

EFFECTS OF PRETREATMENT TREE DOMINANCE AND CONIFER REMOVAL TREATMENTS ON
PLANT SUCCESSION IN SAGEBRUSH COMMUNITIES

BY

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THESIS

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Abstract

In sagebrush (*Artemisia tridentata* Nutt.) communities, the expansion and infilling of conifers decreases perennial vegetation cover and density, and lowers ecosystem resilience and resistance of the shrub-grass dominated state. Successional trajectories following disturbance are highly dependent upon residual species abundance, composition, and resulting structure. Understanding how tree dominance and tree-reduction treatments interact over time will help inform state-and-transition-models to guide management. Juniper (*Juniperus* spp. L.) and pinyon (*Pinus* spp. L.) trees were reduced by prescribed fire and cutting at 10 sites across the western United State. Vegetation cover and density were measured on untreated and treated plots across a gradient of tree dominance index (TDI, defined as tree cover / (tree + shrub + tall grass cover)) 3 and 6 years after treatment. I analyzed responses by functional group using mixed model analysis of covariance, with TDI treated as a covariate. As tree cover increased and TDI approached 0.5 (22% tree cover), shrub cover declined to 25% of the maximum. Three years after treatments, prescribed fire reduced both shrub and perennial herbaceous cover. Although total shrub cover returned to pre-burn percentages 6 years after treatment, it was still much lower than on the unencroached reference state and sagebrush cover was still < 1%. Six years after cut treatments, total shrub cover increased by 7% and sagebrush cover increased by 2.2% compared to no treatment. Tall perennial grasses are especially important in resisting dominance by invasive species such as cheatgrass (*Bromus tectorum* L.). By 6 years after treatment, tall grass and cheatgrass cover both increased on prescribed fire and cut treatments, especially at higher pretreatment TDI. However, ratios of cheatgrass to tall grass cover were much lower on cut than on burn plots. This outcome suggests that system resistance to

cheatgrass dominance is best supported by tree cutting. To retain the shrub, and especially sagebrush, components on a site and increase ecosystem resilience and resistance through increases in tall grasses, I recommend treating at low to mid TDI and using mechanical methods, such as cutting or mastication. Differential effects of prescribed fire compared to mechanical tree reduction, when implemented at different phases of tree dominance, should be incorporated into state-and-transition-models to clarify transitional effects and state outcomes.

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Table of Contents

Introduction	1
Methods.....	7
Results.....	11
Discussion.....	17
Summary	24
Tables and Figures	25
References	37

Introduction

Since the late 1800's, semi-arid lands around the world have been experiencing increased cover of woody vegetation (Archer et al., 1995; Miller and Tausch, 2001; Archer and Predick, 2014). In the western United States (US), woody conifers such as juniper (*Juniperus* spp. L.) and pinyon pine (*Pinus* spp. L.) are expanding and infilling in rangelands at an unprecedented rate (Miller et al., 2000; Brockway et al., 2002; Miller et al., 2008; Floyd and Romme, 2012; O'Connor et al., 2013). In sagebrush (*Artemisia tridentata* Nutt.) communities, the expansion and infilling of juniper and pinyon can lead to altered fire regimes, increased soil erosion, and decreased shrub and herbaceous cover (Burkhardt and Tisdale, 1976; Tausch and West, 1995; Miller et al., 2000; Miller and Tausch, 2001; Bates et al., 2005; Ansley et al., 2006; Pierson et al., 2007; Roundy et al., 2014a). Increased canopy fuel loads (Young et al., 2015) and decreased understory cover (Roundy et al., 2014a) as trees expand and infill may result in severe fire followed by annual weed dominance, increased fire frequency, and loss of ecosystem services.

Woodland expansion can cause declines in many sagebrush obligate species and is considered a threat to greater sage-grouse (*Centrocercus urophasianus*), a species of serious conservation concern (Rowland et al., 2008). Baruch-Mordo et al. (2013) found that sage-grouse leks did not remain active once conifer canopy cover exceeded 4%. Miller et al. (2008) estimated that in the western portion of sage-grouse habitat, 75% of sagebrush steppe encroached by these conifers may become heavily-dominated by trees within 40-50 years.

Tree removal has been used to restore structure and function to these communities (Brockway et al., 2002; O'Connor et al., 2013). However, successional trajectories following disturbance are dependent upon residual species abundance, composition, and resulting structure on a site (Bates et al., 2005; Briske et al., 2008; Bates et al., 2013; Miller et al., 2014 a, 2014b; Roundy et al., 2014a). As tree cover increases, both shrub and herbaceous cover decrease, with shrubs displaying a greater sensitivity (Tausch and West, 1995; Roundy et al., 2014a; Bybee et al., 2016). After tree removal, if shrub and herbaceous cover have already declined, these missing components of the community can be replaced by invasive species (Young et al., 2013a, 2013b, 2014). For this reason, pretreatment tree dominance plays a vital role in steering the successional trajectories of these systems following disturbance (Miller et al., 2000; Archer et al., 2011; Miller et al., 2014a; Roundy et al., 2014a).

State-and-Transition-Models

Resilience theory and state-and-transition-models (STMs) are useful tools for making land management decisions that will improve ecosystem conditions (Bestelmeyer et al., 2003; Stringham et al., 2003; Bestelmeyer et al., 2004; Briske et al., 2008; Bagchi et al., 2013; Chambers et al., 2014b; Miller et al., 2014a). The development of STMs requires an understanding of underlying ecological site potential, ecosystem processes, ecological thresholds, and successional trajectories given pretreatment site conditions and the treatment method employed (Chambers et al., 2014b; Miller et al., 2014b; Roundy et al., 2014a). Ecological resilience describes the ability of a system to regain structure and function after disturbance or stress (Chambers et al., 2014b).

Higher resilience would be indicated by a return to a pre-disturbance or pre-stressed state, as quantified by similar vegetation cover and composition as the reference (pre-disturbance or pre-stressed) state. System resilience is a function of site biotic and environmental characteristics that are currently being characterized by management agencies in the form of ecological site descriptions (Chambers et al., 2014a, 2014b). Resilience for an ecological site is also a function of the type of disturbance or stressor (Roundy et al., 2014a; Bybee et al., 2016), however proposed models for sagebrush steppe systems have not specified effects of different tree reduction treatments on resilience (Chambers et al., 2014b).

Ecological resistance is a system's ability to maintain its current state when exposed to stressors (Briske et al., 2008; Chambers et al., 2014b). Evaluation of management actions (e.g. prescribed fire vs. tree cutting) and successional timing (implementation across a gradient in pretreatment tree dominance) is needed to determine how to best reinforce a restoration trajectory (Briske et al., 2008) toward a reference state considered to be desirable (enhance resilience) and resist a trajectory to an undesirable state (weed dominance). In sagebrush communities, shrubs and perennial bunchgrasses serve to maintain natural fire regimes, resist invasive species, and decrease erosion and can help to increase ecological resistance (Burkhardt and Tisdale, 1976; Tausch and West, 1995; Miller et al., 2000; Miller and Tausch, 2001; Bates et al., 2005; Ansley et al., 2006; Pierson et al., 2007; Roundy et al., 2014a).

Response from Tree Removal Treatments

Following prescribed fire, sites in the Great Basin region typically experience an increase in cheatgrass (*Bromus tectorum* L.), a reduction in fire-intolerant shrubs and short-term

reduction in perennial grasses, with perennial grasses typically recovering within a few years after treatment (Bates et al., 2013; Miller et al., 2013; Chambers et al., 2014b; Miller et al., 2014b; Roundy et al., 2014a). By 3 years after treatment, mechanical treatments, such as cutting or mastication, conducted at low to mid-levels of tree dominance can to increase resistance to cheatgrass, preserve shrub cover and result in a more rapid recovery of perennial herbaceous cover than prescribed fire (Miller et al., 2014b; Roundy et al., 2014a; Bybee et al., 2016). When prescribed fire is used, and when mechanical treatments are implemented at high tree dominance, treatments result in an herbaceous-dominated site 3 years after treatment due to the loss of shrubs from tree infilling or fire (Roundy et al., 2014a).

Cheatgrass

A major concern for sagebrush ecosystems is the potential crossing of a biotic threshold, where, after disturbance, invasive annuals such as cheatgrass dominate, and recovery of perennial vegetation is unlikely without control of invasive annuals and seeding of native species. Structure, abundance, and composition of perennial herbaceous vegetation, especially tall grasses, and biological soil crusts are important in limiting cheatgrass invasion and dominance (Chambers et al., 2007; Blank and Morgan, 2012; Reisner et al., 2013; Miller et al., 2014a). Tall grasses increase resistance to cheatgrass invasion by limiting the availability of gaps for establishment, and reducing water and nutrient availability (Blank and Morgan, 2012; Reisner et al., 2013), whereas biological soil crusts restrict root penetration and growth within interspaces (Serpe et al., 2008). Compared to prescribed fire, mechanical treatments result in greater resistance to cheatgrass dominance through retention of shrubs, increases in tall grasses, and greater cover of biological soil crusts (Miller et al., 2014a, 2014b; Roundy et al.,

2014a; Bybee et al., 2016). Sites in which treatments are conducted at high tree dominance are more likely to experience increases in cheatgrass cover due to lower perennial herbaceous and shrub cover prior to treatment and thus higher availability of resources (Bates et al., 2013). Soil temperature and moisture regimes also influence a site's resistance to invasion, with warm and dry sites displaying lower resistance (Chambers et al., 2014a; Miller et al., 2014a).

Objectives

The Sagebrush Steppe Treatment Evaluation Project (SageSTEP) is a collaborative research effort initiated, in part, to aid in the development of STMs for sagebrush ecosystems by examining ecological responses to vegetation treatments across the Great Basin region. Here, I use SageSTEP data to determine the effects of pretreatment tree dominance and treatment method on plant succession 6 years after tree removal treatments were implemented.

Roundy et al. (2014a) examined the 3-year, post-treatment results of the woodland portion of the SageSTEP study and concluded that to maintain the shrub community; treatments should be implemented at low to mid tree dominance using mechanical treatments that can selectively remove trees, leaving the shrubs intact. If treatments are implemented at high tree dominance using mechanical treatments or at any level of tree dominance using prescribed fire, the community will shift to an herbaceous-dominated site and may require replanting of shrubs. Cheatgrass cover was greatest on prescribed fire treatments, especially when implemented at high pretreatment tree dominance. Cheatgrass cover was lower on mechanical treatments, but increased at high pretreatment tree dominance. Perennial grass

cover exceeded that of cheatgrass at most study locations. Roundy et al. (2014a) concluded that more time after treatment was needed to determine the effects of treatment and pretreatment tree dominance on resistance and resilience of these communities. Further research is needed to determine how fast shrubs recover and whether perennial grasses or cheatgrass dominate over time. My study is an essential follow-up to these results to determine how successional trajectories have changed from 3 to 6 years post-treatment in an effort to predict how these communities will ultimately respond to conifer removal treatments. My study is unique in that it includes data from sites across the Great Basin region representing a wide range of biotic and abiotic characteristics, and because it describes regional vegetation responses to a range of pretreatment tree dominance.

