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Soil depth and precipitation moderate soil textural effects on seedling survival of a foundation shrub species

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Running head: Soil effects on sagebrush seedlings

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Authors' contributions

KV and KN conceived ideas and designed methodology with input from MD, TM, ES, JB, JV, CB, ET; KV, KN collected data; AK, SF analyzed data with input from KV, MD; KV led writing of manuscript. All authors contributed critically to drafts and gave final approval for publication.

Abstract

In drylands, there is a need for controlled experiments over multiple planting years to examine how woody seedlings respond to soil texture and the potentially interactive effects of soil depth and precipitation. Understanding how multiple environmental factors interactively influence plant establishment is critical to restoration ecology and in this case to broad-scale restoration efforts in western US drylands dominated by big sagebrush (*Artemisia tridentata*). We planted sagebrush seedlings across a range of soil textures and depths in the southern portion of the species' range, on the Colorado Plateau. We evaluated survival of repeated plantings of caged and uncaged seedlings over two years across 20 plots in wet vs. average precipitation years at one site, and examined broader patterns of sagebrush seedling survival during an average precipitation year in 56 plots across four sites. First-year survival was >9x higher under wet than average precipitation. Under favorable (wet) conditions, early sagebrush seedling survival was highest on coarser soils, especially those that also had a shallower restrictive layer (e.g., 50-100cm). Under average precipitation, soil texture and depth effects on survival of newly-planted seedlings were much weaker, but older (>1yr) seedlings benefitted from growing on coarser textured soils. It may be possible to increase survival by sheltering seedlings with small mesh cages, which likely improve moisture availability. Our results provide new insights into environmental factors that limit woody seedling survival in drylands and illustrate that planting in wet years and incorporating detailed soil setting information could increase survival of sagebrush seedlings in restoration projects.

Key words: *Artemisia tridentata*; big sagebrush; Colorado Plateau; inverse texture hypothesis; precision restoration; rangelands

Implications for practice:

- Multi-factorial, multi-year experiments can be used to reveal complex interactions among multiple environmental factors that promote or limit restoration success
- Incorporating information on soil physical properties into restoration planning could help identify areas where restoration efforts are most likely to succeed.
- Delineating landscapes according to both soil texture and depth (which strongly influence moisture) could improve success of planting containerized sagebrush seedlings.

Introduction

Drylands worldwide are increasingly threatened by land degradation and climate change, and the effects of multiple interacting ecological drivers must be disentangled in order to achieve conservation and restoration of these systems (Maestre et al. 2016). Especially important, whether in the context of managing natural recruitment or engaging in active restoration, are factors governing plant establishment and eventual transition to adult life stages (Schupp 1995). Chief among these is soil moisture availability, which is a major determinant of dryland plant growth and abundance (Noy-Meir 1973; Sankaran et al. 2008; Schlaepfer et al. 2012), and is especially important for early seedling survival and growth (Harrington 1991; Padilla & Pugnaire 2007).

The timing, duration, amount, and location of soil moisture available to plants is strongly influenced not only by atmospheric precipitation, but by soil texture and depth (Fensham et al. 2015; Duniway et al. 2018; Case et al. 2020). Globally, there is considerable evidence that, under more arid conditions, plant communities are more productive on soils with coarser than finer surface textures due to the rapid percolation of soil moisture below the depths susceptible to surface evaporation (i.e., the "inverse texture hypothesis"; Walter 1964; Noy-Meir 1973; Sala et al. 1988). In deep, coarse-textured soils, it is further hypothesized that deep soil percolation creates soil moisture reservoirs uniquely available to mature deep-rooted woody plants (Knoop & Walker 1985; Kambatuku et al. 2013; Kulmatiski et al. 2020). Less clear is how woody seedlings respond to soil texture and depth because seedlings have less-developed root systems (Gedroc et al. 1996) and are especially sensitive to the positive effects of soil surface moisture (Leffler et al. 2004; O'Connor et al. 2020).

In western North America, understanding how soil texture and depth – and potential interactions with atmospheric precipitation – govern woody plant establishment is highly relevant for conservation and restoration of big sagebrush (*Artemisia tridentata*), a foundational shrub species that covers only half of its original 63 million ha due to wildfire and land conversion (Fig. 1) (Knick et al. 2003). Big sagebrush seedlings are especially sensitive to temperature extremes and soil moisture limitation (Schlaepfer et al. 2014), conditions which are likely to worsen as the region faces increasingly extreme droughts. But knowledge of the factors governing sagebrush seedling dynamics is limited (Schlaepfer et al. 2014) as evidenced by the largely unsuccessful, intensive broadscale restoration efforts throughout much of its range (Arkle et al. 2014; Knutson et al. 2014).

Retrospective analyses of broadscale big sagebrush restoration projects indicate the importance of soil surface moisture (Shriver et al. 2018; O'Connor et al. 2020), as well as soil properties (Williams et al. 2017; Davidson et al. 2019) for seedling establishment, including potential interactions between soil depth and texture. For instance, the combination of finer textured soils and effectively shallower soils (due to restriction layers) may reduce drainage of winter precipitation to the detriment of big sagebrush seedlings that grow poorly on saturated soils (Leffler et al. 2004; Davidson et al. 2019). Conversely, coarser textured soils may be advantageous for seedlings because less moisture is lost to evaporation due to greater downward percolation; but if water infiltration is rapid, bedrock or other water- and root-restricting layers may be necessary to help maintain soil water in the root zone and available for plant uptake.

Studies examining how interactions between soil texture and depth affect seedling survival of big sagebrush – or of woody seedlings in general – are rare (but see Browning et al. 2012), and controlled tests of these interactions even rarer. Moreover, much of our understanding of big sagebrush dynamics comes from the northern portion of the species' range. Much less is known about how soil factors influence sagebrush seedling survival on the Colorado Plateau, which comprises the southern portion of sagebrush range and is governed by different precipitation patterns and soil characteristics (Fig. 1). Even more fundamentally, ecological experiments are rarely initiated in multiple years (Vaughn & Young 2010), making it difficult to test the effect of ambient precipitation and associated "year effects" (Wilson 2015).

We therefore tested how big sagebrush seedling survival responded to different combinations of soil depth and texture on the Colorado Plateau, USA, a region characterized by bedrock-controlled, sandy soils. We hypothesized that 1) survival would be highest in coarser soils with a shallower depth to restrictive layer (~75 cm) due to reduced evaporative soil water loss and improved retention of soil water within the seedling rooting zone and 2) survival would be highest during the earliest period of plant establishment (0-6 mo). We compared responses between two planting years, anticipating that any differences in ambient precipitation would moderate soil effects.

Methods

Study site

Our study was located in San Juan County, southeastern Utah (37.4634° N, 109.7592° W), within the Colorado Plateau physiographic province, which spans 21 million ha across the western USA (Fig. 1). Climate is characterized by cool winters, hot summers and average annual precipitation of 250 mm (Hereford 2002). Study plots were distributed across four shrubland sites located 18 - 64 km from each other and managed by the Bureau of Land Management: Beef Basin (~4,018 ha; 1,904 m asl), Hart's Draw (~14,657 ha; 1,969 m asl), Black Mesa (~2,242 ha;

1,682 m asl), and Alkali Flat (~2,116 ha; 1,712 m asl) (Fig. 1). Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*) was the dominant shrub at all four sites, though Beef Basin had lower densities of living sagebrush due to die-offs over the last three decades (Supplement S1). We established 20 plots each at Beef Basin and Hart's Draw and 8 plots each at Alkali Flat and Black Mesa (56 total). Plots were located in Semidesert Loam (Wyoming Big Sagebrush) or Semidesert Sandy Loam (Wyoming Big Sagebrush) ecological sites (https://edit.jornada.nmsu.edu/), except for six Hart's Draw plots which were Upland Shallow Loam (Pinyon-Utah Juniper) (Table S1).

Study plot characteristics

We sampled and described one soil pedon at the center of each study plot (Supplement S1). We measured pedon depth to a hard lithic contact or maximum depth of auger (~150cm), and calculated a depth-weighted average of percent sand, silt and clay for the top 50 cm, the zone of greatest root biomass for seedlings [Leffler et al. 2004]) (Table S1).We conducted baseline surveys of vegetation, ground cover, animal use, and soil penetration resistance at each plot (Supplement S1).

Study design

We out-planted 3,232 big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis*) seedlings over two years in soils with a range of textures (35-78% sand) and depths (38-168cm) (Table S1). We investigated effects of annual climate cycles by repeating plantings across 20 plots at Beef Basin in what were a wet and average precipitation year (Fig. S1), and we examined broader patterns of sagebrush seedling survival during the average year (Fig. S2) in 56 study plots across four sites.

Seedlings were grown from seed in USDA-ARS, Forage and Range Research Laboratory greenhouses on the Utah State University campus annually during January - April. Seeds were collected from ≥10 mature Wyoming big sagebrush plants at each of the Hart's Draw, Alkali, and Black Mesa plots and the few surviving plants in the Beef Basin plots. Seeds from these different sources were mixed and then sown into sterile peat soil mixture in 21 cm long, 164 cm^3 containers (SC10, Ray Leach cone-tainer, Stuewe & Sons, Inc., Tangent, OR) that were thinned to one seedling. Seedlings were watered regularly and fertilized every two weeks until one month before planting when we gradually reduced frequency of watering to harden them for planting.

In May 2015 we planted 80 seedlings at each of the 20 Beef Basin plots. In May 2016 we planted 30 sagebrush seedlings in Beef Basin plots (in or near microsites where 2015 seedlings had died), 30 in Hart's Draw plots, and 27 in Alkali Flat and Black Mesa plots. A dibble stick was used to make a 20 cm hole. In each plot, seedlings were hand-planted in a 2m x 2m-spaced grid (but if necessary, shifted to ≥5cm outside any existing sagebrush canopy dripline). We applied 60 ml of water at planting and an additional 60 ml one month later. Each seedling was numbered and its height measured (mean ± 1SE: 7.0±0.05 cm in 2015; 5.9±0.04 cm in 2016).

Two-thirds of seedlings at each site were caged with 10 cm x 46 cm plastic mesh seedling protector tubes (Rigid Seedling Protector Tubes, Forestry Suppliers, Inc., Jackson, MS) at the time of planting, attached with a bamboo stick driven into the ground, and secured to the stick with nylon zip ties. If cages had been removed when we returned on subsequent visits, cages were replaced. We removed all cages in May 2017 due to persistent removal of cages by cattle.

Seedlings were censused each fall (October/November) and spring (April/May) through the end of 2018 for survival, height (April/May only), and evidence of herbivory. At planting we measured distance from planted seedling to the three nearest perennial grass or sub-shrubs plants (Supplement S2).

Analyses

For each Beef Basin planting year (2015, 2016), we analyzed seedling survival across different age classes with generalized linear mixed-effects models (GLMMs) using the logistic link function and binomial distribution. We used the “glmer” function in the “lme4” package (Bates et al. 2015) in R version 4.0.3 (R Core Team 2020), which fits models by maximum likelihood (Laplace approximation). For each year we fitted a model with the following fixed effects: age group (0-2, 2-6, 6-14, 14-23, >23 months), caging (caged vs. never caged), soil depth, and sand content (depth-weighted sand content in top 50 cm of soil). Each model included individual within plot as nested random effects. For each age group (i.e., inter-census interval), all seedlings living at the beginning of the interval were included, and seedlings found dead on or before the beginning of the next interval were modeled as dead (survival = 0).

We modeled 2016 planting-year survival (across all four sites) similarly, except individuals nested within plots were additionally nested within site. For height of 2015 Beef Basin plantings, we fit a linear mixed effects model (“lmer” function in the “lme4” package) using restricted maximum likelihood (REML) and used the same model structure described above (except age groups were 0-12, 12-24 and 24-34 months because height was assessed less frequently than survival). Sample size was insufficient to analyze 2016 planting heights. We also separately modeled final survival (i.e., at > 23 months) for wet year Beef Basin seedlings with caging, soil depth, and sand content as fixed effects, and plot as a random effect.

