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Disturbance History, Management, and Seeding Year Precipitation Influences Vegetation Characteristics of Crested Wheatgrass Stands[☆]

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ABSTRACT

Crested wheatgrass (*Agropyron cristatum* [L.] Gaertm. and *Agropyron desertorum* [Fisch.] Schult.) has been seeded across millions of hectares of the sagebrush steppe and is often associated with native species displacement and low biological diversity. However, native vegetation composition of these seedings can be variable. To gain better understanding of the correlation between vegetation characteristics of crested wheatgrass seedings and their seeding history and management, we evaluated 121 crested wheatgrass seedings across a 54 230-km² area in southeastern Oregon. Higher precipitation in the year following seeding of crested wheatgrass has long-term, negative effects on Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young) cover and density. Wyoming big sagebrush cover and density were positively correlated with age of seeding and time since fire. We also found that preseeded disturbance (burned, scarified, plowed, or herbicide) appears to have legacy effects on plant community characteristics. For example, herbicide-treated sites had significantly fewer shrubs than sites that were burned or scarified preseeded. Native vegetation cover and density were greater in grazed compared with ungrazed crested wheatgrass stands. The results of this study suggest a number of factors influence native vegetation cover and density within stands of seeded crested wheatgrass. Though disturbance history and precipitation following seeding can't be modified, management actions may affect the cover and abundance of native vegetation in crested wheatgrass stands. Notably, grazing may reduce monoculture characteristics of crested wheatgrass stands and fire exclusion may promote sagebrush and perennial forbs.

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Introduction

Crested wheatgrass (*Agropyron cristatum* [L.] Gaertm. and *Agropyron desertorum* [Fisch.] Schult.), an introduced perennial bunchgrass, has been seeded across 6–11 million hectares of western North American rangelands (Lesica and DeLuca, 1996; Ambrose and Wilson, 2003; Hansen and Wilson, 2006). Crested wheatgrass was originally seeded in sagebrush (*Artemisia* L.) communities to increase livestock forage and reduce halogeton (*Halogeton glomeratus* [M. Bieb.] C.A. Mey), a plant that is toxic to sheep (Miller, 1943; Miller, 1956; Frischknecht and Harris, 1968; Vale, 1974). Crested wheatgrass is still seeded into sagebrush rangelands following wildfires because of its ability to suppress exotic annual grasses (Arredondo et al., 1998; Davies et al., 2010b). In addition, it often costs less and establishes better than native species (Pellant and Lysne, 2005; Boyd and Davies, 2010; James et al., 2012; Davies et al., 2015); reduces erosion; and increases livestock forage (Dormaar and Smoliak, 1985; Smoliak and Dormaar, 1985; Dormaar et al., 1995).

Although crested wheatgrass may compete effectively with undesirable weed species, its competitiveness can cause formation of near monocultures and significantly decrease cover and richness of native species and reduce wildlife habitat value (Looman and Heinrichs, 1973; Christian and Wilson, 1999; Heidinga and Wilson, 2002). Some crested wheatgrass seedings remain near-monocultures for decades (Hull and Klomp, 1966; Looman and Heinrichs, 1973; Marlette and Anderson, 1986), while others have a higher native vegetation component, particularly shrubs (Reynolds and Trost, 1981; McAdoo et al., 1989; Nafus, 2015). Greater amounts of native vegetation in crested wheatgrass stands are often desired because they correspond to increasing diversity and more suitable habitat for native wildlife (Vale, 1974; Reynolds and Trost, 1981; Parmenter and MacMahon, 1983; McAdoo et al., 1989). Although some of the variation in native vegetation cover and diversity in crested wheatgrass seedings can be explained by site and environmental factors (Raven, 2004; Williams, 2009; Nafus, 2015), it remains unclear why some crested wheatgrass seedings are almost monocultures and others have more native vegetation.

Vegetation characteristics in crested wheatgrass stands may be influenced by precipitation along with preseeded disturbances, including mechanical, burning and herbicide treatments, and postseeded disturbances, including fire and livestock grazing management (Hull and Klomp, 1967; Shown et al., 1969; Cox and Anderson, 2004). Fire,

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herbicide and mechanical treatments were often applied before seeding crested wheatgrass to prepare the soil for seeding and reduce residual vegetation (Vale, 1974). Preseeding disturbance, in combination with seeding year precipitation, may influence the initial recovery of native vegetation species, particularly sagebrush, and establishment of seeded crested wheatgrass (Hull and Klomp, 1967; Cluff et al., 1983; Cox and Anderson, 2004), which, in turn, may affect long-term plant community dynamics. On Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young) sites where crested wheatgrass was not seeded, sagebrush control method influenced long-term recovery of sagebrush (Wambolt and Payne, 1986; Watts and Wambolt, 1996). On sites seeded with crested wheatgrass, however, there is a lack of information about long-term differences in native vegetation cover and abundance associated with preseeding disturbances and seeding year precipitation.

Livestock management after seeding crested wheatgrass may influence plant community dynamics. Although crested wheatgrass is tolerant of grazing and can withstand heavy grazing for many years (Cook et al., 1958; Hull and Klomp, 1966, 1974; Caldwell et al., 1981; Laycock and Conrad, 1981), heavy grazing may favor more grazing-tolerant native bunchgrasses such as Sandberg bluegrass (*Poa secunda* J. Presl) (Hyder and Sawyer, 1951). Heavy spring grazing may be associated with increased shrub cover and reduced crested wheatgrass dominance (Laycock, 1967), whereas moderate grazing in native Wyoming big sagebrush plant communities does not generally appear to alter shrub cover (Rice and Westoby, 1978; Courtois et al., 2004; Yeo, 2005; Davies et al., 2010a; Strand et al., 2014). Information on grazing management, especially grazed compared with ungrazed, influence on native vegetation abundance and cover in crested wheatgrass stands is limited.

