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RESEARCH ARTICLE

Seeding locally sourced native compared to introduced bunchgrasses post-wildfire in frigid Wyoming big sagebrush communities

Kirk W. Davies[1,2], Chad S. Boyd[1]

Perennial grasses are often seeded after disturbances to provide ecosystem services and prevent invasive plant dominance. However, there is widespread disagreement over the use of native compared to introduced grasses. In Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & A. Young) communities, introduced wheatgrasses are often seeded after wildfires because they are less expensive, more available, and establish better than widely available native species. However, locally sourced native bunchgrasses, which likely have adaptations to local conditions, have not been compared to introduced wheatgrasses. We compared drill-seeding locally sourced native bunchgrasses and introduced wheatgrasses after wildfire in frigid Wyoming big sagebrush communities for 3 years. Seeded native and introduced bunchgrasses both increased bunchgrass abundance and cover, even though precipitation was below average the first year post-seeding. Seeding introduced wheatgrasses, however, increased bunchgrass cover and abundance more than seeding native bunchgrasses. Seeding introduced wheatgrasses also limited exotic annual grass abundance and cover, but seeding locally sourced native bunchgrasses did not. Native bunchgrasses are slow growing, thus may limit exotic annual grasses in time. Alternatively, additional treatments, such as exotic annual grass control, may be needed to improve their success. The establishment of seeded native bunchgrasses in Wyoming big sagebrush in a below-average precipitation year is a promising result and suggests further research to improve seeded native vegetation success is warranted. The greater establishment of introduced wheatgrasses and their ability to limit exotic annual grasses suggests that successful introduced species may serve as a model for guiding trait selection in native species.

Key words: ***Artemisia*, crested wheatgrass, drill seeding, exotic annual grass, post-fire restoration**

Implications for Practice

- Locally sourced grasses appear to have adaptations to local conditions as evidenced by their establishment during a below-average precipitation year.
- Competitive introduced species may establish better and limit exotic weeds more than locally sourced native species.
- Additional treatments to control exotic species may be needed when seeding locally sourced vegetation.
- Introduced species that are widely successful in rehabilitation efforts may serve as models for trait identification when developing native species for restoration efforts.

Introduction

Exotic plants have deleterious effects when they invade and dominate native plant communities, including altering fire regimes, disrupting ecosystem processes, degrading native wildlife habitat, and decreasing biodiversity (Gordon 1998; Mack et al. 2000; Davies 2011). Disturbances often facilitate invasive species dominance of plant communities by removing competition and opening safe sites for establishment. To counter this effect, vegetation is commonly seeded after severe disturbances. Seeding success is widely variable and varies in part by the species seeded, thus it is critical to seed species that will establish at given site and also compete with exotic species. Locally sourced native species are expected to have greater establishment and fitness than non-local populations of the same species, likely because they are adapted to local conditions (Bleak et al. 1965;

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Author contributions: KWD, CSB conceived and designed the study; KWD implemented the study and analyzed the data; KWD, CSB wrote and edited the manuscript.

[1]Eastern Oregon Agricultural Research Center, USDA-Agricultural Research Service, Burns, Oregon, USA
[2]Address correspondence to K. W. Davies, email kirk.davies@usda.gov

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Baughman et al. 2019). However, their establishment success and ability to limit exotic species have rarely been compared to widely used introduced species.

The sagebrush steppe of North America is a prime example of an ecosystem at risk of post-disturbance invasion and dominance by exotic plants. This is particularly evident in Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & A. Young) communities where exotic annual grasses can dominate communities after fire if perennial vegetation is substantially reduced (Chambers et al. 2007). Exotic annual grasses are particularly problematic because they alter fire regimes and can limit native species. Exotic annual grasses can promote more frequent fire, because they increase the amount and continuity of highly flammable fine fuels and dry out earlier than native vegetation (Knapp 1995; Brooks 2008; Davies & Nafus 2013). This has devastating impacts because native perennial species are generally intolerant of frequent fire (D'Antonio & Vitousek 1992). Exotic annual grasses are also very competitive with native species, especially at the seedling stage (Nasri & Doescher 1995; Rafferty & Young 2002). Increasing exotic annual grass abundance exponentially decreases plant biodiversity (Davies 2011) and degrades habitat for sagebrush-associated wildlife (Crawford et al. 2004; USFWS 2013). Thus, it is imperative to prevent exotic annual grass invasion and dominance of sagebrush communities.

