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Assessment of Restoration Seedings on Utah Watershed Restoration Initiative Project Sites

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Lacey E. Wilder

ASSESSMENT OF RESTORATION SEEDINGS ON UTAH WATERSHED RESORTATION INITIATIVE PROJECT SITES

by

Lacey E. Wilder

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

Dr. Kari E. Veblen, Ph.D. Major Professor	Dr. Thomas A. Monaco, Ph.D. Committee Member
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UTAH STATE UNIVERSITY
Logan, Utah

2017

ABSTRACT

Assessment of Restoration Seedings on Utah Watershed Restoration Initiative Project Sites

by

Lacey E. Wilder, Master of Science

Utah State University, 2017

Academic Advisor: Dr. Kari E. Veblen
Research Advisor: Dr. Thomas A. Monaco
Department: Wildland Resources

Currently the United States is facing trend of woody species overabundance; specifically in the Western United States the growing amounts of sagebrush, *Artemisia tridentata,* is degrading understory herbaceous vegetation. This pattern requires shrub reduction and seeding to recover ecosystem services. However, there are several complications with shrub reduction treatments, contemporary shrub reduction treatments vary in how they influence soil surface and seedbed conditions and they have variable effects on seeded species performance. It remains unclear which plant species perform best with specific shrub reduction treatments as well as how characteristics of the restoration sites influence seeding success. To address this concern we calculated changes in seeded species abundance following the effects of burning and mechanical shrub reduction treatments. We followed the performance of 15 commonly seeded species at 63 restoration sites across Utah. This study was followed for up to ten years to record two post-treatment timeframes affects on species abundance (1-4 years and 5-10 years). Native shrubs did not increase across these restoration sites, large increases in perennial grasses over time suggest that seeding efforts contributed to enhancing understory herbaceous conditions. While increases in perennial grasses signal the possibility that interference among seeded species may have influenced the results of our assessment.

We then evaluated germination patterns of six commonly seeded restoration species in soils from Wyoming big sagebrush (*A. t.* ssp. *wyomingensis* [Beetle & A. Young] S.L. Welsh) and mountain big sagebrush (*A. t.* ssp. *vaseyana* [Rydb.] Beetle) plant communities that differ in soil texture and soil organic matter. We devised a novel experimental design by regularly wetting soils to a standardized soil water potential (i.e., field capacity; -0.03 MPa) and allowing soil moisture contents to variably fluctuate. Resulting in inherent differences in soil texture and OM between vaseyana and wyomingensis soils translate into fundamental differences in soil water holding capacity. Although species collectively exhibited greater germination in vaseyana soils than wyominensis soil and differences between soils became more pronounced under low soil water, patterns were vastly different among species. My results also highlight that broad differences exist in emergence patterns between species within the same functional groups.

(93 pages)

PUBLIC ABSTRACT

Assessment of Restoration Seedings on Utah Watershed Restoration Initiative Project Sites

Lacey E. Wilder

Overabundance of shrubs poses a major threat to semiarid ecosystems due to degraded understory vegetation. Previous efforts suggest a need for greater understanding of which management practices work best to improve these ecosystems. I sought to develop a better understanding of how the relative performance of commonly seeded species is influenced by three sagebrush removal techniques.

I calculated effect sizes for cover and frequency to estimate relative changes in abundance of 15 common plant species seeded at 63 restoration sites throughout Utah. Shrubs were reduced by fire or mechanical treatment. Effect sizes were assessed using meta-analysis techniques for two post-treatment timeframes. Introduced grasses and shrubs had greater increases in cover and frequency following treatment, respectively. The introduced shrub *Bassia prostrata* experienced the largest increases in abundance following treatments. Forb abundance was highest when treated with fire. Over the long term the fire treatment resulted in greater increases for four of the seven grass species. Large increases in perennial grasses over time suggest that seeding efforts contributed to enhancing understory herbaceous conditions. My results provide new insights regarding the interactive effects of species and shrub-reduction treatments.

Secondly, I evaluated emergence patterns of six commonly seeded restoration species in soils collected from Wyoming big sagebrush (*A. t.* ssp. *wyomingensis* [Beetle & A. Young] S.L. Welsh) and mountain big sagebrush (*A. t.* ssp. *vaseyana* [Rydb.] Beetle) plant communities. I developed a novel experimental design that regularly wetted soils to field capacity and allowed them to naturally dry by evaporation, which resulted in distinct differences in the duration of wet-dry cycles. Results showed that inherent differences in soil texture and organic matter between vaseyana and wyomingensis soils translated into fundamental differences in soil water holding capacity. Although species collectively exhibited greater emergence in vaseyana soils than wyomingensis soil, patterns were vastly different among species and differences between soils became more pronounced under low soil water for two of the test species. I concluded that the manner in which soils and water uniquely influenced emergence patterns provide new insights in species suitability for restoration sites and how inherent soil differences may constrain seeding success.

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Lacey E. Wilder

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CHAPTER 1

INTRODUCTION

Woody species, such as big sagebrush (*Artemisia tridentata* Nutt), have become overabundant in many semiarid ecosystems in the Intermountain Western United States. This shift in vegetation has resulted in degraded understory conditions, including reduced abundance of small-statured shrub plants and herbaceous species (Archer and Predick, 2014). Such degradation of understory conditions has been linked to reduced forage for livestock grazing, poor wildlife habitat, increased soil erosion, (Miller et al., 2014; Chambers et al., 2017), lack of soil stability, and invasion by exotic annual grasses that perpetuate increases in wildfire frequency (D’Antonio and Vitousek, 1992; Van Auken, 2009; Eldridge et al., 2011). To remedy these problems, land managers typically apply shrub-reduction treatments in combination with seeding, but degraded understory conditions and environmental constraints can make it difficult for new species to establish and survive (Ravi et al., 2009; Pierson et al., 2011). Considerable research effort has focused on identifying effective methods of shrub reduction and evaluating suitable restoration species (Archer et al., 2011). In addition, guidelines exist to help restoration practitioners assess restoration sites and choose appropriate management techniques (Pyke et al., 2015). However, there is a tremendous need to comprehensively evaluate *in situ* restoration projects at realistic operational scales to identify the relative performance of seeded species over both the short- and long-term timeframes.

Shrub reduction treatments have not consistently yielded desired improvements in understory vegetation (Miller et al., 2014; Pyke et al., 2015), and shrub density often rapidly returns to pre-treatment levels (Archer et al., 2011). Variable results have been attributed to differences in climate, as well as post-treatment grazing and browsing (Archer et al., 2011; 2017). This is particularly the case for semiarid shrublands and shrub-steppe ecosystems in the Intermountain Region of North America, where pairing among appropriate treatments, adapted seeded species, and restoration sites are not clearly understood (Monsen, 2004; Miller et al., 2014; Brabec et al., 2015). Furthermore, shrub reduction treatments differ in their capacity to create suitable conditions for establishment and persistence of certain species due to contrasting effects on soil surface conditions as well as resource availability (Young et al., 1990; Monsen and Stevens, 2004; Montalvo et al., 2002). This uncertainty can be addressed by retrospectively evaluating past restoration efforts to better understand how disparate treatments influence establishment of seeded species (i.e., Pyke et al., 2013; Knutson et al., 2014; Monaco et al., 2017).

Shrubland and shrub-steppe ecosystems in the western United States have historically been managed to increase perennial herbaceous vegetation to support forage production for livestock, improve wildlife habitat, and reduce fuel loads to prevent wildfires (Hirsch et al., 2012; Hufford and Mealer, 2014; Miller et al., 2014; Dahlgren et al., 2015). Such measures often entail reducing shrub density and cover and seeding of herbaceous species to restore degraded understory vegetation and prevent the invasion by exotic annual species and improve watershed functioning (Miller et al., 2014; Redmond et al., 2014). Without such forms of intervention, degraded sites can experience proliferation of invasive annual grasses that can drive disturbance regimes and impact numerous ecosystem processes (e.g., Hirsch et al., 2012; Miller et al., 2014).

Perhaps the biggest challenge to restoring degraded understory conditions is devising a management scenario that does not lead to further ecosystem degradation. For example, restoration activities can often lead to unintended, negative consequences because some level of disturbance or stress must be applied to the ecosystem in order to reduce shrub dominance and create suitable seedbed conditions for seeded species (Monsen and Stevens, 2004). Thus, because both risk and uncertainty exist when applying restoration treatments to an already degraded system, practitioners must possess a robust understanding of complex ecological processes when developing treatment choices (Leffler and Sheley, 2012). Nonetheless, disturbances are needed that create or mimic natural conditions for the establishment of seeded species (Call and Roundy, 1991). When these conditions are not met, seeded species will not successfully establish and soil disturbances can promote invasion by exotic species that already reside in the ecosystem (Chambers et al., 2017). Gaining knowledge about suitable seedbed conditions for seeded species as well as how treatments support these conditions should be a primary research endeavor, yet we know very little about how consistently these two entities converge when restoration efforts are applied to enhance degraded understory vegetation (Knutson et al., 2014; Germino et al., 2015).

Resilience concepts applied to shrubland and shrub-steppe plant communities in the Intermountain West suggest that a clear dichotomy exists among sagebrush ecosystems such that productive, cold-moist sites that occur at higher elevation are more resilient to environmental perturbations than less productive, warm-dry sites that occur at lower elevation (Chambers et al., 2014). Variation in soils over this gradient may also be responsible for resilience differences among sites, yet the influences of soil properties such as texture, organic matter, and water holding capacity on seedling emergence of common restoration species have not been evaluated. Inquiry into how inherent soil properties influence this critical aspect of restoration will provide new insights into ecosystem resilience and give practical information about species suitability.

OBJECTIVES

My thesis research consisted of a comprehensive assessment of combined shrub reduction-seeding treatments applied at 63 sites throughout Utah between 2003 and 2013 (Study 1) as well as controlled experiments to explore the influence of soils on the emergence of six commonly seeded species (Study 2). For Study 1, I compiled a long-term dataset from the Utah Watershed Restoration Initiative (UWRI) project that included three shrub reduction techniques and 15 different seeded species. My objective was to clarify how shrub reduction treatments influence changes in species abundance (i.e., frequency and cover) in both the short (1-4 yr) and long term (5-10 yr) and address two questions: 1) Do burning and mechanical treatments (aerator and pipe harrow) differentially influence the relative abundance of seeded species? 2) Do native and introduced species differ in relative abundance following shrub reduction? For Study 2, I collected soils from two commonly seeded big sagebrush plant communities in Utah (wyomingensis; dominated by *Artemisia tridentata* ssp. *wyomingensis* [Beetle & A. Young] S.L. Welsh and vaseyana; dominated by *A. t.* ssp. *vaseyana* [Rydb.] Beetle) and conducted experiments to explore how differences in soil texture and organic matter influence emergence patterns. I tested the following two hypotheses: 1) greater water holding capacity of vaseyana soil would result in higher emergence rates, and that 2) this pattern would be more pronounced under low soil water content due to higher evaporation rates in wyomingensis soils.

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CHAPTER 2

INFLUENCES OF BURNING AND MECHANICAL SAGEBRUSH REDUCTION TREATMENTS ON RESTORATION SEEDINGS IN UTAH

ABSTRACT

Overabundance of woody plants in semiarid ecosystems degrades understory herbaceous vegetation and often requires shrub reduction and seeding to recover ecosystem services. However, contemporary shrub reduction treatments vary in how they influence soil surface and seedbed conditions, which in turn have variable effects on seeded species performance. Consequently, it remains unclear which plant species perform best with specific shrub reduction treatments as well as how characteristics of the restoration sites influence seeding success. We calculated changes in seeded species abundance (i.e., frequency and cover) and used meta-analysis techniques to assess the effects of burning and one of two mechanical shrub reduction treatments (i.e., aerator and pipe harrow) on the relative performance of 15 commonly seeded species (comprised of three functional groups; grasses, forbs and shrubs) at 63 restoration sites across five, Level III Ecoregions throughout Utah. Abundance was assessed during two post-treatment timeframes, including short term (1-4 years) and long term (5-10 years). The magnitude of treatment effects on the abundance of seeded species was significantly larger for introduced grasses and shrubs compared to native counterparts. Native grasses and introduced shrubs increased over time, yet the abundance of native shrubs did not change significantly regardless of shrub reduction treatment; however, the introduced shrub *Bassia prostrata* experienced the largest increases in abundance during both timeframes. Forb abundance in the short term was generally lowest in the aerator treatment and highest in the fire treatment followed by the harrow treatment; forb abundance was also highest for the fire treatment in the long term. In general, shrub reduction treatments had similar effects on grass abundance, but over the long term, the fire treatment resulted a greater response compared to the other treatments for four of the seven grass species. Although native shrubs did not increase across this broad array of restoration sites, large increases in perennial grasses over time suggest that seeding efforts contributed to enhancing understory herbaceous conditions. Increases in perennial grasses, coupled with the extraordinary increases in *B. prostrata* (regardless of treatment) signal the possibility that interference among seeded species may have influenced the results of our assessment. Further research is needed to understand the causes of forb mortality over time as well as decipher how greater abundance of introduced species will influence species diversity and successional trajectories of restoration sites.

