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Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems

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Summary

1. Invasive annual grasses alter fire regimes in shrubland ecosystems of the western USA, threatening ecosystem function and fragmenting habitats necessary for shrub-obligate species such as greater sage-grouse. Post-fire stabilization and rehabilitation treatments have been administered to stabilize soils, reduce invasive species spread and restore or establish sustainable ecosystems in which native species are well represented. Long-term effectiveness of these treatments has rarely been evaluated.

2. We studied vegetation at 88 sites where aerial or drill seeding was implemented following fires between 1990 and 2003 in Great Basin (USA) shrublands. We examined sites on loamy soils that burned only once since 1970 to eliminate confounding effects of recurrent fire and to assess soils most conducive to establishment of seeded species. We evaluated whether seeding provided greater cover of perennial seeded species than burned–unseeded and unburned–unseeded sites, while also accounting for environmental variation.

3. Post-fire seeding of native perennial grasses generally did not increase cover relative to burned–unseeded areas. Native perennial grass cover did, however, increase after drill seeding when competitive non-natives were not included in mixes. Seeding non-native perennial grasses and the shrub *Bassia prostrata* resulted in more vegetative cover in aerial and drill seeding, with non-native perennial grass cover increasing with annual precipitation. Seeding native shrubs, particularly *Artemisia tridentata*, did not increase shrub cover or density in burned areas. Cover of undesirable, non-native annual grasses was lower in drill seeded relative to unseeded areas, but only at higher elevations.

4. *Synthesis and applications*. Management objectives are more likely to be met in high-elevation or precipitation locations where establishment of perennial grasses occurred. On lower and drier sites, management objectives are unlikely to be met with seeding alone. Intensive restoration methods such as invasive plant control and/or repeated sowings after establishment failures due to weather may be required in subsequent years. Managers might consider using native-only seed mixtures when establishment of native perennial grasses is the goal. Post-fire rehabilitation provides a land treatment example where long-term monitoring can inform adaptive management decisions to meet future objectives, particularly in arid landscapes where recovery is slow.

Key-words: aerial seeding, *Artemisia tridentata*, *Bromus*, cheatgrass, drill seeding, exotic annuals, non-native annuals, restoration, sagebrush, semi-arid

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Introduction

Ecosystems throughout the world have evolved with periodic disturbance from wildfire, and the extent to which humans manage burned landscapes can have a wide range of ecological and economic consequences (Bowman *et al.* 2011). Introduction of non-native annual grasses has increased the frequency and size of fires, often resulting in dominance of non-native grasses via positive feedbacks (Balch *et al.* 2013). Alteration of fire regimes is expected to continue and may intensify as atmospheric CO_2 increases (Ziska, Reeves & Blank 2005). If left unchecked, wildfire can potentially convert landscapes into novel ecosystems (Brooks *et al.* 2004), increase erosion (Pierson *et al.* 2011) and decrease biological diversity (Davies 2011) or critical wildlife habitat (Knick *et al.* 2003).

Wildfires currently burn two million hectares per year within the Great Basin (US National Interagency Fire Center, 2001–2012 eastern and western Great Basin; http://www.nifc.gov/fireInfo/fireInfo_stats_lightng.html accessed 22 July 2013). Much of this area is managed by the Bureau of Land Management (BLM), which implements an emergency stabilization and rehabilitation (ESR) programme to mitigate potential negative effects of wildfire in Great Basin shrublands. Methods often include aerial or drill seeding with native and non-native perennial grasses, forbs and shrubs. Treatment objectives are to decrease soil erosion, increase desirable perennial plant cover (typically deep-rooted perennial grasses and shrubs), improve wildlife habitat and reduce abundance of invasive plants, particularly non-native annuals (USDI BLM 2007).

Current ESR policy mandates that post-seeding effectiveness monitoring be conducted during the first 3 years after seeding (USDI BLM 2007). Although monitoring programmes can detect initial establishment of seeded species, 3 years is typically insufficient to determine effects on relative species dominance or long-term community trajectories. Few studies have evaluated ecological effects of post-fire seeding in non-forested regions (Pyke, Wirth & Beyers 2013). ESR seeding applications, either owing to techniques used or species sown, may result in unintended consequences that do not become apparent within 3 years. Relative abundance of perennial vs. annual plant species (primarily non-native annual grasses) may strongly influence future fire behaviour by inadvertently modifying fuel loads (Scott & Burgan 2005). In addition, perennial herbaceous species and bare ground are primary determinants of resistance to non-native annual species (Chambers *et al.* 2014) and soil erosion in desert shrublands (Sankey *et al.* 2011); however, if seeding methods result in undesirable impacts on these variables, ESR seeding may have the opposite effect of management objectives. Long-term effectiveness monitoring of ESR treatments also provides an opportunity to inform adaptive management (Williams 2011).

To address these information needs, we quantified vegetation composition at 88 ESR sites within Great Basin shrublands of the semi-arid western USA. Our primary goal was to determine post-fire seeding effects on patterns of cover and density of seeded life forms, cover of undesirable non-native life forms (primarily annual bromes and forbs) and cover of bare ground that would inform future adaptive management decisions. We also investigated the influence of annual precipitation, elevation, topography (i.e. heat load) and time since treatment on ESR seeding outcomes across the study area.

Materials and methods

STUDY SITES AND DATA COLLECTION

We collected ESR records from 19 BLM offices in Idaho, Nevada, Oregon and Utah, and organized it in a geodatabase (Pilliod & Welty 2013) to stratify projects across the Great Basin, USA. Data sufficient to determine the location and basic characteristics (e.g. planned or actual species sown) of seeding treatments were generally available to 1990. Potential ESR sites were stratified by major land resource areas (USDA NRCS 2006), age since seeding and mean annual precipitation and correlated to shrub-dominated ecological sites as defined by USDA NRCS (http://www.nrcs.usda.gov/wps/portal/nrcs/detail/national/landuse/rangepasture/?cid = stelprdb1068392 accessed 17 September 2013). Aerial and drill seeding sites were randomly selected from each stratum and restricted to sites with a single wildfire since 1970 to minimize confounding from repeated burning and seeding. We also restricted sites to loam-type surface textures. This selection process resulted in 100 sites where post-fire seeding was implemented from 1990 to 2003 (Fig. 1; see Table S1, Supporting information). Of these, 27 were aerial and 61 were drill seeding applications (Table 1). Twelve were combinations of aerial-over-drill (AOD) seeding methods (see Table S1, Supporting information) and were not evaluated for purposes of this paper. Although BLM implemented numerous aerial seeding applications during the period of interest, many were not sampled because they were inaccessible, rocky or were in non-shrub communities, which reduced our sample size relative to drill seeding sites.

