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ORIGINAL PAPER

Seeding native species increases resistance to annual grass invasion following prescribed burning of semiarid woodlands

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Abstract Exotic grass invasions are often facilitated by disturbances, which provide opportunities for invasion by releasing pulses of resources available to invaders. Where disturbances such as prescribed fire are used as a management tool, there is a pressing need to identify ecosystem attributes associated with susceptibility to disturbance-induced invasion. In the Great Basin of the western United States, expansion of the exotic annual grass *Bromus tectorum* is transforming native ecosystems. In this study we examined long-term understory plant community responses to experimental prescribed fire and post-fire seeding treatments in Great Basin pinyon-juniper woodlands. We asked (1) how long-term ecosystem resistance to fire-induced *B. tectorum* invasion varies along major abiotic and biotic gradients, and (2) whether post-fire seeding of perennial species promotes perennial plant establishment and increases resistance to invasion. Fourteen years after burning, we found that resistance to invasion was high on relatively cool and moist sites (higher elevation), but that the warmer and drier (low- to mid-elevation) burned sites had become heavily invaded by *B. tectorum*. Post-fire *B. tectorum* dominance was highest in sites with high pre-fire tree cover, where residual and newly established native perennial plant cover was limited following fire. We found that seeding perennial species after burning decreased invasibility in sites with low resistance. Seeding a mix of native perennial shrubs, forbs, and grasses was more effective at increasing perennial cover and inhibiting *B. tectorum* invasion than seeding a mix of non-native perennial grasses. Our results highlight the need for long-term studies to evaluate plant community responses to prescribed fire, as important treatment differences were not captured in a shorter (3–4 year) post-fire monitoring period.

Keywords Biological invasions · Great Basin · Prescribed fire · Resistance to invasion · Restoration · Semiarid woodlands

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Introduction

Exotic grass invasions are transforming structure and function of arid and semi-arid ecosystems worldwide (D'Antonio and Vitousek 1992). Initial invasion is often facilitated by disturbances (Lodge 1993), which increase the quantity of unused resources (Davis et al. 2000) and thus provide niche opportunities for invaders (Shea and Chesson 2002). Ecosystem resistance to invasion varies spatially and temporally and is dependent on the interactions among underlying resource dynamics, the post-disturbance response of resident species, and traits of the invaders (Lonsdale 1999). To facilitate development of effective strategies for addressing exotic grass invasions, there is a pressing need to identify ecosystem attributes associated with resistance to invasion and management options for mitigating invasion risk (Bradley et al. 2010).

Expansion and increasing dominance of the highly flammable invasive annual grass, *Bromus tectorum* L., is transforming native ecosystems in the Great Basin region of the western United States, resulting in increased fire risk (Brooks et al. 2004; Balch et al. 2013) and altering ecosystem processes such as nutrient cycling and soil water flux and storage (Wilcox et al. 2012; Germino et al. 2016). Where Great Basin pinyon-juniper woodlands (*Pinus monophylla* and *Juniperus* spp.) and sagebrush semi-desert (*Artemisia* spp.) overlap, prescribed fire and other tree-reduction measures are often used to maintain native shrub- and grass-dominated habitats and conserve sagebrush obligate animal species (Chambers and Wisdom 2009; Miller et al. 2014). Post-fire management objectives typically prioritize the recovery of perennial herbaceous species that can increase resistance to invasion by exotic annual grasses such as *B. tectorum*. However, fires often accelerate *B. tectorum* invasion (Knapp 1996) and an unfortunate outcome of prescribed fire can be to increase the dominance of *B. tectorum*. Although many understory species are adapted to surviving and reproducing following fire, the dominant shrub and tree species of this region are fire-intolerant and typically killed by fire. Early phenology, rapid growth, and high rates of resource acquisition (Knapp 1996; James 2008; Leffler et al. 2013) allow *B. tectorum* to effectively compete with seedlings of native perennial species for available post-fire resources (Booth et al. 2003; Humphrey and Schupp 2004; Chambers et al. 2016).

Resistance to fire-related *B. tectorum* invasion varies spatially. Landscapes characterized by low resistance to invasion tend to be those in which post-fire establishment of native perennial species is limited or slow (Chambers et al. 2014a). For example, resource-related constraints on seed production limit post-fire perennial seed availability on drier sites (Chambers et al. 2007). Similarly, landscapes in which perennial understory vegetation is competitively suppressed by trees are less likely to have an adequate seed bank for post-fire establishment of perennial understory species (Allen and Nowak 2008; Bates et al. 2014; Roundy et al. 2014a).

Where the post-fire response of native perennial species is constrained by seed availability, seeding treatments can theoretically augment the establishment of perennial species and thus inhibit *B. tectorum* invasion through competition (Pyke et al. 2013). However, seeding treatments are often unsuccessful at establishing the seeded species (Arkle et al. 2014), especially on drier sites where unfavorable abiotic conditions can limit plant establishment regardless of seed availability (Knutson et al. 2014). In other words, seeding treatments are often least successful in those parts of the landscape with lowest resistance to invasion, where they would have the greatest potential to increase invasion resistance if seeding were successful. Even when post-disturbance seeding treatments result in the successful establishment of seeded species, there may be no corresponding reduction in exotic grass cover (Kerns and Day 2014).

We examined understory plant community responses to landscape-scale experimental burning and seeding treatments 14 years after treatment in the Shoshone Mountains, Nevada. Study sites included replicate pairs of control and burned plots arranged along major abiotic (elevation) and biotic (pre-fire tree cover) gradients. Post-fire seeding treatments of native and non-native species were nested within burned plots. Short-term plant community responses 4 years after burning indicated that resistance to fire-induced *B. tectorum* invasion increased with elevation, although post-fire cover of *B. tectorum* was relatively low at all elevations (Urza et al. 2017). Sites with high pre-fire tree cover contained little *B. tectorum* after burning, but native perennial species were also scarce, resulting in sparsely vegetated sites 4 years after fire.

In this study, we revisited permanent sampling plots 14 years after burning to investigate long-term plant community responses to fire and resistance to *B. tectorum* invasion. We asked the following questions: (1) How does prescribed burning affect long-term plant community composition and *B. tectorum* invasion? (2) How does ecosystem resistance to fire-induced *B. tectorum* invasion vary along gradients of elevation and pre-fire tree cover? and (3) Does post-fire seeding of perennial species promote perennial plant establishment and increase resistance to invasion?

