Rangeland Ecology & Management 71 (2018) 695–704

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Original Research

Influence of Land-Use Legacies Following Shrub Reduction and Seeding of Big Sagebrush Sites☆

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ARTICLE INFO

Article history:
Received 27 November 2017
Received in revised form 17 May 2018
Accepted 5 June 2018

Key Words:
chain harrow
sagebrush restoration
sagebrush treatment
seeding
site history

ABSTRACT

Big sagebrush (*Artemisia tridentata* Nutt.) plant communities often require management to reduce shrub density and rehabilitate understory vegetation. We studied vegetation responses to a two-way chain harrow treatment and broadcast seeding of 12 herbaceous species at eight Wyoming big sagebrush (*A. tridentata* Nutt. subsp. *wyomingensis* Beetle & Young) sites. These sites differed in land-use history; five were cultivated for dryland wheat production during the 1950 − 1980s and then seeded with introduced forage grasses (C-S), while three had not been exposed to this land-use legacy (non C-S). Our objective was to evaluate whether the C-S legacy influences the magnitude of vegetation change following contemporary treatment. Before treatment, C-S sites had lower sagebrush cover, higher dead sagebrush cover, and higher broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britton & Rusby) cover than adjacent non C-S sites. Plant community change 3 years after treatment, determined with multivariate ordination analysis of species composition, varied between site histories, and response to treatment was most strongly correlated with reductions in sagebrush cover, increases in perennial grasses, and increases in 10 other herbaceous species—including some undesirable species and four that were seeded in 2010. Five years after treatment, mature sagebrush cover remained reduced for both land-use histories, yet density of sagebrush seedlings and broom snakeweed increased in C-S sites during the second and third years after treatment. In addition, perennial forb cover increased for C-S sites, while perennial grass biomass increased for non C-S sites. Our results emphasize that broad variability in plant community responses to sagebrush reduction and seeding is possible within the same ecological site classification and that legacy effects due to the combination of past cultivation and seeding should be considered when planning restoration projects, including the consideration that seeding may not always be necessary on C-S sites.

Introduction

Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young) plant communities in the western United States provide forage and habitat for wildlife and livestock and have undergone considerable modification since European settlement (West, 1983b; Connelly et al., 2000; Davies et al., 2011b). Today, many plant communities across this broad region have transitioned to alternative stable states characterized by degraded understory conditions, including the replacement of native herbaceous species by invasive annual grasses (Allen-Diaz and Bartolome, 1998; Davies et al., 2012b; Chambers et al., 2017) and reductions in habitat quality for wildlife species (Arkle et al., 2014; Chambers et al., 2017). The severity of these changes varies by plant community type (Williams et al., 2016; Chambers et al., 2017), as well as the type of degradation that has occurred to understory herbaceous vegetation (Ellison, 1960; West, 1983b; Miller and Rose, 1999; Davies et al., 2010). In particular, the duration and magnitude of past disturbances (i.e., livestock grazing, fire, and cultivation for crops) are known to be key drivers of degradation (West, 1988; Chambers et al., 2014a; Morris and Rowe, 2014). However, potential legacies from these historical land uses are less understood (Davies et al., 2011b; Morris and Rowe, 2014) and may potentially influence herbaceous species abundance, sagebrush recovery from disturbances, as well as the success of subsequent rehabilitation efforts (Morris et al., 2011, 2014).

To remediate degraded understory vegetation, shrub reduction treatments are commonly applied in Wyoming big sagebrush plant

☆ Funds to support fencing and treatment applications were provided by Rio-Tinto, Kennecott Utah Copper and the Utah Watershed Restoration Initiative, respectively. We also recognize multiple grants from the R. Harold Burton Foundation to support authors A. J. and M. P.

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https://doi.org/10.1016/j.rama.2018.06.004
1550-7424/Published by Elsevier Inc. on behalf of The Society for Range Management.

communities (Watts and Wambolt, 1996; McDaniel et al., 2005; Beck et al., 2012; Pyke et al., 2014). Because shrub reduction releases soil nutrients and increases water availability that can potentially augment herbaceous species growth (Rittenhouse and Sneva, 1976; Boyd and Svejcar, 2011), it is often assumed that herbaceous production of perennial grass and forb species will increase after shrub reduction (West et al., 1984; Beck and Mitchell, 2000; Crawford et al., 2004; Dahlgren et al., 2006; Davies et al., 2009). Shrub reduction treatments, however, do not consistently rehabilitate understory vegetation, and when they do, treatment effects may be short lived (West and Hassan, 1985; Wambolt et al., 2001; Archer et al., 2011; Archer and Predick, 2014). If native herbaceous species exist in sufficient abundance, understory vegetation can readily increase following shrub reduction treatments (West, 1988; McDaniel et al., 2005; Davies et al., 2007; Chambers et al., 2014a). However, when shrub density is high and understory vegetation is degraded and/or displaced by invasive annual grasses (i.e., cheatgrass, *Bromus tectorum* L.), plant communities often exhibit overall low recovery toward reference state conditions following disturbance (Brown et al., 1985; Chambers et al., 2007, 2014b; Davies and Bates, 2014; Pyke et al., 2014) and shrub removal may actually exacerbate weed species invasion (Davies et al., 2009; Prevéy et al., 2010; Condon et al., 2011; Davies et al., 2011a; Monaco et al., 2017), soil erosion (Johnson et al., 1980; Brown et al., 1985), and loss of wildlife habitat (Davies et al., 2011b; Beck et al., 2012; Arkle et al., 2014; Hess and Beck, 2014). Moreover, while simultaneous shrub reduction and supplemental seeding of perennial species are frequently applied to enhance understory recovery and reduce soil erosion, land-use legacies from prior rehabilitation efforts may influence vegetation changes over time (Johnson and Payne, 1968; Shane et al., 1983).