Perennial grasses are often seeded after fire in these communities to maintain perennial dominance and limit exotic annual grasses. However, there is widespread disagreement over whether native or introduced grasses should be used. The introduced bunchgrasses, crested (*Agropyron cristatum* (L.) Gaertn. and *A. desertorum* [Fisch. Ex Link] Schult) and Siberian wheatgrass (*A. fragile* [Roth] P. Candargy), are commonly seeded after wildfires (Eiswerth et al. 2009; Knutson et al. 2014). These introduced wheatgrasses are often selected instead of native bunchgrasses because they establish better (Robertson et al. 1966; Hull 1974; Wood et al. 1982) and are more available and cost less (Arredondo et al. 1998; Eiswerth et al. 2009; Boyd & Davies 2010). Crested wheatgrass has also been selected because it is highly competitive with exotic annual grasses (Arredondo et al. 1998; Davies et al. 2010). The competitiveness of these introduced wheatgrasses, however, can result in them developing near monocultures that are persistent (Christian & Wilson 1999; Heidinga & Wilson 2002; Nafus et al. 2016). Most efforts to restore native vegetation in these introduced grasslands have failed (Hulet et al. 2010; Fansler & Mangold 2011; Morris et al. 2019). In addition, established native perennial vegetation can also limit exotic annual grasses (Davies & Johnson 2017). Thus, disagreement remains regarding if native or introduced bunchgrasses should be seeded after disturbances, in particular fire, in sagebrush communities at risk of exotic annual grass invasion.

Part of the disagreement arises from knowledge gaps and conflicting reports of the likelihood of seeded native vegetation establishing and persisting. The probability of successfully establishing native vegetation from seed and suppressing exotic annual grasses varies with environmental conditions. For example, the prospect of successfully establishing native perennial vegetation from seed decreases as sagebrush communities become hotter and drier (Knutson et al. 2014; Pilliod et al. 2017). However, seeded native vegetation can be successful in cooler and wetter sagebrush communities and can substantially reduce exotic annual grasses (Davies et al. 2019; Urza et al. 2019). Wyoming big sagebrush communities are generally hotter and drier and are less resistant to exotic annual grass invasion than the other sagebrush communities (Davies 2011; Chambers et al. 2014). Thus, these sagebrush communities often need to be seeded after fire to prevent exotic annual grass dominance, but this is also where it is challenging to establish native perennial vegetation. Locally sourced native species, however, may be more likely to establish and persist than widely available commercial cultivars because of adaptation to local environmental characteristics (Baughman et al. 2019). Locally sourced native species, because of local adaptations, may conceivably establish and persist as well or even better than introduced wheatgrasses. However, comparisons between seeding locally sourced native and introduced perennial grasses are lacking and this knowledge gap needs filled as land managers are tasked with restoring degraded lands and preventing exotic species spread and dominance.

The purpose of the study was to compare seeding introduced and locally sourced native bunchgrasses after wildfire in Wyoming big sagebrush communities for increasing bunchgrass cover and abundance and limiting exotic annual grasses. We hypothesized that (1) seeding bunchgrasses would result in greater bunchgrass cover and density and less exotic annual grass and (2) seeding locally sourced native compared to introduced bunchgrasses would result in greater bunchgrass cover and density and less exotic annual grasses.

Methods

Study Area

The study was conducted in Wyoming big sagebrush communities burned in the Cinder Butte fire 25–35 km west and southwest of Riley, Oregon, USA. The Cinder Butte fire burned 21,231 ha in early August of 2017. The fire completely consumed all fuels at the study sites, even burning shrub stumps below the soil surface. The USDI-Bureau of Land Management and private landowners elected to seed the majority of the burn because of substantial post-fire exotic annual grass risk. Prior to burning, vegetation at the study sites was dominated by Wyoming big sagebrush and native bunchgrasses. Native bunchgrasses included bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), Idaho fescue (*Festuca idahoensis* Elmer), squirreltail (*Elymus elymoides* [Raf.] Swezey), prairie Junegrass (*Koeleria macrantha* [Ledeb.] Schult.), and Sandberg bluegrass (*Poa secunda* J. Presl). Cheatgrass (*Bromus tectorum* L.) was present in low abundance across the study sites prior to the wildfire. Climate across the study area is characteristic of the northern Great Basin with hot, dry summers and cool, wet winters. Long-term (1981–2010) average annual precipitation was 268 mm. Crop-year (October–September) precipitation was 69, 123, and 68% of the long-term average in 2017–2018, 2018–2019, and 2019–2020, respectively (PRISM 2020). Soil temperature regime and moisture class were frigid and aridic, respectively (NRCS 2020). Soils were a gravelly fine sandy loam, well drained, and 60 to >100 cm deep. Elevation ranged from 1,436 to 1,468 m above sea level. Slopes were mild (2–6%) and aspects were northerly. Livestock were excluded for the duration of the study.