INTRODUCTION

Increased woody plant dominance is one of the most pronounced and widespread vegetation shifts within dry-land ecosystems in the last century, and these shifts have negatively impacted understory herbaceous vegetation, habitat suitability for wildlife, forage for livestock, and hydrological functioning (Van Auken, 2009; Eldridge et al., 2011; Wilcox and Thurow, 2006). When woody plants become overabundant in semiarid dry-land ecosystems, as manifested by shrub densities exceeding historical ranges of variation, numerous ecosystem services, such as soil nutrients and soil stability are compromised (Bestelmeyer and Briske, 2012; Archer and Predick, 2014; Wilcox et al., 2017). In addition, soil erosion can increase as a result of degraded understory herbaceous vegetation, which often results in lower restoration potential (Ravi et al., 2009; Pierson et al., 2011). Consequently, remediating herbaceous understory vegetation and achieving a desired shrub density is a major land management challenge (Archer et al., 2017), and often requires land managers to simultaneously reduce shrub abundance and seed restoration sites with a mix of suitable species (Chambers et al., 2014; Knutson et al., 2014; Redmond et al., 2014; Hardegree et al., 2016). However, this restoration strategy relies on the pivotal assumption that shrub reduction treatments will increase resource availability for seeded species as well as support understory species growth. Accordingly, recovery of ecosystem services may become contingent on the success of seedings (Monsen, 2004; Staub et al., 2016), yet a clear understanding of the manifold interactions between shrub reduction treatments and seeded species abundance on such sites does not currently exist (Miller et al., 2014; Pyke et al., 2015).

The fact that shrub reduction has not consistently enhanced understory herbaceous vegetation in many dry-land ecosystems beckons a careful examination of how various treatments influence the factors known to control the success of restoration seedings (Chambers, 2000; Beck et al., 2012; Archer and Predick, 2014). Shrub reduction treatments may differ in their capacity to create suitable conditions for establishment and persistence of certain species due to contrasting effects on soil surface conditions as well as resource availability (Young et al., 1990; Monsen and Stevens, 2004; Montalvo et al., 2002). For example, mechanical shrub removal techniques disturb soil surfaces to a greater extent than non-mechanical treatments such as fire and herbicide treatments (Condon et al., 2011; Chambers et al., 2014). While mechanical treatments are effective at creating furrows and pits that modify hydrology (water infiltration) and improve establishment of seeded species (Hardegree et al., 2016), they also run the risk of proliferating invasive annual species in the short term (Archer and Predick, 2014; Monaco et al., 2017) and can cause excessive loosening of seedbed firmness and soil friability, thereby compromising the success of seedings by altering the depth of seed placement (Monsen and Stevens, 2004). In contrast, the application of fire treatments to burn woody species are typically effective and low cost, yet depending on burn intensity, litter and seeds on the soil surface can be entirely consumed, reducing native seed banks and increasing the erosion potential of treated sites (Frischknecht and Plummer, 1955; Pierson et al., 2013). Fire treatments can also produce resins and waxes that, when deposited on soil surfaces, can create water-repellent soil layers that limit soil water infiltration, increase soil erosion and runoff (DeBano, 2000; Beyers, 2004), and inhibit of seeded species (Miller et al., 2013; Ellsworth et al., 2016). Mechanical and fire treatments can also vary widely in how they impact the resource pools available to residual species in the plant community and, in turn, the seeded species (Leffler and Ryel, 2012; Roundy et al., 2014). Soil water and nutrient availabilities for herbaceous vegetation typically increase following shrub reduction in semiarid shrub and woodland ecosystems (Miller et al., 2014; Rau et al., 2014; Roundy et al., 2014). However, changes in herbaceous production varies with time since treatment (Archer and Predick, 2014) and competition for these resources remain intense (e.g., Blaisdell, 1949), creating a strong biotic filter mediating abundance of seeded species as well as the assembly of post-treatment plant communities (Keddy and Shipley, 1989; Pyke and Archer, 1991; Hulvey and Aigner, 2014).

Numerous shrub reduction and seeding treatments have been explored for semiarid shrublands and shrub-steppe ecosystems, yet much of what we know stems from specific treatments applied to a limited number of sites (Monsen, 2004; Miller et al., 2014; Brabec et al., 2015) and few studies consider treatment and species interactions among functional groups (i.e., shrubs, forbs, grasses) simultaneously across broad ecological regions. Diverse seed mixtures are deemed necessary to increase species diversity, rapidly stabilize soils, and prevent the spread of invasive species (Burton et al., 2006; Sheley and Half, 2006; Davies et al., 2014). Consequently, identifying appropriate seeded-species mixtures that work best with specific shrub reduction treatments will help characterize species and treatment interactions (Knutson et al., 2014; Redmond et al., 2014). While establishment success and subsequent increases in species abundance over time depend on a complex interaction among species in the mix, species traits, and site suitability for individual species (Jones and Johnson, 1998; Monsen, 2004; Calvino-Cancela, 2011), we still know very little about these interactions despite years of site-specific evaluations (Hull, 1971; Keller, 1979; Stevens, 1983). Specifically, there is need to identify general patterns of seeding success and failure among functional groups, so that seed mixtures, seeding techniques, and long-term management efforts can be enhanced and undergo further testing (Jones et al., 2010, Jones et al., 2015; Hardegree et al., 2016). In addition, the relative merits and ecological implications of seeding native and introduced mixes are equally complex (Asay et al., 2001; Pyke et al., 2013; Knutson et al., 2014). In order to refine management options and produce the greatest long-term species diversity of seeded sites (Leger and Baughman, 2015), research is needed to understand interactions among species within native-introduced seed mixes. For example, introduced species may establish more rapidly and interfere with the establishment and growth of native species that exhibit less vigorous seedling growth and development (Waldron et al., 2005; Thompson et al., 2006; Nafus et al., 2016).

Although combined application of shrub reduction treatment and post-treatment seeding is a major component of ecosystem management to enhance herbaceous vegetation in the Western United States (McIver et al., 2014; Redmond et al., 2014), generalizations regarding the relative success of treatments and species combinations are still lacking. To address this need, we examined 63 restoration sites where shrubs were reduced with fire, aerator, and pipe harrow treatments with the goal of identifying patterns in short- and long-term changes in the abundance of species and functional groups (e.g., shrubs, forbs, grasses). We asked the following questions: 1) Do burning and mechanical treatments (aerator and pipe harrow) differentially influence the relative abundance of seeded species? 2) Do native and introduced species differ in relative abundance following shrub reduction?

METHODS AND MATERIALS

To assess the relative performance of seeded species following the application of shrub reduction treatments in Utah, USA, we used data accumulated from Utah Watershed Restoration Initiative (UWRI) project (http://wildlife.utah.gov/range/). The UWRI is a collaborative effort among landowners, private organizations, and state and federal agencies to enhance wildlife and biological diversity and water quality and yield through management approaches such as mechanical vegetation manipulations (UWRI; http://wildlife.utah.gov/watersheds/). Over 1,000 hectares were treated and seeded in Utah between 2003 and 2013 as part of UWRI.

After reviewing metadata from 1,438 completed restoration project sites associated with the UWRI (as of 2013), we selected projects that met the following criteria: 1) both shrub reduction and seeding treatments were applied and 2) both pre- and post-treatment data were available for analysis, with post-treatment data comprised of either short term (1-4 years), long term, (5-10 years), or both timeframes. A total of 63 project sites met these criteria (Table 1); accordingly, we acquired the seeded species list and compiled pre- and post-treatment data that were collected by the Utah Big Game Range Trend Studies Project (Utah Division of Wildlife Resources [DWR]; http://wildlife.utah.gov/range/). Shrub reduction treatments for the 63 sites were categorized as mechanical (aerator and pipe harrow) or fire (natural and prescribed fire). Each project site was also seeded with a custom mix of species deemed most suitable for the environmental, soil, and vegetation conditions, yet a total of 15 perennial species were most commonly seeded for our selection of 63 sites (Table 2). These 15 species included three shrubs, five forbs, and seven grasses (Table 1).

The two mechanical treatments were applied as implements pulled by a rubbertreaded tractor. The aerator consisted of a double drum roller with affixed blades that penetrate the soil and create shallow depressions for water catchment while simultaneously crushing and chopping (RanchWorx®, Palm Harbor, FL, USA). Thus, the aerator roller has low surface disturbance, promotes water infiltration, and creates furrows to trap water and seeds. In contrast, the pipe harrow (regionally known as Dixie Harrow) consists of a series of 2 m x 10 cm diameter pipes with spikes arranged at alternating angles to rip shrubs and cause considerable scarification and disturbance to the soil surface as debris is dragged (Dahlgren et al., 2006). When pulled, the pipes spin, causing the spikes to grade into the soil surface, removing shrubs and breaking up the soil surface. Finally, unlike the two mechanical shrub reduction treatments, fire treatments had little control over fire intensity and the continuity of burned area across sites. Depending on available fuel and subsequent fire intensity, fires typically burn through the vegetation and may also burn the soil surface, consuming seeds and litter. However, most fires typically do not greatly disturb soils other than how it influences litter and duff on the soil surface.

Project sites were primarily seeded using a broadcast method; 46 of the 63 sites dispersed the seed mix from a seed box mounted in front of the rear drum (aerator) or directly from the tractor (pipe harrow). On seven of the 63 sites, a rangeland drill was used for seeding when sites contained fewer standing shrubs (e.g., after fire) and rock obstacles (Appendix 1). Finally, aerial seeding was applied for the remaining 10 sites over rough terrain inaccessible to large ground equipment, or when project sites were subsequently seeded as part of large-scale rehabilitation effort and ground equipment was impractical. Although seed mixes varied among sites, they typically contained a mixture of perennial grasses, forbs, and shrubs.

Pre- and post-treatment cover (grasses and forbs) and frequency (shrubs) of seeded species were monitored with a standard protocol used by the UDWR Range Trend Studies Project (wildlife.utah.gov/about-range-trend). Each site was sampled by establishing one 152.4-m baseline transect in the treatment area. Along this baseline transect, five, 30.5 m belts were placed perpendicularly at predetermined positions (3.4 m, 40.8 m, 78.9 m, 113.0 m, and 150.9 m). A steel stake was placed at the beginning of each belt to ensure consistent placement of future sampling. Vegetation was monitored along each of the five belts within 20, 25 cm x 25 cm nested frequency quadrant frames placed at 1.5 m intervals. Frames were customized with clear markings indicating five nested areas of increasing space: 1) 1%, 2) 5 %, 3) 25 %, 4) 50 %, and 5) 100 %. Using these markings, percentage foliar cover of grass and forb species was estimated visually by assigning species to one of seven possible cover classes: 1) 0.01-1 %, 2) 1.1-5 %, 3) 5.1-25 %, 4) 25.1-50 %, 5) 50.1-75 %, 6) 75.1-95 %, and 7) 95.1-100 %). In addition, shrub abundance was estimated by searching nested areas 1-5 and recording the first area that contained a rooted plant; smaller areas were scored higher, such that nested areas 1-5 were scored from 5-1, respectively. The resulting estimate, nested frequency, was deemed a better source of data to assess seeded shrubs because foliar cover data included mature shrubs that had not been seeded, yet they contained canopies that overtopped smaller seedlings. For each species, we calculated average percentage cover (based on midpoint cover class values) and nested frequency (based on summed scores for each belt) and accompanying standard deviations for each site (*n* = 5).

Statistical Analysis

Mean and standard deviation data for seeded species abundance from the 63 project sites were analyzed using meta-analysis procedures (Gurevitch and Hedges, 1999). Pre- and post-treatment data were used to calculate individual effect size estimates for the predetermined seeded species at each project site for short term (1-4 yr), long term (5-10 yr), or both post-treatment timeframes. Effect sizes were calculated as the natural log of the ratio between post- and pre-treatment (ln[post/pre] = lnRR). Due to inconsistent monitoring years and seeding mix composition, different project sites did not generate effect sizes for the same species and timeframes (Table 1).

Effect sizes were analyzed with R (www.r-project.org) in the RStudio console (www.rstudio.com). Specifically, we used the metafor package to perform meta-analysis with the RMA function (Viechtbauer, 2010) and fixed-effect models to independently evaluate the influence of five moderators (i.e., functional group, species origin, shrub reduction treatment, seeded species identity, and treatment x species) on seeded species abundance. We analyzed fixed-effect models, which make conditional inferences (i.e., only to the set of sites included in the meta-analysis) and used unweighted mean estimates of the true effect sizes (Hedges and Vevea, 1998). These mean lnRR estimates were graphed with 95% confidence intervals to visually compare effects (Nakagawa and Cuthill, 2007). Due to all forbs being introduced species, the effect of origin was analyzed for the grasses and shrubs only. Actual pre- and post-treatment cover and nested frequency values (i.e., mean ± SE) were also summarized by species for each timeframe.

RESULTS

Actual Nested Frequency and Cover Values

Frequency for *Artemisia tridentata* (sagebrush) and *Atriplex canescens* (fourwing saltbrush) changed little between pre- and post-treatment, yet *Bassia prostrata* (forage kochia) increased during post treatment for both timeframes (Figs. 1a, 2a). In contrast, all forbs increased in cover during post treatment in the short term, but over the long term, values declined during post treatment (Figs. 1b, 2b). Grass cover was also highly variable among species; however, even the species with low increases in the short term, showed marked increases during 5-10 yrs post treatment (Figs. 1c, 2c). Pre-treatment values also indicate that numerous species were already present on these sites due to previous restoration efforts (i.e., *A. tridentata*, *B. prostrata*, *L. perenne* (forage kochia), *Medicago sativa* (alfalfa), *Agropyron cristatum* (crested wheatgrass), *Achnatherum hymenoides* (Indian wheatgrass), *Pascopyrum smithii* (Western wheatgrass), *Pseudoroegneria spicata* (bluebunch wheatgrass)) or due to their nativity to sites. By comparison, five of the seeded species were introduced to sites by seedings conducted during our assessment period (i.e., *A. canescens, Melilotus officinalis* (yellow sweetclover), *Onobrychis viciifolia* (sainfoin), *Sanguisorba minor* (small burnet), and *Leymus cinereus*(Great Basin wheatgrass)).

