

RESEARCH ARTICLE

Evaluating strategies for facilitating native plant establishment in northern Nevada crested wheatgrass seedings

J. Kent McAdoo^{1,2}, John C. Swanson³, Peter J. Murphy³, Nancy L. Shaw⁴

Non-native crested wheatgrasses (*Agropyron cristatum* and *A. desertorum*) were used historically within the Great Basin for the purpose of competing with weed species and increasing livestock forage. These species continue to be used in some areas, especially after wildfires occurring in low elevation/precipitation, formerly Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*)/herbaceous communities. Seeding native species in these sites is often unsuccessful, and lack of establishment results in invasion and site dominance by exotic annuals. However, crested wheatgrass often forms dense monocultures that interfere competitively with the establishment of desirable native vegetation and do not provide the plant structure and habitat diversity for wildlife species equivalent to native-dominated sagebrush plant communities. During a 5-year study, we conducted trials to evaluate chemical and mechanical methods for reducing crested wheatgrass and the effectiveness of seeding native species into these sites after crested wheatgrass suppression. We determined that disking treatments were ineffective in reducing crested wheatgrass cover and even increased crested wheatgrass density in some cases. Glyphosate treatments initially reduced crested wheatgrass cover, but weeds increased in many treated plots and seeded species diminished over time as crested wheatgrass recovered. We concluded that, although increases in native species could possibly be obtained by repeating crested wheatgrass control treatments, reducing crested wheatgrass opens a window for invasion by exotic weed species.

Key words: *Agropyron cristatum* and *A. desertorum*, assisted succession, exotic weeds, mechanical and chemical treatments, monocultures, revegetation with native species

Implications for Practice

- Glyphosate treatments can be effective in reducing crested wheatgrass cover, but effectiveness diminishes within a few years as this competitive species recovers.
- Reducing crested wheatgrass opens a window for weed invasion if native seeding fails; successfully established native species may decline as crested wheatgrass recovers.
- Converting crested wheatgrass monocultures to native plant communities may require multiple treatments over time to remove crested wheatgrass plants and seed bank, weed reduction treatments, and/or supplemental seeding or outplanting of native species.

Introduction

Non-native grasses have altered the composition, structure, and function of vegetation over vast areas in dryland ecosystems across the globe (D'Antonio & Vitousek 1992). Although many non-native grasses have been introduced inadvertently, others were, and some have continued to be, selected intentionally for seeding pastures or disturbed wildland landscapes (Joubert & Cunningham 2002; Marshall et al. 2012). These include annual and perennial C3 and C4 species (see Hull 1974; D'Antonio & Vitousek 1992) selected for their ease of establishment, forage production, soil stabilization, and resistance to exotic invasives.

Extensive monocultures of these species, and in some cases their spread into native communities, have resulted in reduced biodiversity, wildlife habitat, and ecosystem services over large areas. Increasing emphasis on conservation and restoration of native communities has led to efforts to control, replace, or reduce the dominance of these non-natives by reestablishing native species. However, control and replacement of such species, such as bulbous bluegrass (*Poa bulbosa* L.) and Lehmann lovegrass (*Eragrostis lehmanniana* Nees), are difficult (Hull 1974; Biedenbender et al. 1995).

In the United States, more than 5 million hectares of semi-arid and arid western rangelands were seeded with non-native crested wheatgrasses (*Agropyron cristatum* (L.) Gaertn. and *A. desertorum*) [Fisch. ex Link] Schult) and Siberian wheatgrass

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(*Agropyron fragile* [Roth] P. Candargy) by the 1990s (Maryland et al. 1992). From the 1950s through the early 1970s, approximately 405,000 ha of sagebrush (*Artemisia* spp.) rangeland in Nevada were converted to crested wheatgrass, (Young et al. 1979) primarily for the purpose of increasing livestock forage and reducing halogeton (*Halogeton glomeratus* [M. Nieb.] C. A. Mey), an exotic plant that is toxic to domestic sheep (Miller 1943). The use of crested wheatgrass has continued in recent years for post-fire rehabilitation (Knutson et al. 2014). Crested wheatgrass is often used for exotic annual grass control (Nafus & Davies 2014) because of its lower cost and relative ease of establishment compared with native perennial grasses (Eiswerth et al. 2009; Boyd & Davies 2010; Davies et al. 2013).

Continued use of crested wheatgrass is controversial (Davies et al. 2011; Fansler & Mangold 2011). Crested wheatgrass often forms dense monocultures (Pyke 1990) and interferes competitively with the establishment of desirable native vegetation (Gunnell et al. 2010; Knutson et al. 2014). Although recent research shows little evidence of substantial changes in ecological processes (such as C and N cycling and soil water availability) when native perennial bunchgrasses are replaced with crested wheatgrass in former sagebrush plant communities (see Davies et al. 2011), crested wheatgrass monocultures do not provide the plant structure and habitat diversity for wildlife species equivalent to sagebrush plant communities (McAdoo et al. 1989). Of considerable concern is that crested wheatgrass has been planted over large areas of current and historic range of the sage-grouse (*Centrocercus urophasianus*) and has negatively impacted this species (Connelly et al. 2000). Because of these concerns, land managers would prefer to use native plant species when revegetating low elevation/precipitation Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) communities (Davies et al. 2015). However, competition from exotic annuals often interferes with establishment of native species and results in the further spread of exotics and increased wildfire risk (Knutson et al. 2014).

