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RESEARCH ARTICLE

Post-Fire Native Seed Use in Western Colorado: A Look at Burned and Unburned Vegetation Communities

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ABSTRACT: Wildfires on public lands in the United States are increasing in size and frequency over time. Government agency post-fire treatments often include seeding of native and nonnative plant species; however, the effectiveness of post-fire seeding has been questioned, and while the importance of using native species has been emphasized, more research on the effects of native seeding post-fire is needed. We sought to understand what characteristics of vegetation communities distinguished burned and unburned areas, and if environmental characteristics of sites would predictably alter community composition. We collected vegetation, ground cover, and environmental data during the summer of 2015 from public lands that burned in wildfires between 2005 and 2012 and were seeded with a native seed mix. We also collected data from unburned comparison areas that were not seeded. We found that biological soil crusts distinguished unburned areas while native forbs, nonnative forbs, and seeded native species distinguished burned areas. Surprisingly, *Bromus tectorum* (cheatgrass) was not important in distinguishing burned from unburned areas. Precipitation the year after fire influenced vegetation communities.

Index terms: cheatgrass, disturbance, invasive plants, public lands, seeding, wildfire

INTRODUCTION

On public lands, federal agencies are directed "to prevent the introduction of invasive species and provide for their control and to minimize the economic, ecological, and human health impacts that invasive species cause" (Executive Office of the President 1999) and significant funding is spent to this end (Pimentel et al. 2005). One cause of the spread of invasive plant species is disturbance, which may facilitate plant invasion (Stohlgren et al. 1999). Disturbance may increase invader performance over native plant performance (Daehler 2003) creating an advantage for invaders in post-disturbance (e.g., fire) environments. Native plant species may have a competitive advantage over nonnative species as disturbance conditions change to more limiting conditions typical of an area. However, a lack of native seeds and/or overwhelming seed inputs by nonnative species can cause a persistence of nonnative species over native species (Daehler 2003).

Fires are increasing in frequency and size in the western United States (Dennison et al. 2014). One common practice after fire on public lands is seeding of both native and nonnative plant species as a means of stabilizing soils and reducing erosion, although there is mounting evidence that seeding is ineffective for soil stabilization in areas characterized by heavy rainfall events (Robichaud et al. 2000; Keeley et al. 2006; Peppin et al. 2011). This practice is meant to protect watersheds and onsite soils, while not inhibiting longer-term site restoration (Robichaud et al. 2000). Seeding is also potentially a cost-effective means, compared to other treatments, of providing competition for nonnative and invasive plant species that may become established after fire (Robichaud et al. 2000). In the western United States one species of particular concern is *Bromus tectorum* L. (cheatgrass), a common annual invasive grass species that has altered fire regimes, creating near monocultures and perpetuating a fire–invasion cycle (e.g., Knapp 1996; Brooks et al. 2004) and an increased rate of fire return (Balch et al. 2013).

Historically, nonnative grass species were planted to reduce shrub cover and increase livestock and game forage through increased grass cover (Scasta et al. 2015). However, in recent years a shift from the use of nonnative perennial grasses to the use of more native plant species, including shrubs, forbs, and grasses, in post-fire seed mixes has occurred (Richards et al. 1998; Executive Office of the President 1999; Pyke et al. 2003; Peppin et al. 2011). Nonnative plant species commonly used in the past, for example *Agropyron* spp. Gaertn., can negatively affect ecosystems (e.g., Christian and Wilson 1999; Scasta et al. 2015). The emphasis on the use of native species is to benefit ecosystem resilience and pollinators, and to maintain ecosystem function (Richards et al. 1998; Presidential Memorandum 2014; BLM 2015). However, the use of native species in restoration has had limited and sometimes unpredictable success (e.g., Banjeree et al. 2006; Grant-Hoffman et al. 2012; Pyke et al. 2013; Knutson et al. 2014; Grant-Hoffman et al. 2015; Jonas et al. in press) and the effects of native seed use post-fire on vegetation communities have been less studied (but see Peppin et al. 2010). Further, native seed use may be affected by how "local" the "native" seed source is (e.g., Jones 2003; Jones and Monaco 2007; Bower et al. 2014; Bucharaova et al. 2017). Obtaining "local" native seed is tempered by practical limitations such as large and unpredictable disturbances, quick timelines, limited budget, and limited seed availability.

We studied areas that burned in wildfires between 2005 and 2012 and were seeded with native seed. We sought to understand what characteristics of the vegetation communities distinguished burned and unburned areas. We hypothesized that the invasive annual cheatgrass would be important and higher in cover in burned areas, as would seeded species. We also sought to determine if certain environmental characteristics would alter vegetation composition.

METHODS

Sampling Area Description

Burned areas that resulted from either naturally or human-caused wildfires, and unburned comparison areas, were located on public lands managed by the Bureau of Land Management within McInnis Canyons National Conservation Area and the Grand Junction Field Office (Figure 1). We sampled burned areas for which seeding information, including seed mix applied, seeding rates, and methods of seed application were available, and that were seeded with a mix of native seeds. Sampling sites were established within burned areas of high burn homogeneity (Table 1, Figure 1). Native seeds were obtained from the Bureau of Land Management seed warehouse in Boise, Idaho, and other vendors for earlier fires, and included some cultivars and some regionally collected seeds (Table 1). We feel that the seed mixes studied here represent

