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Original Research

# Established Perennial Vegetation Provides High Resistance to Reinvasion by Exotic Annual Grasses☆

Kirk W. Davies [a,*], Dustin D. Johnson [b]

[a] Rangeland Scientist, US Department of Agriculture (USDA)–Agricultural Research Service (ARS), Burns, OR 97720, USA
[b] Associate Professor, Oregon State University, Corvallis, OR 97331, USA

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ABSTRACT

Exotic annual grasses have invaded millions of hectares of sagebrush (*Artemisia* L.) steppe in the Great Basin region and degraded wildlife habitat, reduced forage production, and promoted increasingly frequent wildfires. Revegetation after control of exotic annual grasses is needed to restore ecosystem services and break the annual grass-fire cycle. The ability of different common revegetation species and combinations of species to limit reinvasion of annual grasses is relatively unknown. We evaluated five species/combinations of perennial native and introduced bunchgrass and shrub species planted as seedlings after exotic annual grass control at two sites in southeast Oregon. To evaluate resistance to reinvasion, exotic annual grasses were seeded into all treatment plots in the fall two growing seasons after planting. Vegetation characteristics were measured in the third and fourth years after annual grass seeding. Exotic annual grass cover and density were greatly reduced in all treatments where perennial seedlings were planted compared with the control (no seedlings planted). Treatments including crested wheatgrass (*Agropyron desertorum* [Fisch. Ex Link] Schult) generally limited annual grasses more than other treatments. Most notably, forage kochia (*Bassia prostata* [L.] A. J. Scott) reduced exotic annual grasses less than crested wheatgrass and crested wheatgrass planted with forage kochia. This suggests that if forage kochia will be planted, it should be used in conjunction with perennial bunchgrasses in efforts to revegetate exotic annual grass—invaded sagebrush steppe. Established native vegetation also greatly reduced exotic annual grass reinvasion. Though some differences existed among established vegetation treatments, our study highlights that established perennial vegetation prevents redomination by invasives after exotic annual grass control.

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## Introduction

Exotic annual grass invasion, primarily medusahead (*Taeniatherum caput-medusae* [L.] Nevski) and cheatgrass (*Bromus tectorum* L.), is a critical threat to the sagebrush ecosystem and rural communities and wildlife that depend on it (Davies et al., 2011). Exotic annual grass invasion is correlated to reduce biodiversity and reductions in native vegetation (Mack, 1981; Davies, 2011). Invasion by exotic annual grasses also decreases forage production and degrades wildlife habitat (DiTomaso, 2000; Davies and Svejcar, 2008). Perhaps the most devastating impact of exotic annual grass invasion is an increase in wildfire frequency, which is detrimental to native plants that evolved with infrequent fire (D'Antonio and Vitousek, 1992; Mack et al., 2000; Brooks et al., 2004). Exotic annual grasses promote more frequent wildfires by increasing fine fuel biomass and continuity and drying out earlier than native vegetation (Davies and Nafus, 2013). The increase in fire favors exotic annual grasses and creates a grass-fire cycle that promotes their continued dominance of the plant community and may facilitate invasion of surrounding areas as fires spread from invaded to noninvaded communities (D'Antonio and Vitousek, 1992; Brooks et al., 2004).

Revegetation of exotic annual grass—invaded rangelands is needed to break the annual grass-fire cycle and restore ecosystem services. To successfully revegetate annual grass—invaded rangelands, annual grasses must first be controlled to reduce competition for the establishment of perennial vegetation (Davies, 2010; Davies et al., 2013; Nafus and Davies, 2014). Exotic annual grasses can be effectively controlled with pre-emergent herbicides (Monaco et al., 2005; Musil et al., 2005; Elseroad and Rudd, 2011). The effectiveness of preemergent herbicides can be improved by prescribed burning before application to remove litter to improve herbicide-soil contact (Kyser et al., 2007; Davies, 2010; Davies and Sheley, 2011; Sheley et al., 2012). Effective annual grass control is often temporary as these grasses can rapidly reinvade

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* Correspondence: K. W. Davies, USDA-ARS, 67826-A Hwy 205, Burns, OR 97720, USA. Tel.: +1 541 573 4074.
E-mail address: kirk.davies@ars.usda.gov (K.W. Davies).

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treated areas (Monaco et al., 2005; Kyser et al., 2007). Therefore, after successful control of annual grasses, it is imperative to establish perennial vegetation to limit reinvasion.

