# SEED POOL DYNAMICS OF A GREAT BASIN SAGEBRUSH COMMUNITY IN THE CONTEXT OF RESTORATION

by

Kristen M. Pekas

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

of

MASTER OF SCIENCE

in

Ecology

Approved:

| | |
|---|---|
| Eugene W. Schupp<br>Major Professor | Peter B. Adler<br>Committee Member |
| Edward W. Evans<br>Committee Member | Byron R. Burnham<br>Dean of Graduate Studies |

UTAH STATE UNIVERSITY
Logan, Utah

2010

ABSTRACT

Seed Pool Dynamics of a Great Basin Sagebrush Community in the Context of Restoration

by

Kristen M. Pekas, Master of Science

Utah State University, 2010

Major Professor: Eugene W. Schupp
Department: Wildland Resources

Restoration of Great Basin sagebrush communities is often attempted without understanding the potential impacts of either restoration treatments on the seed pool or the seed pool on restoration efforts. In addition, few studies have examined seed pools of the Great Basin and the role of vegetation in structuring seed pool communities. I evaluated soil seed pool dynamics of a Great Basin sagebrush community in a restoration context.

In Chapter 1, I determined the relationship between the compositions of the seed pool and aboveground vegetation and the effect of shrubs (microhabitat effects) and perennial bunchgrass cover (community phase effects) on the seed pool community composition, seed density, and seed pool species richness. To evaluate the relationship between the two communities and the effects of microhabitat and community phase, the aboveground vegetation and the soil seed pools of different community phases and microhabitats were sampled prior to restoration. Similarity and distance metrics and non-metric multidimensional scaling (NMDS) were used to asses the relationship between the two communities. NMDS and analysis of variance (ANOVA) were used to determine the effects of aboveground community phase and microhabitat on the seed pool community. Results suggest that the relationship between the aboveground vegetation and seed pool community compositions varied according to the organizational level used for vegetation. In addition, microhabitat and community phase did influence seed density but not species richness.

I sought to evaluate the effects of restoration treatments on the seed pool community in Chapter 3. To assess the impacts of restoration treatments, the seed pool community before and after treatments was censused. NMDS of the seed pool community and ANOVA on dominant species of the seed pool were performed to determine treatment effects. Results from this research suggest seed pool community composition and seed density varied temporally and spatially. Tebuthiuron and Plateau may have altered community composition whereas prescribed burn affected seed density. This research is applicable for land managers by helping determine the most effective restoration treatment, which will include effects on the seed pool.

(127 pages)

ACKNOWLEDGMENTS

I would like to extend thanks to my advisor, Gene Schupp, for his support and guidance throughout my graduate studies. Thanks to my committee members, Peter Adler and Ted Evans, for their advice and encouragement. I am very grateful for greenhouse and field assistance from fellow graduate students and undergraduate technicians, especially Jeff Burnham, Dara Scherpenisse, Casey Addy, and Dan Zamecnik. I greatly appreciate Susan Durham for her time and insight on statistical issues. Thanks to Leila Shultz, Mary Barkworth, and Michael Piep for helping with plant identification. I would also like to acknowledge my friends and family, especially Char Pekas, John Pekas, Alyssa Pekas, Andy Hill, and Joanna Hsu, who have inspired and reassured my decision to pursue a graduate degree and provided the necessary distractions to keep me sane. This is Contribution Number 41 of the Sagebrush Steppe Treatment Evaluation Project (SageSTEP), funded by the U.S. Joint Fire Science Program. Financial support was also provided by the Utah Agricultural Experiment Station (UAES), and the Utah State University Ecology Center.

Kristen M. Pekas

CONTENTS

# LIST OF TABLES

Table Page

# LIST OF FIGURES

Figure Page

Figure Page

# CHAPTER 1

# INTRODUCTION

Great Basin sagebrush communities are threatened by the invasion of cheatgrass, an exotic, annual grass that was introduced to the U.S. from Eurasia in the late 1800s and was recognized in the Intermountain West by 1900 (Mack and Pyke, 1983; Young and Blank, 1995). Following wildfire, cheatgrass has a competitive advantage over native species; cheatgrass germinates earlier and grows faster, depleting the resources that are available after fire (Melgoza and Nowak, 1991). Cheatgrass densities increase and by early to mid-summer the grass desiccates providing an abundant supply of fine fuels required to spread fires (Knapp, 1996). As a result, the fire frequency increases, creating more disturbed landscapes that cheatgrass can invade (Young and Blank, 1995). Native grasses are not adapted to this increased fire frequency and can not compete with cheatgrass (Knapp, 1996; Brooks and Pyke, 2001).

Wildfires are not exactly rare in the Great Basin, historically occurring every 30 to 100 years (Wright and Bailey, 1982; Brooks and Pyke, 2001). However, in some areas of the Great Basin fire frequency has now increased to 5 year intervals and has become too common for many natives to survive or reestablish (Whisenant, 1990; Knapp, 1996; Brooks and Pyke, 2001). Even though natives usually struggle to survive or reestablish after fire when cheatgrass is present on a site (Knapp, 1996), fire, in addition to other forms of disturbance is used in restoration. Disturbances may activate the seed pool of some desirable species (Bakker et al., 1996a). The seed pool, or seed bank, is the collection of all viable seeds in the soil. Restoration treatments such as fire, herbicide and mowing reduce shrub abundance making resources more available. Therefore, the seed pool may be an important contributor to the recovery of vegetation following restoration treatments, such as serving as a source of new propagules (Nishihiro et al., 2006).

Seed pools of the Great Basin are poorly understood as is their contribution to the aboveground vegetation, but numerous studies have shown that these seed pools vary both spatially and temporally (Thompson and Grime, 1979; Coffin and Lauenroth, 1989; Kemp, 1989). Great Basin seed pools consist of fewer annuals and more perennials than do hot desert seed pools (Kemp, 1989; Guo et al., 1999). Communities dominated by annual species have a higher aboveground-belowground similarity than communities dominated by perennial species (Thompson and Grime, 1979; Ungar and Woodell, 1993; Milberg 1995; Bakker et al., 1996b; Osem et al., 2006). A comparison of aboveground-belowground similarity among vegetation types shows that grasslands, including desert grasslands, have higher similarity than forest and wetland communities (Hopfensperger, 2007).

The aboveground vegetation can also influence the distribution of seeds. The distribution of seeds within desert seed pools is spatially variable, but seeds are generally more abundant under shrubs. Microhabitats beneath shrubs tend to have higher seed densities than shrub interspaces due to seeds settling close to the mother plant (Nelson and Chew, 1977; Guo et al., 1998; Marone et al., 2004; Shaukat and Siddiqui, 2004). Shrubs can decrease wind velocity which traps seeds beneath shrubs (Bullock and Moy, 2004). Litter that has accumulated beneath shrubs can also capture seeds that are being redistributed from interspaces (Chambers and MacMahon, 1994).

Research examining the effects of restoration treatments on the seed pool is lacking, though restoration can potentially alter the seed pool. For example, wildfire can reduce seed densities (Hassen and West, 1986), but the effects of prescribed burn on the seed pool are not well documented. The seed pool will be evaluated within the framework of SageSTEP (Sagebrush Treatment Evaluation Project), a regional scale restoration and fuels reduction experiment evaluating the effectiveness of various treatments (prescribed burn, mowing, and herbicide). The major goal of this project is to determine community thresholds between healthy and unhealthy sagebrush communities within the Great Basin. Sites are located throughout the Great Basin, and plots within each site represent different restoration treatments. Subplots within each plot were chosen based on varying levels of native bunchgrass cover. High native bunchgrass cover (greater than 19 percent) subplots were considered phase 1 communities, intermediate native bunchgrass cover subplots were considered phase 2 communities, and low native bunchgrass cover (less than 10 percent) subplots were considered phase 3 communities. The three community phases allow for determining at which native bunch grass cover a community can restore itself versus requiring active, expensive restoration efforts, such as seeding. Supplemental seeding has varying degrees of success, and vegetation recovery from the seed pool may be as effective (Young et al., 1994; Eiswerth and Shonkwiler, 2006; Floyd et al., 2006; Robichaud et al., 2006; Jessop and Anderson, 2007).

The objective of this research was to evaluate soil seed pool dynamics of a Great Basin sagebrush community in a restoration context. I specifically examined the influences of the aboveground vegetation on the seed pool community and seed distributions. I also investigated the effects of restoration treatments on the seed pool as well as determined if the pre-treatment seed pool or aboveground vegetation is more similar to the vegetation following restoration.

Results from this research have both theoretical and applied implications. Theoretically, this research evaluates how factors aboveground influence the seed pool. Results are also applicable for land managers to help determine the most effective restoration treatment, which will include effects on the seed pool.

**References**

Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M., Thompson, K., 1996a. Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanics Neerlandica 45, 461-490.

Bakker, J.P., Bakker, E.S., Rosen, E., Verweij, G.L., Bekker, R.M., 1996b. Soil seed bank composition along a gradient from dry alvar grassland to Juniperus shrubland. Journal of Vegetation Science 7, 165-176.

Brooks, M.L., Pyke, D., 2001. Invasive plants and fire in the deserts of North America. In: Galley, K.E.M, Wilson, T.P. (Eds.), Proceedings of the Invasive Plant Workshop: The Role of Fire in the Control and Spread of Invasive Species. Tall Timbers Research Station, Tallahassee, Florida, USA, pp. 1-14.

Bullock, J. M., Moy, I.L., 2004. Plants as seed traps: inter-specific interference with dispersal. Acta Oecologica 25, 35-41.

Chambers, J.C., MacMahon, J.A., 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics 25, 263-292.

Coffin, D.P., Lauenroth, W.K., 1989. Spatial and temporal variation in the seed bank of a semiarid grassland. American Journal of Botany 76, 53-58.

Eiswerth, M.E., Shonkwiler, J.S., 2006. Examining post-wildfire reseeding on arid rangeland: A multivariate tobit modelling approach. Ecological Modelling 192, 286-298.

Floyd, M.L., Hanna, D., Romme, W.R., Crews, T.E., 2006. Predicting and mitigating weed invasion to restore natural post-fire succession in Mesa Verde National Park, Colorado, USA. International Journal of Wildland Fire 15, 247-259.

Guo, Q., Rundel, P.W., Goodall, D.W., 1998. Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications. Journal of Arid Environments 38, 465-478.

Guo, Q., Rundel, P.W., Goodall, D.W., 1999. Structure of desert seed banks: comparisons across four North American desert sites. Journal of Arid Environments 42, 1-14.

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

Hopfensperger, K.N., 2007. A review of similarity between seed bank and standing vegetation across ecosystems. Oikos 116, 1438-1448.

Jessop, B.D., Anderson, V.J., 2007. Cheatgrass invasion in salt desert shrublands: benefits of postfire reclamation. Rangeland Ecology & Management 60, 235-243.

Kemp, P.R., 1989. Seed banks and vegetation processes in deserts. In: Leck, M.A., Parker, V.T., Simpson, R.L. (Eds.), Ecology of Soil Seed Pools. Academic Press, New York, pp. 257-282.

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

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

Marone, L., Cueto, V.R., Milesi, F.A., Lopez de Casenave, J., 2004. Soil seed bank composition over desert microhabitats: patterns and plausible mechanisms. Canadian Journal of Botany 82, 1809-1816.

Melgoza, G., Nowak, R.S., 1991. Competition between cheatgrass and two native species after fire: implications from observations and measurements of root distribution. Journal of Range Management 44, 27-33.

Milberg, P., 1995. Soil seed bank after eighteen years of succession from grassland to forest. Oikos 72, 3-13.

Nishihiro, J., Nishihiro, M.A., Washitani, I., 2006. Restoration of wetland vegetation using soil seed banks: lessons from a project in Lake Kasumigaura, Japan. Landscape and Ecological Engineering 2, 171-176.

Nelson, J.F., Chew, R.M., 1977. Factors affecting seed reserves in the soil of a Mojave desert ecosystem, Rock Valley, Nye County, Nevada. American Midland Naturalist 97, 300-320.

Osem, Y., Perevolotsky, A., Kigel, J., 2006. Similarity between seed bank and vegetation in a semi-arid annual plant community: the role of productivity and grazing. Journal of Vegetation Science 17, 29-36.

Robichaud, P.R., Lillybridge, T.R., Wagenbrenner, J.W., 2006. Effects of postfire seeding and fertilizing on hillslope erosion in north-central Washington, USA.

Catena 67, 56-67.

Shaukat, S.S., Siddiqui, I.A., 2004. Spatial pattern analysis of seeds of an arable soil seed bank and its relationship with above-ground vegetation in an arid region. Journal of Arid Environments 57, 311-327.

Thompson, K., Grime, J.P., 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. The Journal of Ecology 67, 893-921.

Ungar, I.A., Woodell, S.R.J., 1993. The relationship between the seed bank and species composition of plant communities in two British salt marshes. Journal of Vegetation Science 4, 531-536.

Whisenant, S.G., 1990. Changing fire frequencies on Idaho's Snake River plains: Ecological and management implications. In: McArthur, E.D., Romney, E.M., Smith, S.D., Tueller, P.T. (Eds.), Symposium on Cheatgrass Invasion, Shrub Die-off, and Other Aspects of Shrub Biology and Management. USDA Forest Service General Technical Report INT-276, pp. 4–10.

Wright, H.A., Bailey, A.W., 1982. Fire Ecology. John Wiley & Sons, New York.

Young, J.A., Blank, R.R., 1995. Cheatgrass and wildfires in the Intermountain West. 1995 Symposium Proceedings. California Exotic Pest Plant Council.

Young, J.A., Blank, R.R., Longland, W.S., Palmquist, D.E., 1994. Seeding Indian ricegrass in an arid environment in the Great Basin. Journal of Range Management 47, 2-7.

# CHAPTER 2

# INFLUENCE OF ABOVEGROUND VEGETATION ON SEED POOL COMPOSITION AND DISTRIBUTION IN A GREAT BASIN SAGEBRUSH COMMUNITY

**Abstract**

The influence of aboveground vegetation on seed density, species richness, and seed pool community composition was studied to understand factors determining seed spatial patterns and seed pool species composition in a Great Basin sagebrush community. Specifically, the relationship between the seed pool and aboveground vegetation and the effect of microhabitat (shrub interspace or beneath shrub) and aboveground community phase (high or low perennial bunchgrass cover) on the seed pool were assessed. The seed pool and aboveground vegetation differed in their most dominant species which resulted in dissimilar species compositions as determined by Sørensen's similarity index and Bray-Curtis distance. In contrast, comparing the seed pool species composition to the aboveground vegetation structure (functional groups) using non-metric multidimensional scaling (NMDS) revealed that there was a correspondence between the two communities. Shrub seed densities were higher beneath shrubs. Communities with higher perennial bunchgrass cover aboveground (phase 1 communities) yielded higher seed densities than those communities with lower perennial bunchgrass cover (phase 3 communities). Microhabitat or community phase did not explain variation in species richness, but richness, as well as seed density, was spatially variable. Therefore, the aboveground vegetation did influence seed densities but not species richness, and the similarity between the seed pool and aboveground vegetation

varied depending on the aboveground organizational level used in comparisons.

## 1. Introduction

The majority of Great Basin species rely on seeds for propagation; however, seed pools of this desert are poorly understood (Kemp, 1989). Seed pools may help re-establish species that have become locally extinct aboveground. Evaluations of North American desert seed pools suggest that those of the Great Basin consist of fewer annual and more perennial species than do hot desert seed pools (Kemp, 1989; Guo et al., 1999). Although maximum seed densities are generally similar among the North American deserts, there are some areas of the Great Basin that appear to have very small seed pools (Hassan and West, 1986).

According to Jurado and Flores (2005), annual species are more likely than perennial species to form persistent seed pools because they tend to produce dormant seeds. This strategy allows the seeds to wait for the proper germination cues which may increase the chance of establishment and survival. However, a long-term seed pooling strategy may be difficult for annuals to achieve because of seed reductions caused by continuous germination and granivory (Kigel, 1995). Due to the nature of perennial species, seeds are less likely to be dormant, and therefore, seed pools tend to be transient. Species that form transient seed pools are at risk of becoming locally extinct, especially if seed input is limited (O'Connor, 1991). Seed inputs can be limited by a number of factors, such as invasive species which may cause native perennial species to produce fewer seeds and die prematurely if the density of the invader is high (Vilà and Gimeno, 2007).

The invasion of cheatgrass has altered the structure and composition of Great

Basin seed pools. Studies examining seed pools of degraded sagebrush communities have shown shifts to greater annual seed abundance with cheatgrass invasion (Young and Evans, 1975; Humphrey and Schupp, 2001). Even in systems that are not considered to be dominated by cheatgrass, introduced species can still account for 20 percent of the total number of seeds in the seed pool (Guo et al., 1999).

The relationship between the seed pool and aboveground vegetation is not well understood in Great Basin sagebrush communities. Plant communities dominated by perennial species usually have relatively low aboveground-belowground similarities, while annual-dominated communities tend to have a greater correspondence between aboveground vegetation and the seed pool (Thompson and Grime, 1979; Ungar and Woodell, 1993; Milberg, 1995; Bakker et al., 1996; Osem et al., 2006). Each year in an annual-dominated community the seedlings germinate from the available seed pool which reflects vegetation of the previous year (Osem et al., 2006).

When comparing the relationship between the seed pool and aboveground vegetation among forest, grassland, and wetland seed pools, grassland standing vegetation is most similar to the seed pools in terms of species composition (Hopfensperger, 2007). In grasslands, extreme environmental conditions may select for species that rely on persistent seed pools, resulting in similar above and belowground communities (Henderson et al., 1988). However, higher similarity between the seed pool and aboveground vegetation in desert grasslands is more likely due to limited dispersal and aggregated seed patterns surrounding parent plants (Shaukat and Siddiqui, 2004). In contrast, some studies have found a lack of correspondence between the seed pool and aboveground vegetation in desert grasslands which has been attributed to different dominant species in the aboveground and seed pool communities (Eriksson and Eriksson, 1997; Kalamees and Zobel, 1997). For example, the most dominant species in the seed pool may be overrepresented due to high production of small seeds (Eriksson and Eriksson, 1997).

The aboveground vegetation not only influences the community composition of the seed pool but also the distribution of the seeds. Although the distribution of seeds within desert seed pools is spatially variable, seeds are generally more abundant under shrub and tree canopies than in interspaces and exhibit an aggregated seed pattern due to seeds settling close to the mother plant (Nelson and Chew, 1977; Guo et al., 1998; Marone et al., 2004; Shaukat and Siddiqui, 2004). A study investigating spatial patterns of species richness found higher species richness at 2 m and 6 m from shrubs (the mid-point and furthest sampling point from shrubs; Feng-Rui, 2008). In pinyon-juniper woodlands, seed densities and species richness were highest in interspaces and the interface between interspaces and litter under trees (Koniak and Everett, 1983). Shrubs and trees affect the spatial distribution of seeds as they can act as a barrier which may alter wind dynamics and subsequent seed deposition patterns. (Guo et al., 1998; Feng-Rui, 2008). Seeds often accumulate beneath shrubs because they decrease wind velocity and physically trap seeds, leading to deposition close to shrubs (Bullock and Moy, 2004). Seeds can also be redistributed from interspaces to litter beneath shrubs by wind and water (phase II dispersal; Chambers and MacMahon, 1994).

This study explores the seed pool and the aboveground vegetation within a Great Basin plant community and how the aboveground vegetation influences the seed pool community composition and seed distributions. Specific goals were to determine the relationship between the compositions of the seed pool and the aboveground vegetation and the effect of shrubs (microhabitat effects) and perennial bunchgrass cover (community phase effects) on the seed pool community composition, seed density, and seed pool species richness.

## 2. Methods

### *2.1. Study site*

Soil seed pool samples were collected from the Onaqui Sagebrush/Cheatgrass SageSTEP research site in Tooele County, Utah, USA, about 40 km south of Tooele, UT (40°11'53"N 112°27'51"W). The Onaqui site is located on the eastern toeslope of the Onaqui mountains at an elevation of 1660-1700 meters. Onaqui has fine-loamy soils (SageSTEP, 2009). Characteristic vegetation of this site includes Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), shadscale saltbush (*Atriplex confertifolia*), yellow rabbitbrush (*Chrysothamnus viscidiflorus*), Sandberg bluegrass (*Poa secunda*), squirreltail (*Elymus elymoides*), Indian ricegrass (*Achnatherum hymenoides*), bluebunch wheatgrass (*Pseudoroegneria spicata*), basin wildrye (*Leymus cinereus*), and cheatgrass (*Bromus tectorum*).

Seed pool germination assays were conducted at the Utah State University Research Greenhouse Facility in Logan, UT.

### *2.2. Experimental design*

Soil seed pool samples were collected 14-17 and 22-24 August 2006 from three plots representing different experimental restoration treatments (control, prescribed burn, and tebuthiuron) within the Onaqui site. An additional Plateau treatment was applied to all plots as a split-plot factor. Samples were collected before treatments were implemented; thus, comparisons of results among treatments reflect spatial variation in seed pools in untreated sagebrush stands. In each plot, subplots with two levels of perennial bunchgrass cover were sampled. Community phases were chosen by dividing the cover of perennial bunchgrasses into 3 ranges. Subplots with greater than 19 percent perennial bunchgrass cover were considered phase 1 communities, those with 10-19 percent bunchgrass cover were considered phase 2, and those with less than 10 percent perennial bunchgrass cover were considered phase 3 communities. Only phase 1 and 3 communities were sampled in order to examine high and low native bunchgrass covers. Four phase 1 subplots and four phase 3 subplots that did not receive Plateau were sampled in the control (CO), prescribed burn (FI), and tebuthiuron (TE) plots, and four phase 1 subplots and four phase 3 subplots that did receive Plateau were sampled in the control plot for a total of 32 subplots. Although the set of the control subplots that did receive Plateau are not from a true plot, I refer to these subplots as the control-Plateau plot (CP).

Within each 0.1-ha (30 x 33 m) subplot, 4, 28-m transects were laid out so as to not interfere with vegetation surveys. Transects ran north-south and were located at 3, 10, 20, and 27 meters from the northwest corner of the subplot. A composite sample consisting of 5 subsamples from within a 25 x 25-cm frame was collected every 3 meters along each of the 4 transects for a total of 10 composite samples per transect and 40 per subplot. Collecting many small samples has been shown to increase the precision of estimates of seed numbers in the soil (Bigwood and Inouye, 1988). If necessary, sampling locations were shifted slightly in order to assure that all 5 subsamples were from the same microhabitat (see below). Subsamples measured 6.1 cm in diameter and were taken to a depth of 4 cm with PVC couplings. Litter and soil layers were collected together. Microhabitat (shrub interspace or beneath shrub) was recorded for each composite sample collected.

### *2.3. Vegetation surveys*

Aboveground vegetation surveys were conducted on transects located at 2, 7, 15, 23, and 28 meters from the northwest corner of each subplot. The line-point intercept method was used to measure the cover of each species present along each transect (Herrick et al., 2005). Species intercepted by the pin were recorded every half meter totaling 60 points per transect and 300 points per subplot. Vegetation surveys were conducted in summer 2006. Nomenclature for all plant species followed the USDA NRCS PLANTS Database (2009).

### *2.4. Evaluating the seed pool*

The germinable seed pool was evaluated by direct germination in a greenhouse following cold-moist stratification, which has been shown to be an efficient and reliable method for determining species presence in the germinable seed pool (Gross, 1990). Each composite sample was moistened to field capacity and kept in an unlighted refrigerator at 2°C. After 60 days of stratification, samples were removed from the refrigerator and spread over a 2-cm layer of sand in planting trays with drainage holes. Planting trays were divided into 3 25.4 X 16.9-cm compartments, each containing one soil sample. Spread out soil samples had a depth of ≈1.3 cm and a volume of 584.49 $cm^3$. Samples were kept moist, and seedlings were identified, counted, and removed as they emerged. Individuals that were not identified in the seedling stage were transplanted and grown until mature.

Due to the high volume of samples collected, not all seed pool samples were evaluated at the same time. Therefore, depending on the availability of greenhouse space, varying numbers of samples were randomly selected from each treatment combination for each germination assay. Eleven of the 40 samples from each treatment combination from the 2006 collection were germinated and evaluated for each of the first and second germination assay. Six samples from the 2006 collection from each treatment combination were germinated and evaluated for the third germination assay. Each germination assay lasted 150 days. Emergence was initially censused for 115 days, at which point emergence was noticeably reduced. Samples were then dried out for 14 days and mixed, after which watering was resumed and emergence was censused for an additional 21 days.

The first germination assay ran from mid-January to mid-June 2007. The second germination assay ran from mid-June to mid-November 2007, and the third germination assay ran from mid-January to mid-June 2008. It was important that the first and third germination assays ran during the same time of year so as to not confound microhabitat and community phase effects with potential seasonal germination effects.

*2.5. Statistical Analysis*

Sørensen's similarity index ($C_s$) and Bray-Curtis distance (*BC*) were calculated in R version 2.6.2 (R Development Core Team, 2008) to compare the seed community to the aboveground community. These two similarity/distance metrics compare two communities in different ways. Sørensen's similarity is based strictly on presence/absence: $C_s=2w/(2w+A+B)$ where *w* is the total number of species found in both communities, *A* is the number of species found aboveground, and *B* is the number of species found belowground. A $C_s$ of 0 represents completely dissimilar communities and $C_s$ of 1 represents identical communities at the level of presence/absence. Bray-Curtis distance incorporates information on relative abundance (or cover). This metric normalizes relative abundance for communities being compared by dividing the absolute differences by the summation:

$$BC = \sum_{i}^{n} | x_{ij} - x_{ik} | / \sum_{i}^{n} x_{ij} + x_{ik}$$

where $x_{ij}$ is the relative abundance of species *i* at community *j*, $x_{ik}$ is the relative abundance of species *i* at community *k*, and *n* is the total number of species. A *BC* of 0 represents most similar communities, and a *BC* of 1 represents most different communities. $C_s$ and *BC* were calculated for the entire site and for each plot using relative cover of the aboveground community and relative abundance of the germinable seed pool community to avoid differences in sampling scales.

To further compare the community composition of the germinable seed pool to that of the aboveground vegetation, data were ordinated by non-metric multidimensional scaling (NMDS) with a Bray-Curtis distance measure using the metaMDS function in the Vegan package in R version 2.6.2 (Oksanen et al., 2008; R Development Core Team, 2008). As with the similarity and distance metrics, relative cover of the aboveground community and relative abundance of the germinable seed pool community were used to avoid differences in sampling scales. Aboveground community structure variables based on functional groups (relative cover of annual forbs, annual grasses, perennial forbs, perennial grasses, *Poa secunda*, shrubs, and trees) were fitted and plotted onto the ordination solution using the envfit function in R and $P < 0.05$ to determine significance (R Development Core Team, 2008). NMDS on densities of germinable seed pool species was also used to compare beneath shrub (S) and shrub interspace (I) community compositions and to compare phase 1 and phase 3 community compositions.

To determine the number of dimensions for each NMDS, stress values were assessed. Stress is a measure of how much the distances in the reduced ordination space depart from the distances in the original p-dimensional space. High stress values indicate a possibility that sites are randomly being placed without any relation to the original distances. Therefore, ordinations with the lowest possible stress are desirable; values up to 20 are acceptable and can be interpreted ecologically (Clarke, 1993). Regardless of the number of dimensions chosen, all figures are shown in two dimensions because the third dimension did not seem to alter results upon inspection.

A mixed-model factorial ANOVA (analysis of variance) was performed to detect differences in total seed density and species richness (total number of species present) between microhabitat and community phase using the MIXED procedure in SAS version 9.1.3 (SAS Institute, 2003) and $P < 0.05$ to determine significance. Plot, microhabitat, and community phase were treated as fixed effects, and subplot was a random effect. The same model was then used to detect seed density differences within each of six functional groups: annual forb, annual grass, perennial forb, perennial grass, *Poa secunda*, and shrub. Functional groups were assigned based on different morphologies and root systems. *Poa secunda* was considered a different functional group than perennial grasses because *P. secunda* has a more shallow root system than other perennial grasses. One tree species (*Tamarix ramosissima*) was found in the germinable seed pool but were not analyzed as a functional group due to very low seed densities and species richness.

Total seed density and species richness across functional groups were square root transformed to meet the assumptions of normality and homogeneity of variance. Seed density within the perennial grass, perennial forb, and annual forb functional groups was square root transformed. Seed density within annual grass, *Poa secunda*, and shrub was log transformed. For significant main effects, least squared means were compared using Tukey's test. For significant interactions, least squared means comparisons between treatment combinations sharing at least one factor level were made using the False Discovery Rate to control for familywise error rate. Least squared means and standard errors were back-transformed for figures.

