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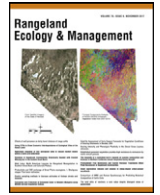
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Variation in Sagebrush Communities Historically Seeded with Crested Wheatgrass in the Eastern Great Basin[☆]



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ABSTRACT

Although crested wheatgrass (*Agropyron cristatum* [L.] Gaertn. & *A. desertorum* [Fisch. ex Link] Schult.) has been one of the most commonly seeded exotic species in the western United States, long-term successional trajectories of seeded sites are poorly characterized, especially for big sagebrush (*Artemisia tridentata* Nutt.) ecosystems in the Great Basin. Interpreting successional trajectories is particularly difficult because many seeded sites were actively managed with subsequent treatments to kill sagebrush and sustain high forage productivity of crested wheatgrass plants. In addition, inherent differences in climate, topography, soils, and disturbance regimes may lead to variable vegetation structure and species composition among seeded sites. To clarify variation in successional trajectories, we measured vegetation composition, plant species diversity, ground cover, and soil properties in 38 historical crested wheatgrass seedings distributed across 146 sampling sites that lacked subsequent sagebrush treatments. The multivariate dataset was analyzed using principal components analysis to identify “defining factors” that best explained variation among sites. Variation was primarily attributed to an inverse relationship between crested wheatgrass and sagebrush abundance ($R^2 = 0.69$; $P < 0.0001$) and their affinity for either silty or sandy soil textures, respectively, as well as a negative association between crested wheatgrass abundance and species diversity ($R^2 = 0.67$; $P < 0.0001$). These results do not support the assumption that crested wheatgrass seedings uniformly remain in vegetation states with low diversity and poor sagebrush reestablishment over the long term (i.e., 43–63 yr). We suggest that a broader interpretation of plant community dynamics is needed while avoiding generalizations of how historically seeded Wyoming big sagebrush sites will respond over time.

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Introduction

Crested wheatgrass (*Agropyron cristatum* [L.] Gaertn & *A. desertorum* [Fisch. ex Link] Schult) is one of the most commonly seeded exotic species in the western United States (Rogler and Lorenz 1983; Pellant et al. 2004). Millions of hectares of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) communities have been seeded since the 1930s throughout the Great Basin, Snake River Plain, and Columbia River Plateau (Astroth and Frischknecht 1984).

Over 12 million hectares of sagebrush lands in Nevada alone have been converted to crested wheatgrass (Rogler and Lorenz 1983; Young et al. 1987). One of the largest examples of this practice was associated with the Halogeton Control Act of 1952 (Tisdale and Zappetini 1953). Through this act, federal funding was granted to land management agencies to plow large expanses of degraded late-seral Wyoming big sagebrush communities in the eastern Great Basin and seed this land with crested wheatgrass to prevent the spread of the invasive species *Halogeton glomeratus* (M. Bieb.) C. A. Mey. (Miller 1956; Pemberton 1986). Abandoned dry-land farms and unproductive sagebrush pastures with little forage value on private and public lands were also seeded with crested wheatgrass during this period (Morris et al. 2014). Crested wheatgrass was the primary seeded species because of its ease of establishment and high grazing and drought tolerance and because seed of native species was unavailable (Blaisdell et al. 1982; Rogler and Lorenz 1983; Salihi and Norton 1987).

Before European settlement into the Intermountain West in the mid-1800s, structural composition of Wyoming big sagebrush plant

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communities was characterized by codominance between sagebrush and native perennial bunchgrasses (West 1988). Wildfire was part of the historical disturbance regime in sagebrush ecosystems and may have been a common practice used by Native Americans (Mensing et al. 2006; McAdoo et al. 2013b). Consequently, Wyoming big sagebrush ecosystems existed with highly variable vegetation structure and species composition depending on climate, topography, soils, and land disturbance regimes (West 1988; Davies et al. 2006; West and Yorks 2006; Benkobi et al. 2007; Davies et al. 2007). With European settlement in the Intermountain Region at the end of the small ice age (Miller and Wigand 1994), vegetation and successional trajectories were drastically altered by a number of pervasive disturbances, including heavy livestock grazing, invasion by exotic annual species, and land cultivation/abandonment associated with grain crop production (Pickford 1932; Daubenmire 1940; Morris et al. 2011). Furthermore, Wyoming big sagebrush sites that were subsequently seeded with crested wheatgrass are generally considered a highly resilient, alternative vegetation state with structural composition that poorly represents recovery toward historical site conditions (Allen-Diaz and Bartolome 1998; Hulet et al. 2010; Fansler and Mangold 2011). However, this interpretation is often based on monotypic crested wheatgrass stands and may be an oversimplification given the climatic and edaphic diversity of ecological sites where crested wheatgrass has been seeded in the Intermountain West.

