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Native Vegetation Composition in Crested Wheatgrass in Northwestern Great Basin☆,☆☆,☆☆☆

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ABSTRACT

Crested wheatgrass, an introduced perennial bunchgrass, has been seeded extensively on the rangelands of western North America. There is a perception that this species is very competitive and that it forms monoculture or low diversity stands where successfully seeded. However, there is limited information on species composition in sites previously seeded to crested wheatgrass. We measured native vegetation and environmental characteristics in areas seeded with crested wheatgrass across the northwestern Great Basin. Plant community composition within these crested wheatgrass stands was variable, from seedings that were near monocultures of crested wheatgrass to those that contained more diverse assemblages of native vegetation, especially shrubs. Environmental factors explained a range of functional group variability from 0% of annual grass density to 56% of large native bunchgrass density. Soil texture appeared to be an important environmental characteristic in explaining vegetation cover and density. Native vegetation was, for all functional groups, positively correlated with soils lower in sand content. Our results suggest environmental differences explain some of the variability of native vegetation in crested wheatgrass stands, and this information will be useful in assessing the potential for native vegetation to co-occupy sites seeded with crested wheatgrass. This research also suggests that crested wheatgrass seedings do not always remain in near monoculture vegetation states as seedings substantially varied in native vegetation composition and abundance with some seeded areas having a more diverse assemblage of native vegetation. In half the sites, there were five or more perennial herbaceous species and 63% of sites contained Wyoming big sagebrush. Although not exclusively true, species most commonly encountered in crested wheatgrass seedings are those that are able to minimize competition with crested wheatgrass via temporal (i.e., Sandberg bluegrass, annual forbs, annual grasses) or spatial (i.e., shrubs) differentiation in resource use.

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Introduction

Crested wheatgrass and desert wheatgrass (*Agropyron cristatum* [L.] Gaertn. and *Agropyron desertorum* [Fisch.] Schult.), hereafter referred to as crested wheatgrass, are closely related introduced bunchgrasses that have been extensively seeded across western North America in an effort to increase livestock forage, decrease wildfires, reduce erosion, and inhibit exotic plant invasions following disturbance (Young and Evans 1986; Heady 1988; D'Antonio and Vitousek 1992; Sheley and Carpinelli 2005). Crested wheatgrass is often selected for seeding because it is more cost-effective and establishes more readily than many native species (Boyd and Davies 2010; James et al. 2012; Davies et al. 2015).

Crested wheatgrass is a strong competitor and may form near monocultures, leading to concerns about native species displacement and low biological diversity (D'Antonio and Vitousek 1992; Christian and Wilson 1999; Krzic et al. 2000). Native species may not disperse well into stands of crested wheatgrass (Marlette and Anderson 1986) and crested wheatgrass is more likely than native bunchgrasses to fill open safe sites (Nafus et al. 2015; Hamerlynck and Davies 2018). Native seedlings that do emerge in crested wheatgrass stands face intense competition and most do not

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persist (Fansler and Mangold 2011). Crested wheatgrass can remain a monoculture stand for > 50 yr (Hull and Klomp 1966; Looman and Heinrichs 1973; Marlette and Anderson 1986) or, in some instances, revert to sagebrush (*Artemisia* L.) dominance (Reynolds and Trost 1981; McAdoo et al. 1989).

It is not clear why native vegetation occurs in some crested wheatgrass seedings but not in others. Many factors are likely important including preseeding community and seedbank composition, seeding success, site characteristics and postseeding management. Preseeding and postseeding management factors are associated with differences in plant community composition on sites seeded with crested wheatgrass (Nafus et al. 2016). Environmental characteristics including soil texture, nutrients, and pH; rockiness; climate; aspect; slope; and elevation can influence vegetative composition (Hinds 1975; Heady 1988; Link et al. 1990; Bansal et al. 2014; Bansal and Sheley 2016; Morris et al. 2019; Raven 2004; Shown et al. 1969; West and Yorks 2006; Williams 2017). Soil texture may be one of the most important environmental characteristics related to the abundance of native vegetation on sites seeded with crested wheatgrass (Raven 2004; Kachergis et al. 2012; Williams 2017). In the northern Great Basin, United States, native vegetation cover and diversity tend to be positively associated with soils higher in silt and clay (Raven 2004; Davies et al. 2007a).

Factors that are associated with greater presence of native vegetation in established stands of crested wheatgrass are of interest because efforts to seed native vegetation into crested wheatgrass stands are largely unsuccessful even when crested wheatgrass is controlled before seeding (Hulet et al. 2010; Fansler and Mangold 2011; McAdoo et al. 2017; Morris et al. 2019). In addition, there is disagreement over the use of crested wheatgrass with proponents stating that natives can coexist with crested wheatgrass and opponents stating that it decreases diversity and displaces natives (Pellant and Lysne 2005; Davies et al. 2011). Thus, there is a critical need for information on the range of plant community characteristics of crested wheatgrass stands, especially since management goals often have an emphasis on increasing species diversity (Pellant and Lysne 2005).

Our objective was to identify environmental factors correlated with native plant density, cover, richness, and diversity and quantify the variability in native vegetation characteristics on sites seeded with crested wheatgrass in semiarid sagebrush steppe. We hypothesized that native vegetation cover, density, and diversity would be positively correlated with finer textured soils, higher elevation, and greater rockiness.