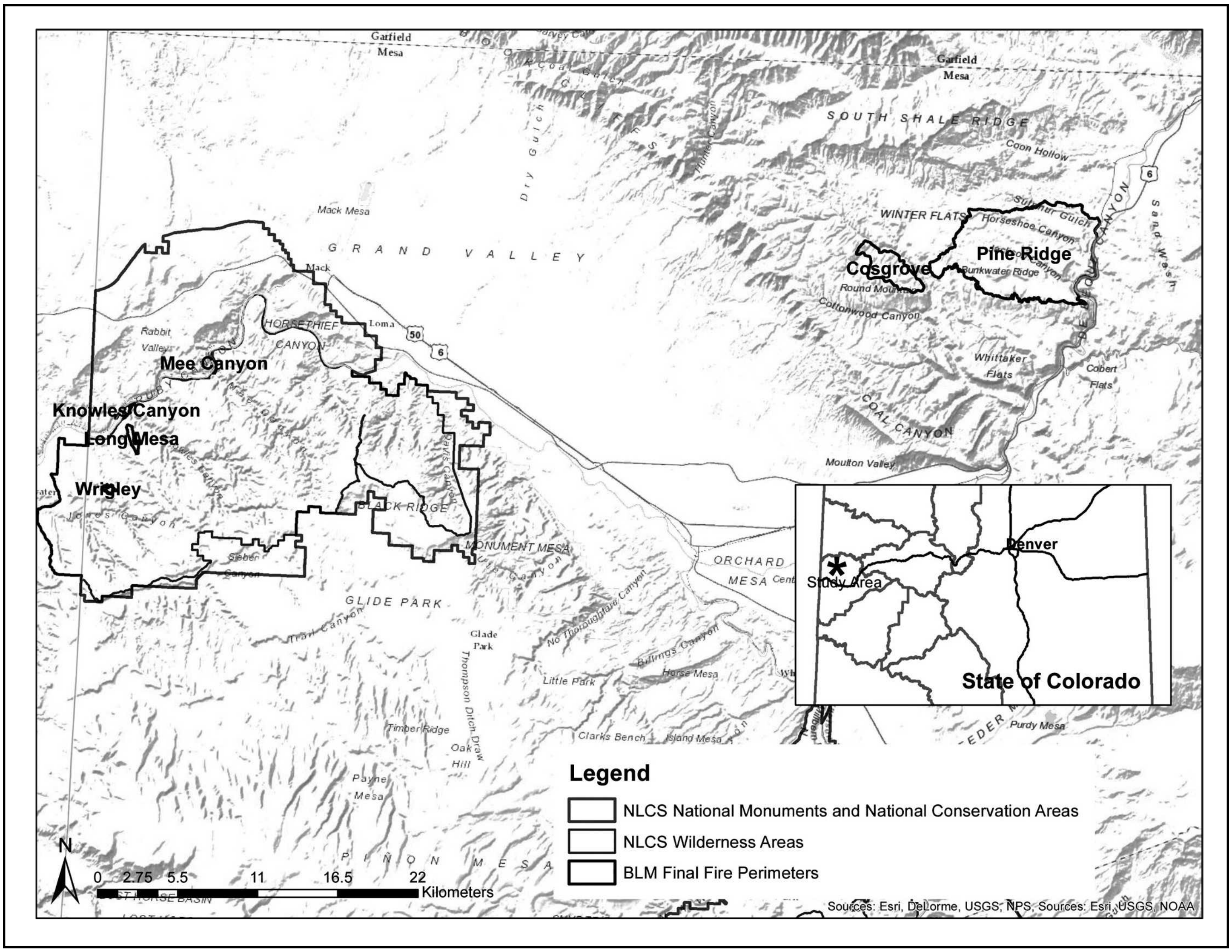

Figure 1. Map of study area.

Table 1. Six areas burned by wildfires were studied through vegetation and ground cover sampling. All areas were seeded with a native seed mix post-fire. Nomenclature follows United Stated Department of Agriculture plants database (accessed October 2016 from http://plants.usda.gov/java/). Cultivar information is listed for each species. "Source identified" materials were fitted as closely as possible to the site of use based on elevation and precipitation.

Burned area	Year burned	Hectares	Mean elevation (meters)	# sites sampled	Vegetation type	Soil type	Species included in seed mix	Seeding method
Mee	2005	25	1508	3	Inter-Mountain Basins Mixed Salt Desert Shrub	Moffat-Shepard-Pennell complex, San Mateo Escavada dry complex	*Achnatherum hymenoides* (Roem. & Schult.) Barkworth (cultivar: Rimrock), *Atriplex canescens* (Pursh) Nutt. (cultivar: Source Identified), *Hesperostipa comata* (Trin. & Rupr.) Barkworth (cultivar: Source Identified), *Sporobolus cryptandrus* Hitchc. (cultivar: Source Identified)	Broadcast and raked into soil @ 12 lbs/acre, September and October 2005
Knowles	2007	37	1335	2	Inter-Mountain Basins Mixed Salt Desert Shrub	Moffat-Shepard-Pennell complex	*Achnatherum hymenoides* (cultivar: Rimrock), *Atriplex canescens* (cultivar: Source Identified), *Elymus elymoides* (Raf.) Swezey (cultivar: Unknown), *Hesperostipa comata* (cultivar: Source Identified), *Sporobolus cryptandrus* (cultivar: Source Identified)	Aerially seeded @13.5 lbs/acre, January 2008
Cosgrove	2011	706	1957	4	Colorado Plateau Pinyon Juniper Woodland	Redcreek Rentsac complex, Yamo moist Redcreek complex	*Achillea millefolium* L. (cultivar: Source Identified), *Achnatherum hymenoides* (cultivar: Nezpar), *Atriplex canescens* (cultivar: Source Identified), *Elymus lanceolatus* (Scribn. & J.G. Sm.) Gould (cultivar: Critana), *Koeleria macrantha* (Ledeb.) Schult. (cultivar: Source Identified), *Linum lewisii* Pursh (cultivar: Maple Grove), *Pascopyrum smithii* (Rydb.) Á. Löve (cultivar: Arriba), *Penstemon palmeri* A. Gray (cultivar: Source Identified)	Aerially seeded @13 lbs/acre, March 2012
Pine Ridge	2012	5240	1718	6	Colorado Plateau Pinyon Juniper Woodland; Inter-Mountain Basins Big Sagebrush Shrubland	Barx loam, Bunkwater very fine sandy loam, Travessilla rock outcrop	*Achillea millefolium* (cultivar: Source Identified), *Achnatherum hymenoides* (cultivar: Rimrock), *Atriplex canescens* (cultivar: Source Identified), *Elymus elymoides* (cultivar: BLM Accession), *Elymus trachycaulus* (cultivar: San Luis), *Linum lewisii* (cultivar: Appar, Maple Grove), *Pascopyrum smithii* (cultivar: Arriba), *Poa secunda* J. Presl (cultivar: UP Accession), *Sporobolus cryptandrus* (cultivar: Source Identified)	Aerially seeded @11 lbs/acre, February 2013
Wrigley	2012	29	1537	3	Inter-Mountain Basins Mixed Salt Desert Shrub	Gladel Bond Rock outcrop complex	*Achillea millefolium* (cultivar: White), *Achnatherum hymenoides* (cultivar: Paloma), *Elymus elymoides* (cultivar: Fish Creek), *Elymus trachycaulus* (cultivar: San Luis), *Linum lewisii* (cultivar: Maple Grove), *Pascopyrum smithii* (cultivar: Arriba), *Poa secunda* (cultivar: Source Identified)	Aerially seeded @11 lbs/acre, February 2013

