Final Report

29 May 2013

"Restoring Natural Fire Regimes at Golden Spike National Historic Site by Developing a Healthy Sagebrush/Grassland Vegetation Community to Prevent the Cheatgrass-Wildfire Cycle/Evaluating Restoration Seeding Techniques Using Native Herbaceous Species in Cheatgrass-Dominated Communities at Golden Spike National Historic Site"

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Final Report

The full details of our experiments and results are contained in the two M.S. theses attached to this report. Here I summarize the major findings and provide a set of preliminary recommendations.

Summary

1) Important note: Initial effects of treatments on perennial grass establishment could not be evaluated because perennial emergence in the year following treatment application was very limited in all treatments; samples were so low that they could not be analyzed. Analyses of cheatgrass from the first year are still possible.

2) Treatment Effects on Cheatgrass

    a. Imazapic pre-emergent herbicide application reduced cheatgrass weights and tiller and spikelet numbers during the first season after application, and these effects were generally greater in plots that were also burned or cleared of sagebrush overstories.

    b. However, in the second season after application, cheatgrass in herbicide-treated plots were larger and with greater tiller and spikelet numbers than in no-herbicide plots. These two results (2 and 3) suggest imazapic can provide a narrow window of opportunity for getting perennials established with reduced competition with cheatgrass, but only a narrow window.

    c. Thinning of sagebrush overstories either resulted in no effects of cheatgrass metrics (50% thinning) or resulted in increases in cheatgrass weights and tiller and spikelet numbers in both the first and second years post-treatment, as well as increased densities during the second growing season (100% thinning).

    d. As expected, burning decreased cheatgrass densities but increased individual cheatgrass weights and tiller and spikelet numbers during both growing seasons. This result is not unusual and again suggests that prescription fires might provide a narrow window of reduced cheatgrass competition for getting perennial grasses established.

    e. Sucrose addition reduced cheatgrass weights and tiller and spikelet numbers during the first season after treatment, but these metrics were increased in sucrose addition subplots during the second growing season. These results were expected based on nitrogen immobilization by microbes stimulated by C addition and once again suggest a narrow window of reduced cheatgrass competition for getting perennial grasses established.

    f. There was some indication AC sequestered herbicide and lessened some of its negative effects on cheatgrass during the first growing season, but there was no evidence that AC had any direct effects on cheatgrass metrics.

3) Treatment Effects on Availabilities of Micronutrient, Macronutrient, and Heavy Metal Soil Ions

    a. During the first time period (November 2008 to March 2009) availabilities of nitrate ($NO3^-$), phosphate ($H2PO4^-$), sulfate ($SO4^{2-}$), potassium (K^+), and manganese (Mn^{2+}) were increased in burned plots and availabilities of $NO3^-$ and $H2PO4^-$ were decreased in sucrose- treated subplots.

   b. In the second time period during the first growing season after treatments (March to June 2009), availabilities of NO_3^- were still greater in burned plots, and availabilities of ammonium (NH_4^+), aluminum (Al_3^+), and lead (Pb_2^+) were now also greater in burned plots. NO_{3-} availabilities were also still lower in sucrose addition subplots.

   c. During the third time period over the second winter post-treatment (November 2009 to March 2010), only availabilities of NO_{3-} and NH_{4+} were assessed. Burned plots still had greater availabilities of NO_{3-}, but no other treatment effects or interactions were significant. There was some indication from comparisons between the first and third time periods that NO_{3-} availabilities increased a great deal in sucrose addition subplots, although this trend was not significant.

   d. These results have implications for restoration. Increased nutrient availability after fire is common and can benefit annual weeds. Increased nitrogen availability in this study lasted at least to the start of the second growing season. The reductions in $NO3^-$ and $H2PO4^-$ with sucrose addition demonstrated nutrient immobilization which is expected to disproportionately harm annuals (see above). This immobilization effect only lasted a single growing season but could reduce cheatgrass vigor and seed production.

4) Treatment Effects on Perennial Grass Emergence

   a. Again, note that emergence the first year following treatment was too little to be meaningful and precluded analyses.

   b. In the third year post-treatment imazapic-treated plots had greater perennial emergence than did plots not receiving imazapic. Such an increase is not surprising given the effects of imazapic on cheatgrass but the reason for the long delay before seeing an effect is not clear.

   c. In the cheatgrass near monoculture sites (but not in the cheatgrass-invaded sagebrush sites) perennial grass emergence was increased in the burned plots two years post-treatment, likely due to the reduction in cheatgrass seed density by the fire (see below).

   d. One of the more important results is that increasing seeding frequency from a single year to 2 and 3 years resulted in increased perennial grasses, with 3 years of seeding yielding the largest increase. This suggests that in such harsh establishment conditions and without the ability to drill seeds into the soil the most effective approach to establishing perennial grasses might simply be to seed multiple years with some establishment occurring each year.

5) Treatment Effects n the Seed Bank

   a. The seed bank was strongly dominated by exotic species with cheatgrass being the most abundant species. In contrast, native perennial grasses were very rare.

   b. In the invaded sagebrush experiment one year post-application, herbicide reduced cheatgrass as well as overall exotic species seed bank densities.

c. In the cheatgrass near-monoculture experiment, the prescribed burn immediately as well as one year post-fire reduced cheatgrass seed bank densities.

d. Sucrose application also reduced cheatgrass seed bank densities one year post-application in the cheatgrass near-monoculture experiment.

e. No treatments were found to affect native species seed bank densities in either experiment.

Preliminary Recommendations

1) Re-establishing a healthy perennial grass understory at Golden Spike National Historic Site is an extreme challenge and will not be easily or quickly accomplished.

2) Several treatments can reduce cheatgrass seed banks; reduce the size, number, and or reproduction of cheatgrass; and potentially improve the chances of perennial establishment. Not all are feasible, economically viable, or ecologically desirable.

    a. **Sucrose application** immobilized both nitrogen and phosphorous, and reduced the vigor of cheatgrass and the seed bank densities of cheatgrass in the cheatgrass near-monoculture experiment. Such reductions have improved the success of perennial establishment in other studies although that was not detected here. However, sucrose is cost-prohibitive, and it is effective only a very short time. Other forms of cheaper easily decomposed carbon (e.g. sugar beet residue, fine saw dust) could be investigated but since the sucrose treatment gave only minimally favorable results it is likely not worth the investment at this time.

    b. **Imazapic application** was effective in both experiments at reducing cheatgrass vigor and in the invaded sagebrush experiment effective at reducing cheatgrass seed bank densities. Further, the reductions in cheatgrass were linked with an increase in perennial grass emergence, although there was a three-year delay in the response of perennials. However, we know from other studies that imazapic can affect desirable perennial emergence and even harm established *Poa secunda* so its use should be with caution.

    c. **Prescribed fire** effectively reduced cheatgrass seed banks in the cheatgrass near-monoculture experiment, but not in the invaded sagebrush experiment. However, prescribed fire increases nutrient availability which is beneficial for exotic weeds and kills sagebrush.

    d. **Thinning,** either partial or complete, did not produce any desirable results, and 100% thinning actually resulted in increased cheatgrass vigor.

    e. Similarly, **activated carbon application** had no effects, positive or negative.

    f. **Recommendations:**

        i. **At this time investment in <u>nutrient immobilization</u> is not advised**.

        ii. **Similarly, there is no justification for investing in <u>thinning sagebrush</u> or applying <u>activated carbon</u>**.

        iii. **<u>Imazapic</u> pre-emergent herbicide application is potentially useful for reducing weed competition <u>in cheatgrass-invaded sagebrush stands</u> while perhaps only minimally harming the existing vegetation. <u>If used, the recommendation is to not seed until the following year</u> – the herbicide should have reduced the cheatgrass and residual effects on seeded perennials should be less**.

        iv. **<u>Prescribed fire</u> is effective at reducing the cheatgrass seed bank densities in**

<u>sites that have been converted to near-cheatgrass monocultures</u> by fire in the past, despite the increased nutrient availability. <u>If crews are available it is recommended to burn these sites prior to seeding</u>. <u>Prescribed fire should not be used on cheatgrass-invaded sagebrush sites, however</u>.

3) Although it requires long-term investment of time and resources, repeated seeding across a number of years appears to be the most promising approach to slowly augment the understory of sagebrush stands to make them more resilient to fire. The suitability of the weather for establishment varies from year to year in a largely unpredictable manner so at the time of seeding (fall) it is not known how suitable the spring/summer conditions will be for establishment. In addition, without an ability to incorporate seeds into the soil it is unlikely that there will be sufficient grass establishment in any single year no matter how suitable the conditions are; establishment of seedlings from broadcast sown seeds is inherently low. Repeated seeding gives the opportunity to slowly add new individuals over several years – more in some years than others, but never substantial numbers. Thus the following preliminary recommendations:

    a. **Preliminary Recommendations:**

        i. **Repeatedly seed the same areas a minimum of three consecutive years. More years if grass densities are increasing but still insufficient**.

        ii. **This requires some investment in monitoring to know the effectiveness of repeated seedings**.

        iii. **Initially concentrate seeding in buffers around roads and parking areas**.

        iv. **However, before making a final recommendation our experimental plots should be censused at least one more time to compare perennial grass densities and/or cover in 1) subplots seeded only once, 2) subplots seeded for three consecutive years, and subplots randomly located outside our seedings**. Although no funding exists for this monitoring I am interested in attempting to do it myself.

8-1-2011

Effects of Non-Surface-Disturbing Treatments for Native Grass Revegetation on Cheatgrass (Bromus tectorum L.) Metrics and Soil Ion Availabilities

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EFFECTS OF NON-SURFACE-DISTURBING TREATMENTS FOR NATIVE GRASS REVEGETATION ON CHEATGRASS (*BROMUS TECTORUM* L.) METRICS AND SOIL ION AVAILABILITIES

by

Jan C. R. Summerhays

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

of

MASTER OF SCIENCE

in

Ecology

Approved:

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2011

ABSTRACT

Effects of Non-Surface-Disturbing Treatments for Native Grass Revegetation on Cheatgrass (*Bromus tectorum* L.) Metrics and Soil Ion Availabilities

by

Jan C. R. Summerhays, Master of Science

Utah State University, 2011

Major Professor: Eugene W. Schupp
Department: Wildland Resources

Several restoration methods intended to increase the success of aerially-seeded perennial grasses were assessed to determine their effects on cheatgrass metrics and soil nutrient bioavailabilities. These methods were: 1) imazapic herbicide application (140 g ai · ha^{-1}, 210 g ai · ha^{-1}, and no application [control]), 2) vegetation manipulation treatments (50% sagebrush overstory thinning, 100% sagebrush overstory thinning, sagebrush overstory and/or vegetative thatch burning, and no manipulation [control]), and 3) alternative seeding treatments (aerial seeding with raking, aerial seeding with activated carbon [AC] addition, aerial seeding with sucrose addition, and regular aerial seeding [control]). Treatments were arranged in 3-way factorial designs, which allowed main effects and interactions between treatments to be assessed. Responses were followed for two growing seasons following treatment.

Main effects of treatments and their interactions on cheatgrass metrics are described in Chapter 2. Herbicide reduced cheatgrass weights and tiller and spikelet numbers in 2009, but these variables were greater than in no-herbicide plots in 2010. Burning decreased cheatgrass densities but increased weights and tiller and spikelet numbers in both years. One hundred percent sagebrush thinning resulted in greater cheatgrass weights and tiller and spikelet numbers in both years and greater densities in 2010. Sucrose addition decreased cheatgrass weights and tiller and spikelet numbers in 2009, but increased these variables in 2010. An interaction between AC and herbicide treatment was observed, with AC potentially sequestering and lessening the negative effect of herbicide on cheatgrass. Aerial seeding with raking and 50% sagebrush thinning treatments were not found to significantly affect cheatgrass either year.

The effects of treatments (herbicide, 50% sagebrush thinning, aerial seeding on snow, and aerial seeding with raking treatments omitted) on soil nutrient availabilities are described in Chapter 3. We used ion exchange resin (IER) membrane probes to measure extractable quantities of 15 ions over three time periods following treatment applications. Burning resulted in short-term increases in many soil nutrient availabilities, including nitrate (NO_3^-), phosphate ($H_2PO_4^-$), and sulfate (SO_4^{2-}). Sucrose addition reduced availabilities of NO_3^- and $H_2PO_4^-$ during the first winter and growing season. No changes were detected with AC addition or 100% sagebrush thinning during any sampling time.

(129 pages)

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Jan C. R. Summerhays

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CHAPTER 1

INTRODUCTION TO RESEACH ON EFFECTS OF NON-SURFACE-DISTURBING TREATMENTS FOR NATIVE GRASS REVEGETATION ON CHEATGRASS (*BROMUS TECTORUM* L.) METRICS AND SOIL ION AVAILABILITIES

Cheatgrass (*Bromus tectorum* L.), an invasive annual grass thought to be native to Mediterranean Europe and parts of Asia, was most likely introduced to the American continent as a contaminant of grain and cattle feed in the mid 1800's (Knapp 1996; Mack 1981). This species was first discovered in the western U.S. in the 1880's and was considered a dominant species on western landscapes by the 1930's (Mack 1981). It is believed that improper livestock grazing practices in the 19th century led to severe reductions in perennial grass and forb cover in western ecosystems, thereby freeing resources for use by cheatgrass (Knapp 1996). Cheatgrass is currently found in all U.S. states and Canadian provinces (USDA, NRCS 2009) and is estimated to occur on approximately 22 million hectares (54 million acres) in the western U.S. (Belnap et al. 2005).

Cheatgrass invasion is highly problematic, especially in sagebrush steppe ecosystems. Cheatgrass is able to germinate, become established, and deplete soil moisture much earlier than native perennial grasses and is therefore easily able to outcompete these species at the seedling stage (Humphrey and Schupp 2004). Because this species' aboveground biomass dries out and becomes extremely flammable earlier in the season, increases in cheatgrass cover and subsequent decreases in fire-resistant perennial grass cover lead to more frequent and intense wildfires than occurred historically (Whisenant 1990; D'Antonio and Vitousek 1992). Shorter fire return intervals exclude sagebrush (*Artemisia tridentata* Nutt.), as this species does not resprout following fire (Knapp 1996). Many perennial grasses are able to survive and resprout following wildfire; however, high fire frequencies begin to exclude even the most fire-tolerant species (Whisenant 1990). Likewise, seeds of perennial plant species are lost from seed banks over time in frequently burned cheatgrass-dominated areas (Humphrey and Schupp 2001), and the establishment of new individuals from seed is greatly inhibited with increasing cheatgrass presence (Humphrey and Schupp 2004) such as accompanies wildfire (Peters and Bunting 1994). Cheatgrass seeds are also lost from seed banks in burned areas (Humphrey and Schupp 2001); however, the stimulated vigor of remaining cheatgrass individuals results in its rapid re-colonization of burned areas over time (Melgoza et al. 1990). These factors make natural reestablishment of perennial species into these areas extremely unlikely.

Augmenting populations of fire-resilient perennial grasses via active reseeding may be necessary to increase the resilience of sagebrush ecosystems so they are able to naturally recover following fire. Surface-disturbing mechanisms, such as drill seeding, are commonly used for perennial grass species seed incorporation in restoration areas. However, site characteristics such as steep slopes, rocky terrain, or the presence of cultural artifacts may make the use of heavy machinery undesirable, unfeasible, or prohibited. In situations such as these, aerial seeding (seeding from aircraft) is generally used; however, success of aerial seeding is generally much lower than with seed incorporation into the soil, and greater amounts of seed are often recommended (Monsen et al. 2004). The overall goal of our research is to determine if certain herbicide treatments, soil amendment additions, and/or vegetation manipulation treatments can alter the resource environment in ways that increase the success of aerially-seeded perennial grass species in cheatgrass-invaded areas.

Complex changes to soil nutrient cycling that both precede and result from cheatgrass invasion may make alterations to the resource environment necessary before successful reestablishment of native perennial species is possible. Anthropogenic soil disturbances such as grazing and agriculture are thought to have unlocked nutrients that had been stored in soil organic matter (SOM) for long periods of time, effectively shifting these ecosystems towards more mineralizing and less immobilizing environments (Haynes and Williams 1993; Norton et al. 2007). Larger quantities of mineralized soil nutrients (especially nitrate, NO_3^-) have been found to disproportionally benefit invasive annual species such as cheatgrass over low-nutrient-adapted native perennial species (Blumenthal 2005; Norton et al. 2007; Vasquez et al. 2008). Cheatgrass' success in the arid West may have been a result of its ability to rapidly colonize these recently disturbed, nutrient-rich areas and outcompete native species that had evolved under more conservative nutrient cycling regimes (Norton et al. 2007).

The physiological and phenological traits of cheatgrass result in changes to the composition and timing of organic matter inputs into the soil in invaded areas (Hooker et al. 2008) that may also inhibit the successful reestablishment of perennial grasses. As cheatgrass is much more shallowly rooted than the native perennial shrub, grass, and forb species it displaces, nitrogen (N) and carbon (C) inputs into the soil become restricted to near-surface soil horizons with increasing cheatgrass dominance (Hooker et al. 2008). Likewise, the annual life history strategy of cheatgrass results in total root turnover yearly, resulting in increased nutrient cycling rates over historical conditions in these shallower soil layers (Booth et al. 2003; Saetre and Stark 2005; Hooker et al. 2008). NO_3^- accumulation has been detected under cheatgrass near-monocultures during summer months (Svejcar and Sheley 2001; Booth et al.2003; Sperry et al. 2006; Hooker et al. 2008); this is thought to be a result of the competitive exclusion of perennial grasses that actively acquire this nutrient longer in the summer (Hooker et al. 2008). Greater NO_3^- availability, greater surface C and N pools, and faster nutrient cycling create conditions well-suited for the continued dominance of cheatgrass in invaded areas.

Methods for increasing the success of seeded perennial grasses though resource environment manipulations have been subject to a great deal of scientific testing in the past few years. Burning, mechanical removal, and herbicide treatment of existing vegetation is done to increase overall resource availability, which could in theory benefit seeded perennial species and increase their chances for establishment. Although wildfires are known to increase cheatgrass presence, prescribed burning could benefit seeded perennials in the short-term by reducing resource competition from established species, increasing soil inorganic N (Blank et al. 1994; Esque et al. 2010) and reducing cheatgrass seed in seed banks (Humphrey and Schupp 2001; Keeley and McGinnis 2007). Sagebrush removal also reduces competitive pressure and increases soil nutrient availability (Blank et al. 2007) and number of days of available soil moisture (Prevéy et al. 2010). The application of imazapic pre-emergent herbicide is also being widely studied to reduce the presence of cheatgrass or other problematic species (Shinn and Thill 2002; Monaco et al. 2005; Kyser et al. 2007; Sheley et al. 2007; Morris et al. 2009). Although its effects on perennial species are variable (Shinn and Thill 2004; Sheley et al. 2007), reductions in cheatgrass presence following application could increase the establishment of seeded native perennials through reduced competition for soil resources.

Other treatments more directly address soil resource availability; soil amendments with C addition and activated carbon (AC) addition may be useful in altering the resource environment in ways that harm invasives and have less effect on natives. Soil C additions are commonly used to stimulate the activity of soil heterotrophic microbes to immobilize soil NO_3^-, thereby disadvantaging high-N adapted invasive annual species such as cheatgrass , although effects on perennial species and the overall success of these experiments have been mixed (Redente et al. 1992; Morghan and Seastedt 1999; Paschke et al. 2000; Blumenthal et al. 2003; Lowe et al. 2004; Corbin and D'Antonio 2004; Prober et al. 2005; Rowe et al. 2009; Perry et al. 2010; James et al. 2011; Mazzola et al. 2011). AC addition to the soil is a fairly new treatment with the potential to decrease cheatgrass presence and benefit native perennials, possibly due to its ability to sequester organic molecules and thereby alter soil nutrient cycling and/or plant-soil feedback signaling (Kulmatiski and Beard 2006; Kulmatiski 2011).

Gaps in understanding exist with many of these treatments in regard to reasonable application rates, how they interact with each other, and their actual effects on cheatgrass and soil ion availabilities. It is the goal of this thesis to present the results of studies testing the effects of the above restoration treatments and their combinations on measures of cheatgrass performance (Chapter 2) and soil ion availabilities (Chapter 3). These results will hopefully provide valuable information to restoration ecologists and land managers making decisions about how to best reincorporate native perennial grass species into cheatgrass-invaded ecosystems to break the cheatgrass-wildfire cycle.

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CHAPTER 2

EFFECTS OF NON-SURFACE DISTURBING RESTORATION TREATMENTS ON CHEATGRASS METRICS IN INVADED SAGEBRUSH ECOSYSTEMS AND FIRE-CONVERTED ANNUAL GRASSLANDS

Abstract. Cheatgrass (*Bromus tectorum* L.), an invasive annual grass, has become established in rangelands in the western U.S., increasing fire frequencies and leading to losses of native plant species over time. Reestablishment of native perennial grasses into these systems to interrupt the cheatgrass-wildfire cycle is inhibited by intense competitive pressure by cheatgrass at the seedling phase; reintroduction of desired species may depend on successful reduction of cheatgrass densities and performance. We tested several restoration treatments intended to increase successful establishment of seeded perennial grasses in cheatgrass-invaded communities. These were: 1) pre-emergent herbicide (imazapic) treatment, 2) vegetation manipulation treatments (burning of sagebrush overstory and/or vegetative thatch, and 50% or 100% thinning of sagebrush overstory), and 3) alternative seeding treatments (sucrose addition, activated carbon [AC] addition), as well as relevant control treatments. The main effects and interactions of these treatments on cheatgrass metrics were followed for two growing seasons after application. Pre-emergent herbicide significantly reduced per individual cheatgrass dry weights, and tiller and spikelet numbers as compared to in no-herbicide plots during the first growing season after treatment; however, these metrics were all significantly greater in herbicide-treated plots than in no-herbicide plots during the second season. Herbicide results were more significant in the first season with removal of sagebrush overstories and cheatgrass thatch. Burning decreased cheatgrass densities and increased mean weights and tiller and spikelet numbers during both growing seasons. Sagebrush 100% thinning increased cheatgrass

weights and tiller and spikelet numbers during the first and second seasons as compared to no manipulation plots, with densities also becoming significantly greater during the second season. Sucrose addition reduced cheatgrass weights, tiller numbers, and spikelet numbers during the first season; however, these metrics were greater and densities were decreased in sucrose addition subplots than in regular aerial seeding subplots during the second season. AC addition resulted in no direct effects on cheatgrass either season; however, AC addition appeared to sequester herbicide and reduce its impact on cheatgrass during the first growing season. This information will be useful to managers deciding how to best assist reestablishment of seeded perennial grasses in cheatgrass-invaded systems.

INTRODUCTION

Cheatgrass (*Bromus tectorum* L.) is an invasive annual grass whose native range includes much of central and Mediterranean Europe, southwest Asia, and extreme northern parts of Africa (Hitchcock 1935; Morrow and Stahlman 1984; Upadhyaya et al. 1986; Novak and Mack 2001). Cheatgrass has become a dominant plant in many communities in the western United States since its first documented occurrences in Idaho, Utah, and Washington in the mid-1890's (Mack 1981; Knapp 1996). Current estimates place cheatgrass invasion at approximately 22 million hectares (54 million acres) in the western U.S. (Belnap et al. 2005a).

Cheatgrass is thought to have been a successful colonizer of western rangelands due mainly to the severe reduction of native perennial grass cover and soil disturbance caused by poor livestock grazing practices beginning in the middle of the 19th century (reviewed in Mack 1981 and Knapp 1996). The reduction of native perennial grass cover by overgrazing increased sunlight, water, and soil nutrient availability for cheatgrass (Mack 1981; Knapp 1996). Likewise, soil disturbance from overgrazing and agriculture created greater soil surface area and increased the activity of soil microbes (Belnap et al. 2005b), which resulted in increased soil resource availability (Norton et al. 2007) and subsequent increased ecosystem invasibility (Davis et al. 2000; Shea and Chesson 2002). Cheatgrass relies on easy-to-access, mineralized forms of soil nutrients for its rapid growth (Norton et al. 2007), and like many other ruderal species, it has evolved mechanisms to allow it to respond quickly to resource pulses and to use abundant nutrients to a greater degree than can slow-growing native perennial plants (Bilbrough and Caldwell 1997; Grime et al. 1997; Blumenthal 2005; Norton et al. 2007; Vasquez et al. 2008).

Fire frequencies have increased dramatically over historical conditions in areas where cheatgrass cover is high and native, fire-resilient perennial grass species have become sparse (Whisenant 1990). Cheatgrass plants generally have a higher specific leaf area, lower root-to-shoot ratio and higher leaf tissue C:N and lignin:N ratios than the perennial species they displace (Evans et al. 2001; Monaco et al. 2003a; James 2008). These factors, coupled with the arid climactic conditions of these sites, result in reduced litter decomposition rates and increased annual accumulation of fine fuels which burn readily and frequently (Knapp 1996; Evans et al. 2001). Sagebrush-steppe ecosystems are especially sensitive to frequent fire; sagebrush does not resprout and germination and reestablishment of both sagebrush and perennial grasses from seed can take many years (Klemmedson and Smith 1964; West and Hassan 1985; Knapp 1996). Natural reestablishment of native plants in cheatgrass-dominated areas is also hindered by a loss of perennial seed bank over time (Humphrey and Schupp 2001). Perennial seeds that do germinate in cheatgrass-dominated areas are easily outcompeted by cheatgrass; this species' early emergence and growth under cool conditions allow it to begin depleting soil moisture before native perennials emerge, making it a better competitor at the seedling establishment stage (Harris 1967; Melgoza et al. 1990; Humphrey and Schupp 2004; Blank 2010). However, mature, established native bunchgrasses are more resistant to the detrimental effects of competition from cheatgrass (Cline et al. 1977; Melgoza et al. 1990; Nasri and Doescher 1995; Humphrey and Schupp 2004).

Active reintroduction of native, fire-resilient perennial grasses that are able to reach maturity may be the key to increasing the resilience of these ecosystems so that they recover following fire rather than convert to near-monocultures of cheatgrass. However, high densities of cheatgrass can make successful reseeding extremely difficult; reducing the size, reproductive capacity, and density of cheatgrass may be necessary before the successful reestablishment of fire-resistant perennials is possible. This is likely especially true in areas where ground disturbing drill-seeding is not feasible or allowed, such as with steep topography or when cultural artifacts are present.

We tested several restoration treatments that have been shown to or are theorized to increase the success of seeded perennial grasses in cheatgrass-invaded areas without the use of soil surface-disturbing mechanisms. These treatments were: 1) pre-emergent herbicide (imazapic) application, 2) vegetation manipulation treatments (burning of sagebrush overstory and/or vegetative thatch, and sagebrush overstory partial or total thinning), and 3) alternative seeding treatments (aerial seeding on snow, aerial seeding with sucrose addition, and aerial seeding with activated carbon [AC] addition). Control treatments were also implemented as appropriate (see Methods). The focus of the present paper is only on how these treatments affected cheatgrass metrics (density, weight, number of tillers, and number of flowering spikelets [a measure of reproductive output]); these results form a foundation for eventually developing an understanding of mechanisms that inhibit or enhance perennial grass seedling establishment. Future work (Reinwald et al., in process) will focus on how cheatgrass metrics within treated plots affected the establishment of seeded native perennial grasses,

Justifications for included treatments are as follows (experimental designs and treatment details are described in the Methods section). As the aerial seeding on snow treatment was not expected to alter cheatgrass metrics, it is omitted from this stage of analysis and not described here.

Imazapic pre-emergent herbicide is effective against invasive grasses such as cheatgrass and medusahead (*Taeniatherum caput-medusae* [L.] Nevski) while still allowing some but variable levels of perennial grass seedling emergence (Shinn and Thill 2002, 2004; Monaco et al. 2005, Kyser et al. 2007; Sheley et al. 2007; Morris et al. 2009; Davies 2010). There is some uncertainty, however, about appropriate rates of application and how this treatment could interact with other restoration treatments.

Burning removes overstory species, which could free resources for use by seeded species. Burning also reduces cheatgrass seed in subsequent seasons (Humphrey and Schupp 2001; Keeley and McGinnis 2007) and increases the availability of inorganic N in the soil (Blank et al. 1994; Esque et al. 2010), both of which may be beneficial for seeded perennial species. Burning also removes thatch, which increases light availability at the soil surface (Zhou and Ripley 1997) potentially for use by perennial seedlings and increases the effectiveness of herbicide on undesirable species (Monaco et al. 2005; Kyser et al. 2007; Sheley et al. 2007). Mechanical sagebrush removal is known to increase soil nutrient levels (Blank et al. 2007) and increase days of available soil moisture (Prevéy et al. 2010), which could increase the availability of these resources to seeded perennial species without the large increases in soil inorganic N or changes to seed banks that occur with burning. It is unknown whether partial thinning of sagebrush might have the same effect as total thinning, however.

Soil C (e.g. sucrose, sawdust) additions have been shown to negatively affect invasive species such as cheatgrass through the reduction of soil inorganic N levels (McLendon and Redente 1992; Zink and Allen 1998; Morghan and Seastedt 1999; Paschke et al. 2000; Blumenthal et al. 2003; Monaco et al. 2003a; Corbin and D'Antonio 2004; Prober et al. 2005; Blumenthal 2009; Brunson et al. 2010; Mazzola et al. 2011). The application of high C materials increases soil C:N ratios and stimulates soil heterotrophic microbe activity (Bengtsson et al. 2003; Knops et al. 2002), which consume the C and immobilize soil inorganic N (nitrate [NO_3^-] and ammonium [NH_4^+]) in their biomass (Baer et al. 2003). Because fast-growing annual species such as cheatgrass thrive with increasing inorganic N availabilities (Vasquez et al. 2008), such N immobilization is thought to be more harmful to them than to slow-growing perennial species that are adapted to low nutrient availability (Wedin and Tilman 1990; McLendon and Redente 1992; Redente et al. 1992). Also, reduced N availability has not been found to inhibit germination of perennial seeds (Monaco et al. 2003b). Sucrose is often used as a C source in experiments due to its constant C content (42.1% C by mass) and its ability to cause rapid immobilization. Although soil C addition can be effective at reducing N availability and invasive species biomasses, these effects are known to be short-term (Zink and Allen 1998; Morghan and Seastedt 1999; Monaco et al. 2003a). Also, the immobilization of soil N may not be able to sufficiently disadvantage invasive annuals in relation to desirable perennials or increase perennial presence in these areas in the long run (James et al. 2011).

AC has also been suggested as a soil additive for use in restoration of cheatgrass-invaded areas. AC is a charcoal-like material with extremely high surface porosity created by super-heating certain carbonaceous materials (e.g. coconut husks or wood); organic molecules are attracted and held inside its micropores via van der Waals forces (Cheremisinoff and Morresi 1978; Marsh 1989). Preliminary trials have shown that high levels of AC incorporated into the soil can reduce cover of cheatgrass and other invasive species (Kulmatiski and Beard 2006; Kulmatiski 2011), although the reasons for this are unclear. The reduction of organic compounds in the soil could result in reduced mineralization rates of nutrients (e.g. Rhodes et al. 2010), which would be expected to disproportionally harm cheatgrass. AC may also sequester organic compounds used as substrate or for growth signaling by microorganisms, thereby interrupting positive plant-soil feedbacks (processes by which plants affect soil structure, chemistry, and biology [Kulmatiski et al. 2008]), that may be occurring under cheatgrass and increasing its persistence in an invaded area (Kulmatiski and Beard 2006; Kulmatiski 2011). It is currently unknown if surface applications of realistic quantities of AC in areas where soil disturbance is precluded would be effective at altering soil nutrient availability and potentially negatively affecting cheatgrass.

Experiments to test the effectiveness of these treatments were established in two distinct plant community types: 1) cheatgrass-invaded areas with intact sagebrush overstories and depleted perennial understories and 2) cheatgrass-dominated areas without sagebrush overstories. The experiment implemented in the area with intact sagebrush cover, referred to as the “sagebrush” experiment, was specifically aimed at determining methods for establishing perennial grasses into the understory of degraded, cheatgrass-invaded sagebrush so they can recover following wildfire instead of converting to cheatgrass near-monocultures. The experiment situated in a cheatgrass-dominated site, referred to as the “cheatgrass” experiment, was aimed at determining how to improve the success of seeding perennial grasses into near-monocultures of cheatgrass. The designs of these experiments allowed us to focus analyses on interactions between treatments, which are currently largely unknown, as well as main effects. Here we address the following questions: 1) How do main effects of treatments alter cheatgrass metrics, 2) How do treatments interact to affect cheatgrass metrics, and 3) What combination of treatments results in the greatest reduction of cheatgrass metrics over the course of the experiments?

