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Original Research

Pretreatment Tree Dominance and Conifer Removal Treatments Affect Plant Succession in Sagebrush Communities☆,☆☆

Rachel E. Williams [a], Bruce A. Roundy [b,*], April Hulet [c], Richard F. Miller [d], Robin J. Tausch [e], Jeanne C. Chambers [f], Jeffrey Matthews [g], Robert Schooley [h], Dennis Eggett [i]

[a] Fish and Wildlife Biologist, US Fish and Wildlife Service, Bishop, CA 93514, USA
[b] Professor, Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT 84602, USA
[c] Assistant Professor, Department of Forest, Rangeland, and Fire Sciences, University of Idaho, Moscow, ID 83844, USA
[d] Professor Emeritus, Department of Animal and Range Science, Oregon State University, Corvallis, OR 97331, USA
[e] Range Scientist, Retired, US Department of Agriculture (USDA) Forest Service, Rocky Mountain Research Station, Reno, NV 89509, USA
[f] Research Ecologist, US Department of Agriculture (USDA) Forest Service, Rocky Mountain Research Station, Reno, NV 89509, USA
[g] Associate Professor, Department of Natural Resources and Environmental Sciences, University of Illinois, Urbana, IL 61801, USA
[h] Assistant Professor, Department of Natural Resources and Environmental Sciences, University of Illinois, Urbana, IL 61801, USA
[i] Associate Research Professor, Department of Statistics, Brigham Young University, Provo, UT 84602, USA

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ABSTRACT

In sagebrush (*Artemisia tridentata* Nutt.) ecosystems, expansion and infilling of conifers decreases the abundance of understory perennial vegetation and lowers ecosystem resilience and resistance of the once shrub grass − dominated state. We prescribed burned or cut juniper (*Juniperus* spp. L.) and pinyon (*Pinus* spp. L.) trees at 10 sites across the western United States. We measured vegetation cover and density on untreated and treated plots 3 and 6 yr after treatment across a gradient of pretreatment tree dominance as quantified by the tree dominance index (TDI); (tree cover)/(tree + shrub + tall grass cover). We analyzed plant responses by functional group using mixed-model analysis of covariance, with TDI treated as a covariate. As tree cover increased and TDI exceeded 0.5, shrub cover declined to < 25% of the maximum on untreated plots. Although total shrub cover recovered on burned plots to untreated percentages 6 yr after treatment, sagebrush cover was still 1.1 − 0.6% on burned plots compared with 13.9 − 0.5% on untreated plots across the range of 0 − 1 TDI. Tall grass cover increased to 25.4 − 9.4% for burn plots and 24.3 − 22.4% on cut plots from 0 − 1 TDI 6 yr after treatment. Cheatgrass (*Bromus tectorum* L.) increased on prescribed fire and on cut treatments, especially at higher pretreatment TDI. However, ratios of cheatgrass to tall grass cover were much lower on cut than burn plots. To retain the shrub, especially sagebrush, components on a site and increase ecosystem resilience and resistance through increases in tall grasses, we recommend treating at low to mid TDI using mechanical methods, such as cutting or mastication. Effects of fire and mechanical treatments implemented at different phases of tree dominance create different successional trajectories that could be incorporated into state-and-transition-models to guide management decisions.

Introduction

Since the late 1800s, semiarid lands around the world have been experiencing increasing cover of woody vegetation (Archer et al., 1995; Miller and Tausch, 2001; Archer and Predick, 2014). In many areas of the western United States, 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.) ecosystems, dominance of juniper and pinyon alters fire regimes, increases soil erosion, decreases shrub and herbaceous cover, and diminishes habitat for certain wildlife species (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; Baruch-Mordo et al., 2013; Roundy et al., 2014a; Roundy et al., 2016). Increased canopy fuel loads (Young et al., 2015) and decreased understory cover (Roundy et al., 2014a) as trees expand and infill can increase fire severity followed by annual weed dominance, increased fire frequency, and loss of ecosystem services.

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* Correspondence: Bruce Roundy, Dept of Plant and Wildlife Sciences, Brigham Young University, 4105 LSB, Provo, UT 84602, USA. Tel.:+1 801 422 8137.
E-mail address: bruce_roundy@byu.edu (B.A. Roundy).

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Drivers for woodland expansion include increases in atmospheric CO_2, altered fire regimes due to fire suppression, and a reduction in fine fuels caused by livestock grazing (Miller and Wigand, 1994; Archer and Predick, 2014). Over the past several thousand years, pinyon and juniper ranges have expanded and contracted in response to changing climatic conditions (Miller and Wigand, 1994; Miller and Tausch, 2001). However, in the past 150 yr, woodland expansion has exceeded rates recorded for the previous 5 000 yr (Miller and Tausch, 2001; Miller et al., 2008). Increased woodland area burned in the past 30 yr has been associated with changes in climate and increases in invasive grasses (Board et al., 2017).

Tree removal is commonly used to restore structure and function to these communities (Brockway et al., 2002; O'Connor et al., 2013; Stephens et al., 2016). However, successional trajectories following disturbance are dependent on disturbance severity and 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., 2014a, 2014b; Roundy et al., 2014a). As tree cover increases, both shrub and herbaceous cover decrease, with relative decreases depending on species composition and ecological site characteristics (Tausch and West, 1995; Roundy et al., 2014a; Bybee et al., 2016). After tree removal, if shrub and herbaceous cover have already declined, missing components of the community may be replaced by invasive species, especially on warmer and drier sites (Young et al., 2013a, 2013b, 2014; Chambers et al., 2014a, 2014b; Miller et al., 2014a). For this reason, pretreatment tree dominance plays a vital role in steering the successional trajectories of these ecosystems following disturbance (Miller et al., 2000; Archer et al., 2011; Miller et al., 2014a; Roundy et al., 2014a). Successional trajectories that appear similar in the short-term (1-5 yr) may diverge when monitored over the long term (5-11 yr). Thus, long-term monitoring is necessary to determine the outcome of these treatments.

State-and-transition-models (STMs) are useful tools for making land management decisions that 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., 2014a, 2014b; Miller et al., 2014a). The development of STMs requires an understanding of underlying ecological site characteristics, ecosystem processes, ecological thresholds, and successional trajectories relative to pretreatment site conditions and the treatment method employed (Chambers et al., 2014a, 2014b; Miller et al., 2014b; Roundy et al., 2014a). Generalized STMs for sagebrush ecosystems have not specified effects of different tree reduction treatments (Chambers et al., 2014b; Miller et al., 2014a). If prescribed fire and mechanical treatments implemented at different phases of tree dominance lead to different successional trajectories and vegetation states, then inclusion of this information in state-and-transition models could better guide land management.

Ecosystem resistance is a system's ability to maintain its current state when exposed to disturbance or stress (Briske et al., 2008; Chambers et al., 2014a, 2014b). However, resistance to annual grass invasion and dominance is of most importance to sagebrush ecosystems because that dominance poses the greatest risk to the system. Exotic annual bromes, such as cheatgrass, can alter fire regimes, soil nitrogen pools, soil microbial communities, and hydrologic conditions leading to degraded site conditions (Brooks et al., 2004; Blank and Morgan, 2012; Bagchi et al., 2013; Reisner et al., 2013; Rau et al., 2008, 2014; Chambers et al., 2014a, 2014b). The major concern is that after disturbance the system passes through a biotic threshold where annual grass dominance results in more frequent and larger fires (Balch et al., 2013), which then requires major intervention by use of herbicides and seeding to restore the system.

Effects of prescribed fire compared with mechanical tree reduction on annual grass resistance depend on initial site conditions and differential treatment effects on perennial shrubs and grasses, seedbanks, and resource availability (Pyke et al., 2010; Bates et al., 2013; Miller et al., 2013; Roundy et al., 2014a). Comparison of these treatments in relation to pretreatment tree dominance is necessary to determine how to best reinforce a restoration trajectory (Briske et al., 2008) toward a desirable state and resist a trajectory to an undesirable state (weed dominance). Deep-rooted perennial (tall) grasses are especially important in limiting cheatgrass invasion and dominance (Chambers et al., 2007; Blank and Morgan, 2012; Reisner et al., 2013; Miller et al., 2014a). Perennial 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).

Compared with prescribed fire, mechanical treatments may result in greater resistance to cheatgrass dominance primarily through retention of shrubs and increases in tall grasses (Miller et al., 2014a, 2014b; Roundy et al., 2014a; Bybee et al., 2016). Sites with high tree dominance are more likely to experience increases in cheatgrass cover after tree reduction due to lower perennial herbaceous and shrub cover and thus higher availability of resources (Bates et al., 2013; Roundy et al., 2014a, 2014b).

Objectives

Our study was a follow-up to the region-wide SageSTEP woodland experiment (McIver and Brunson, 2014) in which effects of tree reduction were reported by Miller et al. (2014b) and Roundy et al. (2014a). Our objective was to determine how successional trajectories have changed from 3 to 6 yr post treatment to better predict how tree-expansion communities will ultimately respond to no-removal or tree-removal treatments. We hypothesized that compared with no treatment and prescribed fire, tree reduction by cutting at low to mid tree dominance will result in a community most similar to the pre-expansion community. This is because 1) on untreated plots, perennial understory cover will continue to decrease with increasing pretreatment tree dominance, 2) on burn treatments cheatgrass cover will continue to increase and shrub cover will remain low, 3) on cut treatments, perennial herbaceous and shrub cover will continue to increase, and 4) on both burn and cut treatments, perennial plant recovery will be highest and cheatgrass cover lowest when treatments are implemented at low to mid tree dominance.

Methods

Study Region and Sites

This study included 10 conifer-expansion or wooded shrubland sites (Romme et al., 2009) located across the Great Basin region (Fig. 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 big sagebrush (*Artemisia tridentata* spp. L.) communities on loamy soils (Roundy et al., 2014b). This current study did not include data from the Stansbury, Utah site originally included in the Miller et al. (2014b) and Roundy et al. (2014a) analyses because that site burned in a wildfire 3 yr after treatment. Elevation, soils, and climate vary widely among sites and across the study region. Sites and environmental conditions were described in detail by McIver et al. (2010), McIver and Brunson (2014), Miller et al. (2014b), and Roundy et al. (2014a, 2014b). The wide distribution of our study sites allows us to determine regional responses to treatments.

