OVERCOMING BARRIERS TO NATIVE SHRUB ESTABLISHMENT ON ABANDONED OIL AND GAS PADS ON THE COLORADO PLATEAU

by

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LIST OF ABBREVIATIONS

Abbreviation Description

CP Colorado Plateau

BLM Bureau of Land Management

SITLA Utah School and Institutional Trust Lands

Administration

USGS United States Geological Survey

hrs hours

A photosynthetic rate

g_s leaf conductance

c_i intercellular CO₂ concentration

cm centimeter

g gram

ds/m decisiemens per meter

 Ψ_{Pre} predawn water potential

 Ψ_{Mid} midday water potential

Y_{Diff} difference between predawn and midday

water potential

PS photosynthesis

SR soil resistance

EC electrical conductivity

 Ψ_{Soil} soil water potential

LE location effects

TSA time since abandonment

Na salt

NS northern sagebrush

SS southern sagebrush

NB northern blackbrush

SB southern blackbrush

GLMER generalized linear mixed effects model

m² square meter

ppt precipitation

min minimum

max maximum

I. COMPARISON OF SOIL PROPERTIES AND PLANT WATER STATUS ON AND OFF ABANDONED OIL AND GAS PADS

Abstract

Dryland ecosystems are increasingly disturbed by human land use practices such as oil and gas extraction. These operations degrade fragile landscapes through removing vegetation and topsoil, which can lead to increased soil compaction and salinity. If affected sites are abandoned after use without reclamation efforts, recovery of native shrubs may take decades. Thus, understanding the barriers to native plant growth and recovery are important for implementing restoration techniques. Using a chronosequence approach to survey abandoned oil and gas pads in Wyoming sagebrush and blackbrush habitats, I evaluated the physiological status of mature shrubs (i.e., predawn water potentials and photosynthetic rates), soil compaction and salinity on abandoned oil and gas pads, compared to off pad reference sites to determine if these qualities changed differentially over time. I also determined whether soil compaction or salinity affected shrub water and photosynthetic processes. In both sagebrush and blackbrush communities, predawn and mid-day water potentials were higher on pads, whereas shrub density was reduced. Plant and soil qualities did not change with time since abandonment, except for blackbrush surface soil moisture which was less dry over time. Increased soil compaction reduced predawn water potentials for plants on pads in blackbrush communities. Salinity was higher on sagebrush pads, but it did not negatively affect shrub physiological status. However, increased salinity in blackbrush communities negatively affected photosynthetic rates for plants on pads. Over time, plant density did not increase, suggesting that there is little dispersal of new recruits away from parent plants. Although poor soil conditions may affect some physiological indicators for

mature plants, there is also a lack of shrub density increase over time. The current patterns of establishment suggest that there are low dispersion distances away from established plants, suggesting that new germinants may be affected more by poor soil qualities.

Introduction

Dryland ecosystems in North America have seen rapid growth in oil and gas development since 2000 (Buto et al. 2010, Allred et al. 2015). Impacts from oil and gas extraction include widespread disturbance across several million hectares, primarily through establishing road networks, removing topsoil and vegetation, and using heavy equipment on site (Allred et al. 2015, Rottler et al. 2018). These operations may alter soil health through the removal of biological soil crusts, increased soil compaction, or increased salinity due to mixing of subsurface material and stockpiled soil. Collectively, these alterations reduce native plant cover and habitat quality (Webb 1983, Taylor and Barr 1991, Webb 2002, Day et al. 2015). After decades of use, oil and gas sites are abandoned, and may take up to a century or more to return to the previous vegetation cover without any restoration efforts (Avirmed et al. 2015).

Well-known barriers to seedling establishment, such as soil compaction and salinization, are especially detrimental to timely vegetation recovery. Concentrated salts can be toxic to some species (Day et al. 2015) and soil compaction increases soil bulk density, which reduces soil water storage and infiltration and may also inhibit root growth, if radicles do not exert enough pressure to expand into compacted soils (Kozlowski 1999, Webb 2002). Together, these effects reduce water availability and uptake, and can increase physiological stress of plants, reducing stomatal openings and

therefore lowering photosynthetic activity (Kozlowski 1999). Applying topsoil or using equipment that decompacts the soil may alleviate these barriers to establishment (Webb 1982, Webb 2002). However, soil may also become decompacted naturally by repeated freeze-thaw cycles, although it may take several decades for desert soils to return to a habitable state (Webb 1983, Taylor and Barr 1991, Kade and Warren 2002).

Elevated salt levels may occur on abandoned well pads if accumulated solutes, usually found deeper in the soil, are exposed during operations and leached into plant root zones (Schladweiler et al. 2004). Increased soil salinity may decrease the amount of soil water uptake by plant roots and can lead to solute accumulation in cells, reducing plant growth and productivity (Oren 1999, Yan et al. 2015). Mature shrubs may be more tolerant to saline soils, but salts in the soil surface can prevent germination and emergence, either through soil surface crusting or toxicity in the root zone (Day et al. 2015). Reclaiming salt affected soils involves leaching salts beyond the plant root zone or amending the soil with chemical or organic matter, and are not as effective as prevention (Flynn and Ulery 2011, Day et al. 2015).

The Colorado Plateau (CP), home to over 200 endemic plant species, has experienced oil and gas development since the early 1900's, but rates have increased dramatically in the past 20 years (Copeland et al. 2017). Due to this region's fragility and susceptibility to rapid degradation, there is an urgent need to develop ecological restoration solutions (Belnap and Lange 2003, Krause et al. 2015). The CP is a shrubdominated cold desert, where most precipitation results from winter snowfall with some additional input of summer monsoon moisture (West 1983a, Comstock and Ehleringer 1992). Precipitation patterns exhibit a north-south gradient with relatively more winter

precipitation in the north and more summer precipitation in the south (Hereford et al. 2002, Schwinning et al. 2008). Seedlings germinate in spring using winter precipitation for early growth and many may not survive the summer, unless both winter and summer rainfall are high (Seager et al. 2007, Schwinning et al. 2008, Copeland et al. 2017, Winkler et al. 2018). Much of the oil and gas extraction occurs in two shrub communities, dominated by Wyoming sagebrush (Artemisia tridentata ssp. wyomingensis) or blackbrush (Coleogyne ramossissima). Both sagebrush and blackbrush have dimorphic root systems, accessing water in shallower soil layers during the cold season and deeper soil layers during the warm season (Smith et al. 1995, Schwinning and Ehleringer 2001, Germino and Reinhardt 2014). During the drought season, plants that are water-limited may be negatively impacted by additional stressors, such as soil compaction or salinity which can be evaluated through measuring plant-available soil water (i.e., predawn water potentials) and leaf gas exchange (i.e., photosynthetic rates) (Schwinning et al. 2005a, b). However, less is known about how the physiological status of these shrubs are affected by altered soil properties resulting from oil and gas operations.

I examined how soil properties differed on and off pads, as a basis for identifying potential barriers to plant emergence, survival, and growth. In addition, I compared physiological indicators (photosynthesis and water potentials) of plants that did successfully establish on oil well pads with mature plants off pads to determine if and how plants on the pad were negatively affected by soil properties. I tested the following specific hypotheses:

- Soil resistance and salinity will be greater on pads than in nearby off pad reference sites.
- 2) Increased soil compaction and salinity will decrease photosynthetic rates and lower plant water potentials during the summer drought season.
- 3) Location effects (i.e., on and off pads) on soil compaction, salinity and physiological indicators will diminish with time since pad abandonment.

Methods

Study Species

The two dominant shrub focal communities include Wyoming sagebrush (*Artemisia tridentata*. spp. *wyomingensis* [Beetle and A. Young] S. L. Welsh) and Blackbrush (*Coleogyne ramosissima* Torr.). Both species form mostly pure stands in association with few grasses, forbs, or other woody species. Wyoming sagebrush is the most common sagebrush species and is found at mid to low elevations (700 m–2150 m) in xeric foothills and valleys from Southern British Colombia to Northern New Mexico, reaching ages between 30–100 years, if undisturbed (Ferguson 1964, Perryman et al. 2001). This species prefers fine-textured soils in medium to shallow soil depths and tolerates low salinity (West 1983a, Shumar and Anderson 1986, Davies et al. 2007, Bowker and Belnap 2008).

Blackbrush, found at mid to low elevations (700 m–1950 m) occupies the transition zone between the CP and Mojave Desert which is a narrow ecotonal band between Southeast California and Southwest Colorado. It is considered a Pleistocene relic and has a life span of several centuries (Pendleton and Meyer 2004, Kitchen et al. 2015). This species is salt intolerant, resistant to disturbed and compacted soils, but generally

found on shallow, well drained soils with exposed bedrock and sand and developed biocrusts on the CP (Anderson 2001, Belnap and Lange 2003, McArthur and Stevens 2004, Munson et al. 2011a, Pendleton et al. 2015).