Within each ESR site, burned–seeded (BS), burned–unseeded (BX) and unburned (UX) treatments were delineated on areas occurring on similar soil map unit components, slopes, aspects and ecological sites. This within-site stratification ensured that potential plant composition and biomass were equivalent across treatments within a site. BX areas were typically located very near (<1 km) or adjacent to BS areas, but were unseeded for various reasons (e.g. land ownership differed, cultural protection or stones preventing equipment access). Within each treatment area, potential plot locations were randomly generated and then visited in random order until three were identified that met within-site stratification criteria. Plots at each ESR project were within close proximity (2–4 km) and had similar livestock grazing histories with the majority (81%) in a single grazing allotment (pasture).

Each plot comprised three 50-m transects in an equally spaced spoke design. Percentage cover of biotic and abiotic components was collected using line-point intercept at 1-m intervals along each transect (Herrick *et al.* 2005). Shrub density by species was

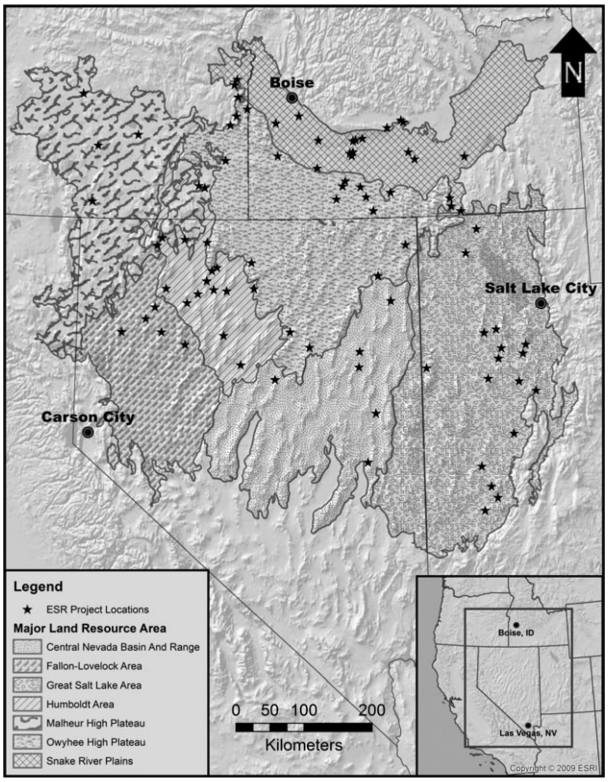

Fig. 1. Locations of Emergency Stabilization and Rehabilitation post-fire seeding sites in Oregon, Idaho, Nevada, and Utah, USA.

Table 1. Number of aerial and drill seeding sites within each major land resource area and their mean elevation and annual precipitation (1 SE)

Major land resource area	Aerial	Drill	Mean elevation (m)	30-year mean annual precipitation (cm)
Central Nevada Basin & Range	3	4	1861 (78)	29·6 (3·7)
Fallon-Lovelock	1	4	1518 (131)	23·5 (5·7)
Great Salt Lake	9	10	1593 (126)	32·0 (4·4)
Humboldt	3	9	1437 (92)	25·1 (3·0)
Malheur High Plateau	2	7	1393 (93)	25·7 (2·6)
Owyhee Plateau	7	13	1457 (183)	29·1 (4·0)
Snake River Plains	2	14	1183 (267)	27·9 (2·8)
Total sites	27	61	1449 (16)	28·4 (0·3)

measured using 2- or 6-m by 50-m belt sampling transects. The 6-m belt was used at BS and BX plots where shrub density was low. Data were collected from April through August of 2011.

DATA ANALYSIS

Vegetation responses were analysed using linear mixed effects modelling (Zuur *et al.* 2009). We first compared cover of all perennial species and cover of all perennial grasses among treatments to identify any general seeding effects or patterns. We then compared seeded species grouped into life form classifications to test for effects resulting from seeding (Table 2; see Tables S2 and S3, Supporting information). If a life form was only seeded at a subset of sites, then only those seeded sites were analysed; this resulted in variable sample sizes (Table 2). Seeded perennial grass species were grouped into native or non-native deep-rooted perennial grasses (DRPG) and *Poa secunda* J. Presl., a shallow-rooted native perennial grass. Native seeded shrubs consisted primarily of species in genera *Artemisia* and *Atriplex* (see Table S3, Supporting information). Density and percentage cover of *Artemisia tridentata* Nutt. were examined, but subspecies were not separated for analyses. At sites seeded with native, non-*Artemisia* shrub species (*Atriplex*, *Purshia* and others), total native shrub cover was evaluated. Cover of *Bassia prostrata* (L.) A.J. Scott was evaluated because it was the only seeded non-native shrub. Non-native PF, although seeded extensively (Table 2), was detected in very low amounts (e.g. cover present at only four of 45 drill sites) and were not analysed. Non-native annual grasses were primarily from the genus *Bromus* and were grouped and evaluated as annual bromes (AB). *Bromus tectorum* L. occurred at all sites, whereas *B. arvensis* L., *B. diandrus* Roth and *B. hordeaceus* L. occurred at two, one and two sites, respectively (see Table S4, Supporting information).