METHODS

Study Site

Golden Spike National Historic Site in Box Elder County, Utah, 32 miles west of Brigham City (lat 41°37′13.73″, long 112°32′50.9″), was historically a sagebrush-steppe ecosystem. Similar to many sagebrush ecosystems, the site and its surrounding land have been subject to over a century of disturbance including grazing, agriculture, landform manipulation, and wild and prescribed fire (Homstad et al. 2000; Thornberry-Ehrlich 2006). These stressors have led to ecological degradation and a sagebrush understory nearly completely lacking in perennial grasses and forbs and dominated by cheatgrass (Monaco 2004). As such, these areas are particularly prone to conversion to cheatgrass-dominated systems by wildfire, as has already happened to some areas within the site (Monaco 2004). Because of the presence of cultural resources, ground-disturbing mechanisms such as drill seeding or use of other heavy machinery are prohibited throughout the site.

General Background

Study plots for the two experiments were established in May 2008. The sagebrush experiment was situated in areas with intact sagebrush cover (52.7% sagebrush cover, data from pre-treatment vegetation surveys of all plots using line-point intercept method). The cheatgrass experiment was located in an area that was burned as part of management activities in 1998 and no longer has a sagebrush overstory. This area had significantly higher pretreatment densities of cheatgrass (115.8 tillers · 100 cm^{-2}, *SE* ± 17.1) than in the sagebrush experiment (21.9 tillers · 100 cm^{-2}, *SE* ± 5.1, $p = 0.0020$; Table 2.1), as is typically found with the loss of sagebrush overstory (Prevéy et al. 2010). However, there were no significant differences between pretreatment measures of cheatgrass individual mean weights, mean tiller numbers, and mean spikelet numbers in the two experiments (Table 2.1).

The experimental designs and treatment factors for these two experiments, discussed separately below, differed due to site characteristics, logistical considerations, and differences in experimental goals. All treatment assignments were made randomly.

Sagebrush Overstory (Sagebrush) Experimental Design and Treatments

In the sagebrush experiment, plots were arranged in four replicate sites, each with eight whole plots. Two replicates were near the park visitor's center and the other two were on a hill adjacent to the east auto tour road. Plots in a replicate were haphazardly distributed across the available area in locations with similar slope, aspect, and vegetative cover. Whole plots were 7 x 19.5 m, with each plot divided lengthwise into three middle (3.5 x 7 m) and two end (4.5 x 7 m) subplots (total number of subplots = 5). A 1.5 x 3 m disturbance-free sampling area was established in the center of each subplot prior to application of treatments, which allowed for 2 m buffers between adjacent sampling areas and between sampling areas and the outside edges of the greater treatment plot.

Four of the eight plots in a replicate were randomly selected to be treated with imazapic (trade name Panoramic 2SL) pre-emergent herbicide. Selected plots were treated with this herbicide on 18 November 2008 using a five nozzle boom sprayer mounted on an all-terrain vehicle and calibrated to deliver 140 g ai · ha^{-1} (2 oz ai · acre^{-1}). At the time of application, fall emergence of cheatgrass was minimal.

Four vegetation manipulation treatments were randomly assigned to whole plots within each herbicide treatment level: 1) burning of sagebrush overstory, cheatgrass thatch, and vegetative understory ('burned'), 2) 100% thinning and removal of sagebrush overstory ('100% thinned'), 3) 50% thinning and removal of sagebrush overstory ('50% thinned'), and 4) no manipulation to sagebrush overstory ('no manipulation'). Thinning and burning treatments were implemented on 25 August and 5 September 2008 by Zion National Park Fire Use Module employees. Burning was done using handheld drip torches; areas outside the desired burn area were wetted before and during burning of plots to prevent the spread of the fire. Thinning and clearing of sagebrush was done with chainsaws, with half of sagebrush individuals in the 50% thinned plots having been pre-marked for removal. Removal of half the individuals in these plots reduced sagebrush cover by 26.0% (44.6% sagebrush cover pre-treatment, 33.1% sagebrush cover post-treatment, data from all 50% thinned plots using line-point intercept method). 'No manipulation' plots were not treated with any of the above vegetation manipulation treatments.

Five seeding treatments were randomly assigned to subplots within a plot: 1) aerial seeding with sucrose ('sucrose addition'), 2) aerial seeding with AC ('AC addition'), 3) aerial seeding over snow, 4) aerial seeding with soil surface raking ('raked'), and 5) regular aerial seeding without any of the above modifications ('regular aerial seeding'). Sucrose addition was at a rate of 360 g · m^{-2} (151.6 g C · m^{-2}) divided between two applications of 180 g · m^{-2} (75.8 g C · m^{-2}) each; the first application was immediately following seeding (20 - 26 October 2008) and the second was the following spring (28 and 29 March 2009). AC addition was done with 12 x 30 mesh size AC derived from superheated coconut husks (AquaSorb CS, Ecologix Environmental Systems), applied at a rate of 100 g · m^{-2} with a handheld spreader immediately after seeding. Again, seeding over snow is included in this treatment structure but omitted from this stage of analysis as it is not expected to alter cheatgrass metrics. The raked treatment, which was meant to serve as a form of control mimicking the effects of drill seeding, involved disturbing the soil surface with a garden rake immediately before and after seed broadcasting. Regular aerial seeding had no additional manipulations beyond seeding.

Each subplot, regardless of seeding treatment, was seeded with the same mix of native grass species: squirreltail (*Elymus elymoides* [Raf.] Swezey), Great Basin wildrye (*Leymus cinereus* [Scribn. & Merr.] A. Löve), needle-and-thread grass (*Hesperostipa comata* [Trin. & Rupr.] Barkworth), Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth), Sandberg bluegrass (*Poa secunda* J. Presl), and bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve ssp. *spicata*), at a rate of 100 viable seeds · $species^{-1}$ · m^{-2}. Pure Live Seed (PLS) rates provided by seed supplier (Granite Seed, Lehi, UT) were used to calculate actual total quantities of seeds to be applied per subplot in order to reach targeted application of viable seeds. All seeding treatments relevant to this stage of analysis were applied between 20 - 26 October 2008. Seeding was done with a handheld seed broadcaster, and pre-weighed packets of seeds were mixed into a set quantity of rice hulls for suspension to ensure adequate distribution within plots. In this experiment, quantities of rice hulls used were 2.5 L for end subplots and

1.75 L for middle subplots. Cardboard shields were used around subplot perimeters to contain the seeding mixture within the desired subplot.

The four seeding treatments, four vegetation manipulation treatments, and two herbicide treatments were arranged in a split-split plot experimental design, which allowed for a total of 32 treatment combinations within each replicate.

Cheatgrass-Dominated (Cheatgrass) Site

Experimental Design and Treatments

Eight 18 x 21 m plots were established in an area dominated by cheatgrass and without sagebrush cover below the eastern end of the east auto tour road. Plots were selected to minimize differences in slope, aspect, and vegetative cover. Plots were situated with their bases (18 m side) running perpendicular to the slope of the hill, in a general NW to SE direction. Each plot was divided into nine 6 x 7 m subplots in a 3 x 3 grid. Each whole plot was randomly assigned to one of two vegetation manipulation treatments: 1) burning of cheatgrass thatch (‘burned’) or 2) no manipulation to cheatgrass thatch (‘no manipulation’), with a total of four plots receiving each treatment. Burning was done on 25 August 2008 by the Zion National Park Fire Use Module.

Each of the nine subplots was assigned a combination of one of three herbicide treatments crossed with one of three seeding treatments. The lowermost row (or ‘strip’) of three subplots in a plot received imazapic at a rate of 210 g ai · ha^{-1} (3 oz ai · acre^{-1}), the middle strip received 140 g ai · ha^{-1} (2 oz ai · acre^{-1}), and the uppermost received no-herbicide. This non-random assignment was made to minimize potential problems of herbicide movement down slope, although we do not expect overland or near-surface water movement to be a factor given the well-drained, gravelly loam texture of underlying soils (USDA NRCS 2011). Herbicide was applied on the same day and in the same manner as in the sagebrush experiment. Each subplot was seeded with the same six perennial grass species at the same rates as in the sagebrush experiment, with 3.25 L of rice hulls used per subplot. The three seeding treatments, randomly assigned to subplots within each strip, were 1) regular aerial seeding, 2) AC addition and 3) sucrose addition. These treatments were applied in the same manner and at the same rates as in the sagebrush experiment. A 1.5 x 3 m disturbance-free sampling zone was established in the center of each subplot, which created 2 m buffers between sampling zones and the edges of subplots.

The three seeding treatments, two vegetation manipulation treatments, and three herbicide treatments were arranged in a split-strip plot experimental design, with seeding treatments nested within herbicide levels. This design allowed for a total of 18 treatment combinations within each replicate.

Data Collection

Subplots were censused for two field seasons after treatment, from 1 - 5 June 2009 and 25 May - 7 June 2010. The lower left portion of each undisturbed sampling area was a 0.5 x 2 m area designated as “Zone 1,” which ran parallel to the left (3 m) side and set 5 cm from the bottom (2 m side) edge of the of the sampling area to make room for soil nutrient probes (see Chapter 3). Densities of cheatgrass tillers were counted in two 10 x 10 cm areas in the lower and upper left corners (along the 2 m side) of this zone. Also within Zone 1, ten individual cheatgrass plants were pulled from the ground, trimmed of roots with scissors, and collected in individual paper bags. These individuals were selected by placing a measuring tape on the ground haphazardly within this zone and choosing the individuals that were closest to each 10-cm mark.

Samples were taken to the lab and dried in a drying oven at 60° C F for 48 hours, weighed, and assessed for number of tillers and number of flowering spikelets per individual.

Statistical Analysis

Data were analyzed using SAS/STAT® 9.2 software (SAS Institute Inc. 2002). We used SAS PROC GLIMMIX to create a generalized linear mixed-model Analysis of Variance (ANOVA) that tested the effects of herbicide, vegetation manipulation treatments, seeding treatments and their interactions within each experiment separately. The factors '*herbtreat*' (level of herbicide treatment), '*vegtreat'* (level of vegetation manipulation treatment) and '*seedtreat*' (level of seeding treatment) were fixed effects and plot number was a random effect. The Tukey-Kramer method for multiple comparisons was used to determine significant differences between treatment combinations at the $\alpha = 0.05$ level. Separate analyses were performed for each variable within each experiment and year. As the 2009 and 2010 field seasons varied in terms of climactic conditions and survey timing, comparisons of variables between years are not made. However, comparisons can be made between the statistical significances of treatment main effects and interactions between years, as this information will show how long specific treatments remained in effect within these experiments.

Response variables were transformed in order to meet the assumptions of normality, symmetry, and homoskedasticity required for ANOVA. In the sagebrush experiment, 'mean density' was square root-(^1/2) transformed, 'mean weight · individual^{-1}' was inverse fourth root- (^-1/4) transformed, 'mean number of tillers · individual^{-1}' was inverse square root- (^-1/2) transformed, and 'mean number of spikelets · individual^{-1}' was log-transformed. In the cheatgrass experiment, all variables were log-transformed. Although significance was determined using transformed data, results in the text and figures are based on analyses using the original (non-transformed) scale for illustrative purposes. Therefore, standard errors (*SE*) reported in the text and in figures do not reflect significance testing of the model.

RESULTS

Mean Cheatgrass Tiller Density

In the sagebrush experiment in 2009 only the *vegtreat* main effect was significant, although the *herbtreat * vegtreat* interaction was marginally significant (Table 2.2). Mean cheatgrass tiller density · 100 cm^{-2} was significantly reduced in burned plots (3.4 ± 0.9; mean ± 1 *SE*) as compared to other vegetation manipulation treatments (50% thinned sagebrush = 11.7 ± 1.5; 100% thinned sagebrush = 15.9 ± 2.4; no manipulation = 11.7 ± 1.3; Fig. 2.1). The near significance of the *herbtreat * vegtreat* interaction was due to herbicide significantly reducing cheatgrass density only in the 100% thinned vegetation treatment (Fig. 2.1).

In the cheatgrass experiment in 2009 the *vegtreat* main effect was significant, as were the *herbtreat * vegtreat* and the *herbtreat * seedtreat* interactions; the *herbtreat* main effect was marginally significant (Table 2.2). Tiller density was less in burned (27.8 ± 3.8) than in no manipulation (89.7 ± 7.4; Fig. 2.2) plots. The *herbtreat * vegtreat* interaction and the marginal *herbtreat* main effect were due to herbicide reducing density only with the combination of 210 g · ha^{-1} in the no manipulation plots; the lower rate of herbicide did not reduce density in no manipulation plots nor was density reduced by any level of herbicide in burned plots (Fig. 2.2). Similarly, the significance of the *herbtreat * seedtreat* interaction was due to 210 g · ha^{-1} herbicide only reducing density within the regular aerial seeding subplots; no level of herbicide reduced tiller density in either sucrose addition or AC addition subplots (Fig. 2.3).

In the sagebrush experiment in 2010 the main effect *vegtreat* was still significant, although the treatment yielding the significance was different; in addition, *seedtreat* was now significant, but the *herbtreat * vegtreat* interaction was no longer significant (Table 2.2). Tiller densities were no longer significantly higher in burned plots (15.9 ± 3.3) than in 50% thinned (10.3 ± 2.0) or no manipulation (11.0 ± 1.9) plots; however, tiller densities were significantly higher in 100% thinned plots (25.1 ± 4.2) than in all other treatments. Tiller densities were lower in sucrose addition subplots (9.4 ± 1.8) than in any other seeding treatment subplots (raked = 17.2 ± 3.7; AC addition = 19.9 ± 3.7; regular aerial seeding = 15.8 ± 2.8).

In the cheatgrass experiment in 2010, *herbtreat* and *vegtreat* main effects were still significant while the *seedtreat* main effect was now also significant (Table 2.2). In contrast to 2009, the *vegtreat* * *seedtreat* interaction was significant while the *herbtreat * vegtreat* and *herbtreat * seedtreat* interactions were no longer significant (Table 2.2). Herbicide at 210 g · ha^{-1} still resulted in significantly reduced tiller densities (19.0 ± 2.8) compared to no-herbicide (28.0 ± 3.2) strips; herbicide at 140 g · ha^{-1} resulted in intermediate densities (25.4 ± 3.2) that did not differ from either no-herbicide or the 210 g · ha^{-1} treatments. Burned plots still had lower tiller densities (16.8 ± 2.1) than did no manipulation plots (31.5 ± 2.5). Tiller densities in sucrose addition subplots (18.8 ± 2.5) were significantly lower than in either AC addition (28.7 ± 3.3) or regular aerial seeding (25.0 ± 3.4) subplots. However, the *vegtreat* * *seedtreat* interaction was significant because a significant reduction in tiller densities in sucrose addition subplots only occurred in burned plots (Fig. 2.4).

Mean Cheatgrass Weight

In the sagebrush experiment in 2009, *herbtreat*, *vegtreat*, and *seedtreat* main effects were all significant, as was the *herbtreat* * *vegtreat* interaction (Table 2.3). Mean weights ·

individual^{-1} were reduced in herbicide-treated plots (0.023 g ± 0.003) as compared to no-herbicide plots (0.132 g ± 0.026). The significant *herbtreat* * *vegtreat* interaction was far more relevant than the significant *vegtreat* main effect; with no-herbicide treatment, cheatgrass in burned plots had significantly greater weights than in all other vegetation manipulation treatments, and cheatgrass in 100% thinned plots had significantly greater weights than those in no manipulation plots (Fig. 2.5). In contrast, mean weights were uniformly very low with herbicide (Fig. 2.5). Weights in sucrose addition subplots (0.024 g ± 0.006) were significantly less than in raked (0.088 g ± 0.030) or regular aerially seeded (0.096 g ± 0.038) subplots; weights in AC addition subplots (0.103 g ± 0.025) were significantly greater than in all other seeding treatment subplots.

In the cheatgrass experiment in 2009, *herbtreat, vegtreat*, and *seedtreat* main effects were significant, as were the *herbtreat * vegtreat* and *herbtreat * seedtreat* interactions (Table 2.3). Mean weights were significantly less with 140 g · ha^{-1} (0.029 g ± 0.004) and 210 g · ha^{-1} (0.025 g ± 0.004) herbicide treatment than with no-herbicide treatment (0.047 g ± 0.009); the two rates of herbicide application did not differ from each other. Weights were significantly greater in burned plots (0.046 g ± 0.007) than in no manipulation plots (0.022 g ± 0.002). However, the *herbtreat * vegtreat* interaction reveals that herbicide at either level significantly reduced cheatgrass weights in burned plots, but not in no manipulation plots (Fig. 2.6). Weights were significantly reduced in sucrose addition subplots (0.016 g ± 0.002) as compared to AC addition (0.046 g ± 0.007) and regular aerial seeding (0.040 g ± 0.007) subplots. The significant *herbtreat * seedtreat* interaction was due to 210 g · ha^{-1} herbicide only decreasing weights in sucrose addition and regular aerial seeding subplots; there was no effect on cheatgrass weights in AC addition subplots when treated with 210 g · ha^{-1} herbicide (Fig. 2.7).

In 2010 in the sagebrush experiment, *herbtreat* and *vegtreat* and main effects were still significant (Table 2.3), although the treatments yielding significances and the direction of treatment effects had changed in some cases. No interactions remained significant (Table 2.3). In this second growing season following treatment, cheatgrass weights were now significantly greater in herbicide plots (0.085 g ± 0.012) than in no-herbicide plots (0.070 g ± 0.016). Cheatgrass weights in burned plots (0.174 g ± 0.030) and 100% thinned plots (0.086 g ± 0.012) were both significantly greater than those in both no manipulation (0.019 g ± 0.002) and 50% thinned (0.030 g ± 0.004) plots. The marginally significant *seedtreat* main effect and *herbtreat * seedtreat* interaction were both due to significantly greater weights in sucrose addition subplots as compared to all other seeding treatment subplots within no-herbicide plots, while there was no difference between seeding treatments in herbicide plots (Fig. 2.8).

In 2010 in the cheatgrass experiment, *herbtreat*, *vegtreat*, and *seedtreat* main effects were all still significant, as was the *herbtreat * seedtreat* interaction (Table 2.3); again, treatments yielding significances and the direction of treatment effects had changed in some instances. The *herbtreat * vegtreat* interaction was no longer significant (Table 2.3). Weights were now significantly greater with 140 g (0.109 g · individual^{-1} ± 0.015) and 210 g · ha^{-1} (0.138 g ± 0.012) herbicide treatments than with no-herbicide treatment (0.065 g ± 0.013); the two rates of herbicide application did not differ from each other. Cheatgrass weights were still greater in burned (0.129 g ± 0.013) than in no manipulation (0.079 g ± 0.009) plots. Cheatgrass in sucrose addition subplots generally had greater weights as compared to AC addition and regular aerial seeding subplots; however, the more important *herbtreat * seedtreat* interaction was due to *seedtreat* effects varying by herbicide level. With no-herbicide treatment, cheatgrass weights in sucrose addition subplots were significantly greater than in both AC addition and regular aerial seeding subplots (Fig. 2.9). With 140 g · ha^{-1} herbicide, weights were only significant different between sucrose addition and AC addition subplots (Fig. 2.9). No difference was found between cheatgrass weights in seeding treatment subplots treated with 210 g · ha^{-1} herbicide (Fig. 2.9).

Mean Number of Tillers

In the sagebrush experiment in 2009, *herbtreat*, *vegtreat*, and *seedtreat* main effects were significant, as were the *herbtreat * vegtreat* and *vegtreat* * *seedtreat* interactions (Table 2.4). Although the main effects *herbtreat* and *vegtreat* were significant, the more explanatory *herbtreat * vegtreat* interaction resulted primarily from herbicide significantly reducing tiller numbers only within burned plots (Fig. 2.10). Additionally, differences between vegetation manipulation treatments were only significant with no-herbicide treatment; without herbicide, tiller numbers were significantly greater in burned plots than in all other treatments and also significantly greater in 100% thinned plots than in 50% thinned or no manipulation plots (Fig. 2.10). With herbicide treatment, differences between vegetation manipulation treatments became non-significant (Fig. 2.10). Similarly, although the main effect of *seedtreat* was significant, the *vegtreat* * *seedtreat* interaction is more informative; sucrose addition reduced tiller numbers below levels found in other seeding treatments only in burned plots (Fig. 2.11).

In the cheatgrass experiment in 2009, *vegtreat* and *seedtreat* main effects were both significant, as was their interaction (Table 2.4). Tiller numbers were greater in burned plots (1.8 tillers ± 0.1) than in no manipulation plots (1.2 tillers ± 0.04). The *seedtreat* main effect was significant due to tiller numbers being reduced in sucrose addition subplots relative to other treatments, but the *vegtreat * seedtreat* interaction reveals that this reduction was only significant in burned plots (Fig. 2.12).

In the sagebrush experiment in 2010, *herbtreat, vegtreat,* and *seedtreat* main effects and the *herbtreat * vegtreat* interaction were all still significant, although the direction of treatment effects was reversed for all three main effects (Table 2.4) in this second season after treatment. The *vegtreat* * *seedtreat* interaction was no longer significant (Table 2.4). In the second growing season after treatment plants had greater tiller numbers with herbicide treatment (3.6 tillers ± 0.4) than without (2.9 tillers ± 0.5), and in burned (6.2 tillers ± 0.9) and 100% thinned (3.8 tillers ± 0.5) plots than in 50% thinned (1.7 tillers ± 0.1) and no manipulation (1.3 tillers ± 0.1) plots. However, the significant *herbtreat * vegtreat* interaction arose because herbicide significantly increased tiller numbers only in the 100% thinned plots; with 100% thinning, tiller numbers in herbicide plots did not differ from those in burned plots while tiller numbers in no-herbicide plots did not differ from those in no manipulation or 50% thinned plots (Fig. 2.13). Tiller numbers were significantly greater in sucrose addition subplots (4.1 tillers ± 0.7) than in AC addition (2.4 tillers ± 0.3) and regular aerial seeding (3.3 tillers ± 0.7) subplots; raked subplots had intermediate tiller numbers (3.3 tillers ± 0.6) that did not differ from any of the other treatments.

In the cheatgrass experiment in 2010, *vegtreat* and *seedtreat* main affects were both still significant, although the direction of the *seedtreat* effect had changed; in addition, the *herbtreat* main effect and the *herbtreat * seedtreat* interaction were now significant, while the *vegtreat* * *seedtreat* interaction no longer was (Table 2.4). Tiller numbers were greatest with 210 g · ha^{-1} herbicide (2.7 tillers ± 0.2), intermediate with 140 g · ha^{-1} herbicide (2.2 tillers ± 0.2), and least with no herbicide (1.6 tillers ± 0.1; all differences significant). Tiller numbers were still greater in burned plots (2.5 tillers ± 0.2) than in no manipulation plots (1.8 tillers ± 0.1). Although *seedtreat* main effect indicated that sucrose increased tiller numbers, the significant *herbtreat * seedtreat* interaction was due to this effect only being significant in no-herbicide subplots (Fig. 2.14).

Mean Number of Spikelets

In 2009 in the sagebrush experiment, *herbtreat*, *vegtreat*, and *seedtreat* main effects were all significant, as was the *herbtreat * vegtreat* interaction (Table 2.5). Although the main effects *herbtreat* and *vegtreat* were significant, the *herbtreat * vegtreat* interaction is more important. Without herbicide treatment, numbers of spikelets were significantly greater in burned plots than in all other vegetation manipulation treatments and significantly greater in 100% thinned plots than in 50% thinned and no manipulation plots (Fig. 2.15). In contrast, the number of spikelets did not differ among vegetation manipulation treatments with herbicide treatment, resulting in herbicide significantly decreasing the number of spikelets in 50% thinned, 100% thinned, and especially burned plots (Fig. 2.15). These results mirror those seen with mean numbers of tillers. Mean numbers of spikelets were significantly less in sucrose addition subplots (4.5 spikelets · individual^{-1} ± 1.1) than in all other seeding treatment subplots (regular aerial seeding = 12.8 spikelets ± 3.1; raked = 12.7 spikelets ± 3.4; AC addition = 15.5 spikelets ± 3.2); the numbers of spikelets in AC addition subplots were significantly greater than in all others.

In the cheatgrass experiment in 2009, *herbtreat, vegtreat*, and *seedtreat* main effects and *herbtreat * vegtreat*, *herbtreat * seedtreat*, and *vegtreat* **seedtreat* interactions were all statistically significant (Table 2.5). Although the significant *herbtreat* main effect indicated that herbicide application decreased spikelet numbers, and the significant *vegtreat* main effect indicated that burning increased spikelet numbers, the more important *herbtreat * vegtreat* interaction was due to herbicide only reducing spikelet numbers in burned plots and, inversely, to burning only increasing spikelet numbers in no-herbicide subplots (Fig. 2.16). Similarly, the significant *vegtreat* * *seedtreat* interaction was a result of burning increasing spikelet numbers significantly only in AC addition subplots (Fig. 2.17). Plants in sucrose addition subplots had significantly fewer spikelets (3.3 spikelets ± 0.6) than did plants in AC addition (9.1 spikelets ± 0.3) and regular aerial seeding (7.4 spikelets ± 1.1) subplots, regardless of herbicide treatment; the significant *herbtreat * seedtreat* interaction was due to sucrose addition subplots having a greater decrease in the number of spikelets when also treated with herbicide than without (Fig. 2.18).

In 2010 in the sagebrush experiment, only *vegtreat* and *seedtreat* main effects remained significant (Table 2.5). Spikelet numbers were significantly greater in burned (18.3 spikelets ± 3.6) and 100% thinned (10.9 spikelets ± 1.8; no difference between burned and 100% thinned) plots compared to no manipulation (2.7 spikelets *SE* ± 0.2) or 50% thinned (4.2 spikelets ± 0.6; no difference between no manipulation and 50% thinned) plots. In this second season following treatment, spikelet numbers in sucrose addition subplots (10.9 spikelets ± 2.6) now were significantly greater than in regular aerial seeding (8.4 spikelets ± 2.5) or raked (7.9 spikelets ± 2.0) subplots; plants in AC addition subplots had intermediate numbers of spikelets (8.9 spikelets ± 2.0) that did not differ from any other seeding treatment.

In the cheatgrass experiment in 2010, *herbtreat, vegtreat*, and *seedtreat* main effects and the *herbtreat * seedtreat* interaction were all still significant, although the treatment yielding the significance was different in some cases; the *herbtreat * vegtreat* and *vegtreat* * *seedtreat* interactions were no longer significant (Table 2.5). Spikelet numbers were significantly greater in subplots with herbicide at 210 g · ha^{-1} (19.6 spikelets ± 2.3) than in subplots with 140 g · ha^{-1} (14.6 spikelets ± 2.4) and subplots with no herbicide (7.8 spikelets ± 1.7); plants in 140 g ·

ha^{-1} herbicide subplots also had significantly greater spikelet numbers than did subplots not treated with herbicide. Spikelet numbers were still significantly greater in burned (18.8 spikelets ± 2.2) than in no manipulation (9.2 spikelets ± 1.0) plots. Although *seedtreat* main effects were significant, the effect depended on the level of *herbtreat*; spikelet numbers were significantly greater in sucrose addition subplots than in AC addition or regular aerial seeding subplots except when also treated with 210 g · ha^{-1} herbicide (Fig. 2.19).

DISCUSSION

Several of the treatments tested in this experiment were effective at either positively or negatively affecting cheatgrass metrics. Interestingly, several interactions among treatments were also evident. Treatment main- and interaction effects during the first year after treatment did not necessarily correspond with results two seasons after treatment; some treatments that initially reduced cheatgrass sizes and densities during the first year resulted in larger and more reproductive cheatgrass the following year. Treatment effects are summarized in Tables 2.6 (sagebrush experiment) and 2.6 (cheatgrass experiment).

Cheatgrass emergence, abundance, and distribution are influenced by various climate and microclimate variables such as temperature and precipitation (Mack and Pyke 1984). In these trials specifically, differences detected between experiments and between times may be correlated with the associated differences in temperature, precipitation, slope, aspect, and soil type. As we did not include these variables as covariates in analyses, their contributions to our findings are unknown. However, preliminary analysis showed that cheatgrass densities were not significantly affected by site slope and aspect (Reinwald et al.; unpublished data).

Perennial grass emergence and establishment was minimal; we therefore believe competitive pressure from perennial grasses was negligible and did not significantly affect cheatgrass metrics. Treatment effects on perennial grass emergence or establishment and subsequent effects of perennial grasses on cheatgrass metrics will not be discussed here.

Herbicide Treatments

Cheatgrass metrics were significantly decreased with herbicide treatment in both experiments during 2009, the first season after application. In 2010, the second season after application, several of these metrics were significantly greater in herbicide-treated plots than in no-herbicide plots in both experiments. Previous studies have also noted reductions in cheatgrass metrics immediately following imazapic application (Shinn and Thill 2002; Baker et al. 2009), as well as decreasing efficacy with time without reapplication (Kyser et al. 2007; Morris et al. 2009; Davies and Sheley 2011). However, increased performance of invasive grasses in the second season following imazapic application has thus far not been reported in published literature.

In the sagebrush experiment during the first season, individual plant mean weights were reduced by 140 g · ha^{-1} herbicide regardless of vegetation manipulation treatment; however, the presence of overstory shrubs may have inhibited herbicide effectiveness on other measures of cheatgrass vigor. Herbicide only significantly reduced densities in 100% thinned plots, spikelet numbers in 50% thinned, 100% thinned, or burned plots, and tiller numbers in burned plots. As imazapic trials are generally done in near-monocultures of invasive annual grasses (e.g. Shinn and Thill 2002; 2004; Monaco et al. 2005; Kyser et al. 2007; Sheley et al. 2007; Morris et al. 2009; Davies 2010; Davies and Sheley 2011), we are aware of no previously reported evidence of shrub overstory inhibition of imazapic. However, inhibitory effects of vegetative litter on imazapic herbicide are well-documented (Monaco et al. 2005; Kyser et al. 2007; Sheley et al. 2007; Davies 2010; Davies and Sheley 2011).

In the cheatgrass experiment in the first season, 140 g · ha^{-1} herbicide did not reduce cheatgrass densities or tiller numbers, even though this area does not have a sagebrush overstory. We believe this is due to higher initial cheatgrass (and by association, litter) densities in the cheatgrass experiment, which potentially resulted in less herbicide contact with the soil and therefore less effectiveness in plots that were not burned. Plots that were burned and treated with 140 g · ha^{-1} herbicide did have lower mean weights and spikelet numbers than those that were treated with herbicide at this rate but not burned. Burning of litter has previously been found to improve the effectiveness of imazapic on invasive annual grasses (Monaco et al. 2005; Kyser et al. 2007; Sheley et al. 2007; Davies 2010; Davies and Sheley 2011). Herbicide at 210 g · ha^{-1} in the cheatgrass experiment did successfully reduce cheatgrass densities in unburned plots in the first season after application; this agrees with previous research (e.g. Shinn and Thill 2002) that showed increasing rates of imazapic application (0, 18, 35, 70, 140, and 280 g · ha^{-1}) resulting in greater cheatgrass control (up to 97%). However, 210 g · ha^{-1} herbicide still had no significant effect on mean tiller numbers in our experiment, and as with 140 g · ha^{-1} herbicide, this rate only significantly decreased mean weights and spikelet numbers in plots that were also burned. Mean density was not decreased by herbicide at any rate in burned plots in either experiment in 2009, however. We believe this is due to the already extremely low cheatgrass densities that resulted from burning treatments.