Methods

Study Area Description

We selected 121 study sites across 54 230 km^2 in southeastern Oregon (Fig. 1). 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 black greasewood (Sarcobatus vermiculatus [Hook.] Torr.). All study locations were seeded with crested wheatgrass 10–50 yr prior, primarily by drill

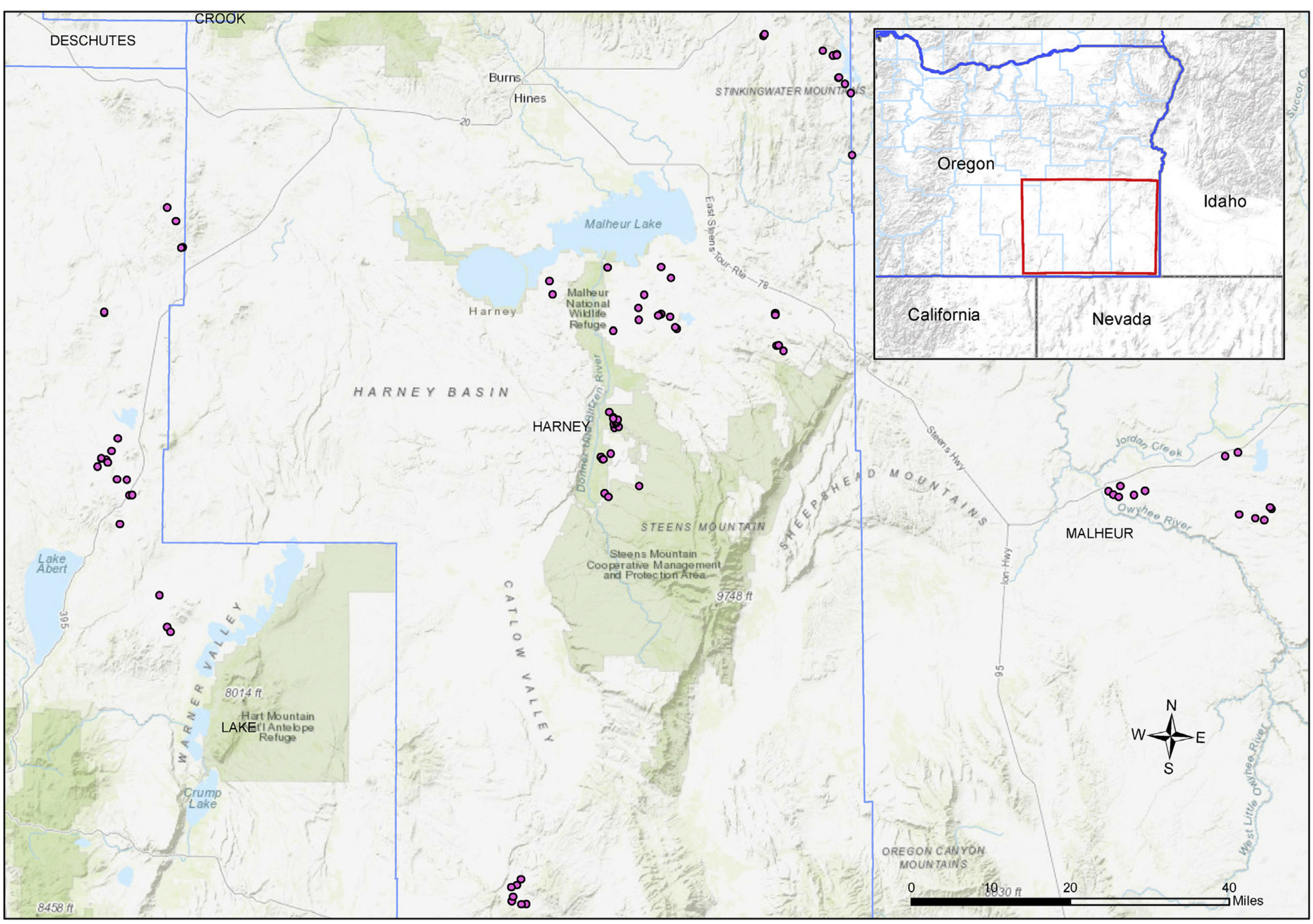

Figure 1. Locations of sites across southeastern Oregon. Pink circles represent areas where crested wheatgrass seedings were sampled.

Figure 2. A near monoculture crested wheatgrass seeding (left) and a Wyoming big sagebrush dominated crested wheatgrass seeding (right).

seeding. Long-term mean annual precipitation for study locations ranged between 200 and 360 mm (with one location at 460 mm) (PRISM Climate Group 2014). Annual precipitation amounts (from 1 October to 30 September) for study locations were 74% and 75% of the long-term average (30 yr) in 2011–2012 and 2012–2013.

Site Selection

Personnel from the US Department of Interior Bureau of Land Management (BLM) of the Burns, Lakeview, and Vale Districts; the US Fish and Wildlife Service, Oregon Department of State Lands; and local ranchers were consulted to obtain locations of all crested wheatgrass seedings in their jurisdiction. Across southeastern Oregon, and within the previously identified seedings, 121 plots were identified so that they occurred across a gradient of environmental conditions to capture a range of crested wheatgrass dominance and variability of native vegetation (Fig. 2). All sites sampled had been identified using land management records. They had been seeded with crested wheatgrass, and only sites that contained at least 0.25-crested wheatgrass plants per m^2 were used in an attempt to ensure that seeding had occurred. The Land Treatment Digital Library was used to verify seeding polygons whenever data was available (Pilliod and Welty 2013).

