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RESEARCH ARTICLE

Landscape and organismal factors affecting sagebrush-seedling transplant survival after megafire restoration

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Larger and more frequent disturbances are motivating efforts to accelerate recovery of foundational perennial species by focusing efforts into establishing island patches to sustain keystone species and facilitate recovery of the surrounding plant community. Evaluating the variability in abiotic and biotic factors that contribute to differences in survival and establishment can provide useful insight into the relative importance of these factors. In the western United States, severe degradation of the sagebrush steppe has motivated substantial efforts to restore native perennial cover, but success has been mixed. In this study, we evaluated survival of more than 3,000 sagebrush seedlings transplanted on 12 patches totaling 650 ha within a 113,000 ha burn area, and related the survival to organismal and subtaxonomic traits, and to landscape variables. Big sagebrush has high intraspecific diversity attributed to subspecies and cytotypes identifiable through ultraviolet (UV)-induced fluorescence, length:width of leaves, or genome size (ploidy). Of these organismal traits, survival was related only to UV fluorescence, and then only so when landscape variables were excluded from analyses. The most significant landscape variable affecting survival was soil taxonomic subgroup, with much lower survival where buried restrictive layers reduce deep water infiltration. Survival also decreased with greater slope steepness, exotic annual grass cover, and burn severity. Survival was optimal where perennial bunchgrasses comprised 8–14% of total cover. These soil, topographic, and community condition factors revealed through monitoring of landscape-level treatments can be used to explain the success of plantings and to strategically plan future restoration projects.

Key words: bunchgrass, cheatgrass, fire, rehabilitation, sagebrush steppe, subspecies, transplants

Implications for Practice

- Deciding where to locate restoration treatments across large and complex landscapes is an ongoing challenge that requires knowledge of how species' ecological requirements vary, especially in relation to physical and biotic-community gradients. Landscape-level restoration trials implemented by managers are key but underutilized opportunities to obtain such information.
- The success of planting sagebrush, a species with high intraspecific diversity, can be enhanced in heterogeneous, megafire landscapes by avoiding planting into soil types with shallow impermeable layers, steep slopes, high burn severity, or high native and exotic grass abundances.
- These factors influence survival more than subtaxonomic variation in transplanted stock, and their effects can help explain mixed establishment success and be considered in setting treatment objectives and metrics for planting success.

Introduction

Spatial variability in restoration outcomes is a primary concern for practitioners, and it can be an important source of insight into the underlying factors contributing to project success or failure (e.g. Brudvig et al. 2017). As disturbances have increased worldwide, the spatial heterogeneity they encompass has also increased. Greater area and heterogeneity within projects cause restoration practitioners (1) to prioritize areas for treatment investment to increase chances of restoration success and (2) to explain the variable outcomes to stakeholders. The needed information for these tasks is often scarce, and difficult or unlikely to be provided from small-plot studies. By evaluating the effects of biotic and abiotic gradients on the variability in outcomes of landscape-scale and operational trials, restoration practitioners could more efficiently implement their limited resources to optimize outcomes and to help define appropriate metrics of success in subsequent trials.

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A key aspect of variability within restoration projects is the patchiness of recovery (Hulvey et al. 2017). Restoration projects are especially challenging in warmer/drier regions of a species' range, and, thus practitioners increasingly recognize the value of attaining initial recovery in patches (vs. continuous cover), considering that patches can serve as wildlife habitat and act as population nuclei for natural regeneration (Longland & Bateman 2002). In large disturbance areas of terrestrial environments, planting foundational species is often used to create such patches and additional degrees of patchiness can result from selective survival of outplants, which refers to seedlings transplanted from nursery to field settings. Spatial variability in planting success can be affected by differences in planting stock that relate to genetic background or rearing conditions, in addition to heterogeneity in landscape features such as topography, soils, and biotic communities (Lesica & Allendorf 1999; Bischoff et al 2010).

Matching appropriate planting source stock to site conditions is considered important for the success of restoration projects (i.e. use of "right plant, at the right place and time"; McKay et al. 2005; Oldfield & Olwell 2015), although few studies address these effects together in real restoration treatments and the variability within them. Acquiring local seed and especially nursery seedlings for planting in time for restoration projects implemented the year after fire is often not possible or pragmatic, especially for megafires. Local seed sources (and thus, native subtaxa and populations) have typically been shown to outperform distant sources in well-cultivated, common garden settings (McKay et al. 2005; Leimu & Fischer 2008; Hereford 2009; Rowe & Leger 2012; Germino et al. 2019) and national restoration programs have accordingly prioritized seed source selection. How seed-source and within-project environmental variability compare in their effects on restoration planting success has received little research despite its importance to managers.

In the western United States, altered fire regimes due to exotic annual grass invasion have greatly impacted the sagebrush steppe ecosystem, resulting in a loss or degradation of half the historic 500,000 km^2 range of sagebrush (*Artemisia* spp.) (Miller et al. 2011; McArthur & Plummer 1978). This loss of habitat has serious implications for obligate sagebrush species such as Greater Sage-Grouse (*Centrocercus urophasianus*), which have been recognized as a serious conservation concern. Big sagebrush (*Artemisia tridentata* Nutt.) is poorly adapted to fire, owing to its inability to resprout after top-kill in addition to short seed longevity and dispersal distances, and thus it often requires restoration intervention after fires (Young & Evans 1989; Wagstaff & Welch 1990). However, postfire efforts to seed sagebrush over the last several decades and across millions of hectares have had mixed results (Knutson et al. 2014; Pilliod et al. 2017; Copeland et al. 2018; Germino et al. 2018). This lack of success relates to unfavorable moisture and temperature conditions or competition from dense stands of exotic or seeded grasses (e.g. Brabec et al. 2017; Germino et al. 2018; Hardegree et al. 2018). Seed availability, germination, and initial seedling survival are frequent demographic bottlenecks for sagebrush, especially after fire (James et al. 2011). One way to overcome these bottlenecks is to outplant seedlings rather than broadcast seed, which generally increases the probability of survival though at a higher cost and effort than seeding (Dettweiler-Robinson et al. 2013), and offers a more targeted approach to reestablishing sagebrush patches.

Widespread species such as big sagebrush often have high intraspecific variation that relates to landscape variation. Sagebrush has three dominant subspecies adapted to different site conditions (McArthur et al. 1988). Chromosomal ploidy number (cytotype), including diploid (2n) and tetraploid (4n), plays an important role in site differentiation and variation in two of the three subspecies and can affect responses to soil water and temperature (McArthur & Sanderson 1999; Brabec et al. 2017). Specifically, polyploid populations of sagebrush can be more adapted than diploids to harsh microclimate conditions such as freezing (Brabec et al. 2017). Moreover, subspecies *A. t. vaseyana* (Rydb.) Beetle is found in relatively cooler and wetter sites at higher elevations, and at lower elevations *A. t. tridentata* Beetle & Young is found where soils are deeper, such as topographic depressions, and *A. t. wyomingesis* Beetle & Young is found on ridges or plateaus that often have shallower soils. Most inferences about population variability for sagebrush and other species have been obtained from common gardens that are cultivated and homogenized compared to spatially variable restoration sites, thus it is unclear how much adaptive variation in sagebrush impacts establishment at landscape scales.