Crested wheatgrass has been considered a “bridge” species that, once established, may facilitate establishment of more desirable and diverse native vegetation (Cox & Anderson 2004; Pellant & Lysne 2005). Cox and Anderson (2004) suggested that crested wheatgrass seeding could “capture” disturbed, former sagebrush-perennial grass communities from weedy species, with such communities subsequently rehabilitated/diversified through “assisted succession” by mechanically or chemically reducing competition from crested wheatgrass and then seeding native species. Recent research by Hulet et al. (2010) in Utah and Fansler and Mangold (2011) in Oregon tested the “assisted succession” hypothesis, with generally unsuccessful results. To further evaluate methods for establishing native plants in crested wheatgrass seedings, we tested mechanical and chemical methods designed to shift the successional trajectory of crested wheatgrass communities in northern Nevada. We used approaches similar to those of Hulet et al. (2010) and Fansler and Mangold (2011), but applied additional herbicide treatments in a different ecological setting and over a longer (5-year) study period. We conducted two trials treated 2 years apart and

tracked precipitation, hoping to reduce response variability and enhance the strength of our inferences. We addressed three questions. First, does mechanical treatment, alone or in combination with glyphosate, favor the establishment of native seeded species in these communities? Second, do various applications of glyphosate suppress crested wheatgrass in favor of seeded native species? Third, do chemical alternatives to glyphosate outperform this popular herbicide in the suppression of crested wheatgrass in favor of seeded native species? We hypothesized that (1) the selected treatments used would decrease crested wheatgrass density and cover; and (2) treatments and seeding would result in measurable establishment of native species within our 5-year study window.

Methods

Study Area

The study site was located in the South Fork State Recreation Area, 24 km southeast of Elko, NV, within the Owyhee High Plateau Major Land Resource Area (MLRA) at an elevation of 1,615 m. Soil is a loam (Orovada Puett association with a sandy loam surface texture). The area is in the Loamy 8–10 PZ ecological site (8–10 inch [203–254 mm] precipitation zone), and was formerly dominated by Wyoming big sagebrush plant communities (USDA-NRCS 2015). Climate in this area is typical of the northern Great Basin, with hot dry summers and precipitation occurring primarily during the cool winter and spring months. Crop-year (October–June) precipitation ranged from 55 to 124% of normal for the 2009–2013 study period (Table S1, Supporting Information). The study area was historically in private ownership, and specific sagebrush reduction methodology is unknown. After sagebrush was controlled, the area was seeded to crested wheatgrass (*Agropyron desertorum*), most likely the “Nordan” cultivar (based on historical records of nearby public land seedings). The area was fenced to exclude livestock grazing in 1989, but wildlife access to the study site was unrestricted.

Vegetation at the site was essentially monotypic crested wheatgrass, with less than 1% shrub cover (McAdoo et al. 2013), only occasional occurrence of Indian ricegrass (*Achnatherum hymenoides* [Roemer & J.A. Schultes] Barkworth) and basin wildrye (*Leymus cinereus* [Scribn. & Merr.] Á. Löve), rare manifestations of native forbs (primarily *Astragalus* spp. [L.] and *Descurainia pinnata* [Walter] Britton), and scattered patches of halogeton. Based on the USDA Natural Resources Conservation Service (NRCS) ecological site description and observations of adjacent unseeded plant communities, pre-conversion vegetation in addition to Wyoming big sagebrush, Indian ricegrass, and basin wildrye would likely have included the following species: needle-and-thread grass (*Heterostipa comata* [Trin. & Rupr.] Barkworth), Sandberg bluegrass (*Poa secunda* J. Presl), bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), spiny hopsage (*Grayia spinosa* [Hook.] Moq.), and various native forb species. No cheatgrass (*Bromus tectorum* L.) was observed within the study areas prior to treatment implementation.

Experimental Design, Treatment Implementation, and Plant Materials

We conducted two 10-ha study trials (Trial 1 and Trial 2) located approximately 0.9 km apart (center to center). Each trial was installed as a randomized block split-plot design with five 2-ha blocks. Each block was divided into five 0.4-ha main plots randomly designated as “untreated” (U) or one of four crested wheatgrass suppression treatments assigned (see below) to each trial. Main plots were further divided into two 0.2 ha split-plots that were randomly selected for either seeding or no seeding. Nonseeded split-plots were included to simulate the outcome of suppression treatments if the seeding treatment failed.

For Trial 1, “disced only” (D) plots were 3-way disced (at right angles and diagonally) during November 2007. In late May 2008, “spring-applied glyphosate” (G) (Roundup Pro®, a post-emergent herbicide that includes surfactant) and “combined discing + glyphosate” (DG) plots were sprayed with glyphosate. In early October 2008, “combined spring + fall-applied glyphosate plots” (GG) were sprayed again with glyphosate. All glyphosate treatments were applied at the rate of 4.7 L/ha. Trial 2 was implemented in 2010, allowing us to adaptively modify treatments informed by Trial 1, which indicated that discing was ineffective at suppressing crested wheatgrass (consistent with results reported by Fansler & Mangold 2011). Hence, we replaced discing with additional herbicide treatments. Crested wheatgrass suppression treatments for Trial 2 consisted of full-rate glyphosate (G), half-rate glyphosate (G/2) at 2.35 L/h, imazapic (I) (Panoramic® 2SL) at 0.73 L/ha, and chlor-sulfuron + sulfometuron methyl (CS) (Landmark®XP) at 0.15 L/ha, all applied in May. The latter two chemicals, applied with a 0.25% v/v nonionic surfactant, can function as both pre- and post-emergent herbicides. We applied them during the active growth period of crested wheatgrass to take advantage of post-emergent action.

For each trial, personnel from the Aberdeen, Idaho NRCS Plant Materials Center seeded randomly selected split-plots with a Truax Rough Rider minimum-till drill at NRCS-recommended rates, in late October 2008 for Trial 1 and late October 2010 for Trial 2. Press wheels and drag chains installed behind disks on the minimum-till drill provided seed–soil contact and seed burial in drill rows for large seeds, whereas patterned imprinter wheels enhanced seed–soil contact in broadcast rows for small seeds. The site-adapted seed mixture included Indian ricegrass, bottlebrush squirreltail, needle-and-thread grass, basin wildrye, Snake River wheatgrass (*Elymus wawawaiensis* J. Carlson & Barkworth), Sandberg bluegrass, Munro globemallow (*Sphaeralcea munroana* [Douglas] Spach), blue flax (*Linum perenne* L.), western yarrow (*Achillea millefolium* L.), Wyoming big sagebrush, and spiny hopsage (see Table S2 for seeding rates and cultivars used). All species seeded were native with the exceptions of Snake River wheatgrass, used because of its adaptation to this low precipitation zone, and blue flax, used as a substitute for Lewis flax (*L. lewisii* Pursh), which was unavailable at the time.