Individual and combinations of perennial species likely vary in their effectiveness at limiting annual grass reinvasion. The introduced bunchgrass, crested wheatgrass (*Agropyron desertorum* [Fisch. Ex Link] Schult), successfully competes with exotic annual grasses (Miller, 1956; Arredondo et al., 1998; McAdoo et al., 2017) and can limit their spread (Davies et al., 2010). Crested wheatgrass has been used successfully to prevent reinvasion (Davies, 2010; Davies et al., 2014), but the ability of other introduced species such as the half-shrub, forage kochia (*Bassia prostata* [L.] A.J. Scott), to reduce reinvasion is largely unknown. Forage kochia has been shown to reduce exotic annual grasses in case studies (Monaco et al., 2003). The use of introduced species in revegetation of sagebrush steppe communities is controversial (Davies et al., 2011). Introduced species can form near-monocultures (Pyke, 1990) and can be highly competitive with native plants (Heinrichs and Bolton, 1950; Schuman et al., 1982; Gunnell et al., 2010). Thus, there is a desire to revegetate annual grass — invaded sagebrush communities with native vegetation (Davies et al., 2015). Established native vegetation can also be competitive with exotic annuals (Clausnitzer et al., 1999; Chambers et al., 2007). However, information regarding the ability of native vegetation to prevent reinvasion after exotic annual grass control is generally lacking.

The purpose of this study was to evaluate the ability of some common native and introduced revegetation species and species mixes to suppress reinvasion by exotic annual grasses after annual grass control. Our objectives were to determine 1) if establishing commonly used species/species mixes reduced exotic annual grass density and cover; 2) if the ability of grass-shrub combinations to suppress exotic annual grasses depended on whether plants were native, introduced, or a combination of native and introduced species; and 3) which introduced species (crested wheatgrass or forage kochia) suppressed exotic annual grass more and if suppression was greater when planted together. We hypothesized that 1) established perennial vegetation would limit exotic annual grass reinvasion, 2) an introduced grass-shrub combination would limit exotic annual grass reinvasion more than a native or an introduced-native grass-shrub combination, and 3) crested wheatgrass and crested wheatgrass-forage kochia combination would suppress exotic annual grass reinvasion more than forage kochia.

## Methods

### *Study Sites*

The study was conducted in southeast Oregon at two sites: the Buck Mountain site and the Warm Springs site located about 65 km southeast and 57 km east of Burns, Oregon, respectively. Climate is typical of the northwest Great Basin with cool, wet winters and hot, dry summers. Long-term (1981 — 2010) average annual precipitation was 287 and 284 mm at Buck Mountain and Warm Springs, respectively (PRISM, 2017). Crop-year (1 October–30 September) precipitation for Buck Mountain was 130%, 72%, 88%, 66%, 94%, and 94% of the long-term average for 2010 — 2011, 2011 — 2012, 2012 — 2013, 2013 — 2014, 2014 — 2015, and 2015 — 2016, respectively (PRISM, 2017). Crop-year precipitation for Warm Springs was 128%, 75%, 96%, 65%, 104%, and 96% of the long-term average for these same time periods (PRISM, 2017). The ecological site at Buck Mountain and Warm Springs was SR Clayey 9-12 PZ (R010XC021OR) and SR Shallow 9-12 PZ (R010XC035OR), respectively (NRCS, 2017). The potential natural vegetation at both sites was dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* [Beetle & A. Young] S. L. Welsh) and bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve) with some Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth) (NRCS, 2017). Soils at Buck Mountain were well drained and ~70 cm deep before encountering a restrictive layer of bedrock. Soils at Warm Springs were also well drained and ~50 cm deep before encountering weathered bedrock. Both sites were relatively flat (< 2%) and 1235 m (Buck Mountain) and 1147 m (Warm Springs) above sea level. Exotic annual grasses, medusahead and cheatgrass, dominated both sites. Both sites had burned in wildfires in the 15 yr before treatment implementation.