Experimental Design and Treatments

We used a randomized complete block design with study sites as the blocks. Within each block, we assigned a cutting treatment (cut), a prescribed fire treatment (burn), and an untreated control to three plots

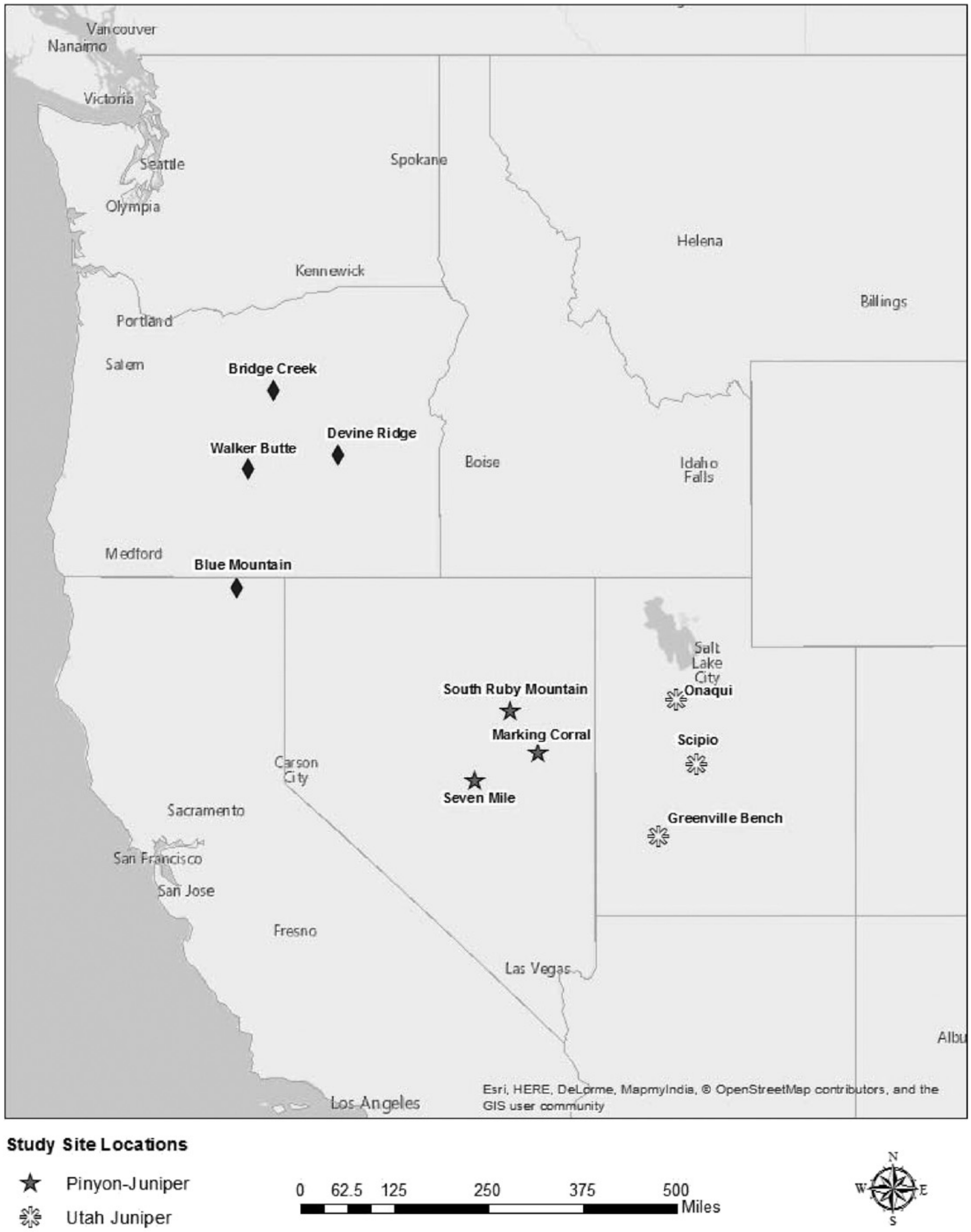

Fig. 1. Study site locations in the Great Basin including predominant tree species on each site. Scipio and Greenville Bench also have pinyon.

(8–20 ha each). All three plots on a site had similar topographic position, soils, and vegetation. Plots were fenced, where necessary, to exclude livestock (Miller et al., 2014b). We applied vegetation treatments in a staggered-start design from 2006 to 2009 and intensively monitored vegetation 3 and 6 yr post treatment.

Fire treatments consisted of low to moderate severity broadcast burns applied between August and November. Cut treatments were completed in the fall following the burn, with the exception of the South Ruby site, where cut treatments were completed the following spring (McIver et al., 2010; Miller et al., 2014b). These treatments involved cutting all trees > 2 m in height and leaving the cut trees on the ground (McIver et al., 2010). Tree canopy cover was reduced to < 5% on burn treatments and to < 1% on cut treatments (Roundy et al., 2014a). We measured daily precipitation on the untreated plot within high tree cover using a tipping bucket rain gage as described by Roundy et al. (2014b).

Vegetation Measurements

We randomly established 15, 0.1-ha (30 × 33 m) subplots within treated and untreated plots (Miller et al., 2014b; Roundy et al., 2014a). Subplots spanned a gradient of tree dominance expressed as tree dominance index (TDI), defined as tree cover/(tree + shrub + tall grass cover). TDI is a useful indicator of pretreatment tree dominance across multiple sites because it expresses pretreatment tree cover relative to cover of all the major competitors for resources (Ryel et al., 2008, 2010; Roundy et al., 2014a, 2014b). We measured vegetation within all subplots before treatment (yr 0) and again 3 and 6 yr post treatment.

Table 1
Ten study sites with dominant species and elevation range.

Study site (abbrev.)	Potential plant community	Elevation (m)
Western juniper		
Blue Mountain (BM)	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)	1500-1700
Bridge Creek (BC)	Basin big sage (*Artemisia tridentata* Nutt. subsp. *tridentata*)/bluebunch wheatgrass-Sandberg bluegrass	800-900
Devine Ridge (DR)	Mountain big sage/Sandberg bluegrass — Thurber's needlegrass — Idaho fescue	1600-1700
Walker Butte (WB)	Mountain big sage/Thurber's needlegrass (*Achnatherum thurberiana* [Piper] Barkworth) — Idaho fescue — squirreltail (*Elymus elymoides* [Raf.] Swezey)	1400-1500
Single-leaf pinyon-Utah juniper		
Marking Corral (MC)	Wyoming big sage (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young)/Thurber's needlegrass	2300-2400
Seven Mile (SV)	Mt. mahogany (*Cercocarpus ledifolius* Nutt)-mountain big sage/bluebunch wheatgrass-muttongrass (*Poa fendleriana* [Steud.] Vasey)	2300-2500
South Ruby (SR)	Wyoming big sage — bitterbrush/bluebunch wheatgrass-Sandberg bluegrass — Thurber's needlegrass	2100-2200
Utah juniper		
Onaqui (OJ)	Wyoming big sage/bluebunch wheatgrass	1700-2100
Colorado pinyon-Utah juniper		
Greenville Bench (GR)	Wyoming big sage/needle and thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth)-bluebunch wheatgrass	1750-1850
Scipio (SC)	Wyoming big sage/bluebunch wheatgrass	1700-1800

We established a 30-m baseline within each subplot with 5 permanent transects placed at 2 m, 7 m, 15 m, 23 m, and 28 m. We used the line-point intercept method (Herrick et al., 2009) 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. We then categorized cover data into shrub; big sagebrush; tall grass; Sandberg bluegrass (*Poa secunda* J. Presl); perennial, annual, and exotic forbs; cheatgrass; and bare ground cover. Tall grass included all native perennial bunchgrasses except Sandberg bluegrass, which has shorter stature and matures earlier in spring and summer than most taller-statured, cool-season bunchgrasses (Majerus et al., 2009). We recorded foliar cover for each functional group or species as a single hit for each point if the point contacted 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.

We measured density of tall perennial bunch grasses, Sandberg bluegrass, nonrhizomatous perennial forbs, and shrub species < 50 mm in height in 0.25-m^2 quadrats every odd-meter along the 7 m, 15 m, and 23 m transects for a total of 45 quadrats per subplot. Along these same transects, all shrubs species > 50 mm in height and within 1 m of the transect (2×30 m) were counted. We estimated tree canopy cover for all trees > 0.5 m in height by measuring the longest crown diameter ($D1$)and the perpendicular crown diameter ($D2$). We then used these measurements to calculate crown area (A) for each tree using the formula:

$$A = \frac{\pi(D1 * D2)}{4}$$

We used the summation of crown area for all trees in the subplot to estimate total tree canopy cover.

Analysis

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

We used the Tukey test to determine differences among treatment, YST, and interaction estimates. To elucidate effects of pretreatment tree dominance on treatment responses, we compared treatment estimates for each YST and YST estimates for each treatment using a Tukey test for each 0.05 increment of the TDI covariate from 0 to 1, representing a range of pretreatment relative tree dominance. Significance of these tests was set at $P < 0.01$ to control the experiment-wise error rate. For these estimates, we included only main effect by TDI covariate interactions that were significant ($P < 0.05$). Even if three-way interaction terms were not significant and were excluded from the model, the models still allowed us to estimate TDI ranges over which treatments varied for each YST. To compare treatment responses with a potential restoration target, we calculated the difference in cover between treatment and 6 YST estimates at different pretreatment TDI with cover estimates for the untreated plot at 0 TDI. Estimated cover responses to the TDI covariate are regression estimates using subplot pretreatment TDI as the independent variable and subplot functional group or species responses as the dependent variables. For untreated plots, cover estimates at 0 TDI should be a reasonable estimate of what could be expected with minimal tree influence.

Results

Weather

October — June precipitation from 2006 to 2013 during the past 6 yr since treatment was generally lower than the 30-yr average (1981 — 2010; PRISM Climate Group, 2016) across the study sites (Fig. 2). An exception was higher precipitation from October 2010 to June 2011, which was associated with heavy spring precipitation.

