FINAL REPORT

Title: Vegetation succession in post-fire seeding treatments

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Francis Kilkenny
U.S. Forest Service, Rocky Mountain Research Station

Jeffrey Ott
U.S. Forest Service, Rocky Mountain Research Station

Danny Summers
Utah Division of Wildlife Resources

Tyler Thompson
Utah Department of Natural Resources

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List of Abbreviations/Acronyms

JFSP = Joint Fire Science Program
ES&R = Emergency Stabilization and Rehabilitation Program
ARS = Agricultural Research Service [seed mix/treatment]
BLM = Bureau of Land Management [seed mix/treatment]
NH = native high diversity seed mix/treatment
NL = native low diversity seed mix/treatment
UB = unburned reference state
USC = unseeded control treatment

Keywords

competition, restoration, wheatgrass, monitoring, succession, plant community, post-fire seeding, seed-mix design, long-term

Acknowledgements

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Abstract:

Seed mixes used for post-fire seeding in the Great Basin are often selected based on short-term rehabilitation objectives, such as ability to rapidly establish and suppress invasive exotic annuals that drive altered fire-regimes via fine build-up (e.g. cheatgrass, *Bromus tectorum* L.), but longer-term considerations are also important, including whether seeded plants persist, continue to suppress invasive weeds, and promote recovery of desired vegetation states. To better understand long-term effects of post-fire seed mixes, we revisited study sites in Tintic Valley, Utah, where seeding experiments had been initiated following a 1999 wildfire. Four different mixes, including two comprised entirely of native species, had been applied using rangeland drills at a shrubland site and aerial seeding followed by chaining at a woodland site. New vegetation data collected in 2015 through 2017 (16+ years post-fire) revealed changes relative to data collected in 2000 through 2002. We found significant increases in total cover of seed-mix species in all treatments, including the unseeded control where these species were present as residual populations or had spread from seeded treatments. Some seeded species, particularly rhizomatous grasses, increased while others declined. Native perennials that were not part of seed mixes had higher recruitment in unseeded treatments and were especially prominent at the higher-elevation aerial seeding site. Exotic annual forb cover decreased in all treatments while cheatgrass increased in some treatments, especially the unseeded control and to a lesser extent native-only seeded treatments. Successional trajectories in community composition differed significantly between seed-mixes that included introduced species and the native-only mixes, which moved toward reference states in unburned areas while the introduced mixes did not. Results indicate that post-fire seeding has lasting effects on vegetation composition and structure, implying that seed mixes should be carefully formulated to promote long-term management objectives. Seed mixes containing competitive introduced species may be especially effective for long-term cheatgrass suppression, but native-only mixes can also serve this purpose while avoiding drawbacks of non-native species introductions, including the altered successional trajectories that move plant communities into novel states that may not support important wildlife habitat. Where recovery of natural vegetation or wildlife habitat is desired, post-fire seeding may not always be needed or may be best accomplished by seeding native species.

Objectives and hypotheses:

We are interested in assessing long-term effects of post-fire seeding on ecosystem restoration and ecosystem services in sagebrush and pinyon-juniper areas of the Great Basin. Establishment of perennial cover and suppression of exotic annual weeds are the primary aims of post-fire seedings in these areas due to concerns over soil stability and fire risk from fine fuel loads. Additional aims of post-fire seeding include restoration of forage resources, wildlife habitat and native plant communities. The overall goal of post-fire seeding is to restore such ecosystem services following fire by directing vegetation succession into a desired trajectory. Our research objective was to determine the effectiveness of different seed mix treatments for meeting these restoration goals, using a seeding experiment at Tintic Valley, Utah (Thompson et al. 2006) as our case study. By re-measuring vegetation attributes originally measured during the early post-fire stage, we planned to document successional trends and assess the degree to which restoration goals were being met 15+ years after seeding.

JFSP Funding Opportunity Notice 15-1-07 called for research that would improve understanding of vegetation succession with implications for fuels management, ecosystem restoration and the provision of ecosystem services. Our research fit these criteria in relation to post-wildfire succession in sagebrush and pinyon-juniper vegetation types of the Great Basin. Exotic annual plants pose the primary hazardous fuels concern in these post-fire environments, while perennial plant establishment is essential to long-term soil stability and resilience to future fire. The type of seed mix applied in post-fire seeding treatments may have an impact on subsequent successional trajectories and the ecosystem services (e.g., soil cover, weed control, wildlife habitat) aligned with the vegetation that develops. Our study addressed these issues directly by comparing vegetation patterns of different seed mix treatments 15+ years after treatments were applied. Our assessment of ecosystem restoration potential and ecosystem services provided by different treatment options will provide managers with guidance when selecting seed mixes for future post-fire seedings.

We had two primary study objectives, each with a set of related questions (see below). To answer these questions we planned to merge original data (2000-2002) and newly-collected data (2015-2017) into a dataset with identifiers linking individual quadrats and belts across years. In addition to directly measured variables (cover, frequency, density and shrub size), we planned to obtain derived measures of community similarity/distance (Oksanen et al. 2014) based on proportional cover, frequency and/or density of species across sample units. We also planned to derive habitat suitability measures from vegetation data using frameworks such as those of Stiver et al. (2010) in the case of sage-grouse (cf. Arkle et al. 2014).

Objective 1

- Questions: Do differences between treatments persist over time? Do treatment means change over time?
- Response variables: cover, density, and frequency of individual species and functional groups (perennials, perennial grasses, annual grasses, shrubs, etc.); shrub size; habitat suitability for big game, sage-grouse and/or other wildlife
- Years included in analysis: 3 and 16 (burned areas only)

Thompson et al. (2006) identified significant differences between treatments and years for measured response variables (including cover, frequency and density of individual species and functional species groups). We planned to repeat this analysis for these same response variables (plus others quantifying habitat suitability) using 3rd year data combined with new data from the 16th year. Results would indicate whether mean values of each variable changed during this span of time and whether relative differences between treatments also changed.

Objective 2

- Questions: How does community composition differ between treatments and change over time? Is composition more stable (fewer year-to-year fluctuations) at a later stage compared to early on following fire and treatment? What is the expected future successional trajectory of the different treatments? How closely do they resemble late-successional reference states?
- Response variable: plant community composition
- Years included in analysis: 1-3 and 16-18 (including new transects from unburned sites)

Using data from all years, we planned to carry out analyses using non-parametric multivariate analysis of variance (Anderson 2001) or similar techniques designed to quantify multivariate differences (Oksanen et al. 2014). These analyses would illuminate successional patterns and trajectories of plant communities over the entire course of the study. Multivariate analyses comparing compositional similarity within years 1-3 to years 16-18 would address the question of year-to-year-to-year stability in these different successional stages. These analyses would incorporate data from unburned transects which represent late successional reference states for comparison with the more recently burned communities. In all, these analyses would be used to assess future successional trajectories of these communities.

Our null hypothesis was that vegetation patterns and treatment differences at years 16-18 would be similar to those previously measured during years 1-3. More likely, however, we expected to detect changes in vegetation structure and composition due to growth of long-lived species and population dynamics of shorter-lived species. For example, maturation of shrub canopies could be expected in treatments where they were seeded (of particular importance for wildlife habitat). Cheatgrass may or may not have been suppressed in the longer-term depending on the persistence and competitive influence of seeded perennials. Certain seeded species could have proved incompatible or poorly adapted to site conditions, and seeded plants could have either inhibited or facilitated entry of other species from the surrounding landscape. Treatments that were previously deemed unsuccessful might have experienced a subsequent rebound due to latent seed germination and population growth of seeded plants. Each of these possibilities were examined.

We were able to meet all data-collection goals for both of our primary objectives. Analysis for objective 1 is mostly complete (see below) and a manuscript has been prepared and will be submitted within a month after this final report is submitted. We have worked on much of the analysis for objective 2 (see below), but will continue with further analyses. Those analyses will be collected in our planned second publication.