Fire is another factor that may influence vegetation composition of crested wheatgrass stands. Wyoming big sagebrush and some native bunchgrass species are not as fire tolerant as crested wheatgrass. Sagebrush is readily killed by fire and is estimated to take decades to centuries to recover (Wambolt and Payne, 1986; Skinner and Wakimoto, 1989; Baker, 2006). Crested wheatgrass burns quickly with little heat transfer into the soil and is therefore more resilient to fire than many native bunchgrass species (DePuit, 1986; Skinner and Wakimoto, 1989). Following fire, crested wheatgrass can take advantage of reduced competition and increase by threefold to sixfold in the next couple of years (Ralphs and Busby, 1979).

Crested wheatgrass has been extensively seeded across millions of acres of historic sage grouse and other sagebrush-associated wildlife habitat and it is, therefore, important to investigate factors that may influence native vegetation in crested wheatgrass stands (Knick et al., 2003; Schroeder et al., 2004; Pellant and Lysne, 2005; Davies et al., 2011). The purpose of this study is to investigate the correlations between plant community characteristics of crested wheatgrass stands and seeding year precipitation, disturbance history, and management. We predicted that increased grazing pressure would be positively associated with higher shrub cover and abundance, and that native vegetation cover and density would be greater on grazed compared with ungrazed crested wheatgrass stands. We also expected native vegetation cover and density would vary by preseeding disturbance and precipitation in the year following seeding and that sites that were seeded or burned more recently would have lower native vegetation cover and density.

Methods

Site Selection

Personnel from the US Department of Interior Bureau of Land Management (BLM) of the Burns, Lakeview, and Vale Districts, Fish and Wildlife Service (USFWS), and the Oregon Department of State

Lands (ODSL) were consulted to obtain locations of all crested wheatgrass seedlings in their jurisdiction. One-hundred and twenty-one sites were located across southeastern Oregon and then measured in June to August of 2012 and 2013. All sites sampled had been identified as having been seeded with crested wheatgrass and contained at least 0.25 crested wheatgrass plants per m² to ensure that they had been successfully seeded.

Study Area

Study sites were selected across a 54 230 km² area in southeastern Oregon. Study locations were generally in Wyoming big sagebrush-bunchgrass ecological sites, though a few locations were more alkaline and had been characterized by shrubs such as spiny hopsage (*Grayia spinosa* [Hook.] Moq.) and greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.). All study locations were seeded with crested wheatgrass 10 to 50 years before sampling largely using drill seeding methods. Long-term annual precipitation for study locations averaged between 200 and 360 mm (PRISM Climatic Group, 2014). Annual precipitation amounts (from 1 October to 30 September) averaged for study locations were 74% and 75% of the long-term average (30 years) in 2011–2012 and 2012–2013, respectively (PRISM Climatic Group, 2014). Precipitation in the study area generally arrives during the cool season, and summers are typically hot and dry. Topography and soils were variable across the study area. Elevation of sites ranged from 819 m to 1739 m above sea level.

Vegetation Characteristics

A randomly located 50 × 60 m plot was used to sample each site. Four parallel 50-m transects were spaced at 20-m intervals perpendicular to the 60-m side of the plot. Herbaceous vegetation basal cover and density were estimated by species inside 40 × 50 cm quadrats located at 3-m intervals on each 50-m transect (starting at 3 m and ending at 45 m, resulting in 15 quadrats per transect and 60 quadrats per plot). We used basal cover as opposed to foliar cover as some sites were grazed before sampling. Basal cover was estimated to the nearest 1% base on markings that segmented the quadrats into 1%, 5%, 10%, 25%, and 50%. Bunchgrasses were considered separate individuals if crowns were separated by > 5 cm. Sandberg bluegrasses (*Poa secunda* J. Presl) were considered separate individuals if there was > 1 cm between crowns. Dead portions within the perimeter of the live portion of the crown were included in the basal cover estimate when they were < 5 cm in diameter. Shrub canopy cover by species was measured using the line intercept method (Canfield, 1941). Shrub canopy gaps < 15 cm were included in cover estimates. Shrub density was determined by counting all individuals rooted in four, 2 × 50 m belt transects centered over each of the four 50-m transects. Species were summarized by functional group: Sandberg bluegrass, crested wheatgrass, large native perennial bunchgrasses, perennial forbs, annual grasses, annual forbs, and shrubs. Some functional groups only contained one species because of unique characteristics. Sandberg bluegrass was analyzed separately because it responds differently to management and disturbance (McLean and Tisdale, 1972; Winward, 1980; Yensen et al., 1992), and it is smaller in stature and develops earlier than other native bunchgrasses in these communities (James et al., 2008). Crested wheatgrass was analyzed separately because it was the only non-native bunchgrass. Species richness was determined by counting all species found in the sixty 40 × 50 cm quadrats. Vegetation diversity was calculated from density measurements using the Shannon-Weiner diversity index (Krebs, 1998). Wyoming big sagebrush was included in the shrub functional group but was also evaluated independently because of its importance to the habitat requirements of many sagebrush-associated wildlife species (Davies et al., 2011).

Explanatory Factors

We used BLM seeding, fire, and management records in conjunction with geographic information system maps available online (USDI-BLM, 2014) in Arc Map 10.0 (ESRI, 2011) to determine grazing, seeding, and fire history for the sites whenever the information was available. Ninety-one sites had seeding year and fire history information. Sixty-three of these sites had information about preseeded disturbance. Four types of preseeded disturbance occurred: fire (31 sites), plowing (8 sites), herbicide (9 sites), and soil scarification (15 sites). Soil scarification involved using chains or harrows to increase bare mineral soil and improve seed-soil contact. Type of herbicide used was not always included in the seeding record but was typically aerially applied 2,4-D, especially on seedings that had been a part of the Vale project (Heady and Bartolome, 1977). Seeding method was not always included in seeding records and, of the sites with records on seeding method, 95% were drill seeded. Therefore, seeding method was not included as an explanatory variable.

Explanatory variables recorded were season of use, stocking rate, distance from water (as a proxy for grazing intensity), number of years since most recent seeding, and number of years since most recent fire. To determine distance from water, we used a combination of field collected records and measurements made from digital BLM records. For each site we also used PRISM (PRISM Climate Group, 2014) to estimate precipitation from September in the year the sites were seeded through August of the following year.

