COMMUNITY AND ECOSYTEM DYNAMICS IN REMNANT AND RESTORED PRAIRIES

by

LAUREL PFEIFER-MEISTER

A DISSERTATION

Presented to the Department of Biology
and the Graduate School of the University of Oregon
in partial fulfillment of the requirements
for the degree of
Doctor of Philosophy

December 2008

University of Oregon Graduate School

Confirmation of Approval and Acceptance of Dissertation prepared by:

Laurel Pfeifer-Meister

Title:

"Community and Ecosystem Dynamics in Remnant and Restored Prairies"

This dissertation has been accepted and approved in partial fulfillment of the requirements for the Doctor of Philosophy degree in the Department of Biology by:

Patrick Phillips, Chairperson, Biology
Barbara Roy, Advisor, Biology
Scott Bridgham, Advisor, Biology
Steven Perakis, Member, Not from U of O
Bart Johnson, Outside Member, Landscape Architecture

and Richard Linton, Vice President for Research and Graduate Studies/Dean of the Graduate School for the University of Oregon.

December 13, 2008

Original approval signatures are on file with the Graduate School and the University of Oregon Libraries.

An Abstract of the Dissertation of

Laurel Pfeifer-Meister for the degree of Doctor of Philosophy

in the Department of Biology to be taken December 2008

Title: COMMUNITY AND ECOSYSTEM DYNAMICS IN REMNANT AND RESTORED PRAIRIES

Approved: _____
Dr. Scott D. Bridgham

Approved: _____
Dr. Barbara "Bitty" A. Roy

Restoration of imperiled ecosystems has emerged as a national priority, but there is little mechanistic understanding of how to restore ecosystems so as to sustain both species diversity and ecosystem function. The main objectives of my dissertation were (i) to develop an understanding of mechanisms that structure upland and wetland prairie plant communities in Oregon's Willamette Valley, with particular focus on edaphic and competitive controls over native and exotic species, and (ii) to apply this knowledge toward more effective restoration of prairie ecosystems. I used a combination of experiments and analysis of natural gradients to examine the effects of succession, competition, and environmental heterogeneity on plant community structure and ecosystem function within a restoration framework.

I conducted a large, replicated field experiment and a retroactive study of previously restored wetland prairies to assess different site preparation techniques. These techniques had variable effectiveness in suppressing the existing vegetation and seed bank, thus providing different initial successional trajectories. However, over time plant community structure converged due to a loss of early-successional species and the increasing dominance of native bunchgrasses; hence, there was a negative relationship between cover of native species and diversity. Only the more extreme treatments, such as topsoil removal, had large impacts on soil functioning. These studies underscore the importance of using a successional framework to guide restoration efforts.

Given the potential importance of competition between native and exotic grasses in structuring prairie vegetation, I used a paired study of field and greenhouse experiments to determine how abiotic factors influence the competitive hierarchies between native and exotic grasses commonly found in upland and wetland prairies. Exotic grasses dominated competitive interactions with the native grasses, but this depended upon nutrient and moisture availability.

Finally, I used a laboratory experiment to determine the seasonal and edaphic controls over nutrient and carbon cycling within a spatially heterogeneous upland prairie. Manipulating moisture and temperature resulted in significant changes in nitrogen, phosphorus, and carbon cycling, particularly in the winter. Under projected future climate change, these changes will likely have large effects on plant community structure.

This dissertation includes my previously published and co-authored materials.

CURRICULUM VITAE

NAME OF AUTHOR: Laurel Pfeifer-Meister

PLACE OF BIRTH: Portland, Oregon

DATE OF BIRTH: September 7, 1978

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon, Eugene, Oregon
Westmont College, Santa Barbara, California

DEGREES AWARDED:

Doctor of Philosophy in Biology, 2008, University of Oregon
Bachelor of Science in Chemistry, 2000, Westmont College
Bachelor of Arts in Biology, 2000, Westmont College

AREAS OF SPECIAL INTEREST:

Restoration Ecology
Community and Ecosystem Ecology

PROFESSIONAL EXPERIENCE:

Graduate Teaching Fellow for Forest Biology, Department of Biology, University of Oregon, Fall 2008, 2003.

Graduate Research Fellow, Department of Biology, University of Oregon, 2004.

Graduate Teaching Fellow for General Biology, Department of Biology, University of Oregon, Spring 2003.

Graduate Teaching Fellow for Biodiversity, Department of Biology, University of Oregon, Winter 2003.

Graduate Teaching Fellow for Ecology, Department of Biology, University of Oregon, Fall 2002.

Chemistry Lab Coordinator and General Chemistry Lab Instructor, Department of Chemistry, Westmont College, 2001-2002.

Undergraduate Research Fellow, Department of Chemistry, Westmont College, 1998.

GRANTS, AWARDS AND HONORS:

Environmental Protection Agency, STAR Fellowship Award, September 2005 to September 2008.

West Eugene Wetlands Award, West Eugene Wetland Partnership, 2006.

National Science Foundation, Predoctoral Fellowship Honorable Mention, 2004.

Graduation with Distinction, *summa cum laude*, Westmont College, 2000.

Presidential Scholarship, Westmont College, September 1996 to May 2000.

Poster Presentation Award, Westmont College, 2000.

Rotary Foundation College Scholarship, Newberg, OR, 1996.

Member of Phi Kappa Phi National Honorary Society.

PUBLICATIONS:

Pfeifer-Meister, L., and S. D. Bridgham. 2007. Seasonal and spatial controls over nutrient cycling in a Pacific Northwest prairie. Ecosystems **10**:1250-1260.

Pfeifer-Meister, L., E. M. Cole, B. A. Roy, and S. D. Bridgham. 2008. Abiotic constraints on the competitive ability of exotic and native grasses in a Pacific Northwest prairie. Oecologia **155**:357-366.

Rosbrugh, I. A., D. W. West, L. E. Pfeifer, N. M. Cook, D. M. Licata, K. A. Martin, and A. M. Nishimura. 2000. Crystallization kinetics of benzophenone and naphthalene multilayers on Al_2O_3 (0001). Surface Science **449**:248-254.

ACKNOWLEDGMENTS

To my advisors, Drs. Scott Bridgham, Bart Johnson, and Bitty Roy, I offer sincere gratitude for their commitment to fostering my development as an ecologist. I wish to thank Scott Bridgham for creating a supportive environment in which to conduct my research, for his accessibility to brainstorm ideas and troubleshoot the inevitable project hiccups, for refining my scientific writing skills, and for his encouragement to think beyond the scope of my individual research—he was an invaluable advisor and reviser! Many thanks to Bart Johnson and Bitty Roy for inviting me to join their ongoing research at Mt. Pisgah, which ultimately led to critical chapters in my dissertation. Bart Johnson challenged me to explore the practical issues of prairie restoration, offered his meticulous attention to scientific protocols, and posed questions that broadened my understanding of the ecological application of my results. Bitty Roy spent countless hours 'cultivating and watering' my botanical knowledge, honed my public speaking and writing skills, and kept me focused on the primary objectives of my research. Together they inspired lively discussion, which improved my experimental design, manuscripts, and the overall quality of my dissertation research.

I also thank the other members of my committee, Drs. Patrick Phillips and Steve Perakis. Patrick served as the chair of my committee and kept me realistic about what I could actually accomplish. He also offered invaluable advice on experimental design and statistical methods. Steve, who willingly drove from Corvallis each year, offered another biogeochemical perspective and helped problem-solve many nutrient methods.

Over the years, many others have been instrumental in the completion of this research. In addition to my advisors, Julie Stewart, Jeff Krueger, Laura Gayton, Santiago Carreño, and Esther Cole have all been co-authors of various manuscripts. Members of the Bridgham, Roy, and Johnson labs have not only provided an intellectual environment in which to conduct my research, but also regularly lent their support in the field and laboratory. In particular, I am grateful to Christy Cherrier for all of her assistance in setting-up a new lab and help in establishing protocols, Karen Sonnenblick for providing company (and assistance) during late nights at school, and Julie Stewart for reading and improving numerous versions of manuscripts. I also thank my cohort, Lisa Turnbull, June Keay, and Julie Toplin, for their support in completing the dreaded first year.

The West Eugene Wetland (WEW) Partnership, Lane Council of Governments, and Friends of Buford Park were also extremely generous with their time, funding, and access to sites. In particular, I offer my gratitude to Jeff Krueger, Eric Wold, Trevor Taylor, Jean Jancitis, Jason Blazar, Paul Gordon, and Ed Alverson—their commitment to restoration efforts in the Willamette Valley is inspirational. This work was supported by the U.S. Environmental Protection Agency through a STAR fellowship and Wetland Program Development Grant.

Finally, I cannot thank my family and friends enough for their patience and unconditional support. They have always encouraged me to pursue my goals and provided the necessary breaks that reminded me life goes beyond my research. My husband, Brent, has realized the true meaning of "for better or for worse", and I am most grateful for his love.

for Irving William Anderson

TABLE OF CONTENTS

Chapter Page

LIST OF FIGURES

LIST OF TABLES

CHAPTER I

INTRODUCTION

Many formerly extensive prairie ecosystems in the United States have been dramatically reduced since Euro-American settlement. Several types, including prairies in Oregon's Willamette Valley, have been listed as critically endangered ecosystems (Noss et al. 1995). Historically, prairies covered much of the Willamette Valley (Hulse et al. 2002, Whitlock and Knox 2002); however, 99% have been severely altered or destroyed by invasion of non-native plants, land development for both agricultural and urban uses, and fire suppression leading to succession to woodlands and forests (Finley 1994, Wilson et al. 1996). As a result, many ecosystem functions have been significantly diminished (e.g., water quality), and a number of species dependent on prairie habitat have been listed as threatened or endangered (e.g., *Aster curtus*, *Erigeron decumbens* var. *decumbens*, *Lomatium bradshawii, Icaricia icarioides fenderi*). For these reasons, the restoration and protection of these ecosystems has become a conservation priority.

Restoration is "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (Society for Ecological Restoration International 2004). Restoration activities are increasingly widespread, although it is a relatively new scientific field (National Research Council 2001, Young et al. 2005). Over the past 20

years, restoration ecologists have begun to integrate basic ecological principles into the practice of restoration. Some of these principles include the role of competition (Seabloom et al. 2003), successional theory and assembly rules (White and Jentsch 2004, Walker et al. 2007), invasion biology (Hoopes and Hall 2002, Seabloom and van der Valk 2003), abiotic factors (Corbin and D'Antonio 2004a), and disturbance ecology (Huston 2004) in structuring ecosystems. However, there is still considerable potential for further integration of ecology into restoration, and restoration practice provides an excellent opportunity to test basic ecological theories (Bradshaw 1987).

The importance of competition in structuring plant communities has long been debated by ecologists (e.g., Connell 1983, Grace 1991, Craine 2005). Some argue that competition becomes more intense under stressful abiotic conditions (Tilman 1988), while others argue that competition becomes less important under stressful abiotic conditions and instead increases with increasing productivity (Grime 1977, Twolan-Strutt and Keddy 1996). If competitive hierarchies vary along environmental gradients, it follows that the abundance and distribution of species would also vary along that gradient. In prairie ecosystems, the ability of aggressive exotic species to competitively exclude native species has been identified as a primary obstacle to successful restoration (Ewing 2002). Previous studies have shown than native species are able to survive in stressful, nutrient-poor environments, but are outcompeted by exotic species under high-resource conditions (Huenneke et al. 1990, Vinton and Burke 1997). However, other studies have shown no effect of the abiotic environment on competitive hierarchies (Bakker and Wilson 2001, Corbin and D'Antonio 2004b). This is still a current debate in

ecology and restoration science, and more empirical evidence is needed to resolve this issue.

Successional theory is one of the oldest concepts in ecology, beginning with the contrasting viewpoints provided by the organismal concept of Clements (1936) and Gleason's individualistic concept (1939). Currently, concepts of alternative stable states and assembly rules have received much attention (Temperton et al. 2004, Schröder et al. 2005). Given that successional theory and assembly rules deal with how communities are constructed, it is not surprising that restoration practitioners have a vested interest in the applicability of these theories, and ecological restoration provides an ideal venue to test these ideas (Sheley et al. 2006).

Invasion by exotic species is recognized as a leading threat to biodiversity and ecosystem functioning (Vitousek et al. 1997, Mack and D'Antonio 1998, Chapin et al. 2000). Furthermore, the potential for successful restoration is seriously comprised by the introduction of exotic species (Zedler 2000). Exotic species are estimated to cost the United States $120 billion per year, and approximately half of endangered and threatened species are considered to be at risk due to the presence of invasive exotic species (Pimentel et al. 2005). In Oregon, it is estimated that greater than 25% of the flora and fauna are non-native species (Meyerson and Mooney 2007). It is important to understand the mechanisms that make some exotic species more invasive than others (e.g., small seed size and high propagule pressure (Rejmanek and Richardson 1996, Zedler and Kercher 2004)), and why certain ecosystems are more invasible than others (e.g., more diverse communities may be more resistant to invasion (Naeem et al. 2000)).

Abiotic factors (e.g., nutrient availability and hydrology) are clearly important in structuring plant communities. Plant distributions are highly correlated with rainfall, temperature, and elevation, and numerous studies have shown that manipulating environmental factors can change plant species composition (e.g., van der Valk et al. 1994, Weltzin et al. 2003, Baer et al. 2005). Restoration attempts often are unsuccessful because of insufficient consideration of the abiotic environment (e.g., trying to establish a wetland community with improper hydrology (Mitsch and Wilson 1996)). To effectively restore and conserve prairies, it is essential to understand how major abiotic processes control plant community structure.

Disturbances can directly affect plant communities, but may also affect them indirectly by altering resource availability (Burke and Grime 1996, Stohlgren et al. 1999). Often land is in a highly-disturbed state prior to restoration, and the practice of restoration can be a form of disturbance as well, both in terms of site preparation (e.g., tilling or topsoil removal) and site management (e.g., fire or mowing). In many cases, restoration practitioners have found that periodic disturbance is necessary to maintain a desired plant community. For example, in Pacific Northwest prairies, fire has been identified as a tool that can favor native species and reduce invasion by woody species (Clark and Wilson 2001, Kaye et al. 2001); however, the intensity and frequency of fire are key determinants of the effectiveness.

Successful conservation and restoration should incorporate all of these ecological principles. No one factor determines the structure and composition of plant communities. Rather, a variety of mechanisms must be considered, including the abiotic environment, competition, succession, the impact of invasive species, and disturbance.

Dissertation Research

The primary objective of my dissertation research was to understand the mechanisms that structure prairie plant communities, with particular attention given to native and aggressive exotic species and their interactions with edaphic controls. To address this objective, I examined the effects of i) succession, ii) competition, and iii) environmental heterogeneity on plant community structure and ecosystem function within a restoration framework. In the following section, I detail the motivation and objectives for each chapter in the remainder of my dissertation.

Chapter II is entitled "Plant community and soil responses to experimental restoration techniques in a wetland prairie." This work is co-authored with Bitty Roy, Bart Johnson, Jeff Krueger, and Scott Bridgham and has been submitted to *Ecological Applications* for publication. Our applied objective in this study was to determine the most successful site preparation techniques for restoring native biodiversity and ecosystem function in a Willamette Valley wetland prairie. Additionally, we used this study to examine i) the role of competition in controlling diversity and the relative abundances of native and exotic plant species, ii) the degree to which plant community structure affected soil function, and iii) whether different restoration treatments might initiate different successional trajectories. To date, no other study has examined the above- and belowground responses to wetland prairie establishment in any detail. We established a large replicated field experiment to examine ten combinations of site preparation techniques in a prior annual ryegrass (*Lolium multiflorum* Lam.) field. We also compared the responses of the experimental treatments to three high-quality remnant wet prairies and the adjacent agricultural field. Site preparation techniques included

various combinations of tilling, herbicide application, solarization, and thermal weed control. Plant (e.g., diversity, cover, and productivity) and soil responses (e.g., microbial biomass, nutrient cycling, and respiration) were measured in the experimental treatments, remnant prairies, and farm field for three years.

In Chapter III, entitled "Restoring wetland prairies: tradeoffs among native plant cover, diversity, and ecosystem functioning," our objective was to assess the effectiveness of two restoration techniques, topsoil removal and solarization, for restoring native plant biodiversity and ecosystem function to agricultural fields that had retained wetland hydrology. We examined previously restored sites that were one to five years old and compared these responses to intact reference wetlands. Solarization and topsoil removal were widely used techniques in the Willamette Valley for wetland prairie restorations beginning in the 1990s. However, the outcomes have never been quantitatively analyzed. In 2005, we sampled three sites each that were restored by solarization or topsoil removal followed by seeding with native species and three remnant prairies. At each site, we measured plant cover, diversity, and productivity, and soil chemical, physical, and functional attributes. This work is co-authored with Bart Johnson, Bitty Roy, Santiago Carreño, Julie Stewart, and Scott Bridgham.

In Chapters IV and V, I examine nutrient dynamics and competitive interactions in an upland remnant prairie on Mt. Pisgah, near Eugene, Oregon, USA. Chapter IV, entitled "Seasonal and spatial controls over nutrient cycling in a Pacific Northwest prairie," is published in *Ecosystems* (Pfeifer-Meister and Bridgham 2007), contains co-authored material with Scott Bridgham, and is copyrighted by Springer Science. Our objective in this study was to understand the degree to which seasonal patterns of

nitrogen, phosphorus, and carbon cycling depend on temperature and moisture availability, and how these seasonal controls vary due to micro-heterogeneity in edaphic conditions. Soil samples were collected seasonally across a south-facing hillslope at Mt. Pisgah. Microbial respiration, net nitrogen mineralization, net nitrification, and phosphorus availability were measured under field conditions and under varied temperature and soil moisture conditions.

Chapter V is entitled "Abiotic constraints on the competitive ability of exotic and native grasses in a Pacific Northwest prairie." This chapter is published in *Oecologia* (Pfeifer-Meister et al. 2008), co-authored with Esther Cole, Bitty Roy, and Scott Bridgham, and copyrighted by Springer-Verlag. Our objective was to test the competitive dynamics among four grass species (two native and two exotic) under varying nutrient and moisture conditions in an upland prairie. Theory suggests that aggressive exotic species are competitively superior in high-quality habitats, and native species are forced to take 'refuge' in low-quality habitats (Hoopes and Hall 2002, Lowe et al. 2003). At the Mt. Pisgah study site, we observed that nutrient poor, wet areas had a higher proportion of native species than nutrient rich, moderately moist areas (unpublished data). Thus, we wanted to test the hypothesis that native species were restricted to these low-quality sites due to the competitive exclusion by exotic species. To test our hypothesis, we preformed a paired-competition study of field and greenhouse experiments on the native perennial grasses, *Danthonia californica* Boland. and *Deschampsia cespitosa* L., and the common exotic grasses, *Schedonorus arundinaceus* (Schreb.) Dumort. and *Lolium multiflorum* Lam. In the field, we examined the effects of aboveground competition on established juvenile plants in four areas of varying nutrient

and moisture conditions, and in the greenhouse, we examined the response of each species in monoculture and interspecific competition trials under experimentally manipulated nutrient and moisture availabilities.

In Chapter VI, I summarize the results from chapters II through V and conclude with implications for restoration.

CHAPTER II

PLANT COMMUNITY AND SOIL RESPONSES TO EXPERIMENTAL RESTORATION TECHNIQUES IN A WETLAND PRAIRIE

A paper submitted to *Ecological Applications* and co-authored with Bitty A. Roy, Bart R. Johnson, and Scott D. Bridgham.

Introduction

Wetland restoration activities are widespread, both on a voluntary basis and as a legal requirement for mitigating the destruction of natural wetlands. However, it is a relatively new field with little accumulated scientific knowledge (National Research Council 2001), and restoration design is often based on anecdotal information and case studies, rather than on rigorous experimental investigations of which restoration techniques are most effective. The few comparative studies that have been conducted often have lacked one or more attributes of good experimental design – randomization, replication, or the inclusion of both treatments and controls. Furthermore, wetland restorations have focused primarily on the establishment of native plant communities, despite a national agenda of no-net-loss of overall wetland function (National Research Council 2001). Even with successful native plant establishment many wetland functions

may be significantly diminished from those of natural wetlands (Simenstad and Thom 1996, Zedler 2003). Moreover, restorations are not always successful in establishing a native plant community; both natural and restored wetlands often are dominated by exotic plant species (National Research Council 2001, Kellogg and Bridgham 2002). For these reasons, wetland restoration provides a challenging venue for testing basic ecological principles in an important applied framework.

Successional theory may offer the most appropriate framework for restoring and maintaining diverse, native communities that are resistant to invasion from exotic species over the long term (Temperton et al. 2004, Walker et al. 2007). Restoration activities try to manipulate, and typically accelerate, secondary succession from a highly disturbed state, generally beginning with suppressing extant vegetation and establishing an initial group of desirable species that are either planted or seeded. The success of these activities in maintaining low cover of exotic plant species is dependent on the effectiveness of site preparation treatments in eliminating the existing plants and seed bank of the site, as they are often dominated by exotic, invasive species. Despite the obvious importance of site preparation, there have been very few studies that have compared different techniques (e.g., Wilson and Gerry 1995, Ewing 2002, Adams and Galatowitsch 2006). Even the best site preparation techniques are only partially effective at eliminating unwanted residual plant species, and there is almost always a continuing invasion of new propagules into a site. Consequently, understanding and directing trajectories of plant community change over time are essential to achieve desirable species diversity and composition. Site preparation techniques may also affect soil properties, which not only will have consequences for ecosystem functioning, but may

provide feedbacks that will determine future plant community successional dynamics. Moreover, there are potential trade-offs between the effectiveness of a particular site preparation technique in removing exotic plants and their seed bank, and impacts on soil functioning. This underscores the importance of following restorations for multiple years and measuring both above- and belowground responses.

The need for reliable, effective approaches to wetland restoration following land use conversion is high. More than 50% of the original wetland area in the contiguous U.S. has been lost to development (Dahl 2006). Wetland losses have been particularly severe in the Willamette Valley in western Oregon. Since 1850, over 97% of wetland prairies in the valley have been converted to agricultural or urban land uses (Hulse et al. 2002). Willamette Valley prairies, which historically comprised 32% of the valley floor and foothills (Hulse et al. 2002), have been listed as a critically endangered ecosystem in the United States (Noss et al. 1995).

Historically, conversion to agriculture has been the primary mode of wetland loss in the U.S., with agricultural activities responsible for 70% of all wetland losses in the last half century (Frayer et al. 1983, Dahl 2000). Similarly, in the Willamette Valley, 70% of wetland losses from the 1980s to the 1990s were due to agriculture (Bernet et al. 1999). The Willamette Valley is the world's largest producer of grass seed and many native wet prairies have been lost to grass seed production. Given their imperiled status, wetland prairies are the focus of extensive restoration efforts in the Willamette Valley, and much of the potentially restorable wetland area is currently in grass seed production.

There have been no published studies of wetland prairie establishment in the Willamette Valley and few conducted elsewhere (e.g., Green and Galatowitsch 2002,

Adams and Galatowitsch 2006). To our knowledge, none of the few existing studies examined the relationships between vegetation and soil processes in any detail. We used a large replicated field experiment to examine the effectiveness of initial site preparation techniques in restoring native plant biodiversity and soil functioning over three years in a prior annual ryegrass (*Lolium multiflorum* Lam.) field. We also compared responses of the experimental treatments to three of the highest quality local intact wetland sites and the adjacent agricultural field. We hypothesized that (1) treatments that most reduced the seed bank would result in a lower cover of exotic species and higher native diversity; (2) even the treatments most successful in establishing diverse native plant communities would have very different community structure from local high-quality reference wetlands; (3) treatments involving more physical disturbance to the soil would have detrimental effects on various aspects of soil functioning; (4) differences in plant community structure and productivity due to the treatments would cause significant differences in soil properties; and (5) restored wetlands would have lower nutrient availability and greenhouse gas emissions than the adjacent agricultural field.

Site Preparation Techniques

To ensure the relevance of site preparation techniques used in this study, we collaborated with the Lane Council of Governments and City of Eugene to conduct a full-day forum that drew on the knowledge of local restoration practitioners to select the restoration methods. Our aim was to test both commonly used and emerging site preparation techniques. The individual techniques were selected so they could be applied

in different combinations to kill the existing vegetation (primarily *L. multiflorum*) and reduce the seed bank. Below is a brief description of each individual method.

Tilling: Tilling is a common restoration practice that reduces existing vegetation through physical disturbance and prepares a site for seeding. This technique has increased native species establishment in some restoration studies (Wilson and Gerry 1995, Barberi 2002), but it may also increase germination of species found in the seed bank by bringing them to the soil surface. This is especially problematic in agricultural fields where the seed bank is almost entirely non-native (Fitzpatrick 2004). Less is known about the effect of tilling on ecosystem function in a restoration context, but studies have shown that tilling can decrease soil microbial biomass and respiration (Potthoff et al. 2005, 2006).

Herbicides: Numerous herbicides have been used in restoration studies, and their application often results in the reduction of invasive species in the short term (Wilson and Gerry 1995, Bakker et al. 2003). Three years post herbicide use, however, the density and biomass of invasive grasses increased in a pothole wetland, with no effect on native grasses and a reduction of native forbs (Sheley et al. 2006). Repeated applications of conventional herbicides have proven more effective than a single application (Morgan 1997). Glyphosate is a typical non-specific herbicide used for these purposes, with an average half-life of 60 days in soils (Feng and Thompson 1990). It has been shown to have little influence on soil microbial biomass and activity at standard application rates (Wardle and Parkinson 1990).

Thermal Weed Control: This technique uses extreme temperatures (500-1000 °C) to kill both the seed bank and the existing vegetation with infrared burners, and thus

is a potential alternative to herbicides (Fitzpatrick 2004). The machine applies a thin film of water to the vegetation and then subjects the plants and seeds to intense heat that is transferred to them through infrared energy, turbulent hot air, and boiling water. Species size, as well as type, affects the success of this technique—smaller vegetation and forbs are more easily eradicated than larger vegetation and grasses (Fitzpatrick 2004). Overall though, this method has been little studied as a restoration technique.

Solarization: Solarization involves trapping heat from the sun underneath plastic for several months to kill the vegetation and the seed bank near the surface of the soil. This technique is most effective when the soil is moist as it conducts heat more efficiently and promotes the germination of seeds (Egley 1990, Fitzpatrick 2004). Studies have found that solarization has helped with the establishment of seeded native forbs and grasses (Bond and Grundy 2001, Wilson et al. 2004, Moyes et al. 2005). Solarization has also been shown to decrease the numbers of certain microbial species (Bendavid-Val et al. 1997, Pinkerton et al. 2000, Wang et al. 2006), but this effect was short lived (Wang et al. 2006).

Methods

Study Sites

Our experimental site was within Coyote Prairie, a 98-ha area located 3 km west of Eugene, OR. This site was an undrained agricultural field (i.e., with intact wetland hydrology) used in the production of *Lolium multiflorum* (annual ryegrass) seed for the past 25 years. The field was tilled and burned annually in the fall until 2003 and fertilized twice annually in the spring with 3.6 to 4.4 g nitrogen m^{-2} yr^{-1}, 1.6 to 2.0 g

phosphorus m^{-2} yr^{-1}, and 3.0 to 3.8 g potassium m^{-2} yr^{-1} until 2004. Coyote Prairie was originally acquired by The Nature Conservancy (TNC) in 2004 and now is owned and managed by the City of Eugene. Our experiment was implemented on a 4.5 ha portion of the field while the remaining area continued to be actively farmed for *L. multiflorum* seed production. The site is relatively flat with a slight slope from east to west of 0.35%. Plots were located randomly across the 4.5-ha site, as well as across 1 ha of the actively farmed adjacent portion. Both the treatment plots and the farm-field plots were arrayed parallel to each other down the slope, and thus had similar water-table depths and surface hydrology. Additionally, we chose the three nearest high-quality remnant prairies as "reference sites." The reference sites included Willow Creek Natural Area (managed by TNC), Oxbow West Prairie (managed by the City of Eugene and the U.S. Bureau of Land Management (BLM)), and the North Greenhill Ashgrove Unit (managed by the City of Eugene and BLM). These sites were all located within 4 km of Coyote Prairie. The soil type for all sites is classified as Natroy series, very-fine, smectitic, mesic Xeric Endoaquerts, and all sites have similar hydrology.

The local climate is Mediterranean with a mean annual daily maximum temperature of 17.2°C, a mean annual daily minimum temperature of 5°C, and a mean annual precipitation of 125 cm, with 113 cm of this falling between October and May (http://www1.ncdc.noaa.gov/pub/data/ccd-data/CCD_2005.pdf). Because of the Mediterranean climate, wetland prairies in this region dry out through June, with peak growing season in mid-June and almost complete senescence of vegetation by mid-July. Established plants of many species begin to green up with the fall rains and continue to

grow throughout the winter. Seedlings of different species emerge at different times throughout the winter and spring.

Experimental Design

We conducted a three-year study to determine the most effective site preparation techniques for wetland prairie restoration. Given the large number of potential treatment combinations, an unbalanced factorial design was chosen that combined and contrasted ten treatment combinations that would be most relevant for local wetland restorations based upon the public forum (Table 2.1). Treatment plots were 15 m by 15 m in size with 5 replicates of each treatment. Buffers of 10 m between the plots and 23 m around the edge of the entire site were established. The buffers were mowed periodically throughout the experiment to reduce seed rain into the plots. The plots were big enough that large pieces of equipment could be used to implement the treatments and thus ensure that the results reflected actual restoration practices. Prior to treatment implementation, the entire 4.5-ha site was mowed twice (on 14 May and 17 June 2004) and the *L. multiflorum* thatch was removed.

A field disk and cultipacker were pulled by a tractor for the tilling treatment. The soil was broken up by running a field disk to a depth of approximately 20 cm in opposite directions on 18 and 23 June 2004. The cultipacker was used on 3 July to homogenize plots for seeding. For the herbicide treatments, glyphosate (Roundup) was applied using a Rears Pul-Tank with 7.5-m booms (Eugene, OR, USA), pulled by an ATV. The summer herbicide application was applied on 20 July and the fall herbicide application on 1 October. For the solarization treatment, trenches were dug around the 15-m by 15-m

experimental plots with a Ditch-Witch (Perry, OK, USA). Clear plastic (6 mil, 15-m width) was placed over the plots, and edges were tucked into the trenches and buried on 21 July 2004. A Sunburst infrared burner (Eugene, OR, USA) was used on 11 August 2004 for the thermal weed control treatment.

Table 2.1. Experimental Design. The original design included ten site preparation treatment combinations, the farm field, and three nearby reference prairies. However, the summer herbicide application had no detectable effect on the plant communities or soil response variables ($p>0.3$). For ease of interpretation, each treatment combination that included summer herbicide was lumped with its equivalent counterpart (e.g., till, summer herbicide has been combined with till), reducing the total treatment combinations from ten to seven.

	Original Treatments		**Collapsed Treatments**
1	Summer Herbicide	1	Control: Summer Herbicide
2	Till	2	Till
3	Till, Summer Herbicide		--
4	Summer Herbicide, Thermal	3	Thermal
5	Till, Thermal	4	Till, Thermal
6	Till, Summer Herbicide, Thermal		--
7	Summer and Fall Herbicide	5	Fall Herbicide
8	Till, Summer and Fall Herbicide	6	Till, Fall Herbicide
9	Till, Solarization	7	Till, Solarization
10	Till, Summer Herbicide, Solarization		--
11	Farm Field	8	Farm Field
12	Reference Prairies	9	Reference Prairies

A seed mix of 15 native graminoid and forb species was sown in all plots with hand broadcasters on 28 October 2004. These species are commonly used for restoration of wet prairies throughout the Willamette Valley. The seed mix included five graminoids, *Agrostis exarata* Trin., *Carex densa* (L. H. Bailey) L. H. Bailey, *Danthonia californica* Bol., *Deschampsia cespitosa* (L.) P. Beauv., and *Juncus tenuis* Willd.; and ten forbs, *Camassia quamash* (Pursh) Greene ssp. *maxima* Gould, *Epilobium densiflorum*

(Lindl.) Hoch & P.H. Raven, *Grindelia integrifolia* DC., *Madia glomerata* Hook., *Microseris laciniata* (Hook.) Sch. Bip., *Plagiobothrys figuratus* (Piper) I.M. Johnst. ex M. Peck ssp. *figuratus*, *Potentilla gracilis* Douglas ex Hook. var. *gracilis*, *Prunella vulgaris* L. ssp. *lanceolata* (W. Bartram) Hultén, *Symphyotrichum hallii* (A. Gray) G.L. Nesom (syn. *Aster hallii)*, and *Wyethia angustifolia* (DC.) Nutt. The overall seeding density of all species in each plot was 850 mg seed/m^2, which is typical of restoration practices within the Willamette Valley.

Within each of the larger 15-m by 15-m plots, three 1-m by 1-m subplots were randomly located to monitor percent cover, species richness, and diversity. In two of these subplots, we also examined the soil functional, physical, and chemical attributes described below.

In each of the three reference wetland sites, we randomly chose five plots within which we randomly placed three 1-m by 1-m subplots. We established five 15-m by 15-m plots in the adjacent farm field, but due to the homogenous nature of the field only one 1-m by 1-m subplot was sampled per plot for plant data and two 1-m by 1-m subplots were sampled for soil variables.

Plant Sampling

In each of the 200 1-m by 1-m subplots (150 experimental treatment, 45 reference, and 5 farm field), percent cover was measured by species using the point-intercept method (Elzinga et al. 1998), and presence/absence was recorded for any species not hit by a pin to calculate species richness and diversity. For the point-intercept method, we constructed 1-m by 1-m aluminum frames with 25 equally spaced pins. Pins

were dropped vertically and each touch by a plant was recorded by species, thus allowing for greater than 100% cover. Plant cover was measured in the experimental restoration plots in mid-June for 3 years after establishment (2005 - 2007), but in 2005 farm field plots were not measured and in 2006 reference sites were not measured. Species nomenclature followed the USDA plant database (http://plants.usda.gov), with the exception of *Schedonorus arundinaceus* (Schreber) Dumortier (syn. *Festuca arundinacea* or *Lolium arundinaceum*), which followed the Flora of North America (Flora of North America Editorial Committee 1993+).

Aboveground net primary productivity (NPP) was estimated in 2006 at peak standing biomass in each of the experimental and farm field subplots. Within each subplot, three 10-cm by 10-cm plots were randomly located and clipped on 20-27 June 2006. The biomass was sorted into graminoids, forbs, woody, and thatch, dried at 60°C for 48 hours, and weighed. Although we did not collect biomass data from the reference sites in 2006, in 2005 biomass was collected in an identical manner at the same time of year in the reference subplots. To estimate belowground NPP, we buried one in-growth root core in each subplot within the experimental treatments (cores were not placed in the farm field or reference sites). Root cores were made of nylon mesh (5-cm diameter, 15-cm tall) and filled with root-free soil from the site. Cores were inserted on 17 September 2005, covered with a small rock, and removed on 3 July 2006 before significant summer dry-season senescence. After removal, in-growth root cores were immediately washed using a hydropneumatic root-washer (Gillison's Variety Fabrication, Benzonia, MI, USA), and roots were dried at 60°C for 48 hours and weighed.

Soil Sampling

We conducted the soil sampling seasonally from the fall of 2005 to the summer of 2006 in the experimental treatments (i.e., in the second year after establishment) and the farm field. Soil sampling was not conducted seasonally in the reference sites because of the logistical limitations of the large number of plots. In the fall (14 October 2005), winter (13 January 2006), and spring (7 April 2006), *in situ* soil respiration was measured using capped PVC chambers (10.16-cm diameter, 35-cm tall). We placed chambers 5-cm in the ground the day before each sampling after all aboveground plant matter was clipped from the chamber location. On the day of the sampling, chambers were closed with a rubber cap, and samples were drawn from the headspace and stored in pre-vacuumed serum bottles sealed with rubber septa. After capping, samples were collected at 0, 30, 60, 90, and 120 minutes from each chamber. Soil temperature was measured at a 5-cm depth adjacent to each chamber at 60 minutes. Gas fluxes in all chambers were measured within a 5-hour period on the same day. In the summer, it was impossible in these hard shrink-swell clay soils to insert gas-tight chambers. Therefore, intact soil cores were collected in the field (5 July 2006), immediately placed in Mason jars fitted with septa, and incubated in the dark in the laboratory at the average *in situ* soil temperature. Gas samples were collected at 0, 30, 60, 90, and 120 min after re-equilibration with the atmosphere and stored as above. An equal volume (20 cc) of the sample that was removed from the headspace of the Mason jars was replaced with N_2 gas. For all seasons, CO_2 and CH_4 were measured with a FID detector with a methanizer and N_2O was measured with an ECD detector on a SRI model 8610C gas chromatograph (Torrance, CA, USA) within one week of sample collection.

In the fall, winter, and spring after chambers were uncapped, we collected a soil core (5.7-cm diameter, 8.5-cm depth) inside the chamber. In the summer, the soil collected for the Mason jars was used for further analysis in the laboratory. In all seasons, an adjacent core was also taken, placed in a Ziploc bag, buried back in its hole and left in the ground for two weeks in order to measure net nitrogen mineralization and net nitrification (Hart et al. 1994). Soils transferred back to the laboratory were stored in a dark incubator at the average *in situ* soil temperature (14.4°C in fall, 8.4°C in winter, 11.3°C in spring, and 17.5°C in summer). The day following gas collection, roots were separated by hand from the soil cores, dried at 60°C for 48 hrs, and weighed to estimate seasonal belowground biomass. On the same day, we extracted sub-samples of soil from each core for $NO_2^- + NO_3^-$ and NH_4^+ using 2 M KCl (Maynard and Kalra 1993) and PO_4^{3-} using 0.5 M $NaHCO_3$ (Kuo 1996). The KCl and $NaHCO_3$ extracts were filtered through Whatman No. 5 and Whatman No. 1 acid-washed filter paper, respectively, and frozen until analysis. To determine net nitrogen mineralization and net nitrification, the soils from the buried bags were extracted for $NO_2^- + NO_3^-$ and NH_4^+ when removed from the ground two weeks later. Net nitrification was calculated as the difference in $NO_2^- + NO_3^-$ and net nitrogen mineralization was calculated as the difference in $NO_2^- + NO_3^-$ and NH_4^+ over the two week incubation. NH_4^+, $NO_2^- + NO_3^-$, and PO_4^{3-} were measured with an Astoria II autoanalyzer (Astoria Pacific International, Clackamas, OR, USA) using the phenate (Solorzano 1969), cadmium reduction (Wood et al. 1967), and ascorbic acid methods (Murphy and Riley 1962), respectively.

