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Long-Term Vegetation Recovery and Invasive Annual Suppression in Native and Introduced Postfire Seeding Treatments[☆]



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ABSTRACT

Seed mixes used for postfire seeding in the Great Basin are often selected on the basis of short-term rehabilitation objectives, such as ability to rapidly establish and suppress invasive exotic annuals (e.g., cheatgrass, *Bromus tectorum* L.). Longer-term considerations are also important, including whether seeded plants persist, continue to suppress invasives, and promote recovery of desired vegetation. To better understand long-term effects of postfire seed mixes, we revisited study sites in Tintic Valley, Utah, where seeding experiments had been initiated after the 1999 Railroad 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 one-way Ely chaining at a woodland site. New vegetation data collected 16 years post fire revealed changes relative to 3 years post fire. 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. Significant increases of seed-mix species cover and density were observed in blocks where seeding treatments had previously been considered unsuccessful. Some seed-mix species, particularly rhizomatous grasses, increased while others declined. Exotic annual forb cover decreased in all treatments while cheatgrass increased in the unseeded control and to a lesser extent in the native-only seeded treatments. Recruitment of non-seed-mix native perennials was highest in the unseeded control. Results indicate that postfire 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 large amounts of competitive introduced species may be especially effective for long-term cheatgrass suppression, but native-only mixes can also serve this purpose to a lesser degree while avoiding drawbacks of non-native species introductions.

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Introduction

The threat of ecosystem degradation associated with wildfires has prompted widespread use of postfire seeding as a rehabilitation tool, especially in the western United States (Peppin et al., 2011; Pyke et al., 2013; Knutson et al., 2014) but also other areas of the world (e.g., Kim et al., 2008; Lamond, 2009; Pickup et al., 2013; Vega et al., 2015; Franca et al., 2016). In the Great Basin region, millions of hectares of public land administered by the US Department of the Interior, 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 after fire (USDI-BLM, 2007). Many seeding treatments have been carried out in semiarid shrubland and woodland sites where invasive exotic annuals, such as cheatgrass (*Bromus tectorum* L.), pose a threat to postfire vegetation recovery (Ott et al., 2003; Pyke et al., 2013). Sites dominated by fire-intolerant (nonresprouting) species of sagebrush (*Artemisia* spp.), juniper (*Juniperus* spp.), and/or pinyon (*Pinus* spp.) are susceptible to postfire proliferation of exotic annuals, especially if fire-resilient (resprouting) native perennials have been depleted due to overgrazing, woodland expansion, or other factors (Young and Evans, 1978; Rew and Johnson, 2010; Davies et al., 2012). In the absence of active postfire 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).

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Postfire 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 undesirable 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., 2011; 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; Hardegree et al., 2011; Robins et al., 2013; Svejcar et al., 2017). However, many of the common US 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 and DeLuca, 1996; Salesman and Thomsen, 2011; Gasch et al., 2016). Native species have increasingly been used for postfire seeding as emphasis has been placed on restoring historical or prefire ecological conditions (Richards et al., 1998; USDI-BLM, 2007; PCA, 2015; Pilliod et al., 2017). Shrubs such as Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) have sometimes been included in postfire seed mixes because of their value for wildlife and other ecosystem services they provide (Lysne, 2005; Knutson et al., 2014; Pilliod et al., 2017).

As a consequence of the ES&R program's short-term focus, assessments of postfire seeding effectiveness have generally been limited to the first 1–3 yr following treatment, with few agency resources dedicated to longer-term monitoring (USDI-BLM, 2007; Pyke et al., 2013). Although this timeframe may be sufficient to assess initial establishment and predict future vegetation development for a site, it fails to consider reactions of plants to a broader range of conditions than those encountered during the early postfire years. Maladaptation of seeded species to site conditions may not be apparent immediately (Millar and Libby, 1989; Bennington et al., 2012), and interactions among seeded species in multispecies mixtures, or between seeded and nonseeded species, may affect long-term vegetation dynamics (Knutson et al., 2014; Nafus et al., 2015). Successful initial establishment of seeded species could be followed by long-term declines (Roché et al., 2008; Rinella et al., 2012; Busby and Southworth, 2014) or, alternatively, seedings initially considered failures could prove successful when revisited at a later date (Herrick et al., 2006; Rinella et al., 2012). Composition of seedings could also shift over time, with some seeded species dying back while others rise to prominence (Hull and Klomp, 1966; Waldron et al., 2005; Nafus et al., 2015).

The relatively few long-term studies of postfire seedings in Great Basin shrublands and woodlands suggest mixed outcomes of seeding efforts. Pyke et al. (2013) reviewed studies ranging from 1 to 10 yr since fire and noted that older seedings (>3 yr) 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. However, Duniway et al. (2015) did not find significant reductions of invasive annuals in yr 4–5 after seeding, despite increases in seeded plants during this timeframe. In a chronosequence study of seeded sites located throughout the Great Basin, Knutson et al. (2014) found that the relationship between seeded plant cover and time since seeding (8–20 yr) could be positive, negative, or insignificant, depending on interacting variables including elevation, seeding method, and seeded species origin. Knutson et al. (2014) also found evidence suggesting that introduced (non-native) seeded species had sometimes outcompeted natives over time. In a related chronosequence study, Arkle et al. (2014) found that postfire seedings in the Great Basin had low sagebrush establishment and generally did not produce quality habitat for greater sage-grouse (*Centrocercus urophasianus*), a species of conservation concern. Range trend monitoring data from Utah revealed instances of increasing

abundance 5–10 yr after fire and seeding, especially of introduced grasses and shrubs, whereas native grasses increased to a lesser degree and native shrub abundance did not change (Wilder et al. in press).

Few studies have used replicated seeding experiments to examine effects of seed mix composition on postfire vegetation recovery in Great Basin shrublands and woodlands, but Thompson et al. (2006) carried out an operational-scale experiment wherein they examined short-term (1–3 yr) effects of seed mix composition by testing four different seed mixes, including conventional ES&R mixes with introduced species and rarely tested mixes containing only native species (Ott et al., 2016; Davies et al., 2019). Thompson et al. (2006) reported establishment of seeded perennials in all seed mix treatments, although establishment differed by species and site, and few plants emerged in two experimental blocks where soils were sandier. 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).

In this paper, we reexamine the experiment initiated by Thompson et al. (2006) to assess outcomes at a later point in time. New data collected from the experimental treatments in 2015 (16 yr post fire) were compared with previous data to determine if and how vegetation characteristics changed during the intervening period. We were interested in the question of long-term seeded plant persistence and the effects of possible shifts in seeded species composition or abundance on invasive exotic annuals and nonseeded native perennials. In considering long-term implications of postfire seeding and seed mix selection, we focus primarily on two common management objectives, suppression of exotic annuals and recovery of natural vegetation including shrub cover (USDI-BLM, 2007).

Methods

Study Area

As described by Thompson et al. (2006), two study sites were selected in areas burned by the July 1999 Railroad wildfire in Tintic Valley, Utah (Fig. 1). A higher elevation site (1769–1799 m) was located near Mud Springs (39°51'–54'N, 112°11'–15'W) on BLM-administered land where pinyon-juniper woodlands were present before the fire. A lower elevation site (1650 m–1680 m) on Utah state land in the vicinity of Jericho (39°42'–45'N, 112°11'–17'W) had been occupied by Wyoming big sagebrush communities prefire. At the higher elevation site (hereafter “Mud Springs”), seeding treatment consisted of aerial seeding followed by chaining, whereas the lower elevation site (hereafter “Jericho”) was seeded using rangeland drills (see later). Treatments were applied at five experimental blocks at each site. No additional fires, seeding treatments, or major disturbances have affected these study sites since 1999, but since 2002 they have been lightly to moderately grazed by cattle at Mud Springs and sheep at Jericho (Table 1). At Jericho, spot-herbicide treatment of scotch thistle (*Onopordum acanthium* L.) was carried out periodically before 2015. Soils are predominantly fine sandy loams at Mud Springs and cobbly, silty, or sandy loams at Jericho (see Table 1).

Weather data for each site were obtained using interpolation models available through the Climate of Western North America computer application (ClimateWNA) version 5.40 (Wang et al., 2016). Mean annual precipitation during the 3 decades before the study (1971–2000) was 368 mm at Mud Springs and 311 mm at Jericho (Table S1; available online at <https://doi.org/10.1016/j.rama.2019.02.001>). At both sites, the study period (2002–2015) was characterized by lower average annual precipitation and higher average temperatures than normals for 1971–2000 (see Table S1). Seasonal precipitation during the study period was on average highest during the spring (Mud Springs, 104 mm; Jericho, 93 mm); lower during fall (Mud Springs, 80 mm; Jericho, 70 mm) and winter (Mud Springs, 90 mm; Jericho, 69 mm); and lowest