Vegetation

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 with 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. Density for all functional groups showed a significant

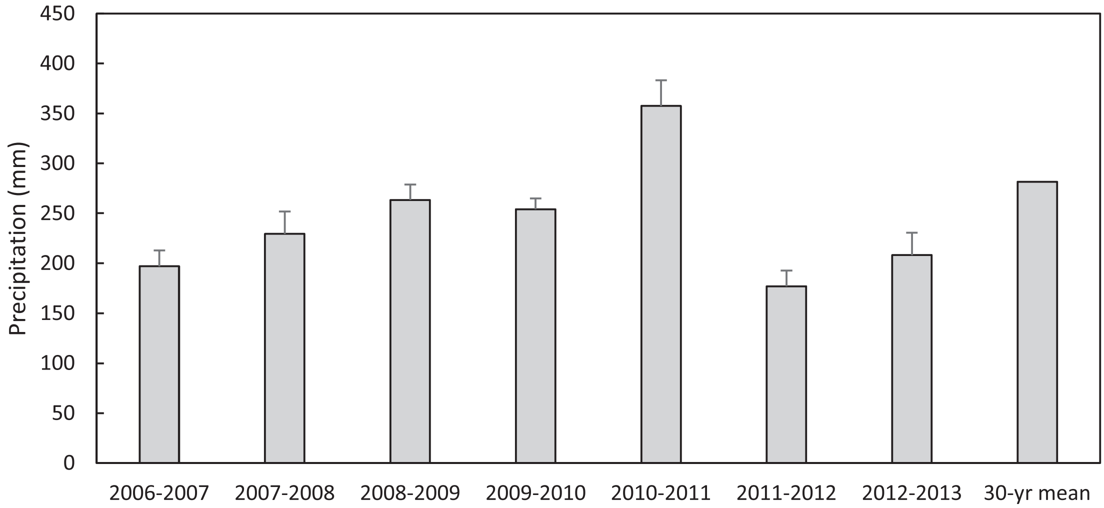

Fig. 2. Average of October through June precipitation for 10 Great Basin study sites with 1 standard error displayed above bars. Thirty-yr average is for 1981 − 2010, PRISM (2016).

interaction ($P < 0.05$) between either treatment with YST or TDI with YST (see Table 2). These results indicate density response over time depended more on treatment method for some variables and more on pretreatment TDI for others. The three-way interaction of treatment, YST, and TDI was significant ($P < 0.001$) for shrub, sagebrush, and tall grass density (see Table 2).

Annual and Exotic Forb Cover

Annual forb cover varied significantly with TDI but not with treatment or YST (see Table 2). The trend at 3 YST was for increased annual forb cover with increasing TDI from 0 to 1 on burned plots (12 − 16%) and cut plots (2.9 − 5.7%) compared with untreated plots (3 − 1.3%).

Table 2
Results for mixed-model analysis of covariance for cover (%) and density (plants m^{-2}) for functional groups and species for untreated plots and burn-and-cut removal treatments in relation to a tree dominance index (TDI) at the time of treatment.

	Annual forb cover				Exotic forb cover				Perennial forb cover				Perennial forb density			
	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P
Treatment (TRTN)	2	18	0.51	0.61	2	66.5	2.6	0.08	2	39.4	1.5	0.23	2	39.5	1.9	0.16
Years since treatment (YST)	1	27	0.14	0.71	1	58.3	3.3	0.07	1	27.2	4.8	**0.04**	1	39.6	10.9	**0.01**
TDIaTDIaTDI	1	455.9	38.5	< **0.0001**	1	448.7	3.4	0.07	1	458.9	41	< **0.0001**	1	452.9	65.5	< **0.0001**
TRTN X YST	2	27	1	0.39	2	44.7	0.55	0.58	2	27.2	1.2	0.33	2	26.8	0.36	0.7
TDI X TRTN	—	—	—	—	2	458.6	6.8	**0.001**	2	466	12.9	< **0.0001**	2	466	4.8	**0.01**
TDI X YST	—	—	—	—	1	451.9	5.1	**0.03**	—	—	—	—	1	449.7	4.8	0.03
TRTN X TDI X YST	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Short grass cover				Short grass density				Tall grass cover				Tall grass density			
	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P
Treatment (TRTN)	2	17.98	0.49	0.62	2	52.6	6.6	**0.003**	2	47.9	0.06	0.94	2	38.3	3.2	**0.05**
Years since treatment (YST)	1	465.6	1.29	0.2568	1	41	7.9	**0.008**	1	42.7	8.2	**0.007**	1	54.9	0.6	0.44
TDIaTDIaTDI	1	454.3	38.29	< **0.0001**	1	456.2	26	< **0.0001**	1	459.2	181.7	< **0.0001**	1	465.6	129.4	< **0.0001**
TRTN X YST	2	—	—	—	2	41	0.3	0.74	2	42.7	0.16	0.86	2	54.8	1.6	0.23
TDI X TRTN	—	—	—	—	—	—	—	—	2	460.1	26	< **0.0001**	—	—	—	—
TDI X YST	—	—	—	—	—	—	—	—	1	449.2	17.1	< **0.0001**	1	458.3	12.4	**0.001**
TRTN X TDI X YST	—	—	—	—	—	—	—	—	2	449	8.7	**0.002**	4	686	3.5	**0.007**
	Perennial grass cover				Perennial herbaceous cover				Sagebrush cover				**Sagebrush density**			
	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P
TRTNaTRTN	2	35.3	0.42	0.66	2	45.6	0.2	0.82	2	40.7	70.1	< **0.0001**	2	38.6	54.2	< **0.0001**
Years since treatment (YST)	1	45.4	7.1	**0.01**	1	41	2.7	0.11	1	27.1	35.1	< **0.0001**	1	74	2.9	0.09
TDI	1	456.1	229.1	< **.0001**	1	462.1	249.1	< **0.0001**	1	462.7	238.3	< **0.0001**	1	461.9	237.1	< **0.0001**
TRTN X YST	2	45.3	1.3	**0.0321**	2	27	0.27	0.76	2	27.1	2.8	**0.08**	2	73.4	6.7	**0.002**
TDI X TRTN	2	465.1	20.9	< **0.0001**	2	463.7	23.8	< **0.0001**	2	469.7	35.8	< **0.0001**	2	470.5	31.5	< **0.0001**
TDI X YST	1	454.4	8.9	**0.003**	1	451.5	11.1	**0.001**	—	—	—	—	1	455.2	8.1	**0.005**
TRTN X TDI X YST	2	454.1	4.4	**0.01**	—	—	—	—	—	—	—	—	2	454.8	6.1	**0.003**
	Total shrub cover				Total shrub density				Cheatgrass cover				Bare ground cover			
	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P
TRTNaTRTN	2	57	50.6	< **0.0001**	2	60.2	40.8	< **0.0001**	2	46.1	9.9	**0.0003**	2	36.6	1.5	0.23
Years since treatment (YST)	1	56.9	20.7	< **0.0001**	1	48.5	0.84	0.37	1	27.1	15.9	**0.0005**	1	26.9	27.8	< **0.0001**
TDI	1	466.3	297.1	< **0.0001**	1	465	324.8	< **0.0001**	1	462.6	15.3	**0.0001**	1	454.7	1.1	0.29
TRTN X YST	2	56.9	3.7	**0.03**	2	48.4	9.3	**0.0004**	2	27.1	1.2	0.32	2	26.9	2.4	0.11
TDI X TRTN	2	447.5	17.3	< **0.0001**	2	445	12.4	< **0.0001**	2	464.9	10.2	< **.0001**	2	464.7	6	**0.003**
TDI X YST	—	—	—	—	1	451.5	29.6	**0.0371**	—	—	—	—	—	—	—	—
TRTN X TDI X YST	3	459.5	3.5	**0.015**	2	451.3	9	< **0.0001**	—	—	—	—	—	—	—	—

NDF, numerator degrees of freedom; DDF, denominator degrees of freedom calculated according to Kenward and Roger (1997); TRTN, treatment; YST, year since treatment; TDI. Bolded values indicate F significance ($P < 0.05$). A dash indicates that a nonsignificant TDI interaction term was not included in the model.

Table 3
Range of pretreatment tree dominance index (TDI) where significant differences ($P < 0.01$) in tree-removal treatments were found for vegetation cover variables 3 and 6 yr after treatment (YST).