Among many factors responsible for variation in shrub dominance and understory degradation in Wyoming big sagebrush plant communities (West, 1983a), past land use has the potential to create legacy effects on vegetation dynamics, shrub cover, species composition, and seed banks (Morris et al., 2011; Morris and Rowe, 2014). For example, cultivation associated with dryland grain production can leave legacy effects on soils and plant community composition, as well as successional trajectories (Morris et al., 2011; Morris, 2012a). In addition, big sagebrush sites exposed to a combined legacy effect of cultivation and seeding with exotic forage grasses consistently show lower density of the native perennial Sandberg bluegrass (*Poa secunda* J. Presl), and in some cases lower sagebrush cover compared to adjacent sites that were only seeded (Morris et al., 2014). Furthermore, exotic forage grasses such as crested wheatgrass (*Agropyron cristatum* [L] Gaertn. and *Agropyron desertorum* [Fisch.] Schult) can reduce establishment of native species yet are known to impede the spread of invasive annual grasses (Schuman et al., 1982; Waldron et al., 2005; Nafus et al., 2015). However, no studies have specifically examined how the effect of cultivation-seeding legacies influence the establishment of subsequent rehabilitation seedings conducted after shrub reduction.

Given that land-use legacies can shape patterns of community assembly after seeding experiments (Brown et al., 2015; Nafus et al., 2016), we hypothesized that big sagebrush lands previously cultivated and seeded with forage grasses respond differently to subsequent shrub reduction and seeding efforts than adjacent lands that did not experience this historical land use. To test this hypothesis, we evaluated short-term responses (i.e., 5 years) of plant species and vegetation composition of Wyoming big sagebrush communities following the application of a combined shrub reduction-seeding treatment to sites with and without a cultivation-seeding legacy in north-central Utah, United States. We asked 3 questions: 1) Which vegetation components and species are most strongly correlated with plant community change following a shrub reduction-seeding treatment? 2) Will changes in vegetation components due to the shrub reduction-seeding treatment vary between sites with and without a cultivation-seeding legacy? 3) Will the abundance of seeded species and preexisting native species vary between sites with and without this legacy? We discuss how understanding land-use legacies can improve our interpretation of short-term recovery of big sagebrush and herbaceous understory species following rehabilitation treatments.

Methods

Study Area

The study was conducted on Barney Ridge, an area of rolling sagebrush foothills on the eastern slope of the Oquirrh Mountains in

Figure 1. Map showing location of eight study sites on Barney Ridge in north-central Utah where chain harrow – seeding treatments were applied in autumn of 2010 (solid gray). Five of our eight sites (i.e., 1–4 and 8) had a cultivation-seeding legacy. Each site also contained untreated control areas (hatched). Solid lines encompassing treatment areas indicted fences to exclude livestock.

north-central Utah, United States (Fig. 1). In 2009, this region became a critical focus area to enhance habitat for wintering deer by the landowners (Rio Tinto, Kennecott Utah Copper) and the Utah Division of Wildlife Resources. Slope and elevation vary between 3 − 15° and 1 650 − 1 700 m, respectively, and climate is characteristic of eastern Great Basin cold desert shrubland ecosystems, where the majority of precipitation arrives as snow in the winter months; summer months are typically hot and dry. Long-term (1985 − 2015) mean annual precipitation and temperature range from 430 mm to 480 mm and 7.8°C to 8.8°C, respectively (http://www.wrcc.dri.edu). Soils on these high alluvial fans are in the Dry Creek Series and classified as Typic Palexerolls with deep freely drained soils, a mollic epipedon, and a xeric moisture regime (Salt Lake Area Soil Survey, available at: www.nrcs.usda.gov/wps/portal/nrcs/surveylist/soils/survey/state/stateId=UT).

On the basis of Ecological Site Descriptions (available at: www.esis.sc.egov.usda.gov), we classified each of the 8 study sites as R028AY310UT Upland Loam (Mountain Big Sagebrush). However, because Barney Ridge is located within a transition zone between mountain and Wyoming big sagebrush ecological sites, we examined *Artemisia* leaf morphology, shape of canopy crown, and inflorescence structure of numerous specimens to determine the prevalence of subspecies across sites. Although we found both subspecies, mountain big sagebrush was rarely identified and Wyoming big sagebrush was deemed the dominant species across Barney Ridge. Hybridization among big sagebrush subspecies has also likely occurred, which is common where populations are sympatric and past disturbance has allowed opportunity for recolonization (Shultz, 2009; Garrison et al., 2013).

During an assessment of Barney Ridge in 2009, we discovered five of our eight sites (i.e., 1–4 and 8; see Fig. 1) were formerly cultivated during the 1950s − 1980s for dryland (nonirrigated) wheat production and seeded with crested and intermediate wheatgrass (*Agropyron cristatum* [L.] Gaertn and *Thinopyrum intermedium* [Host] Barkworth & D.R. Dewey, respectively), before being reverted back to grazing lands in the early 1990s (Tom Giovengo and Gerald Mahoney, personal communication 2 September 2015). Although dryland wheat cultivation was commonly practiced in the past and continues today in the Barney Ridge area, we did not find any evidence of past cultivation for sites 5, 6, and 7, which was confirmed through conversations with former lessees, land-use records at Kennecott Utah Copper, and field reconnaissance specifically looking for the presence of seeded grasses, rock piles, or plow pans (Morris, 2012b). We also emphasize that three of the formerly cultivated sites (i.e., 2 − 4) had more gentle slopes and less of a southern exposure than the other sites. Barney Ridge is currently used for cattle grazing at a moderate level from May to October each year. However, study sites were fenced to prevent any livestock grazing during the first 3 years of our study (2010 − 2013).

Before initiating our study in autumn 2010, percentage cover of big sagebrush (mean ± 1 SE; $n = 144$) averaged 29.4 ± 0.15 across the eight sites. We also encountered broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britton & Rusby), antelope bitterbrush (*Purshia tridentata* [Pursh] DC), yellow rabbitbrush (*Chrysothamnus vicidiflorus* [Hook.] Nutt.), rubber rabbitbrush (*Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird), and gambel oak (*Quercus gambelii* Nutt.), but each contributed < 1% to canopy cover. In addition, average cover of perennial grasses, exotic annual grasses, native forbs, and exotic forbs were 5%, 7%, 2%, and 5%, respectively. Because vegetation varied greatly from Reference State cover percentages for this ecological site (www.esis.sc.egov.usda.gov) (e.g., grasses 35 − 45%, forbs 0 − 10%, and shrubs 10 − 20%), our study sites were collectively considered to represent a degraded vegetation state, thus warranting intervention to assist the recovery of understory vegetation.