For my study, I will discuss ecological resilience and resistance as related to the reference state, or cover and composition on untreated plots at minimal tree cover. Increases in perennial herbaceous cover and shrub cover following conifer removal treatments will signify increased ecosystem resilience, whereas ecological resistance will be indicated by cheatgrass response to treatment and pretreatment tree dominance. My primary question was how did tree reduction treatments and pretreatment tree dominance affect vegetation at 6 years compared to 3 years post treatment? I was especially interested in sagebrush recovery and dominance of perennial herbaceous vegetation as indicators of resilience and lack of cheatgrass cover as an indicator of resistance. I hypothesize that on cut treatments, perennial herbaceous cover and shrub cover will continue to increase and thus limit cheatgrass invasion, indicating higher ecosystem resilience and resistance. On burn treatments, I expect that cheatgrass cover will continue to increase and shrub cover will remain low.

Methods

Study Area

This study consisted of 10 conifer-encroached or wooded shrubland sites (Romme et al., 2009) located across the Great Basin region (Figure 1, Table 1): four western juniper (*Juniperus occidentalis* Hook.) sites in Oregon and northern California, three single-leaf pinyon (*Pinus monophylla* Torr. & Frém.)-Utah juniper (*Juniperus osteosperma* Engelm.) sites in central and eastern Nevada, one Utah juniper site in Utah, and two Colorado pinyon (*Pinus edulis* Engelm.)-Utah juniper sites in Utah (McIver et al., 2010; Miller et al., 2014b; Roundy et al., 2014a, 2014b). These sites all contain sagebrush (*Artemisia* spp. L.) communities on loamy soils (Roundy et al., 2014b).

Elevation, soils, and climate vary widely among sites and across the study region. Elevation is highest in the middle of the Great Basin and lower on the western and eastern edges. Sites in the northwestern portion of the Great Basin consist of basalt-derived soils with the majority of precipitation falling between November and June (McIver et al., 2010; Miller et al., 2014b; Roundy et al., 2014a, 2014b). Sites in the central and eastern portion of the Great Basin include igneous-, metamorphic-, and sedimentary-based soils with less precipitation between November and June, and variable summer precipitation (Roundy et al., 2014a, 2014b). The wide distribution of my study sites allows me to determine regional responses to treatments.

Experimental Design and Treatments

The study design was a randomized complete block with each study site being considered as a block and receiving two treatments and an untreated control. Within each block, both cutting (cut) and prescribed fire (burn) treatments, as well as the untreated control, were randomly assigned to 8-ha to 20-ha plots. All three plots were placed on sites with similar topographic position, soils, and vegetation, and were fenced where necessary, to exclude livestock (Miller et al., 2014b). Vegetation treatments were applied in a staggered-start design from 2006 to 2009, and vegetation was intensively monitored 3 and 6 years post-treatment.

Fire treatments consisted of low to moderate severity broadcast burns applied once between August and November. Cut treatments were applied within six months of fire treatments between the months of September and November (McIver et al., 2010; Miller et al., 2014b). These treatments involved cutting all trees > 2 m in height and leaving the slash on the ground across the contour (McIver et al., 2010). Tree canopy cover was reduced to < 5% on burned treatments and < 1% on mechanical treatments (Roundy et al., 2014a).

Vegetation Measurements

Within each treatment and control plot, 15 0.1-ha (30-m × 33-m) subplots were randomly placed across a tree dominance gradient (Miller et al., 2014b, Roundy et al., 2014a) and marked using steel stakes. Subplots were established and placed to span a gradient of pretreatment tree dominance index (TDI, defined as: tree cover/ [tree + shrub + tall grass cover]). TDI is a useful indicator of pretreatment tree dominance across many sites because it expresses tree cover relative to cover of all the major competitors for resources (Ryel et al.,

2008, 2010; Roundy et al., 2014a, 2014b). Sufficient subplots were located to allow a subset to be randomly selected across the range of TDI. Vegetation was measured within all subplots prior to treatment (year 0) and intensively 3 and 6 years post-treatment. A 30-m baseline was established within each subplot with 5 permanent transects placed at 2 m, 7 m, 15 m, 23 m, and 28 m. The point intercept method (Herrick et al., 2009) was used to sample plant cover by species and ground cover groups every 0.5 m along each transect for a total of 300 points for each subplot and 4,500 points per treatment plot. Cover data were then categorized into shrub, tall grass (deep-rooted), short grass (shallow-rooted; only Sandberg bluegrass (*Poa secunda* J. Presl) was considered short grass in this study), perennial, annual, exotic forb, cheatgrass, and bare ground cover. Foliar cover for each functional group was recorded as a single hit for each point if the point came in contact with any member of that functional group. More than one functional group could be recorded at a single point. Bare ground was only recorded if it was the first and only hit at a point. From these data, percentage of cover for each subplot was calculated.

Density was measured in 0.25-m² quadrats every odd-meter along the 7 m, 15 m, and 23 m transects for tall perennial grasses, nonrhizomatous perennial forbs, and shrub species < 50 mm in height for a total of 45 quadrats per subplot. Tree canopy cover was estimated for all trees > 0.5 m in height by measuring the longest crown diameter and the perpendicular crown diameter. These measurements were used to calculate crown area (*A*) for each tree using the formula $A = \pi(D1 * D2)/4$, where *D1* is the longest crown diameter and *D2* is the perpendicular to *D1*. The summation of crown area for all trees in the subplot was used to estimate total tree canopy cover. All other variables were measured prior to treatment and will

continue for a minimum of 10 years post treatment, with intensive monitoring every 3 years (McIver et al., 2010).

Analysis

I analyzed data by functional group using mixed model analysis of covariance (Littell et al., 2006; Proc Glimmix, SAS v9.4, SAS Institute, Inc., Cary, NC; Roundy et al., 2014a). I normalized non-tree cover data using the logit transformation and density data using the square-root transformation prior to analysis (Warton and Hui, 2011). Treatment and year since treatment (YST; 3 and 6) were considered fixed factors, whereas location was considered random. Because data were only at two points in time, it was not possible to calculate a time series variance structure (repeated measures). By adding subplot as a random term in the model, Proc Glimmix accounted and adjusted for the data correlation between 3 and 6 YST measurements on the same subplots. I considered pretreatment TDI a covariate and it was not transformed. When covariate by main effect interactions were not significant ($P > 0.05$), I removed them from the model (Littell et al., 2006).

I used the Tukey test to determine differences among estimates of treatments when the treatment by YST interaction was significant ($P < 0.05$). When 2-way interactions of treatment or YST with TDI were significant, or when the 3-way interaction of these factors was significant ($P < 0.05$), I compared treatments for each YST using a Tukey test for each 0.05 increment of the TDI covariate from 0 to 1. Significance of these tests was set at $P < 0.01$ to control the experiment-wise error rate. Pretreatment tree cover was regressed over TDI for all subplots across all sites to relate responses to tree cover for this sample of subplots.

Results

Density for all functional groups showed a significant interaction ($P < 0.05$) between either treatment with YST and TDI with YST (Table 2). These results indicate density response over time depended more on treatment method for some variables, and more on pretreatment TDI for others. For most cover variables, the interaction of treatment and YST was significant (Table 2), indicating that cover variables responded differently to treatments at 6 YST compared to 3 YST. In addition, the interaction of treatment and TDI was significant for most cover variables, indicating that response to treatment was also influenced by pretreatment TDI.

Annual forb cover

The interactions of treatment and YST, as well as treatment with TDI, were significant for annual forb cover (Table 2). Annual forb cover was highest on burn plots both 3 and 6 YST and at all TDI (Table 3), though cover decreased from 14.6% to 2.5% on these plots during this same period (Figure 2). By 6 YST, annual forb cover on cut plots had returned to the low levels seen on untreated plots (<1%).

Exotic forb cover

All 2-way interactions of treatment, YST, and TDI were significant for exotic forb cover (Table 2). Exotic forb cover responded similarly to annual forb cover, with highest exotic forb cover occurring on burn plots at low to mid TDI (Table 3). Average exotic forb cover was relatively low across most subplots (<10% on 86% of subplots). However, on some plots, primarily burn plots, exotic forb cover exceeded 30% and was as high as 65.7%. Exotic annual forb cover did not differ between untreated and cut plots at any level of TDI (Table 3, Figure 3).

Perennial forbs

All 2-way interactions with TDI were significant, and the interaction of treatment and YST was marginally significant for perennial forb density (Table 2). Average perennial forb density decreased from 3 to 6 YST on all treatments and across all TDI ranges (Figure 4). Perennial forb density decreased with increasing TDI for all treatments, averaging 8.2% at TDI = 0 to 3.3% at TDI = 1.

The interactions of treatment with YST, as well as treatment with TDI, were significant for perennial forb cover (Table 2). Perennial forb cover averaged < 6.5% across all TDI and treatments, both 3 and 6 YST. Perennial forb cover on cut plots showed little variation across TDI, whereas burn and untreated plots showed higher perennial forb cover at low TDI with cover decreasing as TDI increased (Figure 3).

Cheatgrass cover

All 2-way interactions of treatment, YST, and TDI were significant for cheatgrass cover (Table 2). Cheatgrass increased on treated and untreated plots from 3 to 6 YST, increasing most dramatically on burn plots from 3.0% to 8.6% (Figure 5). At 6 YST, cheatgrass cover was greater on the burn than untreated plots at all TDI and greater than on the cut plots at TDI \leq 0.75 (Table 3). Cutting resulted in greater cheatgrass cover than untreated plots at \geq 0.40 TDI (Table 3, Figure 5).

Short grasses

The interaction of YST and TDI was significant for short grass (Sandberg bluegrass) density, whereas the interaction of YST and treatment was marginally significant (Table 2). Short grass density decreased across all treatments from 3 to 6 YST at all TDI ≥ 0.1 (Figure 4). The interaction of treatment and YST was significant for short grass cover (Table 2). However, short grass cover was not significantly different among treatments or across years.

Tall Grasses

The 3-way interaction of TDI, treatment and YST was significant for tall grass density (Table 2). Tall grass density on untreated plots was not significantly different from that of burn or cut plots. By 6 YST, cut treatments resulted in slightly greater tall grass density (0.6 to 0.8 plants m^{-2}) than burn treatments at all TDI ≥ 0.7 (Table 3, Figure 3).