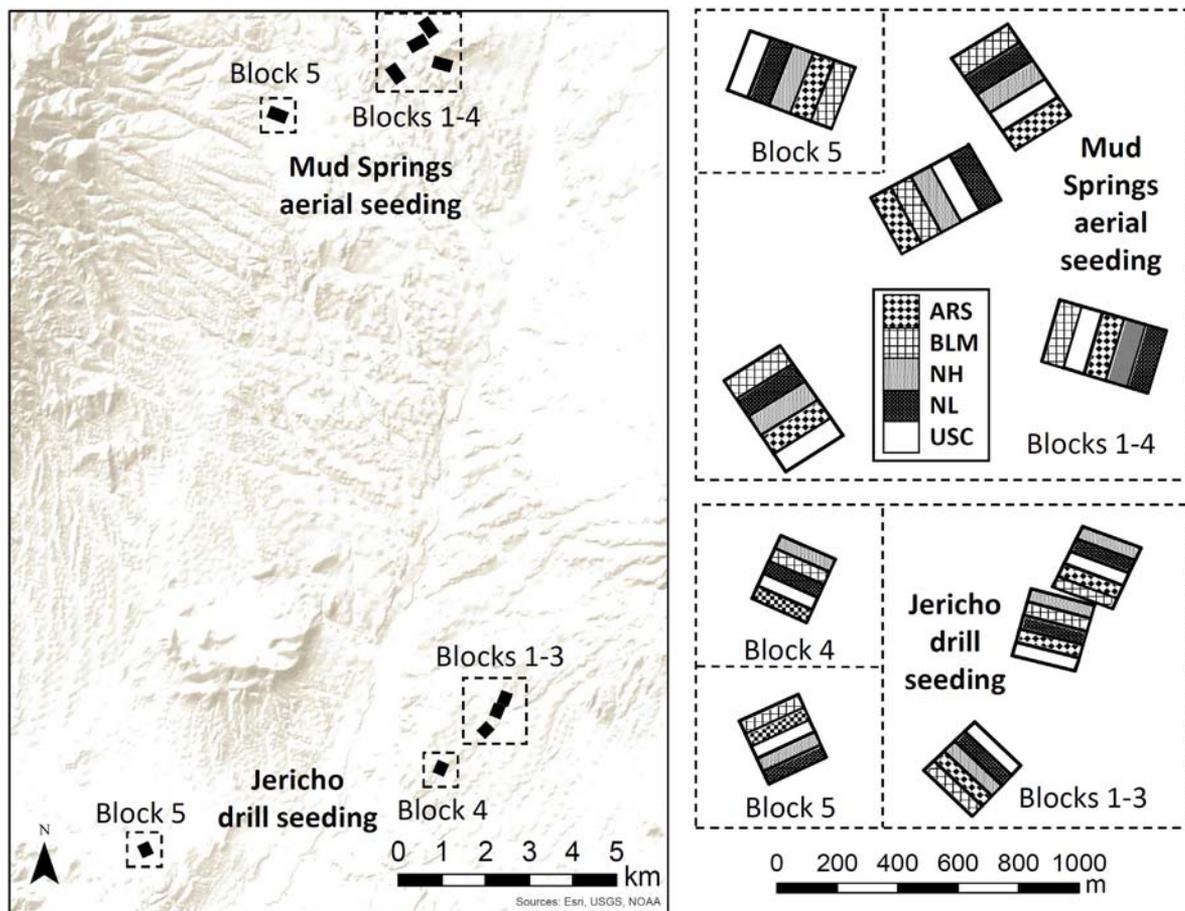


Figure 1. Postfire seeding study sites in Tintic Valley, Utah, showing layout of blocks on the landscape (left) and arrangement of treatments within blocks (right). Treatments: ARS indicates Agricultural Research Service mix; BLM, Bureau of Land Management mix; NH, Native high diversity mix; NL, Native low diversity mix; USC, unseeded control.

during summer (Mud Springs, 56 mm; Jericho, 49 mm). Precipitation was near or below seasonal norms during most years of the study period but was notably above average during one or more seasons of 2004, 2005, 2006, 2008, 2010, 2011, and 2015 (Fig. S1; available online at <https://doi.org/10.1016/j.rama.2019.02.001>). The yrs 2005, 2010, and 2011 were characterized by unusually wet springs (130–184 mm) followed by dry summers (34–65 mm), while the yrs 2007 and 2012–2014 had lower-than-average precipitation during nearly all seasons, especially spring (54–72 mm) (see Fig. S1).

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 (Mud Springs) or 46 m wide (Jericho), within each block (see Fig. 1). Aerial and drill seedings received seed mixes that were similar but not identical in composition and seeding rates (Table 2). Seed mixes were composed of different combinations of native species, defined as accessions, varieties, or cultivars of western North American origin, and/or introduced species native to Eurasia. The BLM supplied a seed mix of seven to eight predominantly introduced species typical of seed mixes commonly used locally at that time (BLM mix; see Table 2). Another seed mix supplied by the Forage and Range Research Laboratory (Logan, Utah) of the US Department of Agriculture, Agricultural Research Service (ARS mix) contained four to six native species and five introduced species (see Table 2) including varieties and cultivars that were being investigated by the agency (Thompson, 2002; Thompson et al., 2006). Two seed mixes formulated

Table 1
Soils classification and livestock grazing at study sites in Tintic Valley, Utah, highlighting differences between blocks located in different grazing allotments.

Site	Block	Soil series ¹	Grazing ²
Mud Springs	1-4	Borvant cobbly loam (2-8% slopes), Doyce silt loam, loamy substratum (2-4% slopes)	Cattle in late spring (May-Jun), late summer/early fall (Jul/Aug-Sep) or fall (Oct-Nov); rested in 2000, 2002, 2003, 2008, 2011, 2012
	5	Borvant cobbly loam (2-8% slopes), Shabliss very fine sandy loam (2-5% slopes)	Cattle in spring (Apr-May); rested in 2000, 2004, 2008, 2012
Jericho	1-4	Truesdale fine sandy loam (2-4% slopes), Linoyer very fine sandy loam (1-2% slopes), Medburn fine sandy loam (2-4% slopes)	Sheep in spring (incidental grazing in Apr during herding movements)
	5	Truesdale fine sandy loam (2-4% slopes)	Sheep in spring (Apr) and fall/early winter (Oct/Nov/Dec/Jan)

¹ Source: USDA-NRCS, 2017.

² Grazing during the period 2000-2015 according to available records (Bureau of Land Management, pers. comm.; Utah Trust Lands Administration, pers. comm.).

Table 2

Seed mix composition and seeding rates at aerial-seeded and drill-seeded sites in Tintic Valley, Utah (after Thompson et al., 2006, Table 1). Inflation-adjusted costs of seed mixes in 1999 (yr of seeding) and 2017 are also shown.

Species	Variety/Cultivar	Origin ¹	PLS ²	Mud Springs aerial seeding				Jericho drill seeding			
				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	0.8E	+	+	+	+	—	—	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
Bluebunch wheatgrass	Goldar	N	0.86	—	3	4.5	4.5	—	—	—	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	0.85E	—	—	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
Cost in 1999 (\$ ha ⁻¹) ⁵				\$53	\$26	\$184	\$79	\$27	\$17	\$136	\$51
Cost in 2017 (\$ ha ⁻¹)				\$38	\$33	\$109	\$43	\$19	\$19	\$88	\$36

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.

⁵ Costs of seed mixes in 1999 are adjusted for inflation to show 2017 dollar equivalents.

by scientists at the US Department of Agriculture Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory (Provo, Utah) consisted entirely of native species (Thompson, 2002; Thompson et al., 2006): one mix with seven to eight species seeded at total bulk seeding rates comparable with 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) (see Table 2).

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 (Thompson et al., 2006). Each drill treatment was seeded using a separate rangeland drill calibrated for its specific seed mix. Drills had standard concave disks, lacked depth-regulator bands, and were pulled by four-wheel-drive tractors (Thompson et al., 2006). In the case of NL and NH treatments, separate drill boxes were used to sow grasses and shrubs in separate rows. Eight of the 10 NL/NH rows were seeded with grasses, one row with the large-seeded shrubs antelope bitterbrush (*Purshia tridentata* [Pursh] DC.) and fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.), and another row with the small-seeded shrub Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young), which was allowed to fall onto the soil surface rather than being dispensed through the disk assembly (Thompson et al., 2006). Forage kochia (*Bassia prostrata* [L.] A.J. Scott) in the ARS drill mix was likewise seeded from a separate box onto the soil surface. Aerial seeding and chaining were accomplished using a helicopter with a gravity-fed broadcast seeder and an Ely-style chain pulled once across treated areas using two crawler tractors (Thompson et al., 2006). Aerial seeding was supplemented by dribbler-seeding of antelope bitterbrush and fourwing saltbush onto treads of the tractors used for chaining (Thompson et al., 2006).

We calculated how much the seed mixes used in this experiment would cost if purchased in the current market and compared results with the original (1999) costs adjusted for inflation. Current seed costs

for most of the varieties used in the experiment were obtained from records of purchases made by the Utah Division of Wildlife Resources (UDWR) in 2017. In a few cases, older varieties that were no longer part of the UDWR inventory were replaced by newer varieties of the same species, or prices were obtained from a local vendor (Table S2; available online at <https://doi.org/10.1016/j.rama.2019.02.001>). Seed costs originally reported by Thompson (2002) were converted to 2017 US dollar amounts using an online inflation adjustment calculator (USDL-BLS, 2018).

Vegetation Data Collection

Vegetation measurements taken during the first 3 yr after the 1999 Railroad Fire (Thompson et al., 2006) were remeasured in August 2015. Quadrats and transects previously sampled were relocated from permanent markers. Each treatment of each block was represented by five 30-m transects with 20, 0.25-m² quadrats positioned at 1.5-m intervals along each transect. Percent canopy cover by species in each quadrat was estimated on a modified Daubenmire cover class scale (1 = ≤1%, 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 for perennial species by counting individual plants rooted in quadrats. For rhizomatous species, individual stems (ramets) were counted.

Species identifications were evaluated following data collection and in some cases rechecked through subsequent field visits and corrected where necessary. Varieties or cultivars of seeded species were 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* [Pursh] Á. Löve; Secar = Snake River [S. R.] wheatgrass, *Elymus wawawaiensis* J. Carlson & Barkworth) (see Table 2). We assume that

most occurrences of these taxa were crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) and bluebunch wheatgrass except in the ARS treatment where Siberian wheatgrass (*Agropyron fragile* [Roth] P. Candargy) and Snake River wheatgrass were part of the seed mixes. Taxonomic nomenclature follows USDA-NCRS (2018).

Data Analysis

We compared data from 2002, the final year reported by Thompson et al. (2006), with data collected in 2015. Analyses focused on assessing changes during the 13-yr interval spanning these years. Unlike Thompson et al. (2006), who excluded two of the five drilled blocks from analysis, we used data from all blocks in our primary analyses, although we also carried out secondary analyses on the two previously excluded blocks. Seeding treatments in the previously excluded blocks had been deemed unsuccessful by Thompson et al. (2006), presumably due to improper seed burial.

