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Seedling emergence patterns of six restoration species in soils from two big sagebrush plant communities

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ABSTRACT.—Despite the critical need to improve degraded herbaceous understory conditions in many semiarid ecosystems, the influence of soil properties on seedling emergence of species seeded in shrubland plant communities is largely unexplored. We evaluated emergence patterns of 6 restoration species in soils from wyomingensis (i.e., Wyoming big sagebrush, *Artemisia tridentata* ssp. *wyomingensis* [Beetle & A. Young] S.L. Welsh) and vaseyana (i.e., mountain big sagebrush, *A. t.* ssp. *vaseyana* [Rydb.] Beetle) plant communities that differed in soil texture, soil organic matter content, and soil water-holding capacity. We conducted 2 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. Our objectives were to compare soil attributes of wyomingensis and vaseyana soils, evaluate whether emergence patterns of restoration species vary within these soils, and determine how these patterns are altered by soil water-content levels. We found differences in soil texture and organic matter between soils and thus soil water-holding capacity: finer-textured vaseyana soils held roughly twofold more water than coarse-textured wyomingensis soils. Seeds in vaseyana soils were exposed to fewer wet-dry cycles compared to wyomingensis soils because of the greater capacity of vaseyana soils to retain water. Restoration species also collectively exhibited greater emergence in vaseyana soils than in wyomingensis soils, yet emergence patterns were vastly different among species, and differences between soils became more pronounced under low soil water for only 2 species. We conclude that the manner in which soils and water uniquely influenced emergence patterns provides new insights into species suitability for restoration sites and how inherent soil differences may constrain seeding success.

RESUMEN.—A pesar de la necesidad imperante de mejorar las condiciones deterioradas de los sotobosques herbáceos en muchos ecosistemas semiáridos, la influencia que tienen las propiedades del suelo, en la aparición de las plántulas de especies sembradas en las comunidades de matorrales es ampliamente inexplorada. Evaluamos los patrones de emergencia de seis especies en restauración en suelos de comunidades de artemisa wyomingensis (*Artemisia tridentata* ssp. *wyomingensis* [Beetle & A. Young] S.L. Welsh) y artemisa vaseyana (*A. t.* ssp. *vaseyana* [Rydb.] Beetle), estas comunidades de plantas difirieron en textura, contenido de materia orgánica y capacidad de retención de agua del suelo. Llevamos a cabo dos experimentos separados en los que se humedecieron los suelos regularmente hasta estandarizar su potencial de agua (i.e. capacidad de campo; -0.03 MPa), dando lugar a diferencias en la evaporación, con el fin de generar distintos patrones cíclicos de humedad/sequía, durante un período de 26–29 días. Nuestros objetivos fueron (1) comparar los atributos de los suelos de wyomingensis y de vaseyana, (2) evaluar si los patrones de emergencia de las especies en restauración varían entre cada tipo de suelo y (3) determinar cómo estos patrones son alterados por el contenido de agua en el suelo. Encontramos diferencias en la textura y en el contenido de materia orgánica entre los distintos tipos de suelos y, por lo tanto, en su capacidad de retención de agua. La textura fina del suelo de artemisa vaseyana retuvo aproximadamente el doble de agua que el suelo con de textura gruesa de artemisa wyomingensis. Las semillas en los suelos de vaseyana fueron expuestas a menos ciclos humedad/sequía en comparación con el suelo de wyomingensis, debido a la mayor capacidad de retención de agua del suelo de vaseyana. En general, las especies en restauración mostraron mayor recuperación en el suelo de vaseyana que en el de wyomingensis. No obstante, los patrones de recuperación difirieron ampliamente entre las especies. Únicamente en dos especies las diferencias entre el suelo se hicieron más pronunciadas por la escasez de agua en el suelo. Concluimos que la forma en que los suelos y el agua influyen en los patrones de emergencia de las especies, proporciona nueva información acerca de la susceptibilidad de las especies en los sitios de restauración y cómo las características inherentes del tipo de suelo pueden limitar el éxito de la siembra.

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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 semidesert 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 (Davies et al. 2007, Meinke et al. 2009, Chaney et al. 2017). For example, 2 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; Meinke et al. 2009) and vary widely in terms of resilience to environmental stress and resistance to invasion by exotic annual grasses, as well as in temperature and precipitation regimes (Wisdom and Chambers 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 higher in 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 in both communities to improve ecosystem health by remediating degraded herbaceous understory conditions (West 1988, Miller et al. 2011). Some species may be more or less suitable for a given community type; thus, inquiry into species performance will identify potential site-specific limitations on seeding success and inform future restoration activities.