Statistics

Step-wise multiple linear regression (JMP, 1989–2007) was used to select models correlating cover and density of functional groups and species diversity and richness with explanatory variables. Two sets of models were created. The first set of models was developed using all of the sites for which seeding year was available (91 sites) without consideration for grazing. In these models, density of functional groups and species diversity and richness were potentially correlated with seeding age (number of years from recorded seeding date to sampling), time since fire (number of years from recorded time since fire to sampling), precipitation (precipitation from September of the year seeded through August of the subsequent year measured in mm), and their interactions: seeding age \times precipitation; seeding age \times years since fire; and precipitation \times years since fire.

The second set of models was developed using the 49 sites that were 1) spring grazed (15 March to 15 May; 29 sites) or 2) spring–summer grazed (15 March to 15 August; 20 sites). For these models the potential explanatory variables were season (spring = 1 or spring–summer = 0), stocking rate (AUMs·ha⁻¹), distance from water (number of meters from nearest livestock available water), and the interactions: season \times stocking rate; season \times distance to water; and stocking rate \times distance to water. There were not enough replicates available to evaluate any other seasons of use. Many crested wheatgrass seedings had variable seasons of use and even multiple seasons of use in some years since their inception. Stocking rate was AUMs·ha⁻¹ averaged from 2001 to 2011 including rest years. This time period was selected over other time periods because grazing records were more complete, management was more consistent, and all sites were crested wheatgrass stands for the entire time period. An average, including rest years, was used in an attempt to capture the long-term grazing pressure on pastures. An initial investigation excluding rest years was not as well correlated with functional groups.

Sandberg bluegrass, crested wheatgrass, large native perennial bunchgrasses (LNPGs), annual grasses, perennial forbs, annual forbs, shrubs, Wyoming big sagebrush, Shannon-Weiner diversity (H'), and species richness were used as response variables to perform stepwise multiple linear regression model selection. The explanatory variables were added and deleted in stepwise fashion using P values to select a

parsimonious model that explained the most variation in response variables resulting in the highest adjusted R^2 value. Factors that did not contribute significantly ($P \leq 0.05$) were excluded from the final model. Data were square root transformed before model selection when necessary to better meet linear regression data distribution assumptions.

To determine whether plant community characteristics differed between grazed and ungrazed crested wheatgrass stands, ungrazed sites ($n = 6$) were blocked with grazed sites ($n = 6$) that had similar location, soil, and time since crested wheatgrass seeding. The same functional and species groups used in model selection were compared between grazed and ungrazed sites using Wilcoxon comparisons (JMP, 1989–2007).

Functional group and species abundance were compared for the four preseeded disturbance methods used on the sites. Because of different sample sizes for groups, Kruskal-Wallis rank sums were used for comparisons. When there was a difference between groups, Wilcoxon comparisons were used to determine which groups differed (JMP, 1989–2007).

Results

Correlations with Age of Seeding, Time Since Fire, and Seeding-Year Precipitation

Shrub canopy cover and density were negatively correlated with precipitation the year after seeding and were positively correlated with seeding age, time since fire, and the interaction between seeding age and time since fire (adj. $R^2 = 0.28, 0.28$, respectively, $P < 0.001$; Tables 1 and 2). Wyoming big sagebrush canopy cover was negatively correlated with precipitation the year after seeding and the interaction between precipitation and time since fire and positively correlated with seeding age, time since fire, and the interaction between seeding age and time since fire (adj. $R^2 = 0.34, P < 0.001$; see Table 1). Wyoming big sagebrush density was positively correlated with time since fire and was negatively correlated with precipitation the year after seeding and the interaction between precipitation and time since fire (adj. $R^2 = 0.34, P < 0.001$; see Table 2). Perennial forb cover was positively correlated with time since fire (adj. $R^2 = 0.11, P < 0.001$; see Table 1). Sandberg bluegrass density was positively correlated with seeding age and negatively correlated with time since fire and the interaction of seeding age and time since fire (adj. $R^2 = 0.19, P = 0.001$; see Table 2).

Age of seeding, time since fire, and precipitation following seeding were not correlated with Shannon-Weiner diversity, species richness, or basal cover of Sandberg bluegrass, perennial forb density, and basal cover or density of large native perennial bunchgrasses, crested wheatgrass, and annual forbs (adj. $R^2 < 0.10, P \geq 0.05$).

Grazing Intensity on Spring- and Spring–Summer–Grazed Sites

Sandberg bluegrass basal cover and density were negatively correlated with higher stocking rates and positively correlated with longer distance from water and the interaction between stocking rate and distance to water (adj. $R^2 = 0.30$ and $0.27, P = 0.003, 0.007$, respectively; Tables 3 and 4). Large native perennial bunchgrass basal cover and density were negatively associated with increased stocking rates (adj. $R^2 = 0.37, 0.37$, respectively, $P < 0.0001$; see Tables 3 and 4).

Crested wheatgrass basal cover was positively correlated with higher stocking rate and negatively correlated with increasing distance from water, as well as the interaction between season of use and distance from water (adj. $R^2 = 0.26, P < 0.003$; see Table 3). Crested wheatgrass density was positively correlated with increasing stocking rate, increasing distance to water, and the interaction between stocking rate and distance to water (adj. $R^2 = 0.21, P = 0.004$; see Table 4). Measured livestock grazing management factors were moderately correlated with exotic annual grass and perennial forb basal cover and density and annual forb density (adj. $R^2 > 0.10 < 0.20, P < 0.05$; see

Table 1

Stepwise multiple linear regression models correlating vegetation cover with historic site characteristics. Herbaceous and shrub vegetation were measured as basal and canopy cover, respectively.