Shrub Reduction Treatment and Broadcast Seeding

To moderately reduce big sagebrush density (ca. 50%) and seed-treated areas, a tractor with a chain harrow implement and a broadcast seeder (Herd Model 2440, Kasco Manufacturing Co. Inc., Shelbyville, IN) was passed two times over each site in October 2010. Chain harrowing is commonly used on similar sagebrush site throughout Utah because it

Figure 2. Photograph of chain harrow − seeding treatment application to eight study sites on Barney Ridge in north-central Utah.

produces relatively lower soil disturbance compared with alternative mechanical treatments (Riginos et al., in review; Wilder et al., in review). The chain harrow consisted of an Ely Chain (Cain, 1971) affixed to a 5-m rail. When dragged over vegetation, it uproots a proportion of older, brittle sagebrush plants; breaks up the soil surface; and improves soil coverage of seeds that are dispersed during the second pass (Fig. 2). The seed mix was composed of both native and introduced species and was applied at 13.3 kg · ha^{-1} pure live seed (Table 1). This seed mixture resembles those typically used on sagebrush sites in Utah, where both native and introduced species are needed to rapidly establish and support wildlife habitat needs, as well as livestock grazing use (Thompson et al., 2006). Portions of each site were neither harrowed nor seeded to provide untreated control areas (see Fig. 1). Control areas were not randomly selected, but they intersected the entire length of each study site and often cut across topographical and vegetation gradients.

Vegetation and Ground Cover Sampling

Shrub species cover and density were sampled in June — July in 2010, 2012, 2013, and 2015. Herbaceous species cover was sampled in July of 2012 and 2013, but because grazing commenced in 2014, subsequent cover measurements were taken in 2015, but only in paired (grazed and nongrazed) plots established at each of the eight sites for a companion study. Within each site, shrub cover and density were measured along 30-m transects randomly placed in treated ($n = 12$) and untreated control areas ($n = 6$). Live and dead Wyoming big sagebrush cover were estimated using line intercept methods (Canfield, 1941); densities of sagebrush and broom snakeweed plants were sampled in belts (1 m × 30 m) that ran parallel to transects (Coulloudon et al., 1999). Sagebrush plants were categorized broadly as either seedlings (≤ 5 cm height) or mature (> 5 cm height). Percentage canopy cover of all herbaceous species was visually estimated at each site within 0.25-m^2 quadrats randomly placed in treated ($n = 60$) and smaller untreated control areas ($n = 18$). Within these quadrats, percentage ground cover for litter and bare soil was also estimated. Also, in 2012 and 2013, all herbaceous vegetation within quadrats was clipped to the height of soil surface and returned to the laboratory, where samples were dried in a convective oven at 60°C for 48 h, sorted by species, and weighed to determine dry mass. Herbaceous species were assigned to four different vegetation categories according to functional group (i.e., annual grass, perennial grass, annual forb, and perennial forb). Quadrat locations were recorded with a global positioning system in 2010, and the same areas, but not the exact locations, were sampled in 2012, 2013, and 2015.

Statistical Analysis

Our experimental design assessed four different conditions created by the combination of two land use histories and two different rehabilitation treatments. To determine which vegetation components and species are most strongly correlated with herbaceous plant community change following the treatment (Question 1), we applied nonmetric multidimensional scaling (NMS) analysis to 2013 data (i.e., 3 years post treatment) because it was the last years both herbaceous and shrub species were sampled. NMS is a procedure that uses species cover data to calculate a distance matrix (dissimilarity between species pairs). On the basis of these distances, the position of sampling location (e.g., sites) within ordination space can be analyzed; sites closer together are more similar in species composition. To construct the dissimilarity matrix, species percentage cover data from the 60 treated and 18 control 0.25 m^2 sampling quadrats at each site were averaged and species that occurred on fewer than two sites were removed from the dataset. The final matrix was 16 rows (8 sites × 2 treatments) × 51 columns (species). We then relativized columns by their maxima in order to standardize the scale of variation across species. Ordination was performed using the Sørensen (Bray-Curtis) distance measure, random starting configurations, 250 runs using real data, and a maximum of 250 runs using random data. Significance of the final stress value (e.g., how well it represented the real distances) was compared with random solutions using a Monte Carlo test with 250 randomizations. Correlations between NMS axes and each species in the main matrix, as well as vegetation categories (shrub, perennial grass, annual grass, perennial forb, annual forb, bare ground, and litter cover), were determined with Pearson's r correlation coefficients. We arbitrarily chose to emphasize coefficients > |0.7| to identify variables with the highest correlation with the ordination results. Overall plant community differences between chain harrow — seeding treatment and the untreated control, as well as between the cultivated and noncultivated sites, were then tested post hoc with one-way PerMANOVA and Multiple Response Permutation Procedures (MRPP), respectively, using the Sørenson distance measure and 9999 permutations for Monte Carlo tests. Analyses were performed using PC-Ord (ver. 7; MjM Software Design, Gleneden Beach, OR) with significance set at $\alpha = 0.05$.

We used two separate analyses to determine whether individual vegetation components varied between sites with a cultivation-seeding legacy (C-S) and those without a cultivation-seeding legacy (non C-S) (Question 2). First, pretreatment differences in shrub canopy cover for sagebrush and broom snakeweed were analyzed with Student's t-tests ($\alpha = 0.05$). Second, post-treatment vegetation components (i.e., density, canopy cover, and biomass of functional groups) and ground cover were assessed using effect size analysis. This latter approach was chosen because our primary goal was to examine whether the direction and magnitude of treatment effects varied between C-S and non C-S sites (Rinella and James, 2010). In addition, effect size analysis was deemed appropriate because our study included 1) unbalanced numbers of cultivated and uncultivated sites, 2) size differences between treated and control areas, and 3) sites with a high degree of spatial variability in topography (e.g., slope degree and aspect) and vegetation. To supplement the interpretation of the effect size analysis, we also present actual values (mean ± SE) for control and treatment areas pooled for C-S and non C-S sites.

