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Impact of Cultivation Legacies on Rehabilitation Seedings and Native Species Re-Establishment in Great Basin Shrublands

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Abstract

Little is known about how cultivation legacies affect the outcome of rehabilitation seedings in the Great Basin, even though both frequently co-occur on the same lands. Similarly, there is little known about how these legacies affect native species re-establishment into these seedings. We examined these legacy effects by comparing areas historically cultivated and seeded to adjacent areas that were seeded but never cultivated, for density of seeded crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) and native perennial grasses, vegetation cover, and ground cover. At half of the sites, historically cultivated areas had lower crested wheatgrass density ($P < 0.05$), and only one site had a higher density of crested wheatgrass ($P < 0.05$). Likewise, the native shrub Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young) had lower cover ($P < 0.05$) in historically cultivated areas at half the sites. Sandberg bluegrass (*Poa secunda* J. Presl.) density was consistently lower in historically cultivated areas relative to those seeded-only. At sites where black greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.) and bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey) were encountered, there was either no difference or a higher density and cover within historically cultivated areas ($P < 0.05$). Likewise, cover of exotic forbs, especially halogeton (*Halogeton glomeratus* [M. Bieb.] C. A. Mey.), was either not different or higher in historically cultivated areas ($P < 0.05$). Bare ground was greater in historically cultivated areas at three sites ($P < 0.05$). These results suggest that cultivation legacies can affect seeding success and re-establishment of native vegetation, and therefore should not be overlooked when selecting research sites or planning land treatments that include seeding and or management to achieve greater native species diversity.

Key Words: crested wheatgrass, exarable fields, land-use legacies, old fields, sagebrush, site history

INTRODUCTION

Despite calls over the last decade for more research into ecological consequences of historical land use, the link between land use and the outcome of restoration efforts remains one of the most poorly investigated topics in the field of restoration ecology (Kettle et al. 2000; Wu and Hobbs 2002; Brudvig 2011). Historical cultivation represents the most extensive and drastic of human land uses because, in comparison to the natural disturbance regimes (e.g., fire) under which ecosystems evolve, the disturbances associated with cultivation (e.g., plowing) are newly introduced to the ecosystem (McIntyre and Hobbs 1999). Therefore, cultivation can degrade both biotic and abiotic properties with ecological consequences (known as “legacies”) that last for decades to millennia (Foster et al. 2003; Cramer et al. 2008). Biotic degradation can alter the assembly of recolonizing native species and thus community assembly (Foster et al. 2003; Cramer et al. 2008). On the other hand, abiotic degradation can alter soil structure, chemistry, and water movement, and ultimately the performance of

colonizing species (Cramer et al. 2008). Plowing mixes soils, which can destroy soil structure, increase erosion potential and organic carbon and nutrient loss, and alter soil chemistry (e.g., pH and salinity), leaving a fundamentally altered abiotic habitat in old fields (McLaughlan 2006; Standish et al. 2006).

Research on cultivation legacies from former wheat-growing regions of Australia, Canada, and the United States reveal that community assembly can be altered for over half a century (Rickard and Sauer 1982; Dormaar and Smoliak 1985; Standish et al. 2007). Species dispersal mode and life history traits are important biotic determinants of these changes (Dyer 2010). For example, wind-dispersed species are sometimes the few native plants to consistently re-establish in old fields (Standish et al. 2006; Morris et al. 2011). Furthermore, because cultivation removes entire plants, species that primarily reproduce vegetatively are less likely to occupy old fields (Dyer 2010; Morris et al. 2011). Consequently, comparisons of vegetation abundance between old fields that have undergone secondary succession and native sites that have never been cultivated indicate that old fields contain lower shrub and forb cover and higher cover of early seral and exotic invasive plants (Rickard and Sauer 1982; Dormaar and Smoliak 1985; Standish et al. 2007). When exotic invasive grasses gain dominance in old fields, secondary succession is stalled for decades (Cramer et al. 2008). For example, the invasive annual grass cheatgrass (*Bromus tectorum* L.) has replaced the native perennial bunch grasses on old fields where it persists for over

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50 yr in the western United States (Daubenmire 1975; Elmore et al. 2006).

