

AN ABSTRACT OF THE THESIS OF

Claire Marie Reed-Dustin for the degree of Master of Science in Rangeland Ecology and Management presented on April 28, 2015.

Title: Long-term fire effects on plant succession and exotic weeds in protected area sagebrush steppe, John Day Fossil Beds National Monument, Oregon

Abstract approved: _____
Ricardo Mata-Gonzalez

The historical function of fire in sagebrush steppe has been altered by 19th century overgrazing, active fire suppression, annual grass invasion and encroachment of woody species. The significance of fire to these systems is known, but research on long-term fire effects are limited. The Sheep Rock management unit of the John Day Fossil Beds National Monument, Oregon offers an opportunity to study long-term (15 year) responses of *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) communities to fire. Using generalized linear mixed models, this study examined responses of *A. tridentata* ssp. *wyomingensis*, *Bromus tectorum* (cheatgrass), *Gutierrezia sarothrae* (broom snakeweed), *Poa secunda* (Sandberg bluegrass), *Pseudoroegneria spicata* (bluebunch wheatgrass) and *Taeniatherum caput-medusae* (medusahead), along gradients of community type and topography through time post-fire. Community types were differentiated between *A. tridentata* ssp. *wyomingensis* dominant plots (brush plots) and *Juniperus occidentalis* (western juniper) dominant plots (forest plots). Cover of *B. tectorum* was greatest in brush plots. *Bromus tectorum* cover increased dramatically 2 years post-burn. At 5 years post-burn cover of *B. tectorum* was 135% of pre-burn cover

in brush plots and 301% of pre-burn cover in forest plots. Analysis determined abundance of *T. caput-medusae* was not enough pre-burn to analyze fire effects. Examination of mean *T. caput-medusae* cover, in plots through time, suggests it is expanding within the Sheep Rock management unit. *Pseudoroegneria spicata* is more abundant in forest plots than in brush plots. In forest plots, *P. spicata* cover decreased by 49% 1 year post-burn, but recovered by 5 years post-burn. In brush plots, cover of *P. spicata* declined, but not significantly through time post-fire. On northern exposures recovery of *P. spicata* cover occurred between 1 and 2 years post-burn, whereas on southern exposures recovery occurred between 2 and 5 years post-burn. The cover of *P. secunda* did not show a dramatic response to fire through time post-burn. Fire reduced *A. tridentata* ssp. *wyomingensis* cover in brush plots by 99% and 100% on northern and southern exposures, respectively. In forest plots, fire reduced *A. tridentata* ssp. *wyomingensis* cover by 86% and 47% on northern and southern exposures, respectively. Similarly, *A. tridentata* ssp. *wyomingensis* density in brush plots declined by 96% on both northern and southern exposures 1 year post-fire. In forest plots fire reduced *A. tridentata* ssp. *wyomingensis* density by 71% on northern exposures and 0% on southern exposures. The cover and density of *A. tridentata* ssp. *wyomingensis* did not change significantly through time after an initial decrease 1 year post-burn, except for density in forest plots, which didn't show significant change through time. *Artemisia tridentata* is a long-lived species and therefore continuation of this study is required to gain a fuller perspective on its long-term response to fire. Cover of *G. sarothrae* declined by 92% in brush plots and by 73% in forest plots. *Gutierrezia sarothrae* cover returned to pre-burn cover by 5 years post-burn in brush plots, but did not recover in forest plots. Topography was not identified as a

significant parameter for *G. sarothrae* cover in response to fire. Similarly to *G. sarothrae* cover, *G. sarothrae* density decreased 1 year post-burn and recovered by 5 years post-burn in brush plots, but it did not recover in forest plots. In contrast to *G. sarothrae* cover, topography was identified as a significant parameter for the response of *G. sarothrae* density. We hypothesize south slopes favor *G. sarothrae* establishment, while north slopes favor increased *G. sarothrae* size, which explains topographic significance for density, but not for cover. Results of this study can be used by land managers to consider species specific responses to fire in both the short and long-term. This information is useful when developing plans for reintroducing fire into *A. tridentata* ssp. *wyomingensis* systems or when developing post-wildfire management strategies.

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Long-term Fire Effects on Plant Succession and Exotic Weeds in Protected Area
Sagebrush Steppe, John Day Fossil Beds National Monument, Oregon

by
Claire Marie Reed-Dustin

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Claire Marie Reed-Dustin, Author

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DEDICATION

The Reed Girls.

Chapter 1 – Introduction

Within North American rangelands, the sagebrush (*Artemisia* sp.) steppe is one of the most imperiled ecosystems (Noss et al. 1995). The cold desert sagebrush system has declined from 25 million hectares pre-European settlement, to about 13 million hectares (Miller et al. 2011, Chambers et al. 2014a). Landscapes that were formerly sagebrush steppe have been lost to overutilization, changes in fire frequency and invasion by annual grasses and woody species (Davies et al. 2011). Within the Great Basin, 2 million hectares are dominated by *Bromus tectorum* (cheatgrass) with high inter-annual variability in abundance (Bradley and Mustard 2005). An additional 30 million hectares of the western United States are occupied by *Juniperus* sp. (juniper), in contrast to an estimated 3 million hectares pre-settlement (Miller and Tausch 2001).

Within the *A. tridentata* (big sagebrush) alliance, *A. tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) communities are the most at-risk of conversion to annual grasslands (Chambers et al. 2014a). *Artemisia tridentata* ssp. *wyomingensis* communities are commonly found in xeric environments, with moderately deep to shallow soils and at low to mid (700 to 2150 meters ASL) elevations (Davies and Bates 2010, Miller et al. 2011). These environmental characteristics create communities with low resilience to disturbance and low resistance to invasion (Chambers et al. 2007). As a result of human preference for moderate climates and flat topography, these systems have been exposed to a high degree of disturbance post-European settlement (Chambers et al. 2007).

Within an ecological site, abiotic and biotic attributes and processes determine the site's resilience and resistance (Miller et al. 2013, Chambers et al. 2014a). Ecosystem resilience is also influenced by the type, characteristics and variability of historical stress

and disturbance (Chambers et al. 2014a). Additionally, these factors apply at plant community scales where slope, aspect and topography act as influential factors (Miller et al. 2013, Chambers et al. 2014a).

Fire is a fundamental natural disturbance and is the primary maintenance mechanism of sagebrush steppe (Wright 1974, Wright and Bailey 1982). Typically, the historical fire return interval within *A. tridentata* ssp. *wyomingensis* communities is defined as between 50 and 100 years (Wright and Bailey 1982). The long-duration fire return interval in *A. tridentata* ssp. *wyomingensis* communities are associated with a high degree of variability, resulting in fire return intervals exceeding 100 years (Miller et al. 2011). Disturbances including overgrazing, fire suppression and annual grass invasion have all fundamentally changed historical fire regimes and subsequently fire effects (Burkhardt and Tisdale 1976, Wright and Bailey 1982, Fleischner 1994, Knapp 1996). For example, increased fuel loads and fuel continuity from *B. tectorum* invasion are associated with reductions in fire return intervals to less than 5 years (Whisenant 1990).

Individual disturbances including overgrazing, fire suppression and annual grass invasion have coupled and interacted to change the condition and/or state of sites. Late 19th and early 20th century overgrazing altered the vegetative community (Fleischner 1994) and reduced fuel accumulations (Burkhardt and Tisdale 1976). Historically, the aridity of *A. tridentata* ssp. *wyomingensis* communities and subsequent slow accumulation of biomass, resulted in long (50-100 year) fire return intervals (Wright and Bailey 1982). By further reducing fuel accumulations, overgrazing effectively acted as a fire suppressant, thereby extending systems further outside their historical fire return

interval. Fire suppression gained significant momentum as a governmental policy with Theodore Roosevelt's presidency and creation of the United States Forest Service in 1905, with the out by "10 AM rule" (Wright and Bailey 1982). Active fire suppression caused further deviation of *A. tridentata* communities to their historical fire return interval. In contrast, annual grass invasion by *B. tectorum* has reduced fire return intervals through increased accumulation of biomass and continuity of fine fuels (Knapp 1996, Chambers et al. 2007). The decrease in length of fire return intervals perpetuates a cycle, which favors increased establishment of *B. tectorum* (D'Antonio and Vitousek 1992).

Overgrazing and annual grass invasion increased homogeneity of vegetative communities. This change in site characteristics, a disturbance in itself, alters existing vegetation, which fundamentally changes the severity, intensity, duration, size, complexity and season of fire (Miller et al. 2013). Thus, when a fire does occur homogeneity of the vegetative community coupled with increased fuel loads, results in a more homogenous burn. In contrast, native communities evolved with heterogeneous fires due to variability in vegetative composition associated with topography and soils at a given site as well as variable time since a previous fire event (Miller and Heyerdahl 2008). Increased fire severity favors re-establishment of invasive annual grasses, before the native perennial community has time to recover (Knapp 1996, Chambers et al. 2007). Therefore, characteristics of a fire ultimately influence post-fire succession, as do pre- and post-burn weather, ecological site characteristics, post-fire disturbance and past land management (Miller et al. 2013).

The interrelationships of disturbance history, post-fire dynamics, invasive species, altered climate regimes and grazing management practices creates a complex situation for land managers. The complexity of the situation is pronounced by low resistance and low resilience in *A. tridentata* ssp. *wyomingensis* communities (Chambers et al. 2014a). A solution for working with system complexity, particularly within the post-fire environment, will require bridging existing gaps between science and management (Chen et al. 2013). The managerial response to dramatic site conversions in sagebrush steppe can benefit by understanding factors determining site's resistance and resilience (Brooks and Chambers 2011). Likewise, managerial response can benefit by understanding long-term fire effects on species of interest within the context of a sites' resistance and resilience. Currently, long-term (> 10 years) fire effects research in the Great Basin is limited (Miller et al. 2013) and is needed for cohesion between the scientific community and land managers (Chen et al. 2013).

Long-term (15 years) fire research conducted in the Sheep Rock management unit of the John Day Fossil Beds National Monument (JDFBNM), Oregon, offers an opportunity to connect scientific research and land managers. Research in the JDFBNM also has an opportunity to aid in filling existing voids in long-term fire effects research (Miller et al. 2013). The Sheep Rock management unit is composed of *A. tridentata* ssp. *wyomingensis* communities and has undergone five, large-scale, prescribed burns between 1999 and 2005. The Sheep Rock unit has an extensive history of both sheep and cattle grazing from 19th century Euro-American settlement of the John Day River Valley to establishment of the JDFBNM in 1975 (Erixson et al. 2011). The native grass community is composed primarily of *Pseudoroegneria spicata* (bluebunch wheatgrass)

and *Poa secunda* (Sandberg bluegrass) and has undergone wide-spread invasion by *B. tectorum* and *Taeniatherum caput-medusae* (medusahead). The native shrub community is primarily composed of *A. tridentata* ssp. *wyomingensis* and *Gutierrezia sarothrae* (broom snakeweed). *J. occidentalis* (western juniper) is present throughout the Sheep Rock management unit, particularly at higher elevations.

Chapter 2: Long-term fire effects on native and invasive grass species cover in protected area sagebrush steppe, John Day Fossil Beds National Monument, Oregon

C.M. Reed-Dustin, R. Mata-Gonzalez and T.J. Rodhouse

Abstract

Historically, fire acted as the primary maintenance mechanism of sagebrush steppe in North America. The role of fire in these systems has been altered, in part by active fire suppression, annual grass invasion and expansion of woody species. The Sheep Rock management unit of the John Day Fossil Beds National Monument, Oregon offers an opportunity to study long-term (15 year) responses of *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) communities to fire. Using generalized linear mixed models this study examined responses of *Bromus tectorum* (cheatgrass), *Taeniatherum caput-medusae* (medusahead), *Pseudoroegneria spicata* (bluebunch wheatgrass) and *Poa secunda* (Sandberg bluegrass) along gradients of community type and topography through time post-fire. Community types were identified as either *A. tridentata* ssp. *wyomingensis* dominant (brush plots) or *Juniperus occidentalis* (western juniper) dominant (forest plots). Cover of *B. tectorum* was greatest in brush plots. *Bromus tectorum* cover increased significantly 5 years post-burn. At 5 years post-burn cover of *B. tectorum* was 135% of pre-burn cover in brush plots and 301% of pre-burn cover in forest plots. Analysis determined abundance of *T. caput-medusae* was not enough pre-burn to analyze fire effects. Examination of mean *T. caput-medusae* cover in plots through time suggests it is expanding within the Sheep Rock management unit. *Pseudoroegneria spicata* is more abundant in forest plots than in brush plots. In forest plots, *P. spicata* cover decreased by 49% 1 year post-burn, but recovered by 5 years post-burn. In brush plots, *P. spicata* cover declined, but not significantly through time post-fire. On northern exposures recovery of *P. spicata* cover occurred between 1 and 2 years post-burn, whereas on southern exposures recovery occurred between 2 and 5 years post-burn. The

cover of *P. secunda* did not show a significant response to fire. Results of this study can be used by land managers to consider species specific responses to fire in both the short and long-term. This type of information is valuable when developing plans for reintroducing fire into *A. tridentata* ssp. *wyomingensis* communities or when developing post-wildfire management strategies.

Introduction

Sagebrush (*Artemisia* sp.) steppe are one of the most imperiled ecosystems in North American rangelands (Noss et al. 1995). Cold desert sagebrush systems have declined from 25 million hectares pre-European settlement to about 13 million hectares (Miller et al. 2011, Chambers et al. 2014a). Within the *A. tridentata* alliance, *A. tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) communities are the most at-risk of conversion to annual grasslands due to low resilience to disturbance and low resistance to invasion (Chambers et al. 2007, Miller et al. 2013, Chambers et al. 2014a).

Ecosystem resilience is influenced by the type, characteristics and variability of historical stress and disturbance (Chambers et al. 2014a). Historically, fire acted as the primary maintenance mechanism of sagebrush steppe (Wright 1974, Wright and Bailey 1982). As a result of evolving with fire, *A. tridentata* ssp. *wyomingensis* communities need fire to maintain long-term resistance to invasion by annual grasses (Davies et al. 2008). The composition, structure and function of sagebrush steppe has been fundamentally altered by disturbances such as overgrazing, fire suppression, invasion of annual grasses and encroachment of woody species (Davies et al. 2011). Alterations that

have and continue to occur in these systems, create complex challenges for land managers when reintegrating fire into these systems and determining post-fire management strategies.

Land managers can gain insight into how a particular site may respond to fire based on the pre-burn vegetation. For example, deep-rooted perennial grasses such as *Pseudoroegneria spicata* (bluebunch wheatgrass) are associated with ecosystem resilience to disturbance and resistance to invasion (Chambers et al. 2007, Davies 2008, Brooks and Chambers 2011, Davies et al. 2011). Within invaded sites the abundance of invasive annual grasses, such as *Bromus tectorum* (cheatgrass) and *Taeniatherum caput-medusae* (medusahead), are inversely correlated with native grass abundance (Davies 2008, Davies et al. 2012). Therefore, utilizing known native perennial and invasive annual grass relationships can be a method for identifying potential site specific responses to fire.

Within the context of using species composition to identify resistant and resilient sites, species specific responses to fire need to be understood. Morphological characteristics are important in determining fire tolerance of species (Pyke et al. 2010). *Pseudoroegneria spicata* is a fire tolerant species due to buds located below the soil surface (Conrad and Poulton 1966). The native, shallow-rooted, perennial grass, *Poa secunda* (Sandberg bluegrass) is also fire tolerant due to an open crown with little biomass accumulation (Miller et al. 2013). In contrast, *B. tectorum* is fire resilient through rapid capitalization on increased post-fire nutrient availability (Davies et al. 2007) through winter root growth (Harris 1967).

Successional modeling suggests a species response to fire will change through time. Short-term (< 5 years) fire responses of native perennial and invasive annual grass species in *A. tridentata* ssp. *wyomingensis* communities are prevalent within the literature. *Pseudoroegneria spicata*'s response to fire in the 1st year post-burn is variable, but it typically recovers to or above pre-burn cover by 2 or 3 years post-burn (Blaisdell 1953, Conrad and Poulton 1966, Wright 1985, Miller et al. 2013). The cover of *P. secunda* is reported to remain unchanged in the 1st through 4th years post-burn (Wright and Klemmedson 1965, Young and Evans 1978, Akinsoji 1988). Cheatgrass typically decreases slightly 1 year post-burn and increases above pre-burn levels by 2 or 3 years post-burn (Young and Evans 1978, Akinsoji 1988, Davies et al. 2007, Mata-Gonzalez et al. 2007). *Taeniatherum caput-medusae* initially increases post-burn, but returns to control equivalents within 3 years post-burn (Young 1972).

