



## Original Research

# Understory Plant Community Responses to Fuel-Reduction Treatments and Seeding in an Upland Piñon-Juniper Woodland<sup>☆</sup>



Caroline A. Havrilla, Akasha M. Faist, Nichole N. Barger<sup>\*</sup>

Ecology & Evolutionary Biology Department, University of Colorado, Boulder, CO 80309-0334, USA

## ARTICLE INFO

## Article history:

Received 18 June 2016

Received in revised form 23 March 2017

Accepted 7 April 2017

## Key Words:

*Bromus tectorum*  
fuel-reduction  
mastication  
piñon-juniper  
prescribed fire  
seeding

## ABSTRACT

Woody plant expansion and infilling into nonwooded rangeland ecosystems have been observed worldwide. Such expansion may lead to declines in herbaceous understory plant communities and increased fuel loads in rangelands. Under the US National Fire Plan, fuel-reduction treatments have been implemented over vast expanses of western forest types to reduce the risk of catastrophic wildfire and restore historical ecosystem structure, function, and diversity. The benefits of fuel-reduction may, however, also carry inherent ecological risk such as promoting non-native species colonization. Here, we compare understory plant community responses to three commonly used fuel-reduction treatments with seeding applications in an upland piñon (*Pinus edulis* Engelm.)–juniper (*Juniperus osteosperma* [Torr.] Little) woodland on the Colorado Plateau: 1) mechanical mastication, 2) lop and slash piled then burned (pile burn), and 3) lop and scatter followed by a broadcast burn (broadcast burn). Data were collected pretreatment (2009) and one (2010), two (2011), and six (2015) growing seasons post treatment. We found while understory perennial herbaceous plant cover remained low 1 and 2 yr post treatment, it increased by > 700% in all fuel-reduction treatment plots six growing seasons post treatment. Furthermore, while we observed minor increases in invasive annual grass, *Bromus tectorum* L. (cheatgrass), colonization in 2010 and 2011, there were substantial increases in *B. tectorum* cover by 2015. *B. tectorum* cover varied among treatments with the greatest cover in the unseeded mastication plot at nearly 30%. Seeding applications did not increase overall seed mix species cover but enhanced seed mix species richness and, thus, may have increased resistance to *B. tectorum* invasion in seeded treatment plots. Our findings offer valuable insights to the ecological consequences of fuel-reduction activities in piñon-juniper woodlands through comparison of common fuel-reduction treatments and seeding applications and highlight differences in understory plant community responses to treatments across short to longer time scales.

© 2017 The Society for Range Management. Published by Elsevier Inc. All rights reserved.

## Introduction

Woody plant expansion and infilling into previously nonwooded rangeland ecosystems has been observed worldwide (Archer et al., 1995, 2001; Van Auken, 2000; Eldridge et al., 2011; Liu et al., 2013). Community shifts from historic grassland, steppe, or savannah into shrubland or woodland impact rangeland ecosystem structure, diversity, and function (Archer et al., 1995; Van Auken, 2000; Knapp et al., 2008; Barger et al., 2011). These changes can be associated with declines in ecosystem herbaceous understory cover and aboveground net primary productivity (Knapp et al., 2008; Barger et al., 2011) resulting in decreased forage production and quality for livestock and wildlife (Clary

and Jameson, 1981; Bates et al., 2005), and increased overstory fuel loads leading to heightened risk of catastrophic wildfire (Young et al., 2015). Thus, fire mitigation strategies and restoration have become foci for rangeland land managers in these ecosystems. In the western United States, fuel management strategies have been implemented under the National Fire Plan to reduce the risk of catastrophic wildfire while restoring these ecosystems to resemble their historical structure, function, and diversity (NFP, 2000). In the context of these goals, increasing understanding of the long-term effects of fuel-reduction treatments on understory plant communities remains a priority of scientists and land managers.

Piñon-juniper woodlands cover ca. 136 million ha of the western United States and have undergone significant recent expansion and increases in stand density. Thus, piñon-juniper woodlands have been among the most widely targeted ecosystems for fuel-reduction and restoration over the last century (Springfield, 1976). Although it is clear that fuel-reduction treatments generally increase resource availability (i.e., water, light, and nutrients) to understory plant communities (Haskins and Gehring, 2004; Owen et al., 2009; Young et al., 2013,

<sup>☆</sup> This research was supported by a US Department of Agriculture National Research Initiative–Managed Ecosystems grant (Proposal 2008-00776) and a National Science Foundation Graduate Research Fellowship (Grant DGE 1144083).

<sup>\*</sup> Correspondence: Nichole N. Barger, Ecology & Evolutionary Biology Dept, University of Colorado, Campus Box 334, Boulder, CO 80309-0334, USA. Tel.: +1 303 483 8239; fax: +1 303 492 8699.

E-mail address: [nichole.barger@colorado.edu](mailto:nichole.barger@colorado.edu) (N.N. Barger).

2014; Roundy et al., 2014a), responses in understory plant cover and species composition may vary considerably by site location and management strategy employed. Treatments that involve prescribed fire, for instance, may promote understory plant growth by temporarily increasing soil nutrient availability (Owen et al., 2009) yet lead to decreased soil fertility over time (Neary et al., 1999). Mulch left behind in mechanical mastication of piñon and juniper trees has been shown to increase understory plant cover by increasing soil stability, moisture, and nutrients (Jacobs and Gatewood, 1999; Owen et al., 2009; Morgan et al., 2014; Young et al., 2013) but alternatively may inhibit plant recolonization by limiting light availability and creating a physical barrier following fuel-reduction treatments (Morgan et al., 2014). Additional factors such as seed bank viability, invasive species presence, species interactions, climatic conditions, and livestock grazing can all contribute to the plant community response to treatment (Barney and Frischknecht, 1974; Allen et al., 2008; Faist et al., 2015).

Disturbance associated with fuel-reduction activities has regularly been shown to promote varying degrees of invasive plant establishment (Haskins and Gehring, 2004; Owen et al., 2009; Ross et al., 2012; Bybee et al., 2016). Although it is not always clear why treatment-associated disturbance creates a pathway for invasion, increased resources are thought to increase plant community invasibility (Vasquez et al., 2008). Increased availability of inorganic nitrogen (N) associated with prescribed burn, for instance, may enable greater competitiveness of invasive annual grasses over native perennial grasses following fuel-reduction treatments. Low understory cover before treatments (Goodrich and Rooks, 1999; Jacobs and Gatewood, 1999; Brockway et al., 2002), in addition to unavoidable removal of standing understory vegetation during management treatments (Osem et al., 2006), may result in a diminished soil seed bank and subsequently decrease the success of post-treatment understory plant establishment. Coupled with the disturbance associated with the removal of overstory plant species, this may further promote the proliferation of invasive non-native plant species (Davenport et al., 1998; Allen et al., 2008; Faist et al., 2015). In piñon-juniper woodlands that have undergone fuel-reduction treatments, an increase in the Eurasian invasive annual grass *Bromus tectorum* L. (*B. tectorum*) can be particularly problematic, as it establishes early in a growing season (Knapp, 1996) and can dominate post-treatment plant communities through successful competition following mastication (Bybee et al., 2016) and prescribed fire (Melgoza et al., 1990; Blank et al., 2007; Pyke et al., 2016). Native species recruiting post-treatment, especially perennial grasses, may experience difficulty competing against *B. tectorum* from the seed stage (Francis and Pyke, 1996; Blank et al., 2015), especially when native seed availability is low.

In an effort to reduce seed availability constraints to understory plant community restoration, seed mixes may be applied in conjunction with fuel-reduction treatments. These seeding applications are costly in terms of time and financial resources (Redmond et al., 2014) and may not be necessary if the seed availability within treated woodlands is sufficient for the restoration of the understory plant community (Jacobs and Gatewood, 1999; Stoddard et al., 2008). Thus, there is a need to better understand understory plant responses to common fuel-reduction treatments and evaluate the effectiveness of seeding applications for restoration so that land managers can better prioritize costly restoration efforts (Allen et al., 2008). A growing number of studies have investigated the effects of fuel-reduction techniques on piñon-juniper understory plant communities with (Stoddard et al., 2008; Redmond et al., 2014; Bybee et al., 2016; DeSandoli et al., 2016; Stephens et al., 2016) and without seeding applications (Fulé et al., 2002; Haskins and Gehring, 2004; Huffman et al., 2009; Owen et al., 2009; Huffman et al., 2013; O'Connor et al., 2013; Young et al., 2013; Miller et al., 2014; Roundy et al., 2014b; Provencher and Thompson, 2014; Bates and Davies, 2016). However, relatively few studies have assessed and compared effects of the most common fuel-reduction treatments (e.g., mastication, broadcast burn, pile burn) on understory plant communities

simultaneously (e.g., Huffman et al., 2013; O'Connor et al., 2013; Provencher and Thompson, 2014; Roundy et al., 2014b) or at time scales longer than the first 1–4 yr following treatment (but see, e.g., Huffman et al., 2013; Bates and Davies, 2016). The overarching goal of this study was thus to evaluate the short- and longer-term (i.e., 6 yr) effectiveness of common fuel-reduction techniques and seeding applications in enhancing native plant responses while resisting colonization of exotic species in an upland piñon-juniper woodland in southeastern Utah. We addressed these questions: 1) How does understory vegetation cover and composition respond to both mechanical and prescribed fire treatments? and 2) Does seeding increase understory cover and alter the species composition to the desired seed mix composition?

## Methods

### Site Description and Experimental Design

This study was conducted on Shay Mesa located on Bureau of Land Management (BLM) land within the Upper Colorado Plateau region of southeastern Utah, United States (37°58'42.97"N, 109°31'52.68"W). The study area at Shay Mesa lies at an elevation of 2237 m, is characterized as an upland shallow loam piñon-juniper ecological site (NRCS, 2004), and is classified as persistent piñon-juniper woodland (Romme et al., 2009). The upland shallow loam piñon-juniper ecological site type is common throughout this region of the Colorado Plateau and is representative of the vegetation types that are commonly targeted for fuel-reduction treatments by the BLM (USDA, 2004). Mean annual precipitation on Shay Mesa is 396 mm and follows a bimodal distribution with monsoonal rains in the summer and snow in the winter, and the mean growing season temperature (March – October) is 14°C (yr 1981 – 2010; <http://www.prism.oregonstate.edu>). Shay Mesa and the entire study site were chained and seeded in 1959 but have since undergone rapid recolonization by the primary overstory species two-needle piñon (*Pinus edulis* Engelm.) and Utah juniper (*Juniperus osteosperma* [Torr.] Little). Other common native plants found within the study site included mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle), broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britton & Rusby), Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth), and blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths). (A full list of the plant species identified within the Shay Mesa experimental site is in Table A1 of the appendix).

In June 2009, fire specialists from the Canyon Country Fire Zone performed three fuel-reduction treatments within randomly designated treatment areas of approximately equal size (~13 ha) within an area of ~40 ha on Shay Mesa: 1) mechanical mastication (mastication), 2) lop and scatter followed by a broadcast burn (broadcast burn), and 3) lop and slash collected in piles and then burned (pile burn). The mastication method used a wood mulcher (or “bullhog”) to remove trees and produce wood mulch. Burn treatments were implemented with drip torches. The broadcast burn treatment involved cutting down trees and spreading the slash across the landscape before a prescribed burn was applied as a backing fire. The pile burn method is similar to the broadcast burn, but instead of spreading the slash, it was placed into piles that were subsequently burned. For both controlled burn treatments, trees were cut in June 2009 and burning was performed 5 months later in November 2009. A control, untreated site was also established within the experimental site boundaries. Plant cover data were collected for comparisons in the summer before each treatment was applied (pretreatment: 2009), as well as one (2010), two (2011), and six (2015) growing seasons after the treatments were applied.