Species were grouped based on origin (native/exotic), longevity (annual/perennial), and whether they had been included in seed mixes. We grouped perennials on the basis of seed-mix inclusion rather than categorizing them as seeded or residual (as done by Thompson et al., 2006) to circumvent the question of whether “seeded” plants actually originated from seeding treatments versus residual populations. “Seed-mix species” were defined as species that had been included in any of the mixes at a given site and, by definition, could thus be present in the unseeded control, either as residuals or invaders from nearby seeding treatments.

For each species and group of interest, we converted cover classes to percent cover values using arithmetic midpoints of the classes. Percent cover values for groups containing multiple species were derived by compositing cover class midpoints across species within quadrats (see formula in Jennings et al., 2009, p. 185) before averaging percent cover across quadrats within transects. In addition to calculating cover on an absolute scale, we calculated relative cover for each seed-mix species as a percentage of total seed-mix cover per transect (using the sum of seed-mix species cover class midpoints as the total, without compositing).

Analyses of cover and density were implemented separately for each site using the MIXED procedure in SAS 9.4 (SAS Institute, Inc., 2012). Measurements taken from quadrats of the same transect were averaged and either $\log(x + 1)$ transformed (density and absolute cover) or arcsine square root transformed (relative cover). Transformed values were used for analysis, but values presented in figures and tables are untransformed. Transects were treated as units of analysis in mixed models with coordinates of transect center points used for spatial adjustment assuming linear spatial covariance. Spatial adjustment is a spatially explicit alternative to using blocks as random variables in mixed models (Littell et al., 1996). We analyzed quadrat cover of each species group by modeling treatment (i.e., seed mix), year, and treatment \times year as fixed effects and used Tukey's HSD at $\alpha = 0.05$ for mean separation. When analyzing cover and density of individual seeded species, we did not test for treatment differences but instead tested only for within-treatment differences between years using contrast statements in SAS (Littell et al., 1996). Cases where mean cover or mean density of a species did not exceed 0.1% or 0.1 m⁻² in one or both years were omitted from analyses.

Results

Seed Mix Costs

The inflation-adjusted cost of the ARS, NH, and NL seed mixes was lower in 2017 than 1999, but the cost of the BLM mix rose slightly (see Table 2). The NH mix remained the most expensive in 2017, but its cost had also dropped the most compared with 1999 (\$75 and \$48

less per ha for aerial and drill, respectively), making its difference from other mixes less extreme (see Table 2). The cost of the NL mix was closer to that of the less expensive ARS and BLM mixes in 2017, differing by \$5–\$17 per ha compared with \$24–\$53 per ha in 1999 (see Table 2). Most of the native grass varieties were less expensive in 2017 than 1999, whereas introduced grasses and native shrubs were more expensive (see Table S2).

Cover by Plant Group

In both 2002 and 2015, perennial cover in seeded treatments (ARS, BLM, NH, and NL) was dominated by seed-mix species. Although seed-mix species composition differed among seeded treatments, total seed-mix perennial cover did not differ significantly between these treatments except that cover was lower in NL than other seeded treatments at Jericho (Fig. 2). At both sites, the USC had lower seed-mix perennial cover than seeded treatments (see Fig. 2). These treatment differences persisted from 2002 to 2015 despite significant changes in seed-mix perennial cover during this time interval (see Fig. 2). At Mud Springs, seed-mix perennial cover increased from 11–13% (2002) to 27–29% (2015) in seeded treatments and 5% (2002) to 15% (2015) in USCs (see Fig. 2). At Jericho, seed-mix perennial cover increased from 3% (2002) to 17% (2015) in NL and 6–8% (2002) to 22–24% (2015) in other seeded treatments (see Fig. 2). Seed-mix perennials were nearly absent from USCs at Jericho in 2002 but increased to 4% cover in 2015 (see Fig. 2).

In contrast to seed-mix species, non-seed-mix perennials attained higher cover in USCs than seeded treatments (see Fig. 2). Non-seed-mix perennial cover increased between years in USC at both Mud Springs (2% in 2002 to 10% in 2015) and Jericho (< 1% in 2002 to 3% in 2015), whereas the seeded treatments had lower cover (< 3%) of non-seed-mix perennials that did not change significantly between years except for increases of 1–2% in the case of NL (see Fig. 2). Much of the non-seed-mix perennial cover was composed of woody species including rubber rabbitbrush (*Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird), yellow rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.), broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britton & Rusby), green ephedra (*Ephedra viridis* Coville), and spiny phlox (*Phlox hoodii* Richardson).

Most annual cover was composed of exotic species; native annuals had < 1% cover that did not differ between treatments and 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* Stapf) at Mud Springs and desert alyssum, Russian thistle (*Salsola tragus* L.), tumbledustard (*Sisymbrium altissimum* L.), and redstem storksbill (*Erodium cicutarium* [L.] L'Hér. ex Aiton) at Jericho. In 2002, exotic annual grass cover was relatively low (< 1% at Mud Springs, 1–4% at Jericho) compared with exotic annual forb cover (2–4% at Mud Springs; 7–22% at Jericho), 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 (see Fig. 2). By 2015, exotic annual grass cover was highest in USC (Mud Springs, 9%; Jericho, 15%), intermediate in NH and NL (Mud Springs, 2–3%; Jericho, 6%), and lowest in ARS and BLM (Mud Springs, 1%; Jericho, 2%) (see Fig. 2). Exotic annual forb cover was likewise highest in USC (14%), followed by NL (5%) and other seeded treatments (1–2%) at Jericho in 2015 (see Fig. 2). At Mud Springs, exotic annual forb cover dropped to 2% in USC and < 1% in seeded treatments by 2015 (see Fig. 2).

Seed-Mix Species Cover and Density Changes

Cover of individual seed-mix species generally increased between 2002 and 2015 in treatments where the species had been seeded, but in some cases, cover decreased or did not change (Table 3). Crested/Siberian wheatgrass, Russian wildrye (*Psathyrostachys juncea* [Fisch.]

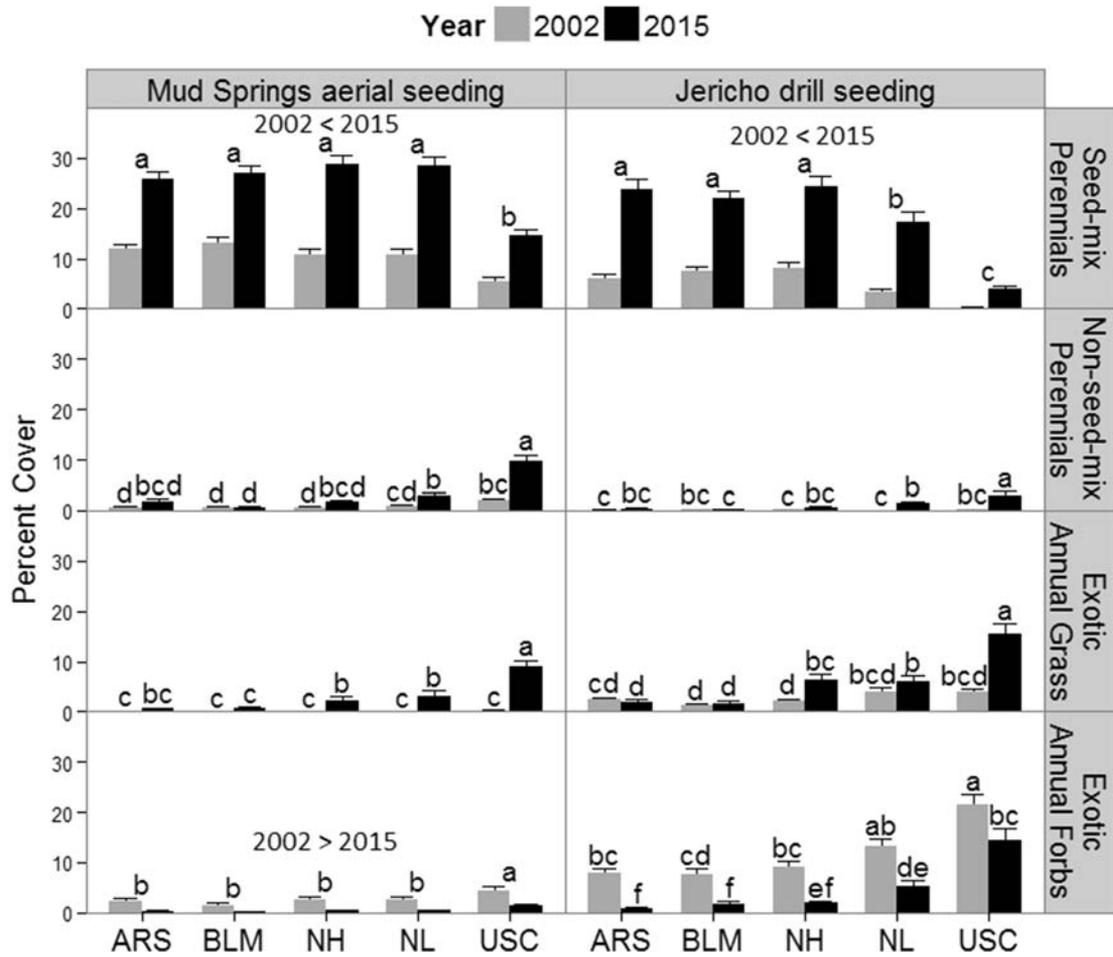


Figure 2. Cover by species group at sites in Tintic Valley, Utah, as recorded 3 yr (2002) and 16 yr (2015) following fire and seeding. Bars indicate means; error bars, standard errors. Within each cell (species groups within sites), means with the same letter are not significantly different ($P < 0.05$). If the treatment \times year interaction was not significant, significance is shown separately for treatment (letters spanning both yr) 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).

