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# Changes in Abundance of Eight Sagebrush-Steppe Bunchgrass Species 13 Yr After Coplanting<sup>☆</sup>

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## ABSTRACT

Stable bunchgrass populations are essential to resilience and restoration of sagebrush steppe rangelands, yet few studies have assessed long-term variation in plant abundance from a known starting point. We capitalized on a previous paddock study by reestablishing in 2011 nine replicate blocks consisting of  $29 \times 29$  grid of cells, each planted in 1998 with a single individual of one of eight sagebrush steppe bunchgrasses, including the widely planted exotic, crested wheatgrass (*Agropyron cristatum*). Plant species and numbers were determined in 2011 for each cell, which were classified as holds or cedes, with ceded cells used to determine species-specific gains. We hypothesized the competitive crested wheatgrass would proportionally occur more in gained cells compared with native grasses. While crested wheatgrass did proportionally hold and gain the greatest number of cells, the relative number of plants within holds and gains was constant across all species, with most plants (80–87%) occurring outside cells originally planted with them. Crested wheatgrass had greater proportions of holds and gains where it was the only species within the cell and showed even presence across all cells planted with other grass species in 1998. Native grasses were underrepresented in 1998 crested wheatgrass cells and sometimes overrepresented in other native species cells. The ratio of total crested wheatgrass to native bunchgrass plants followed a sigmoidal step increase with increasing crested wheatgrass density. These results show population changes in sagebrush steppe bunchgrasses are determined by seed production and emergent seedling survival, both of which are stronger in the exotic bunchgrass. This study also showed that native grasses can maintain presence via seed in areas depending on crested wheatgrass density. This information could help shape management strategies capitalizing on the utility of crested wheatgrass and sustaining desirable levels of native grass productivity and diversity.

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## Introduction

Establishing stable bunchgrass populations enhances long-term restoration success and resilience of sagebrush steppe to degradation, principally due to the ongoing spread of highly competitive exotic invasive annual grasses that can increase fire frequency (Bradley et al., 2006; Davies, 2011; Davies et al., 2011; Boyd and Davies, 2012; Brooks et al., 2016). Restoration success rates in sagebrush steppe are often low, and determining the ecological dynamics and processes associated with restoration outcomes provides critical information for ongoing efforts to maintain the integrity of sagebrush steppe ecosystems for use by livestock, game, and species of concern such as sage grouse (Davies et

al., 2011; James et al., 2013). Of particular importance to these are studies assessing long-term outcomes of plant population dynamics; this presents a problem in that these are rare, and the initial plant community conditions—beyond seeding rates and mixtures—are not well documented (Liston et al., 2003). A recent study by Nafus et al. (2015) showed a widely planted exotic bunchgrass, crested wheatgrass (*Agropyron cristatum* [L] Gaertn), coplanted with 7 native bunchgrasses, attained 10-fold increased density after 13 yr. Only the density of one native grass, Idaho fescue, increased (*Festuca idahoensis* Elmer), while other native bunchgrass densities remained constant or declined from initial planting numbers (Nafus et al., 2015). Nafus et al. (2015) asserted that even though crested wheatgrass is highly competitive, over the long term, coplanted natives can maintain viable population numbers in areas dominated by the exotic grass. Valuable as this study is, Nafus et al. (2015) only reported changes in overall plant density pooled across nine replicated plots, each with a  $29 \times 29$  grid of cells originally containing one adult plant of a single species (Ganskopp et al., 2007), and did not determine cell-by-cell changes in plant abundance. Such information would be valuable, in that the number of plants of

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each species found outside of originally planted cells would show how changes in overall population depend on plant establishment via seed.

Some have considered cold-desert bunchgrasses as long-lived and primarily reliant on vegetative processes to spread and maintain populations (Smith et al., 1997). However, studies have shown that bunchgrasses may not be as long-lived as previously thought and that variation in seed production and establishment from seed is a major component of population growth in native and exotic sagebrush steppe bunchgrasses (Pyke, 1990; Liston et al., 2003). We revisited the Ganskopp et al. (2007) coplanted data grid to determine if changes in plant density documented by Nafus et al. (2015) also varied in the relative proportions of plant abundances inside and outside of originally planted cells. We hypothesized that crested wheatgrass would proportionally occur more in cells outside its original plantings than native grasses, consistent with its marked increase in overall density. Although sagebrush steppe bunchgrasses have high germination rates, crested wheatgrass produces seeds that have higher annual probabilities to transition through emergence, overcoming a key demographic bottleneck to plant recruitment and establishment (James et al., 2011). Crested wheatgrass also possesses ecophysiological mechanisms that optimize soil water and nutrient extraction and water use efficiency, as well as carbon allocation strategies that ameliorate the effects of drought and grazing (Jackson and Caldwell, 1989; Anderson and Toft, 1993; Meays et al., 2000; Gunnell et al., 2010; Mukherjee et al., 2015; Hamerlynck et al., 2016; Denton et al., 2018). Taken together, these attributes likely facilitate crested wheatgrass's ability to spread and hold colonized territory.