Each response variable was evaluated with treatment (BS, BX and UX) as the primary fixed effect. Random effects were MLRA and ESR site within MLRA, in accordance with a split-plot, stratified design. Plots within each treatment at ESR sites were averaged before analysis. Linear models were developed for each response variable using backward elimination from a full model that included treatment, 30-year mean annual precipitation, age of seeding, elevation, heat load and all second-order interaction effects (Zuur *et al.* 2009) to identify potential covariates influencing any observed treatment effects. Mean annual precipitation of plots (1971–2000) was determined from PRISM (2010). Heat load (McCune & Keon 2002) is a unit-less index derived from latitude, slope and aspect. Elevation and 30-year mean annual precipitation were correlated ($r = 0{\cdot}40$, $P < 0{\cdot}01$), but both were retained in model selection to identify potential predictors of ESR success. Although other fine-scale predictors

Table 2. Summary of seeded life forms evaluated using linear mixed modelling. Mean ($\overline{X}$) number of species seeded in each life form per site and the number of sites seeded

Life form seeded	Aerial		Drill	
	Species seeded ($\overline{X}$)	No. of sites (%)	Species seeded ($\overline{X}$)	No. of sites (%)
Native DRPG	1·5	16 (59)	1·6	42 (69)
Non-native DRPG	1·1	13 (48)	1·7	50 (82)
Poa secunda	0·1	3 (11)	0·2	10 (16)
Artemisia tridentata	0·7	18 (67)	0·7	32 (52)
Other native shrubs	0·7	16 (59)	0·4	21 (34)
Bassia prostrata	0·4	11 (41)	0·4	22 (36)
Native PF	0·3	7 (26)	0·4	21 (34)
Non-native PF*	0·8	13 (48)	1·1	45 (74)

DRPG, deep-rooted perennial grass; PF, perennial forb; AF, annual forb.
*Non-native PF was not evaluated – see Materials and methods.

(e.g. post-seeding seasonal precipitation) may have proven useful, we limited covariates to easily determined features (i.e. elevation, heat load) or variables used in stratification (i.e. annual precipitation and age). At each iterative step, nested, reduced models were developed and Bayesian information criterion (BIC) was calculated and compared. A reduced model with the lowest BIC was selected until BIC was no longer reduced by further removal of predictor variables (Table 2). To avoid over-fitting of rarely seeded life forms (20 sites or less), the base model initially included treatment only. Environmental covariates were then added successively until BIC was no longer reduced. *Poa secunda* was a prominent native plant on nearly all sites, but was seeded infrequently (Table 2), so a means-only model of cover was compared among treatments. Response variables were log-transformed as necessary to meet model assumptions, and results presented were back-transformed from predicted means and variances. R computer software was used for statistical computations and linear mixed modelling (R Development Core Team 2012). *T*-statistics and associated *P*-values from linear mixed models are reported for differences between treatments and for coefficients or covariates where appropriate. Modelled relationships and 95% confidence intervals are presented for life form or abiotic responses that had significant ($P < 0{\cdot}1$) treatment or environmental covariation.

Results

CHARACTERISTICS OF SEEDING TREATMENTS

Post-fire aerial and drill seeding treatments were sown with an average of 5·6 and 6·5 species per site (Table 2). Older ESR sites typically had more non-native species in seed mixes than natives, with native species becoming more prevalent at younger sites (see Fig. S1, Supporting information). *Pseudoroegneria spicata* (Pursh) A. Löve and *Agropyron desertorum* (Fisch. ex Link) J.A. Schult. were the most frequently seeded native and non-native DRPG species in both aerial and drill seeding treatments (see Table S2, Supporting information). *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young and *B. prostrata* were the most frequently seeded native and non-native shrubs (see Table S3, Supporting information). Fourteen different native and non-native perennial forb species were seeded; *Achillea millefolium* L. and *Medicago sativa* L. were the most frequently sown species (see Table S3, Supporting information).

Aerial and drill seeding sites ranged from 8 to 21 years since seeded. Mean age of drill and aerial seeding treatments (12·8 and 12·3 years) were similar (see Fig. S1, Supporting information). Aerial seeding sites averaged slightly more annual precipitation than drill seeding sites (29·2 vs. 28·2 cm), but ranges sampled were similar (20·9–41·2 and 20·1–42·6 cm in aerial and drill-seeded areas). Average elevation in aerial seeding areas was over 100 m greater than in drill seeding sites (1548 m vs. 1436 m), but elevation range was similar in both seeding types (897–1956 and 872–1965 m in aerial and drill seeding, respectively). Mean heat load was very similar in aerial (0·94) and drill (0·93) seeding areas.

RESPONSES OF PERENNIAL SPECIES TO SEEDING

At aerial seeding sites, total perennial cover was dependent on age and elevation, and effects of these covariates were interdependent (Table 3; see Fig. S2, Supporting information). Cover of all perennials at aerial seeding sites was not different in BS compared to BX treatments ($t_{44} = 0{\cdot}42$, $P = 0{\cdot}68$). Older burned areas (>12 years) at lower elevations (<1400 m) regardless of seeding treatment tended to lack perennial plant cover. At median sample age (12 years), perennial cover of all aerial treatments increased with elevation, and both burn treatments consistently had less perennial cover than the UX treatment (Fig. 2a). Patterns of perennial cover in drill seeding sites were also complex with several persistent environmental covariates and multiple interactions between predictors (Table 3). At intermediate levels of heat load (0·94) and elevation (1400 m), perennial cover increased with precipitation in all treatments, but this effect was most pronounced in the BS treatment (Fig. 2b). Perennial grass cover at aerial seeding sites was dependent on age, elevation and heat load (Table 3; see Fig. S3, Supporting information). No difference in aerial-seeded perennial grass cover was found in the BS treatment relative to either BX ($t_{43} = 0{\cdot}05$, $P = 0{\cdot}96$) or UX areas ($t_{43} = 0{\cdot}35$, $P = 0{\cdot}73$). Similar to total perennial cover, perennial grass cover was minimal in older aerial seeding treatments (>12 years) at lower elevations (<1350 m; See Fig. S3, Supporting information). At intermediate sampling levels of age and heat load (12 years and 0·94), cover of perennial grass increased with elevation on aerial seeding treatments (Fig. 2c). Perennial grass cover at drill seeding sites was dependent on precipitation and heat load, and the effect of precipitation was also dependent on treatment type (Table 3). At intermediate heat load, cover of perennial grass in BS plots increased rapidly with precipitation (Fig. 2d) and was greater than BX or UX levels when mean annual precipitation was above *c.* 28 cm.