Cultivation legacies have received little scrutiny in the Great Basin in the United States, even though almost a half million hectares of shrubland were converted for wheat and cereal production in the early 20th century and then abandoned two decades later (Morris et al. 2011). For example, only two long-term studies from this region have contrasted vegetation between old fields and adjacent noncultivated land (Elmore et al. 2006; Morris et al. 2011). These studies, conducted on old fields where secondary succession proceeded for 80–90 yr after cultivation ceased, found lower abundances of forbs and the native shrub Wyoming big sagebrush, yet higher abundance of three native shrubs—black greasewood, yellow rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.), and rubber rabbitbrush (*Ericameria nauseosus* [Pall. ex Pursh] G. L. Nesom & Baird)—and the native grass bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey in old fields compared to nearby or adjacent noncultivated land. In contrast, no studies in this region have evaluated native species re-establishment within old fields where active revegetation was conducted after abandonment. This gap in understanding is surprising given the prevalence of rehabilitation seedings that were initiated in the 1930s across the region to revegetate abandoned crop land, stabilize erosion, increase forage production to support livestock in overgrazed areas, and control invasive species (Young and McKenzie 1982; Monsen and MacArthur 1995). This broadscale effort consisted of planting the exotic perennial crested wheatgrass for rehabilitation seedings, a widely successful species most commonly used for revegetation (Young and McKenzie 1982; Pellant et al. 2004; Gunnell et al. 2011). As a result, approximately 2 million ha in the western United States have been seeded with crested wheatgrass (Pellant and Lysne 2005), much of which overlaps old fields where the underlying cultivation history has been mostly forgotten.

Seeding remains a critical component of revegetation efforts in the Great Basin where millions of hectares require restoration (Pellant et al. 2004). Because historical cultivation can alter community assembly in these shrubland ecosystems with observable differences nearly a century later, it is possible that cultivation legacies could affect the outcome of seeding efforts and native species re-establishment. This presumption has not been explored previously in the Great Basin, but testing it has broad implications for improving our understanding of the potential limits to restoration success on old fields. Secondary succession is also an important predictor of the potential to restore diversity in this semiarid ecosystem (Allen 1995), yet studies on the re-establishment of native species into these seedings are lacking (Gunnell et al. 2011). An improved understanding of the factors that limit the success of rehabilitation seedings or native species reassembly within them in the Great Basin is also needed because seeding is an expensive management tool with unpredictable success and frequent failure (Rafferty and Young 2002; Pellant et al. 2004).

To examine if historical cultivation affects seeding success and plant community composition, we identified four areas in the eastern Great Basin where crested wheatgrass seedings overlapped adjacent previously cultivated and noncultivated land, so the dependent factors of soils, climate, historical cultivation practices, seeding methods, postseeding manage-

ment, and other land uses could be held constant. Because crested wheatgrass is broadly adapted to disturbed rangeland conditions in the Great Basin (Young and McKenzie 1982), we hypothesized that crested wheatgrass seedings would not be affected by cultivation legacies. However, given the influence of historical cultivation on secondary succession in Great Basin shrublands (Elmore et al. 2006; Morris et al. 2011), we hypothesized that re-establishment of some native species in old fields would be depressed, while recovery of other native species and exotic species might be facilitated by cultivation legacies.

METHODS

Study Area

Studies were conducted in the northern edge of the Great Basin floristic region in Park Valley, Utah. The average elevation of the Park Valley area, bordered by the Raft River mountain range to the north and the Grouse Creek mountain range on the west, is 1 680 m. Average annual temperatures can range from –18 to 33°C with an average annual precipitation of 25 cm. European settlement began in the late 1860s and early 1870s. Settlers introduced livestock grazing to the area, and the heaviest use occurred prior to the 1930s. In the early 1910s, a land boom associated with dry-land wheat farming spread across the region. As in other parts of the semiarid West, dry farming was not successful in Park Valley, and all of the dry farms were abandoned by the early 1920s (Morris and Monaco 2010; Morris et al. 2011). Many of these old fields were later seeded for rehabilitation using crested wheatgrass and other perennial grass species.

