



Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: <http://www.elsevier.com/locate/rama>

Original Research

Contrasting Effects of Long-Term Fire on Sagebrush Steppe Shrubs Mediated by Topography and Plant Community[☆]Ricardo Mata-González^{a,*}, Claire M. Reed-Dustin^b, Thomas J. Rodhouse^c^a Associate Professor, Department of Animal and Rangeland Sciences, Oregon State University, Corvallis, OR 97331, USA^b Rangeland Management Specialist, US Department of Agriculture — Natural Resource Conservation Service, Goldendale, WA 98620, USA^c Ecologist, Upper Columbia Basin Network, National Park Service, Bend, OR 97001, USA

ARTICLE INFO

Article history:

Received 4 June 2017

Received in revised form 28 November 2017

Accepted 7 December 2017

Key Words:

Artemisia tridentata

broom snakeweed

Gutierrezia sarothrae

John Day Fossil Beds National Monument

restoration of degraded areas

Wyoming big sagebrush

ABSTRACT

The role of fire in restoration of sagebrush plant communities remains controversial mainly because of paucity of information from long-term studies. Here, we examine 15-year post-fire responses of big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and broom snakeweed (*Gutierrezia sarothrae*), the two most abundant native shrubs at the John Day Fossil Beds National Monument, a protected area in north-central Oregon, USA. Fire effects were studied along gradients of topography and community type through time post-burn. Community types were distinguished as brush, plots dominated by big sagebrush and woodland, plots with a significant presence of Western juniper (*Juniperus occidentalis*) trees. Fire reduced big sagebrush cover in brush plots up to 100% and in woodland plots up to 86%. Broom snakeweed cover declined by 92% and 73% in brush plots and woodland plots, respectively. Big sagebrush did not show signs of recovery 15 years after burning regardless of topography and community type while broom snakeweed populations were clearly rebounding and prospering beyond pre-burn levels. Our results showed that an area initially dominated by big sagebrush (cover of big sagebrush 10–20%, cover of broom snakeweed 2–4%) dramatically shifted to an area dominated by broom snakeweed (cover of big sagebrush < 1%, cover of broom snakeweed 5%) in brush-dominated plots. Our results indicated that brush-dominated plots at lower elevation and southern exposures are the least post-fire resilient. We also observed a declining population of big sagebrush on unburned areas, suggesting the lack of post-fire recovery on burned areas was perhaps a result of low seeding potential by extant populations. Although more years of observation are required, these data indicate that recovery time, the encroachment of opportunistic competing shrubs, and the initial condition of vegetation are essential considerations by land managers when prescribing fire in big sagebrush communities.

Published by Elsevier Inc. on behalf of The Society for Range Management.

Introduction

The sagebrush (*Artemisia* sp.) steppe is one of the largest and most threatened ecosystems in North America (Davies et al., 2011). These systems have declined from 25 million ha pre-European settlement to about 13 million ha (Miller et al., 2011; Chambers et al., 2014a). The loss of sagebrush steppe has been primarily due to past land management approaches resulting in overutilization of forage species, invasion by annual grasses and woody species, declines in species diversity, and changes in fire frequency (Davies et al., 2011; Svejcar et al., 2014).

Fire is a common disturbance in sagebrush communities (Miller and Heyerdahl, 2008; Ellsworth et al., 2016). Yet the historic fire return interval, fire behavior, and ultimately fire effects have been altered by changes to preburn plant communities as a result of late 19th and early 20th century overgrazing, active fire suppression, annual grass invasion, and conifer encroachment (Davies et al., 2011; Chambers et al., 2014b). In addition, increased temperatures and earlier springs associated with climate change are correlated with increased wildfire frequency and total burned area throughout the western United States (Westerling et al., 2006; Svejcar et al., 2014).

Increased fire size and frequency in conjunction with burn pattern homogeneity (Miller and Eddleman, 2001; Miller and Heyerdahl, 2008) create barriers to reestablishment for native sagebrush steppe species such as *Artemisia tridentata* after fire. *A. tridentata* is a nonsprouter that establishes by seed and is entirely dependent on neighboring unburned sites, to reestablish on a burned site (Miller et al., 2013). The long-term recovery of *A. tridentata* can be variable depending on subspecies (Lesica et al., 2007). *A. tridentata*

[☆] Funding for this study was provided by the National Park Service Upper Columbia Basin Network and the Pacific Northwest Cooperative Ecosystem Studies Unit under cooperative agreement # P11AC90967.

* Correspondence: Ricardo Mata-González, Department of Animal and Rangeland Sciences, Oregon State University, Corvallis, OR 97331, USA.

E-mail address: ricardo.matagonzalez@oregonstate.edu (R. Mata-González).

ssp. *vaseyana* in Montana has recovered in around 30 yr to preburn levels (Lesica et al., 2007; Mata-Gonzalez et al., 2007; Mata-Gonzalez et al., 2008), but the few long-term reports that exist for ssp. *wyomingensis* seem to indicate a longer recovery time. Lesica et al. (2007) and West and Yorks (2002) concluded that after 18–25 yr post burn the recovery of *A. tridentata* ssp. *wyomingensis* is low to negligible. In addition to its slow recovery after fire, *A. tridentata* ssp. *wyomingensis* communities are generally regarded to exhibit low resilience to disturbance and low resistance to invasion (Chambers et al., 2007; Miller et al., 2013; Chambers et al., 2014a). The slow recovery and low resilience of degraded sagebrush ecosystems may be responsible for declines in populations of sagebrush-obligate wildlife species, such as the Greater sage-grouse (*Centrocercus urophasianus*) (Beck et al., 2009; Dinkins et al., 2014).

Gutierrezia sarothrae Pursh (broom snakeweed) is also a native sagebrush steppe species that, in contrast to *A. tridentata*, can be a postfire sprouter (although a weak one) (Miller et al., 2013), tends to increase its population in response to fire, and remains a dominant shrub component under disturbance (Ralphs and McDaniel, 2011). *G. sarothrae* is a short-lived species that thrives under disturbance, can be toxic to livestock, and is typically dominant on rangelands in poor condition (Thacker et al., 2008). This species is relatively drought tolerant and able to adapt to variations or pulses in soil water conditions (Wan et al., 2002), and once established in a plant community it can be persistent (Thacker et al., 2008).

Prescribed fire remains a controversial tool in shrubland management around the world (van Wilgen et al., 2010; Dalgleish et al., 2015; Ellsworth et al., 2016). Thus understanding both short- and long-term fire effects on shrubland ecosystems is important for conservation efforts and sustainable management. It is especially important to understand the response to fire of native shrubs such as *A. tridentata* and *G. sarothrae* in the sagebrush steppe because of the different functions these species display within vast ecological communities of North America. *A. tridentata* is a foundational long-lived species in sagebrush steppes and plays a fundamental role in the ecosystem's structure and function (Davies et al., 2011; Rodhouse et al., 2014). In contrast, *G. sarothrae* is an opportunistic species that responds rapidly to increased resource availability (Ralphs and Sanders, 2002).

In North America, studies of short-term (< 5 yr) responses of plant species to fire are relatively abundant within the literature, in contrast to long-term (> 10 yr) responses (Miller et al., 2013). Furthermore, often the currently available long-term research utilizes multiple burn sites of different ages in different locations instead of repeated measures on the same site (substitute space for time), lacks unburned control plots, and does not have preburn plant community data (Miller et al., 2013). Information on long-term species responses are needed to bridge gaps between scientific research and management applications (Chen et al., 2013).

Responses of vegetation to fire are likely mediated by topographical conditions because factors such as exposure and elevation modify soil moisture, soil nutrients, and temperatures (Mata-Gonzalez et al., 2002), and thus the degree of resilience of plant communities (Rodhouse et al., 2014). Other factors being equal, plants are more likely to rebound after fire in cooler and moister soils than in warmer and dryer soils (Miller et al., 2013). In addition, the effects of fire on individual species may vary for different community types because species interactions may temper or enhance species responses to disturbance (Engel and Abella, 2011). The objective of this study was to characterize long-term (15-yr) responses of *A. tridentata* subsp. *wyomingensis* and *G. sarothrae*, two important and functionally contrasting native shrubs of the North American sagebrush steppe, to fire, topographical variation, and community type using data with repeated measures on plots through time, unburned controls, and preburn community data. Our study area has low precipitation and mainly aridic soils (see descriptions later), and thus plant community resilience is expected to be inherently low (Chambers et al., 2014b). We hypothesized that the two species of study would show differential recovery responses to

fire through time and that topography and community type would influence their responses.