The 3-way interaction between TDI, treatment and YST was significant for tall grass cover (Table 2). Tall grass cover increased on all treatments from 3 to 6 YST, increasing more dramatically on cut (7.8% cover) and burn (6.0% cover) plots than on untreated (2.8% cover) plots. By 6 YST, both burn (at TDI ≥ 0.55) and cut treatments (at TDI ≥ 0.35) resulted in greater tall grass cover than untreated plots (Table 3). Cut treatments resulted in greater tall grass cover than burn treatments at TDI ≥ 0.55 (Figure 3).

Perennial grass cover

The 3-way interaction between TDI, YST, and treatment was significant for perennial grass cover (Table 2). By 6 YST, cut treatments had the greatest average perennial grass cover

(28.0%), averaging 10.0% more cover than untreated plots. Perennial grass cover was greater on cut treatments 6 YST than burn treatments at $\text{TDI} \geq 0.80$ and untreated plots at $\text{TDI} \geq 0.50$ (Table 3, Figure 3). Burn treatments resulted in greater perennial grass cover than untreated plots only at very high TDI (Table 3).

Total perennial herbaceous cover

The interaction of treatment and TDI was significant for total perennial herbaceous cover (Table 2). Cut treatments and burn treatments resulted in greater total perennial herbaceous cover than untreated at $\text{TDI} \geq 0.40$ and $\text{TDI} \geq 0.55$ respectively (Table 3, Figure 3). Cut treatments resulted in greater total perennial herbaceous cover than burn treatments only at the highest TDI (Table 3).

Sagebrush

The interactions of treatment and YST, as well as treatment and TDI, were significant for sagebrush density. Burn treatments resulted in low sagebrush density (≤ 0.09 plants m^{-2}) across all TDI, even 6 YST (Figure 6). Cut plots resulted in higher sagebrush density 6 YST than burn plots at $\text{TDI} \leq 0.70$ (Table 3). On average and across years, cut treatments resulted in sagebrush densities of 0.29 plants m^{-2} , whereas burns resulted in 0.04 plants m^{-2} and 0.06 plants m^{-2} in years 3 and 6, respectively. Sagebrush density was stable across years on cut treatments, increased on burn treatment (0.016 plants m^{-2}), and decreased on the control (-0.021 plants m^{-2}). Sagebrush density at high TDI (> 0.85) was extremely low (< 0.1 plants m^{-2}) across all treatments and years (Figure 6).

The interactions of treatment and TDI, as well as treatment and YST, were significant for sagebrush cover (Table 2). On burn and untreated plots, sagebrush cover increased less than 0.6% from year 3 to 6, whereas sagebrush cover on cut treatments increased an average of 2.7% (Figure 6). Cut and untreated plots exhibited greater sagebrush cover than burn plots at $\text{TDI} \leq 0.85$ and $\text{TDI} \leq 0.60$ respectively (Table 3). In subplots where TDI exceeded 0.25 (approximately 10% tree cover, Figure 7), sagebrush cover was only 50% of the maximum shrub cover on both untreated and cut plots. Even at 6 YST, untreated plots showed greater sagebrush cover than burn plots at $\text{TDI} \leq 0.60$.

Total shrub density and cover

The 3-way interaction between TDI, YST, and treatment was significant for shrub density (Table 2). Shrub density decreased on untreated plots ($-0.06 \text{ plants m}^{-2}$) and increased on burn ($0.11 \text{ plants m}^{-2}$) and cut ($0.04 \text{ plants m}^{-2}$) plots from 3 to 6 YST. Cut treatments resulted in higher shrub density than burn treatments at $\text{TDI} \leq 0.95$ and untreated plots at $\text{TDI} \geq 0.40$ (Table 3, Figure 6).

The 2-way interactions between treatment and YST, as well as treatment and TDI, were significant for shrub cover (Table 2). Shrub cover increased on cut and burn treatments from 3 to 6 YST (Figure 6). Shrub cover was lower on burn plots than on both cut and untreated plots at $\text{TDI} \leq 0.90$ and $\text{TDI} \leq 0.35$ respectively (Table 3, Figure 6). On plots where TDI exceeded 0.4, shrub cover had declined to less than 50% of the maximum potential cover (approximately 17% tree cover, Figure 7).

Sagebrush seedling density

Across all treatments, the percentage of subplots containing sagebrush seedlings and juveniles (< 5 cm in height) decreased from 3 to 6 YST. The percentage of subplots with sagebrush seedlings was relatively consistent across years on burn plots, but decreased on both untreated and cut plots from 3 to 6 YST (Figure 8). Burn treatments were the only treatments to experience increases in sagebrush density (> 5cm in height) and these increases were relatively small ($0.016 \text{ plants m}^{-2}$), thus decreases in sagebrush seedlings were not due to plants growing > 5cm. Density of seedlings also decreased from 3 to 6 YST on treated and control plots. However, cut and burn treatments had higher sagebrush seedling density than untreated plots in both years (Figure 8).

Bare ground cover

The 2-way interactions of treatment with YST, as well as treatment with TDI, were significant for bare ground cover (Table 2). From 3 to 6 YST, there was a significant reduction in bare ground on treated and untreated plots, with the greatest reduction on cut (8.8%) plots and burn (9.0%) plots (Figure 9). Bare ground on untreated plots 6 YST exceeded that of cut and burn treatments at $\text{TDI} \geq 0.10$ and $\text{TDI} \geq 0.40$ respectively (Table 3).

Deviation from reference state

By using a $\text{TDI} = 0$ for no treatment to represent a reference state, or the idealized restoration target, I was able to graph (Figure 10) the deviations away from this reference state in an attempt to visualize how successful each treatment method, or restoration pathway, was

at moving the community towards the desired condition. Cut treatments 6 YST resulted in conditions most similar to that of the reference state.

Discussion

Shrub Response

Sagebrush communities, and the species that depend on them, are being threatened by the expansion and infilling of juniper and pinyon (Burkhardt and Tisdale, 1976; Miller and Tausch, 2001; Bates et al., 2005; Ansley et al., 2006; Pierson et al., 2007). Shrubs are an important component of these ecosystems and contribute to wildlife habitat as well as biodiversity (Huber et al., 1999; Miller et al., 2005). Sagebrush, in particular, is an important food source for sage-grouse, and other sagebrush obligates (Connelly et al., 2004). As tree cover increased, shrubs were rapidly lost, declining to 25% of the maximum potential cover where tree dominance approached 0.50 (22% tree cover, Figure 7). These results parallel those found in earlier studies (Tausch and West, 1995; Miller et al., 2000). At high TDI, shrub cover was extremely low, and these areas will likely recover slowly following treatment.

Cut treatments had the greatest sagebrush and total shrub cover and also exhibited the greatest increase in shrub cover over time. Total shrub cover on cut plots was double that of untreated plots and triple that of burn plots. However, sagebrush density on cut treatments was not different from untreated plots across years. These results indicate that the major increase in sagebrush cover was the result of canopy expansion of existing shrubs rather than new individuals. This highlights the importance of residual pretreatment plants in directing the successional trajectories of these sites. Furthermore, total shrub density increased on both cut

and burn plots from 3 to 6 YST, whereas sagebrush density remained stable on cut plots and only slightly increased on burn plots. This indicates that sagebrush recruitment is lower than the other shrubs at the study sites, which include fire-tolerant species such as yellow rabbitbrush (*Chrysothamnus viscidiflorus* [Nutt.]).

Burn treatments resulted in a significant loss of shrubs and these plots still had not recovered at 6 YST, especially at high TDI. On burn plots, sagebrush cover remained lower than on untreated plots 6 YST, whereas total shrub cover (sagebrush + all other shrubs) had returned to untreated levels. This difference may indicate that sagebrush cover is much slower to recover following fire than the other, perhaps more fire-tolerant, shrubs such as yellow rabbitbrush (Chambers et al., 2014b). Recovery of sagebrush canopies can take 15 to >50 years to recover following disturbance (Miller et al., 2014b). Thus, given enough time, these shrubs may recover to the higher levels seen on cut treatments.

Little to no viable big sagebrush seeds are carried over in the seed bank from year to year (Young and Evans, 1989; Meyer and Monsen, 1992). In addition, sagebrush germination rates can vary widely and are largely dependent upon climate (Meyer and Monsen, 1992). Thus, the presence of a local seed source is vital for sagebrush recruitment. Cut treatments resulted in the highest percentage of subplots containing sagebrush seedlings, with the percentage of subplots containing seedlings decreasing from 3 (39.9%) to 6 YST (26.9%). Bybee et al. (2016) found similar results with mechanical mastication treatments resulting in higher seedling density than untreated plots. The total percentage of subplots containing sagebrush seedlings declined from 3 to 6 YST from 28.5% to 19.7%. Sagebrush density (> 5 cm height) remained stable on cut treatments, increased on burn treatments and decreased on controls, whereas

the percentage of subplots containing seedlings decreased on both cut and control plots and remained relatively stable on burns. This indicates that the decrease in percentage of subplots containing seedlings is not due to seedlings growing > 5 cm, but rather a decrease in new seedlings. This may be due to differences in weather following treatment and may also reflect greater competition between seedlings and other perennial vegetation 6 YST.

Cheatgrass Invasibility in Relation to Treatment Type and Level of Infilling

Perennial herbaceous vegetation, in particular tall grasses, are vital to maintaining ecosystem resilience and resistance, especially in areas being threatened with cheatgrass invasion (Chambers et al., 2007; Blank and Morgan, 2012; Reisner et al., 2013). There is a clear pattern of decreased perennial vegetation with increasing tree dominance (Roundy et al., 2014a; Bybee et al., 2016). Tree removal can result in increased herbaceous cover, plant species richness and diversity, litter cover, and decreased bare ground (Brockway et al., 2002; O'Connor et al., 2013), which in turn can increase ecosystem resilience and resistance (Chambers et al., 2007; Blank and Morgan, 2012; Reisner et al., 2013).

My findings are consistent with other studies (Ross et al., 2012; O'Connor et al., 2013) showing that disturbance from removing trees, either mechanically or with fire, may lead to increases in cheatgrass due to greater availability of resources and less competition. For example, Young et al. (2013a, 2013b, 2014) found that tree mastication increased soil water availability, inorganic nitrogen availability, and seedling growth of cheatgrass. In the current study, cheatgrass cover increased on treated and untreated plots from 3 to 6 YST. However, cheatgrass cover was nearly 3-fold greater 6 YST and experienced a 5-times greater increase

from 3 to 6 YST on burn plots when compared to cut plots. This increase following burn treatments may be the result of loss of fire-tolerant shrubs and increased soil nutrient and water availability (Chambers et al., 2007). Although cut treatments resulted in slightly higher cheatgrass cover than untreated plots, increases in cheatgrass cover from 3 to 6 YST were significantly lower than on burn plots.

