse, perennial-dominated community.

The results of this experiment demonstrate that removing *E. lehmanniana* causes an increase in relative percent cover of native species, annual species, and forb species. The response varied by site, which could be the result of differences in land use history, precipitation patterns, soil characteristics, or other edaphic factors. In order to ascertain whether differences in responses were the result of various factors, further experimentation modifying these variables is necessary.

Several studies have suggested that the responses observed following a species removal could be the result of indirect effects including the concurrent soil disturbance, breakdown of aboveground or root biomass, and transient responses in nutrient availability (Underwood 1986, Aarssen and Epp 1990, Campbell et al. 1991). The short time span of this study (less than two years post-treatment) precludes determination of

the importance of these effects. Removal of competition for resources including space, light, or nutrients could also be responsible for the response. Further monitoring of the study plots would demonstrate the sites' long-term response to the removal.

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**Table 1.** Repeated measures MANOVA for aboveground vegetation analyses at three sites in southeastern Arizona. The four factors are: Season = post-treatment sampling season (Fall 2003, Spring 2004, Fall 2004), Site = site (Three Links Farm, Coronado NM, Santa Rita Experimental Range), Treatment = herbicide treatment (*E. lehmanniana* removed, control). Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Season.

<b>Response Variable</b>	<b>Source</b>	<b>DF</b>	<b>F value</b>	<b>p</b>
Total percent plant cover	Season*Treatment	2, 78	4.41	<.0001
	Season*Site	4, 78	59.00	0.015
Relative percent native cover	Season*Treatment	2, 81	5.89	0.004
Relative percent nonnative cover	Season*Treatment	2, 88	7.23	0.0012
Relative percent forb cover	Season*Treatment	2, 81	6.73	0.0019
	Season*Site	4, 81	59.09	<.0001
Relative percent grass cover	Season*Treatment	2, 86	7.30	0.0012
	Season*Site	4, 86	62.94	<.0001
Relative percent annual cover	Season*Treatment	2, 77	11.07	<.0001
	Season*Site	4, 77	11.15	<.0001
Relative percent perennial cover	Season*Treatment*Site	4, 88	2.66	0.038
Species richness	Season*Treatment*Site	4, 86	3.33	0.014

**Table 2.** ANOSIM and SIMPER results discriminating within-season species assemblages. R = test statistic indicating relative dissimilarity (0 –1, with 1 = identical composition between groups). “\*” denotes significant ( $P < 0.05$ ) dissimilarity between groups. Percentages reflect proportion of dissimilarity attributable to each species.

Season	Global/Pairwise Test	R	p	Species Differentiation- SIMPER (Percent of Dissimilarity)
SP03	Global	0.369	<.001*	n/a
	CORO-C v. CORO-H	-0.025	0.49	n/a
	SRER-C v. SRER-H	-0.044	0.84	n/a
	TLF-C v. TLF-H.	-0.041	0.671	n/a
FA03	Global	0.797	0.001	n/a
	CORO-C v. CORO-H	0.591	.002*	<i>Eragrostis lehmanniana</i> (37%), <i>Mollugo verticillata</i> (11%), <i>Calliandra eriophylla</i> (11%)
	SRER-C v. SRER-H	0.946	.001*	<i>E. lehmanniana</i> (30%), <i>M. verticillata</i> (16%), <i>Urochloa arizonica</i> (6%)
	TLF-C v. TLF-H.	-0.007	0.444	n/a
SP04	Global	0.706	<.001*	n/a
	CORO-C v. CORO-H	0.618	.001*	<i>E. lehmanniana</i> (48%), <i>C. eriophylla</i> (9%)
	SRER-C v. SRER-H	0.709	.001*	<i>E. lehmanniana</i> (28%), <i>Ambrosia confertiflora</i> (5%), <i>Spermolepis echinata</i> (5%)
	TLF-C v. TLF-H.	0.048	0.26	n/a
FA04	Global	0.705	<.001*	n/a
	CORO-C v. CORO-H	0.46	.002*	<i>E. lehmanniana</i> (27%), <i>C. eriophylla</i> (10%), <i>M. verticillata</i> (6%)
	SRER-C v. SRER-H	0.714	.001*	<i>E. lehmanniana</i> (28%), <i>M. verticillata</i> (8%), <i>U. arizonica</i> (6%), <i>Kallstroemia grandiflora</i> (5%)
	TLF-C v. TLF-H.	0.135	0.139	n/a

**Table 3.** ANOSIM and SIMPER results discriminating within-site/treatment combination species assemblages between treatments. R = test statistic indicating relative dissimilarity (0 –1, with 1 = identical composition between groups). “\*” denotes significant ( $P < 0.05$ ) dissimilarity between groups. Percentages reflect proportion of dissimilarity attributable to each species.

Site/ Treatment	Global/ Pairwise Test	R	p	Species Differentiation- SIMPER (Percent of Dissimilarity)
CORO - Control	Global	0.071	0.067	n/a
	SP03 - FA03	0.074	0.15	n/a
	FA03 - SP04	0.112	0.1	n/a
	SP04 - FA04	-0.055	0.783	n/a
	SP03 - SP04	0.153	0.052	n/a
	FA03 - FA04	0.01	0.362	n/a
SRER - Control	Global	0.338	0.001	n/a
	SP03 - FA03	0.448	<b>0.001*</b>	<i>Eragrostis lehmanniana</i> (7%), <i>Mollugo verticillata</i> (5%)
	FA03 - SP04	0.467	<b>0.001*</b>	<i>E. lehmanniana</i> (5%), <i>M. verticillata</i> (5%)
	SP04 - FA04	0.325	<b>0.001*</b>	<i>E. lehmanniana</i> (4%), <i>Gilia scopulorum</i> (4%)
	SP03 - SP04	0.284	<b>0.001*</b>	<i>G. scopulorum</i> (4%)
	FA03 - FA04	0.256	<b>0.002*</b>	<i>E. lehmanniana</i> (6%), <i>M. verticillata</i> (5%)
TLF - Control	Global	0.978	0.001	n/a
	SP03 - FA03	0.981	<b>0.002*</b>	<i>E. lehmanniana</i> (33%), <i>Sporobolus cryptandrus</i> (9%), <i>E. cilianensis</i> (7%)
	FA03 - SP04	0.957	<b>0.002*</b>	<i>Salsola kali</i> (11%), <i>Eragrostis cilianensis</i> (9%), <i>Sisymbrium irio</i> (8%), <i>Schismus barbatus</i> (7%)
	SP04 - FA04	0.976	<b>0.002*</b>	<i>S. kali</i> (15%), <i>Bouteloua aristidoides</i> (7%), <i>S. barbatus</i> (5%), <i>S. cryptandrus</i> (5%)
	SP03 - SP04	1	<b>0.002*</b>	<i>E. lehmanniana</i> (22%), <i>S. kali</i> (10%), <i>S. cryptandrus</i> (7%), <i>E. cilianensis</i> (7%), <i>S. irio</i> (7%), <i>S. barbatus</i> (6%)
	FA03 - FA04	0.993	<b>0.002*</b>	<i>S. kali</i> (29%), <i>E. cilianensis</i> (8%), <i>B. aristidoides</i> (8%), <i>S. cryptandrus</i> (6%)
CORO - Herbicide	Global	0.337	0.001	n/a
	SP03 - FA03	0.599	<b>0.001*</b>	<i>E. lehmanniana</i> (36%), <i>M. verticillata</i> (11%), <i>Calliandra eriophylla</i> (10%)
	FA03 - SP04	0.234	0.052	n/a
	SP04 - FA04	0.07	0.193	n/a
	SP03 - SP04	0.59	<b>0.001*</b>	<i>E. lehmanniana</i> (46%), <i>C. eriophylla</i> (10%)
	FA03 - FA04	-0.022	0.449	n/a
SRER - Herbicide	Global	0.814	<.0001	n/a
	SP03 - FA03	1	<b>&lt;.0001*</b>	<i>E. lehmanniana</i> (29%), <i>M. verticillata</i> (22%), <i>Kallstroemia grandiflora</i> (8%), <i>Urochloa arizonica</i> (8%)
	FA03 - SP04	0.995	<b>&lt;.0001*</b>	<i>M. verticillata</i> (25%), <i>K. grandiflora</i> (9%), <i>U. arizonica</i> (8%), <i>E. lehmanniana</i> (8%)
	SP04 - FA04	0.723	<b>&lt;.0001*</b>	<i>M. verticillata</i> (11%), <i>E. lehmanniana</i> (9%), <i>U. arizonica</i> (7%)

	SP03 - SP04	0.791	<b>&lt;.0001*</b>	<i>E. lehmanniana</i> (28%), <i>Ambrosia confertiflora</i> (6%)
	FA03 - FA04	0.583	<b>&lt;.0001*</b>	<i>M. verticillata</i> (14%), <i>E. lehmanniana</i> (9%), <i>Boerhavia sp.</i> (6%)
TLF – Herbicide	Global	0.973	<.0001	n/a
	SP03 - FA03	0.865	<b>.002*</b>	<i>E. lehmanniana</i> (33%), <i>E. cilianensis</i> (7%), <i>Cynodon dactylon</i> (5%), <i>Chloris virgata</i> (5%)
	FA03 - SP04	0.961	<b>0.002*</b>	<i>E. cilianensis</i> (9%), <i>S. irio</i> (9%), <i>S. kali</i> (8%)
	SP04 - FA04	1	<b>0.002*</b>	<i>S. kali</i> (18%), <i>B. aristoides</i> (12%)
	SP03 - SP04	0.924	<b>0.002*</b>	<i>E. lehmanniana</i> (21%), <i>S. irio</i> (8%), <i>S. kali</i> (7%), <i>E. cilianensis</i> (5%)
	FA03 - FA04	0.989	<b>0.002*</b>	<i>S. kali</i> (29%), <i>B. aristoides</i> (15%), <i>E. cilianensis</i> (7%)

Table 4. Total seed germinated by sampling event in each of three study sites in southeastern Arizona.

