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REGULAR ARTICLE

Effect of repeated burning on plant and soil carbon and nitrogen in cheatgrass (*Bromus tectorum*) dominated ecosystems

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Abstract
Background and Aims Fire has profound effects on ecosystem properties, but few studies have addressed the effect of repeated burns on soil nutrients, and none have been conducted in cold desert ecosystems where invasion by exotic annual grasses is resulting in greater fire frequency.
Methods In a 5 year study, we examined effects of repeated burning, litter removal, and post-fire seeding on carbon (C) and nitrogen (N) contents in soils, litter, and vegetation in a cheatgrass-dominated Wyoming big sagebrush ecological type. We developed a multivariate model to identify potential mechanisms influencing treatment effects and examine the influence of environmental factors such as precipitation and temperature.
Results We found that repeated burning had strong negative effects on litter C and N contents, but did not reduce soil nutrients or vegetation C and N contents, likely due to cool fire temperatures. There were few effects of litter removal or post-fire seeding. Instead, precipitation and temperature interacted with burning and had the strongest influences on soil N and vegetation C and N contents over time.
Conclusions Management strategies aimed at decreasing litter and seed banks and increasing competitive interactions may be more effective at reducing cheatgrass success than approaches for reducing soil nutrients.

Keywords Cold desert · Invasive annual grasses · Repeated fire · Restoration · Sagebrush · Shrublands

Abbreviations
TMN Total mineral nitrogen

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Introduction

Invasive annual grasses have global effects on fire regimes, plant community composition, and ecosystem processes (Brooks et al. 2004; D'Antonio and Vitousek 1992). Many ecosystems, like North American cold desert shrublands, are exhibiting more frequent fires largely due to invasion of annual grasses and changes in fuel type and continuity (Brooks et al. 2004; D'Antonio and Vitousek 1992; Link et al. 2006). Many native species are intolerant of fire and progressive conversion to invasive annual grass dominance is occurring in low to mid-elevation shrubland types (Chambers et al. 2014). Conversion of cold desert shrublands to invasive annual grasses changes soil physical and chemical properties (Blank et al. 2013) and alters ecosystem processes including soil water flux and storage (Wilcox et al. 2012), nutrient cycling (Rau et al. 2011), and carbon (C) storage (Bradley et al. 2006; Bradley and Mustard 2005). Many of these changes may be creating positive feedbacks that promote further invasion.

Fire may promote annual grass invasion, but also may be an important restoration tool (Baker 2006). Restoration of areas dominated by invasive annual grasses is often difficult because annual grasses such as cheatgrass (*Bromus tectorum*) are highly competitive with seedlings of both native species and introduced cultivars (James et al. 2011; Monaco et al. 2003). Restoration success in these areas depends on reducing competition from cheatgrass. Many methods have been employed to decrease cheatgrass abundance (i.e. prescribed grazing, herbicides, etc.), but effective long-term strategies require reducing the resources available for cheatgrass growth and reproduction. High resource availability, in particular soil mineral nitrogen (N), generally increases cheatgrass success (Chambers et al. 2007; Norton et al. 2004), and decreasing resource availability by restoring a pre-invasion N cycle can reduce the competitive advantage of cheatgrass and favor native species (Blumenthal et al. 2003; Brunson et al. 2010; Mazzola 2008). Repeated burning may be a viable approach for reducing available nutrients and an important component of an integrated restoration strategy.

The influence of burning on soil N is highly dependent on fire severity and frequency. Soil mineral N may temporarily increase following fire due to heat-induced denaturing of soil organic N compounds and increased N mineralization rates (Fig. 1a; Blank et al. 1994; Johnson et al. 2011; Neary et al. 1999) and mineral N may remain elevated for one or more years post-fire (Rau et al. 2007; Stubbs and Pyke 2005). However, frequent fires may ultimately lead to long-term decreases in soil N through progressive nitrogen deficiency. Post-fire pulses in soil nutrients stimulate plant growth and N uptake (Johnson et al. 2011; Monaco et al. 2003) and nutrients contained in biomass can be volatilized in subsequent burns and lost from the system (Fig. 1b). Volatilization of NO_x and NH_3^- from soils can result in further declines in N (Blank and Norton, personal communication; Dodds et al. 1996; Fynn et al. 2003). Unless this volatilized N is replaced by atmospheric deposition, N-fixation, or fertilization, the loss of N from organic material can cause long-term declines in soil mineral N and soil total N contents over time (Fig. 1a and c; Neary et al. 1999; Raison et al. 1985). Repeated burning has caused significant reductions in soil mineral N in pine forests (Binkley et al. 1992; Wright and Hart 1997) and perennial grasslands (Blair 1997; Johnson and Matchett 2001; Ojima et al. 1994); however, no information is currently available on effects of repeated burning in cold desert shrublands.

Soil C contents also can decrease in response to burning (Fig. 1). High severity fires in which temperatures exceed 200 °C can cause C to be volatilized from soils and aboveground biomass (Fig. 1b; Neary et al. 1999; Raison et al. 1985). These decreases in soil C stocks after fire are often long-lived due to removal of fire-intolerant shrubs and trees, which store large amounts of C above- and below-ground (Jackson et al. 2002; Jobbagy and Jackson 2000). Following conversion to annual grass dominance in cold desert shrublands, C contents often increase in near surface soils because annual grasses typically have more roots than shrubs at shallow depths (Ogle et al. 2004). Concentration of C in surface soils increases the potential for future losses of C due to volatilization of organic matter in subsequent fires and topsoil erosion (Fig. 1c; D'Antonio and Vitousek 1992).

Long-term effects of repeated fires on C and N pools can be influenced by several environmental variables, particularly litter accumulation and weather. Replacement of native perennial bunchgrasses by annual grasses such as cheatgrass in cold desert shrublands has significantly increased aboveground litter biomass, often creating continuous and homogeneous litter mats (Booth et al. 2003; Evans et al. 2001; Norton et al. 2004). Accumulated litter typically elevates fuel loads and decreases fire-return intervals (D'Antonio and Vitousek 1992; Knapp 1996; Link et al. 2006). However, depending on its thickness, litter also can act as an insulator and dampen the effects of fire on soil C and N transformations (Facelli and Pickett 1991). Precipitation and temperature interact with litter and influence nutrient

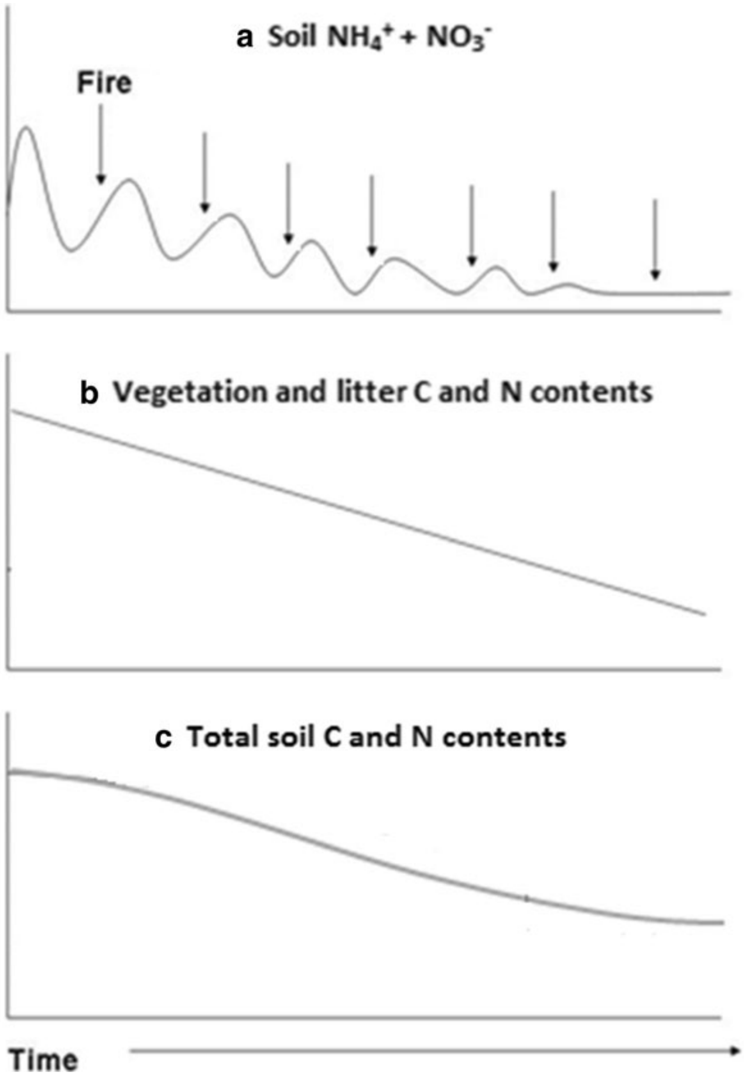


Fig. 1 Hypothesized changes in **a** soil mineral N pre- and post-burn, **b** vegetation and litter C and N contents at peak biomass, and **c** total soil C and N contents at peak biomass over time with repeated burning. *Arrows* in soil mineral N diagram indicate fires

cycling in semi-arid soils. Increased soil water and warmer temperatures typically increase litter and soil organic matter decomposition (Dijkstra and Cheng 2007; Moyano et al. 2013) and net N mineralization (Borken and Matzner 2009; Fierer and Schimel 2002).