Functional group	Comparison	3 YST	6 YST	Comparison	Untreated	Burn	Cut
Annual forb	UT = Burn	≤ 0.75	≤ 0.60	3 YST = 6 YST	≤ 1	None	None
	Burn > UT	≥ 0.80	≥ 0.65	6 YST > 3 YST	None	≤ 1	≤ 1
	UT = Cut	≤ 1	≤ 1				
	Burn = Cut	≥ 0.45	≤ 1				
	Burn > Cut	≤ 0.40	None				
Exotic forb	UT = Burn	≤ 0.75	≤ 1	3 YST = 6 YST	≤ 1	≤ 1	≤ 1
	Burn > UT	≥ 0.80	None				
	UT = Cut	≤ 1	≤ 1				
	Burn = Cut	≤ 1	≤ 1				
Cheatgrass	UT = Burn	≤ 0.15	None	3 YST = 6 YST	≤ 1	≤ 1	≤ 1
	Burn > UT	≥ 0.20	≤ 1				
	UT = Cut	≤ 0.5	≤ 0.5				
	Burn = Cut	≤ 1	≤ 0.05, > 0.35-1				
	Burn > Cut	≤ 1	≥ 0.10 to ≤ 0.30				
Perennial forb	UT = Burn	≤ 1	≤ 1	3 YST = 6 YST	≤ 1	≤ 1	≤ 1
	UT = Cut	≤ 0.75	≤ 1				
	Cut > UT	≥ 0.8	None				
	Burn = Cut	≤ 1	≤ 1				
Sandberg bluegrass	UT = Burn	≤ 1	≤ 1	3 YST = 6 YST	≤ 1	≤ 1	≤ 1
	UT = Cut	≤ 1	≤ 1				
	Burn = Cut	≤ 1	≤ 1				
Tall grass	UT = Burn	≤ 1	≤ 0.65	3 YST = 6 YST	≤ 1	≤ 0.40	≤ 0.60
	Burn > UT	None	≥ 0.70	6 YST > 3 YST	None	≥ 0.45	≥ 0.65
	UT = Cut	≤ 0.45	≤ 0.40				
	Cut > UT	≥ 0.50	≥ 0.45				
	Burn = Cut	≤ 0.60	≤ 0.65				
	Cut > Burn	≥ 0.65	≥ 0.70				
Perennial herbaceous	UT = Burn	≤ 1	≤ 0.70	3 YST = 6 YST	≤ 1	≤ 1	≤ 1
	Burn > UT	None	≥ 0.75				
	UT = Cut	≤ 0.50	≤ 0.45				
	Cut > UT	≥ 0.55	≥ 0.50				
	Burn = Cut	≤ 1	≤ 1				
Sagebrush	UT = Burn	≥ 0.70	≥ 0.60	3 YST = 6 YST	≤ 1	None	None
	Burn < UT	≤ 0.65	≤ 0.55	6 YST > 3 YST	None	≤ 1	≤ 1
	UT = Cut	≤ 1	≤ 1				
	Burn = Cut	≥ 0.85	≥ 0.85				
	Cut > Burn	≤ 0.80	≤ 0.80				
Shrub	UT = Burn	≥ 0.80	≥ 0.40	3 YST = 6 YST	≤ 1	None	≤ 0.40, ≥ 0.9
	Burn > UT	≤ 0.75	≤ 0.35	6 YST > 3 YST	None	≤ 1	≥ 0.45 to 0.85
	UT = Cut	≤ 1	≤ 0.25				
	Cut > UT	None	≥ 0.30				
	Burn = Cut	≤ 1	≥ 0.90				
	Cut > Burn	None	≤ 0.85				
Bare ground	UT = Burn	≤ 1	≤ 0.70	3 YST = 6 YST	≤ 1	≤ 1	None
	Burn > UT	None	≥ 0.75	3 YST > 6 YST	None	None	≤ 1
	UT = Cut	≤ 1	≤ 0.25				
	UT > Cut	≤ 1	≥ 0.30				
	Burn = Cut	≤ 1	≤ 1				

UT, untreated.
None = no significant differences for that comparison.
Comparisons with ≤ 1 indicate that the comparison was significant for the full range of TDI.

At 6 YST, annual forb cover was < 3% for all treatments but was still higher on burned than untreated plots at high TDI (Table 3). The two-way interactions with treatment and YST and TDI and YST were significant for exotic forb cover (see Table 2). Exotic forb cover was < 1% with the exception that burning increased exotic forb cover to 3.3% and cover was higher on burned than on untreated plots at ≥ 0.75 TDI at 3 YST (see Table 3). However, cover decreased on burn plots to equal that on untreated plots by 6 YST. Exotic forb cover was similar on untreated and cut plots at all TDI and YST (see Table 3).

Cheatgrass Cover

Cheatgrass cover varied by all main factors, but the only significant interaction was treatment by TDI (see Table 2). Untreated plots had minimal cheatgrass cover (< 1%) at 3 and 6 YST. Burning increased cheatgrass cover compared with no treatment at ≥ 0.2 TDI at 3 YST and at all TDI at 6 YST (see Table 3, Fig. 3). Cutting increased cheatgrass cover compared with no treatment at ≥ 0.55 TDI at both 3 and 6 YST. By 6 YST, burned plots had greater cheatgrass cover than cut plots at mid TDI (see Fig. 3). Cheatgrass cover on burned plots varied substantially among sites with Walker Butte and Seven Mile having very low cover (< 2%), Scipio and Greenville having high cover (30 − 36%), and all other sites having intermediate cover (7.5 − 17.7%).

Perennial Forbs

Perennial forb cover varied by YST and the treatment by TDI interaction (see Table 2). Perennial forb cover was limited but decreased to 25% of maximum (1.5%, maximum = 6.2% at 0 TDI) at ≥ 0.75 TDI on untreated plots (Fig. 4). Across all treatments and TDI, perennial forb cover decreased slightly ($P < 0.05$) from 3.8% at 3 YST to 3.3% at 6 YST. Perennial forb cover was similar for burned and untreated plots at both 3 and 6 YST (see Table 3). At 3 YST, cut plots had higher perennial forb cover than untreated plots at ≥ 0.8 TDI, but by 6 YST cover was similar on cut and untreated plots for all TDI (see Table 3). Although perennial forb density estimates were statistically similar for different treatments,

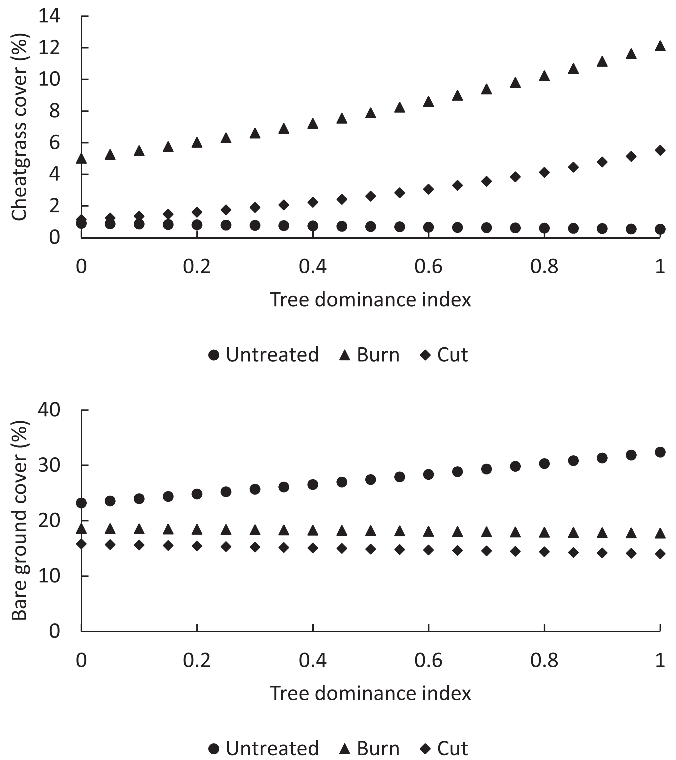

Fig. 3. Cover of cheatgrass (above) and bare ground (below) 6 yr after conifer removal treatment in relation to tree dominance index at the time of treatment.

YST, and TDI (Table 4), TDI by treatment and by YST interactions were significant (see Table 2). Trends are that perennial forb density was higher on untreated plots than on burn and cut plots at low TDI and lower than on burn and cut plots at high TDI (see Fig. 4).

Sandberg Bluegrass

Sandberg bluegrass cover was unaffected by treatment or YST but decreased with increasing TDI (see Tables 2 and 3, Fig. 4). Cover of this species was less sensitive to increasing TDI than other functional groups, decreasing to only 47% of maximum (2.4%, maximum = 5.1%) at a TDI of 1 on untreated plots. Sandberg bluegrass density varied by treatment, YST, and TDI (see Table 2). It had lower density ($P < 0.05$) on the burned (4.5 plants m^{-2}) and cut (4.4 plants m^{-2}) plots than untreated plots (7.8 plants m^{-2}) when averaged across both 3 and 6 YST, and density decreased from 6.6 to 4.4 plants m^{-2} across all treatments from 3 to 6 YST (see Table 3). Sandberg bluegrass density also decreased with increasing TDI on untreated plots but only decreased to 54% of maximum (4.9 plants m^{-2}, maximum = 9 plants m^{-2}) at a TDI of 1.

Tall Grasses

The three-way interaction of treatment, YST, and TDI was significant for tall grass cover (see Table 2). It decreased to 25% of maximum (6.7%, maximum = 26.9%) when TDI ≥ 0.7 on untreated plots (see Fig. 4). Tall grass cover on burned plots was similar to that on untreated plots at 3 YST at all TDI but exceeded that of untreated plots by 6 YST at ≥ 0.7 TDI (see Table 3, Fig. 4). Cut plots had greater tall grass cover than untreated plots at mid and higher TDI both at 3 and 6 YST (see Table 3). Although cut plots had greater tall grass cover than burn plots at 3 and 6 YST, tall grass cover increased on both burn and cut plots from 3 to 6 YST at mid to high TDI (see Table 3). The 3-way interaction of treatment, YST, and TDI was also significant for tall grass density (see Table 2), but interaction estimates did not differ significantly ($P > 0.01$, see Table 4). There was a trend of higher tall grass density on burn and cut than untreated plots at mid to high TDI (see Fig. 4).

Shrubs

Treatments, YST, and TDI all significantly affected total shrub cover (see Table 2). On untreated plots shrub cover was reduced to < 25% of maximum at ≥ 0.5 TDI (5.6%, maximum = 22.5%) (Fig. 5). Shrub cover was reduced by burning but recovered to exceed that of untreated plots at ≤ 0.35 TDI by 6 YST. Total shrub cover increases from 3 to 6 YST on burned plots were modest (3.2% at TDI ≤ 0.35 and 2.2% at ≥ 0.4 TDI). This increase was due to recovery of sprouting shrubs such as green rabbitbrush (*Chrysothamnus viscidiflorus* [Nutt.]).

Total shrub density on untreated plots was reduced to 25% of maximum (0.24 plants m^{-2}, maximum = 0.96 plants m^{-2}) at a TDI ≥ 0.70 (see Fig. 5). While burning reduced shrub density at 3 YST and at ≤ 0.85 TDI, by 6 YST shrub density was similar on untreated and burned plots at ≥ 0.35 TDI, indicating some recruitment on the burned plots (see Table 4, Fig. 5). Shrub density was similar on untreated and cut plots at 3 YST, but by 6 YST shrub density on cut plots was greater than on untreated plots at TDI ≥ 0.55 (see Table 4, Fig. 5).

