

**Interactions of Burn Season and Ecological
Condition on Ecosystem Response to Fire in
Mountain Big Sagebrush Communities:
Information Necessary for Restoration and
Postfire Rehabilitation**

Project No. 01B-3-3-06

Final Report to the Joint Fire Science Program

December 15, 2006

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EXECUTIVE SUMMARY

Overview

A predictive capability of the response of landscapes to fire based upon ecological condition and burn characteristics would be of value for managers concerned with ecosystem restoration or postfire stabilization and rehabilitation. This is particularly true in the Great Basin where fire was historically the dominant disturbance, and landscapes have been dramatically altered in composition, structure, and fire regime. In many sagebrush-dominated landscapes, fire exclusion has resulted in unprecedented rates of juniper encroachment onto lands formerly occupied by grasslands, shrub steppe, or aspen. In contrast, land uses and invasions of exotic annuals have increased the occurrence of fire. Even though the Great Basin is the largest land cover type in the Lower 48 states of the USA, it remains among the least studied. This includes the natural role of fire in its varied ecosystems and how land use, exotic plant invasions, and disruptions of fire regimes have affected ecosystem structure and function.

The primary objective of this research was to determine under what ecological and seasonal conditions would fires facilitate an increase in exotic species and under what conditions do native species positively respond. Knowledge of the ecosystem processes that interact to create the vegetation response to fires is of great importance for ecosystem restoration and maintenance, and to assist managers in implementing proper post fire stabilization and rehabilitation projects.

The research was conducted at the Lava Beds National Monument in northeastern California. To unravel the linkages between fire and environmental characteristics, we measured the fuel, nutrient, and vegetation changes to prescribed fire conducted in two seasons (spring and fall) and in three different states of ecological condition and recent fire history. All experimental units were located in the same common habitat type and soil series (i.e., mountain big sagebrush/bluebunch wheatgrass-Thurber's needlegrass). The different ecological states (condition classes) were: (1) increased fire frequency with a dominance of invaders and exotic annuals (Gillem's Camp site); (2) relatively undisturbed with minor juniper encroachment and exotic grass invasion (Fleener Chimneys site); (3) fire exclusion with juniper encroachment but negligible exotic grass invasion (Merrill Caves site). Fire behavior, fuel and biomass consumption, and vegetation response to spring and fall burning was compared between these three ecological states. Nitrogen cycling response to spring and fall burning was compared between different plant covers at the fire-excluded Merrill Caves site.

Results

Shorter fire return intervals coupled with a heavy historical human use (livestock grazing) have reduced the shrub community at Gillem's Camp and resulted in a fuel load dominated by the invasive annual, cheatgrass. Cheatgrass produces a long-lasting, high continuity fine surface fuel. The live herbaceous biomass formed an important fuels component during both the spring and fall seasons. At the juniper invaded site (Merrill Caves), fire suppression has resulted in a higher accumulation of total above-ground biomass, averaging 19 Mg/ha, largely due to an increase in shrubs, which are important for fire carry. The total above-ground biomass of the relatively undisturbed Fleener Chimneys site was intermediate to the other two sites and within the range expected for sagebrush ecosystems.

Fuel consumption and residual post fire fuels varied in ways that depended upon pre-fire fuel loads and distribution (continuity), and season of burn treatment. The two sites with altered fire regimes, the invasive-dominated Gillem's Camp and the fire-excluded Merrill Caves sites each had high percentage fuel consumption though with different fuel types and loadings.

The season of burn treatment was important at shrub dominated sites but not at the invasive-dominated site. The high rates of consumption during both spring (88%) and fall (78%) seasons at the invasive-dominated site was likely a result of the continued high herbaceous cover from cheatgrass during both spring and fall burns. The seasonal difference in fuel consumption was dramatic at the shrub dominated, fire-excluded site. The spring burn produced very high mortality, and very little surface or shrub fuel remained (84% biomass consumed). In comparison, the fall burn was patchier (48% biomass consumed). Higher spring temperatures were the primary weather difference between spring and fall season fires. The relatively undisturbed site (Fleener Chimneys) experienced a similar result to the fire-excluded site, though patchier fuels distribution produced lower total consumption.

Cheatgrass cover was dramatically reduced (>80%) following both burn seasons in burn as well as control (71%) plots, with little compositional change in the native understory vegetation at the invasive-dominated site (Gillem's Camp). At the relatively undisturbed site (Fleener Chimneys), there was a reduction in native bunchgrass cover (64% decrease), and an increase in native forbs (168% increase) following spring burns, with no changes following fall fires. At the fire-excluded site (Merrill Caves), fire treatments resulted in a decrease in woody plant cover, with no immediate post-fire differences seen in the herbaceous plant community (fall fire treatment).

At the invasive-dominated site, we saw an initial decrease in cheatgrass germination following both spring and fall fires, but this effect was transitory, and by the following year, there were more cheatgrass seeds germinated in burned plots than in controls. We found fewer cheatgrass seedlings germinated in both spring burned plots (-91%) and fall burned plots (-56%) immediately following prescribed fire. However, soils collected one-year post-fire had more cheatgrass germinants in both the spring and fall burn treatments (40% and 59% respectively).

Germination of native forb and bunchgrass species at the relatively undisturbed and the fire-excluded sites generally decreased or showed little change initially following prescribed fire. However, where native forb germination consistently rebounded one-year post-fire, native bunchgrass germination was more variable. One-year post fire at the relatively undisturbed site, native bunchgrass germination increased following the spring burn treatment (24%) and decreased following the fall burn treatment (-57%). It should be noted that the increased germination of native species one-year post-fire was observed following prescribed fires characterized by moderate biomass consumption. The spring fire treatment at the fire-excluded (Merrill Caves) site, characterized by high biomass consumption, resulted in the greatest reduction in germination initially following prescribed fire. One-year post-fire germination data was not available for this treatment.

There was increased reproductive effort in native bunchgrass species following fires in all communities studied. Fire enhanced flowering was not seen in *C. macrocarpus* following spring or fall burns at the relatively undisturbed and fire-excluded sites.

The pools and fluxes of soil mineral N, the forms most readily available for plant uptake, were examined at the fire-excluded (Merrill Caves) site and varied with respect to the season of burn, the time since burn, and the timing of succeeding seasonal-environmental conditions. This study suggests that $\text{NH}_4\text{-N}$ and subsequent nitrification remains high for as long as 13 months or more after fire.

The higher severity and consumption of the spring burn treatment altered the soil conditions more dramatically than the fall burn. The severity of the burn with respect to live plant retention likely played a strong role in the fate of the soil mineral N pools following burn treatment. In fall burn plots, $\text{NH}_4\text{-N}$ was diminished dramatically (-65%) during the fall-wet

season, a time of increased plant and microbial activity and demand for mineral N. Soil $\text{NH}_4\text{-N}$ levels were not significantly reduced during the fall-wet season in the spring burn treatments as high plant mortality likely reduced demand.

The relationship between mineral N soil pools and different vegetation covers was likely related to differences in organic substrate and demand, which varied with season and due to differences in burn treatment severity. Junipers largely survived fall burn treatments because of the lower burn severity and their underlying litter layer remained intact with only minimal consumption. The reduction of mineral N in soil beneath shrubs and in open areas coincided with the fall-wet season, and reflects seasonally changing demand for available N due to increased plant and microbial activity. At the same time, mineral N produced earlier during the dormant season, remained higher beneath juniper, indicating that demand was suppressed where juniper cover and its organic horizon remained intact.

Junipers (as well as shrubs) in plots receiving the spring burn treatment were killed and the underlying litter was largely consumed. Soil mineral N concentrations were retained under all covers through the fall-wet season indicating that the high severity of the spring burn treatment reduced plant demand, and potentially N retention, regardless of cover, unlike the fall burn treatment.

Lessons Learned

The issue of reintroduction of prescribed fire in the sagebrush steppe is complicated by issues such as invasive species, cattle grazing, and increasing woody dominance. As these issues affect both the behavior of the fire itself, and the response of the vegetation communities following fire, they must be considered when developing a prescribed fire plan.

The differences in time since fire, different land use histories and inherent site characteristics resulted in differences in structure including differences in fuel loads and total above-ground biomass. Shorter fire return intervals coupled with a heavy historical human use (livestock grazing) have reduced the shrub community at Gillem's Camp and resulted in a fuel load dominated by the invasive annual, cheatgrass. A longer period since fire at the fire-excluded Merrill Caves site resulted in differences in structure including higher above-ground biomass largely due to an increase in shrubs, and different nitrogen dynamics associated with junipers.

Sites characterized by recent disturbance and/or fuel loads outside the range of natural variation for these ecosystems experienced higher mortality, and fuel and biomass consumption by prescribed fire.

There is now a functioning native bunchgrass, shrub, and forb component at Gillem's Camp that did not exist when there was grazing in the Monument. Total cheatgrass cover was significantly lower one year following burns, and this reduction provides an opportunity for native plants to successfully compete with exotics. In the first post-fire year at this site, we saw an increase in native bunchgrass flowering, demonstrating the ability of these fire adapted plants to flourish in a post-burn environment. However, while cheatgrass germination decreased following both burn treatments this effect was transitory, and by the following year, there were more cheatgrass seeds germinated in burned plots than in controls.

While we saw positive responses at this site following burns, fire should not be used too frequently solely for reduction of cheatgrass, as fire could harm the native plant community if it is applied too often. Native grasses and forbs have been increasing in these low-elevation, degraded areas of the National Monument since the removal of livestock, and with a management policy to maintain the natural fire return interval, this trajectory towards a more native dominated site will continue. In these areas, a good management objective would be to burn (or allow natural fires to burn) for the maintenance of the native plants, rather than for cheatgrass control. In addition, we must caution that this research only extended to one year post-fire. Continued monitoring of

these sites is needed to understand the long-term dynamics of prescribed fire use for cheatgrass control and ecosystem maintenance.

There was no difference in fire behavior, mortality and fuel consumption due to season of burn at the invasive-dominated site, however, the seasonal difference was dramatic at the two sites dominated by shrub fuels, with spring burns producing much higher fuel consumption and mortality. We would expect that in sites where greater quantities of biomass were consumed we would see greater changes in ecosystem properties, such as nutrient retention and plant survival.

While we saw a positive reduction in juniper density due to the high consumption fall burn treatment, shrub fuel reduction was at the high end of management objectives. Due to delayed treatment application, these sites were not revisited one year post-burn to assess the plant community response. Before expanding spring season burns to additional fire-excluded sites, it would be important to determine if the native plant community responds positively to high consumption, particularly if there is the potential for cheatgrass invasion. In these areas, initial burns could be used for juniper control, and then the natural fire return interval should be maintained for continued natural juniper control and ecosystem maintenance. Again, fire could harm the native plant community if it is applied too often.

Chapter 1: Community Composition Response Following Spring and Fall Prescribed Fire at in Mountain Big Sagebrush Ecosystems at Lava Beds National Monument

Lisa M. Ellsworth and J. Boone Kauffman

Abstract

Much of the current management response surrounding wildland and prescribed fire in sagebrush dominated ecosystems has focused on a persistent belief that fire in sagebrush systems results in a loss of native flora and a trend toward dominance by exotic annuals. Fire was historically the dominant disturbance throughout the sagebrush steppe and the plant species that comprised these communities possessed a variety of adaptations facilitating survival to the fire regime. In order to restore ecosystems, land managers will need to reintroduce natural ecosystem processes, including natural disturbance processes. Little has been experimentally quantified on where and to what degree invasive species affect fire effects on species composition. To examine the plant community response to fire, spring and fall prescribed fires were applied to three *Artemisia tridentata* ssp. *vaseyana* (Mountain Big Sagebrush) plant communities with different land use, elevations, and fire histories. These communities were quite different in composition and structure ranging from a dominance of exotic annuals to dominance by native grasses, shrubs, and trees. In invasive-dominated sites, there was a decrease in *B. tectorum* cover following both spring (81% decrease) and fall fires (82% decrease), and no native vegetation composition change. At native dominated sites, there was a reduction in native bunchgrass cover (64% decrease), and an increase in native forbs (168% increase) following spring burns, with no changes following fall fires. In juniper-dominated sites, fire treatments resulted in a decrease in woody plant cover, with no immediate postfire response seen in the herbaceous plant community.

Introduction

Understanding and applying prescribed fire is a critical part of the management of vegetation communities in the Great Basin. In a system which has been dramatically altered by domestic livestock grazing, fire suppression, and introduction of exotic plants, the reintroduction of fire at its natural range of variability may be an effective tool to restore plant communities to their natural compositions. More research is needed to determine the circumstances under which prescribed fire is beneficial to an ecosystem, and under what circumstances it contributes to further degradation and invasion by exotic annuals. These studies are needed as land managers require tools to effectively restore rangelands of the Great Basin including approaches for post wildland fire rehabilitation.

Before Euro-American settlement, fire was frequent throughout rangeland ecosystems (Miller et al 2001). Lightning-ignited fires were common late in the summers, and indigenous groups utilized natural fire as well as set fires to maintain desirable plants, for increased crop productivity, and to manage game species. (Shinn 1980; Young and Blank 1995; Weddell 2001; Griffin 2002). Immediately following the initial settlement by Euroamericans, fire was used excessively, and combined with the introduction of livestock, resulted in degraded rangelands. In response to these practices, policies were established by the early 1900's discouraging ignitions and requiring the suppression of fire (Clark and Starkey 1990). Altering fire regimes changes ecosystems, communities, and population structures, by favoring species more adapted to the new regime or by creating opportunities for invasion (Agee 1993). Overgrazing by domestic livestock

has degraded lands and made them more susceptible to invasion by exotic species. Because livestock consume grasses which were the primary fuels that allowed for sustained ignition and spread, fires were decreased. An increase in time between fires, coupled with land uses such as livestock grazing has resulted in an increase in woody fuels, encroachment of juniper into grasslands and shrub steppe, and a reduction of native bunchgrasses and forbs. Historically, fires were frequent in *A. tridentata* ssp. *vaseyana* communities, occurring approximately every 15-100 years (Miller and Tausch 2001, Miller et al. 2003), and were stand-replacement fires. In the Great Basin two different circumstances arising from a change in fire regime have occurred. Low elevation areas which were overgrazed by domestic livestock or were otherwise affected by anthropogenic disturbance became susceptible to invasion by exotic species, which has been shown to be one of the greatest threats to ecosystem function and species diversity (Vitousek 1990). *Bromus tectorum* (cheatgrass) became a dominant invasive species to western rangelands after the turn of the 20th century. *B. tectorum* was unintentionally introduced into the United States in the early 1900's inside bags of contaminated grain. It has since become the most widespread annual in the semi-arid landscapes of the western United States (Mack 1981). Livestock and *B. tectorum* introductions initiated a cycle of positive feedbacks perpetuating dominance by invasive species (D'Antonio and Vitousek 1992). The introduction of this invasive annual has greatly increased the potential for fires in this environment because it provides a continuous, dry fuel source and lengthens the fire season (Payson et al. 2000). Increased human settlement added to the reduction in fire return interval by providing sources of ignition and further disturbance of the landscape, making it more susceptible to exotic invasion.

In high elevation areas, fire regimes in the Great Basin have been lengthened by fire suppression and domestic livestock grazing. Prior to Euro-American settlement, expansion of *Juniperus occidentalis* (western juniper) is believed to have been limited by fire, drought, and competition with grasses (Kilgore 1981). The introduction of domestic grazing animals in these areas decreased the amount of fine fuels which are necessary for fire spread (Kauffman and Sapsis 1989), thereby reducing fire frequency. Fire exclusion by suppression and reduction of fine fuels within the mountain big sagebrush ecosystem has contributed to the increase in *J. occidentalis* because young junipers do not often survive fire. Restoration of this ecosystem will ultimately require a reintroduction of fire as a necessary means for the maintenance of the native plant communities.

Plant communities in the Great Basin have evolved with fire, and have developed strategies to benefit from the pattern of disturbance caused by the natural fire regime (Kauffman et al. 1997, Wroblecky and Kauffman 2002). Re-introduction of fire into systems where it has been excluded may benefit these plant communities (Kauffman, 1990; Sapsis, 1990). In this paper, I quantified the differences in plant community composition following spring and fall prescribed fire treatments in sites differing in fire and disturbance history, elevation, and plant composition. Community composition preceding fire largely determines the response to and composition following burns. An ability to predict the response of landscapes to fire based upon ecological condition and burn characteristics is useful as land managers seek to restore ecosystem structure and function, including the natural disturbance regime.

Methods

Experimental Design and Data Collection

This study was conducted at Lava Beds National Monument, California, 77 km southeast of Klamath Falls, Oregon (Erhard 1979). All three sites are located in mountain big sagebrush steppe communities within the Monument. Burn treatments (spring and fall plus an unburned control) were applied to three different sites with different landscape settings which had a dominant effect on land use history, and hence, species composition. Fleener Chimneys is

dominated by native perennial grasses and forbs, with predominately *A. tridentata* ssp. *vaseyana* and *Purshia tridentata* (antelope bitterbrush) in the overstory. There is a significant lava flow between this site and water which limited historic grazing. Merrill Caves is characterized by encroachment by *J. occidentalis* in the overstory, with mostly native forbs and bunchgrasses in the herbaceous layer. Gillems Camp has a history of degradation by domestic livestock grazing, and is dominated by *B. tectorum* with a sparse cover of woody vegetation, principally *Chrysothamnus nauseosus* (grey rabbitbrush).

Prescribed fires were applied by Park Service personnel in June, 2003 (spring treatment) and November, 2003 (fall treatment), except at Merrill Caves where spring fire treatments were not applied until June, 2004 due to weather constraints. Treatment units at each site were established as a randomized complete block design. For each combination of site and season of burn, there were five replicate burn plots for a total of 30 burn units (plus 15 unburned controls).

Percent cover of herbaceous vegetation was quantified in 30- 30 X 60 cm microplots (n=150 for each treatment by site combination) at established locations along permanent transects. Pre-fire vegetation cover was measured in July, 2002 (spring treatments) and 2003 (fall and control treatments) and post-fire vegetation cover was measured in 2004 (all plots), during the active growing season. Post-fire herbaceous cover data for spring burns at Merrill Caves was not collected. Each individual was identified to species, and percent cover estimated for each plant rooted within the plot. For shrub species, cover was measured in five 1m by 20 m subplots per plot, adjacent to permanent transects. Taxonomic nomenclature follows Hitchcock and Cronquist (1973).

Data Analysis

For herbaceous vegetation (grasses and forbs) sample units are an average percent cover of microplots (10 per plot in prefire year, increased to 30 per plot in postfire year to ensure a representative sample) taken along five permanent transects per plot, and all analyses are run at the plot level. For shrub species, sample units are an average of percent cover as measured in five subplots (20m by 1m) within each plot (20m by 20m) along permanent transects. All species which occurred in fewer than two sample units were deleted from the analysis, resulting in 62 species remaining in the analysis which reduced noise in the data. All data were transformed using a square root ($p=.5$) power transformation (McCune and Grace 2002), which decreased average skewness of species (from 5.7 to 3.7). After separating the matrix by site, and again removing any species occurring in fewer than two sample units, numbers of species analyzed in each matrix were as follows: Fleener, 42 species; Merrill, 42 species; and Gillems, 32 species. No relativizations were applied to the data because I was interested in studying the effects of fire on absolute cover (total percent cover of each species), rather than relative percent cover (each species relativized by the maximum cover of the most abundant species). Absolute cover provides a better measure of the fire treatment effect, as total plant biomass declined following fire.

Analysis of variance was used to determine whether there was a significant difference between functional group (cheatgrass, native forb, shrub, and perennial bunchgrass) cover before and after spring and fall prescribed fires, as well as between treatment and control groups. Additionally, covers of individual shrub species (*A. tridentata* ssp. *vaseyana*, *C. nauseosus*, *C. viscidiflorus*, *P. tridentata*, and *Tetrademia canescens*), as well as re-sprouting of shrub species were analyzed individually using Analysis of Variance. Multiple comparison tests with a Tukey-Kramer correction factor were used when the one-way ANOVA gave a significant result. The Tukey-Kramer multiple comparison method was used because it provides precise control over the family-wide confidence intervals when pairwise differences of all group means are tested (Ramsey and Schafer 2002). All univariate statistics were analyzed using S+ 6.1 Academic Site Edition.

Multivariate analyses were performed using PC-ORD, Version 4.25. (McCune & Mefford 1999) to test whether there was a difference in community composition between sites, and within sites following spring and fall burn treatments. Sorenson similarity was chosen to represent species distance for all analyses because it has been shown to provide an effective measure for community data sets. Nonmetric Multidimensional Scaling (NMS) was chosen as an ordination technique to reveal patterns which may be present in the data set because it tends to perform well with community data and provides a biologically meaningful explanation for the patterns present (McCune and Grace 2002). All NMS runs were done using the autopilot mode using the slow and thorough setting, and all runs used random starting configurations.

Multi-Response Permutation Procedures for blocked data (MRBP) were used to evaluate the strength of *a priori* groupings of the data by testing the null hypothesis of no difference between groups (fire and control). This technique was used to test for differences between control and fire treatment groups following fire treatments. MRBP generates an A statistic which gives effect size, and a corresponding p-value that shows statistical significance. When $A = 0$, items within groups are homogeneous, when $A > 0$, items within groups are more similar than can be attributed to chance alone, and when $A < 0$, items within groups are more dissimilar than is expected from a random data set.

Indicator species analysis (Dufrene and Legendre 1997) was used to identify species that are unique to burn treatment and control groups. It generates an indicator value (IV) for each species present based on species abundance and relative frequency of each species within the group (fire or control). Indicator values are then tested for significance using a Monte Carlo randomization test (McCune and Grace 2002), and a p-value is generated.

Results

***Bromus tectorum* Cover**

At Gillems Camp, cheatgrass cover significantly decreased not only in spring fire (80% reduction) and fall fires (82% reduction), but also in the control (no burn; 71% reduction) plots following fire ($p < 0.001$ for all prefire/postfire comparisons). Post-fire comparisons between treatments were not significant ($p = 0.12$) (Table 1). These results suggest that annual variability in species cover was greater than burn treatment effects at this site. Cheatgrass cover also decreased following all treatments at Merrill Caves (51% decrease in fall burns; 70% decrease in control plots; $p = 0.46$) and Fleener Chimneys (46% in spring burns; 40% in fall; 32% in control; $p = 0.30$), though none of these comparisons drew statistical significance.

Native Bunchgrass Cover

There was a decrease in cover of bunchgrass species following fire at Fleener Chimneys following spring fire ($p = 0.04$) (Table 1). There was no change in bunchgrass cover at Merrill Caves ($p = 0.42$) or Gillems Camp ($p = 0.12$).

Native Forb Cover

Very little change was observed in native forb cover following fire (Table 1). There was a significant increase from 5% to 13% ($p = 0.02$) in forbs at Fleener Chimneys following spring burns, which was almost entirely due to a large response of the native annual *Phaecelia linearis*.

Shrub Cover

Immediately after fire there is a shift towards an herbaceous plant community (Table 2). There was a decline in the cover of all shrub species following fire. At Gillems Camp, the predominant shrub species was grey rabbitbrush (*Chrysothamnus nauseosus*), which decreased following both spring (from 3.5% to 0.2%; $p < 0.001$) and fall fires (from 3.1% to 0.2%; $p < 0.001$).

Total shrub cover at this site also decreased from 3.6% to 0.2% ($p < 0.001$) following spring fires and from 3.1% to 0.2% ($p < 0.001$) following fall fires.

At Fleener Chimneys, dominant shrub species were *A. tridentata* ssp. *vaseyana*, *P. tridentata*, and *Tetradymia canescens*. Season of burn had little effect on the decreases in percent cover. Total shrub cover decreased following spring burns from 32% to 14% ($p = 0.01$), and decreased following fall burns from 26% to 12% ($p = 0.03$). The relatively high post fire shrub cover here reflects the presence of unburned islands within the study.

Shrub responses to fire at Merrill Caves were driven by a dominance of *A. tridentata* ssp. *vaseyana* and *P. tridentata*. The decrease in cover of these species as well as the total shrub cover was greater following spring fire than fall fire. Total shrub cover decreased from 9% to 0.1% ($p < 0.001$) after spring burns, and from 9% to 2% ($p = 0.02$) following fall burns.

Shrub Mortality and Resprouting

Shrub mortality and shrub resprouting response to fire was not different between spring and fall burns. Over 75% of individual shrubs were killed by fire, regardless of season, but we did see some variability in terms of basal resprouting (Table 3). Although *C. nauseosus* has been reported to be a prolific post-fire sprouting species (Young and Blank 1995), this was not observed during this study. At Gillems Camp, the mortality of this species was 82% following fall fire. No burned individuals of this species sprouted following spring fire (83% of individuals in the sites were top-killed). Merrill Caves and Fleener Chimneys each had one incidence of grey rabbitbrush resprouting.

Tetradymia canescens was a more vigorous sprouter. At Fleener Chimneys, 46% (19 out of 41 individuals) of top-killed shrubs resprouting following spring fires, and 71% (34 of 48) resprouting after fall burns. There were also infrequent incidences of resprouting of *Chrysothamnus viscidiflorus* (green rabbitbrush) and *P. tridentata* (Table 3).

Juniper Mortality

At Gillems Camp, there were 2 small *J. occidentalis* individuals in the fall burn plots, both of which were killed by the fire. At Fleener Chimneys, there was one juniper in the fall burn plots, and it also suffered mortality from the fire treatment. There were no junipers in the spring burn plots at either Gillems or Fleener. At Merrill Caves, we saw a similar mortality response in both spring and fall burns. In spring burn plots, 44.4% (5 out of 9) of junipers were killed by the fire, and in fall burn plots, 46.2% (7 of 13) suffered fire induced mortality.

Does Species Composition Differ Among Sites?

Sample units measured prior to the prescribed fire treatments were ordinated using nonmetric multidimensional scaling (NMS). A two dimensional solution (final stress = 12.52; iterations = 41; final instability = 0.00001) to best described the variation which was seen between plots. The gradient seen along axis 1 ($r^2 = .689$) shows a distinct difference between Gillems Camp and the other two sites (Fig.1). This gradient is largely described by a presence of invasive and early successional species at Gillems Camp (*B. tectorum* $r = -.942$, *Draba verna* $r = -.622$, *C. nauseosus* $r = -.839$, *Lactuca serriola* $r = -.571$) and a presence of shrubs at Merrill Caves and Fleener Chimneys (*P. tridentata* $r = .538$; *A. tridentata* ssp. *vaseyana* $r = .910$). The gradient seen along axis 2 ($r^2 = .199$) separates the species seen at Merrill Caves (*J. occidentalis* $r = -.802$; *Cercocarpus ledifolius* $r = -.660$; *Leptodactylon pungens* $r = -.544$) from those found at Fleener Chimneys. Community composition differed among sites (MRBP: $p < 0.00001$, $A = 0.322$).

Is There a Change in Species Abundance Following Prescribed Fire (Control vs. Burn Treatments)?

A two dimensional ordination in NMS (Fig. 2) gave the best representation of the structure in the total data set (final stress = 15.68; iterations = 77; final instability = 0.00006).