Understanding the effects of fire on C and N pools in invaded cold desert shrubland ecosystems could be key to developing effective management strategies. We developed a multivariate conceptual model of likely effects of repeated burning and important environmental variables (precipitation, temperature, and litter) on soil mineral N and litter and vegetation C and N contents in cold desert shrublands (Fig. 2). The hypothesized mechanisms associated with the paths in the conceptual model were identified based on a priori knowledge from the literature (Table 1). We used a 5 year field study to examine the effects of repeated burning, litter removal, and post-fire seeding with cheatgrass and common wheat (*Triticum aestivum*) on C and N contents in soils, litter, and vegetation. A Wyoming big sagebrush ecological site type was chosen as our study system because this type has exhibited the highest rate of conversion to cheatgrass-dominance. Our analyses addressed two questions: (1) What are the immediate and long-term effects of the treatments on soil mineral N, soil C and N contents, and vegetation and litter C and N contents? and (2) How do environmental factors (precipitation and temperature) influence long-term trends in soil mineral N, soil C and N contents, and vegetation and litter C and N contents? Generalized Linear Mixed-effects Models

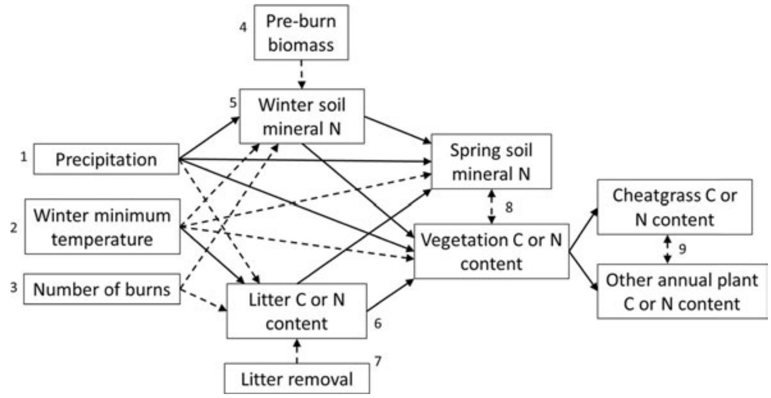


Fig. 2 Path diagram for effects of weather variables and experimental treatments on post-burn and spring soil mineral N, litter N content and vegetation N content. Direct effects are indicated by *one-headed arrows* and correlations are indicated by *two-headed arrows*. Positive effects are indicated by *solid lines* and negative effects by *dashed lines*. Components of the overall hypotheses are described in Table 1

(GLMMs) were used to examine differences in C and N contents among treatments and across time in litter intact and litter removed plots. Structural equation modeling (SEM) was used to evaluate the component hypotheses identified in the conceptual model (Grace 2006; Grace et al. 2009). Implications of the study results for integrated restoration strategies are discussed.

Materials and methods

Study area

Two study sites were located in Humboldt County, Nevada on Bureau of Land Management (BLM) administered land. The Orovada site is located at 1,402 m (436294E, 4598553N), while the Eden Valley site is located at 1,524 m (466314E, 4564313N). Soils at both sites are well-draining, alluvial deposits comprised of fine sandy loams (Denny 2002). The 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 temperatures at these sites typically range from 19 °C in July to −1 °C in January (National Climate Data Center, Coop Id #265818 and #266005, 1970–2010). Both sites are located in the 254–304 mm precipitation zone and most of the 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 characterized as a Wyoming big sagebrush ecological type, dominated by the shrub *Artemisia tridentata* subsp. *wyomingensis*, perennial bunchgrasses including *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 (Charlie Clements, personal communication). 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 study was comprised of two closely related experiments that examined effects of repeated burning on plant and soil C and 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 a year prior to the first burn. Both experiments used a randomized, complete block design. Blocks 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 - unburned litter intact, unburned litter removed, burned only and litter removed, burned and seeded with

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 (Borken and Matzner 2009; Fierer and Schimel 2002). Soil water and N availability are closely coupled in arid and semi-arid systems and together will have a positive effect on plant germination, N uptake, and plant growth/C content (Leffler and Ryel 2012).
2	Low winter temperatures are associated with lower decomposition (Hobbie 1996; Knorr et al. 2005), less mineralization (Rustad et al. 2001), and reduced or delayed plant N uptake and plant growth/C content.
Repeated Burning Effects	
3	Initial effects of repeated burning are a pulse in soil N availability due to heat-induced SOM denaturation (Neary et al. 1999; Raison et al. 1985). 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 and should decrease aboveground C and N contents over time.
4	Fire temperatures in arid ecosystems are strongly affected by type and amount of fuel, with hotter fires occurring in areas with woody fuels and high biomass (Brooks 2002). Hotter fires will result in increased volatilization of above- and belowground N and C (Blair 1997; Neary et al. 1999; Raison et al. 1985) and decreased soil N availability and C contents.
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/C content (Leffler and Ryel 2012). High soil N availability in the winter should carry into the spring.
Litter Effects	
6	Dense litter mats increase soil temperatures, promoting SOM decomposition and soil N availability (Facelli and Pickett 1991), and increase soil moisture, promoting net N mineralization (Facelli and Pickett 1991; Sperry et al. 2006). Dense litter mats also cause seed entrapment and retention (Chambers 2000). Both effects will increase plant success and C and N contents.
7	Litter removal will result in a 3–5 year window of reduced litter biomass.
Seeding and Plant Effects	
8	Vegetation N uptake should decrease soil N availability at peak biomass.
9	Other annual plant C and N content should be negatively correlated with cheatgrass C and N content due to competition (Chambers et al. in press).

cheatgrass and litter removed, and burned and seeded with common wheat and litter removed. The two experiments shared untreated, control plots (unburned litter intact) in order to track natural variation over the course of the study. Each burn and seeding treatment was replicated four times in each experiment and block for a total of 32 treatment plots in the litter intact experiment and 40 treatment plots in the litter removed experiment.

The effects of repeated burning were evaluated pre- and post-burn and at peak biomass production with a Before/After/Control/Impact (BACI) design. 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). 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 the 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 2 years of the study using two methods: 1) pyrometers, i.e., small copper tags striped with Tempilaq® temperature sensitive paints (Tempil, Inc., S. Plainfield, N.J.), 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 2 years.

Seeding was conducted in the fall immediately after the one-time litter removal treatment on the litter removed plots in 2008 and after the 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 annually 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 the 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 (PLS)/m^2. 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.

Sampling

Each plot was divided into two sampling sections - one quarter was reserved for non-destructive sampling and the remaining three quarters were reserved for destructive sampling. Two quadrats (0.1 m^2) were placed in the destructive section in locations that differed with every sampling period to evaluate changes in 1) vegetation biomass and nutritional content, 2) litter biomass and nutrient content, and 3) soil nutrients from extracted soil samples. Samples were taken during peak biomass (mid-late June) and both pre- and post-burn (early-mid September).

Every year, aboveground vegetation and litter were collected from within two quadrats in the destructive section of all treatment plots during the period of peak production just prior to seed dispersal (mid-June). Prior to each burn (early September), vegetation and litter were collected from two additional quadrats. Immediately following each burn (mid-September), litter and ash biomass were collected from two additional quadrats. All samples were returned to the laboratory, oven dried at 60 ° C and weighed. A subsample of each of these samples was analyzed for carbon (C) and N content using a LECO TruSpec CN Analyzer (LECO Corp., St. Joseph, MI, USA) calibrated with a certified EDTA standard (41.02%C and 9.57%N).

Soil samples were taken from each plot to monitor soil N availability during the study. These samples were collected at peak production (early June), prior to the burn treatment (early September), and immediately after the burn treatment (mid-September) from the center of the two quadrats used for destructive vegetation sampling. Following vegetation and litter collection, approximately 100 g of soil was collected to a depth of 5 cm using a trowel and then returned to the laboratory where it was analyzed for available mineral N (NH_4^+ and NO_3^-) using the KCl extraction method (Keeney and Nelson 1987) and quantification using a Lachat® autoanalyzer. The values were reported in units of mmol/kg and were converted to g N/m^2. We summed NH_4^+ and NO_3^- to calculate soil-extracted total mineral N (TMN). In addition, in 2008, 2009, and 2012, a separate portion of the 0–5 cm soil sample was oven-dried, finely ground, and analyzed for %C and %N by dry combustion using a LECO TruSpec CN Analyzer (LECO Corp., St. Joseph, MI, USA) calibrated with a certified soil standard (1.30%C, 0.130%N). The values were reported on an oven-dry mass basis and then converted to g C or g N per m^2.

Plant root simulator (PRS) probes were used to monitor soil NH_4^+ and NO_3^- in each plot during two sampling periods each year - winter (following the burns in mid-September through mid-March) and spring (mid-March through mid-June). Probes consist of anion and cation exchange membranes imbedded separately in plastic stakes. Two probes were placed in the non-destructive section of each plot and, after removal from the field, were sent to Western Ag Innovations (Saskatoon, Canada) for extraction and analysis. At Western Ag, the probes were extracted with 17.5 mL of 0.5 M HCl for 1 h in a zip lock bag, and the extractant was analyzed for NH_4^+ and NO_3^- using a Technicon autoanalyzer (Bran and Lubbe, Inc., Buffalo, NY). The values for both probes were reported in units of μg N/cm^2 of resin area/burial length (i.e. days in the ground) and were converted to ng N/cm^2/sampling period. We summed NH_4^+ and NO_3^- to calculate PRS-extracted TMN. Winter PRS-extracted TMN was chosen for use in conceptual models as the indicator of post-burn soil TMN because, unlike the soil-extracted TMN, it was summed over units of time that were biologically relevant for plants (directly after each burn through mid-March of the following year).