Cover of native DRPG did not differ between BS and BX plots after aerial seeding ($t_{26} = 0{\cdot}96$, $P = 0{\cdot}35$, Fig. 3a) but did increase with elevation regardless of treatment ($t_{26} = 2{\cdot}54$, $P = 0{\cdot}02$, Table 3). Cover of non-native DRPG on aerial seeding sites was positively correlated with mean annual precipitation ($t_{17} = 6{\cdot}28$, $P < 0{\cdot}01$, Table 3); it increased exponentially with mean annual precipitation and became higher than unseeded areas around 28 cm mean annual precipitation (Fig 3b). No native DRPG cover was found in seeded treatments at two sites (mean precipitation: 28·3 cm) seeded aerially with only native DRPG (see Fig. S4a, Supporting information). When native DRPG were sown along with non-native perennial grasses or shrubs (13 sites), native DRPG cover did not differ from BX treatments (BS:BX 6:8%; $t_{21} = 1{\cdot}01$, $P = 0{\cdot}32$, see Fig. S4b, Supporting information). Cover of *P. secunda*, when aerial seeded, was not significantly different between BS and BX treatments ($t_3 = 0{\cdot}56$, $P = 0{\cdot}62$; see Fig. S5a, Supporting information).

Table 3. Final linear mixed effects models used to evaluate vegetation responses of ESR seedings. Sample sizes (*n*) are number of seeding sites evaluated for each response and were restricted to sites sown with the life form

Seeding type	Response variable (% cover unless otherwise noted)*	Final model explanatory fixed effects†	ΔBIC‡
Aerial	Total perennial (n = 27)	Treatment, age (−), elevation (−), age × elevation	41·0
	Perennial grass (n = 27)	Treatment, age (−), elevation (−), heat load (−), age × elevation	42·0
	Native DRPG (n = 16)	Treatment, elevation (+)	2·0
	Non-native DRPG (n = 13)	Treatment, ppt. (+), treatment × ppt.	21·4
	Poa secunda (n = 3)	Treatment	–
	Native SH (n = 16)	Treatment	–
	Bassia prostrata (n = 11)	Treatment, elevation (+)	1·4
	Artemisia tridentata (n = 18)	Treatment	–
	Artemisia tridentata density (n = 17)	Treatment, heat load (−)	5·6
	Native PF (n = 7)	Treatment	–
	AB (n = 27)	Treatment, ppt. (−), heat load (+)	46·8
	Non-native AF (n = 27)	Treatment, elevation (+), heat load (+), heat load × elevation	41·8
	Bare ground (n = 27)	Treatment	57·9
Drill	Total perennial (n = 61)	Treatment, ppt. (−), elevation (+), heat load (−), treatment × ppt., Treatment × heat load, ppt. × elevation, ppt. × heat load	36·1
	Perennial grass (n = 60)	Treatment, ppt. (−), heat load (−), treatment × ppt., ppt. × heat load	50·5
	Native DRPG (n = 42)	Treatment	67·3
	Non-native DRPG (n = 50)	Treatment, ppt. (+), age (+), elevation (−), heat load (−), treatment × ppt., elevation × heat load	36·8
	Poa secunda (n = 10)	Treatment	–
	Native SH (n = 21)	Treatment	–
	Bassia prostrata (n = 22)	Treatment, elevation (+)	0·8
	Artemisia tridentata (n = 31)	Treatment	57·3
	Artemisia tridentata density (n = 32)	Treatment	72·4
	Native PF (n = 7)	Treatment, ppt. (+), elevation (−), heat load (+), treatment × ppt., treatment × elevation, treatment × heat load	21·2
	AB (n = 61)	Treatment, elevation (−), treatment × elevation	40·1
	Non-native AF (n = 60)	Treatment	64·0
	Bare ground (n = 61)	Treatment, age (+), elevation (+), treatment × age	54·1

DRPG, deep-rooted perennial grass; SH, shrub; PF, perennial forb; AB, annual *Bromus* species; AF, annual forb.
*Outliers were removed when necessary, and some sample sizes do not match Table 2.
†ppt. = 30-year mean annual precipitation; (+/−) indicates sign of relationship between response and explanatory variables.
‡Values of ΔBIC indicate differences in Bayesian information criterion between final and initial models used in stepwise selections.

Drill seeding had little effect on cover of native DRPG when averaged across sites (Fig. 3c). However, when native DRPG was sown without non-native perennial grasses or shrubs, native cover was significantly higher in BS than BX treatments (18 vs. 9%) (t_{11} = 2·77, P = 0·02; see Fig. S4c, Supporting information). At 34 drill sites where native DRPG were seeded along with non-native perennial grasses or shrubs, native DRPG cover was low in BS treatments (2%) and did not differ from BX treatments (t_{58} = 0·62, P = 0·54). In contrast, non-native DRPG cover was 13% in BS treatments at these 34 sites (see Fig. S4d, Supporting information). Drill seeding treatments sown with *P. secunda* (10 sites) had lower *P. secunda* cover in BS treatments (9%) than in BX treatments (16%) (t_{18} = 2·22, P = 0·04; see Fig. S5b, Supporting information). Non-native DRPG cover in drill seeding sites (BS) increased with mean annual precipitation (t_{77} = 3·19, P < 0·01, Fig. 3d) and seeding age. Elevation and heat load were inversely associated with non-native DRPG cover and interacted with one another to influence cover (Table 3). At median age (12 years), elevation (1400 m) and heat load (0·94), drill seeding of non-native DRPG increased cover relative to BX areas when mean precipitation was greater than 23 cm (Fig. 3d).