Background:

The threat of ecosystem degradation associated with wildfires has prompted widespread use of post-fire seeding as a rehabilitation tool in the western United States (Peppin et al. 2011; Pyke et al. 2013; Knutson et al. 2014). Millions of hectares of public land in the Great Basin administered by the Bureau of Land Management (BLM) have been seeded in recent decades (Pilliod and Welty 2013; Pilliod et al. 2017) with the intent of reducing soil erosion, suppressing invasive species and establishing desirable perennial plants following fire (USDI-BLM 2007). In many areas of sagebrush and pinyon-juniper fine fuel loads have been amplified by invasive annual weeds, particularly cheatgrass (*Bromus tectorum*) (Suring et al. 2005, Miller et al. 2013). These conditions set the stage for site degradation and cheatgrass proliferation following fire, potentially interrupting natural successional trajectories. Through its competitive influence and alteration of fire frequency, cheatgrass-dominated vegetation can perpetuate itself as an alternative steady state requiring significant management intervention to overcome (Balch et al. 2013, Miller et al. 2013). In the absence of active post-fire management interventions such as seeding, such sites may become trapped in low-diversity, annual-dominated vegetation states prone to recurring fire (Davies et al. 2012; Balch et al. 2013; Davies and Nafus 2013).

Few studies have tracked successional changes in post-fire seedings of the Great Basin for more than a decade, but older seedings (>3 years) provided more consistent evidence that seeded plants were suppressing invasive species than did newer seedings, which suggests that seeded plants are likely to increase and become better competitors over time (Pyke et al. 2013). In a chronosequence study of seeded sites located throughout the Great Basin, Knutson et al. (2014) found that the effect of time since seeding (8-20 years) was minor compared to effects of treatment, elevation and topographic position, although they found that non-native perennial grass cover and bare ground generally increased over time in drill seedings (Knutson et al. 2014). In a related chronosequence study, Arkle et al. (2014) found that post-fire seedings in the Great Basin had low sagebrush establishment and generally did not produce quality habitat for greater sage-grouse. These chronosequence studies expanded the spatial and temporal scale of previous investigations and provided valuable assessments of post-fire seeding practices, but did not account for variation in initial seeded plant establishment and lacked an experimental framework that would allow stronger inference of treatment effects.

Post-fire seedings carried out by the BLM through the Emergency Stabilization and Rehabilitation (ES&R) program (USDI-BLM 2007) have focused on rapid establishment of protective vegetation cover to stabilize soils and outcompete non-desirable species. One consequence of this focus is that managers have generally sought plant materials considered most likely to establish quickly and easily, even if they are not native (Richards et al. 1998; Hardegree et al. 2016; Svejcar et al. 2017). Plants developed for rangeland forage production have often been used for post-fire seeding because of their ease of establishment, competitiveness against invasive annuals, market availability and utility in areas where livestock grazing is the primary land use (Asay et al. 2001; Robins et al. 2013; Hardegree et al. 2016; Svejcar et al. 2017). However, many of the common U.S. rangeland forage species originated on other continents and their use on public lands has been controversial (Richards et al. 1998; Svejcar et al. 2017). Negative long-term effects of these species on ecosystem functioning, biodiversity and wildlife habitat have been documented (Walker et al. 1995; Lesica et al. 1996; Salesman and Thomsen 2011; Gasch et al. 2016). In recent years, native species have increasingly been used for post-fire seeding as increasing emphasis has been placed on restoring historical or pre-fire ecological conditions (Richards et al. 1998; USDI-BLM 2007; PCA 2015). BLM policy stipulates that ES&R treatments should not impair critical habitat for threatened or endangered species (USDI-BLM 2007) such as the greater sage-grouse (*Centrocercus urophasianus*), a candidate for listing under the Endangered Species Act that depends on mature sagebrush stands and diverse forb communities (Miller et al. 2011; Arkle et al. 2014; Dumroese et al. 2015; Finch et al. 2016). Shrubs such as Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) have been included in post-fire seed mixes because of their value for wildlife and other ecosystem services they provide (Lysne 2005), even though they may require specialized seeding techniques to ensure establishment success (Stevens and Monsen 2004; Shaw et al. 2005; J. E. Ott et al. 2017) and may contribute little to site stabilization or weed suppression during early post-fire years.

Operational-scale experiments designed to evaluate post-fire seed mixes are relatively rare. A unique study reported by Thompson et al. (2006) tested multiple seed mixes for Great Basin shrublands and woodlands, including rarely-tested mixes containing only native species. Following a wildfire in Tintic Valley, Utah, in the summer of 1999, the experiment was installed in replicate blocks at two study areas, a sagebrush area receiving rangeland drill treatment and a pinyon-juniper area treated through aerial seeding followed by chaining. Four different seed mixes were applied for comparison within each area: a conventional mix containing primarily introduced species, a mix containing a more balanced combination of introduced and native species, and two entirely native mixes differing by species diversity and seeding rates (Thompson et al. 2006). Vegetation measurements taken during the first three years following treatment (2000-2002) revealed successful establishment of seeded perennials across most seed mix treatments (Thompson et al. 2006). The study provided evidence that both native and introduced seeded species can suppress invasive annuals in areas where they successfully establish, and that growth of newly-established plants may be possible even during drought conditions (Thompson et al. 2006).

At the time of our proposal, 16 years had elapsed since the fire that initiated the Thompson et al. (2006) study and the condition of their treatments had not yet been documented at that time. The intervening years were marked by fluctuating drought cycles and new wildfire incidents throughout the Great Basin (NIFC 2014), although the study areas in Tintic Valley had not re-burned. Our proposal addressed questions as to whether the treatment differences observed during the first three years remained, and whether there had been significant changes in composition of these treatments over time. This study opportunity allowed us to evaluate the effectiveness of the different seed mixes for meeting management objectives such as soil cover, weed suppression and wildlife habitat well beyond the post-fire establishment phase. We proposed to address these questions and issues through re-measurement of vegetation attributes originally collected by Thompson et al. (2006) at the Tintic Valley study areas. The original data from years 1-3 (2000-2002) were supplemented by years 16-18 (2015-2017). Analyses comparing original and re-measured attributes within and between years will provide a broader picture of post-fire seeding effects compared to the original study. This study will likely be relevant beyond its limited geographical area because of the way in which it represents environments, seeding techniques and seeded species common to the larger Great Basin region. This study is unprecedented for its experimental comparisons of operational-scale seeding treatment effects spanning 15+ years, and will provide information applicable to future post-fire rehabilitation strategies on public lands.

Materials and Methods

Study area

Study sites are located in Tintic Valley, Utah, on Bureau of Land Management (BLM) and Utah state-administered lands that burned during the July 1999 Railroad wildfire. As described by Thompson et al. (2006), sites were selected in the vicinity of Jericho (39^{o}42’-45’N, 112^{o}11’-17’W), where drill-seeding treatments were applied to areas where Wyoming big sagebrush communities had been present prior to the fire (‘Drill Site’); and near Mud Springs (39^{o}51’-54’N, 112^{o}11’-15’W) where aerial seeding followed by chaining was applied to areas previously occupied by mixed stands of pinyon-juniper and sagebrush (‘Aerial Site’). Treatments were applied in November 1999 at five experimental blocks at each site. No additional fires, seeding treatments or major disturbances have affected these study sites since 1999, but they have been lightly to moderately grazed by cattle at the Aerial Site and by sheep at the Drill Site. Soils are predominantly fine sandy loams at the Aerial Site and cobbly, silty or sandy loams at the Drill Site.

Seeding treatments

Four treatments differing by seed mix, plus an unseeded control (USC), were applied to randomly-assigned rectangular strips, 213 m long and 73 m wide (Aerial Site) or 46 m wide (Drill Site), within each block (Thompson et al. 2006). Aerial and drill seedings received seed mixes that were similar but not identical in composition and seeding rates (Table 1). Seed mixes were comprised of different combinations of native species, defined as accessions, varieties or cultivars of western North American origin, and/or introduced species derived from Eurasian sources. The BLM Fillmore Field Office supplied a seed mix of 7-8 predominantly introduced species typical of seed mixes commonly used locally for wildfire rehabilitation (BLM mix; Table 1). Another seed mix supplied by the Forage and Range Research Laboratory (Logan, Utah, USA) of the Agricultural Research Service (ARS mix) contained 4-6 native species and 5 introduced species (Table 1). Two seed mixes formulated by scientists at the U.S. Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory (Provo, Utah, USA) consisted entirely of native species: one mix with 7-8 species seeded at total bulk seeding rates comparable to the BLM and ARS mixes (native low diversity mix, NL), and another with 11 species seeded at higher total bulk rates (native high diversity mix, NH) (Table 1).