Many of the studies investigating sagebrush recovery from plantings have been conducted at relatively small scales (Davies et al. 2013; Dettweiler-Robinson et al. 2013; McAdoo et al. 2013). Therefore, there is a need to evaluate variability in outplant success over larger and more variable areas representative of actual restoration sites, with consideration that sagebrush subtaxa may exhibit different survival patterns across the landscape. In the current study, we capitalized on a landscape-scale postfire planting of approximately 420,000 big sagebrush seedlings to determine how much of the variability in survival could be attributed to heterogeneity in (1) static physiographic characteristics of the landscape such as soils and topography, (2) biotic community dynamics, and (3) traits indicating subtaxonomic identity.

Methods

Site and Seedling Stock

The Soda Wildfire burned 113,000 ha of sagebrush steppe with community states varying from intact to exotic annual-grass dominated to seeded bunchgrasses on the Idaho/Oregon state border in August 2015. Planting of 1-year-old big sagebrush seedlings occurred as part of the U.S. Bureau of Land Management's (primary land manager of the area) Emergency Stabilization and Rehabilitation program, with 419,680 seedlings planted by April 2016 across 650 ha of total area in 12 (polygon) areas (mean area/unit = 5 ha; mean seedlings/unit = 44,733 ± 12,916; Fig. 1). Seedlings were either containerized (0.13 L or 8.0 $inch^3$) stock outplanted in October 2015, or bare-root stock outplanted March 2016.

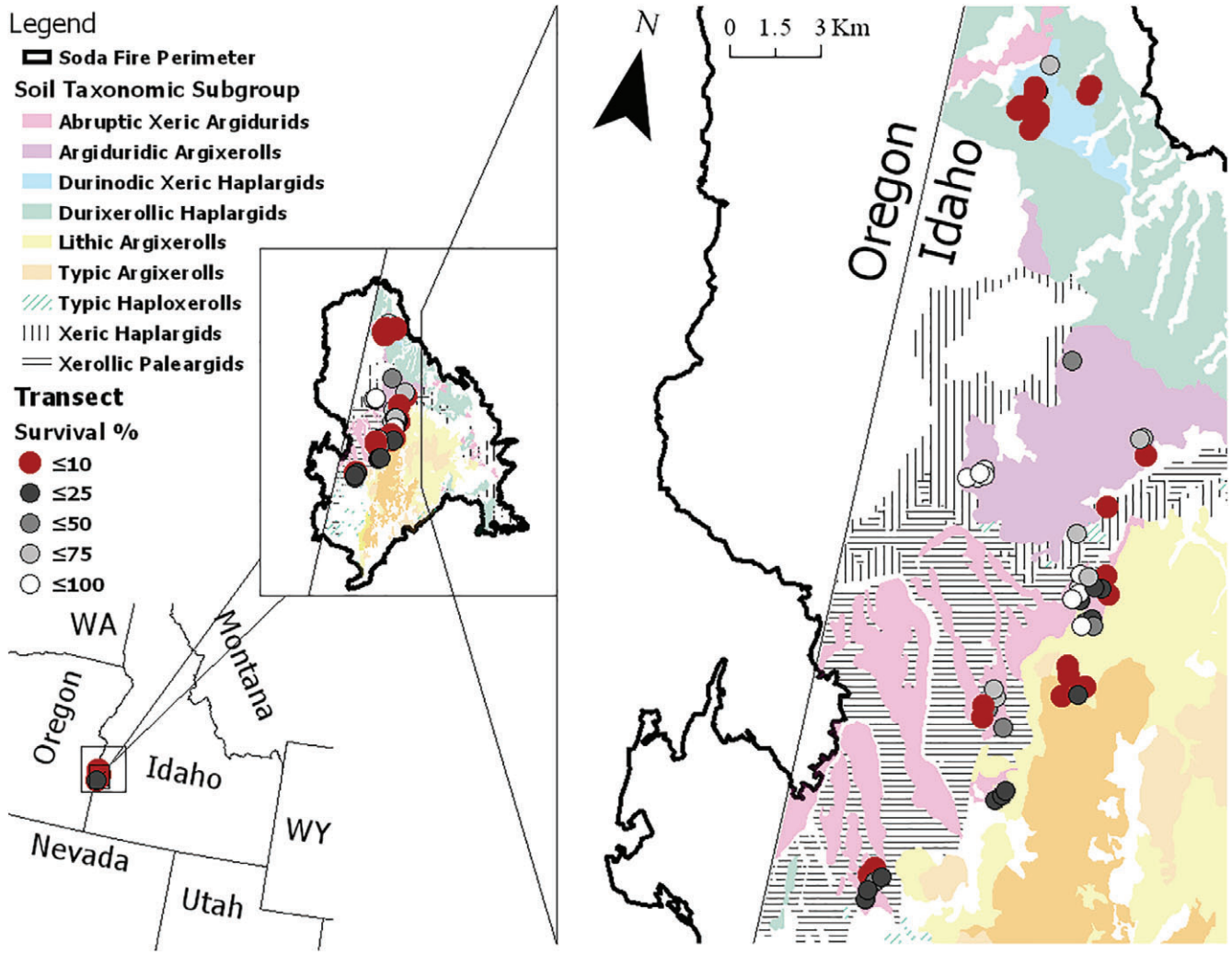

Figure 1. Map of planting units and sagebrush monitoring transects across the Soda fire area (Owyhee Mountains, Idaho, and Oregon). Scale depicts the soil taxonomic subgroup and the proportion of tagged seedlings identified as living during the final monitoring period in fall 2017.

Seedlings were grown at the U.S. Forest Service Lucky Peak Nursery located approximately 100 km to the east (43.581°N, −115.990°W). Holes for seedlings were created with hoedads, using approximately 4 m spacing between outplants distributed over the extent of each planting area/unit. As with any large-scale seeding or planting done in the year after fire, numerous seed sources and nursery stock had to be used. Documentation of all seed sources were not available to us, but according to the agency staff overseeing treatments, the sources were near Twin Falls, Idaho (1,400 MASL) and the Birds of Prey National Conservation Area (800 MASL) for the first planting in fall 2015, and from other undocumented sources in two planting units that occurred in 2016 (2016-A and 2016-B; Table 1).