## 3. Results

### *3.1. Relationship between the germinable seed pool and aboveground vegetation*

A total of 46 species germinated from the seed pool, and 22 species were recorded aboveground (Table A.1; Table A.2). The germinable seed pool and aboveground vegetation were moderately different in terms of species presence at the site scale according to Sørensen's similarity index ($C_s$ = 0.395). Results were similar for all individual plots (CO $C_s$ = 0.375; FI $C_s$ = 0.426; TE $C_s$ = 0.471; CP $C_s$ = 0.326). When incorporating relative abundance, Bray-Curtis distance showed a similar trend where the germinable seed pool and aboveground vegetation were moderately dissimilar at the overall site level and the individual plot levels (Site *BC* = 0.640; CO *BC*=0. 0.622; FI *BC* = 0.596; TE *BC* = 0.618; CP *BC* = 0.712). Both metrics conclude the aboveground-germinable seed pool relationship was the most dissimilar in the CP plot. According to Sørensen's similarity index the aboveground-belowground communities were most similar in the TE plot. However, Bray-Curtis distance identified the FI plot as having the most similar aboveground-belowground communities.

The NMDS with two dimensions was an acceptable representation of the original germinable seed pool data (stress = 9.83). Four of the seven aboveground structure variables (functional groups) were significantly correlated with the germinable seed pool community, with correlations being especially strong for annual grasses and forbs, as expected (Table 2.1). All three annual grass species present in the germinable seed pool (*Bromus tectorum*, *Setaria verticillata*, and *Vulpia octoflora*) were positively correlated with the cover of the aboveground annual grass functional group (Fig. 2.1).

### *3.2. Effects of aboveground community phase and micohabitat on germinable seed pool community, seed densities, and species richness*

#### *3.2.1. Germinable seed pool community*

The NMDS plot constructed to compare microhabitats with three dimensions was an acceptable solution (stress=19.77). Interspace and beneath shrub communities did not display distinct community compositions as indicated by the lack of separation in the ordination plot between the two microhabitats (Fig. 2.2).

The NMDS comparing aboveground community phase required three dimensions to achieve an acceptable stress level of 17.76. There was no obvious separation in phase 1 and phase 3 community compositions (Fig. 2.3).

*3.2.2. Seed density*

ANOVA showed that seed density was significantly affected by aboveground community phase and the plot x microhabitat interaction (Table 2.2). Community phase 1 (higher perennial bunchgrass cover) had significantly higher total seed densities than community phase 3 (Fig. 2.4). The significant plot x microhabitat interaction is explained by a trend for interspaces to have greater densities in FI and TE plots but lower seed densities in the CO plot relative to shrubs (Fig. 2.5).

Perennial grass seed density was significantly affected by aboveground community phase (Table 2.3). Seed density was higher in phase 1 communities (higher perennial bunchgrass cover) than in phase 3 communities (Fig. 2.6). Annual grass seed density was significantly affected by plot (Table 2.3). Seed density in the CP plot was significantly higher than in the FI and TE plots, and seed densities in CP, CO, and FI were significantly higher than in TE (Fig. 2.7). Perennial forb seed density was significantly affected by the plot x microhabitat interaction (Table 2.3). Although no pairwise mean comparisons were statistically significant at the 0.05 probability level, there was a trend for the beneath shrub microhabitat to have greater seed densities in CO and CP but lower densities in FI and TE relative to interspaces (Fig. 2.8). Annual forb seed density was significantly affected by plot, phase, and the plot x microhabitat interaction (Table 2.3). Seed density was significantly higher in the TE than in the CO plot, while densities in the CP and FI plot were intermediate and did not differ from each other or from TE and CO seed densities (Fig. 2.9). Phase 1 communities (higher perennial bunchgrass cover) had significantly more annual forb seeds than phase 3 communities (Fig. 2.10). The significant plot x microhabitat interaction is explained by a trend for interspaces to have greater densities in FI and TE plots but lower seed densities in the CO plot relative to shrubs (Fig. 2.11). *Poa secunda* seed density was significantly affected by community phase, with phase 1 communities having significantly more seeds than phase 3 communities (Table 2.3; Fig. 2.12). Shrub seed density was significantly affected by microhabitat, with more seeds found beneath shrubs than in interspaces (Table 2.3; Fig. 2.13).

### *3.2.3. Species richness*

ANOVA showed that species richness of the germinable seed pool was significantly affected by the plot x microhabitat interaction and the plot x microhabitat x phase interaction (Table 2.2). There seems to be faintly variable patterns among plot and microhabitat, but most of the observed differences were insignificant and not interpreted readily (Fig. 2.14). Although no pairwise mean comparisons were statistically significant at the 0.05 probability level for the plot x microhabitat x phase interaction, this 3-way interaction is explained by a trend for the beneath shrub microhabitat to have higher species richness in CO, CP and FI plots of phase 3 communities and the CO plot of phase 1 communities and lower species richness in the CP plot of phase 1 communities and the TE plot of phase 3 communities relative to interspaces (Fig. 2.15).

## 4. Discussion

### *4.1. Relationship between the germinable seed pool and aboveground vegetation*

Desert grassland germinable seed pool communities may correspond to the aboveground vegetation as a result of limited seed dispersal and clustered seeds surrounding parent plants (Shaukat and Siddiqui, 2004). Results from the similarity and distance metrics did not strongly support these findings. Sørensen's similarity index and Bray-Curtis distance indicate that the germinable seed pool and aboveground community compositions were moderately different at the overall site and individual plot levels. The germinable seed pool and aboveground vegetation only shared 12 of 56 species found. However, for species present in both the germinable seed pool and aboveground vegetation, relative abundances were similar except that *Alyssum desertorum* and *Ceratocephala testiculata* were vastly over-represented in the germinable seed pool and *Artemisia tridentata* aboveground (Table A.1; Table A.2).

Eriksson and Eriksson (1997) have attributed the lack of correspondence between the germinable seed pool and aboveground vegetation to the fact that the dominant species often differ between the two communities. *A. tridentata* was the most dominant species aboveground. Young and Evans (1989) found that no *A. tridentata* seeds germinated from the germinable seed pool when collected before fall when *A. tridentata* seeds mature. In contrast, in the present study *A. tridentata* seeds were found in germinable seed pool samples collected in August, before seed dispersal, but at very low densities. Therefore, *A. tridentata* was overrepresented aboveground, which decreased the similarity between the germinable seed pool and aboveground vegetation. Conversely, *A. desertorum* and *C. testiculata* were abundant in the germinable seed pool but had very low cover aboveground. Species such as *A. desertorum* and *C. testiculata* that produce small abundant seeds generally may be overrepresented in the germinable seed pool (Eriksson and Eriksson, 1997). Also, *A. desertorum* and *C. testiculata* are small annual species which can produce large germinable seed pools and use seed banking as a bet hedging germination strategy (Philippi and Seger, 1989; Gutterman, 2002; Mistro et al., 2005). *A. desertorum* and *C. testiculata* may be maintaining dormant seeds to spread the risk of germination over time allowing seeds to wait for more favorable germination conditions which may increase the chance of establishment and survival. Another possibility for the overrepresentation of *A. desertorum* and *C. testiculata* belowground is the simple fact that these plants were not frequently encountered aboveground during data collection using the line-point intercept method due to their relatively small size (the probability of a pin hitting a smaller plant is lower than the probability of hitting a larger plant) and due to primarily actively growing much earlier in the season than when the aboveground sampling occurred.

In contrast to the similarity and distance metrics, the NMDS suggested that the germinable seed pool and aboveground vegetation were in fact moderately similar. One reason for this disagreement is the organizational level of the aboveground vegetation used in comparisons. For the similarity and distance metrics, relative abundances were compared at the species-level. However, the NMDS compared the relative abundance of each species in the germinable seed pool to the relative abundance of aboveground vegetation functional groups, i.e. aboveground vegetation structure. Therefore, at the species-level the germinable seed pool and aboveground vegetation communities were not very similar, but similarities were considerably greater when comparing germinable seed pool species abundances to the aboveground functional groups. There were a number of species that were only present above or belowground which decreased similarity between the germinable seed pool and aboveground vegetation. However, the differences between each species present in either community were no longer detected when using functional group as the aboveground organizational level of comparison.

The germinable seed pool and aboveground vegetation tend to be more similar in annual communities than in perennial communities (Thompson and Grime, 1979; Ungar and Woodell, 1993; Milberg, 1995; Bakker et al., 1996; Osem et al., 2006). NMDS results from the present study did show a significant correlation between the annual germinable seed pool and aboveground structure, but also a significant correlation between the perennial germinable seed pool and aboveground structure. The unexpected correspondence between the perennial germinable seed pool species and aboveground vegetation structure could simply be a function of the comparison between species and functional groups. As displayed by the similarity and distance metrics, the similarity between germinable seed pool and aboveground species compositions was low. However, comparing germinable seed pool species composition to aboveground structure yielded the opposite result. Although the germinable seed pool and aboveground vegetation were not similar at the species level, the germinable seed pool species composition was similar to the aboveground vegetation functional group categories. For example, *Cirsium* spp. is present in the germinable seed pool but not aboveground yet *Cirsium* spp. is positively correlated with the aboveground perennial forb functional group.

### *4.2. Aboveground community phase and microhabitat effects*

Phase 1 communities (higher perennial bunchgrass cover) had higher total seed density and annual forb seed density than did phase 3 communities (lower perennial bunchgrass cover). Subplots with higher perennial bunchgrass cover may have simply had more plants producing seed, especially annual forbs, which were incorporated into the germinable seed pool. Perennial grass and *P. secunda* seed densities were also higher in phase 1 communities, which was not u considering that phase 1 communities were defined by higher perennial bunchgrass cover.

Shrub was the only functional group significantly affected by microhabitat alone. The beneath shrub microhabitat contained more seeds than interspaces, which is not unusual. Seed densities, especially seeds of shrubs, tend to be higher under shrub canopies due to seeds falling beneath and adjacent to the parent plant (phase I dispersal; Shaukat and Siddiqui, 2004). The patterns between microhabitats for total seed density, perennial forb, and annual forb seed densities varied by plot. Beneath shrub microhabitats in the CO plot (and CP plot for perennial forb seed density) had greater seed densities relative to interspaces, which was the same trend found with shrub seeds. Shrubs might have decreased wind velocity, physically trapping seeds beneath shrubs (Bullock and Moy, 2004). Another explanation for higher beneath shrub densities is seeds could have been transported from interspaces and trapped in the litter beneath shrubs (phase II dispersal; Chambers and MacMahon, 1994). However, the TE and FI plots had greater seed densities in interspaces than beneath shrubs. In TE and FI plots, germination conditions may be more favorable beneath shrubs thereby depleting the soil germinable seed pool. Studies have shown that shrubs may ameliorate the microclimatic conditions by providing shade thereby decreasing soil temperatures and increasing soil moisture by drawing up water from the deep soil profile (Moro et al., 1997; Caldwell et al., 1998). Both of these factors may increase germination and depletion of the germinable seed pool. The fact that plot strongly affected which microhabitat had higher densities suggests that at best there is only a weak microhabitat effect, contrary to what has been found in a number of other studies (Nelson and Chew, 1977; Guo et al., 1998; Marone et al., 2004; Shaukat and Siddiqui, 2004). In fact, the evidence from microhabitats as well as from the overall plot differences suggests strong spatial variability in seed density.

There are few if any studies investigating the spatial pattern of species richness of seeds in desert shrub communities, but Feng-Rui (2008) reported species richness was highest 2 m and 6 m from shrubs. Results from the present research can neither corroborate nor contradict this finding. The significance of the plot x microhabitat x phase interaction without any significant main effects suggests that species richness is spatially variable; while the causes of this variability cannot be determined in this study they do not appear to include microhabitat or phase. In an attempt to explain species richness patterns, I performed a regression analysis in R version 2.6.2 (R Development Core Team, 2008) to determine if species richness varies as a function of seed density; that is, a simple sampling effect. Species richness and seed density were square root transformed. With richness as the response and density as the predictor variable, a linear relationship with density only explains about 0.97 percent ($R^2 = 0.009707$) of the variation in species richness. In addition, the predictor variable (seed density) was not significant ($P = 0.439$), and the regression coefficient for density was extremely low (0.008662). Therefore, richness does not necessarily accumulate with increasing seed density, and species richness was not an artifact of varying seed densities.

The invasive grass *Bromus tectorum* was the most dominant annual grass on site. However, in contrast to expectations, annual grass seed density was not affected by aboveground community phase or microhabitat, but was affected by plot, which demonstrates spatial variability in annual grass and *B. tectorum* seed density at the plot scale. Questions about the effect of restoration treatments on *B. tectorum* are addressed in Chapter 3.

While aboveground community phase and microhabitat did affect seed density, germinable seed pool species composition was not strongly affected by these two factors, or at least NMDS did not detect such effects. Due to variability in seed dispersal patterns among species, distinct germinable seed pool communities as a function of microhabitat and aboveground community phase may not exist.

In conclusion, seed densities were affected by aboveground community phase and microhabitat while species richness and germinable seed pool community composition were not. Both seed density and species richness varied spatially. Species compositions were dissimilar when the germinable seed pool and aboveground vegetation were compared at the species level but were similar when the germinable seed pool was compared to the aboveground vegetation functional groups.

**References**

Bakker, J.P., Bakker, E.S., Rosen, E., Verweij, G.L., Bekker, R.M., 1996. Soil seed bank composition along a gradient from dry alvar grassland to Juniperus shrubland. Journal of Vegetation Science 7, 165-176.

Bigwood, D.W., Inouye, D.W., 1988. Spatial pattern analysis of seed banks: an improved method and optimized sampling. Ecology 69, 497-507.

Bullock, J. M., Moy, I.L., 2004. Plants as seed traps: inter-specific interference with dispersal. Acta Oecologica 25, 35-41.

Caldwell, M.M., Dawson, T.E., Richards, J.H., 1998. Hydraulic lift: consequences of water effluxed from the roots of plants. Oecologia 113, 151-161.

Chambers, J.C., MacMahon, J.A., 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics 25, 263-292.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Austral Ecology 18, 117-143.

Eriksson, Å., Eriksson, O., 1997. Seedling recruitment in semi-natural pastures: the effects of disturbance, seed size, phenology and seed bank. Nordic Journal of Botany 17, 469-482.

Feng-Rui, L., 2008. Presence of shrubs influences the spatial pattern of soil seed banks in desert herbaceous vegetation. Journal of Vegetation Science 19, 537-548.

Gross, K.L., 1990. A comparison of methods for estimating seed numbers in the soil. The Journal of Ecology 78, 1079-1093.

Guo, Q., Rundel, P.W., Goodall, D.W., 1998. Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications. Journal of Arid Environments 38, 465-478.

Guo, Q., Rundel, P.W., Goodall, D.W., 1999. Structure of desert seed banks: comparisons across four North American desert sites. Journal of Arid Environments 42, 1-14.

Gutterman, Y. 2002. Survival Strategies of Annual Desert Plants. Adaptations of Desert Organisms. Springer-Verlag, Berlin, Heidelberg, Germany.

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

Henderson, C.B., Petersen, K.E., Redak, R.A., 1988. Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. The Journal of Ecology 76, 717-728.

Herrick, J.E., Van Zee, J.W., Havstad, K.M., Burkett, L.M., Whitford, W.G., 2005. Monitoring Manual for Grassland, Shrubland and Savanna Ecosystems. USDA-ARS Jornada Experimental Range. The University of Arizona Press, Tucson, Arizona, USA.

Hopfensperger, K.N., 2007. A review of similarity between seed bank and standing vegetation across ecosystems. Oikos 116, 1438-1448.

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

Jurado, E., and Flores, J., 2005. Is seed dormancy under environmental control or bound to plant traits? Journal of Vegetation Science 16, 559-564.

Kalamees, R., Zobel, M., 1997. The seed bank in an estonian calcareous grassland: comparison of different successional stages. Folia Geobotanica 32, 1-14.

Kemp, P.R., 1989. Seed banks and vegetation processes in deserts. In: Leck, M.A., Parker V.T., Simpson, R.L. (Eds.), Ecology of Soil Seed Pools. Academic Press, New York, pp. 257-282.

Kigel, J., 1995. Seed germination in arid and semiarid regions. In: Kigel, J., Galili, G. (Eds.), Seed Development and Germination. Marcel Dekker, New York, pp. 645-699.

Koniak, S., and Everett, R.L., 1982. Seed reserves in soils of successional stages of pinyon woodlands. American Midland Naturalist 108, 295-303.

Marone, L., Cueto, V.R., Milesi, F.A., Lopez de Casenave, J., 2004. Soil seed bank composition over desert microhabitats: patterns and plausible mechanisms. Canadian Journal of Botany 82, 1809-1816.

Milberg, P., 1995. Soil seed bank after eighteen years of succession from grassland to forest. Oikos 72, 3-13.

Mistro, D.C., Rodrigues, L.A.D., Schmid, A.B., 2005. A mathematical model for dispersal of an annual plant population with a seed bank. Ecological Modelling 188, 52-61.

Moro, M.J., Pugnaire, F.I., Haase, P., Puigdefabregas, J., 1997. Effect of the canopy of *Retama sphaerocarpa* on its understorey in a semiarid environment. Functional Ecology 11, 425-431.

Nelson, J.F., Chew, R.M., 1977. Factors affecting seed reserves in the soil of a Mojave desert ecosystem, Rock Valley, Nye County, Nevada. American Midland Naturalist 97, 300-320.

O'Connor, T.G., 1991. Local extinction in perennial grasslands: a life-history approach. The American Naturalist 137, 753-773.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Stevens, M.H.H. 2008. Vegan: Community Ecology Package. R package version 1.13-1. Available from: http://vegan.r-forge.r-project.org/.

Osem, Y., Perevolotsky, A., Kigel, J., 2006. Similarity between seed bank and vegetation in a semi-arid annual plant community: the role of productivity and grazing. Journal of Vegetation Science 17, 29-36.

Philippi, T., Seger, J., 1989. Hedging one's evolutionary bets, revisited. Trends in Ecology & Evolution 4, 41-44.

R Development Core Team, 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.R-project.org.

SageSTEP [Sagebrush Treatment Evaluation Project], 2009. Study site locations: Onaqui sites. Available from: http://www.sagestep.org/locations/onaqui.html.

SAS Institute. 2003. SAS System for Microsoft Windows. SAS Institute, Inc., Cary, North Carolina, USA.

Shaukat, S.S., Siddiqui, I.A., 2004. Spatial pattern analysis of seeds of an arable soil seed bank and its relationship with above-ground vegetation in an arid region. Journal of Arid Environments 57, 311-327.

Thompson, K., Grime, J.P., 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. The Journal of Ecology 67, 893-921.

Ungar, I.A., Woodell, S.R.J., 1993. The relationship between the seed bank and species composition of plant communities in two British salt marshes. Journal of Vegetation Science 4, 531-536.

USDA, NRCS, 2009. The PLANTS Database. National Plant Data Center, Baton Rouge, Louisiana, USA. Available from: http://plants.usda.gov.

Vilà, M., Gimeno, I., 2007. Does invasion by an alien plant species affect the soil seed bank? Journal of Vegetation Science 18, 423-430.

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

Young, J.A., Evans, R.A., 1989. Dispersal and germination of big sagebrush (*Artemisia tridentata*) seeds. Weed Science 37, 201-206.

**Table 2.1** Squared correlation coefficients ($R^2$) and *P*-values of aboveground vegetation structure variables with the seed pool community as determined by non-metric multidimensional scaling (NMDS). Significant *P*-values at the 0.05 level are indicated in bold.

| Aboveground vegetation variable | $R^2$ | *P* |
|---|---|---|
| Perennial grass | 0.2777 | **0.007** |
| Perennial forb | 0.2779 | **0.012** |
| Annual grass | 0.5559 | **<0.001** |
| Annual forb | 0.6844 | **<0.001** |
| *Poa secunda* | 0.0336 | 0.615 |
| Shrub | 0.1257 | 0.130 |
| Tree | 0.1840 | 0.056 |

**Table 2.2** *P*-values for fixed effects of total seed density and species richness. Significant *P*-values at the 0.05 level are indicated in bold.

| Fixed effect | Total seed density | Total species richness |
|---|---|---|
| plot | 0.1222 | 0.0960 |
| phase | **0.0052** | 0.7316 |
| plot*phase | 0.4492 | 0.9826 |
| microhabitat | 0.1161 | 0.6389 |
| plot*microhabitat | **0.0411** | **0.0506** |
| phase*microhabitat | 0.2886 | 0.0718 |
| treatment*phase*microhabitat | 0.1936 | **0.0225** |

**Table 2.3** *P*-values for fixed effects of seed density and species richness within each functional group (AF = annual forb, AG = annual grass, PF = perennial forb, PG = perennial grass, POA = *Poa secunda*, SH = shrub, T = tree). Significant *P*-values at the 0.05 level are indicated in bold.

| Fixed effect | PG | AG | PF | AF | POSE | SH |
|---|---|---|---|---|---|---|
| plot | 0.1797 | **<0.0001** | 0.2042 | **0.0233** | 0.1397 | 0.6478 |
| phase | **0.0125** | 0.1956 | 0.2085 | **0.0039** | **0.0317** | 0.1240 |
| plot*phase | 0.0963 | 0.2997 | 0.8293 | 0.4323 | 0.6312 | 0.9297 |
| microhabitat | 0.9656 | 0.2399 | 0.9700 | 0.0731 | 0.0774 | **0.0053** |
| plot*microhabitat | 0.8793 | 0.5973 | **0.0220** | **0.0221** | 0.5659 | 0.1063 |
| phase*microhabitat | 0.1987 | 0.7189 | 0.1471 | 0.3443 | 0.9007 | 0.8270 |
| plot*phase*microhabitat | 0.6178 | 0.5361 | 0.2123 | 0.4197 | 0.2637 | 0.4709 |

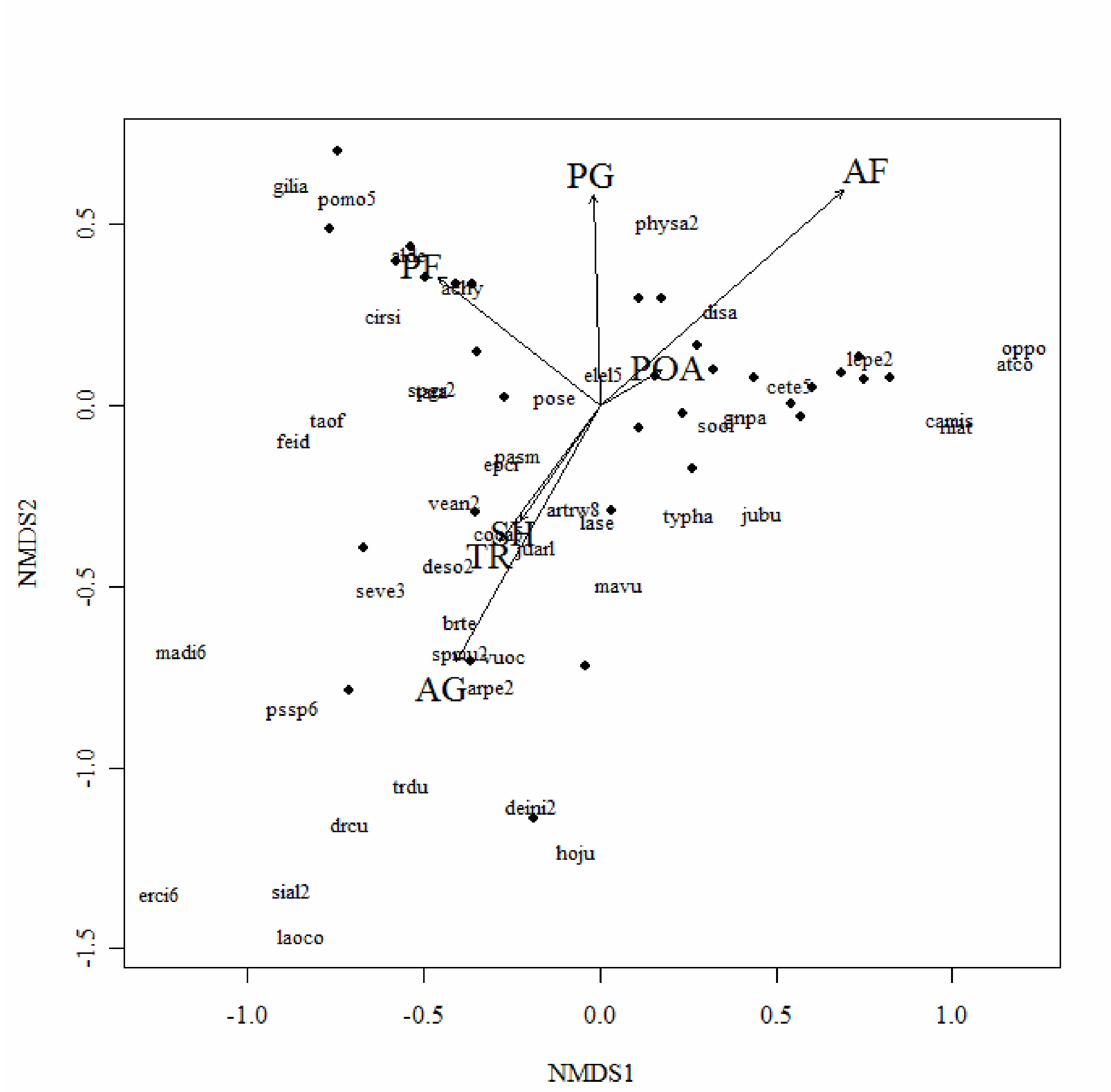


**Figure 2.1** Non-metric multidimensional scaling (NMDS) ordination plot of the germinable seed pool community. Points represent the subplot scores. Species scores are represented by species symbols (USDA, NRCS, 2009). Sold lines represent the fitted aboveground vegetation structure variables (AF = annual forb, AG = annual grass, PF = perennial forb, PG = perennial grass, POA = *Poa secunda*, SH = shrub, TR = tree).

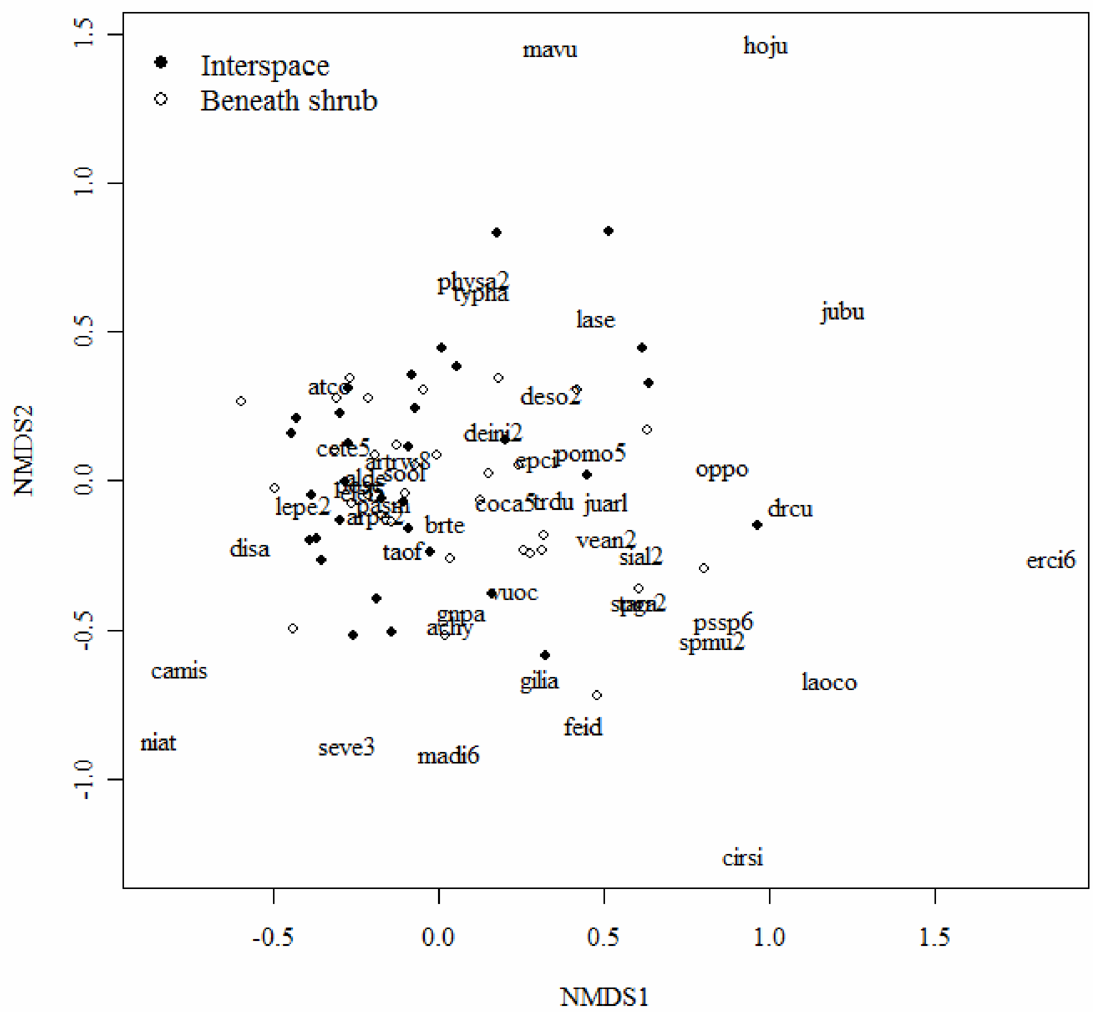


**Figure 2.2** Non-metric multidimensional scaling (NMDS) ordination plot comparing microhabitat. Diamonds represent the subplot scores which are categorized as either shrub interspace or beneath shrub communities. Species scores are represented by species symbols (USDA, NRCS, 2009).