Weather data

Weather data (monthly precipitation, maximum temperatures, and minimum temperatures) were obtained for both sites 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 ten-month period that typically includes the life-cycle of cheatgrass in these systems – from September 1 when fall germination occurs during favorable precipitation years through June 30 when seed maturation occurs. This precipitation was then averaged for the two sites.

Statistical analyses

Separate analyses were used for the litter intact and litter removed experiments to examine the immediate and long-term effects of repeated burning, litter removal, and post-fire seeding on soil-extracted TMN, soil C and N contents, and litter and vegetation C and N contents. For analysis of the immediate effect of burning, the two experiments were analyzed using GLMM. The blocking factor of site was treated as a random effect. The burn and seeding treatments were treated as fixed effects within each site, and plots within sites were treated as random effects. The period of sampling (pre- or post-burn) 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. The analyses of the long-term effects of repeated burning used the same basic analysis; however, period was not included as a fixed effect because there was only one sampling period (peak production). All data were assessed and appropriate link functions were used to meet assumptions of normality and equality of variance. 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 (α=0.05). All analyses were conducted using the GLIMMIX procedure in SAS ver. 9.3.

Structural equation modeling

Structural equation modeling (Grace 2006) was used to evaluate our conceptual model (Fig. 1). Litter and vegetation C and N contents were strongly correlated, and we only show the final model using N contents. Model results using C contents were highly similar. Precipitation from September 1 through June 30 and minimum winter temperature were chosen for use as environmental variables in the model because they were both likely environmental predictors of the study variables. Post-fire seeding was not included in the model because it did not have significant effects on the variables in the GLMMs. Direct effects of one variable on another (one-headed arrows) were calculated as standardized regression coefficients while correlative relationships (two-headed arrows) were calculated as Pearson's correlation coefficients (Sokal and Rohlf 1981). Indirect effects consist of paths from one variable to another mediated by at least one additional variable and were calculated by summing regression coefficients. Evaluation of the conceptual model was determined using Amos 18.0 software (SPSS 2010) and models were assessed using chi-square statistics and the Root Mean Square Error of Approximation (RMSEA), which are complementary measures of model fit. The most parsimonious model (Fig. 10), representing a subset of the full, conceptual model (Fig. 2), was selected based on model fit variables.

Results

Weather

Mean precipitation during the period affecting cheatgrass germination and growth (September 1 through June 30) was highly variable and ranged from 148 to 595 mm (Fig. 3). 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 maximums 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, 70 °C at the soil surface, and 62 °C on top of the litter layer in litter removed plots. Flame temperatures averaged 172 °C and did not differ between litter intact and litter removed plots.

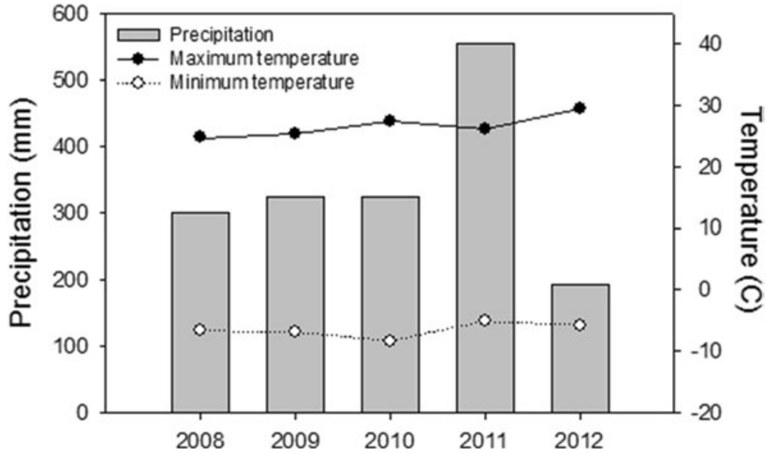


Fig. 3 Average annual precipitation (September 1 through June 30) shown as *bars*, and annual minimum and maximum temperatures illustrated by *lines*

Pre- and post-burn responses to treatments

Vegetation and litter C and N contents

Total vegetation and litter C contents exhibited a year by period interaction in litter intact and litter removed plots (Table 2; Fig. 4). In litter intact plots, C contents were lower in post-burn than pre-burn periods in all years ($p<0.01$). Also, C contents generally decreased across time in both pre- and post-burn periods ($p<0.04$). In litter removed plots, vegetation and litter C contents were lower in post-burn than pre-burn periods in all years ($p<0.03$). Carbon contents in pre-burn periods did not differ in the first 2 years of the study, but decreased in 2011 ($p<0.02$). Carbon contents in post-burn periods were higher in 2010 than 2009, then

Table 2 Results of ANOVAs examining effects of burn and seeding treatments, year, pre- or post-burn sampling period, and their interactions on vegetation and litter carbon and nitrogen contents and soil mineral nitrogen in litter intact and litter removed plots. B = burn/seeding, Y = year, P = period. Values in bold are significant ($p\leq0.05$)

	Vegetation and litter						Soil		
	Carbon content			Nitrogen content			Mineral nitrogen		
	F (Num DF, Den DF)		p	F (Num DF, Den DF)		P	F (Num DF, Den DF)		p
Litter intact plots									
Burn/seeding	2.81	(2,20)	0.084	3.15	(2,20)	0.0645	0.74	(2,20)	0.4896
Year	**90.08**	**(3,147)**	**<.0001**	**82.51**	**(3,147)**	**<.0001**	**7.37**	**(3,146)**	**0.0001**
B x Y	1.10	(6,147)	0.363	**2.56**	**(6,147)**	**0.0217**	1.3	(6,146)	0.2591
Period	**110.68**	**(1,147)**	**<.0001**	**6.11**	**(1,147)**	**0.0146**	0.18	(1,146)	0.6756
B x P	0.30	(2,147)	0.744	0.80	(2,147)	0.4503	1.92	**(2,146)**	0.1504
Y x P	**8.63**	**(3,147)**	**<.0001**	**3.77**	**(3,147)**	**0.0120**	1.42	**(3,146)**	0.2405
B x Y x P	1.37	(6,147)	0.230	0.79	(6,147)	0.5763	1.72	(6,146)	0.1195
Litter removed plots									
Burn/seeding	1.06	(2,20)	0.3649	2.25	(2,20)	0.1313	2.93	**(2,20)**	0.0767
Year	**18.25**	**(4,105)**	**<.0001**	**24.52**	**(4,105)**	**<.0001**	2.26	**(4,105)**	0.1091
B x Y	0.74	(4,105)	0.5680	0.37	(4,105)	0.8313	1.55	(4,105)	0.1926
Period	**61.70**	**(1,105)**	**<.0001**	0.14	(1,105)	0.7057	1.67	(1,105)	0.1986
B x P	2.21	(2,105)	0.1152	3.00	(2,105)	0.0541	**4.79**	**(2,105)**	**0.0102**
Y x P	**3.98**	**(2,105)**	**0.0215**	**4.34**	**(2,105)**	**0.0155**	0.12	(2,105)	0.8914
B x Y x P	0.53	(4,105)	0.7119	0.35	(4,105)	0.8454	1.79	(4,105)	0.1365

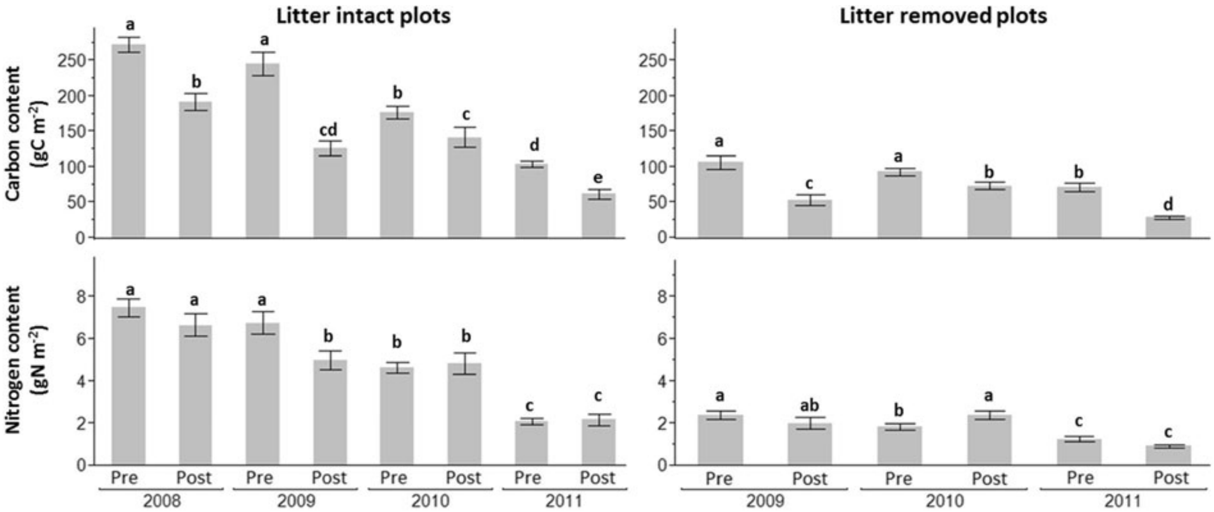


Fig. 4 Changes in pre- and post-burn vegetation and litter C contents (*top panels*) and N contents (*bottom panels*) among study years in litter intact and litter removed plots. *Bars* indicate ± 1 standard error. *Lower-case letters* indicate significant differences among pre- and post-burn time periods among years ($p<0.05$)

decreased below 2009 levels in 2011 ($p<0.03$). There were no differences in vegetation and litter C contents among burned treatments across years or between pre- and post-burn periods in either litter intact or litter removed plots.