Site Selection and Paired Sets

Aerial photographs from the 1950s, 1970s, 1980s, and 2000s, verified against original homestead records, tract books, and land company records, were used to locate old fields that were dry-farmed for cereal production in the early 1910s and abandoned (Morris 2012). Aerial photos were also used to identify dry farms that had been seeded after abandonment and verified with federal records and property owner interviews. Four sites that offered at least one paired set where a seeding overlapped a formerly dry-farmed field (“dry-farmed + seeded” hereafter) and adjacent land that had never been dry-farmed but was seeded-only (“seeded-only” hereafter) were selected for this study (Fig. 1). All paired sets were located on the same slope, soil series, and within the same property ownership so that the age and methods for reseeded (e.g., equipment, time of planting, seeding rate) were always the same. According to archival documents and land owner interviews, these seedings were carried out using standard methods of the day, including tractor-drawn disc plows and rangeland drills (Young and McKenzie 1982). In addition, because the performance of a seeding is highly dependent upon postseeding management practices (Gunnell et al. 2011), consistent property ownership across the paired sets ensured that postseeding management (e.g., grazing, herbicide use) was also the same. Although replication is desirable, in retrospective studies, the “treatments” are applied historically and there is no control over the

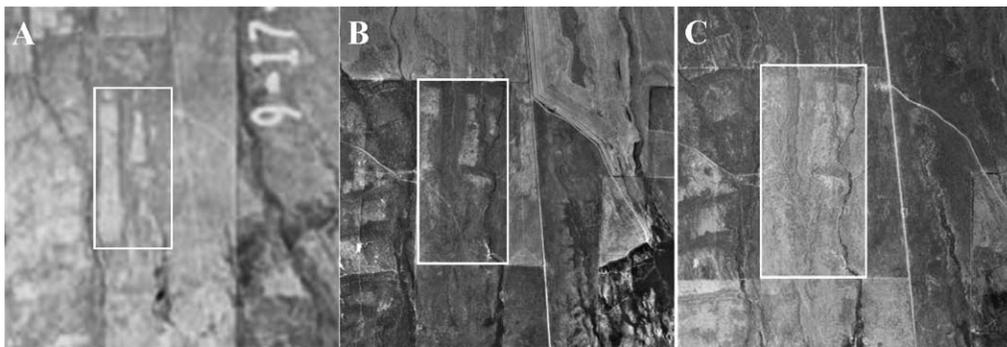


Figure 1. Aerial photographs showing how paired sets were located. Area within the white rectangle was the Grunder homestead, approximately 320 acres. **A**, Dry-farm fields are still visible in 1956 aerial image and **B**, in the 1999 aerial image. **C**, Although fields are slightly obscured, they are still recognizable after the seeding in the 2006 aerial image. This seeding, and others in our study, provide the opportunity to compare vegetation within seedings that overlap previously dry-farmed land (dry-farmed + seeded) and adjacent land that was never cultivated (seeded-only).

number of available sites. The strength of this design is the adjacent pairing of dry-farmed + seeded and seeded-only sites, which provides the closest comparison possible of the cultivation legacy, while controlling for most other variables such as soils, climate, historical cultivation practices, seeding methods, postseeding management, and other land uses (Homburg and Sandor 2011). The four sites were named after the patentee on the homestead (Grunder, Strevell and Taylor) or the land company who sold the property, Pacific Land and Water Company (PLWC) (Table 1). Where homesteaders established more than one field, more than one paired set was available (Grunder, $n=2$; Strevell, $n=1$; PLWC, $n=2$; and Taylor, $n=2$).

Vegetation Sampling and Data Analysis

We collected vegetation and ground cover measurements using 20-m transects ($n=10$) in each condition (dry-farmed + seeded and seeded-only) in June, 2010. Shrub canopy cover was recorded using line intercept (Canfield 1941), and foliar cover of understory vegetation and ground cover was recorded using single-point intercept (100 points per transect) (Bonham 1989). The starting point for each transect was selected randomly from aerial photos in Google Earth and located in the field using global positioning system (GPS) coordinates to ensure sampling was conducted within the boundaries of the old field. All transects were at least 50 m within an old field and away from fence lines or roads to avoid edge effects. Additionally, we selected three random locations along each transect ($n=30$) in each condition to record density of perennial grasses inside a 1-

m^2 frame. Attempts to normalize the data using various transformations were unsuccessful. Therefore, all of the vegetation and ground cover data from paired sets within a site were pooled and analyzed with Wilcoxon Rank Sums tests (JMP 8.0, SAS, Inc.).