Experimental Design and Measurements

A randomized complete block design with five blocks (separated by up to 4 km) was used to evaluate seeding locally sourced native and introduced bunchgrasses after wildfire in Wyoming big sagebrush communities. Each block consisted of three treatments: (1) seeded with native bunchgrasses (Native); (2) seeded with introduced bunchgrasses (Introduced); and (3) unseeded control (Control). Treatments were randomly applied to 7.5 × 100-m plots with a 2 m buffer between treatments. Seeding treatments were applied with a rangeland drill (Laird Welding & Manufacturing Works, Merced, CA) in early December 2017. Drill row centers were 30 cm apart and 5 cm diameter metal pipes were dragged behind the drill to improve soil coverage of seed. The native seed mix was comprised of locally sourced bluebunch wheatgrass, bottlebrush squirreltail, and prairie Junegrass with each species seeded 3.76 kg PLS·ha^{-1} (total = 11.28 kg PLS·ha^{-1}). We considered native species locally sourced if they came from locations that meet the following criteria: (1) were < 100 km from the study sites; (2) at elevations within 100 m of the average elevation of the study sites; and (3) with average annual precipitation ±15% of the study sites. The locally sourced native species were harvested by hand from native plant communities in 2017. Collected seeds were stored in a cool, dry environment until seeding. The introduced seed mix was comprised of crested wheatgrass (Hycrest II) and Siberian wheatgrass (Vavilov) with each seeded at 5.64 kg PLS·ha^{-1} (total = 11.28 kg PLS·ha^{-1}).

Vegetation, bare ground, litter, rock, and biological soil crusts were measured along three 90-m transects spaced at 2, 4, and 6 m along the short edge of the treatment plot in June of 2018, 2019, and 2020. Herbaceous vegetation cover and density, bare ground, rock, litter, and biological soil crust cover were estimated using 0.2 m^{-2} quadrats located at 3-m intervals along the 90-m transects (30 quadrats per transect, 90 quadrats per plot). Cover was estimated based on markings that divided quadrats into 1, 5, 10, 25, and 50% segments. Density was measured by counting all herbaceous plants rooted in the quadrats. Shrub canopy cover was measured using the line intercept method on each of the 90-m transects. Shrub density was measured by counting all shrubs rooted in three 2 × 90-m belt transects positioned over the three 90-m transects.

Statistical Analyses

We used repeated measures analysis of variance using the mixed models procedure in SAS v. 9.4 (SAS Institute Inc., Cary, NC, U.S.A.) with year as the repeated variable. Block and block by treatment interactions were treated as random variables in analyses. We determined the appropriate covariance structure using Akaike's information criterion (Littell et al. 1996). For analyses, herbaceous cover and density were grouped into five plant functional groups: large perennial bunchgrasses, Sandberg bluegrass, exotic annual grasses, perennial forbs, and annual forbs. Sandberg bluegrass was analyzed as a separate plant functional group from the other perennial grasses because it is smaller in stature, phenologically develops earlier, and responds differently to disturbances (McLean & Tisdale 1972; Yensen et al. 1992; James et al. 2008). Cheatgrass was the most common exotic annual grass at the study sites, but some medusahead (*Taeniatherum caput-medusae* (L.) Nevski) and Japanese brome (*Bromus japonicus* Thunb. Ex Murr) were also detected. Exotic annual forbs comprised >75% of the total annual forb cover and density. The perennial forb functional group was comprised of native species. Shrub cover and density were separated into two groups: Wyoming big sagebrush and green rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt). Data that violated assumptions of normality were log or square-root transformed. Original data (i.e. non-transformed) are presented in figures and text. Treatment means were separated using Fisher's protected least significant difference ($p \le 0.05$) and reported with standard errors.

Results

Cover

The interaction between treatment and year was not significant for any measured cover variable (Table S1; $p > 0.050$). Large perennial bunchgrass cover varied by treatment (Fig. 1A; $p = 0.019$) and was greatest in areas seeded with introduced wheatgrasses, followed by areas seeded with native bunchgrasses, and lowest in unseeded controls. Large bunchgrass cover also increased with time ($p < 0.001$). In 2020, introduced wheatgrasses constituted 71% of the large perennial bunchgrass cover in the Introduced treatment. In 2020, bluebunch wheatgrass, prairie Junegrass, and squirreltail (the three seeded species) comprised 57, 8, and 16% of the large bunchgrass total cover and were 26, 21 and 1,171% greater in the Native compared to the Control, respectively. Sandberg bluegrass cover did not vary among treatments ($p = 0.972$), but did among years ($p = 0.050$). Sandberg bluegrass cover was generally greatest in 2019 and lowest in 2018 (data not shown). Exotic annual grass cover varied among treatments and years (Fig. 1B; $p = 0.010$ and < 0.001, respectively). Exotic annual grass cover was less in the Introduced compared to Native and Control treatments ($p = 0.036$ and 0.003, respectively), but did not differ between the Native and Control ($p = 0.148$). Exotic annual grass cover appeared to be increasing with time in Native and Control treatments, but it did not appear to increase from the second to the third year in the Introduced treatment. Perennial forb (solely comprised of native species) cover did not vary among treatments (Fig. 1C; $p = 0.059$) but among years ($p < 0.001$), with it generally greater in 2019 compared to 2018 and 2020. Annual forb (largely comprised of exotic species) cover varied among