Cheatgrass cover was greatest on treated sites at high TDI, likely due to lower cover of perennial grasses, forbs, and shrubs prior to treatments and thus a greater availability of resources following tree removal. Tall grass cover was greater on cut treatments than burn treatments at mid to high levels of TDI. This indicates that mid to high levels of tree infilling puts a system at higher risk of cheatgrass invasion following tree removal treatments, but cut treatments exhibit more resistance to cheatgrass invasion than burn treatments.

Encouraging Ecosystem Resilience and Resistance

Maintaining perennial herbaceous cover and shrub cover is vital for the healthy functioning of sagebrush ecosystems. Tall grasses, in particular, play an important role in increasing ecosystem resilience and resistance (Chambers et al., 2007; Blank and Morgan, 2012; Reisner et al., 2013; Miller et al., 2014a). Tall grasses and cheatgrass use soil water and nitrogen within the same soil depth (Ryel et al., 2008; Leffler and Ryel, 2012; Roundy et al., 2014b). Tree reduction increases time of available water and inorganic nitrogen availability within this depth (Young et al., 2013b, 2014; Roundy et al., 2014b). Therefore, tall grasses are important in reducing resource availability to cheatgrass after tree reduction. Tall grass density was relatively stable between years, only increasing on cut treatments at high TDI. This suggests

that cover increases mainly are due to existing plants increasing their foliar cover and only the result of new recruitment on cut treatments at high TDI.

On cut plots, tall grass cover increased, even at high pretreatment tree dominance. This higher tall grass cover may aid in suppressing cheatgrass and other invasive annuals (Chambers et al., 2007; Blank and Morgan, 2012; Reisner et al., 2013; Miller et al., 2014a). Tall grass cover on burn plots also appeared to be recovering, however at high TDI, tall grass cover remained lower than on cut plots. Higher tall grass cover on cut plots likely plays a role in maintaining lower levels of cheatgrass cover.

Tall grass recovery, and subsequent reduction in bare ground, is critical to reducing erosion in intercanopy areas following tree removal (Williams et al., 2014). Cut and burn treatments resulted in a two-fold greater decrease in bare ground than untreated plots. This indicates that, regardless of treatment, the non-tree vegetation responds favorably to tree removal treatments.

Since I define resilience as the ability to return to a reference, unencroached state, we can visualize the resilience of these sites using Figure 10. These graphs illustrate the cover difference between the unencroached (TDI = 0), untreated condition and the conditions following treatment. Graphs of the untreated plots show a loss of both perennial grass and shrub cover as TDI increases. This is not an artifact of having tall grass and shrub cover as variables in the denominator of TDI. Decreased shrub and tall grass cover could only be considered an artifact of TDI if their absolute cover stayed the same or increased and tree cover increased sufficiently to make them appear to decrease with increasing TDI. It is well

documented that as tree cover increases, shrub and perennial herbaceous cover decrease (Tausch and West, 1995; Miller et al., 2000; Roundy et al., 2014a; Bybee et al., 2016). Also, increased tree cover without decreases in understory plants that use similar resources in a semi-arid, resource-limited system (Roundy et al., 2014b) is unlikely. Thus, tree expansion and infilling move the system away from the reference and desired plant community. The worse-case scenario of waiting to treat these expansion sites is that woody-fuel buildup results in severe fire, subsequent weed dominance and recurrent, frequent fire unless these sites are successfully reseeded to perennial herbs and shrubs by management agencies (Whisenant, 1990; Brooks et al., 2004; Chambers et al., 2014b).

The graphs for treated plots in Figure 10 indicate a definite interaction between TDI and response to treatment relative to the reference state, and lead to important management implications that should be incorporated into state-and-transition-models. On the burn treatment at 6 YST, shrub cover was still far below that of the reference state at all pretreatment TDI. Perennial grass cover on burn treatments was > 10% lower than the reference state at TDI > 0.3 (> 12.5% tree cover). Shrub cover is slower to respond to tree reduction by fire than perennial or annual grass cover so that prescribed fire results in an herbaceous-dominated plant community when implemented at most TDI. Cheatgrass is most likely to dominate when prescribed fire is used at a higher pretreatment TDI where perennial grass cover is lacking. Prescribed fire implemented at low TDI results in lower shrub cover than the reference community. However, the resulting perennial grass-dominated community could have high resilience itself, it just may not provide the functionality of the reference community. When prescribed fire is implemented at intermediate to high TDI where perennial grass cover is

lacking, indications are that resistance to cheatgrass dominance is decreased. In this situation, managers will usually reseed to avoid cheatgrass dominance. Figure 10 also indicates that the cut treatment at 6 YST resulted in the greatest resilience or return to the reference state when implemented at low TDI (< 0.2 TDI or < 9% tree cover) before any shrub cover was lost to encroachment. Since perennial grass cover increased much faster after tree cutting than shrub cover, and especially sagebrush cover, cutting at low to intermediate TDI is necessary to reinforce resilience of the shrub/perennial grass community. Cutting trees at higher TDI's will result in an herbaceous-dominated state which has much lower shrub cover than the reference state, but may be as resilient as either a perennial grass or annual grass-dominated state. The ratio of cheatgrass cover to tall grass cover on cut plots remained stable from 3 to 6 YST, whereas cheatgrass cover increased relative to tall grass cover on both burn and untreated plots. Long-term monitoring will help determine whether or not cutting trees at high TDI or burning at low to intermediate TDI will ultimately result in resistance to cheatgrass dominance.

Summary

To retain the shrub component on a site and increase ecosystem resilience and resistance, I recommend treating at low to mid tree dominance and avoiding prescribed fire. Areas with low levels of tree encroachment ($\text{TDI} < 0.35$, approximately 15% tree cover) could potentially be protected against increases in cheatgrass following cut treatments due to greater perennial herbaceous cover. These results agree with an earlier study that showed a more desirable vegetation response when juniper was treated at or below 20 percent crown cover (Huber et al., 1999).

Burn treatments should be especially avoided in areas in which it is vital to retain the sagebrush for wildlife and where cheatgrass is present. If treatments are delayed until higher TDI ranges, tree removal may result in perennial grassland instead of a grass-shrub mix and require replanting of shrubs. Although cut treatments resulted in greater resilience and resistance through increases in tall grass and shrub cover and greater resistance to cheatgrass, these treatments may require additional follow-up to remove young trees. Differential effects of tree reduction treatments implemented at different phases of tree dominance should be incorporated into state-and-transition-models to better clarify successional trajectories and resulting states. This study highlights the important if pretreatment site conditions on restoration outcomes as well as the importance of long-term monitoring.

Tables and Figures

Table 1. List of 10 sites with dominant species, elevation range, and soils. Mountain big sage (*Artemisia tridentata* Nutt. subsp. *vaseyana* [Rydb.] Beetle), Idaho fescue (*Festuca idahoensis* Elmer), Sandberg bluegrass (*Poa secunda* J. Presl.), bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve), basin big sage (*Artemisia tridentata* Nutt. subsp. *tridentata*), Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), squirreltail (*Elymus elymoides* [Raf.] Swezey), Wyoming big sage (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young), mountain mahogany (*Cercocarpus ledifolius* Nutt), muttongrass (*Poa fendleriana* [Steud.] Vasey), needle and thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth)

Study site	Target vegetation	Elevation
Western juniper		
Blue Mountain	Mountain big sage/Idaho fescue-Sandberg bluegrass-bluebunch wheatgrass	1500-1700 m
Bridge Creek	Basin big sage/bluebunch wheatgrass-Sandberg bluegrass	800-900 m
Devine Ridge	Mountain big sage/Sandberg bluegrass-Thurber's needlegrass-Idaho fescue	1600-1700 m
Walker Butte	Mountain big sage/Thurber's needlegrass-Idaho fescue-squirreltail	1400-1500 m
Single-leaf pinyon-Utah juniper		
Marking Corral	Wyoming big sage/Thurber's needlegrass	2300-2400 m
Seven Mile	Mt. mahogany-mountain big sage/bluebunch wheatgrass-muttongrass	2300-2500 m
South Ruby Mountain	Wyoming big sage-bitterbrush/bluebunch wheatgrass-Sandberg bluegrass-Thurber's needlegrass	2100-2200 m
Utah juniper		
Onaqui	Wyoming big sage/bluebunch wheatgrass	1700-2100 m
Colorado pinyon-Utah juniper		
Greenville Bench	Wyoming big sage/needle and thread-bluebunch wheatgrass	1750-1850 m
Scipio	Wyoming big sage/bluebunch wheatgrass	1700-1800 m

Table 2. Mixed model analysis of covariance results for cover (%) and density (plants m⁻²) for non-tree cover for untreated control plots and burn and cut fuel control treatments in relation to tree dominance at the time of treatment as measured by the covariate tree dominance index. NDF indicates numerator degrees of freedom; DDF, denominator degrees of freedom calculated according to Kenward and Roger (1997).