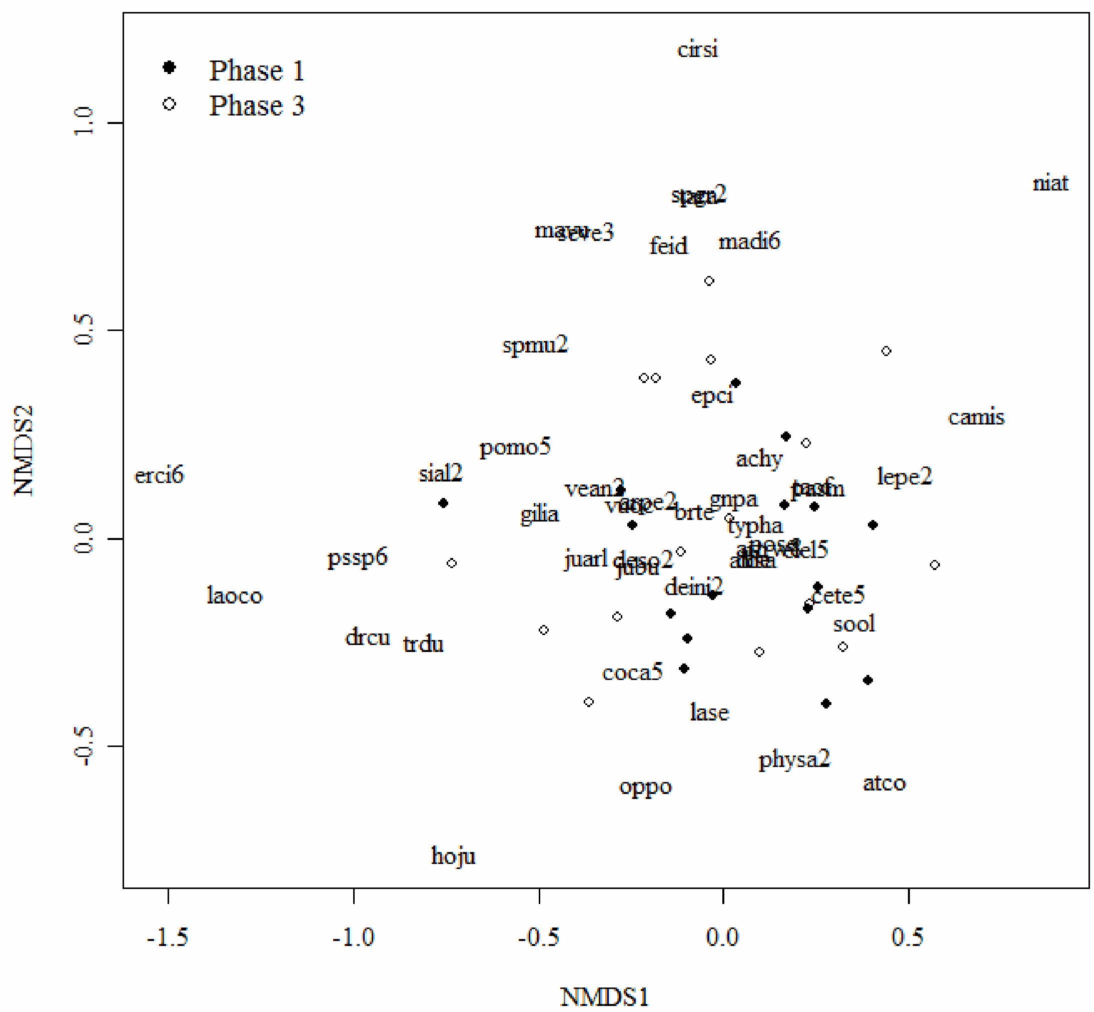


**Figure 2.3** Non-metric multidimensional scaling (NMDS) ordination plot comparing community phase. Diamonds represent the subplot scores which are categorized as either phase 1 or phase 3 communities. Species scores are represented by species symbols (USDA, NRCS, 2009).

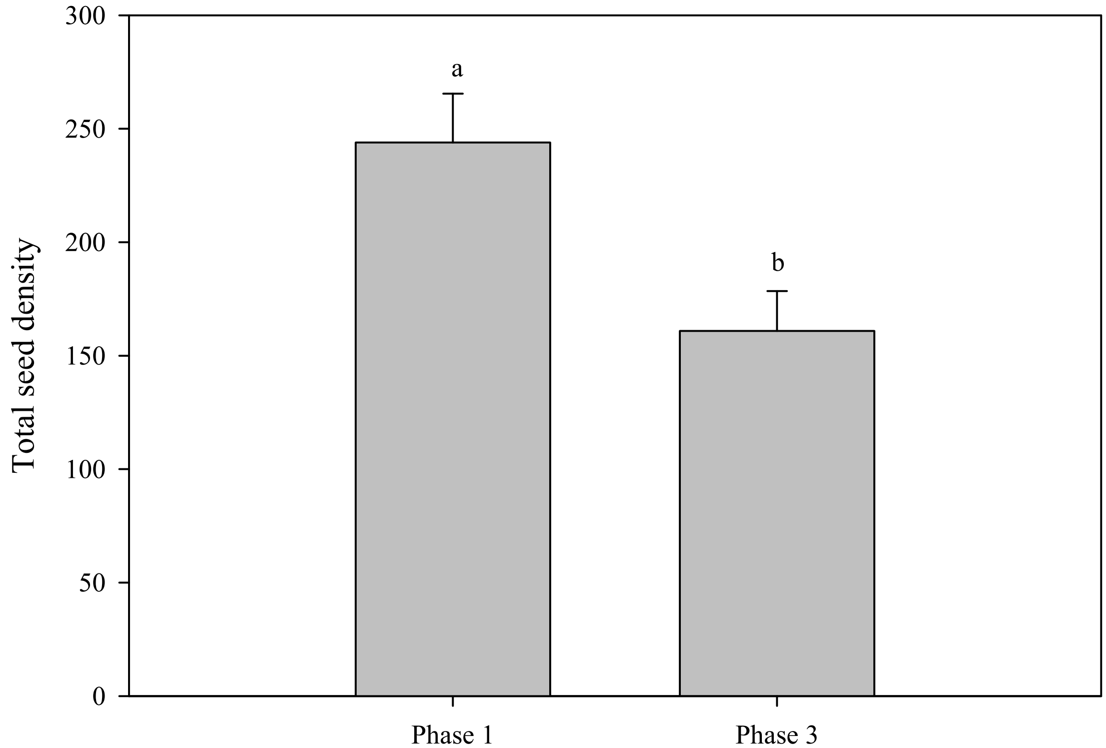


**Figure 2.4** Mean seed density across all plots (+ 1 SE) as affected by community phase. Different letters indicate significant differences ($P < 0.05$).

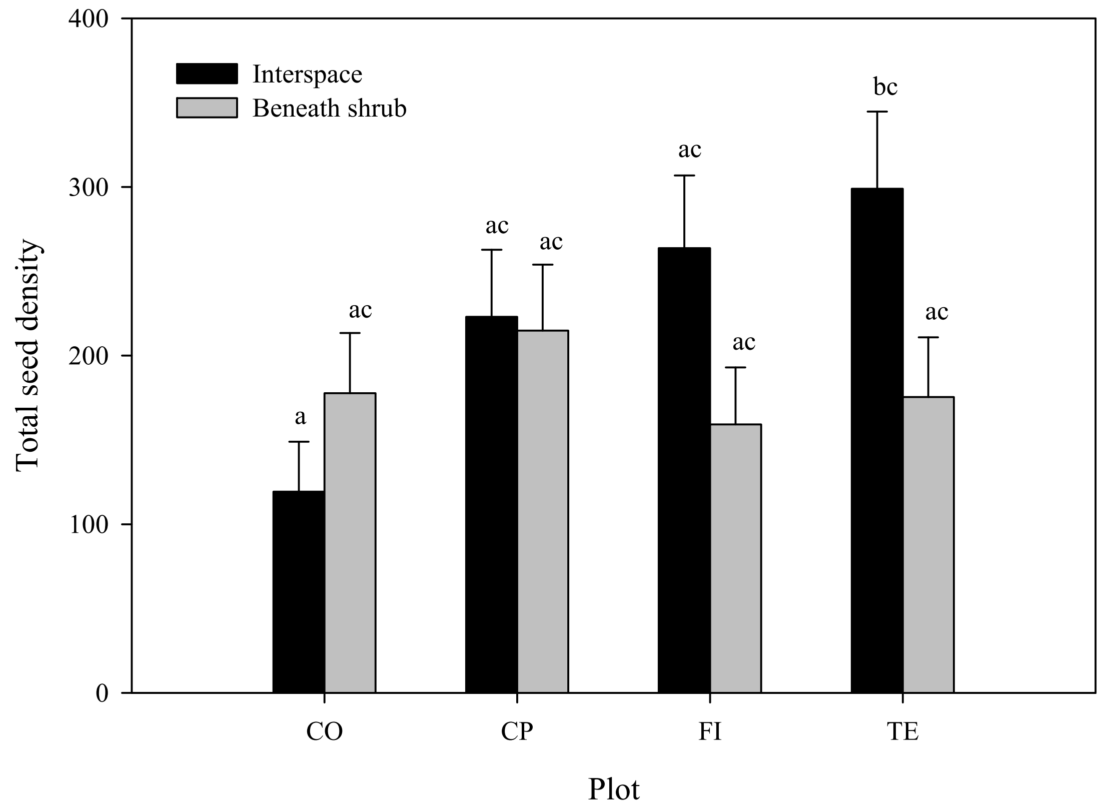


**Figure 2.5** Mean seed density across all plots (+ 1 SE) as affected by microhabitat and plot (CO = Control, CP = Control-Plateau, FI = Prescribed Burn, TE = Tebuthiuron). Different letters indicate significant differences for comparisons between treatment combinations sharing at least one factor level (*P* < 0.05).

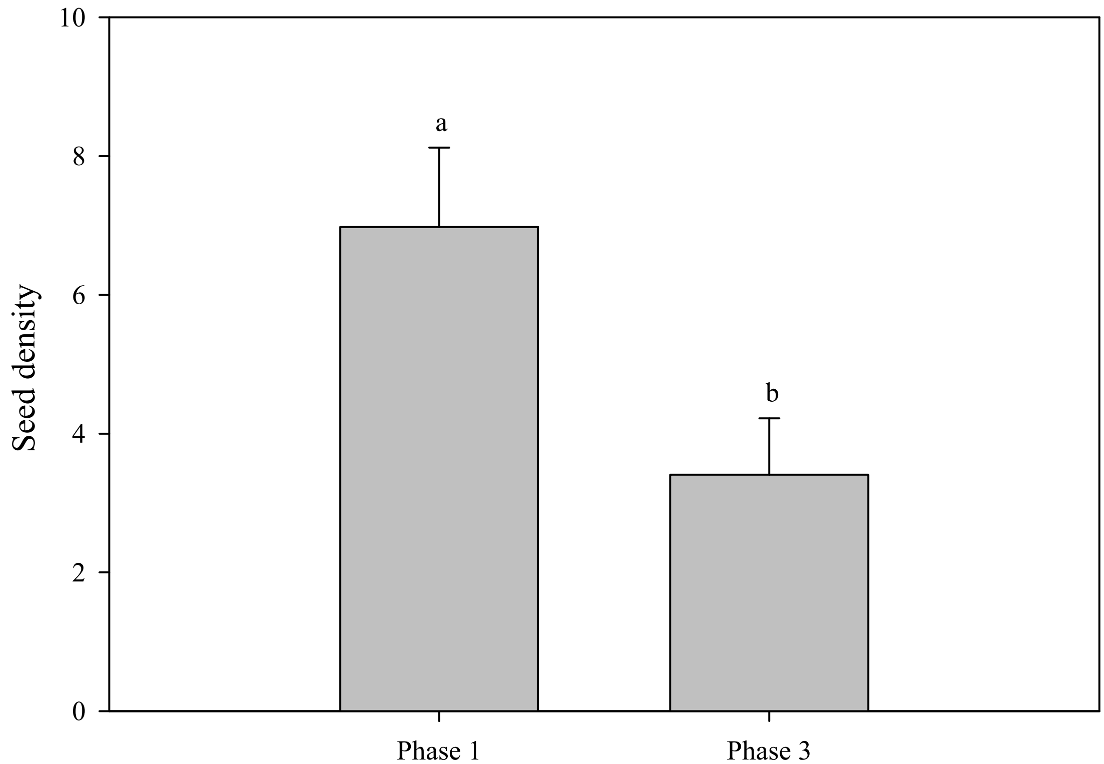


**Figure 2.6** Mean perennial grass seed density (+ 1 SE) as affected by community phase. Different letters indicate significant differences ($P < 0.05$).

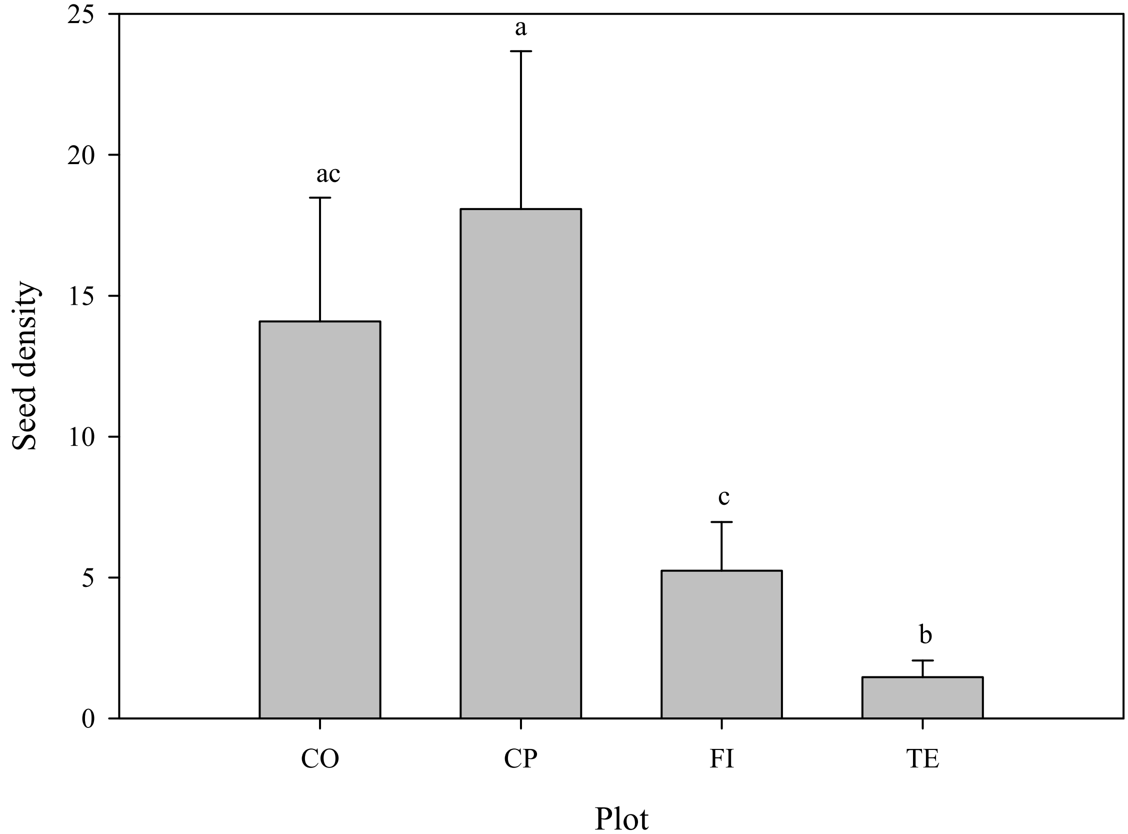


**Figure 2.7** Mean annual grass seed density (+ 1 SE) as affected by plot (CO = Control, CP = Control-Plateau, FI = Prescribed Burn, TE = Tebuthiuron). Different letters indicate significant differences ($P < 0.05$).

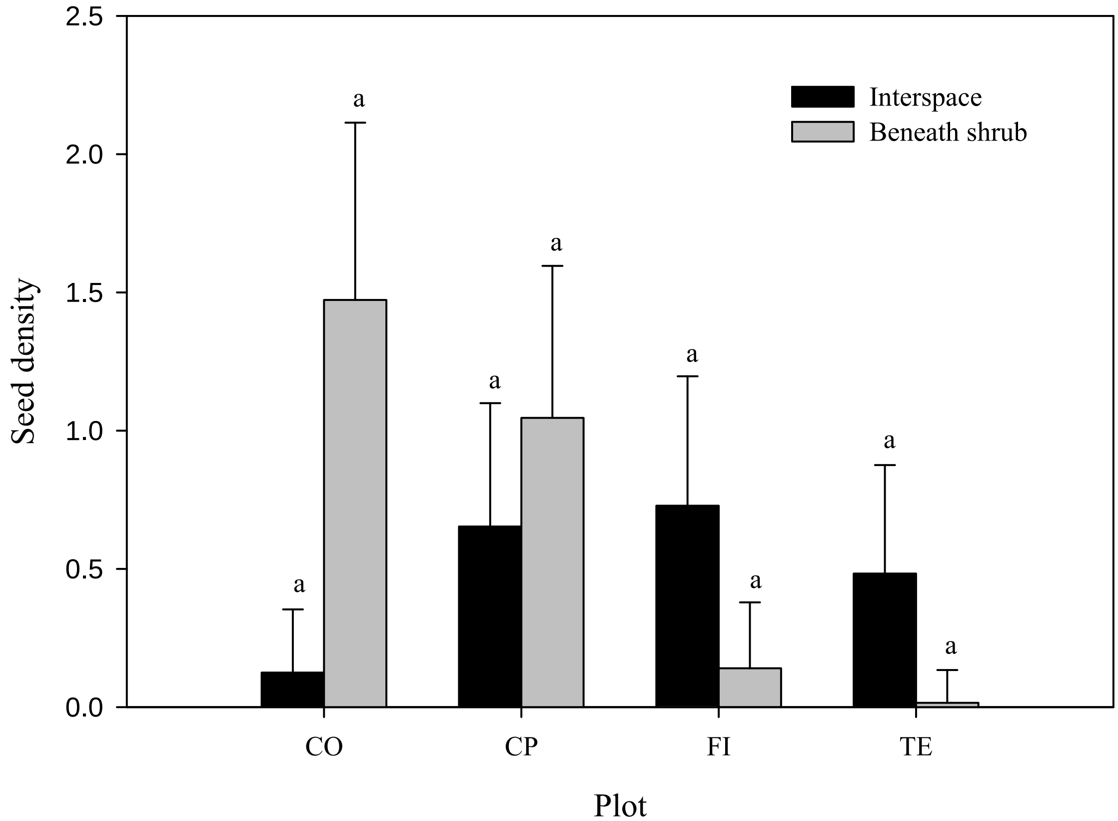


**Figure 2.8** Mean perennial forb seed density (+ 1 SE) as affected by microhabitat and plot (CO = Control, CP = Control-Plateau, FI = Prescribed Burn, TE = Tebuthiuron). Different letters indicate significant differences for comparisons between treatment combinations sharing at least one factor level ($P < 0.05$).

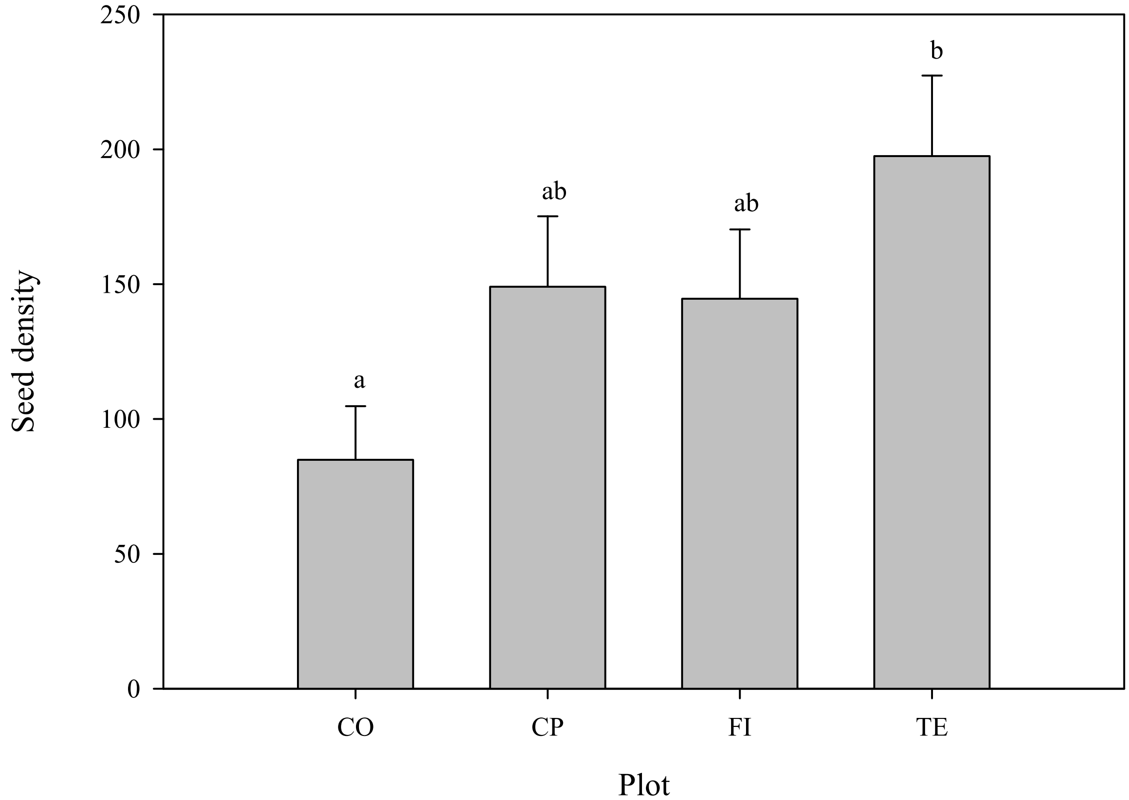


**Figure 2.9** Mean annual forb seed density (+ 1 SE) as affected by plot (CO = Control, CP = Control-Plateau, FI = Prescribed Burn, TE = Tebuthiuron). Different letters indicate significant differences (*P* < 0.05).

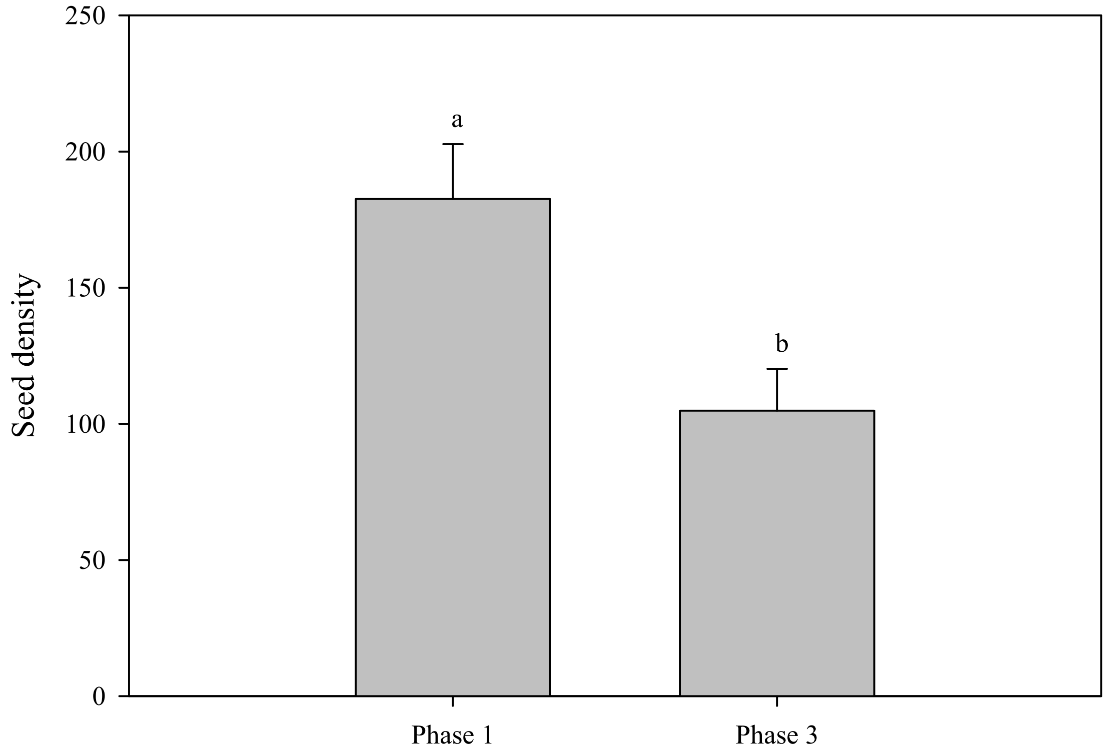


**Figure 2.10** Mean annual forb seed density (+ 1 SE) as affected by community phase. Different letters indicate significant differences (*P* < 0.05).

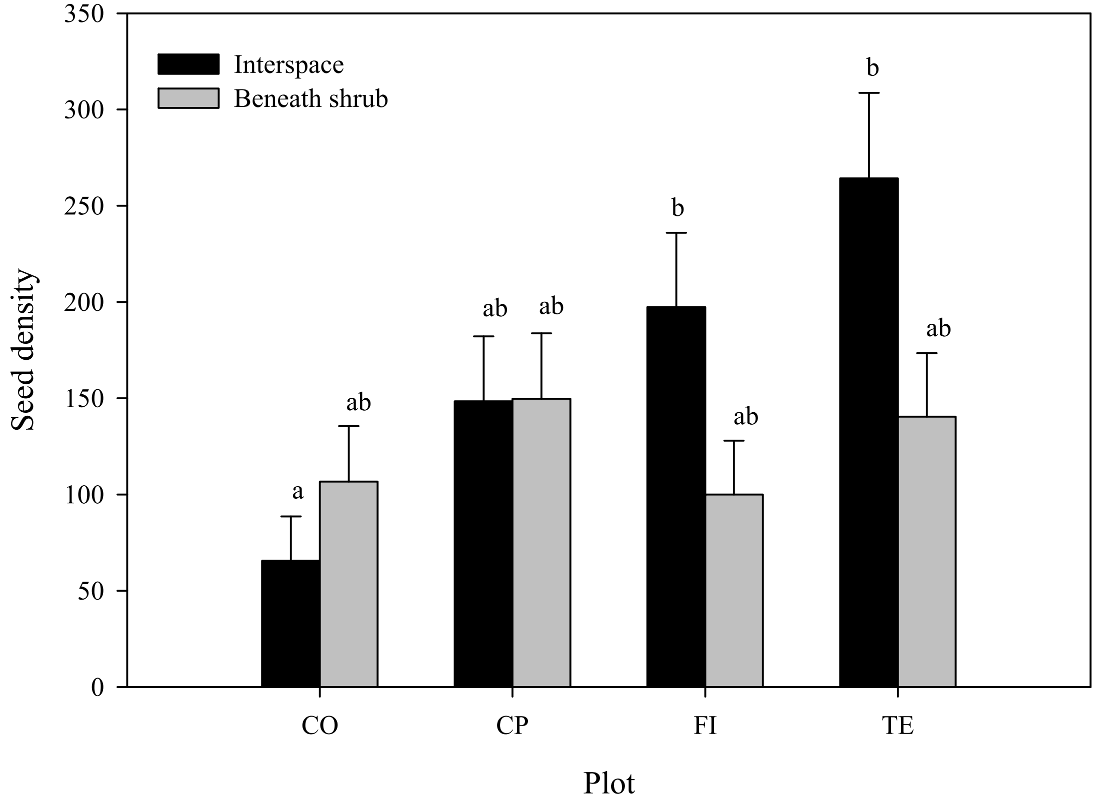


**Figure 2.11** Mean annual forb seed density (+ 1 SE) as affected by microhabitat and plot (CO = Control, CP = Control-Plateau, FI = Prescribed Burn, TE = Tebuthiuron). Different letters indicate significant differences for comparisons between treatment combinations sharing at least one factor level ($P < 0.05$).