Vegetation Sampling

During the summers of 2009, 2010, 2011, and 2013 for Trial 1 and 2012 and 2013 for Trial 2, we used a stratified random sampling design to measure four vegetation parameters: cover and density of crested wheatgrass, cover of exotic weeds, and density of seeded species. We established five 18-m transects spaced 10 m apart in each split-plot. Along each transect, we measured density and canopy cover in 10 frames of 0.25 m² placed at 2-m intervals along each transect. Density of crested wheatgrass and seeded species was determined by counting individual plants within each sampling frame. Cover was estimated using Daubenmire cover classes (Daubenmire 1959) for crested wheatgrass. For exotic weeds, a modified Daubenmire method, including a “0” cover category, was used to more accurately reflect initial weed scarcity (see Hatton et al. 1986). To determine percent cover for each split-plot, we calculated midpoints of the cover classes and averaged them across transects.

We pooled seeded perennial grass data across species for the first growing season (2009) of Trial 1 because species were difficult to distinguish during the seedling stage. This difficulty, along with the high mortality of seeded species observed between the first two growing seasons (similar to that reported by Hulet et al. (2010) and Fansler and Mangold (2011)), led us to delay initial data collection for Trial 2 until the second growing season after seeding. Seeded forb and shrub species were readily identified and recorded by species for both trials in all years.

Statistical Analyses

We assessed the effect of treatment, seeding, and year on cover and density of crested wheatgrass using the linear mixed model procedure (SAS version 9.2, SAS Institute Inc., Cary, NC, U.S.A.). Trials 1 and 2 were initially analyzed separately because they involved different treatments and sampling years. Fixed effects were treatment, seeding, and year and all two-way interactions. The three-way interaction term (treatment × seeding × year) was dropped due to lack of significance and poorer model fit when it was included, as indicated by a higher Akaike information criterion with correction for finite sample size (AIC_C). Because of the split-plot design, block and treatment-by-block were treated as random effects. Year was a repeated effect implemented with unstructured covariance, which produced better fit (lower AIC_C) than did compound-symmetric or first-order autoregressive covariance models. For each response, we compared treatment means pairwise for both Trial 1 and Trial 2, using the Dunn–Sidak method to control for multiple comparisons. Cover percentages were arcsine-square root transformed and densities log-transformed to meet assumptions of ANOVA.

Trials 1 and 2 were not statistically comparable across all treatments because (1) some treatments were unique to each trial; (2) stochastic events (especially precipitation) were different for each trial; and (3) Trial 1 was conducted over a 5-year period compared to only 3 years for Trial 2. Nevertheless, the two trials were conceptually comparable, and we made statistical comparisons between the two trials where appropriate.

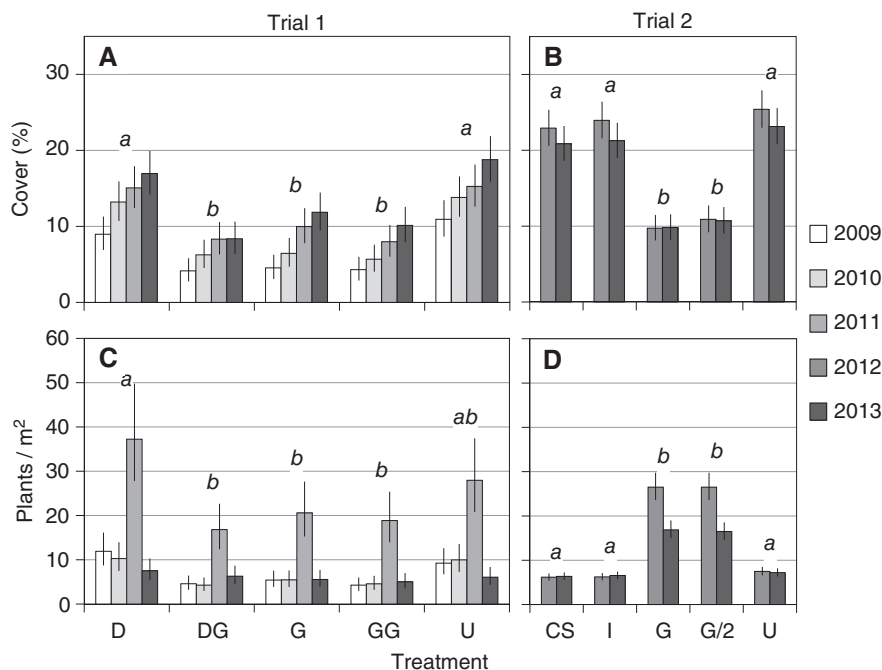


Figure 1. Crested wheatgrass cover and density by treatment and year in two northern Nevada trials. Treatments are discing (D); discing plus glyphosate (DG); glyphosate (G); spring and fall glyphosate (GG); undisturbed (U); chlorsulfuron + sulfometuron methyl (CS); imazapic (I); and half-rate glyphosate (G/2). Bars represent back-transformed means ($\pm 95\%$ CI) from analyses based on arcsine-square root transformed percentages and log-transformed densities. By variable within each trial, treatments (bar groups across years) that do not share a common letter differ significantly ($p < 0.05$, Dunn-Sidak).

Because Trials 1 and 2 shared the glyphosate (G) and control (U) treatments and were sampled in 2013, we tested for a treatment-by-trial interaction on crested wheatgrass cover and density in a single-year split-plot model. We used the same methods to analyze weed cover (total and by species).