Vegetation Characteristics

A 50 × 60 m plot was used to sample each of the 121 sites. Four parallel 50-m transects were located at 20-m intervals along 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. Sampling was conducted between 15 May and 15 July in 2012 and 2013. Due to presampling concerns that grazing might be extensive in crested wheatgrass seedings, we chose to measure basal cover as opposed to foliar cover. Grazing was limited in most sites before sampling and did not affect species identification. Cover was estimated to the nearest 1%. Bunchgrasses were considered separate individuals if there were > 5 cm between clumps and at least 50% of the plant was rooted in the quadrat. Sandberg bluegrasses (*Poa secunda* J. Presl) were considered separate individuals if there was > 1 cm between clumps. Dead portions within the perimeter of the live portion of the crown were included in the basal cover estimate when they were not > 5 cm across. Shrub canopy cover by species was measured using the line intercept method (Canfield 1941). 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 at each plot. Each 2 × 50 m belt transect was centered over one of the four 50-m transects. Individuals were summarized by functional group or individual species as follows: Sandberg bluegrass, crested wheatgrass, large native perennial bunchgrasses, perennial forbs, annual grasses, annual forbs, and shrubs. Sandberg bluegrass was measured separately because of its relatively small stature and early development compared with other native bunchgrasses in these communities (James et al. 2008). As the only non-native bunchgrass, crested wheatgrass was separated at the species level. The functional group/species separations were designed to simplify site characterization and comparisons (Boyd and Bidwell 2002; Davies et al. 2007b). Species richness was determined by summing all species found in the quadrats at each site. 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)

Environmental Factors

A total of 14 environmental variables were measured at each site (Table 1). One 0–15-cm and 15–60-cm soil samples were collected at the plot center in the gaps between vegetation. Two additional 0–15-cm samples were collected, one at 15 m NW and one at 15 m SW from the plot center. Samples were placed in separate bags by

Table 1
Environmental factors and vegetation characteristics measured at or calculated for each of 121 sites located in crested wheatgrass seedings across a 54 230 km^2 area in southeastern Oregon.

Vegetation characteristics	Environmental factors	Calculated parameters
Herbaceous basal cover	Longitude and latitude	Vegetation
Herbaceous density	Slope	Shannon Weiner diversity (H′)
Shrub foliar cover	Elevation	Species richness
Shrub density	Aspect	Environmental
	Soil texture 0-15 cm (% sand, silt, and clay)	Heat load index
	Soil texture 16-60 cm[1] (% sand, silt, and clay)	
	Soil total carbon and nitrogen (0-15 cm) (%)	
	Carbon:nitrogen ratio	
	Soil pH (0-15 cm)	
	Average annual precipitation (30 yr)	
	Average max temperature (April–September)	
	Average min temperature (October–March)	
	Rock (% cover)	
	Gravel (% cover)	

[1] Soil texture (15-60 cm) was originally included in the analysis, but because of missing values in the data and a 99% correlation with the 0-15 cm values, it was removed from the analysis.

depth and location and air dried for further analysis. Soil texture was estimated using the hydrometer method (Bouyoucos 1962). Soil pH from the 0–15-cm soil samples was determined by mixing 5-mg soil samples with 15 mL nanopure H_2O, agitating for 5 min and allowing to settle for 45 min, then stirring vigorously immediately before inserting a Beckman 3 in 1 pH probe (Beckman Coulter, Inc., Brea, CA) into the solution. The total carbon and nitrogen concentration for each 0–15-cm soil sample were determined by oven drying and combusting samples using a LECO CN 2000 (LECO Corp., St. Joseph, MI). The values for the three 0–15-cm depth samples were averaged into a single plot value. Locational coordinates (decimal degrees), slope (degrees), aspect, and elevation (m) were recorded at each site. Longitude, aspect, and slope were used to calculate heat load (McCune and Keon 2002).

Precipitation was estimated for each site using the Precipitation-elevation Regressions on Independent Slopes Model (PRISM Climate Group 2014).

Statistical Analyses

Crested wheatgrass cover and density were regressed against species richness, species diversity, and each of the functional group and Wyoming big sagebrush cover or density (JMP 10.0.2). Stepwise multiple linear regression (JMP 10.0.2) was used to select models correlating basal cover and density of functional groups, species, species diversity and richness with environmental factors. Sandberg bluegrass, crested wheatgrass, large native perennial bunchgrasses (LNPB), 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. Environmental variables (see Table 1) were added and deleted in stepwise fashion using P values to select a parsimonious model that explained the most variation in the response variables resulting in the highest adjusted R^2 value. Environmental factors that did not contribute significantly ($P \geq 0.05$) were excluded from the final model. Because latitude, aspect, and slope were included in the calculation of heat load index, they were not used independently for model selection. Data were square root transformed before model selection when necessary to better meet data distribution assumptions. Parametric statistics were used to describe vegetation characteristics of crested wheatgrass stands. Means were reported with standard errors.

Results

Functional groups/species occurred in the following percentages for the 121 sites: annual forbs (93%), annual grasses (89%), Sandberg bluegrass (85%), shrubs (75%), native perennial forbs (59%), and large native perennial bunchgrasses (LNPBs) (59%). One site contained only crested wheatgrass and a few greasewood plants, while the rest of the sampled sites contained at least three plant species with at least one native species and over half of the sites contained at least 14 plant species. Total species richness, including shrub and herbaceous species, ranged between 2 and 37 species averaging 13.2 ± 0.8 species per site with perennial herbaceous species averaging 6.5 ± 0.4 (Fig. 3). Total species diversity, including shrub and herbaceous species, ranged from 0.002 to 2.23, with total herbaceous and herbaceous perennial species diversity averaging 1.1 ± 0.05 and 0.6 ± 0.05, respectively (see Fig. 3). Squirreltail (*Elymus elymoides* [Raf.] Swezey) and longleaf phlox (*Phlox longifolia* Nutt.) were the most common LNPB and perennial forb, occurring on 35% and 46% of the sites. Slender phlox (*Microsteris gracilis* [Hook.] Greene) was the most common native annual forb and occurred on 64% of the sites. Wyoming big sagebrush was the most common shrub and occurred on 63% of the sites. Large native bunchgrasses and Wyoming big sagebrush occurred together on 49% of the sites, and LNPB, sagebrush, and perennial forbs occurred together on 39% of the sites.

