

RESEARCH ARTICLE

Seed and seedling traits have strong impacts on establishment of a perennial bunchgrass in invaded semi-arid systems

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Great Basin Native Plant Project; National Institute of Food and Agriculture, Grant/Award Number: 2011-38415-31158

Handling Editor: Cate Macinnis-Ng

Abstract

1. Many restoration projects use seeds to found new populations, and understanding phenotypic traits associated with seedling establishment in disturbed and invaded communities is important for restoration efforts world-wide. Focusing on the perennial grass *Elymus elymoides*, a native species common to sagebrush steppe communities in the Western United States, we asked if seed and seedling traits could predict field establishment.
2. We collected seeds from 34 populations from the western Great Basin. In greenhouse studies, we measured variation in seed and seedling characteristics of wild populations and one cultivar. We also quantified abiotic conditions at the collection location and asked if these characteristics predicted survival and other fitness metrics at five planting sites. Planting sites were all near-monocultures of the invasive annual grass *Bromus tectorum*, and all sites experienced similar, below-average precipitation during the experiment.
3. Phenotypic traits were strongly correlated with performance across all sites, with remarkably high predictive power. Seeds from populations with longer roots, larger seeds and earlier emergence were significantly more likely to survive the first growing season ($R^2 = 0.66$, $p < 0.0001$). In contrast, while some abiotic variables at the collection location (e.g. 30-year average summer precipitation and fall minimum temperatures) were associated with field performance at some sites, abiotic variables explained less variation in performance than traits (average $R^2 = 0.22$). Despite the low predictive power of abiotic variables, populations that performed best at each field site were from locations with climate variables similar to planting sites.
4. *Synthesis and applications.* The best seed sources for restoration of *Elymus elymoides* in invaded sites were populations with longer roots, larger seeds and earlier emergence. These easily measured traits were strong predictors of survival in disturbed field sites. While the most successful populations were found in areas with similar abiotic conditions as planting sites, there was phenotypic variation even among populations originating from locations with similar conditions. Thus, our results indicate that abiotic conditions are important considerations when selecting seeds, but these conditions may not sufficiently predict which populations

will establish. Understanding population differences in seedling functional traits can improve predictions of restoration success.

KEYWORDS

adaptation, *Bromus tectorum*, *Elymus elymoides*, functional traits, Great Basin, natural selection, restoration, wild populations

1 | INTRODUCTION

Ecosystem restoration efforts are increasing world-wide, as human society recognizes the value of reclaiming damaged lands (Aronson & Alexander, 2013; IPBES, 2016). Seeds of desirable species are sown across millions of hectares of land in these efforts (e.g. Kiehl, Kirmer, & Shaw, 2014; Peppin, Fulé, Sieg, Beyers, & Hunter, 2010; Pilliod, Welty, & Toevs, 2017). However, establishing plants from seed can be challenging, especially in arid and semi-arid systems, and many seedlings fail (Duniway, Palmquist, & Miller, 2015; Knutson et al., 2014). When competitive invasive species are an established part of the community, as in much of the Western United States (DiTomaso, 2000), the deck can be stacked firmly against successful seedling establishment. Assuring that seeds are well adapted to restoration site conditions is one way to tip the balance towards success (Bucharova et al., 2017).

Using locally adapted seed sources has long been the foundation of restoration efforts (McKay, Christian, Harrison, & Rice, 2005), in recognition that natural selection commonly results in locally adapted ecotypes (Geber & Griffen, 2003; Hereford, 2009; Leimu & Fischer, 2008). Seed transfer zones, which aim to delineate climatically similar areas where seeds can be moved without fitness consequences, are commonly used to streamline this process (Bower, Clair, & Erickson, 2014; Ying & Yanchuk, 2006). However, populations that experience similar abiotic conditions are neither identical nor necessarily optimally adapted to site conditions due to multiple factors, including genetic drift, fluctuating selection, gene flow from neighbouring sites, populations not at equilibrium with site conditions, or lack of variation within populations for adaptive traits (Blows & Hoffmann, 2005; Bridle & Vines, 2007; Kawecki & Ebert, 2004; Lenormand, 2002; McKay et al., 2005). Further, biotic interactions or disturbance history can differ among sites with similar climates, imposing additional selection (Oduor, 2013) or constraining responses to it (Pujol et al., 2018). Thus, even when plant populations have evolved under similar abiotic conditions and fall within the same seed transfer zone, they are likely to differ in phenotypic traits.

Variation in phenotypic traits can be used to predict differences in plant performance (Funk et al., 2017; Poorter & Bongers, 2006; Schroeder-Georgi et al., 2016), and this predictive power is being applied to restoration, with some successes (Clark et al., 2012; Pywell et al., 2003; Sandel, Corbin, & Krupa, 2011). For example, functional trait differences among species such as phenology, plant size, seed mass and specific leaf area can have strong predictive power for plant establishment and persistence in restoration settings, a

clear benefit for planning species mixes for particular types of sites and restoration treatments (Engst, Baasch, & Bruelheide, 2017; Ostertag, Warman, Cordell, & Vitousek, 2015; Zirbel, Bassett, Grman, & Brudvig, 2017). Recognizing intraspecific variation in functional traits (e.g. Siefert et al., 2015) may also be important for fully applying functional trait concepts to restoration (Funk et al., 2017). While variation in functional traits among populations is typically lower than that among species (e.g. Albert et al., 2010), intraspecific variation also provides opportunities for restoration practitioners to select specific populations suited to the conditions in the area to be restored.

