

University of Nevada, Reno

**PLANT-SOIL FEEDBACKS AND INVASION IN SAGEBRUSH STEPPE  
ECOSYSTEMS**

A dissertation submitted in partial fulfillment of the  
requirements for the degree of Doctor of Philosophy in  
Ecology, Evolution and Conservation Biology

by

Rachel O. Jones

Dr. Jeanne C. Chambers/Dissertation Advisor

May, 2014



University of Nevada, Reno  
Statewide • Worldwide

THE GRADUATE SCHOOL

We recommend that the dissertation  
prepared under our supervision by

**RACHEL O. JONES**

entitled

**Plant-Soil Feedbacks And Invasion In Sagebrush Steppe Ecosystems**

be accepted in partial fulfillment of the  
requirements for the degree of

**DOCTOR OF PHILOSOPHY**

Jeanne C. Chambers, Ph. D., Advisor

Elizabeth A. Leger, Ph. D., Co-Advisor

Dale W. Johnson, Ph. D., Committee Member

Thomas P. Albright, Ph. D., Committee Member

Paul S. J. Verburg, Ph. D., Graduate School Representative

David W. Zeh, Ph. D., Dean, Graduate School

May, 2014

## Abstract

Invasion by non-native species is a serious ecological threat and the susceptibility of ecosystems to invasion is often highly correlated with soil resource availability. Understanding the role of plant-soil feedbacks in invaded ecosystems could provide insight into community successional trajectories following invasion and could improve our ability to manage these systems to restore native diversity. My dissertation examined how plant-soil feedbacks and resource availability influence the success of both cheatgrass and native species with three interrelated studies. In a large-scale observational study, I evaluated plant community characteristics as well as soil and plant nutrients associated with progressive cheatgrass invasion in a broadly distributed sagebrush ecological site type. I found that although many nutrient pools did not differ among levels of invasion, soil ammonium ( $\text{NH}_4^+$ ) was negatively affected by increases in cheatgrass cover. Also, cheatgrass nutrient content did not differ across sites indicating that cheatgrass may alter plant available soil nutrients to the detriment of competitors while maintaining its own nutritional content via high nutrient use efficiency and/or soil mining. I also conducted a field experiment to provide a more mechanistic understanding of the role of disturbance on nutrient availability and invasion and to address potential management approaches. I evaluated the effects of 4-5 years of repeated burning, in combination with litter removal and post-fire seeding, on nutrient dynamics and plant responses. Results from my field experiment indicated that repeated burning is unlikely to decrease soil N availability in cheatgrass-dominated systems due to cool fire temperatures that do not volatilize biomass N and strong effects of weather on plant growth and soil processes. Repeated burning and litter removal, however, did have

negative effects on litter biomass and C and N contents which negatively influenced cheatgrass biomass, density and reproduction. In addition, post-fire seeding with common wheat decreased cheatgrass abundance, likely due to competition. Integrated restoration approaches that decrease litter biomass and seed banks and increase competitive interactions may be more effective at reducing annual grasses and establishing desirable perennial species than approaches aimed at reducing soil nutrients. Together, the observational and experimental components of my dissertation indicate that plant-soil feedbacks in arid sagebrush shrublands are complex and that understanding these feedbacks requires both spatial and temporal variability in sampling. Furthermore, the results from these studies provide valuable information on techniques that could facilitate the restoration of cheatgrass-dominated systems to more diverse plant communities.

## Acknowledgments

I would like to express my sincere gratitude and appreciation to my advisor, Dr. Jeanne Chambers for all her guidance and support. I am continually in awe of her knowledge of the Great Basin and was lucky enough to ride in the truck with her on several field trips to and around Winnemucca. I learned so much on those rides! I would also like to thank my co-advisor, Dr. Beth Leger who welcomed me into her lab and was always available whenever I had questions. I really enjoyed being able to walk down the hall to her office for a quick chat about plants, statistics, or really anything on my mind.

I would like to thank my committee members, Dr. Dale Johnson, Dr. Paul Verburg, and Dr. Tom Albright for providing feedback on my dissertation projects and manuscripts. In particular, Dr. Johnson was incredibly involved in the development of many of my projects and taught me much of what I know about soils.

I also must recognize the many individuals who helped collect and analyze the data for my projects. In particular, I must thank Dave Board who was instrumental in the design and implementation of the field experiments and was also always available to me for questions about statistics. I also thank Dr. Bob Blank, Tye Morgan, and the rest of the ARS Great Basin Rangeland Research Unit for their countless hours of help running nutrient analyses and answering my questions about soils. Lastly, I need to thank the numerous technicians that helped out in the field and lab over the past 4 years.

Finally, I would like to thank my friends and family, in particular my husband Gerrad, for their unending love, support, and motivation. You gave me hope when I faltered along the way and reminded me of what was truly important in life. Thank you and I love you!

## Table of Contents

Introduction.....	1
Do soil nutrients change with progressive invasion of cheatgrass ( <i>Bromus tectorum</i> ) into sagebrush communities? .....	7
Effect of repeated burning on plant and soil carbon and nitrogen in cheatgrass ( <i>Bromus tectorum</i> ) dominated ecosystems .....	42
Understanding the role of resource limitation in restoration of sagebrush ecosystems dominated by cheatgrass – a mechanistic approach .....	90
Conclusions.....	145

## Introduction

Invasion by non-native species is one of the most serious biological threats of the 21st century (Mack et al. 2000, Pimentel et al. 2005). Non-native species are one of the top five causes of global biodiversity loss (Wilcove et al. 1998) and it is estimated that the costs of damage recovery and control of invasive species in the United States alone range from \$1.1 to \$137 billion a year (Chapin et al. 2000). The susceptibility of ecosystems to invasion by non-native species is dependent on several interacting factors, including climate, disturbance, and traits of both the resident and invader species (Lonsdale 1999). Initial invasion is often highly correlated with an increase in the amount of unused resources within the system (Davis et al. 2000). As with all plants, invading species must have access to resources such as light, nutrients, and water in order to establish and survive. These resources can become available due to declines in resource use by resident species or because resource supply has increased at a faster rate than resources can be sequestered by resident vegetation (Davis et al. 2000). In many systems, disturbance plays a significant role in altering resource availability via both of these processes. Disturbances such as fire and inappropriate grazing can result in damage to and removal of resident vegetation, decreasing competition for resources (Davis et al. 2000). These same disturbances also can act to increase gross resource supply by altering soil nutrient cycling which, in combination with a decline in uptake by resident species, can leave a surplus of available resources for use by invaders.

The invasion of arid rangelands in the Great Basin of the western United States by cheatgrass (*Bromus tectorum* L) is considered one of the most significant plant invasions in North America (D'Antonio and Vitousek 1992, Knapp 1996). Historically, the

landscape of the Great Basin consisted of arid shrublands dominated by sagebrush (*Artemisia* sp.) and native perennial herbaceous species (West and Young 1999) and ecological resistance to non-native species varied across gradients of available resources (Chambers et al. in press). European settlement in the mid-1800's initiated a series of disturbances that decreased invasion resistance across the landscape (Knapp 1996). Heavy grazing by domestic livestock reduced competition from native perennial herbaceous species (Belsky and Gelbard 2000, Keeley et al. 2003, Diamond 2009, Wisdom and Chambers 2009), formed safe sites (cracks and depressions) for cheatgrass germination (Evans and Young 1970, Facelli and Pickett 1991), and created N enriched soil patches through deposits of urine and dung (Belsky and Gelbard 2000). When cheatgrass was first introduced to the western U.S. from Eurasia in the late 1800's (likely in the hoofs, hair, or bedding of cattle) it encountered a resource-rich environment with reduced perennial herbaceous species that allowed it to rapidly spread and increase in abundance (Knapp 1996). Fine fuels contributed by cheatgrass resulted in the creation of an annual grass fire cycle (Whisenant 1990) which increased resource availability and resulted in progressive increases in the distribution and abundance of cheatgrass (Young and Evans 1978). Currently, over 80% of the rangelands in the Great Basin are invaded to some degree by cheatgrass (Pellant and Hall 1994) and cheatgrass invasion has replaced millions of hectares of native shrub and bunchgrass communities (West 1983, Whisenant 1990, Knapp 1996).

Although fire and grazing disturbances have significantly altered invasion resistance in the Great Basin, restoration of sagebrush shrublands dominated by cheatgrass may benefit from recreating a more conservative N cycle (Blumenthal et al.



2003, Norton et al. 2007, Brunson et al. 2010, Mazzola et al. 2011). My dissertation examined how resource availability influences the success of both cheatgrass and native species with three interrelated studies. In order to gain insight into how cheatgrass invasion is related to plant community characteristics and nutrient availability within the Great Basin, I conducted an observational field study (Chapter 1). In this study, I evaluated the plant community characteristics and soil nutrient availability associated with progressive cheatgrass invasion in a common and widely distributed sagebrush ecological site type. I held soil type constant and surveyed communities that varied in level of invasion: intact native sagebrush, native sagebrush with cheatgrass understory, cheatgrass-dominated, and cheatgrass die-off. I hypothesized that with increasing levels of cheatgrass invasion 1) soil nutrient availability would increase, 2) soil organic matter (SOM) would decrease, 3) cheatgrass nutritional content would increase, and 4) native species (represented by Sandberg bluegrass, *Poa secunda*) nutritional content would decrease. ANOVAs, principal components analysis (PCA), and multiple linear regressions were used to examine differences in soil and plant nutrients among invasion stages and based on the cover of different plant life forms. The results from this study are used to help explain soil changes involved in progressive invasion of cheatgrass in sagebrush ecosystems, and suggest potential mechanisms behind cheatgrass dominance.

In addition to the observational study, I also conducted field experiments to provide a more mechanistic understanding of the role of disturbance on nutrient availability and invasion and to address potential management implications (Chapters 2-3). The experiment outlined in Chapters 2 and 3 evaluated the effects of 4-5 years of repeated burning in a Wyoming big sagebrush ecological site type dominated by

cheatgrass in combination with litter removal and post-fire seeding. Chapter 2 focused primarily on nutrient dynamics and the main questions I sought to address were (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? Chapter 3 focused primarily on plant responses and the main questions I sought to address were (1) What are the direct and indirect effects of management treatments aimed at resource reduction (repeated burning, litter manipulation, seeding an annual competitor) on soil N availability and cheatgrass biomass, density, and reproduction over time? and (2) How do abiotic (precipitation and temperature) and biotic factors (other annual invaders) influence trends in soil N availability and cheatgrass biomass, density, and reproduction over time? In both chapters, I used Generalized Linear Mixed-effects Models (GLMM) to examine differences in nutrients and cheatgrass success among treatments and across time in litter intact and litter removed plots. I also developed multivariate conceptual models of likely effects of environmental variables and treatments on the response variables and evaluate hypothesized mechanisms to determine the immediate and long-term effects of the treatments on nutrient dynamics and cheatgrass success as well as the influence of environmental factors on the long-term trends.

Overall, this research increases our understanding of the role of disturbance and resource availability on the success of cheatgrass invasions in arid sagebrush shrublands. Furthermore, it may provide valuable information on techniques that could facilitate the restoration of cheatgrass dominated systems to more diverse plant communities.

## Literature cited

- Belsky, A. J., and J. L. Gelbard. 2000. Livestock grazing and weed invasions in the arid west. Oregon Natural Desert Association.
- Blumenthal, D. M., N. R. Jordan, and M. P. Russelle. 2003. Soil carbon addition controls weeds and facilitates prairie restoration. *Ecological Applications* **13**:605-615.
- Brunson, J. L., D. A. Pyke, and S. S. Perakis. 2010. Yield responses of ruderal plants to sucrose in invasive-dominated sagebrush steppe of the northern Great Basin. *Restoration Ecology* **18**:304-312.
- Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. *Nature* **405**:234-242.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**:63-87.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**:528-534.
- Diamond, J. M. 2009. Effects of targeted grazing and prescribed burning on fire behavior and community dynamics of a cheatgrass (*Bromus tectorum*)- dominated landscape. Utah State University, Logan, Utah.
- Keeley, J. E., D. Lubin, and C. J. Fotheringham. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications* **13**:1355-1374.
- Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert - History, persistence, and influences to human activities. *Global Environmental Change-Human and Policy Dimensions* **6**:37-52.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522-1536.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* **10**:689-710.
- Mazzola, M. B., J. C. Chambers, R. R. Blank, D. A. Pyke, E. W. Schupp, K. G. Allcock, P. S. Doescher, and R. S. Nowak. 2011. Effects of resource availability and propagule supply on native species recruitment in sagebrush ecosystems invaded by *Bromus tectorum*. *Biological Invasions* **13**:513-526.
- McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. *Bioscience* **38**:794-800.
- Norton, J. B., T. A. Monaco, and U. Norton. 2007. Mediterranean annual grasses in western North America: kids in a candy store. *Plant and Soil* **298**:1-5.
- Pellant, M., and C. Hall. 1994. Distribution of two exotic grasses on intermountain rangelands: status in 1992. Pages 109-112 *in* G. t. r. INT, editor.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* **52**:273-288.

- Singh, R. S., A. S. Raghubanshi, and J. S. Singh. 1991. Nitrogen mineralization in dry tropical savanna- effects of burning and grazing. *Soil Biology & Biochemistry* **23**:269-273.
- West, N. E. 1983. Great Basin-Colorado Plateau sagebrush semi-desert. Pages 331-349 *in* N. E. West, editor. *Temperate deserts and semi-deserts*. Elsevier Publishing Company, Amsterdam, The Netherlands.
- West, N. E., and J. A. Young. 1999. Vegetation of intermountain valleys and lower mountain slopes. Pages 255-284 *in* M. A. Barbour and W. D. Billings, editors. *North American Terrestrial Vegetation*. Cambridge University Press, New York, NY.
- Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. *in* E. M. R. McArthur, S. D. Smith, P. T. Tueller, editor. *Proceedings – Symposium on cheatgrass invasion, shrub die-off and other aspects of shrub biology and management*. USDA General Technical Report INT-276, Ogden, Utah, USA.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* **48**:607-615.
- Wisdom, M. J., and J. C. Chambers. 2009. A landscape approach for ecologically based management of Great Basin shrublands. *Restoration Ecology* **17**:740-749.
- Young, J. A., and R. A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. *Journal of Range Management* **31**:283-289.

Do soil nutrients change with progressive invasion of cheatgrass (*Bromus tectorum*) into sagebrush communities?

Rachel Jones  
Ecology, Evolution and Conservation Biology Graduate Group  
Dept. of Natural Resources & Environmental Science  
University of Nevada, Reno  
1000 Valley Road  
Reno, NV 89512

Jeanne C. Chambers  
US Forest Service, Rocky Mountain Research Station  
920 Valley Road  
Reno, NV 89512

David I. Board  
US Forest Service, Rocky Mountain Research Station  
920 Valley Road  
Reno, NV 89512

Dale W. Johnson  
Dept. of Natural Resources & Environmental Science  
University of Nevada, Reno  
1000 Valley Road  
Reno, NV 89512

## Abstract

Invasive species may alter soil properties, especially nutrient cycling, in ways that differ from native plants. Differences in plant-soil feedbacks between native and invasive species may help explain the success of invasive species and provide insights into community successional trajectories following invasion. We used a large-scale observational study to evaluate plant community characteristics, soil nutrient availability, and plant nutrient contents associated with progressive cheatgrass (*Bromus tectorum* L.) invasion in a broadly distributed sagebrush ecological type -loamy 10-12 precipitation zone/*Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush)/*Achnatherum thurberianum* (Thurber's needlegrass). We held soil type constant and surveyed 25 communities that varied in level of cheatgrass invasion (intact native sagebrush, sagebrush with cheatgrass understory, cheatgrass-dominated, and cheatgrass die-off). We hypothesized that with increasing levels of cheatgrass invasion 1) soil nutrient availability would increase, 2) soil organic matter (SOM) would decrease, 3) cheatgrass nutrient content would increase, and 4) Sandberg bluegrass (*Poa secunda*) nutrient content would decrease. Also, we expected that changes in soil and plant nutrient contents would be related to increasing cover of cheatgrass and decreasing cover of shrubs and native perennial herbaceous species. Results indicate that pools of soil resources such as Ca, Mg, total nitrogen (N), and SOM are not influenced by cheatgrass invasion, but that cheatgrass invasion was associated with decreased mineral N pools, especially of  $\text{NH}_4^+$ . As predicted, cheatgrass nutrient content increased and *P. secunda* nutrient content decreased as level of cheatgrass invasion increased. We also found that cheatgrass maintained a constant N concentration even when soil N changed, indicating

that cheatgrass may maintain nutrient contents via high nutrient use efficiency and/or soil mining while decreasing N availability for competitors. Results of our study along with similar and conflicting results from previous studies on effects of cheatgrass invasion on soil nutrient dynamics also indicate that spatial and temporal variability are extremely important for sampling soils and may affect study outcomes.

### **Key words**

*Artemisia tridentata*, *Poa secunda*, mineral nitrogen, soil organic matter, plant nutrient content, plant community composition

### **Introduction**

Invasive species are a well-documented and ubiquitous threat to biological diversity and ecosystem function (Lonsdale 1999) that can have long-term ecological consequences (Mack et al. 2000). It is well established that plants can modify the soil environment in ways that feedback to vegetation community composition and structure. Plants can affect soil moisture by creating pores in soil through root channeling (Angers and Caron 1998), shading and insulating the soil with litter and canopy cover (Hillel 1998, Raich and Tufekcioglu 2000), and active transpiration (Ehrenfeld et al. 2005). Plants can also alter nutrient cycles and soil resources (Hobbie 1992, Ehrenfeld 2003). Recently, it has been suggested that invasive species may alter soil properties in ways that differ from native plants (Schimel et al. 1991, Schimel et al. 1994, D'Antonio et al. 2009). These differences in plant-soil feedbacks between native and invasive species

may explain the success of invasive species and could provide insights into community successional trajectories following invasion (Ehrenfeld et al. 2001).

A major soil process that can differ between invaded and native ecosystems is nutrient cycling, in particular cycling of carbon (C) and nitrogen (N). For example, many invasive species have high growth rates and nutrient concentrations that can result in increases in rates of litter decomposition, mineralization, and nitrification (Ehrenfeld et al. 2001, Allison and Vitousek 2005, Liao et al. 2008). Also, non-native invasive species can alter the spatial heterogeneity of soil resources such as soil organic C. For example, in arid ecosystems soils beneath shrubs and tussock grasses are often enriched in organic matter and mineral nutrients compared to soil in interspaces because of accumulation of litter under shrubs and adjacent to longer-lived grasses (Schlesinger and Pilmanis 1998, Chambers 2001, Ehrenfeld et al. 2005). Changes to the vegetation community, such as those that occur during invasion of a non-native annual grass, could cause soil resources to become more spatially homogeneous (Cheng et al. 2004). If these changes to the soil environment increase the growth of the non-native species or enhance its competitive advantage over native species, a positive feedback loop could develop that promotes invasion and redirects the successional trajectory of the plant community.

Over the last century, low to mid-elevation sagebrush ecosystems in the Great Basin have been progressively invaded by cheatgrass (*Bromus tectorum* L.). Cheatgrass was first introduced from Eurasia in the late 1800's (Klemmedson and Smith 1964) and was thought to be dispersed in the dung and hair of cattle transported on railroads and in cattle bedding straw (Mack 1981). Intense grazing by domestic livestock removed many of the highly palatable native perennial herbaceous species (Belsky and Gelbard 2000,



Wisdom and Chambers 2009), increased soil resources, and provided the necessary conditions for establishment and spread of cheatgrass. Grazing worked in concert with fire to increase resource availability and promote cheatgrass invasion. Fire in sagebrush ecosystems results in pulses in soil resources, especially ammonium ( $\text{NH}_4^+$ ) (Blank et al. 1994a, Blank et al. 1996, Stubbs and Pyke 2005). Cheatgrass readily established in post-fire systems. The result has been an increase in fine, flammable fuels and the creation of an annual grass-fire cycle characterized by shortened return intervals and larger, more contiguous fires (D'Antonio and Vitousek 1992, Brooks et al. 2004). This fire cycle is resulting in the progressive elimination of sagebrush and other fire-intolerant species and facilitating further cheatgrass invasion (Link et al. 2006). Currently, over 80% of rangelands in the Great Basin are invaded by cheatgrass and more than 60% of intact sagebrush communities are at risk of invasion if disturbed (Pellant and Hall 1994).

Considerable attention has been given to the possibility that cheatgrass may increase soil nutrient availability and provide a positive feedback to its own persistence and spread. However, with the exception of soil N, there is little published research on the topic. Studies comparing soil nutrients in paired native shrubland and cheatgrass-dominated sites have reported increased soil N under cheatgrass monocultures (Booth et al. 2003b, Norton et al. 2004, Blank 2008, Hooker et al. 2008) and attributed it to greater biomass turnover and faster rates of soil N cycling and redistribution of N in surface soils (Hooker et al. 2008). Although few data exist, it has been suggested that cheatgrass invasion may enhance N-fixation by free-living bacteria, increase deposition of N via capture of aeolian sources, or release of N resources via death of competitor species (Blank 2008). Studies examining the effect of cheatgrass invasion in arid  $\text{C}_3$  and  $\text{C}_4$

grasslands found variation in soil N availability over time. In the first several years following invasion, N availability was lower in invaded than non-invaded soils, likely due to increased deposition of cheatgrass litter with high C:N and lignin:N which decreased rates of net N mineralization and nitrification (Evans et al. 2001, Rimer and Evans 2006). Studies at these sites 4 to 8 years after invasion found that soil N availability in invaded communities had increased, potentially due to changes in the activity and composition of bacterial and fungal communities (Belnap and Phillips 2001, Belnap et al. 2005, Schaeffer et al. 2012), as well as SOM decomposition and utilization and redistribution of subsurface nitrate ( $\text{NO}_3^-$ ) by cheatgrass (Sperry et al. 2006).

In previous foundational studies examining the mechanisms by which cheatgrass can influence soil nutrient cycling and feedback to its own invasion, soil samples were typically collected from just one site that contained patches that were either invaded or non-invaded by cheatgrass (Evans et al. 2001, Rimer and Evans 2006, Sperry et al. 2006, Blank 2008). Studies that did sample several locations (Norton et al. 2004) did so over a range of soil types. To our knowledge, no published studies have examined how progressive cheatgrass invasion influences soil and plant nutrients at the plant community or landscape scale. To understand how cheatgrass invasion influences soil nutrients at the plant community or landscape scale, we examined multiple stages of invasion (intact native sagebrush, sagebrush with cheatgrass understory, cheatgrass-dominated, and cheatgrass die-off) at multiple independent locations with the same soil type. This large-scale observational study was designed to evaluate the plant community characteristics, soil nutrient availability, and plant nutrient contents that are associated with progressive cheatgrass invasion in a broadly distributed sagebrush ecological type. Although plant

nutrients are often overlooked in studies of invasion effects on soil nutrients, they are important for understanding the mechanisms involved. We measured the nutritional contents and concentrations of cheatgrass and a native perennial competitor, Sandberg bluegrass (*Poa secunda*). ANOVAs, principal components analysis (PCA) and multiple linear regressions were used to examine differences in soil and plant nutrients among invasion stages and for the different plant life forms. Based on results of previous studies, we hypothesized that with increasing levels of cheatgrass invasion 1) soil nutrient availability would increase, 2) SOM would decrease, 3) cheatgrass nutrient content would increase, and 4) *P. secunda* nutrient content would decrease. In addition, we hypothesized that changes in soil and plant nutrients in response to level of invasion would be related to increasing cover of cheatgrass and decreasing cover of shrubs and native perennial herbaceous species. Tracking these plant-soil feedbacks may help explain the mechanisms involved in the progressive invasion and dominance of cheatgrass in these ecosystems.

## **Methods**

### Site selection

Twenty-one sites were selected that represented three stages of cheatgrass invasion: 1) 8 native intact sites with 0-5% invasion and no recent fires (< 30 years since fire), 2) 5 native sites with 5-20% invasion and no recent fires, and 3) 8 cheatgrass-dominated sites with recent (< 5 years) fire. We also included 4 sites that represent another stage of invasion, cheatgrass die-off, which is a poorly understood phenomenon in which cheatgrass fails to emerge, establish, or reproduce in areas that supported dense

cheatgrass stands in previous years (Baughman and Meyer 2013). The sites that we chose were a year or two post-die-off and had some cheatgrass plants, but still had significantly less cheatgrass biomass than cheatgrass-dominated sites.

Sites were selected after reviewing Bureau of Land Management (BLM) fire and soil maps and consulting with land managers from the BLM Winnemucca Field Office. All sites had approximately the same slope (0-5%) and elevation (1297-1607m), and were located far enough apart to ensure statistical independence (at least 1.5 km distant). Mean temperatures at these sites typically range from 19°C in July to -1°C in January and all sites are located in the 254-304 mm precipitation zone with most of the precipitation arriving as snow in fall and winter (National Climate Data Center). It should be noted that the sites experienced below-average precipitation (79 mm from September 1, 2012-April 30, 2013 and 99 mm from September 1, 2012-June 30, 2013) during the collection year. Unlike previous studies of effects of cheatgrass on soil and plant nutrients, the soils at all sites were similar. Soils were classified as sandy-loam, mixed, superactive, mesic, Durinodic Xeric Haplocambids (Denny 2002). Also, sites were representative of the same ecological site type, which was Loamy 10-12 precipitation zone/*Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush)/*Achnatherum thurberianum* (Thurber's needlegrass). Finally, all the sites had the same current grazing regime, which was grazing from summer through fall.

#### Field sampling

At each site, six 50-m long transects were established parallel to each other and spaced 20 m apart. Shrub cover was measured (described below) and composite samples

of soils and litter biomass were collected along these transects before active growth began in early-mid April 2013. The transects were resampled during peak production in early-mid June 2013 when herbaceous species and ground cover were estimated and composite samples of herbaceous vegetation were collected for nutrient analysis.

Cover of all shrub species was measured along each transect using the line-intercept method. The length of each shrub that intercepted the transect line was measured and then all of the individual lengths were added together to calculate the total shrub distance. Percent shrub cover was determined by dividing the total shrub distance by the total transect distance.

Litter and soil samples were collected systematically every 5m along each transect for a total of 12 samples per transect ( $n = 72$  per site). Prior to collecting soil, litter biomass was removed from a 15x15cm patch at each sampling location along the transect. All samples from two adjacent transects were placed in a bucket and homogenized. A subsample of this material was returned to the lab for analysis ( $n = 3$  subsamples per site). After litter biomass was removed, soil samples were collected from the same locations with a punch auger to a depth of 0-10 cm. All samples from two adjacent transects were placed in a bucket and homogenized. A subsample of this material was returned to the lab for analysis ( $n = 3$  subsamples per site). Litter biomass was oven dried at 60° C, ground in a Udy mill, and then sent to the Soil, Water, and Forage Analytical Laboratory (SWFAL) at Oklahoma State University where it was analyzed for total C and N using a LECO TruSpec CN Analyzer (LECO Corp., St. Joseph, MI, USA). Soil samples were air-dried and sent to SWFAL where they were analyzed for %OM (organic matter) and %TN (total nitrogen) using a LECO TruSpec

CN Analyzer (LECO Corp., St. Joseph, MI, USA), NO<sub>3</sub>-N and NH<sub>4</sub>-N using KCl extraction and quantification with a Lachat® autoanalyzer, Mg and Ca using Mehlich 3 extraction and quantification with a Spectro ICP, and SO<sub>4</sub>-S using calcium phosphate monobasic extraction and quantification with a Spectro ICP.

In June, a 0.1 m<sup>2</sup> quadrat was placed along the transect adjacent to the litter and soil sampling location and was used to visually estimate percent basal and aerial cover of herbaceous vegetation by species, litter, bare ground, rocks, cryptogams, and livestock dung. Standard protocols were used and frequent calibrations among estimators were conducted (Elzinga et al. 1998). These estimates were used to summarize species cover by functional group (i.e., perennial native grasses, perennial native forbs, annual native forbs, annual invasive grasses, and annual invasive forbs). After cover had been estimated, aboveground biomass of cheatgrass, *Poa secunda*, and all other herbaceous plants were harvested from the same quadrats. Samples were homogenized by species for every two transects (n = 3 subsamples per site) as was done for litter and soils. If either cheatgrass or *P. secunda* were not present within the quadrat or sufficient biomass for one of the species was not collected, an additional sample was taken nearby from within the site. Homogenized vegetation subsamples were returned to the lab where they were oven dried at 60°C, ground, and weighed. Vegetation subsamples were then sent to SWFAL for analysis of total C and N using a LECO TruSpec CN Analyzer (LECO Corp., St. Joseph, MI, USA).

Data analysis

In order to determine if soil and plant nutrients differed based on stage of invasion (native intact, native with cheatgrass understory, cheatgrass-dominated, and cheatgrass die-off), least squares ANOVAs were performed using JMP 11 (SAS Institute, Inc, Cary, NC). Data were first assessed and transformed as necessary to meet assumptions of normality. 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 ( $\alpha=0.05$ ).

Principal components analysis (PCA) was used to 1) relate differences in soil nutrients among stages of invasion to plant community composition and microsite characteristic gradients and 2) relate differences in plant nutrients among stages of invasion to soil nutrients and/or to plant community composition and microsite characteristics (JMP 11, SAS Institute, Inc, Cary, NC). Variables were examined for linearity using bivariate scatter plots and were deemed suitable for multivariate ordination (McGarigal et al. 2000). Principal components were not rotated, therefore maximizing the sum of the squared factor loadings. Only principal components with eigenvalues  $> 1.0$  were extracted and only the first two components were retained since the strongest covariation among variables are found within these components (McCune and Grace 2002). Factor loadings  $\geq |0.5|$  were considered important to describe each principal component (McGarigal et al. 2000) and these loadings gave insight into important variables influencing differences in levels of cheatgrass invasion.

After significant factors were determined with PCA, linear regressions were used to 1) determine which of the plant community composition and microsite characteristics were associated with differences in soil resources and 2) determine which of the soil

resources and/or plant community composition and microsite characteristics were associated with differences in plant nutrients (JMP 11, SAS Institute, Inc, Cary, NC). In order to prevent issues associated with multicollinearity, highly correlated variables ( $r > |0.7|$ ) were first removed from analyses which included litter cover, bare ground cover, perennial native grass cover, and annual invasive forb cover. Model selection and model averaging was used to identify candidate models and Akaike information criterion (AIC) was used to compare fit among all candidate models. Multiple regressions were then run to determine the effect of the variables defined in the top models on soil nutrients and plant nutrients.

## Results

### Differences among sites

A PCA analysis of life form covers and other cover variables (litter, bare ground, rocks, etc.) converted the data into two principal components, which together accounted for 56.1% of the total variation from the original variables (Fig 1). Component 1 (eigenvalue [EV] = 5.8749, 45.2% of total variation) generally represented a native to invasive cover gradient. High positive factor loadings ( $> 0.5$ ) included (from highest to lowest) bare ground cover, shrub cover, perennial native grass cover (dominant species- *Poa secunda* and *Elymus elymoides*), cryptogram cover, and perennial native forb cover (dominant species- *Phlox longifolia*). High negative factor loadings ( $< -0.5$ ) included (from highest to lowest) litter cover, annual invasive grass cover (dominant species- *Bromus tectorum*), annual invasive forb cover (dominant species- *Sisymbrium altissimum*), and perennial invasive forb cover (dominant species- unknown thistle).



Component 2 (EV = 1.4139, 10.876% of variation) did not represent a defined cover gradient and had a high positive factor loading for annual native forb cover (dominant species- *Collinsia parviflora*) and a high negative factor loading for gravel cover. A scatter plot of components 1 and 2 revealed that the four stages of invasion (native intact sagebrush, native sagebrush with cheatgrass understory, cheatgrass-dominated, and cheatgrass die-off) grouped predictably based on plant cover and microsite characteristics. Both native intact sagebrush and native sagebrush with cheatgrass understory site types had high cover of shrubs and native herbaceous species. Native intact sagebrush sites had more bare ground and native perennial species cover and native sagebrush sites with cheatgrass understory had more shrub cover. Both cheatgrass-dominated and cheatgrass die-off sites had high cover of invasive species (including *B. tectorum*, *S. altissimum*, and *Ceratocephala testiculata*); however, cheatgrass-dominated sites had more litter and annual invasive grass cover than die-off sites.

#### Effects on soil resources

$\text{NH}_4^+$  was the only soil resource that differed significantly among stages of invasion (Table 1). Native intact sagebrush sites had the highest soil  $\text{NH}_4^+$ , native sagebrush sites with cheatgrass understory and cheatgrass-dominated sites had the lowest soil  $\text{NH}_4^+$ , and cheatgrass-die off sites had intermediate values ( $p < 0.05$ ).  $\text{NO}_3^-$ , which was the dominant form of soil mineral N, was also generally lower in cheatgrass-dominated sites; however this trend wasn't statistically significant ( $p = 0.1636$ ).

Model selection revealed that shrub cover, annual invasive grass cover, and annual native forb cover (which included one species of native mustard, *Descurainia*

*pinnata*) were the most important cover variables associated with soil  $\text{NH}_4^+$  (Table 2). Of these variables, only annual invasive grass cover and annual native forb cover had individually significant relationships with soil  $\text{NH}_4^+$ . Annual invasive grass cover was associated with decreased soil  $\text{NH}_4^+$  while annual native forb cover was associated with increased soil  $\text{NH}_4^+$  (Figure 2).

