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Understory Cover Responses to Piñon–Juniper Treatments Across Tree Dominance Gradients in the Great Basin

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Abstract

Piñon (*Pinus* spp.) and juniper (*Juniperus* spp.) trees are reduced to restore native vegetation and avoid severe fires where they have expanded into sagebrush (*Artemisia tridentata* Nutt.) communities. However, what phase of tree infilling should treatments target to retain desirable understory cover and avoid weed dominance? Prescribed fire and tree felling were applied to 8–20-ha treatment plots at 11 sites across the Great Basin with a tree-shredding treatment also applied to four Utah sites. Treatments were applied across a tree infilling gradient as quantified by a covariate tree dominance index (TDI=tree cover/[tree+shrub+tall perennial grass cover]). Mixed model analysis of covariance indicated that treatment×covariate interactions were significant ($P < 0.05$) for most vegetation functional groups 3 yr after treatment. Shrub cover was most reduced with fire at any TDI or by mechanical treatment after infilling resulted in over 50% shrub cover loss (TDI > 0.4). Fire increased cheatgrass (*Bromus tectorum* L.) cover by an average of 4.2% for all values of TDI. Cutting or shredding trees generally produced similar responses and increased total perennial herbaceous and cheatgrass cover by an average of 10.2% and 3.8%, at TDIs ≥ 0.35 and ≥ 0.45. Cheatgrass cover estimated across the region was < 6% after treatment, but two warmer sites had high cheatgrass cover before (19.2% and 27.2%) and after tree reduction (26.6% and 50.4%). Fuel control treatments are viable management options for increasing understory cover across a range of sites and tree cover gradients, but should be accompanied by revegetation on warmer sites with depleted understories where cheatgrass is highly adapted. Shrub and perennial herbaceous cover can be maintained by mechanically treating at lower TDI. Perennial herbaceous cover is key for avoiding biotic and abiotic thresholds in this system through resisting weed dominance and erosion.

Key Words: brush control, mastication, mechanical treatments, prescribed fire, resilience, state and transition, thresholds

INTRODUCTION

Resilience theory and state-and-transition models have been very useful in organizing approaches to vegetation management and helping us understand the most obvious consequences of planned and natural disturbances (Briske et al. 2006). However, managing for resilience requires an understanding of potential thresholds, triggers, feedback mechanisms, and effects of management actions on successional phases and states. Thus, the application of these models has lagged due to a need to better understand how their concepts apply in specific systems and across landscapes (Bestelmeyer et al. 2009). Although the crossing of certain biotic and abiotic thresholds is recognizable, it is not necessarily easy to recognize when management might be implemented to avoid crossing such thresholds or to improve an at-risk phase.

Expansion and infilling of piñon (*Pinus* spp.) and juniper (*Juniperus* spp.) trees in former sagebrush (*Artemisia* spp. L) steppe increases woody fuels and can reduce cover, density, and seed availability of desirable understory species (Miller and Tausch 2001; Miller et al. 2005). These changes in plant composition can shift communities to at-risk phases, which increase the probability of crossing a biotic threshold when catastrophic fire is followed by invasive weed dominance and recurrent fire (Miller and Tausch 2001; Bates et al. 2013). Likewise, infilling may increase risk of runoff and erosion on erodible sites as diminished understory cover leads to increased connection among bare ground patches and a potential threshold crossing that results in high rates of erosion (Pierson et al. 2010, 2013; Urgeghe et al. 2010; Williams et al. 2013). Although it is usually clear when these thresholds have been crossed on a site, it is not clear at what phase of tree dominance vegetation treatments could have been implemented to avoid crossing these thresholds.

There are well-documented patterns of herbaceous understory loss with increasing woody plant cover (Archer et al. 2011). These patterns depend on how both understory and overstory species modify environmental conditions and use

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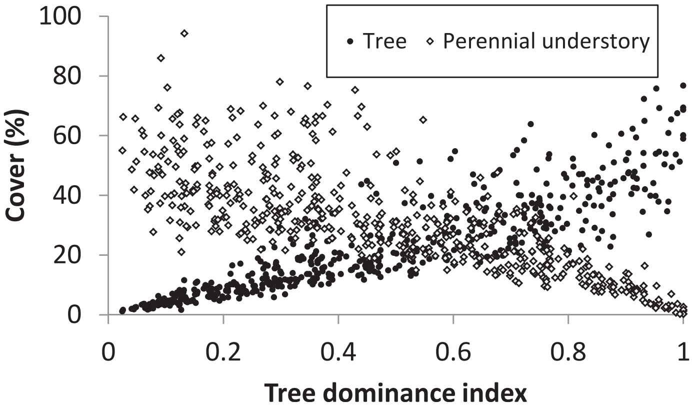

Figure 1. Initial tree and perennial understory cover in relation to tree dominance index (tree cover/[tree+shrub+tall perennial grass cover]) for 11 sagebrush steppe sites encroached by piñon or juniper trees across the Great Basin.

resources in time and space within the environmental context of the site (Archer et al. 2011). For example, as piñon and juniper tree cover and density increase, the decline of shrub and perennial herbaceous cover and biomass may be exacerbated on soils with shallow rooting depth or site aridity (Miller et al. 2000, 2005). Mountain big sagebrush (*Artemisia tridentata* Nutt. subsp. *vaseyana* [Rydb.] Beetle) declines to < 25% of maximum potential as trees increase to 50% of their maximum potential cover (Tausch and West 1995; Miller et al. 2005). Successional theory applied to restoration ecology considers that potential for a restoration pathway is highly dependent on the kind, extent, and dominance of residual species and integrity of ecosystem properties after disturbance (Everett and Sharrow 1985; Briske et al. 2006).

The critical question is how much cover and density of desirable residual plants are needed for community recovery and prevention of weed dominance following tree reduction? Weed dominance is facilitated by an increase in available resources (Davis et al. 2000). Weed dominance in sagebrush communities is resisted by dominance of perennial grasses (Chambers et al. 2007; Blank and Morgan 2012; Reisner et al. 2013), which use soil water and nutrient resources that cheatgrass depends on for growth and seed production (Ryel et al. 2008, 2010). Juniper trees are also major water users (Ryel et al. 2010) and their expansion increases the extent of undercanopy patches of fertility as they accumulate and drop high C : N biomass (Rau et al. 2011). Trees, shrubs, and perennial and annual herbaceous life-forms in sagebrush communities have different rooting depths and access different matric potential ranges of available water. However, critical spring growth depends on a relatively shallow (0–0.3-m) soil depth where roots and nutrients are most concentrated and where N diffusion to roots occurs at soil matric potentials > –1.5 MPa (Ryel et al. 2008, 2010; Leffler and Ryel 2012). Reduction of any major water user in these communities will free up resources for use and expansion by another growth form (Leffler and Ryel 2012). The reduction of woody vegetation generally increases time of available soil water and available N (Bates et al. 2000, 2002; Archer et al. 2011; Young 2012; Young et al. 2013b; Roundy et al. 2014). The extent and kind of residual plants left to use resources freed up by tree reduction or other disturbances should be a major determinant of successional trajectories (Bates et al. 2013).