## Methods

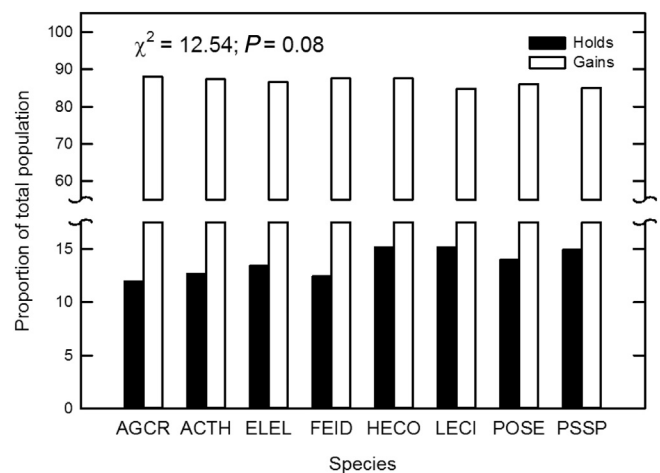
Nine 313-m<sup>2</sup> study plots were established in 1989 for a paddock study in sagebrush steppe cleared of vegetation on the Northern Great Basin Experimental Range (lat 43°28'48.3"N, long 119°42'32.2"W, 1403 m above sea level), located 56 km west of Burns, Oregon (Ganskopp et al., 2007). Average annual precipitation at the site is 286 mm, dominated by rains and snow typically from October to March; soils are a complex of Millican coarse-loamy, mixed Orthodic Durixerolls and Holte coarse-loamy, mixed frigid Orthodic Haploxerolls, with a depth to bedrock or hardpan ranging from 90–150 cm (Lentz and Simonson, 1986; Nafus et al., 2015). Within each plot, eight species of bunchgrass were planted so that each plot contained 2.6 plants or 0.33 plants per species m<sup>-2</sup>, randomly assigned to an evenly spaced grid of 29 rows and columns, giving 800 planted cells and 41 randomly assigned empty gap cells per plot. A single mature plant was transplanted into the center of each cell from the surrounding sagebrush steppe community, characterized by Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* Beetle); these included the native grass species Thurber's needlegrass (*Acnatherum thurberianum* [Piper] Barkworth; ACTH), bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey; ELEM), Idaho fescue (*Festuca idahoensis* Elmer; FEID), needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth; HECO), basin wildrye (*Leymus cinereus* [Scribn. & Merr.] A. Löve; LECI), Sandberg bluegrass (*Poa secunda* J. Presl. POSE), and bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve; PSSP), and one introduced bunchgrass, crested wheatgrass (*Agropyron cristatum* [L.] Gaertn. "Nordan"; AGCR). The site was protected from grazing until 1997, when it was weeded and restocked with transplants when necessary to attain the original plant densities, and used in a livestock forage preference study (Ganskopp et al., 2007). It has been unburned and protected from large animal grazing since 1998 and left to natural processes of recruitment and mortality.

In 2011, the original grids were reestablished in each block and the species and number of all bunchgrasses within each cell were counted. We sorted cells in each block by 1998 species ID and then classified them into two categories: "holds" (1998 species still present in 2011) and "cedes" (species planted in 1998 no longer present). Holds were

classified as "exclusive," with only the original species present, or "mixed" with novel species present, with the identity and number of these recorded. We then classified ceded cells into "gap" and "grass" categories, with the plant species and number recorded. Using the "mixed hold" and "ceded to grass" cells, we were able to determine the total number of cells a species gained outside its original planting, either in an already occupied cell ("gain into hold") or by replacement ("replacement gain"). It should be noted that multiple species could occur within a ceded cell, so the total number of gained cells by a species into a given original planting can exceed the total number of ceded cells.