The roles of soil texture and soil organic matter in determining plant community

dynamics and restoration potential have 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). Sandy soils have high porosity and low water-holding capacity (WHC), while clayey soils have higher bulk density, greater surface area, and higher WHC (Noy-Meir 1973, Lin et al. 1997). Soil organic matter (OM) content also strongly influences WHC of soils and water retention; namely, increasing OM generally increases WHC (Baumann and Bauer 1974, Naeth et al. 1991, Hudson 1994, Huntington 2006). Accordingly, differences in soil texture and OM content between *wyomingensis* and *vaseyana* soils may lead to considerable variation in WHC (i.e., Jensen 1989, 1990).

Seed germination and seedling emergence are recognized as major regulators of restoration success in semiarid ecosystems in the Intermountain West (James et al. 2013, Svejcar et al. 2014). However, little is known regarding how WHC influences germination and seedling emergence 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 by seed enhancements to remedy restoration barriers (Mangold et al. 2007, Hardegee 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. 1990, Brabec et al. 2015). Inherent site differences in WHC among sagebrush soils may dictate the amount of water freely available for seeds to imbibe and germinate (e.g., Evans and Etherington 1990) as well as the matric water potential (i.e., water stress) and retention when soils are exposed to evaporation, all of which directly influence potential germination and seedling emergence of seeds (Doescher et al. 1985, Wuest and Lutcher 2013). Thus, seeds in *wyomingensis* and *vaseyana* soils could experience vastly different soil water conditions, which may become more pronounced under lower soil moisture contents due to greater

water retention and lower evaporation in finer-textured vaseyana soil and more rapid evaporation in coarse-textured wyomingensis soil.

Native species seedling establishment patterns have been correlated with habitat conditions (i.e., elevation, temperature) 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 seedling emergence patterns is poorly understood. Furthermore, controlled experiments have not previously been conducted to develop a mechanistic understanding of how the soil properties known to regulate WHC might influence seedling emergence patterns. To clarify these relationships, we evaluated the effects of vaseyana and wyomingensis soils on emergence patterns of 6 restoration species commonly seeded on degraded sagebrush plant communities in the Intermountain Region. A novel experimental design was developed to account for expected WHC 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 periods of emergence. We tested 3 hypotheses: (1) seedling emergence is higher in vaseyana soils due to greater WHC and water retention than in wyomingensis soils; (2) different seedling emergence patterns develop over time in vaseyana and wyomingensis soils; and (3) differences in seedling emergence patterns between vaseyana and wyomingensis soils become more pronounced under low SWC due to greater evaporation in wyomingensis soils. Assessing emergence patterns of these 2 soils will improve our understanding of species suitability for restoration sites and provide insights into site-related constraints on seeding success.

METHODS

Site Descriptions

Soils from 2 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, Utah

($41^{\circ}49'26.21''$ N, $113^{\circ}17'25.21''$ 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 Semi-desert 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] Å. Löve). Long-term (30-year; 1986–2016) mean 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, Utah ($41^{\circ}33'15.77''$ N, $111^{\circ}57'9.27''$ 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 (30-year; 1986–2016) mean 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 shrub plants

within a single 10 × 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 3 weeks before sieving through a 1-cm wire mesh to remove large organic material and rock.

Air-dried subsamples from each soil ($n = 5$) were analyzed for cation exchange capacity (CEC), organic matter content (OM), WHC (determined by percent soil water content [SWC %] at -0.03 MPa, -1.5 MPa, and soil saturation), pH, and percentages of sand, silt, and clay. CEC and OM were determined with flow injection analysis (Quick Chem 8500, Lachat Instruments, Loveland, CO) using the ammonium replacement method (Gavlak et al. 2005) and the dichromate oxidation method (Walkley and Black 1934), respectively. Percentage SWC values were 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 percent sand, silt, and clay using the slurry and hydrometer 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 pH meter; Thermo Scientific Beverly, MA). To quantify percent 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. The resultant solution was placed into a 1-L cylinder, which was then filled with deionized water. A custom plunger was used to mix the slurry before its temperature ($^{\circ}\text{C}$) and density (g/L) were measured with a Bouyoucos hydrometer (14-331-5C; Thermo Scientific, Beverly, MA) after 30 s and again after 1440 min. Soil variables were compared between soils using the unpaired (i.e., independent samples) 2-sample Student's t test ($\alpha = 0.05$).