Site Description

This study took place on and near abandoned pads throughout eastern Utah on the CP on land under the jurisdiction of U.S. Bureau of Land Management (BLM) and the Utah School and Institutional Trust Lands Administration (SITLA). Experimental sites were located along a geographic range from north to south and encompassed a chronosequence of abandonment from 14 to 59 years. A total of 27 of the 63 experimental sites were previously selected as study sites by the United States Geological Survey (USGS), for which vegetation cover data were available and dates of abandonment had been established (DeFalco et al., in preparation; Table 1.1).

Climate variables used in the analyses were obtained from the PRISM Climate Group, Northwest Alliance for Computational Science & Engineering based at Oregon State University (www.prism.oregonstate.edu; accessed 07/28/2020, period: 1990-2019). During the two years of data collection, sites received lower than average spring and summer precipitation. Precipitation in the northern sagebrush sites averaged 10 mm from April to September 2018, which was 54% lower than the 30-year normal. Precipitation in the southern sagebrush sites averaged 15 mm from April to September 2019, 38% lower 30-year normal. Temperatures averaged 19.3 and 19.6 °C, which were 2% (northern) and 12% (southern) higher than 30-year normal. Precipitation in northern blackbrush sites from April to September 2019 averaged 13 mm, 37% lower than 30-year normal and in southern blackbrush sites 9.5 mm, 39% lower than the 30-year normal. Temperatures

averaged 20 and 21 $^{\circ}$ C for the same time period, which was 1 and 2 % higher than the 30-year normal.

Experimental Design

At each site, within each community type, I randomly selected 5 plants on the pad and 5 plants off the pad in an adjacent undisturbed area approximately 20–30 m away. For each plant, we measured leaf gas exchange (a measure of photosynthetic activity), stem water potentials, (a measure of plant available water in the soil) and three canopy dimensions (diameter 1, perpendicular diameter 2, and height) to estimate canopy volume. I also measured soil resistance (compaction), electrical conductivity (salinity), and soil water potentials on pad and off pad. Target shrub density on and off pad was measured on three 26 m belt transects (2 X 6 m belts) (previously measured by DeFalco et al., in preparation). In blackbrush communities, only five sites were included due to lack of density data, and in sagebrush communities, all 18 sites were included.

The physiological measurements consisted of morning (0800–1200 hrs) leaf gas exchange measurements, using a LI-6400 (or LI-6400XT) Portable Photosynthesis System (LI-COR, Inc., Lincoln, NE, USA) and predawn (0400–0445 hrs) and midday (1000–1200 hrs) plant water potentials, using a pressure chamber (Model 1505D, PMS Instrument Company, Albany, OR USA). Gas exchange variables included photosynthetic rate (A), leaf conductance (g_s), and intercellular CO₂ concentration (c_i) and were measured at near-ambient conditions of light intensity, atmospheric CO₂ concentrations, air temperature and humidity. Both sagebrush and blackbrush have small leaves, therefore entire terminal branches were clamped into the standard 2 cm x 3 cm chamber for measurement, then carefully clipped and placed into moist coin envelopes.

Branches were cold-stored and until they could be optically scanned several days later.

Leaf areas were calculated using WinFOLIA software (Regent Instruments Inc., Quebec,
Canada). Gas exchange and water potentials were measured on the same individuals.

Soil compaction was measured using a dynamic cone penetrometer on three 20 m line-transects distributed radially 5–25 m away from the center of the pad and off pad in the undisturbed vegetation. Measurements were taken at two points per transect (10 m and 20 m). At each point, the cumulative number of strikes per 5 cm increments were tallied until the penetrometer reached 30 cm depth (Herrick and Jones 2002). If a resistance layer stopped the penetrometer above 30 cm depth, the number of strikes to that depth was recorded. The number of strikes to each layer or cumulative number of strikes was converted to soil resistance (Herrick and Jones 2002). Soil samples were taken near the well head at the center and off the pad from one soil core at depths of 0–10 cm, 10-25 cm, 25-40 cm, and 40-60 cm. Samples were placed in glass vials, closed with screw caps, sealed with parafilm, and kept cool until analysis. The water potentials of the soil samples were measured using a WP4-T Dewpoint meter (Decagon Devices, Inc. Pullman, WA). To determine gravimetric soil water content, samples were first weighed, dried at 70 °C for 24 hrs, then re-weighed. Electrical conductivity, a proxy for salinity, was measured from air-dried and sieved soil samples collected at 0–10 cm and 10–25 cm, in a mixture of approximately 20–25 g dry soil and 100–125 ml of deionized water, shaken for three minutes and settled for one minute (Slavich and Petterson 1993). The suspension was measured with an electrical conductivity probe and converted to ds/m, based on a conversion factor through soil texture, determined with the ribbon test (Gibbs 2000) (Milwaukee MW 301 EC Meter, Rocky Mount, NC).

Statistical Analyses

To test hypotheses one and two, i.e., to determine the if abandoned oil and gas pads had negative effects on plant and soils, I conducted linear mixed effects model analysis separately for each shrub species, with location (on or off pad) as the fixed factor and site as the random factor. The response variables included predawn water potentials (Ψ_{Pre}) , midday water potentials (Ψ_{Mid}) , the difference between predawn and midday water potential (Ψ_{Diff}) and leaf photosynthesis rates (PS) as indicators of plant physiological status. Shrub density was the response variable that represented the overall recovery status of the target species. Response variables representing the soil were soil mechanical resistance per 5 cm depth increments (SR), electrical conductivity at 0-25 cm (EC) and soil water potentials in 10-20 cm depth increments (Ψ_{Soil}). Out of nine blackbrush pads, I excluded one electrical conductivity value, as an extreme outlier, based on Tukey's method. I then conducted a linear regression with shrub density as the response and SR or EC as the predictor and time since abandonment and location (on or off pad) as covariates. To determine if density of shrubs effected shrub status, I conducted a linear regression with Ψ_{Pre} or PS as response variables and density, time since abandonment and location as predictors.

To determine potential relationships between soil physical properties and plant physiological variables I conducted regression analyses using location effects as dependent variables. Location effects (LE) were defined as the difference between the on- and off-pad values of a given variable:

LE (X) =
$$X_{On}$$
 - X_{Off} , where X = PS or Ψ_{Pre} (1)

For the independent variables, I used cumulative SR between 0–30 cm (as this was significantly higher on pads compared to references sites) or EC between 0–25 cm, as measured on pads. The rationale was to relate the location effects to actual compaction and salinity measures on pads. We used the slope of the regression to identify whether compaction or salinity on pads increased or decreased location effects.

To test hypothesis three, that location effects diminish over time, I conducted linear regressions between location effects, as defined above, and time since abandonment (TSA, in years) as the predictor.

Results

Across sites, shrub Ψ_{pre} and Ψ_{Mid} were significantly less negative on-pad than off-pad for both sagebrush and blackbrush communities (Table 1.2; Fig. 1.1 A, C). Average PS and Ψ_{Diff} did not differ significantly for either community by location (Table 1.2; Fig. 1.1 B, D). Soil resistance (SR) was overall significantly higher on pads in both communities, in all soil depths from 0–30 cm in sagebrush and 0–20 in blackbrush communities. (Table 1.2; Fig. 1.2). Salinity as measured by electrical conductivity (EC) was significantly higher on pads in the sagebrush community but did not differ between locations in the blackbrush community (Table 1.2; Fig. 1.3). There were no significant differences in Ψ_{Soil} between locations in either community, but Ψ_{Soil} became less negative with depth in both communities (Table 1.2, Fig. 1.4). In both communities, soil water potentials to the measurement depth of 60 cm were much more negative than shrub Ψ_{pre} (Table 1.2). In both communities, target shrub density was significantly higher off pads than on pads (Table 1.2). Density was not affected by SR or EC and similarly did not influence Ψ_{Pre} or PS in either community.

On-pad SR did not affect location effects on Ψ_{pre} for sagebrush, but significantly decreased location effects on Ψ_{pre} in the blackbrush community (Fig. 1.5 A, C; p = 0.03). On-pad SR did not significantly affect location effects on photosynthesis in either community (Fig. 1.5 B, D). Thus, more compacted soils decreased predawn water potentials for blackbrush plants on pads relative to reference sites. On-pad EC increased the location effect on Ψ_{Pre} in sagebrush which means that more compacted soils increased predawn water potentials for plants of pads compared to reference sites, however soil resistance did not have an effect of photosynthesis (Fig. 1.6A, C). In blackbrush, on-pad EC decreased the location effect on PS, without affecting Ψ_{pre} (Fig. 1.6B, D). Thus, higher soil salinity increased soil water availability for sagebrush on pads but diminished the photosynthetic rates for blackbrush on pads.

In the sagebrush community, differences in Ψ_{pre} between pads and reference sites marginally diminished with increasing time since abandonment (p = 0.086) and soil resistance, though not in the blackbrush community. In the blackbrush community, the longer pads were abandoned, surface soils became less dry during summer, compared to reference sites (p = 0.004). In the blackbrush community, location effects on cumulative SR marginally decreased with TSA (p = 0.086), suggesting compaction tended to lessen after abandonment. Density did not change with TSA, suggesting low recruitment rates.