For our first analysis, we determined total number of all plants of each species inhabiting "hold" and "gain" cells pooled across all nine blocks in order to determine how much change from 1998 to 2011 relied purely on plants from seed. We tested for differences between the seven species using chi-square ( $\chi^2$ ; Statistix v.8.0, Analytical Software, Tallahassee, FL); a significant  $\chi^2$  test would indicate the species do not have common proportions of plants distributed between originally planted cells (holds) and colonized cells (gains). We then used one-way analysis of variance (one-way ANOVA, Statistix v.8.0, Analytical Software) to test for differences in the number of exclusive and mixed holds and cedes to gap or other grasses across the original 1998 plantings, using the species-by-replicate block interaction as the error term (F-test df = 7, 64) and  $\alpha$ -adjusted post-hoc means testing using least significant difference (LSD). As species could gain more cells than were ceded, we performed two different analyses for replacement gains. First, we tested to check for differences in replacement gains by AGCR only, mixed (AGCR + other native grass), or native bunchgrasses (NBG; pooled across all native species); this provides an analysis of replacement equivalent to ceded cells. Next, we performed individual ANOVA for total replacement gains by each species, testing for differences in species-specific gains across the original plantings. In both analyses, the species-by-replicate block interaction was used as the error term (F-test df = 6, 56), with  $\alpha$ -adjusted post-hoc means testing made using LSD. To compare replacement gains across 2011 species, we pooled all observations ( $n = 63$  for each species) across the blocks and used one-way ANOVA to test for differences (F-test df = 7, 496), with  $\alpha$ -adjusted post-hoc means testing made using LSD.

We summarized the effect of AGCR density on NBG abundance by first determining the percent of total area of hold and gain cells occupied by 1–5 AGCR plants per cell pooled across all nine blocks; we selected these densities because they were common within all hold and gain areas across all nine blocks. Within each AGCR density class area, the total number of all NBG plants were summed and the ratio of total



**Figure 1.** Percentage of plant populations of seven sagebrush steppe bunchgrasses in 2011 occurring within (Hold) and outside (Gain) cells originally planted in 1998.  $\chi^2$  test-result probability associated with 7 degrees freedom. AGCR indicates crested wheatgrass; ACTH, Thurber's needlegrass; ELEM, bottlebrush squirreltail; FEID, Idaho fescue; HECO, needle-and-thread; LECI, basin wildrye; POSE, Sandberg's bluegrass; and PSSP, bluebunch wheatgrass.

AGCR plants to total NGB plants regressed against AGCR cell<sup>-1</sup> using nonlinear regression (3 parameter sigmoidal, SigmaPlot v. 12.3; Systat Software, Chicago, IL).

## Results

For all species, far more plants in 2011 occurred outside the cells originally planted with them in 1998 and the relative proportions of holds and gains did not significantly differ among the eight species (Fig. 1). In 2011, all holds were lower than original planting numbers and had significant differences in exclusive ( $F_{7,64} = 128.87$ ;  $P \leq 0.01$ ) and mixed holds ( $F_{7,64} = 36.02$ ;  $P \leq 0.01$ ) due to markedly higher holds by AGCR compared with native bunchgrasses, which had similar low exclusive and mixed holds (Fig. 2a). The few significant differences in mixed holds by native grasses were almost exclusively a result of gains by AGCR into these (data not shown). All eight species ceded similar numbers of cells to bare ground ( $F_{7,64} = 1.16$ ;  $P = 0.34$ ), with

**Table 1**

F-test results for total replacement gains by eight bunchgrass species across cells planted with other grass species in 1998 in nine replicate blocks.

Species	F
Crested wheatgrass (AGCR)	1.09
Thurber's needlegrass (ATTH)	6.76*
Bottlebrush squirreltail (ELEL)	2.45*
Idaho fescue (FEID)	6.97*
Needle-and-thread grass (HECO)	10.02*
Basin giant rye (LECI)	9.24*
Sandberg's bluegrass (POSE)	2.03
Bluebunch wheatgrass (PSSP)	3.72*

