

The role of resource limitation in restoration of sagebrush ecosystems dominated by cheatgrass (*Bromus tectorum*)

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Abstract. Success of invasive annual grasses is often linked to increases in resources, and restoration ecologists have suggested that decreasing nitrogen (N) availability and restoring more conservative N cycles with lower N turnover should decrease the competitive advantage of these invaders and facilitate establishment of native perennials. We developed a multivariate conceptual model of the likely effects of environmental factors (precipitation and temperature) and potential management treatments (repeated burning, litter manipulation, and seeding an annual competitor) on soil N availability and success of cheatgrass, the most widespread invader in the western United States. We examined effects of the treatments in a five year field study in a cold desert shrubland. We used generalized linear mixed-effects models to examine differences among treatments over time, and structural equation modeling (SEM) to evaluate component hypotheses of the conceptual model. We hypothesized that burning would result in a pulse in soil available N due to heat-induced soil organic matter denaturation, but that subsequent fires would volatilize soil and biomass N resulting in progressive N deficiency. However, soil available N in burned plots was never lower than pre-burn levels, likely because burn temperatures were too cool to volatilize N from soils or aboveground biomass. Repeated burning decreased litter biomass, but there were generally no differences in soil available N between litter intact and litter removed plots. Litter removal had a negative effect on cheatgrass success likely due to effects on seed entrapment and plant establishment rather than N mineralization. Plots seeded with wheat generally had the lowest cheatgrass success, but available N was similar to other treatments, and decreased cheatgrass success was likely due to competition for other soil nutrients or water and reduced litter. In this semi-arid shrubland, long-term trends in available soil N and cheatgrass success were most strongly associated with precipitation and winter minimum temperatures. Treatments did not result in longer-term decreases in soil N, but indicated that integrated restoration approaches that reduce litter and seed banks and increase competitive interactions may be effective at reducing cheatgrass success and facilitating establishment of natives.

Key words: available nitrogen; cold desert shrubland; invasive annual grasses; litter removal; repeated fire; restoration; seeding.

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INTRODUCTION

Restoration ecologists have suggested that it may be possible to control invasive species and increase the success of native species by managing resource levels (Blumenthal et al. 2003, Suding et al. 2004). Restoration experiments that decreased available nitrogen (N) through topsoil removal (Buisson et al. 2006, Perry et al. 2010), sucrose or other carbon (C) source addition (Morghan and Seastedt 1999, Blumenthal et al. 2003, Suding et al. 2004, Prober et al. 2005, Mazzola et al. 2011), and repeated burning (Ojima et al. 1994, Blair 1997) reduced invasive species abundance and, in some cases, increased native species establishment (Young et al. 1999, Blumenthal et al. 2003, Prober et al. 2005). However, reducing available soil N has not decreased the competitive advantage of invasive species in all studies (Corbin and D'Antonio 2004, Huddleston and Young 2005, James et al. 2011). In most ecosystems, exogenous factors such as weather and endogenous factors such as competitive interactions influence resource availability and restoration outcomes. Thus, to determine the effectiveness of manipulating resources to control invasive species, it is necessary to identify the specific mechanisms influencing resource availability and invasive species success in the ecosystem of interest.

Invasion and expansion of the non-native annual grass, cheatgrass (*Bromus tectorum* L.), is arguably the most widespread invasive species issue in the western United States (D'Antonio and Vitousek 1992, Davies et al. 2011, Chambers et al. 2014a). Initial invasion of cheatgrass is often attributed to increases in resource availability resulting from disturbances such as inappropriate livestock grazing and wildfire (Chambers et al. 2007, Reisner et al. 2013). Traits such as early germination (Roundy et al. 2007), high nutrient use efficiency (Monaco et al. 2003, MacKown et al. 2009), and high growth and reproduction rates (Melgoza and Nowak 1991, Monaco et al. 2003, MacKown et al. 2009, James et al. 2011) allow cheatgrass to benefit from elevated resource levels. Cheatgrass may provide a positive feedback to its own persistence and spread by increasing soil N availability. Higher soil total and mineral N has been observed on cheatgrass dominated sites than on adjacent native shrub-

lands (Booth et al. 2003, Norton et al. 2004, Blank 2008, Hooker et al. 2008), possibly due to greater biomass turnover, faster rates of soil N cycling, and redistribution of mineral N in surface soils (Hooker et al. 2008).

Several authors have suggested that decreasing N availability and restoring a more conservative N cycle with lower N turnover should decrease the competitive advantage of invasive annual grasses like cheatgrass (Blumenthal et al. 2003, Norton et al. 2007, Brunson et al. 2010). In areas dominated by cheatgrass, this could involve direct manipulation of N availability (e.g., sugar amendments or repeated fire), manipulation of litter, or seeding a competitor. Restoration methods for decreasing N availability in cheatgrass-dominated systems typically have involved adding a C source such as sucrose to encourage population growth of soil microbes and immobilize available soil N. Sugar-amendment studies have resulted in reduced N availability, and consequently lower cheatgrass biomass and reproduction (Blumenthal et al. 2003, Blank and Young 2009), but responses are typically short-lived and insufficient for long-term cheatgrass control (Mazzola et al. 2011). Repeated burning is an alternate approach that may reduce soil N for longer time periods as a result of progressive N deficiency (Rau et al. 2007). Both wildfire and prescribed fire are often followed by short-term pulses in NH_4^+ (ammonium) and NO_3^- (nitrate), which can stimulate plant growth and result in increased plant N content in the following growing season (Monaco et al. 2003, Johnson et al. 2011). Repeated burning of this nutrient-rich biomass, along with the litter, may reduce above- and belowground N over time as nutrients in biomass and litter are volatilized and lost from the system (Rau et al. 2007). Also, combustion of soil organic matter (SOM) can cause N to be volatilized and lost directly from soils (Raison et al. 1985, Neary et al. 1999). Repeated burning has reduced available and/or total soil N in studies conducted in a wide variety of ecosystems, including perennial grasslands (Ojima et al. 1994, Blair 1997), heathlands (Adams et al. 1994), and forests (Binkley et al. 1992, Monleon et al. 1997, Wright and Hart 1997, Cheng et al. 2013). However, repeated burning has not reduced soil N in other studies in similar ecosystems (Anderson and Bailey 1980, Coetsee

et al. 2010, Augustine et al. 2014), and neither its effects in ecosystems dominated by invasive annual grasses nor its potential interactions with environmental factors or other restoration treatments have been studied.

Litter can influence nutrient availability and may play an important role in non-native annual grass invasions. Invasion by cheatgrass can significantly increase litter inputs in native sagebrush steppe communities (Evans et al. 2001, Norton et al. 2004). Cheatgrass and other non-native annual plants often have rapid litter turnover, which can increase nutrient availability (especially NO_3^-) in surface and subsurface soil layers (Ehrenfeld 2003, Sperry et al. 2006, Norton et al. 2008). Also, insulation by litter can (1) increase soil temperatures during winter, which promotes SOM decomposition and higher nutrient availability, and (2) elevate soil moisture, which increases N mineralization and reduces NH_4^+ loss (Facelli and Pickett 1991). Finally, litter can retain seeds (Chambers 2000) and create favorable microsites for cheatgrass germination and establishment (Evans and Young 1984).

Rapidly growing annual species with phenology similar to invasive annual grasses have the potential to take up available nutrients and increase soil nutrient loss during repeated burning. Also, they may decrease growth and reproduction of invasive annual grasses via competitive interactions. An effective, integrated restoration approach for improving establishment of native species involves seeding non-native annuals such as common wheat (*Triticum aestivum*) that can serve as cover crops and reduce success of non-native invasive annuals in the first year, and then seeding native species in the following year (Koscelny et al. 1990, Monaco et al. 2003, Herron et al. 2013). Because species like common wheat are typically sterile, competition from these species in the second year and the risk that they will reproduce and become invasive is nil. Seeding an annual competitor such as common wheat may work in tandem with repeated burning to both reduce soil resources and the competitive advantage of cheatgrass.