Seedlings were planted across a wide range of elevations (1,000–1,600 m), aspects (13–344° clockwise from N), mean annual precipitation (281–421 mm/year, 30-year average from gridded data, PRISM Climate Group 2015), plant community, and soil conditions (SSURGO, Soil Survey Staff, Fig. S1, Supporting Information). Soil consists of mollisols (32%) and aridisols (68%) comprised of nine soil-taxonomic subgroups (Table 2). Burn severity across the area ranged from unburned/low (1) to moderate (3) with a median burn severity of low (2; Eidenshink et al. 2007; MTBS 30 m pixel). Annualized weather during the planting and monitoring period did not differ significantly from climatic normal (Fig. 2C & 2D); however, the precipitation during winter and early spring 2017 was the eighth wettest period recorded in the twentieth century (NOAA/NCDC 2018).

Transect Establishment and Seedling Measurements

Fifty-seven 153 m × 8 m belt transects were randomly located and permanently marked across the entire planting area. Transects were surveyed for seedlings during a 6-week period in May–June 2016, prior to the onset of seasonal water deficit and summer drought, (Fig. 1). A total of 3,040 live and dead seedlings (mean = 53 ± 2.5 seedlings/transect) were detected

Table 1. Seedlings were transplanted as part of three different planting units based upon the taxonomic label and site of planting. Significant differences in traits (among rows, within each column) are indicated by differing letters as determined by Kruskal–Wallis test ($p < 0.05$).

Planting Unit	Number of Transects	Year	Stock Type	Proportion Alive (±SE, fall 2017)	Proportion Diploid (±SE)	Average Leaf Length:Width	Average UV Fluorescence (±SE)	Number of Plants per UV Category				
								1	2	3	4	5
2015	9	2015	Container	0.63 (0.099)A	0.66 (0.087)A	3.77 (0.16)	1.23 (0.129)	28	0	2	1	0
2016-A	4	2016	Bare root	0.06 (0.018)B	0.08 (0.075)B	3.39 (0.06)	1.33 (0.141)	21	4	1	1	0
2016-B	36	2016	Bare root	0.26 (0.045)B	0.56 (0.044)A	4.06 (0.10)	1.22 (0.034)	258	32	9	4	1

Table 2. Characteristics of soil taxonomic order, suborder, and subgroups in the study area.

UV Rating	Total Number	Number Dead	Alive:Dead	Diploid (2n)	Tetraploid (4n)	2n:4n
1	247	67	1.05	96	84	1.12
2	25	11	0.69	6	8	0.75
3	11	2	1.46	3	6	0.50
4	5	2	0.59	2	1	
5	1	0		0	1	

in the transects and were marked with 1 cm × 3 cm lightweight metal tags, and remeasured in fall 2016, spring 2017, and fall of 2017. Planted seedlings were very distinct from sagebrush seedlings that had germinated since the fire in the previous 1–4 months, owing to either (1) the larger, narrow, unbranched "popsicle"-like crown, regular spacing, and potting soil of containerized stock or (2) branched but much larger size of bare-root stock, compared to the smaller, more branched, and denser foliage of seedlings that germinated in the field. After June, the risk of confusing planted and nonplanted seedlings increased, and thus we did not establish additional plots. Our sampling did not capture initial mortality from the time of planting to our first measurement (2–7 months, except where dead seedlings were still present). However, the Bureau of Land Management (BLM) conducted implementation monitoring at the time of planting (i.e. "initial abundance") as well as in August of 2016 and spatial patterns of secondary survival reported here correlate well with the BLM's assessment of initial survival to August 2016 (unpublished data on file, Bureau of Land Management, Boise District Office). Survival estimates for the latter three sampling events (fall 2016, spring and fall 2017) were relative to the total number of alive and dead seedlings measured in the initial May 2016 sampling. Eleven transects (530 seedlings) were established to monitor the seedlings planted in fall of 2015 while 46 transects (2,510 seedlings) were established to monitor those planted in the spring of 2016.

At each sampling, we recorded (1) whether seedlings were alive, based on presence of green and turgid leaves, or dead; and (2) plant size, specifically canopy volume as $4/3\ \pi ab^2$, where a and b are half the height and greatest width of the foliar crown (0.5 cm resolution). Vegetation cover within a 1 m^2 quadrat around each seedling was estimated by functional group (all combinations of native or exotic, annual or perennial, grasses or forbs) in 5% increments up to 40% cover, and in 10% increments from 40 to 100% cover.

Tissue Samples

Cytotype based on genome size, ultraviolet (UV) fluorescence (a measure of coumarin concentration, Stevens & McArthur 1974; Richardson et al. 2012), and leaf length:width ratio of evergreen leaves were measured on 362 plants (3–9 seedlings per transect to estimate the subspecies composition of each transect). Three subspecies included (1) mountain big sagebrush, *A.t.* subsp. *vaseyana* (Rydb.) Beetle, found at higher elevations; (2) basin big sagebrush, *A.t.* subsp. *tridentata* Beetle & Young, found at lower elevations in deep and well-drained soils; and (3) Wyoming big sagebrush, *A.t.* subsp. *wyomingensis* Beetle & Young, found on lower-elevation plains and ridges where soils may sometimes be relatively shallower. Given the distinct site characteristics of each subspecies, matching the appropriate subspecies is considered essential to successful seedling establishment (McKay et al. 2005). Moreover, palatability and suitability to wildlife differs among the subspecies, and is related to their differences in foliar compounds (Jaeger et al. 2016). Coumarins favor palatability and occur primarily in mountain big sagebrush, and all subspecies have tetraploid populations but only mountain and basin big sagebrush also has diploid populations (Stevens & McArthur 1974; Rosentreter 2005).

Leafy lateral branches were collected from individual plants, were sealed in plastic bags, and chilled to 4°C until analyzed. The number of samples were adjusted based on the apparent morphological variation (leaf length and stature) of seedlings in each transect, with more sampling in more diverse transects. Tissue samples were collected from nontagged seedlings adjacent to the transect belts, to avoid negatively impacting the survival and growth of monitored seedlings using the same assurances that seedlings were planted as described above. Samples were collected from both living and dead seedlings, and because cytotype analysis cannot be done on dead tissue, we obtained ploidy estimates for 207 of the 362 samples.

