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ARTICLE

Soil surface treatments and precipitation timing determine seedling development across southwestern US restoration sites

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Abstract

Restoration in dryland ecosystems often has poor success due to low and variable water availability, degraded soil conditions, and slow plant community recovery rates. Restoration treatments can mitigate these constraints but, because treatments and subsequent monitoring are typically limited in space and time, our understanding of their applicability across broader environmental gradients remains limited. To address this limitation, we implemented and monitored a standardized set of seeding and soil surface treatments (pits, mulch, and ConMod artificial nurse plants) designed to enhance soil moisture and seedling establishment across RestoreNet, a growing network of 21 diverse dryland restoration sites in the southwestern USA over 3 years. Generally, we found that the timing of precipitation relative to seeding and the use of soil surface treatments were more important in determining seeded species emergence, survival, and growth than site-specific characteristics. Using soil surface treatments in tandem with seeding promoted up to 3× greater seedling emergence densities compared with seeding alone. The positive effect of soil surface treatments became more prominent with increased cumulative precipitation since seeding. The seed mix type with species currently found within or near a site and adapted to the historical climate promoted greater seedling emergence densities compared with the seed mix type with species from warmer, drier conditions expected to perform well under climate change. Seed mix and soil surface treatments had a diminishing effect as plants developed beyond the first season of establishment. However, we found strong effects of the initial period seeded and of the precipitation leading up to each monitoring date on seedling survival over time, especially for annual and perennial forbs. The presence of exotic species exerted a negative influence on seedling survival and growth, but not initial emergence. Our findings suggest that seeded species recruitment across drylands can generally be promoted, regardless of location, by (1) incorporation of soil surface

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treatments, (2) employment of near-term seasonal climate forecasts, (3) suppression of exotic species, and (4) seeding at multiple times. Taken together, these results point to a multifaceted approach to ameliorate harsh environmental conditions for improved seeding success in drylands, both now and under expected aridification.

KEYWORDS
arid and semiarid ecosystems, desert, disturbance, drought, nonnative invasive species, plant recovery, seeding, seedling establishment, site characteristics, vegetation management

INTRODUCTION

Degradation in dryland ecosystems decreases land productivity and biodiversity, creating growing ecological and socioeconomic concerns (Reynolds et al., 2007). Although the restoration of degraded sites has the potential to reverse these negative impacts, land managers and restoration practitioners have struggled to develop strategies that recover desirable plant communities and ecosystem properties in the long term (Hobbs, 2007; Kettenring & Adams, 2011; Suding et al., 2015), particularly in drylands (Shackelford et al., 2021). Land degradation due to anthropogenic and natural disturbances, and the resultant need to restore dryland ecosystems, continue to grow, but comprehensive information about the factors underlying successful revegetation outcomes is often lacking. Deficient understanding is due, in part, to limited monitoring data and duration that restricts our ability to discern factors that lead to success at different spatiotemporal scales (Cooke et al., 2019; Hagger et al., 2017). A lack of knowledge is also due to the inability of most restoration research to identify the general principles that move beyond site-specific insights to inform regional strategies that are applicable across broad environmental gradients (Lindenmayer, 2020).

The effectiveness of restoration treatments, or management actions intended to promote ecosystem recovery, in drylands is dependent on environmental variables that change across space and through time. The type and intensity of disturbance prior to restoration can change resource availability and the physical environment (Grman et al., 2013; Pickett & White, 1985). Following restoration treatments, high spatial and temporal variation in plant water availability in drylands (Loik et al., 2004) is often the primary driver that determines plant recovery patterns (Duniway et al., 2015; Munson et al., 2015; Pyle et al., 2021; Throop et al., 2020). Seedling establishment may increase as mean annual precipitation increases and mean annual temperature decreases (lower evaporative demand) across sites (Shackelford et al., 2021). Within a single site, the high precipitation in the season in which the site was seeded may also increase seedling emergence and can have long-term effects on the trajectory of plant community development (Copeland et al., 2019; Groves et al., 2020). Other site-specific environmental variables, including soil texture and the abundance of exotic species (introduced from a distant historical range and considered noxious by local land managers), can also influence water availability and thus seeded species establishment (Bakker et al., 2003; Muñoz-Rojas et al., 2016). Forecasted climate change trends toward increased warming and drying (Garfin et al., 2013), and increased rainfall variability (Bradford et al., 2020; Thornton et al., 2014), in many drylands will likely have a large effect on future dryland restoration efforts, including potentially altering viable ranges of plant species chosen for restoration.

Within the constraints of low water availability, common restoration methods, such as direct seeding, often have low success rates (Chambers, 2000; Larson et al., 2015; Rowe et al., 2020). Dryland restoration outcomes could be improved upon by testing the use of supplemental treatments that alleviate some of the underlying factors and challenges to plant establishment. There has been a recent push to implement these treatments in tandem with seeding to overcome environmental barriers to seedling emergence, survival, and growth (Dalziell et al., 2022; Kildisheva et al., 2016; Muñoz-Rojas et al., 2016; Rader et al., 2021). For example, manipulating the soil or microenvironment to promote soil moisture, stability, and surface roughness at a restoration site may help to promote the establishment of seeded species (e.g., Muñoz-Rojas et al., 2016; Wubs et al., 2016) and of growth (Rowe et al., 2020). Using additional treatments in tandem with the widely implemented practice of seeding may be key to restoration success, especially under the more arid and variable climate expected in the southwestern USA (Copeland et al., 2021; Young et al., 2021).

Environmental variables that influence whether seedlings emerge, survive, and grow may be unique to a restoration site, or have general effects across a region (Funk, 2021; Grman et al., 2015; James et al., 2019). Furthermore, the effects of soil surface and other restoration treatments may become less important over time as seeded plants develop, or the treatments that are most effective for seedling emergence may be different from the treatments that most effectively help mature plants survive (Chambers, 2000). Environmental variables such as soil texture and precipitation variability can interact with restoration treatments to influence plant development and broader successional dynamics (Brudvig et al., 2017). Despite the importance of treatments and environmental variables influencing different stages of recovery, little research has been conducted to differentiate the relative contribution of these factors to plant stage transitions across sites and over multiple years (James et al., 2011; Larson et al., 2015). Furthermore, because most restoration projects occur at a single location and at a discrete point in time (Vaughn & Young, 2010), and have limited monitoring frequency and duration, our ability to pinpoint bottlenecks to restoration and understand whether the same treatments would work at different sites or over different time periods remains limited. Implementing treatments across sites through multiple years and seasons, and closely tracking different stages of recovery, can inform where and when success can be maximized (Shriver et al., 2018) and promote a prescriptive approach to restoration (Copeland et al., 2021).

Our overall goal was to determine how restoration success, as indicated by the recruitment of seeded species, was influenced by the restoration treatments (including soil surface treatments and seed mix types) and the environmental conditions in which restoration occurred. To address this goal, we harnessed RestoreNet—a restoration field trial network co-produced by land managers and scientists—on degraded sites that span environmental gradients in the southwestern USA (Havrilla et al., 2020). We systematically implemented the same restoration treatments and protocol (Laushman et al., 2022) across 21 RestoreNet sites in the Southwest USA from 2018 to 2020. Our specific objectives were to understand how seeded species emergence, survival, and growth depend on:

1. Restoration treatments, including a seed mix type with species currently found within or near a site and adapted to the historical climate, versus a seed mix type with species from a warmer and drier climate, used with and without additional soil surface treatments (pits, mulch, and ConMod artificial nurse plants).
2. Spatial environmental variables that change across site space (e.g., site characteristics such as mean annual precipitation and soil texture).
3. Temporal environmental variables that change at a specific site through time (e.g., precipitation inputs relative to the date the site was seeded or monitored).

We explored potential interactions among these variables and whether there were differential responses to treatment and environmental variables among seedling emergence, survival, and growth stages. We expected that a seed mix type with species adapted for warm climates relative to each site would be more likely to survive if the site experienced warm and dry conditions following seeding and that soil surface treatments would enhance seedling emergence and growth across all sites.