Regression model with standard errors in parentheses below coefficients	P value	Adj. R ²
POSE = no significant correlations	—	—
AGCR = no significant correlations	—	—
Sqrt LNPG = no significant correlations	—	—
Sqrt AG = no significant correlations	—	—
Sqrt PF = 0.071 + 3.4e ⁻³ (YF) (0.083) (9.9e ⁻⁴)	<0.001	0.11
Sqrt AF = no significant correlations	—	—
Sqrt Shrubs = 3.16 + 6.4e ⁻³ (Age) + 7.3e ⁻³ (YF) - 8.04e ⁻³ (PPT) + 1.1e ⁻³ (Age · YF) (0.8) (0.013) (3.7e ⁻³) (1.9e ⁻³) (3.8e ⁻⁴)	<0.001	0.28
Sqrt Sage = 3.16 + 0.01 (Age) + 0.01 (YF) - 7.5e ⁻³ (PPT) + 8.0e ⁻⁴ (Age · YF) - 1.7e ⁻³ (YF · PPT) (0.8) (0.012) (3.9e ⁻³) (1.8e ⁻³) (3.6e ⁻⁴) (5.1e ⁻⁵)	<0.001	0.34

AF indicates annual forb; AG, annual grass; AGCR, crested wheatgrass; Age, years since seeding crested wheatgrass; LNPG, large native perennial bunchgrass; PF, perennial forb; POSE indicates Sandberg bluegrass; PPT, precipitation (mm) from 1 September the year of seeding to 31 August of the following year; Sage, Wyoming big sagebrush; Shrub, total shrubs; YF, years since fire. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. Correlations were not considered significant if adjusted R² < 0.10 or P > 0.05.

Tables 3 and 4) and were not correlated with annual forb cover (adj R² < 0.10, P > 0.05).

Total shrub canopy cover was negatively correlated with higher stocking rate, greater distance to water, and the interaction between the stocking rate and distance to water (adj. R² = 0.22, P = 0.003; see Table 3). Wyoming big sagebrush canopy cover was negatively correlated with the interaction between stocking rates and season of use (adj. R² = 0.24, P < 0.001; see Table 3). Variability in total shrub density and Wyoming big sagebrush density was moderately well explained by measured livestock grazing management factors (adj. R² < 0.18 and 0.19, P = 0.01 and < 0.001, respectively; see Table 4).

Preseeding Site Disturbance

Preseeding disturbance affected Sandberg bluegrass density (Fig. 1; X² = 28.9; P < 0.001) and basal cover (Fig. 2; X² = 26.43; P < 0.001). Sandberg bluegrass density was greater on sites that were scarified or herbicide treated than on sites that were burned or plowed (P < 0.001) but did not differ between scarified and herbicide treated sites. Sandberg bluegrass basal cover was greater on scarified and herbicide-treated sites than on plowed or burned sites (P ≤ 0.001). Large native perennial bunchgrass, crested wheatgrass, and exotic annual grass density (X² = 5.62, 2.68, 1.93, respectively; P > 0.05) and basal cover (X² = 4.42, 5.67, 2.37, respectively; P > 0.05) did not differ among preseeding disturbances. Perennial forb density was greater on sites that were scarified or herbicide treated than on sites that were burned before seeding (see Fig. 1; X² = 10.90; P ≤ 0.01). Perennial forb density did not differ among other preseeding disturbances (P > 0.05). Perennial forb basal cover did not differ significantly among preseeding disturbances

(see Fig. 2; X² = 2.49; P > 0.05). Annual forb density and basal cover were greater on plowed and herbicide-treated sites than on burned sites (see Figs. 1 and 2; X² = 10.90, 8.47; P < 0.05) but did not differ among other preseeding disturbances (P > 0.05).

Shrub density was greater on scarified and burned sites than on herbicide-treated sites (see Fig. 1; X² = 8.21; P < 0.05). Shrub canopy cover was greater on burned than herbicide-treated sites (X² = 7.83; P < 0.05). On sites where Wyoming big sagebrush was present, scarified sites had greater Wyoming big sagebrush density than burned or herbicide-treated sites (see Fig. 1; X² = 11.3; P ≤ 0.01). Density of Wyoming big sagebrush on plowed sites was not different from any of the other treatments. On sites where Wyoming big sagebrush was present, its canopy cover did not differ between treatments (X² = 11.29; P > 0.05). Rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt., *Ericameria nauseosa* [Pall. ex Pursh] G. L. Nesom and Baird) density and canopy cover were greater on burned sites than on scarified, herbicide-treated and plowed sites (see Figs. 1 and 2; X² = 14.46, 17.74, respectively; P ≤ 0.03). Total species diversity and richness did not differ between preseeding treatments (X² = 6.63; P > 0.05).

Grazed versus Ungrazed

Density of Sandberg bluegrass, native bunchgrasses, and perennial forbs were 6-, 25-, and 22-times greater on grazed compared with ungrazed crested wheatgrass stands (Fig. 3; X² = 6.89, 6.39, 4.67, P = 0.01, 0.01, and 0.03, respectively). Total shrub and Wyoming big sagebrush density were 16-times greater on grazed than ungrazed sites (see Fig. 3; X² = 5.31, 5.64, P = 0.02, 0.02, respectively). Crested

Table 2

Stepwise multiple linear regression models correlating vegetation density (plants · m⁻²) with historic site characteristics.

Regression model with standard errors in parentheses below coefficients	P value	Adj. R ²
POSE = -4.71 + 1.21 (Age) - 0.18 (YF) - 0.025 (Age · YF) (11.99) (0.29) (0.077) (8.3e ⁻³)	0.001	0.19
AGCR = no significant correlations	—	—
Sqrt LNPG = no significant correlations	—	—
Sqrt AG = 9.89 - 0.014 (YF) - 7.4e ⁻³ (PPT) + 1.1e ⁻³ (YF · PPT) (3.91) (0.02) (0.01) (2.9 e ⁻⁴)	0.002	0.13
Sqrt PF = no significant correlations	—	—
Sqrt AF = no significant correlations	—	—
Sqrt Shrubs = 0.85 + 2.4e ⁻³ (Age) + 2.5e ⁻³ (YF) - 2.2e ⁻³ (PPT) + 2.6e ⁻⁴ (Age · YF) (0.23) (3.8 e ⁻³) (1.1e ⁻³) (5.4e ⁻⁴) (1.1e ⁻⁴)	<0.001	0.28
Sqrt Sage = 0.63 + 3.3e ⁻³ (YF) - 2.0e ⁻³ (PPT) - 3.6e ⁻⁵ (YF · PPT) (0.18) (9.8e ⁻⁴) (4.8e ⁻⁴) (1.4e ⁻⁵)	<0.001	0.34

AF indicates annual forb; AG, annual grass; AGCR, crested wheatgrass; Age, years since seeding crested wheatgrass; LNPG, large native perennial bunchgrass; PF, perennial forb; POSE, Sandberg bluegrass; PPT, precipitation (mm) from Sept. 1 the year of seeding to August 31 of the following year; Sage, Wyoming big sagebrush; Shrub, total shrubs; YF, years since fire. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. Correlations were not considered significant if adjusted R² < 0.10 or P > 0.05.