	CORO						SRER						TLF					
	SP03	SU03	FA03	SP04	SU04	FA04	SP03	SU03	FA03	SP04	SU04	FA04	SP03	SU03	FA03	SP04	SU04	FA04
<i>Amaranthus palmeri</i>	0	0	0	0	0	0	1	0	0	0	0	0	2	6	2	2	2	0
<i>Androsace occidentalis</i>	0	0	0	0	0	1	44	49	131	20	95	106	0	0	0	0	0	0
<i>Aristida adscensionis</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Aristida ternipes</i>	0	0	0	3	0	0	0	0	0	7	0	0	0	0	0	1	0	0
<i>Baccharis sarothroides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bouteloua aristidoides</i>	0	0	0	0	0	1	0	0	0	1	4	0	0	0	0	16	57	0
<i>Bouteloua barbata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Bouteloua curtipendula</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bouteloua gracilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
<i>Bouteloua sp.</i>	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0
<i>Chamaesyce sp.</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
<i>Chenopodium sp.</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0
<i>Chamaesyce maculata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chamaesyce micromera</i>	3	0	0	0	2	0	7	0	0	0	0	0	9	6	0	1	1	0
<i>Chamaecrista nictitans</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Chloris virgata</i>	0	0	0	0	0	0	0	0	0	0	0	0	4	2	0	4	8	0
<i>Corydalis aurea</i>	0	0	0	0	0	0	27	40	0	0	0	0	0	0	0	0	0	0
<i>Conyza canadensis</i>	0	0	2	0	0	0	4	1	1	0	0	0	0	0	0	0	0	0
<i>Crassula conniculata</i>	0	1	1	0	2	1	149	269	1804	21	154	1174	1	0	0	0	0	1
<i>Cryptantha angustifolia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cynodon dactylon</i>	0	0	0	0	0	0	0	0	0	2	0	0	21	10	18	4	16	11
<i>Descurainia pinnata</i>	0	0	0	0	0	0	15	1	1	1	2	1	1	0	0	0	1	0
<i>Eriochloa acuminata</i>	0	0	0	0	0	0	0	0	0	3	0	0	13	0	0	0	0	0
<i>Eragrostis sp.</i>	1	0	0	0	0	0	0	0	0	0	0	0	90	36	1	3	5	0
<i>Eragrostis cilianensis</i>	1	0	0	1	0	0	1	0	0	4	0	1	534	888	94	249	467	150
<i>Eriastrum diffusum</i>	6	4	0	0	0	0	98	37	0	0	0	0	0	0	0	0	0	0
<i>Erigeron divergens</i>	1	6	4	7	3	14	5	35	85	19	21	30	0	0	0	4	1	10
<i>Eragrostis intermedia</i>	2	0	2	5	0	0	5	0	0	1	0	0	79	24	1	2	6	1
<i>Eragrostis lehmanniana</i>	61	159	80	95	283	47	465	418	143	455	1868	73	2090	847	299	321	394	54
<i>Euphorbia sp.</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Evolvulus sp.</i>	0	0	0	0	0	0	1	0	0	0	1	3	0	0	0	0	0	0
<i>Gilia sp.</i>	0	0	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0
<i>Gilia sinuata</i>	0	0	0	0	0	0	0	3	0	0	0	17	0	0	0	0	0	0
<i>Gnaphalium palustre</i>	0	0	32	0	0	0	5	3	79	0	2	23	0	0	2	0	0	0
<i>Heterotheca subaxillaris</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Juniperus sp.</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Laennecia coulteri</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lactuca sp.</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Leptochloa panicea</i>	1	0	0	1	0	0	0	0	0	0	0	0	5	26	0	0	7	3

<i>Leptochloa sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Lotus greenei</i>	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0
<i>Lotus humistratus</i>	0	0	0	0	0	0	18	10	0	0	4	22	0	0	0	0	0	0
<i>Lotus sp.</i>	0	0	0	0	0	0	1	0	0	1	14	1	0	0	0	0	0	0
<i>Lupinus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
<i>Mitracarpus breviflorus</i>	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Monolepis nuttalliana</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Mollugo verticillata</i>	6	0	12	23	84	5	490	114	30	692	1841	53	0	0	1	1	0	0
<i>Muhlenbergia sp.</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nothoscordum sp.</i>	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0
<i>Nuttallanthus texanus</i>	0	0	0	0	0	1	11	9	42	0	18	70	0	0	0	0	0	0
<i>Oxalis corniculata</i>	2	2	27	10	37	16	67	25	200	55	38	9	9	8	81	29	17	7
<i>Panicum sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	74	298	15
<i>Pellaea sp.</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Phacelia sp.</i>	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
<i>Physalis longifolia</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Phacelia ramosissima</i>	0	0	0	0	0	0	0	6	1	0	0	0	0	0	0	0	0	0
<i>Plantago patagonica</i>	1	5	5	0	1	9	5	0	1	0	1	3	0	0	0	0	0	0
<i>Polygonum argyrocoleon</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Portulaca halimoides</i>	0	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Portulaca pilosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Portulaca sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0
<i>Portulaca umbraticola</i>	2	0	0	0	3	0	0	1	0	5	0	0	0	2	0	0	0	0
<i>Pseudognaphalium arizonicum</i>	35	64	93	11	49	42	50	70	212	6	25	200	1	0	0	1	0	1
<i>Schismus barbatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
<i>Setaria verticillata</i>	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
<i>Sida abutilifolia</i>	0	0	0	0	0	0	3	0	0	1	21	0	0	0	0	0	0	0
<i>Sisymbrium irio</i>	1	0	0	0	51	0	1	0	1	0	31	0	12	1	8	30	15	41
<i>Solanaceae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sporobolus cryptandrus</i>	0	0	1	6	0	0	0	0	0	1	0	0	6	1	12	63	61	91
<i>Spermolepis echinata</i>	0	0	0	0	0	0	0	5	8	0	68	71	0	0	0	0	0	1
<i>Talinum aurantiacum</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Triodanis perfoliata</i>	0	0	0	0	0	0	0	2	3	0	0	0	0	0	0	0	0	0
unknown forb	0	0	0	0	0	0	1	1	1	1	12	23	0	0	13	1	8	7
unknown grass	0	0	2	1	1	0	0	0	0	0	0	4	0	0	0	2	0	18
unknown	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
<i>Urochloa arizonica</i>	0	0	0	0	1	0	0	2	0	2	10	0	0	0	0	0	0	0
<i>Veronica peregrina</i>	0	0	25	0	0	0	0	0	0	0	0	0	0	6	4	0	0	0
<i>Vulpia octoflora</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
<i>Woodsia sp.</i>	6	2	0	0	0	0	5	3	0	0	0	0	5	0	0	0	0	0

**Table 5.** Repeated measures MANOVA for seed bank analyses at three sites in southeastern Arizona. The four factors are: Group = post-treatment sampling season (Summer 2003, Fall 2003, Spring 2004, Summer 2004, Fall 2004), Site = site (Three Links Farm, Coronado NM, Santa Rita Experimental Range), Treatment = herbicide treatment (*E. lehmanniana* removed, control). Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Group.

<b>Response Variable</b>	<b>Source</b>	<b>DF</b>	<b>F value</b>	<b>p</b>
Germinating seeds	Group*Site	6, 135	17.82	<.0001
Percent graminoid seedlings	Group*Treatment	3, 128	5.26	0.0009
	Group*Site	6, 128	3.39	0.020
Percent perennial seedlings	Group*Treatment*Site	6, 129	2.31	0.029
Percent native seedlings	Group*Treatment*Site	6, 125	3.70	0.0024
Seed bank species richness	Group*Site	7, 148	11.09	<.0001
Percent of seedlings that were <i>E. lehmanniana</i>	Group*Treatment*Site	8, 148	3.11	0.0034

**Table 6.** ANOSIM and SIMPER results discriminating within-season seedbank species assemblages. R = test statistic indicating relative dissimilarity (0 –1, with 1 = identical composition between groups). “\*\*” denotes significant ( $P < 0.05$ ) dissimilarity between groups. Percentages reflect proportion of dissimilarity attributable to each species.

Site/ Treatment	Global/ Pairwise Test	R	p	Species Differentiation- SIMPER (Percent of Dissimilarity)
CORO - Control	Global	0.173	0.001	
	SP03-SU03	-0.015	0.369	
	SU03-FA03	0.255	<b>.03*</b>	<i>Pseudognaphalium arizonicum</i> (8%), <i>Eragrostis lehmanniana</i> (7%), <i>Gnaphalium palustre</i> (6%)
	FA03-SP04	0.242	<b>.031*</b>	<i>P. arizonicum</i> (12%), <i>Mollugo verticillata</i> (6%), <i>Oxalis corniculata</i> (6%), <i>G. palustre</i> (6%), <i>E. lehmanniana</i> (6%)
	SP04-SU04	-0.017	0.554	
	SU04-FA04	0.344	<b>.005*</b>	<i>P. arizonicum</i> (8%), <i>E. lehmanniana</i> (7%), <i>O. corniculata</i> (6%), <i>Plantago patagonica</i> (6%)
SRER - Control	Global	0.58	<b>.001*</b>	
	SP03-SU03	0.308	<b>.001*</b>	<i>Crassula connata</i> (7%), <i>M. verticillata</i> (7%)
	SU03-FA03	0.433	<b>.001*</b>	<i>C. connata</i> (9%), <i>E. lehmanniana</i> (8%), <i>M. verticillata</i> (5%), <i>P. arizonicum</i> (5%)
	FA03-SP04	0.944	<b>.001*</b>	<i>C. connata</i> (15%), <i>M. verticillata</i> (11%), <i>E. lehmanniana</i> (11%), <i>P. arizonicum</i> (7%), <i>Androsace occidentalis</i> (5%)
	SP04-SU04	0.131	0.051	
	SU04-FA04	0.873	<b>.001*</b>	<i>C. connata</i> (12%), <i>E. lehmanniana</i> (12%), <i>M. verticillata</i> (10%), <i>P. arizonicum</i> (7%)
TLF - Control	Global	0.631	<b>.001*</b>	
	SP03-SU03	0.43	<b>.002*</b>	<i>Eragrostis cilianensis</i> (6%)
	SU03-FA03	0.737	<b>.002*</b>	<i>E. cilianensis</i> (8%), <i>O. corniculata</i> (8%)
	FA03-SP04	0.454	<b>.002*</b>	<i>E. cilianensis</i> (5%), <i>Panicum sp.</i> (5%), <i>Sporobolus cryptandrus</i> (5%)
	SP04-SU04	0.252	<b>.035*</b>	<i>Panicum sp.</i> (5%)
	SU04-FA04	0.465	<b>.002*</b>	<i>Panicum sp.</i> (9%), <i>E. lehmanniana</i> (6%), <i>Sisymbrium irio</i> (5%), <i>E. cilianensis</i> (5%), <i>S. cryptandrus</i> (5%)
CORO - Herbicide	Global	0.229	0.001	
	SP03-SU03	0.046	0.258	
	SU03-FA03	0.227	<b>.003*</b>	<i>G. palustre</i> (9%), <i>E. lehmanniana</i> (8%), <i>P. arizonicum</i> (7%), <i>O. corniculata</i> (5%)
	FA03-SP04	0.526	<b>.004*</b>	<i>P. arizonicum</i> (12%), <i>G. palustre</i> (9%), <i>E. lehmanniana</i> (7%), <i>M. verticillata</i> (7%), <i>Erigeron divergens</i> (5%), <i>O. corniculata</i> (5%)
	SP04-SU04	0.146	0.098	
	SU04-FA04	0.144	0.071	
SRER - Herbicide	Global	0.766	<b>.001**</b>	
	SP03-SU03	0.084	0.07	
	SU03-FA03	0.774	<b>.001*</b>	<i>E. lehmanniana</i> (9%), <i>C. connata</i> (9%), <i>M. verticillata</i> (5%)
	FA03-SP04	1	<b>.001*</b>	<i>C. connata</i> (20%), <i>M. verticillata</i> (17%), <i>E. lehmanniana</i> (7%), <i>P. arizonicum</i> (7%)