### *Experimental Design and Measurements*

Treatments were applied at two sites and at each site, arranged in a randomized complete block design with four replications. Before planting seedlings, glyphosate (Pronto Big N' Tuf) was applied at 560 g ai·ha$^{-1}$ in May 2010 and then imazapic (Panoramic, Alligare, LLC, Opelika, AL) was applied at 87.5 g ai·ha$^{-1}$ in early October 2010 to all plots to control exotic annual grasses. Herbicide treatments fully controlled (100%) exotic annual grasses for the 2011 growing season. Fences were constructed at each site to exclude livestock and wildlife. Treatments were applied to 5 × 5 m plots and included 1) unplanted control (control), 2) crested wheatgrass (crested), 3) crested wheatgrass and forage kochia (crested-kochia), 4) forage kochia (kochia), 5) bluebunch wheatgrass and Wyoming big sagebrush (bluebunch-sage), and 6) crested wheatgrass and Wyoming big sagebrush (crested-sage). There was a 1-m buffer between treatment plots. All species were planted as seedlings grown in cone containers (3.8-cm upper diameter and 21-cm tall). Seedlings were started in July 2010 in a greenhouse at the Eastern Oregon Agricultural Research Center in Burns, Oregon. Approximately half of the seedlings were planted in November 2010, and the other half was planted in March 2011. Seedlings were planted at a density of 10 plants·m$^{-2}$ when one species was planted. When two species were planted together, each was planted at a density of 5 plants·m$^{-2}$. Seedlings were planted at a high density to ensure sites would be fully occupied. As plants grow larger, they can self-thin to the appropriate level for the site (Mueggler and Blaisdell, 1955). In the fall of 2012, exotic annual grass (medusahead and cheatgrass) was hand broadcast seeded at 500 PLS·m$^{-2}$ across treatment plots. Exotic annual grass seed was collected from the infestation surrounding each study site; thus, seed composition was representative of the study site. Annual grasses were seeded into treatment plots to ensure that treatments received similar levels of propagule pressure.

Vegetation characteristics were sampled in June of 2015 and 2016. Vegetation foliar cover and density were measured by species in sixteen 40 × 50 cm quadrats (0.2 m$^2$) per treatment plot. Litter cover and bare ground were also measured in the 40 × 50 cm quadrats. The 40 × 50 cm quadrats were demarcated into 1%, 5%, 10%, 25%, and 50% segments to increase the accuracy of cover estimates. Plants were included for density estimates if they were rooted inside the 40 × 50 cm quadrats. Quadrats were located at 1-m intervals on four 5-m transects (starting at 1 m and ending at 4 m), resulting in four quadrats per transect. The 5-m transects were positioned at 1-m intervals in each treatment plot (starting at 1 m and ending at 4 m).

### *Statistical Analyses*

Repeated-measures analysis of variance (ANOVA) employing the mixed models procedure (Proc Mixed SAS v. 9.4, SAS Institute, Cary, NC) was used to compare treatments. Year was the repeated variable, treatment was considered a fixed variable, and site, replication, and site × treatment interaction were treated as random effect variables in analyses. Akaike information criteria were used to select the appropriate covariance structure (compound symmetry) for repeated-measures ANOVAs (Littell et al., 1996). For analyses, vegetation was separated into the following groups: exotic annual grass, perennial bunchgrass, Sandberg bluegrass (*Poa secunda* J. Presl), perennial forbs, annual forbs, and shrubs. Sandberg bluegrass was treated as a separate group from the other bunchgrasses because it is much smaller and matures earlier. The shrub group included sagebrush and forage kochia. Data that violated assumption of ANOVAs were square root transformed to better meet assumptions. In analyses, the control was compared with other treatments, the grass-shrub treatments were compared with one another, and the introduced species planted singularly and together were compared to address our hypotheses. Treatment means were separated using Fisher's Protected LSD method. Treatment means were considered different at $\alpha = 0.05$ and reported with standard errors (S.E.).

## Results

### Control Compared with Other Treatments

Exotic annual grass cover was 5 − 86 times greater in the control treatment than the other treatments (Fig. 1A; $P < 0.001$). Perennial bunchgrass cover was less in the control treatment than the other treatments ($P < 0.050$), except the control did not differ from the bluebunch-sage treatment ($P = 0.886$). Sandberg bluegrass and perennial forb cover did not differ between the control and other treatments ($P > 0.050$). The control had greater annual forb cover compared with the other treatments ($P < 0.005$), except it did not differ from the kochia treatment ($P = 0.439$). Total herbaceous cover was greater in the control treatment compared with the other treatments ($P < 0.001$). Bare ground was less in the control compared with the other treatments ($P < 0.050$). Litter was greater in the control than the crested-kochia and kochia treatments ($P = 0.031$ and 0.008) but did not differ between the control treatment and crested and crested-sage treatments ($P = 0.093$ and 0.204). Litter was less in the control compared with the bluebunch-sage and crested-sage treatments ($P = 0.032$). Shrub cover was less in the control treatment compared with the other treatments ($P < 0.001$), except it did not differ from the crested treatment ($P = 0.960$). The site × treatment and year × treatment interaction did not influence any cover response variables ($P > 0.050$).