In addition to short-term species responses, information on long-term species responses are needed to bridge gaps between science and management (Chen et al. 2013). A synthesis on fire effects in the Great Basin emphasizes the need for long-term (> 10 years) research (Miller et al. 2013). The authors argue currently available long-term research substitutes multiple burn sites of different ages for repeated measures on the same site, lacks unburned control plots and doesn't have pre-burn plant community data (Miller et al. 2013). The objective of our study is to determine long-term (15 years) fire effects on two native perennial (*P. spicata* and *P. secunda*) and two invasive annual (*B. tectorum* and *T. caput-medusae*) grass species. Our study is long-term research with both space and time, unburned controls and pre-burn plant community data. Therefore, we are

attempting to contribute to an existing void in Great Basin fire research as suggested by Miller et al. (2013).

Our specific questions of interest for this study are: How does the response of grass species to fire in *A. tridentata* ssp. *wyomingensis* communities change through time? How does the response vary based on the dominant vegetation type? How does topography influence invasive annual and native perennial grass species response to fire?

Methods

Study Site

This study was conducted in the Sheep Rock management unit of the John Day Fossil Beds National Monument (JDFBNM), 14 kilometers west of Dayville, OR, USA (see Fig. 2.1). The study site is 3,600 hectares located in north-central Oregon's John Day River Valley and is a subunit of the Columbia River Plateau physiographical region (USDI-NPS 2009). The Sheep Rock unit has an extensive history of both sheep and cattle grazing from Euro-American settlement of the John Day River Valley during the 19th century to establishment of the JDFBNM in 1975 (Erixson et al. 2011). The study area ranges in elevation from 610 meters at river valley bottoms to 1,370 meters at the top of steep hills. The Sheep Rock unit is semi-arid with average annual precipitation of approximately 27 centimeters, which falls primarily as rain from October to June (PRISM Climate Group 2004). From 1999 to 2014 in the Sheep Rock unit, 2010 was the wettest year with 36.2 centimeters of precipitation and 2002 was the driest year with 18.6 centimeters of precipitation (see Fig. 2.2) (PRISM Climate Group 2004).

Within the Sheep Rock unit there are 52 identified plant associations, which are differentiated by geographic feature variability (Erixson et al. 2011). Upland woodlands are *Juniperus occidentalis* (western juniper) dominated with an understory of native grasses. Hill slopes and alluvial fans are primarily *A. tridentata* ssp. *wyomingensis* and encroaching *J. occidentalis*. Downslope *P. spicata*, *P. secunda*, *Festuca idahoensis* (Idaho fescue) and *Achnatherum thurberianum* (Thurber's needlegrass) are dominant. Due to low site resistance and resilience, coupled with past land-use disturbance, annual grasses including *B. tectorum* are widely dispersed throughout the JDFBNM. The majority of study plots are located within the following 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.

Experimental Design

Experimental design and monitoring are based on National Park Service's (NPS) fire effects monitoring protocol (USDI-NPS 2003) and have been modified to suit the JDFBNM. Study plot locations were selected using restricted random sampling. Potential plot locations were restricted to areas identified by Youtie and Winward (1977) as either *A. tridentata* or *J. occidentalis* dominant. 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. If a potential plot location exceeded 60% slope it was excluded. *A. tridentata* dominant or brush plots were restricted to having < 10 *J. occidentalis* per hectare and *J. occidentalis* dominant or forest plots were restricted to

having > 10 *J. occidentalis* per hectare (NPS-NOCA 1999). A total of 37 plots ($n_{\text{brush}} = 21$, $n_{\text{forest}} = 16$) were established. The majority of brush plots are currently located within *Bromus tectorum* semi-natural herbaceous or *Pseudoroegneria spicata* – *Balsamorhiza sagittata* – *Poa secunda* herbaceous vegetation alliances (Erixson et al. 2011). The majority of forest plots are currently located within *Juniperus occidentalis*/*Pseudoroegneria spicata* wooded herbaceous vegetation or *Juniperus occidentalis*/*Cercocarpus ledifolius*/*Pseudoroegneria spicata* woodland or *Juniperus occidentalis*/*Artemisia tridentata* ssp. *wyomingensis*/*Pseudoroegneria spicata* wooded herbaceous vegetation alliances (Erixson et al. 2011).

All prescribed fires were burned in early September or early October. Plots are distributed across five prescribed burn units and burned in the fall of the following years: Windy Point 1999 ($n_{\text{brush}} = 6$, $n_{\text{forest}} = 5$), Picture Gorge 2001 ($n_{\text{brush}} = 6$, $n_{\text{forest}} = 3$), Middle Mountain 2002 ($n_{\text{brush}} = 3$, $n_{\text{forest}} = 3$), Rock Creek 2004 ($n_{\text{brush}} = 3$, $n_{\text{forest}} = 3$) and Foree 2005 ($n_{\text{brush}} = 3$, $n_{\text{forest}} = 2$) (see Table A1). As a result of multiple prescribed burns occurring through time, years post-burn in our analysis does not correspond to calendar years. No unburned control plots were initially established. For the purpose of our analysis we treated plots showing no evidence of fire during post-burn monitoring as controls. Of the 37 total plots, 13 plots are treated as controls: Windy Point $n_{\text{brush}} = 0$, $n_{\text{forest}} = 2$; Picture Gorge $n_{\text{brush}} = 2$, $n_{\text{forest}} = 2$; Middle Mountain $n_{\text{brush}} = 1$, $n_{\text{forest}} = 1$; Rock Creek $n_{\text{brush}} = 1$, $n_{\text{forest}} = 2$; Foree $n_{\text{brush}} = 1$, $n_{\text{forest}} = 1$.

All monitoring was conducted during June or July of the particular monitoring year. Brush plots are 5 meters by 30 meters in size and forest plots are 20 meters by 50

meters in size. A point intercept method was applied along the 30 meter (brush) or 50 meter (forest) transect and read every 30 centimeters. All species intercepted at a point were recorded as a hit. All plots have been read pre-burn, 1 year post-burn, 2 years post-burn, 5 years post-burn and the oldest plots have been read 10 years post-burn (Windy Point, Picture Gorge, Middle Mountain and Rock Creek) and 15 years post-burn (Windy Point). 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 at the most recent years post-burn, we read 3 plots at 9 years post-burn and pooled them as 10 years post-burn and 1 plot at 13 years post-burn and pooled it as 15 years post-burn in our analysis (see Table A2) .

Statistical Analysis

All analyses were conducted through construction of generalized linear mixed models (GLMM) using the generalized linear mixed effects model (GLMER) function from the LME4 package (Bates et al. 2014) in R version 10.2.2 (R Core Team 2014). GLMMs were used due to the inherent violation of ANOVA assumptions of normality and equal variance in binomial data. GLMMs allow for violation of these assumptions by defining both a linear predictor and a probability distribution of the observations (Stroup 2014). This is in contrast to a traditional ANOVA which defines an error term in the model equation formula based on assumptions of normality and independence (Stroup 2014).

A model for cover of each species of interest was developed using Burn, Community, Time and Topography as fixed effects and Year as a randomized effect.

Burn is an indicator of a plots burn status, either burned or unburned. Community is an indicator of plot type identified by dominant vegetation, either forest or brush.

Topography is 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). The slope and aspect were calculated from a 10 meter US Geological Survey (USGS) digital elevation model (DEM) 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. Year is included in GLMM construction as a randomized effect to account for inter-annual variability in precipitation between calendar years. Precipitation pre- and post-burn is shown to be an integral factor in post-burn vegetative community response (Miller et al. 2013). Precipitation data from PRISM data indicates a large amount of variability between calendar years over the course of this study in the JDFBNM (see Fig. 2.2). Therefore, including calendar year as a randomized effect in our analysis is an attempt to account for variation due to differences in calendar year precipitation pre- and post-burn, across different burn units.

For cover of each species, likelihood ratio tests, including -2 res log likelihood, Akaike information criterion (AIC) and Bayesian information criterion (BIC), indicated the full model with all interactions, was the best fit. Significant interactions were explored through additional focused models of the full model's component parts. Additionally, post-hoc t-tests were used to determine significant differences in cover of

each species through time and between burned and unburned plots at each monitoring interval. All analyses were interpreted using a $p < 0.05$ significance level.

Results

Bromus tectorum

The fourth-order interaction of Burn \times Community \times Time \times Topography is a significant predictor of *B. tectorum* cover ($z = -3.98$, $p < 0.0001$, see Table 2.1). Focused models were created for both burned and unburned plots to explore significance of the 4-way interaction. The Community \times Time \times Topography interaction in focused models is significant for unburned plots ($z = -3.59$, $p = 0.0003$) and not significant for burned plots ($z = 0.23$, $p = 0.82$). These focused model results indicate significance of the 4th order interaction in the full model stem from unburned plots. As such, the 4-way interaction's significance is likely attributable to random variability, made apparent by a small sample size and inconsistent monitoring in unburned plots, resulting in a lack of replication rather than an actual effect. Other than knowing significant changes did not occur through time in unburned plots, the focus of this study is not to examine their trends through time.

The third-order Burn \times Community \times Topography interaction is significant in the full model ($z = 2.85$, $p = 0.004$, see Table 2.1). To explore the significance of this interaction focused models for unburned and burned plots were created. The Community \times Topography interaction is significant for both unburned ($z = 4.22$, $p < 0.0001$) and burned plots ($z = 8.56$, $p < 0.0001$). This suggests regardless of fire, *B. tectorum* cover within each community type is dependent on topography (see Fig. 2.3). The cover of *B.*

tectorum in brush plots is consistently higher than in forest plots. Within brush plots, southern exposures tend to have a higher cover of *B. tectorum*. Pre-burn cover of *B. tectorum* in burned brush plots on southern exposures was 10% higher than burned brush plots on northern exposures (see Fig. 2.3). This trend continued 15 years post-burn, with 14% greater cover of *B. tectorum* in burned brush plots on southern exposures than on northern exposures (see Fig. 2.3). Similarly, pre-burn cover of *B. tectorum* in forest plots on southern exposures was 7% greater than on northern exposures (see Fig. 2.3). Although, post-burn differences between burned forest plots on northern and southern exposures are not evident (see Fig. 2.3).

The Burn \times Community \times Time interaction is also significant for *B. tectorum* cover ($z = -5.30$, $p < 0.0001$, see Table 2.1) in the full model. This indicates the effect of fire on *B. tectorum* cover within each community type is dependent on time post-burn. To explore the significance of this interaction focused models for both burned and unburned plots were created. The Community \times Time interaction in the focused models is not significant for unburned plots ($z = -1.44$, $p = 0.15$), but is significant for burned plots ($z = 4.98$, $p < 0.0001$). These results indicate within burned plots the effect of time post-burn is dependent on community type. The cover of *B. tectorum* in burned brush plots increased significantly from a mean of $49.25 \pm 6.25\%$ pre-burn to a mean of $66.44 \pm 23.43\%$ at 5 years post-burn (see Table 2.2). The cover of *B. tectorum* in brush plots was not significantly different from pre-burn cover at any other monitoring interval. The cover of *B. tectorum* in burned forest plots also increased significantly from a mean of $12.05 \pm 4.32\%$ pre-burn, to a mean of $36.32 \pm 18.45\%$ by 5 years post-burn (see Table

2.2). At 10 years post-burn cover of *B. tectorum* in forest plots remained significantly higher than pre-burn cover.

Taeniatherum caput-medusae

The fourth-order interaction of Burn \times Community \times Time \times Topography is significant ($z = -2.83$, $p = 0.005$, see Table 2.1) for *T. caput-medusae* cover. Attempts to further explore significance of this interaction through focused models were not possible because of a limited dataset, which led to unidentifiable models. We continued to explore mean cover of *T. caput-medusae* in order to highlight potential utility of this dataset, rather than to explore fire effects.

Graphical examination of means indicates *T. caput-medusae* cover remained relatively stable until 10 and 15 years post-burn in unburned and burned plots, respectively (see Fig. 2.4). In both burned and unburned plots, observed increases in *T. caput-medusae* cover originated in brush plots on northern exposures (see Fig. 2.4). The restriction of observed increases in *T. caput-medusae* cover to brush plots on northern exposures suggests community type and topography are potentially influential factors for *T. caput-medusae* establishment and increase.

The majority of significant increase in burned and unburned brush plots in years 10 and 15 post-burn originates in one unburned plot and one burned plot at each monitoring interval. In the burned brush plot, *T. caput-medusae* cover increased from 0% pre-burn to 44% 15 years post-burn and in the unburned brush plot from 0% pre-burn to 30% 10 years post-burn. Although large increases are isolated to a small subset of plots, *T. caput-medusae* has expanded within the JDFBNM, over the course of this study. Pre-

burn *T. caput-medusae* was present in 4 of 21 brush plots and at 10 years post-burn *T. caput-medusae* was present in 9 of 18 brush plots. Pre-burn *T. caput-medusae* was present in 1 of 16 forest plots and at 10 years post-burn it was present in 3 of 14 forest plots.

Pseudoroegneria spicata

The fourth-order interaction of Burn \times Community \times Time \times Topography for *P. spicata* cover is significant ($z = 5.69$, $p < 0.0001$, see Table 2.1). To further explore significance of this interaction focused models for *P. spicata* cover were created by burn status. The Community \times Time \times Topography interaction in focused models was significant for burned plots ($z = -1.98$, $p = 0.048$) and not significant for unburned plots ($z = 1.50$, $p = 0.13$). These results suggest within burned plots the effect of community type is dependent on topography through time post-burn. To further explore significance of this interaction in burned plots, additional focused models by community type were examined. The Time \times Topography interaction is significant for both burned brush ($z = -2.74$, $p = 0.006$) and burned forest plots ($z = 3.71$, $p = 0.0002$). Cumulatively, these results indicate significance of the 4-way interaction in the full model is the result of fire effects in both community types along topographic gradients through time post-burn.

In contrast to *B. tectorum*, mean cover of *P. spicata* is higher in forest plots rather than in brush plots at each monitoring period (see Fig. 2.5). Pre-burn mean cover of *P. spicata* is higher on northern exposures than on southern exposures in each respective community type (see Fig. 2.5). The time post-burn required for *P. spicata* to recover varied along the topographic gradient. Regardless of community type, post-burn increases

in *P. spicata* cover occurred between 1 and 2 years post-burn on northern exposures and between 2 and 5 years on southern exposures (see Fig. 2.5). For example, mean cover of *P. spicata* in burned forest plots on northern exposures decreased from $33.49 \pm 1.72\%$ pre-burn, to $16.42 \pm 2.26\%$ 1 year post-burn and increased to $23.95 \pm 4.21\%$ at 2 years post-burn (see Fig. 2.5). In contrast, mean *P. spicata* cover in burned forest plots on southern exposures was $31.93 \pm 15.99\%$ pre-burn, decreased to $15.46 \pm 7.96\%$ 1 year post-burn, was $16.47 \pm 8.30\%$ 2 years post-burn and increased to a mean of $28.11 \pm 16.53\%$ at 5 years post-burn (see Fig. 2.5)

Poa secunda

The four-way interaction of Burn \times Community \times Time \times Topography is significant ($z = -2.34$, $p = 0.019$, see Table 2.1) for *P. secunda* cover. To examine significance of this interaction focused models for both community types were studied. The Burn \times Time \times Topography interaction is not significant for brush plots ($z = -0.27$, $p = 0.79$) and is significant for forest plots ($z = -4.31$, $p < 0.0001$). To further explore this interaction additional focused models for burned and unburned plots of each community type were examined. The Time \times Topography interaction from the secondary focused models is significant for burned forest plots ($z = -2.04$, $p = 0.04$), burned brush plots ($z = 5.54$, $p < 0.0001$) and for unburned forest plots ($z = -4.91$, $p < 0.0001$), but not for unburned brush plots ($z = 1.07$, $p = 0.28$). These results suggest within forest plots regardless of fire, the effect of time is dependent on topography. In contrast, these results indicate within brush plots fire results in dependence of the effect of time on topography.

Cumulatively, these results indicate within burned plots of each community type, topographic effects are dependent on time post-burn.

Overall, mean cover of *P. secunda* tended to be higher in forest plots and on northern exposures than brush plots and southern exposures (Fig. 2.6). The cover of *P. secunda* in forest plots on northern exposures declined from $16.39 \pm 4.34\%$ pre-burn to $12.05 \pm 0.55\%$ 1 year post-burn, but peaked at 2 years post-burn with $18.52 \pm 5.42\%$ cover, before declining again (see Fig. 2.6). In forest plots on southern exposures cover of *P. secunda* increased slightly from $8.84 \pm 2.01\%$ pre-burn to $11.04 \pm 1.61\%$ 1 year post-burn (see Fig. 2.6). Similarly to *P. secunda* in forest plots on northern exposures, *P. spicata* in forest plots on southern exposures peaked at 2 years post-burn with $16.87 \pm 7.19\%$ cover, prior to decreasing to $9.44 \pm 5.32\%$ at 5 years post-burn (see Fig. 2.6). Brush plots on northern exposures showed a moderate increase from $10.75 \pm 2.18\%$ pre-burn to $17.25 \pm 4.53\%$ 1 year post-burn, followed by a gradual decline and stabilization (see Fig. 2.6). In contrast, *P. secunda* cover in brush plots on southern exposures declined gradually through time from $7.75 \pm 2.31\%$ pre-burn to $1.75 \pm 1.11\%$ at 15 years post-burn (see Fig. 2.6).