Materials and Methods

Study Site

The study site is part of the John Day Fossil Beds National Monument (hereafter, JDFBNM), which is a protected area managed by the National Park Service of the United States located in north-central Oregon, United States. The site is part of the John Day River Valley and a subunit of the Columbia River Plateau physiographical region (USDI National Park Service, 2009). This study was conducted in the Sheep Rock management unit of the JDFBNM, 14 km west of Dayville, Oregon, United States (Fig. 1). The Sheep Rock unit encompasses 3 648 ha and has a history of both sheep and cattle grazing from 19th century Euro-American settlement of the John Day River Valley to the establishment of the JDFBNM in 1975 (Erixson et al., 2011). The study area ranges in elevation from 610 m at the river valley bottom to 1 370 m at the top of the steep hills. The Sheep Rock unit is semiarid with average annual precipitation of approximately 270 mm. Precipitation falls primarily as rain from November to June with peaks in May and November. From 1999 to 2014, the years of this study, 2010 was the wettest yr and 2002 was the driest yr with 362 mm and 186 mm of precipitation (Fig. 2). Soils of the study area are generally aridic, and most of the study plots are located within the following Natural Resource Conservation Service (NRCS) ecological sites: JD Droughty South 9-12 PZ, JD Droughty North 9-12PZ, JD North 9-12 PZ, and JD Loamy 9-12 PZ.

There are 52 plant associations, primarily defined by geographic variability within the Sheep Rock unit (Erixson et al., 2011). Upland woodlands are dominated by the tree *Juniperus occidentalis* Hook (western juniper) and an understory of native grasses and shrubs. Hill slopes and alluvial fans are primarily dominated by the shrubs *A. tridentata* subsp. *wyomingensis* and *G. sarothrae*, as well as encroaching *J. occidentalis*. Downslope, grasses such as *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass) and *Poa secunda* J. Presl (Sandberg bluegrass) are dominant. Annual grasses including *Bromus tectorum* L. (cheatgrass) and *Taeniatherum caput-medusae* (L.) Nevski (medusahead) are widely dispersed throughout the JDFBNM but are concentrated on southern exposures and flat ground (Rodhouse et al., 2014). Throughout the whole JDFBNM area the most common shrub species are *A. tridentata* subsp. *wyomingensis* and *G. sarothrae*.

Data Collection and Experimental Design

Study plot locations were selected using restricted random sampling. If a potential plot location exceeded 60% slope, it was excluded. Experimental plots were established on areas with different exposure and slope. Our plots were located in areas dominated by *A. tridentata* ssp. *wyomingensis* but some had a significant component of *J. occidentalis*. Thus plot locations were differentially identified as 1) brush plots, those that had fewer than 10 *J. occidentalis* trees per ha and 2) woodland plots, those that had more than 10 *J. occidentalis* trees per ha (Reed-Dustin et al., 2016). The total area of *A. tridentata* or *J. occidentalis* dominant land within a given burn unit was divided into equal-sized polygons corresponding to the desired number of plots of each community type. A single plot was randomly located within each polygon.

A total of 37 plots were established, 21 brush plots and 16 woodland plots (Table 1). Of the 21 brush plots, 5 were unburned controls. Of the 16 woodland plots, 8 were unburned controls. The burned and unburned plots were randomly obtained across five prescribed burn areas and burning took place in the fall (early September to early October) of the following yr: 1999 (6 brush plots, 5 woodland plots); 2001 (6 brush plots, 3 woodland plots); 2002 (3 brush plots, 3 woodland plots); 2004 (3 brush plots, 3 woodland plots); and 2005

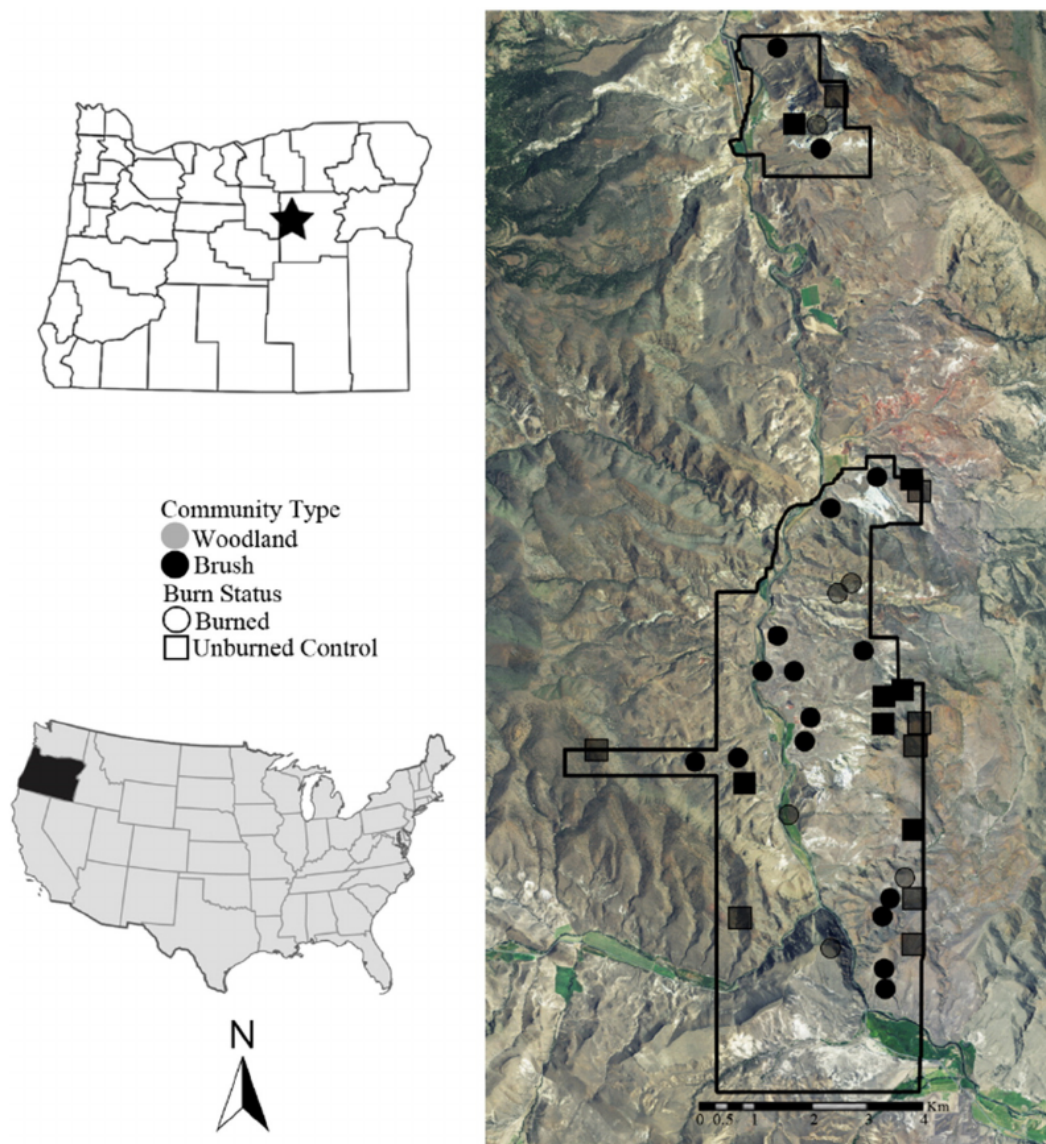


Figure 1. Location of the study plots by community type and burn status within the Sheep Rock Unit of the John Day Fossil Beds National Monument in Oregon, United States.

(3 brush plots, 2 woodland plots). Data collection and monitoring were based on the National Park Service's fire effects monitoring protocol (USDI National Park Service, 2003), modified for the conditions of the JDFBNM. All monitoring was conducted during June or July of the particular monitoring year. All plots were read preburn, 1 yr post burn, 2 yr post burn, and 5 yr post burn, and the oldest plots have been read 10 yr post burn (1999, 2001, 2002, and 2004 prescribed fires) and 15 yr post burn (1999 prescribed fire). Due to monitoring irregularities, not all plots were read consistently on this monitoring interval, particularly unburned control plots. To increase sample size of unburned control plots, we read 3 unburned plots at 9 yr post burn and treated them as 10 yr post burn and 1 unburned plot at 13 yr post burn and treated it as 15 yr post burn in our analysis.