#### Effects on plant nutrients

Plant N contents ( $\text{gN/m}^2$ ) differed significantly among invasion stages for cheatgrass, *P. secunda*, and other herbaceous plants (Table 1). Cheatgrass N content was higher in cheatgrass-dominated and cheatgrass die-off sites than in native intact sagebrush sites while native sagebrush with cheatgrass understory sites had intermediate cheatgrass N contents ( $p < 0.05$ ). *P. secunda* N content was higher in native intact sagebrush sites than cheatgrass-dominated sites while native sagebrush with cheatgrass understory and cheatgrass die-off sites had intermediate *P. secunda* N contents ( $p < 0.05$ ). Other plant N content was higher in cheatgrass-dominated and cheatgrass die-off sites than native sagebrush sites with cheatgrass in the understory while native intact sagebrush sites had intermediate other plant N contents ( $p < 0.05$ ). It should be noted that the composition of other plants differed based on site but was typically composed of non-native annuals in cheatgrass-dominated and cheatgrass die-off sites and native perennials and annuals in native sagebrush sites. Plant N concentrations (%TN) also differed among invasion stages for *P. secunda* and other plants; however there were no significant differences in cheatgrass N concentrations (Table 1). However, because nutrient contents

take mass into consideration and therefore provide a more accurate reflection of plant nitrogen relations, further analysis of nutrient concentrations are not discussed.

Model averaging using soil nutrients as predictor variables revealed few variables that were strongly associated with plant N contents (Table 3). Soil total N (%TN) was the most important variable associated with cheatgrass N content; however, the relationship between the two variables was not significant. Soil  $\text{NH}_4^+$  was the most important variable in relation to *P. secunda* N content and increases in soil  $\text{NH}_4^+$  were weakly associated with increases in *P. secunda* N content (Fig. 3). There were no significant associations between any soil nutrients and other plant N contents

Model averaging using plant and microsite cover as predictor variables revealed many variables that were strongly associated with plant N contents (Table 4). Shrub, gravel, and annual invasive grass covers were the most important variables associated with cheatgrass N content. Of these variables, only shrub cover had an individually significant relationship with cheatgrass N content and increases in shrub cover were associated with decreases in cheatgrass N content (Fig. 4). Perennial native grass and annual invasive grass covers were the most important variables associated with *P. secunda* N content. Of these variables, only annual invasive grass cover had an individually significant relationship with *P. secunda* N content and increases in annual invasive grass cover were associated with decreases in *P. secunda* N content (Fig. 5). Shrub, gravel, rock and annual invasive forb covers were the most important variables associated with other plant N content, however, none of these variables had individually significant relationships with other plant N content.

## Discussion

It is well established that plant-soil feedbacks are often altered following the introduction of non-native species and these changes may explain the persistence and spread of invasive species (Schimel et al. 1991, Ehrenfeld et al. 2001, D'Antonio et al. 2009). In recent years, several studies have been conducted to examine changes in soil resources following invasion by cheatgrass and many of them have found that nutrients such as N are typically elevated in cheatgrass-dominated sites (Norton et al. 2004, Blank 2008, Hooker et al. 2008). However, limited replication and lack of control over pre-existing differences in soil resources may have influenced results. Here we examined plant-soil feedbacks across 25 Great Basin sites that differed in level of cheatgrass invasion, and asked how invasion affected soil resources and plant nutrient contents and concentrations.

### Effects of plant community composition on soil nutrients

Based on the results of previous studies, we hypothesized that soil nutrient availability would increase and SOM would decrease with increasing levels of cheatgrass invasion. However, in our larger-scale study, a majority of soil nutrients, including  $\text{SO}_4^{2-}$ , Ca, Mg, OM, and TN, did not differ among the four stages of invasion. One explanation for our findings could be differences in soil sampling techniques among studies. To maintain consistency, we sampled soils at all sites systematically along transects and then homogenized soil samples to get a soil signature for the entire site. However, other studies have typically collected soils under shrubs and in interspaces because soil resources are often highly heterogeneous across the landscape and accumulate primarily

under shrubs in coppice dune or resource islands (Charley and West 1975, Schlesinger et al. 1996). Therefore, our sampling approach may have averaged out some of the heterogeneity in the sagebrush systems that other studies on effects of cheatgrass invasion on soil nutrients included by sampling based on microsites (e.g., Norton et al. 2004, Blank 2008, Hooker et al. 2008). Another explanation for the similarity in soil nutrients among our sites could be that we sampled similar soils with the same geologic origin that were dominated by sagebrush historically. Soil physical characteristics have a large influence on soil nutrients, especially OM and TN, and the similarity of our sites could help explain our results. For example, finer textured soils tend to store more C and N than coarse grained soils. Therefore, a relatively recent invasion of cheatgrass (<50 years) may not have significantly influenced soil physical characteristics or soil nutrients.

We found that  $\text{NH}_4^+$  differed among invasion stages and was negatively associated with increasing cheatgrass cover. Native sagebrush sites and cheatgrass die-off sites, which both had little to no cheatgrass cover, had the highest amounts of  $\text{NH}_4^+$  while native sagebrush sites with cheatgrass understory and cheatgrass-dominated sites had the lowest amounts of  $\text{NH}_4^+$ . These results are contrary to our hypothesis and to the findings of previous studies which found higher soil mineral N under cheatgrass monocultures compared to uninvaded shrublands (Booth et al. 2003b, Norton et al. 2004, Blank 2008, Hooker et al. 2008) and in grasslands that had been invaded by cheatgrass longer than 4 years (Sperry et al. 2006). However, our findings are similar to those of studies conducted in grasslands in the first years following invasion (Evans et al. 2001, Rimer and Evans 2006, Sperry et al. 2006). These studies attributed lower soil mineral N in cheatgrass-dominated sites to high C:N and lignin:N ratios of cheatgrass litter

compared to native grasses, resulting in reduced net N mineralization. In our study, litter C:N, which was not divided by species but was the combined herbaceous litter collected from sites, did not significantly differ among invasion stages and differences in the quality of litter inputs to soils is not a good explanation for our results. Instead, decreases in  $\text{NH}_4^+$  under high densities of cheatgrass may be related to preferential assimilation of  $\text{NH}_4^+$  by cheatgrass, as found in other studies (Grogan et al. 2000, Johnson et al. 2011). In addition, cheatgrass-dominated soils have been shown to have high rates of nitrification (Norton et al. 2008, Johnson et al. 2011) which could shift the dominant form of mineral N from  $\text{NH}_4^+$  to  $\text{NO}_3^-$  in these systems and result in depleted  $\text{NH}_4^+$ .

It is difficult to determine the reason for the lack of consensus in the literature about the effect of cheatgrass invasion on soil mineral N. One potential explanation could be temporal variability in soil collections across studies. We collected our soils prior to the start of active plant growth in early-mid April to avoid differences in soil nutrients due to plant uptake. Interestingly, studies that also collected soils early in the spring (Evans et al. 2001, Rimer and Evans 2006) had similar findings to ours. In contrast, studies that collected soils in late spring or summer (Norton et al. 2004, Sperry et al. 2006, Blank 2008) had different results than ours, specifically more mineral N in cheatgrass invaded soils. Cheatgrass typically grows early in spring, sets seed and senesces in late spring, and remains dormant through the summer. Greater soil mineral N beneath cheatgrass monocultures in mid-summer therefore could potentially be attributable to continued mineralization but lack of plant N uptake after cheatgrass has senesced. This explanation also was suggested in a study in which soils were sampled throughout the growing season and surface mineral N concentrations in cheatgrass-

dominated sites were only higher than in sagebrush sites in the summer (Hooker et al. 2008). It also has been suggested that hydraulic redistribution can occur through the root systems of fully senesced plants (Leffler et al. 2005) and soil nutrients, particularly  $\text{NH}_4^+$ , are most available to plants when soil water is high enough to facilitate diffusion to root surfaces (Ryel et al. 2010). Therefore, in previous studies, not only could senesced cheatgrass plants have less N uptake than intact shrublands, but they might be increasing surface  $\text{NH}_4^+$  concentrations by increasing soil moisture.

Another potential reason for the difference in findings among studies of the effect of cheatgrass invasion on soil mineral N could be spatial variability and replication. Our study is the first to our knowledge that sampled soil and plant nutrients along a continuum of cheatgrass invasion in a large number of sites. Other studies typically made comparisons of paired intact and cheatgrass-dominated patches situated within the same site (Evans et al. 2001, Norton et al. 2004, Rimer and Evans 2006, Sperry et al. 2006, Blank 2008, Hooker et al. 2008) with little to no spatial replication. Sampling a multitude of sites is time-intensive and costly, however, this sampling scheme makes it more possible to evaluate whether cheatgrass actually altered the soils that it invaded or whether it invaded soil patches within the site with suitable soil nutrients. Also, only comparing uninvaded to heavily invaded sites does not relate cheatgrass-induced soil changes to the density of invasion (Ehrenfeld 2010).

#### Effects on plant nutrients

We hypothesized that cheatgrass nutrient content would increase and *P. secunda* nutrient content would decrease with increasing cheatgrass invasion. Our findings

support these hypotheses and, because nutrient content takes into account plant mass, they are likely explained by differences in the biomasses of these two species in response to competition. Cheatgrass biomass increased and *P. secunda* biomass decreased as the level of cheatgrass invasion increased. Cheatgrass may have had a competitive advantage over *P. secunda* due to high nutrient use efficiency which has been found in previous studies (James et al. 2011) and was indicated in our study by the fact that cheatgrass N concentrations did not differ among invasion stages. In addition, it has been proposed that cheatgrass may be able to maintain high N uptake regardless of plant community composition and soil nutrients because it can access and assimilate recalcitrant forms of soil N via chemical changes caused by plant roots (soil mining; Johnson et al. 2011, Perkins et al. 2011).

The nutrient content of other plants is also likely explained by differences in biomass. Both the species composition and abundance of other plants differed across the levels of cheatgrass invasion. Native intact sagebrush and native sagebrush with cheatgrass in the understory sites typically contained a low biomass of native perennials and annuals while cheatgrass-dominated and cheatgrass die-off sites typically contained a high biomass of invasive annuals. Also, studies comparing the ecophysiological characteristics of native and invasive plants indicate that non-native invaders are more likely to have high growth and nutrient uptake rates than native species (Ehrenfeld 2003). Therefore, sites with a higher composition of invasive species should have higher nutrient contents than sites with a higher composition of native species.

## Conclusions



The results of our study indicate that cheatgrass can alter plant available soil nutrients and may decrease mineral N pools to the detriment of competitors while maintaining its own nutrient concentrations and contents via high nutrient use efficiency and/or soil mining. If these findings are correct, it could provide further insight into the success of cheatgrass invasions. In addition, the results of our study along with similar and conflicting results from previous studies on the role of cheatgrass invasion in soil nutrient dynamics indicate that spatial and temporal variability are extremely important for soil collections and may affect study outcomes. Because of time and budget constraints, scientists often must choose between maximizing spatial variability or temporal variability. We suggest that, in order to increase the generalization of results to the system of interest, spatial variability may be more important; however, the timing of soil collections during the growing season should be selected carefully because of the implications of plant growth and nutrient uptake. Furthermore, because of the potential for pre-existing differences in soils to affect results, soil types should be considered when setting up similar studies. Expanding efforts to sample across time on multiple soil types would clearly increase our understanding of complex plant-soil feedbacks in these invaded systems.

### **Acknowledgement**

We thank M. Hynes, M. Zielinski, R. Burton, and M. Whalen for help with site selection and C. Dencker for help in the field. Funding was provided by the U.S. Forest service with assistance from a UNR GSA research grant awarded to R. Jones. We thank E. Leger, P. Verburg, and T. Albright for valuable comments.

### Literature cited

- Allison, S. D., and P. M. Vitousek. 2005. Responses of extracellular enzymes to simple and complex nutrient inputs. *Soil Biology & Biochemistry* **37**:937-944.
- Angers, D. A., and J. Caron. 1998. Plant-induced changes in soil structure: Processes and feedbacks. *Biogeochemistry* **42**:55-72.
- Baughman, O. W., and S. E. Meyer. 2013. Is *Pyrenophora semeniperda* the cause of downy brome (*Bromus tectorum*) die-offs? *Invasive Plant Science and Management* **6**:105-111.
- Belnap, J., and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: Response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications* **11**:1261-1275.
- Belnap, J., S. L. Phillips, S. K. Sherrod, and A. Moldenke. 2005. Soil biota can change after exotic plant invasion: does this affect ecosystem processes? *Ecology* **86**:3007-3017.
- Belsky, A. J., and J. L. Gelbard. 2000. Livestock grazing and weed invasions in the arid west. Oregon Natural Desert Association.
- Blank, R. R. 2008. Biogeochemistry of plant invasion: A case study with downy brome (*Bromus tectorum*). *Invasive Plant Science and Management* **1**:226-238.
- Blank, R. R., L. Abraham, and J. A. Young. 1994. Soil heating, nitrogen, cheatgrass, and seedbed microsites. *Journal of Range Management* **47**:33-37.
- Blank, R. R., F. L. Allen, and J. A. Young. 1996. Influence of simulated burning of soil-litter from low sagebrush, squirreltail, cheatgrass, and medusahead on water-soluble anions and cations. *International Journal of Wildland Fire* **6**:137-143.
- Booth, M. S., M. M. Caldwell, and J. M. Stark. 2003a. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. *Journal of Ecology* **91**:36-48.
- Booth, M. S., J. M. Stark, and M. M. Caldwell. 2003b. Inorganic N turnover and availability in annual- and perennial-dominated soils in a northern Utah shrub-steppe ecosystem. *Biogeochemistry* **66**:311-330.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *Bioscience* **54**:677-688.
- Chambers, J. C. 2001. *Pinus monophylla* establishment in an expanding *Pinus-Juniperus* woodland: Environmental conditions, facilitation and interacting factors. *Journal of Vegetation Science* **12**:27-40.
- Charley, J. L., and N. E. West. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *Journal of Ecology* **63**:945-963.
- Cheng, X. L., S. Q. An, S. R. Liu, and G. Q. Li. 2004. Micro-scale spatial heterogeneity and the loss of carbon, nitrogen and phosphorus in degraded grassland in Ordos Plateau, northwestern China. *Plant and Soil* **259**:29-37.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**:63-87.

- Denny, D. W. 2002. Soil survey of Humboldt County, Nevada, East Part, part 1. US Department of Agriculture, Natural Resources Conservation Service, Reno, NV, USA.
- D'Antonio, C. M., J. C. Chambers, R. Loh, and J. T. Tunison. 2009. Applying ecological concepts to the management of widespread grass invasions. Pages 123-149 in R. L. Inderjit, editor. *Management of Invasive Weeds*. Springer, Netherlands.
- Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* **6**:503-523.
- Ehrenfeld, J. G. 2010. Ecosystem Consequences of Biological Invasions. *Annual Review of Ecology, Evolution, and Systematics*, Vol 41 **41**:59-80.
- Ehrenfeld, J. G., P. Kourtev, and W. Z. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* **11**:1287-1300.
- Ehrenfeld, J. G., B. Ravit, and K. Elgersma. 2005. Feedback in the plant-soil system. *Annual Review of Environment and Resources* **30**:75-115.
- Elzinga, C. L., D. W. Salzer, and J. W. Willoughby. 1998. Measuring and monitoring plant populations. U.S. Department of the Interior, Bureau of Land Management, Denver, CO.
- Evans, R. D., R. Rimer, L. Sperry, and J. Belnap. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications* **11**:1301-1310.
- Goergen, E. M., E. A. Leger, and E. K. Espeland. 2011. Native Perennial Grasses Show Evolutionary Response to *Bromus tectorum* (Cheatgrass) Invasion. *Plos One* **6**.
- Grogan, P., T. D. Bruns, and F. S. Chapin. 2000. Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. *Oecologia* **122**:537-544.
- Hillel, D. 1998. *Environmental Soil Physics*. Academic, San Diego, CA.
- Hobbie, S. E. 1992. Effects of plant-species on nutrient cycling. *Trends in Ecology & Evolution* **7**:336-339.
- Hooker, T., J. Stark, U. Norton, A. J. Leffler, M. Peek, and R. Ryel. 2008. Distribution of ecosystem C and N within contrasting vegetation types in a semiarid rangeland in the Great Basin, USA. *Biogeochemistry* **90**:291-308.
- Johnson, B. G., D. W. Johnson, J. C. Chambers, and R. R. Blank. 2011. Fire effects on the mobilization and uptake of nitrogen by cheatgrass (*Bromus tectorum* L.). *Plant and Soil* **341**:437-445.
- Klemmedson, J. O., and J. G. Smith. 1964. Cheatgrass (*Bromus Tectorum* L.). *Botanical Review* **30**:226-262.
- Leffler, A. J., M. S. Peek, R. J. Ryel, C. Y. Ivans, and M. M. Caldwell. 2005. Hydraulic redistribution through the root systems of senesced plants. *Ecology* **86**:633-642.
- Liao, C. Z., R. H. Peng, Y. Q. Luo, X. H. Zhou, X. W. Wu, C. M. Fang, J. K. Chen, and B. Li. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytologist* **177**:706-714.
- Link, S. O., W. G. Glendon, and J. L. Downs. 1990. The Effect of Water Stress on Phenological and Ecophysiological Characteristics of Cheatgrass and Sandberg's Bluegrass. *Journal of Range Management* **43**:506-513.
- Link, S. O., C. W. Keeler, R. W. Hill, and E. Hagen. 2006. *Bromus tectorum* cover mapping and fire risk. *International Journal of Wildland Fire* **15**:113-119.

- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522-1536.
- Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America- An ecological chronicle. *Agro-Ecosystems* **7**:145-165.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* **10**:689-710.
- McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.
- McGarigal, K., S. Cushman, and S. Stafford. 2000. Multivariate statistics for wildlife and ecology research. Springer-Verlag, New York, New York, USA.
- Melgoza, G., and R. S. Nowak. 1991. Competition between cheatgrass and 2 native species after fire- Implications from observations and measurements of root distribution. *Journal of Range Management* **44**:27-33.
- Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003. Contrasting responses of intermountain west grasses to soil nitrogen. *Journal of Range Management* **56**:282-290.
- Monaco, T. A., S. B. Monsen, B. N. Smith, and L. D. Hansen. 2005. Temperature-dependent physiology of *Poa secunda*, a cool season grass native to the Great Basin, United States. *Russian Journal of Plant Physiology* **52**:653-658.
- Norton, J. B., T. A. Monaco, J. M. Norton, D. A. Johnson, and T. A. Jones. 2004. Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. *Journal of Arid Environments* **57**:445-466.
- Norton, U., A. R. Mosier, J. A. Morgan, J. D. Derner, L. J. Ingram, and P. D. Stahl. 2008. Moisture pulses, trace gas emissions and soil C and N in cheatgrass and native grass-dominated sagebrush-steppe in Wyoming, USA. *Soil Biology & Biochemistry* **40**:1421-1431.
- Pellant, M., and C. Hall. 1994. Distribution of two exotic grasses on intermountain rangelands: status in 1992. Pages 109-112 in G. t. r. INT, editor.
- Perkins, L. B., D. W. Johnson, and R. S. Nowak. 2011. Plant-induced changes in soil nutrient dynamics by native and invasive grass species. *Plant and Soil* **345**:365-374.
- Phillips, A. J. 2012. Phenotypic plasticity within the native perennial grass, *Poa secunda* (Sandberg bluegrass), an important component of the Western United States sagebrush grassland vegetation. University of Nevada, Reno, Reno, NV.
- Raich, J. W., and A. Tufekcioglu. 2000. Vegetation and soil respiration: Correlations and controls. *Biogeochemistry* **48**:71-90.
- Rimer, R. L., and R. D. Evans. 2006. Invasion of downy brome (*Bromus tectorum* L.) causes rapid changes in the nitrogen cycle. *American Midland Naturalist* **156**:252-258.
- Ryel, R. J., A. J. Leffler, C. Ivans, M. S. Peek, and M. M. Caldwell. 2010. Functional differences in water-use patterns of contrasting life forms in Great Basin steppelands. *Vadose Zone Journal* **9**:548-560.

- Schaeffer, S. M., S. E. Ziegler, J. Belnap, and R. D. Evans. 2012. Effects of *Bromus tectorum* invasion on microbial carbon and nitrogen cycling in two adjacent undisturbed arid grassland communities. *Biogeochemistry* **111**:427-441.
- Schimel, D. S., B. H. Braswell, E. A. Holland, R. McKeown, D. S. Ojima, T. H. Painter, W. J. Parton, and A. R. Townsend. 1994. Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. *Global Biogeochemical Cycles* **8**:279-293.
- Schimel, D. S., T. G. F. Kittel, A. K. Knapp, T. R. Seastedt, W. J. Parton, and V. B. Brown. 1991. Physiological interactions along resource gradients in a tallgrass prairie. *Ecology* **72**:672-684.
- Schlesinger, W. H., and A. M. Pilmanis. 1998. Plant-soil interactions in deserts. *Biogeochemistry* **42**:169-187.
- Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. E. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* **77**:364-374.
- Sperry, L. J., J. Belnap, and R. D. Evans. 2006. *Bromus tectorum* invasion alters nitrogen dynamics in an undisturbed arid grassland ecosystem. *Ecology* **87**:603-615.
- Stubbs, M. M., and D. A. Pyke. 2005. Available nitrogen: A time-based study of manipulated resource islands. *Plant and Soil* **270**:123-133.
- Tausch, R. J., P. E. Wigand, and J. W. Burkhardt. 1993. Viewpoint: Plant Community Thresholds, Multiple Steady States, and Multiple Successional Pathways: Legacy of the Quaternary? *Journal of Range Management* **46**:439-447.
- Wisdom, M. J., and J. C. Chambers. 2009. A landscape approach for ecologically based management of Great Basin shrublands. *Restoration Ecology* **17**:740-749.

Table 1. Means and standard errors for soil and plant nutrients among ecosystem site types. Significant differences among site types indicated with asterisks ( $p < 0.05$ ) and Tukey's comparisons are indicated with upper-case letters.

	Native intact sagebrush	Native sagebrush with cheatgrass	Cheatgrass- dominated	Cheatgrass die-off
<b>A. Soil nutrients</b>				
SO <sub>4</sub> <sup>2-</sup> (kg/ha)	9.77 ± 0.87	12.03 ± 1.1	8.61 ± 0.87	9.02 ± 1.23
Ca <sup>2+</sup> (ppm)	3917.83 ± 358.38	4794.27 ± 453.32	4396.75 ± 358.38	3610.92 ± 506.83
Mg <sup>2+</sup> (ppm)	815.21 ± 47.9	742.4 ± 60.59	822.54 ± 47.9	770.83 ± 67.74
%OM	1.96 ± 0.15	1.78 ± 0.19	1.83 ± 0.15	1.8 ± 0.21
%TN	0.11 ± 0.01	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.01
NH <sub>4</sub> <sup>+</sup> (kg/ha)*	7.39 ± 0.84 <sup>A</sup>	4.34 ± 1.07 <sup>B</sup>	4.47 ± 0.84 <sup>B</sup>	6.13 ± 1.19 <sup>AB</sup>
NO <sub>3</sub> <sup>-</sup> (kg/ha)	7.06 ± 0.69	7.78 ± 0.87	5.38 ± 0.69	7.02 ± 0.97
Total mineral N (kg/ha)	14.45 ± 1.20	12.13 ± 1.51	9.85 ± 1.20	13.14 ± 1.69
<b>B. Plant nutrients</b>				
Litter C:N	43.61 ± 3.2	43.00 ± 4.05	38.53 ± 3.2	51.63 ± 4.52
Cheatgrass N (g/m <sup>2</sup> )*	0.13 ± 0.46 <sup>B</sup>	1.25 ± 0.58 <sup>AB</sup>	3.11 ± 0.46 <sup>A</sup>	3.37 ± 0.65 <sup>A</sup>
Cheatgrass %N	1.09 ± 0.09	0.89 ± 0.10	1.11 ± 0.08	1.24 ± 0.11
<i>Poa secunda</i> N (g/m <sup>2</sup> )*	1.40 ± 0.19 <sup>A</sup>	0.87 ± 0.24 <sup>AB</sup>	0.13 ± 0.19 <sup>B</sup>	0.57 ± 0.27 <sup>AB</sup>
<i>Poa secunda</i> %N*	1.15 ± 0.08 <sup>AB</sup>	0.79 ± 0.12 <sup>B</sup>	1.50 ± 0.17 <sup>A</sup>	1.26 ± 0.14 <sup>AB</sup>
Other plant N (g/m <sup>2</sup> )*	1.51 ± 0.85 <sup>AB</sup>	0.14 ± 1.07 <sup>B</sup>	4.27 ± 0.85 <sup>A</sup>	5.00 ± 1.20 <sup>A</sup>
Other plant %N*	1.30 ± 0.19 <sup>B</sup>	1.54 ± 0.24 <sup>AB</sup>	1.81 ± 0.19 <sup>AB</sup>	2.43 ± 0.27 <sup>A</sup>

Table 2. Model selection results for the associations between plant and microsite cover variables and soil  $\text{NH}_4^+$ . Bold indicates top models ( $> 2.0 \Delta\text{AIC}$  difference from best model). Variables in italics represent individual significance. AIG = annual invasive grass, ANF = annual native forb, PIG = perennial invasive grass, PNF = perennial native forb.

Model	R <sup>2</sup>	AIC	$\Delta\text{AIC}$
<b>Shrubs + <i>AIG</i> + <i>ANF</i></b>	<b>0.62</b>	<b>106.81</b>	--
Shrubs + <i>AIG</i> + <i>ANF</i> + PIG	0.64	109.02	2.21
Shrubs + Gravel + <i>AIG</i> + <i>ANF</i>	0.64	109.08	2.27
Shrubs + <i>AIG</i> + <i>ANF</i> + PNF	0.64	109.24	2.44
Shrubs + Cryptogams + <i>AIG</i> + <i>ANF</i>	0.63	109.64	2.84

Table 3. Model averaging results for the associations between soil nutrients and plant nitrogen contents (gN). Bold indicates top variables. Variables in italics represent individual significance.

Parameter	Estimate	Standard Error
<i>Cheatgrass gN</i>		
SO <sub>4</sub> <sup>2-</sup> (kg/ha)	-0.05	0.08
Ca <sup>2+</sup> (ppm)	0.00	0.00
Mg <sup>2+</sup> (ppm)	0.00	0.00
OM (%)	-0.51	0.76
<b>TN (%)</b>	<b>-22.66</b>	<b>19.73</b>
NH <sub>4</sub> <sup>+</sup> (kg/ha)	-0.02	0.06
NO <sub>3</sub> <sup>-</sup> (kg/ha)	-0.02	0.08
<i>Poa secunda gN</i>		
SO <sub>4</sub> <sup>2-</sup> (kg/ha)	-0.00	0.02
Ca <sup>2+</sup> (ppm)	-0.00	0.00
Mg <sup>2+</sup> (ppm)	-0.00	0.00
OM (%)	0.03	0.19
TN (%)	0.04	4.40
<b><i>NH<sub>4</sub><sup>+</sup> (kg/ha)</i></b>	<b>0.09</b>	<b>0.05</b>
NO <sub>3</sub> <sup>-</sup> (kg/ha)	-0.01	0.03
<i>Other plant gN</i>		
SO <sub>4</sub> <sup>2-</sup> (kg/ha)	-0.07	0.13
Ca <sup>2+</sup> (ppm)	0.00	0.00
Mg <sup>2+</sup> (ppm)	0.00	0.00
OM (%)	-1.06	1.23
TN (%)	-15.43	27.45
NH <sub>4</sub> <sup>+</sup> (kg/ha)	0.01	0.10
NO <sub>3</sub> <sup>-</sup> (kg/ha)	-0.03	0.14



Table 4. Model averaging results for the associations between plant and microsite cover variables and plant nitrogen contents (gN). Bold indicates top variables. Variables in italics represent individual significance.

Parameter	Estimate	Standard Error
Cheatgrass gN		
<i>Shrubs</i>	<b>-0.09</b>	<b>0.04</b>
Bare ground	0.01	0.01
<b>Gravel</b>	<b>-0.02</b>	<b>0.02</b>
Rock	-0.02	0.04
Litter	0.00	0.01
Cryptogams	-0.21	0.23
Perennial native grass	-0.02	0.04
Perennial native forb	-0.04	0.06
Annual native forb	-0.04	0.26
<b>Annual invasive grass</b>	<b>0.31</b>	<b>0.20</b>
Annual invasive forb	-0.00	0.07
<i>Poa secunda</i> gN		
Shrubs	-0.00	0.01
Bare ground	0.00	0.00
Gravel	-0.00	0.01
Rock	0.00	0.01
Litter	-0.00	0.00
Cryptogams	0.04	0.07
<b>Perennial native grass</b>	<b>0.03</b>	<b>0.02</b>
Perennial native forb	-0.01	0.02
Annual native forb	0.01	0.09
<i>Annual invasive grass</i>	<b>-0.24</b>	<b>0.08</b>
Annual invasive forb	-0.01	0.02
Other plant gN		
<b>Shrubs</b>	<b>-0.18</b>	<b>0.07</b>
Bare ground	-0.00	0.03
<b>Gravel</b>	<b>-0.05</b>	<b>0.04</b>
<b>Rock</b>	<b>-0.15</b>	<b>0.10</b>
Litter	-0.00	0.02
Cryptogams	0.02	0.22
Perennial native grass	-0.01	0.05
Perennial native forb	0.06	0.10
Annual native forb	-0.07	0.41
Annual invasive grass	-0.05	0.19
<b>Annual invasive forb</b>	<b>0.21</b>	<b>0.14</b>

## Figure captions

Figure 1. Ordination of 25 sites in community composition space using principal components analysis (PCA). Vectors show the strength and direction of correlations between cover variables and axes. Different symbols and ellipses correspond to the four stages of invasion (sagebrush, sagebrush with cheatgrass, cheatgrass-dominated, and cheatgrass die-off). Principal component 1 represents a gradient from high shrub and perennial native species cover to high invasive species cover. Principal component 2 represents a gradient from high annual native forb cover to high gravel cover. Dashed lines represent component scores of 0. AIG = annual invasive grass, AIF = annual invasive forb, PIF = perennial invasive forb, ANF = annual native forb, PNG = perennial native grass, PNF = perennial native forb, and PIG = perennial invasive grass.

Figure 2. Linear regressions between significant life form covers and soil  $\text{NH}_4^+$ . ANF = annual native forb and AIG = annual invasive grass.

Figure 3. Linear regression between soil  $\text{NH}_4^+$  and *Poa secunda* N content.

Figure 4. Linear regression between shrub cover and cheatgrass N content.

Figure 5. Linear regression between annual invasive grass and *Poa secunda* N content.

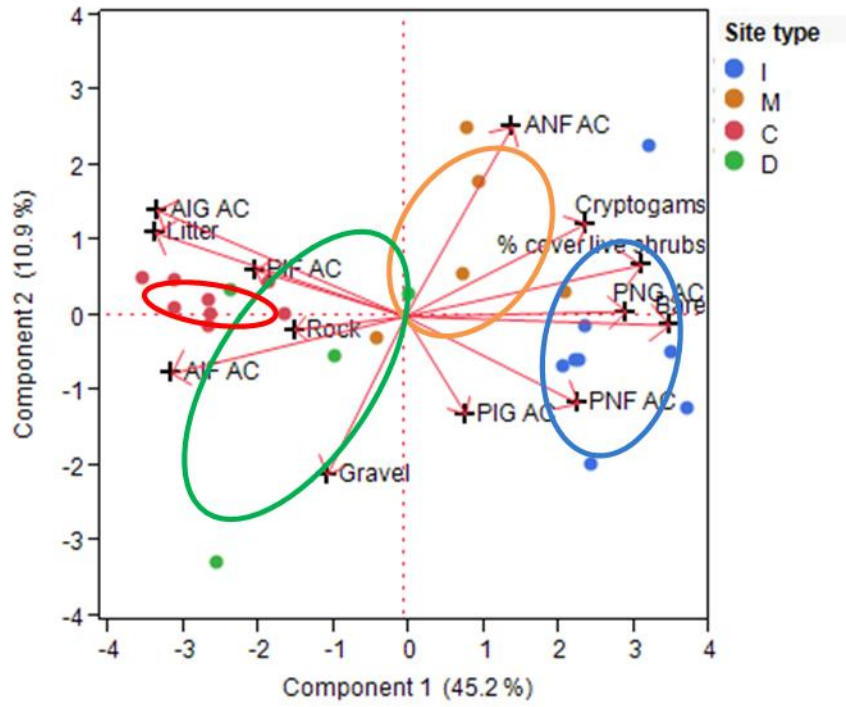


Figure 1.

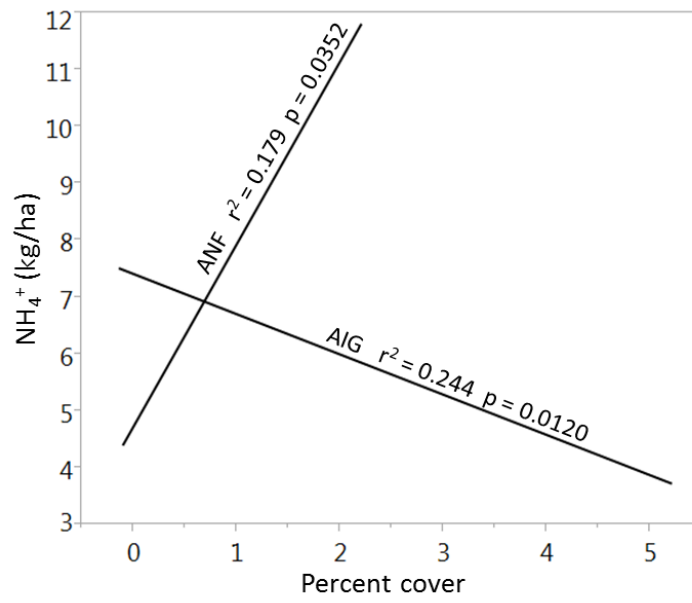


Figure 2.