Plant Species

Six species commonly used in restoration projects in the Great Basin, Rocky Mountain,

and Colorado Plateau ecoregions in the Intermountain West were selected for our study (UWRI; <https://wri.utah.gov/wri>; Lambert 2005, Wilder et al. 2018). These included the shrubs Wyoming and mountain big sagebrush, 2 forbs (alfalfa *Medicago sativa* [L.] and sanfoin *Onobrychis viciifolia* Scop.), and 2 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 (shrubs—wildland collected at Piute/Wayne/Sevier counties in Utah in fall 2016) and Wheatland Seed, Brigham City, Utah (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: Emergence under Field Capacity

To study the influence of sagebrush soils on seed emergence over time, 100 seeds of each species were sown in plastic containers (11 × 11 × 4 cm [L × W × H]) filled with 50 g of either vaseyana or wyomingensis soil (5 replicates × 2 soils × 6 species = 60). This sowing density was chosen because it allowed seeds to be equally spaced 1 cm apart in a 10 × 10 grid and because it allowed for easy calculation of percent emergence as opposed to matching a seeding rate used in restoration. Following seeding recommendations of Jensen et al. (2001), we then covered seeds with either 1 mm of soil (sagebrush) or 3 mm of soil (all other species) and placed unsealed containers in a growth chamber with onboard environmental controls (model PGW132, IntellusUltra C8T, Percival, Perry, IA) 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 2 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 soil water is available and the risk of seedling mortality from freezing temperatures is low (Jensen et al. 2001). We obtained average

TABLE 1. Mean (\pm SE; $n = 5$) soil measures and statistical comparison (unpaired Student's t test and P value) of 2 big sagebrush plant community soils used in seed germination experiments (wyomingensis = Wyoming big sagebrush [*Artemisia tridentata* ssp. *wyomingensis*] and vaseyana = mountain big sagebrush [*A. t.* ssp. *vaseyana*]).

Soil measure	vaseyana soil	wyomingensis soil	t	P
Organic matter (%)	7.86 \pm 0.06	3.78 \pm 0.13	34.23	<0.0001
SWC % (-0.03 MPa)	34.58 \pm 0.49	20.82 \pm 0.36	16.63	<0.0001
SWC % (-1.5 MPa)	15.34 \pm 0.16	6.51 \pm 0.15	52.85	<0.0001
SWC % (saturated soil)	58.90 \pm 0.59	29.43 \pm 0.35	45.90	<0.0001
Sand (%)	15.61 \pm 0.85	65.60 \pm 0.31	-57.11	<0.0001
Silt (%)	47.83 \pm 0.84	23.34 \pm 0.29	26.15	<0.0001
Clay (%)	36.52 \pm 0.43	11.06 \pm 0.09	64.93	<0.0001

hourly air temperature and RH data for Tremonton from the Utah Climate Center (<https://climate.usurf.usu.edu/agweather.php>) and calculated mean daytime (09:00–21:00) and nighttime (21:00–09:00) 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 $\mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$ to prevent high rates of evaporation within the small containers over a 24-h period. To begin the experiment, SWC of each container was adjusted gravimetrically according to values equating to field capacity (i.e., -0.03 MPa) for each soil (i.e., 35% and 21% for vaseyana and wyomingensis soils, respectively; Table 1). Thereafter, we recorded daily low SWC (i.e., after a 24-h period) for each container and readjusted SWC to field capacity by applying water as a fine mist to the soil surface using a spray bottle. In addition, we recorded emergence (based on the appearance of a coleoptile extending 2 mm above the soil surface) for each container for 26 d, a period after which no additional emergence was detected for 3 consecutive days (Supplementary Material 1). Emergence data were assessed for normality and homogeneity of variance, then analyzed for final seedling emergence with mixed-model ANOVA (Hypothesis 1) and repeated measures MANOVA (Hypotheses 2). Both models used a randomized complete block design and were analyzed as a factorial experiment with species and soils as fixed factors and replication as a random effect ($\alpha = 0.05$). Repeated measures analyses tested the null hypothesis that patterns (i.e., profiles) of emergence are the same between the soils. Final emergence values revealed that emergence was generally higher in vaseyana soil compared to wyomingensis soil. Consequently,

we used mean seedling emergence percentages in vaseyana soil as an in situ estimate of maximum species emergence in order to modify sowing densities in Experiment 2.