Contrasts of Functional Group and Species Origin

All three functional groups demonstrated highly significant increases in abundance during both post-treatment timeframes (Table 2; Fig. 3). Increases for grasses and shrubs exceeded those for forbs. Grass and shrub abundance also increased between 1-4 and 5-10 yrs, while forbs slightly declined. The abundance of introduced species exceeded that of native species in both timeframes, especially for shrubs, whose native counterpart showed no net change in either timeframe (Fig. 4). Differences between introduced and native species were most pronounced during in the long term (i.e., 5-10 yrs post treatment).

Interaction Between Species and Treatment

Tests of species, treatment, and the species by treatment interaction were highly significant for all functional groups with the exception of the borderline significant effect of treatment on grasses in the short term (Table 3). *Bassia prostrata* frequency increased much more than the native shrubs and with was more than two fold greater abundance in the fire treatment compared to mechanical shrub removal treatments (Figs. 5a, 6a). Seeded forb cover was also generally higher in the fire treatment, especially for *M. sativa* in both timeframes and *S. minor* during the 5-10 yr timeframe. All forbs except *M. officinalis* also increased in the pipe harrow treatment in the short term, but this effect disappeared in the long term for *M. sativa* and *S. minor*. In contrast, cover for three forb species (i.e., *L. perenne, O. viciifolia,* and *S. minor*) increased in the aerator treatment, but only in the short term. Although the main effect of treatment was not significant for grasses during the 1-4 yrs post-treatment timeframe, treatments influenced grass species differently. For example, *L. cinereus* was not affected by any of the treatments, yet cover of *P. smithii* was higher in the mechanical treatments compared to the fire treatment. The most dramatic variation in grass species among the treatments emerged in the long term when the increases in *A. cristatum, Elymus lanceolatus* (thickspike wheatgrass), *L. cinereus,* and *P. smithii* within the fire treatment exceeded both mechanical treatments. Cover of *A. cristatum* and *Psathyrostachys juncea* (Russian wildrye) was also higher in the pipe harrow treatment compared to the aerator treatment. Although grass abundance was generally lower in the aerator treatment compared to the other treatments in the long term, it improved the overall abundance of four grasses, especially *A. hymenoides*.

DISCUSSION

A consensus exists that the restoration of degraded sagebrush steppe and semiarid shrublands through mechanized approaches and fire, followed by seeding native bunchgrasses, has had limited success (Pyke et al., 2013; Knutson et al., 2014; Svejcar et al., 2017). This is particularly true for sites that have suffered extensive disturbances and alterations to vegetation, soils, and hydrology (Briske et al., 2006; Suding and Hobbs, 2008; Davies et al., 2016) and where current land use may also be perpetuating degraded understory conditions (Morris and Rowe, 2014; Bestelmeyer et al., 2015). Although similar degraded conditions were common throughout the regions evaluated in this study, it is important to emphasize that the particular sites we evaluated encompassed a collection of restoration locations where qualitative attributes of rangeland health (Pyke et al., 2002), as well as conceptual understandings of site resilience to disturbance and resistance to invasion by exotic annual grasses (Miller et al., 2014; Chambers et al., 2017), were generally understood. In fact the restoration sites included in our study have been monitored on a regular five-yr schedule since 1982, and were critically evaluated by a rigorous panel of experts to forecast site suitability prior to initiating shrub reduction and seeding methods (www.wri.utah.gov). Thus, our results present an interpretation of restoration outcomes when many of the typical constraints to restoration success were avoided. Our study provides a clear picture of how shrub reduction treatments differentially influenced the abundance of ten preexisting herbaceous species and five seeded species that had not previously existed on the study sites.

Seeded species identity and shrub reduction treatments strongly interacted, and our results indicated numerous new insights into treatment-species combinations that enhance understory vegetation conditions. First, it is clear that fire treatments promoted the notable increases in *B. prostrata, M. sativa,* and *A. cristatum* as well as long-term increases for three of the perennial grasses. The effectiveness of fire may be related to its greater overall reduction in shrub cover relative to the mechanical treatments at these restoration sites (C. Riginos, unpublished data). Accordingly, competition for soil resources between seeded species and surviving sagebrush plants may have been lower in the fire treatment, offering more favorable conditions for a broad range of species to experience successful growth. Greater increases in seeded species within the fire treatment may also be a consequence of heterogeneous soil surface conditions produced by fire, which often creates mosaics of burned and unburned patches and a greater number of regeneration niches for seeded species (Pyke et al., 2013). Fire, through the combustion of plant biomass and organic matter on the soil surface has also been linked to enriching soils with limiting mineral nutrients that are known to promote seedling growth (Rau et al., 2007; Miller et al., 2013). Fire also creates bare soil surfaces where seeds may have occurred in more favorable safe sites. For example, the most successful seeded species, *B. prostrata*, is known to establish best on bare soils following wildfires, and establishment becomes poor when seeding into thick vegetation or litter (Monaco et al., 2003; Sullivan et al., 2013). In contrast, the mechanical treatments may have buried aerially- and broadcast-dispersed seeds too deep, thus compromising seedling establishment and growth. Accordingly, by creating deep divots, the aerator treatment showed consistently lower species abundances compared to the other treatments. In addition, compared to the aerator, *A. cristatum* showed greater increases in the long term in the pipe harrow treatment that creates small furrows. Lastly, our assessment showed that cover for many of the seeded forbs was higher in the pipe harrow treatment, similar to Dahlgren et al., (2006), who found that the pipe harrow treatment increased forb cover more than 3 % relative to the aerator treatment.

Recent analyses purport that basing the performance of species on geographic origin (i.e., introduced vs native) is a false dichotomy since plant species appear to follow the same ‘rules’ for establishment and growth (Leffler et al., 2014; Lemoine et al., 2016). Our assessment of mixed-species seedings sheds some light on this interpretation by offering a direct examination of species performance when exposed to the same conditions (i.e., rules) within a restoration context. Greater performance of introduced species relative to native species is clearly portrayed from our assessment, suggesting that relative differences between native and introduce species identified nearly 50 years ago still stand (Eckert et al., 1961; Hull, 1971). It is not clear from our data whether introduced species show greater adaptation to the conditions at restoration sites, but traits exhibited by these species, including high seedling vigor, drought tolerance, rapid growth, and recovery from defoliation are often sought in breeding programs (Asay et al., 2001; 2013), and likely contributed to the better performance of introduced species. In contrast, native species seed enhancement programs have focused less on these traits, but typically emphasize selecting for seed and seedling traits to overcome seed production bottlenecks and developing plant materials for distinct geographic locations, all the while having a shorter history of selecting for adaptations such as stress tolerance (Jones and Johnson, 1998; Jones et al., 2015; Leger and Baughman, 2015; Staub et al., 2016). However, despite the lesser performance of native species in our study, four out of the five native grass species showed significant levels of persistence over the long term, suggesting that these currently available and widely utilized seed sources effectively assisted in the recovery of degraded understory conditions. While it is understood that early seedling development is critical for successful species establishment and persistence following brush control in Utah (Plummer, 1943), an ongoing challenge for restoration practitioners will be to better understand how to manipulate seedbed conditions such that poorer performing native species can achieve higher establishment and greater increases following disturbance. In addition, post-treatment management of restoration sites (i.e., livestock grazing and wildlife use) may play a large role in establishment and species persistence patterns. For example, grasses typically dominate initial establishment dynamics after disturbance followed by the recruitment of later successional species (Jentsch et al., 2009; Hoelzle et al., 2012), thus, characterizing the influence of animal use on the persistence of seeded species over time should be emphasized in future research efforts.

Our finding of generally lower establishment and persistence of seeded forbs echoes the concern that this critical component of understory vegetation is a major concern to plant community diversity and provisioning of ecosystem services for big game ungulates and imperiled wildlife species (Wirth and Pyke, 2003; Dumroese et al., 2015; Pennington et al., 2016). The mechanism responsible for lower persistence of forbs is not entirely clear, but because our restoration sites are within critical winter-range habitat for big-game ungulate species, the decline in forb abundance we observed over time may be due to heavy utilization (Scotter, 1980; Dumsoese et al., 2015; Pennington et al., 2016). Nonetheless, even under heavy utilization from big game, our results indicated significant increases in forbs relative to pretreatment conditions that remained evident through the 5-10 yr post-treatment timeframe, particularly from the introduction and establishment of three new species to the understory. These results are promising as they relate to the benefits of provisioning forbs to the diets of big game and sage grouse (*Centrocercus urophasianus*), which are often a primary reason for restoring understory vegetation in this region (Kufeld et al., 2016; Lyons et al., 1996, Dahlgren et al., 2015).

A cautionary result of our assessment is the possibility that the notably greater increases of introduced species may have interfered with either the establishment or growth of native species (i.e., Pyke et al., 2013; Knutson et al., 2014). This speculation is based on the observation of more rapid increases in cover for the most successful species in each functional group (i.e., *B. prostrata, M. sativa,* and *A. cristatum*), while their native counterparts were slower to increase, possibly due to competition. However, disentangling potential interference among seeded species is challenging in this context because seed mixes varied across sites and we did not simultaneously analyze species abundances in the same response years. The relative abundance of *B. prostrata* may be a concern on these restoration sites, especially given its ability to spread within sagebrush ecosystems following disturbances (Gray and Muir, 2013). Subsequent monitoring is needed to determine if vigorous species that rapidly establish diminish over time as native sagebrush plants recover or whether they spread outside of the seeded area into native shrublands (Frischknecht and Plummer, 1955; Sullivan et al., 2013).

IMPLICATIONS

We conclude that all three functional groups experienced notable increases in abundance, but just a few species were actually responsible for these increases. In addition, the greatest increases were observed in introduced species that tended to do better within certain shrub-reduction treatments. The interaction between species and treatment was most dramatic over the long term due to fire having a greater influence than mechanical treatments on species abundance. Based on these results, the influence of potential shrub reduction treatments should be considered on a species by species basis when planning restoration seedings. Because the sites we evaluated had high potential for success, our study offers an unbiased comparison of species-treatment interactions. In addition, greater increases for introduced species signal the need to better understand the long-term implications and potential pitfalls of shifting understory composition from native to introduced species. Future research is also needed to determine how post-treatment wildlife management influences forb persistence. In addition, the greater seeded species increases within the fire treatment beckons the need opportunistically seed sites after wildfires. Lastly, further research is needed to clarify how mechanical treatments influence seedbed conditions, especially for native species that have not been specifically developed for the prevailing anthropogenic disturbances that currently exist within sagebrush ecosystems.

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TABLES AND FIGURES

Table 1
Functional group classification, name, code, and origin for the 15 species evaluated for establishment and persistence on shrub reduction restoration sites in Utah, USA.

Functional	Species	Common name	Species	Origin
Shrub	*Artemisia tridentata* Nutt.	Sagebrush	ARTR	Native
Shrub	*Atriplex canescens* (Pursh) Nutt.	Fourwing	ATCA	Native
Shrub	*Bassia prostrata* (L.) A.J. Scott	Forage Kochia	BAPR	Introduced
Forb	*Linum perenne* L.	Blue Flax	LIPE	Introduced
Forb	*Melilotus officinalis* (L.) Lam.	Yellow	MEOF	Introduced
Forb	*Medicago sativa* L.	Alfalfa	MESA	Introduced
Forb	*Onobrychis viciifolia* Scop.	Sainfoin	ONVI	Introduced
Forb	*Sanguisorba minor* Scop.	Small Burnet	SAMI	Introduced
Grass	*Agropyron cristatum* (L.) Gaertn.	Crested	AGCR	Introduced
Grass	*Psathyrostachys juncea* (Fisch.) Nevski	Russian Wildrye	PSJU	Introduced
Grass	*Achnatherum hymenoides* (Roem. &	Indian Ricegrass	ACHY	Native
Grass	*Elymus lanceolatus* (Scribn. & J.G. Sm.)	Thickspike	ELLA	Native
Grass	*Leymus cinereus* (Scribn. & Merr.) Á.	Great Basin	LECI	Native
Grass	*Pascopyrum smithii* (Rydb.) Á. Löve	Western	PASM	Native
Grass	*Pseudoroegneria spicata* (Pursh) Á. Löve	Bluebunch	PSSP	Native

Table 2

Meta-analysis test of moderators (*Qm*) for studies of functional group (shrub, forb, and grass) and species origin (introduced and native).

	1-4 yr post treatment			5-10 yr post treatment		
Study	Q_m	*df*	*P*-value	Q_m	*df*	*P*-value
Functional group	128.59	2	<0.0001	323.01	2	<0.0001
Origin Shrub	60.60	1	<0.0001	196.48	1	<0.0001
Origin Grass	18.98	1	<0.0001	39.67	1	<0.0001

Table 3
Meta-analysis test of moderators (*Qm*) for studies of species, treatment, and the interaction of species and treatment for three functional groups.

	1-4 yr post treatment			5-10 yr post treatment		
Study	Q_m	*df*	*P*-value	Q_m	*df*	*P*-value
Shrub						
Species	68.67	2	<0.0001	273.29	2	<0.0001
Treatment	35.20	2	<0.0001	30.68	2	<0.0001
S x T	48.15	4	<0.0001	28.12*	2	<0.0001
Forb						
Species	43.60	4	<0.0001	59.81	4	<0.0001
Treatment	63.92	2	<0.0001	44.86	2	<0.0001
S x T	31.62	8	<0.0001	73.73	8	<0.0001
Grass						
Species	228.90	6	<0.0001	208.51	6	<0.0001
Treatment	5.87	2	0.0531	128.36	2	<0.0001
S x T	42.51	12	<0.0001	174.71	12	<0.0001

*The shrub *A. canescens* was removed from analysis of the S x T interaction in the 5-10 yr post-treatment timeframe because all values were zero and models would not converge.