METHODS

Site description

The 21 RestoreNet sites used in this study span seven major dryland ecoregions throughout the southwestern USA (Figure 1) that vary in climate, elevation, potential plant community, soil properties, and initial disturbance type (Table 1). Site mean annual precipitation (MAP) ranges from 98 to 535 mm; mean annual temperature (MAT) ranges from 8.5 to 19.9°C; and elevation ranges from 385 to 2281 m above sea level (Table 1). The sites also fall across a spectrum of precipitation seasonality. Sites in the south and southeast of our study area (Chihuahuan Desert, Madrean Archipelago, Sonoran Basin, and Range) receive up to 57.3% of their annual precipitation from the warm season (July–September) North American Monsoon (monsoon), whereas sites in the west (Mojave Basin and Range) and north (Colorado Plateaus) of our study area receive less warm-season precipitation (as low as 3.9% of annual precipitation) (Table 1). All sites were in areas that had no woody overstory and had the potential to support dryland plant communities including desert scrub, perennial grassland, mesquite savanna, and lower montane pinyon–juniper woodland (based on a compilation of Landfire terrestrial vegetation subclasses [LANDFIRE, 2016; https://landfire.gov/evt.php] and observations of nearby undisturbed sites). Sites varied in soil texture from sand to clay loam. RestoreNet sites were initially disturbed by livestock overgrazing, cropping, wildfire, or vehicle/foot traffic (e.g., recreational off-highway vehicle use, construction vehicle use, or heavy foot traffic) (Table 1). Despite having different disturbance types, disturbances had a similar degree of severity and influence on the initial conditions across sites in that they all had low (<5% canopy cover) initial native perennial plant cover, intact soil horizons and surface integrity, and the potential to support a

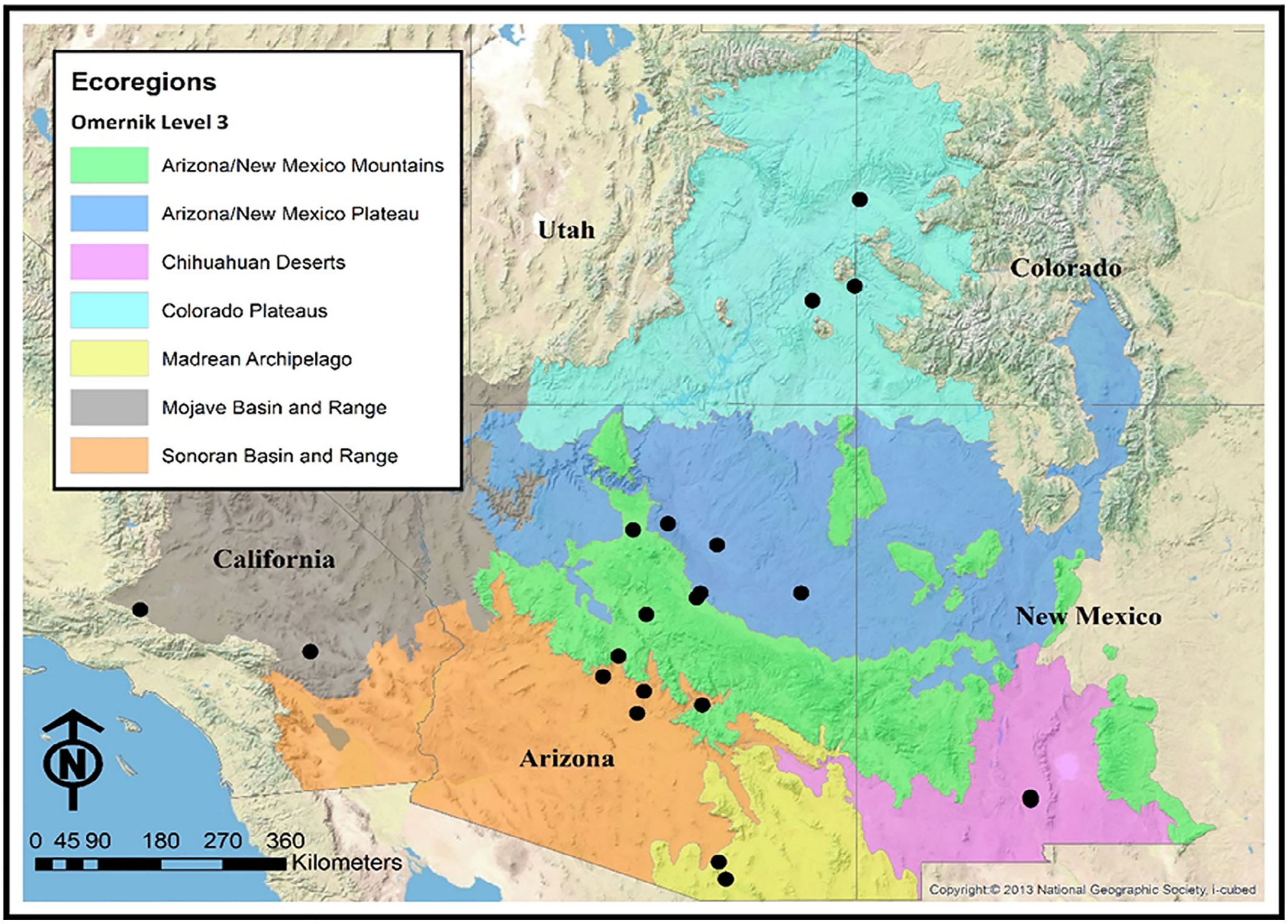

FIGURE 1 The 21 RestoreNet study sites span major ecoregions (Environmental Protection Agency [EPA], 2022) of the southwestern USA and vary in climate, elevation, topography, and potential plant communities.

perennial native plant community. We acknowledge that differences in initial site disturbance might have influenced restoration outcomes in ways that we were not otherwise able to control.

The sites were selected in partnership with local land managers and owners to address degraded areas that they sought to recover through revegetation. Sites were fenced off for a minimum of 30 m × 30 m and a maximum of 50 m × 50 m area (area depended on accessibility) to exclude large herbivores and, if necessary, fine mesh fencing to exclude smaller herbivores. To homogenize initial plant and soil conditions across sites, we used the same methods to prepare each site. All existing vegetation was removed from treatment plots within the exclosure using hand tools and herbicide was spot sprayed onto individual exotic plants as needed to reduce their growth (glyphosate; RangerPro: 41% glyphosate, applied in a 3% mixture) immediately prior to site installation (Laushman et al., 2022). To further minimize the potential for differences among initial site conditions, we installed each site on a flat area (<1% slope) and each plot was raked into a homogenous soil surface prior to receiving treatment.

Restoration treatments

Restoration treatments occurred from 2018 to 2020. The restoration treatments, including seeding and soil surface treatments, occurred either during the warm-season months (July–September) or cool-season months (October–April) to target whether the site received most of its precipitation during the monsoon or winter and spring and based on the expert advice of local site managers (Table 1). The months May and June tended to be extremely dry throughout much of the study region and were not conducive to seeding. The year of treatment installation varied as new partners joined the project network. At six of the sites, where treatments were installed during the warm season of 2018, treatments were re-initiated during the warm season of 2020 to examine the influence of interannual precipitation variability on seedling establishment, while keeping the other environmental site variables constant (Table 1).

At each site, we tested the effect of seeding with one of two different seed mix types independently, or in combination with soil surface treatments. Our experimental

TABLE 1 RestoreNet site name, state, ecoregion, potential plant community, mean annual precipitation (MAP), mean annual temperature (MAT), the percent (%) of annual precipitation that occurs during the North American Monsoon (July–September), soil texture (USDA classification) at 0–10 cm depth, season and year seeded, and initial disturbance type.

State, ecoregion (US EPA, level 3), and site name	Potential plant community	MAP (mm)	Monsoon (%)	MAT (°C)	Elevation (m)	Soil texture (0–10 cm)	Season seeded	Year(s) seeded	Disturbance type
Arizona									
AZ/NM Mtns									
Babbitt PJ	PJ woodland	516	35.1	9.5	1973	Clay loam	Warm	2018, 2020	Overgrazing
Agua Fria Nat. Mon.	Perennial grassland	455	31.7	18.5	1006	Silty clay loam	Warm	2018	Wildfire
Montezuma Well Nat. Mon.	Perennial grassland	383	38.2	16.3	1074	Loam	Warm	2018, 2020	Vehicle/foot traffic
Flying M Ranch	PJ woodland	369	44.8	10.6	1860	Silt loam	Warm	2018, 2020	Overgrazing
AZ/NM Plateau									
BarTBar Ranch	PJ woodland	311	44.1	11.0	1708	Sandy loam	Warm	2018, 2020	Overgrazing
Petrified Forest Nat. Mon.	Perennial grassland	244	44.6	12.6	1642	Sandy loam	Warm	2018, 2020	Overgrazing
Tolani Lake	Perennial grassland	180	45.0	13.0	1497	Sand	Warm	2019	Cropping
Spiderweb	Perennial grassland	171	44.8	13.2	1563	Sandy loam	Warm	2018, 2020	Overgrazing
Utah									
Colorado Plateau									
La Sal	PJ woodland	416	32.2	8.5	2281	Sandy loam	Cool	2018	Wildfire
Salt Desert	Perennial grassland	274	29.7	12.1	1439	Sandy loam	Cool	2018	Overgrazing
Canyonlands Research Center	Desert scrub	225	33.5	12.0	1624	Silty loam	Cool	2018	Cropping
New Mexico									
Chihuahuan Desert									
Creosote (CDRRC)	Desert scrub	297	48.1	16.2	1367	Loamy sand	Warm	2020	Overgrazing
Mesquite (CDRRC)	Mesquite savanna	275	53.3	15.7	1318	Loamy sand	Warm	2020	Vehicle/foot traffic
Arizona									
Madrean Archipelago									
Santa Rita Experimental Range	Mesquite savanna	535	47.7	17.9	1178	Loamy sand	Warm	2019	Overgrazing
Patagonia	Mesquite savanna	486	53.7	16.5	1320	Sandy loam	Warm	2019	Overgrazing
California									
Mojave Basin									
Antelope Valley	Desert scrub	222	3.9	16.7	752	Sandy loam	Cool	2020	Vehicle/foot traffic
29 Palms	Desert scrub	98	27.7	19.7	590	Sand	Cool	2020	Cropping
Arizona									
Sonoran Basin									
Roosevelt Lake	Desert scrub	418	28.6	19.9	762	Sandy loam	Cool	2019	Wildfire