To assess the effectiveness of post-treatment seeding application, the original experimental design was a full factorial experiment with each treatment plot and the untreated area randomly subdivided into seeded and unseeded plots. However, a seeding error occurred, which resulted in all broadcast burn and pile burn plots receiving seeding

treatments. Due to this error, study vegetation response variables to fuel-reduction treatments and seeding applications are examined separately. Specifically, we compare 1) seeded treatment plots (i.e., seeded mastication, broadcast burn, pile burn, and control) to discern differences among seeded fuel-reduction treatments; 2) unseeded mastication and control plots to assess effects of mastication in the absence of seeding; and 3) seeded and unseeded mastication and control plots to determine the relative contribution of seeding to understory plant responses. The seed mixture was created and applied via all-terrain vehicle (ATV) seed spreaders by BLM collaborators. The mixture was composed of a combination of seven native and five non-native plant species (Table 1).

#### Vegetation & Ground Cover

In the spring (May–June) of 2009, before treatment, we randomly established ten, 35-m transects within each of the six plot types, all on slopes of  $\leq 8\%$  and on the same soil type (Bond-Rizno fine sandy loam). Each transect line ran parallel to the contour of the slope. In 2009 (pretreatment), 2010 (one growing season post treatment), 2011 (two growing seasons post treatment), and 2015 (six growing seasons post treatment), we measured plant and soil cover along each transect using the line-point intercept method (Herrick et al., 2005). A pin-flag was dropped at every 50 cm along each transect from a height of  $\sim 1$  m for a total of 70 points/transect. Every plant canopy species or ground cover that the pin-flag hit was recorded, as well as tree and shrub canopies that were directly above the dropped pin-flag. These data were used for the analysis of percent total plant cover, plant functional group cover, and plant species richness.

#### Data Analysis

##### Pretreatment

Pretreatment (2009) plant cover data were analyzed using permutational multivariate analysis of variance (PERMANOVA) to test for community-level differences in plant cover among experimental plots. Pretreatment plant cover data were tested for normality using the Shapiro–Wilk test (Shapiro and Wilk, 1965). Subsequently, treatment data were analyzed using one-way analysis of variance (ANOVA) or nonparametric Kruskal–Wallis tests to test for pretreatment differences in parameters related to plant cover. Kruskal–Wallis tests were used if response variables failed to meet assumptions of normality and homoscedasticity. Statistical significance for all tests was set to  $\alpha = 0.05$ .

##### Post Treatment

Due to the seeding error whereby all broadcast burn and pile burn plots received seeding in 2009, we separate all post-treatment plant

response data analyses in the following ways: First, seeded fuel-reduction treatments (seeded mastication, broadcast burn, pile burn, and control plots) were analyzed together to compare the effects of seeded fuel-reduction treatments on understory plant communities. Secondly, unseeded mastication plots were compared with the unseeded control in an effort to quantify the effects of mastication on understory responses without seeding. Finally, unseeded and seeded mastication and control plots were analyzed separately from broadcast and pile burn plots to directly quantify the effects of seeding on understory plant community responses. All years seeded and unseeded post-treatment data were individually analyzed using PERMANOVA to test for differences in plant cover at the community level. Following PERMANOVA analysis, 2010, 2011, and 2015 post-treatment data were analyzed separately in an effort to meet the assumptions of normality and homoscedasticity. Within each year, treatment and seeding effects were also analyzed separately. ANOVAs or Kruskal–Wallis non-parametric tests were used to assess the differences in response variables among the four seeded fuel-reduction treatment sites (i.e., mastication, broadcast burn, pile burn, and control plots) with subsequent paired comparisons when treatment effects were indicated. Following statistically significant results, pair-wise comparisons were assessed using appropriate parametric post hoc Tukey–Kramer honest significant difference (HSD) or nonparametric pairwise Wilcoxon Sum-Rank tests. All  $P$  values resulting from pairwise Wilcoxon Sum-Rank tests were adjusted using a false discovery rate correction. Differences among seeded and unseeded control and mastication plots by year were analyzed separately using Kruskal–Wallis tests. All statistical tests were done in R (R Core Team, 2015), with  $\alpha = 0.05$ .

## Results

#### Climate Variability

Climate during the study (2009–2015) was highly variable on Shay Mesa (Fig. 1). For instance, 2010 (one growing season post treatment), 2011 (two growing seasons post treatment), and 2015 (six growing seasons post treatment) had abnormally wet winter and/or spring seasons, receiving 99 mm, 38 mm, and 58 mm more total precipitation from December–May than the 1981–2010 long-term average (146 mm; see Fig. 1). The winter-spring precipitation totals in 2012 and 2013 (three and four growing seasons post treatment), however, were low, receiving 16 and 13 mm less than the 1981–2010 average, respectively (see Fig. 1). Notably, the wet winter/spring season of 2015 was also  $2.2^\circ\text{C}$  warmer than the long-term average ( $6.9^\circ\text{C}$ ; see Fig. 1).

#### Pretreatment Understory Plant Community Analysis

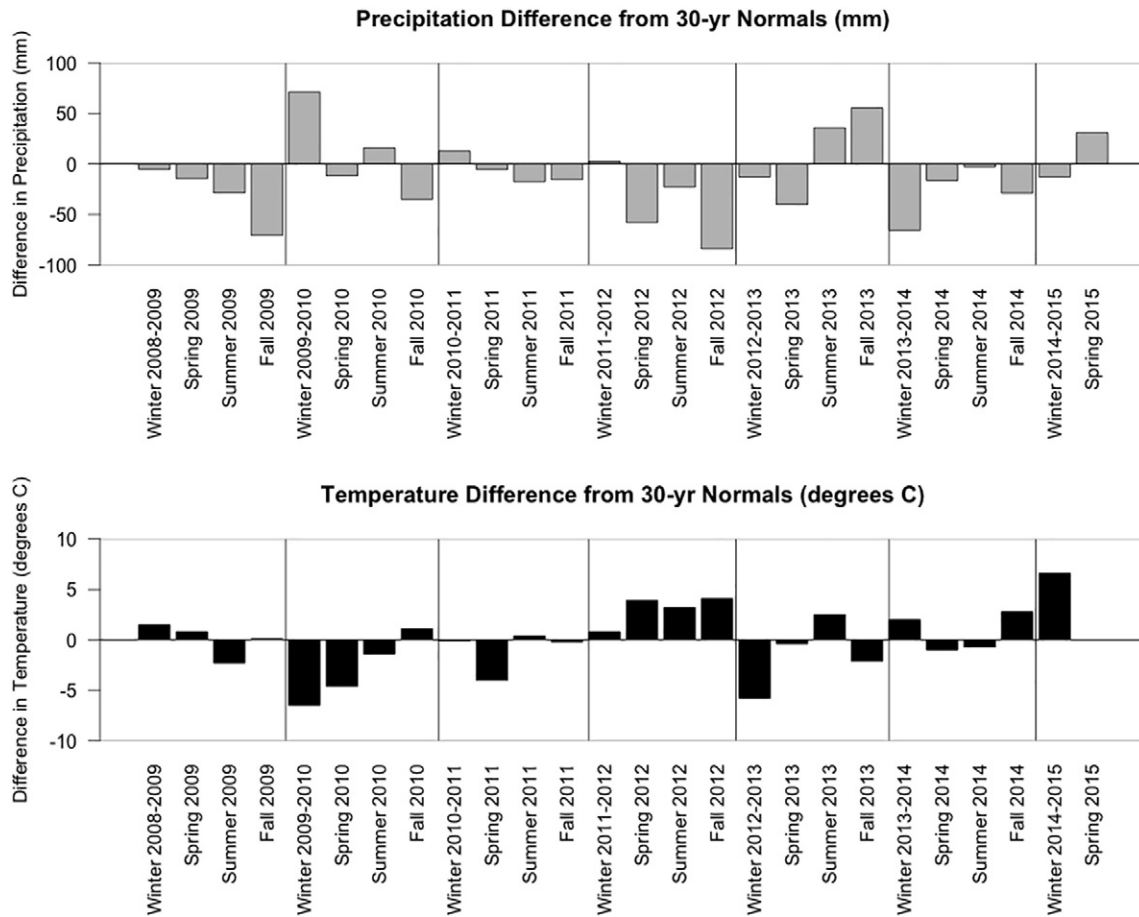
Pretreatment plant communities were similar across all sites in 2009 (PERMANOVA;  $P < 0.001$ ), and there were no statistically significant differences among plant response variables (Kruskal–Wallis/ANOVA; all  $P > 0.05$ ) across treatment plots. Thus, any differences observed in plant community cover and composition in post-treatment years should reflect treatment effects. Specifically, pretreatment tree cover was statistically equal across all experimental plots ( $P = 0.240$ ) at  $\sim 29\%$  (range: 23.1–36.4% cover). Mean herbaceous understory plant cover was equally low across all treatment plots at  $\sim 6\%$  total cover with non-native species cover at averages of 0.1%. Seed mix plant species cover was also low across all plots with averages of  $\sim 2\%$ .

#### Understory Plant Community Response to Fuel-Reduction Treatments with Seeding

In this section, we compare plant community responses among seeded fuel-reduction treatment plots (i.e., seeded control, mastication, broadcast burn, and pile burn). Here, we make no direct comparisons among seeded and unseeded treatment plots due to an error in which

**Table 1**  
Seed mix species applied to seeded treatment plots at Shay Mesa and their relative abundance in the seed mix. All percentages sum to 100%.

Native		
Common name	Scientific name	% Seed mix
Sandberg bluegrass	<i>Poa secunda</i>	18
Indian ricegrass	<i>Achnatherum hymenoides</i>	15
Mountain big sagebrush	<i>Artemisia tridentata</i> ssp. <i>vaseyana</i>	11
Western wheatgrass	<i>Pascopyrum smithii</i>	11
Needle and thread	<i>Hesperostipa comata</i> ssp. <i>comata</i>	3
Winterfat	<i>Krascheninnikovia lanata</i>	2
Antelope bitterbrush	<i>Purshia tridentata</i>	1
Non-native		
Lewis flax	<i>Linum lewisii</i>	14
Sweetclover	<i>Melilotus officinalis</i>	10
Crested wheatgrass	<i>Agropyron cristatum</i>	7
Chickpea milkvetch	<i>Astragalus cicer</i>	6
Sanfoin	<i>Onobrychis viciifolia</i>	2



**Figure 1.** Differences in total precipitation (mm), and mean temperature ( $^{\circ}\text{C}$ ) compared with 30-yr long-term averages (1981–2010) at Shay Mesa, Utah (data from <http://prism.oregonstate.edu>) for winter (December–February), spring (March–May), summer (June–August), and fall (September–November) from December 2009 through May 2015.

all broadcast and pile burn plots were seeded in 2009. To compare understory plant community responses to the three seeded fuel-reduction treatments relative to each other and to the seeded control, we measured understory plant cover and species richness response variables one (2010), two (2011), and six (2015) growing seasons following treatment implementation. Understory plant response variables include the total understory plant community response, which contains native and non-native herbaceous and woody plant species (Table 2). Within the total understory plant cover response, we also report native and non-native plant species cover and percent cover of major plant functional groups. These functional groups include perennial grasses and sedges, perennial forbs, annual grasses, annual forbs, trees, and shrubs. We also report the contributions of seed mix species (see Table 2) and *B. tectorum* to the total understory plant community (Fig. 2).