Continued

a reasonable effort to use appropriate "native" seeds, tempered with practical constraints (Table 1). Burned and unburned areas were categorized by vegetation as determined by the predominant vegetation category based on LANDFIRE data layers in GIS (LANDFIRE 2012). Vegetation types included Inter-Mountain Basins Big Sagebrush Shrubland (sagebrush shrubland), Colorado Plateau Pinyon Juniper Woodland (pinyon-juniper woodland), and Inter-Mountain Basins Mixed Salt Desert Scrub (salt desert scrub). Vegetation types should be seen as a continuum instead of as discrete entities. Vegetation types can overlap and have components of more than one specific type, for example pinyon-juniper encroachment into sagebrush systems (e.g., Miller and Rose 1999; Miller et al. 2008) or scattered juniper in salt desert scrub (Colorado Natural Heritage Program 2005). Soil types sampled include Moffat-Shepard-Pennell complex, San Mateo Escavada dry complex, Redcreek Rentsac complex, Yamo moist Redcreek complex, Barx loam, Bunkwater very fine sandy loam, Travessilla rock outcrop, and Gladel Bond Rock outcrop complex (NRCS 2016; Table 1). Historic fire return for these vegetation types is not always well understood. However, in pinyon-juniper vegetation smaller fires (<10 ha) and drought are thought to have been more prominent disturbances than larger fires (Kennard and Moore 2013). Reported fire return for sagebrush systems is varied. For example, Whisenant (1990) reports intervals between 60 and 110 y, while Miller and Rose (1999) report intervals of 12–15 y in stands shared with ponderosa pines, and Baker (2006) reports 100–240 y for Wyoming big sagebrush. Generally, in the western United States, fire frequency and spatial area are thought to be increasing with climate change and other pressures such as increased fuel continuity due to cheatgrass (Pellant 1990; Brown et al. 2004; Westerling et al. 2006; Dennison et al. 2014). Burn intensity data were only available for two of the six burned areas (Mee and Pine Ridge), and in these areas sampling points were located in "moderate severity" burn areas. Elevation ranged from approximately 1350 m to 1950 m and slope ranged from 0 to 10% (Table 1). Aspects of all sites were south to southwest. All

Table 1. (*Cont'd.*)

Burned area	Year burned	Hectares	Mean elevation (meters)	# sites sampled	Vegetation type	Soil type	Species included in seed mix	Seeding method
Long Mesa	2012	70	1515	3	Inter-Mountain Basins Mixed Salt Desert Shrub	Gladel Bond Rock outcrop complex	*Achillea millefolium* (cultivar: White), *Achnatherum hymenoides* (cultivar: Paloma), *Elymus elymoides* (cultivar: Fish Creek), *Elymus trachycaulus* (cultivar: San Luis), *Linum lewisii* (cultivar: Maple Grove), *Pascopyrum smithii* (cultivar: Arriba), *Poa secunda* (cultivar: Source Identified)	Aerially seeded @11 lbs/acre, February 2013
Unburned Sagebrush	NA	NA	1535	3	Inter-Mountain Basins Big Sagebrush Shrubland	Bunkwater very fine sandy loam, Travessilla rock outcrop	NA	NA
Unburned Pinyon Juniper	NA	NA	1700	3	Colorado Plateau Pinyon Juniper Woodland	Yamo moist Redcreek complex, Travessilla rock outcrop	NA	NA
Unburned Mixed Salt Desert	NA	NA	1546	3	Inter-Mountain Basins Mixed Salt Desert Shrub	Gladel Bond Rock outcrop complex, Moffat-Shepard-Pennell complex, San Mateo Escavada dry complex	NA	NA

sampling areas have historical and current livestock grazing; however grazing was not present from the time of the fire to 3 y post-fire. While livestock grazing can certainly alter vegetation (e.g., Fleischner 1994; Stohlgren et al. 1999) we did not seek to quantify or separate grazing effects. Precipitation in this area is variable in space and time and ranges between average lows of 9 cm and average highs of 39 cm annually, with an overall annual average of 22 cm of total precipitation, with peaks often occurring in spring and fall (Western Regional Climate Center 2016, accessed 20 May 2016). Annual precipitation in the area was 33 cm in 2015 when areas were sampled.

We used GRTS (generalized random tesselation stratified) analysis to randomly place points in burned and unburned comparison areas (Stevens and Olsen 2004). We collected data during the summer of 2015 in six areas that burned in wildfires between 2005 and 2012 and were reseeded with a native seed mix, as well as three unburned comparison areas that were not seeded (Table 1). Burned, unseeded areas were not available for this study. Unburned comparison areas were located within a one-mile buffer of the burned areas and within the three vegetation types represented and on similar soils (Table 1). Burned areas were aerially or broadcast seeded between September and March the year of, or the year following, the fire at similar seeding rates (Table 1). Due to the size of the Pine Ridge fire, two vegetation types were burned, while other fires burned only one vegetation type (Figure 1). Total sampling sites were 9 unburned comparison sites and 21 burned sites for a total of 30 sites sampled. Data were collected once per site in June and July of 2015. We visually estimated percent cover by plant species and ground cover categories in 0.5 m^2 marked quadrats (Daubenmire 1959; Elzinga et al. 1998). Cover was estimated in 5% classes with a 3% and a trace (1%) category. We sampled 25 quadrats per site. Quadrats were located along five 10-m sub-transects perpendicular to a center transect of 25 m. This design was chosen in part to mirror existing BLM data and streamline data collection for maximum use of historical data (Grant-Hoffman et al. in prep).

We also collected environmental variables at each site including slope and aspect. Elevation data were collected from ArcGIS, using a USGS digital elevation model. Precipitation was calculated as a percentage of average for the year of and year following each fire. The closest station with complete data from the years of interest was used: Fruita, Colorado, station for Mee; Colorado National Monument, Colorado, for Knowles, Wrigley, and Long Mesa; Palisade, Colorado, for Pine Ridge; and Grand Junction Walker Field, Colorado, for Cosgrove (Western Regional Climate Center 2016, accessed 14 July 2017).

