EFFECTS OF NON-SURFACE-DISTURBING TREATMENTS FOR NATIVE GRASS REVEGETATION ON

CHEATGRASS (*BROMUS TECTORUM* L.) METRICS AND SOIL ION AVAILABILITIES

by

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ABSTRACT

Effects of Non-Surface-Disturbing Treatments for Native Grass Revegetation on

Cheatgrass (*Bromus tectorum* L.) Metrics and Soil Ion Availabilities

by

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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 $\cdot$ ha^{-1},

210 g ai $\cdot$ 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)

ACKNOWLEDGMENTS

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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 $\cdot$ ha^{-1} (2 oz ai $\cdot$ 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 α = 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 $\cdot$ 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, $140 \text{ g} \cdot \text{ha}^{-1}$ 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 $140 \text{ g} \cdot \text{ha}^{-1}$ 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 $210 \text{ g} \cdot \text{ha}^{-1}$ 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 $280 \text{ g} \cdot \text{ha}^{-1}$) resulting in greater cheatgrass control (up to 97%). However, $210 \text{ g} \cdot \text{ha}^{-1}$ herbicide still had no significant effect on mean tiller numbers in our experiment, and as with $140 \text{ g} \cdot \text{ha}^{-1}$ 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 $\cdot$

$100cm^{-2}$ (mean number of tillers $\cdot$ 100 cm^{-2} divided by mean number of tillers $\cdot$ $individual^{-1}$,

multiplied by mean weight per $individual^{-1}$) in sucrose addition (0.22 g $\cdot$ $100cm^{-2}$ ± 0.06) and

regular aerial seeding (0.33 g $\cdot$ $100cm^{-2}$ ± 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 $\cdot$ $100cm^{-2}$ ± 0.12, regular aerial seeding = 0.95 g $\cdot$ $100cm^{-2}$ ± 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 $\cdot$ 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 $\cdot$ 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 $\cdot$ 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).

Experiment	Cheatgrass metric			
	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

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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, $p \leq 0.05$).

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, $p \leq 0.05$).

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.

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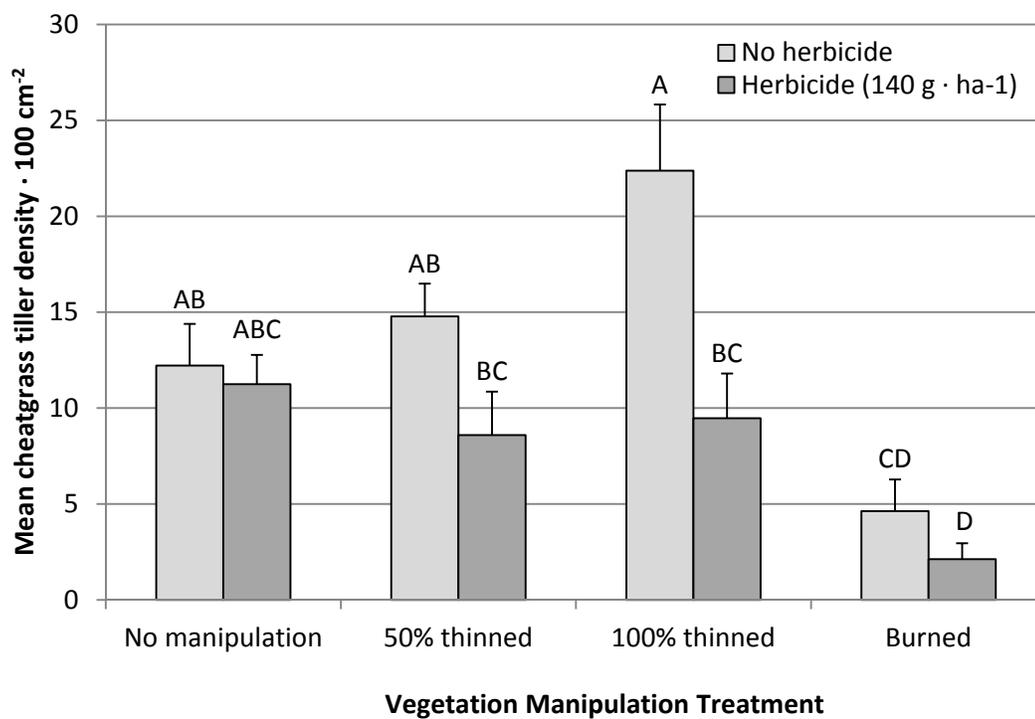
Figure 2.1. Mean cheatgrass tiller density · 100 cm^{-2} (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the sagebrush experiment in 2009. Values with the same letter do not differ significantly from each other.