Our previous work in the Great Basin has identified a set of functional traits (rapid seedling emergence, high root allocation, seed mass, and several aspects of root morphology) that confer an advantage to native perennial grass species growing in former Wyoming sagebrush-dominated sites (Atwater, James, & Leger, 2015; Leger & Baughman, 2015; Leger & Goergen, 2017). These perennial plant communities are experiencing large-scale conversion to invasive annual grasses, particularly *Bromus tectorum* L. (Bradley et al., 2017). Much of the Great Basin is managed by the Bureau of Land Management (BLM), which is the largest seed buyer in the western hemisphere (Mock, Hansen, Coupal, & Menkhous, 2016). The BLM uses these seeds for large-scale seeding treatments across western rangelands, often seeding perennial grasses post-fire, with the goal of reducing weed populations and assisting the return of disturbed sites to perennial systems (USDI BLM, 2007). Thus, any improvements to understanding traits that increase seedling establishment in this system will have immediate application for one of the world's largest ongoing seeding efforts.

Here, we compare first year seedling performance among 35 populations of *Elymus elymoides* (Raf.) Swezey, a primarily self-pollinating, early-seral native perennial grass that grows well under disturbed and invaded conditions (Hironaka & Tisdale, 1963; Jones et al., 2004). Our previous work described characteristics associated with the success of individual plants, but here we ask if we can extend this predictive power to plant populations. This is important for ecological restoration, as populations, rather than individuals, are typically used as sources of propagules (Espeland et al., 2017). We characterized average seed and seedling traits of each population as well as 30-year average temperature, precipitation, soil and water balance characteristics from collection locations, and asked how well functional traits or abiotic factors predicted field establishment at five disturbed, invaded former sagebrush steppe sites in Nevada and Oregon. We expected that phenotypic traits would be correlated with abiotic conditions at the

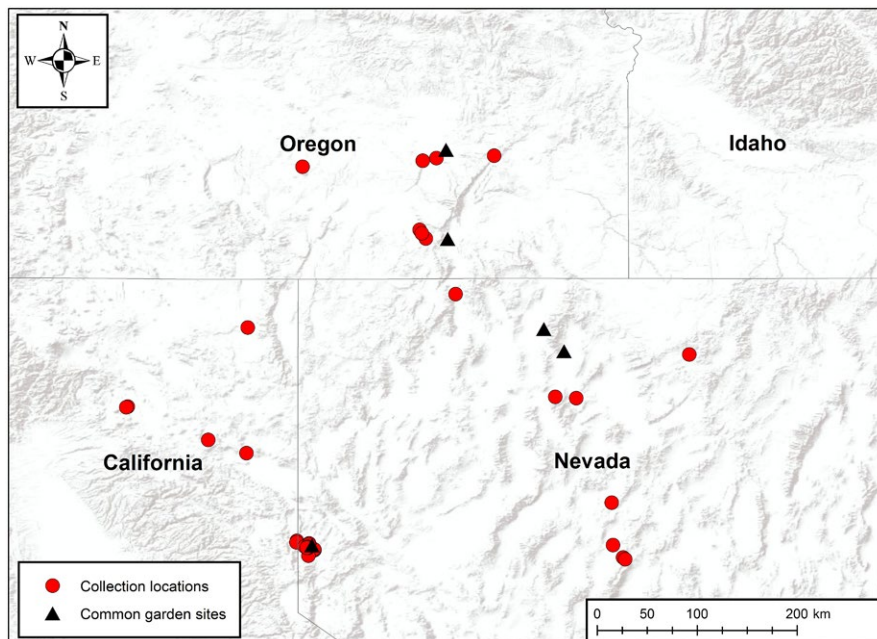


FIGURE 1 Map of *Elymus elymoides* collection locations in Oregon, California and Nevada (circles) and common garden planting sites in Oregon and Nevada (triangles); location details in Appendix S1, Table S1

collection location, and that the most successful phenotypes would be found in locations with abiotic conditions similar to the restoration sites, supporting the common practice of using seed zone delineations for restoration seed sourcing. But further, even among populations from similar abiotic environments, we expected to find variation in phenotypic traits, and consequently, performance in restoration sites. We predicted that populations with rapid seedling emergence and greater root allocation would be found most often in drier locations, and that populations with these characteristics would establish best in *B. tectorum* invaded sites.

2 | MATERIALS AND METHODS

To ask how phenotypic traits affected field establishment, we collected seeds from multiple populations, grew and harvested a subset of these seeds in a greenhouse to describe seedling root characteristics, and then planted seeds into five field sites, where we measured emergence, survival and biomass production over a growing season. Seeds were collected between 25 June and 11 July of 2013 from 34 wild populations of *E. elymoides* that span a range of elevations and climate conditions (Figure 1, Appendix S1, Methods, Table S1). We also included seeds from a commonly seeded, commercially available source, Toe Jam Creek squirreltail (population JJ, in figures), which was originally collected from the NE corner of Nevada (Jones et al., 2004).

2.1 | Measuring traits and environmental characteristics

In the laboratory and greenhouse, we described average seed and seedling phenotypic traits for each population. We measured seed mass in batches of 20 seeds, with 10 replicates per population. Then, 14–20 seeds per population were planted in individual pots in a

Nevada topsoil/sand mix and grown for 10 days in the University of Nevada, Reno greenhouse, at which point roots and shoots of seedlings were harvested, scanned, dried and weighed (Appendix S1, Methods). Traits measured were: time from planting to emergence, total root length, per cent allocation to three root diameter classes, number of root tips, root mass ratio (RMR; root mass/total mass) and specific root length (SRL; total root length in m/root mass in g).