We used the chloroform-fumigation method to determine microbial biomass (Voroney and Winter 1993, Horwath and Paul 1994) on the soils collected from inside

the chambers. The day after collection, sub-samples of soil were extracted with K_2SO_4 to determine initial total carbon and nitrogen. To determine initial phosphorus, we used a sub-sample of the $NaHCO_3$ extracts. We then placed sub-samples of soil in 50-mL centrifuge tubes, added chloroform to lyse microbial cells, and capped tubes for three days. After fumigation, we again extracted soil with K_2SO_4 and $NaHCO_3$ and froze extracts until analysis. To determine total carbon, we used the persulfate digestion method (Wetzel and Likens 2000) on a sub-sample of the K_2SO_4 extracts and measured the CO_2 produced on a LiCOR 7000 infrared gas analyzer (Lincoln, NE, USA) set up to measure discrete injections of CO_2. To determine total nitrogen, a sub-sample of the K_2SO_4 extracts were digested using potassium persulfate (Ameel et al. 1993) and NO_2^- + NO_3^- was measured on the Astoria II autoanalyzer. We determined PO_4^{3-} on the $NaHCO_3$ extracts as above. We calculated the final microbial biomass as the difference between final and initial extracts for C, N, and P, with no extraction efficiency correction factor.

We measured pH using a 1:1 soil-deionized water slurry by weight. Bulk density was determined by weighing the entire cores after collection and correcting for percent moisture by drying a sub-sample at 60°C for 48 hours. We determined soil texture once in the fall of 2005 on dried soils sieved to less than 2-mm diameter. We used the hydrometer method (Gee and Bauder 1986) to calculate percent clay. Percent sand was determined by weight using a 53-μm sieve and percent silt was calculated by difference. We measured total carbon and nitrogen once on dried, ground soils collected in the summer 2006 using a Costech Analytical Technologies 4010 elemental combustion analyzer (Valencia, CA, USA).

Statistical Analyses

To determine the effect of site preparation on the plant communities, data from the three 1-m by 1-m subplots were averaged, with the 15-m by 15-m plot used as the replicate unit for statistical tests (i.e., n=5). Percent cover, species richness, and Simpson's index of diversity (1-D), which considers both species richness and the relative abundance of each species, was calculated for each plot, and repeated-measure ANOVAs were run on the data using SPSS 11.0 for Windows. The between-subject factor was treatment and the within-subject factor was year. Greenhouse-Geiser values are reported to correct for violations of sphericity, and appropriate transformations were used when necessary to normalize the distribution of the residuals. As data from the reference sites and farm field were only available for two of the three years, these treatments could not be included in the repeated-measures analyses. However, when exploring the significant interaction between treatment and year, one-way ANOVAs were run within a year and the reference and farm field data were included in these analyses as appropriate. Tukey's pairwise comparisons were used to explore differences among treatments within a year. Linear least squares regression was used to examine the relationship between native and exotic percent cover and Simpson's index of diversity.

The productivity data were also averaged for each of the 15 by 15-m plots and one-way ANOVA were conducted with treatment as the fixed main effect. Total aboveground NPP, belowground NPP, and grass NPP were natural log transformed and forb NPP was square root transformed to normalize the distribution of the residuals. Belowground NPP did not include the farm field or reference sites in the analysis as in-

growth root cores were not buried in these sites. Tukey's pairwise comparisons were used to explore significant differences among treatments.

We compared plant community structure in the experimental treatments, farm field, and reference sites over the three years using the nonparametric ordination technique non-metric multidimensional scaling (NMS) (McCune and Grace 2002). Community structure was described by creating a matrix of the cover of each species in each plot. Species that were present, but not hit by a pin were assigned a cover of 0.5%. For the NMS analysis, we used the relative Sorensen distance, with Monte Carlo tests (1000 randomized runs), to test for statistical significance. We further tested for community differences among treatments with the multi-response permutation procedure (MRPP) using relative Sorensen distance (McCune and Grace 2002). In addition to a p-value, this nonparametric test gives the chance-correlated within-group agreement, A, an estimate of the effect size. Finally, we performed an indicator species analysis to help describe the axes in our NMS ordinations. Significant indicator species, determined using Monte Carlo tests (1000 randomized runs), are reported with the associated NMS axes loadings for the ordination. To verify that the reference sites and farm field were not driving the significant relationships seen in the ordination and associated tests, we repeated the NMS, MRPP, and indicator species analysis with only the experimental treatments. NMS, MRPP, and indicator species analyses were performed with PC-ORD 4.34 for Windows.

Similar statistical methods were used for the soil response variables. The two 1-m by 1-m subplots were averaged and used as the replicate unit in the experimental treatments and farm field (soil data were not collected in the reference sites). We

performed one-way ANOVAs and used Tukey's pairwise comparisons to examine the effect of treatment on bulk density, total carbon, total nitrogen, and soil texture (% clay, % silt, % sand). We used repeated-measures ANOVAs to determine the effect of treatment and season on nutrient concentrations (NH_4^+, $NO_2^- + NO_3^-$, and PO_4^{3-}), net nitrogen mineralization, net nitrification, microbial biomass (carbon, nitrogen, and phosphorus), soil respiration, % moisture, pH, and belowground biomass. To explore the significant interactions between season and treatment, one-way ANOVAs were conducted within a season with treatment as a fixed factor. For all ANOVAs, appropriate transformations were made to normalize the distribution of the data, and Greenhouse-Geiser values are reported for repeated-measures ANOVAs to correct for violations of sphericity.

Results

The first summer herbicide application had no effect on plant community structure (diversity, richness, cover; $p>0.35$) or measured soil response variables ($p>0.3$). This treatment was ineffective because it was applied after a long period of drought when plants were not actively growing. For ease of interpretation, we have therefore lumped the summer herbicide application with its like counterpart (e.g., till/summer herbicide and till only were combined), thus reducing the total number of treatments from ten to seven (Table 2.1). One treatment had only a summer herbicide application (i.e., it was not applied in combination with any other treatment). For this reason, we subsequently refer to this treatment as 'control: summer herbicide'.

Plant Community Responses

Site preparation treatments created large differences in plant community structure and productivity. However, for the variables measured interannually (species diversity, richness, and cover), the effect of site preparation treatments generally depended upon year (Table 2.2).

Table 2.2. P-values for one-way and repeated-measures ANOVAs for the effect of treatment and year (repeated-measures only) on plant response variables. Values in bold are significant at an alpha <0.05. Aboveground NPP, grass NPP, forb NPP, and thatch include farm field and reference sites. Repeated-measures response variables and belowground NPP include experimental treatment plots only.

One-way ANOVA	**Treatment**		
Total Aboveground NPP	**<0.001**		
Grass NPP	**<0.001**		
Forb NPP	**<0.001**		
Belowground NPP	0.34		
Thatch	**<0.001**		
	Between		**Within**
Repeated-measures ANOVA	**Treatment**	**Year**	**Year*Treatment**
Total Cover	**<0.001**	**<0.001**	**0.003**
Native Cover	**<0.001**	**<0.001**	**<0.001**
Exotic Cover	**<0.001**	**<0.001**	**<0.001**
Species Richness	**<0.001**	**<0.001**	**<0.001**
Native Richness	**<0.001**	**<0.001**	0.956
Exotic Richness	**<0.001**	**<0.001**	**<0.001**
Simpson's Diversity	**<0.001**	**<0.001**	**<0.001**
Native Simpson's Diversity	**<0.001**	**<0.001**	**<0.001**
Exotic Simpson's Diversity	**0.045**	**<0.001**	0.261

In 2005, total plant cover was higher in the till/solarization treatment than in all other experimental treatments except the till-only treatment (data not shown). The till/solarization treatment also had higher native cover than all other treatments in 2005 (Fig. 2.1a). However, in 2006 native cover was lower in the control and till-only

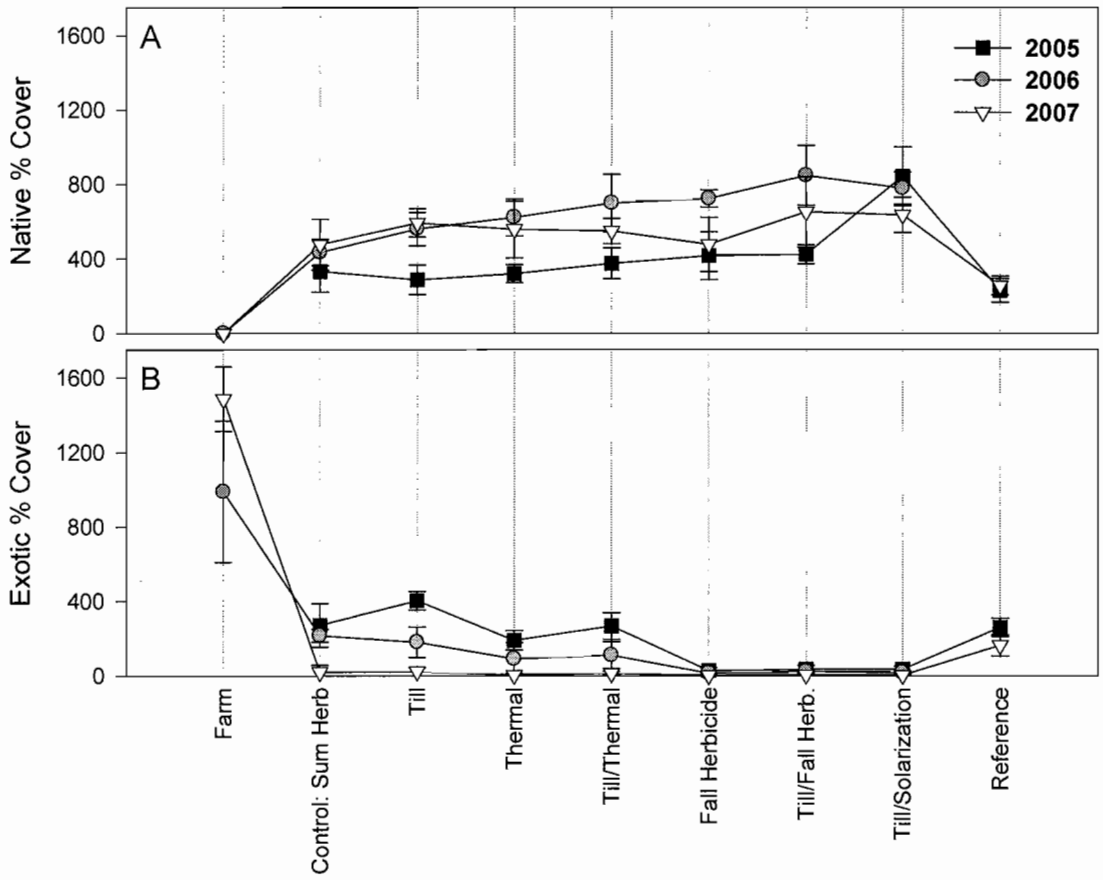


Figure 2.1. Mean native (A) and exotic (B) % cover for experimental treatments, farm field, and reference sites in 2005, 2006, and 2007. Error bars represent 95% confidence intervals. Treatment by year interactions were significant at a $p<0.001$.

treatments and similar in the rest of the experimental treatments. In 2007, we observed no differences among experimental treatments in native cover, but all had significantly higher native cover than the reference sites and farm field. Exotic cover was lower in the till/solarization, fall herbicide, and the till/fall herbicide treatments than in all other experimental treatments in 2005 and 2006, but by 2007 experimental treatment effects were no longer evident (Fig. 2.1b). Interestingly, by 2007, the experimental treatments had substantially lower (15-fold) exotic cover than the reference sites. Not surprisingly,

the farm field had the greatest exotic and total cover in all years measured as it was an almost monotypic field of fertilized *L. multiflorum*.

Overall, species richness was highest in the reference sites and lowest in the farm field (Fig. 2.2a). In 2005 and 2006, the till/solarization treatment had lower total species richness than all other experimental treatments. However, over time richness declined, and by 2007 no differences were detected among experimental treatments. Native species richness varied less among experimental treatments, but like total richness it declined over time in the experimental treatments (Fig. 2.2b). In 2005, the experimental treatments were not significantly different from the reference sites, but by 2007 all experimental treatments had lower native species richness than the reference sites. As there were no native species found in the farm field, native richness was lower in the farm field than in all other treatments. In 2005, exotic richness was lower in the till/solarization treatment than all other experimental treatments, but over time richness declined in all experimental plots and this difference was no longer detectable by 2007 (Fig. 2.2c). The reference site plots had twice as many exotic species as the experimental plots in 2005, and by 2007, declines in the experimental plots left the reference plots with seven times more exotic species.

In 2005, total Simpson's diversity, unlike richness, was not statistically lower in the experimental treatments than the reference sites except in the till-only treatment (Fig. 2.2d). However, by 2007 all treatments except the till and the till/fall herbicide had lower diversity than the reference sites. In 2007, the till/solarization treatment had the lowest diversity among experimental treatments (only marginally lower than the fall herbicide treatment: $p<0.07$), and the farm field had the lowest diversity overall. Native diversity

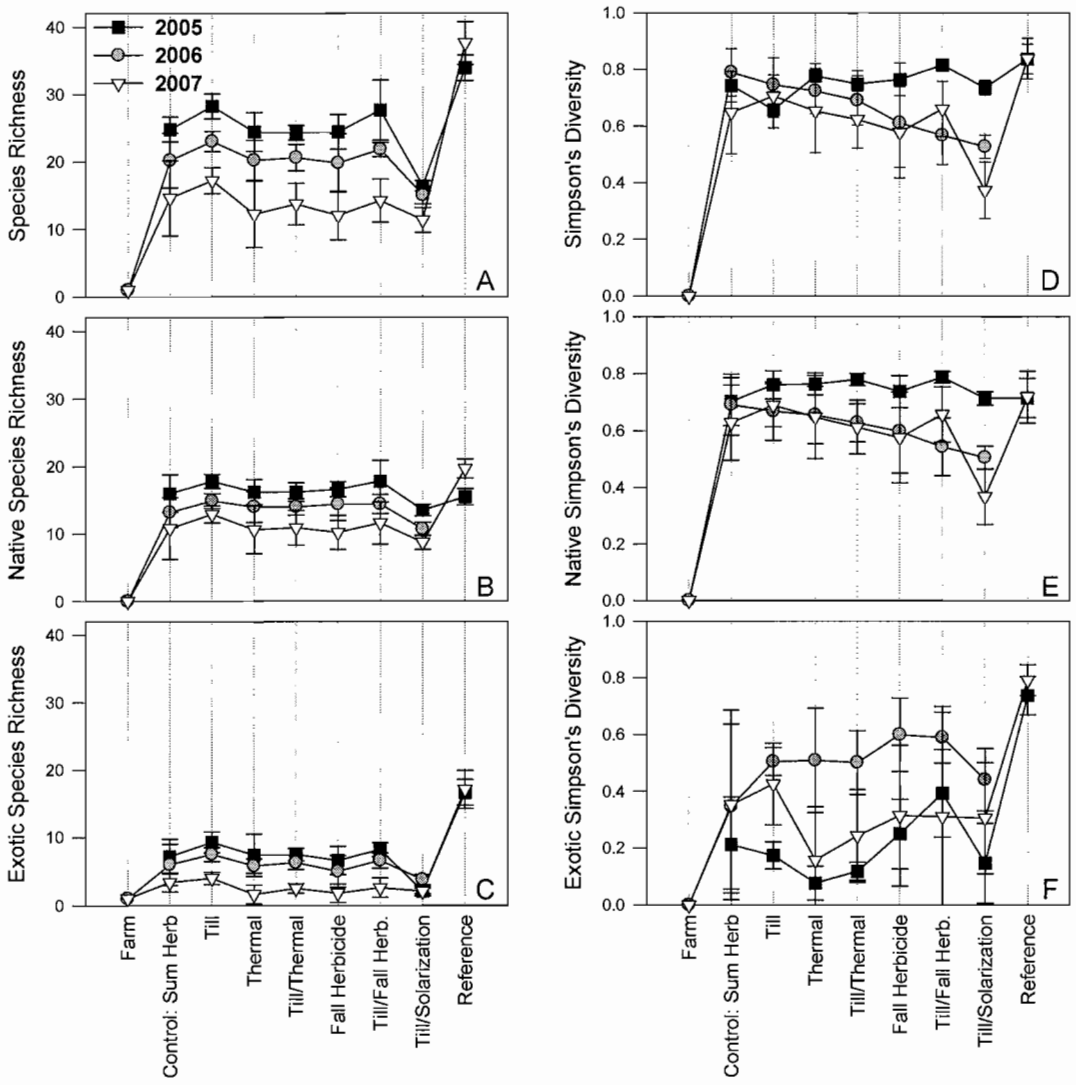


Figure 2.2. Mean overall species richness (A), native species richness (B), exotic species richness (C), overall Simpson's diversity (D), native Simpson's diversity (E), and exotic Simpson's diversity (F) per m^2 for experimental treatments, farm field, and reference sites in 2005, 2006, and 2007. Error bars represent 95% confidence intervals. Treatment by year interaction is significant at $p<0.001$ for all response variables except native species richness and exotic Simpson's diversity.
Note: High values for Simpson's index of diversity indicate high diversity.

followed a similar trend as total diversity (Fig. 2.2e). In 2005, no differences in native diversity in the experimental treatments or reference sites were detected. In 2006, the till/solarization treatment had significantly lower native diversity than the control, and by 2007, the till/solarization treatment was significantly lower than all other treatments (only marginally lower than the fall herbicide treatment: $p<0.08$). Treatment effects on exotic diversity were not dependent upon year (Table 2.2). Experimental treatments were not different from one another; however, the treatments had lower exotic diversity than the reference sites and higher exotic diversity than the farm field (Fig. 2.2f). Over time, unlike exotic richness, exotic diversity increased from 2005 to 2006 but decreased again in 2007. This suggests that though fewer exotic species were found within the plots over time (see Fig. 2.2c), the exotic species remaining became more evenly distributed in 2006 and 2007 when compared to 2005.

Total aboveground NPP was more than three times higher in the farm field than in the experimental treatments and reference sites (Fig. 2.3a). Although the experimental treatments were not significantly different from one another in total aboveground NPP, the till/solarization treatment had higher graminoid NPP than the control or till-only treatments and lower forb NPP than all experimental treatments except the fall herbicide and till/fall herbicide treatments. The farm field also had higher aboveground thatch than the experimental treatments and reference sites (Fig. 2.3b). Belowground NPP did not differ among experimental treatments (Table 2.2), and it was not measured in the farm field or reference sites.

A linear regression was conducted to examine the relationship between cover and diversity as it appeared that plots with high native cover tended to have lower diversity.

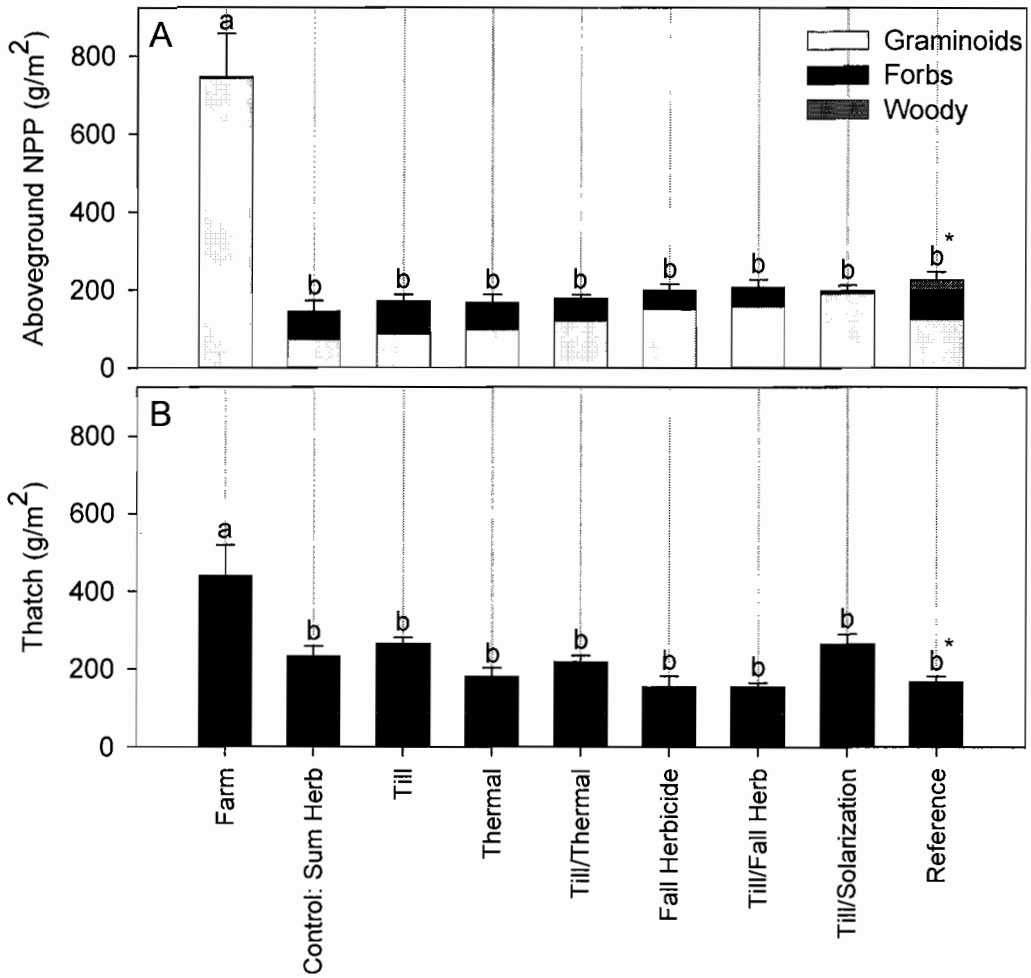


Figure 2.3. Aboveground net primary productivity (A) and thatch (B) in experimental treatments, farm field, and reference sites. Aboveground NPP is further partitioned into graminoids, forbs, and woody biomass. Error bars represent one standard error from the mean and lower case letter differences indicate significant effects ($p<0.05$) among treatments.
Note: Biomass data in the experimental treatments and farm field were collected June of 2006 and biomass data for the references sites were collected in June of 2005.

In 2005, there was not a significant relationship between native cover or exotic cover and diversity (Fig. 2.4a,b). However, a negative association was observed between native cover and diversity in 2006 ($r^2=0.59$, $p<0.001$) and to a lesser extent in 2007 ($r^2=0.24$, $p<0.001$). Plots with high diversity had low native cover and vice versa. This trade-off

appeared to be driven primarily by two dominant native perennial grasses, *Agrostis exarata* and *Deschampsia cespitosa*. When regressing cover of these two species vs. diversity, an even stronger relationship emerged (2006 r^2=0.78, 2007 r^2=0.65; Supplemental Fig. 2.1). Also, the slope of this relationship became more negative over the three years, suggesting an increasing inhibitory effect of the cover of these two native grasses on diversity over time. The opposite pattern was observed with exotic cover and diversity. In 2006 (r^2=0.65, p<0.001) and 2007 (r^2=0.52, p<0.001), plots with higher exotic cover had higher overall diversity (Fig. 2.4b).

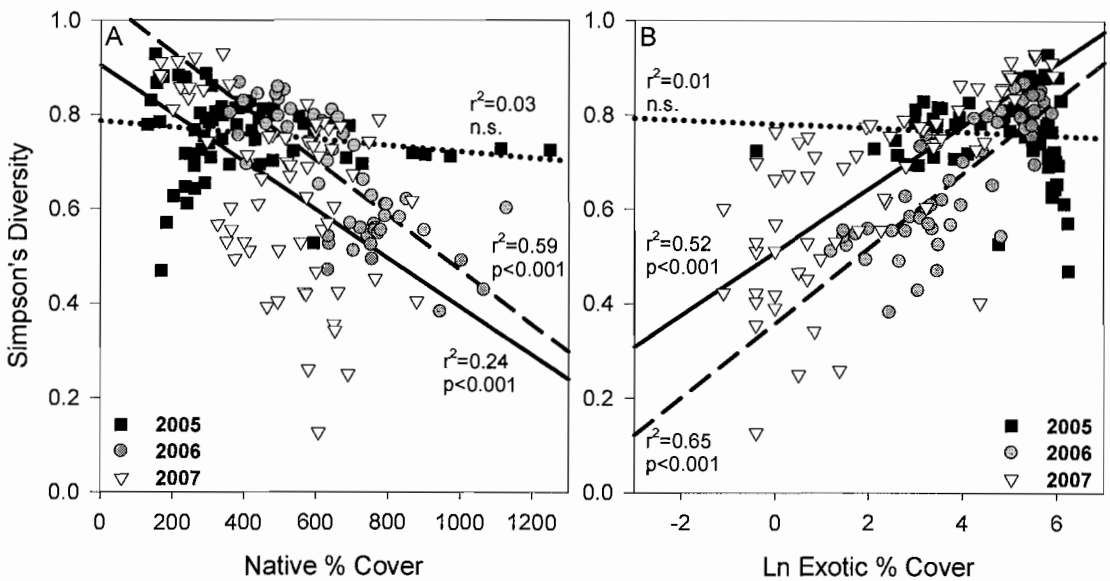


Figure 2.4. Simpson's diversity vs. native % cover (A) and vs. ln exotic % cover (B) in the experimental treatments and reference sites. Regression lines are drawn for 2005 (dotted), 2006 (dashed), and 2007 (solid), and r^2 and p-values are reported.
Note: Farm field was excluded from regression because plots have a Simpson's diversity of zero. High values of Simpson's index of diversity indicate high levels of diversity.

To explore the relationship between plant community structure and treatments, we used NMS to reduce our entire plant data set (i.e., individual species abundances) to two axes (Fig. 2.5). Axis 1 and axis 2 explained 62% and 21% of the variation in plant community structure, respectively (for species loadings on axes see Supplemental Table 2.1), and treatments had significantly different plant community structures ($A=0.52$, $p<0.0001$). From the ordination, it is clear that experimental treatments were more similar to one another in plant community structure than to either the reference sites or farm field. Initially, in 2005, differences in experimental treatments were apparent with the till-only and till/solarization treatments being the most different from one another. However, after three years, the experimental treatment effects were dampened (i.e., points became closer together). Over time the experimental treatments also became more similar to the reference sites, that is, along axis 1, points progressed further right each year, primarily due to a reduction in dominance of seeded annual forbs and *L. multiflorum* in experimental treatments (Supplemental Table 2.1). Additionally, over time plots became increasingly dominated by the native perennial bunchgrasses, *Agrostis exarata* and *Deschampsia cespitosa* (i.e., points progressed further up on Axis 2). Finally, the variance in the experimental treatments was much smaller than the variance in the reference sites, suggesting that plants were more patchily distributed in the reference sites than within the experimental plots.

To understand how plant communities were changing within the experimental treatments, NMS and MRPP were run without the reference and farm field data (Fig. 2.6). Again significant differences were detected among the experimental treatments ($A=0.46$, $p<0.0001$); axis 1 explained 66% of the variation and axis 2 explained 14% of

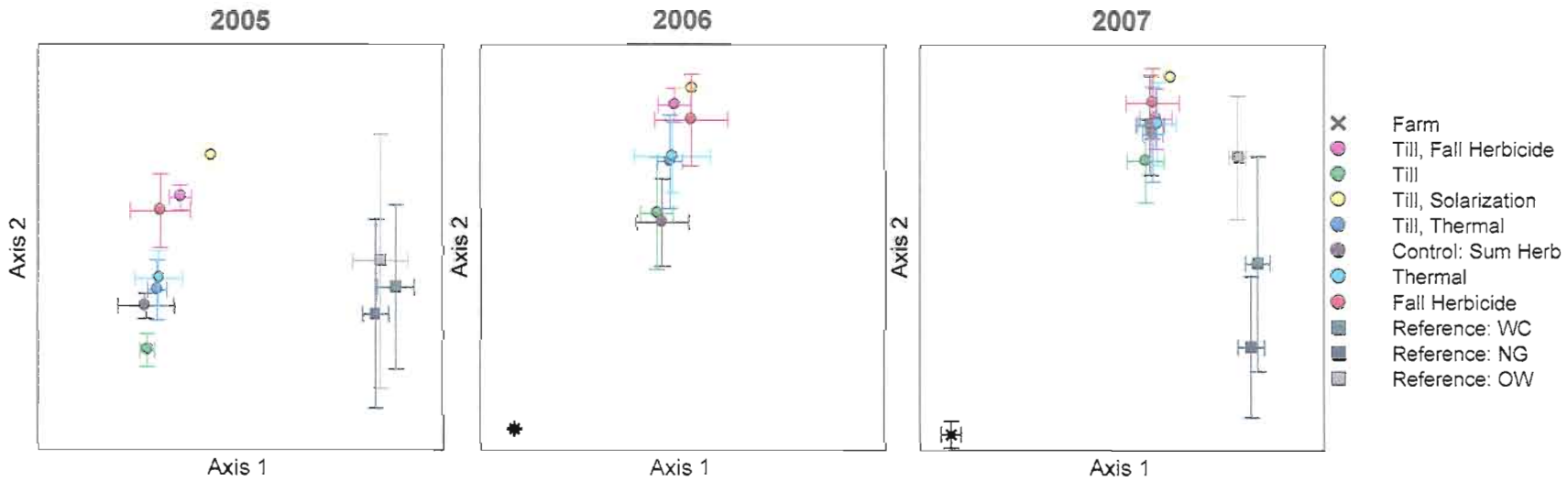


Figure 2.5. Nonmetric multidimensional scaling (NMS) of plant community structure in the experimental treatments, farm field, and reference sites using relative Sorensen distance (A=0.52, p<0.0001). All three years of plant data were ordinated together, but are split for visual clarification (i.e., axes are equivalent for all three panels). Axis 1 explained 62% and axis 2 explained 21% of the variation in plant community structure. Although the analysis was performed on plots, the plot mean and 95% confidence intervals for each treatment are shown for graphic representation. For plant species loadings on axis 1 and 2 see Supplemental Table 2.1.
Note: Plant community structure was not measured in the farm field in 2005 and reference sites were not measured in 2006.

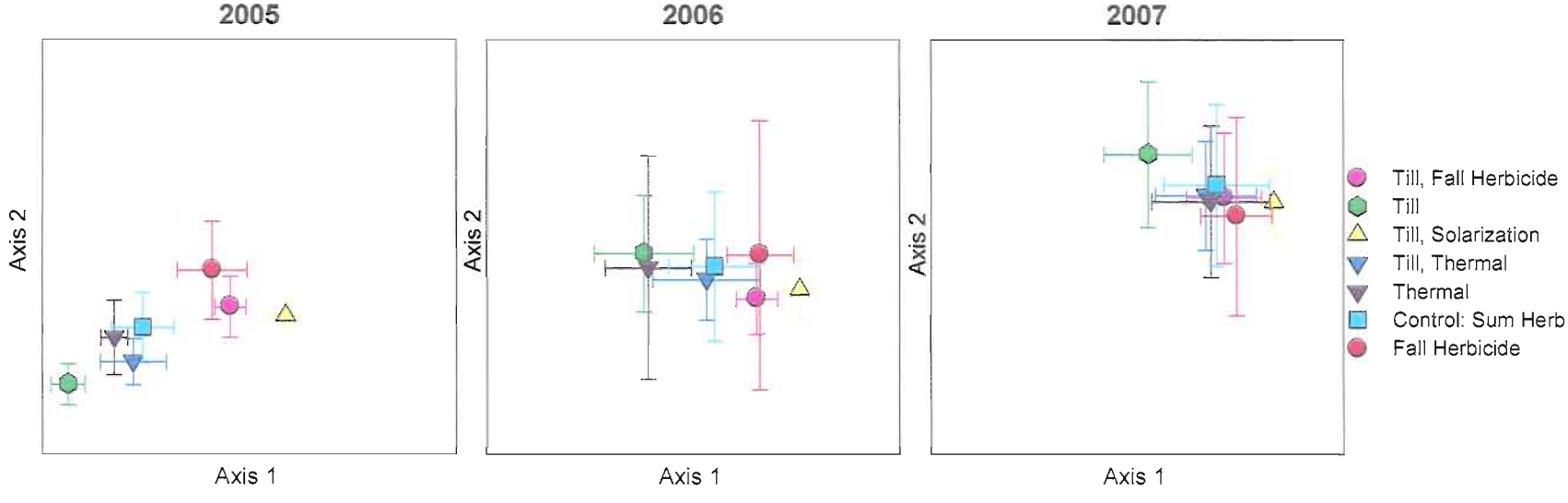


Figure 2.6. Nonmetric multidimensional scaling (NMS) of plant community structure in the experimental treatments only using relative Sorensen distance (A=0.46, $p<0.0001$). All three years of plant data were ordinated together, but are split for visual clarification (i.e., axes are equivalent for all three panels). Axis 1 explained 66% and axis 2 explained 14% of the variation in plant community structure. Although the analysis was performed on plots, the plot mean and 95% confidence intervals for each treatment are shown for graphic representation. For plant species loadings on axis 1 and 2 see Table 2.3.

the variation. As seen in the larger ordination, treatments became more similar in plant community structure over time; however, the relative ordering of treatments remained similar. When examining the axis loadings of significant indicator species (Table 2.3), the till/solarization treatment had plant communities with a higher proportion of perennial graminoids and a lower abundance of annual graminoids, whereas the till, thermal, till/thermal, and control treatments had a higher abundance of forbs and the annual exotic grass, *Lolium multiflorum*. It is also interesting to note that over time, many native annual species considered to be early successional species by local wetland practitioners (e.g., *Plagiobothrys figuratus*, *Juncus bufonius*, and *Gnaphalium palustre*) decreased in abundance and perennial grasses began to dominate plant communities. *L. multiflorum*, the agricultural species originally in the field, also dramatically decreased in abundance over time in all experimental treatments.

Belowground Responses

Overall, many of the belowground responses, including bulk density, total carbon and nitrogen, carbon/nitrogen ratio, soil texture, phosphate availability, microbial biomass phosphorus, and gravimetric percent moisture, showed no effect of treatment (Table 2.4). Additionally, concentrations of nitrous oxide and methane gas never increased above background concentrations over the course of the two-hour incubations in any season, and as a result rates were not statistically different than zero. Not surprisingly, season significantly affected all response variables measured over time (with one exception, microbial biomass phosphorus). However, the purpose of this study

was not to examine these seasonal dynamics, but instead, to understand how the treatment effects varied across seasons.

Table 2.3. Species axis loadings for NMS ordination of experimental treatment plots (see Fig. 6). Only significant ($p<0.05$) indicator species are reported. Native (N) and exotic (E) origin, life history (A: annual, B: biennial, and P: perennial), and functional group (G: graminoid, F: forb, and W: woody) are given for each species.

Species	Axis 1 Loading	Axis 2 Loading	Species Origin	Life History	Funct. Group
Juncus bufonius	-1.09	-0.55	N	A	G
Lolium multiflorum	-0.96	-0.41	E	A	G
Montia linearis	-0.80	-0.48	N	A	F
Rubus armeniacus	-0.79	-0.29	E	P	W
Cirsium vulgare	-0.76	0.10	E	B	F
Cicendia quadrangularis	-0.73	-0.43	N	A	F
Gnaphalium palustre	-0.71	-0.30	N	A	F
Sonchus asper	-0.71	-0.13	E	A	F
Camassia quamash var. maxima	-0.67	-0.22	N	P	F
Hypochaeris radicata	-0.51	0.14	E	P	F
Epilobium densiflorum	-0.47	-0.20	N	A	F
Briza minor	-0.46	0.05	E	A	G
Plagiobothrys figuratus ssp. figuratus	-0.39	0.32	N	A	F
Veronica peregrina var. xalapensis	-0.36	-0.35	N	A	F
Cerastium glomeratum	-0.32	-0.07	E	A	F
Parentucellia viscosa	-0.29	0.11	E	A	F
Centaurium erythraea	-0.24	-0.20	E	A/B	F
Madia glomerata	-0.17	0.50	N	A	F
Juncus tenuis	0.29	0.58	N	P	G
Agrostis exarata	0.33	-0.07	N	P	G
Deschampsia cespitosa	0.52	0.14	N	P	G
Schedonorus arundinaceus	0.55	0.05	E	P	G

Treatment effects on ammonium and nitrate availability depended upon season (Table 2.4). In the fall, both ammonium and nitrate levels were higher in the farm than in the experimental treatment plots (Fig. 2.7). In addition, nitrate availability was lower in the till/ solarization treatment than in all other experimental treatments except the till/fall herbicide treatment (only marginally lower than the control and thermal treatments, $p<0.08$). In the winter, nitrate availability was higher in the thermal treatment than in the

control, till, till/herbicide, till/solarization, and farm field. No differences were detected among nitrate levels in the spring, but in the summer the till/solarization treatment had lower nitrate levels than all other treatments and the farm field had higher nitrate availability than all other treatments. Ammonium levels did not vary significantly among treatments in the winter, spring, or summer.

Table 2.4. P-values for one-way and repeated-measures ANOVAs for the effect of treatment and season (repeated-measures only) on soil response variables. Data were collected in the fall 2005, winter 2006, spring 2006, and summer 2006 in all experimental treatments and farm field. Values in bold are significant at an alpha <0.05.
Note: NA=Not applicable because rates of nitrous oxide and methane production never significantly differed from zero.

One-way ANOVA	**Treatment**		
Bulk Density	0.39		
Total Carbon	0.24		
Total Nitrogen	0.22		
Carbon/Nitrogen Ratio	0.25		
Percent Clay	0.99		
Percent Sand	0.98		
Percent Silt	0.89		
Repeated-measures ANOVA	**Between Treatment**	**Season**	**Within Season*Treatment**
Ammonium	0.611	**<0.001**	**<0.001**
Nitrate	**<0.001**	**<0.001**	**<0.001**
Phosphate	0.70	**<0.001**	0.34
Net Nitrogen Mineralization	**0.006**	**<0.001**	**0.05**
Net Nitrification	**<0.001**	**<0.001**	**<0.001**
Microbial Carbon	**0.005**	**<0.001**	0.32
Microbial Nitrogen	**<0.001**	**<0.001**	0.37
Microbial Phosphorus	0.13	0.59	0.49
Soil Respiration	**<0.001**	**<0.001**	**0.01**
Gravimetric Percent Moisture	0.26	**<0.001**	0.34
pH	**0.005**	**<0.001**	0.33
Belowground biomass	**<0.001**	**<0.001**	**<0.001**
Nitrous oxide flux	NA	NA	NA
Methane flux	NA	NA	NA

The treatment effects for net nitrogen mineralization, net nitrification, and soil respiration also depended upon season (Table 2.4 and Supplemental Fig. 2.2). In the fall, the farm had higher net mineralization rates than all treatments except the till/solarization (marginally higher than the till/herbicide treatment, $p<0.09$). Net nitrogen mineralization rates did not significantly vary among treatments in the winter, spring, or summer. Net nitrification rates were significantly higher in the farm field than all treatments in the fall and summer. In the winter, the thermal treatment had significantly more nitrate immobilization than all treatments. In the spring, no significant differences were detected. Soil respiration did not differ among treatments in the fall, winter, or summer, but in the spring the farm field had higher CO_2 respiration rates than all other treatments.

