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Emergence and early survival of early versus late seral species in Great Basin restoration in two different soil types

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Cheatgrass (*Bromus tectorum*); Ecological resistance; Functional traits; Medusahead (*Taeniatherum caput-medusae*); Niche overlap; Plant–plant interactions; Seedling emergence and survival; Soil–plant relationships

Nomenclature
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Abstract

Questions: How does performance of a native early seral seed mix during early life stages compare to that of a late seral mix when seeded with *Bromus tectorum* or *Taeniatherum caput-medusae*? Does either mix reduce survival of exotic annual grasses during early life stages, and does this effect differ with soil type? Is exotic performance stronger in one soil type, and does native performance when growing with exotics differ between soil types as a result of exotic preference?

Location: University of Nevada Agricultural Research Station, Reno, NV, US.

Methods: We compared seedling emergence and early survival (Nov through May) of two native seed mixes, each composed of grass, forb and shrub functional groups, when growing with *B. tectorum* or *T. caput-medusae* in soils of contrasting texture (sandy loam and clay loam). Natives were also seeded without exotics. Performance of an early seral mix was compared with that of a late seral mix representative of species commonly used in Great Basin restoration.

Results: Comparing emergence and survival probabilities, early seral natives generally outperformed late seral natives when growing with exotics and had earlier emergence timing, although results differed among functional groups and soil types. In contrast, survival probabilities did not differ between the early and late seral mixes when growing without exotics. Within each seed mix, native grasses exhibited the highest emergence probabilities of the functional groups. Natives did not suppress exotics in early life stages. Performance of *B. tectorum* was higher on sandy loam, while *T. caput-medusae* was highly successful in both soil types. Performance of native functional groups differed by soil type when growing with exotics but did not differ when growing without exotics. Survival of native grasses, in particular, was generally higher on sandy loam when growing with exotics.

Conclusions: Findings suggest that the use of early seral natives in areas invaded by exotic annual grasses may improve early seedling survival in the Great Basin, in comparison to the use of later seral species in traditional seed mixes. Variation in native performance in the two soil types may be helpful in tailoring seed mixes to different sites.

Introduction

Native plant communities vary in their ability to resist invasion by exotic species. Resistance to invasion is often thought to be greater in communities with higher native species diversity, where greater niche partitioning and more complete utilization of resources would result in reduced resource availability and thus fewer exotic invaders (Elton 1958; MacArthur & Levins 1967). However, a review of empirical studies challenges this belief, suggesting that increased diversity does not necessarily confer increased resistance to invasion (Levine & D'Antonio 1999). Several studies have shown that plant communities are more resistant to invasion when resident and invading species are of the same functional group and/or have similar resource-use functional traits, a pattern observed across a variety of ecosystems in North America and Europe (Fargione et al. 2003; Turnbull et al. 2005; Young et al.

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2009; Abella et al. 2012). Recent work indicates that increased niche overlap confers increased community resistance to invaders because of increased competition for resources at a local scale (Hooper & Dukes 2010). Success of invaders also varies with abiotic factors, such as differences in soil characteristics (Theoharides & Dukes 2007), and interactions between exotic invaders and native species may also vary from one site to another (Thomsen & D'Antonio 2007). Therefore, knowledge of how plant interactions between functionally similar native and exotic species may vary in different environments would provide important insights for restoration (D'Antonio & Thomsen 2004).

In the Great Basin of the western US, invasion by the exotic annual grasses *Bromus tectorum* (cheatgrass) and *Taeniatherum caput-medusae* (medusahead) and resulting alterations to the fire regime have resulted in conversion of millions of hectares of sagebrush steppe, once dominated by native shrubs and perennial grasses, to annual exotic grasslands (D'Antonio & Vitousek 1992; Pellant & Hall 1994; Bradley & Mustard 2005). Reseeding efforts to restore or rehabilitate after fire are expensive and have generally achieved limited success (Eiswerth & Shonkwiler 2006; Epanchin-Niell et al. 2009). Seed mixtures have traditionally been composed of native species or non-native replacements that would typically be dominant in mid- to late-seral sagebrush steppe (Eiswerth & Shonkwiler 2006; Brown et al. 2008), but competition with exotic annual grasses is thought to be a major barrier to restoration success (Brown et al. 2008). Many native perennial grasses are at a competitive disadvantage during early life stages, when exotics exhibit higher rates of early season growth and resource acquisition (Aguirre & Johnson 1991; Monaco et al. 2003). Furthermore, very low rates of native grass seedling emergence can be a significant recruitment bottleneck in sagebrush steppe (Pyke 1990; Chambers 2000). Survival during early life stages may thus be critical in determining the eventual outcome of restoration reseeding efforts (James et al. 2011).

Ecological restoration may be most effective when one can identify the key functional traits that make an exotic invasive successful and match those key traits with appropriate natives with similar traits (Funk et al. 2008; Drenovsky et al. 2012). Compared to late seral species, the life-history characteristics of early seral species, including annual forbs, may be more closely aligned with those of exotic annual grasses, as they also increase after disturbances such as wildfire (e.g. Goergen & Chambers 2009). For example, similar to *B. tectorum* and *T. caput-medusae*, some native early seral species may have a high probability of germinating in the autumn when there is sufficient soil moisture (Forbis 2010). In addition, traits like earlier seedling emergence and/or faster rates of early growth may help natives survive in the presence of exotic annual grasses (Verdu & Traveset 2005; Rowe & Leger 2011). Because of similarities in functional traits, ecological theory predicts that early seral species would compete more strongly against exotic annual grasses than late seral species (Funk et al. 2008).