Table 3
Stepwise multiple linear regression models correlating cover with stocking rates, distance to water, and grazing season. Herbaceous and shrub vegetation were measured as basal and canopy cover, respectively.

Regression model with standard errors in parentheses below coefficients	P value	Adj. R ²
POSE = 0.73 – 49.33 (AUM) + 6.10e ⁻⁴ (H ₂ O) – 2.08 (S) + 0.094 (AUM · H ₂ O) (1.38) (28.10) (4.3e ⁻⁴) (0.98) (0.039)	0.003	0.30
AGCR = 0.38 + 169.49 (AUM) – 7.6e ⁻⁴ (H ₂ O) + 2.67 (S) + 186.92 (AUM · S) – 3.8e ⁻³ (H ₂ O · S) (1.76) (42.01) (3.6e ⁻⁴) (1.26) (76.99) (1.2e ⁻³)	0.003	0.26
Sqrt LNPG = 0.77 – 20.23 (AUM) – 0.081 (S) – 28.82 (AUM · S) (0.17) (4.18) (0.13) (7.69)	<0.001	0.37
Sqrt AG = 0.10 + 1.1e ⁻⁴ (H ₂ O) + 0.21 (S) – 2.9e ⁻⁴ (H ₂ O · S) (0.10) (6.4e ⁻⁵) (0.10) (1.1e ⁻⁴)	0.030	0.12
Sqrt PF = 0.96 – 12.76 (AUM) – 0.34 (S) (0.17) (3.55) (0.12)	0.003	0.19
Sqrt AF = no significant correlations	–	–
Sqrt Shrubs = 3.38 – 37.76 (AUM) – 1.1e ⁻⁴ (H ₂ O) – 0.045 (AUM · H ₂ O) (0.38) (10.58) (1.9e ⁻⁴) (0.018)	0.003	0.22
Sqrt Sage = 3.38 – 60.47 (AUM) – 0.69 (S) – 69.11 (AUM · S) (0.59) (14.63) (0.45) (26.91)	<0.001	0.24

AF indicates annual forb; AG, annual grass; AGCR, crested wheatgrass; AUM, average AUMS per ha from 2001–2011; H₂O, distance (m) to water; LNPG, large native perennial bunchgrass; PF, perennial forb; POSE, Sandberg bluegrass; S, grazing season (0 = spring-summer; 1 = spring); Sage, Wyoming big sagebrush; Shrub, total shrubs. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. Correlations were not considered significant if adjusted R² < 0.10 or P > 0.05.

wheatgrass, annual grass, and annual forb density did not differ between grazed and ungrazed sites ($X^2 = 0.33, 0.41, 0.49$, respectively, $P > 0.10$).

Basal cover of Sandberg bluegrass and large native bunchgrasses were 4- and 32-fold greater on grazed compared with ungrazed crested wheatgrass stands (Fig. 4; $X^2 = 5.04, P = 0.02$; $X^2 = 6.37, P = 0.01$, respectively). Basal cover of crested wheatgrass was less on grazed compared with ungrazed stands (see Fig. 4; $X^2 = 5.59, P = 0.02$). Basal cover of perennial forbs, annual grasses, and annual forbs did not differ between grazed and ungrazed stands (see Fig. 4; $X^2 = 3.47, 0.10, 0.41$, respectively; $P > 0.05$). Canopy cover of shrubs and Wyoming big sagebrush were 19- and 14-times greater on grazed than ungrazed sites (see Fig. 4; $X^2 = 5.64, 5.04, P = 0.02, 0.02$, respectively).

Discussion

Crested wheatgrass is a strong competitor that can limit exotic annuals (Arredondo et al., 1998; Davies et al., 2010b); however, it also can exclude native vegetation resulting in near-monoculture plant communities (Hull and Klomp, 1966; Looman and Heinrichs, 1973; Marlette and Anderson, 1986). Crested wheatgrass stands can also have more diverse species assemblages (Reynolds and Trost, 1981;

McAadoo et al., 1989; Nafus, 2015). We found that conditions before and immediately after seeding and subsequent postseeding management appear to influence whether crested wheatgrass stands were near-monocultures or more diverse assemblages and which vegetation groups were favored. Precipitation the year following seeding and disturbance before seeding appear to have affected plant community composition in crested wheatgrass stands for decades, suggesting a legacy effect. Grazing management, especially grazed compared with ungrazed, may also greatly influence vegetation characteristics of crested wheatgrass stands.

In general, shrubs and Wyoming big sagebrush cover and density were negatively associated with precipitation in the year following crested wheatgrass seeding. This may be a long-term result of greater initial crested wheatgrass seedling success and lower sagebrush recovery in seeding years with higher than average precipitation (Johnson and Payne, 1968; Shown et al., 1969). Higher precipitation the year following seeding favored increased crested wheatgrass establishment, which likely increases competition experienced by sagebrush seedlings (Shown et al., 1969; Gunnell et al., 2010). Similarly, Rinella et al. (2015) reported that high precipitation in the growing season following seeding appeared to reduce the success of seeded shrubs by increasing grass growth and competition.

Table 4
Stepwise multiple linear regression models correlating vegetation density (plants · m⁻²) with stocking rates, distance to water, and grazing season.