Brush plots were 5×30 m in size, and woodland plots were 20×50 m in size. To determine species cover, the point intercept method was applied along the 30-m (brush) or 50-m (woodland) transect and read every 30 cm. All species intercepted at a point were recorded as a hit. To determine species density, all shrubs within 150 m^2 (brush) or 250 m^2 (woodland) belt transects were counted. The counting unit was an individual shrub even when the plant may have had regrowth. The different size plot for density measurements was a choice based

on operational convenience, but we acknowledge that this may have caused some unwanted small noise in the data analysis. We chose to study *A. tridentata* subsp. *wyomingensis* and *G. sarothrae* because they are the dominant shrub components in the JDFBNM and because they have contrasting niche and life history strategies (foundational long-lived vs. weedy short-lived).

Statistical Analysis

We constructed generalized linear mixed models (GLMMs) using the generalized linear mixed effects model (GLMER) function from the LME4 package (Bates et al., 2014) for analyses in R version 10.2.2 (R Core Team, 2014). Mixed models with binomial links were used to model cover, an improvement over standard normal models (Gaussian or identity link) for cover data bounded between 0 and 1, which presents an inherent violation of analysis of variance assumptions of normality and unequal variance in residuals (Stroup, 2014). We also constructed mixed models with the Poisson link function for modeling counts of shrub density. The mixed modeling capacity provided additional flexibility to model the nested structure of the design, in which repeated observations were made within plots grouped into different

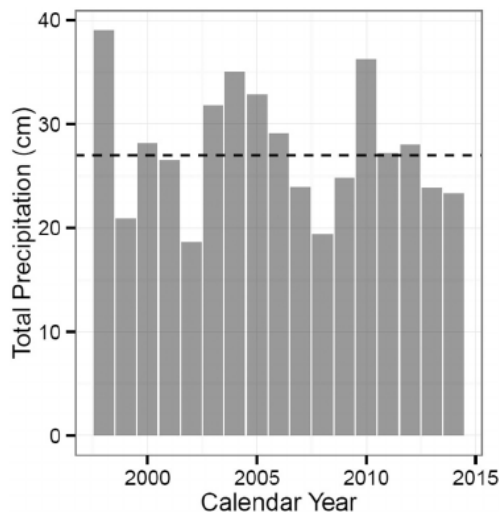


Figure 2. Annual precipitation (cm) in the John Day Fossil Beds National Monument, Oregon during the period of study (1998–2014). The dashed line represents the mean annual precipitation for the site (27 cm) (PRISM Climate Group, 2004).

years. Plots measured within the same year were likely to be correlated because of the common effects of weather; treating year as a random effect explicitly accounted for that process. We also considered a model with an additional random effect included for repeated measures obtained within plots within years (the familiar “repeated-measures” construct). Within-year correlation was much higher than within-plot correlation and model coefficients signs and magnitude did not differ meaningfully between the two model structures. We therefore report results only from the models with a single random effect for year.

A model of cover and density for each species of interest was developed using Burn, Community, Time, and Topography as fixed effects and Year as a randomized effect. Burn was an indicator of a plot burn status, either burned or unburned. Community was an indicator of plot type identified by dominant vegetation, either woodland or brush. Topography was a continuous variable of a combined measure of slope and aspect. It is calculated as $\sin(\text{slope}) \times \cos(\text{aspect})$ where -1 is a steep south-facing slope, 0 is flat, and 1 is a steep north-facing slope, which has been shown to be an important driver of plant community variation in previous studies in the JDFBNM (Rodhouse et al., 2014; Esposito, 2015). The slope and aspect were calculated from a 10-m US Geological Survey digital elevation model in ArcGIS. Time is an indicator of years post burn for which each plot was read, corresponding to the monitoring interval. Calendar years in our analysis do not correspond to year post burn because multiple prescribed fires occurred through time. Time (year) is included in GLMM construction as a randomized effect to account for interannual variability in precipitation, weather patterns, and sampling between calendar years because precipitation before and post burn can be an integral factor in postburn vegetation response (Miller et al., 2013). Precipitation data from PRISM data indicated a large amount of variability between calendar years and not an increasing or decreasing trend over the course of this study in the JDFBNM

Table 1

Timeline of prescribed fire, type of burned plot, and monitoring interval across five burn units (yr).

Prescribed burning	Number of brush plots	Number of woodland plots	Monitoring interval				
			1 yr	2 yr	5 yr	10 yr	15 yr
1999	6	5	2000	2001	2004	2009	2014
2001	6	3	2002	2003	2006	2011	NA
2002	3	3	2003	2004	2007	2012	NA
2004	3	3	2005	2006	2009	2014	NA
2005	3	2	2006	2007	2010	NA	NA

(Reed-Dustin et al., 2016). Likelihood ratio tests, including -2 res log likelihood, Akaike information criterion, and Bayesian information criterion, indicated the full model, with all interactions, was the best fit for cover and density for each species. In addition, post hoc Student's t -tests were used to determine significant differences in cover and density of a species at time or year post burn between other indicators. All analyses were interpreted using a $P < 0.05$ significance level.

Results

Artemisia tridentata ssp. *wyomingensis*

The three-way interactions Burn $\times$ Community $\times$ Topography ($z = 5.14$, $P < 0.0001$) and Burn $\times$ Community $\times$ Time ($z = -7.03$, $P < 0.0001$) were significant for *A. tridentata* cover (Table 2). Cumulatively, these results indicate that effect of community type is dependent on topography and time post burn across both community types. The 1-yr postburn decrease in *A. tridentata* cover was more intense in brush plots (Fig. 3). *A. tridentata* cover decreased 99% on northern exposures and 100% on southern exposures in burned brush plots at 1 yr post burn. In contrast, cover decreased by 86% in woodland plots on northern exposures and by 47% on southern exposures. After an initial decrease, cover of *A. tridentata* remained relatively stable and no signs of recovery were evident in any burned plot. Burning caused the least effect on woodlands with southern exposure with burned and unburned plots in similar *A. tridentata* cover condition through the years.

For *A. tridentata* density, three three-way interactions were significant (Burn $\times$ Time $\times$ Topography, $z = -2.23$, $P = 0.03$; Burn $\times$ Community $\times$ Topography, $z = 16.52$, $P < 0.0001$; Burn $\times$ Community $\times$ Time, $z = -31.20$, $P < 0.0001$, Table 3). Density of *A. tridentata* declined more in brush plots than in woodland plots (Fig. 4). The density of *A. tridentata* in burned brush plots declined by 96% on both northern and southern exposures 1 yr post burn. In burned woodland plots, density of *A. tridentata* declined by 71% on northern exposures and 0% on southern exposures. As for cover, density was least affected in woodland plots with southern exposures.

Unburned plots, regardless of exposure or community type, showed a decline of both cover and density of *A. tridentata* after yr 5 and particularly after yr 10 and 15 (see Figs. 3–4). In some plots the decline was small and not significant, but in others it was of such magnitude that after yr 10 or 15 cover and density were not different from those of burned plots. Thus, if only yr 10 or 15 would have been sampled, no

Table 2

Full generalized linear mixed model z values and P values for cover of each species of interest: *A. tridentata* subsp. *wyomingensis* and *G. sarothrae*. Parameters are whether a plot burned (Bu.), community type (Co.), time post burn (Ti.), and topography (To.) as the combined effect of slope and aspect.