The invasion and success of *B. tectorum* and *T. caput-medusae* appears to be associated with soil type, especially for *T. caput-medusae*, thus it is likely that plant competitive interactions are dependent on soil type as well (e.g. Blank 2010). To date, *T. caput-medusae* invasion has been most closely associated with fine-textured to moderately fine-textured soils, such as clays and clay loams (Young & Evans 1970; Dahl & Tisdale 1975). However, in our companion study, we showed that *T. caput-medusae* can also be highly successful in a more coarse-textured soil, but we did not evaluate emergence or survival during early life stages (Uselman et al. 2014). In contrast, *B. tectorum* is able to grow in most soil types, but it is especially successful on coarse-textured loamy soils, including sandy loams commonly occupied by big sagebrush (Young 2000; Welch 2005). However, it is still unclear how soil type affects interactions between seeded natives and exotic annual grasses and an understanding of these effects is needed to inform restoration in the Great Basin.

Our main objective was to compare seedling emergence and early survival of two native species seed mixes (an early seral mix vs a representative traditional late seral mix, each composed of grass, forb and shrub functional groups) when growing in the presence of two exotic annual grasses (either *B. tectorum* or *T. caput-medusae*), using two different soil types contrasting in texture (a clay loam vs a sandy loam). In our companion study, we reported biomass production, seed production and first-year establishment data (Uselman et al. 2014). In this study, we present a detailed examination of emergence, timing of emergence and early seedling performance because early life stages (i.e. seed and seedling stages) have been found to be the limiting step in other Great Basin restoration projects (James et al. 2011). We evaluated the following hypotheses: first, we hypothesized that the early seral seed mix would be more successful, with higher and earlier emergence and higher survival during early life stages in comparison to the late seral mix when growing in the presence of an exotic annual grass because of greater similarities in functional traits. Second, we hypothesized that the early seral seed mix would have a higher potential suppressive effect on exotic annual grasses in comparison to the late seral seed mix during early life stages, and this effect would be strongest in the soil type to which the exotic is presumed to be least well adapted. Third, we hypothesized that exotics would have higher emergence and survival when growing in the soil type to which the exotic

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is presumed to be most well adapted. Based on anecdotal evidence, we predicted *T. caput-medusae* would be most successful in the clay loam, while *B. tectorum* would be most successful in the sandy loam. For the native seed mixes, we hypothesized that performance would differ by soil type when growing with exotics due to soil preference of the exotics. Given that these natives are relatively widespread, we predicted native performance would not be affected by soil type when growing alone.

Methods

Common garden: experimental design and implementation

To test different species combinations in two different soil types while controlling for environmental conditions, we used a common garden approach. In early October 2010, we sunk soil-filled treepots (6.2 l; 41-cm deep, 15 × 15 cm surface area; TPOT2, Stuewe and Sons, Inc., Tangent, OR, US), containing either a clay loam or sandy loam (see *Soil collection* below), into the ground at the University of Nevada Agricultural Experiment Station in Reno, NV (39°32′ N, 119°48′ W, 1370 m a.s.l.). The site consists of deep, well-drained alluvial soils classified as fine loamy, mixed, superactive, mesic Aridic Argixerolls (USDA Web Soil Survey (http://websoilsurvey.nrcs.usda.gov; accessed 12 May 2010). Pots filled with the two soils were randomly distributed across the 650-m^2 field, with a minimum distance of 45 cm between pots. The study area was fenced with cattle panels lined with 0.64 cm hardware cloth and trenched 30 cm into the ground to exclude small mammals.

Total precipitation for the 2011 water year was 253 mm at the study site, which is higher than the average of 178 mm for Reno, NV (Western Regional Climate Center, DRI), but close to the average range for the Wyoming big sagebrush zone of sagebrush steppe in the Great Basin (i.e. 254–305 mm). For the most part, seasonal patterns in soil moisture followed patterns typical of the Great Basin, with highs in winter and lows in summer. During the study period, soil volumetric water content (0–12 cm) was 8.3 ± 0.3% and 18.3 ± 0.8% in mid-Nov, 24.0 ± 0% and 34.5 ± 2.5% in late Dec, and 7.7 ± 0.3% and 20.0 ± 0.6% by late May in the sandy loam and clay loam, respectively (Uselman et al. 2014). In the sandy loam, the average annual soil temperature was 13.2 °C, varying between −1.4 °C in Dec and 29.7 °C in Jul at 1 cm (data not shown). In the clay loam, the average annual soil temperature was 13.4 °C, varying between −1.7 °C in Dec and 30.7 °C in Jul at 1 cm.

Three separate experiments were performed concurrently to test exotic and native plant performance under the same climatic conditions, using completely randomized designs. Two parallel experiments, one with the exotic annual grass *B. tectorum* and the other with *T. caput-medusae*, were conducted to assess the performance of an early seral native seed mix vs a late seral seed mix (see *Seed mix species selection* below) when growing in the presence of an exotic annual grass. These experiments were also designed to test the relative performance of the two exotic annual grasses when growing with and without natives. In these 2 × 3 factorial experiments, two levels of soil type (clay loam and sandy loam) were crossed with three levels of seed mix (early seral mix, late seral mix and no mix; Table 1a,c). A third experiment was designed to evaluate the performance of natives when growing in the absence of exotics. In this 'No Exotic' experiment, two levels of soil type (clay loam and sandy loam) were crossed with two levels of seed mix (early seral mix and late seral mix; Table 1b).

In October 2010, seeds were precisely sown by hand into one of 20 randomized locations in each pot using a 20-location fixed grid template. In the 'No Exotic' experiment, two species combinations were used: (1) early seral native species only (ten seeds, consisting of two seeds from each of five species) and (2) late seral native species only (ten seeds, consisting of two seeds from each of five species). In the two parallel experiments with exotic grasses, three species combinations were used: (1) exotic species only (ten seeds), (2) exotic and early seral native species together (ten + ten seeds), and (3) exotic and late seral native species together (ten + ten seeds). In the latter experiments, we used an additive design to assess the effect of natives on exotics, maintaining a constant density of the

Table 1. Experimental design for the three concurrent experiments.