	SP04-SU04	0.496	<b>.001*</b>	<i>C. connata</i> (5%)
	SU04-FA04	0.989	<b>.001*</b>	<i>M. verticillata</i> (14%), <i>C. connata</i> (13%), <i>E. lehmanniana</i> (6%), <i>P. arizonicum</i> (5%)
TLF - Herbicide	Global	0.611	.001*	
	SP03-SU03	0.665	<b>.002*</b>	<i>E. cilianensis</i> (7%), <i>E. lehmanniana</i> (5%)
	SU03-FA03	0.889	<b>.002*</b>	<i>O. corniculata</i> (8%), <i>E. cilianensi</i> (7%)
	FA03-SP04	0.239	<b>0.032*</b>	<i>O. corniculata</i> (4%)
	SP04-SU04	0.054	0.31	
	SU04-FA04	0.476	<b>.004*</b>	<i>S. cryptandrus</i> (8%), <i>Panicum sp.</i> (7%), <i>E. lehmanniana</i> (6%), <i>E. cilianensi</i> (6%)

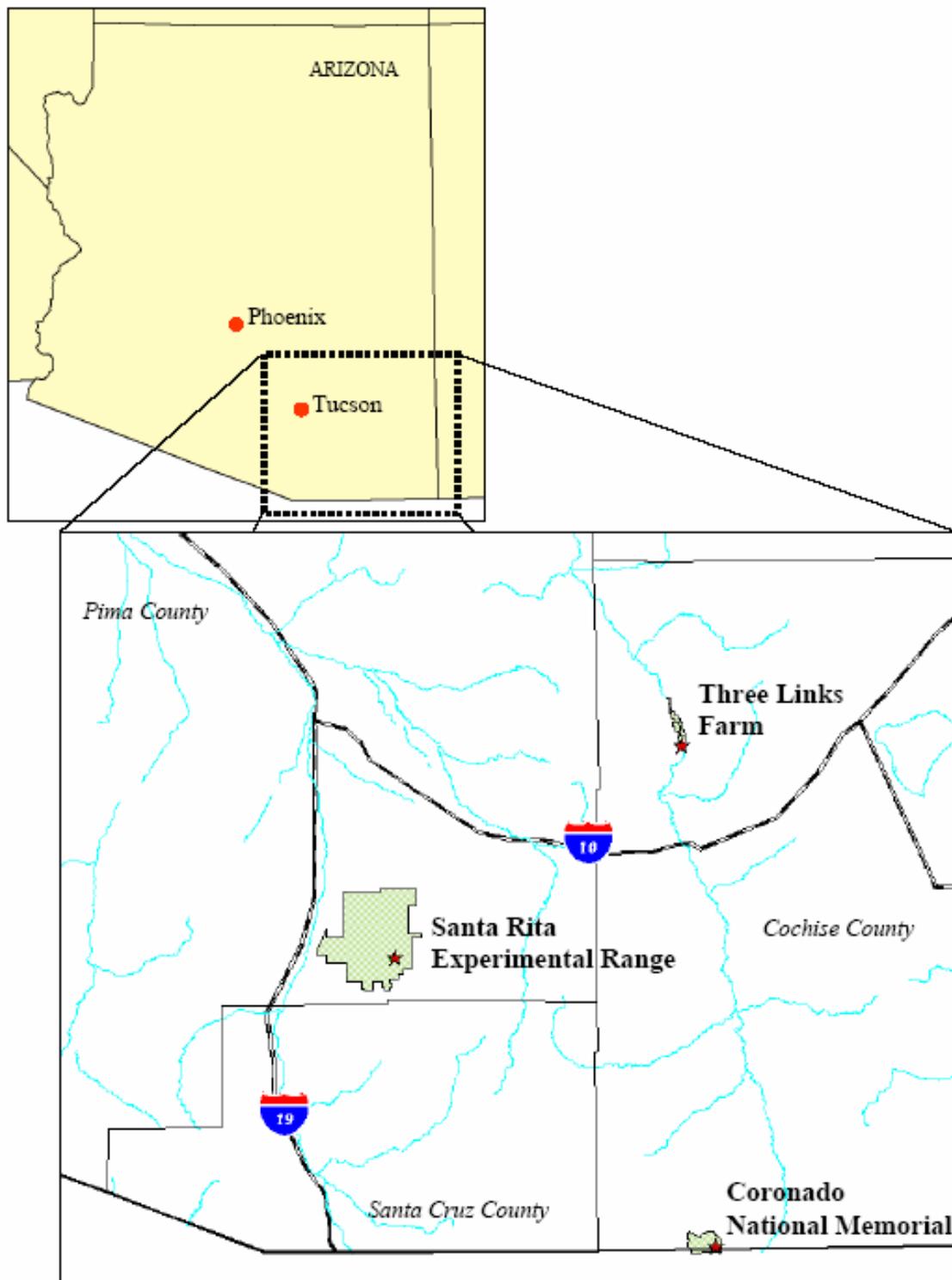
**Table 7.** ANOSIM and SIMPER results discriminating within-site/treatment combination seed bank species assemblages between treatments. R = test statistic indicating relative dissimilarity (0 –1, with 1 = identical composition between groups). “\*” denotes significant ( $P < 0.05$ ) dissimilarity between groups. Percentages reflect proportion of dissimilarity attributable to each species.

Season	Global/Pairwise Test	R	p	Species Differentiation- SIMPER (Percent of Dissimilarity)
SP03	Global	0.597	.001*	n/a
	CORO-C v. CORO-H	0.007	0.329	n/a
	SRER-C v. SRER-H	0.078	0.13	n/a
	TLF-C v. TLF-H	-0.004	0.468	n/a
SU03	Global	0.659	.001*	n/a
	CORO-C v. CORO-H	0.078	0.22	n/a
	SRER-C v. SRER-H	-0.055	0.834	n/a
	TLF-C v. TLF-H	-0.115	0.857	n/a
FA03	Global	0.725	.001*	n/a
	CORO-C v. CORO-H	-0.055	0.697	n/a
	SRER-C v. SRER-H	-0.013	0.519	n/a
	TLF-C v. TLF-H	-0.102	0.857	n/a
SP04	Global	0.631	.001*	n/a
	CORO-C v. CORO-H	-0.14	0.92	n/a
	SRER-C v. SRER-H	0.327	.001*	<i>Molluga verticillata</i> (9%), <i>Eragrostis lehmanniana</i> (8%), <i>Oxalis corniculata</i> (4%)
	TLF-C v. TLF-H	0.015	0.418	n/a
SU04	Global	0.76	.001*	n/a
	CORO-C v. CORO-H	0.228	.015*	<i>M. verticillata</i> (7%), <i>O. corniculata</i> (5%), <i>Erigeron divergens</i> (5%), <i>Pseudognaphalium arizonicum</i> (5%), <i>Eragrostis intermedia</i> (5%)
	SRER-C v. SRER-H	0.45	.001*	<i>E. lehmanniana</i> (8%), <i>M. verticillata</i> (6%), <i>Crassula connata</i> (4%)
	TLF-C v. TLF-H	-0.044	0.649	n/a

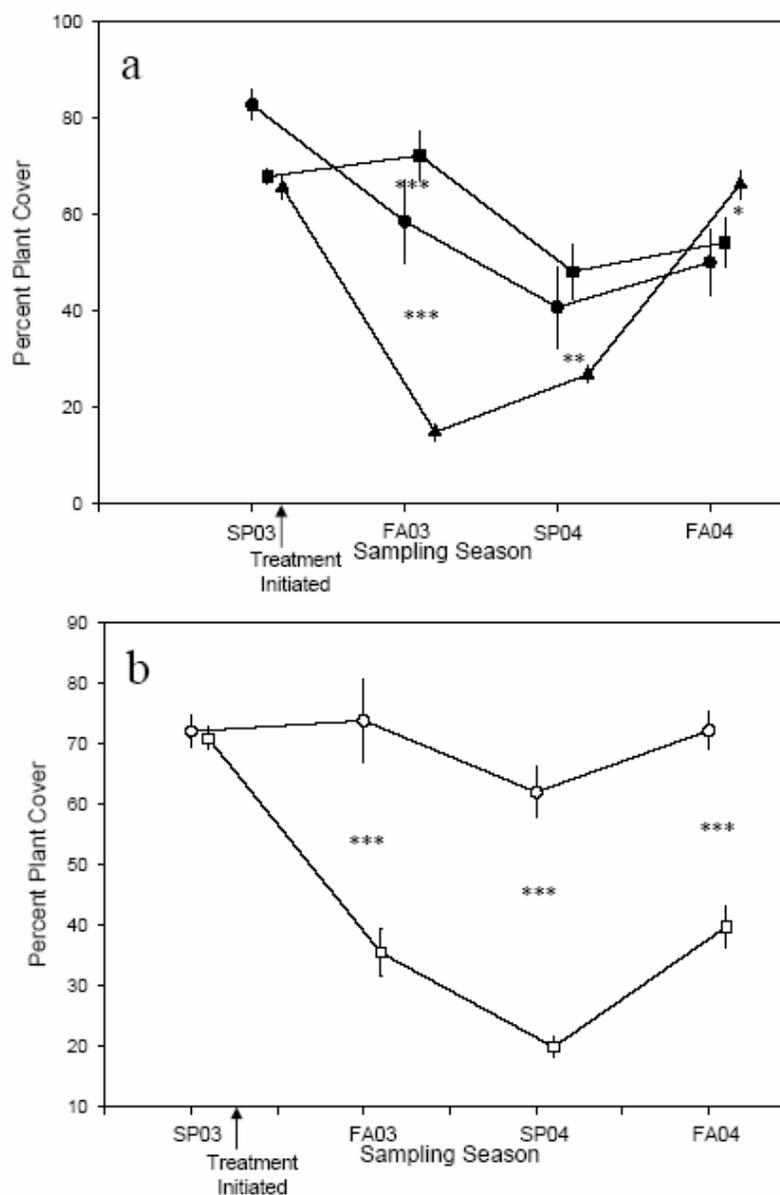
**Table 8.** Results of soils analyses for three *E. lehmanniana*-dominated semi-desert grasslands in southeastern Arizona.