Although research has been conducted on crested wheatgrass ecology, including its competitive ability (Rittenhouse and Sneva 1976; Leonard et al. 2008; Davies et al. 2010), seed banks (Marlette and Anderson 1986; Pyke 1990; Gunnell 2009), and ecological effects in northern prairies (Lesica and DeLuca 1996), little is known about the long-term dynamics of these seeded areas outside the Great Plains and Colorado Plateau (Kachergis et al. 2011; Grant-Hoffman et al. 2012), particularly in the Great Basin Desert Region (Davies et al. 2011; Gunnell et al. 2011; Morris et al. 2014). In the Great Basin, seeded big sagebrush communities can often be dominated by crested wheatgrass in the early stages of succession and experience variable reestablishment of sagebrush and herbaceous forbs in later stages depending on the disturbance regime (Frischknecht and Bleak 1957; Hull Jr. and Klomp 1966; Rittenhouse and Sneva 1976; Nafus et al. 2016). Many seeded communities have been actively managed with subsequent mechanical or chemical treatments to kill sagebrush and other undesired shrubs to sustain high forage productivity for livestock use (Lorenz and Rogler, 1962; Robertson 1969; Robertson et al. 1970; Blaisdell et al. 1982). These management treatments influence the vegetation structure and species composition of many big sagebrush communities, interrupting natural successional pathways and allowing crested wheatgrass to exist in a near monoculture (Hull Jr. and Klomp 1966; West et al. 1979). Furthermore, when successive management treatments and wildfire result in local extinction of native species from the seed bank, they have long-lasting effects on sagebrush communities (Marlette and Anderson 1986; Pyke 1987; Anderson and Inouye 2001) and confound interpretations of vegetation structure, species composition, and successional trajectories over time.

In this study, we evaluated vegetation and soil attributes of historical crested wheatgrass seedings in the northeastern Great Basin in the absence of subsequent management treatments and wildfire effects. To clarify the potential range of successional trajectories in this region, we measured vegetation composition, plant species diversity, ground cover, and soil properties at 146 sites that occurred in thirty-eight 43- to 63-yr-old crested wheatgrass seedings primarily distributed across three Major Land Resource Areas (USDA-NRCS 2006). Our objective was to identify factors that best define variation among historically seeded sites. Given the regional scope of the study, we expected considerable variation in crested wheatgrass and native plant abundances across study sites and believed soil differences would explain much of the variation.

Methods

Study Sites

We conducted a search for historical crested wheatgrass seedings that met the following criteria: 1) successful initial establishment of crested wheatgrass, 2) prescribed burning and natural fire have not occurred since seeding, 3) chemical and mechanical shrub removal treatments have not occurred since seeding, and 4) seedings were > 30 yr old (Williams 2009). We examined management records kept by Bureau of Land Management (BLM) field offices and the Land Treatment Digital Library (Pilliod and Welty 2015) and also visited potential sites to validate these criteria (particularly for any evidence of unreported wildfire occurrence). Seedings were located in the northeastern Great Basin, a region central to seeding efforts associated with the Halogeton Control Act of 1952 (Tisdale and Zappetini 1953). We found a total of 38 seedings that met our criteria. Seedings varied in both age (i.e., yr since seeding between 43- and 63-yr-old) and size (i.e., between 113 and 4149 ha), which extended across topographic gradients. We observed visible differences in shrub cover and proximity to water sources for cattle, which in some cases extended over different pastures. To capture as much of this variation in our analysis, we established four sampling sites within each seeding, except for the four smallest, where we established only two or three. This scheme yielded a total of 146 sampling sites that were considered independent given the high degree of heterogeneity within seedings. Sampling sites were primarily distributed across three Major Land Resource Areas (see Appendix S1; available online at <http://dx.doi.org/10.1016/j.rama.2017.05.003>) on grazing allotments and/or pastures administered by the US Department of Interior, BLM field offices in Cassia and Oneida counties in Idaho, Elko county in Nevada, and Box Elder and Tooele counties in Utah.

Sites were classified and described by the US Department of Agriculture, Natural Resource Conservation Service, Ecological Site Information System (USDA-NRCS 2016a). Sites ranged from 1380 to 1788 m above sea level with most occurring on similar terrain typical of Great Basin Wyoming big sagebrush communities (West 1988). Mean average annual precipitation (1972–2007) ranged from 178 to 382 mm, where precipitation primarily occurs as winter snow and spring rain (WRCC 2015). Regional precipitation for the 2006–2007 growing season when data were collected (1 October to 30 September) was approximately 50% of the 35-yr average. All sites are currently, and have been, grazed by cattle since the late-1800s. Sites occurred on soils typical of Wyoming big sagebrush ecological sites consisting of silt loam, loam, clay loam, and sandy loam texture classes (Williams 2009). Grazing history was quantified by calculating mean animal unit month (AUM), percentage utilization, and characterizing season of use, which were inconsistently reported across allotments between 1969 and 2006 and consequently deemed unsuitable for inclusion in quantitative analyses (Williams 2009).