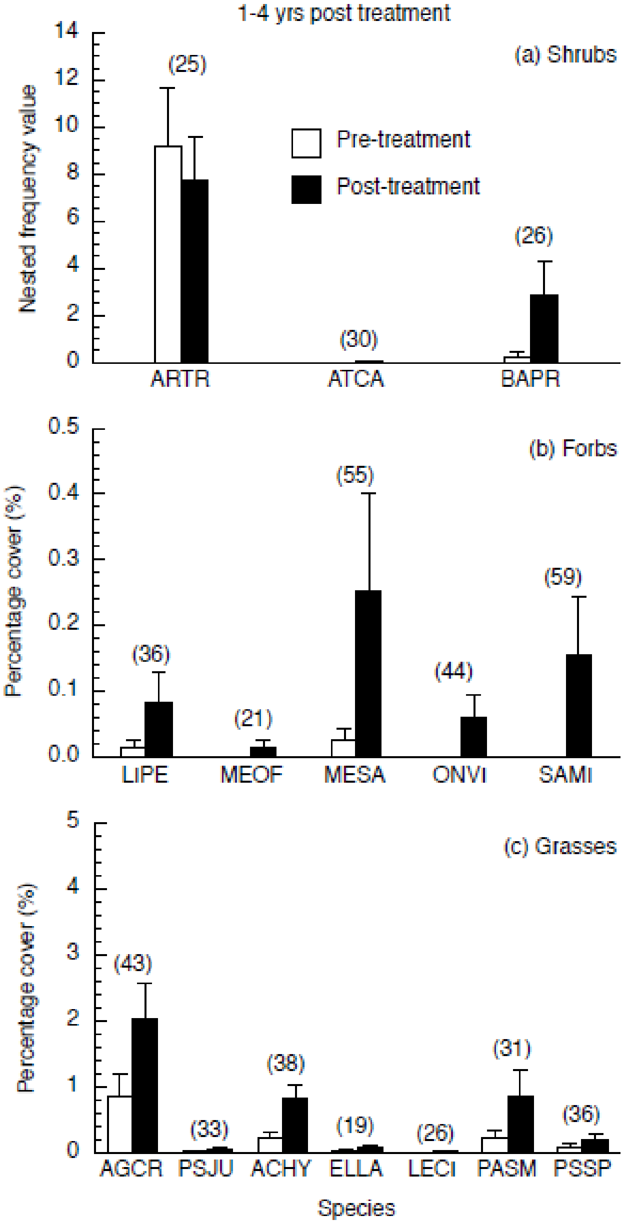

Figure 1. Mean (± SE) nested frequency and cover of 15 seeded species evaluated prior (pre) and 1-4 yr after applying shrub removal-seeding treatments (post). Values in parentheses, directly above bars, indicate the number of sites included in the analysis for each species. Seeded species included three shrubs (a: ARTR, *Artemisia tridentata*; ATCA, *Atriplex canescens*; BAPR, *Bassia prostrata*), five forbs (b: LIPE, *Linum perenne*; MEOF, *Melilotus officinalis*; MESA, *Medicago sativa*; ONVI, *Onobrychis viciifolia*; SAMI, *Sanguisorba minor*), and seven grasses (c: AGCR, *Agropyron cristatum*; PSJU, *Psathyrostachys juncea*; ACHY, *Achnatherum hymenoides*; ELLA, *Elymus lanceolatus*; LECI, *Leymus cinereus*; PASM, *Pascopyrum smithii*; PSSP, *Pseudoroegneria spicata*).

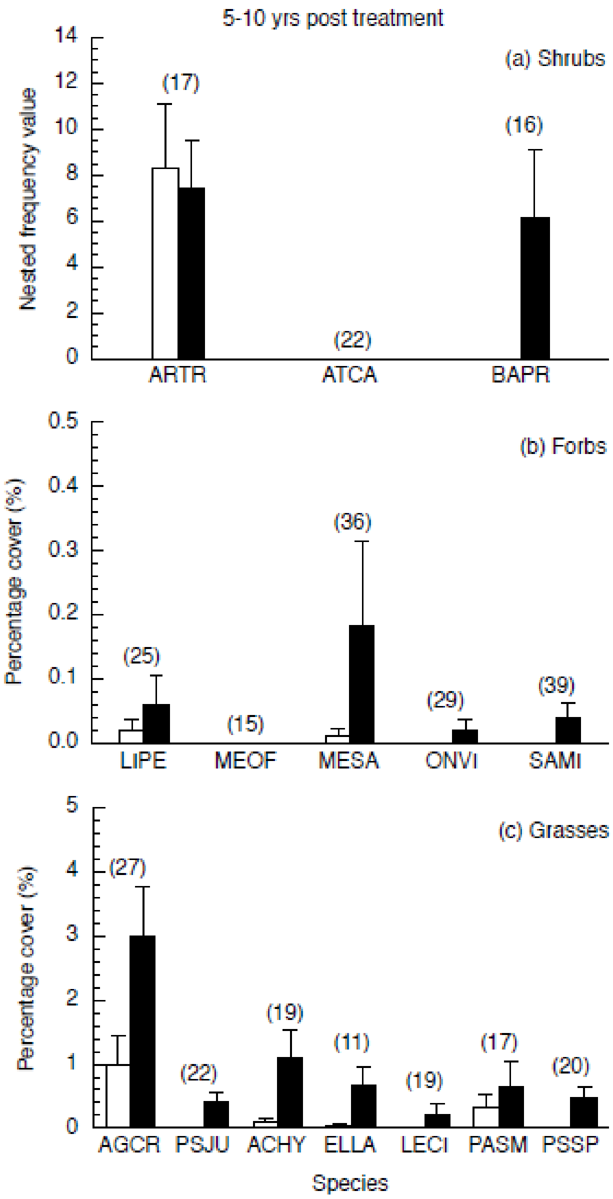

Figure 2. Mean (± SE) nested frequency and cover of 15 seeded species evaluated prior (pre) and 5-10 yr after applying shrub removal-seeding treatments (post). Values in parentheses, directly above bars, indicate the number of sites included in the analysis for each species. Seeded species included three shrubs (ARTR, *Artemisia tridentata*; ATCA, *Atriplex canescens*; BAPR, *Bassia prostrata*), five forbs (LIPE, *Linum perenne*; MEOF, *Melilotus officinalis*; MESA, *Medicago sativa*; ONVI, *Onobrychis viciifolia*; SAMI, *Sanguisorba minor*), and seven grasses (AGCR, *Agropyron cristatum*; PSJU, *Psathyrostachys juncea*; ACHY, *Achnatherum hymenoides*; ELLA, *Elymus lanceolatus*; LECI, *Leymus cinereus*; PASM, *Pascopyrum smithii*; PSSP, *Pseudoroegneria spicata*).

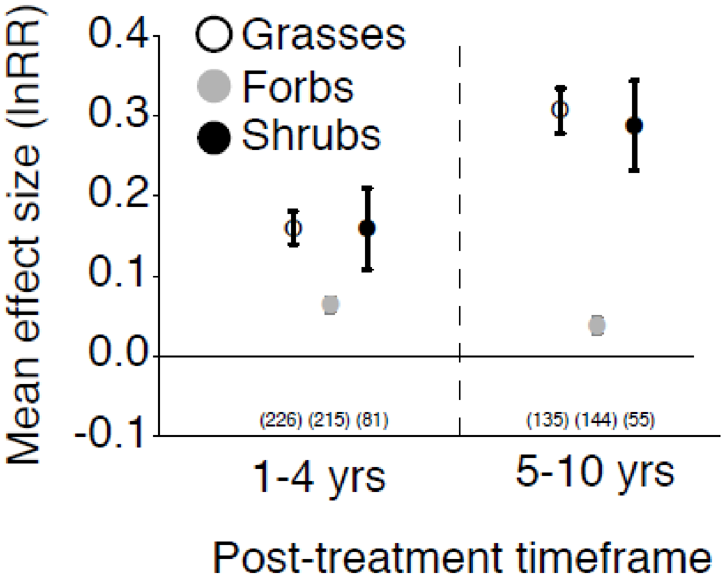

Figure 3. Mean (± 95 % CI) establishment effect size (lnRR = ln[post-treatment/pre-treatment]) for shrubs, forbs, and grasses (pooled for seeded species and shrub reduction treatments) evaluated during two post-treatment timeframes. Values in parentheses, directly below symbols, indicate the number of sites included in meta-analysis of functional groups (Table 2).

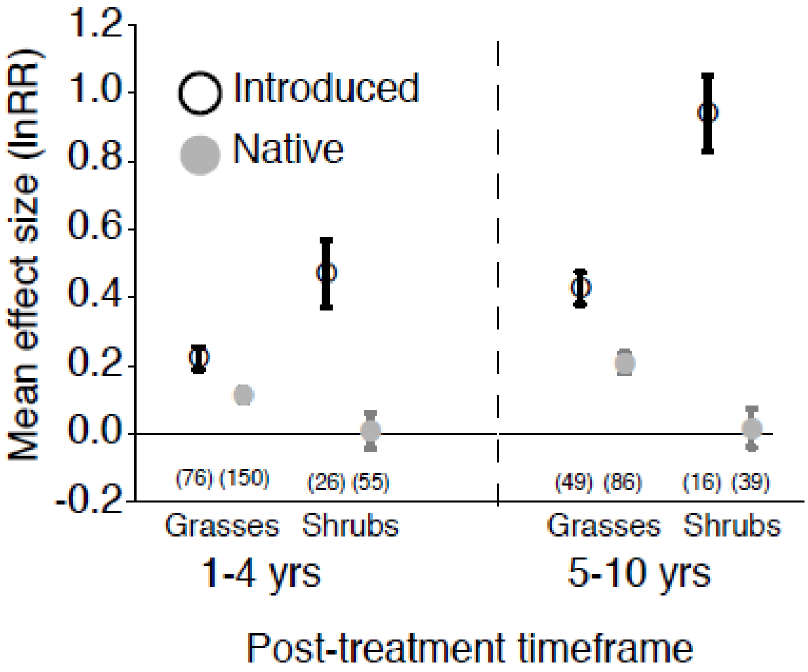

Figure 4. Mean (± 95 % CI) establishment effect size (lnRR = ln[post-treatment/pre-treatment]) for introduced and native species (pooled for seeded species and shrub reduction treatments) evaluated during two post-treatment timeframes. Values in parentheses indicate the number of sites included in meta-analysis of species origin (Table 2).

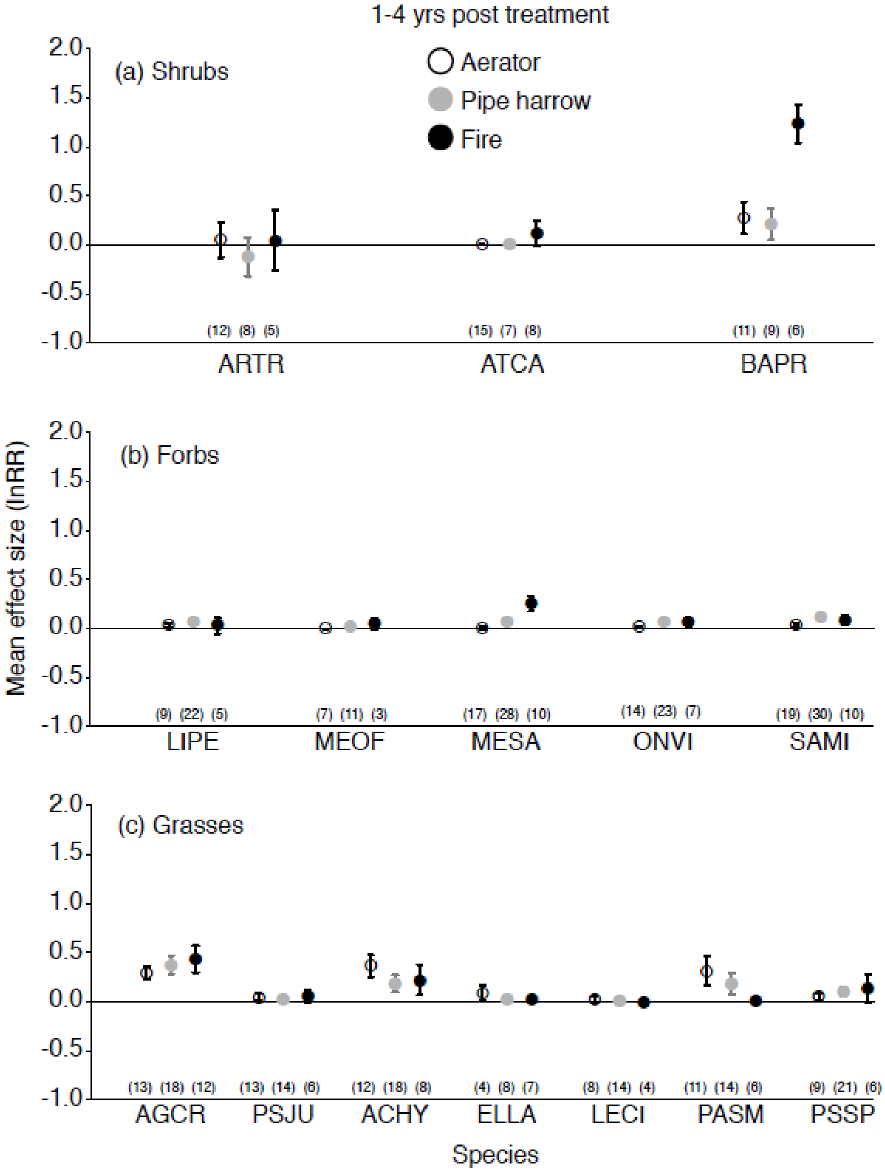

Figure 5. Mean (± 95 % CI) establishment effect size (lnRR = ln[post-treatment/pre-treatment]) for 15 seeded species evaluated 1-4 yr after applying shrub removal-seeding treatments. Values in parentheses indicate the number of sites included in species x treatment meta-analysis (Table 3). Shrub reduction treatments included mechanical (aerator and pipe harrow) and fire methods. Seeded species included three shrubs (a: ARTR, *Artemisia tridentata*; ATCA, *Atriplex canescens*; BAPR, *Bassia prostrata*), five forbs (b: LIPE, *Linum perenne*; MEOF, *Melilotus officinalis*; MESA, *Medicago sativa*; ONVI, *Onobrychis viciifolia*; SAMI, *Sanguisorba minor*), and seven grasses (c: AGCR, *Agropyron cristatum*; PSJU, *Psathyrostachys juncea*; ACHY, *Achnatherum hymenoides*; ELLA, *Elymus lanceolatus*; LECI, *Leymus cinereus*; PASM, *Pascopyrum smithii*; PSSP, *Pseudoroegneria spicata*).