Disturbances in expansion woodlands include broadcast-type natural disturbances such as wildfire and insect outbreaks, or management actions including prescribed fire, chaining, or more selective treatments such as tree reduction by cutting or shredding (Tausch et al. 2009; Evers et al. 2013). Decreases in cover of nonsprouting shrubs and herbaceous vegetation following fire depend on fire intensity and species sensitivity (Pyke et al. 2010; Miller et al. 2013). Typical response to prescribed fire in expansion woodlands is greatly decreased sagebrush cover, initial reduction but eventual recovery of perennial grasses, and a wide range of perennial forb and invasive grass responses depending on residual plants, propagule pressure, and adaptability to the abiotic environment (Bates et al. 2013; Miller et al. 2013, 2014). A few years after prescribed fire or mechanical tree reduction, perennial tall grasses generally return to pretreatment cover or increase unless they had limited initial cover (Bates et al. 2013; Miller et al. 2014). However, there are very few direct side-by-side comparisons evaluating vegetation response between these two treatments in the Great Basin (Miller et al. 2014).

Recognizing the importance of understory residuals to management outcomes, Miller et al. (2005) have categorized tree encroachment into three phases based on relative cover of trees, shrubs, and perennial herbs. However, tree canopy increases and understory cover losses form a continuum (Fig. 1). Management for resilience in conifer-encroached shrublands should be based on understanding where abiotic and biotic thresholds may occur as tree cover increases and understory cover decreases with infilling (Bates et al. 2013). Therefore plant response variables such as cover and biomass must be measured in response to the continuum of tree dominance or cover at the time treatments are implemented. A useful tree dominance index (TDI) would include major resource users in the community, e.g., TDI=tree cover/(tree+shrub+ tall perennial grass cover). This index features the principal competitors for resources (Ryel et al. 2008, 2010) and excludes short grasses such as Sandberg bluegrass (*Poa secunda* J. Presl.) and perennial forbs, which tend to grow early in spring and avoid late-spring effects of limited soil water depleted by the larger growth forms.

A limitation of most studies conducted in the Great Basin is that results and inferences may be specific to the sites studied in a region that has a wide range of abiotic conditions. To best recommend management of tree-encroached shrublands, we need to determine whether there are regional responses to treatments. It is critical to address how vegetation responds to treatments across a tree dominance gradient as we attempt to identify potential thresholds (Bates et al. 2013). Two possible interrelated responses could signal a threshold of tree dominance above which vegetation does not respond favorably to tree control: 1) failure of perennial herbaceous vegetation to increase and 2) dominance of invasive weeds such as cheatgrass. Ultimately, we consider that the community is at risk of crossing a biotic threshold with increased potential for recurrent fire when invasive weed cover exceeds that of desirable perennial species as indicated by continued weed dominance rather than increased desirable perennial dominance over time (Bates et al. 2013). This determination is not possible in a short-term study, but trajectories may still be identified. In this study, we measured the effects of piñon and juniper tree infilling on vegetation response to management treatments designed to reduce or redistribute woody fuels on sites located across a large geographic area. Our objective was to identify ranges of pretreatment tree dominance where vegetation treatments significantly affected understory vegetation response.

METHODS

Study Area

Study sites included four western juniper (*Juniperus occidentalis* Hook.) sites in California and Oregon, three singleleaf piñon (*Pinus monophylla* Torr.& Frém.)–Utah juniper (*Juniperus osteosperma* [Torr.] Little) sites in central Nevada, and two Utah juniper and two Utah juniper–Colorado piñon (*Pinus edulis* Engelm.) sites in Utah (McIver et al. 2010, McIver and Brunson 2014; 2014; Miller et al. 2014). The sites selected have been variously referred to as wooded shrublands (Romme et al. 2009), expansion woodlands (Miller et al. 2008; McIver et al. 2010), or conifer-encroached shrublands (Miller et al. 2014). Trees had invaded sagebrush (*Artemisia* spp.) communities on loamy soils and native species were still present in the understory across a range of tree cover. Sites represented a wide range in elevation, soil, and climatic conditions, but some regional characteristics were evident. Sites followed changes in elevation across the Great Basin from lowest on the west, to highest in the middle, to lower on the east. On the northwestern Great Basin sites, soils were derived from basalt lava flows and the climate was Pacific maritime, with most precipitation falling between November and June (McIver et al. 2010; McIver and Brunson 2014; Rau et al. 2011; Miller et al. 2014). The central and eastern sites included igneous-, metamorphic-, and sedimentary-based soils which were carbonatic, and the climate was more continental, with lower precipitation between November and June, and highly variable summer precipitation mainly in July and August.

Experimental Design and Treatments

Treatments were applied across the region as a randomized complete block, with each of the 11 sites considered a block. We attempted to place treatment plots at each site on the same ecological site and to include a wide range of tree cover (Miller et al. 2014). Plots were fenced where necessary to exclude livestock grazing. At each site in the network, there were three 8–20-ha treatment plots: an untreated control plot, a broadcast burn treatment plot, and a tree cut-and-leave treatment plot. In addition, the four Utah sites had a tree mastication or shred treatment plot as described in Cline et al. (2010). Because plots could not all be burned in the same year (Miller et al. 2014), treatments were applied in 2006, 2007, and 2009 in a stagger-start design (Loughlin 2006). This design avoids the potential restricted inferences associated with implementing all treatments under the same set of climatic conditions. Plots were burned between August and October and trees were cut or shredded from September through November. All trees > 2 m tall were cut or shredded and debris left in place on the ground. Trees were masticated with a Fecon® Bull Hog® attachment (Fecon Inc., Lebanon, OH). Tree canopy cover was reduced to $< 5\%$ in the burn plots and $< 1\%$ in the mechanically treated plots.

Vegetation Measurements

Cover was measured by species, but categorized into shrub, tall grass (deep-rooted), short grass (shallow-rooted, in this study only Sandberg bluegrass was considered short grass), and perennial forb functional groups, as well as annual forbs, cheatgrass, and bare ground. Cover was measured along five permanent 30-m transects placed at 2 m, 7 m, 15 m, 23 m, and 28 m along the 33-m baseline of 15 randomly placed 30×33 m subplots per treatment plot (McIver et al. 2010; Miller et al. 2014). To randomly locate subplots that covered the range in tree cover, we randomly selected more subplots than necessary and then chose subplots from the random population that covered the tree dominance range. All species and bare ground were sampled at 0.5-m intervals along each transect ($n = 300$ points $\cdot$ subplot^{-1} or 4 500 points $\cdot$ treatment plot^{-1}) using the point-intercept method (Herrick et al. 2009). Foliar cover of each functional group was recorded as a single hit at each point if the point came in contact with that functional group. Shrub canopy cover rather than shrub foliar cover was recorded when the point fell within the living canopy perimeter. More than one functional group could be recorded at a single point but only one hit was recorded per functional group or cheatgrass at a single point. Bare ground was recorded only if it was the first and only hit. This method was used to calculate percentage of cover values for each subplot that were continuous, not binomial.

Pretreatment live canopy cover of all trees > 0.5 m tall within each subplot was recorded by measuring the longest (D1) and perpendicular (D2) crown diameters. Crown area (A) was calculated for each tree by $A = \pi (D1 \cdot D2)/4$ (Tausch and Tueller 1990). Tree canopy cover was estimated for each subplot by summing the crown area for each tree in the subplot and dividing by subplot area.