Microbial carbon and nitrogen biomass as well as pH differed significantly among treatments, and these effects were not dependent upon season (Table 2.4 and Supplemental Fig. 2.3). The till/solarization treatment had significantly lower microbial carbon than the till-only, fall herbicide, thermal, and farm field treatments (marginally lower in the till/fall herbicide and control treatments, $p<0.10$). Similarly, microbial nitrogen biomass was lower in the till/solarization treatment than in the till-only, fall herbicide, till/fall herbicide, thermal, till/thermal, and farm field treatments. Finally, the farm field was more acidic than the till/herbicide, till/solarization, and till/thermal treatments.

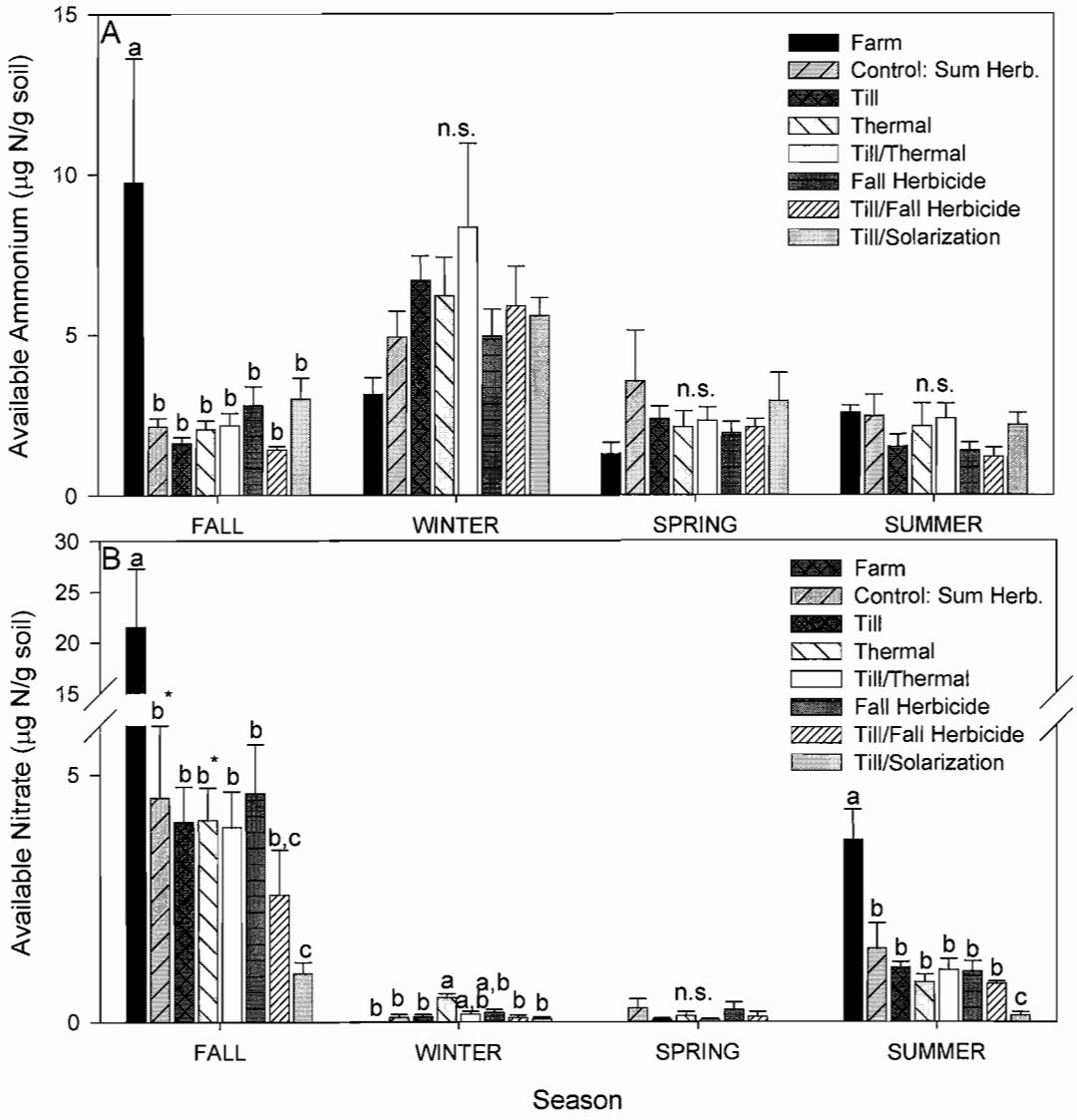


Figure 2.7. Available ammonium (A) and nitrate (B) in the fall 2005, winter 2006, spring 2006, and summer 2006 for the experimental treatments and farm field. Error bars represent one standard error from the mean and lower case letter differences indicate significant ($p<0.05$, $^{*}p<0.10$) effects of treatment within a season.

Discussion

Site preparation techniques, particularly solarization and the fall herbicide application, had large effects on plant communities. Diversity, species richness, plant cover, and productivity varied among treatment type within this wetland, but these effects dampened over time as plant communities became more similar. In particular, the communities became increasingly dominated by perennial native bunchgrasses. After three years, the experimental treatments remained distinctly different from the three reference sites, although there was a trend toward a convergence of plant community structure (Fig. 2.5). Surprisingly, we found few differences among treatments in the many belowground responses measured seasonally. However, soils showed a quick recovery from their former agricultural state. Below, we detail key differences in plant community structure and soil functional, chemical, and physical attributes among site preparation techniques and address our five original hypotheses.

Comparison of Site Preparation Techniques

Our first hypothesis that site preparation treatments that reduced the seed bank (primarily *L. multiflorum*) would result in a lower cover of exotic species and higher native diversity than treatments that solely targeted the existing vegetation was supported initially, although over time competitive dynamics among species appeared to become paramount. Three of our treatments, solarization, fall herbicide application, and thermal weed control, were designed to target the seed bank, although a preliminary seed bank study indicated that the thermal treatment was not effective at reducing the seed bank (results not shown). Initially the solarization and the fall herbicide application were the

most effective treatments for decreasing exotic cover (Fig. 2.1b). Similarly in a California annual grassland, solarization decreased cover and seedling density of the annual exotic grass, *Bromus diandrus* (Moyes et al. 2005). After three years, however, all of the treatments had low exotic cover. This is likely because *L. multiflorum* was not a dominant competitor over multiple growing seasons and no other dominant exotic species significantly colonized the plots during the course of the experiment. *L. multiflorum* has been shown to be competitively superior to native perennial grasses at the seedling stage, including those species planted in this experiment (Pfeifer-Meister et al. 2008), but our results suggest that once established, native perennials out-compete this annual grass. In a California grassland, Corbin and D'Antonio (2004) demonstrated that although competitive interactions initially favored exotic annual grasses, over time the native perennial grasses were able to significantly reduce the productivity of the exotic grasses. Similarly, Seabloom et al. (2003) demonstrated that if native perennial grasses were not recruitment limited, they were able to decrease the biomass and seed production of annual exotic grasses. If the site chosen for our experiment was initially dominated by a more aggressive exotic competitor, the outcome would likely have been different, perhaps with the solarization and fall herbicide treatments being the only site preparation techniques able to maintain low exotic cover as they more effectively eliminated the initial seed bank.

The solarization treatment also gave the highest initial native cover (Fig. 2.1a), but had the lowest native and overall species richness and diversity (Fig. 2.2). Over the dry Pacific Northwest summer, the plastic that covered the solarization plots trapped soil moisture while all other treatment plots dried out. After the plastic was removed in the

fall and plots were seeded, native perennial grasses germinated earliest in the solarization treatment (personal observation). As a result, in 2005 the proportion of the total native cover comprised of native perennial grasses, particularly *Deschampsia cespitosa* and *Agrostis exarata*, was three times greater in the solarization plots (62%) than all other experimental treatments (24%, $p<0.0001$). Additionally, a greater proportion of productivity in the solarization plots was from grass biomass and less from forb biomass (Fig. 2.3a). Thus, there was a trade-off between high abundance of competitive native bunchgrasses and species diversity (including native species diversity) in this treatment. This trade-off is apparently not only due to the specific circumstances of our experiment, as we have observed a similar negative correlation between native bunchgrass cover and species diversity in a number of other restored wetlands that used a variety of initial preparation techniques in local restoration sites (Pfeifer-Meister et al., unpublished data). Based upon the results of our research, local wetland practitioners have attempted to mitigate this trade-off by decreasing the seeding density of native bunchgrasses and planting forb species 1-2 years earlier than grasses to allow time for establishment. It would be interesting to examine to what extent similar dynamics occur in wetlands in other regions with a different suite of native species and climate.

As mentioned above, the fall herbicide application was quite effective at decreasing exotic cover. However, our first July herbicide application had no effect on plant community structure. Other studies have shown that multiple applications of herbicide can be a more effective tool for reducing exotic species than a single application (Morgan 1997). If our first application had been applied earlier in the growing season, before this seasonal wet prairie dried out and *L. multiflorum* senesced,

the double herbicide application may have had a greater effect. Our second fall application was more successful because it was applied after the *L. multiflorum* seed bank had germinated. This highlights the importance of timing in the use of herbicides. In a Washington seasonal wetland, applying glyphosate later in the season was more effective than early-season applications for reducing *Phalaris arundinacea* abundance (Kilbride and Paveglio 1999), and Adams and Galatowitsch (2006) demonstrated that the timing of herbicide application can double the effectiveness of eradicating an exotic grass.

Neither the tilling nor the thermal treatments varied significantly from the control treatment in terms of cover (Fig. 2.1), richness and diversity (Fig. 2.2), productivity (Fig. 2.3), or overall community structure (Figs. 2.5, 2.6). These treatments added no benefit for establishing native plant communities over initial mowing. Tilling brings up the seed bed, which conceivably could promote the establishment of exotic species, although in the public forum to choose site preparation techniques, several local restoration practitioners suggested that repeated tilling over several years might exhaust the seed bank. Given the timing constraints of our funding, we were not able to explore the effects of repeated tilling. Despite the fact that the thermal treatment was advertised as being able to significantly reduce the seed bank, in our study it appeared to have little effect in this regard. Instead, the thermal treatment acted more like a surface fire and was effective at killing small seedlings. To be successful at reducing exotic species, this technique would need to be applied at the time of seed germination.

Our hypothesis that treatments involving more physical disturbance to the soil would have detrimental effects on soil functioning was not supported by our findings. Tilling, the treatment with the greatest physical disturbance effect, had no effect on

belowground function or soil chemical and physical properties. However, it is important to note that over the past 25 years this field was actively tilled, and other studies have shown that tilling can reduce soil microbial biomass carbon, total soil carbon, and soil respiration when compared with soils not previously cultivated (Steenwerth et al. 2002, Potthoff et al. 2005).

We found only modest support for our hypothesis that differences in plant community structure and productivity due to the treatments would cause significant differences in soil properties, as we observed few experimental treatment effects on belowground responses after the first year. Part of this may have been because a year was not long enough for observed changes in plant community composition to affect belowground functional responses. The solarization treatment decreased microbial biomass carbon and nitrogen across all seasons and nitrate availability in the fall and summer (Fig. 2.7b, Supplemental Fig. 2.3). Other studies have shown a decrease in various microbial groups such as bacterivores, fungivores, nematodes, and arbuscular mycorrhizal fungi following solarization (Pinkerton et al. 2000, Schreiner et al. 2001, Wang et al. 2006). In some cases, these results have been attributed to the indirect effects of changes in plant communities rather than the direct effect of solarization (Schreiner et al. 2001). It is unclear in our experiment whether the observed effects were direct or indirect. The thermal treatment resulted in a slight increase in nitrate levels and as a result, an increase in the net immobilization of nitrate in the winter (Fig. 2.7b, Supplemental Fig. 2.2b).

Our hypothesis that restored wetlands would have lower nutrient availability than the adjacent agricultural field was strongly supported. Although the experimental

treatments had minimal effects on belowground responses when compared with one another, the soils were distinctly different from the *L. multiflorum* farm field. In various seasons, the experimental treatments had lower nitrogen availability, net nitrogen mineralization, net nitrification, and soil respiration than the farm field (Fig. 2.7, Supplemental Fig. 2.2). As part of another study, nutrients were also measured in the three reference sites in the spring (Pfeifer-Meister et al., unpublished data). When compared with the experimental treatments, ammonium and nitrate availability did not significantly differ ($p>0.3$), suggesting that after restoration nutrient levels quickly returned to 'natural' levels. Given that many potential wetland restoration sites throughout the U.S. are currently in agriculture and receive fertilization, this is a promising result. However, available nitrogen concentrations returned to low, background levels in the farm field in the winter and spring, and for ammonium also in the summer, suggesting a prudent nutrient management regime (Fig. 2.7). The degree of long-term nutrient enhancement of the soil will depend on the specific management practices within a field, so other sites may maintain higher soil nutrient availability for a longer period post-restoration.

Contrary to our expectations, we did not find that restored wetlands had lower greenhouse gas emissions than the adjacent agricultural field. Fluxes of nitrous oxide and methane in the farm field and in the experimental plots never significantly differed from zero in this study. In a more extensive study of gas emissions and denitrification, we found that fluxes of nitrous oxide and methane and denitrification rates in these wet prairies are co-limited by available nitrogen and labile soil carbon (Pfeifer-Meister et al., unpublished data). Greenhouse gas fluxes have rarely been measured in wetland prairies

or restored wetlands, and to our knowledge, never in a U.S. wetland with such a strong Mediterranean climate (see review by Bridgham et al. 2006). Nitrous oxide emissions are often very high in agricultural fields (Denman et al. 2007), but the prudent nutrient additions appear to have minimized these emissions in our study field. Others have suggested that restored wetlands may provide a strong soil carbon sequestration sink (Euliss et al. 2006), but we have previously cautioned that the greenhouse gas emissions from restored wetlands may nullify any overall positive effects on climate forcing (Bridgham et al. 2006). Our study shows no effect of restoration on carbon sequestration or greenhouse gas emissions one-year post-restoration, but it is likely that other types of restored wetlands will have very different greenhouse gas emissions and carbon sequestration rates. Further research in a variety of wetland types is necessary on this important subject.

Ecological Lessons Learned

In addition to understanding the responses of plant communities and ecosystem functions to the various site preparation techniques, we also gained valuable insight into the underlying ecological mechanisms creating the differences we found. First, it was apparent from our results that over time plant community structure converged among treatments regardless of initial site preparation treatment (Figs. 2.5, 2.6). Additionally, the experimental treatments became more similar to the reference sites each subsequent year due to a reduction in the cover of *L. multiflorum*, a loss of early successional species (including those which were planted), and increasing dominance of perennial grasses (Figs. 2.5, 2.6, Table 2.3). However, as we hypothesized, the community structure in the

treatments remained distinctly different than the reference sites. Other studies have found that restored wetlands retain different community structure than reference wetlands even after 40 years (Kellogg 2002, Seabloom and van der Valk 2003).

To enhance native biodiversity, wetland managers often want to maintain early successional plant species in restored wetlands, but this will likely require periodic disturbance, such as fire (MacDougall and Turkington 2007). Thus, our research demonstrates that an understanding of successional dynamics is essential for effectively directing restored wetlands to a desired plant community condition.

Second, as a result of these successional dynamics, there was a decrease in overall and native plant species diversity over time in all experimental treatments (Fig. 2.2). Experimental treatment plots also never attained the overall or native plant diversity of the reference sites, despite the relatively high cover of exotic plant species in the reference sites. Rather richness and diversity continued to decline in the experimental treatments over time. Our results suggest that this is due to the trade-off seen between the cover of native dominants, particularly native bunchgrasses, and diversity (Fig. 2.4 and Supplemental Fig. 2.1). In a Canadian prairie, diversity also decreased over time following restoration, with particular vulnerability of native forb species (McLachlan and Knipsel 2005). Results from our study and others suggest that future research needs to focus on establishing and maintaining native plant diversity in wetland restorations by actively managing successional trajectories.

Conclusions

We took an ecosystem approach using a replicated experimental design to understand the effects of site preparation—including tilling, herbicide application, solarization, and thermal weed control—on wetland restoration. Overall, we found that the solarization and fall herbicide treatments were particularly effective initially at reducing the exotic plant cover, but over time plant communities converged in all experimental treatments. After three years, native perennial bunchgrasses became the dominant species across experimental treatments and many early successional forb species were lost. Additionally, no experimental treatment had similar plant community structure to reference wetlands, and all treatments had lower overall and native species diversity than reference sites. Future research needs to focus on how generalizable this trade-off between dominant native species' cover and diversity is, and whether it can be mitigated to achieve both high native species cover and diversity.

Contrary to our expectations, none of the common or emerging restoration techniques that we tested had detrimental effects on soil ecosystem function, and the experimental plots quickly moved toward reference wetland conditions. Nutrient levels, mineralization, and respiration rates decreased in the experimental treatments from that of the adjacent farm field. Site preparation may have larger effects on belowground responses when restoring a site not previously cultivated, or with more extreme preparation techniques such as topsoil removal to eliminate the exotic seed bank (Pfeifer-Meister et al., unpublished data).

Based on the convergence of all experimental treatments over time, one might question whether any type of site preparation was necessary prior to seeding on an

agricultural field that had experienced years of active weed suppression. However, the substantial initial differences among the treatments, including functional group cover, richness, and diversity, leaves open the potential that such differences could be maintained or enhanced by careful management during the first years of rapid succession. Such management is not simply an issue of controlling exotics, but also of restraining the increasing dominance of native bunchgrasses. This might be achieved in two ways. First, seed mixes could be manipulated to increase initial diversity, including forbs commonly found in reference sites, which have demonstrated the ability to persist over time, and reducing the levels of native bunchgrasses. Second, selective disturbances could be used during the first years following establishment to guide these systems closer to the richness and diversity of reference communities. Finding ways to mitigate the apparent tradeoff between high native cover and high diversity through an understanding of both site preparation and seeding protocols as part of successional management may be a critical step toward establishing wetland prairie communities with the desired characteristics.

Bridge to Chapter III

In this chapter, we examined the effectiveness of a variety of different site preparation techniques in restoring native plant diversity and ecosystem functioning. We found that over time plant communities converged and that belowground responses quickly recovered to a more 'natural' state. We also observed a significant tradeoff between native cover and diversity. In the following chapter, we explore this relationship further and examine the effects of a more dramatic site preparation technique, topsoil

removal, and solarization on plant communities and soil functioning. We were interested in determining if the relationship between native cover and diversity was generalizable to other wetland prairies. Additionally, we wanted to determine if a more dramatic site preparation technique would also result in minimal belowground responses or if there were larger effects on ecosystem functioning.

CHAPTER III

RESTORING WETLAND PRAIRIES: TRADEOFFS AMONG NATIVE PLANT COVER, DIVERSITY, AND ECOSYSTEM FUNCTIONING

A paper co-authored with Bart R. Johnson, Bitty A. Roy, Santiago Carreño, Julie L. Stewart, and Scott D. Bridgham

Introduction

Restoring wetland prairies is a critical component of wetland conservation efforts. Under Section 404 of the Clean Water Act, the destruction or degradation of wetlands should be mitigated by creating or restoring wetlands elsewhere. Furthermore, the United States federal policy of 'no-net-loss' has a goal of not only maintaining or increasing wetland area, but also no loss of overall wetland function. Despite this goal, few studies have compared the plant communities and soil systems of restored wetland prairies to those of remnant prairies. Evaluations of wetland restoration success frequently take only one or two criteria into account (e.g., high native plant cover), and many functions are ignored (Mitsch and Wilson 1996, National Research Council 2001, Zedler 2003).

Moreover, a number of different site preparation techniques are used in wetland restoration that often lead to very different outcomes in terms of plant community structure and ecosystem function (Fitzpatrick 2004). Additionally, restored or created wetlands may not have similar function or structure to those of 'natural' wetlands (National Research Council 2001, Turner et al. 2001). The net result of these concerns is while the conterminous U.S. experienced a small net increase in wetland area from 1998-2004 (Dahl 2006), the nation may still be experiencing a net loss of wetland function. In this study, we examined above- and belowground responses of restored (1-5 years old) and high quality remnant wetland prairies to understand the effects of mitigation practices on wetland function and structure.

Over the last century, approximately 50% of wetlands have been lost in the conterminous United States (Dahl 2006), with the predominant mechanism being conversion to agriculture (Frayer et al. 1983). Similarly, wetland prairies of Oregon's Willamette Valley have been listed as a critically endangered ecosystem (Noss et al. 1995), with greater than 97% loss since 1850 of this once widespread ecosystem (Hulse et al. 2002). From 1980-1990, 70% of wetland losses in the Willamette Valley were attributed to agricultural activity (Bernet et al. 1999), predominately for commercial grass-seed production. Currently, grass-seed fields comprise much of the restorable wetland area within the Willamette Valley.

Our objective was to assess the effectiveness of two restoration techniques, topsoil-removal and solarization, for restoring native plant biodiversity and ecosystem function to agricultural fields that had retained wetland hydrology. These techniques

were widely used in the southern Willamette Valley for wetland prairie restorations beginning in the 1990s. However, the outcomes have never been quantitatively analyzed.

Topsoil-removal has been employed as a means to eliminate existing vegetation and deplete the upper seed bank (which is typically dominated by exotic species), reduce nutrient levels in heavily fertilized fields, and bring deeply buried viable native species to the soil surface (Tallowin and Smith 2001, Holzel and Otte 2003, Buisson et al. 2008). However, topsoil-removal may also have deleterious effects on ecosystem function because it can increase bulk density and decrease organic matter and available nutrients, leading to lower cover and productivity of desirable plant species (Woodward 1996, Patzelt et al. 2001, Tallowin and Smith 2001).

Solarization uses plastic for several months to trap the heat from solar radiation to kill existing vegetation and the associated seed bank (Horowitz et al. 1983). This technique works best on moist soils, which more effectively conduct heat (Fitzpatrick 2004). Solarization does not involve as intensive or long-lasting a physical disturbance to the soil as does topsoil-removal, although the soil often is tilled prior to applying the plastic. Studies implementing solarization have shown increased establishment of seeded native forbs and grasses and a reduction in exotic species (Wilson et al. 2004, Moyes et al. 2005, Pfeifer-Meister et al. submitted). Other studies have also shown short-lived decreases in microbial community composition and biomass (Bendavid-Val et al. 1997, Wang et al. 2006, Pfeifer-Meister et al. submitted).

In previous research on Willamette Valley wetland prairies, we found that initial differences in plant community structure due to different restoration treatments quickly diminished as plant community structure converged over time (Pfeifer-Meister et al.

submitted). In particular, we observed a trade-off between native plant cover and diversity—areas with high native cover had low diversity and vice versa. This relationship appeared to be primarily driven by the dominant native bunchgrasses found in this ecosystem that provided high native cover and competitively eliminated other native and exotic plant species. At the same time, impacts on belowground functions were relatively minor among the suite of techniques tested, which included solarization but not topsoil-removal. We were interested in determining if these were consistent phenomena in these restored wetland prairies.

In the current study we compared the plant communities and soil function of six restorations (three topsoil-removal and three solarization sites) to those of three nearby, high-quality remnant wetland prairies that served as reference sites. These latter sites were never drained, plowed or otherwise converted to agriculture, and have retained comparatively high levels of historically associated native plant species. They have, however, received varying levels of biodiversity management including prescribed burning, and removal of invasive trees and shrubs. These reference prairies served as a baseline for comparing the relative success of the two restoration techniques. We hypothesized that (1) the removal of topsoil would have deleterious effects on ecosystem function and soil properties, leading to lower productivity than reference wetland prairies, (2) solarization would result in high cover of native species and have minimal effects on belowground processes, and (3) the restored sites, regardless of treatment, would have lower species richness and diversity than the reference prairies.

Methods

Site Selection and Experimental Design

We selected three replicate sites for each of the restoration treatments, topsoil-removal or solarization, and compared these to three of the highest quality wetland prairies available (i.e., reference sites) (Table 3.1). All sites are part of the West Eugene Wetland (WEW) mitigation bank, Oregon, USA. We were constrained by site availability, which meant that the restorations were implemented at different times (between 1-5 yrs. prior to sampling). For the topsoil-removal treatment, the different sites were restored in 1999, 2001, and 2003, and for the solarization treatment, sites were

Table 3.1. Site Selection. Three sites each were selected for topsoil removal, solarization, and reference wetland prairies.
Note: NA= Not Applicable because reference sites were never cultivated.

	Treatment	Site	Prior to Restoration	Year Restored	Owned and Managed
1	Topsoil Removal	North Greenhill	*Lolium multiflorum* field	1999	City of Eugene and BLM
2	Topsoil Removal	Turtle Swale	Unmanaged pasture	2001	City of Eugene and BLM
3	Topsoil Removal	North Greenhill	*Lolium multiflorum* field	2003	City of Eugene and BLM
4	Solarization	North Greenhill	*Lolium multiflorum* field	1999	City of Eugene and BLM
5	Solarization	North Greenhill	*Lolium multiflorum* field	2001	City of Eugene and BLM
6	Solarization	Coyote Prairie	*Lolium multiflorum* field	2004	City of Eugene
7	Reference	Willow Creek	NA	NA	The Nature Conservancy
8	Reference	North Greenhill	NA	NA	City of Eugene and BLM
9	Reference	Oxbow West	NA	NA	City of Eugene and BLM

restored in 1999, 2001, and 2003, and for the solarization treatment, sites were restored in 1999, 2001, and 2004. The 2004 solarization site, Coyote Prairie, was part of an experiment we used in a previous study (Pfeifer-Meister et al. submitted). Despite its recent implementation, it was included because there were only two other solarization sites available for sampling.

Prior to restoration, all sites were either in commercial grass-seed production with *Lolium multiflorum* Lam. or were abandoned pastures. The topsoil-removal treatment was applied using a large excavator, and approximately 10-cm of topsoil was removed from each site. For the solarization treatment, the sites were tilled and then covered with sheets of clear plastic (15-m width, 30-m long) for a minimum of three months, with the edges of the plastic buried in trenches to minimize water evaporation. After site preparation, the six restorations were seeded with a similar mix of native graminoids and forbs. All sites, including the three reference sites, received varying degrees of selective weeding, mowing, and burning that are typical for the management of wetland prairies in this region. The restored sites were never drained, and all sites have hydric soils and similar hydrology.

The climate is Mediterranean with hot, dry summers and mild, wet winters. Mean annual precipitation and temperature are 125 cm and 12°C, respectively (National Climatic Data Center 2005). Because precipitation primarily falls from October to May, these wetland prairies dry out through the summer months, and the water table is more than one meter below the soil surface from July-September. During winter months, the water table is often perched on these shrink-swell clays, with approximately 5-10 cm of

standing water. The primary growing season begins in March, although some species germinate with the fall rains, with almost complete plant senescence by mid-July.

At each of the nine sites, 15 1-m^2 subplots were randomly located within a 225 m^2 portion of the site to measure plant cover, species richness, diversity, and aboveground productivity. Five subplots at each site were also selected to measure soil variables as described below.

Plant Sampling

In July 2005, we determined percent cover of plant species in each 1-m^2 subplot with the point-intercept method (Elzinga et al. 1998). We used 1-m by 1-m frames with 25 equally spaced pins that were dropped vertically, and each plant touch was recorded by species. Because multiple hits were possible for each pin, greater than 100% cover often occurred. Any species not hit by a pin was also recorded as present in the plot to enable calculations of species richness and diversity. Species nomenclature followed the USDA plant database (http://plants.usda.gov), with the exception of *Schedonorus arundinaceus* (Schreber) Dumortier (syn. *Festuca arundinacea* or *Lolium arundinaceum*), which followed the Flora of North America (Flora of North America Editorial Committee 1993+).

We estimated aboveground net primary productivity (NPP) in July 2005 at peak standing biomass by clipping three 10-cm by 10-cm quadrats within each 1-m^2 subplot and sorting the biomass into graminoids, forbs, woody (small shrubs and tree seedlings), and thatch material. The plant material was dried at 60°C for 48 hours and weighed. The three 100-cm^2 quadrats were averaged for each subplot.

Soil Sampling

On 23 April 2005, we measured *in situ* ecosystem CO_2 respiration, CH_4 production, and N_2O production in five 1-m^2 subplots per site. In each plot, we placed PVC chambers (10.2-cm diameter, 35-cm tall) 5 cm in the ground to create good soil contact and sealed the tops with rubber caps fitted with stainless steel compression bands. We collected 20-cm^3 gas samples from the headspace every 30 minutes for two hours after capping. Gas samples were stored in pre-vacuumed serum bottles sealed with rubber septa. After one hour, soil temperature was taken at a 5-cm depth adjacent to each chamber. Gas samples were analyzed on a SRI model 8610C gas chromatograph (Torrance, CA, USA) for N_2O using an ECD detector and for CO_2 and CH_4 using a FID detector with a methanizer.

After gas collection, we removed the chambers and collected soil cores from within the footprint of each chamber using a tulip bulber (5.7-cm diameter, 8.5-cm depth). Soil cores were brought back to the laboratory and stored in a dark incubator at the average soil temperature for all sites (13.8°C). The next day, roots were removed from soil cores by hand and dried at 60°C for 48 hours to estimate belowground biomass. Bulk density was determined by weighing the entire core and correcting for soil moisture by drying a sub-sample at 60°C for 48 hours. We measured pH using a 1:1 soil-deionized water slurry. Two days after soil collection, we extracted sub-samples of soil from each plot for PO_4^{3-} using 0.5 M $NaHCO_3$ (Kuo 1996) and NH_4^+ and $NO_2^- + NO_3^-$ using 2 M KCl (Maynard and Kalra 1993). The soil extracts were filtered through acid-washed filter paper and frozen until analysis. We used an Astoria II autoanalyzer (Astoria Pacific International, Clackamas, OR, USA) to measure available PO_4^{3-} using the ascorbic acid

method (Murphy and Riley 1962), $NO_2^- + NO_3^-$ using the cadmium reduction method (Wood et al. 1967), and NH_4^+ using the phenate method (Solorzano 1969).

Microbial biomass C, N, and P were determined for each soil core using the chloroform-fumigation method (Voroney and Winter 1993, Horwath and Paul 1994). Two days after collection, a soil subsample from each plot was extracted with 0.5 M K_2SO_4 to determine initial total carbon and nitrogen. We used the $NaHCO_3$ extracts to determine initial phosphorus. Soil subsamples were then placed in 50-mL centrifuge tubes, fumigated with chloroform to lyse microbial cells, capped, and stored in an incubator at 13.8°C. After three days, soils from the centrifuge tubes were extracted again. All extracts were frozen until analysis. We used the persulfate digestion method (Wetzel and Likens 2000) and measured the CO_2 produced on a LiCor 7000 infrared gas analyzer (Lincoln, NE, USA) to determine total carbon. Total nitrogen was determined by digesting the K_2SO_4 extracts using the potassium persulfate method (Ameel et al. 1993) and measuring $NO_2^- + NO_3^-$ on the autoanalyzer as previously described. We measured PO_4^{3-} in the $NaHCO_3$ extracts using the ascorbic acid method (Murphy and Riley 1962). Microbial biomass was calculated as the difference between the final and initial extracts for C, N and P, with no extraction efficiency correction factor.

We measured total soil carbon and nitrogen on two sub-samples of dried (60°C for 48 hr), ground soil from each plot using a Costech Analytical Technologies 4010 elemental combustion analyzer (Valencia, CA, USA). To determine soil texture, we sieved dry soils to less than 2-mm diameter. Percent clay was calculated using the hydrometer method (Gee and Bauder 1986), percent sand was determined by weighing the material retained on a 53-μm sieve, and percent silt was calculated as the difference.

To determine arbuscular mycorrhizal fungal colonization of grass roots, we used the fungal-specific stain, trypan blue, and measured percent colonization using the point-intercept method. On 16 May 2005, we collected the plants and associated roots of three native (*Agrostis exarata* Trin., *Danthonia californica* Bol., and *Deschampsia cespitosa* (L.) P. Beauv.) and three exotic grasses (*Anthoxanthum odoratum* L., *Holcus lanatus* L., and *Schedonorus arundinaceus* (Schreber) Dumort.). At each site, ten replicates of each grass species were randomly collected when possible, but not all grasses occurred at all sites. *Deschampsia cespitosa* and *Holcus lanatus* did occur at all sites, and overall sample sizes for native (n=195) and exotic (n=158) grasses were similar. Roots were collected to a depth of approximately 15 cm using a tulip bulber. The roots were washed clean and fixed in 50% ethanol until staining. Prior to staining, the roots were cleared in 10% KOH overnight at room temperature and bleached in alkaline H_2O_2 for 30 minutes. To improve adherence of the stain, the roots were then acidified in 1% HCl. The roots were stained overnight in acidic glycerol containing 0.05% trypan blue and then de-stained in acidic glycerol (Koske and Gemma 1989, Bauer et al. 2003). For each plant, arbuscular mycorrhizal infection rate was determined using the point-intercept method (Giovannetti and Mosse 1980). The roots were cut into 1-cm segments, dispersed evenly over a square grid, and examined under a dissecting microscope (10 – 100x). The presence or absence of infection (including arbuscules, vesicles, and/or hyphae) was determined at each point where the root segments intersected a gridline. A total of 100 grid intersections were scored for each root system.

Statistical Analyses

We used nested one-way ANOVAs to determine the effect of restoration treatment on plant and soil response variables, with the exception of mycorrhizal fungal colonization. The 1-m^2 subplots were nested within sites, so that sites were the replicate unit. In the ANOVA model, sites were treated as a random effect and treatment was a fixed effect. We used Tukey's pairwise comparisons to explore significant treatment effects. To correct for violations of normality, square root transformations were used for exotic cover, exotic richness, total NPP, grass NPP, forb NPP, thatch NPP, belowground biomass, NH_4^+ availability, PO_4^{3-} availability, NO_3^- availability, and ecosystem respiration. A natural log transformation was used for native cover, and Simpson's diversity was squared. For mycorrhizal fungal colonization, mean percent colonization was calculated by site for the two functional groups, native grasses (3 species) and exotic grasses (3 species), and one-way ANOVAs were conducted with treatment as the fixed main effect. Individual ANOVAs were not conducted for each species because every species did not occur at every site. Linear least squares regression was used to examine the relationships of native cover and *Deschampsia cespitosa* cover to Simpson's index of diversity. ANOVAs and regressions were run using SPSS vs. 11.0.

To explore differences in plant community structure among treatments, we used nonmetric multidimensional scaling (NMS), which, unlike other ordination techniques, has no assumption of linear relationships among variables (McCune and Grace 2002). Community structure was described by creating a matrix of the cover of each species in each plot. Species that were present, but not hit by a pin, were assigned a cover of 0.5%. To test for statistical significance of this ordination, we used a Monte Carlo test (1000

randomized runs). We also used the non-parametric technique multi-response permutation procedure (MRPP) to test for community differences among restoration treatments and to obtain an estimate of the effect size, A (McCune and Grace 2002). For both the NMS and MRPP analyses, we used relative Sorensen distance. Only significant indicator species are reported with the associated NMS axes loadings (significance determined using a Monte Carlo test on 1000 randomized runs).

In addition to understanding how plant community structure differed among treatments, we were also interested in how community structure was related to soil response variables. For this, we used the direct gradient ordination technique, canonical correspondence analysis (CCA). Unlike NMS, CCA only accounts for the variation in community structure that is related to the environmental matrix (McCune and Grace 2002) and has the same assumptions as multiple regression. To avoid multicollinearity, soil variables that were highly autocorrelated ($r > 0.6$) were not included in the environmental matrix; autocorrelated variables included percent clay and percent sand ($r = 0.7$), total C and total N ($r = 0.9$), and microbial biomass C, N, and P ($r > 0.6$). Eleven variables were included in the matrix: bulk density, pH, percent moisture, NH_4^+, NO_3^-, and PO_4^{3-} availability, ecosystem respiration, microbial biomass P, total soil C, percent clay, and total percent mycorrhizal colonization. For the plant matrix, species that only occurred in a single plot were eliminated, resulting in a total of 53 species used. To test for a significant relationship between the plant and environmental matrices, we used a Monte Carlo test with 1000 randomized runs. We report linear combinations of the environmental variables (LC scores) for axis loadings. NMS, MRPP, and CCA were all run using PC-ORD vs. 4.34.

Results

Plant Community Responses

Restorations and reference sites differed from one another for species richness, diversity, cover, and productivity (Table 3.2, Figs. 3.1, 3.2). Overall, fewer species were found in the restored sites than in the reference prairies ($p<0.001$). Reference prairies, topsoil-removal sites, and solarization sites averaged 57, 47, and 30 species, respectively, when totaled across the 15 1-m^2 subplots (hereafter called 'per site'). Solarization sites also had fewer native species (mean = 16 per site) than topsoil-removal and reference prairies (mean = 29 per site, $p<0.001$). Plant cover was marginally lower in the topsoil-removal treatment ($p<0.10$) than the reference and solarization sites, and native plant cover was marginally higher in the solarization sites than in the topsoil-removal and reference sites ($p<0.10$). Exotic cover was fourfold higher in the reference sites than the restored sites. Species richness per m^2 was higher in the reference sites than in the restored sites (only marginally lower in the topsoil-removal treatment). Simpson's diversity per m^2 was marginally higher in the reference sites than the solarization treatment. Reference sites also had double the exotic species richness per m^2 of the restored sites and marginally higher exotic Simpson's diversity than the solarization treatment ($p<0.10$). There was no statistical difference in native richness or native diversity among the restored and reference sites.