Materials and methods

Study area

Experimental treatments took place in Underdown Canyon, a west-to-east-draining watershed located on the Humboldt-Toiyabe National Forest in the Shoshone Mountains of central Nevada, USA. Climate is characterized by cold winters in which precipitation falls as snow and warm summers with precipitation falling as rain (Fig. 1a; Western Regional Climate Center 2018). Average annual precipitation increases with elevation, ranging from 23 to 50 cm (Board et al. 2011). Weather was variable during the study period, including wetter-than-average years and periods of drought (Fig. 1b). The underlying geology is welded and non-welded volcanic tuff, and soils on the study sites are classified as coarse loamy mixed frigid typic haploxerolls (Rau et al. 2005). Woodlands of variable density occur in unburned areas throughout Underdown Canyon and are dominated by single-leaf pinyon (*Pinus monophylla*) with lesser amounts of Utah juniper (*Juniperus osteosperma*).

Experimental design and data collection

Underdown Canyon was established as a Joint Fire Sciences Program Demonstration Area to study the ecological effects of landscape-scale prescribed fire treatments. The study used three pairs of adjacent alluvial fans (six fans total, ranging from approx. 1–5 ha) on the north-facing slope of Underdown Canyon. Fan pairs are distributed along an elevational gradient: low (2073 m), mid (2225 m), and high (2347 m). The mid-elevation fans were stratified based on three tree cover categories: low (12% mean cover), moderate (38% mean cover), and high (74% mean cover) (Reiner 2004). The low- and high-elevation fans included only the moderate tree-cover category. One fan within each pair was burned by the USDA Forest Service in May of 2002 and the other remained unburned (control). Relatively cool and moist conditions during the burns (air temperature < 32 °C, relative humidity $> 15\%$, wind speed < 9 m s^{-1}, and gravimetric fuel moisture $< 40\%$) resulted in patchy consumption of vegetation and duff (Rau et al. 2007). Three permanent sampling plots approximately 0.1 ha in size were established in each combination of control/burned, elevation group and tree-cover category, for a total of 30 permanent plots.

Post-fire seeding treatments were nested within the burned plots. Two 100 m^2 seeding subplots were established within each permanent plot for the burned treatments (n = 15 for each seeding treatment). For each pair of seeding subplots, one was seeded with a mix of ten native species, and the other was seeded with a mix of five non-native species. The seed mixes were chosen to represent two common approaches to post-fire restoration: a functionally diverse mix of native species and a less diverse mix of non-native perennial grass species. The native seed mix contained perennial grass, forb, and shrub species which varied in composition among elevations, whereas the non-native seed mix of perennial grasses did not differ among elevations. Seeds were applied at a rate of 60 seeds per species per m^2 in both seeding types. Seeding rates were determined using pure live seeds per gram for each species, which was calculated as the product of filled seeds per gram, percent viability, and percent purity. Seed mixes were broadcast evenly across the seeding subplots in the fall after the burns, and the soil surface was raked to ensure seed-soil contact. This design resulted in four burn/seeding treatments: unburned (control), burned and unseeded, burned and seeded with native species, and burned and seeded with non-native species. Livestock were excluded from the study area between 1995 (7 years prior to treatment) and 2006 (4 years following treatment), although permitted grazing was allowed before and after that period.

We evaluated the response of the vegetation community in 2016, 14 years after burning. Within each permanent plot, 0.25 m^2 quadrats were

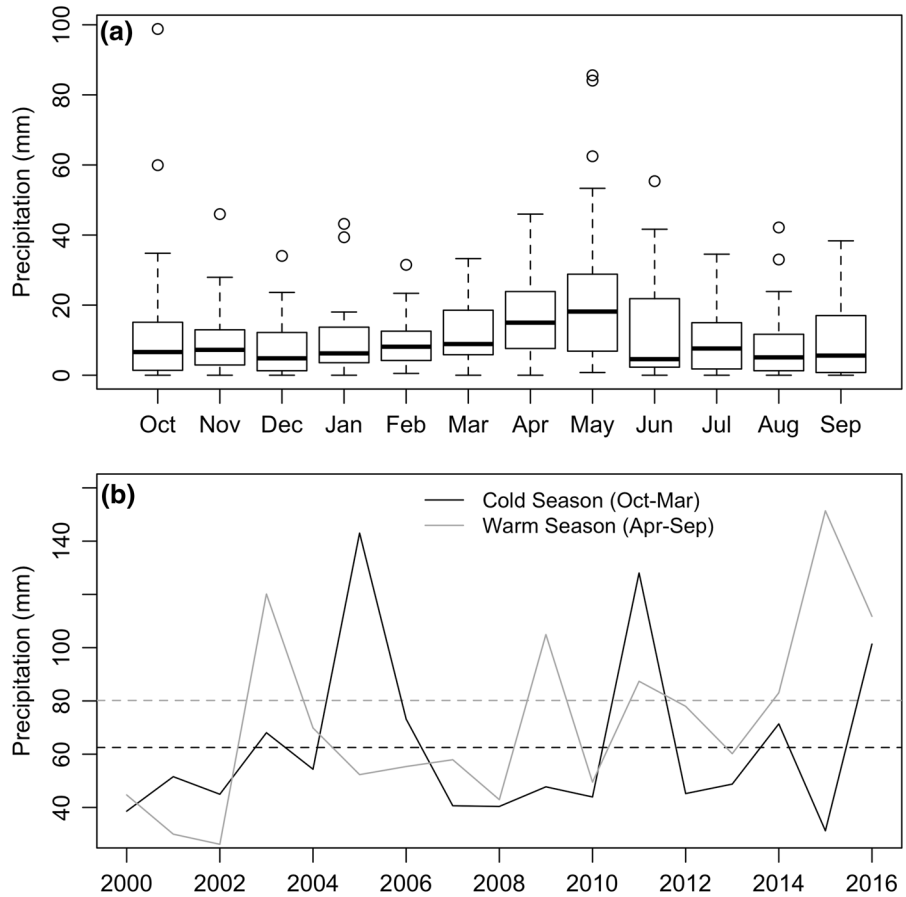

Fig. 1 Monthly and annual precipitation patterns for the study area. **a** Monthly precipitation for the weather record (1987–2018). Bold line is the median, box margins show the interquartile range, whiskers define the 1.5 interquartile range and points are outliers. **b** Annual cold season (October–March; black line) and warm season (April–September; gray line) precipitation over the study period. Dashed lines show the long-term means (1987–2018). Climate data are from the Desatoya Mountain RAWS Weather Station (Western Regional Climate Center 2018) which is located at 1890 m elevation approximately 19 km to the northwest of the study area

systematically located along transect lines that were randomly stratified within each 0.1 ha plot. 15 quadrats were used in the unburned and burned unseeded plots, and 7–8 quadrats were used in the seeded native and seeded non-native subplots. In each quadrat, aerial cover was estimated for each species using 13 cover categories (Daubenmire 1959), and the mid-point of each cover category was chosen to represent percent cover. Plant cover data were also collected from the unburned and burned/unseeded plots in 2001 (pre-fire), 2003, 2004, and 2006 (for more details see Urza et al. 2017). We report results from the earlier time periods where relevant to provide longer-term context for changes in post-fire vegetation.