Leaf length:width ratios were determined by measuring the maximum length and width of persistent leaves using 0.1 mm

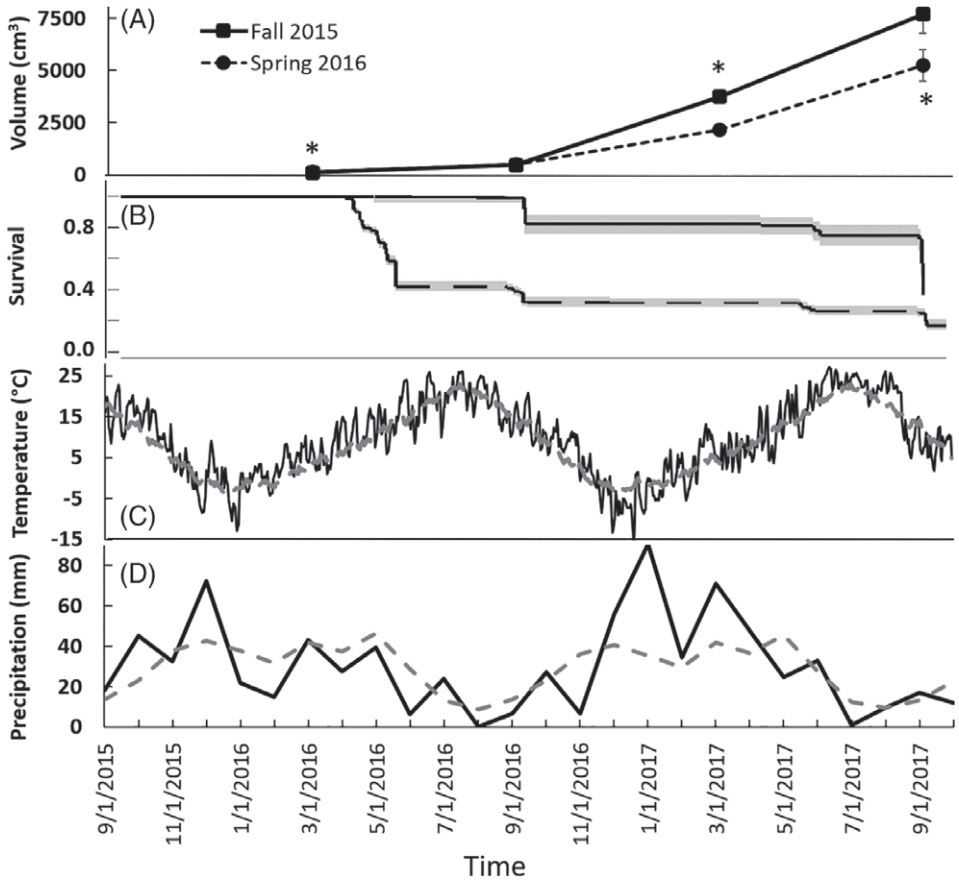

Figure 2. Mean canopy volume (cm^3, ±1SE, A) and proportional survival (±95% CI, B) of sagebrush outplanted in fall (October) 2015 or spring (March) 2016, and corresponding daily weather anomolies (deviation of daily temperature (C) and precipitation (D) from 30-year climate averages). Significant differences ($p < 0.05$) are indicated by asterisks. For separation of survival between cohorts, $p < 0.0001$. Walter-type climate diagram depicting climate normals and study period weather conditions in context of the timing of planting and considerable mortality events is presented in Figure S4 and survival for each transect is presented in Figure S2.

resolution digital calipers. UV fluorescence (fluorescent light emission upon illumination of UV radiation) of ground leaf tissue submerged in water was quantified on a scale from 1 to 5, where 1 indicated no fluorescence (Stevens & McArthur 1974). Genome size was determined from flow cytometry using a Partec Cyflow Space flow cytometer (Partec, Munster, Germany) under UV fluorescence, following Richardson et al. (2012). The mean UV fluorescence value, mean leaf length:width, and the proportion of diploid individuals were calculated for each transect and used as modeling variables.

Statistical Analyses: Step-Wise Modeling at Two Spatial Scales

We used two analyses to address neighborhood community effects on seedlings at two scales: the level of the stand (transect) and at the individual seedling level. The transect-level analyses allowed us to ask questions about how outplant survival and growth related to landscape-level variation between transects, but not about the environment directly around and affecting each seedling (i.e. within-transect variability). Variation in the proportion of seedlings surviving among transects were analyzed using a series of generalized linear mixed models (GLMMs), and analyses at the individual seedling level were analyzed with Cox proportional hazards regression models.

The GLMMs on transect survival were fit to a binomial distribution with spatial planting area unit (polygons in Fig. 1) as a random effect and cohort/type/source as a fixed effect (hereafter referred to as "cohort," its two levels are hereafter labeled "October 2015" or "March 2016"; lme4 package, Bates et al. 2015; all analyses used R v3.4.2, R Core Team 2017). There were not enough replicate transects to provide adequate degrees of freedom for evaluating all factors and factor levels in one GLMM model. Thus, we used a two-stage approach for transect-level analyses in which we first determined which factors within the (1) physiographic, (2) biotic communities, and (3) seedling subtaxonomic trait themes were most explanatory using separate models of seedling survival (to fall 2017) within each theme (Table S1), and then we selected only the significant factors from each model theme for inclusion in one comprehensive synthesis model that would allow us to evaluate the importance of a variable within each theme against the effect of variables in other themes. Model selection within each theme

model was determined using likelihood ratio as a basis to determine if inclusion of each factor improved the model or not as indicated by significant changes ($p < 0.05$) in akaike information criterion.

Factors in the physiographic theme model included soil taxonomic subgroup, soil temperature and moisture regime, soil depth, and generalized soil-water availability from 0 to 5 cm depth, all estimated from the NRCS Soil Web (SSURGO, Soil Survey Staff); heat load (McCune & Keon 2002); slope and topographic wetness index calculated from USGS Digital Elevation Models (as in Germino et al. 2018); and burn severity, defined as "A qualitative assessment of the heat pulse directed toward the ground during a fire. Burn severity relates to soil heating, large fuel and duff consumption, consumption of the litter and organic layer beneath trees and isolated shrubs, and mortality of buried plant parts" (NWCG 2018; MTBS, http://www.mtbs.gov/index.html). The combined stocktype/source/year of planting of seedlings was assessed as a single variable, because confounding difference in planting time between stock type and seedling sources made it impossible to discern the independent effects of stock type or seedling source or planting date. Additionally, maximum vapor pressure deficit, average annual temperature (°C) and precipitation (mm) during the monitoring period, as well as long-term mean annual precipitation (1950–2014, PRISM Climate Group 2015) for each transect were evaluated. None of these factors varied within transects, and so averaging was not required.

Factors in the seedling trait theme model included cytometer value and UV fluorescence rank of tissue samples, average leaf length:width ratio, and cohort (planting year, stock type, and seed source), with the replicate being the average value of all seedlings measured on each transect (i.e. transect was the unit of replication). Differences in the collective leaf taxonomic traits (leaf length:width, UV fluorescence, and ploidy) between cohorts and spatial planting units were evaluated using nonmetric multidimensional scaling (NMDS, "vegan" package, Oksanen et al. 2018) after transforming all values from 0 to 1, where 0 and 1 were the minimum and maximum values for each parameter, respectively.

Factors in the plant-community theme model included the percent cover of each functional group, averaged across for all the 1-m^2 quadrats sampled along each transect. Functional groups consisted of cover by exotic annual grass, perennial grass, bare soil, litter, and forbs.