Big Sagebrush

Big sagebrush cover and density were affected by treatment, YST, and TDI (see Table 2). Big sagebrush cover decreased to 25% of maximum (3.5%, maximum = 13.9%) on untreated plots at TDI ≥ 0.5, while density decreased to 25% of maximum (0.13 plants m^{-2}, maximum = 0.51 plants m^{-2}) at TDI ≥ 0.70 (see Fig. 5). As a nonsprouting species, big sagebrush did not recover as well after burning as sprouting shrubs. Burning decreased sagebrush cover compared with no treatment at low to mid TDI (see Fig. 5). By 6 YST sagebrush cover on burned plots had only increased 0.4% across all TDI. In contrast, cutting maintained sagebrush cover at all TDI and resulted in 2.7% more sagebrush cover at 6 than 3 YST. Burning decreased sagebrush density at all but the highest TDI at 3 YST (see Table 4). However, by 6 YST, untreated and burned plots had similar density at ≥ 0.60 TDI, indicating some recruitment on burned plots (see Fig. 5).

The percentage of subplots with sagebrush seedlings (< 5 cm tall) varied greatly among study sites (Fig. 6). Across both Wyoming and mountain big sagebrush subspecies, treatment was only marginally significant ($P < 0.1$), YST was significant ($P < 0.006$), but the interaction of treatment and YST was not ($P > 0.147$). Across all treatments, the percentage of subplots with seedlings decreased from 30% to 21% from 3 to 6 YST. Across both 3 and 6 YST, untreated plots had 17.9 ± 7.8%, burned plots had 23.9 ± 7.8%, and cut plots had 34.1 ± 7.8% of subplots with seedlings. Seedling density for subplots with seedlings also varied greatly among study sites (see Fig. 6). The Greenville site had more seedlings on burned plots, but most other sites had more seedlings on cut than burned plots. Across all study sites, seedling density was not significant for treatment, but YST was significant ($P< 0.006$), while the interaction of treatment and YST was not significant. Across all treatments, seedling density on subplots with seedlings decreased from 0.99 to 0.25 seedlings m^{-2} from 3 to 6 YST.

Trees

The interaction of treatment and YST was significant for the percentage of subplots with tree seedlings (< 5 cm tall, $P < 0.054$) and saplings (5 − 50 cm tall, $P < 0.001$). For both seedlings and saplings, the percentage of subplots with trees decreased from 3 to 6 YST on untreated plots (13.3 − 4.7% for seedlings; 72.2 − 31.6% for saplings) and increased on burned plots (3.7 − 11.8% for seedlings, 20.1 − 52.6 for saplings) and cut plots (11 − 13% for seedlings, 70.1 − 79.8% for saplings). By 6 YST, burn and cut plots had > 7% more subplots with seedlings and > 21% more subplots with saplings than untreated plots (Fig. 7). Tree seedlings

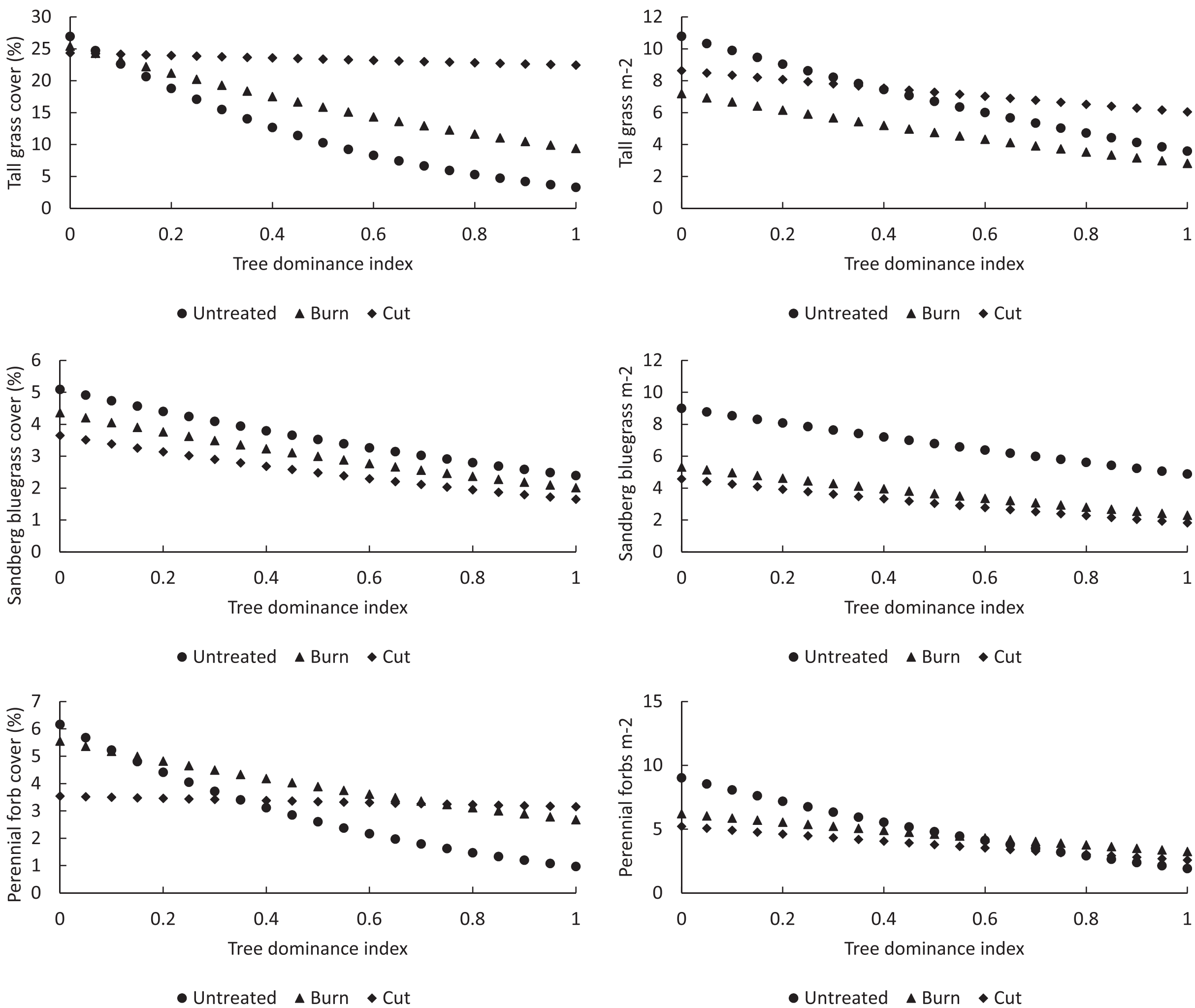

Fig. 4. Cover (left) and density (right) of tall grasses, Sandberg bluegrass, and perennial forbs 6 yr after conifer removal treatment in relation to tree dominance index at the time of treatment.

Table 4
Range of pretreatment tree dominance index (TDI) where significant differences ($P < 0.01$) in tree-removal treatments were found for vegetation density variables 3 and 6 yr after treatment (YST).

Functional group	Comparison	3 YST	6 YST	Comparison	Untreated	Burn	Cut
Perennial forb	UT = Burn	≤ 1	≤ 1	3 YST = 6 YST	≤ 1	≤ 1	≤ 1
	UT = Cut	≤ 1	≤ 1				
	Burn = Cut	≤ 1	≤ 1				
Sandberg bluegrass	UT = Burn	≤ 1	≤ 1	3 YST = 6 YST	≤ 1	≤ 1	≤ 1
	UT = Cut	≤ 1	≤ 1				
	Burn = Cut	≤ 1	≤ 1				
Tall grass	UT = Burn	≤ 1	≤ 1	3 YST = 6 YST	≤ 1	≤ 1	≤ 1
	UT = Cut	≤ 1	≤ 1				
	Burn = Cut	≤ 1	≤ 1				
Sagebrush	UT = Burn	≥ 0.85	≥ 0.60	3 YST = 6 YST	≤ 1	≤ 1	≤ 1
	Burn < UT	≤ 0.80	≤ 0.55				
	UT = Cut	≤ 1	≤ 1				
	Burn = Cut	≥ 0.85	≥ 0.75				
	Burn < Cut	≤ 0.80	≤ 0.70	3 YST = 6 YST	≤ 1	≤ 1	≤ 1
Shrub	UT = Burn	≥ 0.90	≥ 0.35	3 YST = 6 YST	≤ 1	≤ 0.20	≤ 0.85
	Burn < UT	≤ 0.85	≤ 0.30	6 YST > 3 YST	None	≥ 0.25	≥ 0.90
	UT = Cut	≤ 1	≤ 0.50				
	Cut > UT	None	≥ 0.55				
	Burn = Cut	≥ 0.90	≥ 0.90				
	Burn < Cut	≤ 0.85	≤ 0.85				

UT, untreated.
None = no significant differences for that comparison.
Comparisons with ≤ 1 indicate that the comparison was significant for the full range of TDI.

