Utah State University
DigitalCommons@USU

All Graduate Theses and Dissertations | Graduate Studies, School of

5-1-2013

Effects of Non-Surface-Disturbing Restoration Treatments on Native Grass Revegetation and Soil Seed Bank Composition in Cheatgrass-Invaded Sagebrush-Steppe Ecosystems

Alexandra D. Reinwald
Utah State University

Recommended Citation
Reinwald, Alexandra D., "Effects of Non-Surface-Disturbing Restoration Treatments on Native Grass Revegetation and Soil Seed Bank Composition in Cheatgrass-Invaded Sagebrush-Steppe Ecosystems" (2013). *All Graduate Theses and Dissertations.* Paper 1537.
http://digitalcommons.usu.edu/etd/1537

This Thesis is brought to you for free and open access by the Graduate Studies, School of at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact becky.thoms@usu.edu.

UtahStateUniversity
MERRILL-CAZIER LIBRARY

EFFECTS OF NON-SURFACE-DISTURBING RESTORATION TREATMENTS ON NATIVE GRASS REVEGETATION AND SOIL SEED BANK COMPOSITION IN CHEATGRASS-INVADED SAGEBRUSH-STEPPE ECOSYSTEMS

by

Alexandra Dawn Reinwald

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

Dr. Eugene W. Schupp Major Professor	Dr. Thomas A. Monaco Committee Member
Dr. Karin M. Kettenring Committee Member	Dr. Mark R. McLellan Vice President for Research and Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2013

ABSTRACT

Effects of Non-Surface-Disturbing Restoration Treatments on Native Grass Revegetation and Soil Seed Bank Composition in Cheatgrass-Invaded Sagebrush-Steppe Ecosystems

by

Alexandra D. Reinwald, Master of Science

Utah State University, 2013

Major Professor: Eugene W. Schupp
Department: Wildland Resources

The conversion of sagebrush-steppe communities of the Great Basin into cheatgrass-dominated communities is one of the most dramatic ongoing land conversions in North America. Although restoration of these communities is a high priority to landowners and land management agencies, restoration of native vegetation is difficult. Several restoration treatments intended to increase the success of aerially-seeded perennial grasses in cheatgrass-invaded sagebrush ecosystems were assessed to determine their effects on perennial seedling emergence and soil seed bank density and composition. Assessed restoration treatments were: 1) vegetation manipulation (sagebrush thinning and prescribed burning); 2) imazapic herbicide application; 3) seedbed amendments (aerial seeding with activated carbon addition, aerial seeding with sucrose addition); and 4) seeding frequency.

The effects of these treatments were evaluated in two distinct sagebrush shrubland ecosystems in northern Utah. One is characterized as a remnant sagebrush stand with a cheatgrass-dominated understory and the other as a cheatgrass near-monoculture, completely lacking a sagebrush component. In the seed bank study, responses were assessed immediately and 1 year following treatment while in the seedling emergence study, they were assessed 2 and 3 years following treatment.

Main effects of vegetation manipulation, herbicide application, and seedbed addition treatments and their interactions on perennial seedling emergence are described in Chapter 2. The effects of seeding frequency on perennial seedling emergence are also described in Chapter 2. Herbicide demonstrated potential for increasing native perennial grass emergence, although this response was delayed and not seen until 3 years post-application. Burning showed potential for increasing the emergence of perennial grasses 2 years post-burn. Results also suggest that potential exists to increase native perennial grass emergence through an increase in seeding frequency.

In Chapter 3 I evaluated the effects of vegetation manipulation, herbicide application, and seedbed addition on seed pool dynamics. These results suggest that herbicide and sucrose may be useful tools for reducing exotic species richness in cheatgrass-invaded systems. Herbicide also showed potential for reducing cheatgrass seed bank densities. Additionally, results demonstrated that the reductions in cheatgrass seed bank densities observed immediately after fire are still observed 1 year post-burn.

(118 pages)

PUBLIC ABSTRACT

Effects of Non-Surface-Disturbing Restoration Treatments on Native Grass Revegetation and Soil Seed Bank Composition in Cheatgrass-Invaded Sagebrush-Steppe Ecosystems

by

Alexandra D. Reinwald, Master of Science

Utah State University, 2013

Major Professor: Eugene W. Schupp
Department: Wildland Resources

The sagebrush-steppe communities of the Great Basin have been dramatically transformed by the invasion of the non-native annual grass cheatgrass. In many areas of the Great Basin, this invasion has resulted in the loss of native plant species and ultimately the conversion to cheatgrass-dominated communities. As healthy sagebrush communities provide multiple ecosystem services such as diverse wildlife habitat, forage for cattle grazing, and water filtration, restoration of these communities is a high priority to landowners and land management agencies. Established perennial grasses can successfully compete with non-native annual grasses and increase the resistance of plant communities to invasion by non-native annual grasses. As such, re-establishing a healthy native sagebrush understory dominated by perennial grasses may be the key to restoring these communities. However, the restoration of native vegetation is difficult and has been met with limited success.

As a result, I was interested in investigating the effects of several restoration treatments intended to increase the success of aerially-seeded native perennial grasses in cheatgrass-invaded sagebrush communities on perennial seedling emergence and soil seed bank density and composition. The restoration treatments assessed in this study were: 1) vegetation manipulations (50% sagebrush thinning, 100% sagebrush thinning, prescribed burning); 2) imazapic herbicide application (140 g active ingredient $\cdot$ ha^{-1}, 210 g active ingredient $\cdot$ ha^{-1}); 3) soil seedbed amendments (activated carbon addition, sucrose addition); and 4) seeding frequency (2 years of seeding, 3 years of seeding).

Herbicide and prescribed burning demonstrated potential for increasing seeded native perennial grass emergence success. Results also suggest that potential exists to increase native perennial grass emergence through an increase in seeding frequency. Additionally, these results suggest that herbicide and sucrose may be useful tools for reducing exotic species richness in cheatgrass-invaded systems. Herbicide also showed potential for reducing cheatgrass seed bank densities. Results also demonstrated that the reductions in cheatgrass seed bank densities observed immediately after fire are still observed 1 year post-burn.

This study increased our understanding of the effects of some commonly used restoration techniques and seeding frequency on seeded native perennial grass success and seed bank dynamics in Great Basin cheatgrass-invaded sagebrush ecosystems.

ACKNOWLEDGMENTS

I would first like to thank my graduate advisor, Eugene Schupp, for his guidance, support and sense of humor throughout this graduate school journey. Thanks to my committee members, Thomas Monaco and Karin Kettenring, for their advice and commitment to the integrity of this research. I would also like to extend a huge thank you to Suasn Durhman for her limitless patience and assistance with statistical analysis. Thanks to Marsha Bailey for all her administrative support. And a very special thank you to Corrin Liston, Shannon Kay, and the many others that helped in the field, lab, greenhouse, and office making this research possible. Funding for this research was provided by the US National Park Service, the US Geologic Survey, the Utah Agricultural Experiment Station, the Vice Presidential Fellowship at Utah State University, and the Utah State University Ecology Center.

Thank you to my dear friends and family for all your love and support throughout this journey. Thanks also to my fellow graduate students and peers who made this the most enjoyable of experiences. Gigantic thanks to Jan Summerhays, without whom the research process would not have been as smooth, my sanity may have gone out the window, and there certainly would have been less laughter. Lastly, I am grateful to have had the opportunity to pursue a graduate degree when there are so many that are not as fortunate.

Alexandra Reinwald

CONTENTS

Page

ABSTRACT ii

PUBLIC ABSTRACT iv

ACKNOWLEDGMENTS vi

LIST OF TABLES viii

LIST OF FIGURES ix

CHAPTER

1. INTRODUCTION 1

2. EVALUATING RESTORATION TECHNIQUES USING NATIVE PERENNIAL GRASSES IN CHEATGRASS (*BROMUS TECTORUM* L.)-INVADED SAGEBRUSH-STEPPE ECOSYSTEMS 14

3. EVALUATING THE EFFECTS OF RESTORATION TECHNIQUES ON SEED BANK DYNAMICS OF CHEATGRASS (*BROMUS TECTORUM* L.)-INVADED SAGEBRUSH-STEPPE ECOSYSTEMS 52

4. CONCLUSION 101

APPENDICES 106

LIST OF TABLES

Table Page

2.1 Analysis of variance for perennial seedling density in the sagebrush experiment....46

2.2 Analysis of variance for perennial seedling density in the cheatgrass experiment....47

3.1 Analysis of variance for model 1 (2008 pre-treatment and 2008 post-treatment collection times and burning) of the sagebrush experiment 87

3.2 Analysis of variance for model 2 (2008 pre-treatment and 2009 post-treatment collection times and all treatments) of the sagebrush experiment....88

3.3 Analysis of variance for model 1 (2008 pre-treatment and 2008 post-treatment collection times and burning) of the cheatgrass experiment....89

3.4 Analysis of variance for model 2 (2008 pre-treatment and 2009 post-treatment collection times and all treatments) of the cheatgrass experiment....90

3.5 Least squares means comparison estimates of total species richness for model 2 (2008 pre-treatment and 2009 post-treatment collection times and all treatments) of the cheatgrass experiment, assessing the herbicide treatment x seed treatment x collection time interaction 91

A.1 Occurrence of species in the seed bank at the sagebrush experiment. Species frequency (percent of samples in which species was found) and percent of total seed bank for all plots at all three collection times are presented....107

A.2 Occurrence of species in the seed bank at the cheatgrass experiment. Species frequency (percent of samples in which species was found) and percent of total seed bank for all plots at all three collection times are presented....108

LIST OF FIGURES

Figure Page

2.1 Mean 2011 perennial seedling density · 6 m^{-2} (± 95% CI) as affected by herbicide treatment at the sagebrush experiment 48

2.2 Mean perennial seedling density · 6 m^{-2} (± 95% CI) for seed treatment group at the sagebrush experiment in 2010 and 2011 49

2.3 Mean 2010 perennial seedling density · 6 m^{-2} (± 95% CI) as affected by vegetation treatment at the cheatgrass experiment 50

2.4 Mean 2011 perennial seedling density · 6 m^{-2} (± 95% CI) as affected by herbicide treatment at the cheatgrass experiment 51

3.1 Mean *Bromus tectorum* seed bank density · 0.24 L^{-1} of soil (± 95% CI) as affected by herbicide and collection time in model 2 of the sagebrush experiment 92

3.2 Mean exotic species seed bank density · 0.24 L^{-1} of soil (± 95% CI) as affected by herbicide and collection time in model 2 of the sagebrush experiment 93

3.3 a) mean total species richness · 0.24 L^{-1} of soil (± 95% CI) as affected by herbicide and collection time in model 2 of the sagebrush experiment, b) mean native and exotic species richness · 0.24 L^{-1} of soil as affected by herbicide and collection time in model 2 of the sagebrush experiment 94

3.4 Mean *Bromus tectorum* seed bank density · 0.24 L^{-1} of soil (± 95% CI) as affected by vegetation treatment and collection time in model 1 of the cheatgrass experiment 95

3.5 Mean exotic species seed bank density · 0.24 L^{-1} of soil (± 95% CI) as affected by vegetation treatment and collection time in model 1 of the cheatgrass experiment 96

3.6 Mean *Bromus tectorum* seed bank density · 0.24 L^{-1} of soil (± 95% CI) as affected by vegetation treatment and collection time in model 2 of the cheatgrass experiment 97

3.7 Mean exotic species seed bank density · 0.24 L^{-1} of soil (± 95% CI) as affected by vegetation treatment and collection time in model 2 of the cheatgrass experiment 98

3.8 Mean exotic species seed bank density · 0.24 L^{-1} of soil (± 95% CI) as affected by seedbed treatment and collection time in model 2 of the cheatgrass experiment 99

3.9 Mean total species richness · 0.24 L^{-1} of soil (± 95% CI) as affected by the herbicide treatment (a) control, b) 140 g · ha^{-1} c) 210 g · ha^{-1}) x seedbed treatment x collection time interaction in model 2 of the cheatgrass experiment 100

CHAPTER 1

INTRODUCTION

Invasion by exotic species can alter ecosystem processes and threaten the structure and functioning of many ecosystems (D'Antonio and Vitousek 1992). One of the most successful invasive species in the Intermountain West of North America is the annual Eurasian grass *Bromus tectorum* (cheatgrass) (Rimer and Evans 2006). In the Great Basin of the Intermountain West, cheatgrass invasion into *Artemisia tridentata* (sagebrush) shrublands has dramatically transformed species compositions, ecosystem processes, fire regimes and the structure and composition of seed banks (Young and Evans 1975; Whisenant 1990; Humphrey and Schupp 2001). Cheatgrass is considered the most widespread invasive in the sagebrush ecosystems of North America (Mazzola et al. 2008) and is currently found in all U.S. states and Canadian provinces (USDA-NRCS 2012). It is estimated that cheatgrass occupies 22 million hectares (54 million acres) in the western U.S. (Belnap et al. 2005). In the Great Basin specifically, it is estimated to have invaded 10 million hectares (25 million acres) (USDI-BLM 2000), and is spreading at a rate of 14% per year (Duncan et al. 2004).

Healthy sagebrush ecosystems provide multiple ecosystem services such as diverse wildlife habitat, forage for cattle grazing, and water filtration. Restoring these degraded ecosystems is a priority for both ecological and economic reasons. However, restoration of these cheatgrass-invaded sagebrush shrublands has been met with limited success. This limited success is mainly attributed to intense competition for available resources between cheatgrass and seeded perennial grasses (Rummel 1946; Evans 1961)

and a scarcity of native species propagules (Humphrey and Schupp 2001), both of which limit the successful emergence, establishment, and recruitment of perennial grasses.

Initial invasion of cheatgrass is often driven by the reduction of perennial grasses by disturbances such as overgrazing by livestock which frees up space and resources (Knapp 1996). Cheatgrass, a winter annual, is characterized by early germination, rapid growth, prolific seed production, abundant highly flammable fine fuels (Klemmedson and Smith 1964), and great phenotypic plasticity (Young et al. 1987). Due to its early emergence and rapid growth, cheatgrass preemptively attains resources early in the spring prior to later emerging native herbaceous species (Harris 1967; Melgoza et al. 1990; Abraham et al. 2009), making it an aggressive competitor against native vegetation. However, the most significant affect of cheatgrass on sagebrush ecosystems results from its interaction with fire.

Remnant sagebrush systems are dominated by perennial bunchgrasses which are typically widely spaced resulting in a discontinuous fuelbed (Whisenant 1990). Cheatgrass, however, produces abundant highly flammable and often continuous fine fuels which carry fire (Whisenant 1990; D'Antonio and Vitousek 1992). Additionally, cheatgrass has the ability to recover relatively rapidly after fire (Melogza et al. 1990). These attributes of cheatgrass have led to a cheatgrass-wildfire cycle with cheatgrass promoting fire and fire promoting cheatgrass (D'Antonio and Vitousek 1992). Fire return intervals have gone from between 60-110 years in pre-invasion sagebrush communities to 3-5 years under cheatgrass dominance (Whisenant 1990). This altered

cycle is detrimental to native vegetation and it reinforces the dominance of cheatgrass in these sagebrush ecosystems.

Sagebrush is not able to re-sprout post-fire (Young and Evans 1978; Baker 2006) and though perennial grasses are able to, more frequent fires can kill them if they are unable to recover between fires (Stewart and Hull 1949; Whisenant 1990). Depending on the frequency and intensity of fire, post-fire systems can range from intact sagebrush stands with understories dominated by native perennial grasses to cheatgrass near-monocultures. Additionally, over time frequent burns can diminish the seed banks of perennial plant species (Peters and Bunting 1994; Humphrey and Schupp 2001). The resultant changes in the composition and structure of sagebrush shrubland ecosystems has negatively affected native plant and animal populations (Kochert and Pellant 1986; Updike et al.1990; Dobler 1994; Rosentreter 1994; Connelly et al. 2000) as well as greatly reduced plant species diversity (Whisenant 1990). In addition to the ecological consequences of increased fire frequencies, fire suppression and post-fire rehabilitation costs have risen (Stewart and Hull 1949; Roberts 1994), as has the loss of private structures (Pellant 1996).

The key to breaking the fire cycle and preventing a type-conversion may be re-establishing a healthy native herbaceous understory dominated by perennial grasses. Established perennial grasses can successfully compete with exotic annual grasses (Seabloom et al. 2003; Corbin and D'Antonio 2004; Humphrey and Schupp 2004) and increase the resistance of plant communities to invasion by exotic annual grasses (Corbin and D’Antonio 2004; Chambers et al. 2007; Davies et al. 2008).

As intense competition and a scarcity of native species propagules constrain the establishment of perennials, the overall objectives of these studies were to determine if 1) restoration techniques aimed at controlling cheatgrass and altering the resource environment, and 2) increased perennial grass propagule supply can increase the success of seeded native perennial grasses in cheatgrass-invaded sagebrush systems. Additionally, to 3) determine the effects of these restoration treatments on seed bank dynamics.

Sagebrush thinning or removal may reduce competitive pressure for seeded native perennial grass species by increasing nutrient availability (Blank et al. 2007; Boyd and Davies 2010) and/or soil water (Inouye 2006; Prevéy et al. 2010). Previous studies have demonstrated increased establishment (Boyd and Svejcar 2011), cover, and biomass of perennial grasses (Inouye 2006; Bechtold and Inouye 2007; Boyd and Svejcar 2011) with shrub thinning. However, the effects of shrub thinning on perennial grass emergence and seed bank composition and dynamics are largely unknown.

Although fire can harm native vegetation and perpetuate cheatgrass' dominance, it can also create a window of opportunity for the successful establishment of seeded desirable species. Fires in late summer or early fall, after the senescence of native perennial grasses, may have less damage on non-target species relative to spring or summer burns (Dyer and Rice 1997). Prescribed burning can reduce cheatgrass and other overstory species as well as remove the thatch layer, all of which may increase the availability of limiting resources for use by seeded grasses. In addition, fire can destroy cheatgrass seeds and reduce its seed banks (West and Hassan 1985; Hassan and West

1986; Humphrey and Schupp 2001). Burning has also been suggested to enhance the effectiveness of other techniques such as herbicide application by increasing contact with emerging target plants and the soil surface (Washburn et al. 1999; Monaco et al. 2005; Kyser et al. 2007; Sheley et al. 2007).

Herbicide is a common method used for cheatgrass control in invaded rangelands (Pellant 1996; Young and Clements 2000). The pre-emergent herbicide imazapic (chemical family: imidazolinone; mode of action: acetolactate synthase inhibitor) has been suggested for use in restoration efforts as it can reduce cheatgrass and other invasive annual weeds, while still allowing some level of perennial grass emergence (Shinn and Thill 2004; Monaco et al. 2005; Kyser et al. 2007; Morris et al. 2009). Although there is evidence of successful perennial grass emergence in the presence of imazapic, sensitivity of these grasses to imazapic is highly variable among species (Shinn and Thill 2004; Kyser et al. 2007; Sheley et al. 2007). Thus, appropriate application rates that minimize injury to non-target perennial grasses while still controlling cheatgrass need to be determined. Additionally, the effects of imazapic on seed banks of cheatgrass invaded sagebrush ecosystems are still unclear.

It has been suggested that increased soil nitrogen availability allows fast growing annual exotics, like cheatgrass, to dominate disturbed sites (McLendon and Redente 1991; Paschke et al. 2000), while low resource availability often favors native perennial species (Daehler 2003). Therefore, cheatgrass may be disproportionately harmed by nutrient reductions. Thus, treatments that directly manipulate soil resources and reduce cheatgrass growth may be effective restoration tools to increase seeded perennial grass

success (Monaco et al. 2003). Carbon (in readily available forms such as sucrose) and activated carbon (AC) soil amendments are two such treatments. Additions of carbon such as sucrose increase soil microbial nitrogen immobilization thereby decreasing plant available nitrogen (Blumenthal et al. 2003) which can negatively affect invasive early seral species such as cheatgrass (McLendon and Redente 1992; Dakheel et al. 1993; Paschke et al. 2000; Monaco et al. 2003; Beckstead and Augspurger. 2004; Mazzola et al. 2008; Brunson et al. 2010; Mazzola et al. 2011). However, the effects of sucrose on seeded perennial grasses are less clear (Blumenthal et al. 2003; Corbin and D'Antonio 2004).

Very few studies have investigated the effects of AC on invasive and native grasses; however, it has been suggested by Kulmatiski and Beard (2006) for use as a soil manipulation for exotic plant control and native plant restoration. AC is a highly porous material that through adsorption, can tie up plant available nutrients and allelopathic compounds (Inderjit and Callaway 2003), both of which ultimately may be beneficial for native perennial grass establishment. There is evidence that the reduction of alleopathic compounds may reduce the competitive advantage of exotic species relative to native species (Callaway and Aschehoug 2000). Two studies have demonstrated AC's ability to decrease cover of exotics including cheatgrass and increase native perennial grass cover (Kulmatiski and Beard 2006; Kulmatiski 2011). However, the effectiveness of this as a large scale restoration technique has yet to be evaluated. For example, Kulmatiski and Beard (2006) incorporated AC into the top 10 cm of soil at the rate of 1 kg $\cdot$ m^2. This technique would not be feasible or economical on a large scale and incompatible where

soil disturbance is not acceptable. Therefore, the effectiveness of this as a large scale restoration technique has yet to be proven and the effects of surface applications of realistic quantities are unknown.

As seedling establishment, in part, depends on propagule supply (Harper 1977; Picket et al. 1987) and higher densities generally result in higher establishment (Allendorf and Lundquist 2003), seeding rates and seeding frequency may influence the success of re-vegetation efforts (Sheley et al. 1999; Williams et al. 2002; Sheley and Half 2006). Previous studies have demonstrated an increase in perennial grass densities with increased seeding rates (Sheley et al. 1999; Eiswerth and Shonkwiler 2006; Mazzola et al. 2011). Currently, there is limited information on the effectiveness of multiple consecutive years of seeding.

Although extensive research has been conducted investigating the effects of several of these treatments, there remain gaps in knowledge regarding their effects on perennial grass emergence and seed bank dynamics, proper application rates, and the interaction of treatments. In chapter 2, I evaluated the effects of restoration treatments and seeding frequency on native perennial grass emergence. In chapter 3, I evaluated the effects of these same treatments on seed bank densities and composition. I anticipate that these results will define improved strategies and provide valuable information to land mangers and restoration ecologists on increasing the success of restoration efforts aimed at reincorporating native perennial grass species into cheatgrass-invaded sagebrush shrubland ecosystems of the Great Basin.

LITERATURE CITED

Abraham, J. K., J. D. Corbin, and C. M. D'Antonio. 2009. California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. *Plant Ecology* 201:445-456.

Allendorf, F. W., and L. L. Lundquist. 2003. Introduction: population biology, evolution, and control of invasive species. *Conservation Biology* 17:24-30.

Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. *Wildlife Society Bulletin* 34:177–185.

Bechtold, H. A., and R. S. Inouye. 2007. Distribution of carbon and nitrogen in sagebrush steppe after six years of nitrogen addition and shrub removal. *Journal of Arid Environments* 71:122-132.

Beckstead, J., and C. K. Augspurger. 2004. An experimental test of resistance to cheatgrass invasion: limiting resources at different life stages. *Biological Invasions* 6:417-432.

Belnap, J., S. L. Phillips, S. K. Sherrod, and A. Moldenke. 2005. Soil biota can change after exotic plant invasion: does this affect ecosystem processes? *Ecology* 86:3007-3017.