Initial models included all possible three-way interactions. We used the “drop1” function in base R to identify non-significant three-way interaction terms (alpha = 0.05) and replaced them with the two-way interactions contained therein. We repeated this procedure until all non-significant interactions were removed. For survival models, “drop1” performed likelihood ratio tests (LRTs) with a Chi-squared distribution. For the height model, it tested single predictor variable deletions using the Satterthwaite approximation for degrees of freedom. P-values for main effects were calculated using the “summary” function in the “lmerTest” package (Kuznetsova et al. 2017). For survival models, we calculated estimated marginal means with the “emmeans” package (Lenth et al. 2020) and marginal effects using the average-of-marginal-effects method from Kleiber & Zeileis (2008). We centered and scaled all continuous independent variables and sum coded all categorical independent variables prior to modeling.

Results

Precipitation in the three-month period following planting of seedlings in 2015 was more than twice as high as the near-average precipitation in the same period in 2016 (Beef Basin: 162 mm vs. 72 mm; 30-year $\bar{x}$ = 61 mm; values were > 89 mm [$\bar{x}$ + 1 SD] for 4 of 30 years, and one of the last 15 years; Fig. S1). Accordingly, survival 14 months post-planting was 38% for seedlings planted in the wet year (2015) vs. 4% for average-year (2016) plantings (Table 1). By the end of the study, survival declined to 7.0% and 0.3% for wet and average planting years, respectively (Table 1). For both planting years, the greatest absolute mortality occurred within the first growing season after planting (July-Nov, 2-6 month inter-census interval; Fig. 2).

High precipitation year (2015)

During the wet year, seedling survival was improved in soils with greater sand content in the upper 50cm, as well as those with shallower depth to a lithic or restrictive layer (sand content and soil depth, each $p<0.05$, Table S2), though the strength of these effects varied over time post-planting (Table 2). In the two months immediately following planting, when overall survival was high (88%), seedling survival responded positively to sand content in the shallowest soils (Fig. 3a, 0-2 mo.*sand content*soil depth interaction $p<0.05$, Table S2). During the following time period which constituted the first major survival decline (July-Nov, 2-6 month inter-census interval, 53% survival), sandier (coarser) soils were advantageous to seedlings across all soil depths, but that advantage was most pronounced in the shallowest soils (Fig. 3a, left panel, 2-6 mo.*sand content*soil depth interaction $p < 0.05$, Table S2). Specifically, coarser, shallower soils (70% sand and 74 cm depth) increased probability of survival in the 2-6 month inter-census interval by 92% compared to finer, deeper soils (53% sand and 151 cm depth) (Table 2).

In contrast, during a similar time period one year later (14-23 month inter-census interval, 88% survival) coarser soil textures were most beneficial in the deepest soils (Fig. 3a right panel, 14-23 mo.*sand content*soil depth interaction $p<0.05$, Table S2). During this period, when deeper soils were disadvantageous relative to more moderate depths (14-23 mo.*soil depth interaction $p < 0.05$, Table S2), coarser textures reduced the negative effects of deep soils; that is, seedlings in coarse deep soils had similar (high) probability of survival as those growing in shallower soils. During this time period, survival was 88% in coarse, deep soils (53% sand and 151 cm depth, corresponding to 1SD below mean sand content and 1 SD below mean depth of all plots), similar to the 92% survival observed in coarser, shallower soils (Table 2).

For wet year plantings overall probability of survival (i.e., during the final census) was 20% greater on the coarsest- vs. finest-textured soils (Table S3). Coarser soils also were associated with greater overall seedling heights (4.0 cm difference between max and min % sand, Table S1), most strongly for 24-month-old seedlings (5.8 cm difference; Fig. 3b, 24 mo.*sand content interactions $p<0.05$, Table S4). Correlations between model residuals and nearest perennial grass/sub-shrub neighbors were weakly negative (2-6 mo.) and non-significant (14-23 mo.) (Supplement S2).

Average precipitation year (2016)

Precipitation in the three months following 2016 planting for Beef Basin, Alkali Flat, Black Mesa and Hart's Draw, respectively, was 72 mm (30-year $\overline{x} \pm$ 1SE = 61 ± 5 mm), 65 mm (30-year $\overline{x} \pm$ 1SE = 55 ± 6 mm), 58 mm (30-year $\overline{x} \pm$ 1SE = 52 ± 6 mm), and 85 mm (30-year $\overline{x} \pm$ 1SE = 71 ± 6 mm; see also Fig. S1). For sagebrush seedlings planted in the average precipitation year (2016), survival 14 months post-planting ranged from 3% to 14% across the four sites (Table 1). By the end of the study (28 mo.) the only surviving seedlings were at Beef Basin (0.3% survival; Table 1). Seedlings experienced high mortality from the 2-6 mo. inter-census interval through the end of the study (Table 1).

For average precipitation year plantings across all four sites we did not observe the same strong patterns of sandier, shallower soils improving seedling survival as for Beef Basin wet year plantings (main effects of soil depth and sand content, $p>0.05$, Table S5). One similarity, however, was that survival of average year plantings increased with sand content most strongly on the shallowest soils; but this was only true when seedlings were uncaged (Fig. 4a, caging*sand content*depth interaction $p<0.05$, Table S5, S6, Fig. S3). In the deepest soils, survival across the four study sites was only moderately improved by sand content (Fig. 4a, Table S5), though more strongly for caged seedlings in Beef Basin (Table S6, Fig. S3).

Seedlings planted in the drier year also responded negatively to sand content in the 0-2 mo. inter-census interval (Fig. 4b, 0-2 mo.*sand content $p<0.05$, Table S5). Caged seedlings overall, which included high representation from plants in the 0-2 inter-census interval, responded negatively to sandier soils (Fig. 4a; caging*sand content*depth interaction $p<0.05$,

Table S5, S6, Fig. S3). For seedlings that survived to ~1 year, coarser soils improved survival (14-23 mo. inter-census interval).

Caging

Caging improved survival of wet-year plantings throughout the first two years post-planting (Fig. 5a, Table S2), with the strongest positive effects 6-14 mo. following planting when there was a 37% increase in likelihood of surviving 6-14 mo inter-census interval relative to uncaged seedlings (86% caged vs. 63% uncaged; Fig. 5a, caging*6-14 mo. interaction $p<0.05$, Table S2). Final survival (i.e., at >23 mo) was more than twice as high for caged vs. uncaged seedlings, though probability of survival was very low for both groups (5.5% for caged vs. 2.3% for uncaged; Table S3). Caging increased height of wet-year plantings for the 3-year duration of the study (caging effect $p<0.05$, Table S4), though the magnitude of the increase was small (8.59 cm caged vs. 8.03 cm uncaged). For average-year plantings, caging was associated with higher survival of seedlings in the six months following planting ($p<0.05$ for 0-2- and 2-6-month age groups, Fig. 5b), most strongly in shallower, lower-sand content soils (Fig. 4a, Table S5).

Discussion

Consistent with soil texture effects on woody plants in drylands elsewhere (Knoop & Walker 1985; Fravolini et al. 2005; Fensham et al. 2015), abundance of big sagebrush is greatest on coarser soils throughout much of its range in North America (Barnard et al. 2019, but see Nelson et al. 2014), and successional trajectories following disturbance suggest that sagebrush seedling establishment also may be improved under these conditions (Williams et al. 2017). Here we provide new experimental evidence that, in a region characterized by bedrock-controlled landscapes with shallow, sandy soils, early survival of planted seedlings was highest not only on coarse soils, but on soils that were also shallow enough to facilitate retention of soil water within seedling rooting depths. This was true primarily under favorable precipitation conditions, when overall survival of this highly episodic species was > 9x higher than for average precipitation year plantings. Our results indicate it may be possible to improve restoration outcomes in this region by performing targeted plantings on coarser, shallower soils during wet years, particularly if combined with sheltering seedlings.

Soil texture and depth

Similar to responses of mature dryland shrubs to soil texture, sagebrush seedling survival generally was greatest, and seedlings grew tallest, on coarser soils (represented by sand content in upper 50cm). Strong positive effects of coarser textures on survival were especially pronounced during two key time periods: a reduced-survival period during the 2-6 month inter-census interval following planting (July-November) when almost half (47%) of seedlings died, and one year later. In this region, this time period encompasses the summer monsoon, an important growing season for woody plants (Comstock & Ehleringer 1992), and the subsequent dry-down period when young seedlings with undeveloped root systems must rely on moisture in soil surface layers (Donovan & Ehleringer 1992). Although finer textured soils have greater available water holding capacity (AWHC), under dry conditions soil moisture can be less available to plants in these soils due to the relatively large volume of fine pores that retain water at matric potentials unavailable to most plants (e.g., drier than -2 to -3 MPa) (Jensen et al. 1990; Wilder et al. 2019). Thus, in coarser soils, sagebrush seedlings likely experienced increased accessibility to moisture under dry conditions, consistent with Miller et al. (2006) who found that seasonal declines in soil water potential at a nearby site were moderated (less negative) in coarser soils.

Soil depth influences plant growth and establishment by controlling rooting depth and how infiltrated soil moisture is distributed throughout depths (Khumalo et al. 2008; Germino & Reinhardt 2014), and our results uniquely revealed that soil depth moderated sagebrush seedling responses to soil texture. Under hot, dry conditions, soils with coarser surface (0-15cm) textures commonly retain higher moisture at depth than finer textured soils because water is better able to quickly penetrate surface horizons and percolate to depths where evaporative losses are low (Yamanaka & Yonetani 1999; Loik et al. 2004). In the sandy well-drained soils that dominate our study region, newly planted seedlings with shallower and less developed root systems would not be expected to access this water in very deep soils. However, because lithic layers restrict deep soil moisture percolation and root penetration, soils with a shallow or moderately deep restriction layers likely are better at retaining water in the rooting zone of seedlings (Gifford & Shaw 1973; Duniway et al. 2010). Accordingly, we found that the benefits of coarser soils for young (<6 mo) seedlings were most pronounced when soils were also shallow enough to retain moisture at depths more accessible to seedlings, nearly doubling probability of survival relative to finer, deeper soils.

In contrast, when seedlings were assessed one year later, coarser soil textures again had improved survival, but most dramatically on deeper soils -- so much that coarser textures fully compensated for any negative effects of depth and coarser soils yielded high (~90%) probability of survival, regardless of depth. These second-year seedlings likely had deeper and more developed lateral root systems than newly established seedlings (Leffler et al. 2004; Wijayratne 2011), which would have allowed them to harvest soil moisture throughout the soil profile in all but the deepest soils. In the deepest soils, the moisture benefits of coarser soil textures likely provided seedlings with sufficient moisture. However, in the finest textured (and deepest) soils, seedling survival was reduced (to 62%). This was likely due to a combination of higher surface water evaporation, lack of access to deep soil moisture, and dry soil conditions creating very negative soil moisture potentials in finer-textured soils which in turn require greater inputs of infiltrated water to meet both soil and plant moisture deficits. Overall, these results also suggest that sagebrush seedlings become less sensitive to soil surface moisture limitations (*sensu* Leffler et al. 2004) in their second year of growth, and that sites characterized by the deep, coarse-textured soils suitable for mature plants (e.g., Knoop & Walker 1985) may also become suitable for seedlings as young as ~1 year old.