Soil Type	Seed Mix		
	Early Seral (*n*)	Late Seral (*n*)	No Mix (*n*)
(a) *Bromus tectorum* Experiment			
Clay Loam	23	23	15
Sandy Loam	23	23	15
(b) No Exotic Experiment			
Clay Loam	9	9	
Sandy Loam	9	9	
(c) *Taeniatherum caput-medusae* Experiment			
Clay Loam	23	23	15
Sandy Loam	23	23	15

In (a) and (c), treatments composed of exotics only were replicated 15 times (two soil types × 15 replicates = 30) and treatments composed of exotics with natives were replicated 23 times (two soil types × two seed mixes × 23 replicates = 92), for a total of 122 experimental units in each of the two parallel experiments. We increased the replication for treatments composed of a combination of exotics and natives because we anticipated greater variation within these treatments. In (b), the native only treatments were replicated nine times (two seed mixes × two soil types × nine replicates), for a total of 36 experimental units. Treatment replicates were randomly assigned in the field.

target exotic and varying the presence/absence of the potential competitor. This is preferable to using a replacement series, where pot densities are kept constant, as replacement series designs can confound potential effects of intraspecific competition among the exotic seedlings with the effects of interactions with natives (Snaydon 1991). Seeding rates used in this study were within the range of recommended seeding rates suggested for rangelands (Monsen & Stevens 2004). All species combinations and soil types were assigned randomly to locations in the common garden. Grasses were sown to a depth of 1.27 cm, simulating use of a rangeland drill with depth band. Forbs and shrubs were sown to a depth of 0.32 cm to achieve surface to near-surface seeding and ensure seed-to-soil contact in seed placement, simulating usage of a surface seeder or seed dribbler (Stevens & Monsen 2004).

Individual seed locations were monitored weekly to biweekly, using the grid template, for seedling emergence and emerged seedling survival from the date of first emergence in early Nov 2010 through the end of May 2011. Use of the grid template during monitoring also allowed removal of non-seeded individuals originating from the soil seed bank. We were not able to monitor during periods of snow cover. During these periods, the longest monitoring interval was 3 weeks.

Seed mix species selection

Species in the traditional late seral seed mix were selected from species typically used in Great Basin restoration reseedings. This seed mix was entirely perennial species, composed of two forbs, two grasses and one shrub: *Penstemon palmeri* (Scrophulariaceae), *Sphaeralcea grossulariifolia* (Malvaceae), *Elymus wawawaiensis* (Poaceae), *Achnatherum hymenoides* (Poaceae) and *Artemisia tridentata* subsp. *wyomingensis* (Asteraceae). In contrast, we created an early seral seed mix from disturbance-oriented native species common in the Great Basin. The early seral seed mix was composed of two annual forbs, two perennial grasses and one shrub: *Amsinckia tessellata* (Boraginaceae), *Mentzelia veatchiana* (Loasaceae), *Elymus elymoides* (Poaceae), *Poa secunda* (Poaceae) and *Ericameria nauseosa* (Asteraceae). For this mix we focused on annual forbs, rather than annual grasses, as there are very few native annual grasses in these systems (Cronquist et al. 1977). In comparison to the species in the late seral seed mix, the species in the early seral seed mix share more similarities with the exotic annual grasses in emergence and growth phenologies (Appendix S1).

Soil and seed collection

A representative clay loam soil (clayey, smectitic, mesic, Lithic Argixeroll) and a representative sandy loam soil (fine-loamy, mixed, superactive, mesic Durinodic Xeric Haplargid) were collected from multiple field locations in Wyoming big sagebrush communities in northern Nevada, US (USDA Web Soil Survey (http://websoilsurvey.nrcs.usda.gov; accessed 12 May 2010). The clay loam soil was collected from three sites along a 3-km transect off Buffalo Meadows Road, north of the Smoke Creek Desert (ca. 130 km N of Reno, 40°43′ N, 119°48′ W, 1435–1465 m a.s.l.). The sandy loam soil was collected from three sites along a 5-km transect at Bedell Flat (ca. 35 km N of Reno, 39°51′ N, 119°49′ W, 1525–1585 m a.s.l.). Mineral soil was collected from 0 to 15 cm and coarse sieved (12.5 mm) to remove large rocks. For each soil type, the soil collections were thoroughly homogenized in a cement mixer, and filled into pots (see *Common garden: experimental design and implementation* above) by weight to approximate field bulk density (1.3 $g{\cdot}cm^{-3}$ for the clay loam and 1.6 $g{\cdot}cm^{-3}$ for the sandy loam). Both soils were low in fertility in terms of total carbon and nitrogen (following methods described in Blank & Morgan 2012). The sandy loam had 0.45 ± 0.01%C and 0.045 ± 0.004%N; and the clay loam had 0.31 ± 0.01%C and 0.049 ± 0.003%N (mean ± SE, $n = 5$).

Seeds of the early seral seed mix and the two exotic species were hand-collected from multiple wild populations (three to six per species) in northern Nevada in 2010. For each species, the seeds were collected from coarse- to fine-textured soils, at elevations ranging from 1310 to 1585 m. At each seed collection site, mature seeds were collected from a minimum of 20 maternal plants. Seeds of the late seral seed mix were obtained from a commercial vendor (Comstock Seed, Gardnerville, NV, US), following the procedure for a typical restoration reseeding. Seed viability testing using tetrazolium staining (Association of Official Seed Analysts 1988), as detailed in Forbis (2010), was completed after planting in Oct 2010. *Bromus tectorum* seed viability was 91%. Viability of all other species was close to 70% or above, except shrubs (reported in Uselman et al. 2014); shrubs were re-seeded in January 2011 to bring the final addition of viable seed to ca. 100%.