Vegetation Sampling

At each of the 146 sampling sites, a 20 m × 5 m plot was established at least 200 m from fences, roads, water improvements, cultural resources, and disturbed areas identified from management records maintained by the BLM field offices. Plots were placed to avoid rock outcrops, bottom of washes, and steep slopes. Plots were an intensive version of the Modified-Whittaker Plot (Fraser and Keddy 1997) and contained four, nested 1-m² (2 m × 0.5 m) subplots that were sampled during peak herbaceous productivity, corresponding to the period between May and June 2007. Percentage cover (e.g., bare ground, rock, litter, biological soil crust, foliar cover for each plant species in each 1-m² subplot) was estimated using the procedures of Stohlgren et al. (1995). Cover data were collected by one individual (i.e., J. R. Williams) for all sites to minimize sampling bias. The Shannon-Wiener species diversity

index (H') was calculated from plant cover in 1-m² subplots using the following equation: $H' = -\sum p_i \ln p_i$, where p_i is the proportional abundance of a given species. Using species cover data, we calculated total vegetation cover and relative cover for functional group categories (i.e., crested wheatgrass, shrub, forb, grass, native grass, native forb, exotic forb, and annual species) by dividing these categories by total vegetation cover and then multiplying by 100. Nomenclature for all plant species followed that of the US National PLANTS Database (USDA-NRCS 2016b). Data for subplots were averaged to derive mean values for each variable.

Soil Sampling

Four soil samples were collected at each intensive Modified-Whittaker plot by sampling a distance of 2 m diagonally away from each plot corner so as to not disturb the vegetation of plots or trample the soils during plot setup. Surface litter, if present, was removed and two 15-cm diameter × 20-cm deep holes were dug within plant interspaces using a narrow trench shovel. From the side of both holes, a 5-cm wide vertical sliver to 20-cm deep was shaved, placed into a clean 5-gallon bucket, mixed thoroughly, and placed into 1 L-sized plastic bags for storage. Samples were air dried until further analyses.

All soil analyses were performed on air-dry samples sieved to 2 mm. Soil texture was analyzed using the hydrometer method (Gee and Bauder 1986). Soil pH (to the nearest 0.1 pH unit) was determined using an Orion 3-Star bench-top pH meter and electrode (Thermo Scientific, Beverly, MA) and a 1:2 soil-to-water slurry method (Hendershot et al. 1993). Total soil N and C were determined by direct combustion with a LECO CHN-2000 autoanalyzer (LECO Corp., St. Joseph, MI). The four samples from each site were averaged to obtain a single value for soil texture, pH, C, and N.

Statistical Analysis

A total of 20 variables consisting of absolute cover (i.e., bare ground, total vegetation, litter, biological soil crust, and rock); relative vegetation cover (i.e., crested wheatgrass, shrub, native grass, exotic forb, native forb, forb, grass, and annual); Shannon-Wiener species diversity; and soil characteristics (i.e., sand, silt, clay, pH, and total C and N) were included in analyses (see Appendix S1). For interpretive purposes, absolute cover percentages were summarized with box-and-whisker plots to illustrate the range of variability across the 146 sampling sites. Standardizing sites by calculating relative values for vegetation cover categories was deemed essential for planned multivariate and linear regression analyses because sites varied tremendously in total vegetation cover and overall productivity due to their broad geographic distribution and ecological site classification (see Appendix S1).

Data for 146 sampling sites were also analyzed with principal components analysis (PCA) to identify “defining factors” among the 20 variables that most strongly explained the variation among sites. In brief, PCA was chosen because linear relationships were known to exist within our multivariate dataset and most variables fit a normal distribution curve. In addition, PCA identifies factors with the strongest influence on PCA axes (i.e., largest absolute eigenvector values) by placing sampling sites within an orthogonal coordinate system based on defining factors (McCune and Grace 2002). After initial PCA models were run, we used a process to remove factors from the analysis if their eigenvector values were < |0.3| on the first three axes or if a given factor explained equal variation (i.e., > |0.3|) on a secondary axis (O'Rourke and Hatcher 2013). The PCA model was then analyzed again with only the retained defining factors. Final eigenvector scores are shown herein to illustrate their sign and strength for each PCA axis.

The strength of pair-wise relationships between defining factors were evaluated with correlation coefficients (Pearson's r) and null hypothesis tests (i.e., the true correlation coefficient is equal to zero;

$\alpha < 0.05$). In addition, the strongest correlations (i.e., > |0.6|) were further analyzed with curve-fitting software (DeltaGraph ver. 7.0.8 build 5, Red Rock Software Inc., Salt Lake City, UT) to determine whether relationships were linear or quadratic. “Best fit” was determined by comparing R^2 and P values generated from regression equations.