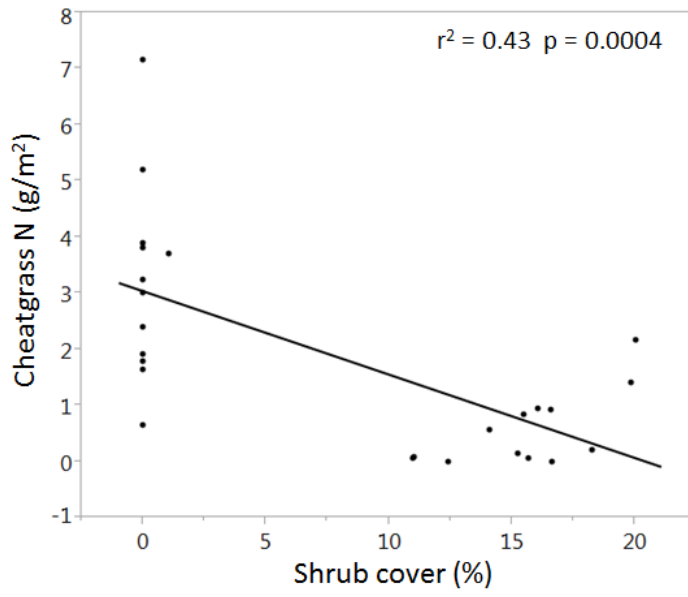


Figure 4.

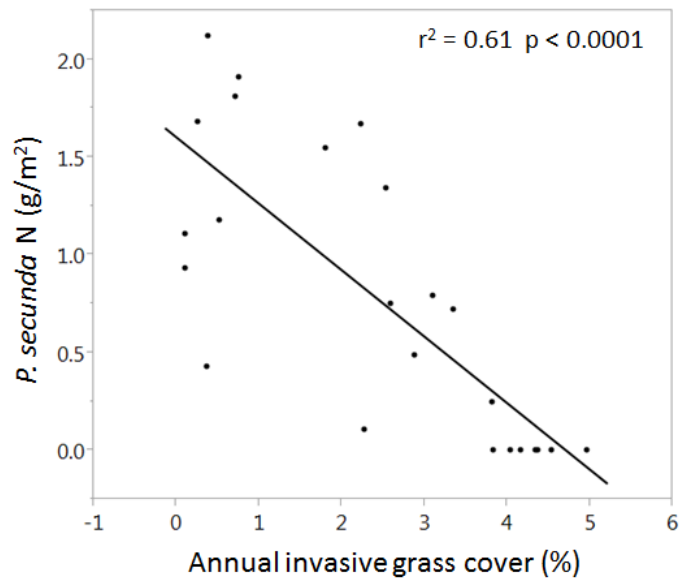


Figure 5.

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

Rachel Jones, corresponding author  
Ecology, Evolution and Conservation Biology Graduate Group  
Dept. of Natural Resources & Environmental Science  
University of Nevada, Reno  
1000 Valley Road  
Reno, NV 89512  
rachel.o.jones@gmail.com  
phone: 775-784-4111  
fax: 775-784-4583

Jeanne C. Chambers  
US Forest Service, Rocky Mountain Research Station  
920 Valley Road  
Reno, NV 89512  
jchambers@fs.fed.us

Dale W. Johnson  
Dept. of Natural Resources & Environmental Science  
University of Nevada, Reno  
1000 Valley Road  
Reno, NV 89512  
dwj@cabnr.unr.edu

Robert R. Blank  
USDA, Agricultural Research Service  
920 Valley Road  
Reno, NV, 89512  
Bob.Blank@ars.usda.gov

David I. Board  
US Forest Service, Rocky Mountain Research Station  
920 Valley Road  
Reno, NV 89512  
dboard@fs.fed.us

Numbers of text pages: 29  
Number of tables: 3  
Number of figures: 10



**Abstract**

**Background and Aims:** Fire has profound effects of 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 five 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.

**Key words**

cold desert, invasive annual grasses, repeated fire, restoration, sagebrush, shrublands

## Abbreviations

Total mineral nitrogen (TMN)

## Introduction

Invasive annual grasses have global effects on fire regimes, plant community composition, and ecosystem processes (D'Antonio and Vitousek 1992, Brooks et al. 2004). Many ecosystems are exhibiting more frequent fires largely due to changes in fuel type and continuity caused by invasion of annual grasses (Keane et al. 2002). In cold desert shrublands where extensive invasion by cheatgrass (*Bromus tectorum*) and other annual grasses has occurred, fine, flammable fuels and fuel continuity have increased and, in areas invaded by cheatgrass, fire return intervals have decreased 2 to 4 fold (D'Antonio and Vitousek 1992, Knapp 1996, Link et al. 2006, Baker 2011, Balch et al. 2013). Because many native species are fire intolerant and there is insufficient time for recruitment between fires, progression conversion to invasive annual grass dominance is occurring in many low to mid-elevation shrubland types (West 1983, Suring et al. 2005, Chambers et al. 2007). Restoration of areas dominated by invasive annual grasses is often difficult. The annual grasses are highly competitive with seedlings of both native species and introduced cultivars because of earlier germination in fall or winter (Aguirre and Johnson 1991, Roundy et al. 2007) high growth and nutrient uptake rates (Melgoza and Nowak 1991, MacKown et al. 2009), and early maturation (Klemmedson and Smith 1964). 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 and Mustard 2005, Bradley et al. 2006). These changes influence ecosystem services and ultimately create positive feedbacks that promote further invasion.

Fire has been instrumental in conversion of cold desert shrublands to invasive annual grasses but it also may be an important restoration tool (Baker 2006). Restoration of cheatgrass-dominated ecosystems depends on reducing cheatgrass abundance while simultaneously providing the conditions necessary for native species establishment. High resource availability, in particular soil mineral nitrogen (N), immediately following fire can increase cheatgrass growth and production and promote cheatgrass invasion (Chambers et al. 2007). In contrast, decreasing nutrient availability and restoring a pre-invasion N cycle can reduce the competitive advantage of cheatgrass and favor native species (Blumenthal et al. 2003, Norton et al. 2007, Mazzola 2008, Brunson et al. 2010). A viable approach for reducing available nutrients may be repeated burning. Repeated burning can cause significant reductions in soil mineral N over time as shown for pine forests (Binkley et al. 1992, Wright and Hart 1997) and perennial grasslands (Ojima et al. 1994, Blair 1997, Johnson and Matchett 2001). However, no information is currently available on the effects of repeated burning in cold desert shrublands.

Repeated burning may result in progressive nitrogen losses over time (Fig. 1). Soil mineral N (typically in the form of ammonium,  $\text{NH}_4^+$ ) may temporarily increase following fire due to heat-induced denaturing of soil organic N compounds and increased N mineralization rates (Fig. 1a; Neary et al. 1999). In cold desert shrublands where resources are often naturally low, soil mineral N can increase immediately following fire (Blank et al. 1994b, Blank et al. 1996, Johnson et al. 2011) and remain elevated for one

or more years post-fire (Stubbs and Pyke 2005, Rau et al. 2007, Rau et al. 2008). Frequent fires however, whether prescribed or naturally promoted by annual grass invasion, may ultimately lead to long-term decreases in soil N as well as annual grass success. These losses can come about through  $\text{NO}_x$  and  $\text{NH}_3$  volatilization from soils or leaching of mobile nitrates ( $\text{NO}_3^-$ ) beyond plant rooting zones (Blank and Norton, personal communication, Dodds et al. 1996, Fynn et al. 2003). Losses result from progressive N deficiency when post-fire pulses in soil nutrients stimulate plant growth and N uptake (Monaco et al. 2003, Johnson et al. 2011) and nutrients contained in biomass are volatilized in subsequent burns (Fig. 1b). Nearly all N contained in organic material that is burned is volatilized and lost from the system causing long-term declines in soil mineral N and soil C and N contents over time (Fig. 1a and 1c) unless the N is replaced by atmospheric deposition, N-fixation, or fertilization (Raison et al. 1985, Blair 1997, Neary et al. 1999).

Soil C contents also can decrease in response to burning (Fig. 1). High severity fires in which temperatures exceed  $200^\circ\text{C}$  can cause C to be volatilized from soils as well as from aboveground biomass (Fig. 1b; Raison et al. 1985, Blair 1997, Neary et al. 1999). These immediate decreases in soil C stocks after fire are often long-lived due to conversion to annual grass dominance and more frequent fires. In fact, it has been proposed that repeated fires caused by annual grass invasion may be converting cold desert shrublands from C sinks to C sources (Bradley et al. 2006, Rau et al. 2011). One of the biggest contributors to C loss is the removal of fire-intolerant shrubs and trees which store large amounts of C aboveground as well as deep in the soil profile (Dobrowolski et al. 1990, Jobbagy and Jackson 2000, Jackson et al. 2002). Following

annual grass invasion, however, C contents are often increased in near surface soils because annual grasses typically have more shallow roots than shrubs (Ogle et al. 2004). Concentration of C in surface soils increases the potential for future losses of C due to topsoil erosion and volatilization in subsequent fires (Fig. 1c; D'Antonio and Vitousek 1992).

Long-term effects of repeated fires on C and N pools are affected by the influence of plant species composition and litter on nutrient cycling. Ecosystems composed of plants with high N uptake rates, such as annual grasses, produce relatively high amounts of N in biomass and are therefore likely to lose more N through volatilization than those systems composed of plants with lower N uptake rates (Boerner 1982). In addition, species composition can influence litter accumulation and alter the effects of repeated burning on soil nutrients. In cold desert shrublands, replacement of native perennial bunchgrasses by annual grasses such as cheatgrass has significantly increased aboveground litter biomass, often creating continuous and homogeneous litter mats (Stewart and Hull 1949, Evans et al. 2001, Booth et al. 2003a, Norton et al. 2004). Accumulated litter typically increases 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).

Cold desert shrubland ecosystems are being rapidly invaded by annual grasses, and understanding the effects of fire on C and N pools in these ecosystems could be key to developing effective management strategies. In a five year field study, we examined 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. We used a Wyoming big sagebrush ecological site type as our study system because this type has exhibited the highest rate of conversion to cheatgrass-dominance. Generalized Linear Mixed-effects Models (GLMMs) were used to examine differences in C and N contents among treatments and across time in litter intact and litter removed plots. Based on a priori knowledge, we developed a multivariate conceptual model of likely effects of environmental factors (precipitation, temperature) and treatments (repeated burning and litter manipulation) on soil mineral N and litter and vegetation C and N contents (Fig. 1). We identified the hypothesized mechanisms associated with the paths in the conceptual model (Table 1) and used structural equation modeling (SEM) to evaluate the component hypotheses identified in the model (Grace 2006, Grace et al. 2009). Together, 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?

## **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 1402 m (436294E, 4598553N), while the Eden Valley site is located at 1524 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 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 in each 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 yrs). 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 yrs). 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 two 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 exists 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 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 PLS/m<sup>2</sup>. 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<sup>2</sup>) 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 lab, 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 100g of soil was collected to a depth of 5 cm using a trowel and then returned to the lab where it was analyzed for available mineral N ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) 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  $\text{gN/m}^2$ . We summed  $\text{NH}_4^+$  and  $\text{NO}_3^-$  to calculate soil-extracted total mineral N (TMN). In addition, in 2008, 2009, and 2012, a separate portion of the 0-5cm 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 gC or gN per  $\text{m}^2$ .

Plant root simulator (PRS) probes were used to monitor soil  $\text{NH}_4^+$  and  $\text{NO}_3^-$  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 one hour in a zip lock bag, and the extractant was analyzed for  $\text{NH}_4^+$  and  $\text{NO}_3^-$  using a Technicon autoanalyzer (Bran and Lubbe, Inc., Buffalo, NY). The values for both probes were reported in units of  $\mu\text{g N/cm}^2$  of resin area/burial length (i.e. days in the ground) and were converted to  $\text{ng N/cm}^2/\text{sampling period}$ . We summed  $\text{NH}_4^+$  and  $\text{NO}_3^-$  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 Generalized Linear Mixed-effects Models (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 ( $\alpha=0.05$ ). 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). Because litter and vegetation C and N contents were strongly correlated, 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. 1), 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 595mm (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.

#### Pre- and post-burn responses to treatments

##### Vegetation and litter C and N contents

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 two years of the study, but decreased in 2011 ( $p < 0.02$ ). Carbon contents in post-burn periods were higher in 2010 than 2009, then 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 were lower than pre-burn contents in 2009 ( $p = 0.0002$ ). In litter removed plots, post-burn N contents were higher than pre-burn contents in 2010 ( $p = 0.0313$ ). 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:  $7.20 \pm 0.76$  gN/m<sup>2</sup>, 2009:  $5.60 \pm 0.76$  gN/m<sup>2</sup>, 2010:  $3.46 \pm 0.76$  gN/m<sup>2</sup>, 2011:  $1.76 \pm 0.76$  gN/m<sup>2</sup>;  $p < 0.05$ ). Also, burned only plots had higher N contents than burned and seeded with cheatgrass plots in 2009 (burned only:  $6.87 \pm 0.76$  gN/m<sup>2</sup>, burned and seeded with cheatgrass:  $5.20 \pm 0.76$  gN/m<sup>2</sup>;  $p < 0.02$ ) and higher than N contents than burned and seeded with cheatgrass and burned and seeded with wheat plots in 2010 (burned only:  $6.14 \pm 0.76$  gN/m<sup>2</sup>, burned and seeded with cheatgrass:  $4.65 \pm 0.76$  gN/m<sup>2</sup>, burned and seeded with wheat:  $3.46 \pm 0.76$  gN/m<sup>2</sup>;  $p < 0.04$ ).

#### 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:  $0.6796 \pm 0.259$  gN/m<sup>2</sup>, 2009:  $1.1806 \pm 0.259$  gN/m<sup>2</sup>, 2010:  $1.0516 \pm 0.259$  gN/m<sup>2</sup>, 2011:  $1.1142 \pm 0.259$  gN/m<sup>2</sup>;  $p < 0.002$ ). 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:  $1.81 \pm 0.3233$  gN/m<sup>2</sup>, pre-burn burned only plots:  $1.0812 \pm 0.3233$  gN/m<sup>2</sup>, post-burn burned only plots:  $1.1124 \pm 0.3233$  gN/m<sup>2</sup>, pre-burn



burned and seeded with cheatgrass plots:  $1.2045 \pm 0.3233$  gN/m<sup>2</sup>, post-burn burned and seeded with cheatgrass plots:  $1.3816 \pm 0.3233$  gN/m<sup>2</sup>;  $p < 0.05$ ).

## Responses to treatments at peak biomass

### Litter C and N contents

Litter C content experienced a 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 ( $p < 0.03$ ). 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 experienced 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 two 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 only differed among years in both 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:  $40.0122 \pm 4.1905$  gC/m<sup>2</sup>, 2009:  $58.5312 \pm 4.1905$  gC/m<sup>2</sup>, 2010:  $96.8284 \pm 4.1905$  gC/m<sup>2</sup>, 2011:  $62.3716 \pm 4.1905$  gC/m<sup>2</sup>, 2012:  $12.2803 \pm 4.1905$  gC/m<sup>2</sup>;  $p < 0.001$ ). 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:  $59.1233 \pm 3.3539$  gC/m<sup>2</sup>, 2010:  $86.284 \pm 3.3539$  gC/m<sup>2</sup>, 2011:  $55.5368 \pm 3.3539$  gC/m<sup>2</sup>, 2012:  $11.2765 \pm 3.3539$  gC/m<sup>2</sup>;  $p < 0.0001$ ).

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:  $0.9803 \pm 0.07848$  gN/m<sup>2</sup>, 2009:  $1.4622 \pm 0.07848$  gN/m<sup>2</sup>, 2010:  $1.9384 \pm 0.07848$  gN/m<sup>2</sup>, 2011:  $1.1472 \pm 0.07848$  gN/m<sup>2</sup>, 2012:  $0.2806 \pm 0.07848$  gN/m<sup>2</sup>;  $p < 0.006$ ). 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:  $1.6068 \pm 0.08952$  gN/m<sup>2</sup>, 2010:  $1.811 \pm 0.08952$  gN/m<sup>2</sup>, 2011:  $1.0068 \pm 0.08952$  gN/m<sup>2</sup>, 2012:  $0.2597 \pm 0.08952$  gN/m<sup>2</sup>;  $p < 0.0001$ ).

### 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 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:  $0.4335 \pm 0.2053$  gN/m<sup>2</sup>, 2009:  $1.3059 \pm 0.2053$  gN/m<sup>2</sup>, 2010:  $0.5516 \pm 0.2053$  gN/m<sup>2</sup>, 2011:  $0.6602 \pm 0.2053$  gN/m<sup>2</sup>, 2012:  $0.7342 \pm 0.2053$  gN/m<sup>2</sup>;  $p < 0.01$ ). 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:  $1.1865 \pm 0.2706$  gN/m<sup>2</sup>, 2010:  $0.4844 \pm 0.2706$  gN/m<sup>2</sup>, 2011:  $0.7107 \pm 0.2706$  gN/m<sup>2</sup>, 2012:  $0.6667 \pm 0.2706$  gN/m<sup>2</sup>;  $p < 0.0001$ ).

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:  $671.37 \pm 121.49$  gC/m<sup>2</sup>, 2009:  $1510.98 \pm 121.49$  gC/m<sup>2</sup>, 2012:  $1436.32 \pm 121.49$  gC/m<sup>2</sup>;  $p < 0.0001$ ). 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 in 2009 ( $p < 0.04$ ). 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 ( $p < 0.04$ ).

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:  $75.7395 \pm$

16.8301 gN/m<sup>2</sup>, 2009: 153.3 ± 16.8301 gN/m<sup>2</sup>, 2012: 132.82 ± 16.8301 gN/m<sup>2</sup>; 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 ± 19.5457 gN/m<sup>2</sup>, 2012: 121.83 ± 19.5457 gN/m<sup>2</sup>; p < 0.0001).

### Structural equation model

The path analyses illustrated the direct and indirect effects of the burning and litter removal treatments and environmental factors on soil TMN and litter and vegetation N contents (Fig. 8). The treatments had both direct and indirect effects on the measured variables. Litter removal had a negative direct effect on litter N content and negative indirect effects on vegetation 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**

### Effects of treatments

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). In our study, however, we found that there were no differences between pre- and post-burn soil TMN in litter intact or litter removed plots. Also, although vegetation N content generally tracked post-burn soil TMN over time, indicating that vegetation was highly responsive to changes in soil N availability as predicted, vegetation and litter N content was not volatilized and lost from the system following burning. Therefore, the prediction that soil TMN would decrease over time due to progressive N deficiency was not

supported. In addition, soil C and N contents were predicted to decrease with burning due to emissions of  $\text{NH}_3$  and  $\text{CO}_2$  from soils; however, total C and N at the end of the study were higher than pre-burn levels.

The failure to achieve immediate decreases in vegetation and litter N content or long-term decreases in soil TMN or total C and N is likely explained by fire temperatures. Fine fuels produced by annual grasses typically burn cooler than woody fuels produced by shrubs and trees. In our study, surface soil temperatures during the burns never exceeded  $70^\circ\text{C}$  and flame temperatures never exceeded  $180^\circ\text{C}$  on either litter intact or litter removed plots. These temperatures are similar to fire temperatures in other burning experiments in annual grass invaded deserts (Patten and Cave 1984, Brooks 2002); however, they are likely too cool to result in sufficient soil heating to denature organic matter or volatilize N from biomass or soils (volatilization temperature of  $200^\circ\text{C}$ , Raison et al. 1985). Instead, a majority of N from combusted biomass was probably left behind in 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 thought to be the primary source of ions into soil solution following a fire, particularly in the case of highly mobile ions such as  $\text{NO}_3^-$  (Grier and Cole 1971). Previous studies have found post-burn soil nutrient increases that could be attributed to N inputs from ash (Brooks 2002, Johnson et al. 2012). In our study, the litter intact plots had high amounts of litter biomass in 2008 and 2009 and, as previously stated, the N from this litter biomass was likely left on the plots as ash following the fire. During the time between the fire and the post-burn soil collection (about one week), some of the N from that ash could have been incorporated into the soil, thereby increasing soil TMN. In

addition, 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, as found in other prescribed burning experiments (Raison et al. 1985, Ojima et al. 1994, Murphy et al. 2006), likely due to the lower volatilization temperature of C. Also, litter C and N contents decreased over time as predicted, 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. These results are supported by findings from previous repeated burn experiments in other systems (Ojima et al. 1994) as well as measurements of C loss following “natural” annual grass fires or prescribed fires (Bradley et al. 2006, Rau et al. 2011). However, 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. Previous studies found that elements left in the ash and soil often experience losses following a fire as a result of off-site particulate transport by wind or water removal (Raison et al. 1985, Malmer 1996, Sankey et al. 2009). Therefore, aeolian (wind) transport may have contributed significantly to litter N loss over time.

In addition to effects of burning, the one-time litter removal treatment 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, as predicted, 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, MacDougall and Turkington 2005, Newingham et al. 2007, Wolkovich et al. 2009) and strong influences on nutrient cycling (Booth et al. 2003a, Ogle et al. 2003, Sperry et al. 2006, Norton et al. 2008). We predicted that litter removal would increase soil TMN directly after fire due to increased soil heating, resulting in significant decreases in soil TMN and vegetation biomass and vegetation C and N contents over time with repeated burning. However, there was generally no difference in soil TMN or soil C and N contents between litter intact and litter removed plots, possibly due to fire temperatures that 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 vegetation, such as seed entrapment and retention and shade and insulation (Chambers and Macmahon 1994, Chambers 2000, Wolkovich et al. 2009), all of which have been shown to increase plant success (Evans and Young 1984, Booth et al. 2003a, Norton et al. 2008). The seeding treatments had very few significant effects on C and N contents in our study; however, seeded plots, especially those 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 unseeded plants (Jones et al. in prep).

#### Effect of weather

Vegetation C and N contents and soil TMN were highly variable among years and were strongly influenced by weather. Precipitation had positive direct effects on post-burn soil TMN and vegetation C:N and a negative direct effect on spring soil TMN.



Also, 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. These effects are likely explained by the influence of soil moisture and temperature on nutrient dynamics (Leffler and Ryel 2012). Microbial activity and net N mineralization are positively affected by soil moisture (Fierer and Schimel 2002, Borken and Matzner 2009); therefore increases in precipitation generally increase soil N availability and consequently, plant N uptake and growth. Microbial activity also is strongly influenced by soil temperatures and, in general, warmer temperatures increase soil N availability (Burke 1989, Evans and Ehleringer 1994, Vinton and Burke 1995, Cui and Caldwell 1997). In our study, precipitation and winter soil temperatures were the predominant factors influencing vegetation C and N contents and 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 there is increasing recognition that fires 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, Rau et al. 2008). It has been suggested that repeated fires could be used to alter soil nutrients and restore annual grass dominated systems which have experienced significant changes in nutrient cycling due to invasion. Results from our study indicate that repeated burning is unlikely to decrease soil N availability in cheatgrass-dominated systems due to cool fire temperatures that do not volatilize biomass

N. In addition, nutrient cycling in arid systems is strongly influenced by weather and therefore results are likely to vary both among years and over time.

Repeated burning did significantly reduce litter C and N contents. Given that vegetation N contents were positively influenced by litter N, management strategies that reduce litter accumulation and litter C and N in the system, such as burning or properly timed grazing, may play an important role in decreasing annual grass success. Moreover, reductions in litter decrease the amount and continuity of fine fuel loads which should decrease the likelihood of future fires, disrupting the annual grass-fire cycle that has been responsible for observed changes to nutrient cycling. In addition, seeding with an annual cover crop such as common wheat can decrease annual grass abundance due to competition, and also can stabilize soils following burning or litter removal. Over time, it may be possible to re-establish native perennial herbaceous species and restore nutrient and fire cycles more typical of sagebrush ecosystems.

### **Acknowledgements**

This study was a collaborative effort among the USFS Rocky Mountain Research Station, University of Nevada, Reno, USDA Agricultural Research Service and Winnemucca District of the Nevada Bureau of Land Management. Research funding was provided through the Rocky Mountain Research Station. We thank T. Morgan, C. Rosner, C. Dencker, and a large number of summer technicians for valuable assistance in the field and lab, and B. Leger, P. Verburg, T. Albright, and B. Rau for valuable comments on earlier drafts of this manuscript.

## References

- Aguirre L, Johnson DA (1991) Influence of temperature and cheatgrass competition on seedling development of 2 bunchgrasses. *Journal of Range Management* 44: 347-354.
- Baker WL (2006) Fire and restoration of sagebrush ecosystems. *Wildlife Society Bulletin* 34: 177-185.
- Baker WL (2011) Pre-EuroAmerican and recent fire in sagebrush ecosystems. In: STKaJW Connelly (ed) *Greater sage-grouse: ecology and conservation of a landscape species and its habitats Studies in avian biology* 38. University of California Press, Berkeley, CA, USA.
- Balch JK, Bradley BA, D'Antonio CM, Gomez-Dans J (2013) Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). *Global Change Biology* 19: 173-183.
- Binkley D, Richter D, David MB, Caldwell B (1992) Soil chemistry in a loblolly longleaf pine forest with interval burning. *Ecological Applications* 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 Science Society of America Journal* 58: 564-570.
- Blank RR, Allen FL, Young JA (1996) Influence of simulated burning of soil-litter from low sagebrush, squirreltail, cheatgrass, and medusahead on water-soluble anions and cations. *International Journal of Wildland Fire* 6: 137-143.
- Blank RR, Morgan T, Clements CD, Mackey BE (2013) *Bromus tectorum* L. invasion: Changes in soil properties and rates of bioturbation. *Soil Science* 178: 281-290.
- Blumenthal DM, Jordan NR, Russelle MP (2003) Soil carbon addition controls weeds and facilitates prairie restoration. *Ecological Applications* 13: 605-615.
- Boerner REJ (1982) Fire and nutrient cycling in temperate ecosystems. *Bioscience* 32: 187-192.
- Booth MS, Caldwell MM, Stark JM (2003) Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. *Journal of Ecology* 91: 36-48.
- Borken W, Matzner E (2009) Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Global Change Biology* 15: 808-824.
- Bradley BA, Houghtonw RA, Mustard JF, Hamburg SP (2006) Invasive grass reduces aboveground carbon stocks in shrublands of the Western US. *Global Change Biology* 12: 1815-1822.
- Bradley BA, Mustard JF (2005) Identifying land cover variability distinct from land cover change: Cheatgrass in the Great Basin. *Remote Sensing of Environment* 94: 204-213.
- Brooks ML (2002) Peak fire temperatures and effects on annual plants in the Mojave Desert. *Ecological Applications* 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. *Restoration Ecology* 18: 304-312.
- Burke IC (1989) Control of nitrogen mineralization in a sagebrush steppe landscape. *Ecology* 70: 1115-1126.
- Chambers JC (2000) Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: Implications for restoration. *Ecological Applications* 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. *Annual Review of Ecology and Systematics* 25: 263-292.
- 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. *Rangeland Ecology & Management*.
- Chambers JC, Roundy BA, Blank RR, Meyer SE, Whittaker A (2007) What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs* 77: 117-145.
- Cui MY, Caldwell MM (1997) A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. *Plant and Soil* 191: 291-299.
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics* 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, NV, USA.
- Dijkstra FA, Cheng W (2007) Moisture modulates rhizosphere effects on C decomposition in two different soil types. *Soil Biology & Biochemistry* 39: 2264-2274.
- Dobrowolski JP, Caldwell MM, Richards JH (1990) Basin hydrology and plant root systems. *Ecological Studies* 80: 243-292.
- Dodds WK, Blair JM, Henebry GM, Koelliker JK, Ramundo R, Tate CM (1996) Nitrogen transport from tallgrass prairie watersheds. *Journal of Environmental Quality* 25: 973-981.
- Evans RA, Young JA (1984) Microsite requirements for downy brome (*Bromus tectorum*) infestation and control on sagebrush rangelands. *Weed Science* 32: 13-17.
- Evans RD, Ehleringer JR (1994) Water and nitrogen dynamics in an arid woodland. *Oecologia* 99: 233-242.
- Evans RD, Rimer R, Sperry L, Belnap J (2001) Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications* 11: 1301-1310.
- Facelli JM, Pickett STA (1991) Plant litter- its dynamics and effects on plant community structure. *Botanical Review* 57: 1-32.

- Fierer N, Schimel JP (2002) Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. *Soil Biology & Biochemistry* 34: 777-787.
- Fynn RWS, Haynes RJ, O'Connor TG (2003) Burning causes long-term changes in soil organic matter content of a South African grassland. *Soil Biology & Biochemistry* 35: 677-687.
- Grace JB (2006) *Structural equation modeling and natural systems*. Cambridge University Press, Cambridge.
- Grier CC, Cole DW (1971) Influence of slash burning on ion transport in soil. *Northwest Science* 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.
- Jackson RB, Banner JL, Jobbagy EG, Pockman WT, Wall DH (2002) Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* 418: 623-626.
- Jobbagy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* 10: 423-436.
- Johnson BG, Johnson DW, Chambers JC, Blank RR (2011) Fire effects on the mobilization and uptake of nitrogen by cheatgrass (*Bromus tectorum* L.). *Plant and 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 Science* 177: 338-344.
- 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 Ecology and Management* 220: 155-165.
- Johnson LC, Matchett JR (2001) Fire and grazing regulate belowground processes in tallgrass prairie. *Ecology* 82: 3377-3389.
- Jones RO, Chambers JC, Board DI, Johnson DW, Blank RR (in prep) Understanding the role of resource limitation in restoration of sagebrush ecosystems dominated by cheatgrass - a mechanistic approach.
- Keane RE, Ryan KC, Veblen TT, Allen CD, Logan J, Hawkes B (2002) Cascading effects of fire exclusion in Rocky Mountain ecosystems: a literature review. In: FS U.S. Department of Agriculture, Rocky Mountain Research Station (ed) RMRS-GTR-91, Fort Collins, Colorado.
- Keeney DR, Nelson DW (1987) Nitrogen—inorganic forms. In: AL Page (ed) *Methods of Soil Analysis, Part 2 Chemical and Microbiological Properties*. American Society of Agronomy, Madison, Wisconsin USA.
- Klemmedson JO, Smith JG (1964) Cheatgrass (*Bromus Tectorum* L.). *Botanical Review* 30: 226-262.
- Knapp AK, Seastedt TR (1986) Detritus accumulation limits productivity of tallgrass prairie. *Bioscience* 36: 662-668.
- Knapp PA (1996) Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert - History, persistence, and influences to human activities. *Global Environmental Change-Human and Policy Dimensions* 6: 37-52.