Table 1
Seed mix composition and pure live seed application rate for broadcast seeding of eight study sites on Barney Ridge in north-central Utah, United States

Common name	"Variety"/Germplasm	Scientific name	Pure live seed rate (kg · ha^{-1})
Western yarrow	Great Northern	*Achillea millefolium* L. var. *occidentalis* DC.	0.22
Blue flax	"Appar"	*Linum perenne* L.	0.65
Alfalfa	"Ladak"	*Medicago sativa* L.	0.69
Sainfoin	"Eski"	*Onobrychis viciifolia* Scop.	0.23
Small burnet	"Delar"	*Sanguisorba minor* Scop.	1.82
Crested wheatgrass	"Hycrest II"	*Agropyron cristatum* (L.) Gaertn.	1.76
Bottlebrush squirreltail	Rattlesnake	*Elymus elymoides* (Raf.) Swezey	0.43
Thickspike wheatgrass	"Bannock"	*Elymus lanceolatus* (Scribn. & J.G. Sm.) Gould	1.29
Western wheatgrass	"Rosana"	*Pascopyrum smithii* (Rydb.) Á. Löve	1.74
Sandberg bluegrass	Mountain Home	*Poa secunda* J. Presl	0.44
Bluebunch wheatgrass	Anatone	*Pseudoroegneria spicata* (Pursh) Á. Löve	1.53
Intermediate wheatgrass	"Luna"	*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey	0.92

For our effect size statistic, we calculated natural log response ratio (lnRR) of shrub density, canopy cover, ground cover, and biomass where lnRR for each site = ln (treated/untreated). We then performed a meta-analysis of each variable using the *metafor* package for R (Viechtbauer, 2010). In brief, this analysis calculates a weighted mean effect size: mean lnRR = Σw_i lnRR$_i$/Σw_i, where lnRR$_i$ and w_i are effect size and weight (inverse variance), respectively. Effect sizes were analyzed with the RMA function and REML (restricted maximum likelihood) method. Mixed-effects models were used to test the significance ($\alpha = 0.05$) of effect size estimates (z-test; H_0: $\mu = 0$) for non C-S and C-S sites and examine the difference between site histories (Q_M-test; H_0: $\mu = 0$). Site history was considered the fixed variable and replications were treated as a random effect.

Differences in cover of seeded forbs, resident native grasses, and previously seeded grasses between C-S and non C-S sites (Question 3) were determined using 2013 data with Wilcoxon rank sums tests (χ^2 test; $df = 1$; $\alpha = 0.05$) using JMP ver. 13 (SAS Institute Inc. Cary, NC). This approach was chosen because no suitable data transformations could adequately improve normality or homogeneity of variances for individual species data. We emphasize that differences in seeded species cover between non C-S and C-S sites are not entirely due to establishment of new seedlings from our 2010 seeding because in addition to past seedings of crested and intermediate wheatgrass on C-S sites, four of the seeded species were encountered on Barney Ridge before applying chain harrow-seeding treatments. Thus, to assess the abundance of seeded species, we focus attention on four introduced forb species (i.e., sanfoin, alfalfa, small burnet, and blue flax) and two perennial grasses (i.e., western and thickspike wheatgrass) that did not exist on any site before our study.

Results

Plant Community Change

Final NMS ordination of plant community composition 3 years after treatment (i.e., 2013) was based on a stress value of 8.87 and a significant 2-axis solution (Fig. 3; $P = 0.048$, instability of 0.0000, and 73 iterations. The ordination revealed that NMS Axis 1 ($R^2 = 0.607$) was negatively correlated with shrub cover ($r = -0.753$) and positively correlated with perennial grass cover ($r = 0.865$) (Table 2). In contrast, Axis 2 ($R^2 = 0.329$) was positively correlated with bare ground ($r = -0.724$) and negatively correlated with perennial forb cover ($r = 0.879$) (see Table 2). Plant communities were significantly different between treatments (perMANOVA $F = 3.99$; $P = 0.0047$), and distances between C-S and non C-S sites in ordination space were also significant (MRPP $A = 0.17$; $P = 0.00004$). While sites generally responded in the same fashion to chain harrow − seeding treatment, as illustrated by movement from lower left to upper right in ordination space, the magnitude of overall plant community change varied among sites (see Fig. 3). The C-S plant communities with lower pretreatment shrub cover generally experienced less change due to chain harrow seeding than the non C-S plant communities with steeper slope, greater proportional southern exposure, and higher initial shrub cover.

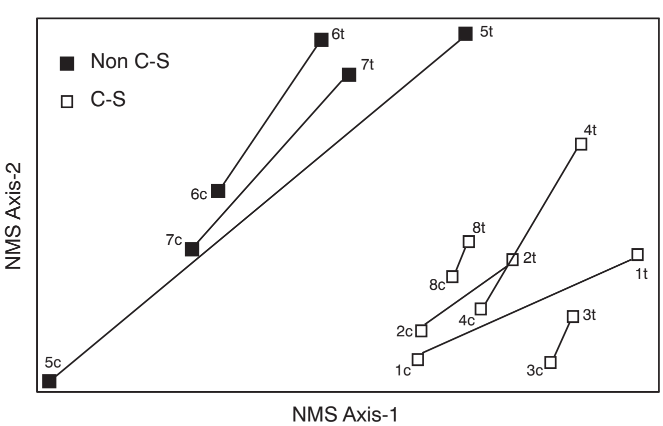

Figure 3. Nonmetric multidimensional scaling (NMS) ordination of the eight study sites on Barney Ridge in north-central Utah three years after treatment (see Fig. 1). Symbols represent plant community locations in "species space" for control ("c") and chain harrow-seeding treatment ("t") areas for five historically cultivated and seeded sites (C-S) and three sites without this land-use legacy (Non C-S). Ordination was based on percentage cover data for 51 species common among the eight sites. The correlation of species, functional groups, bare ground, and litter with NMS ordination axes is shown in Table 2.