In 2010, the second season following application, herbicide treatment had the opposite effect compared to 2009 on some cheatgrass metrics in both experiments. In the sagebrush experiment, mean weights of cheatgrass individuals were increased in herbicide-treated plots regardless of vegetation manipulation treatment, and mean tiller numbers were significantly increased by herbicide in 100% thinned plots relative to in plots not treated with herbicide in 2009. In the cheatgrass experiment, decreased densities with 210 g · ha^{-1} herbicide were still apparent in the second season, two full growing seasons after application, regardless of whether or not the plot was burned initially. However, cheatgrass in plots treated with either rate of herbicide now had greater mean weights, tiller and spikelet numbers than those in no-herbicide plots, also regardless of whether or not the plot was burned. Weights, tiller numbers, and spikelet numbers were all significantly greater in 210 g · ha^{-1} herbicide plots than even in 140 g · ha^{-1} plots. Cheatgrass is known to be highly plastic in its growth patterns in response to environmental conditions (Rice and Mack 1991), and densities and shoot biomasses of cheatgrass are known to be inversely related (Nasri and Doescher 1995). Reduced densities of cheatgrass in herbicide plots may have reduced intraspecific competition for resources and allowed individual cheatgrass to grow to larger sizes in both experiments in 2010. As a post-hoc analysis, we assessed differences in estimated mean biomass · $100cm^{-2}$ (mean number of tillers · 100 cm^{-2} divided by mean number of tillers · $individual^{-1}$, multiplied by mean weight per $individual^{-1}$) in the sagebrush experiment in 2010 and found that no-herbicide plots still had higher estimated mean biomass (0.44 g · 100 cm^{-2} ± 0.05) than herbicide plots (0.16 g · 100 cm^{-2} ± 0.03; $p < 0.0001$, $n = 160$). This was due to significantly higher mean densities in no-herbicide plots, even though individuals in herbicide plots were significantly larger. The difference between estimates of mean biomass in 140 g · ha^{-1} herbicide (1.05 g · 100 cm^{-2} ± 0.12), 210 g · ha^{-1} herbicide (1.01 g · 100 cm^{-2} ± 0.06), and no-herbicide (0.83 g · 100 cm^{-2} ± 0.07) plots in the cheatgrass experiment in 2010 was not significant ($p = 0.3166$, $n = 72$), indicating a roughly equal tradeoff between densities and individual cheatgrass sizes in this experiment.

Vegetation Manipulation Treatments

Sagebrush Thinning and Clearing. Partial (50%) thinning of sagebrush had no effect on cheatgrass metrics during either the first or second season after treatment. This may be due to 50% removal of sagebrush individuals resulting in less than a 50% reduction in cover. In contrast, cheatgrass in 100% thinned plots had greater mean weights, mean numbers of tillers, and mean numbers of spikelets than those in no manipulation plots during both post-treatment seasons. Removal of overstory shrubs is known to increase availabilities of NO_3^- and other soil nutrients (Blank et al. 2007) as well as light and soil water (Prevéy et al. 2010), all of which can contribute to increased cheatgrass growth. Heightened cheatgrass success has been previously found in areas where sagebrush is removed to increase forage production or for other management reasons (Blumenthal et al. 2006; Prevéy et al. 2010).

Burning of Sagebrush Overstory and/or Vegetative Thatch. When not treated with herbicide, burning reduced densities of cheatgrass in both the sagebrush and cheatgrass experiments during the first season after treatment. In the second season, densities were still lower in the cheatgrass experiment but had returned to levels not significantly different than in no manipulation plots in the sagebrush experiment. Although post-fire conditions favor invasive grasses such as cheatgrass (Melgoza et al. 1990; D'Antonio and Vitousek 1992), cheatgrass seed densities in seed banks are reduced (Humphrey and Schupp 2001) and cheatgrass presence is generally patchy (Ratzlaff and Anderson 1995) during the first few years after fire occurrence. Burning significantly increased individual cheatgrass mean weights, mean numbers of tillers, and mean numbers of spikelets in both experiments in the first season after treatment, and all these results persisted through the second season. Increased availabilities of N, P, and S, are commonly observed following fire (Christensen 1973; Christensen and Muller 1975; Giovaninni and Lucchesi 1997; Castelli and Lazzari 2002; Chapter 3). Increased nutrient availabilities, especially bioavailable forms of N, have been shown to positively influence cheatgrass biomasses (McLendon and Redente 1992; Redente et al. 1992; Vasquez et al. 2008). Reduced densities in these experiments during the first season after treatment may have also partially accounted for increased sizes of cheatgrass individuals, as happened in some instances with herbicide application.

Although burning positively affected cheatgrass individuals (while negatively affecting cheatgrass densities) in our experiments, our results also show that herbicide was able to reduce cheatgrass weights and tiller and spikelet numbers in burned plots to levels not significantly different than in no manipulation plots for a year following application. Imazapic herbicide application has been shown to be effective elsewhere to control increased invasive grass biomasses post-fire, although repeated applications are suggested for more complete invasive grass control following fire (Monaco et al. 2005).

Seeding Treatments

Soil Surface Raking. Soil disturbance by raking at these sites did not significantly affect cheatgrass densities, mean weights, mean numbers of tillers or mean numbers of spikelets in either experiment in either sampling season. Although soil surface disturbance is considered beneficial to cheatgrass via changes to soil nutrient availability (Norton et al. 2007), we found no evidence that slight ground disturbance was in any way beneficial or detrimental to cheatgrass in our plots.

Sucrose Addition. During the first season after application, cheatgrass individuals in sucrose addition subplots had smaller mean weights, mean number of tillers, and mean numbers of spikelets than those in regular aerial seeding subplots, while densities were not significantly affected. Although little data exists on C addition impacts to cheatgrass specifically (but see Paschke et al 2000; Rowe et al. 2009; Mazzola et al. 2011), invasive species densities, shoot biomasses, seed production, and tiller numbers have been found to be significantly reduced during the first growing season post C addition (Paschke et al. 2000; Blumenthal et al. 2003; Monaco et al. 2003a; Blumenthal 2009; Rowe et al. 2009; Brunson et al. 2010; Mazzola et al. 2011). In the second season after sucrose addition, cheatgrass densities were reduced and plants generally had greater mean weights, numbers of tillers, and numbers of spikelets than those in regular aerial seeding subplots. Mazzola et al. (2011) also found significant increases in biomass and seed production of individual cheatgrass plants the second year following C addition; however, this significance disappeared when these variables were assessed on a per area basis. In fact, we also found no significant difference between estimates of mean biomass · 100cm^{-2} (mean number of tillers · 100 cm^{-2} divided by mean number of tillers · individual^{-1}, multiplied by mean weight per individual^{-1}) in sucrose addition (0.22 g · 100cm^{-2} ± 0.06) and regular aerial seeding (0.33 g · 100cm^{-2} ± 0.07; $p = 0.1734$; $n = 64$) subplots in the sagebrush experiment in 2010. The same was also true in the cheatgrass experiment (sucrose addition = 0.96 g · 100cm^{-2} ± 0.12, regular aerial seeding = 0.95 g · 100cm^{-2} ± 0.11; $p = 0.9328$; $n = 48$). This indicates that decreased densities caused by sucrose addition were compensated for by per individual increases in biomass in 2010. Immobilized nutrients that were potentially rereleased in the second year following treatments may have also contributed increases to individual cheatgrass sizes in 2010 (see Chapter 3).

AC Addition. Studies by Kulmatiski and Beard (2006) and Kulmatiski (2011) reported significant decreases in invasive species cover with AC incorporation 10 cm into the soil at a rate of 1 kg · m^{-2} that were believed to be a result of the interruption of important plant-soil feedbacks. Our application of AC at the soil surface (100 g · m^{-2}) resulted in no such cheatgrass biomass reductions. The lack of response with our AC treatment could either be due to our treatment methods or to plant-soil feedbacks not being a large reinforcing factor for cheatgrass at our study site. Rowe and Brown (2008) found no detectable inhibition of perennial seed establishment in former cheatgrass-dominated soils, indicating that plant-soil feedbacks might not be an obstacle to perennial establishment in all cheatgrass-invaded areas.

In the cheatgrass experiment in 2009, 210 g · ha^{-1} herbicide did not reduce cheatgrass weights in AC addition subplots as it did in regular aerial seeding and sucrose treated subplots. We believe this is due to AC sequestering imazapic herbicide, which has an organic chemical structure, and thereby lessening its negative effects on cheatgrass. Also in the cheatgrass experiment in the first season after treatment, spikelet numbers in AC addition subplots in burned plots were significantly greater than in AC addition subplots in no manipulation plots. We believe these findings may be due to a non-statistically significant three-way interaction; herbicide is better able to reduce cheatgrass vigor in burned plots, and therefore AC's ability to sequester this herbicide and lessen its effect on cheatgrass would be more pronounced in burned plots. In the sagebrush experiment in 2009, significant increases in cheatgrass weights and spikelet numbers were detected in AC addition subplots as compared to regular aerial seeding and sucrose addition subplots. Although the *herbtreat* * *seedtreat* interaction was non-significant for these variables (Tables 2.3, 2.5), mean weights in herbicide-treated plots tended to be higher in AC addition subplots than in raked and regular aerial seeding subplots (differences non-significant). Also suggestive of AC sequestering herbicide is that no cheatgrass metrics were significantly different in AC addition subplots than in other seeding treatment subplots during the second growing season, when negative herbicide effects were also no longer detectable.

IMPLICATIONS

Some treatments tested in these experiments may positively influence emergence and establishment of seeded perennial species, primarily through a reduction in competition from cheatgrass. Herbicide application and sucrose addition were both effective at reducing cheatgrass weights, tiller numbers, and spikelet numbers, and burning reduced cheatgrass densities. While these effects may be beneficial to seeded perennials, there is a short window of opportunity (potentially less than one year) for perennial establishment before cheatgrass may again come to dominate a treated area.

Other treatments may actually lead to an immediate increase in cheatgrass vigor, and a reduced opportunity for establishment of seeded perennials. AC addition may have sequestered herbicide and thereby reduced its negative effects on cheatgrass. Total sagebrush thinning resulted in larger and denser cheatgrass, which would increase competitive pressure on seeded perennial species instead of freeing resources for their use. Burning reduced cheatgrass densities and potentially freed light, water, and soil resources for use by perennial species; however, increased resource availability and sizes and reproductive capacities of remaining cheatgrass individuals will most likely lead to eventual cheatgrass dominance in burned plots in the absence of established perennials. The results of these trials will be beneficial to restoration ecologists and land managers making decisions about how to best reincorporate native perennial grass species into cheatgrass-invaded areas.

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Table 2.1. Comparisons of initial cheatgrass metrics between the sagebrush and cheatgrass experiments. Values with the same letter in a column do not differ significantly from each other (α = 0.05).

	Cheatgrass metric			
Experiment	Mean density of tillers · 100 cm^{-1}	Mean weight (g) · $individual^{-1}$	Mean number of tillers · $individual^{-1}$	Mean number of spikelets · $individual^{-1}$
Sagebrush	21.9 ± 5.1^{B}	0.06 ± 0.03^{A}	1.6 ± 0.4^{A}	8.3 ± 3.7^{A}
Cheatgrass	115.8 ± 17.1^{A}	0.03 ± 0.003^{A}	1.2 ± 0.08^{A}	5.5 ± 0.6^{A}

Table 2.2. Analysis of variance for the variable 'Mean density of tillers · 100 cm^{-1}' for both sagebrush and cheatgrass experiments during 2009 and 2010 (bold font denotes significance, $p \leq 0.05$).

Effect	Sagebrush experiment (square root transformation)								Cheatgrass experiment (log transformation)							
	2009				2010				2009				2010			
	df		*F*	*p*	*df*		*F*	*p*	*df*		*F*	*p*	*df*		*F*	*p*
Vegtreat	3	81	23.22	**<0.0001**	3	81	7.01	**0.0003**	1	24	17.44	**0.0003**	1	24	8.72	**0.0069**
Herbtreat	1	3	5.35	0.1038	1	3	7.16	0.0753	2	12	3.7	0.0561	2	12	11.52	**0.0016**
Seedtreat	3	9	1.78	0.2203	3	9	10.26	**0.0029**	2	12	0.66	0.5366	2	12	10.07	**0.0027**
Herbtreat * Vegtreat	3	81	2.72	0.0501	3	81	2.1	0.1063	2	24	5.11	**0.0142**	2	24	1.7	0.2037
Herbtreat * Seedtreat	3	81	0.7	0.5563	3	81	1.42	0.2438	4	24	2.87	**0.0446**	4	24	1.12	0.3720
Vegtreat * Seedtreat	9	81	0.84	0.5814	9	81	1.05	0.4095	2	24	0.59	0.5603	2	24	4.85	**0.0170**
Herbtreat * Vegtreat * Seedtreat	9	81	1.08	0.3870	9	81	0.64	0.7589	4	24	0.78	0.5498	4	24	1.73	0.1767

Table 2.3. Analysis of variance for the variable 'Mean weight of cheatgrass (g) · individual^{-1}' for both sagebrush and cheatgrass experiments during 2009 and 2010 (bold font denotes significance, $p \leq 0.05$).

Effect	Sagebrush experiment (inverse 4th root [^-1/4] transformation)								Cheatgrass experiment (log transformation)							
	2009				2010				2009				2010			
	df		*F*	*p*	*df*		*F*	*p*	*df*		*F*	*p*	*df*		*F*	*p*
Vegtreat	3	81	21.76	**<0.0001**	3	81	39.89	**<0.0001**	1	24	12.52	**0.0017**	1	24	9.27	**0.0056**
Herbtreat	1	3	47.28	**0.0063**	1	3	16.28	**0.0274**	2	12	15.42	**0.0005**	2	12	29.47	**<0.0001**
Seedtreat	3	9	117.1	**<0.0001**	3	9	3.65	0.0571	2	12	49.68	**<0.0001**	2	12	16.08	**0.0004**
Herbtreat * Vegtreat	3	81	4.75	**0.0042**	3	81	2.22	0.0926	2	24	3.52	**0.0458**	2	24	0.06	0.9466
Herbtreat * Seedtreat	3	81	1.3	0.2797	3	81	2.69	0.0516	4	24	2.85	**0.0457**	4	24	4.41	**0.0082**
Vegtreat * Seedtreat	9	81	0.53	0.8505	9	81	0.51	0.8603	2	24	2.19	0.1333	2	24	1.05	0.3640
Herbtreat * Vegtreat * Seedtreat	9	81	0.49	0.8760	9	81	0.83	0.5903	4	24	0.55	0.7009	4	24	0.58	0.6769

Table 2.4. Analysis of variance for the variable 'Mean number of tillers · individual^{-1}' for both sagebrush and cheatgrass experiments during 2009 and 2010 (bold font denotes significance, *p* ≤ 0.05).

Effect	Sagebrush experiment (inverse square root [^-1/2] transformation)						Cheatgrass experiment (log transformation)					
	2009			2010			2009			2010		
	df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Vegtreat	3 81	38.86	**<0.0001**	3 81	54.8	**<0.0001**	1 24	20.8	**0.0001**	1 24	3.91	0.0595
Herbtreat	1 3	38.81	**0.0083**	1 3	77.9	**0.0031**	2 12	1.17	0.3435	2 12	41.4	**<0.0001**
Seedtreat	3 9	12.57	**0.0014**	3 9	5.38	**0.0214**	2 12	20.1	**0.0001**	2 12	12.3	**0.0012**
Herbtreat * Vegtreat	3 81	14.23	**<0.0001**	3 81	3.05	**0.0334**	2 24	2.06	0.15	2 24	2.67	0.0897
Herbtreat * Seedtreat	3 81	0.76	0.5181	3 81	1.93	0.1310	4 24	1.38	0.2706	4 24	2.94	**0.0411**
Vegtreat * Seedtreat	9 81	2.01	**0.0484**	9 81	0.57	0.8165	2 24	3.89	**0.0344**	2 24	1.13	0.3409
Herbtreat * Vegtreat * Seedtreat	9 81	0.72	0.6896	9 81	1.12	0.3584	4 24	0.64	0.6413	4 24	1.39	0.2680

Table 2.5. Analysis of variance for the variable 'Mean number of spikelets · individual^{-1}' for both sagebrush and cheatgrass experiments during 2009 and 2010 (bold font denotes significance, *p* ≤ 0.05).

Effect	Sagebrush experiment (log transformation)						Cheatgrass experiment (log transformation)					
	2009			2010			2009			2010		
	df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Vegtreat	3 81	27.69	**<0.0001**	3 81	19.6	**<0.0001**	1 24	11.9	**0.0021**	1 24	12.5	**0.0017**
Herbtreat	1 3	189.6	**0.0008**	1 3	2.22	0.2334	2 12	10.5	**0.0023**	2 12	31.4	**<0.0001**
Seedtreat	3 9	76.91	**<0.0001**	3 9	6.32	**0.0135**	2 12	63	**<0.0001**	2 12	20.4	**0.0001**
Herbtreat * Vegtreat	3 81	11.08	**<0.0001**	3 81	0.89	0.4504	2 24	3.64	**0.0416**	2 24	0.97	0.3921
Herbtreat * Seedtreat	3 81	0.3	0.8263	3 81	2.38	0.0759	4 24	3.05	**0.0364**	4 24	4.27	**0.0094**
Vegtreat * Seedtreat	9 81	0.57	0.8170	9 81	0.3	0.9714	2 24	4.61	**0.0202**	2 24	0.45	0.641
Herbtreat * Vegtreat * Seedtreat	9 81	0.32	0.9645	9 81	0.75	0.6620	4 24	0.9	0.4817	4 24	0.86	0.5032

Table 2.6. Summary of treatment effects on response variables in the sagebrush experiment in 2009 and 2010. Plus signs (+) indicate a positive effect, minus signs (-) indicate a negative effect, and zeros indicate no significant effect.

Treatment	2009				2010			
	Mean densities	Mean weights	Mean tiller numbers	Mean spikelet numbers	Mean densities	Mean weights	Mean tiller numbers	Mean spikelet numbers
140 g · ha-^{1} herbicide (vs. no herbicide)	- (in 100% thinned plots only)	-	- (in burned plots only)	- (in 50% thinned, 100% thinned, and burned plots only)	0	+	+ (in 100% thinned plots only)	0
Burning (vs. no manipulation)	-	+ (in no-herbicide plots only)	+ (in no-herbicide plots only)	+ (in no-herbicide plots only)	0	+	+	+
50% thinning (vs. no manipulation)	0	0	0	0	0	0	0	0
100% thinning (vs. no manipulation)	0	+ (in no-herbicide plots only)	+ (in no-herbicide plots only)	+ (in no-herbicide plots only)	+	+	+ (in herbicide-treated plots only)	+
Raking (vs. regular aerial seeding)	0	0	0	0	0	0	0	0
Sucrose addition (vs. regular aerial seeding)	0	-	- (in burned plots only)	-	-	+ (in no-herbicide plots only)	+	+
AC addition (vs. regular aerial seeding)	0	+	0	+	0	0	0	0

Table 2.7. Summary of treatment effects on response variables in the cheatgrass experiment in 2009 and 2010. Plus signs (+) indicate a positive effect, minus signs (-) indicate a negative effect, and zeros indicate no significant effect.

Treatment	2009				2010			
	Mean densities	Mean weights	Mean tiller numbers	Mean spikelet numbers	Mean densities	Mean weights	Mean tiller numbers	Mean spikelet numbers
140 g · ha^{-1} herbicide (vs. no herbicide)	0	- (in burned plots only)	0	-(in burned plots only)	0	+	+	+
210 g · ha^{-1} herbicide (vs. no herbicide)	- (in no manipulation plots or regular aerial seeding subplots only)	- (in burned plots or regular aerial seeding and sucrose addition subplots only)	0	-(in burned plots only)	-	+	+	+
Burning (vs. no manipulation)	-	+(in no-herbicide strips only)	+	+ (in AC addition subplots and no-herbicide strips only)	-	+	+	+
Sucrose addition (vs. regular aerial seeding)	0	-	- (in burned plots only)	-	-	+ (in no-herbicide plots only)	+ (in no-herbicide plots only)	+ (in no-herbicide and 140 g · ha^{-1} herbicide subplots only)
AC addition (vs. regular aerial seeding)	0	0	0	0	0	0	0	0

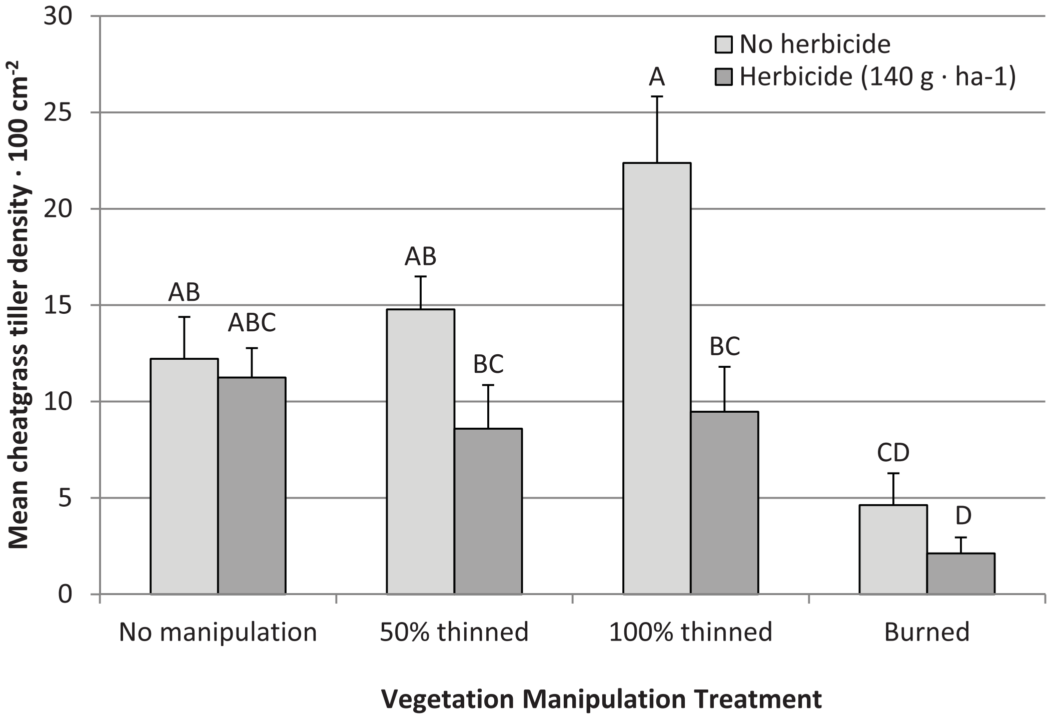

Figure 2.1. Mean cheatgrass tiller density · 100 cm^{-2} (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the sagebrush experiment in 2009. Values with the same letter do not differ significantly from each other.

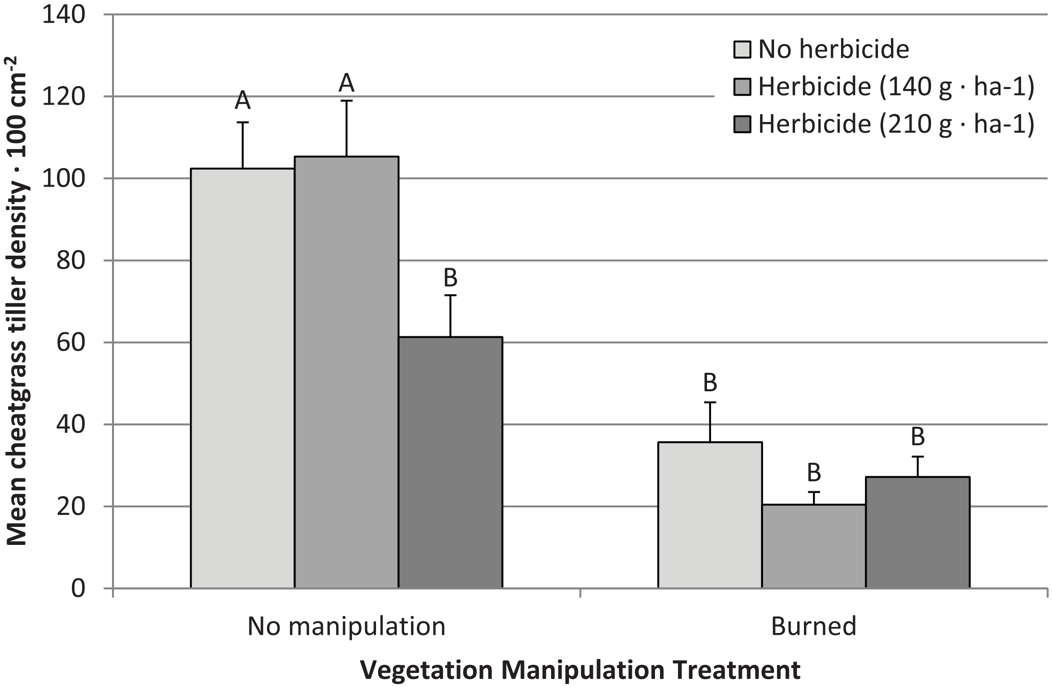

Figure 2.2. Mean cheatgrass tiller density · 100 cm^{-2} (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.

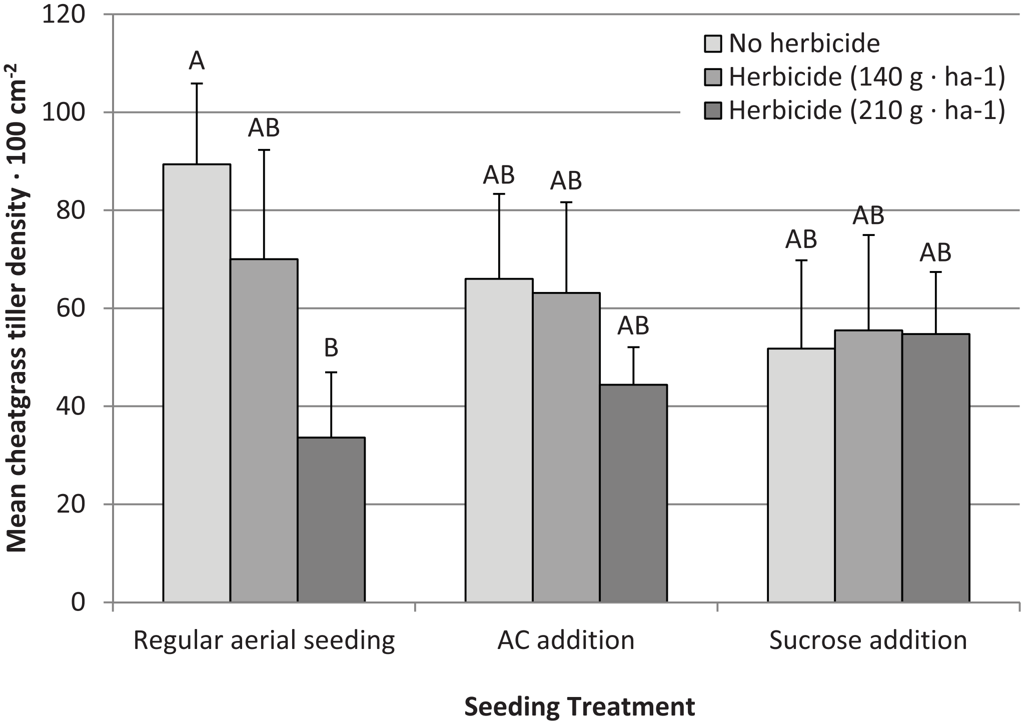

Figure 2.3. Mean cheatgrass tiller density · 100 cm^{-2} (+ *SE*), showing the interaction between *herbtreat* and *seedtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.

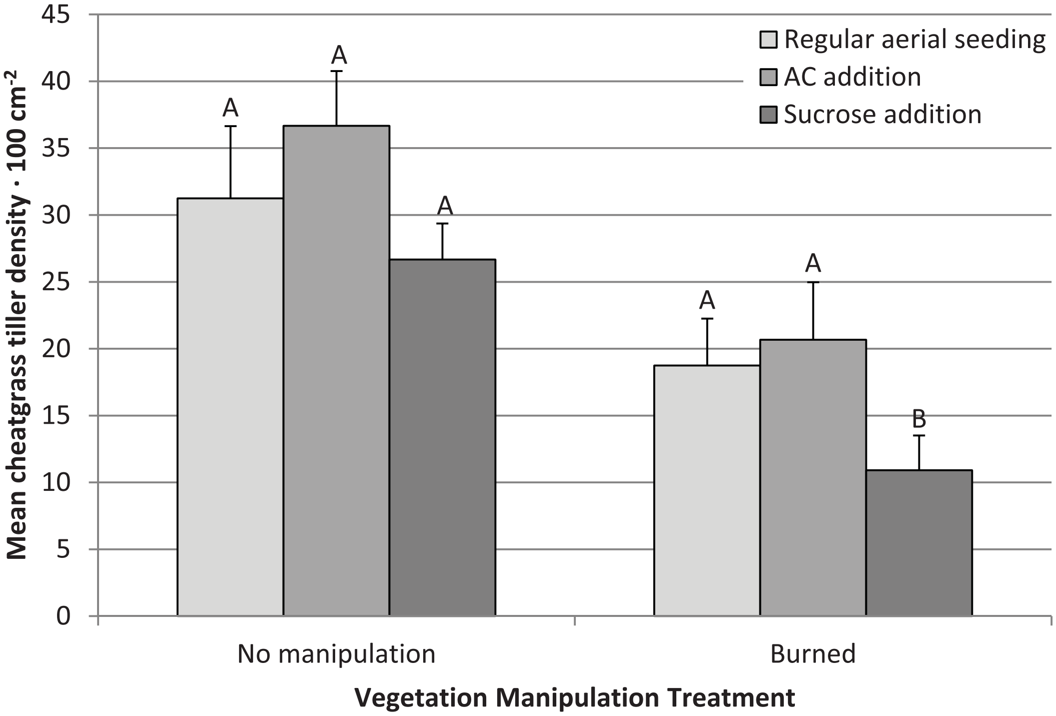

Figure 2.4. Mean cheatgrass tiller density · 100 cm^{-2} (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the cheatgrass experiment in 2010. Values with the same letter do not differ significantly from each other.

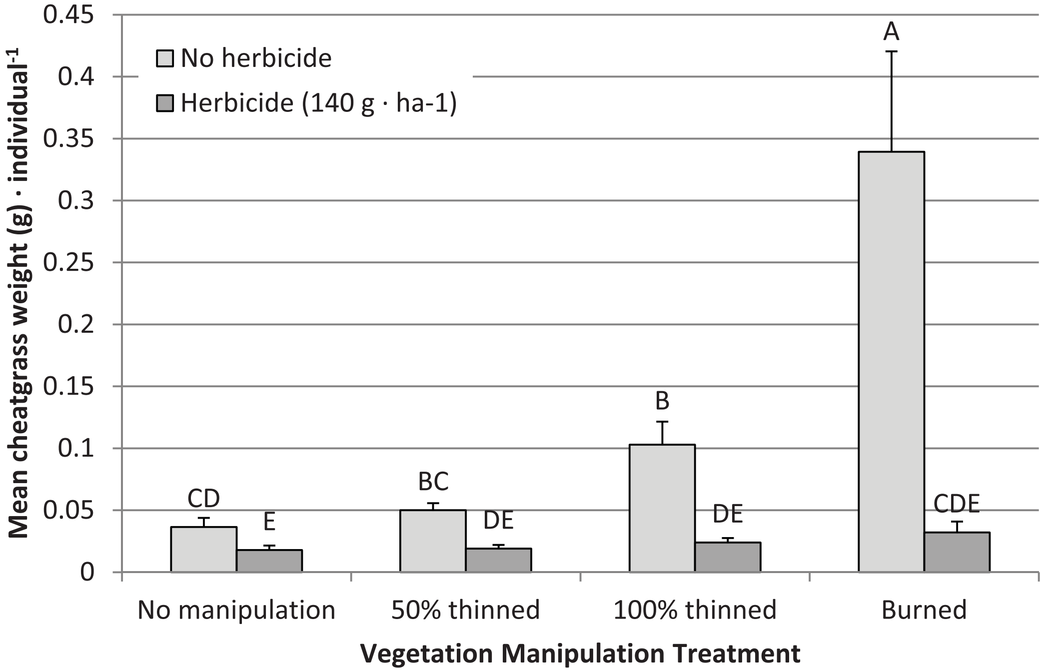

Figure 2.5. Mean weight (g) · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the sagebrush experiment in 2009. Values with the same letter do not differ significantly from each other.