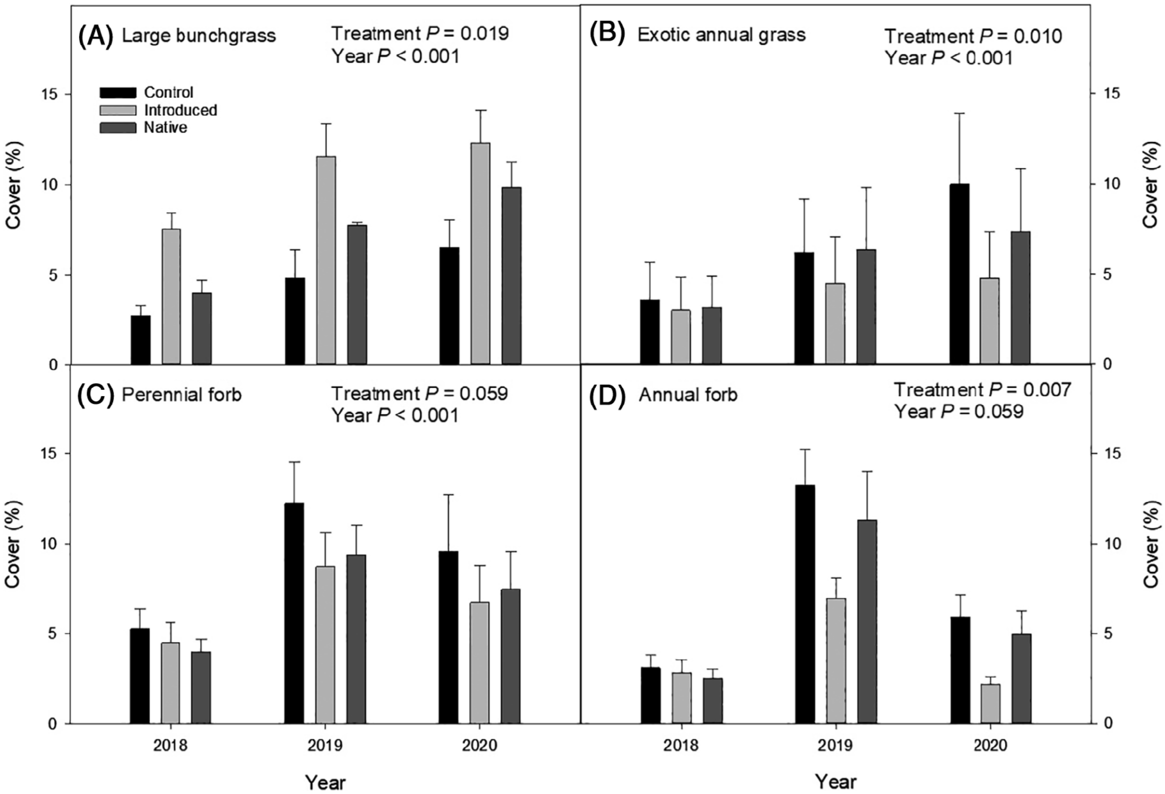

Figure 1. (A–D) Plant functional group cover (mean + SE) in drill-seeded locally sourced native bunchgrasses (Native), drill-seeded introduced bunchgrasses (Introduced), and control (Control) treatments in 2018, 2019, and 2020.

treatments and years (p = 0.007 and < 0.001, respectively). Annual forb cover was less in the Introduced compared to Native and Control treatments (Fig. 1D; p = 0.019 and 0.002, respectively), but was similar between Native and Control treatments (p = 0.178). Annual forb cover was generally greater in 2019 than 2018 and 2020. Sagebrush and green rabbitbrush cover was low (0 to <0.6%) in all sampling years and did not vary among treatments (data not shown; p = 0.410 and 0.230). Sagebrush cover was also similar among years (p = 0.383). Green rabbitbrush cover was less in 2018 than 2019 and 2020 (p = 0.022). Bare ground, rock, and litter cover did not vary among treatments (data not shown; p = 0.105, 0.161, and 0.583, respectively), but did vary among years (p < 0.001). In general, bare ground and rock decreased and litter increased with time. Biological soil crust cover was extremely low (< 0.20%) and did not vary among treatments (data not shown; p = 0.519). Biological soil crust cover declined over time (p = 0.006).

Density

The interaction between treatment and year was not significant for any measured density variable (Table S2; p > 0.050). Large perennial bunchgrass density varied among treatments and years (Fig. 2A; p < 0.001 and 0.020). Large bunchgrass density was on average 1.5- to 2.3-fold greater in the Introduced treatment compared to Native and Control treatments (p = 0.005 and < 0.001) and 1.6-fold greater in the Native compared to the Control (p = 0.024). In general, bunchgrass density was greater in 2018 compared to 2019 and 2020. In the Introduced treatment in 2020, introduced wheatgrasses constituted 68% of the total large bunchgrass cover. The seeded native species drove the increase in large perennial bunchgrass density in the Native treatment. In 2020, bluebunch wheatgrass, prairie Junegrass, and squirreltail contributed 44, 10, and 21% to large bunchgrass total density and increased 10, 22 and 713% in the Native treatment compared to the Control, respectively. Sandberg bluegrass density was similar among treatments (p = 0.827), but was less in 2020 than other years (p < 0.001). Exotic annual grass density varied among treatments (Fig. 2B; p = 0.008), with exotic annual grasses being greater in Control and Native treatments compared to the Introduced treatment (p = 0.003 and 0.013, respectively). At the end of the study (2020), exotic annual grasses were 1.6- and 1.5-fold greater in Control and Native treatments than the Introduced treatment, respectively. Exotic annual grass density was similar between Control and Native treatments (p = 0.343). Density of exotic annual grasses increased with time (p < 0.001). Perennial forb (solely comprised of native species) density did not vary among treatments (Fig. 2C; p = 0.376) and was generally less in 2018 than 2019 and 2020 (p = 0.041). Annual forb (largely comprised of exotic species) density varied among treatments and years