(Continues)

TABLE 1 (Continued)

State, ecoregion (US EPA, level 3), and site name	Potential plant community	MAP (mm)	Monsoon (%)	MAT (°C)	Elevation (m)	Soil texture (0–10 cm)	Season seeded	Year(s) seeded	Disturbance type
McDowell Sonoran Preserve	Desert scrub	371	27.1	20.7	799	Sandy loam	Cool	2019	Vehicle/foot traffic
Lake Pleasant	Desert scrub	311	31.9	21.3	539	Sandy loam	Cool	2019	Vehicle/foot traffic
Scottsdale CC	Desert scrub	245	31.7	22.4	385	Sandy clay loam	Cool	2019	Cropping

Abbreviations: AZ, Arizona; CA, California; CC, community college; CDRRC, Chihuahuan Desert Rangeland Research Center; Mtns, mountains; Nat. Mon., National Monument; NM, New Mexico; PJ, pinyon–juniper; USDA, United States Department of Agriculture; US EPA, United States Environmental Protection Agency; UT, Utah.

design included four restoration treatments (seeding alone, seeding with connectivity modifiers, seeding with mulch, and seeding in pits) with four replicate plots for each treatment ($N = 16$) × two seed mix types ($N = 32$), which, along with four control plots (no seed or other treatment), composed a total of 36 plots. At each of our 21 sites, we randomly assigned one of four treatments, and a control, to 2 m × 2 m permanently marked plots, including:

1. seeding alone;
2. seeding with connectivity modifiers ("ConMods" are small physical barriers made from wire hardware cloth that mimic nurse plants and are designed to retain litter, nutrients, and seeds as well as provide a favorable microclimate for seedlings; Okin et al., 2015);
3. seeding with wood mulch spread to loosely cover over the soil surface (to increase soil moisture and provide seed and seedling protection; Kader et al., 2019);
4. seeding in pits, or shallow 40 × 40 cm depressions that are 10 cm deep to capture and retain water (Laushman et al., 2022), four pits were installed per plot with one in each quadrant equidistance from each other;
5. no seeding or soil surface treatments (control).

Seed was broadcast by hand on its own or following the installation of the other soil surface treatments. The permanently marked plots were installed in rows that were spaced 1 m apart.

Each soil surface treatment was conducted with one of two different eight-species seed mix types composed of grasses, forbs, and shrubs. Seed mixes were composed of high-priority native species that are generally adapted for the dry conditions of the southwestern USA and tailored for each RestoreNet site in partnership with the local land manager or owner at each site (Laushman et al., 2022; Appendix S1: Table S1). Seeds were purchased from commercial vendors depending on availability and region (Appendix S1: Table S1) and any recommended pretreatments to break dormancy were applied. One eight-species seed mix type contained species currently found within or near a site and adapted to the historical climate, and a second eight-species seed mix type contained species selected to be suitable for a slightly warmer and drier climate than the historical site climate. The respective seed mix types "cool" and "warm" were based on the temperature niche distributions of species obtained from occurrence records (Butterfield et al., 2017; Havrilla et al., 2020; Appendix S1: Table S1). Plots were seeded with eight species to align with seed mix recommendations for the region and at a seeding rate recommended by the seed company for each species.

Site monitoring

Following treatment installation, we monitored seedling recruitment (density and height) at each RestoreNet site. Seedling density (number) and average height (mm) of each species were measured inside a small (25 cm × 25 cm) permanently marked subplot within each plot using a standardized monitoring protocol (Laushman et al., 2022). This smaller monitoring subplot area was designated to closely track plant emergence and growth, which would have been difficult within the much larger plot area. Seedlings were identified by species and, when species could not be identified we indicated whether they were seeded, unseeded, or unknown. Site monitoring frequency varied from every 0.5 months to twice annually for up to 2.5 years (falling between fall 2018 and spring 2021), generating 13,989 unique plant densities by species observations. Monitoring frequency and duration varied among sites based on available resources and site accessibility. All sites were monitored at least once (and up to 10 times) within 4 months of seeding to capture the initial emergence of the seeded species. The integrity of the soil surface treatments was noted for each plot at each monitoring visit (e.g., percent mulch remaining), but was not amended.

Response variables

Using the density and height measurements of seeded species obtained at each monitoring visit at all 21 sites, we calculated three response variables. We calculated the seedling density during the emergence stage (seedlings that appeared above the soil surface 0–5.5 months since seeding) as the summed density of all seeded species within each subplot for each monitoring period at each site. We combined all seeded species within each subplot together for the emergence stage, because it was often difficult to identify plant species very early in their development, although often clear whether the plant was seeded or not.

We then calculated the seedling density during the survival stage (seedlings that persisted through the first growing season; >5.5 months since seeding) as the density of seeded individuals per subplot, discriminated at the individual species level because plant identification was more consistent than the emergence stage. However, we examined seedling survival using functional groups, rather than species, as not all the same species were seeded across sites. The 5.5-month cut-off between the emergence and survival stages was based on the time it took seedling density at most sites to begin to decline, indicating that most of the emergence had concluded for the first season of growth. Furthermore, because some of our sites were monitored infrequently (e.g., only two times annually), we wanted to ensure that we represented an "emergence stage" monitoring period from each site. The 5.5-month cut-off also aligned with other studies on plant demographic transitions (e.g., James et al., 2011).

Last, we calculated the growth (change in height) of seeded individuals between monitoring periods as the natural log of the difference between the average height of all seeded individuals of the same species in a monitoring period relative to their average height from the previous monitoring period. To calculate the growth of each seeded species, we used height measurements from all monitoring periods up through 15 months since seeding, to capture growth in both the emergence and the survival stages. We selected a cut-off of 15 months of monitoring, as this was the point at which growth leveled off at most sites, and/or a new cohort of seedlings was germinating.

Explanatory variables

In correspondence with our objectives, we generated three categories of explanatory variables that might explain differences in seeded-plant density and height over time. Our explanatory variable categories were: (1) seeding and soil surface treatment variables; (2) spatial environmental variables (e.g., site characteristics that change across space); and (3) temporal environmental variables (variables that are relative to the time of seeding or monitoring at a site) (Appendix S1: Table S2).

Seeding and soil surface treatment variables

Seeding and soil surface treatment variables included our restoration treatments (seeding, seeding with ConMods, seeding with mulch, or seeding in pits) with two different seed mix types (cool or warm relative to average conditions of the site). We also examined the plant functional groups of the seeded species measured in monitoring: annual forbs, cool-season (C_3) grasses, warm-season (C_4) grasses, perennial nonleguminous forbs, leguminous perennial forbs, and shrubs so that we could compare among sites where different species were seeded. We also included the period seeded, which indicates the year and season the restoration treatments occurred, categorized as either warm-season or cool-season months.

Spatial environmental variables

Spatial environmental variables are site characteristics and include soil texture, elevation, potential plant community, MAP, MAT, the proportion of precipitation that occurs during the warm season (monsoon), the initial source of disturbance (overgrazing, previous cropping, wildfire, or vehicle/human traffic), the density of exotic species at the time of monitoring, exotic species influence (height × density, which quantifies how much space they occupied) at the time of monitoring, density of nonseeded species (exotics and natives that naturally recruited) at the time of monitoring, the average height of exotic species at the time of monitoring, and average seeded species density in the emergence stage (for the survival and growth models). Exotic species densities were considered spatial environmental variables because this measurement characterizes the potential for nonnative exotic species at each site generated from the soil seed bank, which varied more strongly across sites than through time. The percent sand and clay of a site were derived from three composite samples, randomly taken from a 0–10 cm depth at each site; the soils were categorized into high and low categories of sand and clay content according to the soil texture triangle (clay above 25% was considered "high" [clay loam and finer]; sand above 50% was considered "high" [captures most of the "sandy" textural classes]). All climate data were extracted from PRISM (PRISM Climate Group, 2021, Oregon State University, https://prism.oregonstate.edu) using site coordinates. MAP, MAT, and the proportion of monsoon relative to MAP were based on 30-year (1981–2010) site averages.