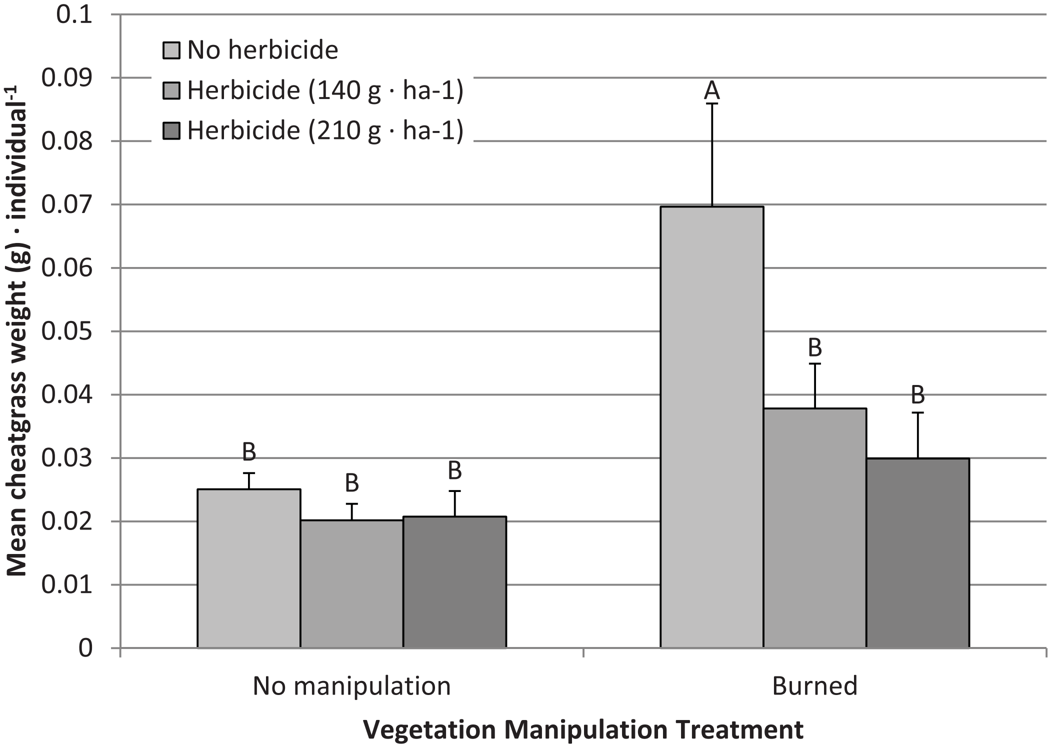

Figure 2.6. Mean weight (g) · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.

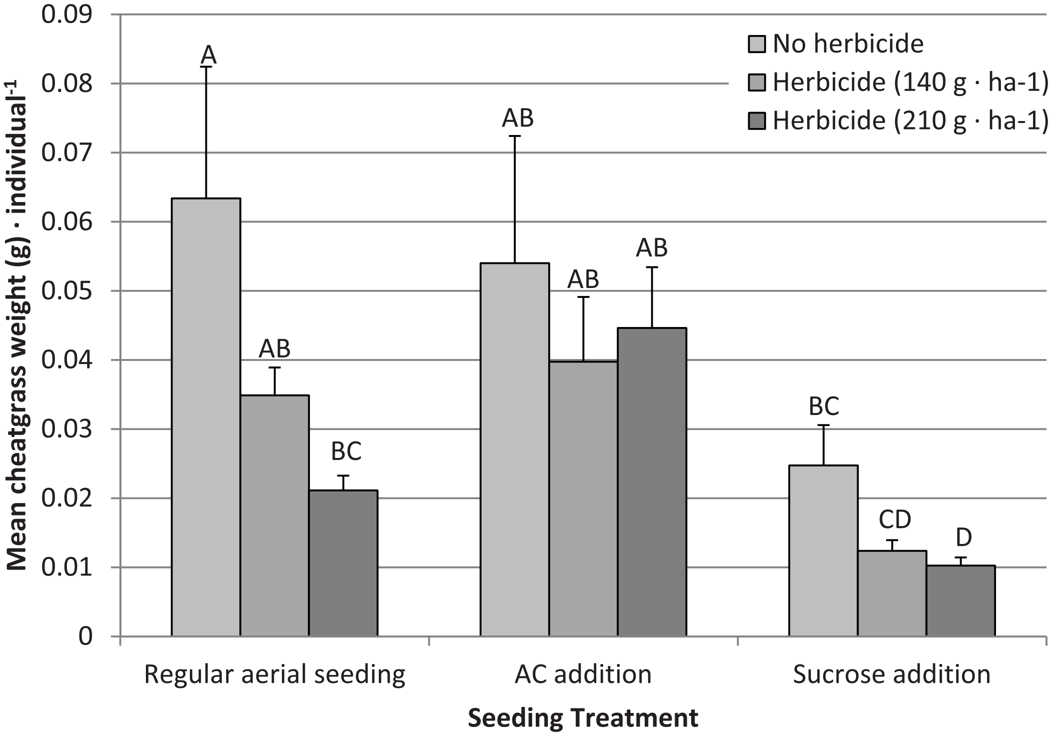

Figure 2.7. Mean weight (g) · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *seedtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.

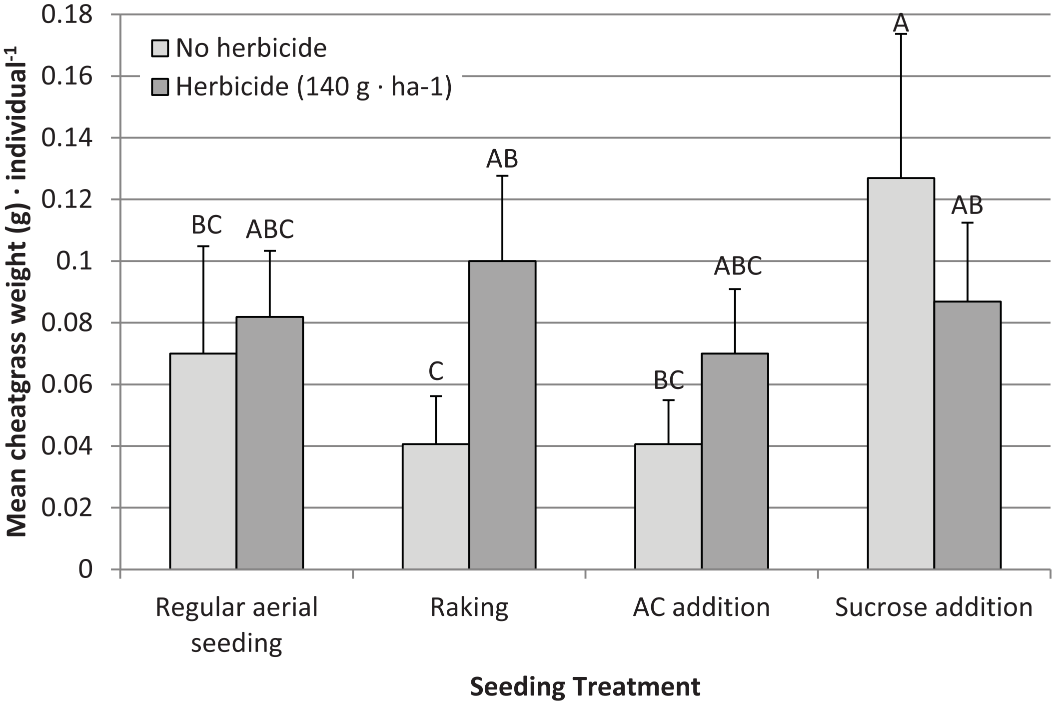

Figure 2.8. Mean weight (g) · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *seedtreat* in the sagebrush experiment in 2010. Values with the same letter do not differ significantly from each other.

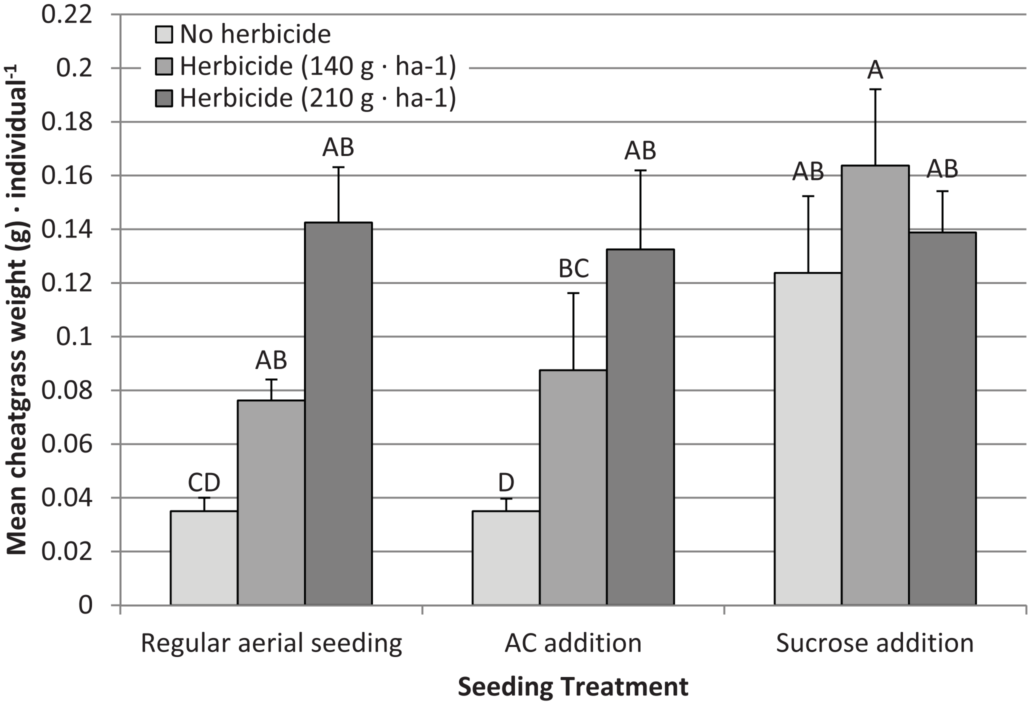

Figure 2.9. Mean weight (g) · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *seedtreat* in the cheatgrass experiment in 2010. Values with the same letter do not differ significantly from each other.

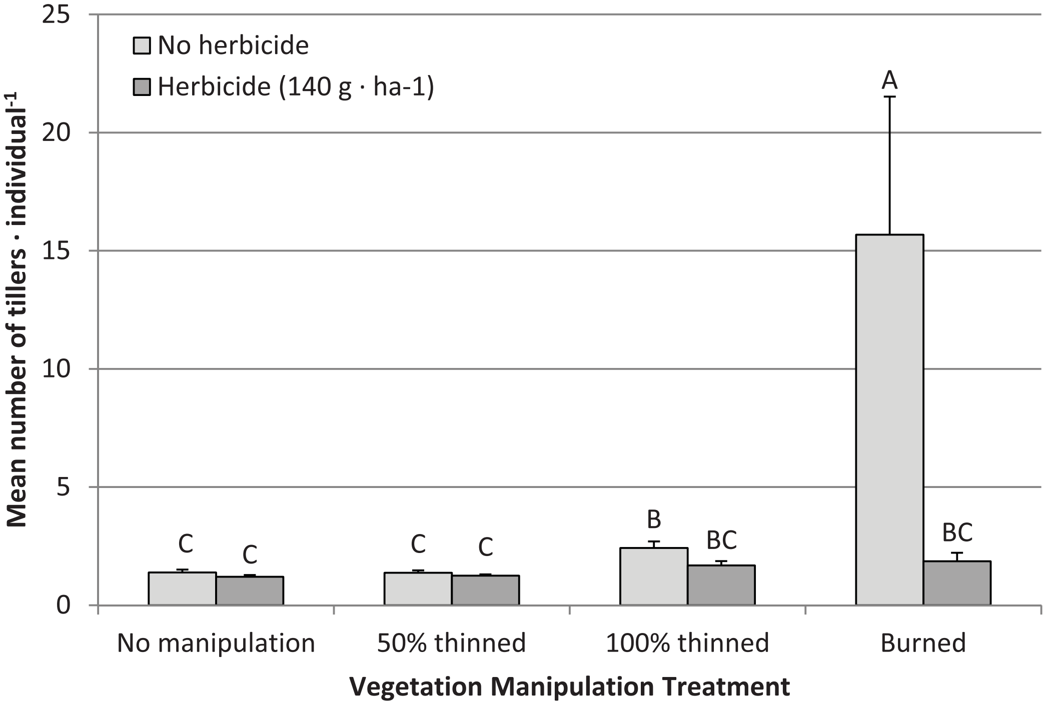

Figure 2.10. Mean number of tillers · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the sagebrush experiment in 2009. Values with the same letter do not differ significantly from each other.

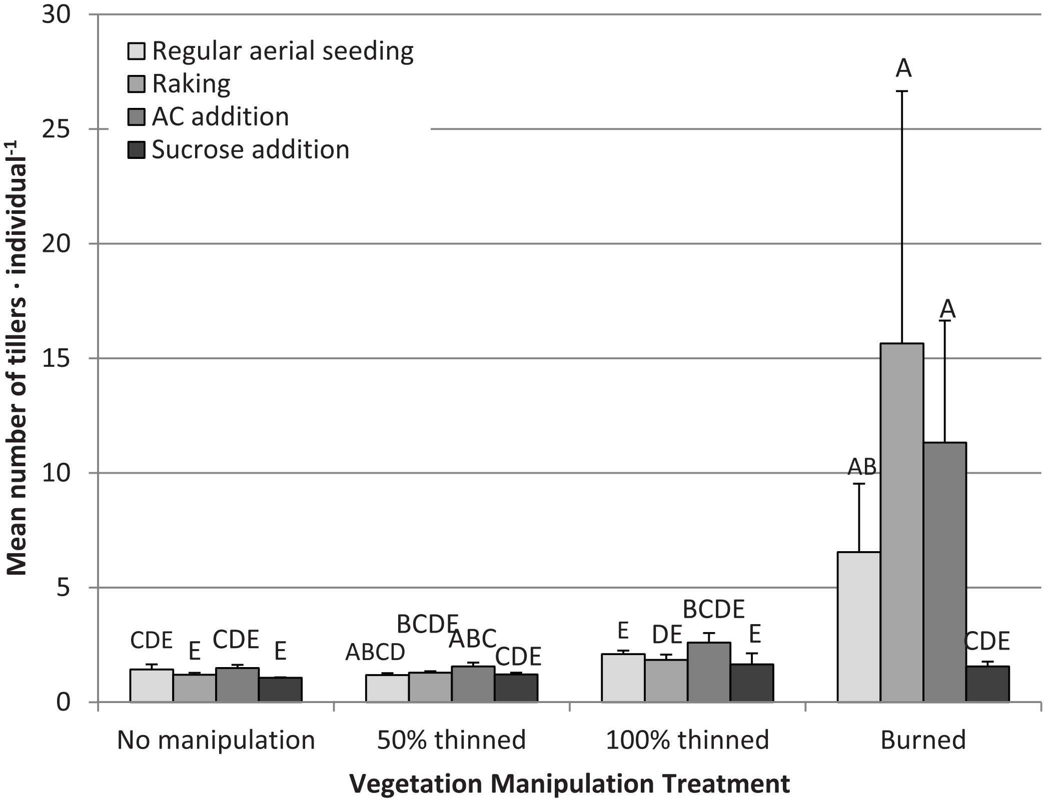

Figure 2.11. Mean number of tillers · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the sagebrush experiment in 2009. Values with the same letter do not differ significantly from each other.

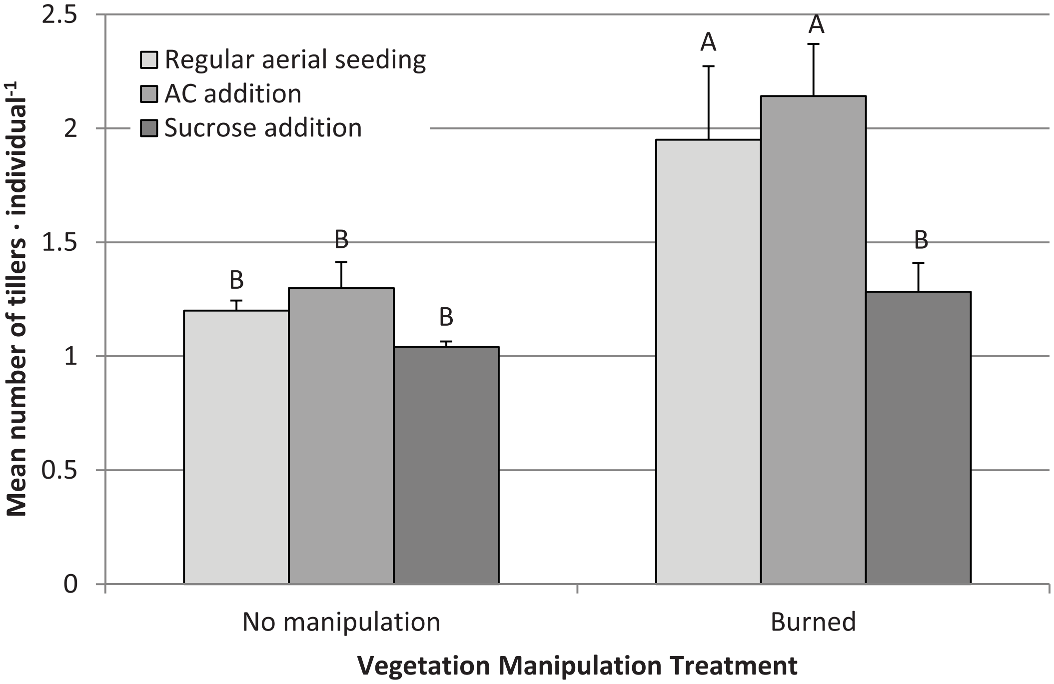

Figure 2.12. Mean number of tillers · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.

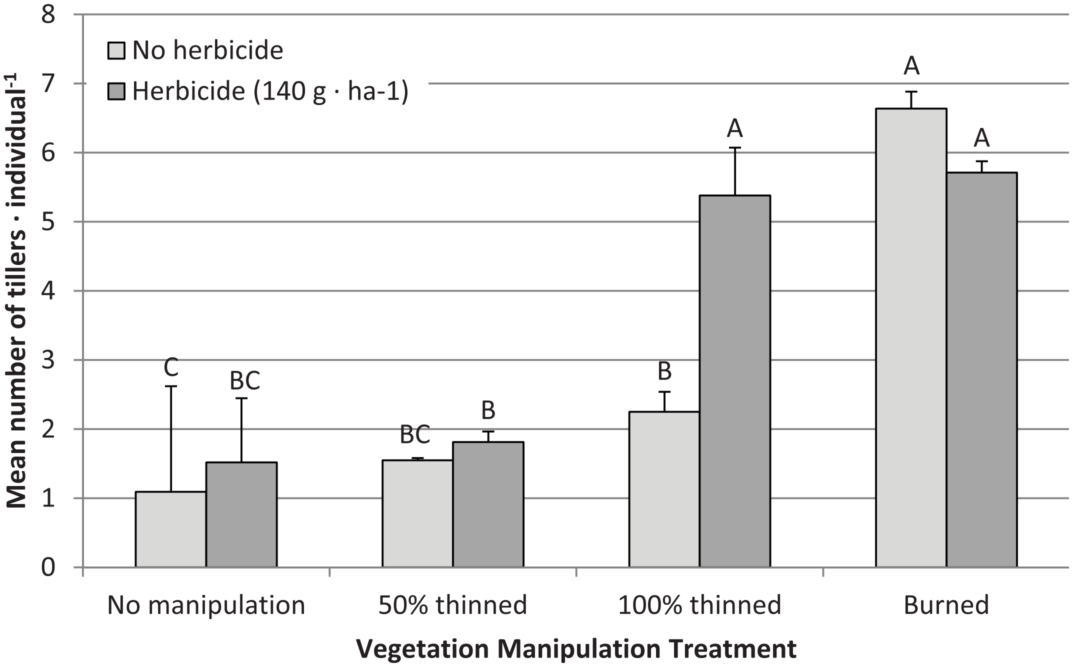

Figure 2.13. Mean number of tillers · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the sagebrush experiment in 2010. Values with the same letter do not differ significantly from each other.

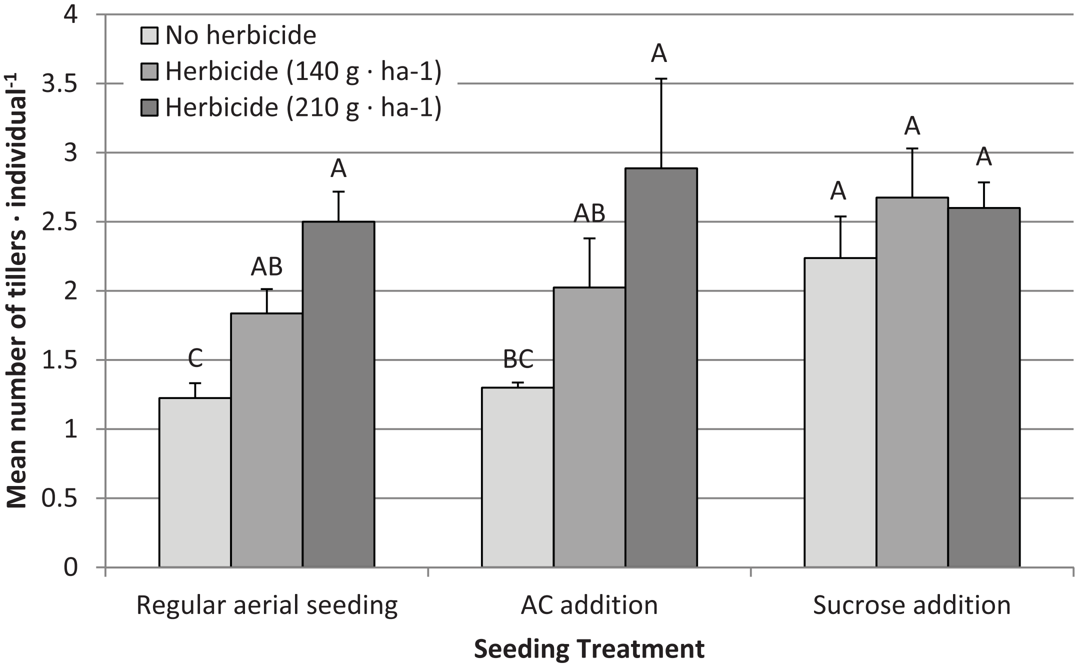

Figure 2.14. Mean number of tillers · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *seedtreat* in the cheatgrass experiment in 2010. Values with the same letter do not differ significantly from each other.

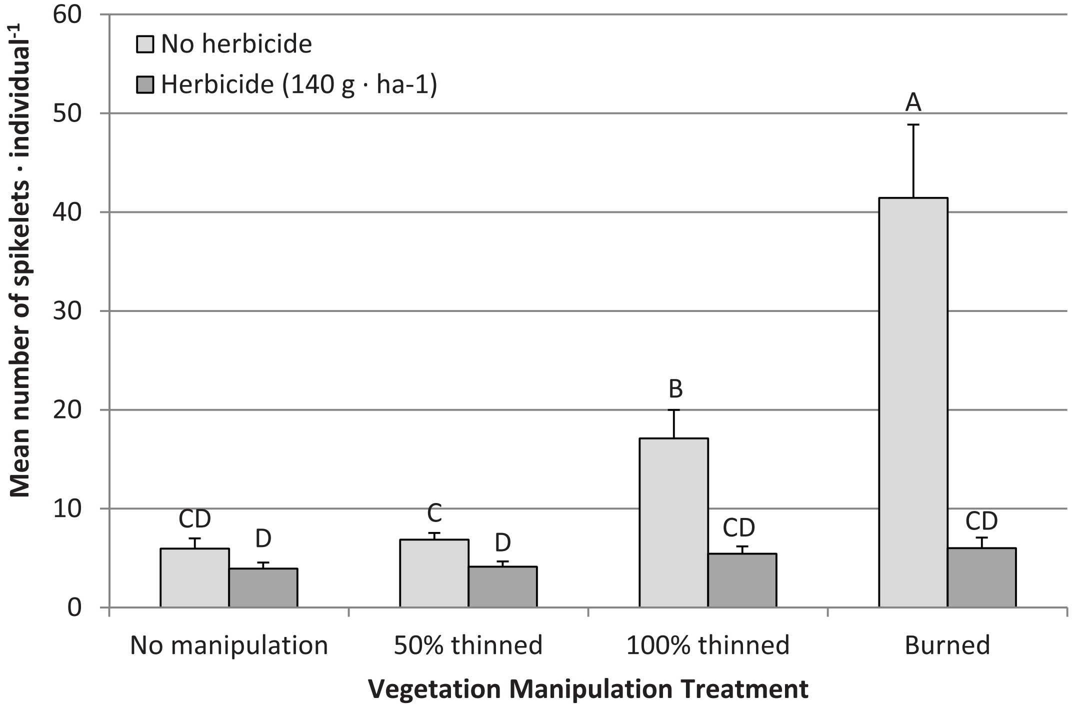

Figure 2.15. Mean number of spikelets · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the sagebrush experiment in 2009. Values with the same letter do not differ significantly from each other.

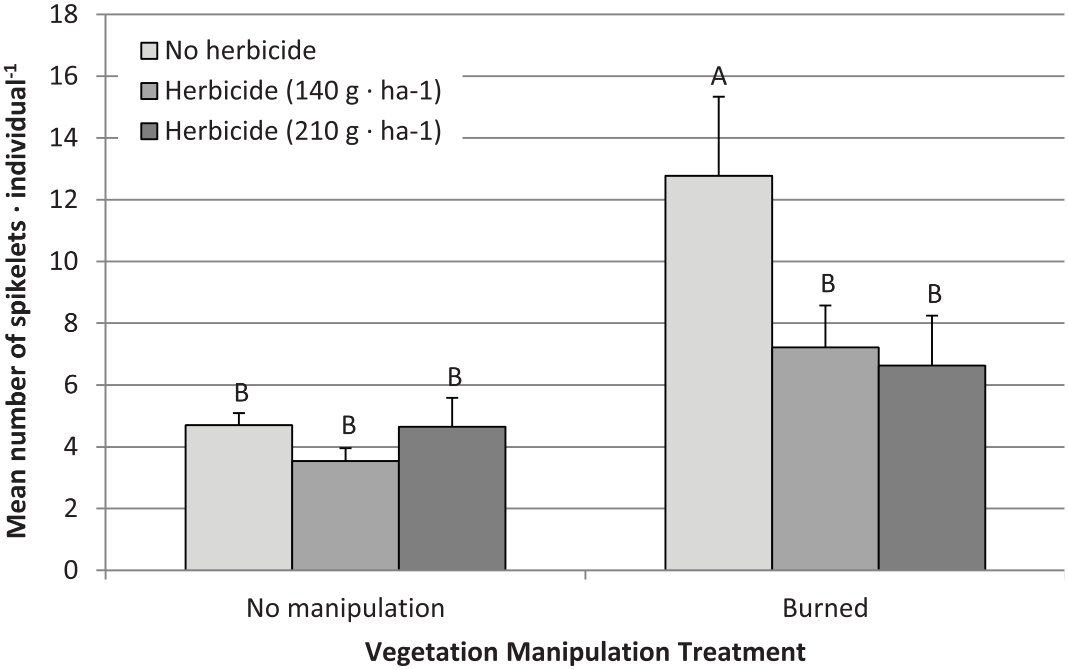

Figure 2.16. Mean number of spikelets · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.

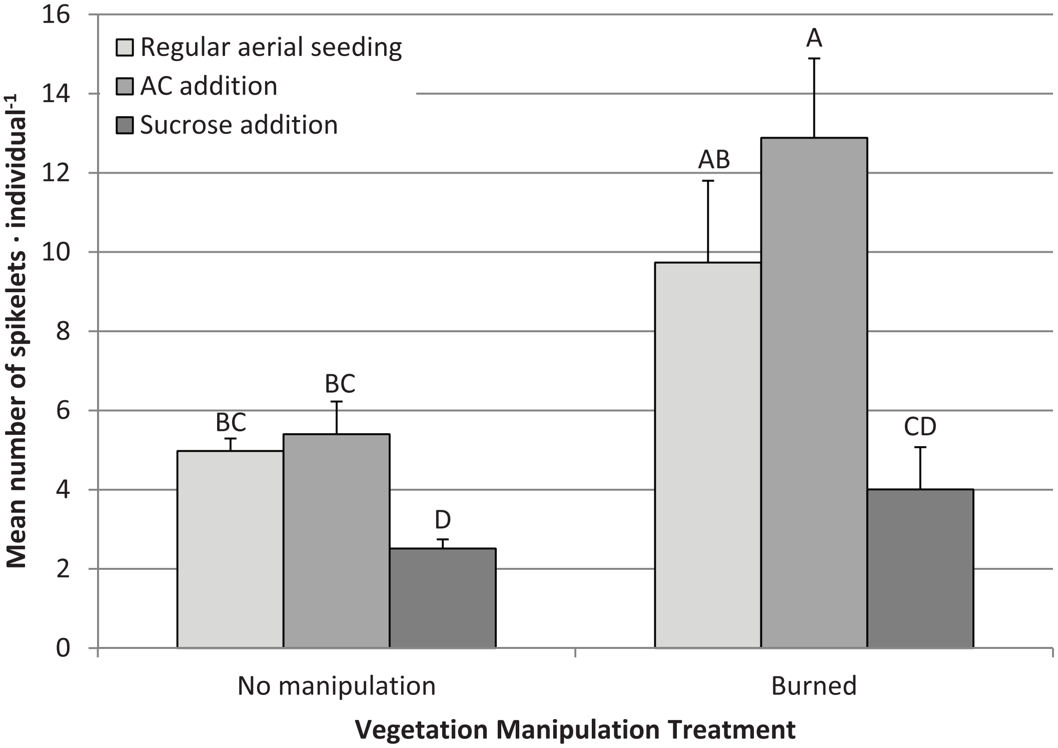

Figure 2.17. Mean number of spikelets · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.

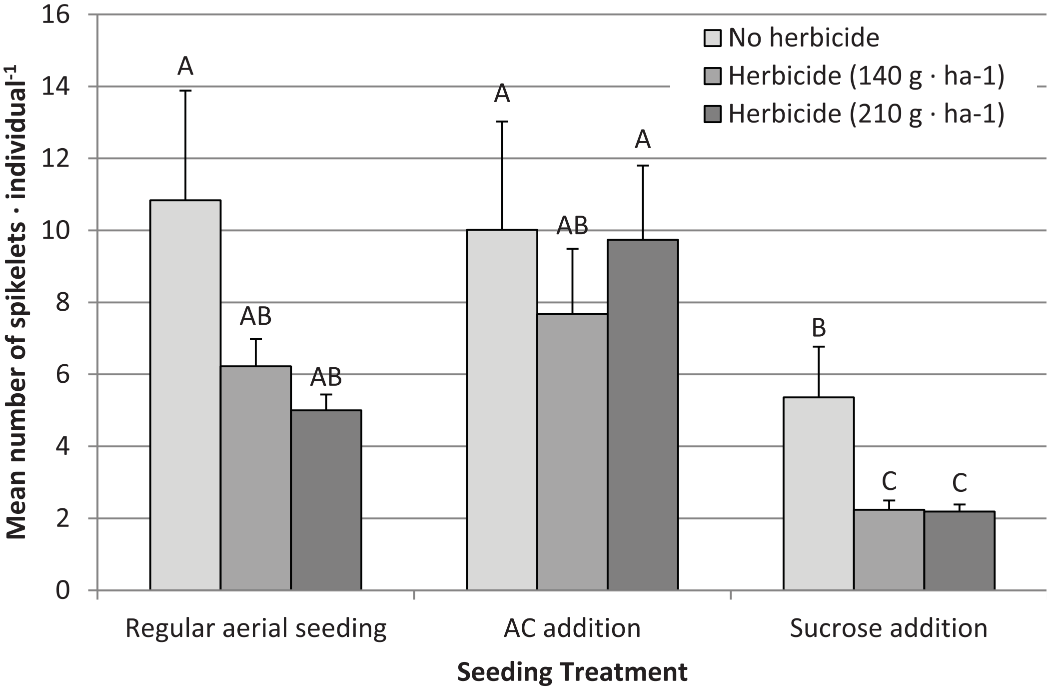

Figure 2.18. Mean number of spikelets · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *seedtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.