Discussion

Our analysis supports current literature suggesting native perennial and invasive annual grass species respond differently to fire and differently in the post-fire environment (Miller et al. 2013). Our analysis uses GLMMs to determine long-term (15 year) fire effects on cover of two invasive annual grasses, *B. tectorum* and *T. caput-*

medusae and two native perennial grasses, *P. spicata* and *P. secunda*, in an *A. tridentata* ssp. *wyomingensis* community. The overall lack of significance in response of each species between years post-burn in unburned control plots, suggests measured differences are in fact burn effects rather than the result of confounding factors.

Bromus tectorum

Bromus tectorum cover declined slightly, but not significantly 1 year post-burn, increased above pre-burn cover by 2 years post-burn and did not change appreciably thereafter. Decreases or maintenance of *B. tectorum* cover 1 year post-burn are common throughout the literature and across different *A. tridentata* complexes (Young and Evans 1978, Young and Miller 1985, Akinsoji 1988, Davies et al. 2007, Mata-Gonzalez et al. 2007). Increases in cover of *B. tectorum* 2 or 3 years post-burn are also common throughout the literature (Davies et al. 2007, Mata-Gonzalez et al. 2007, Young and Evans 1978, Young and Miller 1985). An increase in *B. tectorum* cover post-burn, is attributed to increased resource availability in the post-fire environment (Davies et al. 2007). Young and Evans (1978) reported increased vigor in *B. tectorum* plants 1 year post-burn, despite a decrease in plant density, which ultimately contributes to an increase in *B. tectorum* density 2 years post-burn.

Studies on long-term responses of *B. tectorum* to prescribed fire are limited in the literature, particularly those with both space and time gradients well represented (Miller et al. 2013). A study by West and York (2002) reported cover of *B. tectorum* fluctuated between <1% and 20% during the 6th through 19th years post-burn, in response to annual precipitation. Model simulations by Mata-Gonzalez et al. (2007) show *B. tectorum* lost

community dominance after 15 years post-burn due to increased competition with reestablished shrubs. In our study, cover of *B. tectorum* increased above pre-burn cover by 2 years post-burn and showed no drastic change between 2 and 15 years post-burn. Unlike West and York (2002), we didn't observe a significant fluctuation in mean cover of *B. tectorum* between years post-burn. If fluctuations due to annual variations in moisture regimes did exist, they are likely masked by evaluation of means across multiple calendar years within the same year post-burn. There is not a significant difference in *B. tectorum* cover between any year pre- or post-burn in unburned plots, suggesting long-term increase in *B. tectorum* cover is an actual fire effect rather than the result of variation in annual moisture regimes. Also, unlike simulations by Mata-Gonzalez et al. (2007), *B. tectorum* remained dominant in study plots at 15 years post-burn. Mata-Gonzalez et al. (2007) reported a decrease in *B. tectorum* cover as shrubs recovered, which is a possible explanation for differences in our results. In the JDFBNM, we have not observed evidence of shrub cover recovery.

Throughout the 16 year duration of this study burned brush plots consistently had a higher cover of *B. tectorum* than burned forest plots. Prior to burning, brush plots had 4 times higher *B. tectorum* cover than forest plots. Rodhouse et al. (2014) reported annual grasses are weakly associated with lower elevations in the JDFBNM. The mean elevation of brush plots is 802 meters and mean elevation of forest plots is 956 meters. This difference in elevation suggests a probable explanation for the observed difference in *B. tectorum* cover between community types. Higher elevations are more resistant to annual grass invasion because of cooler and wetter conditions favoring increased productivity, in turn allowing for native species to better compete with annual species (Miller et al. 2013,

Chambers et al. 2014a). Also, high elevation sites are less accessible and likely didn't experience cultivation and livestock grazing prior to establishment of the JDFBNM (Erixson et al. 2011).

Similarly to high elevations, north slopes tend to be more resistant to annual grass invasion than south slopes (Chambers et al. 2014a). The susceptibility of a site to *B. tectorum* invasion is greatest on sites with more variation in resource availability (Chambers et al. 2007). Lower elevation *A. tridentata* ssp. *wyomingensis* communities experience variability in resources due in response to variability in annual precipitation (Chambers et al. 2007). We observed a higher mean cover of *B. tectorum* on southern exposures than on northern exposures in burned brush plots. This factor coupled with the significance of topography on burned brush plots, but not on unburned brush plots indicates the importance of topography in affecting a sites resistance to invasion following fire.

Taeniatherum caput-medusae

Increases in *T. caput-medusae* cover were not observed until 10 and 15 years post-burn in either unburned or burned plots, respectively. This pattern suggests results are not fire effects and are rather results of another factor. It appears *T. caput-medusae* abundance pre-burn was not enough to influence fire effects. Presently, *T. caput-medusae* is still relatively rare in some areas of the JDFBNM (Rodhouse et al. 2014).

Taeniatherum caput-medusae affects fire behavior and therefore fire effects through increased fuel accumulation and direct competition with native fuel sources. These accumulations have previously been shown to be a causal mechanism for mortality of

native species and for establishment of *T. caput-medusae* monocultures post-fire (George 1992, Young 1992). Thus, for *T. caput-medusae* to have had a significant post-burn response, the pre-burn abundance may need to be more substantial.

The plots with significant increases in *T. caput-medusae* cover had relatively flat topography, which is consistent with other findings in the JDFBNM (Rodhouse et al. 2014, Esposito 2015). *Taeniatherum caput-medusae* has high soil moisture requirements for germination and is thus typically associated with clayey soils (Dahl and Tisdale 1975). The lack of *T. caput-medusae* establishment in forest plots is therefore potentially due to a lack of soil moisture because soils at forest sites tended to be rockier and shallower. Increased establishment of *T. caput-medusae* in some brush plots is likely due to the presence of clay soils. Additionally, grazing and cultivation history at low elevation sites increased susceptibility of brush plots to *T. caput-medusae* establishment through decreased community resistance to invasion.

Pseudoroegneria spicata

Pseudoroegneria spicata is one of the most fire tolerant native perennial grass species in the Great Basin region (Miller et al. 2013). The observed decrease in *P. spicata* cover 1 year post-burn and return to pre-burn cover by 2 years post-burn is consistent with the existing literature. A review of Great Basin fire literature by Miller et al. (2013) determined 86% of studies reported a decrease in deep-rooted perennial grasses 1 year post-burn and 90% reported recovery to pre-burn levels within 2 and 5 years post-burn. Fire tolerance of *P. spicata* and its ability for rapid recovery have been attributed to increased reproductive effort (Uresk et al. 1976, Sapsis 1990, Ellsworth and Kauffman

2010). Although isolated to north slopes in the JDFBNM, Sapsis (1990) reported 5.2% mortality of *P. spicata* 1 year post-burn and a significant increase of flowering inflorescences by 2 years post-burn.

In burned plots cover of *P. spicata* is dependent on the combined effects of community type, topography and time. Previous studies in the JDFBNM reported *P. spicata* is strongly correlated with topography and with steep north slopes (Rodhouse et al. 2014, Esposito 2015). In contrast to *B. tectorum*, *P. spicata* cover is consistently greater in burned forest plots than in burned brush plots. Rodhouse et al. (2014) reported *P. spicata* is moderately associated with higher elevations in the JDFBNM. This is opposite of the trend identified for *B. tectorum* cover. The mean elevation of brush plots is 802 meters and the mean elevation of forest plots is 956 meters. This fact in conjunction with Rodhouse et al.'s (2014) findings suggest cover differences between community types are influenced by elevation differences. High elevation plots tend to have cooler and wetter conditions favoring increased productivity. This allows native perennial species like *P. spicata* to better compete with invasive annual grasses such as *B. tectorum* (Chambers et al. 2007, Miller et al. 2013, Chambers et al. 2014a). The observed inverse relationship between *P. spicata* and *B. tectorum* cover between community types is consistent with literature suggesting an inverse relationship between invasive annuals and native perennial grass abundance (Davies 2008, Davies et al. 2012). *Pseudoroegneria spicata* is associated with increased site resilience to disturbance and resistance to invasion (Chambers et al. 2007, Davies 2008, Brooks and Chambers 2011, Davies et al. 2011). The relatively low cover of *B. tectorum* in plots with relatively high cover of *P. spicata* is consistent with increased resistance to invasion of comparatively intact sites.

Poa secunda

Response of *P. secunda* to fire varied between community types and topography. Overall response of *P. secunda* in any combination of community type and topography was not particularly dramatic. Although limited, literature reports little effect of fire on *P. secunda* (Miller et al. 2013). Studies have reported no significant change in *P. secunda* cover, density and basal area between 1 and 4 years post-burn (Wright and Klemmedson 1965, Young and Evans 1978, Akinsoji 1988). Lack of *P. secunda* response to fire can be explained by morphology. *Poa secunda* has an open crown and accumulates a limited amount of biomass. The morphology is thereby able to limit fire intensity and duration on individual plants (Miller et al. 2013).

Within burned plots a strong relationship between *P. secunda* cover and time post-burn, topography and community type is identified. Higher *P. secunda* cover is observed in forest plots on northern and southern exposures and brush plots on northern exposures whereas *P. secunda* in brush plots on southern exposures declined in cover through time. Previous research in the JDFBNM reported *P. secunda* to be most common on north slopes (Esposito 2015) and moderately associated with higher elevations (Rodhouse et al. 2014). Our findings of greater cover of *P. secunda* in higher elevation forest plots and on northern exposures at lower elevations are consistent with these previous studies. Fuel loads and competition from a high and increasing cover of *B. tectorum* in brush plots on southern exposures, may explain the gradual decline in *P. secunda* cover through time on the same sites.

Conclusions

The results of this study indicate within the JDFBNM, *A. tridentata* ssp. *wyomingensis* community resilience to fire varies along environmental gradients such as elevation and topography. The observed long-term responses of *B. tectorum*, *T. caput-medusae*, *P. spicata*, and *P. secunda* cover to fire are consistent with previous literature. The cover of *B. tectorum* increased 2 years post-burn and did not change significantly thereafter. The cover of *P. spicata* returned to pre-burn cover by 2 years post-burn. The cover of *P. secunda* did not show a dramatic response to fire in either the short- or long-term. For each species, community type, topography and time post-burn are significant determinants of their response to fire. Therefore, the effect of community type and topography need to be important considerations for prescribed fire in the JDFBNM and other *A. tridentata* ssp. *wyomingensis* sites. These characteristics reflect site disturbance history, ecological site characteristics, pre-burn weather and current vegetation, which are fundamental factors influencing post-burn community response (Miller et al. 2013, Chambers et al. 2014a).

Artemisia tridentata ssp. *wyomingensis* communities are least resilient to disturbance and least resistant to annual grass invasion of the *A. tridentata* complex (Miller and Eddleman 2000, Chambers et al. 2014a). The abundance of foundational species such as *P. spicata* in the JDFBNM (Rodhouse et al. 2014) is strongly correlated with a sites' resistance to invasion (Chambers et al. 2007, Brooks and Chambers 2011, Davies et al. 2011). In this study greater cover of *B. tectorum* was observed at lower elevation sites and greater cover of *P. spicata* was observed at high elevation sites. It is

likely that post-settlement land-use at lower elevation sites created disturbances which reduced the system's resistance to invasion. Reduced resistance created an opportunity for establishment of invasive annual grasses, like *B. tectorum*. The establishment and eventual dominance of *B. tectorum* caused a biotic threshold to be crossed (Chambers et al. 2014b). Threshold crossing initiates a cycle where resilience and resistance are continuously reduced because the community is no longer able to function within its historical range of variability (Chambers et al. 2014b). The reduction in resilience, contributed to a relatively recent establishment of *T. caput-medusae* in the JDFBNM. Despite inherently low resilience and resistance of *A. tridentata* ssp. *wyomingensis* communities, a relatively intact native perennial grass community at higher elevation forest sites has buffered resilience of the forest sites through time and following fire.

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Figures

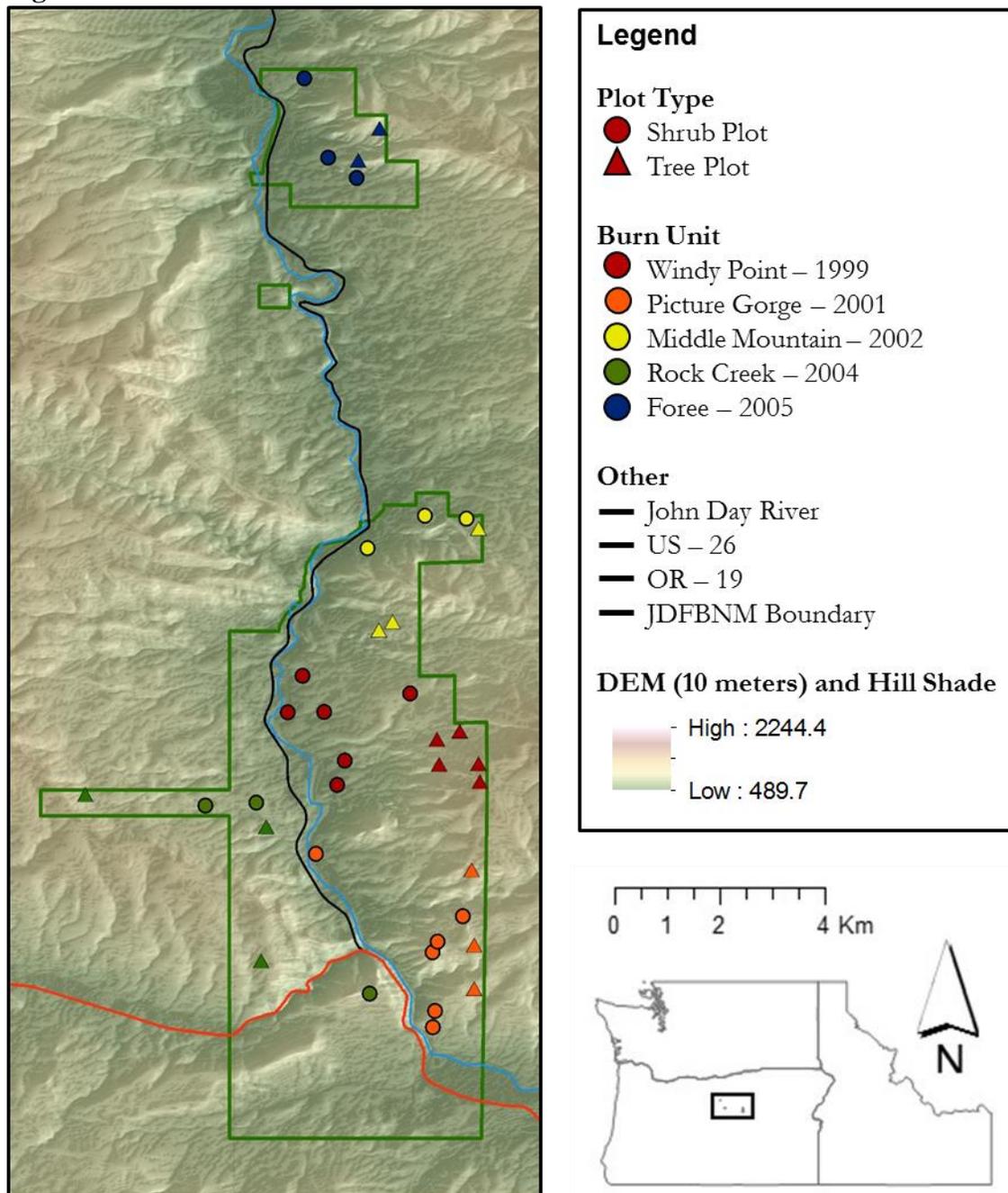


Figure 2.1- Sheep Rock unit of the John Day Fossil Beds National Monument, located in north-central, Oregon, USA. The map shows study plot locations within the monument differentiated between forest (triangles) and brush (circles). Five separate prescribed burn units exist within the Sheep Rock unit: Windy Point 1999 (red), Picture Gorge 2001 (orange), Middle Mountain 2002 (green), Rock Creek 2004 (blue) and Foree 2005 (purple).