Temporal environmental variables

Temporal environmental variables were those related to changes over time and included time since seeding, period seeded (a combination of year and season [warm season vs. cool season]), and precipitation variables. Daily precipitation records from PRISM (PRISM Climate Group, 2021, Oregon State University) during the study period were aggregated at different windows of time that were hypothesized to be biologically important to seedling emergence, survival, and growth, and in relation to seeding and monitoring events, from daily records (Robinson et al., 2013): precipitation through 1, 2, and 3 months after seeding; precipitation 1 month prior to monitoring; cumulative precipitation since seeding; cumulative precipitation since the previous monitoring event; a ratio of cumulative precipitation since seeding or since the previous monitoring event relative to the historical precipitation for the site over the same period (whether it was wetter or drier relative to what the site experienced over the long term); daily average precipitation since seeding; and daily average precipitation since the monitoring event.

Model construction and statistical analysis

We constructed three statistical models corresponding to our three response variables, a seedling emergence model, a seedling survival model, and a seedling growth model. To reduce the number of explanatory environmental and treatment variables from the pool of all considered explanatory variables for each model, account for potential multicollinearity in our models, and correctly assign variable importance (Murray & Conner, 2009), we selected variables for inclusion in final models using a three-step process. First, we examined the univariate relationships between individual explanatory and response variables (seedling emergence density, seedling survival density, and plant growth) and dropped explanatory variables that were not significant to eliminate spurious variables in the final models. Second, to understand explanatory variable importance, we created hierarchical partitioning (*hier.part* package; Nally & Walsh, 2004) submodels using the previously selected significant variables within each explanatory variable category (restoration treatment variables, spatial environmental variables, and temporal environmental variables). Within each submodel, we selected the variables that explained the most variation, or ≥5% of independent effects on R^2 within their category (Graham, 2003), and dropped any variables that had <5% independent effects on R^2. Finally, using the top-ranking explanatory variables derived from the submodels, we built our three final models (Appendix S1: Table S2).

To account for the excess of zeros in the density data due to sites where no emergence or survival occurred, we used zero-inflated negative binomial models for the final emergence model and final survival model (Martin et al., 2005). We fitted a negative binomial distribution with a log link for the positive (non-zero) density to account for our data being right skewed and overdispersed in the emergence and survival models (*glmmTMB* package; Brooks et al., 2017). In the zero-inflation portion of the emergence model we used period seeded (combination of year and season) and cumulative precipitation because we observed that some monitoring periods and seasons received little or no precipitation, resulting in many plots with no seedling emergence. We used seeded species emergence as a variable in the survival model, and plots with no emergence could not have survived. For the zero-inflated variables in the survival model, we used the average density of seedlings found in each plot from the emergence stage and precipitation since the last monitoring.

We built the growth model using a generalized linear mixed model (GLMM; *LME4* package; Bates et al., 2015). The natural log change in height data was normally distributed so the growth model was fit with a Gaussian distribution. We included "site ID:plot ID" as a random effect in all models in which unique plots were nested within each site to account for repeated measures of the same plots through time, spatial autocorrelation of measurements from the same site, and variation due to the site-level variables we were not able to measure. We presented untransformed values for ease of interpretation.

For each of the three models, we estimated marginal (fixed effects) and conditional (fixed and random effects) R^2 (*r2_nakagawa* package; Nakagawa et al., 2017). For significant categorical variables within each model, we applied a Tukey honestly significant difference (HSD) multiple pairwise comparison (TukeyHSD in R; Yandell, 1997). For significant interactions between continuous and categorical variables (e.g., precipitation × treatment types), we compared the slopes of the regressions using a lsmeans post hoc test (*lsmeans* package; Lenth, 2016). All analyses were conducted in R version 4.0.5 (R Core Team, 2020).

RESULTS

There was high intra- and interannual precipitation variability at study sites with extreme wet and dry conditions compared with the historical (1981–2010) averages at each site during the months following seeding (Table 2). Across all seasons and monitoring periods, of the plots that experienced plant recruitment, ~44% had at least one exotic plant species and 35% had at least one seeded-plant species. In total, 84 unique seeded species emerged across all sites.

Overall, restoration treatment variables (soil surface treatment, seed mix type, and seeded-plant functional group) and temporal environmental variables (precipitation, time since seeding, and period seeded) explained the most variation in seeded-plant emergence, survival, and growth, while spatial environmental variables explained less (Figure 2). Treatment and environmental variables explained 29% of the variance in seedling emergence, 46% in seedling survival, and 12% in seedling growth (marginal R^2), while unaccounted-for site variables explained an additional 19%–38% (conditional R^2). For seedling emergence, we found that soil surface treatment, time since seeding, and cumulative precipitation were the strongest explanatory variables, followed by period seeded, exotic species density, and seed mix type (Figure 2). For seedling survival, we found that precipitation since the previous monitoring period was the strongest explanatory variable, followed by the period seeded, then seeded-plant functional group, soil surface treatment, initial seedling emergence, and exotic species density (Figure 2). For seedling growth, we found that the seeded-plant functional group was the strongest explanatory variable, followed by the time since seeding, cumulative precipitation, exotic species influence, and soil sand content (Figure 2).

TABLE 2 Percent of seasonal precipitation (mean ± SE) relative to historical averages (1981–2010) at each site during period seeded (>100% indicates a wetter-than-average period; <100% indicates a drier than average period), and the percent of plots with seedling emergence (0–5.5 months since treatment) of seeded species corresponding to each period.

Period seeded	Seasonal precipitation compared with historical (%)	Plots with seeded species emergence (%)
Warm season 2018	117 ± 9	41
Cool season 2018/2019	58 ± 19	16
Warm season 2019	46 ± 8	8
Cool season 2019/2020	145 ± 17	62
Warm season 2020	55 ± 11	6

Seedling emergence

All soil surface treatment types significantly increased the emergence of seeded species relative to the control ($p < 0.001$ for all) (Table 3). The pit treatment resulted in the greatest density of seeded species (average of 57 seedlings/m^2; ~3× greater seedling density than seed only), followed by the mulch treatment (35 seedlings/m^2; ~1.8× greater seedling density than seed only), with ConMod and seed-only treatments resulting in the lowest densities (~19 seedlings/m^2 for both treatments). The cool seed mix type resulted in ~1.7× greater emerged seedlings than the warm seed mix type (51 vs. 29 seedlings/m^2; $p = 0.008$).

The period seeded explained the additional variation in seedling emergence. Seedling density was greatest for sites seeded in the cool season 2019/2020 (56 seedlings/m^2), followed by the warm season 2018 (33 seedlings/m^2) and the cool season 2018/2019 (29 seedlings/m^2). Sites seeded in the warm seasons of 2019 and 2020 had the lowest seedling emergence (5 and 9 seedlings/m^2, respectively). Soil surface treatments interacted with the period seeded to explain seedling emergence densities (Figure 3). For sites seeded in the warm season of 2018, the pit treatment resulted in the highest number of seedlings, the mulch treatment produced the second highest, while ConMods performed equally to seed only but better than the control. For sites seeded in the cool season of 2018/2019 and the cool season of 2019/2020, all treatments performed better than the control, but no one treatment performed significantly better than the others. For sites seeded in the warm season of 2019 and the warm season of 2020, no treatment performed significantly better than the control (Figure 3 shows all pairwise comparisons).

Seedling emergence density was positively correlated with cumulative precipitation since seeding (slope = 1 seedling/m^2 per 6 cm of precipitation; $r = 0.27$, $p < 0.0001$) and time (months) since seeding (slope = 10 seedlings/month; $r = 0.19$, $p < 0.0001$) (Table 3). Soil surface treatments interacted with cumulative precipitation to explain the seedling emergence of seeded species ($R^2 = 0.25$, $p < 0.001$) where all treatments increased seedling densities more with increasing cumulative precipitation than the control (Figure 4), and seedling emergence increased in pits more with increasing cumulative precipitation (slope = 1 seedling per 2 cm of precipitation) compared with mulch, ConMod, and seed only ($p < 0.001$). Seed mix type also interacted with cumulative precipitation ($R^2 = 0.17$, $p < 0.0001$), such that seeded species densities increased with increasing cumulative precipitation in plots seeded with the cool seed mix type (1 seedling/m^2 per 4 cm precipitation) at a higher