Seeding native shrubs had little effect on shrub cover (Figs 4 and 5). Subspecies of *A. tridentata* were sown at 18 and 32 aerial and drill seeding sites, but *A. tridentata* cover did not differ from comparable BX areas (t_{29} = 0·05, P = 0·96 and t_{51} = 0·60, P = 0·55 for aerial and drill seeding sites; Fig. 4a,b). A similar result was

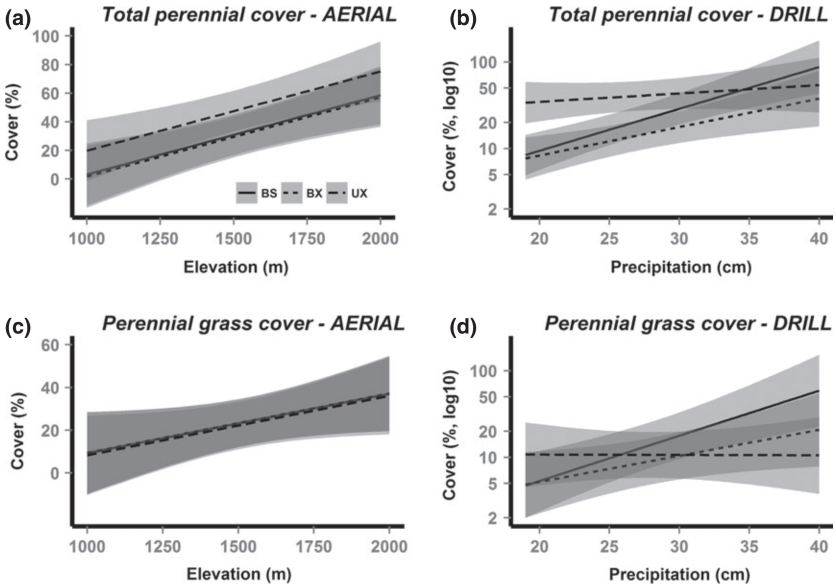

Fig. 2. Cover of all perennial life forms (a, b) and perennial grasses (c, d) in burned–seeded (BS), burned–unseeded (BX) and unburned (UX) treatments at aerial and drill projects. Other significant model covariates not shown (Table 3) were held constant at intermediate values (precipitation: 28 cm, age: 12 years, elevation: 1400 m, heat load: 0·94). Different letters represent significant differences ($P < 0{\cdot}05$) between treatments. Shaded bands are 95% confidence intervals, and darker areas represent overlap.

found for *A. tridentata* density in aerial and drill seeding sites (Fig. 4c,d). *A. tridentata* density in aerial seeding sites decreased in all treatments as heat load index increased ($t_{26} = 3{\cdot}17$, $P < 0{\cdot}01$; Fig. 4c). Sowing native shrubs other than *A. tridentata* also did not increase native shrub cover relative to BX areas (Aerial $t_{26} = 0{\cdot}31$, $P = 0{\cdot}76$; Drill $t_{33} = 0{\cdot}58$, $P = 0{\cdot}56$, Fig. 5a,b). Cover of the non-native shrub *B. prostrata* increased with elevation (Aerial $t_{16} = 1{\cdot}76$, $P = 0{\cdot}10$; Drill $t_{32} = 2{\cdot}19$, $P = 0{\cdot}04$; Fig. 5c,d) and both aerial and drill seeding (Aerial BS:BX $t_{16} = 3{\cdot}01$, $P < 0{\cdot}01$; Drill BS:BX $t_{32} = 2{\cdot}94$, $P < 0{\cdot}01$; Table 3).

Native PF cover was typically low (<5%) at aerial and drill projects. Native PF cover did not differ between BS and BX treatments at seven aerial seeding sites where this life form was seeded ($t_9 = 0{\cdot}56$, $P = 0{\cdot}59$), and no covariates affected this relationship (Table 3; see Fig. S6, Supporting information). At 20 drill locations seeded with native PF, cover was dependent on annual precipitation, elevation and heat load, and these relationships interacted with treatment type (Table 3; see Fig. S6, Supporting information). Native PF cover increased with increased precipitation, but little difference was found between BS and BX treatments at intermediate project elevation and heat load. Heat load was also positively associated with native PF cover at drill BS locations, whereas elevation was inversely related to cover of this life form.

RESPONSES OF NON-NATIVE ANNUALS & BARE GROUND TO SEEDING

Annual brome (AB) and non-native annual forb (AF) cover differed among treatments and with seeding method (Fig. 6). On aerial sites, AB and non-native AF cover

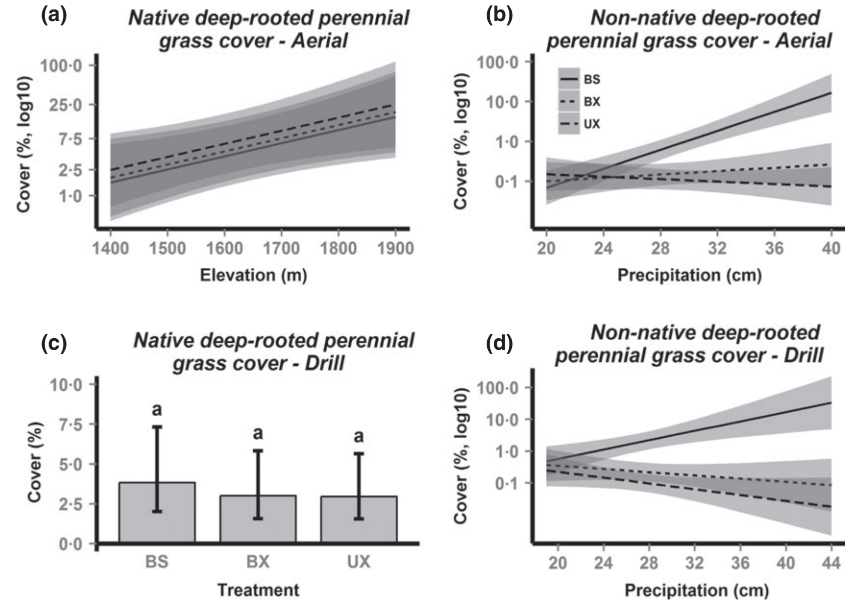

Fig. 3. Native and non-native deep-rooted perennial grass (DRPG) cover in burned–seeded (BS), burned–unseeded (BX) and unburned (UX) treatments at aerial (a, b) and drill (c, d) projects. For drill-seeded non-native DRPG (d), other significant model covariates (Table 3) were held constant at intermediate values (see Fig. 2). Different letters represent significant differences ($P < 0{\cdot}05$) between treatments. Shaded bands/bars are 95% confidence intervals, and darker areas represent overlap.