Analysis

To determine an appropriate response model, we graphed functional group cover as the dependent variable across both pretreatment tree cover and TDI (TDI = tree cover/[tree cover - shrub cover + tall perennial grass cover]) for each site and for all sites using subplot data as individual points (e.g., Fig. 1). We noted a continuous linear or curvilinear response of functional group cover to pretreatment tree cover or TDI for both untreated and treated plots. Analysis of covariance is well suited to determine effects of a continuous covariate (TDI or tree cover) on treatment differences (Littell et al. 2006). Therefore, mixed-model analysis of covariance and Proc Glimmix (SAS version 9.3, SAS Institute, Inc., Cary, NC) were used to determine significance of treatments, covariates, and interactions using F tests from maximum likelihood estimation (Littell et al. 2006). Variables analyzed were functional cover groups, including shrubs, tall perennial grass, short perennial grass, total perennial grass, perennial forbs, total perennial forbs and grasses, annual forbs, cheatgrass, and bare ground. Blocks (sites) were considered random and treatments fixed,

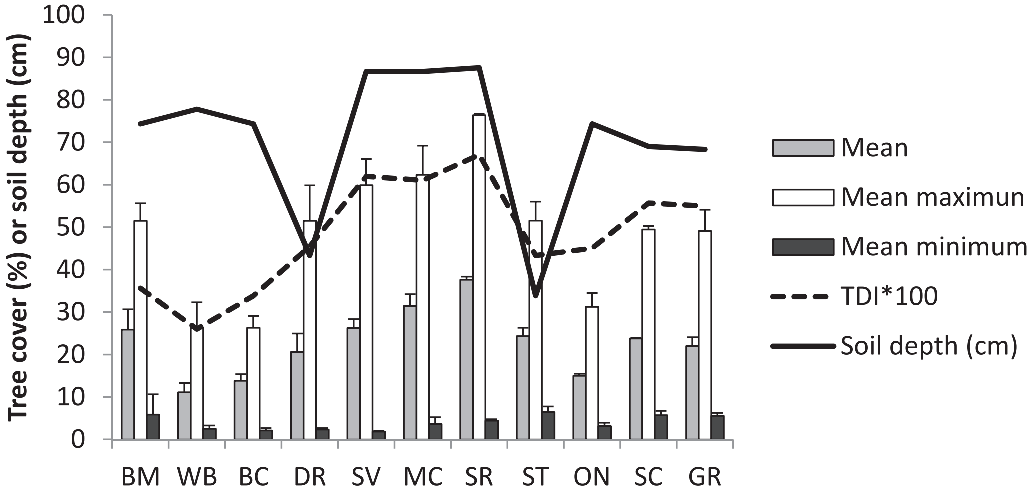

Figure 2. Mean, maximum, and minimum tree cover for 11 piñon or juniper sites across the Great Basin arranged form northwest on the left to southeast on the right. TDI indicates tree dominance index (tree cover/[tree+shrub+tall perennial grass cover]). Tree cover means and standard errors and TDI means calculated from three to four treatment plot means at each site. Soil depth means calculated from 9 to 12 cores per site. BM indicates Blue Mountain; WB, Walker Butte; BC, Bridge Creek; DR, Devine Ridge; SV, Seven Mile; MC, Marking Corral; SR, South Ruby; ST, Stansbury; ON, Onaqui; SC, Scipio; and GR, Greenville.

while subplots were considered subsamples. To provide the strongest inferences, we analyzed the data in a number of ways. Analysis of covariance was conducted comparing untreated and treated plots at 2 yr and 3 yr posttreatment and also using the difference between 2-yr and 3-yr posttreatment and pretreatment cover for each subplot. For each of these analyses of covariance, two covariates were analyzed separately: pretreatment tree cover and TDI.

We analyzed data for 2 yr and 3 yr after treatment separately for each year because each year included different sites. All 11 sites were analyzed 2 yr after treatment, but only nine sites were analyzed 3 yr after treatment. The Stansbury site burned in a wildfire before the third year and the South Ruby site had not completed 3 yr since treatment by the time the current analysis was completed.

Cover data were normalized using the arcsine square root transformation prior to statistical analysis. Observation of residual plots indicated assumptions were met for analysis of covariance. Covariates were not transformed. Each subplot provided a covariate value and values for functional group and cheatgrass cover variables. Subplots are considered as subsamples measured across main plot treatments to provide responses associated with a range of covariate values and are legitimate data points for analysis of covariance (Littell et al. 2006). When treatment by covariate interactions were found to be significant ($P < 0.05$), the Tukey test was used to determine significant differences among treatments for each 0.05 increment of TDI or each 5% increment of pretreatment tree cover. This was specifically relevant to our main objective of determining the pretreatment tree cover or TDI ranges where functional group cover responses varied significantly among treatments. We adjusted for false positives from multiple comparisons by using a value of $P < 0.01$. Model estimates of functional group response variables were back-transformed for graphing posttreatment response.

Our study did not have within-site replication of treatments to directly test site by treatment and covariate interactions. However, we plotted subplot data and used simple regressions to make inferences about response of specific sites relative to regional responses. For example, to assess relationships of TDI and perennial herbaceous cover to cheatgrass cover, we regressed TDI and perennial herbaceous cover on cheatgrass cover for specific sites. We similarly regressed cheatgrass : perennial herbaceous cover ratio on pretreatment TDI. Our inferences based on these regressions are restricted to the specific sites analyzed, but may be important in helping us determine the kinds of sites that are more or less resistant to weed dominance and why.

RESULTS

Pretreatment Differences

Sites varied in mean and mean maximum tree cover and TDI before treatment implementation as calculated across pretreatment plots (Fig. 2). Two western juniper sites, Walker Butte and Bridge Creek, as well as the Onaqui juniper site in Utah, had < 35% maximum tree cover. The other two western juniper sites, Blue Mountain and Devine Ridge, and the three remaining juniper or juniper–piñon Utah sites—Scipio, Greenville, and Stansbury—had intermediate tree cover (mean maximum of 46–51%). The highest maximum tree cover group (mean maximum 57–75%) included only the central Nevada piñon–juniper sites, Marking Corral, Seven Mile, and South Ruby. Soil depths ranged from 68 cm to 78 cm for most sites, but were deeper (86–88 cm) for the central Nevada sites and shallower (33–43 cm) for the Stansbury and Devine Ridge sites (Fig. 2). Precipitation was generally highest on the western juniper sites, lowest on the piñon–juniper sites in Nevada, and intermediate for the juniper–piñon sites in Utah (McIver and Brunson 2014). Based on 30-yr estimates from PRISM Climate Group (2011), exceptions were Walker Butte, which had exceptionally low precipitation for western juniper, and Stans-

Table 1. Probability > F for understory 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. Analyses were conducted separately for pretreatment, 2 yr, and 3 yr after treatment.

	Shrub	Tall grass	Short grass	Total grass	Forb	Total perennial herbaceous	Annual cheatgrass	Bare ground
Pretreatment (11 sites)								
T[1]	0.514	**0.0142**	0.1565	**0.0014**	0.4152	0.1264	0.7488	0.5059
TDI	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	**0.0026**	< **0.0001**
T × TDI	0.3069	0.609	**0.0134**	**0.0177**	0.4757	0.1603	0.7947	0.2093
Pretreatment (9 sites)								
T	0.0512	0.327	0.2559	0.0727	0.4414	0.6921	0.8156	0.0999
TDI	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	**0.0425**	< **0.0001**
T × TDI	0.0559	0.9576	**0.0088**	0.1223	0.8093	0.3814	0.6371	0.0124
Posttreatment year 2 (11 sites)								
T	< **0.0001**	**0.0011**	0.786	**0.0046**	0.1107	0.095	0.142	0.4898
TDI	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	0.6655	**0.0169**
T × TDI	< **0.0001**	0.4356	0.5241	0.0791	**0.0003**	**0.0213**	**0.022**	0.1308
Posttreatment year 3 (9 sites)								
T	< **0.0001**	0.3075	0.1263	0.1451	0.1308	0.8481	**0.0484**	0.3023
TDI	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	**0.0013**	0.2266
T × TDI	< **0.0001**	**0.0099**	0.0845	**0.0219**	< **0.0001**	**0.0002**	**0.0055**	0.2044

[1]T indicates treatment; TDI, tree dominance index. Bolded values indicate F significance ($P < 0.05$).