For seeded species, we assessed the effect of treatment, year, and treatment-by-year on log-transformed density using repeated-measures analysis of variance. Each species was analyzed separately, and we ran analyses for total seeded species, perennials, and forbs. For each response, we compared treatment means pairwise for each trial, again using Dunn-Sidak to control for multiple comparisons. As for crested wheatgrass and weed cover, we compared seeded species density in 2013 by trial and treatment for the glyphosate (G) and untreated (U) plots. In the species-specific analyses, a large number of zeroes in Trial 1 for seven species and for all seeded species in Trial 2 led to non-normal residuals and suspect statistical conclusions.

Results

Crested Wheatgrass Suppression

All treatments that included glyphosate reduced crested wheatgrass cover compared to no treatment (U). Cover was significantly lower in DG, G, and GG than in D and U treatments in Trial 1 ($F_{[4,16]} = 20.4$, $p < 0.001$; Fig. 1A) and lower in G and G/2 than in other herbicide treatments (CS and I) and U in Trial 2 ($F_{[4,16]} = 82.6$, $p < 0.001$; Fig. 1B), averaging about 50% less

than U. However, crested wheatgrass density responded differently to glyphosate in the two trials. In Trial 1, all glyphosate treatments reduced crested wheatgrass density compared to D (by almost half), but no treatment significantly reduced density below U ($F_{[4,16]} = 6.3$, $p = 0.003$; Fig. 1C). Conversely, in Trial 2, glyphosate (G and G/2) treatments nearly tripled density compared to U and the other herbicides ($F_{[4,16]} = 140.3$, $p < 0.001$; Fig. 1D), which were all similar. There was a trial ($F_{[1,66]} = 6.7$, $p = 0.012$) and treatment-by-trial interaction for crested wheatgrass density in 2013 ($F_{[1,66]} = 34.7$, $p < 0.001$; only G and U included).

Crested wheatgrass cover increased relatively consistently across all treatments over the years in Trial 1 (year, $F_{[3,152]} = 99.2$, $p < 0.001$; year-by-treatment, $F_{[12,152]} = 1.6$, $p = 0.102$), while decreasing slightly in nonglyphosate treatments in the second sampling year of Trial 2 (year, $F_{[1,64]} = 12.7$, $p = 0.001$; year-by-treatment, $F_{[4,64]} = 2.0$, $p = 0.102$; Fig. 1A & B). Unlike cover, crested wheatgrass density spiked in 2011 in Trial 1 ($F_{[3,152]} = 202.8$, $p < 0.001$; Fig. 1C) and in 2012 in Trial 2 ($F_{[1,64]} = 88.8$, $p < 0.001$; Fig. 1D). The magnitude of these spikes differed by treatment in both trials, producing year-by-treatment interactions ($p < 0.001$). By 2013, G treatment had reduced crested wheatgrass cover compared to U more effectively in Trial 2 (by 58%) than in Trial 1 (by 45%), driving a trial effect ($F_{[1,66]} = 10.6$, $p = 0.002$) and a treatment-by-trial interaction ($F_{[1,66]} = 31.6$, $p < 0.001$). This comparison is between three growing seasons after treatment for Trial 2 versus five for Trial 1.

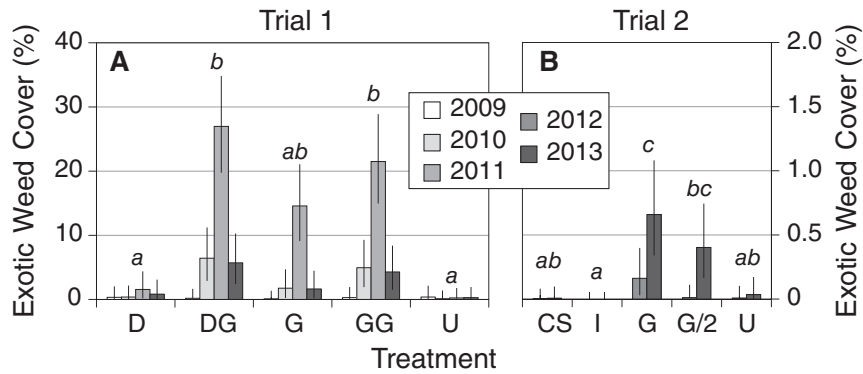


Figure 2. Total exotic weed cover by treatment and year in two northern Nevada trials. Treatments are discing (D); discing plus glyphosate (DG); glyphosate (G); spring and fall glyphosate (GG); undisturbed (U); chlorsulfuron + sulfometuron methyl (CS); imazapic (I); and half-rate glyphosate (G/2). Bars represent back-transformed means ($\pm 95\%$ CI) from analyses based on arcsine-square root transformed percentages and log-transformed densities. Within each trial, treatments (bar groups across years) that do not share a common letter differ significantly ($p < 0.05$, Dunn–Sidak). Note differences in scale between left and right vertical axes.

Response of Exotic Weeds

Exotic weed establishment was generally favored by glyphosate treatments that suppressed crested wheatgrass cover. We detected five weed species in Trial 1 and four in Trial 2. Weed cover values ranged from 0–28% in Trial 1 and 0–0.7% in Trial 2, with halogeton and tumble mustard (*Sisymbrium altissimum* L.) greatest in cover. Cheatgrass occurred at extremely low cover in both trials ($< 0.1\%$ across treatments). In Trial 1, we found significantly greater total weed cover across years (by 10-fold) in DG and GG treatments compared to D and U, with G treatment falling between these two groups ($F_{[4,16]} = 9.1$, $p < 0.001$; Fig. 2A). Similarly, for Trial 2, exotic weed cover was significantly greater (by an order of magnitude) in G as compared to CS, I, and U treatments, with G/2 falling between these two groups ($F_{[4,16]} = 9.6$, $p < 0.001$; Fig. 2B). However, with cover being less than 1% for all treatments in Trial 2, the biological significance of these differences is questionable. In Trial 1, weed cover increased in 2011 (a relatively wet year, Table S1), evidenced especially in the glyphosate treatments (Fig. 2A) and resulting in a significant effect of year ($F_{[3,152]} = 39.74$, $p < 0.001$) and year-by-treatment ($F_{[12,152]} = 6.1$, $p < 0.001$).