We developed a multivariate conceptual model of the likely effects of environmental factors (precipitation and temperature) and restoration treatments (repeated burning, litter manipula-

tion, seeding an annual competitor) on soil N availability and cheatgrass establishment, growth, and reproduction (Fig. 1). We identified hypothesized mechanisms associated with the paths in the conceptual model (Table 1), and examined the effects of environmental factors and restoration treatments in a five year field study. We used a Wyoming big sagebrush ecological site type dominated by cheatgrass because this plant community has exhibited the highest rate of conversion to cheatgrass-dominance. Our analyses addressed two questions. (1) What are the direct and indirect effects of restoration treatments aimed at resource reduction (repeated burning, litter manipulation, seeding an annual competitor) on soil N availability and cheatgrass success over time? (2) How do abiotic (precipitation and temperature) and biotic factors (other annual invaders) influence soil N availability and cheatgrass success over time? Generalized linear mixed-effects models (GLMMs) were used to examine differences in soil N availability, litter, cheatgrass, common wheat, and other annual plants among treatments and across time. Structural equation modeling (SEM) was used to evaluate the component hypotheses in the conceptual model (Grace et al. 2009). We used our results to suggest integrated restoration strategies.

METHODS

Study area

Two study sites were located in Humboldt County, Nevada, on land administered by the Bureau of Land Management (BLM). The Eden Valley site is located at 1524 m above sea level (466314 E, 4564313 N) while the Orovada site is located at 1402 m above sea level (436294 E, 4598553 N). Soils at both sites are well-drained and occur on alluvial fans with a veneer of loess ranging in texture from silt loam to fine sandy loam (Denny 2002). Soils at Eden Valley are classified as coarse-loamy, mixed, superactive, mesic, Durinodic Xeric Haplocambids while the soils at Orovada are classified as sandy-skeletal, mixed, mesic Xeric Haplocambids (Denny 2002). Mean daily temperatures typically range from 29°C in July to -6°C in January (National Climate Data Center, Coop Id #265818 and #266005, 1970–2010). Sites are located in the 254–304 mm

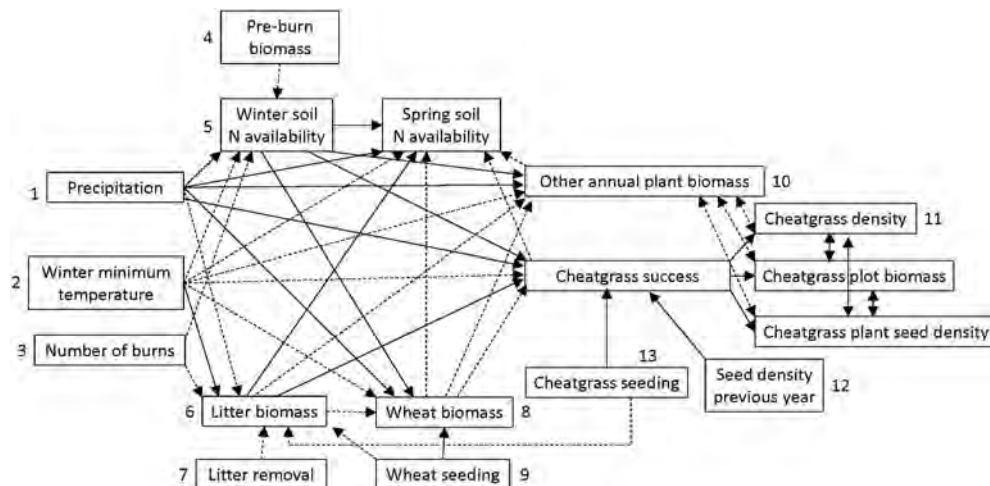


Fig. 1. Hypothesized path models for effects of weather variables and experimental treatments on winter and spring soil N availability, litter biomass, wheat biomass, other annual plant biomass, and cheatgrass density, biomass per plot, and seed density per plant. Direct effects are indicated by one-headed arrows and two-directional correlations are indicated by two-headed arrows. Positive effects are indicated by solid lines and negative effects by dashed lines. Components of the overall hypotheses, which are indicated by the numbers, are described in Table 1.

precipitation zone and most precipitation arrives as snow in fall and winter (National Climate Data Center, Coop Id #265818 and #266005, 1970–2010). Grazing by livestock occurred from the late 1800s until fall 2002 for the Eden Valley site and until summer of 1999 for the Orovada site when the study sites were enclosed by fences to exclude cattle.

Historically, vegetation at both sites was a Wyoming big sagebrush ecological site type dominated by natives, including the shrub *Artemisia tridentata* subsp. *wyomingensis*, perennial bunchgrasses such as *Poa secunda*, *Elymus elymoides*, *Pseudoroegneria spicata* and *Leymus cinereus*, and forbs such as *Crepis acuminata* and *Lupinus argenteus* (West and Young 1999). Conversion to cheatgrass dominance occurred after an extensive wildfire in 1999 at the Eden Valley site and by at least 1985 at the Orovada site. Currently, no shrubs occur on the sites and residual perennial herbaceous species consist primarily of the native grass, *P. secunda*. Also, several species of introduced annual forbs (e.g., *Descuriana sophia*, *Erodium cicutarium*, *Sisymbrium altissimum*) occur in varied abundance on the sites.

Experimental design

The experimental design was comprised of two closely related experiments that examined effects of repeated burning and post-fire seeding on cheatgrass success and soil N. A litter intact experiment examined the effect of repeated burning and post-fire seeding, while a litter removed experiment examined the effect of repeated burning and post-fire seeding on plots that had litter removed. Both experiments were initiated in 2008, but sampling began in 2008 on the litter intact experiment and in 2009 on the litter removed experiment. The two experiments used a randomized, complete block design and were conducted in close proximity to one another. The blocks for both experiments were the two sites, Eden Valley and Orovada. The litter intact experiment had four burn and seeding treatments: unburned, burned only, burned and seeded with cheatgrass, and burned and seeded with common wheat. The litter removed experiment had five treatments: litter intact unburned, litter removed unburned, litter removed and burned only, litter removed and burned and seeded with cheatgrass, and litter removed and burned and seeded with common wheat. The two experiments shared untreated, control plots

Table 1. Components of hypotheses represented by multivariate conceptual model.

Path	Hypothesized mechanism
Environmental effects	
1	Increased soil water availability due to higher precipitation results in increases in litter and soil organic matter decomposition (Dijkstra and Cheng 2007, Moyano et al. 2013) and net N mineralization (Fierer and Schimel 2002, Borke and Matzner 2009). Soil water and N availability are closely coupled in arid and semi-arid systems and together will have a positive effect on plant establishment, N uptake, and growth (Leffler and Ryel 2012).
2	Low winter temperatures are associated with lower decomposition (Fierer et al. 2005) and less N mineralization in winter (Rustad et al. 2001) and reduced or delayed plant N uptake.
Repeated burning effects	
3	Initial effects of repeated burning are a pulse in soil N availability due to heat-induced SOM denaturation (Raison et al. 1985, Neary et al. 1999). Subsequent fires volatilize N in aboveground biomass and soils resulting in a decrease in available soil N over time (progressive N deficiency) (Monaco et al. 2003, Rau et al. 2007). Repeated burning also consumes litter biomass over time, especially when a thick litter mat is present.
4	Fire temperatures in arid ecosystems are strongly affected by type and amount of fuel, with higher temperatures occurring in areas with woody fuels and high biomass (Brooks 2002). Hotter fires will result in increased volatilization of above- and belowground N (Raison et al. 1985, Blair 1997, Neary et al. 1999) and decrease soil N availability.
5	Nitrogen is often an important limiting factor to plant productivity in arid ecosystems and increases in soil N availability will increase plant N uptake and growth (Leffler and Ryel 2012). High soil N availability in the winter will carry into spring.
Litter effects	
6	Dense litter mats modulate soil temperatures, promoting SOM decomposition and soil N availability (Facelli and Pickett 1991), and increase soil moisture, promoting net N mineralization (Knapp and Seastedt 1986, Facelli and Pickett 1991, Sperry et al. 2006). Dense litter mats also cause seed entrapment and retention (Chambers 2000). Both effects will increase cheatgrass success.
7	Litter removal will result in a 3–5 year window of reduced litter biomass and will decrease cheatgrass success.
Seeding and plant effects	
8	High annual wheat biomass and N uptake will decrease spring soil N availability and decrease the plant density, biomass and seed density of phenologically similar plant species due to competition (Koscelny et al. 1990, Blackshaw 1994, Monaco et al. 2003).
9	Wheat seeding will increase wheat biomass but decrease litter biomass due to disturbance caused by seeding.
10	Other annual plant biomass will be negatively correlated with cheatgrass plant density, biomass, and seed density due to competition (Chambers et al. 2014b).
11	Cheatgrass density will be positively correlated with cheatgrass biomass per plot, but will be negatively correlated with cheatgrass seed density per plant due to strong intraspecific competition (self-thinning theory; Yoda et al. 1963, White et al. 2007, Deng et al. 2008).
12	High seed density from the previous year will increase cheatgrass plant density, biomass, and seed density due to high propagule pressure.
13	Cheatgrass seeding will increase cheatgrass plant density, biomass, and seed density due to high propagule pressure and decrease litter biomass due to disturbance caused by seeding.