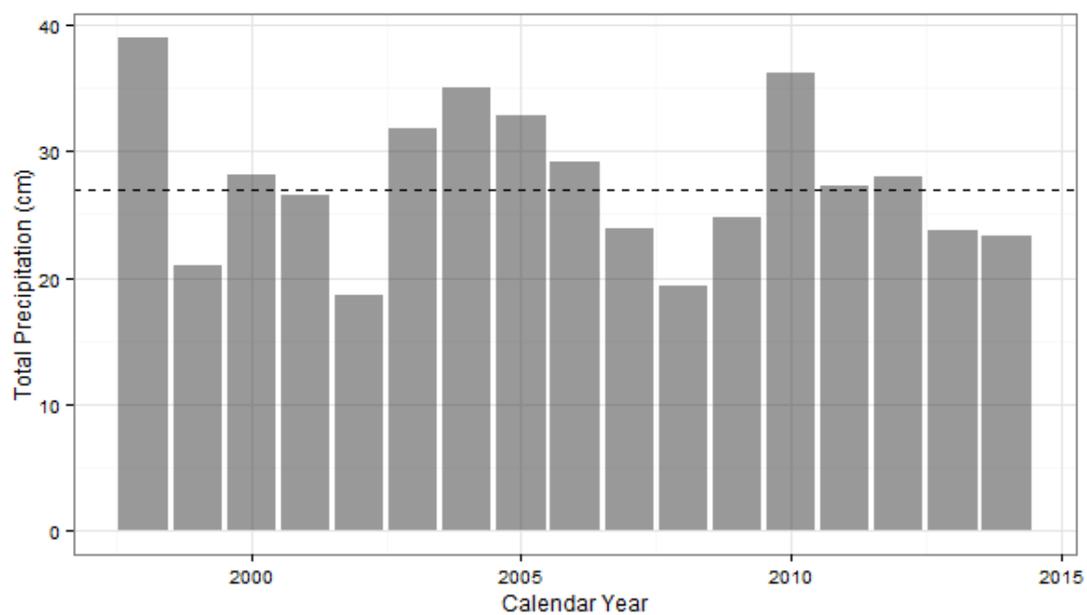


Figure 2.2 – Total annual precipitation (cm) in the John Day Fossil Beds National Monument, Oregon from 1998 to 2014. Mean annual precipitation is 27 cm (dashed line).

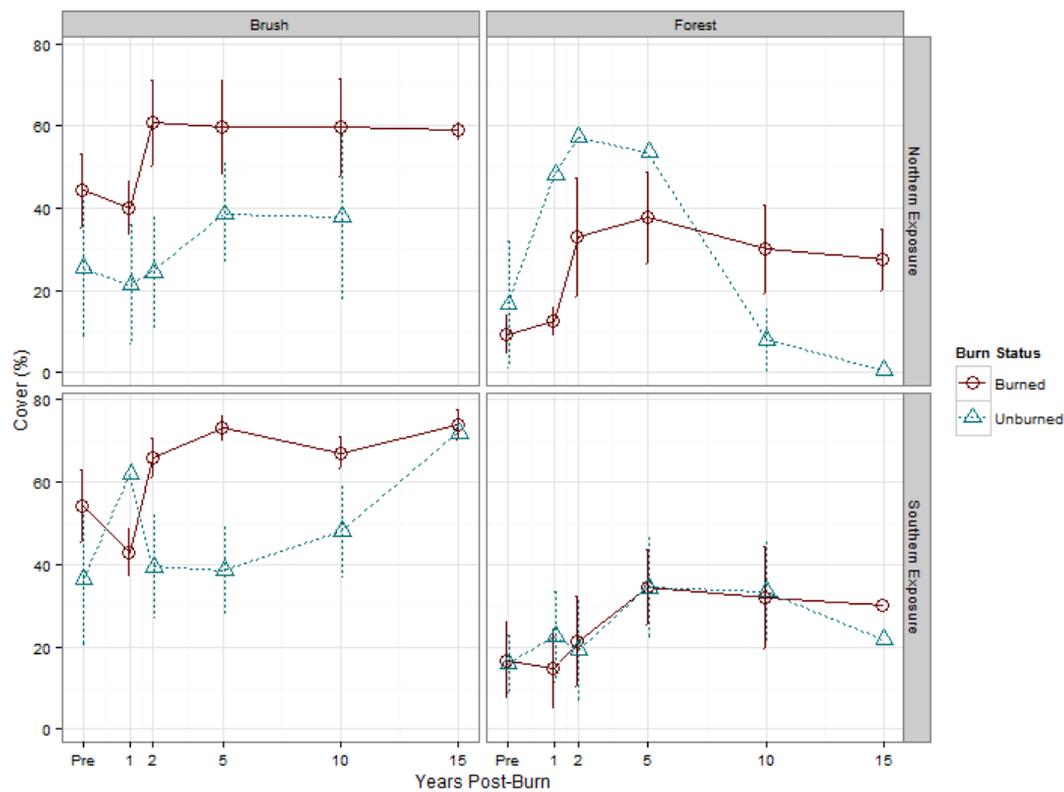


Figure 2.3 – *B. tectorum* cover (mean \pm SE) through time post-burn with both burned (red circles with solid lines) and unburned (blue triangles with dashed lines) plots. *B. tectorum* cover is differentiated between brush plots (left column), forest plots (right column), northern exposures (top) and southern exposures (bottom). Topography is analyzed as a continuous variable, but for purposes of graphical representation it is grouped into northern and southern exposures.

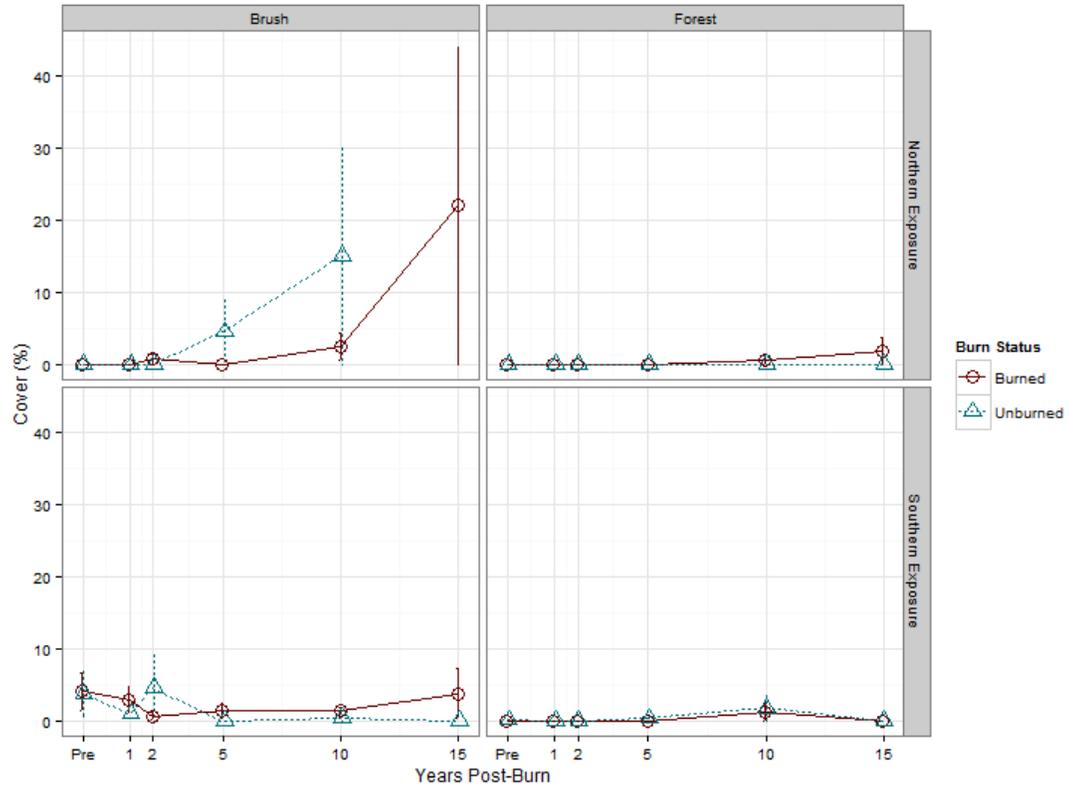


Figure 2.4 – *T. caput-medusae* cover (mean \pm SE) through time post-burn with both burned (red circles with solid lines) and unburned (blue triangles with dashed lines) plots. *T. caput-medusae* cover is differentiated between brush plots (left column), forest plots (right column), northern exposures (top) and southern exposures (bottom). Topography is analyzed as a continuous variable, but for purposes of graphical representation it is grouped into northern and southern exposures.

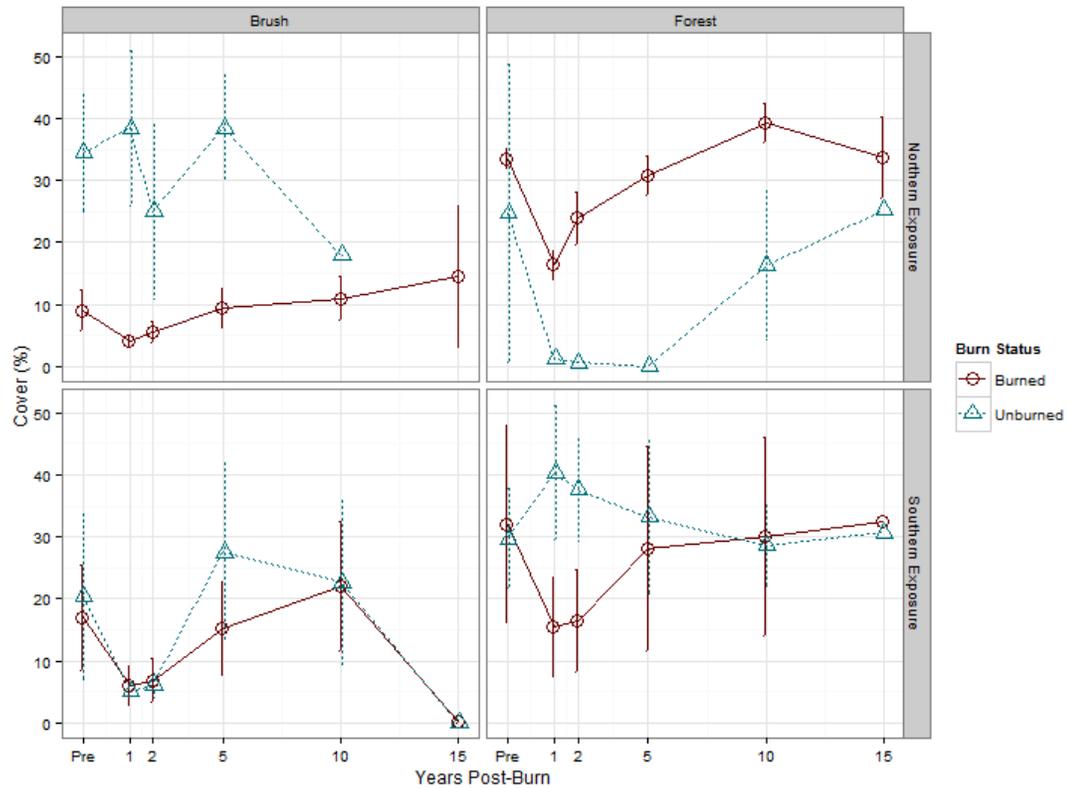


Figure 2.5 – *P. spicata* cover (mean \pm SE) through time post-burn with both burned (red circles with solid lines) and unburned (blue triangles with dashed lines) plots. *P. spicata* cover is differentiated between brush plots (left column), forest plots (right column), northern exposures (top) and southern exposures (bottom). Topography is analyzed as a continuous variable, but for purposes of graphical representation it is grouped into northern and southern exposures.

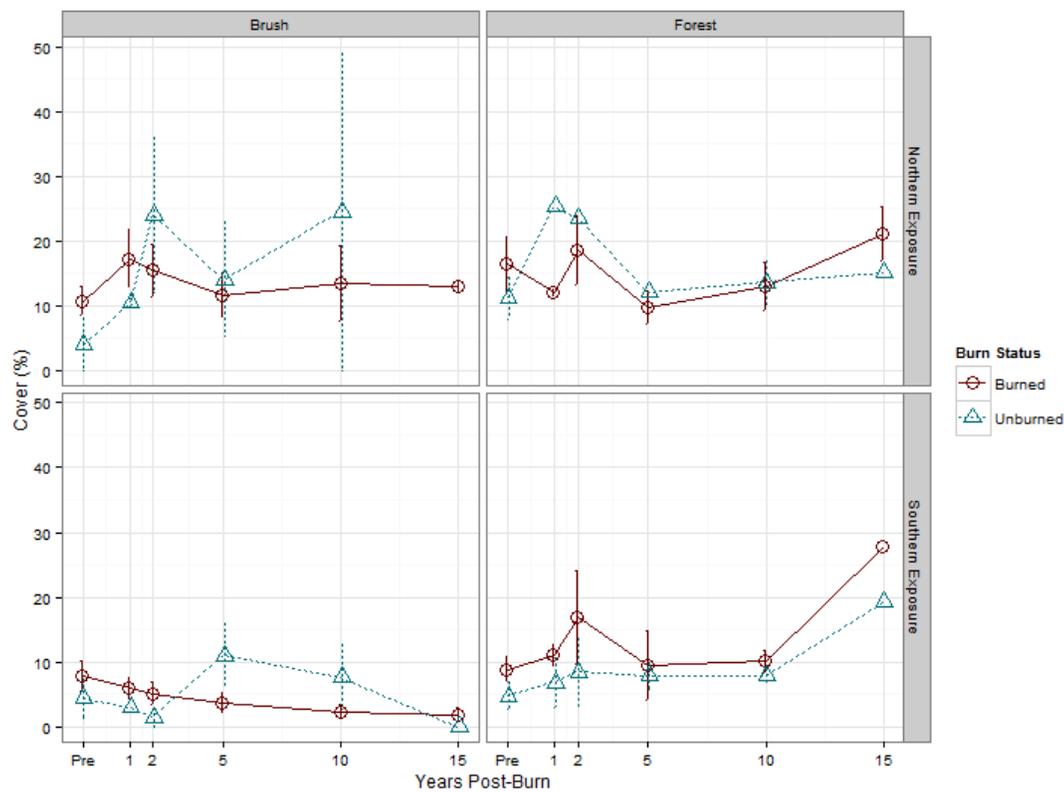


Figure 2.6 – *P. secunda* cover (mean \pm SE) through time post-burn with both burned (red circles with solid lines) and unburned (blue triangles with dashed lines) plots. *P. secunda* cover is differentiated between brush plots (left column), forest plots (right column), northern exposures (top) and southern exposures (bottom). Topography is analyzed as a continuous variable, but for purposes of graphical representation it is grouped into northern and southern exposures.

Table

Parameter	Full Model Results for Each Grass Species of Interest							
	<i>Bromus tectorum</i>		<i>Taeniatherum caput-medusae</i>		<i>Pseudoroegneria spicata</i>		<i>Poa secunda</i>	
	z value	Pr (> z)	z value	Pr (> z)	z value	Pr (> z)	z value	Pr (> z)
(Intercept)	-2.98	0.003	-6.96	<0.0001	-16.49	<0.0001	-14.78	<0.0001
Burn	-4.54	<0.0001	5.84	<0.0001	12.74	<0.0001	-1.53	0.13
Community	-16.47	<0.0001	-3.45	0.0005	13.27	<0.0001	1.30	0.19
Time	4.06	<0.0001	4.42	<0.0001	0.91	0.36	-1.55	0.12
Time ²	-7.32	<0.0001	-1.06	0.29	4.53	<0.0001	-1.00	0.31
Topography	-7.23	<0.0001	-4.28	<0.0001	-7.59	<0.0001	3.26	0.001
Burn × Community	8.70	<0.0001	-0.74	0.46	-11.05	<0.0001	1.42	0.16
Burn × Time	-0.07	0.94	-4.80	<0.0001	-5.84	<0.0001	4.89	<0.0001
Burn × Topography	3.26	0.001	-2.36	0.02	4.42	<0.0001	1.50	0.13
Community × Time	4.78	<0.0001	1.94	0.05	-0.24	0.81	4.86	<0.0001
Community × Topography	4.14	<0.0001	-0.58	0.57	7.90	<0.0001	-1.86	0.06
Time × Topography	-0.15	0.88	4.76	<0.0001	5.71	<0.0001	5.78	<0.0001
Burn × Community × Time	-5.30	<0.0001	1.11	0.27	3.09	0.002	-4.54	<0.0001
Burn × Community × Topography	2.85	0.004	2.41	0.02	-7.80	<0.0001	2.92	0.003
Burn × Time × Topography	-0.11	0.91	3.79	0.0002	-6.79	<0.0001	-0.24	0.81
Community × Time × Topography	0.30	0.76	0.43	0.66	-3.05	0.002	-4.55	<0.0001
Burn × Community × Time × Topography	-3.98	<0.0001	-2.83	0.005	5.69	<0.0001	-2.34	0.019

Table 2.1 – Full GLMM model z-values and p-values of each parameter for each species of interest: *B. tectorum*, *T. caput-medusae*, *P. spicata* and *P. secunda*.