Although there is a suggestion of a treatment effect within sites from this visual representation, the overriding site differences in sites make it difficult to see a pattern in the data. Therefore, data was therefore separated into three site-specific matrices and fire treatment effects were looked at individually.

Fleener Chimneys

Prescribed fires at Fleener Chimneys were difficult to ignite, carried poorly, and resulted in a patchy burn pattern. Most shrubs, however, were ignited, resulting in large mortality of shrub species (Table 3), as well as a decrease in percent cover (Table 2). Spring fires resulted in a large increase in native forbs (Table 1), particularly *P. linearis*.

NMS was used to illustrate the patterns of species distribution seen at Fleener Chimneys following burn treatments. A three dimensional solution best described the variation which was seen between plots (final stress = 15.76; iterations = 112; final instability = 0.00010). A gradient was visible between the sample units corresponding to the pre-burn plots and those following burn treatments (Fig. 3). The gradient seen along Axis 3 (Fig. 4) weakly separates control plots from treatment plots. Because these samples were taken during two different years, it may be difficult to assess whether the shift seen here is actually a fire effect, or if it can be attributed, at least in part, to yearly variation in species composition. When only the post fire data was represented by NMS (Figure 5), a three dimensional solution (final stress = 9.96; iterations = 74; final instability = 0.00001) illustrated the separation of the spring burn treatment from the fall burn and control treatments.

The lack of separation between fall and control treatments reiterates what was observed in the field. During fall fires at this site, fuel moisture was high and temperatures were low (Appendix 1). Fire personnel working on the fire had a very difficult time igniting plant material, and fire spread was limiting. The gradient seen along axis 1 ($r^2 = .514$) seems to be explained by the separation of the spring burns from the fall and control plots. Species which had r values greater than 0.5 were assessed for their role in the gradients observed. The end of the gradient representing spring burn plots was characterized by species which responded positively to fire (*Phaecelia linearis* $r = -.886$; *Vulpia* spp. $r = -.580$; *Descurania pinnata* $r = -.638$; *Mentzelia albicaulis* $r = -.809$; *Plagybothrys tenellus* $r = -.864$) and the gradient representing both fall and control plots were characterized by both higher shrub cover (*A. tridentata* $r = .690$) and increased bunchgrass cover (*Poa sandburgii* $r = .755$; *Stipa occidentalis* $r = .540$). A difference was seen between spring and fall burns and control groups (MRBP: $p = 0.0006$, $A = 0.151$). Indicator species analysis revealed three species which were common only in the spring burn treatment following fire ($p < 0.05$): *Plagybothrys tenellus* (Indicator value = 85), *Epilobium minutum* (57), and *Phaecelia linearis* (78), and two species were unique to fall burn treatments: *Artemisia tridentata* (43) and *Tetradymia canescens* (62). One species was distinct to the control treatment, *Stipa occidentalis* (45).

Merrill Caves

Following fall prescribed burns at Merrill Caves, there were no fire effects apparent in the species composition of herbaceous vegetation (Table 1). There was a significant decrease in cover of dominant shrub species, *A. tridentata* (spring, $p < 0.001$; fall, $p = 0.001$) and *P. tridentata* (spring, $p < 0.001$; fall, $p < 0.001$) (Table 2) as well as high mortality of these species (Table 3) following both spring and fall prescribed fires.

A three dimensional solution (final stress = 13.02; iterations = 77; final instability = 0.00001) best described the patterns which were seen in the species composition data at Merrill Caves. In Figure 5, a gradient along axis 3 ($r^2 = .465$) is visible between the sample units corresponding to the pre-burn plots and those following fall burn treatments. Because these samples were taken during two different years, it may be difficult to assess whether the shift seen here is actually a fire effect, or if it can be attributed, at least in part, to yearly variation in species composition, particularly because the same shift can be observed in the control plots. When only

the post fire data was represented by NMS (Figure 6), a two dimensional solution (final stress = 12.52; iterations 127; final instability = 0.00001) illustrated the separation of the fall burn treatment from control plots. After a 175 degree rotation, the gradient seen along axis 1 ($r^2 = .301$) seems to represent the separation of the fall burns from the control plots. Species which had r values greater than 0.5 were assessed for their role in the gradients present. The end of the gradient representing fall burn plots was characterized by species which respond positively to fire (*B. tectorum* $r = -.574$; *Mentzelia albicaulis* $r = -.636$; *Leptodactylon pungens* $r = -.727$; *Phacelia linearis* $r = -.624$). The end of the gradient representing control plots was characterized by species which do not initially respond positively to fire (*Penstemon speciosa* $r = .508$, *Draba verna* $r = .636$). Although there were species that contributed to the gradient seen on axis 2 ($r^2 = .492$) (*Calochortus macrocarpus* $r = -.705$; *Crepis acuminata* $r = -.790$; *Phlox hoodii* $r = -.722$, there was no obvious explanation for this gradient. The high correlations appear to be due to high cover of these species in few plots, as evidenced by species overlays. A difference was seen between fall burns and control plots (MRBP: $p = 0.007$, $A = 0.090$). Indicator species analysis revealed two species which were common only in the control plots ($p < 0.05$): *Purshia tridentata* (Indicator value = 80), and *Leptodactylon pungens* (80). One species was distinct to the fall burn treatment, *Mentzelia albicaulis* (77).

Gillems Camp

Fires at Gillems Camp were of high intensity and severity, top-killing most vegetation. There were few unburned islands in these burn plots. Shrub cover following both spring and fall fires were significantly reduced, and mortality was high. There were significant reductions in *B. tectorum* cover between prefire and postfire years in spring ($p < 0.001$) and fall burns ($p < 0.001$) as well as in control ($p = 0.01$) plots. There were no significant changes in perennial bunchgrasses or native forbs due to fire treatments.

Ordination of sample units from Gillems Camp in species space using NMS showed a differentiation between pre-burn and post burn communities (Figure 7). Because there may be large annual variation contributing to the spread of points seen, the post fire data was examined further in an additional NMS ordination (Figure 8). The end of axis 1 representing spring burn plots was characterized by species which respond positively to fire (*Phlox hoodii* $r = .500$; *Descurainia pinnata* $r = .542$; *Sisymbrium altissimum* $r = .503$), and the end of the gradient representing control plots was characterized by increased shrub cover (*C. nauseosus* $r = -.728$), and annual grasses (*B. tectorum* $r = -.673$) and forbs (*Draba verna* $r = -.851$). There was a difference observed between spring and fall burns and control plots (MRBP: $p = 0.0038$, $A = 0.110$). There was a difference as well between spring and fall burn treatments (MRBP: $p = A = 0.07$, $p = 0.038$). Indicator species analysis revealed species which were common only in the spring burn treatment ($p < 0.05$): *D. pinnata* (Indicator value = 69), and *S. altissimum* (53), and three species which were distinct to the control plots, *B. tectorum* (45), *D. verna* (39), and *C. nauseosus* (87).

Discussion

Based on the results which were demonstrated by both multivariate analyses and analysis of variance, it was shown that site difference described many of the differences seen in herbaceous plant composition, with fire treatment describing the variation within site. Many species which are common to the degraded site, Gillems Camp, are annuals which are common following disturbance such as invasive weeds *S. altissimum* and *Lactuca serriola*. Conversely, in areas where native plants are still successfully competing with exotics, and fire has been maintained at a return interval which is within its normal range of variation, an increase in native forbs was measured following fire treatments such as those seen at Fleener Chimneys and Merrill Caves (*P. linearis*, *Mentzelia albicaulis*, and *Crepis acuminata*). The effect of the fire treatment

at Merrill Caves was largely affected by the mortality of Western Juniper, and the subsequent release of resources for understory vegetation. Management goals in areas which have increased in *J. occidentalis* cover are to reduce tree cover with fire or other methods.

Responses of plant species to fire are a function of the adaptations that species have for resilience, resistance, and reestablishment following fire (Kauffman 1990; Wroblewski and Kauffman, 2002). Degraded, lower elevation sites dominated by exotic species are a higher risk for invasion, and coupled with an increased fire return interval, can become further dominated by invasives with disturbance (D'Antonio and Vitousek 1996). However, if there is adequate native seed source, perennial native bunchgrass species and native forbs can utilize the short window following fire to inhabit microsites previously occupied by cheatgrass and become established. Areas under current management at the Lava Beds National Monument, where the fire return interval is more frequent than it was historically and where there is a native component would benefit from keeping the fire return interval within its historic range of variability, and allowing native seed to recolonize the site.

Higher elevation, native-dominated sites also would benefit from the reintroduction of fire at its natural range of variability. Fire shifts the composition from dominance of woody vegetation to that of grasses and herbs and results in a short-term flush of nutrients to be used by herbaceous vegetation, resulting in an increase in bunchgrasses and forbs in postfire years. (John Wilson, personal communication) Understanding site differences in mountain big sagebrush systems and how those differences influence prescribed fire behavior and species response is critical when these tools are applied in a management context.

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Table 1: Herbaceous plant cover following prescribed fire at the Lava Beds National Monument: Lowercase letters indicate statistically significant groups ($p < 0.05$).

Gillems Camp Percent Cover						
	<i>Bromus tectorum</i>		perennial bunchgrasses		native forbs	
	mean	SE	mean	SE	mean	SE
spring pre	33.50 (a)	2.26	10.2 (a)	1.82	1.94 (a)	1.39
spring post	6.54 (b)	0.37	3.11 (a)	1.01	1.71 (a)	0.85
fall pre	41.14 (a)	1.62	9.82 (a)	2.30	1.00 (a)	0.17
fall post	7.22 (b)	1.04	5.50 (a)	1.18	1.85 (a)	0.55
control pre	40.22 (a)	7.58	7.10 (a)	2.97	2.89 (a)	0.40
control post	11.71 (b)	1.79	6.80 (a)	1.48	1.28 (a)	0.38
Fleener Chimneys Percent Cover						
	<i>Bromus tectorum</i>		perennial bunchgrasses		native forbs	
	mean	SE	mean	SE	mean	SE
spring pre	0.88 (a)	0.43	16.56 (a)	3.27	4.81 (a)	1.67
spring post	0.46 (a)	0.18	5.92 (b)	1.37	12.99 (b)	3.98
fall pre	1.65 (a)	0.86	13.80 (a)	3.15	4.79 (a)	0.94
fall post	0.99 (a)	0.29	9.68 (a,b)	1.55	3.42 (a)	0.94
control pre	0.53 (a)	0.14	9.22 (a,b)	2.33	6.52 (a)	1.92
control post	0.36 (a)	0.11	9.55 (a,b)	0.52	3.26 (a)	0.68
Merrill Caves Percent Cover						
	<i>Bromus tectorum</i>		perennial bunchgrasses		native forbs	
	mean	SE	mean	SE	mean	SE
fall pre	4.05 (a)	2.29	6.73 (a)	2.18	5.82 (a)	1.92
fall post	1.99 (a)	0.52	7.17 (a)	1.31	5.8 (a)	1.44
control pre	2.52 (a)	1.44	5.65 (a)	1.77	3.14 (a)	0.35
control post	0.76 (a)	0.16	5.76 (a)	0.99	3.86 (a)	1.27

Table 2: Shrub percent covers before and after burn treatments. Lowercase letters indicate statistically significant differences between groups.

	<i>Artemisia tridentata</i>		<i>Chrysothamnus nauseosus</i>		Gillems Camp Shrub Cover		<i>Furshia tridentata</i>		<i>Tetradymia canescens</i>		Total shrub covers	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
spring pre	0.08 (a)	0.05	3.47 (a)	0.66	0.00 (a)	0.00	0.00 (a)	0.00	0.03 (a)	0.03	3.59 (a)	0.68
spring post	0.00 (a)	0.00	0.17 (b)	0.06	0.00 (a)	0.00	0.00 (a)	0.00	0.00 (a)	0.00	0.47 (b)	0.06
fall pre	0.00 (a)	0.00	3.05 (a)	1.07	0.00 (a)	0.00	0.02 (a)	0.02	0.00 (a)	0.00	3.07 (a)	1.09
fall post	0.00 (a)	0.00	0.23 (b)	0.17	0.00 (a)	0.00	0.00 (a)	0.00	0.00 (a)	0.00	0.23 (b)	0.17
control	0.00 (a)	0.00	2.74 (a)	0.48	0.00 (a)	0.00	0.01 (a)	0.01	0.01 (a)	0.01	2.76 (a)	0.48
					Fleener Chimneys Shrub Cover							
	<i>Artemisia tridentata</i>		<i>Chrysothamnus nauseosus</i>		Chrysothamnus viscidiflorus		<i>Furshia tridentata</i>		<i>Tetradymia canescens</i>		Total shrub covers	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
spring pre	23.00 (a)	2.83	0.13 (a)	0.07	0.12 (a)	0.04	6.46 (a)	3.96	1.73 (a)	0.97	31.61 (a)	6.37
spring post	11.89 (a)	2.25	0.04 (a)	0.03	0.04 (a)	0.02	1.55 (a)	0.90	0.25 (b)	0.21	13.77 (b)	1.41
fall pre	20.20 (a)	4.31	0.43 (a)	0.31	0.24 (a)	0.09	3.27 (a)	1.89	2.11 (a)	0.83	26.24 (a,b)	4.13
fall post	9.31 (a)	1.93	0.00 (a)	0.00	0.02 (a)	0.02	2.33 (a)	1.48	0.10 (b)	0.10	11.76 (b)	0.85
control	21.21 (a)	2.66	1.02 (a)	0.88	0.18 (a)	0.08	5.51 (a)	1.73	3.67 (a)	1.44	31.6 (a)	2.50
					Merrill Caves Shrub Cover							
	<i>Artemisia tridentata</i>		<i>Chrysothamnus nauseosus</i>		Chrysothamnus viscidiflorus		<i>Furshia tridentata</i>		<i>Tetradymia canescens</i>		Total shrub covers	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
spring pre	3.76 (a)	0.49	0.02 (a)	0.01	0.04 (a)	0.02	2.65 (a)	0.74	0.00 (a)	0.00	8.53 (a)	0.60
spring post	0.12 (b)	0.12	0.00 (a)	0.00	0.00 (a)	0.00	0.00 (b)	0.00	0.00 (a)	0.00	0.12 (b)	0.12
fall pre	4.32 (a)	0.38	0.06 (a)	0.04	0.00 (a)	0.00	1.33 (a)	0.44	0.00 (a)	0.00	8.72 (a)	1.83
fall post	1.54 (b)	0.49	0.00 (a)	0.00	0.00 (a)	0.00	0.30 (a,b)	0.32	0.00 (a)	0.00	2.20 (b,c)	0.69
control	3.76 (a)	0.82	0.01 (a)	0.00	0.18 (a)	0.04	2.50 (a)	0.70	0.00 (a)	0.00	6.70 (a,e)	1.28

Table 3: Shrub mortality and resprouting following prescribed fire of selected shrub species (*C.nauseosus*, *C.viscidiflorus*, *P.tridentata*, and *T.canescens*).

Gillems Camp	spring				fall					
	prefire (N)	mortality (N)	% mortality	resprout (N)	% resprout	prefire (N)	mortality (N)	% mortality	resprout (N)	% resprout
<i>C.nauseosus</i>	131	109	83.2	0	0	103	84	81.6	5	6.0
<i>C.viscidiflorus</i>	1	1	100.0	0	0	0	X	X	X	X
<i>P.tridentata</i>	0	X	X	X	X	1	1	100.0	0	X
<i>T.canescens</i>	2	2	100.0	0	0	0	X	X	X	X
Fleener Chimneys	spring				fall					
	prefire (N)	mortality (N)	% mortality	resprout (N)	% resprout	prefire (N)	mortality (N)	% mortality	resprout (N)	% resprout
<i>C.nauseosus</i>	9	7	77.8	1	14.3	9	9	100.0	0	0.0
<i>C.viscidiflorus</i>	15	12	80.0	3	25.0	23	22	95.7	0	0.0
<i>P.tridentata</i>	17	10	58.8	0	0.0	23	14	60.9	1	7.1
<i>T.canescens</i>	42	41	97.6	19	46.3	51	48	94.1	34	70.8
Merrill Caves	spring				fall					
	prefire (N)	mortality (N)	% mortality	resprout (N)	% resprout	prefire (N)	mortality (N)	% mortality	resprout (N)	% resprout
<i>C.nauseosus</i>	3	2	66.7	X	X	8	3	37.5	1	33.3
<i>C.viscidiflorus</i>	8	8	100.0	X	X	0	X	X	X	X
<i>P.tridentata</i>	25	24	96.0	X	X	17	17	100.0	1	5.9
<i>T.canescens</i>	0	X	X	X	X	0	X	X	X	X

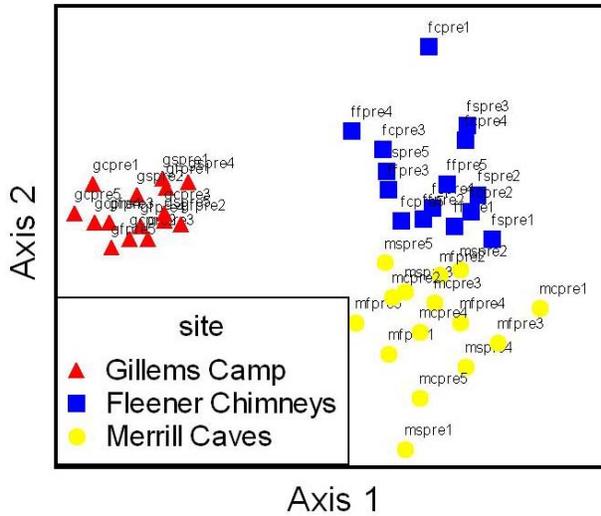


Figure 1: Before burn treatments, sites occupy different areas of NMS ordination space, indicating that plant communities are more similar within a site than they are across sites. Symbols correspond to the vegetation composition in one treatment plot. Axis 1 shows a separation of Gillem's Camp (left) plots from plots at other sites (right). Axis 2 further separates plots at Fleener Chimneys (top) from plots at Merrill Caves (bottom)

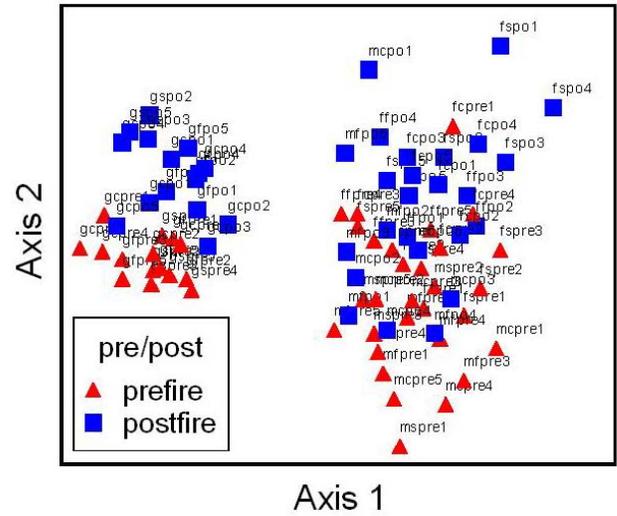


Figure 2: While there is some evidence of a treatment effect shown on Axis 2 of this NMS representation, site differences overshadowed fire responses when comparing the three locations of this study. Gillem's Camp (left) occupies a different area of ordination space than Fleener Chimneys and Merrill Caves (right). For further analyses, each site was looked at individually. Symbols correspond to the vegetation composition in one treatment plot.

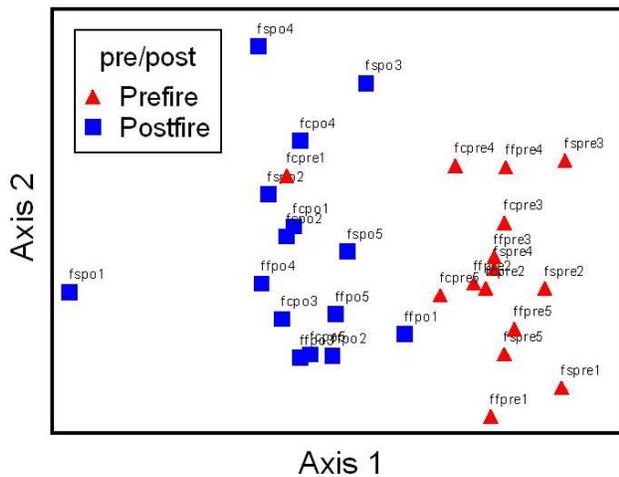


Figure 3: Vegetation composition shifts following spring and fall fires at Fleener Chimneys. In this NMS representation, Axis 1 was the strongest gradient – separating pre-treatment plots from post-treatment plots. However, control plots also show this change. Symbols correspond to the vegetation composition in one treatment plot.

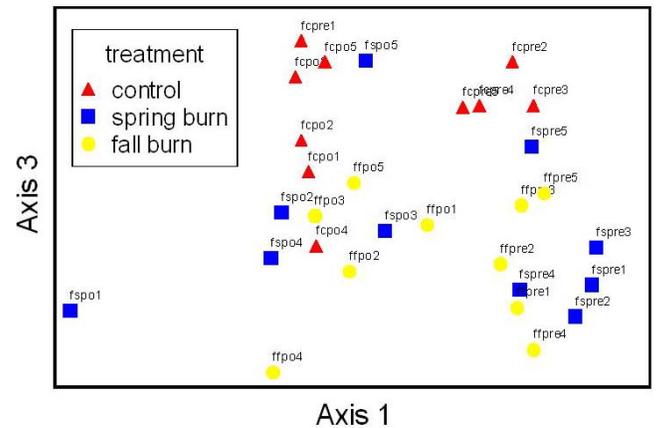


Figure 4: Control plots weakly separate from treatment plots in this NMS ordination representing vegetation composition shifts following spring and fall fires at Fleener Chimneys. Axis 3 shows a separation of pre and post treatment control plots (top) from treatment plots (bottom). Symbols correspond to the vegetation composition in one treatment plot.

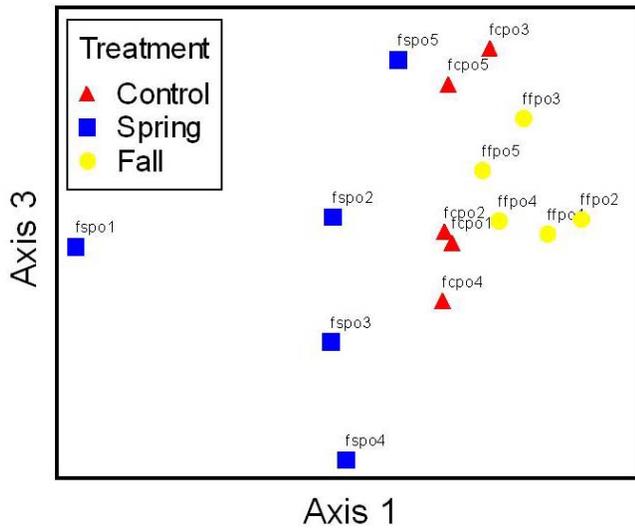


Figure 5: Vegetation composition at Fleener Chimneys differed between treatments following fire. Plots burned in the spring separate Axis 1 from fall and control plots (NMS). Fall burns were low in intensity and severity, causing them to remain more similar to the control plots. Symbols correspond to the vegetation composition in one treatment plot.

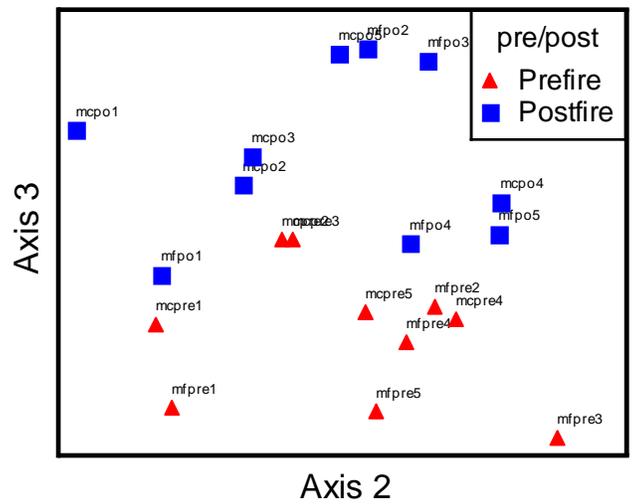


Figure 6: Spring fire and Control plots shift in NMS ordination space (along Axis 3) following prescribed burns at Merrill Caves. Symbols correspond to the vegetation composition in one treatment plot. Composition change in control plots may indicate yearly variation.

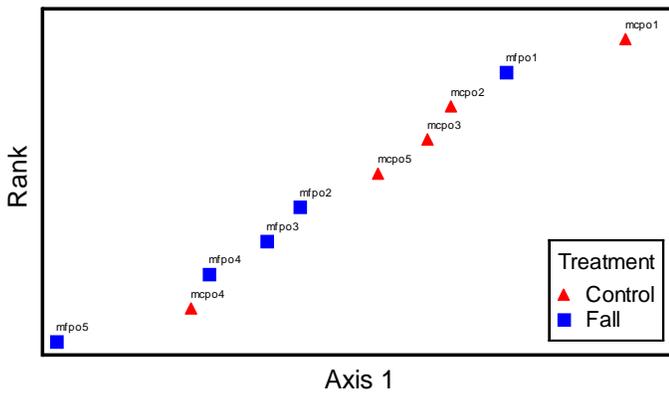


Figure 7: Merrill Caves postfire: In this 1-dimensional NMS solution, there is weak separation of the fall burn and control plots. Symbols correspond to the vegetation composition in one treatment plot.

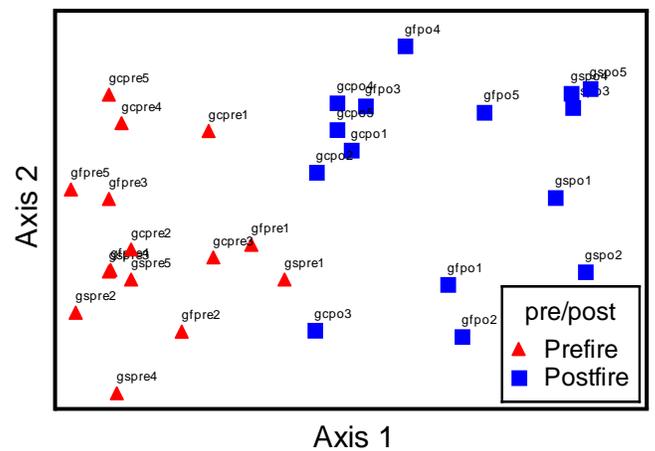


Figure 8: Gillems Camp fire response: While there is a separation of prefire and postfire plots in this NMS diagram, control plots also show this shift, although to a lesser degree. Spring fire plots move the farthest in ordination space from their prefire counterparts. Symbols correspond to the vegetation composition in one treatment plot.