Data analyses

To quantify the effects of the burning and seeding treatments on vegetation composition, species cover data from 2016 were aggregated into six functional groups: annual forbs, annual grasses (*B. tectorum*), perennial forbs, perennial graminoids, sprouting perennial shrubs, and non-sprouting perennial shrubs. Percent cover was summed by functional group within each sampling quadrat, then averaged within each plot. We used linear mixed models fit by maximum likelihood with the *lme4* package in R version 3.3.3 (Bates et al. 2015; R Core Team 2015). Cover for each functional group (square-root-transformed) was the response variable and the burn/seeding treatment was the fixed effect, while elevation, tree cover, and the interaction of both elevation and tree cover with burn/seeding treatment were treated as random effects. All predictor variables were categorical: burn/seeding treatment had four levels (unburned, burned unseeded, burned seeded native, and burned seeded non-native), elevation had three levels (low, mid, and high), and tree cover had three levels (low, moderate, and high). The residuals for all models were visually inspected

for normality and homogeneity to ensure that the assumptions of linear models were met. p values for predictor variables were calculated using parametric bootstrapping with the PBmodcomp function in the *pbkrtest* package (Halekoh and Højsgaard 2017), which simulates data from a null model without the term of interest and uses likelihood ratio tests on nested models (with and without the term of interest) to compare the null distribution to the true data. All parametric bootstraps were run with 10,000 simulations. We used a critical alpha level of 0.05 to determine the statistical significance of each predictor.

To quantify the effect of the seeding treatments on post-fire cover of the seeded species, we compared 2016 cover from burned plots that were seeded after burning with those that were unseeded. For each seeded species at each elevation, we calculated mean differences in cover between the seeded and unseeded subplots in each burn plot and used paired t-tests to calculate p values.

Results

Perennial graminoid cover (Fig. 2a) was not consistently affected by the burn/seeding treatment (treatment; $p = 0.14$; Table 1). Instead, the treatment effect varied among tree cover classes (tree cover * treatment; $p = 0.01$). In sites with low tree cover, perennial graminoid cover was highest in the unburned plots (mean 15%), lowest in the burned unseeded plots (5%), and intermediate in the burned seeded plots (7–10%). In sites with moderate or high tree cover, perennial graminoid cover was relatively low in both unburned and burned unseeded plots (5–6%), but was substantially higher in plots seeded with either native (11% at moderate tree cover) or non-native (13% at high tree cover) species. Perennial graminoid cover was positively related to elevation (elevation; $p = 0.001$), with a mean of 13% cover at the high elevation site and 7% and 8% at the low and mid elevation sites, respectively. The treatment effect did not vary among elevations (elevation * treatment; $p = 0.12$).

Bromus tectorum was the only annual grass (Fig. 2b) found in any of the study plots, so results for annual grass cover are synonymous with *B. tectorum* cover. Annual grass cover differed among burn/seeding treatments ($p < 0.001$; Table 1). Unburned plots had the lowest cover (mean < 1%), followed by burned plots seeded with native species (2%), burned plots seeded with non-native species (5%), and burned plots that were unseeded (11%). Annual grass cover was negatively related to elevation ($p < 0.001$), and the treatment effect differed significantly among elevations (elevation * treatment; $p = 0.003$). At the low elevation site, the burned unseeded plots had higher annual grass cover (mean 4.6%) than the unburned plots (0%), with generally low values in plots seeded with either native or non-native species (< 1%). At the mid elevation, burned plots that were either unseeded (19%) or seeded with non-native species (11%) had much higher annual grass cover than the unburned plots (1%) and burned plots seeded with native species (2%). At the high elevation, annual grasses were effectively absent in all plots. There was no effect of tree cover ($p = 0.51$) or the tree cover by treatment interaction ($p = 0.11$).

The effect of the burn/seeding treatments on **perennial forb** cover (Fig. 3a) differed among elevations (elevation * treatment; $p = 0.002$; Table 1). At the low elevation site, unburned plots had much lower perennial forb cover (mean < 1%) than burned plots (8–10%), while the differences between burned and unburned plots were smaller at the mid and high elevation sites. At all elevations, burned plots seeded with native species had the highest perennial forb cover. For all treatment types combined, perennial forb cover was positively related to elevation ($p = 0.001$) and negatively related to pre-fire tree cover ($p < 0.001$).

Annual forb cover (Fig. 3b) did not differ among burn/seeding treatments ($p = 0.06$; Table 1). Annual forb cover was positively related to elevation ($p = 0.01$) and was lower at the low elevation (mean 0.2%) than at the mid or high elevation (0.6% and 1% respectively). There was no effect of tree cover ($p = 0.13$) or the tree cover by treatment interaction ($p = 0.39$). Nearly all annual forb cover was comprised of native species at all elevations.

Non-sprouting shrubs consisted of *Artemisia tridentata* ssp. *wyomingensis* at the low elevation, and *A. tridentata* ssp. *vaseyana* and *A. arbuscula* at the mid and high elevations. Non-sprouting shrub cover (Fig. 4a) differed significantly among burn/seeding treatments ($p = 0.002$; Table 1), and was substantially higher in burned plots that were seeded with native species (mean 15%) than in the other treatment groups