Drill seeding was carried out on 12 November 1999, aerial seeding on 19 November 1999, and chaining over a period lasting from late November 1999 to February 2000. Further details on seeding operations were described by Thompson et al. (2006).

Data collection

Vegetation measurements taken from experimental treatments during the first three years following the 1999 Railroad Fire (Thompson et al. 2006) were re-measured during the summer field seasons of 2015, 2016, and 2017. Transects previously sampled were relocated from permanent markers. Each transect (treatment within a block) was represented by 5 belts (30 m) with 20 quadrats (0.25-m^2) positioned at 1.5 m intervals along each belt. Measurements of cover, density and nested frequency were taken at each quadrat following the range trend methodology of the Utah Department of Wildlife Resources (DWR 2015). Percent canopy cover by species in each quadrat was estimated on a modified Daubenmire cover class scale (1 = 1% or less, 2 = 1.1-5%, 3 = 5.1-15%, 4 = 15.1-25%, 5 = 25.1-50%, 6 = 50.1-75%, 7 = 75.1-95%, and 8 = 95.1-100%). Density data were collected in 2015 by counting individuals of all perennial species rooted in quadrats. Measurements of shrub density, height and line-intercept were also taken from broader areas aligned with belts in 2015.

Additional data were collected in 2017 from unburned areas in the vicinity of the burned treatments. We located unburned stands dominated by sagebrush and/or pinyon-juniper vegetation to serve as late-successional reference states. New transects were established in these areas where cover and nested frequency data were collected from quadrats using the same methods as the burned treatments. Measurements of shrub density and size were also collected along belts in the unburned areas.

Varieties or cultivars of seeded species where not differentiated, including different forms of the crested/Siberian wheatgrass complex (*Agropyron* spp.) and different bluebunch wheatgrass varieties that have recently been recognized as different species (Whitmar and Goldar = bluebunch wheatgrass, *Pseudoroegneria spicata*; Secar = Snake River wheatgrass, *Elymus wawawaiensis*) (Table 1). Nomenclature in this report follows USDA-NRCS (2018).

Table 1. Seed mix composition and seeding rates at aerial-seeded and drill-seeded sites in Tintic Valley, Utah (after Thompson et al. 2006, Table 1).

				Aerial Site				Drill Site			
Species	Variety/Cultivar	Origin[1]	PLS[2]	ARS[3]	BLM	NH	NL	ARS	BLM	NH	NL
Alfalfa	Rangelander	I	0.56	3[4]	—	—	—	1.5	—	—	—
Alfalfa (inoculated)	Ladak	I	0.92	—	—	—	—	—	0.6	—	—
Antelope bitterbrush	—	N	0.8 E	+	+	+	+	—	—	1.1	1.1
Basin wildrye	Magnar	N	0.86	—	—	3	—	—	—	2.2	—
Bluebunch wheatgrass	Whitmar	N	0.85 E	—	—	4.5	4.5	—	—	2.2	2.2
Bluebunch wheatgrass	Goldar	N	0.86	—	3	4.5	4.5	—	—	2.2	2.2
Snake river wheatgrass	Secar	N	0.89	2.5	—	—	—	1.3	—	—	—
Crested wheatgrass	Hycrest	I	0.85	—	4.5	—	—	—	2.2	—	—
Crested wheatgrass (hybrid)	CD II	I	0.93	3.6	—	—	—	1.8	—	—	—
Forage kochia	Immigrant	I	0.71	0.8	—	—	—	0.4	—	—	—
Fourwing saltbush	—	N	0.32	+	+	+	+	—	0.6	1.1	1.1
Indian ricegrass	Rimrock	N	0.92	1.2	—	—	—	0.6	—	—	—
Indian ricegrass	Nezpar	N	0.85 E	—	—	3	3	—	—	2.2	2.2
Intermediate wheatgrass	Luna	N	0.92	—	3	—	—	—	2.2	—	—
Needle and thread	VNS	N	0.88	—	—	3	—	—	—	2.2	—
Russian wildrye	Bozoisky	I	0.86	3	3	—	—	1.5	2.2	—	—
Sandberg bluegrass	—	N	0.85	—	—	3	1.5	—	—	2.2	—
Siberian wheatgrass	Vavilov	I	0.89	3.8	—	—	—	1.9	—	—	—
Smooth brome	Lincoln	I	0.81	—	3	—	—	—	—	—	—
Squirreltail	VNS	N	0.77	—	—	3	—	—	—	2.2	—
Tall wheatgrass	Alkar	I	0.83	—	3	—	—	—	2.2	—	—
Thickspike wheatgrass	Critana	N	0.93	1.2	—	—	—	0.6	—	—	—
Western wheatgrass	Rosanna	N	0.85 E	2.4	—	3	3	1.2	—	2.2	1.1
Western wheatgrass	Aribba	N	0.88	—	—	—	—	—	1.1	—	—
Wyoming big sagebrush	—	N	0.14	—	—	3	1.5	—	—	2.2	1.1

[1]Origin: I indicates introduced species; N, native species.
[2]PLS indicates pure live seed; E, percentage unknown but expected to be at least what is listed.
[3]Seed-mix treatments: ARS indicates Agricultural Research Service mix; BLM, Bureau of Land Management mix; NH, Native high-diversity mix; NL, Native low-diversity mix.
[4]Seeding rates shown are in kg ha^{-1}; + indicates seeds dribbled onto tractor treads at total rate of 2.2 kg ha^{-1}.

Data analysis

In our first set of analyses, we combined data from 2002 (the final year of the earlier study by Thompson et al. 2006) and 2015 (the first year of our current study) and assessed changes in cover and density of plant species (or groups) during the 13-year interval spanning these years. Species were grouped based on origin (native/exotic), longevity (annual/perennial), and whether they had been included in seed mixes. For each species and group of interest, we converted cover classes to percent cover values using arithmetic midpoints of the classes. Analyses of cover and density were implemented separately for each site using the MIXED procedure in SAS 9.3 (SAS Institute, Inc 2011). We analyzed quadrat cover of each species group by modeling treatment (i.e. seed mix), year, and treatment × year as fixed effects and used Tukey's HSD at alpha = 0.05 for mean separation.

A second set of analyses utilized multivariate data from all years and all recorded plant species. We analyzed plant community composition of seeded and non-seeded treatments and assessed successional trends of these treatments across years using unburned communities as late-successional reference states. Non-metric multidimensional scaling (NMDS), an ordination technique appropriate for ecological data (McCune and Grace 2002), was used to extract the primary axes of variation in community composition for easy visualization. Separate NMDS analyses were carried out for each study site using transects (unique combinations of treatment, block and year) as sample units and percent cover (average of cover class midpoints) as a measure of abundance for each species. The Bray-Curtis index (Krebs 1999) was used to calculate community similarity. We used the *Vegan* package in R (R Core Team 2014) to carry out these analyses.

Results and Discussion:

Photos illustrating vegetation states at the two study sites in 2015 are provided in Fig. 1-2. This is followed by presentation of results related to cover of major plant species groups (seed-mix perennials, non-seed-mix perennials, and exotic annual grasses/forbs) compared across treatments and years (2002 vs. 2015) (Fig. 3). We then summarize changes in cover and density of individual seeded species between 2002 and 2015 (Fig. 4) followed by results of plant community analyses spanning all sampling years (2000-2002 and 2015-2017) (Fig. 5).