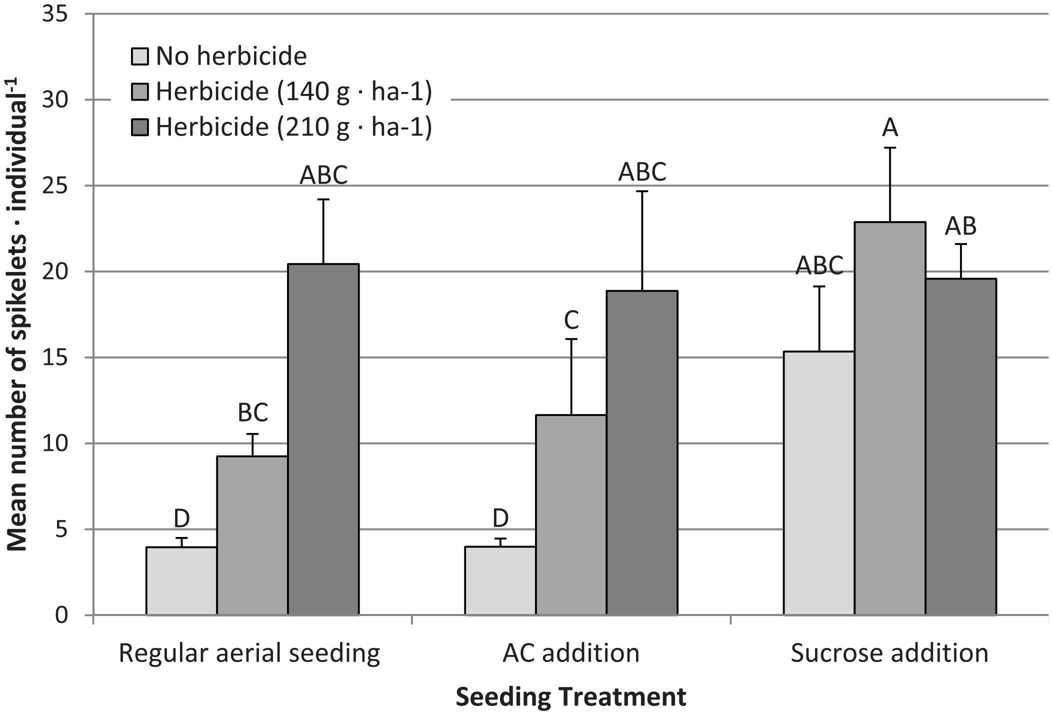

Figure 2.19. Mean number of spikelets · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *seedtreat* in the cheatgrass experiment in 2010. Values with the same letter do not differ significantly from each other.

CHAPTER 3

CHANGES TO SOIL ION AVAILABILITY FOLLOWING RESTORATION TREATMENTS IN CHEATGRASS-INVADED ECOSYSTEMS

Abstract. Many acres of rangelands in the western U.S. have been colonized by the invasive annual grass cheatgrass (*Bromus tectorum* L.), resulting in shorter fire return intervals and a loss of native ecosystem components. Efforts to reintroduce native, fire-resilient perennial species into cheatgrass-invaded communities may require addressing underlying changes to soil nutrient availabilities that accompany and reinforce cheatgrass dominance and/or altering soil nutrient availability in ways that increase the relative competiveness of desired species. We tested the effects of three seeding treatments (sucrose addition, activated carbon [AC] addition, and regular aerial seeding [control]), and three vegetation manipulation treatments (100% sagebrush thinning, sagebrush overstory and/or vegetative thatch burning, and no manipulation [control]) on ion exchange resin (IER)-extractable quantities of 15 plant-available soil ions over three sampling time periods that spanned 16 months following treatment applications. We also followed the effects of sucrose addition and burning and their interactions on IER-extractable quantities of nitrate (NO_3^-) and ammonium (NH_4^+) only for an additional winter season. Sucrose addition applied by itself or after burning reduced availability of soil NO_3^- and $H_2PO_4^-$ during the first year after treatment and increased NO_3^- availability during the second winter. No changes to soil chemistry were detected with AC addition or 100% sagebrush thinning. Burning of vegetative overstories and cheatgrass thatch resulted in a suite of changes to soil chemistry, most importantly short-term increases in soil NO_3^-, phosphate ($H_2PO_4^-$), and sulfate (SO_4^{2-}). Information on changes to soil ion availabilities following treatments will help land managers and restoration practitioners decide how best to reestablish perennial grasses in these systems.

INTRODUCTION

The invasive grass species cheatgrass (*Bromus tectorum* L.), a native of Mediterranean Europe, southwest Asia, and extreme northern parts of Africa (Hitchcock 1935; Morrow and Stahlman 1984; Upadhyaya et al. 1986; Novak and Mack 2001), has invaded approximately 22 million hectares (54 million acres) in the western U.S. (Belnap et al. 2005). Cheatgrass was first documented in western states in the mid 1890's and was most likely inadvertently brought to the U.S. on several occasions via ship ballast and the importing of grain and livestock feed (Mack 1981; Knapp 1996). Cheatgrass invasion is a threat to sagebrush (*Artemisia tridentata* Nutt.) shrublands, resulting in increased wildfire intensities, spatial extents, and frequencies as cheatgrass becomes dominant (Whisenant 1990). Sagebrush is not able to resprout following fire, and its reestablishment from seed can take many years (Klemmedson and Smith 1964; West and Hassan 1985; Knapp 1996). Seeds of perennial plant species are also lost from seed banks over time in these systems (Humphrey and Schupp 2001). Therefore, increased fire frequencies result in the conversion of cheatgrass-invaded areas to near monocultures of cheatgrass with time (Whisenant 1990).

Cheatgrass has been able to invade and maintain dominance in extensive areas of the western U.S. mainly due to the degradation of native sagebrush steppe by overgrazing and agricultural practices common since the 19th century (Knapp 1996). With the severe reduction of understory components such as native perennial grasses in these ecosystems, cheatgrass was able to colonize and take advantage of newly available space and resources (Mack 1981; Knapp 1996). Soil disturbance from overgrazing and agriculture also contributes to the ability of cheatgrass to colonize and maintain dominance in western ecosystems (Davis et al. 2000; Shea and Chesson 2002; Norton et al. 2007). Soil disturbance and the subsequent unlocking of pools of long-held soil organic matter (SOM) disproportionately benefit cheatgrass; like other ruderal species, cheatgrass relies on higher quantities of bioavailable soil nutrients (namely inorganic forms of nitrogen [N]) than do slow-growing native perennials (Grime et al. 1997; Blumenthal 2005; Norton et al. 2007). In addition, cheatgrass exhibits early emergence and can grow under very cool conditions, which allow it to deplete soil moisture early and outcompete native perennials at the seedling stage (Harris 1967; Melgoza et al. 1990; Humphrey and Schupp 2004; Blank 2010).

Established perennial native bunchgrasses are more resistant to cheatgrass competition (Cline et al. 1977; Melgoza et al. 1990; Nasri and Doescher 1995; Humphrey and Schupp 2004). Active reintroduction of native, fire-resilient perennial grasses into cheatgrass-dominated ecosystems may be the key to breaking the cheatgrass-wildfire cycle in these areas. However, changes to quality, timing, and amounts of organic matter inputs in cheatgrass-invaded ecosystems create a positive-feedback loop that further increases cheatgrass’ dominance and complicates reintroduction of perennial species (Booth et al. 2003). Higher rates of root turnover and subsequent increased inputs of C and N into near-surface soil horizons occur in cheatgrass-dominated sites, which results in faster rates and shallower distribution of C and N cycling as well as proportionally larger soil surface C and N pools over time (Booth et al. 2003; Saetre and Stark 2005; Hooker et al. 2008). Accumulation of nitrate (NO_3^-) has been measured in near-surface soils under cheatgrass during summer months (Svejcar and Sheley 2001; Booth et al.2003; Sperry et al. 2006; Hooker et al. 2008) which may be a result of the exclusion of slower-growing perennial grasses that use this nutrient longer during the growing season (Hooker et al. 2008). Faster, shallower cycling and greater near- surface availability of soil nutrients (especially

NO_3^-) reinforce the competitive dominance cheatgrass has over native perennial grasses in invaded systems (Booth et al. 2003).

Certain restoration treatment methods are aimed at addressing underlying soil nutrient conditions, especially increased concentrations of inorganic N in the soil, which lead to and reinforce cheatgrass dominance. Although results are somewhat mixed, nutrient immobilization via additions of carbon (C) has been shown to be an effective method for reducing the sizes and densities of invasive species individuals while still allowing emergence of seedlings of native perennial grasses in at least some cases (Redente et al. 1992; Paschke et al. 2000; Blumenthal et al. 2003; Lowe et al. 2004; Corbin and D'Antonio 2004; Prober et al. 2005; Mazzola et al. 2008; Rowe et al. 2009; Perry et al. 2010; Mazzola et al. 2011). The addition of C (in the form of compost, shredded wood, sucrose, or other high C:N materials) stimulates the activity of soil heterotrophic microbes which temporarily take up ('immobilize') soil nutrients for use in their biomass (Bengtsson et al. 2003; Knops et al. 2002). Most soil C addition trials have been focused on reducing the availability of inorganic N; decreased concentrations of inorganic N in the soil are thought to disproportionately harm annual invasive species such as cheatgrass while leaving perennial species relatively unaffected (Wedin and Tilman 1990; McLendon and Redente 1992; Redente et al. 1992; Paschke et al 2000; Monaco et al. 2003; but see James et al. 2011). As immobilization effects on cheatgrass are temporary (Bakker and Wilson 2004; Prober et al. 2005), soil C additions are not a sufficient remediation treatment alone for ecosystems heavily invaded by cheatgrass (Morghan and Seastedt 1999); reincorporation of low-N adapted native species is necessary for more long-term stabilization of N levels (Perry et al. 2010; Mazzola et al. 2011).

Activated carbon (AC), a charcoal-like material with extremely high surface porosity, has also been suggested as a soil additive to be used to indirectly negatively impact cheatgrass and other exotic weeds without harming native perennial species. Preliminary tests indicate that AC incorporated into the soil at high concentrations can reduce cheatgrass cover (Kulmatiski and Beard 2006; Kulmatiski 2011), although chemical mechanisms for these effects are not well understood. Due to its high surface porosity, AC is able to sequester organic compounds inside its micropores via van der Waals forces (Cheremisinoff and Morresi 1978; Marsh 1989); the sequesteration of chemical substrates used during plant-microbe interactions may directly disadvantage invasive species such as cheatgrass (Kulmatiski and Beard 2006; Kulmatiski 2011). Also, the reduction of organic compounds in the soil (namely N and P in the form of amino acids) could result in reductions in mineralization rates (e.g. Rhodes et al. 2010) and nutrient availability over time, which could negatively impact cheatgrass in a similar fashion as occurs with microbial immobilization. It is unknown whether surface applications of economically realistic quantities of AC would be effective at altering soil nutrient availability and potentially negatively affecting cheatgrass in areas where soil disturbance is precluded.

Other commonly used management techniques in sagebrush ecosystems, whether or not intended for the reestablishment of native perennials, can have implications for soil nutrient availability. Burning temporarily increases the availability of inorganic forms of N, P, and sulfur (S), which could create better conditions for the germination and establishment of desired perennial species if not outcompeted for these resources by cheatgrass (Blank et al. 1994). Burning also may temporarily reduce cheatgrass soil seed banks (Humphrey and Schupp 2001). Likewise, mechanical clearing of sagebrush overstories may have the effect of freeing light and soil resources that could be made available to perennial grass seedlings without fire-induced changes to soil N.

As part of an overall goal of determining optimum restoration treatment combinations for perennial grass reestablishment, this stage of our research addresses the effects of soil sucrose addition, soil AC addition, sagebrush and vegetative cover burning, and sagebrush mechanical removal on soil ion availability through time. The experimental designs allowed us to determine main effects of treatments as well as interactions between treatments.

METHODS

Study Site

Golden Spike National Historic Site is located in Box Elder County, Utah, 32 miles west of Brigham City (lat 41°37′13.73″, long 112°32′50.9″). This historic site, managed by the National Park Service, marks the spot of the completion of the transcontinental railroad in 1869. The park and its surrounding area, which were historically sagebrush-steppe ecosystems, have been subject to disturbance activities such as grazing, agriculture, landform manipulation, and wild and prescribed fire since the arrival of European settlers over a century ago (Homstad et al. 2000; Thornberry-Ehrlich 2006). Because of these disturbances, the perennial grass component of the sagebrush ecosystem has been severely degraded and, in many places, almost completely lost (Monaco 2004). Because of this, cheatgrass has been able to establish and become a dominant part of the understories of these ecosystems (Monaco 2004). Much of the acreage of the site still maintains a sagebrush overstory; however, some areas of the park have already lost the sagebrush overstory and been converted to cheatgrass near-monocultures due to fire. As this park is an historic site with abundant archaeological resources, soil-disturbing treatments are not allowed.

General Background

Study plots for two related experiments were established in May 2008. These experiments were implemented with an overall goal of determining how best to reestablish native perennial grasses into cheatgrass-invaded ecosystems in the absence of soil disturbing treatments, with initial objectives of determining the effects of these treatments on cheatgrass metrics (Chapter 2) and soil ion availabilities.

The first experiment, referred to as the 'sagebrush' experiment, was arranged in four replicates established in areas with intact sagebrush cover. Two of the replicates, called the 'Hill' replicates, were located on a hill above the east auto tour road. The other two, called the 'VC' replicates, were located near the park visitor's center. Each replicate consisted of eight plots, each measuring 19.5 x 7 m and divided linearly into five subplots (three 3.5 x 7 m interior subplots and two 4.5 x 7 m subplots on the ends). Half of the plots in each replicate were treated with herbicide. Four vegetation manipulation treatments, burning, 100% thinning, 50% thinning, and no manipulation were assigned randomly to one herbicide plot and one no-herbicide plot. Five seeding treatments were randomly assigned at the subplot level within each plot: regular aerial seeding, aerial seeding with raking, aerial seeding with sucrose addition, aerial seeding with activated carbon (AC) addition, and aerial seeding on snow. This created a split-split plot experimental design, with herbicide treatment occurring at the half-replicate level, vegetation manipulation occurring at the whole plot level, and seeding treatments occurring at the subplot level. This design allowed for a total of 32 treatment combinations within each replicate. A 1.5 x 3 m disturbance-free sampling zone was established in the center of each subplot, which created 2 m buffers between adjacent sampling areas and between sampling areas and the outside border of the greater whole plot.

The second experiment, referred to as the ‘cheatgrass’ experiment, was established in an area that was subject to a prescribed burn in 1998 and thereby converted to a near-monoculture of cheatgrass without a sagebrush overstory. This experiment was arranged in four replicates of two plots each, each whole plot measuring 18 x 21 m and divided into nine 6 x 7 m subplots in a 3 x 3 grid. One plot in each replicate was burned and the other was left as a control. Herbicide was applied to subplots in the two lowest 1 x 3 subplot strips within each whole plot. Three seeding treatments, regular aerial seeding, aerial seeding with sucrose addition, and aerial seeding with AC addition, were randomly assigned to subplots within each strip. This created a strip-split plot design, with vegetation manipulation treatment occurring at the whole plot level, herbicide application occurring at the strip-plot level, and seeding treatments occurring at the subplot level with the three treatments nested within herbicide strips. Eighteen total treatment combinations occurred within each replicate of this experiment. Disturbance-free sampling zones measuring 2 x 3 m were established in the center of each subplot in this experiment, creating 2 m buffers from each disturbance-free sampling zone to the edge of its subplot.

As the present study is focused on treatments most likely to alter soil ion availability, not all treatments are included in this phase of analysis. In the sagebrush experiment, we included three vegetation manipulation treatments, burning of sagebrush and vegetative overstory (‘burning’), 100% thinning and removal of sagebrush (‘100% thinning’), and no manipulation to sagebrush overstory (‘no manipulation’) applied at the plot level. We also included three seeding treatments: 1) aerial seeding with sucrose addition (‘sucrose addition’),

2) aerial seeding with AC addition (‘AC addition’), and 3) regular aerial seeding (‘regular aerial seeding’) applied at the subplot level, resulting in a 3 x 3 factorial design. In the cheatgrass experiment, we used two vegetation manipulation treatments (‘burning’ and ‘no manipulation’) at the plot level and three seeding treatments (‘sucrose addition’, ‘AC addition’, and ‘regular aerial seeding’) at the subplot level, resulting in a 2 x 3 factorial design.

Soil Survey Information

Soil survey information for eastern Box Elder County, Utah shows four soil types occurring within the boundaries of these experiments (USDA NRCS 2011; Table 3.1). All are located on fan remnants and lake terraces and are composed of limestone, quartzite, and sandstone. The VC replicates in the sagebrush experiment occur on Kearns-Stingal complex (KgD), 6 to 10% slopes, and Kerns silt loam (KeB), 1 to 3% slopes, which are both non-saline, well-drained, and with high available water capacity, a maximum of 20% calcium carbonate ($CaCO_3$) content, and a pH range of 8.0 to 9.2. Plots in the Hill replicates in the sagebrush experiment all occur on Sterling gravelly loam (SsB), 1 to 6% slopes, which is non-saline and somewhat excessively drained with low available water capacity, a maximum of 35% $CaCO_3$ content, and a pH range of 7.7 to 8.1. Plots in the cheatgrass experiment all occur on Abela gravelly loam (ABE), 10 to 20% slopes, well-drained, non-saline to slightly saline, and with low available water capacity, a maximum $CaCO_3$ content of 40%, and a pH range of 8.3 to 9.2.

Treatment Methods

Vegetation Manipulation Treatments. 100% thinning of sagebrush was done via chainsaws by the Zion National Park Fire Use Module. All sagebrush within selected sagebrush plots were cut off at the ground and removed from plots. Prescribed burning was also done by the Zion National Park Fire Use Module using handheld drip torches; areas outside the desired burn area were wetted before and during burning to contain fire spread. Vegetation manipulation treatments were done on 25 August 2008 in the cheatgrass experiment and on 5 September 2008 in the sagebrush experiment.

Seeding Treatments. All subplots were seeded with the same mixture of six native grass species (see Chapter 2). AC (12 x 30 mesh size) from superheated coconut husks (AquaSorb CS, Ecologix Environmental Systems) was applied at a rate of 100 g · m^{-2} immediately following seeding on 20 - 26 October 2008. Sucrose was applied at a rate of 360 g · m^{-2} (151.6 g C · m^{-2}) divided between two applications of 180 g · m^{-2} (75.8 g C · m^{-2}) each, the first applied from 20 - 26 October 2008 and the second from 28 to 29 March 2009. Sucrose was used as a C source because of its constant C content and ability to cause rapid immobilization.

Data Collection

Soil ion data were collected using Plant Root Simulator™ (PRS) probes (Western Ag Innovations, Inc., Saskatoon, Canada). PRS probes are composed of ion exchange resin (IER) membranes in plastic casings. IER membranes, each measuring 10 cm^2, use electrostatic attraction to attract and adsorb bioavailable ions from the surrounding soil solution over the length of burial time (WAI 2007). At the end of the burial period, probes are removed, rinsed thoroughly with deionized water, placed in labeled resealable plastic bags, and sent back to Western Ag Innovations for processing. During processing, IER-extracted ions are removed from the membranes using a weak acid or salt solution, and the concentrations of these ions in solution are assessed. PRS probes collected data on the IER-extractable quantities of 15 micro- and macronutrient ions and heavy metals: nitrate (NO_3^-), ammonium (NH_4^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^+), phosphate ($H_2PO_4^-$), iron (Fe^{3+}), manganese (Mn^{2+}), copper

(Cu^{2+}), zinc (Zn^{2+}), borate ($B[OH]_4^{3+}$), sulfate (SO_4^{2-}), lead (Pb^{2+}), aluminum (Al^{3+}), and cadmium (Cd^{2+}). NO_3^- and NH_4^+ are inorganic (bioavailable) forms of N, a plant-essential macronutrient. $H_2PO_4^-$ (bioavailable form of phosphorus, P), K^+, Ca^{2+}, SO_4^{2-} , and Mg^{2+} are also plant-essential macronutrients, while Fe^{3+}, Mn^{2+}, Cu^{2+}, $B(OH)_4^{3+}$, and Zn^{2+} are plant-essential micronutrients. Pb^{2+}, Al^{3+}, and Cd^{2+} are heavy metals not essential for plant growth that can cause toxicity in plants in relatively small quantities. Data are reported in units of $\mu g \cdot 10\ cm^{-2} \cdot \text{burial length}^{-1}$.

We measured extracted quantities of ions in three time periods. The first time period ('Time 1'; 22-23 Nov 2008 to 17-19 March 2009) closely followed application of experimental treatments and therefore measured their immediate effects on soil nutrient availabilities. Only one round of sucrose (180 $g \cdot m^{-2}$, half of total amount) had been applied up to this point. The second time period ('Time 2'; 17-19 March 2009 to 9-11 June 2009) measured ions during the first active growing season following treatment applications. Both rounds of sucrose application (for a total of 360 $g \cdot m^{-2}$) had been applied before this time period began. The third time period ('Time 3'; 20 Nov 2009 to 20 March 2010) occurred one full season after initial treatment applications to determine residual effects of treatments on quantities of IER-extractable ions. During Time 3, only NO_3^- and NH_4^+ were analyzed. Additionally, mechanically cleared plots in the sagebrush experiment and AC addition subplots in both experiments were omitted during Time 3. This round of sampling was done to determine the length of treatment effects on N observed during preliminary data analysis of Times 1 and 2.

One set of probes, each containing an anion-collecting and a cation-collecting probe, was put into the ground in each of the four corners of the undisturbed sampling area within each selected subplot. Probes were inserted following protocols for *in situ* collection from Western Ag Innovations, namely assuring complete contact between probe membranes and the soil (WAI 2007). Handheld trowels were occasionally used to prepare holes when the ground was too rocky or hard to insert probes directly. The four sets of probes in a subplot were analyzed as a composite to give the mean IER-extractable quantity of each ion in the subplot.

Statistical Analysis

Data were analyzed using SAS/STAT® 9.2 software (SAS Institute Inc. 2002). Initial differences in IER-extractable quantities of ions between sagebrush and cheatgrass experiments were determined by comparing untreated subplots in both experiments (regular aerial seeding subplots in no manipulation plots, n=4 in each experiment) during Time 1. For these analyses, we used SAS PROC GLM to create analysis of variance (ANOVA) models for all of the soil ions using the factor '*experiment*' ('sagebrush' or 'cheatgrass') as a class explanatory variable.

We used SAS PROC GLIMMIX to create generalized linear mixed-model ANOVAs to test the effects of vegetation manipulation and seeding treatments, as well as their interactions, within each experiment separately. '*Vegtreat*' (level of vegetation manipulation treatment) and '*seedtreat*' (level of seeding treatment) were fixed effects, and '*rep*' (replicate number) was a random effect. Random effects for Times 1 and 2 also included *rep* * *vegtreat* and *rep** *vegtreat* * *seedtreat* in the sagebrush experiment and *rep* * *vegtreat* in the cheatgrass experiment. Random effects for Time 3 in the sagebrush experiment also included *rep* * *vegtreat*. Random factors varied by experiment and time period due to differing experimental designs. The Tukey-Kramer method for multiple comparisons was used to determine significant differences between treatment combinations at $\alpha = 0.05$ level. The response variables (IER-extractable quantities of each ion, in units of $\mu g \cdot 10\ cm^{-2} \cdot$ burial length $^{-1}$) were transformed in order to meet the assumptions of normality, symmetry, and homoskedasticity of residuals required for ANOVA (Table 3.2). Some data points (one in the sagebrush experiment and five in the cheatgrass experiment) from Time 3 were lost due to labels detaching from samples during shipping, causing the dataset to be unbalanced. However, PROC GLIMMIX can handle unbalanced datasets when ADJUST = TUKEY is specified.

We analyzed ion data for each time period separately. We also compared NO_3^- and NH_4^+ data between Time 1 and Time 3 in both experiments to determine trends in the availabilities over time, both with and without treatments, with '*time*' (sampling time period) included as a repeated measure. Only data from subplots sampled in both Time 1 and Time 3 were included in these analyses (i.e. only sucrose addition and regular aerial seeding subplots within burned and no manipulation plots).

RESULTS

Differences between Initial Quantities of IER-Extractable Ions

There were no significant differences (all $p > 0.05$) in the initial quantities of Al^{3+}, $B(OH)_4^{3+}$, Ca^{2+}, Cd^{2+}, Fe^{3+}, K^+, Mg^{2+}, Mn^{2+}, NO_3^- , $H_2PO_4^-$, and SO_4^{2-} between experiments (data from Time 1, regular aerial seeding subplots within no manipulation plots only). Quantities of Cu^{2+}, Zn^{2+}, and Pb^{2+} were significantly greater in the cheatgrass experiment than the sagebrush experiment, and quantities of NH_4^+ were significantly greater in the sagebrush experiment than the cheatgrass experiment (Table 3.3).

Time 1- First Winter after Treatment

The majority (>50%) of samples of Pb^{2+} and Cd^{2+} in both experiments, of Cu^{2+} in the sagebrush experiment, and of NH_4^+ in the cheatgrass experiment were at or below method detection limits of PRS probes; we therefore did not analyze availability of these ions in the appropriate experiments. All values in this section are in units of $\mu g \cdot 10\ cm^{-2} \cdot 17\ weeks^{-1}$.

In the sagebrush experiment, the *seedtreat* main effect was significant for NO_3^- and the *vegtreat* main effect was significant for $H_2PO_4^-$, SO_4^{2-}, Mn^{2+}, and K^+ (Table 3.4). Quantities of IER-extractable NO_3^- were significantly less in sucrose addition subplots (11.7 µg ± 2.7; mean ± 1 *SE*) than in regular aerial seeding (51.6 µg ± 8.8) or AC addition (56.5 µg ± 13.4) subplots. Quantities of IER-extractable $H_2PO_4^-$, SO_4^{2-}, and K^+ were significantly greater in burned than no manipulation and 100% thinned plots (Table 3.5). Quantities of Mn^{2+} were significantly greater in burned plots than in no manipulation plots; 100% thinning resulted in intermediate Mn^{2+} quantities not significantly different from either of the other vegetation manipulation treatments (Table 3.5).

In the cheatgrass experiment, *vegtreat* and *seedtreat* main effects and the *seedtreat* * *vegtreat* interaction were significant for NO_3^- and $H_2PO_4^-$, while only the *vegtreat* main effect was significant for SO_4^{2-} (Table 3.4). Sucrose addition significantly decreased quantities of NO_3^- and $H_2PO_4^-$ as compared to AC addition and regular aerial seeding (Table 3.6). Burning increased quantities of NO_3^-, $H_2PO_4^-$, and SO_4^{2-} as compared to no manipulation plots (Table 3.7). The significant *seedtreat* * *vegtreat* interactions for NO_3^- and $H_2PO_4^-$ were due to sucrose addition decreasing quantities of these ions in burned plots to levels not significantly different from no manipulation plots while not affecting quantities in no manipulation plots (Figs. 3.1-3.2).

Time 2- First Summer after Treatment

The majority (>50%) of reported IER-extractable quantities of Cd^{+2} and SO_4^{2-} in both experiments and of Pb^{2+} in the sagebrush experiment were at or below method detection limits of PRS probes and were therefore excluded from analysis. All IER-extractable quantities in this section are in units of $\mu g \cdot 10\ cm^{-2} \cdot 12\ weeks^{-1}$.

In the sagebrush experiment, the *seedtreat* main effect for NO_3^- and the *vegtreat* main effect for $H_2PO_4^-$, SO_4^{2-}, K^+ and Mn^{2+} were no longer significant. However, the *vegtreat* main effect for NO_3^- and Al^{3+} and the v*egtreat* * *seedtreat* interaction for NH_4^+ and Ca^{2+} were now significant (Table 3.8). Quantities of NO_3^- and Al^{3+} were both now significantly greater in burned plots than in 100% thinned or no manipulation plots (Table 3.9). The significant *vegtreat* * *seedtreat* interaction for NH_4^+ and Ca^{2+} resulted from the no manipulation, 100% thinned, and burned plots responding differently, but non-significantly, to the seeding treatments (Figs. 3.3-3.4).

In the cheatgrass experiment, the *seedtreat* main effect was still significant for NO_3^-, no longer significant for $H_2PO_4^-$, and now significant for Mn^{2+} and Cu^{2+} (Table 3.8). The *vegtreat* main effect was no longer significant for NO_3^-, $H_2PO_4^-$, and SO_4^{2-} but was now significant for NH_4^+, Al^{3+}, and Pb^{2+} (Table 3.8). The *seedtreat* * *vegtreat* interaction was no longer significant for NO_3^- and $H_2PO_4^-$ but was now significant for Fe^{3+} (Table 3.8). Quantities of IER-extractable NO_3^- were significantly lower in sucrose addition subplots (11.5 µg ± 4.3) than in AC addition subplots (34.3 µg ± 5.7); NO_3^- quantities in regular aerial seeding subplots (26.8 µg ± 8.7) were intermediate and not significantly different than in the other two seeding treatments. In contrast, quantities of Mn^{2+} and Cu^{2+} were both significantly greater in sucrose addition subplots than in AC addition or regular aerial seeding subplots (Table 3.10). Quantities of NH_4^+ were significantly decreased in burned plots (2.0 µg ± 0.1) as compared to in no manipulation plots (2.7 µg ± 0.2); quantities of Al^{3+} and Pb^{2+} were both significantly greater in burned plots (Al^{3+} = 50.8 µg ± 1.9 vs. 44.2 µg ± 1.3; Pb^{2+} = 0.8 µg ± 0.1 vs. 0.5 µg ± 0.1; burned vs. no manipulation, respectively). The significant *seedtreat* * *vegtreat* interaction for Fe^{3+} was due to quantities of this ion being greatest in AC addition subplots and lowest in regular aerial seeding subplots within no manipulation plots, and the reverse in burn plots, though no significant differences existed (Fig. 3.5).

Time 3- Second Winter after Treatment

No main effects or interactions were significant in either the sagebrush or cheatgrass experiments (Table 3.11).

Time 1 and 3 Differences

For these analyses, we compared quantities of IER-extractable NO_3^- and NH_4^+ between Time 1 and Time 3, the first and second winters after treatment implementation, with experiments analyzed separately. Values in this section are in units of $\mu g \cdot 10\ cm^{-2} \cdot 17\ weeks^{-1}$.

In the sagebrush experiment, the *vegtreat* main effect was significant for NO_3^-, the *time* main effect was significant for both NH_4^+ and NO_3^-, and the *time* * *seedtreat* interaction was significant for NO_3^- (Table 3.12). Quantities of NO_3^- were greater at both times in burned (83.3 µg ± 19.1) than in no manipulation (47.9 µg ± 11.0) plots. Quantities of NH_4^+ were significantly greater in Time 1 than in Time 3 (8.7 µg ± 0.8 vs. 5.2 µg ± 0.4, respectively), while quantities of NO_3^- were significantly less in Time 1 than in Time 3 (32.6 µg ± 7.5 vs. 99.6 µg ± 18.7, respectively). The significant *time* * *seedtreat* interaction for NO_3^- was due to quantities of this ion being significantly greater in Time 3 than in Time 1 in the sucrose addition subplots but equivalent (at intermediate levels) in the regular aerial seeding subplots in the two time periods (Fig. 3.6).

In the cheatgrass experiment, the *vegtreat* main effect and the *time* * *seedtreat* interaction were significant for NO_3^-, while the *time* main effect was significant for NH_4^+ (Table 3.12). As in the sagebrush experiment, quantities of NO_3^- were greater in burned (73.4 µg ± 24.1) than in no manipulation (42.9 µg ± 9.4) plots at both times. Quantities of NH_4^+ were less during Time 1 (2.6 µg ± 0.8) than Time 3 (5.8 µg ± 0.9), the opposite of what was found in the sagebrush experiment. The significant *time* * *seedtreat* interaction was due to quantities of NO_3^- in sucrose addition subplots being significantly less than in regular aerial seeding subplots during Time 1, but increasing significantly from Time 1 to Time 3 to a level indistinguishable from that in regular aerial seeding plots in either time period (Fig. 3.7). Quantities of NO_3^- also decreased significantly between Time 1 and Time 3 in regular aerial seeding subplots (Fig. 3.7).

DISCUSSION

Some treatments evaluated in this experiment affected soil ion availabilities either positively or negatively. Interactions between some of the plot-level and subplot-level treatments were also present.

Mobility of soil ions depends a great deal on soil temperature and moisture level (Barber 1995; Alam 1999). In these trials specifically, differences detected between experiments and between times may be correlated with the associated differences in soil temperatures and moisture levels. As we did not measure these variables and include them as covariates in analyses, their contributions to our findings are unknown.