We observed no treatment effects in understory plant cover response variables in the first growing season post treatment (2010) aside from the expected obvious declines in woody 12 species cover in all seeded fuel-reduction treatment plots relative to the seeded control, which remained low (1–3% cover; see Table 2) across all growing seasons. However, by 2011 mean total understory plant cover was more than threefold higher ( $P < 0.001$ ; see Table 2) in the three seeded fuel-reduction treatments relative to the seeded control (mastication = 20%, broadcast burn = 24%; pile burn = 18%; control = 5%; see Table 2). This increase in total understory cover was accompanied by an increase in understory plant species richness ( $P < 0.05$ ; Table 3) in all seeded fuel-reduction treatment plots relative to the seeded control. Seeded mastication and broadcast burn plots had higher species richness relative to the seeded pile burn and control plots ( $P = 0.04$  each;

see Table 3). By 2015, total understory plant cover remained higher in the seeded treatments relative to the seeded control ( $P < 0.001$ ; see Table 2) and differed among fuel-reduction treatment types with total understory cover higher ( $P = 0.03$ ; see Table 2) in the pile burn plots at 66% relative to the mastication and broadcast burn plots both at 46% cover. In 2015, species richness was also higher ( $P < 0.05$ ; see Table 3) in all seeded treatment plots relative to the seeded control and was highest in the pile burn plot. This result suggests seeded fuel-reduction treatments increase understory plant diversity.

In 2011 and 2015 differences between native understory plant cover in seeded treatment and control plots were primarily attributed to increases in perennial grass and sedge cover in all treatment plots. Specifically, all seeded treatments resulted in high recruitment of native perennial bunchgrasses *Achnatherum hymenoides* and *Pascopyrum smithii* relative to the seeded control. By 2011 perennial grass and sedge cover was higher (5–11%;  $P < 0.05$ ; see Table 2) in all seeded fuel-reduction treatments relative to the seeded control ( $0.86\% \pm 0.23\%$ ). Notably, perennial grass and sedge cover was statistically higher in the seeded broadcast and mastication plots compared with the pile burn (see Table 2). By 2015 cover of perennial grasses and sedges increased to ~31–38% cover in seeded treatment plots, while their cover remained low in the seeded control plot at only  $2.1\% \pm 0.86\%$ . Perennial forb cover showed slightly higher ( $P = 0.05$ ; see Table 2) recruitment in the seeded mastication plot relative to the seeded control and burn treatments in 2011. However, by 2015 there were no differences in perennial forb, annual forb, or shrub cover among seeded treatments. During the first two growing seasons, annual grass cover remained low in seeded treatment plots (2011 average ~2.4%; see Table 2). However, by 2015, there were notable differences in

**Table 2**

Means (and standard errors) of understory vegetative cover (%) by functional groups for the six treatments in post-treatment yr 2010, 2011, and 2015. Total understory plant cover includes herbaceous and woody native and non-native plant cover. Within the total understory plant response, we also note the relative contributions of native and non-native plant cover, major plant functional groups (e.g., perennial grasses and sedges, annual grasses), and seed mix species. Uppercase letters A–C indicate statistically different means for the comparison of unseeded and seeded plots (Control, Mastication) at  $\alpha = 0.05$ . Lowercase letters a–c indicate statistically different means for the within-year comparison of seeded plots. No between-year comparisons are shown.

	Comparison of unseeded and seeded plots		Comparison of seeded plots			
	Control unseeded	Mastication unseeded	Control seeded	Mastication seeded	Broadcast burn seeded	Pile burn seeded
<b>Total understory</b>						
2010	8.14 (2.61) A	3.43 (1.30) A	5.71 (1.28) Aa	4.43 (1.53) Aa	4.29 (1.79) a	8.14 (1.73) a
2011	7.78 (2.45) A	23.57 (4.02) B	4.86 (1.07) Aa	19.71 (1.90) Bb	23.71 (8.28) b	18.43 (2.19) b
2015	7.43 (2.29) A	71.04 (3.71) B	6.57 (2.64) Aa	45.86 (4.59) Cb	46.00 (6.86) b	66.29 (4.74) c
<b>Non-native</b>						
2010	0.14 (0.14) A	0.57 (0.38) A	0.00 (0.00) Aa	0.29 (0.19) Aa	0.57 (0.32) a	0.29 (0.29) a
2011	0.32 (0.29) A	3.86 (1.48) AB	0.14 (0.14) ABa	3.71 (0.83) ACb	5.14 (2.15) c	3.86 (0.80) c
2015	0.00 (0.00) A	29.00 (7.35) B	0.14 (0.14) Aa	3.29 (0.64) Cb	8.71 (2.88) b	18.57 (5.32) c
<b>Native</b>						
2010	8.00 (1.81) A	2.86 (1.28) A	5.71 (1.28) Aa	4.14 (1.45) Ab	3.71 (1.52) bc	7.73 (1.70) c
2011	7.00 (2.45) A	19.71 (3.22) B	4.71 (1.00) Aa	16.29 (1.61) Bb	19.00 (6.14) b	15.14 (1.54) b
2015	7.42 (2.29) A	47.86 (3.89) B	6.71 (2.80) Aa	42.57 (4.74) Bb	37.43 (4.71) b	47.71 (3.73) b
<b>Annual grasses</b>						
2010	0.00 (0.00) A	0.57 (0.38) A	0.00 (0.00) Aa	0.43 (0.22) Aa	0.57 (0.32) a	0.29 (0.29) a
2011	0.00 (0.00) A	4.43 (1.54) B	0.00 (0.00) Aa	1.29 (0.72) Aa	3.57 (2.06) a	2.29 (0.86) a
2015	0.00 (0.00) A	30.71 (7.47) B	0.00 (0.00) Aa	2.00 (0.77) Ca	5.86 (2.45) ab	16.57 (5.39) b
<b>Perennial grasses and sedges</b>						
2010	1.43 (0.56) A	0.43 (0.30) A	1.14 (0.42) Aa	0.57 (0.23) Aa	0.71 (0.38) a	1.43 (0.48) a
2011	2.70 (1.52) A	5.14 (1.33) A	0.86 (0.23) Aa	8.43 (1.87) Abc	11.85 (4.80) c	5.86 (1.54) b
2015	3.14 (1.47) A	35.43 (4.17) B	2.14 (0.86) Aa	37.71 (4.59) Cb	31.43 (5.55) b	38.00 (4.04) b
<b>Annual forbs</b>						
2010	0.71 (0.57) A	1.14 (0.67) A	0.00 (0.00) Aa	0.57 (0.23) Aa	1.29 (0.86) a	1.00 (0.37) a
2011	0.16 (0.14) A	7.86 (2.13) A	0.00 (0.00) Aa	2.00 (0.96) Aa	3.57 (1.72) a	3.71 (1.28) a
2015	0.00 (0.00) A	4.00 (1.06) B	0.29 (0.19) Aa	1.43 (0.30) Ba	2.71 (1.45) a	1.86 (0.52) a
<b>Perennial forbs</b>						
2010	2.00 (0.71) A	0.71 (0.38) A	2.14 (0.68) Aa	0.43 (0.30) Aa	0.57 (0.32) a	0.57 (0.23) a
2011	1.75 (0.58) A	3.43 (1.52) AB	0.71 (0.32) Aa	5.43 (1.18) Bb	3.43 (1.22) ab	2.00 (0.44) ab
2015	2.70 (0.77) A	1.90 (0.51) A	1.14 (0.51) Aa	2.43 (0.74) Aa	1.86 (0.77) a	2.43 (1.00) a
<b>Shrubs</b>						
2010	4.00 (1.20) A	0.57 (0.38) A	2.43 (0.95) Aa	2.43 (0.93) Aa	1.14 (0.59) a	4.86 (1.23) a
2011	3.17 (1.06) A	2.71 (0.86) A	3.29 (0.95) Aa	2.57 (0.79) Aa	1.71 (0.36) a	4.71 (1.66) a
2015	1.86 (0.85) A	7.43 (1.31) B	3.29 (2.07) Aa	2.29 (0.57) Aa	4.14 (0.62) a	7.43 (1.67) a
<b>Trees</b>						
2010	26.14 (4.44) A	1.28 (1.28) B	31.14 (3.91) Aa	0.71 (0.44) Bb	3.29 (1.89) b	1.28 (1.14) b
2011	26.57 (3.34) A	1.14 (1.14) B	28.29 (3.61) Aa	0.14 (0.14) Bb	2.14 (2.14) b	1.29 (0.99) b
2015	23.14 (2.82) A	1.00 (1.00) B	29.27 (3.32) Aa	0.00 (0.00) Bb	2.86 (2.86) b	2.14 (1.99) b
<b>Seed mix species</b>						
2010	0.43 (0.22) A	0.14 (0.14) A	0.86 (0.32) Aa	0.00 (0.00) Aa	0.43 (0.22) a	0.86 (0.32) a
2011	0.63 (0.39) A	3.71 (1.15) AB	0.95 (0.57) ABa	10.00 (2.36) Bb	11.43 (2.65) b	7.14 (1.81) b
2015	1.46 (0.66) A	29.57 (3.71) B	1.86 (0.78) Aa	33.86 (4.81) Bb	31.86 (5.59) b	40.00 (4.97) b

*B. tectorum* response among seeded fuel-reduction treatment types with cover nearly threefold higher in the pile burn (16.29%  $\pm$  5.13%; see Fig. 2) relative to broadcast burn (5.86%  $\pm$  2.45%; see Fig. 2) and mastication (1.57%  $\pm$  0.65%; see Fig. 2) plots. Notably, *B. tectorum* was absent in the seeded control in all monitored growing seasons. These results show a trend of increased *B. tectorum* recruitment as a consequence of the fuel-reduction activities in this study.

#### Understory Plant Community Response to Mastication (Without Seeding)

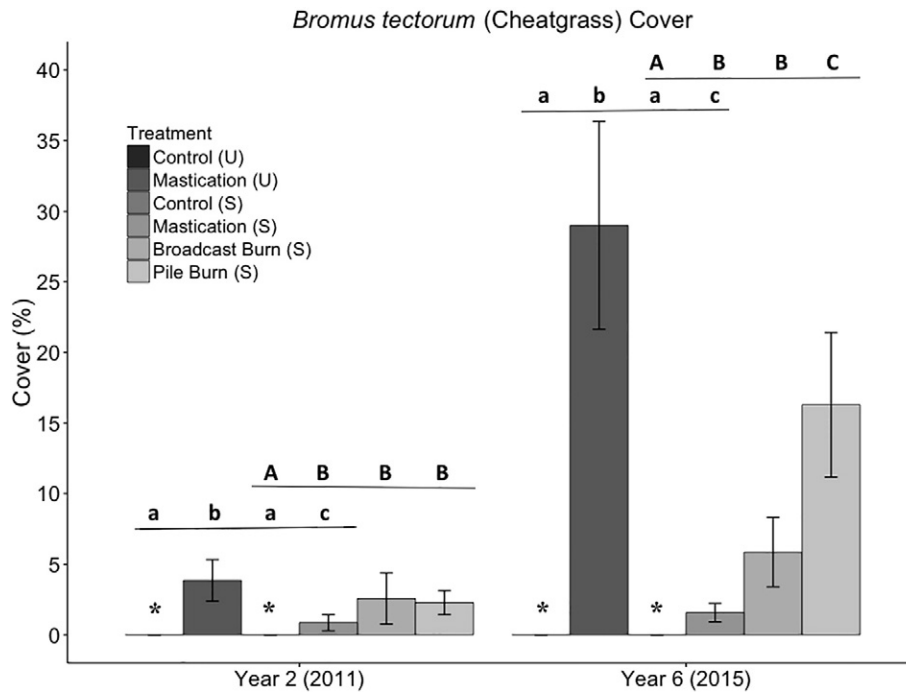
To directly quantify understory plant community responses to mastication in the absence of seeding, we compared understory plant responses in the unseeded mastication plot to unseeded control. After two growing seasons (2011), unseeded mastication increased understory plant cover, resulting in threefold higher total understory plant cover (23.71%  $\pm$  8.28%;  $P < 0.01$ ; see Table 2) relative to the unseeded control (7.78%  $\pm$  2.45%). Continuing this trend, by the sixth growing season post treatment (2015) the unseeded mastication treatment had 9.5-fold higher total understory plant cover (71.04%  $\pm$  3.71%;  $P < 0.001$ ; see Table 2) relative to the unseeded control (7.43%  $\pm$  2.29%).