By the end of the study (2013), 5-year post-treatment, total exotic weed cover in Trial 1 was 8 to 12 times greater in two of the three glyphosate treatments, GG and DG, than in U ($F_{[4,16]} = 7.5$, $p = 0.001$; Fig. 3A), two of the same treatments that also reduced crested wheatgrass cover (Fig. 1). Likewise, G treatment in Trial 2 (3-year post-treatment) had significantly more exotic weed cover than CS, I, and U, with G/2 falling between the two groups ($F_{[4,16]} = 8.0$, $p = 0.001$; Fig. 3C). By 2013, halogeton and tumble mustard were the primary exotic weeds in both trials. Halogeton cover was numerically greater in glyphosate treatments (Fig. 3B & D), but variable among plots in both trials, indicating no significant differences by treatment ($F_{[4,16]} \leq 2.7$, $p \geq 0.068$). Tumble mustard cover was consistently greater after the DG treatment in Trial 1 and after both the G and G/2 treatments in Trial 2 ($F_{[4,16]} \geq 5.8$, $p \leq 0.005$; Fig. 3B & D).

Seeded Species Establishment

In Trial 1, the density of seeded species averaged across years was significantly higher (by approximately 70%) in DG, G, and GG treatments than in U, with D falling between these groups ($F_{[4,20]} = 4.8$, $p = 0.007$; Fig. 4A). Similarly, in Trial 2, though measured values were an order of magnitude lower than in Trial 1, G treatment had significantly (16 times) higher densities of seeded species than CS, I, and U treatments, with G/2 falling between these groups ($F_{[4,20]} = 5.1$, $p = 0.005$; Fig. 4B). In Trial 1, the surge of establishment in 2009 was followed by sharp mortality in 2010 and thereafter, with larger die-offs in D and U plots (year, $F_{[3,20]} = 151.7$, $p < 0.001$; year-by-treatment, $F_{[12,20]} = 3.8$, $p = 0.004$; Fig. 4A). In Trial 2, mortality from 2012 to 2013 was lower but significant across treatments ($F_{[1,20]} = 7.0$, $p = 0.015$; Fig. 4B). Because of heavy mortality, by 2013 in Trial 1 (5-year post-seeding) the effect of treatment was marginal on total seeded density ($F_{[4,20]} = 2.7$, $p = 0.062$) but was still significant for seeded perennial grasses ($F_{[4,20]} = 3.1$, $p = 0.039$), driven by the almost 2-fold difference between the DG treatment and U (Fig. 5, top). By 2013 in Trial 2 (3-year post-seeding), total seeded and seeded perennial grass densities were significantly to marginally higher in G and G/2 than in the other treatments ($F_{[4,20]} \geq 4.8$, $p \leq 0.007$; Fig. 5, bottom). When comparing the effect of only G treatment versus U on seeded densities in 2013 across trials, no effect of trial ($F_{[1,36]} \leq 0.9$, $p \geq 0.348$), treatment ($F_{[1,36]} \leq 0.16$, $p \geq 0.690$), or treatment-by-trial ($F_{[1,36]} \leq 1.2$, $p \geq 0.275$) was found on seeded total, perennial grass, or forb species.

Establishment of seeded species was more successful in Trial 1 than in Trial 2. Across treatments 2 years after seeding, total densities were roughly 600% higher in Trial 1 than in Trial 2 (0.88 vs. 0.14 plants/m²; Fig. 4A & B, 2010 vs. 2012, respectively). However, by 2013 (5-year and 3-year post-treatment for Trials 1 and 2, respectively), total seeded densities were only about 40% higher in Trial 1 than in Trial 2 (0.14 vs. 0.10 plants/m²). Across years and treatments, total densities of seeded species ranged from 0 to 15.7 plants/m² in Trial 1 (grasses: 0–15.4, forbs: 0–1.5) and from 0–1.1 plant/m² in

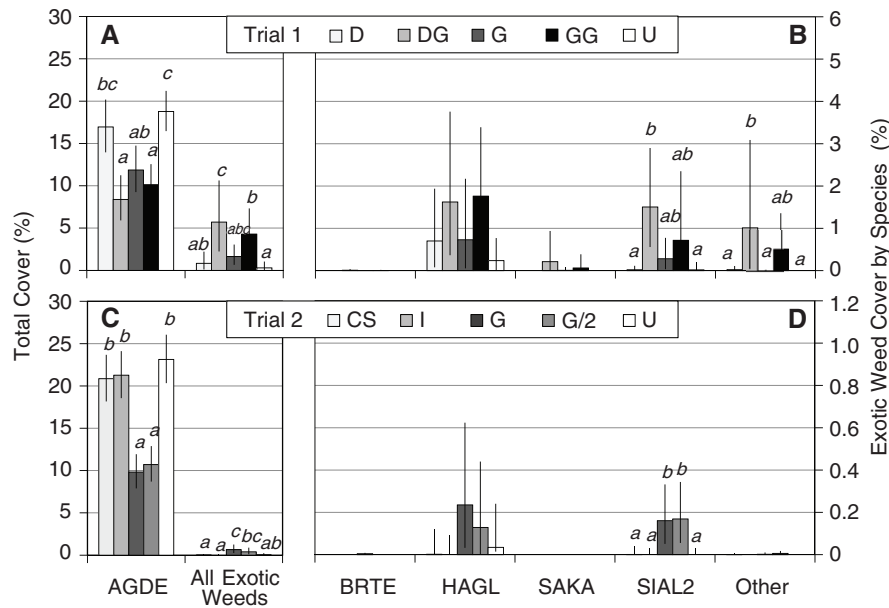


Figure 3. Crested wheatgrass and exotic weed cover in the final growing season (2013) for Trial 1 (5 years post-treatment) and Trial 2 (3 years post-treatment), northern Nevada. The right-side panels (B) and (D) show weed cover by species. Treatments are discing (D); discing plus glyphosate (DG); glyphosate (G); spring and fall glyphosate (GG); undisturbed (U); chlorsulfuron + sulfometuron methyl (CS); imazapic (I); and half-rate glyphosate (G/2). Bars represent back-transformed means ($\pm 95\%$ CI) from analyses based on arcsine-square root transformed percentages. By vegetation category within each trial, treatments that do not share a common letter differ significantly ($p < 0.05$, Dunn–Sidak). Species abbreviations are: AGDE, crested wheatgrass; BRTE, cheatgrass; HAGL, halogeton; SAKA, Russian thistle; and SIAL2, tumble mustard. Note differences in scale between left and right vertical axes.