We described abiotic conditions at the collection location for each population. Using 30-year (1981–2010) average temperature and precipitation data from the PRISM Climate Group (<http://prism.oregonstate.edu/>), USDA gridded SSURGO soils data (USDA, 2013) and a digital elevation model, we calculated average annual and seasonal maximum and minimum temperatures, mean monthly temperature, annual and seasonal precipitation totals and several additional variables from a water balance model (Appendix S1, Methods) for each collection location and the five common garden sites. For the common garden sites, we also gathered temperature and precipitation values over the timeframe of this experiment: summer and fall of 2013, and winter and spring of 2014.

Variables were standardized to a mean of 0 and standard deviation of 1 for analysis so that coefficients were directly comparable. Because many of the variables measured were highly correlated, we used principal component analysis as a method to select a subset of phenotypic traits and environmental variables for use in further analysis. A single seed or seedling trait strongly associated with each of the first six principal components was selected, resulting in the selection of six traits with correlations of 0.75 or less (Table S2, Figure S1). These included total root length, RMR, SRL, % allocation to medium diameter roots (0.2–0.4 mm), seed mass and emergence timing. Next, a single abiotic variable strongly associated with each of the first five principal components was selected, resulting in five traits with correlations <0.75 (Table S3, Figure S2). These included average vapour pressure deficit (VPD; higher values indicate greater water

limitation on plant growth), monthly actual evapotranspiration (AET; higher values indicate sites with greater plant productivity), rain per month (mm of monthly precipitation falling as rain, rather than snow), fall minimum temperature and total summer precipitation.

2.2 | Field methods

After describing trait and environmental characteristics for each population, we tested field performance in five sites (Fields, OR: 42.3493°N, -118.6472°W; Diamond Crater, OR: 43.1510°N, -118.6622°W; Orovada, NV: 41.5419°N, -117.7824°W; Paradise, NV: 41.3425°N, -117.6012°W; and Peavine, NV: 39.6056°N, -119.9005°W). Before planting, 250 seeds from each population were glued to toothpicks with Titebond II Premium Wood Glue, and seeds on toothpicks were planted directly into the ground to allow tracking of sown seeds. Each of 35 populations were planted into 10 blocks between 24 and 26 October 2013, with five seeds per population randomly assigned a position within each block, resulting in 1,750 seeds planted at each of five field sites. These sites are former Wyoming sagebrush steppe communities with sandy loam soils, and all are currently dominated by *B. tectorum*. Thirty-year average precipitation varied between ~190 and 315 mm of annual precipitation (Table S1).

To determine whether seeds emerged and survived the first growing season, we monitored *E. elymoides* emergence five times at each site, every 3–5 weeks beginning in January and ending in early June, with exact monitoring timing dependent on weather and logistical constraints. A final census of seedling presence at each site occurred during the first week of June; any seedling present at this time is considered to have survived the first growing season. At the June census, we noted whether each seedling was senescent or green ('greenness'). Above-ground biomass ('biomass') was harvested, dried at 40°C for 1 week and weighed. To describe differences in competitive environment at each site, we quantified *B. tectorum* seed bank densities at the time of planting and biomass of *B. tectorum* in June (Appendix S1, Methods).

2.3 | Data analysis

We asked whether seed and seedling traits were correlated with environmental conditions at collection sites by conducting Pearson's correlation tests between phenotypic traits and collection site environmental variables. To test for nonlinear relationships, environmental variables were also included as squared values in these correlations.

To describe differences in plant emergence, survival and greenness among planting sites, we analysed total emergence (sum of emergence between January and June), survival and greenness on a per seed/seedling basis using generalized linear models, with response variables modelled with a binomial distribution. Models included planting site, block (nested within planting site), source population and the site $\times$ source population interaction. Differences in biomass were analysed with a mixed model, with planting site, block

(nested within planting site, random factor), source population and the site $\times$ source population interaction included in the model. The Paradise Valley planting site was excluded from biomass analyses due to the small number of surviving plants, which precluded model convergence. Biomass from the remaining sites was log transformed to meet model assumptions.

To determine trait and environmental variables most strongly associated with performance across sites, we used a model selection approach, followed by model averaging (using a zero-averaging approach) to estimate the relative strength of each predictor variable if multiple (>3) best models were identified. For model selection, multiple regression analyses were conducted between seed/seedling traits or collection site abiotic variables as model predictors, with the following three response variables calculated for each block: per cent surviving seedlings, per cent of seedlings green in June and above-ground biomass. To test for site-specific responses, the site and site $\times$ predictor variable interactions were included in the model selection process. Preliminary analysis of the relationships between seed/seedling traits and survival and biomass indicated that most relationships were linear, with the exception of a few quadratic relationships. Emergence timing had a quadratic relationship with greenness, so a squared term was included in candidate models along with linear terms. Similarly, a squared term for fall minimum temperature was included in candidate models for survival. For seed and seedling traits, site $\times$ trait interactions were not included in best models, so results are presented for response variables across all five sites. For collection site abiotic variables, there were extensive site $\times$ abiotic variable interactions for all response variables. For ease of interpretation and to reduce model complexity, we created models separately for each site rather than report and interpret site by environment interactions from this larger model. This approach improves our ability to accurately describe what is happening at each site, but limits our ability to generalize across sites or extrapolate to unmeasured sites. To assess the strength of the relationship between traits or environmental factors and field performance in the best models, we report coefficients for non-zero variables from model averaging (i.e. coefficients for which confidence intervals did not overlap zero), significance of individual non-zero terms and model fit (R^2); these R^2 values are used to assess relative fit.

Finally, we asked whether the most successful populations originated from environments similar to planting sites. We conducted a principal component analysis with the abiotic variables, and calculated the Euclidean distance between overall abiotic conditions at each source population and abiotic conditions at each planting site, based on the first two principal components. We then used regression analysis to ask whether this distance affected survival, greenness and biomass. We then did the same for the two environmental variables that were most closely related to field performance: fall minimum temperature and summer precipitation.