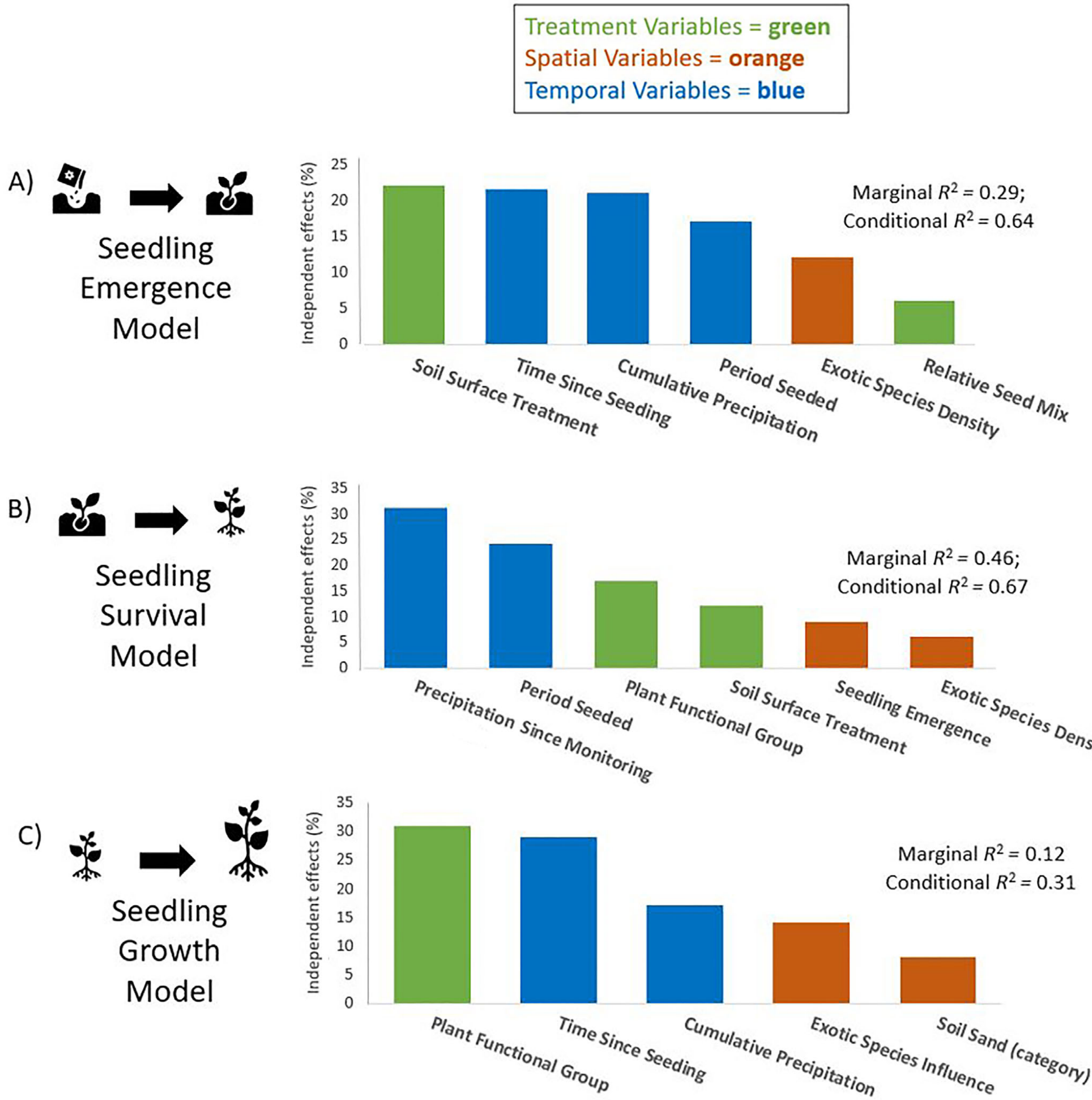

FIGURE 2 Independent effects (%) of each treatment and environmental variable (colored by variable type) on marginal R^2 (fixed effects) and conditional R^2 (fixed and random effects) for the (A) seedling emergence, (B) seedling survival, and (C) growth models.

rate compared with plots seeded with the warm seed mix type (1 seedling/m^2 per 9 cm precipitation) (Table 3).

Seeded species density in the emergence stage was positively correlated with the density of exotic species (slope = 1 seeded seedling increase per nine exotic seedlings; $r = 0.18$, $p < 0.001$, Figure 5A). Although it was not significant in the final model, sites with high clay content (>25% clay) tended to have greater seedling emergence than those with low clay content in the spatial environmental variable submodel.

Seedling survival

All soil surface treatments significantly increased seedling density in the survival stage of seeded species relative to the control ($p < 0.001$ for all treatments; Table 4). As with the emergence stage, the pit treatment resulted in the greatest density of seedling survival, with more than twice the density of surviving seedlings compared with seed only; mulch and ConMod treatments had the second highest seedling densities, and seed-only plots resulted in the lowest

TABLE 3 Seedling emergence (density of seeded species <5.5 months since treatment) model results.

Seedling emergence model (density)[a]	*df*	Estimate	Standard error	*z*/*t*-value	*p* value	Pairwise comparisons
Intercept		0.57	0.68	0.84	0.39	
Soil surface treatment	**4**				**<0.001**	
ConMod		1.19	0.2	29.4	0.001	C
Mulch		2.29	0.3	36.4	<0.001	B
Pits		3.61	0.3	37.5	<0.001	A
Seed only		1.16	0.3	26.8	0.002	C
Seed mix type (cool-warm)	**1**	**−0.22**	**0.08**	**−4.447**	**0.008**	
Period seeded	**4**				**<0.001**	
Warm season 2018		2.09	0.67			B
Cool season 2018/2019		1.85	0.92	0.35	0.03	B
Warm season 2019		0.35	0.82	0.57	<0.001	C
Cool season 2019/2020		3.62	0.53	−0.38	0.02	A
Warm season 2020		0.62	0.67	2.21	<0.001	C
Soil surface treatment × Period seeded	**16**				**<0.001**	
Soil surface treatment × Cumulative precipitation	**4**				**<0.001**	
ConMod × precipitation		0.01	0.004	−2.98	0.02	B
Mulch × precipitation		0.02	0.004	−4.49	0.001	B
Pits × precipitation		0.03	0.004	−7.81	<0.001	A
Seed only × precipitation		0.01	0.004	−2.84	0.04	B
Seed mix type (cool-warm) × cumulative precipitation	**1**	**0.01**	**0.002**	**5.03**	**<0.001**	
Density of exotic plants (no. individuals/plot)	**1**	**0.01**	**0**	**5.58**	**<0.001**	
Cumulative precipitation since seeding	**1**	**0.02**	**0**	**17.2**	**<0.001**	
Time since seeding (months)	**1**	**0.41**	**0.03**	**12.91**	**<0.001**	
Residuals:	2836					
Zero-inflated (presence/absence)						
Intercept		−1.58	0.76	−2.07	0.03	
Cumulative precipitation since seeding	**1**	**−0.04**	**0.001**	**−10.87**	**<0.001**	
Period seeded	**4**				**<0.001**	
Warm season 2018						
Cool season 2018/2019		2.89	1.78	1.70	0.56	
Warm season 2019		4.29	1.51	2.86	<0.001	
Cool season 2019/2020		3.03	0.71	4.19	0.25	
Warm season 2020		5.29	1.23	4.31	<0.001	

Note: Bold values and explantory variables indicate significant main effects and interactions. Different letters indicate significant Tukey HSD pairwise differences for categorical explanatory variables and significant differences in slope for categorical × continuous explanatory variable interactions. The results of the zero-inflated portions of the emergence model are reported below the positive (non-zero) density results and the significant explanatory variables should be interpreted as explaining presence versus absence of seeded species from plots.

[a]Marginal $R^2 = 0.29$; Conditional $R^2 = 0.64$.

densities. Seed mix type did not explain differences in seedling survival. Instead, functional groups of the seeded species explained seedling survival densities with seeded annual forbs and cool-season grasses having higher densities than shrubs (Table 4).

Survival of seeded species also depended on the period seeded ($p < 0.001$; Figure 3). In the survival stage, seeded-plant density was greatest at the sites seeded in the cool season of 2018/2019 (despite low initial emergence rates), followed by sites seeded in the warm season