(unburned litter intact) in order to track natural variation during the study. Each burn and seeding treatment was replicated four times in each experiment in each block for a total of 32 treatment plots in the litter intact experiment and 40 treatment plots in the litter removed experiment for both sites. All plots were completely randomized within experiments. Effects of repeated burning were evaluated at peak biomass production with a before/after/control/impact (BACI) design (Stewart-Oaten et al. 1986) to

clearly assess the interaction of treatment with time. Samples were collected the year before the first burn and the year after each subsequent burn (2008 through 2012 for the litter intact experiment; 2009 through 2012 for the litter removed experiment). Control plots were monitored each study year.

Treatments

In the litter intact experiment, all plots were undisturbed at the beginning of the study.

Burning and seeding treatments were initiated in 2008 and continued through 2011 (4 years). In the litter removed experiment, litter was raked off of the study plots and removed from the area once at the beginning of the study in fall 2008. Seeding treatments were initiated in 2008, but for logistical reasons, burning treatments began in 2009 and were continued through 2011 (3 years). Treatment plots were circular, 3.2 m in diameter, and located approximately 5 m apart. Burn treatments were conducted in mid-September of each year by BLM fire management personnel. Burn barrels that were 3.5 m in diameter (see Korfmacher et al. [2003] for a detailed description of the burn barrels) were placed around each designated treatment plot and standing vegetation within that plot was ignited with a propane torch. To ensure consistency between sites and to monitor treatment effects, peak fire temperatures were evaluated during the first two years of the study using two methods: (1) pyrometers, i.e., small copper tags striped with Tempilaq® temperature sensitive paints (Tempil, South Plainfield, N.J.) that were placed at the soil surface, 2 cm below the soil surface, and on top of the litter layer if one existed and (2) an infrared temperature gun (Omegascope OS530le) aimed at the base of the flames. Variability in burn temperatures was minimal and we stopped monitoring fire temperatures after the first two years.

Seeding was conducted in the fall immediately after the one-time litter removal on litter removed plots in 2008 and after all burn treatments on both litter intact and litter removed plots. Prior to seeding, cheatgrass seeds were collected adjacent to the study area for each site and cleaned to maximize number of filled seeds. Seeds of common wheat were purchased from Comstock Seed located in Gardnerville, NV. Standard tetrazolium tests (AOSA) were conducted on both species to determine seed viability (Peters 2000), which was 89% or higher in all years. For all seeded plots, furrows spaced 30 cm apart were cut into mineral soil across the entire plot. Furrows of plots seeded with cheatgrass were 2.5 cm deep while furrows seeded with common wheat were 4 cm deep, reflecting the different seed sizes and germination requirements of the two species. Seeds of both species were hand broadcast over the furrows in the appropriate plots at a rate of 600

Pure Live Seed per m². After the seeds were sown, the furrows were closed with a hoe. The plot was then rolled with a sod roller to ensure that the seed made good contact with the soil. It was assumed that the lack of procedural controls to test effects of litter removal and seeding treatments alone would not affect the response.

Sampling

Vegetation sampling periods included (1) mid-late June when peak biomass and seed production were measured, and (2) early-mid September when pre-burn biomass (fuel loads) were determined. In each sampling period, two quadrats (0.1 m²) were placed in each treatment plot in locations that had not been sampled previously.

In the mid-late June sampling period, cheatgrass and wheat density were counted, and aboveground biomass of cheatgrass, wheat, and all other species (referred to hereafter as other annual plant biomass) were harvested separately in all treatment plots. Other annual plant biomass was harvested and combined into one sample that included primarily the introduced annual forbs listed in the study area description. After aboveground biomass was harvested, litter was collected in all treatment plots. In the lab, cheatgrass samples were sorted into reproductive (filled and unfilled seeds) and vegetative biomass. Each portion of the cheatgrass samples, and the other biomass and litter samples, were then oven dried for 48 hours at 60°C and weighed. Viability of filled seed was assessed from a subsample (~200 seeds) from each site prior to drying. Average cheatgrass plant biomass and seed density per plant values were calculated by dividing total plot biomass and total plot seed density values by plant density within the plot.

In the pre-burn sampling period, aboveground vegetation and litter were collected a few days prior to the fall burns to assess pre-burn biomass as a measure of fuel loads. Aboveground biomass of all plants was harvested and combined into one sample and then litter was collected. Total vegetation and litter biomass were then oven dried and weighed, and the weights were summed to calculate total pre-burn biomass.

Plant root simulator (PRS) probes (Western Ag

Innovations, Saskatoon, Canada) were used to monitor soil N availability (NH_4^+ and NO_3^-) in each plot during two sampling periods in each year: (1) winter (post-burn in mid-September through mid-March) when annual plant germination and establishment may have occurred, but growth and N uptake are typically minimal, and (2) spring (mid-March through mid-June) when annual plant growth and N uptake is typically highest. Soil N availability was not monitored from mid-June to September because precipitation in our study area is minimal, annual plants have senesced, and N availability typically does not influence growth and reproduction. Probes consisted of either anion or cation exchange membranes embedded in plastic stakes. One set of probes (one anion and one cation probe) was placed in portions of the plots where there was no destructive vegetation sampling. After removal from the field, the probes were sent to Western Ag Innovations for extraction and analysis. The probes were extracted with 17.5 mL of 0.5 M HCl for one hour in a zipper closure bag, and the extractant was analyzed for NH_4^+ and NO_3^- using a Technicon autoanalyzer (Bran and Lubbe, Buffalo, NY). The values for both probes were reported in units of $\mu\text{g N}/\text{cm}^2$ of resin area/burial length (i.e., days in the ground) and were converted to $\text{ng N}/\text{cm}^2/\text{day}$. We summed NH_4^+ and NO_3^- to calculate total soil N availability.

Weather data

Weather data (monthly precipitation, maximum temperatures, and minimum temperatures) were gathered for each site in each of the study years (2008–2012) from the PRISM Climate Group (<http://prism.oregonstate.edu>) using the latitude/longitude of the sites. Maximum and minimum temperatures were calculated for each year and then averaged for the two sites. Precipitation was summed for the 10-month period that typically includes the life-cycle of cheatgrass (and other common annual plants) in these systems: from September 1 when fall germination occurs during favorable precipitation years through June 30 when seed maturation and senescence occurs. Precipitation also was averaged for the two sites.

Data analyses

Separate analyses were used for the litter intact

and litter removed experiments to examine main and interactive effects of burn and seeding treatments and years on (1) winter and spring soil N availability ($\text{NH}_4^+ + \text{NO}_3^-$), (2) mid-late June values of litter biomass, wheat biomass, other annual plant biomass, and cheatgrass density, biomass, and seed density per plot, and (3) mid-late June values of cheatgrass biomass and seed density per plant. The two experiments were analyzed using generalized linear mixed effects models (GLMM). An initial GLMM examined the interaction between burn and seeding treatments and site and indicated no significant differences in treatments among sites. Site was therefore used as a blocking factor in the models. Site and plots within sites were treated as random effects while burn and seeding treatments and year of sampling (year of burn for burned plots) were treated as fixed effects. The experimental unit was the sample from each period for each plot. All data were assessed and appropriate link functions were used to meet assumptions of normality and equality of variances. For results with significant effects, mean comparisons were performed using Tukey adjusted least square means for multiple comparisons and considered significant at the 95% confidence level ($\alpha = 0.05$). These mean comparisons are illustrated in the figures. All analyses were conducted using the GLIMMIX procedure in SAS version 9.3 (SAS Institute, Cary, NC).