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.
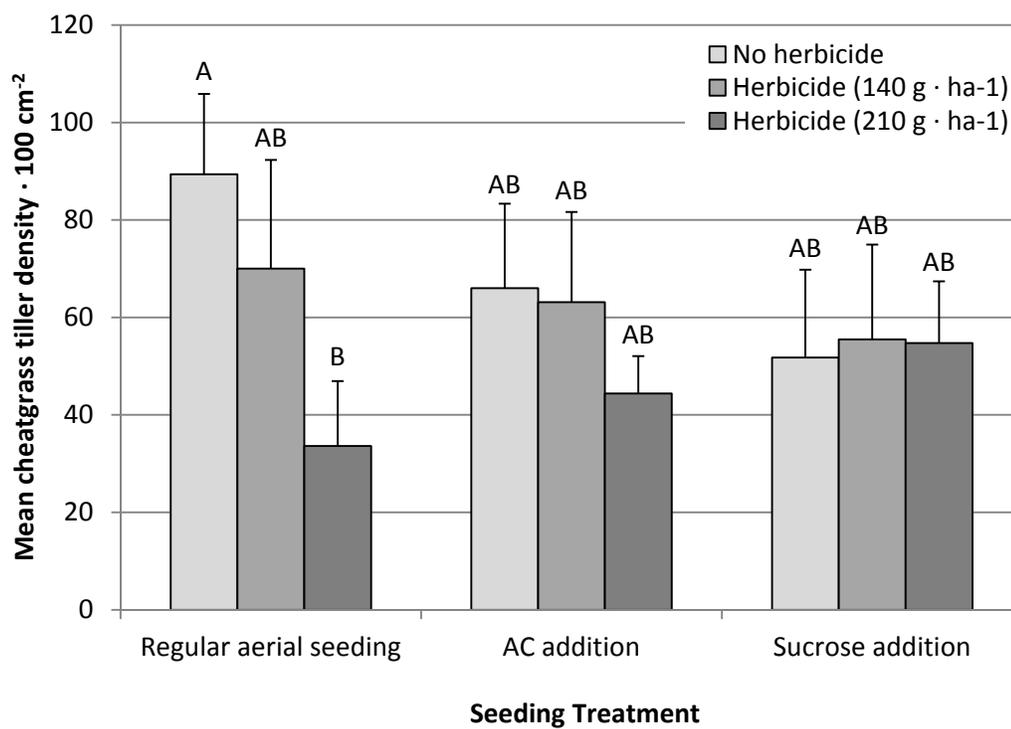
Figure 2.3. Mean cheatgrass tiller density · 100 cm^{-2} (+ *SE*), showing the interaction between *herbtreat* and *seedtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.
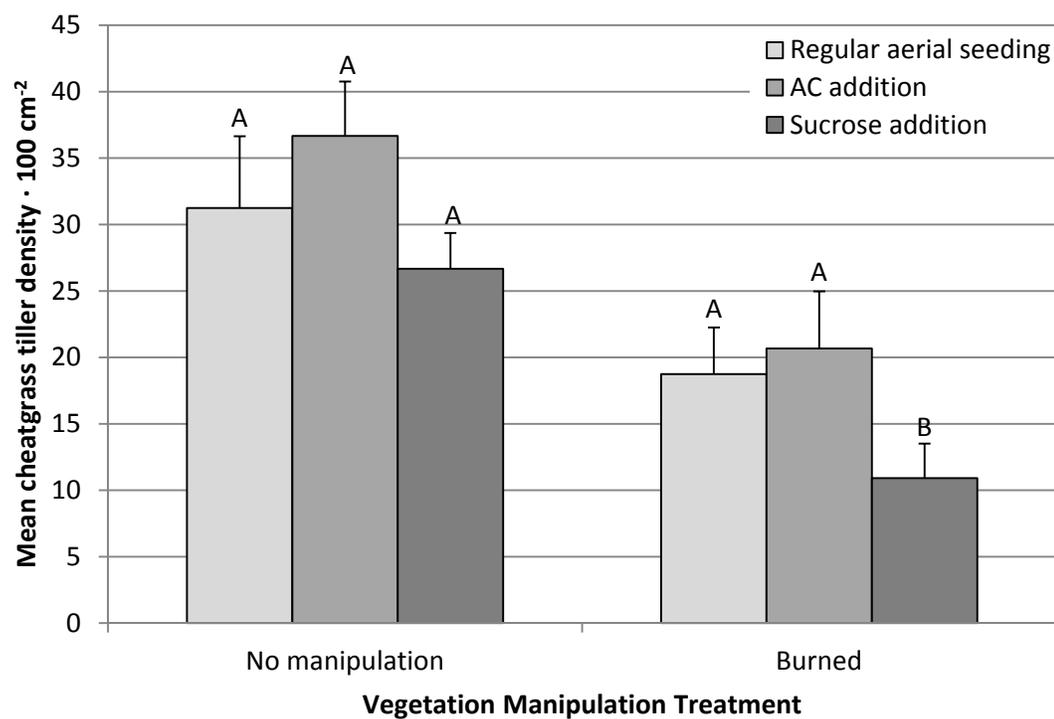
Figure 2.4. Mean cheatgrass tiller density · 100 cm^{-2} (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the cheatgrass experiment in 2010. Values with the same letter do not differ significantly from each other.
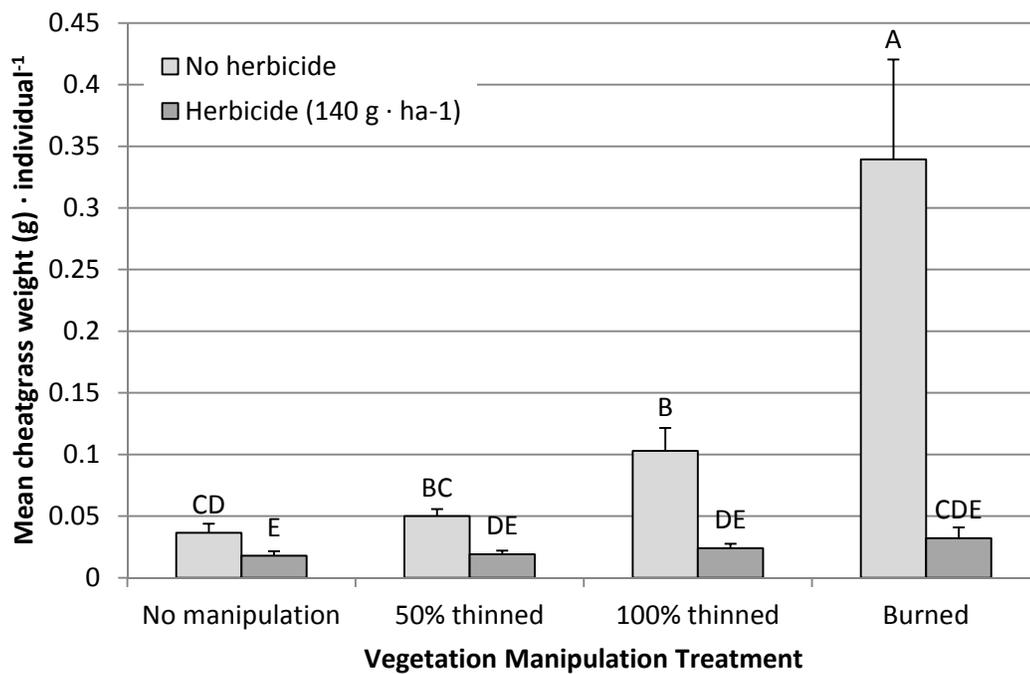
Figure 2.5. Mean weight (g) · cheatgrass individual[-1] (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the sagebrush experiment in 2009. Values with the same letter do not differ significantly from each other.
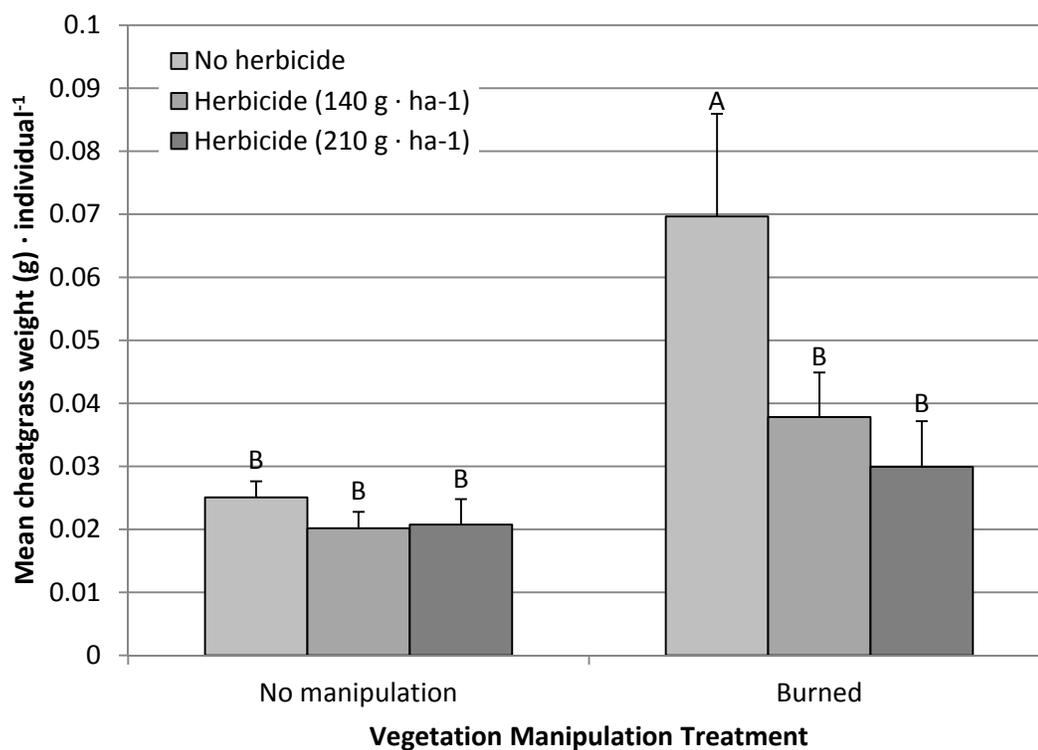
Figure 2.6. Mean weight (g) · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.
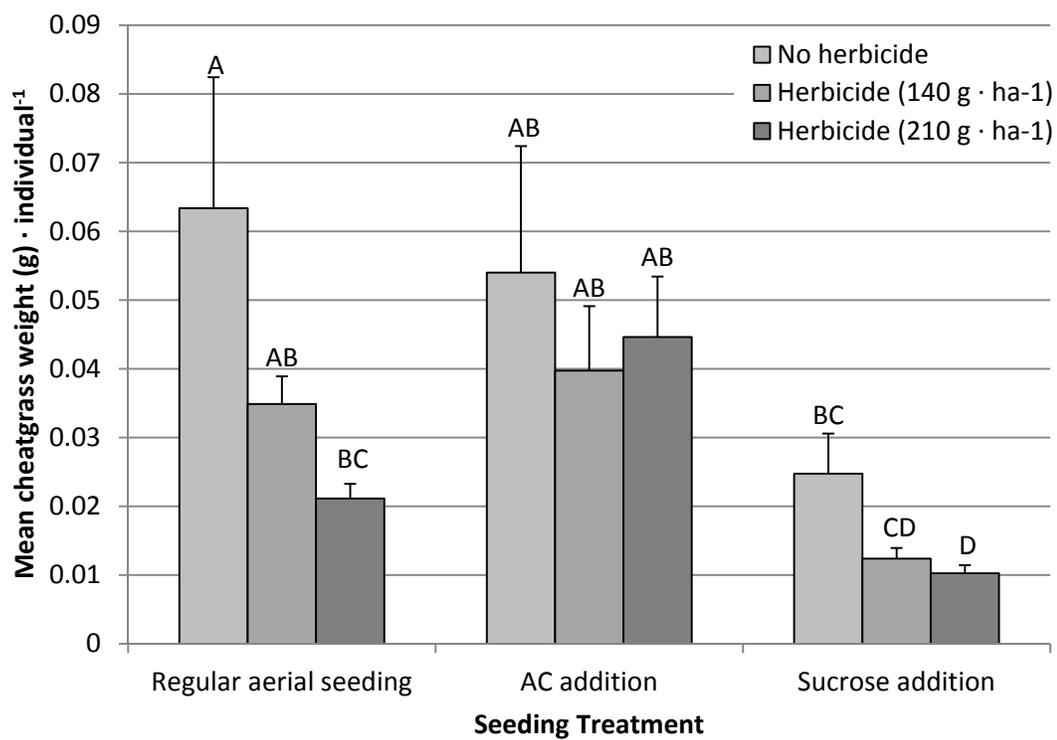