Parameter	<i>Artemisia tridentata</i> subsp. <i>wyomingensis</i>		<i>Gutierrezia sarothrae</i>	
	z value	$P(> z)$	z value	$P(> z)$
(Intercept)	−3.86	0.0001	−5.60	<0.0001
Burn	0.80	0.42	2.75	0.006
Community	−0.84	0.40	2.77	0.006
Time	−11.45	<0.0001	1.04	0.30
Time ²	4.12	<0.0001	1.66	0.10
Topography	4.29	<0.0001	−1.58	0.11
Bu. $\times$ Co.	−0.62	0.54	−2.89	0.004
Bu. $\times$ Ti.	8.68	<0.0001	−2.61	0.009
Bu. $\times$ To.	−4.00	<0.0001	0.88	0.38
Co. $\times$ Ti.	7.59	<0.0001	−3.13	0.002
Co. $\times$ To.	−5.37	<0.0001	0.74	0.46
Ti. $\times$ To.	−0.76	0.45	1.02	0.31
Bu. $\times$ Co. $\times$ Ti.	−7.03	<0.0001	2.33	0.02
Bu. $\times$ Co. $\times$ To.	5.14	<0.0001	−0.07	0.94
Bu. $\times$ Ti. $\times$ To.	0.65	0.52	−0.31	0.76
Co. $\times$ Ti. $\times$ To.	1.24	0.22	−1.45	0.15
Bu. $\times$ Co. $\times$ Ti. $\times$ To.	−1.45	0.15	0.58	0.56

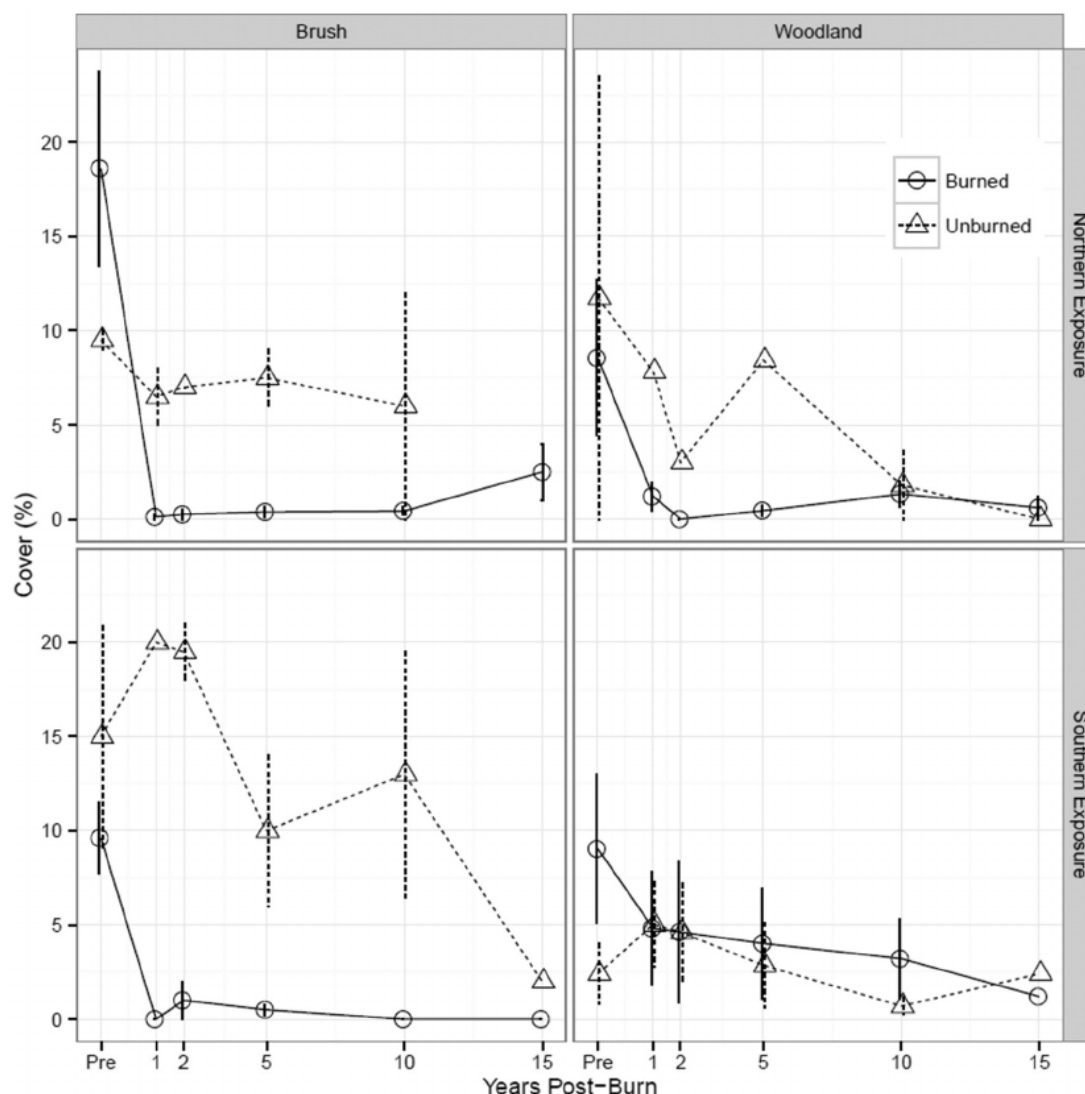


Figure 3. Cover of *Artemisia tridentata* ssp. *wyomingensis* (mean $\pm$ SE) through time post fire at different community types and gradients of topography in John Day Fossil Beds National Monument, Oregon, United States. Topography was analyzed as a continuous variable, but for purposes of graphical representation it is grouped into northern and southern exposures.

Table 3

Full generalized linear mixed model z values and P values for density of each species of interest: *A. tridentata* subsp. *wyomingensis* and *G. sarothrae*. Parameters are whether a plot burned (Bu.), community type (Co.), time post burn (Ti.), and topography (To.) as the combined effect of slope and aspect.

Parameter	<i>Artemisia tridentata</i> subsp. <i>wyomingensis</i>		<i>Gutierrezia sarothrae</i>	
	z value	$P(> z)$	z value	$P(> z)$
(Intercept)	43.76	< 0.0001	16.16	< 0.0001
Burn	11.13	< 0.0001	2.41	0.02
Community	−14.46	< 0.0001	6.40	< 0.0001
Time	−47.97	< 0.0001	−53.63	< 0.0001
Time ²	−0.87	0.38	23.29	< 0.0001
Topography	0.79	0.43	−16.73	< 0.0001
Bu. $\times$ Co.	−4.27	< 0.0001	−20.31	< 0.0001
Bu. $\times$ Ti.	40.52	< 0.0001	8.09	< 0.0001
Bu. $\times$ To.	11.90	< 0.0001	11.86	< 0.0001
Co. $\times$ Ti.	38.01	< 0.0001	−12.78	< 0.0001
Co. $\times$ To.	−8.25	< 0.0001	−8.95	< 0.0001
Ti. $\times$ To.	−3.68	0.0002	−6.52	< 0.0001
Bu. $\times$ Co. $\times$ Ti.	−31.20	< 0.0001	−7.58	< 0.0001
Bu. $\times$ Co. $\times$ To.	16.52	< 0.0001	12.29	< 0.0001
Bu. $\times$ Ti. $\times$ To.	−2.23	0.03	6.10	< 0.0001
Co. $\times$ Ti. $\times$ To.	−0.27	0.79	−5.78	< 0.0001
B. $\times$ C. $\times$ Ti $\times$ To.	0.58	0.56	−12.06	< 0.0001

vegetation differences associated with burning would have been detected on these areas.

Gutierrezia sarothrae

The third-order Burn $\times$ Community $\times$ Time interaction was significant for *G. sarothrae* cover ($z = 2.33$, $P = 0.02$, see Table 2). However, topography did not influence these effects. In burned brush plots, cover of *G. sarothrae* declined significantly from a mean of $3.12\% \pm 0.77\%$ cover before burn, to a mean of $0.25\% \pm 0.14\%$ cover 1 yr post burn (Fig. 5). The cover of *G. sarothrae* at 5 yr post burn increased in burned brush plots and was no longer significantly different from preburn cover. The increase in cover continued at yr 10 and 15 post fire. In burned woodland plots, cover of *G. sarothrae* declined significantly on the first and second yr after the fire, from $3.16\% \pm 1.24\%$ cover before burn to $0.09\% \pm 0.09\%$ at 2 yr post burn. As in the brush plots, the cover of *G. sarothrae* in woodland plots showed signs of recovery, but at a much slower pace. At 10 and 15 yr post burn, cover was greater than that at yr 2, but not yet reaching the preburn levels.