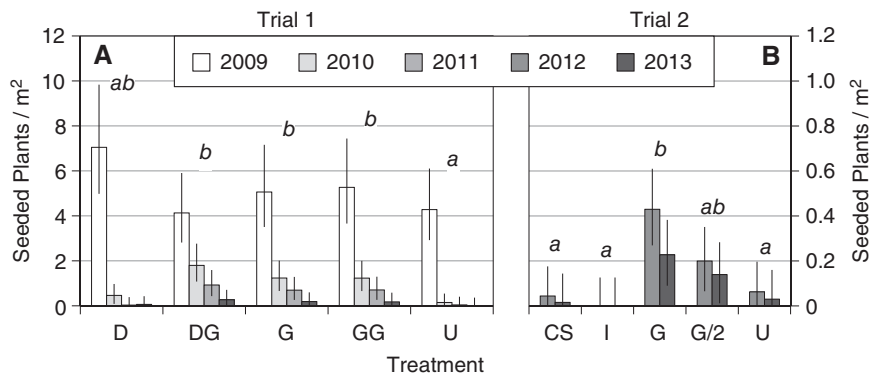


Figure 4. Total seeded species density by treatment and year in two northern Nevada trials. Treatments are discing (D); discing plus glyphosate (DG); glyphosate (G); spring and fall glyphosate (GG); undisturbed (U); chlorsulfuron + sulfometuron methyl (CS); imazapic (I); and half-rate glyphosate (G/2). Bars represent back-transformed means ($\pm 95\%$ CI) from analyses based on arcsine-square root transformed percentages and log-transformed densities. Within each trial, treatments (bar groups across years) that do not share a common letter differ significantly ($p < 0.05$, Dunn–Sidak). Note differences in scale between left and right vertical axes.

Trial 2 (grasses: 0–0.8, forbs: 0–0.2). Of the 11 species seeded (Table S2), we initially found 10 in Trial 1: Wyoming big sagebrush, all six perennial grasses, and all three forbs. In Trial 2, we detected seven: Wyoming big sagebrush, four perennial grasses, and two forbs. Spiny hopsage did not establish in either trial.

Notwithstanding statistical limitations of the species-specific seeding analyses, the most abundant seeded native grasses across years in Trial 1 were basin wildrye, bottlebrush squirreltail, and Indian ricegrass, and the most abundant seeded forb was Munro’s globemallow. However, by 2013, only six seeded herbaceous species remained in Trial 1, with Indian ricegrass

absent, leaving basin wildrye, squirreltail, and Munro’s globemallow as the dominant seeded native species (Fig. 5, top). In Trial 2, only four herbaceous seeded species remained by 2013, with the same three seeded native species being most abundant (Fig. 5, bottom). These three were more consistently present in the DG and G treatments. Marginally or significantly higher densities for basin wildrye in Trial 1 and bottlebrush squirreltail in Trial 2 were observed in glyphosate-treated plots compared to other treatments (Fig. 5). We recorded no establishment of native species within any unseeded split-plots.

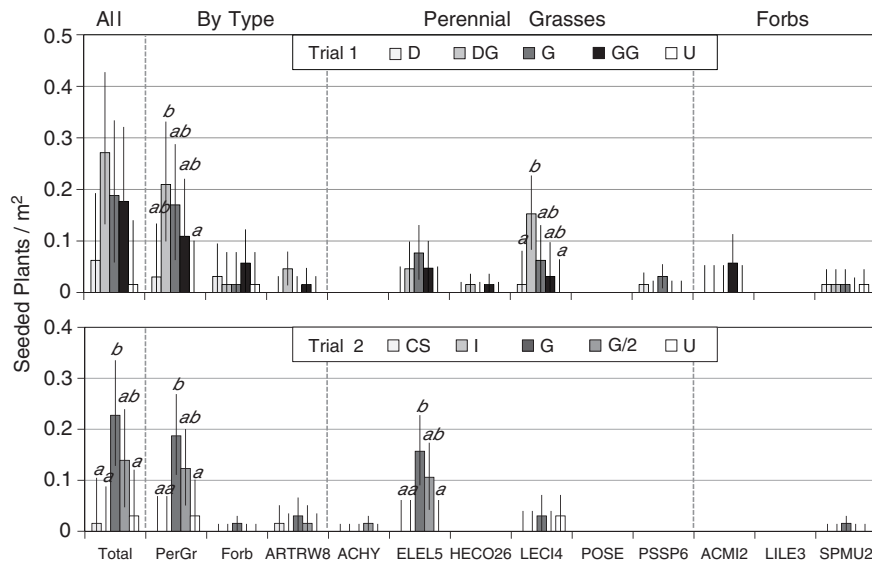


Figure 5. Density of seeded native species in the final growing season (2013) for Trial 1 and Trial 2 (5 and 3 years post-treatment and seeding, respectively), northern Nevada. Treatments are discing (D); discing plus glyphosate (DG); glyphosate (G); spring and fall glyphosate (GG); undisturbed (U); chlorsulfuron + sulfometuron methyl (CS); imazapic (I); and half-rate glyphosate (G/2). Bars represent back-transformed means ($\pm 95\%$ CI) from analyses based on log-transformed densities. By vegetation category within each trial, treatments that do not share a common letter differ significantly ($p < 0.05$, Dunn–Sidak). Abbreviations are: PerGr, all perennial grasses; Forb, all forb species; ARTRW8, Wyoming big sagebrush; ACHY, Indian ricegrass; ELEL5, bottlebrush squirreltail; HECO26, needle-and-thread grass; LECI4, basin wildrye; POSE, Sandberg’s bluegrass; ELWA2, Snake River wheatgrass; ACMI2, western yarrow; LIPE2, blue flax; SPMU2, munro globemallow. Spiny hopsage (not shown) did not establish in either trial.