	Annual forb cover ^b				Exotic forb cover ^b				Perennial forb cover ^b				Perennial forb density ^b			
	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P
TRTN ^a	2	58.65	22.19	<.0001	2	61.38	5.26	0.0078	2	39.59	1.56	0.2234	2	39.5	1.93	0.1589
YST ^a	1	901.1	541.43	<.0001	1	900.3	49.24	<.0001	1	463.9	20.89	<.0001	1	459.6	5.39	0.0207
TDI ^a	1	924.4	0.07	0.7923	1	920.3	1.7	0.1927	1	457.8	40.74	<.0001	1	448.5	64.74	<.0001
TRTN X YST	2	901.2	12.36	<.0001	2	900.3	4.74	0.0089	2	463.9	4.84	0.0083	2	461.6	2.76	0.0641
TDI X TRTN	2	772.6	8.57	0.0002	2	750.9	3.31	0.037	2	464.8	12.87	<.0001	2	455.4	4.79	0.0087
TDI X YST	-	-	-	-	1	900.3	6.67	0.01	-	-	-	-	1	463.2	4.29	0.0388
TRTN X TDI X YST	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Short grass cover ^b				Short grass density ^b				Tall grass cover				Tall grass density ^b			
	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P
TRTN ^a	2	17.98	0.49	0.62	2	17.9	6.53	0.0074	2	48.48	0.06	0.9431	2	38.41	3.28	0.0486
YST ^a	1	465.6	1.29	0.2568	1	459.3	2.89	0.0897	1	458.4	13.34	0.0003	1	459.1	0.31	0.5798
TDI ^a	1	454.3	38.29	<.0001	1	451.5	24.58	<.0001	1	456.3	182.27	<.0001	1	455.3	131.19	<.0001
TRTN X YST	2	465.6	6.69	0.0014	2	461.3	2.45	0.0873	2	458.3	1.01	0.3648	2	459	5.08	0.0066
TDI X TRTN	-	-	-	-	-	-	-	-	2	457.1	25.57	<.0001	-	-	-	-
TDI X YST	-	-	-	-	1	462.6	8.17	0.0045	1	461.8	18.9	<.0001	-	-	-	-
TRTN X TDI X YST	-	-	-	-	-	-	-	-	2	461.7	6.09	0.0025	5	697.6	3.77	0.0023
	Perennial grass cover				Perennial herbaceous cover ^b				Sagebrush cover ^b				Sagebrush density ^b			
	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P
TRTN ^a	2	35.4	0.42	0.6621	2	45.8	0.22	0.8029	2	40.71	70.03	<.0001	2	38.62	54.28	<.0001
YST ^a	1	461.7	17.58	<.0001	1	465.6	103.78	<.0001	1	461.9	158.69	<.0001	1	459.9	0.41	0.522
TDI ^a	1	454.5	226.96	<.0001	1	459.4	246.32	<.0001	1	461.4	239.05	<.0001	1	460.4	237.76	<.0001
TRTN X YST	0	461.6	3.46	0.0321	2	465.5	1.89	0.152	2	461.9	12.54	<.0001	2	459.9	15.62	<.0001
TDI X TRTN	2	463.5	21.27	<.0001	2	461	24.09	<.0001	2	468.5	35.91	<.0001	2	469.1	31.45	<.0001
TDI X YST	1	465.4	6.2	0.0131	-	-	-	-	-	-	-	-	-	-	-	-
TRTN X TDI X YST	2	465.3	3.03	0.0492	-	-	-	-	-	-	-	-	-	-	-	-
	Total shrub cover ^b				Total shrub density				Cheatgrass cover ^b				Bare ground cover ^b			
	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P
TRTN ^a	2	56.89	50.29	<.0001	2	59.88	40.38	<.0001	2	46.15	9.88	0.0003	2	36.6	1.44	0.2499
YST ^a	1	464.5	276.53	<.0001	1	456.6	1.15	0.2834	1	463.5	11.76	0.0007	1	465.4	275.2	<.0001
TDI ^a	1	465	298.77	<.0001	2	456.6	23.53	<.0001	1	459.6	15.85	<.0001	1	451.6	1.29	0.2559
TRTN X YST	2	464.5	63.15	<.0001	1	462	324.47	<.0001	2	465.4	16.3	<.0001	2	465.3	23.09	<.0001
TDI X TRTN	2	446.7	17.36	<.0001	2	442.9	12.35	<.0001	2	461.8	10.67	<.0001	2	461.6	6.21	0.0022
TDI X YST	-	-	-	-	1	458.6	4.37	0.0371	1	466.9	10.33	0.0014	-	-	-	-
TRTN X TDI X YST	-	-	-	-	2	458.5	7.5	0.0006	-	-	-	-	-	-	-	-

^a TRTN indicates treatment; TDI, tree dominance index; YST, year since treatment. Bolded values indicate F significance ($p < 0.05$).

^b Reduced model

Table 3. Range of the pretreatment tree dominance index (TDI) covariate where significant differences ($P < 0.01$) in tree removal treatments were found for vegetation cover variables 6 years after treatment. Comparisons with ≤ 1 indicate that the comparison was significant for all values of TDI.

Variable	Year 6 Response	TDI	Variable	Year 6 Response	TDI
Annual forb cover^a	Burn > cut	≤ 1	Sagebrush cover^a	Cut > burn	≤ 0.85
	Burn > untreated	≤ 1		Untreated > burn	≤ 0.60
	Cut > untreated	1		Cut = untreated	≤ 1
Exotic forb cover^a	Burn > cut	≥ 0.15	Total shrub cover^a	Cut > burn	≤ 0.90
	Burn > untreated	≥ 0.40		Untreated > burn	≤ 0.35
	Cut = untreated	≤ 1		Cut > untreated	≥ 0.20
Perennial forb cover^a	UT = B	≤ 1	Perennial forb density^a	Burn = cut	≤ 1
	C > UT	≥ 0.90		Burn = untreated	≤ 1
	C = B	≤ 1		Cut = untreated	≤ 1
Cheatgrass cover^a	Burn > cut	≤ 0.75	Short grass density^a	Burn = cut	≤ 1
	Burn > untreated	≤ 1		Burn = untreated	≤ 1
	Cut > untreated	≥ 0.40		Untreated > cut	≤ 0.95
Short grass cover^a	Burn = cut	≤ 1	Tall grass density^a	Cut > burn	≥ 0.7
	Burn = untreated	≤ 1		Untreated = burn	≤ 1
	Cut = untreated	≤ 1		Cut = untreated	≤ 1
Tall grass cover	Cut > burn	≥ 0.55	Total shrub density	Cut > burn	≤ 0.95
	Burn > untreated	≥ 0.55		Untreated > burn	≤ 0.40
	Cut > untreated	≥ 0.35		Cut > untreated	≥ 0.40
Perennial grass cover	Cut > burn	≥ 0.80	Sagebrush density^a	Cut > burn	≤ 0.70
	Burn > untreated	≥ 0.95		Untreated = burn	≤ 1
	Cut > untreated	≥ 0.50		Cut = untreated	≤ 1
Total perennial herbaceous cover^a	Cut > burn	≥ 1	Bareground^a	Cut = burn	≤ 1
	Burn > untreated	≥ 0.55		Untreated > burn	≥ 0.40
	Cut > untreated	≥ 0.40		Untreated > cut	≥ 0.10

^aReduced model



Study Site Locations

- ★ Pinyon-Juniper
- ✱ Utah Juniper
- ◇ Western Juniper

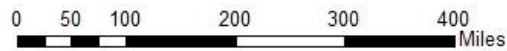


Figure 1. Study site locations in the Great Basin including predominant tree species on each site.

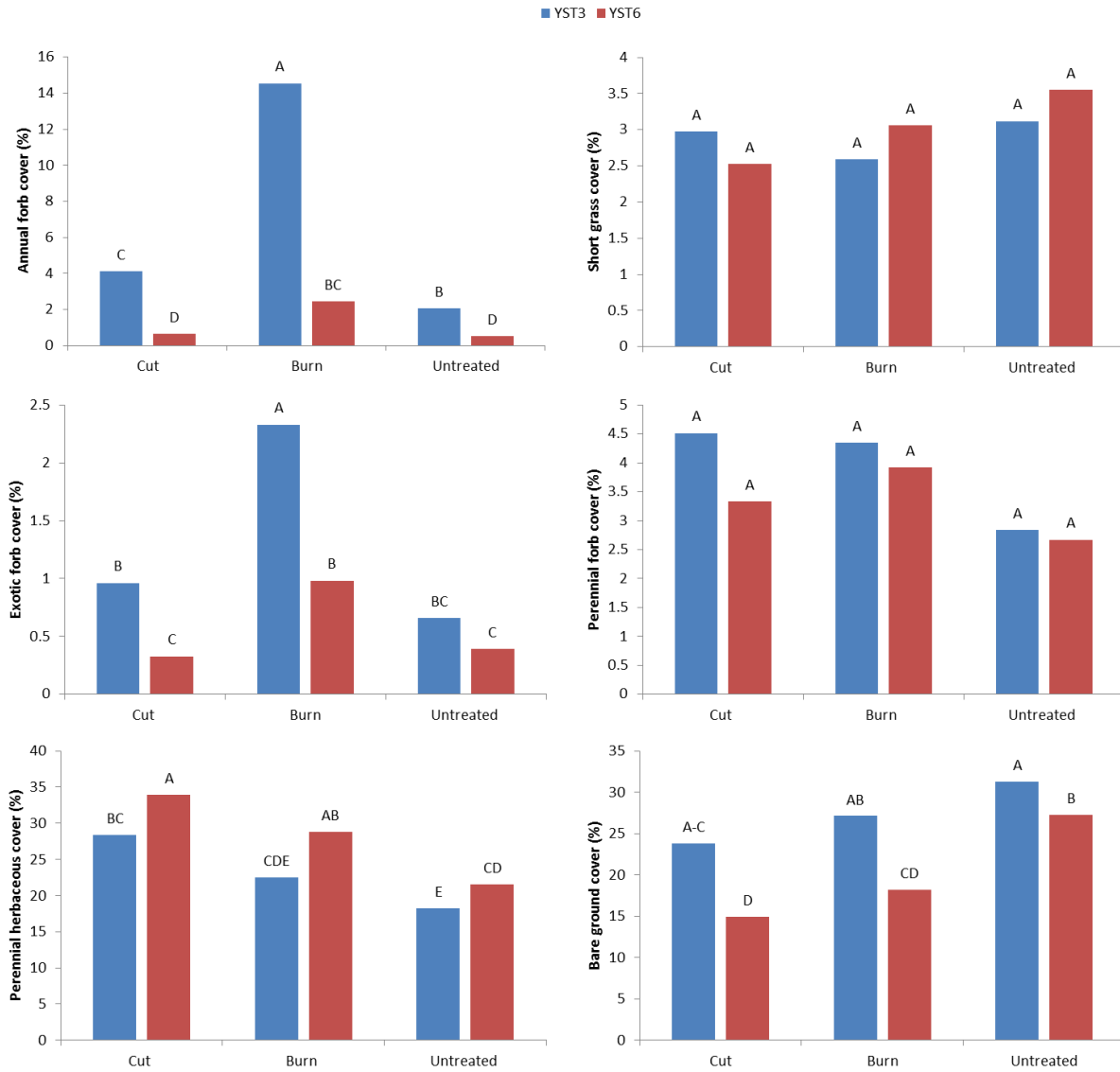


Figure 2. Vegetation cover 3 and 6 years after treatment in relation to treatment method. Different letters denote significant differences identified through Tukey's test.