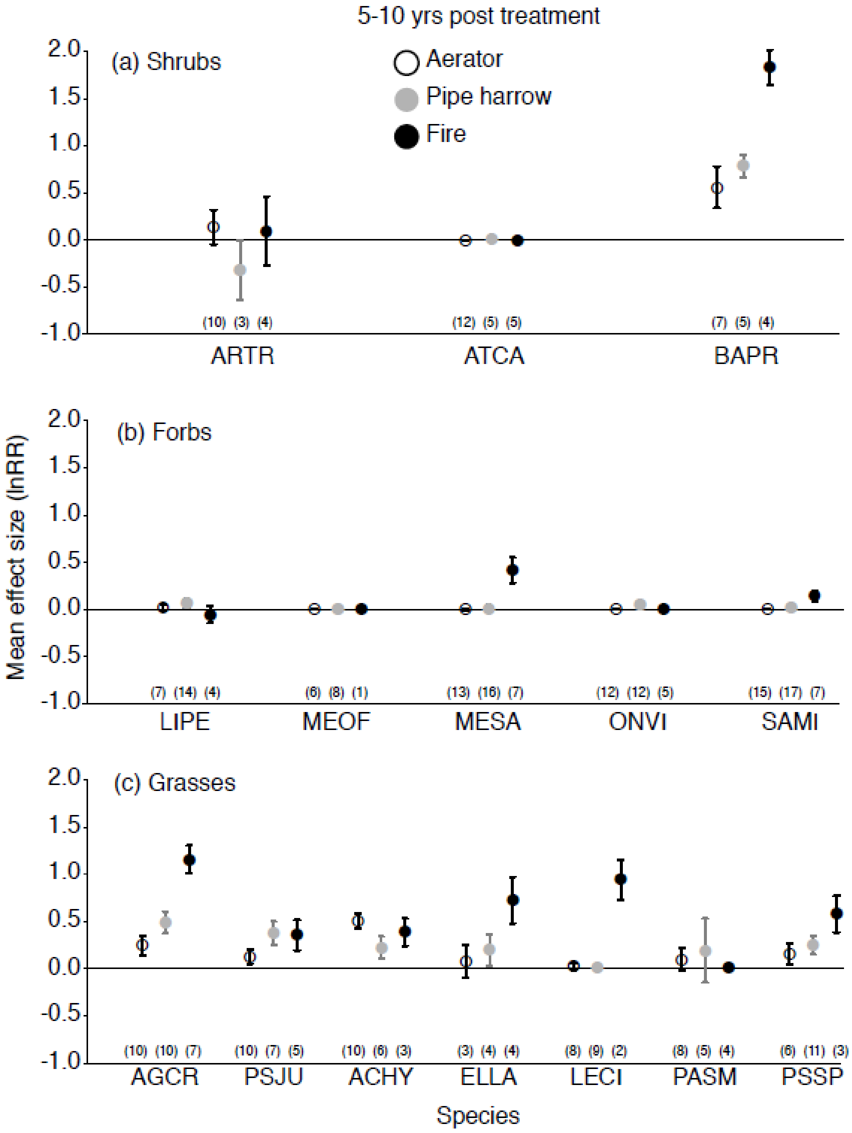

Figure 6. Mean (± 95 % CI) establishment effect size (lnRR = ln[post-treatment/pre-treatment]) for 15 seeded species evaluated 5-10 yr after applying shrub removal-seeding treatments. Values in parentheses indicate the number of sites included in species x treatment meta-analysis (Table 3). Shrub reduction treatments included mechanical (aerator and pipe harrow) and fire methods. Seeded species included three shrubs (a: ARTR, *Artemisia tridentata*; ATCA, *Atriplex canescens*; BAPR, *Bassia prostrata*), five forbs (b: LIPE, *Linum perenne*; MEOF, *Melilotus officinalis*; MESA, *Medicago sativa*; ONVI, *Onobrychis viciifolia*; SAMI, *Sanguisorba minor*), and seven grasses (c: AGCR, *Agropyron cristatum*; PSJU, *Psathyrostachys juncea*; ACHY, *Achnatherum hymenoides*; ELLA, *Elymus lanceolatus*; LECI, *Leymus cinereus*; PASM, *Pascopyrum smithii*; PSSP, *Pseudoroegneria spicata*).

CHAPTER 3

INFLUENCE OF MOUTAIN AND WYOMING BIG SAGEBRUSH PLANT COMMUNITY SOILS ON SEEDLING EMERGENCE PATTERNS OF SIX RESTORATION SPECIES

ABSTRACT

The influences of soil properties on recruitment of restoration species seeded to improve degraded herbaceous understory conditions in big sagebrush (*Artemisia tridentata* Nutt.) plant communities are largely unexplored. We evaluated emergence patterns of six commonly seeded restoration species in soils from Wyoming big sagebrush (*A. t.* ssp. *wyomingensis* [Beetle & A. Young] S.L. Welsh) and mountain big sagebrush (*A. t.* ssp. *vaseyana* [Rydb.] Beetle) plant communities that differed in soil texture, soil organic matter content, and soil water holding capacities. We conducted two separate experiments that regularly wetted soils to standardized soil water potentials (i.e., field capacity; -0.03 MPa) and allowed differences in evaporation to create distinct wet-dry watering pattern cycles over a 26-29 d period. We hypothesized that greater water holding capacity of vaseyana soil would result in higher emergence than wyomingensis soil, and that this pattern would be more pronounced under low soil water content due to higher evaporation in wyomingensis soils. Results supported our assumption that inherent differences in soil texture and organic matter between soils translate into fundamental differences in soil water holding capacity: finer-textured vaseyana soils held roughly two-fold more water than course-textured wyomingensis soils. On the other hand, seeds in vaseyana soils were exposed to less frequent watering and less frequent wet-dry cycles compared to wyomingensis soils. Although species collectively exhibited greater emergence in vaseyana soils than wyomingensis soil, patterns were vastly different among species and differences between soils became more pronounced under low soil water for only two species. Consequently, both hypotheses were rejected due to variable responses among species. We conclude that the manner in which soils and water uniquely influenced emergence patterns provides new insights in species suitability for restoration sites and how inherent soil differences may constrain seeding success.

INTRODUCTION

The Intermountain Region in the western United States is home to expansive big sagebrush (*Artemisia tridentata* Nutt.) ecosystems, which occupy an extraordinary variety of environmental conditions (West, 1983; Davies et al., 2006). This variety encompasses plant communities in semi-desert shrublands, shrub-steppe, and upland foothills and woodlands, as well as high mountain plateaus (West, 1988; Miller et al., 2011). Furthermore, big sagebrush plant communities are often dominated, and thus classified, by different subspecies (West, 1983; Shultz, 2009), with distinct affinities to environmental factors, topographic position, and soils (Meinke et al., 2009; Davies et al., 2007; Chaney et al., 2017). For example, two major subspecies—Wyoming big sagebrush (*A. t.* ssp. *wyomingensis* [Beetle & A. Young] S.L. Welsh; hereafter wyomingensis) and mountain big sagebrush (*A. t.* ssp. *vaseyana* [Rydb.] Beetle; hereafter vaseyana)—generally occupy different topographic positions (i.e., lower and higher elevation sites, respectively), and vary widely in resilience to environmental stress and resistance to invasion by exotic annual grasses as well as temperature and precipitation regimes (Wisdom and Chamber, 2009; Chambers et al., 2017). In addition, soils occurring in both plant communities are considered well drained, but soils found in vaseyana sagebrush communities are typically deeper, finer-textured and have higher organic matter (Jensen, 1990; Mahalovich and McArthur, 2004; McArthur, 2005; Davies, et al. 2007). In contrast, coarser soils found in wyomingensis sagebrush communities drain more rapidly and experience higher rates of evaporation due to higher sand and lower organic matter content (Bauer, 1974; Kuss, 1986; Wang et al., 2016). Despite these documented differences, relatively little is known about how variation in soil properties influences recruitment opportunities of restoration species that are actively seeded to improve ecosystem health by remediating degraded herbaceous understory conditions (West, 1988; Miller et al., 2011).

The roles of soil texture and soil organic matter in determining plant community dynamics and restoration potential has gained recognition in the last few decades (Bronick and Lal, 2005; Heneghan et al., 2008; Baer et al., 2010). Soil texture is a crucial soil property that directly influences moisture content, porosity, bulk density, organic matter stability, cation exchange capacity, and nutrient availability (Bauer, 1974; Tuller and Or, 2004; Saxton and Rawls, 2006). Consequently, sandy soils have high porosity and low water-holding capacity (WHC), but clayey soils have higher bulk density, greater surface area, and higher WHC (Noy-Meir, 1973; Lin et al., 1997). Soil organic matter content also strongly influences WHC of soils and water retention (Baumann and Bauer, 1974; Naeth et al., 1991; Hudson, 1994; Huntington, 2006). Accordingly, inherent differences in soil texture and OM content between wyomingensis and vaseyana soils may lead to considerable variation in soil water holding capacity (i.e, Jensen, 1989; 1990).

Seed germination and seedling emergence are recognized as major regulators of restoration success in semi-arid ecosystems in the Intermountain West (James et al. 2013; Svejcar et al. 2014). However, little is known regarding how WHC capacity influences germination and seedling growth of commonly seeded species in this region. Although seeded species success can be improved by soil surface modifications to increase the number of favorable microsites for seed germination and emergence, as well as seed enhancements to remedy restoration barriers (Mangold et al., 2007; Hardegree et al., 2016; Madsen et al., 2016), site specific factors, such as soil properties, can have overriding effects on germination and emergence patterns of seeded species (Stevens, 1983; Young et al., 1989; Brabec et al., 2015). For example, inherent site differences in WHC among sagebrush soils may interact with soil water availability, such that as moisture declines, the amount of water freely available for seeds to imbibe and germinate will vary among sites (e.g., Evans and Etherington, 1990). These differences in soil texture and WHC among also dictate matric water potential (i.e., water stress), which directly influence germination potential of seeds (Doescher et al., 1985; Wuest and Lutcher, 2013). Thus, seeds germinating and emerging in wyomingensis and vaseyana soils could experience vastly different wet-dry cycling at given water potentials. If true, the effects of inherent soil differences on these processes would become more pronounced under lower soil moisture contents due to greater water retention and lower evaporation in finer-textured vaseyana soil and more frequent wet-dry cycling in coarse-textured wyomingensis.

Native species germination patterns have been correlated with habitat conditions in big sagebrush plant communities (Meyer and Monsen, 1992; Kitchen and Monsen, 1994; Hardegree and Van Vactor, 1999), yet the influence of soil properties on species germination and emergence patterns is poorly understood. To clarify these relationships, we evaluated the effects of vaseyana and wyomingensis soils on emergence patterns of six restoration species commonly seeded on degraded sagebrush plant communities in the Intermountain Region. A novel experimental design was developed to account for soil water holding capacity differences between soils by regularly wetting soils to standardized soil water potentials (i.e., field capacity; -0.03 MPa) and allowing differences in evaporation rates to create distinct wet-dry cycles over a 26-29 d period. We hypothesized that 1) greater water holding capacity of vaseyana soils would result in higher emergence, and that 2) this pattern would be more pronounced under low soil water content due to higher evaporation in wyomingensis soils. We anticipated that evaluating emergence patterns of these two soils would improve our understanding of species suitability for restoration sites and provide insights into site-related constraints on seeding success.