Discussion

Crested Wheatgrass Reduction Treatment Effectiveness

Our hypothesis that the selected treatments would decrease crested wheatgrass density and cover was only partially supported by our data. Although the effects of glyphosate treatments were transient, they generally produced the best control of crested wheatgrass. A comparison of our results with similar studies in Utah (Hulet et al. 2010) and Oregon (Fansler & Mangold 2011) demonstrates the variability in treatment responses among various sites within low elevation Wyoming big sagebrush communities. Nevertheless, results of all three studies indicated that, no matter how effective a specific treatment might be for initially reducing crested wheatgrass, these effects diminish steadily over time, resulting in increasing competition from crested wheatgrass that may interfere with establishment and persistence of seeded native species. Interestingly, the *Agropyron desertorum* “Nordan” cultivar used in our study is considered more susceptible to control with glyphosate herbicide than the other commonly planted *Agropyron cristatum* “Fairway” and “Hycrest” cultivars (Lym & Kirby 1991). Repeated applications may be necessary because crested wheatgrass may recover following treatment (Hansen & Wilson 2006).

Crested wheatgrass plants recovering after control treatments benefit from reduced competition and produce numerous tillers and seedheads (Ambrose & Wilson 2003; Wilson & Partel 2003). High seed production from crested wheatgrass plants remaining after glyphosate treatment and cover reduction (still apparent in 2011) and increased resource availability could

have also contributed to increased seedlings in a wet year (see Ambrose & Wilson 2003). Therefore, the increase in crested wheatgrass density observed in 2011 may have been the result of seedlings responding to a relatively wet spring (101 mm precipitation), but increased seedlings would not necessarily increase cover. Fall application of glyphosate (Trial 1) might have been more effective with greater soil moisture, but July–September precipitation (29 mm) prior to October spraying was not enough to produce green-up. Looking at both trials, all three of the herbicides were labeled for post-emergent action, but only glyphosate had any impact. Also, many of the crested wheatgrass fragments caused by discing may have survived (see Fansler & Mangold 2011), keeping both cover and density measurements high.

Response of Exotic Weeds

Exotic weeds were more responsive to treatments in Trial 1 than Trial 2. This may have been caused by any one or a combination of the following factors: (1) level of weed infestation before treatment; (2) proximity of off-site weed source to trial location; (3) timing of treatments as related to precipitation patterns; (4) effectiveness of crested wheatgrass control treatment, which could have reduced competition and allowed more weed cover; and/or (5) pre-emergent weed control potential of CS and I herbicides used in Trial 2. Based on measurements in untreated (U) plots and pre-experiment reconnaissance, exotic weed cover was minimal in both trial areas before treatment implementation, but a small patch of tumble mustard was observed within 0.2-km west of the Trial 1 area and was

likely introduced into the area by prevailing westerly winds. Regarding precipitation patterns, both trials were seeded during years of above normal crop-year precipitation. However, precipitation for Trial 1 in 2009 was 32% higher in spring (April–June) and 93% higher in summer (July–September) as compared to that for Trial 2 in 2011 (see Table S1). High spring precipitation results in high germination and vigorous growth of exotic winter annual weeds, including tumble mustard (Eckert et al. 1974; Allen & Meyer 2014). Regarding treatment effectiveness, three of the four crested wheatgrass control treatments used in Trial 1 (all including glyphosate) initially reduced crested wheatgrass cover significantly, and two of the four treatments in Trial 2 (both involving glyphosate) were similarly effective on crested wheatgrass cover as compared to untreated areas. Finally, the I herbicide (Trial 2) with its 120-day half-life, though applied in May as a post-emergent treatment 5 months before seeding, could have had some residual pre-emergent control potential and may have reduced weed emergence, especially during the first growing season after seeding. Higher weed cover in G treatment compared to CS and I treatments lends some validity to this possibility. However, the issue is complicated by the significant reduction of crested wheatgrass by G treatment, as compared to CS and I treatments, resulting in less competition for invading weeds. The CS herbicide, with a half-life less than that of G herbicide, would have had negligible effect.

Other studies have shown that native species establishment and survival can be seriously compromised if persistent seed banks of crested wheatgrass or weeds are not adequately reduced prior to seeding (Henderson & Naeth 2005; Hulet et al. 2010). More specifically, researchers have issued caution regarding the risk of cheatgrass invasion after crested wheatgrass reduction (Hulet et al. 2010; Davies et al. 2013), particularly if the seeded native species are not successfully established. Cheatgrass invasion was not the greatest exotic weed threat during our study. However, even though this species was undetected before treatment implementation, by study's end (2013) there was a minor expression of cheatgrass across treatments. Tumble mustard became the dominant exotic weed in all three glyphosate treatments during 2011 (for Trial 1), the third growing season after crested wheatgrass reduction and concurrent with 124% of normal crop-year precipitation (Table S1). Tumble mustard declined precipitously after 2011 but was the co-dominant exotic species with halogeton by study's end.