Seed-mix perennial cover, 2002 vs. 2015

In both 2002 (the 3rd year after fire and seeding) and 2015, perennial cover in seeded treatments (ARS, BLM, NH and NL) was dominated by seed-mix species (Fig. 1-2). Although seed-mix species composition differed among seeded treatments, total seed-mix perennial cover did not differ significantly between these treatments either year except that cover was lower in NL than other seeded treatments at the Drill Site (Fig. 3). At the Aerial Site, seed-mix perennial cover in seeded treatments increased from 11-14% (2002) to 27-30% (2015) (Fig. 3). At the Drill Site, seed-mix perennial cover increased from 3% (2002) to 18% (2015) in NL and 6-8% (2002) to 23-25% (2015) in other seeded treatments (Fig. 3). The overall increase in seed-mix perennial cover at these sites indicates that plants introduced through seeding (at least some of the species; see below) were adapted to establish, compete, grow and/or reproduce under the sequence of environmental conditions they encountered. Given that seedling establishment is often the most mortality-prone phase for plants in semiarid environments of the Great Basin (James et al. 2011), the presence of seedlings during the early years following seeding will in many cases foretell continued persistence and growth of established individuals.

At both sites, the unseeded control (USC) had significantly lower seed-mix perennial cover than the seeded treatments (Fig. 3), as expected given that USC did not receive seed from mixes except for unintentional drift associated with aerial seeding. Some of the seed-mix perennials recorded in USC at the Aerial Site likely arrived through seed drift, especially Wyoming big sagebrush which became well-established in USC at one of the blocks where seed could have drifted from the adjacent NH treatment. Other seed-mix perennials could have originated from residual populations that survived the fire rather than from seed mixes per se. Western wheatgrass (*Pascopyrum smithii*), Indian ricegrass (*Achnatherum hymenoides*), squirreltail (*Elymus elymoides*) and Sandberg bluegrass (*Poa secunda*) are among the species that appear to have had a presence at the sites prior to the fire as well as being reintroduced by seeding. At the Aerial Site, seed-mix perennial cover increased from 5% (2002) to 15% (2015) in USC (Fig. 3). Seed-mix perennials were nearly absent from USC at the Drill Site in 2002, but increased to 4% cover in 2015 (Fig. 3).

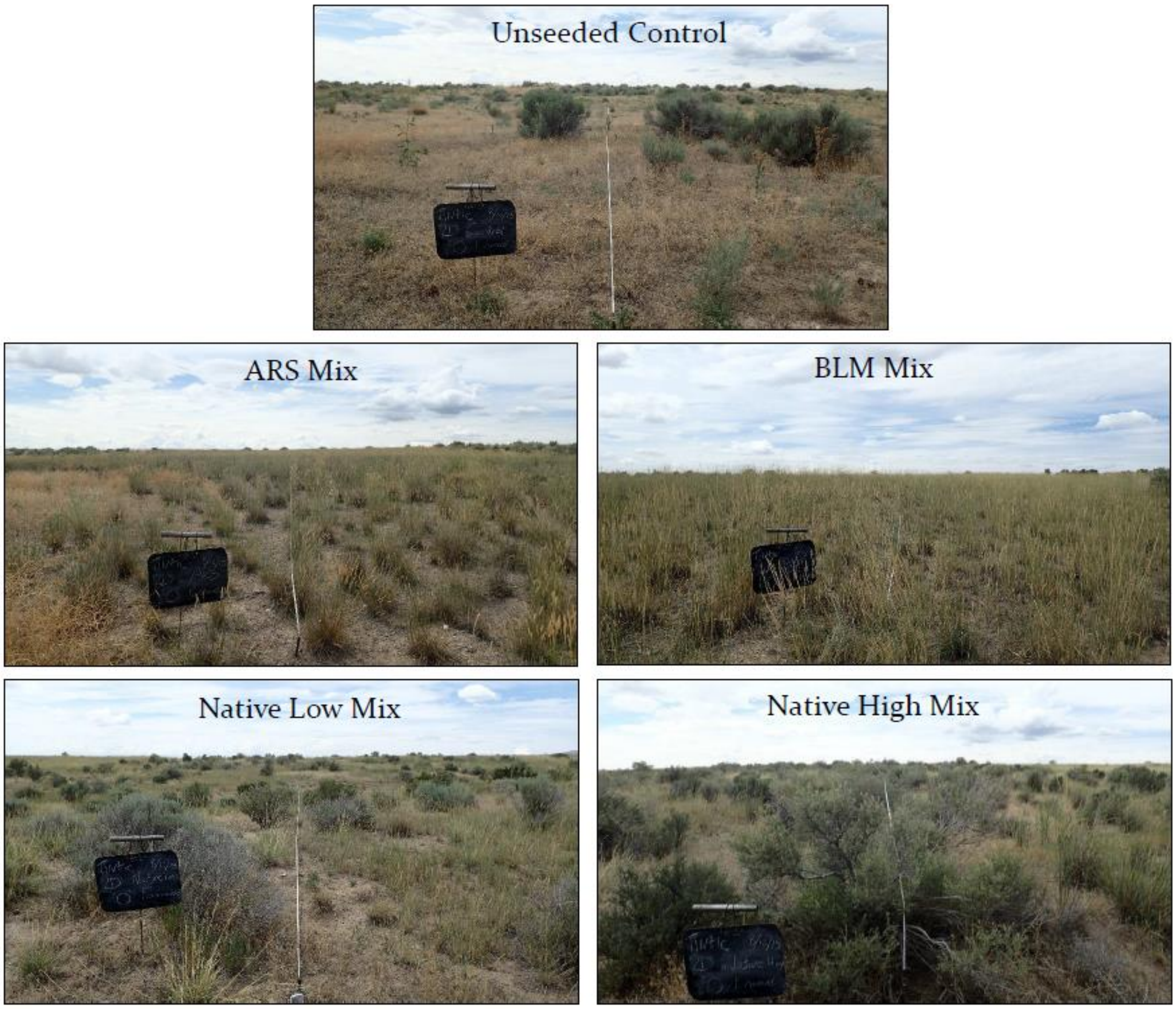

Figure 1. Photos illustrating vegetation states in treatments at the Jericho drill seeding site, Tintic Valley, Utah, in August 2015. Photos were taken from adjacent transects of a single block and face the same direction. Credits: Utah Division of Wildlife Resources Range Trend Crew.