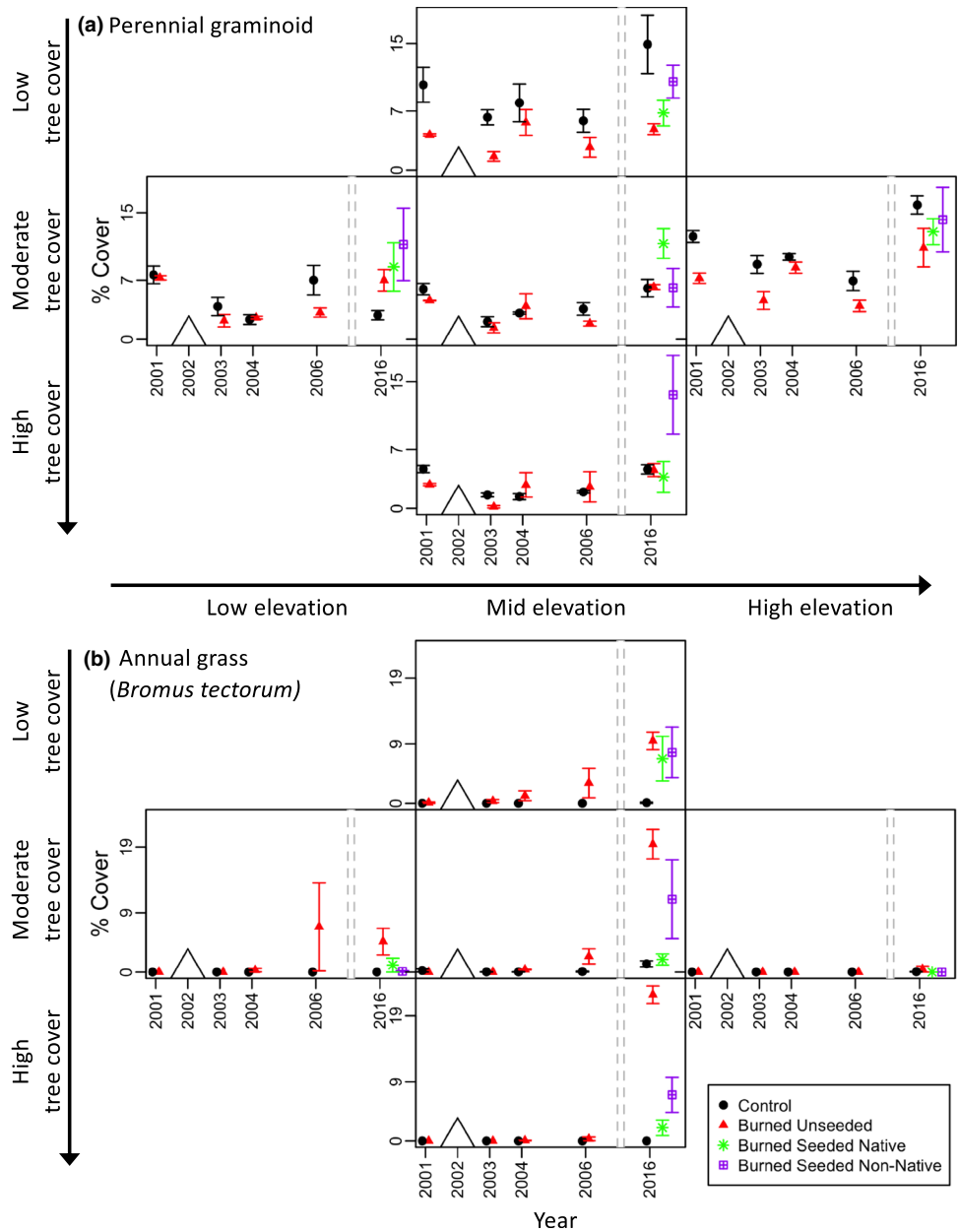

Fig. 2 Time series of **a** perennial graminoid and **b** annual grass (*B. tectorum*) cover along gradients of pre-fire tree cover and elevation. Data shown as mean ± 1 SE. Large triangle shows year of burn treatment. Data from years 2001–2006 for control and burned unseeded sites were published in Urza et al. (2017)

(4–7%). The treatment effect varied by tree cover class (tree cover * treatment; $p = 0.04$). In sites with low pre-fire tree cover, non-sprouting shrub cover was high in the unburned plots (mean 16%) and was reduced by burning (4–8%) except where burned plots were seeded with native species (15%). In sites with moderate and high pre-fire tree cover, non-sprouting shrub cover was relatively low in both unburned and burned unseeded plots (0–6%) and was much higher in burned plots seeded with native species (18–22%). There was no effect of elevation ($p = 0.99$) or the elevation by treatment interaction ($p = 0.64$).

Sprouting shrub cover (Fig. 4b) had a highly significant burn/seeding treatment predictor variable ($p < 0.001$; Table 1). Burning resulted in increased sprouting shrub cover, regardless of post-fire seeding treatment. Burned plots, regardless of seeding treatment, averaged 10–12% sprouting shrub cover, compared to 2% in the unburned plots. Sprouting shrub cover was negatively related to pre-fire tree cover ($p = 0.001$), with lower cover in plots with high pre-fire tree cover. There was no effect of elevation on sprouting shrub cover ($p = 0.08$), though the composition of sprouting shrub species differed somewhat among elevations. *Chrysothamnus viscidiflorus* was the most common sprouting shrub species found in burned plots at all elevations. *Symphoricarpos oreophilus* was also found in burned plots at the mid and high elevation, and burned plots at the low elevation contained *Ericameria nauseosa*, *Tetradymia canescens*, and *Sambucus nigra.*

The effectiveness of the seeding treatments for increasing cover of the seeded species was highly variable (Table 2). For the native seed mix, individual species responses varied by elevation. At all elevations, seeding increased cover of *A. tridentata*, though the strength of the effect was substantially higher at the mid elevation site. Seeding resulted in slightly higher cover of two native perennial forb species (*Lupinus alpestris* and *Eriogonum umbellatum*) but had no effect on others (*Eriogonum heracleoides*, *Penstemon palmeri*, *Sphaeralcea munroana*, and *Linum lewisii*). Seeding effects on native perennial graminoid species varied with elevation, although seeded plots had slightly lower cover of *Elymus elymoides* than unseeded plots at all elevations. From the non-native seed mix, only two seeded perennial graminoid species successfully established (*Agropyron cristatum* and *Bromus inermis*).

Taken together, the plant functional group responses indicate important long-term effects of the burning and seeding treatments on plant community composition (Fig. 5). Burning resulted in increased cover of non-native annual grasses (*B. tectorum*) and sprouting shrubs and decreased cover of non-sprouting shrubs (*Artemisia* spp.). However, there were important long-term differences in plant community responses to burning and seeding across the environmental gradients (elevation and pre-fire tree cover) included in the study (Fig. 5). At low and mid elevations, burning increased total understory plant cover, including both native species and invasive annual grasses (Fig. 5, center and center left), while at the high elevation, the composition of burned plots closely resembled that of unburned plots, regardless of seeding treatment (Fig. 5, center right). At the mid elevation site, pre-fire tree cover was strongly related to post-fire plant community composition. The annual grass response to burning was similar for all tree cover groups, but all native plant functional groups were

Table 1 Results from linear mixed models predicting plant functional group cover (square-root transformed)

Predictor	Perennial graminoid cover χ^2 (p)	Annual grass (*B. tectorum*) cover	Perennial forb cover	Annual forb cover	Non-sprouting shrub cover	Sprouting shrub cover
Burn-seed treatment	5.92	43.76	8.05	8.10	16.06	19.75
	(0.135)	(**< 0.001**)	(0.051))	(0.055)	(**0.002**)	(**< 0.001**)
Elevation	8.04	27.78	10.70	4.83	0.00	1.67
	(**0.001**)	(**< 0.001**)	(**0.001**)	(**0.010**)	(0.99)	(0.084)
Elevation * burn-seed treatment	6.47	20.92	17.31	1.98	0.88	0.29
	(0.117)	(< **0.001**)	(**0.002**)	(0.518)	(0.635)	(0.867)
Tree cover	0.16	0	15.16	1.06	1.37	9.00
	(0.326)	(0.511)	(**< 0.001**)	(0.129)	(0.085)	(**0.001**)
Tree cover * burn-seed treatment	10.56	4.78	3.62	2.23	7.96	2.82
	(**0.012**)	(0.114)	(0.348)	(0.387)	(**0.042**)	(0.425)