Vegetation and litter N contents exhibited a year by period interaction in litter intact and litter removed plots (Table 2; Fig. 4). In litter intact plots, post-burn N contents in 2009 were lower than pre-burn contents ($p<0.01$). In litter removed plots, post-burn N contents in 2010 were higher than pre-burn contents ($p<0.04$). Nitrogen contents in both litter intact and litter removed plots generally decreased across time in both pre- and post-burn periods ($p<0.04$). Differences in vegetation and litter N contents among burned treatments occurred across years in litter intact plots, but there were no differences in N contents among burned treatments in litter removed plots (Table 2). In litter intact plots, N contents generally decreased over time in all burned treatments, but especially in burned and seeded with wheat plots (2008: 7.20±0.76 gN/m^2, 2009: 5.60±0.76 gN/m^2, 2010: 3.46±0.76 gN/m^2, 2011: 1.76±0.76 gN/m^2; $p<0.05$). Also, burned only plots had higher N contents than burned and seeded with cheatgrass plots in 2009 (burned only: 6.87±0.76 gN/m^2, burned and seeded with cheatgrass: 5.20±0.76 gN/m^2; $p<0.02$), and higher N contents than burned and seeded with cheatgrass and burned and seeded with wheat plots in 2010 (burned only: 6.14±0.76 gN/m^2, burned and seeded with cheatgrass: 4.65±0.76 gN/m^2, burned and seeded with wheat: 3.46±0.76 gN/m^2; $p<0.04$).

Soil-extracted mineral N

Soil-extracted TMN in the top 5 cm of soil exhibited a significant main effect for year in litter intact plots and a burn and seeding treatment by period interaction in litter removed plots (Table 2; Fig. 5). In litter intact plots, soil-extracted TMN was higher than pre-burn levels in all post-burn years, regardless of period or burn and seeding treatment (2008: 0.68±0.26 gN/m^2, 2009: 1.18±0.26 gN/m^2, 2010: 1.05±0.26 gN/m^2, 2011: 1.11±0.26 gN/m^2; $p<0.002$). In litter removed plots, pre-burn soil-extracted TMN in burned and seeded with wheat plots was higher than pre- or post-burn soil-extracted TMN in burned only and burned and seeded with cheatgrass plots (pre-burn burned and seeded with wheat plots: 1.81±0.32 gN/m^2, pre-burn burned only plots: 1.08±0.32 gN/m^2, post-burn burned only plots: 1.11±0.32 gN/m^2, pre-burn burned and seeded with cheatgrass plots: 1.20±0.32 gN/m^2, post-burn burned and seeded with cheatgrass plots: 1.38±0.32 gN/m^2; $p<0.05$).

Responses to treatments at peak biomass

Litter C and N contents

Litter C content exhibited year by burn and seeding treatment interactions in both litter intact and litter removed plots (Table 3; Fig. 6). In litter intact plots, litter C content generally decreased over time in all plots

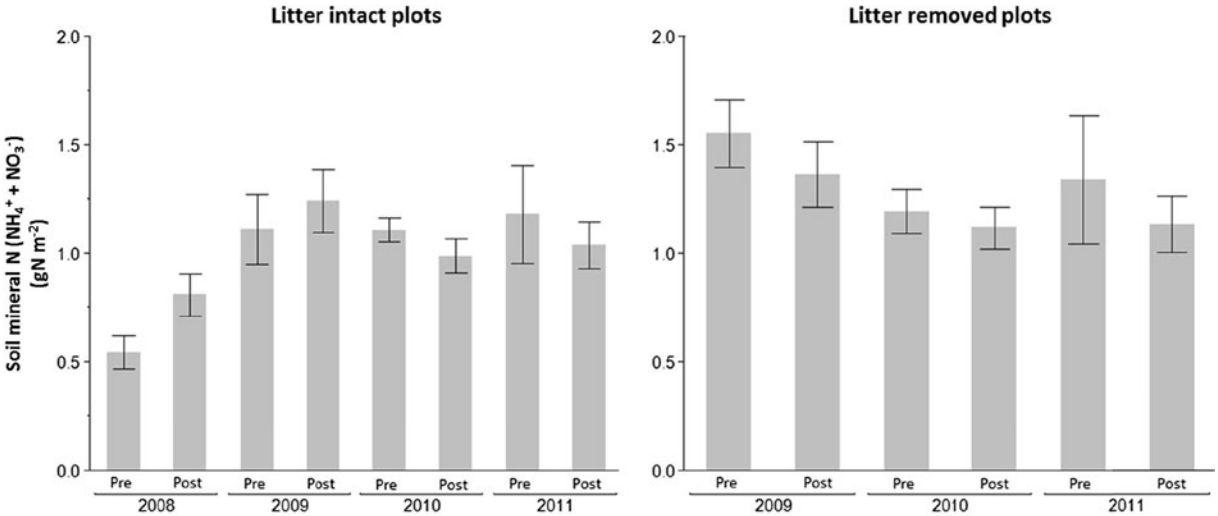


Fig. 5 Changes in pre- and post-burn soil mineral N in the top 5 cm of soil among years in litter intact and litter removed plots. *Bars* indicate ± 1 standard error. *Lower-case letters* indicate significant differences among pre- and post-burn time periods among years ($p<0.05$)

($p<0.03$). There were no significant trends over time in litter removed plots. Unburned litter intact plots had higher litter C content than burned litter intact plots in post-burn years ($p<0.02$) and higher litter C content than all litter removed plots in all years ($p<0.05$). Also, unburned litter removed plots had higher litter C content than litter removed plots that were burned and seeded with wheat in 2010 and 2011 ($p<0.04$).

Litter N content exhibited separate burn and seeding treatment and year effects in litter intact plots and a year by burn and seeding treatment interaction in litter removed plots (Table 3; Fig. 6). In litter intact plots, litter N content decreased over time ($p<0.05$) and unburned plots had higher litter N content than burned plots ($p<0.0001$). In litter removed plots, litter N content in burned only plots decreased in the final 2 years ($p<0.05$) but there was no difference in litter N content over time in unburned, burned and seeded with cheatgrass, or burned and seeded with wheat plots. Unburned, litter intact plots had higher litter N content than unburned, litter removed plots in 2009 and 2010 ($p<0.0001$) and higher litter N content than burned litter removed plots in all years ($p<0.01$).

Vegetation C and N contents

Vegetation C contents at peak biomass differed only among years in litter intact and litter removed plots (Table 3; Fig. 7). In litter intact plots, C contents averaged across all burn and seeding treatments were higher than pre-burn levels in 2009, 2010, and 2011, and then decreased below pre-burn levels in 2012 (2008: 40.01±4.19 gC/m^2, 2009: 58.53±4.19 gC/m^2, 2010: 96.83±4.19 gC/m^2, 2011: 62.37±4.19 gC/m^2, 2012: 12.28±4.19 gC/m^2; $p<0.001$). In litter removed plots, C contents averaged across all burn and seeding treatments were higher than pre-burn levels in 2010 and then decreased to at or below pre-burn levels in 2011 and 2012 (2009: 59.12±3.35 gC/m^2, 2010: 86.28±3.35 gC/m^2, 2011: 55.54±3.35 gC/m^2, 2012: 11.28±3.35 gC/m^2; $p<0.0001$).

Vegetation N contents at peak biomass only differed among years in both litter intact and litter removed plots (Table 3; Fig. 7). In litter intact plots, N contents averaged across all burn and seeding treatments were higher than pre-burn levels in 2009, 2010, and 2011, and then decreased below pre-burn levels in 2012 (2008: 0.98±0.08 gN/m^2, 2009: 1.46±0.08 gN/m^2, 2010: 1.94±0.08 gN/m^2, 2011: 1.15±0.08 gN/m^2, 2012: 0.28±0.08 gN/m^2; $p<0.006$). In litter removed plots, N contents averaged across all burn and seeding treatments did not differ from pre-burn levels in 2010 and then decreased to at or below pre-burn levels in 2011 and 2012 (2009: 1.61±0.09 gN/m^2, 2010: 1.81±0.09 gN/m^2, 2011: 1.01±0.09 gN/m^2, 2012: 0.26±0.09 gN/m^2; $p<0.0001$).