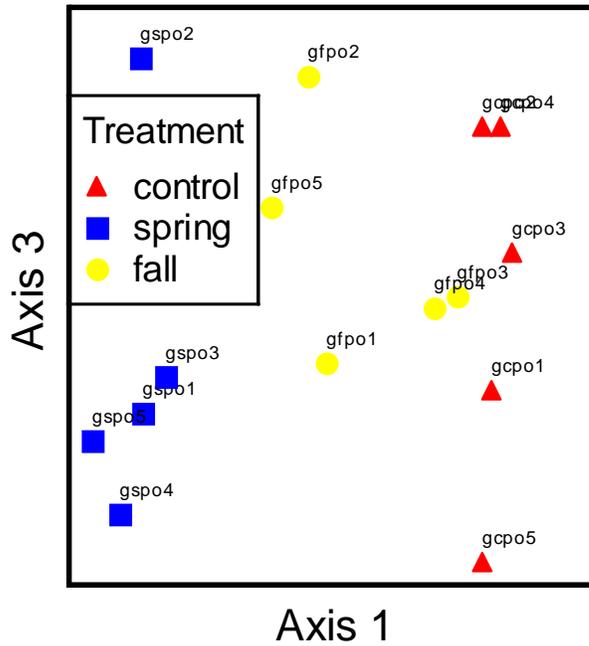


Figure 9: NMS demonstrates a clear separation of control, fall, and spring burn plots along Axis 1 for Gillems Camp plots. The end of the axis representing spring burns corresponds to an increase in species that increase following high intensity fire (*S.altissimum*, *D.pinnata*) and the control end of the axis corresponds to higher percent covers of *C.nauseosus* and *B.tectorum*. Symbols correspond to the vegetation composition in one treatment plot.

Chapter 2: Soil Seedbank Response to Prescribed Fire in Sagebrush-dominated Ecosystems at Lava Beds National Monument, California

Lisa M. Ellsworth and J. Boone Kauffman

Abstract

Anthropogenic land use alterations such as livestock grazing and fire suppression have greatly altered sagebrush grasslands of the Great Basin, facilitating invasion of exotic annuals, increases in woody species, and losses of native species. The reintroduction of fire at its natural interval (coupled with the elimination of exotic herbivores) may be integral to the restoration of sagebrush ecosystems such as has been done at the Lava Beds National Monument. Little is known how prescribed fire affects the soil seed bank in sagebrush-dominated ecosystems. To address this, we quantified the emergence of *Bromus tectorum* (cheatgrass) seedlings as well as emergence of seedlings of functional groups (native forbs, bunchgrasses, and shrubs) in a seedbank germination study following spring and fall prescribed burns at Lava Beds National Monument, California. At a cheatgrass dominated site (Gillems Camp), we found 91% fewer cheatgrass seedlings germinated in spring burned sites than in controls immediately following spring prescribed burns. However, soils collected one-year post fire had an increase in cheatgrass germinants (40%) and exotic forbs (55%) when compared to unburned controls. Following fall burns at this site there was a similar response, with a 56% immediate reduction in cheatgrass (as compared to control) and a 59% higher number of cheatgrass and 58% higher number of exotic forb germinants one year following fires. There was an increase in native forbs following spring burns (94%) and fall burns (45%) at a site dominated by native plants (Fleener Chimneys). Native bunchgrass seed germination declined following spring fire in sites dominated by native vegetation (79%), and in sites where *Juniperus occidentalis* (western juniper) dominated (Merrill Caves) (71%). Seedbank populations were largely populated with annual species from the respective sites, with more dramatic effects seen following higher severity spring fires.

Introduction

The response of landscapes to fire is dependant upon on the condition of the site, the existing plant community, and the soil seedbank which will generate postfire vegetation. The ability to predict these responses is of value for managers concerned with ecosystem restoration or postfire stabilization and rehabilitation. Landscapes and fire regimes in the Great Basin have been altered in the last century by fire suppression, disturbance by domestic livestock grazing, and introduction of exotic species. Understanding the relationships between ecological condition, burn season, and seedbank and vegetation communities allow managers to effectively implement prescribed burning strategies.

The Great Basin has seen two different shifts in plant community structure related to altered fire regimes. Many areas with a history of overgrazing by domestic livestock became susceptible to invasion and dominance by exotic grasses, most commonly *Bromus tectorum*. In other areas, mostly at higher elevations fire suppression has resulted in an expansion of western juniper (*Juniperus occidentalis*) into the shrub steppe.

Invasion by a non-native species (both plants and animals) can be one of the greatest threats to ecosystem function and species diversity (Vitousek 1990). In sites where ecological restoration is a high land management priority, such as National Parks, exotic herbivores are often removed as a means of preservation and restoration. Restoration of ecosystem processes including fire is another important component. However, invasive plant species can be problematic. Cheatgrass (*B. tectorum*) became a dominant invasive species on western USA

rangelands just after the turn of the 20th century (Mack 1981). As described by D'Antonio and Vitousek (1992), disturbance and alien invasion may begin a cycle of positive feedbacks between grass and fire. Cheatgrass was unintentionally introduced into the United States in the early 1900's inside bags of contaminated grain (Young and Clements 2004). The combination of land degradation due to domestic livestock grazing, human population expansion, and increases in exotic annuals, has resulted in a decrease of native species in many areas of the sagebrush steppe ecosystem. Increased human settlements, roads, and railways added to the reduction in fire interval by providing sources of ignition and making it even susceptible to exotic invasion.

Fire regimes in other areas of the Great Basin have been lengthened by fire suppression and domestic livestock grazing. Prior to Euro-American settlement, expansion of *J. occidentalis* is believed to have been limited by fire, drought, and competition with grasses (Kilgore 1981). The introduction of domestic grazing animals in these areas decreased the amount of fine fuels which are necessary for fire spread (Kauffman and Sapsis 1989), thereby reducing fire intensity and frequency. Fire exclusion by suppression and reduction of fine fuels from the *Artemisia tridentata* ssp. *vaseyana* (mountain big sagebrush) ecosystem has contributed to the occupation of *J. occidentalis* because young junipers (<30 years) do not often survive fire. The current rate of *J. occidentalis* encroachment onto sites formerly occupied by bunchgrasses and sagebrush has exceeded rates of expansion from the 5000 years preceding (Miller and Wigand 1994). Restoration in this ecosystem may require a reintroduction of fire as a necessary means for the maintenance of the native plant communities and a return to a properly functioning ecosystem.

Changes in germination following fire can occur by a variety of mechanisms. Fire burns seeds on the soil surface, in the litter, and on standing vegetation, but it can also serve to increase germination through scarification, increases in inorganic nitrogen, and increased sunlight (due to a reduction in shade) (Baskin and Baskin 1998). Alteration of seedbanks by fire can have an effect on postfire vegetation germination and recovery.

Because the response of seedbanks to fire largely predicts the composition of new germinants in the first post-fire year, it is important to understand any differences that season of burn and site condition may have on seedbank populations. In this study, I seek to answer the following questions: 1) Is there a difference in soil seedbank populations following prescribed fire in *A. tridentata* ssp. *vaseyana* ecosystems of differing compositions? 2) Does season of burn (spring or fall) have an effect on seedbank response to prescribed fire? Germination following fire largely predicts future vegetation composition, so understanding the response of seedbank populations to fire treatments is necessary as land managers seek to understand and implement fire as a tool for restoration.

Methods

The study was conducted at Lava Beds National Monument, California, 77 Km southeast of Klamath Falls, Oregon. This area ranges in elevation from 1228 meters along the shore of Tule Lake in the northeast to 1725 meters at the southwest corner. (Erhard 1979). The climate is cool and semi-arid, with an average annual precipitation of 39 cm (Miller et al 2003) and a temperature range from -1° C in January to 20° C in July (Erhard 1979). Most fires occur from July to September, when dry thunderstorms often coincide with high temperatures and low fuel moisture contents. The geology of the monument is unique, with basaltic lava flows and cinder cones scattered across the landscape. The monument is located on the north face of Medicine Lake shield volcano, which has erupted periodically over the last 500,000 years, and most recently erupted approximately 1100 years BP. Soils are of volcanic origin, shallow with basaltic outcrops (Erhard 1979). The study areas were dominated by *A. tridentata* spp. *vaseyana* in the overstory, and *Pseudoroegneria spicata* and *Achnatherum therberianum* in the understory. This study was conducted in three sites of the same habitat type (Erhard) but with different land use

histories and current species composition. Fleener Chimneys is dominated by native perennial grasses and forbs, with predominately *A. tridentata* spp. vaseyana and *Purshia tridentata* in the overstory. Merrill Caves is characterized by encroachment by *J. occidentalis* in the overstory, with mostly native forbs and bunchgrasses in the herbaceous layer. Gillems Camp has a history of degradation by domestic livestock grazing, and is dominated by exotics, with a high percent cover of *B. tectorum*, and little woody vegetation.

Experimental Design

The experiment was established as a randomized complete block design. Five experimental blocks were established at each of three sites (Gillems Camp, Fleener Chimneys, and Merrill Caves) at the Lava Beds National Monument. Each block contains three sub-blocks (plots) in which spring and fall prescribed fire treatments as well as unburned controls were applied. For burn treatments, the area that was burned was at least 5 m wider than the plot in every direction. Each block was established with a steel fence post marking corners and documented with a GPS unit. Experimental units were all located within mountain big sagebrush shrublands with an understory of perennial bunchgrass plants (*Pseudoroegneria spicata*, *Achnatherum therberianum*, *Elymus elymoides*).

Spring burns at Fleener Chimneys and Gillems Camp were conducted in June, 2003. Due to weather constraints during 2003, spring burns at Merrill Caves were not conducted until June, 2004. Fall burns at all sites took place in November, 2003. Although environmental conditions (temperature, relative humidity) were warmer and drier during the spring burns than in the fall burns (Appendix 1), it did not result in significantly different fire behavior measures. Both spring and fall fires burned in a mosaic pattern, burning some areas and leaving others unburned. As temperatures increased and relative humidity decreased throughout the days of the burns, rate of spread, flame lengths, and fireline intensity increased (Appendix 1).

Seedbank Sampling

To quantify the difference in soil seedbanks following spring and fall fires, we collected 5 - 20 x 20 x 5 cm blocks of surface soils from all treatment and control plots following the prescribed fires (N= 25 for each site/treatment combination). Samples were collected again one year following fires in both spring and fall seasons. Samples were placed in 25 x 50 cm flat trays over a 2.5 cm layer of vermiculite. Florescent lights were placed over trays at a cycle of 12 hours light/12 hours dark to encourage maximum germination of seeds. The seedlings that germinated within 90 days were counted and identified to species. Seedlings were removed from trays as they became identifiable, and any species that could not be identified within the 90- day germination period was allowed to grow longer until it could be identified. Because there were many species that occurred at densities too low for statistical analysis, species were combined into functional groups (bunchgrasses, shrubs, native forbs, exotic forbs, and cheatgrass) for statistical comparisons. We recognize this could result in spurious results because species of the same functional group could possess different response characteristics to fire. Analysis of Variance was run on these groups in order to test the null hypothesis of no difference between burn treatments groups and control groups.

Results

Prescribed spring fire resulted in a significant decrease ($p < 0.001$) in the soil seed bank of *B. tectorum* immediately following fire at Gillems Camp. Treatment plots had 832 germinants/m², while 9016 seedlings germinated per square meter in unburned control plots. No significant differences were seen in germination following fall fires (965 germinants/m² in fall postfire plots; 2200 germinants/m² in control plots; $p = 0.26$; Table 1). One year following fire at this site, there

was no significant difference in cheatgrass germination between spring burn (8017 germinants/m²) and control plots (5132 germinants/m²) ($p=0.42$) or fall burn (4615 germinants/m²) and control plots (1887 germinants/m²) ($p=0.17$).

Following spring fires at Gillems Camp, there was a significant increase ($p<0.001$) in number of exotic forbs germinated one year following fire in all fire and control plots (when compared to immediately following fire). Because germination in the control plots increased significantly, this is likely a year effect. There was a large increase in germination of exotic annual mustard *Draba verna* which accounted for most of the exotic forb germination one year following fire. One year following prescribed fire treatments, we saw a decrease in native forb germination in fall fire (80% decrease; $p=0.03$) and control plots (89% decrease; $p<0.001$), when compared to immediate postfire seedbank germination. There were no significant differences between fire and control groups in germination of native shrub or native bunchgrass functional groups.

At Fleener Chimneys, which was dominated by native shrubs, bunchgrasses, and forbs, we saw a large flush of both native and exotic forbs in the year following prescribed fires, with few other changes in seedbank germination (Table 2). There was a significant increase ($p<0.001$) in native forb germinant response one year following spring fires. In burned plots there were 1607 seeds germinated per square meter, and in control plots there were 91 seeds germinated. There was also a significant increase ($p<0.001$) in germination of exotic forbs seeds between immediate postburn samples, and those taken one year following treatments for both spring fire, fall fires, and control plots. This is almost entirely attributed to a large number of *Draba verna* seedlings in both burn and control plots in the year following fire. Immediately following fire, there was a significant difference ($p<0.001$) in germination of native bunchgrasses between spring burn (6 germinants/m²) and control plots (28 germinants/m²). There were no significant differences between fire and control plots for *B. tectorum* or native shrub germination (Table 2).

At the site characterized by encroachment of western juniper with a heavy dominance of shrubs (Merrill Caves), spring fires caused significant declines in the germinant density of native bunchgrasses and exotic forbs (Table 3). There was a significant difference in density of native bunchgrasses ($p=0.03$) between spring fire (7 germinants/m²) and control plots (78 germinants/m²). Also immediately following spring fires, there was a significant difference ($p=0.01$) in exotic forb density between spring burn (285 germinants/m²) and control plots (1058 germinants/m²). No comparable fire effects were seen following fall fires. There were no significant differences between groups for any of the other groups examined (*B. tectorum*, native forbs, or native shrubs) immediately following prescribed fire. Because the spring burns at this site did not occur until one year later than at Gillems Camp or Fleener Chimneys, we do not have any one year post fire recovery data for this site.

Discussion

The immediate post-fire response of the soil seedbank must be interpreted cautiously. Seeds in the litter, on the soil surface, or attached to flowering stalks are likely killed during fires when they are exposed to temperatures greater than 100° C (Baskin and Baskin 1998), resulting in low germination the first growing season following fire. However, there was a very resilient response of *B. tectorum*, where there were many individuals with few seeds produced in unburned areas, and few individual plants following burns, but each produced abundant crops of seeds. This density dependant reproductive strategy likely accounts for the increase in cheatgrass germination one year following fire. Following burns from 1975 to 1978, in the northern, cheatgrass dominated areas of Lava Beds National Monument, Olson et al (1980) found no significant change in *B. tectorum* cover as compared to controls, but found a significant reduction in viable *B. tectorum* seeds (1980). Exotic forbs have been documented to briefly dominate a site

following disturbance (Bunting 2002), but forb richness tends to then increase in the post-burn recovery period.

Seed sources of native species also reestablish quickly following fire. Sapsis found that by the second post-fire year in sagebrush habitats at John Day Fossil Beds, numbers of *P. spicata* and *Festuca idahoensis* seed culms had returned to their preburn levels (1990). While we saw few increases in native species the year following prescribed burns, we saw an increase in reproductive culms in native bunchgrass species, demonstrating the resilience of those species to fire (Ellsworth 2006). Wroblesky and Kauffman found increases in reproductive structures (flowers, racemes, umbels) in native forb species in the year following prescribed burns in *Artemisia tridentata* ssp. *wyomingensis* habitats at Hart Mountain Wildlife Refuge (2003). In species composition studies at Lava Beds National Monument, we found a reduction in woody plant cover, but few changes in herbaceous vegetation in either native or exotic dominated communities, indicating that the existing vegetation on a site is a good predictor of the vegetation that will be present in the seedbank and in the community composition following fire (Ellsworth 2006).

In the initial years after removal of grazing, studies conducted at Lava Beds National Monument showed that the high cheatgrass seed load inhibited the establishment of native bunchgrasses (Olson et al 1980; Martin et al 1980; Erhard 1980). However, passive restoration (livestock exclusion) and the re-introduction of fire into the National Monument have resulted in an increase in native flora when compared to these previous studies (Ellsworth 2006).

The increase in native forb germination following spring burns at Fleener Chimneys mirrors the response that was evident in the field a year after burns. The increased nitrogen availability at this site likely contributed to the flush of annual native forbs measured (Wilson pers comm.) and is probably a transitory fire effect. The decrease in native bunchgrass seed germination seen immediately following spring burns at both Fleener Chimneys and Merrill Caves may be due to the high intensity and severity of the spring fires. Because these communities have healthy, intact bunchgrass components, with a demonstrated ability to maintain or increase reproductive effort (Sapsis 1980; Ellsworth 2006), there will be adequate seed source for native bunchgrasses to germinate and flourish in the post-fire environment. With a decreased litter layer, there are more opportunities for seeds to become established, facilitating the postburn transition to an herbaceous community.

Juniper and shrub mortality will largely determine the regeneration response of the understory in juniper dominated sites. At Merrill Caves, the increase in woody vegetation that occurred in the years preceding the prescribed fire of this study at this site likely led to a decline in forb species in the understory, thick sage and bitterbrush covers, and an increasingly closed canopy. Almost half of the juniper individuals in both spring and fall fires were killed by the burn treatments (Ellsworth 2006), which results in increases of available water and nutrients for understory vegetation, light availability, and microsites for seed germination and seedling establishment.

Sagebrush systems of the Great Basin are composed of plants which display adaptations to a regime of frequent fire. Some perennial forbs and shrubs resprout from belowground growth points (*Tetradymia canescens*, *Crepis acuminata*), bunchgrasses display fire-enhanced flowering (*Pseudoroegneria spicata*, *Elymus elymoides*), while many annual species exist following fire due to their persistence in the seedbank. Condition of the site prior to the burns largely determined the composition of the soil seedbank. Even in sites dominated by *B. tectorum*, native species maintained a presence in the seedbank. The post-fire environment provides an opportunity for them to become re-established. Sites which are dominated by native plants had few significant differences in seedbank germination between control and treatment plots.

Season of burn had no lasting impact on the germination response of the seedbank. While higher intensity spring burns tended to reduce seedbank populations immediately following fires, these effects were no longer seen one year after the burns. This shows that these

plants are accustomed to a regime of frequent fire and can maintain a similar herbaceous vegetation composition following a fire event. Based on these results, season of burn is less of a management concern than is the need to restore and maintain the natural fire return interval.

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Table 1: Seeds germinated per square meter at Gillems Camp. Lowercase letters represent statistically distinct ($p < 0.05$) groups.

germinants per square meter		cheatgrass		native forbs		exotic forbs		native shrubs		native bunchgrasses	
		mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Gillems Postfire	spring	832.00 (a)	159.17	31.00 (a)	12.59	30.00 (a)	13.51	0.00 (a)	0.00	1.00 (a)	1.00
	control	9015.50 (b)	857.87	90.25 (a)	71.97	74.75 (a)	19.91	0.00 (a)	0.00	5.00 (a)	3.16
	fall	965.00 (a)	221.40	1346.00 (b)	292.80	32.25 (a)	19.95	2.00 (a)	2.00	5.25 (a)	2.75
	control	2200.00 (a,c)	504.49	1225.00 (b)	248.18	14.00 (a)	7.97	15.00 (a)	8.37	7.00 (a)	2.55
Gillems Recovery	spring	8017.00 (b)	1170.18	14.00 (a)	10.65	1818.00 (b,c)	334.13	0.00 (a)	0.00	4.00 (a)	1.87
	control	5132.00 (b,c)	1046.19	8.00 (a)	2.00	4069.00 (c)	711.00	0.00 (a)	0.00	29.00 (a)	15.52
	fall	4615.00 (b,c)	1066.81	267.00 (a)	120.98	2919.00 (b,c)	810.95	0.00 (a)	0.00	11.00 (a)	3.67
	control	1887.00 (a,c)	288.12	140.00 (a)	50.17	1225.00 (b)	337.10	0.00 (a)	0.00	10.00 (a)	4.18

Table 2: Seeds germinated per square meter at Fleener Chimneys. Lowercase letters represent statistically distinct ($p < 0.05$) groups.

germinants per square meter		cheatgrass		native forbs		exotic forbs		native shrubs		native bunchgrasses	
		mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Fleener Postfire	spring	79.00 (a)	46.83	257.00 (a)	42.83	3.00 (a)	2.00	20.00 (a)	7.07	6.00 (a)	4.85
	control	523.00 (a)	205.54	114.00 (a)	51.17	4.00 (a)	2.92	10.00 (a)	3.54	28.00 (b)	8.46
	fall	93.00 (a)	40.52	454.00 (a)	88.18	0.00 (a)	0.00	48.00 (a)	14.63	3.00 (a)	1.22
	control	136.00 (a)	45.84	680.00 (a,b)	252.10	2.00 (a)	2.00	38.00 (a)	8.46	2.00 (a)	1.22
Fleener Recovery	spring	245.00 (a)	136.40	1607.00 (b)	502.99	3209.00 (b)	997.48	11.00 (a)	5.57	85.00 (b)	20.68
	control	485.00 (a)	209.42	91.00 (a)	25.02	2696.00 (b)	680.90	52.50 (a)	21.15	65.00 (b)	13.04
	fall	309.00 (a)	118.43	797.00 (a,b)	260.74	482.00 (c)	160.30	13.00 (a)	6.63	12.00 (a)	3.39
	control	298.25 (a)	124.62	438.25 (a)	152.42	597.25 (c)	330.43	21.75 (a)	7.50	28.00 (b)	28.00

Table 3: Seeds germinated per square meter at Merrill Caves. Lowercase letters represent statistically distinct ($p < 0.05$) groups.

germinants per square meter		cheatgrass		native forbs		exotic forbs		native shrubs		native bunchgrasses	
		mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Merrill Postfire	spring	27.00 (a)	16.02	182.00 (a)	63.18	285.00 (a)	145.76	4.00 (a)	4.00	7.00 (a)	4.90
	control	810.00 (a)	280.44	349.00 (a)	144.66	1058.00 (b)	342.81	12.00 (a,b)	10.79	78.00 (b)	26.15
	fall	199.25 (a)	100.44	274.50 (a)	69.52	0.00 (a)	0.00	37.00 (a,b)	8.46	8.00 (a)	3.39
	control	222.50 (a)	39.89	391.00 (a)	132.19	0.00 (a)	0.00	53.50 (b)	19.68	2.00 (a)	1.22
Merrill Recovery	fall	355.00 (a)	121.75	912.00 (a)	351.96	142.00 (a)	93.01	12.00 (a,b)	8.46	3.00 (a)	2.00
	control	267.00 (a)	110.47	522.00 (a)	184.04	122.00 (a)	43.03	8.00 (a,b)	4.64	10.00 (a)	7.75

Chapter 3: Effects of Spring and Fall Prescribed Fire on Native Bunchgrass and Mariposa Lily Density and Reproductive Effort in Mountain Big Sagebrush Ecosystems at Lava Beds National Monument

Lisa M. Ellsworth and J. Boone Kauffman

Abstract

Much of the current research surrounding the reintroduction of fire in sagebrush dominated ecosystems has focused on a persistent myth that fire in sagebrush systems results in a loss of native flora and a trend toward dominance by exotic annuals. However, fire was historically the dominant disturbance throughout the sagebrush steppe and the plant communities found in these systems show a variety of adaptations to a frequent fire regime. In this paper we examined the reproductive and density responses of three native bunchgrasses (*Pseudoroegneria spicata*, *Achnatherum therberianum*, and *Elymus elymoides*) as well as one native forb, *Calochortus macrocarpus*, to both spring and fall prescribed fire in three sagebrush systems (native dominated, cheatgrass dominated, and juniper encroachment sites). Density responses of the bunchgrass species were variable and inconclusive only one year following burns, underscoring a need for longer term monitoring. No significant increase in flowering was seen in *C. macrocarpus* one year following spring or fall burns at the native dominated sites or following fall burns at juniper-encroachment sites. Reproductive effort increased in all bunchgrass species following both spring and fall fires in all communities studied, demonstrating that maintaining the natural disturbance regime in these fire-adapted ecosystems is beneficial to the native biota.

Introduction

The landscapes of the Great Basin have undergone dramatic changes in vegetation structure and composition largely due to anthropogenic land use alterations. Prior to European settlement, fire was a common disturbance in rangeland systems. Lightning was seasonally common, and fires were used by Native American peoples to enhance desirable vegetation, for wildlife habitat management, and for pest control (Shinn 1980; Griffin 2002). Immediately following settlement by early homesteaders, increased ignitions combined with abusive grazing practices resulted in degraded rangelands. In response to these practices, policies were established by the early 1900's requiring suppression of fire (Clark and Starkey 1990). More than a century of fire suppression has resulted in an increase in fuels, encroachment of juniper into grasslands and shrub steppes, and a reduction of native bunchgrasses and forbs. Overgrazing by domestic livestock has increased susceptibility to invasion by exotic species.

The knowledge that plant communities have evolved in response to fire in these ecosystems has often been neglected or overlooked (Champlin 1982). Historically, fires were frequent, stand replacing fires in the sagebrush grasslands of the Great Basin, occurring at intervals of less than 30 years in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) ecosystems (Miller et al 2000). Natural fire return intervals in these systems have been altered by fire suppression, livestock grazing, and the introduction of exotic species. The Great Basin has seen two different shifts in structure related to changes in fire regimes. Low-elevation areas which were overgrazed by domestic livestock or otherwise disturbed became susceptible to invasion and dominance by exotic grasses, whereas many higher elevation sites have seen an expansion of western juniper (*Juniperus occidentalis*) into the shrub steppe.

Invasion by a non-native species can be one of the greatest threats to ecosystem function and species diversity (Vitousek 1990). Cheatgrass (*Bromus tectorum*) became such a threat to the rangelands of the western United States just after the turn of the 20th century. As described by

D'Antonio and Vitousek (1992), disturbance and alien invasion begin a cycle of positive feedbacks between grass and fire. Cheatgrass was unintentionally introduced into the United States in the early 1900's inside bags of contaminated grain (Young and Clements 2004). It has since become the most widespread annual in the semi-arid landscapes of the western United States (Mack 1981). The combination of land degradation due to domestic livestock grazing, human population expansion, and increases in exotic annuals, has resulted in a decrease of native species in many areas of the sagebrush steppe ecosystem. The introduction of cheatgrass has greatly increased the potential for fires in this environment because its phenology of early dormancy provides a dry fuel source and lengthens the fire season (Payson et al. 2000) by increasing dry fuels much earlier in the season. Increased human settlements, roads, and railways added to the reduction in fire interval by providing sources of ignition and making it even susceptible to exotic invasion.

Fire regimes in other areas of the Great Basin have been lengthened by fire suppression and domestic livestock grazing. Prior to Euro-American settlement, expansion of western juniper (*Juniperus occidentalis*) is believed to have been limited by fire, drought, and competition with grasses (Kilgore 1981). The introduction of domestic grazing animals in these areas decreased the amount of fine fuels which are necessary for fire spread (Kauffman and Sapsis 1989), thereby reducing fire intensity and frequency. Fire exclusion by suppression and reduction of fine fuels from the mountain big sagebrush ecosystem has contributed to the occupation of western juniper because young junipers (<30 years) do not often survive fire. The current rate of western juniper encroachment onto sites formerly occupied by bunchgrasses and sagebrush has exceeded rates of expansion from the 5000 years preceding (Miller and Wigand 1994). Restoration in this system may require a reintroduction of fire as a necessary means for the maintenance of the native plant communities and a return to a properly functioning ecosystem.