The four-way Burn $\times$ Community $\times$ Time $\times$ Topography interaction was significant for *G. sarothrae* density ($z = -12.06$, $P < 0.0001$, see Table 3). These results are in contrast to *G. sarothrae* cover, which did not show a significant effect of topography. Overall, density of *G. sarothrae* was higher,

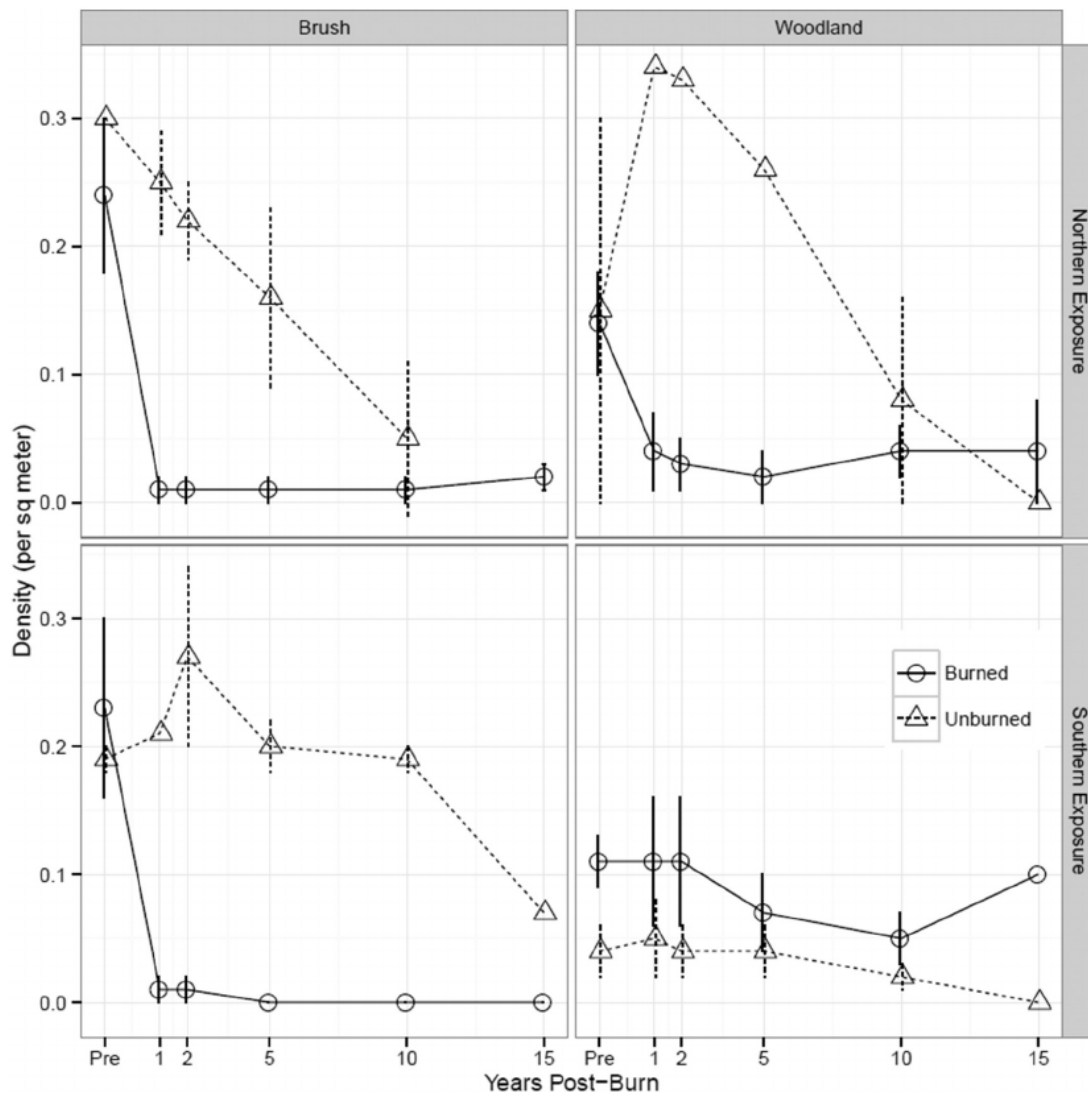


Figure 4. Density of *Artemisia tridentata* ssp. *wyomingensis* (mean $\pm$ SE) through time post fire at different community types and gradients of topography in John Day Fossil Beds National Monument, Oregon, United States. Topography was analyzed as a continuous variable, but for purposes of graphical representation it is grouped into northern and southern exposures.

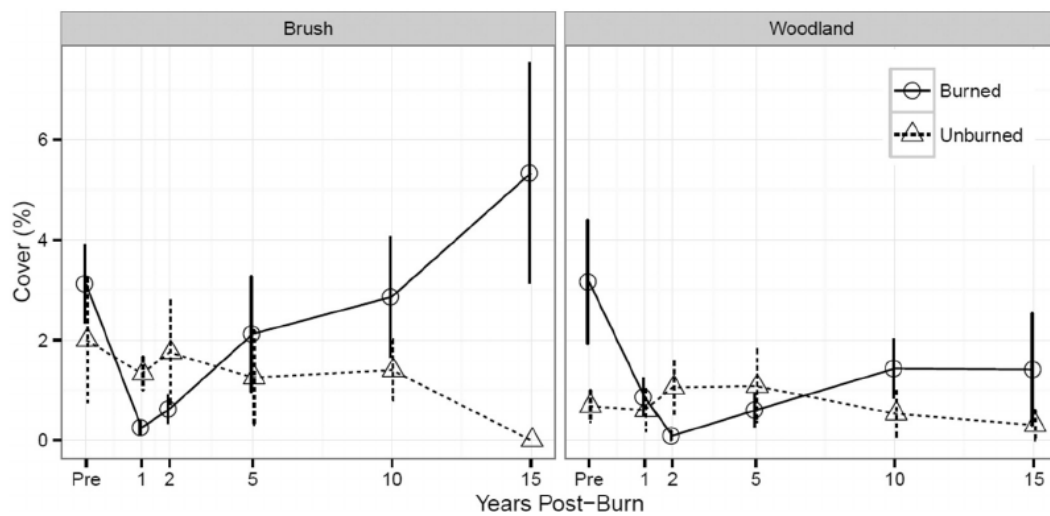


Figure 5. Cover of *Gutierrezia sarothrae* (mean $\pm$ SE) through time post fire at different community types in John Day Fossil Beds National Monument, Oregon, United States.