Structural equation modeling

Structural equation modeling (Grace 2006) was used to evaluate our conceptual model (Fig. 1). The model included two environmental variables (growing season precipitation and winter minimum temperature), four restoration treatments (burning, litter removal, seeding with wheat, and seeding with cheatgrass), and eight response variables which had also been analyzed with GLMM (winter and spring soil N availability as well as mid-late June values of cheatgrass density, cheatgrass biomass, wheat biomass, litter biomass, and other annual plant biomass per plot, and cheatgrass seed density per plant). Cheatgrass biomass per plot was chosen to represent N uptake by the population and the potential for progressive N deficiency over time, while seed density per plant was selected to represent individual plant success (Chambers et

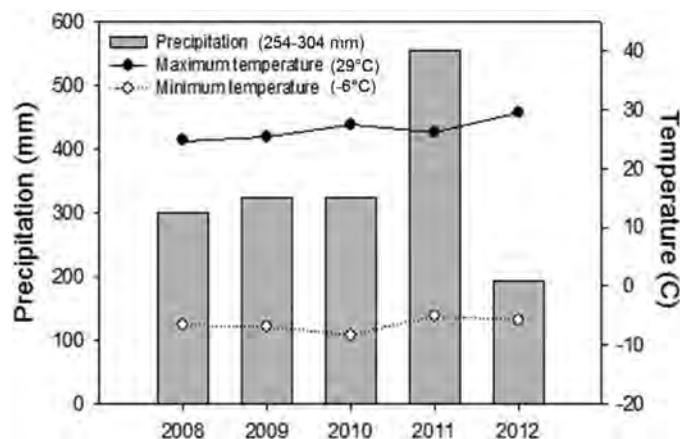


Fig. 2. Precipitation for the ten-month period that typically includes the life-cycle of cheatgrass in cold desert shrublands (September 1 through June 30) shown as bars, and annual minimum and maximum temperatures are illustrated by lines. Average precipitation and minimum and maximum temperatures for the study area are written in parentheses in the figure legend.

al. 2007). The model also included two additional explanatory variables: pre-burn biomass or fuel load, and previous year's cheatgrass seed density or the propagule pool. The GLMM analyses showed that the samples were reasonably independent of plots across years. Direct effects of one variable on another (one-headed arrows) were calculated as standardized regression coefficients, while correlative relationships in which both variables have an effect on each other (two-headed arrows) were calculated as Pearson's correlation coefficients (Sokal and Rohlf 1981). Indirect effects consisted of paths from one variable to another mediated by at least one additional variable and were calculated by summing regression coefficients. The most parsimonious model representing a subset of the full, hypothesized path model (Fig. 1) was determined using Amos 18.0 software (SPSS 2010); model fit was assessed using chi-square statistics and Root Mean Square Error of Approximation (RMSEA). Path coefficients were calculated to illustrate the direct relationships between variables.

RESULTS

Weather and fire temperatures

Mean precipitation during the period of cheatgrass germination and growth (September 1 through June 30) ranged from 148 to 595mm

(Fig. 2). The highest precipitation during this period was in 2011 and the lowest precipitation was in 2012. Minimum and maximum temperatures during this period also exhibited inter-annual variability with maxima ranging from 23° to 32°C and minimums ranging from -4° to -9°C.

Burning resulted in temperatures averaging 40°C at 2 cm below the soil surface, 66°C at the soil surface, and 59°C on top of the litter layer in litter intact plots. Temperatures were 42°C at 2 cm below the soil surface and 70°C at the soil surface in litter removed plots. Flame temperatures averaged 172°C in both litter intact and litter removed plots.

Effect of treatments on litter biomass and soil available nitrogen

Litter biomass exhibited a strong year by burn and seeding treatment interaction in litter intact and litter removed plots (Table 2; Fig. 3). Mean comparisons showed that unburned litter intact plots varied over time, but maintained higher litter biomass than all other treatments in almost all years (Fig. 3). Litter intact plots that were repeatedly burned lost 30–50% litter biomass in each year of the experiment regardless of seeding treatment, and had litter biomass in 2012 that was similar to plots where litter was initially removed. Litter removal in 2008 reduced initial litter biomass in litter removed plots to almost zero. Unburned litter removed plots slowly

Table 2. Results of GLMMs examining effects of burn and seeding treatment, time, and their interaction on soil, litter and plant measurements in litter intact and litter removed plots.

Metric	Burn/seeding		Year		Burn/seeding × Year	
	F	df	F	df	F	df
Litter intact plots						
Litter biomass	16.74***	3, 27	67.97***	4, 112	3.85***	12, 112
Winter soil N availability (NH ₄ ⁺ + NO ₃ ⁻)	6.59**	3, 27	12.7***	3, 82	1.28	9, 82
Spring soil N availability (NH ₄ ⁺ + NO ₃ ⁻)	2.19	3, 27	3.38*	3, 83	2.12*	9, 83
Cheatgrass density	12.89***	3, 27	11.97***	4, 112	3.01**	12, 112
Cheatgrass biomass per plot	9.02**	3, 27	23.14***	4, 112	3.14**	12, 112
Cheatgrass biomass per plant	3.82*	3, 27	4.13**	4, 112	2.55**	12, 112
Cheatgrass seed density per plot	6.45**	3, 27	43.6***	4, 112	2.5**	12, 112
Cheatgrass seed density per plant	4.38*	3, 27	19.33***	4, 112	2.93**	12, 112
Wheat biomass	N/A		4.76**	3, 29	N/A	
Other annual plant biomass	1.02	3, 27	15.09***	4, 99	2.10*	12, 99
Litter removed plots						
Litter biomass	39.02***	4, 34	7.60**	3, 105	4.51***	12, 105
Winter soil N availability (NH ₄ ⁺ + NO ₃ ⁻)	6.71**	4, 34	24.61***	3, 100	0.89	12, 100
Spring soil N availability (NH ₄ ⁺ + NO ₃ ⁻)	3.51*	4, 34	2.87*	3, 102	2.76**	12, 102
Cheatgrass density	12.51***	4, 34	13.83***	3, 104	1.23	12, 104
Cheatgrass biomass per plot	6.13**	4, 34	16.3***	3, 105	1.65	12, 105
Cheatgrass biomass per plant	3.18*	4, 34	6.53**	3, 104	1.46	12, 104
Cheatgrass seed density per plot	4.24**	4, 34	66.21***	3, 105	2.81**	12, 105
Cheatgrass seed density per plant	4.25**	4, 34	32.92***	3, 104	2.23*	12, 104
Wheat biomass	N/A		3.66*	3, 31	N/A	
Other annual plant biomass	3.40*	4, 34	15.14***	3, 100	1.00	12, 100

*p < 0.05; **p < 0.01; ***p < 0.001.

regained litter biomass throughout the experiment and had four times more litter biomass in 2012 than litter removed plots that were burned every year (Fig. 3).

The dominant form of total soil available N was NO₃⁻ and total soil N availability (NH₄⁺ + NO₃⁻) generally followed trends in NO₃⁻ in both winter and spring. Therefore, only total soil N availability is shown. Annual trends in winter soil N availability in both litter intact and litter removed plots were similar over time and among treatments (Table 2, Fig. 4). In general, winter soil N availability was higher in 2010 than 2009, but 2011 and 2012 levels were similar to those in 2009. Also, winter soil N availability was higher in burned than unburned plots regardless of seeding treatment.

Winter soil N availability was higher than spring soil N availability in all years in litter intact ($F_{3,214} = 9.96$, $p < 0.0001$) and litter removed plots ($F_{3,265} = 10.58$, $p < 0.0001$). Spring soil N availability in both litter intact and litter removed plots was generally similar among years for all burn and seeding treatments with a few exceptions (Table 2; Fig. 4). In 2009 in litter intact plots, spring soil N availability in burned only plots was higher than in unburned and

burned and seeded with wheat plots in 2012 in both litter intact and litter removed plots, spring soil N availability in plots that were burned and seeded with wheat was higher than in all other treatment plots.

Effect of treatments on cheatgrass (plot scale)

Cheatgrass density was significantly decreased by initial litter removal and was generally lower in litter removed plots than in unburned, litter intact plots throughout the study (Table 2, Fig. 5). In litter removed plots, overall density increased after treatment implementation through 2011 and then decreased in 2012. Few differences existed among treatments. Burned and seeded with wheat plots had lower overall densities than the other treatments in litter removed plots and, in 2009 through 2012, had lower densities than most of the other treatments in the litter intact plots.