Soil mineral N and soil C and N contents

Soil-extracted TMN at peak biomass only differed among years in litter intact plots and litter removed plots (Table 3; Fig. 8). In litter intact plots, soil-extracted TMN averaged across all burn and seeding treatments

Table 3 Results of ANOVAs examining effects of burn and seeding treatments, year, and their interaction on litter and vegetation carbon and nitrogen contents, soil mineral nitrogen, and total soil carbon and nitrogen contents at peak biomass in litter intact and litter removed plots. B = burn/seeding, Y = year. Values in bold are significant ($p \leq 0.05$)

	Litter			Vegetation			Mineral soil			Total soil		
	$F_{(\text{Num DF, Den DF})}$		P	$F_{(\text{Num DF, Den DF})}$		P	$F_{(\text{Num DF, Den DF})}$		P	$F_{(\text{Num DF, Den DF})}$		P
Carbon												
Litter intact plots												
Burn/seeding	**12.62**	**(3,27)**	**<.0001**	0.68	(3,27)	0.5713	N/A			1.36	(3,27)	0.2748
Year	**93.87**	**(4,111)**	**<.0001**	**68.38**	**(4,112)**	**<.0001**	N/A			**83.11**	**(2,56)**	**<.0001**
B x Y	**2.11**	**(12,111)**	**0.0214**	0.88	(12,112)	0.568	N/A			2.07	(6,56)	0.0707
Litter removed plots												
Burn/seeding	**31.01**	**(4,34)**	**<.0001**	1.48	(4,34)	0.23	N/A			0.38	(4,34)	0.8204
Year	**14.57**	**(3,100)**	**<.0001**	**85.72**	**(3,105)**	**<.0001**	N/A			**6.56**	**(1,35)**	**0.0149**
B x Y	**4.79**	**(12,100)**	**<.0001**	0.97	(12,105)	0.4828	N/A			**2.99**	**(4,35)**	**0.0318**
Nitrogen												
Litter intact plots												
Burn/seeding	**7.72**	**(3,27)**	**0.0007**	0.88	(3,27)	0.4646	1.53	(3,27)	0.2296	1.16	(3,27)	0.3429
Year	**72.46**	**(4,111)**	**<.0001**	**61.83**	**(4,112)**	**<.0001**	**45.43**	**(4,112)**	**<.0001**	**71.22**	**(2,56)**	**<.0001**
B x Y	1.38	(12,111)	0.1872	0.73	(12,112)	0.7165	1.29	(12,112)	0.2353	1.31	(6,56)	0.2697
Litter removed plots												
Burn/seeding	**27.85**	**(4,34)**	**<.0001**	2.01	(4,34)	0.1147	0.34	(4,34)	0.8497	0.16	(4,34)	0.9556
Year	**16.38**	**(3,100)**	**<.0001**	**83.24**	**(3,105)**	**<.0001**	**21.56**	**(3,105)**	**<.0001**	**26.48**	**(1,35)**	**<.0001**
B x Y	**4.33**	**(12,100)**	**<.0001**	1.69	(12,105)	0.0782	1.21	(12,105)	0.2837	0.84	(4,35)	0.5079

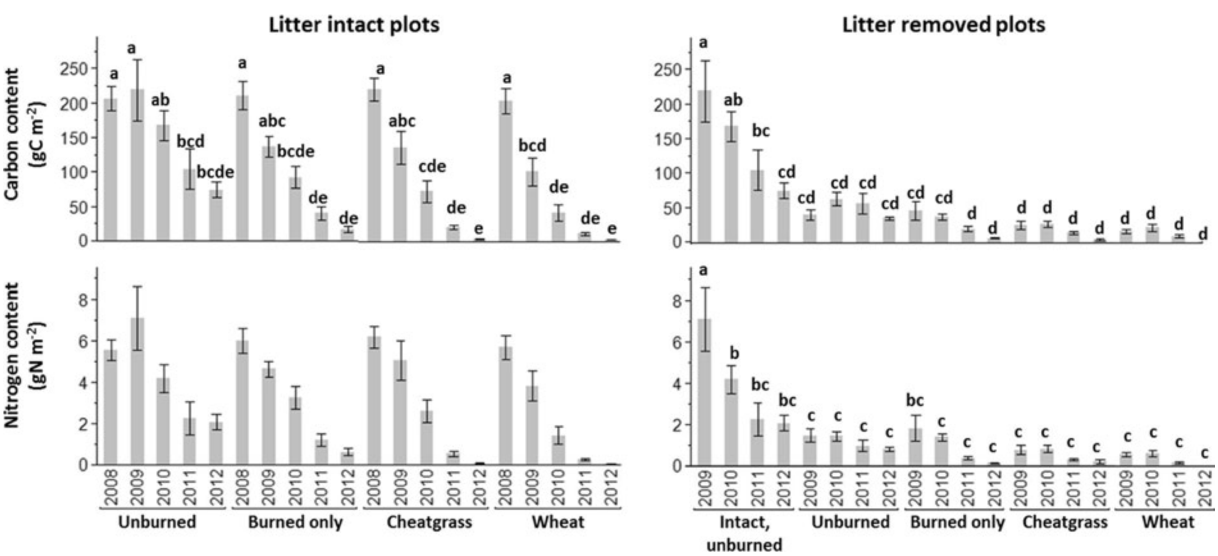


Fig. 6 Changes in litter C contents (*top panels*) and N contents (*bottom panels*) at peak biomass among years and among burn and seeding treatments in litter intact and litter removed plots. *Bars* indicate ± 1 standard error. *Lower-case letters* indicate significant differences among burn and seeding treatments among years ($p<0.05$)

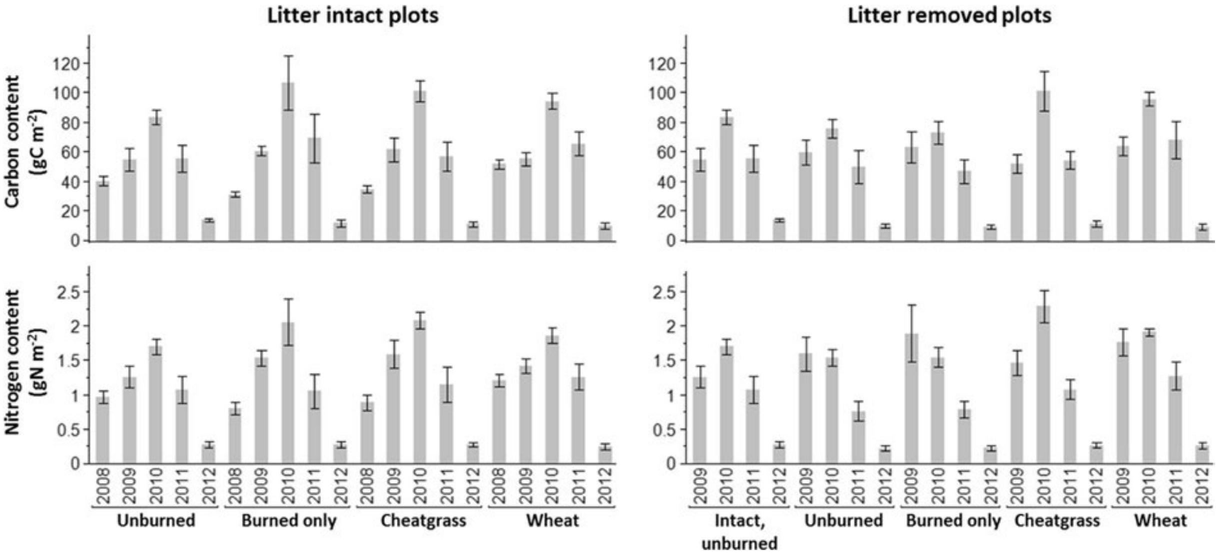


Fig. 7 Changes in vegetation C contents (*top panels*) and N contents (*bottom panels*) at peak biomass among burn and seeding treatments and among years in litter intact and litter removed plots. *Bars* indicate ± 1 standard error

was higher in 2009 than 2008, decreased to its lowest level in 2010, and then returned to at or above pre-burn levels in 2011 and 2012 (2008: 0.43±0.20 gN/m^2, 2009: 1.31±0.20 gN/m^2, 2010: 0.55±0.20 gN/m^2, 2011: 0.66±0.20 gN/m^2, 2012: 0.73±0.20 gN/m^2; p<0.01). In litter removed plots, soil-extracted TMN averaged across all burn and seeding treatments was lower in 2010 than 2009 and then increased in 2011 and 2012 but remained below 2009 levels (2009: 1.19±0.27 gN/m^2, 2010: 0.48±0.27 gN/m^2, 2011: 0.71±0.27 gN/m^2, 2012: 0.67±0.27 gN/m^2; p<0.0001).