Regression model with standard errors in parentheses below coefficients	P value	Adj. R ²
POSE = 42.05 – 449.61 (AUM) + 4.1e ⁻³ (H ₂ O) – 17.63 (S) + 0.66 (AUM · H ₂ O) (11.25) (228.71) (3.5e ⁻³) (7.95) (0.32)	0.007	0.27
AGCR = 4.22 + 110.13 (AUM) + 4.2e ⁻⁴ (H ₂ O) (1.25) (35.09) (6.4e ⁻⁴)	0.004	0.21
Sqrt LNPG = 1.63 – 38.98 (AUM) – 0.32 (S) – 46.74 (AUM · S) (0.31) (7.53) (0.23) (13.84)	0.001	0.37
Sqrt AG = 1.21 + 2.4e ⁻³ (H ₂ O) + 2.93 (S) + 6.0e ⁻³ (H ₂ O · S) (1.60) (9.8e ⁻⁴) (1.60) (1.8e ⁻³)	0.005	0.19
Sqrt PF = 2.43 – 38.34 (AUM) – 1.66 (S) (0.70) (14.81) (0.54)	0.009	0.15
Sqrt AF = 8.88 – 3.96 (S) (1.18) (1.53)	0.010	0.19
Sqrt Shrubs = 1.20 – 12.45 (AUM) – 4.2e ⁻⁵ (H ₂ O) + 2.2e ⁻⁵ (H ₂ O · S) (0.19) (3.71) (6.4e ⁻⁵) (1.2e ⁻⁴)	0.010	0.19
Sqrt Sage = 0.95 – 14.89 (AUM) – 0.25 (S) – 12.79 (AUM · S) (0.17) (4.08) (0.13) (7.50)	0.008	0.18

AF indicates annual forb; AG, annual grass; AGCR, crested wheatgrass; AUM, average AUMS per ha from 2001 to 2011; H₂O = distance (m) to water; LNPG, large native perennial bunchgrass; PF, perennial forb; POSE, Sandberg bluegrass; S, grazing season (0 = spring-summer; 1 = spring); Sage, Wyoming big sagebrush; Shrub, total shrubs. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. Correlations were not considered significant if adjusted R² < 0.10 or P > 0.05.

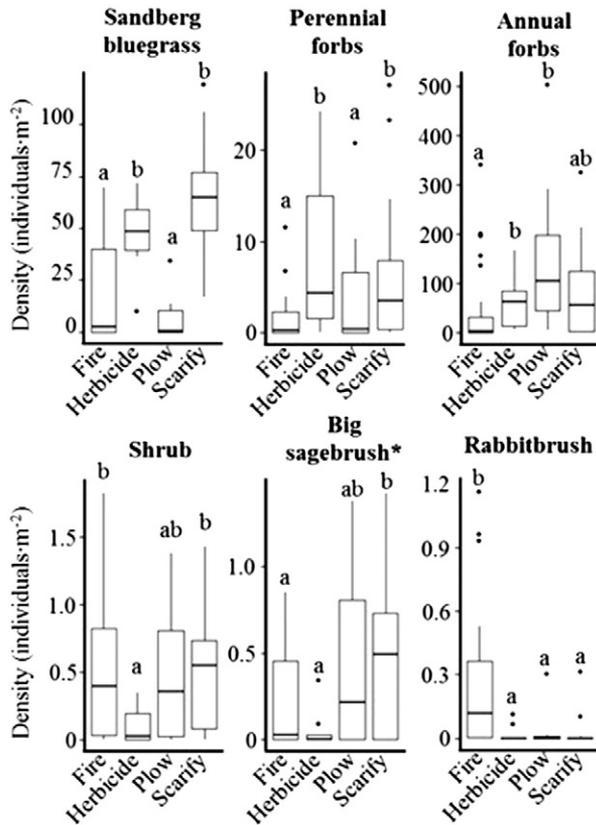


Fig. 1. Density (individuals·m⁻²) of Sandberg bluegrass, perennial forbs, annual forbs, shrubs, Wyoming big sagebrush, and rabbitbrush on sites that were burned ($n = 31$), herbicide treated ($n = 9$), plowed ($n = 8$), or scarified ($n = 15$) before seeding crested wheatgrass. Preseeding disturbance significantly ($P < 0.05$ using Kruskal-Wallis rank sum comparisons) influenced shown plant groups. Different letters indicate significant differences at $P < 0.05$. The upper and lower ends of the box correspond to the first and third quartiles (the 25th and 75th percentiles). Whiskers extend from the 25th and 75th percentiles to the lowest or highest value that is within 1.5 · the interquartile range. Data beyond the end of the whiskers are outliers and plotted as points (as specified by Tukey).

The positive relationship between Wyoming big sagebrush cover and density and time since fire was in agreement with our expectations. Similarly, other authors have reported that Wyoming big sagebrush is typically slow to recover after fire (Cluff et al., 1983; Wambolt and Payne, 1986; Wambolt et al., 2001; Beck et al., 2009). Thus, the greater the time since last fire, the more sagebrush has recovered. Although crested wheatgrass responds positively to fire (Ralphs and Busby, 1979), we did not find any evidence suggesting that time since fire was related to crested wheatgrass cover or abundance.

The majority of the crested wheatgrass seedlings for which we were able to obtain actual use records were grazed in the spring or from the spring through summer. On these sites, crested wheatgrass density was positively associated with higher stocking rate. In contrast, cover and density of Sandberg bluegrass and large native perennial bunchgrass were negatively associated with higher stocking rates. Large native perennial bunchgrasses are typically negatively impacted by repeated, intense grazing early in the spring in sagebrush communities of the Intermountain West (Strand et al., 2014). Although Sandberg bluegrass often increases as other native bunchgrasses decrease with heavy grazing in sagebrush communities (Hyder and Sawyer, 1951; Krzic et al., 2000), we did not find evidence that it increased with increased stocking rates. Our results could be interpreted to indicate that crested wheatgrass was responding favorably and native bunchgrasses were responding negatively to higher stocking densities as crested wheatgrass is known to be very tolerant to grazing and can withstand heavy grazing for multiple years (Cook et al., 1958; Hull and Klomp, 1966, 1974; Caldwell et al., 1981; Laycock and Conrad,