Exotic annual grass density was 24 − 93 times greater in the control treatment compared with the other treatments (Fig. 1B; $P < 0.001$). Perennial bunchgrass density was less in the control than other treatments ($P < 0.050$), except the control did not differ from the bluebunch-sage and kochia treatments ($P = 0.554$ and 0.182). Sandberg bluegrass and perennial forb density did not differ between the control and other treatments ($P > 0.050$). Annual forb density was 6 − 17 times greater in the control than other treatments ($P < 0.001$). Shrub density was less in the control than the other treatments ($P < 0.050$), except the crested treatment ($P = 0.998$). The site × treatment and year × treatment interaction did not influence any density response variables ($P > 0.050$).

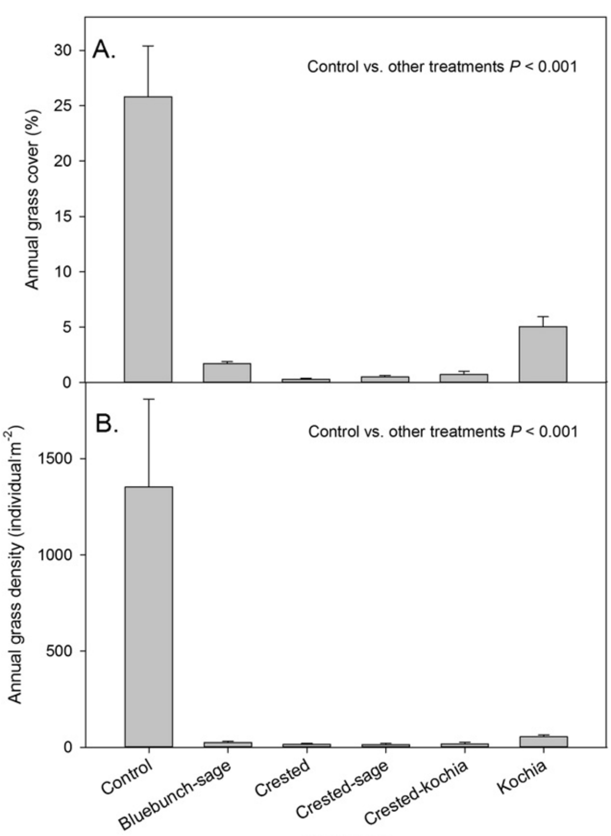


**Fig. 1.** Average exotic annual grass foliar cover (**A**) and density (**B**) with standard error across treatments summarized for 2015 and 2016. Treatments were planted with seedlings after exotic annual grass control, 2 yr later seeded with exotic annual grasses, and then sampled in the third and fourth years after seeding. Control indicates no vegetation planted; Bluebunch-sage, bluebunch wheatgrass and Wyoming big sagebrush seedlings planted; Crested, crested wheatgrass seedlings planted; Crested-sage, crested wheatgrass and Wyoming big sagebrush seedlings planted; Crested-kochia, crested wheatgrass and forage kochia seedlings planted; Kochia, forage kochia seedlings planted.

### Grass-Shrub Combinations

Exotic annual grass and perennial bunchgrass cover varied among treatments (see Fig. 2A and B; $P = 0.037$ and 0.033). Exotic annual grass cover was 2.4 − 3.4-fold greater in the bluebunch-sage treatment compared with the crested-kochia and crested-sage treatments ($P = 0.035$ and 0.018) but did not differ between the crested-kochia and crested-sage treatments ($P = 0.508$). Exotic annual grass cover, however, was relatively low (< 2%) in all grass-shrub combinations. Perennial bunchgrass cover was 4.9 − 7.7-fold greater in the crested-sage and crested-kochia treatments compared with the bluebunch-sage treatment ($P = 0.050$ and 0.014). We did not detect a statistically significant difference in perennial bunchgrass cover between the crested-kochia and crested-sage treatments ($P = 0.071$). Sandberg bluegrass, perennial forb, and annual forb cover did not vary among treatments ($P = 0.398$, 0.241, and 0.199). Total herbaceous vegetation cover and litter varied among grass-shrub combinations ($P = 0.012$ and 0.043). Total herbaceous vegetation cover was 2.6 and 2.9 times greater in the crested-kochia treatment than the crested-sage and bluebunch-sage treatments ($P = 0.009$ and 0.007) but did not differ between the crested-sage and bluebunch-sage treatments ($P = 0.716$). Litter was less in the crested-kochia treatment than the bluebunch-sage and crested-sage treatments ($P = 0.026$ and 0.030), but we did not detect a difference between the crested-sage and bluebunch-sage treatments ($P = 0.884$). Bare ground did not differ among treatments ($P = 0.095$). Shrub cover (sagebrush and forage kochia) varied among treatments ($P = 0.001$). Shrub cover was 4.8 − 5.3 times greater in the bluebunch-sage (31.9% ± 2.5%) and crested-sage (35.0% ± 3.1%) treatments compared with the crested-kochia (6.6% ± 2.6%) treatment ($P = 0.001$ and 0.001) but did not differ between the bluebunch-sage and crested-sage treatments ($P = 0.311$).