Data analysis

Logistic regression analysis was performed on the emergence and survival of individual seedlings in all three experiments using the GLIMMIX procedure for generalized linear mixed models in SAS (v 9.2; SAS Institute Inc., Cary, NC, US). Tukey-Kramer adjustments were made for multiple comparisons when appropriate. Models for exotics included the following fixed factors: seed mix and soil type. Models for natives included the following fixed factors: seed mix, soil type and functional group. The natives models for survival included all two-way interactions

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between factors; the three-way interaction could not be included because the logistic regressions failed to converge due to quasi-complete or complete separation. This occurred as a result of one or more functional group treatment combinations having zero survival (Fig. 3; Allison 2008). All other models included all possible interactions between factors. Initially, we included species as a random factor nested within functional group and seed mix, but the logistic regressions failed to converge due to quasi-complete or complete separation. This occurred as a result of the poor emergence and survival of some species of forbs and shrubs, i.e. zero counts (Appendices S2 and S3; Allison 2008). Consequently, models were run without the effect of species, but functional group was retained in the analyses. Although species could not be included in the statistical analysis, species-level data are presented in Appendices S2 and S3.

In the logistic regression analysis, the probability of an event (P) is modelled by linearizing binary responses. This is done by calculating the logit or the log(odds) = log [P/(1–P)], of the probability of an event (e.g. survival = P) over the probability of non-occurrence (e.g. death = 1–P). For example, the odds of survival for *B. tectorum* (when growing without natives) in clay loam was [0.581/(1–0.581)], whereas the odds of survival in sandy loam was [0.726/(1–0.726)] (Appendix S3). To compare survival of *B. tectorum* between the two soils, the ratio of these two odds is calculated (Hosmer & Lemeshow 2000; Agresti 2002). This provides a measure of the likelihood of survival between the two soil types. In this example, the odds ratio of *B. tectorum* survival in clay loam compared to sandy loam is calculated as:

$$\left(0.581 \Big/ (1-0.581)\right) \Big/ \left(0.726 \Big/ (1-0.726)\right) = \left(0.581 \Big/ 0.419\right) \Big/ \left(0.726 \Big/ 0.274\right) = 0.52$$

The interpretation is that *B. tectorum* is 0.52 times as likely to survive in clay loam as sandy loam. For ease of interpretation, we inverted to give an odds ratio more than one (e.g. 0.52/1 → 1/0.52 = 1.9), interpreted as *B. tectorum* is 1.9 times as likely to survive in sandy loam as clay loam.

ANOVA was used to assess treatment differences in timing of emergence (days to emergence after seeding), both for exotics and for natives, using the same model structure described above. Prior to statistical analysis, timing of emergence data were log-transformed to meet the assumptions of homogeneity of variance and normal distribution of residuals. We also summarized the emergence timing data in order to categorize each species as predominantly emerging in the autumn ('autumn-emerging') or later ('spring-emerging'). The date of 12/21/2010 was used as the end of autumn, based on natural breaks in emergence pulses. ANOVA was used to examine the effect of emergence timing on survival probability of natives by experiment.

Data were analysed using SAS (v 9.2; SAS Institute) or JMP (v 9.0; SAS Institute) statistical analysis software, with $\alpha = 0.05$ set as the significance level. Figures and tables show mean ± 1 SE.

Results

Seedling emergence

Emergence of natives was higher for early vs late seral grasses and shrubs, but it was similar for early and late seral forbs, indicated by significant seed mix by functional group interactions in the *B. tectorum* and 'No Exotic' experiments (Table 2, Fig. 1). The seed mix by functional group interaction also indicated that within each seed mix, emergence was generally different for the functional groups considered, with the exception that the emergence of late seral forbs and late seral shrubs were not significantly different from each other in all of the experiments, including the *T. caput-medusae* experiment (Table 2, Fig. 1). Natives were 1.6 or 2.1 times more likely to emerge in sandy loam than in clay loam when growing in the presence of either *B. tectorum* or *T. caput-medusae*, respectively. In contrast, soil type had no effect on emergence in the 'No Exotic' experiment.

Timing of native emergence was significantly earlier for the early vs late seral mix, and it was earliest for the native grasses vs forbs or shrubs, in the 'No Exotic' experiment (Table 2, Fig. 2). In the *B. tectorum* and *T. caput-medusae* experiments, significant seed mix by functional group interactions indicated that timing of native emergence was earlier for the early vs late seral grasses and forbs, but similar for shrubs (Table 2, Fig. 2). This seed mix by functional group interaction also indicated that, within each seed mix, timing of emergence was earliest for grasses compared to forbs and shrubs. In the *B. tectorum* experiment, there was also a significant seed mix by soil type interaction, such that timing of emergence was earlier in sandy loam than clay loam for the early seral seed mix, but not for the late seral mix. In addition, timing of emergence was earlier in sandy loam than clay loam for native grasses but not for the other native functional groups in the *B. tectorum* experiment (soil type by functional group interaction). In the *T. caput-medusae* experiment, timing of native emergence was earlier on sandy loam vs clay loam. The three-way seed mix by soil type by functional group interaction was not significant in the *B. tectorum* or *T. caput-medusae* experiments. There were no significant interaction terms in the 'No Exotic' experiment. When averaged across the

Table 2. Logistic regression and ANOVA results for emergence, timing of emergence, and survival. Natives models (A) are shown for the (i) *B. tectorum*, (ii) *T. caput-medusae* and (iii) No Exotic experiments. Exotics models (B) are shown for the (i) *B. tectorum* and (ii) *T. caput-medusae* experiments.