Table 2
Pearson's r correlation coefficients > |0.7| among vegetation cover, ground cover, and species and NMS ordination axes for eight plant communities 3 years after application of a chain harrow − seeding treatment (2013). *Asterisks* denote seeded species. See results for scientific names of species

Pearson's r			
NMS Axis 1 ($r^2 = 0.607$)		NMS Axis 2 ($r^2 = 0.329$)	
Vegetation or ground category			
Shrub	−0.753	Bare ground	−0.724
Perennial grass	0.865	Perennial forb	0.879
Species			
Wyoming big sagebrush	−0.902	Prickly lettuce	0.706
Bulbous bluegrass	0.797	Blue flax*	0.721
		Douglas' knotweed	0.720
		Cheatgrass	0.722
		Dalmatian toadflax	0.780
		Small burnet*	0.788
		Bluebunch wheatgrass*	0.852
		Western aster	0.853
		Field brome	0.882
		Western yarrow*	0.906

A few vegetation categories and species were strongly correlated with NMS axes (r > |0.7|; see Table 2). Plant community changes along Axis 1 were correlated with perennial grass and shrub cover, which were primarily attributed to treatment effects on bulbous bluegrass (*Poa bulbosa* L.) and Wyoming big sagebrush, respectively. Alternatively, plant community changes along Axis 2 were correlated with perennial forb cover and bare ground, as well as 10 herbaceous species including four species seeded in 2010 (see Table 1; blue flax, *Linum perenne* L.; bluebunch wheatgrass, *Pseudoroegneria spicata* [Pursh] Á. Löve; small burnet, *Sanguisorba minor* Scop.; and western yarrow, *Achillea millefolium* [L.] var. *occidentalis* DC.), three undesirable invasive species (cheatgrass; Dalmatian toadflax, *Linaria dalmatica* [L.] Mill; field brome, *Bromus arvensis* L.), and three common exotic annual forb species (prickley lettuce, *Lactuca serriola* L.; Douglas' knotweed, *Polygonum douglasii* Greene ssp. *douglasii;* western aster, *Symphyotrichum ascendens* [Lindl.] G.L. Nesom).

Treatment Effects on Vegetation and Ground Cover

Before applying the rehabilitation treatment, C-S sites had lower live sagebrush cover ($t = 5.5$, $df = 94$; $P < 0.0001$), greater dead sagebrush cover ($t = -2.0$, $df = 94$; $P < 0.05$), and greater broom snakeweed cover ($t = -6.1$, $df = 94$; $P < 0.0001$; Fig. 4) than non C-S sites, yet the magnitude of these differences was rather small. In contrast, relative to the control, the rehabilitation treatment led to significant changes in herbaceous components; including twofold increases in both perennial forbs and annual grasses (Table 3; Fig. 5b). Most parameters, however, were similar between C-S and non − C-S site types, with a few exceptions (Q_M tests; see Table 3). For example, perennial grass cover increased much more following application of the rehabilitation treatment at the non − C-S sites (i.e., 8%) than the C-S sites (3%) (see Table 3; Fig. 5b). Lastly, the response of bare ground was markedly different between the two site histories; namely, non − C-S sites experienced greater reductions (40%) than C-S sites (see Table 3; Fig. 5c).

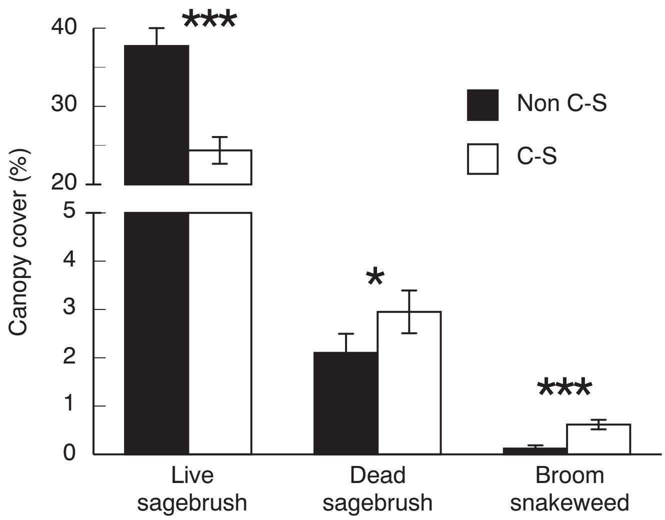

Figure 4. Mean (± 1 SE; $n = 18$) Big sagebrush cover, dead sagebrush cover, and broom snakeweed cover for five historically cultivated and seeded sites (C-S) and three sites without this land-use legacy (Non C-S) in autumn 2010 before applying the chain harrow—seeding treatment on Barney Ridge in north-central Utah. *Asterisks* above bars indicate significant differences between noncultivated and cultivated sites (*$P < 0.05$ and ***$P < 0.001$).

Treatment Effects on Abundance of Seeded Forbs and Preexisting Species

Three years after applying the chain harrow—seeding treatment, seeded forb cover was either similar between the site histories or significantly greater on non—C-S than C-S sites (i.e., blue flax and small burnet; Table 4). In contrast, cover of crested and intermediate wheatgrass (i.e., previously seeded after cultivation was abandoned in the early 1990s) was lower on non—C-S than C-S sites. Consequently, total cover of seeded perennial grasses remained higher on C-S compared with non—C-S sites ($\chi^2 = 47.94$; $P < 0.0001$), concealing the increases of individual seeded species on the latter sites.

Discussion

Our study supports the assumption that simultaneous application of mechanical shrub-reduction treatments and seeding can reduce sagebrush and increase herbaceous understory vegetation components (Blaisdell et al., 1982; Archer et al., 2011), as well as the contention that reducing Wyoming big sagebrush when understory conditions are degraded may increase the risk of further exotic annual grass dominance (e.g., cheatgrass) (Davies et al., 2011a; Monaco et al., 2017). Site history, however, influenced these short-term responses as illustrated by the chain harrow—seeding treatment, causing greater relative increases in the herbaceous understory for non—C-S compared with C-S sites that had been seeded previously. Although we contend that this legacy is a primary factor for differences among sites, we emphasize that three of the formerly cultivated sites (i.e., 2—4) had more gentle slopes and less of a southern exposure than the other sites, which may have compounded how past land use affected historical shrub community and favored the establishment of previously seeded exotic perennial grasses. Despite herbaceous understory increases at non—C-S sites, understory recovery to values within the range of reference ecological site conditions (e.g., grasses 35—45% and forbs 0—10%;

Table 3
Mean effect size and results of meta-analyses by vegetation and ground cover variable for sites with and without (non) a cultivation-seeding legacy. Mean effect size and lower and upper 95% confidence interval (CI) bounds are reported as the natural log response ratio between the chain harrow—seeding treatment and the untreated control. Actual mean values are shown in Fig. 5. Mean effect sizes are tested against a *z*-distribution and differences between non—C-S and C-S sites are measured with the Q_M statistic; *asterisks* indicate significance (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$)