<b>Sample</b>	<b>pH</b>	<b>EC (mmohs/cm)</b>	<b>Phosphorus (ppm)</b>	<b>Total Organic Carbon (%)</b>	<b>Potassium (ppm)</b>	<b>Nitrogen (NH<sub>4</sub><sup>+</sup>) (ppm)</b>
CORO 1	5.36	0.24	7.36	0.91	19.18	32.08
CORO2	5.93	0.15	16.36	0.66	14.16	35.20
SRER 1	6.01	0.31	17.02	0.84	22.88	30.04
SRER 2	6.42	0.24	21.28	0.74	23.73	51.21
TLF	6.65	0.42	14.44	1.42	33.46	27.82

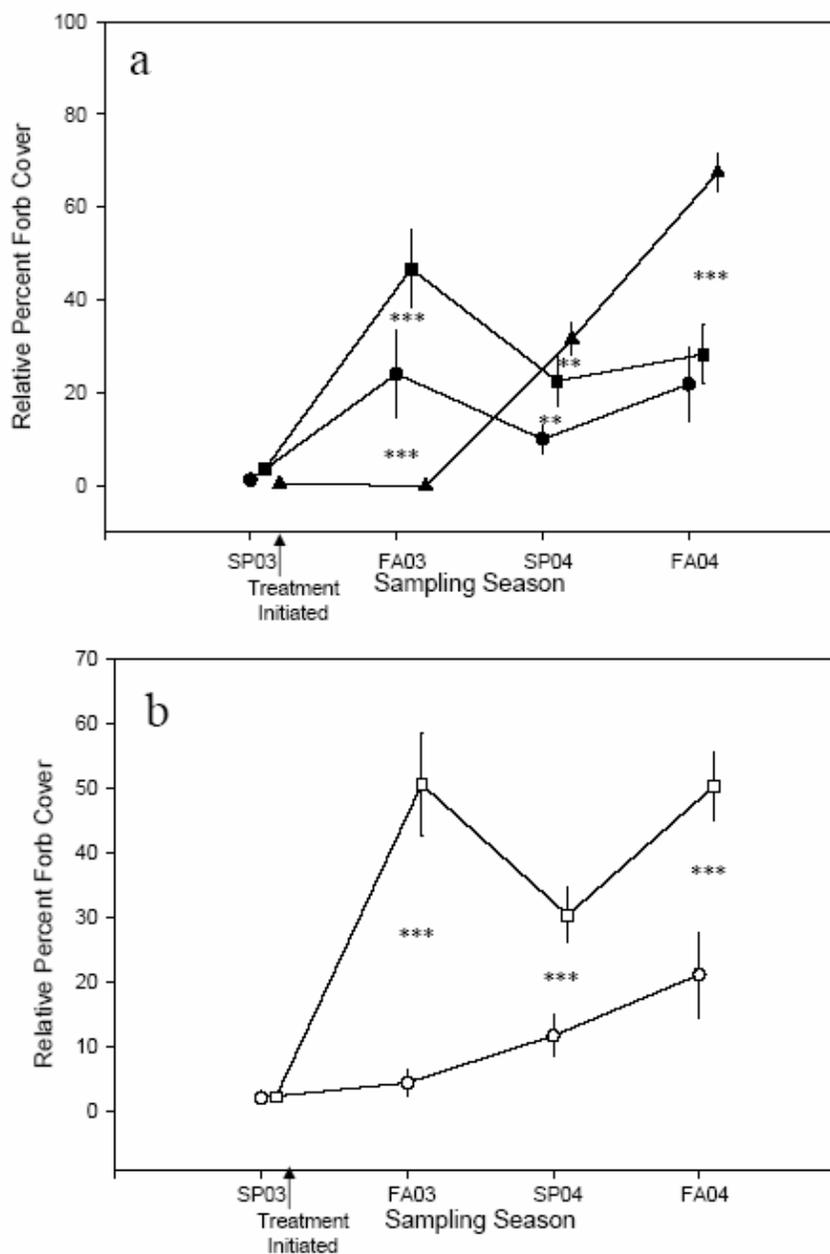
**Figure 1.** Location of grass removal study sites in southeastern Arizona.



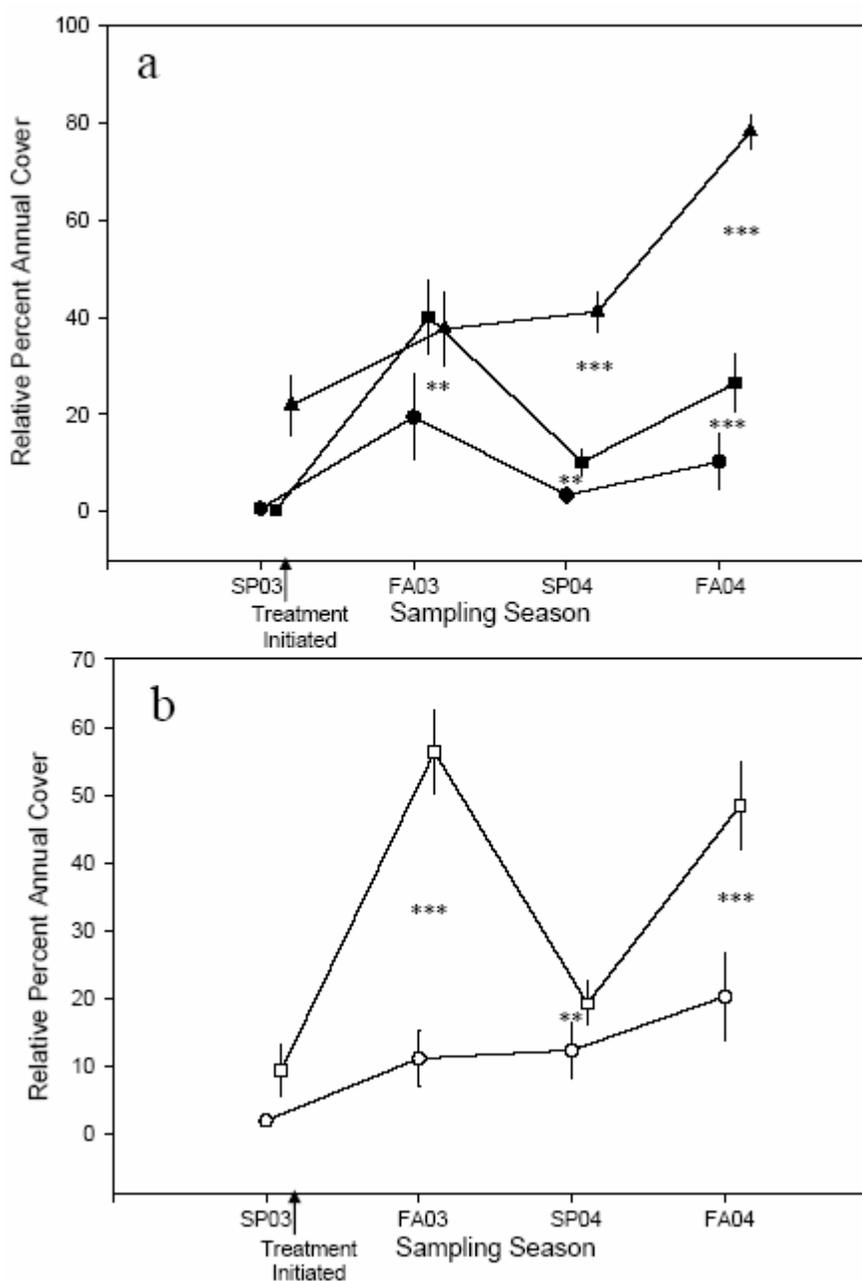
**Figure 2.** Effects of site (a) and treatment (b) on total plant cover (mean $\pm$ SE) before (SP03) and after removing *Eragrostis lehmanniana* from three sites in southeastern Arizona. SP = Spring, FA = Fall; sampling seasons 2003 and 2004. Filled circles = Coronado National Memorial, filled squares = Santa Rita Experimental Range, filled triangles = Three Links Farm. Open circles = control plots, open squares = treated plots. \*, \*\*, and \*\*\* denote significant within season effects ( $p < 0.05$ ,  $p < 0.01$  and  $p < 0.001$ , respectively). See Table 1 for more detailed information.