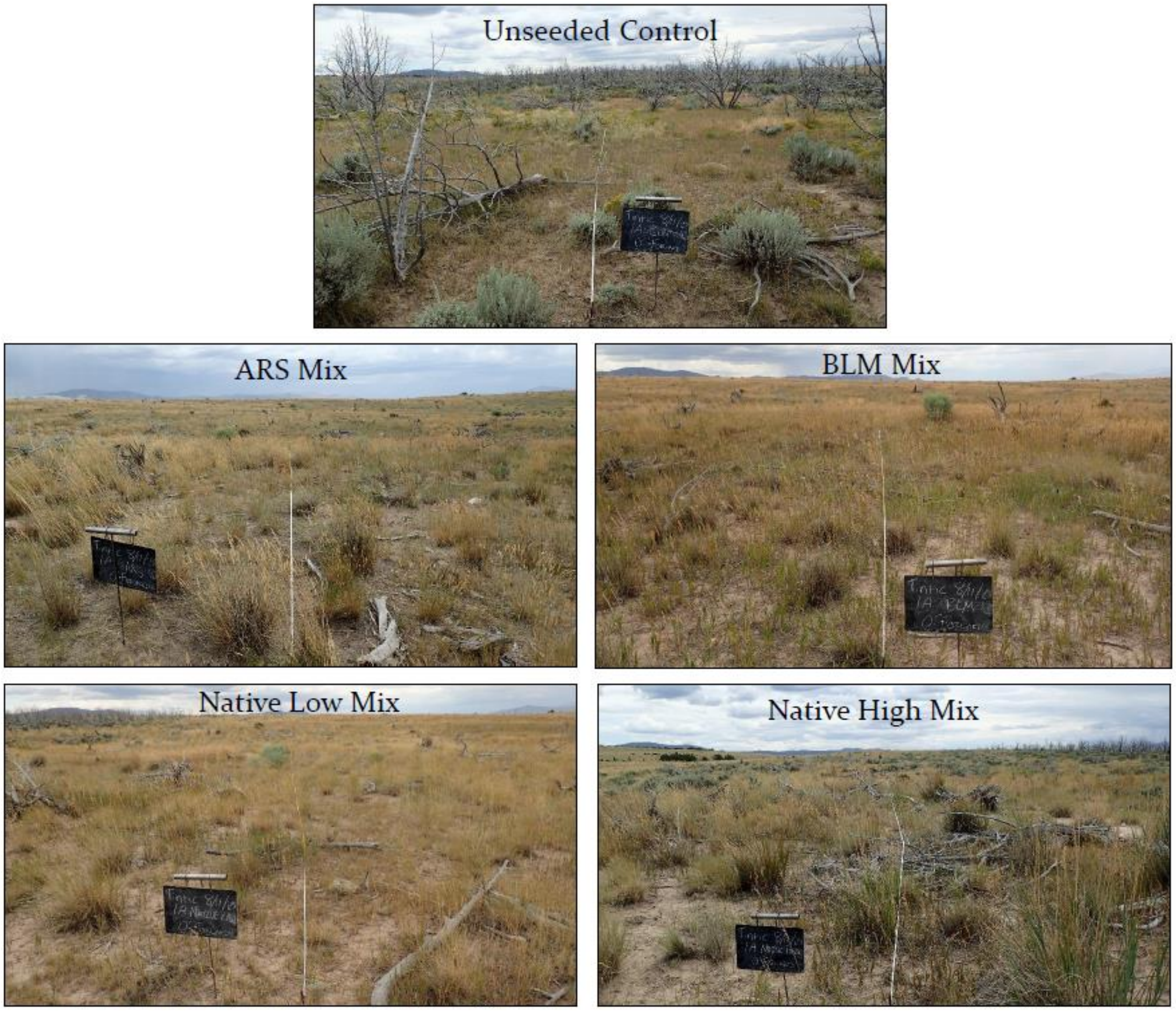

Figure 2. Photos illustrating vegetation states in treatments at the Mud Springs aerial seeding site, Tintic Valley, Utah, in August 2015. Photos were taken from adjacent transects of a single block and face the same direction. Credits: Utah Division of Wildlife Resources Range Trend Crew.

Non-seed-mix perennial cover, 2002 vs. 2016

Many native perennial species that were not part of the seed mixes were also present at the study sites, especially in the USC treatment. Non-seed-mix perennial cover increased between years in USC at both the Aerial Site (2% in 2002 to 10% in 2015) and the Drill Site (1% in 2002 to 3% in 2015), whereas the ARS, BLM and NH treatments had lower cover (<1%) that did not change significantly between years at either site (Fig. 3). This indicates that non-seed-mix perennials were capable of colonizing the burned areas but their recruitment appeared to be inhibited by competition with seed-mix species in the seeded treatments. Much of the non-seed-mix perennial cover was composed of woody species including rubber rabbitbrush (*Ericameria nauseosa*), yellow rabbitbrush (*Chrysothamnus viscidiflorus*), broom snakeweed (*Gutierrezia sarothrae*), green ephedra (*Ephedra viridis*) and spiny phlox (*Phlox hoodii*).

At the Aerial Site, total perennial cover in USC reached levels similar to the seeded treatments in 2015 due to the combination of seed-mix and non-seed-mix perennials that became established. Although perennials in USC were not as effective at suppressing exotic annuals as those of seeded treatments (see below), they demonstrate the potential for natural vegetation recovery following fire at favorable sites. The higher-elevation Aerial Site exhibited higher resilience to fire disturbance and greater resistance to exotic annual invasion (Chambers et al. 2014; Ellsworth et al. 2016) in comparison to the lower-elevation Drill Site which had few residual perennials and became dominated by exotic annuals in unseeded areas.

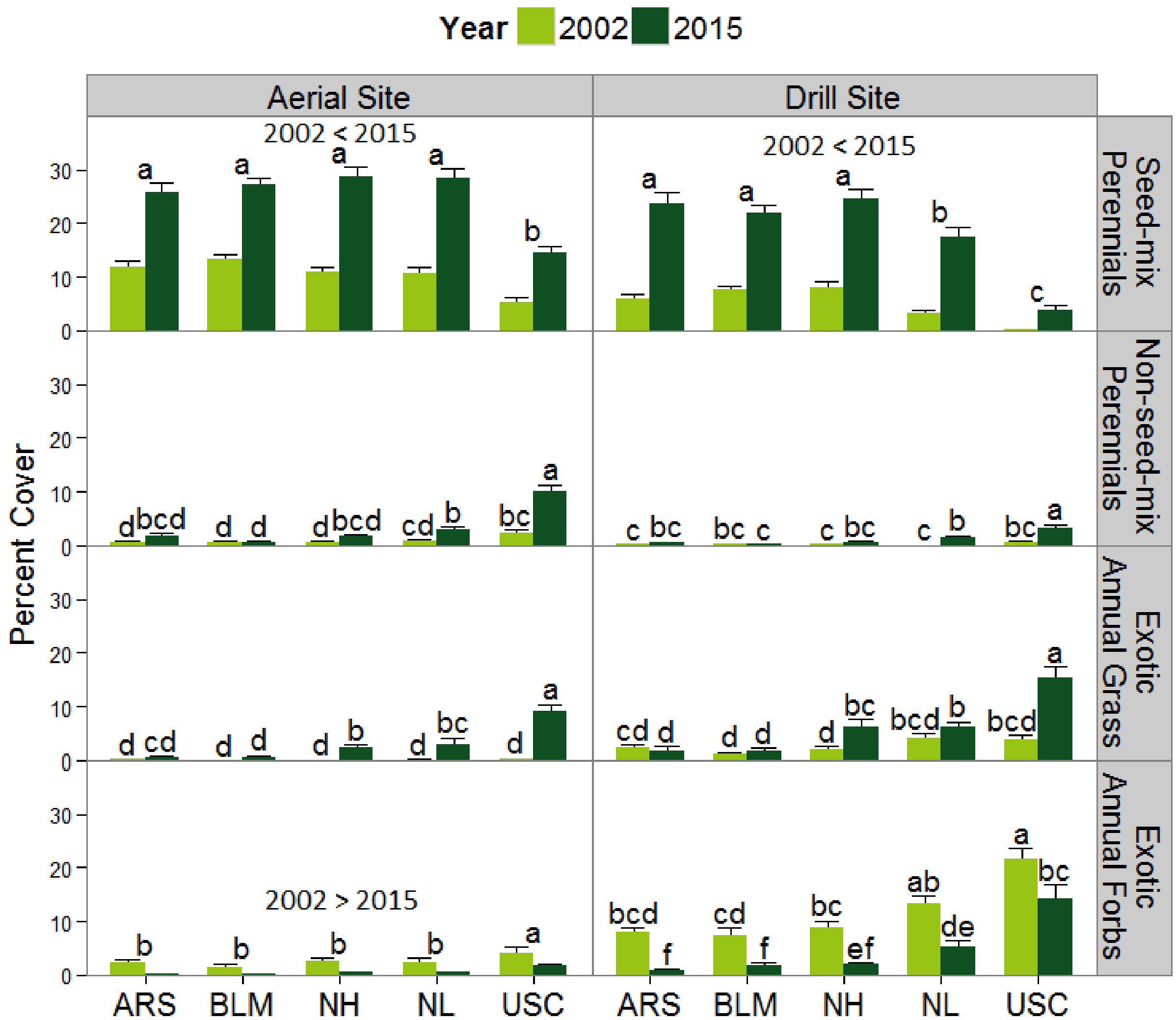

Figure 3. Cover by species group at sites in Tintic Valley, Utah, as recorded 3 years (2002) and 16 years (2015) following fire and seeding. Bars indicate means; error bars, standard errors. Within each cell, means with the same letter are not significantly different ($P < 0.05$). If the treatment × year interaction was not significant, significance is shown separately for treatment (letters spanning both years) and year (text in cell). Treatments: ARS indicates Agricultural Research Service mix; BLM, Bureau of Land Management mix; NH, Native high diversity mix; NL, Native low diversity mix; USC, unseeded control. Graphed using R package 'ggplot2' (Wickham 2009, R Core Team 2014).