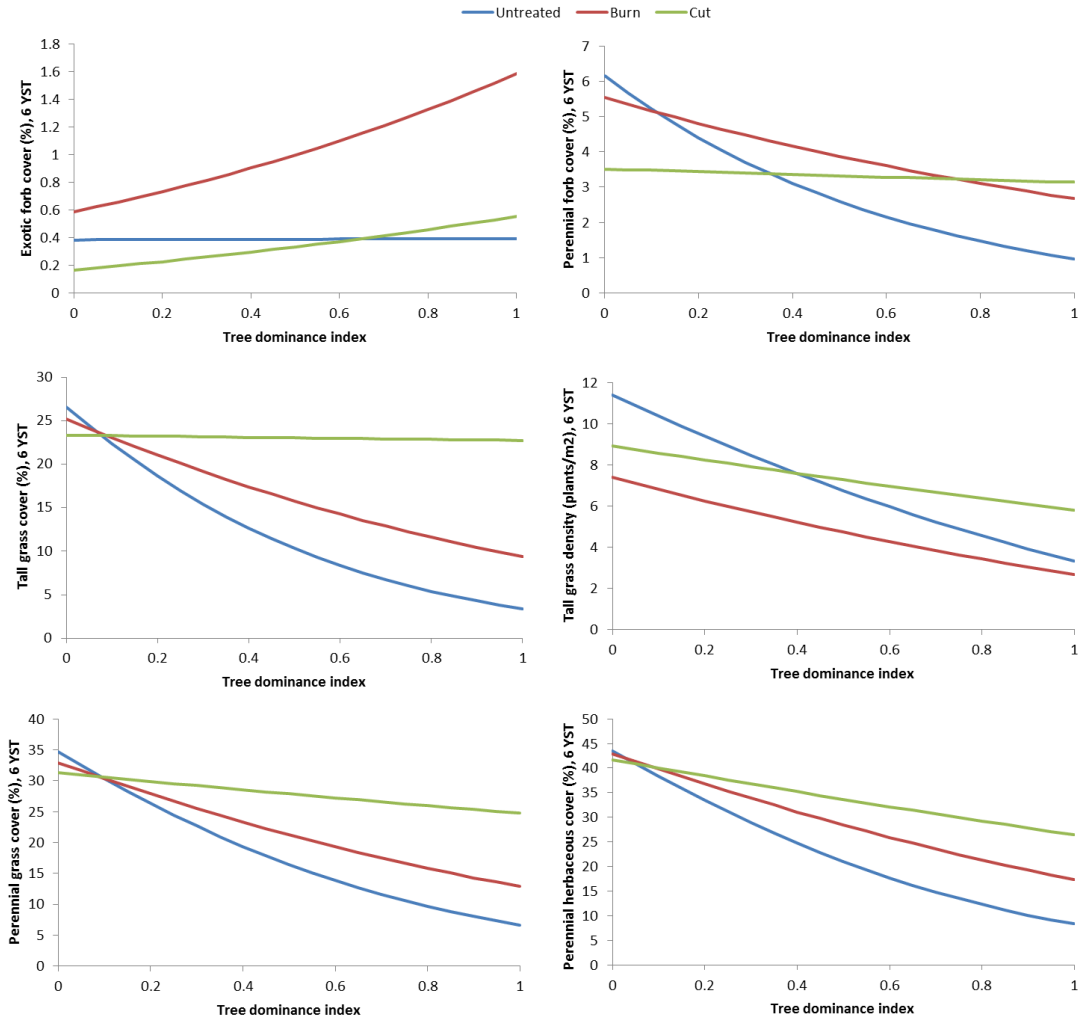


Figure 3. Vegetation cover 6 years after treatment in relation to treatment method and tree dominance index.

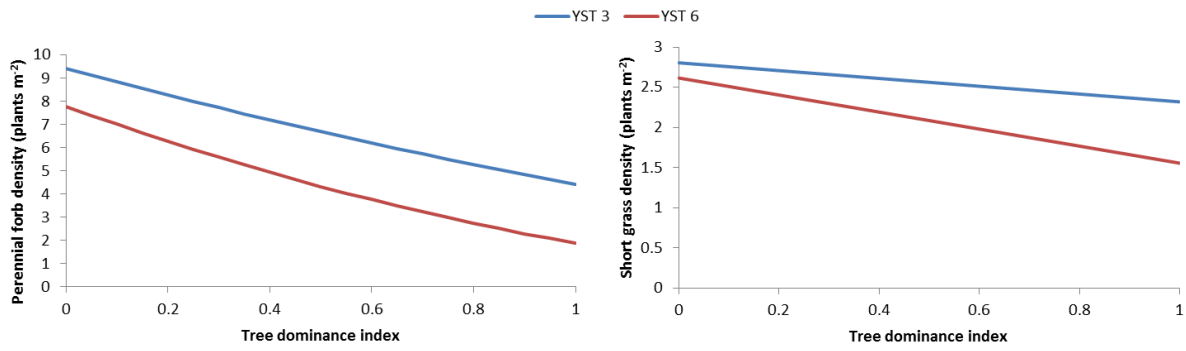


Figure 4. Vegetation cover 3 and 6 years after treatment in relation to tree dominance index.

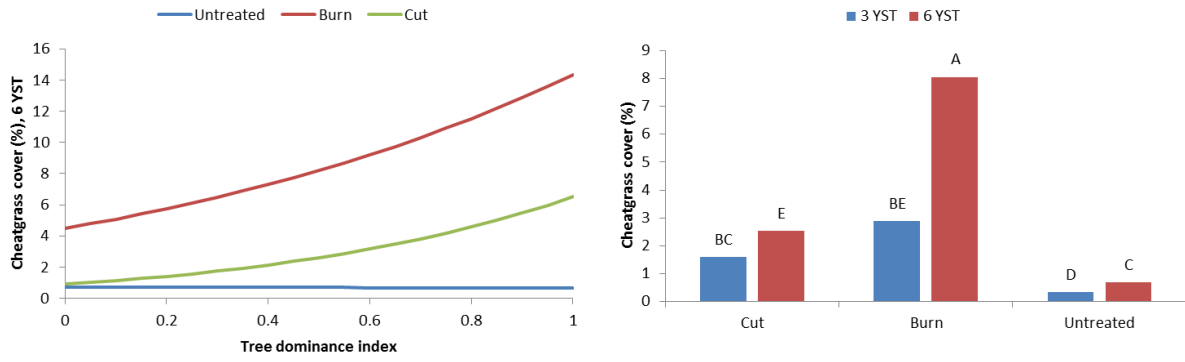


Figure 5. The graph on the left depicts cheatgrass cover 6 years after treatment in relation to tree dominance index and treatment method. The graph on the right depicts cheatgrass cover in relation to treatment type and year since treatment. Different letters denote significant differences identified through Tukey's test.

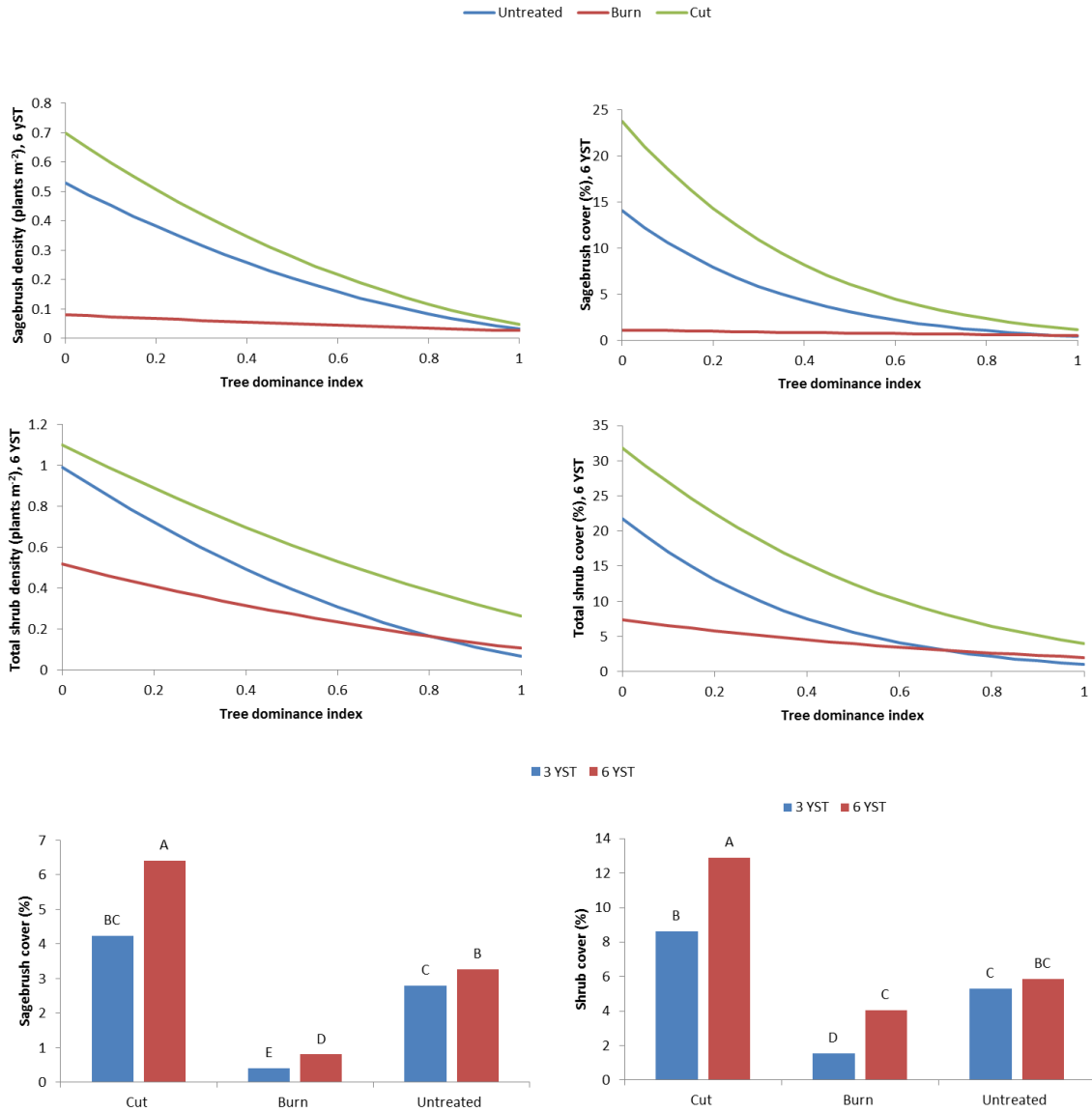


Figure 6. Upper graphs depict vegetation cover 6 years after treatment in relation to tree dominance index. The lower graphs depict vegetation cover in relation to years since treatment and treatment method. Different letters denote significant differences identified through Tukey's test.