Results

Variation Among Sampling Sites

Mean ground cover across sites was dominated by roughly equal percentages of bare ground (39.7%) and total vegetation (36.4%) (Fig. 1, a). The remainder of ground cover, in decreasing percentage, consisted of litter (12.3%), biological soil crust (7.5%), and rock (4.1%). Mean cover of crested wheatgrass (17.1%) exceeded that for shrub (12.2%), but both vegetation categories showed considerable variability among the 146 sites with values ranging from < 1% to > 35% (see Fig. 1,

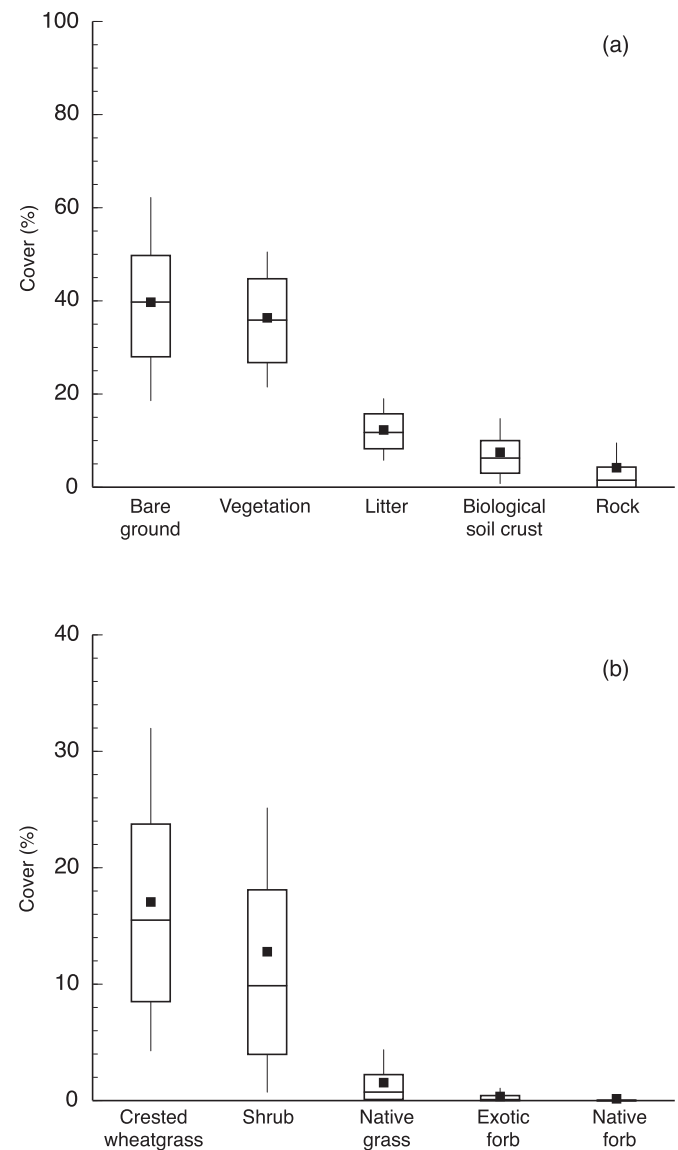


Figure 1. Box-and-whisker plots showing percentage total cover (a) and vegetation cover of functional groups (b) for 146 sites historically seeded with crested wheatgrass in eastern Great Basin, United States. For each variable, top, bottom, and middle lines of the box correspond to the 75th, 25th, and median, respectively; vertical lines extending from the bottom and top of the box correspond with the 10th and 90th percentiles, respectively; and the black squares indicate the mean value. Note differences in y-axis scale.

b). Sites exhibited low annual species cover (i.e., 2.8% of vegetation cover; see Appendix S1) and near absence of native forb plant species (0.8%; see Fig. 1, b). Annual species cover consisted almost entirely of downy brome (*Bromus tectorum* L.). On the other hand, exotic forb cover (1.7%) exceeded native forb cover, yet both were far less abundant than native grasses, which were present at most sites and averaged 4.6% cover (see Fig. 1, b). Native grass cover was almost entirely composed of Sandberg bluegrass (*Poa secunda* J. Presl).

Of the 20 variables directly measured or calculated for the 146 sampling sites, 8 defining factors emerged from PCA (Table 1). The PCA solution explained 81.3% of total variation among sites on three axes. Axes were best defined by variation in the following: Axis 1 (33.4%), associations between soil texture and site productivity (i.e., total vegetation cover and bare ground); Axis 2 (29.6%), associations among crested wheatgrass cover, sagebrush cover, and species diversity; and Axis 3 (18.3%), associations among exotic forb cover, species diversity, and site productivity.