Precipitation

Climate conditions affect the ultimate trajectory of plant establishment in restoration settings (Stuble et al. 2017), and sagebrush establishment is driven by episodic moisture availability (Urza et al. 2021). Accordingly, we found that first-year survival of sagebrush seedlings was > 9x higher for wet- than average-year plantings in Beef Basin. Although it is possible that lower average-year survival of Beef Basin seedlings was partially due to their being planted in the (potentially less favorable) microsites where plants had failed to establish the previous year, average-year survival nonetheless was similarly low across all four sites. These overall weaker effects of soil texture and depth on average-year seedlings suggest that texture and depth – which moderate moisture availability - are only important once minimum moisture requirements are met. Low overall survival (≤ 3% at ~ 2 years post planting) also likely limited our ability to detect statistical effects.

Sagebrush seedlings have narrow moisture requirements (Schlaepfer et al. 2014), underscoring the important roles of soil texture and depth for providing moisture during good establishment years. Our results also highlight the importance of climate forecasting efforts (e.g., https://climate.northwestknowledge.net/downscaledForecast/), particularly given the low frequency of above-average precipitation years (i.e., once every 7.5 years; see Results). Notably, however, our results also reveal that above average precipitation during the initial year of establishment does not overcome drier conditions in subsequent years; the cohort of seedlings planted during a wet year (38% survival at >1 year post-planting) ultimately yielded only 7% establishment at >3 years post-planting (but 16% in soils with >70% sand).

Caging

Providing sufficient water to plants is a major hurdle for successful dryland restoration (Hardegree et al. 2018), and we found that structural barriers may be an effective way to mitigate moisture loss and improve sagebrush seedling establishment. Caging improved probability of early sagebrush seedling survival by 37% and more than doubled the (low) final probability of survival (relative to uncaged), even after cages were removed. We attribute the benefits of caging to shading (cooler leaf temperatures and lower transpiration rates), protection from wind and saltating sands, and the retention of plant litter helping capture and harvest precipitation (David 2013; Fick et al. 2016). Although we observed minimal herbivory to plants in any year (maximum of ~8% of wet-year and 2% of average-year seedlings during any census), we cannot rule out the possibility that cages protected seedlings from herbivory. Maintaining cages may not only protect seedlings from herbivores, but also provide moisture benefits to older seedlings (Ludwig & Tongway 1996).

Applications to ecological restoration

Precision restoration approaches are intended to improve restoration outcomes in variable environments by targeting specific limitations to plant establishment (Copeland et al. 2021), and our results highlight the summer moisture period as critical for sagebrush seedling survival. We have shown that delineating landscapes according to both soil texture and depth (which strongly influence moisture) could help identify areas where planting containerized seedlings – a cost-intensive restoration approach that is increasingly being used in broadscale restoration projects (e.g., Davidson et al. 2019) – is most likely to succeed. Mapping soil texture has been suggested as a guide for shrubland management elsewhere (Wonkka et al. 2016), and high resolution raster-based maps of soil physical properties (30-m resolutions; e.g., Nauman & Duniway 2020a; Brungard et al. 2021) are increasingly available. This information can be used to help prioritize areas for restoration (Fig. 1; Supplement S3) because soil texture and depth are relatively simple measures that can be used to delineate landscapes and serve as an accessible, common language between land managers and researchers.

We suggest that targeting coarser, shallower soils, in wet years and in conjunction with use of shelters, could improve sagebrush restoration efforts in this region – and that similar approaches could be fruitful elsewhere, but with important caveats: 1) optimal soil texture-depth conditions in an ideal (wet) year did not overcome the effects of subsequent drought years, 2) optimal conditions for early plant establishment may not be the same as for long-term persistence, and 3) a different choice of plant materials (e.g., use of seed collected on-site vs. commercially-available seeds) could influence how sagebrush seedling establishment responds to soil properties. Nonetheless, the fact remains that early plant establishment is an unavoidably critical period that dictates, sometimes by precluding, the possibility of long-term success of restoration projects. This is particularly true in our study area, the Colorado Plateau, where spring and summer soil moisture availability is expected to further decrease in the coming years.

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Table 1. Survival of sagebrush seedlings that were planted in May of a wet (2015, Beef Basin site only) vs. average (2016, all four sites) precipitation year. Number (n) and percent survival (%) since previous time step (with % of originally planted seedlings in parentheses) from planting through the end of the study in September 2018 (40 months and 28 months post-planting, respectively for 2015 and 2016).

	Planted	2 mo		6 mo		14 mo		>23 mo		Study end	
	n	n	%	n	%	n	%	n	%	n	%
Beef Basin (2015)	1627	1431	88%	754	53% (46%)	613	81% (38%)	541	88% (33%)	114	21% (7%)
Beef Basin (2016)	597	406	68%	128	32% (21%)	26	20% (4%)	7	27% (1%)	2	29% (0.3%)
Alkali Flat (2016)	216	176	81%	60	34% (28%)	23	38% (11%)	7	30% (3%)	0	0% (0%)
Black Mesa (2016)	216	199	92%	58	29% (27%)	7	12% (3%)	4	57% (2%)	0	0% (0%)
Hart's Draw (2016)	600	583	97%	213	37% (36%)	84	39% (14%)	4	5% (1%)	0	0% (0%)

Table 2. Modeled probability of survival of sagebrush seedlings planted in Beef Basin in 2015 (wet year) across 0-2, 2-6, 6-14, 14-23 and >23 month post-planting inter-census intervals in coarser, shallower vs. finer, deeper soils. Coarser, shallower soils are represented by 70% sand and 74 cm depth, corresponding to 1SD > mean sand content and 1SD < mean depth of all plots. Finer, deeper soils are 53% sand and 151 cm depth, corresponding to 1SD < mean sand content and 1SD > mean depth of all plots.

	SURVIVAL	
	coarser, shallower	**finer, deeper**
0-2 mo	94%	89%
2-6 mo	69%	36%
6-14 mo	84%	59%
14-23 mo	92%	62%
>23 mo	22%	8%

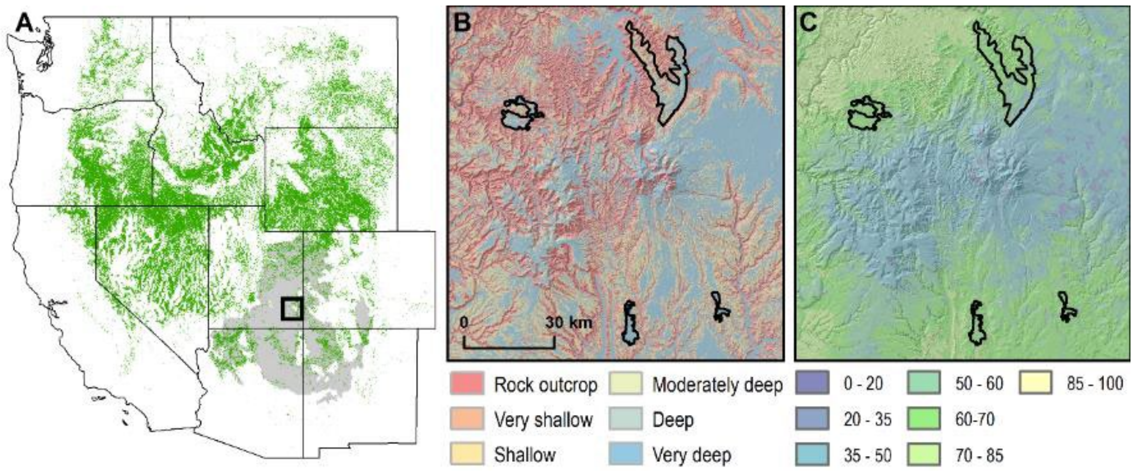

Figure 1. A) Location of study area (black box) within the Colorado Plateau (grey), with respect to the broader sagebrush ecosystem (green), and western US states (black lines). The soil depth (B) and surface sand content (C) of the study sites (black outlines; Beef Basin in upper left, Hart's Draw upper right, Alkali Flat bottom right, and Black Mesa bottom left) and surrounding areas. Sagebrush ecosystem from LANDFIRE Existing Vegetation Type (Hanser 2011), soil depth based on soil taxonomic depth classes and mapped by Brungard et al. (2021), and sand is depth-weighted percent by weight from 0-15 cm from Nauman et al. (2020).

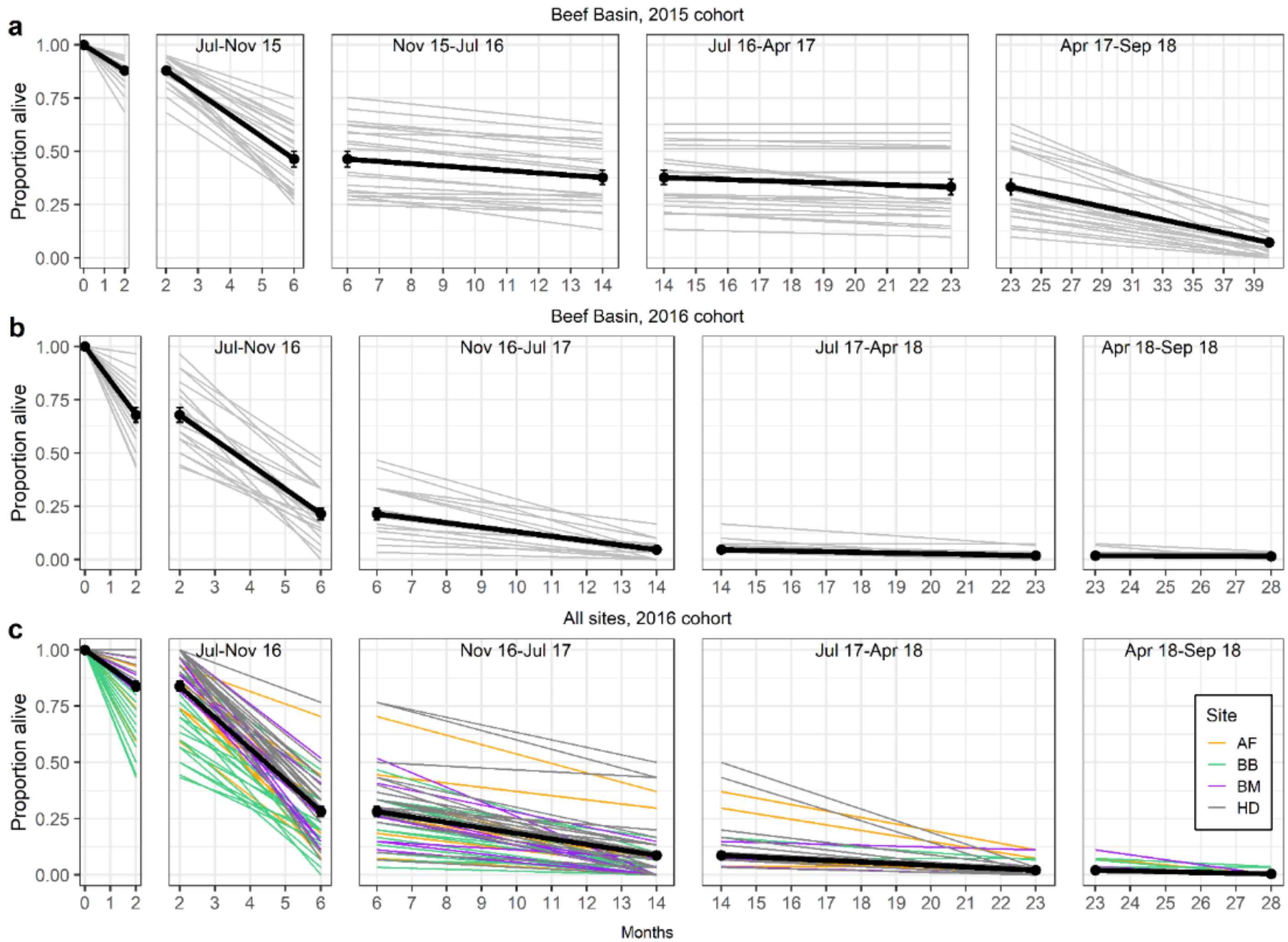

Figure 2. Sagebrush seedling survival across 0-2, 2-6, 6-14, 14-23 and >23 month post-planting inter-census intervals. a) Beef Basin 2015 (wet year) and b) Beef Basin 2016 (average precipitation year) show plot-wise (grey lines) and mean (black line + 1 SE) survival across time, by months-since-planting. c) All sites 2016 (average precipitation year) shows plot-wise (colored lines) and mean (black line + 1 SE) survival across time, by time-since-planting, for seedlings planted at four sites: Alkali Flat (AF), Beef Basin (BB), Black Mesa (BM), and Hart's Draw (HD).