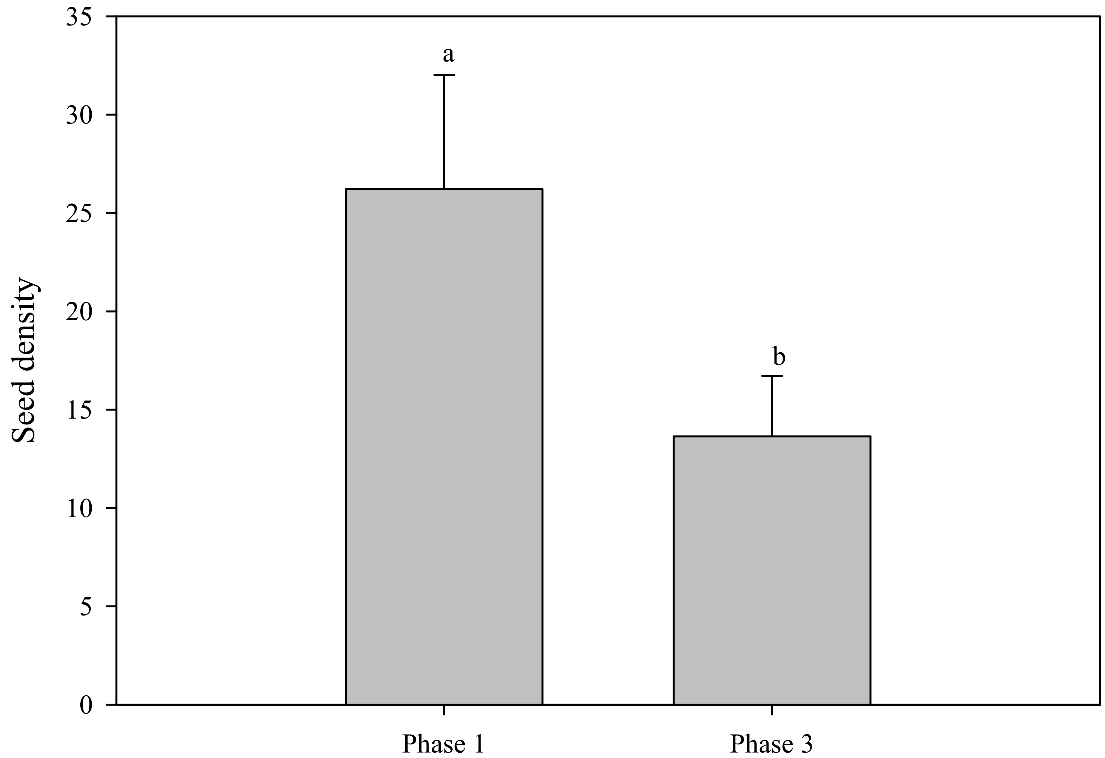


**Figure 2.12** Mean *Poa secunda* seed density (+ 1 SE) as affected by community phase. Different letters indicate significant differences ($P < 0.05$).

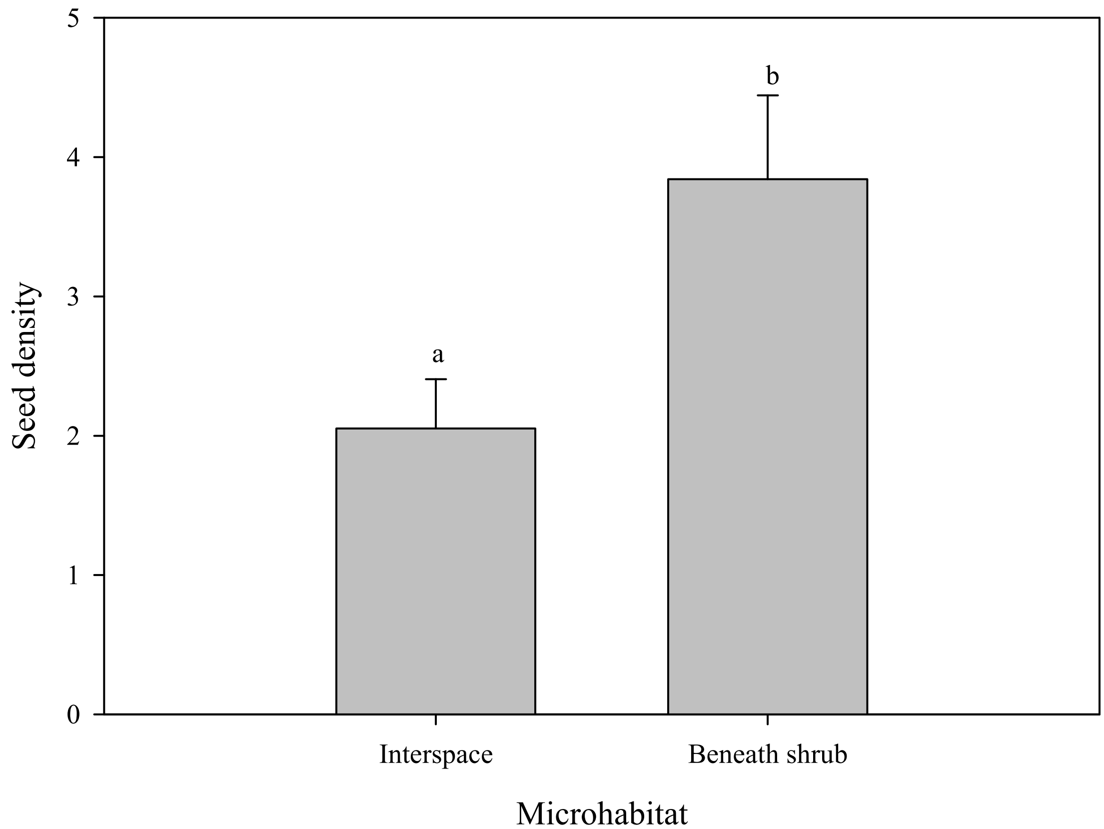


**Figure 2.13** Mean shrub seed density (+ 1 SE) as affected by microhabitat. Different letters indicate significant differences ($P < 0.05$).

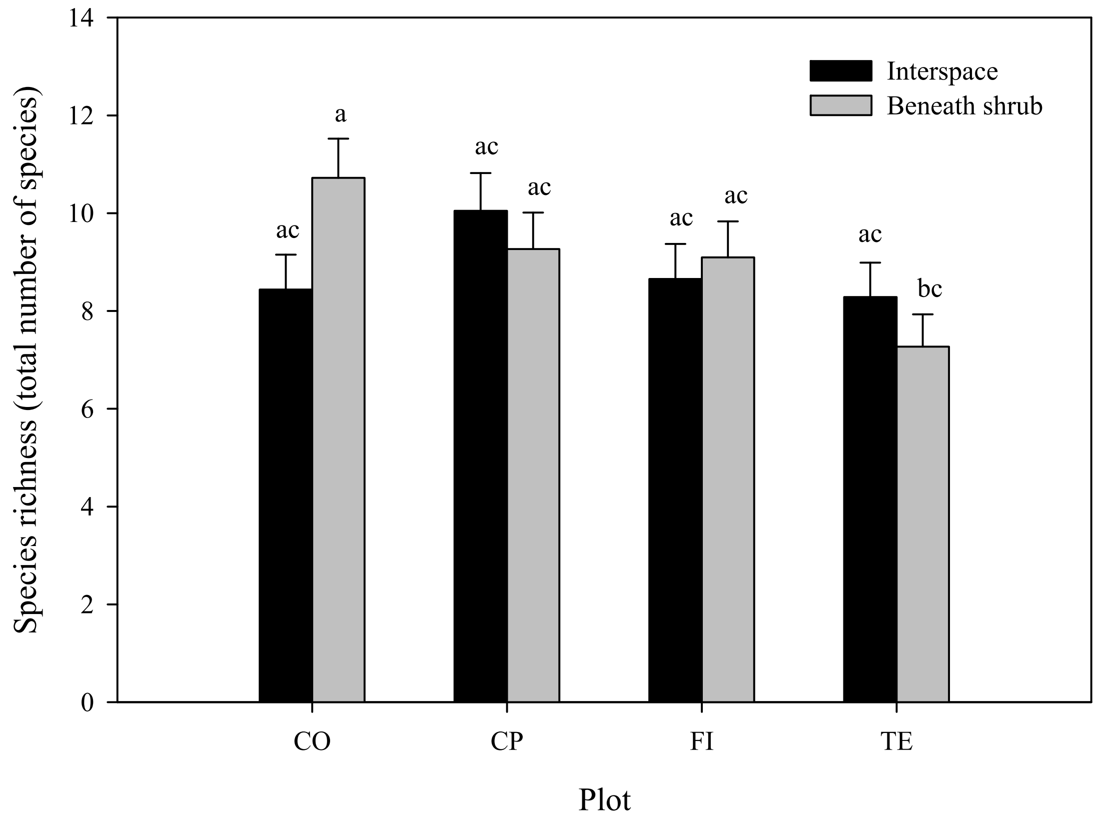


**Figure 2.14** Mean species richness (+ 1 SE) as affected by microhabitat and plot (CO = Control, CP = Control-Plateau, FI = Prescribed Burn, TE = Tebuthiuron). Different letters indicate significant differences for comparisons between treatment combinations sharing at least one factor level (*P* < 0.05).

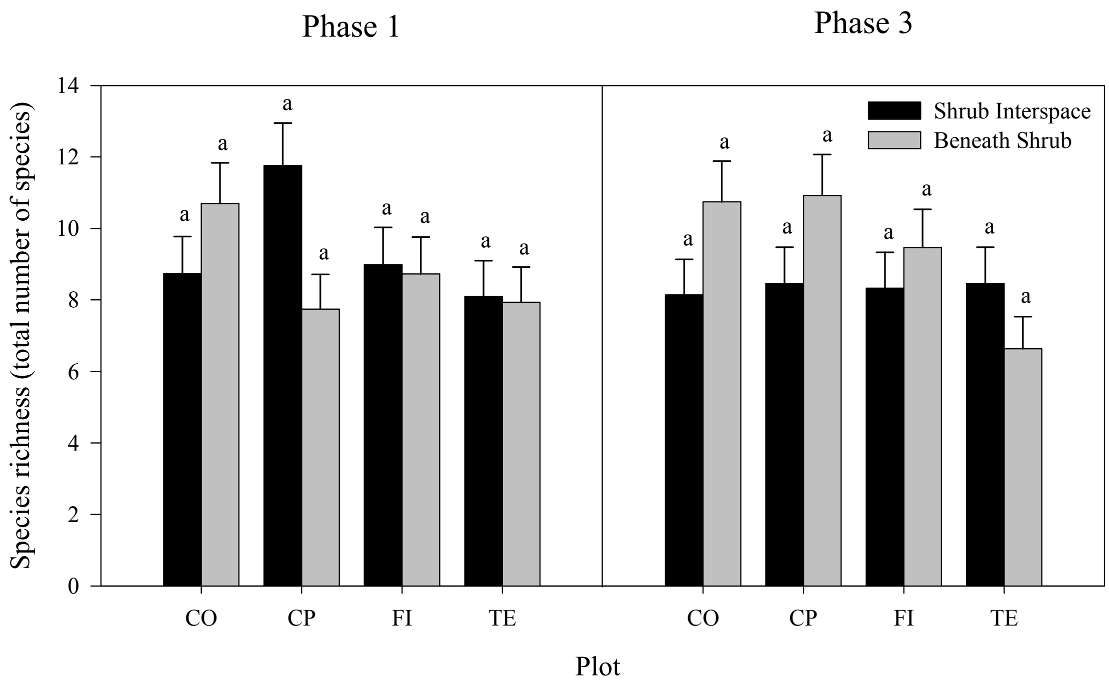


**Figure 2.15** Mean species richness (+ 1 SE) as affected by microhabitat, phase, and plot (CO = Control, CP = Control-Plateau, FI = Prescribed Burn, TE = Tebuthiuron). Different letters indicate significant differences for comparisons between treatment combinations sharing at least one factor level ($P < 0.05$).

# CHAPTER 3

# EFFECTS OF SAGEBRUSH RESTORATION TREATMENTS ON A GREAT BASIN SEED POOL COMMUNITY


## Abstract

The influence of sagebrush restoration on Great Basin vegetation dynamics has been well documented but the impacts of treatments on the seed pool community has not received as much attention. The effects of restoration treatments (prescribed burn, tebuthiuron herbicide, and Plateau® herbicide) on seed pool community composition and dominant seed pool species densities were evaluated. In addition I determined whether the pre-treatment seed pool or the aboveground vegetation was more similar to the vegetation following the restoration treatment. *Alyssum desertorum*, *Bromus tectorum*, *Ceratocephala testiculata*, and *Poa secunda* dominated the seed pool community. The seed pool community shifted after restoration treatments, especially in the tebuthiuron and Plateau treatments. Prescribed burn was the only treatment that affected seed density. The post-treatment vegetation community was more similar to the pre-treatment vegetation than to the pre-treatment seed pool community, and perennial comparisons were as similar as the annual comparisons. Results suggest seed pool community composition and seed density were temporally and spatially variable. Furthermore, tebuthiuron and Plateau may have altered community composition whereas prescribed burn affected seed density. This research also implies that the pre-existing vegetation may be a better indicator of the vegetation community following restoration than is the seed pool community.

## 1. Introduction

The Great Basin, a cold desert, is the largest North American desert, covering an area of approximately 409,000 $km^2$ (Graham, 1999). This desert provides habitat for many endemic plants and animals (Scott et al., 1998). During the past century, the health of this ecosystem has dramatically declined as a result of exotic grass invasion, altered fire regime, conversion to agriculture, livestock grazing, and climate change (D'Antonio and Vitousek, 1992; Hemstrom et al., 2002). Some consider certain ecosystems of the Great Basin to be critically endangered (Noss et al., 1995).

The invasive cheatgrass (*Bromus tectorum*) has contributed to changes in community structure and dynamics. Cheatgrass is a winter annual introduced to the U.S. from Eurasia by the late 1800s, probably as a contaminant in grain seed (Mack and Pyke, 1983; Young and Allen, 1997). Excessive and improper grazing enhanced the dispersal and eventual dominance of cheatgrass (Young and Clements, 2007). Grazing was common after fire which reduces the vigor of perennial grasses, and with sagebrush removed this created an opportunity for cheatgrass to successfully invade (Stewart and Hull, 1949). Cheatgrass is a prolific seed producer and can easily form persistent seed pools. Once established, densities can reach high levels that increase the chance of igniting fires (Young and Clements, 2007). Cheatgrass is highly flammable, more so than the native species, and provides fine fuels which contribute to the spread of fires (Stewart and Hull, 1949; D'Antonio and Vitousek, 1992). These fires often spread to and burn healthy sagebrush communities that have not been heavily invaded (Stewart and Hull, 1949). *B. tectorum* recovers quickly following fires by producing high seed densities and outcompeting native species for resources (D'Antonio and Vitousek, 1992).

This grass-fire cycle continues, and as a result, cheatgrass dominance has spread, and fires have become more frequent.

Management decisions of the past have created challenges for current and future land managers. For example, overgrazing has led to decreased competitive ability of many native grasses which has contributed to both the increase in shrub abundance and cheatgrass colonization (Olson and Whitson, 2002; Chambers et al., 2007). Some common land management options used to help restore degraded systems include herbicide and prescribed burning which can achieve a variety of goals depending on the type and dose of herbicide and the timing of the fire. The herbicide tebuthiuron can selectively thin shrubs at low doses (Whitson and Alley, 1984). Studies using tebuthiuron as a shrub control agent have shown that the number of species does not change as a result of tebuthiuron application, although as shrub abundance decreases grass abundance increases (Whitson and Alley, 1984; Olson and Whitson, 2002). This shift in abundances can be problematic if cheatgrass is present. A study that measured the cover of cheatgrass and perennial grasses 11 years after herbicide application showed that the proportional increase of cheatgrass cover was much greater than that of perennial grasses (Blumenthal et al., 2006). This result indicates that cheatgrass has the ability to exploit resources made available by shrub thinning which may increase the cover of cheatgrass relative to perennial grasses. To our knowledge, no studies have investigated the effects of tebuithiuron on the seed pool community within the Great Basin. However, researchers investigating the effects of tebuthiuron on seed pools of northern Australia floodplains have found that tebuthiuron reduced forb and *Mimosa pigra* emergence (Lane et al., 1997).

Plateau® (imazapic) is another herbicide used in restoration, which can suppress cheatgrass growth and control cheatgrass populations (Shinn and Thill, 2002; Morris et al., 2009). In addition, Plateau has been shown to be instrumental in establishing perennial species, but if cheatgrass is not reduced below a critical threshold, an increase in precipitation can augment the recovery of cheatrass to pre-treatment levels (Morris et al., 2009). Plateau tends to affect annuals more than perennials, and there is extensive variation among perennial species in sensitivity to Plateau (Shinn and Thill, 2002; Sheley et al., 2007). No studies have determined the effects of Plateau on Great Basin seed pools, to our knowledge.

Prescribed fire also has been used by land managers to reduce shrub abundance (Keeley, 2006). Even low intensity fires can result in high shrub mortality (Baker, 2006). Fire creates a pattern of burned and unburned patches (Baker, 2006). There are a number of factors that can contribute to the likelihood of an area burning, including the amount of fine fuels, fuel moisture, and wind. The timing or season in which the fire occurs can also influence fire patterns and produce very different results. Fall burns have been shown to produce greater flame length, rate of spread, and fire intensity than spring burns (Sapsis and Kauffman, 1991). However, these differences may not lead to differences in percent consumption (Sapsis and Kauffman, 1991).

Prescribed burning can result in the replacement of shrubs by grasses, which is a favorable outcome if the emerging grasses are native species. However, if cheatgrass is present, fire can assist in its spread (Keeley, 2006; Davies et al., 2008). Prescribed burning can increase the availability of safe sites which can be readily colonized by invaders (Davies et al., 2008). Cheatgrass can successfully compete with native grasses for water and nutrients following fire (Melgoza and Nowak, 1991). Studies looking at the effects of wildfire on sagebrush communities have shown that the pulse in nutrients, light, and water gives understory herbaceous species the chance to germinate and establish. West and Hassan (1985) found that herbaceous growth doubled one year after fire, mainly due to increased cheatgrass cover. However, perennial grass levels returned to those recorded prior to burning. A similar result was found in a longer term study; cheatgrass cover increased within the first few years after fire, but perennial grass cover subsequently increased to dominate the landscape (West and Yorks, 2002).

Not only can cheatgrass take advantage of post-fire conditions by outcompeting native species for newly available resources, but the increase in abundance helps populations persist by providing the fine fuels that ignite and spread fires (Young and Evans, 1978). However, fire can be an effective management tool for controlling invasive species populations, such as cheatgrass, if the fire kills all adult plants and eliminates the seed pool (Brooks and Pyke, 2001). Cheatgrass seeds are relatively short-lived and do not develop long-lived seed pools, so local extinction of cheatgrass populations could be possible if there is 100 percent mortality caused by fire (Mack and Pyke, 1983; Brooks and Pyke, 2001). However, fires tend to create burned and unburned patches, which suggests that cheatgrass will survive in unburned patches and produce seeds that can be dispersed to burned areas (Baker, 2006). In addition, cheatgrass seeds can survive in burned patches, especially when burns occur after seed has matured and fallen to the ground (Klemmedson and Smith, 1964; Young et al., 1972). Even when fire kills cheatgrass seeds and greatly reduces the seed pool, seed densities can quickly return to pre-fire levels (Hassan and West, 1986; Humphrey and Schupp, 2001).

Restoration strategies often involve disturbances that create opportunities for regeneration and germination of seeds from the seed pool (Kotanen, 1996). Seed pools may be used to manage the existing vegetation and to predict the aboveground vegetation response to restoration (van der Valk and Pederson, 1989; Olano et al., 2005). The seed pool can be an indicator of community composition and the relative abundance and distribution of species (Welling et al., 1988; van der Valk and Pederson, 1989). Using the seed pool as a means of vegetation management is only possible if seeds of desirable species are present, seeds of unwanted species are absent or uncommon, and conditions are suitable for germination and establishment of desirable species (van der Valk and Pederson, 1989). Even though restoration may provide more suitable conditions for colonization, restoration treatments may potentially alter the seed pool community. Studies investigating the effects of restoration treatments on the seed pool community within the Great Basin are limited.

This study was designed to evaluate the effects of sagebrush restoration on a Great Basin seed pool community. Specifically, the following research questions were addressed: (1) What is the effect of restoration treatments on seed pool community composition and dominant seed pool species densities? (2) Is the post-treatment vegetation community following restoration more similar to the pre-treatment seed pool or pre-treatment aboveground vegetation?

## 2. Methods

### *2.1. Study site*

Soil seed pool samples were collected from the Onaqui site (40°11'53"N

112°27'51"W) which is one of several Sagebrush/Cheatgrass sites being used in the large-scale fuels reduction and restoration experiment, SageSTEP. The Onaqui site is located on the eastern toeslope of the Onaqui mountains, Tooele County, Utah, USA, at an elevation of 1660-1700 meters. Onaqui has fine-loamy soils (SageSTEP, 2009), and Wyoming big sagebrush (*Artemisia tridentata* ssp. *Wyomingensis*), shadscale saltbush (*Atriplex confertifolia*), yellow rabbitbrush (*Chrysothamnus viscidiflorus*), Sandberg bluegrass (*Poa secunda*), squirreltail (*Elymus elymoides*), Indian ricegrass (*Achnatherum hymenoides*), bluebunch wheatgrass (*Pseudoroegneria spicata*), basin wildrye (*Leymus cinereus*), and cheatgrass (*Bromus tectorum*) were common on the site.

Seed pool germination assays were conducted in a greenhouse at the Utah State University Research Greenhouse Facility in Logan, UT.

*2.2. Experimental design*

Soil seed pool samples were collected from 30 X 33 m subplots within 3, 75-acre treatment plots (control, prescribed burn, and tebuthiuron). In addition, a pre-emergent herbicide, Plateau® (imazapic), was applied as a split-plot treatment with half of the subplots within a treatment plot being treated with Plateau. Community phase was determined by the native bunchgrass cover where subplots with higher relative native bunchgrass cover (> 19 percent) were considered phase 1 communities, and subplots with lower (< 10 percent) were considered phase 3 communities. Four subplots for each community phase were sampled totaling eight subplots per treatment plot and 32 subplots overall. Treatments will be referred to as control (CO), tebuthiuron (TE), prescribed burn (FI), and control-Plateau (CP; the control subplots that received a Plateau treatment). The Tebuthiuron treatment, designed to reduce the shrub canopy by approximately 50 percent, was applied late November 2006 at a rate of 1.5 lbs/acre (1681.28 g/ha). The Plateau treatment, designed to severely reduce cheatgrass establishment, was applied early November 2006 at a rate of 6 oz/acre (420.32 g/ha). The prescribed burn, which occurred the week of 24 September 2006, blackened about 65 percent of the entire plot and 75-80 percent of each subplot.

Within each subplot, 4, 28-m transects that ran north-south were laid out so as to not interfere with annual vegetation surveys. Transects were located at 3, 10, 20, and 27 m from the northwest corner of the subplot. A composite sample consisting of 5 subsamples within a quarter-meter square frame was collected every 3 m along the 4 transects for a total of 40 composite samples per subplot. Microhabitat (beneath shrub or interspace) was recorded for each sample. Sampling locations were occasionally shifted slightly to ensure that all 5 subsamples were from the same microhabitat. Subsamples measured 6.1 cm in diameter and were taken to a depth of 4 cm with PVC couplings. Litter and soil layers were collected together.

Pre-treatment seed pool samples were collected from all subplots on 14-17 and 22-24 August 2006. On 3-5 November 2006, shortly after the fire but before application of herbicides, soil cores were collected 0.5 meters from the original sampling locations from only the control and prescribed burn subplots to detect immediate effects of the fire. All subplots were resampled 1 meter from original sampling locations one growing season after treatment implementation on 1-2 and 7-8 August 2007.

### *2.3. Vegetation surveys*

The line-point intercept method was used to measure the aboveground vegetation cover of each species present along transects located at 2, 7, 15, 23, and 28 meters from the northwest corner of each subplot (Herrick et al., 2005). Vegetation surveys conducted in summer 2006 were used to represent the pre-treatment vegetation community, and surveys conducted in summer 2007 were used to represent the post-treatment vegetation community. Nomenclature for all plant species followed USDA, NRCS (2009).

*2.4. Evaluating the seed pool*

The germinable seed pool was evaluated by direct germination in a greenhouse following cold-moist stratification. Samples were moistened to field capacity and kept in an unlighted refrigerator at 2°C. After 60 days of cold-moist stratification, samples were removed from the refrigerator. Soil samples were then spread over a 2-cm layer of sand in planting trays with drainage holes. Planting trays were divided into 3 equal compartments. Each compartment contained one composite soil sample. Therefore, each planting tray contained 3 composite soil samples. Soil sample dimensions measured 25.4 X 16.9 cm with a depth of 1.3 cm and a volume of 584.49 $cm^3$. Samples were kept moist with daily watering. Seedlings were identified, counted, and removed. Nomenclature for all germinable seed pool species followed USDA, NRCS (2009). Individuals that were not identified in the seedling stage were transplanted and fertilized until mature.

All seed pool samples were not evaluated at the same time due to the high volume of samples collected. The availability of greenhouse space determined the number of samples for each germination assay. Eleven samples representing each treatment combination from the 2006 collection were germinated and evaluated for the first and second germination assays. Six samples from the 2006 collection and 11 samples from the 2007 collection representing each treatment combination were germinated and evaluated for the third germination assay. Each germination assay lasted 150 days. Emergence was initially censused for 115 days, at which point emergence was noticeably reduced. Samples were then dried out for 14 days to break dormancy and mixed, after which watering was resumed and emergence was censused for an additional 21 days.

The first germination assay ran approximately from mid January to mid June 2007. The second germination assay ran from mid June to mid November 2007, and the third germination assay ran from mid January to mid June 2008. It was important that the first and third germination assays ran during the same time of year so as to not confound treatment effects with potential seasonal effects.

*2.5. Statistical Analysis*

To detect treatment effects, non-metric multidimensional scaling (NMDS) of Bray-Curtis distance in species composition was employed using the metaMDS function in the Vegan package in R version 2.6.2 (Oksanen et al., 2008; R Development Core Team, 2008). Seed densities for each species were used in NMDS. Stress values were assessed to determine the number of dimensions. Stress is a measure of the mismatch between the distance in the original p-dimensional space and the distance in the reduced ordination space. A lower stress indicates a better match between the two distances, and a stress < 20 corresponds to a usable and interpretable solution (Clarke, 1993). All figures, regardless of the number of dimensions used, were shown in two dimensions because the third dimension did not seem to alter results upon inspection.

Mixed-model factorial ANOVAs (analysis of variance) were performed using the MIXED procedure in SAS version 9.1.3 to determine the effects of restoration treatments on seed density of the four most dominant species, *Alyssum desertorum*, *Bromus* *tectorum*, *Ceratocephala testiculata*, and *Poa secunda* (SAS Institute, 2003). Treatment, phase, microhabitat and collection time (pre-treatment 2006, post-treatment 2006, and post-treatment 2007) were treated as fixed effects, and subplot was a random effect. Phase and microhabitat effects were addressed in Chapter 2 and were only included in these models to incorporate the design structure and not because they were factors of major interest. The research questions of this chapter addressed treatment effects and not microhabitat or community phase effects. Therefore, results for all significant effects and interactions are presented in the Results section, but the interpretation of treatment and collection time effects and interactions involving both of these factors are the focus of the Results and the Discussion sections. In particular, a significant treatment x collection time interaction was considered indicative of a treatment effect on seed density.