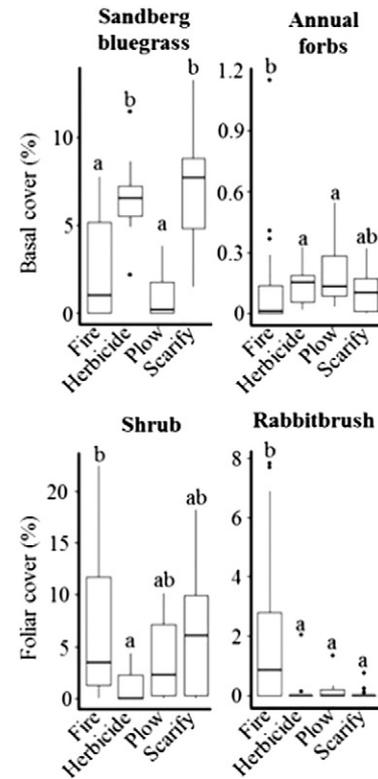


Fig. 2. Basal cover (%) of Sandberg bluegrass and annual forbs, and canopy cover (%) of shrubs and rabbitbrush on sites that were burned ($n = 31$), herbicide treated ($n = 9$), plowed ($n = 8$), or scarified ($n = 15$) before seeding crested wheatgrass. Preseeding disturbance significantly ($P < 0.05$ using Kruskal-Wallis rank sum comparisons) influenced shown plant groups. Different letters indicate significant differences at $P < 0.05$. The upper and lower ends of the box correspond to the first and third quartiles (the 25th and 75th percentiles). Whiskers extend from the 25th and 75th percentiles to the lowest or highest value that is within 1.5 · the interquartile range. Data beyond the end of the whiskers are outliers and plotted as points (as specified by Tukey).

1981). However, this doesn't explain why Sandberg bluegrass, a grazing tolerant bunchgrass, was negatively correlated with increasing stocking rates. It is more probable that the association between stocking rates and crested wheatgrass was a result of greater stocking rates being assigned to seedings with more crested wheatgrass (i.e., greater forage production and less native vegetation) (Dormaer and Smoliak, 1985; Smoliak and Dormaer, 1985). Stocking rates are generally higher on seedings that have more crested wheatgrass and less shrubs because of greater forage availability (Booth, 2015; Miller, 2015).

Sagebrush and total shrub results further support our speculation that higher stocking rates were assigned to stands with more crested wheatgrass, not that higher stocking rates were causing an increase in crested wheatgrass. Sagebrush and other shrubs would be expected to increase as grazing pressure increases because grazing would place herbaceous vegetation at a competitive disadvantage with ungrazed shrubs (Van Auken, 2000), but we found that total shrub and Wyoming big sagebrush cover was lower on sites with higher stocking rates. This suggests that in our situation, stocking rate is not a good substitute for grazing pressure. Lower shrub and Wyoming big sagebrush cover and greater crested wheatgrass in pastures with greater stocking rates support our speculation that higher stocking rates were assigned to pastures with greater crested wheatgrass productivity. Furthermore, total shrub cover was greater on sites that were closer to water where livestock pressure was concentrated, which is what would be expected as increasing grazing pressure favors shrubs (Van Auken, 2000). As sagebrush cover increases, crested wheatgrass productivity decreases (Hull and Klomp, 1974; Rittenhouse and Sneva, 1976), which would reduce the amount of forage for livestock resulting in decreased

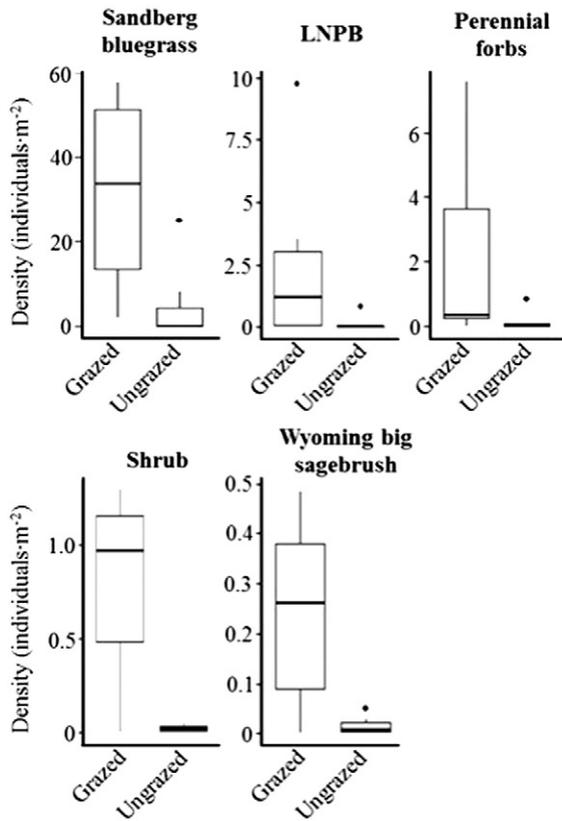


Fig. 3. Density (individuals·m⁻²) of Sandberg bluegrass, large native perennial bunchgrasses (LNPB), perennial forbs, shrubs, and Wyoming big sagebrush on crested wheatgrass seedlings that were grazed ($n = 6$) or ungrazed ($n = 6$). Grazed and ungrazed sites had similar soil texture, location, seeding age, and time since fire. Plant groups that are shown differed between grazing and ungrazed areas ($P < 0.05$ using Wilcoxon rank sums). The upper and lower ends of the box correspond to the first and third quartiles (the 25th and 75th percentiles). Whiskers extend from the 25th and 75th percentiles to the lowest or highest value that is within 1.5 · the interquartile range. Data beyond the end of the whiskers are outliers and plotted as points (as specified by Tukey).

stocking rates. The increased shrub cover with greater livestock pressure (i.e., closer to water) and higher sagebrush cover on spring-through summer-grazed sites are in agreement with prior studies that found increased sagebrush cover under season-long or summer grazing (Robertson et al., 1970; Angell, 1997) with little increase in shrub cover on spring-grazed sites (Robertson et al., 1970).