METHODS AND MATERIALS

Site Descriptions

Soils from two different big sagebrush plant communities in northern Utah, dominated by either Wyoming *(Artemisia tridentata ssp. wyomingensis*) or mountain (*Artemisia tridentata ssp. vaseyana*) big sagebrush, were collected for use in this study. The Wyoming big sagebrush plant community was located near Park Valley in Box Elder County, UT (41° 49’ 26.21” N, 113° 17’ 25.21” W), at 1680 m elevation, on a 3 % south-facing slope. The parent material is derived from alluvium; soils are in the Kapod and Donnardo series and classified as loamy-skeletal, mixed, superactive, mesic Calcic Argixerolls and loamy-skeletal, mixed, superactive, mesic Typic Argixerolls, respectively (Box Elder County, Western Part; http://websoilsurvey.nrcs.usda.gov/app/). The plant community was classified as Semidesert Gravelly Loam (Wyoming Big Sagebrush) North (R028AY215UT; Ecological Site Information System; https://esis.sc.egov.usda.gov). Vegetation resembled a Wyoming big sagebrush-dominated phase, with a number of less common species including, rubber rabbitbrush (*Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird), bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey ssp. *elymoides*), and bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve). Long-term mean (30-year; 1986-2016) annual precipitation and air temperature are 368.3 mm and 7.8 °C, respectively (Box Elder County, Western Part; http://websoilsurvey.nrcs.usda.gov/app/).

The mountain big sagebrush plant community was located near Mantua in Box Elder County, UT (41° 33’ 15.77” N, 111° 57’ 9.27” W), at 1800 m elevation, on a 10 %

north-facing slope. The parent material was quartzite alluvium derived from sandstone; soils are part of the Hendricks series and classified as fine-silty, mixed, superactive, mesic Pachic Argixerolls (Box Elder County, Eastern Part; http://websoilsurvey.nrcs.usda.gov/app/). Current vegetation was classified as Mountain Loam (Mountain Big Sagebrush) (R047XA430UT; Ecological Site Information System https://esis.sc.egov.usda.gov); vegetation resembled a mountain big sagebrush-dominated phase with bluebunch wheatgrass (*P. spicata*) and a number of less common species including mountain snowberry (*Symphoricarpos oreophilus* A. Gray) and prairie junegrass (*Koeleria macrantha* [Ledeb.] Schult). Long-term mean (30-year; 1986-2016) annual precipitation and air temperature were 622.3 mm and 6.1 °C, respectively (Box Elder County, Eastern Part; http://websoilsurvey.nrcs.usda.gov/app/).

Soil Collection and Analysis

Soil was excavated to a depth of 20 cm from the interspace areas between dominant shrubs within a single 10 m x 10 m area at each plant community, excluding the top litter layer, until 100 L of soil was obtained. Soils were transported to a greenhouse, homogenized by mixing, and air-dried for three weeks before sieving through a 1-cm wire mesh to remove larger organic material and rock.

Air-dried subsamples from each soil (n = 5) were analyzed for cation exchange capacity (CEC), organic matter content (OM), percentage soil water content (SWC % at -0.03 MPa, -1.5 MPa, and soil saturation.), pH, and texture. CEC and OM were determined with flow injection analysis (Quick Chem 8500, Lachat Instruments, Loveland, Colorado, USA) using the ammonium replacement method (Gavlak et al.,

2005) and the dichromate oxidation method (Walkley and Black, 1934), respectively. Percentage SWC values was measured with the pressure plate method (Gavlak et al., 2005) at -0.03 MPa and the samples were allowed to equilibrate for 24 h. For permanent wilting point, the pressure plate was set at -1.5 MPa and allowed to equilibrate for 48 h. SWC % values are expressed gravimetrically (i.e., the weight of water as a fraction of the total soil wet weight; Bittelli, 2011). Samples were also analyzed for pH and texture (i.e., percentage sand, silt, and clay) using the hydrometer and slurry methods, respectively (Gee and Bauder, 1986; Thomas, 1996). For pH, 15 g of soil was mixed with 30 mL of deionized water, shaken at 100 rpm for 30 min, then measured with a pH meter (Orion 3 star bench-top pH meter; Thermo Scientific). To quantify percentage sand, silt, and clay, 50 g of soil was mixed with a 100-mL sodium hexametaphosphate–water solution and 250 mL of deionized water and shaken at 150 rpm for 1 h, placed into a 1-L cylinder, and filled with deionized water. A custom plunger was used to mix the slurry before measuring its temperature and density ($g \cdot L^{-1}$) with a Bouyoucos hydrometer (14-331-5C; Thermo Scientific, Beverly, MA) after 30 s and again after 1,440 min (Table 4). Soil variables for each soil were compared statistically using the unpaired (i.e., independent samples) two-sample Student's *t*-test ($p = 0.05$).

Plant Species

Six species commonly used in restoration projects in Great Basin, Rocky Mountain, and Colorado Plateau ecoregions in the Intermountain West were selected for our study (UWRI; http://wildlife.utah.gov/watersheds/; Lambert 2005). These included the shrubs Wyoming and mountain big sagebrush, two forbs (alfalfa; *Medicago sativa*

[L.] and sanfoin; *Onobrychis viciifolia* Scop.), and two perennial grasses (bluebunch wheatgrass; (*Pseudoroegneria spicata*). and “Hycrest II” crested wheatgrass; *Agropyron cristatum* [L.] Gaertn). Seeds for the study were obtained from Great Basin Research Center and Seed Warehouse, Ephraim, Utah, USA (shrubs; wildland collected at Piute/Wayne/Sevier counties in Utah in fall 2016) and Wheatland Seed Brigham City, Utah, USA (forbs and grasses; commercially produced in Utah 2015). Seeds were hand cleaned and selected for consistency in shape and size prior to experiments.

Experiment 1

To study the influence of sagebrush soils on cumulative seed emergence, 100 seeds of each species were sown in plastic containers (11 cm x 11 cm x 4 cm) filled with 50 g of either vaseyana or wyomingensis soil (*n* = 5). We then covered seeds with either 1 mm of soil (i.e., sagebrush) or 3 mm of soil (i.e., all other species) and placed unsealed containers in a growth chamber with onboard environmental controls (model PGW132, IntellusUltra C8T, Percival, Perry, IA 50220) for photosynthetically active radiation (PAR), air temperature, and relative humidity (RH %). The chamber was set to a 12/12 h day/night regime, and temperature and RH values were chosen to mimic a springtime regime (e.g., 15 April to 15 May) for Tremonton, Utah, a site located geographically between the two plant communities where soils were obtained. Spring conditions were mimicked due to the fact that these species are typically sown with fall-dormant seeding to promote spring emergence when SWC is available and the risk of seedling mortality from freezing temperatures is low (Jensen et al. 1999). We obtained average hourly air temperature and RH data for Tremonton from the Utah Climate Center (https://climate.usurf.usu.edu/agweather.php) and calculated mean daytime (0900 – 2100) and nighttime (2100 - 0900) values for a 4-year period (2013-2016). Based on these calculations, we set the day/night temperature and RH to 14.6/8.4 °C and 50.9/70.8 %, respectively. Daytime PAR was set to an uncharacteristically low PAR value of 100 μmol · m^{-2} · s^{-1} to prevent high rates of evaporation within containers over a 24 h period. SWC of each container was adjusted gravimetrically according to pre-determined field capacity values for each soil (-0.03 MPa; Table 4). We recorded daily low SWC (i.e., after a 24 h period) of each container for 26 d and readjusted SWC to field capacity. In addition, we recorded emergence (based on the appearance of a coleoptile extending 2 mm above the soil surface) for each container. Cumulative emergence data were assessed for normality and homogeneity of variance, then analyzed with repeated measures MANOVA as a factorial experiment using a completely randomized design ($p = 0.05$). We also analyzed total seedling emergence and learned that emergence was generally higher in vaseyana compared to wyomingensis soil. Consequently, we used mean maximum seedling emergence in vaseyana soil as a proxy estimate of seed purity for each species for use in Experiment 2.

Experiment 2

To study the interactive influence of soil water content and sagebrush soil on cumulative seedling emergence over a 29-d period, we followed the same procedures of Experiment 1, but to minimize intraspecific competition with the small containers, seeds were sown at a lower density and total soil weight within containers was increased to 200 g. A greater amount of soil in containers increased soil volume and allowed us to create distinct watering levels that could be maintained feasibly over a 24 h period. In addition, using seed purity estimates obtained from Experiment 1, a standard sowing density was calculated for each species to potentially yield 30 seedlings per container. A total of 140 containers were prepared for the experiment (2 soils x 2 water levels x 6 species + a non-sown control x 5 replicates).

Distinct water levels were created by adjusting daily SWC to either field capacity (high treatment) or to the midpoint between field capacity and the permanent wilting point (low treatment). Midpoint SWC levels for vaseyana and wyomingensis soils were 25.0 and 13.7 %, respectively. Thus, unlike Experiment 1, adjustments were not made each day, but only when the SWC of at least one container from a species-water level combination reached permanent wilting point due to evaporation. Gravimetric SWC and seedling emergence was recorded daily even if water adjustments were not necessary. Cumulative emergence data were assessed for normality and homogeneity of variance and analyzed as a factorial experiment using a randomized complete block design with repeated measures MANOVA ($p = 0.05$).

RESULTS

Soil Properties and Water Content

Differences between vaseyana and wyomingensis soils were highly significant (Table 4). Organic matter, CEC, as well as silt and clay content of vaseyana soil were typically two-fold higher than wyomingensis soil (Table 4). On the other hand, sand content of wyomingensis soil was nearly four-fold higher than vaseyana soil.

Consequently, vaseyana soils required nearly twice the amount of water to attain the same soil water potential (i.e., field capacity; -0.03 MPa) and, thus, SWC of vaseyana soils remained much higher relative to wyomingensis soils for both experiments (Fig. 7). Even when distinct soil water levels were applied in Experiment 2, the low water level of vaseyana soil maintained higher daily-low SWC than both water levels of the wyomingensis soil. Vaseyana soil also retained water longer than wyomingensis soil based on the fact that the number of watering events was approximately double for wyomingensis compared to vaseyana soil in both the high (9.0 ± 0.0 vs 14.1 ± 0.1; $t = 36.0$, $df = 6$, $P < 0.0001$) and low water level treatment (14.0 ± 0.3 vs 25.0 ± 0.6; $t = 15.2$, $df = 6$, $P < 0.0001$).

Emergence Patterns

In Experiment 1, emergence was significantly greater in the vaseyana than wyomingensis soil, yet species exhibited vastly different patterns in the two soils (Table 5; Fig. 8). Final emergence percentage was much higher in vaseyana soil for both sagebrush subspecies compared to the wyomingensis soil, but not for the other four species. Emergence was also notably higher for *M. sativa* and *A. cristatum* in vaseyana soil, but only during the midpoint of the experiment. In addition, emergence of *O. viciifolia* and *P. spicata* was not significantly affected by the different sagebrush soils, although values for *P. spicata* in the wyomingensis soil showed a marked increase over vaseyana soil between Days 20 and 26 of the experiment. Consequently, although emergence patterns were significantly different between vaseyana and wyomingensis soils (Table 5), final values (mean ± SE pooled for species) differed by less than 4 % (i.e, 61.8 ± 5.2 vs 58.6 ±7.3, respectively).

Although water was added less frequently in Experiment 2 relative to Experiment 1, the patterns of species emergence and how they were influenced by soils were similar. Emergence of all species was generally more rapid and higher for the combination of high water and vaseyana soil, yet a number of exceptions were observed (Fig. 9). For example, unlike the other species, final emergence of *P. spicata* in wyomingensis soil exceeded vaseyana soil regardless of soil water level. In addition, *O. viciifolia,* and *A. cristatum* showed greater emergence in wyomingensis compared to vaseyana soil under low water. Water levels also modulated germination patterns differently among species (Fig. 9, Table 6). Significant differences between soils were not found for either sagebrush subspecies or *O. viciifolia* under the high water level. In contrast, emergence patterns were different between soils, regardless of water level, for *M. sativa*, *P. spicata,* and *A. cristatum*. However, differences between soils were more pronounced under low water only for *O. viciifolia* and *P. spicata*. Although emergence patterns were significantly different between vaseyana and wyomingensis soils (Table 6), final values (mean ± SE pooled for species) were similar under high water (56.0 ± 5.0 vs 55.5 ± 5.9), but quite different under low water (32.8 ± 3.6 vs 50.2 ± 5.2), respectively.

DISCUSSION

My results support the assumption that the inherent properties of soil texture and OM between vaseyana and wyomingensis soils translate into fundamental differences in soil water holding capacity (i.e., Bauer 1974; Lin et al. 1997) and suggest a number of important considerations relevant to seed emergence patterns. First, fine-textured vaseyana soils held more water (i.e., roughly two-fold higher SWC) than coarse-textured wyomingensis soils. Thus, differences in evaporation created fluctuating SWC conditions and highly variable seed emergence patterns for a broad range of restoration species. For example, the variability in SWC between soils, exposed germinating seeds in vaseyana soils to less frequent watering and less frequent wet-dry cycles compared to wyomingensis soils. In addition, this signature difference in SWC became more pronounced in the low water level treatment for two of the study species. Second, because soils and species strongly interacted, our hypotheses were not supported; not all species experienced higher emergence rates in vaseyana soil and differences between soils were not consistently more pronounced under the low water treatment. The emergence patterns observed under these experimental conditions provide insight into species suitability for restoration sites and how inherent soil differences may constrain seeding success.