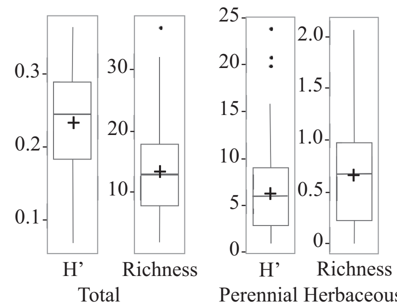

Figure 3. Boxplot showing total and perennial herbaceous Shannon-Weiner Diversity (H′) and species richness across 121 crested wheatgrass stands sampled in southeastern Oregon. The median is shown as the *solid black line,* the mean is depicted as a *gray cross.* The upper and lower ends of the box correspond 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.

Cover varied widely among and within herbaceous functional groups (Fig. 4). Fifty percent of the sites contained at least 2.4% Sandberg bluegrass cover, which ranged from 0% to 13%. Cover of LNPB ranged from 0% to 10%, although 50% of the sites contained < 1% LNPB cover. Cover of crested wheatgrass was > 5% on 50% of the sites and ranged from < 1% to 19%. Shrub cover ranged from 0% to 27%, and 50% of the sites had at least 3.4% cover. Sagebrush cover was > 10% on 15% of the sites.

Density varied widely among and within functional groups (Fig. 5). Density of Sandberg bluegrass ranged from 0 to 119 plants $\cdot$ m^{-2}, and 50% of the sites contained at least 17.4 Sandberg bluegrass plants $\cdot$ m^{-2}. Forty-three percent of sites contained no LNPB individuals. Of the sites containing LNPB, 55% had < 1 LNPB plant $\cdot$ m^{-2} and 45% had LNPB densities between 1 and 10 plants $\cdot$ m^{-2}. Density of shrubs ranged from 0 to 2 plants $\cdot$ m^{-2}. Density of crested wheatgrass ranged from 0.25 to 22 plants $\cdot$ m^{-2}, and half of the sites had > 7.6 crested wheatgrass plants $\cdot$ m^{-2}. Density of annual forbs and grasses ranged from 0 to 769 plants $\cdot$ m^{-2} and 0 to 757 plants $\cdot$ m^{-2}, respectively.

Functional Group Correlations

There was no correlation between crested wheatgrass cover or density and species richness or species diversity ($P > 0.05$). Crested wheatgrass density was not correlated with the density of any herbaceous functional group ($P > 0.05$). Crested wheatgrass cover was not correlated with the basal cover of any herbaceous functional group ($P > 0.05$). Foliar cover of shrubs was negatively correlated with cover of crested wheatgrass (adj. $R^2 = 0.26$, $P < 0.001$). Wyoming big sagebrush cover was negatively correlated with crested wheatgrass cover (adj. $R^2 = 0.24$, $P < 0.001$).

Sandberg bluegrass density was positively correlated with LNPB density (adj. $R^2 = 0.90$, $P < 0.001$). LNPB density was positively correlated with perennial forb density (adj. $R^2 = 0.29$, $P < 0.001$).

Multiple Linear Regression

Sandberg bluegrass cover and density were positively associated with higher silt in the soil and more eastern longitudes (Tables 2 and 3). Sandberg bluegrass cover was also positively correlated with elevation (see Table 2). Cover of crested wheatgrass was positively correlated with total carbon, a higher C:N ratio, and more alkaline soils. Cover of crested wheatgrass was negatively

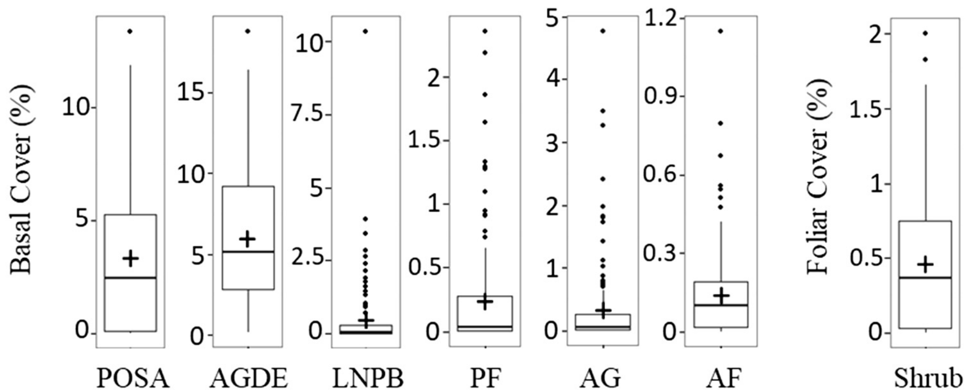

Figure 4. Boxplot showing the percent basal cover of Sandberg bluegrass (POSA), crested wheatgrass (AGDE), large native perennial bunchgrass (LNPB), perennial forbs (PF), annual grass (AG), and annual forbs (AF) and foliar cover (%) of shrubs across 121 crested wheatgrass stands sampled in southeastern Oregon. The median is shown as the *solid black line*, and the mean is depicted as a *gray cross*. 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.

correlated with silt and gravel cover (see Table 2). Crested wheatgrass density was weakly correlated with measured environmental variables (see Table 2). LNPB density was associated with silty, more acidic soils and more eastern sites (see Table 3). LNPB cover was weakly correlated with measured environmental variables (adj $R^2 = 0.19$, $P < 0.05$; see Table 3). Perennial forb cover and density were negatively correlated with sandy, more acidic soils (see Tables 2 and 3). Perennial forb cover was positively correlated with soil carbon and gravel cover (see Table 2). Perennial forb density was positively correlated with rock cover (see Table 3). Annual forb cover was positively correlated with clay and average annual precipitation but negatively correlated with gravel cover (see Table 2). Annual forb density was not significantly correlated with any measured environmental variables ($P > 0.05$). Shrub cover and density were negatively correlated with sandiness and average annual precipitation and positively correlated with elevation (see Tables 2 and 3). Shrub density was higher in neutral to slightly acidic soil (see Table 3). Wyoming big sagebrush canopy cover and density were weakly correlated with environmental variables (see Tables 2 and 3). Sagebrush cover was positively correlated with gravel cover and negatively correlated with sand, soil pH, and average annual precipitation (see Table 2).