Aboveground net primary productivity was lower in the topsoil-removal treatment than the reference sites (Fig. 3.2). Additionally, productivity varied significantly among functional groups. The reference and solarization sites had more than twice the graminoid biomass of the topsoil-removal sites ($p<0.001$), and the solarization treatment

Table 3.2. Nested ANOVA results for the effect of restoration treatment on plant and soil response variables (df 2,6). P-values in bold are significant at an alpha<0.05. *Note: NA= Not Applicable because rates of methane and nitrous oxide production never significantly differed from zero.*

Plant Response Variables	**F**	***p***
Total Cover	3.77	0.087
Native Cover	4.16	0.074
Exotic Cover	23.61	**0.001**
Species Richness	9.65	**0.013**
Native Species Richness	0.73	0.521
Exotic Species Richness	10.91	**0.010**
Simpson's Diversity	4.61	0.061
Native Simpson's Diversity	2.54	0.159
Exotic Simpson's Diversity	4.36	0.068
Total Aboveground NPP	6.10	**0.036**
Grass NPP	8.63	**0.017**
Forb NPP	4.88	**0.055**
Aboveground Thatch	23.04	**0.001**
Soil Response Variables	**F**	***p***
Bulk Density	3.38	0.100
pH	7.28	**0.025**
Clay	0.18	0.843
Sand	0.23	0.798
Silt	0.07	0.936
Soil Moisture	3.30	0.108
Belowground Biomass	1.44	0.309
Total Soil Carbon	15.19	**0.004**
Total Soil Nitrogen	9.11	**0.015**
Ammonium Availability	0.50	0.628
Nitrate Availability	2.48	0.164
Phosphate Availability	78.34	**<0.001**
Ecosystem CO_2 Respiration	5.54	**0.043**
Methane Flux	NA	NA
Nitrous Oxide Flux	NA	NA
Microbial Biomass Carbon	27.52	**<0.001**
Microbial Biomass Nitrogen	24.81	**<0.001**
Microbial Biomass Phosphorus	13.39	**0.006**
Mycorrhizal Colonization of Native Grasses	6.59	**0.031**
Mycorrhizal Colonization of Exotic Grasses	2.99	0.141

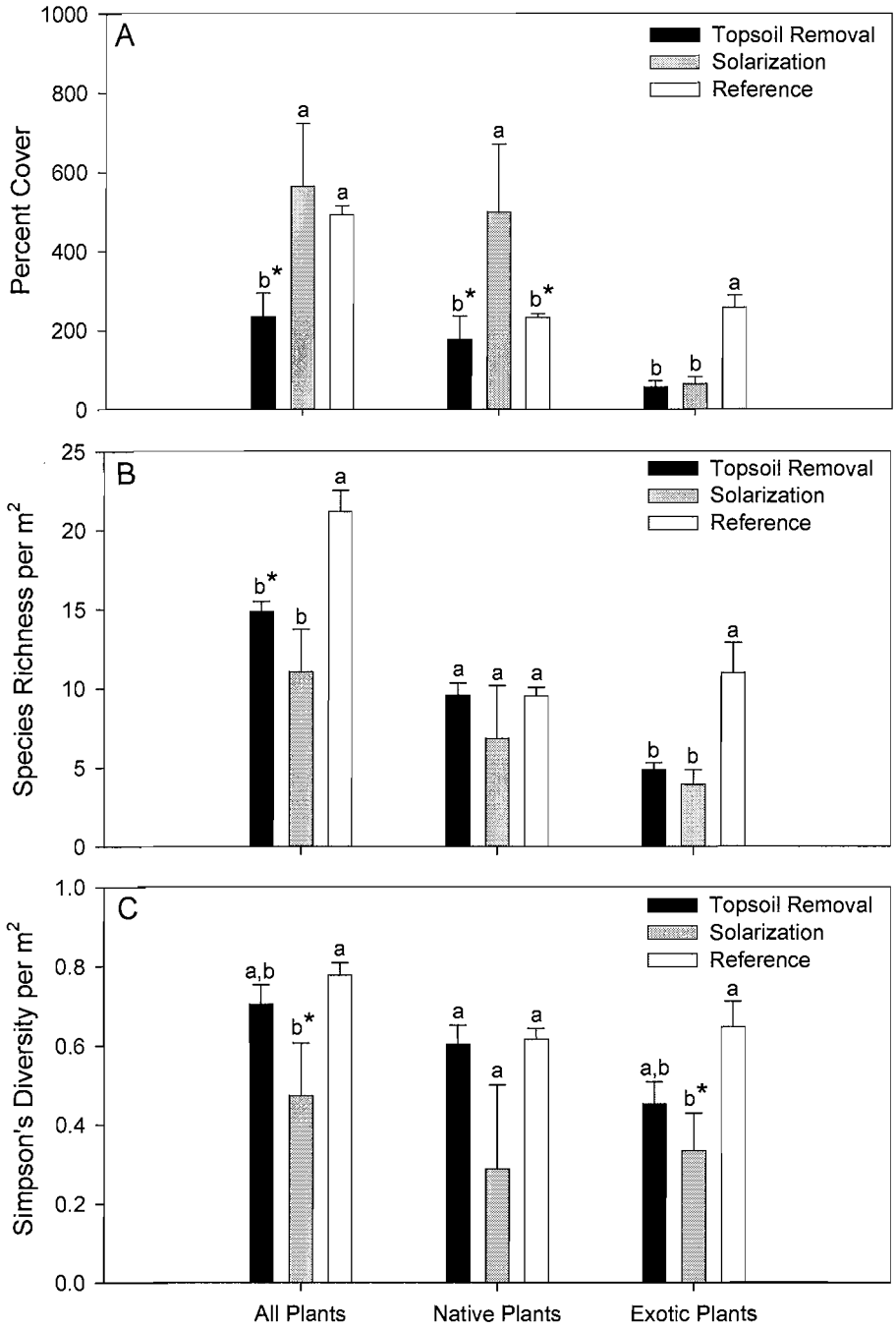


Figure 3.1. Mean percent cover (A), species richness (B), and Simpson's diversity (C) for restoration treatments by plant group (e.g., all, native, or exotic). Error bars represent one standard error and lower case letter differences indicate significant ($p<0.05$, $*p<0.10$) effects of treatment within a plant group.
Note: High values of Simpson's index of diversity indicate high levels of diversity.

had substantially less forb biomass than the reference and topsoil-removal treatments ($p<0.001$). Woody species were found only at the reference sites. Finally, the solarization treatment (mean = 348 g/m^2) had more than twice as much thatch biomass as the reference (mean = 166 g/m^2) and topsoil-removal (mean = 145 g/m^2) sites ($p<0.005$, results not shown).

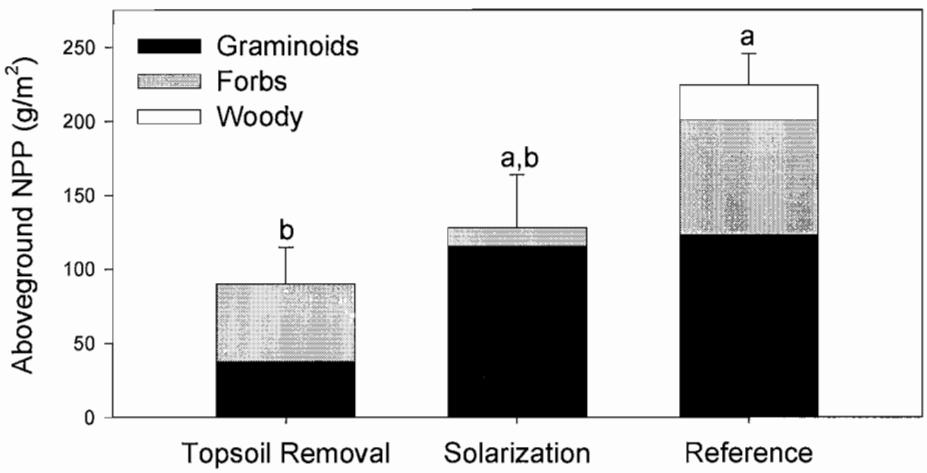


Figure 3.2. Mean aboveground net primary productivity (NPP) in restoration treatments. NPP is further partitioned into graminoids, forbs, and woody biomass. Error bars represent one standard error of total aboveground NPP, and lower case letter differences indicate significant effects ($p<0.05$) among treatments.

When all treatment types are considered together, there was a significant tradeoff between high native cover and high Simpson's diversity, i.e., plots with high native plant cover tended to have lower overall diversity ($r^2 = 0.39$, $p < 0.001$, Fig. 3.3). This negative trend also was observed within each treatment, although the slope of reference prairies was not as steep (data not shown). This tradeoff appeared to be primarily driven by the dominant native perennial bunchgrass, *Deschampsia cespitosa* (Fig. 3.3b). In general, the solarization sites had higher cover of *D. cespitosa* and lower overall diversity, and the

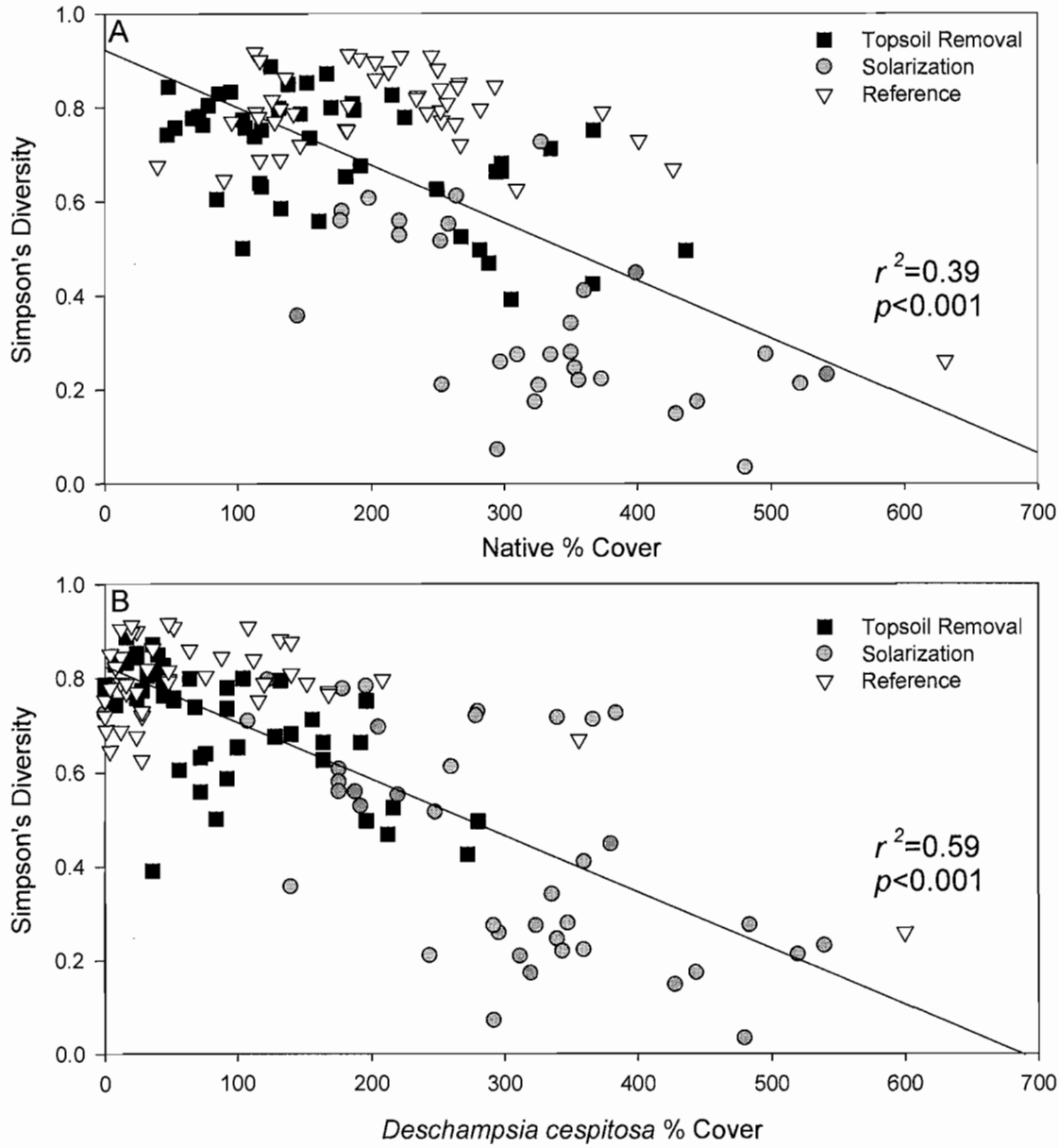


Figure 3.3. Simpson's diversity vs. percent native cover (A) and vs. percent *Deschampsia cespitosa* cover (B) in all treatments (n=135).
Note: High values of Simpson's index of diversity indicate high levels of diversity.

reference sites had the highest diversity and lowest *D. cespitosa* cover. When regressing *D. cespitosa* percent cover with Simpson's diversity, we were able to explain 20% more of the variation ($r^2 = 0.59$, $p < 0.001$) than when using total native cover.

The restored sites also had substantially different plant community structure than the reference sites ($A = 0.16$, $p < 0.0001$, Fig. 3.4). The nonmetric multidimensional scaling (NMS) ordination extracted two axes from the plant data set that explained 65% of the variation in plant community structure. Axis 1 explained 40% of this variation and primarily represented a life history gradient (Supplemental Table 3.1). Plots loading negatively on this axis (e.g., reference wetland prairie plots) had a greater abundance of perennial species, and plots loading positively on this axis (e.g., solarization and topsoil-removal plots) had a greater abundance of annual species. Axis 2 explained 25% of the variation and did not separate treatments clearly, but instead, the youngest restored site (solarization at Coyote Prairie) was significantly different from all other sites. This site was dominated by native species, with the exception of the exotic annual grass, *Lolium multiflorum*.

Belowground Responses

Overall, both restoration treatments differed significantly from the reference prairies in belowground processes; however, the topsoil-removal treatment generally had the most dramatic effects on soil properties when compared to the reference prairies (Table 3.2, Figs. 3.5, 3.6). In all treatments, the headspace concentrations of the greenhouse gases nitrous oxide and methane remained at atmospheric concentrations over the course of the two-hour field measurements (i.e., flux equaled zero).

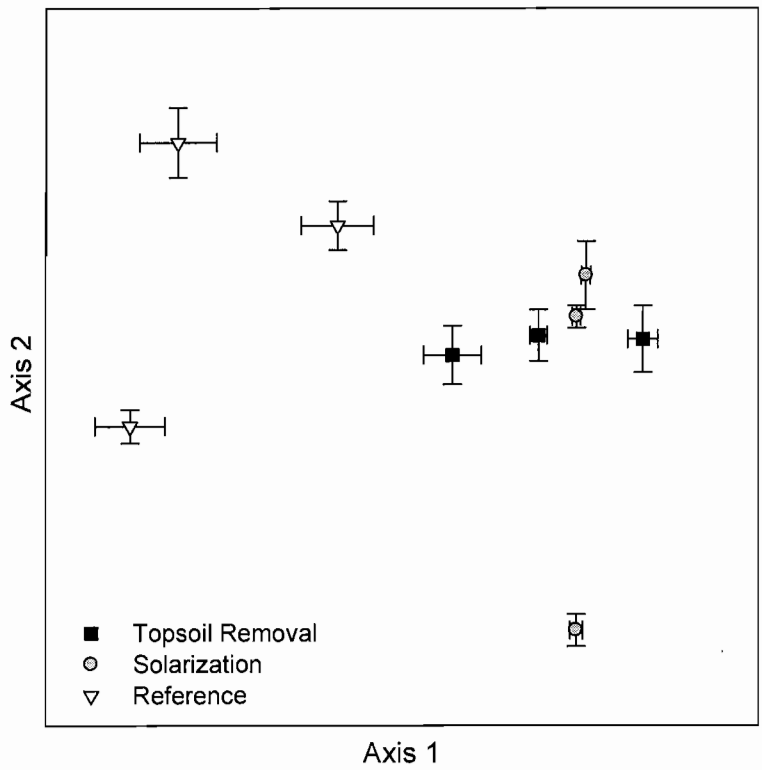


Figure 3.4. Nonmetric multidimensional scaling (NMS) of plant community structure in restoration treatments using relative Sorenson distance. Axis 1 explained 40% and axis 2 explained 25% of the variation in plant community structure (A=0.16, P<0.0001). Although the analysis was performed on plots, the plot mean and standard error for each site are shown for graphic representation.

Ecosystem respiration was significantly higher in the solarization sites than the topsoil-removal and reference prairies (Fig. 3.5a). Phosphate availability was also highest in the solarization sites, and the reference prairies had the lowest available phosphorus (Fig. 3.5b). The topsoil-removal treatment had approximately half the total carbon and total nitrogen of the solarization and reference prairies (Fig. 3.5c, d). Microbial biomass carbon, nitrogen, and phosphorus were substantially lower in the topsoil-removal sites, with reference prairies having the most microbial biomass

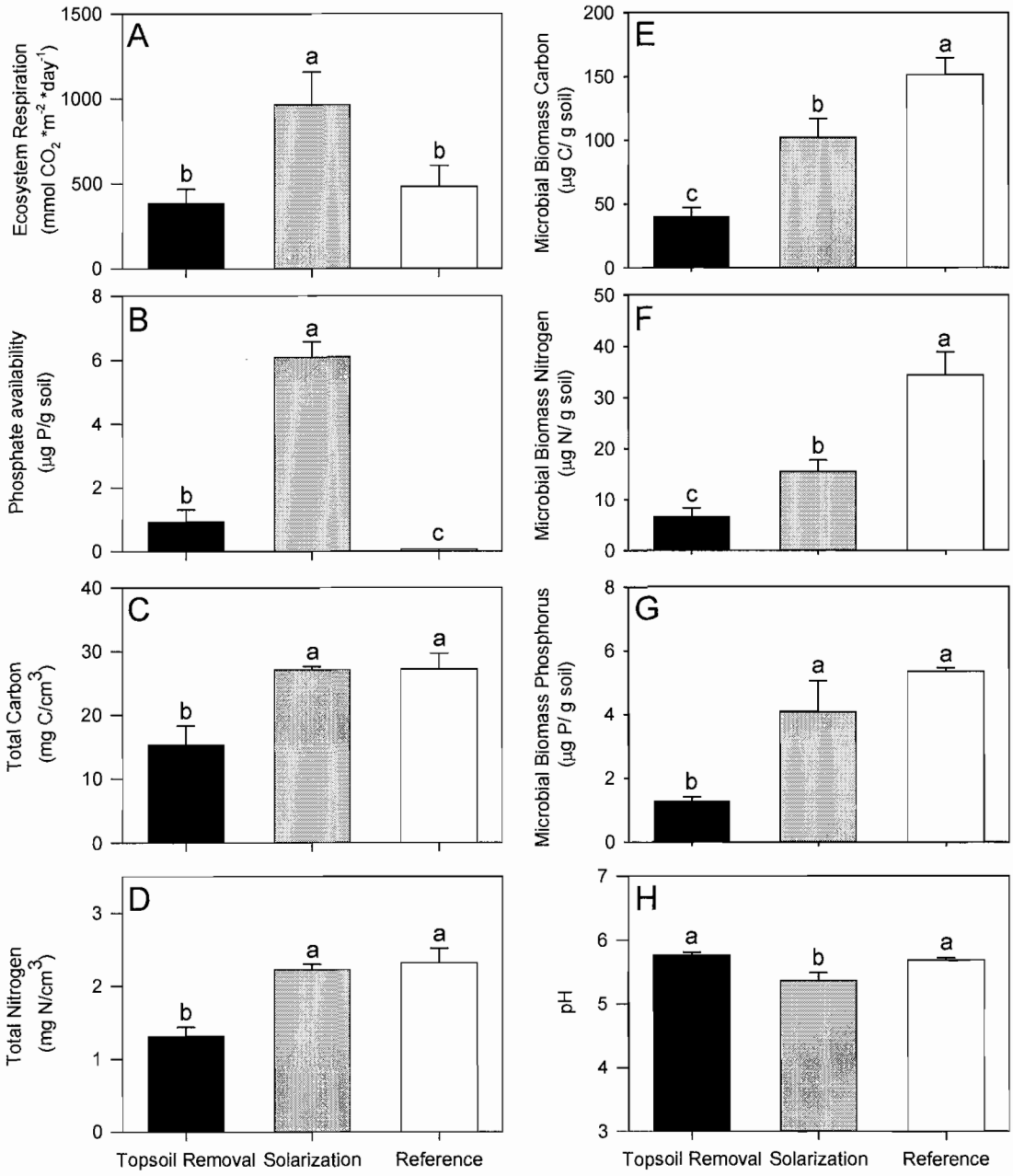


Figure 3.5. Mean ecosystem respiration (A), phosphate availability (B), total soil carbon (C), total soil nitrogen (D), microbial biomass carbon (E), microbial biomass nitrogen (F), microbial biomass phosphorus (G), and pH (H) in the restoration treatments. Error bars represent one standard error, and lower case letter differences indicate significant (p<0.05) effects among treatments.

(Fig. 3.5e-g). The solarization treatment had a slightly lower pH than the topsoil-removal and reference prairies (Fig, 3.5h). In addition, bulk density was marginally higher in the topsoil-removal sites (mean =1.46 g/cm^3) than in the reference prairies (mean= 1.21 g/cm^3, p =0.09), and soil moisture was marginally higher in the reference prairies (mean= 32%) than in topsoil-removal sites (mean = 24%, p =0.09).

Arbuscular mycorrhizal fungal colonization differed among treatments but only for the native grasses (Fig. 3.6). In the native grasses, the topsoil-removal treatment had approximately 15% less colonization than the reference prairies and solarization sites. Native and exotic grasses had approximately the same amount of colonization by mycorrhizal fungi (mean = 40%).

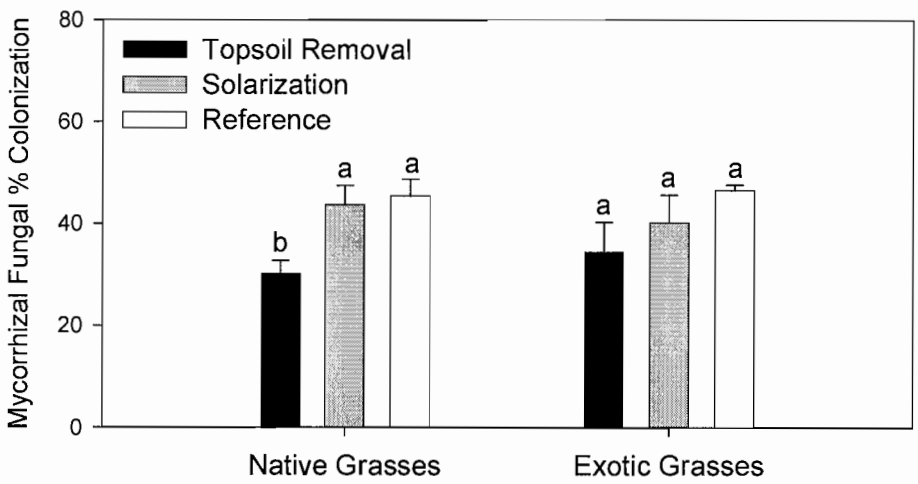


Figure 3.6. Mean mycorrhizal fungal percent colonization in native and exotic grasses in the restoration treatments. Error bars represent one standard error and lower case letter differences indicate significant (p<0.05) treatment effects within a grass type.

Canonical correspondence analysis (CCA) revealed a significant relationship between plant community structure and edaphic factors (p <0.010, Fig. 3.7). Axis 1 explained 12% of the variation in plant community structure, and axis 2 explained 7%, whereas species-environment correlations were 0.94 and 0.87 for axes 1 and 2, respectively. As in the NMS, axis 1 was primarily a perennial-annual gradient with the lowest negative loadings dominated by perennial species and the highest positive

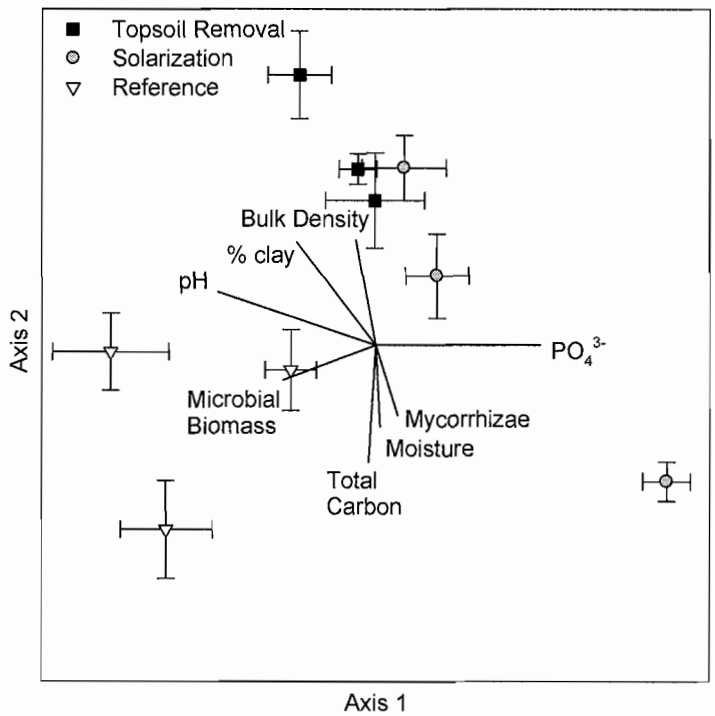


Figure 3.7. Canonical Correspondence Analysis of fifty-three plant species using eleven environmental variables (pH, bulk density, percent moisture, ammonium, phosphate, nitrate, respiration, mycorrhizal fungal % colonization, microbial biomass P, total soil C, and % clay). Axis one and axis two explained 12% and 7% of the variation in plant community structure, respectively. Only vectors with a $r^2 > 0.25$ are shown. Although the analysis was performed on plots, the plot mean and standard error for each site are shown for graphic representation.

loadings dominated by annual species, particularly native annuals (see Supplemental Table 3.2). Soil variables loading most heavily on axis 1 included (in order of absolute magnitude of loading): phosphate availability, pH, microbial biomass, and to a lesser extent, percent clay. Axis 2 did not have a clear gradient of plant functional groups. Soil variables loading most heavily on axis 2 included (in order): total carbon, bulk density, percent clay, percent moisture, and mycorrhizal fungal percent colonization. Reference prairie plots tended to group in the lower left quadrant of community space, and restored plots tended to group in the upper middle of community space, with the exception of the young solarization plots (Coyote prairie) which fell out in the lower right quadrant. Reference prairie plots were distinguished by a high abundance of perennial species (as in the NMS) and were associated with higher microbial biomass and pH (i.e., more basic). Reference prairie plots also tended to have higher total carbon, moisture availability, and mycorrhizal colonization than the restored plots, with the exception of Coyote Prairie which also loaded negatively on axis 2. The topsoil-removal plots loaded slightly more negatively on axis 1 than the solarization plots and were associated with higher bulk density and percent clay and lower total carbon, % moisture, and mycorrhizal colonization. The solarization plots were associated with the highest phosphate availability.

Discussion

Despite the large variation in site history and management regimes within a treatment type, we observed substantial differences in plant and soil properties among treatments. The restored sites differed from the reference prairies both in plant

community structure and ecosystem function; however, the two site preparation treatments, topsoil-removal and solarization, varied in different ways. In general, the solarization sites had high cover of native graminoids and lower overall species richness and diversity. Solarization sites also had the highest available phosphate and ecosystem respiration. Although the topsoil-removal sites had similar diversity as the reference prairies, they were much less productive and had low plant cover, likely because of the substantial differences in belowground processes discussed below. In the following paragraphs, we address each of our original hypotheses, highlight important mechanisms controlling plant community structure, and conclude with implications for restoration.

Our first hypothesis, that the removal of topsoil would have deleterious effects on ecosystem function and soil properties and thus be less productive than reference prairies, was strongly supported. The microbial community was significantly reduced in the topsoil-removal sites, with lower microbial biomass and mycorrhizal colonization of native grasses (Figs. 3.5, 3.6). These sites had half the total carbon and nitrogen of reference prairies (Fig. 3.5). Similarly, in a European wet meadow, organic matter was drastically reduced after topsoil-removal (Holzel and Otte 2003). The topsoil-removal sites also had higher bulk density and lower soil moisture than reference prairies. Woodward (1996) attributed lower soil moisture following topsoil-removal to a decrease in soil porosity from compaction and thus greater evaporation. In our previous research in the West Eugene Wetlands, we found only minimal effects of belowground responses to site preparation, but none of these techniques (e.g., herbicide application) involved as intensive physical disturbance to the soil structure (Pfeifer-Meister et al. submitted).

Likely as a result of these dramatic differences in edaphic conditions, the topsoil-removal sites had half the aboveground productivity of the reference prairies (Fig. 3.2), particularly of graminoid species. Total plant cover was also substantially lower in the topsoil-removal sites (Fig. 3.1). Other studies have found similar results. In a United Kingdom wetland prairie, productivity was significantly reduced after topsoil-removal (Tallowin and Smith 2001), and Patzelt et al. (2001) found plant cover continually decreased with greater depths of topsoil-removal in wet fen meadows. Unlike cover, species diversity was not lower in topsoil-removal sites, but instead was similar to reference prairies on a 1-m^2 scale. On a site scale, however, fewer species were observed in the topsoil-removal sites than reference prairies, although no difference was found in native richness.

Our second hypothesis, that solarization would result in high cover of native species and have minimal effects on belowground processes, was somewhat supported by our findings. The solarization sites did have the highest mean native plant cover and significantly less exotic cover than the reference prairies (Fig. 3.1). Total cover and productivity did not differ between the solarization sites and reference prairies (Fig. 3.2). Despite surpassing reference prairies in native cover, solarization sites were far less speciose with approximately half the species found in reference prairies (Fig. 3.1). These sites were also dominated by graminoid species, particularly native bunchgrasses (Fig. 3.2). Similar results were observed in a previous study of wetland prairie restoration in the West Eugene Wetlands (Pfeifer-Meister et al. submitted, both studies included the 2004 solarization plots) and in a California annual grassland (Moyes et al. 2005). Moyes et al. found that solarization significantly reduced cover of an exotic annual grass and

increased survival of two native perennial bunchgrasses, but forb seedling density was significantly reduced. The decrease in forb productivity that we observed (Fig. 3.2) appeared to be the result of native perennial bunchgrasses outcompeting forb species. These grasses contributed to the twofold increase in thatch found that, together with the high levels of bunchgrass cover, may have created an environment that reduced subsequent forb recruitment. Reduced recruitment would have particularly strong effects on the abundance of annual species.

As hypothesized, many soil characteristics did not differ between solarization and reference prairies, but we did detect a few differences. Solarization sites had higher ecosystem respiration and phosphate availability, a slightly more acidic pH, and lower microbial biomass carbon and nitrogen (Fig. 3.5). Other studies implementing solarization have found a decrease in the microbial community, with lower nematode abundance (Wang et al. 2006) and arbuscular mycorrhizal infection (Bendavid-Val et al. 1997), but these effects were generally short-lived (weeks to months). We examined older sites (1-5 yrs post restoration), so it was surprising that a decrease in microbial biomass was still detectable. This decrease was not as severe as the decrease found in the topsoil-removal sites, and no decrease in mycorrhizal colonization was detected in the solarization sites. The prior land use (e.g., *Lolium multiflorum* fields) of the solarization sites could explain the higher phosphate availability as these sites were likely fertilized regularly prior to restoration.

We found modest support for our third hypothesis, that restored sites, regardless of treatment, would have lower species richness and diversity than the reference prairies. Both restoration treatments (particularly solarization) had lower species richness (both on

a m^2 scale and totaled across the 15 subplots), but only the solarization sites had lower Simpson's diversity (Fig. 3.1). We found no differences in native species richness and diversity between the topsoil-removal and reference sites, but the solarization treatment had fewer native species when totaled across the 15 subplots. Exotic species richness was lower in both restored treatments than in the reference prairies. Many other studies have found that restored sites have significantly lower diversity than reference sites (e.g., Seabloom and van der Valk 2003, McLachlan and Knipsel 2005, Pfeifer-Meister et al. submitted).

One important mechanism for the lower diversity observed in the restored sites may be the dominance attained by native perennial bunchgrasses. We observed a significant tradeoff between cover of *Deschampsia cespitosa*, a common perennial bunchgrass, and diversity (r^2 =0.59). The solarization sites were dominated by this grass species and had the lowest overall diversity, whereas the reference prairies had the lowest cover of *D. cespitosa* and the highest diversity. We observed a similar tradeoff in previous research of Willamette Valley prairies (Pfeifer-Meister et al. submitted), suggesting this is a general trend within these wetland prairies.

Further research is needed to understand why restored sites are particularly vulnerable to native perennial bunchgrass dominance and reference sites are not. Potential mechanisms include (i) seed limitation within remnants as a consequence of historical losses of bunchgrasses, or (ii) the more variable microtopography of remnant prairies. In California, it has been hypothesized that grazing by cattle may have led to the decrease in native perennials, but experimental studies, have given conflicting results for the impact of grazing on native bunchgrasses (Daphne A. Hatch 1999, Kimball and

Schiffman 2003, Seabloom et al. 2003b). In California grasslands, seed limitation has also been recognized as a primary obstacle to reestablishing native grasses and forbs (Hamilton et al. 1999, Seabloom et al. 2003a). However, it is important to note that California grasslands have been invaded predominately by annual grasses, whereas the primary invaders of Pacific Northwest prairies are perennial grasses. Microtopographic heterogeneity has also been identified as a mechanism increasing diversity and richness in wetland communities (Vivian-Smith 1997). The reference prairies in this experiment had much greater spatial variability with hummocks and deep channels, whereas the restored sites tended to be flat surfaces with little microtopographic variation. Consistent with this explanation, the reference prairies also exhibited greater site-level variability in plant community structure than did the restored sites. Future experiments could test these two hypotheses by introducing topographic heterogeneity into restorations and by manipulating seed mixes to include varying levels of native bunchgrasses.

In addition to the many univariate differences in treatments, the ordinations revealed large differences in plant community structure and environmental variables between the restored and reference sites (Fig. 3.4, 3.7). Interestingly, the restored treatments did not substantially differ from one another in plant community structure, with the exception of the young solarization, though these sites differed from one another in total cover and productivity. Instead, a similar set of species were found in all of the restoration sites. We observed a similar convergence of plant communities in ten different restoration treatments after three years (Pfeifer-Meister et al. submitted). Moreover, a different set of edaphic factors were more strongly associated with plant communities in the restored sites (e.g., high phosphate availability) than in the remnant

prairies (e.g., high microbial biomass, soil carbon; Fig. 3.7). In general, the restored sites had a higher abundance of annual species, whereas reference sites were dominated by perennial graminoids, forbs, and woody species (many of which were exotic, see Supplemental Table 1). This may be reflective of the restorations being relatively young and that many early-successional species, particularly annuals, are still found in these sites. Nevertheless, we previously observed that three years was ample time for many early-successional species to be lost (Pfeifer-Meister et al. submitted).

The higher proportion of exotic species found in the reference prairies (Fig. 3.2) could be a result of several mechanisms. It may be explained partially by the differences in site-management. Restored sites may have experienced more selective weeding of invasive species, as this is a typical practice within the Willamette Valley. This is likely not the only mechanism though, as we observed in an experimental study with no post-restoration management significantly lower exotic cover and diversity in restored plots than in remnant prairies (Pfeifer-Meister et al. submitted). The lower proportion of exotics could also be a consequence of the young age of the restorations. Over time the restorations could accumulate more exotics as they disperse into the sites from elsewhere. It is interesting to note, that although the reference prairies had a large abundance of exotic species, native species were not excluded and were able to persist at relatively high abundance. Understanding what factors allow for this persistence could have important implications for wetland restoration.

Conclusions

We found large differences between restored sites and reference prairies in both plant community structure and ecosystem functioning despite the relatively small sample size. Moreover, we observed important tradeoffs between the two site preparation treatments despite different post-restoration management regimes in each site. The removal of topsoil significantly altered ecosystem functioning, with substantially lower aboveground productivity, microbial biomass, mycorrhizal infection of native grasses, and total soil carbon and nitrogen than either the reference prairies or solarization sites. However, these sites were more similar to reference prairies in terms of diversity and species richness than solarization sites. The solarization treatment, on the other hand, had minimal effects on belowground responses and surpassed the reference prairies in terms of native plant cover, particularly of native perennial bunchgrasses, but these sites were substantially less diverse and speciose. In no case, did restored wetlands, even up to 5 years after establishment, resemble high-quality reference wetlands in terms of plant community structure or ecosystem function, suggesting that mitigation for loss of natural wetlands may result in progressive loss of wetland function.

Our study highlights the importance of considering multiple criteria when determining the 'success' of mitigation projects. If only one criterion (e.g., high cover of native species) is examined, restorations could be deemed 'successful' despite having dramatically different ecosystem functioning than high-quality remnant prairies. Such a simplistic metric of success not only glosses over the impacts of restoration treatments on key ecosystem functions, but also ignores important potential tradeoffs should establishing high cover of native bunchgrasses suppress overall species diversity, as we

observed. Further research is needed to better understand the mechanisms causing the tradeoff between diversity and native bunchgrass cover, and why restored sites are particularly susceptible to native bunchgrass dominance. Establishing wetland prairie restorations that can sustain both high native cover and high species diversity over time with relatively low amounts of maintenance is a key challenge that remains to be solved.

Bridge to Chapter IV

In this chapter, we examined how restoration techniques affected plant community structure and ecosystem functioning by comparing previously restored sites to three remnant prairies. We found that even after five years restored prairies differed from remnant prairies in terms of plant structure and ecosystem functioning. We also found that various edaphic factors (e.g., moisture availability and phosphate availability) were strongly associated with plant communities, suggesting these factors may be important in controlling plant species distributions. Furthermore, within the remnant prairies, we observed large variation in plant communities (i.e., a patchy distribution of plant species), and we hypothesized that this may be due to microtopographic variation within these sites. In an upland prairie, Mt. Pisgah, we observed similar environmental heterogeneity and patchy distributions of plants. In particular, native species appeared to be restricted to low 'quality' habitats, and exotic species appeared to be found in high 'quality' habitats. For these reasons, we were interested in understanding if environmental heterogeneity was important in determining the distribution of native and

exotic species across the prairie. We also wanted to determine the underlying controls of carbon and nutrient cycling across this heterogeneous site. In the following chapters, we explore how nutrient and moisture availability influence competitive hierarchies between native and exotic grasses, and we determine the controls over nutrient cycling and availability.

CHAPTER IV

SEASONAL AND SPATIAL CONTROLS OVER NUTRIENT CYCLING IN A PACIFIC NORTHWEST PRAIRIE

A paper published in *Ecosystems* and co-authored with Scott D. Bridgham.

Pfeifer-Meister, L. E. and S. D. Bridgham. 2007. *Ecosystems* 10(8): 1250-1260.