- Korfmacher JL, Chambers JC, Tausch RJ, Roundy BA, Meyer SE, Kitchen S (2003) Technical Note: A technique for conducting small-plot burn treatments. *Journal of Range Management* 56: 251-254.
- Leffler AJ, Ryel RJ (2012) Resource pool dynamics: conditions that regulate species interactions and dominance. In: TA Monaco, RL Sheley (eds) *Invasive plant ecology and management Linking processes to practice*. CAB International, Cambridge, MA, USA.
- Link SO, Keeler CW, Hill RW, Hagen E (2006) *Bromus tectorum* cover mapping and fire risk. *International Journal of Wildland Fire* 15: 113-119.
- MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86: 42-55.
- MacKown CT, Jones TA, Johnson DA, Monaco TA, Redinbaugh MG (2009) Nitrogen uptake by perennial and invasive annual grass seedlings: nitrogen form effects. *Soil Science Society of America Journal* 73: 1864-1870.
- Malmer A (1996) Hydrological effects and nutrient losses of forest plantation establishment on tropical rainforest land in Sabah, Malaysia. *Journal of Hydrology* 174: 129-148.
- Mazzola MB (2008) Spatio-temporal heterogeneity and habitat invasibility in sagebrush steppe ecosystems. PhD dissertation. University of Nevada, Reno, Reno, NV, USA.
- Melgoza G, Nowak RS (1991) Competition between cheatgrass and 2 native species after fire- Implications from observations and measurements of root distribution. *Journal of Range Management* 44: 27-33.
- Monaco TA, Johnson DA, Norton JM, Jones TA, Connors KJ, Norton JB, Redinbaugh MB (2003) Contrasting responses of intermountain west grasses to soil nitrogen. *Journal of Range Management* 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 Biology & Biochemistry* 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 Science* 171: 181-199.
- Neary DG, Klopatek CC, DeBano LF, Ffolliott PF (1999) Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management* 122: 51-71.
- Newingham BA, Vidiella P, Belnap J (2007) Do soil characteristics or microhabitat determine field emergence and success of *Bromus tectorum*? *Journal of Arid Environments* 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. *Journal of Arid Environments* 57: 445-466.
- Norton JB, Monaco TA, Norton U (2007) Mediterranean annual grasses in western North America: kids in a candy store. *Plant and Soil* 298: 1-5.
- Norton U, Mosier AR, Morgan JA, Derner JD, Ingram LJ, Stahl PD (2008) Moisture pulses, trace gas emissions and soil C and N in cheatgrass and native grass-

- dominated sagebrush-steppe in Wyoming, USA. *Soil Biology & Biochemistry* 40: 1421-1431.
- 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. *Biological Invasions* 6: 365-377.
- Ogle SM, Reiners WA, Gerow KG (2003) Impacts of exotic annual brome grasses (*Bromus* spp.) on ecosystem properties of northern mixed grass prairie. *American Midland Naturalist* 149: 46-58.
- 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. *Journal of Range Management* 37: 277-280.
- Peters J (2000) Tetrazolium testing handbook. Contribution no. 29 to The handbook on seed testing. Association of Official Seed Analysts, Lincoln, NE, USA.
- Raison RJ, Khanna PK, Woods PV (1985) Mechanisms of element transfer to the atmosphere during vegetation fires. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 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. *Journal of Arid Environments* 71: 362-375.
- Rau BM, Chambers JC, Blank RR, Johnson DW (2008) Prescribed fire, soil, and plants: Burn effects and interactions in the central great basin. *Rangeland Ecology & Management* 61: 169-181.
- 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. *Rangeland Ecology & Management* 64: 139-147.
- Reilly MJ, Wimberly MC, Newell CL (2006) Wildfire effects on beta-diversity and species turnover in a forested landscape. *Journal of Vegetation Science* 17: 447-454.
- Roundy BA, Hardegree SP, Chambers JC, Whittaker A (2007) Prediction of cheatgrass field germination potential using wet thermal accumulation. *Rangeland Ecology & Management* 60: 613-623.
- Sankey JB, Germino MJ, Glenn NF (2009) Relationships of post-fire aeolian transport to soil and atmospheric conditions. *Aeolian Research* 1: 75-85.
- Sokal RR, Rohlf FJ (1981) *Biometry- the principles and practice of statistics in biological research*. W. H. Freeman and Co.
- Sperry LJ, Belnap J, Evans RD (2006) *Bromus tectorum* invasion alters nitrogen dynamics in an undisturbed arid grassland ecosystem. *Ecology* 87: 603-615.
- Stewart G, Hull AC (1949) Cheatgrass (*Bromus tectorum* L.) - an ecologic intruder in southern Idaho. *Ecology* 30: 58-74.
- Stubbs MM, Pyke DA (2005) Available nitrogen: A time-based study of manipulated resource islands. *Plant and Soil* 270: 123-133.
- Suring LH, Wisdom MJ, Tausch RJ, Miller RF, Rowland MM, Schueck L, Meinke CW (2005) Modeling threats to sagebrush and other shrubland communities. *Habitat*

- threats in the sagebrush ecosystems: methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Lawrence, Kansas, USA.
- Vinton MA, Burke IC (1995) Interactions between individual plant-species and soil nutrient status in shortgrass steppe. *Ecology* 76: 1116-1133.
- West NE (1983) Great Basin-Colorado Plateau sagebrush semi-desert. In: NE West (ed) *Temperate deserts and semi-deserts*. Elsevier Publishing Company, Amsterdam, The Netherlands.
- West NE, Young JA (1999) Vegetation of Intermountain valleys and lower mountain slopes. In: MA Barbour, WD Billings (eds) *North American Terrestrial Vegetation*. 2<sup>nd</sup> ed. edn. Cambridge University Press, New York, NY.
- 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. *Journal of Vegetation Science* 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.



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

Path	Hypothesized mechanism
1	High soil water due to increased 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, Borken 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 germination, N uptake, and growth (Leffler and Ryel 2012).
2	Low winter temperatures are associated with higher snowfall and therefore more soil water which will have effects described in Path 1.
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 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.
4	Fire temperatures in arid ecosystems are strongly affected by the microhabitat fuel gradient, with hotter fires occurring in areas of 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 should carry into the spring.
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 (Knapp and Seastedt 1986, Facelli and Pickett 1991, Sperry et al. 2006).
7	Manually removing litter from some plots at the beginning of the experiment should cause them to have reduced litter biomass throughout the experiment.
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).

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 ( $p \leq 0.05$ ).

	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	<b>90.08</b> (3,147)	<b>&lt;.0001</b>		<b>82.51</b> (3,147)	<b>&lt;.0001</b>		<b>7.37</b> (3,146)	<b>0.0001</b>
B x Y	1.10 (6,147)	0.363		<b>2.56</b> (6,147)	<b>0.0217</b>		1.3 (6,146)	0.2591
Period	<b>110.68</b> (1,147)	<b>&lt;.0001</b>		<b>6.11</b> (1,147)	<b>0.0146</b>		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	<b>8.63</b> (3,147)	<b>&lt;.0001</b>		<b>3.77</b> (3,147)	<b>0.0120</b>		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	<b>18.25</b> (4,105)	<b>&lt;.0001</b>		<b>24.52</b> (4,105)	<b>&lt;.0001</b>		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	<b>61.70</b> (1,105)	<b>&lt;.0001</b>		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		<b>4.79</b> (2,105)	<b>0.0102</b>
Y x P	<b>3.98</b> (2,105)	<b>0.0215</b>		<b>4.34</b> (2,105)	<b>0.0155</b>		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

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 <sub>(Num DF, Den DF)</sub>		P	F <sub>(Num DF, Den DF)</sub>		P	F <sub>(Num DF, Den DF)</sub>		P	F <sub>(Num DF, Den DF)</sub>		P
Carbon												
Litter intact plots												
Burn/seeding	<b>12.62</b>	(3,27)	<b>&lt;.0001</b>	0.68	(3,27)	0.5713	N/A			1.36	(3,27)	0.2748
Year	<b>93.87</b>	(4,111)	<b>&lt;.0001</b>	<b>68.38</b>	(4,112)	<b>&lt;.0001</b>	N/A			<b>83.11</b>	(2,56)	<b>&lt;.0001</b>
B x Y	<b>2.11</b>	(12,111)	<b>0.0214</b>	0.88	(12,112)	0.568	N/A			2.07	(6,56)	0.0707
Litter removed plots												
Burn/seeding	<b>31.01</b>	(4,34)	<b>&lt;.0001</b>	1.48	(4,34)	0.23	N/A			0.38	(4,34)	0.8204
Year	<b>14.57</b>	(3,100)	<b>&lt;.0001</b>	<b>85.72</b>	(3,105)	<b>&lt;.0001</b>	N/A			<b>6.56</b>	(1,35)	<b>0.0149</b>
B x Y	<b>4.79</b>	(12,100)	<b>&lt;.0001</b>	0.97	(12,105)	0.4828	N/A			<b>2.99</b>	(4,35)	<b>0.0318</b>
Nitrogen												
Litter intact plots												
Burn/seeding	<b>7.72</b>	(3,27)	<b>0.0007</b>	0.88	(3,27)	0.4646	1.53	(3,27)	0.2296	1.16	(3,27)	0.3429
Year	<b>72.46</b>	(4,111)	<b>&lt;.0001</b>	<b>61.83</b>	(4,112)	<b>&lt;.0001</b>	<b>45.43</b>	(4,112)	<b>&lt;.0001</b>	<b>71.22</b>	(2,56)	<b>&lt;.0001</b>
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	<b>27.85</b>	(4,34)	<b>&lt;.0001</b>	2.01	(4,34)	0.1147	0.34	(4,34)	0.8497	0.16	(4,34)	0.9556
Year	<b>16.38</b>	(3,100)	<b>&lt;.0001</b>	<b>83.24</b>	(3,105)	<b>&lt;.0001</b>	<b>21.56</b>	(3,105)	<b>&lt;.0001</b>	<b>26.48</b>	(1,35)	<b>&lt;.0001</b>
B x Y	<b>4.33</b>	(12,100)	<b>&lt;.0001</b>	1.69	(12,105)	0.0782	1.21	(12,105)	0.2837	0.84	(4,35)	0.5079

## Figure captions

Figure 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.

Figure 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.

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

Figure 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  $\pm 1$  standard error. Lower-case letters indicate significant differences among pre- and post-burn time periods among years ( $p < 0.05$ ).

Figure 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  $\pm 1$  standard error. Lower-case letters indicate significant differences among pre- and post-burn time periods among years ( $p < 0.05$ ).

Figure 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  $\pm 1$  standard error. Lower-case letters indicate significant differences among burn and seeding treatments among years ( $p < 0.05$ ).

Figure 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  $\pm 1$  standard error.

Figure 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  $\pm 1$  standard error.

Figure 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  $\pm 1$  standard error. Lower-case letters indicate significant differences among burn and seeding treatments among years ( $p < 0.05$ ).

Figure 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.

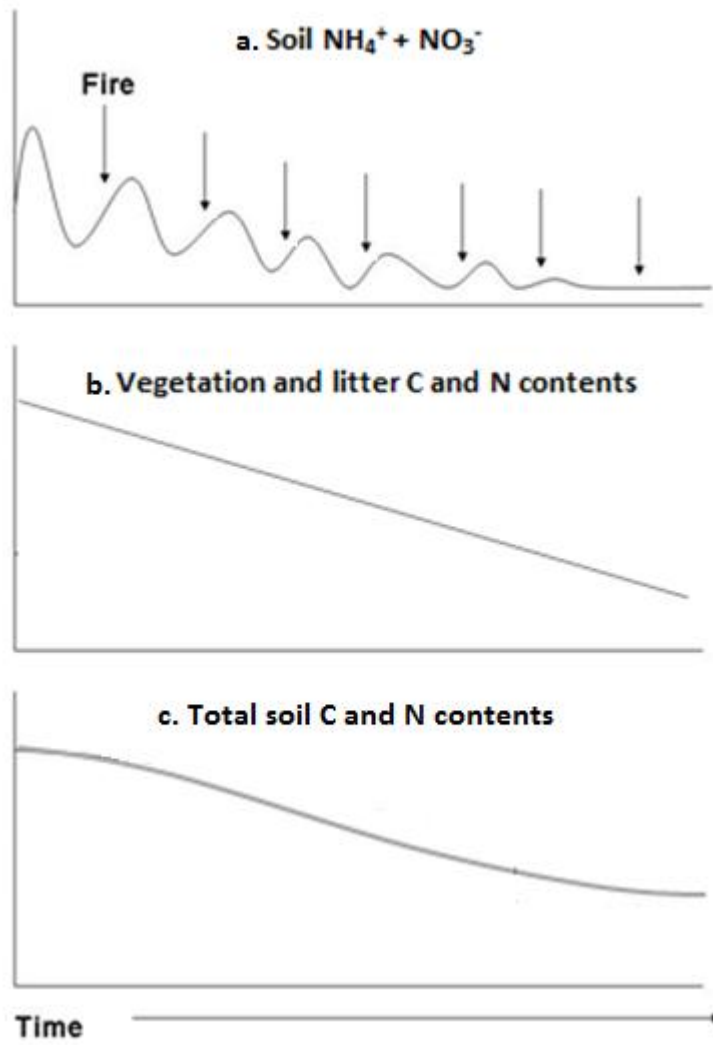


Figure 1.

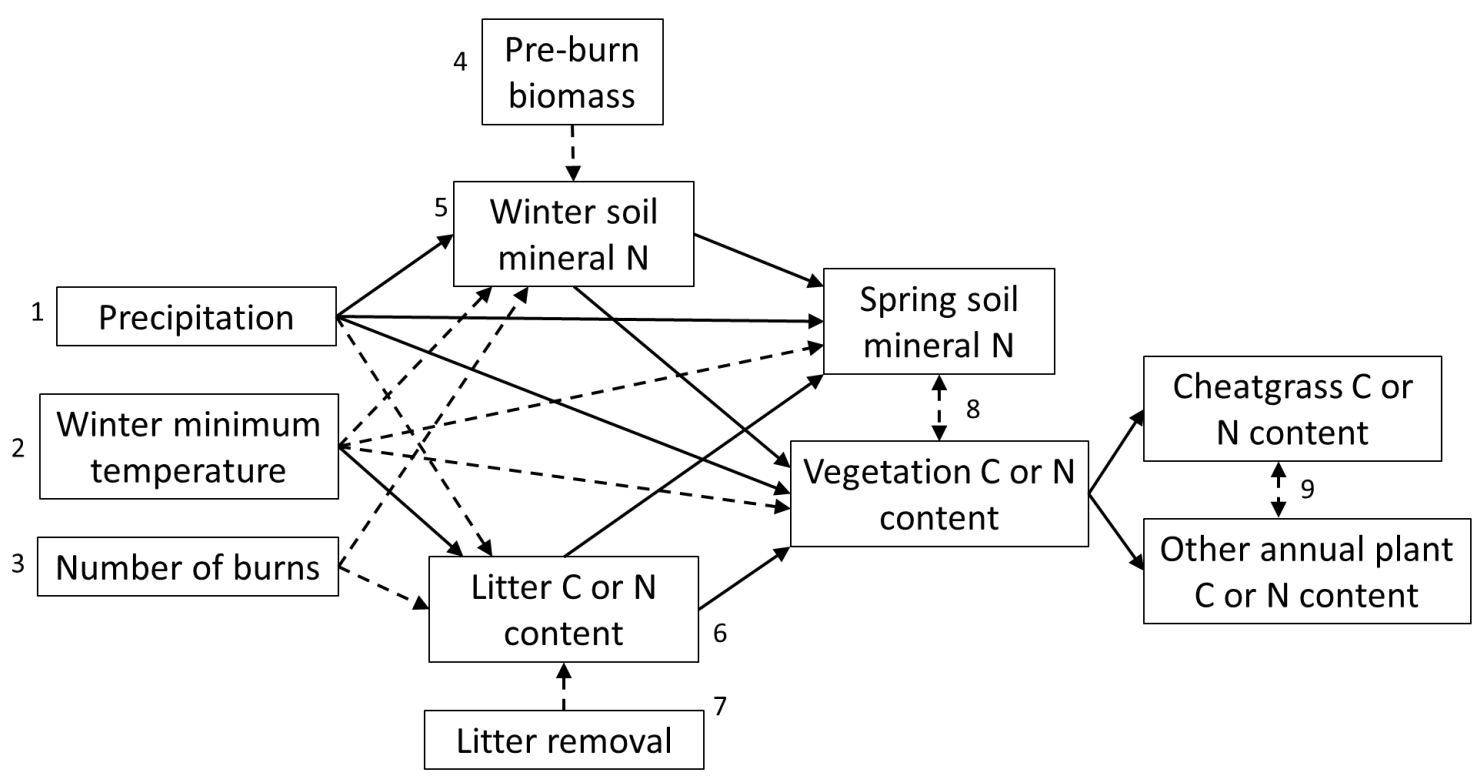


Figure 2.

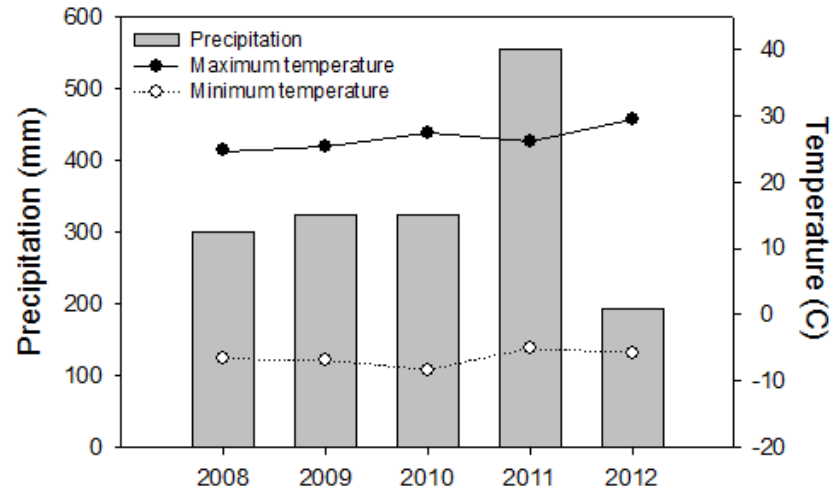


Figure 3.



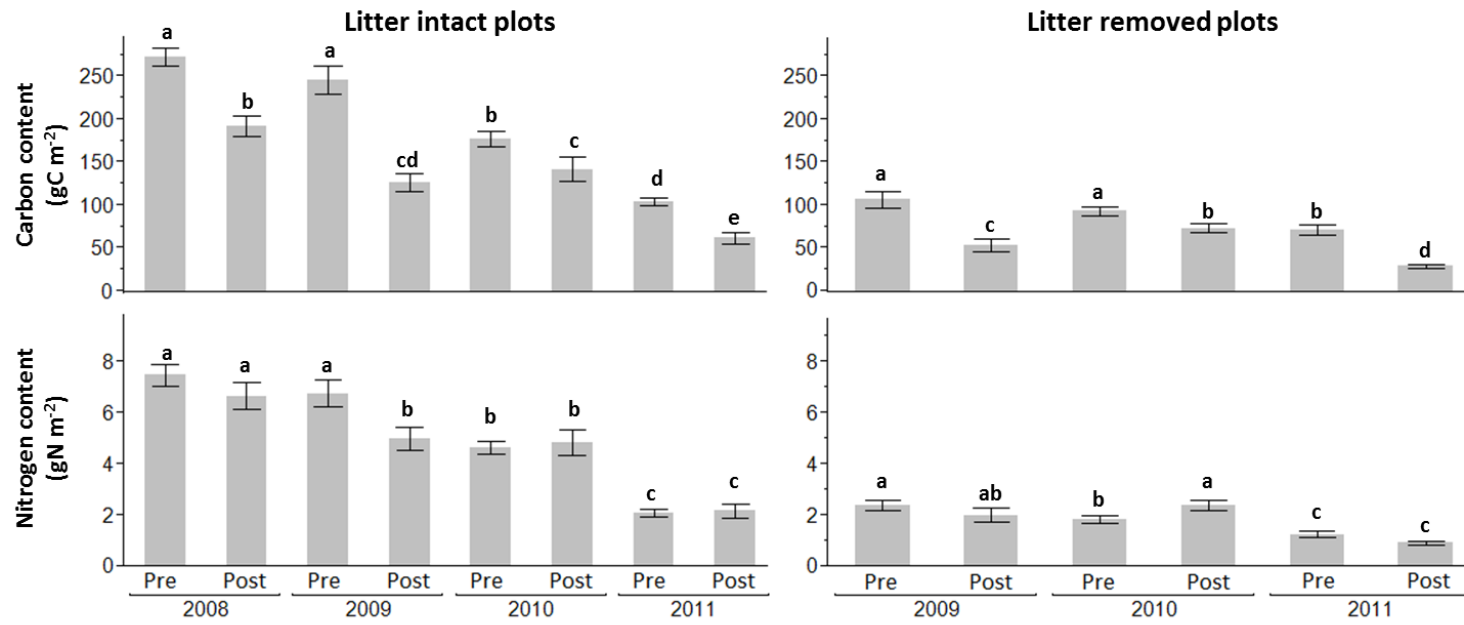


Figure 4.

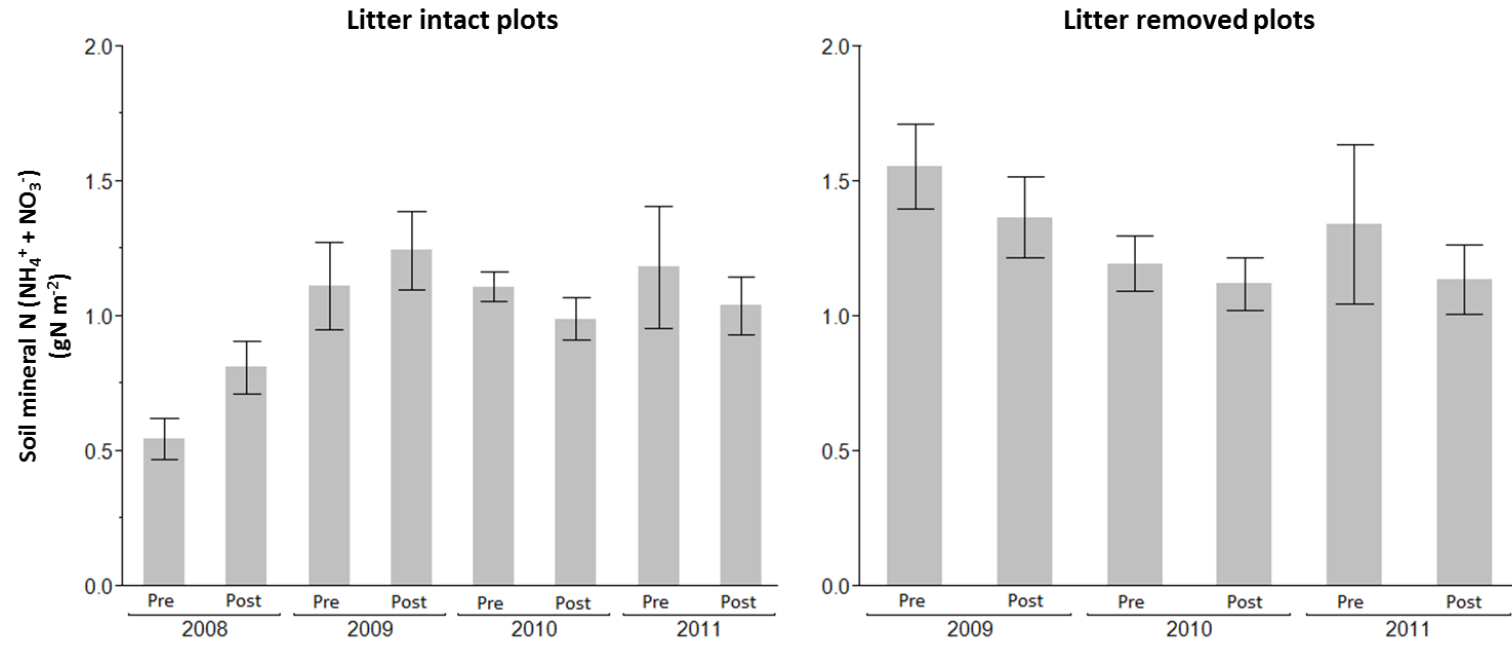


Figure 5.

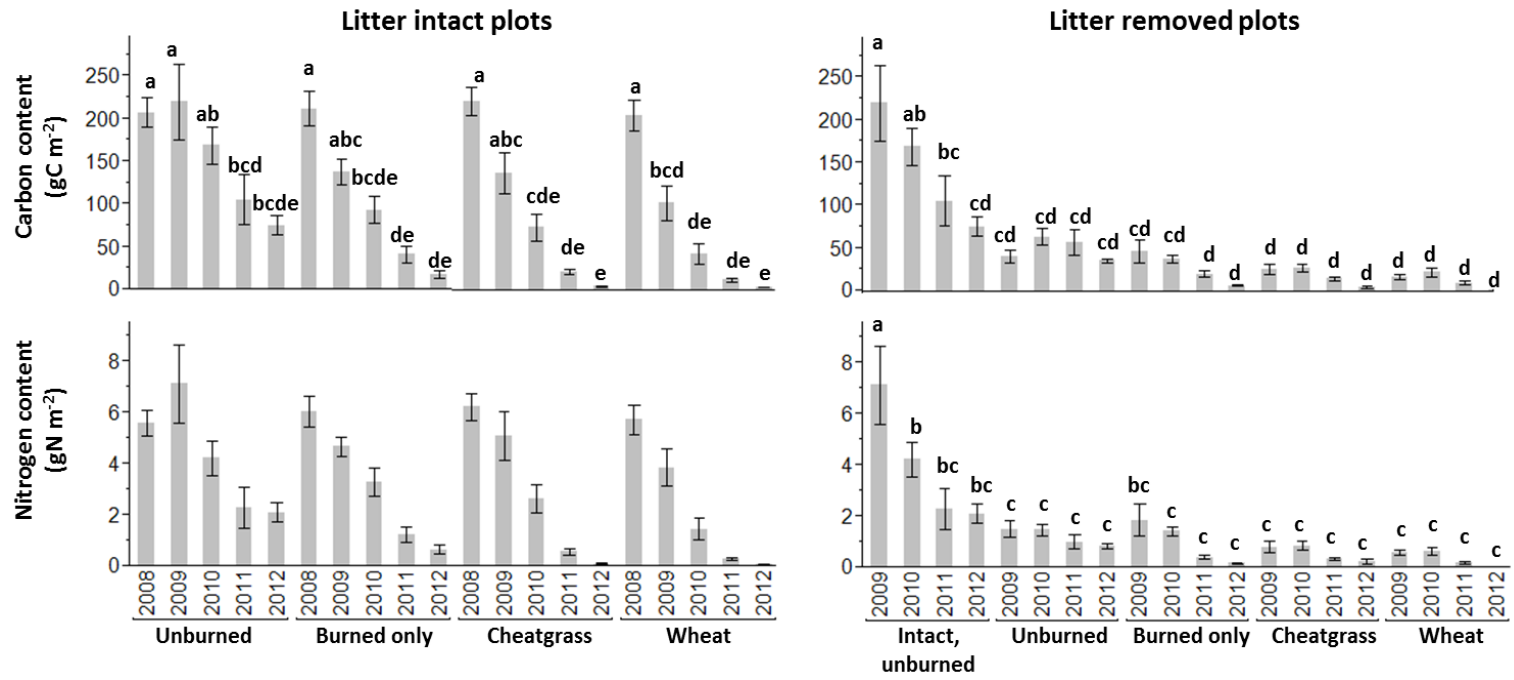


Figure 6.

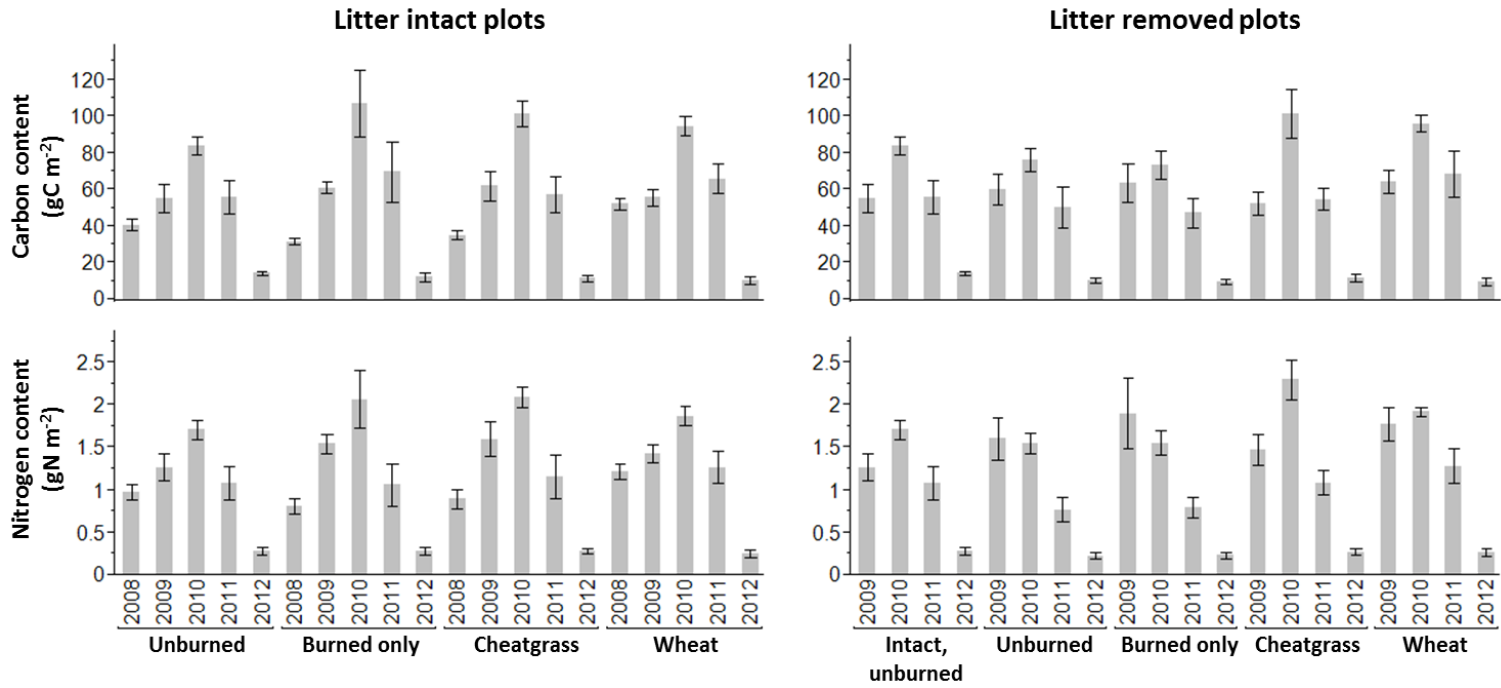


Figure 7.

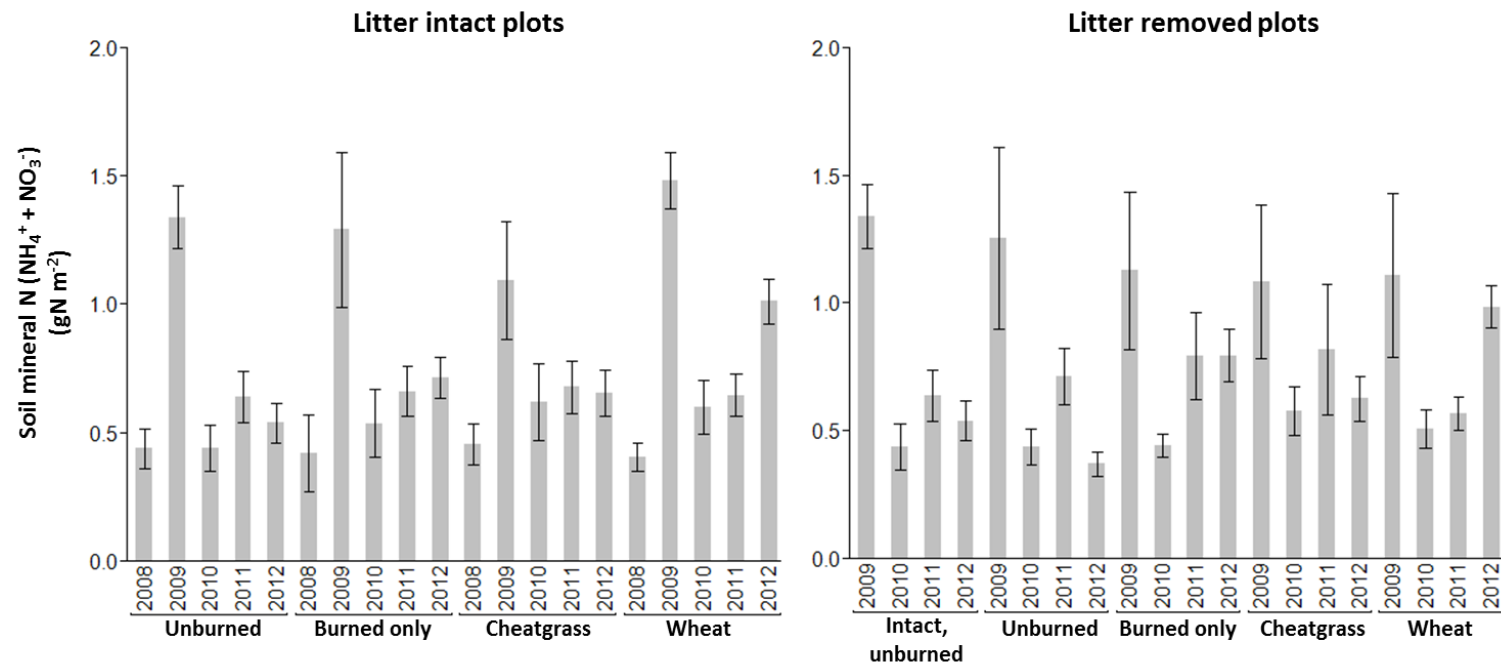


Figure 8.

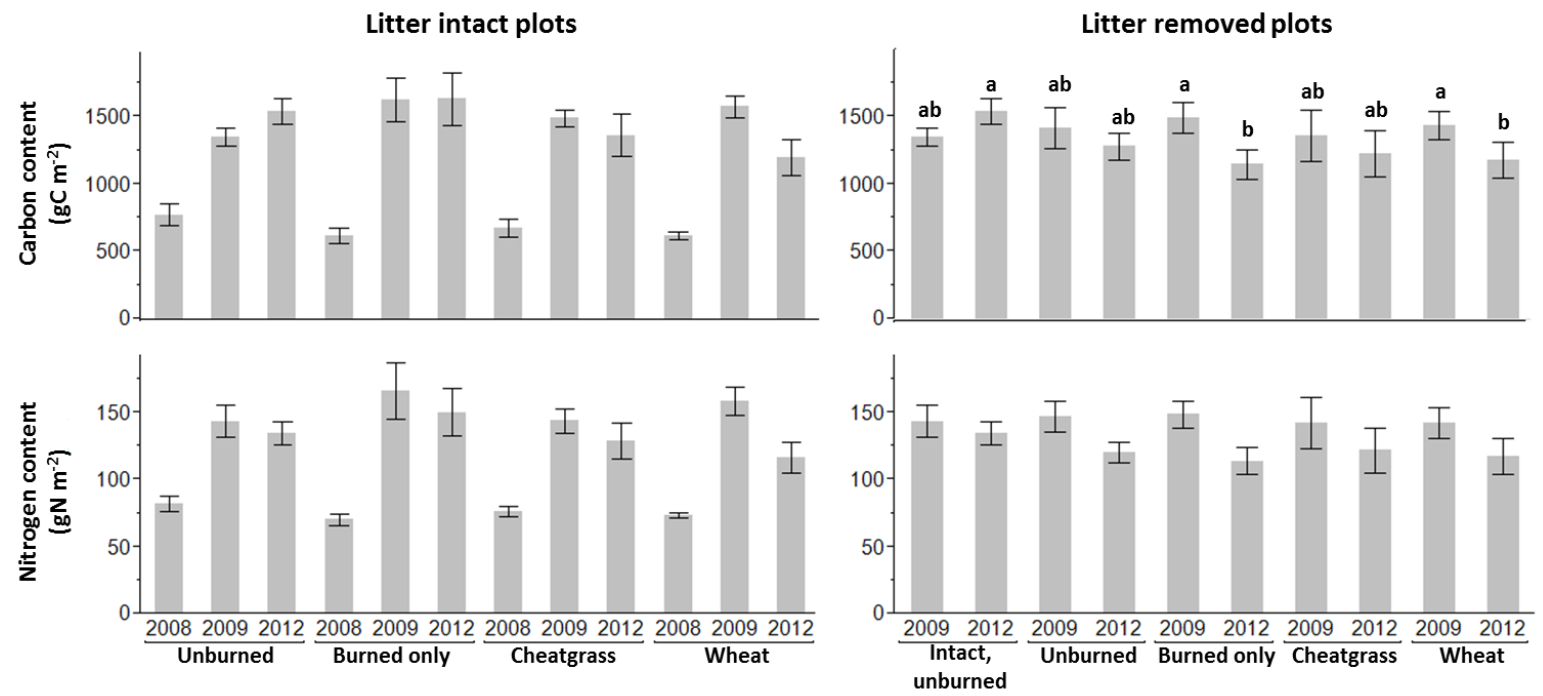


Figure 9.