Plant communities in the Great Basin have evolved in response to a natural fire regime, and have developed strategies to benefit from the resulting pattern of disturbance (Kauffman et al 1997, Pendergrass et al 1999, Wrobley and Kauffman 2002). Re-introduction of fire into systems where it has been excluded may benefit these plant communities. Increased flowering has been observed following fire in grasses of high deserts east of the Oregon Cascades (Kauffman 1990). Champlin (1983) observed significant increases in basal area of bluebunch wheatgrass (*Pseudoroegneria spicata*) and Sandberg's bluegrass (*Poa sandbergii*) two years after burning in mountain big sagebrush (*Artemisia tridentata vaseyana*) communities at Lava Beds National Monument. Conversely, he found decreases in basal area of Thurber's needlegrass (*Achnatherum thurberianum*) and Idaho fescue (*Festuca idahoensis*) following fire. Sapsis (1990) found that both fall and spring burning reduced the frequency of annual grasses in basin big sagebrush-bluebunch wheatgrass communities at John Day Fossil Beds National Monument, while having no effect on the frequency of perennial grasses. Conversely, Wright and Klemmedson (1965) found that early summer burns only provided a temporary setback for cheatgrass, and harmed perennial grass species.

In this study, I seek to answer the following research questions: 1) Is there a change in reproductive effort of three bunchgrass species and one native forb following prescribed fire at the Lava Beds National Monument? 2) Is there a differential effect of prescribed fire on reproductive effort of these species due to the season of burn? 3) Is the response of these species to fire different in study areas with a different land use history and plant composition?

I hypothesize that 1) Reproductive effort will increase in bunchgrass and forb species following prescribed fire. 2) There will be a differential response due to season of burn. Plants burned in the fall will have higher reproductive effort than those burned in the spring following fires because they were not burned during the active growing season. 3) Sites in good condition and dominated by native plants will demonstrate a greater reproductive effort than sites in which the plant communities have been altered by fire suppression and invasion of exotic plants.

Methods

This research was conducted at Lava Beds National Monument, California, 77 Km southeast of Klamath Falls, Oregon. This area ranges in elevation from 1228 meters along the shore of Tule Lake in the northeast to 1725 meters at the southwest corner. (Erhard 1979). The climate is cool and semi-arid, with a microclimate and precipitation gradient that increases with elevation. Average annual precipitation is 39 cm (Miller et. al 2003) and the average temperature ranges from -1° C in January to 20° C in July (Erhard 1979). Most fires occurs from July to September, when dry thunderstorms often coincide with high temperatures and low fuel moisture contents. The geology of the monument is unique, with basaltic lava flows and cinder cones scattered across the landscape. The monument is located on the north face of Medicine Lake shield volcano, which has erupted periodically over the last 500,000 years, and most recently erupted approximately 1100 years BP. Soils are of volcanic origin, shallow with basaltic outcrops (Ehrard 1979). The study areas were dominated by mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana*) in the overstory, and *Pseudoroegneria spicata* and *Achnatherum therberianum* in the understory. Fleener Chimneys is dominated by native perennial grasses and forbs, with predominately sagebrush and bitterbrush in the overstory. Merrill Caves is characterized by encroachment by western juniper in the overstory, with mostly native forbs and bunchgrasses in the herbaceous layer. Gillems Camp has a history of degradation by domestic livestock grazing, and is dominated by exotics, with a high percent cover of cheatgrass, and little woody vegetation

Experimental Design and Bunchgrass Sampling

The experiment was established as a randomized complete block design. Five experimental blocks were established at each of three sites (Gillems Camp, Fleener Chimneys, and Merrill Caves) at the Lava Beds National Monument. Each block contains three sub-blocks (plots) in which spring and fall prescribed fire treatments as well as unburned controls were applied. For burn treatments, the area that was burned was at least 5 m wider than the plot in every direction. Each block was established with a steel fence post marking corners and documented with a GPS unit. Experimental units were all located within mountain big sagebrush shrublands with an understory of perennial bunchgrass plants (*Pseudoroegneria spicata*, *Achnatherum therberianum*, *Elymus elymoides*). The different sites represent the following ecological conditions: 1) Merrill Caves: Fire exclusion with significant juniper encroachment and minor exotic grass invasion; 2) Fleener Chimneys: Fire exclusion with little juniper encroachment or exotic grass invasion; 3) Gillems Camp: Increased fire frequency with a dominance of invaders and exotic annuals.

Spring burns at Fleener Chimneys and Gillems Camp were conducted in June, 2003. Due to weather constraints during 2003, spring burns at Merrill Caves were not conducted until June, 2004. Fall burns at all sites took place in November, 2003. Although environmental conditions (temperature, relative humidity) were warmer and drier during the spring burns than in the fall burns (Appendix 1), it did not result in significantly different fire behavior measures. Both spring and fall fires burned in a mosaic pattern, burning some areas and leaving others unburned. As temperatures increased and relative humidity decreased throughout the days of the burns, rate of spread, flame lengths, and fireline intensity increased.

Bunchgrass species which were studied to quantify reproductive effort following fire include the most abundant native bunchgrasses (*Pseudoroegneria spicata*, *Elymus elymoides*, and *Achnatherum therberianum*) and one forb, Mariposa lily (*Calochortus macrocarpus*). In burn and control plots, at least 15 individuals of each selected species were measured as they were encountered within a 5-m wide transect located adjacent to a permanent transect in each burn unit. Length of the transect was as long as necessary to encounter 15 individuals. At least 50 individuals of each species were measured in each burn -treatment combination at each site. In

burned units, only individuals which showed evidence of the burn were counted. For each selected individual I counted the number of flowering culms (bunchgrasses) and flowers (forbs) per plant. These measurements were taken during peak flowering of plants (late in the growing season). Measurements were made each year (immediately preceding spring fires and one year following fire).

Density of bunchgrass individuals was calculated from microplot measurements along five permanent transects in each unit. Each transect contained two 30 x 60 cm microplots (n=50 for each treatment). Measurements of bunchgrass density were made during the growing season. Spring units were measured in July, 2002 (prefire) and June and July, 2004 (postfire), with the exception of Merrill Caves, which had no postfire measurements taken. Fall and Control units were measured in June and July, 2003 (prefire) and in June and July, 2004 (postfire).

Analysis

Bunchgrass species

All statistical analyses were accomplished using S+ 6.1 Academic Site Edition (Insightful Corp). In order to determine whether there was a treatment effect within sites, Analysis of Variance (Ramsay and Schafer, 2002) was used at Fleener Chimneys and Gillems Camp to determine whether there was a significant difference between spring burn, fall burn, and control plots. A multiple comparison test (Tukey-Kramer) was used if the F-test for treatment effect was significant at the $p < .05$ significance level. Because there is no post fire data for spring burns at Merrill Caves, a two sample t-test was used to determine whether there was a significant difference between fall burn and control plots. In sites where there is no spring prefire data for a species, a two sample t-test was used to determine whether there was a difference in percent change between fall and control plots.

Analysis of Variance among all site/treatment combinations was used to determine whether there was a difference in treatment effect (as evidenced by number of reproductive culms per individual in fire and control treatments) between sites following prescribed fire. A multiple comparison test (Tukey-Kramer) was used if the F-test was significant at the $p < .05$ significance level to distinguish which site/treatment combinations were significantly different from one another.

Mariposa lily

Analysis of Variance was used to test whether there was a significant difference in number of flowers of *Calochortus macrocarpus* following spring and fall prescribed fire treatments between treatment and control plots within a site. Samples at Gillems Camp were excluded from the analysis due to insufficient sample sizes. An additional Analysis of Variance including all site/treatment combinations was examined to determine whether any significant difference in percent change could be attributed to a treatment effect or to site differences.

Bunchgrass density

To determine whether there was a difference in bunchgrass density in different site/treatment combinations, Analysis of Variance was used to test across sites and examine any interaction between fire treatment and site history. Additionally, to determine whether there was a treatment effect within a site, ANOVA was also used to reveal differences between control and spring and fall burned plots.

Results

Bunchgrass Density

Fire did not result in a significant change in bunchgrass density in either spring or fall burn treatments (Table 1). There was no significant differences between either within site comparisons (treatment vs. control, prefire vs. postfire) or across site comparisons (all site/treatment combinations included in analysis). While none of these results show a statistically significant difference, there is suggestion of some trends in the results. Densities of *E. elymoides* and *A. therberianum* decreased in all spring (*E. elymoides*: Gillems, $p=0.49$; Fleener, $p=0.50$; *A. therberianum*: Gillems, $p=0.15$; Fleener, $p=0.57$) and fall (*E. elymoides*: Gillems, $p=0.46$; Fleener, $p=0.50$; Merrill, $p=0.79$; *A. therberianum*: Gillems, $p=0.15$; Fleener, $p=0.57$; Merrill, $p=0.77$) treatment plots, as well as in unburned controls. Initial post-fire densities, however, may not be indicative of a longer term fire effect.

Reproductive Response to Prescribed Fire

Bunchgrass species:

At the site dominated by exotic annuals (Gillems Camp), there was no significant difference in reproductive effort (as evidenced by average number of flowering culms per plant) in *E. elymoides* ($p=0.13$) or *A. therberianum* ($p=0.43$). A difference in fire enhanced flowering between preburn and postburn plots was seen in *P. spicata* at this site ($p=0.05$) following fall prescribed fire, however postfire comparisons between burn and control plots were not significant ($p=0.09$).

In areas of good ecological condition (Fleener Chimneys), there was an overall increase in reproductive effort of all studied bunchgrass species (Table 2). There was a significant difference (increase following fire from 0.85 to 9.13) in number of flowering culms per plant of *P. spicata* in fall postfire plots when compared to both prefire plots and control plots ($p=0.03$ for fall prefire vs. fall postfire; $p=0.05$ for fall postfire vs. control postfire). There was no significant difference in reproductive response following fire in *E. elymoides* either within years between treatments ($p=0.11$), or between prefire and postfire years ($p=0.23$). *A. therberianum* reproductive effort was significantly different between fall prefire plots and fall postfire plots, showing an increase of 0.02 to 3.69 flowering culms per individual ($p=0.01$). However, there was no significant difference in this species between control and burn plots in the year following fire ($p=0.08$).

At Merrill Caves, which is characterized by expansion of western juniper, there was fire enhanced flowering seen following fall fires in every species studied. As spring fires were burned a year late, there is not data to test whether this same trend holds for spring burns. Significant differences ($p<0.001$) were found between postfire fall and control plots in *P. spicata* response, as well as a significant difference ($p=0.05$) between prefire and postfire plots within the fall burn treatments. Also significant ($p=0.05$) was the difference between fall and control treatments in *A. therberianum* and the difference ($p=0.03$) between prefire and postfire plots. *E. elymoides* response in fall postfire plots was significantly different ($p=0.05$) from prefire plots, although not significantly different from controls ($p=0.10$). No data were collected following spring burn treatments at this site due to the difference in burning years.

Mariposa lily:

Among examined individuals of the Mariposa lily (*Calochortus macrocarpus*), I found no significant difference in reproductive response (measured in average number of flowers per plant) following fire treatments at Fleener Chimneys ($p=0.96$) or at Merrill Caves ($p=0.17$) (Table 3). At Gillems Camp there were too few individuals to provide an adequate sample size, and this site was thus removed from the analysis. When all site/treatment combinations were analyzed together, there were no combinations that were significantly different ($p=0.38$). These results

indicate that there is no evidence of fire enhanced flowering of *Calochortus macrocarpus* one year following fire, nor is there evidence of a difference in flowering due to site.

Discussion

Fire in the sagebrush ecosystem functions to structurally to decrease woody vegetation and shift the plant community towards an herbaceous, grass-dominated state. In the absence of shrub and juniper cover, grasses and forbs are able to utilize available nutrient resources and colonize microsites previously occupied by woody species. While fire can stimulate vegetative growth of bunchgrass species (Sapsis, 1990), it has also been shown to enhance sexual reproduction (Kauffman and Sapsis 1989), and to increase microsites for seed establishment by the removal of surface litter and overstory competition.

Gillems Camp

The interactions of degraded landscapes, altered fire regimes, and invasive species make it difficult to predict the potential for recovery in cheatgrass dominated landscapes. Invasive plants have been shown to first cause altered fire regimes by changing fuel conditions and then flourish under the new conditions they create (Brooks et. al. 2004). While the reintroduction of the natural fire regime is critical to the restoration of the sagebrush ecosystem, in low-precipitation areas that have been degraded by anthropogenic disturbance, it is difficult to predict the role that fire will play in the recovery of these systems. The removal of sheep and cattle grazing within the National Monument in 1974 started a trend toward reestablishment of native plants in the system, decreasing the pattern of cheatgrass invasion that was evident in the late 1970's (Erhard 1979). While the abundance of native plants has increased, there is still a dominance of invasive plants such as *Bromus tectorum* and *Sisymbrium altissimum* at Gillems Camp. Prescribed burning in these areas can shift the competitive advantage toward native plant establishment immediately following fires due to the nutrient pulses and increased microsites, as long as there is a sufficient native seed source.

While the variability of density response to fire treatments was pronounced in all studied bunchgrass species, fire did not result in a significant mortality of bunchgrass species when compared to unburned control.. This large range of variability may be attributed to the mosaic nature of the burn; some areas may have increased in density due to a nutrient pulse following burn treatment coupled with a decrease in surface litter, while other areas remained unburned, and still others burned with such high severity that seedling establishment one year following the fire treatments was decreased.

Contrary to the variability seen in density response following both spring and fall burn treatments, every studied bunchgrass species consistently decreased in percent cover following both spring and fall fire treatments, while in control plots there was an increase in the cover of *E. elymoides* and *P. spicata* (Ellsworth and Kauffman, 2006). These results indicate that while many established individuals likely decrease in size due to consumption of aboveground biomass or were killed by the fire treatments, there were a large number of seedlings established in the burn treatments.

Previous studies (Sapsis 1990) have shown that there is more damage sustained to individual bunchgrasses which are burned when they are metabolically active and more vulnerable to injury by fire. When above-ground growing points are subjected to high temperatures, there is a higher incidence of mortality than would be expected if the plant was burned following the active growing season. Bunchgrass species may exhibit lower reproductive effort following early season fires than their late season counterparts because most energy early in the season has gone into vegetative growth. These physiological responses of an individual plant to fire were observed only in *Achnatherum therberianum* results at Gillems Camp.

Because of the continuous fuel loads due to an abundance of cheatgrass, high intensity fires at this site were more damaging to this thin-bladed species, resulting in a lower reproductive effort in fire-damaged individuals following spring burns when compared to both individuals burned in the fall and unburned individuals. Spring fires though, have been shown (Wills 2000, Moyes et.al. 2005) to be more effective than their later season counterparts at reducing annual grass cover due to timing the burn before annual grass seed has set, thus diminishing the seedbank. While these results demonstrate the fire adaptations that many bunchgrass species in the shrub steppe have evolved, it is necessary to continue monitoring these communities, as one post fire year is not long enough to estimate the trajectory of recovery following the prescribed burn.

Fleener Chimneys

In areas of the sagebrush steppe which remain fairly pristine, we predicted that native plants would respond positively to the reintroduction of fire at its natural return interval. A shift in composition from shrub-dominated communities to herbaceous dominance occurs throughout the sagebrush-bunchgrass ecosystem following fire. Prior to fire, the Fleener Chimneys site remained dominated by native shrubs, perennial bunchgrasses, and native forbs, and had not suffered from significant encroachment by western juniper or invasion by cheatgrass. Because these plants are adapted to a regime of frequent, low-intensity fires, the positive response of bunchgrasses at this site suggests a positive functional role for prescribed fires to maintain the natural fire return interval. This maintains the dynamics of the native plant associations. The increase in reproductive effort of all studied bunchgrass species that we saw at this site demonstrates the response of these fire-adapted species. It is likely that the pulse of nutrients present following fire resulted in enhanced flowering. The variability in density response that was seen at this site, as well as the change in reproductive effort seen in control plots demonstrates that annual variability, as well as disturbance, can have an effect on the reproductive output of these species.

While our results show no significant change in density for studied species, this may largely be a transient immediate post-fire effect, and warrants further monitoring. Other studies have shown that in relatively intact, native bunchgrass communities, fire resulted in an immediate reduction in density, followed by an increase in subsequent years, largely due to seedling success in a post-burn environment (Sapsis 1990, Marty et al 2005). In a remnant population of California native bunchgrass *Nassella pulchra*, Marty et. al. found an initial 10% decrease in density immediately following burn, and 2 years later, seedling density was 100% higher in burned plots than in the unburned controls (2005). Sapsis (1990) also found that increased seedling establishment of *P. spicata* and *F. idahoensis* following prescribed burning in sagebrush communities was characteristic of native bunchgrass (*P. spicata*, *F. idahoensis*) communities at John Day Fossil Beds National Monument, Oregon.

We found very few significant differences in vegetation response at this site which can be attributed to season of burn. Both spring and fall fires resulted in an increase in reproductive effort in studied species, and there was an equally variable bunchgrass density response. Weather during spring burns was warmer and drier, resulting in lower fine fuel moistures, but the patchy vegetation structure prevented the fire from spreading quickly and kept fireline intensities relatively low. In areas where native vegetation remains dominant, and the fire regime is intact, season of burn may be less of a managerial concern than the need for maintenance of the fire return interval. Initial post-fire changes in response of all studied bunchgrass species indicate that they are fire adapted species and are likely to survive and benefit from both spring and fall fires.

Merrill Caves

Livestock grazing beginning in the late nineteenth century altered the fire regime within the park, removed much of the fine fuels that were necessary to carry fire, and damaged the native bunchgrasses and forbs. With less frequent fire events, western juniper (*Juniperus occidentalis*) greatly increased its distribution and density in this sagebrush steppe habitat, and changed the functioning of the plant communities that it occupies (Miller and Rose 1999; Miller and Tausch 2001). As juniper increased, it altered water and nutrient availability, and shrubs, forbs, and bunchgrasses decline, shifting the structure of the community outside of its historical range of variability (Miller et al 2000).

With the reintroduction of fire into juniper-dominated landscapes, we expected to see a shift back towards a larger herbaceous plant component. Our results show that the native bunchgrasses in this community increased more in reproductive effort following fire than in the unburned controls. We attribute this to resources (water, nutrients, light availability) that were released from decreased juniper trees and shrubs as well as the nutrient pulse seen following fire. Potential for germination of the increased seed source is expected to increase as more light and belowground resources become available for herbs, grasses, and shrubs (Belsky 1996).

Miller et al (2000) has shown that with increasing juniper dominance, there is a decrease in both species diversity and herbaceous cover coupled with an increase in bare ground. While prescribed fire treatments alone here resulted in increases in bunchgrass reproductive effort in the first year following fire, previous work (Rasmussen et al 1986, Ansley and Rasmussen 2005) suggests that in some cases mechanical treatment may be necessary prior to fire to effectively manage juniper competition. Further monitoring of this site would be beneficial to determine how long a positive fire effect is evident in this system.

There is a persistent myth in fire ecology that fire in the sagebrush steppe serves to degrade the native plant communities and increase dominance of invasive grasses. Our results show that native grass species can survive fire and even benefit from the increased nutrients and decreased litter and canopy cover that is present in postfire environments. While a need for longer term monitoring following prescribed fire is imperative, initial post fire response suggests that fire adapted species will respond positively to prescribed fire when applied at the natural range of variability.

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Table 1: There was no significant change in bunchgrass density in response to spring and fall prescribed burn treatments at Lava Beds National Monument.

	Gillems Camp Bunchgrass Density Response (individuals per square meter)							
	<i>Elymus elymoides</i>		<i>Pseudoroegneria spicata</i>		<i>Poa sandbergii</i>		<i>Achnatherum thurbarianum</i>	
	mean	SE	mean	SE	mean	SE	mean	SE
spring prefire	0.22 (a)	0.14	1.00 (a)	0.32	7.11 (a)	2.07	6.89 (a)	3.92
spring postfire	0.11 (a)	0.11	0.56 (a)	0.25	7.56 (a)	3.01	0.78 (a)	0.52
fall prefire	1.00 (a)	0.54	0.44 (a)	0.21	5.89 (a)	1.29	2.00 (a)	0.67
fall postfire	0.56 (a)	0.25	0.89 (a)	0.89	5.56 (a)	1.04	1.89 (a)	0.97
control prefire	1.33 (a)	0.94	1.89 (a)	0.42	6.00 (a)	1.40	1.33 (a)	0.65
control postfire	1.00 (a)	0.54	0.11 (a)	0.11	5.78 (a)	1.42	0.89 (a)	0.48
	Fleener Chimneys Bunchgrass Density Response (individuals per square meter)							
	<i>Elymus elymoides</i>		<i>Pseudoroegneria spicata</i>		<i>Poa sandbergii</i>		<i>Achnatherum thurbarianum</i>	
	mean	SE	mean	SE	mean	SE	mean	SE
spring prefire	1.33 (a)	0.45	3.89 (a)	1.08	5.00 (a)	1.35	1.56 (a)	0.81
spring postfire	0.89 (a)	0.57	1.89 (a)	0.85	7.89 (a)	2.05	1.33 (a)	0.62
fall prefire	2.11 (a)	0.77	2.56 (a)	0.82	9.56 (a)	3.33	2.33 (a)	0.32
fall postfire	1.33 (a)	0.52	1.89 (a)	0.45	9.44 (a)	3.25	1.67 (a)	0.43
control prefire	1.33 (a)	0.45	1.67 (a)	0.58	4.78 (a)	1.25	2.67 (a)	0.64
control postfire	0.67 (a)	0.21	2.67 (a)	0.69	6.78 (a)	2.68	2.56 (a)	0.85
	Merrill Caves Bunchgrass Density Response (individuals per square meter)							
	<i>Elymus elymoides</i>		<i>Pseudoroegneria spicata</i>		<i>Poa sandbergii</i>		<i>Achnatherum thurbarianum</i>	
	mean	SE	mean	SE	mean	SE	mean	SE
fall prefire	1.44 (a)	0.65	2.22 (a)	0.43	6.67 (a)	2.29	2.67 (a)	0.81
fall postfire	1.00 (a)	0.54	3.78 (a)	1.07	6.56 (a)	1.57	1.22 (a)	0.54
control prefire	0.67 (a)	0.21	1.89 (a)	0.42	2.67 (a)	0.62	2.00 (a)	0.91
control postfire	0.55 (a)	0.18	1.11 (a)	0.47	5.22 (a)	1.15	1.56 (a)	0.64

Table 2: Bunchgrass reproductive effort following spring and fall fires at Lava Beds National Monument. Units are individuals per square meter. We saw increased numbers of reproductive culms per bunchgrass individual following spring and fall prescribed fire in sagebrush systems at Lava Beds National Monument.

Gillems Camp Bunchgrass Reproductive Response						
	<i>Elymus elemoides</i>		<i>Pseudoroegneria spicata</i>		<i>Achnatherum thurbarianum</i>	
	mean	SE	mean	SE	mean	SE
spring prefire	X	X	X	X	4.55 (a)	1.62
spring postfire	17.82 (a)	3.46	15.97 (a,b)	3.92	2.21 (a)	0.81
fall prefire	20.37 (a)	2.8	8.94 (a)	4.95	4.43 (a)	0.75
fall postfire	29.27 (a)	4.89	30.83 (b)	6.99	6.26 (a)	1.24
control prefire	43.56 (a)	21.43	9.04 (a)	2.30	5.71 (a)	2.41
control postfire	29.97 (a)	4.77	17.88 (a,b)	1.42	5.01 (a)	0.84
Fleener Chimneys Bunchgrass Reproductive Response						
	<i>Elymus elemoides</i>		<i>Pseudoroegneria spicata</i>		<i>Achnatherum thurbarianum</i>	
	mean	SE	mean	SE	mean	SE
spring prefire	3.91 (a)	0.47	X	X	1.76 (a,b)	0.38
spring postfire	8.10 (a)	2.38	1.80 (a)	0.63	2.26 (a,b)	0.88
fall prefire	3.00 (a)	0.51	0.85 (a)	0.33	0.02 (a)	0.29
fall postfire	4.87 (a)	0.68	9.13 (b)	3.14	3.69 (b)	0.47
control prefire	2.22 (a)	0.46	1.46 (a)	0.42	1.45 (a,b)	0.39
control postfire	3.40 (a)	0.54	1.97 (a)	0.84	1.49 (a,b)	0.51
Merrill Caves Bunchgrass Reproductive Response						
	<i>Elymus elemoides</i>		<i>Pseudoroegneria spicata</i>		<i>Achnatherum thurbarianum</i>	
	mean	SE	mean	SE	mean	SE
spring prefire	1.95 (a)	0.36	X	X	3.07 (a,b)	0.26
spring postfire	X	X	X	X	X	X
fall prefire	2.90 (a)	0.76	1.66 (a)	0.72	1.35 (a)	0.31
fall postfire	8.97 (b)	1.84	12.91 (b)	1.75	6.15 (b)	2.09
control prefire	1.81 (a)	0.53	1.97 (a)	0.89	1.12 (a)	0.34
control postfire	5.43 (a,b)	0.6	3.10 (a)	0.94	0.95 (a)	0.26

Table 3: Reproductive response of *Calochortus macrocarpus* to prescribed fire treatments. Units are individuals per square meter. Lowercase letters represent statistically significant groups.

	Fleener Chimneys		Merrill Caves	
	mean	SE	mean	SE
spring prefire	1.41 (a)	0.07	1.52 (a)	0.07
spring postfire	1.76 (a)	0.10	X	X
fall prefire	1.50 (a)	0.14	1.43 (a)	0.07
fall postfire	1.72 (a)	0.17	1.89 (a)	0.10
control prefire	1.85 (a)	0.04	1.69 (a)	0.08
control postfire	1.78 (a)	0.13	2.10 (a)	0.10

Chapter 4: Fuel Loads, Fire Behavior, Total Biomass and Consumption

J. Boone Kauffman, John Wilson, and Lisa M. Ellsworth

Introduction

The Great Basin big sagebrush (*Artemisia tridentata*) desert is the largest semiarid ecosystem in the western USA covering about 100 million ha (247 million acres) (Blaisdell et al. 1982). Even though the Great Basin is the largest land cover type in the lower 48 states of the USA, it remains among the least studied. This includes the natural role of fire across its varied landscapes and how land use, exotic plant invasions, and disruptions of fire regimes have affected ecosystem structure and function.

Natural fire regimes of big sagebrush dominated landscapes are generalized as short to moderate-return interval, stand-replacement fires. The mean fire-return interval (MFRI) is highly variable due to the wide variation of topography, climate and vegetation composition. Miller and Tausch (2001) and Wright and Bailey (1982) suggest that Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis*) has a MFRI of 50 to 100 years. In contrast, mountain big sage (*Artemisia tridentata* spp. *vaseyana*) is often ecotonal to ponderosa pine (*Pinus ponderosa*) forests. As these forests are known to have a fire regime of frequent low intensity surface fires (5-10 year MFRI) it is reasonable to assume that the fire-return interval in mountain big sage is similar (12-25 years; Miller et al. 1998; Miller and Tausch 2001). If true, then the biota of mountain big sagebrush ecosystems are likely adapted to frequent fires.