Soil C content only differed among years in litter intact plots and exhibited a burn and seeding treatment by year interaction in litter removed plots (Table 3; Fig. 9). In litter intact plots, soil C content averaged across all burn and seeding treatments was higher in 2009 and 2012 than pre-burn levels (2008: 671.37± 121.49 gC/m^2, 2009: 1,510.98±121.49 gC/m^2, 2012: 1,436.32±121.49 gC/m^2; p<0.0001). In litter removed plots, soil C content was higher in burned only and burned and seeded with wheat plots in 2012 than in burned only and burned and seeded with wheat plots

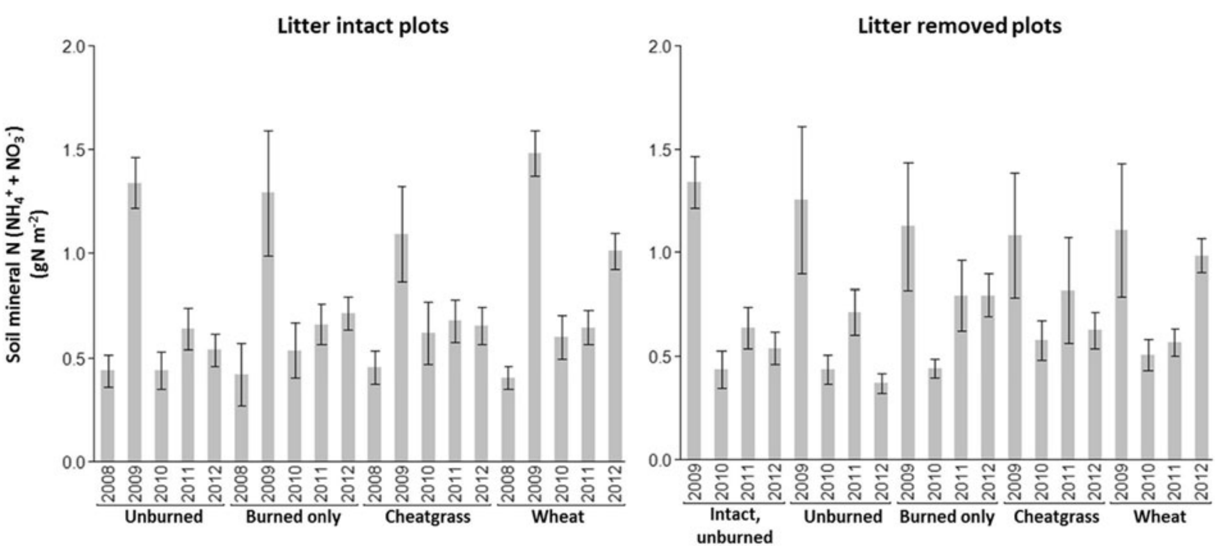


Fig. 8 Changes in soil mineral N in the top 5 cm of soil at peak biomass among burn and seeding treatments and among years in litter intact and litter removed plots. *Bars* indicate ± 1 standard error

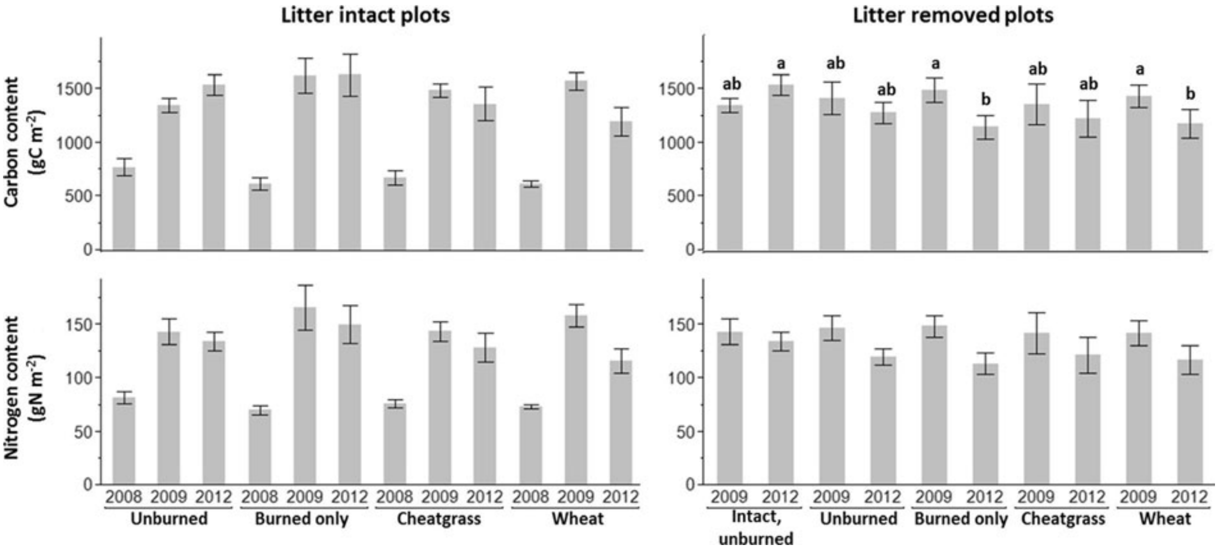


Fig. 9 Changes in soil C contents (*top panels*) and N contents (*bottom panels*) in the top 5 cm of soil at peak biomass among burn and seeding treatments and among years in litter intact and litter removed plots. *Bars* indicate ± standard error. *Lower-case letters* indicate significant differences among burn and seeding treatments among years ($p<0.05$)

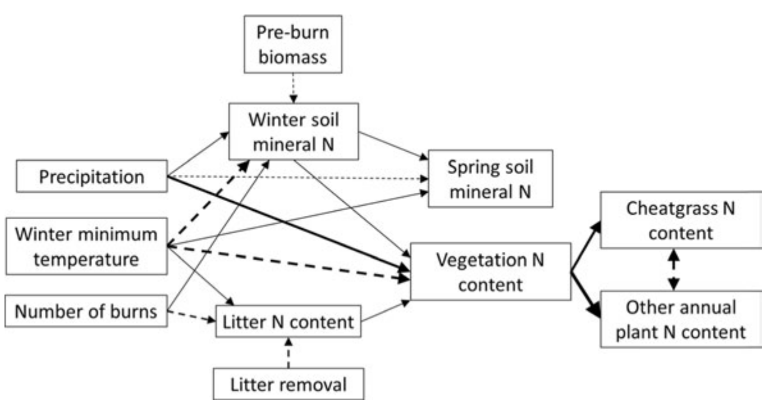
in 2009 (burned only plots 2009: 1,495.34±190.55 gC/m^2, burned only plots 2012: 1,151.02±190.55 gC/m^2, burned and seeded with wheat plots 2009: 1436.71±190.55 gC/m^2, burned and seeded with wheat plots 2012: 1,180.74±190.55 gC/m^2; $p<0.04$). Also, unburned litter intact plots had higher soil C content in 2012 than burned only and burned and seeded with wheat litter removed plots in 2012 (unburned litter intact plots: 1,545.41±190.55 gC/m^2, burned only litter removed plots: 1151.02±190.55 gC/m^2, burned and seeded with wheat litter removed plots: 1,180.74±190.55 gC/m^2; $p<0.04$).

Soil N content only differed among years in litter intact and litter removed plots (Table 3; Fig. 9). In litter intact plots, soil N contents averaged across all burn and seeding treatments was higher in 2009 and 2012 than pre-burn levels (2008: 75.74±16.83 gN/m^2, 2009: 153.30±16.83 gN/m^2, 2012: 132.82±16.83 gN/m^2; $p<0.004$). In litter removed plots, soil N content averaged across all burn and seeding treatments was higher in 2009 than 2012 (2009: 145.09±19.55 gN/m^2, 2012: 121.83±19.55 gN/m^2; $p<0.0001$).

Structural equation model

The path analyses illustrated direct and indirect effects of burning and litter removal treatments and environmental factors on soil TMN and litter and vegetation N contents (Fig. 10). Litter removal had a negative direct effect on litter N content and negative indirect effects on vegetation

Fig. 10 Path diagram for effect of climatic variables and experimental treatments on post-burn and spring soil mineral N, and litter and vegetation N contents. 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



N content, particularly cheatgrass N content. Burning, expressed as number of burns in our model, had a negative direct effect on litter N content and a positive direct effect on winter soil TMN. Burning had a negative indirect effect on vegetation N content, due to the positive effect of litter N content, and a positive indirect effect on spring soil TMN, due to the positive effect of winter soil TMN. Cheatgrass and other annual plant N contents were negatively correlated. The burning and litter removal treatments had similar effects on litter C contents but did not have significant direct or indirect effects on vegetation C content (data not shown).

Environmental factors such as fuel loads and weather conditions also affected our measured variables. Pre-burn biomass, which is representative of fuel load, was generally higher in litter intact plots (data not shown) and had a negative direct effect on winter soil TMN. The weather variables, precipitation received from September 1 through June 30 and winter minimum temperature, had significant direct and indirect effects. Precipitation had positive direct effects on winter soil TMN and vegetation N contents and a negative direct effect on spring soil TMN. Precipitation had positive indirect effects on both vegetation N content and soil TMN at peak biomass, due to positive effects of winter soil TMN on those variables. Minimum winter temperature had negative direct effects on winter soil TMN and vegetation N contents but positive direct effects on litter N content and spring soil TMN. Minimum winter temperature had negative indirect effects on vegetation N content and spring soil TMN, due to positive effects of winter soil TMN on those variables. Precipitation and temperature had similar effects on litter and vegetation C contents (data not shown).

Discussion

Fire can have profound effects of ecosystem properties, but very few studies have been conducted to address the role of repeated burns in altering soil nutrients, and none have been conducted in cold desert ecosystems where progressive invasion of exotic annual grasses is resulting in annual grass-fire cycles. In addition, although soil and vegetation nutrients are temporally variable and strongly influenced by environmental factors which also vary over time, few long-term studies have been conducted.

This research allowed us to identify mechanisms associated with treatments aimed at reducing soil N availability and restoring pre-invasion above- and belowground C and N contents and to track changes in these nutrient pools over time. Structural equation modeling revealed that a multivariate approach was necessary to clarify effects of treatments and abiotic environmental factors (precipitation and temperature) on soil N availability and C and N contents. 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.