Shown are likelihood ratio test χ^2 values for each predictor, with p values calculated from parametric bootstrapping listed parenthetically. All predictors are categorical factors. Burn-seed treatment levels: unburned, burned unseeded, burned seeded native, and burned seeded non-native. p values are bolded where < 0.05

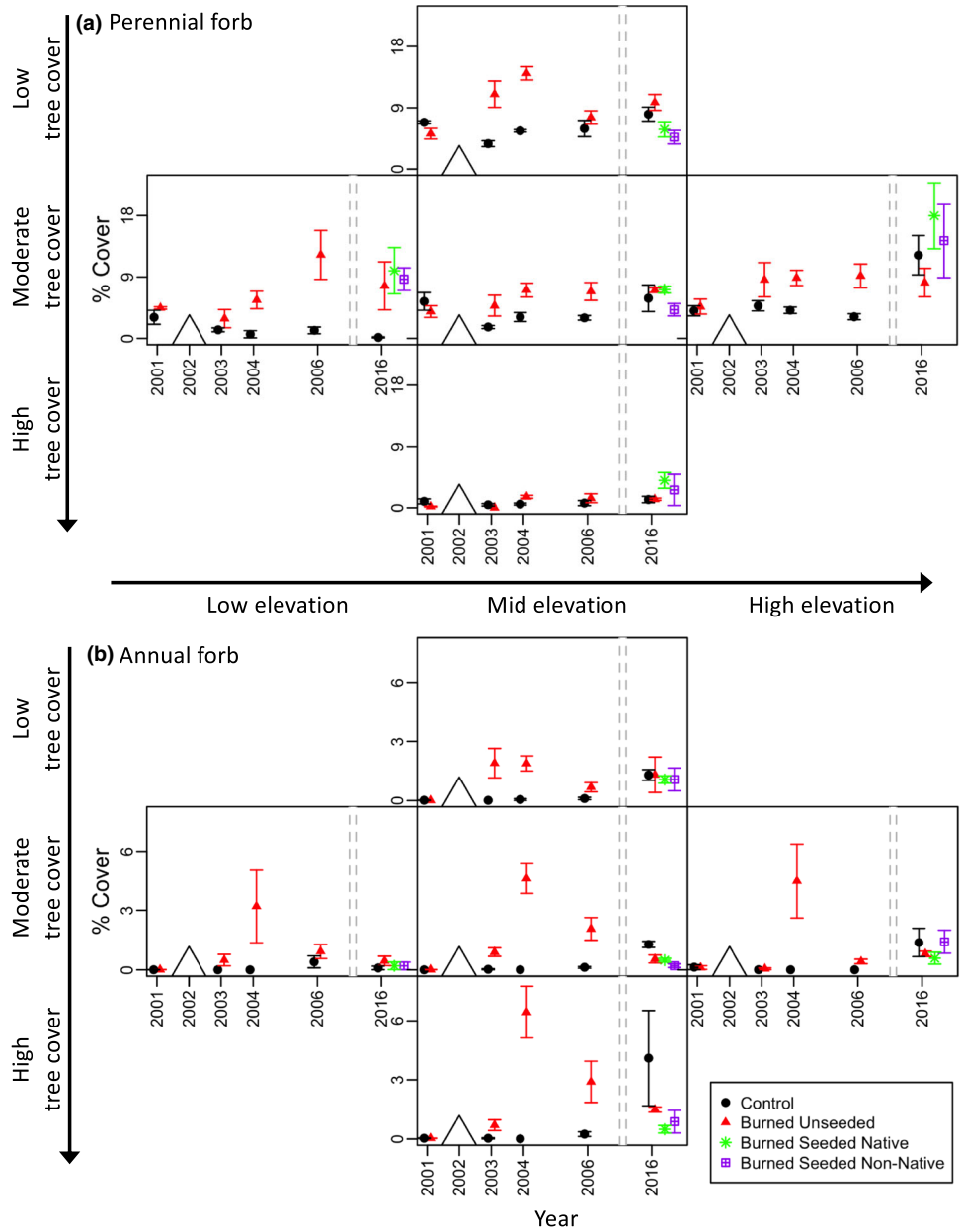

Fig. 3 Time series of **a** perennial forb and **b** annual forb cover along gradients of pre-fire tree cover and elevation. Data shown as mean ± 1 SE. Large triangle shows year of burn treatment. Data from years 2001–2006 for control and burned unseeded sites were published in Urza et al. (2017)

negatively related to pre-fire tree cover, so burned plots with high pre-fire tree cover were more dominated by annual grasses (Fig. 5, bottom center). For site types that experienced a large post-fire increase in annual grass cover (lower elevations, especially those with high pre-fire tree cover), burned plots that were seeded after fire had lower annual grass dominance than unseeded burned plots, reflecting a smaller increase in invasive annual grasses and/or higher perennial cover. The strongest seeding effects were in plots that were seeded with a functionally diverse mix of native species, while seeding with a mix of non-native grasses had generally weaker effects on post-fire plant community composition (Fig. 5).