Exotic annual cover, 2002 vs. 2015

Most annual cover was comprised of exotic species (native annuals had <1% cover that did not differ between treatments or years at either site). Exotic annual grass cover was predominately cheatgrass with trace amounts of other exotic brome grasses. Exotic annual forbs were primarily desert alyssum (*Alyssum desertorum*) at the Aerial Site and desert alyssum, Russian thistle (*Salsola tragus*), tumblemustard (*Sisymbrium altissimum*) and redstem storksbill (*Erodium cicutarium*) at the Drill Site. In 2002, exotic annual grass cover was relatively low (<1% at Aerial Site, 1-4% at Drill Site) compared to exotic annual forb cover (2-4% at Aerial Site; 8-23% at Drill Site), but the pattern shifted in 2015 as exotic annual forbs declined in all treatments while exotic annual grass increased in the NH, NL and USC treatments (Fig. 3). By 2015, exotic annual grass cover was highest in USC (Aerial Site, 9%; Drill Site, 15%), intermediate in NH and NL (Aerial Site, 2-3%; Drill Site, 6%), and lowest in ARS and BLM (Aerial Site, 1%; Drill Site, 2%) (Fig. 3). 2015 exotic annual forb cover at the Drill Site was likewise highest in USC (15%), followed by NL (5%) and other seeded treatments (1-2%) (Fig. 3). At the Aerial Site, exotic annual forb cover dropped to 2% in USC and <1% in seeded treatments by 2015 (Fig. 3).

These results suggest that cheatgrass gained a competitive advantage over other exotic annuals as time passed following fire at these sites, but that both cheatgrass and other exotic annuals were suppressed to varying degrees by perennial species of the seed mixes. The degree of exotic annual suppression was generally higher in the mixes with introduced perennials (ARS, BLM) than in the native-only mixes (NH, NL), possibly due to the presence in the ARS and BLM mixes of particularly competitive cultivars of introduced grass species (Aguirre and Johnson 1991, Francis and Pyke 1996; Whitson and Koch 1998). 2015 exotic annual grass percent cover in the native-only mixes was 2%-5% higher than ARS and BLM, but was still 6%-9% less than respective unseeded controls. Overall, cheatgrass cover in all seeding treatments at both sites was held under 10%, below the threshold where it is considered a detrimental component of the plant community and well-below the threshold (~60%) where cheatgrass dominance is especially likely to increase the risk of fire (Pellant and Hall 1994, Balch et al. 2013). In terms of exotic forb suppression, the NH and NL mixes performed just as well as the ARS and BLM mixes at the Aerial Site and the NH mix performed just as well at the Drill Site.

Seed-mix species cover and density, 2002 vs. 2015

Cover and of individual seed-mix species (data not shown) generally increased between 2002 and 2015 in treatments where the species had been seeded, but in some cases, cover decreased or did not change. Crested/Siberian wheatgrass, Russian wildrye (*Psathyrostachys juncea*), intermediate wheatgrass (*Thinopyrum intermedium*), smooth brome (*Bromus inermis*), needle-and-thread (*Hesperostipa comata*) and basin wildrye (*Leymus cinereus*) each increased wherever they were seeded. Western wheatgrass cover increased in the ARS, NH and NL treatments. Cover of bluebunch/Snake River wheatgrass, Indian ricegrass and Sandberg bluegrass did not change in seed-mix treatments at the Aerial Site but decreased at the Drill Site. Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) increased in cover in the NH treatment at the Aerial Site but not the Drill Site, in contrast to fourwing saltbush (*Atriplex canescens*) and antelope bitterbrush (*Purshia tridentata*) whose cover increased in NH and/or NL at the Drill Site but not the Aerial Site. By 2015, many of the fourwing saltbush and antelope bitterbrush plants at the Drill Site had grown to mature size with the result that NH and NL were distinctively more shrub-dominated than other treatments (Fig. 1).

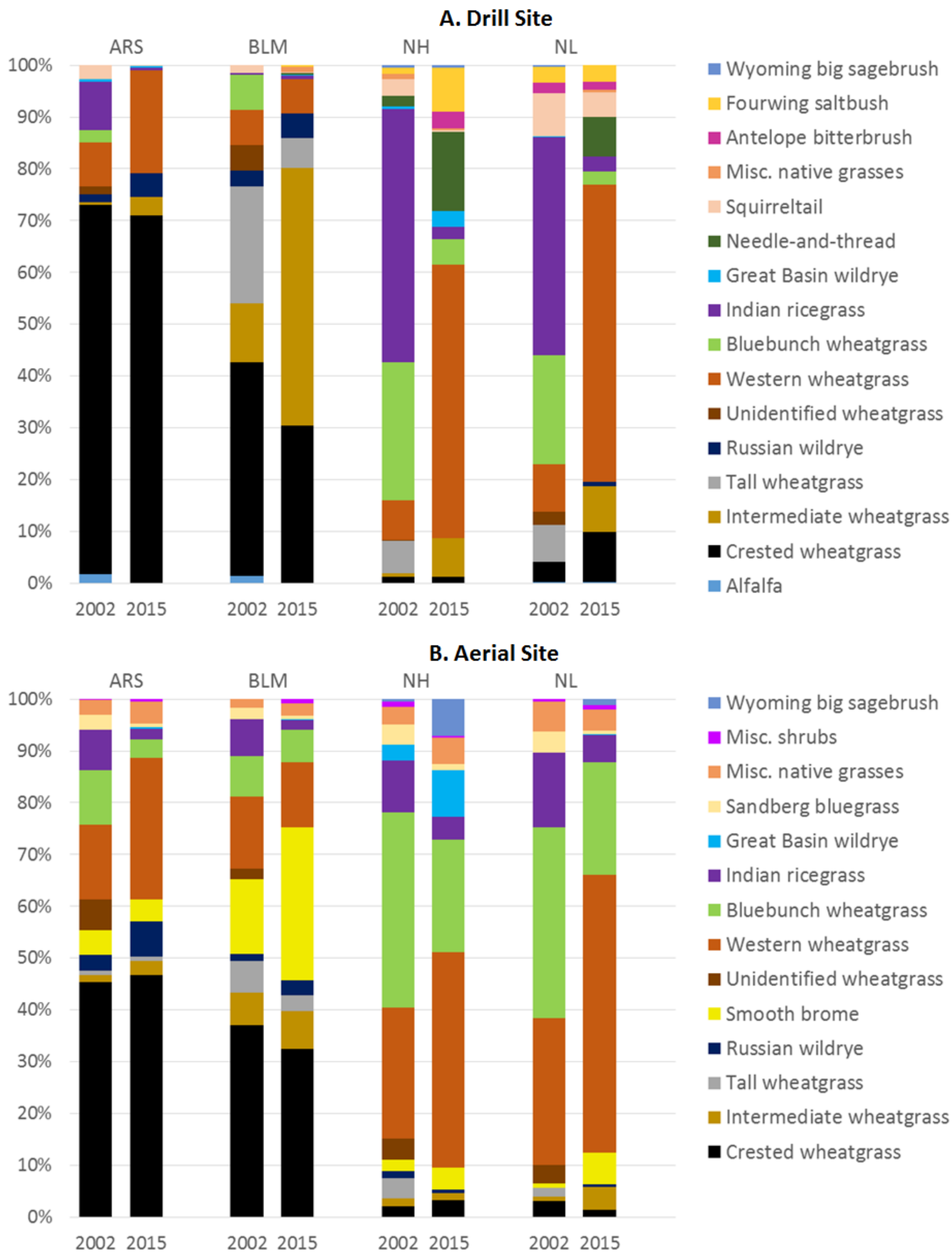

Figure 4. Relative cover of seeded species (percent of total by treatment and year) at sites in Tintic Valley, Utah, as recorded 3 years (2002) and 16 years (2015) following fire and seeding. A, Jericho drill seeding site; B, Mud Springs aerial seeding site. Treatments: ARS indicates Agricultural Research Service mix; BLM, Bureau of Land Management mix; NH, native high diversity mix; NL, native low diversity mix.