Source	Emergence			Timing of Emergence[a]			Survival		
	df[b]	*F*	*P*[c]	*df*	*F*	*P*	*df*	*F*	*P*
(A) Natives									
(i) *B. tectorum* Expt.									
Seed Mix	1,898	46.93	**<0.001**	1,384	23.64	**<0.001**	1,386	2.65	0.10
Soil Type	1,898	8.98	**0.003**	1,384	12.24	**<0.001**	1,386	13.16	**<0.001**
Functional Group	2,898	95.02	**<0.001**	2,384	65.35	**<0.001**	2,386	17.39	**<0.001**
Mix × Soil	1,898	0.28	0.59	1,384	5.14	**0.02**	1,386	8.10	**0.005**
Mix × Funct. grp.	2,898	10.29	**<0.001**	2,384	8.32	**<0.001**	2,386	1.36	0.26
Soil × Funct. grp.	2,898	1.57	0.21	2,384	9.03	**<0.001**	2,386	18.30	**<0.001**
Mix × Soil × Funct. grp.	2,898	1.59	0.20	2,384	1.39	0.25	–	–	–
(ii) *T. caput-medusae* Expt.									
Seed Mix	1,908	71.02	**<0.001**	1,406	18.19	**<0.001**	1,408	6.09	**0.01**
Soil Type	1,908	17.58	**<0.001**	1,406	12.65	**<0.001**	1,408	6.82	**0.009**
Functional Group	2,908	98.55	**<0.001**	2,406	89.17	**<0.001**	2,408	13.78	**<0.001**
Mix × Soil	1,908	0.96	0.33	1,406	0.05	0.83	1,408	0.73	0.39
Mix × Funct. grp.	2,908	6.40	**0.002**	2,406	6.63	**0.002**	2,408	0.83	0.44
Soil × Funct. grp.	2,908	1.27	0.28	2,406	1.44	0.24	2,408	21.62	**<0.001**
Mix × Soil × Funct. grp.	2,908	1.39	0.25	2,406	0.04	0.96	–	–	–
(iii) No Exotic Expt.									
Seed Mix	1,348	31.43	**<0.001**	1,150	3.84	**0.05**	1,152	0.27	0.61
Soil Type	1,348	0.10	0.75	1,150	3.22	0.07	1,152	0.89	0.35
Functional Group	2,348	42.19	**<0.001**	2,150	53.22	**<0.001**	2,152	1.52	0.22
Mix × Soil	1,348	0.58	0.45	1,150	0.16	0.69	1,152	0.23	0.63
Mix × Funct. grp.	2,348	3.51	**0.03**	2,150	1.21	0.30	2,152	1.86	0.16
Soil × Funct. grp.	2,348	2.00	0.14	2,150	1.90	0.15	2,152	5.35	**0.006**
Mix × Soil × Funct. grp.	2,348	1.28	0.28	2,150	0.07	0.93	–	–	–
(B) Exotics									
(i) *B. tectorum* Expt.									
Seed Mix	2,1214	2.00	0.14	2,762	0.36	0.70	2,762	3.15	**0.04**
Soil Type	1,1214	29.43	**<0.001**	1,762	168.45	**<0.001**	1,762	17.72	**<0.001**
Mix × Soil	2,1214	2.42	0.09	2,762	0.63	0.53	2,762	0.21	0.81
(ii) *T. caput-medusae* Expt.									
Seed Mix	2,1214	0.31	0.73	2,1115	1.18	0.31	2,1115	0.01	0.99
Soil Type	1,1214	6.13	**0.01**	1,1115	607.02	**<0.001**	1,1115	0.00	0.97
Mix × Soil	2,1214	1.29	0.27	2,1115	0.01	0.99	2,1115	0.02	0.98

[a]Timing of emergence (days to emergence after seeding) was log-transformed for this analysis.

[b]Degrees of freedom (*df*), indicated as numerator *df*, denominator *df*.

[c]Bolded *P*-values indicate significant ($P < 0.05$) model effects.

three experiments, the observed emergence timing of all species generally fit expected seasonal patterns (Appendix S1), with two exceptions: *A. tessellata* was categorized as autumn/spring emerging and *A. hymenoides* as spring emerging.

Seed mix did not affect emergence of either *B. tectorum* or *T. caput-medusae* (Table 2, Fig. 1). *Bromus tectorum* was 1.9 times as likely to emerge in sandy loam relative to clay loam. Emergence of *T. caput-medusae* was also significantly higher in sandy loam than clay loam, although emergence was generally very high in all treatment combinations (92% average; Fig. 1). Timing of exotic emergence was significantly earlier in sandy loam than clay loam, in both the *B. tectorum* and *T. caput-medusae* experiments (Table 2, Fig. 2). Overall, the average time to emergence was 28 days for *T. caput-medusae* vs 39 days for *B. tectorum*.

Survival during early life stages

Early seedling survival of the early seral natives was higher than that of late seral natives in sandy loam, but not in clay loam in the *B. tectorum* experiment (seed mix by soil type interaction; Table 2, Fig. 3). In the *T. caput-medusae* experiment, early seral natives were 2.3 times as likely to survive as the late seral natives, averaged across both soil types (Table 2, Fig. 3). In contrast, in the 'No Exotic' experiment, the early and late seral natives exhibited similar survival when growing without exotics (Table 2, Fig. 3). In

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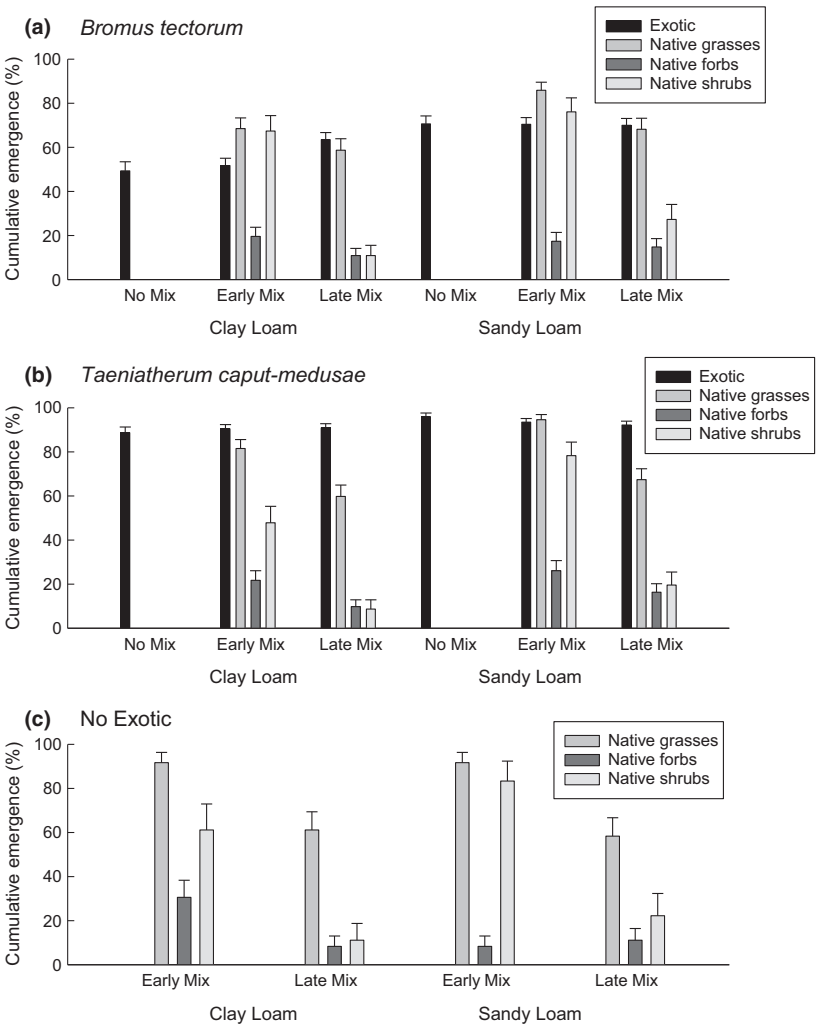