Fire is considered to be the most important natural disturbance that maintained the shrub steppe prior to Euroamerican settlement (West 1999, Kauffman and Sapsis 1989). There have been dramatic changes in the composition and structure of sagebrush dominated communities in the last 130 years and this change has largely been attributed to alteration in fire regimes, grazing by domestic livestock, climatic changes, and increases in atmospheric CO₂ (Miller and Tausch 2001). Areas formerly occupied by native bunchgrass and sagebrush/bunchgrass communities have been replaced by pinyon-juniper woodlands or exotic annual grasslands.

In the Great Basin there are two scenarios of fire regime change. In some areas the increased presence of human settlement (ignition sources) coupled with the invasion of highly flammable exotic annual grasses has greatly increased the fire frequency in landscapes. Cheatgrass (*Bromus tectorum*) is the most widespread annual in the Great Basin. Cheatgrass may extend the fire season in this ecosystem because it senesces earlier than perennials and may be susceptible to fire 1-2 months longer in the fall (Payson et al. 2000).

The second scenario of altered fire regimes comes from fire exclusion. Miller and Rose (1999) reported that fire occurrences in South-central Oregon were significantly reduced after the introduction of livestock. The rate of western juniper (*Juniperus occidentalis*) encroachment onto sites formerly occupied by grasslands and sagebrush steppe in the past 130 years has been unprecedented in the last 5000 years (Miller and Wigand 1994).

Restoration of fire intervals to the natural range of variability is needed for the restoration of native ecosystem structure and function in this ecosystem. The difficulty lies in the knowledge of under what circumstances are fires (as well as wildland fires for resource benefits) beneficial to the maintenance and restoration of Sagebrush-dominated ecosystems and under what circumstances do they degrade biotic composition. A basic need of land managers is better information on range and variation of fuel loads, and the fire behavior among the sagebrush-dominated communities during differing seasons of burn. We sampled fuels and fire behavior of three mountain big sagebrush ecosystems with dramatically different species compositions, structures and land use histories. The objectives of this study addressed the following research questions.

- What are the effects of altering fire regime and land use history on above ground biomass (fuel loads)?
- Do ecosystems in different ecological states (condition) differentially respond to prescribed fire in terms of fire behavior and biomass consumption?
- Do burns conducted at different seasons differentially affect the response of ecosystems to fire in terms of fire behavior and biomass consumption?

Methods

The study area was located at the Lava Beds National Monument, California. This was an ideal area for study because of the presence of a wide variety of Great Basin plant community stands in varying states of ecological condition (Erhard 1980). Some areas historically were subjected to high levels of livestock grazing and increased fire while other areas reflect decades of fire suppression but without a history of overgrazing. In addition, this landscape is representative of much of the sagebrush steppe of southeast Oregon, northwest Nevada, and Northeastern California.

All experimental sites were classified as mountain big sage/bluebunch wheatgrass - Thurber's needlegrass habitat types but with different land use histories and hence, current species composition and structure (Table 1). These three "states" of ecological condition were characterized as 1 (Gillem's Camp) past overgrazing by domestic livestock with severe exotic grass dominance and increased fire frequency - dominated by Gray rabbitbrush (*Chrysothamnus nauseosus*)/cheatgrass with few natives in the composition and fuel load; 2 (Fleener Chimneys) limited fire exclusion, little history of domestic livestock use due to distance to water and lava flows - dominance of Sagebrush/ native bunchgrasses with some alien annuals; and 3 (Merrill Caves) Fire exclusion but little exotic grass invasion - <5% cover of cheatgrass where native bunchgrasses were dominant (Erhard 1980). With fire exclusion, the Merrill Caves site is experiencing juniper encroachment.

The soils are shallow inceptisols, and are all volcanic in origin with a large amount of pumice in evidence. The sites range in elevation from 1220 m to 1480 m with <30% slopes. The climate is cool, semi-arid with the majority (> 90%) of precipitation occurring in winter. Arid summers produce severe fire weather from July to September. During this time, dry lightning storms are common occurrences.

The research was established as a randomized complete block design with a factorial analysis (Fig. 1). The 3 X 3 factorial included the three differing states of ecological condition and two seasons of burning (spring and fall prescribed fires as well as a control - unburned plots). For each combination, there were five replicate burn plots for a total of 30 burn units (and 15 unburned controls).

Prefire Fuel Loads

Fires in big sagebrush communities are typically stand-replacing and therefore we defined the fuel loads to be equivalent to the total aboveground biomass. Fuel loads were measured prior to burn treatment to characterize the effect of land use history, and immediately following treatment to determine the effects of season on quantity of fuel consumed and the quantity remaining. The pre-fire fuel load was partitioned into the following categories: litter, fine fuels, herbaceous fine fuels, shrubs, trees (juniper) and dead and down woody fuels.

Methods of fuel load determination, consumption and fire behavior follow closely those described in Sapsis and Kauffman (1991). Five parallel, 20 m, permanent, sampling transects were established 5 m apart in each plot. Prior to burning, organic horizons (litter and duff layers), herbaceous fine fuels, and woody fuels were collected in 30 x 60 cm subplots (n= 8 for each plot) established between the permanent transects, and 1 m to the interior of the transects. Samples

were then dried at 65°C for at least 48 hours and weighed to determine fuel biomass on a dry weight basis.

The biomass (fuel load) of shrubs was determined from measurement of the cover and volume of all shrubs in 5 - 1 x 20 m subplots placed adjacent to the permanent transects. For each shrub rooted within the plot, we calculated elliptical crown area and volume based on shrub canopy diameter and height. Elliptical crown area was computed as:

$$A = (W1 * W2 * \pi) / 4$$

where A is the crown area, W1 is the longest crown dimension, and W2 is the longest crown dimension perpendicular to W1. Shrub volume was then calculated as the elliptical area multiplied by the measured height. Shrub biomass was then calculated from regression equations using shrub volume as the independent variable, developed for the dominant shrubs; mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana*), antelope bitterbrush (*Purshia tridentata*) and gray rabbitbrush (*Chrysothamnus nauseosus*) (Table 1). The equation for mountain big sagebrush came from Champlin (1991). We developed the equations for bitterbrush and gray rabbit brush through destructive sampling of 20 plants of each species. Biomass for green rabbitbrush (*Chrysothamnus viscidiflorus*) and gray horsebrush (*Tetradymia canescens*) was calculated using the gray rabbitbrush equation. Biomass for all other shrub species was calculated using the antelope bitterbrush equation.

Postfire Biomass/ Fuel Consumption

We sampled post-fire fuel loads immediately following burn treatment using similar methods as pre-fire fuels. Post-fire surface fuels (herbaceous, organic horizon, and woody debris) were collected in 30 x 60 cm subplots located 2.5 m from the transect pole and 1 m to the exterior of the transects. In addition to live shrubs, burned residual standing shrub biomass in each 1 x 20 m subplot was measured utilizing a modified reference method (Andrew et al. 1979). The total amount of biomass consumed by fire broken down by individual component (i.e., the combustion factor) was calculated as the percent of prefire fuels that were not present in postfire measurements.

Fuel Moisture and Fire Behavior

The spring burns for the Gillem's Camp and Fleenor Chimneys sites and all fall burns were conducted in 2003 (Table 2). The spring burn at Merrill Caves was conducted in June, 2004. Temperature, relative humidity, in-stand windspeed, and wind direction were measured at the time of ignition, and at approximately 30 minute intervals during the actual burn. Each treatment block was burned using drip torches in a strip-head or spot firing pattern. Within each plot, fire behavior was visually estimated during the fires by NPS Fire Effects Monitors (FEMO). This included rates of spread (ROS, m/min.), total flaming duration (sec), flame residence time (sec), flame length (FL, m), and flame depth (FD, m). From the observations above, we calculated fireline intensity (FI) which is defined as the rate of heat release per unit length of fireline and related to flame length by Rothermel and Deeming (1980) as follows:

$$FI \text{ (kW/m)} = 258 \text{ (FL)}^{2.17}$$

The reaction intensity (RI), defined as the heat released per unit area of flaming front was calculated as follows:

$$RI \text{ (kW/m}^2\text{)} = FI / FD$$

Statistical Analysis

Statistical analysis for the within site differences in fuel consumption between the spring and fall burn treatments was performed using a two sample t-Test assuming unequal variances. Statistical analysis for the difference between sites was performed using ANOVA (F-protected Fishers LSD). The significance level was set at 0.10.

Results

Pre-fire Fuel Loads

Pre-burn fuel loads varied greatly among sites with a total biomass ranging from 6.6 to 21.6 Mg/ha (Table 3). Fuel loads also differed with season (Table 3). The fire excluded, Merrill Caves site, with the lowest apparent fire-return interval, was highest in biomass, particularly that of woody species. The relatively undisturbed Fleener Chimneys site, with a history of limited livestock grazing and fire suppression, was intermediate in total biomass (~9-10 Mg/ha). The Gillem's Camp site, which was characterized by a history of high levels of livestock grazing, a dominance of exotic annuals and a high fire frequency, was lowest in aboveground biomass (~7 Mg/ha). Total fuel loads decreased along this gradient (Figure 2).

While the increases in total biomass along the gradient from Gillem's Camp to Merrill Caves can be explained largely due to increases in shrub biomass, fine surface fuels (i.e. herbaceous plus litter) were highest at the cheatgrass invaded Gillem's Camp. At this site fine surface fuels were approximate in mass to the shrub fuel biomass, and comprised ~46% of the total fuel load. Fine surface fuels, decreased along the gradient of severity of past land use, comprising ~16% of the total fuel load at the fire excluded Merrill Caves site. Only at the Gillem's Camp site did the herbaceous component comprise a substantial part of the total fuels. While litter biomass was similar across all sites, it comprised the greatest percentage of total fuels at the Gillem's Camp site.

Fine surface fuels also varied considerably depending upon the season of burn. Herbaceous fuel, dominated by cheatgrass, was a significant fuel component (14% and 20% of total fuels respectively) in both the spring and fall at the Gillem's Camp site (Figure 3). Herbaceous fuels comprised a lesser proportion (<5%) of the total aboveground biomass at the two less disturbed sites, especially during the fall. At Gillem's Camp and at Fleener Chimneys litter fuels were greater during fall burns (2.09 and 2.81 Mg/ha) compared to spring burns (1.45 and 0.79 Mg/ha). The reverse was true for the fire excluded Merrill Caves site where litter fuel was greater in the spring burn (3.04 Mg/ha) compared to the fall burn (1.70 Mg/ha).

In contrast to the pattern of fine surface fuels, shrub fuel mass increased in biomass and dominance with an increased fire-return interval and lessened history of human disturbances. The shrub component, which comprised a little more than half the total fuels at the Gillem's Camp site, dominated the biomass at the less disturbed Fleener Chimneys and Merrill Caves sites, comprising 71% and 70% of the total fuels respectively (Table 3).

The surface wood debris was only of minor importance as a fuel component at all three sites. Wood mass ranged from 0.2 to 2.9 Mg/ha. Wood debris followed the same trend as the shrub component, comprising a low of 6% at Gillem's Camp to as much as 13% at Merrill Caves.

Fire Behavior

Weather conditions and fuel moisture contents were similar among the three sites during the Spring and Fall burns. We did measure differences between season of burn with the same site. A notable difference between burn seasons was the higher temperatures during the spring burns (13.8 – 28.3°C) compared to the fall burns (6.1 – 15.6°C) (Tables 4 and 5).

Mean fireline intensity was highest at Merrill Caves and lowest at Fleener Chimneys for both spring and fall season burns (Table 4). The higher fireline intensity at Merrill Caves was

likely related to the higher quantity of fine fuels on shrubs (live leaves) coupled with the quantity of fine herbaceous mass which would be consumed by the flaming front and thus contributing to the fireline intensity. The higher fireline intensity at Gillem's Camp compared to Fleener Chimneys was likely due to the high quantity of grass mass at this site. In addition the fuels at the Fleener Chimneys site were patchier and less continuous with greater areas of bare ground. Fireline intensity was similar for spring and fall season burn comparisons at all sites.

Biomass Consumption by Prescribed Fires

Site Comparison

Fuels biomass consumption largely depended upon the different fuel loading and distribution of the different sites. Consumption as a percentage of total pre-fire biomass was lowest at the Fleener Chimneys site for both spring (48%) and fall season (27%) burns (Figure 5). Despite the lower site biomass, fuels consumed at Gillem's Camp equaled that of Fleener Chimneys due to the high rate of consumption for both the spring (88%) and fall (78%) burns. Due in part to the highest cover of shrub fuels and therefore the highest total biomass, the Merrill Caves site had the highest total quantity of biomass consumed by fire.

Fine surface fuel consumption was lowest at Fleener Chimneys and is largely due to the patchy discontinuous arrangement of the fuel loads at this site. While fine surface fuel consumption was >80% for both spring and fall season burns at Gillem's Camp and Merrill Caves, at Fleener Chimneys consumption was <40% (Figure 5).

Season of Burn

The percentage of total fuels consumed was different between spring and fall treatments only at the Merrill Caves site (2-sided p-value = 0.027). Total biomass consumption was comparable between spring and fall season burn treatments at all three sites (Table 6), however, the percentage of total fuel consumption reflected the total biomass consumed only at Gillem's Camp and Fleener Chimneys. At the shrub-dominated Merrill Caves site the percentage of total biomass consumed was considerably greater for the spring burn treatment (84%) compared to the fall (48%) even though there was no difference in total biomass consumed (Figure 5). The basis for this difference lies in a difference in pre-fire biomass between the two treatments at this site.

In a comparison of burn season, the shrub fuel component generally mirrored total fuel consumption in both the quantity consumed and as a percent consumed (Fig. 5), only showing a difference in percent consumption between spring and fall burn treatments at the Merrill Caves site (2-sided p-value = 0.044). Likewise, the percentage of fine surface fuels consumed was different between spring and fall treatments only at the Merrill Caves site (2-sided p-value = 0.084).

Discussion

Fuels

Total fuel loads in the mountain big sagebrush communities varied by over three fold (6.7- to 19 Mg/ha). The differences in time since fire, different land use histories and inherent site characteristics resulted in differences in structure including differences in fuel loads and total above-ground biomass. Differences were largely due to increases in shrubs at the sites with less fire and land use disturbances in their history. This range in fuel loads for the mountain big sagebrush communities in this study was similar to the variation in fuel loads of basin big sagebrush (*Artemisia tridentata* subsp. *Tridentata*) communities in central Oregon (Sapsis and Kauffman 1991). The aboveground biomass of basin big sagebrush/perennial bunchgrass communities at John Day Fossil Beds National Monument in central Oregon ranged from 5 to 12 Mg/ha (Sapsis and Kauffman 1991).

Shrub fuels, particularly attached dead fuels and fine live fuels are important fuels components that influence fire behavior (Debano et al. 1998). The Merrill Caves site averaged twice the shrub biomass (14.1 Mg/ha) as the Fleener Chimneys site (6.71 Mg/ha) and nearly four times that of the cheatgrass invaded Gillem's Camp site (3.62 Mg/ha). The total shrub consumption at this site was 9.1 Mg/ha and these differences are reflected in fireline intensity and other parameters of fire behavior. Fire in sagebrush ecosystems consumes shrub vegetation and enhances the cover of the fire-adapted bunchgrasses (Kauffman and Sapsis 1989, Kauffman 1990).

The high shrub biomass (14.1 Mg/ha) at the Merrill Caves site may be indicative of a long fire-free period in a productive site. The shrub mass for this site was not only greater for this study but is greater in mass than many other sampled sites. Shrub biomass for Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis*) (3.19 – 3.65 Mg/ha) in SE Oregon, and basin big sagebrush (2.93 - 6.07 Mg/ha) in central-eastern Oregon were considerably lower (Wroblewski and Kauffman 2003, Sapsis and Kauffman 1991).

Herbaceous (live) biomass formed an important fuels component during both the spring and fall seasons at the cheatgrass dominated Gillem's Camp site. Cheatgrass produced a continuous fine surface fuel, load allowing for a uniform spread of fire (Whisenant 1990). This is largely the result of heavy historical human use (livestock grazing in close proximity to surface water) that reduced the shrub community at Gillem's Camp and resulted in a fuel load dominated by the annual cheatgrass.

Consumption and Fire Behavior

Fuel consumption and residual post fire fuels varied in predictable ways that depended upon pre-fire fuel loads and distribution (coverage), and season of burn treatment

The total quantity of fuel consumed appeared to be related not only to prefire fuel quantities but also to fuel coverage and continuity. The Gillem's Camp and Merrill Caves sites each had high percentage fuel consumption but with quite different fuel types and loadings. While Merrill Caves derived fuel coverage from its well-developed shrub community, cheatgrass provided a continuous fuel at Gillem's Camp. Fleener Chimneys, which was intermediate in total fuels and had twice the shrub biomass as Gillem's Camp, but had a patchy herbaceous coverage resulting in minimal fire carry and half the fuel consumption as measured by percentage of total biomass.

The seasonal difference in fuel consumption was dramatic at the Merrill Caves site. The spring burn produced very high mortality with a very high combustion factor; very little fuel, shrub or fine surface fuel, remained. In comparison, the fall burn was patchier consuming only 48% of the total fuels, and produced moderate shrub mortality. Higher fuel moisture content during the fall treatment likely contributed to the lower consumption at the Merrill Caves site. Fall season prescribed fires at the high end of moisture content and weather conditions also produced a similar patchy result in southeastern Oregon with 47% of treatment areas burned during a prescribed fire (Wroblewski and Kauffman 2003). Though lower in total consumption, the Fleener Chimneys site experienced a similar difference with the spring burn shrub consumption higher compared to the fall burn.

Since fuel loads were seasonally similar for these shrub dominated sites at Lava Beds, the difference in consumption was likely related to the higher temperatures during the spring burn (13.8 – 25.6°C) compared to the fall burn (6.1 – 15.6°C) and differences in fuel moisture content. The other weather and topographic variables were not different between seasons. Sapsis and Kauffman (1991) found no difference in percentage of total biomass consumed in a comparison of spring and fall burns of sagebrush communities in central Oregon. However, at their sites, greener spring fuels burned due to higher temperatures and lower humidity compared to fall burns.

The high rates of consumption (>80%) during both seasons at Gillem's Camp despite low total biomass, was likely a result of the continued high herbaceous cover from cheatgrass during both spring and fall burns. This is likely due to the rapid rate of fuel dry down for the dead cheatgrass compared to other sites which have a higher proportion of their fuel load composed of shrub fuels.

With low fuel moisture, seasonal differences in temperature do not appear to affect the high fuel consumption at cheatgrass invaded sites where high fine dead surface fuels exist. However, fire weather, temperature in this case, does appear to affect fire spread and fuel consumption where shrub fuels dominate, particularly at older sites that have accumulated greater fuels biomass.

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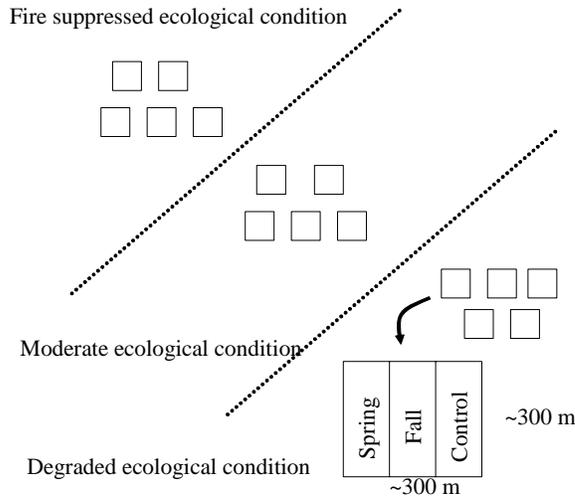


Figure 1. Experimental layout of the study. Five blocks were established in each ecological condition. Each block contained a spring burn, a fall burn, and a control (no burn) treatment. The three ecological conditions were not immediately adjacent to one another.

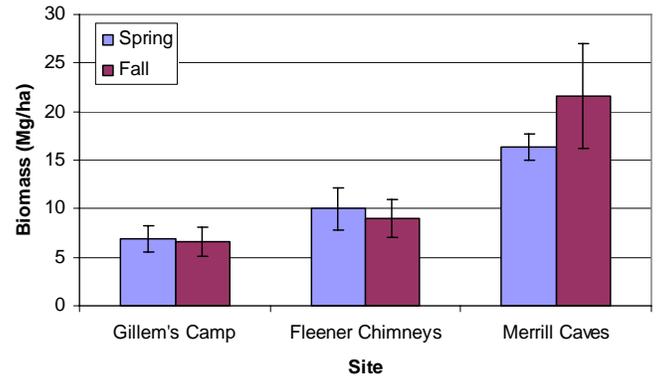


Figure 2. Total fuels biomass (Mg/ha) for spring and fall season burns at each site. Means \pm 1SE.

Table 1. Shrub biomass equations for total shrub biomass (kg) using measured volume (m^3).

Shrub Species	Equation	r^2
<i>Artemisia tridentata</i> ssp. <i>vaseyana</i> ¹	total biomass = (188.46 + 2588.75*volume)/1000	0.8991
<i>Purshia tridentata</i> ²	total biomass = 1.5438*volume	0.9626
<i>Chrysothamnus nauseosus</i> ²	total biomass = 2.6833*volume	0.8626

¹Champlin 1991.

²This study.

Table 2. Burn treatment dates and fuel models for research sites (Powell 2003, Rasmussen 2003).

Site	Spring Burn Date	Fall Burn Date	Fuel Model
Gillem's Camp	6/25-26/2003	11/12-13/2003	continuous bed of cheatgrass
Fleener Chimneys	6/25/2003	11/12/2003	patchy shrubs and bunchgrasses
Merrill Caves	6/2004	11/18/2003	patchy shrubs and bunchgrasses, widely spaced juniper and mtn. mahogany

Table 3. Total aboveground biomass partitioned into individual fuel components and sampled before and after Spring and Fall prescribed fires at the Lava Beds National Monument. Numbers are means (Mg/ha) \pm 1SE.

	Spring		Fall	
	Pre-fire	Post-fire	Pre-fire	Post-fire
Gillems Camp				
Fine Surface Fuels				
Litter (dead)	1.45 \pm 0.79	0.27 \pm 0.09	2.09 \pm 0.22	0.49 \pm 0.22
Herbaceous (live)	0.83 \pm 0.25	0.01 \pm 0.01	1.03 \pm 0.15	0.0
Total	2.28 \pm 0.33	0.28 \pm 0.09	3.13 \pm 0.19	0.49 \pm 0.22
Total Wood Debris	0.61 \pm 0.54	0.04 \pm 0.02	0.19 \pm 0.10	0.11 \pm 0.05
Shrub Biomass	4.00 \pm 0.88	0.43 \pm 0.08	3.23 \pm 1.33	0.64 \pm 0.20
Total Biomass	6.89 \pm 1.34	0.74 \pm 0.13	6.55 \pm 1.49	1.24 \pm 0.29
Ash		1.20 \pm 0.43		1.07 \pm 0.29
Fleener Chimneys				
Fine Surface Fuels				
Litter (dead)	0.79 \pm 0.18	0.51 \pm 0.19	2.81 \pm 0.96	1.74 \pm 0.50
Herbaceous (live)	0.31 \pm 0.05	0.24 \pm 0.05	0.0	0.0
Total	1.10 \pm 0.21	0.75 \pm 0.24	2.81 \pm 0.96	1.74 \pm 0.50
Total Wood Debris	1.27 \pm 0.46	0.33 \pm 0.19	0.36 \pm 0.26	0.26 \pm 0.10
Shrub Biomass	7.61 \pm 1.77	3.34 \pm 0.42	5.81 \pm 1.09	3.95 \pm 0.87
Total Biomass	9.98 \pm 2.16	4.43 \pm 0.69	8.98 \pm 1.98	5.96 \pm 0.70
Ash		1.03 \pm 0.27		0.74 \pm 0.16
Merrill Caves				
Fine Surface Fuels				
Litter (dead)	3.04 \pm 0.94	0.15 \pm 0.15	1.70 \pm 0.82	0.34 \pm 0.07
Herbaceous (live)	0.16 \pm 0.01	0.02 \pm 0.01	0.0	0.0
Total	3.20 \pm 0.93	0.17 \pm 0.15	1.70 \pm 0.82	0.34 \pm 0.07
Total Wood Debris	2.02 \pm 0.36	0.36 \pm 0.17	2.89 \pm 0.56	1.13 \pm 0.35
Shrub Biomass	11.16 \pm 1.55	2.02 \pm 0.54	17.03 \pm 6.09	8.04 \pm 2.61
Total Biomass	16.39 \pm 1.37	2.55 \pm 0.82	21.62 \pm 5.35	9.51 \pm 2.52
Ash		1.23 \pm 0.35		

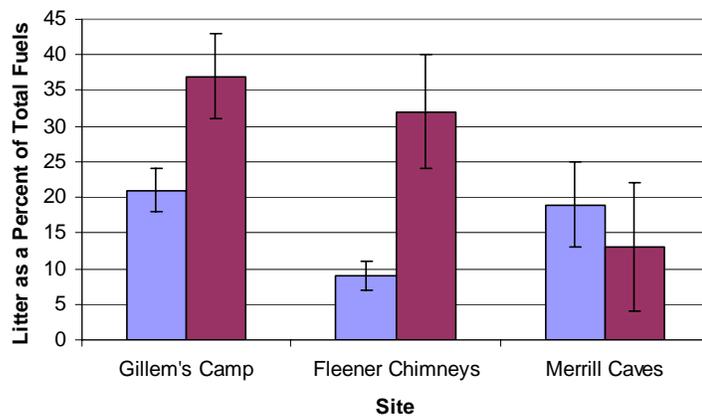
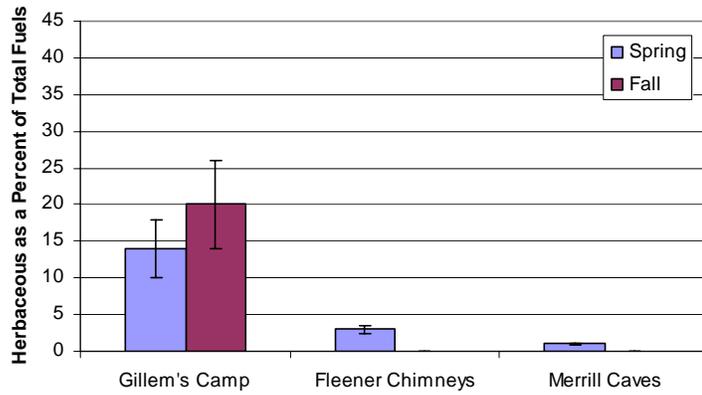


Figure 3. Herbaceous (top) and litter (bottom) fine surface fuels as a percentage of total fuels comparing spring and fall burn treatments for each site. Means \pm 1SE.

Table 4. Fire weather and fire behavior of spring burns (Rasmussen 2003) at the Lava Beds National Monument. Fire weather presented as range (minimum – maximum) of observations. Fire behavior presented as mean of observations \pm 1SE.