Statistical Analyses

Nonmetric multidimensional scaling was used to analyze vegetation and ground cover categories: bare ground, litter, rock, biological soil crust, standing dead wood, cheatgrass, native forbs, nonnative plants excluding cheatgrass, native grass, native shrubs, native trees, seeded species, previously planted nonnative species (most notably *Agropyron cristatum* [L.] Gaertn. [crested wheatgrass], a native of Russia that has been widely introduced in the western United States [Rogler and Lorenz 1983]) (metaMDS in R package vegan; R Core Team 2017), using the Bray–Curtis distance and 9999 runs. Vegetation and ground cover categories were averaged over the 25 quadrats per site, making N=30 (sites). Environmental factors (burn status: burned or unburned; vegetation type: sagebrush shrublands, pinyon-juniper woodlands, mixed salt desert scrub), and vectors (precipitation in the year of the fire, precipitation the year after the fire) were then fitted to the resulting ordination (envfit in R package vegan; R Core Team 2017). It is noted that we could not distinguish between native individuals from the applied seed mix versus individuals from the seed bank in burned areas. Therefore, cover estimates of species included in the seed mixes may be high. However, cover estimates of native species included in seed mixes were also calculated in unburned areas, which were not seeded, and used in analyses for comparisons. We assumed that if cover of species included in the seed mixes in burned areas was significantly higher than cover of these same species in unburned, unseeded areas, that this increase in burned areas was due at least in part to seeding efforts. Seeded species were included only in the seeded response variable to preclude double counting.

Significant vectors and factors were further analyzed with permutational multivariate analysis of variance (adonis in R package vegan; R Core Team 2017) using Euclidean (vectors) or Bray–Curtis (factors) methods. Normality of data was checked with quantile–quantile plots of residuals (qqnorm in R; R Core Team 2017); most data reasonably met normality assumptions and transformations were not performed (Hothorn and Everitt 2014). Where normality was questionable (native tree, native grass, previously planted nonnative variables), data were log transformed, however transformation did not change significance at P=0.05 level, and results from untransformed data are used. Data reasonably met homogeneity of variance assumptions as tested with Levene's test (P = 0.10; library 'car', 'leveneTest' in R; R Core Team 2017).

Given significant differences in MANOVA analyses, to further determine which specific vegetation groups were driving groupings, we performed protected ANOVAs for specific vegetation categories (aov in R [R Core Team 2017]; Zar 1999; Scheiner and Gurevitch 2001; Hothorn and Everitt 2014). By using variance component mixed modeling, we were able to attribute variation in data to fixed components, vegetation type, and burn status. We were also able to attribute variation in data to the random component precipitation in the year following the fire (Zar 1999; Scheiner and Gurevitch 2001; Hothorn and Everitt 2014). Precipitation in the year following fire was used to determine if precipitation patterns in the year following the disturbance and seeding effort could explain variation in certain vegetation groups. For example, if a fire was followed by a dry year we might expect higher cover of invasive annuals, whereas a wet year following fire may contribute to higher cover of native perennial grasses. ANOVA models included vegetation categories of interest as response variables and significant explanatory variables from permutational MANOVA analyses (burn status, vegetation type, precipitation the year after the fire, and a burn status by vegetation interaction). We considered a vegetation by burn status interaction since we expected that some trends may be significant regardless of vegetation type. For example, cover of cheatgrass may be higher in burned areas regardless of which vegetation type was burned, while others may be dependent on vegetation type (e.g., shrubs may increase more in mixed salt desert scrub than in pinyon juniper vegetation). While precipitation during the year of the fire and precipitation the year after the fire were both significant in permutational MANOVA analyses, they were highly correlated (simple scatterplot matrix, 'pairs' in R; R Core Team 2017). We therefore use precipitation the year after the fire, which showed stronger relationships with specific vegetation categories, in our ANOVA analysis models. Tukey's honest significant difference was used to determine differences between vegetation types when appropriate (TukeyHSD in R; R Core Team 2017).

Species richness was determined for each site in the Pine Ridge burned area for Colorado Plateau Pinyon Juniper Woodland and Inter-Mountain Basins Big Sagebrush Shrubland, and compared using *t* tests between burned and unburned areas. Histograms showed data were reasonably normal (hist in R; R Core Team 2017), therefore data were not transformed. We did not test Inter-Mountain Basins Mixed Salt Desert Scrub due to an unequal number of burned and unburned sample sites, which could skew species richness estimates. To quantify the effectiveness of seeding plant species commonly used in seed mixes, we tallied the number of sites (presence/absence) where we found plant species that had been seeded at that sample site, the number of sample sites where a plant species had been seeded but not found, and the number of sample sites where plant species commonly used in seed mixes had been found but not seeded (Table 2). As in all of our analyses, we could not distinguish between native individuals from the applied seed mix and individuals from the seed bank in burned areas. However, by including presence of species both where they were seeded and where they were not seeded, we hoped to indicate a potential seeding effect.

RESULTS

Nonmetric multidimensional scaling showed stress values of 0.11 and a stress plot showed reasonable scatter around a regression between original dissimilarities and the reduced dimensions distances. Nonmetric multidimensional scaling and ordination found that the vectors related to precipitation the year of the fire, and precipitation the year after the fire, were both significant ($P < 0.01$, data not shown); the factors burn status ($P < 0.01$, Figure 2) and vegetation type ($P = 0.03$, Figure 3) were also significant. Permutational

Table 2. Plant species commonly found in seed mixes used in the six burned areas studied. Shown are the number of sites where a particular species was seeded; the number and percentage of sites where it was and seeded and found during vegetation cover sampling in 2015; and the number and percentage of sites where it was not seeded but found during vegetation cover sampling in 2015. Light gray indicates species found where seeded in at least 30% of sites, termed "good re-seeders." Dark gray indicates species found in at least 30% of sites where they were not seeded, termed "good re-colonizers." One perennial grass species, *Pascopyrum smithii*, was both a "good re-seeder" and a "good re-colonizer." Nomenclature follows United States Department of Agriculture plants database (accessed October 2016 from http://plants.usda.gov/java/).