Blank, R. R., J. Chambers, B. Roundy, and A. Whittaker. 2007. Nutrient availability in rangeland soils: influence of prescribed burning, herbaceous vegetation removal, overseeding with *Bromus tectorum*, season, and elevation. *Rangeland Ecology & Management* 60:644-655.

Blumenthal, D. M., N. R. Jordan, and M. P. Russelle. 2003. Soil carbon addition controls weeds and facilitates prairie restoration. *Ecological Applications* 13:605-615.

Boyd, C. S., and K. W. Davies. 2010. Shrub microsite influences post-fire perennial grass establishment. *Rangeland Ecology & Management* 63:248-252.

Boyd, C. S., and T. J. Svejcar. 2011. The influence of plant removal on succession in Wyoming big sagebrush. *Journal of Arid Environments* 75:734-741.

Brunson, J. L., D. A. Pyke, and S. S. Perakis. 2010. Yield response of ruderal plants to sucrose in invasive-dominated sagebrush steppe of the northern Great Basin. *Restoration Ecology* 18:304-312.

Callaway, R. M., and E. T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290:521-523.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs* 77:117-145.

Connelly, J. W., M.A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage Sage Grouse populations and their habitats. *Wildlife Society Bulletin* 28:967-985.

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.

Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology Evolution and Systematics* 34:183-211.

Dakheel, A. J., S. R. Radosevich, and M. G. Barbour. 1993. Effect of nitrogen and phosphorus on growth and interference between *Bromus tectorum* and *Taeniatherum asperum*. *Weed Research* 33:415-422.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasion by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.

Davies, K. W., R. L. Sheley, and J. D. Bates. 2008. Does fall prescribed burning *Artemisia tridentata* steppe promote invasion or resistance to invasion after a recovery period? *Journal of Arid Environments* 72:1073-1082.

Dobler, F. C. 1994. Washington State shrub-steppe ecosystem studies with emphasis on the relationship between nongame birds and shrub and grass cover densities. *In*: S. B. Monsen and S. G. Kitchen [comps.]. Proceedings: Ecology and management of annual rangelands; 18- 22 May 1992; Boise, ID, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-GTR-313. p. 149-161.

Duncan, C. A., J. J. Jachetta, M. L. Brown, V. F. Carrithers, J. K. Clark, J. M. Ditomaso, R. G. Lym, K. C. McDaniel, M. J. Renz, and P. M. Rice. 2004. Assessing the economic, environmental, and societal losses from invasive plants on rangeland and wildlands. *Weed Technology* 18:1411-1416.

Dyer, A. R., and K. J. Rice. 1997. Intraspecific and diffuse competition: the response of *Nassella pulchra* in a California grassland. *Ecological Applications* 7:484-492.

Eiswerth, M. E., and J. S. Shonkwiler. 2006. Examining post-wildfire reseeding on arid rangeland: a multivariate tobit modeling approach. *Ecological Modeling* 192:286-298.

Evans, R. A. 1961. Effects of different densities of downy brome (*Bromus tectorum*) on growth and survival of crested wheatgrass (*Agropyron desertorum*) in the greenhouse. *Weeds* 9:216-223.

Harper, J. L. 1977. Population biology of plants. London, UK: Academic Press. 892 p.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs* 37:89-111.

Hassan, M. A., and N. E. West. 1986. Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. *Ecology* 67:269-272.

Humphrey, L. D., and E. W. Schupp. 2001. Seed banks of *Bromus tectorum*-dominated communities in the Great Basin. *Western North American Naturalist* 61:85-92.

Humphrey, L. D., and E. W. Schupp. 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* 58:405-422.

Inderjit, and R. M. Callaway. 2003. Experimental designs for the study of allelopathy. *Plant and Soil* 256:1-11.

Inouye, R. S. 2006. Effects of shrub removal and nitrogen addition on soil moisture in sagebrush steppe. *Journal of Arid Environments* 65:604-618.

Klemmedson, J. O., and J.G. Smith. 1964. Cheatgrass (*Bromus tectorum* L). *Botanical Review* 30:226-262.

Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin desert - history, persistence, and influences to human activities. *Global Environmental Change-Human and Policy Dimensions* 6:37-52.

Kochert, M. N., and M. Pellant. 1986. Multiple use in the Snake River Birds of Prey Area. *Rangelands* 8: 217-220.

Kulmatiski, A., and K. H. Beard. 2006. Activated carbon as a restoration tool: potential for control of invasive plants in abandoned agricultural fields. *Restoration Ecology* 14:251-257.

Kulmatiski, A. 2011. Changing soils to manage plant communities: activated carbon as a restoration tool in ex-arable fields. *Restoration Ecology* 19:102-110.

Kyser, G. B., J. M. DiTomaso, M. P. Doran, S. B. Orloff, R. G. Wilson, D. L. Lancaster, D. F. Lile, and M. L. Porath. 2007. Control of medusahead (*Taeniatherum caputmedusae*) and other annual grasses with imazapic. *Weed Technology* 21:66-75.

Mazzola, M. B., K. G. Allcock, J. C. Chambers, R. R. Blank, E. W. Schupp, P. S. Doescher, and R. S. Nowak. 2008. Effects of nitrogen availability and cheatgrass competition on the establishment of Vavilov Siberian wheatgrass. *Rangeland Ecology & Management* 61:475-484.

Mazzola, M. B., J. C. Chambers, R. R. Blank, D. A. Pyke, E. W. Schupp, K. G. Allcock, P. S. Doescher, and R. S. Nowak. 2011. Effects of resource availability and propagule supply on native species recruitment in sagebrush ecosystems invaded by *Bromus tectorum*. *Biological Invasions* 13:513-526.

McLendon, T., and E. F. Redente. 1992. Effects of nitrogen limitation on species replacement dynamics during early secondary succession on a semiarid sagebrush site. *Oecologia* 91:312-317.

Melgoza, G., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83:7-13.

Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003. Contrasting responses of intermountain west grasses to soil nitrogen. *Journal of Range Management* 56:282-290.

Monaco, T. A., T. M. Osmond, and S. A. Dewey. 2005. Medusahead control with fall- and spring-applied herbicides on northern Utah foothills. *Weed Technology* 19:653-658.

Morris, C., T. A. Monaco, and C. W. Rigby. 2009. Variable impacts of imazapic rate on downy brome (*Bromus tectorum*) and seeded species in two rangeland communities. *Invasive Plant Science and Management* 2:110-119.

Paschke, M. W., T. McLendon, and E. F. Redente. 2000. Nitrogen availability and old-field succession in a shortgrass steppe. *Ecosystems* 3:144-158.

Pellant M. 1996. Cheatgrass: the invader that won the west. Boise, ID, USA: Bureau of Land Management, Interior Columbia Ecosystem Management Project. 22 p.

Peters, E. F. and S. C. Bunting. 1994. Fire conditions pre- and post-occurrence of annual grasses on the Snake River Plain. *In*: S. B. Monsen and S. G. Kitchen [comps.]. Proceedings: Ecology and management of annual rangelands; 18- 22 May 1992; Boise, ID, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-GTR-313. p. 31-36.

Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms and pathways of succession. *Botanical Review* 53:335-371.

Prevey, J. S., M. J. Germino, N. J. Huntly, and R. S. Inouye. 2010. Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe. *Plant Ecology* 207:39-51.

Rimer, R. L., and R. D. Evans. 2006. Invasion of downy brome (*Bromus tectorum L.*) causes rapid changes in the nitrogen cycle. *American Midland Naturalist* 156:252-258.

Roberts, T.C., Jr. 1994. Resource impacts of cheatgrass and wildfires on public lands and livestock grazing. *In*: S. B. Monsen and S. G. Kitchen [comps.]. Proceedings: Ecology and management of annual rangelands; 18- 22 May 1992; Boise, ID, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-GTR-313. p. 167-169.

Rosentreter, R. 1994. Displacement of rare plants by exotic grasses. *In*: S. B. Monsen and S. G. Kitchen [comps.]. Proceedings: Ecology and management of annual rangelands; 18- 22 May 1992; Boise, ID, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-GTR-313. p. 170-175.

Rummel, R. S. 1946. Some effects of competition from cheatgrass brome on crested wheat-grass and bluestem wheatgrass. *Ecology* 27:159-167.

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.

Sheley, R. L., M. F. Carpinelli, and K. J. R. Morghan. 2007. Effects of imazapic on target and non-target vegetation during re-vegetation. *Weed Technology* 21:1071-1081.

Sheley, R. L., and M. L. Half. 2006. Enhancing native forb establishment and persistence using a rich seed mixture. *Restoration Ecology* 14:627-635.

Sheley, R. L., J. S. Jacobs, and R. P. Velagala. 1999. Enhancing intermediate wheatgrass establishment in spotted knapweed infested rangeland. *Journal of Range Management* 52:68-74.

Shinn, S. L., and D. C. Thill. 2004. Tolerance of several perennial grasses to imazapic. *Weed Technology* 18:60-65.

Stewart, G., and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.) an ecologic intruder in southern Idaho. *Ecology* 30:58-74.

Updike, D. R., Loft, E. R., and F. A. Hall. 1990. *In*: D. E. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller [comps.]. Proceedings: Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 5-7 April 1989; Las Vegas, NV, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-276. p. 41-46.

USDA-NRCS. 2012. The PLANTS database. Available at: http://plants.usda.gov/java/profile?symbol=BRTE. Accessed 17 August 2012.

USDI-BLM. 2000. The Great Basin: healing the land. Boise, ID, USA: National Interagency Fire Center. 36 p.

Washburn, B. E., T. G. Barnes, and J. D. Sole. 1999. No-till establishment of native warm-season grasses in tall fescue fields: fire-year results indicate value of new herbicide. *Ecological Restoration* 17:40-45.

West, N. E., and M. A. Hassan. 1985. Recovery of sagebrush-grass vegetation following wildfire. *Journal of Range Management* 38:131-134.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. *In*: D. E. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller [comps.]. Proceedings: Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 5-7 April 1989; Las Vegas, NV, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-276. p. 4-10.

Williams, M. I., G. E. Schuman, A. L. Hild, and L. E. Vicklund. 2002. Wyoming big sagebrush density: effects of seeding rates and grass competition. *Restoration Ecology* 10:385-391.

Young, J. A., and C. D. Clements. 2000. Cheatgrass control and seeding. *Rangelands* 22:3-7.

Young, J. A., and R. A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. *Journal of Range Management* 31:283-289.

Young, J.A., R.A. Evans, R.E. Eckert, Jr., and B.L. Kay. 1987. Cheatgrass. *Rangelands* 9: 266-270.

CHAPTER 2

EVALUATING RESTORATION TECHNIQUES USING NATIVE PERENNIAL GRASSES IN CHEATGRASS (*BROMUS TECTORUM* L.)-INVADED SAGEBRUSH-STEPPE ECOSYSTEMS

Abstract

Much of the sagebrush ecosystem of western North America has been converted to exotic annual grasslands, particularly dominated by the Eurasian grass *Bromus tectorum* (cheatgrass). The invasion of cheatgrass into sagebrush shrublands of the Great Basin has resulted in increased fire frequency and a loss of native species. As cheatgrass is a strong competitor at the seedling stage, efforts to reintroduce native fire-resilient perennial species into cheatgrass-invaded communities have been met with limited success. In field experiments conducted in northern Utah, I investigated the effects, two and three years post-treatment, of burning, sagebrush thinning, imazapic herbicide, and sucrose and activated carbon seedbed amendments on native perennial grass emergence in a cheatgrass-invaded sagebrush site and a cheatgrass near-monoculture site. Additionally, I compared seedling emergence from plots seeded one, two, and three consecutive years in the cheatgrass-invaded sagebrush site. Restoration techniques were aimed at controlling cheatgrass and altering the resource environment in ways that could increase the success of seeded perennial grasses.

In the cheatgrass near-monoculture site, native perennial grass emergence was significantly enhanced both two years post-burning and three years post-herbicide

application. In the cheatgrass-invaded sagebrush site, native perennial grass emergence was significantly enhanced three years post-herbicide application. Plots that were seeded two consecutive years had significantly higher native perennial grass emergence than did those that were seeded a single year and plots seeded three consecutive years had even higher perennial emergence. These results demonstrate that burning and herbicide may be useful restoration tools for increasing native perennial grass emergence in sagebrush systems invaded by cheatgrass. Additionally, results demonstrate that increasing seeding frequency increases native perennial grass emergence.

INTRODUCTION

Cheatgrass is said to be the most widespread invasive in the sagebrush ecosystems of North America (Mazzola et al. 2008). It is estimated that cheatgrass has invaded 10 million hectares (25 million acres) of the Great Basin (USDI-BLM 2000), and is spreading at a rate of 14% per year (Duncan et al. 2004). Cheatgrass invasion is a threat to *Artemisia tridentata* (sagebrush) shrublands of the Great Basin. Increased cheatgrass dominance results in increased fire frequency, size, and severity, and a subsequent loss of native species (Whisenant 1990; Knapp 1996; Chambers 2008). Restoration of cheatgrass-invaded sagebrush shrublands has been difficult under these highly altered fire regimes and with the competitive pressure exerted on native species by cheatgrass (Evans 1961; Whisenant 1990).

Cheatgrass is an annual Eurasian grass that was unintentionally introduced to the United Sates in the late 1800’s (Mack 1981). Severe livestock overgrazing of the

sagebrush ecosystems of the Intermountain West starting in the late 1800's (Knapp 1996) greatly reduced native herbaceous cover which lead to an increase in resource availability. Cheatgrass was able to take advantage of the reduced competition and freed resources and rapidly spread across the degraded landscape occupying open niches (Billings 1952; Knapp 1996). Once introduced and established in the Great Basin, fire insured the continued dominance of cheatgrass in these sagebrush ecosystems.

Fire regimes in the Great Basin have been dramatically altered by the invasion of cheatgrass (Chambers 2008). Cheatgrass produces highly abundant flammable fine fuels which increase the rate of fire spread as well as the size, severity and frequency of fires (Stewart and Hull 1949; D'Antonio and Vitousek 1992; Knapp 1996; Link et al. 2006). In many parts of the Great Basin a cheatgrass-wildfire cycle exists with cheatgrass promoting fire and fire promoting cheatgrass (D'Antonio and Vitousek 1992); historically, pre-invasion sagebrush communities had fire return intervals of 60-110 years whereas under cheatgrass dominance they are 3-5 years (Whisenant 1990). This altered fire cycle can be detrimental to native vegetation which is not adapted to such frequent fire.

Because sagebrush does not re-sprout post-fire and must re-establish from seed, recovery can take many years (Young and Evans 1978; Baker 2006). Likewise, native perennial grasses, depending on the species and frequency of fire, can be injured or killed by fire (Stewart and Hull 1949; Wright and Klemmedson 1965; Harris 1967; Young and Evans 1978). Additionally, through time this altered cycle diminishes the perennial seed bank (Peters and Bunting 1994). Unlike native vegetation, cheatgrass is well adapted to

fire (Melgoza et al. 1990; Ziska et al. 2005) and in the near absence of a native seed bank (Humphrey and Schupp 2001) it recovers and preemptively fills unoccupied resource niches (Melgoza et al. 1990; D'Antonio and Vitousek 1992; Knapp 1996).

Even if native species are able to germinate, cheatgrass is highly competitive for soil resources; its early germination and rapid growth allow it to deplete resources prior to later emerging native species thereby outcompeting them at the seedling stage (Klemmedson and Smith 1964; Harris 1967; Melgoza et al. 1990; Abraham et al. 2009). However, established perennial grasses can successfully compete with exotic annual grasses (Booth et al. 2003; Seabloom et al. 2003; Corbin and D'Antonio 2004b; Humphrey and Schupp 2004) and increase the resistance of plant communities to invasion by exotic annual grasses (Corbin and D'Antonio 2004b; Chambers et al. 2007; Davies et al. 2008).

The key to breaking the cheatgrass-wildfire cycle and preventing a type-conversion may be re-establishing the perennial grass component into these degraded systems. However, efforts to reintroduce native perennial grasses have had limited success when annuals such as cheatgrass are present at high densities (Dyer and Rice 1999). Therefore, controlling cheatgrass density may be critical for successful establishment of native perennial grasses.

The reintroduction of native perennial grasses into degraded landscapes is often attempted by seeding and is commonly done via rangeland drill which creates furrows that seeds are deposited in thereby incorporating seeds into the soil surface (Haferkamp et al. 1987). This method causes surface disturbance and may not be suitable in areas with

cultural artifacts present or rocky/steep terrains. In areas where rangeland drills are not acceptable, an alternative is aerial (from aircraft) or broadcast seeding. However, in some studies the success of re-vegetation via broadcast seeding was lower than with techniques which incorporate seed into the soil (Clary 1988; MacDonald 1999; Sheley et al. 2001).

As early season competition for water is a primary obstacle to native perennial species seedling establishment and survival (Evans 1961; Harris 1967; Harris and Wilson 1970; Melgoza et al. 1990; Humphrey and Schupp 2004), reducing competition that seeded perennials face should increase emergence and survival. It has been suggested that in sagebrush-dominated systems, thinning of shrubs may increase establishment (Boyd and Svejcar 2011) and cover and biomass (Inouye 2006; Bechtold and Inouye 2007; Boyd and Svejcar 2011) of perennial grasses. This has been suggested to be the result of decreased competition for soil water (Inouye 2006) and/or an increase in nutrient availability (Blank et al. 2007; Boyd and Davies 2010). However, other studies (e.g. Prevey et al. 2010) have demonstrated that the removal of shrubs increases cheatgrass cover, which could negatively affect perennial grass emergence. Although there is evidence of shrub removal being beneficial for established perennial grasses, its effect on seedling emergence is less clear.

Prescribed burning, either alone or as part of an integrated approach, is commonly used as a tool to control invasive annual grass species (Klemmedson and Smith 1964). It has been shown to reduce aboveground cheatgrass density as well as destroy its seeds and reduce its seed banks, although this reduction is often short lived and seed banks and

aboveground vegetation can recover in one growing season (West and Hassan 1985; Hassan and West 1986; Humphrey and Schupp 2001). Seeded perennial grasses may benefit from the removal of thatch via burning; thatch can reduce seedling germination, emergence and survival (Fowler 1988; Facelli and Pickett 1991; Foster 1999; Jutila and Grace 2002). Burning also removes overstory species which may increase the availability of limiting resources for use by seeded grasses. Additionally, burning may enhance the effectiveness of other techniques such as herbicide application by increasing contact with emerging target plants and the soil surface (Washburn et al. 1999; Monaco et al. 2005; Kyser et al. 2007; Sheley et al. 2007).

In invaded rangelands, herbicide is commonly used to control cheatgrass (Pellant 1996; Young and Clements 2000). The herbicide imazapic (chemical family: imidazolinone; mode of action: acetolactate synthase inhibitor), applied as a pre-emergent herbicide, selectively targets annual species (Davison and Smith 2007; Elseroad and Rudd 2011) and there is evidence that it can reduce cheatgrass and other invasive annual grasses, while still allowing some level of perennial grass emergence (Shinn and Thill 2004; Monaco et al. 2005; Kyser et al. 2007; Morris et al. 2009). However, sensitivity of perennial grasses to imazapic is highly variable with application rate and among species (Shinn and Thill 2004; Kyser et al. 2007; Sheley et al. 2007). Currently, appropriate application levels and effects on seeded perennial grass emergence are still unclear.

Slow growing native perennial grasses in sagebrush ecosystems are adapted to low nutrient levels and have been shown to successfully compete with invasive annual

grasses under low nutrient conditions (McLendon and Redente 1992). In contrast, increased nitrogen levels have been shown to favor fast growing exotic annuals, such as cheatgrass (Brooks 2003; Vasquez et al. 2008a; Vasquez et al. 2008b). Therefore, it is expected that cheatgrass would be disproportionately harmed by low nitrogen levels (Monaco et al. 2003). Soil carbon amendments in the form of sawdust or sucrose have been suggested for use as a tool to reduce plant available nitrogen and thereby enhance the competitive ability of perennial grasses. Soil carbon amendments stimulate the activity of soil heterotrophic microbes which immobilize soil nitrogen and thereby decrease plant available nitrogen (Blumenthal et al. 2003). Several studies have demonstrated negative effects of carbon amendments on invasive early seral species (McLendon and Redente 1992; Dakheel et al. 1993; Paschke et al. 2000; Monaco et al. 2003; Beckstead and Augspurger 2004; Mazzola et al. 2008; Mazzola et al. 2011).

Sucrose is often used as a carbon source in experiments as it contains consistent quantities of carbon per unit weight and is readily decomposable which allows for rapid immobilization. Though carbon amendments have been shown to be successful at reducing nitrogen availability and cheatgrass growth and density, the effect is usually short lived and the window of opportunity for native perennial establishment is likewise short (Brown et al. 2008; Mazzola et al. 2008; Summerhays 2011). Additionally, there have been mixed results as to its effectiveness as a tool in the restoration of native perennial grasses (McLendon and Redente 1992; Blumenthal et al. 2003; Corbin and D’Antonio 2004a).

Activated carbon (AC) has also been suggested as a soil addition for use in restoration of exotic invaded communities (Kulmatiski and Beard 2006). AC is a highly porous material, often derived from superheated coconut husk or wood, which readily adsorbs organic compounds. The high surface porosity of AC allows it, through adsorption, to tie up plant available nutrients and allelopathic compounds (Inderjit and Callaway 2003), both of which ultimately may be beneficial for native perennial grass establishment. Preliminary studies have shown that high levels of AC incorporated into the soil can decrease the cover of cheatgrass and other exotics as well as increase native perennial grass cover (Kulmatiski and Beard 2006; Kulmatiski 2011). However, incorporating AC into the soil would be an incompatible application method where soil disturbance is not acceptable. Currently it is unknown whether surface application of economically realistic quantities of AC will have similar positive effects on perennial establishment.

As recruitment of native perennial grasses in cheatgrass-invaded systems is limited by propagule supply (Humphrey and Schupp 2001), seed addition should increase recruitment rates. For example, several studies have demonstrated increases in perennial grass densities with increased seeding rates (Sheley et al. 1999; Eiswerth and Shonkwiler 2006; Mazzola et al. 2011). Thus, seeding frequency will likely influence the success of re-vegetation efforts. However, there is limited information on the effectiveness of multiple consecutive years of seeding.

Survival of seeded native perennial grasses was difficult to measure and likely extremely low so in this study I focused on the density of native perennial grass

emergence. Previous studies from this experiment investigated the effects of these restoration treatments on aboveground cheatgrass densities (Summerhays 2011). The goals of this study were to determine if: 1) burning or sagebrush thinning enhances seeded native perennial grass emergence in future years, 2) herbicide application enhances seeded native perennial grass emergence in future years, 3) activated carbon or sucrose soil amendments enhance seeded native perennial grass emergence in future years, and 4) if repeated seeding (2 and 3 consecutive years) increases seeded native perennial grass emergence when compared to a single seeding? In addition to the main effects of these restoration treatments, the experimental design allowed me to examine the interactions between treatments.