Year Post-Burn	Mean Cover of <i>Bromus tectorum</i> (% \pm SE)			
	Brush Plots		Forest Plots	
	Burned	Unburned	Burned	Unburned
Pre-Burn	49.25 \pm 6.25 Aa	32.00 \pm 10.37 Aa	12.05 \pm 4.32 Aa	16.04 \pm 5.83 Aa
1 Year Post-Burn	41.44 \pm 4.22 Aa	35.00 \pm 15.88 Aa	13.43 \pm 4.01 Aac	28.92 \pm 10.10 Aa
2 Years Post-Burn	63.31 \pm 5.53 Aacd	32.00 \pm 8.67 Ba	27.97 \pm 9.04 Aad	28.77 \pm 12.76 Aa
5 Years Post-Burn	66.44 \pm 23.43 Abde	38.50 \pm 13.33 Ba	36.32 \pm 18.45 Abde	38.19 \pm 22.61 Aa
10 Years Post-Burn	63.36 \pm 6.06 Aace	44.00 \pm 9.01 Aa	30.72 \pm 7.67 Abcdf	27.18 \pm 9.80 Aa
15 Years Post-Burn	69.00 \pm 3.98 ace	72.00 \pm NA	28.31 \pm 4.44 Aaef	11.14 \pm 10.54 Aa

Table 2.2- *B. tectorum* percent cover (mean \pm SE) through year post-burn between brush and forest plots and burned and unburned plots. Different capital letters denote significant differences ($p < 0.05$) between burned and unburned plots of each community type within a given year post-burn. Different lower case letters denote significant differences ($p < 0.05$) between years post-burn within each combination of community type and burn status.

Chapter 3: Long-term fire effects on *Artemisia tridentata* ssp. *wyomingensis* and *Gutierrezia sarothrae* cover and density in protected area sagebrush steppe, John Day Fossil Beds National Monument, Oregon

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Abstract

Fire is a fundamental ecosystem process in sagebrush steppe. The role of fire in these systems has been altered by overgrazing, active fire suppression and annual grass invasion following Euro-American settlement of the western United States. The Sheep Rock management unit of the John Day Fossil Beds National Monument, Oregon offers an opportunity to study long-term (15 year) responses of shrub cover and density to fire in *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) communities. Using generalized linear mixed models we examined fire effects on *A. tridentata* ssp. *wyomingensis* and *Gutierrezia sarothrae* (broom snakeweed) along gradients of community type and topography through time post-burn. Community types are distinguished by *A. tridentata* ssp. *wyomingensis* dominant or brush plots and *Juniperus occidentalis* (western juniper) dominant or forest plots. Fire reduced *A. tridentata* ssp. *wyomingensis* cover in brush plots by 99% on northern exposures and 100% on southern exposures. In forest plots, fire reduced *A. tridentata* ssp. *wyomingensis* cover by 86% and 47% on northern and southern exposures, respectively. Similarly, *A. tridentata* ssp. *wyomingensis* density in brush plots declined by 96% on both northern and southern exposures. In forest plots, fire reduced *A. tridentata* ssp. *wyomingensis* density by 71% and 0% on northern and southern exposures, respectively. The cover and density of *A. tridentata* ssp. *wyomingensis* did not change significantly after a 1 year post-burn decrease, except for in burned forest plots on southern exposures which didn't show significant change through time. The cover of *G. sarothrae* declined by 92% in brush plots and by 73% in forest plots. *Gutierrezia sarothrae* cover recovered to pre-burn cover by 5 years post-burn in brush plots, but did not recover in forest plots until 15 years post-

burn. Topography was not identified as a significant determinant of *G. sarothrae* response to fire. Similarly, to *G. sarothrae* cover, *G. sarothrae* density decreased 1 year post-burn and continued a gradual increase thereafter. In contrast to *G. sarothrae* cover, topography was identified as a significant determinant of *G. sarothrae* density response to fire. We hypothesize southern exposures favor *G. sarothrae* establishment, while northern exposures favor increased *G. sarothrae* size which explains the significance of topography for density and not cover. Due to a long life span, continuation of this study is required to gain a fuller perspective of *A. tridentata* ssp. *wyomingensis* recovery potential in these communities. Results of this study can be used by land managers to consider short and long-term species specific responses to fire. This information is useful when developing plans for reintroducing fire into *A. tridentata* ssp. *wyomingensis* systems or when developing post-wildfire management strategies.

Introduction

Sagebrush (*Artemisia* sp.) steppe is one of the most threatened rangeland ecosystems in North America (Noss et al. 1995). Cold desert sagebrush systems have declined from 25 million hectares pre-European settlement to about 13 million hectares (Miller et al. 2011, Chambers et al. 2014). The post-settlement loss of sagebrush steppe is primarily due to Euro-American land-use (West and Young 2000). Euro-American land-use resulted in overutilization, changes in fire frequency and invasion by annual grasses and woody species in sagebrush steppe (Davies et al. 2011). Within the *A. tridentata* (big sagebrush) alliance *A. tridentata* ssp. *wyomingensis* (Wyoming big sagebrush)

communities are most at-risk due to low resilience to disturbance and low resistance to invasion (Chambers et al. 2007, Miller et al. 2013, Chambers et al. 2014).

Fire is a fundamental disturbance, important for maintenance of *A. tridentata* communities (Wright 1974). Typically, the historical fire return interval within *A. tridentata* ssp. *wyomingensis* communities is defined as between 50 and 100 years (Wright and Bailey 1982). The long-duration fire return interval in *A. tridentata* ssp. *wyomingensis* communities are associated with a high degree of variability, resulting in fire return intervals exceeding 100 years (Miller et al. 2011). The historical fire return interval, fire behavior and ultimately fire effects have been altered by changes to pre-burn plant communities as a result of late 19th and early 20th century overgrazing, active fire suppression and annual grass invasion (Davies et al. 2011). In addition to these factors, increased temperatures and earlier and longer growing seasons associated with climate change, are correlated with increased wildfire frequency and total burned area throughout the western United States (Westerling et al. 2006). Pre-settlement, heterogeneity of burn patterns resulted in heterogeneity of plant community successional stages across a landscape. This heterogeneity further perpetuated heterogeneity of burn patterns due to differential fuel accumulation (Miller and Eddleman 2001, Miller and Heyerdahl 2008). Post-settlement changes, such as increased fuel continuity from annual grass invasion, have resulted in larger, more continuous fires. Therefore, creating homogeneity of plant community successional stages across a site following fire (Miller and Eddleman 2001, Miller and Heyerdahl 2008).

Increased fire size in conjunction with burn pattern homogeneity creates barriers to reestablishment for species such as *A. tridentata* after fire (Miller et al. 2013). *Artemisia tridentata* reestablishes by seed and is entirely dependent on neighboring unburned sites to reestablish on a burned site (Miller et al. 2013). Recovery of *A. tridentata* is dependent on fire severity and distance to seed source (Blaisdell 1953). The long-term recovery of *A. tridentata* ssp. *wyomingensis* is documented as negligible at 20 years post-burn (West and Yorks 2002). Ultimately, post-fire *A. tridentata* recovery is dependent on seed dissemination and soil moisture content at time of establishment (Miller et al. 2013). In contrast, *Gutierrezia sarothrae* (broom snakeweed) tends to increase in response to fire and remains a dominant shrub component until *A. tridentata* or *Juniperus* sp. (juniper) reestablishes (Ralphs and McDaniel 2011). *Gutierrezia sarothrae* is considered a weedy species and is typically dominant on rangelands in poor condition prior to burning (Thacker et al. 2008). Both species are native shrubs, but *A. tridentata* ssp. *wyomingensis* is a long-lived, fire intolerant species and *G. sarothrae* is a short-lived, fire resilient species.

Understanding both short and long-term fire effects on *A. tridentata* ssp. *wyomingensis* and *G. sarothrae* is important for land managers, due to the different roles these species serve within a community. *Artemisia tridentata* is a foundational species in sagebrush steppe and as such plays a fundamental role in the ecosystem's structure and function (Gaston 2011). For example, *A. tridentata* create an island of fertility beneath their canopy with increased levels of carbon, nitrogen and potassium compared to shrub canopy interspaces (Burke et al. 1989, Chambers 2001). The fertility islands play a critical role in post-fire community response through increased seedling establishment

(Boyd and Davies 2010). Therefore, *A. tridentata* ssp. *wyomingensis* contributes to heterogeneity of herbaceous vegetation through modification of microsites and resource availability (Davies et al. 2007). In contrast, *G. sarothrae* is a weedy species and shows pulse establishment in response to increased resource availability such as overgrazing, fire and precipitation (Ralphs and Sanders 2002). Thus, understanding short and long-term responses of these shrub species can provide overall insight into the general response of a community to fire.

Studies of short-term (< 5 years) responses of species are relatively abundant within the literature, in contrast to long-term (> 10 years) responses (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). A synthesis on fire effects in the Great Basin emphasizes the need for long-term (>10 years) research (Miller et al. 2013). The authors argue most currently available long-term research substitutes multiple burn sites for repeated measures on the same site, lacks unburned control plots and doesn't have pre-burn plant community data (Miller et al. 2013). The objective of this study is to characterize long-term (15 year) responses of *A. tridentata* ssp. *wyomingensis* and *G. sarothrae* to fire using data with repeated measures on plots through time, unburned controls and pre-burn community data. We are thereby attempting to contribute to an existing void in Great Basin fire research.

Our questions of interest include the following: How does *A. tridentata* ssp. *wyomingensis* cover and density change immediately post-fire and through 15 years post-fire? Does *A. tridentata* ssp. *wyomingensis* show signs of recovery within 15 years post-

burn? How does *G. sarothrae* cover and density respond to fire? Does the response of *G. sarothrae* persist for 15 years post-burn?

Methods

Study Site

This study was conducted in the Sheep Rock management unit of the John Day Fossil Beds National Monument (JDFBNM), 14 kilometers west of Dayville, OR, USA (see Figure 3.1). The study site is 3,600 hectares located in north-central Oregon's John Day River Valley and is a subunit of the Columbia River Plateau physiographical region (USDI-NPS 2009). The Sheep Rock unit has an extensive history of both sheep and cattle grazing from 19th century Euro-American settlement of the John Day River Valley to establishment of the JDFBNM in 1975 (Erixon et al. 2011). The study area ranges in elevation from 610 meters at the river valley bottom to 1,370 meters at the top of steep hills. The Sheep Rock unit is semi-arid with mean annual precipitation of approximately 27 centimeters, which falls primarily as rain from October to June (PRISM Climate Group 2004). From 1999 to 2014 in the Sheep Rock unit, 2010 was the wettest year with 36.2 centimeters of precipitation and 2002 was the driest year with 18.6 centimeters of precipitation (see Figure 3.2) (PRISM Climate Group 2004).

Within the Sheep Rock Unit there are 52 identified plant associations, which are primarily differentiated by geographic feature variability (Erixon et al. 2011). Upland woodlands are *Juniperus occidentalis* (western juniper) dominated, with an understory of native grasses. Hill slopes and alluvial fans are primarily *A. tridentata* ssp. *wyomingensis*

and encroaching *J. occidentalis*. Downslope *Pseudoroegneria spicata* (bluebunch wheatgrass), *Poa secunda* (Sandberg bluegrass), *Festuca idahoensis* (Idaho fescue) and *Achnatherum thurberianum* (Thurber's needlegrass) are dominant. Due to low site resistance and resilience, coupled with past land-use disturbance, annual grasses including *Bromus tectorum* (cheatgrass) and *Taeniatherum caput-medusae* (medusahead) are widely dispersed throughout the JDFBNM. The majority of study plots are located within the following 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.

Experimental Design

Experimental design and monitoring are based on the National Park Service's (NPS) fire effects monitoring protocol (USDI-NPS 2003) and have been modified to suit the JDFBNM. Study plot locations were selected using restricted random sampling. Potential plot locations were restricted to areas identified by Youtie and Winward (1977) as either *A. tridentata* or *J. occidentalis* dominant. The total area of *A. tridentata* or *J. occidentalis* dominant land within a given burn unit, was divided into equal sized polygons corresponding to a desired number of plots of each community type. A single plot was randomly located within each polygon. If a potential plot location exceeded 60% slope it was excluded. *Artemisia tridentata* dominant or brush plots were restricted to having < 10 *J. occidentalis* per hectare and *J. occidentalis* dominant or forest plots were restricted to having > 10 *J. occidentalis* per hectare (NPS-NOCA 1999). A total of 37 plots ($n_{\text{brush}} = 21$, $n_{\text{forest}} = 16$) were established. The majority of brush plots are located within *Bromus tectorum* semi-natural herbaceous or *Pseudoroegneria spicata* –

Balsamorhiza sagittata – *Poa secunda* herbaceous vegetation alliances (Erixson et al. 2011). The majority of forest plots are located within *Juniperus occidentalis*/*Pseudoroegneria spicata* wooded herbaceous vegetation or *Juniperus occidentalis*/*Cercocarpus ledifolius*/*Pseudoroegneria spicata* woodland or *Juniperus occidentalis*/*Artemisia tridentata* ssp. *wyomingensis*/*Pseudoroegneria spicata* wooded herbaceous vegetation alliances (Erixson et al. 2011).

All prescribed fires were burned in early September or early October. Plots are distributed across five prescribed burn units and burned in the fall of the following years: Windy Point 1999 ($n_{\text{brush}} = 6$, $n_{\text{forest}} = 5$), Picture Gorge 2001 ($n_{\text{brush}} = 6$, $n_{\text{forest}} = 3$), Middle Mountain 2002 ($n_{\text{brush}} = 3$, $n_{\text{forest}} = 3$), Rock Creek 2004 ($n_{\text{brush}} = 3$, $n_{\text{forest}} = 3$) and Foree 2005 ($n_{\text{brush}} = 3$, $n_{\text{forest}} = 2$) (see Table A1). As a result of multiple prescribed burns occurring through time, year post-burn in our analysis does not correspond to calendar year. No unburned control plots were initially established. For the purpose of our analysis we treated plots with no evidence of fire during post-burn monitoring as controls. Of the 37 total plots, we have treated 13 as controls: Windy Point $n_{\text{brush}} = 0$, $n_{\text{forest}} = 2$; Picture Gorge $n_{\text{brush}} = 2$, $n_{\text{forest}} = 2$; Middle Mountain $n_{\text{brush}} = 1$, $n_{\text{forest}} = 1$; Rock Creek $n_{\text{brush}} = 1$, $n_{\text{forest}} = 2$; Foree $n_{\text{brush}} = 1$, $n_{\text{forest}} = 1$.

All monitoring was conducted during June or July of the particular monitoring year. Brush plots are 5 meters by 30 meters in size and forest plots are 20 meters by 50 meters in size. To determine species cover a point intercept method was applied along the 30 meter (brush) or 50 meter (forest) transect and read every 30 centimeters. All species intercepted at a point are recorded as a hit. To determine species density, all shrubs

within 150 meter² (brush) or 250 meter² (forest) belt transects were counted. All plots have been read pre-burn, 1 year post-burn, 2 years post-burn, 5 years post-burn and the oldest plots have been read 10 years post-burn (Windy Point, Picture Gorge, Middle Mountain and Rock Creek) and 15 years post-burn (Windy Point). 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 at the most recent years post-burn, we read 3 plots at 9 years post-burn and pooled them as 10 years post-burn and 1 plot at 13 years post-burn and pooled it as 15 years post-burn in our analysis (see Table A2) .

Statistical Analysis

All analyses were conducted through construction of generalized linear mixed models (GLMM) using the generalized linear mixed effects model (GLMER) function from the LME4 package (Bates et al. 2014) in R version 10.2.2 (R Core Team 2014). GLMMs were used due to inherent violation of ANOVA assumptions of normality and equal variance in binomial and Poisson distribution data. GLMMs allow for violation of these assumptions by defining both a linear predictor and a probability distribution of the observations (Stroup 2014). This is in contrast to a traditional ANOVA which defines the error term in a model equation formula based on assumptions of normality and independence (Stroup 2014).

A model for cover and density of each species of interest was developed using Burn, Community, Topography and Time as fixed effects and Year as a randomized effect. Burn is an indicator of a plots burn status, either burned or unburned. Community

is an indicator of plot type identified by dominant vegetation, either forest or brush. Topography is 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). The slope and aspect were calculated from a 10 meter US Geological Survey (USGS) digital elevation model (DEM) in ArcGIS. Time is an indicator of year post-burn for which each plot was read corresponding to the monitoring interval. Calendar year in our analysis do not correspond to year post-burn because multiple prescribed fires occurred through time. Year is included in the constructed GLMMs as a randomized effect to account for inter-annual variability in precipitation between calendar years. Precipitation pre- and post-burn is an integral factor in post-burn vegetative community response (Miller et al. 2013). Precipitation data from PRISM data indicates a large amount of variability between calendar years over the course of this study in the JDFBNM (see Fig. 3.2). Therefore, including calendar year as a randomized effect is an attempt to account for variation due to differences in calendar year precipitation pre- and post-burn, across different burn units.