Experiment 2: Emergence under Variable Water Levels

To study the interactive influence of soil water content and sagebrush soil on seedling emergence patterns, we followed the same procedures of Experiment 1, but to minimize intraspecific competition within the small containers, seeds were sown at a lower density and emergence was tracked over a 29-d period, a period after which no additional emergence was detected for 3 additional days (Supplementary Material 1). Using maximum emergence estimates obtained from Experiment 1, sowing density was calculated for each species in order to potentially yield 30 seedlings per container. Total soil weight within containers was increased to 200 g; increased soil volume allowed us to create distinct watering levels that could be maintained feasibly over a 24-h period. A total of 120 containers were prepared for the experiment (2 soils \times 2 water levels \times 6 species \times 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 were recorded daily even if water adjustments were not necessary. Seedling emergence data were assessed for normality

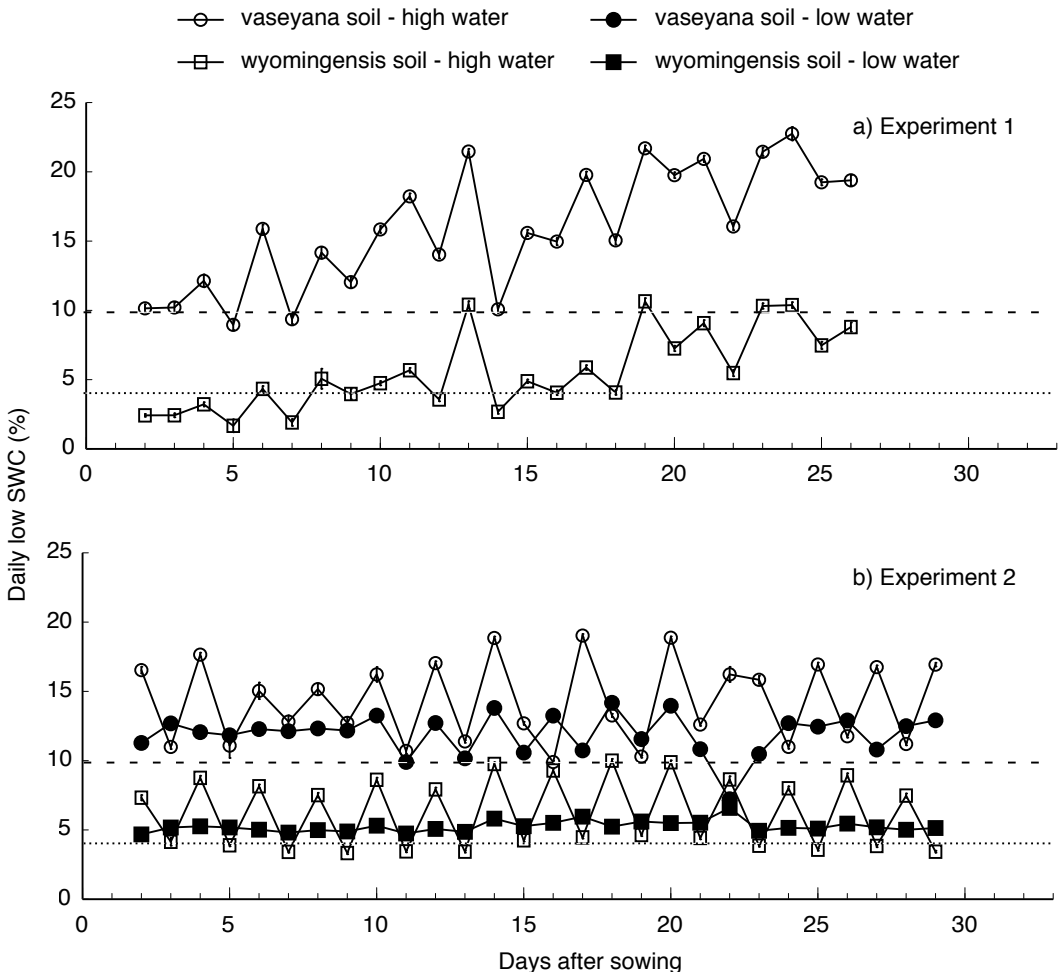


Fig. 1. Analysis of daily-low percent soil water content (SWC) in Experiments 1 and 2. Dashed and dotted lines indicate SWC values at the permanent wilting point (i.e., -1.5 MPa) for vaseyana (mountain big sagebrush, *Artemisia tridentata* ssp. *vaseyana*) and wyomingensis (Wyoming big sagebrush, *A. t.* ssp. *wyomingensis*) soils, respectively. Experiment 1 had one water level (i.e., high water content) and Experiment 2 incorporated 2 water levels (i.e., high and low water content).

and homogeneity of variance and analyzed as described in Experiment 1, but with the additional factor of water level in order to test Hypothesis 3. Statistical analyses in both experiments were conducted in JMP ver. 13 (SAS Institute Inc., Cary, NC).