		Non—C-S sites			C-S sites			
			95% CI			95% CI		
Variable	Year	Effect size	Lower	Upper	Effect size	Lower	Upper	Q_M
Mature sagebrush density	2012	−0.81	−2.14	0.51	−0.29***	−0.47	−0.12	0.95
	2013	−0.96	−2.20	0.29	−0.67***	−1.04	−0.31	0.33
	2015	−0.52*	−0.98	−0.06	−0.40**	−0.67	−0.14	0.15
Seedling sagebrush density	2012	2.06	−1.65	5.77	2.98*	0.53	5.43	0.16
	2013	−3.55	−7.26	0.16	2.84*	0.25	5.43	8.14**
	2015	−0.05	−0.78	0.68	−0.26	−1.08	0.56	0.18
Broom snakeweed density	2012	2.68	−1.28	6.64	1.19*	0.19	2.19	0.86
	2013	1.22	−3.26	5.70	0.85***	0.23	1.48	0.06
	2015	1.12	−0.25	2.49	0.35	−0.16	0.85	1.09
Mature sagebrush cover	2012	−1.34***	−1.86	−0.82	−0.85**	−1.45	−0.25	1.21
	2013	−1.24***	−1.86	−0.62	−0.92**	−1.56	−0.28	0.42
	2015	−1.79***	−2.80	−0.77	−1.28***	−1.58	−0.97	1.45
Perennial grass cover	2012	0.29	−0.17	0.75	0.19**	0.06	0.32	0.09
	2013	0.53*	0.02	1.05	0.07	−0.04	0.18	6.19*
Perennial forb cover	2012	1.813	−0.21	3.84	1.27***	0.88	1.67	0.31
	2013	1.64	−0.32	3.61	1.12**	0.34	1.90	0.22
Annual grass cover	2012	1.29*	0.08	2.50	0.49	−0.11	1.09	1.31
	2013	1.02***	0.65	1.39	0.85***	0.40	1.29	0.40
Annual forb cover	2012	0.67	−0.16	1.50	0.40	−0.08	0.88	0.24
	2013	0.11	−0.18	0.41	0.26	−0.16	0.67	0.39
Perennial grass biomass	2012	0.54**	0.20	0.89	−0.04	−0.42	0.34	3.22
	2013	1.06**	0.31	1.81	0.33	−0.03	0.69	3.77
Perennial forb biomass	2012	2.49	−0.28	5.26	1.71***	1.28	2.13	0.52
	2013	1.48*	0.14	2.83	1.62***	1.07	2.18	0.01
Annual grass biomass	2012	2.33*	0.35	4.32	2.18***	1.00	3.36	0.02
	2013	1.43***	0.92	1.93	1.58***	1.04	2.12	0.17
Annual forb biomass	2012	0.67	−0.16	1.50	0.40	−0.08	0.88	0.24
	2013	0.16	−0.27	0.60	0.76**	0.29	1.23	3.39
Bare ground	2012	−0.53***	−0.73	−0.34	−0.23***	−0.34	−0.13	9.56**
	2013	−1.32***	−1.71	−0.93	−0.44***	−0.60	−0.28	22.20***
Litter cover	2012	−0.27	−0.82	0.28	−0.27	−0.64	0.10	0.06
	2013	0.32*	0.03	0.62	0.12	−0.19	0.43	0.85