We also evaluated the relationship of outplant size and surrounding plant community conditions (within the 1 m^2 area) to survival of each seedling using a semi-parametric Cox proportional hazard regression model ("survival" package, Therneau & Lumley 2015). Data were clustered by transect, and seedling cohort was a fixed effect. The interval censored analysis can provide a "hazard of death" or "hazard ratio" that informs the parameters influence on the probability that an individual seedling will experience mortality while holding all other factors constant. Between-group comparisons were tested using Kaplan–Meier log-rank survival analysis.

Lastly, classification and regression trees (CART, "rpart" package, Therneau et al. 2017) were used to identify thresholds in slope, precipitation, and exotic annual grass and perennial bunchgrass densities on outplant seedling survival.

Results

Seedling Growth and Survival

Nearly half of the 3,040 outplanted seedlings we sampled (i.e. not including BLM data) were dead upon our first sampling in May–June 2016 (46% mortality, leaving 1,402 live plants; Fig. S2B). Thereafter, approximately 9% of remaining seedlings died between each sampling event. By fall 2017, 26% of the 3,040 seedlings we initially marked and detected were still alive. Ending survival in fall 2017 was 58% for the containerized seedlings planted in the fall of 2015 and 23% for bare-root seedlings planted in spring of 2016 (effect of cohort, log-rank, $p < 0.0001$; Fig. 2B). These survival statistics accounts for 210 seedlings removed from analysis because tags were no longer attached to subject plants. Nearly half of the tags (90) were recovered in the general vicinity of transects and were presumably relocated by animals such as crows (*Corvid* sp.). An additional 24 plants of the 210 seedlings removed from analysis (12%) had been uprooted or severely impacted by burrowing animals. Less than 1% of seedlings showed evidence of frost heaving (which can lift the soil-root plug aboveground) and there were no relationships of frost heaving to survival (Table S2).

Mean canopy volume at the first sampling event was 130.7 (±1.01) cm^3 for all sagebrush outplants, 106.9 (±2.07) cm^3 for the containerized seedlings outplanted in fall 2015, and 142.2 (±1.86) cm^3 for bare-root seedlings outplanted in spring 2016 ($p < 0.0001$; Fig. 2A). Mean relative growth rate for the 2015 containerized seedlings was 1.7 times greater than for the 2016 bare-root seedlings ($p = 0.014$), resulting in larger canopy volumes by fall 2017 for the 2015 containerized seedlings ($7{,}681.5 \pm 735\ cm^3$) compared to the 2016 bare-root seedlings ($5{,}260.7 \pm 569\ cm^3$, Fig. 2A). By the last sampling in fall 2017, mean height and width were 24.3 ± 0.37 and 15.1 ± 0.35 cm for all surviving seedlings, respectively. Initial seedling canopy volume did not relate to seedling survival (Table S2).

Physiographic Model

Soil taxonomic subgroup, precipitation (30-year climate average), the slope of the site, and burn severity affected survival (Table S1). Survival probabilities predicted by the models were greatest for argiduridic argixerolls (survival probability approximately 70%) and least for durixerollic haplargids (approximately 2%, Fig. 3). Survival had a curvilinear relationship to precipitation variability among transects (Fig. 4) with an optimum range of 300–350 mm/year and maxima at 340 mm/year according to the CART model (Fig. 5B). Survival decreased with slope steepness and appeared optimal where slopes were less than 8° according to the CART model. Seedling survival decreased with burn severity (Fig. 4). The effect of burn severity may be related to community cover, specifically having a positive relationship to perennial grass cover ($p < 0.0001$) and bare

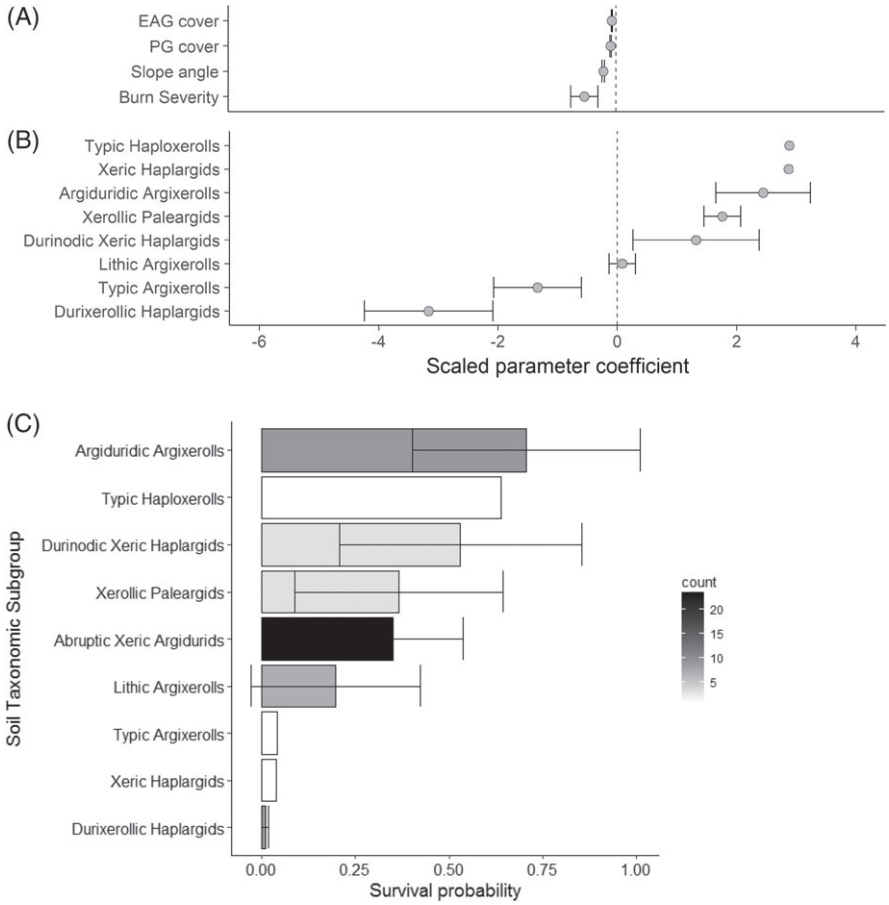

Figure 3. Scaled parameter coefficient plot depicting the influence of each factor on the proportion of seedling survival for (A) continuous variables and (B) individual subgroups of soil taxonomy. Coefficients greater than zero indicate the factor has a positive relationship to survival, and more negative values indicate the factor is associated with less survival. Significant factors do not have errors overlapping zero. (C) Predicted survivability (±1SD) based upon soil taxonomic class. Greyscale shows the number of transects with that soil type (legend). EAG and PG are exotic annual and perennial grasses, respectively.

soil exposure, albeit marginally ($p = 0.09$). Sites that burned at low intensity (burn severity of 2) had significantly more exotic annual grass cover ($p = 0.02$).