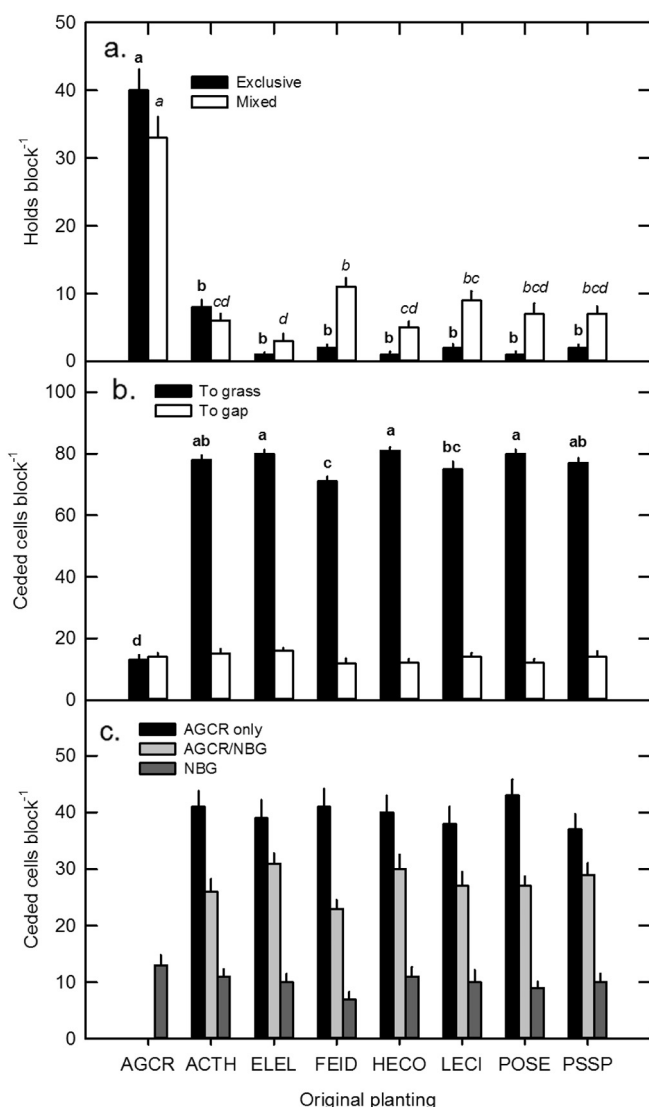
\* Indicates significance at 0.05, F-test degrees freedom = 6, 56.

significant differences between the species in cedes to grasses ( $F_{7,64} = 200.0$ ;  $P < 0.01$ ). AGCR ceded lower than natives. FEID ceded least of NGB of NGBs, intermediate LECI, and similar others (Fig. 2b). The average number of cells ceded did not differ across the original plantings to AGCR ( $F_{6,56} = 0.50$ ;  $P = .080$ ), mixed ( $F_{6,56} = 1.7$ ;  $P = 0.14$ ), or pooled NGB conditions ( $F_{7,64} = 1.07$ ;  $P = 0.39$ ; Fig. 2c). On a species-by-species basis, replacement gains in 2011 significantly varied across original plantings for all grasses except crested wheatgrass and Sandberg's bluegrass (Table 1). The significant variation in other grasses was due primarily to lower replacement of crested wheatgrass by any native grass, though there were some cases in which some native grasses had higher gains in cells ceded by other native grasses (Fig. 3). However, most of these gains were made in the form of mixed gains with the exotic crested wheatgrass (data not shown). While Sandberg's bluegrass did not show significant replacement gain variation (see Table 1), it also had low gains into crested wheatgrass cells (Fig. 4d). Pooled across all the blocks, replacement gains differed significantly among species in 2011 ( $F_{7,496} = 2049.0$ ;  $P \leq 0.01$ ), with crested wheatgrass cells averaging much higher gains than native grasses and Idaho fescue having significantly higher gains compared with other native grasses (Table 2).