Nevski), pubescent wheatgrass (*Thinopyrum intermedium* [Host] Barkworth & D.R. Dewey), smooth brome (*Bromus inermis* Leyss.), needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth), and basin wildrye (*Leymus cinereus* [Scribn. & Merr.] Á. Löve) each increased wherever they were seeded (see Table 3). Western wheatgrass (*Pascopyrum smithii* [Rydb.] Á. Löve) cover increased in the ARS, NH, and NL treatments but did not change significantly in BLM (see Table 3). Thickspike wheatgrass (*Elymus lanceolatus* [Scribn. & J.G. Sm.] Gould) cover increased in ARS at Mud Springs after having not been recorded (possibly due to misidentification) in 2002 (see Table 3). Cover of bluebunch/S. R. wheatgrass and Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth) did not change in seed-mix treatments at Mud Springs (see Table 3), but at Jericho, Indian ricegrass decreased in all treatments where it was seeded (ARS, NH, and NL) and bluebunch/S. R. wheatgrass decreased in the NH treatment (see Table 3). Tall wheatgrass (*Thinopyrum ponticum* [Podp.] Z.-W. Liu & R.-C. Wang) cover increased where it had been seeded (BLM) at Mud Springs but not Jericho, where it decreased (see Table 3). Squirreltail (*Elymus elymoides* [Raf.] Swezey) and Sandberg bluegrass (*Poa secunda* J. Presl) did not have significant cover changes in treatments where they were seeded. Wyoming big sagebrush cover increased in the NH treatment at Mud Springs but not Jericho (see Table 3), in contrast to fourwing saltbush and antelope bitterbrush, whose cover increased in NH and/or NL at Jericho but not Mud Springs (see Table 3).

Cover of some seed-mix species increased in treatments where they had not been seeded. Crested/Siberian wheatgrass and smooth brome were present and increased in the NH, NL, and/or USC treatments, although their cover remained lower in these treatments compared with ARS and BLM treatments, where they had been part of the seed mix (see Table 3). Needle-and-thread, squirreltail, western wheatgrass, and Wyoming big sagebrush also increased in some treatments where they had not been seeded, especially USC, where cover of these species approached or exceeded that of seeded treatments in some cases (see Table 3).

In most cases where a species changed cover between 2002 and 2015, density also changed in the same direction (Table 4). However, there were some cases where cover increases were not accompanied by density increases, notably crested/Siberian wheatgrass in Jericho BLM treatment, tall wheatgrass in Mud Springs BLM, and the seeded shrubs fourwing saltbush and antelope bitterbrush in Jericho NH (see Table 4). In other cases, cover did not change significantly while density increased (e.g., pubescent wheatgrass and smooth brome in Mud Springs ARS) or decreased (e.g., bluebunch/S. R. wheatgrass in NL and Mud Springs NH) (see Table 4). Density increases were most pronounced for the rhizomatous grasses western wheatgrass, pubescent wheatgrass, and smooth brome, which rose from 1 to 12 stems m^{-2} (2002) to 25–65 stems m^{-2} (2015) in several instances (see Table 4).

Table 3
Percent cover (mean ± standard error) of seeded species at sites in Tintic Valley, Utah, as recorded 3 years (2002) and 16 years (2015) following fire and seeding. Significant ($P < 0.05$) changes between years (Δ) are shown for each species and treatment (+ indicates increase; -, decrease). Underlined values indicate the species was seeded in a given treatment (see Table 1). Trace amounts of forage kochia are omitted.

	ARS ¹		BLM		NH		NL		USC	
	2002	2015 (Δ)	2002	2015 (Δ)	2002	2015 (Δ)	2002	2015 (Δ)	2002	2015 (Δ)
Mud Springs aerial seeding										
Alfalfa	<0.1 ²	0	0	<0.1	0	0	0	0	0	0
Antelope bitterbrush	<0.1	0	0	0	<0.1	<0.1	0	0	0	0
Basin wildrye	0	0.1 ± 0.1	0	0.2 ± 0.1	0.3 ± 0.1	3.1 ± 0.6 (+)	0	<0.1	0	0.1 ± 0.1
Bluebunch/S. R. wheatgrass	1.3 ± 0.3	0.8 ± 0.3	1.4 ± 0.4	1.6 ± 0.5	4.1 ± 0.6	6.0 ± 0.9	4.8 ± 1.1	6.4 ± 1.3	0.1 ± 0.1	<0.1
Crested/Siberian wheatgrass	5.8 ± 0.9	13 ± 1.4 (+)	0.9 ± 0.6	9.5 ± 0.9 (+)	0.3 ± 0.2	0.8 ± 0.3 (+)	0.1 ± <0.1	0.3 ± 0.1	<0.1	1.1 ± 0.3 (+)
Fourwing saltbush	<0.1	0.1 ± 0.1	<0.1	0.2 ± 0.1 (+)	0.1 ± 0.1	0.1 ± 0.1	<0.1	0.4 ± 0.2	0	0
Indian ricegrass	0.8 ± 0.2	0.6 ± 0.2	0.9 ± 0.4	0.5 ± 0.1	1.3 ± 0.3	1.4 ± 0.4	1.5 ± 0.3	1.3 ± 0.4	1.1 ± 0.3	2.0 ± 0.5
Needle-and-thread	<0.1	0.2 ± 0.1	<0.1	0.3 ± 0.3	0.1 ± 0.1	0.7 ± 0.3 (+)	<0.1	0.5 ± 0.2 (+)	<0.1	1.1 ± 0.4 (+)
Pubescent wheatgrass	0.2 ± 0.1	0.6 ± 0.2	1.0 ± 0.4	2.4 ± 0.4 (+)	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0	0.6 ± 0.4
Russian wildrye	0.4 ± 0.1	1.6 ± 0.4 (+)	0.1 ± 0.1	0.7 ± 0.1 (+)	0.2 ± 0.1	0.1 ± 0.1	<0.1	0.1 ± 0.1	0	0
Sandberg bluegrass	0.3 ± 0.1	0.2 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.4 ± 0.1	0.4 ± 0.2	0.4 ± 0.1	0.3 ± 0.1	0.4 ± 0.2	0.7 ± 0.2 (+)
Smooth brome	0.5 ± 0.2	1.0 ± 0.4	2.1 ± 0.4	8.2 ± 1.2 (+)	0.3 ± 0.2	1.2 ± 0.5 (+)	0.1 ± 0.1	1.7 ± 0.8 (+)	0	0.4 ± 0.2
Squirreltail	0.2 ± 0.1	0.1 ± <0.1	0.2 ± 0.1	0.1 ± <0.1	0.2 ± 0.1	0.6 ± 0.2	0.4 ± 0.2	0.6 ± 0.2	0.5 ± 0.2	2.0 ± 0.6 (+)
Tall wheatgrass	0.2 ± 0.1	0.2 ± 0.1	0.7 ± 0.2	1.3 ± 0.3 (+)	0.5 ± 0.2	<0.1 (-)	<0.1	0	<0.1	<0.1
Thickspike wheatgrass	0	1.1 ± 0.8 (+)	0	<0.1	0	0.2 ± 0.1	0	0.2 ± 0.2	0	0
Western wheatgrass	2.0 ± 0.6	7.5 ± 1.3 (+)	1.9 ± 0.5	3.4 ± 1.1	2.8 ± 0.6	14 ± 2.1 (+)	3.2 ± 0.9	17 ± 2.1 (+)	3.2 ± 1.2	5.5 ± 1.5 (+)
Wyoming big sagebrush	0	0	0	0	0.1 ± <0.1	2.0 ± 0.5 (+)	0	0.3 ± 0.2	<0.1	1.3 ± 1.0 (+)
Jericho drill seeding										
Alfalfa	0.2 ± 0.1	0	0.1 ± <0.1	0	0	0	<0.1	<0.1	<0.1	0
Antelope bitterbrush	0	0	0	0	<0.1	0.6 ± 0.3 (+)	0.1 ± <0.1	0.3 ± 0.3	0	0
Basin wildrye	<0.1	0	0	<0.1	0.1 ± 0.1	0.7 ± 0.2 (+)	<0.1	0	0	0
Bluebunch/S. R. wheatgrass	0.3 ± 0.3	<0.1	0.4 ± 0.2	0	2.7 ± 0.5	1.2 ± 0.3 (-)	1.1 ± 0.4	0.7 ± 0.3	<0.1	0
Crested/Siberian wheatgrass	4.1 ± 0.7	18 ± 1.7 (+)	3.0 ± 0.4	6.8 ± 0.9 (+)	0.1 ± <0.1	0.3 ± 0.1	0.2 ± 0.1	1.8 ± 0.5 (+)	0	0.7 ± 0.2 (+)
Fourwing saltbush	0	0	0	0.1 ± 0.1	0.2 ± 0.2	2.1 ± 0.6 (+)	0.1 ± 0.1	0.5 ± 0.2 (+)	0	0
Indian ricegrass	0.6 ± 0.2	0.1 ± <0.1 (-)	0.1 ± 0.1	0.1 ± 0.1	3.7 ± 0.6	0.4 ± 0.3	1.1 ± 0.2	0.2 ± 0.1 (-)	<0.1	0.5 ± 0.3
Needle-and-thread	0	<0.1	0	0.1 ± <0.1	0.2 ± 0.1	3.3 ± 0.9 (+)	0	0.6 ± 0.3 (+)	0	1.2 ± 0.6 (+)
Pubescent wheatgrass	<0.1	0.1 ± 0.1	1.1 ± 0.4	12 ± 1.3 (+)	<0.1	<0.1	0	0.3 ± 0.2	0	0.3 ± 0.2
Russian wildrye	0.1 ± 0.1	0.6 ± 0.3 (+)	0.2 ± 0.1	1.0 ± 0.2 (+)	0	<0.1	0	0.1 ± 0.1	0	0
Sandberg bluegrass	<0.1	0	0	0	0.1 ± <0.1	<0.1	0	<0.1	<0.1	0
Squirreltail	0.2 ± 0.1	<0.1	0.1 ± 0.1	<0.1	0.2 ± 0.1	0.1 ± 0.1	0.1 ± <0.1	1.0 ± 0.5 (+)	0.1 ± 0.1	1.2 ± 0.5 (+)
Tall wheatgrass	0	0	1.8 ± 0.5	0.7 ± 0.2 (-)	0.3 ± 0.3	0	0.3 ± 0.2	0	0	0
Thickspike wheatgrass	0	0	0	0	0	0.1 ± 0.1	0	0	0	0
Western wheatgrass	0.4 ± 0.1	5.6 ± 1.6 (+)	0.6 ± 0.3	1.4 ± 0.6	0.7 ± 0.2	16 ± 2.2 (+)	0.4 ± 0.2	12 ± 1.6 (+)	0	<0.1
Wyoming big sagebrush	0	0	0	0	<0.1	0.1 ± 0.1	<0.1	0	0	0

¹ 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.