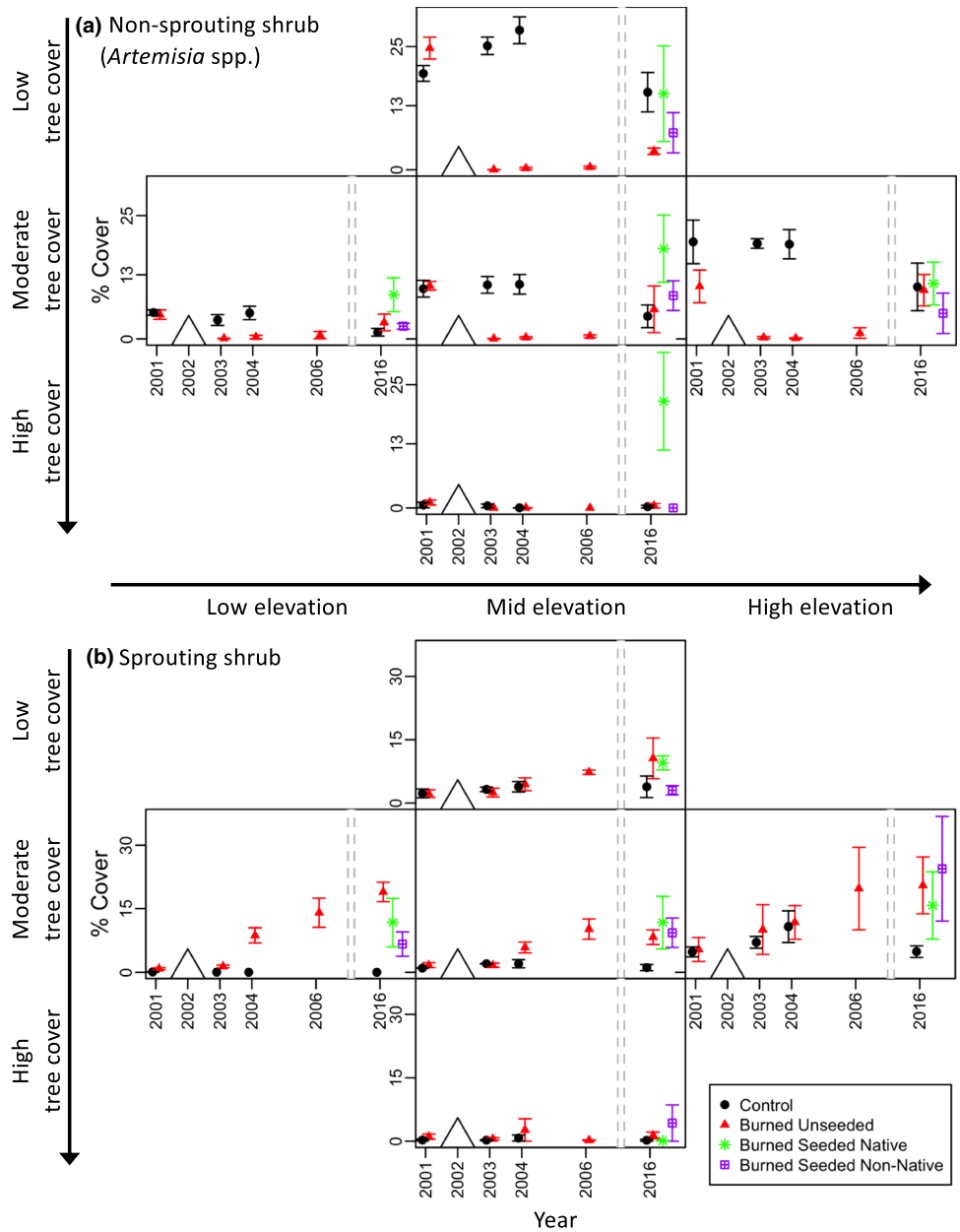

Fig. 4 Time series of **a** non-sprouting shrub (*Artemisia* spp.) and **b** sprouting shrub cover along gradients of pre-fire tree cover and elevation. Data shown as mean ± 1 SE. Large triangle shows year of burn treatment. Data from years 2001–2006 for control and burned unseeded sites were published in Urza et al. (2017)

Discussion

Abiotic and biotic context drives long-term resistance to annual grass invasion after burning

Our results show that prescribed burning facilitated the long-term invasion of *Bromus tectorum*, a fire-adapted annual grass (Fig. 5). Disturbance increases susceptibility to invasion by creating niche opportunities (Shea and Chesson 2002). Fire removes resident trees and shrubs (Miller et al. 2013), reducing resource uptake and thus providing a pulse of available resources (Davis et al. 2000). Companion studies from the same Demonstration Area showed that near-

Table 2 Effect of seeding treatment on post-fire cover of seeded species

Seeded species	Functional group	Low elevation Mean difference (p value)	Mid elevation	High elevation
Native seed mix				
Elymus elymoides	Perennial graminoid	− 0.12 (0.78)	− 0.85 (0.09)	− 0.82 (0.04)
Festuca idahoensis	Perennial graminoid	[a]	0[b]	2.58 (0.24)
Poa secunda	Perennial graminoid	− 0.37 (0.89)	1.22 (0.09)	0.43 (0.51)
Pseudoroegneria spicata	Perennial graminoid	2.57 (0.40)	1.33 (0.09)	0[b]
Hesperostipa comata	Perennial graminoid	− 0.49 (0.42)	0.32 (0.38)	0[b]
Eriogonum heracleoides	Perennial forb	0[b]	0[b]	0[b]
Eriogonum umbellatum	Perennial forb	1.50 (0.38)	0.28 (0.75)	0.61 (0.56)
Lupinus alpestris	Perennial forb	0.25 (0.91)	1.89 (0.04)	2.98 (0.28)
Penstemon palmeri	Perennial forb	0[b]	[a]	[a]
Sphaeralcea munroana	Perennial forb	0[b]	[a]	[a]
Linum lewisii	Perennial forb	[a]	0.00 (0.35)	0[b]
Artemisia tridentata wyomingensis	Non-sprouting shrub	3.43 (0.55)	[a]	[a]
Artemisia tridentata vaseyana	Non-sprouting shrub	[a]	14.33 (0.01)	1.35 (0.66)
Non-native seed mix				
Agropyron cristatum	Perennial graminoid	0.95 (0.42)	2.54 (0.03)	0.17 (0.42)
Bromus inermis	Perennial graminoid	4.48 (0.32)	1.78 (0.08)	0.25 (0.22)
Dactylis glomerata	Perennial graminoid	0[b]	0[b]	0[b]
Phleum pratense	Perennial graminoid	0[b]	0[b]	0[b]
Thinopyrum intermedium	Perennial graminoid	0[b]	0[b]	0[b]

For each species seeded at each elevation, results of paired t tests are shown (mean difference = burned seeded plots − burned unseeded plots). For both mixes, seeds were applied at a rate of 60 seeds per species per m^2

[a]Species not included in seed mix

[b]Species included in seed mix, but not observed during vegetation surveys

surface soil nutrients (inorganic nitrogen and phosphorus) remained elevated for 2–3 years after prescribed fire (Rau et al. 2007). *B. tectorum*'s early phenology, rapid growth rate, and high reproductive capacity allow it to take advantage of fire-induced resource pulses and undergo rapid population growth where the underlying abiotic environment is suitable (James 2008; Chambers et al. 2016). The long-term data consistently showed trends of increasing *B. tectorum* cover through time in invaded sites (Fig. 2b), but it is possible that higher-than-normal spring precipitation resulted in relatively high *B. tectorum* abundance in the 2016 observation year (Fig. 1b).