Total species richness was associated with lower soil carbon, higher soil nitrogen, and a lower C:N ratio (Table 4). Perennial herbaceous species richness was positively correlated with total soil carbon (Table 5). Perennial herbaceous species diversity was associated with lower total soil carbon and a lower C:N ratio (see Table 5). Richness and diversity were associated with more neutral to slightly acidic soils (see Tables 4 and 5). Herbaceous perennial, total species richness, and total species diversity were negatively correlated with sand. Perennial herbaceous diversity was associated with higher clay content. Richness and diversity were positively correlated with rock cover (see Tables 4 and 5). Total species diversity was positively correlated with higher elevations, and perennial herbaceous species diversity was positively correlated with sites with a higher heat load index.

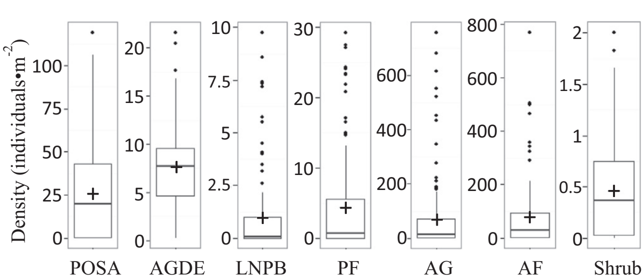

Figure 5. Boxplot showing density (plants·m^{-2}) of Sandberg bluegrass (POSA), crested wheatgrass (AGDE), large native perennial bunchgrass (LNPB), perennial forbs (PF), annual grass (AG), annual forbs (AF), and shrubs across 121 crested wheatgrass stands sampled in southeastern Oregon. The median is shown as the *solid black line*, and the mean is depicted as a *gray cross*. 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.

Discussion

Introduced perennial bunchgrasses have been used extensively in revegetation projects across the United States, in part because of their ability to compete against undesirable species (Frischknecht 1968; Davies et al. 2010). However, this competitiveness may also lead to decreased biodiversity of desirable native species (Marlette and Anderson 1986; D'Antonio and Vitousek 1992; Christian and Wilson 1999; Krzic et al. 2000), leading to a general assumption that areas seeded with crested wheatgrass will become monocultures. Although true in some cases, we found variable native vegetation presence on sites seeded with crested wheatgrass. Near-monoculture stands of crested wheatgrass existed, but some stands had relatively abundant native vegetation, especially shrubs (Fig. 2). Correlations between environmental variables and vegetation characteristics suggest that variability in cover and abundance of native vegetation in crested wheatgrass stands is, in part, likely related to environmental differences (see Tables 2 and 3). Environmental variability, as well as management differences (Nafus et al. 2016; Williams et al. 2017), may explain why some authors (Looman and Heinrichs 1973; Marlette and Anderson 1986) have reported that seeding crested wheatgrass results in near monocultures and others have found more diverse assemblages (Reynolds and Trost 1981; McAdoo et al. 1989; Williams et al. 2017). Correlations between environmental factors and native vegetation may be useful to identify where native vegetation is more likely to coexist with crested wheatgrass and where crested wheatgrass monocultures are more likely to develop.

Functional groups/individual species responded differently to environmental characteristics. Environmental factors were not correlated with the variability in annual grass density, whereas 56% of the variability of LNPB density was explained by environmental factors (see Table 3). Perennial forb and Sandberg bluegrass basal cover and density variability were also fairly well explained by environmental factors ($R^2 = 0.44–0.49$). Environmental

Table 2
Multiple linear regression models for Sandberg bluegrass, crested wheatgrass, large native perennial bunchgrasses (LNPB), annual grass, perennial forb, and annual forb basal cover and shrub and Wyoming big sagebrush (ArtrWy) foliar cover. Direction of association (+ or −), correlations, and (SE) are shown for environmental variables selected using mixed model selection. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. Only functional groups that had an adjusted $R^2 > 0.10$ were included in the table. All coefficients of variation (R^2) were significant at $P < 0.05$.

Functional group basal cover (%)	AdjR^2	Intercept	Silt (%)	Sand (%)	Clay (%)	Nitrogen (%)	Carbon (%)	C:N ratio	pH	Sqrt (Gravel cover [%])	Sqrt (Rock cover [%])	Longitude (decimal degrees)	Elevation (m)	Precipitation (mm)
Sandberg bluegrass	0.46	+ 219.13 (41.89)	+ 0.10 (0.018)									+ 1.89 (0.36)	+ $4.2e^{-3}$ ($1.4e^{-3}$)	
Crested wheatgrass	0.30	− 12.33 (6.51)	− 0.10 (0.023)				+ 34.00 (7.96)	+ 0.81 (0.20)	+ 1.89 (0.78)	− 0.86 (0.22)				
Sqrt (LNPB)	0.19	+ 2.37 (0.70)		− $7.0e^{-3}$ ($2.7e^{-3}$)					− 0.28 (0.11)	+ 0.11 (0.032)				
Sqrt (Annual grass)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sqrt (Perennial forb)	0.44	+ 2.73 (0.45)		− $5.8e^{-3}$ ($1.6e^{-3}$)			+ 1.66 (0.71)		− 0.35 (0.065)	+ 0.40 (0.019)				
Sqrt (Annual forbs)	0.20	− 0.067 0.15			+ $8.0e^{-3}$ ($2.0e^{-3}$)					− 0.039 (0.013)				+ $1.1e^{-3}$ ($5.4e^{-4}$)
Sqrt (Shrubs)	0.20	11.15 (3.20)		− 0.022 ($1.4e^{-3}$)									+ $2.3e^{-3}$ ($6.7e^{-4}$)	− 0.017 ($4.2e^{-3}$)
Sqrt (ArtrWy)	0.22	+ 14.2 (3.18)		− 0.017 ($7.2e^{-3}$)					− 1.40 (0.34)	+ 0.19 (0.090)				− 0.011 ($4.4e^{-3}$)