Analyses were conducted using the *lme4* package in program R version R 3.3.1 (Bates, Maechler, & Walker, 2016) and in JMP version

12.1.0 (SAS Institute Inc, 2015), using a p -value of 0.05 to determine significance.

3 | RESULTS

3.1 | Phenotypic variation and correlations with site characteristics

Populations differed significantly in all seed, phenology, biomass and root traits ($p < 0.0001$ for all analyses; Appendix S1, Table S4). There were significant correlations between plant traits and climate variables at the original collection location for all traits except RMR (Appendix S1, Table S5). Traits with the greatest number of significant correlations with environmental variables were seed mass and emergence timing: seeds germinated more quickly when they were collected from locations with less rain per month, higher VPD, lower AET and lower fall minimum temperatures. Populations with lower seed mass were collected from locations with more summer precipitation, lower monthly rain and intermediate AET and fall minimum temperatures. Populations with the highest SRL were collected from locations with more summer precipitation and lower VPD. Allocations to medium diameter roots were highest in locations with higher fall minimum temperatures and in areas with higher VPD. Populations producing the longest roots were found in locations with intermediate fall minimum temperatures, with a trend ($p < 0.10$) towards longer roots in locations with less summer precipitation.

3.2 | Common garden conditions and field performance

Cumulative precipitation across the 10-month growing season was low at all sites, ranging from 149 to 164 mm at Peavine, Fields and Paradise, and 189 and 199 mm, respectively, at Orovada and Diamond (Figure 2a). Sites differed in initial *B. tectorum* seed banks ($F_{4,45} = 13.1$, $p < 0.0001$), with the most seeds at Paradise and the fewest at Diamond and Orovada (Table S1b). *Bromus tectorum* productivity differed among sites ($F_{4,20} = 12.6$, $p < 0.0001$) but was unrelated to seed bank density, with Fields producing significantly less biomass than all other sites (Appendix S1, Table S1b).

Planting sites differed significantly in total *E. elymoides* emergence ($\chi^2(3) = 696$, $p < 0.0001$), survival ($\chi^2(3) = 182$, $p < 0.0001$), greenness ($\chi^2(3) = 202$, $p < 0.0001$; Figures 2b and 3) and biomass ($F_{3,37} = 39.5$, $p < 0.0001$; Appendix S1, Results). Paradise had lower emergence and persistence of *E. elymoides* than did the other four sites, and Diamond and Orovada had the greatest emergence, survival and number of green plants (Figure 3).

In the field sites, *E. elymoides* source populations differed in biomass ($F_{34,1014} = 12.3$, $p < 0.0001$), ranging from an average of less than 1 mg for the smallest population to over 4.5 mg for the largest, with an average of 2.3 mg across all populations (Appendix S1, Table S1). These differences were consistent across sites, with no site $\times$ population interaction for biomass ($P > 0.2122$). Populations also differed in total emergence, survival and greenness, and there were

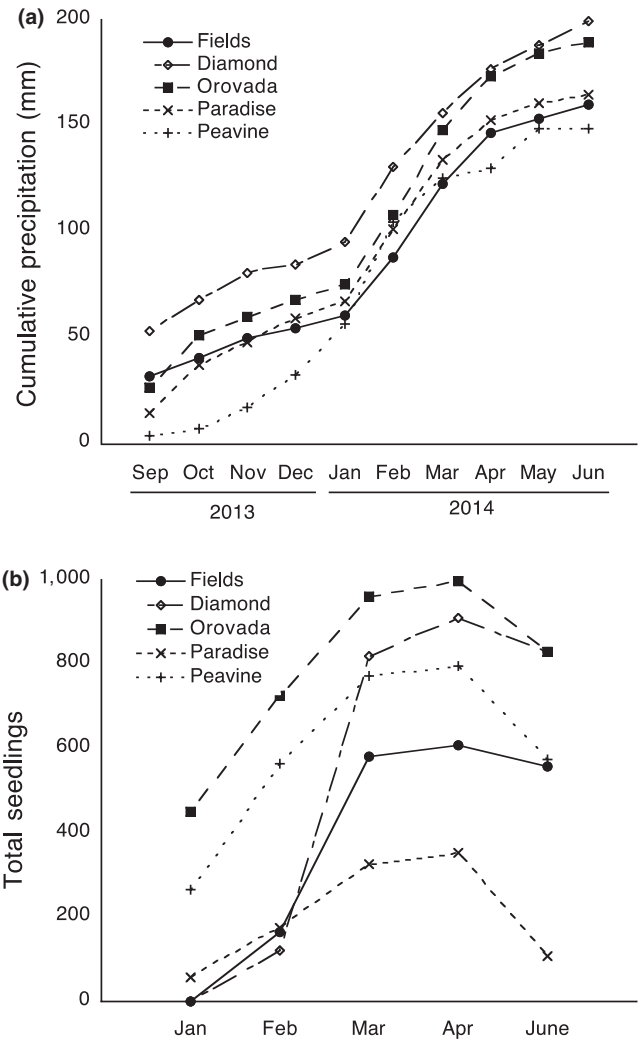


FIGURE 2 (a) Cumulative precipitation and (b) total number of seedlings at each site. Sites were planted in October 2013, monitored monthly from January to June 2014 and harvested in June 2014. In 2013, sites received between 120 and 170 mm total precipitation; in 2014, total precipitation ranged from 245 to 290 mm

significant site $\times$ population interactions for these three responses (all $p < 0.0001$, $\chi^2(34) = 202$, $\chi^2(34) = 122$, $\chi^2(34) = 134$ respectively). Some populations were consistent in their performance, with, for example, high survival at all sites (Figure 4; populations W, U, E, BB, A and Y), while others had much more variable survival among sites, ranking at some sites among the best and at other sites among the worst populations (e.g. populations I and F). Nine populations were above the 75% quartile for survival across sites (Appendix S1, Table S1). The only commercially available seed source, population JJ, survived at or below average at all planting sites (Figure 4).