Not all treatments were represented in each collection time; therefore, subsets of the data were analyzed in order to attain complete factorial models. Model 1 included all four treatments and the pre-treatment 2006 and post-treatment 2007 collection times. Model 2 included the control and prescribed burn treatments and all three collection times. Statistical significance was set at the 0.05 probability level.

Data for all models were log-transformed, and least squared means and standard errors were back-transformed for figures. For significant main effects, least squared means were compared using Tukey’s test. For significant interactions, least squared means comparisons between treatment combinations sharing at least one factor level were made using the False Discovery Rate to control for familywise error rate.

Sørensen’s similarity index ($C_s$) and Bray-Curtis (*BC*) distance were calculated in R version 2.6.2 to determine if the germinable seed pool or the aboveground vegetation before treatment was more similar to the aboveground vegetation after treatment (R Development Core Team, 2008). The relative abundance of the seed community before treatment was compared to the relative cover of the aboveground community after treatment, and the relative cover of the aboveground vegetation was compared before and after treatment. The similarity/distance metrics were calculated for the whole germinable seed pool and aboveground vegetation communities, the annual germinable seed pool and aboveground vegetation communities, and the perennial germinable seed pool and aboveground vegetation communities within each treatment plot. Sørensen's similarity is based strictly on presence/absence: $C_s=2w/(2w+A+B)$ where $w$ is the total number of species found in both communities, $A$ is the number of species found aboveground, and $B$ is the number of species found belowground. A $C_s$ of 0 represents completely dissimilar communities and $C_s$ of 1 represents identical communities at the level of presence/absence. Bray-Curtis distance which incorporates relative abundance normalizes relative abundance for communities being compared by dividing the absolute differences by the summation:

$$BC = \sum_{i}^{n} | x_{ij} - x_{ik} | / \sum_{i}^{n} x_{ij} + x_{ik}$$

where $x_{ij}$ is the relative abundance of species $i$ at community $j$, $x_{ik}$ is the relative abundance of species $i$ is at community $k$, and $n$ is the total number of species. A $BC$ of 0 represents most similar communities and a $BC$ of 1 represents most different communities.

## 3. Results

### *3.1. Treatment effects on germinable seed pool community composition and dominant germinable seed pool species*

#### *3.1.1. Germinable seed pool community*

The NMDS required three dimensions to achieve an acceptable stress level of 19.80. Although there was only moderate separation among the four treatments, there was a more obvious separation between the pre and post-treatment community compositions within each treatment, including the CO treatment, indicating a temporal shift in community composition (Fig. 3.1; see Table A.1 and Table A.3 for relative abundance of species present in the germinable seed pool community before and after treatment implementation). However, pre-treatment and post-treatment subplots within the CO and FI treatments were more similar in terms of community composition than the CP and TE treatments, suggesting that fire did not affect community composition as much as did tebuthiuron and Plateau.

#### *3.1.2. Dominant germinable seed pool species*

ANOVA showed that *A. desertorum* seed density was not significantly affected by treatment but was significantly affected by phase, microhabitat, and collection time for model 1 (all treatments, 2 collections times) and collection time and the phase x collection time interaction for model 2 (2 treatments, all collection times) (Table 3.1; Table 3.2). *A. desertorum* seed density was significantly higher in phase 1 communities (greater perennial grass cover), beneath shrub microhabitats, and in the pre-treatment

2006 collection time for model 1 (Fig. 3.2a; Fig. 3.3a; Fig. 3.4a). In model 2, *A. desertorum* seed density was significantly higher for the pre-treatment 2006 collection time (Fig. 3.5a; Fig. 3.6). In phase 1 communities, seed densities significantly decreased from pre-treatment 2006 to post-treatment 2006 but did not change post-treatment 2007 (Fig. 3.6). In phase 3 communities, seed densities also significantly decreased from pre-treatment 2006 to post-treatment 2006 to a density equal to that in phase 1 communities. However, seed density continued to significantly decrease post-treatment 2007 (Fig. 3.6), which contributes to the significant interaction.

*B. tectorum* seed density was significantly affected by treatment, collection time, and the treatment x collection time interaction for model 1 (all treatments, 2 collection times) and treatment, collection time, the treatment x microhabitat interaction, the treatment x collection time interaction, the microhabitat x collection time interaction, and the treatment x microhabitat x collection time interaction for model 2 (2 treatments, all collection times) (Table 3.1; Table 3.2). Pre-treatment 2006 samples had significantly higher *B. tectorum* seed densities than post-treatment 2007 samples, and the CO and CP treatments had significantly higher seed densities than the FI and TE treatments (Fig. 3.4b; Fig. 3.7a; Fig. 3.8a). *B. tectorum* seed density differed more among treatments in the pre-treatment 2006 collection time than the post-treatment 2007 collection time with seed densities in the FI and TE treatments being significantly different than densities in the CO and CP treatments (Fig. 3.7a). Seed density significantly decreased from the pre-treatment 2006 to the post-treatment 2007 collection time in all treatments with the greatest decrease in the FI plot (Fig. 3.7a). For model 2 (2 treatments, all collection times), *B. tectorum* seed density was significantly higher in the CO treatment and the pre-treatment 2006 collection time (Fig. 3.9a; 3.5b). In the pre-treatment 2006 collection time, the CO treatment contained more seeds than the FI, but in the post-treatment 2006 collection time (immediately after the fire) densities of *B. tectorum* decreased in the FI treatment but not the CO treatment. However, in the post-treatment 2007 collection time densities were equally low in both treatments yielding a significant treatment x collection time interaction (Fig. 3.10a). The significant treatment x microhabitat x collection time interaction showed that beneath shrub microhabitats were more affected by treatment and collection time than interspaces. In the post-treatment 2006 collection time, seed density in the CO treatment remained unchanged from pre-treatment 2006. However, seed density significantly decreased in the FI treatment, but only beneath shrubs. By post-treatment 2007, seed density decreased to equally low levels for both treatments and both microhabitats (Fig. 3.11).

*C. testiculata* seed density was significantly affected by treatment, microhabitat, collection time, the treatment x phase x microhabitat interaction, and the phase x microhabitat x collection time interaction for model 1 (all treatments, 2 collection times) and treatment, phase, microhabitat, collection time, the treatment x collection time interaction, and the phase x microhabitat x collection time interaction for model 2 (2 treatments, all collection times) (Table 3.1; Table 3.2). For model 1, *C. testiculata* seed density was significantly higher in the TE and FI treatments, interspace microhabitats, and the pre-treatment 2006 collection time (Fig. 3.8b; Fig. 3.3b; 3.5c). The significant treatment x phase x microhabitat interaction in model 1 and the phase x microhabitat x collection time interactions in model 1 and model 2 do not directly address my questions of interest. Additionally, these interactions were not explained readily. The changes that occurred in *C. testiculata* seed density across combinations of treatment, microhabitat, and phase and combinations of phase, microhabitat, and collection time were likely a reflection of strong spatial and temporal variation in seed densities (Fig.3.12; Fig. 3.13; Fig. 3.16). For model 2, *C. testiculata* seed density was significantly higher in the FI treatment, phase 3 communities, interspace microhabitats, and the pre-treatment 2006 collection time (Fig. 3.9b; Fig. 3.14; Fig. 3.15; 3.5c). The significant treatment x collection time interaction showed that the reduction in *C. testiculata* seed density between pre-treatment 2006 and post-treatment 2006 was greater in the FI treatment than the CO treatment. However, in the post-treatment 2007 collection time, density increased significantly in the FI treatment but not in the CO treatment (Fig. 3.10b).

*P. secunda* seed density was significantly affected by phase, collection time, the treatment x collection time interaction, the microhabitat x collection time interaction, and the treatment x phase x microhabitat x collection time interaction for model 1 (all treatments, 2 collection times) and treatment, the treatment x collection time interaction, and the treatment x phase x microhabitat x collection time for model 2 (2 treatments, all collection times) (Table 3.1; Table 3.2). For model 1, *P. secunda* seed density was significantly higher in phase 1 than in phase 3 communities (Fig. 3.2b). Pre-treatment 2006 seed densities were significantly higher than post-treatment 2007 seed densities (Fig. 3.4d). In fact, *P. secunda* seed density was significantly higher in pre-treatment 2006 samples than in post-treatment 2007 samples in all treatment plots, with the greatest difference in density between collection times occurring in the FI plot (Fig. 3.7 b). However, seed density did not differ among treatments within each collection time (Fig. 3.7 b). The significant treatment x phase x microhabitat x collection time interaction showed that changes in seed density following the pre-treatment 2006 collection time varied in a complex manner as a function of treatment, microhabitat, and phase (Fig. 3.17). Seed densities decreased in the post-treatment 2007 collection and the decrease tended to be greater in interspaces than beneath shrubs, although the actual amount of reduction depended on both phase and treatment. The patterns resulting from this interaction were not interpreted readily. For model 2, seed density significantly decreased from pre-treatment 2006 to post-treatment 2006 and then remained unchanged in the post-treatment 2007 samples; the decrease was greater in the FI treatment than in the CO treatment, producing the collection time x treatment interaction (Fig. 3.10c). The significant treatment x collection time interaction seems to be the dominant force driving the patterns in the significant 4-way interaction, though the actual response varied depending on phase and microhabitat. The mostly insignificant shifts among phases and microhabitats did not reveal a ready explanation (Fig. 3. 18). Interestingly, the only evidence for an increase in seed density following a full growing season (post-treatment 2006 to post-treatment 2007) was in the FI treatment, beneath shrubs, in phase 1 communities; whether this is biologically meaningful is unclear.

### *3.2. Similarity between pre-treatment germinable seed pool or aboveground vegetation and post-treatment vegetation*

The pre-treatment vegetation and the post-treatment vegetation were more similar than the pre-treatment germinable seed pool and post-treatment vegetation across all treatments and within each treatment for annuals, perennials, and both life histories combined at the level of species presence/absence according to Sørensen's similarity (a $C_s$ of 0 represents completely dissimilar communities and $C_s$ of 1 represents identical communities at the level of presence/absence) (Table 3.3). For the pre-treatment germinable seed pool-post-treatment vegetation comparison, the perennial community was more similar than the annual community across all treatments combined and within the FI and TE treatments, whereas the annual community was more similar than the perennial community in the CO and CP treatments. For the pre-treatment vegetation-post-treatment vegetation comparison, the perennial community was more similar than the annual community across all treatments combined and within each treatment individually.

When incorporating relative abundance, Bray-Curtis distance showed a similar trend where the pre-treatment vegetation and the post-treatment vegetation were more similar than the pre-treatment germinable seed pool and post-treatment vegetation (a *BC* of 0 represents most similar communities and a *BC* of 1 represents most different communities) (Table 3.4). This trend occurred across all treatments and within the CO, CP, and TE treatments for annuals, perennials, and both life histories combined, and within the FI treatment for annuals (Table 3.4). However, the pre-treatment-germinable seed pool and the post-treatment vegetation were more similar than the pre-treatment vegetation and post-treatment vegetation in the FI treatment for the perennials. For the pre-treatment germinable seed pool-post-treatment vegetation comparison, the perennial community was more similar than the annual community in the CP, FI, and TE treatments, whereas the annual community was more similar than the perennial community across all treatments and within the CO treatment. For the pre-treatment vegetation-post-treatment vegetation comparison, the perennial community was more similar than the annual community across all treatments and within the CO, CP, and TE treatments, whereas the annual community was more similar than the perennial community in the FI treatment.

## 4. Discussion

### *4.1. Treatment and collection time effects*

NMDS results showed a moderate distinction among treatments suggesting spatial variability in germinable seed pool composition. Desert germinable seed pools often reveal a high degree of spatial heterogeneity (Henderson et al., 1988; Coffin and Lauenroth, 1989; Kemp, 1989). However, the NMDS plot showed a more obvious distinction between pre-treatment and post-treatment communities for all individual treatments. This result indicates a shift in community composition from before to after treatment. Disturbances such as restoration treatments may alter the community composition of the germinable seed pool (Stark et al., 2006). In the present study, tebuthiuron and Plateau seem to have affected germinable seed pool composition while fire did not as indicated by the greater distance between pre-treatment and post-treatment subplots in tebuthiuron and Plateau than in prescribed burn and control which were similar. It is not surprising that Plateau would alter the germinable seed pool community composition given that it tends to have greater effects on annuals than on perennials and that there is extensive variation among perennial species in sensitivity (Shinn and Thill, 2002; Sheley et al., 2007). However, the apparent shift in community composition following tebuthiuron application is surprising. Although this result may be an artifact, it strongly suggests a need for further research on the effect of tebuthiuron on seeds.

The difference in collection time could also be driving this shift in community composition and would explain why shifts occurred in all treatments, even the CO treatment. The germinable seed pool can vary greatly depending on season and year (Thompson and Grime, 1979; Coffin and Lauenroth, 1989). Yearly climate variability affects seed production, dispersal patterns, seed predation, and germination from the germinable seed pool, all of which can alter germinable seed pool community composition (Went, 1949; Brown et al., 1975; Chambers and MacMahon, 1994). Temperatures between 2006 and 2007 did not differ much; however, 2007 was drier than 2006, especially in April (Table A.5; Table A.6). Seed reserves do change over time (Thompson and Grime, 1979; Henderson et al., 1988; Coffin and Lauenroth, 1989), and in this study, changes in seed reserves may be due to the changes in precipitation between 2006 and 2007, with different species responding differently to the decreased precipitation in 2007, resulting in different germinable seed pool communities.

Evaluating the treatment x collection time interaction for the dominant germinable seed pool species may reveal if treatments affected seed densities. Although fire did not seem to alter germinable seed pool species compositions, in model 1 (all treatments, 2 collection times), fire (and fire only) did appear to alter both *B. tectorum* and *P. secunda* seed densities one growing season after treatment. The changes in both *B. tectroum* and *P. secunda* seed density after one growing season for the CP and TE treatment were less than the changes in density for the CO treatment suggesting that Plateau and tebuthiuron did not impact seed density for either species. In contrast, changes in seed density between 2006 and 2007 were greater in the FI than in the CO treatments, implying that fire decreased seed densities for both *B. tectorum* and *P. secunda*. The short-term response of *B. tectorum* to fire concurs with the findings of Hassan and West (1986). Fire can initially reduce germinable seed pools of *B. tectorum* by killing a large proportion of the seeds (Hassen and West, 1986; Young et al., 1987; Humphrey and Schupp, 2001).

Model 2 (2 treatments, all collections times) results demonstrate that fire immediately reduced *B. tectorum* seed densities beneath shrubs but not in interspaces, likely because of the greater fuel load (litter) beneath shrubs. As in other studies, these results indicate that fire kills cheatgrass seeds beneath shrub due to shrubs burning (Young and Evans, 1976, 1978; Young et al., 1976). In addition, fire may not kill as many seeds in interspaces because the lack of litter makes fires less intense (Young et al., 1976; Young and Evans, 1978). Studies have shown that seeds that do survive fire may produce more vigorous plants which can in turn replenish the germinable seed pool in one growing season (Hassen and West, 1986; Young et al., 1987; Humphrey and Schupp, 2001). However, there was no evidence of an increase in *B. tectorum* seed density after one growing season in the present study, probably because of the dry year, especially spring, in 2007.

Although aboveground cheatgrass density can increase 11 years after tebuthiuron application (Blumenthal et al., 2006), the immediate effects of this herbicide on cheatgrass germinable seed pools remains unknown. Results from Model 1 do not provide evidence of tebuthiuron reducing cheatgrass germinable seed pools. Interestingly, Plateau, a pre-emergent herbicide designed to target annuals, did not reduce cheatgrass seed density. Thus, if Plateau reduced emergence of cheatgrass and the other dominant annual *C. testiculata*, it did not reduce it enough to affect population-level seed production. Although little is known about *C. testiculata* growth and reproduction, *B. tectorum* is extremely plastic in growth and has been shown to compensate extremely well for reduced density with increased per capita growth and seed production (Palmblad, 1968).

Model 2 (2 treatments, all collection times) also showed a decrease in *P. secunda* and *C. testiculata* seed densities immediately after fire. Seed densities remained the same after one growing season for *P. secunda*, while the results for *C. testiculata* depended on treatment. *C. testiculata* seed density increased one growing season after the fire but remained the same in the control. The effect of fire on *P. secunda* seed density is not well documented, but reductions in *P. secunda* seedling emergence after fire has been observed (Champlin, 1982). In addition, Hassan and West have reported smaller *Poa* spp. germinable seed pools in burned plots (1986). Therefore, fire may have reduced *P.secunda* seed densities. The effect of fire on *C. testiculata* seed density remains largely unknown but results from this research suggest that fire reduces *C. testiculata* seed density, but that density can increase fairly quickly in the high-resource conditions following fire.

The significant treatment main effect for *B. tectorum* and *C. testiculata* suggests that seed densities of these two species vary spatially. *B. tectorum* seed density was significantly higher in the CO and CP treatments than the FI and TE treatments for model 1 and significantly higher in the CO than the FI treatment in model 2. *C. testiculata* seed density was significantly higher in the FI and TE treatments than the CO and CP for model 1 and significantly higher in the FI than the CO treatments in model 2. CO and CP treatment plots are in reality in the same plot so it is not surprising that they have similar densities, at least pre-treatment.

All species responded to variation in collection time. For all species and in both models, pre-treatment 2006 seed densities were significantly higher than the other collection times. Seeds collected in the fall of 2006 (post-treatment 2006) might exhibit a different degree of dormancy that did not break as easily, which would explain the immediate post-treatment decrease in seed density in the control treatment, even though the reduction was not as great as in the prescribed burn for at least some species. However, this does not clarify why seed densities were low in the summer of 2007 (post-treatment 2007). Similar to the differences in community composition between collection times, seed densities of all species could vary temporally due to variation in environmental conditions, specifically the decrease in precipitation between 2006 and 2007. Water stress could be limiting plant growth and seed production resulting in lower seed densities in 2007 relative to 2006 when precipitation was higher. Other studies have attributed lower seed production to water stress (French and Turner, 1991; Munns, 2002). Another possibility is that greenhouse conditions were more favorable in the first two germination assays resulting in higher germination rates and ultimately higher seed densities for the pre-treatment 2006 collection time since a greater proportion of pre-treatment 2006 samples were represented in the first two germination assays. However, given the very large differences in densities between pre-treatment 2006 and post-treatment 2007 samples it is unlikely that this can be the sole explanation.

### *4.2. Similarity between germinable seed pool or aboveground vegetation and post-treatment vegetation*

As indicated by both Sørensen's similarity and Bray-Curtis distance, the post-treatment vegetation community was more similar to the pre-treatment vegetation community than to the germinable seed pool community. This result is not surprising considering that the pre-treatment vegetation contains many individuals that will remain present aboveground the following year. Also, the pre-existing vegetation represents those species that can germinate and establish while the germinable seed pool contains seeds that may or may not germinate. For example, a number of wetland species (*Polypogon monspeliensis, Tamarix ramosissima*, *Typha spp.*, *Veronica anagallis-aquatica*; Table A.1; Table A.3) were present in the germinable seed pool but were not represented aboveground (Table A.2; Table A.4), most likely due to unfavorable germination conditions in the field. However, the pre-treatment germinable seed pool and the post-treatment vegetation were more similar than the pre-treatment vegetation and post-treatment vegetation in the FI treatment for the perennials according to Bray Curtis distance. The fire reduced aboveground vegetation biomass substantially. Therefore the pre-treatment germinable seed pool could have been more similar to the post-treatment vegetation because the changes in aboveground biomass before and after fire were greater. The reduction in vegetation in combination with perennials not recovering quickly after fire could cause a dissimilarity in the pre- and post-treatment vegetation communities.

The annual germinable seed pool and vegetation communities were more similar than the perennial community in CO and CP treatments according to Sørensen's similarity index and across all treatments combined and within the CO treatment according to Bray-Curtis distance. Each year in an annual-dominated community the seedlings germinate from the available germinable seed pool which reflects vegetation of the previous year (Osem et al., 2006). However, both the similarity and distance metrics showed the majority of perennial germinable seed pool-post-treatment vegetation comparisons being more similar the annual germinable seed pool-post-treatment vegetation comparisons. This result does not strongly support findings from previous studies that document plant communities dominated by perennial species having lower aboveground-belowground similarities than communities dominated by annuals (Thompson and Grime, 1979; Ungar and Woodell, 1993; Milberg, 1995; Bakker et al., 1996; Osem et al., 2006). However most of these studies are not assessing the relationship between the germinable seed pool of one year and aboveground vegetation of a different year. These generalizations developed from previous studies may not apply to the present study. Additionally, germination conditions in the field might not have been suitable for annuals so seeds remained dormant in the germinable seed pool. Annual seeds may have more selective germination requirements because these plants only produce seeds once (Jurado and Flores, 2005). Thus, if environmental conditions were unfavorable for annual germination, more annuals would be represented belowground than aboveground. Therefore the annual germinable seed pool and vegetation may differ more than the perennial germinable seed pool and vegetation.

In general, the perennial pre-treatment and post-treatment vegetation was also more similar than the annual pre-treatment and post-treatment vegetation. This result is not unusual since perennials can remain aboveground for multiple years while annuals may die after one growing season. Therefore the annual community aboveground is expected to change more over time. However, Bray-Curtis distance showed that the annual vegetation before and after treatment was more similar than the perennial vegetation before and after treatment in the FI treatment. The majority of aboveground biomass was destroyed by the fire. It is not surprising that the annuals recovered more quickly in cover following fire.

In conclusion, the germinable seed pool community composition shifted following restoration treatment application in all treatment plots, but especially in the tebuthiuron and Plateau plots. These results suggest that the germinable seed pool composition varied spatially and temporally, and tebuthiuron and Plateau may have affected germinable seed pool composition while fire did not. However, prescribed burn did reduce *B. tectorum*, *P. secunda*, and *C. testicultata* seed densities. There was no evidence of tebuthiuron or Plateau affecting seed densities of dominant species, which suggests that the potential effects of tebuthiuron on germinable seed pool community composition might be an artifact and that if Plateau reduced annual emergence it was not enough to reduce population-level seed production. All four dominant species were affected by collection time where pre-treatment 2006 samples had higher seed densities than the other collection times, suggesting temporal variability in seed density. The post-treatment vegetation community was more similar to the pre-treatment vegetation than the pre-treatment germinable seed pool community, which suggests that the pre-existing vegetation may be a better indicator of the vegetation community following restoration than the germinable seed pool community.

**References**

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

Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M., Thompson, K., 1996. Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanics Neerlandica 45, 461-490.

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

Brooks, M.L., Pyke, D., 2001. Invasive plants and fire in the deserts of North America. In: Galley, K.E.M, Wilson, T.P. (Eds.), Proceedings of the Invasive Plant Workshop: The Role of Fire in the Control and Spread of Invasive Species. Tall Timbers Research Station, Tallahassee, Florida, USA, pp. 1-14.

Brown, J.H., Grover, J.J., Davidson, D.W., and Lieberman, G.A., 1975. A preliminary study of seed predation in desert and montane habitats. Ecology 56, 987-992.

Chambers, J.C., MacMahon, J.A., 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics 25, 263-292.

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

Champlin, Mark R. 1982. Big sagebrush (*Artemisia tridentata*) ecology and management with emphasis on prescribed burning. Dissertation, Oregon State University, Corvallis, Oregon, USA.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Austral Ecology 18, 117-143.

Coffin, D.P., Lauenroth, W.K., 1989. Spatial and temporal variation in the seed bank of a semiarid grassland. American Journal of Botany 76, 53-58.

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

Davies, K.W., Sheley, R.L., Bates, J.D., 2008. Does fall prescribed burning *Artemisia tridentata* steppe promote invasion or resistance to invasion after a recovery period? Journal of Arid Environments 72, 1076-1085.

French R.J., Turner N.C., 1991. Water deficits change dry matter partitioning and seed yield in narrow-leafed lupins (*Lupinus angustifolius* L.). Australian Journal of Agricultural Research 42, 471–484.

Graham, A., 1999. Late Cretaceous and Cenozoic History of North American Vegetation. Oxford University Press, New York.

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

Hemstrom, M.A., Wisdom, M.J., Hann, W.J., Rowland, M.M., Wales, B.C., Gravenmier, R.A., 2002. Sagebrush-steppe vegetation dynamics and restoration potential in the Interior Columbia Basin, U.S.A. Conservation Biology 16, 1243-1255.

Henderson, C.B., Petersen, K.E., and Redak, R.A., 1988. Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. The Journal of Ecology 76, 717-728.

Herrick, J.E., Van Zee, J.W., Havstad, K.M., Burkett, L.M., Whitford, W.G., 2005. Monitoring manual for grassland, shrubland and savanna ecosystems. USDA-ARS Jornada Experimental Range. The University of Arizona Press, Tucson, Arizona, USA.

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

Jurado, E., and Flores, J., 2005. Is seed dormancy under environmental control or bound to plant traits? Journal of Vegetation Science 16, 559-564.

Keeley, J.E., 2006. Fire management impacts on invasive plants in the western United States. Conservation Biology 20, 375-384.

Kemp, P.R., 1989. Seed banks and vegetation processes in deserts. In: Leck, M.A., Parker V.T., Simpson, R.L. (Eds.), Ecology of Soil Seed Pools. Academic Press, New York, pp. 257-282.

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

Kotanen, P.M., 1996. Revegetation following soil disturbance in a California meadow: the role of propagule supply. Oecologia 108, 652-662.

Lane, A.M., Williams, R.J., Muller, W.J., Lonsdale, W.M., 1997. The effects of the herbicide tebuthiuron on seedlings of *Mimosa pigra* and native floodplain vegetation in northern Australia. Austral Ecology 22, 439-447.

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

Melgoza, G., Nowak, R.S., 1991. Competition between cheatgrass and two native species after fire: implications from observations and measurements of root distribution. Journal of Range Management 44, 27-33.

Milberg, P., 1995. Soil seed bank after eighteen years of succession from grassland to forest. Oikos 72, 3-13.

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

Munns, R., 2002. Comparative physiology of salt and water stress. Plant, Cell & Environment 25, 239-250.

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

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Stevens, M.H.H., 2008. Vegan: Community Ecology Package. R package version 1.13-1. Available from: http://vegan.r-forge.r-project.org/.

Olano, J.M., Caballero, I., Loidi, J., Escudero, A., 2005. Prediction of plant cover from seed bank analysis in a semi-arid plant community on gypsum. Journal of Vegetation Science 16, 215-222.

Olson, R.A., Whitson, T.D., 2002. Restoring structure in late-successional sagebrush communities by thinning with tebuthiuron. Restoration Ecology 10, 146-155.

Osem, Y., Perevolotsky, A., Kigel, J., 2006. Similarity between seed bank and vegetation in a semi-arid annual plant community: the role of productivity and grazing. Journal of Vegetation Science 17, 29-36.

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

R Development Core Team, 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Available from: http://www.R-project.org.

SageSTEP [Sagebrush Treatment Evaluation Project], 2009. Study site locations: Onaqui sites. Available from: http://www.sagestep.org/locations/onaqui.html.

Sapsis, D.B., Kauffman, J.B., 1991. Fuel consumption and fire behavior associated with prescribed fires in sagebrush ecosystems. Northwest Science 65.

SAS Institute. 2003. SAS System for Microsoft Windows. SAS Institute, Inc., Cary, North Carolina, USA.

Scott, M.J., Bilyard, G.R., Link, S.O., Ulibarri, C.A., Westerdahl, H.E., Ricci, P.F., Seely, H.E., 1998. Valuation of ecological resources and functions. Environmental Management 22, 49-68.

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

Shinn, S.L., Thill, D.C., 2002. The response of yellow starthistle (*Centaurea solstitialis*), annual grasses, and smooth brome (*Bromus inermis*) to imazapic and picloram. Weed Technology 16, 366-370.

Stark, K.E., Arsenault, A., and Bradfield, G.E., 2006. Soil seed banks and plant community assembly following disturbance by fire and logging in interior Douglas-fir forests of south-central British Columbia. Canadian Journal of Botany 84, 1548-1560.

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

Thompson, K., Grime, J.P., 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. The Journal of Ecology 67, 893-921.

Ungar, I.A., Woodell, S.R.J., 1993. The relationship between the seed bank and species composition of plant communities in two British salt marshes. Journal of Vegetation Science 4, 531-536.

USDA, NRCS. 2009. The PLANTS Database. National Plant Data Center, Baton Rouge, Louisiana, USA. Available from: http://plants.usda.gov.

van der Valk, A.G., Pederson, R.L., 1989. Seed banks and the management and restoration of natural vegetation. In: Leck, M.A., Parker V.T., Simpson, R.L. (Eds.), Ecology of Soil Seed Pools. Academic Press, New York, pp. 329-346.