Table 2. Range of the pretreatment tree dominance index (TDI) covariate where significant differences ($P<0.01$) in fuel control treatments were found for vegetation cover variables for 2 and 3 yr after treatment. The shred treatment was implemented only on Utah sites, while all other treatments were implemented on all sites. Comparisons with ≤ 1 indicate that the comparison was significant for all values of TDI.

Cover variable	Year 2 response	TDI[1]	Year 3 response	TDI
Shrub	Burn < untreated	< 0.9	Burn < untreated	≤ 0.75
	Cut = untreated	≤ 1	Cut > untreated	0.3–0.75
	Shred = untreated	≤ 1	Shred = untreated	≤ 1
	Cut > burn	≤ 1	Cut > burn	≤ 0.75
	Shred > burn	≤ 0.65	Shred > burn	≤ 0.65
	Cut > shred	≤ 0.05	Cut > shred	≤ 0.35
Tall grass	Burn = untreated	≤ 1	Burn = untreated	≤ 1
	Cut > untreated	≤ 1	Cut > untreated	≥ 0.15
	Shred > untreated	≤ 0.85	Shred > untreated	≤ 1
	Cut > burn	≤ 1	Cut > burn	≥ 0.35
	Shred > burn	≤ 0.55	Shred = burn	≤ 1
	Cut = shred	≤ 1	Cut = shred	≥ 0.05
Total perennial herbaceous	Burn = untreated	≤ 1	Burn > untreated	≥ 0.7
	Cut > untreated	≥ 0.25	Cut > untreated	≥ 0.35
	Shred > untreated	0.4–0.85	Shred = untreated	≤ 1
	Cut > burn	≥ 0.05	Cut = burn	≤ 1
	Shred > burn	≤ 0.5	Shred = burn	≤ 1
	Cut = shred	≤ 1	Cut = shred	≤ 1
Cheatgrass	Burn > untreated	≥ 0.55	Burn > untreated	≤ 1
	Cut > untreated	1	Cut > untreated	≥ 0.45
	Shred = untreated	≤ 1	Shred > untreated	≥ 0.55
	Cut = burn	≤ 1	Cut = burn	≤ 1
	Shred = burn	≤ 1	Shred = burn	≤ 1
	Cut = shred	≤ 1	Cut = shred	≤ 1

[1]TDI indicates tree dominance index.

bury, which had exceptionally high precipitation for Utah juniper.

Before treatment, plots were generally statistically similar ($P > 0.05$) for most understory cover variables across all sites or blocks in the region (Table 1). An exception was that tall grass and total perennial grass cover varied among treatment plots for the 11 sites used to compare treatment plots 2 yr after treatment (Table 1). Third-year data for the South Ruby and Stansbury sites were not available, and when these two sites were excluded from the pretreatment analysis, there were no significant pretreatment differences (Table 1). Pretreatment functional group cover generally decreased ($P < 0.05$) with increasing TDI for both the 11- and 9-site analyses. Cover decreased to < 50% of maximum cover (TDI = 0) at TDI > 0.4 for shrubs and > 0.7 for perennial herbs. The pretreatment treatment by covariate interaction was generally not significant, except for short grass cover for both the 11- and 9-site analyses and for total grass cover for the 11-site analysis (Table 1). Lack of differences in pretreatment plots, consistency of covariate significance, and lack of significant treatment by covariate interactions for pretreatment data across the region allow us to conclude that posttreatment differences among treatments are a result of the treatments themselves, rather than preexisting differences.

Posttreatment Responses

Although the functional group cover responses were analyzed two different ways, results were similar using either TDI or tree cover as covariates. For simplicity we include results from all analyses in Tables S1 and S2 and Figure S1 (available online at http://dx.doi.org/10.2111/REM-D-13-00018.s1; http://dx.doi.org/10.2111/REM-D-13-00018.s2; http://dx.doi.org/10.2111/REM-D-13-00018.s3). Here we present only results of the posttreatment analysis using TDI as the covariate (Tables 1 and 2; Fig. 3). Treatment by covariate interactions became more obvious during the third than during the second year after

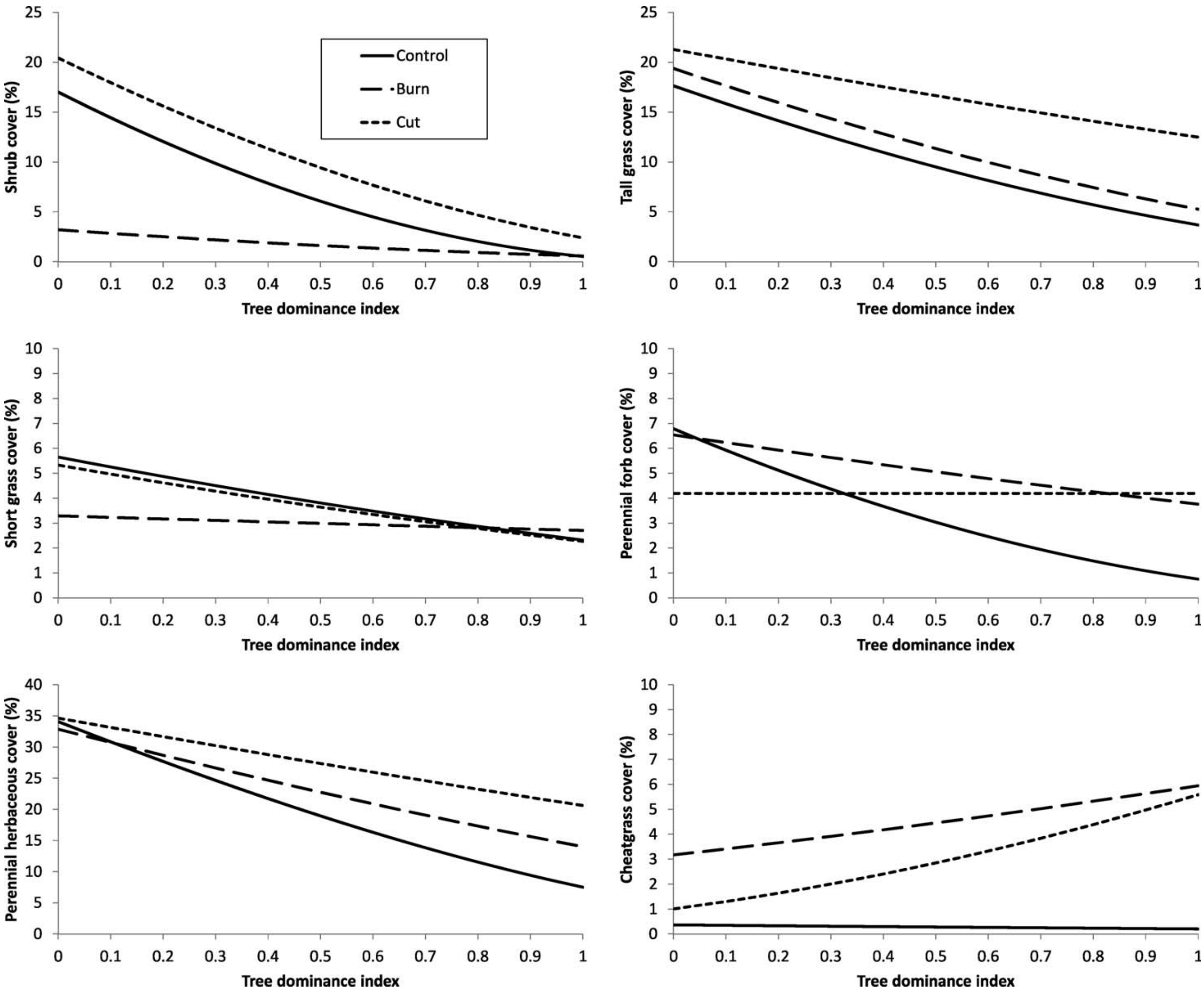

Figure 3. Vegetation cover 3 yr after treatment in relation to pretreatment tree dominance index.

treatment (Table 1). By the third year after treatment, the treatment by TDI covariate interaction was significant ($P < 0.05$) for all cover variables except bare ground and short grass cover (Table 1). The treatment by covariate interaction was also significant ($P < 0.01$) for annual forb cover. Significance of the treatment by covariate interaction indicates that treatment responses must be compared at specific TDI covariate values to determine ranges of TDI over which treatments differ or not.