Discussion

Through observing abandoned oil and gas sites in aerial images and with on-theground surveys it is noticeable that arid lands, once denuded and frequented by heavy vehicles, take a very long time to recover. Here we examined to what extent changes in soil properties, particularly the slow reversal of compaction, elevated salt levels, and the negative effects on plant performance, were contributing to barriers created following oil and gas disturbance.

As expected, soils were more compacted on pads than off pads at all measured depths in sagebrush communities and the top 20 cm for blackbrush communities. In both sagebrush and blackbrush communities, cumulative soil resistance to 30 cm was more than doubled on pads, despite differences in native soil resistance (Table 1.2). Other studies also showed that the majority of compaction occurs within the top 30 cm on sandy loams (Kozlowski 1999). High soil resistance can reduce root growth and penetration through hardpan layers and in these water-limited areas, may hinder the initial establishment of seedlings (Alameda and Villar 2009). Mature plants may have roots past the compacted layers or increased root plasticity that can overcome the soil resistance. Above this layer, freeze-thaw cycles, penetration of roots of herbaceous species, and burrowing animals may reverse compaction after abandonment, but may take long periods of time for complete compaction reversal through all soil layers (Webb 2002).

We also expected soil to have higher electrical conductivities (or salinity) on pads than off pads, especially where in arid regions, salt crusts may form more readily without water runoff or leaching (Mason et al. 2011), but found this to be the case only in the sagebrush community (Table 1.2, Fig. 1.3). The reason for the difference is unclear but could be due to differences in soil amendments or patchiness across the pad. For example, when soil is reapplied onto pads after operations, soluble salts present in the soil mixture may leach into the surface soil layers and under previous reclamation criteria, salinity levels tended to be higher (Rutherford et al. 2005, Pennock et al. 2015, Lupardus

et al. 2020). Salt contamination could also result from spillages during extraction operations, which can explain some of the variation in salt levels between sampling points. Elevated soil salinity can be exacerbated by compacted soils, decreasing water infiltration, which prevents water uptake by new seedlings (Lupardus et al. 2020). High salt (Na) concentrations can form crusts on the soil surface, and increased solutes combined with limited water, can be toxic to plants during the germination and seedling phase (Day et al. 2015). Prevention of soil salinity is the best option, however, if not possible, then reducing plant osmotic stress through increasing organic matter composition or leaching salts may improve soil structure.

Despite greater compaction in sagebrush, established shrubs had significantly higher Ψ_{pre} values, suggesting they were less water-stressed on pads and photosynthetic rates were unaffected (Table 1.2A). In contrast to the second hypothesis, increased salinity positively affected shrub photosynthesis on pads (Fig. 1.6B), but the mechanism for this is unclear. It may be related to root water uptake in deeper soil layers, bypassing the highest level of soil salinity. In partial support of the second hypothesis, compaction negatively affected blackbrush Ψ_{pre} values for plants on pads, despite higher Ψ_{pre} for plants on pads (Table 1.2B, Fig. 1.5C). Based on their values relative to soil water potentials above 60 cm, water uptake at the time of measurement occurred below 60 cm depth at the times of measurement, both on and off pad. Thus, differences in Ψ_{pre} were probably related to differences in water availability below the zone of compaction and maximum salinity. Across the sampled pads, comparison of plant abundance on and off pads in the same region found that sagebrush shrubs were 72% less abundant and blackbrush 99% less abundant on pads, respectively. Thus, one explanation for the

improved water status of shrubs on pads was reduced competition for water due to greater inter-shrub distances.

Site variability in compaction and salinity allowed us to examine in more detail whether physiological characteristics were at all related to the degree of soil degradation. In some species, moderate levels of soil compaction can increase root to soil contact allowing for increased water and nutrient uptake but is more likely to impede root growth and water infiltration (Kozlowski 1999, Bassett et al. 2005, Alameda and Villar 2009). Generally, EC values at 0-25 cm were below the threshold level of sagebrush salinity tolerance at 1.8 dS/m¹, however some individual sites showed higher EC values than the threshold tolerance (West 1983a). Commonly, EC values peak at depths of 15-30 cm, due to the movement of solutes with precipitation (Schladweiler et al. 2004). Thus, increasing salinity is predicted to have had negative effects on sagebrush through hindering water uptake from the soil (Yan et al. 2015), and the opposite occurred in this study, where elevated salt levels increased positive location effects on sagebrush shrub Ψ_{Pre} (Fig. 1.6A). This leads to the conclusion that increased salinity did not per se affect established plants, however increased salinity may have negatively affected seedling recruitments, and fewer established seedlings meant less competition for established adults.

In the blackbrush community, no such positive effects in response to soil compaction or salinity were found. In fact, even just slightly more compaction and saline soils diminished positive location effects on Ψ_{pre} and PS, respectively (Figs. 1.5C, 1.6D). In accordance with blackbrush's noted compaction and salt intolerance (Summers et al. 2009, Pendleton et al. 2015). Thus, even though shrubs had higher water potentials on pads, increased compaction may be lowering the degree to how much plant- available soil

water can be taken up. Higher salt levels may have prevented positive location effects on photosynthesis PS. Blackbrush is able to photosynthesize at high temperatures with sufficient soil water uptake, however with small increases in soil salinity, water uptake may be reduced (Summers et al. 2009).

Contrary to what I predicted, in general, both plant physiological status and soil status did not change with time since abandonment except for moderate differences in Ψ_{pre} for sagebrush and slightly less compaction over time on blackbrush pads. Although other studies have seen little changes in pad recovery over time (Avirmed et al. 2015), these results focuses on the plant-soil water dynamics. An unexpected but statistically strong and consistent result was that surface soil water potentials became more similar on and off pad over time in the blackbrush community. Although average soil water potentials were not significantly different due to the great amount of variation, surface Ψ_{Soil} on-pad was on average 20 MPa lower than off pad (Table 1.2 B). This difference would not have affected plant water status, as plants are obtaining water at deeper soil layers (based on a comparison of Ψ_{pre} and Ψ_{Soil}), but it is an interesting indicator of physical changes at the soil surface, perhaps the formation of a soil crust that decreases soil evaporation (Belnap and Lange 2003).

The overall patterns of very limited recovery over time that we observed on disturbed pads are generally consistent with observations reported in the literature (Avirmed et al. 2015, Rottler et al. 2018, Rottler et al. 2019, Lupardus et al. 2020). Other studies have reported other indices or drivers of slow recovery, including soil organic matter (Mason et al. 2011, Minnick and Alward 2015), microbial activity (Mummey et al.

2002), microclimate (Barnard et al. 2019) and invasive species competition (Davies et al. 2011, Svejcar et al. 2017) that can affect shrub recruitment.

Restoration Implications

This study has demonstrated that pad locations are not per se overtly hostile to adult blackbrush and sagebrush shrubs, but there is likely to be a severe recruitment bottleneck on pads that maintains low shrub densities for decades after abandonment (Meyer and Pendleton 2005, Alameda and Villar 2009, Germain et al. 2018). Assuming all established plants emerged post abandonment, plants that did manage to establish may have taken advantage of rare cracks through the compacted layer to reach uncompacted and uncontaminated soil water sources. Although compaction and salinity are unlikely to be the only factors that inhibited recruitment, however based on other study results, it can be suggested that the reported levels of compaction and salinity were substantial enough to have had a negative impact on seedlings (Kozlowski 1999, Bassett et al. 2005, Flynn and Ulery 2011, Gasch et al. 2014, Yan et al. 2015). Treatments that alleviate subsoil compaction include loosening soils through tilling or ripping, adding organic or coarse material and reducing grazing (Kozlowski 1999, Bolling and Walker 2000). Decreasing saline soils without amendments may require longer periods to allow precipitation to leach solutes through the soil, which may result in higher salinity levels in lower root zone layers (Flynn and Ulery 2011, Day et al. 2015). However, if seedlings are able to establish, they may tolerate increased saline levels in lower soil layers. Additionally, "islands" for seed recruitment may enhance the ability of the pioneer plants to gain cover on pads while the general soil conditions are still poor (Eldridge et al. 2012, Minnick and Alward 2012, McAdoo et al. 2013, Hulvey et al. 2017, Lupardus et al. 2020). However,

the presence of mature shrubs, as seen in this study, provides evidence that the absence of nurse plants, are not prohibitive obstacles to recruitment, but without them recovery could take longer (Padilla and Pugnaire 2006). Therefore, the creation of macropores through the compaction layer could have positive effects on seedling establishment. Ideally, such methods would be used in conjunction with seed applications or the planting of nursery seedlings.