Within the total understory cover response by 2015, the unseeded mastication treatment resulted in over sixfold higher native plant

species cover (47.86%  $\pm$  3.89%;  $P = 0.01$ ; see Table 2) relative to the unseeded control (7.42%  $\pm$  2.29%). In the unseeded mastication plot, perennial grasses and sedge, annual forb, and shrub cover increased by factors of 11 (35.43%  $\pm$  4.17%), 4 (4.00%  $\pm$  1.06%), and 4 (7.43%  $\pm$  1.31%), respectively, compared with the unseeded control (3.14%  $\pm$  1.47%, 0.00%  $\pm$  0.00%, 1.86%  $\pm$  0.85%; all  $P < 0.01$ ; see Table 2). Overall, herbaceous perennial plant cover comprised 53% and 79% of relative plant cover in the unseeded mastication and control, respectively, by 2015. Along with these increases, non-native plant cover also increased 30-fold (29.00%  $\pm$  7.35%; see Table 2) in the unseeded mastication relative to the unseeded control (0.00%  $\pm$  0.00%). *B. tectorum* contributed to a majority (91%) of this non-native plant cover response. Indeed, while *B. tectorum* remained absent in the unseeded control for all growing seasons, the unseeded mastication treatment resulted in 26.36%  $\pm$  3.71% *B. tectorum* cover by 2015. Notably, *B. tectorum* cover in the unseeded mastication plot was the highest among all seeded and unseeded fuel-reduction treatments.

#### Understory Plant Community Responses to Seeding Application

To quantify the relative contribution of seeding to the understory response in mastication and control plots, we compared the cover and



**Figure 2.** Mean post-treatment *B. tectorum* cover for the six treatments two (2011) and six (2015) growing seasons post treatment. Pretreatment (2009) and one growing season (2010) post treatment are not shown because there were no treatment effects in these years. In 2011 and 2015, there was 0% cover of *B. tectorum* in unseeded and seeded control plots (denoted by “\*”). Lowercase letters a – c indicate statistically different means for the comparison of unseeded and seeded plots at  $\alpha = 0.05$ . Uppercase letters A – C indicate statistically different means for the within-year comparison of seeded plots. Bars represent  $\pm 1$  standard error of the mean ( $n = 10$ ). No between-year comparisons are shown.

species richness of the 12 seeded plant species (see Table 1) in both the unseeded versus seeded controls and the unseeded versus seeded mastication plots. While we cannot ultimately determine which individual plants recruited from the seed mix versus the preexisting seed bank on Shay Mesa, these comparisons allow us to gauge the relative contribution of seeding to seed mix species recruitment in the post-treatment landscape.

We found no differences in plant cover or richness responses between seeded and unseeded control plots in any years sampled (see Tables 2 and 3). This suggests that seeding applications may not significantly enhance understory plant communities in persistent piñon-juniper woodlands when fuel-reduction treatments are not applied in combination with seeding.

While there was no effect of seeding in control plots, we observed differences in understory plant community cover and composition between the unseeded and seeded mastication plots. There were no differences in total understory plant cover in the first (2010) and second (2011) growing season post treatment. However, by 2015 there was a significant seeding effect ( $P = 0.03$ ; see Table 2) whereby total understory cover was highest at  $71.04\% \pm 3.71\%$  in the unseeded mastication compared with the seeded mastication plot ( $45.86\% \pm 4.59\%$ ; see Table 2). Within their total understory plant cover responses, unseeded and seeded mastication treatments produced distinct understory plant communities by the sixth growing season post treatment. By 2015 the seeded mastication treatment resulted in marginally greater cover of perennial grass and sedges ( $37.71\% \pm 4.59\%$ ;  $P = 0.04$ ; see Table 2)

**Table 3**  
Means (and standard errors) of total understory, non-native, native, and seed mix plant species richness for six treatments in post-treatment yr 2010, 2011, and 2015. Uppercase letters A – C indicate comparison of unseeded and seeded plots at  $\alpha = 0.05$ . Lowercase letters a – c indicate statistically different means for the comparison of seeded plots.

Treatment	Comparison of unseeded and seeded plots					
	Control unseeded	Mastication unseeded	Comparison of seeded plots			
			Control seeded	Mastication seeded	Broadcast burn seeded	Pile burn seeded
<b>Total understory</b>						
2010	3.20 (0.65) A	1.50 (0.56) B	2.70 (0.52) Aab	2.10 (0.66) ABa	2.00 (0.88) ab	3.40 (0.60) b
2011	2.80 (0.68) A	6.10 (0.98) B	1.80 (0.29) Ca	7.40 (0.52) Bb	5.80 (0.84) c	6.80 (0.71) bc
2015	2.60 (0.58) A	8.00 (0.65) B	2.30 (0.56) Aa	7.30 (0.47) Bb	6.60 (0.45) b	8.30 (0.50) c
<b>Non-native</b>						
2010	0.10 (0.10) A	0.20 (0.13) A	0.00 (0.00) Aa	0.20 (0.13) Ab	0.30 (0.15) b	0.10 (0.10) ab
2011	0.10 (0.10) A	0.60 (0.16) B	0.10 (0.10) Aa	1.40 (0.16) Cb	1.70 (0.42) b	1.80 (0.25) b
2015	0.00 (0.00) A	1.00 (0.15) B	0.10 (0.10) Aa	1.10 (0.18) Bb	1.20 (0.25) b	1.70 (0.26) c
<b>Native</b>						
2010	3.10 (0.59) A	1.30 (0.54) B	2.70 (0.52) ACab	1.90 (0.60) BCa	1.70 (0.75) a	3.30 (0.58) b
2011	2.70 (0.52) A	5.50 (0.86) B	1.70 (0.26) Ca	6.00 (0.56) Bb	4.10 (0.57) c	5.00 (0.49) bc
2015	2.60 (0.58) A	7.00 (0.60) B	1.60 (0.43) Aa	6.20 (0.47) Bbc	5.40 (0.43) b	6.60 (0.40) c
<b>Seed mix</b>						
2010	0.30 (0.15) A	0.10 (0.10) B	0.30 (0.15) Aa	0.00 (0.00) Bb	0.30 (0.15) a	0.60 (0.22) a
2011	0.40 (0.22) AB	0.80 (0.20) A	0.30 (0.15) Ba	2.90 (0.50) Cb	2.70 (0.47) b	2.20 (0.51) b
2015	0.50 (0.17) A	2.00 (0.26) B	0.50 (0.17) Aa	3.40 (0.45) Cb	3.30 (0.21) b	3.60 (0.37) b

and threefold lower shrub cover ( $2.29\% \pm 0.57\%$ ;  $P = 0.03$ ; see Table 2) relative to perennial grass and sedge ( $35.43\% \pm 4.17\%$ ) and shrub ( $7.43\% \pm 1.31\%$ ) in the unseeded mastication treatment. Overall, herbaceous perennial plant cover was ~53% and ~88% in the unseeded and seeded mastication plots, respectively. Annual grass cover was additionally > 15-fold higher in the unseeded mastication treatment ( $30.71\% \pm 7.47\%$ ;  $P = 0.01$ ; see Table 2) at 44% cover relative to the seeded mastication treatment ( $2.00\% \pm 0.77\%$ ). This difference in annual grass cover was driven vastly by proliferation of *B. tectorum* in the unseeded mastication plot (see Fig. 2). Indeed, *B. tectorum* accounted for 86% of all annual grass cover in the unseeded mastication plot and comprised  $26.36\% \pm 3.71\%$  of unseeded mastication ground cover (see Fig. 2). Conversely, *B. tectorum* cover in the seeded mastication remained low ( $1.57\% \pm 0.65\%$ ). Lower cover of *B. tectorum* in the seeded mastication plot suggests seeding applications may pose a barrier to annual grass proliferation following mastication as a fuel-reduction treatment.

In addition to analyzing differences in plant functional groups between unseeded and seeded mastication plots, we also specifically compared seed mix species cover and richness. Interestingly, while there was no significant seeding effect on mean seed mix species cover between unseeded and seeded mastication treatments, seed mix species richness was higher ( $P = 0.05$ ; see Table 3) in the seeded mastication plot relative to the unseeded mastication plot both two and six growing seasons post treatment. This result may suggest that while the applied seed mix did not increase cover of seed mix species, seeding contributed to higher plant community diversity in seeded plots.

## Discussion

Our results highlight differences in understory plant community responses to common fuel-reduction treatments (i.e., mastication, broadcast burn, pile burn) with seeding applications in an upland piñon-juniper woodland on Shay Mesa within the Colorado Plateau region of southeastern Utah. We found short-term (1–2 growing seasons) herbaceous understory plant recruitment responded similarly across all seeded fuel-reduction treatments and followed trends consistent with the results of similar studies comparing understory vegetation responses in piñon-juniper woodlands to fuel-reduction treatments. Six growing seasons post treatment, however, we found seeded fuel-reduction treatments produced differences in understory plant community composition, specifically in differing annual grass cover. Additionally, comparisons between unseeded and seeded mastication plots suggest seeding applications may contribute to native over non-native plant recruitment following treatment.

### Plant Community Response to Fuel-Reduction Treatments with Seeding

Primary goals when implementing fuel-reduction treatments in piñon-juniper woodlands on public lands include reducing woody overstory fuel loads and enhancing herbaceous understory plant communities. In assessment of the first goal, we analyzed overstory tree cover before and after fuel-reduction treatment. Importantly, pretreatment (2009) average tree (piñon and juniper) cover was statistically equivalent across treatment plots at about 29%. Pretreatment tree cover has been shown by others to influence understory abundance and the trajectory of post-treatment understory plant responses (Bates et al., 2005; Dhaemers, 2006; Bates et al., 2014; Miller et al., 2014; Roundy et al., 2014b). As pretreatment tree cover was approximately equivalent for all plots in our study, we can assume that all differences in post-treatment understory plant responses represent treatment effects rather than pretreatment tree cover differences. Following treatment, we found all fuel-reduction treatments were similarly successful in decreasing piñon-juniper woody fuel loads and resulted in low reestablishment of tree cover one, two, and six growing seasons post treatment (see Table 2). Fuel-reduction treatments reduced post-treatment tree cover to an average of 1.3% across treatments in 2010,

and that tree cover remained at 1.5% through 2015. This suggests that since fuel-reduction treatment implementation in 2009, there has been relatively low tree reestablishment on Shay Mesa.