Biotic Community Model

Outplant survival was negatively related to exotic annual grass cover and hyperbolic in its relationship with perennial grass cover (Fig. 4, see Table S1 for mean and range of community cover). According to the CART model results, outplant survival was favored by perennial grasses where they had 8.1–14% cover and declined when perennial grass (PG) cover was below 8.1 and above 14% (Fig. 5A). The negative effect of exotic annual grass cover was more strongly correlated with survival for the transects planted in 2015 ($r^2 = 0.78$, $p = 0.0003$) than for transects planted in 2016 ($r^2 = 0.11$, $p = 0.027$).

Subtaxonomic Trait Effects

Half of all seedlings sampled were diploid (2n; 52%) for both seedling cohorts ($p = 0.50$), although significantly more tetraploid (4n) individuals were identified from the 2016-A planting units (Table 1; $p = 0.001$ for differences among transects, and $p = 0.0003$ for differences among planting unit). Leaf length:width ratio varied among transects ($p < 0.0001$) but not cohorts ($p = 0.30$) or planting unit type ($p = 0.10$). UV fluorescence values ranged from 1 to 5 (none to maximum fluorescence, respectively), with 5% of samples from 13 transects having UV fluorescence levels diagnostic of subspecies *vaseyana* (>2 for UV score).

UV fluorescence did not differ between seedlings that were alive or dead in the first sampling event ($p = 0.65$; Table 3). Multivariate trait combinations (UV, ploidy, leaf length:width ratio; NMDS; Fig. S3) did not vary between cohorts ($p = 0.94$) but were distinct between planting units ($p = 0.002$; Table 1) due primarily to variation in ploidy. However, the GLMM revealed that survival was related only to UV fluorescence and none of the other factors in the seedling trait model ($p < 0.0001$, Table S1).

Synthesis Mixed Model

The following factors were statistically significant ($p < 0.05$) variables from each of the three theme models and therefore

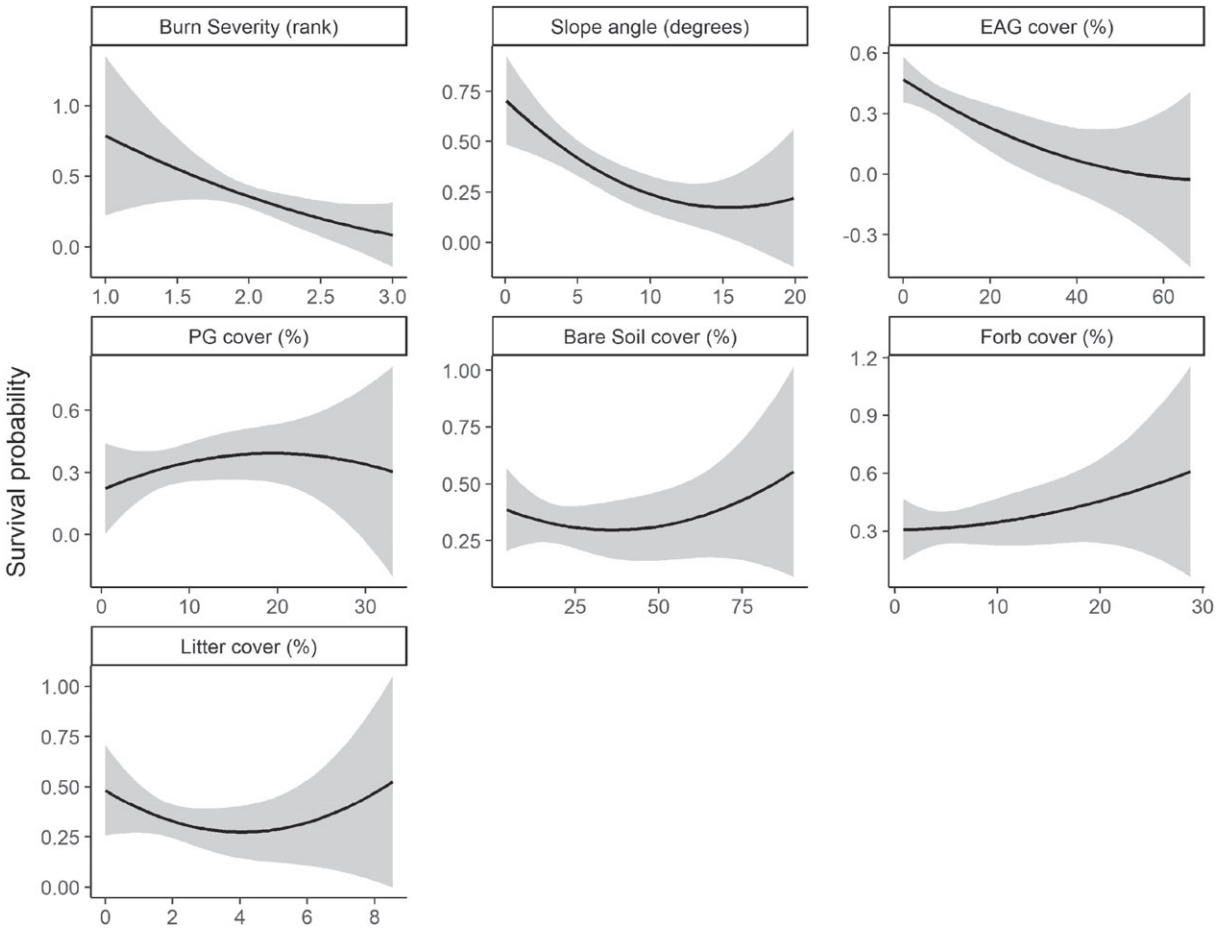

Figure 4. Partial dependence plots of significant, continuous variables affecting seedling survival. Burn severity, slope angle (degrees), exotic annual grass (EAG, %), perennial grass (PG, %), bare soil (%), forb (%), and litter cover (%). X-axis titles and units are shown in the header for each panel.

were used in the full combined comprehensive, "synthesis model" of seedling survival: (1) UV fluorescence from the seedling trait model, (2) soil subgroup, precipitation, slope, burn severity from the physiographic model, and (3) seedling cohort, exotic annual, and perennial grass cover from the competition model. Ultimately, UV fluorescence, precipitation, and cohort did not significantly contribute to the model accuracy and were therefore excluded in the full model (Table S1, bottom).

To verify that the significantly higher survival of containerized seedlings planted in the fall of 2015 was not falsely inflating the significance of soil taxonomic subgroup, models were re-run on a reduced dataset containing only transects planted in the spring of 2016, in which case soil taxonomic subgroup, slope, and exotic annual and perennial grass cover were significant explanatory factors but burn severity was not.