Even without the challenge of poor soil quality, return to pre-disturbance shrub density is naturally slow in both communities, upwards of 100 years, if not reclaimed (Avirmed et al. 2015, Rottler et al. 2018, Rottler et al. 2019, Lupardus et al. 2020). Wyoming sagebrush recruitment fluctuates interannually, based on available resources, and seeds often fall within 1m of the canopy, limiting dispersal (Young and Evans 1989, Meyer and Monsen 1992). Blackbrush recruitment requires two successive years of above-average precipitation, followed by mast seeding, and subsequent burial by rodents, where germination is limited by moisture and predation (Meyer and Pendleton 2005, Pendleton et al. 2015). Although slow recovery is common, this suggest that disturbances on abandoned oil and gas pads may have long lasting effects on late-successional shrub communities that should be progressing towards recovery (Rottler et al. 2019). Thus, hostile soil conditions on pads might be hindering survival during the phase of development, (germination, seedling growth) in which plants depend on water stored in the top 30 cm of soils. Restoration methods that bypass these initial recruitment limitations may allow for a quicker establishment of shrub cover. For example, planting shrubs from larger containers or using bareroot stock plants that have deeper roots may bypass the initial seedling stage mortality, which occurs at the highest rate during the first year (Dettweiler-Robinson et al. 2013, McAdoo et al. 2013, Clements and Harmon 2019). If those plants survive and produce seeds, there is still a high probability of low germination, but the odds may increase with greater mature shrub establishment.

Determining potential barriers to plant establishment and growth based on microsite differences can inform future decisions on restoration methods in oil and gas pad revegetation.

II. RESTORATION TREATMENT EFFECTS ON PLANT STOCK SURVIVAL OF WYOMING BIG SAGEBRUSH AND BLACKBRUSH ON ABANDONED OIL AND GAS PADS

Abstract

Ecological restoration in arid lands of abandoned oil and gas pads has had limited success but can be improved by considering site- and species-specific barriers to restoration and developing cost-effective techniques that overcome those barriers. I examined the efficacy and economic tradeoffs of different restoration methods and their combinations in establishing Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis) and blackbrush (Coleogyne ramosissima) on abandoned oil and gas exploration pads in Utah, USA, along a north-south biotic and abiotic gradient. Soil surface treatments (i.e., decompaction by drilling holes through compacted soil layers, digging soil depressions), herbivore deterrents (debris cover, wire cages), and three types of plant propagules (greenhouse raised transplants, locally harvested wildlings, and seeds) were examined. Finally, due to the different costs associated with treatment and plant material options, I also tested whether the preference ranking of various methods in terms of total cost differed from the preference ranking of methods based on survival rates. Northern populations had higher first-year survival in sagebrush communities and there was no effect of decompaction at any location. For sagebrush, no seeded plants survived the first year and wildlings did not significantly differ in transplant survivorship in both northern and southern populations. In northern locations, soil depressions did not affect transplant survival and the effect of added debris was negative. In southern locations, soil depressions had a significant positive effect on transplant survival, while debris had a marginally significant positive effect. For blackbrush, no wildling survived

in northern locations, and few survived in southern locations, while emerging seedlings survived in both locations. In both northern and southern locations, depression and debris treatments had significant or marginally significant positive effects on transplant survival. Seedling emergence and survival in both the north and south was strongly increased by cages while the addition of debris decreased emergence and depressions had mixed effects on emergence and survival. Overall, sagebrush wildlings had the highest first-year survival and were associated with the lowest cost of restoration, regardless of geographic location. Blackbrush transplants in the depression & debris treatment had the highest first-year survival in both north and south, nonetheless, seeds in cages were more costeffective. My experiments demonstrate that while ecologically well-founded treatments can improve the survival of transplants, far greater restoration success can be achieved through the appropriate selection of plant propagules. Wildlings were not feasible in blackbrush, likely because vital taproots cannot be successfully extracted during harvest, but wildlings were a successful source material in sagebrush. By contrast, sagebrush did not establish well from seeds but blackbrush seeds did emerge and survive when caged. Furthermore, geographic location did not affect the best economic choice of plant material. These results question the use of costly transplants in the restoration of oil and gas pads. By virtue of being denuded islands in a sea of healthy vegetation, source populations for wildlings are generally close and herbivores may be disincentivized to visit patches of low vegetation cover.

Introduction

One of the great challenges in ecological restoration is the successful reintroduction of native plants, which requires significantly reducing natural and

manmade barriers to establishment and seedling survival (Munson et al. 2011b, Avirmed et al. 2015). Barriers to plant establishment accumulate when land has been used for other purposes, such as oil and gas extraction, mining, and recreation (Pocewicz et al. 2011, Copeland et al. 2017). Under these land uses, recruitment barriers include decreased shelter from harsh climate conditions, increased herbivory, and altered edaphic factors. For example, soil compaction is especially common on abandoned oil and gas pads (Maxwell 2021, Ch. I), which increases bulk density, reduces both soil water storage capacity and infiltration rates and may also inhibit root growth, if radicles do not exert enough pressure to expand into compacted soils (Kozlowski 1999, Webb 2002). Together, these effects reduce plant water availability and increase physiological stress (Kozlowski 1999, Webb 2002). Barriers to establishment and seedling survival can be mitigated by applying a range of restoration techniques, for example, reducing soil compaction through applying topsoil or mechanically decompacting the soil (Webb 1982, Webb 2002). While soil compaction can be reversed naturally by repeated freezethaw cycles, it may take several decades for compacted desert soils to return to a habitable state (Webb 1983, Taylor and Barr 1991, Kade and Warren 2002). Some of these strategies can be implemented at minimal effort or cost, while others involve substantial investment of time and resources (Copeland et al. 2018). Thus, identifying the "best restoration methods", which varies by agency may be defined by vegetation cover, species composition, or plant survival. Best methods for any given case require a careful weighing of costs relative to benefits over time, which depends on agency budget limitations. Although research on cost-benefit considerations is growing, in restoration

research, studies considering both ecological success and monetary costs are still relatively rare (Boyd and Davies 2012, Kimball et al. 2015, Copeland et al. 2018).

In arid lands, moisture deficit is arguably the most detrimental factor with respect to seedling survivorship and is typically unpredictable in any given year. In cold deserts, such as the Colorado Plateau, seeds usually germinate in winter or early spring when soil water is at a maximum, but seedlings rarely survive the first summer dry season (Comstock and Ehleringer 1992, Meyer and Pendleton 2005). Surviving the critical first drought season requires vigorous growth, particularly of tap roots during the spring augmented by above-average rainfall through summer (Schwinning et al. 2005a). Within the Southwestern United States, areas at lower latitudes and elevations usually have lower precipitation and higher temperatures than higher latitudes or elevations, suggesting that throughout the ranges of many plant species, establishment and early survivorship is relatively more constrained by harsh climate conditions on the drier end of the climate spectrum and relatively more constrained by granivory and herbivory on the opposite end (Hereford et al. 2002, Schwinning et al. 2008). For example, in blackbrush restoration, caging seeds increased survivorship at higher elevations and in proximity to nurse plants at lower elevations (Jones et al. 2014).

Restoration methods often address the problems associated with low soil moisture through supplemental irrigation, reducing interspecific competition with nonnative species through herbicide application and reducing herbivory by use of exclusion cages (Davies et al. 2013, Jones et al. 2014, Brabec et al. 2015, Grant-Hoffman and Plank 2021), but the application of one or more of these methods may not consider how the effectiveness of methods may change with geography and/or climate range. Other

techniques aimed at improving water supply involve the modification of the soil surface in an attempt to locally increase water infiltration and run-on or to shade the soil surface to reduce soil evaporation where seedlings grow (Chambers and MacMahon 1994). For example, small depressions dug in the soil can increase local accumulation of snow or rain (Evans and Young 1987, Chambers 2000, García-Ávalos et al. 2018). As well, depressions can entrap native seeds, as would naturally occur in soil crevices, near rocks or in animal burrows (Reichman 1979, Eckert et al. 1986). Other surface modifying techniques include adding surface mulch or debris (dead shrubs, grass, rocks), which may provide nutrients and surface protection, decrease evaporation and erosion, and hide seedlings from potential predators (Rotundo and Aguiar 2005, Stoddard et al. 2008, Minnick and Alward 2012).

A second significant factor which limits restoration outcomes is seed and seedling predation (Brown et al. 1979, Meyer and Pendleton 2005). If seeds escape granivory, by the local granivore community, rodents and lagomorphs can then consume emerging or young woody plants, before they develop secondary plant compounds that deter herbivory (Pendleton et al. 2015). Seed predation can be reduced by burying seeds in soil and herbivory can be reduced by protective caging or fencing (DeFalco et al. 2009, Abella et al. 2012). If these measures are not achievable, rock piles or coarse, spikey debris may be used to deter herbivores or decrease plant apparency to foragers (Belnap and Sharpe 1995). In some cases, planting seeds under adult shrubs or "nurse plants" may facilitate seedling growth (Padilla and Pugnaire 2006). Alternatively, it is possible that co-seeding or planting additional fast-growing woody plant seeds may outcompete target species for available nutrients and moisture (Ralphs 2011).