In assessment of the second goal, we first compared understory plant community responses to seeded fuel-reduction treatments. While we cannot directly quantify the effects of broadcast and pile burn treatments in the absence of seeding, we are able to discern relative treatment effects by comparing the seeded mastication, broadcast burn, and pile burn treatments to the seeded control. All seeded treatments were successful in increasing herbaceous understory plant cover one (2010), two (2011), and six (2015) growing seasons post treatment, though the magnitude of these increases and resulting understory plant community composition varied by treatment across years. Short-term (1–2 growing season) herbaceous understory responses to seeded fuel-reduction treatments in this study follow trends similar to those reported in other studies comparing understory plant responses to fuel-reduction treatments (both seeded and unseeded) and untreated controls in piñon-juniper woodlands. With few exceptions (Owen et al., 2009), studies indicate that herbaceous understory cover typically increases in the first 1–3 yr following mastication (Ross et al., 2012; Young et al., 2013; Redmond et al., 2014; Bybee et al., 2016; Stephens et al., 2016), broadcast burn (Ross et al., 2012; O'Connor et al., 2013; Redmond et al., 2014), and pile burn (Ross et al., 2012; O'Connor et al., 2013; Redmond et al., 2014) fuel-reduction treatments.

On the basis of ecological site descriptions, the potential understory plant cover in upland piñon-juniper woodlands is 55% (NRCS, 2004). However, such restoration targets are often not met by the first 1–3 growing seasons following treatment. Our study results, for instance, showed an average of only 20% total understory plant cover with 12% herbaceous perennial cover two growing seasons post treatment. While there were no differences in perennial herbaceous cover in 2010, there was slightly greater perennial grass and sedge cover in seeded broadcast burn (~12%; see Table 2) relative to the seeded pile burn (~6%) plot in 2011. Overall, lower perennial responses 1–3 yr following treatment may be because this time window is too soon to detect substantial establishment and growth of perennials (Bates et al., 2005, 2007).

Despite the modest response of perennial species in 2010 and 2011, by 2015 we observed more substantial increases in perennial herbaceous understory plant cover across seeded fuel-reduction treatments (~38%; see Table 2) that were on the magnitude of established restoration goals for upland piñon-juniper woodlands (NRCS, 2004). Delayed increases in perennial understory cover over longer time scales are consistent with other longer-term studies in piñon-juniper woodlands that assess vegetation dynamics following fuel-reduction treatments (e.g., 5 yr, O'Connor et al., 2013; 10 yr, Bates and Davies, 2016). Studies demonstrate that the perennial understory is often slow to recover following fuel-reduction with low perennial cover in the first to third growing seasons followed by more substantial increases 5–10 yr post treatment. Within the perennial response, we found large responses in perennial grass and sedge cover 6 yr post treatment but no substantial increases in perennial forb cover over time. This result of low perennial forb cover is consistent with other piñon-juniper removal studies (Owen et al., 2009; Provencher and Thompson, 2014), but it conflicts with other observations of significant increases in perennial forb cover by 2–3 growing seasons post treatment (Tausch and Tueller, 1977; O'Connor et al., 2013). Others have shown annual forbs tend to dominate early successional, post-fuel-reduction piñon-juniper understory plant communities and then decline as perennial species cover increases over time (Bates et al., 2000; Bates and Svejcar, 2009). We conversely found no substantial increase in annual cover across fuel-reduction treatments 1–2 yr following treatment and observed generally low forb cover across all post-treatment years (see Table 2). Low annual forb cover may be potentially due to below-average annual precipitation observed in 2011, 2012, and 2014 on Shay Mesa (see Fig. 1).

### *B. tectorum* Response to Seeded Fuels-Reduction Treatments

Although we found all seeded fuel-reduction treatments to be similarly successful in enhancing cover of the herbaceous understory, we did observe differences in native versus non-native understory plant community composition among treatments by 2015. Specifically, there were large differences in the response of *B. tectorum* among seeded fuel-reduction treatments. *B. tectorum* was all but absent from this piñon-juniper woodland before treatment in 2009 and remained entirely absent in both unseeded and seeded control plots in all years monitored (see Fig. 2). In the first two growing seasons following treatment, *B. tectorum* cover remained relatively low with an average of relative cover of ~9% in 2011 among all seeded treatments. However, by 2015 *B. tectorum* cover increased significantly across all seeded treatment plots, reaching ~15% average relative cover (see Fig. 2). Overall, these results suggest a delayed response of *B. tectorum* in seeded fuel-reduction treatment plots.

Delayed *B. tectorum* colonization following fuel-reduction treatments reflects a consistent trend reported in other short and longer-term piñon-juniper fuel-reduction studies (O'Connor et al., 2013; Roundy et al., 2014b; Miller et al., 2014; Stephens et al., 2016). In our study, we postulate increases in *B. tectorum* cover over time are likely due to a combination of several factors. First, *B. tectorum* has been shown to respond positively to above-average levels of precipitation in the winter and spring when accompanied by above-normal seasonal temperatures (Zelikova et al., 2013). As there was a warm winter and above-average precipitation in spring 2015 (see Fig. 1), it is possible that the observed increases in *B. tectorum* cover in 2015 were in part due to favorable climatic factors. Differences in pretreatment *B. tectorum* cover among treatment plots are additionally often thought to contribute to post-treatment *B. tectorum* colonization (Roundy et al., 2014b). However, there were no differences in pretreatment *B. tectorum* cover across plots on Shay Mesa. Therefore, our results suggest differences in the microenvironments produced by the fuel-reduction treatments themselves led to observed differences in *B. tectorum* invasion.

By 2015, *B. tectorum* cover was the main driver of differences in understory plant community cover between seeded fuel-reduction treatments. Despite similar perennial plant responses among seeded treatments in 2015 (33–40% cover; see Table 2), *B. tectorum* contributed to a staggering 25% of relative understory cover in seeded pile burn plots and only 13% and 3% in the seeded broadcast burn and mastication plots, respectively. The result of high *B. tectorum* colonization following pile burning supports similar studies that report dense patches of *B. tectorum* surrounding pile burned areas in treated piñon-juniper woodlands (Haskins and Gehring, 2004; Owen et al., 2009; Ross et al., 2012). In contrast to the seeded pile burn treatment, *B. tectorum* cover remained relatively low in seeded broadcast burn and mastication plots at  $5.86\% \pm 2.45\%$  and  $1.57\% \pm 0.65\%$ , respectively. The seven-fold increase in *B. tectorum* cover between 2011 and 2015 in the seeded pile burn treatment suggests short- and longer-term monitoring efforts can show very different snapshots of understory plant community response to different fuel-reduction techniques and highlights that longer-term monitoring may be needed to adequately capture nuances in ecological responses to fuel-management strategies.

In comparison of the two burn treatments, unlike the seeded pile burning, seeded broadcast burning was not associated with large increases in *B. tectorum* colonization. While *B. tectorum* proliferation is common in postfire landscapes, this result is surprising and conflicts with similar studies that have shown greater *B. tectorum* colonization following broadcast burning relative to pile burning (O'Connor et al., 2013; Redmond et al., 2014). Differences in early post-treatment community assembly may underlie the observed differences in *B. tectorum* between seeded broadcast and pile burn plots. Low perennial plant recruitment following fire often drives *B. tectorum* colonization in postfire landscapes (Tausch, 1999; Dhaemers, 2006; Bates et al., 2006; Condon et al., 2011; Roundy et al., 2014b). In 2011 we did observe lower

perennial grass and sedge cover in the pile burn plot ( $5.86\% \pm 1.54\%$ ; see Table 2) relative to the broadcast burn plot ( $11.85\% \pm 4.80\%$ ; see Table 2). Thus, while perennial grass and sedge cover became statistically equivalent in seeded broadcast and pile burn plots by 2015 (~35%; see Table 2), it is possible that lower perennial cover in the pile burn in the second growing season post treatment may have increased pile burn plot susceptible to *B. tectorum* colonization during later post-treatment community assembly.

Our results suggest differences in the microenvironments produced by seeded broadcast and pile burning may have differentially impacted native and non-native plant community assembly in postfire landscapes. Broadcast and pile burning techniques share commonalities. For instance, both broadcast and pile burning can generate pulses of available nutrients that promote exotic plant invasion, specifically nitrophilic species like *B. tectorum* (Blank et al., 2007; Owen et al., 2009; DeSandoli et al., 2016). Burning can additionally increase soil erosion (Neary et al., 1999) and create vegetation-depleted burn scars (Korb et al., 2004; Halpern et al., 2014) with diminished soil seed banks (Neary et al., 1999; Allen et al., 2008). Thus, burning may pose barriers to postfire native plant establishment and favor establishment of non-native species with more efficient dispersal mechanisms (Grime, 1977). Despite commonalities, however, there are also differences between broadcast and pile burn treatments that may have contributed to differential *B. tectorum* invasion. Unlike broadcast burning, which burns slash spread across the landscape, pile burning burns slash only in discrete piles. This practice can leave interspaces between the piles intact with the intention that unburned interspaces may then provide propagules for the recolonization of vegetation. However, slash piles associated with pile burning can burn longer and at higher temperatures compared with broadcast burning. Such localized high intensity fire (over 300°C) has the potential to sterilize soil, and may lead to increased mortality of plant roots and seeds (Neary et al., 1999). For these reasons, pile burning may decrease re-establishment of native vegetation within the first few years post-treatment (Blank et al., 2007; Owen et al., 2009; Fornwalt and Rhoades, 2011). It is possible that the observed limited perennial grass colonization 1 and 2 yr post treatment (see Table 2) in pile burn plots may have contributed to higher *B. tectorum* invasion in the pile burn plot compared with seeded broadcast burn treatment.

Mechanical mastication with seeding resulted in a strong native understory plant cover response ( $47.71\% \pm 3.73\%$ ; see Table 2) and produced significantly lower *B. tectorum* cover ( $1.57\% \pm 0.65\%$ ; see Fig. 2) compared with broadcast and pile burn treatments. These results are consistent with other studies in piñon-juniper woodlands that indicate mastication is a successful means of reducing overstory fuel-loads and enhancing understory plant communities (Ross et al., 2012; Young et al., 2013; Redmond et al., 2014; Bybee et al., 2016; Stephens et al., 2016). Mechanical mastication may differentially affect the recruitment of native and exotic plant species for several reasons. First, as mastication does not involve burning, it may leave more residual vegetation and seed propagules behind from the pretreatment plant community relative to prescribed burning treatments. This may also promote soil stability and more rapid native plant recruitment in the post-treatment landscape relative to burn treatments. Following treatment, layers of mulch associated with mastication can alter the surrounding microenvironment by creating a physical barrier hindering native plant recruitment and survival (Rhoades et al., 2012; Faist et al., 2015) and may obstruct plant access to light. Alternatively, mulch can encourage native plant recruitment following treatment by promoting soil stability, higher soil moisture and nutrient content, and cooler soil microclimate relative to areas lacking mulch (Chambers et al., 2007; Owen et al., 2009; Rhoades et al., 2012; Robichaud et al., 2013). Mulching can also temporarily reduce soil available N (Perry et al., 2010; Rhoades et al., 2012). This mechanism may depress the establishment of invasive exotic plant species with high N demand (Perry et al., 2010) and has been specifically shown to reduce *B. tectorum* germination (Wicks, 1997).



### Understory Plant Response to Seeding Applications

We cannot be certain which individual plants recruited from the seed mix versus the seed bank on Shay Mesa following fuel-reduction treatments. However, by comparing unseeded and seeded mastication plots, we can infer the relative contribution of seeding applications to the understory response to mastication treatments. We found unseeded and seeded mastication plots produced similar understory plant communities, with only slight differences in herbaceous perennial plant cover (~37% and ~40% respectively; see Table 2). However, in stark contrast to the seeded mastication treatment, the unseeded mastication treatment resulted in a staggering increase in *B. tectorum* cover. In accordance with other studies that have shown seeding treatments help reduce proliferation of non-native annual species following fuel-reduction activities and fire (Beyers, 2004; Floyd et al., 2004; Hunter et al., 2006; Thompson et al., 2006; DeSandoli et al. 2016), we found seed application with mastication treatments produced 15-fold lower *B. tectorum* cover than mastication alone (see Fig. 2). Seed applications are often used as a restoration tool to increase herbaceous plant establishment by supplementing depleted seed banks following fuel-reduction treatments (Poulsen et al., 1999). By increasing native plant cover, seeding applications following fuel-reduction treatments have been shown to decrease community vulnerability to exotic plant invasion (Floyd et al., 2004; Thompson et al., 2006; DeSandoli et al. 2016).