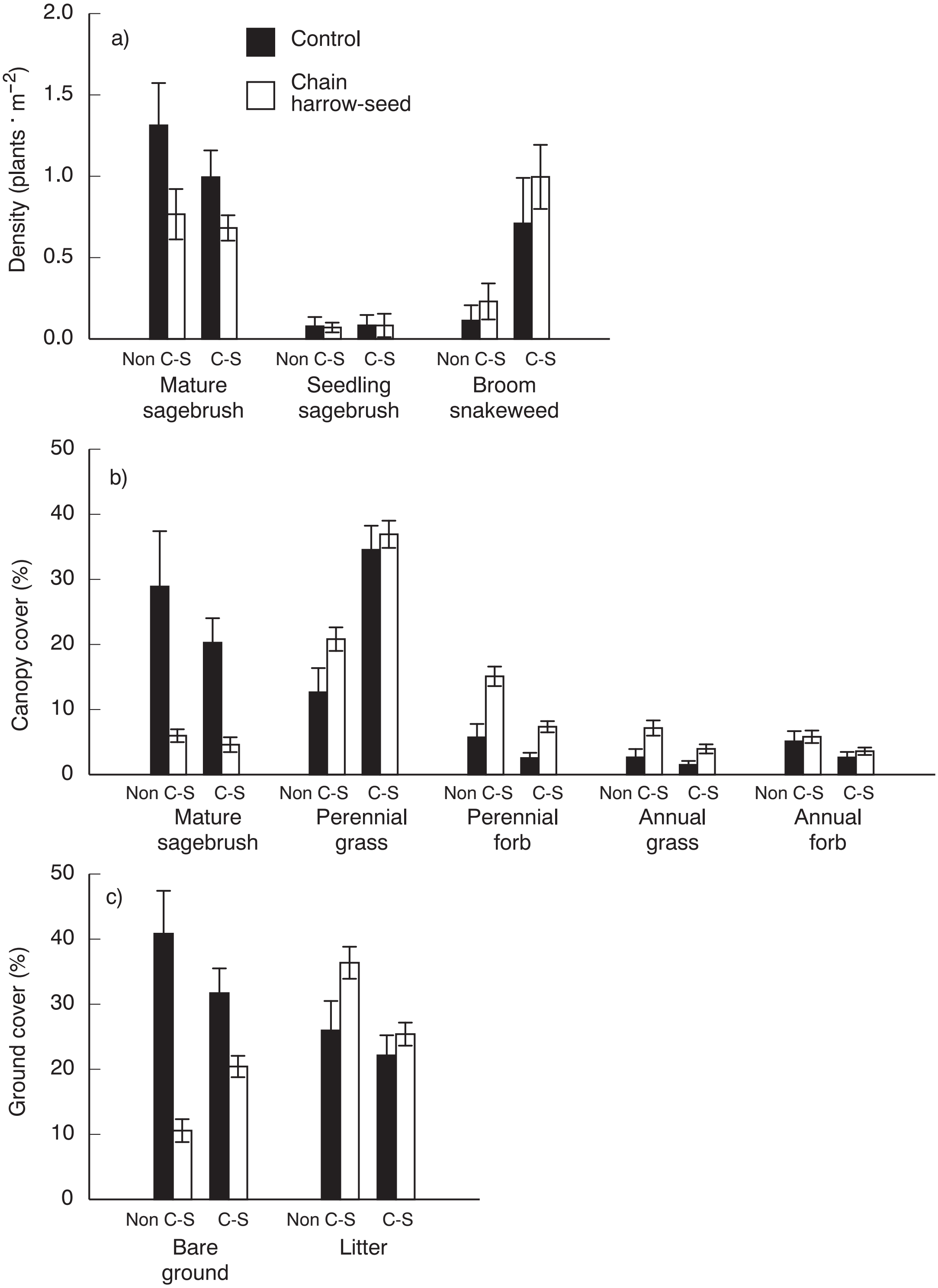

Figure 5. Mean (± 95% confidence interval) density (a), canopy cover (b), and ground cover (c) measured for five historically cultivated and seeded sites (C-S) and three sites without this land-use legacy (Non C-S) on Barney Ridge in north-central Utah following the application of a chain harrow-seeding treatment. Shrub density and mature sagebrush canopy cover were measured in 2015, while all other cover values were measured in 2013. Statistical significance of the treatment and land use legacy were tested by calculating mean effect sizes (i.e., natural log response ratio between the chain harrow-seeding treatment and the untreated control) and performing meta-analysis of each response variable (see Table 3).

https://esis.sc.egov.usda.gov) was realized to a greater extent for C-S sites, primarily due to the greater abundance of perennial grasses that were seeded more than 20 years ago. Site history also affected the magnitude of change in plant communities in response to sagebrush reduction and seeding, which was much more pronounced for non − C-S than C-S sites. Greater overall plant community change following treatment for non − C-S sites was attributed to many vegetation components, including higher cover for 6 of the 12 seeded species and much lower bare ground in non − C-S sites. These results suggest that in addition to considering site-to-site variation, which is typical of large-scale shrub reduction efforts (Wambolt and Payne, 1986; Arkle et al., 2014). Land managers, thus, should not overlook how land-use legacies may affect both pretreatment vegetation and expected outcomes following the application of sagebrush reduction treatments. Next, we discuss

Table 4
Percentage cover (± 95% confidence intervals [CIs]) of seeded combined forbs, individual forb species, seeded combined grasses, and individual grass species for five historically cultivated and seeded sites (C-S) and three non — C-S sites on Barney Ridge in north-central Utah, United States 3 years (2013) after application of a chain harrow — seeding treatment. Within a row, differences between non — C-S and C-S sites were determined with Wilcoxon one-way rank sums analysis (χ^2 test; $df = 1$; *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ns = not significant; >, <, and — symbols indicate whether cover values were greater than, less than, or equitable between non — C-S and C-S sites), respectively. See Table 1 for scientific names of species

	Non — C-S sites			C-S sites		
Species	Mean (n = 180)	95% CI		Mean (n = 298)	95% CI	χ^2
Western yarrow	1.00	0.41	>	0.33	0.16	23.41***
Blue flax†	1.94	0.59	>	0.87	0.30	38.53***
Alfalfa†	0.02	0.03	—	0.12	0.10	2.21
Sainfoin†	0.45	0.19	—	0.43	0.20	2.46
Small burnet†	3.27	0.54	>	2.06	0.47	29.45***
Forbs (total)	6.68	1.00	>	3.80	1.22	46.92***
Crested wheatgrass*	0.72	0.32	<	5.03	0.93	39.54***
Bottlebrush squirreltail	0.12	0.13	>	0	0	4.99*
Thickspike wheatgrass†	0.87	0.31	—	1.70	0.61	3.67
Western wheatgrass†	0.28	0.32	—	0.17	0.20	0.39
Sandberg bluegrass	5.28	1.14	>	2.43	0.58	18.98***
Bluebunch wheatgrass	1.36	0.47	>	0.30	0.17	45.33***
Intermediate wheatgrass*	0.43	0.24	<	7.41	1.26	81.38***
Grasses (total)	9.30	1.20	<	17.03	1.45	47.94***

* Crested and intermediate wheatgrass were previously seeded in the early 1990s after cultivation and dryland wheat production was ceased.
† Four forb and two grass species were not present on sites before seeding.

how the C-S legacy influences short-term changes in plant community and vegetation composition experienced after applying rehabilitation efforts.

Plant Community Change

Greater overall change in non — C-S than C-S plant communities in response to chain harrow seeding was due to relatively larger reductions in sagebrush and bare ground, as well as relatively larger increases in perennial grass and forbs (see Table 2). On one hand, the greater reductions in sagebrush cover and density were likely a consequence of higher pretreatment sagebrush cover values for non — C-S sites (see Fig. 5); increases in perennial grass and forb cover were associated with greater increases in native species and a number of seeded species within understory conditions that lacked previously established exotic perennial grasses. On the other hand, previously established perennial grasses in the understory of C-S sites resulted in lower plant community change compared with non — C-S sites in response to the combined canopy and ground disturbance we imposed. However, annual grass (i.e., cheatgrass) biomass increased in both C-S and non — C-S sites following the disturbance of chain harrow — seeding treatments (see Table 3; Fig. 5), suggesting that even though C-S sites exhibited lower overall plant community change, they were not impervious to annual grass invasion following removal of sagebrush (i.e., Davies et al., 2011a; Pyke et al., 2014).