Repeated burning effects

We hypothesized that burning would result in an immediate pulse in post-fire soil TMN due to heat-induced organic matter denaturation, followed by an increase in plant N uptake and plant and litter N contents in the following growing season (Monaco et al. 2003). Subsequent fires were predicted to volatilize biomass C and N, resulting in decreases in N inputs to soils over time (progressive N deficiency; Rau et al. 2007). However, there were no differences between pre- and post-burn soil TMN in litter intact or litter removed plots. Although vegetation N content generally tracked post-burn soil TMN over time indicating that vegetation was highly responsive to changes in soil N availability, vegetation and litter N contents were not volatilized and lost from the system following burning. Also, total C and N at the end of the study were higher than pre-burn levels and did not decrease with burning.

Fire temperature likely explains the failure to achieve immediate decreases in vegetation and litter N content, or longer term decreases in soil TMN, total C, or total N. Fine fuels produced by annual grasses typically burn cooler than woody fuels produced by shrubs and trees. In our study, surface soil temperatures during burns never exceeded 70 °C and flame temperatures never exceeded 180 °C on either litter intact or litter removed plots. These temperatures are similar to fire temperatures in other burning experiments in annual grass invaded deserts (Brooks 2002; Patten and Cave 1984), but lower than those in sagebrush-dominated ecosystems (Korfmacher et al. 2003; Neary et al. 1999). The cooler soil temperatures in our burns were likely insufficient to denature organic matter or volatilize N from biomass or soils (volatilization temperature of 200 °C, Raison et al. 1985). Instead, a majority of N from combusted biomass was probably left behind as ash on the plots and may have contributed to the general, though non-significant, post-burn increase in soil TMN in litter intact plots in 2008 and 2009. Ash incorporation is a primary source of ions in soil solution following a fire, particularly highly mobile ions such as NO_3^- (Grier and Cole 1971), and previous studies have attributed post-burn soil nutrient increases to N inputs from ash (Brooks 2002; Johnson et al. 2012). During the time between the fire and the post-burn soil collection (about 1 week), some of the N from ash could have been incorporated into the soil, thereby increasing soil TMN. Also, small particles of N-rich ash may have been left behind on the soil surface during ash collection (which was done by hand) and then collected along with soil during soil sampling.

Burning did result in an immediate loss of vegetation and litter C content, likely due to the lower volatilization temperature of C (Murphy et al. 2006; Ojima et al. 1994; Raison et al. 1985). Also, litter C and N contents decreased over time, especially in burned litter intact plots. The declines in C content in burned plots are likely due to progressive volatilization of litter C and depletion of litter biomass with successive burns as found in repeated burn experiments in other systems (Ojima et al. 1994) and from measurements of C loss following wildfire and prescribed fire in cheatgrass-dominated systems (Bradley et al. 2006; Rau et al. 2011). However, the decreases in litter N content were probably not attributable to volatilization losses because of the relatively cool fire temperatures. Instead, losses of litter N during the experiment were likely due to combustion of relatively immobile litter into highly mobile ash that was subsequently transported off-site by wind or water (Malmer 1996; Sankey et al. 2009).

Litter and seeding effects

Litter removal and the annual post-fire seeding treatments also had effects on C and N contents. Litter removal had a significant and persistent negative effect on litter C and N contents measured on an area basis, and litter N content had a positive effect on vegetation N content. Cheatgrass and other annual grasses are often positively influenced by litter because of its microsite effects (Facelli and Pickett 1991; Newingham et al. 2007; Wolkovich et al. 2009) and strong influences on nutrient cycling (Booth et al. 2003; Sperry et al. 2006). However, there was generally no difference in soil TMN or soil C and N contents between litter intact and litter removed plots, likely because fire temperatures were too cool to result in significant soil heating even in litter removed plots. The positive effects of litter on vegetation, therefore, were likely a result of the physical influences of litter on seed entrapment and retention, soil temperature, and soil water availability (Chambers 2000; Chambers and MacMahon 1994; Wolkovich et al. 2009). The seeding treatments had very few significant effects on C and N contents; however, plots seeded with common wheat generally had the largest decreases in vegetation and litter N contents over time and the lowest soil TMN likely due to competition for soil resources with cheatgrass (Jones et al. in process).

Environmental effects

Precipitation and winter soil temperatures were the predominant factors influencing vegetation C and N contents and soil TMN, undoubtedly due to the effects of soil water and temperature on nutrient dynamics (Leffler and Ryel 2012). Precipitation had positive direct effects on post-burn soil TMN and vegetation C:N and a negative direct effect on spring soil TMN. Microbial activity and net N mineralization are positively affected by soil moisture (Borken and Matzner 2009; Fierer and Schimel 2002); therefore increases in precipitation generally result in higher soil N availability and plant N uptake and growth. The negative effect of precipitation on spring soil TMN was likely due to more favorable growing conditions and higher plant N uptake. Minimum winter temperature had negative direct effects on post-burn soil TMN and vegetation C:N and a positive direct effect on spring soil TMN. Microbial activity is strongly influenced by soil temperatures and, in general, warmer temperatures increase soil N availability (Hobbie 1996; Knorr et al. 2005; Rustad et al. 2001). Colder winter temperatures likely decreased or delayed plant uptake resulting in higher spring soil TMN.

Synthesis

Prescribed fire has often been used as a management tool to restore community structure in systems with historically frequent fires (Reilly et al. 2006) and fire can have major and long-lasting effects on C and N contents of vegetation and soils and on nutrient cycling (Grogan et al. 2000; Johnson et al. 2005; Rau et al. 2007). We hypothesized that repeated fires could be used to alter soil nutrients and restore semi-arid ecosystems that have experienced annual grass invasion and changes in nutrient cycling. Our results indicate that repeated burning is unlikely to decrease soil N availability in cheatgrass-dominated systems because fire temperatures are too cool to volatilize biomass and soil N. Also, nutrient cycling and nutrient availability in semi-arid ecosystems are strongly influenced by weather and effects of repeated burning are likely to vary both among years and over time.

Our study does provide insights into integrated strategies for restoring pre-invasion nutrient cycles in Wyoming big sagebrush ecosystems (Mangold 2012; Sheley and Krueger-Mangold 2003). Vegetation (cheatgrass) N contents were positively influenced by litter N, and repeated burning significantly reduced litter C and N contents. Thus, the first component of an integrated restoration strategy for cheatgrass-dominated systems may be reducing litter and litter C and N through repeated burning as shown here, or through prescription livestock grazing (Frost and Launchbaugh 2003). The second component may be seeding with grasses to prevent rapid post-disturbance increases in cheatgrass seed banks and to stabilize soils to limit erosion. Our companion research shows that sterile cover crops like common wheat decrease cheatgrass densities, biomass, and reproduction in the first year after seeding (Jones et al. *in process*) without the threat of out-competing native species that introduced species like crested wheatgrass (*Agropyron cristatum*) pose (Knutson et al. in press). The last component of an integrated restoration strategy is to seed native perennial species. In arid and semi-arid systems with low and variable precipitation, more than one intervention may be required to successfully restore native ecosystems.

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References

Baker WL (2006) Fire and restoration of sagebrush ecosystems. Wildl Soc Bull 34:177–185

Binkley D, Richter D, David MB, Caldwell B (1992) Soil chemistry in a loblolly longleaf pine forest with interval burning. Ecol Appl 2:157–164

Blair JM (1997) Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. Ecology 78: 2359–2368

Blank RR, Allen F, Young JA (1994) Extractable anions in soils following wildfire in a sagebrush-grass community. Soil Sci Soc Am J 58:564–570

Blank RR, Morgan T, Clements CD, Mackey BE (2013) *Bromus tectorum* L. invasion: changes in soil properties and rates of bioturbation. Soil Sci 178:281–290

Blumenthal DM, Jordan NR, Russelle MP (2003) Soil carbon addition controls weeds and facilitates prairie restoration. Ecol Appl 13:605–615

Booth MS, Caldwell MM, Stark JM (2003) Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. J Ecol 91:36–48

Borken W, Matzner E (2009) Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Glob Chang Biol 15:808–824

Bradley BA, Mustard JF (2005) Identifying land cover variability distinct from land cover change: cheatgrass in the Great Basin. Remote Sens Environ 94:204–213

Bradley BA, Houghtonw RA, Mustard JF, Hamburg SP (2006) Invasive grass reduces aboveground carbon stocks in shrublands of the Western US. Glob Chang Biol 12:1815–1822

Brooks ML (2002) Peak fire temperatures and effects on annual plants in the Mojave Desert. Ecol Appl 12:1088–1102

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. Bioscience 54:677–688

Brunson JL, Pyke DA, Perakis SS (2010) Yield responses of ruderal plants to sucrose in invasive-dominated sagebrush steppe of the northern Great Basin. Restor Ecol 18:304–312

Chambers JC (2000) Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: implications for restoration. Ecol Appl 10:1400–1413

Chambers JC, MacMahon JA (1994) A day in the life of a seed-movements and fates of seeds and their implications for natural and managed systems. Annu Rev Ecol Syst 25:263–292

Chambers JC, Roundy BA, Blank RR, Meyer SE, Whittaker A (2007) What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecol Monogr 77:117–145

Chambers JC, Bradley BA, Brown CS, D'Antonio C, Germino MJ, Grace JB, Hardegree SP, Miller RF, Pyke DA (2014) Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of Western North America. Ecosystems 17:360–375

Chambers JC, Miller RF, Board DI, Pyke DA, Roundy BA, Grace JB, Schupp EW, Tausch RJ (in press) Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. Rangel Ecol Manag

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass fire cycle, and global change. Annu Rev Ecol Syst 23:63–87