Went, F.W., 1949. Ecology of desert plants. II. The effect of rain and temperature on germination and growth. Ecology 30, 1-13.

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

West, N.E., Yorks, T.P., 2002. Vegetation responses following wildfire on grazed and ungrazed sagebrush semi-desert. Journal of Range Management 55, 171-181.

Welling, C.H., Pederson, R.L., van der Valk, A.G., 1988. Recruitment from the seed bank and the development of zonation of emergent vegetation during a drawdown in a prairie wetland. Journal of Ecology 76, 483.

Whitson, T.D., Alley, H.P., 1984. Tebuthiuron effects on *Artemisia* spp. and associated grasses. Weed Science 32, 180-184.

Young, J.A., Allen, F.L., 1997. Cheatgrass and range science: 1930-1950. Journal of Range Management 20, 530-535.

Young, J.A., Clements, C.D., 2007. Cheatgrass and grazing rangelands. Rangelands 29, 15-20.

Young, J.A., Evans, R.A., 1976. Responses of weed populations to human manipulations of the natural environment. Weed Science 24, 186-190.

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

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

Young, J.A., Evans, R.A., Major, J., 1972. Alien plants in the Great Basin. Journal of Range Management 25, 194-201.

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

**Table 3.1** Model 1 *P*-values for fixed effects for seed density of *A. desertorum* (ALDE), *B. tectorum* (BRTE), *C. testiculata* (CETE5), and *P. secunda* (POSE). Significant *P*-values at the 0.05 level are indicated in bold.

| Fixed effect | ALDE | BRTE | CETE5 | POSE |
|---|---|---|---|---|
| treatment | 0.1584 | **<0.0001** | **<0.0001** | 0.6399 |
| phase | **0.0146** | 0.1273 | 0.0720 | **0.0432** |
| treatment*phase | 0.0785 | 0.1062 | 0.4840 | 0.6979 |
| microhabitat | **0.0358** | 0.3251 | **0.0007** | 0.8827 |
| treatment*microhabitat | 0.7172 | 0.5568 | 0.2338 | 0.9860 |
| phase*microhabitat | 0.6275 | 0.4941 | 0.1393 | 0.5640 |
| treatment*phase*microhabitat | 0.8267 | 0.8935 | **0.0015** | 0.8932 |
| collection time | **<0.0001** | **<0.0001** | **<0.0001** | **<0.0001** |
| treatment*collection time | 0.6678 | **0.0002** | 0.3114 | **0.0541** |
| phase*collection time | 0.6909 | 0.9437 | 0.1248 | 0.2766 |
| treatment*phase*collection time | 0.8197 | 0.7021 | 0.2414 | 0.4228 |
| microhabitat*collection time | 0.7250 | 0.0615 | 0.4922 | **0.0303** |
| treatment*microhabitat*collection time | 0.9197 | 0.7869 | 0.0760 | 0.3103 |
| phase*microhabitat*collection time | 0.3875 | 0.5953 | **0.0011** | 0.3960 |
| treatment*phase*microhabitat*collection time | 0.8088 | 0.1472 | 0.8575 | **0.0344** |

**Table 3.2** Model 2 *P*-values for fixed effects for seed density of *A. desertorum* (ALDE), *B. tectorum* (BRTE), *C. testiculata* (CETE5), and *P. secunda* (POSE). Significant *P*-values at the 0.05 level are indicated in bold.

| Fixed effect | ALDE | BRTE | CETE5 | POSE |
|---|---|---|---|---|
| treatment | 0.0843 | **0.0002** | **0.0074** | 0.8748 |
| phase | 0.0645 | 0.2530 | **0.0435** | 0.6928 |
| treatment*phase | 0.1963 | 0.6461 | 0.5006 | 0.1516 |
| microhabitat | 0.9840 | 0.8190 | **0.0121** | 0.3870 |
| treatment*microhabitat | 0.0564 | **0.0251** | 0.0595 | 0.4973 |
| phase*microhabitat | 0.5556 | 0.4177 | 0.4233 | 0.9318 |
| treatment*phase*microhabitat | 0.5156 | 0.4827 | 0.3996 | 0.5969 |
| collection time | **<0.0001** | **<0.0001** | **<0.0001** | **<0.0001** |
| treatment*collection time | 0.5030 | **0.0001** | **0.0032** | **0.0233** |
| phase*collection time | **0.0511** | 0.9513 | 0.1638 | 0.1165 |
| treatment*phase*collection time | 0.8608 | 0.2169 | 0.8982 | 0.3702 |
| microhabitat*collection time | 0.0727 | **0.0173** | 0.5162 | 0.1962 |
| treatment*microhabitat*collection time | 0.3807 | **0.0103** | 0.7288 | 0.2322 |
| phase*microhabitat*collection time | 0.8377 | 0.8759 | **0.0012** | 0.5836 |
| treatment*phase*microhabitat*collection time | 0.4097 | 0.0818 | 0.2932 | **0.0179** |

**Table 3.3** Sørensen's similarity index ($C_s$) comparing the presence/absence of species in the seed pool community before treatment to the presence/absence of species in the aboveground community after treatment, and the presence/absence of species in the aboveground vegetation before and after treatment for the annual community, perennial community, and both annual and perennial communities. $C_s$ was calculated for all treatments combined and each treatment separately. A $C_s$ of 0 represents completely dissimilar communities and $C_s$ of 1 represents identical communities at the level of presence/absence.

| Life History | Comparison | All treatments | CO | CP | FI | TE |
|---|---|---|---|---|---|---|
| Annual | pre-treatment seed pool-post-treatment vegetation | 0.4474 | 0.5000 | 0.4000 | 0.5000 | 0.3750 |
| Annual | pre-treatment vegetation-post-treatment vegetation | 0.6667 | 0.6000 | 0.6667 | 0.7273 | 0.6667 |
| Perennial | pre-treatment seed pool-post-treatment vegetation | 0.4545 | 0.3571 | 0.2727 | 0.6667 | 0.6000 |
| Perennial | pre-treatment vegetation-post-treatment vegetation | 0.8378 | 0.7619 | 0.8000 | 0.8750 | 0.9412 |
| Both | pre-treatment seed pool-post-treatment vegetation | 0.4540 | 0.4255 | 0.3333 | 0.5789 | 0.5000 |
| Both | pre-treatment vegetation-post-treatment vegetation | 0.7788 | 0.7097 | 0.7586 | 0.8148 | 0.8462 |

**Table 3.4** Bray-Curtis distance (*BC*) comparing the relative abundance of the seed pool community before treatment to the relative cover of the aboveground community after treatment, and the relative cover of the aboveground vegetation before and after treatment for the annual community, perennial community, and both annual and perennial communities. *BC* was calculated for all treatments combined and each treatment separately. A *BC* of 0 represents most similar communities and a *BC* of 1 represents most different communities.

| Life History | Comparison | All treatments | CO | CP | FI | TE |
|---|---|---|---|---|---|---|
| Annual | pre-treatment seed pool-post-treatment vegetation | 0.6612 | 0.4888 | 0.8295 | 0.5423 | 0.7316 |
| Annual | pre-treatment vegetation-post-treatment vegetation | 0.4053 | 0.2853 | 0.5383 | 0.3580 | 0.4736 |
| Perennial | pre-treatment seed pool-post-treatment vegetation | 0.6868 | 0.8018 | 0.7411 | 0.3830 | 0.5802 |
| Perennial | pre-treatment vegetation-post-treatment vegetation | 0.2922 | 0.2706 | 0.2244 | 0.5399 | 0.1876 |
| Both | pre-treatment seed pool-post-treatment vegetation | 0.6453 | 0.5781 | 0.8031 | 0.4927 | 0.6750 |
| Both | pre-treatment vegetation-post-treatment vegetation | 0.3289 | 0.2752 | 0.3229 | 0.4712 | 0.2720 |

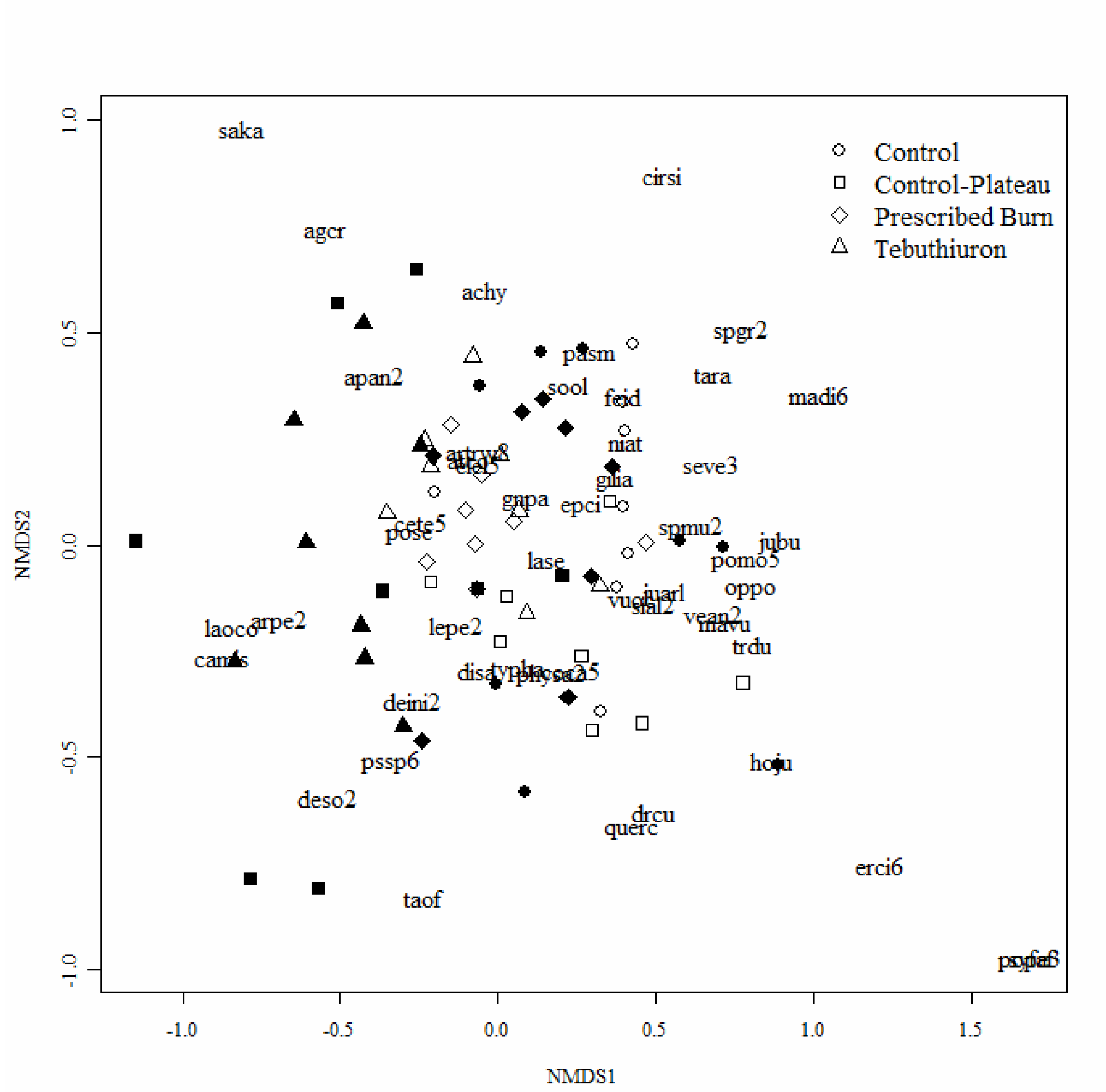


**Figure 3.1** Non-metric multidimensional scaling (NMDS) ordination plot of the germinable seed pool community. Points represent the subplot scores. Species scores are represented by species symbols (USDA, NRCS, 2009). Open symbols represent the pre-treatment community and solid symbols represent the post-treatment community.

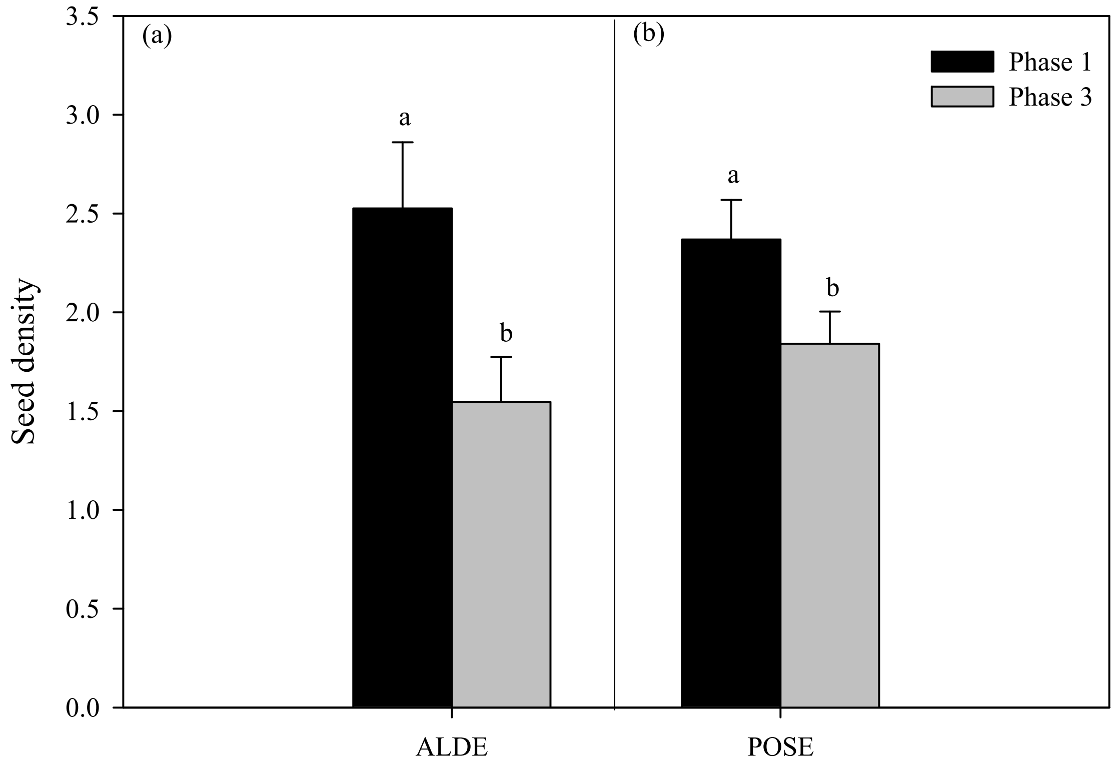


**Figure 3.2** Model 1 mean seed density of (a) *A. desertorum* and (b) *P. secunda* (+ 1 SE) as affected by community phase. Different letters indicate significant differences within each species ($P < 0.05$).

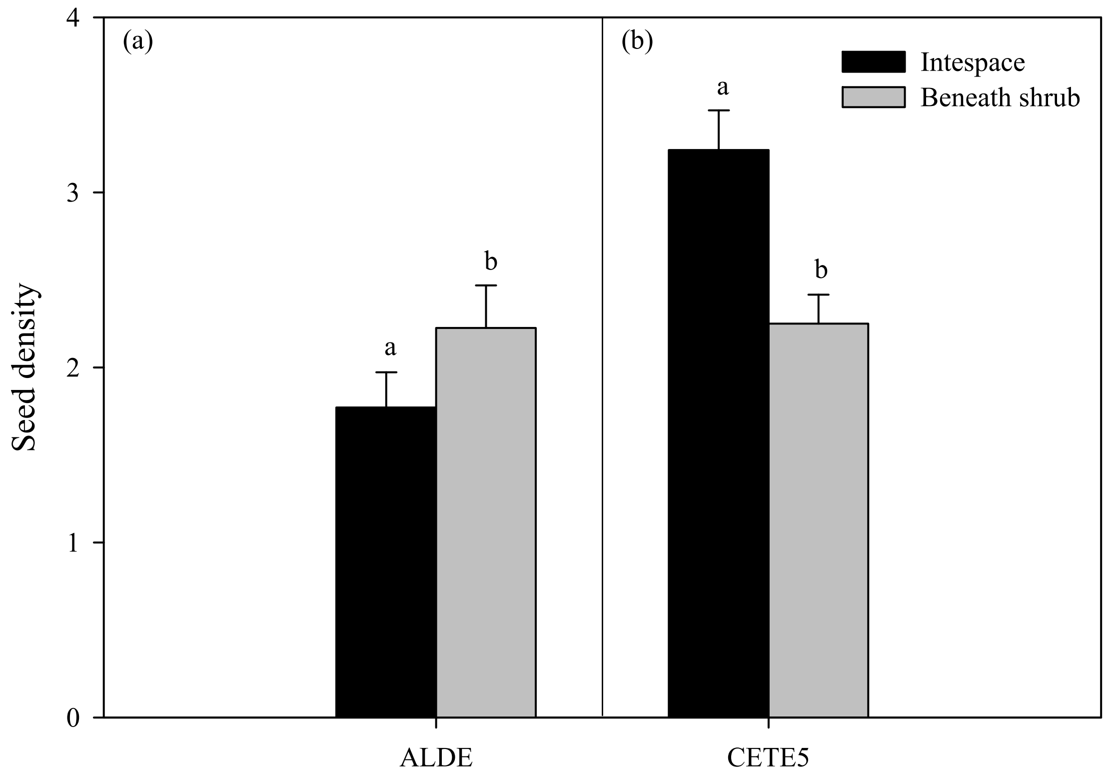


**Figure 3.3** Model 1 mean seed density of (a) *A. desertorum* and (b) *C. testiculata* (+ 1 SE) as affected by microhabitat. Different letters indicate significant differences within each species ($P < 0.05$).

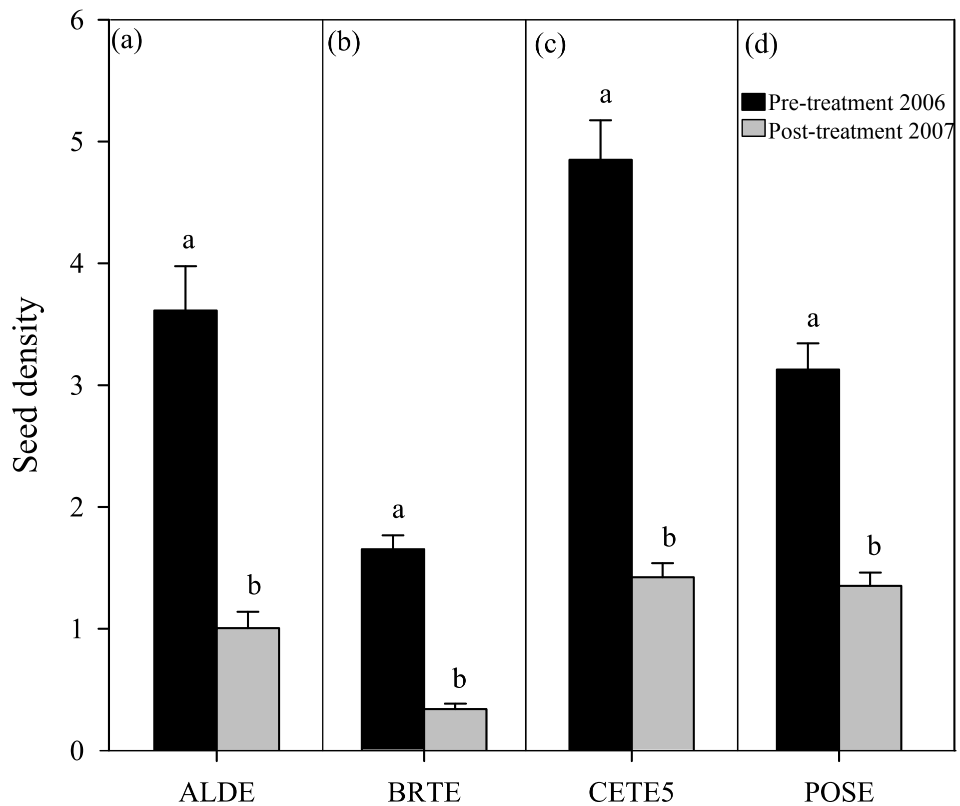


**Figure 3.4** Model 1 mean seed density of (a) *A. desertorum*, (b) *B. tectorum*, (c) *C. testiculata*, and (d) *P. secunda* (+ 1 SE) as affected by collection time. Different letters indicate significant differences within each species ($P < 0.05$).

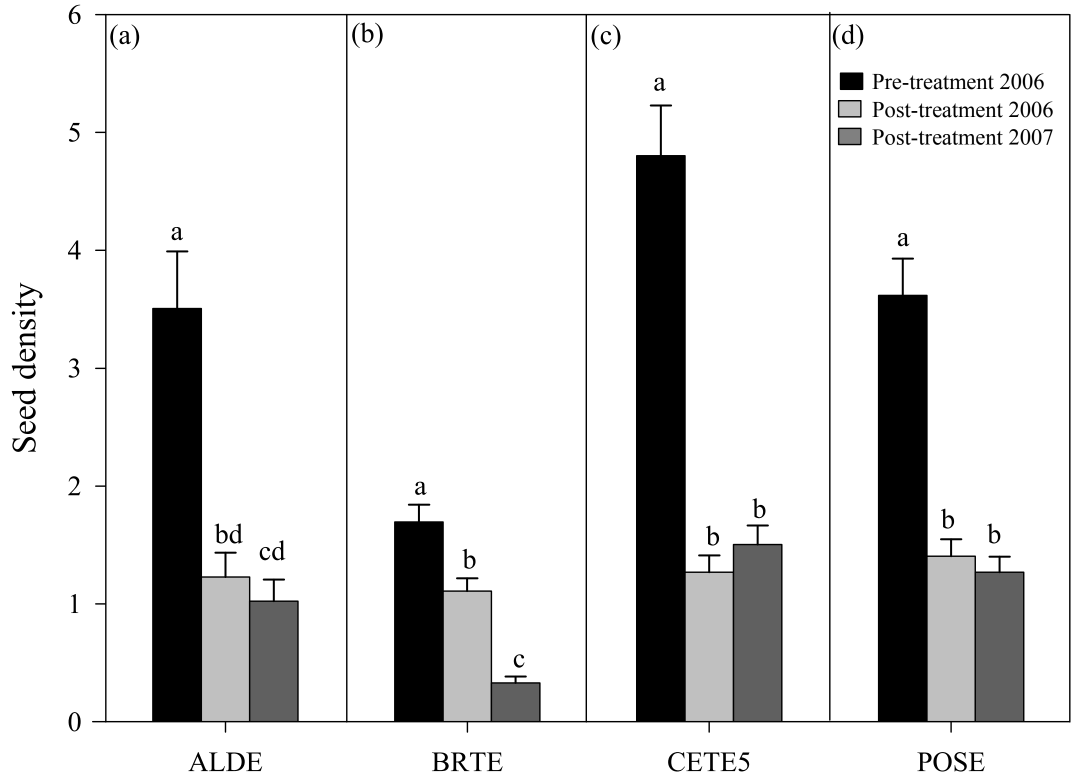


**Figure 3.5** Model 2 mean seed density of (a) *A. desertorum*, (b) *B. tectorum*, (c) *C. testiculata*, and (d) *P. secunda* (+ 1 SE) as affected by collection time. Different letters indicate significant differences within each species ($P < 0.05$).

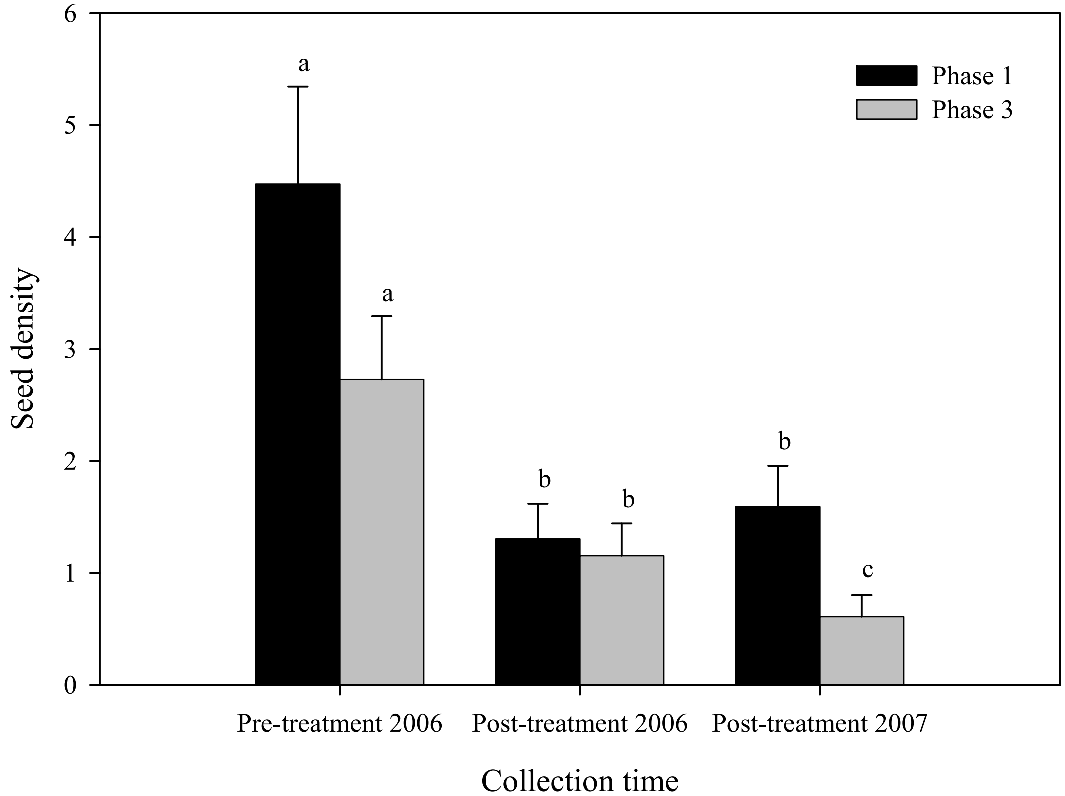


**Figure 3.6** Model 2 mean seed density of *A. desertorum* (+ 1 SE) as affected by community phase and collection time. Different letters indicate significant differences for comparisons between treatment combinations sharing at least one factor level ($P < 0.05$).

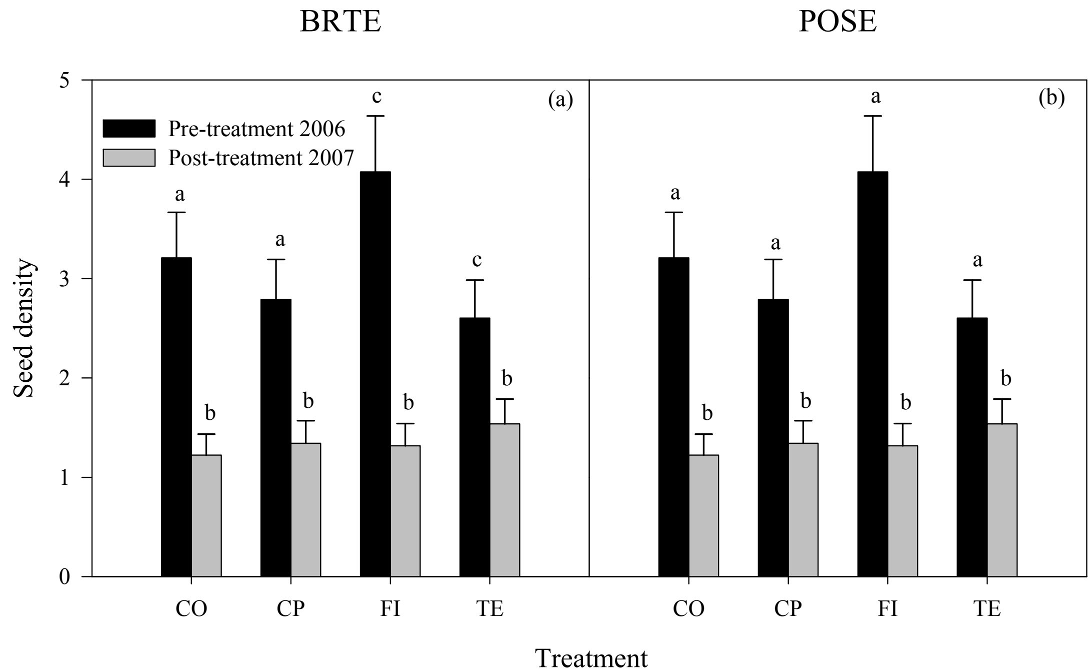


**Figure 3.7** Model 1 mean seed density of (a) *B. tectorum* and (b) *P. secunda* (+ 1 SE) as affected by collection time and treatment (CO = Control, CP = Control-Plateau, FI = Prescribed Burn, TE = Tebuthiuron). Different letters indicate significant differences for comparisons between treatment combinations sharing at least one factor level ($P < 0.05$).