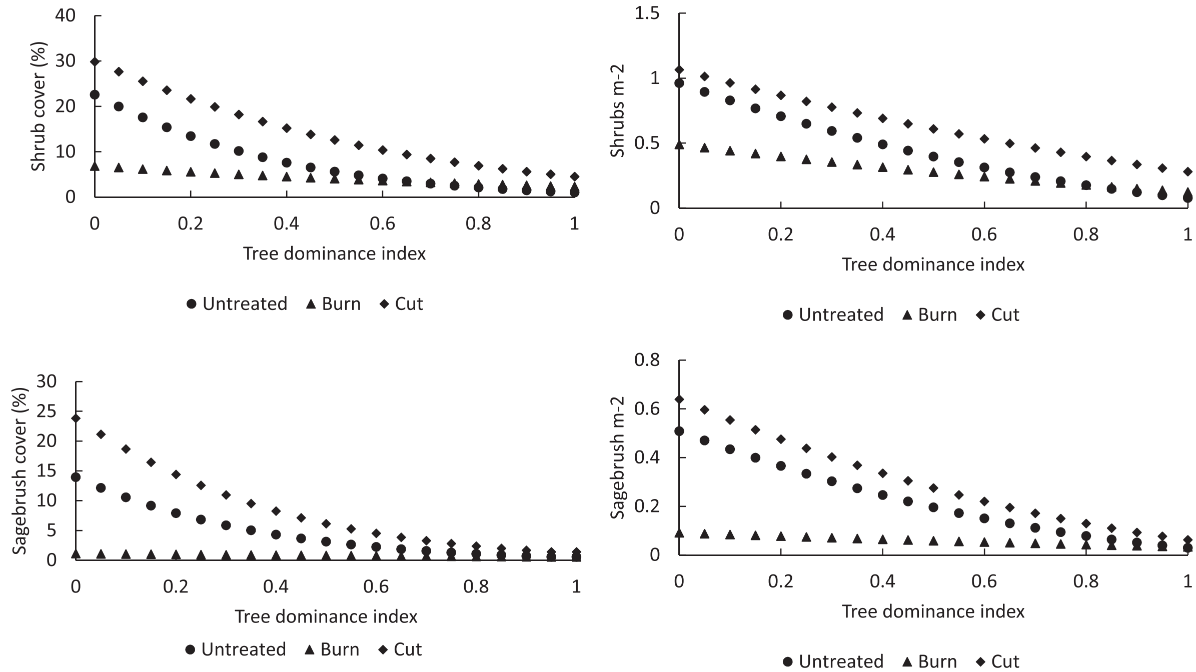

Fig. 5. Cover (left) and density (right) of all shrubs and big sagebrush 6 yr after conifer removal treatment in relation to tree dominance index at the time of treatment.

were encountered on all but the South Ruby and Scipio study sites while saplings were found on all but the South Ruby site. There was a much higher percentage of subplots with saplings than seedlings, and sapling density was much higher than seedling density on subplots with trees for all treatments (see Fig. 7). By 6 YST, seedling and sapling density on subplots with trees was similar among treatments (see Fig. 7).

Bare Ground Cover

Bare ground was similar for untreated, burned, and cut plots at 3 YST (see Table 3). By 6 YST, both burned and cut plots had less bare ground than untreated plots at > 0.75 and 0.3 TDI (see Fig. 3).

Cover Comparison with Potential Restoration Target

For untreated plots in good ecological condition, cover estimates at 0 TDI should be a reasonable estimate of what could be expected with minimal tree influence. Proximity to the potential restoration target can be estimated by calculating the difference between functional group cover for each treatment and pretreatment TDI and that of the restoration target (Fig. 8). For untreated plots, deviations from the target became more negative for shrubs and tall grasses with increasing TDI. Cover of perennial groups and species on both burn and cut treatments moved closer to the target at 6 YST than at 3 YST. By 6 YST, the burn treatment still lacked tall grass and especially shrub cover compared with the target and had higher cheatgrass cover. Deviations of the burn treatment from the target were greatest from mid to high TDI.

By 6 YST, the cut treatment had cover most similar to that of the target for the perennial functional groups (see Fig. 8). Cut plots had tall grass and shrub cover that was more similar to the target than untreated and burned plots and had less cheatgrass cover than the burn treatment. Differences between the target and the cut treatment were greatest at high TDI. The target community cover estimates (untreated plots at TDI = 0, 6 YST) consisted of 35% for perennial grass, 22% for shrubs, and 6% for perennial forbs. These cover estimates equate to relative perennial cover of 55% for grasses, 35% for shrubs, and 10% for forbs. Increasing tree cover on untreated plots resulted in diminished shrub and perennial grass cover and a tree-dominated community. At mid to high TDI, the burn treatment resulted in a perennial herbaceous-dominated plant community, with cheatgrass cover increasing with increasing pretreatment TDI. By 6 YST, shrub cover on the burn treatment was recovering but still well below the target. In contrast, shrub cover was maintained on the cut treatment, except at mid to higher TDI. Cutting at low to mid TDI resulted in the greatest proximity to the restoration target. For the cut treatment at 0.05 − 0.4 TDI at 6 YST, cover estimates were 29.7% for perennial grasses, 21.9% for shrubs, and 3.4% for perennial forbs. These equate to relative perennial cover of 54% for grasses, 40% for shrubs, and 6% for perennial forbs. Compared with the relative perennial cover of the target community, the cut treatment was similar in relative cover for perennial grasses but higher in shrub cover and lower in forb cover. However, if cutting is done at > 0.4 TDI, by 6 YST perennial cover was 26.4% for grasses, 8.2% for shrubs, and 3.2% for forbs, equating to relative perennial cover of 70% for grasses, 22% for shrubs, and 8% for forbs.

Discussion

No Treatment

Increasing pretreatment tree dominance on untreated plots had no effect on annual forbs, exotic forbs, or cheatgrass cover but decreased cover and density of all perennial functional groups that were analyzed. Of the perennial functional groups, shrub cover in general and big sagebrush cover in particular were most sensitive to increasing tree dominance (< 25% maximum cover at ≥ 0.5 TDI). Tall grass and perennial forb cover was more sensitive than Sandberg bluegrass cover to increasing tree dominance. Perhaps trees are less competitive with Sandberg blue grass because of its early maturation. Miller et al. (2005) have related relative tree dominance to phase categories to help categorize management options. At Phase I, perennial shrubs and herbs dominate with scattered trees. At Phase II, trees and perennial shrubs and herbs share dominance, while at Phase III, trees dominate. TDI values for Phase I, II, and III could be equated to 0 − 0.34, > 0.34 − 0.67, and > 0.67. Across all pretreatment subplots for our 10 sites, perennial understory cover variation decreased while tree cover variation increased with increasing TDI (Roundy et al., 2014a). Therefore, there may be a wide range of tree cover and understory perennial cover for a given range of TDI across sites. Despite the variability, perennial understory loss with increasing

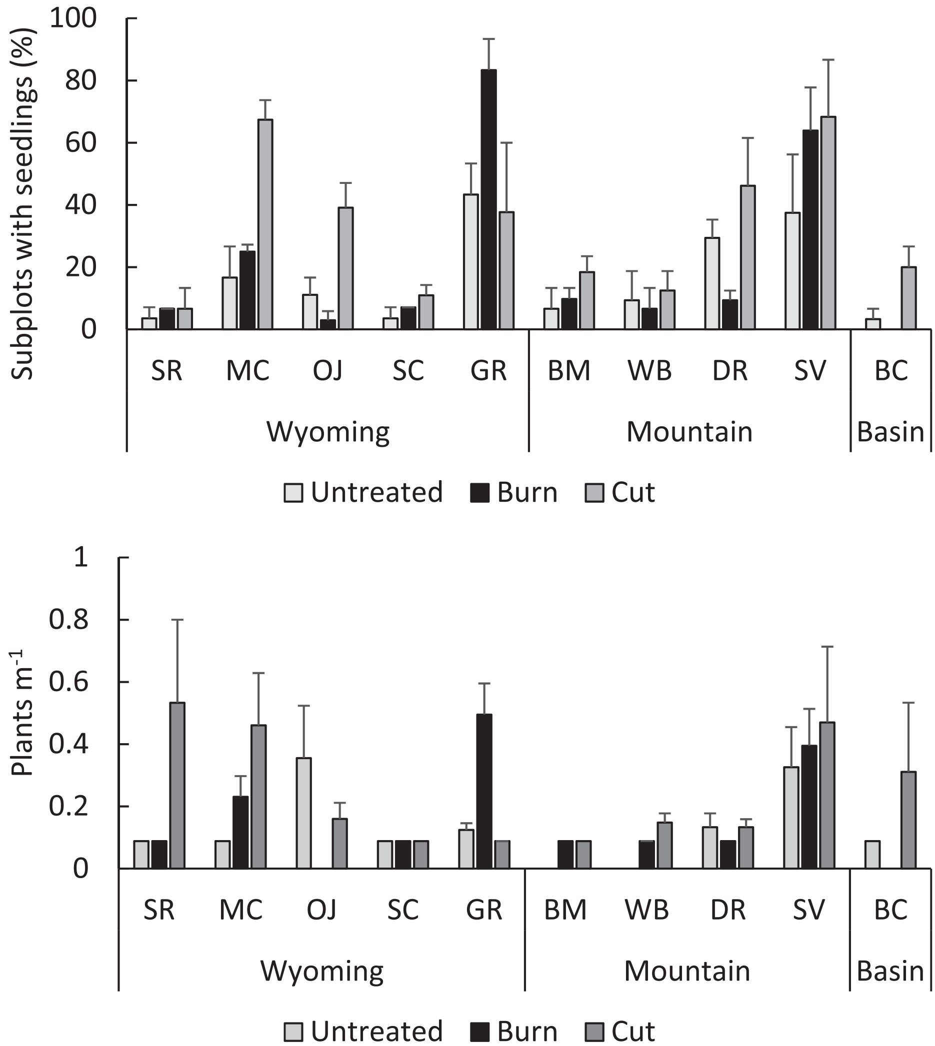

Fig. 6. Percentage of subplots with sagebrush seedlings (above) and density of sagebrush seedlings 3 and 6 yr (YST) since tree reduction treatments (below) for Wyoming and mountain big sagebrush sites (abbreviations in Table 1). Bars are 1 SE.

tree dominance is robust enough to conclude that tree reduction should be implemented at Phase I and early Phase II to avoid significant loss of shrub and sagebrush cover. In addition, tree reduction should be implemented at Phase II to early Phase III to avoid significant loss of perennial herbaceous cover. The tree effects we found parallel those found in earlier studies (Tausch and West, 1995; Miller et al., 2000; Bybee et al., 2016). Continued tree expansion and infilling will not only move the community farther away from the restoration target (see Fig. 8) but also result in high canopy fuel loads (Young et al., 2015). High-intensity fire in Phase II and III communities could lead to the crossing of a biotic threshold into annual weed dominance and subsequent high-frequency fire (Young et al., 2015), especially on warmer and drier sites (Chambers et al., 2014b). Increasing tree dominance to a Phase III woodland can also lead to greater intercanopy erosion and the crossing of an abiotic threshold on some sites (Petersen and Stringham, 2008; Williams et al., 2014; Roundy et al., 2016).