Species	# of sites seeded	# sites found seeded	%sites found/ seeded	# found not seeded	% sites found/ not seeded
Achillea millefolium L.	16	7	44	0	0
Achnatherum hymenoides (Roem. & Schult.) Barkworth	21	9	43	1	11
Atriplex canescens (Pursh) Nutt.	15	5	33	0	0
Elymus elymoides (Raf.) Swezey	14	0	0	3	33
Elymus lanceolatus (Scribn. & J.G.) Gould	4	0	0	0	0
Elymus trachycaulus (Link) Gould ex Shinners	12	2	17	0	0
Hesperostipa comata (Trin. & Rupr.) Barkworth	5	0	0	7	78
Koeleria macrantha (Ledeb.) Schult.	4	0	0	0	0
Linum lewisii Pursh	16	11	69	1	11
Pascopyrum smithii (Rydb.) Á. Löve	16	11	69	3	33
Penstemon palmeri A. Gray	4	0	0	0	0
Poa secunda J. Presl	12	0	0	3	33
Sporobolus cryptandrus (Torr.) A. Gray	11	6	55	4	44

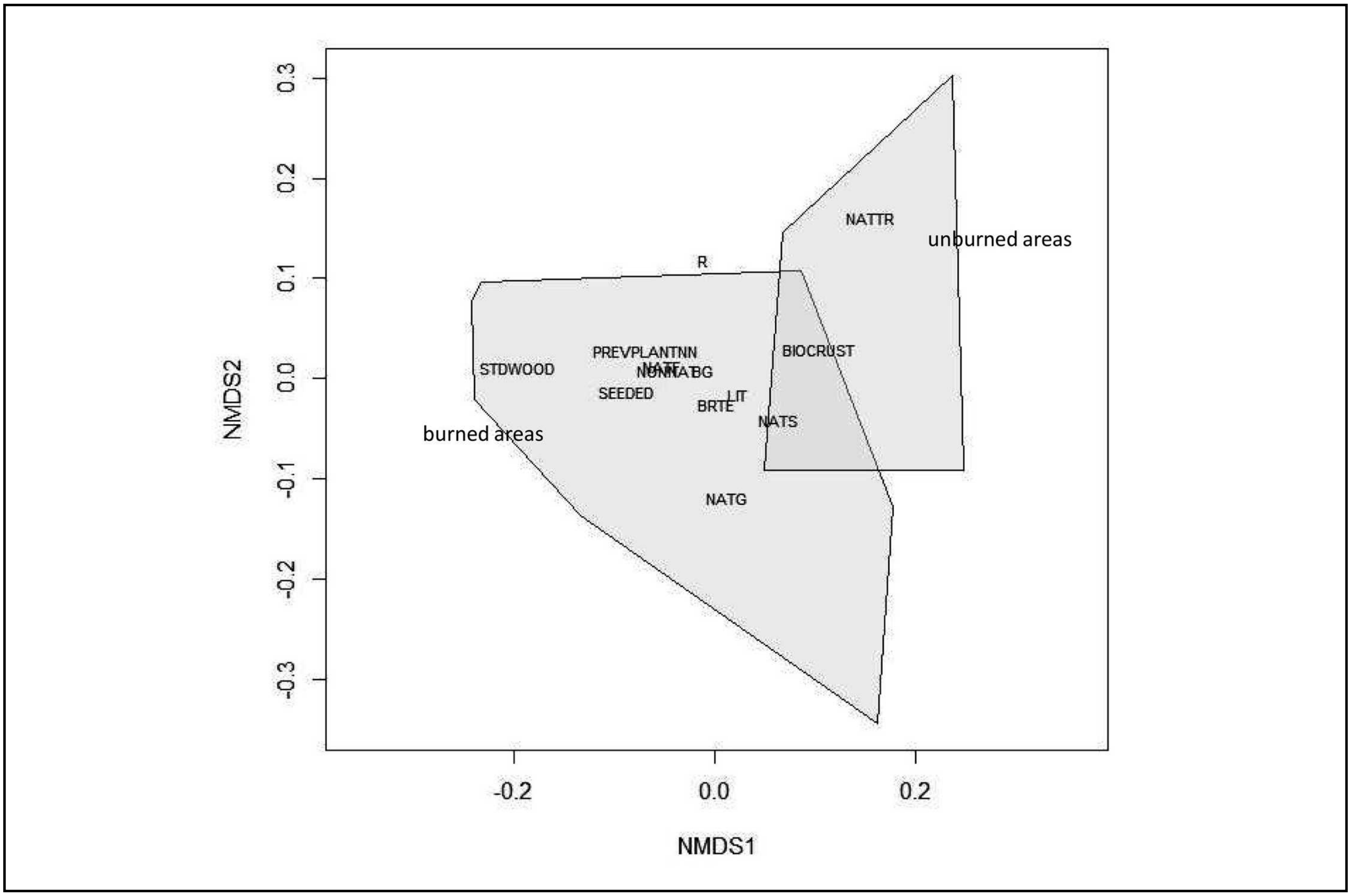

Figure 2. Significant factors in nonmetric multidimensional scaling ordination ($P < 0.05$). Gray boxes represent burn status (burned or unburned). R = rock; LIT = litter; BG = bare ground; BIOCRUST = biological soil crusts including moss, lichen, and cyanobacteria; NATTR = native trees; NATS = native shrubs; NATG = native grasses; NATF = native forbs; STDWOOD = standing dead wood; SEEDED = native plant species included in seed mixes applied to burned areas, cover of these species was also calculated for unburned areas; PREVPLANTNN = nonnative species planted in previous management actions, most notably crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.); BRTE = *Bromus tectorum* L.; NONNAT = nonnative species excluding *B. tectorum*.

multivariate analyses of variance further showed that for vegetation categories the three vegetation types were significantly different from each other ($P < 0.05$ for all tests), which was expected.