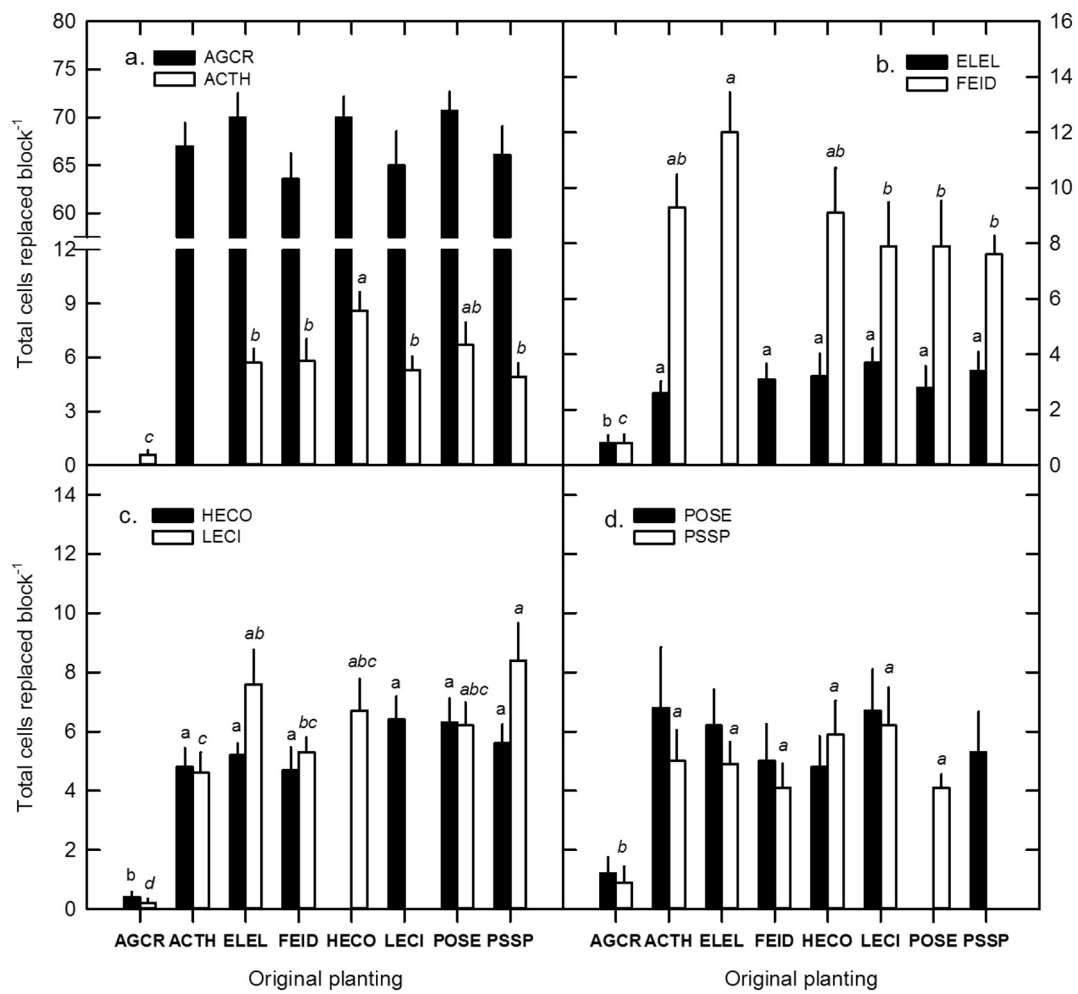
Cells with 1–5 AGCR plants occupied 77.7% of the total study area, with the bulk of this area, 69.8%, consisting of cells with 1–3 AGCR plants (Fig. 4). Within this area, total plant AGCR:NGB ratios were similar between holds and gains with 1–2 AGCR plants, with a slight increase in AGCR:NGB in the area with 3 AGCR plants per cell (see Fig. 4). Cells with 4–5 AGCR plants made up 7.9% of the total area, with a sharp rise in AGCR:NGB ratios, especially in cells held by AGCR from 1998 through 2011, contributing to significant sigmoidal relationship between AGCR:NGB with AGCR density class (see Fig. 4).

## Discussion

Contrary to our expectations, crested wheatgrass plants did not proportionally occur more outside of cells originally planted with it in 1998 compared with native grass species. Rather, the overwhelming majority of plants of all species, in some cases nearly 90%, occurred outside of cells originally planted with them in 1998 (Fig. 1). This indicates that the consequences of population dynamics to plant community composition over this 13-yr period in our study plots were dominated by variation in plant establishment from seed. This supports longer-term studies by Liston et al. (2003), where isozyme analyses showed that 60–70% of bunchgrass population growth over 37 yr was accounted for by sexual reproduction, not vegetative clonal spread, and demographic studies showing population growth in these grasses are strongly determined by seed production and seedling survival through the emergent period (Pyke, 1990; James et al., 2011). Indeed, our results extend findings from these studies, as even species with declining populations in our plots consist primarily of individuals established from seed. For crested wheatgrass, population gains likely reflect the cumulative effects of delayed timing of seed release that can increase crested wheatgrass presence in the seed bank (Pyke, 1990) and higher interannual

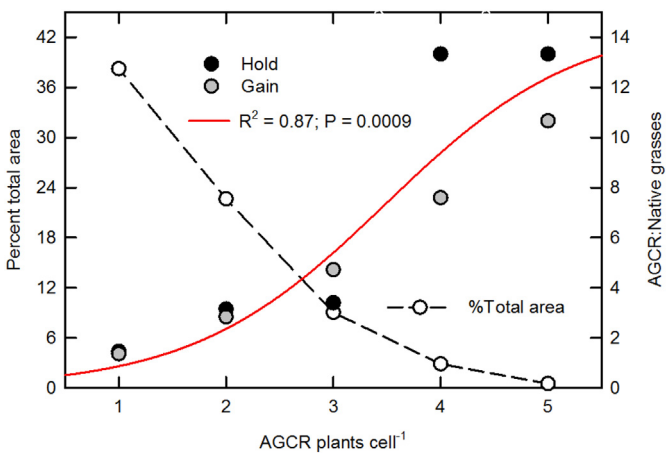


**Figure 2.** Average number of cells (a) held, either exclusively by original species or with a novel species, and cells ceded to (b) bare ground (gap) or one or more other grasses (grass). (c) Cells ceded to grass occupied exclusively by crested wheatgrass, crested wheatgrass with one or more native grasses, or other native grasses. Each bar is the mean of nine replicate blocks, error bars are  $\pm 1$  S.E. of the mean, and letters differ across original plantings (LSD; one-way analysis of variance). AGCR indicates crested wheatgrass; ACTH, Thurber's needlegrass; ELEL, bottlebrush squirreltail; FEID, Idaho fescue; HECO, needle-and-thread; LECI, basin wildrye; POSE, Sandberg's bluegrass; and PSSP, bluebunch wheatgrass.