METHODS

Study Area

Field experiments took place at Golden Spike National Historic Site in Box Elder County, Utah, approximately 51 km west of Brigham City (lat 41°37’13.73”, long 112°32’50.9”). This Site marks the spot of the completion of the transcontinental railroad in 1869 and due to the presence of cultural artifacts, ground-disturbing mechanisms such as drill seeding are prohibited throughout the site. Mean annual precipitation is 30 - 35 cm and mean annual temperature is 7 - 9.5 °C (USDA-NRCS 2011). As with much of the sagebrush steppe ecosystem in the Great Basin, this area has been subjected to disturbance by heavy livestock and agriculture use (Homstad et al. 2000). These disturbances along with increased fire frequency have resulted in heavily

degraded sagebrush understories almost completely lacking a perennial grass component and often dominated by cheatgrass. Consequently, these areas are highly prone to conversion to cheatgrass monocultures by wildfire. Parts of the Site have already been converted to cheatgrass monocultures.

All study plots were located on old lake terraces of the prehistoric lake Bonneville; elevation ranged from 1413 m to 1508 m. Two distinct experiments were established, one in a cheatgrass-invaded sagebrush site (sagebrush experiment) and the other in a cheatgrass near-monoculture site (cheatgrass experiment). The sagebrush experiment was located in areas with intact sagebrush; pre-treatment sagebrush cover averaged 52.7%. The cheatgrass experiment was located in an area burned by Site management in 1998; this area has a complete absence of sagebrush. Pre-treatment cheatgrass density was much higher in the cheatgrass experiment (116 tillers · 100 cm^{-2}) than the sagebrush experiment (22 tillers · 100 cm^{-2}). Experimental designs differed between the sagebrush and cheatgrass experiments due to landscape constraints and vegetation characteristics. Study plots for the two experiments were established May 2008. The experimental methods here follow those outlined by Summerhays (2011).

Sagebrush Experiment Methods

The sagebrush experiment had a total of four replicates, each containing eight plots; two replicates were located along the Site's East auto tour and the other two near the visitor's center. Plots in a replicate were haphazardly placed on the landscape in areas with similar aspect, slope and vegetation cover. Plots were 7 x 19.5 m; each plot was divided into two 4.5 x 7 m end subplots and three 3.5 x 7 m interior subplots. Each

subplot had a central 1.5 x 3 m undisturbed sampling area leaving a 2-m buffer between adjacent subplot sampling areas and outside edges of the plot. The arrangement of treatments created a split-split plot experimental design, with herbicide treatment occurring at the half-replicate level, vegetation manipulation occurring at the whole plot level, and seeding treatments occurring at the subplot level.

Four of the eight plots in each replicate were randomly selected for imazapic pre-emergent herbicide treatment. Imazapic was applied at a rate of 140 g active ingredient · ha^{-1} (2 oz · $acre^{-1}$) using a five nozzle boom sprayer mounted on an all terrain vehicle. The herbicide treatment was applied on 18 November 2008.

There were four vegetation treatments, each of which was randomly applied to one herbicide and one no herbicide plot: 1) no manipulation to vegetation (‘control’); 2) prescribed burn to remove sagebrush overstory, vegetative understory, and vegetative thatch (‘burn’); 3) 50% thinning and removal of sagebrush overstory (‘50% thinning’); and 4) 100% thinning and removal of sagebrush overstory (‘100% thinning’). The thinning and burning treatments were implemented on 25 August and 5 September 2008, respectively, by the Zion National Park Fire Use Module. Burning was done using handheld drip torches and was confined to the area of the plot by wetting the perimeter of plots. Thinning was done using chainsaws; in the 50% thinning, removed individuals were selected in advance and marked. All cut plant material was removed from plots.

Five seedbed treatments were applied randomly to subplots in each plot: 1) seeding alone (‘control’); 2) seeding with sucrose (‘sucrose’); 3) seeding with activated carbon (‘AC’); 4) seeding on snow (‘snow’); and 5) seeding with raking into soil

('raking'). Sucrose was applied at a rate of 360 g · m^{-2} (151.6 g C · m^{-2}) divided between two applications of 180 g · m^{-2}; the first application was 20 - 26 October 2008, immediately following seeding, and the second was 28 - 29 March 2009. AC derived from superheated coconut husks (AquaSorb CS, Ecologix Environmental Systems; 12 x 30 US standard mesh size) was applied at a rate of 100 g · m^{-2} with a handheld spreader 20 - 26 October 2008, immediately following seeding. Raking was implemented immediately before and after broadcast seeding.

Each subplot, regardless of seedbed treatment, was seeded with the following five native grasses: bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve ssp. *spicata*), Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth), Great Basin wildrye (*Leymus cinereus* [Scribn. & Merr.] A. Löve), needle-and-thread grass (*Hesperostipa comata* [Trin. & Rupr.] Barkworth), Sandberg bluegrass (*Poa secunda* J. Presl), and squirreltail (*Elymus elymoides* [Raf.] Swezey). Seed was applied at a rate of 100 viable seeds · $species^{-1}$ · m^{-2}. Pure Live Seed rates provided by seed supplier (Granite Seed, Lehi, UT, US) were used to calculate number of viable seeds. Seeds were mixed with rice hulls (2.5 L larger end subplots and 1.75 L smaller interior subplots) for suspension and to ensure even distribution within plots. All subplots were seeded using handheld broadcast seeders 20 - 26 October 2008, and in the control, sucrose, and activated carbon subplots 16 - 18 October 2009 and 23 - 25 October 2010. Cardboard shields were used around subplot perimeters to contain seeding mixture within the desired subplot.

Raking was meant to serve as a form of control mimicking the effects of drill seeding. However, its effects on perennial grass emergence, along with those of the snow treatment, were not evaluated in this study; these treatment plots were only seeded in the first year when emergence was so low analyses could not be conducted. Rather, they were used in comparisons of seeding frequency.

Cheatgrass Experiment Methods

The cheatgrass experiment had a total of eight plots located below the Site's East auto tour. Plots were haphazardly placed on the landscape in areas with similar aspect, slope, and vegetation cover. Plots were 18 x 21 m and arranged so that the bottom (21 m) ran perpendicular to the slope. Each plot was divided into three 7 x 18 m strips across the plot perpendicular to the slope; and each strip was partitioned into three 7 x 6 m subplots. Each subplot had a central 2 x 3 m undisturbed sampling area leaving a 4 m buffer between adjacent subplot sampling areas and outside edges of the plot. Treatment arrangement created a split-split plot design, with vegetation manipulation treatment occurring at the whole plot level, herbicide application occurring at the strip- level, and seeding treatments occurring at the subplot level.

A burn treatment was randomly allocated to four of the eight plots; the burn involved 100% blackening of the entire plot. The burn was done by the Zion National Park Fire Use Module using handheld drip torches and was confined to the area of the plot by wetting the plot perimeter. The burn treatment was implemented on 25 August 2008. Within each plot each imazapic pre-emergent herbicide treatment was applied to a 7 m x 18 m strip. Herbicide was applied at three levels: 1) no herbicide ('control'); 2)

140 g active ingredient · ha^{-1} ('2 oz · $acre^{-1}$'); and 3) 210 g active ingredient · ha^{-1} ('3 oz · $acre^{-1}$'). To reduce chances of herbicide drift and leaching, the control strip was always the most uphill strip, the 2 oz · $acre^{-1}$ concentration was applied to the middle strip, and the 3 oz · $acre^{-1}$ concentration was applied to the most downhill strip. The herbicide treatment was applied 18 November 2008 using a five nozzle boom sprayer mounted on an all terrain vehicle.

Three seedbed treatments were applied randomly to the three subplots within each herbicide strip: 1) seeding alone ('control'); 2) seeding with sucrose ('sucrose'); and 3) seeding with AC ('AC'). Sucrose was applied at a rate of 360 g · m^{-2} (151.6 g C · m^{-2}) divided between two applications of 180 g · m^{-2}; the first application was 20 - 26 October 2008, immediately following seeding, and the second was 28 - 29 March 2009. AC was applied at a rate of 100 g · m^{-2} with a handheld spreader 20 - 26 October 2008 immediately following seeding.

The mixture of five native perennial grasses described above was seeded using handheld broadcast seeders in all subplots 20 - 26 October 2008, 16 - 18 October 2009, and 23 - 25 October 2010. Seeds were sown at a rate of 100 viable seeds · $species^{-1}$ · m^{-2}. The mixture was seeded with 3.25 L of rice hulls per subplot. Cardboard shields were used around subplots to contain seeding mixture within the subplot.

Sampling

The density of emerging native perennial grass seedlings (hereafter, perennial seedling density) was measured over a 1.5 x 2 m designated area contained within the larger sampling area 1 - 5 June 2009, 25 May - 7 June 2010 and 25 May - 14 June 2011.

Seedling densities in 2009 were extremely low, including zero in many quadrats, due to poor emergence, high early mortality, or both. Due to poor plant performance, data collected in 2009 could not be analyzed. Therefore, I was unable to assess the effects of treatments on seedling emergence the first season following treatment. Perennial seedlings were not recorded by species as it was too difficult to identify grasses at the seedling stage and only individuals that were assumed to be seedlings (basal diameter ≤ 1.0 cm) were recorded.

Statistical Analyses

Due to experimental design differences, analyses were run separately for each experiment. In the sagebrush experiment, the effects of vegetation, herbicide, and seedbed treatments on 2010 and 2011 perennial seedling density were assessed using an analysis of variance (ANOVA) of a 3-way factorial in a randomized block design, with whole plots in blocks, and subsamples (within blocks). Vegetation, herbicide and seedbed treatment were fixed-effects factors and replicates, plots, and subplots were random-effects factors. Replicates were blocks. The whole plot unit was plot as defined above in methods; the whole plot factors were vegetation treatment and herbicide treatment. The subplot unit was subplot as defined above; the subplot factor was seedbed treatment.

In the cheatgrass experiment, the effects of vegetation, herbicide and seedbed treatments on 2010 and 2011 perennial seedling density were assessed using an ANOVA of a 3-way factorial in a split-split plot design. Plots, strips, and subplots were random effects factors. Vegetation, herbicide, and seedbed treatments were fixed effects factors.

The whole plot unit was plot as defined above in methods; the whole plot factor was vegetation treatment. The subplot unit was a strip; the subplot factor was herbicide treatment. The sub-subplot unit was subplot; the sub-subplot factor was seedbed treatment.

An analysis, using only data from the sagebrush experiment, was run to test the effects of multiple consecutive years of seeding on perennial seedling density. For this analysis, a mean perennial density in 2010 and 2011 from subplots AC, sucrose and control (additional seed) was compared to the mean perennial density in 2010 and 2011 from subplots snow and raking (no additional seed). The statistical model is as described above for the sagebrush experiment.

Significances were based on $\alpha = 0.05$. For significant main effects, least squared means were compared using the Tukey-Kramer method. All data analyses were computed using SAS/STAT Version 9.2 in the SAS System for Windows (SAS Institute Inc. 2007). ANOVA's were computed using the GLIMMIX procedure. Comparisons of seeding frequency were computed using the LSMESTIMATE statement in the GLIMMIX procedure. To better meet assumptions of normality '2010 and 2011 perennial seedling density' and '2010 and 2011 additional seed and no additional seed' in the sagebrush experiment were square root transformed. In the cheatgrass experiment, '2010 and 2011 perennial seedling densities' were natural log transformed. Least squared means and confidence intervals (CI) presented in text and figures were back-transformed.

Three entire plots in the sagebrush experiment were left out of the analyses; these plots had a disproportionately high number of perennial seedlings due to high densities of introduced crested wheatgrass (*Agropyron cristatum*) from previous National Park Service re-vegetation efforts. All snow and raked sub-plots in the sagebrush experiment were left out of the ANOVA model testing the effects of treatments and treatment interactions as they were only seeded in 2008.

RESULTS

Treatment Effects

In the sagebrush experiment, herbicide significantly affected 2011 perennial seedling density (Table 2.1). Relative to control, herbicide increased 2011 perennial seedling density (Fig. 2.1). In the cheatgrass experiment, 2010 perennial seedling density exhibited a vegetation treatment effect (Table 2.2); densities were significantly higher in burned plots than control plots (Fig. 2.2). In 2011 there was a significant herbicide effect on perennial seedling density in the cheatgrass experiment (Table 2.2). Both levels of herbicide increased perennial seedling density relative to the control (Fig. 2.3); however, the two levels of herbicide did not differ from each other.

Seeding Frequency

There was a significant difference in mean perennial seedling densities between the re-seeded and non re-seeded treatment groups in both 2010 ($p<.0001$) and 2011 ($p<.0001$). 2010 perennial seedling density was significantly higher in the re-seeded treatment group than the non re-seeded treatment group (Fig. 2.4). Additionally, re-

seeded subplots had significantly more perennial seedlings in 2011 after 3 years of seeding than in 2010 after 2 years of seeding (Fig. 2.4). Although not significant, there was a visible reduction in perennial seedlings from 2010 to 2011 in the non-re-seeded subplots (Fig. 2.4).

DISCUSSION

Vegetation Manipulation

Results indicated that in the cheatgrass experiment two years post burn (2010), burning enhanced perennial seedling density with burned plots having roughly twice the number of perennial seedlings as control plots. In a separate analysis of these experiments, Summerhays (2011) found 2010 cheatgrass densities to be significantly lower in burned than unburned plots. This lower density of cheatgrass in burned plots may have resulted in reduced interspecific competition for resources and thus higher perennial densities. These results are supported by other studies (e.g. Mazzola et al. 2008) showing increased perennial grass seedling density with reduced cheatgrass seeding density. Likewise, many studies have shown cheatgrass competition to reduce perennial grass seedling survival and establishment (Rummel 1946; Harris 1967; Nelson et al.1970; Aguirre and Johnson 1991).

Interestingly, the length of treatment effect provided by burning was longer than that seen in most studies and certainly longer than expected. As cheatgrass populations usually rebound quickly after fire (West and Hassan 1985; Hassan and West 1986; Humphrey and Schupp 2001), the burn in my study may have been more intense, perhaps

resulting in conditions that were in some way still not suitable for increased cheatgrass densities 2 years post-burn.

In the sagebrush experiment, none of the vegetation treatments affected perennial seedling density in either year. Though vegetation treatment did not have a significant effect in the sagebrush experiment, the mean number of perennial seedlings was highest in control plots ($14.1 \cdot 3\ m^{-2}$) and lowest in 100% thin ($8.6 \cdot 3\ m^{-2}$). Results from Summerhays (2011) showed that 2010 cheatgrass densities were significantly higher in 100% thinned plots than in control plots, perhaps explaining the observed lower perennial seedling densities in these plots. Other studies have shown that in areas where sagebrush has been removed cheatgrass is more abundant (Blumenthal et al. 2006; Prevey et al. 2010), and it has been suggested that sagebrush plays an important role in reducing invasions and maintaining native vegetation (Prevey et al. 2010).

Most studies that have demonstrated a positive effect of shrub removal on perennial grasses have been focused on already established grasses and not seedling emergence (Inouye 2006; Bechtold and Inouye 2007; Boyd and Svejcar 2011). However, in a study by Chambers and Linnerooth (2001), grass and sedge emergence was highest in unburned sagebrush sub-canopies when other microsites (burned sagebrush sub-canopies and burned and unburned interspace) had lower soil water availability or more extreme temperatures. These findings suggest that shrubs are beneficial to emerging perennial grasses and removal of them may decrease their success, in contrast to my original prediction.

Herbicide Application

Two years post-treatment (2010), there was no evidence of an herbicide effect in either experiment. However, 3 years post-treatment (2011) results demonstrate greater perennial seedling densities in herbicide treatments in both the cheatgrass and sagebrush experiment. As Summerhays (2011) did not collect data on 2011 cheatgrass metrics, it was unknown if cheatgrass densities were lower in herbicide plots that year. The cause of this delayed response in perennial seedlings to herbicide is unclear and the result may be spurious.

Sucrose & Activated Carbon Addition

No evidence of sucrose enhancing perennial seedling densities either 2 years or 3 years post-application was detected. Reductions in nitrogen via sucrose have been shown to be short lived (Mazzola et al. 2008; Rowe et al. 2009; Mazzola et al. 2011; Summerhays 2011), perhaps explaining why I did not detect any effect. In a separate analysis of soil ions from this experiment, Summerhays (2011) reported reduced levels of nitrogen the first summer after treatment (2009) but by the second winter after treatment (2010) levels were similar to those in controls plots. As the perennial seedling data in 2009 were not suitable for analysis, their response to the observed reduction in nitrogen 1 year post-sucrose application was unknown. However, 1 year post-sucrose application at a rate similar to ours, Mazzola et al. (2011) saw no evidence of perennial grasses being favored by the low nitrogen conditions created by sucrose addition.

In a separate analysis of cheatgrass from this experiment, Summerhays (2011) reported significantly smaller and less reproductive cheatgrass individuals in 2009 (1 year

post-application) and larger more reproductive individuals at lower densities in 2010 in sucrose subplots. The pattern observed in 2010, which has been observed in other studies of sucrose effects on cheatgrass (Mazzola et al. 2008; Mazzola et al. 2011), demonstrates an equal tradeoff between biomass/reproductive output and density. Thus, even though densities were reduced in 2010, this likely did not lead to the competitive release of perennial grass seedlings. As Summerhays (2011) did not collect data on 2011 cheatgrass metrics or soil ions, their status 3 years post-sucrose application was unknown.

In addition to time since application, the lack of a sucrose effect on perennial seedlings may be due to low application rates. For example, Blumenthal et al. (2003) began seeing increases in native perennial grasses above 1000 g C $\cdot$ m^{-2} with the most benefits seen at the highest level of 3346 g C $\cdot$ m^{-2}. Herein the present study as well as in Mazzola et al. (2011) sucrose was applied at a rate of $\approx$150 g C $\cdot$ m^{-2}. Lastly, even if the reduction in nitrogen did increase perennial seedling densities one year post-application, the fact that 2 years post application there was no effect would suggest that repeated applications may be necessary to benefit seeded perennial grasses.

There was no evidence of an AC affect on perennial grass densities. Likewise, Summerhays (2011) did not detect any changes in soil ions or cheatgrass with the addition of AC. As with sucrose, the lack of an affect of AC on perennial seedling densities may have been attributed to time since application or low application rates. Studies by Kulmatiski and Beard (2006) and Kulmatiski (2011) reported significant decreases in exotic species cover and increases in perennial grass cover with AC

incorporated into the top 10 cm of soil at a rate of 1 kg · m^{-2}, a rate ten times as high as ours.

Seeding Frequency

Results revealed that seeding multiple consecutive years in cheatgrass-invaded sagebrush sites increased perennial seedling densities when compared to seeding a single year. As suggested by Bakker et al. (2003), spreading seeding over multiple years may help address among-year variation in establishment. Though there is limited information available on the effects of seeding multiple years, several studies have demonstrated increases in perennial grass establishment with increasing seeding rates within a year (Sheley et al. 1999; Bakker et al. 2003; Eiswerth and Shonkwiler 2006; Mazzola et al. 2011). As very few seedlings apparently survived from year to year and large increases in seedling density with repeated seeding were still observed, likely only a small portion of the viable seeds were emerging each year.

It has been suggested that low seeding rates may help explain the high rate of failure in re-vegetation efforts in weed infested rangelands (Sheley et al. 1999). Most re-vegetation studies of weed infested rangelands use agronomic seeding rates that are designed to optimize crop yield (Zimdall 1980). In a study by Sheley et al. (1999), intermediate wheatgrass failed to establish by the second growing season when sown at near the recommended seeding rate of 500 seeds m^{-2} but establishment was greatly increased at five and 25 times the recommended rate. My findings, as well as those of others (Sheley et al. 1999; Bakker et al. 2003; Eiswerth and Shonkwiler 2006), suggest

that higher seeding rates and/or multiple years of seeding improve the chances of successful re-vegetation.

IMPLICATIONS

Very few of the treatments tested in this experiment were effective at increasing the success of native perennial grass emergence two and three years after treatment. Native grass emergence, abundance, distribution and survival are influenced by both climatic and landscape characteristics (Lauenroth et al. 1994; Chambers 2000; Bakker et al. 2003). Thus, abiotic factors such as, precipitation, temperature, slope, aspect, and edaphic characteristics as well as biotic factors such as, cheatgrass density and biomass, sagebrush density and seed consumers likely interacted to influence seeded perennial grass emergence and perhaps explained some of the observed variation in perennial seedling density.

Results demonstrated that burning in cheatgrass near-monocultures can improve the success of perennial grass emergence. These results in combination with those of Summerhays (2011) suggest that in cheatgrass near-monocultures, decreasing cheatgrass density is critical for increasing the success of seeded perennial grass emergence. Therefore, treatments that reduce cheatgrass density may be tools that can improve the chances of successful reintroduction of native perennial grasses via seeding in cheatgrass near-monocultures.

In both cheatgrass near-monocultures and cheatgrass-invaded sagebrush sites, herbicide was effective at enhancing perennial seedling emergence three years post application. This delayed response was surprising and the explanation for it is unclear.

The strongest result in this study is that seeding success may be enhanced by increasing seeding rates and/or consecutive years of seeding. Thus, future work should focus on finding appropriate seeding rates for native perennial grasses in cheatgrass-invaded sagebrush systems. Additionally, future work should consider the effects of abiotic (overstory dynamics, edaphic variables, climatic variables) and biotic (density and biomass of other species) factors on seeding success in these systems.

As data were collected 2 and 3 years post restoration treatments, the effects of some treatments may have diminished by 2010 and even more so by 2011. Summerhays (2011) found that many treatments negatively affected cheatgrass in 2009 but in many cases by 2010 cheatgrass had rebounded and in some cases even increased compared to untreated controls. My results combined with Summerhays' (2011) results suggest that many of these treatments have a short window of opportunity for increasing success of seeding efforts. This is consistent with results from other studies showing short lived effects of fire (Humphrey and Schupp 2001), herbicide (Kyser et al. 2007; Morris et al. 2009), and sucrose (Monaco et al. 2003; Mazzola et al. 2008; Brown et al. 2008) on cheatgrass reduction. Some treatments may have not been successful at enhancing perennial seedling emergence as their effects on cheatgrass density or soil nutrients only lasted a single year. Given this single year treatment effect, different results may have been seen had 2009 perennial grass seedling data been successfully collected.

As many of the tested treatments have a short window of opportunity for increasing the success of seeding efforts, future work should address the effects of repeated treatment applications. Additionally, the difficulty of re-establishing desirable species within cheatgrass-invaded communities, combined with the ability of cheatgrass to recover after disturbance or treatment, suggests that follow-up treatments or alternative management approaches should be explored. And as likely very few native seedlings survived from year to year, future work should focus on increasing survival and establishment of seeded perennial grasses.

LITERATURE CITED

Abraham, J. K., J. D. Corbin, and C. M. D'Antonio. 2009. California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. *Plant Ecology* 201:445-456.

Aguirre, L., and D. A. Johnson. 1991. Influence of temperature and cheatgrass competition on seedling development of 2 bunchgrasses. *Journal of Range Management* 44:347-354.

Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. *Wildlife Society Bulletin* 34:177–185.

Bakker, J. D., S. D. Wilson, J. M. Christian, X. D. 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.

Bechtold, H. A., and R. S. Inouye. 2007. Distribution of carbon and nitrogen in sagebrush steppe after six years of nitrogen addition and shrub removal. *Journal of Arid Environments* 71:122-132.

Beckstead, J., and C. K. Augspurger. 2004. An experimental test of resistance to cheatgrass invasion: limiting resources at different life stages. *Biological Invasions* 6:417-432.

Billings, W. D. 1952. The environmental complex in relation to plant growth and distribution. *The Quarterly Review of Biology* 27:251-265.