Considering all three axes, a total of 20 significant pairwise correlations were found (Fig. 2). The strongest correlations (i.e., $> |0.6|$) included inverse relationships between sand and silt content ($r = -0.940$), crested wheatgrass and shrub cover ($r = -0.830$), total vegetation cover and bare ground ($r = -0.772$), and crested wheatgrass cover and diversity ($r = -0.636$); all of which confirm the primary importance of PCA axes 1 and 2. In contrast, correlation coefficients between the defining factors identified for PCA axis 3 were all < 0.4 yet emphasized exotic forb cover correlations with bare ground ($r = 0.226$) and species diversity ($r = 0.285$). Other significant correlations that help explain the combined importance of PCA axes 1 and 2 include crested wheatgrass associations with bare ground ($r = 0.227$) and soil silt content ($r = 0.172$) and shrub cover associations with species diversity ($r = 0.287$), soil sand content ($r = 0.215$), and soil silt content ($r = -0.274$).

Regressions of crested wheatgrass cover with shrub cover and species diversity revealed different relationships. The relationship between crested wheatgrass cover and sagebrush cover was best described as linear (Fig. 3, a). In contrast, the relationship between crested wheatgrass cover and species diversity was best defined by a quadratic curve (see Fig. 3, b).

Table 1

Results of Principal Components Analysis (PCA) based on 20 soil and vegetation variables for the 146 Wyoming big sagebrush sampling sites in the eastern Great Basin, United States, that were historically seeded with crested wheatgrass. The PCA solution identified three axes, whose eigenvalues explained 81.3% of the total variance in the dataset. Bolded values represent “defining factors” for each axis based on eigenvectors $> |0.3|$; dashes indicate when eigenvectors are below this value for all three axes.

	Axis 1	Axis 2	Axis 3
Eigenvalues	3.9	3.3	1.9
Total variance (%)	33.4	29.6	18.3
Shrub cover (%)	-0.003	0.562	-0.053
Forb cover (%)	—	—	—
Grass cover (%)	—	—	—
Crested WG cover (%)	-0.120	-0.599	-0.169
Native grass cover (%)	—	—	—
Native forb cover (%)	—	—	—
Exotic forb cover (%)	0.031	-0.049	0.730
Annual cover (%)	—	—	—
Total vegetation cover (%)	0.474	0.064	-0.339
Diversity (H')	0.248	0.392	0.351
Biol. soil crust cover (%)	—	—	—
Bare ground (%)	-0.477	-0.136	0.341
Litter cover (%)	—	—	—
Rock cover (%)	—	—	—
Sand (%)	-0.491	0.242	-0.232
Silt (%)	0.479	-0.297	0.166
Clay (%)	—	—	—
Total soil carbon (%)	—	—	—
Total soil nitrogen (%)	—	—	—
Soil pH	—	—	—

Discussion

Our results demonstrate the wide variability in vegetation composition, plant diversity, and ground cover that can develop over the long term across a broad range of sites historically seeded with crested wheatgrass. Although highly variable, the 146 sites portrayed low cover of annual species and native forbs and an inverse relationship between shrub and crested wheatgrass cover. Low annual species cover contrasts with a previous study that found several historically seeded areas were dominated by the annual grass downy brome (*Bromus tectorum* L.) (Allen-Diaz and Bartolome 1998). However, low abundance of annual species and native forb cover in our study may be a consequence of a region-wide drought in 2006–2007, and we cannot rule out the potential for increased dominance of annual species on these sites in years with higher precipitation. Low cover of native forb species across our sampling sites is consistent with ecological site descriptions for many Wyoming big sagebrush plant communities, as well as other studies that report low persistence of forbs in crested wheatgrass seedings (Grant-Hoffman et al. 2012). Low native forbs may also be a consequence of cultural disturbances such as plowing and disking that limit their reestablishment (Morris et al. 2011; Morris et al. 2014). It is also possible that the low abundance of native forb species is a consequence of soil conditioning by crested wheatgrass that limits the growth of native forbs (Jordan et al. 2008; Perkins and Hatfield 2014) or insect herbivory on native forbs within crested wheatgrass seedings (Branson and Sword 2009). The strong inverse relationship we observed between shrub and crested wheatgrass cover across a broad range of sites also emphasizes the importance of competition in determining the relative abundance of grasses and shrubs in sagebrush ecosystems (Hull Jr. and Klomp 1974; Anderson and Inouye 2001) and counters the assumption that rehabilitation seedings conducted within Wyoming big sagebrush plant communities will remain in alternate vegetation states dominated by crested wheatgrass. Understanding the defining factors responsible for ecological site variation and plant community trajectories will greatly improve our ability to manage these lands in the future where land-use goals consider a broad array of ecosystem services.