Relative percent cover of seed-mix species shifted as the net result of each species' cover changes between 2002 and 2015 (Fig. 4). Species that did not increase in absolute cover during this period, including Indian ricegrass, bluebunch/Snake River wheatgrass, tall wheatgrass, Sandberg bluegrass and squirreltail, generally decreased in relative cover as other species such as western wheatgrass, intermediate wheatgrass, smooth brome, Russian wildrye, basin wildrye and Wyoming big sagebrush became more dominant (Fig. 4). Relative cover of crested/Siberian wheatgrass did not change significantly in most treatments (Fig. 4) despite increases in absolute cover (data not shown).

In most cases where a species changed cover between 2002 and 2015, density also changed in the same direction (data not shown). Density increases were most pronounced for the rhizomatous grasses western wheatgrass, intermediate wheatgrass and smooth brome, which rose from 1-12 plants m^{-2} (2002) to 22-59 plants m^{-2} (2015) in several instances. This may indicate that rhizomatous spread is a key trait fostering population growth in Great Basin ecosystems. In particular, rhizomatous spread may allow persistence and expansion in years when seeds may have difficulty germinating due to lack of precipitation or other biotic and abiotic factors.

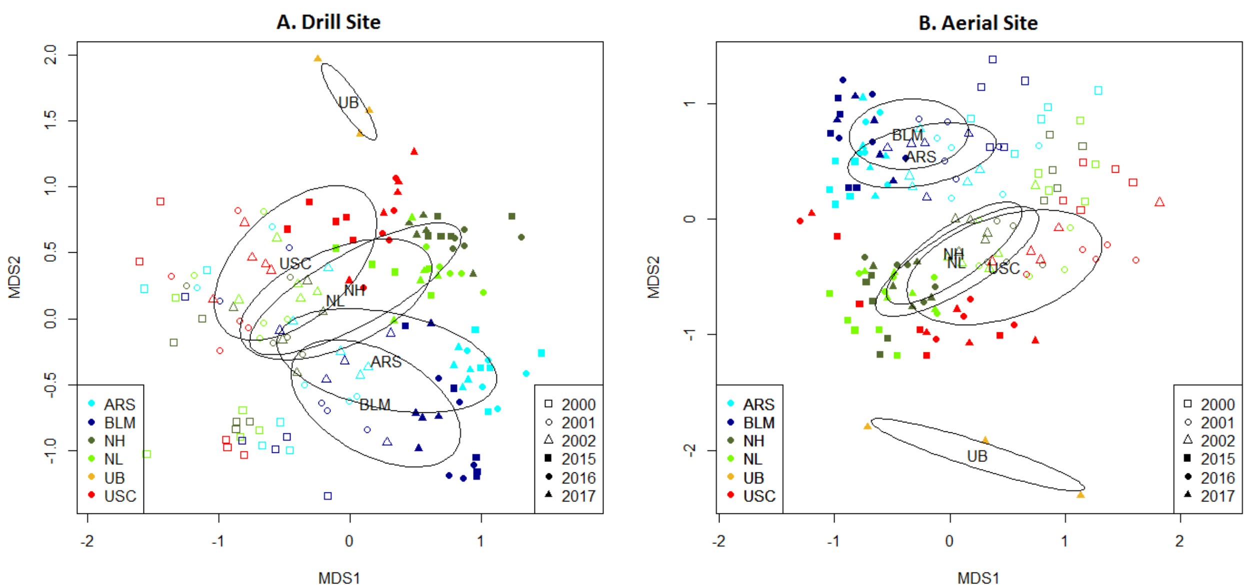

Figure 5. Ordination diagrams for plant communities at sites in Tintic Valley, Utah, illustrating compositional differences among seeded and unseeded burned treatments and changes over time in relation to unburned reference states. Axes are compositional gradients derived from non-metric multidimensional scaling in two dimensions with the Bray-Curtis index of similarity. A, Jericho drill seeding site; B, Mud Springs aerial seeding site. Treatments: ARS indicates Agricultural Research Service mix; BLM, Bureau of Land Management mix; NH, native high diversity mix; NL, native low diversity mix; UB, unburned reference; USC, unseeded control. Years 2000-2002 and 2015-2017 are different sampling periods following fire and seeding that took place in 1999.

Plant community composition in 2000-2002 and 2015-2017

Differences in community composition between treatments and years were evident from ordination analyses. At both sites, the first two ordination axes were associated with time since fire and treatment type (Fig. 5). At the Drill Site, there was extensive overlap in community composition across burned treatments during the first three years following fire (2000-2002), but these treatments had largely diverged from one another by years 16-18 (2015-2017) (Fig. 5A). The successional trajectories of the ARS and BLM treatments took them farther away from the unburned reference state whereas the NH, NL and USC mostly followed trajectories that led them closer to it, both at the Drill Site (Fig. 5A) and the Aerial Site (Fig. 5B). At the Aerial Site, the BLM and ARS treatments formed a distinct cluster that differed in community composition from the other treatments during both early and later years (Fig. 5B). The NH and NL treatments at the Aerial Site had high overlap in community composition and similar successional trajectories (Fig. 5B). Community composition of the USC treatment at the Aerial Site varied widely and partially overlapped the NH and NL treatments (Fig. 5B).

Conclusions and Implications for Management/Policy and Future Research:

This study shows that post-fire seeding can have lasting effects on successional patterns in Great Basin plant communities. While the abundance and dominance of particular species are likely to change over time, the initial seed mix can have a strong influence on later plant community composition. This emphasizes the importance of designing seed mixes that take into account probable long-term successional trajectories, and of implementing long-term monitoring of post-fire seedings whenever possible. Given that the most common post-fire seeding treatments in the Great Basin are through BLM's ES&R program, and that few restoration treatments are carried after these treatments are applied, it should be noted that these initial seeding treatments are often the only chance to shift plant community succession toward positive outcomes. Studies like this one can help in predicting future succession in post-fire seedings. Lessons from this study are:

1. *Post-fire seeding is useful but some recovery is possible without seeding*
2. *Native-only mixes can be nearly as effective in suppressing invasive annuals*
3. *Interference between seed-mix species can affect successional trajectories*
4. *Some seeded species may be more adapted to site conditions than others*
5. *Successional trajectories of conventional mixes may lead to novel plant communities*

Post-fire seeding is useful but some recovery is possible without seeding

While post-fire seeding is often useful, some management goals can be achieved through natural recovery. This study showed that seeding of both conventional mixes and native-only seed mixes suppressed exotic annuals, such as cheatgrass, which is a desired outcome. However, at favorable sites, native perennials, including shrubs, became dominant in the absence of seeding. This was especially true for the USC at the aerial site, with both greater exotic annual suppression and greater natural recovery of native perennials than the USC at the drill site. This was likely due to the richer soils, higher elevation and higher precipitation of the aerial site, factors which have all been to shown to contribute to greater resistance and resilience. Additionally, the successional trajectories of the unseeded controls were similar to the successional trajectories of the native-only mixes, both of which trended toward the unburned reference state at both the aerial and drill sites. This suggests that natural recovery can lead to some desired management goals. This will, of course, depend on the potential for exotic annual invasion, which may require seeding to achieve desired levels of suppression. Other studies in the literature, specifically resistance and resilience models (Chambers et al. 2014, Miller et al. 2015), are likely to help managers decide when seeding is appropriate and when natural recovery may be an option. However, the resistance and resilience models currently available as management tools tend to be course-grained and often require local knowledge for optimal use.

Additionally, current resistance and resilience models are based on abiotic factors, such as soil moisture conditions. While these factors are important, our data show how important initial plant community composition, including residual seedbanks and root-stocks that remain after fires as well as added seed, is to future successional trajectories. We suggest that further research be done into understanding how plant community dynamics and composition, both historical and current, can affect post-fire recovery will be useful in making seeding decisions.