RESULTS

Soil Properties and Water Content

Differences between vaseyana and wyomingensis soils were highly significant (Table 1, Supplementary Material 2). Organic matter as well as the silt and clay content of vaseyana

soil were typically twofold higher than those of wyomingensis soil (Table 1). Sand content of wyomingensis soil was roughly fourfold higher than of 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, WHC (i.e., SWC at predetermined water potential) of vaseyana soils remained much higher relative to wyomingensis soils for both experiments (Fig. 1). Even when distinct soil water levels were applied in Experiment 2, the low water level of vaseyana soil maintained higher daily-low percent SWC than

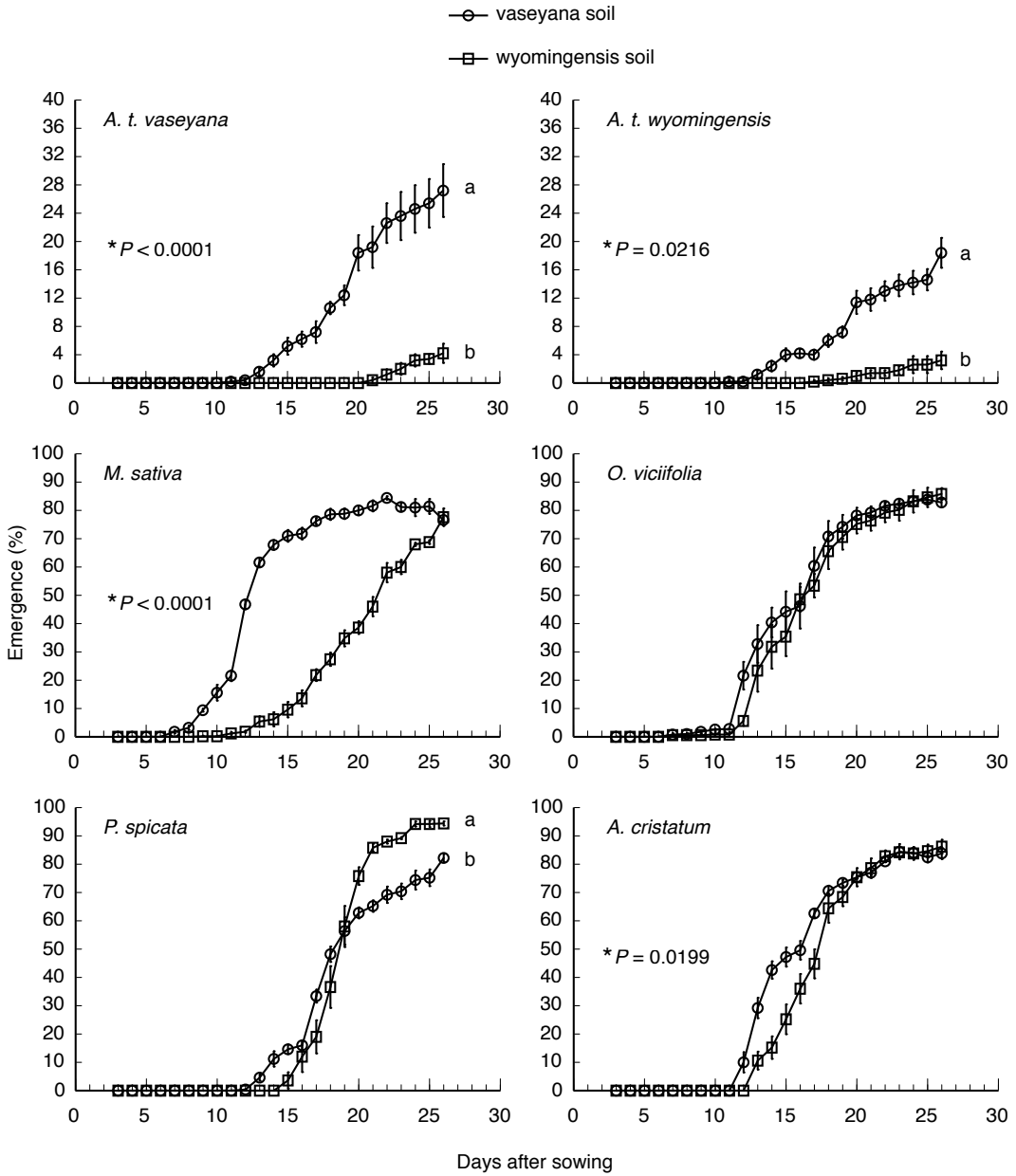


Fig. 2. Daily percent emergence (mean \pm SE) of 6 species (*Artemisia tridentata vaseyana*, *A. t. wyomingensis*, *Medicago sativa*, *Onobrychis viciifolia*, *Pseudoroegneria spicata*, and *Artemisia cristatum*) in Experiment 1. Emergence was assessed daily for 26 d in vaseyana (mountain big sagebrush, *Artemisia tridentata* ssp. *vaseyana*) and wyomingensis (Wyoming big sagebrush, *A. t. ssp. wyomingensis*) soils. *P* values indicate significant differences between soils and lower-case letters indicate significant differences between final emergence values. Note that different *y*-axis scales are used.

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 (i.e., mean \pm SE, pooled across species) was approximately dou-

ble 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 ; $t = 15.2$, $df = 6$, $P < 0.0001$).

TABLE 2. Results of MANOVA showing degrees of freedom (df), *F* statistics, and *P* values for the effects of sagebrush community soil (wyomingensis = Wyoming big sagebrush [*Artemisia tridentata* ssp. *wyomingensis*] and vaseyana = mountain big sagebrush [*A. t.* ssp. *vaseyana*]) on germination of 6 species in Experiment 1.

Effect	df	<i>F</i>	<i>P</i>
Soil	1, 48	83.68	<0.0001
Species	5, 48	290.52	<0.0001
Soil * Species	5, 48	26.01	<0.0001

Seedling Emergence

In Experiment 1, seedling emergence was significantly higher in vaseyana soil than in wyomingensis soil, and species exhibited vastly different patterns in the 2 soils (Fig. 2, Table 2). Final emergence percentages were much higher in vaseyana soil for both sagebrush subspecies compared to the wyomingensis soil, but not for the other 4 restoration 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 patterns of *O. viciifolia* and *P. spicata* were not significantly affected by the different sagebrush soils, although patterns 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 2), final percentage values (mean \pm SE, pooled for species) differed by <4% (i.e., 61.8 \pm 5.2 vs. 58.6 \pm 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 was generally rapid and high for the combination of high water and vaseyana soil for many species, yet a number of exceptions were observed (Fig. 3). For example, unlike the other species, final emergence of *P. spicata* in wyomingensis soil exceeded that in vaseyana soil regardless of soil water level. In addition, *O. viciifolia* showed greater emergence in wyomingensis than in vaseyana soil under low water. Water levels also modulated emergence patterns differently among species (Fig. 3, Table 3). Significant differences in seedling emergence patterns between soils were not found for either sagebrush subspecies or *O. viciifolia* under the high water

level. In contrast, emergence patterns for *M. sativa*, *P. spicata*, and *A. cristatum* were different between soils, regardless of water level. However, differences between soils were more pronounced under low water only for *O. viciifolia* and *P. spicata*. Although pooled-species emergence patterns were significantly different between vaseyana and wyomingensis soils (Table 3), final percentage values (mean \pm SE, pooled for species) were similar under high water (56.0 \pm 5.0 vs. 55.5 \pm 5.9), but quite different under low water (32.8 \pm 3.6 vs. 50.2 \pm 5.2).

DISCUSSION

Our results support the assumption that variations in 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 that these differences suggest a number of important considerations relevant to seed emergence patterns. First, finer-textured vaseyana soils had greater WHC (roughly twofold higher SWC) than coarser-textured wyomingensis soils. Thus, differences in evaporation between soils created fluctuating SWC conditions and highly variable seedling emergence patterns for a broad range of restoration species. For example, differences in SWC between soils exposed germinating seeds in vaseyana soils to fewer watering events and less frequent wet-dry cycles compared to wyomingensis soils. In addition, this signature difference in SWC between soils became more pronounced on emergence in the low water level treatment for 2 of the study species. Second, because soils and species strongly interacted, we rejected our 3 hypotheses because all species did not experience higher emergence rates in vaseyana soil, all species did not experience different emergence patterns in the 2 soils, and differences in emergence patterns between soils were not consistently more pronounced under the low water treatment. Collectively, the rejection of these hypotheses clearly illustrates that there is still much to be learned about the influence of inherent soil properties on seedling emergence of important restoration species.