Exotic annual grass density did not differ among grass-shrub combinations (Fig. 2C; $P = 0.717$). Perennial bunchgrass density varied among grass-shrub combinations (Fig. 2D; $P = 0.035$). Perennial bunchgrass density was 2.8 and 4.5 times greater in the crested-kochia treatment compared with the crested-sage and bluebunch-sage treatments ($P = 0.038$ and 0.017) but did not differ between the crested-sage and bluebunch-sage treatments ($P = 0.412$). Sandberg bluegrass, perennial forb, and annual forb density did not vary among grass-shrub combinations ($P = 0.315$, 0.130, and 0.130). We did not detect a difference in shrub density among grass-shrub combinations ($P = 0.385$). The site × treatment and year × treatment interaction did not influence vegetation cover and density ($P > 0.050$).

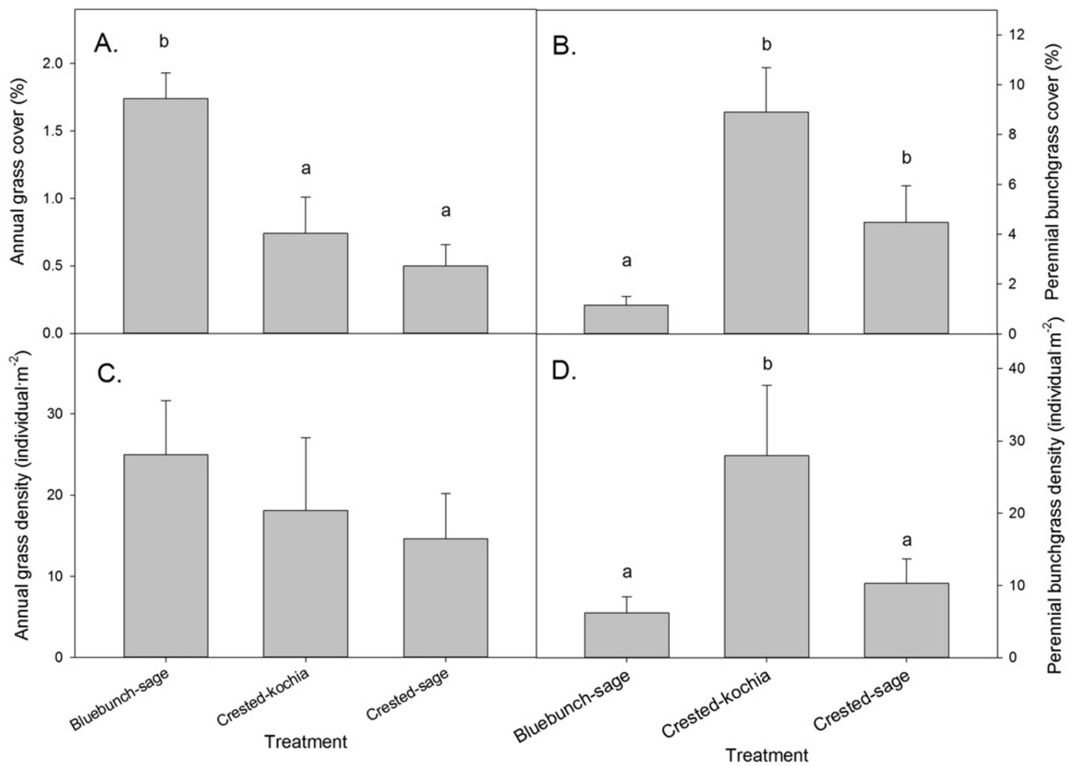


**Fig. 2.** Average exotic annual grass and bunchgrass foliar cover (**A** & **B**) and density (**C** & **D**) with standard error across treatments summarized for 2015 and 2016. Bluebunch-sage indicates bluebunch wheatgrass and Wyoming big sagebrush seedlings planted; Crested-kochia, crested wheatgrass and forage kochia seedlings planted; Crested-sage, crested wheatgrass and Wyoming big sagebrush seedlings planted. Different lowercase letters signify differences ($P < 0.05$) among treatments for response variable.