Another approach to restoration is to bypass the most vulnerable seed and/or early seedling stages by transplanting older plants, such as greenhouse raised seedlings or bareroot stock, harvested from nursery grown adult plants. Another less studied option includes transplanting wildlings, which are young plants or root stock harvested in the wild, typically from undisturbed areas in the vicinity of the restoration sites. Although this latter method adds labor costs for finding, collecting, and moving the plant materials, costs are lower than raising seedlings in a greenhouse, while the survivorship of wildlings and greenhouse transplants may be similar (Shumar and Anderson 1987, McAdoo et al. 2013). Furthermore, locally collected wildlings may also be adapted with more-developed root systems. However, quantitative studies on wildling transplant success are rare and have only been conducted on small scales (Shumar and Anderson 1987, McArthur and Stevens 2004, McAdoo et al. 2013).

Recovery plans including a combination of plant propagule types and soil modifications may reap unequal benefits for different species across climate ranges. For example, in northern populations, survival rates may increase for depressions and debris treatments, but given reduced overall low water limitation (higher winter precipitation and colder temperatures), debris by itself may sufficiently deter herbivores to constitute the most cost-effective method of increasing survival rates. Conversely, for southern populations, which face severe water limitations (lower precipitation and greater year-round temperatures), the combined treatment of soil depressions plus debris cover could increase survival rates in a cost-efficient manner. Further, germinating seeds and resulting seedlings may have far greater mortality from granivory and herbivory especially in northern ranges, respectively, than transplants and wildlings, irrespective of

location. Sagebrush wildlings and greenhouse transplants might have similar mortality rates as both are similarly sized during outplanting. Finally, while it may be beneficial to implement all known techniques for improving microsite conditions, the beneficial effects per method on survival may not be additive while their costs are. Therefore, on a limited budget, fewer restoration techniques applied to a greater area may optimize the intended outcome of widespread shrub reestablishment.

There is typically a tradeoff between those methods that improve restoration outcomes and the feasibility and cost of application over large areas. For example, controlling invasive species before planting on a large scale may be much more expensive than seeding or transplanting alone, but could reduce competition with native species(Munson et al. 2015). However, the cost-benefit ratio of a restoration effort can only be evaluated after sufficient time has elapsed which is required to assess the mortality rate for introduced propagules. For example, the per-acre cost of broadcasting seeds is initially much less than outplanting greenhouse grown transplants, but it is unclear whether the cost per surviving plant will be lower for the seeding method, as illustrated by Wyoming sagebrush (Artemisia tridentata ssp. wyomingensis). For example, commercially grown Wyoming sagebrush plants initially cost \$2.00-\$10.00 per plant, depending on size. Assuming survival rates of 10%–65% depending on size, time of planting, climate, and soil type (Kleinman and Richmond 2000, McAdoo et al. 2013, Clements and Harmon 2019), establishment of 100 seedlings would minimally cost \$2000, or \$20 per plant. By comparison, a 1lb. bag of Wyoming sagebrush seeds may cost \$20 and contain approximately 2 million seeds, but each seed may have less than a 1 in 10,000 chance to germinate and survive the first year. However, even if just 20 plants

establish, the per-plant cost would be \$1 (Lysne and Pellant 2004, Lysne 2005). Other dominant shrub propagules may not be commercially (or locally) available either as seed or transplant, which would increase their per-propagule cost, because seeds would have to be collected from the wild and transplants produced at a smaller scale. Furthermore, species differ in intrinsic survivorship and respond to restoration interventions differently. For example, blackbrush (*Coleogyne ramosissima*) has a lower first-year survivorship than sagebrush without intervention (Abella et al. 2012). However lower survivorship in the absence of intervention suggests the possibility of a greater response to intervention. Thus, it is not clear what specific intervention could be most effective for a given species as successful strategies for one species may not be as successful for other species, even in the same climate. Best practices must therefore be fine-tuned at the species and geographic location scale according to efficiency, cost, and propagule type.

Multidimensional cost-benefit analysis such as those conducted by Boyd and Davies (2012), and Powell et al. (2017) are critically needed to evaluate alternate restoration methods and combinations. However, state and federal agencies typically adhere to the concept of 'best management practice', commonly defined as a method that has proven to reliably and quickly lead to a "desired result" (Kimball et al. 2015, Winkler et al. 2018). Moreover, land-management agencies that are engaged in ecological restoration often follow different guidelines, have different management objectives, and often variable statements of what constitutes a desired result (e.g., restoring shrub communities to any degree with respect to plant cover in the first three years may be considered a desirable result). For example, the Bureau of Land Management (BLM) has the "Gold Book" which includes guidelines for specific restoration treatments, such as

salvaging topsoil and revegetation with a seed mix of native plant species and other fast-growing perennials, but little information describing effective techniques for ecological communities composed of long-lived, woody perennials and the costs and/or time associated with implementing these meeting guidelines and meeting goals (Agriculture 2007, Svejcar et al. 2017). Therefore, while there are numerous restoration tools and methods available across varying guidelines, there is no clear framework to determine which techniques (or combination thereof) would produce the highest number of surviving plants at the lowest cost.

To address this knowledge gap in ecological restoration, the overarching goal for my research is to develop a generalizable decision support framework, based on population-based measures of success (e.g., first-year propagule survival), area-based costs (e.g., USD per acre) and an ecologically based spectrum of restoration methods that are sensitive to climate and edaphic constraints, community characteristics and the autecology of the target species. Here, I develop such a framework through experimentation with two dominant shrubs on the Colorado Plateau.

Herein, our objectives are to examine for two prominent Colorado Plateau Desert shrubs, Wyoming sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* [Beetle & Young] Welch) and blackbrush (*Coleogyne ramosissima*) the differences in survivorship of three propagule types (seeds, transplanted seedlings, and wildlings), as a function of three soil surface mitigation treatments (decompaction, soil depressions, adding debris, or herbivore exclusion cages in the case of direct seeding). We implement the same experimental design for each of these species which are distributed across a latitudinal climate gradient. I focused on testing the following central hypotheses:

- 1) Decompaction will have positive effects at all locations for both species.
- 2) In general, the addition of debris in northern populations and the addition of depressions in southern populations will have the greatest impact on survival rates compared to no treatments, irrespective of propagule (transplant or seedling).
- 3) Transplants will have greater survival rates than wildlings since wildlings may be injured in the extraction. Both transplants and wildlings will have higher survival rates than emerged seedlings, based on their initial size advantage.
- 4) Seedling emergence and survival will strongly depend on the presence of cages.
- 5) The combination methods producing the greatest survival will not necessarily be the combination of methods that minimizes the cost of restoration and best practice may be species- and location-specific.

Methods

Site Selection

I obtained research permits for six abandoned oil and gas exploration pads, (henceforth sites) in Utah, U.S.A., all of which had little to no shrub presence on pads, irrespective of time since abandonment (Table 2.1). Precipitation and temperature varied across locations (Table 2.2). All sites were located on either BLM or School and Institutional Trust Lands Administration (SITLA). All sites were situated in open rangeland with access to livestock or recreation.

Plant Materials

The seeds used to raise seedlings in the greenhouse were collected by USGS collaborators in fall 2017 for sites NS1 and SS1 (i.e., northern, or southern sagebrush 1, respectively), and summer 2018 for sites NB1, NB2, SB1, and SB2 (i.e., northern, or

southern blackbrush 1, 2, respectively). The seeds used for direct seeding were collected in fall 2017 (NS1 and NS2), summer 2019 (NB1, NB2, SB1, and SB2) and, then stored at 4-5 °C until used for planting (Table 2.1). Seeds were collected and outplanted near their respective collection locations

Wildling plants, defined as naturally occurring juveniles of ca. 10-30 cm above-ground height, were collected from areas adjacent to the oil and gas exploration pads. Plants were harvested using a sharpshooter shovel to lift as much of the taproot as possible. Plants were stored in plastic bags and replanted within approximately two hrs. after excavation.

Greenhouse Procedures

Sagebrush transplants were raised at the Texas State University greenhouse, San Marcos, TX. Blackbrush seedlings were raised in a greenhouse in Boulder City, NV.

Sagebrush seeds from the northern range were germinated September–December 2018 and November 2019 in a growth chamber at 10 °C for 10–15 days, before transplanting individual seedlings into plant bands (n = 400). Seeds from the southern populations were germinated April–December 2018 and November 2019 and individual seedlings were placed into plant bands[©] (n = 1000) (Monarch Manufacturing, INC, Salida, CO, USA with dimensions 30.5L x 30.5W x 10.2H cm). Southern population blackbrush seeds were germinated December–March 2018 (n = 500) and northern populations from December–March 2019 (n = 500), both in greenhouse conditions. At both greenhouses, plant bands were filled with a 3:1:1 mix of sand, manure compost and perlite. Each seedling was tagged with a unique ID number and initial root crown diameters were measured to track growth of individual plants. One week before outplanting, seedlings

were moved outdoors to acclimatize and then transported to their respective ouplanting locations in Utah at three different times, depending on permit, volunteer, and transplant availability (Table 2.1).