Blank, R. R., J. Chambers, B. Roundy, and A. Whittaker. 2007. Nutrient availability in rangeland soils: influence of prescribed burning, herbaceous vegetation removal, overseeding with *Bromus tectorum*, season, and elevation. *Rangeland Ecology & Management* 60:644-655.

Blumenthal, D. M., N. R. Jordan, and M. P. Russelle. 2003. Soil carbon addition controls weeds and facilitates prairie restoration. *Ecological Applications* 13:605-615.

Blumenthal, D. M., U. Norton, J. D. Derner, and J. D. Reeder. 2006. Long-term effects of tebuthiuron on *Bromus tectorum*. *Western North American Naturalist* 66:420-425.

Booth, M. S., M. M. Caldwell, and J. M. Stark. 2003. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. *Journal of Ecology* 91:36-48.

Boyd, C. S., and K. W. Davies. 2010. Shrub microsite influences post-fire perennial grass establishment. *Rangeland Ecology & Management* 63:248-252.

Boyd, C. S., and T. J. Svejcar. 2011. The influence of plant removal on succession in Wyoming big sagebrush. *Journal of Arid Environments* 75:734-741.

Brooks, M. L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology* 40:344-353.

Brown, C. S., V. J. Anderson, V. P. Claassen, M. E. Stannard, L. M. Wilson, S. Y. Atkinson, J. E. Bromberg, T. A. Grant, III, and M. D. Munis. 2008. Restoration ecology and invasive plants in the semiarid west. *Invasive Plant Science and Management* 1:399-413.

Chambers, J. C. 2000. Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: implications for restoration. *Ecological Applications* 10:1400-1413.

Chambers, J. C. 2008. Fire and the Great Basin. *In*: J. C. Chambers, A. Evenden, and N. Devoe [comps.]. Collaborative management and research in the Great Basin: examining the issues and developing a framework for action. Fort Collins, CO, USA: US Department of Agriculture, Forest Service, General Technical Report RMRS-GTR-204. p. 33-37.

Chambers, J. C., and A. R. Linnerooth. 2001. Restoring riparian meadows currently dominated by *Artemisia* using alternative state concepts: the establishment component. *Journal of Applied Vegetation Science* 4:157–166.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs* 77:117-145.

Clary, W. P. 1988. Plant density and cover response to several seeding techniques following wildfire. Ogden, UT, USA: US Department of Agriculture, Forest Service, Research Note INT-384. 6 p.

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.

Dakheel, A. J., S. R. Radosevich, and M. G. Barbour. 1993. Effect of nitrogen and phosphorus on growth and interference between *Bromus tectorum* and *Taeniatherum asperum*. *Weed Research* 33:415-422.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasion by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.

Davison, J. C. and E. G. Smith. 2007. Imazapic provides 2-year control of weedy annuals in a seeded Great Basin fuel break. *Native Plants Journal* 8:91-95.

Duncan, C. A., J. J. Jachetta, M. L. Brown, V. F. Carrithers, J. K. Clark, J. M. Ditomaso, R. G. Lym, K. C. McDaniel, M. J. Renz, and P. M. Rice. 2004. Assessing the economic, environmental, and societal losses from invasive plants on rangeland and wildlands. *Weed Technology* 18:1411-1416.

Dyer, A. R., and K. J. Rice. 1999. Effects of competition on resource availability and growth of a California bunchgrass. *Ecology* 80:2697-2710.

Eiswerth, M. E., and J. S. Shonkwiler. 2006. Examining post-wildfire reseeding on arid rangeland: a multivariate tobit modeling approach. *Ecological Modeling* 192:286-298.

Elseroad, A. C., and N. T. Rudd. 2011. Can Imazapic increase native species abundance in cheatgrass (*Bromus tectorum*) invaded native plant communities? *Rangeland Ecology and Management* 64:641-648.

Evans, R. A. 1961. Effects of different densities of downy brome (*Bromus tectorum*) on growth and survival of crested wheatgrass (*Agropyron desertorum*) in the greenhouse. *Weeds* 9:216-223.

Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. *Botanical Review* 57:1-32.

Foster, B. L. 1999. Establishment, competition and the distribution of native grasses among Michigan old-fields. *Journal of Ecology* 87:476-489.

Fowler, N. L. 1988. What is a safe site: neighbor, litter, germination date, and path effects. *Ecology* 69:947-961.

Haferkamp, M. R., D. C. Ganskopp, R. F. Miller, and F. A. Sneva. 1987. Drilling versus imprinting for establishing crested wheatgrass in the sagebrush-bunchgrass steppe. *Journal of Range Manage* 40:524–530.

Harper, J. L. 1977. Population biology of plants. London, UK: Academic Press. 892 p.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs* 37:89-111.

Harris, G. A., and A. M. Wilson. 1970. Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. *Ecology* 51:530-534.

Hassan, M. A., and N. E. West. 1986. Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. *Ecology* 67:269-272.

Humphrey, L. D., and E. W. Schupp. 2001. Seed banks of *Bromus tectorum*-dominated communities in the Great Basin. *Western North American Naturalist* 61:85-92.

Humphrey, L. D., and E. W. Schupp. 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* 58:405-422.

Inderjit, and R. M. Callaway. 2003. Experimental designs for the study of allelopathy. *Plant and Soil* 256:1-11.

Inouye, R. S. 2006. Effects of shrub removal and nitrogen addition on soil moisture in sagebrush steppe. *Journal of Arid Environments* 65:604-618.

Jutila, H. M., and J. B. Grace. 2002. Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. *Journal of Ecology* 90:291-302.

Klemmedson, J. O., and J.G. Smith. 1964. Cheatgrass (*Bromus tectorum* L). *Botanical Review* 30:226-262.

Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin desert - history, persistence, and influences to human activities. *Global Environmental Change-Human and Policy Dimensions* 6:37-52.

Kulmatiski, A. 2011. Changing soils to manage plant communities: activated carbon as a restoration tool in ex-arable fields. *Restoration Ecology* 19:102-110.

Kulmatiski, A., and K. H. Beard. 2006. Activated carbon as a restoration tool: potential for control of invasive plants in abandoned agricultural fields. *Restoration Ecology* 14:251-257.

Kyser, G. B., J. M. DiTomaso, M. P. Doran, S. B. Orloff, R. G. Wilson, D. L. Lancaster, D. F. Lile, and M. L. Porath. 2007. Control of medusahead (*Taeniatherum caputmedusae*) and other annual grasses with imazapic. *Weed Technology* 21:66-75.

Lauenroth, W. K., O. E. Sala, D. P. Coffin, and T. B. Kirchner. 1994. The importance of soil-water in the recruitment of *Bouteloua gracilis* in the shortgrass steppe. *Ecological Applications* 4:741-749.

Link, S. O., C. W. Keeler, R. W. Hill, and E. Hagen. 2006. Bromus tectorum cover mapping and fire risk. *International Journal of Wildland Fire* 15:113-119.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L into Western North America: an ecological chronicle. *Agro-Ecosystems* 7:145-165.

Macdonald, L. 1999. Wildfire rehabilitation in Utah. *In*: S. B. Monsen and R. Stevens [comps.]. Proceedings: Ecology and management of pinyon- juniper communities within the interior west; 15-18 September 1997; Provo, UT, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, RMRS-P-9. p. 410–411.

Mazzola, M. B., K. G. Allcock, J. C. Chambers, R. R. Blank, E. W. Schupp, P. S. Doescher, and R. S. Nowak. 2008. Effects of nitrogen availability and cheatgrass competition on the establishment of Vavilov Siberian wheatgrass. *Rangeland Ecology & Management* 61:475-484.

Mazzola, M. B., J. C. Chambers, R. R. Blank, D. A. Pyke, E. W. Schupp, K. G. Allcock, P. S. Doescher, and R. S. Nowak. 2011. Effects of resource availability and propagule supply on native species recruitment in sagebrush ecosystems invaded by *Bromus tectorum*. *Biological Invasions* 13:513-526.

McLendon, T., and E. F. Redente. 1992. Effects of nitrogen limitation on species replacement dynamics during early secondary succession on a semiarid sagebrush site. *Oecologia* 91:312-317.

Melgoza, G., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83:7-13.

Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003. Contrasting responses of intermountain west grasses to soil nitrogen. *Journal of Range Management* 56:282-290.

Monaco, T. A., T. M. Osmond, and S. A. Dewey. 2005. Medusahead control with fall- and spring-applied herbicides on northern Utah foothills. *Weed Technology* 19:653-658.

Morris, C., T. A. Monaco, and C. W. Rigby. 2009. Variable impacts of imazapic rate on downy brome (*Bromus tectorum*) and seeded species in two rangeland communities. *Invasive Plant Science and Management* 2:110-119.

Nelson, J. R., A. M. Wilson, and C. J. Goebel. 1970. Factors influencing broadcast seeding in bunch-grass range. *Journal of Range Management* 23:163-170.

Paschke, M. W., T. McLendon, and E. F. Redente. 2000. Nitrogen availability and old-field succession in a shortgrass steppe. *Ecosystems* 3:144-158.

Pellant, M. 1996. Cheatgrass: the invader that won the west. Boise, ID, USA: Bureau of Land Management, Interior Columbia Ecosystem Management Project. 22 p.

Peters, E. F. and S. C. Bunting. 1994. Fire conditions pre- and post-occurrence of annual grasses on the Snake River Plain. *In*: S. B. Monsen and S. G. Kitchen [comps.]. Proceedings: Ecology and management of annual rangelands; 18- 22 May 1992; Boise, ID, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-GTR-313. p. 31-36.

Prevey, J. S., M. J. Germino, N. J. Huntly, and R. S. Inouye. 2010. Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe. *Plant Ecology* 207:39-51.

Rowe, H. I., C. S. Brown, and M. W. Paschke. 2009. The Influence of soil inoculum and nitrogen availability on restoration of high-elevation steppe communities invaded by *Bromus tectorum*. *Restoration Ecology* 17:686-694.

Rummel, R. S. 1946. Some effects of competition from cheatgrass brome on crested wheat-grass and bluestem wheatgrass. *Ecology* 27:159-167.

SAS Institute. 2007. SAS System for Microsoft Windows. SAS Institute, Inc., Cary, NC, USA.

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.

Sheley, R. L., M. F. Carpinelli, and K. J. R. Morghan. 2007. Effects of imazapic on target and non-target vegetation during re-vegetation. *Weed Technology* 21:1071-1081.

Sheley, R. L., J. S. Jacobs, and D. E. Lucas. 2001. Re-vegetating spotted knapweed infested rangeland in a single entry. *Journal of Range Management* 54:144-151.

Sheley, R. L., J. S. Jacobs, and R. P. Velagala. 1999. Enhancing intermediate wheatgrass establishment in spotted knapweed infested rangeland. *Journal of Range Management* 52:68-74.

Shinn, S. L., and D. C. Thill. 2004. Tolerance of several perennial grasses to imazapic. *Weed Technology* 18:60-65.

Stewart, G., and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.) an ecologic intruder in southern Idaho. *Ecology* 30:58-74.

Summerhays, J. C. R. 2011. Effects of non-surface-disturbing treatments for native grass revegetation on cheatgrass (*Bromus tectorum L.*) metrics soil ion availabilities [thesis]. Logan, UT, USA: Utah State University. 130 p.

USDA-NRCS. 2011. Official Soil Series Descriptions. Available at: https://soilseries.sc.egov.usda.gov/OSD_Docs/A/ABELA.html. Accessed 29 December 2011.

USDI-BLM. 2000. The Great Basin: healing the land. Boise, ID, USA: National Interagency Fire Center. 36 p.

Vasquez, E., R. Sheley, and T. Svejcar. 2008a. Creating invasion resistant soils via nitrogen management. *Invasive Plant Science and Management* 1:304-314.

Vasquez, E., R. Sheley, and T. Svejcar. 2008b. Nitrogen enhances the competitive ability of cheatgrass (*Bromus tectorum*) relative to native grasses. *Invasive Plant Science and Management* 1:287-295.

Washburn, B. E., T. G. Barnes, and J. D. Sole. 1999. No-till establishment of native warm-season grasses in tall fescue fields: fire-year results indicate value of new herbicide. *Ecological Restoration* 17:40-45.

West, N. E., and M. A. Hassan. 1985. Recovery of sagebrush-grass vegetation following wildfire. *Journal of Range Management* 38:131-134.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. *In*: D. E. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller [comps.]. Proceedings: Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 5-7 April 1989; Las Vegas, NV, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-276. p. 4-10.

Wright, H. A., and J. O. Klemmedson. 1965. Effect of fire on bunchgrasses of the sagebrush-grass region in southern Idaho. *Ecology* 46:680-688.

Young, J. A., and C. D. Clements. 2000. Cheatgrass control and seeding. *Rangelands* 22:3-7.

Young, J. A., and R. A. Evans. 1978. Population-dynamics after wildfires in sagebrush grasslands. *Journal of Range Management* 31:283-289.

Zimdahl, R. L. 1980. Weed-crop competition: a review. Corvallis, Oregon, USA: International Plant Protection Center, Oregon State University. 195 p.

Ziska, L. H., J. B. Reeves, and B. Blank. 2005. The impact of recent increases in atmospheric CO2 on biomass production and vegetative retention of cheatgrass (*Bromus tectorum*): implications for fire disturbance. *Global Change Biology* 11:1325-1332.

Table 2.1. Analysis of variance for perennial seedling density in the sagebrush experiment (bold font denotes significance, $p \leq 0.05$). Vegtreat = vegetation treatment, herbtreat = herbicide treatment, seedtreat = seedbed treatment.

		2010		2011	
Effect	*df*	*F*	*p*	*F*	*p*
vegetation treatment	3, 21	1.08	0.38	0.46	0.72
herbicide treatment	1, 21	0.10	0.75	4.78	**0.04**
herbtreat*vegtreat	3, 21	1.01	0.41	0.68	0.57
seedbed treatment	2, 42	1.92	0.16	2.27	0.12
seedtreat *vegtreat	6, 42	0.83	0.56	1.51	0.20
seedtreat *herbtreat	2, 42	1.20	0.31	1.08	0.35
seedtreat *herbtreat*vegtreat	6, 42	1.04	0.41	1.10	0.38

Table 2.2. Analysis of variance for perennial seedling density in the cheatgrass experiment (bold font denotes significance, $p \leq 0.05$). Vegtreat = vegetation treatment, herbtreat = herbicide treatment, seedtreat = seedbed treatment.

		2010		2011	
Effect	*df*	*F*	*p*	*F*	*p*
vegetation treatment	1	9.61	**0.02**	0.71	0.43
herbicide treatment	2	1.53	0.26	8.93	**0.00**
herbtreat*vegtreat	2	2.57	0.12	1.32	0.30
seedbed treatment	2	1.44	0.25	0.7	0.51
seedtreat*vegtreat	2	0.77	0.47	3.05	0.06
seedtreat *herbtreat	4	1.05	0.39	0.93	0.46
seedtreat *herbtreat*vegtreat	4	0.33	0.86	0.63	0.65

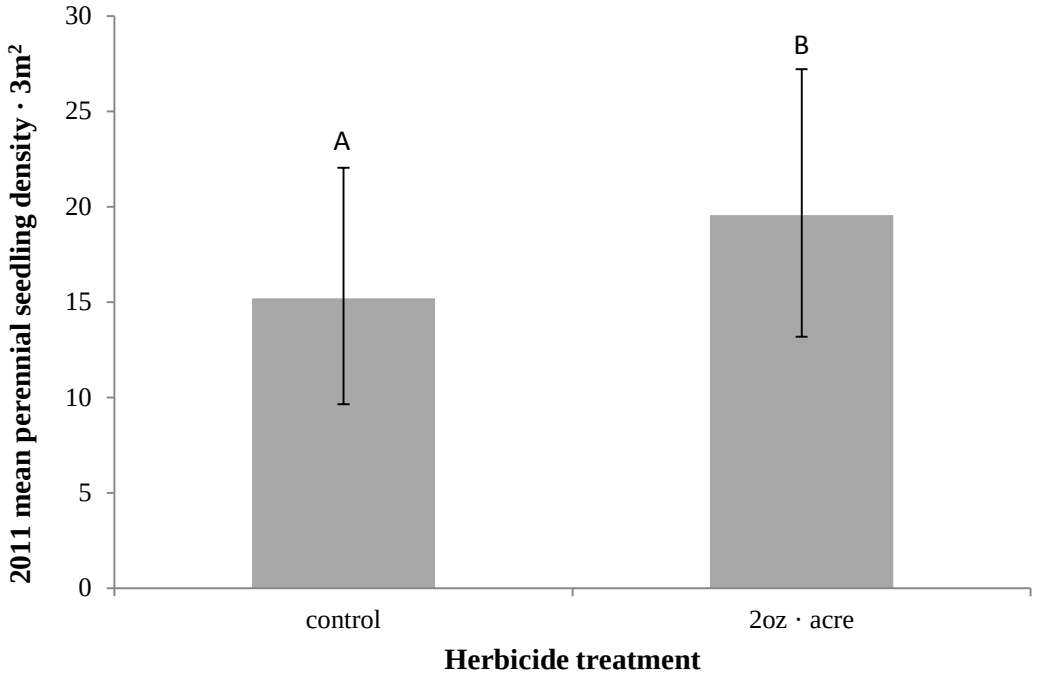

Figure 2.1. Mean 2011 perennial seedling density · $3m^{-2}$ (± *95% CI*) as affected by herbicide treatment at the sagebrush experiment. Values with different letters differ significantly from each other.

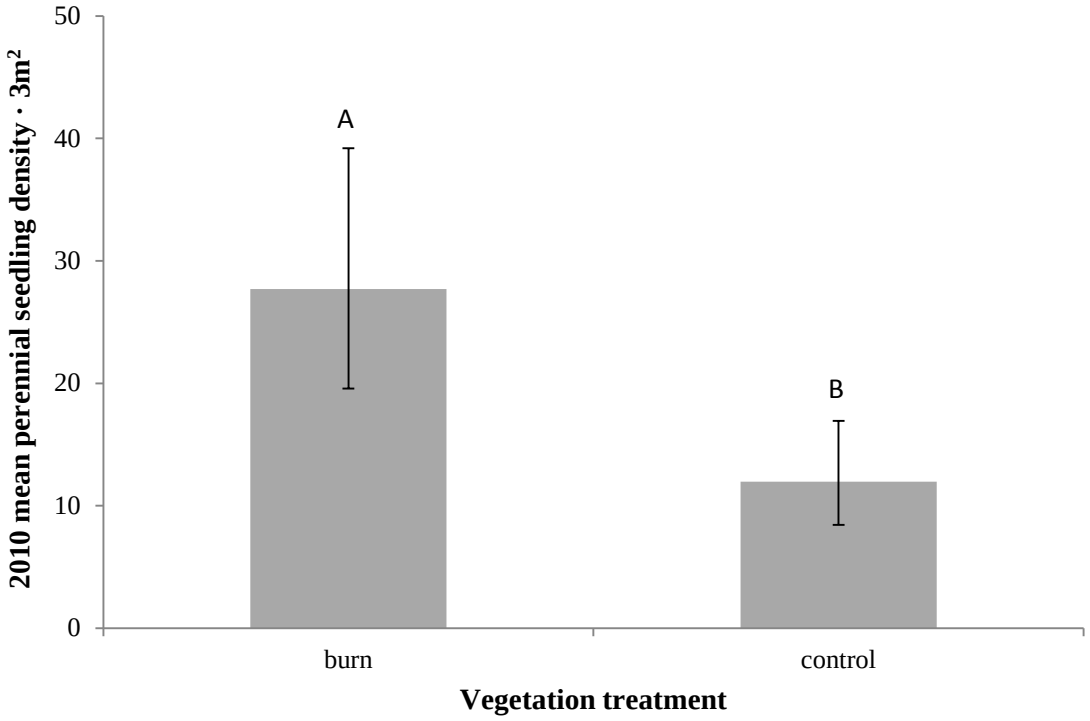

Figure 2.2. Mean 2010 perennial seedling density · $3m^{-2}$ (± *95% CI*) as affected by vegetation treatment at the cheatgrass experiment. Values with different letters differ significantly from each other.

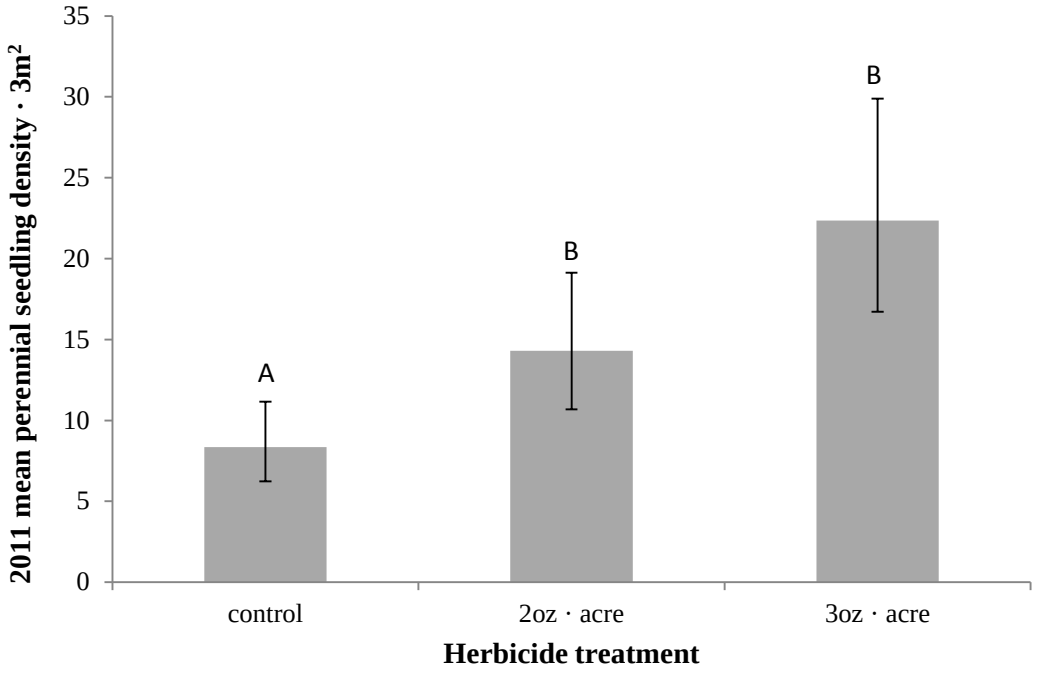

Figure 2.3. Mean 2011 perennial seedling density · $3m^{-2}$ (± *95% CI*) as affected by herbicide treatment at the cheatgrass experiment. Values with different letters differ significantly from each other.