Cheatgrass biomass and seed density at the plot scale followed the same general patterns over time (Table 2, Fig. 5). Except for litter removed, burned and seeded with cheatgrass plots, cheatgrass biomass was lower in litter removed plots than in unburned litter intact plots, and cheatgrass seed densities were lower

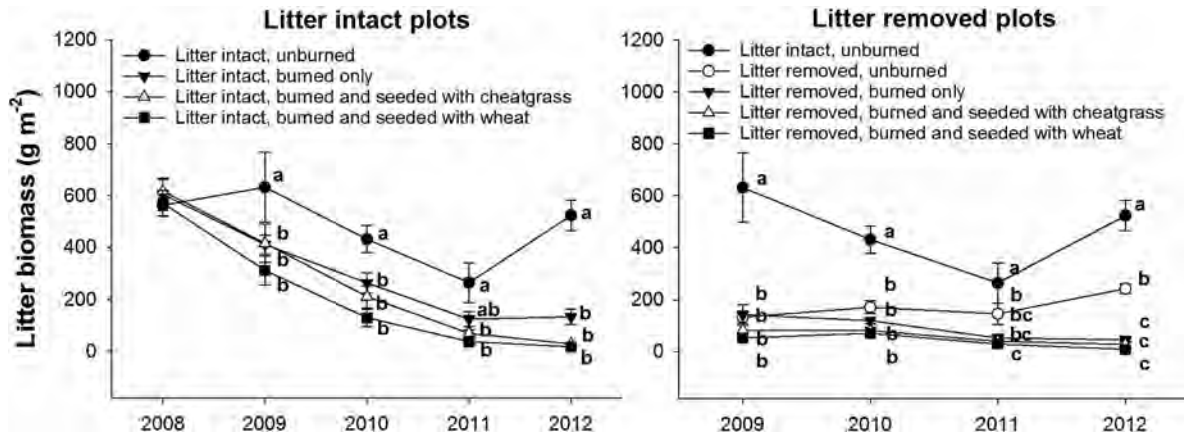


Fig. 3. Changes in litter biomass among study years and burn and seeding treatments in litter intact and litter removed plots. Bars indicate ± 1 SE and lowercase letters indicate significant differences among treatments within years ($p \leq 0.05$).

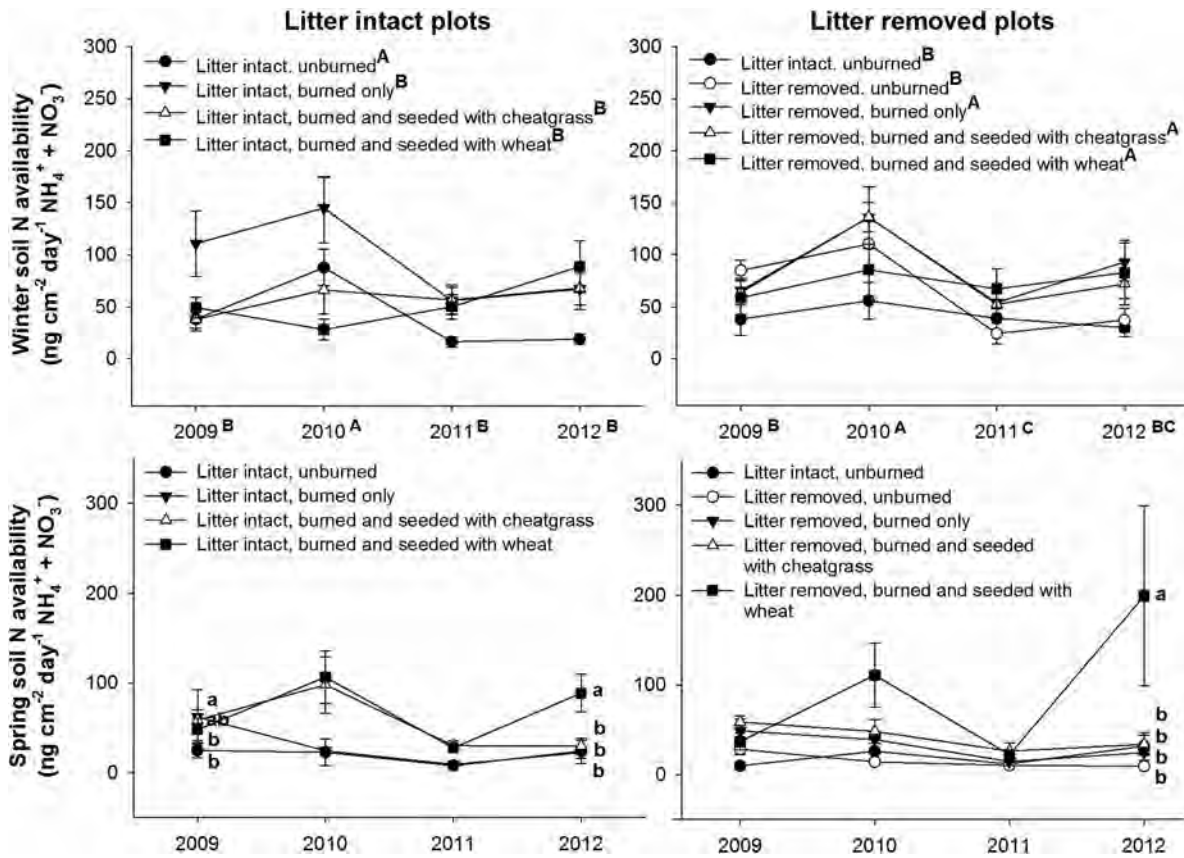


Fig. 4. Changes in winter (September–March) and spring (March–June) soil N availability among years and burn and seeding treatments in litter intact and litter removed plots. Bars indicate ± 1 SE. Lowercase letters next to lines indicate significant differences among treatments, compared separately for each year ($p \leq 0.05$). Upper-case letters written as superscripts in legend and along x-axis indicate significant main effects of treatments and year ($p \leq 0.05$).