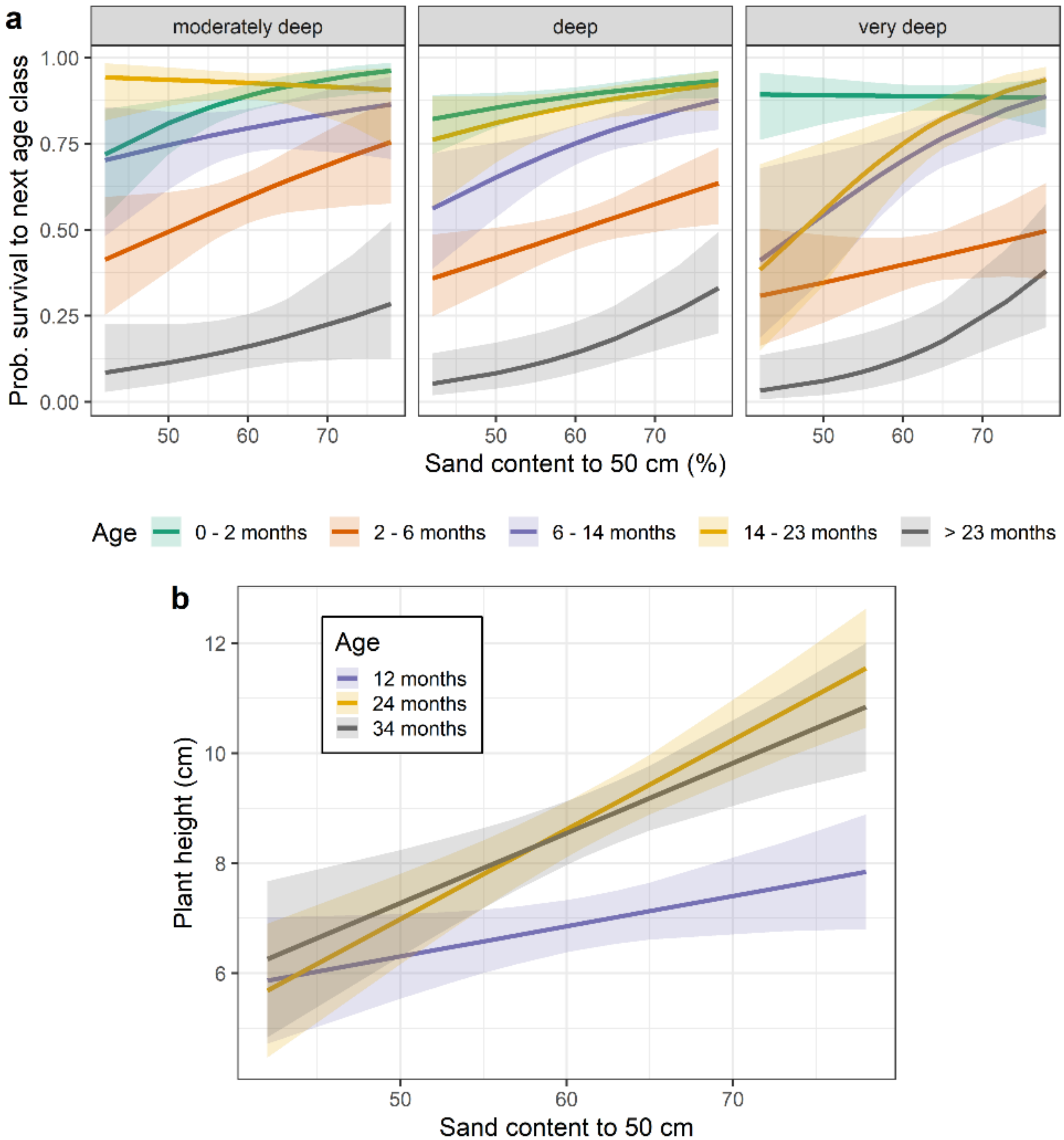

Figure 3. Responses of sagebrush seedlings planted in Beef Basin in 2015 (wet year). a) Modeled probability of survival for different age classes across sand content and soil depths. Moderately deep, deep and very deep correspond, respectively, to 74 cm, 113 cm, and 151 cm, which correspond to mean soil depth (113 cm) plus or minus one standard deviation (151, 74). Lines indicate the predicted probability of survival, and shaded areas represent the 95% confidence interval; b) Plant heights across sand content at 12, 24 and 34 months following planting. Lines indicate the predicted height, and shaded areas represent the 95% confidence interval.

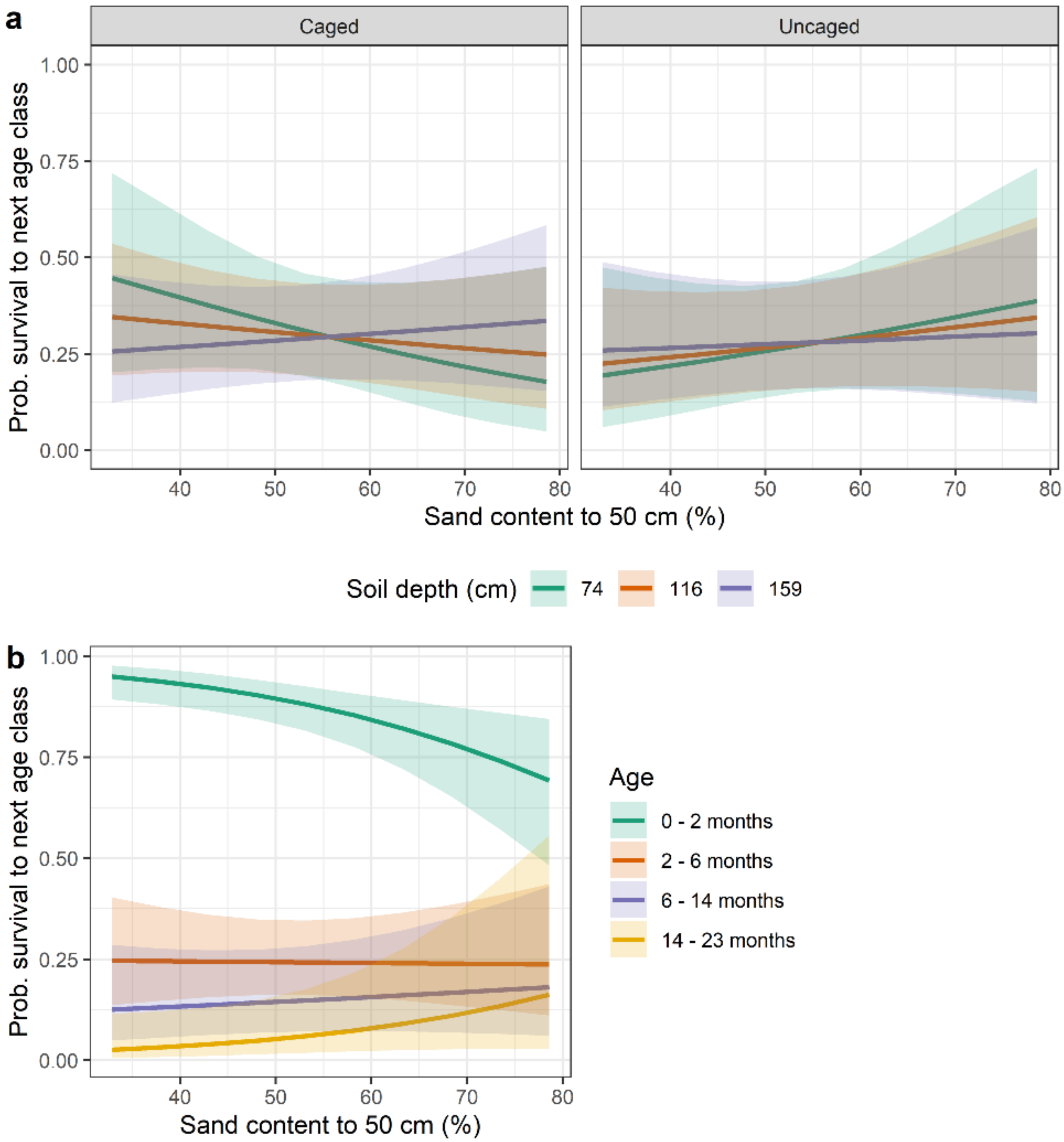

Figure 4. Modeled probability of survival for sagebrush seedlings planted at four study sites (Alkali Flat, Beef Basin, Black Mesa, and Hart’s Draw) in 2016, an average precipitation year. a) with and without caging across sand contents and soil depths and b) across sand content and time periods post-planting (0-2, 2-6, 6-14 and 14-23 mo). In a) soil depths represent mean soil depth and the mean plus or minus one standard deviation. Lines indicate predicted probability of survival, and shaded areas represent the 95% confidence interval.

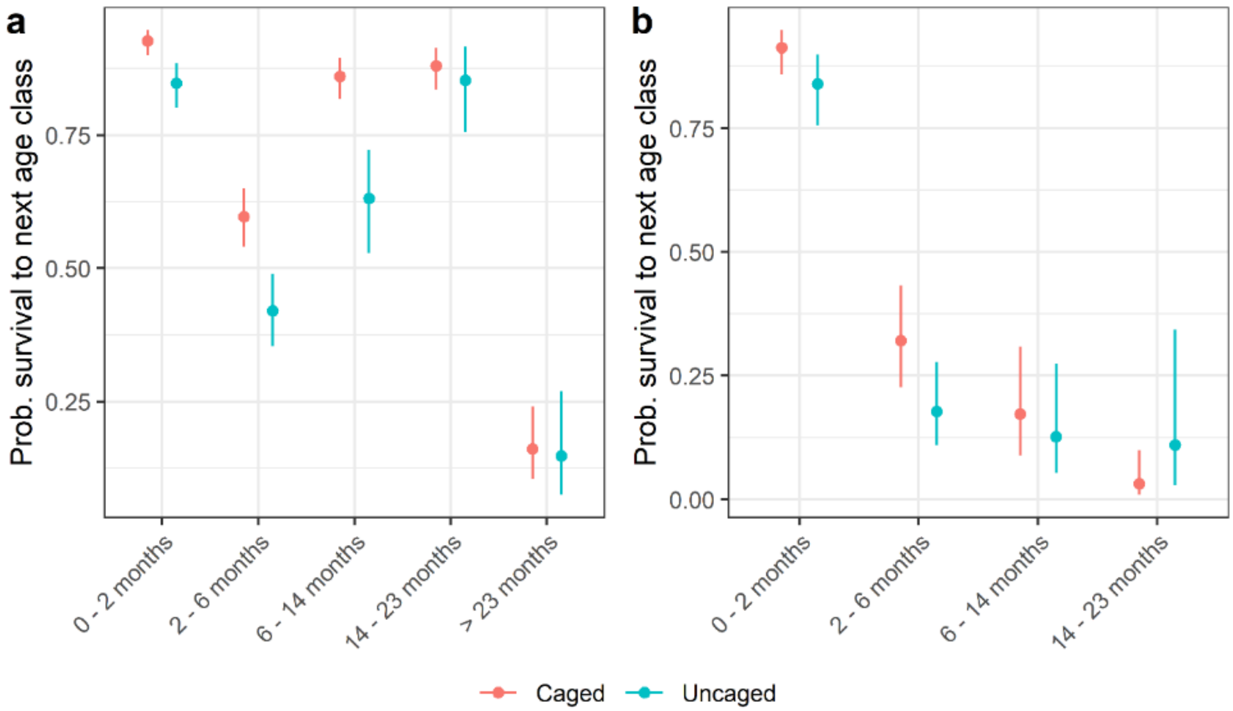

Figure 5. Responses of sagebrush seedlings a) planted in Beef Basin in 2015 (wet year) and b) across four study areas in 2016 (average precipitation year). Modeled probability of survival with vs. without cages across different age classes. Points represent survival probabilities predicted using estimated marginal means. Lines represent the 95% confidence interval.