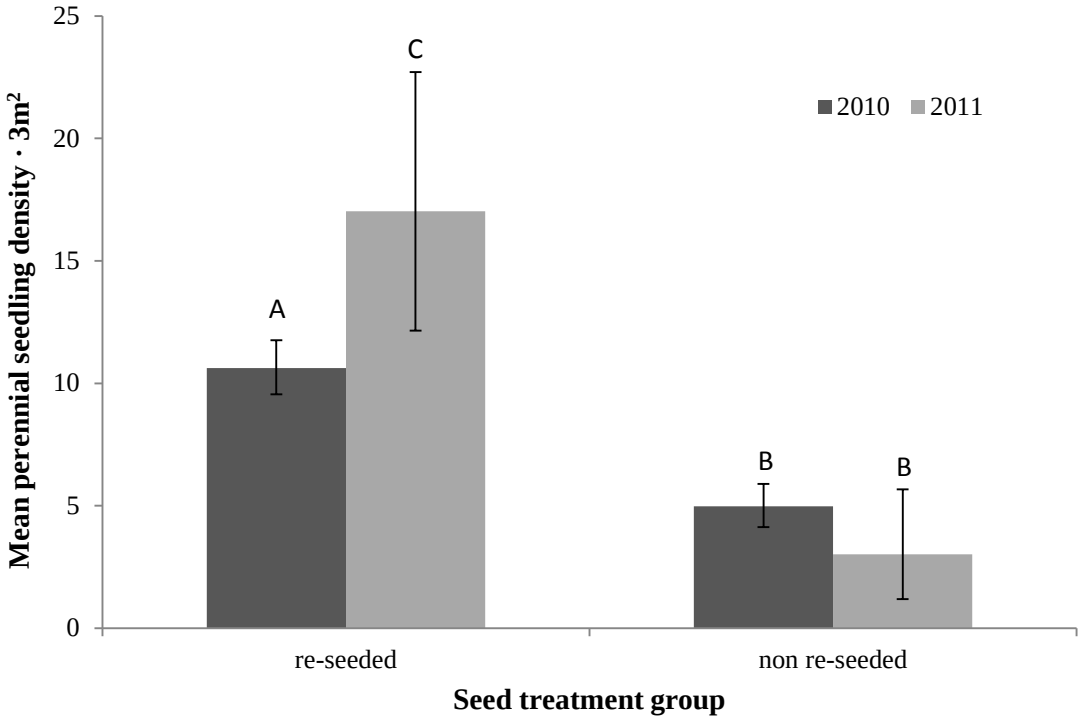

Figure 2.4. Mean perennial seedling density · $3m^{-2}$ (± *95% CI*) for seed treatment group at the sagebrush experiment in 2010 and 2011. Values with different letters differ significantly from each other.

CHAPTER 3

EVALUATING THE EFFECTS OF RESTORATION TECHNIQUES ON SEED BANK DYNAMICS OF CHEATGRASS (*BROMUS TECTORUM* L.) INVADED SAGEBRUSH-STEPPE ECOSYSTEMS

Abstract

The exotic annual grass *Bromus tectorum* (cheatgrass) has invaded millions of acres of sagebrush shrubland communities in the Western U.S., increasing fire frequencies and displacing native species. The reintroduction of native perennial grasses into these degraded systems is inhibited by intense competition for available resources between cheatgrass and seeded perennial grasses. However, once established, fire-resilient perennial grasses can effectively compete with cheatgrass. Thus, controlling cheatgrass may be necessary for the successful establishment of native perennial grasses.

As most control strategies for cheatgrass are driven by the principle of depleting the soil seed bank, I investigate the effects of several restoration techniques used to restore cheatgrass-invaded communities on the seed bank dynamics of a cheatgrass-invaded sagebrush site (sagebrush experiment) and cheatgrass near-monoculture site (cheatgrass experiment). The restoration treatments investigated were: prescribed fire, sagebrush thinning (50% and 100%), pre-emergent herbicide (imazapic) application, and two seedbed amendments (sucrose and activated carbon). Seed banks were sampled before treatments were applied, immediately post-fire in the burn and control treatments,

and one year post treatments for all treatments; species densities were quantified by monitoring seedling emergence from these seed bank samples in a greenhouse.

In the sagebrush experiment one year post-application, herbicide reduced cheatgrass and exotic species seed bank densities as well as species richness. This reduction in species richness was attributed to a reduction in exotic species richness. In the cheatgrass experiment, burning immediately as well as one year post-fire reduced cheatgrass seed bank densities. Sucrose also reduced cheatgrass seed bank densities one year post-application in the cheatgrass experiment. Additionally in the cheatgrass experiment, sucrose and imazapic both reduced species richness one year post-application. This reduction in species richness was also attributed to a reduction in exotic species richness. No treatments were found to affect native species seed bank densities in either experiment.

INTRODUCTION

In *Artemisia tridentata* (sagebrush) shrublands of the Intermountain West of North America, the exotic annual grass cheatgrass has displaced native species as well as altered ecosystem processes, fire regimes, and the structure and composition of seed banks (Young and Evans 1975; Whisenant 1990; Knapp 1996; Humphrey and Schupp 2001). Cheatgrass is said to be the most ubiquitous, and in many areas most dominant, invasive in the sagebrush ecosystems of the Intermountain West (Mack 1981). Cheatgrass has invaded 22 million hectares (54 million acres) in the western U.S. (Benlap

et al. 2005), and is spreading at a rate of 14% per year in the Great Basin (Duncan et al. 2004).

Cheatgrass, an invasive annual grass native to Eurasia, was unintentionally introduced to the United Sates in the late 1800's (Mack 1981). Degradation of the sagebrush ecosystems of the Intermountain West, caused by severe overgrazing and agricultural practices starting in the late 1800's, allowed cheatgrass to establish throughout these areas (Knapp 1996). The resultant reduction in native herbaceous understory species and increase in resource availability allowed cheatgrass to rapidly spread across the degraded landscape and occupy open niches (Billings 1952; Knapp 1996). The invasion of cheatgrass into sagebrush shrublands has transformed species compositions, ecosystem processes, fire regimes and the structure and composition of seed banks (Young and Evans 1975; Whisenant 1990; Humphrey and Schupp 2001). Restoration of these cheatgrass-invaded sagebrush shrublands has been met with limited success, which is mainly attributed to competition from cheatgrass limiting the successful establishment of seeded perennial grasses (Evans 1961).

Cheatgrass is a winter annual characterized by early germination, rapid growth, prolific seed production, and abundant highly flammable fine fuels (Klemmedson and Smith 1964). Its seeds are capable of remaining dormant and forming a small persistent seed bank, although most germinate the year of dispersal (Hulbert 1955; Monsen 1994; Pyke 1994; Pyke and Novak 1994). Due to its early germination and rapid growth, cheatgrass preemptively attains resources early in the spring prior to later emerging native herbaceous species (Harris 1967; Melgoza et al. 1990; Abraham et al. 2009),

making it an aggressive competitor against establishing native vegetation. However, the most detrimental effect of cheatgrass is its effect on the fire cycle.

Cheatgrass' highly abundant fine fuels and ability to rapidly recover to pre-fire densities after fire have led to a cheatgrass-wildfire cycle with cheatgrass promoting fire and fire promoting cheatgrass (Young and Evans 1978; D'Antonio and Vitousek 1992). Fire return intervals have gone from between 60-110 years in pre-invasion sagebrush communities to 3-5 years under cheatgrass dominance (Whisenant 1990). Over time this altered cycle diminishes the perennial seed bank (Peters and Bunting 1994) and converts high diversity native shrublands to low diversity exotic grasslands (Brooks and Pyke 2001). Ultimately this altered cycle reinforces the dominance of cheatgrass in these sagebrush ecosystems.

Cheatgrass is well adapted to frequent fire (Melgoza et al. 1990; Ziska et al. 2005) and in the near absence of a native seed bank (Humphrey and Schupp 2001) recovers and preemptively utilizes limiting soil resources (Melgoza et al. 1990; D'Antonio and Vitousek 1992; Knapp 1996). Unlike cheatgrass, native perennial grasses and shrubs found in sagebrush communities are not adapted to such short fire return intervals; depending on the species, frequent fires either damage or kill the natives (Stewart and Hull 1949; Wright and Klemmedson 1965; Harris 1967; Young and Evans 1978). Under highly altered fire regimes and competitive pressure from cheatgrass, natural recovery is limited.

As established perennial grasses have been shown to successfully compete with exotic annual grasses (Booth et al. 2003; Seabloom et al. 2003; Corbin and D'Antonio

2004; Humphrey and Schupp 2004), actively reintroducing and establishing perennial grasses may be the key to breaking the cheatgrass-wildfire fire cycle and preventing a type-conversion. As such, controlling cheatgrass density both in the seed bank and standing vegetation may be critical for successful establishment of native perennial grasses. As most control strategies for cheatgrass are driven by the principle of depleting the soil seed bank (Ogg 1994), management techniques used to restore cheatgrass-invaded communities should be investigated to determine their effects on the seed bank. Thus, the goal of this study was to evaluate the effects of several restoration techniques aimed at controlling cheatgrass and altering the resource environment in ways that could increase the success of seeded perennial grasses on the seed bank dynamics of two Great Basin sagebrush communities.

Prescribed fire is one such technique that can be an effective tool for controlling invasive species, such as cheatgrass, if it kills most plants or greatly reduces the seed bank (Whelan 1995; Brooks and Pyke 2001). As cheatgrass does not develop long-lived seed banks and approaches zero density in the spring (Mack and Pyke 1983; Pyke 1994), greatly reducing the seed bank may be possible if there is near 100 % mortality caused by fire prior to dispersal (Brooks and Pyke 2001). However, even when fires greatly reduce cheatgrass seed banks, they can quickly recover to pre-fire or greater levels (Young and Evans 1985; Hassan and West 1986; Brooks and Pyke 2001; Humphrey and Schupp 2001). Through a reduction in competition and release of resources (Brooks and Pyke 2001; Blank et al. 2007), burning may increase native and exotic species reproductive output. Additionally, burning may enhance the effectiveness of herbicide application by

increasing contact with emerging target plants and the soil surface (Washburn et al. 1999; Monaco et al. 2005; Kyser et al. 2007; Sheley et al. 2007).

The removal of sagebrush is known to increase nutrient availability (Blank et al. 2007; Boyd and Davies 2010) as well as decrease competition for soil water (Inouye 2006), both of which may benefit seeded perennial species. Several studies have demonstrated an increase in perennial grass cover and biomass after the thinning of sagebrush (Inouye, 2006; Bechtold and Inouye 2007; Boyd and Svejcar 2011). However, increases in cheatgrass cover after shrub removal have also been observed (Blumenthal et al. 2006; Prevey et al. 2010). Although several studies have investigated the effects of shrub removal on aboveground vegetation, effects on seed banks in cheatgrass-invaded communities are unknown.

Herbicides have long been used in cheatgrass control efforts (Pellant 1996; Young and Clements 2000). The herbicide imazapic, applied as a pre-emergent herbicide, selectively targets annual species (Davison and Smith 2007; Elseroad and Rudd 2011) and although its effects on perennial grasses are variable (Shinn and Thill 2004; Kyser et al. 2007; Sheley et al. 2007), imazapic has been shown to successfully control cheatgrass and other invasive annual grasses (Monaco et al. 2005; Kyser et al. 2007; Morris et al. 2009). If imazapic can reduce emergence of cheatgrass enough to affect population level seed production there is potential for imazapic to deplete cheatgrass seed banks. Currently, there is limited information on the effects of imazapic on the seed banks of cheatgrass-invaded sagebrush ecosystems.

Other treatments that directly manipulate soil resources and reduce the competitive advantage of cheatgrass may be effective restoration tools for depleting cheatgrass seed banks. Two such treatments are carbon (in readily available forms such as sucrose) and activated carbon (AC) soil amendments. Carbon additions increase soil microbial nitrogen immobilization thereby decreasing plant available nitrogen (Blumenthal et al. 2003). Low resource availability often favors native perennial species over annual or short-lived exotic species (Daehler 2003) and fast growing exotic annuals, such as cheatgrass, greatly increase in biomass, density, and competitive ability with increasing nitrogen availability (Brooks 2003; Vasquez et al. 2008a, 2008b). Therefore, it is expected that cheatgrass will be disproportionately harmed by nutrient reductions which may result in reduced seed production. Sucrose is often used as a carbon source in experiments due to its constant carbon content and its readily decomposable nature which allows for rapid immobilization. Soil carbon additions, such as sucrose, have been shown to negatively affect invasive early seral species such as cheatgrass (McLendon and Redente 1992; Dakheel et al. 1993; Paschke et al. 2000; Monaco et al. 2003; Beckstead and Augspurger 2004; Mazzola et al. 2008; Mazzola et al. 2011).

AC as a soil addition has been suggested for use as a restoration tool in exotic invaded communities (Kulmatiski and Beard 2006). AC is a charcoal-like material with high surface porosity which readily adsorbs organic compounds such as plant available nutrients and allelopathic compounds (Inderjit and Callaway 2003). The adsorption of plant available nutrients could negatively impact cheatgrass in the same way that microbial immobilization does. Also, the reduction in allepoathic compounds may be

beneficial for native species as there is evidence that the reducing them may reduce the competitive advantage of exotics (Callaway and Aschehoug 2000). A few studies have demonstrated AC's ability to decrease cover of exotics including cheatgrass and increase native perennial grass cover (Kulmatiski and Beard 2006; Kulmatiski 2011). However, these studies incorporated AC at high rates into the surface layer of the soil which would not be feasible or economical at a large scale. It is currently unknown what the effects of AC applied at the soil surface at a more realistic quantity will be on the seed banks of cheatgrass-invaded ecosystems. Any of these treatments that reduce cheatgrass seed bank densities, and therefore potentially reduce aboveground cheatgrass density, could potentially result in an increase in native species seed bank densities and/or richness.

As research examining the effects of restoration treatments on seed banks is lacking, this study aimed to evaluate the effects of several restoration techniques on seed bank densities and species richness in cheatgrass-invaded communities. In particular, the immediate and 1 year post-fire effects of prescribed fire, and the 1 year post-treatment effects of sagebrush thinning, herbicide application, and two seedbed amendments (sucrose and activated carbon) on seed bank densities and species richness were examined. Previous studies from this experiment investigated the effects of these restoration treatments on aboveground cheatgrass densities and soil ion availability (Summerhays 2011) and seeded perennial grass emergence (chapter 2).

METHODS

Study Area

Soil seed bank samples were collected from Golden Spike National Historic Site in Box Elder County, Utah, approximately 51 km west of Brigham City (lat 41°37’13.73”, long 112°32’50.9”). This area is located on old Lake Terraces of prehistoric Lake Bonneville; elevation ranged from 1413 m to 1508 m. Mean annual precipitation is 33 cm and mean annual temperature is 8 °C (USDA-NRCS 2011). This area was historically a sagebrush steppe ecosystem but disturbance caused by heavy livestock grazing, agriculture use, and landform manipulation diminished much of the perennial grass component (Homstad et al. 2000). In some areas of the Site there are remnant sagebrush stands with cheatgrass-dominated understories while in others repeated fire has resulted in a conversion to cheatgrass near-monocultures. Seed bank germination assays were conducted at the Utah State University Research Greenhouse Facility in Logan, UT.

In May 2008, study plots for the two distinct experiments were established; one experiment was located in cheatgrass-invaded sagebrush sites (sagebrush experiment) and the other in a cheatgrass near-monoculture site (cheatgrass experiment). These experiments were implemented with the overall goal of assessing the effectiveness of several restoration treatments in re-establishing native perennial grasses into cheatgrass-invaded ecosystems in the absence of soil disturbing treatments. Experimental designs and treatment factors differed between the experiments due to landscape

constraints and vegetation characteristics. The experimental methods here follow those outlined by Summerhays (2011).

Sagebrush Experiment Methods

The sagebrush experiment had a total of four replicates; two replicates were located along the Site's East auto tour and the other near the visitor center. Replicates were located in remnant sagebrush stands with cheatgrass-dominated understories; pre-treatment sagebrush cover averaged 52.7% and cheatgrass density averaged 22 tillers · 100 cm^{-2}. Each replicate contained eight plots which were haphazardly placed on the landscape in areas with similar aspect, slope, and vegetation cover. Plots measured 19.5 x 7m and were divided linearly into five subplots, two end subplots (4.5 x 7 m) and three interior subplots (3.5 x 7 m). Each subplot contained a central 1.5 x 3 m undisturbed sampling area which left a 2-m buffer between adjacent subplot sampling areas and the outside edges of the plot. Treatment assignments created a split-split plot experimental design, with herbicide treatment occurring at the half-replicate level, vegetation manipulation occurring at the whole plot level, and seeding treatments occurring at the subplot level.

Half of the plots in each replicate were randomly selected for imazapic herbicide treatment; herbicide was applied at a rate of 140 g active ingredient · ha^{-1} ('2 oz · $acre^{-1}$'). Imazapic was applied 18 November 2008 using a five nozzle boom sprayer mounted on an all terrain vehicle.

Four vegetation treatments were randomly applied to whole plots within each herbicide treatment: 1) no manipulation to vegetation ('control'); 2) prescribed burn to

remove sagebrush overstory, vegetative understory, and vegetative thatch ('burn'); 3) 50% thinning and removal of sagebrush overstory ('50% thinning'); and 4) 100% thinning and removal of sagebrush overstory ('100% thinning'). The Zion National Park Fire Use Module implemented the thinning and burning treatments on 25 August and 5 September 2008, respectively. Burning was done using handheld drip torches; the plot perimeter was wetted to prevent the spread of fire. Thinning and clearing of sagebrush was done with chainsaws; in the 50% thin plots individuals to be removed were selected in advance and marked. All cut plant material was removed from plots.

Three seedbed treatments were randomly assigned to subplots within a plot: 1) seeding alone ('control'); 2) seeding with sucrose ('sucrose'); and 3) seeding with activated carbon ('AC'). Sucrose addition was at a rate of 360 $g \cdot m^{-2}$ (151.6 $g\ C \cdot m^{-2}$) divided between two applications of 180 $g \cdot m^{-2}$ each; the first application was, immediately following seeding (20 - 26 October 2008), and the second was the following spring (28 - 29 March 2009). Sucrose was broadcast by hand. AC, derived from superheated coconut husks (AquaSorb CS, Ecologix Environmental Systems; 12 x 30 US standard mesh size), was applied at a rate of 100 $g \cdot m^{-2}$ with a handheld broadcast seeder immediately following seeding (20 - 26 October 2008).

A mixture of five native perennial grasses was seeded using handheld broadcast seeders in all subplots 20 - 26 October 2008, 16 - 18 October 2009 and 23 - 25 October 2010. The seed mixture contained: bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve ssp. *spicata*), Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth), Great Basin wildrye (*Leymus cinereus* [Scribn. & Merr.] A. Löve),

needle-and-thread grass (*Hesperostipa comata* [Trin. & Rupr.] Barkworth), Sandberg bluegrass (*Poa secunda* J. Presl), and squirreltail (*Elymus elymoides* [Raf.] Swezey). Seeds were sown at a rate of 100 viable seeds · species^{-1} · m^{-2}. Number of viable seeds was calculated using Pure Live Seed rates provided by seed supplier (Granite Seed, Lehi, UT, US). Seeds were mixed with 2.5 L (larger end subplots) or 1.75 L (smaller interior subplots) of rice hulls for suspension to ensure an even distribution within plots. Seeding mixture was contained within the subplot using cardboard shields around the subplot perimeter.

Cheatgrass Experiment Methods

The cheatgrass experiment was located below the Site's East auto tour in an area burned by Site management in 1998; this area has a complete absence of sagebrush and pre-treatment cheatgrass density averaged 116 tillers · 100 cm^{-2}. The cheatgrass experiment had a total of eight 18 x 21 m plots which were haphazardly placed on the landscape in areas with similar aspect, slope, and vegetation cover and were situated so that the bottom (21 m) ran perpendicular to the slope. Each plot was divided into three 7 x 18 m strips across the plot perpendicular to the slope, and each strip was divided into three 7 x 6 m subplots. Each subplot contained a central 2 x 3 m undisturbed sampling area which left a 2-m buffer between adjacent subplot sampling areas and the outside edges of the plot. Treatment arrangement created a split-split plot design, with vegetation manipulation treatment occurring at the whole plot level, herbicide application occurring at the strip- level, and seeding treatments occurring at the subplot level.

Four of the eight plots were randomly selected for a burn treatment; the burn blackened 100% of the selected plots. The burn was done 25 August 2008 by the Zion National Park Fire Use Module using handheld drip torches; the plot perimeter was wetted to prevent the spread of fire.

Within each plot, each 7 x 18 m strip received one of three imazapic herbicide treatments: 1) no herbicide ('control'), 2) 140 g active ingredient · ha^{-1} ('2 oz · $acre^{-1}$'), and 3) 210 g active ingredient · ha^{-1} ('3 oz · $acre^{-1}$'). The herbicide levels were assigned non-randomly to reduce chances of herbicide drift and leaching; the control strip was always the most uphill strip, the 2 oz · $acre^{-1}$ concentration was applied to the middle strip, and the 3 oz · $acre^{-1}$ concentration was applied to the most downhill strip. Herbicide was applied on 18 November 2008 using a five nozzle boom sprayer mounted on an all terrain vehicle.

Each of the three subplots within each herbicide strip was randomly assigned one of the following seedbed treatments: 1) seeding alone ('control'), 2) seeding with sucrose ('sucrose'), and 3) seeding with AC ('AC'). These seeding treatments were applied at the same rates and in the same manner as described above in the sagebrush experiment.

The same mixture of five native perennial grasses as described above was seeded at a rate of 100 viable seeds · $species^{-1}$ · m^{-2} mixed with 3.25 L of rice hulls per subplot. All subplots were seeded using handheld broadcast seeders on 20 - 26 October 2008, 16 - 18 October 2009, and 23 - 25 October 2010. Cardboard shields were used around subplots to contain seeding mixture within the subplot.

Sampling

Pre-treatment seed bank soil samples were collected prior to any treatment or seeding on 25 August 2008 (2008 pre-treatment). In addition, two sets of post-treatment seed bank samples were collected. To determine the immediate effects of the burn treatment on seed banks, seed bank samples were collected following the application of the vegetation treatment (2008 post-treatment) on 27 August 2008 in the cheatgrass experiment and on 9 September 2008 in the sagebrush experiment. Then to determine the delayed effects of all treatments, additional seed bank samples were collected the following year (2009 post-treatment) on 19 - 20 September 2009. In the sagebrush experiment, 2008 pre-treatment samples were collected from all plots in the control, sucrose, and AC subplots, resulting in 96 samples. Post-treatment samples from 2008 were collected from burn and control plots only in the control, sucrose, and AC subplots, resulting in 48 samples. In 2009, samples were collected from the control, sucrose, and AC subplots of all plots, resulting in 96 samples. In the cheatgrass experiment, 2008 pre-treatment, 2008 post-treatment, and 2009 post-treatment samples were collected in all subplots of all plots resulting in 72 samples per collection time.

Seed Bank Data Collection

Soil cores were taken with a 6-cm diameter soil tin to a depth of 3 cm. Putty knives were inserted beneath the tin to keep the soil core from falling out when the tin was removed. In 2008, samples were collected from one random location within the buffer area of each subplot. At each location a 25 x 25 cm frame was placed and a core was collected from the outside of each corner of the frame. The four sub-samples were

combined in a sealed plastic bag as one bulk sample; the samples were then air dried in the lab. In 2009, samples were a bulk collection from three locations in the buffer area of each subplot. Samples were taken from the right and left lower corners of the central sampling area and in the center above the sampling area. At each location a 25 x 25 cm frame was placed on the ground, avoiding any signs of previous sampling, and a core was collected from the outside of each corner of the frame. All four cores per location from all three locations in a subplot were placed together in a sealed plastic bag for a bulk sample of 12 cores. Samples were then taken to the lab and air dried.