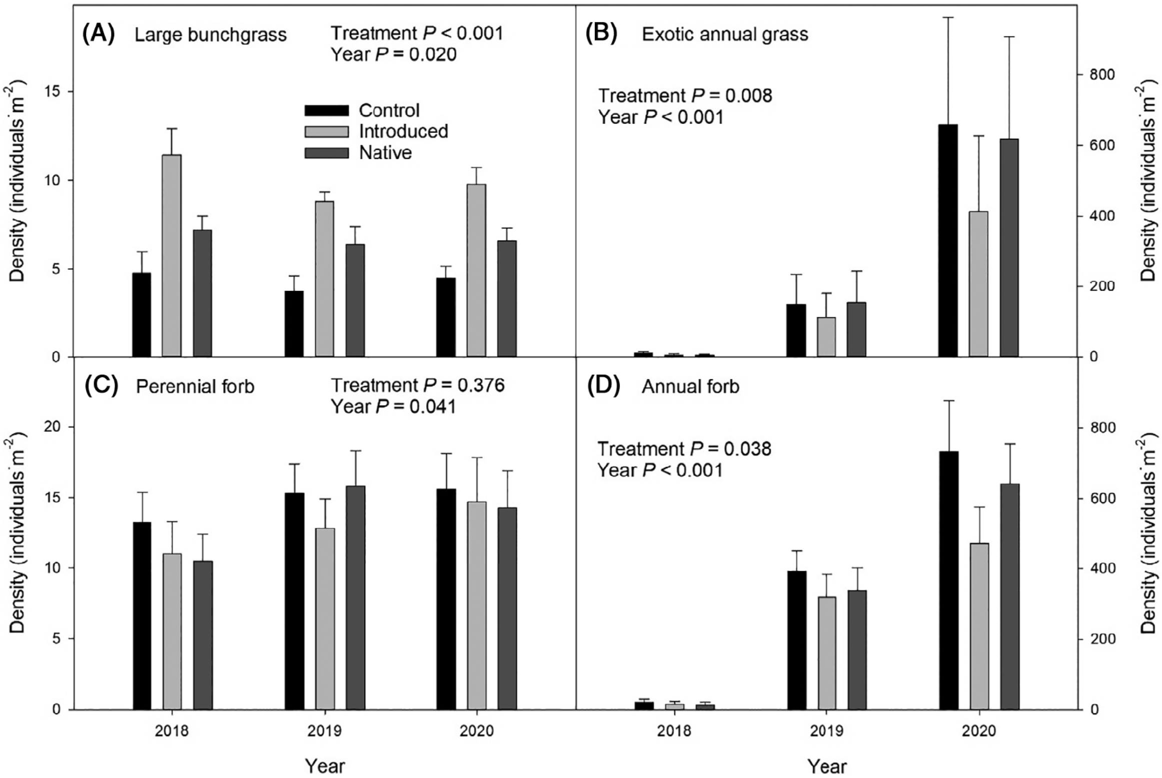

Figure 2. (A–D) Plant functional group density (mean + SE) in drill-seeded locally sourced native bunchgrasses (Native), drill-seeded introduced bunchgrasses (Introduced), and control (Control) treatments in 2018, 2019, and 2020.

(Fig. 2D; p = 0.038 and < 0.001, respectively). In general, annual forb density was greatest in the Control and least in the Introduced treatment and increased with time. Sagebrush and green rabbitbrush density did not vary among treatments or years ($p > 0.050$).

Discussion

Seeding perennial bunchgrasses after wildfire in frigid Wyoming big sagebrush communities increased bunchgrass abundance and cover even though the first-year precipitation was below average. This is counter to expectations that seedings are generally unsuccessful in below-average precipitation years (Hardegree et al. 2011). However, above-average precipitation the next year may have been crucial for their persistence. These results suggest that locally sourced native and introduced bunchgrasses can be successfully seeded in some Wyoming big sagebrush communities in less than ideal precipitation years. However, there are a few caveats that need to be acknowledged. First, the soil temperature regime was frigid for the study sites, thus these results may not apply to hotter sites. Second, exotic annual grasses were not abundant immediately after burning, which likely also contributed to the success of seeded bunchgrasses. Exotic annual grasses are highly competitive with bunchgrasses at the seedling stage, which can prevent their establishment (Nasri & Doescher 1995; Rafferty & Young 2002; Humphrey & Schupp 2004). The establishment of bunchgrasses, especially native bunchgrasses, from seed in Wyoming big sagebrush communities after wildfire in our study is encouraging, as restoration of these communities is often a management challenge (Svejcar et al. 2017), but should not lead to assumptions that bunchgrass establishment from seed will be similar in other sagebrush communities.