Supporting Information. Veblen, K.E. et al. Soil depth and precipitation moderate soil textural effects on seedling survival of a foundation shrub species. *Restoration Ecology*.

Table S1
Table S2
Table S3
Table S4
Table S5
Table S6
Figure S1
Figure S2
Figure S3

Table S1. Soil pedon texture and depth for Alkali Flat (AF), Beef Basin (BB), Black Mesa (BM), and Hart's Draw (HD). Depth-weighted average (DWA) of the soil texture elements sand, silt and clay for the soil pedon augured at each experimental plot. DWA calculated for the entire augured soil pedon and to 50cm depth (primary rooting zone for sagebrush). Pedon depth is the depth to a hard lithic contact (less than 150cm) or to maximum depth of auger (~150cm). Soil texture based on the USDA classification system. USDA NRCS Ecological Site Description (ESD) codes and names are included. Asterisks indicate sites where Decagon soil moisture probes were deployed. See Supplement S1 for further methodological details.

		Entire Pedon				**To 50 cm or lithic contact**					
Plot	**Pedon Depth (cm)**	**Texture Class**	**% Sand**	**% Silt**	**% Clay**	**Texture Class**	**% Sand**	**% Silt**	**% Clay**	**ESD code**	**ESD name**
AFCD2	159+	Loam	48.4	30.0	21.6	Sandy Clay Loam	51.3	22.4	26.3	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
AFCD4	155+	Loam	51.8	28.6	19.6	Loam	50.6	28.7	20.7	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
AFCD7*	158+	Loam	48.9	30.2	20.9	Loam	48.1	28.4	23.5	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
AFCS1	99	Loam	50.3	28.0	21.7	Sandy Clay Loam	49.0	27.9	23.1	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
AFCS2	84	Loam	44.9	34.4	20.8	Loam	45.8	33.1	21.2	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
AFSID1	160+	Fine Sandy Loam	61.9	18.8	19.3	Sandy Clay Loam	65.0	13.6	21.4	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
AFSID2	140	Clay Loam	44.8	25.8	29.4	Clay Loam	41.2	25.1	33.7	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
AFSID3*	160+	Loam	52.0	23.6	24.5	Sandy Clay Loam	46.9	24.5	28.6	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)

BBCD1	150+	Fine Sandy Loam	69.6	11.2	19.3	Fine Sandy Loam	73.1	9.8	17.1	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BBCD2	147+	Fine Sandy Loam	58.5	23.0	18.5	Fine Sandy Loam	55.5	25.4	19.1	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BBCD3*	150+	Fine Sandy Loam	63.6	17.7	18.7	Sandy Clay Loam	62.6	17.4	20.0	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BBCD4*	140	Sandy Clay Loam	61.9	17.6	20.5	Sandy Clay Loam	61.3	17.7	21.0	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BBCD5	148+	Loam	44.8	32.5	22.7	Loam	49.9	29.9	20.2	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
BBCS1*	69	Fine Sandy Loam	65.8	17.8	16.4	Fine Sandy Loam	65.2	18.7	16.1	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BBCS2	82	Sandy Clay Loam	60.1	15.1	24.8	Sandy Clay Loam	56.3	16.2	27.5	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BBCS3*	104	Sandy Clay Loam	59.7	19.7	20.5	Sandy Clay Loam	56.9	21.9	21.3	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BBCS4	64	Fine Sandy Loam	72.5	13.5	14.1	Fine Sandy Loam	72.9	13.4	13.7	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BBCS5	61	Fine Sandy Loam	63.8	17.0	19.2	Fine Sandy Loam	61.0	19.1	19.9	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BBSD1*	145+	Sandy Clay Loam	53.8	25.7	20.5	Sandy Clay Loam	60.2	19.4	20.5	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
BBSD2	150+	Sandy Clay Loam	67.7	10.8	21.5	Sandy Clay Loam	65.0	13.2	21.8	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
BBSD3*	147+	Very Fine Sandy Loam	66.5	17.6	15.9	Very Fine Sandy Loam	65.2	16.4	18.4	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)

BBSD4	150+	Fine Sandy Loam	76.5	8.8	14.8	Fine Sandy Loam	77.9	9.4	12.8	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BBSD5	147+	Sandy Clay Loam	69.6	9.2	21.1	Sandy Loam	73.4	7.1	19.5	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
BBSS1*	89	Clay Loam	39.5	33.0	27.5	Loam	42.2	32.5	25.3	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BBSS2	70	Sandy Clay Loam	54.3	19.4	26.4	Sandy Clay Loam	54.9	19.2	25.9	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BBSS3	147+	Sandy Clay Loam	61.1	15.3	23.5	Sandy Clay Loam	60.2	17.0	22.8	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
BBSS4	87	Sandy Clay Loam	53.5	22.5	24.0	Sandy Clay Loam	53.1	23.0	23.9	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BBSS5*	50	Sandy Clay Loam	54.6	19.9	25.5	Sandy Clay Loam	54.6	19.9	25.5	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BMCD1	158+	Loam	52.4	23.8	23.8	Sandy Clay Loam	50.1	25.3	24.6	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
BMCD2	168+	Loam	39.7	33.5	26.8	Loam	42.7	31.8	25.5	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BMCD4*	154+	Loam	36.5	38.3	25.2	Clay Loam	39.8	31.7	28.5	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BMCS1	148+	Loam	36.2	39.6	24.2	Loam	34.6	39.7	25.8	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
BMCS2	132	Loam	44.3	32.4	23.3	Loam	39.5	34.8	25.6	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BMCS4	131	Loam	26.2	47.0	26.8	Clay Loam	34.8	36.5	28.7	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)

BMSD1	158+	Sandy Clay Loam	60.0	18.7	21.3	Sandy Loam	56.2	23.8	19.9	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
BMSD3*	160+	Loam	28.0	47.0	25.1	Loam	34.6	42.3	23.1	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
HDCD1	116	Clay Loam	42.1	26.7	31.2	Clay Loam	42.2	27.3	30.4	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
HDCD2*	148+	Clay Loam	36.9	28.9	34.2	Clay Loam	34.8	31.3	33.9	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
HDCD3	130	Loam	43.4	33.9	22.7	Sandy Clay Loam	52.2	25.8	21.9	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
HDCD4*	150+	Sandy Clay Loam	54.6	19.4	26.1	Sandy Clay Loam	49.0	24.3	26.7	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
HDCD5	133	Sandy Clay Loam	50.2	24.8	25.0	Loam	44.4	30.1	25.4	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
HDCS1	46	Sandy Clay Loam	55.3	21.4	23.4	Sandy Clay Loam	55.3	21.4	23.4	R035XY315UT	Upland Shallow Loam (Pinyon-Utah Juniper)
HDCS2	72	Clay Loam	47.4	24.9	27.7	Sandy Clay Loam	45.7	26.9	27.4	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
HDCS3*	47	Sandy Clay Loam	56.2	20.2	23.7	Sandy Clay Loam	56.2	20.2	23.7	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
HDCS4	45	Sandy Clay Loam	48.2	25.3	26.5	Sandy Clay Loam	48.2	25.3	26.5	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
HDCS5*	47	Loam	44.7	29.0	26.3	Loam	44.7	29.0	26.3	R035XY315UT	Upland Shallow Loam (Pinyon-Utah Juniper)
HDSD1	151+	Fine Sandy Loam	72.7	8.8	18.6	Sandy Clay Loam	67.2	11.4	21.4	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)

HDSD2*	153+	Fine Sandy Loam	71.9	11.1	17.0	Sandy Clay Loam	64.6	14.1	21.3	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
HDSD3*	153+	Sandy Clay Loam	65.4	13.5	21.1	Sandy Clay Loam	62.5	15.7	21.8	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
HDSD4	155+	Sandy Loam	62.9	18.3	18.9	Sandy Loam	57.4	22.9	19.6	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
HDSD5	121	Sandy Clay Loam	51.4	22.3	26.3	Sandy Clay Loam	51.6	22.6	25.9	R035XY216UT	Semidesert Sandy Loam (Wyoming Big Sagebrush)
HDSS1*	45	Sandy Clay Loam	56.0	21.4	22.6	Sandy Clay Loam	56.0	21.4	22.6	R035XY315UT	Upland Shallow Loam (Pinyon-Utah Juniper)
HDSS2	77	Sandy Clay Loam	53.1	24.9	22.0	Sandy Clay Loam	51.9	27.1	21.1	R035XY315UT	Upland Shallow Loam (Pinyon-Utah Juniper)
HDSS3*	95	Sandy Clay Loam	59.5	14.0	26.5	Sandy Clay Loam	59.3	15.2	25.5	R035XY209UT	Semidesert Loam (Wyoming Big Sagebrush)
HDSS4	38	Sandy Clay Loam	54.4	22.8	22.8	Sandy Clay Loam	54.4	22.8	22.8	R035XY315UT	Upland Shallow Loam (Pinyon-Utah Juniper)
HDSS5	44	Sandy Clay Loam	49.1	26.2	24.8	Sandy Clay Loam	49.1	26.2	24.8	R035XY315UT	Upland Shallow Loam (Pinyon-Utah Juniper)

Table S2. Beef Basin survival 2015 (wet year) model estimates and effects. Marginal effects, expressed in terms of probability, are reported for (scaled) continuous variables and their interactions. Estimated marginal means (EMMs), expressed in terms of probability, are reported for categorical variables and interactions involving only categorical variables.