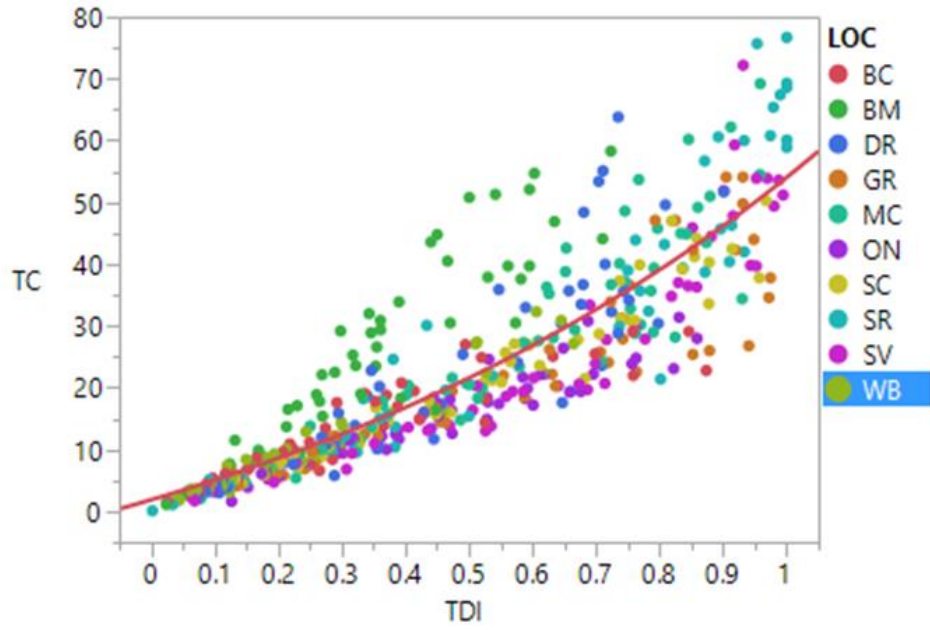


Figure 7. Regression showing relationship of pre-treatment tree cover (TC) to tree dominance index (TDI). BC indicates Bridge Creek; BM, Blue Mountain; DR, Devine Ridge; GR, Greenville; MC, Marking Corral; ON, Onaqui; SC, Scipio; SR, South Ruby; SV, Seven Mile; WB, Walker Butte.

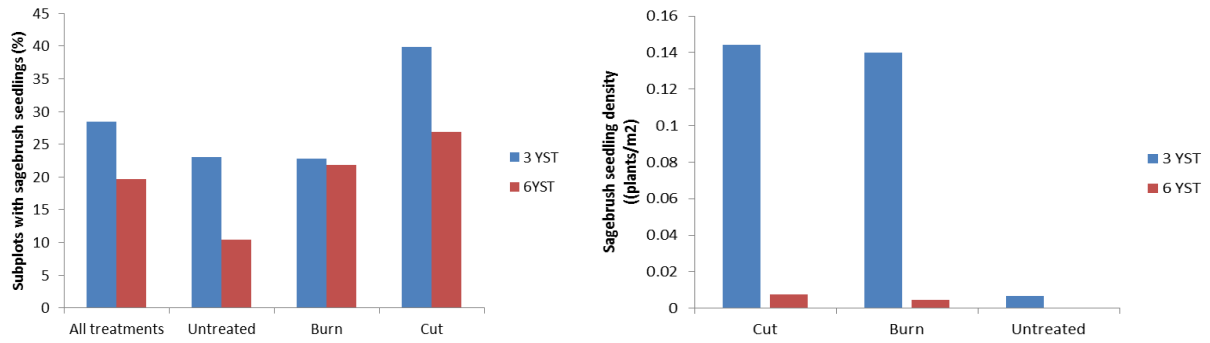


Figure 8. Percentage of subplots containing sagebrush seedlings 3 and 6 years since treatment

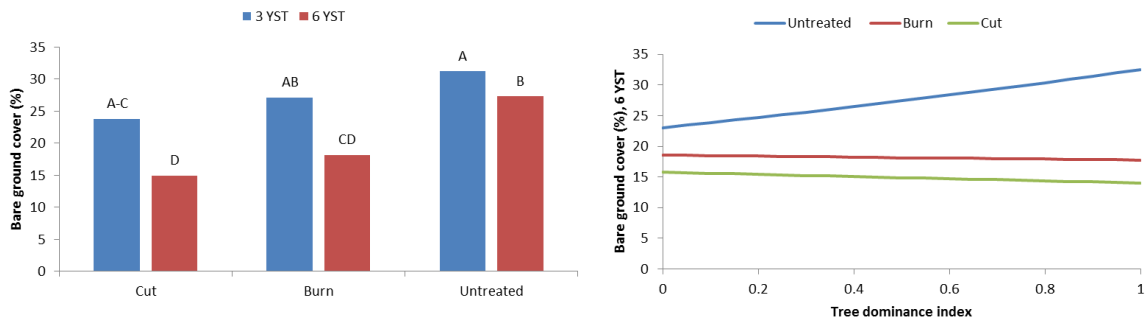


Figure 9. The left graph depicts bare ground cover in relation to treatment method and years since treatment. The right graph depicts bare ground cover in relation to treatment method and tree dominance index. Different letters denote significant differences identified through Tukey's test.

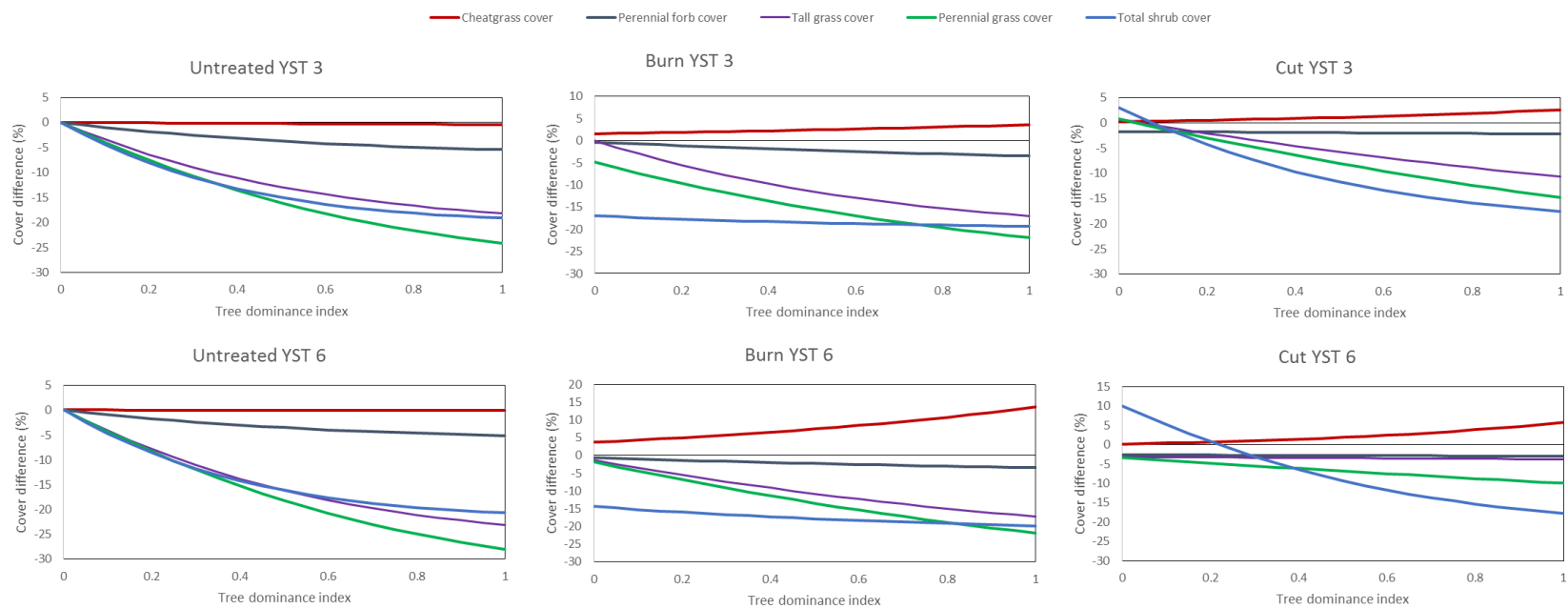


Figure 10. Differences between post-treatment functional group cover (%) and pre-treatment functional group cover at TDI = 0 across treatment types and years. Differences indicate how far a functional group cover is from the unencroached plant community or idealized restoration target.

References

- Ansley, R.J., H.T. Wiedemann, M.J. Castello, and J.E. Slosser. 2006. Herbaceous restoration of juniper dominated grasslands with chaining and fire. *Rangeland Ecology & Management*, 59(2):171-178.
- Archer, S.R. and K.I. Predick. 2014. An ecosystem services perspective on brush management: research priorities for competing land-use objectives. *Journal of Ecology*, 102: 1394-1407.
- Archer, S., D.S. Schimel, and E.A. Holland. 1995. Mechanisms of shrubland expansion: land use, climate or CO₂? *Climatic Change*, 29: 91-99.
- Archer, S.R., K.W. Davies, T.E. Fulbright, K.C. McDaniel, B.P. Wilcox, and K.I. Predick. 2011. Brush management as a rangeland conservation strategy: a critical evaluation. *Conservation benefits of rangeland practices*. Washington, DC, USA: US Department of Agriculture Natural Resources Conservation Service. p 105-170.
- Bagchi, S., D.D. Briske, B.T. Bestelmeyer, and X.B. Wu. 2013. Assessing resilience and state-transition models with historical records of cheatgrass *Bromus tectorum* invasion in North American sagebrush-steppe. *Journal of Applied Ecology*, 50: 131-1141.
- Baruch-Mordo, S., J.S. Evans, J.P. Severson, D.E. Naugle, J.D. Maestas, J.M. Kiesecker, M.J. Falkowski, C.A. Hagen, and K.P. Reese. 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. *Biological Conservation*, 167: 233-241.
- Bates, J.D., R.F. Miller, and T. Svegcar. 2005. Long-term successional trends following western juniper cutting. *Rangeland Ecology and Management*, 58(5): 533-541.
- Bates, J.D., R.N. Sharp, and K.W. Davies. 2013. Sagebrush steppe recovery after fire varies by development phase of *Juniperus occidentalis* woodland. *International Journal of Wildlife Fire* doi:10.1071/WF12206
- Bestelmeyer, B.T., J.R. Brown, K.M. Havstad, R. Alexander, G. Chavez, and J.E. Herrick. 2003. Development and use of state-and-transition models for rangelands. *Journal of Range Management*, 56(2): 114-126.
- Bestelmeyer, B.T., J.E. Herrick, J.R. Brown, D.A. Trujillo, and K. M. Havstad. 2004. Land management in the American Southwest: a state-and-transition approach to ecosystem complexity. *Environmental Management* 34(1): 38-51.