**Figure 3.** Average total number of cells gained by replacement for (a) crested wheatgrass (AGCR) and Thurber's needlegrass (ACTH), (b) bottlebrush squirreltail (ELEL) and Idaho fescue (FEID), (c) needle-and-thread (HECO) and basin wildrye (LECI), and (d) Sandberg's bluegrass (POSE) and bluebunch wheatgrass (PSSP). Each bar is the average of nine replicate blocks and includes gains from exclusive and mixed species replacements; error bars indicate  $\pm 1$  S.E.; letters indicate significant differences within a species across the original cell plantings (least significant difference; one-way analysis of variance). AGCR indicates crested wheatgrass; ACTH, Thurber's needlegrass; ELEL, bottlebrush squirreltail; FEID, Idaho fescue; HECO, needle-and-thread; LECI, basin wildrye; POSE, Sandberg's bluegrass; and PSSP, bluebunch wheatgrass.

probability of seedlings transitioning through emergence (James et al., 2011). This likely enhanced establishment of crested wheatgrass plants capable of contributing to greater seed-bank representation.



**Figure 4.** Percentage of the study area occupied by crested wheatgrass (AGCR) (open symbols, dashed line) and the proportion of total AGCR to native bunchgrasses plants within these areas from AGCR holds (black symbols) and gains (gray symbols) from 1998 to 2011. The fitted sigmoidal relationship is to data pooled across AGCR holds and gains.

Our study area also experienced greater numbers of years of low rainfall following 1998, consistent with trends across other Western US ecoregions (Cook et al., 2010; McAuliffe and Hamerlynck, 2010; Moran et al., 2014). The greater proportion of crested wheatgrass holds from 1998 to 2011 (see Fig. 3) may reflect lower mortality compared with native grasses over the 1998–2011 period, consistent with studies demonstrating greater drought tolerance of crested wheatgrass compared with native bunchgrasses (Anderson and Toft, 1993; Meays et al., 2000; Hamerlynck et al., 2016; Denton et al., 2017). Survival of established plants through drought would facilitate population

**Table 2**  
Average total replacement gains made between 1998 and 2011 pooled across all blocks coplanted with eight sagebrush steppe bunchgrass species. Each value is the mean of 63 observations. Standard error of the mean is presented in parentheses. Letters differ significantly at  $P < 0.05$  (least significance difference from one-way analysis of variance).

Species	Replacement gains (cells block <sup>-1</sup> )
Crested wheatgrass (AGCR)	67 (1.0) a
Thurber's needlegrass (ATTH)	5 (0.4) c
Bottlebrush squirreltail (ELEL)	2 (0.2) d
Idaho fescue (FEID)	8 (0.6) b
Needle-and-thread grass (HECO)	5 (0.3) c
Basin giant rye (LECI)	6 (0.5) c
Sandberg's bluegrass (POSE)	5 (0.5) c
Bluebunch wheatgrass (PSSP)	4 (0.4) c



growth potential. Indeed, crested wheatgrass holds had a higher frequency of cells occupied by four or more crested wheatgrass plants than did native bunchgrass holds, even those in Idaho fescue, the only native species that grew in population (data not shown). This is reflected in the high AGCR:NBG ratios in crested wheatgrass hold areas consisting of cells with 4–5 crested wheatgrass plants compared with gain areas with the similar numbers of plants (see Fig. 4). This could indicate greater seedling establishment around older plants that persisted through dry years; however, we would need to account for the degree of self-replacement within any given cell to determine if this were the case. If these cells are occupied by plants established in 1998, the reproductive output by these, coupled with greater seedling emergence and higher establishment of reproductively viable plants in gained territory alluded to above, would give crested wheatgrass a strong competitive advantage over native grasses.