Site resistance to invasion depends on the ability of resident species to compete with the invader for resources (Davis et al. 2000), which varies based on the abiotic and biotic context. The lack of replication of the elevational gradient in this study limits the scope of inference to the Underdown Canyon study area. However, our results are consistent with many other studies that have found that resistance to fire-induced *B. tectorum* invasion increases with elevation (Chambers et al. 2007; Condon et al. 2011; Miller et al. 2013; Taylor et al. 2014). *B. tectorum* was observed in the drier (low- to mid-elevation) sites shortly after burning (Urza et al. 2017) and gradually increased in abundance over time, demonstrating that these site types have relatively low resistance to invasion (Fig. 2b). In contrast, after 14 years the high elevation site showed no invasion after burning and a robust response from a diverse suite of native plant species, indicating high resilience to burning and resistance to invasion.

The relationship between resistance to invasion and elevation may be explained by multiple related mechanisms. For example, cold soil temperatures at

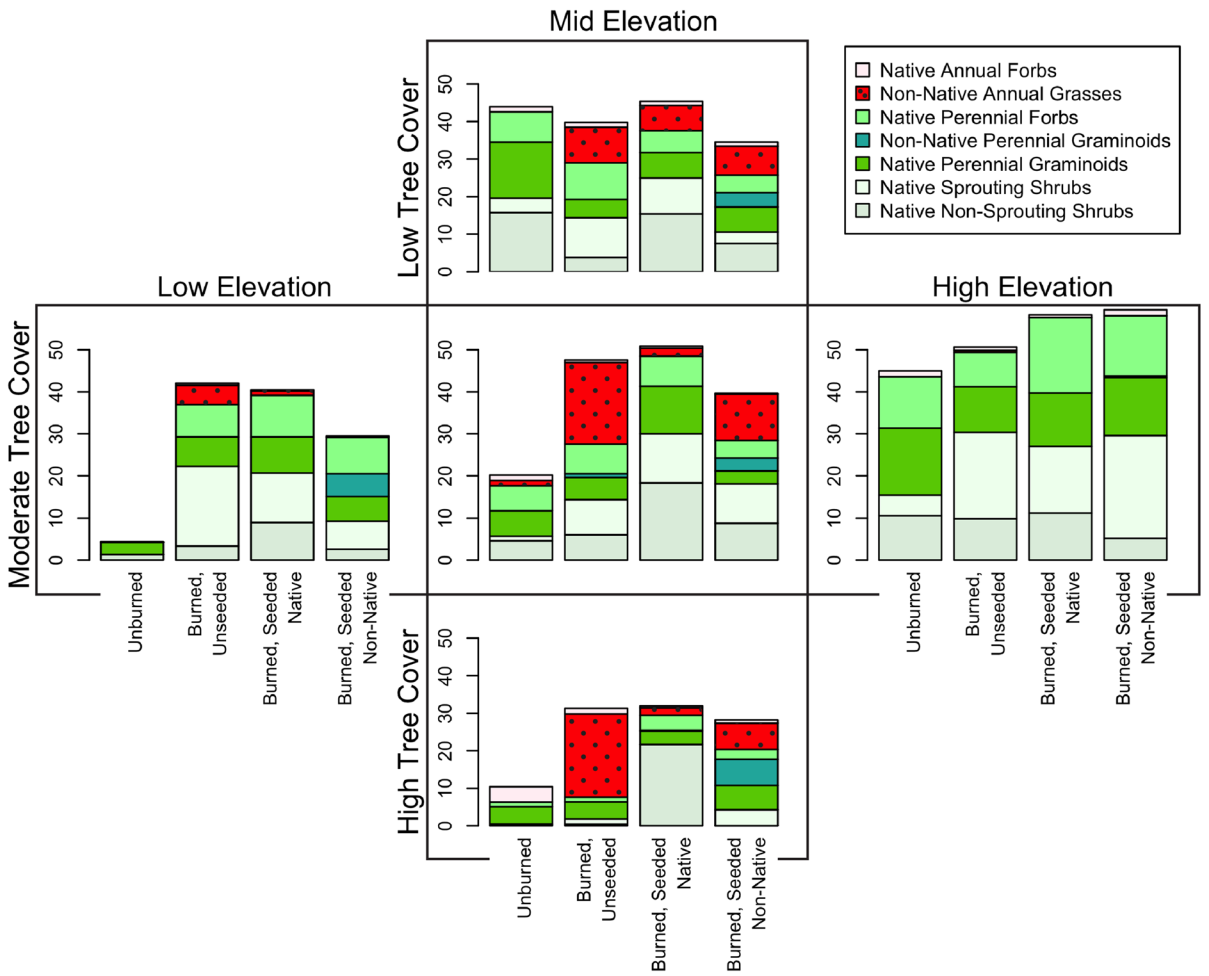

Fig. 5 Plant community composition by functional group from 2016 (14 years after burning). Each panel represents mean cover (%) for burn/seeding treatments within all combinations of elevation and pre-fire tree cover. The center row of panels represents the elevational gradient (for sites with moderate pre-fire tree cover) and the center column of panels represents the gradient of pre-fire tree cover (for sites at the mid elevation)

the high elevation are likely outside the range of suitable climate for *B. tectorum*, directly limiting its ability to establish and reproduce, whereas warmer soil temperatures at the low elevation are highly suitable for *B. tectorum* (Chambers et al. 2007). Additionally, lower resource availability at lower elevations, combined with a history of intensive grazing, results in lower productivity of the native community (West 1983). As a result, the native community may lack the capacity to take advantage of resource pulses such as those that become available after fire, thus reducing biotic resistance to invasion (Rejmanek 1989). Finally, the lower elevation sites may have had higher propagule pressure from nearby *B. tectorum* populations after the burn treatments were implemented, allowing the invader to establish more quickly after burning.

We found that at the mid elevation site, post-fire *B. tectorum* dominance was highest where pre-fire tree cover was high. In tree-dominated sites, the pre-fire absence of understory vegetation results in a weak ecological memory after burning, and post-fire recovery of native understory species can be significantly delayed if seed dispersal is limited or physical soil conditions impede establishment (Condon et al. 2011; Roundy et al. 2014a). Although burning released abundant soil nutrient resources through the removal of trees and residual *Artemisia* spp. (Rau et al.

2007, 2014; Roundy et al. 2014b), sites with high pre-fire tree cover were still sparsely vegetated 4 years after burning (Urza et al. 2017), providing ample opportunity for invasion. Once *B. tectorum* dispersed to the site, the availability of abundant resources and a relative lack of competition from native species facilitated dominance of the plant community by the invader (Fig. 5). Our results are consistent with other studies showing that pinyon-juniper woodland sites at low to mid elevations with high pre-fire tree cover are less resistant to *B. tectorum* invasion (Bates et al. 2014; Roundy et al. 2014a; Reed-Dustin et al. 2016). It is unclear why *B. tectorum* invasion was delayed in our study compared to other examples from the literature, but it is possible that its initial spread was dispersal-limited during this period (Simberloff 2009). Cattle grazing and wood harvest were prohibited in Underdown Canyon for 4 years after burning, but these and other anthropogenic disturbances resumed at high intensity once restrictions were eased and may have facilitated the increase in *B. tectorum*.