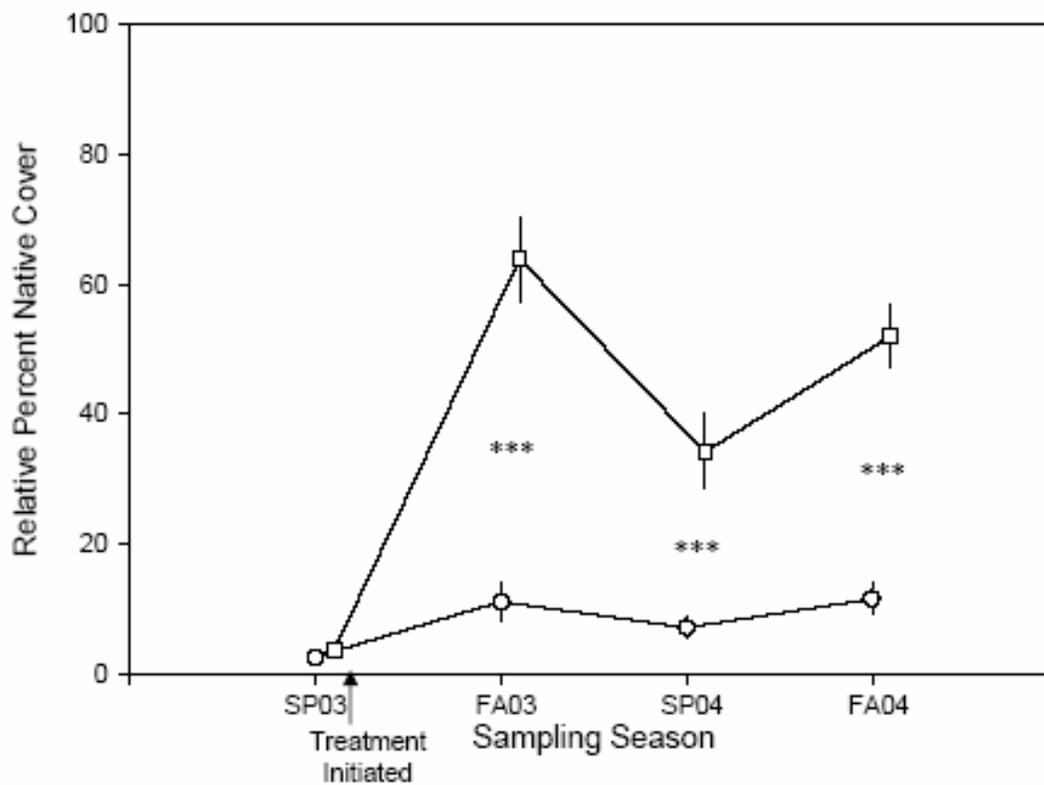
**Figure 3.** Effects of site (a) and treatment (b) on relative percent forb cover (mean $\pm$ SE) before (SP03) and after removing *Eragrostis lehmanniana* from three sites in southeastern Arizona. SP = Spring, FA = Fall; sampling seasons 2003 and 2004. Filled circles = Coronado National Memorial, filled squares = Santa Rita Experimental Range, filled triangles = Three Links Farm. Open circles = control plots, open squares = treated plots. \*, \*\*, and \*\*\* denote significant within season effects ( $p < 0.05$ ,  $p < 0.01$  and  $p < 0.001$ , respectively). See Table 1 for more detailed information.



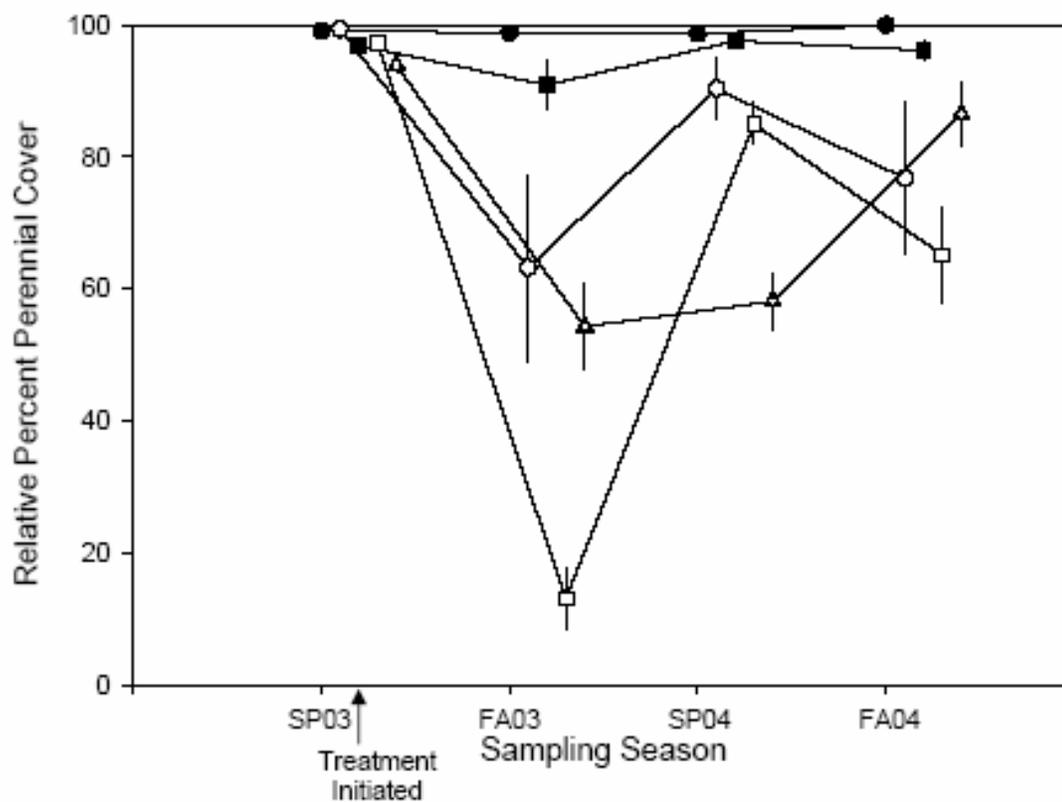
**Figure 4.** Effects of site (a) and treatment (b) on relative percent annual cover (mean $\pm$ SE) before (SP03) and after removing *Eragrostis lehmanniana* from three sites in southeastern Arizona. SP = Spring, FA = Fall; sampling seasons 2003 and 2004. Filled circles = Coronado National Memorial, filled squares = Santa Rita Experimental Range, filled triangles = Three Links Farm. Open circles = control plots, open squares = treated plots. \*, \*\*, and \*\*\* denote significant within season effects ( $p < 0.05$ ,  $p < 0.01$  and  $p < 0.001$ , respectively). See Table 1 for more detailed information.



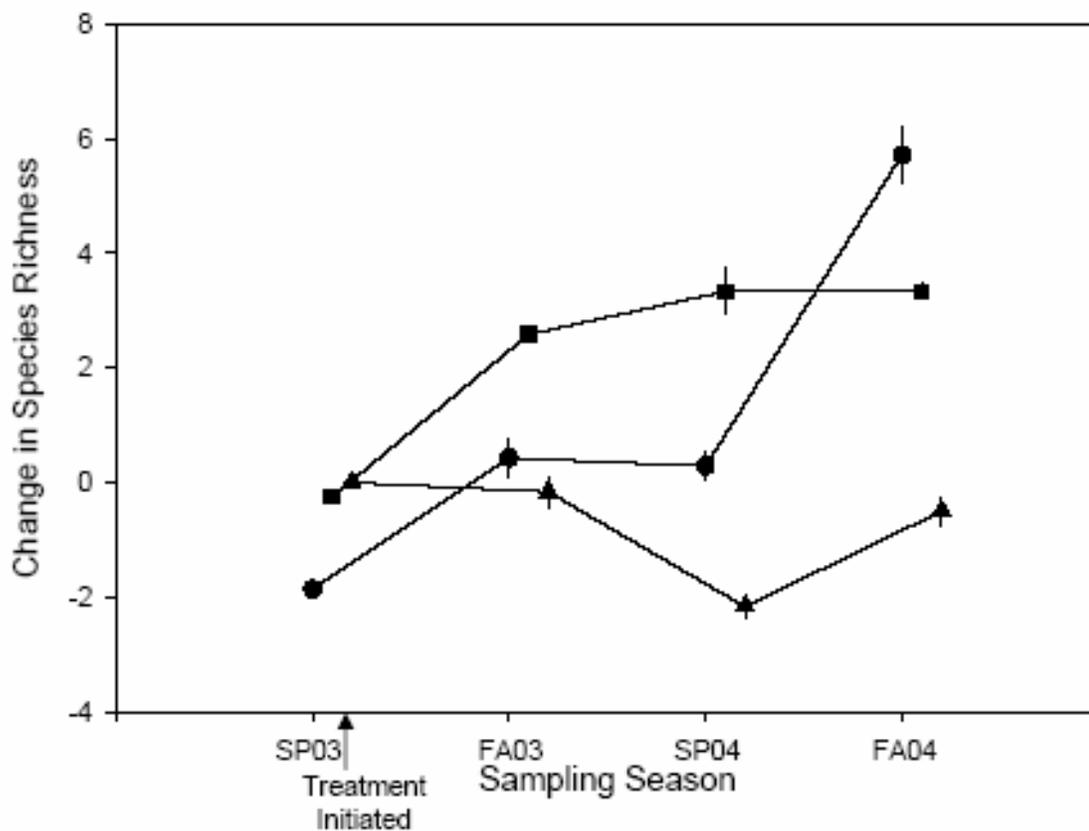
**Figure 5.** Effects of treatment on relative percent native cover (mean $\pm$ SE) before (SP03) and after removing *Eragrostis lehmanniana* from three sites in southeastern Arizona. SP = Spring, FA = Fall; sampling seasons 2003 and 2004. Open circles = control plots, open squares = treated plots. \*, \*\*, and \*\*\* denote significant within season effects ( $p < 0.05$ ,  $p < 0.01$  and  $p < 0.001$ , respectively). See Table 1 for more detailed information.