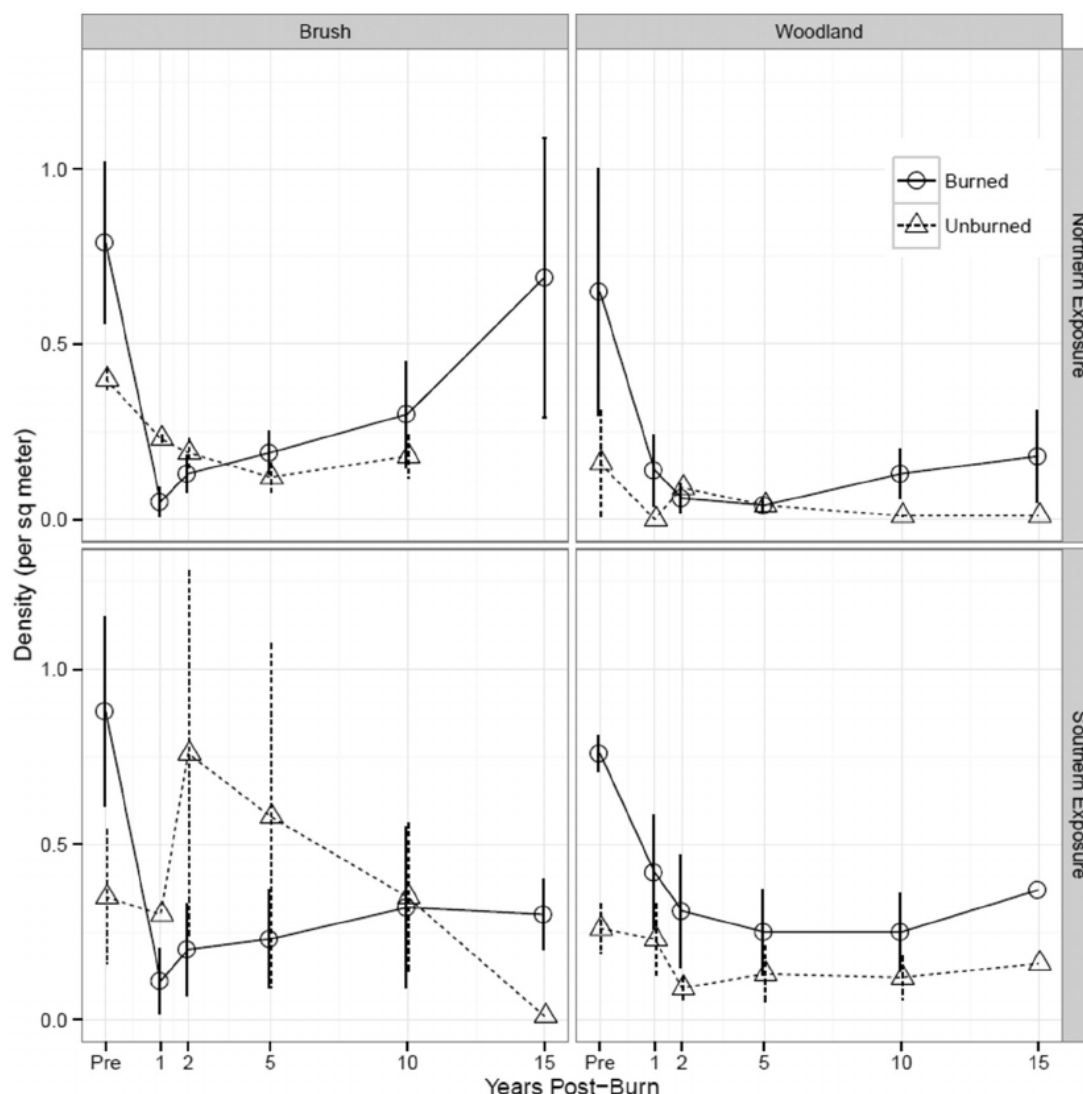


Figure 6. Density of *Gutierrezia sarothrae* (mean $\pm$ SE) through time post fire at different community types and gradients of topography in John Day Fossil Beds National Monument, Oregon, United States. Topography was analyzed as a continuous variable, but for purposes of graphical representation it is grouped into northern and southern exposures.

at least twice, than that of *A. tridentata* (see Fig. 4 and Fig. 6). Burning caused a decline in *G. sarothrae* density in all conditions, but the decline in brush plots was more pronounced than in woodland plots (see Fig. 6). In brush plots on both northern and southern exposures, *G. sarothrae* density bottomed out 1 year post burn. The mean density of *G. sarothrae* continued to recover through time post burn on northern and southern exposures in burned brush plots. In burned woodland plots on both northern and southern exposures, *G. sarothrae* declined gradually through time post burn and bottomed out at 5 yr post burn. *G. sarothrae* density continued to recover in burned woodland plots through time, but not to the degree of brush plots.

Unlike *A. tridentata*, cover and density of *G. sarothrae* in unburned areas remained fairly stable and did not change substantially through the 15 yr post fire of the study (see Figs. 5 and 6). Only density of *G. sarothrae* in brush areas with southern exposure showed a tendency to increase in yr 2 and 5, but with large variation. Therefore, the cause behind the changes in unburned *A. tridentata* through the years did not have a similar effect on *G. sarothrae*.

Discussion

Our hypothesis that both shrub species would respond differently to fire and the postfire environment was confirmed by the results. In short, *A. tridentata* subsp. *wyomingensis* did not show signs of recovery after

15 yr of burning while *G. sarothrae* populations were clearly rebounding and prospering beyond preburn levels. Our hypothesis that topography and community type would influence the vegetation rate of recovery was also supported by our results.

The cover and density of *A. tridentata* subsp. *wyomingensis* across both community types declined dramatically 1 yr post burn. The significant decline in cover and density 1 yr post burn is consistent with literature reports (Watts and Wambolt, 1996; Ellsworth et al., 2016). Over the course of this study, neither *A. tridentata* ssp. *wyomingensis* cover nor density showed any appreciable change following the dramatic decrease 1 yr post burn. Similarly, studies have reported no significant postburn recovery in *A. tridentata* ssp. *wyomingensis* cover after 18–30 yr (Watts and Wambolt, 1996; West and Yorks, 2002; Lesica et al., 2007). Seemingly, the 15-yr time frame of this study is not necessarily long enough to determine if *A. tridentata* subsp. *wyomingensis* will recover in the JDFBNM. Yet for *A. tridentata* ssp. *wyomingensis* to become reestablished and achieve preburn levels in the near future, the observed declines in cover and density should have started to show a reversal of trend by yr 15 post burn. Ellsworth et al. (2016) reported some evidence that *A. tridentata* subsp. *wyomingensis* started to recover 17 yr post fire in southeast Oregon. However, that postfire recovery amounted to only 2.3% cover in *A. tridentata* subsp. *wyomingensis* (Ellsworth et al., 2016). Our results, on the other hand, showed little or no evidence of recovery for this subspecies.

The recovery of *A. tridentata* is dependent on proximity of burned sites to seed sources and seed dissemination from neighboring populations (Miller et al., 2013). Recent vegetation monitoring shows *A. tridentata* subsp. *wyomingensis* cover in the JDFBNM is low (Rodhouse, 2010), which coincides with the observed decline in the condition of *A. tridentata* ssp. *wyomingensis* in the unburned plots across our studied area. The extensive prescribed fires and the history of heavy grazing mediating weed invasion in the JDFBNM have likely contributed to a small extant population size. The limited source population for *A. tridentata* subsp. *wyomingensis* might limit the speed of reestablishment.

Results indicated that fire effects were influenced by topography and community type on *A. tridentata* subsp. *wyomingensis* cover and density. Woodland (*J. occidentalis*) sites are typically restricted to rocky outcrops with low productivity (Miller and Rose, 1999). These conditions limit fuel continuity and protect *J. occidentalis* from fire (Miller and Rose, 1999). The mean elevation of brush plots is 802 m, and the mean elevation of woodland plots is 956 m. The difference in elevation between community types has likely played a role in their differential responses to fire. Higher elevations are more resistant to invasion because of cooler and wetter conditions, allowing native species to better compete with annual species (Chambers et al., 2014a; Miller et al., 2013; Rodhouse et al., 2014) and because higher elevations are typically less subject to anthropogenic disturbance (Averett et al., 2016). Erixson et al. (2011) suggested that areas at higher elevations of the JDFBNM were likely more insulated from historic grazing and cultivation than areas at lower elevations. Cover of *B. tectorum* is greater in brush plots than in woodland plots and on north slopes than south slopes (Reed-Dustin et al., 2016), perhaps also because of differential shading effect. Therefore, we suggest the somewhat limited effect of fire on *A. tridentata* ssp. *wyomingensis* cover at higher elevation woodland sites and on south slopes with respect to brush plots was related to fuel continuity. Fuel continuity at lower-elevation brush sites was probably not a limiting factor, thus allowing topography to be influential.

Across all plots, cover of *G. sarothrae* declined 1 yr post burn, which has been previously observed (Parmenter, 2008). Contrary to the lack of postfire recovery observed in *A. tridentata*, the cover of *G. sarothrae* showed signs of a clear rebound; returning to preburn levels by 5 yr post burn in brush plots and with a clear trend of recovery, although slower, in woodland plots. Previous studies in the Great Basin suggest *G. sarothrae* increases in response to fire and remains dominant in the community until *A. tridentata* or other dominant shrubs get reestablished (Pechanec and Stewart, 1954; Ralphs and McDaniel, 2011; Morris and Leger, 2016). Our 15-yr study can only confirm that an area initially dominated by *A. tridentata* ssp. *wyomingensis* (cover of *A. tridentata* 10–20%, cover of *G. sarothrae* 2–4%) can dramatically shift to an area dominated by *G. sarothrae* (cover of *A. tridentata* < 1%, cover of *G. sarothrae* 5%) in brush-dominated plots. This seems to confirm observations suggesting *G. sarothrae* increases significantly post fire, particularly in *A. tridentata* subsp. *wyomingensis* communities (Thacker et al., 2008), which is likely related to its capacity for sprouting (although weak) after fire (Miller et al., 2013) and ability to thrive under disturbance (Ralphs and McDaniel, 2011).