Differences in soil texture and OM content between wyomingensis and vaseyana soils directly influenced evaporative water loss (e.g., Bauer, 1974; Saxton and Rawls, 2006) and exposed germinating seeds to different wet-dry cycles. While rapid evaporation of moisture is known to limit germination of semiarid plant species (e.g., Frasier et al., 1997), alternating wet-dry cycles accelerates germination and seedling emergence (Zhu et al., 2013), but responses can vary widely among species native to the Intermountain Region (Bleak and Keller, 1972; Kastner et al., 1981). Furthermore, the influence of alternating wet-dry cycles on germination rates (e.g., Doescher et al., 1985; Evers and Parsons, 2003) depends on the interval length between rewetting events (Fay and Schultz, 2009; Gao et al., 2014). In both of our experiments, interval lengths were greater for vaseyana soil and rewetting occurred more frequently in wyomingensis soils. In addition, seeds in Experiment 2 were exposed to 6 and 11 more wet-dry cycles in the high and low water treatments compared to the vaseyana soils, respectively. These differences in wet-dry cycles provide an important clarification when interpreting emergence patterns overall (i.e., pooled-species responses) as well as for individual species.

Considerable variation in emergence patterns among species necessitated rejecting Hypothesis 1 that greater water holding capacity of vaseyana soil would lead to higher emergence compared to the coarser wyomingensis soil. In fact, differences between soils were evident for only four species in Experiment 1, and among these, only the two sagebrush subspecies clearly illustrated greater final emergence values in vaseyana soil. Considering both experiments together, only *M. sativa* and *A. cristatum* responded according to our first hypothesis. We speculate that greater emergence in vaseyana than wyomingensis soil for both sagebrush subspecies in Experiment 1 was a consequence of less rapid evaporation experienced between watering intervals in vaseyana soil (e.g., Gill and Jalota, 1996), which reduced the chances of dry soils desiccating seeds between watering intervals, especially since they were planted more shallowly compared to Experiment 2. Sagebrush seeds are very small compared to the other species, and require shallow seeding depths (Walck et al., 2008; Meyer, 1994;

Daws et al., 2008). Thus, rapid emergence under the higher and less fluctuating water conditions of vaseyana soil may be a mechanism to reduce the risk of drought induced mortality of these species. On the other hand, consistently more rapid emergence of the broadly adapted *M. sativa* and *A. cristatum* in vaseyana soil suggests that both species benefited from the buffered, i.e., less extreme changes in daily SWC provided by finer textured, vaseyana soils. Less wet-dry cycling in the vaseyana soil over the course of our experiments likely improved *M. sativa* emergence by increasing the rate of imbibition (i.e., Hegarty, 1977), a process known to strongly control germination speed and consistency in the this legume species (Chon et al., 2004; Yacoubi et al., 2011). Greater emergence of *A. cristatum* in vaseyana soil also appears to be related to higher soil water retention in finer soils. This aggressive forage grass has been shown to be most productive and maintain dominance on silty loam compared to sandy loam soils in the Intermountain Region (Shown et al., 1969; Williams et al. *in press*). In addition, previous research illustrated that supplementing clayey field soils with sand to reduce water-holding capacity resulted in significant reductions in crested wheatgrass germination and seedling emergence (Mangold and Sheley, 2007).

Water content of surface-soil horizons can fluctuate greatly from day to day in sagebrush ecosystems (Obrist et al., 2004; Ivans et al., 2006), and can vary by vegetation type (Castelli et al., 2000; Ducas et al., 2011), particularly during spring conditions that coincide with seed germination and seedling emergence of seeded species (Schlaepfer et al., 2015). Soil water depletion can be rapid if not recharged by precipitation or through hydraulic redistribution. Such diel fluctuation in soil surface water conditions can be extreme, and reflects daytime depletion due to evaporation and transpiration and nocturnal resupply by hydraulic redistribution and both liquid and vapor flow along temperature and pressure potential gradients (Caldwell et al., 1998; Schelde et al.,1998). These environmental gradients make it difficult to measure soil water conditions at the soil surface, yet from modeling, we know that fluctuations in water and temperature strongly regulate seed germination patterns (Flerchinger and Hardegree, 2004; Hardegree et al., 2013). When soils become dry and are not recharged, available soil water conditions are not suitable for seeded species germination and may lead to desiccation and mortality of emerged seedlings (Evans et al., 1970 Abbott and Roundy, 2003; James and Svejcar, 2010; James et al., 2011). Although pooled-species emergence patterns suggested that differences between soils became more pronounced under low water in Experiment 2, the second hypothesis must be rejected because species-level patterns did not consistently respond as expected. In fact, *O. viciifolia* and *P. spicata* were the only two species with more pronounced differences between soils under low water; however, surprisingly, both species showed higher emergence rates in wyomingensis soil. A mechanism for these unexpected results is difficult to speculate, but it is possible that longer interval lengths spent at suboptimal water conditions in vaseyana soil reduced emergence relative to coarser, wyomingensis soil that was recharged more frequently due to higher evaporation rates. Greater emergence of *P. spicata* in wyomingensis soil than vaseyana soil regardless of water level also agrees with a previous report that showed ~two-fold greater germination in sandy compared to clay soil (Madsen et al., 2012).

Further research that expressly varies the temporal dynamics of wet-dry cycles is needed to characterize germination and emergence patterns in soils of different textures.

IMPLICATIONS

My results showing variable species emergence patterns for vaseyana and wyomingensis soils provides a greater understanding of species suitability for restoration sites and new insights into site-related constraints on seeding success. Emergence was generally greater in vaseyana soil and within the high water treatment, yet the low water treatment did not seem to prevent any of the species from emerging. In a few cases, the magnitude of differences in emergence between the two soil was greater under low water treatments, which was likely caused by alternating wet/dry cycles promoting water imbibition and increasing germination. My results also highlight that broad differences exist in emergence patterns between species within the same functional groups. Further research is needed to characterize the role of soil texture and how it influences the temporal dynamics of alternating wet/dry cycles. Such information could assist in determining the suitability of sites for proposed restoration seedings as well as selecting the most appropriate species to plant.

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TABLES AND FIGURES

Table 4

Mean (± SE; *n* = 5) soil measures and statistical comparison (unpaired Student's *t*-test and *P*-value) of two big sagebrush plant community soils used in seed germination experiments.

Soil measure	vaseyana soil	wyomingensis soil	*t*-ratio	*P*-value
Organic matter (%)	7.86 (0.06)	3.78 (0.13)	34.23	<0.0001
CEC (meq/100g)	41.92 (0.22)	19.62 (0.15)	85.32	<0.0001
SWC % (-0.03 MPa)	34.58 (0.49)	20.82 (0.36)	16.63	<0.0001
SWC % (-1.5 MPa)	15.34 (0.16)	6.51 (0.15)	52.85	<0.0001
SWC % (saturated soil)	58.90 (0.59)	29.43 (0.35)	45.90	<0.0001
pH	7.30 (0.03)	7.91 (0.01)	-18.60	<0.0001
Sand (%)	15.61 (0.85)	65.60 (0.31)	-57.11	<0.0001
Silt (%)	47.83 (0.84)	23.34 (0.29)	26.15	<0.0001
Clay (%)	36.52 (0.43)	11.06 (0.09)	64.93	<0.0001

Table 5

Results of MANOVA showing degrees of freedom (*df*), *F* statistics, and *p*-values for the effects of sagebrush community soil (i.e., vaseyana and wyomingensis) on germination of six species in Experiment 1.

Effect	*Df*	*F*	*p-value*
Soil	1,48	83.68	<0.0001
Species	5,48	290.52	<0.0001
Soil*Species	5,48	26.01	<0.0001

Table 6

Results of MANOVA showing degrees of freedom (*df*), *F* statistics, and *p*-values for the effects of sagebrush community soil (i.e., vaseyana and wyomingensis) and soil water content levels on germination of six species in Experiment 2.

Effect	*Df*	*F*	*p*-value
Soil	1,92	2.07	0.1536
Species	5,92	87.19	<0.0001
Water	1,92	63.77	<0.0001
Soil*Species	5,92	22.59	<0.0001
Soil*Water	1,92	12.56	<0.0001
Water*Species	5,92	6.42	<0.0001
Soil*Species*Water	5,92	3.10	0.0124

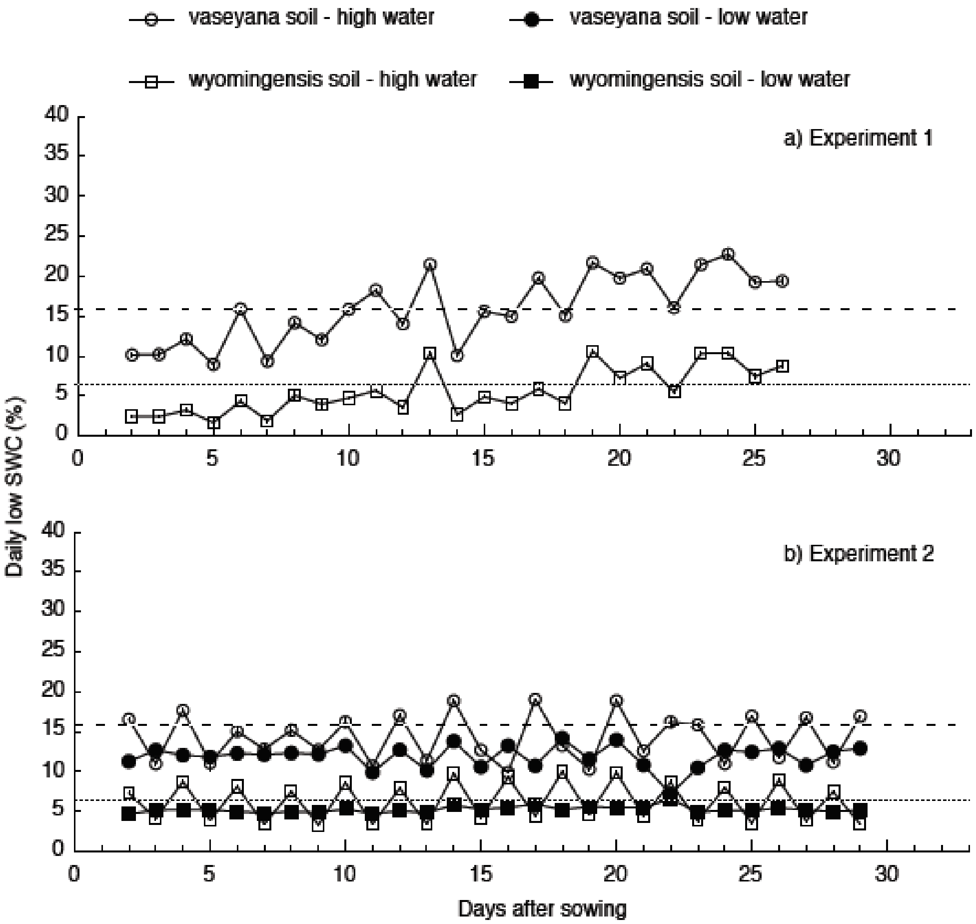

Figure 7. Analysis of daily low soil water content percentages in experiments one and two. Dashed and dotted lines indicate SWC % values at permanent wilting point (i.e., -1.5 MPa) for vaseyana and wyomingensis soils, respectively. Experiment 1 had one water level (i.e., high water content) and Experiment 2 incorporated two water levels (i.e., high and low).

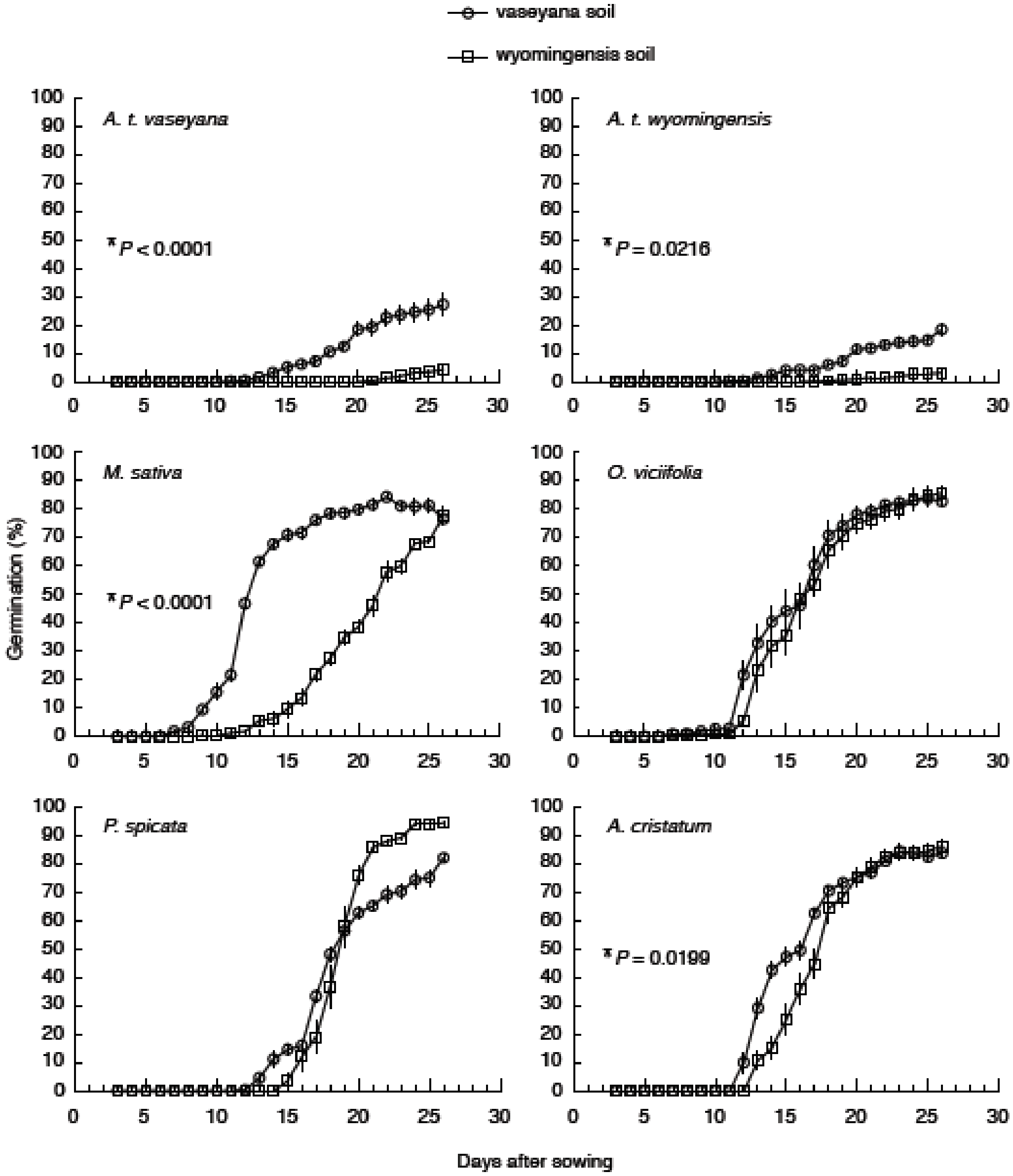

Figure 8. Cumulative daily mean (± SE) percentage emergence of *A. t. vaseyana*, *A. t. wyomingensis, M. sativa, O. viciifolia, P. spicata,* and *A. cristatum* in Experiment 1. Emergence was assessed daily for 26 days in vaseyana and wyomingensis soils; *P*-values indicate significant differences between soils ($P < 0.05$).