Unburned areas were characterized by the presence of biological soil crusts and native trees, while burned areas were characterized by native forbs, as well as nonnative forbs, and seeded species (Figure 2). There was a significant interaction between burn status and vegetation type for native trees, driven by no trees found in sagebrush shrublands, few trees found in mixed salt desert scrub, and abundant trees in pinyon juniper vegetation types ($F = 21.01$, $P < 0.01$; Tukey's HSD $P < 0.05$ for all vegetation types). There was significantly higher cover of biological soil crusts ($F = 35.82$, $P < 0.01$, Figure 4) and native trees ($F = 65.74$, $P < 0.01$, data not shown) in unburned areas compared to burned areas. Living native trees were found only in unburned areas. Cover of native forbs ($F = 6.36$, $P = 0.02$, Figure 4), nonnative cover ($F = 8.94$, $P = 0.01$, Figure 4), and seeded species ($F = 6.24$, $P = 0.02$, Figure 4) were significantly higher in burned areas (Figure 4).

Pinyon-juniper woodlands were characterized by higher cover of native trees and standing dead wood, while sagebrush areas were characterized by higher cover of cheatgrass and nonnative planted species (driven by crested wheatgrass), and lower cover of native forbs (Figure 3). Cover of native forbs ($F = 3.71$, $P = 0.04$), cheatgrass ($F = 9.00$, $P = 0.001$), and nonnative planted species ($F = 5.93$, $P = 0.008$), most notably crested wheatgrass, were significantly different between vegetation types. Native forbs were significantly lower in sagebrush shrublands than in pinyon-juniper woodlands (Tukey's HSD, $P = 0.04$), but not in sagebrush shrublands compared to mixed salt desert scrub (Tukey's HSD, $P = 0.11$). Mean cover of cheatgrass was 14% in sagebrush areas vs. 10% in pinyon juniper and 6% in mixed salt desert scrub; the difference between sagebrush shrublands and mixed salt desert scrub was significant (Tukey's HSD, $P = 0.001$). The interaction of burn status and vegetation was marginally significant for cheatgrass ($F = 2.81$, $P = 0.08$). In both

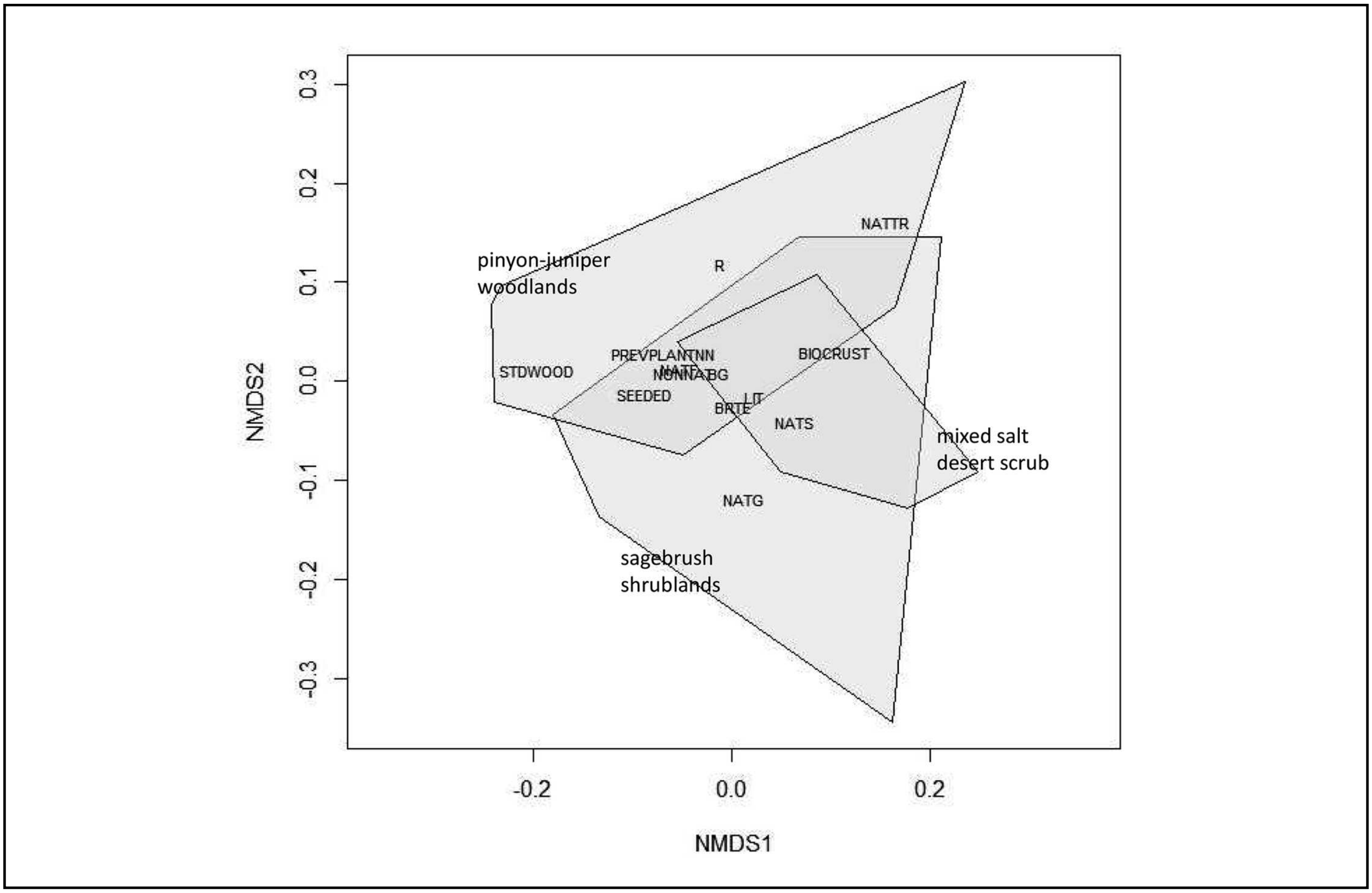

Figure 3. Significant factors in nonmetric multidimensional scaling ordination ($P < 0.05$). Gray boxes represent vegetation types. Vegetation types include Inter-Mountain Basins Big Sagebrush Shrubland (sagebrush shrubland), Colorado Plateau Pinyon Juniper Woodland (pinyon-juniper woodland), and Inter-Mountain Basins Mixed Salt Desert Scrub (salt desert scrub). Abbreviations are the same as in Figure 2.