Cox Proportional Hazards Model

The mortality hazard ratio for individual seedlings was predicted to increase 3% with each 10% increase in the cover of bare soil ($p = 0.0184$) and was 3.7 times greater for spring-planted, bare-root seedlings than for fall-planted, containerized seedlings ($p < 0.0001$, Table S2).

Discussion

Similar to other studies on postfire sagebrush planting (e.g. Dettweiler-Robinson et al. 2013), approximately one-quarter of seedlings survived, under the generally average-to-favorable weather conditions of our study years, and insights from which seedlings survived or perished were gleaned from the combination of stand- and plant-level analyses. Differences in the relative importance of each factor theme to survival were evident, with very strong effects of soil type compared to plant community composition and especially organismal traits that indicate subtaxonomic identity or cytotype and thus might be expected to influence survival patterns.

Soil Mapping Unit Effects

Stark differences in soils resulting from parent material are known to influence restoration treatments (e.g. Abella et al. 2014), but few studies have evaluated how mapped variation in soil type affects restoration seedings (e.g. Gornish & Ambrozio dos Santos 2015), and even fewer have evaluated soil type effects for planning intensive planting treatments. We found that differences in soils that are not always evident viewing a

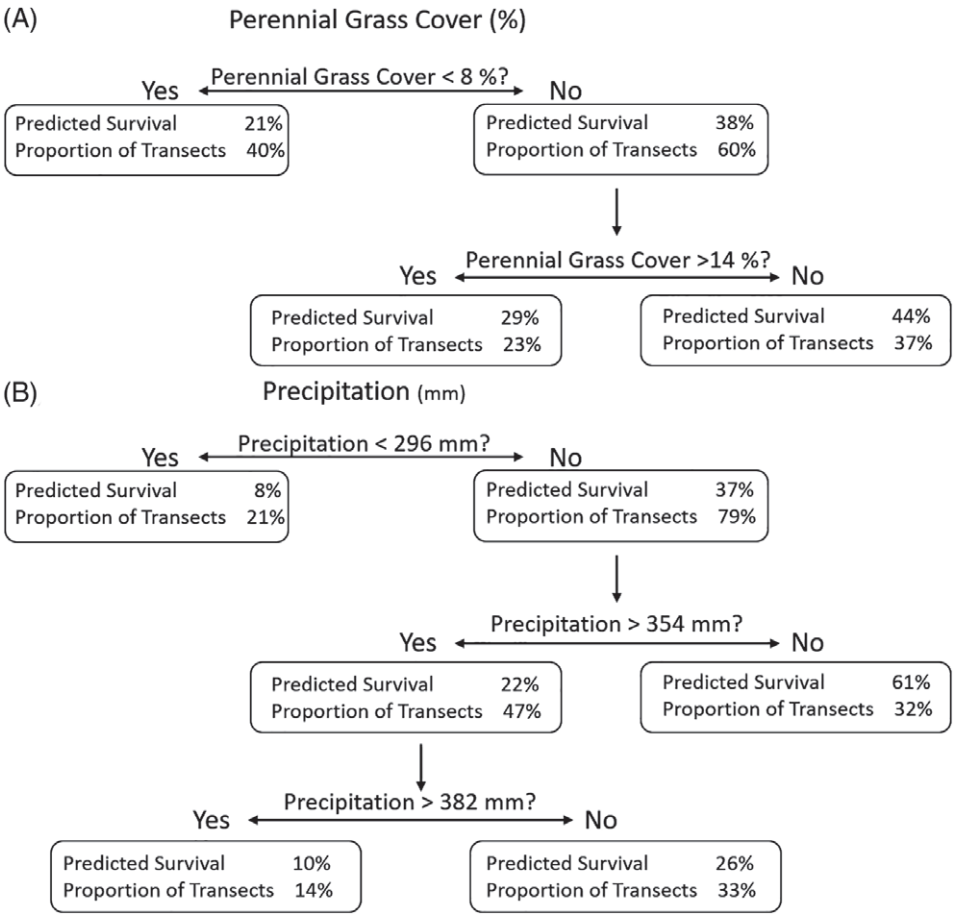

Figure 5. Classification and regression trees (CART) results of seedling survival in relation to perennial grass cover (%, A) and precipitation (mm/year, B). The percent of seedlings predicted to survive (predicted survival) and the percent of transects that meet the conditions (proportion of transects) are depicted in boxes.

landscape and instead generally require a soil map (or soil pits) to identify had very strong effects on sagebrush outplant survival. The relatively greater survival of outplants we observed on argiduridic argixerolls compared to other soil types also may relate to soil moisture, although not in a way that is attributable to soil moisture class. Within argixerolls, greater survival occurred on the aridic argiduridic compared to typic (semiarid) subgroup. Similarly, within haplargids, greater survival on the durinodic xeric compared to durixerollic suborders cannot be due to differences in their temperature and moisture regime, as they both had relatively low precipitation and high temperatures and vapor pressure deficit compared to the other soil types. Both of these haplargids have a buried silica and calcium carbonate horizon, but this layer is poorly developed and thus more penetrable (for water storage and root penetration) in its "durinodic" form compared to its well-developed and thus more impenetrable "duripan" form that prevails in the durixerollic soil class and which limits root growth and air and water movement (Blank et al. 1998; Wilson 2015). Thus, soils with restrictive layers that reduce infiltration to the deep soil layers that sagebrush is known to rely on, and at the same time cause less drainage and thus saturation and anoxic conditions in shallow soils that sagebrush is proposed to be intolerant of (Germino & Reinhart 2014), reduced survival of outplants. Soil hydrology may also explain the negative effects of slope on sagebrush survival, considering that run-off is greater and thus infiltration less on slopes.

Fire Severity and Biotic Community Effects

Burn severity can be highly variable in space and, although maps of burn severity are not as reliable in sagebrush steppe as in other habitats (Sparks et al. 2015), they nonetheless are one of the primary sources of information for planning treatments. The lower survival of outplanted seedlings in transects mapped as having higher burn severity could relate to increases in available nitrogen following fire (Rau et al. 2008), which would agree with Herriman et al.'s (2016) observation of reduced sagebrush seedling survival with fertilization that can favor competing herbs (Melgoza et al. 1990; Chambers et al. 2007; Vasquez et al. 2008). Fire can also exacerbate drought stress by reducing infiltration due to formation of hydrophobic soil surfaces (Doerr et al. 2000; Shakesby & Doerr 2006; Madsen et al. 2012).

Table 3. Survival and ploidy (numbers of plants) and ratios of alive:dead and 2n:4n of all sagebrush outplant seedlings as a function of their UV fluorescence rating. Cytotype cannot be determined from dead seedlings, and so sample sizes and populations differ for the ploidy and survival analyses. UV fluorescence differs significantly between cytotype ($p = 0.0001$) but not by seedling status (living vs. dead; $p = 0.65$).