Experimental Design

The field experiment consisted of a split-plot block design, where blocks were replicated three times on all pads (note that two blocks were planted in SS1 in the first spring and one block was planted the second spring; Table 2.1). Blocks consisted of a 17 m x 8 m rectangular area divided into two halves, one of which was randomly selected for the decompaction treatment (Fig. 2.1). The two halves were further split into two areas: a 8 m x 8 m area for the transplant experiments and a 1 m x 8 m strip for the direct seeding experiment. Each 8 m x 8 m square plot was subdivided into four quadrats of equal area, which were randomly assigned to one of four treatment combinations: control (no further treatment), depression, debris cover, depression & debris cover. Transplants were planted into all treatment combinations, but wildlings were only planted in the control plots on both the decompacted and un-decompacted sides of the block (Fig. 2.1).

The strips at each block that were set aside for the seeds were subdivided into four 2 m x 1 m plots (Fig. 2.1), to implement the same four treatment combinations used in the transplant experiment. However, within each plot, three additional treatments were implemented: no additional treatment, an herbivore exclusion cage (made of wire mesh), and a third treatment in which the target species seeds were mixed with seeds of a common subshrub, which may also be considered a nurse plant species: either broom snakeweed (*Gutierrezia sarothrae*) or rubber rabbitbrush (*Ericameria nauseosa*),

depending on seed availability. Snakeweed and rabbitbrush were purchased commercially (Granite seed).

Depressions of dimensions 40 cm x 80 cm x 10 cm for transplants or 10 cm X 10 cm x 5 cm for seed (W X L X H) were excavated within which transplants or seeds would later be planted. For the debris treatment, dead woody litter, and forbs (as available on each site) were placed around the transplants. In a final step, all plants in all treatments were protected in ca. 10 cm tall conical structures built from dead branches and *Salsola* sp. (tumbleweed), to discourage herbivory.

The decompaction treatment was applied after outplanting and was implemented by using a jackhammer (Bosch, 35 lbs.) with a pointed bar attachment to create 20 cm x 5 cm (depth x diameter) holes in the soil throughout the decompaction side of the block in a ca 1 m grid pattern. Apart from penetrating past the compacted layer, we expected some benefit from the vibrations to create micro fissures and loosen the soil.

Outplanting Procedures

Since transplants were raised as a series of cohorts in greenhouses, they differed in age at the time of outplanting. Southern populations of blackbrush and sagebrush were 3–9 months old, northern populations of blackbrush were 7–9 months old, and northern populations of sagebrush were 3–15 months old. To control for the effects of age and size variation at the plot response level both transplants and wildlings were stratified into four size classes (based on root collar diameter) and distributed between plots so that each plot approximately equal numbers of transplants per size class. Plantings were conducted in March 2019, November, and December 2019, followed by the last planting in March 2020 (Table 2.1). Due to the lower availability of blackbrush transplants and northern

sagebrush transplants, only eight individuals were transplanted into each quadrat clustered in pairs of two (i.e., two per depression), compared to 16 transplants for the southern sagebrush pad, clustered in pairs of four (i.e., four per depression; Fig. 2.1). Due to high herbivory within northern blackbrush sites the first 30 days, additional transplants were subsequently planted to replace original transplants (for total number of transplants per site, see Table 2.1).

Transplants were slipped from bottomless bands with the entire root system and as much of the greenhouse soil mix as possible into 30 cm deep holes dug using a 12-inch soil auger and carefully backfilled with native soil, which previously had been wetted and crumbled to facilitate root-soil contact. Wildlings were planted in the same way as greenhouse transplants using local soil. Wildling root collar diameters were measured at the time of outplanting (measured with Mitutoyo Corp. digital calipers, in mm).

Sagebrush seeds were spread on soil surface and hand raked into soil (n = 1000 seeds per replicate). Blackbrush seeds were buried in caches 2 cm - 3 cm below the soil surface (n = 20 seeds per cache). Snakeweed and rabbitbrush seeds were spread on soil surface and hand raked into soil (n = 200 seeds per replicate).

Monitoring

Transplants and wildlings were marked with unique tag ID and their locations within blocks were mapped. At each site, a rain gauge was installed to monitor precipitation (Tru-chek rain gauge) and at least one Ibutton was suspended (approx. 0.5 m above ground) to monitor hourly air temperature and humidity (iButtonLink Technology). Environmental data were also collected from PRISM Climate Group for each of the outplanting locations to compare monthly and yearly precipitation and

temperature among sites (Northwest Alliance for Computational Science & Engineering, Oregon State University) (Table 2.2). Site visits were conducted between May 2019 and April 2021, where each site was visited up to eight times depending on accessibility. During each visit, each plant was scored as live or dead; if alive, plants were visually ranked for percentage of brown leaves and percentage of canopy affected by mammalian herbivore damage based on severed twigs or stems with tooth marks (range: 0 = no damage, 1 = minimal branches browsed, 2 = several branches browsed, 3=many branches browsed, 4 = only stump remains, 5 = plant missing). Root collar growth was measured for living plants (Mitutoyo Corp. digital calipers, in mm). Seedling emergence and survival was monitored up to four times between March 2020 and April 2021.

Statistical Analyses

Transplant survival by treatment

The two species were examined separately, as were the southern and northern locations since they were planted separately and from different greenhouse cohorts. From exploratory data analysis to test the first hypothessis, I determined that the decompaction treatment was not significant across experimental designs and henceforth this treatment was omitted from analyses. Additionally, interactive treatment effects were not significant (possibly due to limited sample size) and were not included in the analysis.

Within species and geographic location, I conducted Kaplan-Meier survivorship curves (R package, 'KMsurv', 'survminer', 'survival') to analyze survivorship over time from planting (up to 1.5 years after planting) for both depressions and debris treatments.

To determine treatment effects on survival for the second hypothesis, I directly compared survival at the end of the study using a generalized linear mixed effects model

(GLMER, R package 'lme4') with a binomial distribution based on the status at approximately 1.5 years after planting (0 = live, 1 = dead) as the response variables, with block as the random factor and the two categorical treatment factors (depression (1 = yes, 0 = no), debris (1 = yes, 0 = no) nested within block. I used size class as a covariate to account for initial variation in age and size at the time of transplanting.

Transplants versus Wildling survival

Species and geographic locations were analyzed separately. I conducted Kaplan-Meier survivorship analysis to compare the survival of transplant and wildlings in the control treatment for each species and each geographic location up to 1.5 years after planting. To test the third hypothesis, I directly compared survival at the endpoint of the experiment using a GLMER with a binomial distribution based on the status at the final visit approximately 1.5 years after planting (0 = live, 1 = dead) as the response variable, propagule type as a fixed factor, and block as a random factor.

Seedling emergence and survival by treatment

No sagebrush seeds germinated in any plot. No subshrubs (snakeweed or rabbitbrush) emerged in blackbrush communities and therefore was included in the control treatment (i.e., no cage) to double the sample size. To test the fourth hypothesis, I conducted a linear mixed effects model for each location with proportion of seeds emerged or the survival of emerged seedlings as a function of cage, depression, and debris all treated as fixed factors, and interactions between cage and depression and cage and debris, and block as random factors. Cage presence, depression and debris were nested within block.

Costs are species- and location-specific

To determine the potential cost-benefit tradeoffs of the various treatments and plant propagule types for the fifth hypothesis, I developed a cost table, which included per-propagule cost, per-propagule survival, and estimated associated cost items. I assumed a fixed target density for first-year survivors to estimate the total restoration cost per land area, which I then ranked to determine the most cost-effective restoration method based on results of this experiment. However, target densities as well as cost factors can easily be modified to custom fit different applications. Although no sagebrush seeds emerged, I added an example of a low survival rate based on a previous study, with no extra treatments to determine an associated cost.

Assumed throughout was the price of a worker making \$17 per hour, which is calculated with time in the following set of variables. (A) The cost of each propagule was estimated by the amount of time it took to collect the number of seeds needed to establish 1 plant per square meter, time propagating 100 transplants in the greenhouse, and time to collect 48 wildlings per location in the field. (B) Survival per propagule was calculated as the proportion survived for one year out of the total planted. (C) The target density was assumed as 10 plants per 10 m². (D) The propagules required to achieve target density was calculated as (C)/(B). (E) The propagule cost per 10 m² at the target density (D) was calculated (A)*(C). (F) The ground preparation costs were based on time to implement each treatment for the target density and cages were assumed to be \$1 per unit. (G) Transportation costs were calculated in equation (1), where the carrying capacity was assumed that a large vehicle can carrying up to 1000 plants and the cost would be \$100 per vehicle. It was calculated as:

(eq. 1) $\frac{\text{Propagules required to achieve target density}}{\text{Carrying capacity of vehicle}} * \text{Cost of vehicle}$

(H) The total costs per 10 m² were calculated as: (E)+(F)+(G). (I) The total costs per pad calculated how many plants would be need across a 1-acre pad, assuming the target density above: (H)*40.