Denny DW (2002) Soil survey of Humboldt County, Nevada, East Part, part 1. US Department of Agriculture, Natural Resources Conservation Service, Reno

Dijkstra FA, Cheng W (2007) Moisture modulates rhizosphere effects on C decomposition in two different soil types. Soil Biol Biochem 39:2264–2274

Dodds WK, Blair JM, Henebry GM, Koelliker JK, Ramundo R, Tate CM (1996) Nitrogen transport from tallgrass prairie watersheds. J Environ Qual 25:973–981

Evans RD, Rimer R, Sperry L, Belnap J (2001) Exotic plant invasion alters nitrogen dynamics in an arid grassland. Ecol Appl 11:1301–1310

Facelli JM, Pickett STA (1991) Plant litter- its dynamics and effects on plant community structure. Bot Rev 57:1–32

Fierer N, Schimel JP (2002) Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. Soil Biol Biochem 34:777–787

Frost RA, Launchbaugh KL (2003) Prescription grazing for rangeland weed management: a new look at an old tool. Rangelands 25:43–47

Fynn RWS, Haynes RJ, O'Connor TG (2003) Burning causes long-term changes in soil organic matter content of a South African grassland. Soil Biol Biochem 35:677–687

Grace JB (2006) Structural equation modeling and natural systems. Cambridge University Press, Cambridge

Grace JB, Youngblood A, Scheiner SM (2009) Structural equation modeling and ecological experiments. In: Miao S, Carstenn S, Nungesser M (eds) Real world ecology: large-scale and long-term case studies and methods. Springer Verlag, New York

Grier CC, Cole DW (1971) Influence of slash burning on ion transport in soil. Northwest Sci 45:100–106

Grogan P, Bruns TD, Chapin FS (2000) Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. Oecologia 122:537–544

Hobbie SE (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. Ecol Monogr 66: 503–522

Jackson RB, Banner JL, Jobbagy EG, Pockman WT, Wall DH (2002) Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418:623–626

James JJ, Drenovsky RE, Monaco TA, Rinella MJ (2011) Managing soil nitrogen to restore annual grass-infested plant communities: effective strategy or incomplete framework? Ecol Appl 21:490–502

Jobbagy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol Appl 10:423–436

Johnson LC, Matchett JR (2001) Fire and grazing regulate belowground processes in tallgrass prairie. Ecology 82: 3377–3389

Johnson DW, Murphy JF, Susfalk RB, Caldwell TG, Miller WW, Walker RF, Powers RF (2005) The effects of wildfire, salvage logging, and post-fire N-fixation on the nutrient budgets of a Sierran forest. Forest Ecol Manag 220:155–165

Johnson BG, Johnson DW, Chambers JC, Blank RR (2011) Fire effects on the mobilization and uptake of nitrogen by cheatgrass (*Bromus tectorum* L.). Plant Soil 341:437–445

Johnson BG, Johnson DW, Miller WW, Board DI (2012) The effects of ash influx on burned and unburned soil water-extractable nutrients using a mechanical vacuum extractor. Soil Sci 177:338–344

Jones RO, Chambers JC, Board DI, Johnson DW, Blank RR (in process) Understanding the role of resource limitation in restoration of sagebrush ecosystems dominated by cheatgrass - a mechanistic approach

Keeney DR, Nelson DW (1987) Nitrogen–inorganic forms, sec. 33–3, extraction of exchangeable ammonium, nitrate, and nitrite. In: Page AL et al (eds) Methods of soil analysis: part 2, chemical and microbiological properties agronomy, a series of monographs, no9 pt2. Soil Science Society of America, Madison

Knapp PA (1996) Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert – history, persistence, and influences to human activities. Global Environ Chang 6:37–52

Knorr W, Prentice IC, House JI, Holland EA (2005) Long-term sensitivity of soil carbon turnover to warming. Nature 433: 298–301

Knutson KC, Pyke DA, Wirth TA, Arkle RS, Pilliod DS, Brooks ML, Chambers JC, Grace JB (in press) Long-term effects of seeding after wildfire on vegetation composition in Great Basin shrub steppe. J Appl Ecol

Korfmacher JL, Chambers JC, Tausch RJ, Roundy BA, Meyer SE, Kitchen S (2003) Technical note: a technique for conducting small-plot burn treatments. J Range Manag 56:251–254

Leffler AJ, Ryel RJ (2012) Resource pool dynamics: conditions that regulate species interactions and dominance. In: Monaco TA, Sheley RL (eds) Invasive plant ecology and management linking processes to practice. CAB International, Cambridge

Link SO, Keeler CW, Hill RW, Hagen E (2006) *Bromus tectorum* cover mapping and fire risk. Int J Wildland Fire 15:113–119

Malmer A (1996) Hydrological effects and nutrient losses of forest plantation establishment on tropical rainforest land in Sabah, Malaysia. J Hydrol 174:129–148

Mangold JM (2012) Revegetation: using current technologies and ecological knowledge to manage site availability, species availability, and species performance. In: Monaco T, Sheley R (eds) Invasive plant ecology and management: linking processes to practice. CABI Invasive Plant Series MPG Books Group, Reading

Mazzola MB (2008) Spatio-temporal heterogeneity and habitat invasibility in sagebrush steppe ecosystems. PhD disseration. University of Nevada, Reno, Reno, NV, USA

Monaco TA, Johnson DA, Norton JM, Jones TA, Connors KJ, Norton JB, Redinbaugh MB (2003) Contrasting responses of intermountain west grasses to soil nitrogen. J Range Manag 56:282–290

Moyano FE, Manzoni S, Chenu C (2013) Responses of soil heterotrophic respiration to moisture availability: an exploration of processes and models. Soil Biol Biochem 59:72–85

Murphy JD, Johnson DW, Miller WW, Walker RF, Blank RR (2006) Prescribed fire effects on forest floor and soil nutrients in a Sierra Nevada forest. Soil Sci 171:181–199

Neary DG, Klopatek CC, DeBano LF, Ffolliott PF (1999) Fire effects on belowground sustainability: a review and synthesis. Forest Ecol Manag 122:51–71

Newingham BA, Vidiella P, Belnap J (2007) Do soil characteristics or microhabitat determine field emergence and success of *Bromus tectorum*? J Arid Environ 70:389–402

Norton JB, Monaco TA, Norton JM, Johnson DA, Jones TA (2004) Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. J Arid Environ 57:445–466

Ogle SM, Ojima D, Reiners WA (2004) Modeling the impact of exotic annual brome grasses on soil organic carbon storage in a northern mixed-grass prairie. Biol Invasions 6:365–377

Ojima DS, Schimel DS, Parton WJ, Owensby CE (1994) Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. Biogeochemistry 24:67–84

Patten DT, Cave GH (1984) Fire temperatures and physical characteristics of a controlled burn in the upper Sonoran desert. J Range Manag 37:277–280

Peters J (2000) Tetrazolium testing handbook. Contribution no. 29 to the handbook on seed testing. Association of Official Seed Analysts, Lincoln

Raison RJ, Khanna PK, Woods PV (1985) Mechanisms of element transfer to the atmosphere during vegetation fires. Can J Forest Res 15:132–140

Rau BM, Blank RR, Chambers JC, Johnson DW (2007) Prescribed fire in a Great Basin sagebrush ecosystem: Dynamics of soil extractable nitrogen and phosphorus. J Arid Environ 71:362–375

Rau BM, Johnson DW, Blank RR, Lucchesi A, Caldwell TG, Schupp EW (2011) Transition from sagebrush steppe to annual grass (*Bromus tectorum*): influence on belowground carbon and nitrogen. Rangel Ecol Manag 64:139–147

Reilly MJ, Wimberly MC, Newell CL (2006) Wildfire effects on beta-diversity and species turnover in a forested landscape. J Veg Sci 17:447–454

Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen JHC, Gurevitch J, Gcte N (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543–562

Sankey JB, Germino MJ, Glenn NF (2009) Relationships of post-fire aeolian transport to soil and atmospheric conditions. Aeolian Res 1:75–85

Sheley RL, Krueger-Mangold J (2003) Principles for restoring invasive plant-infested rangeland. Weed Sci 51:260–265

Sokal RR, Rohlf FJ (1981) Biometry- the principles and practice of statistics in biological research. W. H. Freeman and Co, San Francisco

Sperry LJ, Belnap J, Evans RD (2006) *Bromus tectorum* invasion alters nitrogen dynamics in an undisturbed arid grassland ecosystem. Ecology 87:603–615

Stubbs MM, Pyke DA (2005) Available nitrogen: a time-based study of manipulated resource islands. Plant Soil 270:123–133

West NE, Young JA (1999) Vegetation of intermountain valleys and lower mountain slopes. In: Barbour MA, Billings WD (eds) North American terrestrial vegetation, 2nd edn. Cambridge University Press, New York

Wilcox BP, Turnbull L, Young MH, Williams CJ, Ravi S, Seyfried MS, Bowling DR, Scott RL, Germino MJ, Caldwell TG, Wainwright J (2012) Invasion of shrublands by exotic grasses: ecohydrological consequences in cold versus warm deserts. Ecohydrology 5:160–173

Wolkovich EM, Bolger DT, Cottingham KL (2009) Invasive grass litter facilitates native shrubs through abiotic effects. J Veg Sci 20:1121–1132

Wright RJ, Hart SC (1997) Nitrogen and phosphorus status in a ponderosa pine forest after 20 years of interval burning. Ecoscience 4:526–533