For cover and density of each species likelihood ratio tests, including -2 res log likelihood, Akaike information criterion (AIC) and Bayesian information criterion (BIC) indicated the full model with all interactions is the best fit. Significant interactions were explored through additional focused models of the full model's component parts. In addition, post-hoc 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 third-order Burn \times Community \times Topography interaction is significant for *A. tridentata* ssp. *wyomingensis* cover ($z = 5.14$, $p < 0.0001$, see Table 3.1). To explore significance of this interaction, focused models were examined by burn status. The Community \times Topography interaction in focused models is significant for both burned ($z = -3.12$, $p = 0.002$) and unburned plots ($z = 7.22$, $p < 0.001$). Further focused models indicate Topography is significant for unburned brush ($z = -2.51$, $p = 0.01$), unburned forest ($z = 6.30$, $p < 0.0001$) and burned brush plots ($z = 5.13$, $p < 0.0001$) and not significant for burned forest plots ($z = -1.02$, $p = 0.31$). Cumulatively these results indicate in burned plots the effect of community type is dependent on topography, but topography is a significant predictor for burned brush and not for burned forest plots. The 1 year post-burn decrease in *A. tridentata* ssp. *wyomingensis* cover is most dramatic in brush plots (see Fig. 3.3). *Artemisia tridentata* ssp. *wyomingensis* cover decreased 99% on northern exposures and 100% on southern exposures in burned brush plots at 1 year post-burn (see Fig. 3.3). In contrast, cover decrease was 86% in forest plots on northern exposures and 47% on southern exposures (see Fig. 3.3). After an initial decrease, cover of *A. tridentata* ssp. *wyomingensis* remained relatively unchanged through 15 years post-burn (see Fig. 3.3).

The three-way interaction of Burn \times Community \times Time for *A. tridentata* ssp. *wyomingensis* cover is significant ($z = -7.03$, $p < 0.0001$, see Table 3.1). Focused models by community type indicate the Burn \times Time interaction is significant for both brush ($z = 9.69$, $p < 0.0001$) and forest plots ($z = 3.11$, $p = 0.002$). Together, these results suggest fire effects are dependent on time post-burn across both community types for *A. tridentata* ssp. *wyomingensis* cover. Cover of *A. tridentata* ssp. *wyomingensis* in burned brush plots declined significantly from a mean of $14.12 \pm 2.90\%$ pre-burn, to $0.06 \pm 0.06\%$ 1 year post-burn (see Table 3.3). Similarly, cover of *A. tridentata* ssp. *wyomingensis* in burned forest plots declined significantly from a mean of $8.73 \pm 2.77\%$ pre-burn to $2.75 \pm 1.39\%$ 1 year post-burn (see Table 3.3).

For *A. tridentata* ssp. *wyomingensis* density the three-way Burn \times Time \times Topography interaction is significant ($z = -2.23$, $p = 0.026$, see Table 3.2). Focused models indicate the Time \times Topography interaction is significant for both unburned ($z = -11.45$, $p < 0.0001$) and burned plots ($z = -2.29$, $p = 0.02$). In contrast to *A. tridentata* ssp. *wyomingensis* cover, these results indicate burn effects through time post-burn are dependent on topography for *A. tridentata* ssp. *wyomingensis* density (see Fig. 3.4).

The three-way Burn \times Community \times Topography ($z = 16.52$, $p < 0.0001$, see Table 3.2) interaction is also significant for *A. tridentata* density. Focused models show a significant Community \times Topography interaction for both burned ($z = -15.77$, $p < 0.0001$) and unburned plots ($z = 25.08$, $p < 0.0001$). Further, focused models show a significant effect of Topography on both burned brush ($z = 11.14$, $p < 0.0001$) and burned forest ($z = -14.02$, $p < 0.0001$) plots. This is in contrast to focused models for *A.*

tridentata cover, which show a lack of significance for the effect of topography on burned forest plots. Together these results indicate, regardless of fire the effect of topography is dependent on community type. Density of *A. tridentata* ssp. *wyomingensis* declined most in brush plots and on northern exposures (see Fig. 3.4). The density of *A. tridentata* ssp. *wyomingensis* in burned brush plots declined by 96% on northern exposures and by 96% on southern exposures 1 year post-burn (see Fig. 3.4). In burned forest plots, density of *A. tridentata* ssp. *wyomingensis* declined by 71% on northern exposures and 0% on southern exposures (see Fig. 3.3).

The Burn \times Community \times Time ($z = -31.20$, $p < 0.0001$, see Table 3.2) interaction is also significant for *A. tridentata* ssp. *wyomingensis* density. Focused models by community type show the Burn \times Time interaction is significant for both brush ($z = 37.72$, $p < 0.0001$) and forest plots ($z = 3.53$, $p = 0.0004$). These results suggest regardless of community type, the effect of fire is dependent on time post-burn. Within burned forest plots density of *A. tridentata* ssp. *wyomingensis* declined, but not significantly from a mean of 0.13 ± 0.03 shrubs per meter² pre-burn, to 0.07 ± 0.03 shrubs per meter² 1 year post-burn (see Table 3.4). In burned forest plots, density of *A. tridentata* ssp. *wyomingensis* declined significantly from pre-burn density to a mean of 0.04 ± 0.02 shrubs per meter² at 5 years post-burn and 0.04 ± 0.01 shrubs per meter² at 10 years post-burn (see Table 3.4). The density of *A. tridentata* ssp. *wyomingensis* in burned brush plots declined significantly from a mean of 0.23 ± 0.04 shrubs per meter² pre-burn, to 0.01 ± 0.00 shrubs per meter² 1 year post-burn and did not change significantly thereafter (see Table 3.4).

Gutierrezia sarothrae

For *G. sarothrae* cover, the third-order Burn \times Community \times Time interaction is significant ($z = 2.33$, $p = 0.02$, see Table 3.1). In focused models by community type, the Burn \times Time interaction is significant for brush plots ($z = -2.63$, $p = 0.008$) and is not significant for forest plots ($z = 1.18$, $p = 0.24$). These results indicate, the effect of burning is dependent on time for brush plots, but is not dependent on time for forest plots. In burned brush plots, cover of *G. sarothrae* declined significantly from a mean of $3.12 \pm 0.77\%$ cover pre-burn, to a mean of $0.25 \pm 0.14\%$ cover 1 year post-burn (see Fig. 3.5). The cover of *G. sarothrae* at 5 years post-burn increased to $2.12 \pm 1.15\%$ in burned brush plots and was no longer significantly different from pre-burn cover (see Fig. 3.5). In burned forest plots cover of *G. sarothrae* declined significantly from $3.16 \pm 1.24\%$ cover pre-burn, to $0.86 \pm 0.37\%$ cover 1 year post-burn and ultimately bottomed-out at 2 years post-burn with a mean cover of $0.09 \pm 0.09\%$ (see Fig. 3.5). The cover of *G. sarothrae* in forest plots showed signs of recovery at 10 years post-burn with an increase to a mean of $1.43 \pm 0.57\%$ cover, but remained significantly different from pre-burn cover (see Fig. 3.5).

The four-way Burn \times Community \times Time \times Topography interaction is significant for *G. sarothrae* density ($z = -12.06$, $p < 0.0001$, see Table 3.2). Focused models by community type show the Burn \times Time \times Topography interaction is not significant for brush plots ($z = 0.41$, $p = 0.68$) and is significant for forest plots ($z = -8.49$, $p < 0.0001$). The focused models indicate the effect of burning is dependent on time and topography in forest plots and not in brush plots. Although, within brush plots all two-way interactions

are significant. These results are in contrast to *G. sarothrae* cover, which did not show a significant effect of topography. Overall, density of *G. sarothrae* tends to be higher in brush plots and on southern exposures. Similarly in pattern to *A. tridentata* ssp. *wyomingensis*, *G. sarothrae* density in burned brush plots declined 94% on northern exposures and 88% on southern exposures compared to 78% in burned forest plots on northern exposures and 45% on southern exposures (see Fig. 3.6). In brush plots on both northern and southern exposures *G. sarothrae* density bottomed-out 1 year post-burn with 0.05 ± 0.10 shrubs per meter² and 0.11 ± 0.26 shrubs per meter², respectively (see Fig. 3.6). The mean density of *G. sarothrae* continued to recover through time post-burn on northern and southern exposures in burned brush plots (see Fig. 3.6). In burned forest plots on both northern and southern exposures, *G. sarothrae* declined gradually through time post-burn and bottomed-out at 5 years post-burn with 0.04 ± 0.05 shrubs per meter² and 0.25 ± 0.21 shrubs per meter², respectively (see Fig. 3.6). *Gutierrezia sarothrae* density continued to recover in burned forest plots through time, but not to the degree of brush plots (see Fig. 3.6).

Discussion

Our analysis uses GLMMs to determine the long-term (15 year) response of native shrubs to prescribed fire in the JDFBNM. As the literature suggests both shrub species responded differently to fire and in the post-fire environment. The overall lack of significance in response of each species between years post-burn in unburned control

plots, suggests measured differences are in fact burn effects rather than results of confounding factors.

Artemisia tridentata ssp. *wyomingensis*

The cover and density of *A. tridentata* ssp. *wyomingensis* across both community types, declined dramatically 1 year post-burn. The significant decline in cover and density 1 year post-burn is consistent with literature reporting *A. tridentata* fire intolerance (Blaisdell 1953, Wright 1972, Winward 1985). A previous fire study in the JDFBNM reported similar results with 100% reduction in *A. tridentata* density 1 year post burn, although their results are restricted to north slopes (Sapsis 1990).

Over the course of this study, neither *A. tridentata* cover nor density showed any appreciable change following the dramatic decrease 1 year post-burn. The response of *A. tridentata* ssp. *wyomingensis* to fire is reportedly variable by site (Wambolt et al. 2001) and ultimately dependent on seed dissemination and soil moisture content at time of seedling establishment (Miller et al. 2013). Some studies have reported no significant change in *A. tridentata* ssp. *wyomingensis* cover after an initial post-burn decrease at 18 years (West and Yorks 2002) and 32 years (Wambolt et al. 2001) post-fire. Others have reported recovery of *A. tridentata* ssp. *wyomingensis* to pre-burn cover by 30 years post-burn (Harniss and Murray 1973, Watts and Wambolt 1995). The longevity of studies reporting *A. tridentata* ssp. *wyomingensis* recovery are twice as long as this study. Therefore, the 15 year time frame of this study is not long enough to see if *A. tridentata* ssp. *wyomingensis* will recover in the JDFBNM. Although, if *A. tridentata* ssp. *wyomingensis* is going to reestablish in the near future, the observed declines in cover

and density should begin to show a reversal in trend. To date, evidence of a trend reversal has not been detected. The recovery of *A. tridentata* is dependent on proximity of burned sites to seed sources and seed dissemination from neighboring populations (Blaisdell 1953, Miller et al. 2013). Vegetation monitoring shows *A. tridentata* ssp. *wyomingensis* cover in the JDFBNM is low to negligible (Rodhouse et al. 2010). The history of grazing coupled with extensive prescribed fires in the JDFBNM have likely contributed to a small extant population size. The limited population which *A. tridentata* ssp. *wyomingensis* can reestablish from will inevitably reduce the speed of, if not the possibility of reestablishment.

Results suggest response of *A. tridentata* ssp. *wyomingensis* density through time post-burn is dependent in part on topography. The amount of solar radiation a site receives varies based on slope and aspect. Variability in solar radiation influences plant community composition, even over relatively small elevation gradients (Mata-Gonzalez et al. 2002). Previous studies in the JDFBNM identified significance of the combined effects of slope and aspect on plant community composition (Rodhouse et al. 2014, Esposito 2015). In addition, results indicate topographic effects on *A. tridentata* ssp. *wyomingensis* cover and density differ by community type and time since fire. The effect of fire on *A. tridentata* ssp. *wyomingensis* cover is dependent on topography in burned brush plots, but not in burned forest plots. *Juniperus occidentalis* dominated 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 meters and the mean elevation of forest plots is 956 meters. 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 (Miller et al. 2013, Chambers et al. 2014). Also higher elevations of the JDFBNM were likely insulated from historical grazing and cultivation (Erixson et al. 2011). Cover of *B. tectorum* is greater in brush plots than in forest plots and on northern than southern exposures. Therefore, we hypothesize the effect of fire on *A. tridentata* cover at higher elevation juniper sites and on south slopes is limited by fuel continuity, while fuel continuity at lower elevation brush sites is not a limiting factor, thus allowing topography to be influential.

Gutierrezia sarothrae

Across all plots, cover of *G. sarothrae* declined 1 year post-burn. This result is consistent with literature indicating *G. sarothrae* susceptibility to fire (Britton and Ralphs 1979, Gatewood 1992). The cover of *G. sarothrae* returned to pre-burn cover by 5 years post-burn in brush plots. In contrast, cover of *G. sarothrae* in forest plots did not return to pre-burn cover until 15 years post-burn. The results of this study are contradictory to others on *G. sarothrae* in the Great Basin. Studies suggest *G. sarothrae* increases in response to fire and remains dominant in the community until *A. tridentata* reestablishes (Pechanec and Blaisdell 1954, Ralphs and McDaniel 2011). Our study results are more similar to those from the desert Southwest. One Southwest study suggests *G. sarothrae* will reestablish gradually through time if seedlings establishment doesn't occur within 1 to 2 years post-burn (McDaniel et al. 2000). Other studies suggest *G. sarothrae* increases significantly post-fire, particularly in *A. tridentata* ssp. *wyomingensis* communities

(Thacker et al. 2008). The observations further suggest increases would be amplified by grazing history and annual grass invasion in the JDFBNM (Thacker et al. 2008). The difference in elevation between community types and the subsequent lack of disturbance at high elevations sites with less invasive annual grass establishment may explain slower recovery of *G. sarothrae* at higher elevation sites. Furthermore, *P. spicata* is an effective deterrent to *G. sarothrae* establishment (Thacker et al. 2008). The greater abundance of *P. spicata* in forest plots than in brush plots may explain a slower increase of *G. sarothrae* at higher elevations.

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 year post-burn and showed varying degrees of increase across community types and topographic gradients thereafter. The recovery of *G. sarothrae* cover, but not density suggests individual *G. sarothrae* plants are larger post-burn than they were pre-burn. Unlike *G. sarothrae* cover, topography is a significant interaction parameter for *G. sarothrae* density. *Gutierrezia sarothrae* does not conserve water under increased soil water stress and responds negatively to drought (Wan et al. 1993, Thacker et al. 2008, Ralphs and McDaniel 2011). Lack of drought tolerance suggests *G. sarothrae* would be more successful on northern aspects than on southern aspects and on higher elevation forest plots than on lower elevation brush plots. Our analysis, does not show consistent significant differences between community types or topography. The literature does not provide a clear rationale for why topography would be significant for density and not for cover. Plot means indicate southern exposures in the JDFBNM appear to be more conducive to *G. sarothrae* establishment than northern exposures. 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. We hypothesize more individual *G. sarothrae* established on south slopes, but their size is limited by nutrient and water availability. In contrast, we hypothesize establishment of *G. sarothrae* on north slopes was limited by greater site resistance, but increased nutrient availability favored increased size of individual *G. sarothrae* on north slopes. We believe this is a possible explanation for the significance of topography for *G. sarothrae* density and not cover. Additional studies with data on *G. sarothrae* size along topographic gradients are needed to further explore these results.

Conclusion

Overall, 15 years is not enough time to full characterize long-term responses of *A. tridentata* ssp. *wyomingensis* and *G. sarothrae* to fire. Our results show a rapid decline in the short-term and negligible long-term recovery of *A. tridentata* ssp. *wyomingensis*. The results of our analysis show no signs of *A. tridentata* ssp. *wyomingensis* recovery within the first 15 years post-burn. To gain a fuller perspective of *A. tridentata* ssp. *wyomingensis* recovery potential this study should be continued. The longevity of recovery time, needs to be considered by land managers when prescribing fire in *A. tridentata* ssp. *wyomingensis* communities. Return of *G. sarothrae* to pre-burn cover within this study's time-frame, but not above pre-burn cover should also be of consideration to land managers when burning. These results are inconsistent with Great Basin literature and will require additional study. In addition, continuation of this study

may illuminate the source of variation between *G. sarothrae* cover and density with respect to topography.