Fig. 1. Cumulative percentage emergence from seed (from the date of first emergence in early Nov 2010 through the end of May 2011) for each functional group, shown by soil type and by seed mix for the (**a**) *Bromus tectorum* experiment, (**b**) *Taeniatherum caput-medusae* experiment and (**c**) 'No Exotic' experiment with only natives. Mean ± SE.

addition, survival of native forbs and shrubs was higher in clay loam than sandy loam, but survival of grasses was higher in sandy loam than clay loam, when growing in the presence of either *B. tectorum* or *T. caput-medusae*, as indicated by significant soil type by functional group interactions. This interaction also indicated that native grasses had higher survival than forbs and shrubs in the sandy loam but similar survival in the clay loam, and this pattern was also observed in the 'No Exotic' experiment.

In the experiments with exotics, survival was significantly higher for natives that emerged in the autumn vs those that emerged after the end of autumn. Autumn emerging natives were 2.5 or 3.3 times as likely to survive compared to spring emerging natives when growing with *B. tectorum* ($F = 19.38_{1,394}$, $P < 0.001$) or *T. caput-medusae* ($F = 32.42_{1,416}$, $P < 0.001$), respectively. In contrast, when natives were growing alone in the 'No Exotic' experiment, timing of emergence did not affect survival ($F = 1.17_{1,160}$, $P = 0.28$).

The exotic *B. tectorum* had higher survival when growing with early or late seral natives than when growing alone (Table 2, Fig. 3). In addition, *B. tectorum* was twice as likely to survive in sandy loam as in clay loam. *Bromus tectorum* had notably low survival on the clay loam (64% average; Fig. 3). Contrary to our expectations, survival of *T. caput-medusae* was not affected by soil type, nor was it affected by seed mix (Table 2, Fig. 3). Survival of *T. caput-medusae* was generally very high (97% average; Fig. 3). Neither exotic appeared to suffer any significant suppression due to competition with natives.

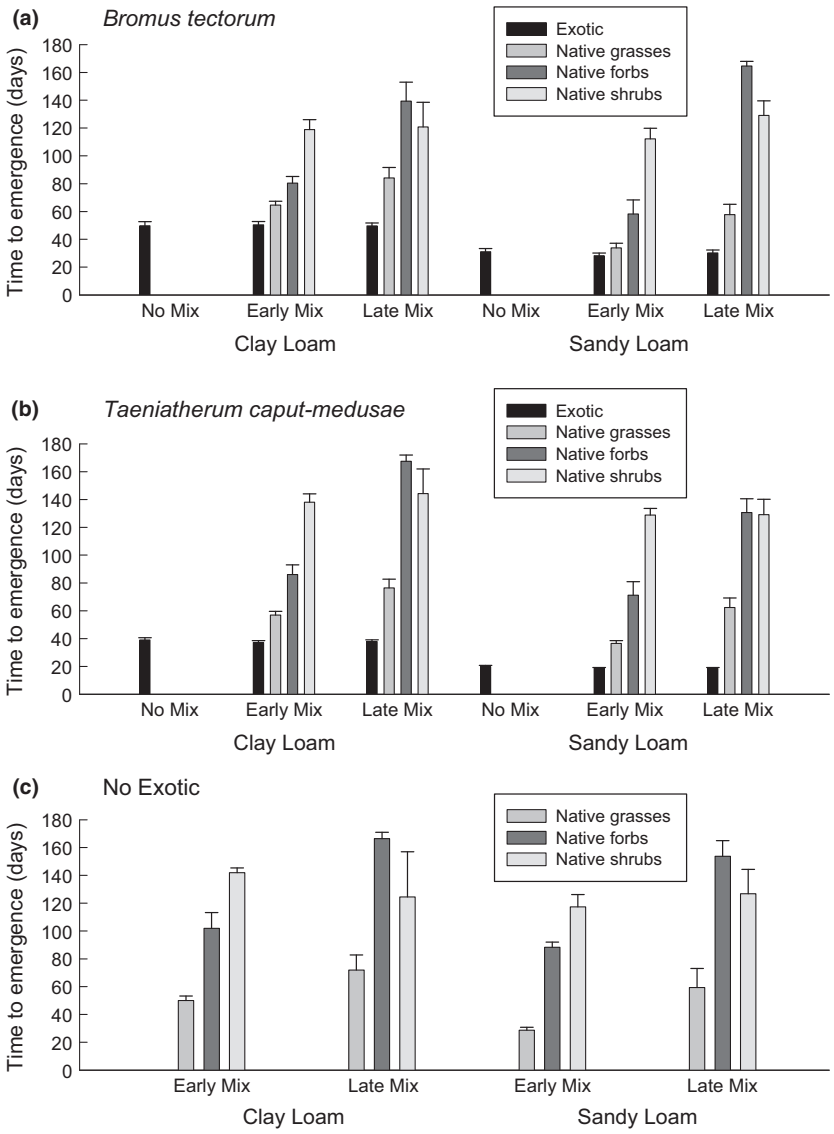

Fig. 2. Emergence timing (number of days from seeding to emergence) for functional groups, shown by soil type and by seed mix for the (**a**) *Bromus tectorum* experiment, (**b**) *Taeniatherum caput-medusae* experiment and (**c**) 'No Exotic' experiment with only natives. Mean ± SE.