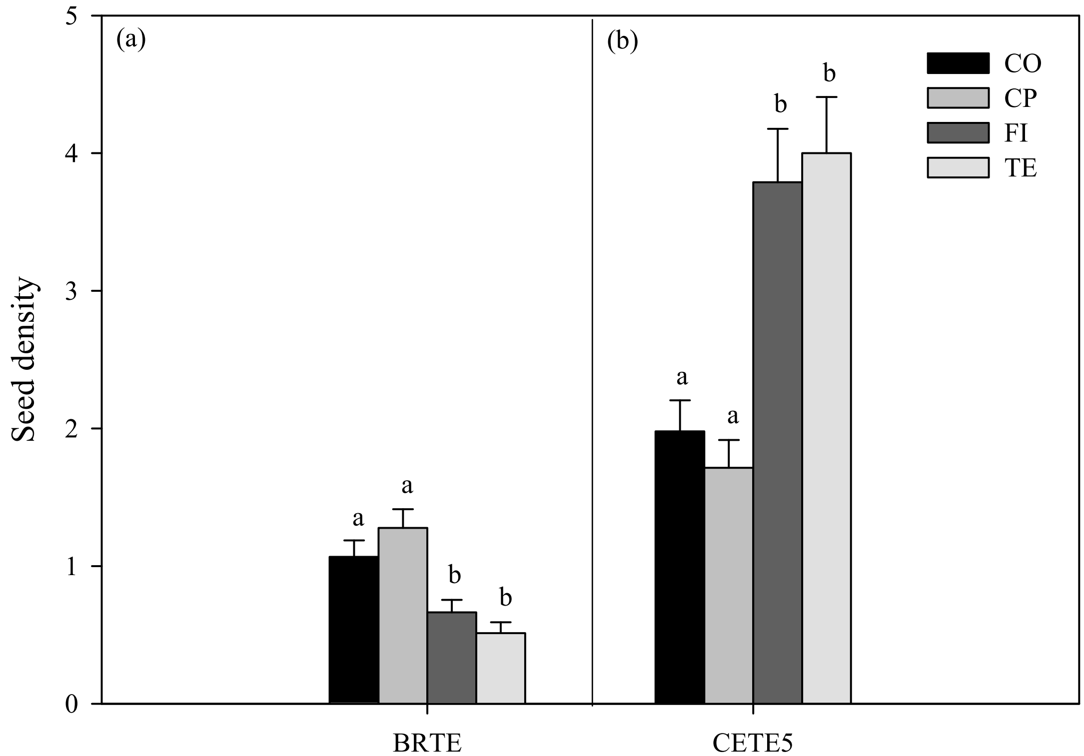


**Figure 3.8** Model 1 mean seed density of (a) *B. tectorum* and (b) *C. testiculata* (+ 1 SE) as affected by treatment (CO = Control, CP = Control-Plateau, FI = Prescribed Burn, TE = Tebuthiuron). Different letters indicate significant differences within each species ($P < 0.05$).

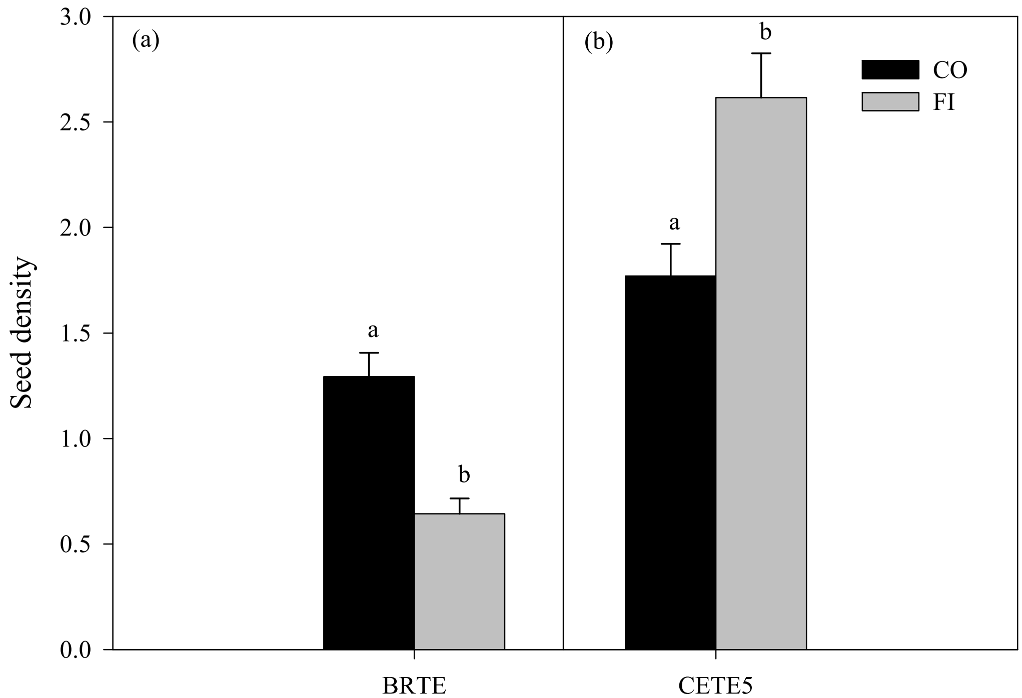


**Figure 3.9** Model 2 mean seed density of (a) *B. tectorum* and (b) *C. testiculata* (+ 1 SE) as affected by treatment (CO = Control, FI = Prescribed Burn). Different letters indicate significant differences within each species ($P < 0.05$).

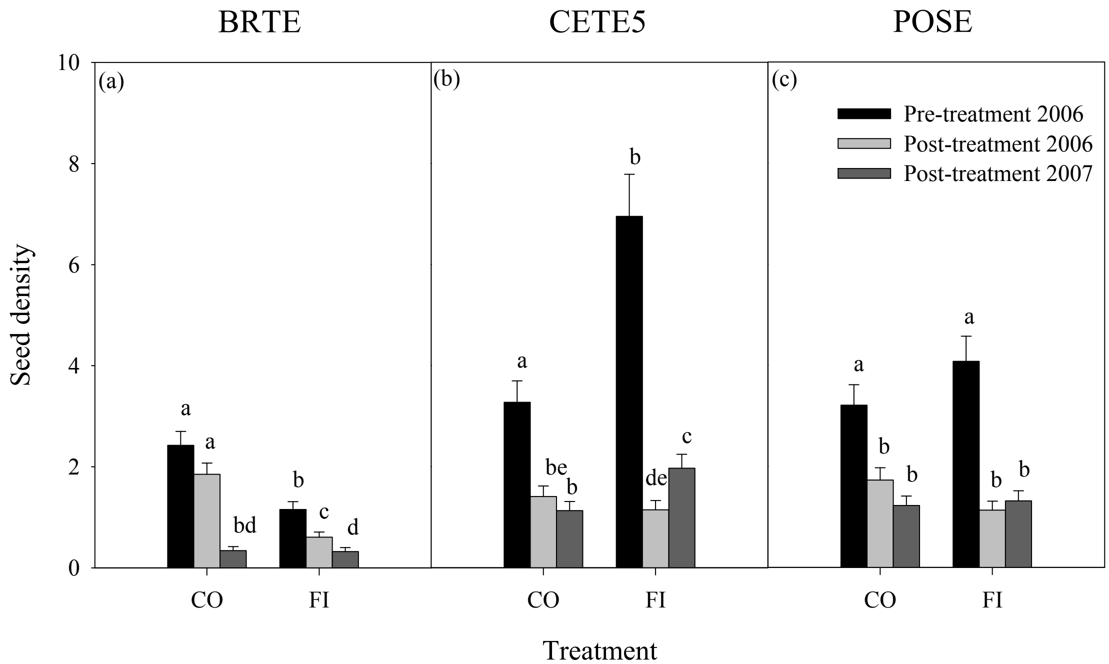


**Figure 3.10** Model 2 mean seed density of (a) *B. tectorum*, (b) *C. testiculata*, and (c) *P. secunda* (+ 1 SE) as affected by collection time and treatment (CO = Control, FI = Prescribed Burn). Different letters indicate significant differences for comparisons between treatment combinations sharing at least one factor level within each species ($P < 0.05$).

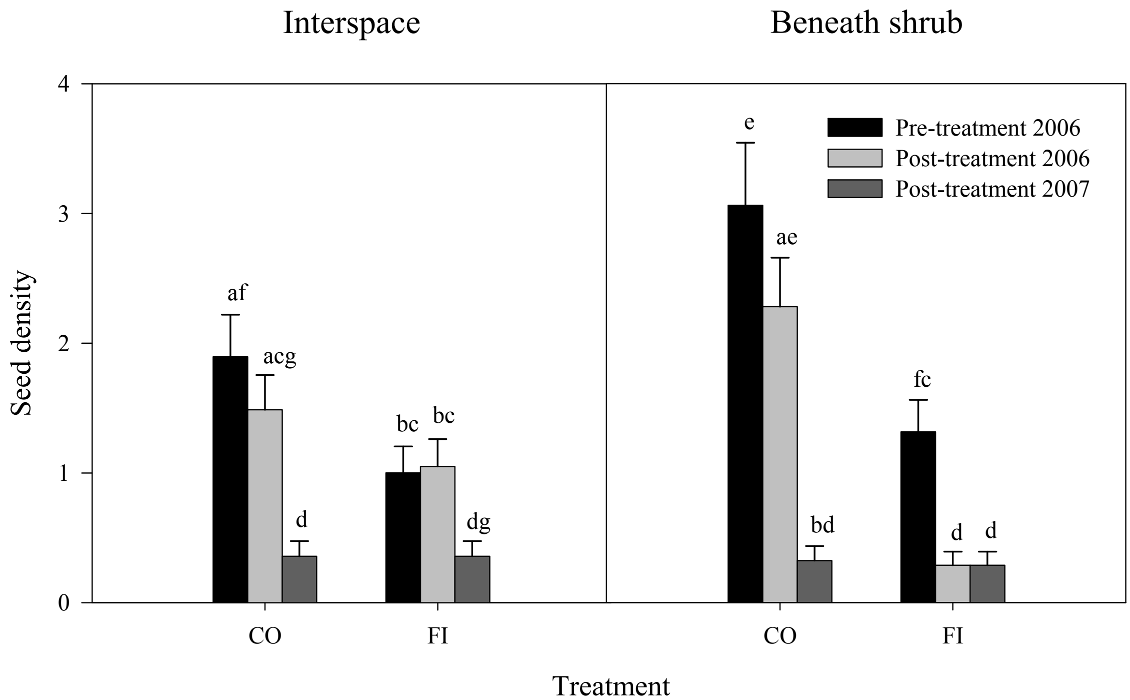


**Figure 3.11** Model 2 mean seed density of *B. tectorum* (+ 1 SE) as affected by microhabitat, collection time, and treatment (CO = Control, FI = Prescribed Burn). Different letters indicate significant differences for comparisons between treatment combinations sharing at least one factor level ($P < 0.05$).

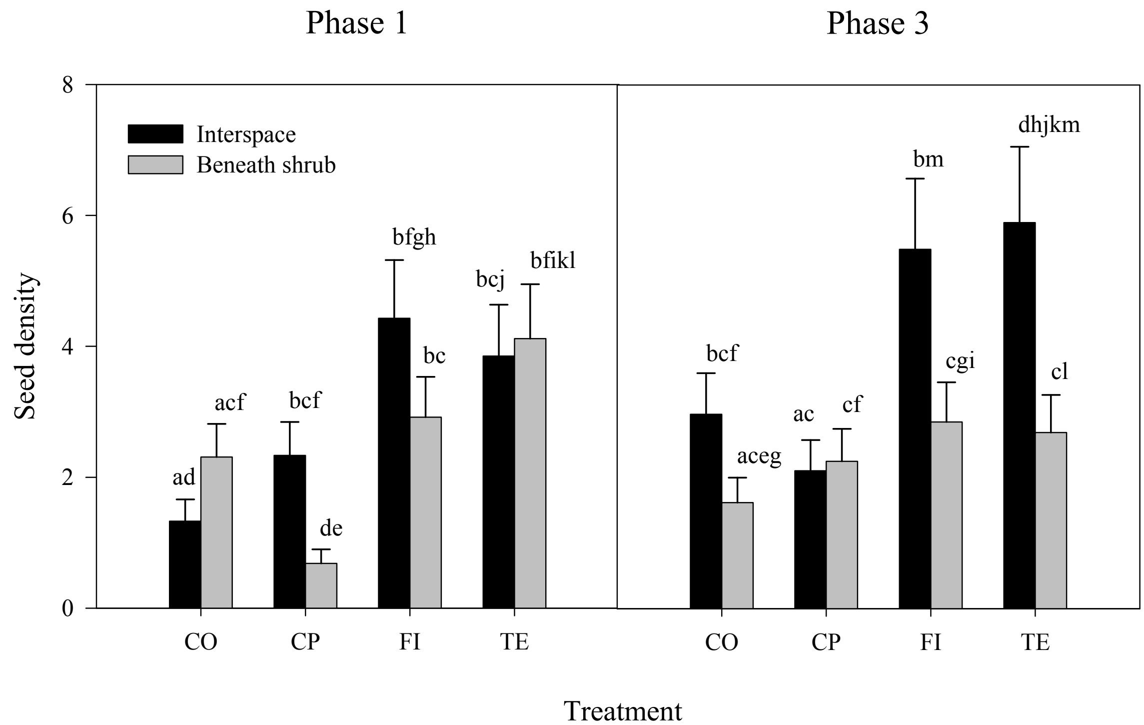


**Figure 3.12** Model 1 mean seed density of *C. testiculata* (+ 1 SE) as affected by phase, microhabitat, and treatment (CO = Control, CP = Control-Plateau, FI = Prescribed Burn, TE = Tebuthiuron). Different letters indicate significant differences for comparisons between treatment combinations sharing at least one factor level ($P < 0.05$).

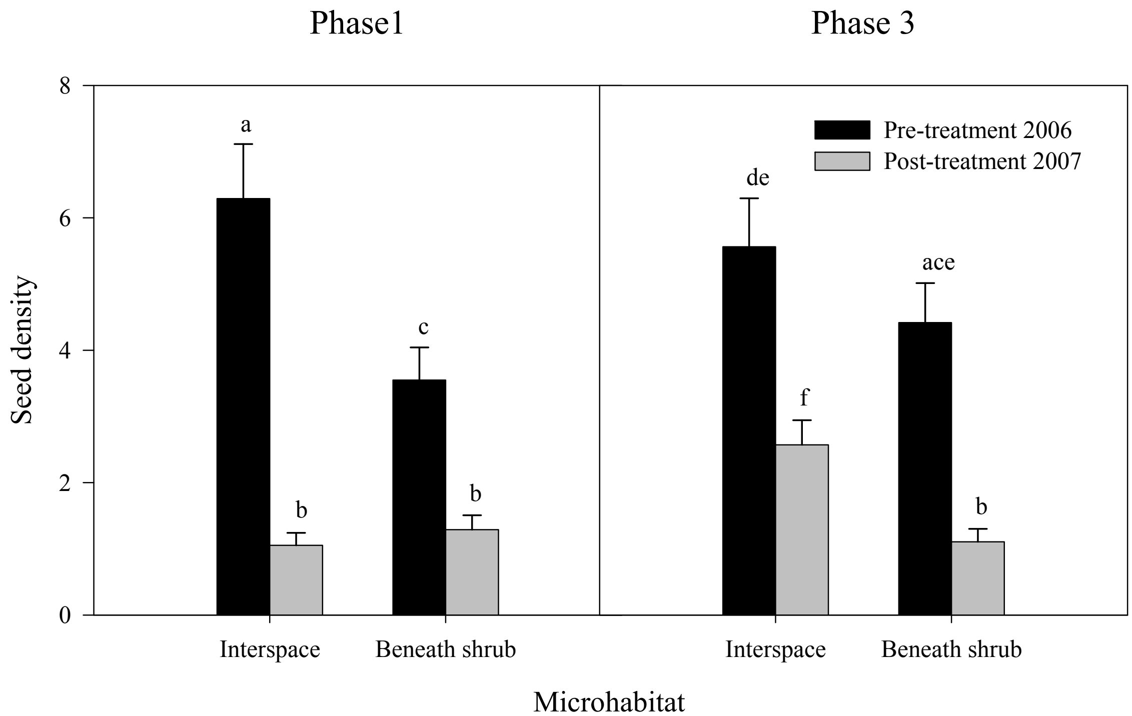


**Figure 3.13** Model 1 mean seed density of *C. testiculata* (+ 1 SE) as affected by phase, microhabitat, and collection time. Different letters indicate significant differences comparisons between treatment combinations sharing at least one factor level ($P < 0.05$).

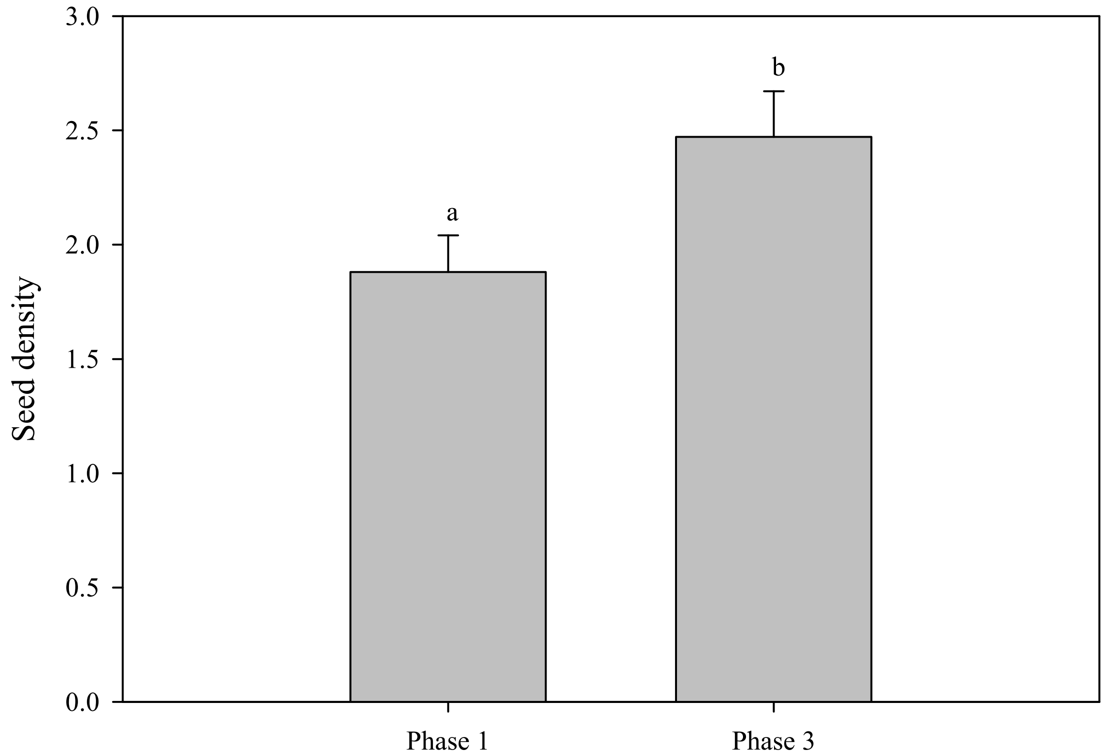


**Figure 3.14** Model 2 mean seed density *C. testiculata* (+ 1 SE) as affected by community phase. Different letters indicate significant differences ($P < 0.05$).

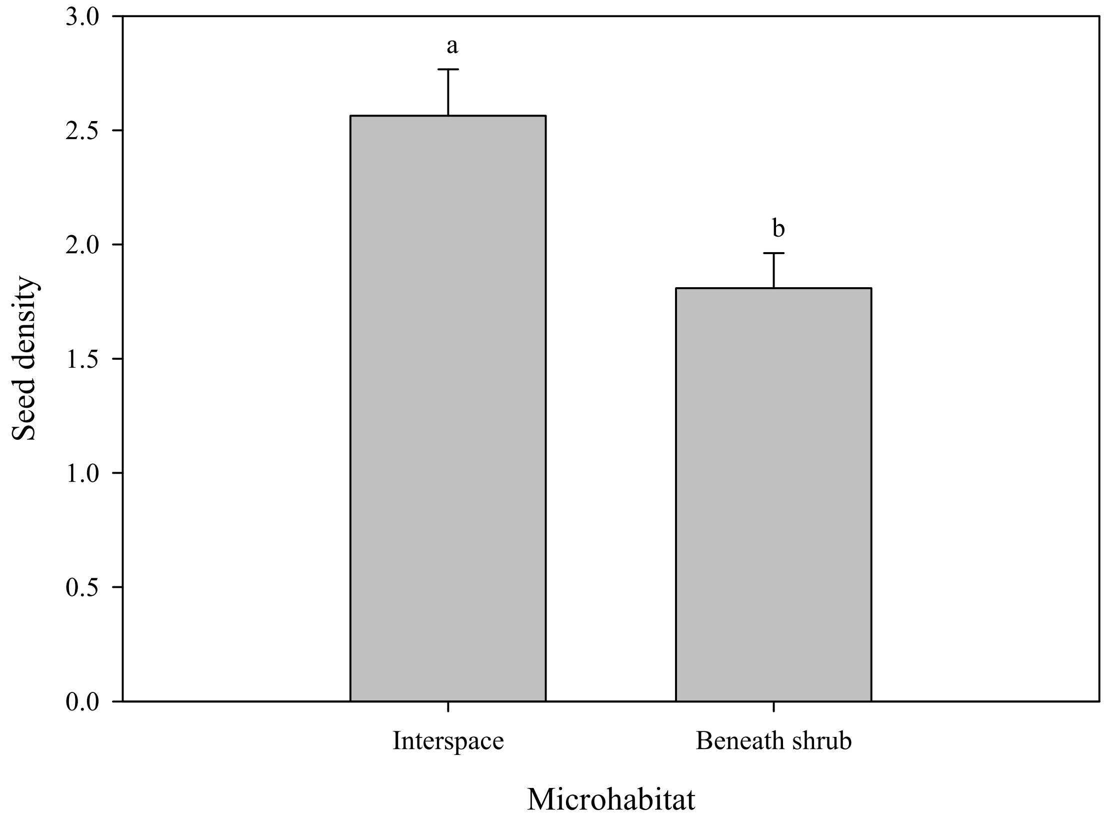


**Figure 3.15** Model 2 mean seed density *C. testiculata* (+ 1 SE) as affected by microhabitat. Different letters indicate significant differences ($P < 0.05$).

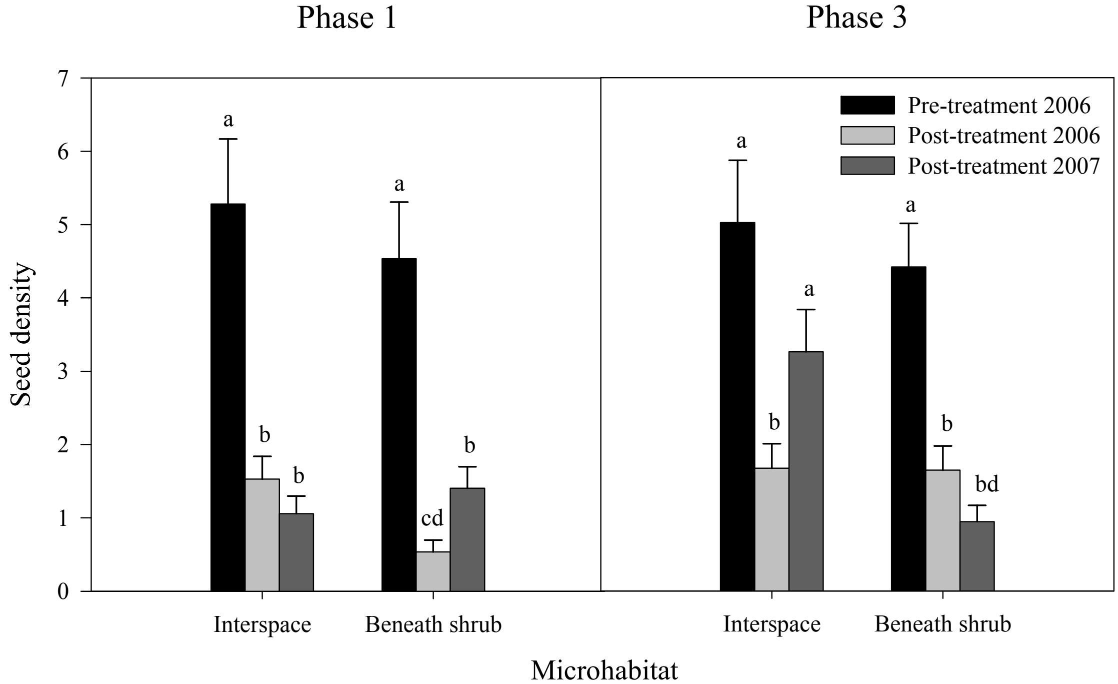


**Figure 3.16** Model 2 mean seed density of *C. testiculata* (+ 1 SE) as affected by phase, microhabitat, and collection time. Different letters indicate significant differences comparisons between treatment combinations sharing at least one factor level ($P < 0.05$).

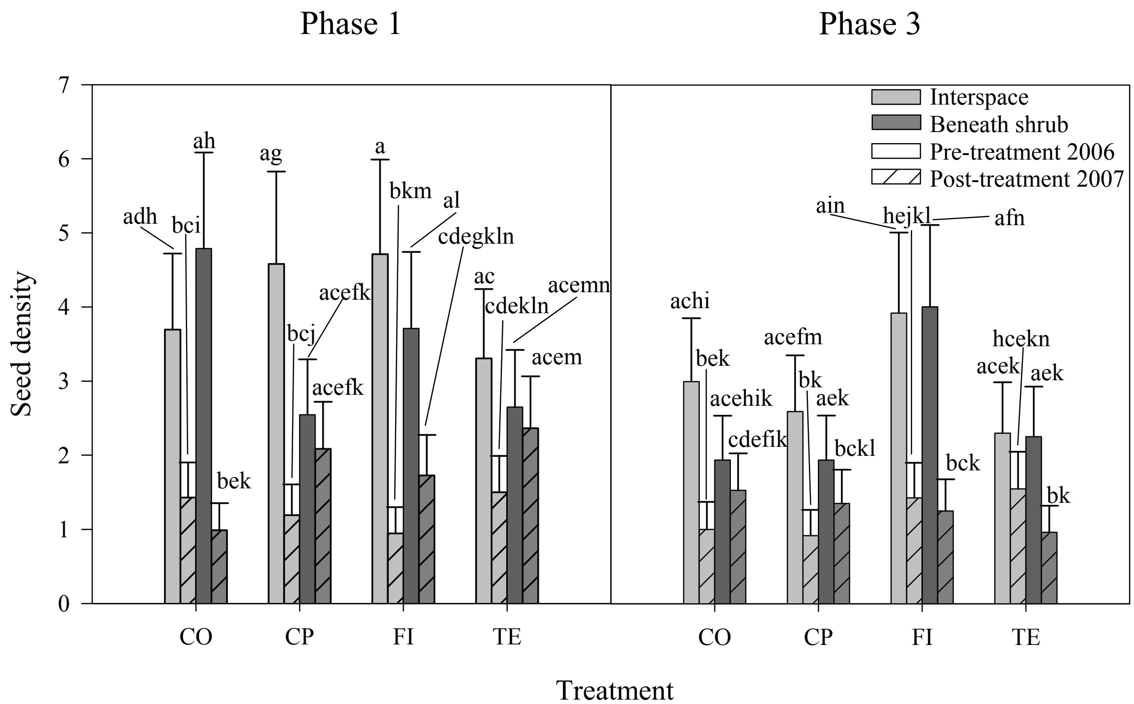


**Figure 3.17** Model 1 mean seed density of *P. secunda* (+ 1 SE) as affected by phase, microhabitat, collection time, and treatment (CO = Control, CP = Control-Plateau, FI = Prescribed Burn, TE = Tebuthiuron). Different letters indicate significant differences comparisons between treatment combinations sharing at least one factor level ($P < 0.05$).