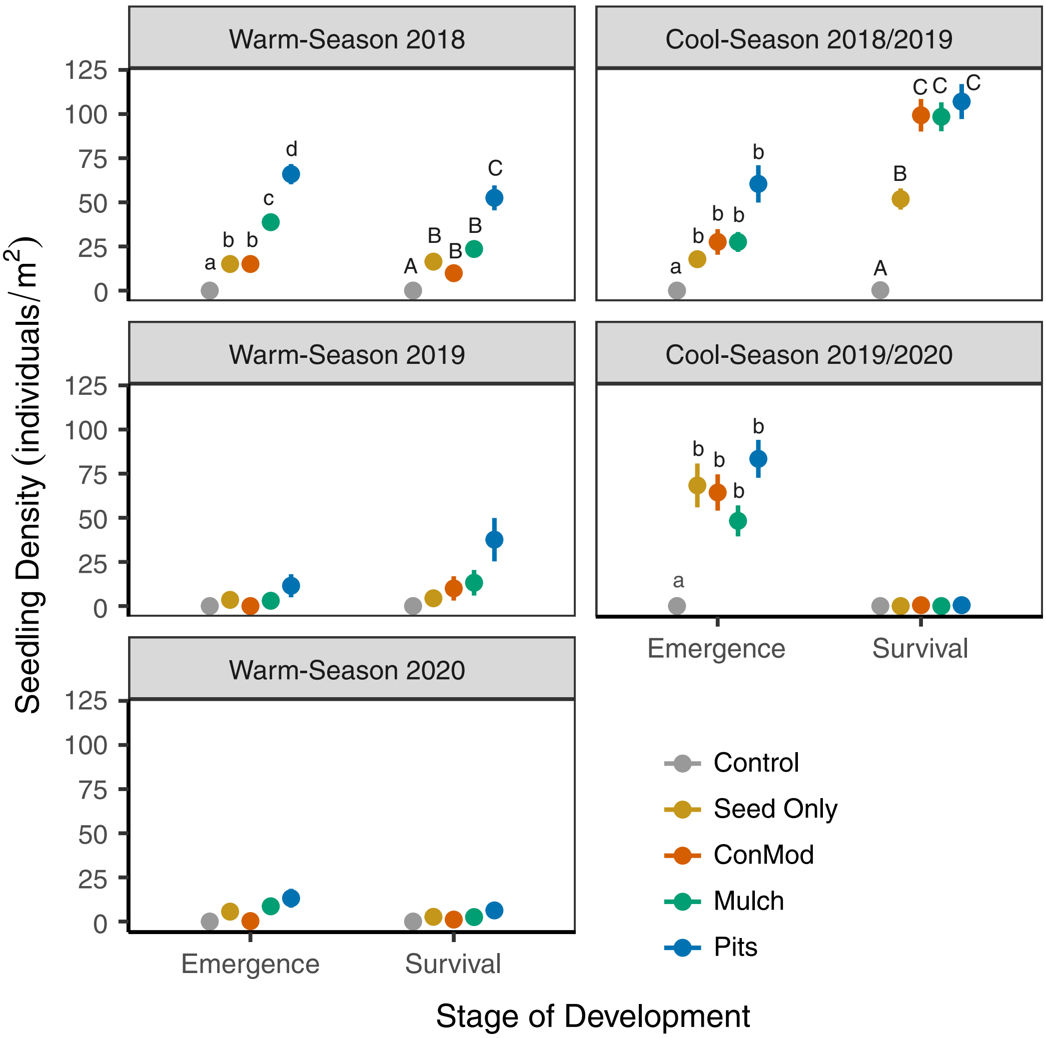

FIGURE 3 Mean ± SE of seedling density during the emergence and survival stages according to the period seeded (panels). Different letters are shown when the seedling densities were significantly different among treatment types within the same period seeded (e.g., warm season 2018) and stage (emergence = lowercase letters, survival = uppercase letters). Seedling density (*y*-axis) scales vary among period seeded.

of 2018. The warm seasons of 2019 and 2020 had low survival densities (similar to emergence stage patterns). Sites seeded in the cool season of 2019/2020 had the lowest survival densities (1 seedling/m^2), despite high initial emergence rates. Soil surface treatments interacted with the period seeded to explain seeded species survival ($p < 0.001$; Figure 3). The soil surface treatments tended to improve survival in the cool season of 2018/2019, with pit treatments resulting in the greatest survival densities in the warm season of 2018. Total precipitation since the last monitoring period was positively correlated with seedling survival ($r = 0.08$, $p = 0.003$; slope = 1 seedling/m^2 per 4 cm precipitation). Total precipitation since the last monitoring period interacted with the plant functional group, whereby annual forb densities increased the most with increased precipitation (1 seedling/m^2 per 6.6 cm), followed by perennial forbs (1 seedling/m^2 per 11 cm); and the response (slope) of cool-season grasses, warm-season grasses, leguminous perennial forbs, and shrubs did not differ from zero or from each other as precipitation increased (Figure 6A).

In contrast with seedling emergence, seeded species densities in the survival stage were weakly negatively correlated with the density of exotic species ($r = -0.04$; $p < 0.001$; slope = 1 seeded seedling decrease per 16 exotic seedlings) (Figure 5B). Additionally, average seeded species densities in the survival stage were positively correlated with initial seedling emergence densities ($r = 0.13$, $p < 0.001$; slope = 1 seedling survived per four seedlings that emerged). Time since seeding did not influence seedling survival, nor did other site-level spatial environmental variables such as MAP, MAT, elevation, and soil texture (Table 4).

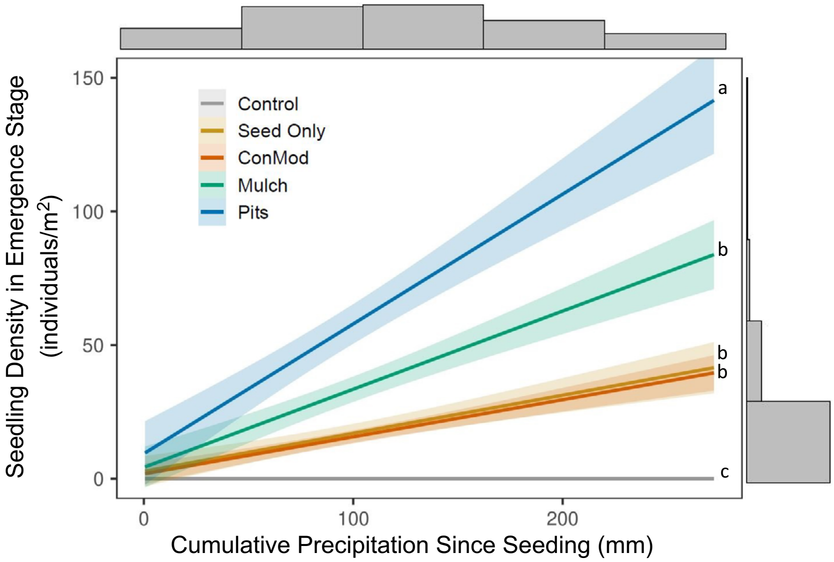

FIGURE 4 Seedling density in the emergence stage increased as cumulative precipitation since seeding increased in all treatment types compared with the control across all sites. Significantly different slopes are indicated by different letters. Pits had a higher rate of emergence as precipitation increased relative to the other treatments. The histograms along the axes indicate the density of data points.

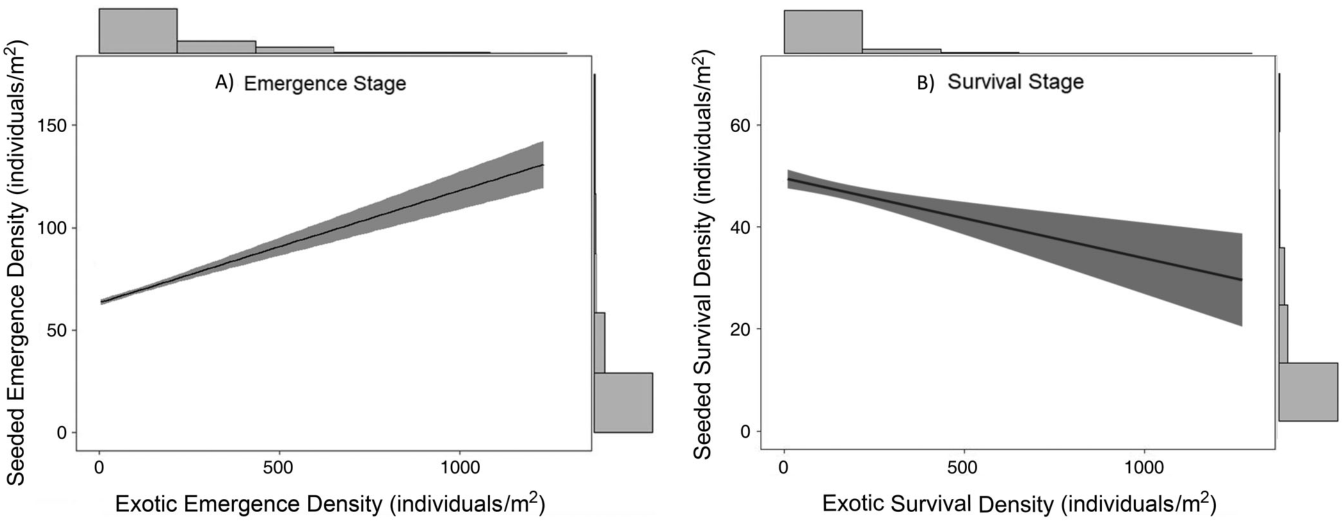

FIGURE 5 Seedling density of seeded species was (A) positively related to exotic plant density in the emergence stage ($r = 0.18$, $p < 0.001$), and (B) negatively related to exotic plant density in the survival stage ($r = -0.04$, $p < 0.001$). The histograms along the axes indicate the density of data points.

Seedling growth

Perennial forbs, followed by warm-season grasses, experienced the most growth between monitoring periods (9.5 and 7.6 mm average growth, respectively; Table 5). Leguminous perennial forbs, cool-season grasses, and shrubs experienced less growth between monitoring periods (6.5, 2.8, and 1.5 mm growth, respectively). Cumulative precipitation since seeding was the precipitation variable that best explained seeded species growth ($r^2 = 0.19$, $p < 0.001$; slope = 0.7 mm growth per 1 cm precipitation). Cumulative precipitation also interacted with seeded species functional groups, whereby perennial forbs put on the most growth in response to increased precipitation (slope = 1.2 mm growth per 1 cm increased precipitation), while the other functional types did not increase at a rate different from each other (Figure 6B).