Introduction

Numerous studies have shown the importance of temperature, moisture, and edaphic factors such as pH, soil texture, and organic matter in controlling carbon, nitrogen, and phosphorus cycling, but results conflict regarding the relative importance of these factors seasonally and spatially in different prairie ecosystems (e.g., Schimel and Parton 1986, Pastor et al. 1987, Franzluebbers et al. 2002, Wan and Luo 2003, Booth et al. 2005). Most of these studies have been conducted in grasslands with a mid-continental climate. Far fewer studies have investigated grasslands with a Mediterranean climate, and, to our knowledge, no study has examined perennial-dominated prairies with a Mediterranean climate, such as occur in the Pacific Northwest, USA. These different types of prairies may not respond similarly to future climatic forcing. Therefore

knowledge of the full spectrum of responses of prairie habitats to variable moisture and temperature will require a better understanding of grasslands with a Mediterranean climate, particularly those dominated by perennials.

Within the U.S., prairies with a Mediterranean climate occur only in California and the Pacific Northwest. These West Coast prairies are quite different from those in mid-continental areas of the U.S. in terms of climate, nutrient inputs, and species composition. In general, Midwest prairies have deeper soils, are dominated by warm season (C_4) grasses, and most of the precipitation falls in the spring and summer months (Porazinska et al. 2003, Fitzpatrick 2004). In contrast, West Coast prairies have cool season (C_3) grasses, a rainy season that begins in the fall and ends in the spring, and often shallow soils. As a result of the climatic differences, the primary growing season of West Coast prairies is during the winter and spring months in contrast to the summer growing season in the Midwest (Xu and Baldocchi 2004). Inorganic nitrogen (N) deposition from nitrate and ammonium is also much higher in Midwest prairies (2-7 kg N/ha) than West Coast prairies (0-2 kg N/ha) (National Atmospheric Deposition Program 2005). Among West Coast prairies, the climate of Oregon upland prairies is wetter and cooler than California prairies (National Climatic Data Center 2005). Furthermore, although all West Coast prairies were historically dominated by perennial bunchgrasses, invasion by exotic annual grasses in California has resulted in predominantly annual grasslands (Buisson et al. 2006), whereas western Oregon prairies continue to be dominated by perennial grasses.

Over the past century, the Pacific Northwest has seen an increase in temperature of 0.5 to 1.5°C and a 10% increase in precipitation (Parson 2001). In the next fifty years,

climate change models predict an increase in mean annual temperature of 3°C in this region, with most of the warming expected to occur in winter months. Predicted changes in precipitation vary more among models, but most agree that precipitation will increase in the winter, and summers will experience little change or a slight decrease in the Pacific Northwest (Parson 2001). These changes in climate will likely have complex effects, both direct and indirect, on nutrient cycling and will vary among ecosystems and spatially within ecosystems.

Therefore, our objective was to understand the degree to which seasonal patterns of carbon, nitrogen, and phosphorous cycling depend on temperature and soil moisture availability, and how these seasonal controls vary due to micro-heterogeneity in edaphic conditions, within an upland prairie in Oregon, USA. We collected soils seasonally across an upland prairie hillslope and measured microbial respiration, net nitrogen mineralization, net nitrification, and phosphorus availability under field conditions and under varied temperature and soil moisture conditions in the laboratory. The treatments were designed to tease apart the effects of soil moisture and temperature as seasonal controls over nutrient cycling.

Methods

Study Site

Field sampling was conducted in a remnant upland prairie at Mt. Pisgah, located within the 930-ha Howard Buford Recreation Area, approximately 11 km southeast of Eugene, Oregon. The summit of Mt. Pisgah is at 467-m elevation, while the study site is located at the base of the south facing slope at 190-m elevation. The slope and aspect of

the site are 7% and 154°, respectively. The climate is Mediterranean with a mean annual temperature of 12°C, and a mean annual precipitation of 117 cm, falling primarily between October and May (National Climatic Data Center 2005). Plots were located randomly across a 6-ha hillslope dominated by grasses and forbs with occasional *Quercus garryana* (white oak). Areas with *Q. garryana* were excluded to restrict sampling to prairie. Dominant species include exotic grasses *Bromus japonicus* and *Schedonorus arundinaceus,* the native grass *Danthonia californica,* and native forbs *Lomatium nudicaule,* and *Wyethia angustifolia*; however, more than 550 plant species have been identified within this recreational area (Friends of Buford Park 2000). Across the hillslope, many of the native species appeared to be restricted to areas characterized by shallow, rocky, or heavy clay soils, whereas exotics appeared to be abundant in more mesic areas. The soil is classified as Philomath series, clayey, smectitic, mesic, shallow, vertic haploxerolls and the average soil depth is 43 cm, but ranges between 7 and 100 cm. For other edaphic site characteristics, see Table 4.1.

Experimental Design

We conducted a 1-year study to determine seasonal controls over carbon and nutrient cycling in this upland prairie. Sixteen 9 by 5-m plots were randomly established. Within each of these plots, four 1 by 1-m subplots were randomly chosen to seasonally measure (August 28, 2003; January 25, 2004, and May 6, 2004) microbial respiration, net nitrogen mineralization, net nitrification, and phosphorous availability. In the fall of 2002, half of the plots were burned as part of an earlier experiment (Johnson and Roy,

Table 4.1. Seasonal means (± standard error) of site characteristics at Mt. Pisgah (Lane County, Oregon). Lower case letter differences indicate significant effects ($p<0.05$) of site characteristics among seasons. pH, % clay, % sand, % silt, total % carbon, and total % nitrogen were measured once in August 2003.

	Gravimetric % Moisture	% Field Capacity	Temp. (°C)	Initial NH_4^+ (μg N/ g soil)	Initial NO_3^- (μg N/ g soil)	pH	% Clay	% Sand	% Silt	Total % Carbon	Total % Nitrogen
August 2003	9.2 ±0.4c	12.1±0.4c	19	9.1±0.3a	0.7±0.1b	6.5±0.02	56.5±0.5	16.7±0.3	26.7±0.8	3.4±0.05	0.27±0.004
January 2004	50.8±0.7a	66.9±0.7a	5	2.3±0.2b	2.4±0.2a	--	--	--	--	--	--
May 2004	21.9±0.5b	28.9±0.5b	13	1.8±0.2b	0.8±0.1b	--	--	--	--	--	--

unpublished data), but in no case did the burn create significant differences in the response variables measured in this paper (p range: 0.11-0.44, n=64).

On each sampling date, we collected soils from the 64 1-m^2 subplots, brought them back to the laboratory, and separated them into three treatments: 1) field temperature and field moisture, 2) field temperature and 60% field capacity moisture, and 3) 19°C and field moisture. The treatments were designed to sort out the relative importance of soil moisture and temperature as seasonal controls over microbial respiration, net nitrogen mineralization, net nitrification, and phosphorus availability. Field temperature was considered to be the average monthly temperature in which soils were collected from the sixteen plots, and field moisture was the gravimetric moisture content of soils when collected. Field capacity was determined on soil from each subplot in the summer of 2003 prior to implementation of the experiment by saturating soils with deionized water twice, covering, allowing them to drain for 2 hours, and drying at 105°C for 48 hours. Gravimetric field moisture, field capacity, and temperature on each sampling date are given in Table 1. As field temperature in August was 19°C, treatments 1 and 3 were the same.

Field Sampling and Incubation Set-up

On each sampling date, two cores were taken per 1-m^2 subplot to a depth of 15 cm with a soil auger (5-cm width). These cores were homogenized into one sealed plastic bag and brought back to the laboratory. Once large roots and small rocks were removed from the soil cores by hand, the soils were weighed into wide-mouth Mason jars and incubated for 2 weeks in a dark incubator at the appropriate temperature. The lids of

the Mason jars were drilled with 1.25-cm diameter holes, and glass wool was stuffed into these holes to allow air exchange while minimizing moisture loss. In the summer and spring, soils were wetted to achieve the 60% field capacity in treatment 2, but in winter the soils were air-dried to achieve 60% field capacity. While waiting for soils to dry (under winter conditions), all soils were kept at field temperature. In all cases, the incubations began no more than 5 days after soils were originally collected. To maintain appropriate moisture levels throughout the duration of the experiment, deionized water was added every 2 days to the Mason jars. The evaporation of water never exceeded more than 1% of total soil moisture.

Soil Analyses

On the first and last day (day 14) of the lab incubations, separate subsamples of soil were removed and extracted for $NO_2^- + NO_3^-$ and NH_4^+ using 2 M KCl (Maynard and Kalra 1993). The KCl extracts were filtered through Whatman No. 5 acid-washed filter paper and frozen until analysis. Net nitrification is the difference in $NO_2^- + NO_3^-$ over the two week incubation, whereas net nitrogen mineralization is the difference over the two weeks in $NO_2^- + NO_3^- + NH_4^+$. On the last day of the incubation, soils were extracted with 0.5 M $NaHCO_3$ to determine phosphorus availability (Kuo 1996). Similarly, these extracts were filtered through acid-washed Whatman No. 42 filter paper and frozen until analysis. NH_4^+, $NO_2^- + NO_3^-$, and PO_4^{3-} were measured with an Astoria II autoanalyzer (Astoria Pacific International, Clackamas, OR, USA) using the phenate (Solorzano 1969), cadmium reduction (Wood et al. 1967), and ascorbic acid methods (Murphy and Riley 1962), respectively.

To determine microbial respiration, the Mason jars were closed with septa for 24 hours on days 1, 7, and 14 of the incubation. A 10-cc gas sample was taken from the headspace initially and 24 hours later; the initial headspace sample was replaced with 10-cc of N_2 gas. Gas samples were immediately run on a Li-COR 6400 infrared gas analyzer set-up to measure discrete injections of CO_2. Headspace CO_2 concentrations were corrected for dissolution into soil water based upon soil moisture content and soil pH (Stumm and Morgan 1981). The difference in CO_2-C over the course of 24 hours was considered microbial respiration. Over the course of the incubation, respiration rates decreased. However, to simplify the many complex interactions between time and treatments, cumulative μg C/ g soil/day for the entire 2-week incubation was calculated for final statistical analyses.

Soil texture, pH, total carbon, and total nitrogen were determined once on soils collected in each of the subplots on August 28, 2003. pH was determined immediately after collection using a 1:1 soil-deionized water slurry. For soil texture analysis, dried soils (105˚C for 48 hours) were sieved to less than 2-mm (10 mesh) diameter. To calculate percent clay, we used the hydrometer method (Gee and Bauder 1986). Percent sand was calculated by weight using a 53-μm sieve (270 mesh). Percent silt was calculated by difference. We determined total carbon and nitrogen on dried, ground soil using a Costech Analytical Technologies 4010 elemental combustion analyzer (Valencia, CA, USA).

Statistical Analyses

To determine the controls over microbial respiration, net nitrogen mineralization, net nitrification, and phosphorus availability, a repeated-measures ANOVA was run for each response variable using SPSS 11.0 for Windows. The between-subject factors included treatment and plot, and the within-subject factor was season. To meet the normality assumption of ANOVA, microbial respiration and phosphorus availability were square-root transformed for analysis and back-transformed for presentation. All other residuals were normally distributed and the assumption of sphericity was not violated.

To deconvolve the many significant interactions with plot and season, a multiple regression approach was used on the field-condition data set (treatment 1). This allowed us to explore how seasonal and edaphic factors affected nutrient cycling across the hillslope. Akaike Information Criterion (AIC) was employed to select the best models. AIC is derived from Kullback-Leibler information and maximum likelihood theories, and does not use traditional hypothesis testing (Anderson et al. 2000, Burnham and Anderson 2002). Instead, the most probable model has the lowest AIC score. Based on this model, one can calculate the differences in AIC scores (Δ AIC) to determine the likelihood of each model being the best correlative relationship, allowing comparison between multiple models simultaneously, as opposed to traditional stepwise regression where only a single model is presented, even if it is only marginally better than other candidate models. The corrected AIC score (AIC_c) accounts for any bias from the large number of parameters relative to sample size. Additionally, Akaike's weights (ω) can be used to standardize the AIC scores between 0 and 1, and determine the probability of any given model being the best model (e.g., a ω of 0.7 indicates that 70% of the time that particular model would be

selected). Following convention, we used a criterion of a $\omega \geq 0.1$ to determine the most probable models in our data set (Burnham and Anderson 2002). AIC values were calculated using SAS 9.1 (SAS Institute). All AIC_c, ΔAIC_c, and ω values were then calculated using equations from Burnham and Anderson (2002) in a Microsoft Excel spreadsheet. To avoid multicollinearity, predictors that were highly autocorrelated (r >0.7) were not included in the models; autocorrelated variables included % clay, % sand, and % silt (r >0.85), total C and total N (r = 0.91), and % moisture and temperature (r = -0.93). Parameters included in all models were % moisture, total C, pH, and % clay. In addition to these parameters, inorganic nitrogen and phosphorus were included for microbial respiration, inorganic phosphorus was included for net nitrogen mineralization and net nitrification, and inorganic nitrogen was included for phosphorus availability.

Results

Season significantly affected all variables measured (Table 4.2). The experimental treatments had a direct effect on microbial respiration, nitrification, and phosphorous availability, but not nitrogen mineralization. However in all cases, treatment effects depended upon season (Table 4.2, Fig. 4.1). The effect of season on all response variables depended on plot, and was thus site specific (Table 4.2). The initial inorganic nitrogen also differed among seasons (Table 4.1). In the summer, ammonium was the dominant form of inorganic nitrogen, and nitrate levels were low. In the winter, nitrate and ammonium were available in approximately equal concentrations, and in the spring both ammonium and nitrate concentrations were low, but ammonium was the dominant form.

Table 4.2. P-values from repeated-measures ANOVAs for the effect of season, treatment, and plot on microbial respiration, net nitrogen mineralization, net nitrification, and phosphorus availability. Values in bold are significant at an alpha <0.05.

	Microbial Respiration (μg C/g soil/day)	Net Nitrogen Mineralization (μg N/g soil/day)	Net Nitrification (μg N/g soil/day)	Phosphorus availability (μg P/g soil)
Between				
Treatment	**<0.001**	0.842	**<0.001**	**<0.001**
Plot	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Treatment*Plot	**0.004**	**<0.001**	**<0.001**	0.310
Within				
Season	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Season*Treatment	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Season*Plot	**<0.001**	**<0.001**	**<0.001**	**0.002**
Season*Treatment*Plot	**<0.001**	**0.004**	**<0.001**	**0.002**

Microbial Respiration

Under field conditions (treatment 1), microbial respiration was lower during the summer than during the winter or spring (Fig. 4.1). In the summer, increasing moisture content to 60% field capacity increased microbial respiration. In the winter, highest respiration rates were achieved through increasing the temperature from 5 to 19°C. The soils were at 67% field capacity in the winter, and drying the soils to 60% field capacity decreased microbial respiration. In the spring, increasing moisture from 29% to 60% field capacity or increasing temperature to 19°C led to an equivalent increase in respiration.

To disentangle the significant interaction between season and plot (Table 4.2), AIC was employed. Using our criterion, there were two probable models, which explained between 75-76% of the variation (Table 4.3). The most likely model included % moisture, % clay, total carbon, and inorganic nitrogen and phosphorus. The alternative

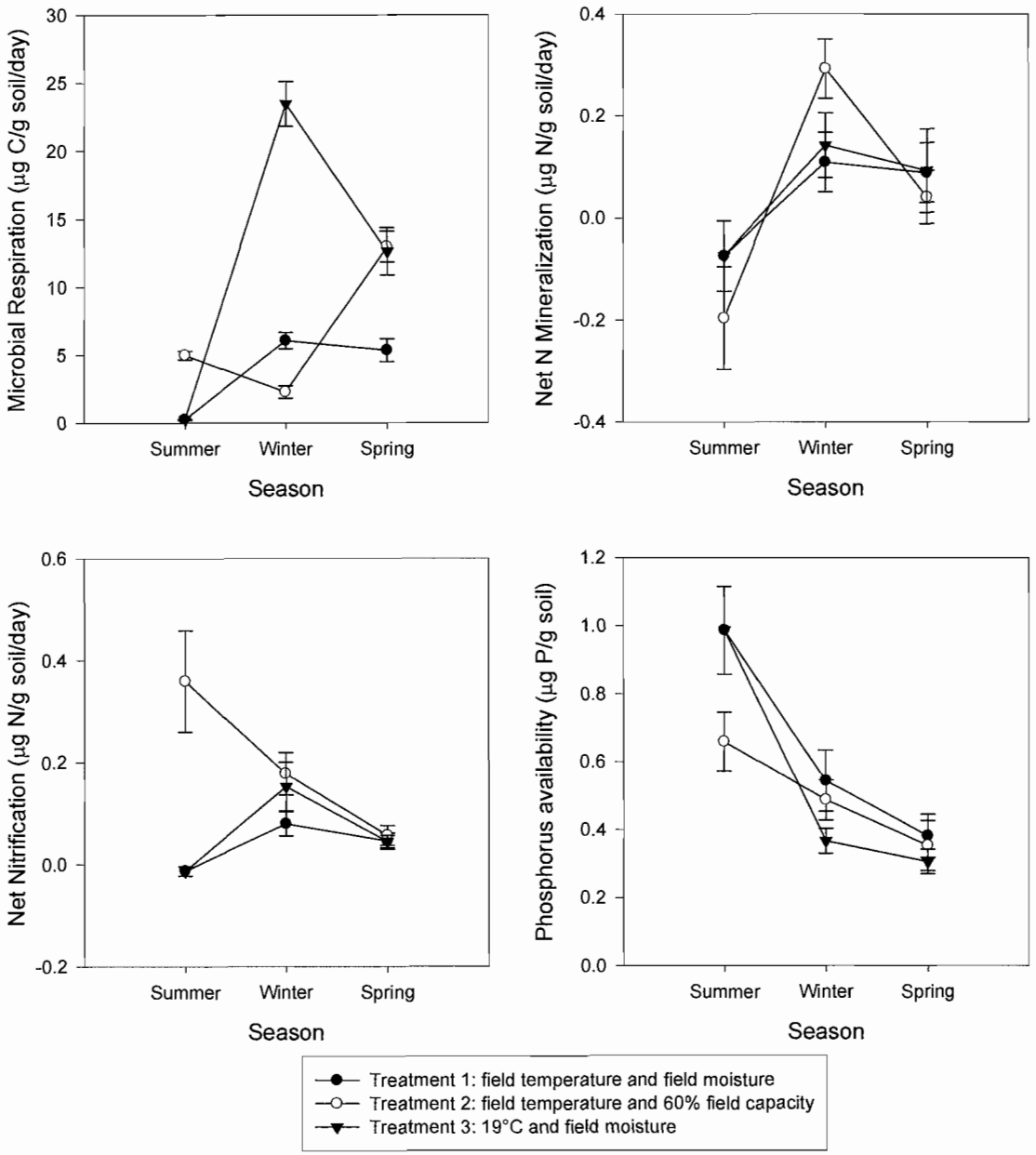


Figure 4.1. Significant interactions between season and treatments for microbial respiration, net nitrogen (N) mineralization, net nitrification, and phosphorus availability. Error bars represent 95% confidence intervals. Treatments 1 and 3 were the same in the summer, as field temperature was 19 °C. Negative numbers for net nitrogen mineralization and net nitrification indicate a net immobilization of nitrogen and positive numbers indicate a net mineralization of nitrogen.

model also included pH. Percent moisture explained the largest proportion of the total variance, with an average partial R^2 of 65% (Fig. 4.2). Total carbon, inorganic nitrogen, % clay, inorganic phosphorus, and pH only explained a small amount of the variance, with average partial R^2's of 4, 2.5, 2, 1, and 0.5%, respectively.

Table 4.3. Candidate models describing patterns of microbial respiration, net nitrogen mineralization, net nitrification, and phosphorus availability where K is the number of parameters, Δ AIC_c is the change in the Akaike's corrected Information Criterion, and ω is the Akaike's weight (see methods for statistical description). A criterion of $\omega \geq 0.1$ was used to determine candidate models. Positive and negative signs denote the direction of individual correlations.

Model	K	Δ AIC_c	ω	R^2
Microbial Respiration (µg C/g soil/day)				
Moisture +Total C +Clay -Inorganic N -Inorganic P	5	0	0.54	0.75
Moisture +Total C +Clay -Inorganic N -Inorganic P +pH	6	0.58	0.41	0.76
Net Nitrogen Mineralization (µg N/g soil/day)				
Moisture -Total C	2	0	0.23	0.18
Moisture -Total C -Clay	3	1.18	0.13	0.19
Moisture -Total C -Clay -pH	4	1.20	0.13	0.19
Moisture -Total C -pH	3	1.62	0.10	0.18
Net Nitrification (µg N/g soil/day)				
Moisture +Clay -Inorganic P	3	0	0.27	0.29
Moisture +Clay	2	0.03	0.26	0.29
Moisture +Clay -Inorganic P +Total C	4	1.95	0.10	0.29
Phosphorus availability (µg P/g soil)				
-Moisture +Total C +pH +Inorganic N	4	0	0.27	0.35
-Moisture +pH +Inorganic N +Clay	4	0.41	0.22	0.34
-Moisture +pH +Inorganic N	3	1.10	0.16	0.33
-Moisture +Inorganic N +Clay	3	1.30	0.14	0.33
-Moisture +Total C +pH +Inorganic N +Clay	5	1.34	0.14	0.35

Net Nitrogen Mineralization

Similar to microbial respiration, under field conditions net nitrogen mineralization was lowest during the summer (with net immobilization of nitrogen), with no detectable difference in the winter and spring (Fig. 4.1). In the summer and spring, the moisture and

temperature treatments had no effect. However, in the winter, drying the soils to 60% field capacity increased net nitrogen mineralization.

The results from the AIC led to four probable models (Table 4.3, Fig. 4.2). Soil moisture (avg. partial R^2= 16.5%) and total carbon (avg. partial R^2= 2%) were always important predictors of net nitrogen mineralization. Some models also included % clay and pH, but they explained < 1% of additional variance. However, no model had high explanatory power, with the best model explaining 19% of the variance (Table 4.3).

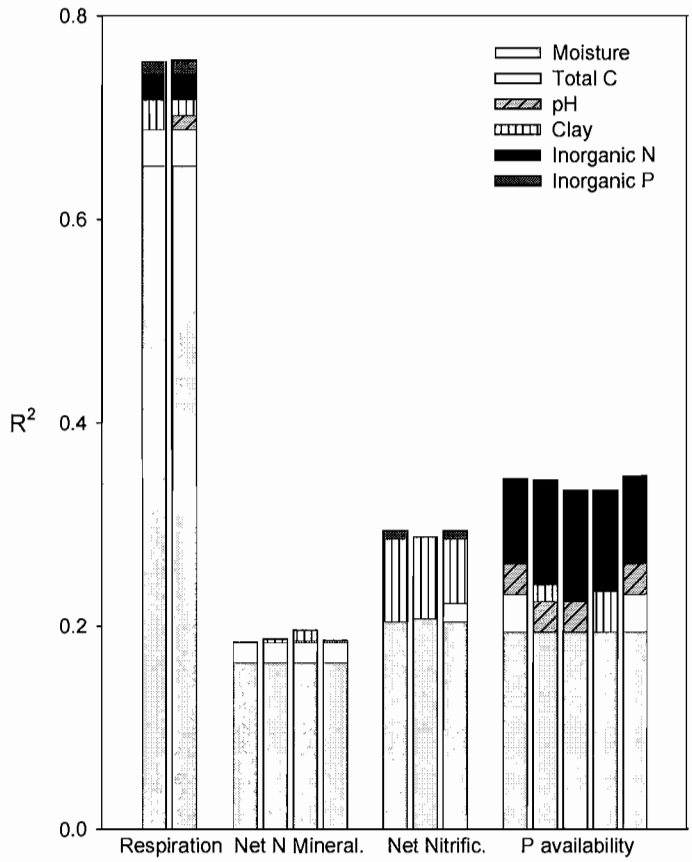


Figure 4.2. Candidate models describing patterns of microbial respiration, net nitrogen (N) mineralization, net nitrification, and phosphorus availability under field temperature and moisture conditions. The total bar height represents the total R^2 for each response variable, which are further partitioned into the partial R^2 for the individual predictors.

Net Nitrification

Under field conditions, net nitrification followed the same trends as both microbial respiration and nitrogen mineralization with the lowest nitrification rates in the summer (Fig. 4.1). In contrast to net nitrogen mineralization, increasing moisture content in the summer caused a 30-fold increase in net nitrification. Additionally, drying the soils in the winter increased net nitrification, suggesting that nitrification is limited by both too little and too much water in different seasons. Increasing the temperature never significantly affected nitrification rates, nor were there any treatment effects on nitrification rates in the spring.

The three probable models for net nitrification all explained 29% of the variation (Table 4.3, Fig. 4.2). The best model included % moisture and % clay. Alternative models included inorganic phosphorus and total carbon. As was the case for microbial respiration and net nitrogen mineralization, % moisture explained the largest portion of the variance (avg. partial $R^2 = 21\%$), with clay only explaining 7% of the variance, and inorganic phosphorus and total carbon explaining an even smaller amount (avg. partial $R^2<1\%$).

Phosphorus Availability

Unlike the other response variables, phosphorus availability was higher in the summer than in the winter or spring when incubated under field conditions. In the summer, wetting the soils decreased phosphorus availability. In the winter, increasing the temperature decreased phosphorus availability. In the spring, the moisture and temperature treatments had no effect.

From the AIC results, the five best models explained between 33 and 35% of the variance (Table 4.3, Fig. 4.2). All models included % moisture (avg. partial $R^2 = 19.5\%$) and inorganic nitrogen (avg. partial $R^2 = 10\%$). The most probable model also included total carbon (avg. partial $R^2 = 1.5\%$) and pH (avg. partial $R^2 = 2.5\%$). Three of the alternative models also included % clay (avg. partial $R^2 = 1\%$).

Discussion

To our knowledge, this is the first study to examine nutrient dynamics in a perennial-dominated prairie with a Mediterranean climate. The availability of nutrients is clearly important in structuring plant communities in this prairie as they have been shown to affect the competitive hierarchies between native and exotic grass species (Pfeifer-Meister et al. 2008). We found the expected seasonal variation in microbial respiration, net nitrogen mineralization, net nitrification, and phosphorus availability, but the underlying causes of this seasonal variation were complex. The relative importance of the soil moisture and temperature treatments varied among response variables, plot, and season. The degree to which abiotic factors explained the plot effect also differed among response variables (R^2 range: 0.18-0.76, Table 4.2). In all cases, soil moisture was the best predictor (Fig. 4.2), but it was highly correlated with temperature (which we did not use in the AICs), so soil moisture probably acted as an overall indicator of seasonal environmental effects.

Microbial Respiration

Overall, respiration rates under field conditions (~ 0.5 μmol $C/m^2/s$) were lower than prairies throughout the country (1.4-8 μmol $C/m^2/s$) (Luo et al. 1996, Raich and Tufekcioglu 2000, Franzluebbers et al. 2002, Wan and Luo 2003). Seasonally, respiration rates were lower in the summer than winter or spring. This result is similar to California prairies (Luo et al. 1996), but differs from Midwest prairies where respiration rates are lowest in the winter months and highest in summer months (Raich and Tufekcioglu 2000, Wan and Luo 2003). The most likely explanation is that the rainy season occurs during the winter and spring on the West Coast as opposed to the summer rainy season in the Midwest. Depending on season, soil moisture and/or temperature limited respiration rates. Not surprisingly, in the summer moisture was limiting; a 25% increase in soil moisture led to a 20-fold increase in respiration rates. In the winter, a decrease in soil moisture led to a decrease in respiration suggesting that microbial activity was not inhibited by excessive soil moisture, even at 67% water holding capacity, and an increase in temperature led to the highest respiration rates in this study (24 μg C/g soil/day). As winters are expected to get warmer and wetter in the Pacific Northwest (Parson 2001), these (and similar Mediterranean grasslands) may end up becoming a net source of atmospheric CO_2. In the spring, both a small increase in soil moisture and a 6°C increase in temperature led to an increase in respiration rates. A meta-analysis of ecosystem warming experiments also showed that increased temperature significantly increased soil respiration (Rustad et al. 2001). However, in a tallgrass prairie, Luo et al. (2001) demonstrated that over time the soil respiration response to warming decreased as the soil community acclimated.

To understand how seasonal controls and micro-heterogeneity in edaphic conditions explained differences in respiration rates, we used a multiple regression approach. However, we were limited in interpreting the seasonal controls as only soil moisture could be included in the models due to the high correlation (r = -0.93) between soil moisture and temperature. Overall, the most probable models explained a high proportion of the variance (75-76%), with soil moisture explaining most of this (partial R^2 =65%). Other studies have observed this high correlation with soil moisture. For example, in a tallgrass prairie in Oklahoma, soil moisture explained 59% of the variation in soil CO_2 efflux (Liu et al. 2002) and in a California grassland, belowground respiration was positively correlated with moisture (R^2=0.66) (Luo et al. 1996). In addition to soil moisture and temperature, organic matter is also considered a major control and has been shown to influence respiration rates (Bridgham and Richardson 1992, Raich and Tufekcioglu 2000, Flanagan et al. 2002, Franzluebbers et al. 2002, Wan and Luo 2003). In our study, total carbon was positively correlated with soil respiration, but, on average, explained only 4% of the variation. Other edaphic factors, including soil texture, inorganic nitrogen and phosphorus, and pH, explained even less of the variation in respiration rates (0.5-2.5%).

Net Nitrogen Mineralization

In general, net nitrogen mineralization was low in this prairie (average: 0.0041 $g/m^2/day$; range:-0.008-0.012 $g/m^2/day$), perhaps due to the high clay content and low organic matter of these soils. As with soil respiration, mineralization rates under field conditions were lower in the summer than the spring and winter. This same pattern has

been seen in other Mediterranean prairies (Taylor et al. 1982, Davidson et al. 1990, Jamieson et al. 1998, 1999), but in Midwest grasslands the seasonal effect is often reversed (Wedin and Tilman 1990). Surprisingly, increasing temperature never affected net nitrogen mineralization. Many studies have seen a positive correlation with soil temperature and mineralization rates (MacDonald et al. 1995, Updegraff et al. 1995, Burke et al. 1997), and in a meta-analysis of soil warming experiments, an increase in soil temperature led to a 46% average increase in net nitrogen mineralization (Rustad et al. 2001). However, as warming experiments typically occur over a much longer time-frame, this increase could be explained by the indirect effects of warming on other factors (i.e. changes in soil moisture or litter quality and quantity). In our study, a decrease in soil moisture in the winter led to a 3-fold increase in net nitrogen mineralization rates. This is likely due to the decrease in microbial activity (seen in respiration rates) resulting in a decrease in nitrogen immobilization.

Moisture and total carbon were always significant in explaining the seasonal variation in net nitrogen mineralization rates across the hillslope, with pH and clay sometimes explaining <1% of the variation. However, no model explained more than 19% of the variation. Other studies with similar sets of variables have shown similarly low correlations. For example, in a transect of grasslands from Colorado to Kansas, temperature, site, and moisture explained 24% of the variation in net nitrogen mineralization (Barrett et al. 2002). The predictability of nitrogen mineralization may be improved by separating net nitrogen mineralization into its component parts of gross mineralization and gross immobilization. However, soil moisture explained only 18% of the variation in gross nitrogen mineralization rates in a California annual grassland

(Hungate et al. 1997). Other studies have shown a higher correlation with net nitrogen mineralization and climatic variables (r^2 =0.69-0.91), but the soils were collected from plant monocultures (Cassman and Munns 1980, Taylor et al. 1982). Indeed, Wedin and Tilman (1990) demonstrated that by including plant species differences along with environmental factors in their regression model, they could explain 88% of the variation in net nitrogen mineralization.

Net Nitrification

Net nitrification followed the same seasonal trends as net nitrogen mineralization, and nitrification rates were also never affected by an increase in temperature. This lack of response to an increase in temperature has been demonstrated in soil warming experiments (Peterjohn et al. 1994, Shaw and Harte 2001). Despite the fact that mineralization rates did not respond to an increase in soil moisture during the summer, there was a 30-fold increase in net nitrification, suggesting that the large initial pool of ammonium was quickly nitrified in the presence of adequate soil moisture (Table 4.1). The opposite effect was seen in the winter, where a decrease in moisture availability increased net nitrification, indicating that excessive soil moisture in winter may inhibit nitrification in these prairies. At low summer moisture levels, gross nitrification is likely the limiting step, and at high moisture levels, either a decrease in nitrification or an increase in denitrification due to anaerobic micro-sites could lead to the decrease in net nitrification observed. However, as respiration rates did not decrease at the high moisture availability, denitrification is the most probable explanation. Schimel and Parton (1986) also demonstrated that nitrification is inhibited at higher water potentials more than

ammonification. In the spring, when plants are most actively growing and competing for nutrients, the treatments had no effect on nitrification rates which may reflect the low overall nitrogen availability (Table 4.1).

Soil moisture and % clay content explained the most variation in net nitrification, and both were positively correlated with nitrification rates. Potential nitrification is often limited by moisture availability (Robertson 1982, Davidson et al. 1990), and a positive correlation with soil moisture is common (e.g., Shaw and Harte 2001). Clay, with its high water tension (Hillel 1998), could also increase moisture availability to microbes under dry conditions. The high cation exchange capacity of clays (Chapin et al. 2002) could also explain the correlation found. Despite the positive relationships with moisture and clay, 70% of the variance remained unexplained. As there is a large biotic gradient across this hillslope (unpublished data), species effects on litter quality and belowground competition for nutrients could explain this missing variance (Wedin and Tilman 1990). It may also be explained by the opposing environmental effects on gross nitrification versus microbial immobilization and denitrification.

Phosphorus Availability

Due to the strong geochemical sorption of phosphorus, net mineralization rates are difficult to interpret (Bridgham et al. 1998, Kellogg et al. 2006). However, changes in phosphorus availability over time are important for understanding how phosphorus may limit productivity and structure plant communities. When incubated under field conditions, phosphorus availability was higher in the summer than the winter or spring, as opposed to microbial respiration, net nitrification, and net nitrogen mineralization.

This same seasonal pattern has been reported in a California annual grassland (Hooper and Vitousek 1998). In the summer, increasing moisture decreased phosphorus availability, and in the winter, increasing temperature decreased phosphorus availability. As microbial activity increased under these conditions (evidenced in respiration rates), it follows that phosphate would be incorporated into microbial biomass and become unavailable.

The results of the AIC analyses suggest that moisture availability and inorganic nitrogen are major controls of phosphorus availability across this hillslope, and to a lesser extent pH, total carbon, and clay content. In a study that manipulated moisture and organic matter, Braschi et al. (2003) demonstrated that increases in moisture could decrease phosphate availability and that increases in organic matter could increase phosphate availability. Similarly, in our study phosphorus availability was negatively correlated with moisture and positively correlated with total carbon. The positive correlation between phosphorus availability and inorganic nitrogen may suggest that microbial communities are co-limited by these nutrients. As the soils across this hillslope range from slightly acidic to neutral (pH range: 5.5-6.8), it is not surprising that a positive correlation was found between phosphorus availability and pH. The availability of phosphorus decreases at low pH because of sorption onto the surface of clays and iron and aluminum oxides (Chapin et al. 2002).

Conclusions

We have demonstrated complex seasonal controls over microbial respiration, nitrogen cycling, and phosphorus availability in an upland Oregon prairie. The few

related studies from California grasslands suggest similar sets of seasonal controls over these processes in Mediterranean grasslands. In our study, the relative importance of temperature and moisture varied among response variables, season, and sampling site. Overall, our results suggest that in Pacific Northwest prairies microbial respiration is limited by low temperatures in the winter and spring and by low soil moisture year-round. Net nitrogen mineralization and net nitrification are never limited by soil temperature, but both are limited by excessive soil moisture in winter, and net nitrification is also limited by low soil moisture in the summer. Factors that enhance microbial respiration tended to decrease soil phosphorus availability. It is likely that these seasonal dynamics have strong effects on plant community structure and the competitive dynamics of native and exotic plant species in these prairies (Pfeifer-Meister et al. 2008).

Considering current climate models for the Pacific Northwest, we would expect climate change to have the largest direct effects on carbon, nitrogen, and phosphorus cycling in the winter as all response variables measured responded to a change in moisture and/or temperature in this season. Under warmer, wetter winter conditions, we would expect soil respiration to increase and plant-available nitrogen and phosphorus to decrease. As plants are actively growing during the winter in the Pacific Northwest, these changes will have large effects on community structure, which in turn could feedback to nutrient cycling processes. To effectively restore and conserve the remaining prairies of the Pacific Northwest, it is essential to understand how major ecosystem processes will respond to changes in climatic factors and how they may interact with other edaphic factors to structure plant communities.

Bridge to Chapter V

In this chapter, we determined the seasonal and spatial controls over nutrient cycling in an upland prairie, Mt. Pisgah. Carbon, nitrogen, and phosphorus cycling were all limited by temperature and/or moisture in various seasons. Additionally, these rates were associated with other edaphic factors that varied considerably across the site. We hypothesized that this environmental heterogeneity was an important control over plant community structure, particularly over the distribution of native and exotic species. More specifically, we hypothesized that native species were being excluded from the high-quality habitats (i.e., nutrient-rich, moderately moist areas) and forced to take refuge in the nutrient-poor, wet areas. In Chapter V, we test this hypothesis by examining the competitive dynamics of two native and two exotic grasses in the field and in the greenhouse under varied nutrient and moisture conditions.

CHAPTER V

ABIOTIC CONSTRAINTS ON THE COMPETITIVE ABILITY OF NATIVE AND EXOTIC GRASSES IN A PACIFIC NORTHWEST PRAIRIE

A paper published in *Oecologia* and co-authored with Esther M. Cole, Bitty A. Roy and Scott D. Bridgham.

Pfeifer-Meister, L., E. Cole, B. A. Roy, and S. Bridgham. 2008. *Oecologia* 155: 357-366.

Introduction

Invasion by exotic species is recognized as a leading threat to native biodiversity and ecosystem functioning (Vitousek et al. 1997, Mack and D'Antonio 1998, Chapin et al. 2000). In prairie ecosystems, invasive species have been identified as a primary obstacle to successful restoration, and this has been attributed to their ability to competitively exclude native species (Ewing 2002). In particular, theory suggests that invasive species are competitively superior in high quality habitats (i.e., high nutrient and mesic moisture conditions), forcing native species to take 'refuge' in low quality habitats (Hoopes and Hall 2002, Lowe et al. 2003). However, empirical evidence to support this theory has been equivocal. Understanding how competition between native and exotic species interacts with abiotic factors to structure plant communities will be important for the conservation of native prairies.