Prescribed fire reduced shrub cover relative to the untreated control at all but the upper ranges of TDI where there was limited shrub cover at time of treatment (Fig. 3; Table 2). By 3 yr after treatment, the maximum difference in shrub cover between untreated control and burn treatments was 13.8% at a TDI of 0 (0% tree cover). Cutting or shredding maintained similar or greater shrub cover as on the untreated control plots and also resulted in greater shrub cover than the burn plots, especially at low to mid TDI (Fig. 3; Table 2). Burning had no effect on tall grass cover relative to the untreated control 2 yr and 3 yr after treatment (Fig. 3; Table 2). Cutting increased tall grass cover relative to untreated control plots for most values of TDI. Maximum increase in tall grass cover for cut compared to no treatment after 3 yr was 8.8% at a TDI of 1 (Fig. 3). Understory response to shredding was generally similar to that of cutting, although cutting maintained 11% and 5% higher shrub cover than shredding in years 2 and 3 at low to mid TDI (Fig. 3; Table 2). Cutting produced greater tall grass cover than burning at all ranges of TDI in year 2, and at mid to high ranges of TDI by year 3 (Fig. 3; Table 2). Shredding produced greater tall grass cover than burning at low to mid ranges of TDI in year 2, but produced similar cover as burning in year 3. Tall grass cover on cut and shred plots was similar for most ranges of TDI (Fig. 3; Table 2). Short grass cover differed significantly among treatments before treatment implementation (Table 1). Posttreatment differences among treatments were small (Fig. 3), and Tukey tests showed no significant differences among treatments in short grass cover for any ranges of TDI. Perennial forb cover was much lower than perennial grass cover (Fig. 3),

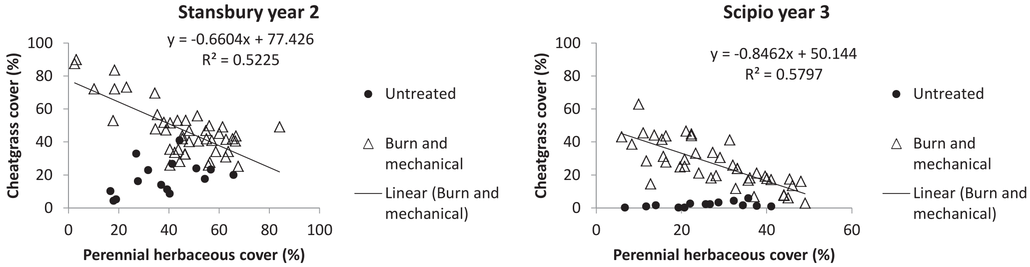

Figure 4. Cheatgrass cover in relation to perennial herbaceous cover on untreated and burned or mechanically treated plots on two sites with high cheatgrass cover.

but had a significant ($P < 0.05$) treatment by TDI covariate interaction (Table 2). Three years after treatment, perennial forb cover was greater on burn than untreated plots at a TDI ≥ 0.6, and was greater on cut than untreated plots at a TDI of ≥ 0.7(Fig. 3).

Total perennial herbaceous cover was composed primarily of tall and short grass cover and therefore showed a similar response to treatment as did tall grass cover (Fig. 3; Table 2). Total perennial herbaceous cover was similar for untreated and burn plots 2 yr after treatment but was higher on the burn than untreated plots at mid to high ranges of TDI 3 yr after treatment (Fig. 3; Table 2). The cut treatment had higher cover than the untreated control at mid to high ranges of TDI and greater cover than burn plots at all but the lowest TDI (< 0.05). Maximum increase in year 3 for cutting compared to no treatment was 13.1% at a TDI of 1, and for cutting compared to burning was 6.6% at a TDI of 1. Perennial herbaceous cover was statistically similar on shred and cut plots (Table 2).

Across the region, cheatgrass cover was limited on untreated control and pretreatment plots, but varied slightly with TDI (Table 1; Fig. 3). After treatment, cheatgrass cover increased mainly at mid to high TDI, although by year 3 cheatgrass was higher on burned than on untreated plots at all values of TDI (Table 2). Burning or mechanical treatments resulted in similar increases in cheatgrass cover, but across the region actual cover increases were small ($< 4.2\%$ on burn and cut plots, and $< 13.8\%$ on shred plots by the third year; Fig. 3). Burning increased cheatgrass cover relative to no treatment at lower pretreatment TDI than did cutting (Table 2). Annual forb cover was also limited on untreated plots and decreased with increasing TDI, ranging from 4% to 1% at low to high TDI. After treatment, annual forb cover increased with increasing pretreatment TDI. Burning increased annual forb cover by 10% to 15% from low to high TDI. Mechanical treatments increased annual forb cover by 2% to 5 % at mid to high TDI.

Our experimental design using sites as blocks does not specifically allow testing of site by treatment interactions. However, because it is highly relevant to a possible threshold crossing to cheatgrass dominance, cheatgrass cover among sites should be reported and inferences made for specific sites. Most sites had limited cheatgrass cover both before and 3 yr after treatment, except for Stansbury and Scipio. Pretreatment cheatgrass cover percentages from highest to lowest were as follows (mean percentage ± SE): Stansbury, 27.2 ± 1.8%; Scipio, 19.2 ± 1.6%; Devine Ridge, 4.6 ± 0.6%; Bridge Creek, 2.5 ± 0.6%; Greenville Bench, 2.2 ± 0.5%; Blue Mountain, 1.9 ± 0.4%; Onaqui, 0.9 ± 0.3%; South Ruby, 0.3 ± 0.7%; Walker Butte, 0.2 ± 0.1%; Marking Corral, 0.1 ± 0.3%; and Seven Mile, 0. Although these percentages are low for most sites, 7 of the 11 sites had some subplots that had $> 8\%$ cheatgrass cover. For example, Devine Ridge had 11 subplots with $> 8\%$ and Bridge Creek and Onaqui each had one subplot with $> 20\%$ cheatgrass cover. Plotting and regressing pretreatment cheatgrass cover as a function of TDI indicated very weak association of these two variables for most sites ($r^2 = 0.0004$ to 0.16). Slopes were limited (0.029% to 5.97% per 0.1 TDI), and were negative for 7 of the 10 sites that had some cheatgrass cover. In contrast, Stansbury had a strong negative association between cheatgrass cover and TDI ($r^2 = 0.52$, slope $= -39.9\%$). At Stansbury in year 2 (year 3 values not available because the site burned in a wildfire), cheatgrass cover percentages averaged, 18.6 ± 2.7 on untreated subplots, 59.6 ± 5.3 on the burn, and 41.2 ± 1.6 on the mechanically treated subplots. At Scipio, cheatgrass cover percentages in year 3 averaged 2.0 ± 0.4 on the untreated subplots, 25.5 ± 3.2 on the burn, and 27 ± 2.6 on mechanically treated subplots. The Devine Ridge site, which had the maximum average cheatgrass cover of all the remaining sites, had posttreatment cheatgrass percentages on burned and mechanically treated plots of 13.5 ± 1.7 and 2.1 ± 1.1, respectively, in year 3.