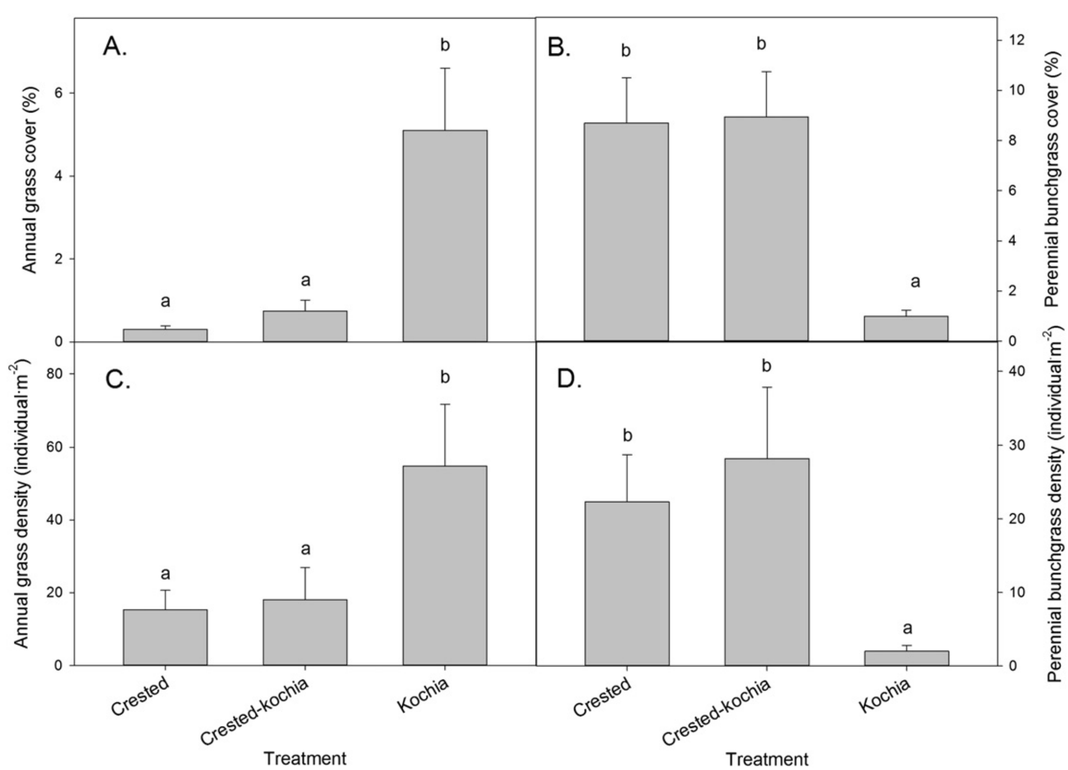


**Fig. 3.** Average exotic annual grass and bunchgrass foliar cover (**A** & **B**) and density (**C** & **D**) with standard error across treatments summarized for 2015 and 2016. Crested indicates crested wheatgrass seedlings planted; Crested-kochia, crested wheatgrass and forage kochia seedlings planted; Kochia, forage kochia seedlings planted. Different lowercase letters signify differences ($P < 0.05$) among treatments for response variable.

*Crested and Kochia*

Exotic annual grass and perennial bunchgrass cover differed among treatments (Fig. 3A and D; $P = 0.034$ and 0.021). Exotic annual grass cover was 16.3 and 6.8 times greater in the kochia treatment compared with the crested and crested-kochia treatments ($P = 0.019$ and 0.026) but did not differ between the crested and crested-kochia treatments ($P = 0.750$). Bunchgrass cover was approximately ninefold greater in the crested and crested-kochia treatments compared with the kochia treatment ($P = 0.014$ and 0.013). Perennial bunchgrass cover was similar between the crested and crested-kochia treatments ($P = 0.907$). Sandberg bluegrass, perennial forb, annual forb, total herbaceous, litter, and bare ground cover did not differ among treatments ($P > 0.050$). Shrub cover varied among treatments ($P = 0.011$). Shrub cover was greater in the kochia (18.7% ± 5.3%) treatment than the crested (0.2% ± 0.1%) and crested-kochia (6.6% ± 2.6%) treatments ($P < 0.001$ and 0.006) and greater in the crested-kochia treatment compared with the crested treatment ($P = 0.008$).