Multiple studies have stressed the dependence of competition upon environmental conditions such as water, light, and nutrient availability (e.g., Lowe et al. 2003, Suding et al. 2004a, 2004b, Kluse and Allen Diaz 2005). However, results vary regarding how abiotic factors affect the ability of exotic species to competitively exclude native species. A variety of mechanisms can explain why the population sizes of native and exotic grasses may be negatively correlated (Parker et al. 1993). In some cases, native species are able to survive in stressful, low-nutrient environments, but are out-competed by aggressive exotics under high resource conditions (Huenneke et al. 1990, Maron and Connors 1996, Vinton and Burke 1997, Hamilton et al. 1999). For example, fertilization treatments that promoted growth in *Festuca idahoensis*, a perennial grass native to Pacific Northwest prairies, also facilitated success among aggressive exotic species, thereby reducing the positive effects on *F. idahoensis* (Ewing 2002). Similarly, some native perennial forbs and grasses in northern California were out-competed and replaced by exotic annual grasses in high nutrient environments, but were able to persist in low quality habitats (Murphy and Ehrlich 1986). In contrast, other studies show no effect of abiotic factors on competitive hierarchies between native and invasive plants. In northern California, the reduction of available nitrogen did not decrease the competitive suppression of native perennial bunchgrasses by exotic perennial and annual grasses over the course of two years (Corbin and D'Antonio 2004). Furthermore, water availability had no effect on the competitive outcome between a native and exotic grass in Canada (Bakker and Wilson 2001).

In previous research we observed large differences in the relative abundance of native and exotic plants in a remnant upland prairie in the Willamette Valley, Oregon

(unpublished data). In a multiple regression analysis, soil moisture and inorganic nitrogen availability explained 63% of the variation in the proportion of native to exotic species biomass ($p=0.003$). Areas with a high proportion of native biomass were wet and had low nitrogen availability, whereas a higher proportion of exotics were found in drier, nutrient-rich sites. We hypothesized native species were restricted to these low quality (nutrient poor and wet) sites due to competitive exclusion by exotic species. Therefore, the objective of our study was to test the competitive dynamics among four grass species under varying nutrient and moisture conditions. We examined two native perennial grasses, *Danthonia californica* and *Deschampsia cespitosa*, and two common exotics, *Schedonorus arundinaceus* and *Lolium multiflorum*. We hypothesized competitive hierarchies would change depending on abiotic conditions. Specifically, we predicted that the two invasive, exotic grasses would have greater competitive ability at high nutrient, moderate moisture conditions resulting in the displacement of native species from these environments. We performed a paired study of field and greenhouse experiments to test our hypotheses. In the field competition experiment, we examined the effects of aboveground competition, inferred from the removal of neighbors, on established juvenile plants in four areas in a remnant upland prairie. However, within this prairie, soil moisture, nutrient availability, and other environmental variables covaried in complicated ways, so that it was difficult to determine how abiotic factors affected competitive hierarchies in the field. Hence, we also performed a greenhouse experiment in which we experimentally manipulated nutrients and moisture and examined the response of each species in monoculture and interspecific competition trials.

Methods

Site Description

We conducted the field component of the study on Mt. Pisgah, a small mountain located within Lane County's Howard Buford's Recreation Area, approximately 11 km from Eugene, Oregon. Mt. Pisgah is vegetated primarily by oak savannah and upland prairie interspersed with Douglas fir (*Pseudotsuga menziesii*) infill. Four 9-m by 5-m blocks were randomly located at approximately 190-m elevation in an upland prairie across a 6.1-ha area on a south-facing hill-slope at the base of the 467-m high Mt. Pisgah. Across the site, soil attributes varied considerably. Soil depth ranged from 8-106 cm with a mean of 43 cm, % clay ranged from 42-68 with a mean of 57%, total % carbon ranged from 1.8-5.2 with a mean of 3.4%, and pH ranged from 5.6-7.1 with a mean of 6.5 (for soil methods see Pfeifer-Meister and Bridgham 2007).

The Willamette Valley is characterized by a Mediterranean climate with wet winters and mild, dry summers. Over the past 30 years, the mean annual daily maximum and minimum temperatures were 17.2°C and 5.0°C, respectively, and mean annual precipitation was 117 cm (National Climatic Data Center 2005).

Species Description

Danthonia californica Boland. is a tufted, native perennial bunchgrass (Pojar and MacKinnon 1994). Culms grow 30 to 100-cm tall bearing 2 to 5 spikelets on average (Hitchcock 1971). This species is commonly found from low to high elevations across a continuum of wet to dry prairie (Pojar and MacKinnon 1994), ranging from California to British Columbia along the west coast of North America (Hitchcock 1971).

Deschampsia cespitosa L. is a densely tufted, native perennial bunchgrass with 20 to 120-cm tall culms. This grass is found commonly from sea level to alpine elevations spanning a wet to dry prairie continuum (Pojar and MacKinnon 1994), although it is more common in wet environments. Within wetland habitats, *D. cespitosa* is found along the west coast of North America, as well as the northeastern United States (Hitchcock 1971).

Lolium multiflorum Lam. is a winter annual that germinates in the fall and generally flowers and produces seed the following spring (Pojar and MacKinnon 1994). Introduced from Europe, this species is grown extensively for commercial seed production, and its harvestable area covers over 47,000 ha of the Willamette Valley (Young 2005). *L. multiflorum* has spread across low elevation habitats in the Willamette Valley (Pojar and MacKinnon 1994), and its range extends along the west coast of North America (Hitchcock 1971). *L. multiflorum* culms can grow to 100-cm tall and typically have 10 to 20 spikelets per stalk (Hitchcock 1971). The earliest specimen at the Oregon State University Herbarium that documented the occurrence of *L. multiflorum* in the Willamette Valley was from 1884.

Schedonorus arundinaceus (Schreb.) Dumort., formerly *Festuca arundinacea* or *Lolium arundinaceum,* is an exotic perennial introduced from Europe for agricultural purposes (Pojar and MacKinnon 1994). The area occupied by cultivated fields of *S. arundinaceus* has increased from 4,000 hectares in 1979 to over 57,000 hectares in 2003 (Young 2005). *S. arundinaceus* is abundant in low to mid-elevation habitats, frequently colonizing fields, meadows, roadsides, or other disturbed areas (Pojar and MacKinnon

1994), with a range that extends along the west and east coasts of North America (Hitchcock 1971). *S. arundinaceus* is a tufted grass with flat, wide leaves and culms 50 to 100-cm tall (Pojar and MacKinnon 1994). The earliest specimen at the Oregon State University Herbarium that documented this Eurasian grass in the Willamette Valley was from 1918.

Field Competition Experiment

Our initial design called for experimental manipulation of competition on 12 naturally occurring juveniles of each grass species per 9-m by 5-m block. However, blocks were chosen randomly, and *D. cespitosa*, *L. multiflorum*, and *S. arundinaceus* juveniles were only found in two of the four blocks (n=24), and *D. californica* juveniles were located in all blocks (n=48). Substitute grass species were not available that occurred in all four blocks, and we decided to accept uneven occurrence of species in blocks rather than bias block selection.

A wire mesh ring, 5 cm in height and 23 cm in diameter, encircled each juvenile target plant. Juvenile individuals were classified by small size (2-5 cm tall) and small number (1-3) of emergent shoots. We established three levels of aboveground competition by clipping all vegetation surrounding the target individual within the ring for 100% competition reduction, clipping two diagonally oriented quarter sections for 50% competition reduction, and not clipping for 0% competition reduction. Clipping commenced on March 13, 2004 at the beginning of the growing season and was maintained every week until each species reached peak standing biomass. At the end of the experiment, length, width, and vegetative height of each target plant was measured *in*

situ to evaluate growth morphology. Length was the longest horizontal dimension of the plant, while width was the horizontal distance perpendicular to the length. *L. multiflorum*, the only non-perennial in the study, produces reproductive stalks exclusively. Thus, in analyses of basal area:height ratio, we used the reproductive height for *L. multiflorum* while using vegetative height for all other species. In addition to measurements of plant morphology, each target plant was also clipped at the base and dried at 60°C for 48 h. We harvested *D. californica* on May 31, *S. arundinaceus* and *L. multiflorum* on June 9, and *D. cespitosa* on June 16, 2004, the date at which each species reached peak standing biomass. We weighed the dry aboveground biomass of each plant and separated out the seeds produced. Seeds were cleaned and counted by hand or by using a Pfeuffer Contador seed counter (Kitzigen, Germany).

To evaluate significant effects of competition on aboveground biomass and basal area:height ratio, we analyzed data from each species separately using a two-way ANOVA with competition as a fixed main effect and block as a random main effect. As seed count was highly correlated with aboveground biomass (r =0.92), only biomass data is presented, but similar trends were observed for both variables. We log-transformed all data to normalize the distribution of residuals and used Tukey's pairwise comparisons to evaluate significant differences among competition levels within a species. All statistical analyses were performed using SPSS 11.0 for Windows.

Greenhouse Competition Experiment

In the greenhouse, we examined the growth of each grass species in monoculture and in all combinations of pairwise competition. These competition treatments were

crossed with three levels of soil moisture and two levels of soil nutrient availability that were representative of field conditions. Each treatment contained four replicate pots. We obtained seeds from local suppliers of native plants or from fields near the location of the study site. Seeds obtained commercially represented genotypes from local prairies within the southern Willamette Valley. The seeds were cold-treated at 5° C for 30 days and then germinated at 20° C for 10 days in Petri dishes wetted with giberellic acid solution (1000 mg/L) to ensure greater germination success and similar germination dates (Atwater 1980; Roy et al. 1999). We used fine-grain sand for the soil substrate, and placed four germinated seeds 5 cm away from their nearest neighbor in a square formation. Seeds were planted in circular pots 16.5 cm in diameter and 18-cm deep. Monoculture pots included four plants of the same species. Interspecific competition pots contained two plants of a given species on opposite corners of the competition square and two plants of another species in the remaining corners.

Each competition treatment was crossed with two levels of nutrient availability and three levels of moisture, representing a continuum from wet to dry prairie. In the high moisture treatment, we placed pots in slightly larger containers and maintained the water level at 2.5 cm below the soil surface. Water was replaced bi-weekly. In the medium moisture treatment, we watered pots to field capacity every other day. To allow establishment of seedlings, we initially maintained plants in the low moisture treatment in the same manner as plants in the medium moisture treatment. Eight weeks into the experiment we reduced the frequency of water applications to twice a week in the low moisture treatment pots. We established the water schedule by a visual examination of

wilting in the plants. Our goal was to induce water stress without causing high mortality. All water added was deionized.

We based the low nutrient treatment upon calculations of *in situ* nutrient uptake into vegetation in the portion of the remnant prairie with the lowest nutrient availability and lowest productivity, while the high nutrient treatment was ten times that concentration. In the low nutrient treatment, we added 50 mg N and 3 mg P per pot in the form of NH_4NO_3 and Na_2HPO_4, respectively. We added potassium, calcium, magnesium, and trace nutrients in equal amounts to all treatments based on ratios dictated by standard Hoagland's solution (Hoagland and Arnon 1938), so that plants were limited only by nitrogen and phosphorus. Nutrients were added weekly in 100-mL aliquots of solution with deionized water.

The greenhouse was unheated, but was cooled when the temperature rose above 33 °C, thus the temperatures varied between 4.4 and 35 °C, conditions typical of the growing season within the Willamette Valley (National Climatic Data Center 2005). The light system simulated a 16-hour photoperiod. All pots were randomly assigned positions in the greenhouse and were moved bi-weekly so that environmental variation and shading by neighboring plants was randomized. The experiment spanned 90 days. At the end of the experiment, plants were harvested by separating the above- and belowground biomass for each species. The biomass was dried for 48 hours at 60°C and weighed. The few plants that died prior to the end of the experiment were immediately removed and dried.

We examined all species in monoculture using a three-way ANOVA to evaluate significant effects of species, nutrients, and moisture on total biomass using SPSS 11.0 for Windows. Within species, we used a three-way ANOVA and Tukey's pairwise

comparisons to evaluate significant effects of competition, nutrients, and moisture on total biomass and root:shoot ratio. To determine the importance of intra- and interspecific competition on total biomass, relative competitive yield (RCY) was calculated for each species combination as

$$RCY = Y_{ij}/Y_i$$

where Y_{ij} is the mean biomass of individuals of species *i* grown with species *j* and Y_i is the mean biomass of individuals of species *i* grown in monoculture (Harper 1977; Wetzel and van der Valk 1998). A RCY greater than one indicates that intraspecific competition had a greater effect on total biomass than interspecific competition, and a value less than one indicates that interspecific competition had a greater effect on total biomass than intraspecific competition. To test whether individual species combinations were significantly different than one, one-sample t-tests were performed. For all analyses, pots were used as the replicate unit, and data were log-transformed to normalize the distribution of the residuals.

Results

Field Experiment

Overall, differing degrees of aboveground vegetation removal affected the growth patterns in three of the four species (Table 5.1, Fig. 5.1). *Danthonia californica*, a native, did not produce more aboveground biomass in response to a reduction in neighbors, but plants with fewer neighbors had a greater basal area:height ratio, i.e., they were wider and shorter (Table 5.1, Fig. 5.1). Removing vegetation had no effect on aboveground biomass or the basal area:height ratio of *D. cespitosa*, the other native species (Table 5.1,

Fig. 5.1). However, *D. cespitosa* grew marginally taller (p=0.055) with more neighbors (data not shown). *Lolium multiflorum,* an exotic annual, was the only species to show an aboveground biomass response to vegetation removal, with the most aboveground biomass in the 100% aboveground competition reduction treatment (Table 5.1, Fig. 5.1). Similarly, the basal area:height ratio was greatest in the 100% competition reduction treatment (Fig. 5.1). *Schedonorus arundinaceus*, an exotic perennial, had a greater basal area:height ratio with 100% neighbor removal than in the 0% competition reduction treatment (Table 5.1, Fig. 5.1).

Table 5.1. Results of two-way ANOVA for aboveground biomass and basal area:height ratio of each species in the field experiment, p-values <0.05 are in bold.

	D. californica			*D. cespitosa*			*L. multiflorum*			*S. arundinaceus*		
	F	df	p	F	df	p	F	df	p	F	df	P
Aboveground Biomass												
Competition	0.50	2	0.63	0.23	2	0.81	7.16	2	**0.005**	1.27	2	0.44
Block	15.3	3	**0.003**	3.46	1	0.20	2.46	1	0.13	4.52	1	0.17
Competition*Block	0.92	6	0.49	1.01	2	0.38	2.80	2	0.087	0.39	2	0.69
Basal Area:Height Ratio												
Competition	21.8	2	**0.002**	2.19	2	0.14	14.2	2	**0.002**	18.8	2	**0.050**
Block	3.77	3	0.078	0.32	1	0.58	0.38	1	0.60	0.82	1	0.46
Competition*Block	0.98	6	0.45	2.09	2	0.15	1.08	2	0.36	0.16	2	0.85

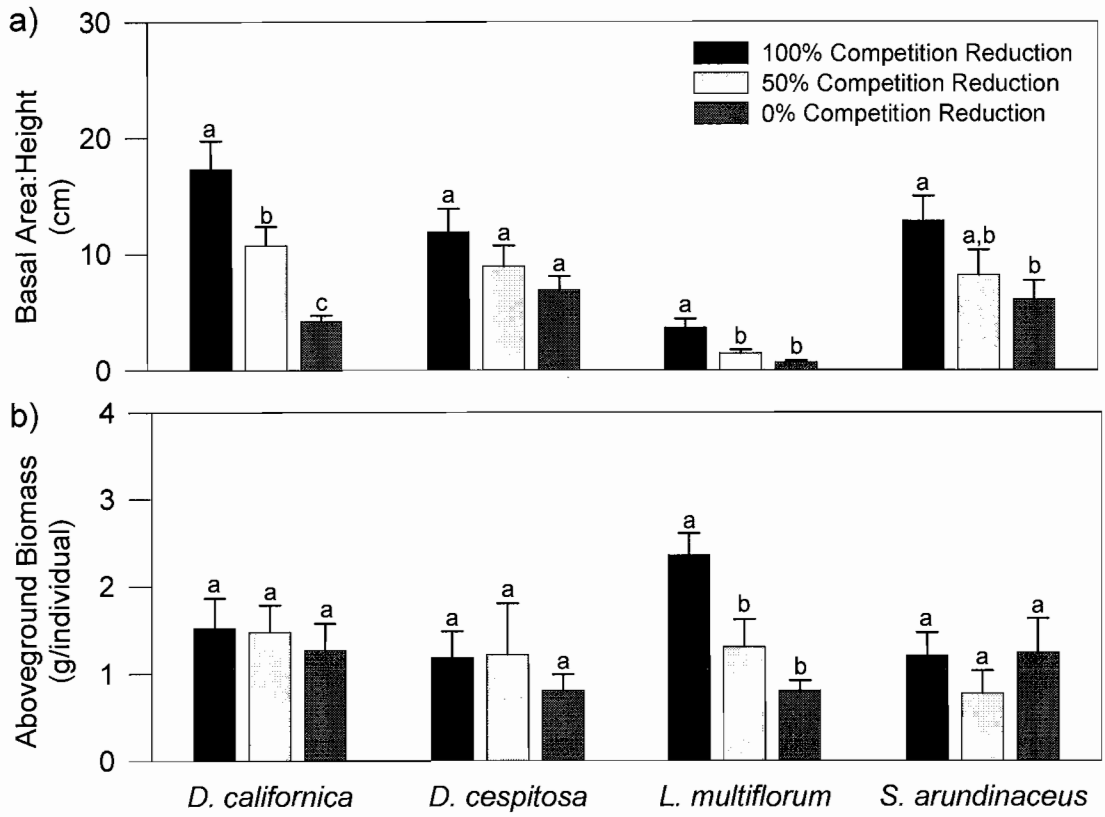


Figure 5.1. Basal area:height (a) and aboveground biomass (b) of *Danthonia californica* (n=16), *Deschampsia cespitosa* (n=8), *Lolium multiflorum* (n=8), and *Schedonorus arundinaceus* (n=8) for 0, 50, and 100% competition reduction in the field. Error bars represent one standard error from the mean. Lower case letter differences indicate significant effects ($p < 0.05$) of competition within a species.

Greenhouse Experiment

Plants in Monoculture

To evaluate species growth responses to the nutrient and moisture treatments in the absence of the interspecific competition treatments, we analyzed results separately for the monoculture pots. Nutrient availability, moisture availability, species, and all of the interactions among these main effects significantly affected plant biomass ($p<0.017$).

Despite the significant interactions, clear differences in the amount of biomass produced by different species were evident (overall means = *D. californica* 0.0315 g ± 0.006, *D. cespitosa* 0.287 g ± 0.059, *S. arundinaceus* 2.629 g ± 0.325, *L. multiflorum* 3.688 g ± 0.059). In monoculture, native species produced less biomass than exotics ($p<0.001$), and *L. multiflorum*, the only annual, produced significantly more biomass than the three perennial species ($p<0.001$). Treatment effects on the species are discussed subsequently in terms of plants grown in combination with other species.

Interspecific Competition (Two-Species Polycultures)

The effect of nutrients on total biomass production in *D. californica* depended on moisture level (Table 5.2, Fig. 5.2). *D. californica* was only able to exploit the increase in nutrients in the high moisture treatment. The competition treatment alone or in interaction with the nutrient or moisture treatments had no effect on *D. californica* (Table 5.2, Fig. 5.3). The ratio of roots to shoots depended upon moisture treatment; a greater proportion of the biomass was allocated to roots in the low moisture treatment than in the high moisture treatment (Table 5.2, Fig. 5.4).

Similarly, *D. cespitosa* responded positively to high nutrient concentrations only in the high moisture treatment (Table 5.2, Fig. 5.2). *D. cespitosa* produced more biomass in monoculture than when grown with the exotic annual, *L. multiflorum* ($p=0.027$), but the effect of the competition treatment never depended upon abiotic treatments (Table 5.2, Fig. 5.3). The root:shoot ratio of *D. cespitosa* decreased with higher nutrient availability (Table 5.2, Fig. 5.4).

Table 5.2. Results of three-way ANOVA for total biomass and root:shoot ratio of each species in the greenhouse experiment, p-values<0.05 are in bold.

	D. californica			*D. cespitosa*			*L. multiflorum*			*S. arundinaceus*		
	F	df	p	F	df	p	F	df	p	F	df	P
Total Biomass												
Nutrients	2.34	1	0.13	12.2	1	**0.001**	191.2	1	**<0.001**	58.9	1	**<0.001**
Moisture	5.91	2	**0.004**	9.25	2	**<0.001**	0.53	2	0.59	3.29	2	**0.043**
Competitor Identity	0.46	3	0.71	3.28	3	**0.026**	5.77	3	**<0.001**	20.7	3	**<0.001**
Nutrients*Moisture	3.07	2	**0.053**	5.10	2	**0.009**	0.36	2	0.70	15.2	2	**<0.001**
Nutrients*Comp.	1.28	3	0.29	0.47	3	0.71	4.91	3	**0.004**	4.68	3	**0.005**
Moisture*Comp.	0.42	6	0.86	1.95	6	0.084	1.50	6	0.19	8.07	6	**<0.001**
Nutr.*Moist.*Comp.	0.52	6	0.74	0.33	6	0.92	0.59	6	0.74	0.91	6	0.49
Root:Shoot Ratio												
Nutrients	0.56	1	0.46	7.57	1	**0.008**	5.40	1	**0.023**	79.1	1	**<0.001**
Moisture	3.42	2	**0.038**	0.28	2	0.76	2.30	2	0.11	1.57	2	0.22
Competitor Identity	0.82	3	0.49	1.80	3	0.16	1.18	3	0.32	2.14	3	0.10
Nutrients*Moisture	0.87	2	0.42	1.44	2	0.25	0.71	2	0.50	1.75	2	0.18
Nutrients*Comp.	0.50	3	0.67	1.40	3	0.25	0.35	3	0.79	1.19	3	0.32
Moisture*Comp.	1.05	6	0.40	0.55	6	0.77	1.07	6	0.39	2.83	6	**0.016**
Nutr.*Moist.*Comp.	0.55	6	0.77	0.73	6	0.63	0.45	6	0.84	0.84	6	0.54

Although *L. multiflorum* biomass was consistently greater in the high nutrient treatment, the effect of the competition treatment differed between low and high nutrient conditions (Table 5.2, Fig. 5.3). Under high nutrient conditions, *L. multiflorum* was able to produce more biomass when grown with *S. arundinaceus* than in monoculture. However, under low nutrient treatments, *L. multiflorum* produced more biomass when grown with *D. californica*. *L. multiflorum* allocated more biomass belowground in the low nutrient treatment than in the high nutrient treatment (Table 5.2, Fig. 5.4).

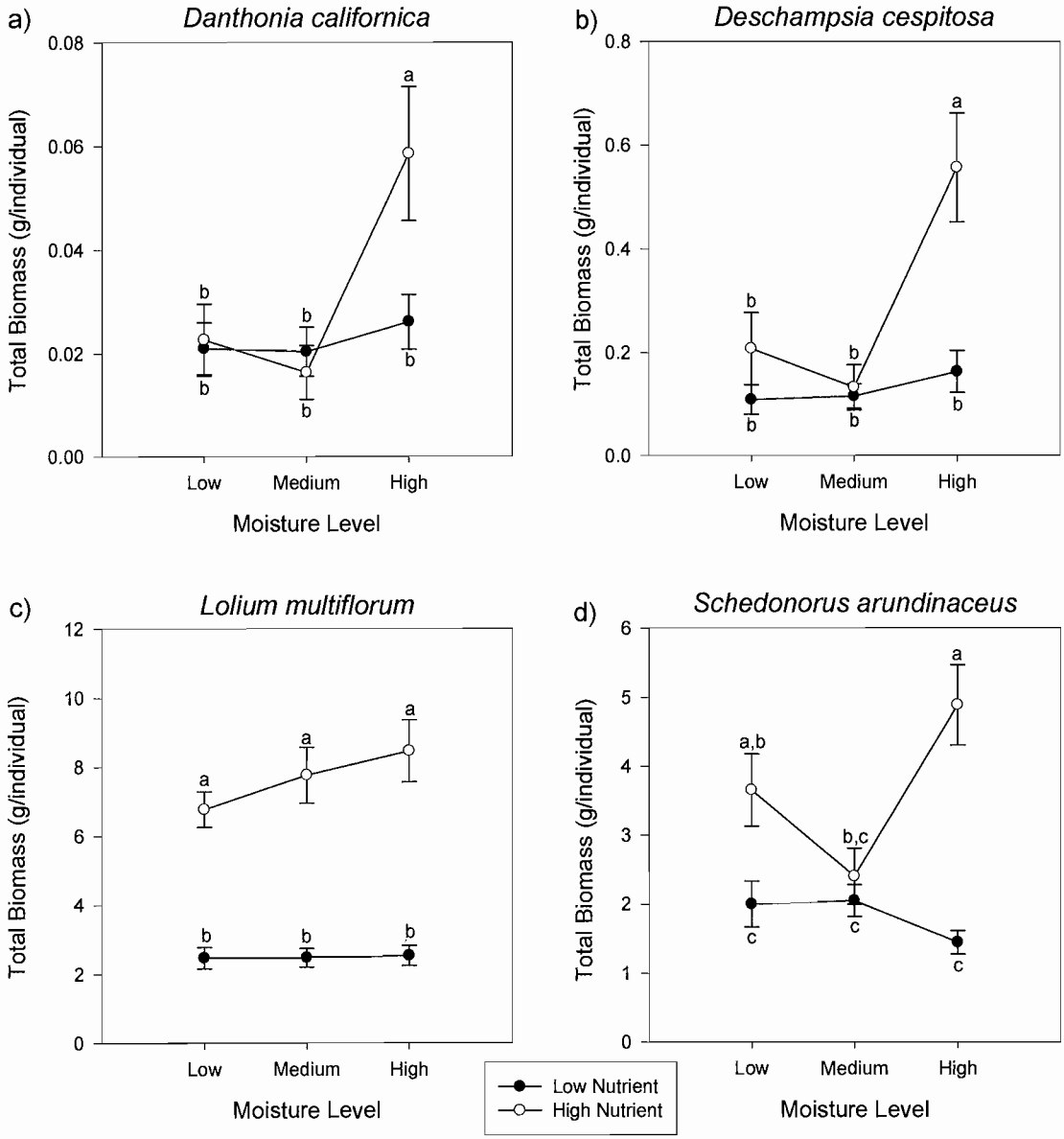


Figure 5.2. Interaction between nutrients and moisture in the greenhouse experiment for total biomass of a) *Danthonia californica*, b) *Deschampsia cespitosa*, c) *Lolium multiflorum*, and d) *Schedonorus arundinaceus* (n=16) across all species combinations. Error bars represent one standard error from the mean. Different lower case letters indicate significant ($p < 0.05$) treatment effects.

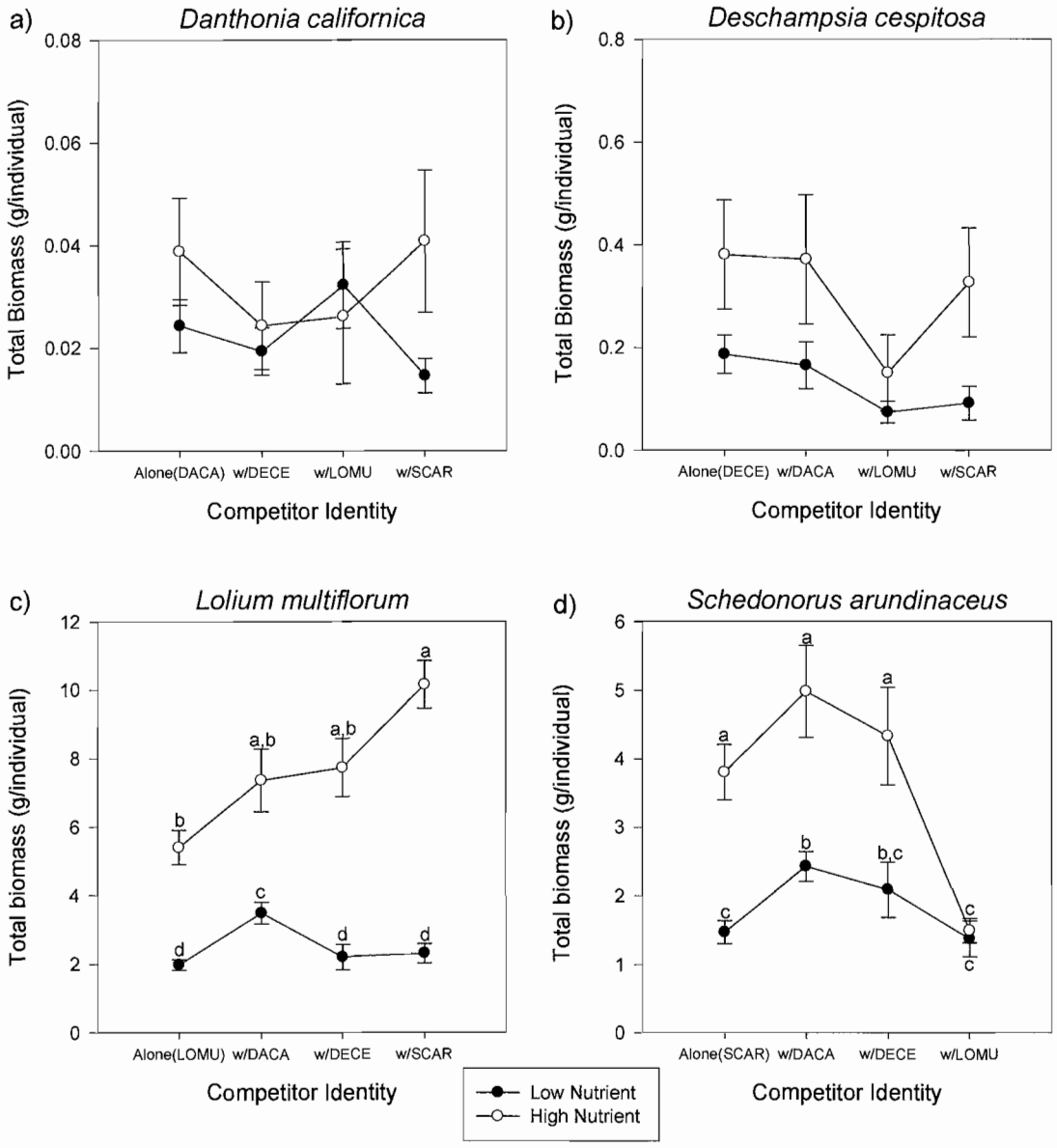


Figure 5.3. Total biomass per individual of a) *Danthonia californica*, b) *Deschampsia cespitosa*, c) *Lolium multiflorum*, and d) *Schedonorus arundinaceus* among competition levels (monoculture: Alone; Interspecific competition: w/SCAR = with *S. arundinaceus*, w/LOMU= *L. multiflorum*, w/DACA= with *D. californica*, w/DECE= with *D. cespitosa*) for low and high nutrient concentrations in the greenhouse (n=12). Error bars represent one standard error from the mean, and lower case letter differences indicate significant effects ($p<0.05$).

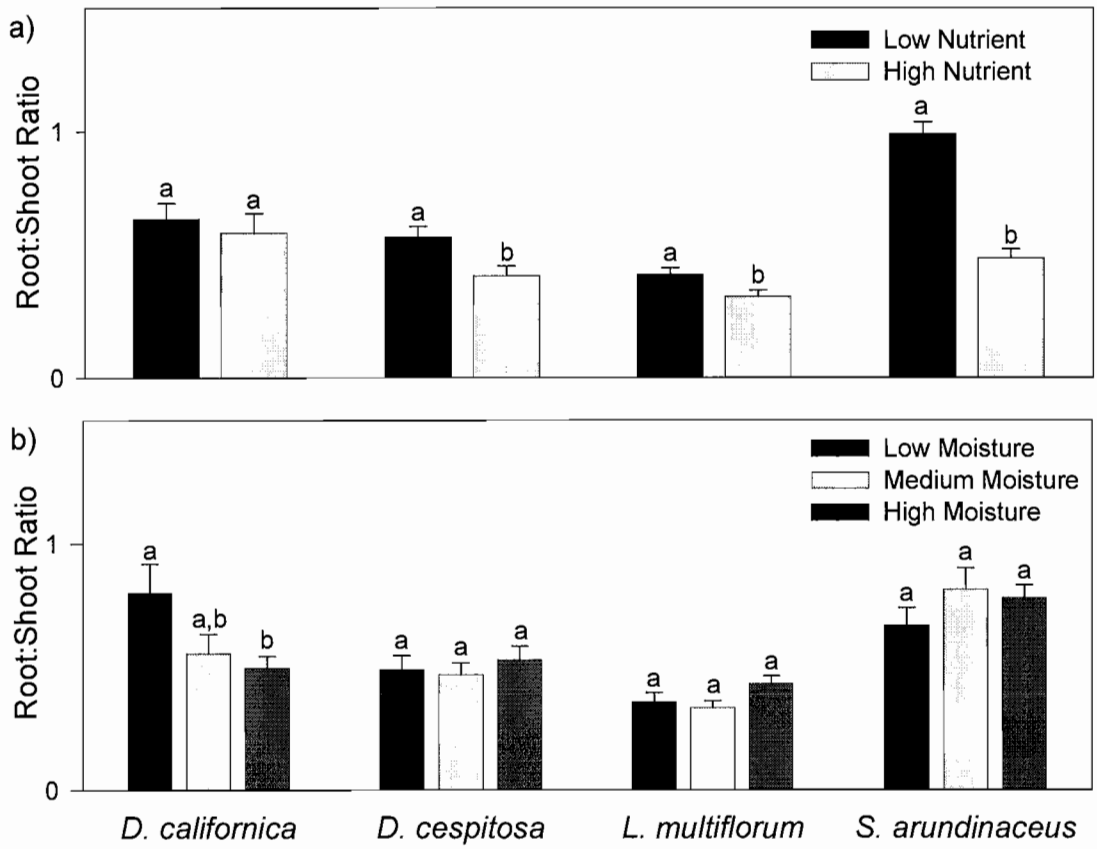


Figure 5.4. Ratio of roots to shoots in the greenhouse of *Danthonia californica*, *Deschampsia cespitosa*, *Lolium multiflorum*, and *Schedonorus arundinaceus* among nutrient concentrations (panel a, n=48) and moisture levels (panel b, n=32). Error bars represent one standard error from the mean, and lower case letter differences indicate significant effects ($p<0.05$) within species.

Total biomass of *S. arundinaceus* within moisture treatments depended on nutrient availability (Table 5.2, Fig. 5.2). Under high nutrient conditions, *S. arundinaceus* had greater total biomass in the high moisture treatment than in the medium moisture treatment. There were no differences in total biomass among moisture levels in the low nutrient treatment. Additionally, the response of *S. arundinaceus* to the

competition treatment depended on nutrient availability (Table 5.2, Fig. 5.3). Total biomass did not differ between low and high nutrient levels when grown with *L. multiflorum*, suggesting that competition with *L. multiflorum* prevented *S. arundinaceus* from capitalizing on the increase in nutrient concentrations. Finally, the effect of the competition treatment on total biomass of *S. arundinaceus* also depended on moisture availability (Table 5.2). When grown with *D. cespitosa*, *S. arundinaceus* produced more biomass in the low moisture treatment than in the medium moisture treatment. When grown with *L. multiflorum*, the least amount of biomass was produced in the low moisture treatment. A greater proportion of biomass was allocated to roots in the low nutrient treatment (Table 5.2, Fig. 5.4). Additionally, the effect of the competition treatment on the root:shoot ratio depended upon moisture level; plants grown with *L. multiflorum* had a greater proportion of roots in the medium moisture treatment than in the low moisture treatment ($p=0.043$).

Relative Competitive Yield

The relative competitive yield (RCY) for each species was calculated across all nutrient and moisture treatments to determine the importance of intra- and interspecific competition on total biomass (Fig. 5.5). For the two exotic species, *L. multiflorum* and *S. arundinaceus*, the RCY was greater than one, suggesting intraspecific competition had a greater effect on total biomass than interspecific competition, with one exception: when *S. arundinaceus* was grown with *L. multiflorum*, the RCY was less than one ($p<0.01$), suggesting interspecific competition was more important than intraspecific competition. For the two native species, *D. californica* and *D. cespitosa*, the RCY was either less than or not significantly different than one, suggesting intraspecific competition never exerted

a greater influence on total biomass than interspecific competition. For *D. californica*, the RCY was less than one when grown with *D. cespitosa* ($p<0.05$), and for *D. cespitosa*, the RCY was less than one when grown with the two exotics, *L. multiflorum* and *S. arundinaceus* ($p<0.05$).

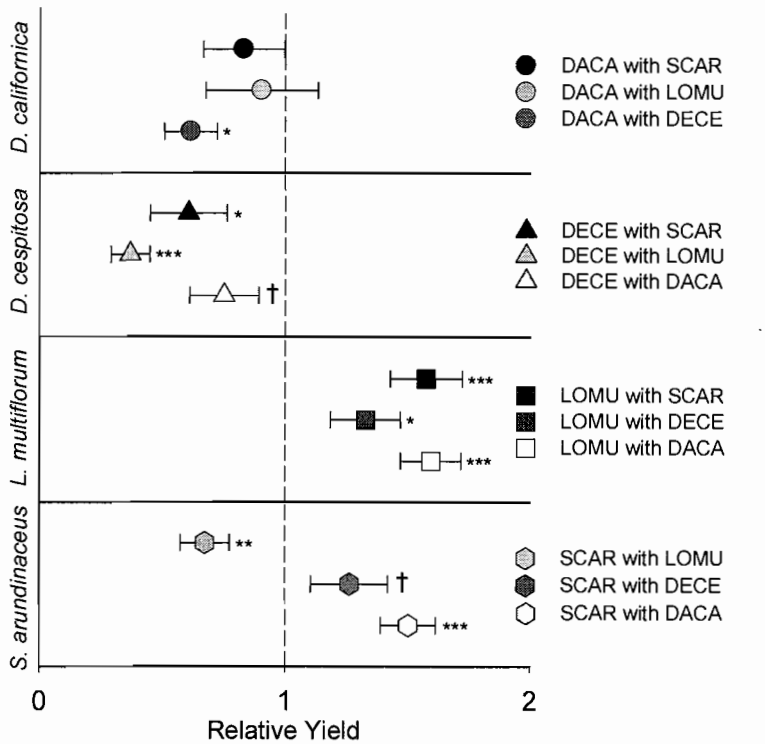


Figure 5.5. Total biomass relative competitive yield (± standard error) for *Danthonia californica* (DACA), *Deschampsia cespitosa* (DECE), *Lolium multiflorum* (LOMU), and *Schedonorus arundinaceus* (SCAR) in the greenhouse (n=24). Values less than one indicate that interspecific competition is greater than intraspecific competition and values greater than one indicate that intraspecific competition is greater than interspecific competition. Each species combination was tested if significantly different than one (* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$, † = $p<0.10$).