Intercept estimate	Std. error of intercept estimate (logit)	P-value of intercept	Marginal R^2	Conditional R^2
0.70	0.13	< 0.001***	0.36	0.39

Predictors	Estimate (logit)	Std. error of estimate (logit)	EMM (prob.)	P-value
Uncaged	-0.31	0.06	0.60	< 0.001***
Caged	0.31	0.06	0.73	< 0.001***
Age 0 - 2 months	1.42	0.17	0.89	< 0.001***
Age 2 - 6 months	-0.67	0.09	0.51	< 0.001***
Age 6 - 14 months	0.47	0.10	0.76	< 0.001***
Age 14 - 23 months	1.17	0.14	0.87	< 0.001***
Age > 23 months	-2.40	0.21	0.15	< 0.001***
Uncaged x Age 0 - 2 months	-0.09	0.08	0.85	0.245
Uncaged x Age 2 - 6 months	-0.04	0.07	0.42	0.538
Uncaged x Age 6 - 14 months	-0.32	0.09	0.63	< 0.001***
Uncaged x Age 14 - 23 months	0.20	0.13	0.85	0.128
Uncaged x Age > 23 months	0.26	0.12	0.15	0.024*
Caged x Age 0 - 2 months	0.09	0.08	0.93	0.245
Caged x Age 2 - 6 months	0.04	0.07	0.60	0.538
Caged x Age 6 - 14 months	0.32	0.09	0.86	< 0.001***
Caged x Age 14 - 23 months	-0.20	0.13	0.88	0.128
Caged x Age > 23 months	-0.26	0.12	0.16	0.024*

Predictor	Estimate (logit)	Std. error of estimate (logit)	Marginal effect (prob.)	P-value
Soil depth	-0.29	0.11	-0.04	0.008**
Sand content	0.35	0.11	0.05	< 0.001***
Soil depth x Sand content	0.08	0.11	0.01	0.461
Age 0 - 2 months x Soil depth	0.24	0.09	0.04	0.010**
Age 2 - 6 months x Soil depth	-0.13	0.07	-0.02	0.064
Age 6 - 14 months x Soil depth	0.07	0.09	0.01	0.476
Age 14 - 23 months x Soil depth	-0.35	0.12	-0.05	0.004**
Age > 23 months x Soil depth	0.17	0.10	0.03	0.094
Age 0 - 2 months x Sand content	-0.09	0.08	-0.01	0.282
Age 2 - 6 months x Sand content	-0.08	0.07	-0.01	0.221

Age 6 - 14 months x Sand content	0.05	0.10	0.01	0.581
Age 14 - 23 months x Sand content	-0.04	0.12	-0.01	0.737
Age > 23 months x Sand content	0.16	0.11	0.02	0.143
Age 0 - 2 months x Soil depth x Sand content	-0.36	0.09	-0.05	< 0.001***
Age 2 - 6 months x Soil depth x Sand content	-0.16	0.07	-0.02	0.025*
Age 6 - 14 months x Soil depth x Sand content	0.09	0.10	0.01	0.400
Age 14 - 23 months x Soil depth x Sand content	0.35	0.13	0.05	0.007**
Age > 23 months x Soil depth x Sand content	0.09	0.11	0.01	0.416

Table S3. Beef Basin seedling survival at >23 mo for 2015 (average year). Marginal effects are used to interpret (scaled) continuous variables, and estimated marginal means (EMMs) are used to interpret categorical variables

Intercept estimate	Std. error of intercept estimate (logit)	P-value of intercept	Marginal R^2	Conditional R^2
-3.28	0.27	< 0.001***	0.16	0.33

Predictors	Estimate (logit)	Std. error of estimate (logit)	EMM (prob.)	P-value
Uncaged	-0.44	0.12	0.023	< 0.001***
Caged	-0.44	0.12	0.055	< 0.001***

Predictor	Estimate (logit)	Std. error of estimate (logit)	Marginal effect (prob.)	P-value
Soil depth	-0.46	0.25	-0.028	0.066
Sand content	0.77	0.25	0.047	0.002

Table S4. Beef Basin seedling height 2015 (wet year) model estimates and effects.

Intercept estimate	Std. error of intercept estimate	P-value of intercept	Marginal R^2	Conditional R^2
8.31	0.24	< 0.001***	0.19	0.66

Predictors	Estimate	Std. error of estimate	P-value
Uncaged	-0.28	0.13	< 0.031*
Caged	0.28	0.13	< 0.031*
Soil depth	0.133	0.25	0.595
Age 12 months	-1.31	0.09	< 0.001***
Age 24 months	0.73	0.09	< 0.001***
Age 34 months	0.57	0.12	< 0.001***
Sand content	0.97	0.24	< 0.001***
Age 12 months * sand content	-0.51	0.09	< 0.001***
Age 24 months * sand content	0.40	0.09	< 0.001***
Age 34 months * sand content	0.10	0.11	0.363

Table S5. Seedling survival for all sites in 2016 (average year). Marginal effects are used to interpret (scaled) continuous variables and their interactions, and estimated marginal means (EMMs) are used to interpret categorical variables

Intercept estimate	Std. error of intercept estimate (logit)	P-value of intercept	Marginal R^2	Conditional R^2
-0.91	0.31	0.003**	0.43	0.57

Predictors	Estimate (logit)	Std. error of estimate (logit)	EMM (prob.)	P-value
Uncaged	-0.06	0.09	0.27	0.475
Caged	0.06	0.09	0.30	0.475
Age 0 - 2 months	2.91	0.37	0.88	< 0.001***
Age 2 - 6 months	-0.23	0.13	0.24	0.068
Age 6 - 14 months	-0.84	0.17	0.15	< 0.001***
Age 14 - 23 months	-1.85	0.37	0.06	< 0.001***
Uncaged x Age 0 - 2 months	-0.285	0.10	0.84	0.005**
Uncaged x Age 2 - 6 months	-0.33	0.10	0.18	< 0.001***
Uncaged x Age 6 - 14 months	-0.12	0.13	0.13	0.332
Uncaged x Age 14 - 23 months	0.73	0.21	0.11	< 0.001***
Caged x Age 0 - 2 months	0.28	0.10	0.91	0.005
Caged x Age 2 - 6 months	0.33	0.10	0.32	< 0.001***
Caged x Age 6 - 14 months	0.12	0.13	0.17	0.332
Caged x Age 14 - 23 months	-0.73	0.21	0.03	< 0.001***

Predictor	Estimate (logit)	Std. error of estimate (logit)	Marginal effect (prob.)	P-value
Soil depth	-0.01	0.12	-0.002	0.910
Sand content	0.01	0.15	0.002	0.928
Soil depth x Sand content	0.05	0.145	0.008	0.706
Age 0 - 2 months x Sand content	-0.49	0.10	-0.07	< 0.001***
Age 2 - 6 months x Sand content	-0.02	0.09	-0.004	0.778
Age 6 - 14 months x Sand content	0.08	0.11	0.01	0.443
Age 14 - 23 months x Sand content	0.43	0.19	0.07	0.023*
Uncaged x Soil depth	0.03	0.05	0.005	0.506
Caged x Soil depth	-0.03	0.05	-0.005	0.506
Uncaged x Sand content	0.12	0.06	0.02	0.036*
Caged x Sand content	-0.12	0.06	-0.02	0.036*
Uncaged x Sand content x Soil depth	-0.14	0.06	-0.02	0.034*
Caged x Sand content x Soil depth	0.14	0.06	0.02	0.034*

Table S6. Beef Basin seedling survival for 2016 (average year). Marginal effects are used to interpret (scaled) continuous variables and their interactions, and estimated marginal means (EMMs) are used to interpret categorical variables.

Intercept estimate	Std. error of intercept estimate (logit)	P-value of intercept	Marginal R^2	Conditional R^2
-0.75	0.29	0.009**	0.22	0.61

Predictors	Estimate (logit)	Std. error of estimate (logit)	EMM (prob.)	P-value
Uncaged	0.002	0.14	0.32	0.985
Caged	-0.002	0.14	0.32	0.985
Age 0 - 2 months	1.50	0.33	0.68	< 0.001***
Age 2 - 6 months	-0.16	0.18	0.29	0.369
Age 6 - 14 months	-0.80	0.23	0.17	< 0.001***
Age 14 - 23 months	-0.54	0.45	0.21	0.228
Uncaged x Age 0 - 2 months	-0.23	0.15	0.63	0.117
Uncaged x Age 2 - 6 months	-0.09	0.15	0.27	0.570
Uncaged x Age 6 - 14 months	0.38	0.21	0.24	0.068
Uncaged x Age 14 - 23 months	-0.06	0.35	0.21	0.860
Caged x Age 0 - 2 months	0.23	0.15	0.73	0.117
Caged x Age 2 - 6 months	0.09	0.15	0.30	0.570
Caged x Age 6 - 14 months	-0.38	0.21	0.13	0.068
Caged x Age 14 - 23 months	0.06	0.35	0.23	0.860

Predictor	Estimate (logit)	Std. error of estimate (logit)	Marginal effect (prob.)	P-value
Soil depth	-0.0001	0.11	-0.00002	0.999
Sand content	-0.004	0.12	-0.0007	0.975
Soil depth x Sand content	0.03	0.12	0.006	0.812
Uncaged x Soil depth	-0.004	0.07	-0.0009	0.951
Caged x Soil depth	0.004	0.07	0.0009	0.951
Uncaged x Sand content	-0.01	0.07	-0.003	0.859
Caged x Sand content	0.01	0.07	0.003	0.859
Uncaged x Sand content x Soil depth	-0.18	0.08	-0.04	0.020
Caged x Sand content x Soil depth	0.18	0.08	0.04	0.020

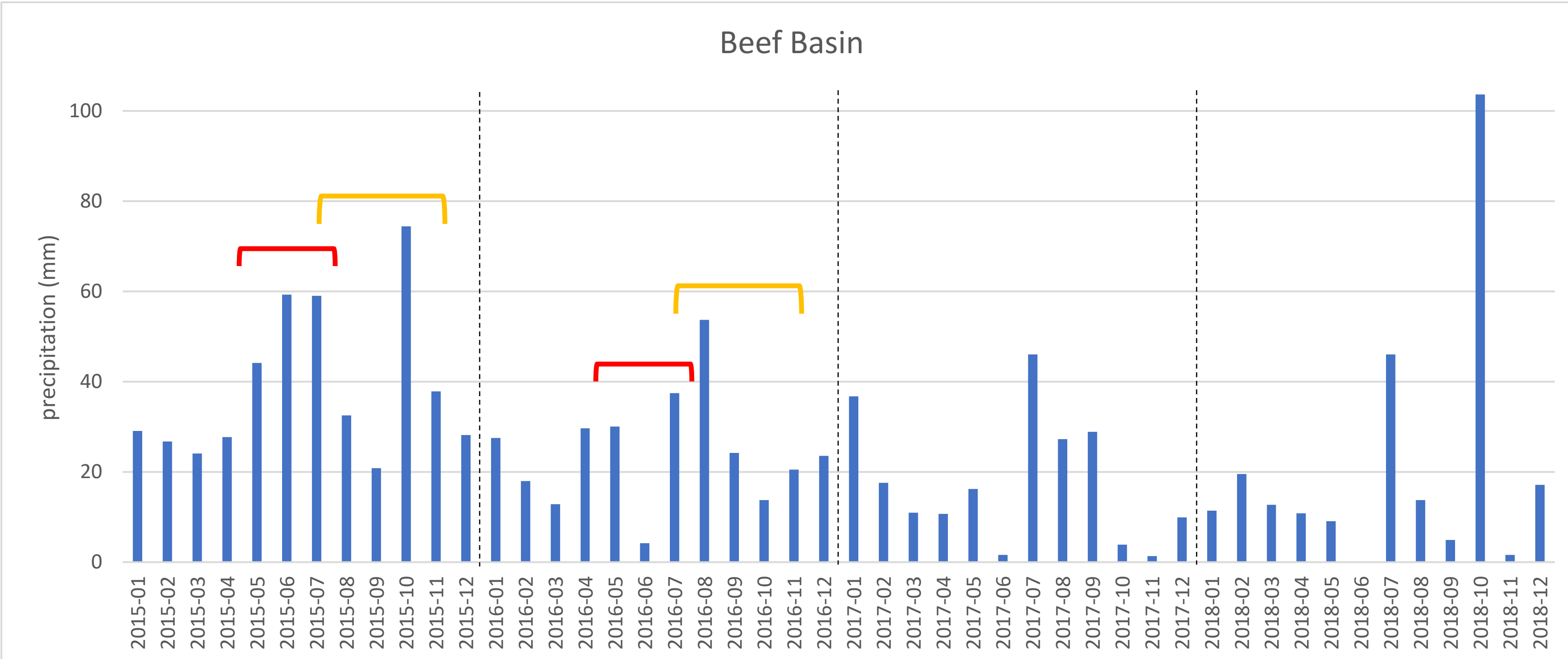

Figure S1. Monthly precipitation in Beef Basin between January 2015 and December 2018 (http://prism.oregonstate.edu). Sagebrush seedlings were planted in April/May 2015 and 2016 and monitored through the end of 2018. Red brackets indicate 3 months following planting of seedlings in each year, and yellow brackets indicate the period when newly planted seedlings encountered a strong survival bottleneck.