RESULTS

Even though some of the sites were seeded with a mix of species, crested wheatgrass was the only surviving seeded perennial grass at all of the sites. There was less than 1% cover of native forbs across all sites and conditions (data not shown). At the Grunder site (Fig. 2), there was more bare ground ($n=20$; $Z=-4.34$, $P<0.05$), less litter ($n=20$; $Z=2.05$, $P<0.05$), less cheatgrass ($n=20$; $Z=1.77$, $P<0.10$), and less Wyoming big sagebrush cover in dry-farmed + seeded than in seeded-only conditions ($n=20$; $Z=1.96$, $P<0.05$). Conversely, there was five times more exotic forb cover ($n=20$; $Z=-4.36$, $P<0.001$) and nearly 10 times more black greasewood cover ($n=20$; $Z=-5.11$, $P<0.01$) in dry-farmed + seeded than in the seeded-only conditions. The density of crested wheatgrass was three times lower in the dry-farmed + seeded areas at this site ($n=60$; $Z=2.43$, $P<0.05$), and Sandberg bluegrass density was also lower ($n=60$; $Z=2.43$, $P<0.05$). The difference in seeding success between dry-farmed + seeded and seeded-only conditions at the Grunder site was strikingly visible on the landscape. In contrast, the Strevell site (Fig. 2) had no significant differences in ground or vegetation cover and a slightly higher density of crested wheatgrass in dry-farmed +

Table 1. Characteristics and history of the four sites used in this study (NRCS 1993, 2010).

Site name	Soil classification	Soil series	Potential plant community	Year dry farming initiated	Year of seeding
Grunder	coarse-loamy, mixed, superactive, mesic Durinodic Xeric Haplocalcid	Kunzler	Wyoming big sagebrush and black greasewood	1914	1992
Strevell	coarse-loamy, mixed, superactive, mesic Xeric Argidurid	Lembos	Wyoming big sagebrush and bluebunch wheatgrass	1914	1974
Public Land and Water Company (PLWC)	coarse-loamy, mixed, superactive, mesic Xeric Argidurid	Lembos	Wyoming big sagebrush and bluebunch wheatgrass	ca. 1911	1987
Taylor	coarse-loamy, mixed, superactive, mesic Xeric Argidurid	Lembos	Wyoming big sagebrush and bluebunch wheatgrass	1913 and 1914	2007