SPRING BURNS	Fleener Chimneys (June 2003)	Gillems Camp (June 2003)	Merrill Caves (June 2004)
Weather			
Temperature (°C)	13.8 – 24.4	16.7 – 28.3	20.6 – 25.6
Relative Humidity (%)	30-54	28-53	27-58
Wind Speed (m/s)	1.3 – 3.6	1.3 – 2.2	0.4 – 0.9
Fine Fuel Moisture (%)	6.7 \pm 0.7	6.7 \pm 1.2	4-11
Fire Behavior			
Rate Of Spread (m/min)	0.6	1.8	<0.1
Flame Length (m)	0.7 \pm 0.1	1.0 \pm 0.2	0.609 – 6.096
Flame Zone Depth (m)	0.5 \pm 0.1	0.2 \pm 0.04	0.305 – 1.83
Fireline Intensity (kW/m)	121 \pm 29	376 \pm 149	157.4 – 1573.8
Reaction Intensity (kW)	164 \pm 25	1280 \pm 743	516.0 – 860.0

Table 5. Fire weather and fire behavior of fall burns (Powell 2003). Fire weather presented as range (minimum – maximum) of observations. Fire behavior presented as mean of observations \pm 1SE.

FALL BURNS	Fleener Chimneys (November 2003)	Gillems Camp (November 2003)	Merrill Caves (November 2003)
Weather			
Temperature (°C)	6.1-10.6	7.2-11.7	7.8-15.6
Relative Humidity (%)	60-53	55-41	68-30
Wind Speed (m/s)	0 – 1.8	0.4 – 2.7	0 – 2.7
Fine Fuel Moisture (%)	10.1 \pm 0.4	9.8 \pm 0.6	9.8 \pm 0.9
Fire Behavior			
Rate Of Spread (m/min)	<0.1	0.2	<0.1
Flame Length (m)	0.9 \pm 0.1	1.4 \pm 0.3	2.0 \pm 0.3
Flame Zone Depth (m)	1.0 \pm 0.2	0.6 \pm 0.3	0.7 \pm 0.1
Fireline Intensity (kW/m)	231 \pm 25	702 \pm 193	1263 \pm 398
Reaction Intensity (kW)	232 \pm 26	1916 \pm 782	1605 \pm 346

Table 6. Fuel biomass consumption. Means (Mg/ha) \pm 1SE following prescribed fires at the Lava Beds National Monument. Different lower-case letters signify a significant difference between sites (two sided p-value for ANOVA with a 0.1 significance level). No significant differences were detected between burn season treatments (two-sided p-value for a two sample t-Test with a 0.1 significance level).

Biomass Consumed	Gillem's Camp	Fleener Chimneys	Merrill Caves
Spring Prescribed Burn			
Fine Surface Fuels	2.00 \pm 0.36a	0.36 \pm 0.17b	3.03 \pm 0.98a
Wood Fuels	0.57 \pm 0.24a	0.93 \pm 0.40ab	1.67 \pm 0.52b
Shrub Fuels	3.58 \pm 0.82a	4.27 \pm 1.89a	9.15 \pm 1.37b
Total Fuels	6.15 \pm 1.27a	5.55 \pm 2.31a	13.84 \pm 1.63b
Fall Prescribed Burn			
Fine Surface Fuels	2.63 \pm 0.29	1.46 \pm 1.06	1.36 \pm 0.87
Wood Fuels	0.20 \pm 0.09a	0.33 \pm 0.33a	1.92 \pm 0.87b
Shrub Fuels	3.24 \pm 1.38	1.86 \pm 0.40	8.99 \pm 6.62
Total Fuels	5.31 \pm 1.51ab	3.04 \pm 1.46a	12.11 \pm 6.18b

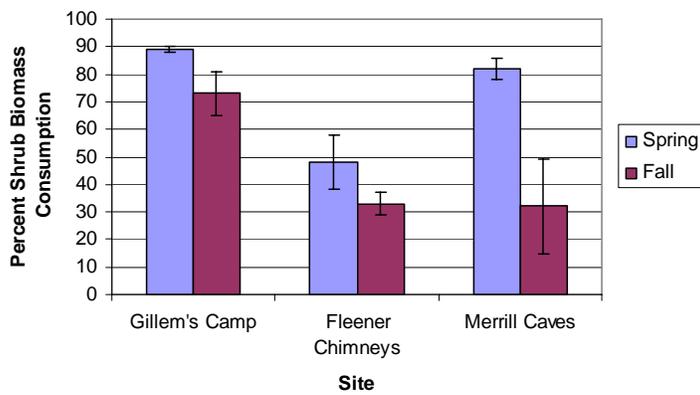
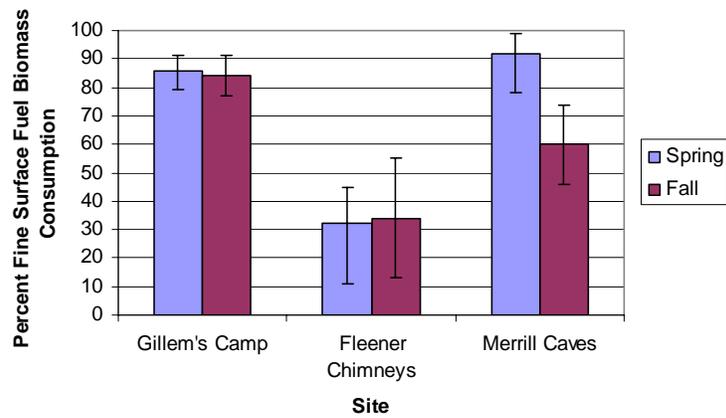
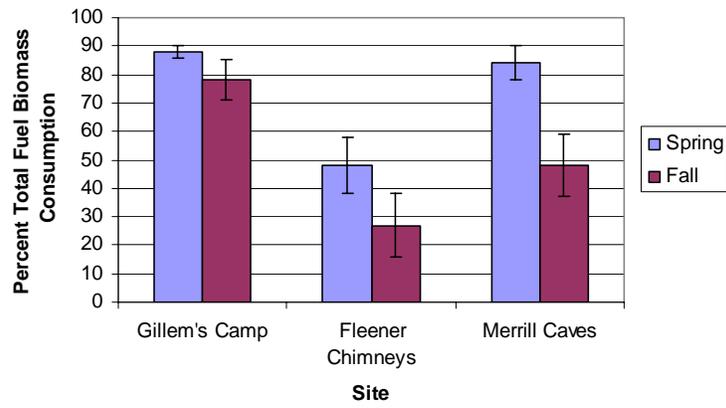


Figure 5. Percent consumption of total fuels biomass (top), fine surface fuel biomass (middle) and shrub biomass (bottom), comparing spring and fall season burn treatments at the Lava Beds National Monument. Data are means \pm 1SE.

Chapter 5: Effects of Prescribed Fire on Soil N Dynamics

John Wilson and J. Boone Kauffman

Introduction

It is of great importance in fire management planning for ecosystem restoration to understand the role of nutrient bioavailability in relation to the ecosystem processes. It is generally recognized that of all plant nutrients, nitrogen has the most impact on plant growth. Mineral nitrogen, the form most available for plant uptake makes up less than one percent of total soil nitrogen in natural ecosystems (Chapin et al. 2002). As an interactive factor, nutrient availability both controls and responds to ecosystem processes such as plant growth, community composition, and decomposition rates. Understanding these interactive processes is particularly important with respect to monitoring the recovery and interactions of vegetation following prescribed or wildland fires.

Fire dramatically alters the pools and fluxes of nitrogen. The low total N of xeric ecosystems reflects low total organics, and mineral N, the form most available for plant uptake, is further limited by ecosystem aridity and therefore tightly conserved (Skujins 1981). Fire exclusion promotes the dominance of woody species (Kauffman and Sapsis 1989) and the accumulation of organic material that serve as the primary nutrient substrate (Doescher et al. 1984). Fire disrupts tight nutrient cycling, often making nitrogen more available for a period, but also accelerating ecosystem losses of total nitrogen. Many early seral species in the post fire environment are also N-fixers (legumes, ceanothus) that function in N-reaccumulation in the post fire environment (Kauffman 1990). Land changes such as grazing or altering fire regimes could result in the loss of these early seral native species which would affect ecosystem dynamics of plant available nitrogen.

Altered fire regimes due to fire exclusion in the mountain big sagebrush (*Artemisia tridentata vaseyana*) ecosystem have dramatically altered ecosystem structure and composition including the increased distribution and density of western juniper (*Juniperus occidentalis*) on 3.2 million hectares across eastern Oregon, NE California, SW Idaho and NW Nevada (Miller and Tausch 2001). This has come with a concomitant decrease in shrubs, grasses, and herbs adapted to a more frequent occurrence of fire. Juniper seedlings are readily killed by fire, but the native shrub and understory community, adapted to the natural fire regime, resprout following fire or quickly reinvade sites via seed dispersal. Restoration of fire intervals to the natural range of variability has been proposed for the restoration of native ecosystem structure and function in this ecosystem. We hypothesize that the higher growth, flowering, and reproductive response of native species that has been found in burned compared to unburned areas (See chapters in this report and also Kauffman 1990, Wroblewski and Kauffman 2002) was due to greater nutrient, especially N, availability to plants following fire. In addition, it has also been suggested that exotic annual grasses are more likely to invade sites where N availability is high (Burke and Grime 1996).

Community structure and composition across landscapes are shaped by the interactions of fire, potential vegetation and nutrient resources through time. Remarkably, few studies have quantified fire effects on the nutrient status in sagebrush communities (Blank et al. 1994; Kauffman et al. 1997). To understand the environmental conditions following fire in a fire excluded, western juniper invaded sagebrush community type we quantified the amount and duration of change in plant available and total nitrogen soil pools following prescribed fires conducted at two different seasons (spring and fall). The objectives of the research were to quantify the dynamics and linkages between fire and N availability which could assist in the determination of what ecological and seasonal conditions would fires facilitate an increase in

native species abundance (proper restoration or preservation) as opposed to activities which may favor increases in exotic species.

We addressed these objectives through the following research questions:

- How do fires occurring at different seasons differentially affect the response of ecosystems to fire in terms of soil N cycling?
- How do different types of plant cover or total fuel load affect post fire soil N cycling?

Methods

The study area was located at the Lava Beds National Monument, California. We examined N-cycling in western juniper invaded, mountain big sage/bluebunch wheatgrass - Thurber's needlegrass habitat. The above ground biomass (16.4-21.6 Mg/ha, this study) was dominated by the shrub component including mountain big sagebrush, antelope bitterbrush (*Purshia tridentata*) and gray rabbitbrush (*Chrysothamnus nauseosus*) (Table 1). This landscape is representative of much of the juniper invaded, sagebrush steppe associated with fire exclusion of southeast Oregon, northwest Nevada, and northeastern California.

The research was established as a randomized complete block design with a factorial analysis (The 3 X 4 factorial included two seasons of burning (spring and fall prescribed fires as well as control - unburned plots); and four vegetative covers (western juniper, antelope bitterbrush; an N-fixing shrub, and mountain big sagebrush; a non-N-fixing shrub, as well as open/no cover with bare ground). There were five replicate plots of each of the three burn (and control) treatments. Vegetative cover samples were combined for season of burn analysis. The four cover types were sampled (three sub-samples each) in each of the 15 plots for a total of 60 sampled treatments. Soils were sampled three different seasons following the burn treatments (Table 2).

We used the buried bag method (Eno 1960, Binkley and Hart 1989) to examine net N-mineralization differences in the top 10 cm of soil. We examined differences in N mineralization among burns conducted during different seasons (spring and fall prescribed burns) and due to differences in vegetation cover. Mineralized nitrogen (NH_4^+ -N and NO_3^- -N) is the form most available for plant uptake, and net mineralization measures the changes in the available soil pool. The availability of mineral-N in soil is also dependent upon the quantity of total nitrogen and carbon, and dissolved organic nitrogen (DON). In addition labile DON may provide an additional direct source of plant available nutrients (Schimel and Bennett 2004).

The buried bag method excludes plant uptake from the process (Eno 1960), and measures the in-situ potential for producing plant available-N in excess of microbial demand. Net mineralization was determined by first collecting samples to determine the initial soil pool, and then incubating soil samples over a season to determine the change in the soil pool relative to the initial quantity. Positive net values indicate soil solution mineral-N was produced (mineralized) in excess of microbial demand (immobilization). Negative net values indicate that soil solution mineral-N was immobilized by soil microbes in excess of that mineralized.

The buried bag method involved extracting samples of the top 10 cm of soil with a corer from beneath the canopy of the specified vegetation cover. Soil cores were placed into resealable, breathable, polyethylene bags and then replaced in the hole from which the soil was extracted, for in-situ incubation. The bags allowed for the transfer of oxygen and carbon dioxide but not the transfer of liquid. Separate soil samples were collected simultaneously with each bag placement (collected at the incubation start date, Table 2) to determine the initial soil pool of mineral-N which also served as a measure soil N concentrations (Ellingson et al. 2000). Initial soil samples collected for each seasonal buried bag sampling period (collected at the incubation start date, Table 2) were also used for mineral-N, DON, and total C/N analysis.

Following field collection, mineral-N was extracted from all soil samples in the laboratory using 0.5 M K_2SO_4 (Jonasson et al. 1996). Soil sample extracts analyzed for DON were digested first with alkaline persulfate to convert all DON and NH_4^+ -N to NO_3^- -N (Cabrera and Beare 1993). Soil samples analyzed for microbial biomass were first split, with one sample fumigated with chlorine (to lyse microbes). Both splits were then extracted as above and digested with alkaline persulfate to convert DON (and NH_4^+ -N) into NO_3^- -N (Cabrera and Beare 1993). Nitrate in the unfumigated samples was a measure of DON, while NO_3^- -N in the fumigated samples measured the microbial biomass, after subtracting NO_3^- -N of the corresponding DON sample.

Extract analysis for NH_4^+ -N (Astoria Pacific International-a 2002, Astoria Pacific International-b 2002), and NO_3^- -N (Astoria-Pacific International-c 2002) was performed using an ALPKEM Rapid Flow Analyzer at the Oregon State University Department of Fisheries and Wildlife Lab. Samples were analyzed for total C and N by the induction furnace method (Nelson and Sommers 1996) on a Carlo-Erba NCS element analyzer at the Oregon State University Department of Fisheries and Wildlife Lab.

Standard statistical analysis for difference among treatments was performed using 2-way ANOVA (multiple comparisons by F-protected Fishers LSD). Differences among cover types were determined by using 1-way ANOVA (F-protected Fishers LSD). The significance level was set at 0.10.

Results

Fire Treatment Effects – Mineral-N

Prescribed fire resulted in a 4 to 7-fold increase in available forms of mineral-N for both burn treatments during the summer-dry sampling (1 September 2004) post burn (Figure 1). Total available N (NH_4^+ -N + NO_3^- -N) in the top 10 cm of soil increased by 35.6 mg/kg soil in the fall burn and by 18.9 mg/kg soil in the spring burn. Post-burn, plant available mineral-N was significantly greater in both burn treatments compared to the control during all three sampling seasons (Figure 1). Control mineral-N values were very low, and gradually decreased seasonally from late summer-dry to winter-cold. Ammonium, which is increased during fires via the process of pyromineralization, was significantly higher in both burn treatments compared to the control (Table 3).

Among burn treatments, soil mineral-N was significantly higher in the fall burn treatment compared with the spring burn treatment during the late summer-dry season primarily due to significantly higher NO_3^- -N concentrations (Table 4). The disparity in NO_3^- -N concentrations shows that significant nitrification of the NH_4^+ -N pulse has already occurred in the fall burn treatment, but has yet to occur in the more recent spring burn treatment.

Mineral-N concentrations in the fall burn treatment dropped precipitously (65% of NH_4^+ -N and 83% of NO_3^- -N) from the late summer-dry to the initial sampling for the winter-cold season, while the spring burn treatment concentrations experienced a more gradual decrease, which leveled off between fall-wet and winter-cold season (Figure 1). By the time of winter-cold season sampling, mineral-N for the burn treatments was reversed, with spring burn treatment concentrations higher than fall burn treatment concentrations. Differences between treatments are attributed to the differences in vegetation cover due to differences in fire severity, and possibly differences in phenology due to time since fire. The mineral-N in the fall burn plots diminished at a time of increased plant and microbial activity and thus increased demand. However, the soil NH_4^+ -N remained essentially level during the fall-wet season on the spring burn treatments where high aboveground plant mortality and little aboveground growth reduced demand. The reduction of soil NO_3^- -N in both treatments during the fall-wet season suggests microbial sequestration or an additional pathway of loss.

Fire Treatment Effects – N Mineralization

Fires and time since fire had a significant influence on soil N mineralization rates. Net soil mineralization, determined for all plant covers combined, was consistently highest (p-value = 0.030) in the spring burn treatment (i.e. sites most recently burned; Figure 2). The highest levels for all treatments occurred during the fall-wet season suggesting the response to the moisture influx (Figure 3) by soil microbes. Net mineralization in the control was consistently negative or near zero indicating a constant state of low N substrate availability and turnover. More specifically, with one exception, rates of ammonification were negative or near zero for all treatments across seasons (Table 5). The spring burn treatment, showing a recent fire effect, experienced a positive spike during fall-wet season, which was significantly greater (p-value = 0.001) than the other treatments. Nitrification rates were generally positive indicating that nitrifying bacteria were more active than the bacteria that assimilated nitrate (Table 6). Nitrification rates for the more recent spring burn treatment were significantly greater than the other treatments during the summer and winter seasons suggesting greater activity related to the more recent NH_4^+ -N pulse of the spring burn. The rates of microbial assimilation of mineral-N during the winter season were not different (p-value = 0.717) between fall burn (2.37 mg/kg soil/mo), spring burn (1.98 mg/kg soil/mo) and control (2.77 mg/kg soil/mo).

Fire Treatment Effects – Total C, N and DON

Post-burn soil total carbon and nitrogen concentrations were not significantly different between the three treatments, and the low C/N ratios do not suggest soil N deficiency (Brady and Weil 2004) (Table 7). Likewise, soil dissolved organic nitrogen (DON) was not significantly different between treatments, though there was an apparent decrease following the fall-wet season (Table 8). Prescribed fires did not appear to affect these parameters to a significant degree.

Cover Treatment Effects – Mineral-N

Consistent differences were found in the distribution of plant available mineral N (NH_4^+ -N + NO_3^- -N) with respect to species of plant cover in unburned controls. Mineral N was 2 to 6 times greater under juniper cover than the very low concentrations found in open areas and under shrub cover (Figure 4). Prescribed fire resulted in dramatic increases in soil mineral N across the treatment areas regardless of plant cover type. Of the burn treatments, only the fall burn treatments following the onset of fall-wet season precipitation showed substantial differences in soil mineral N concentration between juniper and other cover types. No such trends were apparent in the spring burn treatments. In the fall burn treatment as with the controls, demand for available mineral N was likely greater in areas uninsulated by thick juniper litter, leaving higher concentrations of mineral N in soil beneath junipers. However, the higher biomass consumption and the lower amount of aboveground plant growth in the spring burn treatment likely reduced overall demand, leaving the higher, fire-generated mineral N concentrations elevated throughout.

We found that plant cover had a significant effect on soil mineral-N composition. Significant differences occurred only in the fall-wet and winter-cold sampling seasons. In the fall burn treatment as with the control, both NH_4^+ -N and NO_3^- -N soil concentrations were significantly higher under juniper cover at the beginning the fall-wet season (Tables 9 and 10). Relative to other vegetation cover, significantly higher NH_4^+ -N and NO_3^- -N soil concentrations were retained under juniper into the winter-cold season in the fall burn treatment, but not in the control. At the same time, soil NO_3^- -N concentration under juniper dropped precipitously (75%) compared to the reduction in soil NH_4^+ -N concentration (24%) indicating potential demand or additional pathways of NO_3^- -N loss.

Cover Effects – N mineralization

We found that plant cover had a significant effect on soil N mineralization rates. The most notable differences occurred in the fall burn treatment during the fall-wet season and the

winter-cold season where the combined ($\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$) mineralization rate in soil under juniper was negative (<3.0 mg/kg soil/mo) while rates under the other covers were distinctly positive (1.2-7.0 mg/kg soil/mo) (Figure 5). Combined N mineralization rates under different plant cover types in controls were negative or near zero, with rates under juniper consistently lowest, though not significantly so. The ammonification rate in controls was negative or near zero (Table 11), during all seasons, under all covers, while the nitrification rate was minimally positive under all covers following the onset of the fall-wet season (Table 12). Control treatment nitrification rates were lowest in soil under juniper, significantly so during the winter-cold season.

The difference in the N mineralization rates under different covers in the fall burn treatment during the fall-wet season was primarily due to the significantly lower ammonification rate in soils under juniper (Table 11). The addition of labile litter (and fine roots) from senescing herbs and shrubs in conjunction with increased soil moisture following the onset of the fall-wet season may have contributed to the higher (and variable) ammonification rates in soils under shrubs and in open areas compared to soils under juniper.

The ammonification rate in soil under different plant cover types in the spring burn treatment shifted from negative or near zero rates during the late summer-dry season, to positive rates during the fall-wet season. The positive ammonification rate under all cover types was likely a continuing legacy of increased mineralization following the more recent prescribed fire. Microbial activity was likely limited by low soil moisture during the summer-dry season and low soil temperature during the winter-cold season.

Soils under all cover types in all treatments experienced positive nitrification rates during the fall-wet season, however we found significant differences between covers only in the spring burn treatment where soil under juniper had the lowest rates and soil under bitterbrush the highest. Positive nitrification rates continued under all cover types in all treatments during the winter-cold season, with significant differences between cover types found in both the fall burn and control treatments, where once again soil under juniper had the lowest rates and soil under bitterbrush the highest. Despite higher $\text{NH}_4^+\text{-N}$ availability in soil under juniper cover (Table 9), nitrifier activity was consistently higher under the other covers. The availability of $\text{NH}_4^+\text{-N}$ is generally considered the most important direct determinant of nitrification rate (Chapin et al. 2002), though other limitations have also been proposed including allelopathic inhibition (Rice 1979) which may be the case here under juniper cover.

Cover Treatment Effects – Total C, N and DON

Both burn treatments were similar to controls in that total C, N and DON were higher in soils under juniper compared to open areas. DON is the immediate precursor of microbial-mediated mineral N and levels are related in part to soil total N (Chapin et al. 2002). One significant difference occurred in the total C and N under sagebrush where the levels in the fall burn treatment were approximately twice those in the spring burn treatment.

Conclusions

Fire Treatment

The pools and fluxes of mineral N, the forms most readily available for plant uptake, varied with respect to the season of burn, the time since burn, and the timing of succeeding seasonal-environmental conditions. The effects of the spring burn were dramatically different from the fall burn by producing significantly higher plant mortality and greater percent biomass consumption. In addition, succeeding environmental conditions differed immediately following the fires where the spring burn (late spring) was just before the summer-dry season and the fall burn was followed by the fall-wet and winter-cold seasons. In arid ecosystems, both plant

activity and microbial mediated N mineralization varies seasonally with high activity during wet and warm periods (Skujins 1981), and during periods of moisture fluctuation (Bolton et al. 1990).

While both spring and fall season burns were expected to produce immediate ammonium pulses via pyromineralization, the subsequent use and transformation of this pool was different for the two treatments. We were surprised there was such a high concentration of NH_4^+ -N in the fall treatments more than nine months after fire. Typically, concentrations of NH_4^+ -N are high immediately after fire and decrease in short order. For example Ellingson and Kauffman (2000) reported that NH_4^+ -N concentrations in the top 10 cm of soil were no different than control levels three months after burning. However in the sagebrush-dominated ecosystem of this study we found that NH_4^+ -N remains high for as long as 13 months after fire. For the fall season burn, which occurred during the wettest season, soil microbial activity may have ensued immediately, but was likely limited during the following winter-cold season. Meanwhile, significant mineralization in the spring burn treatment appears to have been delayed through the summer-dry season until the fall-wet season. Blank et al. (1994) found that NO_3^- -N concentrations increased one year following fire in a big sagebrush ecosystem in northwestern Nevada. While NO_3^- -N concentrations had already increased substantially by the summer following the fall burn treatment, nitrification of the NH_4^+ -N pulse was still greater than control rates 13 months after fire.

The severity of the burn with respect to live plant retention likely played a strong role in the fate of the mineral N pools. In fall burn plots, NH_4^+ -N was diminished dramatically during the fall wet season, a time of increased plant and microbial activity and demand for mineral N. Soil NH_4^+ -N levels were not significantly reduced during the fall-wet season in the spring burn treatments as high plant mortality likely reduced demand. Despite positive net nitrification, both treatments lost soil NO_3^- -N during the wet season indicating microbial immobilization or other pathways of loss such as denitrification or leaching. Both burn treatments produced a pulse of plant available mineral N, however the spring burn treatment had higher mortality and consumed a higher percentage of biomass, and therefore total N. The fall burn treatment, with its lower consumption, had greater post-fire plant cover which increased the demand for plant available N. The fall burn treatment therefore may have retained a higher percentage of its fire generated mineral N pulse.

Cover Treatment

The relationship between mineral N soil pools and different vegetation covers was likely related to differences in organic substrate, and demand which varied with season and due to differences in burn treatment severity. Nutrients including total N have been found to be spatially variable (Skujins 1981) and higher under shrub canopies compared to interspace areas in Great Basin shrublands (Doescher et al. 1984). At the juniper invaded Merrill Caves control site, soil mineral N (NH_4^+ -N and NO_3^- -N) and DON were likewise spatially variable. The highest concentrations of DON, the immediate precursor of mineral N, were found under juniper which sequestered N in thick organic horizons in the immediate understory. Microbial activity and plant uptake might be expected to be greater under juniper compared with surrounding areas due to the greater quantity of substrate under juniper. However, N mineralization was generally lower under juniper, and dramatic reductions in mineral N concentrations occurred outside juniper cover in the fall burn and control treatments. Allelopathic inhibition of microbial mediated processes due to plant cover is one mechanism suggested elsewhere for reduced N mineralization rates (Rice 1979).

Junipers largely survived fall burn treatments because of the lower burn severity and the underlying litter layer remained intact with only minimal consumption. The reduction of mineral N in soil beneath shrubs and open areas coincided with the fall-wet season, and reflects seasonally changing demand for available N due to increased plant and microbial activity. At the same time, mineral N produced earlier during the dormant season, remained higher beneath

juniper, indicating that demand was suppressed where juniper cover and its organic horizon remained intact.

The higher severity and consumption of the spring burn treatment altered the soil conditions more dramatically than the fall burn. Junipers (as well as shrubs) in plots receiving the spring burn treatment were killed and the underlying litter was largely consumed. Soil mineral N concentrations were retained under all covers through the fall-wet season indicating that the high severity of the spring burn treatment reduced plant demand, and potentially N retention, regardless of cover, unlike the fall burn treatment. In addition, the resulting convergence of N mineralization rates in soils under juniper and shrubs after the spring burn treatment indicates that juniper mortality along with the consumption of the associated organic horizon (which released sequestered biomass) reduced the suppressive effect of juniper on N mineralization rates.

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Table 1. A description of environmental variables and prescribed fire treatments at the Merrill Caves research site at Lava Beds National Monument.