Across the region, cheatgrass cover was too low to make inferences about associated effects of perennial herbaceous cover (Fig. 3). At Stansbury and Scipio, cheatgrass cover had no significant correlation with perennial herbaceous cover on untreated plots (Fig. 4; Stansbury: $r^2 = 0.17$, $P = 0.129$, Scipio: $r^2 = 0.21$, $P = 0.104$). However, on treated plots at both Stansbury and Scipio, cheatgrass cover significantly ($P < 0.0001$) decreased with increasing perennial herbaceous cover (Fig. 4). Stansbury had higher perennial herbaceous and cheatgrass cover than Scipio, but at both sites cheatgrass cover was high on treated plots, even with high perennial herbaceous cover (Fig. 4). For example, when perennial herbaceous cover was 20%, cheatgrass cover was 87% at Stansbury and 36% at Scipio (Fig. 4). Although cheatgrass cover was high on treated plots at both sites, it especially increased at Scipio when pretreatment TDI was > 0.7 (Fig. 5).

DISCUSSION

Should Treatments Target a Specific Phase of Infilling?

Although many woody plants provide significant ecosystem values and services, woody plant encroachment is generally considered to lower ecosystem values of grasslands, shrub-

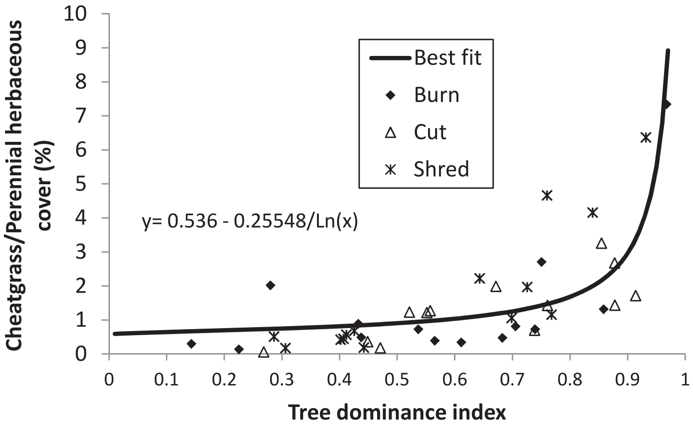

Figure 5. Ratio of cheatgrass to perennial herbaceous cover in relation to pretreatment tree dominance index for burn, cut, and shred tree control treatments at Scipio, Utah ($r^2 = 0.64$).

steppe, and savannas (Archer et al. 2011). In the case of piñon and juniper tree encroachment into sagebrush communities, major concerns are that both valuable woody and herbaceous understory plants are depleted, and that increased fuel loads will result in high-severity fire, high mortality of understory vegetation, and weed dominance by invasive annuals. Resilience is the ability to regain, whereas resistance is the capacity to retain functional processes and components after disturbance (Chambers et al. 2014). Functional processes are assessed by measuring vital ecosystem attributes, which are useful in determining thresholds within successional models (Aronson et al. 1993a, 1993b; Pellant et al. 2005). Vegetation components considered vital to system function may indicate system resilience and successional trajectories. Because perennial herbs are a key component of sagebrush steppe systems (Miller et al. 2013, 2014; Pierson et al. 2013; Reisner et al. 2013; Williams et al. 2013; Chambers et al. 2014), failure of this component to increase in density and cover after tree reduction could indicate that infilling passed a biotic threshold prior to the implementation of treatments. Resilience-based management for conifer-encroached shrublands suggests that treatments need to be applied well before a biotic or abiotic threshold is crossed (Briske et al. 2006; Chambers et al. 2014). Because perennial herbaceous cover is critical to avoiding a biotic threshold of weed dominance and an abiotic threshold of interspace erosion, it is important to consider effects of vegetation treatments on the trajectory of perennial herbaceous cover.

Both prescribed fire and mechanical treatments by nature or design selectively reduce certain life forms or species. Burning decreased shrub cover at all but the advanced phases of infilling (high TDI) where shrub cover was already minimal, while cutting or shredding maintained or increased shrub cover at all phases, and increased perennial herbaceous cover most at mid to upper phases of infilling. This absolute increase in cover at mid and upper phases of infilling was a result of lower cover at these phases on untreated plots and high cover response after treatment (Fig. 3). For example, at year 3 and at a TDI of 0.1, total perennial herbaceous cover was 30.8%, 30.7%, and 33.2% on untreated, burned, and cut plots, respectively, across the region. However, at a mid TDI of 0.5, cover values were 19%, 22.8%, and 27.4%, and at an upper TDI of 0.95 they were 8.4%, 14.8%, and 21.3% for untreated, burned, and cut plots. These increases of cover above those on untreated plots for burn and cut treatments would be 3% and 8.4% at 0.5 TDI, and 6.4% and 12.9% at 0.95 TDI. Although burning and cutting greatly increased perennial herbaceous cover compared to the untreated plots at mid and high TDI, they did not increase absolute cover above that at low pretreatment TDI (34%) where encroachment was just beginning.

Across the region, shrub cover was reduced by tree infilling to a minimum at lower TDI than was perennial herbaceous cover. This varies from the model of Barney and Frischknecht (1974) where shrubs, not perennial herbs, were considered to be the last life form to survive tree infilling. Shrub cover did not necessarily decrease at a higher rate than perennial herbaceous cover with increased infilling, but was initially lower (Fig. 3). Because 50% of shrub cover was lost at a TDI > 0.4, and because fire greatly reduces shrub and especially sagebrush cover, maintenance of the shrub component requires using mechanical treatments instead of fire, and implementing those treatments at low to mid TDI. Prescribed fire at any TDI, or mechanical treatments implemented at mid to high TDI will result in a herbaceous-dominated plant community with more or less perennials or annuals. Maximum shrub cover returned 36–46 yr after fire in these systems in Utah (Barney and Frischknecht 1974). Mountain big sagebrush recovers 15–100 yr after fire, depending on postfire cool-season precipitation (Nelson et al. 2013), whereas Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & Young) recovery is limited (Miller et al. 2013). Sagebrush species accounted for 68% of the total shrub cover and 50% of the shrub density on our sites (Miller et al. 2014). Burning piñon or juniper encroachment areas may increase cover of sprouting shrubs (Bates et al. 2013; Miller et al. 2013; Chambers et al. 2014), but not species of big sagebrush, which do not sprout and must establish from seed (Miller et al. 2013). Both burning and cutting increased sagebrush seedling density by the third year after treatment on our sites (Miller et al. 2014). There is some evidence that manual cutting may be less damaging to shrub cover than shredding, which is done using a tractor and could crush some shrubs. Cutting had 4.8% higher shrub cover than shredding at low to mid ranges of TDI 3 yr after treatment (Table 2).