Treatment Effects on Vegetation and Ground Cover

The mechanisms responsible for increases we observed in broom snakeweed and sagebrush seedling density in 2012 and 2013 at C-S but not non — C-S sites are not clearly understood but may have been a consequence of preexisting differences in seed bank composition as opposed to differential emergence from seed banks due to competition experienced by emerging shrubs. Higher initial abundance of broom snakeweed before applying treatments indicates that preexisting populations were higher on C-S sites and that this species continued to be more abundant compared with non — C-S sites into 2015 (Fig. 5a). In contrast, it is unlikely that increases in seedling density of big sagebrush and broom snakeweed were a result of differences in competition experienced by emerging shrubs because C-S sites had much higher grass cover than non — C-S, which is known to provide strong competition with emerging shrub seedlings (Robertson, 1947; Frischknecht and Bleak, 1957; Gunnell et al., 2010). While perennial grass biomass increased in response to treatment on non — C-S sites (possibly due to depleted understory conditions that existed before treatment), an opposite response for C-S sites is likely a result of the understory already being dominated by introduced forage grasses, which are known to compete with seeded native species (Waldron et al., 2005; Nafus et al., 2015). Furthermore, because seeded forb species that were not previously present on sites generally established more readily on non — C-S sites, where relative decreases in bare ground were greater, these sites were more predisposed to understory herbaceous vegetation release following treatment relative to C-S sites, which agrees with other sagebrush reduction studies (Sturges, 1986; Olson and Whitson, 2002; Davies et al., 2012b). We also surmise that by 2013, the general increase in herbaceous cover and biomass, and thus decreased bare ground, was responsible for increased litter cover only for the non — C-S sites (Davies et al., 2012b; Williams et al., 2014; Pierson et al., 2015). Lastly, perennial forb cover increased in response to treatment for both site histories, but more so at C-S sites, and this response appears to be due to six, nonseeded species that were more prevalent at the C-S sites.

Treatment Effects on Seeding and Resident Species

Greater establishment of two perennial forbs (blue flax and small burnet) and greater increases in cover of three seeded native grasses that were already present (i.e., bluebunch wheatgrass, Sandberg bluegrass, and bottlebrush squirreltail) in non — C-S sites than C-S sites provides further evidence that site history is a major determinant of short-term restoration outcomes. In addition, these results are encouraging since forbs are important for wildlife forage (Connelly et al., 2000; Crawford et al., 2004; Dumroese et al., 2015) and perennial grasses help reduce soil erosion (Beyers, 2004) and invasion by exotic annual grasses (Chambers et al., 2014a) and provide critical forage for livestock and wildlife (Urness et al., 1983; Austin et al., 1994; Gregg et al., 1994), as well as hiding cover for wildlife species (Gregg et al., 1994; Rhodes et al., 2010; Shirk et al., 2017). Greater establishment from the seeding was likely due to the absence of competition in the understory in non — C-S sites. In contrast, lower seeding establishment of the forb species that were not previously present at C-S sites is probably a consequence of competition from previously seeded crested wheatgrass, which has been shown to limit establishment of other species from seedbanks (Marlette and Anderson, 1986; Gunnell et al., 2010). Our results showed that previously seeded intermediate and crested wheatgrass cover were still abundant at C-S sites and likely reduced the ability of resident native perennial grasses to increase due to competition for limiting resources (Schuman et al., 1982; Francis and Pyke, 1996; Morris et al., 2014). Despite these potential species interactions, our results showed that crested and intermediate wheatgrass contributed to increases in herbaceous perennial cover and biomass at C-S sites in the short term (5 years). Increases in perennial grass help meet management objectives and restoration goals for the site, and our results suggest that sites with a cultivation legacy, especially one that is followed by seeding of exotic forage grasses may not require seeding as part of contemporary restoration efforts.

Management Implications

Wyoming big sagebrush communities can be improved by moderate shrub reduction followed by seeding, yet we emphasize that long-term assessments (i.e., > 5 years) are required to determine site trajectories in response to Wyoming big sagebrush reduction (Davies et al., 2012a) and to determine whether treatment sites begin to resemble reference state conditions for a given ecological site (Forbis et al., 2007). Although none of the eight sites in our study achieved understory vegetation resembling reference state conditions over the 5 years following treatment, considerable improvements were noted, but these varied depending on site history. Most importantly, our study emphasizes that land-use legacy effects strongly dictate the magnitude of change in vegetation and species composition experienced on restoration sites. We also emphasize that managers can expect contemporary shrub reduction and seeding treatments to yield greater changes (including greater decreases in bare ground, more dramatic increases in resident native species, and higher rates of seeded species not previously present on restoration sites) on sites that have not experienced a historical cultivation-seeding legacy. Documenting legacy effects from previous land use is becoming increasingly easier with the advent of online tools and resources (Morris and Monaco, 2011; Morris, 2012b; Pilliod et al., 2017) and can assist with restoration planning and setting realistic management goals and expectations. Increases for native grasses and two of the seeded forbs not previously found on study sites indicate that meeting management goals for greater understory native species abundance and increasing forb diversity (Ziegenhagen and Miller, 2009) will be more attainable for sites that have not experienced a C-S legacy. In addition, the robust increases of previously seeded forage grasses following the application of chain harrow-seeding treatments on C-S sites suggest that seeding may not be necessary on such sites and that the benefits to forage production and soil stabilization provide promising conditions to support future livestock grazing and habitat needs for wildlife. We conclude that contemporary chain harrow − seeding treatments improved understory conditions. Although increases in cheatgrass are a common occurrence when applying shrub reduction techniques (Monaco et al., 2017), we did not consider it a hindrance to the understory recovery on these sites. This speculation is based on the fact that perennial grass cover either remained very high in C-S sites (i.e., > 30%) or increased in non − C-S sites due to the combination of treatment and seeding (see Fig. 5; Table 3); increasing levels of perennial grass cover can result in simultaneous reductions in annual grass cover (Anderson and Inouye, 2001). Consequently, we recommend applying less-intensive rehabilitation treatments at lower-elevation Wyoming big sagebrush sites where understory vegetation may be more degraded and therefore cannot adequately provide resistance to cheatgrass invasion (Davies et al., 2012b; Chambers et al., 2017).

Acknowledgments

Many Utah State University students assisted with fieldwork and sample processing, including Joe Lamb, Sarahi Felix, Kyle Becker, Mike Grant, Merilynn Schantz, and Tom Green. We are grateful to Ann Neville at Rio-Tinto, Kennecott Utah Copper for providing logistical support and access to private lands. We also recognize current lessee Shamus Haws, for his assistance and support in carrying out our study. We also thank previous lessees, Tom Giovengo and Gerald Mahoney, who participated in interviews to ascertain land-use history and past cultivation activities on Barney Ridge. Lesley Morris provided expertise into interpreting site history designations, and Kari Veblen offered valuable suggestions to improve our manuscript.

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