Post-fire seeding increased resistance to invasion

We found that seeding perennial species after burning decreased invasibility in sites with low resistance and greatly inhibited *B. tectorum* invasion (Figs. 2, 5). After disturbance, rapid plant establishment or regrowth moderates the pulse of resources that are available, thus limiting opportunities for invasion (Davis et al. 2000; Shea and Chesson 2002). For the low- and mid-elevation sites, especially those dominated by trees before fire, burned plots that were seeded had higher perennial cover and only a small fraction of the *B. tectorum* cover seen in unseeded plots 14 years later. We found that seeding a mix of native shrubs, grasses, and forbs more effectively inhibited invasion than seeding non-native grass species commonly used in restoration. However, the native seed mix had higher species richness and a higher total seeding rate than the non-native mix, so it is possible that the greater inhibition of *B. tectorum* invasion with the native mix was due to higher densities of seeded species. In our study, the effect of the seeding treatments on post-fire cover of individual seeded species was small and differed across sites (Table 2), yet the cumulative effect of seeding on vegetation composition was substantial (Fig. 5). Higher perennial cover, regardless of species, appeared to be important for inhibiting *B. tectorum* invasion (Fig. 5), but these results demonstrate the challenge of predicting exactly which species will successfully establish. This suggests that using a high seeding rate with a diverse mix of species that represents multiple plant functional groups adapted to the environmental conditions of the site can increase the likelihood of successful perennial establishment and improve the outcome of seeding treatments. In areas that are not invaded before treatment, seeding only native species limits competition from non-natives and can result in more successful restoration of native vegetation (Knutson et al. 2014).

Although the link between perennial herbaceous vegetation cover and resistance to *B. tectorum* invasion is well established (Chambers et al. 2007, 2014b; James et al. 2008; Condon et al. 2011; Davies et al. 2012; Bates et al. 2014; Roundy et al. 2014a, 2018), successful inhibition of invasion from post-fire seeding has not often been observed. Instead, other studies have shown that management-scale seeding treatments are often unsuccessful at establishing the seeded species (Pyke et al. 2013; Arkle et al. 2014), particularly for native species at lower elevations (Knutson et al. 2014; Davies et al. 2015). The success of our seeding treatments was likely a result of several factors. First, a heavy seed rate combined with our method of seed application—broadcast seeding and surface mixing with minimal soil disturbance—likely contributed to high rates of establishment of seeded species. Minimizing surface disturbance reduces the loss of residual bunchgrasses that survived burning (Ott et al. 2016), and using heavy seed rates with a minimum-till imprinter—a mechanized analog to our application method—has been found to be the most successful approach for seeding *A. tridentata* (Ott et al. 2017). Second, the weather conditions following the burn may have been particularly favorable for plant establishment at lower elevations, where the effectiveness of post-fire seeding tends to be unpredictable (Knutson et al. 2014; Ott et al. 2016). Even when seeds are available, post-fire *A. tridentata* establishment requires favorable weather conditions immediately following fire (Ziegenhagen and Miller 2009; Nelson et al. 2014). Precipitation was above average in both the winter and summer following the burn (Fig. 1b), which likely promoted successful establishment of *A. tridentata* and the other seeded species.

Finally, the effect of seeding was likely strengthened by prolonged protection from post-fire cattle grazing. Cattle grazing was excluded from Underdown Canyon for 4 years after burning, in contrast to the typical management prescription of 2 years of post-fire grazing deferment (Miller et al. 2014). Mature perennial grasses are highly effective competitors with *B. tectorum* (Booth et al. 2003; Humphrey and Schupp 2004; Chambers et al. 2007), but improper grazing during the active growing season can impede perennial grass establishment after fire (Kerns et al. 2011) and disperse seeds of invasive species (Schiffman 1997). Grazing deferment or exclusion can slow the arrival of *B. tectorum* to a burned site and help ensure that seeded perennial grasses have the ability to outcompete this invader (Reisner et al. 2013). Our data do not allow us to isolate the effect of cattle on the establishment and growth of native competitors, but suggest that the role of grazing on fire-facilitated invasions should be explored further.

Management implications

The results of our study contribute to the growing consensus that susceptibility to fire-induced *B. tectorum* invasion is greatest at lower elevations and where native perennial species are lacking in the understory (Davies et al. 2012; Chambers et al. 2014a, 2016; Taylor et al. 2014). However, our results also highlight the need for more long-term studies to evaluate plant community responses to prescribed fire. Four years after burning, annual grass cover was lowest on sites with high pre-fire tree cover, where only trace amounts of *B. tectorum* were observed (Urza et al. 2017), whereas the opposite result was observed after 14 years.

To reduce the risk of invasion, fire should be avoided in the drier portions of the landscape, especially where tree dominance or improper grazing practices have resulted in depauperate understory vegetation (Chambers et al. 2014a; Miller et al. 2014). When fire cannot be avoided in these types of sites, seeding native perennial shrubs and grasses after burning may speed recovery and reduce the risk of *B. tectorum* invasion. However, the positive results from our seeding treatments could be challenging to reproduce at typical management scales, as post-fire seeding treatments are often unsuccessful in increasing establishment of native species or preventing invasion of *B. tectorum* (Pyke et al. 2013; Knutson et al. 2014). Post-fire seeding success tends to be higher on moister sites (Knutson et al. 2014; Germino et al. 2018), so on drier sites, repeated seeding may be needed to achieve management objectives (Shriver et al. 2018).

Several factors need to be considered when seeding sites with inherently low resistance to invasion and depauperate understories. Success is more likely with a heavy seeding rate (Ott et al. 2017), and although some surface soil disturbance is required to gain sufficient seed-to-soil contact, minimizing the severity of soil disturbance with low-impact drill seeders reduces the loss of important residual bunchgrasses and shrubs whose roots survive the fire and can resprout (Ott et al. 2016). Native-only seed mixes should be used if restoring native vegetation is a management goal, because non-natives tend to outcompete native species when they are seeded together (Knutson et al. 2014). Locally-adapted seeds or varieties with traits that improve field performance should be used to the extent possible (Brabec et al. 2017; Leger and Goergen 2017). Finally, our results suggest that prolonged protection from post-fire grazing may improve the effectiveness of seeding treatments, especially in drier sites characterized by low resilience to fire and resistance to invasion.

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