Discussion

As predicted, the early seral seed mix generally outperformed the late seral mix when growing with the exotic annual grasses during early life stages, which has implications for improving restoration reseeding methods in the Great Basin. Greater similarity in functional traits between early seral natives and exotics likely contributed to the higher seedling emergence and survival of the early seral natives when growing with the exotics; although soil type and functional group also influenced plant performance (Figs 1 and 3). Similar to our results, research conducted in arid to mesic grasslands and shrublands have found that similarity in functional traits improves native plant community resistance to invasion, likely due to more intense competition for resources (Fargione et al. 2003; Turnbull et al. 2005; Young et al. 2009; Hooper & Dukes 2010; Abella et al. 2012). Our finding that early seral natives generally emerged sooner than late seral natives (except shrubs; Fig. 2) and that autumn-emerging natives had higher survival when growing with exotics provides additional support for our hypothesis that functional similarity would increase performance, and highlights the importance of emergence timing as a factor affecting early seedling performance. The earlier phenology of the early seral seed mix in our study may have given the early seral

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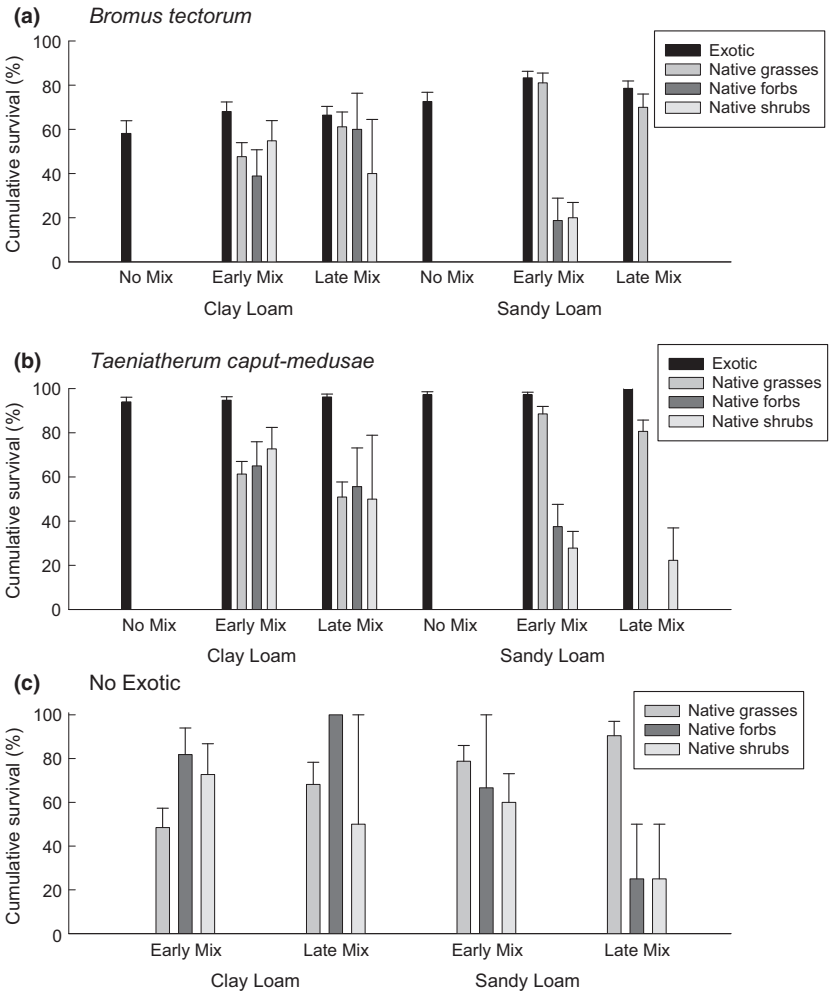

Fig. 3. Cumulative percentage survival (of emerged seedlings) for functional groups, shown by soil type and by seed mix for the (**a**) *Bromus tectorum* experiment, (**b**) *Taeniatherum caput-medusae* experiment and (**c**) 'No Exotic' experiment with only natives. Mean ± SE. Note that for two treatment combinations survival is 100% (±0 SE).

natives a greater advantage to preempt limited resources and thus better compete against the exotic annual grasses during early life stages (Ross & Harper 1972).

The early seral seed mix demonstrated superior seedling survival when growing with the exotics, suggesting that the advantage of using early seral species would be in invaded areas. Early and late seral species were able to perform relatively equally under more benign, annual grass-free experimental conditions, but when growing with exotics, the early seral species were able to outperform late seral ones. These results are important because most restoration in the Great Basin occurs in locations where *B. tectorum* and/or *T. caput-medusae* are currently present in the seed bed and/or surrounding vegetation, and these are conditions where use of early seral natives would be most beneficial. Many trials for native seed selection are conducted in weed-free common gardens (e.g. Wilson et al. 2008), and notably, these are the conditions where the higher survival of the early serals would not have been expressed, and thus not identified. The weaker performance of the late seral seed mix, composed of species traditionally used in restoration, suggests that use of early seral natives may improve restoration reseeding outcomes. Researchers in the northern Great Basin have found very poor emergence of commonly used late seral species, indicating that failure at this early life stage would limit restoration success (James et al. 2011; Boyd & James 2013). Taken together, our findings suggest that selection criteria for restoration materials must consider the ability to successfully emerge and survive during early life stages in the presence of exotic annual grasses, not only the ability to withstand harsh environmental conditions in the Great Basin. If seeded species cannot survive these critical first

life stages when growing with exotics, then they cannot be useful for restoration.