Figure 2.7. Mean weight (g) · cheatgrass individual[-1] (+ *SE*), showing the interaction between *herbtreat* and *seedtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.
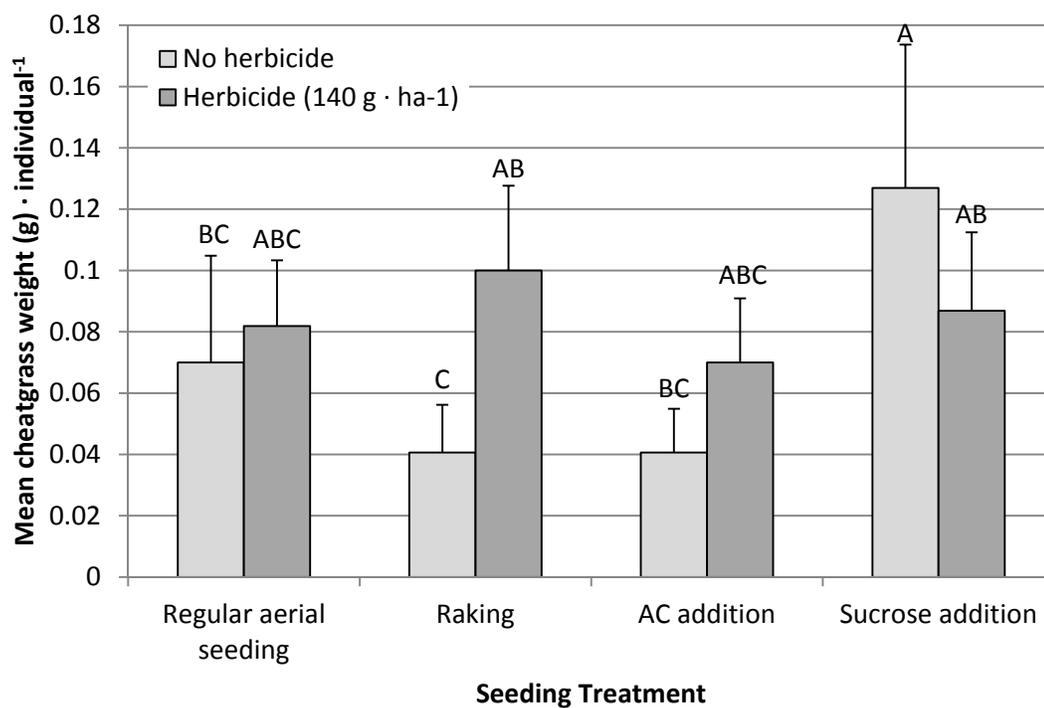
Figure 2.8. Mean weight (g) · cheatgrass individual[-1] (+ *SE*), showing the interaction between *herbtreat* and *seedtreat* in the sagebrush experiment in 2010. Values with the same letter do not differ significantly from each other.
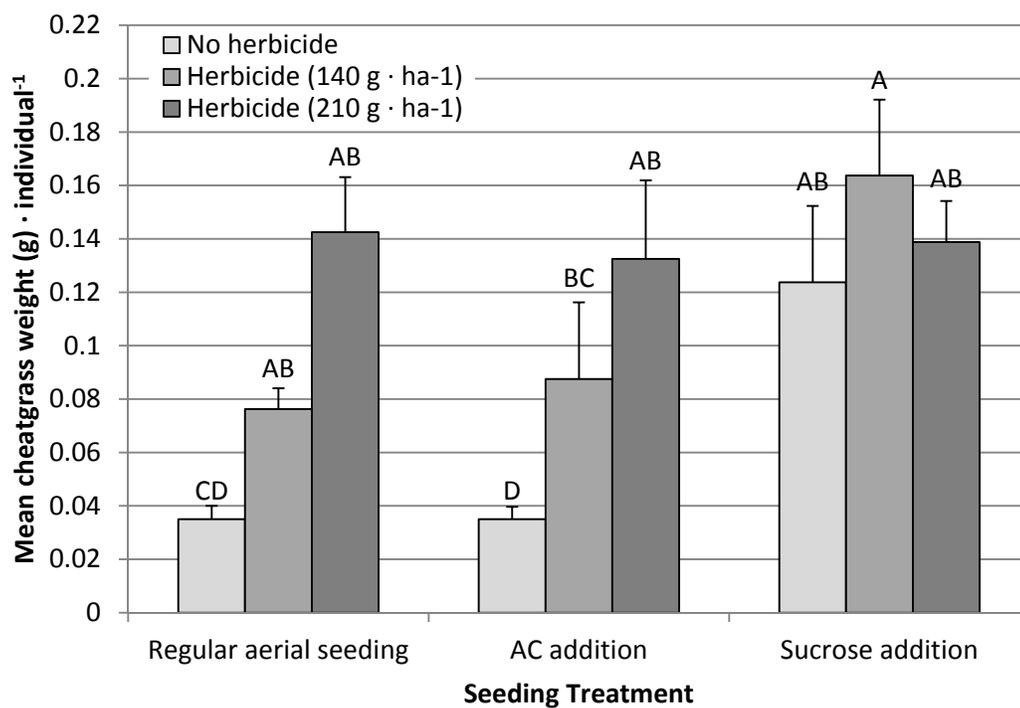
Figure 2.9. Mean weight (g) · cheatgrass individual[-1] (+ *SE*), showing the interaction between *herbtreat* and *seedtreat* in the cheatgrass experiment in 2010. Values with the same letter do not differ significantly from each other.
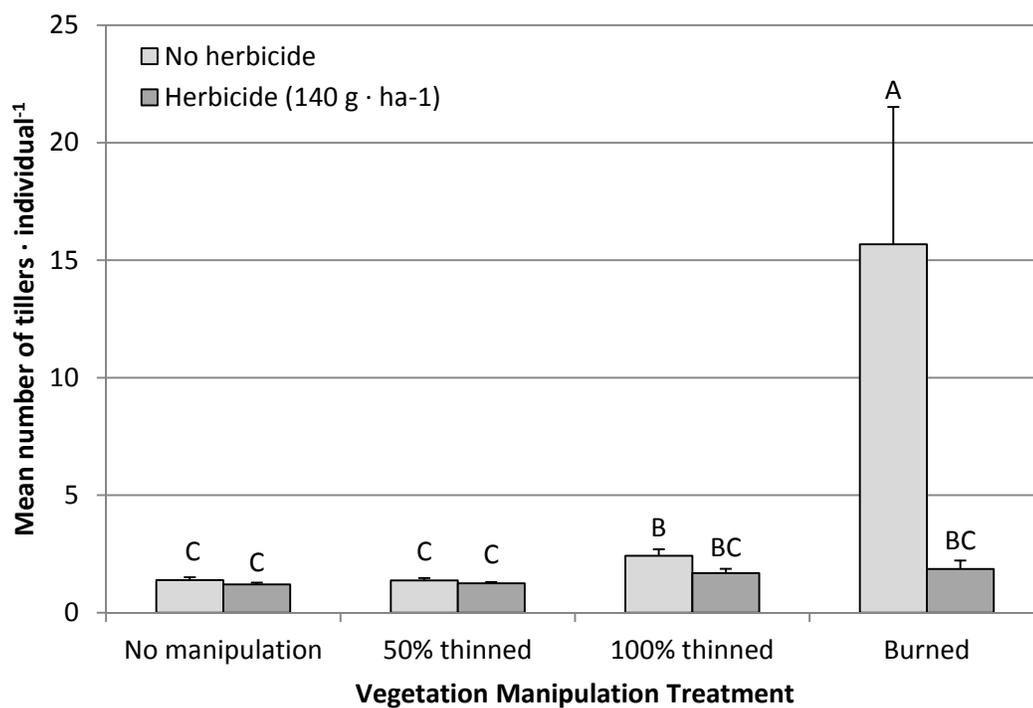
Figure 2.10. Mean number of tillers · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the sagebrush experiment in 2009. Values with the same letter do not differ significantly from each other.
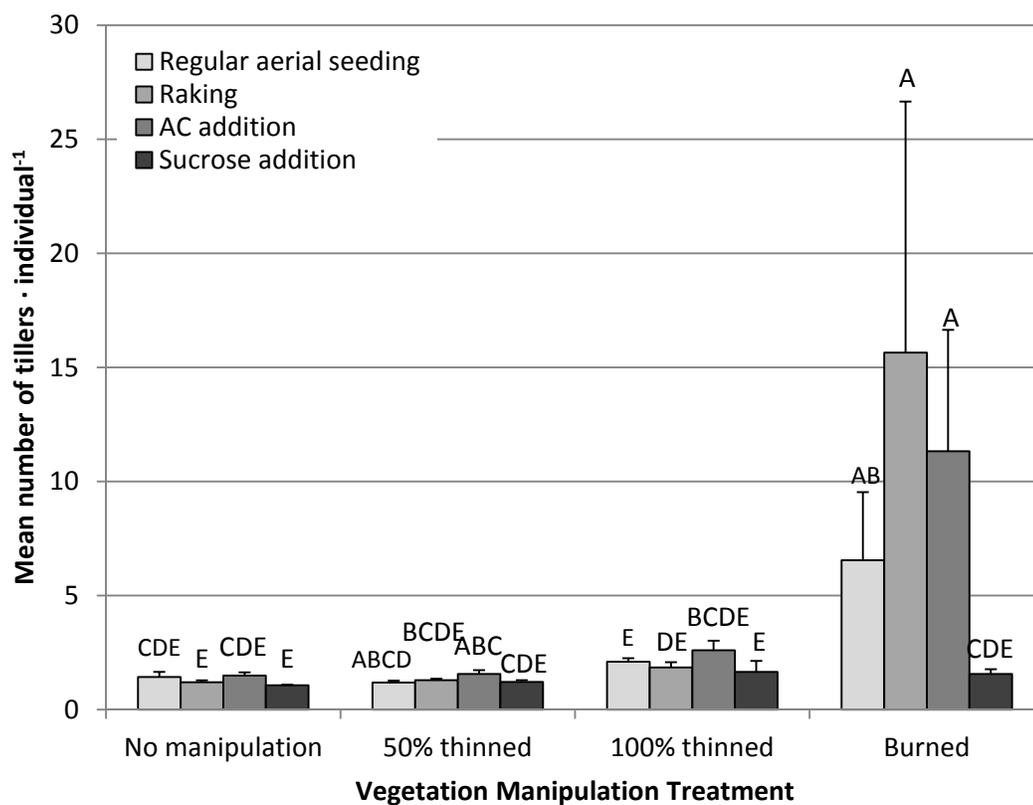