Table 3
Multiple linear regression models for Sandberg bluegrass, crested wheatgrass, large native perennial bunchgrasses (LNPB), annual grass, perennial forb, annual forb, shrub, and Wyoming big sagebrush (ArtrWy) abundance (plants $\cdot$ m^{-2}). Direction of association (+, −), correlations, and (SE) are shown for environmental variables selected using mixed model selection. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. Only functional groups that had an adjusted $R^2 > 0.10$ were included in the table. All coefficients of variation (R^2) were significant at $P < 0.05$.

Functional group density (plants $\cdot$ m^{-2})	AdjR^2	Intercept	Silt (%)	Sand (%)	Clay (%)	Nitrogen (%)	Carbon (%)	C:N ratio	pH	Sqrt (Gravel cover [%])	Sqrt (Rock cover [%])	Longitude (decimal degrees)	Elevation (m)	Precipitation (mm)
Sandberg bluegrass	0.49	+ 1291.38 (278.75)	+ 0.92 (0.14)									+ 10.94 (2.33)		
Crested wheatgrass	0.11	+ 7.06 (1.10)	− 0.060 (0.027)			+ 3.31 (0.88)								
Sqrt (LNPB)	0.56	+ 142.62 (29.80)	+ 0.11 (0.015)						− 1.34 (0.45)			+ 1.12 (0.25)		
Sqrt (annual grass)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sqrt (perennial forb)	0.45	+ 12.56 (1.66)		− 0.039 ($6.2e^{-3}$)					− 1.44 (0.26)		+ 0.19 (0.098)			
Sqrt (annual forbs)	0.14	+ 232.98 (72.80)			+ 0.16 (0.055)							+ 1.94 (0.61)	+ 0.010 ($4.7e^{-3}$)	
Sqrt (shrubs)	0.20	+ 3.04 (0.87)		− $4.9e^{-3}$ ($2.0e^{-3}$)					− 0.30 (0.093)				+ $6.0e^{-4}$ ($1.8e^{-4}$)	− $3.9e^{-3}$ ($1.1e^{-3}$)
Sqrt (ArtrWy)	0.18	+ 3.34 (0.79)		− $4.5e^{-3}$ ($1.8e^{-3}$)					− 0.33 (0.087)	+ 0.047 (0.022)				− $2.3e^{-3}$ ($1.1e^{-3}$)

Table 4
Multiple linear regression models for total species richness and total Shannon-Weiner diversity (H′), direction of association (+, −), correlations, and (SE) are shown for environmental variables selected using mixed-model selection. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. All coefficients of variation (R^2) were significant at $P < 0.05$.

All species	Adj R^2	Intercept	Silt (%)	Sand (%)	Clay (%)	Nitrogen (%)	Carbon (%)	C:N ratio	pH	Sqrt (Gravel cover [%])	Sqrt (Rock cover [%])	Longitude (decimal degrees)	Elevation (m)	Precipitation (mm)
Richness	0.50	+ 77.89 (10.69)		− 0.071 (0.031)		+ 14.44 (3.97)	− 76.96 (33.57)	− 2.29 (0.65)	− 6.58 (1.35)		+ 1.91 (0.48)			
Diversity	0.37	+ 3.91 (0.82)		− 0.011 ($2.5e^{-3}$)					− 0.48 (0.11)		+ 0.10 (0.038)		+ $5.8e^{-4}$ ($2.3e^{-4}$)	

Table 5
Multiple linear regression models for perennial herbaceous species richness and perennial herbaceous Shannon-Weiner diversity (H′). Direction of association (+, −), correlations, and (SE) are shown for environmental variables selected using mixed-model selection. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. All coefficients of variation (R^2) were significant at $P < 0.05$.

Perennial herbaceous species	Adj R^2	Intercept	Silt (%)	Sand (%)	Clay (%)	Nitrogen (%)	Carbon (%)	C:N ratio	pH	Sqrt (Gravel cover [%])	Sqrt (Rock cover [%])]	Longitude (decimal degrees)	Elevation (m)	Heat Load Index
Richness	0.45	+ 34.42 (5.52)		− 0.061 (0.019)			+ 28.86 (8.36)		− 4.32 (0.81)		+ 0.90 (0.30)			
Diversity	0.48	+ 1.17 (1.47)			+ 0.016 ($4.0e^{-3}$)	+ 1.23 (0.26)	− 7.41 (2.25)	− 0.19 (0.042)	− 0.30 (0.090)		+ 0.082 (0.032)			+ 2.73 (1.33)
Perennial herbaceous species	Adj R^2	Intercept	Silt (%)	Sand (%)	Clay (%)	Nitrogen (%)	Carbon (%)	C:N ratio	pH	Sqrt (Gravel cover [%])	Sqrt (Rock cover [%])	Longitude (decimal degrees)	Elevation (m)	Heat Load Index
Richness	0.45	+ 34.42 (5.52)		− 0.061 (0.019)			+ 28.86 (8.36)		− 4.32 (0.81)		+ 0.90 (0.30)			
Diversity	0.48	+ 1.17 (1.47)			+ 0.016 ($4.0e^{-3}$)	+ 1.23 (0.26)	− 7.41 (2.25)	− 0.19 (0.042)	− 0.30 (0.090)		+ 0.082 (0.032)			+ 2.73 (1.33)

characteristics did not always explain the diversity of native vegetation in crested wheatgrass seedings, which was not unexpected as competition and management also have a substantial influence on plant community composition and dynamics (Grant-Hoffman et al. 2012; Morris et al. 2014; Nafus et al. 2016).