Variation Among Sampling Sites

As expected, soil properties, particularly soil texture, explained most of the variation among sites. The abundance of shrub and crested wheatgrass cover across sites was primarily influenced by soil texture, with crested wheatgrass favoring silty sites and shrubs favoring more sandy sites. These results are likely a consequence of differences in soil preference between shrub and grass growth forms (Jensen 1990; Dodd et al. 2002) and agree with the observations that shrubs become dominant with increasing sand content or can replace herbaceous species as silt content is lost due to desertification in semiarid grasslands (Peters 2002; Li et al. 2006). Lower crested wheatgrass abundance on sandy soils may also be related to low water holding capacity, which is known to reduce its seedling emergence in shrub-steppe soils (Mangold and Sheley 2007). Furthermore, sand content and coarser soils were found to be negatively associated with total herbaceous productivity and soil water holding capacity across the Wyoming big sagebrush alliance in the northern Great Basin, United States (Davies et al. 2007; Reisner et al. 2013). Although a previous study in southwestern Montana, United States, concluded that soil texture was not a significant determinant of sagebrush reestablishment within crested wheatgrass seedings (Johnson and Payne 1968), our findings across a broader range of sites are consistent with a study in a sagebrush steppe plant community in the Colorado Plateau, United States, where differences in species composition between two ecological sites were primarily attributed to soil texture (Kachergis et al. 2012). Our results also agree with a study in southwest Texas, United States, that found woody plants quickly regained dominance on course-textured soils, but grasses

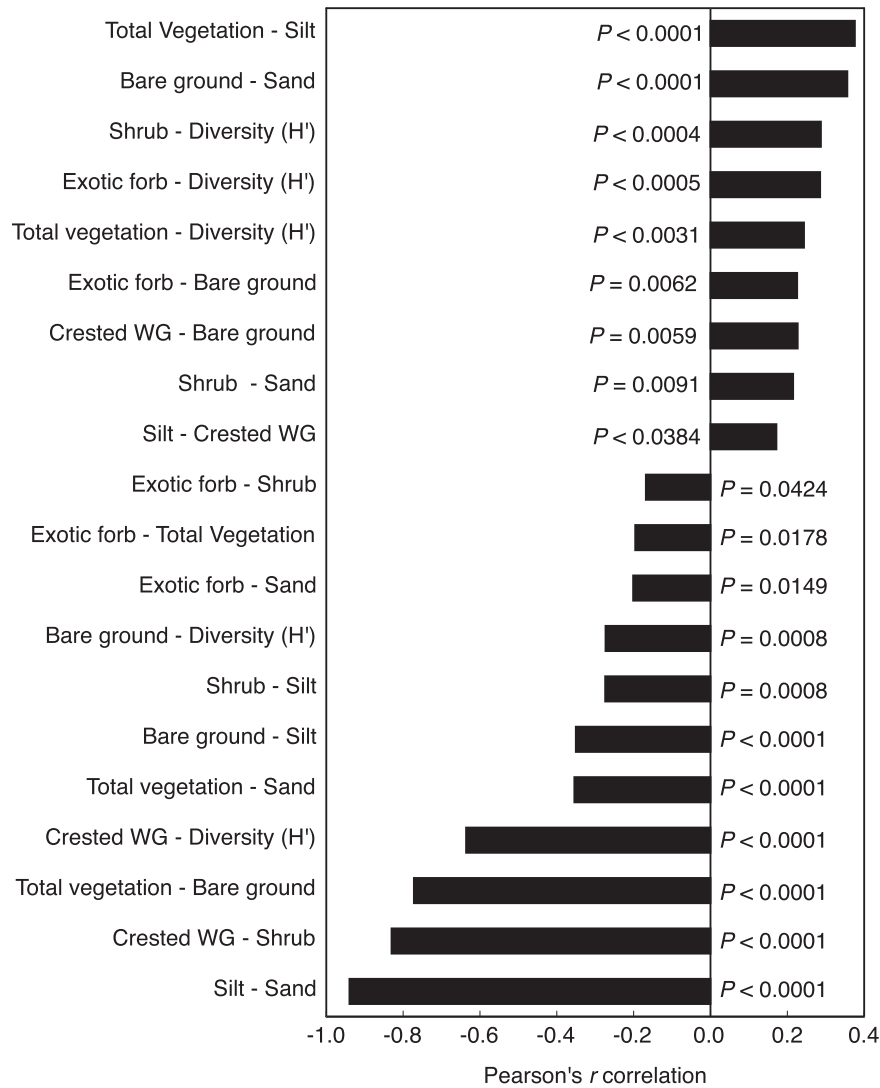


Figure 2. Pairwise correlations ($P < 0.05$) between “defining factors” (see Table 1) measured for 146 Wyoming big sagebrush sites historically seeded with crested wheatgrass in eastern Great Basin, United States.

continued dominance on fine-textured soils following uniform brush removal treatments (Wonkka et al. 2016).