	Fall 2003 Burn	Spring 2004 Burn
Elevation (m)	1450-1480	1450-1480
Slope (%)	<30	<30
Aspect	SE	SE
Soils	Shallow-volcanic	Shallow-volcanic
Fuel Model	patchy shrubs and bunch grasses, widely spaced juniper and mountain mahogany	
Date Burned	18 November 2003	June 2004
Prefire aboveground biomass (Mg/ha)	21.62	16.39
Biomass Consumed (Mg/ha)	12.11	13.84
Biomass Consumed (% of total)	56	84

Table 2. Buried bag seasonal incubation periods and recorded temperatures and precipitation. Daily temperature data was obtained from NOAAs Western Regional Climate Center website (<http://www.wrcc.dri.edu/index.html>). Incubation period beginning and ending precipitation values were obtained from the RAWS (Remote Automated Weather Stations ROMAN (Real-time Observation Monitor and Analysis Network) Indian Well site via MESOWEST STATION INTERFACE website (http://www.raws.wrh.noaa.gov/cgi-bin/roman/meso_base.cgi?stn=IDWC1&time=GMT). RAWS is operated by the U. S. Forest Service and Bureau of Land Management, and the data is distributed through NOAA.

	Seasonal Incubation Periods		
	Summer-Dry	Fall-Wet	Winter-Cold
Incubation Start Date	1 September 2004	21 October 2004	14 December 2004
Incubation Length (days)	42	43	78
Time Since Fall (18 November 2003) Burn (days)	288	338	392
Time Since Spring (June 2004) Burn (days)	~78	~128	~182
Daily Average Temperature (°C)	14.9	3.0	1.9
Precipitation Total (mm)	5.5	75.2	36
Precipitation Rate (mm/day)	0.13	1.75	0.46

Table 3. Soil NH₄⁺-N (mg/kg soil) between burn treatments for all cover types combined, for three sampling season dates following prescribed fire at Lava Beds National Monument. Numbers are means (±1SE). P-value from 2-way ANOVA. Different lower-case letters signify a significant difference between treatments (<0.1).

Sampling Date	Fall 2003 Burn ¹	Spring 2004 Burn ²	Control (no burn)	P-value
1 September 2004	19.39 ± 3.96a	16.10 ± 2.47a	3.61 ± 1.36b	0.001
21 October 2004	9.66 ± 1.70a	10.89 ± 1.71a	2.24 ± 0.75b	<0.001
14 December 2004	6.87 ± 1.25a	13.51 ± 1.83b	2.06 ± 0.71c	<0.001

¹Fall 2003 burn occurred November 18, 2003.

²Spring 2004 burn occurred June 2004.

Table 4. Soil NO₃⁻-N (mg/kg soil) between burn treatments for all cover types combined, for three sampling season dates following prescribed fire at Lava Beds National Monument. Numbers are means (±1SE). P-value from 2-way ANOVA. Different lower-case letters signify a significant difference between treatments (<0.1).

Date	Fall 2003 Burn	Spring 2004 Burn	Control (no burn)	P-value
Sept-01-2004	22.55 ± 1.48a	7.08 ± 0.98b	2.71 ± 0.31c	<0.001
Oct-21-2004	9.23 ± 2.43a	4.76 ± 0.84b	2.54 ± 0.68b	<0.001
Dec-14-2004	3.89 ± 0.86a	3.21 ± 0.38a	1.21 ± 0.19b	<0.001

¹Fall 2003 burn occurred November 18, 2003.

²Spring 2004 burn occurred June 2004.

Table 5. Soil ammonification rate (mg/kg soil/mo) between burn treatments for all cover types combined, during three sampling seasons following prescribed fire at the Lava Beds National Monument. Numbers are means (±1SE). P-value from 2-way ANOVA. Different lower-case letters signify a significant difference (<0.1).

Sample Season	Fall 2003 Burn	Spring 2004 Burn	Control (no burn)	p-value
Summer-Dry 2004	-0.05 ± 2.20	-0.67 ± 1.46	-1.21 ± 0.72	0.847
Fall-Wet 2004	-0.28 ± 0.83a	4.42 ± 1.55b	-0.14 ± 0.44a	0.001
Winter-Cold 2004/05	-1.20 ± 0.82	-1.07 ± 0.71	-0.82 ± 0.62	0.934

¹Fall 2003 burn occurred 18 November 2003.

²Spring 2004 burn occurred June 2004.

Table 6. Soil nitrification rate (mg/kg soil/mo) between burn treatments for all cover types combined, during three sampling seasons following prescribed fire at the Lava Beds National Monument. Numbers are means (±1SE). P-value from 2-way ANOVA. Different lower-case letters signify a significant difference (<0.1) between treatments within the same sampling period.

Sample Season	Fall 2003 Burn	Spring 2004 Burn	Control (no burn)	p-value
Summer-Dry 2004	-2.36 ± 0.93a	1.58 ± 0.86b	-0.06 ± 0.35b	0.017
Fall-Wet 2004	2.76 ± 1.05a	2.18 ± 0.29a	0.82 ± 0.44b	0.028
Winter-Cold 2004/05	1.58 ± 0.30a	2.34 ± 0.22b	0.60 ± 0.16c	<0.001

¹Fall 2003 burn occurred November 18, 2003.

²Spring 2004 burn occurred June 2004.

Table 7. Soil total carbon (%) and nitrogen (%), and C/N ratios between burn treatments for all cover types combined, following prescribed fire at the Lava Beds National Monument. Numbers are means (±1SE). P-value from 2-way ANOVA. Significant difference set at 0.1.

	Fall 2003 Burn	Spring 2004 Burn	Control (no burn)	P-value
% Carbon	3.56 ± 0.38	3.26 ± 0.40	3.23 ± 0.39	0.582
% Nitrogen	0.268 ± 0.028	0.233 ± 0.024	0.228 ± 0.024	0.242
C/N Ratio	13.28 ± 0.43	13.68 ± 0.35	13.87 ± 0.30	0.273

¹Fall 2003 burn occurred November 18, 2003.

²Spring 2004 burn occurred June 2004.

Table 8. DON (mg/kg soil) between burn treatments for all cover types combined, for three sampling season dates following prescribed fire at the Lava Beds National Monument. Numbers are means ($\pm 1SE$). P-value from 2-way ANOVA. Significant difference set at 0.1.

Sampling Date	Treatment			P-value
	Fall 2003 Burn	Spring 2004 Burn	Control (no burn)	
Sept-01-2004	12.01 \pm 1.57	16.17 \pm 3.20	13.74 \pm 6.65	0.798
Oct-21-2004	13.84 \pm 4.79	12.57 \pm 1.93	12.12 \pm 3.78	0.919
Dec-14-2004	8.47 \pm 2.78	5.45 \pm 1.59	8.17 \pm 2.46	0.280

¹Fall 2003 burn occurred November 18, 2003.

²Spring 2004 burn occurred June 2004.

Table 9. Soil NH₄⁺-N (mg/kg soil) among different cover types for each burn treatment, during three sampling seasons following prescribed fire at the Lava Beds National Monument. Numbers are means ($\pm 1SE$). P-value from 2-way ANOVA. Different lower-case letters signify a significant difference (<0.1).

Sampling Date/ Burn Treatment	Plant Cover				P-value
	<i>Juniper occidentalis</i>	<i>Artemesia tridentata</i>	<i>Purshia tridentata</i>	Open	
1 September 2004					
Fall 2003 Burn ¹	20.79 \pm 8.25	8.27 \pm 2.81	26.92 \pm 13.00	21.59 \pm 6.68	0.481
Spring 2004 Burn ²	18.30 \pm 6.37	10.62 \pm 1.69	15.30 \pm 4.41	20.18 \pm 5.38	0.534
Control (no burn)	6.60 \pm 5.19	2.72 \pm 0.66	2.01 \pm 0.42	3.10 \pm 0.85	0.630
21 October 2004					
Fall 2003 Burn ¹	17.96 \pm 4.83a	4.65 \pm 1.46b	8.87 \pm 3.24b	7.18 \pm 4.16b	0.095
Spring 2004 Burn ²	13.73 \pm 4.41	13.62 \pm 2.69	9.09 \pm 3.53	7.12 \pm 1.87	0.406
Control (no burn)	5.96 \pm 3.07a	0.97 \pm 0.10b	0.71 \pm 0.12b	1.31 \pm 0.32b	0.087
14 December 2004					
Fall 2003 Burn ¹	15.82 \pm 6.71a	1.13 \pm 0.48b	4.14 \pm 1.98b	6.41 \pm 1.85b	0.058
Spring 2004 Burn ²	14.92 \pm 4.61	11.90 \pm 2.96	14.05 \pm 4.08	13.18 \pm 6.36	0.972
Control (no burn)	3.97 \pm 2.34	1.21 \pm 0.30	1.39 \pm 0.25	1.65 \pm 0.53	0.369

¹Fall 2003 burn occurred November 18, 2003.

²Spring 2004 burn occurred June 2004.

Table 10. Soil NO₃⁻-N (mg/kg soil) among different cover types for each burn treatment, during three sampling seasons following prescribed fire at the Lava Beds National Monument. Numbers are means (±1SE). P-value from 2-way ANOVA. Different lower-case letters signify a significant difference (<0.1).

Sampling Date/ Burn Treatment	<i>Juniper occidentalis</i>	<i>Artemesia tridentata</i>	<i>Purshia tridentata</i>	Open	P-value
Sept-01-2004					
Fall 2003 Burn ¹	27.67 ± 5.37	15.55 ± 1.99	28.01 ± 5.57	18.99 ± 4.50	0.176
Spring 2004 Burn ²	7.72 ± 2.77	5.87 ± 0.42	7.99 ± 1.49	6.74 ± 0.55	0.784
Control (no burn)	2.67 ± 1.27	2.74 ± 0.48	2.70 ± 0.53	2.71 ± 0.58	1.000
Oct-21-2004					
Fall 2003 Burn ¹	13.96 ± 2.70a	4.36 ± 0.77b	12.78 ± 2.89ac	5.82 ± 2.89bc	0.080
Spring 2004 Burn ²	5.40 ± 2.29	3.78 ± 0.64	6.33 ± 1.73	3.54 ± 1.11	0.557
Control (no burn)	5.72 ± 2.02a	1.59 ± 0.47b	1.17 ± 0.21b	1.67 ± 1.00b	0.044
Dec-14-2004					
Fall 2003 Burn ¹	6.89 ± 2.07a	1.72 ± 0.28b	3.99 ± 0.91ab	2.94 ± 0.87b	0.048
Spring 2004 Burn ²	4.34 ± 1.18a	2.51 ± 0.25bc	3.96 ± 0.42ab	2.02 ± 0.28c	0.065
Control (no burn)	1.09 ± 0.14	1.48 ± 0.48	1.45 ± 0.13	0.82 ± 0.18	0.304

¹Fall 2003 burn occurred November 18, 2003.

²Spring 2004 burn occurred June 2004.

Table 11. Soil ammonification rate (mg/kg soil/mo) among different cover types for each burn treatment, during three sampling seasons following prescribed fire at the Lava Beds National Monument. Numbers are means (±1SE). P-value from 2-way ANOVA. Different lower-case letters signify a significant difference (<0.1).

Sampling Season/ Burn Treatment	<i>Juniper occidentalis</i>	<i>Artemesia tridentata</i>	<i>Purshia tridentata</i>	Open	P-value
Summer-Dry 2004					
Fall 2003 Burn ¹	3.66 ± 3.64	-1.56 ± 1.51	-0.36 ± 4.86	-1.91 ± 5.49	0.771
Spring 2004 Burn ²	-0.77 ± 2.05	-1.81 ± 0.92	-3.89 ± 0.99	3.77 ± 4.01	0.172
Control (no burn)	-2.95 ± 2.52	-0.96 ± 0.63	0.17 ± 0.67	-1.12 ± 0.41	0.459
Fall-Wet 2004					
Fall 2003 Burn ¹	-5.10 ± 1.35a	0.47 ± 0.75b	0.46 ± 1.28b	3.06 ± 2.17b	0.009
Spring 2004 Burn ²	9.18 ± 3.88	2.78 ± 1.23	3.07 ± 1.03	2.65 ± 2.44	0.204
Control (no burn)	-0.56 ± 1.65	0.25 ± 0.46	-0.06 ± 0.23	-0.20 ± 0.30	0.931
Winter-Cold 2004/05					
Fall 2003 Burn ¹	-3.39 ± 2.13	0.28 ± 0.52	-1.49 ± 1.22	-0.19 ± 1.82	0.369
Spring 2004 Burn ²	-0.89 ± 0.43	0.23 ± 1.90	-1.86 ± 2.00	-1.75 ± 1.96	0.810
Control (no burn)	-2.94 ± 2.37	-0.02 ± 0.31	-0.05 ± 0.17	-0.33 ± 0.30	0.285

¹Fall 2003 burn occurred November 18, 2003.

²Spring 2004 burn occurred June 2004.

Table 12. Soil nitrification rate (mg/kg soil/mo) among different cover types for each burn treatment, during three sampling seasons following prescribed fire at the Lava Beds National Monument. Numbers are means (± 1 SE). P-value from 2-way ANOVA. Different lower-case letters signify a significant difference (<0.1).

Sampling Season/ Burn Treatment	<i>Juniper occidentalis</i>	<i>Artemisia tridentata</i>	<i>Purshia tridentata</i>	Open	P-value
Summer-dry 2004					
Fall 2003 Burn ¹	-1.92 \pm 4.36	-2.15 \pm 1.32	-4.79 \pm 3.03	-0.58 \pm 2.51	0.795
Spring 2004 Burn ²	0.71 \pm 0.77	0.33 \pm 0.36	2.44 \pm 1.93	2.85 \pm 1.75	0.496
Control (no burn)	0.65 \pm 1.00	-0.13 \pm 0.56	-0.23 \pm 0.28	-0.52 \pm 0.46	0.613
Fall-wet 2005					
Fall 2003 Burn ¹	1.46 \pm 1.74	3.40 \pm 1.49	2.29 \pm 0.68	3.90 \pm 1.46	0.612
Spring 2004 Burn ²	0.83 \pm 0.56a	1.58 \pm 0.59a	4.04 \pm 1.19b	2.28 \pm 0.31ab	0.042
Control (no burn)	0.29 \pm 1.57	1.35 \pm 0.31	0.95 \pm 0.20	0.70 \pm 0.36	0.830
Winter-Cold 2004/05					
Fall 2003 Burn ¹	0.16 \pm 0.82a	1.33 \pm 0.15ab	2.70 \pm 0.33c	2.14 \pm 0.34bc	0.010
Spring 2004 Burn ²	1.77 \pm 0.57	2.66 \pm 0.70	3.10 \pm 0.49	1.85 \pm 0.25	0.254
Control (no burn)	0.06 \pm 0.18a	0.75 \pm 0.36bc	1.23 \pm 0.38b	0.36 \pm 0.07ac	0.049

¹Fall 2003 burn occurred November 18, 2003.

²Spring 2004 burn occurred June 2004.

Table 13. Soil total carbon (%) and nitrogen (%), and C/N ratios between different cover types for each burn treatment, following prescribed fire at the Lava Beds National Monument. Numbers are means (± 1 SE).

Treatment		<i>Juniper occidentalis</i>	<i>Artemisia tridentata</i>	<i>Purshia tridentata</i>	Open
Fall 2003 Burn	% Carbon	3.57 \pm 0.46	4.51 \pm 0.63	NA	2.60 \pm 0.44
	% Nitrogen	0.261 \pm .023	0.347 \pm 0.056	NA	0.195 \pm 0.029
	C/N Ratio	13.59 \pm 0.83	13.28 \pm 0.72	NA	12.97 \pm 0.49
Spring 2004 Burn	% Carbon	4.12 \pm 0.83	2.58 \pm 0.28	3.76 \pm 0.70	2.58 \pm 0.28
	% Nitrogen	0.287 \pm 0.053	0.188 \pm 0.016	0.270 \pm 0.043	0.188 \pm 0.015
	C/N Ratio	14.07 \pm 0.41	13.58 \pm 0.40	13.48 \pm 0.40	13.58 \pm 0.49
Control-No Burn	% Carbon	3.86 \pm 0.27	3.38 \pm 0.66	3.30 \pm 0.55	2.38 \pm 0.61
	% Nitrogen	0.261 \pm .016	0.232 \pm 0.039	0.238 \pm .038	0.180 \pm .043
	C/N Ratio	14.59 \pm 0.37	14.16 \pm 0.40	13.73 \pm 0.55	13.00 \pm 0.45

¹Fall 2003 burn occurred November 18, 2003.

²Spring 2004 burn occurred June 2004.

Table 14. DON (mg/kg soil) among different cover types for each burn treatment, during three sampling seasons following prescribed fire at the Lava Beds National Monument. Numbers are means ($\pm 1SE$). P-value from 2-way ANOVA. Different lower-case letters signify a significant difference (<0.1).

Sampling Season/ Burn Treatment	<i>Juniper occidentalis</i>	<i>Artemesia tridentata</i>	<i>Purshia tridentata</i>	Open	P-value
Sept-01-2004					
Fall 2003 Burn ¹	8.75 \pm 2.75	11.99 \pm 0.82	20.05 \pm 6.55	7.24 \pm 2.97	0.130
Spring 2004 Burn ²	20.12 \pm 5.93	13.99 \pm 4.26	18.93 \pm 4.40	11.62 \pm 2.17	0.492
Control (no burn)	38.19 \pm 27.47	7.09 \pm 0.88	6.02 \pm 1.39	3.68 \pm 0.66	0.276
Oct-21-2004					
Fall 2003 Burn ¹	26.56 \pm 15.21	7.87 \pm 0.93	15.33 \pm 3.30	5.60 \pm 1.16	0.263
Spring 2004 Burn ²	22.62 \pm 8.01	10.16 \pm 1.80	11.58 \pm 3.89	5.93 \pm 1.16	0.104
Control (no burn)	34.37 \pm 11.72a	5.19 \pm 1.30b	4.32 \pm 0.63b	4.60 \pm 2.80b	0.006
Dec-14-2004					
Fall 2003 Burn ¹	16.45 \pm 6.20	4.69 \pm 1.49	7.51 \pm 3.31	5.22 \pm 2.21	0.139
Spring 2004 Burn ²	6.97 \pm 1.42	4.89 \pm 2.58	5.51 \pm 2.51	4.40 \pm 1.27	0.825
Control (no burn)	13.43 \pm 4.38	6.71 \pm 2.31	7.84 \pm 2.44	4.71 \pm 1.97	0.222

¹Fall 2003 burn occurred November 18, 2003.

²Spring 2004 burn occurred June 2004.

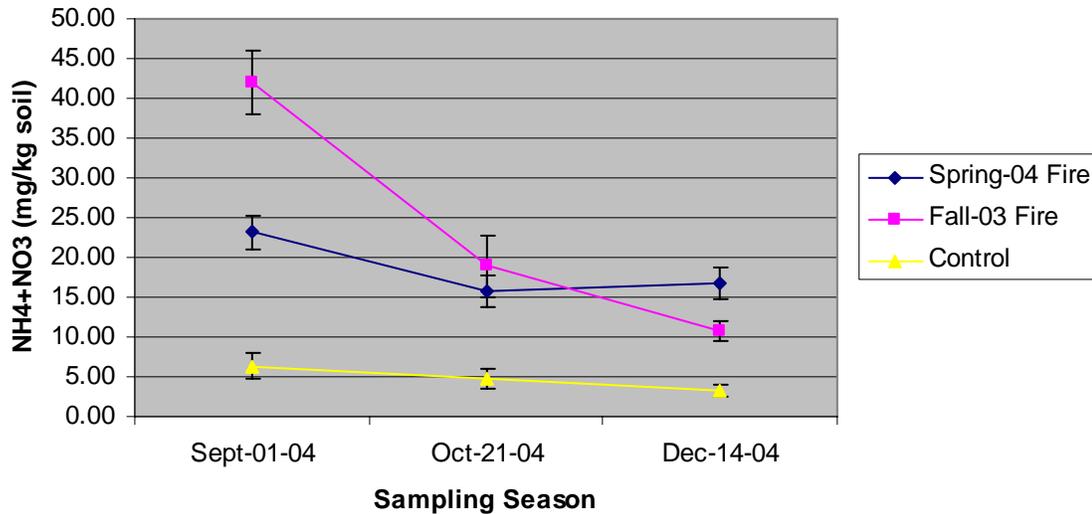


Figure 1. Soil mineral-N (mg/kg soil) between burn treatments for all cover types combined, for three sampling season dates following prescribed fire at Lava Beds National Monument. Numbers are means ($\pm 1SE$). The fall prescribed fire was conducted on 18 November 2003 and the spring prescribed fire occurred in June 2004.

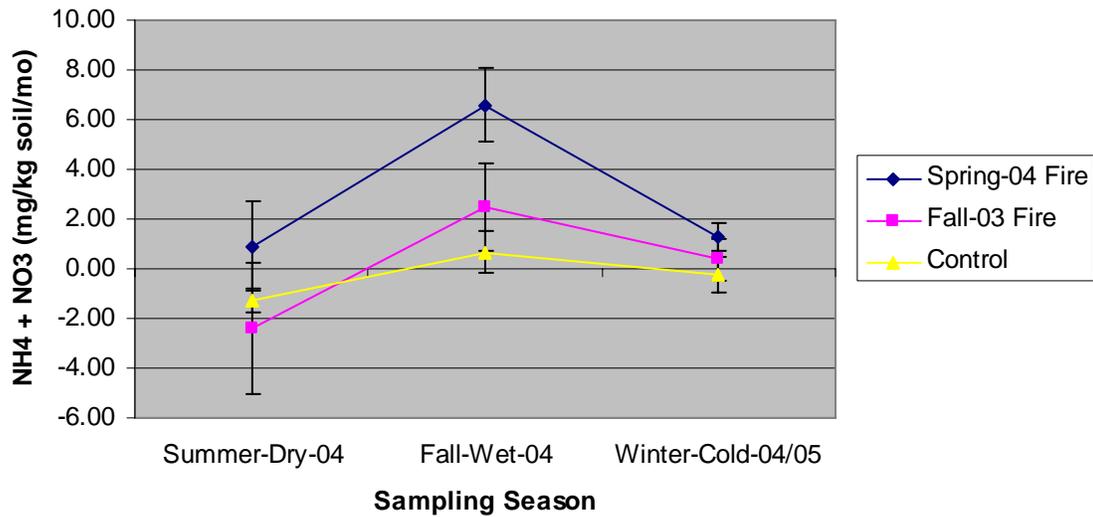


Figure 2. Soil N-mineralization rate (mg/kg soil/mo) between burn treatments for all cover types combined, during three sampling seasons following prescribed fire at the Lava Beds National Monument. Numbers are means \pm 1SE.

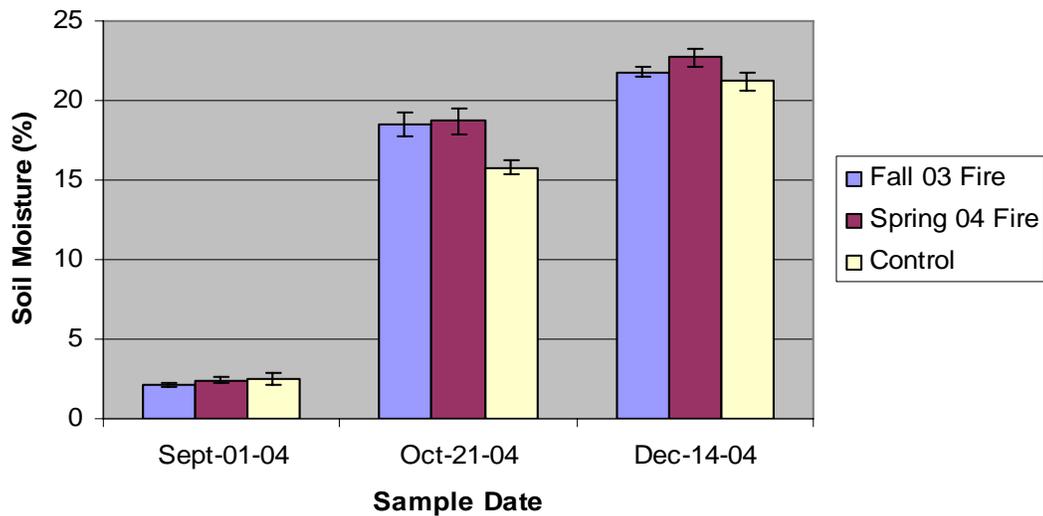


Figure 3. Soil moisture (%) between burn treatments for all cover types combined, during three sampling seasons following prescribed fire at the Lava Beds National Monument. Numbers are means \pm 1SE.

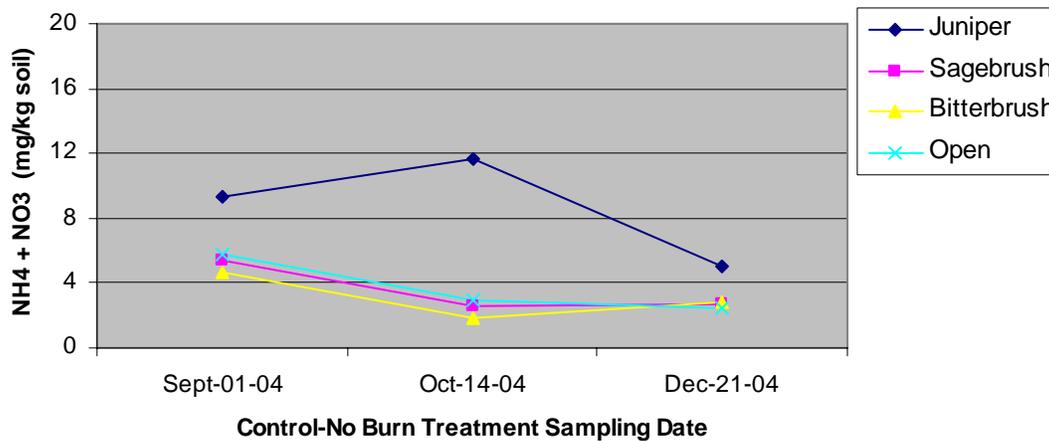
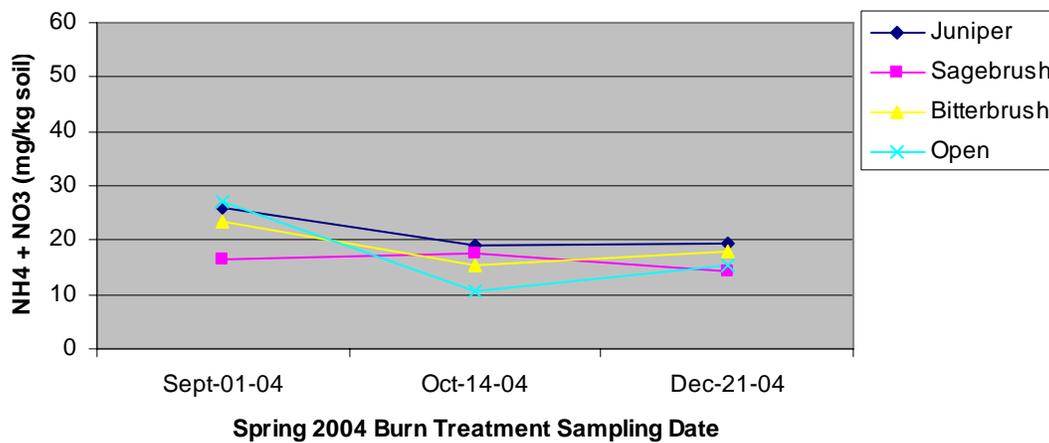
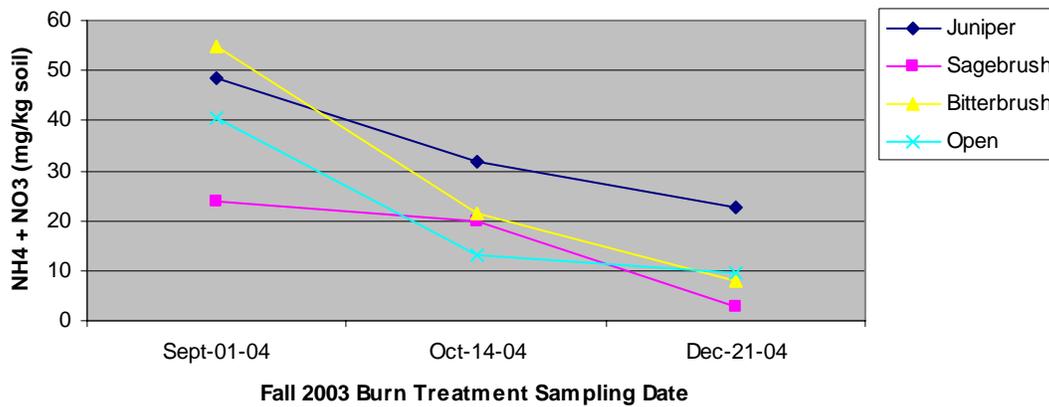


Figure 4. Soil mineral-N (mg/kg soil) between cover types for each burn treatment (fall 2003 burn, spring 2004 burn and control – no burn), for three sampling season dates following prescribed fire at Lava Beds National Monument. Numbers are means.