Interestingly, though, there were no differences in total understory or seed mix species cover between the seeded and unseeded mastication plots across growing seasons (see Table 2). This suggests seed applications did not increase overall understory plant establishment in seeded plots. We found, however, both seed mix and non-native species richness was higher in the seeded compared with unseeded mastication plot 2 and 6 yr post treatment (see Table 2). This could imply that differences in mastication plot invasibility may be attributed to differences in plant functional and species diversity contributed by the seed mix rather than differences in cover. Plant community diversity has been widely hypothesized to promote ecosystem resilience and decrease susceptibility to persistent exotic plant invasions at small spatial scales (Naem et al., 2000; Diaz and Cabido, 2001; Kennedy et al., 2002; Kuebbing et al., 2013). Seed mix perennial herbaceous species *Agropyron cristatum* (crested wheatgrass), *Poa secunda* (Sandburg bluegrass), *Linum lewisii* (Lewis flax), and *Onobrychis vicicifolia* (sanfoin) and shrubs *Purshia tridentata* (antelope bitterbrush) and *A. tridentata* (mountain big sagebrush) recruited in the seeded mastication plot but were entirely absent from the unseeded mastication plot.

Our results suggest non-native perennial plant diversity associated with the applied seed mix may have been important in determining site-specific susceptibility to *B. tectorum* invasion following mechanical mastication. With non-native perennial plant species present in the applied seed mix (see Table 1), we found seeding enhanced non-native perennial species diversity in the seeded mastication plot. Perennial plant establishment can reduce soil resource availability (e.g., soil nutrients, biological root space) to levels at which annual grasses are no longer competitive (Wedin and Tilman, 1990; Prober and Lunt, 2009). Interestingly, we found *A. cristatum*, a non-native, agronomic, drought-tolerant perennial bunchgrass at the greatest abundance among seed mix species in the seeded mastication plot in both 2011 and 2015. This result was consistent with Redmond et al.'s (2013) finding of high relative recruitment of *A. cristatum* following seeding and fuel-reduction treatments in a similar upland piñon-juniper woodland on the Colorado Plateau. *A. cristatum* is a strong competitor with other species during the establishment period (USDA, NRCS, 2016), and has been shown to suppress *B. tectorum* colonization (Francis and Pyke, 1996; Blank et al., 2015). Our result of decreased invasive grass cover following seeding of native and agronomic plant species is supported by a recent study in a Great Basin Ponderosa Pine ecosystem that showed the seeding of agronomic grass species decreased undesired non-native plant recruitment following pile burning (DeSandoli et al.

2016). The use of agronomic species for restoration is controversial. Agronomic grass species can stabilize soils and suppress establishment of other non-native plant species. However, seeding of such species can also lead to establishment of self-sustaining monocultures and depletion of local biodiversity as shown with *A. cristatum* in other ecosystems (Redente et al., 1989). Hence, early recruitment of *A. cristatum* and other seed mix species during the establishment period may have served as a possible mechanism whereby *B. tectorum* was suppressed in the seeded mastication plot. However, considering use of fast-establishing agronomic species in restoration efforts should be approached with caution.

Our results support mechanical mastication as a successful fuel-reduction strategy with the potential to encourage seed mix species recruitment by contributing to favorable microenvironment for native plant recruitment by stabilizing the soil surface, conserving soil moisture, and moderating soil microclimate (Massman et al., 2006; Miller and Seastedt, 2009; Owen et al., 2009; Ross et al., 2012; Young et al., 2013; Pierson et al., 2014; Stephens et al., 2016). However, as we observed the unseeded mastication plot to have the highest post-treatment invasion of *B. tectorum* among all treatments on Shay Mesa, our results also imply the potential importance of seeding when implementing mastication treatments. To place these results into a broader context, though, we also recognize that in addition to microenvironmental changes caused by mastication treatments, larger-scale climatic differences may also contribute to site-specific invasibility in the post-treatment landscape as noted in prior studies. Bybee et al. (2016), for instance, observed low *B. tectorum* invasion and successful native plant recruitment following unseeded mastication treatments across a wide range of piñon-juniper sites. Collectively, results from our study suggest applying seed mix in conjunction with mastication may be an effective management tool to promote establishment of native and seed mix species while decreasing colonization of undesirable invasive annual grasses like *B. tectorum* during the establishment period of post-treatment plant community assembly.

### Management Implications

Increased piñon-juniper woodland stand density has led to decreased herbaceous understory plant communities, diminished livestock and wildlife forage, and increased the risk of high-severity wildfire in the western United States. Thus exists an evident need for effective fuel-reduction strategies in these ecosystems. Management under the National Fire Plan has focused on reducing the risk of catastrophic fire while restoring historic cover of understory plant communities (NFP, 2000). However, these goals must be weighed against the potential risks of fuel-management strategies to decrease ecosystem stability and increase cover of invasive plant species like *B. tectorum*. Once established, *B. tectorum* may persist in ecosystems causing long-term impacts on ecological function including altered ecosystem N dynamics (Sperry et al., 2006), changes in soil biota (Belnap and Phillips, 2011), decreased forage quality for wildlife and livestock (Knapp, 1996), and increased risk of wildfire (Link et al., 2006).

Our results showed seeded mastication, broadcast burn, and pile burn fuel-reduction treatments to be successful in both reducing woody overstory fuel loads and increasing herbaceous understory cover 6 yr post treatment in an upland semiarid piñon-juniper woodland on the Colorado Plateau. Differences in treatment-associated disturbance regimes, however, produced understory plant communities with dramatically different levels of *B. tectorum* invasion. Specifically, pile burning with seeding resulted in high proliferation of *B. tectorum* when compared with other seeded treatment types. Seeding seems to contribute to lowering site invasibility in the post-treatment landscape. In our direct comparison of seeded and unseeded mastication, the seeded mastication plot had higher seed mix species richness than its unseeded counterpart, a difference that corresponded to nearly 15-fold lower *B. tectorum* cover than in the unseeded mastication plot, and the lowest cover across all treatments implemented. This indicates seeding

applications used in conjunction with fuel-reduction activities may be worth associated time and financial investments to prevent against *B. tectorum* proliferation in post – fuel-reduction piñon-juniper woodlands. Given our current understanding, we suggest mechanical mastication with seeding application may be the most effective fuel-reduction treatment to promote native over non-native understory plant establishment in similar upland piñon-juniper woodlands. Mastication is additionally generally less expensive than prescribed burning treatments (i.e., broadcast and pile burning) and has been shown to yield a greater ecological return on investment relative to burn treatments (Provencher and Thompson, 2014). Our study offers longer-term data on piñon-juniper understory plant community responses to fuel-reduction activities than many existing studies and suggests monitoring communities over longer time scales may strengthen our ability to draw robust conclusions about longstanding ecological consequences of fuel-reduction activities.

## Acknowledgments

We would like to thank Mark Miller and Jeff Herrick, who offered critical assistance with field methodologies in the early stages of this project, and Brian Keating, Gabe Bissonette, Paul Plemons, and Jason Kirks from the Canyon Country District of the Utah BLM for their support in the initial setup and maintenance of the experimental site. Additionally, Heidi Guenther assisted with this project as part of her master's thesis, and Melinda Markin offered critical assistance with field plant identification. Other members of Barger lab field crews also helped greatly with project data collection and processing.

## Appendix A

**Table A1**

Plant species identified within the Shay Mesa experimental site during the 4 yr of sampling: 2009 (pretreatment), 2010 (one growing season post treatment), 2011 (two growing seasons post treatment), and 2015 (six growing seasons post treatment).

Symbol	Scientific name	Common name
<b>Trees</b>		
JUOS	<i>Juniperus osteosperma</i>	Utah juniper
PIED	<i>Pinus edulis</i>	Two-needle pinyon
<b>Shrubs</b>		
ARTRV	<i>Artemisia tridentata</i> ssp. <i>vaseyana</i>	Mountain big sagebrush
CEMO2	<i>Cercocarpus montanus</i>	Alderleaf mountain mahogany
CHVI8	<i>Chrysothamnus viscidiflorus</i>	Yellow rabbitbrush
EPVI	<i>Ephedra viridis</i>	Mormon tea
ERMI4	<i>Eriogonum microthecum</i>	Slender buckwheat
ERNA10	<i>Ericameria nauseosa</i>	Rubber rabbitbrush
OPPO	<i>Opuntia polyacantha</i>	Plains pricklypear
PUTR2	<i>Purshia tridentata</i>	Antelope bitterbrush
YUAN2	<i>Yucca angustissima</i>	Narrowleaf yucca
YUHA	<i>Yucca harrimaniana</i>	Spanish bayonet
<b>Perennial forbs</b>		
ARFE3	<i>Arenaria fendleri</i>	Fendler's sandwort
ARPE2	<i>Arabis perennans</i>	Perennial rockcress
ASAM5	<i>Astragalus amphioxys</i>	Crescent milkvetch
ASMO7	<i>Astragalus mollissimus</i>	Woolly locoweed
CANU3	<i>Calochortus nuttallii</i>	Sego lily
CHER2	<i>Chaetopappa ericoides</i>	Rose heath
CHFE3	<i>Chamaesyce fendleri</i>	Fendler's sandmat
CRFL6	<i>Cryptantha flavoculata</i>	Roughseed cryptantha
ERAL4	<i>Eriogonum alatum</i>	Winged buckwheat
ERPU2	<i>Erigeron pumilus</i>	Shaggy fleabane
GUSA2	<i>Gutierrezia sarothrae</i>	Broom snakeweed
HEVIM3	<i>Heterotheca villosa</i> var. <i>minor</i>	Hairy false goldenaster
HYFI	<i>Hymenopappus filifolius</i>	Fineleaf hymenopappus
LEMO2	<i>Lepidium montanum</i>	Mountain pepperweed