Once dried, soil samples were put through a Fisher Scientific sieve (nominal opening 4.75mm) to remove rocks and plant debris. Each bulk sample was then thoroughly mixed to homogenize the soil sample. Then from each bulk sample a 0.24 L (1 cup) subsample was removed and mixed with 0.24 L (1 cup) of vermiculite. These subsamples were then moistened to field capacity and placed in an unlighted refrigerator at 2 °C for 60 days of cold-moist stratification. After 60 days, subsamples were removed from the refrigerator and each 0.48 L subsample (1:1 soil:vermiculite) was divided in half for two replicate sub-sub-samples per subsample and placed in 15 cm (6 in) diameter pots lined with landscape fabric. Hereafter these sub-sub-samples will be referred to as samples. Pots were labeled and placed in the greenhouse according to a completely randomized layout generated by the PLAN procedure in SAS/STAT Version 9.2 in the SAS System for Windows (SAS Institute Inc. 2007). Soils were kept moist by a sprinkler system which ran twice daily for a total of 20 minutes and greenhouse temperatures were maintained between 21 - 23 C°.

Seed Bank Germination

A single germination trial, including samples from all three collection times, ran for 308 days beginning 22 February 2010. Emergence was censused several times weekly for 115 days. Pots were then dried out for 14 days, then mixed, and watering was re-initiated after which emergence was censused for an additional 67 days. Samples were again dried for 36 days, then mixed, and watering was re-initiated after which emergence was censused for an additional 76 days. Seedlings were identified, counted, and removed as they emerged. Individuals that could not be identified in the seedling stage were transplanted into larger pots, fertilized, watered, and grown until mature. Density was measured as numbers $\cdot$ 0.24 L^{-1} of soil. Although seed bank densities are referred to in this chapter the data reflect only the germinable fraction of the seed bank given the germination treatments applied.

Statistical Analysis

Not all treatment categories were represented in each collection time; therefore, two separate statistical analyses were used. One model (hereafter, Model 1) assessed the immediate effects of burning prior to the implementation of herbicide and seedbed treatments by comparing 2008 pre-treatment and 2008 post-treatment collection times. The second model (hereafter, Model 2) assessed the effects of all treatments (vegetation, herbicide, and seedbed amendments) one year after treatments were applied by comparing 2008 pre-treatment and 2009 post-treatment collection times.

Due to experimental design differences, analyses of cheatgrass seed bank density, exotic species seed bank density, native species seed bank density, and total species

richness were run separately for each experiment. In the sagebrush experiment, model 1 compared burning to control vegetation treatments using an analysis of variance (ANOVA) of a 1-way factorial in a randomized block design, with whole plots in replicates, subsamples within replicates, and repeated (2008 pre-treatment versus 2008 post-treatment) measures. In model 2, the effects of vegetation, herbicide, and seedbed treatments on each response variable were assessed using an ANOVA of a 3-way factorial in a randomized block design, with whole plots in replicates, subsamples within replicates, and repeated (2008 pre-treatment versus 2009 post-treatment) measures. Replicates, plots, and subplots were random-effects factors. Vegetation, herbicide, seedbed treatments, and collection time were fixed-effects factors. Replicates were blocks. The whole plot unit was plot as defined above in methods; the whole plot factors were vegetation treatment and herbicide treatment. The subplot unit was subplot as defined above; the subplot factor was seedbed treatment. The experimental unit for collection time was a repeated measure on a subplot.

In the cheatgrass experiment, model 1 assessed the effects of burning to control vegetation treatments on each response variable using an ANOVA of a 1-way factorial in a completely randomized design with subsamples (strips & subplots) within plots, and repeated (2008 pre-treatment versus 2008 post-treatment) measures. In model 2, the effects of vegetation, herbicide, and seedbed treatments on each response variable were assessed using an ANOVA of a 3-way factorial in a split-split plot design, with repeated (2008 pre-treatment versus 2009 post-treatment) measures. Plots, strips, and subplots were random-effects factors. Vegetation, herbicide, and seedbed treatments and

collection time were fixed-effects factors. The whole plot unit was plot as defined above in methods; the whole plot factor was vegetation treatment. The subplot unit was a strip; the subplot factor was herbicide treatment. The sub-subplot unit was subplot; the sub-subplot factor was seedbed treatment. The experimental unit for time as a fixed-effects factor was a repeated measure on a sub-subplot.

Significances were based on $\alpha = 0.05$. A significant interaction involving any treatment and collection time indicated a treatment effect on seed density; main effects are not of interest and thus are not discussed.

Data analyses were computed using the GLIMMIX procedure in SAS/STAT Version 9.2 in the SAS System for Windows (SAS Institute Inc. 2007). Pertinent contrasts were computed as needed to aid in interpretation of interactions; family-wise Type I error was controlled using the SIMULATE option in the GLIMMIX procedure. Data for all response variables were square-root transformed prior to analysis to better meet assumptions of normality and homogeneity of variance. Least squared means and confidence intervals were back-transformed for figures.

Three entire plots in the sagebrush experiment were left out of the analyses; these plots had a disproportionately high number of perennial seedlings due to high densities of introduced crested wheatgrass (*Agropyron cristatum*) from previous National Park Service re-vegetation efforts. Additionally, several samples from the sagebrush experiment were mislabeled and therefore left out of the analysis. In total, the sagebrush experiment had 171 samples in model 1 and 87 samples in model 2. Total species richness was low in both experiments (Table A.1 and A.2) as was its variance within

collection times. Therefore, I was unable to analyze native species richness separately from exotic. However, when an interaction for total species richness was found, raw data patterns were examined to determine if source of significance was due to changes in native species richness, exotic species richness, or both. As cheatgrass usually accounted for the majority of the total exotic species seed bank density (Table A.1 and Table A.2), results for cheatgrass and exotic species density were often similar.

RESULTS

Sagebrush Experiment

There was no evidence of an immediate burn effect on seed bank densities or total species richness for any response variable in the sagebrush experiment (model 1 vegetation treatment x collection time interaction, Table 3.1). One year following treatment, cheatgrass and exotic species seed bank densities as well as total species richness exhibited an herbicide effect (model 2 herbicide treatment x collection time interaction, Table 3.2). Both cheatgrass and exotic species seed densities in the herbicide treatment significantly decreased from 2008 pre-treatment to 2009 post-treatment relative to the control (Fig. 3.1, Fig. 3.2). Similarly, total species richness was reduced from 2008 pre-treatment to 2009 post-treatment in the herbicide treatment relative to the control (Fig. 3.3a, b). Based on visual evaluation of the data set, the reduction appeared to be driven by the effect of herbicide on exotic species richness, although statistical analysis was not possible.

A small *p*-value for total species richness suggested that vegetation treatment and seedbed treatment might interact in their effects (model 2 seed treatment x vegetation treatment x collection time interaction, Table 3.2). Based on inspection of data patterns, results of post-hoc tests, and lack of meaningful biological interpretation, it was decided that significance merely reflected random noise.

Cheatgrass Experiment

In the cheatgrass experiment, there was an immediate effect of burning on cheatgrass and exotic species seed bank densities (model 1 vegetation treatment x collection time interaction, Table 3.3). Relative to the control, burning reduced both cheatgrass and exotic species seed bank densities from 2008 pre-treatment to 2008 post-treatment (Fig. 3.4, Fig. 3.5). There was no evidence of an effect of burning on either native species seed bank density or on total species richness (Table 3.3).

One year post-treatment, effects of both burning (model 2 vegetation treatment x collection time, Table 3.4) and seedbed treatment (model 2 seedbed treatment x collection time interaction, Table 3.4) were evident. From 2008 pre-treatment to 2009 post-treatment, both cheatgrass and exotic species seed densities were reduced in the burn treatment relative to the control (Fig. 3.6, Fig. 3.7). Exotic species seed density also responded to seedbed treatment, decreasing between collection times in sucrose plots relative to both control ($p = 0.0018$) and AC addition (AC) ($p = 0.0224$) plots; there was no evidence of an effect of AC relative to the control ($p = 0.6255$) (Fig. 3.8).

There was evidence of an herbicide treatment x vegetation treatment x collection time interaction for native species density between 2008 pre-treatment and 2009 post-

treatment (Table 3.4). This significance was due to the oddly low mean for 2008 pre-treatment density of burned, herbicide control plots relative to both the burned, 2 oz · acre^{-1} herbicide and the burned, 3 oz · acre^{-1} herbicide plots. As there were no other meaningful biological patterns, I suspect that the significance of the interaction is likely spurious.

The effect of seedbed treatment on the change in total species richness from 2008 pre-treatment to 2009 post-treatment interacts with herbicide treatment (model 2 seedbed treatment x herbicide treatment x collection time interaction, Table 3.4; Table 3.5). In the absence of herbicide, sucrose addition decreased total species richness relative to the control; there was no evidence of an effect of AC addition relative to the control (Fig. 3.9a). Whereas, with herbicide application at either rate (2 oz · acre^{-1}, 3 oz · acre^{-1}) total species richness was reduced, regardless of seedbed treatment (Figs. 3.9b and 3.9c). The significant decrease in no herbicide (control) with sucrose subplots appeared to be due to a reduction in exotic species richness.

DISCUSSION

Immediate Effects (model 1)

Sagebrush Experiment

Interestingly, in the sagebrush experiment, burning did not immediately reduce cheatgrass or exotic species seed bank densities. In contrast, Hassan and West (1986) observed a reduction in cheatgrass seed bank density six weeks post fire perhaps because their fire was more intense, as evident by the complete removal of aboveground

vegetation. In my study, the sagebrush sites had visibly less litter and more inter-space than the cheatgrass site. Thus, results may be attributed to lower fuel continuity and litter resulting in a less intense fire and therefore fewer destroyed seeds (Young et al. 1976; Young and Evans 1978).

Cheatgrass Experiment

In contrast to the sagebrush experiment, burning immediately reduced cheatgrass seed bank densities in the cheatgrass experiment. Likewise, these same patterns were observed for the exotic species seed bank densities. These findings are consentient with other studies that demonstrate a reduction in the seed bank of cheatgrass and other exotic species immediately following fire (Young et al. 1976; Hassan and West 1986; Humphrey and Schupp 2001; Pekas 2010).

Longer-term Effects (model 2)

Sagebrush Experiment

Similar to the immediate effects, results do not provide evidence of burning reducing cheatgrass or exotic species seed bank densities 1 year post-treatment in the sagebrush experiment. As there was no affect of burning immediately post-fire, it follows that there was no affect 1 year post-fire. Alternatively, even if burning did destroy a large portion of the seed bank, studies have demonstrated that reduced post-fire populations of cheatgrass can respond to a reduction in competition with more reproductively vigorous plants which can replenish the seed bank in sometimes as little as one growing season (Palmblad 1968; Young and Evans 1978; Hassan and West 1986;

Young et al. 1987; Humphrey and Schupp 2001). In contrast to the seed bank results, Summerhays (2011) did find a reduction in cheatgrass densities one year following (June 2009) the burn; she also found an increase in the mean number of spikelets per individual. It is likely that increased reproduction per individual exactly compensated for the reduction in number of individuals as has been found in other studies (e.g. Palmblad 1968), resulting in equal seed production in both burn and control treatments.

Likewise, results did not provide evidence of sagebrush thinning affecting cheatgrass or exotic species seed bank densities. The results for 50% thinning are consistent with those of Summerhays (2011) who found no effect of 50% thinning on cheatgrass. However, she did find an increase in mean number of spikelets per individual and no change in density one year after (June 2009) 100% thinning. Cheatgrass success has been shown to increase with shrub removal (Blumenthal et al. 2006; Prevey et al. 2010); this is likely due to an increase in plant available nutrients following overstory shrub removal (Blank et al. 2007). As the increase in spikelets seen by Summerhays (2011) did not result in a subsequent seed bank density increase, it was likely not a great enough increase in seed bank densities to detect with the sampling used in this study.

One year post-treatment, results demonstrate that herbicide reduced both cheatgrass and exotic species seed bank densities. Additionally, herbicide reduced total species richness, which was attributed to a reduction in exotic species richness. These results are not surprising as imazapic is intended to target exotic annuals (Shinn and Thill 2004; Sheley et al. 2007). These results also follow those of Summerhays (2011) who found a reduction in mean number of spikelets and no change in density one year post

(June 2009) herbicide application. However, these results disagree with those of the one Great Basin seed bank study that looked at the effects of imazapic on seed bank dynamics which found no affect on cheatgrass seed bank densities (Pekas 2010). These contradicting results are particularly interesting as Pekas applied imazapic at a rate three times that of the rate applied in this study.

Results also demonstrated that, one year post-treatment, seedbed treatments did not affect cheatgrass, exotic species or native species seed bank densities, or total species richness. Although no data exists on effects of carbon addition on cheatgrass seed banks, cheatgrass cover, growth, and seed production have been found to be significantly reduced the first growing season post carbon addition (Monaco et al. 2003; Mazzola et al. 2008; Rowe et al. 2009; Mazzola et al. 2011). The lack of response in cheatgrass and exotic species seed bank densities in this study are also surprising given that Summerhays (2011) found sucrose to decrease quantities of plant available nitrogen in these plots during the first winter/spring after treatment (March 2009) leading to a reduction in mean number of spikelets one year post application (June 2009) while densities were not affected. Based on her results and those of others, a reduction in seed input into the seed bank was expected. However, the reduction in spikelets seen by Summerhays may not have been large enough to cause a subsequent reduction in seed bank densities sufficiently large to be significant.

There was no affect of AC on seed bank densities or richness. To my knowledge there are no studies examining the effects of AC on seed banks. However, Summerhays (2011) found no effect of AC addition on plant available soil nutrients or cheatgrass

density and reproductive output. Kulmatiski and Beard (2006) found a reduction in cheatgrass cover after AC seedbed amendments which they attributed to the interruption of plant-soil feedbacks. The lack of an AC effect on cheatgrass in this study could be due to the application method or plant-soil feedbacks not being an important controlling factor for cheatgrass in these study sites. Additionally, Kulmatiski and Beard (2006) did not look at the affects of AC on cheatgrass reproductive output. As cheatgrass is known to respond plastically to reductions in competition with more reproductively vigorous plants (Palmblad 1968; Mazzola et al. 2011), the reduction in cover seen by Kulmatiski and Beard (2006) may have been compensated for by increased per individual reproductive output.

Cheatgrass Experiment

Cheatgrass and exotic species seed bank densities were still reduced in burned plots one year post-burn. Densities in the control treatment were also significantly reduced, although not nearly to the same extent, which may be attributed to a dry spring in 2009. These results are consistent with others that demonstrated reduced cheatgrass seed banks one year following fire (Humphrey and Schupp 2001; Pekas 2010).

Interestingly, cheatgrass seed bank density was not reduced by herbicide regardless of application rate. Although these results contrast with those from the sagebrush experiment, they are consistent with those of Pekas (2010) who found no affect of imazapic on cheatgrass seed bank densities. Summerhays (2011) found a reduction in mean cheatgrass spikelets in herbicide plots that were burned while cheatgrass densities were not affected. As there was no evidence of herbicide interacting with burning, this

reduction in spikelets may not have not been great enough to reduce seed bank densities sufficiently to detect.

One year post treatment, reduction in cheatgrass seed bank densities were found in sucrose subplots, in contrast to results from the sagebrush experiment. This is likely due to a reduction in plant available nutrients which may have reduced cheatgrass reproductive output. This is supported by findings of Summerhays (2011) who found reduced levels of plant available nitrogen during the first winter after treatment (March 2009) as well as the first summer after treatment (June 2009) which apparently resulted in reduced numbers of spikelets per individual but no affect on density. These findings are also consistent with other studies that have shown a reduction in seed production one year post-sucrose application (Mazzola et al. 2008, 2011).

The reductions in cheatgrass seed bank densities were not different between AC and the control suggesting that AC did not affect seed bank densities. This is also supported by Summerhays (2011) who did not see a reduction in any of the plant available nutrients assessed or cheatgrass reproductive output with the addition of AC.

Interestingly, Summerhays saw a reduction in spikelets in sucrose subplots in both experiments. In this study however, a reduction in cheatgrass seed bank densities was only seen in the cheatgrass experiment. This could perhaps be the result of a larger reduction in spikelets in the cheatgrass experiment than the sagebrush experiment resulting in a subsequent larger reduction in seed bank densities.

The seedbed treatment x herbicide treatment x collection time interaction for species richness demonstrated that either sucrose with no herbicide or either level of

imazapic, regardless of seedbed treatment, reduced total species richness equally. In other words, either herbicide or sucrose addition resulted in a reduction in total species richness, but that the combination of the two did not reduce richness further than either alone. This reduction in total species richness was attributed to a loss in exotic species, not native. This is not surprising as both imazapic and reduced plant available nutrients caused by sucrose addition are thought to disproportionately harm invasive annuals.

In this study, no treatments were found to affect native species seed bank densities in either model or experiment. This may be attributed to the low richness and densities and therefore low variance in time. This is not surprising as cheatgrass invasion into sagebrush systems is known to displace native species and reduce diversity (Stewart and Hull 1949; Harris 1967; Whisenant 1990; Anderson and Inouye 2001). Additionally, cheatgrass-invaded sagebrush systems have been shown to have low native species seed bank densities (Young and Evans 1975; Humphrey and Schupp 2001).

IMPLICATIONS

These results demonstrate that herbicide may be a useful tool for reducing exotic species richness as well as cheatgrass and other exotic species densities in the seed bank of cheatgrass-invaded sagebrush communities. Additionally, these results demonstrate that burning may be a useful tool for reducing cheatgrass and other exotic species seed bank densities in cheatgrass near-monocultures and that the effect of burning can be seen immediately as well as one year post treatment. However, this still leaves only a narrow window of opportunity for establishing perennial grasses post-fire and if that fails,

subsequent burning may be necessary to control cheatgrass at levels suitable for the establishment of desirable species.

Results also suggest that immobilization of plant available nutrients via sucrose addition may be a useful restoration tool for reducing seed bank densities of exotic species, including cheatgrass, in cheatgrass near-monocultures. However, the application of sucrose to large areas of disturbed sagebrush shrublands is not an economically feasible restoration tool. The application of other materials, such as sawdust, that have the ability to stimulate microbial growth and immobilize soil nitrogen might be feasible. Also, sucrose and herbicide were found to be equally useful restoration tools for reducing exotic species seed bank richness in cheatgrass near-monocultures. As these two techniques were equally successful at reducing exotics, but not additive, land managers would need to decide which is more cost effective as well as practical to apply on a large scale.

As with other studies examining the effects of restoration treatments on seed bank dynamics of cheatgrass-dominated systems (Humphrey and Schupp 2001), native species richness and seed bank densities were found to be very low in this study. This perhaps explains why I did not detect any treatment effects on native species. This suggests that augmenting native species seed banks in these systems is vital for successful restoration. Additionally, as native grasses were seeded into all plots I was unable to assess their effect on native species richness. Thus, future studies should include control seeding plots.

As cheatgrass can rebound quickly after a reduction in seed bank densities, future studies should address the effects of restoration treatments on seed bank dynamics beyond one growing season. Most importantly, I would like to determine if any of the short term effects on the seed bank dynamics create conditions more conducive to establishing desirable plants. This could be addressed by including information on aboveground establishment success of desirable species.

LITERATURE CITED

Abraham, J. K., J. D. Corbin, and C. M. D'Antonio. 2009. California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. *Plant Ecology* 201:445-456.

Anderson, J. E., and Inouye, R. S. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological Monographs* 71:531-556.

Bechtold, H. A., and R. S. Inouye. 2007. Distribution of carbon and nitrogen in sagebrush steppe after six years of nitrogen addition and shrub removal. *Journal of Arid Environments* 71:122-132.

Beckstead, J., and C. K. Augspurger. 2004. An experimental test of resistance to cheatgrass invasion: limiting resources at different life stages. *Biological Invasions* 6:417-432.

Belnap, J., S. L. Phillips, S. K. Sherrod, and A. Moldenke. 2005. Soil biota can change after exotic plant invasion: does this affect ecosystem processes? *Ecology* 86:3007-3017.

Billings, W. D. 1952. The environmental complex in relation to plant growth and distribution. *The Quarterly Review of Biology* 27:251-265.

Blank, R. R., J. Chambers, B. Roundy, and A. Whittaker. 2007. Nutrient availability in rangeland soils: influence of prescribed burning, herbaceous vegetation removal, overseeding with *Bromus tectorum*, season, and elevation. *Rangeland Ecology & Management* 60:644-655.

Blumenthal, D. M., N. R. Jordan, and M. P. Russelle. 2003. Soil carbon addition controls weeds and facilitates prairie restoration. *Ecological Applications* 13:605-615.

Blumenthal, D. M., U. Norton, J. D. Derner, and J. D. Reeder. 2006. Long-term effects of tebuthiuron on *Bromus tectorum*. *Western North American Naturalist* 66:420-425.

Booth, M. S., M. M. Caldwell, and J. M. Stark. 2003. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. *Journal of Ecology* 91:36-48.

Boyd, C. S., and K. W. Davies. 2010. Shrub microsite influences post-fire perennial grass establishment. *Rangeland Ecology & Management* 63:248-252.

Boyd, C. S., and T. J. Svejcar. 2011. The influence of plant removal on succession in Wyoming big sagebrush. *Journal of Arid Environments* 75:734-741.

Brooks, M. L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology* 40:344-353.

Brooks, M. L., and D. Pyke. 2001. Invasive plants and fire in the deserts of North America. *In*: K. E. M. Galley and T.P. Wilson [eds.]. Proceedings of the invasive plant workshop: the role of fire in the control and spread of invasive species. Tallahassee, FL, USA: Tall Timbers Research Station. p. 1-14.

Callaway, R. M., and E. T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290:521-523.

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.

Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology Evolution and Systematics* 34:183-211.

Dakheel, A. J., S. R. Radosevich, and M. G. Barbour. 1993. Effect of nitrogen and phosphorus on growth and interference between *Bromus tectorum* and *Taeniatherum asperum*. *Weed Research* 33:415-422.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasion by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.

Davison, J. C., and E. G. Smith. 2007. Imazapic provides 2-year control of weedy annuals in a seeded Great Basin fuel break. *Native Plants Journal* 8:91-95.

Duncan, C. A., J. J. Jachetta, M. L. Brown, V. F. Carrithers, J. K. Clark, J. M. Ditomaso, R. G. Lym, K. C. McDaniel, M. J. Renz, and P. M. Rice. 2004. Assessing the economic, environmental, and societal losses from invasive plants on rangeland and wildlands. *Weed Technology* 18:1411-1416.

Elseroad, A. C., and N. T. Rudd. 2011. Can Imazapic increase native species abundance in cheatgrass (*Bromus tectorum*) invaded native plant communities? *Rangeland Ecology and Management* 64:641-648.

Evans, R. A. 1961. Effects of different densities of downy brome (*Bromus tectorum*) on growth and survival of crested wheatgrass (*Agropyron desertorum*) in the greenhouse. *Weeds* 9:216-223.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs* 37:89-111.

Hassan, M. A., and N. E. West. 1986. Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. *Ecology* 67:269-272.

Homstad, C., J. Caywood, and P. Nelson. 2000. Cultural landscape report: Golden Spike National Historic Site, Box Elder County, Utah. Denver, CO, USA: National Park Service, Intermountain Region. 140 p.

Humphrey, L. D., and E. W. Schupp. 2001. Seed banks of *Bromus tectorum*-dominated communities in the Great Basin. *Western North American Naturalist* 61:85-92.

Humphrey, L. D., and E. W. Schupp. 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* 58:405-422.

Hulbert, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual bromegrasses. *Ecological Monographs* 25:181-213.

Inderjit, and R. M. Callaway. 2003. Experimental designs for the study of allelopathy. *Plant and Soil* 256:1-11.