Results

Transplants

Overall transplant survival in sagebrush after the first year was 44% in the northern populations and 27% in the southern populations. Larger size class plants had generally greater survivorship, but the effect was more pronounced in the southern compared to northern populations (Table 2.3a). Northern sagebrush had significantly lower survival in the debris treatment and southern sagebrush survival marginally increased with debris (Fig. 2.3a) but significantly increased with depressions (Table 2.3a; Fig. 2.2a). Overall blackbrush transplant survival was 22% in northern population and 16% in the southern populations, and survival increased with larger transplants (Table 2.3b). In contrast to northern sagebrush, northern blackbrush survival increased significantly for the depression treatment (Table 2.2b; Fig. 2.2b) and both depression and debris treatments were significantly positive in southern populations (Table 2.3b; Fig. 2.3b).

Transplants versus Wildlings

Overall, sagebrush wildling survival was 75% in the northern population and 25% survival in the southern populations. There were no significant differences in survival

between transplants and wildlings in the control plots for northern or southern populations (p = 0.116 and p = 0.380, respectively; Fig. 2.4a). Wildling survival did not differ between size classes in either population. Blackbrush wildings were significantly lower in the south (p = 0.01), and there were no survivors in the northern populations (Fig. 2.4b).

Seed Emergence and Seedling Survival

No sagebrush seeds germinated or emerged. In the northern locations, 80% of blackbrush seeds that emerged also survived across treatments, and only 19% of those seeds that emerged survived in the south. In both blackbrush populations, cages significantly increased both seed emergence and survival. In the north and south, the interaction between debris and cages significantly decreased seed emergence, however the interaction between depressions and cages significantly increased seed emergence in the south but decreased seedling survivorship (Tables 2.4 and 2.5).

Cost Table

The costs of planting greenhouse transplants for both sagebrush and blackbrush was much higher than outplanting wildlings or seeds, respectively. Northern sagebrush was more cost-effective when outplanting wildlings and costs increased with additional surface treatments, where transplants with depressions and debris were most expensive (Table 2.6a). Although no sagebrush seeds emerged in this study, an example of surviving seedlings from another study (Lysne and Pellant 2004) suggests that at low survival rates, sagebrush seeding costs would be lower than transplants but not wildlings. However, the chances of survival are minimal in most years when seeding sagebrush. The least expensive option for southern sagebrush was wildlings followed by transplants

in depressions, and the no treatment option was the most expensive per surviving plant (Table 2.6b).

Northern blackbrush was most cost-effective when seeds were planted in depressions within cages. Costs rose sevenfold when planting greenhouse transplants within depressions and adding debris, but at survival increased 3x with this approach (Table 2.6c). Southern blackbrush was most cost-effective when planting seeds within cages, followed by wildings, and transplants with depressions and debris (Table 2.6d). However, transplants with depressions and debris had a higher survival rate than seeds or wildlings.

Discussion

Western North America oil and gas disturbances has affected over 3 million hectares in the past two decades, and the need for reclamation and restoration is critical, however it is unclear what techniques will be both successful across the landscape and cost effective (Allred et al. 2015, Rottler et al. 2018). Restoration is both difficult to gauge and difficult to achieve, and is limited by climatic conditions, plant establishment and soil conditions. I wanted to examine the effects of implementing restoration treatments that bypass the initial barriers to plant establishment, such as compaction, water availability, and herbivory or granivory. Here I tested different soil mitigation techniques (soil depressions, adding debris, decompaction) on the establishment and survival of two dominant shrub species, Wyoming sagebrush and blackbrush, and three plant propagule types across a geographic gradient on abandoned oil and gas pads across the Colorado Plateau.

Surface Treatment Effects

Although restoration treatments significantly affected transplant and seedling survival, the specific predictions of the first hypothesis were generally not supported. For example, decompaction in and of itself did not increase survival for any propagule type. However, it is possible that the effects of decompaction could be amplified in future years by freeze thaw cycles, improving infiltration and water availability in deeper soil layers.

Furthermore, I predicted that soil depressions would be more beneficial in drier southern locations but instead found that depressions increased transplant survival across all blackbrush populations and for southern sagebrush. Counterintuitively, depressions increased the emergence of seedling but subsequently decreased survivorship in southern locations. Depressions can increase water infiltration into the soil because they accumulate precipitation and snowfall, allowing for deeper roots to uptake soil water (Chambers 2000). Even in drier years, soil depressions may increase water availability. In 2019, spring and summer precipitation was higher than in 2020 (Table 2.2), suggesting that the pads that were planted in spring 2019 had advantage over those planted the following fall or spring.

I also predicted that northern locations would benefit more from the addition of debris than southern locations. Instead, debris negatively affected transplant survival in sagebrush and only marginally increased blackbrush survival in northern regions.

However, in the southern locations, debris marginally increased survival for sagebrush and significantly increased survival for blackbrush transplants. Debris also negatively affected emergence rates of caged blackbrush seedlings in northern and southern

populations (Table 2.4) but this did not translate into significant positive effects on seedling survival (Table 2.5). The variable effect of debris cover suggests that it affected survival predominantly through shading, with too much cover hindering the development of northern populations, but potentially reducing stress levels in southern populations.

Regardless of treatment, the size at which plants were transplanted and block had pervasive effects on survival. Larger transplants can survive the initial changes in soil conditions, as their roots are more established (Herriman et al. 2016, Clements and Harmon 2019). Older seedlings may also produce greater concentrations of secondary compounds, deterring predation (Provenza and Malechek 1983, West 1983a). The block effects highlight the difficulty of improving survival odds through ground preparation in desert restoration, given the high degree of spatial and individual variability, which may often dominate restoration outcomes, even in the most well-planned experimental designs (Aguiar and Sala 1999, Boyd and Davies 2012, Minnick and Alward 2012).

Transplants versus Wildlings

The hypothesis that wildlings could be a viable alternative to greenhouse grown transplants was generally supported for sagebrush but rejected for blackbrush, where wildlings exhibited poor survival in comparison with greenhouse grown emerged seedlings. This result suggests that small blackbrush wildlings while they may be older and have well-developed root systems, are too large to be successfully extracted and thus not able to survive transplanting (Pendleton et al. 2015, Scoles-Sciulla et al. 2015). Sagebrush wildlings and transplant survival did not differ significantly differ in either location. Sagebrush wildlings were easy to collect at various sizes and ages and may have had more intact roots when transplanted, resulting in similar survival rates to greenhouse

grown transplants (Shumar and Anderson 1987, McArthur and Stevens 2004).

Interestingly, counter to long term climate records, the northern sagebrush location had lower precipitation and higher temperature maximums than the southern site, indicating that there may be other factors contributing to survival (Table 2.1).

Cage Effect for Seeds

As hypothesized based on previous experiments (Jones et al. 2014), successful blackbrush restoration from seeds required granivore/herbivore exclusion cages. However, sagebrush seeds did not germinate or establish with or without cages confirming the results of (Brabec et al. 2015, Grant-Hoffman and Plank 2021) who found that seeding sagebrush had limited success in restoration treatments, due to short term seed viability or insufficient abiotic conditions. By contrast, herbivore species are a primary determinate of seedling establishment in blackbrush supporting the findings of (Meyer and Pendleton 2005).

Survival Rankings versus Cost Rankings

Under a scenario where the effects of individual restoration interventions have additive costs but nonadditive effects on survival, simpler treatments generating lower survival may be more cost-effective. Secondly, low per-propagule costs could overcome low survival odds in the cost calculations. With some caveats, this hypothesis was supported. The use of sagebrush wildings lowered restoration costs by an order of magnitude in both the north and south, compared to the next best cost option with respect to similar survival (transplant without further treatment). However, since treatment effects were not implemented with wildlings, it is possible that additional treatment effects could have increased wilding survival and lowered the cost, though unlikely given

the moderate magnitude of treatment effects on transplant survival. Since there was had no seed emergence, we were unable to attach a cost to restoration by seeding. However, considering the low seeding survival rates observed in other studies (Lysne and Pellant 2004, Brabec et al. 2015), costs are likely magnitudes higher compared with establishing wildlings, but this may depend on the year and the viability of seeds.

Based on comparative survival across transplants and caged blackbrush seedlings, the control treatment was approximately as cost-effective or better than the more elaborate depression and debris treatments (Table 2.6). Overall, however, the choice of propagule was the most consequential factor in the cost calculation. Using caged blackbrush seeds lowered the restoration cost approximately sevenfold (north) and fourfold (south) compared to the best transplant option and additional treatment had either no effect on cost or increased the cost of restoration. For blackbrush, the relatively small differences between survival of caged seedlings and transplants favored direct seeding as the preferred restoration option. In contrast, for sagebrush, the high survivorship of wildlings combined with the ease of onsite harvesting dominated the cost calculation.

Restoration Implications

The costs of restoration are difficult to assess when time to recovery takes many years. Projected long recovery times have been shortened by choosing fast growing grasses and forbs for seed mixes and outplantings, even in shrublands (Svejcar et al. 2017). Forbs and grasses establish ground cover quicker than shrubs, but are often the first to die during drought, thus returning the restoration area to the bare, erosion-prone state prior to restoration (Munson et al. 2011b, Winkler et al. 2019). In order to begin the

trajectory of pad recovery through restoration, more funds and treatment efforts could be invested upfront to restore a plant community of drought-tolerant species. However, with a higher upfront cost comes more responsibility to use monetary resources wisely, so that the largest amount of land can be revegetated. This requires a framework that integrates biological and economic factors and variables (Allen 1995, Schuman et al. 2005, Andersen and Coupal 2009, Powell et al. 2017).