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Figures

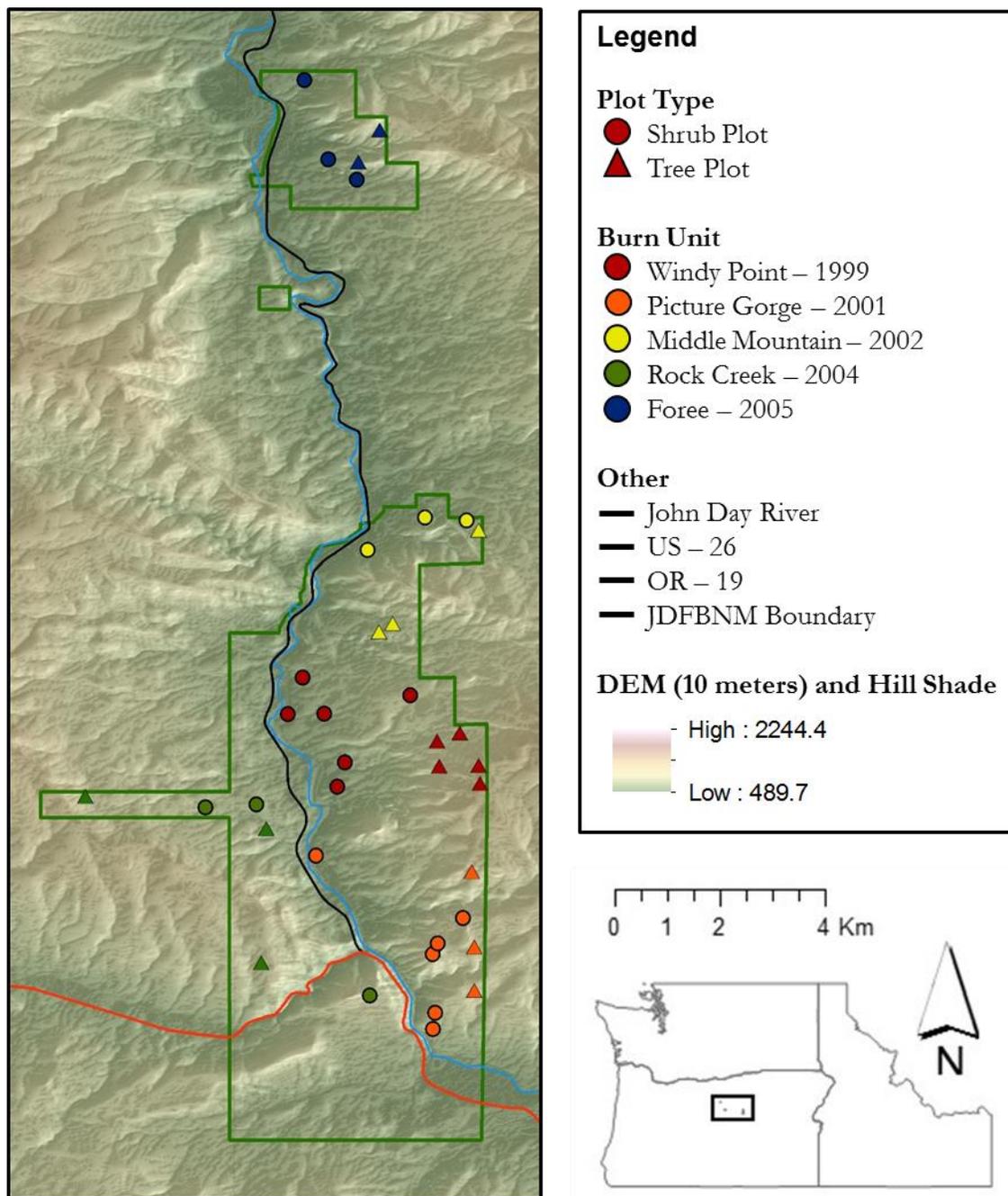


Figure 3.1 – Sheep Rock unit of the John Day Fossil Beds National Monument, located in north-central, Oregon, USA. The map shows study plot locations within the monument differentiated between forest (triangles) and brush (circles). Five separate prescribed burn units exist within the Sheep Rock unit: Windy Point 1999 (red), Picture Gorge 2001 (orange), Middle Mountain 2002 (green), Rock Creek 2004 (blue) and Foree 2005 (purple).

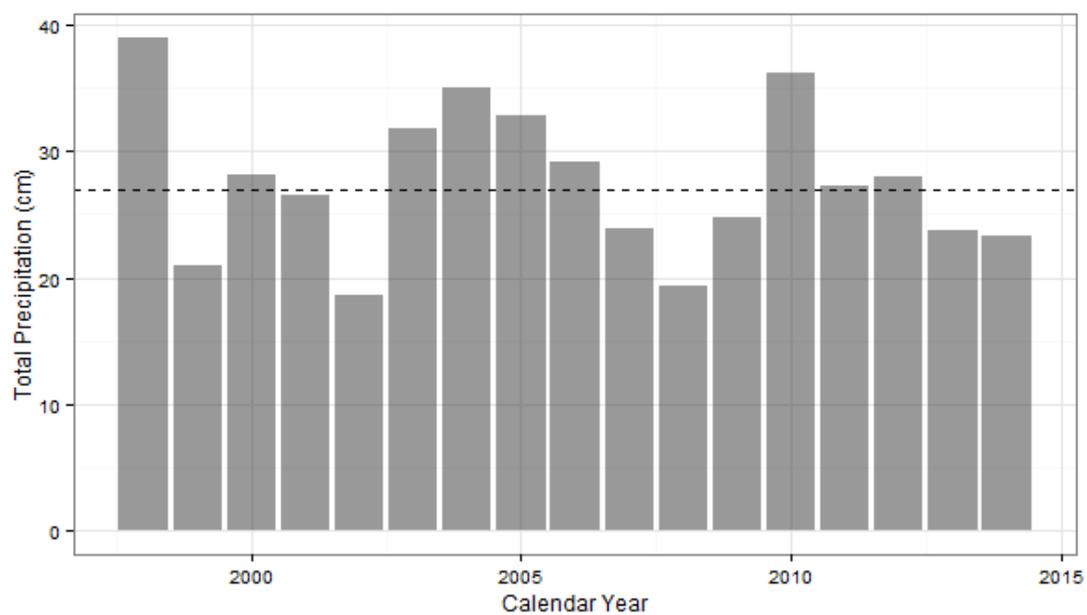


Figure 3.2 – Total annual precipitation (cm) in the John Day Fossil Beds National Monument, Oregon from 1998 to 2014. Mean annual precipitation is 27 cm (dashed line).

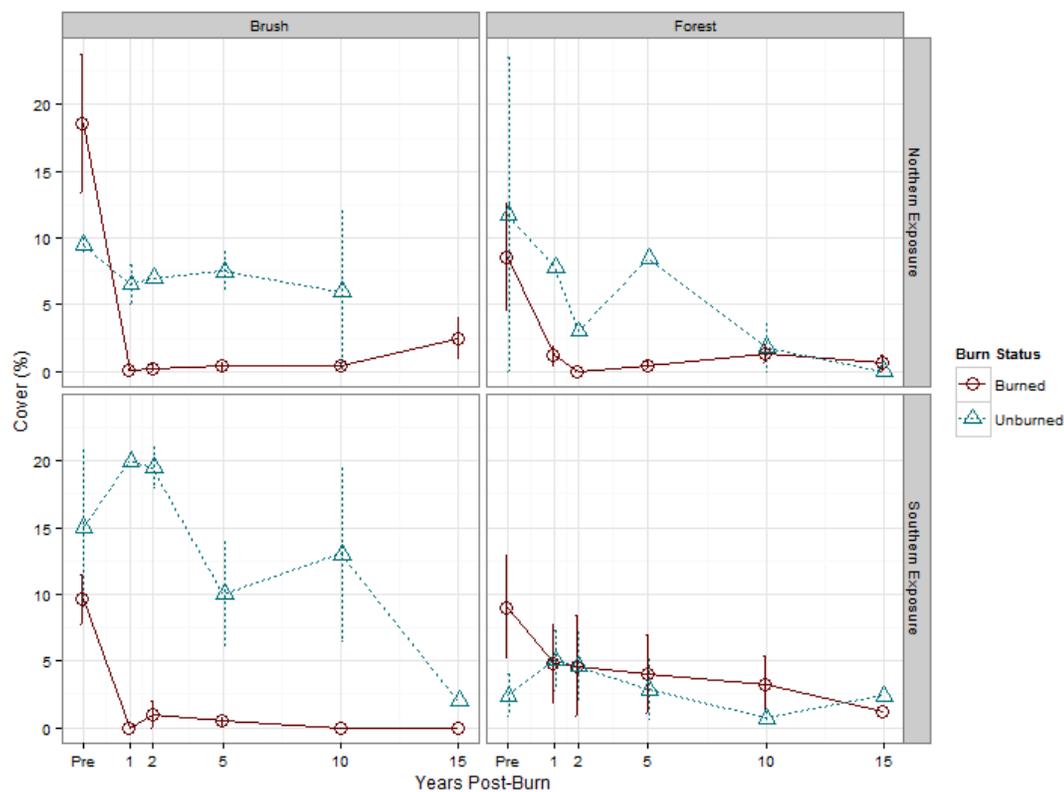


Figure 3.3 – *A. tridentata* ssp. *wyomingensis* cover (mean \pm SE) through time post-burn with both burned (red circles with solid lines) and unburned (blue triangles with dashed lines) plots. *A. tridentata* ssp. *wyomingensis* cover is differentiated between brush plots (left column), forest plots (right column), northern exposures (top) and southern exposures (bottom). Topography is analyzed as a continuous variable, but for purposes of graphical representation it is grouped into northern and southern exposures.

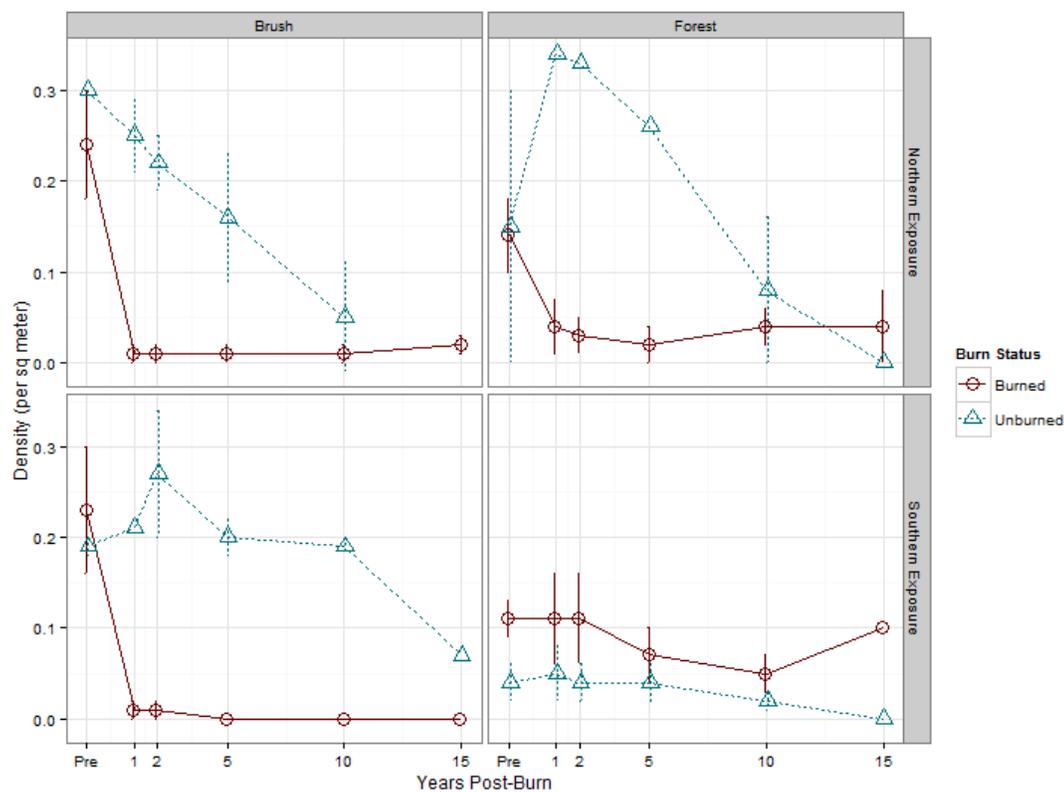


Figure 3.4 – *A. tridentata* ssp. *wyomingensis* density (mean \pm SE) through time post-burn with both burned (red circles with solid lines) and unburned (blue triangles with dashed lines) plots. *A. tridentata* ssp. *wyomingensis* density is differentiated between brush plots (left column), forest plots (right column), northern exposures (top) and southern exposures (bottom). Topography is analyzed as a continuous variable, but for purposes of graphical representation it is grouped into northern and southern exposures.

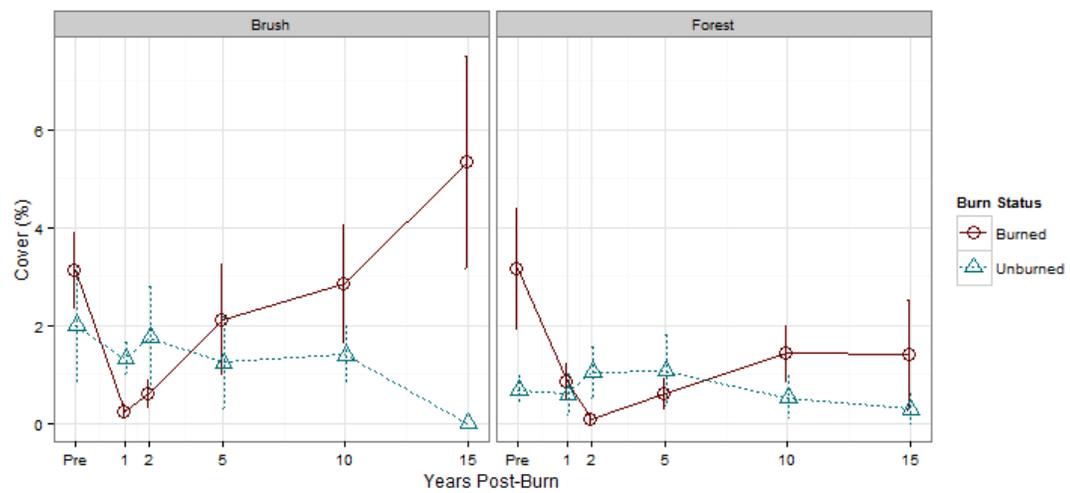


Figure 3.5 – *G. sarothrae* cover (mean \pm SE) through time post-burn with both burned (red circles with solid lines) and unburned (blue triangles with dashed lines) plots. *G. sarothrae* cover is differentiated between brush (left column) and forest plots (right column).

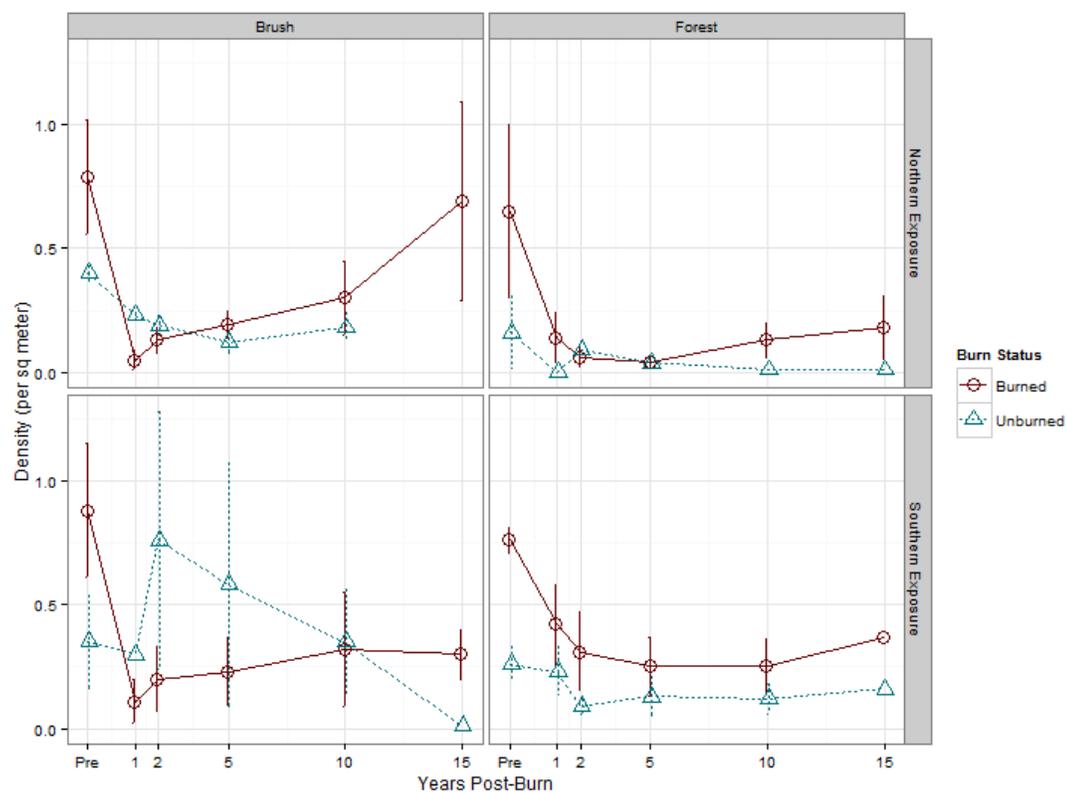


Figure 3.6 – *G. sarothrae* density (mean \pm SE) through time post-burn with both burned (red) and unburned (blue) plots. *G. sarothrae* density is differentiated between brush plots (left column), forest plots (right column), northern exposures (top) and southern exposures (bottom). Topography is analyzed as a continuous variable, but for purposes of graphical representation it is grouped into northern and southern exposures.