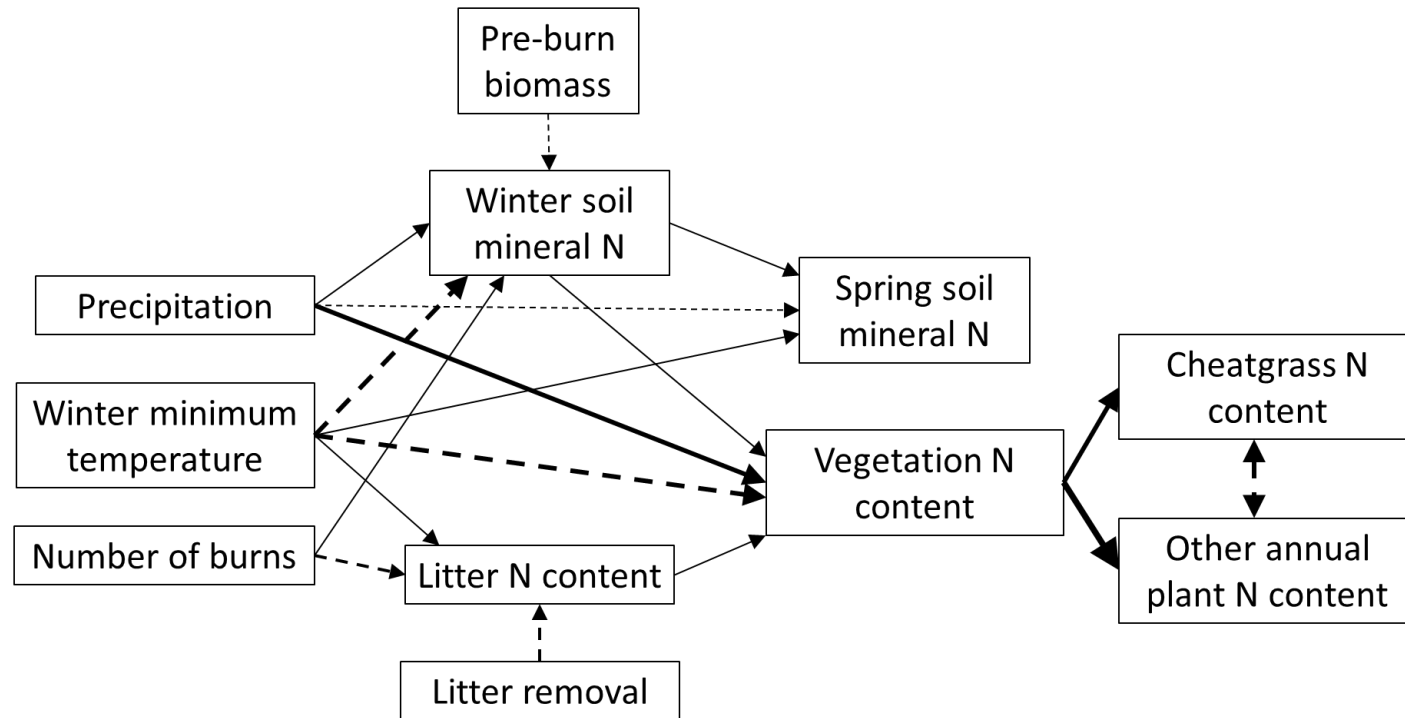


Figure 10.

Understanding the role of resource limitation in restoration of sagebrush ecosystems dominated by cheatgrass – a mechanistic approach

Rachel Jones<sup>1</sup>

Ecology, Evolution and Conservation Biology Graduate Group  
Dept. of Natural Resources & Environmental Science  
University of Nevada, Reno  
1000 Valley Road  
Reno, NV 89512

Jeanne C. Chambers<sup>2</sup>

US Forest Service, Rocky Mountain Research Station  
920 Valley Road  
Reno, NV 89512

David I. Board<sup>3</sup>

US Forest Service, Rocky Mountain Research Station  
920 Valley Road  
Reno, NV 89512

Dale W. Johnson<sup>4</sup>

Dept. of Natural Resources & Environmental Science  
University of Nevada, Reno  
1000 Valley Road  
Reno, NV 89512

Robert R. Blank<sup>5</sup>

USDA, Agricultural Research Service  
920 Valley Road  
Reno, NV, 89512

<sup>1</sup>rachel.o.jones@gmail.com

<sup>2</sup>jchambers@fs.fed.us

<sup>3</sup>dboard@fs.fed.us

<sup>4</sup>dwj@cabnr.unr.edu

<sup>5</sup>Bob.Blank@ars.usda.gov



## Abstract

Invasion and expansion of cheatgrass (*Bromus tectorum* L.) into cold desert shrublands is often linked to increases in resources, and restoration ecologists have suggested that decreasing nitrogen (N) availability and restoring a more conservative nitrogen cycle should decrease the competitive advantage of cheatgrass. Repeated burning decreases soil carbon (C) and available N in grassland and forest systems, but use of repeated burning to decrease soil resources in cheatgrass-dominated systems has not been tested. In a five year field study, we examined effects of repeated burning, litter removal, and seeding with an annual competitor (common wheat) after burning on soil available N, litter and cheatgrass biomass, and plant and seed density. We used generalized linear mixed-effects models to examine differences among treatments over time. We developed a multivariate conceptual model of effects of environmental factors (precipitation, temperature) and restoration treatments on soil available N and cheatgrass success. 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 biomass N resulting in progressive N deficiency over time. However, soil available N in burned plots was never lower than pre-burn levels, likely because surface soil temperatures during burns were too cool to cause volatilization of N from soils or aboveground biomass. Repeated burning did decrease litter biomass, but there was generally no difference in soil available N between litter intact and litter removed plots. Litter did have 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 soil available N was similar to

other treatments and decreased cheatgrass success was likely due to competition for other soil nutrients or water as well as 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. Restoration approaches aimed at decreasing litter and seed banks and increasing competitive interactions may be more effective at reducing cheatgrass success than current approaches for reducing soil N.

### **Key words**

cold desert, invasive annual grasses, repeated fire, restoration, sagebrush, shrublands

### **Introduction**

Invasion of non-native plant species is often closely linked to resource availability (Daehler 2003), and 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). Disturbances and weather events that result in resource pulses often facilitate initial invasion of non-native species (Vitousek et al. 1996, Davis et al. 2000), and many invasive species have physiological characteristics like rapid resource uptake and high growth rates that allow them to take advantage of higher nutrient availability and rapidly occupy high-resource sites (Seabloom et al. 2003, Pyšek and Richardson 2007). Recent research in controlled greenhouse environments indicates that invasive species from a broad array of plant groups have higher nutrient use efficiency than native species even in relatively low resource environments (Funk and Vitousek 2007, James et al. 2011). Consequently, these authors have questioned the

efficacy of using nutrient manipulation as a restoration tool. Nevertheless, field-based restoration experiments that decrease 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, Mazzola et al. 2011), and repeated burning (Ojima et al. 1994, Blair 1997) have been effective in decreasing invasive species abundance and, in many cases, increasing native species establishment (Young et al. 1999, Blumenthal et al. 2003, Mazzola et al. 2011). In native ecosystems, exogenous factors such as weather and endogenous factors such as competitive interactions influence resource availability and restoration outcomes. 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, *Bromus tectorum* L. (cheatgrass), across the western U.S. is often attributed to increases in resource availability. Historically, two of the most significant factors contributing to changes in resource availability in western ecosystems are inappropriate livestock grazing and wildfires (Miller et al. 2011). Livestock grazing that results in soil surface disturbance or depletes native perennial grasses and forbs can result in increases in soil nutrient and water availability (Chambers et al. 2007). In turn, elevated resource availability can result in an increase in woody species dominance and, consequently, when wildfires occur, high woody fuel loads can cause an increase in fire severity and, ultimately, pulses in soil resources, especially soil N availability (Stubbs and Pyke 2005). Soil N availability can increase immediately following wildfire (Blank et al. 1994b, Blank et al.

1996, Johnson et al. 2011) and remain elevated for as long as three years (Stubbs and Pyke 2005, Rau et al. 2007). Cheatgrass possesses many life history traits and physiological characteristics, 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) that make it well-adapted to benefit from resource pulses. Cheatgrass biomass and seed production can increase 2 to 6 times following fire in intact ecosystems and 10 to 30 times in ecosystems with depleted perennial herbaceous species (Chambers et al. 2007). Once established, cheatgrass creates a highly flammable and continuous fuel bed that contributes to larger, more frequent fires and, ultimately, an annual grass-fire cycle that can facilitate progressive conversion of the landscape to cheatgrass (D'Antonio and Vitousek 1992, Link et al. 2006).

Several authors have suggested that decreasing N availability and restoring a more conservative N cycle 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 (sugaring and 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 soil microbes to rapidly expand their population and thereby immobilize available soil N pools. Sugaring experiments have resulted in significant reductions in N availability and cheatgrass biomass and reproduction (Blumenthal et al. 2003, Blank and Young 2009), but the responses were typically short-lived and insufficient for long-term cheatgrass control (Mazzola et al.

2011). Repeated burning using prescribed fire is an alternate approach that may reduce soil nutrients for longer time periods as a result of progressive N deficiency. Both natural and prescribed fires are often followed by a short-term pulse in soil nutrients, especially ammonium ( $\text{NH}_4^+$ ) and nitrate ( $\text{NO}_3^-$ ) which stimulate cheatgrass growth and can result in an increase in cheatgrass N content (Monaco et al. 2003, Johnson et al. 2011). Repeated burning of this nutrient-rich biomass, along with the litter, may result in a loss of above- and belowground N over time as nutrients in biomass and litter are volatilized and lost from the system (Rau et al. 2007). Unvolatilized nutrients are deposited as ash onto the soil surface and can later be removed by wind or water (Blank et al. 1994b, Blank et al. 1996, Blank and Zamudio 1998). Also, depending on fire severity, 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). Studies in perennial grasslands (Ojima et al. 1994, Blair 1997) and pine forests (Binkley et al. 1992, Monleon et al. 1997, Wright and Hart 1997) demonstrated significant reductions in available and total soil N following repeated burning, and it has been suggested that an increase in fire frequency could eventually decrease soil N availability in cheatgrass systems. However, the effects of repeated burning in cheatgrass-dominated ecosystems and its potential interactions with environmental factors or other restoration treatments are unknown.

Litter may play an important role in cheatgrass invasion dynamics. Cheatgrass invasion significantly increases litter biomass in native sagebrush steppe communities (Evans et al. 2001, Norton et al. 2004) and litter can provide positive feedbacks to cheatgrass invasion by altering nutrient cycling (Norton et al. 2008) and increasing establishment (Evans and Young 1984). Cheatgrass and other non-native annual plants

have rapid litter turnover which can increase nutrient availability (especially  $\text{NO}_3^-$ ) in surface and subsurface soil layers (Ehrenfeld 2003, Sperry et al. 2006, Norton et al. 2008). Also, litter can have indirect effects on nutrient availability through its insulating effects. Insulation by litter can increase soil temperatures during the winter and promote soil organic matter (SOM) decomposition and higher nutrient availability, and elevate soil moisture which increases N mineralization and reduces ammonia loss (Facelli and Pickett 1991). In addition, litter can retain seeds (Chambers 2000) and create favorable microsites for cheatgrass seed germination and establishment (Evans and Young 1984). Reductions in cheatgrass litter should decrease soil N availability and cheatgrass success.

Rapidly growing annual species with phenology similar to cheatgrass have the potential to take up available nutrients and increase soil nutrient loss during repeated burning. Also, they may decrease cheatgrass growth and reproduction via competitive interactions. Non-native annuals such as common wheat (*Triticum aestivum*) are frequently used as cover crops and can reduce the success of non-native annuals and improve the likelihood of native species establishment (Koscelny et al. 1990, Herron et al. 2001, Monaco et al. 2003). In addition, common wheat is typically sterile therefore the risk that it will become invasive is low. Seeding an annual competitor such as common wheat could work in tandem with repeated burning to both reduce soil resources and the competitive advantage of cheatgrass.

We used a mechanistic approach to examine effects of repeated burning, litter manipulation, and competition on soil N availability and cheatgrass establishment, growth, and reproduction. In a five year field study, we examined the effects of repeated burns in litter intact and litter removed experiments and of competition by seeding

common wheat and cheatgrass into experimental plots after burning. Generalized Linear Mixed-effects Models (GLMMs) were used to examine differences in soil N availability, litter biomass, cheatgrass density, biomass and seed density, common wheat biomass, and other annual plant biomass among treatments and across time. Based on a priori knowledge, we developed a multivariate conceptual model of the likely effects of environmental factors (precipitation, temperature) and management treatments (repeated burning, litter manipulation, seeding an annual competitor) on soil nitrogen availability and cheatgrass success (density, biomass, seed production) (Fig. 1) and identified the hypothesized mechanisms associated with the paths in the conceptual model (Table 1). We used structural equation modeling (SEM) to evaluate the component hypotheses identified in the conceptual model (Grace et al. 2009). Our analyses addressed two questions: (1) What are the direct and indirect effects of management treatments aimed at resource reduction (repeated burning, litter manipulation, seeding an annual competitor) on soil N availability and cheatgrass success over time? and (2) How do abiotic (precipitation and temperature) and biotic factors (other annual invaders) influence trends in soil N availability and cheatgrass success over time? These questions were addressed in a Wyoming sagebrush ecological site type dominated by cheatgrass because this plant community has exhibited the highest rate of conversion to cheatgrass-dominance.

## **Methods**

### **Study area**

Two study sites were located in Humboldt County, Nevada on Bureau of Land Management (BLM) administered land. The Orvada site is located at 1402 m

(436294E, 4598553N), while the Eden Valley site is located at 1524 m (466314E, 4564313N). 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). 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, the vegetation at both sites was characterized as a Wyoming sagebrush ecological site 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. 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. The 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 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 in each 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 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). 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 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 two 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 exists 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 the 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 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 PLS/m<sup>2</sup>. 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<sup>2</sup>) were placed in the destructive section in locations that differed with every sampling period to evaluate changes in 1) cheatgrass density, biomass, and seed production, 2) annual wheat density and biomass, 3) other annual plant biomass, 4) litter biomass, and 5) soil nutrients. Samples were taken during peak biomass (mid-late June) as well as both pre- and post-burn (early-mid September).

### Vegetation and litter

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 prior to seed dispersal (mid-June). Cheatgrass and wheat density were

counted, and aboveground biomass of cheatgrass, wheat, and all other species were harvested separately in all treatment plots. After aboveground biomass was harvested, litter was collected in all treatment plots. In the lab, cheatgrass samples were sorted into filled seed and vegetative biomass. Each portion of the cheatgrass samples, as well as the other biomass and litter samples, was then oven dried at 60°C and weighed. Viability of filled seed was assessed from a subsample (~200 seeds) from each site prior to drying. Cheatgrass plant biomass and seed density values were calculated by dividing total plot biomass and seed density by plant density.

Aboveground vegetation and litter also were collected directly prior to fall burns to assess pre-burn biomass. Aboveground biomass of all plants was harvested in 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.

## Soils

Plant root simulator (PRS) probes were used to monitor soil N availability ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) 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 one hour in a zip lock bag, and the extractant was analyzed for  $\text{NH}_4^+$  and  $\text{NO}_3^-$  using a Technicon autoanalyzer (Bran and Lubbe, Inc., Buffalo, NY). The values for

both the probes were reported in units of  $\mu\text{g N/cm}^2$  of resin area/burial length (i.e. days in the ground) and were converted to  $\text{ng N/cm}^2/\text{day}$ . We summed  $\text{NH}_4^+$  and  $\text{NO}_3^-$  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 between 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 between the two sites.

#### Statistical 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 soil N availability ( $\text{NH}_4^+ + \text{NO}_3^-$ ), litter biomass, wheat biomass, other annual plant biomass, and cheatgrass density, cheatgrass biomass and seed density per plot, and cheatgrass biomass and seed density per plant. The two experiments were analyzed using Generalized Linear Mixed-effects Models (GLMM). The blocking factor of site was treated as a random effect. The burn and seeding treatments were treated as a fixed effect within each site, and plots within sites were treated as random effects. The year of

sampling (year of burn for burned plots) was treated as a fixed effect. 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 ( $\alpha=0.05$ ). All analyses were conducted using the GLIMMIX procedure in SAS ver. 9.3 (SAS Institute, Cary NC).

### Structural equation modeling

Structural equation modeling (Grace 2006) was used to evaluate our conceptual model (Fig. 1). 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 representing a subset of the full, hypothesized path models (Fig. 1) was selected based on model fit statistics. Path coefficients were calculated, which demonstrate the direct relationships between variables. Cheatgrass growth and reproduction were represented in the model by total cheatgrass biomass per plot and seed density per plant. Cheatgrass biomass and seed density were strongly correlated at both

the plot and plant scale. These particular variables (biomass per plot and seed density per plant) were chosen because of their importance in previous studies of cheatgrass success (Chambers et al. 2007). Also, cheatgrass biomass per plot is representative of N uptake by the population and the potential for progressive N deficiency over time while seed density per plant is representative of individual plant success.

## **Results**

### Weather and fire temperatures

Mean precipitation during the period affecting 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 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 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

Litter biomass exhibited a strong year by burn and seeding treatment interaction in litter intact and litter removed plots (Table 2; Fig. 3). Unburned litter intact plots maintained higher litter biomass than all other treatments in all years ( $p < 0.05$ ). Litter intact plots that were repeatedly burned lost 30-50% litter biomass 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 regained litter biomass throughout the experiment and had four times more litter biomass in 2012 than litter removed plots that were burned every year ( $p = 0.0009$ ).

#### Soil N availability

Total soil N availability ( $\text{NH}_4^+ + \text{NO}_3^-$ ) in both winter and spring generally followed trends in  $\text{NO}_3^-$ .  $\text{NO}_3^-$  was the dominant form of total soil available N, and therefore only total soil N availability is shown. Winter soil N availability exhibited separate burn and seeding treatment and year effects in litter intact and litter removed plots (Table 2; Fig. 4). In litter intact and litter removed plots, all burn and seeding treatments had higher winter soil N availability in 2010 than 2009 but 2011 and 2012 levels were similar to those in 2009 ( $p < 0.0001$ ). Winter soil N availability was higher in burned than unburned plots regardless of seeding treatment ( $p < 0.05$ ) and there was no difference in winter soil N availability between litter intact plots and litter removed plots.

Spring soil N availability exhibited a year by burn and seeding treatment interaction in litter intact and litter removed plots (Table 2; Fig. 4). In litter intact and litter removed plots, spring soil N availability in all burn and seeding treatments was



generally similar among years. Exceptions were that in litter intact plots in 2009, soil N availability in burned only plots was higher than in other burned treatment plots ( $p < 0.001$ ), and in litter intact and litter removed plots in 2012, soil N availability in plots that were burned and seeded with wheat was higher than in all other treatment plots ( $p < 0.0001$ ). There was no difference in spring soil N availability between litter intact plots and litter removed plots. Winter soil N availability was higher than spring soil N availability in all years.

#### Effect of treatments on vegetation

##### Cheatgrass (plot scale)

Cheatgrass density per plot exhibited a year by burn and seeding treatment interaction for litter intact plots, and significant main effects for burn and seeding treatments and year in litter removed plots (Table 2; Fig. 5). In litter intact plots, densities in all plots except for those that were burned and seeded with wheat increased in the first three years after burning with a peak in 2011, the wet year, and then decreased to pre-burn levels in 2012 ( $p < 0.05$ ). In contrast, densities in plots that were burned and seeded with wheat were generally similar throughout the first four years of the experiment and then declined in 2012 ( $p < 0.04$ ). Also, although initial densities in litter intact plots were similar among all treatments, densities in burned and seeded with wheat plots were lower than all other treatments in the last three years ( $p < 0.05$ ). Litter removed plots had similar trends across years (peak in density in 2011) and among burn and seeding treatments (lowest densities in burned and seeded with wheat plots).

However, densities were generally lower in litter removed plots than in unburned, litter intact plots ( $p < 0.01$ ).

Cheatgrass biomass and seed density per plot followed the same general patterns over time. Biomass exhibited year by burn and seeding treatment interactions in litter intact plots and significant main effects for burn and seeding treatment and year in litter removed plots (Table 2; Fig. 5). Seed density exhibited year by burn and seeding treatment interactions in both litter intact and litter removed treatments (Table 2; Fig. 5). In litter intact plots, biomass and seed density in unburned, burned only and burned and seeded with cheatgrass plots increased in the first two post-burn years and then decreased to or below pre-burn levels in 2012 ( $p < 0.05$ ). In burned and seeded with wheat plots, biomass and seed density were similar from 2008 to 2010 and then decreased in 2011 and 2012 ( $p < 0.04$ ). Differences in biomass and seed density among burn and seeding treatments in litter intact plots occurred in 2010, 2011 and 2012 when biomass and seed density were highest in burned only and/or burned and seeded with cheatgrass plots and lowest in burned and seeded with wheat plots ( $p < 0.05$ ). In litter removed plots, biomass was highest in 2010 and lowest in 2011 and 2012 ( $p < 0.03$ ). Also, biomass was lowest in litter removed plots that were burned and seeded with wheat and highest in unburned, litter intact and burned and seeded with cheatgrass plots ( $p < 0.05$ ). Seed density increased in 2010 and then decreased to or below pre-burn levels in 2011 and 2012 in plots that were burned and seeded with cheatgrass ( $p < 0.04$ ). Seed density in unburned, burned only, and burned and seeded with wheat plots was similar from 2009 to 2010 and decreased to or below pre-burn levels in 2011 and 2012 ( $p < 0.001$ ). Differences in seed density among burn and seeding treatments in litter intact plots occurred in two years. In

2010 and 2012 burned and seeded with cheatgrass plots and/or unburned litter intact plots had higher seed density than unburned, burned only, and burned and seeded with wheat plots ( $p < 0.05$ ).

#### Cheatgrass (plant scale)

Cheatgrass biomass and seed density per plant followed the same general patterns over time. Biomass exhibited a strong year by burn and seeding treatment interaction for litter intact plots and separate burn and seeding treatment and year effects for litter removed plots. Seed density exhibited strong year by burn and seeding treatment interactions in both litter intact and litter removed treatments (Table 2; Fig. 6). In litter intact plots, biomass and seed density in burned only and burned and seeded with cheatgrass plots increased in the first post-burn year and then decreased to or below pre-burn levels by 2012 ( $p < 0.05$ ). Biomass and seed density in unburned and burned and seeded with wheat plots were similar to pre-burn levels in the first two post-burn years and then decreased to or below pre-burn levels in the final post-burn years ( $p < 0.04$ ). Differences in biomass and seed density among burn and seeding treatments occurred in several years. In 2009, burned only plots had higher biomass and seed density than unburned and burned and seeded with wheat plots ( $p < 0.04$ ). In 2010, burned and seeded with cheatgrass plots had higher seed density than unburned plots ( $p < 0.03$ ). In 2011, burned and seeded with wheat plots had higher biomass and seed density than unburned plots and burned and seeded with cheatgrass plots ( $p < 0.02$ ). In litter removed plots, biomass was generally highest in 2009 and 2010 and lowest in 2011 and 2012 ( $p < 0.05$ ). Also, plots that were burned and seeded with wheat and cheatgrass generally had

the highest biomass, especially compared to unburned litter intact plots ( $p < 0.04$ ). Litter removed plots had higher seed density than litter intact plots in 2009 ( $p < 0.002$ ), but decreased significantly in 2010 after the first burn ( $p < 0.03$ ) and did not equal seed densities in litter intact plots until 2012.

#### Wheat and other annual plants

Wheat biomass in plots burned and seeded with wheat exhibited changes in biomass across years (Table 2; Fig. 7). In both litter intact and litter removed plots, wheat biomass increased from 2009 to 2010 and then decreased in 2011 and 2012 ( $p < 0.05$ ).

Other annual plant biomass exhibited a year by burn and seeding treatment interaction in litter intact plots and significant main effects of burn and seeding treatment and year in litter removed plots (Table 2; Fig. 7). In litter intact plots, annual plant biomass other than cheatgrass generally increased in all burned treatments in the first three post-burn years (2009-2011), and then decreased to pre-burn levels in 2012 ( $p < 0.05$ ). In unburned litter intact plots other annual plant biomass was generally similar among years, except for an increase in 2010 ( $p < 0.05$ ). In litter removed plots, the only difference in other annual plant biomass among burn and seeding treatments was in 2011 when plots that were burned and seeded had the highest biomass and unburned plots generally had the lowest biomass ( $p < 0.03$ ). In litter removed plots, other annual plant biomass generally increased from 2009 to 2010 and then decreased to or below pre-burn levels in 2011 and 2012 ( $p < 0.02$ ). Also, unburned litter intact plots and burned litter removed plots that were seeded with wheat generally had lower other annual plant

biomass than unburned litter removed plots and litter removed plots that were burned only and burned and seeded with cheatgrass ( $p < 0.05$ ).

#### Structural equation model

The path analyses illustrated the direct and indirect effects of the treatments and abiotic and biotic factors on our measured variables (Fig. 8). Litter removal, burning, and seeding with wheat or cheatgrass had both direct and indirect effects on our measured variables. Litter removal had a negative direct effect on litter biomass, negative indirect effects on cheatgrass biomass per plot and seed density per plant which were positively affected by litter biomass, and positive indirect effects on wheat and other annual plant biomass which were negatively affected by litter biomass. Burning, expressed as number of burns in our model, had a large negative direct effect on litter biomass and, consequently, a negative indirect effect on cheatgrass biomass per plot and positive indirect effect on wheat and other annual plant biomass. Burning had a smaller positive direct effect on winter soil N availability, and a negative indirect effect on cheatgrass density but 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 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 N availability. Seed density from the previous

year, which is representative of 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.

The abiotic factors, precipitation received from September 1 through June 30 and winter minimum temperature, had strong direct and indirect effects. Precipitation had positive 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, but negative direct effects on litter biomass and spring soil N availability. Precipitation had positive indirect effects on cheatgrass seed density per plant, due to the effect of precipitation on winter soil N availability, and a positive indirect effect on other annual plant biomass, due to the effect of precipitation on litter biomass. Precipitation had negative indirect effects on wheat biomass and cheatgrass density, due to the effect of precipitation on winter soil N availability, and negative indirect effects 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. Minimum winter temperature had negative indirect effects on cheatgrass seed density per plant, due to the effect of temperature on winter soil N availability. 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**

There is debate in the literature about the efficacy of using nutrient manipulation as a management strategy. Controlled greenhouse experiments indicate that reducing soil resources will not decrease the competitive advantage of invasive species (Funk and Vitousek 2007, James et al. 2011) while field experiments have found that decreasing soil N availability is effective at decreasing invasive species abundance, at least in the short-term (Ojima et al. 1994, Blair 1997, Blumenthal et al. 2003, Suding et al. 2004, Buisson et al. 2006, Perry et al. 2010, Mazzola et al. 2011). However, there has yet to be an approach developed that restores pre-invasion nutrient cycling over the long term

This research allowed us to identify the mechanisms associated with treatments aimed at reducing soil N availability and cheatgrass success, and to evaluate 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. In particular, the effects of repeated burning were not as anticipated

(discussion below), and precipitation and temperature mediated the effects of all treatments in these climatically variable ecosystems.

#### Treatment effects

We found that cheatgrass biomass and seed density, both per plot and per plant, generally tracked winter soil N availability over time, indicating that cheatgrass was highly responsive to changes in soil N availability and exhibited a high degree of plasticity in plant size and seed production as found elsewhere (Chambers et al. 2007, Mazzola et al. 2011). However, hypotheses concerning the long-term effects of burning on soil N availability and cheatgrass success were not supported. We had hypothesized that burning would result in an immediate pulse in soil N availability due to heat-induced SOM 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 N, resulting in decreases in N inputs to soils over time (progressive N deficiency) (Rau et al. 2007). In our study, winter soil N availability was higher than spring soil N availability in all years, especially in burned plots, likely due to predicted SOM denaturation as well as 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. The lack of a long-term response to burning may be partly explained by fire temperatures. Surface soil temperatures during the burns never exceeded 70°C and flame temperatures never exceeded 180°C on either litter intact or litter removed plots. Although hotter fire temperatures and more short-term N mobilization and volatilization can occur in sagebrush ecosystems that have woody fuels (Johnson et al. 2011),



temperatures documented in our study are typical of fires 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. submitted).

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). Also, litter mats can increase soil moisture and modulate extreme temperatures (Facelli and Pickett 1991, Newingham et al. 2007, Wolkovich et al. 2009), both of which may enhance net N mineralization. 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). Also, over time litter biomass gradually recovered on the litter removal plots and by the end of the study was similar to that on burned litter intact plots.

The litter removal treatment did have a significant negative effect on cheatgrass plot biomass and plant seed density, likely due to the effect of litter on cheatgrass seed entrapment and retention and on plant establishment and growth rather than on 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). The

initial effect of litter removal in our study likely resulted in a significant reduction in the seed bank of cheatgrass. Moreover, litter removal may have shifted the competitive balance between species in the system. Dense litter mats, such as those produced by cheatgrass, trap most seeds and typically prevent large seeded species from reaching mineral soil to germinate, while small-seed species often have insufficient reserves to emerge through the dense litter. Cheatgrass, however, has long awns that allow it to work through litter and gain an advantage in germination and growth (Stewart and Hull 1949). Removal of the litter mat may have removed the competitive advantage of cheatgrass thereby reducing its success while increasing the biomass of the small-seeded annual forbs on the site.

Cheatgrass success also was influenced by post-burn seeding and competition from wheat and other unseeded annual plants. 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 highly elevated in plots seeded with wheat 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  $\text{NH}_4^+$ , in cold desert shrublands are most available to plant roots in shallow soil depths and are available primarily 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. in press).

Our path analyses indicated that effects of soil available N differed depending on whether cheatgrass variables were measured on a plant versus plot basis. In our model, winter soil N availability had a negative direct effect on density, a positive direct effect on plant seed density, and no effect on plot biomass. Also, cheatgrass density was positively correlated with plot biomass but negatively correlated with seed density per plant. 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) and has been observed in other research on cheatgrass (Mazzola et al. 2011). As a result, the 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 resources are made available by mortality of some individuals in the population (White et al. 2007). These results show that the choice to measure plant variables on a plot versus plant basis can influence the interpretation of study results, and may partly explain the differences in

interpretation between greenhouse experiments that measure plant variables and field studies that largely measure plot variables to evaluate effects of resource manipulation.

#### 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 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). It is noteworthy that 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. Short-term depletions in cheatgrass seed banks after disturbance are often followed by large increases in following years (Humphrey and Schupp 2001, Mazzola et al. 2011). Our data also indicate that all available resources are likely utilized by individual plants well before peak plant and seed bank densities are reached.

## Synthesis

Our study provides insights into the mechanisms influencing resource availability and cheatgrass success in Wyoming big sagebrush ecosystems as well as potential approaches for restoring pre-invasion nutrient cycles. Results of our treatments indicate that repeated burning is unlikely to decrease soil N availability in cheatgrass-dominated systems due to cool fire temperatures that do not volatilize biomass N and only partially consume litter layers (Jones et al. submitted). In fact, cool fire 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 in arid and semi-arid ecosystems. Although repeated burning did not decrease soil N availability, it 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 is a factor that should be considered when evaluating if restoration practices like seeding will succeed. Seeding with a competitor, annual wheat, significantly decreased cheatgrass plot variables and other plant biomass, but it did not reduce available soil N and thus had no effect on cheatgrass plant variables. The large overall decrease in cheatgrass success at the plot scale indicates that 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. Our results indicate that studies evaluating effects of N manipulations should monitor weather variables and soil water availability and are best repeated over time to incorporate differences among years. The success of restoration species also depends on weather, and restoration seeding should be conducted during favorable periods of weather and repeated over time if necessary (Hardegree et al. 2003, Roundy et al. 2007).