Figure 2.11. Mean number of tillers · cheatgrass individual[-1] (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the sagebrush experiment in 2009. Values with the same letter do not differ significantly from each other.
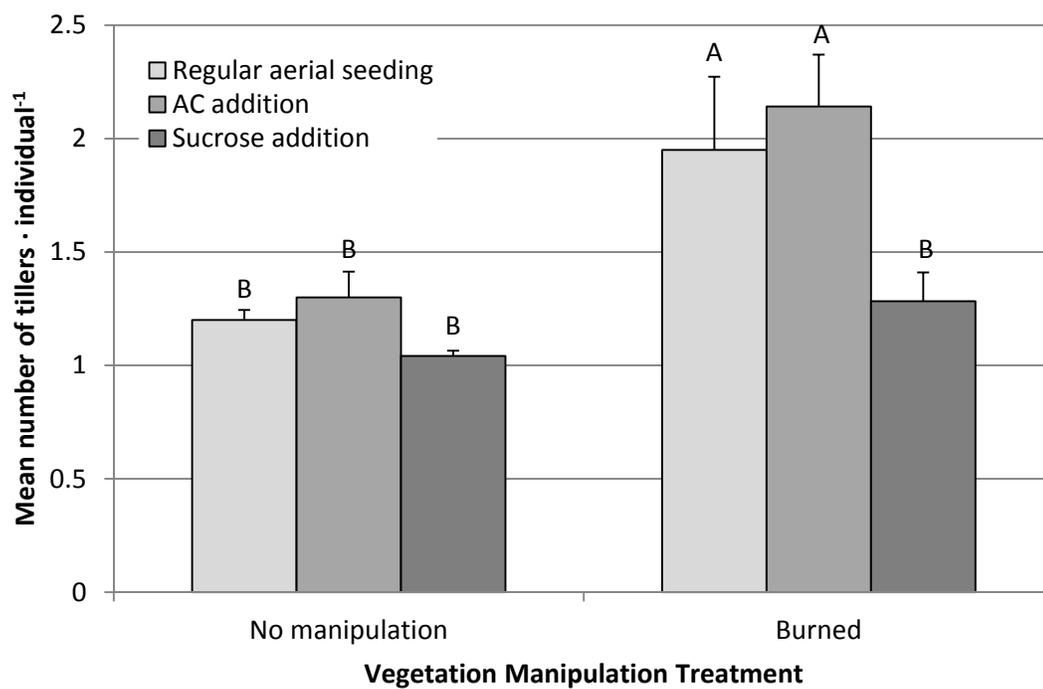
Figure 2.12. Mean number of tillers · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.
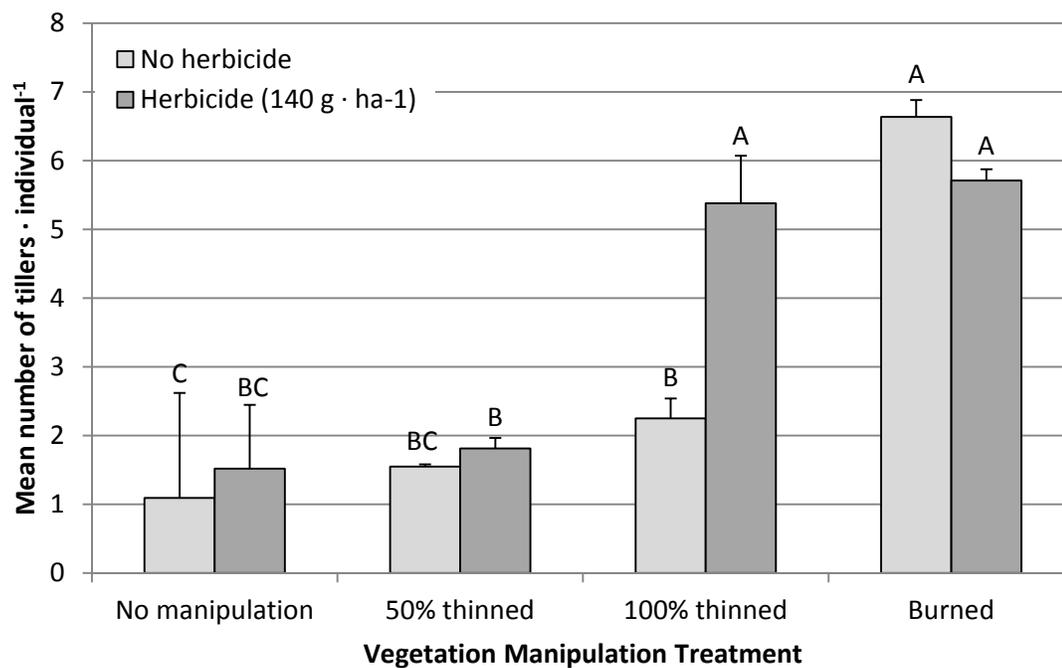
Figure 2.13. Mean number of tillers · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the sagebrush experiment in 2010. Values with the same letter do not differ significantly from each other.
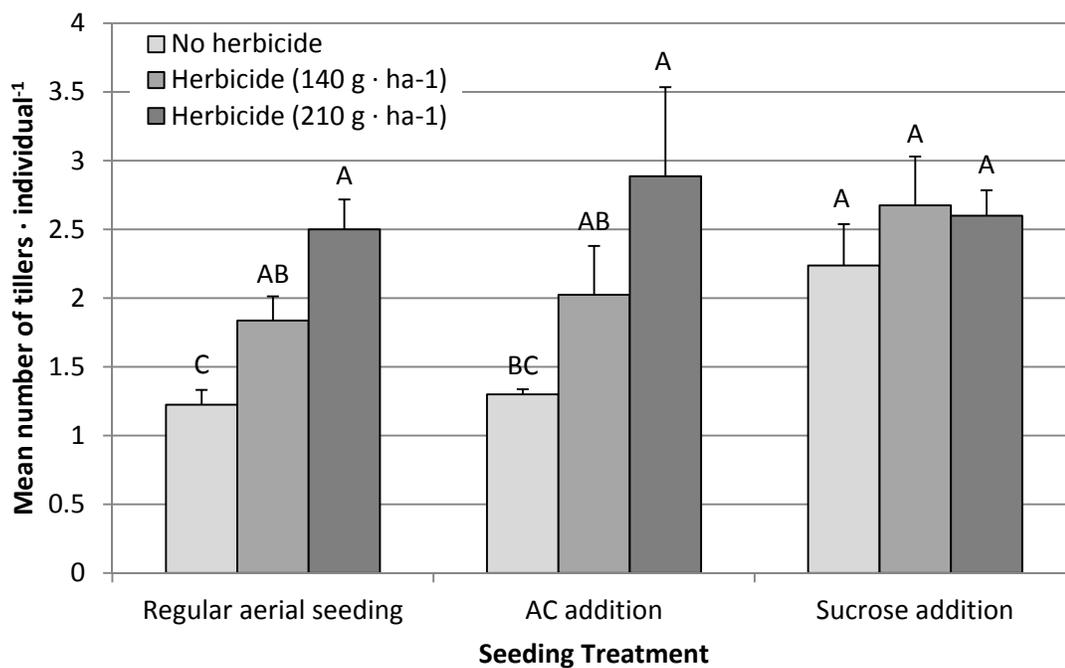
Figure 2.14. Mean number of tillers · cheatgrass individual[-1] (+ *SE*), showing the interaction between *herbtreat* and *seedtreat* in the cheatgrass experiment in 2010. Values with the same letter do not differ significantly from each other.
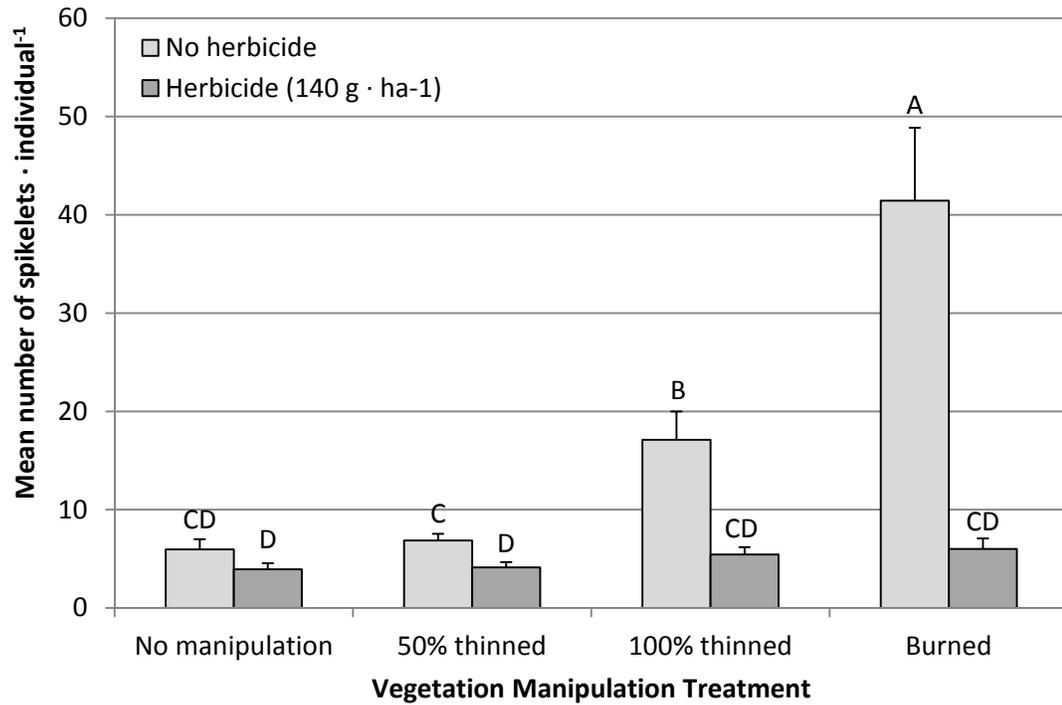
Figure 2.15. Mean number of spikelets · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the sagebrush experiment in 2009. Values with the same letter do not differ significantly from each other.