Discussion

The paired field and greenhouse studies strengthened our ability to understand how competition interacted with abiotic environmental variables to determine species

dominance in a remnant prairie. In the field experiment, we were able to determine if competition, inferred from a removal of neighbors, is important within the natural environment, but as many environmental variables covary and are not easily isolated in the field, we moved to the greenhouse to tease apart how nutrients, moisture, and competition interacted to determine species dominance. Previous research conducted in 2003 and 2004 (unpublished data) showed the relative distribution of native and exotic species was correlated with moisture and nutrient availability, with a higher proportion of native species biomass occurring in nutrient poor, wet sites. In the mesic areas, exotic grasses appeared to form dense monocultures (Simpson's diversity vs. exotic grass biomass; r =-0.69, p =0.003), which we hypothesized was due to the competitive exclusion of native species from these environments. The exclusion of native species could also be explained by their limited seed availability, rather than by their low competitive ability (Seabloom et al. 2003a, 2003b). However, neighboring stands of each species provided ample seed supply across the prairie, so seed limitation was unlikely within our study area.

In our field experiment, we verified the four grass species were competing within the natural environment. The amount of aboveground competition influenced plant morphology; all four species grew to cover at least a marginally larger area and/or shorter height when surrounding vegetation was removed. These changes in morphology will likely translate into increased biomass and seed count during successive seasons due to increased light capture ability (Schmitt and Dudley 1996). Similarly, Wilson and Shay (1990) found that basal circumference increased in perennial grasses when neighbors were removed in a Canadian mixed-grass prairie. *L. multiflorum*, the only non-perennial,

was able to capitalize on the reduction in competition to produce more aboveground biomass which was highly correlated (r =0.92) with seed production.

The greenhouse experiment supported our main hypothesis that competitive hierarchies change with abiotic conditions, but only for the two exotic grasses. The competitive success of *L. multiflorum* and *S. arundinaceus* depended upon nutrient availability (Fig. 5.3), and the competitive success of *S. arundinaceus* further depended upon moisture. However, the details of these interactions did not clearly support our more specific hypothesis that aggressive exotic species have a greater competitive ability at high nutrient, moderate moisture conditions. Under low nutrient conditions, *L. multiflorum* produced the most biomass when in competition with *D. californica*, whereas in high nutrient treatments, *L. multiflorum* produced the most biomass when in competition with *S. arundinaceus*. *L. multiflorum* is the stronger competitor of the two exotics as it was able to prevent *S. arundinaceus* from capitalizing on high nutrient availability (Fig. 5.3). This was also supported in the relative competitive yield calculations, where intraspecific competition always had a greater effect on *L. multiflorum* than interspecific competition, and the only competitive interaction for *S. arundinaceus* that had a greater influence on total biomass than intraspecific competition was with *L. multiflorum*. *L. multiflorum* is an annual, and this may reflect annual grasses being generally more competitive than perennial grasses under high nutrient conditions. For example, Lowe et al. (2003) showed that as nitrogen availability increased, the annual exotic grass *Bromus tectorum* dominated the native perennial grass *Bouteloua gracilis*, and intraspecific competition was more significant than interspecific competition for the exotic grass while the reverse was true for the native grass.

Abiotic factors never affected the competitive outcome for the two native species, *D. cespitosa* and *D. californica* in the greenhouse. The native *D. cespitosa* was least competitive when in combination with *L. multiflorum*, but this did not depend on moisture or nutrient conditions. In general, the two native species attained a much smaller size than the two invasive species, and their biomass production and allocation appeared to be primarily controlled by abiotic factors and not competition (Figs. 5.2, 5.4). Although this result is consistent with findings in other West Coast prairies (Bakker and Wilson 2001, Corbin and D'Antonio 2004), some studies have observed an interaction between abiotic factors and competition for native species. For example, in a California montane meadow, the competitive ability of *D. cespitosa* decreased at very low soil moisture (Kluse and Allen Diaz 2005). In a California grassland, the native perennial, *Sporobolus airoides*, had lower survival at higher ammonium concentrations when in competition with the exotic annual, *Bromus diandrus* (Hoopes and Hall 2002). However, in this latter study, differences in timing of establishment could explain this effect. Rather than planting germinated seedlings into their competition plots, seeds were scattered and allowed to establish naturally. In our study site, the annual exotic grasses, including *L. multiflorum*, germinate much earlier than the perennial natives (personal observation). As we did not consider timing of germination in our experiment, we are not able to rule out the possibility that natives are excluded from the mesic habitats due to differences in establishment dates.

Three of the grasses had the greatest growth response to high nutrients at the highest moisture level (Fig. 5.2). The exception was *L. multiflorum,* which consistently produced more biomass under high nutrient conditions regardless of moisture

availability. In addition, *D. cespitosa*, *L. multiflorum*, and *S. arundinaceus* allocated more resources belowground in the low nutrient treatment, and *D. californica* had a higher root:shoot ratio in the low moisture treatment than in the high moisture treatment (Fig. 5.4). The competitiveness of *S. arundinaceus* depended on moisture, but in a complicated manner that did not support our hypothesis.

The field experiment supported the importance of competition *in situ*, and the greenhouse experiment supported our main hypothesis that competitive hierarchies change depending on abiotic conditions, but only for the two exotic species. However, our more specific hypothesis, that the aggressive exotic species, *S. arundinaceus* and *L. multiflorum,* have a greater competitive ability at high nutrient, moderate moisture conditions, was not consistent with the results from the greenhouse experiment. Furthermore, we found no support that native species were preferentially excluded from nutrient rich, moderately wet environments, but we can not rule out timing of germination as an important factor in contributing to the exclusion of native species in the field. The large average size of *L. multiflorum* when grown in monoculture, its large absolute and relative response to nutrient additions irrespective of moisture conditions, and its greater overall competitiveness in the greenhouse pairs support a conclusion that this invasive species is a very potent competitor with both native and exotic species. However, the competitive ability of perennial species may increase over multiple growing seasons. The factors contributing to plant community structure are complex, but our experiment shows that even within a single growing season, competition, nutrients, and moisture influence plant success and determine interactions between native and exotic species.

CHAPTER VI

CONCLUSIONS AND RESTORATION IMPLICATIONS

"The next century will, I believe, be the era of restoration in ecology."—E.O. Wilson

Restoration ecology is an emerging discipline and provides an ideal opportunity to test basic ecological theories. Over the past twenty years, ecologists have begun testing theories of succession, competition, disturbance, and invasion within a restoration framework, but there is still considerable potential for integration. With this dissertation, I attempt to advance this emerging field and build upon the collective knowledge base by examining multiple controls over plant community structure and ecosystem functioning. In particular, I examined the roles of succession, competition, and environmental heterogeneity in structuring plant communities and controlling ecosystem function within remnant and restored prairies of the Willamette Valley, Oregon.

Summary of Results

1. In restored wetland prairies, site preparation techniques resulted in different initial successional trajectories of plant communities, but over time, these communities converged due to a loss of early-successional species and the increasing dominance of native perennial bunchgrasses. The net result was a progressive

decrease in diversity each year. Site preparation techniques also had minimal impacts on belowground function, with the exception of topsoil removal, which, even after five years, resulted in significantly less microbial biomass, mycorrhizal colonization, and net primary productivity than other treatments.

2. Restored wetland prairies never attained the overall species richness found in high-quality remnant wet prairies. In the restored sites, native perennial bunchgrasses dominated plant communities, which resulted in a tradeoff with species diversity. Areas of high diversity tended to have low native cover, particularly of native bunchgrasses, and vice versa. Finding ways to mitigate this tradeoff between high native cover and high diversity through an understanding of both site preparation and seeding protocols as part of successional management may be a critical step toward establishing wetland prairie communities with the desired characteristics.
3. Remnant prairies had higher exotic species cover, diversity, and productivity than restored prairies, suggesting that current site preparation techniques are effective in initially eliminating the exotic vegetation and seed bank. However, it is not clear that restored sites will remain resistant to invasion over the long term without active management.
4. Wetland prairies of the Willamette valley were not significant producers of the greenhouse gasses, methane and nitrous oxide. In every season, rates of methane and nitrous oxide production were zero. This is apparently due to a co-limitation of nitrate and carbon in these systems (unpublished data).

5. The competitive hierarchies for exotic grasses (commonly found in both upland and wetland prairies) were dependent upon nutrient and/or moisture availability within a single growing season. Although abiotic factors affected the growth and reproduction of native grasses, the competitive outcomes were not influenced by nutrient and moisture availability. Instead, in the first year of growth, native perennial grasses were poor competitors with exotic grasses regardless of abiotic conditions. However, the competitive ability of native perennials may increase over multiple years, particularly with exotic annuals.
6. In an upland prairie, carbon, nitrogen, and phosphorus cycling were controlled by temperature and/or moisture, and various edaphic factors (e.g., total carbon and percent clay content). Microbial respiration, net nitrogen mineralization, net nitrification, and phosphorus availability all responded to experimentally manipulated temperature and moisture treatments, particularly in the winter. As current climate change models predict warmer, wetter winters in the Pacific Northwest, my results suggest that we would see an increase in soil respiration and decrease in plant-available nitrogen and phosphorus during these months.

Implications for Restoration and Conservation

Understanding the complex interactions between biotic and abiotic factors in controlling ecosystem function and plant community structure is essential for effective restoration in general and conservation of Willamette Valley prairies in particular. My results suggest that succession, competition, and environmental heterogeneity all are important controls of plant community structure and thus, should be considered when

attempting to restore diverse wet and dry prairie ecosystems. In particular, it is important to develop a successional framework for managing plant community change over time. This begins with site preparation treatments to control exotic species and establish native plant diversity. However, my results suggest that successful initial establishment of native species may need to be followed by other types of management disturbances over time, such as fire, to help maintain diversity by reducing the dominance of highly competitive species.

When restoring a site, it also is important to consider the criteria for 'success' of mitigation projects. If only one criterion is examined, restorations could be deemed 'successful' despite having dramatically different ecosystem functioning and diversity than high-quality remnant prairies. For example, if mitigation success is based solely upon high native plant cover, my results suggest that heavily seeding with native perennial bunchgrasses would likely meet this criterion, but at a cost to diversity. If the ultimate goal is a highly diverse native community, then allowing forbs and other subdominant species to establish first, followed by a light seeding of native bunchgrasses may be a more appropriate approach. Furthermore, once plants have been established, periodic disturbances may be necessary to maintain the subdominant native species. Establishing prairie restorations that can sustain both high cover and high species diversity with relatively low amounts of maintenance is a challenge that remains to be resolved.

One promising finding is that restored wetland prairies with intact hydrology relatively rapidly attained a more 'natural' belowground state, resembling soil functioning in the remnant prairies. For the soil variables measured, I observed minimal

impacts on belowground functions after site preparation, with the exception of the more intensive technique, topsoil-removal. These results suggest restoration practitioners can focus on establishing diverse, productive plant communities and that 'soil functioning will follow' as long as the site preparation does not involve a significant disruption to the soil structure and the hydrology is intact. Further research is needed to determine what impacts site preparation may have on specific members of the soil microbial community.

Once restored, land managers must also consider the competitive hierarchies between native and exotic species, and how these hierarchies will be influenced by the abiotic environment. My results suggest that exotic grasses are competitively superior to native grasses in a single growing season; however, further research is needed to determine if this is true over multiple growing seasons and for native versus exotic forbs as well. Determining under what conditions native species may be competitively superior will be important for maintaining native populations in remnant and restored prairies. Finally, it is necessary to consider how a changing climate will affect plant community structure and ecosystem function. I began to touch on this by determining how changing moisture and temperature conditions affected nutrient cycling, but this area warrants further research, including how a changing climate will affect plant species distributions.

In conclusion, one measure of successful ecological research is the degree to which the findings are employed to solve real-world environmental problems. The research presented in this dissertation is already informing local restoration activities. As one City of Eugene employee stated, "This work has transformed the way prairie

restoration is done in the Willamette Valley" (Trevor Taylor, Wetlands Program Supervisor).

APPENDIX A

CHAPTER II SUPPLEMENTAL TABLES AND FIGURES

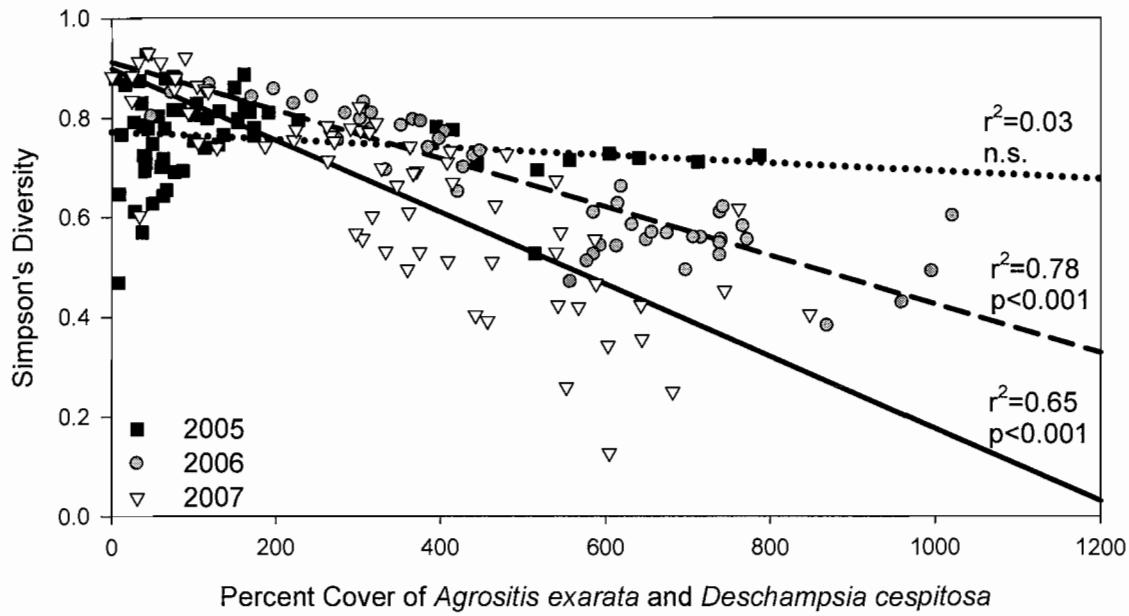
Supplemental Table 2.1. Species axis loadings for NMS ordination of experimental treatments, reference sites, and farm field (see Fig. 2.5). Only significant ($p<0.05$) indicator species are reported. Native (N) and exotic (E) origin, life history (A: annual, B: biennial, and P: perennial), and functional group (G: graminoid, F: forb, and W: woody) are given for each species.

Species	Axis 1 Loading	Axis 2 Loading	Species Origin	Life History	Functional Group
Lolium multiflorum	-1.07	-0.97	E	A	G
Juncus bufonius	-0.74	-0.64	N	A	G
Epilobium densiflorum	-0.48	-0.16	N	A	F
Cicendia quadrangularis	-0.43	-0.32	N	A	F
Sonchus asper	-0.37	-0.34	E	A	F
Lactuca serriola	-0.36	-0.26	E	A/B	F
Carex densa	-0.30	0.02	N	P	G
Madia elegans	-0.13	0.21	N	A	F
Agrostis exarata	-0.05	0.46	N	P	G
Hypochaeris radicata	-0.03	-0.22	E	P	F
Madia glomerata	0.11	0.00	N	A	F
Prunella vulgaris	0.14	0.08	N	P	F
Deschampsia cespitosa	0.22	0.47	N	P	G
Rumex crispus	0.24	-0.30	E	P	F
Cynosurus cristatus	0.44	0.06	E	P	G
Eryngium petiolatum	0.55	-0.39	N	P	F
Symphyotrichum hallii	0.62	-0.20	N	P	F
Parentucellia viscosa	0.65	-0.15	E	A	F
Potentilla gracilis var. gracilis	0.69	-0.38	N	P	F
Rubus armeniacus	0.71	-0.32	E	P	W
Centaurium erythraea	0.78	-0.25	E	A/B	F
Camassia quamash var. maxima	0.94	-0.46	N	P	F
Hypericum perforatum	0.97	-0.76	E	P	F
Centaurium muhlenbergii	0.98	-0.11	N	A/B	F
Bromus hordeaceus	0.99	-0.71	E	A	G
Danthonia californica	1.00	-0.32	N	P	G
Myosotis discolor	1.01	-0.88	E	A	F

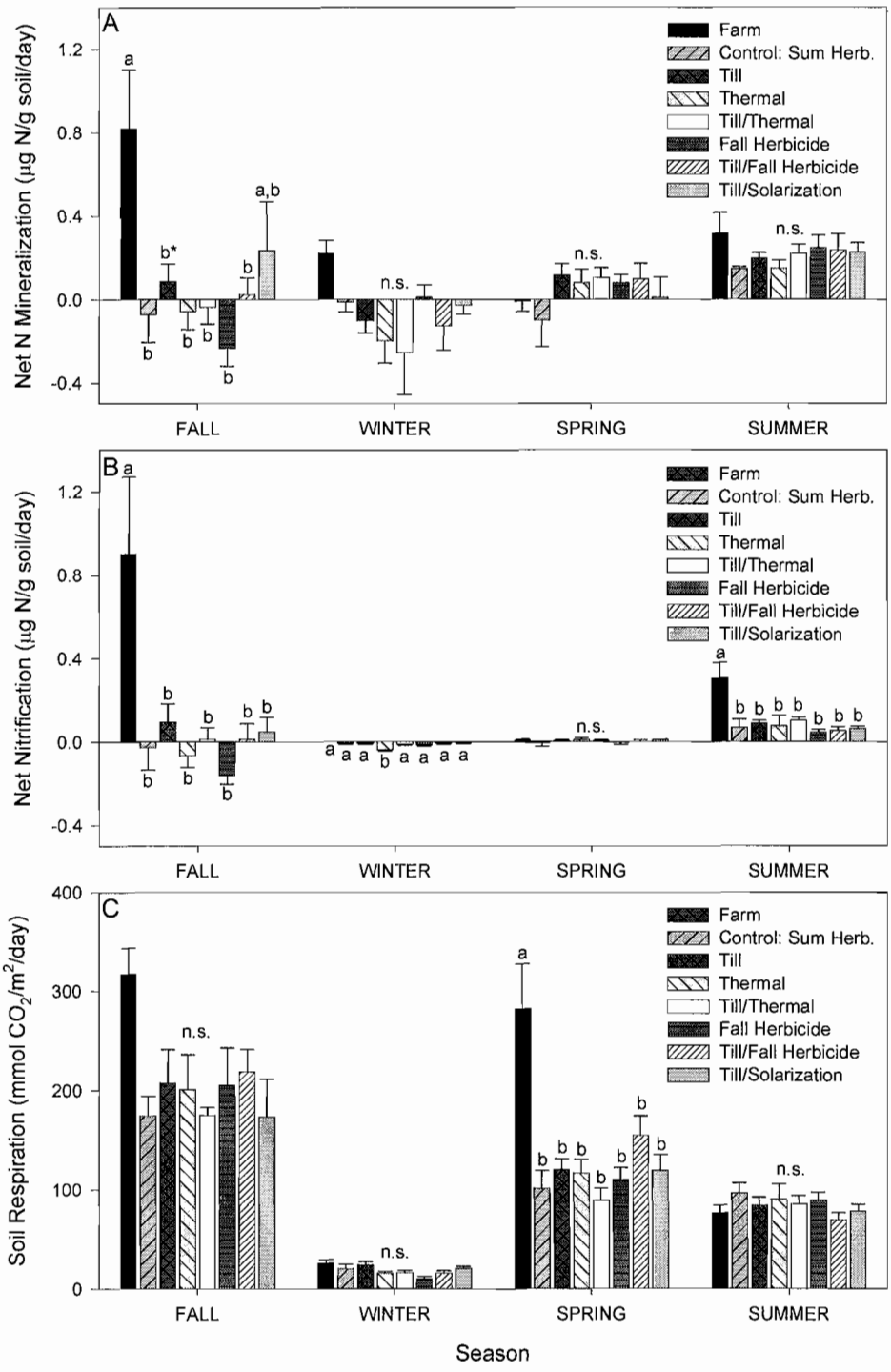
Supplemental Table 2.1 (continued)

Species	Axis 1 Loading	Axis 2 Loading	Species Origin	Life History	Functional Group
Daucus carota	1.02	-0.77	E	B	F
Rhamnus purshiana	1.03	-0.84	N	P	F
Rumex acetosella	1.03	-0.08	E	P	F
Rosa multiflora	1.04	-0.82	E	P	W
Holcus lanatus	1.04	-0.42	E	P	G
Vicia hirsuta	1.05	-0.75	E	A	F
Vicia sativa	1.05	-0.75	E	A	F
Amelanchier alnifolia	1.05	-0.63	N	P	F
Triteleia hyacinthine	1.08	-0.60	N	P	F
Crataegus monogyna	1.08	-0.06	E	P	W
Anagallis arvensis	1.09	-0.58	E	A/B	F
Rubus laciniatus	1.09	-0.06	E	P	W
Eriophyllum lanatum	1.10	-0.37	N	P	F
Juncus acuminatus	1.10	0.22	N	P	G
Agrostis stolonifera	1.11	-0.61	E	P	G
Geranium molle	1.12	-0.68	E	A/B/P	F
Sisyrinchium idahoense	1.12	-0.28	N	P	F
Geranium columbinum	1.13	-0.88	E	A	F
Juncus nevadensis	1.13	-0.14	N	P	G
Vicia tetrasperma	1.13	-0.52	E	A	F
Erigeron decumbens	1.14	-0.88	N	P	F
Schedonorus arundinaceus	1.14	-0.73	E	P	G
Allium amplectens	1.16	-0.24	N	P	F
Saxifraga oregano	1.16	-0.13	N	P	F
Plantago lanceolata	1.16	-0.52	E	P	F
Lotus unifoliolatus	1.16	-0.40	N	A	F
Leucanthemum vulgare	1.16	-0.69	E	P	F
Navarretia intertexta	1.18	0.04	N	A	F
Galium parisiense	1.18	-0.54	E	A	F
Luzula comosa	1.19	-1.12	N	P	G
Aira caryophyllea	1.20	-0.61	E	A	G
Leontodon taraxacoides	1.21	-0.55	E	P	F
Aster curtus	1.22	-1.03	N	P	F
Anthoxanthum odoratum	1.23	-0.63	E	P	G
Lotus formosissimus	1.23	-0.54	N	P	F
Zigadenus venenosus	1.23	-0.32	N	P	F
Mentha pulegium	1.24	-0.51	E	P	F
Sidalcea cusickii	1.24	-0.59	N	P	F
Rosa nutkana	1.24	-0.75	N	P	W
Achillea millefolium	1.24	-1.20	N	P	F
Dichanthelium acuminatum	1.24	-0.60	N	P	G
Linum bienne	1.25	-0.45	E	A/B	F
Fragaria virginiana	1.27	-0.35	N	P	F
Bromus arvensis	1.27	-0.35	E	A	G
Veronica scutellata	1.29	-0.44	N	P	F

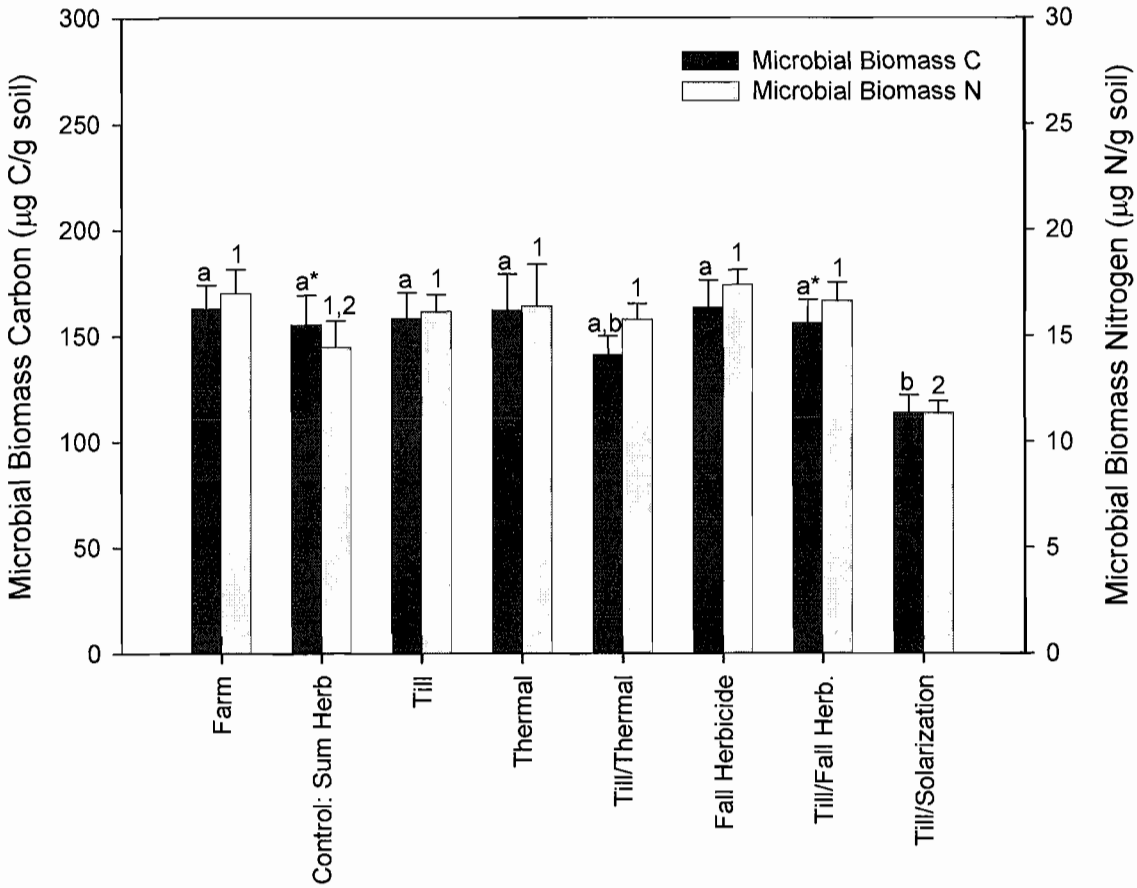
Supplemental Figure 2.1. Simpson's diversity vs. percent cover of *Agrostis exarata* and *Deschampsia cespitosa* in the experimental treatments and reference sites. Regression lines are drawn for 2005 (dotted), 2006 (dashed), and 2007 (solid) and r^2 and p-values are reported.
Note: Farm field is excluded from regression because plots have a Simpson's diversity of zero.
High values of Simpson's index of diversity indicate high levels of diversity.



Supplemental Figure 2.2. Net nitrogen (N) mineralization (A), net nitrification (B), and soil respiration (C) in the fall 2005, winter 2006, spring 2006, and summer 2006 for experimental treatments and farm field. Error bars represent one standard error from the mean and lower case letter differences indicate significant ($p<0.05$, $^{*}p<0.10$) effects of treatment within a season.



Supplemental Figure 2.3. Microbial biomass carbon and nitrogen in experimental treatments and farm field. Error bars represent one standard error from the mean and lower case letter (carbon) and number (nitrogen) differences indicate significant effects ($p<0.05$, $*p<0.10$) among treatments. *Note differences in magnitude of y-axes.*



APPENDIX B

CHAPTER III SUPPLEMENTAL TABLES

Supplemental Table 3.1. Species axes loadings for NMS ordination of restoration treatments (see Fig. 3.5). Only significant indicator species ($P < 0.05$) are reported. Native (N) and exotic (E) origin, life history (A: annual, B: biennial, and P: perennial), and functional group (G: graminoid, F: forb, and W: woody) are given for each species. Axis loading values greater than 0.5 are in bold and values less than -0.5 are underlined and in bold.

Species	Axis 1 Loading	Axis 2 Loading	Species Origin	Life History	Funct. Group
Hypericum perforatum	**-1.19**	0.17	E	P	F
Rosa nutkana	**-1.11**	0.14	N	P	W
Anthoxanthum odoratum	**-1.11**	-0.18	E	P	G
Fraxinus latifolia	**-1.10**	**0.65**	N	P	W
Zigadenus venenosus	**-1.07**	-0.28	N	P	F
Dichanthelium acuminatum ssp. fasciculatum	**-1.03**	-0.46	N	P	G
Crataegus monogyna x suksdorfi	**-1.00**	0.26	E	P	W
Sisyrinchium idahoense	**-1.00**	-0.09	N	P	F
Mentha pulegium	**-0.88**	-0.12	E	P	F
Leucanthemum vulgare	**-0.87**	**0.61**	E	P	F
Daucus carota	**-0.79**	**0.65**	E	B	F
Schedonorus arundinaceus	**-0.76**	**0.73**	E	P	G
Danthonia californica	**-0.75**	0.02	N	P	G
Symphyotrichum hallii	**-0.73**	**0.60**	N	P	F
Galium parisiense	**-0.71**	0.23	E	A	F
Potentilla gracilis var. gracilis	**-0.69**	**0.64**	N	P	F
Vicia tetrasperma	**-0.62**	0.40	E	A	F
Plantago lanceolata	**-0.61**	0.27	E	P	F
Sonchus asper	**-0.61**	0.23	E	A	F
Lotus formosissimus	**-0.60**	-0.13	N	P	F
Briza minor	**-0.58**	-0.04	E	A	G
Centaurium erythraea	**-0.54**	0.24	E	A/B	F
Rubus armeniacus	**-0.50**	0.34	E	P	W
Aira caryophyllea	-0.47	0.43	E	A	G
Linum bienne	-0.45	-0.11	E	A/B	F
Juncus nevadensis	-0.45	0.31	N	P	G
Leontodon taraxacoides	-0.36	0.29	E	P	F
Hypochaeris radicata	-0.27	0.32	E	P	F

Supplemental Table 3.1 (continued)

Species	Axis 1 Loading	Axis 2 Loading	Species Origin	Life History	Funct. Group
Cirsium vulgare	0.07	**0.95**	E	B	F
Orthocarpus bracteosus	0.13	0.02	N	A	F
Microsteris gracilis	0.21	-0.31	N	A	F
Parentucellia viscosa	0.23	0.44	E	A	F
Juncus tenuis	0.23	-0.01	N	P	G
Wyethia angustifolia	0.23	0.15	N	P	F
Holcus lanatus	0.24	0.24	E	P	G
Grindelia integrifolia	0.24	-0.28	N	P	F
Deschampsia cespitosa	0.33	-0.09	N	P	G
Poa compressa	0.36	-0.30	E	P	G
Hordeum brachyantherum	0.38	-0.46	N	P	G
Lolium multiflorum	0.40	**-0.99**	E	A	G
Agrostis exarata	0.41	**-0.91**	N	P	G
Epilobium densiflorum	0.42	**-0.89**	N	A	F
Poa annua	0.42	**-0.95**	E	A	G
Carex densa	0.43	-0.23	N	P	G
Madia glomerata	0.44	**-0.93**	N	A	F
Plagiobothrys figuratus ssp. figuratus	0.44	**-0.86**	N	A	F
Moenchia erecta	0.45	0.09	E	A	F
Madia elegans	0.48	-0.05	N	A	F
Downingia elegans	**0.50**	-0.33	N	A	F
Epilobium brachycarpum	**0.50**	0.18	N	A	F
Deschampsia danthonioides	**0.54**	-0.20	N	A	G
Lotus unifoliolatus	**0.60**	0.41	N	A	F
Gnaphalium palustre	**0.61**	-0.14	N	A	F
Centunculus minimus	**0.66**	-0.01	E	A	F
Agrostis stolonifera	**0.71**	0.02	E	P	G

Supplemental Table 3.2. Species axes loadings for CCA ordination of restoration and reference prairies (see Fig. 3.7). Native (N) and exotic (E) origin, life history (A: annual, B: biennial, and P: perennial), and functional group (G: graminoid, F: forb, and W: woody) are given for each species. Axis loading values greater than 1.0 are in bold and values less than -1.0 are underlined and in bold.

Species	Axis 1 Loading	Axis 2 Loading	Species Origin	Life History	Funct. Group
Rosa multiflora	**-2.29**	0.77	E	P	W
Fraxinus latifolia	**-2.29**	**-3.66**	N	P	W
Plantago lanceolata	**-1.97**	**-1.23**	E	P	F
Leucanthemum vulgare	**-1.83**	-0.38	E	P	F
Potentilla gracilis var. gracilis	**-1.81**	-0.47	N	P	F
Daucus carota	**-1.75**	-0.14	E	B	F
Schedonorus arundinaceus	**-1.66**	-0.06	E	P	G
Eryngium petiolatum	**-1.65**	-0.58	N	P	F
Anthoxanthum odoratum	**-1.51**	**-1.37**	E	P	G
Dichanthelium acuminatum ssp. fasciculatum	**-1.32**	**-1.96**	N	P	G
Anagallis arvensis	**-1.25**	-0.83	E	A	F
Sisyrinchium idahoense var. idahoense	**-1.25**	-0.78	N	P	F
Vicia tetrasperma	**-1.24**	-0.59	E	A	F
Galium parisiense	**-1.22**	**-1.08**	E	A	F
Symphyotrichum hallii	**-1.21**	-0.38	N	P	F
Danthonia californica	**-1.20**	**-1.39**	N	P	G
Hypericum perforatum	**-1.18**	-0.01	E	P	F
Mentha pulegium	**-1.14**	-0.66	E	P	F
Centaurium erythraea	**-1.07**	0.30	E	A/B	F
Lotus formosissimus	**-1.03**	0.01	N	P	F
Crataegus suksdorfii	-0.94	**-1.68**	N	P	W
Hypochaeris radicata	-0.92	0.93	E	P	F
Rubus armeniacus	-0.86	-0.66	E	P	W
Zigadensus venenosus var. venenosus	-0.85	**-2.00**	N	P	F
Aira carophyllea	-0.83	0.06	E	A	G
Rosa nutkana var. nutkana	-0.69	-0.42	N	P	W
Briza minor	-0.68	-0.16	E	A	G
Juncus sp.	-0.58	0.27	N	P	G
Leontodon taraxacoides	-0.56	0.21	E	P	F
Eriophyllum lanatum	-0.47	**1.55**	N	P	F
Madia sp.	-0.44	**1.05**	N	A	F
Grindelia integrifolia	-0.39	**1.85**	N	P	F
Prunella vulgaris var. lanceolata	-0.31	-0.02	N	P	F
Juncus tenuis	-0.27	**1.64**	N	P	G
Holcus lanatus	-0.17	0.31	E	P	G
Lotus unifoliolatus var. unifoliolatus	-0.11	0.61	N	A	F
Cirsium vulgare	-0.07	0.06	E	B	F
Parentucellia viscose	-0.04	0.20	E	A	F
Madia elegans	0.09	0.84	N	A	F
Ranunculus sp.	0.10	**1.71**	N	P	F
Veronica scutellata	0.16	**1.42**	N	P	F
Microseris laciniata	0.20	0.99	N	P	F
Deschampsia cespitosa	0.28	0.82	N	P	G
Rumex salicifolius var. salicifolius	0.31	**1.97**	N	P	F
Agrostis stolliniferus	0.34	**1.94**	E	P	G
Epilobium brachycarpum	0.40	0.40	N	A	F
Vulpia bromoides	**1.07**	-0.17	E	A	G
Agrostis exarata	**1.54**	**-1.18**	N	P	G
Epilobium ciliatum	**1.62**	**-1.06**	N	A	F

Supplemental Table 3.2 (continued)

Species	Axis 1 Loading	Axis 2 Loading	Species Origin	Life History	Funct. Group
Epilobium densiflorum	**1.67**	**-1.02**	N	A	F
Plagiobothrys figuratus ssp. figuratus	**1.73**	**-1.37**	N	A	F
Lolium multiflorum	**1.82**	**-1.39**	E	A	G
Madia glomerata	**1.98**	**-1.32**	N	A	F

REFERENCES

Chapter I

Baer, S. G., S. L. Collins, J. M. Blair, A. K. Knapp, and A. K. Fiedler. 2005. Soil herogeneity effects on tallgrass prairie community hterogeneity: an application of ecological theory to restoration ecology. Restoration Ecology **13**:413-425.

Bakker, J., and S. D. Wilson. 2001. Competitive abilities of introduced and native grasses. Plant Ecology **157**:117-125.

Bradshaw, A. D. 1987. Restoration: the acid test for ecology. Pages 23-29 *in* W. R. Jordan, M. E. Gilpin, and J. D. Aber, editors. Restoration Ecology: A Synthetic Approach to Ecological Research. Cambridge University Press, Cambridge, UK.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology **77**:776-790.

Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. Nature **405**:234-242.

Clark, D. L., and M. V. Wilson. 2001. Fire, mowing, and hand-removal of woody species in restoring a native wetland prairie in the Willamette Valley of Oregon. Wetlands **21**:135-144.

Clements, F. E. 1936. Nature and Structure of the climax. Journal of Ecology **24**:252-284.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist **122**:661-696.

Corbin, J. D., and C. M. D'Antonio. 2004a. Can carbon addition increase competitiveness of native grasses? A case study from California. Restoration Ecology **12**:36-43.

Corbin, J. D., and C. M. D'Antonio. 2004b. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology **85**:1273-1283.

Craine, J. M. 2005. Reconciling plant strategy theories of Grime and Tilman. Journal of Ecology **93**:1041-1052.

Ewing, K. 2002. Effects of initial site treatments on early growth and three-year survival of Idaho fescue. Restoration Ecology **10**:282-288.

Finley, K. K. 1994. Hydrology and related soil features of three Willamette valley wetland prairies. M.S. Oregon State University, Corvallis, OR.

Gleason, H. A. 1939. The individualistic concept of the plant association. American Midland Naturalist **21**:92-110.

Grace, J. B. 1991. A clarification of the debate between Grime and Tilman. Functional Ecology **5**:583-587.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist **111**:1169-1194.

Hoopes, M. F., and L. M. Hall. 2002. Edaphic factors and competition affect pattern formation and invasion in a California grassland. Ecological Applications **12**:24-39.

Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of Soil Resources on Plant Invasion and Community Structure in Californian Serpentine Grassland. Ecology **71**:478-491.

Hulse, D., J. Baker, and S. Gregory. 2002. Willamette River Basin Planning Atlas: Trajectories of Environmental and Ecological Change. Oregon State University Press, Corvallis, OR.

Huston, M. A. 2004. Management strategies for plant invasions: manipulating productivity, disturbance, and competition. Diversity and Distributions **10**:167-178.

Kaye, T. N., K. L. Pendergrass, K. Finley, and J. B. Kauffman. 2001. The effect of fire on the population viability of an endangered prairie plant. Ecological Applications **11**:1366-1380.

Lowe, P. N., W. K. Lauenroth, and I. C. Burke. 2003. Effects of nitrogen availability on competition between *Bromus tectorum* and *Bouteloua gracilis*. Plant Ecology **167**:247-254.

Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution **13**:195-198.

Meyerson, L. A., and H. A. Mooney. 2007. Invasive alien species in an era of globalization. Frontiers in Ecology and the Environment **5**:199-208.

Mitsch, W. J., and R. F. Wilson. 1996. Improving the success of wetland creation and restoration with know-how, time, and self-design. Ecological Applications **6**:77-83.

Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos **91**:97-108.

National Research Council. 2001. Compensating for Wetland Losses under the Clean Water Act. National Academy Press, Washington D.C.

Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. 28, U.S. National Biological Service, Washington D.C.

Pfeifer-Meister, L., and S. D. Bridgham. 2007. Seasonal and spatial controls over nutrient cycling in a Pacific Northwest prairie. Ecosystems **10**:1250-1260.

Pfeifer-Meister, L., E. M. Cole, B. A. Roy, and S. D. Bridgham. 2008. Abiotic constraints on the competitive ability of exotic and native grasses in a Pacific Northwest prairie. Oecologia **155**:357-366.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics **52**:272-288.

Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology **77**:1655-1661.

Schröder, A., L. Persson, and A. M. De Roos. 2005. Direct experimental evidence for alternative stable states: a review. Oikos **110**:3-19.

Seabloom, E. W., E. T. Borer, V. L. Boucher, R. S. Burton, K. L. Cottingham, L. Goldwasser, W. K. Gram, B. E. Kendall, and F. Micheli. 2003. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. Ecological Applications **13**:575-592.

Seabloom, E. W., and A. G. van der Valk. 2003. Plant diversity, composition, and invasion of restored and natural prairie pothole wetlands: implications for restoration. Wetlands **23**:1-12.

Sheley, R. L., J. M. Mangold, and J. L. Anderson. 2006. Potential for successional theory to guide restoration of invasive-plant-dominated rangeland. Ecological Monographs **76**:365-379.

Society for Ecological Restoration International. 2004. The SER International Primer on Ecological Restoration, Version 2. http://www.ser.org/content/ecological_restoration_primer.asp.

Stohlgren, T. J., L. D. Schell, and B. V. Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in rocky mountain grasslands. Ecological Applications **9**.

Temperton, V. M., R. J. Hobbs, T. Nuttle, and S. Halle, editors. 2004. Assembly Rules and Restoration Ecology: Bridging the Gab between Theory and Practice. Island Press, Washington D.C.

Tilman, D., editor. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press; Ewing : California Princeton Fulfillment Services [Distributor], Princeton.

Twolan-Strutt, L., and P. A. Keddy. 1996. Above- and belowground competition intensity in two contrasting wetland plant communities. Ecology **77**:259-270.

van der Valk, A. G., L. Squires, and C. H. Welling. 1994. Assessing the impacts of an increase in water level on wetland vegetation. Ecological Applications **4**:525-534.

Vinton, M. A., and I. C. Burke. 1997. Contingent effects of plant species on soils along a regional moisture gradient in the Great Plains. Oecologia **110**:393-402.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science **277**:494-499.

Walker, L. R., J. Walker, and R. J. Hobbs, editors. 2007. Linking Restoration and Ecological Succession. Springer, New York, NY.

Weltzin, J. F., S. D. Bridgham, J. Pastor, J. Chen, and C. Harth. 2003. Potential effects of warming and drying on peatland plant community composition. Global Change Biology **9**:1-11.

White, P. S., and A. Jentsch. 2004. Disturbance, succession and community assembly in terrestrial plant communities. Pages 342-366 *in* V. Temperton, R. J. Hobbs, T. Nuttle, and S. Halle, editors. Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice. Island Press, Washington, DC.

Whitlock, C., and M. A. Knox. 2002. Prehistoric burning in the Pacific Northwest: Human versus climatic influences. Pages 195-231 *in* T. R. Vale, editor. Fire, Native Peoples, and the Natural Landscape. Island Press, Washington D.C.

Wilson, M. V., E. R. Alverson, D. L. Clark, R. H. Hayes, C. A. Ingersol, and M. B. Naughton. 1996. Willamette valley natural areas network. Restoration and Management Notes **13**:26-28.

Young, T. P., D. A. Peterson, and J. J. Clary. 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. Ecology Letters **8**:662-673.

Zedler, J. B. 2000. Progress in wetland restoration ecology. Trends in Ecology & Evolution **15**:402-407.

Zedler, J. B., and S. Kercher. 2004. Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences **23**:431-452.

Chapter II

Adams, C. R., and S. M. Galatowitsch. 2006. Increasing the effectiveness of reed canary grass (*Phalaris arundinacea* L.) control in wet meadow restorations. Restoration Ecology **14**:441-451.

Ameel, J. J., R. P. Axler, and O. C. J. 1993. Persulfate digestion for determination of total nitrogen and phosphorus in low-nutrient waters. American Environmental Laboratory **10/93**:7-11.

Bakker, J. D., S. D. Wilson, J. M. Christian, X. Li, L. G. Ambrose, and J. Waddington. 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. Ecological Applications **13**:137-153.

Barberi, P. 2002. Weed management in organic agriculture: are we addressing the right issues? Weed Research (Oxford) **42**:177-193.

Bendavid-Val, R., H. D. Rabinowitch, J. Katan, and Y. Kapulnik. 1997. Viability of VA-mycorrhizal fungi following soil solarization and fumigation. Plant and Soil **195**:185-193.

Bernet, J. A., J. M. Eilers, B. J. Eilers, E. Blok, S. G. Daggett, and K. F. Bierly. 1999. Recent wetland trends (1981/82-1994) in the Willamette Valley Oregon, USA. Wetlands **19**:545-559.

Bond, W., and A. C. Grundy. 2001. Non-chemical weed management in organic farming systems. Weed Research (Oxford) **41**:383-405.

Bridgham, S. D., J. P. Megonigal, J. K. Keller, N. B. Bliss, and C. Trettin. 2006. The carbon balance of North American wetlands. Wetlands **26**:889-916.

Corbin, J. D., and C. M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology **85**:1273-1283.

Dahl, T. E. 2000. Status and Trends of Wetlands in the Conterminous United States, 1986 to 1997. Fish and Wildlife Service, U.S. Department of the Interior, Washington D. C.

Dahl, T. E. 2006. Status and trends of wetlands in the conterminous United States 1998-2004. U.S. Department of the Interior; Fish and Wildlife Service, Washington, D.C.

Denman, K. L., G. Brasseur, A. Chidthaisong, P. Ciais, P. M. Cox, R. E. Dickinson, D. Hauglustaine, C. Heinze, E. Holland, D. Jacob, U. Lohmann, S. Ramachandran, P. L. da Silva Dias, S. C. Wofsy, and X. Zhang. 2007. Couplings between changes in the climate system and biogeochemistry. Pages 499-587 *in* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Egley, G. H. 1990. High-temperature effects on germination and survival of weed seeds in soil. Weed Science **38**:429-435.

Elzinga, C. L., D. W. Salzer, and J. W. Willoughby. 1998. Measuring and monitoring plant populations. USDI Bureau of Land Management, National Business Center, Denver, CO.

Euliss, N. H., R. A. Gleason, A. Olness, R. L. McDougal, H. R. Murkin, R. D. Robarts, R. A. Bourbonniere, and B. G. Warner. 2006. North American prairie wetlands are important nonforested land-based carbon storage sites. Science of the Total Environment **361**:179-188.

Ewing, K. 2002. Effects of initial site treatments on early growth and three-year survival of Idaho fescue. Restoration Ecology **10**:282-288.

Feng, J. C., and D. G. Thompson. 1990. Fate of glyphosate in a Canadian forest watershed: persistence in foliage and soils. Journal of Agriculture and Food Chemistry **38**.

Fitzpatrick, G. S. 2004. Techniques for restoring native plant communities in upland and wetland prairies in the Midwest and West coast regions of North America. Report to the City of Eugene-Parks and Open Space Division, Eugene, Oregon.

Flora of North America Editorial Committee, editor. 1993+. Flora of North America North of Mexico, New York and Oxford.

Frayer, W. E., T. J. Monahan, D. C. Bowden, and F. A. Graybill. 1983. Status and Trends of Wetlands and Deepwater Habitats in the Conterminous United States, 1950s to 1970s. Colorado State University, Fort Collins, CO.

Gee, G. W., and J. W. Bauder. 1986. Particle-size analysis. Pages 377-411 *in* A. Klute, editor. Methods of Soil Analysis Part 1: Physical and Mineralogical Methods. American Society of Agronomy, Madison, WI.

Green, E. K., and S. M. Galatowitsch. 2002. Effects of *Phalaris arundinacea* and nitrate-N addition on the establishment of wetland plant communities. Journal of Applied Ecology **39**:134-144.

Hart, S. C., J. M. Stark, E. A. Davidson, and M. K. Firestone. 1994. Nitrogen mineralization, immobilization, and nitrification. Pages 985-1018 *in* R. W. Weaver, S. Angle, P. S. Bottomley, D. Bezdicek, S. Smith, M. A. Tabatabai, and A. Wollum, editors. Methods of Soil Analysis, Part 2. Microbiological and Biochemical Properties. Soil Science Society of America, Madison, WI.

Horwath, W. R., and E. A. Paul. 1994. Microbial Biomass. Pages 763-767 *in* R. W. Weaver, J. S. Angle, and P. S. Bottomley, editors. Methods of Soil Analysis: Part 2 Microbiological and Biochemical Properties. Soil Science Society of America, Inc., Madison, WI.

Hulse, D., J. Baker, and S. Gregory. 2002. Willamette River Basin Planning Atlas: Trajectories of Environmental and Ecological Change. Oregon State University Press, Corvallis, OR.

Kellogg, C. H. 2002. Plant community succession and invasion in restored freshwater marshes. Ph.D. dissertation. University of Notre Dame, Notre Dame, IN.

Kellogg, C. H., and S. D. Bridgham. 2002. Colonization during early succession of restored freshwater marshes. Canadian Journal of Botany **80**:176-185.

Kilbride, K., and F. Paveglio. 1999. Integrated pest management to control reed canarygrass in seasonal wetlands of southwestern Washington. Wildlife Society Bulletin **27**:292-297.

Kuo, S. 1996. Phosphorus. Pages 869-920 *in* D. L. Sparks, A. L. Page, P. A. Helmke, R. H. Loeppert, R. N. Soltanpour, M. A. Tabatabai, C. T. Johston, and M. E. Sumner, editors. Methods of Soil Analysis, Part 3: Chemical Methods. Soil Society of America, Madison, WI.

MacDougall, A. S., and R. Turkington. 2007. Does the type of disturbance matter when restoring disturbance-dependent grasslands? Restoration Ecology **15**:263-272.

Maynard, D. G., and Y. P. Kalra. 1993. Nitrate and exchangeable ammonium nitrogen. Pages 25-38 *in* M. R. Carter, editor. Soil Sampling and Methods of Analysis. Lewis Publishers, Boca Raton, FL.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MJM, Gleneden Beach, Oregon.

McLachlan, S. M., and A. L. Knipsel. 2005. Assessment of long-term tallgrass prairie restoration in Manitoba, Canada. Biological Conservation **124**:75-88.

Morgan, J. P. 1997. Plowing and seeding. *in* S. Packard and C. F. Mutel, editors. The tallgrass restoration handbook: for prairies, savannas, and woodlands. Island Press, Covelo, California.

Moyes, A. B., M. S. Witter, and J. A. Gamon. 2005. Restoration of native perennials in a California annual grassland after prescribed spring burning and solarization. Restoration Ecology **13**:659-666.

Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of phosphates in natural waters. Analytica Chimica Acta **27**:31-36.

National Research Council. 2001. Compensating for Wetland Losses under the Clean Water Act. National Academy Press, Washington D.C.

Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. 28, U.S. National Biological Service, Washington D.C.

Pfeifer-Meister, L., E. M. Cole, B. A. Roy, and S. D. Bridgham. 2008. Abiotic constraints on the competitive ability of exotic and native grasses in a Pacific Northwest prairie. Oecologia **155**:357-366.

Pinkerton, J. N., K. L. Ivors, M. L. Miller, and L. W. Moore. 2000. Effect of soil solarization and cover crops on populations of selected soilborne plant pathogens in Western Oregon. Plant Disease **84**:952-960.

Potthoff, M., L. E. Jackson, K. L. Steenwerth, I. Ramirez, M. R. Stromberg, and D. E. Rolston. 2005. Soil biological and chemical properties in restored perennial grassland in California. Restoration Ecology **13**:61-73.

Potthoff, M., K. L. Steenwerth, L. E. Jackson, R. E. Drenovsky, K. M. Scow, and R. G. Joergensen. 2006. Soil microbial community composition as affected by restoration practices in California grassland. Soil Biology & Biochemistry **38**:1851-1860.

Schreiner, R. P., K. L. Ivors, and J. N. Pinkerton. 2001. Soil solarization reduces arbuscular mycorrhizal fungi as a consequence of weed suppression. Mycorrhiza **11**:273-277.

Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences of the United States of America **100**:13384-13389.

Seabloom, E. W., and A. G. van der Valk. 2003. Plant diversity, composition, and invasion of restored and natural prairie pothole wetlands: implications for restoration. Wetlands **23**:1-12.

Sheley, R. L., J. M. Mangold, and J. L. Anderson. 2006. Potential for successional theory to guide restoration of invasive-plant-dominated rangeland. Ecological Monographs **76**:365-379.

Simenstad, C. A., and R. M. Thom. 1996. Functional equivalency trajectories of the restored Gog-le-hi-te estuarine wetland. Ecological Applications **6**:38-56.

Solorzano, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnology and Oceanography **14**:799-801.

Steenwerth, K. L., L. E. Jackson, F. J. Calderon, M. R. Stromberg, and K. M. Scow. 2002. Soil microbial community composition and land use history in cultivated and grassland ecosystems of coastal California. Soil Biology & Biochemistry **34**:1599-1611.

Temperton, V. M., R. J. Hobbs, T. Nuttle, and S. Halle, editors. 2004. Assembly Rules and Restoration Ecology: Bridging the Gab between Theory and Practice. Island Press, Washington D.C.

Voroney, R. P., and J. P. Winter. 1993. Soil Microbial Biomass C and N. Pages 277-286 *in* M. R. Carter, editor. Soil Sampling and Methods of Analysis. Lewis Publishers, Boca Raton, FL.

Walker, L. R., J. Walker, and R. J. Hobbs, editors. 2007. Linking Restoration and Ecological Succession. Springer, New York, NY.

Wang, K. H., R. McSorley, and N. Kokalis-Burelle. 2006. Effects of cover cropping, solarization, and soil fumigation on nematode communities. Plant and Soil **286**:229-243.

Wardle, D. A., and D. Parkinson. 1990. Effects of three herbicides on soil microbial biomass and activity. Plant and Soil **122**:21-28.

Wetzel, R. G., and G. E. Likens. 2000. Limnological Analyses, Third edition. Springer-Verlag, New York.

Wilson, M. V., C. A. Ingersol, M. G. Wilson, and D. L. Clark. 2004. Why pest plant control and native plant establishment failed: a restoration autopsy. Natural Areas Journal **24**:23-31.

Wilson, S. D., and A. K. Gerry. 1995. Strategies for mixed-grass prairie restoration: Herbicide, tilling, and nitrogen manipulation. Restoration Ecology **3**:290-298.

Wood, E. D., F. A. J. Armstrong, and F. A. Richards. 1967. Determination of nitrate in sea water by cadmium-copper reduction to nitrite. Journal of the Marine Biological Association of the United Kingdom **47**:23-31.

Zedler, J. B. 2003. Wetlands at your service: reducing impacts of agriculture at the watershed scale. Frontiers in Ecology and the Environment **2**:65-72.

Chapter III

Ameel, J. J., R. P. Axler, and O. C. J. 1993. Persulfate digestion for determination of total nitrogen and phosphorus in low-nutrient waters. American Environmental Laboratory **10/93**:7-11.

Bauer, C. R., C. H. Kellogg, S. D. Bridgham, and G. S. Lamberti. 2003. Mycorrhizal colonization across hydrologic gradients in restored and reference freshwater wetlands. Wetlands **23**:961-968.

Bendavid-Val, R., H. D. Rabinowitch, J. Katan, and Y. Kapulnik. 1997. Viability of VA-mycorrhizal fungi following soil solarization and fumigation. Plant and Soil **195**:185-193.

Bernet, J. A., J. M. Eilers, B. J. Eilers, E. Blok, S. G. Daggett, and K. F. Bierly. 1999. Recent wetland trends (1981/82-1994) in the Willamette Valley Oregon, USA. Wetlands **19**:545-559.

Buisson, E., S. Anderson, K. D. Holl, E. Corcket, G. F. Hayes, A. Peeters, and T. Dutoit. 2008. Reintroduction of Nassella pulchra to California coastal grasslands: Effects of topsoil removal, plant neighbour removal and grazing. Applied Vegetation Science:195-204.

Dahl, T. E. 2006. Status and trends of wetlands in the conterminous United States 1998-2004. U.S. Department of the Interior; Fish and Wildlife Service, Washington, D.C.

Daphne A. Hatch, J. W. B., Jeffrey S. Fehmi, Deborah S. Hillyard,. 1999. Effects of Burning and Grazing on a Coastal California Grassland. Restoration Ecology **7**:376-381.

Elzinga, C. L., D. W. Salzer, and J. W. Willoughby. 1998. Measuring and monitoring plant populations. USDI Bureau of Land Management, National Business Center, Denver, CO.

Fitzpatrick, G. S. 2004. Techniques for restoring native plant communities in upland and wetland prairies in the Midwest and West coast regions of North America. Report to the City of Eugene-Parks and Open Space Division, Eugene, Oregon.

Flora of North America Editorial Committee, editor. 1993+. Flora of North America North of Mexico, New York and Oxford.

Frayer, W. E., T. J. Monahan, D. C. Bowden, and F. A. Graybill. 1983. Status and Trends of Wetlands and Deepwater Habitats in the Conterminous United States, 1950s to 1970s. Colorado State University, Fort Collins, CO.

Gee, G. W., and J. W. Bauder. 1986. Particle-size analysis. Pages 377-411 *in* A. Klute, editor. Methods of Soil Analysis Part 1: Physical and Mineralogical Methods. American Society of Agronomy, Madison, WI.

Giovannetti, M., and B. Mosse. 1980. An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. New Phytologist **84**:498-500.

Hamilton, J. G., C. Holzapfel, and B. E. Mahall. 1999. Coexistence and interference between a native perennial grass and a non-native annual grasses in California. Oecologia **121**:518-526.

Holzel, N., and A. Otte. 2003. Restoration of a species-rich flood meadow by topsoil removal and diaspore transfer with plant material. Applied Vegetation Science **6**:131-140.

Horowitz, M., Y. Regev, and G. Herzlinger. 1983. Solarization for Weed Control. Weed Science **31**:170-179.

Horwath, W. R., and E. A. Paul. 1994. Microbial Biomass. Pages 763-767 *in* R. W. Weaver, J. S. Angle, and P. S. Bottomley, editors. Methods of Soil Analysis: Part 2 Microbiological and Biochemical Properties. Soil Science Society of America, Inc., Madison, WI.

Hulse, D., J. Baker, and S. Gregory. 2002. Willamette River Basin Planning Atlas: Trajectories of Environmental and Ecological Change. Oregon State University Press, Corvallis, OR.

Kimball, S., and P. M. Schiffman. 2003. Differing Effects of Cattle Grazing on Native and Alien Plants. Conservation Biology **17**:1681-1693.

Koske, R. E., and J. N. Gemma. 1989. A modified procedure for staining roots to detect VA mycorrhizas. Mycorrhizal Research **92**:486-488.

Kuo, S. 1996. Phosphorus. Pages 869-920 *in* D. L. Sparks, A. L. Page, P. A. Helmke, R. H. Loeppert, R. N. Soltanpour, M. A. Tabatabai, C. T. Johston, and M. E. Sumner, editors. Methods of Soil Analysis, Part 3: Chemical Methods. Soil Society of America, Madison, WI.

Maynard, D. G., and Y. P. Kalra. 1993. Nitrate and exchangeable ammonium nitrogen. Pages 25-38 *in* M. R. Carter, editor. Soil Sampling and Methods of Analysis. Lewis Publishers, Boca Raton, FL.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MJM, Gleneden Beach, Oregon.

McLachlan, S. M., and A. L. Knipsel. 2005. Assessment of long-term tallgrass prairie restoration in Manitoba, Canada. Biological Conservation **124**:75-88.

Mitsch, W. J., and R. F. Wilson. 1996. Improving the success of wetland creation and restoration with know-how, time, and self-design. Ecological Applications **6**:77-83.

Moyes, A. B., M. S. Witter, and J. A. Gamon. 2005. Restoration of native perennials in a California annual grassland after prescribed spring burning and solarization. Restoration Ecology **13**:659-666.

Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of phosphates in natural waters. Analytica Chimica Acta **27**:31-36.

National Climatic Data Center. 2005. NOAA, Ashville, North Carolina. http://www1.ncdc.noaa.gov/pub/data/ccd-data/CCD_2005.pdf. Cited 29 May 2006.

National Research Council. 2001. Compensating for Wetland Losses under the Clean Water Act. National Academy Press, Washington D.C.

Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. 28, U.S. National Biological Service, Washington D.C.

Patzelt, A., U. Wild, and J. Pfadenhauer. 2001. Restoration of wet fen meadows by topsoil removal: Vegetation development and germination biology of fen species. Restoration Ecology **9**:127-136.

Pfeifer-Meister, L., B. A. Roy, B. R. Johnson, and S. D. Bridgham. submitted. Plant community and soil responses to experimental restoration techniques in a wetland prairie. Ecological Applications.

Seabloom, E. W., E. T. Borer, V. L. Boucher, R. S. Burton, K. L. Cottingham, L. Goldwasser, W. K. Gram, B. E. Kendall, and F. Micheli. 2003a. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. Ecological Applications **13**:575-592.

Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003b. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences of the United States of America **100**:13384-13389.

Seabloom, E. W., and A. G. van der Valk. 2003. Plant diversity, composition, and invasion of restored and natural prairie pothole wetlands: implications for restoration. Wetlands **23**:1-12.

Solorzano, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnology and Oceanography **14**:799-801.

Tallowin, J. R. B., and R. E. N. Smith. 2001. Restoration of a *Cirsio-Molinietum* fen meadow on an agriculturally improved pasture. Restoration Ecology **9**:167-178.

Turner, R. E., A. M. Redmond, and J. B. Zedler. 2001. Count It by acre or function-Mitigation adds up to net loss of wetlands. National Wetlands Newsletter **23**:5-16.

Vivian-Smith, G. 1997. Microtopographic heterogeneity and floristic diversity in experimental wetland communities. Ecology **85**:71-82.

Voroney, R. P., and J. P. Winter. 1993. Soil Microbial Biomass C and N. Pages 277-286 *in* M. R. Carter, editor. Soil Sampling and Methods of Analysis. Lewis Publishers, Boca Raton, FL.

Wang, K. H., R. McSorley, and N. Kokalis-Burelle. 2006. Effects of cover cropping, solarization, and soil fumigation on nematode communities. Plant and Soil **286**:229-243.

Wetzel, R. G., and G. E. Likens. 2000. Limnological Analyses, Third edition. Springer-Verlag, New York.

Wilson, M. V., C. A. Ingersol, M. G. Wilson, and D. L. Clark. 2004. Why pest plant control and native plant establishment failed: a restoration autopsy. Natural Areas Journal **24**:23-31.

Wood, E. D., F. A. J. Armstrong, and F. A. Richards. 1967. Determination of nitrate in sea water by cadmium-copper reduction to nitrite. Journal of the Marine Biological Association of the United Kingdom **47**:23-31.

Woodward, C. L. 1996. Soil compaction and topsoil removal effects on soil properties and seedling growth in Amazonian Ecuador. Forest Ecology and Management **82**:197-209.

Zedler, J. B. 2003. Wetlands at your service: reducing impacts of agriculture at the watershed scale. Frontiers in Ecology and the Environment **2**:65-72.

Chapter IV

Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: Problems, prevalence, and an alternative. Journal of Wildlife Management **64**:912-923.

Barrett, J. E., R. L. McCulley, D. R. Lane, I. C. Burke, and W. K. Lauenroth. 2002. Influence of climate variability on plant production and N-mineralization in Central US grasslands. Journal of Vegetation Science **13**:383-394.

Booth, M. S., J. M. Stark, and E. Rastetter. 2005. Controls on nitrogen cycling in terrestrial ecosystems: A synthetic analysis of literature data. Ecological Monographs **75**:139-157.

Braschi, I., C. Ciavatta, C. Giovannini, and C. Gessa. 2003. Combined effect of water and organic matter on phosphorus availability in calcareous soils. Nutrient Cycling in Agroecosystems **67**:67-74.

Bridgham, S. D., and C. J. Richardson. 1992. Mechanisms controlling soil respiration (CO_2 and CH_4) in southern peatlands. Soil Biology & Biochemistry **24**:1089-1099.

Bridgham, S. D., K. Updegraff, and J. Pastor. 1998. Carbon, nitrogen, and phosphorus mineralization in northern wetlands. Ecology **79**:1545-1561.

Buisson, E., K. D. Holl, S. Anderson, E. Corcket, G. F. Hayes, F. Torre, A. Peteers, and T. Dutoit. 2006. Effect of seed source, topsoil removal, and plant neighbor removal on restoring California coastal prairies. Restoration Ecology **14**:569-577.

Burke, I. C., W. K. Lauenroth, and W. J. Parton. 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. Ecology **78**:1330-1340.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference, Second edition. Springer-Verlag, New York.

Cassman, K. G., and D. N. Munns. 1980. Nitrogen mineralization as affected by soil moisture, temperature, and depth. Soil Science Society of America Journal **44**:1233-1237.

Chapin, F. S., P. A. Matson, and H. A. Mooney. 2002. Principles of Terrestrial Ecosystem Ecology. Springer-Verlag, New York.

Davidson, E. A., J. M. Stark, and M. K. Firestone. 1990. Microbial-production and consumption of nitrate in an annual grassland. Ecology **71**:1968-1975.

Fitzpatrick, G. S. 2004. Techniques for restoring native plant communities in upland and wetland prairies in the Midwest and West coast regions of North America. Report to the City of Eugene-Parks and Open Space Division, Eugene, Oregon.

Flanagan, L. B., L. A. Wever, and P. J. Carlson. 2002. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. Global Change Biology **8**:599-615.

Franzluebbers, K., A. J. Franzluebbers, and M. D. Jawson. 2002. Environmental controls on soil and whole-ecosystem respiration from a tallgrass prairie. Soil Science Society of America Journal **66**:254-262.

Friends of Buford Park. 2000. HBRA Plant List. http://www.bufordpark.org/hbraplantlist.htm. Cited 12 June 2007.

Gee, G. W., and J. W. Bauder. 1986. Particle-size analysis. Pages 377-411 *in* A. Klute, editor. Methods of Soil Analysis Part 1: Physical and Mineralogical Methods. American Society of Agronomy, Madison, WI.

Hillel, D. 1998. Environmental Soil Physics: Fundamentals, Applications, and Environmental Considerations. Academic Press; Elsevier Science & Technology Books, San Diego.

Hooper, D. U., and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. Ecological Monographs **68**:121-149.

Hungate, B. A., F. S. Chapin, H. Zhong, E. A. Holland, and C. B. Field. 1997. Stimulation of grassland nitrogen cycling under carbon dioxide enrichment. Oecologia **109**:149-153.

Jamieson, N., D. Barraclough, M. Unkovich, and R. Monaghan. 1998. Soil N dynamics in a natural calcareous grassland under a changing climate. Biology and Fertility of Soils **27**:267-273.

Jamieson, N., R. Monaghan, and D. Barraclough. 1999. Seasonal trends of gross N mineralization in a natural calcareous grassland. Global Change Biology **5**:423-431.

Kellogg, L. E., S. D. Bridgham, and D. Lopez-Hernandez. 2006. A comparison of four methods of measuring gross phosphorus mineralization. Soil Science Society of America Journal **70**:1349-1358.

Kuo, S. 1996. Phosphorus. Pages 869-920 *in* D. L. Sparks, A. L. Page, P. A. Helmke, R. H. Loeppert, R. N. Soltanpour, M. A. Tabatabai, C. T. Johston, and M. E. Sumner, editors. Methods of Soil Analysis, Part 3: Chemical Methods. Soil Society of America, Madison, WI.

Liu, X. Z., S. Q. Wan, B. Su, D. F. Hui, and Y. Q. Luo. 2002. Response of soil CO_2 efflux to water manipulation in a tallgrass prairie ecosystem. Plant and Soil **240**:213-223.

Luo, Y. Q., R. B. Jackson, C. B. Field, and H. A. Mooney. 1996. Elevated CO_2 increases belowground respiration in California grasslands. Oecologia **108**:130-137.

Luo, Y. Q., S. Q. Wan, D. F. Hui, and L. L. Wallace. 2001. Acclimatization of soil respiration to warming in a tall grass prairie. Nature **413**:622-625.

MacDonald, N. W., D. R. Zak, and K. S. Pregitzer. 1995. Temperature effects on kinetics of microbial respiration and net nitrogen and sulfur mineralization. Soil Science Society of America Journal **59**:233-240.

Maynard, D. G., and Y. P. Kalra. 1993. Nitrate and exchangeable ammonium nitrogen. Pages 25-38 *in* M. R. Carter, editor. Soil Sampling and Methods of Analysis. Lewis Publishers, Boca Raton, FL.

Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of phosphates in natural waters. Analytica Chimica Acta **27**:31-36.

National Atmospheric Deposition Program. 2005. Annual Summary. http://nadp.sws.uiuc.edu/. Cited 27 October 2006.

National Climatic Data Center. 2005. NOAA, Ashville, North Carolina. http://www1.ncdc.noaa.gov/pub/data/ccd-data/CCD_2005.pdf. Cited 29 May 2006.

Parson, E. A. 2001. Potential consequences of climate variability and change for the Pacific Northwest. Pages 247-280 *in* N. A. S. Team, editor. Climate Change Impacts on the United States: the Potential Consequences of Climate Variability and Change. Cambridge University Press, Cambridge, UK.

Pastor, J., M. A. Stillwell, and D. Tilman. 1987. Nitrogen mineralization and nitrification in four Minnesota old fields. Oecologia **71**:481-485.

Peterjohn, W. T., J. M. Melillo, P. A. Steudler, K. M. Newkirk, F. P. Bowles, and J. D. Aber. 1994. Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. Ecological Applications **4**:617-625.

Pfeifer-Meister, L., E. M. Cole, B. A. Roy, and S. D. Bridgham. 2008. Abiotic constraints on the competitive ability of exotic and native grasses in a Pacific Northwest prairie. Oecologia **155**:357-366.

Porazinska, D. L., R. D. Bardgett, M. B. Blaauw, H. W. Hunt, A. N. Parsons, T. R. Seastedt, and D. H. Wall. 2003. Relationships at the aboveground-belowground interface: plants, soil biota, and soil processes. Ecological Monographs **73**:377-395.

Raich, J. W., and A. Tufekcioglu. 2000. Vegetation and soil respiration: Correlations and controls. Biogeochemistry **48**:71-90.

Robertson, G. P. 1982. Factors regulating nitrification in primary and secondary succession. Ecology **63**:1561-1573.

Rustad, L. E., J. L. Campbell, G. M. Marion, R. J. Norby, M. J. Mitchell, A. E. Hartley, J. H. C. Cornelissen, and J. Gurevitch. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia **126**:543-562.

Schimel, D. S., and W. J. Parton. 1986. Microclimate controls of nitrogen mineralization and nitrification in shortgrass steppe soils. Plant and Soil **93**:347-357.

Shaw, M. R., and J. Harte. 2001. Response of nitrogen cycling to simulated climate change: differential responses along a subalpine ecotone. Global Change Biology **7**:193-210.

Solorzano, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnology and Oceanography **14**:799-801.

Stumm, W., and J. J. Morgan. 1981. Aquatic Chemistry, Second edition. John Wiley and Sons, New York.

Taylor, A. A., J. Defelice, and D. C. Havill. 1982. Seasonal variation in nitrogen availability and utilization in an acidic and calcareous soil. New Phytologist **92**:141-152.

Updegraff, K., J. Pastor, S. D. Bridgham, and C. A. Johnston. 1995. Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. Ecological Applications **5**:151-163.

Wan, S. Q., and Y. Q. Luo. 2003. Substrate regulation of soil respiration in a tallgrass prairie: Results of a clipping and shading experiment. Global Biogeochemical Cycles **17**.

Wedin, D. A., and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial grasses. Oecologia **84**:433-441.

Wood, E. D., F. A. J. Armstrong, and F. A. Richards. 1967. Determination of nitrate in sea water by cadmium-copper reduction to nitrite. Journal of the Marine Biological Association of the United Kingdom **47**:23-31.

Xu, L., and D. D. Baldocchi. 2004. Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. Agricultural and Forest Meteorology **1232**:79-96.

Chapter V

Atwater, B. R. 1980. Germination, dormancy and morphology of the seeds of herbaceous ornamental plants. Seed Science and Technology **8**:523-573.

Bakker, J., and S. D. Wilson. 2001. Competitive abilities of introduced and native grasses. Plant Ecology **157**:117-125.

Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. Nature **405**:234-242.

Corbin, J. D., and C. M. D'Antonio. 2004. Can carbon addition increase competitiveness of native grasses? A case study from California. Restoration Ecology **12**:36-43.

Ewing, K. 2002. Effects of initial site treatments on early growth and three-year survival of Idaho fescue. Restoration Ecology **10**:282-288.

Hamilton, J. G., C. Holzapfel, and B. E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. Oecologia **121**:518-526.

Harper, J. L. 1977. Population Biology of Plants. Academic Press, London.

Hitchcock, A. S. 1971. Manual of the Grasses of the United States, 2nd edition. Dover Publications, Mineola.

Hoagland, D. R., and A. I. Arnon. 1938. The water-culture method for growing plants without soil. University of California College of Agriculture. Circular **347**:1-39.

Hoopes, M. F., and L. M. Hall. 2002. Edaphic factors and competition affect pattern formation and invasion in a California grassland. Ecological Applications **12**:24-39.

Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of Soil Resources on Plant Invasion and Community Structure in Californian Serpentine Grassland. Ecology **71**:478-491.

Kluse, J. S., and B. H. Allen Diaz. 2005. Importance of soil moisture and its interaction with competition and clipping for two montane meadow grasses. Plant Ecology **176**:87-99.

Lowe, P. N., W. K. Lauenroth, and I. C. Burke. 2003. Effects of nitrogen availability on competition between *Bromus tectorum* and *Bouteloua gracilis*. Plant Ecology **167**:247-254.

Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution **13**:195-198.

Maron, J. L., and P. G. Connors. 1996. A native nitrogen-fixing shrub facilitates weed invasion. Oecologia **105**:302-312.

Murphy, D. D., and P. R. Ehrlich. 1986. Conservation biology of California's remnant native grasslands. Pages 250-272 *in* H. A. Mooney and J. A. Drake, editors. The Ecology of Biological Invasions of North America and Hawaii. Springer, New York.

National Climatic Data Center. 2005. NOAA, Ashville, North Carolina. http://www1.ncdc.noaa.gov/pub/data/ccd-data/CCD_2005.pdf. Cited 29 May 2006.

Parker, I. M., S. K. Mertens, and D. W. Schemske. 1993. Distribution of 7 Native and 2 Exotic Plants in a Tallgrass Prairie in Southeastern Wisconsin - the Importance of Human Disturbance. American Midland Naturalist **130**:43-55.

Pfeifer-Meister, L., and S. D. Bridgham. 2007. Seasonal and spatial controls over nutrient cycling in a Pacific Northwest prairie. Ecosystems **10**:1250-1260.

Pojar, J., and A. MacKinnon. 1994. Plants of the Pacific Northwest Coast: Washington, Oregon, British Columbia and Alaska. Lone Pine Publishing USA; Holt : Partners Publishers Group [Distributor], Auburn.

Roy, B. A., M. L. Stanton, and S. M. Eppley. 1999. Effects of environmental stress on leaf hair density and consequences for selection. Journal of Evolutionary Biology **12**:1089-1103.

Schmitt, J., and S. A. Dudley. 1996. Testing the adaptive plasticity hypothesis for plant responses to neighbors. Plant Species Biology **11**:59-67.

Seabloom, E. W., E. T. Borer, V. L. Boucher, R. S. Burton, K. L. Cottingham, L. Goldwasser, W. K. Gram, B. E. Kendall, and F. Micheli. 2003a. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. Ecological Applications **13**:575-592.

Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003b. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences of the United States of America **100**:13384-13389.

Suding, K. N., J. R. Larson, E. Thorsos, H. Steltzer, and W. D. Bowman. 2004a. Species effects on resource supply rates: do they influence competitive interactions? Plant Ecology **175**:47-58.

Suding, K. N., K. D. LeJeune, and T. R. Seastedt. 2004b. Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorus availability. Oecologia **141**:526-535.

Vinton, M. A., and I. C. Burke. 1997. Contingent effects of plant species on soils along a regional moisture gradient in the Great Plains. Oecologia **110**:393-402.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science **277**:494-499.

Wetzel, P. R., and A. G. van der Valk. 1998. Effects of nutrients and soil moisture on competition between *Carex stricta*, *Phalaris arundinacea*, and *Typha latifolia*. Plant Ecology **138**:179-190.

Wilson, S. D., and J. M. Shay. 1990. Competition, fire, and nutrients in a mixed-grass prairie. Ecology **71**:1959-1967.

Young, W. T. 2005. Grass Seed Production in Oregon. http://cropandsoil.oregonstate.edu/seed-ext/Pub/or_prod.html. Cited 29 May 2006.