Initial Differences Between Soil Nutrient Availabilities In the Two Experiments

Data from untreated subplots during the first sampling time period showed significantly lower availability of NH_4^+ and greater availabilities of Cu^{2+}, Zn^{2+}, and Pb^{2+} in the cheatgrass experiment as compared to the sagebrush experiment. These differences are potentially due to the prescribed burn in the cheatgrass experiment area in 1998 and the long-term consequences of conversion to a cheatgrass near-monoculture. Brye (2006) also reported increased availability of Cu^{2+} over time in soils under annually-burned tallgrass prairies; however, availabilities of Zn^{2+} were unchanged during the 12-year study period. Rau et al. (2008) did find significant increases in Zn^{2+} availabilities following burning of pinyon and juniper woodlands and sagebrush shrublands, but this effect only lasted one year post-burn. We were not able to find research pertaining to changes in soil Pb^{2+} with burning. These three ions are known to become bound to cation exchange sites in SOM (Johnson and Richter 2010); the combustion of SOM with burning (Wohlgemuth et al. 2006) could therefore increase the solubility of these ions in the soil solution. Long-term depletions of SOM have been observed in cheatgrass-dominated areas (Norton et al. 2004); SOM in soils in this area are likely to still be quite impoverished despite ten years having passed since the burn and when this data was collected (2008-2009). This may explain why availabilities of these ions are still greater at this site than the sagebrush experiment area. Solubility of these heavy metal ions is known to be reduced with increasing soil pH (Reddy et al. 1977; Sinha et al. 1978). However, soils in the cheatgrass site are generally more alkaline (pH 8.3 - 9.2) than in the sagebrush experiment (Hill replicate pH = 7.7 - 8.1; VC replicate pH = 8.0 - 9.2). Increased availabilities of these ions in the cheatgrass site are not therefore explained by differences in soil alkalinity between the two experiments.

We are unsure of the reason for decreased NH_4^+ availability in the cheatgrass-dominated cheatgrass experiment. Previous studies have either found no difference between NH_4^+ concentrations in cheatgrass soils as compared to sagebrush soils (Saetre and Stark 2005; Hooker et al. 2008; Johnson et al. 2010) or higher concentrations of NH_4^+ under cheatgrass soils (Booth et al. 2003; Adair et al. 2010). It is possible that potentially greater SOM levels in the sagebrush experiment result in greater resupply rates of NH_4^+ than in the SOM-poor soils assumed to occur in the cheatgrass experiment area (Booth et al. 2005).

Effects of Sucrose Addition

Sucrose addition resulted in significantly decreased quantities of IER-extractable NO_3^- during the first winter after treatment (Time 1) in both experiments. Quantities of NO_3^- were still reduced in sucrose addition subplots in the cheatgrass experiment during the first summer after treatment (Time 2). By the second winter after treatment (Time 3) NO_3^- levels in sucrose addition subplots had returned to a level not significantly different than those found in the regular aerial seeding subplots in both experiments. The reduction of NO_3^- over the course of the first two phases indicates that sucrose did in fact stimulate the activity of soil heterotrophic microbes and induce temporary immobilization. Previous studies have also shown short-term decreases in soil NO_3^- with sucrose addition in cheatgrass-dominated (Mazzola et al. 2008; Rowe et al. 2009; Mazzola et al. 2011) and other communities (McLendon and Redente 1992; Paschke et al 2000; Monaco et al. 2003). There is also some indication in our data that in both experiments soil NO_3^- availability increased in sucrose addition subplots to levels greater than in regular aerial seeding subplots during Time 3, suggesting N immobilization over the short term might result in a pulse of N later; however, this increase did not bring NO_3^- availability to levels significantly different than in regular aerial seeding subplots (Figs. 3.6-3.7).

Quantities of IER-extractable $H_2PO_4^-$ were also significantly reduced in sucrose addition subplots in the cheatgrass experiment during the first winter after treatment (Time 1). This effect did not continue in the cheatgrass experiment in Time 2 or occur in the sagebrush experiment during either time (quantities of $H_2PO_4^-$ were not assessed in Time 3). Immobilization of soil P following C addition has been found in some (Jonasson et al. 1996; Wu et al. 2007) but not all (McLendon and Redente 1991; Mazzola et al. 2008; Mazzola et al. 2011) previous studies that measured this nutrient.

IER-extractable quantities of Mn^{2+} and Cu^{2+} were increased significantly in sucrose addition subplots during Time 2 as compared to regular aerial seeding subplots. There was no change in the IER-extractable quantities of these ions in Time 1, and these ions were not assessed during Time 3. We do not know the reason for these increases, although they might indicate a release of these ions following immobilization even though the reductions via immobilization, which would have occurred during Time 1, were not statistically detectable. We are aware of no literature reporting Mn^{2+} or Cu^{2+} immobilization with sucrose addition, but these ions are generally not assessed in C addition trials.

Effects of AC Addition

We did not detect an effect of AC addition in either experiment on the IER-extractable quantities of any of the ions assessed, and therefore we were not able to find any soil chemistry bases for the results of studies by Kulmatiski and Beard (2006) and Kulmatiski (2011) that utilized AC for control of cheatgrass and other exotic species. However, this may be accounted for by our lower rate of AC use and our application method (on the soil surface instead of tilled in to the soil column), which were tested as more realistic options for large-area AC application.

Effects of Sagebrush Thinning

Sagebrush overstory removal has been found to increase availabilities of NO_3^-, Ca^{2+} and Mg^{2+} in the soil (Blank et al. 2007). However, for the duration of this experiment no quantities of any of the measured soil ions were significantly different in plots where sagebrush was removed as compared to no manipulation plots. Significantly increased cheatgrass mean weights, numbers of tillers, and numbers of spikelets found in these plots during previous analyses (Chapter 2) may therefore be correlated with increases in the availability of other resources, such as sunlight and water (Prevéy et al. 2010), which occur with sagebrush removal. Shrub removal has been found to increase days of available water in subsurface soils (Schlesinger et al. 1987; Whittaker et al. 2008); cheatgrass is better able to take advantage of soil water than are native perennial species (Melgoza et al. 1990) and could in theory be disproportionally benefited by this increase.

Effects of Vegetative Burning

During Time 1, burned plots had significantly greater quantities of $H_2PO_4^-$, SO_4^{2-} , Mn^{2+}, Ca^{2+}, and K^+ in the sagebrush experiment and of NO_3^- , $H_2PO_4^-$, and SO_4^{2-} in the cheatgrass experiment. Also in Time 1 in the cheatgrass experiment, sucrose addition in burned plots significantly reduced quantities of NO_3^- and $H_2PO_4^-$ to levels not significantly different than in no manipulation plots. During Time 2, quantities of NO_3^-, $H_2PO_4^-$, and Al^{3+} in the sagebrush experiment and Al^{3+} and NH_4^+ and Pb^{2+} in the cheatgrass experiment were significantly increased in burned plots. In Time 3, no soil ion differences were detected in burned plots in either experiment (only NH_4^+ and NO_3^- were assessed in Time 3).

Increases in availabilities of soil ions are commonly observed post-fire (Christensen 1973; Christensen and Muller 1975; DeBano and Klopatek 1988; Blank et al. 1994, 1996; Giovaninni and Lucchesi 1997; Rau et al. 2007, 2008; Esque et al. 2010). Increases in availabilities of NH_4^+, SO_4^{2-}, and $H_2PO_4^-$ are due to organic matter combustion and denaturing of amino acids and proteins in SOM with elevated soil temperatures (DeBano and Klopatek 1988; Blank et al. 1994; Certini 2005; Wohlgemuth et al. 2006; Moghaddas and Stevens 2007). Increased NO_3^- availabilities are a result of heightened soil temperatures stimulating activity of soil bacteria, leading to greater mineralization of soil organic N and oxidation of NH_4^+ (Hobbs and Schimel 1984). Burning is known to increase soil availabilities of organically-bound ions like Mn^{2+}, Al^{3+}, K^+, and Ca^{2+} as plant material is converted to ash (Hough 1981; Wohlgemuth et al. 2006; Pereida and Ubeda 2010). Increases in Pb^{2+} availability in burned plots might be due to the degradation of SOM and subsequent reduction of its cation exchange capacity (Wohlgemuth et al. 2006), which would increase the mobility of cations such as Pb^{2+} formerly held on exchange sites (Johnson and Richter 2010).

As described in Chapter 2, cheatgrass in burned plots had significantly greater mean weights and mean number of tillers and spikelets than those in no manipulation plots in both experiments. The accelerated growth of cheatgrass in these areas may be explained partially by heightened availability of these soil ions, probably in addition to the increases in sunlight and soil water availability with the removal of overstory species and the reduced cheatgrass densities (Prevéy et al. 2010).

IMPLICATIONS

Sucrose addition resulted in significantly decreased soil nutrient quantities after application, but treatment effects were short-lived. As shown in Chapter 2, the effects of sucrose addition on cheatgrass metrics were also temporary; reductions in mean weights and tiller and spikelet numbers occurred during the first growing season after application but these metrics were increased in sucrose addition subplots during the second growing season. A trend of increased NO_3^- availability was apparent in Time 3 in sucrose addition plots in both experiments, and although this increase was not statistically significant, it is possible that it was enough to stimulate cheatgrass biomass production during the second growing season. If sucrose addition is to be used, efforts should be made to incorporate perennial grass seedlings as quickly as possible following application as heightened soil nutrient availability following the cessation of immobilization could again create conditions suited to cheatgrass competitive dominance.

Increases in soil nutrient quantities were observed in burned plots, with treatment effects on NO_3^- significant during all three sampling time periods. Burning can reduce cheatgrass seed in seed banks (Humphrey and Schupp 2001) resulting in decreased post-fire densities; however, heightened soil nutrient availability following fire may stimulate growth of individual plants. As described in Chapter 2, cheatgrass densities were significantly lower but individuals were larger and with greater reproductive capacity in burned plots than in no manipulation (unburned) plots during both seasons. We believe there is a narrow window of opportunity for establishing desirable species into burned areas, as post-burn soil nutrient conditions and increased reproductive capacity of remaining cheatgrass individuals favor the eventual reestablishment and dominance of this species without intervention.

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Table 3.1. Site and soils information for experimental areas in Golden Spike National Historic Site. Data from soil series descriptions (USDA NRCS 2011).

Experiment	Vegetation	Rep	Soil series name	Texture (0 - 60 inches)	Taxonomic class	pH	Drainage class	Available water capacity	Max $CaCO_3$	Max salinity
Cheatgrass	Cheatgrass-dominated	All	Abela gravelly loam, 10 to 20% slopes	Gravelly loam to extremely gravelly sandy loam	Loamy-skeletal, mixed, superactive, mesic Typic Calcixerolls	8.3 - 9.2	Well-drained	Low (about 5.6 inches)	40%	Nonsaline to slightly saline (0.0 to 8.0 mmhos · cm^{-1})
Sagebrush	Sagebrush overstory	Hill 1 and 2	Sterling gravelly loam, 1 to 6% slopes	Gravelly loam to extremely cobbly loam	Loamy-skeletal, mixed, superactive, mesic Typic Calcixerolls	7.7 - 8.1	Somewhat excessively drained	Low (about 5.5 inches)	35%	Nonsaline (0.0 to 2.0 mmhos · cm^{-1})
		VC 1	Kearns-Stingal complex, 6 to 10% slopes	Silt loam to loam	Fine-silty, mixed, superactive, mesic Calcic Haploxerolls	8.0 - 9.2	Well-drained	High (about 11.0 inches)	20%	Nonsaline (0.0 to 2.0 mmhos · cm^{-1})
		VC 2	Kearns silt loam, 1 to 3% slopes	Silt loam to loam	Fine-silty, mixed, superactive, mesic Calcic Haploxerolls	8.0 - 9.2	Well-drained	High (about 11.0 inches)	20%	Nonsaline (0.0 to 2.0 mmhos · cm^{-1})

Table 3.2. Data variable transformations for both experiments.

	Soil ion								
Experiment	NO_{3-}	NH_4^+	$H_2PO_4^-$	SO_4^{2-}	K^+	Ca^{2+}	Mg^{2+}	Fe^{3+}	Mn^{2+}
Sagebrush	square root (^1/2)	square root (^1/2)	log	log	log	log	log	log	log
Cheatgrass	square root (^1/2) (*log-transformed in Time 3*)	square root (^1/2)	square root (^1/2)	log	inverse square root (^-1/2)	square root (^1/2)	inverse square root (^-1/2)	square root (^1/2)	inverse (^-1)

	Soil ion					
Experiment	$B[OH]_4^{3+}$	Zn^{2+}	Cu^{2+}	Al^{3+}	Pb^{2+}	Cd^{2+}
Sagebrush	square root (^1/2)	log	inverse (^-2)	inverse cube root (^-1/3)	none	none
Cheatgrass	square root (^1/2)	log	none	inverse cube root (^-1/3)	none	none

Table 3.3. Mean IER-extractable quantities (µg · 10 cm^{-2} · 17 weeks^{-1}) ± *SE*'s, of soil ions that are significantly different between the sagebrush and cheatgrass experiments. Ions not listed were not significantly different between experiments. Values with the same letter in a column do not differ significantly from each other (α = 0.05).

	Soil ion			
Experiment	NH_4^+	Cu^{2+}	Zn^{2+}	Pb^{2+}
Sagebrush	6.1 µg ± 1.1^A	0.2 µg ± 0.0^B	0.7 µg ± 0.1^B	0.1 µg ± 0.1^B
Cheatgrass	1.4 µg ± 1.0^B	0.4 µg ± 0.1^A	1.3 µg ± 0.2^A	0.5 µg ± 0.1^A

Table 3.4. Analysis of variance of Time 1 *vegtreat* and *seedtreat* main effects and their interactions on availabilities of soil ions within the sagebrush and cheatgrass experiments. Significant *p*-values (α = 0.05) are in bold font.

				Soil ion													
		dF		NO_3^-		NH_4^+		$H_2PO_4^-$		SO_4^{2-}		K^+		Ca^{2+}		Mg^{2+}	
Experiment	Source	num	den	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Sagebrush	Seedtreat	2	18	10.26	**0.0011**	0.51	0.6061	1.90	0.1781	1.59	0.2310	0.74	0.4914	0.96	0.4015	0.45	0.6443
	Vegtreat	2	6	3.38	0.1041	3.79	0.0861	93.86	**<.0001**	17.16	**0.0033**	29.56	**0.0008**	4.73	0.0584	0.68	0.5433
	Vegtreat* Seedtreat	4	18	0.43	0.7831	1.46	0.2564	0.65	0.6371	0.91	0.4797	1.54	0.2319	0.73	0.5842	2.38	0.0904
Cheatgrass	Seedtreat	2	12	15.79	**0.0004**	data insufficient		8.53	**0.0050**	2.27	0.1458	0.66	0.5362	0.26	0.7754	2.09	0.1669
	Vegtreat	1	3	25.76	**0.0148**			42.01	**0.0075**	25.46	**0.0150**	0.10	0.7755	0.26	0.6474	0.00	0.9842
	Vegtreat* Seedtreat	2	12	5.92	**0.0162**			4.22	**0.0410**	1.73	0.2187	0.59	0.5687	0.72	0.5070	0.95	0.4140

				Soil ion													
		dF		Fe^{3+}		Mn^{2+}		$B[OH]_4^{3+}$		Zn^{2+}		Cu^{2+}		Al^{3+}		Pb^{2+} and Cd^{2+}	
Experiment	Source	num	den	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Sagebrush	Seedtreat	2	18	1.60	0.2290	1.46	0.2589	0.15	0.8631	0.06	0.9444	data insufficient		0.08	0.9207	data insufficient	
	Vegtreat	2	6	2.38	0.1731	6.42	**0.0323**	0.52	0.6189	0.62	0.5681			0.87	0.4655		
	Vegtreat* Seedtreat	4	18	0.56	0.6927	0.31	0.8700	0.89	0.4895	1.63	0.2095			0.81	0.5350		
Cheatgrass	Seedtreat	2	12	1.14	0.3529	0.62	0.5541	1.17	0.3428	1.70	0.2240	0.47	0.6339	1.07	0.3749	data insufficient	
	Vegtreat	1	3	1.12	0.3675	0.18	0.7003	0.94	0.4044	1.94	0.2578	1.00	0.3910	1.21	0.3509		
	Vegtreat* Seedtreat	2	12	3.45	0.0656	1.45	0.2737	0.43	0.6590	0.07	0.9367	1.11	0.3626	0.11	0.8968		

Table 3.5. Mean IER-extractable quantities (μg · 10 cm^{-2} · 17 $weeks^{-1}$) ± *SE*'s, of soil nutrient ions that differed between vegetation manipulation treatments in the sagebrush experiment in Time 1. Values with the same letter in a column do not differ significantly from each other (α = 0.05).

	Soil ion			
Treatment	$H_2PO_4^-$	SO_4^{2-}	Mn^{2+}	K^+
Burned	27.0 μg ± 2.6^A	34.1 μg ± 8.1^A	3.6 μg ± 0.7^A	190.1 μg ± 15.2^A
100% thinned	11.0 μg ± 0.8^B	9.1 μg ± 1.9^B	1.5 μg ± 0.3^{AB}	117.7 μg ± 20.2^B
No manipulation	9.6 μg ± 0.9^B	9.5 μg ± 1.7^B	1.3 μg ± 0.3^B	116.4 μg ± 11.9^B

Table 3.6. Mean IER-extractable quantities (μg · 10 cm^{-2} · 17 $weeks^{-1}$) ± *SE*'s, of soil nutrient ions in the cheatgrass experiment in Time 1 that differed with seeding treatments. Values with the same letter in a column do not differ significantly from each other (α = 0.05).

	Soil ion	
Treatment	NO_3^-	$H_2PO_4^-$
Sucrose addition	20.9 μg ± 6.1^B	10.1 μg ± 1.1^B
AC addition	115.8 μg ± 27.5^A	19.6 μg ± 2.7^A
Regular aerial seeding	113.3 μg ± 33.0^A	17.9 μg ± 2.3^A

Table 3.7. Mean IER-extractable quantities (μg · 10 cm^{-2} · 17 $weeks^{-1}$) ± *SE*'s, of soil nutrient ions in the cheatgrass experiment in Time 1 that differed with vegetation manipulation treatments. Values with the same letter in a column do not differ significantly from each other (α = 0.05).

	Soil ion		
Treatment	NO_3^-	$H_2PO_4^-$	SO_4^{2-}
Burned	126.4 μg ± 27.9^A	19.1 μg ± 2.4^A	24.5 μg ± 4.0^A
No manipulation	40.2 μg ± 6.1^B	12.6 μg ± 1.1^B	11.6 μg ± 2.6^B

Table 3.8. Analysis of variance of Time 2 *vegtreat* and *seedtreat* main effects and their interactions on availabilities of soil ions within the sagebrush and cheatgrass experiments. Significant *p*-values (α = 0.05) are in bold font.

				Soil ion													
Experiment	Source	dF		NO_3^-		NH_4^+		$H_2PO_4^-$		SO_4^{2-}		K^+		Ca^{2+}		Mg^{2+}	
		num	den	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Sagebrush	Seedtreat	2	18	2.65	0.0984	0.76	0.4836	2.69	0.0951	data insufficient		1.42	0.2669	1.30	0.2980	1.62	0.2248
	Vegtreat	2	6	21.76	**0.0018**	0.31	0.7413	4.69	0.0594			3.48	0.0994	1.70	0.2597	2.03	0.2126
	Vegtreat* Seedtreat	4	18	0.12	0.9738	4.44	**0.0114**	2.04	0.1323			1.23	0.3344	3.34	**0.0327**	1.51	0.2401
Cheatgrass	Seedtreat	2	12	4.06	**0.0451**	0.45	0.6499	0.15	0.8612	data insufficient		2.55	0.1190	1.12	0.3581	1.14	0.3507
	Vegtreat	1	3	0.70	0.4648	34.54	**0.0098**	0.48	0.5365			4.21	0.1324	4.89	0.1139	0.67	0.4739
	Vegtreat* Seedtreat	2	12	0.16	0.8533	0.59	0.5686	0.18	0.8346			2.25	0.1477	1.07	0.3737	0.05	0.9472

				Soil ion															
Experiment	Source	dF		Fe^{3+}		Mn^{2+}		$B[OH]_4^{3+}$		Zn^{2+}		Cu^{2+}		Al^{3+}		Pb^{2+}		Cd^{2+}	
		num	den	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Sagebrush	Seedtreat	2	18	0.08	0.921	1.94	0.1720	0.15	0.8578	0.95	0.4066	0.75	0.4866	0.52	0.6035	data insufficient		data insufficient	
	Vegtreat	2	6	3.96	0.0799	4.22	0.0717	0.14	0.8718	1.46	0.3048	0.46	0.6532	9.62	**0.0134**				
	Vegtreat* Seedtreat	4	18	1.54	0.2332	0.53	0.7166	0.60	0.6703	2.86	0.0538	0.27	0.8948	0.61	0.6592				
Cheatgrass	Seedtreat	2	12	0.83	0.4589	6.02	**0.0155**	0.29	0.7556	1.32	0.3033	7.00	**0.0097**	0.68	0.5234	2.43	0.1297	data insufficient	
	Vegtreat	1	3	0.74	0.4536	1.58	0.2971	0.77	0.4440	0.20	0.6848	1.59	0.2967	14.04	**0.0332**	16.67	**0.0265**		
	Vegtreat* Seedtreat	2	12	3.98	**0.0473**	1.92	0.1895	2.67	0.1098	0.72	0.5068	3.00	0.0878	1.52	0.2587	3.03	0.0859		

Table 3.9. Mean IER-extractable quantities (µg · 10 cm^{-2} · 17 weeks^{-1}) ± *SE*'s, of soil ions in the sagebrush experiment in Time 2 that differed with vegetation manipulation treatments. Values with the same letter in a column do not differ significantly from each other (α = 0.05).

	Soil ion	
Treatment	NO_3^-	Al^{3+}
Burned	109.7 µg ± 22.5^A	46.1 µg ± 1.1^A
100% thinned	30.9 µg ± 8.0^B	40.7 µg ± 1.5^B
No manipulation	16.4 µg ± 4.7^B	40.3 µg ± 1.5^B

Table 3.10. Mean IER-extractable quantities (µg · 10 cm^{-2} · 17 weeks^{-1}) ± *SE*'s, of soil nutrient ions in the cheatgrass experiment in Time 2 that differed with seeding treatments. Values with the same letter in a column do not differ significantly from each other (α = 0.05).

	Soil ion	
Treatment	Mn^{2+}	Cu^{2+}
Sucrose addition	3.4 µg ± 0.4^A	0.43 µg ± 0.05^A
AC addition	1.6 µg ± 0.2^B	0.30 µg ± 0.04^B
Regular aerial seeding	2.0 µg ± 0.4^B	0.33 µg ± 0.04^B

Table 3.11. Analysis of variance of Time 3 *vegtreat* and *seedtreat* main effects and their interactions on availabilities of soil nutrient ions within the sagebrush and cheatgrass experiments. Significant *p*-values (α = 0.05) are in bold font.

				Soil ion			
		dF		NO_3^-		NH_4^+	
Experiment	Source	num	den	F	p	F	p
Sagebrush	Seedtreat	1	5	1.83	0.2338	1.95	0.2210
	Vegtreat	1	3	6.76	0.0803	0.66	0.4747
	Vegtreat *Seedtreat	1	5	0.97	0.3708	0.03	0.8739
Cheatgrass	Seedtreat	1	1	31.22	0.1128	0.47	0.6183
	Vegtreat	1	3	1.00	0.3917	1.42	0.3185
	Vegtreat *Seedtreat	1	1	6.26	0.2421	0.36	0.657

Table 3.12. Analysis of variance of *seedtreat*, *vegtreat*, and t*ime* main effects and their interactions on availabilities of NO_3^- and NH_4^+ within the sagebrush and cheatgrass experiments. Significant *p*-values (α = 0.05) are in bold font.

		dF		Soil ion			
				NO_3^-		NH_4^+	
Experiment	Source	num	den	F	p	F	p
Sagebrush	Vegtreat	1	6	6.86	**0.0396**	1.50	0.2663
	Seedtreat	1	6	0.10	0.7600	1.49	0.2681
	Vegtreat *Seedtreat	1	6	0.61	0.4639	1.97	0.2103
	Time	1	11	32.01	**0.0001**	12.16	**0.0051**
	Time*Vegtreat	1	11	0.14	0.7159	3.96	0.0722
	Time*Seedtreat	1	11	16.47	**0.0019**	0.66	0.4349
Cheatgrass	Vegtreat	1	6	75.01	**0.0001**	0.16	0.7061
	Seedtreat	1	6	0.80	0.4064	0.00	0.9529
	Vegtreat *Seedtreat	1	6	2.94	0.1370	0.10	0.7580
	Time	1	7	0.07	0.7999	6.90	**0.0341**
	Time*Vegtreat	1	7	0.71	0.4260	1.71	0.2320
	Time*Seedtreat	1	7	24.69	**0.0016**	0.49	0.5077

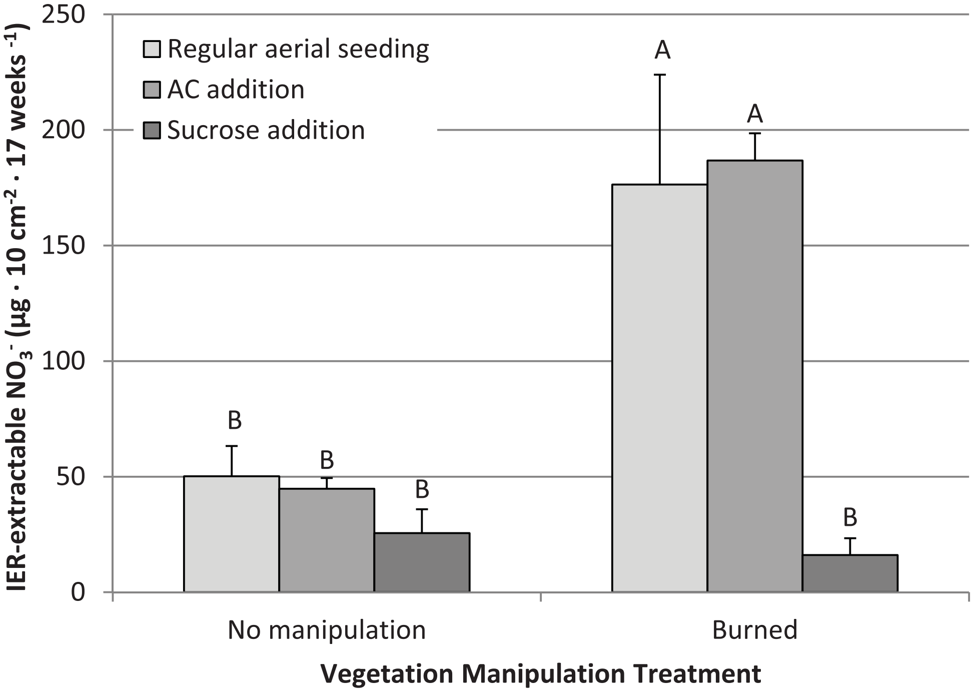

Figure 3.1. Mean quantities of IER-extractable NO_3^- (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the cheatgrass experiment in Time 1. Values with the same letter do not differ significantly from each other.

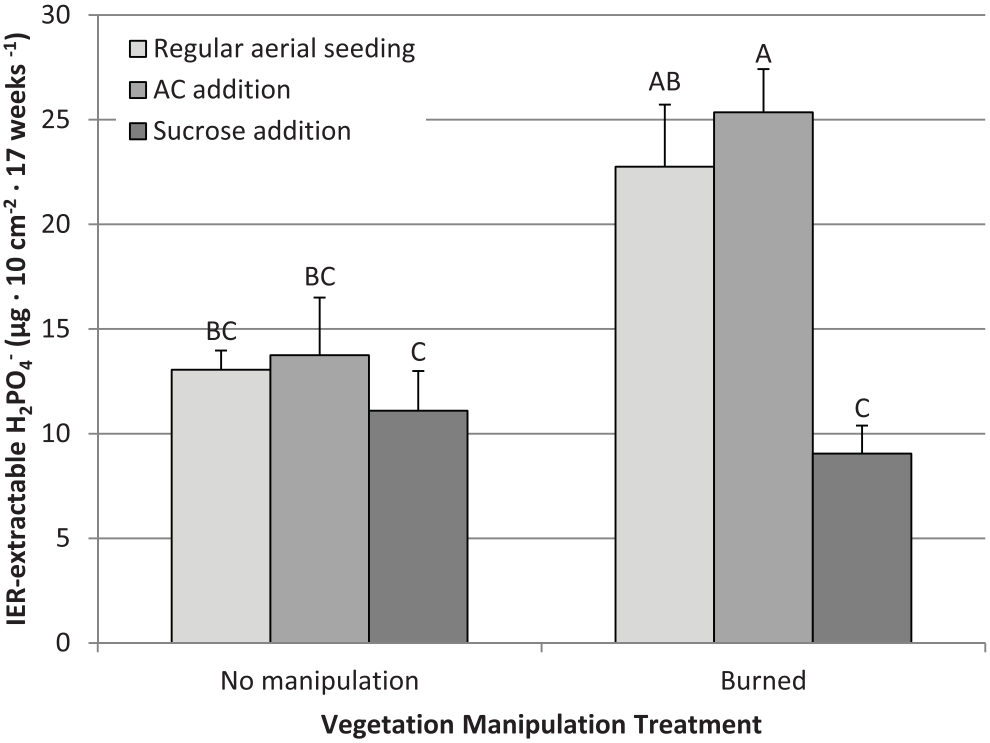

Figure 3.2. Mean quantities of IER-extractable $H_2PO_4^-$ (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the cheatgrass experiment in Time 1. Values with the same letter do not differ significantly from each other.

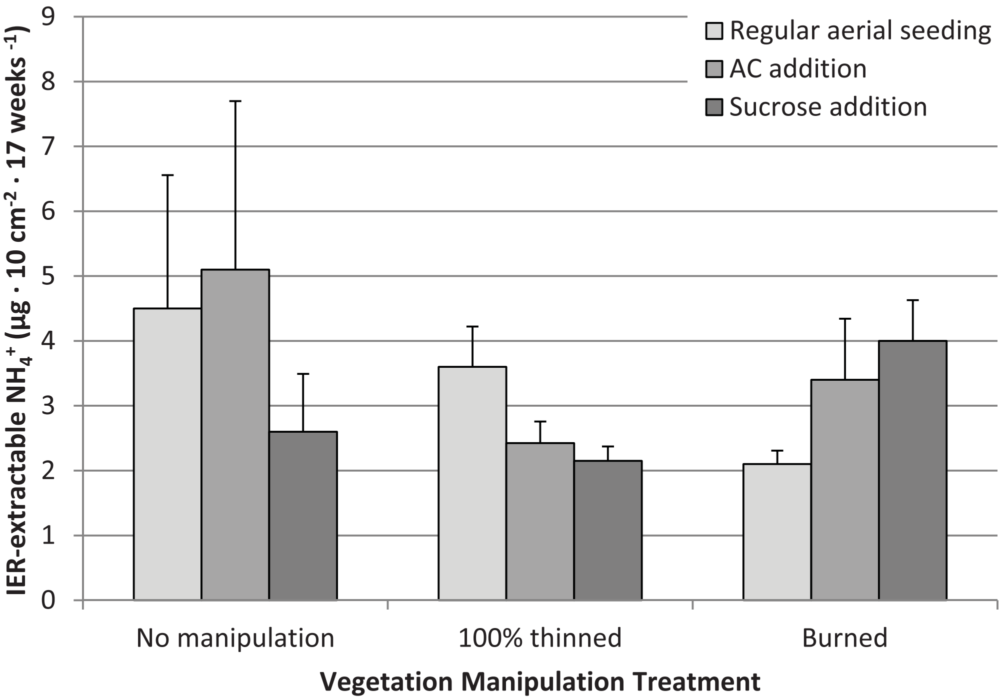

Figure 3.3. Mean quantities of IER-extractable NH_4^+ (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the sagebrush experiment in Time 2.