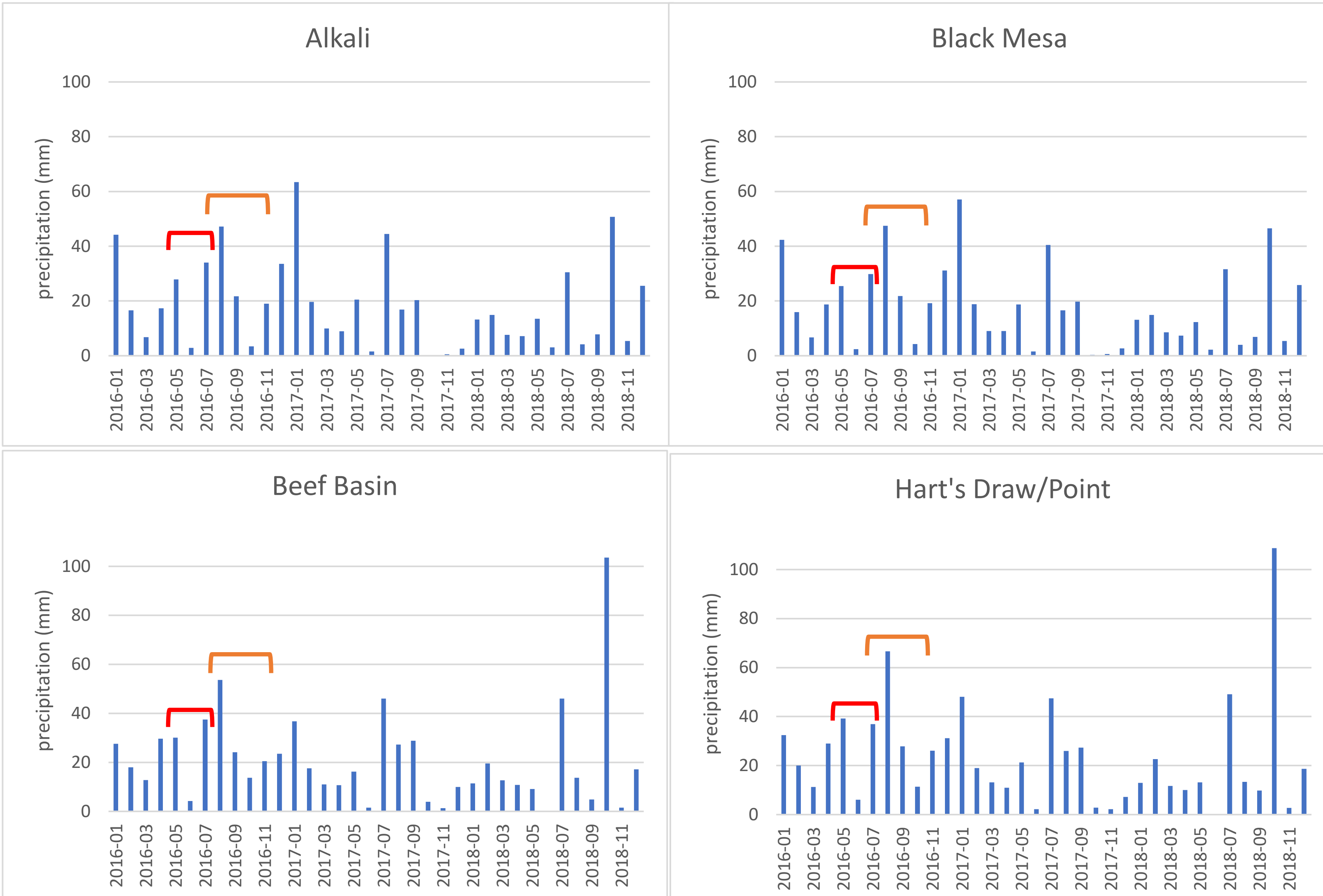

Figure S2. Monthly precipitation in Alkali, Black Mesa, Beef Basin, and Hart's Draw/Point study sites between January 2016 and December 2018 (http://prism.oregonstate.edu). Sagebrush seedlings were planted in April/May 2016 and monitored through the end of 2018. Red brackets indicate 3 months following planting of seedlings, and yellow brackets indicate the period when newly planted seedlings encountered a strong survival bottleneck.

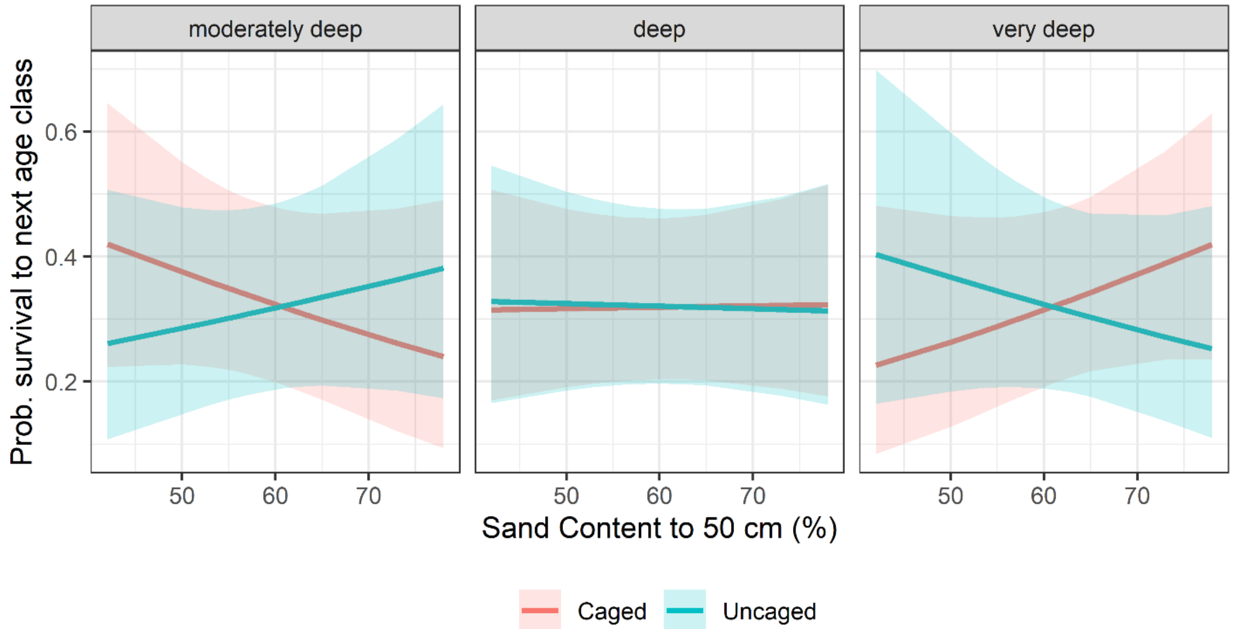

Figure S3. Probability of survival with and without caging across sand contents and soil depths for sagebrush seedlings planted in Beef Basin in 2016, an average precipitation year. Moderately deep, deep and very deep correspond, respectively, to 78 cm, 115 cm, and 153 cm, which are mean soil depth (115) and mean soil depth plus or minus one standard deviation (153, 78). Lines indicate the predicted probability of survival and shaded areas represent the 95% confidence interval.

Supporting Information. Veblen, K.E. et al. Soil depth and precipitation moderate soil textural effects on seedling survival of a foundation shrub species. *Restoration Ecology*.

Supplement S1. Site characteristics
Supplement S2. Neighboring perennials
Supplement S3. Soil mapping

Supplement S1. Site characteristics

At each of the 56 study plots, using an auger, we sampled one soil pedon at the center of the plot. We identified soil structure and estimated root density for the top 25 cm of each soil in the field and identified genetic soil horizons (Schoeneberger et al. 2012). Soil samples from each genetic horizon were air-dried and sieved <2 mm. Particle size distribution (clay, silt, sand) was measured using the hydrometer method (Gavlak et al. 2013) after carbonates and soluble salts were removed with a sodium acetate solution buffered to pH 4.5. In May/June 2016 we measured soil penetration resistance in the 56 seedling plots using a soil impact penetrometer to a depth of 25cm, with strikes measured every 5cm of depth (Herrick et al. 2017). At a subset of sites (see Table S1), we monitored soil moisture with Decagon EC-5 soil moisture probes and a Decagon EM50b logger with measurements every four hours between December 2015 and September 2018.

We conducted baseline surveys of vegetation and animal use in May 2015 (Beef Basin) and May 2016 (Hart's Draw, Alkali Flat, and Black Mesa) along transects that ran perpendicular to the slope of the site. Surveys were conducted in Beef Basin along four 20m transects spaced four meters apart, in Hart's Draw along three 12m transects spaced four meters apart, and in Alkali and Black Mesa along two 16m transects spaced four meters apart. We made visual estimates of cover class (1-5, 6-25, 25-50, 51-75, 76-95, 96-100%) for all plants identified to species in 1m x 1m quadrats. Quadrats were placed every 5 m in Beef Basin, every 3m at Hart's Draw, and every 4m at Alkali Flat and Black Mesa to yield 8-12 quadrats per plot. Along these transects we also assessed: mature shrub density by species and height class (≤ 15cm vs. >15 cm tall) along four-meter wide belt transects; perennial grass density along two-meter wide belt transects; pin hits of biological soil crusts, litter and bare ground on a 25cm x 25cm 25-point gridded crust frame placed every two meters; and ungulate and lagomorph pellet counts (piles for ungulates, individual pellets for lagomorphs) along two-meter wide belt transects.

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Table i. Means and standard errors for site characteristics at Beef Basin (BB), Hart's Draw (HD), Alkali Flat (AF), and Black Mesa (BM) study sites. Min/Max % sand across the four sites, respectively were: 42-78, 35-67, 41-65, 35-56. Min/Max pedon depths across the four sites, respectively, were 50-150, 38-155, 84-160, 131-168 cm.

	BB		HD		AF		BM		Variable definitions
	mean	SE	mean	SE	mean	SE	mean	SE	
pedon depth (cm)	115	9	98	10	139	11	151	5	Pedon depth
sand to 50cm (cm)	61	2	52	2	50	2	42	3	% Sand to 50cm (depth-weighted average)
sand (%)	61	2	54	2	50	2	40	4	% Sand (weighted average)
silt (%)	18	2	22	1	28	2	35	4	% Silt (weighted average)
clay (%)	21	1	24	1	22	1	25	1	% Clay (weighted average)
elev (m)	1904	11	1969	11	1712	13	1682	13	Elevation
# pen strikes to 10cm	27	2	28	1	21	2	25	3	# strikes for penetrometer to reach 10 cm
deer/elk pellets (#/m)	0.11	0.02	0.23	0.03	0.35	0.06	0.22	0.04	# deer and elk pellets / total transect length
rabbit pellets (#/m)	2.84	0.40	2.61	0.22	2.47	0.29	1.71	0.19	# rabbit pellets / total transect length
cow pellets (#/m)	0.08	0.01	0.06	0.01	0.06	0.02	0.04	0.01	# cow pellets / total transect length
A. tridentata density (#/m)	0.25	0.03	0.75	0.07	0.71	0.09	1.08	0.17	# all sagebrush plants / total transect length
A. tridentata ≤ 15cm density (#/m)	0.08	0.01	0.08	0.01	0.06	0.01	0.23	0.11	# all sagebrush plants <15 cm / total transect length
A. tridentata > 15cm density (#/m)	0.17	0.02	0.68	0.06	0.65	0.08	0.85	0.07	# all sagebrush plants > 15 cm / total transect length
Perennial grass density (#/m)	2.89	0.29	0.82	0.15	0.56	0.21	1.68	0.54	Grass density (# / total linear transect length)
A. tridentata cover (%)	1	0	17	2	17	3	24	5	visual estimate, 1 m x 1m frames; mean calculated from center points of cover classes
exotic annual cover (%)	2	1	1	0	17	7	0	0	visual estimate (BRTE and ERCI), 1 m x 1m frames; mean calculated from center points of cover classes
bunchgrass cover (%)	28	1	30	2	3	1	11	4	visual estimate, 1 m x 1m frames; mean calculated from center points of cover classes