**Table A1** (continued)

Symbol	Scientific name	Common name
LILE3	<i>Linum lewisii</i>	Lewis flax
LIPA5	<i>Lithophragma parviflorum</i>	Smallflower woodland-star
MEMU3	<i>Mentzelia multiflora</i>	Adonis blazingstar
ONVI	<i>Onobrychis vicifolia</i>	Sainfoin
PAMU11	<i>Packera multilobata</i>	Lobeleaf groundsel
PEPU7	<i>Petradoria pumila</i>	Rock goldenrod
PESP	<i>Penstemon speciosus</i>	Royal penstemon
PEUT	<i>Penstemon utahensis</i>	Utah penstemon
PHAC4	<i>Physaria acutifolia</i>	Sharpleaf twinpod
PHHO	<i>Phlox hoodii</i>	Spiny phlox
SPCO	<i>Sphaeralcea coccinea</i>	Scarlet globemallow
STCO6	<i>Streptanthus cordatus</i>	Heartleaf twistflower
TAOF	<i>Taraxacum officinale</i>	Common dandelion
TEACA2	<i>Tetranneuris acaulis</i> var. <i>acaulis</i>	Stemless four-nerve daisy
TEIV	<i>Tetranneuris ivesiana</i>	Stemless woollybase
TOIN	<i>Townsendia incana</i>	Silvery townsendia
<b>Annual forbs</b>		
ALLE7	<i>Aliciella leptomeria</i>	Sand gilia
CETE5	<i>Ceratocephala testiculata</i>	Curvseed butterwort
CHFR3	<i>Chenopodium fremontii</i>	Fremont's goosefoot
COWR2	<i>Cordylanthus wrightii</i>	Wright's bird's beak
CRPT	<i>Cryptantha pterocarya</i>	Wingnut cryptantha
DRNE	<i>Draba nemorosa</i>	Woodland draba
ERCE2	<i>Eriogonum cernuum</i>	Nodding buckwheat
LAMA9	<i>Lappula marginata</i>	Margined stickseed
LAOC3	<i>Lappula occidentalis</i>	Flatspine stickseed
LASE	<i>Lactuca serriola</i>	Prickly lettuce
MACA2	<i>Machaeranthera canescens</i>	Hoary tansyaster
MEOF	<i>Melilotus officinalis</i>	Sweetclover
PHIV	<i>Phacelia ivesiana</i>	Ives' phacelia
PLPA2	<i>Plantago patagonica</i>	Woolly plantain
SAC08	<i>Salsola collina</i>	Slender Russian thistle
SIAL2	<i>Sisymbrium altissimum</i>	Tall tumbledustard
TRDU	<i>Trigopogon dubius</i>	Yellow salsify
<b>Perennial grasses</b>		
ACHY	<i>Achnatherum hymenoides</i>	Indian ricegrass
AGCR	<i>Agropyron cristatum</i>	Crested wheatgrass
ARPU9	<i>Aristida purpurea</i>	Purple threeawn
BOGR2	<i>Bouteloua gracilis</i>	Blue grama
ELELB2	<i>Elymus elymoides</i>	Squirreltail
HECOC8	<i>Hesperostipa comata</i>	Needle and thread
PASM	<i>Pascopyrum smithii</i>	Western wheatgrass
PLJA	<i>Pleuraphis jamesii</i>	James' galleta
POFE	<i>Poa fendleriana</i>	Muttongrass
POSE	<i>Poa secunda</i>	Sandberg bluegrass
TRMU	<i>Tridens muticus</i>	Slim tridens
<b>Annual grasses</b>		
BRTE	<i>Bromus tectorum</i>	Cheatgrass
VUOC	<i>Vulpia octoflora</i>	Sixweeks fescue

## References

- Allen, E.A., Chambers, J.C., Nowak, R.S., 2008. Effects of a spring prescribed burn on the soil seed bank in sagebrush steppe exhibiting pinyon-juniper expansion. *Western North American Naturalist* 68 (3), 265–277.
- Archer, S., Schimel, D.S., Holland, E.A., 1995. Mechanism of shrubland expansion: land use, climate or CO<sub>2</sub>. *Climate Change* 29, 91–99.
- Archer, S., Boutton, T.W., Hibbard, K.A., 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. *Global Biogeochemical Cycles in the Climate System* 115–138.
- Barger, N.N., Archer, S.R., Campbell, J.L., Huang, C.Y., Morton, J.A., Knapp, A.K., 2011. Woody plant proliferation in North American drylands: a synthesis of impacts on ecosystem carbon balance. *Journal of Geophysical Research: Biogeosciences* 116 (G4).
- Barney, M.A., Frischknecht, N.C., 1974. Vegetation changes following fire in the pinyon-juniper type of west-central Utah. *Journal of Range Management* 27 (2), 91–96.
- Bates, J.D., Davies, K.W., 2016. Seasonal burning of juniper woodlands and spatial recovery of herbaceous vegetation. *Forest Ecology and Management* 361, 117–130.
- Bates, J.D., Svejcar, T.J., 2009. Herbaceous succession after burning of cut western juniper trees. *Western North American Naturalist* 69 (1), 9–25.
- Bates, J.D., Miller, R.F., Svejcar, T.J., 2000. Understory dynamics in cut and uncut western juniper woodlands. *Journal of Range Management* 119–126.
- Bates, J.D., Miller, R.F., Svejcar, T., 2005. Long-term successional trends following western juniper cutting. *Rangeland Ecology & Management* 58, 533–541.

- Bates, J.D., Miller, R.F., Davies, K.W., 2006. Restoration of quaking aspen woodlands invaded by western juniper. *Rangeland Ecology & Management* 59 (1), 88–97.
- Bates, J.D., Miller, R.F., Svejcar, T., 2007. Long-term vegetation dynamics in a cut western juniper woodland. *Western North American Naturalist* 67 (4), 549–561.
- Bates, J.D., Sharp, R.N., Davies, K.W., 2014. Sagebrush steppe recovery after fire varies by development phase of *Juniperus occidentalis* woodland. *International Journal of Wildland Fire* 23 (1), 117–130.
- Belnap, J., Phillips, S.L., 2011. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications* 11, 1261–1275.
- Beyers, J.L., 2004. Postfire seeding for erosion control: effectiveness and impacts on native plant communities. *Conservation Biology* 18 (4), 947–956.
- Blank, R.R., Chambers, J., Roundy, B., Whittaker, A., 2007. Nutrient availability in rangeland soils: influence of prescribed burning, herbaceous vegetation removal, overseeding with *Bromus tectorum*, season, and elevation. *Rangeland Ecology & Management* 60 (6), 644–655.
- Blank, R.R., Morgan, T., Allen, F., 2015. Suppression of annual *Bromus tectorum* by perennial *Agropyron cristatum*: roles of soil nitrogen availability and biological soil space. *AoB Plants* 7, plv006.
- Brockway, D.G., Gatewood, R.G., Paris, R.B., 2002. Restoring grassland savannas from degraded pinyon-juniper woodlands: effects of mechanical overstory reduction and slash treatment alternatives. *Journal of Environmental Management* 64, 179–197.
- Bybee, J., Roundy, B.A., Young, K.R., Hulet, A., Roundy, D.B., Crook, L., Aanderud, Z., Eggett, D.L., Cline, N.L., 2016. Vegetation response to piñon and juniper tree shredding. *Rangeland Ecology & Management* 69 (3), 224–234.
- Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E., Whittaker, A., 2007. What makes Great Basin sagebrush ecosystems invulnerable by *Bromus tectorum*? *Ecological Monographs* 77, 117–145.
- Clary, W.P., Jameson, D.A., 1981. Herbage production following tree and shrub removal in the pinyon-juniper type of Arizona. *Journal of Range Management* 34, 109–113.
- Condon, L., Weisberg, P.J., Chambers, J.C., 2011. Abiotic and biotic influences on *Bromus tectorum* invasion and *Artemisia tridentata* recovery after fire. *International Journal of Wildland Fire* 20 (4), 597–604.
- Davenport, D.W., Breshears, D.D., Wilcox, B.P., Allen, C.D., 1998. Viewpoint: sustainability of piñon-juniper ecosystems—a unifying perspective of soil erosion thresholds. *Journal of Range Management* 51 (2), 231–240.
- DeSandoli, L., Turkington, R., Fraser, L.H., 2016. Restoration of slash pile burn scars to prevent establishment and propagation of non-native plants. *Canadian Journal of Forest Research* 46 (8), 1042–1050.
- Dhaemers, J.M., 2006. Vegetation recovery following spring prescribed fire in pinyon-juniper woodlands of central Nevada: effects of elevation and tree cover. ProQuest, Ann Arbor, MI, USA.
- Diaz, S., Cabido, M., 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16 (11), 646–655.
- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whittford, W.G., 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters* 14 (7), 709–722.
- Faist, A.M., Stone, H., Tripp, E.A., 2015. Impacts of mastication: soil seed bank responses to a forest thinning treatment in three Colorado (USA) conifer forest types. *Forests* 6 (9), 3060–3074.
- Floyd, M.L., Hanna, D.D., Romme, W.H., 2004. Historical and recent fire regimes in piñon-juniper woodlands on Mesa Verde. *Forest Ecology and Management* 198, 269–289.
- Fornwalt, P.J., Rhoades, C.C., 2011. Rehabilitating slash pile burn scars in upper Montane forests of the Colorado Front Range. *Natural Areas Journal* 31 (2), 177–182.
- Francis, M.G., Pyke, D.A., 1996. Crested wheatgrass-cheatgrass seedling competition in a mixed-density design. *Journal of Range Management* 49, 432–438.
- Fulé, P.Z., Waltz, A.E.M., Covington, W.W., Smith, H.B., Springer, J.D., Heinlein, T.A., Huisinga, K.D., Moore, M.M., 2002. Comparing ecological restoration alternatives: Grand Canyon, Arizona. *Forest Ecology and Management* 107, 19–41.
- Goodrich, S., Rooks, D., 1999. Control of weeds at a pinyon-juniper site by seeding grasses. In: Monsen, S.B., Stevens, R. (Eds.), *Proceedings: ecology and management of pinyon-juniper communities within the interior West*. Proceeding RMRS-P-9. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT, USA, p. 403–307.
- Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111 (982), 1169–1194.
- Halpern, C.B., Antos, J.A., Beckman, L.M., 2014. Vegetation recovery in slash-pile scars following conifer removal in a grassland-restoration experiment. *Restoration Ecology* 22 (6), 731–740.
- Haskins, K.E., Gehring, C.A., 2004. Long-term effects of burning slash on plant communities and arbuscular mycorrhizae in a semi-arid woodland. *Journal of Applied Ecology* 41, 379–388.
- Herrick, J.E., Van Zee, J.W., Havstad, K.M., Burkett, L.M., Whittford, W.G., 2005. *Monitoring manual for grassland, shrubland & savanna ecosystems, volume i: quick start*. University of Arizona Press, Tucson, AZ, USA, pp. 9–13.
- Huffman, D.W., Fulé, P.Z., Crouse, J.E., Pearson, K.M., 2009. A comparison of fire hazard mitigation alternatives in pinyon-juniper woodlands of Arizona. *Forest Ecology and Management* 257, 628–235.
- Huffman, D.W., Stoddard, M.T., Springer, J.D., Crouse, J.E., Chancellor, W.W., 2013. Understory plant community responses to hazardous fuels reduction treatments in pinyon-juniper woodlands of Arizona, USA. *Forest Ecology and Management* 289, 478–488.
- Hunter, M.E., Omi, P.N., Martinson, E.J., Chong, G.W., 2006. Establishment of non-native plant species after wildfires: effects of fuel treatments, abiotic and biotic factors, and post-fire grass seeding treatments. *International Journal of Wildland Fire* 15 (2), 271–281.
- Jacobs, B.F., Gatewood, R.G., 1999. Restoration studies in degraded pinyon-juniper woodlands of north-central New Mexico. In: Monsen, S.B., Stevens, R. (Eds.), *Proceedings: ecology and management of pinyon-juniper communities within the interior West*. Proceeding RMRS-P-9. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT, USA; pp. 294–298 (Available at: [http://www.fs.fed.us/rm/pubs/rmrs\\_p009/rmrs\\_p009\\_294\\_298.pdf](http://www.fs.fed.us/rm/pubs/rmrs_p009/rmrs_p009_294_298.pdf)). Accessed 3 May 2016.
- Kennedy, T.A., Naem, S., Howe, K.M., Knops, J.M.H., Tilman, D., Reich, P., 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417, 636–638.
- Knapp, P.A., 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert: history, persistence, and influences to human activities. *Global Environmental Change* 6 (1), 37–52.
- Knapp, A.K., Briggs, J.M., Collins, S.L., Archer, S.R., Bret-Harte, M.S., Ewers, B.E., Cleary, M.B., 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology* 14 (3), 615–623.
- Korb, J.E., Johnson, N.C., Covington, W.W., 2004. Slash pile burning effects on soil biotic and chemical properties and plant establishment: recommendations for amelioration. *Restoration Ecology* 12 (1), 52–62.
- Kuebbing, S., Rodriguez-Cabal, M.A., Fowler, D., Breza, L., Schweitzer, J.A., Bailey, J.K., 2013. Resource availability and plant diversity explain patterns of invasion of an exotic grass. *Journal of Plant Ecology* 6 (2), 141–149.
- Link, S.O., Keeler, C.W., Hill, R.W., Hagen, E., 2006. *Bromus tectorum* cover mapping and fire risk. *International Journal of Wildland Fire* 15 (1), 113–119.
- Liu, F., Archer, S.R., Gelwick, F., Bai, E., Boutton, T.W., Wu, X.B., 2013. Woody plant encroachment into grasslands: spatial patterns of functional group distribution and community development. *PloS One* 8 (12), e84364.
- Massman, W.J., Frank, J.M., Jiménez Esquín, A.E., Stromberger, M.E., Shepperd, W.D., 2006. Long term consequences of a controlled slash burn and slash mastication to soil moisture and CO<sub>2</sub> at a southern Colorado site. 27th Conference on Agricultural and Forest Meteorology. American Meteorological Society, Boston, MA, USA (Available at: <http://ams.confex.com/ams/pdfpapers/111082.pdf>). Accessed May 3, 2016.
- Melgoza, G., Nowak, R.S., Tausch, R.J., 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83 (1), 7–13.
- Miller, E.M., Seastedt, T.R., 2009. Impacts of woodchip amendments and soil nutrient availability on understory vegetation establishment following thinning of a ponderosa pine forest. *Forest Ecology and Management* 258 (3), 263–272.
- Miller, R.F., Ratchford, J., Roundy, B.A., Tausch, R.J., Hulet, A., Chambers, J., 2014. Response of conifer-encroached shrublands in the Great Basin to prescribed fire and mechanical treatments. *Rangeland Ecology & Management* 67, 468–481.
- Morgan, P., Moy, M., Droske, C.A., Lentile, L.B., Lewis, S.A., Robichaud, P.R., Hudak, A.T., 2014. Vegetation response after post-fire mulching and native grass seeding. *Fire Ecology* 10 (3) (Available at: <http://www.treesearch.fs.fed.us/pubs/48604>).
- Naem, S., Knops, J.M., Tilman, D., Howe, K.M., Kennedy, T., Gale, S., 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91 (1), 97–108.
- Natural Resource Conservation Service (NRCS), 2004. Major Land Resources Area: Colorado and Green River Plateaus. US Department of Agriculture Natural Resources Conservation Service (Available at: [http://www.nrcs.usda.gov/wps/portal/nrcs/detail/ut/technical/landuse/pasture/?cid=nrcs141p2\\_034190](http://www.nrcs.usda.gov/wps/portal/nrcs/detail/ut/technical/landuse/pasture/?cid=nrcs141p2_034190)). Accessed 1 September 2015).
- Near, D.G., Klopatek, C.C., DeBano, L.F., Ffolliott, P.F., 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management* 122, 51–71.
- O'Connor, C., Miller, R., Bates, J.D., 2013. Vegetation response to western juniper slash treatments. *Environmental Management* 52 (3), 553–566.
- Osem, Y., Perevolotsky, A., Jaime, K., 2006. Similarity between seed bank and vegetation in a semi-arid annual plant community: the role of productivity and grazing. *Journal of Vegetation Science* 17, 29–36.
- Owen, S.M., Sieg, C.H., Gehring, C.A., Bowker, M.A., 2009. Above- and belowground responses to tree thinning depend on the treatment of tree debris. *Forest Ecology and Management* 259, 71–80.
- Pierson, F.B., Williams, C.J., Kormos, P.R., Al-Hamdan, O.Z., 2014. Short-term effects of tree removal on infiltration, runoff, and erosion in woodland-encroached sagebrush steppe. *Rangeland Ecology & Management* 67 (5), 522–538.
- Perry, L.G., Blumenthal, D.M., Monaco, T.A., Paschke, M.W., Redente, E.F., 2010. Immobilizing nitrogen to control plant invasion. *Oecologia* 163 (1), 13–24.
- Poulsen, C.L., Walker, S.C., Stevens, R., Monsen, S.B., Stevens, R., 1999. Soil seed banking in pinyon-juniper areas with differing levels of tree cover, understory density and composition. *Proceedings: Ecology and Management of Pinyon-Juniper Communities within the Interior West*. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, RMRS-P-9, Ogden, UT, USA; pp. 141–145 (Available at: [http://www.fs.fed.us/rm/pubs/rmrs\\_p009/rmrs\\_p009\\_141\\_145.pdf](http://www.fs.fed.us/rm/pubs/rmrs_p009/rmrs_p009_141_145.pdf)). Accessed 3 May 2016.
- Prober, S.M., Lunt, I.D., 2009. Restoration of *Themeda australis* swards suppresses soil nitrate and enhances ecological resistance to invasion by exotic annuals. *Biological Invasions* 11, 171–181.
- Provencher, L., Thompson, J., 2014. Vegetation responses to pinyon-juniper treatments in eastern Nevada. *Rangeland Ecology & Management* 67 (2), 195–205.
- Pyke, D.A., Chambers, J.C., Beck, J.L., Brooks, M.L., Mealor, B.A., 2016. Land uses, fire, and invasion: exotic annual *Bromus* and human dimensions. *Exotic brome-grasses in arid and semiarid ecosystems of the western US*. Springer International Publishing, New York, NY, USA, pp. 307–337.
- R Core Team, 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (Available at: <https://www.R-project.org/>).
- Redente, E.F., Biondini, M.E., Moore, J.C., 1989. Observations on biomass dynamics of a crested wheatgrass and native shortgrass ecosystem in southern Wyoming. *Journal of Range Management* 113–118.