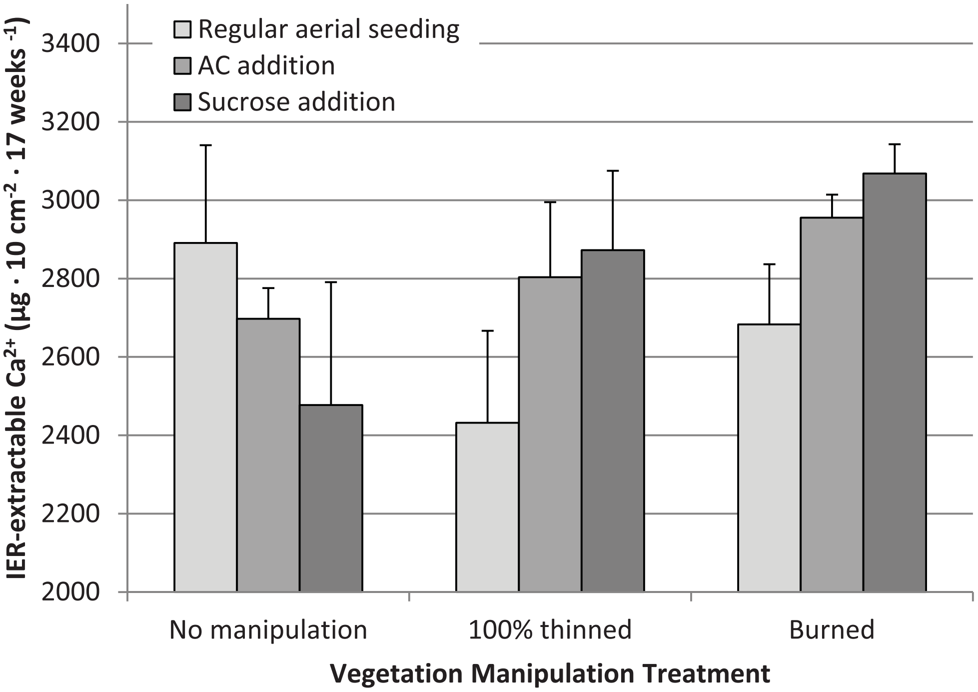

Figure 3.4. Mean quantities of IER-extractable Ca^{2+} (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the sagebrush experiment in Time 2.

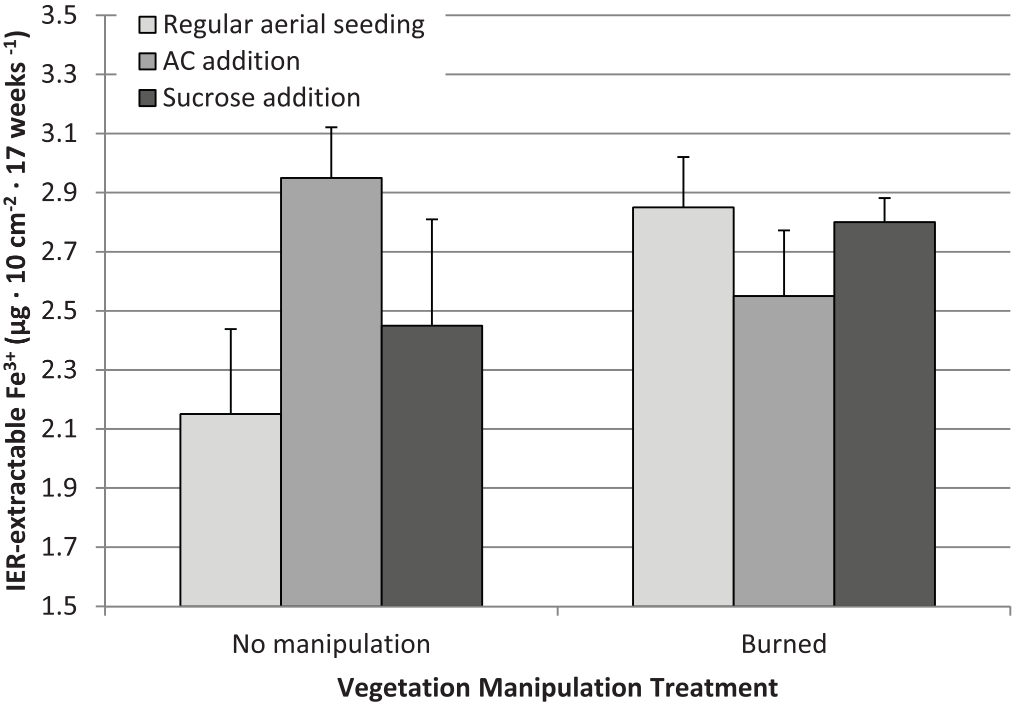

Figure 3.5. Mean quantities of IER-extractable Fe^{3+} (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the cheatgrass experiment in Time 2.

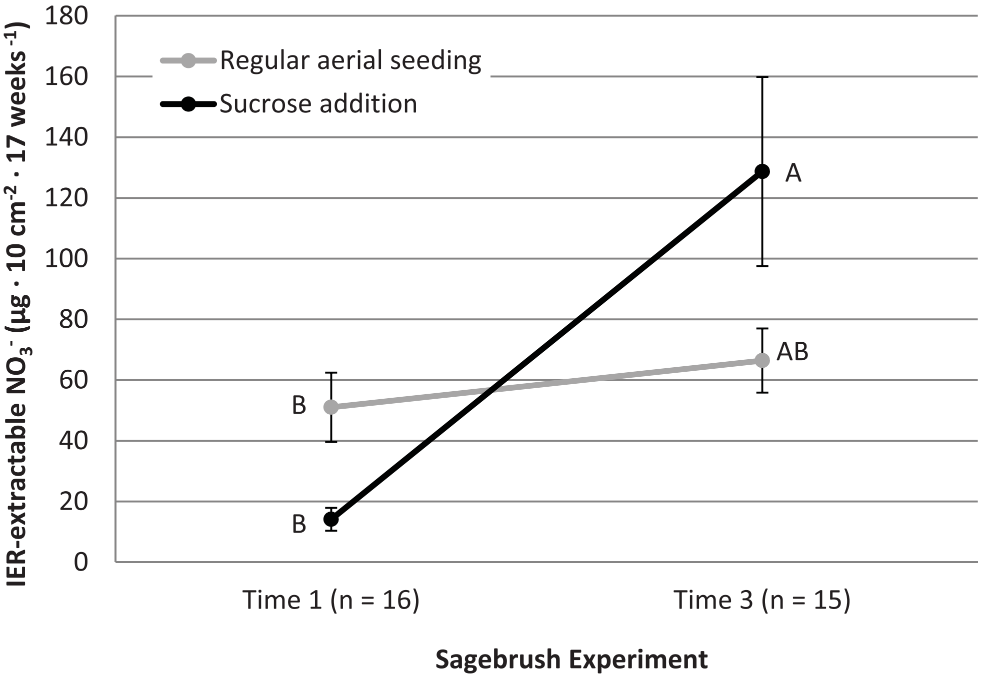

Figure 3.6. Mean quantities of IER-extractable NO_3^- (± *SE*) in regular aerial seeding and sucrose addition subplots during Time 1 and Time 3 in the sagebrush experiment. Values with the same letter do not differ significantly from each other.

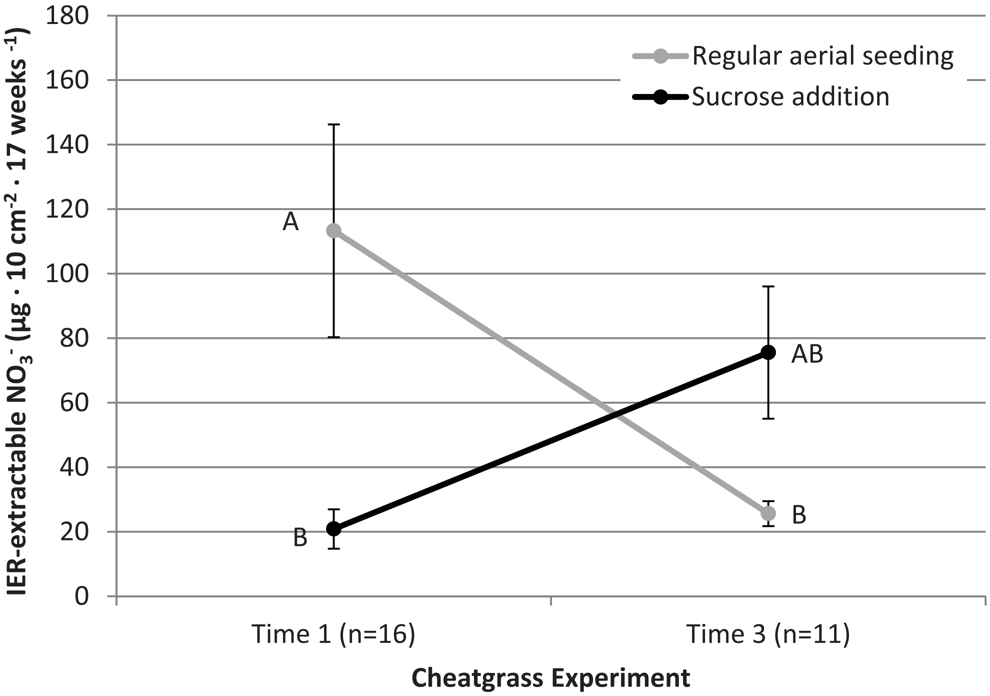

Figure 3.7. Mean quantities of IER-extractable NO_3^- (± *SE*) in regular aerial seeding and sucrose addition subplots during Time 1 and Time 3 in the cheatgrass experiment. Values with the same letter do not differ significantly from each other.

CHAPTER 4

CONCLUSION

Cheatgrass invasion in sagebrush shrub ecosystems has increased fire frequencies and intensities, resulting in a loss of sagebrush overstories and herbaceous perennial species in these areas (Whisenant 1990; Knapp 1996). The reestablishment of fire-resilient perennial grass species into cheatgrass-invaded areas may be necessary to interrupt the cheatgrass-wildfire cycle and to protect these areas from conversion to cheatgrass monocultures. However, this will most likely require reducing competitive pressure from cheatgrass as well as addressing changes to soil nutrient availabilities that accompany its invasion. In this thesis I described the effects of non-surface-disturbing techniques aimed at altering the resource environment in ways that could increase the success of seeded perennial species. Specifically, I examined how these treatments alter cheatgrass metrics (Chapter 2) and soil nutrient availabilities (Chapter 3), as this information may be crucial for the understanding of conditions that facilitate or inhibit perennial seedling establishment. Treatments were tested in two experimental areas, one with an intact sagebrush overstory with a degree of cheatgrass invasion and one in a near-monoculture of cheatgrass that was type-converted by fire in 1998.

In Chapter 2 I describe the effects of herbicide application (140 $g \cdot ha^{-1}$ and 210 $g \cdot ha^{-1}$), burning, sagebrush 50% and 100% thinning, sucrose addition, activated carbon (AC) addition, and respective control treatments on cheatgrass metrics for two growing seasons. Herbicide application reduced cheatgrass weights and tiller and spikelet numbers during the first season after application, and these effects were generally greater in plots that were also burned or cleared of sagebrush overstories. In the second season after application, cheatgrass in herbicide-treated plots were larger and with greater tiller and spikelet numbers than in no-herbicide plots. Partial (50%) thinning of sagebrush overstories did not result in any significant changes to cheatgrass metrics in either growing season. Total (100%) thinning of sagebrush overstories resulted in increases in cheatgrass weights and tiller and spikelet numbers both seasons, as well as increased densities during the second growing season. Burning decreased cheatgrass densities but increased individual cheatgrass weights and tiller and spikelet numbers during both growing seasons. Sucrose addition reduced cheatgrass weights and tiller and spikelet numbers during the first season after treatment, but these metrics were increased in sucrose addition subplots during the second growing season. There was some indication AC sequestered herbicide and lessened some of its negative effects on cheatgrass during the first growing season, but AC itself was not believed to have direct effects on cheatgrass metrics.

In Chapter 3 I describe the effects of these same treatments (herbicide treatment and 50% sagebrush thinning omitted) on the availabilities of micronutrient, macronutrient, and heavy metal soil ions. We used *in situ* burials of plant root simulator (PRS) probes (Western Ag Innovations, Saskatoon, SK, Canada) to assess the supply rates of these nutrients over three time periods following treatment applications. During the first time period, which occurred from November 2008 to March 2009, availabilities of nitrate (NO_3^-), phosphate ($H_2PO_4^-$), sulfate (SO_4^{2-}), potassium (K^+), and manganese (Mn^{2+}) were increased in burned plots and availabilities of NO_3^- and $H_2PO_4^-$ were decreased in sucrose- treated subplots. Sucrose addition subplots in burned plots had availabilities of NO_3^- and $H_2PO_4^-$ that were not significantly different than in unburned (no manipulation) plots. In the second time period, which occurred during the first growing season after treatments (March to June 2009), availabilities of NO_3^- were still greater in burned plots, and availabilities of ammonium (NH_4^+), aluminum (Al_3^+), and lead (Pb^{2+}) were now also greater in burned plots. NO_3^- availabilities were also still lower in sucrose addition subplots, and availabilities of Mn^{2+} and copper (Cu^{2+}) were now significantly greater in sucrose addition subplots. Sucrose addition subplots in burned plots had availabilities of NH_4^+, calcium (Ca^{2+}), and iron (Fe^{3+}) that tended to be higher than in regular aerial seeding subplots in burned plots, although differences were not significant. During the third time period, which occurred over the second winter post-treatment (November 2009 to March 2010), only availabilities of NO_3^- and NH_4^+ were assessed. Burned plots still had greater availabilities of NO_3^-, but no other treatment effects or interactions were significant. There was some indication from comparisons between the first and third time periods that NO_3^- availabilities increased a great deal in sucrose addition subplots, although this trend was not significant. There was no effect of 100% sagebrush thinning or AC addition on any of the soil nutrients during any of the time periods.

The results of these studies indicate that some of the treatments were effective at altering the resource environment in ways that could potentially affect seeded perennials, while some were not. As herbicide treatment reduced cheatgrass presence for a year following application, this treatment could provide a short window for perennial grass establishment. Burning reduced densities and increased the availabilities of some soil nutrients (NO_3^-, NH_4^+, $H_2PO_4^-$, SO_4^{2-}, K^+, Mn^{2+}, and Al^{3+}), which probably accounted for much of the increases in individual cheatgrass weights and tiller and spikelet numbers observed during both growing seasons after treatment. If cheatgrass could be prevented from taking advantage of increased soil nutrients and growing to larger sizes, well-timed burning could also provide a window of opportunity for seeded perennial establishment. Sagebrush 50% thinning did not result in any changes to cheatgrass metrics or soil ion availabilities, but 100% thinning increased cheatgrass mean densities, weights, and tiller and spikelet numbers during all seasons without alterations to soil ion availabilities. This treatment would therefore not be recommended for use in perennial grass seeding establishment in cheatgrass-invaded areas. Sucrose addition was successful at immobilizing soil nutrients, namely NO_3^- and $H_2PO_4^-$, and reducing cheatgrass mean weights and tiller and spikelet numbers through the first growing season after application. However, during the second winter, NO_3^- availabilities tended to be greater than before sucrose treatment, indicating an end of immobilization and a re-release of this nutrient. This fact, coupled with decreased cheatgrass densities, may have accounted for increased cheatgrass individual metrics observed during the second growing season. As with herbicide treatment, sucrose addition may be a valuable tool for temporarily disadvantaging cheatgrass and providing a short window for perennial grass reestablishment. AC addition was not found to alter soil ion availabilities or to affect cheatgrass directly in any way, although there was some indication that it lessened the effect of herbicide on cheatgrass via sequestration. Surface application of AC is also therefore not recommended for use in areas where herbicide will also be used to control cheatgrass or other invasives. We hope the results of these experiments will be useful to land managers and restoration practitioners attempting to reestablish perennial grasses into cheatgrass-invaded areas to disrupt the cheatgrass-wildfire cycle.

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

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

by

Alexandra Dawn Reinwald

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

of

MASTER OF SCIENCE

in

Ecology

Approved:

Dr. Eugene W. Schupp Major Professor	Dr. Thomas A. Monaco Committee Member
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UTAH STATE UNIVERSITY
Logan, Utah

2013

ABSTRACT

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

by

Alexandra D. Reinwald, Master of Science

Utah State University, 2013

Major Professor: Eugene W. Schupp
Department: Wildland Resources

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

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

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

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

(118 pages)

PUBLIC ABSTRACT

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

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

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

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

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

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Alexandra Reinwald

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CHAPTER 1

INTRODUCTION

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

Healthy sagebrush ecosystems provide multiple ecosystem services such as diverse wildlife habitat, forage for cattle grazing, and water filtration. Restoring these degraded ecosystems is a priority for both ecological and economic reasons. However, restoration of these cheatgrass-invaded sagebrush shrublands has been met with limited success. This limited success is mainly attributed to intense competition for available resources between cheatgrass and seeded perennial grasses (Rummel 1946; Evans 1961) and a scarcity of native species propagules (Humphrey and Schupp 2001), both of which limit the successful emergence, establishment, and recruitment of perennial grasses.

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

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

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

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

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

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

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

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

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

It has been suggested that increased soil nitrogen availability allows fast growing annual exotics, like cheatgrass, to dominate disturbed sites (McLendon and Redente 1991; Paschke et al. 2000), while low resource availability often favors native perennial species (Daehler 2003). Therefore, cheatgrass may be disproportionately harmed by nutrient reductions. Thus, treatments that directly manipulate soil resources and reduce cheatgrass growth may be effective restoration tools to increase seeded perennial grass success (Monaco et al. 2003). Carbon (in readily available forms such as sucrose) and activated carbon (AC) soil amendments are two such treatments. Additions of carbon such as sucrose increase soil microbial nitrogen immobilization thereby decreasing plant available nitrogen (Blumenthal et al. 2003) which can negatively affect invasive early seral species such as cheatgrass (McLendon and Redente 1992; Dakheel et al. 1993; Paschke et al. 2000; Monaco et al. 2003; Beckstead and Augspurger. 2004; Mazzola et al. 2008; Brunson et al. 2010; Mazzola et al. 2011). However, the effects of sucrose on seeded perennial grasses are less clear (Blumenthal et al. 2003; Corbin and D'Antonio 2004).

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

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

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

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CHAPTER 2

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

Abstract

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

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

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

INTRODUCTION

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

Cheatgrass is an annual Eurasian grass that was unintentionally introduced to the United Sates in the late 1800's (Mack 1981). Severe livestock overgrazing of the sagebrush ecosystems of the Intermountain West starting in the late 1800’s (Knapp 1996) greatly reduced native herbaceous cover which lead to an increase in resource availability. Cheatgrass was able to take advantage of the reduced competition and freed resources and rapidly spread across the degraded landscape occupying open niches (Billings 1952; Knapp 1996). Once introduced and established in the Great Basin, fire insured the continued dominance of cheatgrass in these sagebrush ecosystems.

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

Because sagebrush does not re-sprout post-fire and must re-establish from seed, recovery can take many years (Young and Evans 1978; Baker 2006). Likewise, native perennial grasses, depending on the species and frequency of fire, can be injured or killed by fire (Stewart and Hull 1949; Wright and Klemmedson 1965; Harris 1967; Young and Evans 1978). Additionally, through time this altered cycle diminishes the perennial seed bank (Peters and Bunting 1994). Unlike native vegetation, cheatgrass is well adapted to fire (Melgoza et al. 1990; Ziska et al. 2005) and in the near absence of a native seed bank (Humphrey and Schupp 2001) it recovers and preemptively fills unoccupied resource niches (Melgoza et al. 1990; D'Antonio and Vitousek 1992; Knapp 1996).

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

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

The reintroduction of native perennial grasses into degraded landscapes is often attempted by seeding and is commonly done via rangeland drill which creates furrows that seeds are deposited in thereby incorporating seeds into the soil surface (Haferkamp et al. 1987). This method causes surface disturbance and may not be suitable in areas with cultural artifacts present or rocky/steep terrains. In areas where rangeland drills are not acceptable, an alternative is aerial (from aircraft) or broadcast seeding. However, in some studies the success of re-vegetation via broadcast seeding was lower than with techniques which incorporate seed into the soil (Clary 1988; MacDonald 1999; Sheley et al. 2001).

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

Prescribed burning, either alone or as part of an integrated approach, is commonly used as a tool to control invasive annual grass species (Klemmedson and Smith 1964). It has been shown to reduce aboveground cheatgrass density as well as destroy its seeds and reduce its seed banks, although this reduction is often short lived and seed banks and aboveground vegetation can recover in one growing season (West and Hassan 1985; Hassan and West 1986; Humphrey and Schupp 2001). Seeded perennial grasses may benefit from the removal of thatch via burning; thatch can reduce seedling germination, emergence and survival (Fowler 1988; Facelli and Pickett 1991; Foster 1999; Jutila and Grace 2002). Burning also removes overstory species which may increase the availability of limiting resources for use by seeded grasses. Additionally, burning may enhance the effectiveness of other techniques such as herbicide application by increasing contact with emerging target plants and the soil surface (Washburn et al. 1999; Monaco et al. 2005; Kyser et al. 2007; Sheley et al. 2007).

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

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

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

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

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

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

METHODS

Study Area

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

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

Sagebrush Experiment Methods

The sagebrush experiment had a total of four replicates, each containing eight plots; two replicates were located along the Site's East auto tour and the other two near the visitor's center. Plots in a replicate were haphazardly placed on the landscape in areas with similar aspect, slope and vegetation cover. Plots were 7 x 19.5 m; each plot was divided into two 4.5 x 7 m end subplots and three 3.5 x 7 m interior subplots. Each subplot had a central 1.5 x 3 m undisturbed sampling area leaving a 2-m buffer between adjacent subplot sampling areas and outside edges of the plot. The arrangement of treatments created a split-split plot experimental design, with herbicide treatment occurring at the half-replicate level, vegetation manipulation occurring at the whole plot level, and seeding treatments occurring at the subplot level.

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

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

Five seedbed treatments were applied randomly to subplots in each plot: 1) seeding alone ('control'); 2) seeding with sucrose ('sucrose'); 3) seeding with activated carbon ('AC'); 4) seeding on snow ('snow'); and 5) seeding with raking into soil (‘raking’). Sucrose was applied at a rate of 360 g · m^{-2} (151.6 g C · m^{-2}) divided between two applications of 180 g · m^{-2}; the first application was 20 - 26 October 2008, immediately following seeding, and the second was 28 - 29 March 2009. AC derived from superheated coconut husks (AquaSorb CS, Ecologix Environmental Systems; 12 x 30 US standard mesh size) was applied at a rate of 100 g · m^{-2} with a handheld spreader 20 - 26 October 2008, immediately following seeding. Raking was implemented immediately before and after broadcast seeding.

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

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

Cheatgrass Experiment Methods

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

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

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

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

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

Sampling

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

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

Statistical Analyses

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

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

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

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

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

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

RESULTS

Treatment Effects

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

Seeding Frequency

There was a significant difference in mean perennial seedling densities between the re-seeded and non re-seeded treatment groups in both 2010 ($p<.0001$) and 2011 ($p<.0001$). 2010 perennial seedling density was significantly higher in the re-seeded treatment group than the non re-seeded treatment group (Fig. 2.4). Additionally, re-seeded subplots had significantly more perennial seedlings in 2011 after 3 years of seeding than in 2010 after 2 years of seeding (Fig. 2.4). Although not significant, there was a visible reduction in perennial seedlings from 2010 to 2011 in the non-re-seeded subplots (Fig. 2.4).

DISCUSSION

Vegetation Manipulation

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

Interestingly, the length of treatment effect provided by burning was longer than that seen in most studies and certainly longer than expected. As cheatgrass populations usually rebound quickly after fire (West and Hassan 1985; Hassan and West 1986; Humphrey and Schupp 2001), the burn in my study may have been more intense, perhaps resulting in conditions that were in some way still not suitable for increased cheatgrass densities 2 years post-burn.

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

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

Herbicide Application

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

Sucrose & Activated Carbon Addition

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

In a separate analysis of cheatgrass from this experiment, Summerhays (2011) reported significantly smaller and less reproductive cheatgrass individuals in 2009 (1 year post-application) and larger more reproductive individuals at lower densities in 2010 in sucrose subplots. The pattern observed in 2010, which has been observed in other studies of sucrose effects on cheatgrass (Mazzola et al. 2008; Mazzola et al. 2011), demonstrates an equal tradeoff between biomass/reproductive output and density. Thus, even though densities were reduced in 2010, this likely did not lead to the competitive release of perennial grass seedlings. As Summerhays (2011) did not collect data on 2011 cheatgrass metrics or soil ions, their status 3 years post-sucrose application was unknown.

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

There was no evidence of an AC affect on perennial grass densities. Likewise, Summerhays (2011) did not detect any changes in soil ions or cheatgrass with the addition of AC. As with sucrose, the lack of an affect of AC on perennial seedling densities may have been attributed to time since application or low application rates. Studies by Kulmatiski and Beard (2006) and Kulmatiski (2011) reported significant decreases in exotic species cover and increases in perennial grass cover with AC incorporated into the top 10 cm of soil at a rate of 1 kg · m^{-2}, a rate ten times as high as ours.

Seeding Frequency

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

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

IMPLICATIONS

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

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

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

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

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

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

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

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

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

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

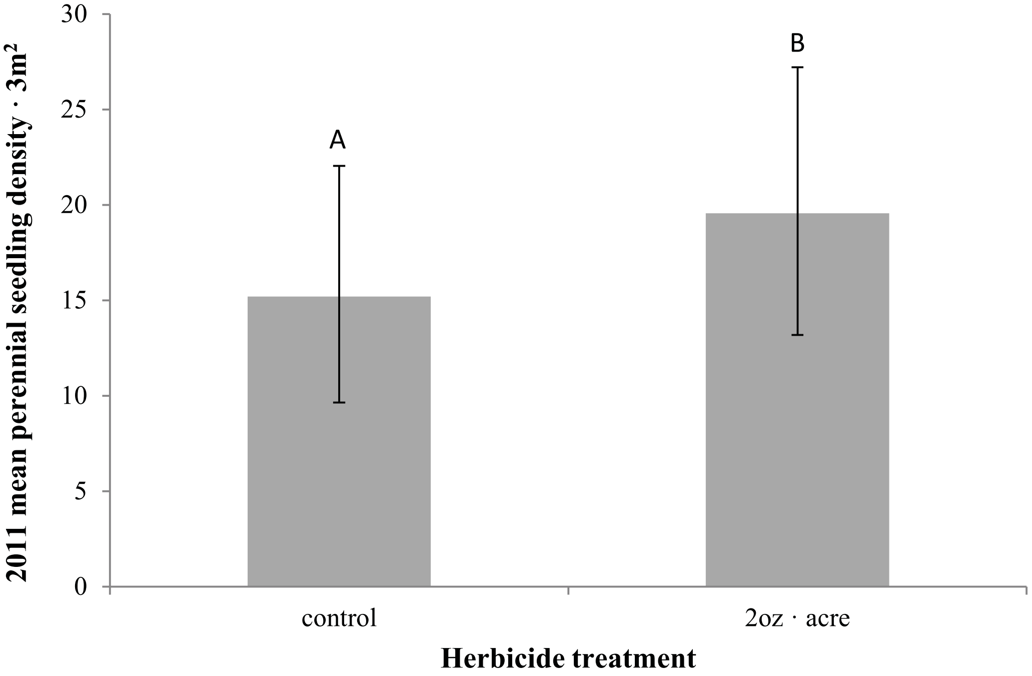

Figure 2.1. Mean 2011 perennial seedling density · $3m^{-2}$ (± *95% CI*) as affected by herbicide treatment at the sagebrush experiment. Values with different letters differ significantly from each other.

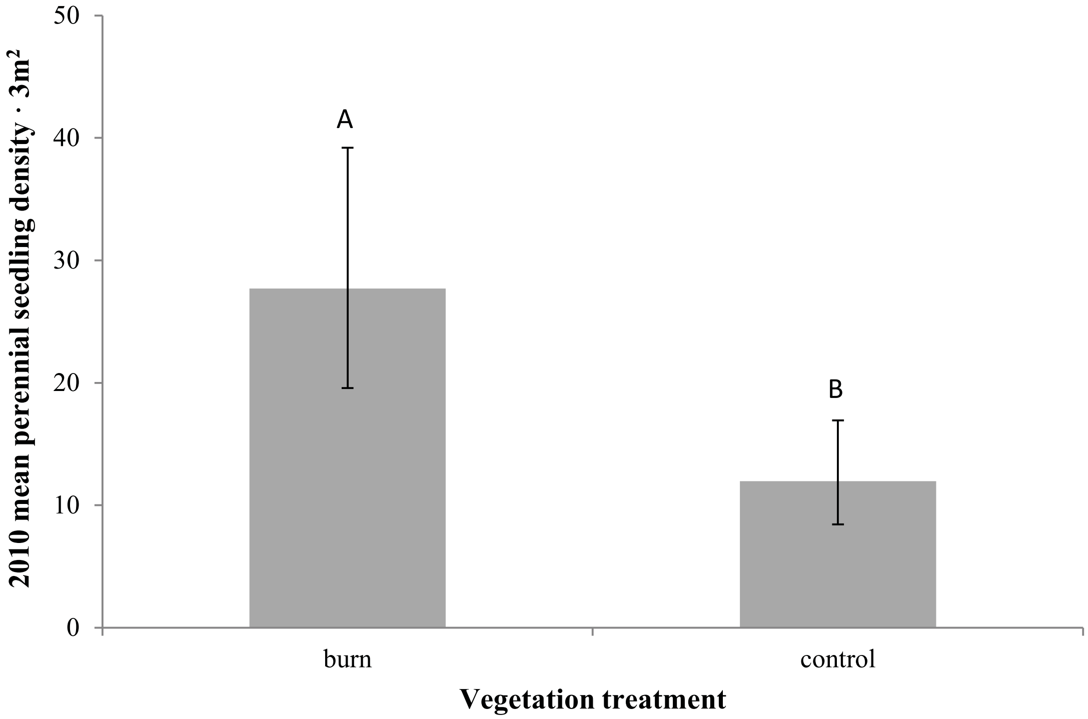

Figure 2.2. Mean 2010 perennial seedling density · $3m^{-2}$ (± *95% CI*) as affected by vegetation treatment at the cheatgrass experiment. Values with different letters differ significantly from each other.

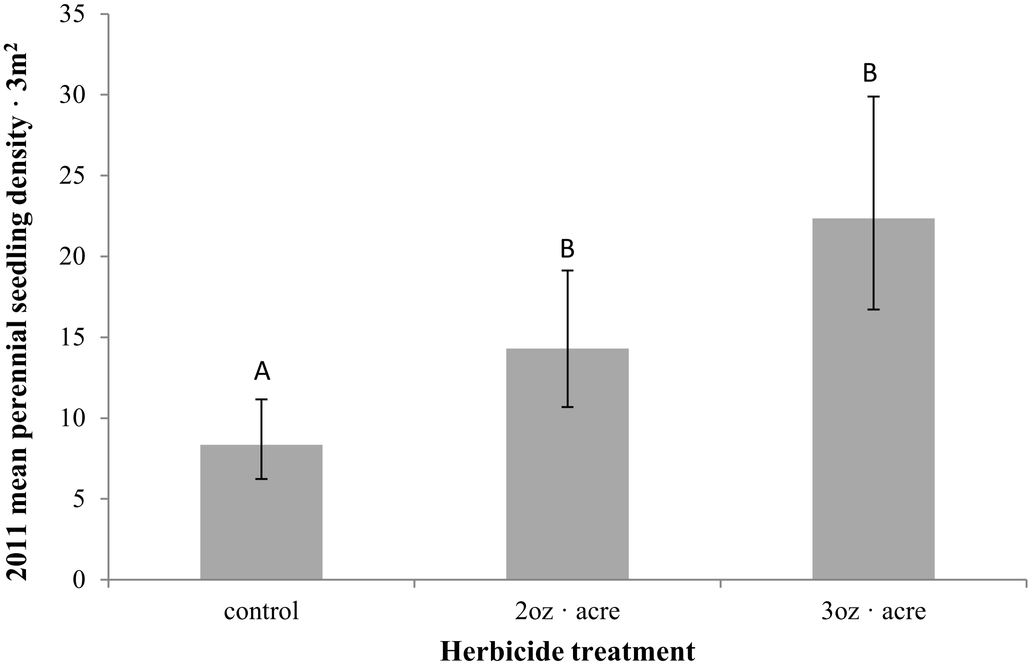

Figure 2.3. Mean 2011 perennial seedling density · $3m^{-2}$ (± *95% CI*) as affected by herbicide treatment at the cheatgrass experiment. Values with different letters differ significantly from each other.