Perennial herbs are critical components for the sagebrush steppe ecosystem. Abundant perennial grasses resist cheatgrass dominance (Chambers et al. 2007, 2014; Bates et al. 2005, 2011; Blank and Morgan 2012; Reisner et al. 2013; Miller et al. 2014) and increase infiltration in interspaces between shrub and tree mounds (Pierson et al. 2010, 2013; Williams et al 2013). Therefore perennial herbaceous, and especially grass, cover is key for resistance to crossing a biotic threshold to weed dominance and frequent fire, as well as for resistance to soil loss and crossing an abiotic threshold. Increases in perennial herbaceous cover occurred mainly from growth of residual plants, rather than new seedlings (Miller et al. 2014) and were probably the result of a longer period of soil water availability and growth in the spring associated with reduced water use and interception of precipitation by trees (Bates et al. 2000; Roundy et al. 2014). Mechanical treatments increased tall grass and perennial herbaceous cover earlier after treatment at lower phases of infilling, and by over twice the amount as did burning during the first 2–3 yr after treatment (Fig. 3). Miller et al. (2014) reported that burning initially decreased perennial herbaceous cover on these sites, but that cover recovered by the third year after treatment. In a study of western juniper woodlands on Steens Mountain, southeastern Oregon, Bates et al. (2013) found recovery of perennial herbaceous cover after burning Phase II (codominant trees with shrubs and perennial herbs) woodlands, but Phase III (dominant trees) woodlands had limited perennial herbaceous cover both before and after severe fire. We expect continued recovery of perennial herbaceous cover on our sites where cheatgrass cover is limited and residual perennials are already well adapted to the environmental conditions (Rew and Johnson 2010).

There are both advantages and disadvantages of fire compared to mechanical tree control. Shrubs, perennial herbs, and biological soil crusts respond better to mechanical treatments than to fire over the short term (Miller et al. 2014), but neither cutting nor shredding reduces woody ground fuels as well as burning (Young et al. 2014). Trees may recover more quickly after mechanical treatments than after fire. Resources made available by tree reduction may be used by tree seedlings (Chambers et al. 1999), small trees that were not treated, or trees sprouting from incomplete mechanical treatment. Tree cover reached 16% 71 yr after fire in Utah woodlands (Barney and Frischknect 1974). Infilling after chaining steadily reduced growth of understory cover and production starting at 5–8 yr after treatment (Tausch and Tueller 1977). Studies of mechanical treatments suggest that western juniper will return to dominance within 50 yr (Bates et al. 2005, 2006; O'Connor et al. 2013). Thus, mechanical tree control treatments will especially require follow-up maintenance to continue providing fuel control and understory benefits.

Both cutting and shredding reduce canopy fuels but increase surface fuels by maintaining shrub biomass, converting woody canopy fuels to down-and-dead 10-h and 100-h fuels, and by increasing herbaceous fuels (Young et al. 2014). Redistribution of fuels from the canopy to the ground may reduce wildfire spread and facilitate containment, but when a wildfire does occur, it may increase burning time and temperatures near the soil surface, resulting in higher fire severity. Increased fire severity could kill seeds and growing points of desirable vegetation and weeds and ultimately reduce perennial shrub and herbaceous cover as happened on the Stansbury site in this study. Because of this risk, some managers are conducting follow-up prescribed fire after mechanical treatments to avoid burning shrubs, reduce woody ground fuels, and favor desired vegetation (Brockway et al. 2002; Bates et al. 2006; Bates and Svejcar 2009; O'Conner et al. 2013). Posttreatment wildfires might create an opportune time to seed areas that have limited perennial residuals because high fire severity can reduce the cheatgrass seed bank (Young and Evans 1978). Seeding mountain big sagebrush steppe after prescribed fire to reduce encroached western juniper can greatly increase perennial grass abundance and decrease abundance of cheatgrass (Davies et al. 2014).

In the short term, we did not discover a tree-infilling point at which perennial herbaceous plants failed to respond positively to tree reduction. Whether this increase is sufficient to lead to continued dominance by native perennials rather than invasive weeds remains to be seen. The hope is that increased growth and cover of desirable perennials (increased resilience) will prevent weed dominance (reinforced resistance). The greatest increase in perennial herbaceous cover occurred when trees were reduced at the highest phase of infilling that we measured and was associated with the greatest increase in time of soil water availability in the resource growth pool at that phase (Roundy et al. 2014). This increase in perennial herbaceous cover at higher phases of infilling was not sufficient to deplete soil water in the resource growth pool as well as the untreated plant community or vegetation treated at lower and mid phases of infilling (Roundy et al. 2014). This result leaves a concern that weeds could use these resources to invade and dominate before perennial species can increase fast enough to use the extra resources and resist weed dominance. Also, an abiotic threshold of soil loss may be crossed with advanced tree infilling as runoff is concentrated through interconnecting bare intercanopy areas with low infiltration rates (Pierson et al. 2013; Williams et al. 2013). As shown by these authors, fire reduces infiltration rates in canopy areas but increases them in intercanopy areas when perennial herbaceous cover increases.

Cheatgrass Invasibility in Relation to Site, Treatment, and Infilling

The most obvious crossing of a biotic threshold with western juniper infilling is signaled by a change in fire regime resulting from fuel structural changes and replacement of native with exotic plants and seed pools (Bates et al. 2013; Miller et al. 2005). Three major factors interrelate in affecting annual weed invasion and dominance: weed adaptation to the abiotic environment, resource availability for weed use, and weed presence and propagule pressure. Cheatgrass dominance is more likely where environmental conditions best meet its requirements for germination, growth, and seed production (e.g., on sites that fit its fundamental niche well; Chambers et al. 2013). Although Roundy et al. (2007) found that cheatgrass germination requirements are generally met across a wide range of environmental conditions on Great Basin sagebrush rangelands, Chambers et al. (2007) found that cheatgrass growth and seed production were minimal on higher-elevation sites with low degree days and greatest on lower-elevation sites with greater degree days. Cheatgrass N uptake is greater than that of native perennial grasses at warmer temperatures (Leffler et al. 2013). Warmer temperature conditions at lower elevations or on south-facing slopes are sometimes associated with both lower perennial grass cover and higher cheatgrass cover (Rickard 1975; Koniak and Everett 1983; Everett and Sharrow 1985; Zouhar 2003; Condon et al. 2011). Warmer temperatures are obviously associated with cheatgrass adaptation, but only if there is sufficient time of available water for seed production and seedling establishment. Although the potential for cheatgrass dominance increases from frigid (cool) to mesic (warm) soil temperature regimes (Chambers et al. 2014), frigid soils on the warm end of the soil temperature gradient may support cheatgrass dominance after severe fire that decreases perennial grass density (Bates et al. 2013). Cheatgrass cover both before and after tree reduction treatments was highest on our Stansbury and Scipio sites. In an ordination of seasonal soil water and temperature for these sites (Roundy et al. 2014), both Stansbury and Scipio were warmer, while Stansbury was wet and Scipio dry in relation to the other sites. Soil temperature regimes were classified as cool mesic for Stansbury and as warm mesic for Scipio. We expect that our warmer sites are most at risk to cheatgrass dominance unless constrained by lack of resource availability associated with perennial herbaceous growth.

Cheatgrass dominance is constrained within the range of sites that it is more or less adapted to by perennial herbaceous competitors (realized niche; Chambers et al. 2007, 2013). Cheatgrass and other invasive species are most likely to invade and dominate where resources are not consistent enough to support high cover and growth of perennial competitors (Davis et al. 2000). In addition to having temperatures that are less favorable to cheatgrass, higher-elevation Wyoming big sagebrush, mountain big sagebrush, and mountain brush communities with higher productivity and more consistent resource availability are more resilient and recover both sagebrush and perennial herbaceous dominance after disturbance much better than drier and lower-elevation Wyoming sagebrush and salt desert shrub communities (Chambers et al. 2013, 2014).