Integrated restoration approaches that decrease litter biomass and seed banks and increase competitive interactions may be more effective at reducing annual grasses and establishing desirable perennial species than current approaches aimed at reducing soil nutrients. One restoration approach that has proven successful in cheatgrass-dominated areas is assisted succession. Assisted succession is a multi-stage restoration process that can be used immediately following disturbances such as wildfire or intensive grazing by livestock, both of which reduce cheatgrass seed banks and litter mats (Frost and Launchbaugh 2003). The first stage of assisted succession is seeding with grasses to prevent rapid post-disturbance increases in cheatgrass seed banks and stabilize soils to limit erosion. Introduced perennial species such as crested wheatgrass (*Agropyron cristatum*) have historically been seeded in this first stage because these species are strong competitors for available soil nutrient and water resources and can decrease cheatgrass cover on certain ecological types (Cox and Anderson 2004, Waldron et al. 2005, Blank and Morgan 2012). However, species like crested wheatgrass usually reduce the cover of residual natives (Knutson et al. submitted) and often form near monocultures with their own suite of ecological costs (Christian and Wilson 1999, Heidinga and Wilson 2002, Davison and Smith 2005). Our study shows that sterile cover crops like common

wheat decrease cheatgrass densities, biomass, and reproduction in the first year after seeding, but lack the threat of out-competing native species and therefore may be better choices for the first stage of assisted succession. In the second stage of assisted succession, native perennial species can be seeded (Cox and Anderson 2004). Our findings, and those of others, suggest that reducing cheatgrass abundance sufficiently to enable native species establishment will require an integrated approach that involves reducing litter and seeding a competitor, and that more than one intervention may be needed on sites with low and variable precipitation.

### **Acknowledgements**

This study was a collaborative effort among the USFS Rocky Mountain Research Station, University of Nevada, Reno, USDA Agricultural Research Service and Winnemucca District of the Nevada Bureau of Land Management. Research funding was provided through the Rocky Mountain Research Station. We thank T. Morgan, C. Rosner, C. Dencker, and a large number of summer technicians for valuable assistance in the field and lab, and B. Leger, P. Verburg, and T. Albright for valuable comments on earlier drafts of this manuscript.

### **Literature Cited**

- Aguirre, L., and D. A. Johnson. 1991. Influence of temperature and cheatgrass competition on seedling development of 2 bunchgrasses. *Journal of Range Management* **44**:347-354.
- Allison, S. D., and P. M. Vitousek. 2005. Responses of extracellular enzymes to simple and complex nutrient inputs. *Soil Biology & Biochemistry* **37**:937-944.
- Angers, D. A., and J. Caron. 1998. Plant-induced changes in soil structure: Processes and feedbacks. *Biogeochemistry* **42**:55-72.
- Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. *Wildlife Society Bulletin* **34**:177-185.

- Baker, W. L. 2011. Pre-EuroAmerican and recent fire in sagebrush ecosystems. Pages 185–201 in S. T. K. a. J. W. Connelly, editor. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in avian biology 38. University of California Press, Berkeley, CA, USA.
- Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gomez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). *Global Change Biology* **19**:173-183.
- Baughman, O. W., and S. E. Meyer. 2013. Is *Pyrenophora semeniperda* the cause of downy brome (*Bromus tectorum*) die-offs? *Invasive Plant Science and Management* **6**:105-111.
- Belnap, J., and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: Response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications* **11**:1261-1275.
- Belnap, J., S. L. Phillips, S. K. Sherrod, and A. Moldenke. 2005. Soil biota can change after exotic plant invasion: does this affect ecosystem processes? *Ecology* **86**:3007-3017.
- Belsky, A. J., and J. L. Gelbard. 2000. Livestock grazing and weed invasions in the arid west. Oregon Natural Desert Association.
- Binkley, D., D. Richter, M. B. David, and B. Caldwell. 1992. Soil chemistry in a loblolly longleaf pine forest with interval burning. *Ecological Applications* **2**:157-164.
- Blackshaw, R. E. 1994. Rotation affects downy brome (*Bromus tectorum*) in winter wheat (*Triticum aestivum*). *Weed Technology* **8**:728-732.
- Blair, J. M. 1997. Fire, N availability, and plant response in grasslands: A test of the transient maxima hypothesis. *Ecology* **78**:2359-2368.
- Blank, R. R. 2008. Biogeochemistry of plant invasion: A case study with downy brome (*Bromus tectorum*). *Invasive Plant Science and Management* **1**:226-238.
- Blank, R. R., L. Abraham, and J. A. Young. 1994a. Soil heating, nitrogen, cheatgrass, and seedbed microsites. *Journal of Range Management* **47**:33-37.
- Blank, R. R., F. Allen, and J. A. Young. 1994b. Extractable anions in soils following wildfire in a sagebrush-grass community. *Soil Science Society of America Journal* **58**:564-570.
- Blank, R. R., F. L. Allen, and J. A. Young. 1996. Influence of simulated burning of soil-litter from low sagebrush, squirreltail, cheatgrass, and medusahead on water-soluble anions and cations. *International Journal of Wildland Fire* **6**:137-143.
- Blank, R. R., and T. Morgan. 2012. Mineral nitrogen in a crested wheatgrass stand: Implications for suppression of cheatgrass. *Rangeland Ecology & Management* **65**:101-104.
- Blank, R. R., T. Morgan, C. D. Clements, and B. E. Mackey. 2013. *Bromus tectorum* L. invasion: Changes in soil properties and rates of bioturbation. *Soil Science* **178**:281-290.
- Blank, R. R., and J. A. Young. 2009. Plant-soil relationships of *Bromus tectorum* L.: Interactions among labile carbon additions, soil invasion status, and fertilizer. *Applied and Environmental Soil Science* **2009**:7 pages.
- Blank, R. R., and D. C. Zamudio. 1998. The influence of wildfire on aqueous-extractable soil solutes in forested and wet meadow ecosystems along the eastern front of the Sierra-Nevada range, California. *International Journal of Wildland Fire* **8**:79-85.



- Blumenthal, D. M., N. R. Jordan, and M. P. Russelle. 2003. Soil carbon addition controls weeds and facilitates prairie restoration. *Ecological Applications* **13**:605-615.
- Boerner, R. E. J. 1982. Fire and nutrient cycling in temperate ecosystems. *Bioscience* **32**:187-192.
- Booth, M. S., M. M. Caldwell, and J. M. Stark. 2003a. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. *Journal of Ecology* **91**:36-48.
- Booth, M. S., J. M. Stark, and M. M. Caldwell. 2003b. Inorganic N turnover and availability in annual- and perennial-dominated soils in a northern Utah shrub-steppe ecosystem. *Biogeochemistry* **66**:311-330.
- Borken, W., and E. Matzner. 2009. Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Global Change Biology* **15**:808-824.
- Bradley, B. A., R. A. Houghton, J. F. Mustard, and S. P. Hamburg. 2006. Invasive grass reduces aboveground carbon stocks in shrublands of the Western US. *Global Change Biology* **12**:1815-1822.
- Bradley, B. A., and J. F. Mustard. 2005. Identifying land cover variability distinct from land cover change: Cheatgrass in the Great Basin. *Remote Sensing of Environment* **94**:204-213.
- Brooks, M. L. 2002. Peak fire temperatures and effects on annual plants in the Mojave Desert. *Ecological Applications* **12**:1088-1102.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *Bioscience* **54**:677-688.
- Brunson, J. L., D. A. Pyke, and S. S. Perakis. 2010. Yield responses of ruderal plants to sucrose in invasive-dominated sagebrush steppe of the northern Great Basin. *Restoration Ecology* **18**:304-312.
- Buisson, E., K. D. Holl, S. Anderson, E. Corcket, G. F. Hayes, F. Torre, A. Peteers, and T. Dutoit. 2006. Effect of seed source, topsoil removal, and plant neighbor removal on restoring California coastal prairies. *Restoration Ecology* **14**:569-577.
- Burke, I. C. 1989. Control of nitrogen mineralization in a sagebrush steppe landscape. *Ecology* **70**:1115-1126.
- Chambers, J. C. 2000. Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: Implications for restoration. *Ecological Applications* **10**:1400-1413.
- Chambers, J. C. 2001. *Pinus monophylla* establishment in an expanding *Pinus-Juniperus* woodland: Environmental conditions, facilitation and interacting factors. *Journal of Vegetation Science* **12**:27-40.
- Chambers, J. C., and J. A. Macmahon. 1994. A day in the life of a seed- movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics* **25**:263-292.
- Chambers, J. C., R. F. Miller, D. I. Board, D. A. Pyke, B. A. Roundy, J. B. Grace, E. W. Schupp, and R. J. Tausch. in press. Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. *Rangeland Ecology & Management*.

- Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs* **77**:117-145.
- Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. *Nature* **405**:234-242.
- Charley, J. L., and N. E. West. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *Journal of Ecology* **63**:945-963.
- Cheng, X. L., S. Q. An, S. R. Liu, and G. Q. Li. 2004. Micro-scale spatial heterogeneity and the loss of carbon, nitrogen and phosphorus in degraded grassland in Ordos Plateau, northwestern China. *Plant and Soil* **259**:29-37.
- Christian, J. M., and S. D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the northern Great Plains. *Ecology* **80**:2397-2407.
- Cox, R. D., and V. J. Anderson. 2004. Increasing native diversity of cheatgrass-dominated rangeland through assisted succession. *Journal of Range Management* **57**:203-210.
- Cui, M. Y., and M. M. Caldwell. 1997. A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. *Plant and Soil* **191**:291-299.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**:63-87.
- Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annual Review of Ecology and Systematics* **34**:183-211.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**:528-534.
- Davison, J., and E. Smith. 2005. Living with fire, crested wheatgrass: hero or villain in reclaiming disturbed rangelands. Page 4. University of Nevada Cooperative Extension Service, Reno, NV, USA.
- Deng, J. M., T. Li, G. X. Wang, J. Liu, Z. L. Yu, C. M. Zhao, M. F. Ji, Q. Zhang, and J. Q. Liu. 2008. Trade-Offs between the Metabolic Rate and Population Density of Plants. *Plos One* **3**:7.
- Denny, D. W. 2002. Soil survey of Humboldt County, Nevada, East Part, part 1. US Department of Agriculture, Natural Resources Conservation Service, Reno, NV, USA.
- Diamond, J. M. 2009. Effects of targeted grazing and prescribed burning on fire behavior and community dynamics of a cheatgrass (*Bromus tectorum*)- dominated landscape. Utah State University, Logan, Utah.
- Dijkstra, F. A., and W. Cheng. 2007. Moisture modulates rhizosphere effects on C decomposition in two different soil types. *Soil Biology & Biochemistry* **39**:2264-2274.
- Dobrowolski, J. P., M. M. Caldwell, and J. H. Richards. 1990. Basin hydrology and plant root systems. *Ecological Studies* **80**:243-292.

- Dodds, W. K., J. M. Blair, G. M. Henebry, J. K. Koelliker, R. Ramundo, and C. M. Tate. 1996. Nitrogen transport from tallgrass prairie watersheds. *Journal of Environmental Quality* **25**:973-981.
- Ducas, L. P., S. B. Jones, A. J. Leffler, and R. J. Ryel. 2011. Associations of near-surface soil moisture and annual plant community dynamics. *Natural Resources and Environmental Issues* **17**:12.
- D'Antonio, C. M., J. C. Chambers, R. Loh, and J. T. Tunison. 2009. Applying ecological concepts to the management of widespread grass invasions. Pages 123-149 in R. L. Inderjit, editor. *Management of Invasive Weeds*. Springer, Netherlands.
- Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* **6**:503-523.
- Ehrenfeld, J. G. 2010. Ecosystem Consequences of Biological Invasions. *Annual Review of Ecology, Evolution, and Systematics*, Vol 41 **41**:59-80.
- Ehrenfeld, J. G., P. Kourtev, and W. Z. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* **11**:1287-1300.
- Ehrenfeld, J. G., B. Ravit, and K. Elgersma. 2005. Feedback in the plant-soil system. *Annual Review of Environment and Resources* **30**:75-115.
- Elzinga, C. L., D. W. Salzer, and J. W. Willoughby. 1998. Measuring and monitoring plant populations. U.S. Department of the Interior, Bureau of Land Management, Denver, CO.
- Evans, R. A., and J. A. Young. 1970. Plant Litter and Establishment of Alien Annual Weed Species in Rangeland Communities. *Weed Science* **18**:697-703.
- Evans, R. A., and J. A. Young. 1984. Microsite requirements for downy brome (*Bromus tectorum*) infestation and control on sagebrush rangelands. *Weed Science* **32**:13-17.
- Evans, R. D., and J. R. Ehleringer. 1994. Water and nitrogen dynamics in an arid woodland. *Oecologia* **99**:233-242.
- Evans, R. D., R. Rimer, L. Sperry, and J. Belnap. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications* **11**:1301-1310.
- Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter- its dynamics and effects on plant community structure. *Botanical Review* **57**:1-32.
- Fierer, N., J. M. Craine, K. McLauchlan, and J. P. Schimel. 2005. Litter quality and the temperature sensitivity of decomposition. *Ecology* **86**:320-326.
- Fierer, N., and J. P. Schimel. 2002. Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. *Soil Biology & Biochemistry* **34**:777-787.
- Frost, R. A., and K. L. Launchbaugh. 2003. Prescription grazing for rangeland weed management: a new look at an old tool. *Rangelands* **25**:43-47.
- Funk, J. L., and P. M. Vitousek. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* **446**:1079-1081.
- Fynn, R. W. S., R. J. Haynes, and T. G. O'Connor. 2003. Burning causes long-term changes in soil organic matter content of a South African grassland. *Soil Biology & Biochemistry* **35**:677-687.
- Goergen, E. M., E. A. Leger, and E. K. Espeland. 2011. Native Perennial Grasses Show Evolutionary Response to *Bromus tectorum* (Cheatgrass) Invasion. *Plos One* **6**.

- Grace, J. B. 2006. Structural equation modeling and natural systems. Cambridge University Press, Cambridge.
- Grace, J. B., A. Youngblood, and S. M. Scheiner. 2009. Structural equation modeling and ecological experiments. Pages 19–45 in S. C. S. Miao, and M. Nungesser, editor. Real World Ecology: Large-Scale and Long-Term Case Studies and Methods. Springer Verlag, New York, NY.
- Grier, C. C., and D. W. Cole. 1971. Influence of slash burning on ion transport in soil. Northwest Science **45**:100-106.
- Grogan, P., T. D. Bruns, and F. S. Chapin. 2000. Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. Oecologia **122**:537-544.
- Hardegee, S. P., G. N. Flerchinger, and S. S. Van Vactor. 2003. Hydrothermal germination response and the development of probabilistic germination profiles. Ecological Modelling **167**:305-322.
- Heidinga, L., and S. D. Wilson. 2002. The impact of an invading alien grass (*Agropyron cristatum*) on species turnover in native prairie. Diversity and Distributions **8**:249-258.
- Herron, G. J., R. L. Sheley, B. D. Maxwell, and J. S. Jacobsen. 2001. Influence of nutrient availability on the interaction between spotted knapweed and bluebunch wheatgrass. Restoration Ecology **9**:326-331.
- Hillel, D. 1998. Environmental Soil Physics. Academic, San Diego, CA.
- Hobbie, S. E. 1992. Effects of plant-species on nutrient cycling. Trends in Ecology & Evolution **7**:336-339.
- Hooker, T., J. Stark, U. Norton, A. J. Leffler, M. Peek, and R. Ryel. 2008. Distribution of ecosystem C and N within contrasting vegetation types in a semiarid rangeland in the Great Basin, USA. Biogeochemistry **90**:291-308.
- Humphrey, L. D., and E. W. Schupp. 2001. Seed banks of *Bromus tectorum*-dominated communities in the Great Basin. Western North American Naturalist **61**:85-92.
- Jackson, R. B., J. L. Banner, E. G. Jobbagy, W. T. Pockman, and D. H. Wall. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature **418**:623-626.
- James, J. J., R. E. Drenovsky, T. A. Monaco, and M. J. Rinella. 2011. Managing soil nitrogen to restore annual grass-infested plant communities: effective strategy or incomplete framework? Ecological Applications **21**:490-502.
- Jobbagy, E. G., and R. B. Jackson. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications **10**:423-436.
- Johnson, B. G., D. W. Johnson, J. C. Chambers, and R. R. Blank. 2011. Fire effects on the mobilization and uptake of nitrogen by cheatgrass (*Bromus tectorum* L.). Plant and Soil **341**:437-445.
- Johnson, B. G., D. W. Johnson, W. W. Miller, and D. I. Board. 2012. The effects of ash influx on burned and unburned soil water-extractable nutrients using a mechanical vacuum extractor. Soil Science **177**:338-344.
- Johnson, D. W., J. F. Murphy, R. B. Susfalk, T. G. Caldwell, W. W. Miller, R. F. Walker, and R. F. Powers. 2005. The effects of wildfire, salvage logging, and post-fire N-fixation on the nutrient budgets of a Sierran forest. Forest Ecology and Management **220**:155-165.

- Johnson, L. C., and J. R. Matchett. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. *Ecology* **82**:3377-3389.
- Jones, R. O., J. C. Chambers, D. I. Board, D. W. Johnson, and R. R. Blank. in prep. Understanding the role of resource limitation in restoration of sagebrush ecosystems dominated by cheatgrass - a mechanistic approach.
- Jones, R. O., J. C. Chambers, D. W. Johnson, R. R. Blank, and D. I. Board. submitted. Effect of repeated burning on plant and soil carbon and nitrogen in cheatgrass (*Bromus tectorum*) dominated ecosystems. *Plant and Soil*.
- Keane, R. E., K. C. Ryan, T. T. Veblen, C. D. Allen, J. Logan, and B. Hawkes. 2002. Cascading effects of fire exclusion in Rocky Mountain ecosystems: a literature review. Fort Collins, Colorado.
- Keeley, J. E., D. Lubin, and C. J. Fotheringham. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications* **13**:1355-1374.
- Keeney, D. R., and D. W. Nelson. 1987. Nitrogen—inorganic forms. Pages 643-698 in A. L. Page, editor. *Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties*. American Society of Agronomy, Madison, Wisconsin USA.
- Klemmedson, J. O., and J. G. Smith. 1964. Cheatgrass (*Bromus Tectorum* L.). *Botanical Review* **30**:226-262.
- Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *Bioscience* **36**:662-668.
- Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert - History, persistence, and influences to human activities. *Global Environmental Change-Human and Policy Dimensions* **6**:37-52.
- Knutson, K. C., D. A. Pyke, T. A. Wirth, R. S. Arkle, D. S. Pilliod, M. L. Brooks, J. C. Chambers, and J. B. Grace. submitted. Long-term effects of seeding after wildfire on vegetation composition in Great Basin shrub steppe. *Journal of Applied Ecology*.
- Korfmacher, J. L., J. C. Chambers, R. J. Tausch, B. A. Roundy, S. E. Meyer, and S. Kitchen. 2003. Technical Note: A technique for conducting small-plot burn treatments. *Journal of Range Management* **56**:251-254.
- Koscelny, J. A., T. F. Peeper, J. B. Solie, and S. G. Solomon. 1990. Effect of wheat (*Triticum aestivum*) row spacing, seeding rate, and cultivar on yield loss from cheat (*Bromus tectorum*). *Weed Technology* **4**:487-492.
- Leffler, A. J., M. S. Peek, R. J. Ryel, C. Y. Ivans, and M. M. Caldwell. 2005. Hydraulic redistribution through the root systems of senesced plants. *Ecology* **86**:633-642.
- Leffler, A. J., and R. J. Ryel. 2012. Resource pool dynamics: conditions that regulate species interactions and dominance. Pages 57-78 in T. A. M. a. R. L. Sheley, editor. *Invasive plant ecology and management. Linking processes to practice*. CAB International, Cambridge, MA, USA.
- Liao, C. Z., R. H. Peng, Y. Q. Luo, X. H. Zhou, X. W. Wu, C. M. Fang, J. K. Chen, and B. Li. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytologist* **177**:706-714.

- Link, S. O., W. G. Glendon, and J. L. Downs. 1990. The Effect of Water Stress on Phenological and Ecophysiological Characteristics of Cheatgrass and Sandberg's Bluegrass. *Journal of Range Management* **43**:506-513.
- Link, S. O., C. W. Keeler, R. W. Hill, and E. Hagen. 2006. *Bromus tectorum* cover mapping and fire risk. *International Journal of Wildland Fire* **15**:113-119.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522-1536.
- MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* **86**:42-55.
- Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America- An ecological chronicle. *Agro-Ecosystems* **7**:145-165.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* **10**:689-710.
- MacKown, C. T., T. A. Jones, D. A. Johnson, T. A. Monaco, and M. G. Redinbaugh. 2009. Nitrogen uptake by perennial and invasive annual grass seedlings: nitrogen form effects. *Soil Science Society of America Journal* **73**:1864-1870.
- Malmer, A. 1996. Hydrological effects and nutrient losses of forest plantation establishment on tropical rainforest land in Sabah, Malaysia. *Journal of Hydrology* **174**:129-148.
- Mazzola, M. B. 2008. Spatio-temporal heterogeneity and habitat invasibility in sagebrush steppe ecosystems. PhD dissertation. University of Nevada, Reno, Reno, NV, USA.
- Mazzola, M. B., J. C. Chambers, R. R. Blank, D. A. Pyke, E. W. Schupp, K. G. Allcock, P. S. Doescher, and R. S. Nowak. 2011. Effects of resource availability and propagule supply on native species recruitment in sagebrush ecosystems invaded by *Bromus tectorum*. *Biological Invasions* **13**:513-526.
- McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.
- McGarigal, K., S. Cushman, and S. Stafford. 2000. Multivariate statistics for wildlife and ecology research. Springer-Verlag, New York, New York, USA.
- Melgoza, G., and R. S. Nowak. 1991. Competition between cheatgrass and 2 native species after fire- Implications from observations and measurements of root distribution. *Journal of Range Management* **44**:27-33.
- Miller, R., S. Knick, D. Pyke, C. Meinke, S. Hanser, M. Wisdom, and A. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145–185 in S. Knick and J. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. *Studies in Avian Biology*, Vol. 38. University of California Press, Berkeley, CA.
- Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003. Contrasting responses of intermountain west grasses to soil nitrogen. *Journal of Range Management* **56**:282-290.
- Monaco, T. A., S. B. Monsen, B. N. Smith, and L. D. Hansen. 2005. Temperature-dependent physiology of *Poa secunda*, a cool season grass native to the Great Basin, United States. *Russian Journal of Plant Physiology* **52**:653-658.

- Monleon, V. J., K. Cromack, and J. D. Landsberg. 1997. Short- and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **27**:369-378.
- Morghan, K. J. R., and T. R. Seastedt. 1999. Effects of soil nitrogen reduction on nonnative plants in restored grasslands. *Restoration Ecology* **7**:51-55.
- Moyano, F. E., S. Manzoni, and C. Chenu. 2013. Responses of soil heterotrophic respiration to moisture availability: An exploration of processes and models. *Soil Biology & Biochemistry* **59**:72-85.
- Murphy, J. D., D. W. Johnson, W. W. Miller, R. F. Walker, and R. R. Blank. 2006. Prescribed fire effects on forest floor and soil nutrients in a Sierra Nevada forest. *Soil Science* **171**:181-199.
- Neary, D. G., C. C. Klopatek, L. F. DeBano, and P. F. Ffolliott. 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management* **122**:51-71.
- Newingham, B. A., P. Vidiella, and J. Belnap. 2007. Do soil characteristics or microhabitat determine field emergence and success of *Bromus tectorum*? *Journal of Arid Environments* **70**:389-402.
- Norton, J. B., T. A. Monaco, J. M. Norton, D. A. Johnson, and T. A. Jones. 2004. Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. *Journal of Arid Environments* **57**:445-466.
- Norton, J. B., T. A. Monaco, and U. Norton. 2007. Mediterranean annual grasses in western North America: kids in a candy store. *Plant and Soil* **298**:1-5.
- Norton, U., A. R. Mosier, J. A. Morgan, J. D. Derner, L. J. Ingram, and P. D. Stahl. 2008. Moisture pulses, trace gas emissions and soil C and N in cheatgrass and native grass-dominated sagebrush-steppe in Wyoming, USA. *Soil Biology & Biochemistry* **40**:1421-1431.
- Ogle, S. M., D. Ojima, and W. A. Reiners. 2004. Modeling the impact of exotic annual brome grasses on soil organic carbon storage in a northern mixed-grass prairie. *Biological Invasions* **6**:365-377.
- Ogle, S. M., W. A. Reiners, and K. G. Gerow. 2003. Impacts of exotic annual brome grasses (*Bromus* spp.) on ecosystem properties of northern mixed grass prairie. *American Midland Naturalist* **149**:46-58.
- Ojima, D. S., D. S. Schimel, W. J. Parton, and C. E. Owensby. 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry* **24**:67-84.
- Patten, D. T., and G. H. Cave. 1984. Fire temperatures and physical characteristics of a controlled burn in the upper Sonoran desert. *Journal of Range Management* **37**:277-280.
- Pellant, M., and C. Hall. 1994. Distribution of two exotic grasses on intermountain rangelands: status in 1992. Pages 109-112 in G. t. r. INT, editor.
- Perkins, L. B., D. W. Johnson, and R. S. Nowak. 2011. Plant-induced changes in soil nutrient dynamics by native and invasive grass species. *Plant and Soil* **345**:365-374.

- Perry, L. G., D. M. Blumenthal, T. A. Monaco, M. W. Paschke, and E. F. Redente. 2010. Immobilizing nitrogen to control plant invasion. *Oecologia* **163**:13-24.
- Peters, J. 2000. Tetrazolium testing handbook. Contribution no. 29 to The handbook on seed testing. Association of Official Seed Analysts, Lincoln, NE, USA.
- Phillips, A. J. 2012. Phenotypic plasticity within the native perennial grass, *Poa secunda* (Sandberg bluegrass), an important component of the Western United States sagebrush grassland vegetation. University of Nevada, Reno, Reno, NV.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* **52**:273-288.
- Pyšek, P., and D. M. Richardson. 2007. Traits associated with invasiveness in alien plants: where do we stand? Pages 97–125 in W. Nentwig, editor. *Biological invasions*. Springer-Verlag, Berlin.
- Raich, J. W., and A. Tufekcioglu. 2000. Vegetation and soil respiration: Correlations and controls. *Biogeochemistry* **48**:71-90.
- Raison, R. J., P. K. Khanna, and P. V. Woods. 1985. Mechanisms of element transfer to the atmosphere during vegetation fires. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **15**:132-140.
- Rau, B. M., R. R. Blank, J. C. Chambers, and D. W. Johnson. 2007. Prescribed fire in a Great Basin sagebrush ecosystem: Dynamics of soil extractable nitrogen and phosphorus. *Journal of Arid Environments* **71**:362-375.
- Rau, B. M., J. C. Chambers, R. R. Blank, and D. W. Johnson. 2008. Prescribed fire, soil, and plants: Burn effects and interactions in the central great basin. *Rangeland Ecology & Management* **61**:169-181.
- Rau, B. M., D. W. Johnson, R. R. Blank, A. Lucchesi, T. G. Caldwell, and E. W. Schupp. 2011. Transition From Sagebrush Steppe to Annual Grass (*Bromus tectorum*): Influence on Belowground Carbon and Nitrogen. *Rangeland Ecology & Management* **64**:139-147.
- Reilly, M. J., M. C. Wimberly, and C. L. Newell. 2006. Wildfire effects on beta-diversity and species turnover in a forested landscape. *Journal of Vegetation Science* **17**:447-454.
- Rimer, R. L., and R. D. Evans. 2006. Invasion of downy brome (*Bromus tectorum* L.) causes rapid changes in the nitrogen cycle. *American Midland Naturalist* **156**:252-258.
- Roundy, B. A., S. P. Hardegree, J. C. Chambers, and A. Whittaker. 2007. Prediction of cheatgrass field germination potential using wet thermal accumulation. *Rangeland Ecology & Management* **60**:613-623.
- Rustad, L. E., J. L. Campbell, G. M. Marion, R. J. Norby, M. J. Mitchell, A. E. Hartley, J. H. C. Cornelissen, J. Gurevitch, and N. Gcte. 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.
- Ryel, R. J., A. J. Leffler, C. Ivans, M. S. Peek, and M. M. Caldwell. 2010. Functional differences in water-use patterns of contrasting life forms in Great Basin steppe lands. *Vadose Zone Journal* **9**:548-560.



- Sankey, J. B., M. J. Germino, and N. F. Glenn. 2009. Relationships of post-fire aeolian transport to soil and atmospheric conditions. *Aeolian Research* **1**:75-85.
- Schaeffer, S. M., S. E. Ziegler, J. Belnap, and R. D. Evans. 2012. Effects of *Bromus tectorum* invasion on microbial carbon and nitrogen cycling in two adjacent undisturbed arid grassland communities. *Biogeochemistry* **111**:427-441.
- Schimel, D. S., B. H. Braswell, E. A. Holland, R. McKeown, D. S. Ojima, T. H. Painter, W. J. Parton, and A. R. Townsend. 1994. Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. *Global Biogeochemical Cycles* **8**:279-293.
- Schimel, D. S., T. G. F. Kittel, A. K. Knapp, T. R. Seastedt, W. J. Parton, and V. B. Brown. 1991. Physiological interactions along resource gradients in a tallgrass prairie. *Ecology* **72**:672-684.
- Schlesinger, W. H., and A. M. Pilmanis. 1998. Plant-soil interactions in deserts. *Biogeochemistry* **42**:169-187.
- Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. E. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* **77**:364-374.
- Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences of the United States of America* **100**:13384-13389.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry- the principles and practice of statistics in biological research*. 2nd edition. W. H. Freeman and Co.
- Sperry, L. J., J. Belnap, and R. D. Evans. 2006. *Bromus tectorum* invasion alters nitrogen dynamics in an undisturbed arid grassland ecosystem. *Ecology* **87**:603-615.
- Stewart, G., and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.) - an ecologic intruder in southern Idaho. *Ecology* **30**:58-74.
- Stubbs, M. M., and D. A. Pyke. 2005. Available nitrogen: A time-based study of manipulated resource islands. *Plant and Soil* **270**:123-133.
- Suding, K. N., K. D. LeJeune, and T. R. Seastedt. 2004. Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorus availability. *Oecologia* **141**:526-535.
- Suring, L. H., M. J. Wisdom, R. J. Tausch, R. F. Miller, M. M. Rowland, L. Schueck, and C. W. Meinke. 2005. Modeling threats to sagebrush and other shrubland communities. Pages 114-149 *Habitat threats in the sagebrush ecosystems: methods of regional assessment and applications in the Great Basin*. Alliance Communications Group, Lawrence, Kansas, USA.
- Tausch, R. J., P. E. Wigand, and J. W. Burkhardt. 1993. Viewpoint: Plant Community Thresholds, Multiple Steady States, and Multiple Successional Pathways: Legacy of the Quaternary? *Journal of Range Management* **46**:439-447.
- Vinton, M. A., and I. C. Burke. 1995. Interactions between individual plant-species and soil nutrient status in shortgrass steppe. *Ecology* **76**:1116-1133.
- Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and G. D. Tilman. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications* **7**:737-750.

- Vitousek, P. M., C. M. Dantonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* **84**:468-478.
- Waldron, B. L., T. A. Monaco, K. B. Jensen, R. D. Harrison, A. J. Palazzo, and J. D. Kulbeth. 2005. Coexistence of native and introduced perennial grasses following simultaneous seeding. *Agronomy Journal* **97**:990-996.
- West, N. E. 1983. Great Basin-Colorado Plateau sagebrush semi-desert. Pages 331-349 *in* N. E. West, editor. *Temperate deserts and semi-deserts*. Elsevier Publishing Company, Amsterdam, The Netherlands.
- West, N. E., and J. A. Young. 1999. Vegetation of intermountain valleys and lower mountain slopes. Pages 255-284 *in* M. A. Barbour and W. D. Billings, editors. *North American Terrestrial Vegetation*. Cambridge University Press, New York, NY.
- Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. *in* E. M. R. McArthur, S. D. Smith, P. T. Tueller, editor. *Proceedings – Symposium on cheatgrass invasion, shrub die-off and other aspects of shrub biology and management*. USDA General Technical Report INT-276, Ogden, Utah, USA.
- White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution* **22**:323-330.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* **48**:607-615.
- Wilcox, B. P., L. Turnbull, M. H. Young, C. J. Williams, S. Ravi, M. S. Seyfried, D. R. Bowling, R. L. Scott, M. J. Germino, T. G. Caldwell, and J. Wainwright. 2012. Invasion of shrublands by exotic grasses: ecohydrological consequences in cold versus warm deserts. *Ecohydrology* **5**:160-173.
- Wisdom, M. J., and J. C. Chambers. 2009. A landscape approach for ecologically based management of Great Basin shrublands. *Restoration Ecology* **17**:740-749.
- Wolkovich, E. M., D. T. Bolger, and K. L. Cottingham. 2009. Invasive grass litter facilitates native shrubs through abiotic effects. *Journal of Vegetation Science* **20**:1121-1132.
- Wright, R. J., and S. C. Hart. 1997. Nitrogen and phosphorus status in a ponderosa pine forest after 20 years of interval burning. *Ecoscience* **4**:526-533.
- Yoda, K., T. Kira, H. Ogawa, and K. Hozumi. 1963. Self thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology*, Osaka City University **14**:106-129.
- Young, J. A., R. R. Blank, and D. C. Clements. 1999. Nitrogen enrichment and immobilization influences on the dynamics of annual grass community. Pages 279-281 *in* *People and rangelands, building the future*. Proceedings of the VI International Rangeland Congress, Townsville, Queensland, Australia July 19-23.
- Young, J. A., and R. A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. *Journal of Range Management* **31**:283-289.