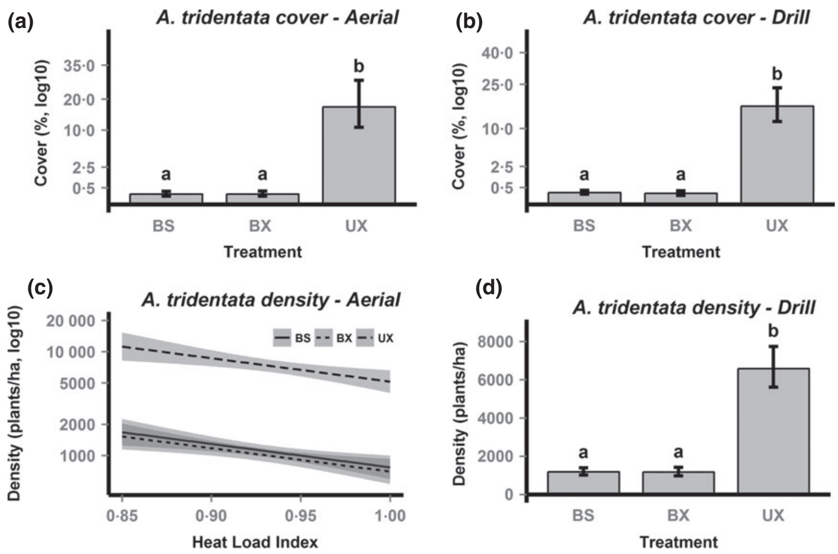

Fig. 4. *Artemisia tridentata* cover (a, b) and density (c, d) in burned–seeded (BS), burned–unseeded (BX) and unburned (UX) treatments at aerial and drill projects. Different letters represent significant differences ($P < 0{\cdot}05$) between treatments. Shaded bands/bars are 95% confidence intervals, and darker areas represent overlap.

were lower in UX than BS or BX treatments (Fig. 6a,c), and seeding had no effect on AB or non-native AF cover in the burn area (AB: $t_{44} = 1{\cdot}48$, $P = 0{\cdot}15$; non-native AF: $t_{43} = 0{\cdot}82$, $P = 0{\cdot}42$). Lower annual precipitation and higher heat loads increased AB cover at aerial sites (Table 3). AB cover at drill seeding sites decreased as elevation increased ($t_{98} = 4{\cdot}03$, $P < 0{\cdot}01$), and this relationship interacted with treatment (Table 3, Fig. 6b). Mean AB cover at 1000 m elevation was greater than 60% regardless of burning or drill seeding, but decreased more rapidly in BS and UX treatments than BX treatments as elevation increased (Fig. 6b). No environmental covariates affected cover of non-native AF at drill seeding sites (Table 3), and cover was reduced by nearly one-third in the seeded area (BS vs. BX: $t_{99} = 3{\cdot}09$, $P < 0{\cdot}01$; Fig. 6d).

Unburned areas had over twice the cover of bare ground found on burned areas at aerial seeding sites (Fig. 7a), and seeding had no impact on burned area bare ground cover (BS vs. BX; $t_{46} = 0{\cdot}62$, $P = 0{\cdot}54$). No covariates affected bare ground cover at aerial seeding sites (Table 3). Percentage bare ground in all drill treatments increased with elevation and age, but the effect of age was also treatment-dependent (Table 3). At young seeding age (8–12 years), bare ground was higher in BS treatments than in BX (Fig. 7b). At older ages (>12 years), predicted bare ground was similar in drill-seeded BS and BX treatments (see Fig. S7, Supporting information).

Discussion

Post-fire seeding applications had mixed effectiveness in meeting ESR objectives. Increased perennial cover from seeding was dependent on the life form seeded and the type of seeding implemented. Older aerial seeding sites at low elevations had little to no perennial cover, which may have resulted from poor seeding success followed by

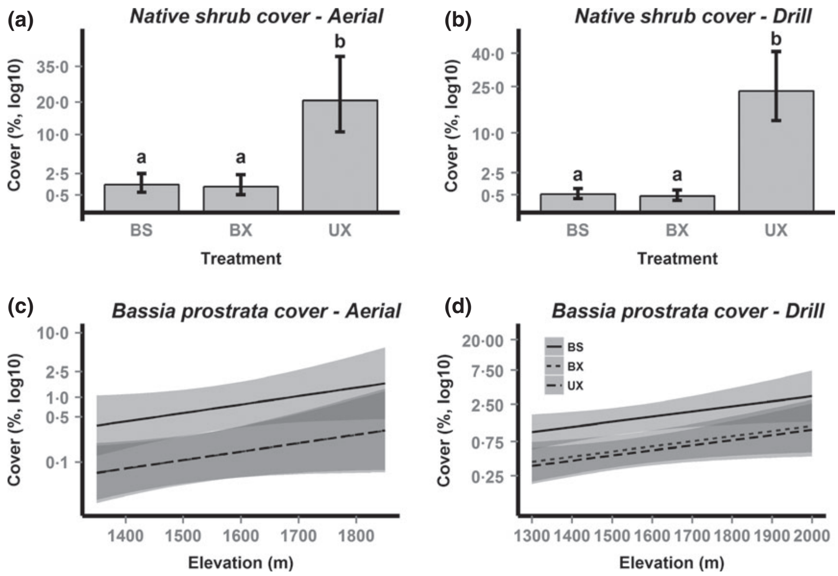

Fig. 5. Native shrub (a, b) and *Bassia prostrata* cover (c, d) in burned–seeded (BS), burned–unseeded (BX) and unburned (UX) treatments at aerial and drill seeding sites. Different letters represent significant differences ($P < 0{\cdot}05$) between treatments. Shaded bands/bars are 95% confidence intervals, and darker areas represent overlap.