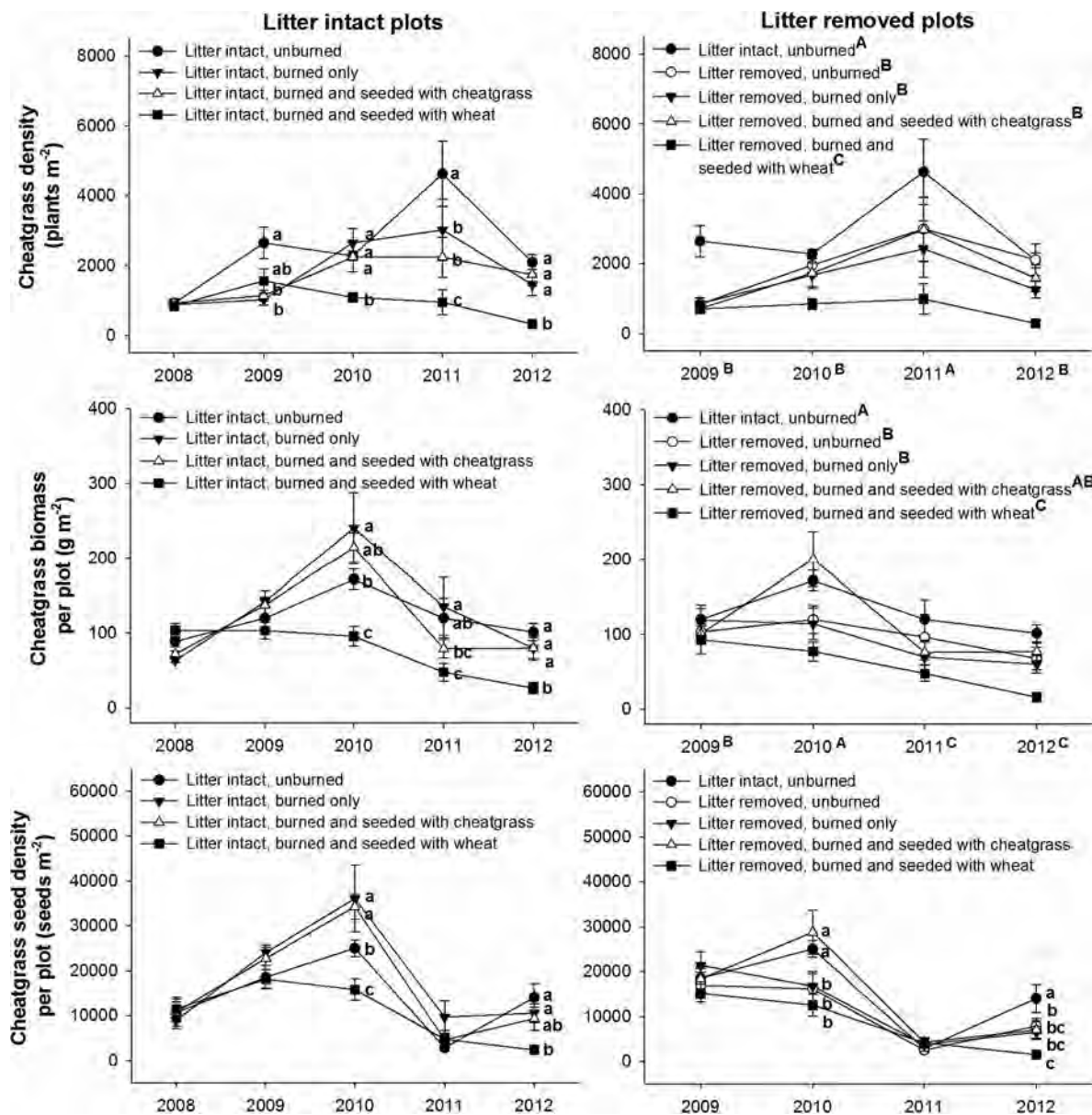


Fig. 5. Changes in cheatgrass density, biomass per plot, and seed density per plot among study years and burn and seeding treatments in litter intact and litter removed plots. Bars indicate + 1 standard error. Lowercase letters next to lines indicate significant differences among treatments, compared separately for each year ($p \leq 0.05$). Upper-case letters written as superscripts in legend and along x-axis indicate significant main effects of treatments and year ($p \leq 0.05$).

in litter removed plots than unburned litter intact plots in 2010 and 2012. Biomass and seed density in both litter intact and litter removed plots tended to increase after treatment implementation through 2010 and then decline in 2011 and 2012. In 2010, the high production year, biomass

and seed densities were highest in burned only and burned and seeded with cheatgrass plots in litter intact plots. Seed densities in 2010 were highest in unburned and burned and seeded with cheatgrass plots in the litter removed experiment. Plots that were burned and seeded

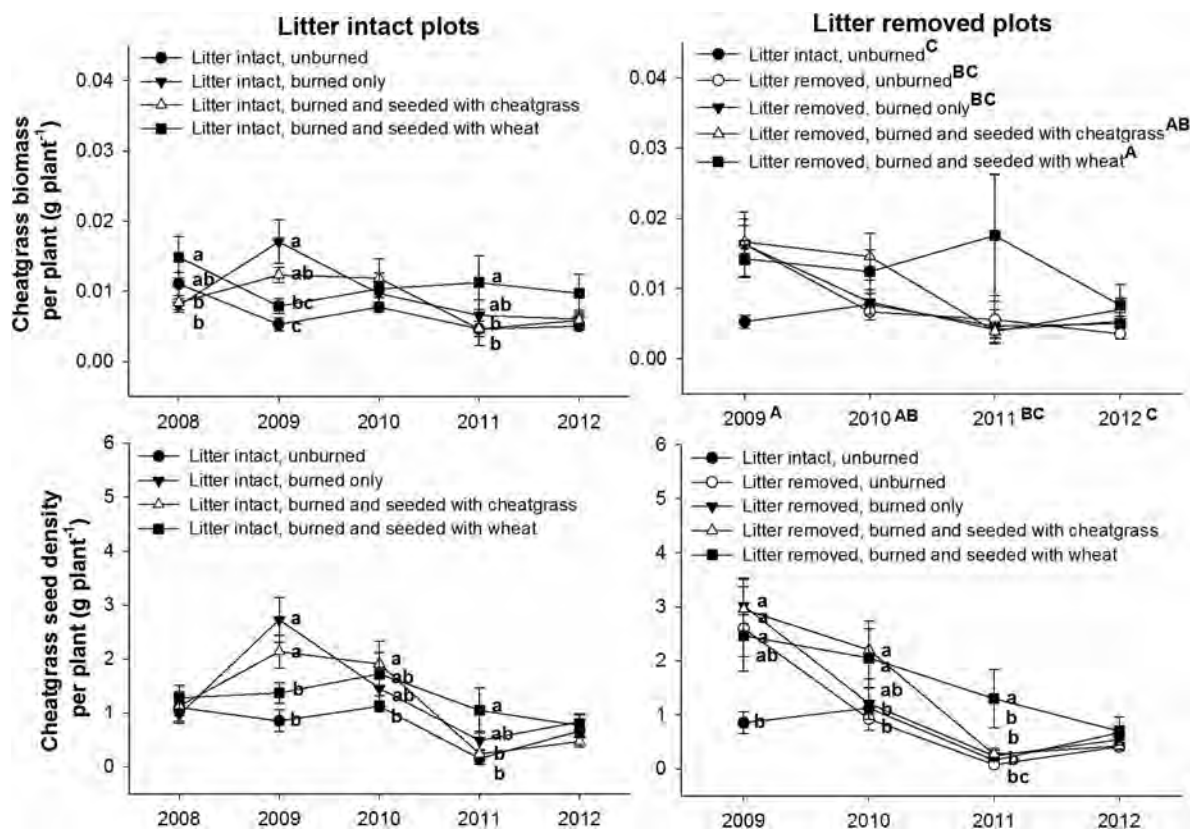


Fig. 6. Changes in cheatgrass biomass per plant and seed density per plant among study years and burn and seeding treatments in litter intact and litter removed plots. Bars indicate ± 1 SE. Lowercase letters next to lines indicate significant differences among treatments, compared separately for each year ($p \leq 0.05$). Upper-case letters written as superscripts in legend and along x-axis indicate significant main effects of treatments and year ($p \leq 0.05$).

with wheat had the lowest biomass overall in litter removed plots, and had the lowest biomass in 2010 and 2012 in litter intact plots. These plots also tended to have the lowest seed densities in both litter removed and litter intact treatments.

Effect of treatments on cheatgrass (plant scale)

Cheatgrass biomass and seed density per plant showed almost opposite trends to cheatgrass biomass and seed density per plot (Table 2, Fig. 6). Litter removal tended to result in higher overall biomass and in higher seed density than in litter intact, unburned plots. Overall plant biomass in litter removed plots was as high in 2009 as 2010 and was lowest in 2012. Plant seed density in litter removed plots showed a similar trend. In litter intact plots, a significant burn and seeding treatment by year interaction existed and

differences among years were less clear. Treatments that had the highest plant biomass and seed densities across years in both litter removed and litter intact plots were generally burned and seeded with wheat followed by burned and seeded with cheatgrass.

Effect of treatments on wheat and other annual plants

Wheat biomass in plots burned and seeded with wheat exhibited identical patterns in litter intact and litter removal treatments (Table 2; Fig. 7). Wheat biomass increased from 2009 to 2010 and was intermediate in 2011 and 2012.

Litter removal resulted in an increase in other annual plant biomass relative to litter intact, unburned plots for all treatments except burned and seeded with wheat (Table 2; Fig. 7). Overall