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

Path	Hypothesized mechanism
1	High soil water due to increased precipitation results in increased plant litter and soil organic matter decomposition (Dijkstra and Cheng 2007, Moyano et al. 2013) and net N mineralization (Fierer and Schimel 2002, Borken 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 germination, N uptake, and growth (Leffler and Ryel 2012).
2	Low winter temperatures are associated with higher snowfall and therefore more soil water which will have effects described in Path 1.
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 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 the microhabitat fuel gradient, with hotter fires occurring in areas of 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 should carry into the spring.
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 (Knapp and Seastedt 1986, Facelli and Pickett 1991, Sperry et al. 2006). Dense litter mats also cause seed entrapment and retention (Chambers 2000).
7	Manually removing litter from some plots at the beginning of the experiment should cause them to have reduced litter biomass throughout the experiment.
8	High annual wheat biomass and N uptake will decrease spring soil N availability and decrease the 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 should increase wheat biomass but decrease litter biomass due to disturbances caused by the furrows used to facilitate seeding.
10	Other annual plant biomass should be negatively correlated with cheatgrass density, biomass, and seed density due to competition (Chambers et al. in press).
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 density, biomass, and seed density due to high propagule pressure.
13	Cheatgrass seeding should increase cheatgrass density, biomass, and seed density due to high propagule pressure and decrease litter biomass due to disturbances caused by furrows used to facilitate seeding.

**Table 2. Results of ANOVAs examining effects of burn and seeding treatment, time, and their interaction on soil, litter and plant measurements in litter intact and litter removed plots. Values in bold are significant ( $p \leq 0.05$ ).**

	Burn/seeding			Year			Burn/seeding x Year		
	F (Num DF, Den DF)	P		F (Num DF, Den DF)	P		F (Num DF, Den DF)	P	
Litter intact plots									
Litter biomass	<b>16.74</b> (3,27)	<b>&lt;0.0001</b>		<b>67.97</b> (4,112)	<b>&lt;0.0001</b>		<b>3.85</b> (12,112)	<b>&lt;0.0001</b>	
Winter soil N availability (NH <sub>4</sub> <sup>+</sup> + NO <sub>3</sub> <sup>-</sup> )	<b>6.59</b> (3,27)	<b>0.0017</b>		<b>12.7</b> (3,82)	<b>&lt;0.0001</b>		1.28 (9,82)	0.2588	
Spring soil N availability (NH <sub>4</sub> <sup>+</sup> + NO <sub>3</sub> <sup>-</sup> )	2.19 (3,27)	0.112		<b>3.38</b> (3,83)	<b>0.0221</b>		<b>2.12</b> (9,83)	<b>0.0365</b>	
Cheatgrass density	<b>12.89</b> (3,27)	<b>&lt;0.0001</b>		<b>11.97</b> (4,112)	<b>&lt;0.0001</b>		<b>3.01</b> (12,112)	<b>0.0011</b>	
Cheatgrass biomass per plot	<b>9.02</b> (3,27)	<b>0.0003</b>		<b>23.14</b> (4,112)	<b>&lt;0.0001</b>		<b>3.14</b> (12,112)	<b>0.0007</b>	
Cheatgrass biomass per plant	<b>3.82</b> (3,27)	<b>0.021</b>		<b>4.13</b> (4,112)	<b>0.0037</b>		<b>2.55</b> (12,112)	<b>0.0051</b>	
Cheatgrass seed density per plot	<b>6.45</b> (3,27)	<b>0.0019</b>		<b>43.6</b> (4,112)	<b>&lt;0.0001</b>		<b>2.5</b> (12,112)	<b>0.0060</b>	
Cheatgrass seed density per plant	<b>4.38</b> (3,27)	<b>0.0123</b>		<b>19.33</b> (4,112)	<b>&lt;0.0001</b>		<b>2.93</b> (12,112)	<b>0.0014</b>	
Wheat biomass		N/A		<b>4.76</b> (3,29)	<b>0.0093</b>			N/A	
Other annual plant biomass	1.02 (3,27)	0.3986		<b>15.09</b> (4,99)	<b>&lt;0.0001</b>		<b>2.10</b> (12,99)	<b>0.0235</b>	
Litter removed plots									
Litter biomass	<b>39.02</b> (4,34)	<b>&lt;0.0001</b>		<b>7.60</b> (3,105)	<b>0.0001</b>		<b>4.51</b> (12,105)	<b>&lt;0.0001</b>	
Winter soil N availability (NH <sub>4</sub> <sup>+</sup> + NO <sub>3</sub> <sup>-</sup> )	<b>6.71</b> (4,34)	<b>0.0004</b>		<b>24.61</b> (3,100)	<b>&lt;0.0001</b>		0.89 (12,100)	0.5567	
Spring soil N availability (NH <sub>4</sub> <sup>+</sup> + NO <sub>3</sub> <sup>-</sup> )	<b>3.51</b> (4,34)	<b>0.0168</b>		<b>2.87</b> (3,102)	<b>0.0401</b>		<b>2.76</b> (12,102)	<b>0.0028</b>	
Cheatgrass density	<b>12.51</b> (4,34)	<b>&lt;0.0001</b>		<b>13.83</b> (3,104)	<b>&lt;0.0001</b>		1.23 (12,104)	0.2697	
Cheatgrass biomass per plot	<b>6.13</b> (4,34)	<b>0.0008</b>		<b>16.3</b> (3,105)	<b>&lt;0.0001</b>		1.65 (12,105)	0.0888	
Cheatgrass biomass per plant	<b>3.18</b> (4,34)	<b>0.0252</b>		<b>6.53</b> (3,104)	<b>0.0004</b>		1.46 (12,104)	0.1496	
Cheatgrass seed density per plot	<b>4.24</b> (4,34)	<b>0.0068</b>		<b>66.21</b> (3,105)	<b>&lt;0.0001</b>		<b>2.81</b> (12,105)	<b>0.0023</b>	
Cheatgrass seed density per plant	<b>4.25</b> (4,34)	<b>0.0067</b>		<b>32.92</b> (3,104)	<b>&lt;0.0001</b>		<b>2.23</b> (12,104)	<b>0.0154</b>	
Wheat biomass		N/A		<b>3.66</b> (3,31)	<b>0.0247</b>			N/A	
Other annual plant biomass	<b>3.40</b> (4,34)	<b>0.0192</b>		<b>15.14</b> (3,100)	<b>&lt;0.0001</b>		1.00 (12,100)	0.4529	

## Figure captions

Figure 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 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.

Figure 2. Average annual precipitation (September 1 through June 30) shown as bars, and annual minimum and maximum temperatures illustrated by lines.

Figure 3. Changes in litter biomass among study years and burn and seeding treatments in litter intact and litter removed plots. Bars indicate  $\pm 1$  standard error and lower-case letters indicate significant differences among treatments within years ( $p \leq 0.05$ ).

Figure 4. Changes in winter (Sept-March) and spring (March-June) soil N availability among years and burn and seeding treatments in litter intact and litter removed plots. Bars indicate  $\pm 1$  standard error. Lower-case 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 ( $p \leq 0.05$ ).

Figure 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  $\pm 1$  standard error. Lower-case 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 ( $p \leq 0.05$ ).

Figure 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  $\pm 1$  standard error. Lower-case 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 ( $p \leq 0.05$ ).

Figure 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  $\pm 1$  standard error. Lower-case 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 ( $p \leq 0.05$ ).

Figure 8. Path diagrams for effect 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.

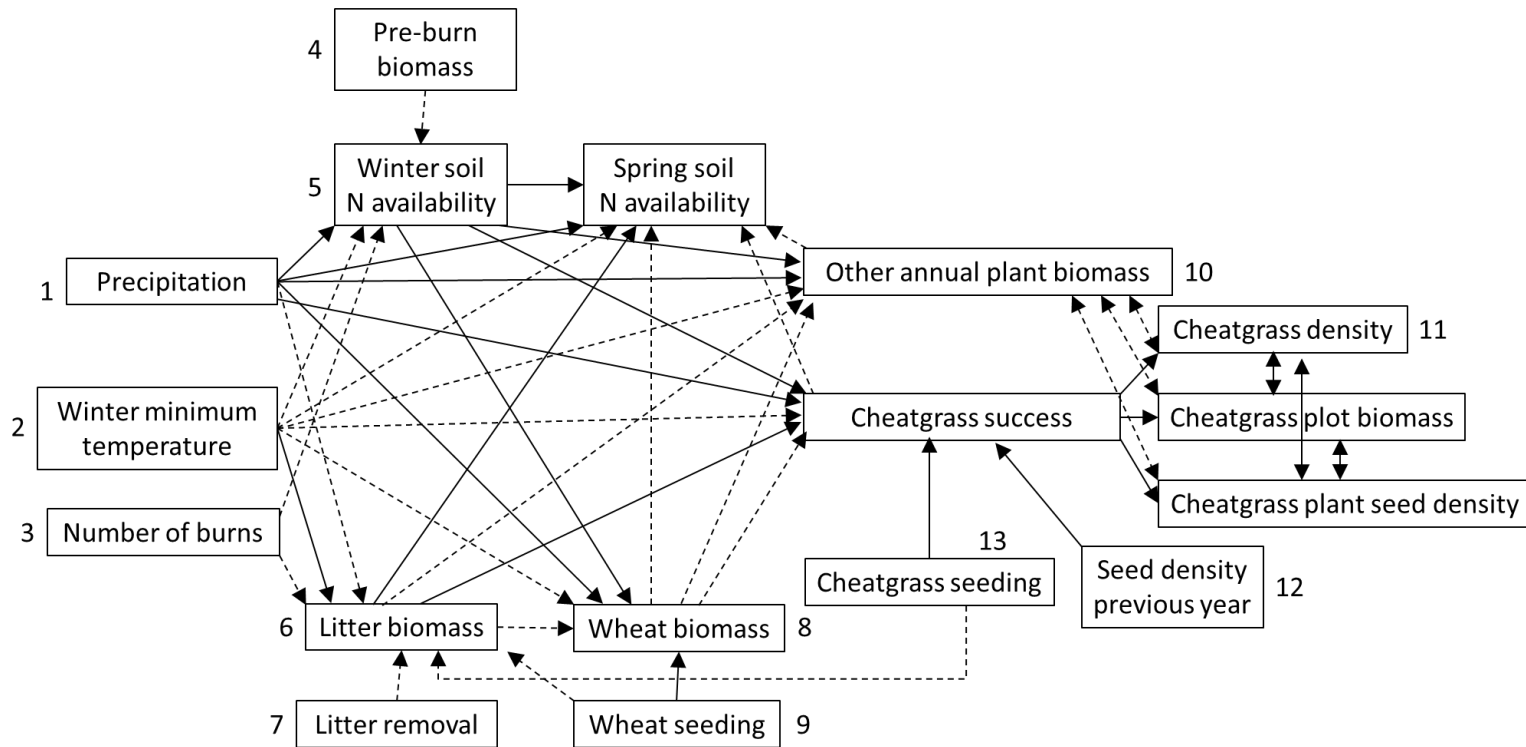


Figure 1.

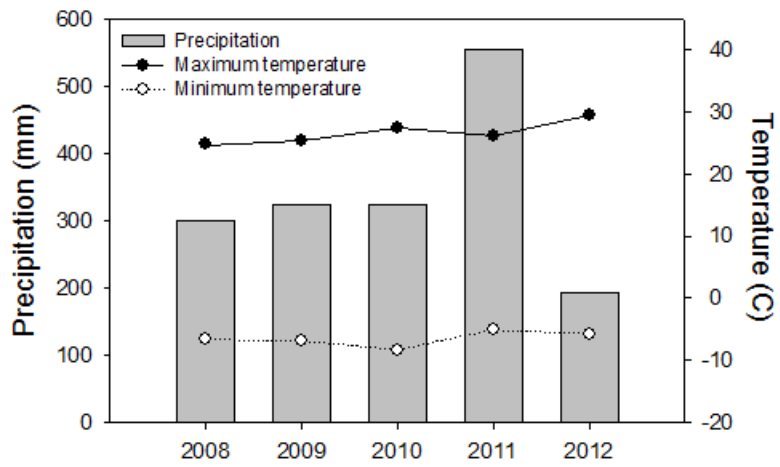


Figure 2.



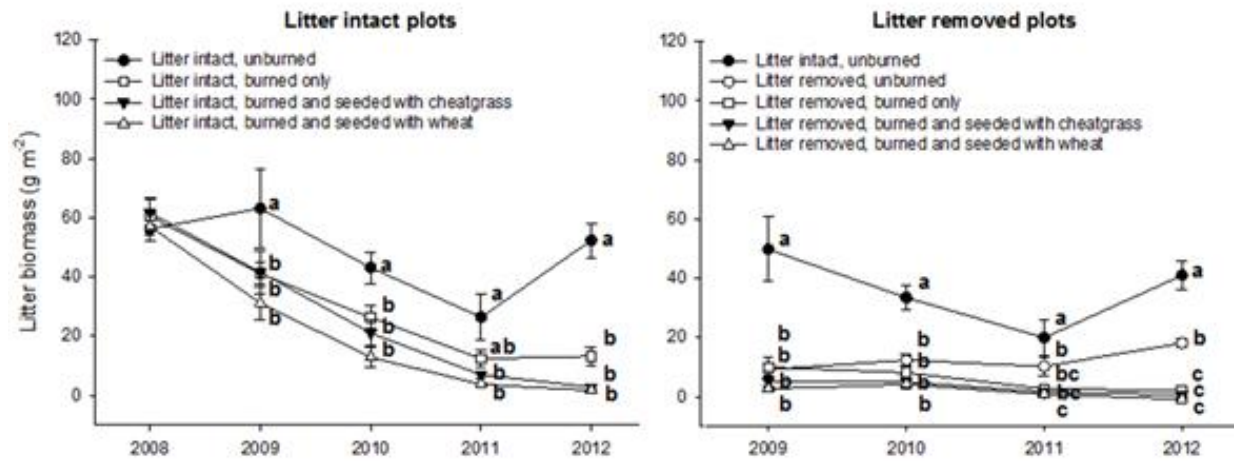


Figure 3.

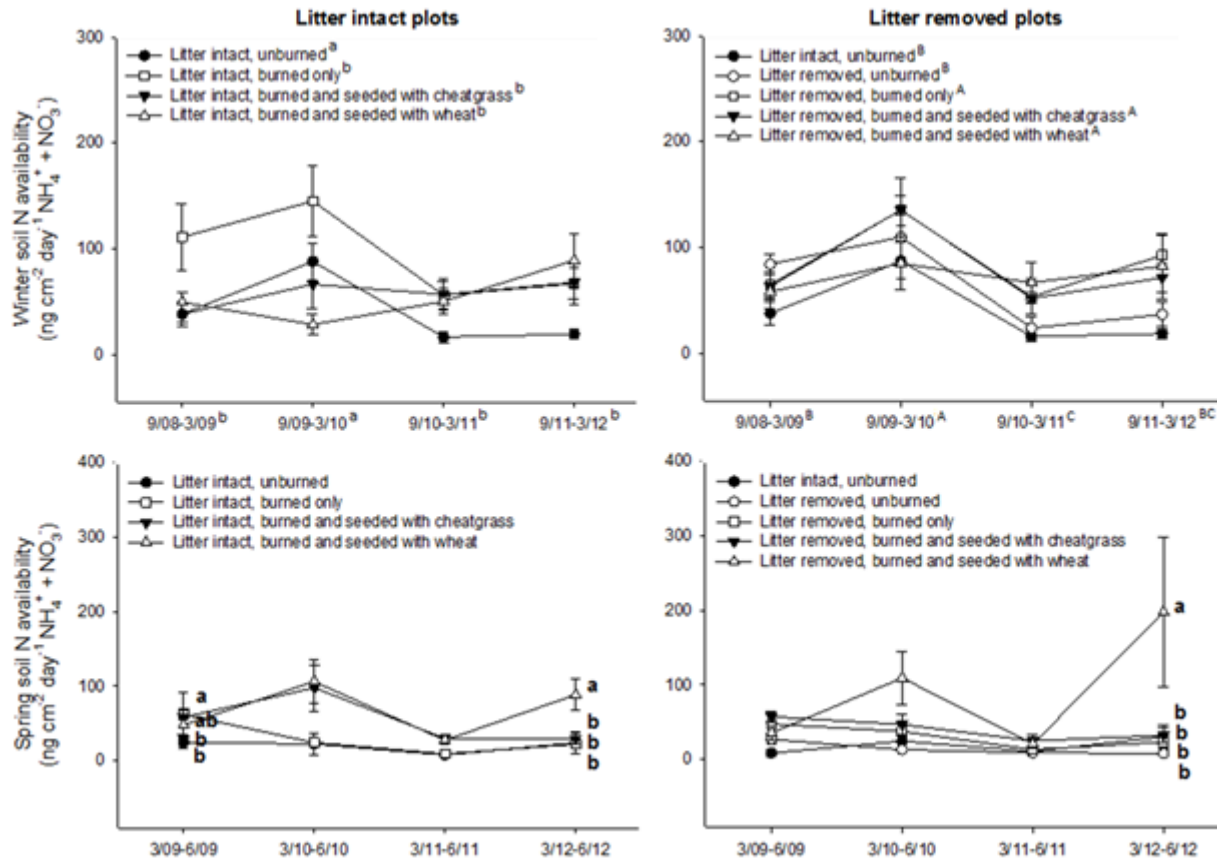


Figure 4.

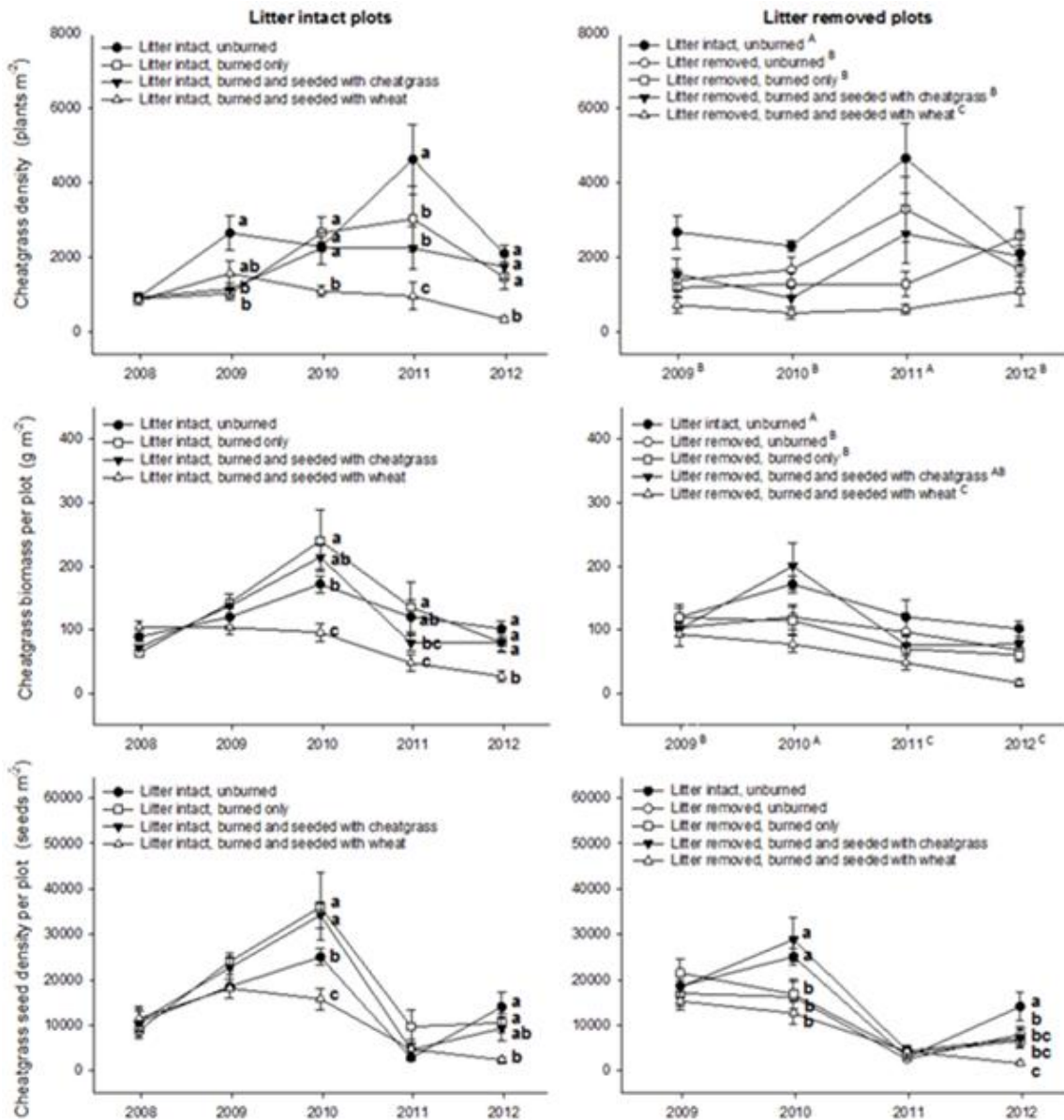


Figure 5.

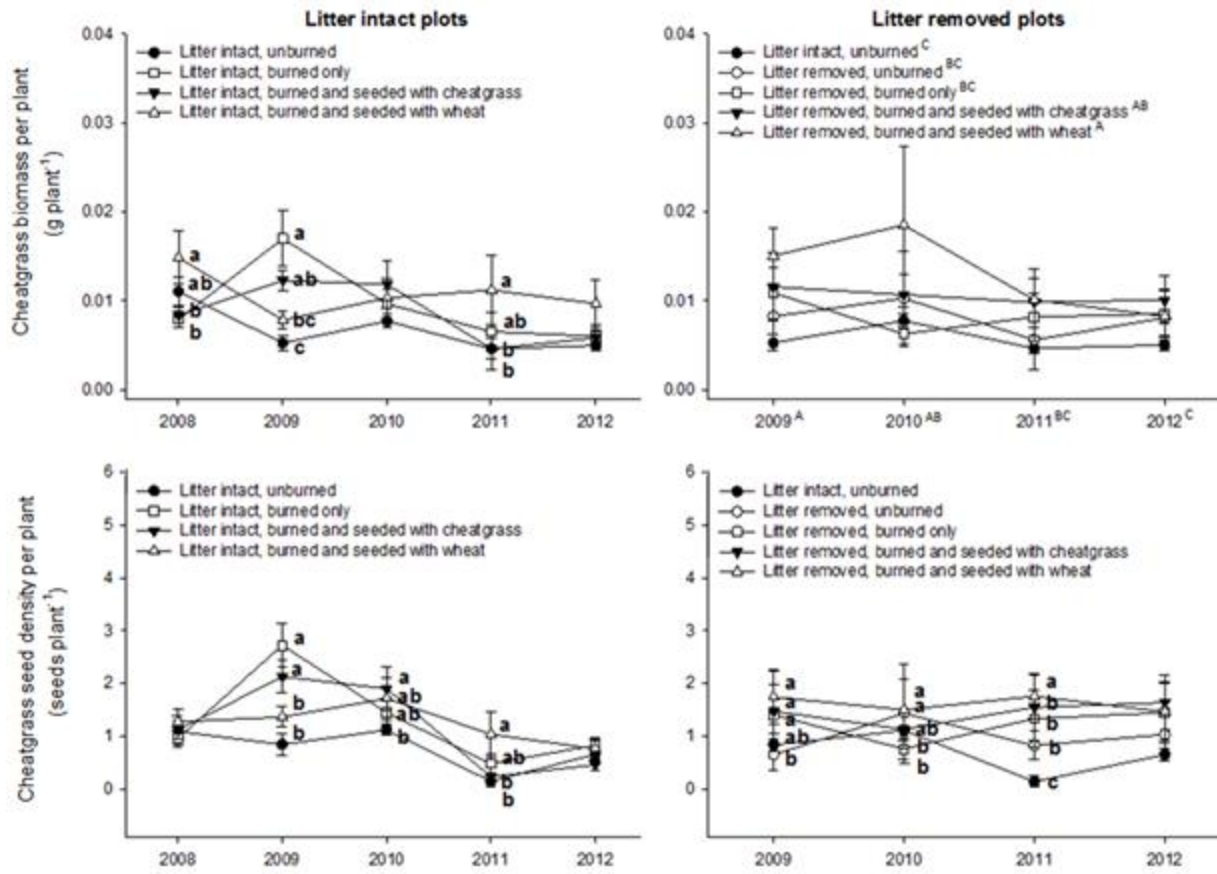


Figure 6.

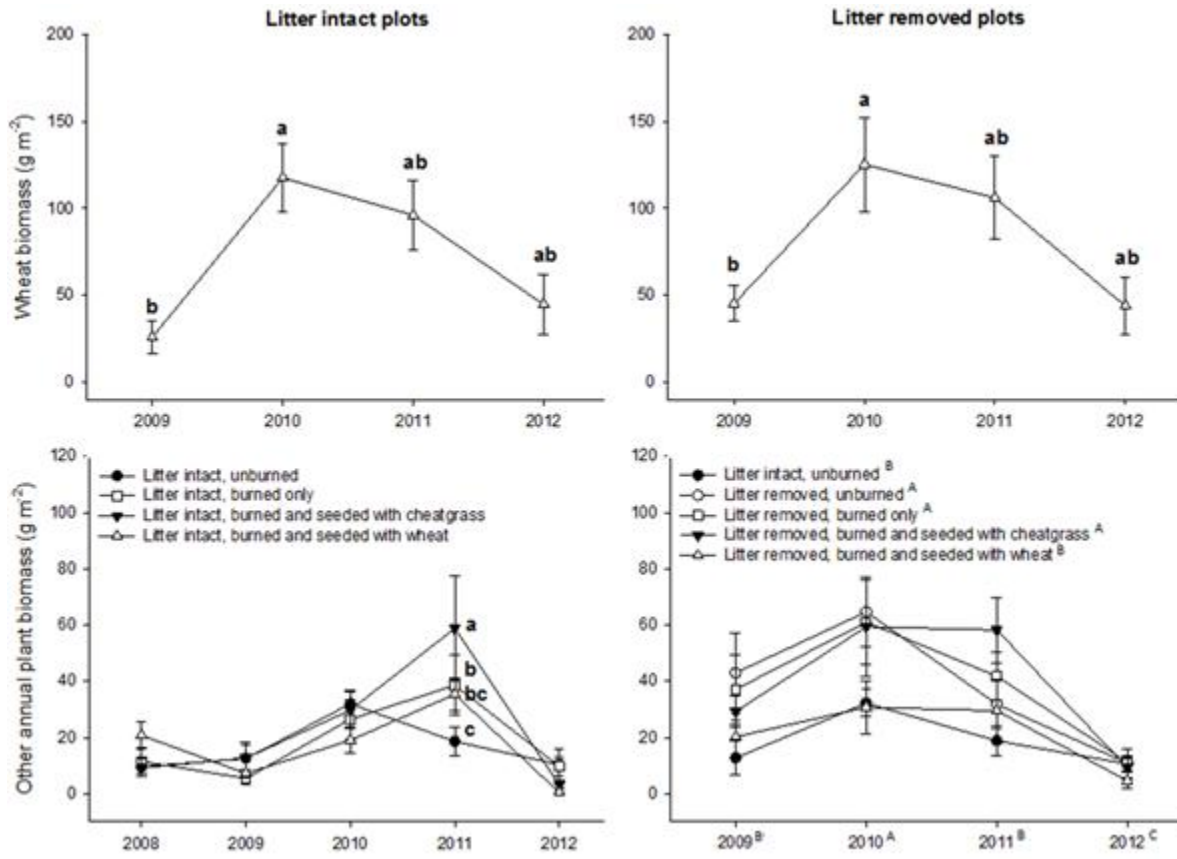


Figure 7.

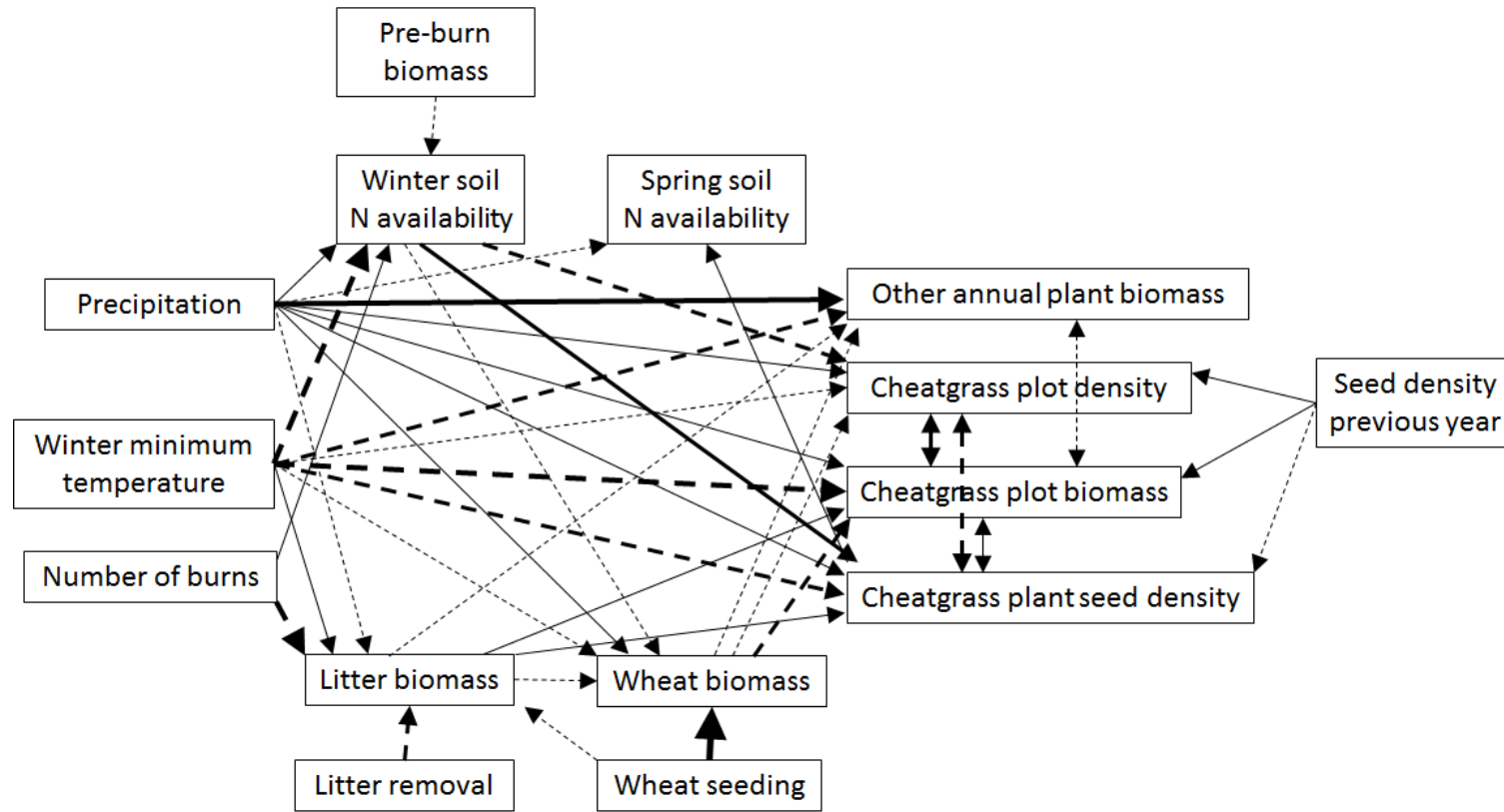


Figure 8.

## Conclusions

Understanding the role of plant-soil feedbacks in invaded ecosystems could provide insight into community successional trajectories following invasions and could improve our ability to manage these systems to restore native diversity. The overall goal of my dissertation was to examine the interactions between soil resource availability, native plant community composition and the invasibility of cheatgrass. The specific goals were to evaluate 1) the plant community characteristics and plant and soil nutrients associated with progressive cheatgrass invasion and 2) the effectiveness of repeated burning, litter manipulation, and competition as management tools to restore a more conservative nitrogen (N) cycle and reduce cheatgrass abundance.

It has been suggested that invasive species may alter soil nutrient cycling in ways that differ from native species (Schimel et al. 1991, Schimel et al. 1994, D'Antonio et al. 2009). In arid rangelands of the western U.S., considerable attention has been given to the possibility that cheatgrass may increase soil nutrient availability and provide a positive feedback to its own persistence. Previous studies examining the effects of cheatgrass invasion on soil nutrients, however, have had several limitations including poor spatial variability and replication and inconsistency in soil type. I conducted a large-scale observational study in which plant community composition and plant and soil nutrients were sampled in 25 sites that varied in their level of cheatgrass invasion but had the similar soils and environmental characteristics. I found that, although many nutrient pools (ex. Ca, Mg, total N, and soil organic matter) did not differ among levels of invasion likely due to overriding effects of soil type, soil ammonium ( $\text{NH}_4^+$ ) was negatively affected by increases in cheatgrass cover, potentially due the high C:N of its

litter. In addition, although the nutrient contents of *Poa secunda* (Sandberg bluegrass) and other herbaceous species differed among levels of invasion likely due to competitive interactions, cheatgrass nutrient content was the same across sites, which was not as predicted. These results indicate that cheatgrass may alter plant available soil nutrients to the detriment of competitors while maintaining its own nutritional content via high nutrient use efficiency and/or soil mining. Not only do these findings provide further insight into the success of cheatgrass invasions, but they could be useful when considering cheatgrass management approaches.

Restoration of sagebrush shrublands dominated by cheatgrass may be possible by re-establishing a more conservative nutrient cycling (Blumenthal et al. 2003, Norton et al. 2007, Brunson et al. 2010, Mazzola et al. 2011). 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 there is increasing recognition that fires can also 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, Rau et al. 2008). Results from my field experiment on the effects of repeated burning, litter removal, and post-fire seeding, however, indicated that repeated burning is unlikely to decrease soil N availability in cheatgrass-dominated systems due to cool fire temperatures that do not volatilize biomass N. Instead, long-term trends in nutrient cycling and plant success in my study appeared to be strongly influenced by weather, specifically precipitation and minimum winter temperature. 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.