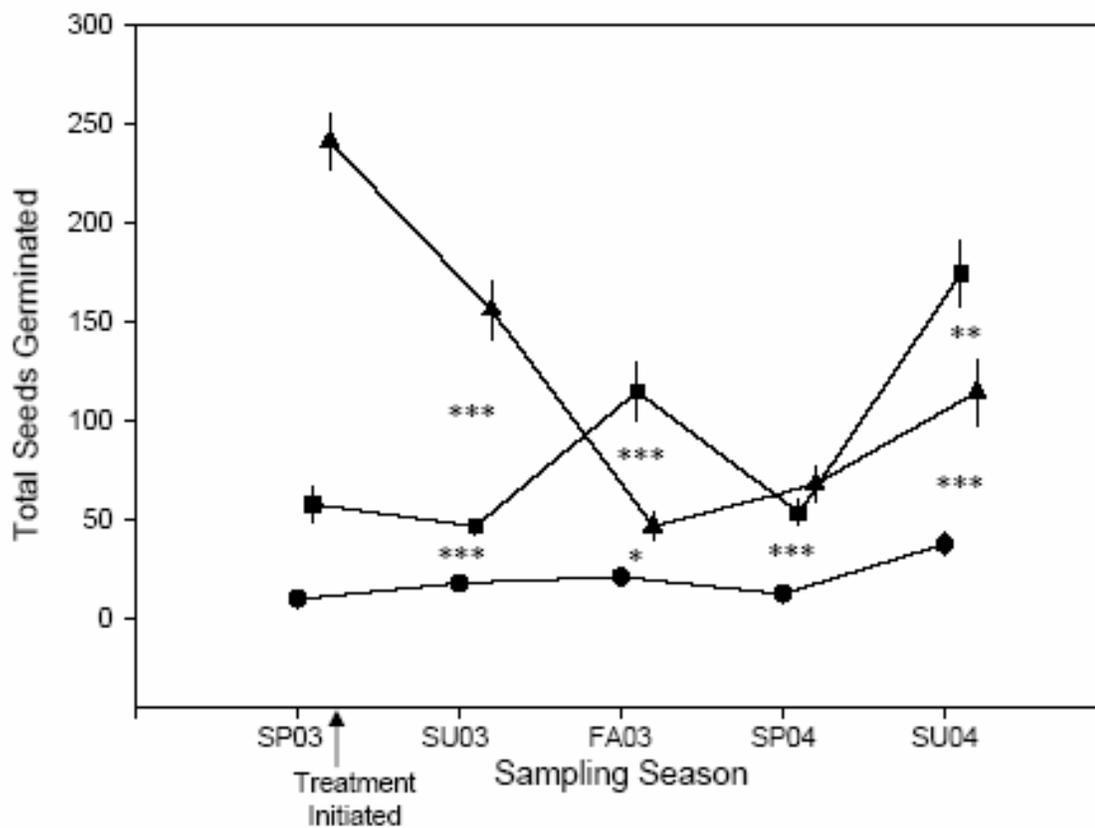
**Figure 6.** Effects of site and treatment on relative percent perennial cover (mean $\pm$ SE) before (SP03) and after removing *Eragrostis lehmanniana* from three sites in southeastern Arizona. SP = Spring, FA = Fall; sampling seasons 2003 and 2004. Circles = Coronado National Memorial, squares = Santa Rita Experimental Range. Filled symbols = control plots, open symbols = treated plots. Dotted triangles = Three Links Farm; treated and control plots combined due to no significant differences. See Table 1 for more detailed information.



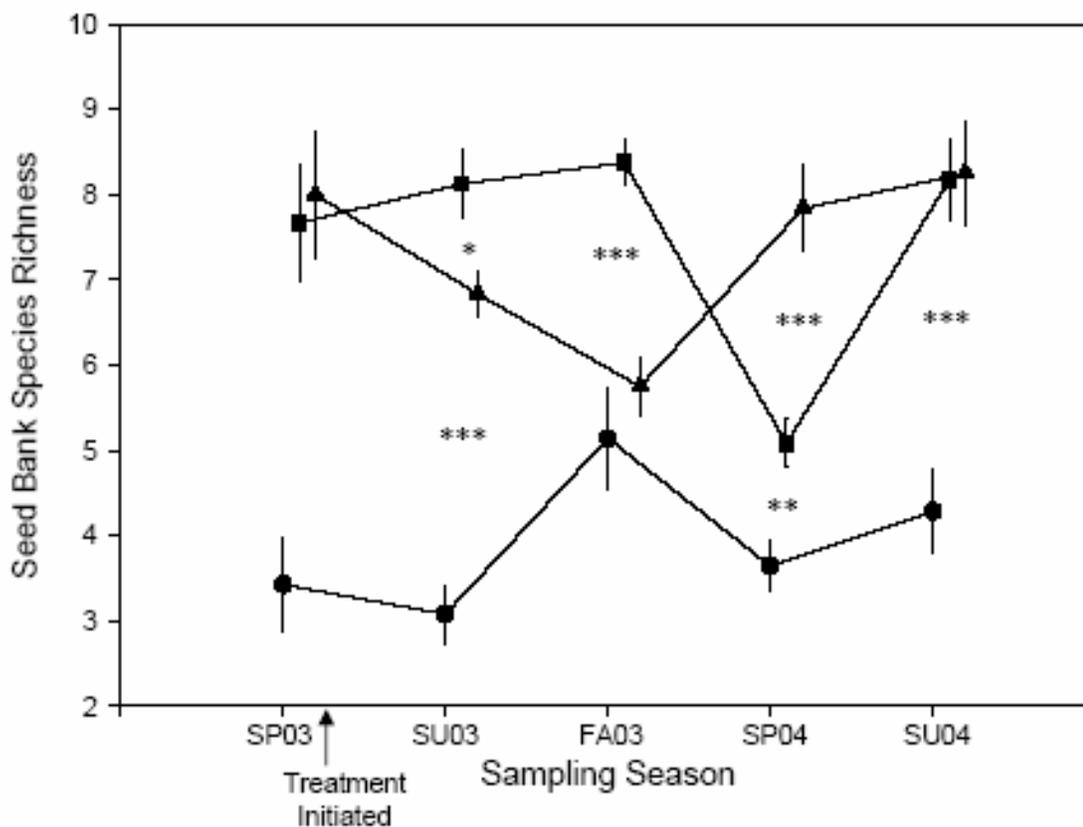
**Figure 7.** Effects of site and treatment on species richness of aboveground vegetation (mean $\pm$ SE) before (SP03) and after removing *Eragrostis lehmanniana* from three sites in southeastern Arizona, represented as departure from control plots. SP = Spring, FA = Fall; sampling seasons 2003 and 2004. Circles = Coronado National Memorial, squares = Santa Rita Experimental Range.



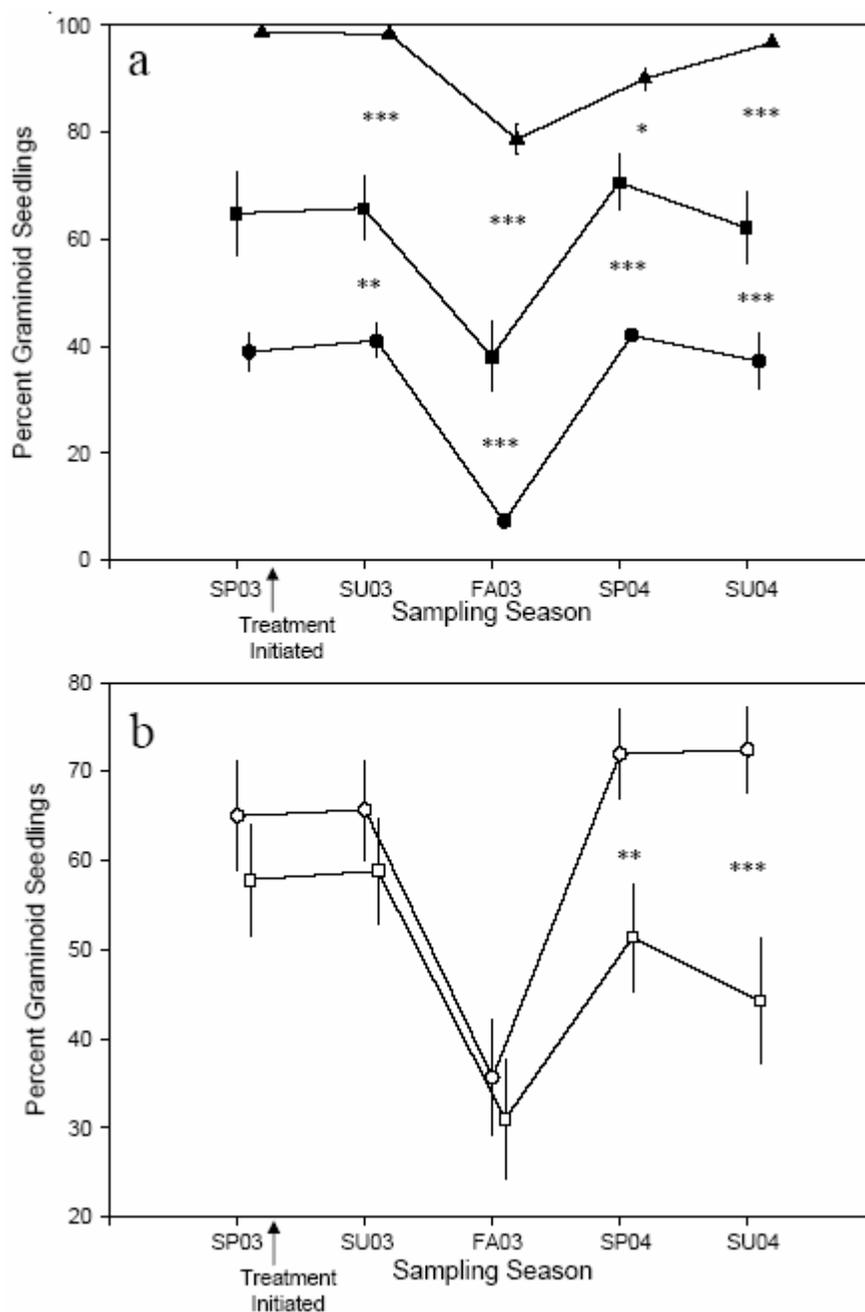
**Figure 8.** Effects of site on total seeds germinated (mean±SE) before (SP03) and after removing *Eragrostis lehmanniana* from three sites in southeastern Arizona. SP = Spring, SU = Summer, FA = Fall; sampling seasons 2003 and 2004. Circles = Coronado National Memorial, squares = Santa Rita Experimental Range, triangles = Three Links Farm. \*, \*\*, and \*\*\* denote significant within season effects ( $p < 0.05$ ,  $p < 0.01$  and  $p < 0.001$ , respectively). See Table 1 for more detailed information.