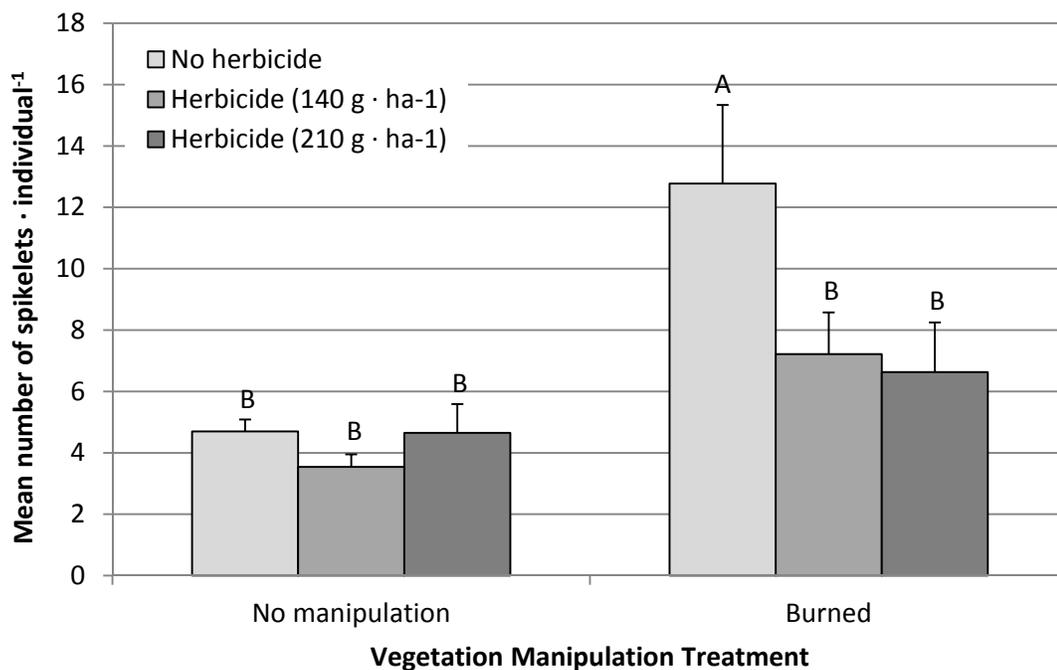
Figure 2.16. Mean number of spikelets · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *vegtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.
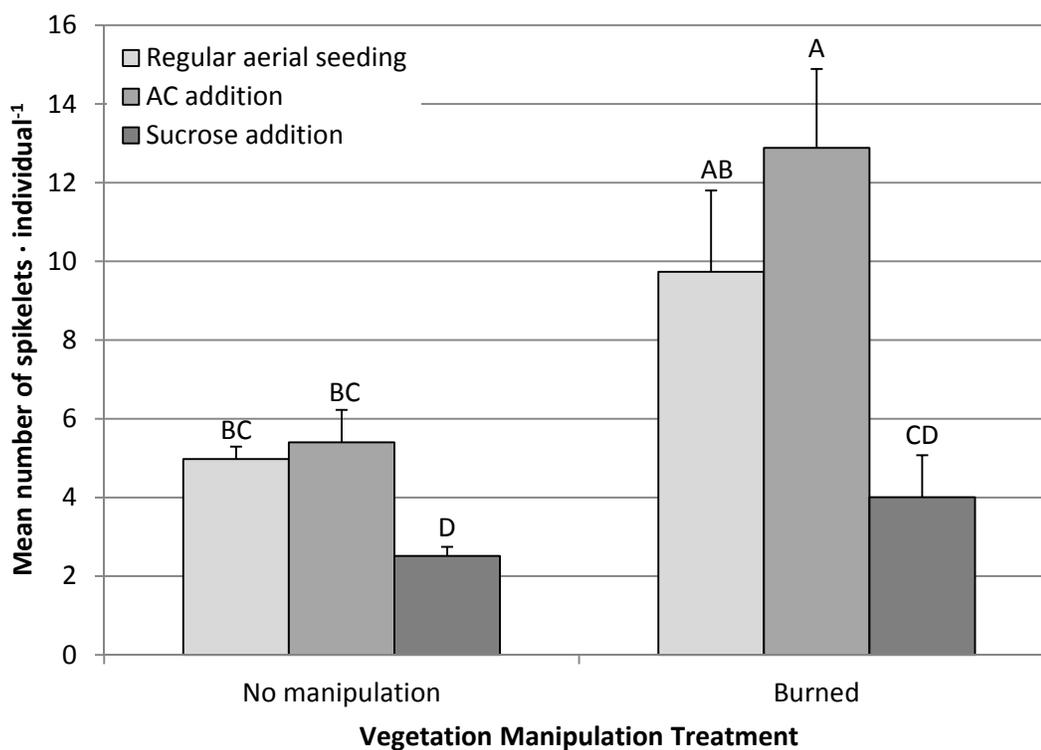
Figure 2.17. Mean number of spikelets · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.
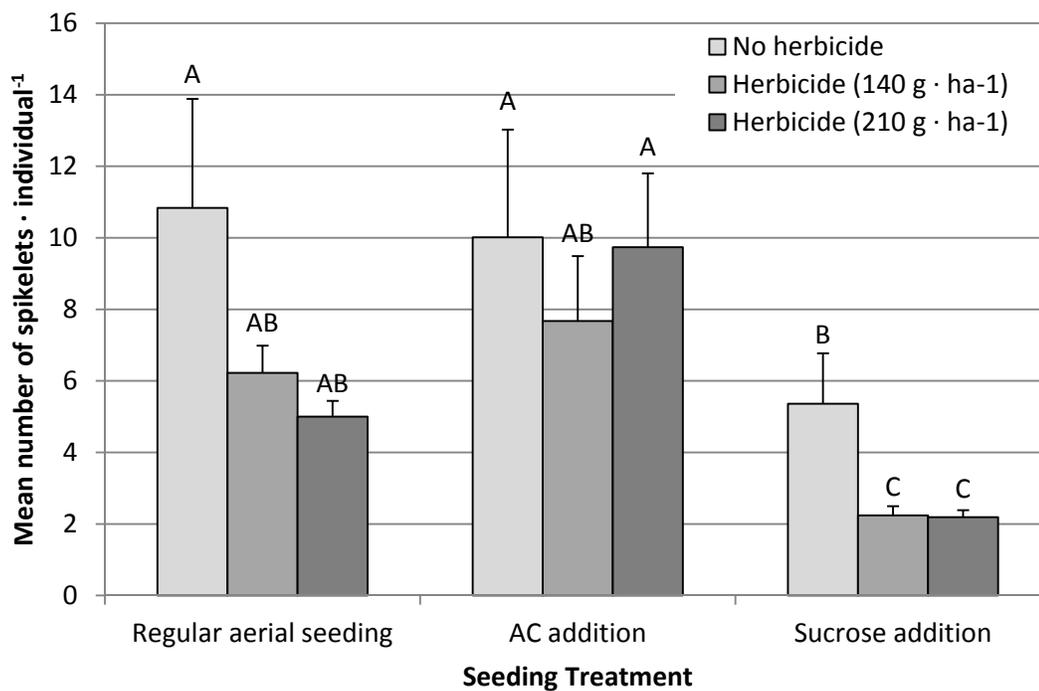
Figure 2.18. Mean number of spikelets · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *seedtreat* in the cheatgrass experiment in 2009. Values with the same letter do not differ significantly from each other.
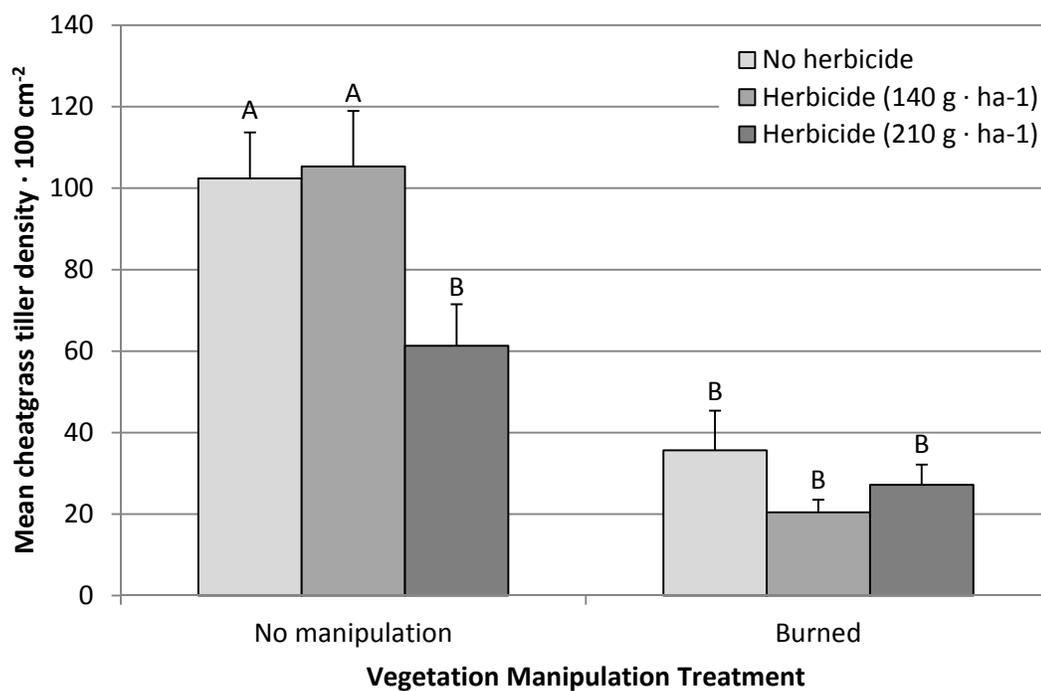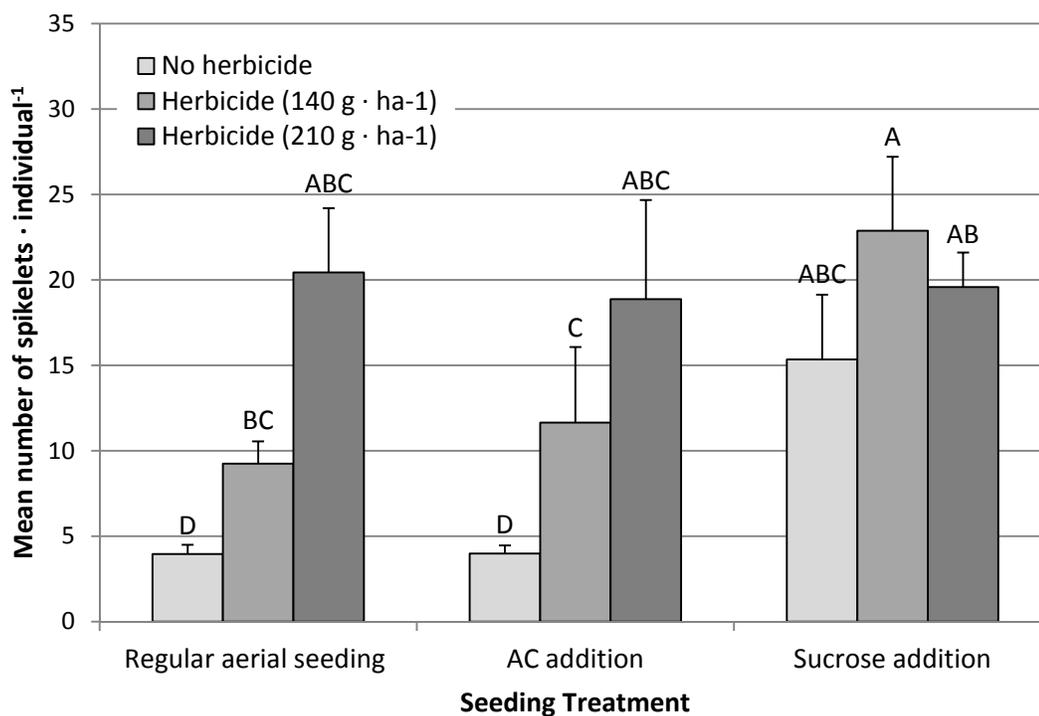
Figure 2.19. Mean number of spikelets · cheatgrass individual^{-1} (+ *SE*), showing the interaction between *herbtreat* and *seedtreat* in the cheatgrass experiment in 2010. Values with the same letter do not differ significantly from each other.