Dead ARTR cover (%)	8	1	8	1	9	2	10	4	visual estimate, 1 m x 1m frames; mean calculated from center points of cover classes
BSC (%)	2	1	14	2	5	1	4	2	# biological soil crust hits / 25 points on crust frame
Litter (%)	54	2	48	2	56	8	46	3	# litter points / 25 points on crust frame
Bare (%)	19	3	36	2	38	8	50	2	# Bare points / 25 points on crust frame

Table ii. Percent (%) Volumetric Water Content (VWC; mean ± 1SE) at 5, 15, 50 and 100 cm soil depths at eight Beef Basin sites with low (≤ 60%) and high (> 60%) sand content. For each site in each of two years (2016, 2017), readings were averaged across 4-hour intervals between Sept 1 and Nov 30. For each year-soil depth combination, a t-test was used to test for VWC differences in low vs. high sand content sites (n = 4 sites each for low and high sand, except n = 3 for < 60% sand at 100 cm).

	depth	***< 60% sand (n=4)***	***> 60% sand (n=4)***	**t**	**p**
2016	5 cm	6.1 ± 0.7	8.0 ± 0.7	2.00	0.09
	15 cm	7.6 ± 0.01	8.5 ± 0.6	0.77	0.47
	50 cm	4.0 ± 0.4	4.5 ± 0.8	0.51	0.63
	100 cm	5.5 ± 1.2	3.6 ± 0.5	1.60	0.16
2017	5 cm	3.5 ± 1.1	5.4 ± 0.6	1.60	0.17
	15 cm	6.9 ± 0.9	7.7 ± 0.8	0.70	0.51
	50 cm	4.0 ± 0.6	4.6 ± 0.7	0.69	0.51
	100 cm	5.0 ± 0.01	3.6 ± 0.7	1.10	0.31

Supplement S2. Neighboring perennials

At the time of planting we measured distance from each planted sagebrush seedling to the three nearest perennial grass or sub-shrub plants. The most common perennial grass neighbors were *Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths, *Sporobolus cryptandrus* (Torr.) A. Gray, and *Hesperostipa comata* (Trin. & Rupr.) Barkworth, and the only sub-shrub was *Gutierrezia sarothrae* (Pursh) Britt. & Rusby, corresponding respectively to 47%, 25%, 8% and 10% of neighbors.

We explored the potential effect of perennial grasses (which also rely on moisture at shallower depths, Gremer et al. 2018) on survival for 2015 (wet year) Beef Basin seedlings during the 2-6 month and 14-23 month inter-census intervals, the time of year when most seedlings died and when grasses are most active. At the individual seedling scale, we examined Pearson correlations between model residuals and mean distance from seedling to the three nearest perennial grass/sub-shrub neighbors. We also calculated Pearson correlations between the mean of model residuals for each plot and two plot-scale metrics: density of all perennial grasses and cover of perennial bunchgrasses (i.e., excluding *B. gracilis*). The correlation between model residuals and mean distance from seedling to its three nearest perennial grass/sub-shrub neighbors was significantly but very weakly negative for the 2-6 month inter-census interval ($r = -0.05$, $p = 0.04$), while correlations between residuals and perennial grass cover and density at the site level were non-significantly negative during this time period (perennial grass density $r = -0.27$, $p = 0.26$; perennial bunchgrass cover $r = -0.28$, $p = 0.24$). For the 14-23 months interval, correlations were all non-significant (distance to neighbors = 0.003, $p = 0.94$; density $r = -0.02$, $p = 0.94$; cover $r = 0.17$, $p = 0.47$).

Gremer, J. R., C. Andrews, J. R. Norris, L. P. Thomas, S. M. Munson, M. C. Duniway, and J. B. Bradford. 2018. Increasing temperature seasonality may overwhelm shifts in soil moisture to favor shrub over grass dominance in Colorado Plateau drylands. Oecologia **188**:1195-1207.

Supplement S3. Soil mapping

To move beyond current soil survey data (which are often coarse and/or inaccurate) we used digital soil mapping to make spatially explicit predictions of key soil variables (soil depth, water holding capacity) across the study sites. This work was already completed for Beef Basin prior to the current study, and here we mapped the Hart's Draw, Black Mesa, and Alkali sites and surrounding region. We selected a total of 80 sites within the Hart's Draw (40), Alkali Flat (20), and Black Mesa (20) sites, using Conditioned Latin Hypercube Sampling (cLHS), a stratified random sampling scheme which selects representative sample locations to capture soil variability (Brungard and Boettinger 2010). At each of these sites in May and June 2017, we augured a soil pedon and identified the soil horizons according to Schoeneberger et al. (2012)). We identified the structure and root density in each horizon located in the upper 25 cm in each soil pit. We transported soil samples for each horizon to the lab and estimated soil texture by hand texturing methods and measured the color, pH, and effervescence of each soil horizon according to Schoeneberger et al. (2012). At each site, we identified the major vegetation cover that each soil pedon was located within.

At 60 of the soil pedon sites, we also conducted more intensive vegetation surveys along three 30 m transects, 10 m apart, run perpendicular to the slope and centered around the soil pit. We followed the same methods we used for the 56 experimental plots for densities of shrubs, sub-shrubs and bunchgrasses, as well as large ungulates and lagomorphs. To sample vegetation we assessed percent cover of plants to the species level using line-point intercept along each transect, with pin drops every 0.5m.

The sampled pedon observations were supplemented with observations from three national-extent soil databases to produce the most accurate soil maps (Somarathna et al. 2017). Machine learning (McBratney et al. 2003, Brungard et al. 2015) was then used to derived predictive relationships between key soil properties from the soil pedon observations and environmental covariates from terrain analysis, spectral responses, and geospatial environmental variables at 30m spatial resolution. Key soil variables were determined to be soil depth and the weighted average sand content (%) in the upper 50 cm.

Spatial predictions of soil depth classes were made for the entire upper Colorado River Basin using a regional modeling approach, whereby sub-models for each physiographic region were built and subsequently merged to produce predictions with low uncertainty (Brungard et al. 2021). Spatial predictions of the weighted average sand content (%) in the upper 50 cm were derived from (Nauman and Duniway 2020). Spatial predictions of sand content at the following depth increments: 0, 5, 15, 30, and 60 cm were then integrated using triangular integration (Hengl et al. 2017). Weights were derived by the fractional proportion of the depth increment over the total depth increments. Because only the upper 50 cm were desired the spatial predictions of sand content at 60 cm were weighted only to 50 cm.

Weighted sand content in the upper 50 cm was subsequently masked to 1) areas that were between 50 and 100 cm deep, and 2) where soils were > 100 cm deep. Depth-masked weighted-average sand contents predictions were subsequently further restricted to areas which were deemed similar to the original project areas to avoid significant model extrapolation (Fig. i). This was done by first masking the predictions to areas that were between 1500m and 2200m elevation to approximate areas with potentially similar climate. Secondly, the predictions were further restricted to only areas that had weighted-sand content values that fell between 30% and 85%. These were +- ~ 5% of the predicted sand values found in each study area. Thirdly, these areas were constrained to a general physiographic area surrounding the original project areas. This area was visually chosen by looking at aerial imagery to identify areas with landforms similar to the study areas. This area very generally followed the Colorado River on the north and west, the San Juan River on the south, and the Dolores River on the east.

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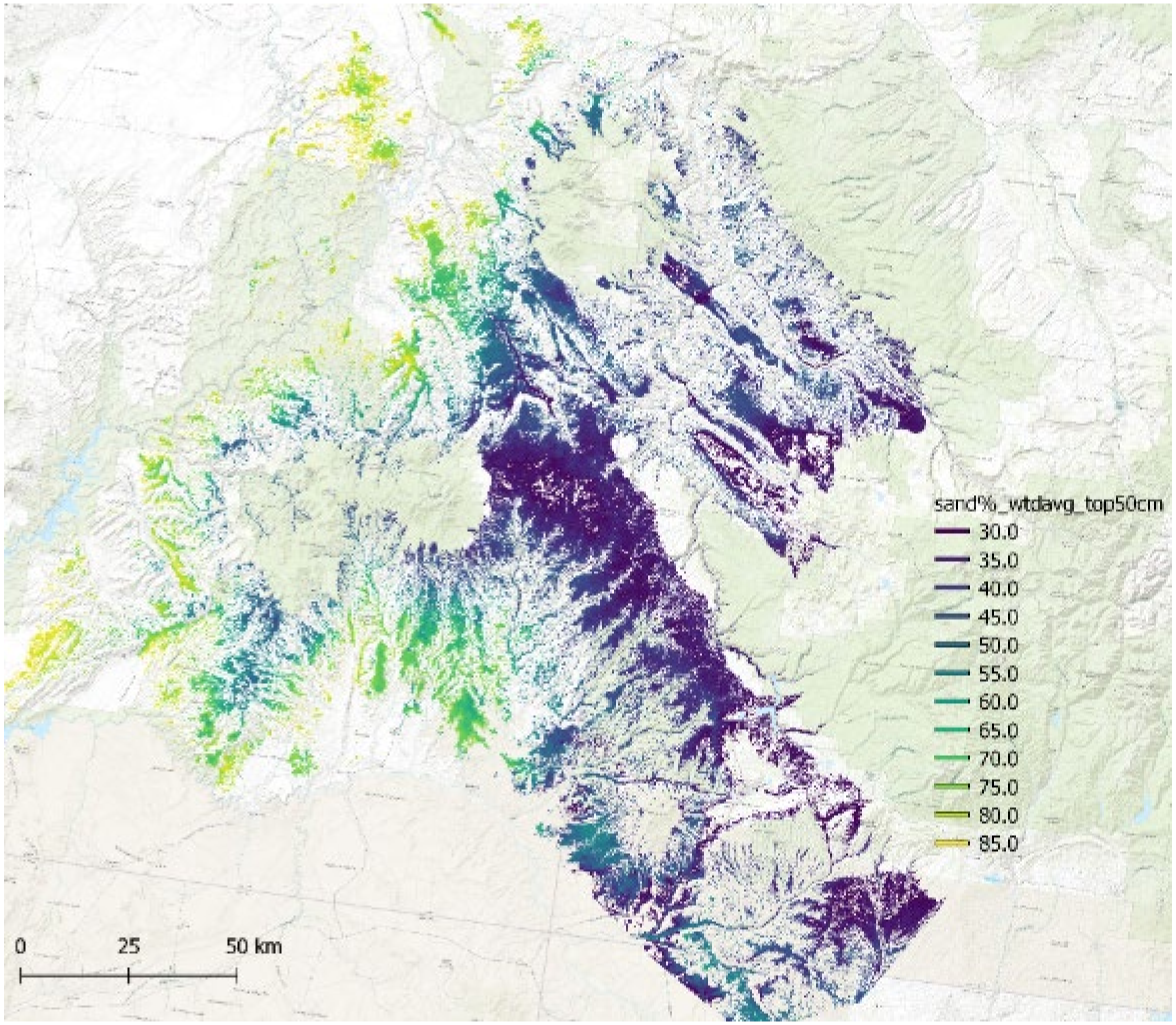

Figure i. Weighted average sand content in the upper 50 cm for soils > 100 cm deep. Predictions were restricted to areas that were similar to the three study areas based on elevation and sand content. Predictions of weighted average sand content in the upper 50 cm for soils between 50 and 100 cm are also included on this map, but are not distinguishable on this map)