3.3 | Trait and abiotic variable correlations with field performance

Seed and seedling traits were highly predictive of survival across all field sites, with R^2 values for the best models across field sites

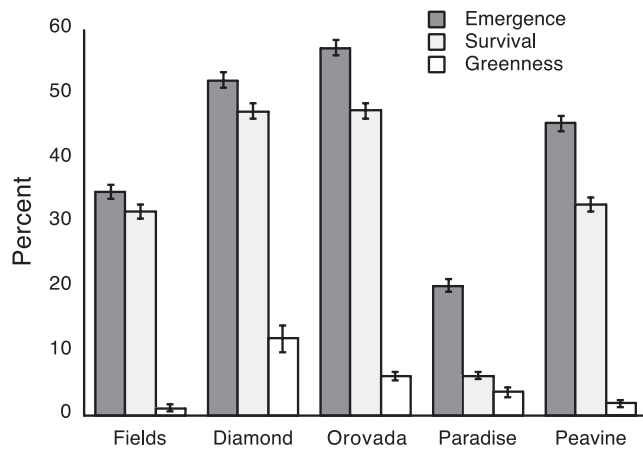


FIGURE 3 Means and standard errors for per cent emergence, survival or per cent of seedlings that were green in June (greenness) at planting sites, based on averages per block

between 0.61 and 0.67 (Table 1a). Populations with larger seed mass, longer root lengths (Figure 5a) and earlier emergence timing were most likely to survive (Figure 5d), and model averaging confirmed that these three variables had consistently strong effects (Table 1a). Phenotypic traits also predicted greenness across all field sites, with R^2 values for best models between 0.51 and 0.59 (Table 1b). Populations with larger seeds, lower RMR (Figure 5b), intermediate emergence timing and lower SRL remained green longer in the season, as identified by model averaging (Table 1b). Finally, seed mass (Figure 5c), root length and RMR were important for predicting biomass across sites (Table 1c), with R^2 values between 0.64 and 0.69.

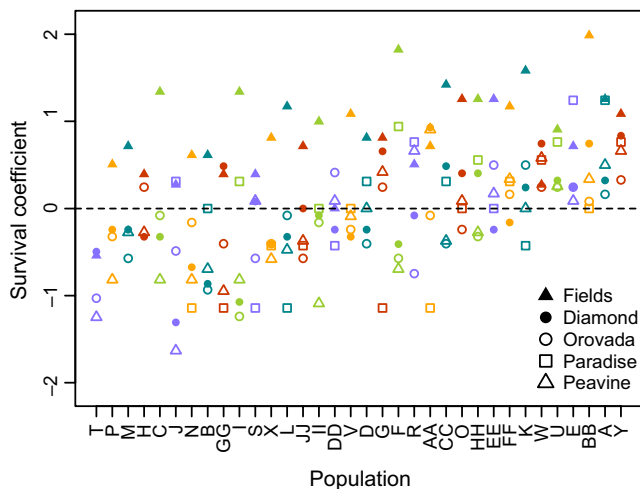


FIGURE 4 Survival coefficients from logistic models for each population by planting site combination, indicating relative survival across five planting sites; the y-axis is on the log-odds scale. Values above 0 indicate that the population had higher performance than a reference population (Q, data not shown), which had approximately average survival at each planting site, while values below 0 indicate lower performance. Mean survival coefficients for each planting site are: Fields, 0.9; Diamond, -0.03; Orovada, -0.2; Paradise, -2.5; Peavine, -0.2. Note that survival coefficients for the first five populations (T-C) at Paradise were below -2, and are not shown here

Because site $\times$ abiotic variable interactions were abundant, models of the effects of collection location abiotic variables on performance measures were run separately for each site. Overall, the explanatory power of these models, as measured by R^2 values, was much lower than trait models (R^2 values for survival were 0.06–0.42; greenness, 0.15–0.23; biomass, 0.09–0.30, Table 2). For some sites and responses (greenness or biomass at Paradise, greenness at Peavine), no abiotic variables were able to predict responses (Table 2). Abiotic variable/response variable relationships that were important at multiple sites included fall minimum temperatures for predicting survival (with intermediate values favoured at some sites), and lower summer precipitation, greater rain per month and greater AET positively related to biomass in some sites (Table 2). Despite the low predictive power of individual variables, overall, populations that performed best at each field site were those with climate variables most similar to planting sites. For each planting site, at least one of our three response variables (survival, greenness, biomass) was significantly predicted by the magnitude of the environmental distance (determined either across all five abiotic variables or just in fall minimum temperatures and summer precipitation) between source populations and each planting site, with significant negative slopes between 0.32 and 0.58 indicating greater performance of populations with a better match to climate conditions in the year of our experiments (Table 3).

4 | DISCUSSION

Abiotic factors strongly influence the evolution of diversity, impacting species distributions and genetic variation below the species level, frequently resulting in locally adapted populations with distinct phenotypic traits (Geber & Griffen, 2003; Hereford, 2009; Leimu & Fischer, 2008). In a common garden study in highly invaded habitats in the western Great Basin, we observed multiple lines of evidence of adaptation of wild populations to local abiotic conditions, including trait/environment correlations and collection location abiotic factors significantly related to field performance, supporting the use of abiotic factors to delineate seed transfer zones for restoration. But, as predicted, we observed phenotypic trait variation even among populations originating from similar abiotic conditions, and we saw much greater predictive power (greater significance of individual factors and higher R^2 values indicating better model fit) from trait/performance models than from home environment/planting site models. When selection is strong, as it appeared to be in these dry, invaded sites, and when there is high among-population variation, which may be more likely for early-seral, selfing species (Loveless & Hamrick, 1984; Nybom, 2004), there is the potential for identifying population-level differences in phenotypic traits that have strong effects on native seedling establishment.