Grazed crested wheatgrass seedlings had higher shrub cover and density than ungrazed seedlings and less crested wheatgrass basal cover. This is consistent with Marlette and Anderson (1986), who found crested wheatgrass maintained a near monoculture for over 50 years in an ungrazed seeding. Our results also, in general, support speculation by Busso and Richards (1995) that intense grazing can create openings in the plant community that allow niche differentiated species such as Wyoming big sagebrush to establish. Crested wheatgrass can inhibit Wyoming big sagebrush and rabbitbrush establishment and growth (Gunnell et al., 2010). Thus, reducing crested wheatgrass cover and density can improve sagebrush seedling establishment and growth (Davies et al., 2013). Once established, shrubs are able to coexist with crested wheatgrass and provide a potential seed source for continued shrub establishment (Frischknecht and Harris, 1968; Gunnell et al., 2010). Similar to native shrubs, Sandberg bluegrass and large native perennial bunchgrass cover and density were higher on grazed than ungrazed sites. This suggests, as with shrubs, that grazing may be beneficial by reducing the competitiveness of crested wheatgrass and creating openings where native vegetation can establish.

Our results suggest that preseedling disturbances had legacy effects on plant community characteristics. Perennial and annual forbs were

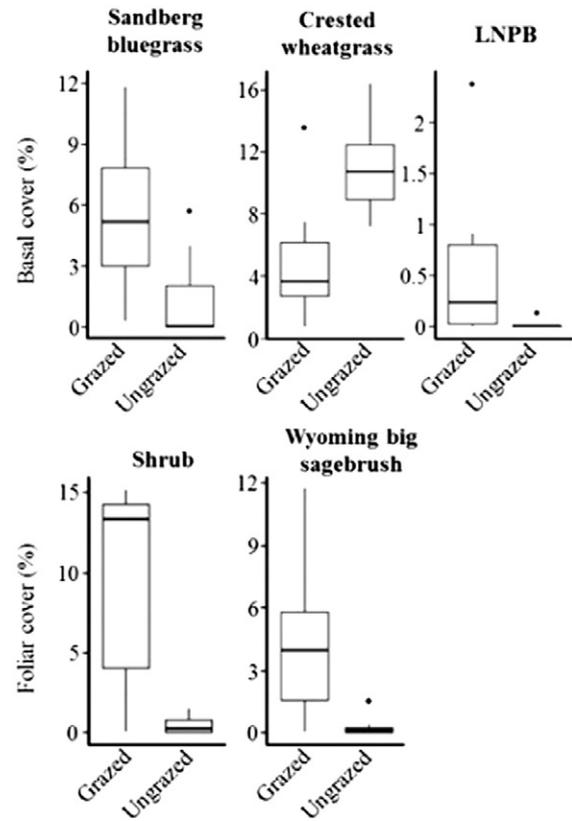


Fig. 4. Basal cover (%) of Sandberg bluegrass, crested wheatgrass, and large native perennial bunchgrasses (LNPB) and canopy cover (%) of shrubs and Wyoming big sagebrush on crested wheatgrass seedlings that were grazed ($n = 6$) or ungrazed ($n = 6$). Grazed and ungrazed sites had similar soil texture, location, seeding age and time since fire. Plant groups that are shown differed between grazing and ungrazed areas ($P < 0.05$ using Wilcoxon rank sums). The upper and lower ends of the box correspond to the first and third quartiles (the 25th and 75th percentiles). Whiskers extend from the 25th and 75th percentiles to the lowest or highest value that is within 1.5 · the interquartile range. Data beyond the end of the whiskers are outliers and plotted as points (as specified by Tukey).

lower on sites that were burned before seeding, suggesting a long-term negative impact of preseedling fire on forbs. Shrub density and cover were higher on burned sites than on herbicide-treated sites, largely due to high abundance of rabbitbrush on burned sites. On sites without sagebrush, rabbitbrush was the most abundant shrub species. Rabbitbrush often recovers quickly following fire because it resprouts (Wambolt et al., 2001) and frequent fire is often associated with increased rabbitbrush density (Bunting et al., 1987). Sites that were treated with herbicide had the lowest shrub abundance, which is expected because broadleaf herbicides used to control sagebrush often controlled other shrubs including rabbitbrush (Robertson and Cords, 1957; Tueller and Evans, 1969).

Prior research reports conflicting results when comparing effects of different treatments on sagebrush. Wambolt and Payne (1986) found that spraying had a more negative impact on sagebrush than burning, but Cluff et al. (1983) found that burning was the most effective method for removing Wyoming big sagebrush. We did not find any difference in Wyoming big sagebrush cover or density among burned, sprayed, or plowed sites. Wyoming big sagebrush density was greater on scarified sites than on burned or sprayed sites, suggesting that more plants either survived scarification or recruitment was greater following scarification than burning or herbicide treatment.

Our data was collected across sites with variable edaphic, topographic, and climatic characteristics. Even with large site variation, we found associations between vegetation characteristics and disturbance history, precipitation the year following seeding, and management. These effects may interact with site and environmental characteristics.

Unfortunately, sample size limitations prevented us from investigating the role of interactions among management, disturbance history, and seeding year precipitation, as well as their interaction with environmental site characteristics.

Management Implications

Our results suggest that prior disturbance history and seeding year precipitation produce legacy effects in crested wheatgrass stands. Our results also suggest that grazing influenced the cover and abundance of native vegetation and that without grazing, crested wheatgrass stands may have low diversity of native vegetation. On the basis of our findings, the best management option to promote increases in native vegetation in crested wheatgrass communities is to apply grazing treatments and limit fires in these stands. In contrast, if the management goal is to maintain high production of crested wheatgrass to provide forage for livestock, then periodic fires may maintain crested wheatgrass dominance. In addition, grazing management may need to be tailored (e.g., deferred-rotational grazing, lower utilization, periodic rest) to maintain crested wheatgrass's competitiveness. Further research evaluating the effects of different grazing management strategies on vegetation in crested wheatgrass stands may prove valuable in assisting efforts to meet management goals in these stands.

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