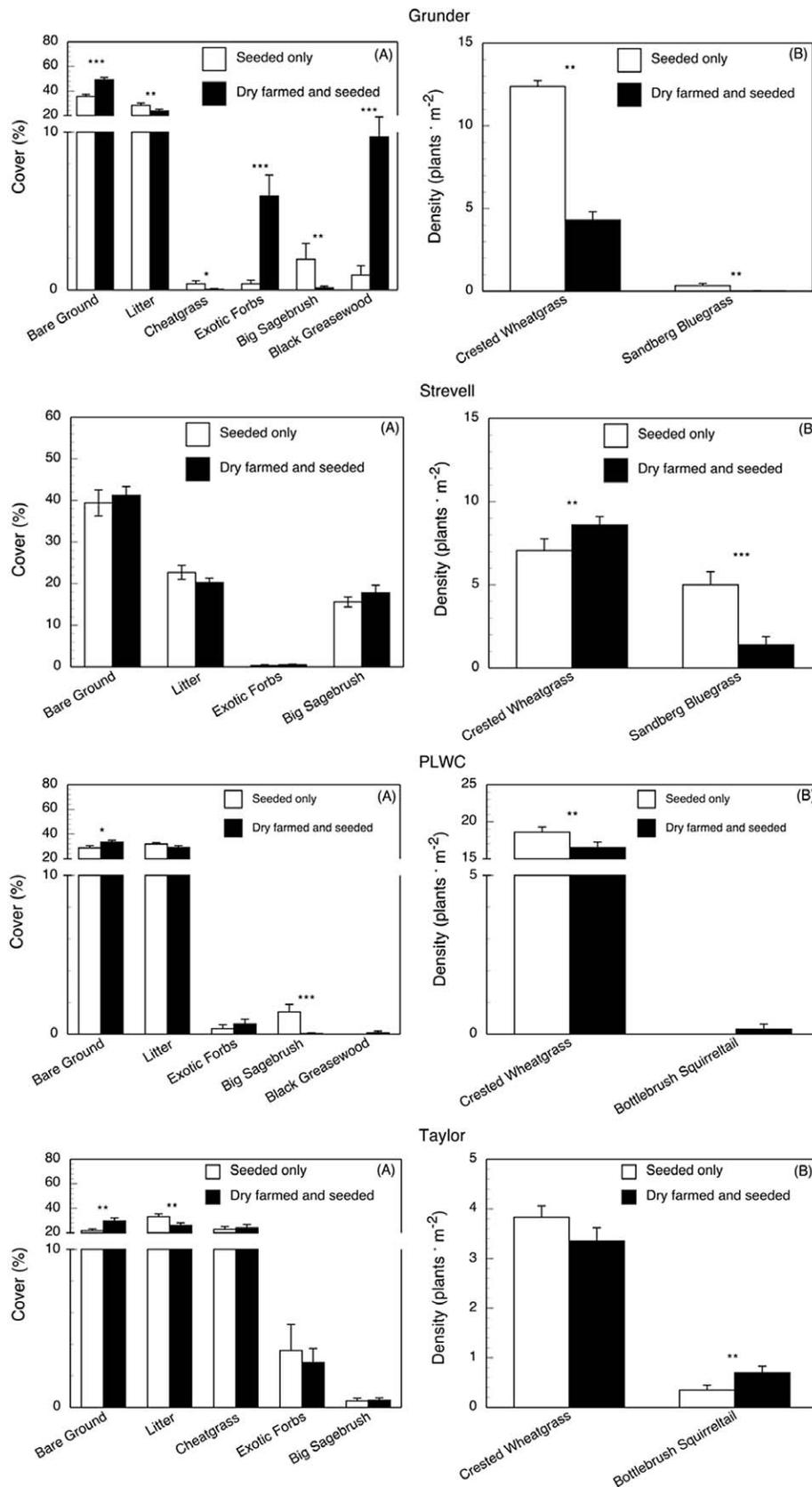


Figure 2. (A) Percent cover of bare ground, litter, and vegetation and (B) density of crested wheatgrass and native grasses for seeded-only and dry-farmed + seeded paired sets at four sites in the Great Basin. Asterisks indicate significance of Wilcoxon Rank Sums tests; * $P < 0.10$, ** $P < 0.05$, and *** $P < 0.01$.

seeded than in seeded-only condition ($n=30$; $Z=-2.10$, $P<0.05$). However, density of Sandberg bluegrass was three times lower in the dry-farmed + seeded condition ($n=30$; $Z=3.48$, $P<0.01$). The PLWC site (Fig. 2) had more bare ground ($n=20$; $Z=-1.75$, $P<0.10$), less big sagebrush ($n=20$; $Z=2.68$, $P<0.01$), and a lower density of crested wheatgrass ($n=60$; $Z=2.17$, $P<0.05$) in dry-farmed + seeded compared to seeded-only conditions. Bottlebrush squirreltail was only encountered in the dry-farmed + seeded areas at this site. Finally, the Taylor sites (Fig. 2) had significantly more bare ground ($n=20$; $Z=-2.49$, $P<0.05$) and less litter cover ($n=20$; $Z=2.09$, $P<0.05$) in dry-farmed + seeded than seeded-only conditions. Density of crested wheatgrass did not differ between the dry-farmed + seeded and seeded-only. However, there was a significantly higher density of bottlebrush squirreltail in the dry-farmed + seeded conditions ($n=60$; $Z=-2.17$, $P<0.05$).