Though seeded locally sourced native and introduced bunchgrasses both established, effects varied by seed mix. All three locally sourced native bunchgrasses were able to establish and persist at our study sites, but seeding introduced bunchgrasses resulted in greater bunchgrass abundance and cover. This was likely the result of introduced wheatgrasses establishing better and growing faster than locally sourced native bunchgrasses. Introduced wheatgrasses generally establish better than widely available native bunchgrasses (Hull 1974; Asay et al. 2003; Boyd & Davies 2010;). However, to our knowledge, this is the first comparison of seeding introduced wheatgrasses with locally sourced native bunchgrasses. Introduced wheatgrasses also generally grow faster than native bunchgrasses because of physiological advantages (James et al. 2012; Hamerlynck et al. 2016, 2020). Seed mix selection is undoubtedly a critical post-fire management decision and success will vary by the species included.

Seed mix also had differing effects on exotic annual grasses and annual forbs, predominately non-native species. Seeding native bunchgrasses did not decrease exotic annual grass or annual forb cover and density in the three growing seasons post-fire. In contrast, seeding introduced bunchgrasses substantially limited exotic annual grasses and annual forbs. From the second to third year, exotic annual grass cover did not change in areas seeded with introduced bunchgrasses, but exotic annual grass cover appeared to still be increasing in the other treatments. Similarly, others have found that introduced wheatgrasses are competitive with exotic annual grasses (Arredondo et al. 1998; Davies et al. 2010; Davies & Johnson 2017). Native bunchgrasses in semi-arid rangelands are generally slow-growing (Holmes & Rice 1996; James et al. 2009), thus they may limit exotic annual grasses in the future, assuming they continue to increase in cover (e.g. Ott et al. 2019). In support of this speculation, established native vegetation has been demonstrated to limit exotic annuals in other studies (Davies & Johnson 2017; Davies et al. 2019; Urza et al. 2019), though introduced wheatgrasses generally reduced exotic annual grasses more than other perennial vegetation (Davies & Johnson 2017). Seeding introduced wheatgrasses limited exotic annual grasses more than seeding native bunchgrasses in the 3 years post-seeding, but longer-term evaluations are needed to determine if seeded native bunchgrasses will limit exotic annuals in time and to better understand the long-term effects of seeding introduced wheatgrasses.

Alternatively, locally sourced native bunchgrass success may be improved by including treatments to control exotic annual grasses. Exotic annual grasses preempt resource use by growing earlier and more rapidly than many native species (Melgoza et al. 1990; Humphrey & Schupp 2004), thus control of exotic annual grasses can result in increases in co-existing vegetation. For example, pre-emergent herbicide control of exotic annual grasses increased co-existing native bunchgrasses (Davies & Sheley 2011). Targeted grazing could also be used to reduce exotic annual grass abundance and encourage perennial grasses (Schmelzer et al. 2014; Porensky et al. 2020). Bunchgrasses overlap substantially with exotic annual grasses in resource acquisition patterns (James et al. 2008) and are, therefore, critical to limiting them (Chambers et al. 2007; Davies 2008). Further increases in native bunchgrasses should limit exotic annual grasses; it just may require short-term control of exotic annuals to allow native bunchgrasses to increase to the point they preempt enough resources to reduce exotic annual grasses.

Our results support assumptions that locally sourced native species likely have adaptions to local environments which translate into successful establishment and persistence (e.g. Baughman et al. 2019). Establishing locally sourced native bunchgrasses in Wyoming big sagebrush communities in a below-average precipitation year suggests that native species can play a larger role in post-fire revegetation efforts in more semiarid rangelands. Additional selection criteria and breeding to improve native species success is warranted. For example, locally sourced native species that have adapted to competition from invasive species may improve restoration success in invaded-rangelands (Leger 2008; Goergen et al. 2011; Leger et al. 2019). Selecting for traits that have proven beneficial in establishment and persistence in restoration attempts could also improve success (Kulpa & Leger 2013). The greater abundance and cover of seeded introduced wheatgrasses and subsequent reductions in exotic annuals suggest that selecting native species with traits similar to successful introduced species may be a way to achieve greater success.