Variation among sampling sites was also explained by the relationships among crested wheatgrass, bare ground, and species diversity. We attribute the positive correlation between crested wheatgrass and bare ground and the negative correlation between crested wheatgrass and species diversity to the competitive ability of crested wheatgrass (Evans et al. 1970; Gunnell et al. 2010). Crested wheatgrass regularly spaces itself, increasing bare ground (Rayburn and Monaco 2011), and is known to competitively exclude grasses, forb, and shrub species in many regions (Bakker and Wilson 2001; Grant-Hoffman et al. 2012; Lavin et al. 2013; Nafus et al. 2015). Furthermore, low species diversity within historical crested wheatgrass seedings is widely recognized in the central grasslands of North America (Henderson and Naeth 2005), and this pattern can last for several decades on sagebrush sites in central Utah, United States (Stevens 1987; Vernon et al. 2001). However, our results show that considerable variation in species diversity exists among study sites. Increasing cover of crested wheatgrass has previously been accompanied by direct declines in native plant species (Krzic et al. 2000; Heidinga and Wilson 2002), yet our results are the first to illustrate that a threshold possibly exists when vegetation is dominated by 30–40% crested wheatgrass cover (see Fig. 3, b). Our data indicate that species diversity slightly increases with crested wheatgrass cover

below this threshold, yet it steeply declines above this threshold, as crested wheatgrass becomes the dominant vegetation component.

Species diversity across the sampling sites in our study was primarily a function of the abundance of exotic forbs that showed affinity to bare ground. However, generally low native and exotic forb cover across our study sites is consistent with previous reports in crested wheatgrass seedings (Marlette and Anderson 1986; Johnson 2008) and may be a consequence of low establishment rates (Hull Jr. 1974), low persistence when seeded simultaneously with crested wheatgrass (Waldron et al. 2005; Grant-Hoffman et al. 2012), high competitive ability of crested wheatgrass (Leonard et al. 2008; Leffler et al. 2014), and soil conditioning by crested wheatgrass that facilitates its own growth and reduces growth of native forbs (Jordan et al. 2008). Although species diversification efforts in crested wheatgrass seedings have primarily focused on reestablishing sagebrush (Davies et al. 2013), overall paucity of native forb cover across our sites indicates that future efforts should also emphasize forbs given their recognized role in shrub steppe ecosystems (Pokorny et al. 2004; Parkinson et al. 2013). For example, greater sage-grouse (*Centrocercus urophasianus*) depend on forbs, as well as the insects associated with them, for the majority of their spring and early summer diet (Drut et al. 1994; Gregg et al. 2008; Dumroese et al. 2015). Forbs are also important for maintaining both species and genetic diversity of pollinators (Black et al. 2011) and reducing susceptibility