- Redmond, M.D., Cobb, N.S., Miller, M.E., Barger, N.N., 2013. Long-term effects of chaining treatments on vegetation structure in piñon-juniper woodlands of the Colorado Plateau. *Forest Ecology and Management* 305, 120–128.
- Redmond, M.D., Zelikova, T.J., Barger, N.N., 2014. Limits to understory plant restoration following fuel-reduction treatments in a piñon-juniper woodland. *Environmental Management* 54 (5), 1139–1152.
- Rhoades, C.C., Battaglia, M.A., Rocca, M.E., Ryan, M.G., 2012. Short-and medium-term effects of fuel reduction mulch treatments on soil nitrogen availability in Colorado conifer forests. *Forest Ecology and Management* 276, 231–238.
- Robichaud, P.R., Lewis, S.A., Wagenbrenner, J.W., Ashmun, L.E., Brown, R.E., 2013. Post-fire mulching for runoff and erosion mitigation: Part I: effectiveness at reducing hillslope erosion rates. *Catena* 105, 75–92.
- Romme, W.H., Allen, C.D., Bailey, J.D., Baker, W.L., Bestelmeyer, B.T., Brown, P.M., Miller, R.F., 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon-juniper vegetation of the western United States. *Rangeland Ecology & Management* 62 (3), 203–222.
- Ross, M.R., Castle, S.C., Barger, N.N., 2012. Effects of fuels reductions on plant communities and soils in a piñon-juniper woodland. *Journal of Arid Environments* 79, 84–92.
- Roundy, B.A., Young, K., Cline, N., Hulet, A., Miller, R.F., Tausch, R.J., Chambers, J.C., Rau, B., 2014a. Piñon-juniper reduction increases soil water availability of the resource growth pool. *Rangeland Ecology & Management* 67 (5), 495–505.
- Roundy, B.A., Miller, R.F., Tausch, R.J., Young, K., Hulet, A., Rau, B., Jessop, B., Chambers, J.C., Eggett, D., 2014b. Understory cover responses to piñon-juniper treatments across tree dominance gradients in the Great Basin. *Rangeland Ecology & Management* 67 (5), 482–494.
- Shapiro, S.S., Wilk, M.B., 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52, 591–611.
- Sperry, L.J., Belnap, J., Evans, R.D., 2006. *Bromus tectorum* invasion alters nitrogen dynamics in an undisturbed arid grassland ecosystem. *Ecology* 87 (3), 603–615.
- Springfield, H.W., 1976. Characteristics and management of southwestern piñon-juniper ranges: the status of our knowledge. In: Paulsen Jr., H.A. (Ed.), *Range management in the central and southern Rocky Mountains: a summary of the status of our knowledge by range ecosystems* (No. RM-160).
- Stephens, G.J., Johnston, D.B., Jonas, J.L., Paschke, M.W., 2016. Understory responses to mechanical treatment of piñon-juniper in northwestern Colorado. *Rangeland Ecology & Management* 69 (5), 351–359.
- Stoddard, M.T., Huffman, D.W., Alcoze, T.M., Fulé, P.Z., 2008. Effects of slash on herbaceous communities in piñon-juniper woodlands of northern Arizona. *Rangeland Ecology & Management* 61, 485–495.
- Tausch, R.J., 1999. Transitions and thresholds: influences and implications for management in piñon and juniper woodlands. *Proceedings of the US Department of Agriculture. Report RMRS-P-9. US Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA*, pp. 361–365.
- Tausch, R.J., Tueller, P.T., 1977. Plant succession following chaining of piñon-juniper woodlands in eastern Nevada. *Journal of Range Management* 44–49.
- Thompson, T.W., Roundy, B.A., McArthur, E.D., Jessop, B.D., Waldron, B., Davis, J.N., 2006. Fire rehabilitation using native and introduced species: a landscape trial. *Rangeland Ecology & Management* 59 (3), 237–248.
- USDA National Fire Plan, 2000. National Fire Plan. US Department of Agriculture forests and rangelands (Available at: <https://www.forestandrangelands.gov/resources/overview/>. Accessed 15 August 2016).
- USDA, NRCS, 2004. Major Land Resource Area D-35, Ecological Site Description: Upland Shallow Loam (P-J). Site ID: 035XY315UT. NRCS State Office, Salt Lake City, UT, USA, p. 9.
- USDA, NRCS, 2016. The PLANTS Database. National Plant Data Team, Greensboro, NC, USA: 27401-4901 USA. <http://plants.usda.gov> (Accessed 1 June 2016).
- Van Auken, O.W., 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31 (1), 197–215.
- Vasquez, E., Sheley, R., Svejcar, T., 2008. Creating invasion resistant soils via nitrogen management. *Invasive Plant Science and Management* 1 (3), 304–314.
- Wedin, D.A., Tilman, D., 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* 84, 433–441.
- Wicks, G.A., 1997. Survival of downy brome (*Bromus tectorum*) seed in four environments. *Weed Science* 225–228.
- Young, K.R., Roundy, B.A., Eggett, D.L., 2013. Plant establishment in masticated Utah juniper woodlands. *Rangeland Ecology & Management* 66 (5), 597–607.
- Young, K.R., Roundy, B.A., Eggett, D.L., 2014. Mechanical mastication of Utah juniper encroaching sagebrush steppe increases inorganic soil N. *Applied and Environmental Soil Science*:2014 <http://dx.doi.org/10.1155/2014/632757>.
- Young, K.R., Roundy, B.A., Bunting, S.C., Eggett, D.L., 2015. Utah juniper and two-needle piñon reduction alters fuel loads. *International Journal of Wildland Fire* 24 (2), 236–248.
- Zelikova, T.J., Huffbauer, R.A., Reed, S.C., Wertig, T., Fettig, C., Belnap, J., 2013. Evolutionary responses of *Bromus tectorum* to climate change: implications for biological invasions. *Ecology and Evolution* 3 (5), 1374–1387.