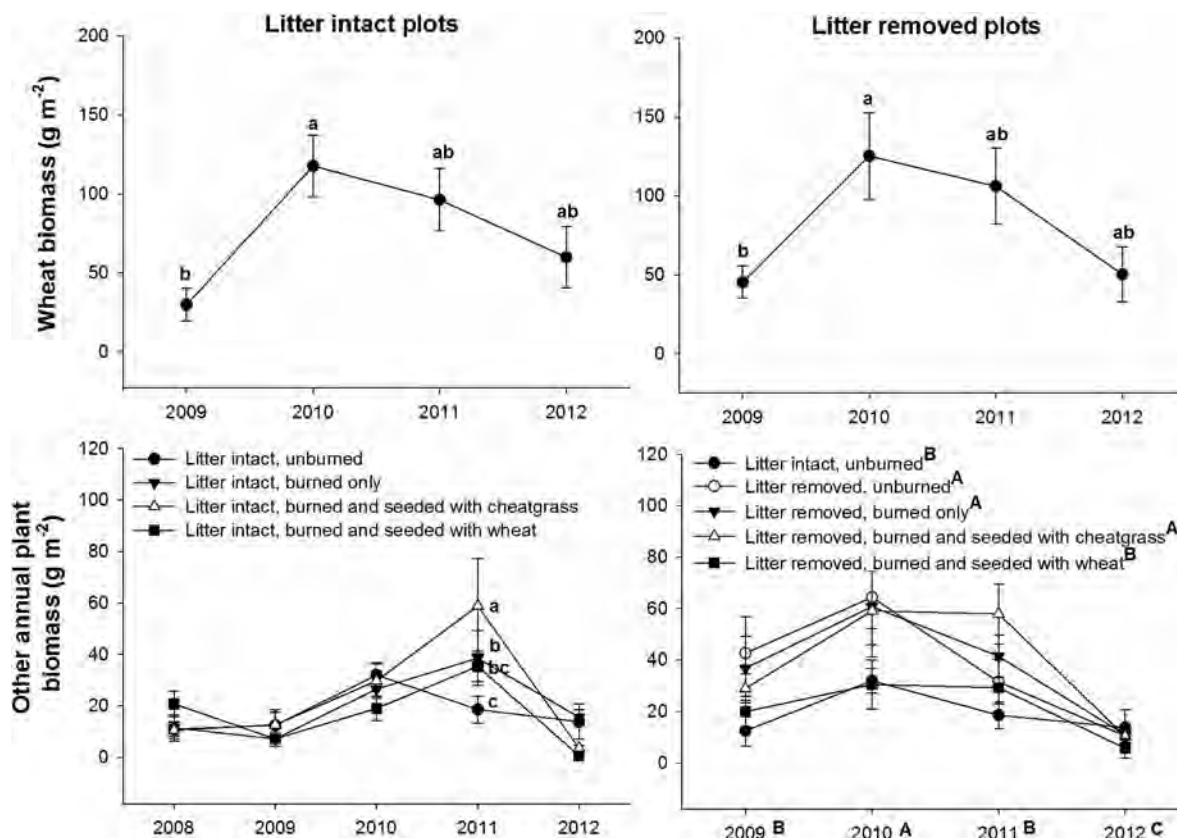


Fig. 7. Changes in wheat and other annual plant biomass among study years and, for other annual plant biomass, burn and seeding treatments in litter intact and litter removed plots. Bars indicate ± 1 SE. Lowercase letters next to lines indicate significant differences among treatments, compared separately for each year ($p \leq 0.05$). Upper-case letters written as superscripts in legend and along x-axis indicate significant main effects of treatments and year ($p \leq 0.05$).

biomass of other annual plants was highest in 2010 and lowest in 2012 in litter removed plots, but a year by burn/seeding treatment interaction existed for litter intact plots and differences among years were less clear. In the litter removed experiment, annual plant biomass was lowest in litter intact, unburned plots and in burned and seeded with wheat plots, and highest in unburned, burned only, and burned and seeded with cheatgrass plots. In the litter intact experiment, other annual plant biomass was lowest in unburned plots and highest in burned and seeded with cheatgrass plots but only in 2011 which received high precipitation.

Structural equation model

The final model included all of the factors from

the conceptual model, except for the cheatgrass seeding treatment which had no significant effects on any response variables (Fig. 8). Based on the path analyses, our treatments (litter removal, burning, and seeding with wheat) had both direct and indirect effects on our measured variables. Litter removal had a negative direct effect on litter biomass. Cheatgrass biomass per plot and seed density per plant were positively affected by litter biomass, and therefore litter removal had negative indirect effects on these variables. Similarly, wheat and other annual plant biomass were negatively affected by litter biomass, and therefore litter removal had positive indirect effects on these variables. Burning, expressed as number of burns in our model, had a large negative direct effect on litter biomass

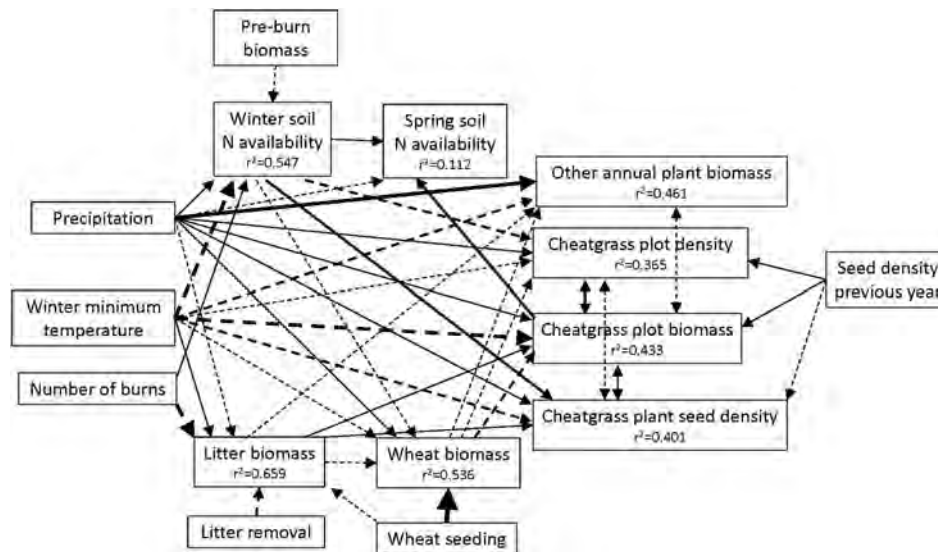


Fig. 8. Structural equation model of effects of weather variables and experimental treatments on winter soil N availability, spring N availability, litter biomass, wheat biomass, other annual plant biomass, and cheatgrass density, biomass per plot, and seed density per plant. Direct effects are indicated by one-headed arrows and correlations are indicated by two-headed arrows. Positive effects are indicated by solid lines and negative effects are indicated by dashed lines. Only significant paths are included. Line thickness corresponds to standardized regression weights. Squared multiple correlations (r^2 values) are included to indicate the fraction of variance of each dependent variable that is explained by the independent variables.

and, consequently, a negative indirect effect on cheatgrass biomass per plot and positive indirect effects on wheat biomass and other annual plant biomass. Burning had a small positive direct effect on winter soil N availability and, consequently, a negative indirect effect on cheatgrass density and a positive indirect effect on cheatgrass seed density per plant. Post-burn seeding with wheat had a positive direct effect on wheat biomass and a negative direct effect on litter biomass. Wheat seeding had negative indirect effects on cheatgrass density, cheatgrass biomass per plot, and other annual plant biomass, which were all negatively affected by wheat biomass.

Biotic factors outside of our treatments also affected our measured variables. Pre-burn biomass, which is a measure of fuel load, was generally higher in litter intact plots (data not shown) and had a negative direct effect on winter soil N availability. Seed density from the previous year, which represents the propagule pool, had positive direct effects on cheatgrass density and cheatgrass biomass per plot and a negative direct effect on cheatgrass seed density per plant.

Other annual plant biomass was negatively correlated with cheatgrass biomass per plot, but was not correlated with cheatgrass density or cheatgrass seed density per plant.

Precipitation received from September 1 through June 30 had positive direct effects on winter soil N availability, wheat biomass, other annual plant biomass, cheatgrass density, cheatgrass biomass per plot, and cheatgrass seed density per plant, but negative direct effects on litter biomass and spring soil N availability. Precipitation also had many indirect effects that were relatively small when compared to the positive effects of precipitation. Consequently, these effects were only discussed if the indirect effect was in opposition to the direct effect. Precipitation had negative indirect effects on wheat biomass and cheatgrass density, due to the effect of precipitation on winter soil N availability, and a negative indirect effect on cheatgrass biomass per plot, due to the effect of precipitation on litter biomass. Minimum winter temperatures had a positive direct effect on litter biomass and negative direct effects on winter soil

N availability, wheat and other annual plant biomass, cheatgrass density, cheatgrass biomass per plot, and cheatgrass seed density per plant. As with precipitation, minimum winter temperature also had many minor indirect effects that were only discussed if the indirect effect was in opposition to the direct effect. Minimum winter temperatures had positive indirect effects on wheat biomass and cheatgrass density, due to the effect of temperature on winter soil N availability, and positive indirect effects on other annual plant biomass and cheatgrass biomass per plot, due to the effect of temperature on litter biomass.

DISCUSSION

We identified mechanisms associated with treatments aimed at reducing soil N availability and cheatgrass success, and evaluated the efficacy of these treatments for restoring sagebrush ecosystems. Structural equation modeling revealed that a multivariate approach was necessary to clarify effects of treatments and abiotic environmental factors (precipitation and temperature) on N availability and plant performance. Results of the path analyses were generally consistent with the GLMMs, and illustrated the importance of direct and indirect effects in determining treatment outcomes. However, not all of our results were consistent with the hypothesized mechanisms (Table 1), indicating the importance of critical tests of resource limitation hypotheses for focal ecosystems.