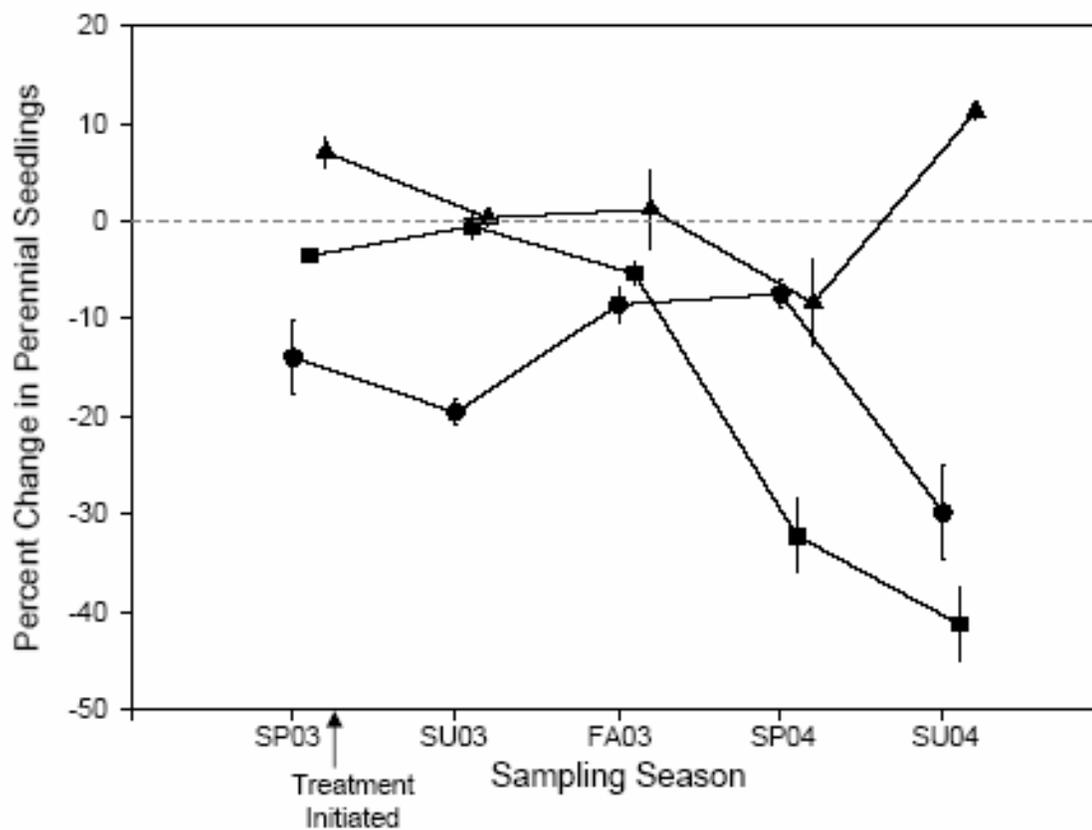
**Figure 9.** Effects of site on seed bank species richness (mean $\pm$ SE) before (SP03) and after removing *Eragrostis lehmanniana* from three sites in southeastern Arizona. SP = Spring, SU = Summer, FA = Fall; sampling seasons 2003 and 2004. Circles = Coronado National Memorial, squares = Santa Rita Experimental Range, triangles = Three Links Farm. \*, \*\*, and \*\*\* denote significant within season effects ( $p < 0.05$ ,  $p < 0.01$  and  $p < 0.001$ , respectively). See Table 1 for more detailed information.



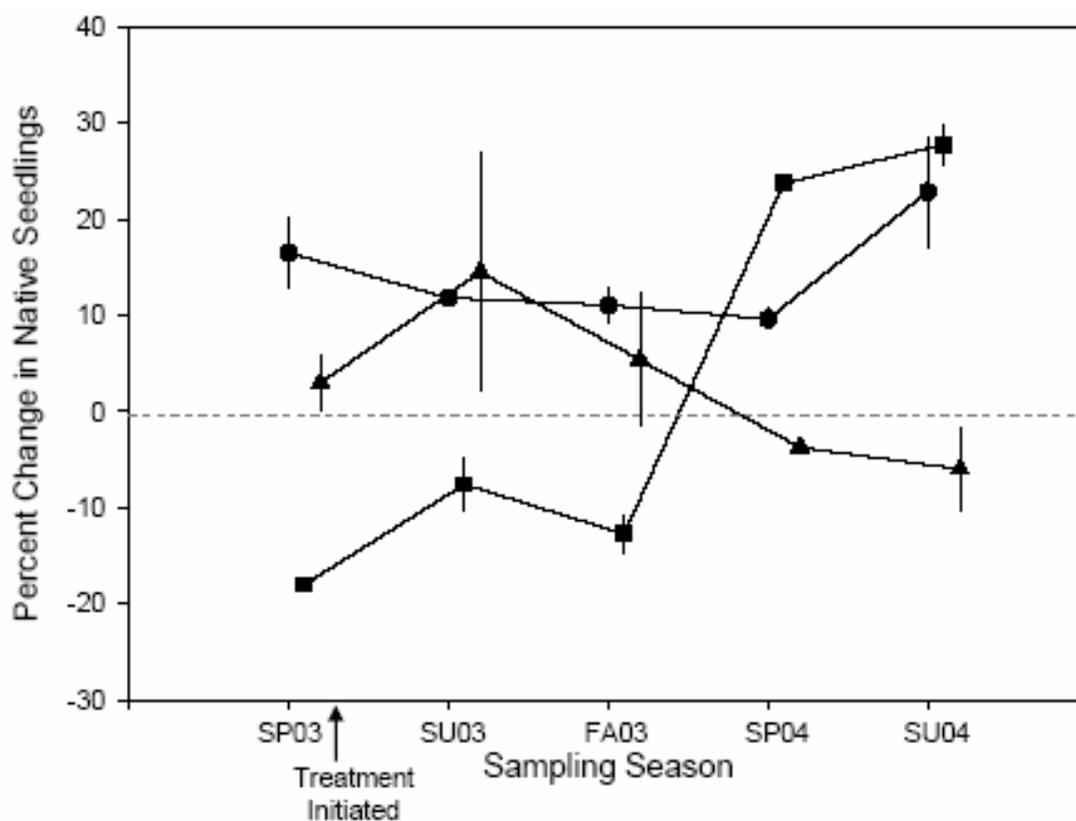
**Figure 10.** Effects of site (a) and treatment (b) on relative percent grass seedlings (mean±SE) before (SP03) and after removing *Eragrostis lehmanniana* from three sites in southeastern Arizona. SP = Spring, SU = Summer, FA = Fall; sampling seasons 2003 and 2004. Circles = Coronado National Memorial, squares = Santa Rita Experimental Range, triangles = Three Links Farm. Open circles = control plots, open squares = treated plots. \*, \*\*, and \*\*\* denote significant within season effects ( $p < 0.05$ ,  $p < 0.01$  and  $p < 0.001$ , respectively). See Table 1 for more detailed information.



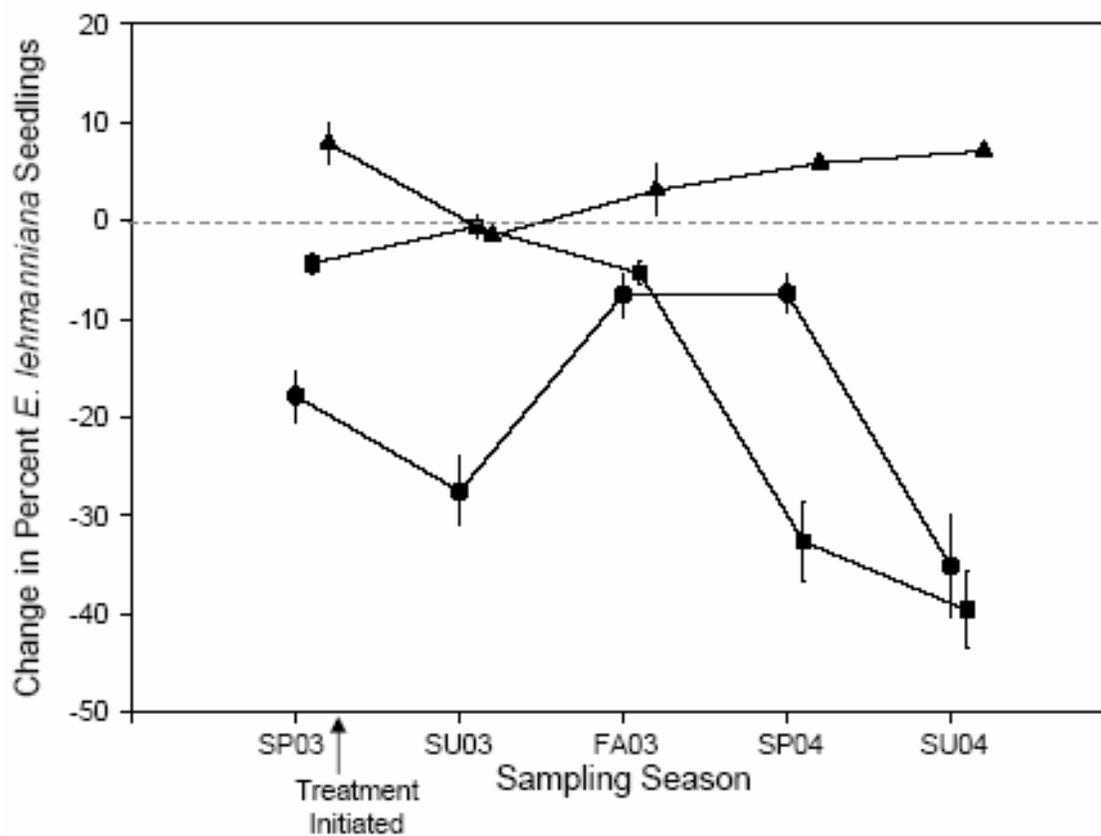
**Figure 11.** Effects of site and treatment on relative percent perennial seedlings (mean $\pm$ SE) before (SP03) and after removing *Eragrostis lehmanniana* from three sites in southeastern Arizona, represented as departure from control plots. SP = Spring, SU = summer, FA = Fall; sampling seasons 2003 and 2004. Circles = Coronado National Memorial, squares = Santa Rita Experimental Range, triangles = Three Links Farm.