It is possible that the current dominance gained by *G. sarothrae* is lost over time in the absence of fire (Morris and Leger, 2016), but such predictability is also challenged by climate change and the expected increase of late-fall to early-spring precipitation in sagebrush areas (Palmquist et al., 2016). It is well established that *G. sarothrae* populations are highly responsive to increased fall and spring precipitation (Ralphs and Sanders, 2002; Ralphs and McDaniel, 2011). In general, an opportunistic species such as *G. sarothrae* would be better equipped to respond to precipitation changes or disturbance than a slow-grow, foundational species such as *A. tridentata*.

The slower recovery of *G. sarothrae* in woodland plots than in brush plots is perhaps a result of the greater abundance of grasses such as *P. spicata* in woodland plots at higher elevations in our study area (Reed-Dustin et al., 2016), given that *P. spicata* is an effective competitor

and deterrent to *G. sarothrae* establishment (Thacker et al., 2008). Furthermore, the typically lower disturbance levels at higher elevation (Averett et al., 2016) would also explain the slower recovery of *G. sarothrae* in woodland areas (Ralphs and McDaniel, 2011).

The response of *G. sarothrae* density to fire is more complex than *G. sarothrae* cover. Like *G. sarothrae* cover, the density of *G. sarothrae* decreased dramatically 1 yr post burn and showed varying degrees of increase across community types and topographic gradients thereafter. The higher recovery of *G. sarothrae* cover but lower recovery of density suggests individual *G. sarothrae* plants are larger post burn than they were before burn. Plot means indicate southern exposures in the JDFBNM appear to be more conducive to *G. sarothrae* establishment than northern exposures. This was also reported by Mata-Gonzalez et al. (2002) in desert mountains. The reduced resilience of south slopes to disturbance and lack of *P. spicata* on south slopes would favor the establishment of *G. sarothrae* over north slopes (Reed-Dustin et al., 2016). Our results suggest that more individuals of *G. sarothrae* became established on south slopes, but their size was limited by nutrient and water availability. In contrast, our results indicate that the establishment of *G. sarothrae* on north slopes was limited by greater site resistance, but increased nutrient availability favored increased size of individuals of this species.

The noticeable decline in cover and density in unburned *A. tridentata* ssp. *wyomingensis* populations through time was unexpected. In some cases burned and unburned populations were not different at yr 10 and 15 post fire. The decline of this species in unburned populations may be related to the extensive prescribed fires and weed invasion in the area (Rodhouse, 2010). In fact, previous work has shown that dominance by annual grasses hinders the natural establishment of *A. tridentata* (Mata-Gonzalez et al., 2008). Other potential causes for the decline of unburned *A. tridentata* populations could be browsing by native ungulates as observed in other protected areas (Singer and Renkin, 1995; Boccadori et al., 2008) or pests such as the argo moth (Evers et al., 2013). However, these causes are only speculations because our study was not designed to elucidate the causes of vegetation change in unburned populations. Whatever the cause, the lack of vigorous *A. tridentata* extant populations is likely a restricting factor that adds to the slow recovery process after fire.

Implications

Our results show a rapid decline post fire and negligible long-term recovery (15 yr) of *A. tridentata* ssp. *wyomingensis* concurrent with increasing dominance of *G. sarothrae* in our study area. Also, we did not see signs of recovery of *A. tridentata* ssp. *wyomingensis* for the foreseeable future, corroborating the low resilience of this plant community (Chambers et al., 2014a). The recovery time needs to be considered by land managers when prescribing fire in *A. tridentata* ssp. *wyomingensis* communities. We agree with previous reports (Baker, 2006; Beck et al., 2009) that managers should avoid burning, especially in relation to preserving the habitat for wildlife species of concern. Other studies have shown signs of recovery of *A. tridentata* ssp. *wyomingensis* 17 yr post fire (Ellsworth et al., 2016) reportedly as a result of good-condition neighboring stands, which favored the natural seeding and recruitment of this subspecies. Our study was conducted in an area with overall declining populations of *A. tridentata* ssp. *wyomingensis* despite protection from livestock grazing since 1975 (Rodhouse, 2010). A clear indication of such decline was the low cover and density of *A. tridentata* ssp. *wyomingensis* in unburned plots. As suggested by Wright (1990), for plant communities to be responsive to fire they need to be in good ecological condition. Thus, the use of prescribed fire as a tool for rangeland restoration should be carefully analyzed and restricted to areas with relatively intact plant communities and a high degree of postfire resiliency. Restoring native vegetation, for example by reseeding, should be an important goal before considering fire for management of many degraded areas.

Even though our 15-yr study is comparatively long term for an ecological study, it is not long enough to fully characterize long-term responses of *A. tridentata* ssp. *wyomingensis* and *G. sarothrae* to fire. To gain a fuller perspective, this study should be continued, especially because it represents a real long-term study with no time-for-space substitution and with monitoring through intervals of time. As a complement to this continuing study, we suggest evaluating the observed overall decline in *A. tridentata* ssp. *wyomingensis* in the study area by analyzing its potential causes.

Acknowledgments

We thankfully acknowledge the monitoring vegetation work of Cedar Drake, Karen Kopper, and their NPS field crews through the years. We also thankfully acknowledge the field assistance of Matthew Hovland, Daniel Esposito, and Devin Stucki, as well as the assistance with figure formatting by David Prado-Tarango.