Inouye, R. S. 2006. Effects of shrub removal and nitrogen addition on soil moisture in sagebrush steppe. *Journal of Arid Environments* 65:604-618.

Klemmedson, J. O., and J.G. Smith. 1964. Cheatgrass (*Bromus tectorum* L). *Botanical Review* 30:226-262.

Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin desert - history, persistence, and influences to human activities. *Global Environmental Change-Human and Policy Dimensions* 6:37-52.

Kulmatiski, A. 2011. Changing soils to manage plant communities: activated carbon as a restoration tool in ex-arable fields. *Restoration Ecology* 19:102-110.

Kulmatiski, A., and K. H. Beard. 2006. Activated carbon as a restoration tool: potential for control of invasive plants in abandoned agricultural fields. *Restoration Ecology* 14:251-257.

Kyser, G. B., J. M. DiTomaso, M. P. Doran, S. B. Orloff, R. G. Wilson, D. L. Lancaster, D. F. Lile, and M. L. Porath. 2007. Control of medusahead (*Taeniatherum caputmedusae*) and other annual grasses with imazapic. *Weed Technology* 21:66-75.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L into Western North America: an ecological chronicle. *Agro-Ecosystems* 7:145-165.

Mack, R. N., and D. A. Pyke. 1983. The demography of *Bromus tectorum*: variation in time and space. *Journal of Ecology* 71:69-93.

Mazzola, M. B., K. G. Allcock, J. C. Chambers, R. R. Blank, E. W. Schupp, P. S. Doescher, and R. S. Nowak. 2008. Effects of nitrogen availability and cheatgrass competition on the establishment of Vavilov Siberian wheatgrass. *Rangeland Ecology & Management* 61:475-484.

Mazzola, M. B., J. C. Chambers, R. R. Blank, D. A. Pyke, E. W. Schupp, K. G. Allcock, P. S. Doescher, and R. S. Nowak. 2011. Effects of resource availability and propagule supply on native species recruitment in sagebrush ecosystems invaded by *Bromus tectorum*. *Biological Invasions* 13:513-526.

McLendon, T., and E. F. Redente. 1992. Effects of nitrogen limitation on species replacement dynamics during early secondary succession on a semiarid sagebrush site. *Oecologia* 91:312-317.

Melgoza, G., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83:7-13.

Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003. Contrasting responses of intermountain west grasses to soil nitrogen. *Journal of Range Management* 56:282-290.

Monaco, T. A., T. M. Osmond, and S. A. Dewey. 2005. Medusahead control with fall- and spring-applied herbicides on northern Utah foothills. *Weed Technology* 19:653-658.

Monsen, S. B. 1994. The competitive influences of cheatgrass (*Bromus tectorum*) on site restoration. *In*: S. B. Monsen and S. G. Kitchen [comps.]. Proceedings: Ecology and management of annual rangelands; 18- 22 May 1992; Boise, ID, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-GTR-313. p. 43-50.

Morris, C., T. A. Monaco, and C. W. Rigby. 2009. Variable impacts of imazapic rate on downy brome (*Bromus tectorum*) and seeded species in two rangeland communities. *Invasive Plant Science and Management* 2:110-119.

Ogg, A. G., Jr. 1994. A review of the chemical control of downy brome. *In*: S. B. Monsen and S. G. Kitchen [comps.]. Proceedings: Ecology and management of annual rangelands; 18- 22 May 1992; Boise, ID, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-GTR-313. p. 194 -196.

Palmblad, I. G. 1968. Competition in experimental populations of weeds with emphasis on the regulation of population size. *Ecology* 49:26-34.

Paschke, M. W., T. McLendon, and E. F. Redente. 2000. Nitrogen availability and old-field succession in a shortgrass steppe. *Ecosystems* 3:144-158.

Pekas, K. 2010. Seed pool dynamics of a Great Basin sagebrush community in the context of restoration [thesis]. Logan, UT, USA: Utah State University. 127 p.

Pellant, M. 1996. Cheatgrass: the invader that won the west. Boise, ID, USA: Bureau of Land Management, Interior Columbia Ecosystem Management Project. 22 p.

Peters, E. F., and S. C. Bunting. 1994. Fire conditions pre- and post-occurrence of annual grasses on the Snake River Plain. *In*: S. B. Monsen and S. G. Kitchen [comps.]. Proceedings: Ecology and management of annual rangelands; 18- 22 May 1992; Boise, ID, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-GTR-313. p. 31-36.

Prevey, J. S., M. J. Germino, N. J. Huntly, and R. S. Inouye. 2010. Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe. *Plant Ecology* 207:39-51.

Pyke, D. A. 1994. Ecological significance of seed banks with special reference to alien annuals. *In*: S. B. Monsen and S. G. Kitchen [comps.]. Proceedings: Ecology and management of annual rangelands; 18-22 May 1992; Boise, ID, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-GTR-313. p. 197-201.

Pyke, D. A., and S. J. Novak. 1994. Cheatgrass demography: establishment attributes, recruitment, ecotypes, and genetic variability. *In*: S. B. Monsen and S. G. Kitchen [comps.]. Proceedings: Ecology and management of annual rangelands; 18-22 May 1992; Boise, ID, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-GTR-313. p. 12-21.

Rowe, H. I., C. S. Brown, and M. W. Paschke. 2009. The Influence of soil inoculum and nitrogen availability on restoration of high-elevation steppe communities invaded by *Bromus tectorum*. *Restoration Ecology* 17:686-694.

SAS Institute. 2007. SAS System for Microsoft Windows. SAS Institute, Inc., Cary, NC, USA.

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.

Sheley, R. L., M. F. Carpinelli, and K. J. R. Morghan. 2007. Effects of imazapic on target and non-target vegetation during re-vegetation. *Weed Technology* 21:1071-1081.

Shinn, S. L., and D. C. Thill. 2004. Tolerance of several perennial grasses to imazapic. *Weed Technology* 18:60-65.

Stewart, G., and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.) an ecologic intruder in southern Idaho. *Ecology* 30:58-74.

Summerhays, J. C. R. 2011. Effects of non-surface-disturbing treatments for native grass revegetation on cheatgrass (*Bromus tectorum L.*) metrics soil ion availabilities [thesis]. Logan, UT, USA: Utah State University. 130 p.

USDA-NRCS. 2011. Official Soil Series Descriptions. Available at: https://soilseries.sc.egov.usda.gov/OSD_Docs/A/ABELA.html. Accessed 29 December 2011.

Vasquez, E., R. Sheley, and T. Svejcar. 2008a. Creating invasion resistant soils via nitrogen management. *Invasive Plant Science and Management* 1:304-314.

Vasquez, E., R. Sheley, and T. Svejcar. 2008b. Nitrogen enhances the competitive ability of cheatgrass (*Bromus tectorum*) relative to native grasses. *Invasive Plant Science and Management* 1:287-295.

Washburn, B. E., T. G. Barnes, and J. D. Sole. 1999. No-till establishment of native warm-season grasses in tall fescue fields: fire-year results indicate value of new herbicide. *Ecological Restoration* 17:40-45.

West, N. E., and M. A. Hassan. 1985. Recovery of sagebrush-grass vegetation following wildfire. *Journal of Range Management* 38:131-134.

Whelan, R. J. 1995. The ecology of fire. Cambridge, UK: Cambridge University Press. 346 p.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. *In*: D. E. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller [comps.]. Proceedings: Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 5-7 April 1989; Las Vegas, NV, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-276. p. 4-10.

Wright, H. A., and J. O. Klemmedson. 1965. Effect of fire on bunchgrasses of the sagebrush-grass region in southern Idaho. *Ecology* 46:680-688.

Young, J. A., and C. D. Clements. 2000. Cheatgrass control and seeding. *Rangelands* 22:3-7.

Young, J. A., and R. A. Evans. 1975. Germinability of seed reserves in a big sagebrush community. *Weed Science* 23:358-364.

Young, J. A., and R. A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. *Journal of Range Management* 31:283-289.

Young, J. A., R. A. Evans, and R. A. Weaver. 1976. Estimating potential downy brome competition after wildfires. *Journal of Range Management* 29:322-325.

Young, J.A., R.A. Evans, R.E. Eckert, Jr., and B.L. Kay. 1987. Cheatgrass. *Rangelands* 9: 266-270.

Ziska, L. H., J. B. Reeves, and B. Blank. 2005. The impact of recent increases in atmospheric CO2 on biomass production and vegetative retention of cheatgrass (*Bromus tectorum*): implications for fire disturbance. *Global Change Biology* 11:1325-1332.

Table 3.1. Analysis of variance for model 1 (2008 pre-treatment and 2008 post-treatment collection times and burning) of the sagebrush experiment (bold font denotes significance, $p \leq 0.05$). † denotes interaction terms that are relevant for assessing hypotheses. Vegtreat = vegetation treatment, collection = collection time.

		Bromus tectorum seed bank density		exotic species seed bank density		native species seed bank density		total species richness	
Effect	*df*	*F*	*p*	*F*	*P*	*F*	*p*	*F*	*p*
vegtreat	1, 3	4.11	0.14	6.34	0.09	0.04	0.86	1.74	0.28
collection	1, 6	1.26	0.31	4.39	0.08	0.46	0.52	4.72	0.07
†vegtreat*collection	1, 6	1.54	0.26	3.00	0.13	2.66	0.15	4.06	0.09

Table 3.2. Analysis of variance for model 2 (2008 pre-treatment and 2009 post-treatment collection times and all treatments) of the sagebrush experiment (bold font denotes significance, $p \leq 0.05$). † denotes interaction terms that are relevant for assessing hypotheses. Vegtreat = vegetation treatment, herbtreat = herbicide treatment, seedtreat = seedbed treatment, collection = collection time.

		Bromus tectorum seed bank density		exotic species seed bank density		native species seed bank density		total species richness	
Effect	*df*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
vegtreat	3, 18	3.59	**0.03**	3.05	**0.06**	0.60	0.62	0.31	0.82
herbtreat	1, 18	2.03	0.17	5.71	**0.03**	6.67	**0.02**	4.76	**0.04**
herbtreat*vegtreat	3, 18	0.46	0.72	0.12	0.95	0.25	0.86	0.10	0.96
seedtreat	2, 42	4.16	**0.02**	3.79	**0.03**	0.78	0.47	3.29	**0.05**
seedtreat*vegtreat	6, 42	0.13	0.99	0.52	0.79	1.60	0.17	1.49	0.20
seedtreat*herbtreat	2, 42	0.55	0.58	1.69	0.20	0.51	0.60	0.04	0.96
seedtreat*herbtreat*vegtreat	6, 42	0.22	0.97	0.57	0.75	0.58	0.75	1.18	0.33
collection	1, 60	0.87	0.36	0.12	0.73	4.20	**0.04**	28.14	**<.0001**
†vegtreat*collection	3, 60	0.11	0.95	0.48	0.70	2.36	0.08	1.46	0.23
†herbtreat*collection	1, 60	12.09	**0.00**	16.55	**0.00**	1.36	0.25	8.95	**0.00**
†herbtreat*vegtreat*collection	3, 60	1.32	0.28	0.92	0.44	0.98	0.41	0.22	0.88
†seedtreat*collection	2, 60	0.74	0.48	0.66	0.52	0.44	0.64	0.14	0.90
†seedtreat*vegtreat*collection	6, 60	2.11	0.07	2.08	0.07	1.27	0.28	2.38	**0.04**
†seedtreat*herbtreat*collection	2, 60	0.68	0.51	0.42	0.66	2.47	0.09	1.13	0.33
†seedtreat*herbtreat*vegtreat*collection	6, 60	0.61	0.72	0.97	0.45	0.53	0.78	0.60	0.73

Table 3.3. Analysis of variance for model 1 (2008 pre-treatment and 2008 post-treatment collection times and burning) of the cheatgrass experiment (bold font denotes significance, $p \leq 0.05$). † denotes interaction terms that are relevant for assessing hypotheses. Vegtreat = vegetation treatment, collection = collection time.

		Bromus tectorum seed bank density		exotic species seed bank density		native species seed bank density		total species richness	
Effect	*df*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
vegtreat	1, 6	8.34	**0.03**	3.39	0.12	0.00	0.99	2.28	0.18
collection	1, 6	18.01	**0.01**	12.52	**0.01**	2.07	0.20	5.48	**0.06**
†vegtreat*collection	1, 6	25.43	**0.00**	16.58	**0.01**	0.57	0.48	0.73	0.43

Table 3.4. Analysis of variance for model 2 (2008 pre-treatment and 2009 post-treatment collection times and all treatments) of the cheatgrass experiment (bold font denotes significance, $p \leq 0.05$). † denotes interaction terms that are relevant for assessing hypotheses. Vegtreat = vegetation treatment, herbtreat = herbicide treatment, seedtreat = seedbed treatment, collection = collection time.

		Bromus tectorum seed bank density		exotic species seed bank density		native species seed bank density		total species richness	
Effect	*df*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
vegtreat	1, 6	0.71	0.43	0.33	0.59	3.09	0.13	1.56	0.26
herbtreat	2, 12	1.83	0.20	2.65	0.11	6.90	**0.01**	0.80	0.47
herbtreat*vegtreat	2, 12	0.57	0.58	1.34	0.30	0.04	0.96	0.57	0.58
seedtreat	2, 36	0.61	0.55	0.61	0.55	0.63	0.54	0.98	0.38
seedtreat*vegtreat	2, 36	0.29	0.75	1.34	0.27	0.46	0.64	0.04	0.96
seedtreat*herbtreat	4, 36	0.16	0.96	0.40	0.80	0.48	0.75	1.29	0.29
seedtreat*herbtreat*vegtreat	4, 36	0.57	0.69	0.73	0.58	1.51	0.22	1.43	0.24
collection	1, 54	86.48	**<.0001**	217.69	**<.0001**	14.24	**0.00**	94.65	**<.0001**
†vegtreat*collection	1, 54	20.49	**<.0001**	32.74	**<.0001**	0.75	0.39	2.28	0.14
†herbtreat*collection	2, 54	0.09	0.92	1.54	0.22	0.51	0.60	2.71	0.08
†herbtreat*vegtreat*collection	2, 54	0.98	0.38	0.83	0.44	3.26	**0.05**	0.68	0.51
†seedtreat*collection	2, 54	2.96	0.06	7.36	**0.00**	0.12	0.88	0.59	0.56
†seedtreat*vegtreat*collection	2, 54	0.39	0.68	1.25	0.30	0.54	0.59	1.68	0.20
†seedtreat*herbtreat*collection	4, 54	0.91	0.46	0.79	0.54	0.55	0.70	2.91	**0.03**
†seedtreat*herbtreat*vegtreat*collection	4, 54	0.12	0.97	0.09	0.99	0.34	0.85	1.29	0.29

Table 3.5. Least squares means comparison estimates of total species richness for model 2 (2008 pre-treatment and 2009 post-treatment collection times and all treatments) of the cheatgrass experiment, assessing the herbicide treatment x seed treatment x collection time interaction (bold font denotes significance, $p \leq 0.05$).

		seeding alone (control)			sucrose			activated carbon	
Effect	*df*	*t*	*p*	*df*	*t*	*p*	*df*	*t*	*p*
no herbicide (control)	54	0.83	0.41	54	4.83	**<.0001**	54	0.81	0.42
herbicide 2 oz • acre^{-1}	54	3.46	**0.00**	54	3.19	**0.00**	54	4.31	**<.0001**
herbicide 3 oz • acre^{-1}	54	4.86	**<.0001**	54	3.24	**0.00**	54	3.65	**0.00**

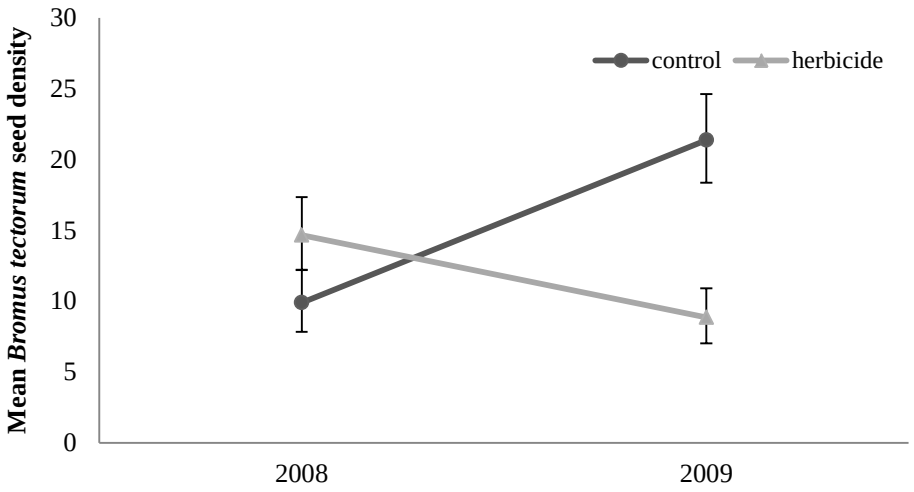

Figure 3.1. Mean *Bromus tectorum* seed bank density · 0.24 L^{-1} of soil (± *95% CI*) as affected by herbicide and collection time in model 2 of the sagebrush experiment.

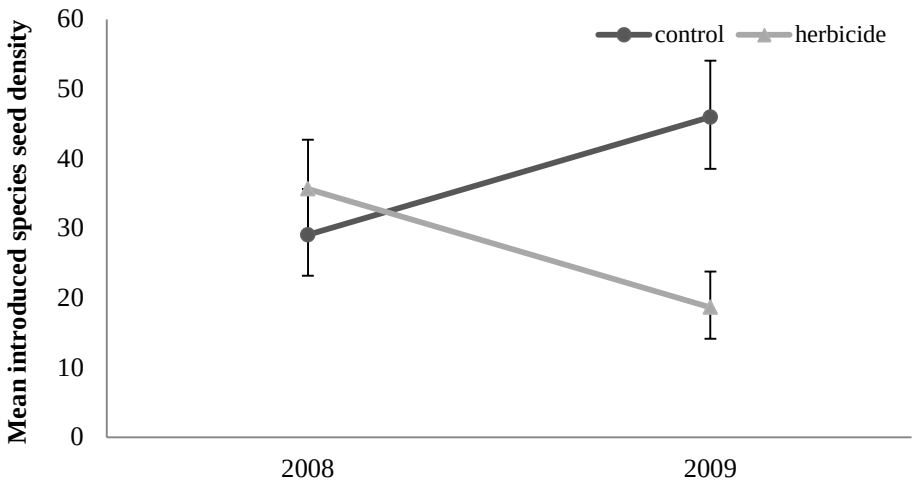

Figure 3.2. Mean exotic species seed bank density · 0.24 L^{-1} of soil (± *95% CI*) as affected by herbicide and collection time in model 2 of the sagebrush experiment.

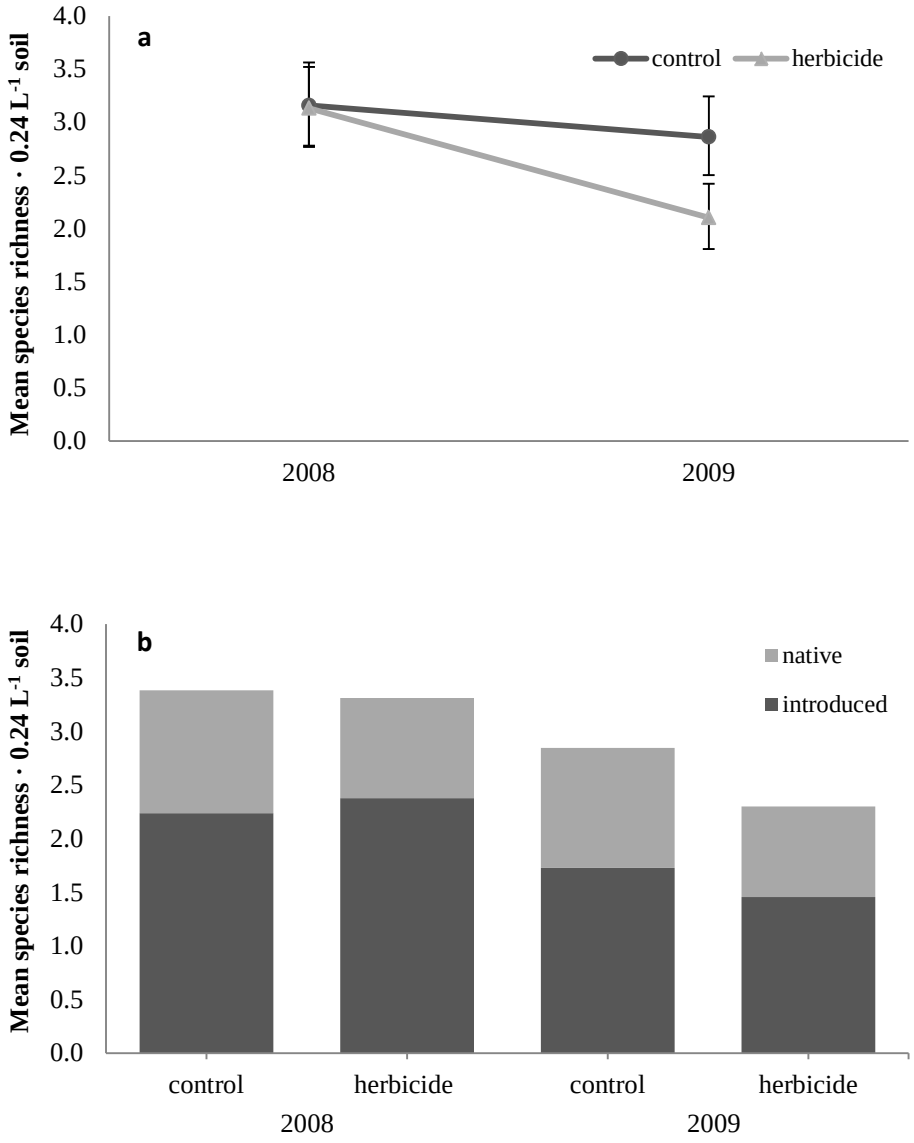

Figure 3.3. a) mean total species richness · 0.24 L^{-1} of soil (± *95% CI*) as affected by herbicide and collection time in model 2 of the sagebrush experiment, b) mean native and exotic species richness · 0.24 L^{-1} of soil as affected by herbicide and collection time in model 2 of the sagebrush experiment.

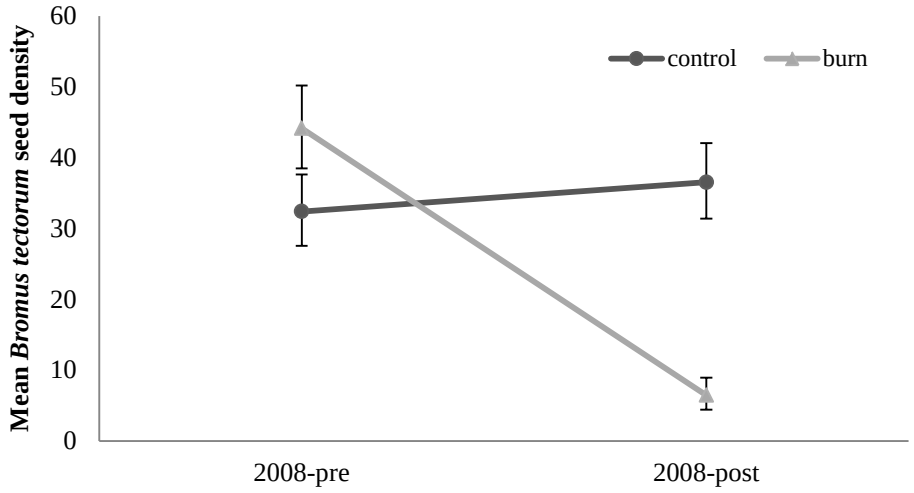

Figure 3.4. Mean *Bromus tectorum* seed bank density · $0.24L^{-1}$ of soil (± *95% CI*) as affected by vegetation treatment and collection time in model 1 of the cheatgrass experiment.