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LITERATURE CITED

Arredondo JT, Jones TA, Johnson DA (1998) Seedling growth of intermountain perennial and weedy annual grasses. Journal of Range Management 51:584–389

Asay KH, Chatterton NJ, Jensen KB, Jones TA, Waldron BL, Horton WH (2003) Breeding improved grasses for semiarid rangelands. Arid Land Research and Management 17:469–478

Baughman OW, Agneray AC, Forister ML, Kilkenny MF, Espeland EK, Fiegener R, et al. (2019) Strong patterns of intraspecific variation and local adaptation in Great Basin plants revealed through a review of 75 years of experiments. Ecology and Evolution 9:6259–6275

Bleak AT, Frishknecht NC, Plummer AP, Eckert RE (1965) Problems in artificial and natural revegetation of the arid shadscale vegetation zone of Utah and Nevada. Journal of Range Management 18:59–65

Boyd CS, Davies KW (2010) Shrub microsite influences post-fire perennial grass establishment. Rangeland Ecology and Management 63:248–252

Brooks ML (2008) Plant invasions and fire regimes. Pages 33–45.In: Zouhar K, Smith JK, Sutherland S, Brooks ML (eds) Wildland fire in ecosystems: fire and nonnative invasive plants. USDA – Forest Service, Rocky Mountain Research Station Technical Reports, RMRS-GRT-42, Fort Collins, CO

Chambers JC, Bradley BA, Brown CS, D'Antonio C, Germino MJ, Grace JB, Hardegree SP, Miller RF, Pyke DA (2014) Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. Ecosystems 17:360–375

Chambers JC, Roundy BA, Blank RR, Meyer SE, Whittaker A (2007) What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs 77:117–145

Christian JM, Wilson SD (1999) Long-term ecosystem impacts of an introduced grass in the northern Great Plains. Ecology 80:2397–2407

Crawford JA, Olson RA, West NE, Mosley JC, Schroeder MA, Whitson TD, Miller RF, Gregg MA, Boyd CS (2004) Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2–19

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87

Davies KW (2008) Medusahead dispersal and establishment in sagebrush steppe plant communities. Rangeland Ecology and Management 61:110–115

Davies KW (2011) Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass. Oecologia 167:481–491

Davies KW, Bates JD, Boyd CS (2019) Post-wildfire seeding to restore native vegetation and limit exotic annuals: an evaluation in juniper-dominated sagebrush steppe. Restoration Ecology 27:120–127

Davies KW, Johnson DD (2017) Established perennial vegetation provides high resistance to reinvasion by exotic annual grasses. Rangeland Ecology and Management 70:748–754

Davies KW, Nafus AM (2013) Exotic annual grass invasion alters fuel amounts, continuity and moisture content. International Journal of Wildland Fire 22:353–358

Davies KW, Nafus AM, Sheley RL (2010) Non-native competitive perennial grass impedes the spread of an invasive annual grass. Biological Invasions 12:3187–3194

Davies KW, Sheley RL (2011) Promoting native vegetation and diversity in exotic annual grass infestations. Restoration Ecology 19:159–165

Eiswerth ME, Krauter K, Swanson SR, Zielinski M (2009) Post-fire seeding on Wyoming big sagebrush ecological sites: regression analyses of seeded nonnative and native species densities. Journal of Environmental Management 90:1320–1325

Fansler VA, Mangold JM (2011) Restoring native plants to crested wheatgrass stands. Restoration Ecology 19:16–23

Goergen EM, Leger EA, Espeland EK (2011) Native perennial grasses show evolutionary response to *Bromus tectorum* (cheatgrass) invasion. PLos One 6:e18145

Gordon DR (1998) Effects of invasive, non-indigenous plant species on ecosystem processes: lesson from Florida. Ecological Applications 8:975–989

Hamerlynck E, Denton E, Davies KW, Boyd C (2020) Photosynthetic regulation in seed heads and flag leaves of exotic and native sagebrush steppe bunchgrasses. Conservation Physiology 7:coz112

Hamerlynck EP, Sheley RL, Davies KW, Svejcar TJ (2016) Postdefoliation ecosystem carbon and water flux and canopy growth dynamics in sagebrush steppe bunchgrasses. Ecosphere 7:e01376

Hardegree SP, Jones TA, Roundy BA, Shaw NL, Monaco TA (2011) Assessment of range planting as a conservation practice. Pages 171–212.In: Briske DD (ed) Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps. Allen Press, Inc., Lawrence, Kansas.

Heidinga L, Wilson SD (2002) The impact of an invading alien grass (*Agropyron cristatum*) on species turnover in native prairie. Diversity and Distributions 8:249–258

Holmes TH, Rice KJ (1996) Patterns of growth and soil-water utilization in some exotic annuals and native perennial bunchgrasses of California. Annuals of Botany 78:233–243

Hulet A, Roundy BA, Jessop B (2010) Crested wheatgrass control and native plant establishment in Utah. Rangeland Ecology and Management 63:450–460

Hull AC (1974) Species for seeding arid rangeland in southern Idaho. Journal of Range Management 27:216–218

Humphrey LD, Schupp EW (2004) Competition as a barrier to establishment of a native perennial grass (*Elmus elymoides*) in alien annual grass (*Bromus tectorum*) communities. Journal of Arid Environments 58:405–422

James JJ, Davies KW, Sheley RL, Aanderud ZT (2008) Linking nitrogen partitioning and species abundance to invasion resistance in the Great Basin. Oecologia 156:637–648