References

- Averett, J.P., McCune, B., Parks, C.G., Naylor, B.J., DelCurto, T., Mata-González, R., 2016. Non-native plant invasion along elevation and canopy closure gradients in a middle Rocky Mountain ecosystem. *PLoS ONE* 11 (1), e0147826.
- Baker, W.L., 2006. Fire and restoration of sagebrush ecosystems. *Wildlife Society Bulletin* 34, 177–185.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. *lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.1–7.
- Beck, J.L., Connelly, J.W., Reese, K.P., 2009. Recovery of greater sage-grouse habitat features in Wyoming big sagebrush following prescribed fire. *Restoration Ecology* 17, 393–403.
- Boccardi, S.J., White, P.J., Garrott, R.A., Borkowski, J.J., Davis, T.L., 2008. Yellowstone pronghorn alter resource selection after sagebrush decline. *Journal of Mammals* 89, 1031–1422.
- Chambers, J.C., Roundy, B., Blank, R., Meyer, S., Whittaker, A., 2007. What makes Great Basin sagebrush ecosystems invulnerable by *Bromus tectorum*? *Ecology Monographs* 77, 117–145.
- Chambers, J.C., Bradley, B.A., Brown, C.S., D'Antonio, C.D., Germino, M.J., Grace, J.B., Hardegree, S.P., Miller, R.F., Pyke, D.A., 2014a. Resilience to stress and disturbance and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. *Ecosystems* 17, 360–375.
- Chambers, J.C., Pyke, D.A., Maestas, J.D., Pellant, M., Boyd, C.S., Campbell, S.B., Espinosa, S., Havlina, D.W., Mayer, K.E., Wuenschel, A., 2014b. Using resistance and resilience concepts to reduce impacts of invasive annual grasses and altered fire regimes on the sagebrush ecosystem and greater sage-grouse: a strategic multi-scale approach. Gen. Tech. Rep. RMRS-GTR-326. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA 73 p.
- Chen, X., Emery, N., Garcia, E.S., Hanan, E.J., Hodges, H.E., Martin, T., Meyers, M.A., Peavey, L.E., Peng, H., Santamaria, J.S., Uyeda, K.A., Anderson, S.E., Tague, C., 2013. Perspectives on disconnects between scientific information and management decisions on post-fire recovery in western US. *Environmental Management* 52, 1415–1426.
- R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Dalgleish, S.A., Van Etten, E.J.B., Stock, W.D., Knuckey, C., 2015. Fuel dynamics and vegetation recovery after fire in semiarid Australian shrubland. *International Journal of Wildland Fire* 24, 613–623.
- Davies, K.W., Boyd, C.S., Beck, J.L., Bates, J.D., Svejcar, T.J., Gregg, M.A., 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. *Biology Conservation* 144, 2573–2584.
- Dinkins, J.B., Conover, M.R., Kirol, C.P., Beck, J.L., Frey, S.N., 2014. Greater sage-grouse (*Centrocercus urophasianus*) select habitat based on avian predators, landscape composition, and anthropogenic features. *Condor* 116, 629–642.
- Ellsworth, L.M., Wroblewski, D.W., Kauffman, J.B., Reis, S.A., 2016. Ecosystem resilience is evident 17 years after fire in Wyoming big sagebrush ecosystems. *Ecosphere* 7 (12), e01618.
- Engel, E., Abella, S.R., 2011. Vegetation recovery in a desert landscape after wildfires: influences of community type, time since fire and contingency effects. *Journal of Applied Ecology* 48, 1401–1410.
- Erixson, J.A., Cogan, D., Von Loh, J., 2011. Vegetation inventory project: John Day Fossil Beds National Monument. Natural Resource Technical Report NPS/UCBN/NRTR–2011/419. National Park Service, Fort Collins, CO, USA.
- Esposito, D.M., 2015. Geographic variation in distribution and cover of principle native and non-native plant species along gradients of topography, climate, and disturbance in protected-area sagebrush steppe communities of the Columbia Plateau [thesis]. Oregon State University, Corvallis, OR, USA.
- Evers, L.B., Miller, R.F., Doescher, P.S., Hemstrom, M., Neilson, R.P., 2013. Simulating current successional trajectories in sagebrush ecosystems with multiple disturbances using a state-and-transition modeling framework. *Rangeland Ecology & Management* 66, 313–329.
- Lesica, P., Cooper, S.V., Kudray, G., 2007. Recovery of big sagebrush following fire in southwest Montana. *Rangeland Ecology & Management* 60, 261–269.
- Mata-Gonzalez, R., Pieper, R.D., Cardenas, M.M., 2002. Vegetation patterns as affected by aspect and elevation in small desert mountains. *The Southwestern Naturalist* 47, 440–448.
- Mata-Gonzalez, R., Hunter, R.G., Coldren, C.L., McLendon, T., Paschke, M.W., 2007. Modelling plant growth dynamics in sagebrush steppe communities affected by fire. *Journal of Arid Environments* 69, 144–157.
- Mata-Gonzalez, R., Hunter, R.G., Coldren, C.L., McLendon, T., Paschke, M.W., 2008. A comparison of modeled and measured impacts of resource manipulations for control of *Bromus tectorum* in sagebrush steppe. *Journal of Arid Environments* 72, 836–846.
- Miller, R.F., Eddleman, L.E., 2001. Spatial and temporal changes of sage grouse habitat in the sagebrush biome. Report Technical Bulletin 151. Oregon State University Agricultural Experiment Station, Corvallis, OR, USA.
- Miller, R.F., Heyerdahl, E.K., 2008. Fine-scale variation of historical fire regimes in sagebrush-steppe and juniper woodland: an example from California, USA. *International Journal of Wildland Fire* 17, 245–254.
- Miller, R.F., Rose, J.A., 1999. Fire history and western juniper encroachment in sagebrush steppe. *Journal of Range Management* 52, 550–559.
- Miller, R.F., Knick, S.T., Pyke, D.A., Meinke, C.W., Hanser, S.E., Wisdom, M.J., Hild, A.L., 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. In: Knick, S.T., Connelly, J.W. (Eds.), *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology Vol. 38. University of California Press, Berkeley, CA, USA, pp. 145–185.
- Miller, R.F., Chambers, J.C., Pyke, D.A., Pierson, F.B., Williams, J.C., 2013. Fire effects on vegetation and soils in the Great Basin: response and site characteristics. General Technical Report. RMRS-GTR-308. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Morris, L.R., Leger, E.A., 2016. Secondary succession in the sagebrush semidesert 66 years after fire in the Great Basin, USA. *Natural Areas Journal* 36, 187–193.
- Palmquist, K.A., Schlaepfer, D.R., Bradford, J.B., Lauenroth, W.K., 2016. Mid-latitude shrub steppe plant communities: climate change consequences for soil water resources. *Ecology* 97, 2342–2354.
- Parmenter, R.R., 2008. Long term effects of a summer fire on desert grassland plant demographics in New Mexico. *Rangeland Ecology & Management* 61, 156–168.
- Pechanec, J.F., Stewart, G., 1954. Sagebrush burning good and bad. *Farmers' Bulletin No. 1948*. US Department of Agriculture, Washington, DC, USA.
- PRISM Climate Group, 2004. Oregon State University. Available at: <http://prism.oregonstate.edu>. Accessed Feb 4, 2014.
- Ralphs, M.H., McDaniel, K.C., 2011. Broom snakeweed (*Gutierrezia sarothrae*): toxicology, ecology, control, and management. *Invasive Plant Science Management* 4, 125–132.
- Ralphs, M.H., Sanders, K.D., 2002. Population cycles of broom snakeweed in the Colorado Plateau and Snake River plains. *Journal of Range Management* 55, 406–411.
- Reed-Dustin, C.M., Mata-Gonzalez, R., Rodhouse, T.J., 2016. Long-term fire effects on native and invasive grasses in protected area sagebrush steppe. *Rangeland Ecology & Management* 69, 257–264.
- Rodhouse, T.J., 2010. Sagebrush steppe vegetation monitoring in Craters of the Moon National Monument and Preserve, Hagerman Fossil Beds National Monument, John Day Fossil Beds National Monument, and Lake Roosevelt National Recreation Area: 2009 Annual Report. Natural Resource Technical Report NPS/UCBN/NRTR–2010/302. National Park Service, Fort Collins, CO, USA.
- Rodhouse, T.J., Irvine, K.M., Sheley, R.L., Smith, B.S., Hoh, S., Esposito, D.M., Mata-Gonzalez, R., 2014. Predicting foundation bunchgrass species abundances: model-assisted decision-making in protected-area sagebrush steppe. *Ecosphere* 5, 108.
- Singer, F.J., Renkin, R.A., 1995. Effects of browsing by native ungulates on the shrubs in big sagebrush communities in Yellowstone National Park. *Great Basin Nature* 55, 201–212.
- Stroup, W., 2014. Rethinking the analysis of non-normal data in plant and soil science. *Agronomy* 4, 106–117.
- Svejcar, T., Boyd, C., Davies, K., Madsen, M., Bates, J., Sheley, R., Marlow, C., Bohnert, D., Borman, M., Mata-González, R., Buckhouse, J., Stringham, T., Perryman, B., Swanson, S., Tate, K., George, M., Ruyle, G., Roundy, B., Call, C., Jensen, K., Launchbaugh, K., Gearhart, A., Vermeire, L., Tanaka, J., Derner, J., Frasier, G., Havstad, K., 2014. Western land managers will need all available tools for adapting to climate change, including grazing: a critique of Beschta and others. *Environmental Management* 53, 1035–1038.
- Thacker, E.T., Ralphs, M.H., Call, C.A., Benson, B., Green, S., 2008. Invasion of broom snakeweed (*Gutierrezia sarothrae*) following disturbance: evaluating change in a state and-transition model. *Rangeland Ecology & Management* 61, 263–268.
- USDI National Park Service, 2003. Fire Monitoring Handbook. Fire Management Program Center, National Interagency Fire Center, Boise, ID, USA. 274 p.
- USDI National Park Service, 2009. John Day Fossil Beds National Monument, Oregon: General management plan/environmental assessment. USDI, Denver, CO, USA. 101 p.
- Wan, C., Yilmaz, I., Sosebee, R.E., 2002. Seasonal soil-water availability influences snake-weed root dynamics. *Journal of Arid Environments* 51, 255–264.
- Watts, M.J., Wambolt, C.L., 1996. Long-term recovery of Wyoming big sagebrush after four treatments. *Journal of Environmental Management* 46, 95–102.
- West, N.E., Yorks, P., 2002. Vegetation responses following wildfire on grazed and ungrazed sagebrush semi-desert. *Journal of Range Management* 38, 131–134.
- Westerling, A., Hidalgo, H., Cayan, D., Swetnam, T., 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313, 940–943.
- van Wilgen, B.W., Forsyth, G.G., De Klerk, H., Das, S., Khuluse, S., Schmitz, P., 2010. Fire management in Mediterranean-climate shrublands: a case study from the Cape fynbos, South Africa. *Journal of Applied Ecology* 47, 631–638.
- Wright, H. A. 1990. Role of fire in the management of Southwestern ecosystems. In: Krammes, J. S. [technical coordinator]. Effects of fire management of Southwestern Natural Resources. General Technical Report RM-191. Fort Collins, CO, USA: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. p. 1–5.