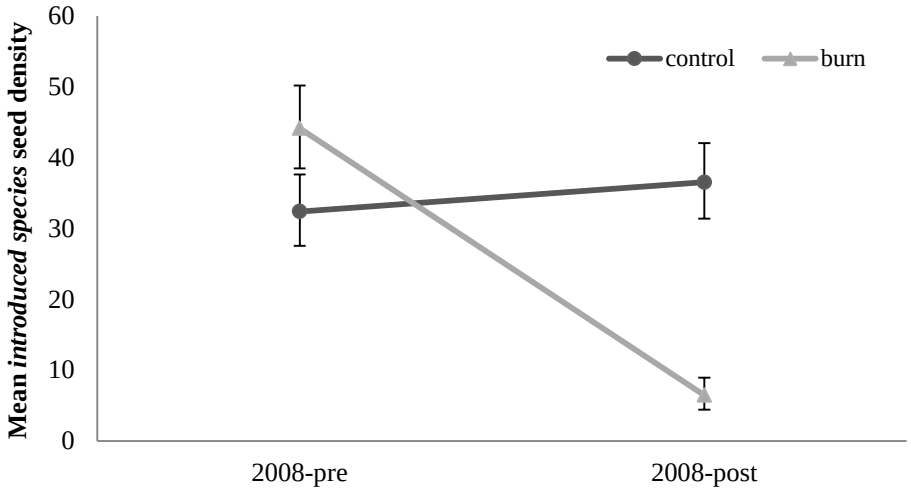

Figure 3.5. Mean exotic species seed bank density · $0.24L^{-1}$ of soil (± *95% CI*) as affected by vegetation treatment and collection time in model 1 of the cheatgrass experiment.

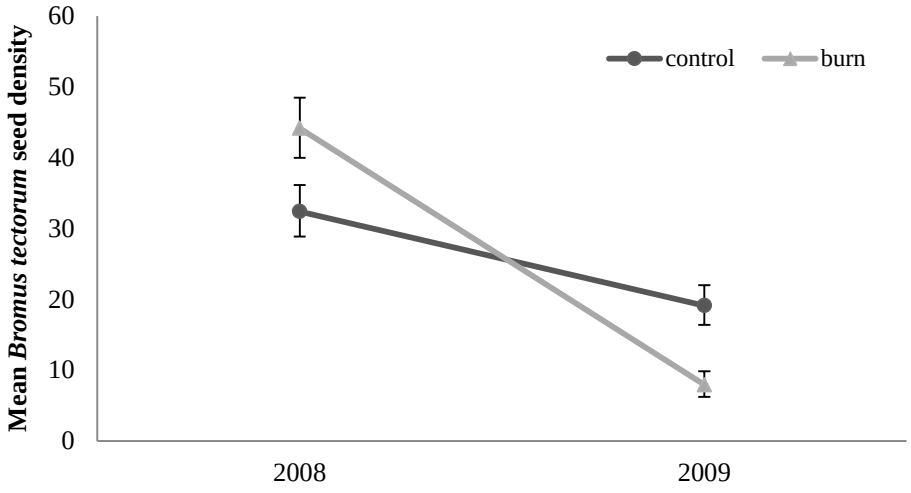

Figure 3.6. Mean *Bromus tectorum* seed bank density · $0.24L^{-1}$ of soil (± *95% CI*) as affected by vegetation treatment and collection time in model 2 of the cheatgrass experiment.

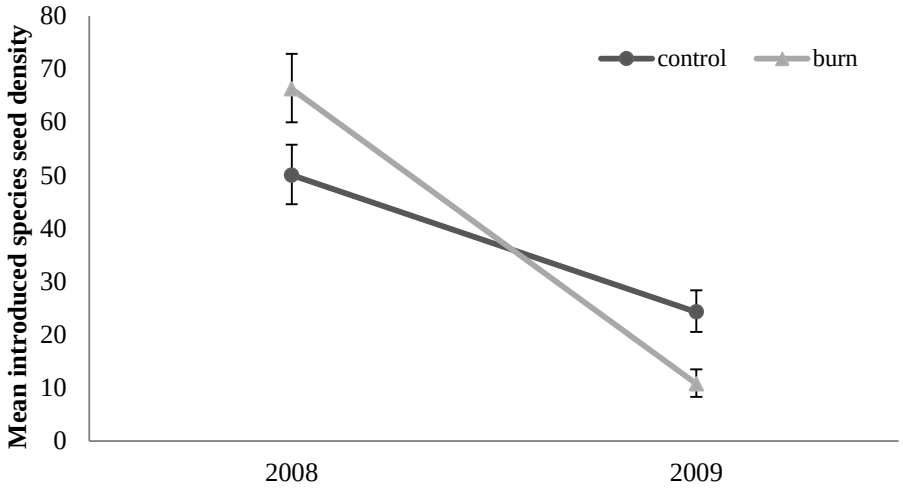

Figure 3.7. Mean exotic species seed bank density · $0.24L^{-1}$ of soil (± *95% CI*) as affected by vegetation treatment and collection time in model 2 of the cheatgrass experiment.

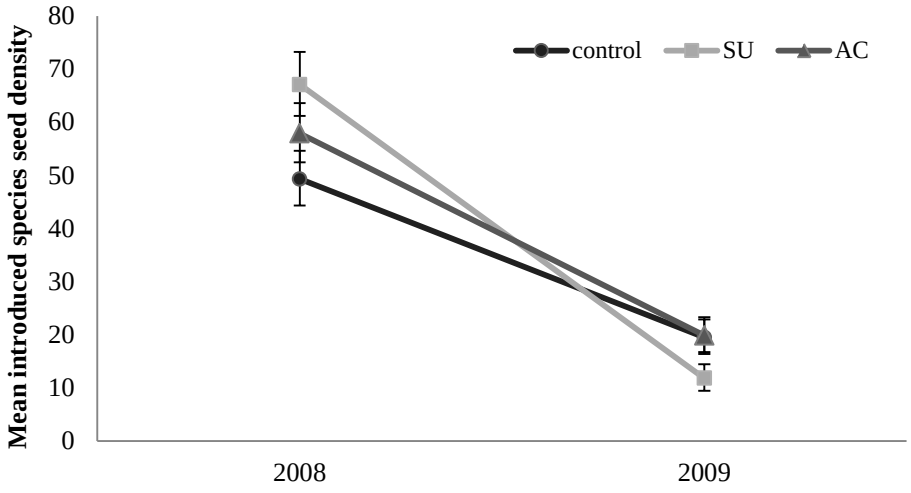

Figure 3.8. Mean exotic species seed bank density · $0.24L^{-1}$ of soil (± *95% CI*) as affected by seedbed treatment and collection time in model 2 of the cheatgrass experiment.

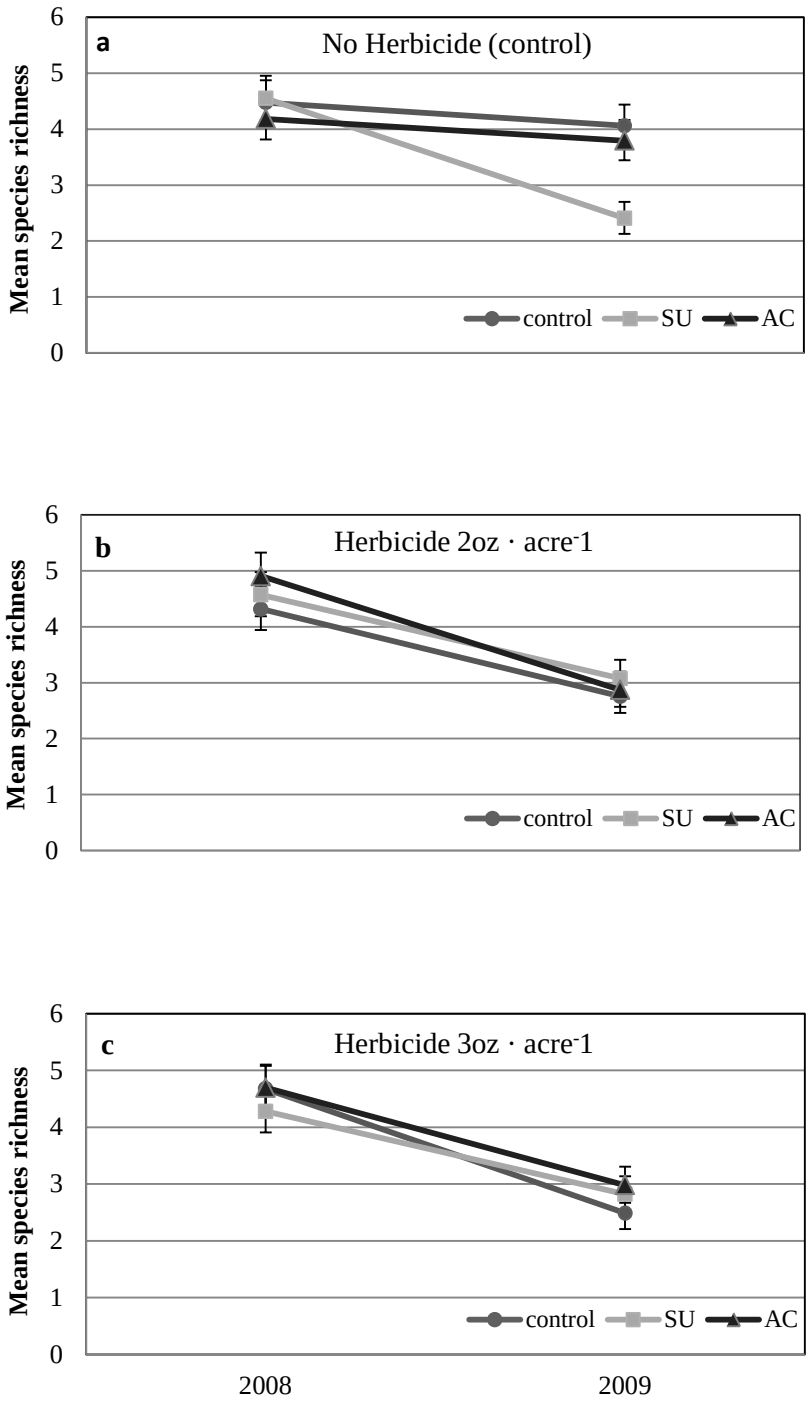

Figure 3.9. Mean total species richness · 0.24 L^{-1} of soil (± *95% CI*) as affected by the herbicide treatment (a) control, b) 2 oz · acre c) 3 oz · acre) x seedbed treatment x collection time interaction in model 2 of the cheatgrass experiment.

CHAPTER 4

CONCLUSION

Cheatgrass is ubiquitous throughout the Great Basin of the Intermountain West (Knapp 1996); the consequences of its invasion into sagebrush-steppe ecosystems have been an increase in fire frequency and intensity, decreased species diversity, degradation of ecological function, and economic loss (Stewart and Hull 1949; Whisenant 1990; D'Antonio and Vitousek 1992; Roberts 1994; Knapp 1996; Pellant 1996). It has recently been suggested that 58 percent of sagebrush in the Great Basin is at moderate or high risk of being displaced by cheatgrass (Rowland et al. 2010). Primarily due to a loss of habitat, conservation and restoration of these sagebrush ecosystems are of special concern to State and Federal resource management agencies (Knick et al. 2003).

The key to restoring these systems may be re-introducing the native perennial grass component as perennial grasses have demonstrated the ability to successfully compete with cheatgrass (Booth et al. 2003; Humphrey and Schupp 2004). However, previous attempts to restore native plant species to these invaded sagebrush systems have had low success mainly due to resource competition from cheatgrass to native species at the seedling stage (Rummel 1946; Evans 1961; Mazzola et al. 2008). I evaluated the effects of several restoration treatments aimed at altering the resource environment in ways that could benefit seeded native perennial grasses on 1) perennial grass emergence, and 2) seed bank densities and richness. Additionally, I evaluated 3) the effects of seeding frequency on perennial grass emergence. Treatments, including seeding

frequency, were evaluated in two distinct experimental sites in northern Utah, one a cheatgrass-invaded sagebrush site, the other a cheatgrass near-monoculture.

In Chapter 2, I evaluated the effects of burning, sagebrush thinning (50% and 100%), imazapic herbicide (2 oz · acre^{-1}' and 3 oz · acre^{-1}'), and sucrose and activated carbon (AC) seedbed amendments on native perennial grass emergence in both experimental sites 2 and 3 years post-treatment. Additionally, I compared seedling emergence between plots seeded one, two and three consecutive years in the cheatgrass-invaded sagebrush site.

Results suggested that herbicide may be a useful tool for increasing the emergence of native perennial grasses in both cheatgrass-invaded sagebrush systems and cheatgrass near-monocultures. However, as this increase was not seen until 3 years post-herbicide application, further investigation into the cause of this delay is needed. Burning also showed promise as a tool for increasing perennial grass emergence in cheatgrass near-monocultures. As with herbicide, burning provided a longer than expected window of opportunity for increased perennial grass emergence. This may have been attributed to the severity of the burn or some other unaccounted for effect of the burn, however further investigation is needed to substantiate this.

Perhaps the most interesting and valuable findings in this chapter were those from the seeding frequency comparisons. Increasing seeding frequency from a single year to 2 and 3 years resulted in increased perennial grass emergence with 3 years of seeding yielding the largest increase. Since environmental conditions vary from year to year and

are hard to predict, seeding multiple consecutive years may increase the probability of seeding in a year that is ‘favorable’ for seeded grasses.

As success was only measured in terms of emergence, it is unknown whether any of these treatments that demonstrated usefulness would lead to higher establishment rates and ultimately increase the density of mature perennial grasses.

The effects of restoration treatments on seed banks are largely unknown and most control strategies for cheatgrass are driven by the principle of depleting the soil seed bank. Therefore in Chapter 3, I investigated the effects of burning, sagebrush thinning (50% and 100%), imazapic herbicide (2 oz · acre^{-1} and 3 oz · acre^{-1}), sucrose and AC seedbed amendments on the seed bank dynamics of both experimental sites.

Results from this study demonstrated that herbicide may be an effective tool for reducing seed bank densities of exotic species such as cheatgrass as well as exotic species seed bank richness in cheatgrass-dominated sagebrush systems. Additionally, in cheatgrass near-monocultures burning reduced cheatgrass seed bank densities immediately as well as one year post burn. Results also demonstrated that, sucrose and imazapic were equally useful tools for reducing exotic species richness in the seed banks cheatgrass near-monocultures.

None of the treatments tested in this study showed potential for use as tools to increase native species densities or richness in cheatgrass invaded sagebrush systems. This was likely due to the typically low native richness and density observed in these invaded systems. The low native richness and density seen in the seed bank study in combination with results from the seeding frequency comparisons in chapter 2 highlight

the need for revegetation efforts in cheatgrass invaded communities to augment native species.

Due to the variability in both space and time of abiotic and biotic factors, as well as the often short windows of opportunity provided by restoration treatments, adaptive management will likely be necessary for successful restoration. Additionally, more complete knowledge of the abiotic and biotic interactions that affect plant establishment in these invaded systems will prove crucial for increasing the success of restoration efforts. Collectively, these studies increased our understanding of the effects of some commonly used restoration techniques and propagule supply on the emergence of native perennial grasses and seed bank dynamics in Great Basin cheatgrass-invaded sagebrush ecosystems.

LITERATURE CITED

Booth, M. S., M. M. Caldwell, and J. M. Stark. 2003. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. *Journal of Ecology* 91:36-48.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasion by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.

Evans, R. A. 1961. Effects of different densities of downy brome (*Bromus tectorum*) on growth and survival of crested wheatgrass (*Agropyron desertorum*) in the greenhouse. *Weeds* 9:216-223.

Humphrey, L. D., and E. W. Schupp. 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* 58:405-422.

Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin desert - history, persistence, and influences to human activities. *Global Environmental Change-Human and Policy Dimensions* 6:37-52.

Knick, S.T., D.S. Dobkin, J.T. Rotenberry, M.A. Schroeder, W.M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105: 611-634.

Mazzola, M. B., K. G. Allcock, J. C. Chambers, R. R. Blank, E. W. Schupp, P. S. Doescher, and R. S. Nowak. 2008. Effects of nitrogen availability and cheatgrass competition on the establishment of Vavilov Siberian wheatgrass. *Rangeland Ecology & Management* 61:475-484.

Pellant, M. 1996. Cheatgrass: the invader that won the west. Boise, ID, USA: Bureau of Land Management, Interior Columbia Ecosystem Management Project. 22 p.

Roberts, T.C., Jr. 1994. Resource impacts of cheatgrass and wildfires on public lands and livestock grazing. *In*: S. B. Monsen and S. G. Kitchen [comps.]. Proceedings: Ecology and management of annual rangelands; 18- 22 May 1992; Boise, ID, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-GTR-313. p. 167-169.

Rowland, M.M., L.H. Suring, and M.J. Wisdom. 2010. Assessment of habitat threats to shrublands in the Great Basin: a case study. *In*: J. M. Pye, M. H. Rauscher, Y. Sands, D. C. Lee, and J. S. Beatty [eds.]. Proceedings: Advances in threat assessment and their application to forest and rangeland management. Portland, OR, USA: US Department of Agriculture, Forest Service, General Technical Report PNW-GTR-802. p. 673-685.

Rummel, R. S. 1946. Some effects of competition from cheatgrass brome on crested wheat-grass and bluestem wheatgrass. *Ecology* 27:159-167.

Stewart, G., and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.) an ecologic intruder in southern Idaho. *Ecology* 30:58-74.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. *In*: D. E. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller [comps.]. Proceedings: Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 5-7 April 1989; Las Vegas, NV, USA. Ogden, UT, USA: US Department of Agriculture, Forest Service, General Technical Report INT-276. p. 4-10.

APPENDICES

Table A.1. Occurrence of species in the seed bank at the sagebrush experiment. Species frequency (percent of samples in which species was found) and percent of total seed bank for all plots at all three collection times are presented.

		2008 pre-treatment		2008 immediate post-treatment		2009 1-yr. post-treatment	
Species	Nativity	Frequency %	% Total seed bank	Frequency %	% Total seed bank	Frequency %	% Total seed bank
Achnatherum hymenoides	Native	1.15	0.03				
Alyssum desortorum	Intro					1.25	0.01
Arabidopsis thaliana	Intro	3.45	0.92	6.52	0.53	4.38	0.12
Artimesia tridentata	Native	29.89	1.41	26.09	1.75	41.88	0.79
Bromus briziformis	Intro	1.15	0.05			3.13	0.09
Bromus tectorum	Intro		38.44	80.43	37.18	98.75	48.35
Carex sp.	Native	2.30	0.05			1.88	0.02
Chamaesyce serpyllifolia	Native	2.30	0.05			3.75	0.06
Cryptantha pterocarya	Native	1.15	0.03			0.63	0.01
Draba cuneifolia	Native	32.18	2.25	45.65	7.28	40.00	2.19
Draba verna	Intro	52.87	31.78	54.35	27.47	51.25	18.29
Elymus elymoides	Native	1.15	0.03	4.35	0.30	23.13	0.69
Erodium cicutarium	Intro					0.63	0.01
Gutierrezia sarothrae	Native	5.75	0.14	4.35	0.23	5.63	0.08
Helianthus annuus	Native	3.45	0.08	2.17	0.08	9.38	0.14
Hesperostipa comata	Native					0.63	0.01
Holesteum umbellatum	Intro	40.23	12.10	34.78	4.48	40.63	4.81
Juncus torreyi	Native					1.25	0.01
Lactuca serriola	Intro	2.30	0.05	2.17	0.08	34.38	0.71
Lithophragma parviflorum	Native	3.45	1.14			8.13	1.77
Penstemon sp.	Native	2.30	0.05			0.63	0.01
Physaria sp.	Native	12.64	0.57	4.35	0.15	21.25	0.70
Poa bulbosa	Intro	2.30	0.08	4.35	0.46	10.00	0.43
Poa pratensis	Intro					1.88	0.03
Poa secunda	Native	2.30	0.08			9.38	0.21
Ranunculus testiculatus	Intro	37.93	10.34	32.61	19.80	58.75	19.63
Sisymbrium altissimum	Intro					2.50	0.05
Sporobolus cryptandrus	Native					1.25	0.03
tragopogon dubius	Intro					0.63	0.01
Tyhpa sp.	Native					1.25	0.01
Vulpia octoflora	Native	3.45	0.32	2.17	0.23	15.63	0.72

Table A.2. Occurrence of species in the seed bank at the cheatgrass experiment. Species frequency (percent of samples in which species was found) and percent of total seed bank for all plots at all three collection times are presented.

		2008 pre-treatment		2008 immediate post-treatment		2009 1-yr. post-treatment	
Species	Nativity	Frequency %	% Total seed bank	Frequency %	% Total seed bank	Frequency %	% Total seed bank
Alyssum desortorum	Intro	1.39	0.02	1.39	0.03		
Arabidopsis thaliana	Intro	1.39	0.02	2.78	0.12	1.39	0.06
Artimesia tridentata	Native					1.39	0.03
Bromus briziformis	Intro					1.39	0.06
Bromus tectorum	Intro	100.00	60.37	95.83	52.83	100.00	63.28
Chamaesyce serpyllifolia	Native	1.39	0.02			4.17	0.14
Cryptantha pterocarya	Native	1.39	0.02	1.39	0.03	9.72	0.34
Draba cuneifolia	Native	61.11	2.46	52.78	2.47	75.00	4.34
Draba verna	Intro	37.50	3.09	34.72	5.65	41.67	1.96
Epilobium ciliatum	Native	4.17	0.06	2.78	0.06		
Erodium cicutarium	Intro	6.94	0.10	13.89	0.35	36.11	2.18
Gutierrezia sarothrae	Native	5.56	0.14	8.33	0.24	15.28	0.42
Helianthus annuus	Native	97.22	7.23	91.67	10.18	93.06	11.25
Hesperostipa comata	Native					6.94	0.14
Holesteum umbellatum	Intro	87.50	25.36	72.22	26.49	55.56	8.79
Lactuca serriola	Intro	2.78	0.04	1.39	0.03	50.00	2.41
Lappula occidentalis	Native					4.17	0.08
Leymus cinereus	Native					4.17	0.08
Lithophragma parviflorum	Native					1.39	0.17
Physaria sp.	Native	27.78	0.65	8.33	0.26	25.00	0.67
Poa bulbosa	Intro			2.78	0.06	11.11	0.64
Poa pratensis	Intro					2.78	0.06
Poa secunda	Native					13.89	0.56
Ranunculus testiculatus	Intro	5.56	0.10	2.78	0.09	12.50	0.34
Sisymbrium altissimum	Intro	8.33	0.16	11.11	0.74	20.83	0.76
Sporobolus cryptandrus	Native			1.39	0.06	6.94	0.25
tragopogon dubius	Intro					1.39	0.03
Tyhpa sp.	Native					1.39	0.03
Vulpia octoflora	Native	8.33	0.14	8.33	0.32	18.06	0.95