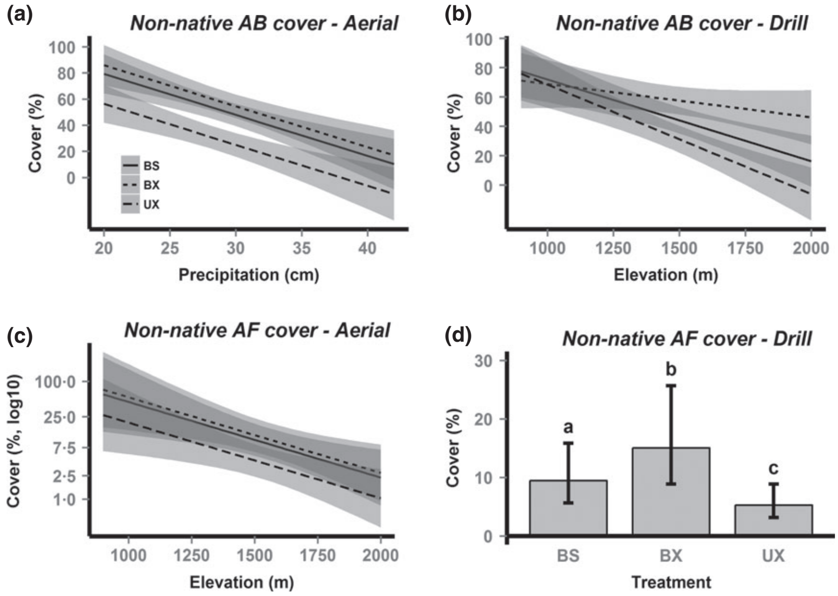

Fig. 6. Annual *Bromus* (AB) and non-native annual forb (AF) cover in burned–seeded (BS), burned–unseeded (BX) and unburned (UX) treatments at aerial (a, c) and drill (b, d) seeding sites. Heat load index at aerial seeding sites had a positive relationship with AB and non-native AF cover and was held constant (0·94) for predictions in (a) and (c). Different letters represent significant differences ($P < 0{\cdot}05$) between treatments. Shaded bands/bars are 95% confidence intervals, and darker areas represent overlap.

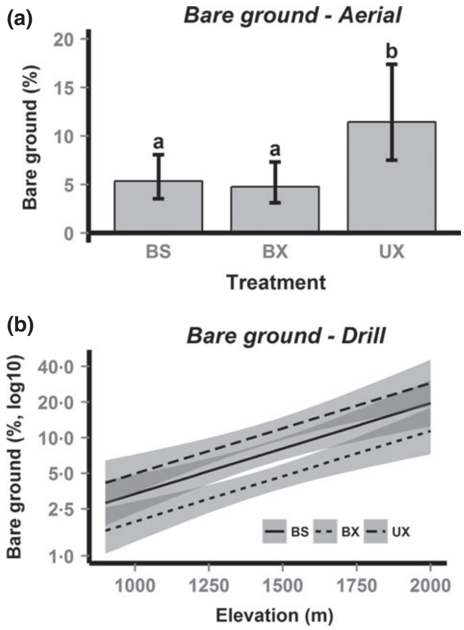

Fig. 7. Percentage bare ground (a, b) in burned–seeded (BS), burned–unseeded (BX) and unburned (UX) treatments at aerial and drill seeding sites. Age of seeding sites also had a significant relationship with percentage bare ground at drill seeding sites (Table 3) and was held constant (12 years since seeding) for predictions in (b). Different letters represent significant differences ($P < 0{\cdot}05$) between treatments. Shaded bands/bars are 95% confidence intervals, and darker areas represent overlap.

intense livestock grazing to reduce annual plant fuel loads. Sowing native perennial grasses after fires had little effect on long-term cover, regardless of precipitation or elevation. However, aerial and drill seeding sites with higher precipitation or elevation did increase non-native perennial grass cover. One explanation reasonably supported by our data is that non-native perennial grasses commonly used in post-fire seed mixes are more competitive than seeded native species (Chambers, Brown & Williams 1994). Competitive traits such as higher seed production and more rapid soil water extraction in non-native *A. desertorum* and *A. cristatum* (Eissenstat & Caldwell 1988; Pyke 1990) can interfere with growth and establishment of native perennial grasses (Gunnell *et al.* 2010). Although results were limited to relatively few sites, we found greater native DRPG cover when these species were drill-seeded in the absence of non-native perennial species, suggesting future native DRPG seeding applications might benefit if sown without non-native competitors. Non-native DRPG were also occasionally found in unburned areas (8·0% and 17·5% of aerial and drill UX treatments, respectively), which may indicate potential expansion from treated areas.

Seeding *P. secunda* had a negative effect on cover of this species in drill seeding sites. To our knowledge, this is the first information reported on post-fire seeding of *P. secunda*. Our observations indicate that *P. secunda* is among the native species most likely to survive wildfires, and pulling a seed drill across lands where *P. secunda* already exists may result in up-rooting of existing plants with little establishment of seeded individuals. Tests of minimum-till rangeland drills are being conducted, which may reduce loss of potentially important wildfire survivors (Shaw *et al.* 2012).

Competitive dominance and interference from non-native annual bromes is a common justification for sowing non-native DRPG in post-fire rehabilitation projects (McArthur 2004). Our results indicate that non-native DRPG cover in aerial and drill seeding sites increased with mean annual precipitation, but only drill-seeded sites showed any concomitant decline in annual bromes and then only at elevations above 1300 m. Not only were non-native DRPG aerial seeding treatments ineffective at reducing annual brome cover, but in locations with <24–28 cm of precipitation, the seeded species often failed to establish.