Average exotic species influence (height × density of exotic species) was positively correlated with change in

TABLE 4 Seedling survival (density of seeded species 5.5–24 months since treatment) model results.

Survival model (density)[a]	*df*	Estimate	Standard error	*z*/*t*-value	*p* value	Pairwise comparisons
Intercept		0.7	0.33	2.10	0.04	
Soil surface treatment	**4**				**<0.001**	
ConMod		0.71	0.4	5.53	0.02	B
Mulch		0.75	0.4	5.54	<0.001	B
Pits		1.13	0.4	5.99	<0.001	A
Seed only		0.51	0.5	5.25	0.05	C
Functional group	**5**				**0.03**	
Annual forb		0.07	0.51			A
Cool-season grass		0.13	0.32	0.15	0.98	A
Warm-season grass		−0.12	0.31	0.24	0.92	AB
Perennial forb		0.02	0.32	−0.31	0.16	AB
Leguminous perennial forb		−0.06	0.32	−0.51	0.72	AB
Shrub		−0.49	0.45	−0.82	0.003	B
Period seeded	**4**				**<0.001**	
Warm season 2018		0.56	0.21			B
Cool season 2018/2019		1.21	0.29	2.07	0.04	A
Warm season 2019		0.22	0.52	−0.68	<0.001	C
Cool season 2019/2020		0.04	0.99	−4.08	<0.001	D
Warm season 2020		0.23	0.51	−0.14	<0.001	C
Functional group × precipitation since last monitoring	**5**				**0.02**	
Annual forb × precipitation		0.013	0.001			A
Cool-season grass × precipitation		0.003	0.001	−0.87	0.54	BC
Warm-season grass × precipitation		−0.002	0.002	1.99	0.34	BC
Perennial forb × precipitation		0.006	0.001	−2.29	0.19	B
Legume × precipitation		0.001	0.002	0.47	0.97	BC
Shrub × precipitation		0	0.011	0.21	0.69	C
Soil surface treatment × period seeded	**16**				**<0.001**	
Density of exotic plants	**1**	**−0.004**	**0.001**	**5.34**	**<0.001**	
Seeded species emergence (average/plot)	**1**	**0.27**	**0.04**	**7.51**	**<0.001**	
Precipitation since last monitoring	**1**	**0.002**	**0.001**	**2.53**	**0.003**	
Residuals:	5416					
Zero-inflated (presence/absence)						
Intercept		0.93	0.47	1.96	0.05	
Average seeded density in emergence stage	**1**	**−5.01**	**0.68**	**−7.42**	**<0.001**	
Precipitation since last monitoring	**1**	**−0.02**	**0.01**	**−3.75**	**<0.001**	

Note: Bold values and explantory variables indicate significant main effects and interactions. Different letters indicate significant Tukey HSD pairwise differences for categorical explanatory variables and significant differences in slope for categorical × continuous explanatory variable interactions. The results of the zero-inflated portions of the emergence model are reported below the positive (non-zero) density results and the significant explanatory variables should be interpreted as explaining presence versus absence of seeded species from plots.
[a]Marginal $R^2 = 0.48$; Conditional $R^2 = 0.67$.

seeded species height ($r = 0.13$, $p < 0.001$). The growth of seeded species was also explained by the percent sand content at a site; sites with high sand (>50%) resulted in an average of 4 mm of more plant growth between monitoring periods than seeded species growing in sites with low sand ($p = 0.003$).

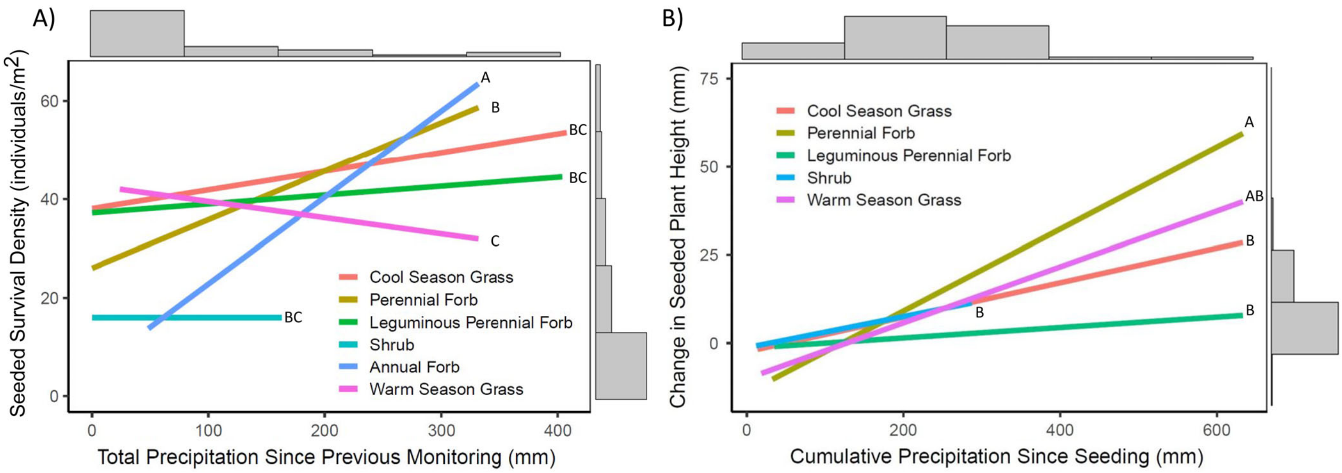

FIGURE 6 (A) Seedling density of seeded species in the survival stage according to plant functional group relative to precipitation between monitoring periods (how wet or dry the recent period had been). (B) The change in height (growth) of seeded species between monitoring periods according to plant functional type relative to cumulative precipitation since seeded. Different letters indicate significantly different slopes. The histograms along the axes indicate the density of data points.

DISCUSSION

Seedling emergence

Using soil surface treatments in tandem with seeding strongly enhanced seedling emergence densities, and this effect interacted with the amount of cumulative precipitation since seeding. We found that when precipitation following soil surface treatment implementation and seeding was low, not only was seedling emergence from seeding alone low, but none of the soil surface treatments were able to significantly bolster seedling emergence. As cumulative precipitation since seeding increased during the emergence stage, all the soil surface treatments increased seedling emergence, with the pit treatment producing the greatest emergence relative to the other treatments. This result expands on previous findings of Havrilla et al. (2020) by showing the effectiveness of small depressions at dryland sites across the southwestern USA and in multiple treatment years. Pits capture water and enhance soil moisture for prolonged durations, which has been found to be key to improving restoration success in drylands (Muñoz-Rojas et al., 2016; Rader et al., 2021). Furthermore, when cumulative precipitation was low, neither seed mix type performed particularly well, but as cumulative precipitation increased, the cool seed mix type (containing species well suited for the historical site climate conditions and currently found within or near a site) had higher seedling emergence than the warm seed mix type. These results suggest that soil surface treatments or using a seed mix type comprised of species adapted for a warmer and drier climate cannot overcome the barrier of a particular site or season with exceptionally low precipitation, but instead, soil surface treatments serve to amplify the effect of precipitation if it increases following seeding.

Surprisingly, spatial environmental variables (those that vary across site or region) such as MAP, MAT, elevation, ecoregion, potential plant community, and soil texture did not explain much variance in the emergence of seeded species. We had initially expected sites with high MAP, low MAT (and therefore low evaporative demand), and soils with high infiltration rates to have high emergence due to their capacity to generate elevated soil moisture availability. Instead, temporal environmental variables, including precipitation since seeding, time since seeding, and period seeded, were more predictive of emergence densities. Our sites had high rainfall variability over space and across seasons, therefore MAP did not represent rainfall dynamics each year, and our results suggest that aligning restoration actions with favorable seasonal precipitation is key to improving the efficacy of restoration outcomes (Hardegree et al., 2018). We do not suggest that climate and soil setting are unimportant, but that variation in seedling emergence can be better captured by finer temporal resolution weather data. These results may provide a reason for optimism among restoration practitioners, as a favorable precipitation year or season offers opportunities for restoration success even in arid systems.

Our results support those of Grman et al. (2013) who found that restoration outcomes were determined more by management decisions (e.g., soil surface treatment or seed mix type applied) and site history (e.g., time since restoration) than by specific site or landscape characteristics. There is often emphasis for land managers and restoration practitioners to tailor restoration treatment

TABLE 5 Seedling growth (change in height between monitoring periods) model results.