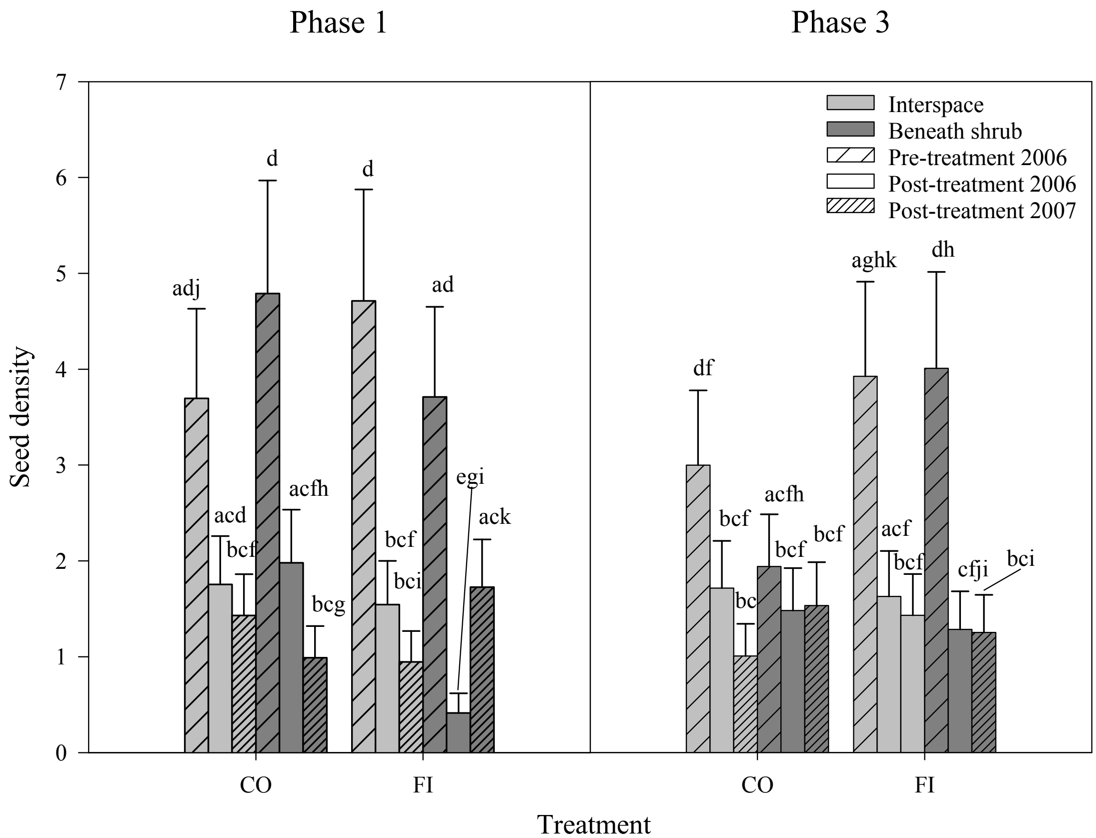


**Figure 3.18** Model 2 mean seed density of *P. secunda* (+ 1 SE) as affected by phase, microhabitat, collection time, and treatment (CO = Control, FI = Prescribed Burn) . Different letters indicate significant differences comparisons between treatment combinations sharing at least one factor level ($P < 0.05$).

# CHAPTER 4

# CONCLUSION

Degraded sagebrush communities in the Great Basin are at risk of conversion to cheatgrass-dominated systems. Habitat degradation has been a result of agricultural use, livestock grazing, exotic grass invasion, and altered fire regime (D'Antonio and Vitousek, 1992; Anderson and Inouye, 2001; Hemstrom et al., 2002). Great Basin restoration strategies often involve a disturbance such as prescribed fire or herbicide that reduces shrub abundance making resources more available. Disturbances can also activate the seed pool by creating opportunities for regeneration and germination of seeds from the seed pool (Kotanen, 1996; Bakker et al., 1996). The seed pool can serve as an important source of new propagules following restoration (Nishihiro et al., 2006). However, prior to this study, the effects of aboveground vegetation variables and restoration treatments on seed pools within the Great Basin have not been well documented.

In Chapter 2, I examined the influence of the aboveground vegetation on seed density, species richness, and seed pool community composition. The relationship between the seed pool and aboveground vegetation compositions differed according to the aboveground vegetation organizational level used for comparisons. When comparison between the two communities were made on the species level (using Sørensen's similarity index and Bray-Curtis distance) the seed pool and aboveground vegetation were dissimilar. In contrast, when using functional groups as the aboveground organizational level (in NMDS), the seed pool and the aboveground vegetation were moderately similar.

The effects of microhabitat (shrub interspace or beneath shrub) and aboveground community phase (high or low perennial bunchgrass cover) were also assessed. Shrubs were the only functional group affected by microhabitat alone with seed density being greater beneath shrubs than in interspaces, as expected. However seed density between micohabitat was influenced by plot, which demonstrates spatial variability in seed distributions. Total seed density, as well as annual forb, perennial grass, and *P. secunda* seed densities were higher in communities with higher perennial bunchgrass cover (phase 1 communities) than in communities with lower perennial bunchgrass cover (phase 3 communities). Variation in species richness was not well explained by microhabitat or community phase but appeared to vary spatially.

Chapter 3 evaluated the effects of restoration treatments on the seed pool as well as determined whether the pre-treatment seed pool or the aboveground vegetation was more similar to the vegetation following restoration. Both herbicides (tebuthiuron and Plateau) may have altered the community composition. In addition, the seed pool varied temporally as indicated by distinct pre-treatment and post-treatment communities in all treatments, including the control. Prescribed burn decreased seed densities of *B. tectorum*, *C. testiculata,* and *P. secunda*. The timing of soil seed pool collection did affect all four dominant species, *Alyssum desertorum*, *Bromus tectorum*, *Ceratocephala testiculata*, and *Poa secunda*. Collections before treatment (pre-treatment 2006) contained significantly more seeds than any other collection time which was likely due to temporal variability in the seed pool. Lastly, the post-treatment vegetation community was more similar to the pre-treatment vegetation community than the pre-treatment seed pool community, suggesting that the pre-existing vegetation is a better indicator of the vegetation following restoration than the seed pool.

One common theme throughout this research was the variability in the seed pool, both spatially and temporally. This variability makes it difficult to develop generalization about Great Basin seed pool communities. Nonetheless, I have provided evidence that aboveground vegetation variables do play a role in soil seed pool dynamics. Initial effects of restoration showed herbicides may have altered the seed pool community whereas prescribed fire decreased seed densities. However the long-term contribution of the seed pool to the aboveground still remains unclear. A long-term seed pool study may help determine how the effects of restoration treatments on the seed pool community influence the vegetation response to restoration.

**References**

Anderson, J.E., 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.

Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M., Thompson, K., 1996. Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanics Neerlandica 45, 461-490.

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

Hemstrom, M.A., Wisdom, M.J., Hann, W.J., Rowland, M.M., Wales, B.C., Gravenmier, R.A., 2002. Sagebrush-steppe vegetation dynamics and restoration potential in the Interior Columbia Basin, U.S.A. Conservation Biology 16, 1243-1255.

Kotanen, P.M., 1996. Revegetation following soil disturbance in a California meadow: the role of propagule supply. Oecologia 108, 652-662.

Nishihiro, J., Nishihiro, M.A., Washitani, I., 2006. Restoration of wetland vegetation using soil seed banks: lessons from a project in Lake Kasumigaura, Japan. Landscape and Ecological Engineering 2, 171-176.

# APPENDICES

**Table A.1** Relative abundance of species present in the germinable seed pool community prior to treatment implementation.

| Species | Symbol | Relative abundance | Functional group |
|---|---|---|---|
| *Ceratocephala testiculata* | cete5 | 40.5066 | annual forb |
| *Alyssum desertorum* | alde | 24.1800 | annual forb |
| *Poa secunda* | pose | 14.0844 | perennial grass |
| *Bromus tectorum* | brte | 8.6232 | annual grass |
| *Elymus elymoides* | elel5 | 2.8235 | perennial grass |
| *Descurainia incana ssp. incisa* | deini2 | 2.1972 | annual forb |
| *Artemisia tridentata ssp. wyomingensis* | artrw8 | 2.1647 | shrub |
| *Vulpia octoflora* | vuoc | 1.5161 | annual grass |
| *Sisymbrium altissimum* | sial2 | 1.2608 | annual forb |
| *Erodium cicutarium* | erci6 | 1.0447 | annual forb |
| *Typha spp.* | typha | 0.1705 | perennial forb |
| *Sphaeralcea munroana* | spmu2 | 0.1294 | perennial forb |
| *Conyza canadensis* | coca5 | 0.1287 | annual forb |
| *Lactuca serriola* | lase | 0.1202 | annual forb |
| *Epilobium ciliatum* | epci | 0.1187 | perennial forb |
| *Draba cuneifolia* | drcu | 0.1021 | annual forb |
| *Sonchus oleraceus* | sool | 0.0941 | annual forb |
| *Achnatherum hymenoides* | achy | 0.0926 | perennial grass |
| *Juncus arcticus ssp. littoralis* | juarl | 0.0534 | perennial forb |
| *Pascopyrum smithii* | pasm | 0.0463 | perennial grass |
| *Veronica anagallis-aquatica* | vean2 | 0.0421 | perennial forb |
| *Atriplex confertifolia* | atco | 0.0401 | shrub |
| *Lappula occidentalis* | laoco | 0.0395 | annual forb |

**Table A.1 continued** Relative abundance of species present in the germinable seed pool community prior to treatment implementation.

| Species | Symbol | Relative abundance | Functional group |
|---|---|---|---|
| *Arabis perennans* | arpe2 | 0.0390 | perennial forb |
| *Festuca idahoensis* | feid | 0.0342 | perennial grass |
| *Taraxacum officinale* | taof | 0.0325 | perennial forb |
| *Descurainia sophia* | deso2 | 0.0291 | annual forb |
| *Marrubium vulgare* | mavu | 0.0267 | perennial forb |
| *Pseudoroegneria spicata* | pssp6 | 0.0265 | perennial grass |
| *Tamarix ramosissima* | tara | 0.0254 | tree |
| *Camissonia spp.* | camis | 0.0242 | annual forb |
| *Digitaria sanguinalis* | disa | 0.0188 | annual grass |
| *Cirsium spp.* | cirsi | 0.0183 | perennial forb |
| *Nicotiana attenuata* | niat | 0.0159 | annual forb |
| *Matricaria discoidea* | madi6 | 0.0158 | annual forb |
| *Opuntia polyacantha* | oppo | 0.0154 | shrub |
| *Tragopogon dubius* | trdu | 0.0151 | annual forb |
| *Lepidium perfoliatum* | lepe2 | 0.0131 | anuual forb |
| *Sphaeralcea grossulariifolia* | spgr2 | 0.0127 | perennial forb |
| *Hordeum jubatum* | hoju | 0.0125 | perennial grass |
| *Setaria verticillata* | seve3 | 0.0123 | annual grass |
| *Juncus bufonius* | jubu | 0.0096 | annual forb |
| *Physaria spp.* | physa2 | 0.0083 | annual forb |
| *Polypogon monspeliensis* | pomo5 | 0.0062 | annual grass |
| *Gnaphalium palustre* | gnpa | 0.0056 | annual forb |
| *Gilia spp.* | gilia | 0.0040 | annual forb |

**Table A.2** Relative abundance of species present in the aboveground community prior to treatment implementation.

| Species | Symbol | Relative cover | Functional group |
|---|---|---|---|
| *Artemisia tridentata ssp. wyomingensis* | artrw8 | 29.2396 | shrub |
| *Poa secunda* | pose | 16.1771 | perennial grass |
| *Bromus tectorum* | brte | 13.0729 | annual grass |
| *Elymus elymoides* | elel5 | 10.4271 | perennial grass |
| *Ceratocephala testiculata* | cete5 | 10.3229 | annual forb |
| *Lepidium lasiocarpum* | lela | 4.6042 | annual forb |
| *Pascopyrum smithii* | pasm | 2.3646 | perennial grass |
| *Achnatherum hymenoides* | achy | 1.5000 | perennial grass |
| *Atriplex confertifolia* | atco | 0.5729 | shrub |
| *Descurainia incana ssp. incisa* | deini2 | 0.5000 | annual forb |
| *Ipomopsis congesta* | ipco5 | 0.3021 | perennial forb |
| *Sisymbrium altissimum* | sial2 | 0.1667 | annual forb |
| *Leymus cinereus* | leci4 | 0.0833 | perennial grass |
| *Chrysothamnus viscidiflorus* | chvi8 | 0.0729 | shrub |
| *Sphaeralcea munroana* | spmu2 | 0.0625 | perennial forb |
| *Opuntia polyacantha* | oppo | 0.0625 | shrub |
| *Juniperus osteosperma* | juos | 0.0417 | tree |
| *Sphaeralcea grossulariifolia* | spgr2 | 0.0313 | perennial forb |
| Unidentified annual exotic forb | ukfe2 | 0.0104 | annual forb |
| *Astragalus eurekensis* | aseu4 | 0.0104 | perennial forb |
| *Lathyrus pauciflorus* | lapau | 0.0104 | perennial forb |
| Unidentified annual exotic forb | ukhe1 | 0.0104 | annual forb |

**Table A.3** Relative abundance of species present in the germinable seed pool community after treatment implementation.

| Species | Symbol | Relative abundance | Functional group |
|---|---|---|---|
| *Ceratocephala testiculata* | cete5 | 32.4159 | annual forb |
| *Poa secunda* | pose | 22.1622 | perennial grass |
| *Alyssum desertorum* | alde | 20.2713 | annual forb |
| *Bromus tectorum* | brte | 5.7618 | annual grass |
| *Descurainia incana ssp. incisa* | deini2 | 5.6692 | annual forb |
| *Artemisia tridentata ssp. wyomingensis* | artrw8 | 3.9586 | shrub |
| *Elymus elymoides* | elel5 | 2.5891 | perennial grass |
| *Sisymbrium altissimum* | sial2 | 1.5297 | annual forb |
| *Vulpia octoflora* | vuoc | 1.3613 | annual grass |
| *Achnatherum hymenoides* | achy | 0.5473 | perennial grass |
| *Pseudoroegneria spicata* | pssp6 | 0.4104 | perennial grass |
| *Lactuca serriola* | lase | 0.4009 | annual forb |
| *Typha spp.* | typha | 0.3805 | perennial forb |
| *Taraxacum officinale* | taof | 0.3108 | perennial forb |
| *Camissonia spp.* | camis | 0.2976 | annual forb |
| *Sonchus oleraceus* | sool | 0.2855 | annual forb |
| *Epilobium ciliatum* | epci | 0.2136 | perennial forb |
| *Arabis perennans* | arpe2 | 0.1329 | perennial forb |
| *Lappula occidentalis* | laoco | 0.1268 | annual forb |
| *Sphaeralcea munroana* | spmu2 | 0.1228 | perennial forb |
| *Juncus arcticus ssp. littoralis* | juarl | 0.1186 | perennial forb |
| *Agropyron cristatum* | agcr | 0.1092 | perennial grass |
| *Conyza canadensis* | coca5 | 0.1004 | annual forb |
| *Draba cuneifolia* | drcu | 0.0909 | annual forb |
| *Tamarix ramosissima* | tara | 0.0757 | tree |
| *Descurainia sophia* | deso2 | 0.0694 | annual forb |
| *Nicotiana attenuata* | niat | 0.0533 | annual forb |
| *Erodium cicutarium* | erci6 | 0.0531 | annual forb |
| *Apocynum androsaemifolium* | apan2 | 0.0496 | perennial forb |
| *Pascopyrum smithii* | pasm | 0.0481 | perennial grass |
| *Veronica anagallis-aquatica* | vean2 | 0.0457 | perennial forb |
| *Salsola kali* | saka | 0.0446 | annual forb |
| *Polygonum persicaria* | pope3 | 0.0332 | annual forb |
| *Symphyotrichum falcatum* | syfaf | 0.0332 | perennial forb |
| *Hordeum jubatum* | hoju | 0.0258 | perennial grass |
| *Matricaria discoidea* | madi6 | 0.0258 | annual forb |
| *Cirsium spp.* | cirsi | 0.0223 | perennial forb |
| *Gilia spp.* | gilia | 0.0195 | annual forb |
| *Quercus spp.* | querc | 0.0187 | tree |
| *Opuntia polyacantha* | oppo | 0.0144 | shrub |

**Table A.4** Relative abundance of species present in the aboveground community after treatment implementation.

| Species | Symbol | Relative cover | Functional group |
|---|---|---|---|
| *Artemisia tridentata ssp. wyomingensis* | artrw8 | 18.6889 | shrub |
| *Ceratocephala testiculata* | cete5 | 8.8556 | annual forb |
| *Bromus tectorum* | brte | 8.4111 | annual grass |
| *Poa secunda* | pose | 8.3333 | perennial grass |
| *Elymus elymoides* | elel5 | 3.6333 | perennial grass |
| *Alyssum desertorum* | alde | 2.0667 | annual forb |
| *Pascopyrum smithii* | pasm | 1.4889 | perennial grass |
| *Achnatherum hymenoides* | achy | 0.9889 | perennial grass |
| *Ipomopsis congesta* | ipco5 | 0.3333 | perennial forb |
| *Atriplex confertifolia* | atco | 0.2333 | shrub |
| *Sisymbrium altissimum* | sial2 | 0.0778 | annual forb |
| *Lathyrus pauciflorus* | lapau | 0.0444 | perennial forb |
| *Opuntia polyacantha* | oppo | 0.0444 | shrub |
| *Descurainia incana ssp. incisa* | deini2 | 0.0444 | annual forb |
| *Lepidium perfoliatum* | lepe2 | 0.0333 | annual forb |
| *Juniperus osteosperma* | juos | 0.0222 | tree |
| *Leymus cinereus* | leci4 | 0.0222 | perennial grass |
| *Cryptantha spp.* | crypt | 0.0111 | annual forb |
| *Chrysothamnus viscidiflorus* | chvi8 | 0.0111 | shrub |
| *Tetradymia canescens* | teca2 | 0.0111 | shrub |
| *Allium spp.* | alliu | 0.0111 | perennial forb |

**Table A.5** Monthly and annual total precipitation averages (mm) measured by regional climate stations nearest to the Onaqui site. Blank cells indicate missing data.

| Station | Year | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Annual |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tooele, UT | 2000 | 44.96 | 61.48 | 39.87 | 49.02 | 42.67 | 1.27 | 12.44 | 34.78 | 62.99 | 74.43 | 23.11 | 21.85 | 468.87 |
| Tooele, UT | 2001 | 23.88 | 41.9 | 73.65 | 61.2 | 8.13 | 18.54 | 50.03 | 14.48 | 8.13 | 17.52 | 67.04 | 56.14 | 440.64 |
| Tooele, UT | 2002 | 23.87 | 4.57 | 56.13 | 87.11 | 23.37 | 10.42 | 10.91 | 2.03 | 51.82 | 41.92 | 25.15 | 8.12 | 345.42 |
| Tooele, UT | 2003 | 21.09 | 40.12 | 65.52 | 48.25 | 44.45 | 22.62 | 4.32 | 5.84 | 3.05 | 12.7 | 34.79 | 90.69 | 393.44 |
| Tooele, UT | 2004 | 16.76 | 117.09 | 18.28 | 85.1 | 27.19 | 20.06 | 4.06 | 11.43 | 20.07 | 92.72 | 31.23 | 7.37 | 451.36 |
| Tooele, UT | 2005 | 73.15 | 45.21 | 74.42 | 67.06 | 191.28 | 30.99 | 0 | 10.93 | 14.47 | 27.95 | 24.13 | 29.73 | 589.32 |
| Tooele, UT | 2006 | 70.62 | 28.19 | 83.07 | 75.18 | 18.03 | 21.84 | 41.13 | 10.16 | 52.57 | 57.65 | 15.75 | 33.78 | 507.97 |
| Tooele, UT | 2007 | 42.92 | 45.22 | 64.76 | 9.9 | 22.61 | 18.04 | 56.13 | 14.48 | 41.91 | 28.19 | 11.94 | 82.54 | 438.64 |
| Grantsville, UT | 2000 | 25.39 | 44.44 | 10.41 | 22.6 | 22.85 | 0.76 | 10.92 | 49.52 | 47 | 45.46 | 11.93 | 9.65 | 300.93 |
| Grantsville, UT | 2001 | 9.4 | 19.81 | | 21.08 | 1.27 | 3.81 | 39.38 | 8.88 | 6.85 | 4.57 | 39.12 | 23.87 | |
| Grantsville, UT | 2002 | 6.61 | 0.76 | 23.38 | 43.92 | 14.73 | 2.54 | 14.73 | 3.56 | 24.9 | 14.48 | 23.35 | 6.86 | 179.82 |
| Grantsville, UT | 2003 | 8.39 | | 17.28 | 22.36 | 25.15 | 10.66 | 10.92 | 6.6 | 2.55 | 2.29 | 28.21 | 41.41 | |
| Grantsville, UT | 2004 | 9.9 | 39.12 | 9.14 | 38.35 | 26.67 | 15.75 | 13.46 | 7.63 | 25.91 | 74.41 | 24.89 | 8.14 | 293.37 |
| Grantsville, UT | 2005 | 41.16 | 28.95 | 29.96 | 64.25 | 63.76 | 24.13 | | 5.85 | 5.33 | 8.13 | 16.76 | 18.03 | |
| Grantsville, UT | 2006 | 26.41 | 14.46 | 36.83 | 50.28 | 15.24 | 9.65 | 8.62 | 26.15 | 36.33 | 41.65 | 15.75 | 21.85 | 303.22 |
| Grantsville, UT | 2007 | 16.5 | 14.47 | 30.74 | 5.58 | 19.31 | 10.41 | 30.98 | 9.65 | 14.73 | 39.11 | 4.06 | 24.63 | 220.17 |
| Garfield, UT | 2000 | 51.82 | 60.96 | 38.33 | 40.9 | 44.96 | 12.45 | 26.16 | 84.32 | 43.94 | 57.4 | 44.7 | 37.33 | 543.27 |
| Garfield, UT | 2001 | | 35.04 | 41.66 | 49.03 | 4.31 | 43.43 | 92.2 | 18.8 | 3.3 | 14.22 | 100.58 | 56.38 | |
| Garfield, UT | 2002 | 17.28 | 6.85 | 45.98 | 86.12 | 34.29 | 8.13 | 5.83 | 7.88 | 46.48 | 30.74 | | 11.17 | |
| Garfield, UT | 2003 | 14.22 | 27.68 | 26.93 | 37.33 | 39.62 | 13.72 | 19.05 | 8.13 | | 11.43 | 50.31 | 64.25 | |
| Garfield, UT | 2004 | 10.42 | 57.15 | 26.15 | 83.3 | 34.8 | 10.41 | 6.1 | 7.87 | 53.08 | 108.7 | 29.2 | 9.4 | 436.58 |
| Garfield, UT | 2005 | 46.47 | 48.25 | | 76.95 | 123.45 | 65.03 | 4.32 | 10.92 | 9.14 | 33.53 | 29.97 | 32.26 | |
| Garfield, UT | 2006 | 37.09 | 18.53 | 57.39 | 69.35 | 29.97 | 22.6 | 15.23 | 35.56 | 72.89 | 44.45 | 31.99 | 25.65 | 460.7 |
| Garfield, UT | 2007 | 23.87 | 39.87 | 28.96 | 11.43 | 35.06 | 30.48 | 27.43 | 7.88 | 46.22 | 56.14 | 10.92 | 50.8 | 369.06 |

**Table A.6** Monthly and annual mean temperature (°C) measured by regional climate stations nearest to the Onaqui site. Blank cells indicate missing data.

| Station | Year | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Annual |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tooele, UT | 2000 | 2.5 | 4.7 | 6.2 | 13.2 | 17.1 | 22.8 | 27.6 | 26.9 | 19.1 | 11.8 | 0.6 | 0.9 | 12.8 |
| Tooele, UT | 2001 | 2.4 | 1.7 | 7.4 | 10.7 | 18.2 | 22.2 | 26.1 | 26.7 | 22 | 14.3 | 6.2 | 2.2 | 12.6 |
| Tooele, UT | 2002 | 1.5 | 0.6 | 4.2 | 11.5 | 16.2 | 22.8 | 28.1 | 24.9 | 19.1 | 10.1 | 3.6 | 1.8 | 11.7 |
| Tooele, UT | 2003 | 4.2 | 2.4 | 7.2 | 10.2 | 16.1 | 22.3 | 29.1 | 27 | 19.9 | 15.3 | 2.5 | 1.1 | 13.1 |
| Tooele, UT | 2004 | 4.6 | 1.3 | 9.2 | 11.1 | 16.1 | 21.4 | 25.7 | 23.7 | 18.7 | 12 | 3.4 | 0.2 | 11.3 |
| Tooele, UT | 2005 | 0.3 | 1.4 | 5.9 | 10 | 14.9 | 18.9 | 27.4 | 24.8 | 18.8 | 12.2 | 5.1 | 0.2 | 11.7 |
| Tooele, UT | 2006 | 1.6 | 1.2 | 4.9 | 11.9 | 17.7 | 23.6 | 27.9 | 25.1 | 17.7 | 10.4 | 5.6 | 0.6 | 12.3 |
| Tooele, UT | 2007 | 4.3 | 3.3 | 8.2 | 11.7 | 18.2 | 23.5 | 28.3 | 26.6 | 19.2 | 11.2 | 6 | 1.9 | 12.5 |
| Grantsville, UT | 2000 | 1.4 | 3.4 | 4.5 | 11 | 15.4 | 21.6 | 26.2 | 25.9 | 17.2 | 10.9 | 0.1 | 0.6 | 11.4 |
| Grantsville, UT | 2001 | 3.5 | 0.3 | | 9.1 | 16.8 | 20.5 | 25.6 | 24.9 | 20.2 | 12.5 | 5.4 | 3.5 | |
| Grantsville, UT | 2002 | 2.9 | 2.9 | 2.7 | 9.9 | 14 | 21.4 | 27 | 23.5 | 18.2 | 9.3 | 2.3 | 0.6 | 10.3 |
| Grantsville, UT | 2003 | 2.5 | | 6.4 | 9.5 | 14.9 | 20.6 | 28.2 | 26 | 18.1 | 13.7 | 2 | 0.5 | |
| Grantsville, UT | 2004 | 5.9 | 2.7 | 7.5 | 10.8 | 15.2 | 20.8 | 25.3 | 23.4 | 17.5 | 11.6 | 3.1 | 1 | 10.5 |
| Grantsville, UT | 2005 | 0.1 | 0.3 | 5.2 | 8 | 14.3 | 18.7 | | 24.3 | 17.3 | 11.2 | 4.6 | 1.3 | |
| Grantsville, UT | 2006 | 0 | 0.2 | 4 | 10.3 | 16 | 22.3 | 27.4 | 23.8 | 16.1 | 9.6 | 4.4 | 2.2 | 11 |
| Grantsville, UT | 2007 | 7.1 | 1.7 | 6.7 | 9.8 | 16.5 | 21.5 | 27.5 | 25.7 | 18.3 | 9.8 | 4.6 | 2.6 | 11 |
| Garfield, UT | 2000 | 3.1 | 5.1 | 6.7 | 14 | 18.3 | 24.4 | 28.9 | 27.6 | 20.7 | 13.2 | 2 | 1.4 | 13.8 |
| Garfield, UT | 2001 | | 2.6 | 8.8 | 11.6 | 19.7 | 23.6 | 27.9 | 27.8 | 22.8 | 15.1 | 7.5 | 0.6 | |
| Garfield, UT | 2002 | 1 | 0.7 | 5.5 | 12.4 | 17.4 | 24.1 | 29.7 | 26.3 | 20.4 | 11.5 | | 2.6 | |
| Garfield, UT | 2003 | 4.3 | 2.9 | 8.7 | 11.3 | 17.9 | 23.4 | 30.3 | 27.8 | | 15.4 | 3.5 | 1.8 | |
| Garfield, UT | 2004 | 3.9 | 1.2 | 9.8 | 12.4 | 17.2 | 22.8 | 27.6 | 24.7 | 19.3 | 12.5 | 4.4 | 0.9 | 12.2 |
| Garfield, UT | 2005 | 0.5 | 1.9 | | 10.7 | 15.9 | 20.4 | 28.7 | 26.5 | 19.4 | 12.8 | 5.9 | 0.2 | |
| Garfield, UT | 2006 | 1.2 | 1.5 | 5.3 | 12.7 | 18.2 | 24.6 | 29.1 | 26.3 | 18.3 | 11.3 | 6.1 | 0.2 | 12.9 |
| Garfield, UT | 2007 | 4 | 3.5 | 8.7 | 12.7 | 18.5 | 24.4 | 30 | 27.9 | 20.4 | 11.6 | 6.5 | 1.4 | 13.2 |