Prescribed Fire

Functional groups all responded somewhat differently to prescribed fire over time, and these responses were affected by pretreatment tree dominance. Shrub cover and density were initially reduced by prescribed fire but had recovered to equal or exceeded that on untreated plots at low – mid TDI by 6 YST. Shrub recovery was mainly for sprouting shrubs such as green rabbitbrush and Saskatoon serviceberry (*Amelanchier alnifolia* [Nutt.] Nutt ex M. Roem) as observed by (Chambers et al., 2014b) 4 yr after treatment. In contrast, big sagebrush had limited recovery even at 6 YST. Recovery of sagebrush canopies can take 15 to > 50 yr following fire depending on seed source and site conditions (Miller et al., 2014b).

Three yr after treatment, Miller et al. (2014b) noted higher sagebrush seedling densities for this study on both burn and cut treatments than untreated plots and also higher densities for mountain big sagebrush sites with frigid soils than Wyoming or basin big sagebrush sites with mesic soils. In a separate study, Chambers et al. (2017) found similar results on burned plots. In our study, the percentage of subplots with sagebrush seedlings varied by study site but was generally greater on cut than burned plots (see Fig. 6). Seedling density on subplots with seedlings followed the same trend and decreased from 3 to 6 YST. Across all of our study sites, untreated big sagebrush density at 0 TDI was 0.51 plants m^{-2} at 6 YST. This density is similar to that for mature Wyoming big sagebrush and half of the density for mountain big sagebrush reported by Davies and Bates (2010) in southeast Oregon. Ziegenhagen and Miller (2009) estimated that one-fourth to one-third of preburn sagebrush density was needed the first few years after wildfire for mountain big sagebrush to recover in southeastern Oregon and northwestern Nevada. In our study, density of seedlings exceeded this potential recovery threshold on only two Wyoming big sagebrush

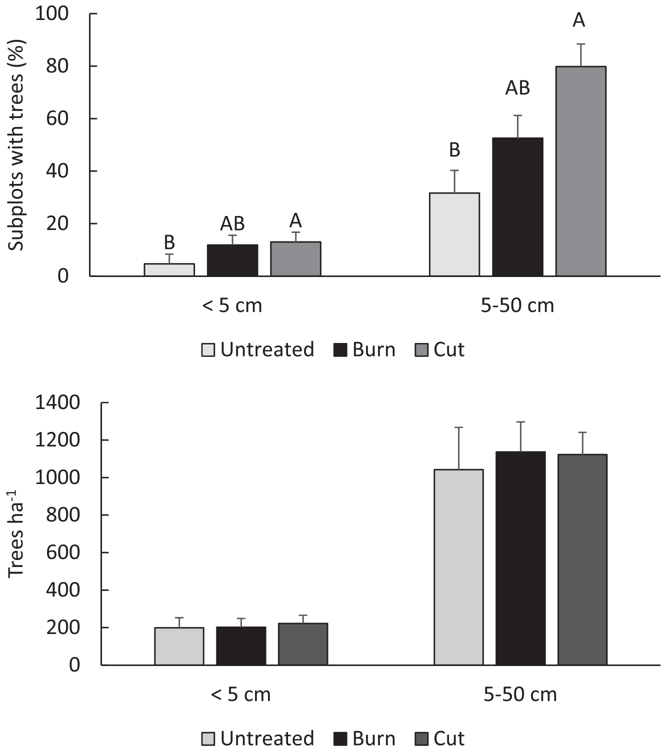

Fig. 7. Percentage of subplots with trees < 5 and 5-50 cm tall (above) and density of trees (below) 6 yr after treatment. Bars are 1 SE, and similar letters above bars indicate no significant difference ($P > 0.05$) in treatments.

sites and on one mountain big sagebrush site at 6 YST. Seed source, availability, and viability; weather conditions; soil water availability; and competing species all influence sagebrush establishment (Young and Evans, 1989; Meyer and Monsen, 1992; Boltz, 1994; Perryman et al., 2001; Ziegenhagen and Miller, 2009; Boyd and Obradovich, 2014; Miller et al., 2014b; Brabec et al., 2015). Increased perennial grass cover on treated plots (see Fig. 4), as well as lower precipitation for most years since treatment (see Fig. 2) may have contributed to decreases in seedling density (Davies et al., 2013; Chambers et al., 2017). Seedling establishment and recovery of big sagebrush after fire is clearly undependable.

Prescribed fire affected herbaceous functional groups in various ways. It initially increased annual and exotic forb cover and decreased tall grass cover (Miller et al., 2014b). This increase in annual and exotic forb cover was still evident at 3 YST, especially at high TDI (see Table 3). By 6 YST cover for the two annual functional groups was low (< 3%, Fig. 3). Tall grass cover continued to follow a recovery pathway over time by equaling at 3 YST, then exceeding at 6 YST that on untreated plots, especially at high TDI. The period of increased annual herbaceous cover after fire may be longer or shorter, depending on perennial herbaceous cover and aspect (Barney and Frischknect, 1974; Koniak, 1985). Miller et al. (2014b) have noted that, for tree expansion areas in the Great Basin region, tall grasses typically recover 2 − 3 yr after fire. However, fire intensity, season of burning, species composition, and many other factors affect tall grass response to fire (Miller et al., 2013). Bates et al. (2011) found that perennial grass seedlings were establishing sufficiently in later successional western juniper (*Juniperus occidentalis* Hook.) woodlands 3 yr after a cut-then-burn treatment to achieve full recovery. However, Chambers et al. (2017) found that reductions of perennial grasses, which is caused by not only pinyon and juniper expansion but also inappropriate livestock grazing, resulted in highly significant decreases (40 − 62%) in perennial native grass and forb cover on burned and control plots in both Wyoming big sagebrush and mountain big sagebrush sites over a decade after treatment. In that study, lack of perennial grass recovery was associated with big sagebrush competition.

In contrast to annual and exotic forbs, cheatgrass cover on burned plots increased from 3 to 6 YST across all but the highest TDI, where high variability among sites may have resulted in lack of statistical significance (see Fig. 3, Table 3). Short-term increases in annual forb and cheatgrass cover and decreases in perennial grass cover the first few years after burning pinyon and juniper are typical (Miller et al., 2014b; Bates et al., 2017), as is high variability in cheatgrass response among sites (Bates et al., 2013; Chambers et al., 2014b; Roundy et al., 2014a). Because perennial grasses compete for the same soil water and nutrients in time and space (Ryel et al., 2010; Leffler and Ryel, 2012; Roundy et al., 2014b), they are especially important in maintaining cheatgrass resistance (Chambers et al., 2007, 2014a, 2014b, 2017). Across all sites, cheatgrass to tall grass cover ratios on burned plots were < 1 at TDI ≤ 0.8 at 6 YST, indicating that tall grasses should continue to reduce cheatgrass cover on most of our sites. Although cheatgrass cover increased on burn plots from 3 to 6 YST, so did tall grass cover so that cheatgrass to tall grass cover ratios were similar at 3 and 6 YST. Typically, cheatgrass cover decreases as perennial grass cover increases with time since fire (Barney and Frischknect, 1974; Miller et al., 2014b). Also, cheatgrass is consistently lower on mountain big sagebrush sites with cool frigid soils than on Wyoming or basin big sagebrush sites with mesic soils (Chambers et al., 2014b, 2017).

Both perennial forb and Sandberg bluegrass cover and density were less sensitive to increasing TDI than shrubs and perennial grasses in our study. Perhaps that is one reason that they did not respond nearly as well to tree reduction by fire as did tall grasses. The increase in tall grass cover after fire may have suppressed short grasses, perennial forbs, and sagebrush recruitment, especially at high TDI. From numerous studies, Bates et al. (2017) noted that while annual forbs increased most after fire, perennial forb response to tree reduction was similar for mechanical and burn treatments and highly dependent on site potential.

Although prescribed fire has the liability of slow recovery of shrubs and especially sagebrush, it has the advantage of reducing woody fuel loads and eliminating most of the trees much better than mechanical methods (Young et al., 2013a, 2013b). Effectiveness of fire in reducing fuels varies with season of ignition, with cool-season burns only consuming smaller fuel size classes (Bates et al., 2014). Fire may increase cheatgrass on some warmer sites with lower resistance, but on wetter and cooler sites with high perennial grass cover and where sagebrush cover is not a priority, it will enhance the perennial herbaceous community and reduce the risk of high-intensity fire (Chambers et al., 2014b; Young et al., 2014).

Mechanical Treatment

A major advantage of mechanical tree reduction by cutting or mastication over prescribed fire is that it maintains shrub cover. Shrubs are an important component of sagebrush steppe ecosystems and contribute to wildlife habitat, as well as biodiversity (Huber et al., 1999; Miller et al., 2005). The negative effects of tree expansion are of major concern for sagebrush obligate wildlife species (Miller et al., 2017). Cutting increased total shrub cover compared with untreated plots at ≥ 0.3 TDI (4.3% untreated, 10.1% cut). Some of this difference was due to greater shrub cover on the cut than untreated plots before treatment (at ≥ 0.3 TDI, estimated shrub cover was 6.3% for untreated and 7% for cut plots pretreatment). Sagebrush cover and density, however, were not increased by cutting. Therefore, cutting should not be expected to result in rapid recovery of sagebrush when initiated at mid to high tree dominance.