Soil texture appeared to be the most prominent environmental factor in regression models. Soil texture was included in the best regression models for cover and density of all plant functional groups. Other studies in the Great Basin have also suggested that soil texture might be one of the most important variables predicting herbaceous composition (Raven 2004; Davies et al. 2007a; Bansal et al. 2014; Bansal and Sheley 2016; Williams et al. 2017), possibly because it affects moisture availability. Sandier soil has a lower water-holding capacity and retains less water in the root zone than finer-textured soil (Shown et al. 1969). Crested wheatgrass, because it exploits soil moisture and nutrients more quickly than native bunchgrasses, may therefore be better able to take advantage of limited moisture in sandier soils than many native herbaceous species (Eissenstat and Caldwell 1988). Intact sagebrush sites with sandy soils generally have lower native herbaceous vegetation and less sagebrush cover than sites with finer-textured soils (Davies et al. 2006; Davies et al. 2007a); suggesting some of this effect may be inherent regardless of whether or not crested wheatgrass was seeded on these sites.

Unlike Williams et al. (2017), who found a strong negative relationship between crested wheatgrass cover and species diversity, we did not find an association between crested wheatgrass and perennial herbaceous species richness and diversity. Overall, we found lower species richness and diversity than others have found in relatively intact Wyoming big sagebrush communities across the northwestern Great Basin. The average perennial herbaceous species richness and diversity in intact Wyoming big sagebrush communities were 14.4 species and 1.6, respectively (Davies and Bates 2010b). This was about three times as high as the average richness (5.5) and diversity (0.6) we found on sites seeded to crested wheatgrass. Krzic et al. (2000) also found reduced species diversity in fields seeded with crested wheatgrass than on nearby native vegetation sites. This study was not designed to test the effects of seeding crested wheatgrass on community richness and diversity as seedings were not compared with unseeded communities. Although our results suggest that crested wheatgrass may reduce species richness and diversity, the lack of comparison to nearby unseeded communities means that the lower richness and diversity cannot be conclusively attributed to crested wheatgrass. The low richness and diversity in our study sites may be an artifact of plant community composition at the time of seeding since many seedings were implemented after a disturbance that reduced native vegetation. The land-use legacy (e.g., historic cultivation, shrub removal, fire) of a site may favor long-term persistence of crested wheatgrass and reduced vegetative composition and structure (Morris et al. 2014; Nafus et al. 2016, Williams et al. 2017).

Richness and species diversity on our sites were positively correlated with rockiness (see Tables 4 and 5). Rocks may create microhabitats and therefore multiple niches (Milchunas and Noy-Meir 2002; Lambrinos et al. 2006), convey protection from herbivores, and catch seeds to recolonize overgrazed microsites (Milchunas and Noy-Meir 2002; Golodets et al. 2011). Rocks can also affect soil hydrology as water can accumulate on the underside of surface and subsurface rocks to provide a more persistent water source (Hamerlynck et al. 2002). In addition, rockiness of a site may influence initial seeding success as increased site rockiness may negatively affect drill seeding effectiveness (Call and Roundy 1991) and may influence the soil texture by decreasing wind erosion. Soil sand content can increase as a result of wind erosion, leading to decreases in soil carbon and nitrogen availability (Li et al. 2009). Site rockiness may be tied to management legacy effects that favor native vegetation (see Morris et al. 2014). These same legacy effects may also make it more difficult to implement management actions, such as seeding, to increase vegetation diversity.

Large native bunchgrasses were the least likely functional group to occur in the sampled crested wheatgrass communities. This may be because LNPBs 1) may have been negatively impacted by overgrazing (Caldwell et al. 1981; Mack and Thompson 1982; Brewer et al. 2007) before seeding crested wheatgrass or 2) are generally less competitive than crested wheatgrass (Bakker and Wilson 2001) and are less likely to occupy open spaces than crested wheatgrass (Hamerlynck and Davies 2018). We were, in most cases, unable to determine preseeding plant community composition at sampled sites but speculate that many may have had low LNPB density before seeding crested wheatgrass. Large native bunchgrasses were likely not only depleted in the community before seeding of crested wheatgrass but were also subsequently less likely to reestablish due to crested wheatgrass competition (Heady 1988; Pyke 1990; Fansler and Mangold 2011). Although 10% of our sampled sites had a higher density of native bunchgrasses than of crested wheatgrass, we found, overall, few LNPBs in most stands of crested wheatgrass. Native bunchgrasses do not generally increase when seeded in conjunction with non-native perennial grasses, such as crested wheatgrass (Knutson et al. 2014; Nafus et al. 2015). Large native bunchgrasses can be difficult to establish in crested wheatgrass–dominated plant communities, even with management to reduce crested wheatgrass (Hulet et al. 2010; Fansler and Mangold 2011) as natives generally have low establishment and crested wheatgrass rapidly recovers (McAdoo et al. 2017).