Differences in soil texture and OM content between wyomingensis and vaseyana soils directly influenced evaporative water loss

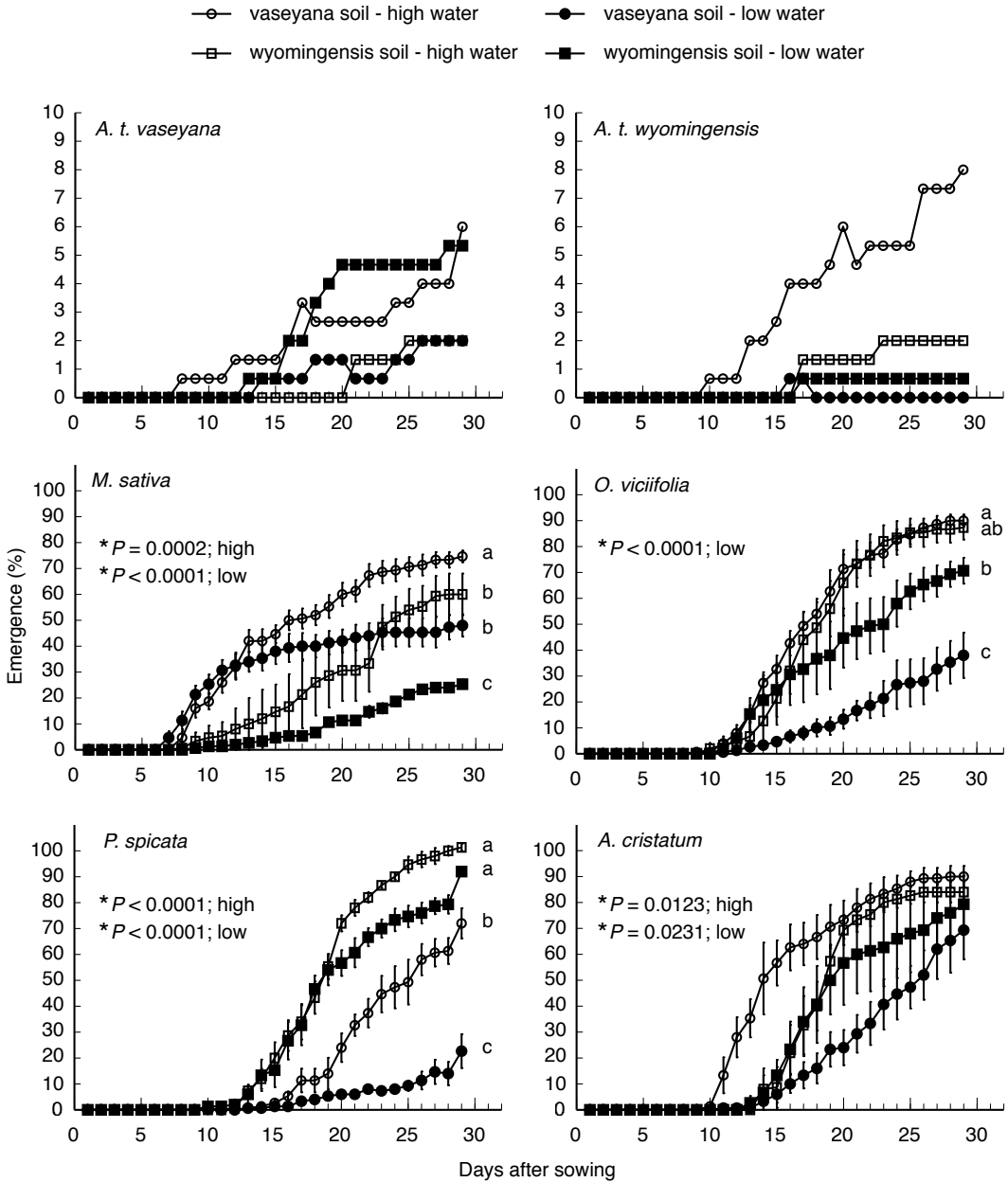


Fig. 3. Daily percent emergence (mean \pm SE) of 6 species (*Artemisia tridentata vaseyana*, *A. t. wyomingensis*, *Medicago sativa*, *Onobrychis viciifolia*, *Pseudoroegneria spicata*, and *Artemisia cristatum*) in Experiment 2. Emergence was assessed daily for 29 d in vaseyana (mountain big sagebrush, *Artemisia tridentata* ssp. *vaseyana*) and wyomingensis (Wyoming big sagebrush, *A. t. ssp. wyomingensis*) soils. Within water content levels, P values indicate significant differences between soils, and lowercase letters indicate significant differences between final emergence values. Note that for easier viewing, error bars are not shown for sagebrush emergence values. Also note that different y -axis scales are used.