Tree reduction increases time of soil water availability during the critical spring growing season and this increase is greatest where pretreatment tree cover is highest and understory cover least (Roundy et al. 2014). Increased soil water availability after tree reduction at high phases of infilling continues at least 4 yr after treatment (Roundy et al. 2014). Burning increases soil temperatures and mechanically treating trees modifies the microenvironment to support both increased weed and perennial plant growth (Young et al. 2013a, Roundy et al. 2014). Tree reduction also increases available N (Bates et al. 2000, 2002; Young 2012). Whether desirable perennial plants or weeds such as cheatgrass use these resources and dominate over the long term could be highly dependent on the phase of infilling at which treatments are applied. In the study of Bates et al. (2013), cheatgrass dominated burned Phase III western juniper woodlands where perennial grass cover was low ($< 3\%$) both before and after fire, and the high-severity fire reduced density by 95%. In contrast, Phase II woodlands with about 10% perennial grass cover prior to burning recovered and were not dominated by cheatgrass after moderate-severity fire. This led the authors to conclude that their Phase III woodlands had crossed a recovery threshold. They considered that burned woodlands would recover their native species composition if densities exceed 1 perennial grass plant $\cdot$ $m^{-2}$and 5 perennial forb plants $\cdot$ m^{-2}. High fire severity and the associated mortality of perennial grasses on the Phase III woodlands in this study may have been increased by felling a third of the trees and letting them dry over the summer before conducting the prescribed fire.

Increases in annual weed cover the first few years after tree reduction treatments may give way to perennial dominance in time, but differential site conditions and posttreatment management result in a wide array of long-term responses in dominance from annual weeds to desirable perennials (Bates et al. 2000; Bates et al. 2013; Miller et al. 2005, 2014). Across our regional study, cheatgrass cover was increased by burning at low to high phases of infilling, and at mid to high phases of infilling by mechanical treatments (Fig. 3; Table 2). By 3 yr after treatment, cheatgrass cover increased across the region to a maximum of 5.9% on burned plots and a maximum of 5.6% on cut plots at a TDI of 1 (Fig. 3). Cheatgrass dominance affects fire potential, behavior, and frequency (Brooks 2008), and has been predicted to increase the likelihood of fire by $> 60\%$ when cover exceeds 20% (Link et al. 2006). Cheatgrass cover can vary widely among years ranging from $< 5\%$ on dry years to almost 25% on wet years on the same site (Bates et al. 2007). Because most of our sites had much higher total perennial herbaceous than cheatgrass cover, we may conclude that tree reduction did not put most of our sites at risk by 3 yr after treatment. Although perennial herbaceous cover increased most when trees were reduced at high pretreatment TDI, the increase in cover after 3 yr did not result in as high an absolute cover (14% on burn plots, 20.6% on cut plots) as was present at the lowest TDI and initial phases of infilling (34%; Fig. 3). Bybee (2013) found that cheatgrass cover was usually $< 10\%$ on tree-shredded sites that had $> 30\%$ perennial herbaceous cover. The ultimate dominance of perennial herbaceous species or cheatgrass and other weeds may take some years to express on most of our sites and will be driven by environmental and management conditions over time.

The Stansbury and Scipio sites had the highest cheatgrass cover before treatment and also had the highest posttreatment cheatgrass cover, which underscores the importance of propagule pressure to postdisturbance weed dominance (Davies and Sheley 2007; Davies and Johnson 2011). The pattern of increased cheatgrass cover in relation to pretreatment infilling varied for the two sites. By 2 yr after treatment, Stansbury had high cheatgrass cover on untreated and treated subplots and cheatgrass cover actually decreased with increasing pretreatment TDI. At this site, cheatgrass cover was high enough on all treated plots, regardless of pretreatment TDI, to cause high susceptibility to fire. By 3 yr after treatment at Scipio, cheatgrass cover was limited on untreated plots, but increased with increasing pretreatment TDI on treated plots. On treated plots at both sites, cheatgrass cover decreased with increasing perennial herbaceous cover (Fig. 4). Cheatgrass cover at both sites was high, even with high perennial herbaceous cover. At Scipio, the ratio of cheatgrass : perennial herbaceous cover on treated plots increased exponentially above a pretreatment TDI of 0.7 (Fig. 5). Cheatgrass : perennial herbaceous cover ratios would still be considered high (> 0.5) at all pretreatment TDIs at this site (Fig. 5). At Stansbury and Scipio and on a number of other sites we observed that cheatgrass cover and growth was limited in small patches (< 5 m diameter) of high perennial grass cover, indicating a smaller scale (30×33 m) of perennial herbaceous constraint on cheatgrass than we measured at the subplot scale and graphed in Figure 4. This suggests that increases in perennial cover could reduce cheatgrass cover over time on these sites. High environmental suitability to cheatgrass supported high cheatgrass cover and propagule pressure before tree reduction at the Stansbury and Scipio sites. This led to high cheatgrass cover when resource availability was increased by tree reduction.

MANAGEMENT IMPLICATIONS

Managers of sagebrush steppe systems want to know which fuel control treatments will produce the most favorable vegetation response, and at which phase of infilling treatments should be applied. Favorable vegetation responses are increased native shrub, perennial grass, and perennial forb cover, and decreased invasive weed cover. Managers also are concerned that treatment at an advanced phase of infilling could result in weed dominance. Over the short term (3 yr after treatment), we found that mechanical treatments of cutting and shredding trees maintained shrub cover when applied at lower phases of infilling and increased perennial herbaceous cover when applied at mid to high phases of tree infilling. Burning decreased shrub cover at all but upper phases of infilling where it was already limited by infilling and slightly increased perennial herbaceous cover at mid to high phases of infilling. However, response of perennial herbaceous cover to burning was lower in magnitude and was delayed more years after treatment than response to mechanical treatments. Burning increased cheatgrass cover at low to high phases of infilling whereas mechanical treatments increased cheatgrass cover at mid to high phases of infilling. To maintain shrub cover we recommend mechanically treating at low to mid phases of infilling. Where maintaining shrubs in not a major objective, many sites that have lost shrub cover due to advanced infilling will still have increased perennial herbaceous cover after tree reduction. Where sites appear susceptible to high weed dominance, as indicated by mesic (warm) to warm frigid (cool) soil temperature regimes, high pretreatment weed cover, or limited perennial herbaceous cover, we recommend mechanical treatment. If these sites are burned, or mechanically treated with low perennial herbaceous cover, we recommend seeding in conjunction with tree control. Perennial herbaceous cover is critical to resisting weed dominance, as well as to maintaining high infiltration rates and avoiding erosion in interspaces between shrubs and trees.

Although mechanical treatments had better shrub and perennial herbaceous response than prescribed fire, they also leave more surface fuels. These fuels could increase subsequent wildfire severity, resulting in decreased perennial cover and potential weed dominance. Because of the potential risk of plant mortality when wildfires burn mechanical fuel treatments, some managers are using cool-season patch burns and other follow-up burning strategies to reduce mechanically treated fuels. Especially after mechanical treatment, trees begin infilling with the growth of seedlings, untreated small trees, and growth of branches or buds not removed by treatment. Thus, tree control treatments will require follow-up maintenance to continue providing fuel control and understory benefits. Most significantly for our study, we have shown that perennial herbaceous plants have responded favorably to tree control treatments across a range of sites in the Great Basin, and that response has occurred at mid to high phases of infilling. This may be reassuring to land managers who must apply treatments across a landscape composed of various phases of infilling. Considering that nontreatment can lead to near complete loss of residuals and high-severity wildfires on some encroachment sites, our results suggest that although fuel control treatments will be most beneficial in the early to mid phases of tree encroachment, they may still be viable management options for increasing understory cover across a range of sites and tree cover gradients.

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