DISCUSSION

Our first hypothesis, that crested wheatgrass seedings would not be affected by cultivation legacies, was not confirmed by results from the four sites. Alternatively, our results suggest that crested wheatgrass seedings can be affected by cultivation legacies, depending on site-specific factors. The hypothesis that community assembly of some native species in old fields can be hampered while recovery of others can be facilitated by cultivation legacies, was confirmed by our results. These results suggest that old fields might take even longer than seeded-only sites to diversify over time through secondary succession, an important factor for restoration planning (Cramer et al. 2008). Exotic species cover was greater in the most recent seedings, consistent with expectations that these species dominate early stages of postdisturbance succession. However, exotic forbs were most favored in the dry-farmed + seeded rather than seeded-only conditions at Grunder, even though the most recent soil disturbance associated with the seeding (i.e., disking) was completed at the same time and in the same manner across both conditions.

Although this study was not designed to make comparisons among sites, the patterns in ground cover were fairly consistent. Three of the four sites had more bare ground, and half of them trended toward less litter in dry-farmed + seeded sites than in seeded-only areas. The amounts of bare ground and litter cover are important ecological indicators of site stability (de Soyza et al. 2000). For example, more bare ground typically indicates greater potential for wind and water erosion and loss of soil resources (Weltz et al. 1998; de Soyza et al. 2000). Conversely, litter is a ground-cover variable highly correlated to reducing erosion potential on rangelands (Pierson et al. 2007). Reduced vegetation and litter cover can also lead to higher soil surface temperatures and increased soil moisture evaporation (Jury et al. 1991). Together, these patterns in ground cover can create feedbacks between abiotic properties of soils on previously dry-farmed + seeded areas that disfavor both seeded and native species.

Response of Crested Wheatgrass

Our finding that underlying cultivation legacies can affect the outcome of crested wheatgrass seedings is surprising, given its

long history of development and use in revegetation of old fields (Young and McKenzie 1982; Dormaar and Smoliak 1985; Monsen and MacArthur 1995). The only other study that reports the outcome of seeding on previously cultivated land in this region found greater crested wheatgrass cover on five previously cultivated seedings compared to seeded-only sites (Williams 2010). However, Williams (2010) did not make comparisons within the same soils, and because the previously cultivated seedings had higher silt fractions than noncultivated seedings, soil texture was credited with this outcome. Additional testing is needed to define which mechanisms might be limiting (or enhancing) the long-term performance of the crested wheatgrass. However, given the responses at our sites, we suspect these mechanisms will likely be related to altered abiotic factors in the soils, because cultivation is well known for producing legacies in soil physical and chemical properties (Standish et al. 2006). For example, cultivation has the tendency to raise soil pH as well as increase the content of salts and sodium on the surface due to mixing of soils with lower soil horizons where these values are higher (Cook 1961; Cronin and Williams 1966). Salinity can limit crested wheatgrass seeding establishment in rangelands, especially in greasewood plant communities where soils can have both saline and sodic conditions (Rollins et al. 1968). Soil chemical legacies might have played a role in the highly contrasting density of crested wheatgrass between dry-farmed + seeded and seeded-only conditions at the Grunder site, a moderately saline soil where exchangeable sodium percentage increases with depth (NRCS 2010). Finally, differences in historical cultivation practices and equipment can generate different land-use legacies, even across the same soil type (Coffin et al. 1996; Buisson and Dutoit 2004). Therefore, increased density of crested wheatgrass in the old field at Strevell and decreased density of crested wheatgrass in the old fields at PLWC could be due to differences in soil legacies created by differing farming practices.

Response of Native Species

Our results showed that community assembly of some native species in old fields is hampered, while recovery of others is facilitated by cultivation legacies, a finding consistent with old field studies in Australia (Cramer et al. 2008) and within the study region (Elmore et al. 2006; Morris et al. 2011). Higher bottlebrush squirreltail and black greasewood abundance but lower abundance of Sandberg bluegrass and Wyoming big sagebrush in the dry-farmed + seeded condition compared to seeded-only were consistent with their responses in previous studies on old fields (Elmore et al. 2006; Morris et al. 2011). Although more testing is required to address the mechanisms generating these patterns, we propose that the grass response is due to altered biotic factors (e.g., dispersal and seed banking). Greater density of the perennial grass bottlebrush squirreltail in the dry-farmed + seeded relative seeded-only condition has been observed before in this region and has been attributed to its wind dispersal (Hironaka and Tisdale 1963; Morris et al. 2011). The three-fold reduction in density of Sandberg bluegrass in our study is congruent with observations that cultivation slows re-establishment of this grass within the region (Hironaka and Tisdale 1963; Williams 2010; Morris et

al. 2011) and in cultivated grasslands in California (Stromberg and Griffin 1996). Sandberg bluegrass is one of the few perennial grasses in the Great Basin that form a substantial seed bank (Allen and Nowak 2008), which annual plowing could bury and deplete because the seed is relatively small and emergence is inhibited below 3 cm (Evans et al. 1977).