² Values less than 0.1 but greater than 0 are indicated by '<0.1'; otherwise values are rounded to the nearest tenth (if less than 10) or whole number (if greater than 10).

Although cover and density of seed-mix species appeared to be generally lower in Jericho blocks 4–5 compared with the site as a whole, significant increases occurred even in these blocks, which had previously been considered failed seedings (Table 5). Western wheatgrass, crested/Siberian wheatgrass, pubescent wheatgrass, Russian wildrye, and needle-and-thread each increased in cover and density in all treatments of Jericho blocks 4–5 where they had been seeded (see Table 5). In some of these cases, cover and density were more than an order of magnitude higher in 2015 than in 2002 (e.g., western wheatgrass cover increased from 0.2% [2002] to 18.9% [2015] and needle-and-thread from 0.1% [2002] to 6.0% [2015] in the NH treatment of these blocks) (see Table 5).

Relative Cover of Seed-Mix Species in Seeded Treatments

Relative percent cover of seed-mix species shifted as the net result of each species' cover changes between 2002 and 2015 (Fig. 3). Species that did not increase in absolute cover during this period (see Table 3), including Indian ricegrass, bluebunch/S. R. wheatgrass, Sandberg bluegrass, alfalfa (*Medicago sativa* L.), and in some instances tall wheatgrass and squirreltail, generally decreased in relative cover as other species became more dominant, such as western wheatgrass, pubescent wheatgrass, smooth brome, Russian wildrye, basin wildrye, needle-and-thread, fourwing saltbush, and Wyoming big sagebrush (see Fig. 3). Relative cover of crested/Siberian wheatgrass did not change significantly in the ARS and BLM

treatments (see Fig. 3) despite increases in absolute cover (see Table 3).

In the ARS treatment, crested/Siberian wheatgrass was the dominant seed-mix species in both 2002 and 2015, accounting for ca. 46% of the seeded cover at Mud Springs and ca. 73% at Jericho (see Fig. 3). Remaining seed-mix cover at Mud Springs ARS was codominated in 2002 by western wheatgrass, bluebunch/S. R. wheatgrass, and Indian ricegrass, which each had 8–14% of the relative cover, but by 2015, western wheatgrass had risen to 27% while bluebunch/S. R. wheatgrass and Indian ricegrass had only 3% each (see Fig. 3). A similar shift occurred at Jericho ARS, where western wheatgrass increased from 9% to 21% relative cover while Indian ricegrass decreased from 9% to <1% between 2002 and 2015 (see Fig. 3). Russian wildrye relative cover also increased in the ARS treatment at Mud Springs (3% in 2002, 6% in 2015) (see Fig. 3).

The BLM treatment was characterized by roughly equivalent relative cover of crested/Siberian wheatgrass at Mud Springs and Jericho in 2002 (ca. 39%) and 2015 (ca. 32%), but the two sites differed with respect to relative cover of other species within and between years (see Fig. 3). At Mud Springs BLM, smooth brome increased from 14% relative cover in 2002 to become codominant with crested/Siberian wheatgrass at 30% in 2015, while western wheatgrass remained secondary with ca. 13% both years (see Fig. 3). At Jericho BLM, pubescent wheatgrass increased from 11% relative cover in 2002 to become the dominant species with 53% in 2015, in contrast

Table 4

Density m⁻² (mean ± standard error) of seeded species at sites in Tintic Valley, Utah, as recorded 3 years (2002) and 16 years (2015) following fire and seeding. Significant (P < 0.05) changes between years (Δ) are shown for each species and treatment (+ indicates increase; -, decrease). Underlined values indicate the species was seeded in a given treatment (see Table 1). Trace amounts of forage kochia are omitted.

	ARS ¹		BLM		NH		NL		USC	
	2002	2015 (Δ)	2002	2015 (Δ)	2002	2015 (Δ)	2002	2015 (Δ)	2002	2015 (Δ)
Mud Springs aerial seeding										
Alfalfa	<0.1 ²	0	0	<0.1	0	0	0	0	0	0
Antelope bitterbrush	<0.1	0	0	0	<0.1	0	0	0	0	0
Basin wildrye	0	<0.1	0	<0.1	<u>0.1 ± <0.1</u>	<u>0.8 ± 0.1 (+)</u>	0	<0.1	0	0
Bluebunch/S. R. wheatgrass	<u>1.7 ± 0.7</u>	<u>0.4 ± 0.1 (-)</u>	<u>2.1 ± 0.8</u>	<u>0.7 ± 0.3 (-)</u>	<u>4.1 ± 0.7</u>	<u>2.7 ± 0.5 (-)</u>	<u>4.0 ± 0.9</u>	<u>2.3 ± 0.6 (-)</u>	0.2 ± 0.1	<0.1
Crested/Siberian wheatgrass	<u>5.3 ± 0.9</u>	<u>9.5 ± 1.2 (+)</u>	<u>4.0 ± 0.5</u>	<u>7.1 ± 0.6 (+)</u>	<u>0.2 ± 0.1</u>	<u>0.7 ± 0.3</u>	<u>0.1 ± 0.1</u>	<u>0.2 ± 0.1</u>	<0.1	0.9 ± 0.3 (+)
Fourwing saltbush	<0.1	<0.1	0	<0.1	<u>0.1 ± <0.1</u>	<0.1	0	0	0	0
Indian ricegrass	<u>0.5 ± 0.1</u>	<u>0.5 ± 0.2</u>	<u>0.3 ± 0.1</u>	<u>0.3 ± 0.1</u>	<u>0.6 ± 0.1</u>	<u>0.6 ± 0.1</u>	<u>0.8 ± 0.2</u>	<u>0.7 ± 0.2</u>	0.5 ± 0.1	1.0 ± 0.2 (+)
Needle-and-thread	<0.1	0.3 ± 0.2	<0.1	0.2 ± 0.2	<u>0.1 ± 0.1</u>	<u>0.7 ± 0.3 (+)</u>	<0.1	0.3 ± 0.1	<0.1	0.9 ± 0.3 (+)
Pubescent wheatgrass	0.1 ± 0.1	3.2 ± 1.4 (+)	<u>0.6 ± 0.2</u>	<u>6.4 ± 0.8 (+)</u>	0.2 ± 0.1	0.7 ± 0.6	0.2 ± 0.1	0.5 ± 0.3	0	3.1 ± 2.3
Russian wildrye	<u>0.2 ± 0.1</u>	<u>0.8 ± 0.2 (+)</u>	<u>0.1 ± <0.1</u>	<u>0.5 ± 0.1 (+)</u>	0.2 ± 0.1	<0.1	<0.1	<0.1	0	0
Sandberg bluegrass	<u>0.9 ± 0.3</u>	<u>0.6 ± 0.2</u>	<u>0.9 ± 0.3</u>	<u>1.5 ± 0.8</u>	<u>1.1 ± 0.3</u>	<u>1.2 ± 0.5</u>	<u>1.3 ± 0.3</u>	<u>0.7 ± 0.2</u>	0.9 ± 0.3	1.8 ± 0.4 (+)
Smooth brome	0.6 ± 0.3	6.3 ± 3.2 (+)	<u>4.3 ± 0.7</u>	<u>39 ± 5.5 (+)</u>	<u>0.5 ± 0.2</u>	<u>4.9 ± 2.0 (+)</u>	<u>0.2 ± 0.2</u>	<u>5.9 ± 2.5 (+)</u>	0	1.2 ± 0.6
Squirreltail	0.3 ± 0.1	0.1 ± <0.1	0.1 ± <0.1	0.1 ± <0.1	<u>0.2 ± 0.1</u>	<u>0.5 ± 0.1</u>	0.4 ± 0.1	0.7 ± 0.2	0.6 ± 0.2	2.4 ± 0.4 (+)
Tall wheatgrass	0.3 ± 0.2	0.1 ± 0.1	<u>0.5 ± 0.2</u>	<u>0.7 ± 0.2</u>	0.6 ± 0.3	<0.1 (-)	0.1 ± 0.1	0	<0.1	<0.1
Thickspike wheatgrass	0	2.3 ± 1.0 (+)	0	0.2 ± 0.1	0	0.7 ± 0.6	0	0.4 ± 0.3	0	0
Western wheatgrass	<u>5.8 ± 1.6</u>	<u>31 ± 5.3 (+)</u>	6.7 ± 2	16 ± 5.8	<u>10 ± 2.5</u>	<u>48 ± 6.7 (+)</u>	<u>12 ± 3.0</u>	<u>65 ± 8.2 (+)</u>	11 ± 3.6	32 ± 9.4 (+)
Wyoming big sagebrush	0	0	0	0	<0.1	<u>0.2 ± 0.1 (+)</u>	0	<0.1	0	0.4 ± 0.3 (+)
Jericho drill seeding										
Alfalfa	<u>0.2 ± 0.1</u>	0 (-)	<u>0.2 ± 0.1</u>	0 (-)	0	0	<0.1	<0.1	<0.1	0
Antelope bitterbrush	0	0	0	0	<0.1	<0.1	<0.1	<0.1	0	0
Basin wildrye	<0.1	0	0	<0.1	<0.1	<u>0.3 ± 0.1 (+)</u>	<0.1	0	0	0
Bluebunch/S. R. wheatgrass	<u>0.4 ± 0.4</u>	<0.1	0.5 ± 0.3	0	<u>3.3 ± 0.8</u>	<u>0.3 ± 0.1 (-)</u>	<u>0.7 ± 0.2</u>	<u>0.1 ± 0.1 (-)</u>	<0.1	0
Crested/Siberian wheatgrass	<u>2.9 ± 0.4</u>	<u>8.6 ± 0.8 (+)</u>	<u>3.0 ± 0.4</u>	<u>3.0 ± 0.3</u>	0.1 ± <0.1	0.1 ± <0.1	0.1 ± 0.1	0.8 ± 0.2 (+)	0	0.3 ± 0.1
Fourwing saltbush	0	0	0	0	<0.1	<0.1	<0.1	<0.1	0	0
Indian ricegrass	<u>0.4 ± 0.1</u>	<0.1 (-)	<0.1	0.1 ± 0.1	<u>2.9 ± 0.5</u>	<u>0.1 ± 0.1 (-)</u>	<u>0.6 ± 0.1</u>	<u>0.1 ± <0.1 (-)</u>	<0.1	0.2 ± 0.1
Needle-and-thread	0	<0.1	0	<0.1	<u>0.2 ± 0.1</u>	<u>2.1 ± 0.5 (+)</u>	0	0.4 ± 0.2	0	0.5 ± 0.2 (+)
Pubescent wheatgrass	<0.1	0.5 ± 0.5	<u>1.0 ± 0.3</u>	<u>37 ± 4.9 (+)</u>	<0.1	0.1 ± 0.1	0	0.4 ± 0.2	0	0.9 ± 0.8
Russian wildrye	<u>0.1 ± <0.1</u>	<u>0.3 ± 0.1 (+)</u>	<u>0.2 ± 0.1</u>	<u>0.5 ± 0.1 (+)</u>	0	<0.1	0	<0.1	0	0
Sandberg bluegrass	<0.1	0	0	0	<u>0.4 ± 0.1</u>	<0.1 (-)	0	<0.1	<0.1	0
Squirreltail	0.1 ± 0.1	<0.1	0.1 ± <0.1	<0.1	<u>0.3 ± 0.1</u>	<u>0.1 ± 0.1</u>	0.1 ± <0.1	0.8 ± 0.4 (+)	0.1 ± <0.1	0.8 ± 0.3 (+)
Tall wheatgrass	0	0	<u>1.3 ± 0.4</u>	<u>0.2 ± 0.1 (-)</u>	0.1 ± 0.1	0	0.2 ± 0.1	0	0	0
Thickspike wheatgrass	0	0	0	0	0	0.1 ± 0.1	0	0	0	0
Western wheatgrass	<u>0.9 ± 0.3</u>	<u>25 ± 5.8 (+)</u>	<u>1.9 ± 1</u>	<u>4.4 ± 1.8</u>	<u>2.3 ± 0.8</u>	<u>54 ± 8.2 (+)</u>	<u>1.4 ± 0.6</u>	<u>44 ± 5.6 (+)</u>	0	0.4 ± 0.3
Wyoming big sagebrush	0	0	0	0	<0.1	<0.1	<0.1	0	0	0