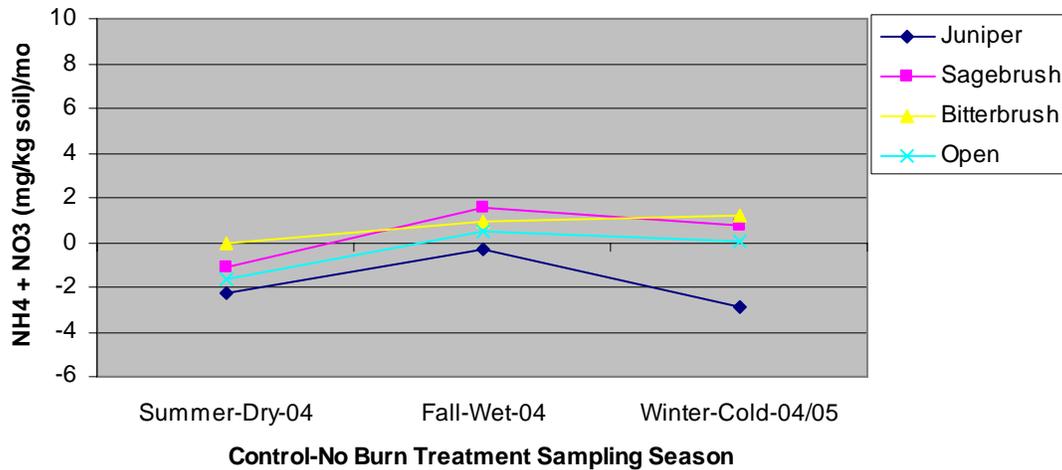
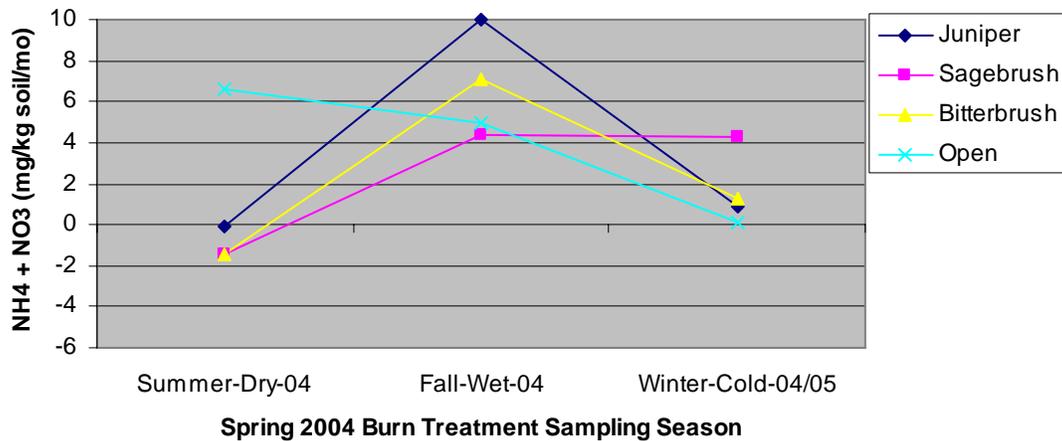
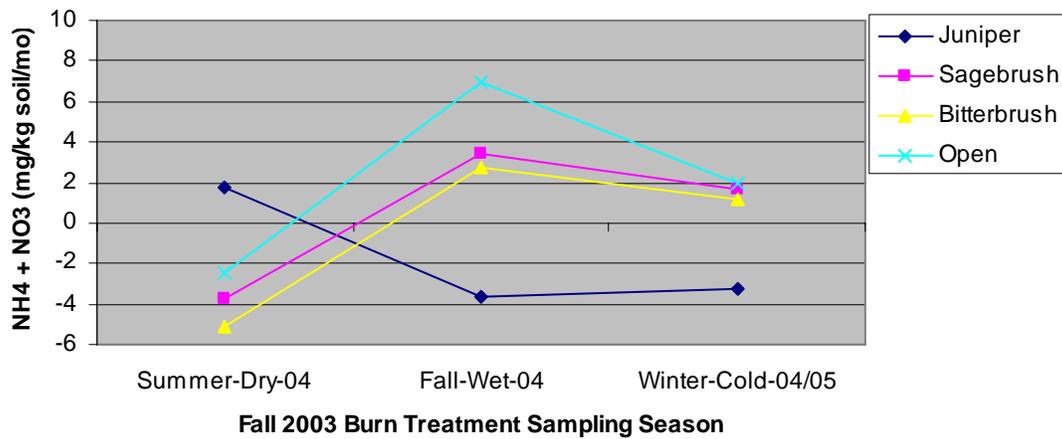


Figure 5. Soil N-mineralization rate (mg/kg soil/mo) between cover types for each burn treatment (fall 2003 burn, spring 2004 burn and control – no burn), for three sampling season dates following prescribed fire at Lava Beds National Monument. Numbers are means.

Conclusions and Lessons Learned

The issue of reintroduction of prescribed fire in the sagebrush steppe is complicated by issues such as invasive species, cattle grazing, and increasing woody dominance. As these issues affect both the behavior of the fire itself, and the response of the vegetation communities following fire, they must be considered when developing a prescribed fire plan.

Domestic livestock grazing has been removed from Lava Beds National Monument for the last 30 years, alleviating the plant communities within the Monument from this disturbance pressure. Since that time, there has already been a dramatic response in the native plant communities to this passive restoration. Research conducted in the years following removal of livestock showed a complete dominance of cheatgrass in degraded, low-elevation areas where cattle and sheep were common (Erhard 1979; Martin et al 1980; Olsen et al 1980). While we still saw higher cheatgrass covers in these degraded areas (Gillems Camp) compared to other areas in the Monument, there is now a functioning native bunchgrass, shrub, and forb component that did not exist when grazing was present.

At Gillems Camp, we saw an initial decrease in cheatgrass germination following both spring and fall fires, but this effect was transitory, and by the following year, there were more cheatgrass seeds germinated in burned plots than in controls. Total cheatgrass covers, however, were significantly lower one year following fire in burned plots (both spring and fall) than in their unburned control counterparts. This reduction in cheatgrass cover provides an opportunity for native plants to successfully compete with exotics. In the first post-fire year at this site, we saw an increase in native bunchgrass flowering, demonstrating the ability of these fire adapted plants to flourish in a post-burn environment.

The dry, continuous fuel source provided by cheatgrass can shorten the fire return interval, and while we saw positive responses at this site following burns, fire should not be used too frequently solely for reduction of cheatgrass, as fire could harm native plants if it is applied too often. Native grasses and forbs have been increasing in these low-elevation, degraded areas of the National Monument since the removal of livestock, and with a management policy to maintain the natural fire return interval, this trajectory towards a more native dominated site will continue. In these areas, a good management objective would be to burn (or allow natural fires to burn) for the maintenance of the native plants, rather than for cheatgrass control.

In our sites dominated by native shrubs, forbs, and bunchgrasses (Fleener Chimneys), fire frequency is not outside its historical range of variability, and fires at this site reduced shrub cover and shifted composition towards a larger native bunchgrass and forb component. There was a significant increase in number of native forbs that germinated following both spring and fall fires. While there was a reduction in number of bunchgrass seeds germinated following fire, the fire-enhanced flowering seen at this site will quickly replenish the bunchgrass component of the soil seedbank. These sites were likely never grazed, as there are lava flows preventing the movement of domestic animals, and the fire return interval here has been maintained. Fire here serves to shift vegetation composition from a large shrub component to a grassland community and to prevent the establishment of western juniper. Maintaining a fire return interval of less than 30 years would continue to prevent woody dominance and keep these sites in near pristine condition.

In areas where burns are less frequent than they were historically, western juniper and shrub species are dominant, decreasing the herbaceous vegetation component (Merrill Caves). Management objectives in these sites are to reduce woody cover by applying prescribed fire, and then maintain the fire return interval at its historical range of variability. In fires at this site, these objectives were largely met. We saw high juniper mortality and a decrease in shrub covers. Fire-enhanced flowering was seen in all studied bunchgrass species following fire, and large amounts of duff and litter were removed by fires, opening up microsites for germination. Young (<30 year

old) junipers do not survive fire, so managing to prevent juniper encroachment requires re-burning these areas at least every 30 years.

We saw few differences in fire effects between spring and fall burns. Spring burns tended to move more quickly and consumed greater amounts of biomass, while fall fires were difficult to ignite due to cold temperatures, but vegetation response was comparable. These results suggest that season of burn may be less of a managerial concern than the need for maintenance of the fire return interval.

Caution should be taken in extrapolating these results outside the context of the Lava Beds National Monument. The unique lava substrate and absence of grazing make this a unique system within the Great Basin. Longer term monitoring will be necessary to determine the impacts of these prescribed fires on the recovery of these ecosystems.

APPENDICES:

Appendix 1: Lava Beds National Monument Weather Data

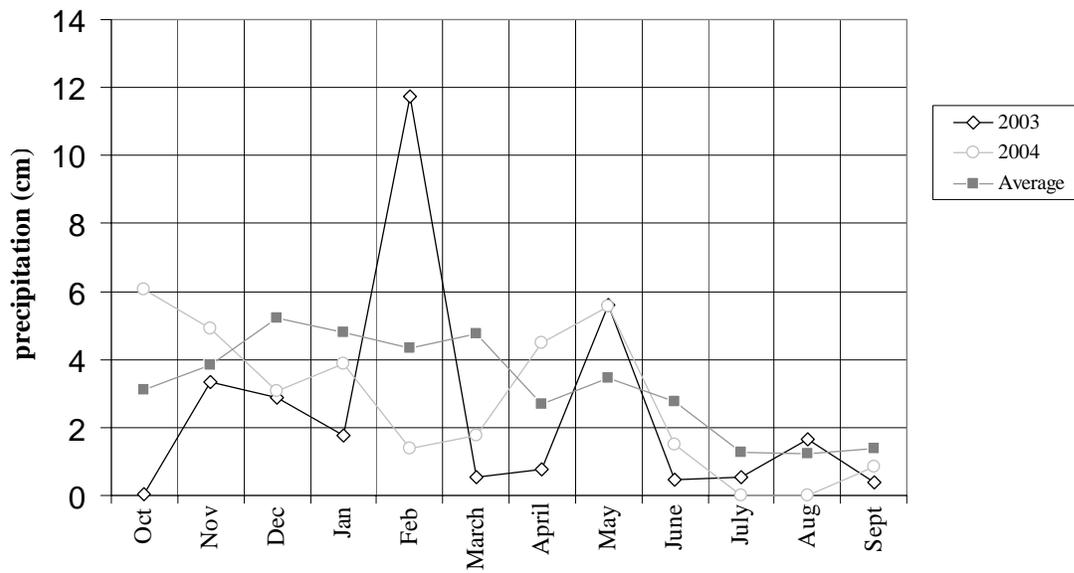


Figure 1: Monthly precipitation (in cm) for Lava Beds National Monument. Data for years of field sampling (2003, 2004) are shown as well as 58 year average. Precipitation was measured at park headquarters (NPS, unpublished data, Lava Beds Data File)

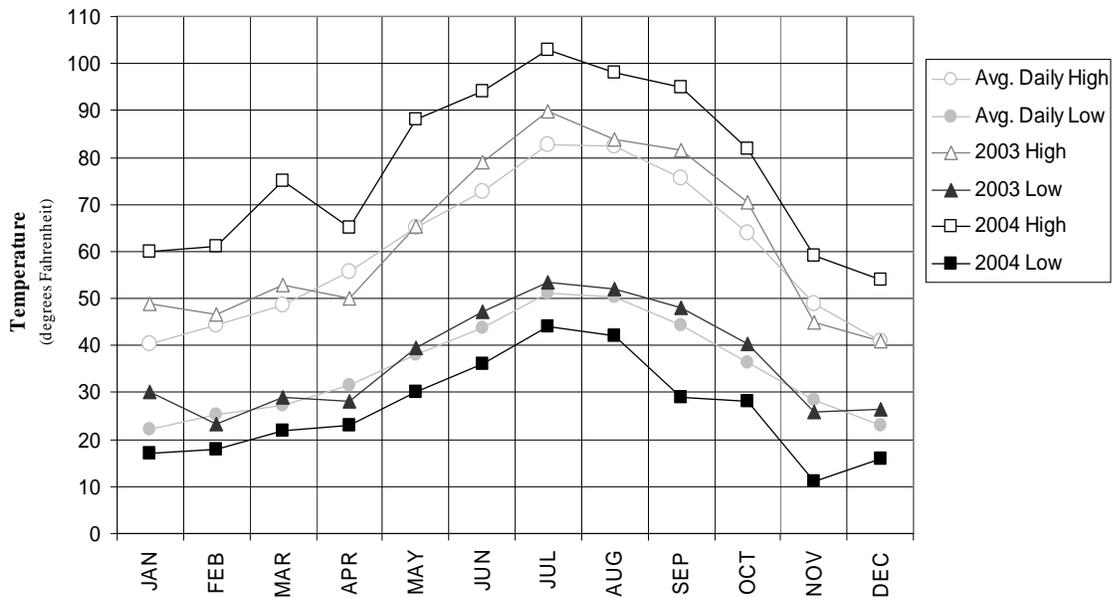


Figure 2: Temperature data for Lava Beds National Monument. Data collected at Park Headquarters. Monthly high and low temperatures are shown (in degrees F) for years of field sampling (2003, 2004) as well as 58 year average (NPS, unpublished data, Lava Beds Data File).

Table 1: Continued

	Gillens Camp						Fleener Chimneys						Merrill Caves					
	Spring		Fall		Control		Spring		Fall		Control		Spring		Fall		Control	
	pre	post	pre	post	pre	post	pre	post	pre	post	pre	post	pre	post	pre	post	pre	post
<i>Poa</i>	mean	3.82	2.41	4.32	2.50	4.00	2.78	2.06	0.85	3.05	3.64	1.34	2.83	1.46	2.06	1.99	1.04	1.83
	SE	1.20	0.76	0.90	0.57	1.34	0.67	0.48	0.36	0.96	1.38	0.47	0.66	0.46	0.90	0.27	0.25	0.30
<i>Pseudoroegneria</i>	mean	3.02	0.30	1.76	0.73	0.18	1.11	8.93	0.26	7.12	0.21	2.20	0	5.00	2.37	3.29	2.88	1.53
	SE	0.95	0.15	1.27	0.68	0.18	0.82	3.06	0.18	2.16	0.21	1.18	0	2.43	1.35	1.41	0.67	0.89
<i>Stipa</i>	mean	0	0	0	0	0	0	1.95	0.98	0	1.23	0.72	2.67	0	0.08	0	0	0.04
	SE	0	0	0	0	0	0	1	0.33	0	0.33	0.72	0.43	0	0.08	0	0	0.04
<i>Artemisia</i>	mean	0.40	0	0	1.80	0	0	0.13	5.34	20.19	14.42	13.12	7.47	17.85	21.78	7.57	9.90	2.57
	SE	0.25	0	0	0.56	0	0	0.07	1.52	4.32	3.12	3.17	0.99	3.29	2.17	2.51	2.69	0.86
<i>Tridentata</i>	mean	17.26	0.01	15.00	0	5.66	2.74	0.12	0.01	0.43	0.11	0	0.01	0.08	0.30	0.05	0	0.17
	SE	3.30	0.01	5.39	0	2.14	1.05	0.04	0.01	0.31	0.11	0	0.01	0.06	0.21	0.05	0	0.17
<i>Clysothamnus</i>	mean	0.07	0	0	0.85	0	0	0.12	0.10	0.29	0.20	0.26	0.23	0.19	0.04	0.01	0	0
	SE	0.07	0	0	0.66	0	0	0.04	0.05	0.12	0.10	0.19	0.14	0.12	0.04	0.01	0	0
<i>Prunus</i>	mean	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0.04	0	0	0
	SE	0	0	0	0	0	0	0	0	0	0	0	0	0.25	0.04	0	0	0
<i>Emerginata</i>	mean	0	0	0.11	0	0	0.57	6.46	0.35	3.05	2.71	0.12	1.93	12.86	6.63	1.39	4.62	4.31
	SE	0	0	0.11	0	0	0.57	3.96	0.19	1.64	1.38	0.12	1.22	3.98	2.18	0.76	1.54	1.88
<i>Ribes</i>	mean	0	0	0	0	0	0	0.18	0	0	0	0	0	3.62	0.22	0	0	0.57
	SE	0	0	0	0	0	0	0.18	0	0	0	0	0	2.17	0.20	0	0	0.57
<i>Tetralymia</i>	mean	0.15	0.03	0	0	0	0	1.73	0.18	2.14	0.42	0	0.03	0	0	0	0.12	0
	SE	0.14	0.03	0	0	0	0	0.97	0.14	0.82	0.14	0	0.03	0	0	0	0.12	0
<i>Cercocarpus</i>	mean	0	0	0	0	0	0	0	0	0	0	0	0	5.24	14.79	6.10	3.72	1.43
	SE	0	0	0	0	0	0	0	0	0	0	0	0	3.21	5.66	4.75	2.31	1.41
<i>Juniperus</i>	mean	0	0	0.26	0	0.05	0.05	0	0	0.03	0	1.32	1.32	15.04	10.98	5.38	10.06	6.78
	SE	0	0	0.16	0	0.05	0.05	0	0	0.03	0	0.82	0.82	11.1	5.10	3.40	2.79	2.78
<i>Carex</i>	mean	0	0	0	0	0	0	0	0	0	0	0	0	0.16	0	0	0	0.07
	SE	0	0	0	0	0	0	0	0	0	0	0	0	0.16	0	0	0	0.07

Table 1: Continued

	Fleener Chimneys		Gillems Camp		Merrill Caves	
	control post	spring recovery post	control post	spring recovery post	control post	spring recovery post
<i>Epilobium minutum</i>	mean 5.00	24.00 2.00	1.00 1.00	2.00 0.00	3.00 3.00	0.00 0.00
	SE 3.16	24.00 2.00	1.00 1.00	1.22 0.00	3.00 3.00	0.00 0.00
<i>Festuca idahoensis</i>	mean 0.00	0.00 3.00	0.00 0.00	0.00 0.00	0.00 0.00	0.00 0.00
	SE 0.00	2.00 2.00	0.00 2.00	0.00 0.00	2.00 2.00	0.00 0.00
<i>Lactuca serriola</i>	mean 4.00	1.00 2.00	62.00 1.85	10.00 2.24	13.00 8.00	2.00 1.22
	SE 2.92	0.00 1.00	1.85 0.00	2.24 1.00	8.00 0.00	1.22 1.00
<i>Mertzelia albicaulis</i>	mean 0.00	0.00 0.00	0.00 0.00	1.00 1.00	0.00 0.00	1.00 1.00
	SE 0.00	0.00 0.00	0.00 0.00	1.00 1.00	0.00 0.00	1.00 1.00
<i>Phacelia linearis</i>	mean 38.00	54.00 159.00	0.00 1477.00	0.00 0.00	0.00 0.00	76.00 33.00
	SE 12.10	19.20 50.13	516.58 0.00	0.00 0.00	0.00 0.00	67.37 20.77
<i>Phacelia ramosissima</i>	mean 0.00	10.00 0.00	32.00 0.00	0.00 0.00	0.00 0.00	38.00 41.00
	SE 0.00	6.52 0.00	17.86 0.00	0.00 0.00	0.00 0.00	36.76 24.67
<i>Plagiobothrys tenellus</i>	mean 46.00	4.00 164.00	21.00 0.00	0.00 0.00	0.00 0.00	0.00 1.00
	SE 43.51	2.92 152.79	13.08 0.00	0.00 0.00	0.00 0.00	0.00 1.00
<i>Poa secunda</i>	mean 19.00	21.00 6.00	19.00 5.00	8.00 8.00	1.00 1.00	1.00 1.00
	SE 9.67	8.28 4.85	4.85 3.16	6.82 6.82	1.00 1.00	1.00 1.00
<i>Pseudrocragma spicata</i>	mean 0.00	14.00 0.00	38.00 0.00	1.00 1.00	0.00 0.00	6.00 21.00
	SE 0.00	6.20 0.00	23.54 0.00	1.00 1.00	0.00 0.00	4.85 15.20
<i>Sisymbrium altissimum</i>	mean 0.00	2.00 2.00	1.00 1.00	125.00 17.00	358.00 0.00	0.00 0.00
	SE 0.00	1.22 2.00	1.00 1.00	75.17 7.00	127.25 0.00	0.00 0.00
<i>Vulpia spp.</i>	mean 3.00	3.00 0.00	0.00 0.00	3.00 0.00	9.00 0.00	0.00 0.00
	SE 3.00	3.00 0.00	0.00 0.00	2.00 0.00	6.00 0.00	0.00 0.00
unknown forb	mean 7.00	21.00 2.00	46.00 69.00	5.00 5.00	3.00 3.00	52.00 256.00
	SE 3.74	12.88 1.22	27.18 27.18	1.58 1.58	3.00 3.00	32.50 119.24

Table 2: Continued

	Fleener Chimneys				Gillems Camp				Merrill Caves					
	post	recovery	post	fall	control	post	recovery	post	fall	control	post	recovery	post	fall
<i>Festuca idahoensis</i>	mean	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	1.00	0.00	2.00	0.00	0.00
	SE	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	1.00	0.00	2.00	0.00	0.00
<i>Holosteum umbellatum</i>	mean	3.00	0.00	0.00	0.00	1.00	1.00	2.00	0.00	7.00	0.00	0.00	0.00	0.00
	SE	3.00	0.00	0.00	0.00	1.00	1.00	2.00	0.00	7.00	0.00	0.00	0.00	0.00
<i>Koeleria macrantha</i>	mean	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	SE	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lactuca scariola</i>	mean	0.00	0.00	0.00	1.00	6.00	16.00	11.00	18.00	0.00	0.00	0.00	0.00	0.00
	SE	0.00	0.00	0.00	1.87	12.59	7.81	9.82	0.00	0.00	0.00	0.00	0.00	0.00
<i>Malva neglecta</i>	mean	0.00	1.00	0.00	0.00	0.00	26.00	0.00	0.00	0.00	38.00	0.00	0.00	0.00
	SE	0.00	1.00	0.00	0.00	0.00	26.00	0.00	0.00	0.00	20.65	0.00	0.00	0.00
<i>Mentzelia albicaulis</i>	mean	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.00	0.00	0.00	4.00	0.00
	SE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.85	0.00	0.00	4.00	0.00
<i>Nicotiana attenuata</i>	mean	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	23.00	0.00	0.00
	SE	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.54	0.00	0.00
<i>Phacelia linearis</i>	mean	1.00	46.00	6.00	315.00	0.00	0.00	0.00	0.00	41.00	11.00	14.00	1.00	0.00
	SE	1.00	21.99	4.85	202.16	0.00	0.00	0.00	0.00	22.47	6.00	7.00	1.00	0.00
<i>Phacelia ramosissima</i>	mean	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
	SE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
<i>Plagiobothrys tenellus</i>	mean	180.00	22.00	27.00	22.00	1.00	4.00	0.00	0.00	8.00	4.00	2.92	12.00	0.00
	SE	122.60	19.60	19.85	11.25	1.00	2.45	0.00	0.00	5.61	1.87	28.27	12.00	0.00
<i>Poa secunda</i>	mean	1.00	11.00	3.00	13.00	2.00	6.00	0.00	2.00	13.00	4.00	4.00	10.00	0.00
	SE	1.00	5.34	2.00	8.46	1.22	3.67	0.00	1.22	9.43	2.92	2.92	6.52	0.00
<i>Pseudoroegneria spicata</i>	mean	0.00	28.00	1.00	4.00	3.00	4.00	1.00	6.00	0.00	0.00	0.00	1.00	0.00
	SE	0.00	28.00	1.00	1.87	2.00	2.92	1.00	3.67	0.00	0.00	0.00	1.00	0.00
<i>Purshia tridentata</i>	mean	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
	SE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
<i>Sisymbrium altissimum</i>	mean	2.00	2.00	0.00	1.00	14.00	7.00	35.00	41.00	0.00	0.00	0.00	0.00	0.00
	SE	2.00	2.00	0.00	1.00	14.00	1.22	17.54	26.71	0.00	0.00	0.00	0.00	0.00
<i>Stephanomeria tenuifolia</i>	mean	0.00	0.00	0.00	0.00	0.00	0.00	4.00	2.00	0.00	0.00	0.00	0.00	0.00
	SE	0.00	0.00	0.00	0.00	0.00	0.00	1.87	1.22	0.00	0.00	0.00	0.00	0.00
<i>Vulpia sp.</i>	mean	0.00	0.00	0.00	2.00	0.00	0.00	1.00	1.00	0.00	0.00	1.00	0.00	0.00
	SE	0.00	0.00	0.00	2.00	0.00	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00
unknown forb	mean	1.00	353.00	5.00	364.00	0.00	56.00	4.00	17.00	6.00	452.00	7.33	747.00	0.00
	SE	1.00	154.45	3.16	76.52	0.00	33.07	2.92	8.60	2.92	173.57	2.82	243.12	0.00