Exotic annual grass and perennial bunchgrass density varied among treatments (see Fig. 3C and D; $P = 0.049$ and 0.030). Annual grass density was 3.6 and 6.0 times greater in the kochia treatment compared with the crested and crested-kochia treatments ($P = 0.037$ and 0.046) but did not differ between the crested and crested-kochia treatments ($P = 0.840$). Perennial bunchgrass density was more than 10 times greater in the crested and crested-kochia treatments compared with the kochia treatment ($P = 0.032$ and 0.014) but was similar between the crested and crested-kochia treatments ($P = 0.397$). Sandberg bluegrass, perennial forb, and annual forb densities did not vary among treatments ($P > 0.050$). Shrub density differed among treatments ($P = 0.018$) with fewer shrubs occurring in the crested treatment compared with the crested-kochia and kochia treatments ($P = 0.034$ and 0.007). Shrub density did not differ between the crested-kochia and kochia treatments ($P = 0.138$). The site × treatment and year × treatment interaction did not influence vegetation cover and density ($P > 0.050$).

## Discussion

Established native and introduced perennial vegetation limited reinvasion by exotic annual grasses whether planted individually or in combinations. Perennial vegetation limited exotic annual grass cover to < 5% compared with > 25% in the control (no perennial vegetation established) treatment. Similarly, Davies (2010) and Davies et al. (2015) found that successful establishment of perennial grasses limited exotic annual grass reinvasion. The high exotic annual grass cover in the control treatment suggests that without establishment of perennial vegetation after control, annual grasses will reinvade and dominate sagebrush steppe communities. This is in agreement with other studies showing exotic annual grasses often quickly reinvade and dominate sagebrush steppe if perennial vegetation is not established after control (Monaco et al., 2005; Sheley et al., 2012; Davies et al., 2015). Therefore, control of exotic annual grasses should, in most situations, only be implemented if establishment of perennial vegetation is also planned.

The ability of different grass-shrub combinations to suppress exotic annual grass cover varied; however, all combinations resulted in exotic annual grass cover of < 2%. In addition, exotic annual grass density did not differ among grass-shrub combination even though one of the combinations was solely composed of natives. Our research indicates that established native species can resist reinvasion by exotic annual grasses. However, native species generally do not establish as well as introduced species in low-elevation sagebrush communities (Robertson et al., 1966; Hull, 1974; Eiswerth et al., 2009; Boyd and Davies, 2010) and when seeded after annual grass control may fail to establish perennial-dominated communities (Davies et al., 2015). Considering prior research and our current study, the critical issue limiting the use of natives in revegetation after exotic annual grass control in the sagebrush steppe is the establishment of seeded native vegetation, not its ability to compete with exotic annual grasses once established. Thus, improving the ability of native vegetation to establish from seed through improved selection and possibly seed and seeding enhancement technologies (e.g., Madsen et al., 2016) represent important strategies for bolstering the utility of native species for revegetation of exotic annual grass — invaded sagebrush communities. Our research also highlights the potential value in evaluating the performance of additional native sagebrush steppe species and mixes for revegetation of annual grass — prone areas.

In addition, it would be valuable to evaluate different densities of established perennial vegetation, especially when coestablished with other vegetation to determine the effects of varying densities on reinvasion resistance and each other. For example, as Wyoming big sagebrush cover increases, bunchgrass productivity declines (Rittenhouse and Sneva, 1976). Similarly, our results suggest that the high planting density of sagebrush, which translated to high sagebrush cover, may have limited coplanted perennial bunchgrasses. Sagebrush cover exceeding 30% is more than double the average cover found in intact Wyoming big sagebrush communities (Davies et al., 2006). Thus, we strongly suspect that sagebrush competition was limiting resources for coplanted bunchgrasses.