Repeated burning effects

We found that cheatgrass biomass and seed density, both per plot and per plant, generally tracked winter soil N availability over time, reaffirming that cheatgrass is highly responsive to changes in soil N availability and exhibits a high degree of plasticity in plant size and seed production (Chambers et al. 2007, Mazzola et al. 2011). However, our hypothesis that repeated burning would result in progressive N deficiency (Rau et al. 2007) was not supported. Winter soil N availability was higher than spring soil N availability in all years, especially in burned plots, likely due to predicted SOM denaturation and greater plant N uptake during the spring period (Neary et al. 1999). However, soil N

availability in burned plots was never lower than pre-burn levels. Surface soil temperatures during burns never exceeded 70°C and flame temperatures never exceeded 180°C on either litter intact or litter removed plots. Although higher fire temperatures and more short-term N mobilization and volatilization can occur in sagebrush ecosystems with woody fuels (Johnson et al. 2011), fire temperatures in our study were typical of those in annual grass dominated systems (Brooks 2002), and were likely too cool to result in complete or even partial volatilization of N (volatilization temperature of 200°C; Raison et al. 1985) from mineral soils or aboveground biomass (Jones et al. 2015).

Repeated burning did significantly decrease litter biomass over time, but contrary to our hypothesis, there was generally no difference in soil N availability between litter intact and litter removed plots. A key function of litter consists of releasing nutrients to the soil through decomposition (Ogle et al. 2003, Sperry et al. 2006, Norton et al. 2008). Litter mats may enhance net N mineralization by increasing soil moisture and modulating extreme temperatures (Facelli and Pickett 1991, Newingham et al. 2007, Wolkovich et al. 2009). The litter removal treatment, which involved raking the litter from the soil surface, may have resulted in sufficient disturbance of the soil surface to cause a small, short-term increase in N availability, thus offsetting the potential initial decrease in N availability due to litter removal (Vitousek et al. 1997).

Litter effects

The litter removal treatment did have a significant negative effect on cheatgrass plot biomass and plant seed density as predicted, but this was likely due to the effect of litter on cheatgrass seed entrapment and retention and on plant establishment and growth rather than N mineralization. Litter can increase plant establishment by preventing movement of surface soils and seeds, providing shade and insulation, and moderating soil temperatures (Chambers and MacMahon 1994, Chambers 2000, Wolkovich et al. 2009) and has been shown to increase cheatgrass success (Evans and Young 1984, Norton et al. 2008). Dense litter mats, such as those produced by cheatgrass, can trap most seeds but they typically prevent large seeded

species from reaching mineral soil to germinate and small-seed species from emerging through the dense litter due to insufficient energy reserves. Because cheatgrass has long awns, it can work through litter and gain an advantage in germination and growth (Stewart and Hull 1949). However, cheatgrass has short-lived seeds (2–3 years) and the majority of the seed bank is stored in the litter or on the soil surface (Thill et al. 1984). Removal of the litter mat and raking the soil surface likely removed most of the cheatgrass seed bank.

Seeding and competitive effects

Post-burn seeding and competition from wheat and other unseeded annual plants influenced cheatgrass success largely as predicted. Plots seeded with wheat after burns generally had the lowest cheatgrass density, biomass, and seed density per plot, and cheatgrass plants were typically limited to areas between the rows of wheat. Soil N availability in wheat seeded plots generally did not differ from other treatments, except in 2012 when spring soil N availability was elevated due to poor wheat establishment (Fig. 7). Thus, other soil nutrients or soil water may have been more limiting than soil N availability. Although invasive annual grasses often have higher nutrient use efficiency than other species, they do not appear to have higher water use efficiency (Funk and Vitousek 2007, James et al. 2011) and cheatgrass may have been negatively affected by competition with wheat for soil water. Also, plots seeded with wheat may have had lower cheatgrass success due to reduced litter biomass and lower seedling establishment. Other annual plant biomass was negatively correlated with cheatgrass biomass per plot, and this relationship was likely due to direct competition for soil resources. Nutrients, particularly NH_4^+ , in cold desert shrublands are most available to plant roots in shallow soil depths when soil water is high enough to facilitate diffusion to root surfaces (Ryel et al. 2010). Cold-adapted annuals in these systems generally utilize soil water and nutrients from this same resource pool (Ryel et al. 2010). Disturbances like fire that reduce litter and cheatgrass seed density and increase available soil nutrients and water can shift the competitive balance in favor of invasive annual forbs (Ducas

et al. 2011, Chambers et al. 2014b).

Treatment effects of soil available N differed depending on whether cheatgrass variables were measured on a plant versus plot basis. Cheatgrass density was positively correlated with plot biomass, but negatively correlated with seed density per plant as observed in other research on cheatgrass (Mazzola et al. 2011). Negative correlations between population size and individual plant size and reproduction can be attributed to intraspecific competition and self-thinning (Yoda et al. 1963, White et al. 2007, Deng et al. 2008); biomass of individual plants within a population increases until a size-dependent critical density is reached where all available resources are exploited, and further growth is possible only if mortality increases resource availability (White et al. 2007). Also, the peak in cheatgrass density lagged behind the peak in plot biomass and seed density, likely as a result of increases in propagule availability and effects of intraspecific competition over time (Humphrey and Schupp 2001, Mazzola et al. 2011). Thus, all available resources are likely utilized by individual plants well before peak plant and seed bank densities are reached. Measuring plant variables on a plot versus plant basis and at different intervals following treatment can influence interpretation of study results, and may partly explain differences in interpretations of the effects of resource manipulation on invasive annual grasses between greenhouse experiments that measure plant variables and field studies that largely measure plot variables.

Environmental effects

Long-term trends in soil N availability and cheatgrass success were most strongly influenced by weather. High winter minimum temperatures resulted in low winter soil N availability and overall low cheatgrass success while high precipitation resulted in high winter soil N availability, cheatgrass success, and other annual plant biomass. Warmer temperatures can increase microbial activity, which in turn increases plant litter and SOM decomposition (Fierer et al. 2005) and net N mineralization (Rustad et al. 2001). However, temperature effects on plant litter and SOM decomposition are strongly influenced by soil water availability (Dijkstra

and Cheng 2007, Moyano et al. 2013) and net N mineralization and soil N availability generally increase with increasing soil water availability (Cui and Caldwell 1997, Fierer and Schimel 2002, Borken and Matzner 2009). Higher soil N and water availability in years with high precipitation and low minimum winter temperatures resulted in greater success of cheatgrass as expected for this winter annual (Hardegee et al. 2003, Roundy et al. 2007).

Synthesis

Our study provides insights into the mechanisms influencing resource availability and cheatgrass success and into approaches for restoring pre-invasion nutrient cycles. Due to cool fire temperatures that do not volatilize biomass N and only partially consume litter mats (Jones et al. 2015), repeated burning is unlikely to decrease soil N availability in cheatgrass-dominated systems. In fact, cool wildfire temperatures that have minor effects on soils but increase N availability in cheatgrass-dominated systems may provide further explanation for the success of cheatgrass invasions. Repeated burning did decrease litter biomass over time. Litter biomass had positive direct effects on cheatgrass plot and plant variables as found elsewhere (Evans and Young 1984, Norton et al. 2008), and initial amount of litter should be considered when evaluating if restoration practices like seeding will succeed. Also, seeding with a competitor, annual wheat, significantly decreased cheatgrass and other plant biomass at the plot scale, likely due to competition for water resources. Thus, seeding with an annual competitor may be a highly useful component of an overall restoration approach.

In this semi-arid ecosystem, weather, specifically precipitation and minimum winter temperature, had the strongest effects on soil N availability and cheatgrass success over time. Higher soil water availability in wet years coupled with warmer winter temperatures provide favorable conditions for plant litter and SOM decomposition and N mineralization, as well as germination and growth of cheatgrass. Studies evaluating effects of N manipulations should monitor weather variables and soil water availability and examine differences among years.

Our results show that integrated restoration approaches that decrease litter biomass and seed banks and increase competitive interactions may be more effective at reducing invasive annual grasses and establishing desirable perennial species than approaches that attempt to manipulate soil N directly. A successful integrated restoration approach may include reducing litter through repeated burning (Jones et al. 2015) or through prescribed grazing (Frost and Launchbaugh 2003), seeding with sterile cover crops like common wheat to decrease cheatgrass reproduction and, thus, seed banks, and then seeding the desired native perennial species. Monitoring treatment outcomes is an important component of an integrated restoration strategy in semi-arid ecosystems, and on sites with low and variable precipitation, more than one intervention may be needed to achieve restoration success.

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