This competitive advantage is also reflected in the similar, high number of gains made by crested wheatgrass in 2011 across cells planted with native grasses in 1998 and the consistent underrepresentation of native grasses into cells originally planted with this exotic grass (see Fig. 3). The fact that crested wheatgrass had more exclusive holds and greater numbers of cells ceded exclusively to it (see Fig. 2) is suggestive of competitive exclusion. Some native grasses tended to show greater replacement gains in cells planted with other native grass species (see Fig. 3). This might be a consequence of the randomization scheme of Ganskopp et al. (2007). However, given that crested wheatgrass was prevalent, if not dominant, across most of the study area by 2011 (see Fig. 4), and that most of these gains occurred concurrently in cells with crested wheatgrass, this may also reflect a degree of continuing competitive displacement imposed by the exotic grass. If so, the step-function declines in native grass abundance with increasing crested wheatgrass density (see Fig. 4) could eventually lead to a decline in native bunchgrass diversity as well, as occurs with increasing density of exotic annual grasses in sagebrush steppe communities (Davies, 2011).

## Implications

This study highlights how the use of crested wheatgrass should be carefully matched with management objectives. Crested wheatgrass is highly effective in halting invasive annual spread and restoring watershed functionality and integrity following fire or remediation of woody plant encroachment (Monsen and McArthur, 1995; Davies et al., 2010). High densities of crested wheatgrass in such areas would present a formidable challenge to establishing desirable native bunchgrass species. Our results indicate a threshold crested wheatgrass density above which increased seeding levels of native grasses would likely not be effective, much as occurs in areas dominated by high densities of exotic annuals (Schantz et al., 2016). However, for other revegetation or conservation efforts, this study shows, as did Nafus et al. (2015), that native grasses can maintain a considerable presence in areas planted with crested wheatgrass. Furthermore, this study extends these findings by showing that the level of native grass presence follows 1) long-term patterns in plant establishment following sexual reproduction and 2) densities of crested wheatgrass. The latter could be important, in that livestock grazing can promote native plant diversity in crested wheatgrass – dominated sagebrush steppe (Nafus et al., 2016) and there could be a window in which grazing in such areas might be most effective. This information might optimize management seeding and planting strategies that could capitalize on the utility of crested wheatgrass but still sustain native grass productivity and diversity desired in sagebrush steppe rangelands. Caution should be used in generalizing our results to all natural sagebrush steppe ecosystems. Though overall plant densities increased from 1998 to 2011 (Nafus et al., 2015), these are low compared with mature sagebrush steppe (Liston et al., 2003), even following severe fire (Hulet et al., 2015). However, our findings are valuable for restoration efforts aimed at reclaiming highly disturbed sagebrush steppe systems.