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 $\mu g \cdot 10\ cm^{-2} \cdot burial\ length^{-1}$.

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 α = 0.05 level. The response variables (IER-extractable

quantities of each ion, in units of µg · 10 cm^{-2} · 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 $\mu g \cdot 10 \text{ cm}^{-2} \cdot 17 \text{ weeks}^{-1}$.

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 µg · 10 cm^{-2} · 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

$\mu g \pm 19.1$) than in no manipulation (47.9 $\mu g \pm 11.0$) plots. Quantities of NH_4^+ were significantly

greater in Time 1 than in Time 3 (8.7 $\mu g \pm 0.8$ vs. 5.2 $\mu g \pm 0.4$, respectively), while quantities of

NO_3^- were significantly less in Time 1 than in Time 3 (32.6 $\mu g \pm 7.5$ vs. 99.6 $\mu g \pm 18.7$,

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 $\mu g \pm 24.1$)

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).

<center>IMPLICATIONS</center>

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.

Experiment	Soil ion								
	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)

Experiment	Soil ion					
	$B[OH]_4^{3+}$	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 ($\mu g \cdot 10\ cm^{-2} \cdot 17\ weeks^{-1}$) ± *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 ($\alpha = 0.05$).

| Experiment | Soil ion | | | |
	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 ($\alpha = 0.05$) are in bold font.

Experiment	Source	dF num	dF den	NO_3^- F	NO_3^- p	NH_4^+ F	NH_4^+ p	$H_2PO_4^-$ F	$H_2PO_4^-$ p	SO_4^{2-} F	SO_4^{2-} p	K^+ F	K^+ p	Ca^{2+} F	Ca^{2+} p	Mg^{2+} F	Mg^{2+} 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

Experiment	Source	dF num	dF den	Fe^{3+} F	Fe^{3+} p	Mn^{2+} F	Mn^{2+} p	$B[OH]_4^{3+}$ F	$B[OH]_4^{3+}$ p	Zn^{2+} F	Zn^{2+} p	Cu^{2+} F	Cu^{2+} p	Al^{3+} F	Al^{3+} p	Pb^{2+} and Cd^{2+} F	Pb^{2+} and Cd^{2+} 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 ($\mu g \cdot 10 \text{ cm}^{-2} \cdot 17 \text{ weeks}^{-1}$) ± *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 ($\alpha = 0.05$).

Treatment	Soil ion			
	$H_2PO_4^-$	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 ($\mu g \cdot 10 \text{ cm}^{-2} \cdot 17 \text{ weeks}^{-1}$) ± *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 ($\alpha = 0.05$).

Treatment	Soil ion	
	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 ($\mu g \cdot 10 \text{ cm}^{-2} \cdot 17 \text{ weeks}^{-1}$) ± *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 ($\alpha = 0.05$).