Our data support findings by Chambers *et al.* (2007) who noted that *B. tectorum* increases with decreasing elevation and increasing heat load. This indicates that cooler, wetter environments in the Great Basin are more resistant to *B. tectorum* establishment. These areas also may be more resilient to disturbances like overgrazing or fire (Chambers *et al.* 2014). Thus, managers might consider whether cost of seeding at low elevations or at sites with low annual precipitation will provide sufficient benefit in reducing annual bromes, as these areas have both low probability of establishing DRPG and low resistance to non-native annuals. Should managers deem seeding necessary on low elevation or extremely arid sites, they might consider alternative methods to establish perennials, as annual weather variation may not provide sufficient precipitation for initial establishment.

Aerial seeding applications without any method to cover seeds did not provide sufficient establishment of non-native DRPG to significantly impact annual bromes. Stevens & Monsen (2004) have argued that aerial seeding treatments require some form of soil disturbance (e.g. harrowing or chaining) to gain sufficient seed-to-soil contact for seeds to escape predation, imbibe, germinate and establish. However, past studies have found mixed effectiveness of chaining or harrowing after aerial seeding (Ott, McArthur & Roundy 2003; Thompson *et al.* 2006).

A primary justification for rehabilitation projects is to reduce post-fire soil erosion. Soil erosion effects are rarely measured directly (Pyke, Wirth & Beyers 2013), but erosion reductions are often assumed through increased plant cover associated with reseeding. We found that soil protection after fire on these lands was largely achieved from increased annual plant cover at lower elevation sites and by increased perennial cover (primarily perennial grasses) at higher mean annual precipitation sites. In addition, because herbaceous perennial plant cover does not adequately protect most sites immediately after fire (Miller *et al.* 2012), the likelihood of gaining erosion protection through seeding perennial herbaceous plants remains low until adequate establishment and growth provide protective cover over multiple years. Our results indicate that long-term perennial establishment to meet ESR erosion reduction goals was more likely achieved at wetter, high-elevation sites.

Aerial or drill seeding native shrubs did not increase shrub cover or density relative to burned areas that were not seeded. *A. tridentata* cover did not exceed 5% in any of the fifty ESR seeding areas where this species was sown. Although establishment of mature *A. tridentata* stands can take several decades (Miller *et al.* 2013), little increase in cover or density of this species 8–21 years after seeding suggests alternative strategies, such as transplanting, may be required to establish meaningful populations (McAdoo, Boyd & Sheley 2013). While our results suggest that *B. prostrata* seeding can increase shrub cover, concerns have emerged regarding its potential spread to unseeded areas (Gray & Muir 2013).

Several study limitations should be considered and indicate future research needs. We did not account for temporal or spatial patterns of interannual variability in wildfire or climate, which may bias seeding success or failure rates based on years when fires and seeding applications were more frequent (e.g. spike of ESR projects sampled in 1999, which was a year with increased fire activity that was followed by below-average precipitation in subsequent years). Treatment timing and seeding technique can also influence post-fire seeding success (Eiswerth & Shonkwiler 2006), but we were unable to completely account for these effects. Our long sampling period (April–August) may have also resulted in some loss of annual cover (primarily forbs) in later months.

We were unable to evaluate grazing management practices that likely affected long-term ESR seeding outcomes. Grazing management data were not consistently available for all years or locations similar to other studies (Veblen *et al.* 2014). Standard ESR practice by BLM is to allow a seeding at least 2 years rest from grazing to allow establishment; however, grazing has been cited as a potential reason for seeding failure long term (Eiswerth & Shonkwiler 2006) and warrants further investigation.

Post-fire ESR seeding treatments did provide a long-term increase in cover of perennial grasses and at times reduced non-native brome and forb cover. These effects, however, were primarily limited to locations drill-seeded with non-native grasses at higher elevation or precipitation sites (locations where non-native annuals are typically less problematic). Seeding treatments at lower, drier locations were less likely to result in establishment of perennial grasses and were more likely to be dominated by introduced annual grasses. In these locations, intensive methods of restoration (e.g. pre-treatment invasive plant control) may be required to effectively establish seeded species. Although we found ESR shrub establishment efforts to be largely ineffective, foundational species like *Artemisia tridentata* should not be abandoned in post-fire restoration efforts. Instead, managers might consider alternative strategies, such as transplanting, use of native-only seed mixes or prioritization of seeding towards favourable sites (e.g. high annual precipitation), to achieve project goals.

Successful adaptive management requires monitoring effectiveness of management actions to meet objectives (Williams 2011). Effectiveness monitoring of single projects provides limited information for adaptive management without input from additional projects. Evaluation of multiple projects under variable conditions over time provides a comprehensive understanding of success and failure that can inform future management decisions and improve long-term outcomes. Our findings suggest the ESR programme on BLM-managed federal lands may benefit from an adaptive management approach to improve seeding success. Other land treatment projects with comparable goals and objectives (e.g. restoration, mitigation and fuels management) may also benefit from a similar approach to improve management decisions.

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Data accessibility

Data and associated metadata have been archived at the USGS SAGEMAP site (http://sagemap.wr.usgs.gov/ESR_Chrono.aspx).

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1. Number of sites and seeded species by nativity and year.

Fig. S2. Predicted total perennial plant cover (aerial burned–seeded).

Fig. S3. Predicted perennial grass (PG) cover (aerial burned–seeded).

Fig. S4. Cover of native deep-rooted perennial grasses with and without non-native seeded species.

Fig. S5. Cover of *Poa secunda*.

Fig. S6. Cover of native perennial forbs.

Fig. S7. Predicted bare ground (%) in relation to age and elevation (drill burned–seeded and burned–unseeded).

Table S1. Locations and features of Emergency Stabilization and Rehabilitation projects.

Table S2. Summary of seeded perennial grass species.

Table S3. Summary of seeded perennial forb and shrub species.

Table S4. Species and genera detected.