We observed a small number of populations that performed well in all sites, which may represent 'general-purpose genotypes' (Baker, 1974). Adaptive phenotypic plasticity in response to local conditions is hypothesized to be one mechanism behind such genotypes

TABLE 1 Model selection and model averaging results for models testing effects of seed and seedling characteristics on (a) survival, (b) per cent of seedlings that were green in June (greenness) and (c) biomass, averaged across five field sites in western Nevada and southeastern Oregon. Significance of each individual predictor variable is indicated with * ($p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) for model selection, and coefficients from model averaging with standard errors that overlap zero (i.e. coefficients not significantly different from zero) are shown in *italics*

Best models	R ²	AIC	Delta AIC
(a) Survival			
Length*, Seed mass**, Emerge*	0.6648	72.13	–
Length**, Seed mass**	0.6176	74.00	1.87
Length*, SRL, Seed mass**, Emerge*	0.6741	74.07	1.94
Model averaging coefficients: 0.54 Seed mass, 0.27 Length, –0.21 Emerge, 0.04 SRL			
(b) Greenness			
RMR*, Seed mass**, Emerge ² *	0.5696	80.87	–
SRL**, RMR**, Emerge ² *	0.5573	81.86	0.99
SRL, RMR*, Seed mass, Emerge ² *	0.5899	82.11	1.24
RMR, Seed mass**, Emerge, Emerge ² *	0.5857	82.4661	1.59
Seed mass***, Emerge ² *	0.5083	82.7999	1.93
Model averaging coefficients: 0.35 Seed mass, –0.25 RMR, 0.17 Emerge ² , –0.14 SRL, 0.03 Emerge			
(c) Biomass			
Length*, Seed mass***, Emerge	0.6758	70.95	–
RMR*, Seed mass***	0.6490	71.00	0.05
Length, Seed mass***	0.6402	71.86	0.91
Length, RMR, Seed mass***	0.6602	72.60	1.65
RMR*, Seed mass***, Emerge	0.6578	72.85	1.89
Length, RMR, Seed mass***, Emerge	0.6852	72.86	1.90
Model averaging coefficients: 0.64 Seed mass, 0.15 Length, –0.09 RMR, 0.05 Emerge			

(Richards, Bossdorf, Muth, Gurevitch, & Pigliucci, 2006), and future studies could determine if the populations we observed to have greater than average success across all sites are more phenotypically plastic than others. Because conditions were so consistently arid across sites during this experiment and had similar levels of invasive plant competition, we caution that a different suite of traits could be associated with success under different conditions that favour, for example, competitive ability rather than stress tolerance (wetter years, different soil types, less-invaded sites), as has been observed in other studies (Engst et al., 2017). However, given the many hectares of arid, invaded landscapes in the Great Basin (Bradley et al., 2017), and the volume of seeding efforts in this region (Pilliod et al., 2017), identifying populations that are good at establishing from seed in dry years in invaded sites could have significant ecosystem benefits.

Our experiment used wild-collected seeds, and observed differences among populations could be influenced by maternal-environment effects. One area where maternal environment is well known to influence plants is in seed mass (Roach & Wulff, 1987), which, in our study, had strong positive effects on all measured responses. In previous work, structural equation modelling indicated that the effects of seed mass on *E. elymoides* seedling performance were due to more indirect effects on other phenotypic traits than direct effects on plant survival (Atwater et al., 2015). Influence of maternal environment on seed mass can vary among species, and even among populations of the same species (Bischoff & Müller-Schärer, 2010). We observed similar variation in our collections, which were

gathered in a dry year: we grew a small subset of these populations to produce and weigh F1 seed from plants grown in a common environment, and results were highly variable: seed mass of population A decreased by 26%, population M and L both increased by 18% and population C did not change (A. C. Agneray and E. A. Leger, unpubl. data). Thus, given our results to date, further investigation into the genetic vs. environmental contributions to seed mass in this species is warranted, as is understanding direct and indirect relationships among seed mass and other phenotypic traits, including possible trade-offs between seed size and other life-history characteristics (Moles & Westoby, 2004).

Timing of emergence can have strong impacts on seedling survival, and here, as in other studies, we observed that early emergence leads to increased survival (Verdú & Traveset, 2005). Early emergence can be detrimental in some cases, such as in areas with variable precipitation (Bartolome, 1979; Vieira, de Lima, Sevilha, & Scariot, 2008), and optimal emergence time may vary among years. In our trait/environment correlations, we observed that populations that emerged earliest were collected from drier, less productive locations, similar to other studies (Thomson, King, & Schultz, 2017; Vaughn & Young, 2015). Root length had strong effects on survival and biomass, potentially because seedlings with longer roots were able to track soil-water availability as it dries down during the spring and summer (Fernandez & Caldwell, 1975; Peek, Leffler, Ivans, Ryell, & Caldwell, 2005). The longest roots were favoured under our extreme field conditions, but in a previous experiment measuring selection within a single field site, we observed that plants with