¹ 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.

² Values less than 0.1 but greater than 0 are indicated by '<0.1'; otherwise values are rounded to the nearest tenth (if less than 10) or whole number (if greater than 10).

to tall wheatgrass, which decreased from 23% to 3% during this interval (see Fig. 3). Western wheatgrass maintained ca. 7% relative cover at Jericho BLM both years, but bluebunch/S. R. wheatgrass declined from 7% to 0% (see Fig. 3).

The two native treatments (NH and NL) had similar patterns of relative cover for the dominant species bluebunch/S. R. wheatgrass, Indian ricegrass, and western wheatgrass (see Fig. 3). With the exception of western wheatgrass at Jericho, these three species had been seeded at identical rates in NH and NL (see Table 2). At Mud Springs, NH and NL treatments both had ca. 37% relative cover of bluebunch/S. R. wheatgrass, ca. 27% western wheatgrass, and ca. 12% Indian ricegrass in 2002 (see Fig. 3). By 2015, bluebunch/S. R. wheatgrass and Indian ricegrass relative cover had dropped to ca. 22% and ca. 5%, respectively, while western wheatgrass increased to 42% in NH and 58% in NL, in native treatments at Mud Springs (see Fig. 3). A similar shift occurred between 2002 and 2015 in native treatments at Jericho, where Indian ricegrass decreased from ca. 45% to ca. 2% relative cover and bluebunch/S. R. wheatgrass decreased from ca. 24% to ca. 4%, whereas western wheatgrass increased from ca. 8% to ca. 63% (see Fig. 3).

Species that were seeded at higher rates in NH than NL generally increased significantly in NH but not NL, resulting in noticeably higher cover (both absolute and relative) in NH by 2015 (see Fig. 3, Table 3). At Mud Springs, basin wildrye increased from 3% to 10%

relative cover and Wyoming big sagebrush increased from < 1% to 7% relative cover in the NH treatment but maintained low cover (< 2%) in NL (see Fig. 3). At Jericho, needle-and-thread increased from 2% to 15% relative cover in NH compared with a 0% to 8% increase in NL (see Fig. 3). Antelope bitterbrush and fourwing saltbush at Jericho likewise increased to a greater extent in NH than NL (see Fig. 3, Table 3) despite being seeded at identical rates in these two treatments (see Table 2). On the other hand, squirreltail at Jericho had noticeably lower cover in NH (relative cover: 3% in 2002, < 1% in 2015) than NL (relative cover: 8% in 2002, 5% in 2015) (see Fig. 3, Table 3), even though it had not been seeded in the latter treatment. Relative cover of smooth brome and crested/Siberian wheatgrass also increased significantly in NL at the Mud Springs and Jericho, respectively (Fig. 3), even though these species were not part of the NL seed mix.

Discussion

Following 3 yr of vegetation monitoring, Thompson et al. (2006) concluded that postfire aerial- and drill-seeding treatments had for the most part been successful at establishing perennial species and suppressing exotic annuals. Above-average precipitation during the winter and early spring following seeding likely contributed to this outcome, as most successful seedings have historically occurred in

Table 5
Seeded species cover (%) and density (m⁻²), means ± standard errors, at drill blocks 4–5 in Tintic Valley, Utah, as recorded 3 years (2002) and 16 years (2015) following fire and seeding. Significant ($P < 0.05$) changes between years (Δ) are shown for each species and treatment (+ indicates increase; -, decrease). Underlined values indicate the species was seeded in a given treatment (see Table 1). Trace amounts of alfalfa, antelope bitterbrush, fourwing saltbush, forage kochia and thickspike wheatgrass are omitted from this table.

	ARS ¹		BLM		NH		NL		USC	
	2002	2015 (Δ)	2002	2015 (Δ)	2002	2015 (Δ)	2002	2015 (Δ)	2002	2015 (Δ)
Cover										
Basin wildrye	0.1 ± <0.1 ²	0	0	<0.1	0	0.2 ± 0.1 (+)	0	0	0	0
Bluebunch/S. R. wheatgrass	0	0	0.2 ± 0.2	0	0.4 ± 0.2	0.6 ± 0.4	<0.1	0.8 ± 0.6	0	0
Crested/Siberian wheatgrass	1.6 ± 0.3	13 ± 1.8 (+)	1.7 ± 0.4	6.7 ± 1.4 (+)	<0.1	0.1 ± 0.1	0	0.8 ± 0.3 (+)	0	1.0 ± 0.5 (+)
Indian ricegrass	0.1 ± <0.1	<0.1	0	0	1.3 ± 0.3	0 (-)	0.2 ± 0.1	0.2 ± 0.2	0	0
Needle-and-thread	0	0	0	<0.1	0.1 ± 0.1	6.0 ± 1.7 (+)	0	1.1 ± 0.8 (+)	0	0.4 ± 0.2
Pubescent wheatgrass	<0.1	0.3 ± 0.2	0.3 ± 0.2	9.7 ± 2.1 (+)	<0.1	0	0	<0.1	0	0
Russian wildrye	<0.1	0.2 ± 0.2	0.4 ± 0.3	1.5 ± 0.5 (+)	0	0	0	0	0	0
Sandberg bluegrass	0	0	0	0	<0.1	<0.1	0	0.1 ± <0.1 (+)	0	0
Squirreltail	0.1 ± 0.1	<0.1	0.2 ± 0.2	<0.1	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.1	2.3 ± 1.0 (+)	0.1 ± 0.1	2.0 ± 1.0 (+)
Tall wheatgrass	0	0	1.7 ± 0.5	0.2 ± 0.2 (-)	0.2 ± 0.2	0	0.3 ± 0.3	0	0	0
Western wheatgrass	0.5 ± 0.3	10 ± 3.4 (+)	1.3 ± 0.7	3.3 ± 1.4	0.2 ± 0.1	19 ± 4.0 (+)	0.4 ± 0.3	12 ± 2.8 (+)	0	<0.1
Wyoming big sagebrush	0	0	0	0	<0.1	0	0	0	0	0
Density										
Basin wildrye	<0.1	0	0	0	0	0.1 ± 0.1	0	0	0	0
Bluebunch/S. R. wheatgrass	0	0	0.1 ± 0.1	0	0.4 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0	0
Crested/Siberian wheatgrass	1.7 ± 0.4	8.2 ± 1.8 (+)	1.8 ± 0.4	3.5 ± 0.6 (+)	<0.1	0.1 ± 0.1	0	0.3 ± 0.1	0	0.4 ± 0.1
Indian ricegrass	0.1 ± 0.1	0	0	0	1.5 ± 0.4	0 (-)	0.2 ± 0.1	0.1 ± <0.1	0	0
Needle-and-thread	0	0	0	<0.1	0.1 ± 0.1	4.0 ± 0.9 (+)	0	0.6 ± 0.3	0	0.2 ± 0.1
Pubescent wheatgrass	<0.1	1.4 ± 1.2	0.3 ± 0.2	29 ± 6 (+)	0.1 ± 0.1	0	0	<0.1	0	0
Russian wildrye	0	0.1 ± 0.1	0.2 ± 0.1	0.7 ± 0.3 (+)	0	0	0	0	0	0
Sandberg bluegrass	0	0	0	0	<0.1	<0.1	0	0.1 ± 0.1	0	0
Squirreltail	0.1 ± 0.1	0	0.1 ± <0.1	<0.1	0.1 ± <0.1	0.3 ± 0.2	0.1 ± <0.1	1.9 ± 0.9 (+)	<0.1	1.2 ± 0.6 (+)
Tall wheatgrass	0	0	1.2 ± 0.4	0.1 ± 0.1 (-)	0.1 ± 0.1	0	0.3 ± 0.3	0	0	0
Western wheatgrass	0.6 ± 0.4	44 ± 12 (+)	4.0 ± 2.4	11 ± 3.8 (+)	0.4 ± 0.2	60 ± 15 (+)	1.3 ± 1.3	43 ± 10 (+)	0	<0.1
Wyoming big sagebrush	0	0	0	0	<0.1	0	0	0	0	0

¹ 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.