Contrary to our prediction, *B. tectorum* and *T. caput-medusae* were not suppressed by the natives growing with them during early life stages. In the case of *B. tectorum*, survival was higher when the exotic was growing with natives as compared to when growing without natives (Fig. 3), suggesting possible facilitation by native species. Survival of *T. caput-medusae* was neither negatively nor positively affected by the natives. In this study, we focused on emergence and survival during early life stages, so the native perennials did not reach maturity during the time frame of the experiments. Some native perennial grasses are effective competitors and may have a suppressive effect on exotic annual grasses when they are mature and established (Borman et al. 1991; Booth et al. 2003; Humphrey & Schupp 2004; Chambers et al. 2007; Davies 2008; Blank & Morgan 2012). Although the exotics were not competitively suppressed during early life stages, it is notable that the natives, particularly the early seral natives, were able to persist with the exotic annual grasses (Fig. 3). In our companion study, we found that the early seral seed mix significantly reduced annual biomass and seed production of *T. caput-medusae* (Uselman et al. 2014), so exotic performance was negatively impacted by the early seral natives in later life-history stages.

Soil type affected exotic and native performance and interactions, but our findings did not support all of our predictions. The emergence and survival of *B. tectorum* was higher in sandy loam relative to clay loam (Figs 1 and 3), as predicted, suggesting that *B. tectorum* has a preference for more coarse-textured soils over finer-textured soils. We suspect that this may be related to increased root exposure in the clay loam, where we observed increased frost heaving and cracking of surface soils, as would be expected in a smectitic clay loam with high shrink–swell potential (Hillel 1998). Compared to roots of *T. caput-medusae*, roots of *B. tectorum* are more fibrous and have a relatively poorly developed endodermis, rendering them more vulnerable to desiccation when exposed or when soils dry down (Hironaka 1961; Harris 1977). Contrary to our prediction, the performance of *T. caput-medusae* was very good in both soils. In terms of emergence, *T. caput-medusae* exhibited a statistical preference for sandy loam over clay loam, while survival of the exotic was not affected by soil type (Figs 1 and 3). However, both emergence and survival were very high for all treatments, indicating that it performs well in either soil type and suggesting that *T. caput-medusae* may be capable of expanding its current range (Dahl & Tisdale 1975; Young 1992). As predicted, native performance did not differ by soil type when growing without exotics, but emergence was higher in sandy loam than clay loam when growing in the presence of exotics (Fig. 1). Native grasses also had significantly higher survival in sandy loam while forbs and shrubs had higher survival in clay loam when growing with exotics, but not when growing without exotics (Fig. 3). Because the performance of natives in the two soil types differed only when seeded with exotics, it appears that plant–plant interactions between the natives and exotics were important in determining emergence and survival probabilities of natives in the different soil types. This result highlights the importance of testing plant interactions in multiple soil types, as outcomes of native–exotic plant interactions differed in our study. Additionally, the result that certain functional groups performed better in one of the soils when growing with exotics could be helpful for designing seed mixes at different sites.

Our finding that native grasses exhibited the highest performance of all the native functional groups confirms that grasses play an important role in restoration in Great Basin ecosystems. Both early and late seral grasses emerged earlier and had higher probabilities of emergence than native forbs or shrubs (Figs 1 and 2). Survival of grasses was also higher than forbs and shrubs on sandy loam (Fig. 3). In contrast, emergence of the native forb *S. grossulariifolia* was 0–6% in our study, and almost every individual died during the study period (Appendices S2 and S3), so the utility of this species for restoration appears limited under our experimental conditions. Certain functional groups, or even specific species, may play an instrumental role in resisting the invasion process (Tilman 1997; Levine & D'Antonio 1999). Grasses, in particular, have been found to be a key functional group in resistance to invasion (Fargione et al. 2003; Thomsen & D'Antonio 2007). For example, squirreltail species (*Elymus elymoides* and *Elymus multisetus*) are capable of invading and persisting in sites dominated by *B. tectorum* and *T. caput-medusae* (Hironaka & Tisdale 1963; Hironaka & Sindelar 1973). In comparison to the grasses, the native forbs generally did not perform as well as expected, with the exception of the early seral *A. tessellata*, which had the earliest emergence phenology of all the forbs (Appendices S1–S3). The poor performance of certain species in this study suggests that it may be advisable to use a higher seeding rate or perhaps to replace poor performers (i.e. *M. veatchiana* in the early seral mix) with a different species in the seed mix, although we note that performance may differ under other growing conditions.

Management implications

Our findings suggest that the use of early seral species may improve native survival and growth in the Great

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Basin, in comparison to the use of later seral species in traditional seed mixes. Given their better performance when growing with exotics during early life stages, early seral species may have a higher chance of persisting in communities where exotic annual grasses are present, although future research is needed to evaluate long-term native survival. Additionally, native grasses were particularly successful when growing with exotic annual grasses, relative to native forbs and shrubs, suggesting an important role in restoration in these systems. Our results showing differences in native performance in the two soil types may be helpful in tailoring seed mixes to different sites. For example, restoration reseedings emphasizing early seral native grasses, in particular, may be more successful in more coarse-textured soils, such as sandy loams. It should, however, be noted that neither the early nor the late seral seed mix suppressed the exotic annual grasses during the earliest life stages, although we did see some evidence of suppression at later life stages (Uselman et al. 2014). Additional research is needed to determine whether the use of early seral natives in restoration reseedings will facilitate succession to later seral native vegetation (Brown et al. 2008).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Comparison of growth form and phenology for species in the early and late seral seed mixes and for the two exotic species.

Appendix S2. Cumulative percent emerged (of seeded) by treatment for each species (mean ± SE).

Appendix S3. Cumulative percent survived (of emerged) by treatment for each species (mean ± SE).

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