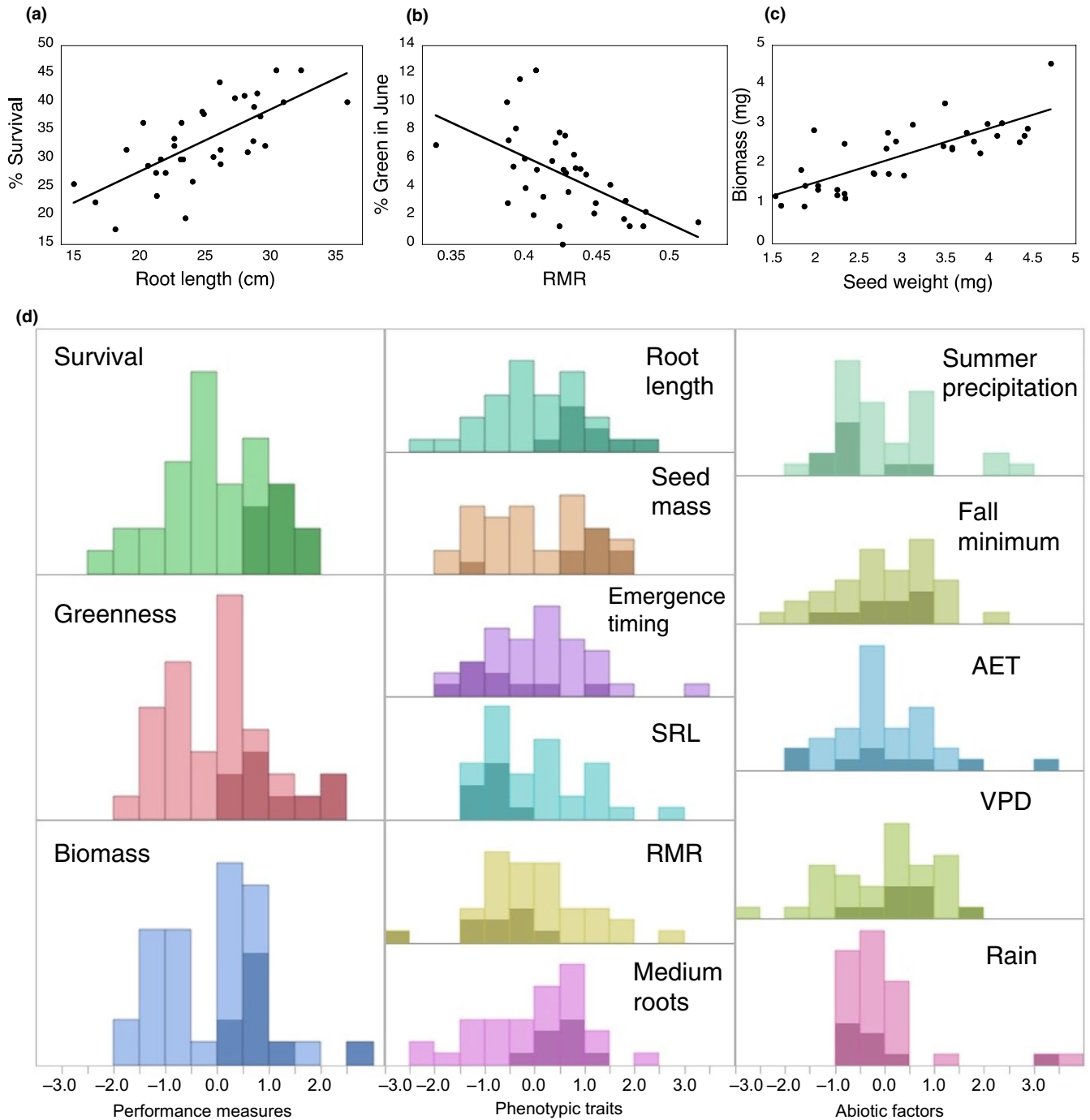


FIGURE 5 Example trait/performance relationships between (a) root length and survival, (b) RMR and per cent of seedlings that were green in June (greenness), and (c) seed weight and above-ground biomass and (d) histograms of standardized values of each of these three performance metrics, phenotypic traits and collection location abiotic variables. In (d), nine populations above the 75th quartile of survival across sites are highlighted in all panels, showing where these populations lie in the distribution of each variable (e.g. longer roots, larger seeds, etc.)

intermediate root lengths had the highest fitness, indicating that population means can be close to the local optimum (Atwater et al., 2015). Root length was highly correlated with other phenotypic traits not included in this analysis, including the number of root tips (correlation coefficient of 0.825), a trait that we have observed to be important in other studies (Atwater et al., 2015; Leger & Goergen, 2017). Populations with lower RMR were green later in the growing

season and had higher above-ground biomass, which may indicate increased allocation to above-ground structures; it remains to be seen if this is a successful long-term strategy in these sites. With this highly selfing species, it is challenging to determine how individual traits contribute to performance, but similar studies on outcrossing species would allow the breeding designs necessary to understand selection on individual traits.

TABLE 2 Standardized coefficients from model averaging for effects of collection location abiotic variables on three performance measures (survival, greenness in June and biomass). Values are presented for coefficients with confidence intervals that did not overlap zero, from models run separately at each site. R^2 values indicate overall fit of a model containing only non-zero predictors, and bold text indicates significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) of each individual predictor variable in these models

	Fields	Diamond	Orovada	Paradise	Peavine
Survival					
AET ^a	–	–	–	0.14	–0.31*
Rain ^b	–	–	–	0.11	–
Fall min.	–	0.27*	–	–	0.11
Fall min. ²	–0.11	–0.25	–0.21*	–	–0.42**
Summer precip.	–	–0.10	–	–0.31*	–
R^2	0.0662	0.3629	0.0921	0.2620	0.4175
Greenness					
AET ^a	–0.41*	0.15	–	–	–
Fall min.	0.12	–0.23	–	–	–
Summer precip.	–	–	–0.28*	–	–
R^2	0.2296	0.1606	0.1500	–	–
Biomass					
AET ^a	0.17	0.26*	–	–	–
Fall min.	0.15	–	–	–	–
Summer precip.	–0.17	–0.38*	–0.55***	–	–0.16
R^2	0.2282	0.2841	0.2966	–	0.0914

^aActual evapotranspiration. ^bAmount of precipitation falling as rain.