² Values less than 0.1 but greater than 0 are indicated by '<0.1'; otherwise values are rounded to the nearest tenth (if less than 10) or whole number (if greater than 10).

above-average precipitation years (Hardegreve et al., 2011). Although perennial establishment at Jericho was minimal in two of the five blocks and relatively low in the NL treatment, the overall pattern of high perennial establishment in seeding treatments (relative to USC, where exotic annuals were more abundant) was interpreted as a successful outcome (Thompson et al., 2006). Different seed mixes resulted in different plant assemblages, and some seeded species established more successfully than others, but the total amount of cover attained by seeded species was nevertheless similar across seeding treatments (Thompson et al., 2006). Thompson et al. (2006) also noted that seeded species and residual perennials were more abundant at Mud Springs, whereas annuals (mostly exotic annual forbs) were more abundant at Jericho by the end of their monitoring period. These site differences could have been partially due to different effects of aerial/chain versus drill-seeding techniques (e.g., different levels of seed burial and ground disturbance), but the experiment was not designed to compare effects of these seeding techniques, which are appropriate for different types of sites (Thompson et al., 2006; Wilder et al. in press).

Our reanalysis of third-yr (2002) data largely reconfirmed the results and conclusions of Thompson et al. (2006), even though we used a different statistical approach and a more complete data set that included previously omitted drill-seeded blocks. Because we grouped plants differently than Thompson et al. (2006), our results provide additional details regarding vegetation patterns at the study sites. We note that “residuals” recorded in the USC treatment by Thompson et al. (2006) were dominated by some of the same species that had been included in one or more of the seed mixes (e.g., western wheatgrass, Indian ricegrass, squirreltail, Sandberg bluegrass). Some of these seed-mix perennials recorded in USC could have inadvertently arrived from the

seeding treatments, especially with aerial seeding, where seed drift is possible. However, we suspect that many of them did in fact originate from residual populations that survived the fire, which means that residuals were likely also present in the seeded treatments and contributed to the “seed-mix” cover and density patterns we observed.

The effects of seeding were still evident in 2015 despite significant changes in plant cover and density. The overall increase in seeded perennial cover and persistence of many seeded species over the 2002–2015 interval demonstrates that postfire seedings can have lasting effects on vegetation composition and structure. Other studies evaluating long-term effects of postfire seedings or other seeding treatments in semiarid ecosystems have also shown increasing dominance of seeded species over time (e.g., Walker et al., 1995; Newman and Redente, 2001; Rinella et al., 2012; Pyke et al., 2013; Knutson et al., 2014; Wilder et al. in press), although long-term declines have also been documented (Rinella et al., 2012; Busby and Southworth, 2014). The outcome we observed, in which seedings shifted the successional trajectory toward dominance by seeded plants, indicates that at least some of the seeded species were well 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. Even in cases where initial establishment of seeded plants is minimal, as in Jericho blocks 4–5 of our study, the effect of those individuals that manage to establish (possibly combined with ungerminated seed) may be magnified over time if conditions favoring growth and recruitment subsequently arise.

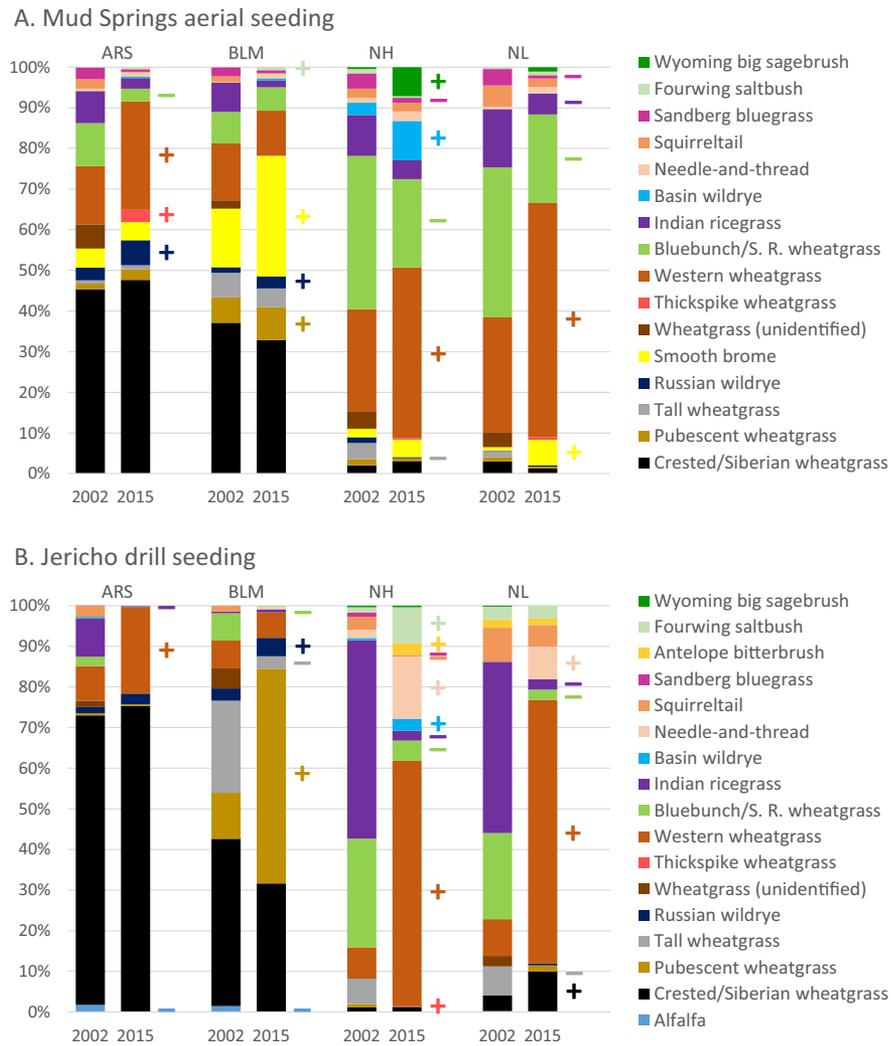


Figure 3. Relative cover of seeded species and groups (percent of total by treatment and year) at sites in Tintic Valley, Utah, as recorded 3 yr (2002) and 16 yr (2015) after fire and seeding. **A,** Mud Springs aerial seeding site; **B,** Jericho drill seeding site. Symbols “+” and “-” indicate significant ($P < 0.05$) increase or decrease, respectively, in relative cover between 2002 and 2015 for species/treatment to left of symbol. Significant decreases of unidentified wheatgrass due to improved identification in 2015 are not shown. Treatments: ARS indicates Agricultural Research Service mix; BLM, Bureau of Land Management mix; NH, Native high diversity mix; NL, Native low diversity mix.

Results for Jericho blocks 4–5, where seeded plants increased to an unexpected degree, challenge the assumption that seedings with low initial establishment will inevitably remain “failures” in the absence of subsequent seeding attempts (Knutson et al., 2014; Ott et al., 2016). Although this assumption is clearly valid for many situations, our results highlight the possibility that marginally successful seedings can become measurably more successful over time. Because the long-term outcome of most “failures” and “partially successful” postfire seedings in the Great Basin has not been systematically documented (Pilliod et al., 2017), the extent to which such changes may have occurred elsewhere in the region is currently unknown.

In the absence of seeding, natural succession can be disrupted by exotic annuals, especially in areas where exotic annual propagule pressure is high and postfire recovery of native perennials is delayed (Young and Evans, 1978; D’Antonio and Vitousek, 1992; Reisner et al., 2013; Chambers et al., 2016; Davies et al., 2019). The USC treatment at Jericho showed this tendency for exotic annual invasion, with cheatgrass becoming codominant with Russian thistle and other exotic annual forbs by 2015. Cheatgrass also increased between 2002 and 2015 at Mud Springs, but not to the same extent as at Jericho and without the accompanying exotic annual forbs. Mud Springs also differed from Jericho in having higher perennial cover in the USC treatment. These patterns indicate that the higher-elevation Mud Springs site had higher resilience

to fire disturbance and resistance to exotic annual invasion, possibly due to a more favorable growing regime and greater abundance of residual native perennials (Chambers et al., 2014; Miller et al., 2015; Ellsworth et al., 2016).

In 2015, at both sites, exotic annual cover was lower in the seeding treatments than USCs, indicating that seed-mix species continued to suppress exotic annuals beyond the early postfire years. Above-average spring precipitation in 2015 (117–125 mm; see Fig. S1) may have favored growth of cheatgrass and other cool-season annuals and thus accentuated this contrast. 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 ($\approx 60\%$) where cheatgrass dominance is especially likely to increase the risk of fire (Pellant and Hall, 1994; Balch et al., 2013). Although we did not directly measure fuel characteristics such as biomass, continuity, and moisture content, we assume that reductions in cheatgrass cover indicate that seeding treatments had lower fine fuel loads and lower susceptibility to fire ignition and spread than USC treatments (Davies and Nafus, 2013).