Perennial forbs were less common on sandy soil. Sandy soil was similarly associated with lower perennial forb cover in intact sagebrush communities (Davies et al. 2006), possibly because competition may be exacerbated on sandy soils that have lower soil water and nutrient availability (Binkley and Vitousek 1989). Crested wheatgrass may also limit perennial forbs as it can be highly competitive with forb species and has been used to prevent reinvasion by exotic forb species in Montana (Sheley and Carpinelli 2005). Similarly to our findings, Williams et al. (2017) also found relatively few native perennial forbs in crested wheatgrass seedings.

Annual forbs, annual grasses, and Sandberg bluegrass, the three most prevalent herbaceous functional groups in stands of crested wheatgrass, tend to avoid resource limitations by growing earlier in the season, when resources are more plentiful (Ludlow 1989; Volaire et al. 2009). The ability to temporally avoid competition for resources may explain their success in crested wheatgrass stands relative to plant functional groups that are more likely to have to compete directly with crested wheatgrass when resources are limited (e.g., large native bunchgrasses). In addition, these functional groups are often found to increase as a result of overgrazing (Hubbard 1951), which likely preceded the planting of crested wheatgrass in many cases. Therefore, it is probable that these early growing species were abundant on many of these sites before seeding (Heady 1988).

Wyoming big sagebrush constituted the majority of the shrub cover (74%) and density (62%). Plant communities with higher numbers of shrubs, most of which were Wyoming big sagebrush, tended to be associated with soils higher in silt and lower in precipitation. It is possible that in our case, shrubs tended to dominate sites with less precipitation because shrubs were able to access moisture deeper in the soil profile that was less accessible to herbaceous vegetation, giving shrubs a competitive advantage on these sites (Jensen et al. 1990; Dodd et al. 2002). Alternatively, sites with lower precipitation may have had lower initial crested wheatgrass establishment and therefore lower crested wheatgrass competition, allowing sagebrush to more rapidly recover (Shown et al. 1969; Gunnell et al. 2010).

Wyoming big sagebrush cover was negatively associated with crested wheatgrass cover. Other researchers have also found this negative relationship between crested wheatgrass and sagebrush cover (e.g., Rittenhouse and Sneva 1976; Williams et al. 2017). Sagebrush seedlings establish and grow better in locations where crested wheatgrass cover is reduced (Gunnell et al. 2010; Newhall et al. 2011; Davies et al. 2013). Environmental characteristics that affect water-holding capacity may influence the ability of Wyoming big sagebrush to establish and persist, even in low crested wheatgrass cover (Morris et al. 2019).

However, only 22% of the variation in Wyoming big sagebrush cover was explained by environmental variables. Our data suggest that sagebrush is recruiting into crested wheatgrass stands as most stands had sagebrush removed before seeding, and it is now present in 63% of the stands with 15% of the stands having 10% or higher sagebrush cover. This is important because the addition of Wyoming big sagebrush to crested wheatgrass stands diversifies community structure and improves habitat for sagebrush-dependent wildlife (McAdoo 1989; Kennedy et al. 2009) and can help provide valuable winter habitat (Connelly et al. 2000).

Most communities seeded to crested wheatgrass were degraded, burned in a wildfire, and/or treated in an attempt to remove shrub species before seeding (Heady 1988); thus, low native vegetation cover and abundance at some sites may have been an artifact of management before seeding. The type and severity of disturbance, as well as plant composition before seeding, likely affects current plant composition (Burke and Grime 1996). Regrettably, complete historical management and disturbance information and preseeding plant community were unavailable for all 121 sites. A parallel study using a subset of plots with information about management history found that fire, time since seeding, grazing, and other management actions are associated with variation in community composition (see Nafus et al. 2016). However, regardless of confounding management factors, we found that soil texture was the factor most strongly associated with differences in community composition.

Management Implications

Our results suggest that general assumptions that seeding crested wheatgrass will always result in the formation of monoculture stands are not supported. Environmental variables, particularly soil texture, and management (Nafus et al. 2016) have substantial influence on native plant abundance and cover in crested wheatgrass communities. Our results indicate that site characteristics can have variable effects on native species density, cover, and diversity and that, in most cases, at least some native vegetation can co-occupy rangelands seeded with crested wheatgrass. In general, we observed that the species most commonly encountered in sites seeded with crested wheatgrass tend to be those that are able to minimize competition with crested wheatgrass via temporal (i.e., Sandberg bluegrass, annual forbs, annual grasses) or spatial (i.e., shrubs) differentiation in resource use. Attempts to diversify crested wheatgrass stands should likely focus on these species. Increasing native vegetation in existing crested wheatgrass seedings can be difficult (Hulet et al. 2010; Fansler and Mangold 2011; McAdoo et al. 2017). Knowledge of which factors are more likely to lead to higher cover and diversity of desirable native vegetation may assist land managers to determine where diversifying crested wheatgrass stands is possible. For example, our results suggest that native vegetation may be more successful on sites with fine-textured soils. Management efforts to diversify seedings could be targeted toward sites where conditions are more favorable for coexistence of native vegetation with crested wheatgrass and possibly focus on species or functional groups that show more aptitude for coexisting with crested wheatgrass. Wyoming big sagebrush, for example, was found on the majority of study sites, and its reestablishment can restore shrub steppe characteristics not found in introduced grasslands. There are crested wheatgrass stands where species diversity and richness are low, but more than half the stands we sampled had five or more perennial herbaceous species and 63% contained Wyoming big sagebrush. Efforts to diversify other competitive, introduced grass seedings should likely focus on species that have temporal or spatial differentiation of resource use with the seeded species. These efforts could also be aided by research determining which site characteristics increase the probability of success.

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