Seedling growth (change in height) model[a]	*df*	Estimate	Standard error	*t*-value	Pr (>χ^2)	Pairwise comparisons
Intercept		−0.56	3.45	−0.45		
Functional group	**4**				**<0.001**	
Cool-season grass		0.06	0.03	−0.42		B
Warm-season grass		0.16	0.03	−0.51		AB
Perennial forb		0.25	0.02	5.57		A
Leguminous perennial forb		0.08	0.03	−0.23		B
Shrub		0.05	0.06	0.56		B
Cumulative precipitation since seeding	**1**	**0.001**	**0.001**	**2.28**	**0.01**	
Cumulative precipitation × functional group	**5**				**<0.001**	
Cool-season grass × precipitation		0.0006	0.0002	−0.32		B
Warm-season grass × precipitation		0.0011	0.0003	−0.25		AB
Perennial forb × precipitation		0.0019	0.0002	−1.69		A
Legume × precipitation		0.0008	0.0003	−1.21		B
Shrub × precipitation		0.0009	0.001	0.09		B
Sand category (high–low)	**1**	**−0.09**	**0.02**	**−4.01**	**0.003**	
Average exotic plant height	**1**	**0.13**	**0.01**	**1.55**	**<0.001**	
Months since seeding	**1**	**0.003**	**0.001**	**0.35**	**<0.001**	
Residual:	3215					

Note: Bold values and explantory variables indicate significant main effects and interactions. Different letters indicate significant Tukey HSD pairwise differences for categorical explanatory variables and significant differences in slope for categorical × continuous explanatory variable interactions.
[a]Marginal $R^2 = 0.12$; Conditional $R^2 = 0.31$.

plans to site-specific characteristics (e.g., Metzger et al., 2017). However, incorporating all possible site variables into restoration planning can be difficult, especially across large areas with multiple stakeholders (Hagger et al., 2017) and when needing to allocate limited resources (Wilson et al., 2011). Although our analyses did not include all possible site-specific characteristics, our results show that, in dryland ecosystems of the southwestern USA, site characteristics may be less important than seasonal precipitation patterns in determining seeding and restoration outcomes. Therefore, general restoration treatments that increase water availability in dryland settings may increase success across large regions, given that there is adequate seasonal precipitation.

Seedling survival

While seedling emergence partially determined seeded species survival, high seeded-plant densities in the emergence stage did not necessarily lead to high seeded-plant densities in the survival stage. This finding contrasts with other studies that have found that initial seedling establishment is key in determining survival outcomes at a restoration site (e.g., Larson et al., 2015). For example, we found that an initial wetter-than-average cool season in 2019/2020 encouraged high seedling emergence, but survival subsequently dropped after a period of drought. Our results indicate that germinants require periodic wet conditions to establish successfully. Our finding that seasonal precipitation patterns drive plant recruitment, is a common finding in dryland restoration studies (e.g., Duniway et al., 2015; James et al., 2019; Pyle et al., 2021). However, at some periods and sites, such as those seeded in the cool season of 2018/2019, seedling survival densities increased relative to seedling emergence densities, suggesting that there were additional recruitment events, as reported in a previous study (Rowe et al., 2022). Our study expands these previous results by comparing restoration success among multiple plant life stages over several years of seeding across many sites.

Our results emphasize that trajectories of plant establishment are highly variable in drylands as plants move through developmental stages (James et al., 2011). We found that not all treatment and environmental variables that were important in the emergence stage were critical to the survival stage (supporting Howard & Goldberg, 2001). For example, soil surface treatments were much more important in explaining density in the emergence stage than in the survival stage. Although pits remained the best treatment to increase survival densities, the diminishing effects of mulch could be due to the materials being lost to wind over time. The interactions between seeded and exotic species also shifted between developmental stages. In the emergence stage, seeded-plant density was positively correlated with exotic plant density, suggesting that seeded and weedy species are taking advantage of the same conditions to emerge (Stohlgren et al., 2003). In the survival stage, however, there was a negative correlation, indicating that the exotic and seeded species may have been large enough to compete for aboveground and belowground resources (D'antonio & Meyerson, 2002). To counter the negative effect of exotic species, restoration practitioners could consider applying a seed mix that includes species that have traits that can suppress or outcompete exotic plants (Farrell et al., 2021; Funk & Wolf, 2016), suppress exotic propagule sources (Hess et al., 2019; Uselman et al., 2015), use priority effects through manipulating seeding timing (Weidlich et al., 2021; Young et al., 2017), reduce the use of treatments that encourage exotic species (Havrilla et al., 2020; Rowe et al., 2022), or control the exotics after they emerge (Kimball et al., 2015).

Plant functional groups differed in their survival densities and responsiveness to precipitation. While annual and perennial forbs had relatively high emergence and large increases with increasing precipitation, warm-season grasses and shrubs were less responsive. However, once successfully established, shrubs and warm-season grasses may tolerate warm and dry conditions (Munson & Lauenroth, 2012). Further research on understanding how land managers can design seed mixes to take advantage of the trade-offs of fast growth in favorable resource periods and high survival rates in low resource periods (Funk, 2021; Larson et al., 2015) can improve long-term restoration outcomes. Incorporation of how these traits shift from seedling to mature plants can also help to improve restoration success (Havrilla et al., 2021). RestoreNet will continue to monitor restoration outcomes to test which species and plant functional groups persist over longer periods of time.

Seedling growth

In this study, we used the increase in the height of seeded species between monitoring periods as a proxy for the overall growth and health of the plants. As expected, plants tended to grow larger over time and with more precipitation, but responses varied by plant functional group and in different soil types. Perennial forbs were more responsive to precipitation compared with the other functional groups and sites in the high sand category (>50% sand) tended to have more rapid seedling growth. Perennial forbs are known to rapidly increase following restoration treatments under favorable precipitation (Munson & Lauenroth, 2012) and are critical for the recovery of diversity. High growth in sandier soils supports the inverse texture hypothesis (Sala et al., 1988) where water in dryland ecosystems can escape high evaporative demand at the soil surface through infiltration in sandy soils, leading to more water availability for developing roots. Conversely, although it was not used in the final model, sites in the high clay category had higher seedling emergence than those with low clay. We attributed this result to the high water-holding capacity of clay soils, which likely led to a greater duration of sufficient soil moisture in contact with seeds to induce emergence. While it was somewhat surprising that neither the soil surface treatment nor the seed mix type explained variation in seedling growth, growth is probably more dependent on individual species and their traits. The relatively low marginal and conditional R^2 of our growth model further indicates that there are other variables that we did not characterize that are driving seeded-plant growth over time.

Management implications

Water availability is key to restoration success in dryland ecosystems, and a lack of precipitation at any stage of a plant's early development can be detrimental. As drought events are expected to increase in duration, intensity, and frequency across drylands (Schlaepfer et al., 2017), our research suggests that there are multiple opportunities to improve restoration outcomes by increasing the chances of favorable soil moisture. Application of soil surface treatments that help to capture and retain water can enhance plant development at multiple life stages to improve overall plant recruitment. These treatments may be especially effective for land management if they are scalable to larger areas, including the use of large cultipacker and imprinter equipment to create pits, mulch blowers and spreaders, and seeding underneath nurse plants or other suitable microsites that increase water availability.

There has been a call to adopt weather-centric adaptive management approaches for dryland restoration by emphasizing flexibility in treatment plans (Brudvig et al., 2017; Shriver et al., 2018). As we found period seeding largely explained seedling emergence and survival, seeding across multiple years and seasons can be implemented as a bet-hedging strategy that increases the odds that seedlings emerge and receive the precipitation they need to survive. At six of our sites, we repeated the same treatments in different years (warm season 2018 vs. warm season 2020) and found that our treatment results varied widely, as a response to changes in weather patterns between treatment periods. This result is more generally supported by a literature review conducted by Vaughn and Young (2010), who found that less than 5% of ecological restoration studies repeated treatments over multiple years but, of the few that did, more than three-quarters of those studies saw significant interactions between treatments and year of initiation. Future research that incorporates repeat treatments at the same site over time will better elucidate the effects of intra- and interannual climate variation and is a promising opportunity for future research.

Although we found that precipitation within certain time windows was important in determining seeding success, timing restoration activities to coincide with favorable seasonal weather conditions presents a challenge for restoration practitioners because it is difficult to predict weather patterns with fine enough resolution to integrate these into management decisions (Clark et al., 2001; Hagger et al., 2018; Hardegree et al., 2018). However, technology, modeling, and tools for climate and weather forecasts in relation to land management actions are becoming more accurate and widely accessible (Bradford et al., 2020; Lewis et al., 2021). For example, in the southwestern USA, land managers can use resources such as the Climate Assessment for the Southwest (CLIMAS, https://climas.arizona.edu/sw-climate), which provides North American Monsoon and other near-term weather forecasts based on climate models.

Our research suggests that a land manager or restoration practitioner in dryland settings can implement generalizable strategies that work well across sites and stages of plant development. While site-specific details, such as soil texture, disturbance history, and the potential plant community, still need to be considered, we found that the timing of treatments and precipitation are key to successful restoration outcomes across dryland sites. The RestoreNet framework allows for further restoration treatments to be tested across environmental gradients, across space and through time, to determine when and where they will be effective.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data generated from this study (Farrell & Munson, 2022) are available at USGS ScienceBase at https://doi.org/10.5066/P9G7XRIK.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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