sagebrush and mixed salt desert scrub areas percent cover of cheatgrass was similar in burned and unburned areas. In sagebrush shrublands the mean cover of cheatgrass in burned areas was 13.8%, and mean cover in unburned areas was 14.2%. In mixed salt desert scrub, the mean cover of cheatgrass in burned areas was 6.1% vs. 5% in unburned areas. In pinyon juniper areas the average cover of cheatgrass in burned areas was 12.5% while the average cover of cheatgrass in unburned areas was 3.5%. Pinyon juniper sites had significantly more nonnative plant cover than mixed salt desert scrub ($F = 4.81$, $P = 0.02$; Tukey's HSD, $P = 0.02$). Sagebrush shrublands were not significantly different from either pinyon juniper or mixed salt desert scrub sites in cover of nonnative species. Not surprisingly, native shrubs were most abundant in sagebrush shrublands followed by mixed salt desert scrub, then pinyon juniper ($F = 3.85$, $P = 0.04$; Tukey's HSD sagebrush and pinyon juniper $P = 0.05$, Tukey's HSD mixed salt desert scrub and pinyon juniper $P = 0.08$). Also not surprisingly, native trees were most abundant in pinyon juniper sites, scarce in mixed salt desert shrub, and absent in sagebrush shrublands; all differences were significant ($F = 65.74$, $P < 0.01$; Tukey's HSD $P < 0.05$). Previously planted nonnative species, most notably crested wheatgrass, had significantly higher cover in sagebrush shrublands as compared to mixed salt desert scrub, where they were absent (Tukey's HSD $P = 0.01$).

Cover of nonnative species excluding cheatgrass was significantly lower when precipitation was higher the year after the fire ($F = 9.73$, $P = 0.005$); litter was marginally lower in the same circumstances ($F = 3.25$, $P = 0.08$). Cover of native shrubs did not significantly increase with higher precipitation the year after the fire ($F = 2.15$, $P = 0.16$).

In Colorado Plateau Pinyon Juniper Woodlands, species richness was significantly higher in burned areas than unburned comparison areas ($t = 3.58$, $P = 0.02$), but was not significantly different between burned and unburned comparison areas for Inter-mountain Basins Big Sagebrush shrubland ($t = 0.13$, $P = 0.90$; data not shown). Plant species that were included in seed mixes but not found in any of the sampled sites were two grasses, *Elymus lanceolatus* and *Koeleria macrantha*, and one forb, *Penstemon palmeri* (Table 2). Plant species that were found in at least 30% of the areas where they were seeded were termed "good re-seeders" and were

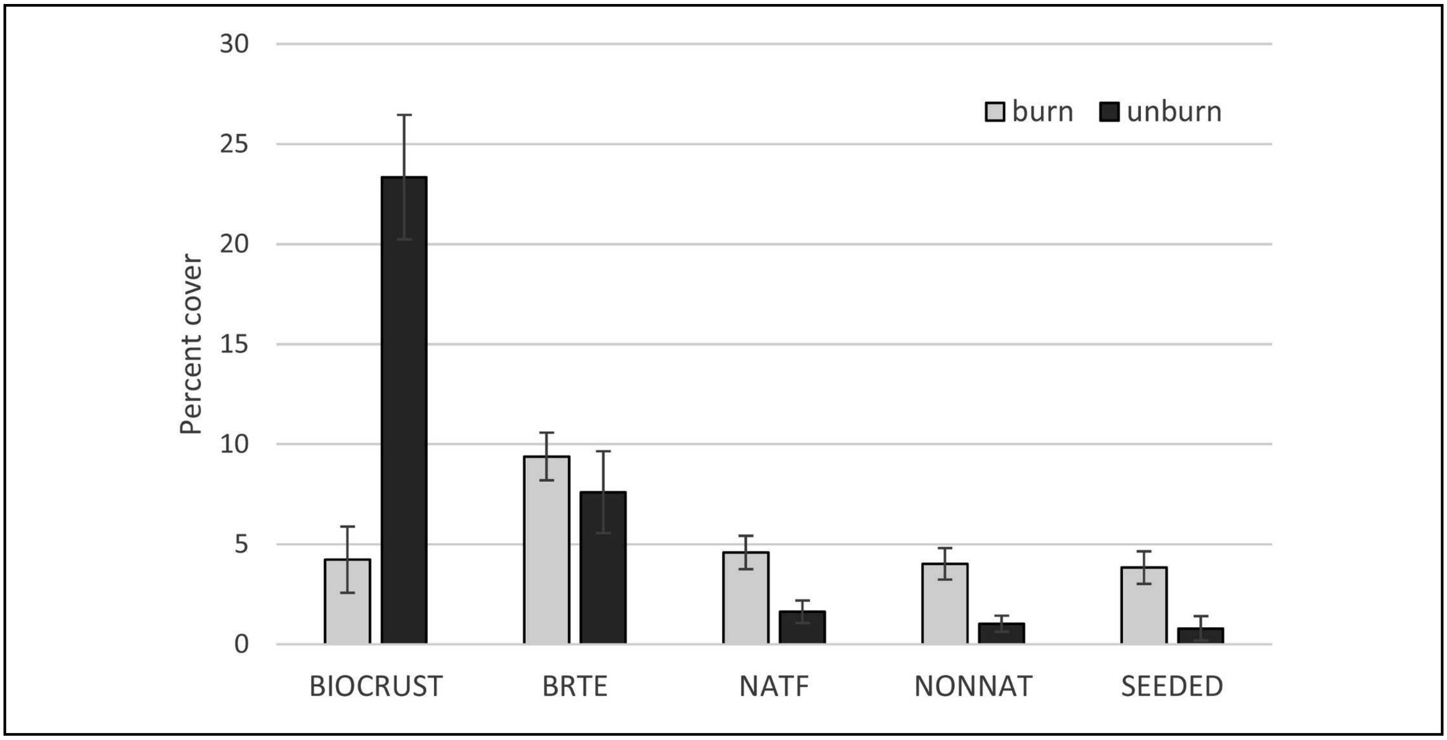

Figure 4. Differences in select ground cover and cover of vegetation categories between burned and unburned areas. BIOCRUST = biological soil crust; BRTE = *Bromus tectorum* L., cheatgrass; NATF = native forbs; NONNAT = nonnative species excluding cheatgrass; NATG = native grasses; SEEDED = native species included in seed mixes which were used in burned areas only, burn = areas burned by wildfire and seeded with native seed, unburn = unburned, unseeded areas. All differences except BRTE are significant (*P* < 0.05). Shown are averages and standard error.