It is also possible that native shrub responses to cultivation are related to changes in abiotic factors (e.g., soil chemistry). When cultivation leads to higher pH, salinity, and sodicity, species with unique adaptations to these conditions will achieve greater colonization. For example, cultivation favors recolonization of black greasewood and slows the re-establishment of Wyoming big sagebrush (Morris et al. 2011). Old fields tend to have few if any species that reproduce vegetatively, because plowing destroys most of the root system (Dyer 2010). Black greasewood has the capacity to resprout from adventitious buds located in the root crown, yet its primary mode of colonization and reproduction is through seed (Robertson 1983). Black greasewood seeds have adaptive mechanisms that allow them to establish localized water potential gradients that create favorable conditions for germination in the presence of high salt concentrations (Romo and Eddleman 1985). In contrast to black greasewood, such changes in soil chemistry might disfavor Wyoming big sagebrush, which is less tolerant of saline and high pH soils than greasewood (Fireman and Hayward 1952). Future research should focus on the mechanism for these patterns in native species re-establishment.

Response of Exotic Species

Greater overall cover of exotic species in the most recently disturbed (i.e., seeded) sites, Taylor and Grunder, is consistent with generalizations about community assembly of disturbed areas. Cultivation often favors the abundance of annual exotic species because their life-history traits enable them to grow fast, produce abundant seed, and survive disturbance more so than longer-lived perennial species (Baker 1974; Campbell and Grime 1992). However, the fact that exotic forbs were favored in the previously dry-farmed + seeded conditions at the Grunder site in comparison to the seeded-only conditions indicates that cultivation legacies (possibly abiotic changes) might have altered community assembly because the most recent disturbance (disking for seeding) was performed at the same time, and in the same manner, across both conditions. Halogeton, the dominant exotic forb at the Grunder site, can be favored at disturbed sites, including old fields, because it is one of the few species that can tolerate the accumulation of salts and sodium moved from the lower soil horizons to the surface during cultivation (Williams 1960; Cronin and Williams 1966). Williams (2010) also found two-fold higher exotic herbaceous cover in previously cultivated crested wheatgrass seedings than in seeded-only sites.

IMPLICATIONS

Our study has several important implications for rehabilitation and restoration seeding in the Great Basin. First, negative responses of both seeded and native species to the legacy of cultivation demonstrates why the history and location of this land use should be considered a priori to conducting any study

or land management treatment. Our results suggest that the success of crested wheatgrass seedings can be affected by cultivation legacies. Because these legacies can influence crested wheatgrass, their potential to affect seeding success of native species should also be investigated. In addition, researchers should determine cultivation history of study and restoration sites so that seeding techniques are not inadvertently confounded with cultivation legacies, a task that can be accomplished using internet search (Morris 2012). Because land-use legacies create differences in initial conditions in vegetation and soils, failure to account for these differences will lead to misinterpretation of management and treatment effects (Kettle et al. 2000; Anderson 2008). Second, unassisted succession of native species into crested wheatgrass seedings that were previously cultivated can take longer than sites that were seeded-only because altered biotic and abiotic factors can continue to favor exotic invasive species in some locations. Understanding these relationships will be important as diversification of crested wheatgrass seedings is pursued in the Great Basin (Fansler and Mangold 2011). Finally, the potential for cultivation legacies to remain for nearly a century in sagebrush ecosystems of the Great Basin (Elmore et al. 2006; Morris et al. 2011), in combination with the results from this study, raise important questions about whether or not additional soil disturbances from seeding (e.g., plowing, tilling, and disking) have cumulative impacts on biotic and abiotic processes that further delay re-establishment of native species diversity.

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