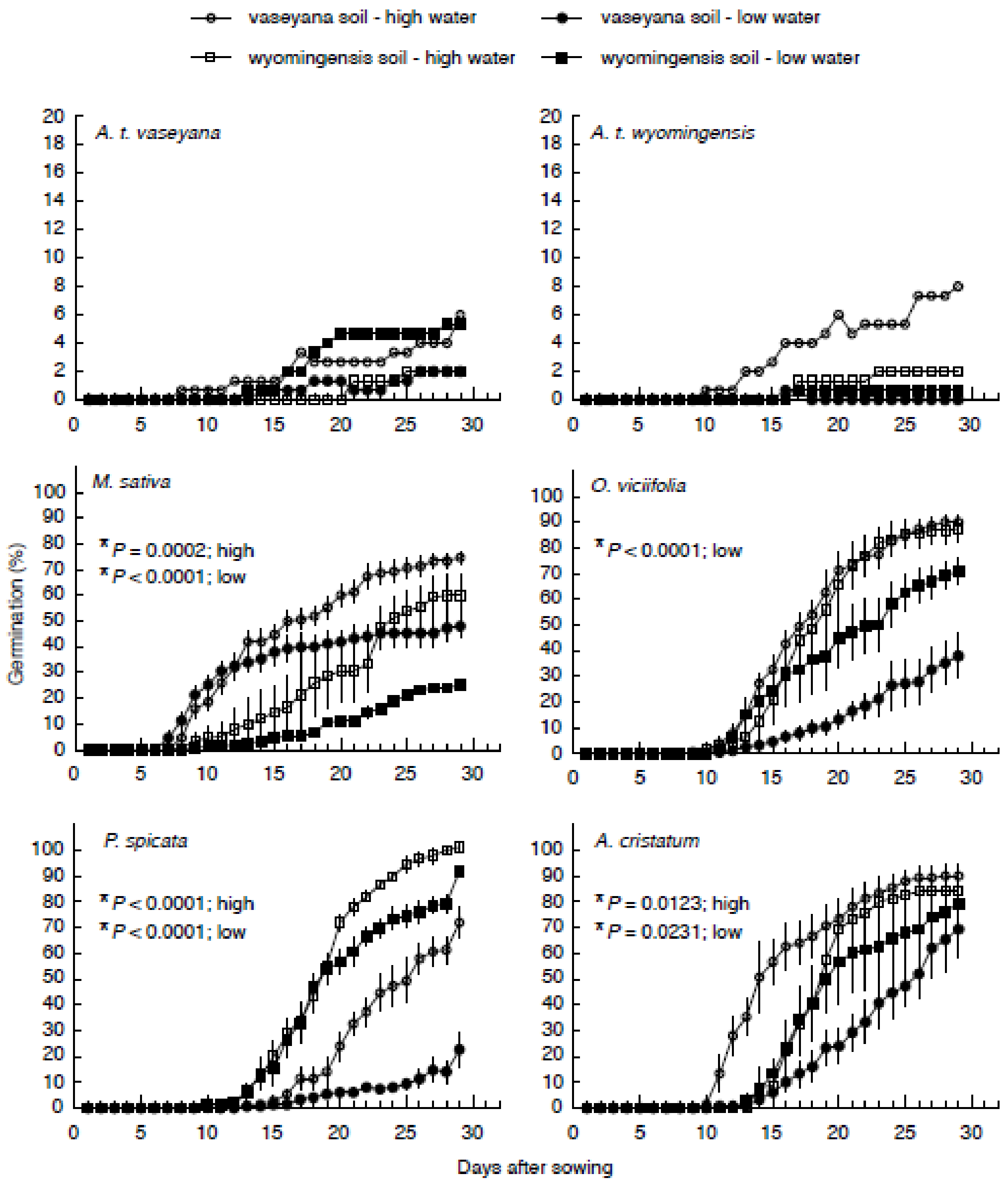

Figure 9. Cumulative daily mean (± SE) percentage emergence of *A. t. vaseyana*, *A. t. wyomingensis*, *M. sativa*, *O. viciifolia*, *P. spicata*, and *A. cristatum* in Experiment 2. Emergence was assessed daily for 29 days in vaseyana and wyomingensis soils maintained at high and low soil water content; within a water content level, *P*-values indicate significant differences between soils ($P < 0.05$).

CHAPTER 4

CONCLUSION

Sagebrush (*Artemisia tridentata* Nutt.) ecosystems are managed to balance the relative dominance of woody shrub species and herbaceous species, prevent environmental damage, and promote a broad range of ecosystem services (Van Auken, 2009; Eldridge et al., 2011; Archer et al., 2017). My research sheds light on how shrub removal treatments and restoration seedings help remediate degraded understory conditions, which has been a long standing challenge to managing sagebrush ecosystems (Monsen, 2004). In Chapter 2, seeded grasses experienced greater increases in abundance after shrub removal than forbs and shrubs; however, these increases were primarily driven by a single, high performing species within each functional group. Increases over time were also higher for introduced species compared to native species. The interaction between species identity and treatment was most dramatic over the long term (5-10 yrs), primarily due to fire having a greater influence on seeded species than the mechanical treatments

In Chapter 3, I determined how soils from two different big sagebrush plant communities (i.e., wyomingensis; *Artemisia tridentata ssp. wyomingensis* and vaseyana; *Artemisia tridentata ssp. vaseyana*) influence emergence patterns of six commonly seeded restoration species. My study identified that differences in soil texture and organic matter (OM) created fundamental differences in soil water holding capacities and evaporation between vaseyana and wyomingensis soils. I found that finer-textured vaseyana soils held more water than course-textured wyomingensis soils, yet at a given soil water content (SWC), seeds in vaseyana soil were exposed to greater water stress (Jensen, 1990; McArthur, 2005). There was large variation in the emergence patterns among species, thus, greater water holding capacity of vaseyana soils did not necessarily lead to higher emeregence compared to coarser wyomingensis soil. In a second experiment, I varied SWC to determine whether SWC and soil type had interactive effects on seedling emergence. Results showed strong interaction between these factors; however, species did not consistently show higher emergence in vaseyana soil and only a few species experienced greater differences between soils under the SWC treatment. Emergence was generally greater in vaseyana soil and within the high water treatment, yet the low water treatment did not seem to prevent any of the species from emerging. In a few cases, the magnitude of differences in emergence between the two soils was greater under low water treatments, which was likely caused by alternating wet/dry cycles promoting water imbibition and increasing germination. These findings provide greater understanding of species suitability for restoration sites and new insights into site-related constraints on seeding success.

My findings can help researchers and restoration practitioners understand which species perform best at big sagebrush project sites. Furthermore, fundamental differences in emergence patterns between soils from commonly rehabilitated big sagebrush sites suggests that further research is needed to characterize soils based on the temporal dynamics of alternating wet/dry cycles. Such information could assist in determining the suitability of sites for proposed restoration seedings as well as selecting the most appropriate species to plant.

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APPENDICES

Appendix 1. Summary of project sites showing treatment type, seeding method (A, aerial; B, broadcast; and D, drill), seeding/treatment year, and general site characteristics.

Project Site	Treatment	Seeding method	Years pre- and post-monitoring	Elevation (m)	Aspect
Brown’s Field	Aerator	D	2008-2011	1712	NW
Brown’s Park db Drum	Aerator	B	2005-2008, 2012	1661	SW
Cache Cave 1	Aerator	B	2004-2007, 2011	2003	N
Cache Cave 2	Aerator	B	2004-2007, 2012	1996	N
Consumer Bench	Aerator	B	2004-2009, 2012	1859	S
Consumer Bench 2	Aerator	B	2005-2008, 2012	1867	NE
Consumer Bench North	aerator	B	2004-2009, 2012	1829	N
Deadman Greenstrip	aerator	D	2007-2011	1768	S
Deep Creek	aerator	A, D	2005-2008, 2011	1676	NE
Duck Creek 1	aerator	B	2003-2006, 2011	2222	NW
Duck Creek 3 Low	aerator	B	2003-2006, 2009	2012	NE
Dugout	aerator	B	2004-2008, 2013	1999	NW
Hart Draw Flat 1	aerator	B	2005-2008, 2013	1935	N
Hart Draw Flat 2	aerator	B	2005-2008, 2013	1935	SW
Harts Draw	aerator	B	2004-2009	1951	SW
Harts Windmill	aerator	B	2005-2008, 2013	1920	W
Porphyry Bench	aerator	B	2004-2009	1920	W
Purple Cabin	aerator	A	2005-2008, 2013	2134	N
Upper Porphyry	aerator	B	2004-2007, 2012	1929	NE
Anderson Dixie	pipe harrow	B	2007-2010, 2011	1570	W
Beaver Easement Harrow	pipe harrow	B, A	2008-2011	1920	S
Bell Draw Dixie	pipe harrow	B	2006-09, 2010	2103	NE
Brush Creek Dixie	pipe harrow	D	2010-2012	1756	SE
Buckskin Valley Highway	pipe harrow	B	2005-2008, 2013	2172	W
Chew Dixie	pipe harrow	B	2006-2009	2347	NW
Diagonal/Electric Harrow	pipe harrow	B	2008-2009, 2010	1736	Flat
East Pasture Harrow	pipe harrow	B	2007-2012	1768	W
Elbow Ranch 1	pipe harrow	B, D	2004-2012	1868	W
Fountain Green Dixie	pipe harrow	B	2006-2010	1768	SW
Hamlin Valley Harrow	pipe harrow	B	2008-2011	2621	SE
Harvey John Mesa	pipe harrow	B	2006-2010	2164	SW
Ibapah Harrow	pipe harrow	B	2007-2012	1835	W
Ibapah Harrow (2)	pipe harrow	B	2008-2012	1798	W
Lower Dog Flat	pipe harrow	B	2004-2009, 2013	2469	S
Mountain Home Seeding	pipe harrow	B	2003-2008, 2013	2286	NW
North Narrows Dixie	pipe harrow	B	2008-2010, 2013	2065	W
North Spring	pipe harrow	B	2006-2010	1890	S
Panguitch East Beach	pipe harrow	B, A	2004-2007, 2012	2134	SW

P-Hill Dixie	pipe harrow	B	2005-2008, 2013	1920	E
Poverty Dixie	pipe harrow	B	2005-2010, 2013	1798	N
Row of Pines Exclosure A	pipe harrow	B	2004-2009, 2013	2454	SE
Sage Valley Dixie	pipe harrow	B	2006-2008, 2010	1890	NE
Scofield Dixie	pipe harrow	B	2008-2011	2398	NE
SITLA Dixie	pipe harrow	B	2006-2009, 2010	2073	SE
SITLA Dixie 2	pipe harrow	B	2006-2012	2073	SE
South Narrows	pipe harrow	B	2004-2007, 2012	2045	S
Stateline North	pipe harrow	B	2006-2009, 2013	2036	E
Trout Creek Dixie	pipe harrow	B	2006-2010	2332	W
West Stuntz	pipe harrow	B	2006-2010, 2013	2393	NW
Wildcat Dixie Harrow	pipe harrow	B	2008-2010, 2013	2578	N
Yergy	pipe harrow	S	2003-2008	2176	Flat
Big Cedar Cove	fire	A	2003-2008, 2013	1844	SW
Big Hollow	fire	A	1997-2002, 2007	1966	SE
Buckskin 1	fire	A	2005-2008, 2013	1925	N
Doubleup Hollow	fire	A	2003-2008, 2013	2323	S
Mouth of Blacksmith Fork	fire	A	2006-2011	1494	W
Pack Creek	fire	B	2007-2010	1798	N
Peter’s Canyon	fire	B	2007-2010	2957	SE
Quacking Aspen Spring	fire	A, B	1999-2004, 2010	2073	NW
Tintic Knapweed Control	fire	D	2008-2011	1798	E
Tobin Bench	fire	A	2003-2008, 2013	1417	E
Wide Canyon	fire	A	2003-2008	1682	W
Hereford 1	fire	D, A	2005-2008, 2013	1631	SW
Coldwater 1	fire	D	2005-2009, 2013	1451	E