Tables

Parameter	Full Model Results for Shrub Cover			
	<i>Artemisia tridentata</i> <i>ssp. wyomingensis</i>		<i>Gutierrezia</i> <i>sarothrae</i>	
	z value	Pr (> z)	z value	Pr (> 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
Burn × Community	-0.62	0.54	-2.89	0.004
Burn × Time	8.68	<0.0001	-2.61	0.009
Burn × Topography	-4.00	<0.0001	0.88	0.38
Community × Time	7.59	<0.0001	-3.13	0.002
Community × Topography	-5.37	<0.0001	0.74	0.46
Time × Topography	-0.76	0.45	1.02	0.31
Burn × Community × Time	-7.03	<0.0001	2.33	0.02
Burn × Community × Topography	5.14	<0.0001	-0.07	0.94
Burn × Time × Topography	0.65	0.52	-0.31	0.76
Community × Time × Topography	1.24	0.22	-1.45	0.15
Burn × Community × Time × Topography	-1.45	0.15	0.58	0.56

Table 3.1 – Full GLMM model z-values and p-values of each parameter for cover of each species of interest: *A. tridentata* *ssp. wyomingensis* and *G. sarothrae*.

Parameter	Full Model Results for Shrub Density			
	<i>Artemisia tridentata</i> <i>ssp. wyomingensis</i>		<i>Gutierrezia</i> <i>sarothrae</i>	
	z value	Pr(> z)	z value	Pr(> z)
(Intercept)	43.76	<0.0001	16.16	<0.0001
Burn	11.13	<0.0001	2.41	0.016
Community	-14.46	<0.0001	6.4	<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
Burn × Community	-4.27	<0.0001	-20.31	<0.0001
Burn × Time	40.52	<0.0001	8.09	<0.0001
Burn × Topography	11.90	<0.0001	11.86	<0.0001
Community × Time	38.01	<0.0001	-12.78	<0.0001
Community × Topography	-8.25	<0.0001	-8.95	<0.0001
Time × Topography	-3.68	0.0002	-6.52	<0.0001
Burn × Community × Time	-31.20	<0.0001	-7.58	<0.0001
Burn × Community × Topography	16.52	<0.0001	12.29	<0.0001
Burn × Time × Topography	-2.23	0.026	6.1	<0.0001
Community × Time × Topography	-0.27	0.79	-5.78	<0.0001
Burn × Community × Time × Topography	0.58	0.56	-12.06	<0.0001

Table 3.2 – Full GLMM model z-values and p-values of each parameter for density of each species of interest: *A. tridentata* *ssp. wyomingensis* and *G. sarothrae*.

Year Post-Burn	Mean Cover of <i>A. tridentata</i> ssp. <i>wyomingensis</i> (% \pm SE)			
	Brush Plots		Forest Plots	
	Burned	Unburned	Burned	Unburned
Pre-Burn	14.12 \pm 2.90 Aa	12.80 \pm 3.48 Aa	8.73 \pm 2.77 Aa	4.74 \pm 2.94 Aa
1 Year Post-Burn	0.06 \pm 0.06 Ab	11.00 \pm 4.58 Ba	2.75 \pm 1.39 Ab	5.72 \pm 1.75 Aa
2 Years Post-Burn	0.62 \pm 0.51 Ab	13.25 \pm 3.66 Ba	1.98 \pm 1.70 Ab	4.22 \pm 1.86 Aa
5 Years Post-Burn	0.44 \pm 0.18 Ab	8.75 \pm 1.88 Ba	1.98 \pm 1.32 Ab	3.98 \pm 2.08 Aa
10 Years Post-Burn	0.21 \pm 0.11 Ab	10.20 \pm 4.39 Ba	2.03 \pm 0.87 Ab	0.98 \pm 0.51 Aa
15 Years Post-Burn	0.83 \pm 0.65 b	2.00 \pm NA	0.80 \pm 0.40 Ab	1.20 \pm 1.20 Aa

Table 3.3 – *A. tridentata* ssp. *wyomingensis* cover (mean \pm SE) through year post-burn between brush and forest plots and burned and unburned plots. Different capital letters denote significant differences ($p < 0.05$) between burned and unburned plots of each plot type within a given year post-burn. Different lower case letters denote significant differences ($p < 0.05$) between years post-burn within each combination of plot type and burn status.

Year Post-Burn	Mean Density (per sq meter) of <i>A. tridentata</i> ssp. <i>wyomingensis</i> (\pm SE)			
	Brush Plots		Forest Plots	
	Burned	Unburned	Burned	Unburned
Pre-Burn	0.23 \pm 0.04 Aa	0.23 \pm 0.03 Aa	0.13 \pm 0.03 Aa	0.07 \pm 0.04 Aa
1 Year Post-Burn	0.01 \pm 0.00 Ab	0.23 \pm 0.03 Ba	0.07 \pm 0.03 Aac	0.12 \pm 0.08 Aa
2 Years Post-Burn	0.01 \pm 0.00 Ab	0.25 \pm 0.04 Ba	0.07 \pm 0.03 Aac	0.11 \pm 0.08 Aa
5 Years Post-Burn	0.01 \pm 0.00 Ab	0.18 \pm 0.03 Ba	0.04 \pm 0.02 Abcd	0.08 \pm 0.04 Aa
10 Years Post-Burn	0.01 \pm 0.01 Ab	0.14 \pm 0.04 Bb	0.04 \pm 0.01 Abc	0.03 \pm 0.02 Aa
15 Years Post-Burn	0.01 \pm 0.00 b	0.07 \pm NA	0.06 \pm 0.03 Aad	0.00 \pm 0.00 Aa

Table 3.4 – *A. tridentata* ssp. *wyomingensis* density (mean \pm SE) per meter² through year post-burn differentiated between brush and forest plots and burned and unburned plots. Different capital letters denote significant differences ($p < 0.05$) between burned and unburned plots of each plot type within a given year post-burn. Different lower case letters denote significant differences ($p < 0.05$) between years post-burn within each combination of plot type and burn status.

Chapter 4: General Conclusions

This study analyzed short and long-term responses of *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush), *Bromus tectorum* (cheatgrass), *Gutierrezia sarothrae* (broom snakeweed), *Poa secunda* (Sandberg bluegrass), *Pseudoroegneria spicata* (bluebunch wheatgrass) and *Taeniatherum caput-medusae* (medusahead) to prescribed fire in the Sheep Rock management unit of the John Day Fossil Beds National Monument, Oregon. This study is relatively unique within long-term sagebrush steppe fire effects literature because the dataset includes unburned control plots, repeated measures on individual plots through time and pre-burn plant community data (Miller et al. 2013). The pre-burn cover of each species was not significantly different between burned and unburned plots, which indicates fuel loads were not a significant reason for differences in burn status between plots. Analysis indicated cover and density of each species did not change significantly with time since fire. This result suggests variations detected within burned plots are in fact fire effects. The dominant plant community type, topography defined as the combined effect of aspect and slope and time post-burn were all identified as significant parameters in determining individual species response to fire. Analysis of *T. caput-medusae* was not fully possible because the pre-burn abundance within study plots was minimal.

Artemisia tridentata ssp. *wyomingensis* cover and density declined 1 year post-burn, which is consistent with documented *A. tridentata* fire intolerance (Blaisdell 1953, Wright 1972, Winward 1985). The cover and density showed no appreciable changes from 1 through 15 years post-burn. The response varied between community types and was less severe in higher elevation forest plots than in lower elevation brush plots. This

result is attributed to higher elevation *Juniperus occidentalis* (western juniper) sites having less fuel continuity (Miller and Rose 1999), which limited potential fire effects in these sites.

Bromus tectorum cover increased dramatically 2 years post-burn and did not show significant changes thereafter. The significant increase in *B. tectorum* cover is partially attributed to low resistance of *A. tridentata* ssp. *wyomingensis* to invasion, particularly following a disturbance like fire (Chambers et al. 2007, Miller et al. 2013, Chambers et al. 2014). The effect of topography on *B. tectorum* cover was dependent on community type. The mean cover of *B. tectorum* tended to be greater in low elevation brush plots than in high elevation forest plots. Both high elevations and north slopes tend to be more resistant to *B. tectorum* invasion than their low elevation and south slope counterparts due to cooler and wetter conditions (Miller et al. 2013, Chambers et al. 2014). Historic livestock grazing at low elevation sites in the JDFBNM likely reduced the resistance of the vegetative community to annual grass invasion (Erixson et al. 2011).

Gutierrezia sarothrae cover and density declined dramatically 1 year post-burn. By 5 years post-burn cover of *G. sarothrae* recovered in brush plots, but by 10 years post-burn density of *G. sarothrae* did not recover in brush plots. Neither cover nor density of *G. sarothrae* recovered in forest plots. Typically *G. sarothrae* is associated with disturbed sites (Thacker et al. 2008). The lack of *G. sarothrae* recovery on higher elevation forest plots is therefore attributable to a lack of livestock grazing history in higher elevations contributing to a relatively more intact site (Erixson et al. 2011). Topography was a significant predictor of *G. sarothrae* density, but not cover. We

hypothesize this is the result of south slopes favoring the establishment of more *G. sarothrae* plants, while north slopes favor the establishment of less, but larger *G. sarothrae* plants.

Poa secunda showed minimal change with time since fire. This result is consistent with literature indicating its morphology, of an open crown with low fuel accumulation, limits the potential for fire effects on the species (Miller et al. 2013). Yet, within forest plots the effect of fire is dependent on time post-burn and topography. This can be explained by previous research findings in the JDFBNM concluding *P. secunda* is more prevalent at higher elevations and on north slopes (Rodhouse et al. 2014, Esposito 2015). In our dataset we detect higher mean cover of *P. secunda* in higher elevation plots and in brush plots on north slopes.

Pseudoroegneria spicata decreased 1 year post-burn, but recovered by 2 years post-burn. The moderate decline 1 year post-burn of *P. spicata* is the result of tolerance due to buds located below the soil surface (Miller et al. 2013). The rapid recovery of *P. spicata* is attributable to increased reproductive effort following fire (Uresk et al. 1976, Sapsis 1990, Ellsworth and Kauffman 2010). In addition to time post-burn, in burned plots the post-burn response of *P. spicata* is dependent on community type and topography. Through time cover of *P. spicata* was consistently greater in higher elevation forest plots. This is inferred to be the result of cooler and wetter conditions at higher elevations and on north slopes (Chambers et al. 2007, Miller et al. 2013 and Chambers et al. 2014) and a lack of livestock grazing history at higher elevations within the JDFBNM (Erixson et al. 2011).

Post-fire plant community succession is influenced by pre- and post-fire weather, ecological site characteristics, fire severity, post-fire disturbance and current vegetation which is influenced by disturbance history (Miller et al. 2013). Therefore, understanding individual species in the pre-burn communities' response to fire is a source of information for land managers in determining post-fire community succession. In this study community type, time post-burn and topography were identified as significant factors for determining individual species responses to fire in the JDFBNM. The significance of these interactions differentially influenced individual species responses to fire. Thus, when land managers are planning future prescribed burns in the JDFBNM or in similar *A. tridentata* ssp. *wyomingensis* communities' potential variation in species and community response along environmental gradients needs to be considered. Being able to consider these factors gives land managers an opportunity to better prioritize and tailor their response to smaller scales within their larger management area.

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Appendix

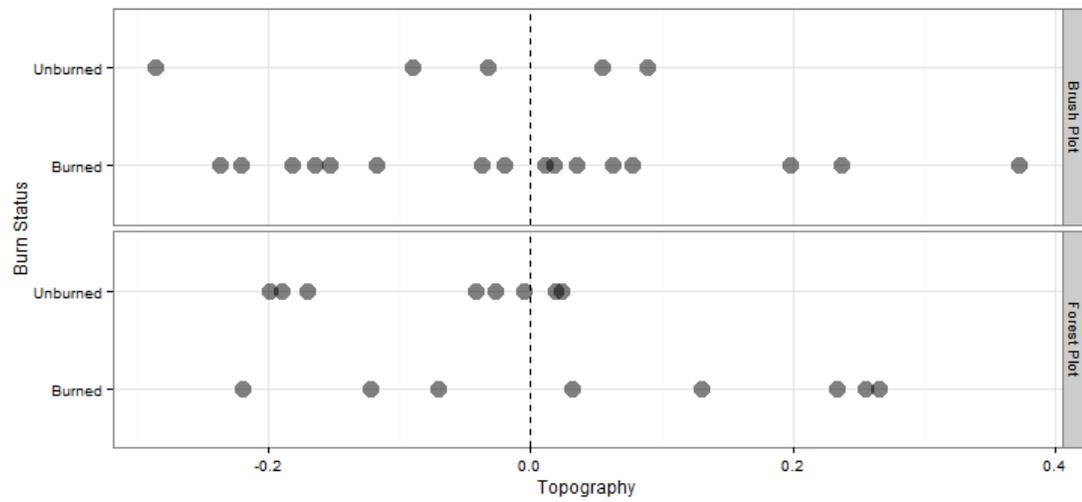


Figure A1 – Distribution of study plots across the topographic gradient, differentiated between unburned and burned plots within brush plots (top figure) and forest plots (bottom figure).

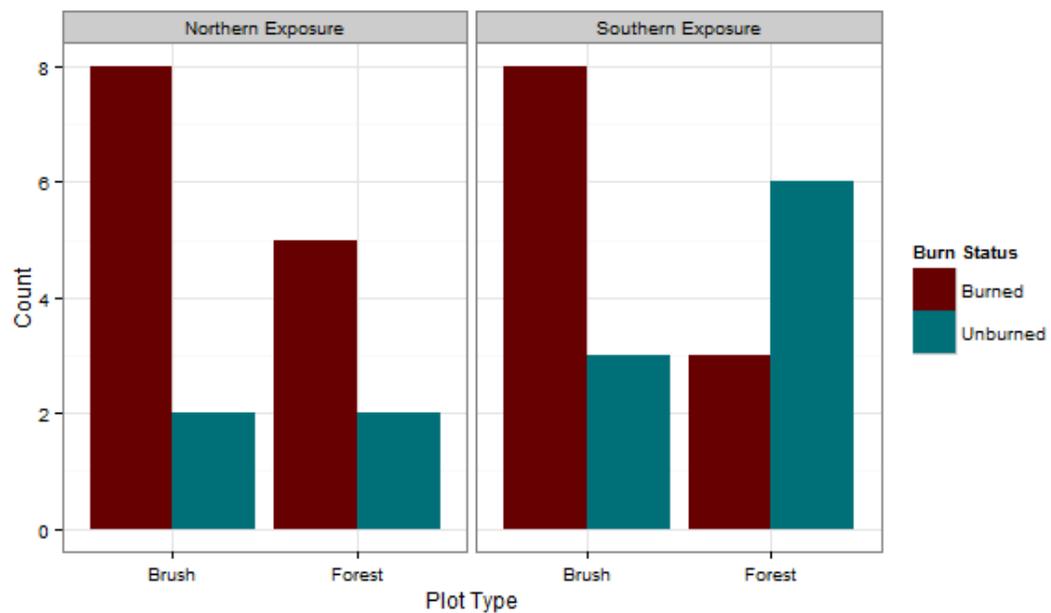


Figure A2- Counts of plot numbers split between northern exposures (left) and southern exposures (right) and differentiated between burned (red) and unburned (plots) and community type within each figure. Topographic data is analyzed across a continuous scale, but for purposes of graphical representation it is split between northern and southern exposures.

Burn Unit	Number of Plots of Each Community Type by Burn Status					
	Brush		Forest		Total	
	Burned	Unburned	Burned	Unburned	Burned	Unburned
Windy Point	n=6	n=0	n=3	n=2	n=9	n=2
Picture Gorge	n=4	n=2	n=1	n=2	n=5	n=4
Middle Mountain	n=2	n=1	n=2	n=1	n=4	n=2
Rock Creek	n=2	n=1	n=1	n=2	n=3	n=3
Foree	n=2	n=1	n=1	n=1	n=3	n=2
Total	n=16	n=5	n=8	n=8	n=24	n=13

Table A1 – The number (n) of plots within each burn unit (Windy Point [1999], Picture Gorge [2001], Middle Mountain [2002], Rock Creek [2004] and Foree [2005]), divided by burned and unburned plots for both brush and forest community types and totaled across community types.

Plots of Each Community Type, Burn Status and Topography Monitored								
Burn Year	Brush				Forest			
	Burned		Unburned		Burned		Unburned	
	North	South	North	South	North	South	North	South
Pre-Burn	n=8	n=8	n=2	n=3	n=5	n=3	n=2	n=6
1 Year	n=8	n=8	n=2	n=1	n=4	n=3	n=1	n=3
2 Years	n=8	n=8	n=2	n=2	n=4	n=3	n=1	n=3
5 Years	n=8	n=8	n=2	n=2	n=4	n=3	n=1	n=4
10 Years	n=7	n=7	n=2	n=3	n=5	n=3	n=2	n=6
15 Years	n=2	n=4	n=0	n=1	n=2	n=1	n=1	n=1

Table A2 – The number (n) of plot actually monitored in each year post-burn (pre-burn, 1 year, 2 years, 5 years, 10 years and 15 years post-burn), split between brush and forest plot types, burned and unburned plots and between north and south aspects. Topographic data is analyzed across a continuous scale, but for purposes of graphical representation it is split between northern and southern exposures.