Soil Order	*Description*	*Suborder*	*Feature*	*Subgroup*	*Features*
Aridisols	Arid climates: moisture to sustain plant growth for no more than 90 consecutive days	Argids	Clay accumulation	Durinodic Xeric Haplargids	One or more horizons that have 20% or more durinodes. Fine-loamy particle size. Discontinuous weakly cemented very gravelly loam.
	Often accumulate $CaCO_3$			Durixerollic Haplargids	Well-established duripan, cemented by silica, with its upper boundary within 100 cm. Clayey-skeletal particle size. Medium to high surface run-off. Abundant gravel and cobble in subsurface horizons.
				Xeric Haplargids	Do not have lithic contact nor significant sandy particle size class nor durinodes within 50 cm. Fine-loamy particle size. Increasing alkalinity with depth to very alkaline.
				Xerollic Paleargids	Abrupt textural change. Fine particle size. Very slow permeability.
		Durids	Silica accumulation and cementation	Abruptic Xeric Argidurids	Significant increase in clay content within a short distance. Fine particle size.
Mollisols	Often associated with grasslands	Xerolls	Dry summers, moist winter	Argiduridic Argixerolls	Thin clay subsoil horizon and 20% or more durinodes within 100 cm. Clayey-skeletal particle size. Slightly to strongly alkaline. Relatively deep.
	Contain organic matter and nutrients			Lithic Argixerolls	Shallow lithic contact. Clayey-skeletal particle size. Very high surface run-off.
				Typic Argixerolls	Deep soils that is not more than 20% durinodes. Clayey-skeletal particle size. Slow permeability. Medium to rapid run-off.
				Typic Haploxerolls	Little development in the subsoil. Many have horizons with accumulated secondary carbonates. Neutral to slightly acidic.

The probability that an individual seedling would suffer mortality ("hazard ratio"; Case et al. 2002) was found to increase significantly with the increasing cover of bare soil and correspondingly less exotic-annual or native-bunchgrass cover in sagebrush steppe. Bare soil is usually greater following more severe burning and may confer less water infiltration (Sankey et al. 2012), and more exposure to high sunlight and vapor deficits, potentially causing greater water stress. The effects of bare soil (and, conversely, community cover) appeared to be complicated by species' identity of the surrounding vegetation, with generally negative effects for exotic annual grasses and a hyperbolic relationship with perennial bunchgrasses. Notably, both relationships generally resemble observations made on sagebrush seedlings that emerged from seed on the same study site (Germino et al. 2018). Exotic annual grasses generally have negative, competitive effects on young perennials with root systems overlapping the shallow fibrous roots of exotic annual grasses (Melgoza et al. 1990). Most literature on sagebrush responses to perennial bunchgrasses has found negative and implicitly competitive relationships (e.g. Eissenstat & Caldwell 1988; Gunnell et al. 2010; Davies et al. 2013). Our data are more consistent with Germino et al.'s (2018) finding that a positive relationship between native bunchgrasses and sagebrush might be expected in low-productivity settings (low grass abundances), whereas negative relationships are expected when grass cover exceeds some threshold abundance. Competitive interactions with grasses may also differ with stock type (McAdoo et al. 2013) or with subspecies identity of sagebrush outplants (Newhall et al. 2011) and identifying their separate effects will require additional research.

The effects of surrounding grasses on sagebrush are influenced by treatments that often accompany planting, such as preemergent herbicides to reduce exotic annual grasses or seeding of perennial grasses and livestock management decisions that affect the abundance of these grasses. Our findings suggest that co-treatments that reduce exotic annuals or high abundances of perennial bunchgrasses might be expected to increase sagebrush outplant survival. The timing of planting relative to the recovery of grasses, which can occur within a year but often requires 2 years, may affect grass-sagebrush interactions and thus outplant survival.

Organismal and Subtaxonomic Effects

The greater survival of the 2015 cohort despite their relatively smaller sizes upon planting may relate to another aspect of stock type, specifically an advantage of being containerized or planted in the fall. The planting size:survival relationship for sagebrush has varied among studies, with Dettweiler-Robinson et al. (2013) finding no effects, and others suggesting that differences in soil treatments such as tilling (Herriman et al. 2016) or season of planting (McAdoo et al. 2013) modulate the relationship. Differences in the survival of containerized compared to bare-root stock types depend on plant and soil conditions and context; bare-root seedlings are susceptible to handling and transport stresses and require sufficient moisture, while containerized are considered more prone to frost heaving (McKay 1997; Shaw 2004; Dettweiler-Robinson et al. 2013; McAdoo et al. 2013) although we did not detect that frost heaving affected survival. Seedlings planted in the fall have more time to develop adequate root systems before drought stress but must be able to tolerate the rapid onset of chilling and frost heaving. In contrast, seedlings planted in the spring may have less time to develop extensive root systems capable of competing for limited water resources with the rapid onset of seasonal drought.

Planting seedlings can be an effective means of accelerating the recovery of foundational species such as big sagebrush following wildfire, although a variety of biotic and abiotic stressors can limit success. Removing all stressors through site selection will usually not be possible. However, our results indicate several ways that sagebrush planting success could be optimized with spatially strategic planning, specifically selecting sites for planting with low burn severity, minimal slope, intermediate cover of exotic annual and perennial grasses, and soil mapping units without impermeable horizons. These factors appear relatively important compared to taxonomic variation, at least with respect to the range of variation and lack of experimental control in the management treatment we evaluated. Results from studies such as ours can help provide realistic expectations for success and can suggest levels of investment and the number of replantings that might be necessary to achieve restoration objectives. This is especially true when restoration conditions are suboptimal yet restoration planting must proceed, such as where sagebrush needs to be increased on or near priority wildlife habitat.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Factors, and their mean (SE), range of values observed, and significance in the seedling trait, physiographic, and competition models (top) and the coefficient estimate, coefficient standard error, and significance of factors included in the full comprehensive model.

Table S2. Cox proportional hazards analysis on the probability of individual seedling mortality ($r^2 = 0.115$, Wald test = 37.36, $p < 0.0001$).

Figure S1. Site/transect variation in precipitation (mm, A), heatload (unitless, B), slope angle (°, C), elevation (m, D), aspect (°, E), and topographic wetness index (TWI, unitless, F).

Figure S2. Comparison of survival reported here for the first sampling interval (May/June to fall 2016) to survival calculated from Bureau of Land Management's monitoring from when seedlings were outplanted to August of 2016 (A) and the proportion of living seedlings over time for data reported here, by transect number and the number of seedlings (B).

Figure S3. Nonmetric multidimensional scaling (NMDS) ordination of tissue sample results of UV fluorescence rating, cytometer value, and leaf length:width ratio in relation to planting unit (A) and cohort (B).

Figure S4. Climate and weather patterns of the planting area. Climate data is derived from 30-year averages (1981–2010) for precipitation (mm, solid gray) and temperature (°C, dashed gray).

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