(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. 1987), alternating wet-dry cycles have been found to accelerate germination and seedling emergence (Zhu et al. 2014); still, responses can vary

TABLE 3. Results of MANOVA showing degrees of freedom (df), *F* statistics, and *P* values for the effects of sagebrush community soil (wyomingensis = Wyoming big sagebrush [*Artemisia tridentata* ssp. *wyomingensis*] and vaseyana = mountain big sagebrush [*A. t.* ssp. *vaseyana*]) and soil water content levels on germination of 6 species in Experiment 2.

Effect	df	<i>F</i>	<i>P</i>
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

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. 2015). In both of our experiments, interval lengths were greater for vaseyana soil, while 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 wyomingensis high and low water treatments, respectively, compared to the vaseyana soils. 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 final emergence values and emergence patterns among species necessitated rejecting Hypotheses 1 and 2. Instead, we found that the greater WHC of vaseyana soil did not consistently lead to higher emergence or distinct emergence patterns compared to the coarser wyomingensis soil. In fact, emergence differences between soils were evident for only 4 of the 6 species in Experiment 1 (Fig. 2), and of these, only the sagebrush subspecies clearly illustrated greater final emergence values in vaseyana soil. Considering both experiments together, only *M. sativa* and *A. cristatum* responded according to Hypothesis 2. We speculate that the greater emergence in vaseyana soil than in wyomingensis soil for both sagebrush subspecies in Experiment 1, where seeds were planted more shallowly than in Experiment 2, exposed seeds to more rapid evaporation between

watering intervals in wyomingensis soil than in vaseyana soil (e.g., Gill and Jalota 1996), which increased the chances of dry soils desiccating seeds between watering intervals. Sagebrush seeds are very small compared to the seeds of other species in our study, and require shallow seeding depths (Meyer 1994, Walck et al. 2008, Daws et al. 2008). Thus, rapid emergence under the higher SWC 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, a process known to strongly control germination speed and consistency in this legume (Hegarty 1977, 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 to maintain dominance on silty loam soils compared to sandy loam soils in the Intermountain Region (Shown et al. 1969, Williams et al. 2017). In addition, previous research has illustrated that supplementing 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 (Obriest 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 soils are not recharged by precipitation or through hydraulic redistribution. Such diel fluctuation in soil surface water conditions can be extreme, and it reflects (1) daytime depletion due to evaporation and transpiration and (2) nocturnal recharge by hydraulic redistribution and flow of vapor and liquid 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 Hardegee 2004, Hardegee 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, Hypothesis 3 must be rejected because not all individual species responded this way. In fact, *O. viciifolia* and *P. spicata* were the only species with more pronounced differences between soils under low water; however, surprisingly, both species showed higher emergence rates in wyomingensis soil, rather than in vaseyana soil. A mechanism for these unexpected results is difficult to speculate on, but it is possible that longer interval lengths spent at suboptimal water conditions in vaseyana soil reduced emergence relative to coarser wyomingensis soil, which 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 twofold greater germination in sandy compared to clayey 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 and for different species.

Implications

Our results, which show variable species emergence patterns for vaseyana and wyomingensis soils, provide a greater understanding of the mechanisms influencing species suitability for restoration sites and offer new insights into site-related constraints on seedling success. In particular, our observations indicate that a given seed mix will behave differently on wyomingensis versus vaseyana soils. 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 2 soils was greater under low water treatments, which was likely caused by alternating wet-dry cycles promoting water imbibition and increasing germination. This information has relevance to those interested in how drought and climate could change seedling emergence in restoration sites (Wilder et al. 2018). In addition, the variation between species in response to water and soil factors demonstrates that restoration seed mixes could be potentially improved by matching species to specific soil types. To expedite this endeavor, further research is needed to characterize the role of soil texture on seedling emergence of a broader range of important restoration species, while accounting for its influence on the temporal dynamics of alternating wet-dry cycles. Ultimately, this approach could assist in determining the suitability of sites for proposed restoration seedlings, as well as in selecting the most appropriate species to plant.

SUPPLEMENTARY MATERIAL

Two online-only supplementary files accompany this article (scholarsarchive.byu.edu/wnan/vol79/iss2/9).

SUPPLEMENTARY MATERIAL 1. Actual numbers of seeds sown and emergents for 6 species grown in different sagebrush community soils.

SUPPLEMENTARY MATERIAL 2. Mean cation exchange capacity and soil pH compared statistically between 2 big sagebrush plant community soils used in seed germination experiments.

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