- Blank, R.R. and T. Morgan. 2012. Suppression of *Bromus tectorum* by established perennial grasses: potential mechanisms – part 1. *Applied Environmental Soil Science* 2012:1-9.
- Briske, D.D., B.T. Bestelmeyer, T.K. Stringham, and P.L. Shaver. 2008. Recommendations for development of resilience-based state-and-transition-models. *Rangeland Ecology and Management*, 61(4): 359-367.
- Brockway, D.G., R.G. Gatewood, and R.B. Paris. 2002. Restoring grassland savannas from degraded pinyon-juniper woodlands: effect of mechanical overstory reduction and slash treatment alternatives. *Journal of Environmental Management*, 64: 179-197.
- Brooks, M.L., C.M. D'Antonio, D.M. Richardson, J.B. Grace, J.E. Keeley, J.M DiTomaso, R.J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *American Institute of Biological Sciences*, 54(7): 677-688.
- Burkhardt, J.W. and E.W. Tisdale. 1976. Causes of juniper invasion in southwestern Idaho. *Ecology*, 57: 472-484.
- Bybee, J., B.A. Roundy, K.R. Young, A. Hulet, D.B. Roundy, L. Crook, Z. Aanderud, D.L. Eggett, and N.L. Cline. 2016. Vegetation response to piñon and juniper tree shredding. *Rangeland Ecology and Management*, 69: 224-234..
- Chambers, J.C., B.S. Roundy, R.R. Blank, S.E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invisable by *Bromus tectorum*? *Ecological Monographs*, 77(1): 117-145.
- Chambers, J.S, B.A. Bradley, C.S. Brown, C. D'Antonio, M.J. Germino, J.B. Grace, S.P. Hardegree, R.F. Miller, and D.A. Pyke. 2014a. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. *Ecosystems*, 17: 360-375
- Chambers, J.C., R.F. Miller, D.I. Board, D.A. Pyke, B.A. Roundy, J.B. Grace, E.W. Schupp, and R.J. Tausch. 2014b. Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. *Rangeland Ecology and Management*, 67: 440-454.
- Connelly, J.W., S.T. Knick, M.A. Schroeder, and S.J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Cheyenne, WY, USA: Western Association of Fish and Wildlife Agencies. Unpublished report.
- Floyd, M.L. and W.H. Romme. 2012. Ecological restoration priorities and opportunities in pinion-juniper woodlands. *Ecological Restoration*, 30(1): 37-49.

- Herrick, J.E., J.W. Van Zee, K.M. Havstad, L.M. Burkett, and W.G. Whitford. 2009. Monitoring manual for grassland, shrubland, and savannah ecosystems. *Range Ecology and Management*, 66: 313-329.
- Huber, A., S. Goodrich, and K. Anderson. 1999. Diversity with successional status in the pinyon-juniper/mountain mohogany/bluebunch wheatgrass community type near Dutch John, Utah. In: Monsen, S.B., Stevens, R. (Eds.), *Proceedings: ecology and management of pinyon-juniper communities within the interior west; 15-18 September 1997*; Brigham Young University, Provo, Utah, USA. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, RMRS-P-9, Ogden, UT, USA, pp. 114-117.
- Kenward, M.G., and J.K. Roger. 1997. Small sample interference for fixed effects from restricted maximum likelihood. *Biometrics*, 53: 983-997.
- Leffler, A. L. and R. J. Ryel. 2012. Resource pool dynamics: conditions that regulate species interactions and dominance. In Monaco, T. A. and Sheley, R. L. (Eds.), *Invasive plant ecology and management. Linking processes to practice*. Oxfordshire, UK: CAB International.
- Littell, R.C., G.A. Milliken, W.W. Stroup, R.D. Wolfinger, and O. Schabenberger. 2006. *SAS for Mixed Models, Second Edition*. Cary, NC: SAS Institute Inc.
- Mclver, J.D., M. Brunson, S.C. Bunting, and others. 2010. The Sagebrush Steppe Treatment Evaluation Project (SageSTEP): a test of state-and-transition theory. Gen. Tech. Rep. RMRS-GTR-237. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 16 p.
- Meyer, S.E. and S.B. Monsen. 1992. Big sagebrush germination patterns: subspecies and population differences. *Journal of Range Management*, 45: 87-93.
- Miller, R.F., T.J. Svejcar, and J.A. Rose. 2000. Impacts of western juniper on plant community composition and structure. *Journal of Range Management*, 56(6): 574-585.
- Miller, R.F., J.D. Bates, T.J. Svejcar, F.B. Pierson, and L.E. Eddleman. 2005. *Biology, ecology, and management of western juniper*. Oregon State University Agricultural Experiment Station, Technical Bulletin 152.
- Miller, R.F., R.J. Tausch, E.D. McArthur, D.D. Johnson, and S.C. Sanderson. 2008. Age structure and expansion of piñon-juniper woodlands: a regional perspective in the Intermountain West. Res. Pap. RMRS-RP-69. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 15 p.

- Miller, R.F., J.C. Chambers, D.A. Pyke, F.B. Pierson, and J.C. Williams. 2013. Fire effects on vegetation and soils in the Great Basin Region and the role of site characteristics. Fort Collins, CO, USA: US Department of Agriculture, Forest Service, Rocky Mountain Station. RMRS-GTR-308. 136 p.
- Miller, R.F., J.C. Chambers, and M. Pellant. 2014a. A field guide for selecting the most appropriate treatment in sagebrush and piñon-juniper ecosystems in the Great Basin: Evaluating resilience to disturbance and resistance to invasive annual grasses, and predicting vegetation response. Gen. Tech. Rep. RMRS-GTR-322-rev. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 68 p.
- Miller, R.F., J. Ratchford, B.A. Roundy, R.J. Tausch, A. Hulet, and J. Chambers. 2014b. Response of conifer-encroached shrublands in the Great Basin to prescribed fire and mechanical treatments. *Rangeland Ecology and Management*, 67(5): 468-481.
- Miller, R.F. and R.J. Tausch. 2001. The role of fire in pinyon and juniper woodlands: a descriptive analysis. K.E.M Galley and T.P. Wilson (eds.). *Proceedings of the Invasive Species Workshop: The Role of Fire in the Control and Spread of Invasive Species. Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management. Miscellaneous Publication No. 11: 15-30*, Tall Timber Research Station, Tallahassee, FL.
- O'Connor, C., R. Miller, and J.D. Bates. 2013. Vegetation response to western juniper slash treatments. *Environmental Management*, 52: 553-566.
- Pierson, F.B., J.D. Bates, T.J. Svejcar, and S.P. Hardegree. 2007. Runoff and erosion after cutting western juniper. *Society for Range Management*, 60(3): 285-292.
- Reisner, M.D., J. B. Grace, D.A. Pyke, and P.S. Doescher. 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. *Journal of Applied Ecology*, 50: 1039-1049.
- Ross, M.R., S.C. Castle, and N.N. Barger. 2012. Effects of fuels reductions on plant communities and soils in a piñon-juniper woodland. *Journal of Arid Environments*, 79: 84-92.
- Roundy, B.A., R.F. Miller, R.J. Tausch, K. Young, A. Hulet, B. Rau, B. Jessop, J.C. Chambers, and D. Eggett. 2014a. Understory cover responses to piñon –juniper treatments across tree dominance gradients in the Great Basin. *Rangeland Ecology & Management* 67:482-494.
- Roundy, B.A., K. Young, N. Cline, A. Hulet, R.F. Miller, R.J. Tausch, J.C. Chambers, and B. Rau. 2014b. Piñon-juniper reduction increases soil water availability of the resource growth pool. *Rangeland Ecology and Management*, 67: 495-505.

- Rowland, M.M., L.H. Suring, R.J. Tausch, S. Geer, and M.J. Wisdom. 2008. Characteristics of western juniper encroachment into sagebrush communities in central Oregon. USDA Forest Service Forestry and Range Sciences Laboratory, La Grande, Oregon 97850, USA. 23 pp.
- Ryel, R. J., C. Y. Ivans, M. S. Peek, and A. J. Leffler. 2008. Functional differences in soil water pools: a new perspective on plant water use in water-limited systems. *Progress in Botany*, 69:397-422.
- Ryel, R. J., A. J. Leffler, C. Ivans, M. S. Peek, and M. M. Caldwell. 2010. Functional differences in water-use patterns of contrasting life forms in Great Basin steppelands. *Vadose Zone Journal*, 9:548-560.
- Serpe, M.D., S.J. Zimmerman, L. Deines, and R. Rosentreter. 2008. Seed water status and root tip characteristics of two annual grasses on lichen-dominated biological soil crusts. *Plant and Soil*, 303: 191-205.
- Stringham, T.K., W.C. Krueger, and P.L. Shaver. 2003. State and transition modeling: an ecological process approach. *Journal of Range Management*, 56(2): 106-113.
- Tausch, R.J. and N.E. West. 1995. Plant species composition patterns with differences in tree dominance on a southwestern Utah pinyon-juniper site. In: D.W. Shaw, E.F. Aldon, and C. LoSapio [Tech. Coords.]. *Proceedings – desired future conditions for pinyon-juniper ecosystems*. Fort Collins, CO, USA: US Department of Agriculture, Forest Service, GTR RM-258. p. 16-23.
- Warton, D. and F.K. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, 92(1): 3-10.
- Whisenant, S.G. 1990. Changing fire frequencies on Idaho's Snake River Plain: ecological and management implications. Logan, UT, USA: US Department of Agriculture, Forest Service, Intermountain Research Center. General Technical Report, INT-276.
- Williams, C.J., F.B. Pierson, O.Z. Al-Hamdan, P.R. Kormos, S.P. Hardegree, and P.E. Clark. 2014. Can wildfire serve as an ecohydrologic threshold-reversal mechanism on juniper-encroached shrublands. *Ecohydrology*, 7: 453-477.
- Young, J.A. and R.A. Evans. 1989. Dispersal and germination of big sagebrush (*Artemisia tridentata*) seeds. *Weed Science*, 37(2): 201-206.

- Young, K. R., B. A. Roundy, S.C. Bunting, and D. L. Eggett. 2015. Utah juniper and two-needle piñon reduction alters fuel loads. *International Journal of Wildland Fire*, 24: 236-248.
- Young, K. R., B. A. Roundy, and D. L. Eggett. 2014. Mechanical mastication of Utah juniper encroaching sagebrush steppe increases inorganic soil N. *Applied and Environmental Soil Science*, <http://dx.doi.org/10.1155/2014/632757>.
- Young, K. R., B. A. Roundy, and D. L. Eggett. 2013a. Plant establishment in masticated Utah juniper woodlands. *Rangeland Ecology and Management*, 66:597-607.
- Young, K. R., B. A. Roundy, and D. L. Eggett. 2013b. Tree reduction and debris effects of mastication on soil climate variables in Utah. *Forest Ecology and Management*, 310: 777-785.