The degree of exotic annual suppression was generally higher in the mixes with introduced species (ARS, BLM) than in the native-only mixes (NH, NL), possibly due to greater competitiveness of the introduced species. Previous work has demonstrated that introduced

perennial grasses, including species and varieties of the ARS and BLM mixes such as Hycrest crested wheatgrass, can be strong competitors against exotic annuals (Aguirre and Johnson, 1991; Francis and Pyke, 1996; Whitson and Koch, 1998; Ott et al., 2003; Davies and Johnson, 2017). Certain native perennials have also been shown to be competitive and capable of suppressing exotic annuals (Booth et al., 2003; Porensky et al., 2014; Ott et al., 2016; Davies and Johnson, 2017). At Mud Springs, we found that the native-only mixes were equally effective as the ARS/BLM mixes at suppressing exotic annual forbs and nearly as effective (differing by ca. 2% cover) at suppressing exotic annual grasses (i.e., cheatgrass). At Jericho, exotic annual grass cover in 2015 was ca. 4% higher in the native-only mixes than ARS/BLM, suggesting that the native-only mixes were less effective at suppressing exotic annual grasses at a site where exotics had a stronger foothold, although exotic annual grass cover was still reduced by ca. 9% in the native-only mixes compared with USCs. Exotic annual forbs at Jericho were also suppressed in a manner similar to exotic annual grasses, except that the NH mix performed just as well as the ARS and BLM mixes. These results suggest that mixes containing competitive introduced species may be appropriate for areas where the risk of exotic annual invasion is high and maximal suppression is desired, but that in other circumstances, native-only mixes can be a viable alternative for suppressing exotic annuals. It may be possible to optimize native seed mixes to meet weed suppression objectives by increasing seeding rates, as exemplified by the NH mix, and/or by using native plant materials selected for competitive ability against exotic annuals (Goergen et al., 2011; Barak et al., 2015).

In practice, seed mixes used in ES&R seedings have nearly always included introduced grass species, particularly *Agropyron* spp. such as crested wheatgrass and Siberian wheatgrass, while the frequency of native seedings has been low and has only increased recently (Knutson et al., 2014; Pilliod et al., 2017). Lower monetary cost appears to be one of the main reasons that introduced species have been preferred over natives, although our examination of seed mix costs in 1999 versus 2017 indicates that native seed is currently more affordable than it once was for many species. The added cost of native seed may be worth the investment if long-term management goals include priorities for which native mixes are better suited, such as the recovery of plant communities that support wildlife habitat (Arkle et al., 2014; Dumroese et al., 2015; Finch et al., 2016). Previous studies have pointed out that plants native to western North America can be adversely affected by competition with introduced grasses (Marlette and Anderson, 1986; Walker et al., 1995; Gunnell et al., 2010; Salesman and Thomsen, 2011; Nafus et al., 2015; McAdoo et al., 2017; Ott et al., 2017a), and once established, competitive introduced grasses may be difficult to remove or control (Hulet et al., 2010; Salesman and Thomsen, 2011; Davies et al., 2013; McAdoo et al., 2017), so managers should be cautious about seeding these grasses at sites where natural vegetation recovery is a long-term objective.

Competitive interactions between introduced and native perennial grasses (Walker et al., 1995; Waldron et al., 2005; Nafus et al., 2015) may account for some of the changes in grass species abundance and dominance we observed, but more generally, these changes can be attributed to species' differing abilities to thrive and compete under site conditions. Some of the plant materials that were seeded may have been poorly adapted for long-term persistence at the study sites, possibly as a consequence of nonlocal origin, leading to declining abundance of established plants over time (Millar and Libby, 1989; Bennington et al., 2012). For example, the bluebunch and Snake River wheatgrass varieties used in this study all originated from southeastern Washington (Monsen et al., 2003) and are genetically and adaptively distinct from local populations in western Utah (Larson et al., 2004; St. Clair et al., 2013; Massatti et al., 2018), suggesting that varieties that were more closely matched to environments similar to the Tintic Valley may have performed better. This could also be the case with Indian ricegrass because both seeded varieties originated outside of the Great Basin (Ogle

et al., 2013). Squirreltail performed better in USC and NL, where its presence was likely due to locally adapted residual populations, than in NH, where it had been seeded. On the other hand, rhizomatous species (pubescent wheatgrass, smooth brome, and western wheatgrass) tended to show large increases in cover between 2002 and 2015 in the mixes where they were seeded, as well as some plots where they were not seeded. Although these species were not the only notable increasers in this study, the fact that all three seeded rhizomatous species performed well may indicate that rhizomatous spread is a key trait fostering population growth in Great Basin ecosystems. 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. The period between 2002 and 2015 was a fairly dry period with several extended droughts (see Fig. S1; Table S2). Western wheatgrass tended to have a large increase in relative cover, especially in the native seedings, suggesting that it may be highly competitive with other seeded species. This may or may not be desirable depending on management goals.

One of the concerns related to the use of competitive perennial grasses in postfire seedings is their potential competitive interference with shrubs that provide ecosystem services and habitat for wildlife (Arkle et al., 2014; Knutson et al., 2014; Porensky et al., 2014). To reduce competitive interference, shrub seeds can be placed in spatially segregated microsites, such as separate drill rows, when seeded simultaneously with competitive grasses (e.g., Brabec et al., 2015; Ott et al., 2016). This strategy was followed at the Jericho drill seeding and likely contributed to the successful establishment and subsequent increase of antelope bitterbrush and fourwing saltbush (though not Wyoming big sagebrush and forage kochia). Unexpectedly, antelope bitterbrush and fourwing saltbush were more successful in NH than NL at Jericho despite equivalent seeding rates. This result suggests that the net effect of higher cover and diversity of native perennial grasses in NH was positive rather than negative, possibly because perennial grasses shielded these shrubs from harsher competition with invasive annuals during the establishment phase (Holmgren, 1956; Hall et al., 1999). Other shrub species, in contrast, fared better in areas with fewer perennial grasses. We infer that seed-mix perennial grasses inhibited non-seed-mix shrubs at both study sites because these shrubs increased most in USCs where seed-mix grass cover was lowest. The non-seed-mix shrubs were primarily species such as rubber rabbitbrush, yellow rabbitbrush, broom snakeweed, and green ephedra that are known to readily colonize burned areas (West and Yorks, 2002; Thacker et al., 2008; Morris and Leger, 2016).

Wyoming big sagebrush is an important shrub of Great Basin ecosystems that generally recolonizes slowly after fire (Wambolt et al., 2001; Beck et al., 2009; Schlaepfer et al., 2014) and can be difficult to establish through seeding (Lysne, 2005; Brabec et al., 2015; Ott et al., 2017b). At Jericho, Wyoming big sagebrush was recorded in trace amounts only in treatments where it had been seeded (NH and NL), suggesting that residual seed sources were deficient and that seeding was only marginally effective, possibly due to suboptimal drill-seeding techniques (Ott et al., 2017b) or poorly adapted plant materials (Brabec et al., 2015). At Mud Springs, residual sagebrush seed was likely also in short supply, but conditions favored establishment of seeded Wyoming big sagebrush. During the span of the study, many recently established Wyoming big sagebrush plants at Mud Springs matured and probably became seed sources for new recruitment (Schlaepfer et al., 2014). Wyoming big sagebrush increased in two treatments at Mud Springs: NH, where it had been seeded at a high rate, and USC, where its presence was likely due to seed drift from adjacent seeded treatments. Assuming seed drift occurred, Mud Springs USC can be viewed as an unintentional aerial seeding of sagebrush that proved reasonably successful in a setting where chaining had not been implemented and competition from seeded perennial grasses was low. The lack of parallel sagebrush establishment in other treatments at Mud Springs where sagebrush was nominally not seeded (ARS and BLM) suggests that seed drift did not

affect these treatments to the same extent as USC and/or that seeded grasses in these treatments were inhibiting sagebrush (Blaisdell, 1949; Gunnell et al., 2010; Nafus et al., 2016). Competitive inhibition of sagebrush by seeded grasses may have also occurred in NL, resulting in minimal sagebrush establishment despite seeding, and in NH, where a higher seeding rate may have partially compensated for competitive losses by ensuring that more seeds reached open microsites within the matrix of establishing seeded grasses (Ott et al., 2017b). Our interpretation is that seeded grasses can limit sagebrush establishment, but this limitation can be overcome with high seeding rates, at least when competition with coseeded grasses is not too severe. There may be a trade-off in seed-mix design between mixes that optimize exotic annual suppression and mixes that allow for adequate sagebrush recruitment, due to the competitive spectrum of perennial grasses that are used (Porensky et al., 2014; Nafus et al., 2016). This relationship should be studied further.

Implications

This study shows that postfire 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 postfire seedings whenever possible. Studies like this one can help in predicting future succession in postfire seedings. Lessons from this study are as follows: 1) Conventional mixes containing introduced species can be effective for long-term suppression of exotic annuals. In areas where exotic annual suppression overrides other management concerns, their continued use may be warranted. 2) Native seed mixes can establish, persist, and suppress invasive annuals nearly as effectively as conventional seed mixes. Thus, as more native seed enters the market and reduces costs, native mixes may be seen as a viable option for post-fire seeding. 3) Some seeded species and germplasm 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. In addition, some species, such as Indian ricegrass and bluebunch wheatgrass, declined over time. This could be due to competition with other seed-mix species or adaptive mismatch to site conditions. 4) Seeded stands containing competitive perennial grasses may interfere with recruitment of other seeded and nonseeded species, including shrubs. While these perennial grasses can be highly effective at suppressing exotic annuals, suppression of shrub recruitment could lead to a long-term trade-off and should be taken into consideration. If sagebrush is included in seed mixes containing these grasses, high seeding rates may be necessary to ensure sagebrush establishment.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.rama.2019.02.001>.

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