Treatment	Soil ion		
	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 num	dF den	NO_3^- F	NO_3^- p	NH_4^+ F	NH_4^+ p	$H_2PO_4^-$ F	$H_2PO_4^-$ p	SO_4^{2-} F	SO_4^{2-} p	K^+ F	K^+ p	Ca^{2+} F	Ca^{2+} p	Mg^{2+} F	Mg^{2+} 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 num	dF den	Fe^{3+} F	Fe^{3+} p	Mn^{2+} F	Mn^{2+} p	$B[OH]_4^{3+}$ F	$B[OH]_4^{3+}$ p	Zn^{2+} F	Zn^{2+} p	Cu^{2+} F	Cu^{2+} p	Al^{3+} F	Al^{3+} p	Pb^{2+} F	Pb^{2+} p	Cd^{2+} F	Cd^{2+} 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 ($\mu g \cdot 10 \text{ cm}^{-2} \cdot 17 \text{ weeks}^{-1}$) $\pm$ *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 ($\alpha = 0.05$).

	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 ($\mu g \cdot 10 \text{ cm}^{-2} \cdot 17 \text{ weeks}^{-1}$) $\pm$ *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 ($\alpha = 0.05$).

	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 ($\alpha = 0.05$) are in bold font.

		dF		Soil ion			
				NO_3^-		NH_4^+	
Experiment	Source	num	den	F	p	F	p
	Seedtreat	1	5	1.83	0.2338	1.95	0.2210
Sagebrush	Vegtreat	1	3	6.76	0.0803	0.66	0.4747
	Vegtreat *Seedtreat	1	5	0.97	0.3708	0.03	0.8739
	Seedtreat	1	1	31.22	0.1128	0.47	0.6183
Cheatgrass	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
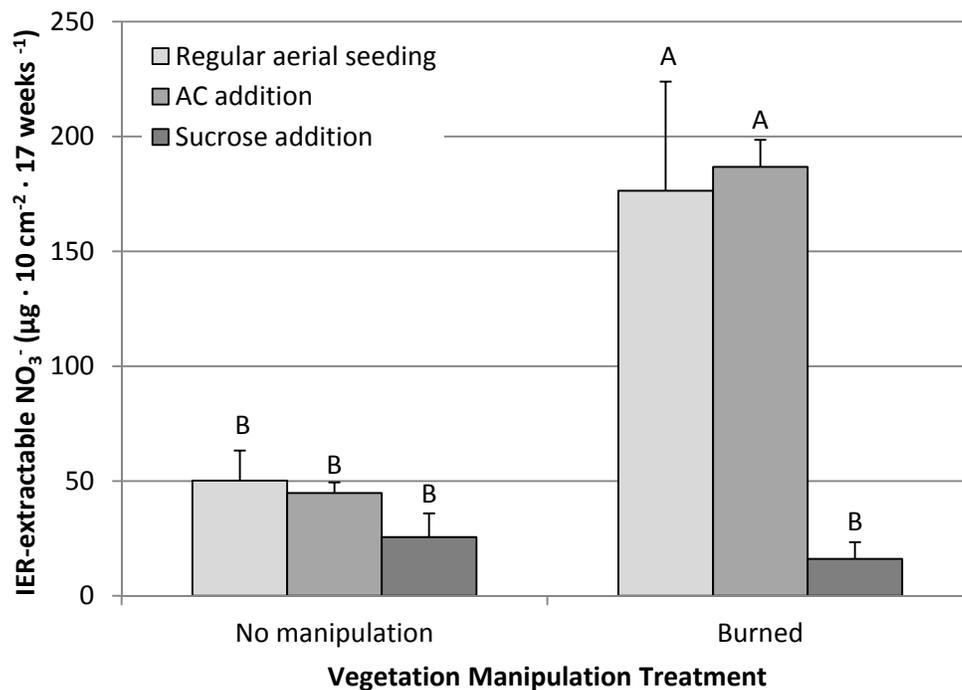
Figure 3.1. Mean quantities of IER-extractable NO_3^- (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the cheatgrass experiment in Time 1. Values with the same letter do not differ significantly from each other.
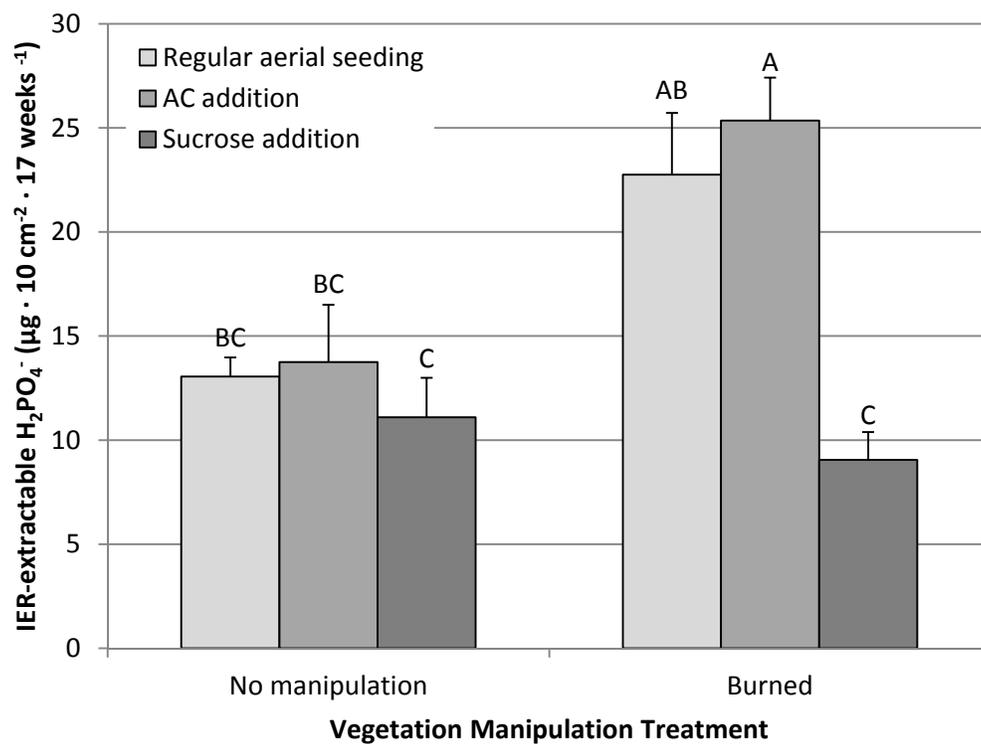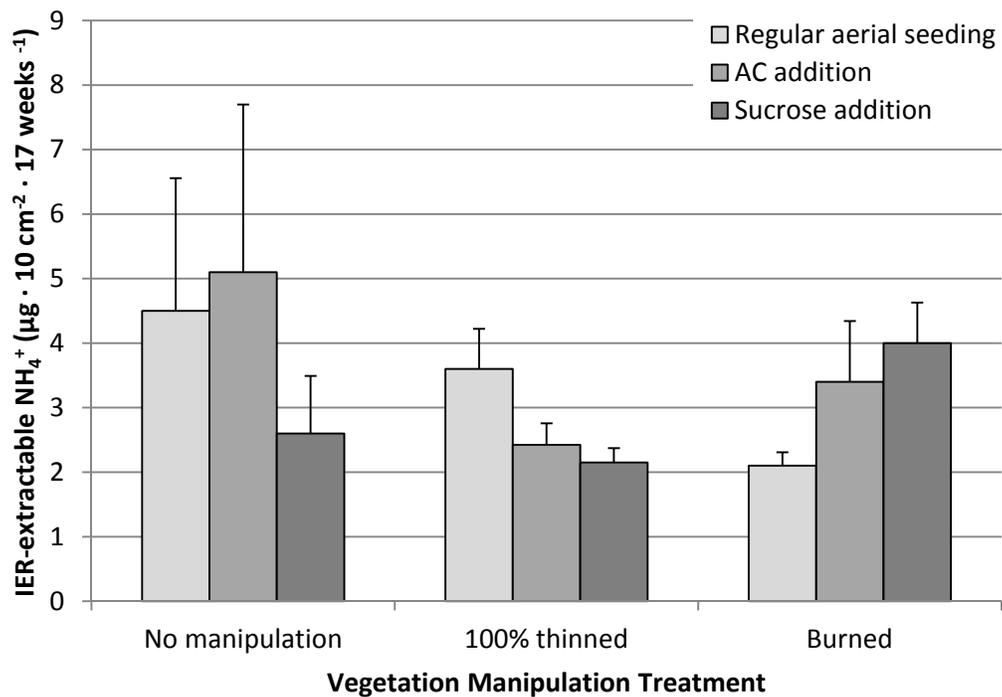
Figure 3.2. Mean quantities of IER-extractable $H_2PO_4^-$ (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the cheatgrass experiment in Time 1. Values with the same letter do not differ significantly from each other.