James JJ, Mangold JM, Sheley RL, Svejcar T (2009) Root plasticity of native and invasive Great Basin species in response to soil nitrogen heterogeneity. Plant Ecology 202:211–220

James JJ, Rinella MJ, Svejcar T (2012) Grass seedling demography and sagebrush steppe restoration. Rangeland Ecology & Management 65:409–417

Knapp PA (1995) Intermountain West lightning-caused fires: climatic predictors of area burned. Journal of Range Management 48:85–91

Knutson KC, Pyke DA, Wirth TA, Arkle RS, Pilliod DS, Brooks ML, Chambers JC, Grace JB (2014) Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. Journal of Applied Ecology 51:1414–1424

Kulpa SM, Leger EA (2013) Strong natural selection during plant restoration favors an unexpected suite of plant traits. Evolutionary Applications 6:510–523

Leger EA (2008) The adaptive value of remnant native plants in invaded communities: an example from the Great Basin. Ecological Applications 18:1226–1235

Leger EA, Atwater DZ, James JJ (2019) Seed and seedling traits have strong impacts on establishment of a perennial bunchgrass in invaded semi-arid systems. Journal of Applied Ecology 56:1343–1354

Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1996) SAS system for mixed models. SAS Institue Inc, Cary, NC

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10:689–710

McLean A, Tisdale EW (1972) Recovery rate of depleted range sites under protection from grazing. Journal of Range Management 25:178–184

Melgoza G, Nowak RS, Tausch RJ (1990) Soil-water exploitation after fire – competition between *Bromus tectorum* (cheatgrass) and 2 native species. Oecologia 83:7–13

Morris C, Morris LR, Monaco TA (2019) Evaluating the effectiveness of low soil-disturbance treatments for improving native plant establishment in stable crested wheatgrass stands. Rangeland Ecology and Management 72: 237–248

Nafus AM, Svejcar TJ, Davies KW (2016) Disturbance history, management, and seeding year precipitation influences vegetation characteristics of crested wheatgrass stands. Rangeland Ecology and Management 69:248–256

Nasri M, Doescher PS (1995) Effect of competition by cheatgrass on shoot growth of Idaho fescue. Journal of Range Management 48:402–405

NRCS (2020) Web Soil Survey. http://websoilsurvey.sc.egove.usda.gov/App/WebSoilSurvey.aspx (accessed 1 Dec 2020)

Ott JE, Kilkenny FF, Summers DD, Thompson TW (2019) Long-term vegetation recovery and invasive annual suppression in native and introduced postfire seeding treatments. Rangeland Ecology and Management 72:640–653

Pilliod DS, Welty JL, Arkle RS (2017) Refining the cheatgrass-fire cycle in the Great Basin: precipitation timing and fine fuel composition predict wildfire trends. Ecology and Evolution 7:8126–8151

Porensky LM, Baughman O, Williamson MA, Perryman BL, Madsen MD, Leger EA (2020) Using native grass seedling and target spring grazing to reduce low-level *Bromus tectorum* invasion on the Colorado Plateau. Biological Invasions 23:705–722

PRISM (2020) PRISM Climate Group Database. http://prism.nacse.org/explorer/ (accessed 16 Nov 2020)

Rafferty DL, Young JA (2002) Cheatgrass competition and establishment of desert needlegrass seedlings. Journal of Range Management 55:70–72

Robertson JH, Eckert RE, Bleak AT (1966) Responses of grasses seeded in an *Artemisia tridentata* habitat in Nevada. Ecology 47:187–194

Schmelzer L, Perryman B, Bruce B, Schultz B, McAdoo K, McCuin G, Swanson S, Wilker J, Conley K (2014) Case study: reducing cheatgrass (*Bromus tectorum* L.) fuel loads using fall cattle grazing. The Professional Animal Scientists 30:270–278

Svejcar T, Boyd C, Davies K, Hamerlynck E, Svejcar L (2017) Challenges and limitations to native species restoration in the Great Basin, USA. Plant Ecology 218:81–94

Urza AK, Weisberg PJ, Chambers JC, Board D, Flake SW (2019) Seeding native species increases resistance to annual grass invasion following prescribed burning of semiarid woodlands. Biological Invasion 21: 1993–2007

USFWS (2013) Pages 108. Sage-grouse (*Centrocercus urophasianus*) conservation objectives: final report. U.S. Fish and Wildlife Service, Denver, CO

Wood KM, Eckert RE, Blackburn W, Peterson FF (1982) Influence of crusting soil surfaces on emergence and establishment of crested wheatgrass, squirreltail, Thurber needlegrass, and fourwing saltbrush. Journal of Range Management 35:282–287

Yensen E, Quinney DL, Johnson K, Timmerman K, Steenhof K (1992) Fire, vegetation changes, and population fluctuations of Townsend's ground squirrels. American Midland Naturalist 128:299–312

Supporting Information

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

Table S1. Cover group results from mixed model repeated-measure ANOVA.
Table S2. Density group results from mixed model repeated-measure ANOVA.

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