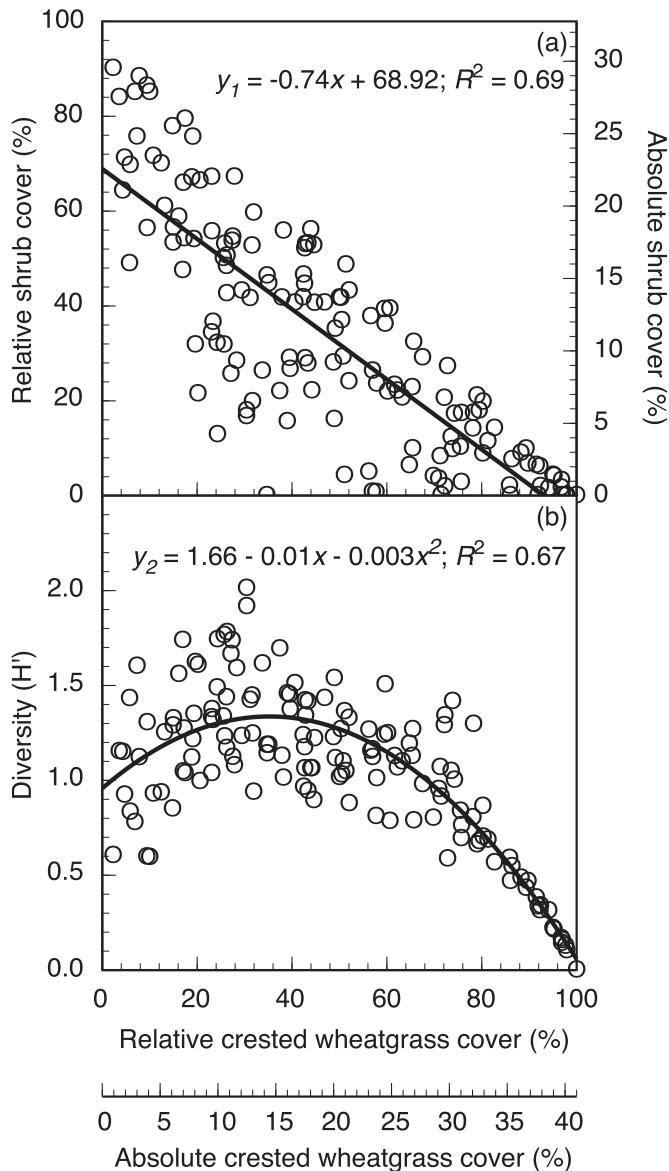


Figure 3. Linear and quadratic relationships between relative crested wheatgrass cover (x) and shrub cover (y_1 ; a) and Shannon-Wiener diversity (H') (y_2 ; b), respectively, for 146 sites historically seeded with crested wheatgrass in eastern Great Basin, United States. Labels scaled to absolute cover are shown for comparison with other reports. Both regressions represent significant best-fit predictions ($P < 0.0001$).

to invasion by non-native species (Chambers et al. 2007; Leffler et al. 2014; Leger et al. 2014).

Although our study design did not allow us to determine the underlying mechanisms responsible for the variation we observed among sites, previous studies report the strong influences of disturbance history (Nafus et al. 2016), current management, and environmental variation (Chase 2003; Hobbs et al. 2007; Kachergis et al. 2011; Evers et al. 2012; Grman et al. 2013). Interestingly, the primary defining factor in our study included soil texture, which can be either inherent to a site or altered by soil disturbances. Variation in soil texture has also been an indicator of historical land uses like cultivation (Morris et al. 2011; Kachergis et al. 2012). For example, plowing mixes soil (Morris et al. 2016) and increases soil sand content by subsequent wind erosion and loss of lighter soil fractions (Hull Jr. and Klomp 1967; Li et al. 2006). Variable effects of different land treatments associated with sagebrush reduction and seeding crested wheatgrass (e.g., plowing, herbicide, fire) can also influence plant community trajectories (Allen-

Diaz and Bartolome 1998; Kachergis et al. 2011; Ripplinger et al. 2015), yet further experimentation is needed to clarify their influence across our study area. We also suggest that variable plant community trajectories on historically seeded rangelands may be associated with the amount of site degradation that occurred before seeding, climatic differences among sites over time, size and age of the seeding (Johnson and Payne 1968; Nafus et al. 2016), and grazing management after seeding (Jackson and Hobbs 2009; Grman et al. 2013). Vegetation structure and species composition of Great Basin rangelands seeded with crested wheatgrass can also be dependent upon land-use history (Morris and Rowe 2014) and the kind of postseeding shrub reduction it received (Pellant and Lysne 2005; Gunnell et al. 2011). Finally, the long-term establishment of different crested wheatgrass cultivars and the influence of variable grazing pressure are two additional factors that may influence the successional trajectories of historical seedings (Asay et al. 2001; Iwaasa et al. 2014).

Management Implications

Our results reveal several important implications for management of historically seeded shrubland ecosystems. First, our results indicate that successional trajectories in the absence of confounding management factors in these seeded Wyoming big sagebrush communities are highly variable and primarily attributed to site differences in soil texture, as has been shown for numerous other semiarid regions. Consequently, the assumption that crested wheatgrass seedings will remain in a low diversity state and experience uniformly low sagebrush reestablishment is not supported by our results. Furthermore, future management to expedite sagebrush reestablishment within similar plant communities may experience greater success in sites with courser soils that better support shrubs (Jensen 1990; Dodd et al. 2002). Although we found clear evidence of sagebrush reestablishment among our study sites, we still lack a complete understanding of temporal dynamics of these recruitment processes and the influences of land-use history and environmental variation. Second, the broad range of variation in crested wheatgrass and sagebrush cover we observed across sites during the 43–63 yr after sagebrush removal and seeding may assist in the development of future state-and-transition models. For example, our results suggest that seeding in and of itself is not an irreversible transition to a resilient alternative state uniformly dominated by crested wheatgrass (Davies et al. 2011; Kachergis et al. 2011). Our results indicate that generalizations of how historically seeded Wyoming big sagebrush sites will respond over the long term should be avoided. Consequently, land managers should not assume that all historical seedings would respond similarly to management efforts (Kachergis et al. 2012). This suggestion particularly applies to diversification efforts within crested wheatgrass seedings to meet specific wildlife habitat needs (Pellant and Lysne 2005; McAdoo et al. 2013a). Lastly, given the long-term stability of introduced forage grasses in many semiarid regions in North America (Scasta et al. 2015), there is immense need to better understand ecological consequences of rehabilitation seedings in sagebrush ecosystems (Morris and Rowe 2014) and identify ways to best manage them for multiple ecosystem services (Allen-Diaz and Bartolome 1998; D'Antonio and Meyerson 2002; Nafus et al. 2015). Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.rama.2017.05.003>.

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