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.
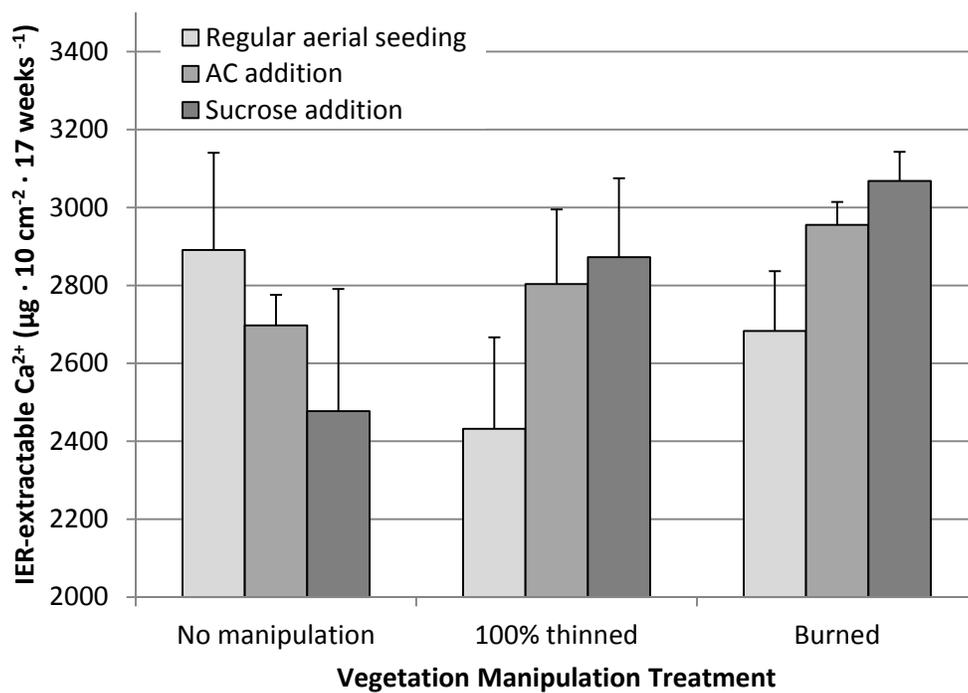
Figure 3.4. Mean quantities of IER-extractable Ca^{2+} (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the sagebrush experiment in Time 2.
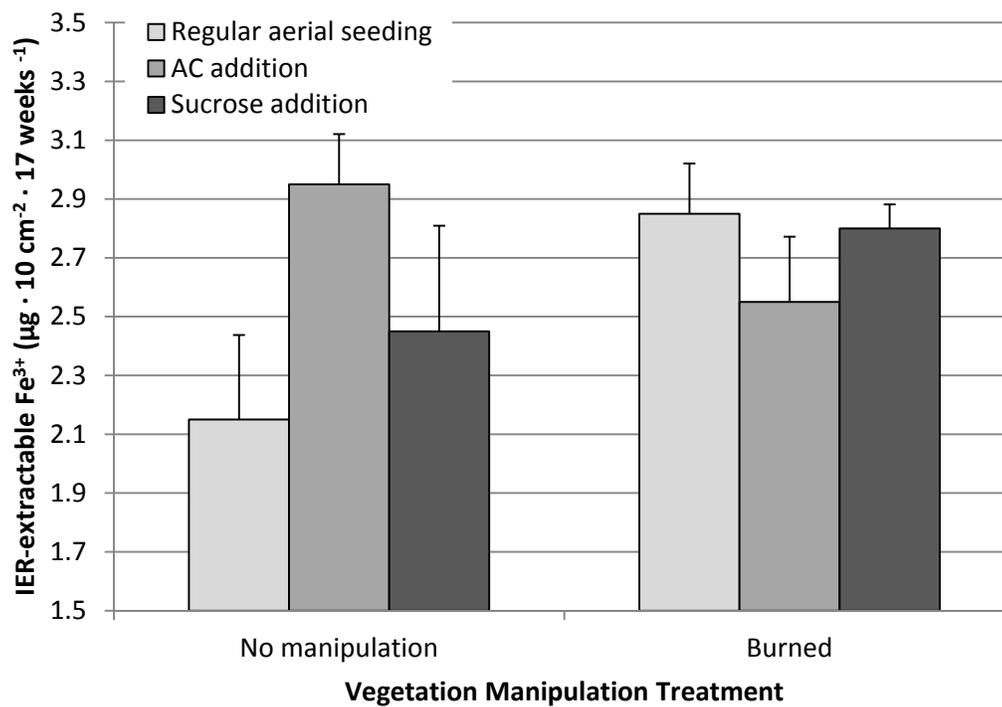
Figure 3.5. Mean quantities of IER-extractable Fe^{3+} (+ *SE*), showing the interaction between *vegtreat* and *seedtreat* in the cheatgrass experiment in Time 2.

Figure 3.6. Mean quantities of IER-extractable NO_3^- ($\pm$ *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.
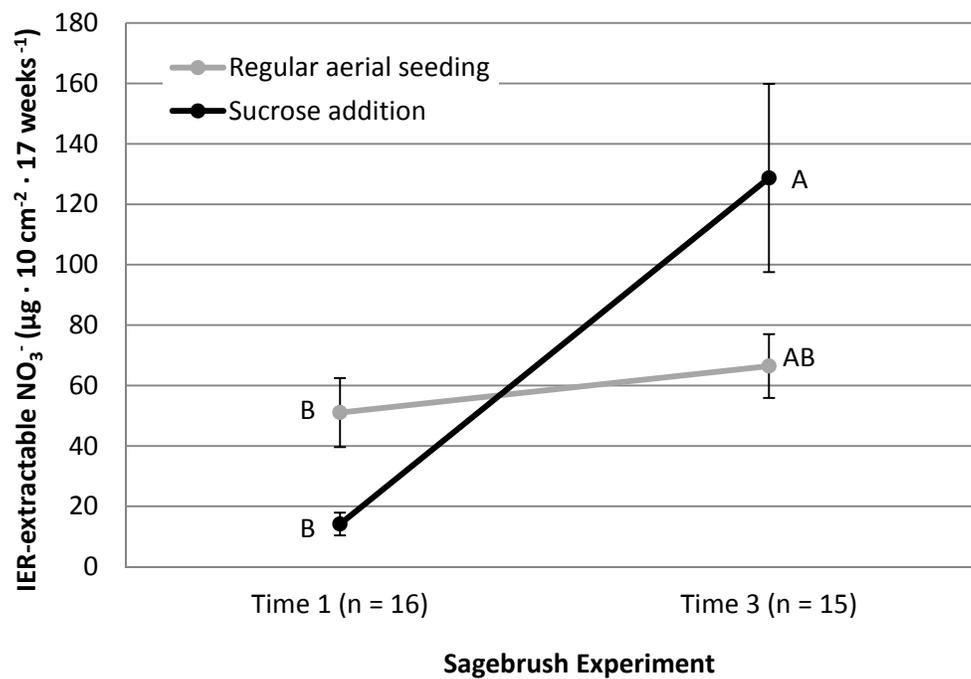
Figure 3.7. Mean quantities of IER-extractable NO_3^- ($\pm$ *SE*) in regular aerial seeding and sucrose addition subplots during Time 1 and Time 3 in the cheatgrass experiment. Values with the same letter do not differ significantly from each other.
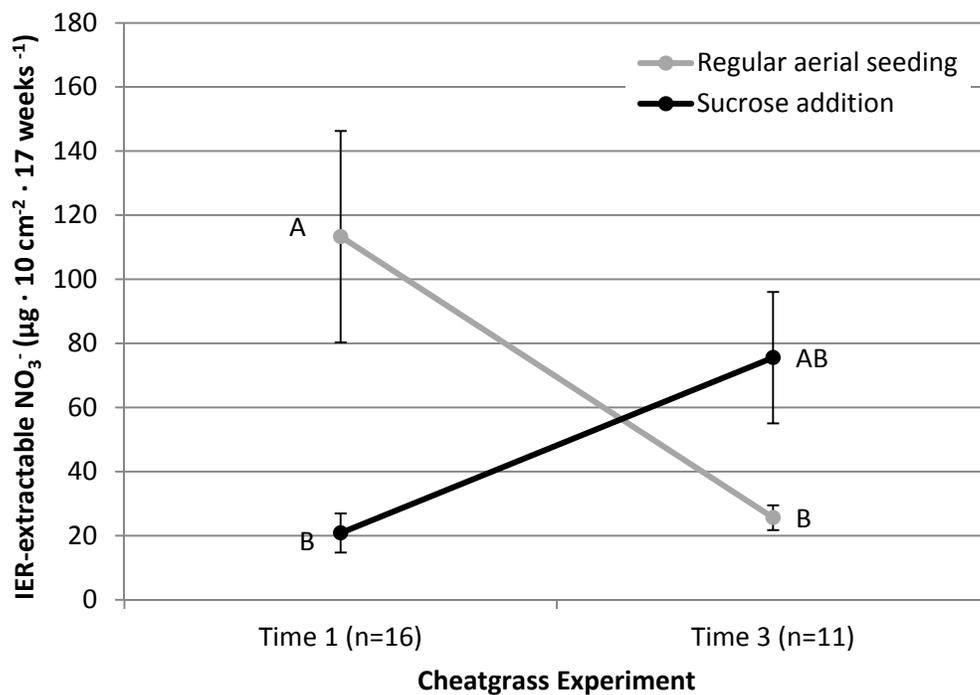
CHAPTER 4

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 · ha^{-1} and 210 g · 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.

LITERATURE

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