Although repeated burning did not have the predicted outcomes for soil N, there were significant effects of the treatments on litter and vegetation. Repeated burning reduced litter biomass and C and N contents over time which had negative effects on cheatgrass biomass, density and reproduction. The one time litter removal treatment also had a negative effect on litter biomass and C and N contents, however, litter removed plots that were not burned experienced recovery of litter over time. In addition, I found that seeding with an annual cover crop such as common wheat decreased annual grass abundance, likely due to competition. Therefore, integrated restoration approaches that decrease litter biomass and seed banks and increase competitive interactions may be more effective at reducing annual grasses and establishing desirable perennial species than current approaches aimed at reducing soil nutrients. One such restoration approach that has proven successful in cheatgrass-dominated areas is assisted succession. Assisted succession is a multi-stage restoration process in which grasses are initially seeded to prevent rapid post-disturbance increases in cheatgrass seed banks and stabilize soils to limit erosion (Cox and Anderson 2004, Waldron et al. 2005, Blank and Morgan 2012) and then native perennial species can be seeded (Cox and Anderson 2004). However, given my findings on temporal variability in soil nutrients, I speculate that the success of restoration seeding strongly depends on weather and should be conducted during favorable periods of weather and repeated over time if necessary (Hardegree et al. 2003, Roundy et al. 2007).

Together, the observational and experimental components of my dissertation indicate that plant-soil feedbacks are incredibly complex and understanding these feedbacks requires both spatial and temporal variability in sampling. Because

precipitation and temperature have significant effects on soil nutrients, future studies should closely monitor weather variables and soil water availability and measurements should be repeated over time to incorporate differences within and among years. In addition, soil physical properties can have significant effects on nutrient dynamics so studies examining effects of cheatgrass on soils should focus on sites that share similar soil type.

### Literature cited

- Aguirre, L., and D. A. Johnson. 1991. Influence of temperature and cheatgrass competition on seedling development of 2 bunchgrasses. *Journal of Range Management* **44**:347-354.
- Allison, S. D., and P. M. Vitousek. 2005. Responses of extracellular enzymes to simple and complex nutrient inputs. *Soil Biology & Biochemistry* **37**:937-944.
- Angers, D. A., and J. Caron. 1998. Plant-induced changes in soil structure: Processes and feedbacks. *Biogeochemistry* **42**:55-72.
- Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. *Wildlife Society Bulletin* **34**:177-185.
- Baker, W. L. 2011. Pre-EuroAmerican and recent fire in sagebrush ecosystems. Pages 185–201 *in* S. T. K. a. J. W. Connelly, editor. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in avian biology 38. University of California Press, Berkeley, CA, USA.
- Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gomez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). *Global Change Biology* **19**:173-183.
- Baughman, O. W., and S. E. Meyer. 2013. Is *Pyrenophora semeniperda* the cause of downy brome (*Bromus tectorum*) die-offs? *Invasive Plant Science and Management* **6**:105-111.
- Belnap, J., and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: Response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications* **11**:1261-1275.
- Belnap, J., S. L. Phillips, S. K. Sherrod, and A. Moldenke. 2005. Soil biota can change after exotic plant invasion: does this affect ecosystem processes? *Ecology* **86**:3007-3017.
- Belsky, A. J., and J. L. Gelbard. 2000. Livestock grazing and weed invasions in the arid west. Oregon Natural Desert Association.
- Binkley, D., D. Richter, M. B. David, and B. Caldwell. 1992. Soil chemistry in a loblolly longleaf pine forest with interval burning. *Ecological Applications* **2**:157-164.
- Blackshaw, R. E. 1994. Rotation affects downy brome (*Bromus tectorum*) in winter wheat (*Triticum aestivum*). *Weed Technology* **8**:728-732.

- Blair, J. M. 1997. Fire, N availability, and plant response in grasslands: A test of the transient maxima hypothesis. *Ecology* **78**:2359-2368.
- Blank, R. R. 2008. Biogeochemistry of plant invasion: A case study with downy brome (*Bromus tectorum*). *Invasive Plant Science and Management* **1**:226-238.
- Blank, R. R., L. Abraham, and J. A. Young. 1994a. Soil heating, nitrogen, cheatgrass, and seedbed microsites. *Journal of Range Management* **47**:33-37.
- Blank, R. R., F. Allen, and J. A. Young. 1994b. Extractable anions in soils following wildfire in a sagebrush-grass community. *Soil Science Society of America Journal* **58**:564-570.
- Blank, R. R., F. L. Allen, and J. A. Young. 1996. Influence of simulated burning of soil-litter from low sagebrush, squirreltail, cheatgrass, and medusahead on water-soluble anions and cations. *International Journal of Wildland Fire* **6**:137-143.
- Blank, R. R., and T. Morgan. 2012. Mineral nitrogen in a crested wheatgrass stand: Implications for suppression of cheatgrass. *Rangeland Ecology & Management* **65**:101-104.
- Blank, R. R., T. Morgan, C. D. Clements, and B. E. Mackey. 2013. *Bromus tectorum* L. invasion: Changes in soil properties and rates of bioturbation. *Soil Science* **178**:281-290.
- Blank, R. R., and J. A. Young. 2009. Plant-soil relationships of *Bromus tectorum* L.: Interactions among labile carbon additions, soil invasion status, and fertilizer. *Applied and Environmental Soil Science* **2009**:7 pages.
- Blank, R. R., and D. C. Zamudio. 1998. The influence of wildfire on aqueous-extractable soil solutes in forested and wet meadow ecosystems along the eastern front of the Sierra-Nevada range, California. *International Journal of Wildland Fire* **8**:79-85.
- Blumenthal, D. M., N. R. Jordan, and M. P. Russelle. 2003. Soil carbon addition controls weeds and facilitates prairie restoration. *Ecological Applications* **13**:605-615.
- Boerner, R. E. J. 1982. Fire and nutrient cycling in temperate ecosystems. *Bioscience* **32**:187-192.
- Booth, M. S., M. M. Caldwell, and J. M. Stark. 2003a. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. *Journal of Ecology* **91**:36-48.
- Booth, M. S., J. M. Stark, and M. M. Caldwell. 2003b. Inorganic N turnover and availability in annual- and perennial-dominated soils in a northern Utah shrub-steppe ecosystem. *Biogeochemistry* **66**:311-330.
- Borken, W., and E. Matzner. 2009. Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Global Change Biology* **15**:808-824.
- Bradley, B. A., R. A. Houghton, J. F. Mustard, and S. P. Hamburg. 2006. Invasive grass reduces aboveground carbon stocks in shrublands of the Western US. *Global Change Biology* **12**:1815-1822.
- Bradley, B. A., and J. F. Mustard. 2005. Identifying land cover variability distinct from land cover change: Cheatgrass in the Great Basin. *Remote Sensing of Environment* **94**:204-213.
- Brooks, M. L. 2002. Peak fire temperatures and effects on annual plants in the Mojave Desert. *Ecological Applications* **12**:1088-1102.

- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *Bioscience* **54**:677-688.
- Brunson, J. L., D. A. Pyke, and S. S. Perakis. 2010. Yield responses of ruderal plants to sucrose in invasive-dominated sagebrush steppe of the northern Great Basin. *Restoration Ecology* **18**:304-312.
- Buisson, E., K. D. Holl, S. Anderson, E. Corcket, G. F. Hayes, F. Torre, A. Peteers, and T. Dutoit. 2006. Effect of seed source, topsoil removal, and plant neighbor removal on restoring California coastal prairies. *Restoration Ecology* **14**:569-577.
- Burke, I. C. 1989. Control of nitrogen mineralization in a sagebrush steppe landscape. *Ecology* **70**:1115-1126.
- Chambers, J. C. 2000. Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: Implications for restoration. *Ecological Applications* **10**:1400-1413.
- Chambers, J. C. 2001. *Pinus monophylla* establishment in an expanding *Pinus-Juniperus* woodland: Environmental conditions, facilitation and interacting factors. *Journal of Vegetation Science* **12**:27-40.
- Chambers, J. C., and J. A. Macmahon. 1994. A day in the life of a seed- movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics* **25**:263-292.
- Chambers, J. C., R. F. Miller, D. I. Board, D. A. Pyke, B. A. Roundy, J. B. Grace, E. W. Schupp, and R. J. Tausch. in press. Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. *Rangeland Ecology & Management*.
- Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invisable by *Bromus tectorum*? *Ecological Monographs* **77**:117-145.
- Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. *Nature* **405**:234-242.
- Charley, J. L., and N. E. West. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *Journal of Ecology* **63**:945-963.
- Cheng, X. L., S. Q. An, S. R. Liu, and G. Q. Li. 2004. Micro-scale spatial heterogeneity and the loss of carbon, nitrogen and phosphorus in degraded grassland in Ordos Plateau, northwestern China. *Plant and Soil* **259**:29-37.
- Christian, J. M., and S. D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the northern Great Plains. *Ecology* **80**:2397-2407.
- Cox, R. D., and V. J. Anderson. 2004. Increasing native diversity of cheatgrass-dominated rangeland through assisted succession. *Journal of Range Management* **57**:203-210.
- Cui, M. Y., and M. M. Caldwell. 1997. A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. *Plant and Soil* **191**:291-299.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**:63-87.

- Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annual Review of Ecology Evolution and Systematics* **34**:183-211.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**:528-534.
- Davison, J., and E. Smith. 2005. Living with fire, crested wheatgrass: hero or villain in reclaiming disturbed rangelands. Page 4. University of Nevada Cooperative Extension Service, Reno, NV, USA.
- Deng, J. M., T. Li, G. X. Wang, J. Liu, Z. L. Yu, C. M. Zhao, M. F. Ji, Q. Zhang, and J. Q. Liu. 2008. Trade-offs between the metabolic rate and population density of plants. *Plos One* **3**:7.
- Denny, D. W. 2002. Soil survey of Humboldt County, Nevada, East Part, part 1. US Department of Agriculture, Natural Resources Conservation Service, Reno, NV, USA.
- Diamond, J. M. 2009. Effects of targeted grazing and prescribed burning on fire behavior and community dynamics of a cheatgrass (*Bromus tectorum*)- dominated landscape. Utah State University, Logan, Utah.
- Dijkstra, F. A., and W. Cheng. 2007. Moisture modulates rhizosphere effects on C decomposition in two different soil types. *Soil Biology & Biochemistry* **39**:2264-2274.
- Dobrowolski, J. P., M. M. Caldwell, and J. H. Richards. 1990. Basin hydrology and plant root systems. *Ecological Studies* **80**:243-292.
- Dodds, W. K., J. M. Blair, G. M. Henebry, J. K. Koelliker, R. Ramundo, and C. M. Tate. 1996. Nitrogen transport from tallgrass prairie watersheds. *Journal of Environmental Quality* **25**:973-981.
- Ducas, L. P., S. B. Jones, A. J. Leffler, and R. J. Ryel. 2011. Associations of near-surface soil moisture and annual plant community dynamics. *Natural Resources and Environmental Issues* **17**:12.
- D'Antonio, C. M., J. C. Chambers, R. Loh, and J. T. Tunison. 2009. Applying ecological concepts to the management of widespread grass invasions. Pages 123-149 in R. L. Inderjit, editor. *Management of Invasive Weeds*. Springer, Netherlands.
- Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* **6**:503-523.
- Ehrenfeld, J. G. 2010. Ecosystem Consequences of Biological Invasions. *Annual Review of Ecology, Evolution, and Systematics*, Vol 41 **41**:59-80.
- Ehrenfeld, J. G., P. Kourtev, and W. Z. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* **11**:1287-1300.
- Ehrenfeld, J. G., B. Ravit, and K. Elgersma. 2005. Feedback in the plant-soil system. *Annual Review of Environment and Resources* **30**:75-115.
- Elzinga, C. L., D. W. Salzer, and J. W. Willoughby. 1998. Measuring and monitoring plant populations. U.S. Department of the Interior, Bureau of Land Management, Denver, CO.
- Evans, R. A., and J. A. Young. 1970. Plant Litter and Establishment of Alien Annual Weed Species in Rangeland Communities. *Weed Science* **18**:697-703.

- Evans, R. A., and J. A. Young. 1984. Microsite requirements for downy brome (*Bromus tectorum*) infestation and control on sagebrush rangelands. *Weed Science* **32**:13-17.
- Evans, R. D., and J. R. Ehleringer. 1994. Water and nitrogen dynamics in an arid woodland. *Oecologia* **99**:233-242.
- Evans, R. D., R. Rimer, L. Sperry, and J. Belnap. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications* **11**:1301-1310.
- Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter- its dynamics and effects on plant community structure. *Botanical Review* **57**:1-32.
- Fierer, N., J. M. Craine, K. McLaughlan, and J. P. Schimel. 2005. Litter quality and the temperature sensitivity of decomposition. *Ecology* **86**:320-326.
- Fierer, N., and J. P. Schimel. 2002. Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. *Soil Biology & Biochemistry* **34**:777-787.
- Frost, R. A., and K. L. Launchbaugh. 2003. Prescription grazing for rangeland weed management: a new look at an old tool. *Rangelands* **25**:43-47.
- Funk, J. L., and P. M. Vitousek. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* **446**:1079-1081.
- Fynn, R. W. S., R. J. Haynes, and T. G. O'Connor. 2003. Burning causes long-term changes in soil organic matter content of a South African grassland. *Soil Biology & Biochemistry* **35**:677-687.
- Goergen, E. M., E. A. Leger, and E. K. Espeland. 2011. Native Perennial Grasses Show Evolutionary Response to *Bromus tectorum* (Cheatgrass) Invasion. *Plos One* **6**.
- Grace, J. B. 2006. Structural equation modeling and natural systems. Cambridge University Press, Cambridge.
- Grace, J. B., A. Youngblood, and S. M. Scheiner. 2009. Structural equation modeling and ecological experiments. Pages 19–45 in S. C. S. Miao, and M. Nungesser, editor. *Real World Ecology: Large-Scale and Long-Term Case Studies and Methods*. Springer Verlag, New York, NY.
- Grier, C. C., and D. W. Cole. 1971. Influence of slash burning on ion transport in soil. *Northwest Science* **45**:100-106.
- Grogan, P., T. D. Bruns, and F. S. Chapin. 2000. Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. *Oecologia* **122**:537-544.
- Hardegree, S. P., G. N. Flerchinger, and S. S. Van Vactor. 2003. Hydrothermal germination response and the development of probabilistic germination profiles. *Ecological Modelling* **167**:305-322.
- Heidinga, L., and S. D. Wilson. 2002. The impact of an invading alien grass (*Agropyron cristatum*) on species turnover in native prairie. *Diversity and Distributions* **8**:249-258.
- Herron, G. J., R. L. Sheley, B. D. Maxwell, and J. S. Jacobsen. 2001. Influence of nutrient availability on the interaction between spotted knapweed and bluebunch wheatgrass. *Restoration Ecology* **9**:326-331.
- Hillel, D. 1998. *Environmental Soil Physics*. Academic, San Diego, CA.
- Hobbie, S. E. 1992. Effects of plant-species on nutrient cycling. *Trends in Ecology & Evolution* **7**:336-339.

- Hooker, T., J. Stark, U. Norton, A. J. Leffler, M. Peek, and R. Ryel. 2008. Distribution of ecosystem C and N within contrasting vegetation types in a semiarid rangeland in the Great Basin, USA. *Biogeochemistry* **90**:291-308.
- Humphrey, L. D., and E. W. Schupp. 2001. Seed banks of *Bromus tectorum*-dominated communities in the Great Basin. *Western North American Naturalist* **61**:85-92.
- Jackson, R. B., J. L. Banner, E. G. Jobbagy, W. T. Pockman, and D. H. Wall. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* **418**:623-626.
- James, J. J., R. E. Drenovsky, T. A. Monaco, and M. J. Rinella. 2011. Managing soil nitrogen to restore annual grass-infested plant communities: effective strategy or incomplete framework? *Ecological Applications* **21**:490-502.
- Jobbagy, E. G., and R. B. Jackson. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* **10**:423-436.
- Johnson, B. G., D. W. Johnson, J. C. Chambers, and R. R. Blank. 2011. Fire effects on the mobilization and uptake of nitrogen by cheatgrass (*Bromus tectorum* L.). *Plant and Soil* **341**:437-445.
- Johnson, B. G., D. W. Johnson, W. W. Miller, and D. I. Board. 2012. The effects of ash influx on burned and unburned soil water-extractable nutrients using a mechanical vacuum extractor. *Soil Science* **177**:338-344.
- Johnson, D. W., J. F. Murphy, R. B. Susfalk, T. G. Caldwell, W. W. Miller, R. F. Walker, and R. F. Powers. 2005. The effects of wildfire, salvage logging, and post-fire N-fixation on the nutrient budgets of a Sierran forest. *Forest Ecology and Management* **220**:155-165.
- Johnson, L. C., and J. R. Matchett. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. *Ecology* **82**:3377-3389.
- Jones, R. O., J. C. Chambers, D. I. Board, D. W. Johnson, and R. R. Blank. in prep. Understanding the role of resource limitation in restoration of sagebrush ecosystems dominated by cheatgrass - a mechanistic approach.
- Jones, R. O., J. C. Chambers, D. W. Johnson, R. R. Blank, and D. I. Board. submitted. Effect of repeated burning on plant and soil carbon and nitrogen in cheatgrass (*Bromus tectorum*) dominated ecosystems. *Plant and Soil*.
- Keane, R. E., K. C. Ryan, T. T. Veblen, C. D. Allen, J. Logan, and B. Hawkes. 2002. Cascading effects of fire exclusion in Rocky Mountain ecosystems: a literature review. Fort Collins, Colorado.
- Keeley, J. E., D. Lubin, and C. J. Fotheringham. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications* **13**:1355-1374.
- Keeney, D. R., and D. W. Nelson. 1987. Nitrogen—inorganic forms. Pages 643-698 in A. L. Page, editor. *Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties*. American Society of Agronomy, Madison, Wisconsin USA.
- Klemmedson, J. O., and J. G. Smith. 1964. Cheatgrass (*Bromus Tectorum* L.). *Botanical Review* **30**:226-262.
- Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *Bioscience* **36**:662-668.

- Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert - History, persistence, and influences to human activities. *Global Environmental Change-Human and Policy Dimensions* **6**:37-52.
- Knutson, K. C., D. A. Pyke, T. A. Wirth, R. S. Arkle, D. S. Pilliod, M. L. Brooks, J. C. Chambers, and J. B. Grace. submitted. Long-term effects of seeding after wildfire on vegetation composition in Great Basin shrub steppe. *Journal of Applied Ecology*.
- Korfmacher, J. L., J. C. Chambers, R. J. Tausch, B. A. Roundy, S. E. Meyer, and S. Kitchen. 2003. Technical Note: A technique for conducting small-plot burn treatments. *Journal of Range Management* **56**:251-254.
- Koscelny, J. A., T. F. Peeper, J. B. Solie, and S. G. Solomon. 1990. Effect of wheat (*Triticum aestivum*) row spacing, seeding rate, and cultivar on yield loss from cheat (*Bromus tectorum*). *Weed Technology* **4**:487-492.
- Leffler, A. J., M. S. Peek, R. J. Ryel, C. Y. Ivans, and M. M. Caldwell. 2005. Hydraulic redistribution through the root systems of senesced plants. *Ecology* **86**:633-642.
- Leffler, A. J., and R. J. Ryel. 2012. Resource pool dynamics: conditions that regulate species interactions and dominance. Pages 57-78 in T. A. Monaco and R. L. Sheley, editors. *Invasive plant ecology and management. Linking processes to practice*. CAB International, Cambridge, MA, USA.
- Liao, C. Z., R. H. Peng, Y. Q. Luo, X. H. Zhou, X. W. Wu, C. M. Fang, J. K. Chen, and B. Li. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytologist* **177**:706-714.
- Link, S. O., W. G. Glendon, and J. L. Downs. 1990. The Effect of Water Stress on Phenological and Ecophysiological Characteristics of Cheatgrass and Sandberg's Bluegrass. *Journal of Range Management* **43**:506-513.
- Link, S. O., C. W. Keeler, R. W. Hill, and E. Hagen. 2006. *Bromus tectorum* cover mapping and fire risk. *International Journal of Wildland Fire* **15**:113-119.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522-1536.
- MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* **86**:42-55.
- Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America- An ecological chronicle. *Agro-Ecosystems* **7**:145-165.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* **10**:689-710.
- MacKown, C. T., T. A. Jones, D. A. Johnson, T. A. Monaco, and M. G. Redinbaugh. 2009. Nitrogen uptake by perennial and invasive annual grass seedlings: nitrogen form effects. *Soil Science Society of America Journal* **73**:1864-1870.
- Malmer, A. 1996. Hydrological effects and nutrient losses of forest plantation establishment on tropical rainforest land in Sabah, Malaysia. *Journal of Hydrology* **174**:129-148.
- Mazzola, M. B. 2008. Spatio-temporal heterogeneity and habitat invasibility in sagebrush steppe ecosystems. PhD dissertation. University of Nevada, Reno, Reno, NV, USA.



- Mazzola, M. B., J. C. Chambers, R. R. Blank, D. A. Pyke, E. W. Schupp, K. G. Allcock, P. S. Doescher, and R. S. Nowak. 2011. Effects of resource availability and propagule supply on native species recruitment in sagebrush ecosystems invaded by *Bromus tectorum*. *Biological Invasions* **13**:513-526.
- McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.
- McGarigal, K., S. Cushman, and S. Stafford. 2000. Multivariate statistics for wildlife and ecology research. Springer-Verlag, New York, New York, USA.
- Melgoza, G., and R. S. Nowak. 1991. Competition between cheatgrass and 2 native species after fire- Implications from observations and measurements of root distribution. *Journal of Range Management* **44**:27-33.
- Miller, R., S. Knick, D. Pyke, C. Meinke, S. Hanser, M. Wisdom, and A. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145–185 in S. Knick and J. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. *Studies in Avian Biology*, Vol. 38. University of California Press, Berkeley, CA.
- Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003. Contrasting responses of intermountain west grasses to soil nitrogen. *Journal of Range Management* **56**:282-290.
- Monaco, T. A., S. B. Monsen, B. N. Smith, and L. D. Hansen. 2005. Temperature-dependent physiology of *Poa secunda*, a cool season grass native to the Great Basin, United States. *Russian Journal of Plant Physiology* **52**:653-658.
- Monleon, V. J., K. Cromack, and J. D. Landsberg. 1997. Short- and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **27**:369-378.
- Morghan, K. J. R., and T. R. Seastedt. 1999. Effects of soil nitrogen reduction on nonnative plants in restored grasslands. *Restoration Ecology* **7**:51-55.
- Moyano, F. E., S. Manzoni, and C. Chenu. 2013. Responses of soil heterotrophic respiration to moisture availability: An exploration of processes and models. *Soil Biology & Biochemistry* **59**:72-85.
- Murphy, J. D., D. W. Johnson, W. W. Miller, R. F. Walker, and R. R. Blank. 2006. Prescribed fire effects on forest floor and soil nutrients in a Sierra Nevada forest. *Soil Science* **171**:181-199.
- Neary, D. G., C. C. Klopatek, L. F. DeBano, and P. F. Ffolliott. 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management* **122**:51-71.
- Newingham, B. A., P. Vidiella, and J. Belnap. 2007. Do soil characteristics or microhabitat determine field emergence and success of *Bromus tectorum*? *Journal of Arid Environments* **70**:389-402.
- Norton, J. B., T. A. Monaco, J. M. Norton, D. A. Johnson, and T. A. Jones. 2004. Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. *Journal of Arid Environments* **57**:445-466.
- Norton, J. B., T. A. Monaco, and U. Norton. 2007. Mediterranean annual grasses in western North America: kids in a candy store. *Plant and Soil* **298**:1-5.

- Norton, U., A. R. Mosier, J. A. Morgan, J. D. Derner, L. J. Ingram, and P. D. Stahl. 2008. Moisture pulses, trace gas emissions and soil C and N in cheatgrass and native grass-dominated sagebrush-steppe in Wyoming, USA. *Soil Biology & Biochemistry* **40**:1421-1431.
- Ogle, S. M., D. Ojima, and W. A. Reiners. 2004. Modeling the impact of exotic annual brome grasses on soil organic carbon storage in a northern mixed-grass prairie. *Biological Invasions* **6**:365-377.
- Ogle, S. M., W. A. Reiners, and K. G. Gerow. 2003. Impacts of exotic annual brome grasses (*Bromus* spp.) on ecosystem properties of northern mixed grass prairie. *American Midland Naturalist* **149**:46-58.
- Ojima, D. S., D. S. Schimel, W. J. Parton, and C. E. Owensby. 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry* **24**:67-84.
- Patten, D. T., and G. H. Cave. 1984. Fire temperatures and physical characteristics of a controlled burn in the upper Sonoran desert. *Journal of Range Management* **37**:277-280.
- Pellant, M., and C. Hall. 1994. Distribution of two exotic grasses on intermountain rangelands: status in 1992. Pages 109-112 in G. t. r. INT, editor.
- Perkins, L. B., D. W. Johnson, and R. S. Nowak. 2011. Plant-induced changes in soil nutrient dynamics by native and invasive grass species. *Plant and Soil* **345**:365-374.
- Perry, L. G., D. M. Blumenthal, T. A. Monaco, M. W. Paschke, and E. F. Redente. 2010. Immobilizing nitrogen to control plant invasion. *Oecologia* **163**:13-24.
- Peters, J. 2000. Tetrazolium testing handbook. Contribution no. 29 to The handbook on seed testing. Association of Official Seed Analysts, Lincoln, NE, USA.
- Phillips, A. J. 2012. Phenotypic plasticity within the native perennial grass, *Poa secunda* (Sandberg bluegrass), an important component of the Western United States sagebrush grassland vegetation. University of Nevada, Reno, Reno, NV.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* **52**:273-288.
- Pyšek, P., and D. M. Richardson. 2007. Traits associated with invasiveness in alien plants: where do we stand? Pages 97-125 in W. Nentwig, editor. *Biological invasions*. Springer-Verlag, Berlin.
- Raich, J. W., and A. Tufekcioglu. 2000. Vegetation and soil respiration: Correlations and controls. *Biogeochemistry* **48**:71-90.
- Raison, R. J., P. K. Khanna, and P. V. Woods. 1985. Mechanisms of element transfer to the atmosphere during vegetation fires. *Canadian Journal of Forest Research- Revue Canadienne De Recherche Forestiere* **15**:132-140.
- Rau, B. M., R. R. Blank, J. C. Chambers, and D. W. Johnson. 2007. Prescribed fire in a Great Basin sagebrush ecosystem: Dynamics of soil extractable nitrogen and phosphorus. *Journal of Arid Environments* **71**:362-375.
- Rau, B. M., J. C. Chambers, R. R. Blank, and D. W. Johnson. 2008. Prescribed fire, soil, and plants: Burn effects and interactions in the central great basin. *Rangeland Ecology & Management* **61**:169-181.

- Rau, B. M., D. W. Johnson, R. R. Blank, A. Lucchesi, T. G. Caldwell, and E. W. Schupp. 2011. Transition From Sagebrush Steppe to Annual Grass (*Bromus tectorum*): Influence on Belowground Carbon and Nitrogen. *Rangeland Ecology & Management* **64**:139-147.
- Reilly, M. J., M. C. Wimberly, and C. L. Newell. 2006. Wildfire effects on beta-diversity and species turnover in a forested landscape. *Journal of Vegetation Science* **17**:447-454.
- Rimer, R. L., and R. D. Evans. 2006. Invasion of downy brome (*Bromus tectorum* L.) causes rapid changes in the nitrogen cycle. *American Midland Naturalist* **156**:252-258.
- Roundy, B. A., S. P. Hardegree, J. C. Chambers, and A. Whittaker. 2007. Prediction of cheatgrass field germination potential using wet thermal accumulation. *Rangeland Ecology & Management* **60**:613-623.
- Rustad, L. E., J. L. Campbell, G. M. Marion, R. J. Norby, M. J. Mitchell, A. E. Hartley, J. H. C. Cornelissen, J. Gurevitch, and N. Gcte. 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.
- Ryel, R. J., A. J. Leffler, C. Ivans, M. S. Peek, and M. M. Caldwell. 2010. Functional differences in water-use patterns of contrasting life forms in Great Basin steppelands. *Vadose Zone Journal* **9**:548-560.
- Sankey, J. B., M. J. Germino, and N. F. Glenn. 2009. Relationships of post-fire aeolian transport to soil and atmospheric conditions. *Aeolian Research* **1**:75-85.
- Schaeffer, S. M., S. E. Ziegler, J. Belnap, and R. D. Evans. 2012. Effects of *Bromus tectorum* invasion on microbial carbon and nitrogen cycling in two adjacent undisturbed arid grassland communities. *Biogeochemistry* **111**:427-441.
- Schimel, D. S., B. H. Braswell, E. A. Holland, R. McKeown, D. S. Ojima, T. H. Painter, W. J. Parton, and A. R. Townsend. 1994. Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. *Global Biogeochemical Cycles* **8**:279-293.
- Schimel, D. S., T. G. F. Kittel, A. K. Knapp, T. R. Seastedt, W. J. Parton, and V. B. Brown. 1991. Physiological interactions along resource gradients in a tallgrass prairie. *Ecology* **72**:672-684.
- Schlesinger, W. H., and A. M. Pilmanis. 1998. Plant-soil interactions in deserts. *Biogeochemistry* **42**:169-187.
- Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. E. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* **77**:364-374.
- Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences of the United States of America* **100**:13384-13389.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry- the principles and practice of statistics in biological research*. W. H. Freeman and Co.
- Sperry, L. J., J. Belnap, and R. D. Evans. 2006. *Bromus tectorum* invasion alters nitrogen dynamics in an undisturbed arid grassland ecosystem. *Ecology* **87**:603-615.

- Stewart, G., and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.) - an ecologic intruder in southern Idaho. *Ecology* **30**:58-74.
- Stubbs, M. M., and D. A. Pyke. 2005. Available nitrogen: A time-based study of manipulated resource islands. *Plant and Soil* **270**:123-133.
- Suding, K. N., K. D. LeJeune, and T. R. Seastedt. 2004. Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorus availability. *Oecologia* **141**:526-535.
- Suring, L. H., M. J. Wisdom, R. J. Tausch, R. F. Miller, M. M. Rowland, L. Schueck, and C. W. Meinke. 2005. Modeling threats to sagebrush and other shrubland communities. Pages 114-149 *Habitat threats in the sagebrush ecosystems: methods of regional assessment and applications in the Great Basin*. Alliance Communications Group, Lawrence, Kansas, USA.
- Tausch, R. J., P. E. Wigand, and J. W. Burkhardt. 1993. Viewpoint: Plant Community Thresholds, Multiple Steady States, and Multiple Successional Pathways: Legacy of the Quaternary? *Journal of Range Management* **46**:439-447.
- Vinton, M. A., and I. C. Burke. 1995. Interactions between individual plant-species and soil nutrient status in shortgrass steppe. *Ecology* **76**:1116-1133.
- Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and G. D. Tilman. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications* **7**:737-750.
- Vitousek, P. M., C. M. Dantonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* **84**:468-478.
- Waldron, B. L., T. A. Monaco, K. B. Jensen, R. D. Harrison, A. J. Palazzo, and J. D. Kulbeth. 2005. Coexistence of native and introduced perennial grasses following simultaneous seeding. *Agronomy Journal* **97**:990-996.
- West, N. E. 1983. Great Basin-Colorado Plateau sagebrush semi-desert. Pages 331-349 *in* N. E. West, editor. *Temperate deserts and semi-deserts*. Elsevier Publishing Company, Amsterdam, The Netherlands.
- West, N. E., and J. A. Young. 1999. Vegetation of Intermountain valleys and lower mountain slopes. Pages 255-284 *in* M. A. Barbour and W. D. Billings, editors. *North American Terrestrial Vegetation*. Cambridge University Press, New York, NY.
- Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. *in* E. M. R. McArthur, S. D. Smith, P. T. Tueller, editor. *Proceedings – Symposium on cheatgrass invasion, shrub die-off and other aspects of shrub biology and management*. USDA General Technical Report INT-276, Ogden, Utah, USA.
- White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution* **22**:323-330.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* **48**:607-615.
- Wilcox, B. P., L. Turnbull, M. H. Young, C. J. Williams, S. Ravi, M. S. Seyfried, D. R. Bowling, R. L. Scott, M. J. Germino, T. G. Caldwell, and J. Wainwright. 2012.

- Invasion of shrublands by exotic grasses: ecohydrological consequences in cold versus warm deserts. *Ecohydrology* **5**:160-173.
- Wisdom, M. J., and J. C. Chambers. 2009. A landscape approach for ecologically based management of Great Basin shrublands. *Restoration Ecology* **17**:740-749.
- Wolkovich, E. M., D. T. Bolger, and K. L. Cottingham. 2009. Invasive grass litter facilitates native shrubs through abiotic effects. *Journal of Vegetation Science* **20**:1121-1132.
- Wright, R. J., and S. C. Hart. 1997. Nitrogen and phosphorus status in a ponderosa pine forest after 20 years of interval burning. *Ecoscience* **4**:526-533.
- Yoda, K., T. Kira, H. Ogawa, and K. Hozumi. 1963. Self thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University* **14**:106-129.
- Young, J. A., R. R. Blank, and D. C. Clements. 1999. Nitrogen enrichment and immobilization influences on the dynamics of annual grass community. Pages 279-281 *in* People and rangelands, building the future. Proceedings of the VI International Rangeland Congress, Townsville, Queensland, Australia July 19-23.
- Young, J. A., and R. A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. *Journal of Range Management* **31**:283-289.