TABLE 3 Relationships between environmental distance and three performance measures (survival, greenness in June and biomass) for each population at each planting site. Overall distance is the Euclidean distance between each population's collection location and each planting site based on two principal components created from five abiotic variables. Fall min., summer pre. distance is the same calculation, considering only differences in fall minimum temperatures (x-axis) and summer precipitation (y-axis). Values are the slope of the regression line between environmental distance and performance. Significant relationships are bolded (* $p < 0.05$, ** $p < 0.01$)

Site	Survival				Greenness				Biomass			
	Overall distance		Fall min., summer pre. distance		Overall distance		Fall min., summer pre. distance		Overall distance		Fall min., summer pre. distance	
	Slope	R^2	Slope	R^2	Slope	R^2	Slope	R^2	Slope	R^2	Slope	R^2
Fields	0.06	0.04	0.06	0.00	–0.07	0.06	–0.22	0.05	0.03	0.01	–0.33*	0.12
Diamond	–0.01	0.00	0.01	0.00	0.00	0.00	–0.49*	0.17	0.14*	0.12	–0.38	0.10
Orovada	0.04	0.02	0.23	0.04	–0.09	0.09	–0.35	0.09	–0.04	0.02	–0.58**	0.25
Paradise	0.00	0.00	–0.45*	0.18	0.07	0.05	0.02	0.00	0.07	0.06	–0.06	0.00
Peavine	–0.06	0.04	–0.42*	0.17	–0.07	0.05	–0.20	0.04	–0.07	0.06	–0.32*	0.10

The ability to establish from seed under arid conditions has long been recognized as important in cultivar selection for restoration in the Great Basin (e.g. Johnson, Rumbaugh, & Asay, 1981), and in some systems, cultivars can outperform wild-collected seeds (Gallagher & Wagenius, 2016). In our study, however, the commercially available cultivar had average or below-average performance relative to wild collections. One reason may be that field performance has not always been the primary selection criteria for cultivar development in this region, and many plants available for use in rangeland seedings were chosen for other factors such as forage quality, biomass and seed production under agronomic conditions (Leger & Baughman, 2015). The results from this experiment indicate room for improvement in seed source for *E. elymoides*, and several of our experimental populations

would be excellent candidates for use in restoration. Similar studies could determine if it is possible to similarly identify promising populations of other important rangeland restoration species.

Finally, we focused on the seed-seedling transition, an important stage for plant regeneration (Postma & Ågren, 2016) and key for restoration from seed, but survival beyond the seedling stage is clearly important. Following experimental seedings over time can be challenging, as low survival at this stage in invaded arid systems precludes sufficient sample sizes for comparing performance among populations across other life-history stages (Waser & Price, 1985). An experimental strategy that combines direct seeding, as employed here, directly alongside transplanting of juvenile plants from the same populations (e.g. Johnson, Cashman, & Vance-Borland, 2012)

could allow for identifying trade-offs among fitness at different life-history stages and identification of populations that perform optimally across life-history stages, and we recommend future studies that combine these two approaches.

5 | CONCLUSIONS

The wild populations we surveyed were highly variable, and we observed very strong relationships between population-level phenotypic traits and field performance. Though variables associated with average climate and soil properties at the location of origin were also important, they were much less reliable predictors of performance than direct measures of phenotype. It is possible that more precise measures of site abiotic variables would have yielded better overall predictive power, but the amount of phenotypic variation we observed in plants from even similar average climate conditions suggests that other factors are maintaining variation in fitness-related phenotypic traits (Geber & Griffen, 2003). Our field study found that seed size, root length and emergence timing were important characteristics for seedling establishment in altered sites. While focusing on climate of origin was an effective first step for selecting seed sources for restoration in this system, field trials identified multiple populations of *E. elymoides* that are promising seed sources for restoration in disturbed Great Basin systems. Similar studies can be used to test population suitability for restoration from seed in any ecosystem, and focusing on seedling traits, as we have done here, could help increase success in challenging restoration scenarios world-wide.

ACKNOWLEDGEMENTS

This project was funded by a USDA Rangelands Grant 2011-38415-31158, the USDA-Hatch program through the University of Nevada, Reno, and the Great Basin Native Plant Project. Thanks to Riley Anderson, Lindsey Boyer, Meghan Whitman and Bryce Wehan for assistance with seed collection and processing, and Scot Ferguson, Owen Baughman, Todd Erickson, Jason Sprott and Britney Trimble for assistance with planting and data collection, the BLM for facilitating work on public land and Tom Dilts for providing his CWD calculator.

AUTHORS' CONTRIBUTIONS

E.A.L. and J.J.J. conceived the ideas, and secured research funding; E.A.L., D.Z.A. and J.J.J. designed the methodology; E.A.L. and D.Z.A. implemented the field experiment and collected data; E.A.L. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.771q160> (Leger, Atwater, & James, 2019).

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SUPPORTING INFORMATION

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How to cite this article: Leger EA, Atwater DZ, James JJ. Seed and seedling traits have strong impacts on establishment of a perennial bunchgrass in invaded semi-arid systems. *J Appl Ecol.* 2019;56:1343–1354. <https://doi.org/10.1111/1365-2664.13367>