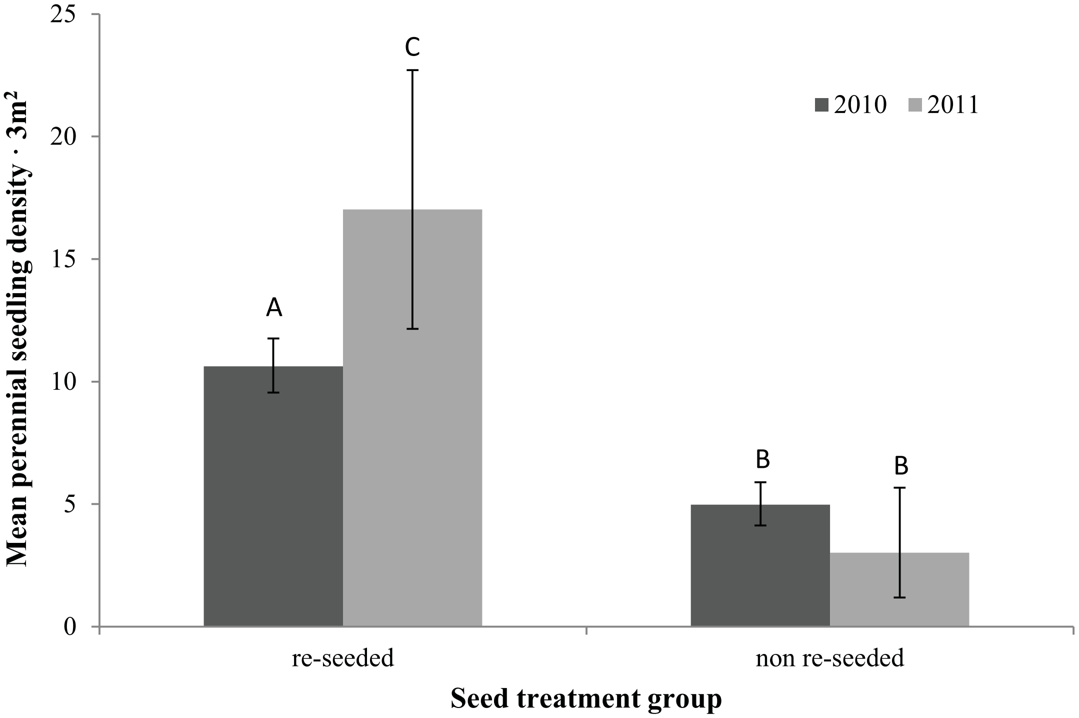

Figure 2.4. Mean perennial seedling density · 3m^{-2} (± *95% CI*) for seed treatment group at the sagebrush experiment in 2010 and 2011. Values with different letters differ significantly from each other.

CHAPTER 3

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

Abstract

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

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

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

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

INTRODUCTION

In *Artemisia tridentata* (sagebrush) shrublands of the Intermountain West of North America, the exotic annual grass cheatgrass has displaced native species as well as altered ecosystem processes, fire regimes, and the structure and composition of seed banks (Young and Evans 1975; Whisenant 1990; Knapp 1996; Humphrey and Schupp 2001). Cheatgrass is said to be the most ubiquitous, and in many areas most dominant, invasive in the sagebrush ecosystems of the Intermountain West (Mack 1981). Cheatgrass has invaded 22 million hectares (54 million acres) in the western U.S. (Benlap et al. 2005), and is spreading at a rate of 14% per year in the Great Basin (Duncan et al. 2004).

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

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

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

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

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

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

Prescribed fire is one such technique that can be an effective tool for controlling invasive species, such as cheatgrass, if it kills most plants or greatly reduces the seed bank (Whelan 1995; Brooks and Pyke 2001). As cheatgrass does not develop long-lived seed banks and approaches zero density in the spring (Mack and Pyke 1983; Pyke 1994), greatly reducing the seed bank may be possible if there is near 100 % mortality caused by fire prior to dispersal (Brooks and Pyke 2001). However, even when fires greatly reduce cheatgrass seed banks, they can quickly recover to pre-fire or greater levels (Young and Evans 1985; Hassan and West 1986; Brooks and Pyke 2001; Humphrey and Schupp 2001). Through a reduction in competition and release of resources (Brooks and Pyke 2001; Blank et al. 2007), burning may increase native and exotic species reproductive output. Additionally, burning may enhance the effectiveness of herbicide application by increasing contact with emerging target plants and the soil surface (Washburn et al. 1999; Monaco et al. 2005; Kyser et al. 2007; Sheley et al. 2007).

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

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

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

AC as a soil addition has been suggested for use as a restoration tool in exotic invaded communities (Kulmatiski and Beard 2006). AC is a charcoal-like material with high surface porosity which readily adsorbs organic compounds such as plant available nutrients and allelopathic compounds (Inderjit and Callaway 2003). The adsorption of plant available nutrients could negatively impact cheatgrass in the same way that microbial immobilization does. Also, the reduction in allepoathic compounds may be beneficial for native species as there is evidence that the reducing them may reduce the competitive advantage of exotics (Callaway and Aschehoug 2000). A few studies have demonstrated AC's ability to decrease cover of exotics including cheatgrass and increase native perennial grass cover (Kulmatiski and Beard 2006; Kulmatiski 2011). However, these studies incorporated AC at high rates into the surface layer of the soil which would not be feasible or economical at a large scale. It is currently unknown what the effects of AC applied at the soil surface at a more realistic quantity will be on the seed banks of cheatgrass-invaded ecosystems. Any of these treatments that reduce cheatgrass seed bank densities, and therefore potentially reduce aboveground cheatgrass density, could potentially result in an increase in native species seed bank densities and/or richness.

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

METHODS

Study Area

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

In May 2008, study plots for the two distinct experiments were established; one experiment was located in cheatgrass-invaded sagebrush sites (sagebrush experiment) and the other in a cheatgrass near-monoculture site (cheatgrass experiment). These experiments were implemented with the overall goal of assessing the effectiveness of several restoration treatments in re-establishing native perennial grasses into cheatgrass-invaded ecosystems in the absence of soil disturbing treatments. Experimental designs and treatment factors differed between the experiments due to landscape constraints and vegetation characteristics. The experimental methods here follow those outlined by Summerhays (2011).

Sagebrush Experiment Methods

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

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

Four vegetation treatments were randomly applied to whole plots within each herbicide treatment: 1) no manipulation to vegetation ('control'); 2) prescribed burn to remove sagebrush overstory, vegetative understory, and vegetative thatch (‘burn’); 3) 50% thinning and removal of sagebrush overstory (‘50% thinning’); and 4) 100% thinning and removal of sagebrush overstory (‘100% thinning’). The Zion National Park Fire Use Module implemented the thinning and burning treatments on 25 August and 5 September 2008, respectively. Burning was done using handheld drip torches; the plot perimeter was wetted to prevent the spread of fire. Thinning and clearing of sagebrush was done with chainsaws; in the 50% thin plots individuals to be removed were selected in advance and marked. All cut plant material was removed from plots.

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

A mixture of five native perennial grasses was seeded using handheld broadcast seeders in all subplots 20 - 26 October 2008, 16 - 18 October 2009 and 23 - 25 October 2010. The seed mixture contained: bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve ssp. *spicata*), Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth), Great Basin wildrye (*Leymus cinereus* [Scribn. & Merr.] A. Löve), needle-and-thread grass (*Hesperostipa comata* [Trin. & Rupr.] Barkworth), Sandberg bluegrass (*Poa secunda* J. Presl), and squirreltail (*Elymus elymoides* [Raf.] Swezey). Seeds were sown at a rate of 100 viable seeds · species^{-1} · m^{-2}. Number of viable seeds was calculated using Pure Live Seed rates provided by seed supplier (Granite Seed, Lehi, UT, US). Seeds were mixed with 2.5 L (larger end subplots) or 1.75 L (smaller interior subplots) of rice hulls for suspension to ensure an even distribution within plots. Seeding mixture was contained within the subplot using cardboard shields around the subplot perimeter.

Cheatgrass Experiment Methods

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

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

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

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

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

Sampling

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

Seed Bank Data Collection

Soil cores were taken with a 6-cm diameter soil tin to a depth of 3 cm. Putty knives were inserted beneath the tin to keep the soil core from falling out when the tin was removed. In 2008, samples were collected from one random location within the buffer area of each subplot. At each location a 25 x 25 cm frame was placed and a core was collected from the outside of each corner of the frame. The four sub-samples were combined in a sealed plastic bag as one bulk sample; the samples were then air dried in the lab. In 2009, samples were a bulk collection from three locations in the buffer area of each subplot. Samples were taken from the right and left lower corners of the central sampling area and in the center above the sampling area. At each location a 25 x 25 cm frame was placed on the ground, avoiding any signs of previous sampling, and a core was collected from the outside of each corner of the frame. All four cores per location from all three locations in a subplot were placed together in a sealed plastic bag for a bulk sample of 12 cores. Samples were then taken to the lab and air dried.

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

Seed Bank Germination

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

Statistical Analysis

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

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

In the cheatgrass experiment, model 1 assessed the effects of burning to control vegetation treatments on each response variable using an ANOVA of a 1-way factorial in a completely randomized design with subsamples (strips & subplots) within plots, and repeated (2008 pre-treatment versus 2008 post-treatment) measures. In model 2, the effects of vegetation, herbicide, and seedbed treatments on each response variable were assessed using an ANOVA of a 3-way factorial in a split-split plot design, with repeated (2008 pre-treatment versus 2009 post-treatment) measures. Plots, strips, and subplots were random-effects factors. Vegetation, herbicide, and seedbed treatments and collection time were fixed-effects factors. The whole plot unit was plot as defined above in methods; the whole plot factor was vegetation treatment. The subplot unit was a strip; the subplot factor was herbicide treatment. The sub-subplot unit was subplot; the sub-subplot factor was seedbed treatment. The experimental unit for time as a fixed-effects factor was a repeated measure on a sub-subplot.

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

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

Three entire plots in the sagebrush experiment were left out of the analyses; these plots had a disproportionately high number of perennial seedlings due to high densities of introduced crested wheatgrass (*Agropyron cristatum*) from previous National Park Service re-vegetation efforts. Additionally, several samples from the sagebrush experiment were mislabeled and therefore left out of the analysis. In total, the sagebrush experiment had 171 samples in model 1 and 87 samples in model 2. Total species richness was low in both experiments (Table A.1 and A.2) as was its variance within collection times. Therefore, I was unable to analyze native species richness separately from exotic. However, when an interaction for total species richness was found, raw data patterns were examined to determine if source of significance was due to changes in native species richness, exotic species richness, or both. As cheatgrass usually accounted for the majority of the total exotic species seed bank density (Table A.1 and Table A.2), results for cheatgrass and exotic species density were often similar.

RESULTS

Sagebrush Experiment

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

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

Cheatgrass Experiment

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

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

There was evidence of an herbicide treatment x vegetation treatment x collection time interaction for native species density between 2008 pre-treatment and 2009 post-treatment (Table 3.4). This significance was due to the oddly low mean for 2008 pre-treatment density of burned, herbicide control plots relative to both the burned, 2 oz · acre^{-1} herbicide and the burned, 3 oz · acre^{-1} herbicide plots. As there were no other meaningful biological patterns, I suspect that the significance of the interaction is likely spurious.

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

DISCUSSION

Immediate Effects (model 1)

Sagebrush Experiment

Interestingly, in the sagebrush experiment, burning did not immediately reduce cheatgrass or exotic species seed bank densities. In contrast, Hassan and West (1986) observed a reduction in cheatgrass seed bank density six weeks post fire perhaps because their fire was more intense, as evident by the complete removal of aboveground vegetation. In my study, the sagebrush sites had visibly less litter and more inter-space than the cheatgrass site. Thus, results may be attributed to lower fuel continuity and litter resulting in a less intense fire and therefore fewer destroyed seeds (Young et al. 1976; Young and Evans 1978).

Cheatgrass Experiment

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

Longer-term Effects (model 2)

Sagebrush Experiment

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

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

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

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

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

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

There was no affect of AC on seed bank densities or richness. To my knowledge there are no studies examining the effects of AC on seed banks. However, Summerhays (2011) found no effect of AC addition on plant available soil nutrients or cheatgrass density and reproductive output. Kulmatiski and Beard (2006) found a reduction in cheatgrass cover after AC seedbed amendments which they attributed to the interruption of plant-soil feedbacks. The lack of an AC effect on cheatgrass in this study could be due to the application method or plant-soil feedbacks not being an important controlling factor for cheatgrass in these study sites. Additionally, Kulmatiski and Beard (2006) did not look at the affects of AC on cheatgrass reproductive output. As cheatgrass is known to respond plastically to reductions in competition with more reproductively vigorous plants (Palmblad 1968; Mazzola et al. 2011), the reduction in cover seen by Kulmatiski and Beard (2006) may have been compensated for by increased per individual reproductive output.

Cheatgrass Experiment

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

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

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

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

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

The seedbed treatment x herbicide treatment x collection time interaction for species richness demonstrated that either sucrose with no herbicide or either level of imazapic, regardless of seedbed treatment, reduced total species richness equally. In other words, either herbicide or sucrose addition resulted in a reduction in total species richness, but that the combination of the two did not reduce richness further than either alone. This reduction in total species richness was attributed to a loss in exotic species, not native. This is not surprising as both imazapic and reduced plant available nutrients caused by sucrose addition are thought to disproportionately harm invasive annuals.

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

IMPLICATIONS

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

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

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

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

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

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

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

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

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

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

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

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

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

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

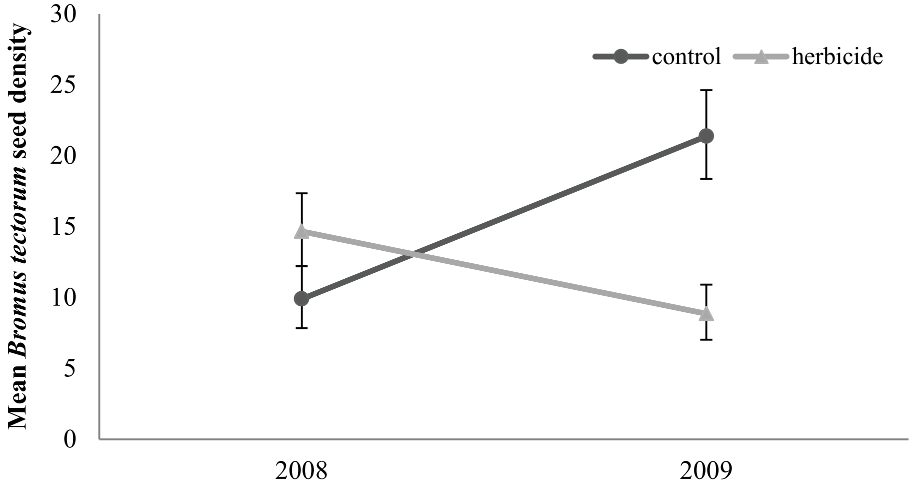

Figure 3.1. Mean *Bromus tectorum* seed bank density · 0.24 L^{-1} of soil (± *95% CI*) as affected by herbicide and collection time in model 2 of the sagebrush experiment.

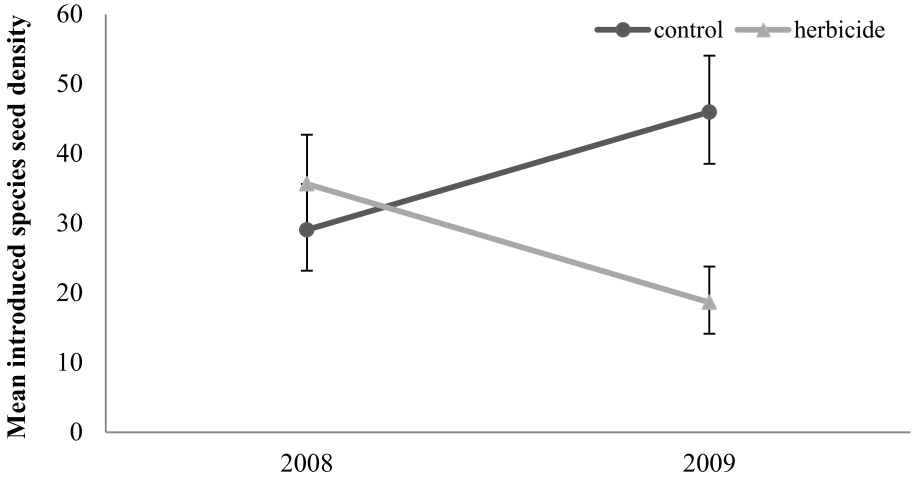

Figure 3.2. Mean exotic species seed bank density · 0.24 L^{-1} of soil (± *95% CI*) as affected by herbicide and collection time in model 2 of the sagebrush experiment.

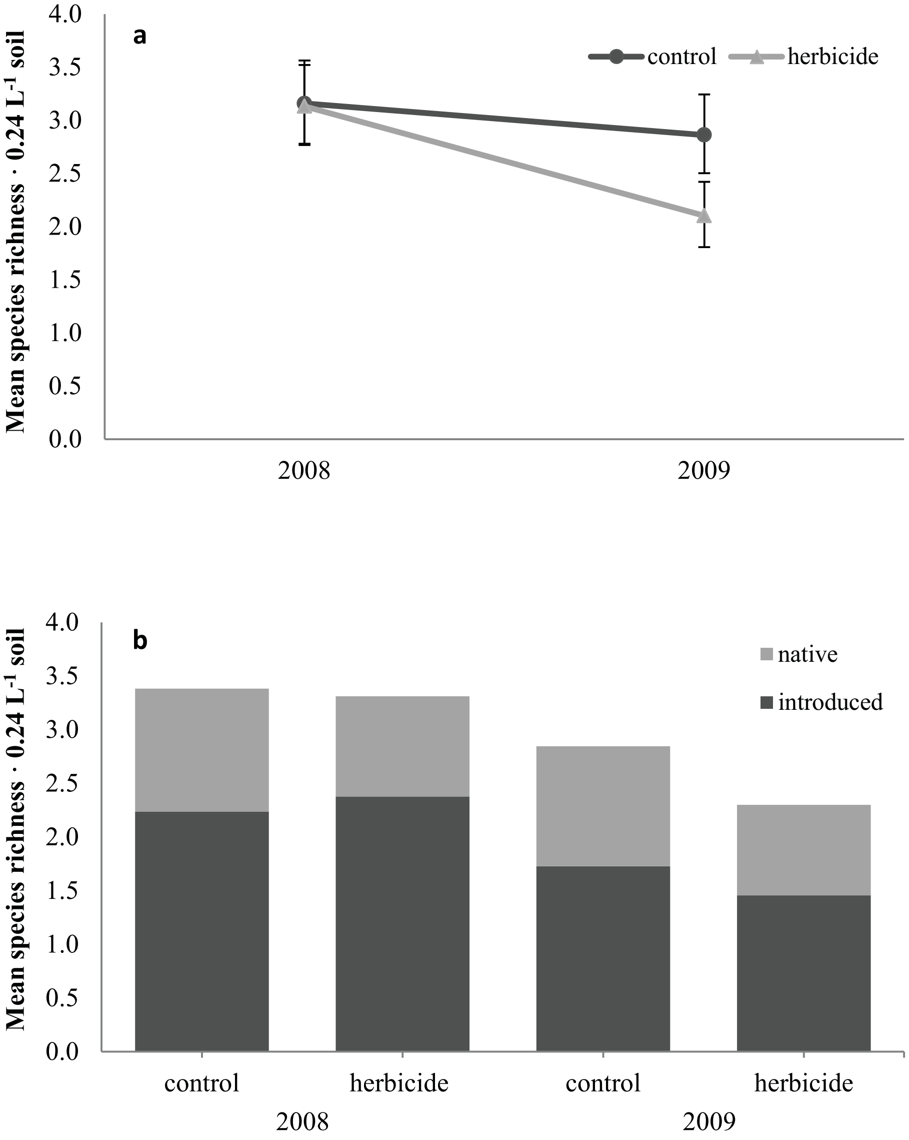

Figure 3.3. a) mean total species richness · 0.24 L^{-1} of soil (± *95% CI*) as affected by herbicide and collection time in model 2 of the sagebrush experiment, b) mean native and exotic species richness · 0.24 L^{-1} of soil as affected by herbicide and collection time in model 2 of the sagebrush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

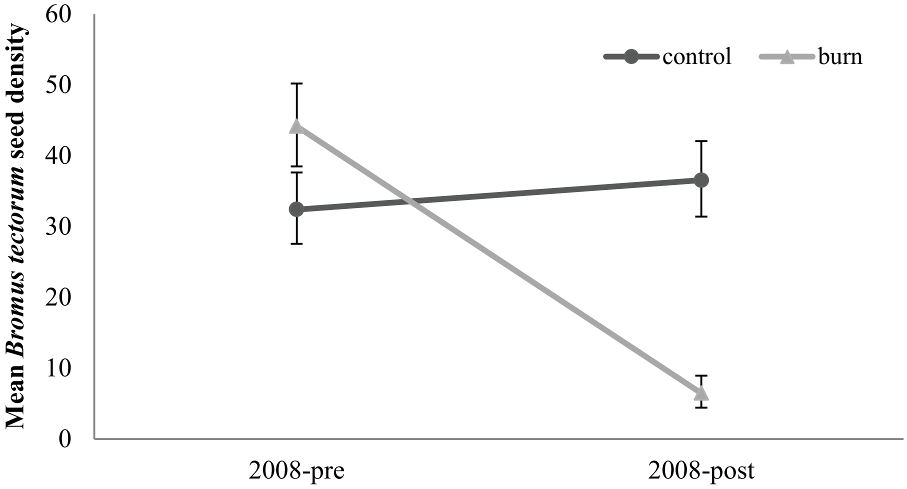

Figure 3.4. Mean *Bromus tectorum* seed bank density · 0.24L^{-1} of soil (± *95% CI*) as affected by vegetation treatment and collection time in model 1 of the cheatgrass experiment.

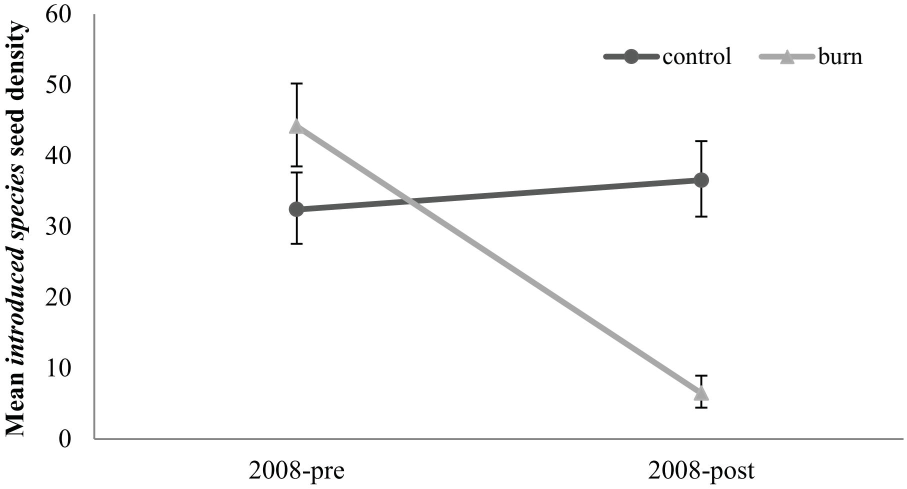

Figure 3.5. Mean exotic species seed bank density · $0.24L^{-1}$ of soil (± *95% CI*) as affected by vegetation treatment and collection time in model 1 of the cheatgrass experiment.

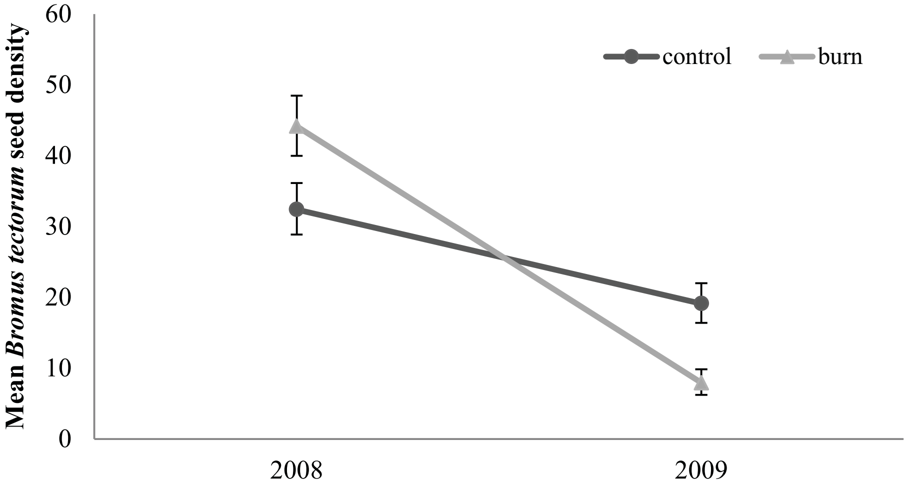

Figure 3.6. Mean *Bromus tectorum* seed bank density · 0.24L^{-1} of soil (± *95% CI*) as affected by vegetation treatment and collection time in model 2 of the cheatgrass experiment.

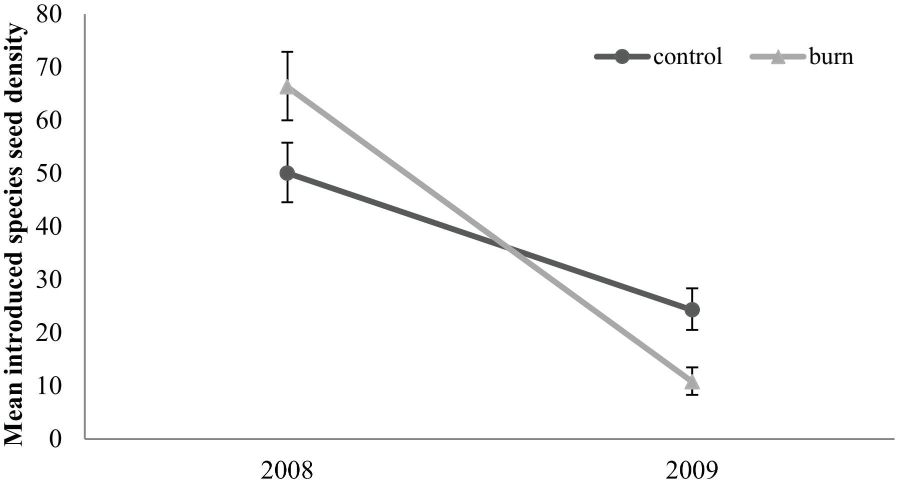

Figure 3.7. Mean exotic species seed bank density · 0.24L^{-1} of soil (± *95% CI*) as affected by vegetation treatment and collection time in model 2 of the cheatgrass experiment.

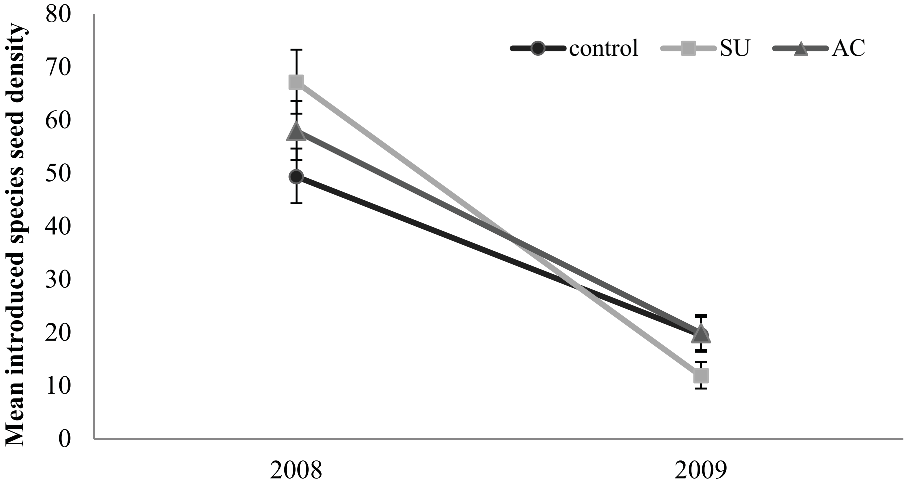

Figure 3.8. Mean exotic species seed bank density · 0.24L^{-1} of soil (± *95% CI*) as affected by seedbed treatment and collection time in model 2 of the cheatgrass experiment.

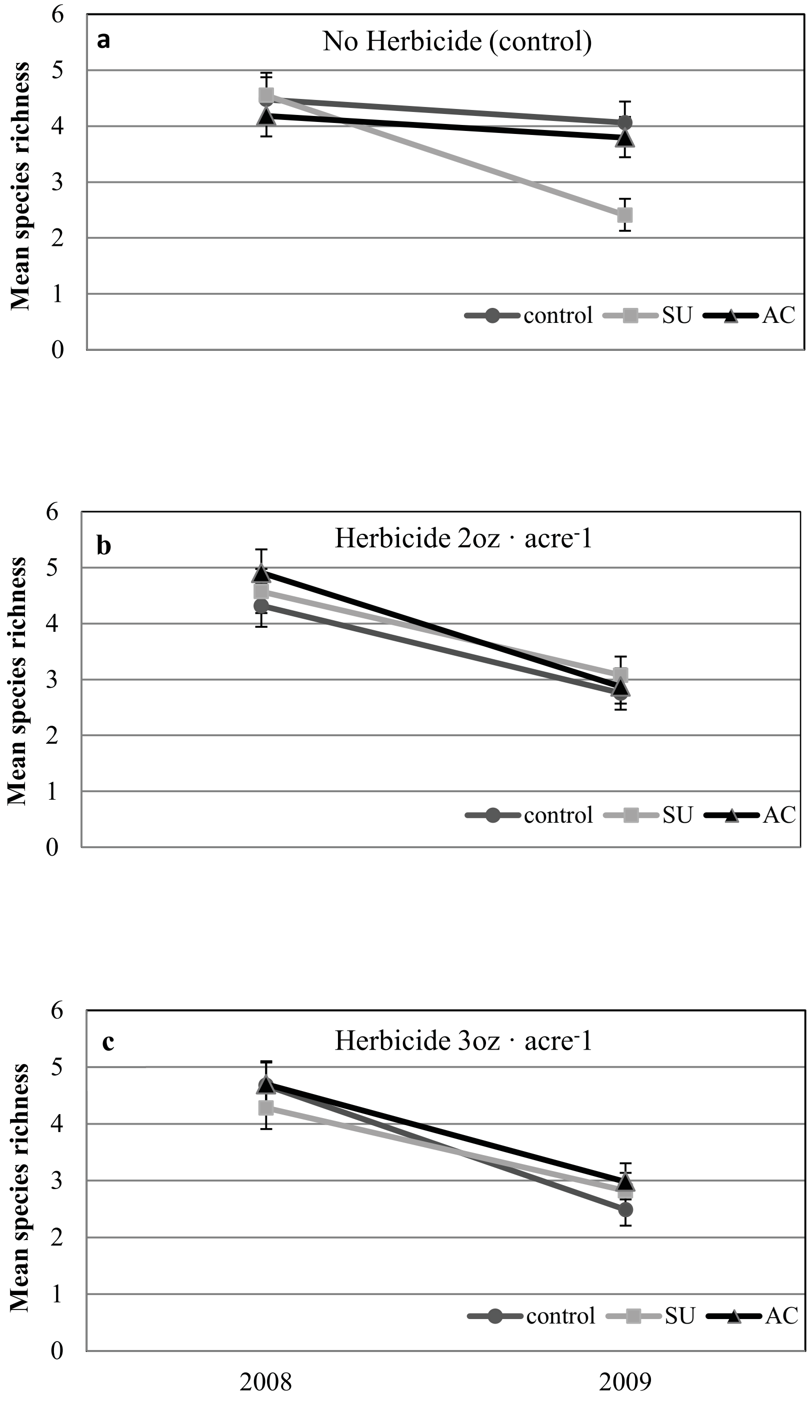

Figure 3.9. Mean total species richness · 0.24 L^{-1} of soil (± *95% CI*) as affected by the herbicide treatment (a) control, b) 2 oz · acre c) 3 oz · acre) x seedbed treatment x collection time interaction in model 2 of the cheatgrass experiment.

CHAPTER 4

CONCLUSION

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

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

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

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

Perhaps the most interesting and valuable findings in this chapter were those from the seeding frequency comparisons. Increasing seeding frequency from a single year to 2 and 3 years resulted in increased perennial grass emergence with 3 years of seeding yielding the largest increase. Since environmental conditions vary from year to year and are hard to predict, seeding multiple consecutive years may increase the probability of seeding in a year that is ‘favorable’ for seeded grasses.

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

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

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

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

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

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APPENDICES

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

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

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

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