## References

- Anderson, J.E., Toft, N.L., 1993. Depletion of soil moisture by two cold-desert bunchgrasses and effects on photosynthetic performance. *Great Basin Naturalist* 53, 97–106.
- Boyd, C.S., Davies, K.W., 2012. Spatial variability in cost and success of revegetation in a Wyoming big sagebrush community. *Environmental Management* 50, 441–450.
- Bradley, B.A., Houghton, R.A., Mustard, J.F., Hamburg, S.P., 2006. Invasive grass reduces aboveground carbon stocks in shrublands of the Western US. *Global Change Biology* 12, 1815–1822.
- Brooks, M.L., Brown, C.S., Chambers, J.C., D'Antonio, C.M., Keeley, J.E., Belnap, J., 2016. Exotic annual *Bromus* invasions: comparisons among species and ecoregions in the Western United States. In: Germino, M.J., Chambers, J.C., Brown, C.S. (Eds.), *Exotic brome-grasses in arid and semiarid ecosystems of the western US*. Springer Series on Environmental Management, Springer International Publishing, Cham, Switzerland, pp. 11–60.
- Cook, E.R., Seager, R., Heim, R.R., Vose, R.S., Herweijer, C., Woodhouse, C., 2010. Megadroughts in North America: placing IPCC projections of hydroclimatic change in long-term palaeoclimate context. *Journal of Quarterly Science* 25, 48–61.
- Davies, K.W., 2011. Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass. *Oecologia* 167, 481–491.
- Davies, K.W., Nafus, A.M., Sheley, R.L., 2010. Non-native competitive perennial grass impedes the spread of an invasive annual grass. *Biology Invasions* 12, 3187–3194.
- Davies, K.W., Boyd, C.S., Beck, J.L., Bates, J.D., Svejcar, T.J., Gregg, M.A., 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. *Biology Conservation* 144, 2573–2584.
- Denton, E.M., Smith, B.S., Hamerlynnck, E.P., Sheley, R.L., 2018. Seedling defoliation: effect of intensity and frequency on performance and survival. *Rangeland Ecology & Management* 71, 25–34.
- Ganskopp, D., Aguilera, L., Varva, M., 2007. Livestock forage conditioning among six great basin grasses. *Rangeland Ecology & Management* 60, 71–78.
- Gunnell, K.T., Monaco, T.A., Call, C.A., Ransom, C.V., 2010. Seedling interference and niche differentiation between crested wheatgrass and contrasting native great basin species. *Rangeland Ecology & Management* 63, 443–449.
- Hamerlynnck, E.P., Smith, B.S., Sheley, R.L., Svejcar, T.J., 2016. Compensatory photosynthesis, water-use efficiency and biomass allocation of defoliated exotic and native bunchgrass seedlings. *Rangeland Ecology & Management* 69, 206–214.
- Hulet, A., Boyd, C.S., Davies, K.W., Svejcar, T.J., 2015. Prefire (preemptive) management to decrease fire-induced bunchgrass mortality and reduce reliance of postfire seeding. *Rangeland Ecology & Management* 68, 437–444.
- Jackson, R.B., Caldwell, M.M., 1989. The timing and degree of root proliferation in fertile soil microsites for three cold-desert perennials. *Oecologia* 81, 149–153.
- James, J.J., Svejcar, T.J., Rinella, M.J., 2011. Demographic processes limiting seedling recruitment in arid grassland restoration. *Journal of Applied Ecology* 48, 961–969.
- James, J.J., Sheley, R.L., Erickson, T., Rollins, K.S., Taylor, M.H., Dixon, K.W., 2013. A systems approach to restoring degraded drylands. *Journal of Applied Ecology* 50, 730–739.
- Lentz, R.D., Simonson, G.H., 1986. A detailed soil inventory and associated vegetation of Squaw Butte Range Experimental Station. Oregon Ag. Exp. Sta. Special Report 760 Corvallis, OR, USA: 184 p.
- Liston, A., Wilson, B.L., Robinson, W.A., Doescher, P.S., Harris, N.R., Svejcar, T., 2003. The relative importance of sexual reproduction versus clonal spread in an aridland bunchgrass. *Oecologia* 137, 216–225.
- McAuliffe, J.R., Hamerlynnck, E.P., 2010. Perennial plant mortality in the Sonoran and Mojave Deserts in response to severe, multi-year drought. *Journal of Arid Environments* 74, 885–896.
- Meays, C.L., Laliberte, A.S., Doescher, P.S., 2000. Defoliation response of bluebunch and crested wheatgrass: why we cannot graze these two species in the same manner. *Rangelands* 22, 16–18.
- Monsen, S.B., McArthur, E.D., 1995. Implications of early intermountain range and watershed practices. In: Roundy, B.A., McArthur, E.D., Haley, J.S., Mann, D.K. (Eds.), *Proceedings: Wildland Shrub and Arid Land Restoration Symposium*, October 19–21, 1993, Las Vegas, NV, USA: General Technical Report INT-GTR-315. USDA US Forest Service Intermountain Research Station, Ogden, UT, USA, pp. 16–25.
- Moran, M.S., Ponce Campos, G.E., Huete, A., McClaran, M.P., Zhang, Y., Hamerlynnck, E.P., Augustine, D.J., Gunter, S.A., Kitchen, S.G., Peters, D.P.C., Starks, P.J., Hernandez, M., 2014. Functional response of U.S. grasslands to the early 21st century drought. *Ecology* 95, 2121–2133.
- Mukherjee, J.R., Jones, T.A., Adler, P.B., Monaco, T.A., 2015. Contrasting mechanisms of recovery from defoliation in two Intermountain-native bunchgrasses. *Rangeland Ecology & Management* 68, 485–493.
- Nafus, A.M., Svejcar, T.J., Ganskopp, D.C., Davies, K.W., 2015. Abundances of co-planted native bunchgrasses and crested wheatgrass after 13 years. *Rangeland Ecology & Management* 68, 211–214.
- Nafus, A.M., Svejcar, T.J., Davies, K.W., 2016. Disturbance history, management, and seeding year precipitation influences vegetation characteristics of crested wheatgrass stands. *Rangeland Ecology & Management* 69, 248–256.
- Pyke, D., 1990. Comparative demography of co-occurring introduced and native tussock grasses: persistence and potential expansion. *Oecologia* 82, 537–543.
- Schantz, M.C., Sheley, R.L., James, J.J., Hamerlynnck, E.P., 2016. Role of dispersal timing and frequency in annual grass invaded Great Basin ecosystems: how modifying seeding strategies increases restoration success. *Western North American Naturalist* 76, 36–52.
- Smith, S.D., Monson, R.K., Anderson, J.E., 1997. *Physiological ecology of North American desert plants*. Springer-Verlag, Berlin and Heidelberg, Germany; New York, NY, USA 286 p.