the grasses *Achnatherum hymenoides*, *Pascopyrum smithii*, and *Sporobolus cryptandrus*; forbs *Achillea millefolium*, *Linum lewisii*; and the shrub *Atriplex canescens* (Table 2). It is noted that we cannot definitively state that the presence of these species indicates recruitment from applied seed versus recruitment from the seedbank; however, we assume that presence of a species where seeded indicated some recruitment from seed. The grass *Elymus trachycaulus* was found in 17% of the sites where it was seeded (Table 2). Plant species that were found in ≥30% of the areas where they were not seeded, and could therefore not have resulted from added seed, were termed "good re-colonizers" and were the grasses *Elymus elymoides*, *Hesperostipa comata*, *Pascopyrum smithii*, and *Poa secunda* (Table 2). Conversely to good "re-seeders," we assumed these species were good colonizers from an existing seedbank or existing plants. We did not distinguish if "good re-colonizers" resulted from seed or resprouting. Nomenclature follows United States Department of Agriculture plants database (http://plants.usda.gov/java/).

DISCUSSION

In our study, unburned areas were characterized by biological soil crusts, while burned areas were characterized by the presence of unseeded native and nonnative forbs, as well as seeded species. Haubensak et al. (2009) also found that biological soil crusts were lower in burned areas, while nonnative species were higher in burned sites, compared to unburned sites in salt desert scrub in the Great Basin. Seeded species, including native perennial grasses, forbs, and shrubs, had significantly higher cover in burned areas compared to unburned areas in our study. Further, seeded native species were important, as shown by results of nonmetric multidimensional scaling and ANOVA analyses, in distinguishing burned and unburned areas, implying that seeding is having a measurable effect on burned areas. Thompson et al. (2006) found increased seeded species cover and density when a high diversity native seed mix was applied after fire. Unseeded burned controls were not available for this study and other studies have found few significant effects of seeding compared to burned, unseeded controls. For example, Knutson et al. (2014) found that seeding native perennial grasses did not increase grass cover compared to burned unseeded areas in the Great Basin and that perennial cover was dependent more on elevation and age of burned area, and generally increased with elevation and precipitation.

Although cheatgrass is of management concern in all three vegetation types in these areas, cheatgrass was not a significant vegetative factor in distinguishing burned from unburned sites, with an average of less than 10% cover (Figure 4). A lack of a significant relationship between cheatgrass and burn status suggests that fire was not the most important factor in determining cheatgrass cover of sites. The ability of cheatgrass to invade and/or dominate a site can be complex and dependent on several variables (Chambers et al. 2007; Kulpa et al. 2012; Sherrill and Romme 2012; Chambers et al. 2014), and while fire may be important, fire alone is not enough to predict cheatgrass response. The significant relationship between seeded native species, native forbs, and nonnative species indicates that natural regeneration processes, management actions (seeding), and other nonnative species, for example *Salsola kali* L., *Sisymbrium altissimum* L., and *Halogeton glomeratus* (<M. Bieb.) C.A. Mey., are playing an important role in the vegetation communities of sites. As opportunities for native species are opened after disturbance (fire), so are opportunities for nonnative and invasive species (e.g., Alpert et al. 2009). In about 50% of studies comparing burned seeded areas to burned unseeded areas, invasive species decreased in older seeded areas (> 3 y; Pyke et al. 2013), and more research is needed to determine under what conditions seeding may curtail plant invasion.

Species richness was significantly higher in burned areas for pinyon juniper areas but not for sagebrush areas. Crested wheatgrass, which was previously planted as a part of management actions, was present in some of our sites and most common in sagebrush sites. Both crested wheatgrass and cheatgrass can compete with native grasses (e.g., Chambers et al. 2007; Gunnell et al. 2010). This competition may have contributed to the similar species richness in burned and unburned sagebrush sites. Our failed seeding results in the sagebrush shrubland sites suggest a reduced ability of native species to respond after fire in this vegetation type. Both the seed bank and seed rain (seeds entering a site) can be important in seedling establishment after disturbance (Thompson 2000). Alba et al. (2015) found a positive response of nonnative species to wildfire coupled with a negative effect of wildfire on native species and stressed the importance of native seed banks. More research into appropriate seeding materials and seeding techniques in areas with aggressive nonnatives, either those that were introduced purposefully or accidentally, is needed in order to increase native species diversity and cover in sagebrush shrublands, which are particularly susceptible to large, environmentally damaging fires (Balch et al. 2013).

Increased precipitation in early post-fire years may decrease the time needed for a site to add structural complexity after a fire, as suggested by a weak positive relationship between cover of native shrubs and precipitation the year after the fire. Other studies have also found that perennial plant cover increases with increased precipitation in the Great Basin (Knutson et al. 2014). Structural heterogeneity can increase diversity and increased diversity is generally thought to increase ecosystem resilience through functional redundancy (e.g., Gunderson 2000). While shrubs can be an important component of these systems, artificial seeding of shrubs may not increase shrub cover in the Great Basin (Knutson et al. 2014). In our study, nonnative species were lower in cover when precipitation was higher just after fires. This may be because of an increased ability of native species to compete with nonnative (especially annual) species with increased precipitation.

Contrary to what we originally hypothesized, cheatgrass was not statistically important in distinguishing burned and unburned sites. Additionally, precipitation was important in influencing certain aspects of the vegetation community. While precipitation cannot easily be manipulated by management, understanding how it is likely to affect the vegetation community can influence what management actions are taken after a fire. For example, more research into seeds and restoration techniques for shrubs, especially in lower precipitation years and lower elevations, is warranted. Native seed mixes in our study provided an (indirectly) measurable if not prodigious impact on burned areas. The use of native seed mixes may be a useful management tool in promoting diversity in vegetation communities without overwhelming existing seed banks, and we have identified some plant species that may be beneficial to include in seed mixes in this area.

Future studies could include a closer look at how the vegetation community reacts to disturbance and artificial seeding at short time scales (less than 5 y). As suggested by James and Svejcar (2010), more direct evaluations of artificial seeding success in burned areas versus natural recovery are needed. While this longer-term study provides evidence of natural recovery, a study with burned sites that were not seeded could look more specifically at unaltered natural recovery vs. assisted recovery via artificial seeding of natives. The use of native seed to supplement local native seed banks after fire is an important management tool which can be better understood with further study.

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