Seeded Species Establishment

Our hypothesis that crested wheatgrass reduction treatments and seeding would result in successful establishment of native plant species was partially supported by our data. By reducing crested wheatgrass (in the short term), all glyphosate treatments except G/2 initially resulted in higher densities of all seeded species combined in both Trial 1 and Trial 2 as compared to untreated plots. However, the gradual but significant annual increase in crested wheatgrass cover over 5 years in Trial 1 and the corresponding decline in seeded native species over time underscores findings of other studies indicating competition

from introduced species like crested wheatgrass can be reduced but not eliminated (Bakker et al. 2003), and that non-native perennial grasses are more competitive than native species (Chambers et al. 1994). The competitive traits of crested wheatgrass, including high seed production and seed bank domination (Pyke 1990), as well as rapid soil water extraction and rapid nutrient acquisition (Gunnell et al. 2010), are mechanisms that interfere with the growth and establishment of native perennial grasses. According to Knutson et al. (2014), seedings at lower, relatively drier locations are less likely to result in establishment of perennial grasses. The literature is replete with statements and conclusions indicating that introduced bunchgrasses generally have higher establishment rates than native bunchgrasses in sagebrush-dominated and formerly sagebrush-dominated plant communities (e.g. Robertson et al. 1966; Hull 1974; Boyd & Davies 2010). If persistent seed banks of crested wheatgrass are not sufficiently reduced before seeding, native species establishment and persistence may be seriously jeopardized (Henderson & Naeth 2005; Hulet et al. 2010), with crested wheatgrass potentially out-recruiting native grasses by many orders of magnitude (Nafus et al. 2015). During our study, we routinely observed numerous crested wheatgrass seedlings from seed germination as well as tillers from established plants.

Previous research has shown the difficulty of successfully seeding native forbs in crested wheatgrass stands (Hulet et al. 2010; Fansler & Mangold 2011). Competition from crested wheatgrass as well as poor forb establishment and persistence can all be influencing factors. Establishing forbs even in areas without crested wheatgrass is often difficult (Pyke 1990; Leger et al. 2014; Ott et al. 2016). Persistence of I herbicide treatment, with its half-life of 120 days, could have somewhat negatively impacted native seeded species establishment during the first year. However, the significant reduction of crested wheatgrass by G treatment as compared to CS and I treatments, resulting in less competition for emerging seeded species, was more likely the primary reason for disparity in seeded species establishment among herbicide treatments.

Although sagebrush establishment during this study was very weak (<0.1 shrub/m²) and there were no significant differences among treatments by the end of the study, the few sagebrush that survived in areas where crested wheatgrass had been initially reduced by the various treatments may be ecologically important nevertheless (Brabec et al. 2015). Similarly, Davies et al. (2013) reported surviving densities of sagebrush seeded into crested wheatgrass stands controlled with glyphosate to be 0.07/m². Most mortality of seeded sagebrush occurs during the first year after seeding (Young & Evans 1989; Boyd & Obradovich 2014; Schlaepfer et al. 2014), presenting one of the most difficult restoration challenges (Brabec et al. 2015). Our study area also experienced high populations of black-tailed jackrabbits (*Lepus californicus*) from at least 2009–2011, during which time numerous sagebrush transplants were harvested (cut at ground level) by jackrabbits in an adjacent study site (McAdoo et al. 2013). Because of the affinity that jackrabbits have for both succulent herbaceous vegetation (McAdoo et al. 1987) and shrubs (Fagerstone et al. 1980), we assume

that jackrabbits impacted the survival of our seeded species, including sagebrush.

Herbaceous species are notoriously competitive with sagebrush during the first season of establishment (Young & Evans 1989; Boyd & Obradovich 2014), and therefore sagebrush restoration in areas dominated by perennial grasses may require targeted reduction of grass competition (Boyd & Svejcar 2010). However, after sagebrush has established it has high persistence in crested wheatgrass communities due to niche differentiation between these species (Gunnell et al. 2010). The importance of this shrub for sagebrush-dependent wildlife species is well-documented, and the addition of sagebrush into crested wheatgrass seedings leads to greater diversity of habitat structure important to a variety of wildlife species (McAdoo et al. 1989; Kennedy et al. 2009). Although alternative strategies for sagebrush establishment (e.g. from planting stock) are being implemented successfully in some areas (Davies et al. 2013; McAdoo et al. 2013), these techniques have practical and economic limitations, so the need for improving sagebrush survival from seed remains paramount.

Management Implications

Our study underscores the challenges of diversifying crested wheatgrass monocultures in semiarid Wyoming big sagebrush sites so that they may provide a wider range of ecological services—including habitat more suitable for sagebrush-obligate wildlife species. Our research and that of others indicate that reduction of crested wheatgrass is possible but will be transient over time. Leveraging our finding about initial crested wheatgrass reduction with glyphosate, we would recommend future research such as following glyphosate treatment with pre-emergent imazapic treatment to control exotic annuals and crested wheatgrass seed germination, then seeding and outplanting sagebrush after residual effects of imazapic have subsided. Other adaptive management approaches, including the use of livestock grazing to reduce crested wheatgrass and enhance native species establishment (Nafus et al. 2016), should also be evaluated. Because seeding native species is often less than successful in arid sites (Knutson et al. 2014), the more readily established crested wheatgrass (Robertson et al. 1966; Boyd & Davies 2010) may often be the likely candidate for seeding (Davies 2010), especially since this species can limit exotic annual grasses at low elevations (Davies et al. 2015). However, researchers are gradually making strides in the realm of native seed adaptation (Johnson et al. 2010; Bower et al. 2014) and seeding technology (Boyd & Lemos 2015; Madsen et al. 2016). Therefore, seeding site-adapted native species following plant community disturbance still holds promise for restoring native plants in Wyoming big sagebrush plant communities.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Precipitation (mm) by quarter for water year and crop year, 2008–2013, for two seeding trials* at South Fork State Recreation Area, Nevada (from South Fork State Recreation Area Weather Station and Database).

Table S2. Seeded species and pure live seed (PLS) seeding rates for treatments at South Fork State Recreation Area, Nevada, planted in late October 2008 for Trial 1 and late October 2010 for Trial 2.