Native-only mixes can be nearly as effective in suppressing exotic annuals

Native-only seed mixes can establish, persist and suppress invasive exotic annuals, such as cheatgrass. This study demonstrates that conventional mixes that include introduced grasses are effective at exotic annual suppression, as they were designed to be, but it also shows that native-only mixes can be nearly as effective. Additionally, all seed mixes continued to effectively suppress annual exotics over the long-term. This shows that seeding is an effective long-term tool to help disrupt the cheatgrass-fire cycle; even when native species are used, which has not always been believed to be the case (Asay et al. 2001). Managers have some trade-offs to consider when deciding whether to use mixes that include introduced species or to use native-only mixes. Conventional mixes are often less expensive, and somewhat more effective at suppressing exotic annuals, while native-only mixes are often more expensive, and somewhat less effective at suppressing exotic annuals. However, conventional seed mixes may have long-term effects that are not desirable, particularly if the goal is to restore plant communities that are ecologically similar to plant communities that have not been disturbed (see below). Research has shown that seedings using conventional mixes have not generally been effective at rehabilitating sage-grouse habitat (Arkle et al. 2014), and our study indicates that native-only mixes are more likely to have successional trajectories that move toward desired reference states. Thus, we suggest that research prioritizing native plant material development to increase restoration effectiveness and lower cost will be important to the long-term restoration of the Great Basin ecosystems. As more native seed enters the market and reduces costs, native-only mixes should be seen as a viable option for post-fire seeding.

Interference between seed-mix species can affect successional trajectories

Seeded stands containing competitive perennial grasses may interfere with recruitment of other seeded and non-seeded species, including shrubs. In this study, the relative abundances of the seeded species shifted over time. Some of this may be due to differences in adaptation to site conditions (see below), but many of these shifts were likely due to competitive interactions. This study corroborates the growing literature that shows that these competitive interactions are important to the long-term successional trajectories of post-fire seedings (e.g. Nafus et al. 2015). For seeded species, long-term dominance, persistence or loss should be a consideration when designing seed mixes, particularly when certain species may promote management objectives better than others. For example, forb species are necessary for sage grouse chick rearing and other habitat considerations (Dumroese et al. 2015), but if perennial grasses suppress natural or seeded forbs then habitat recovery objectives may not be met over the long-term. Additionally, while these perennial grasses can be highly effective at suppressing exotic annuals, suppression of shrub recruitment could lead to a long-term trade-offs as well, and should be taken into consideration. Sagebrush recovery in the NH treatments indicated that high seeding rates may be needed to ensure sagebrush establishment, information which could help managers. There is some evidence from our study, and more evidence from the literature (Knutson et al. 2014;

Nafus et al. 2015), that some introduced grasses, such as *Agropyron* spp., have particularly suppressive effects on desirable species. Further research is needed into how these competitive interactions affect the long-term trajectories of post-fire seedings, especially across multiple environments. These kinds of data will inform seed mix design, so that more optimal mixes can be developed that meet as many management goals as possible.

Some seeded species may be more adapted to site conditions than others

Some seeded species and germplasms may be better able to persist and increase over time at a given site than others. In this case, rhizomatous grasses tended to increase over time, possibly due to the ability to recruit during drought. Additionally, some species, such as Indian ricegrass, declined over time. This could be due to competition with other seed-mix species or due to adaptive mismatch to site conditions, or both. It should be noted that many of the native germplasm releases were originally collected at locations that were quite distant from the sites in this study, indicating that these materials may not have been adapted to conditions at the study sites. While significant work has been put in to selecting and developing native plant materials, particularly perennial grasses, much less attention has been paid to selecting for traits that lead to success in the extreme conditions that characterize the Great Basin than to selecting for traits that are desirable in maximizing seed production in an agronomic setting (Leger and Baughman 2015). Therefore, more attention should be paid to promoting adaptive traits in plant material development. Studies on species-wide adaptive genetic variation (e.g. St. Clair et al. 2013) may prove particularly useful in searching for genes and traits that could bolster the future of plant material development. Next generation genomic technology in combination with common garden studies can target specific genetic associations that may prove useful in native plant selection programs.

Successional trajectories of conventional mixes may lead to novel plant communities

While the use of introduced species in seed mixes can help suppress exotic annuals, over the long-term inclusion of these species is likely to generate novel plant communities that are dissimilar to the Great Basin plant communities that have formed over evolutionary history. The successional trajectories of the conventional mixes not only separated from the native-only mixes and the USC but also trended away from the plant community composition at the unburned reference sites. The inclusion of these species themselves adds a novel element, however the fact that these trajectories continue to diverge from the reference state indicates that interactions between the seeded species and naturally recovering native species were also affected, especially over the long-term period in this study. The fact that seeding introduced species can shift successional trajectories to such a degree should be considered in any seed mix design and post-fire treatment plans. This is especially the case if the successional trajectories of conventional seedings inhibit ecosystem services, such as the recovery of wildlife habitat. Studies have shown that sage grouse habitat has often failed to recover in many ES&R seedings, even up to twenty years later, and that use of introduced perennial grasses may be part of the reason (Arkle et al. 2014; Knutson et al. 2014). Our study adds to this understanding by showing, through an operational scale experiment, that the successional trajectories of conventional mixes can move away from desirable reference conditions via long-term species-to-species interactions. Together, this suggests that seed mixes should be designed with the understanding that the long-term plant community shift could be significant, including the possible generation of novel and possibly undesirable, ecosystems. More research is needed on the long-term successional trajectories of seedings to help determine the likelihood these patterns given seed mix design decisions.

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Appendix A: Contact Information for Key Project Personnel

Francis Kilkenny
Research Biologist, U.S. Forest Service, Rocky Mountain Research Station, Boise, ID
208-373-4376
ffkilkenny@fs.fed.us

Jeffrey Ott
Research Geneticist, U.S. Forest Service, Rocky Mountain Research Station, Boise, ID
208-373-4353
jeott@fs.fed.us

Danny Summers
Habitat Restoration Coordinator, Utah Division of Wildlife Resources, Ephraim, UT
435-283-4441
dannysummers@utah.gov

Tyler Thompson
Watershed Program Director, Utah Department of Natural Resources
801-538-4876
tylerthompson@utah.gov

Appendix B**: **List of Completed/Planned Scientific/Technical Publications/Science Delivery Products: Identify scientific/technical publications that were produced during the course of the project, to include:

Completed:

1. Ott, J. E. September 2017. Strategies and equipment for large-scale, multi-species native seedings in North American drylands. VII World Conference on Ecological Restoration, Iguassu, Brazil.

2. Ott, J. E., and F. F. Kilkenny. November 2017. Long-term vegetation recovery and invasive annual suppression in native and introduced post-fire seeding treatments. Great Basin Native Plant Project Annual Meeting, Reno, NV.

3. Ott, J. E., and F. F. Kilkenny, D. Summers, and T. Thompson. February 2018. Long-term effects of post-fire seed mixes: revisiting a large-scale seeding experiment in Tintic Valley, Utah. 71st Annual Meeting, Society for Range Management, Reno, NV.

4. Kilkenny, F. F. January 2018. Long-term consequences of using nonnative species in post-fire restoration and fuel breaks: how implicit goals can define “success” or “failure.” Idaho Native Plant Society Pahove Chapter, Boise, ID.

5. Kilkenny, F. F. February 2018. Long-term consequences of using nonnative species in post-fire restoration and fuel breaks. Brown Bag Lunch USFWS Office, Boise, ID.

Planned:

1. Refereed Publication 1 - “Long-term vegetation recovery and invasive annual suppression in native and introduced post-fire seeding treatments” for Rangeland Ecology and Management. Manuscript completed, submission April 2018.

2. Refereed Publication 2 – “Successional trajectories of post-fire seeding treatments in Great Basin shrublands and woodlands” for Applied Vegetation Science. Manuscript in progress, submission planned summer 2018.

3. Ott, J. E., F. F. Kilkenny, D. Summers, and T. Thompson. July 2018. Effects of seeding treatments on vegetation succession following fire in semiarid ecosystems of the Great Basin. International Association for Vegetation Science 61st Annual Symposium, Bozeman, MT.

4. Webinar for Great Basin Fire Science Exchange (JFSP funded) on management implications of successional changes in seedings 15 years after fire. Webinars will be recorded and made available on the GBFSE website (http://www.gbfiresci.org/). Fall 2018.

5. Data from all years in standardized format. Fall 2018.

6. Management brief on long-term seeding success in sagebrush steppe using data and finding collected for this study in conjunction with a review of other studies. Spring 2019.