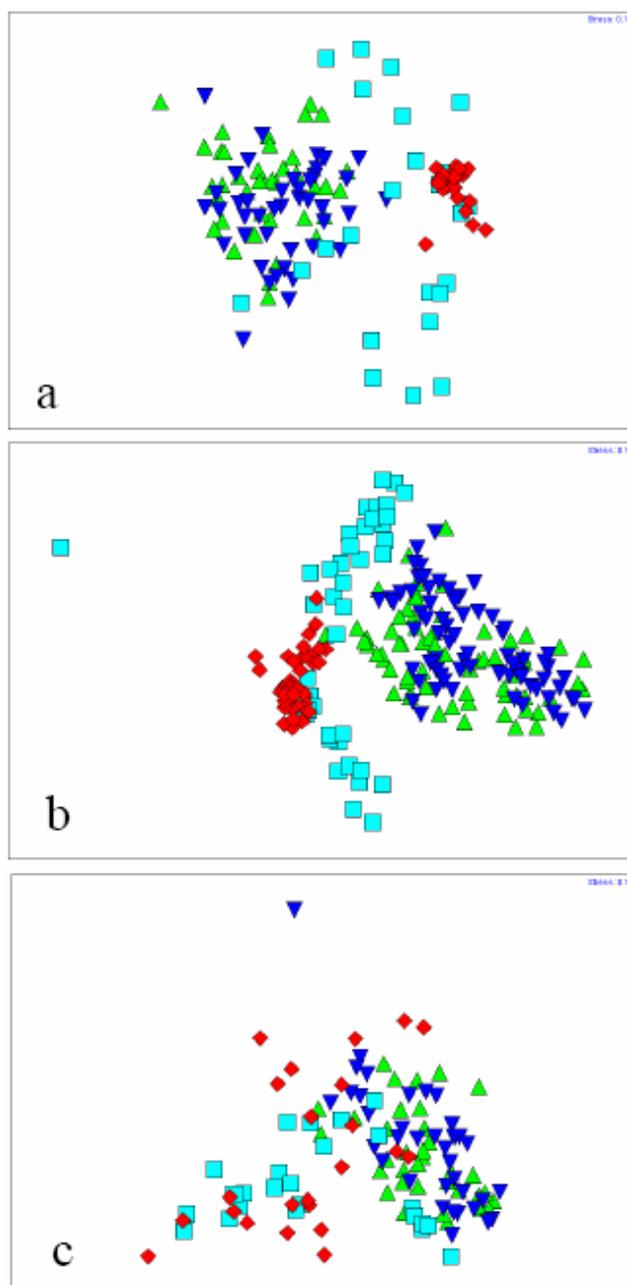
**Figure 12.** Effects of site and treatment on relative percent native seedlings (mean $\pm$ SE) before (SP03) and after removing *Eragrostis lehmanniana* from three sites in southeastern Arizona, represented as departure from control plots. SP = Spring, SU = summer, FA = Fall; sampling seasons 2003 and 2004. Circles = Coronado National Memorial, squares = Santa Rita Experimental Range, triangles = Three Links Farm.



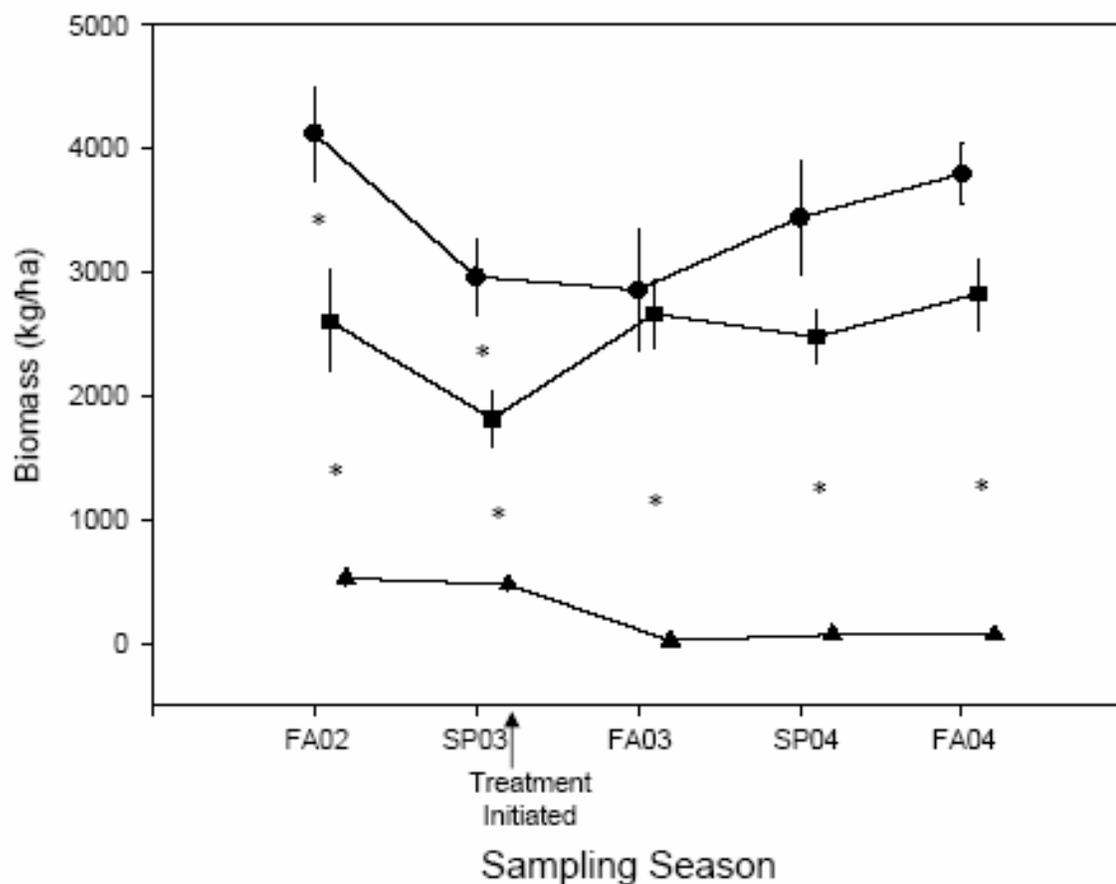
**Figure 13.** Effects of site and treatment on percent of seedlings that were *E. lehmanniana* (mean $\pm$ SE) before (SP03) and after removing *Eragrostis lehmanniana* from three sites in southeastern Arizona, represented as departure from control plots. SP = Spring, SU = summer, FA = Fall; sampling seasons 2003 and 2004. Circles = Coronado National Memorial, squares = Santa Rita Experimental Range, triangles = Three Links Farm.



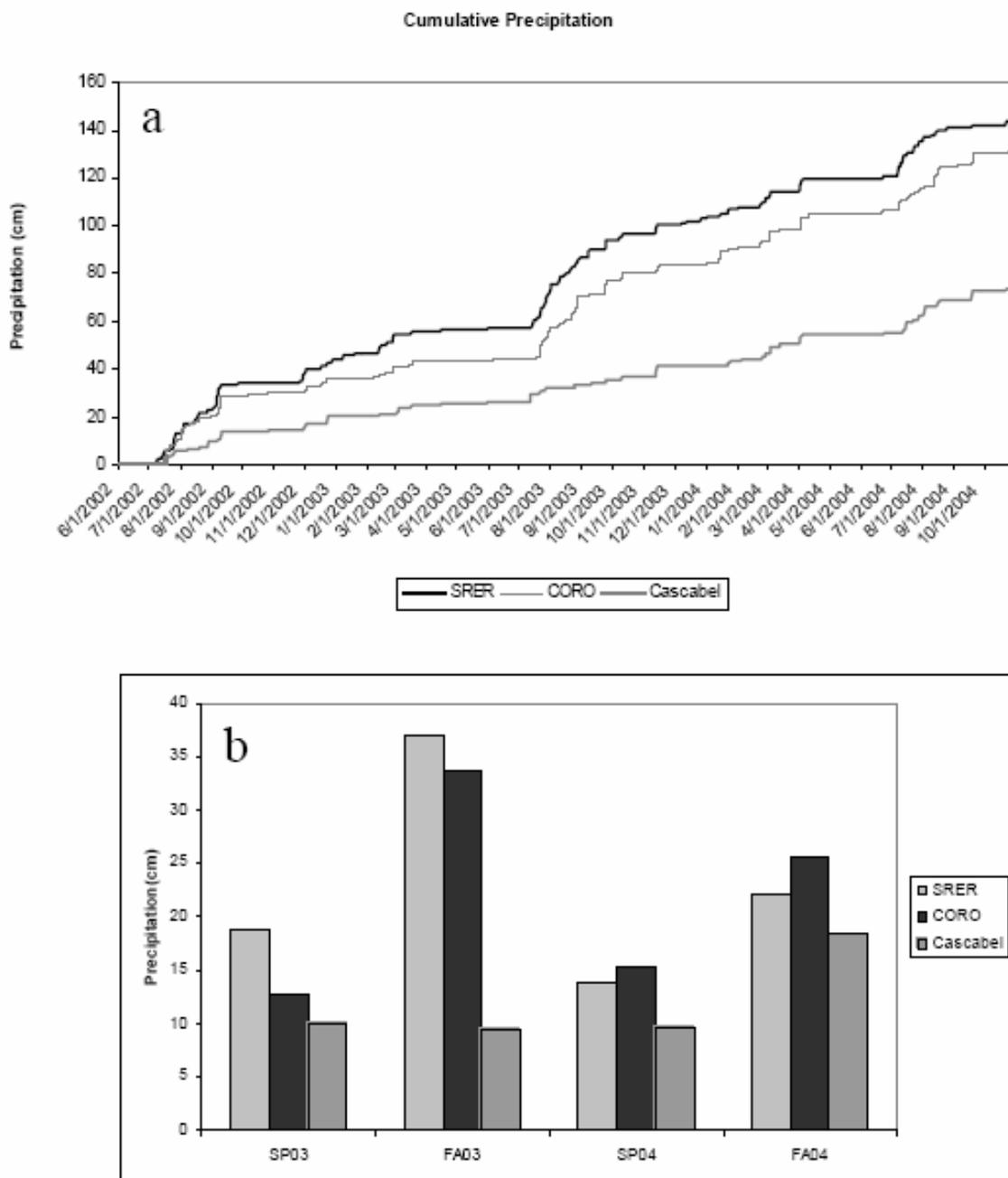
**Figure 14.** Non-metric multi-dimensional scaling (NMS plots of above-ground plant communities and seed bank communities in a nonnative grass removal experiment in southeastern Arizona for all sampling seasons together; a=CORO, b=SRER, c=TLF. Green triangles represent samples of seed banks from control plots; blue triangles are seed bank samples from treated plots. Red diamonds represent above-ground communities in control plots; light blue squares are above-ground communities in treated plots.



**Figure 15.** Biomass (mean±SE) of *E. lehmanniana* at the three study locations over the course of the experiment before (SP03) and after removing *Eragrostis lehmanniana* from three sites in southeastern Arizona. SP = Spring, SU = Summer, FA = Fall; sampling seasons 2003 and 2004. Circles = Coronado National Memorial, squares = Santa Rita Experimental Range, triangles = Three Links Farm. \* denotes significant within season effects ( $p < 0.05$ ). See Table 1 for more detailed information.



**Figure 16.** Cumulative precipitation (a) and seasonal total precipitation (b) at three study locations over the course of a nonnative grass removal experiment in southeastern Arizona.



**Figure 17.** Monthly totals of winter (a) and monsoon season (b) precipitation at Coronado National Memorial and the Santa Rita Experimental Range, two of the study locations in a nonnative grass removal study in southeastern Arizona.