Forage kochia has been widely recommended for seeding in the Great Basin to compete with exotic annual grasses (Stevens et al., 1985; McArthur et al., 1990; Monsen and Turnipseed, 1990; Clements et al., 1997). Similarly, our results show that forage kochia can suppress exotic annual grasses; however, crested wheatgrass and crested wheatgrass-forage kochia communities were more resistant to reinvasion by exotic annual grasses. Including a perennial bunchgrass in the revegetation plant community is probably crucial to resisting exotic annual grass invasion because of high niche overlap between perennial and annual grasses (James et al., 2008). Perennial bunchgrasses are often the most important plant group to limiting exotic annual grasses in sagebrush steppe communities (Chambers et al., 2007; Davies, 2008). Though we did not test niche separation, our results suggest that there is more separation between forage kochia and exotic annual grasses than bunchgrasses and exotic annual grasses. In support of this assertion, Leonard et al. (2008) reported that cheatgrass compared with forage kochia competed more for soil nitrate with crested wheatgrass. The ability of forage kochia, at times, to establish in exotic annual grasslands without control of exotic annual grasses (McArthur et al., 1990; Monsen and Turnipseed, 1990) further suggests a large degree of niche separation between forage kochia and exotic annual grasses. Therefore, for the best suppression of exotic annual grasses, it appears that perennial bunchgrasses should be included in revegetation efforts that use forage kochia.

An additional concern with only seeding forage kochia after annual grass control is that forage kochia exhibits sporadic establishment in the Great Basin (Haferkamp et al., 1990; Sheley et al., 2007). Forage kochia establishment has, at times, been poor after annual grass control with preemergent herbicides (Morris et al., 2009; Davies et al., 2015). However, Clements et al. (1997) estimated that forage kochia had a 70% chance of success when seeded on suitable sites, though crested wheatgrass chance of success was 80%. Therefore, to increase the likelihood of successful revegetation after annual grass control, we recommend that forage kochia and other similar species be used only in combination with other species in revegetation attempts.

Crested wheatgrass appears to be a strong competitor with exotic annual grasses. Treatments that included crested wheatgrass generally limited reinvasion of annual grasses more than other treatments. It has been well established that crested wheatgrass can effectively compete with exotic annuals and promote resistance to invasive species (Miller, 1956; Arredondo et al., 1998; Davies, 2010; Davies et al., 2015). Crested wheatgrass is generally considered a more effective competitor with exotic annuals in the sagebrush ecosystem than native bunchgrasses because it is better at acquiring soil resources (Aguirre and Johnson, 1991; Van Auken et al., 1992; Bilbrough and Caldwell,

1997) and can increase photosynthetic water-use efficiency following defoliation (Hamerlynck et al., 2016). The success of crested wheatgrass in limiting exotic annuals may also be partially attributed to its high recruitment potential. For example, crested wheatgrass outrecruited native bunchgrasses by 10-fold over a 13-yr period (Nafus et al., 2015). Our results affirm that established crested wheatgrass communities are highly resistant to exotic annual grass invasion.

## Implications

Established introduced or native perennial vegetation appears to convey resistance to reinvasion by exotic annual grasses following their control in sagebrush steppe communities. The viability of seeding native vegetation after exotic annual grass control in low-elevation sagebrush communities, however, is currently constrained by low establishment success and high costs (Davies et al., 2011; James et al., 2011; Nafus and Davies, 2014). In areas of high priority for restoration of native vegetation, bypassing the seed to seedling stage by planting seedlings may be a viable method for restoration after exotic annual grass control. We caution against solely using forage kochia as a revegetation species because resistance to exotic annual grass invasion was greater when a perennial bunchgrass was also established with kochia. As expected, established crested wheatgrass greatly limits exotic annual grass expression and, therefore, provides high resistance to exotic annual grass reinvasion after control. In addition, crested wheatgrass can be a cost-effective species to seed after annual grass control to establish a perennial-dominated plant community. However, it can be difficult to establish native vegetation in crested wheatgrass communities (Hulet et al., 2010; McAdoo et al., 2017). As such, managers should determine if established crested wheatgrass communities meet their long-term management goals. Coseeding crested wheatgrass and sagebrush may be a possible approach to have a high probability of limiting exotic annual grass reinvasion and establishing a native-introduced plant community that provides many of the same ecosystem services as a native community, such as sagebrush-obligate wildlife habitat, reliable livestock forage, and a reduced likelihood of frequent wildfires. Though there are numerous combinations of native, introduced, and native-introduced species that could be evaluated for revegetating annual grass — invaded sagebrush steppe, our research demonstrates that successful establishment of perennial vegetation greatly reduces reinvasion by exotic annual grasses. Therefore, management should focus on ensuring that species selected for revegetation successfully establish, which may necessitate that more costly and labor-intensive methods be implemented for species that are prone to failing to establish when seeded.

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