Cutting favored tall grasses compared with shrubs when implemented at higher tree dominance in our study. Cutting increased tall grass cover while fire reduced it the first few years after treatment (Miller et al., 2014b). Tall grass density did not differ significantly ($P > 0.01$) on cut plots from 3 to 6 YST, but the trend was positive, especially at ≥ 0.60 TDI. Miller et al. (2014b) did not find any increase in tall grass

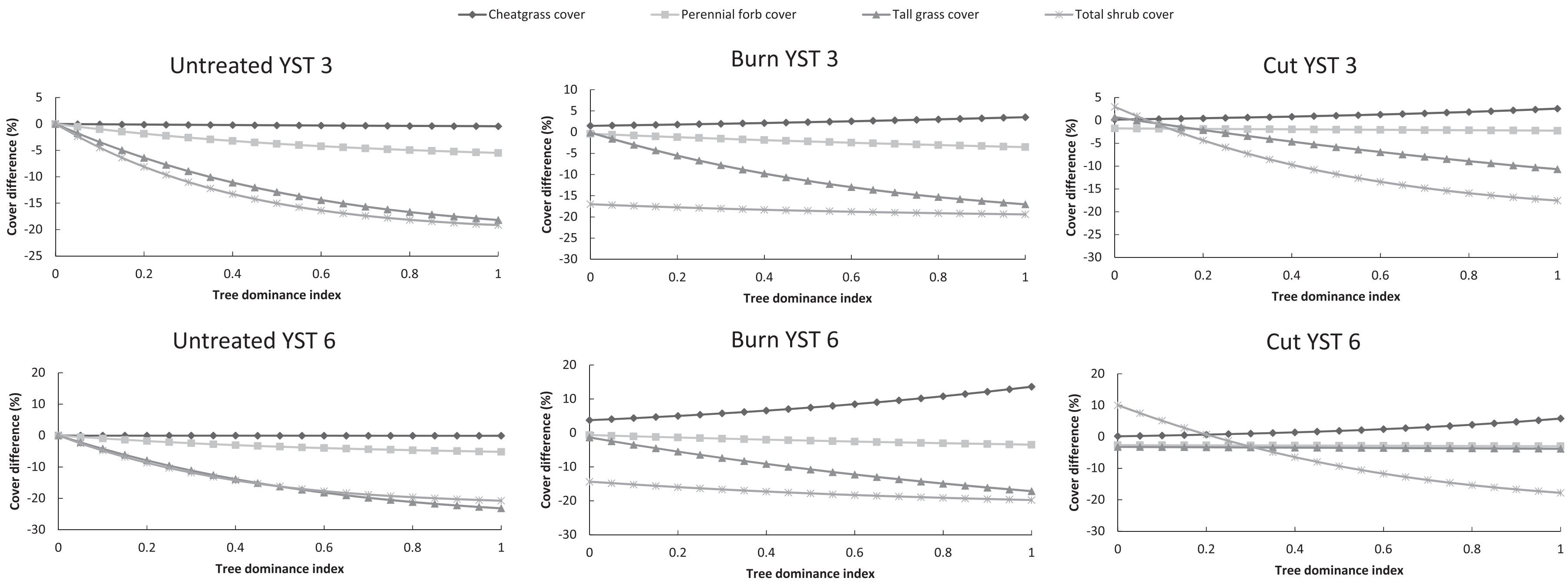

Fig. 8. Differences between 3 and 6 yr post treatment functional group cover (%) and untreated functional group cover at tree dominance index (TDI) = 0 for different conifer removal treatments. Differences indicate how far mean functional group cover is from the unencroached plant community or idealized restoration target.

density on cut plots in our study from 0 to 3 YST. Others have reported initial increases in perennial grass cover were a result of increased plant size and not density (Everett and Sharrow, 1985; Bates et al., 2000). Increased tall grass cover on plots cut at high tree dominance may also result from lack of shrub cover and therefore greater soil water availability for grasses (Roundy et al., 2014b).

Cutting resulted in less cheatgrass cover than did prescribed fire in our study, probably due to low severity of disturbance and increased tall grass cover, especially at high TDI. Perennial herbaceous vegetation, particularly tall grass, is 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). At ≥ 0.5 TDI and 6 YST, cheatgrass to tall grass cover ratios ranged from 0.5 to 1.3 on burned plots and 0.1 to 0.2 on cut plots in our study.

Tree debris after cutting can provide favorable sites for annual grass establishment (Bates et al., 2007). Mechanical treatments also increase resource availability and support seedling establishment (Bates et al., 2000, 2002; Young et al., 2013a, 2013b, 2014; Roundy et al., 2014a, 2014b; Stephens et al., 2016). Both treatments are associated with higher cheatgrass cover on warmer and drier sites and where competition from perennial grasses is lower (Chambers et al., 2007, 2014b, 2017).

A major disadvantage of cutting trees is that all size classes of canopy fuels are placed on the ground (Young et al., 2014). This could result in subsequent high-severity wildfire and high herbaceous plant mortality. In contrast to cutting, mastication reduces large canopy fuels to small-size classes (Shakespear, 2014; Young et al., 2014). This may not reduce total fuels, but it facilitates fire suppression by bringing fire out of the canopy and down to the ground. Since effects of cutting and mastication on understory vegetation are generally similar (Bybee et al., 2016), mastication might be a better option than cutting when fire suppression is a priority.

Another disadvantage of both cutting and mastication is that residue trees and tree seedlings will require some kind of retreatment over time. Animal or bird dispersal of pinyon and juniper seeds, as well as residual shrubs serving as nurse plants, facilitate establishment of tree seedlings after tree reduction (Chambers et al., 1999; Redmond and Barger, 2013). Bates et al. (2005) found that 13 yr after cut treatments, about two-thirds of western juniper trees had reestablished from seed while one-third were from small individuals missed in the initial treatment. Studies have estimated that mechanically treated western juniper sites will return to tree dominance within 50 yr (Bates et al., 2005; O'Connor et al., 2013). Boyd et al. (2017) estimated that prescribed fire had twice the duration time (100 yr) as tree-cutting treatments for reducing conifers. Because of the need to reduce almost all trees for predator avoidance and to maintain sagebrush for sage-grouse *(Centrocercus urophasianus)*, they recommended a combination of treatments. Bristow et al. (2014) found that juniper preceded pinyon in naturally reforesting chained areas in Nevada. Clearly, retreatment will be necessary to maintain advantages of mechanical treatments. Lopping of small trees after mechanical treatments could greatly increase project life and should be inexpensive compared with large-tree treatments (Provencher and Thompson, 2014). Mechanical treatments may also support more ground cover and better watershed protection than prescribed fire, especially during the first few years after treatment (Cline et al., 2010; Pierson et al., 2015).

Restoration Trajectories and Targets

Six yr after treatment, deviations from the potential restoration target were much less for the cut treatment than for no treatment or prescribed fire (see Fig. 6). Both tree dominance and fire reduce shrubs, especially sagebrush, and fail to support a mixed shrub-grass community in comparison with tree cutting. However, to best retain the shrub and perennial grass components, trees should be cut at early to mid TDI (Phases I and II). A major advantage of prescribed fire over no treatment is that it greatly reduces woody fuel loads (Young et al., 2014). Prescribed fire and mechanical methods both increase herbaceous fuel loads (Young et al., 2014; Shakespear, 2014). After applying prescribed fire initially or as a follow-up to mechanical treatments, wildfire suppression should be easier and wildfire intensity much less than in untreated woodlands, especially those with high tree dominance.

Understory succession after fire (Barney and Frischknect, 1974) and after cutting (Bates et al., 2000) followed a pattern of multiple entry points where species and abundance at the time of treatment had a major effect on relative dominance after treatment. Our shrub and especially sagebrush data fit this pattern with slow recovery at high pretreatment tree dominance. On the other hand, we have been surprised at the strong recovery of tall grasses, even at high pretreatment tree dominance. Perennial grass recovery after tree reduction at high tree dominance can be highly variable (Bates et al., 2011, 2013, 2014). Bates et al. (2005) noted changing dominance of Sandberg blue grass, other perennial grasses, and cheatgrass over time after cutting western juniper, and after 13 years, eventual perennial grass dominance. They considered that dominance by annual grass reported in other studies (Evans and Young, 1985; Young et al., 1985) was due to lack of perennial grass density when trees were cut. In a follow-up to that same study, Bates et al. (2017) reported declines in perennial grass density and yield, as well as increases in annual grass yield 25 yr after tree cutting. They attributed these changes to increases in shrub and tree cover and density and considered that the treatment had an effective life span of 25 − 30 yr. Redmond et al. (2013) reported that 20 − 40 yr after chaining pinyon-juniper trees and seeding on the Colorado Plateau, both sagebrush and the seeded crested wheatgrass (*Agropyron cristatum* L. [Gaertn.]) had high cover. Differences in long-term outcomes underscore the need for monitoring.

Of major concern is post-treatment cheatgrass dominance, which varied widely in our study with site and tree dominance at time of treatment but was highest on burned plots. Across our study sites, tall grasses had higher cover than cheatgrass, especially on cut plots. Our study indicates that high resistance (as indicated by lower cheatgrass cover) and high resilience (as indicated by higher perennial grass and shrub cover) are better supported by tree cutting than prescribed fire. This conclusion assumes that tree cutting and other mechanical treatments will be followed by enhanced fire suppression and by small tree and, where necessary, additional fuel-control treatments. Our sites had either very limited cheatgrass cover both before and 6 YST or they had intermediate or high cheatgrass cover 6 YST. While we expect that most of our sites will continue on a restoration pathway toward mixed shrub-perennial grass or at least perennial grass dominance, monitoring should be continued and vegetation outcomes for different sites should be related to both biotic and abiotic variables.

Management Implications

To retain the shrub component on sagebrush sites and increase ecosystem resilience and resistance, we recommend tree cutting or other mechanical tree reduction at Phase I to early Phase II expansion (low to mid TDI). Tree reduction at Phase II to early Phase III expansion (mid TDI) results in mainly annual or perennial herbaceous cover and a lack of sagebrush. Prescribed fire best controls trees and woody fuels and can be effective for increasing perennial herbaceous cover on cooler and wetter sites where risk of cheatgrass is minimal. Prescribed fire should be avoided where sagebrush is considered an important component and on warmer sites where cheatgrass risk is high. If treatments are delayed to Phase III expansion (high TDI), tree reduction may result in an annual or perennial grassland instead of a grass-shrub mix and may therefore require revegetation. Grass, forb, and shrub revegetation on these areas has been successful after tree reduction (Redmond et al., 2013; Bybee et al., 2016; Davies et al., 2014; Davies and Bates, 2017; Havrilla et al., 2017). Weedy sites are still candidates for tree reduction if accompanied by herbaceous weed control and revegetation. Not treating these sites could result in annual weed dominance after wildfire. Although cut treatments resulted in greater resilience through increases in tall grass and shrub cover, as well as greater resistance to cheatgrass, these treatments require additional follow-up to remove missed and new saplings.

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