To my knowledge, there are no tools available that would help land managers determine how to guide the investment of limited funds, where establishment success and cost calculations vary with propagule type, species ecology and climate region within the species' range. Here, I demonstrated how even a low-precision approach to calculating the costs of restoration related expenses, combined with experimentally determined perpropagule survival odds, can inform restoration recommendations. The methodology is generalizable and could be improved by further research that considers stochastic annual survival odds, market trends and differences in the cost structures of restoration conditions. For example, it is likely that the cost structure differs between the restoration of oil and gas exploration plots, which are patchily distributed disturbances within a background of otherwise intact vegetation, and large, contiguous burn areas.

Furthermore, the study demonstrates that considerations of species' biology and autecology can dominate restoration decisions, rather than aspects of the application of treatments to restoration sites. A small seeded species, such as sagebrush, may rarely reach critical size in the first season, but beyond a critical size could persist long term (Meyer 1994). Together with the fact that excavation rarely kills a small sagebrush outright, transplanting wildlings is a promising option for species with similar biology.

Greenhouse-raised transplants are categorically more costly than wildings. However, greenhouse grown plants may be available at larger quantities, with reliable survival rates and thus may still be a best choice option for the restoration of large contiguous burn areas.

Blackbrush produces relatively large, robust seeds but exhibits masting, which is challenging when the timing of seed demand does not overlap masting years (Pendleton et al. 2015). Masting is a challenge for both seed sourcing and growing greenhouse transplants, although it may be possible to raise a bulk-quantities of transplants from seeds collected in masting years. Blackbrush transplants do not require cages to survive, nevertheless, when seeds are available it is more cost effective to seed directly and cage than to take seeds to the greenhouse for raising transplants and outplanting at some future time. Perhaps a mixed strategy could be considered, which could make transplants available in non-masting years.

There are several propagule and treatment combinations that can be applied during restoration. Given the range of potential restoration options, the wise investment of limited resources requires the integration of biological, economic, and stochastic considerations (such as bet hedging). The decision tool illustrated in table 2.6 is a first step towards allowing restoration practitioners to strategize across the largest possible decision space.

Tables

Table 1.1. Chronosequence site information for a) Wyoming sagebrush and b) blackbrush. This includes API # (American Petroleum Institute well ID number), date surveyed, county, field office, latitude and longitude, elevation (feet), year of abandonment (YOA), and time since abandonment (TSA, in years) for a) Wyoming sagebrush and b) blackbrush.

API#	Survey Date	Geo. Range	County	Field Office	Latitude	Longitude	Elevation	YOA	TSA
4304731425	7/22/2018	North	Uintah	Vernal	40.2657	-109.435	5083	1984	35
4304731671	8/3/2018	North	Uintah	Vernal	40.2469	-109.4478	5119	1985	34
4304731276	7/10/2018	North	Uintah	Vernal	40.3037	-109.6901	5098	1982	37
4304710631	7/11/2018	North	Uintah	Vernal	40.3592	-109.5923	5303	1961	58
4304720309	7/19/2018	North	Uintah	Vernal	40.3626	-109.6681	5235	1968	51
4304730128	7/20/2018	North	Uintah	Vernal	40.3949	-109.7364	5463	1973	46
4304730191	7/23/2018	North	Uintah	Vernal	40.135	-109.3198	5357	1974	45
4304715307	7/24/2018	North	Uintah	Vernal	40.1967	-109.179	5765	1986	33
4304731083	8/4/2018	North	Uintah	Vernal	40.1792	-109.2826	5608	1993	26
4304731109	8/5/2018	North	Uintah	Vernal	40.1319	-109.1597	5497	1981	38
4304715309	8/7/2018	North	Uintah	Vernal	40.1677	-109.198	5604	1992	27
4303730309	7/12/2019	South	San Juan	Monticello	38.18276	-109.4152	5879	1978	41
4303730109	7/17/2019	South	San Juan	Monticello	38.06755	-109.5013	6494	1973	46
4303731826	7/22/2019	South	San Juan	Monticello	37.59330	-109.54134	5944	2002	17
4303710224	8/6/2019	South	San Juan	Monticello	37.4741	-109.5147	5432	1960	59
4303731087	8/7/2019	South	San Juan	Monticello	37.46300	-109.3516	5361	1984	35
4303730047	8/8/2019	South	San Juan	Monticello	37.56117	-109.37872	5809	1974	45
4303730036	8/9/2019	South	San Juan	Monticello	37.56847	-109.36462	5841	1969	50

b)

API#	Survey Date	Geo. Range	County	Field Office	Latitude	Longitude	Elevation	YOA	TSA
4301931332	6/28/2019	North	Grand	Moab	38.5224	-109.8463	4965	2005	14
4301930276	7/23/2019	North	Grand	Moab	38.69576	-109.926	5048	1976	43
4301910931	8/10/2019	North	Grand	Moab	38.59924	-109.9648	5202	1964	55
4303730617	8/11/2019	North	San Juan	Moab	38.4269	-109.582	5441	1981	38
4303731002	6/27/2019	South	San Juan	Monticello	37.22081	-109.9202	5062	1984	35
4303731339	7/21/2019	South	San Juan	Monticello	37.36538	-109.5418	4706	1987	32
4303730203	7/8/2019	South	San Juan	Monticello	37.23257	-109.9304	5183	1974	45
4303731483	7/19/2019	South	San Juan	SITLA	37.7372	-110.274	5190	1992	27
4303730163	7/18/2019	South	San Juan	SITLA	37.3112	-109.47	4609	1974	45

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Table 1.2. Location effects for all measured variables. Shown are means with 95% confidence intervals in brackets for the A) sagebrush community; B) blackbrush community. *P*-values correspond to the comparisons of means on and off pad with site as a random factor.

Sagebrush	On pad	Off pad	P value
$\Psi_{\operatorname{Pre}}(\operatorname{MPa})$	-3.08 (-3.71, -2.44)	-3.71 (-4.40, -3.02)	0.003
$\Psi_{\mathrm{Mid}}(\mathrm{MPa})$	-3.97 (-4.47, -3.48)	-4.47 (-5.12, -3.82)	0.019
$\Psi_{\mathrm{Diff}}(\mathrm{MPa})$	0.77 (0.55, 1.00)	0.83 (0.63, 1.03)	0.615
Photosynthesis rates (µmol m ⁻² s ⁻¹)	6.40 (4.81, 7.98)	5.36 (3.74, 6.98)	0.100
Shrub density (plant/m²)	0.74 (0.44, 1.03)	1.72 (1.19, 2.23)	0.003
Cum. soil resistance at 30cm (J)	2107 (1696, 2517)	899 (717, 1082)	< 0.001
Soil resistance 0-5 cm (J)	69.69 (49.96, 89.41)	28.20 (21.77 34.63)	< 0.001
Soil resistance 5-10 cm (J)	222.86 (174.59, 271.13)	83.45 (72.42, 94.47)	< 0.001
Soil resistance 10-15 cm (J)	400.06 (298.72, 501.40)	139.78 (120.89, 158.66)	< 0.001
Soil resistance 15-20 cm (J)	415.00 (276.59, 553.38)	168.96 (140.45, 197.47)	< 0.001
Soil resistance 20-25 cm (J)	496.30 (384.74, 607.86)	211.61 (157.71, 265.51)	< 0.001
Soil resistance 25-30 cm (J)	502.91 (398.64, 607.18)	267.39 (174.54, 360.25)	< 0.001
Electrical conductivity 0-25 cm (dS/m ²)	1.37 (1.02, 1.73)	0.80 (0.53, 1.07)	< 0.001
$\Psi_{\text{Soil}} 0 - 10 \text{ cm (MPa)}$	-82.73 (-112.96, -52.50)	-66.05 (-91.07, -41.04)	0.212
Ψ_{Soil} 10 – 25 cm (MPa)	-35.79 (-49.55, -22.02)	-33.74 (-48.56, -18.92)	0.744
Ψ _{Soil} 25 - 40 cm (MPa)	-13.81 (-20.51, -7.12)	-13.53 (-20.69, -6.38)	0.910
Ψ _{Soil} 40 - 60 cm (MPa)	-8.54 (-13.17, -3.90)	-11.06 (-15.10, -7.02)	0.163

Blackbrush	On pad	Off pad	P value
$\Psi_{\text{Pre}}(\text{MPa})$	-3.05 (-3.86, -2.24)	-4.38 (-6.22, -2.53)	0.031
$\Psi_{ m Mid}(m MPa)$	-4.93 (-5.90, -3.95)	-6.12 (-7.72, -4.51)	0.012
$\Psi_{\mathrm{Diff}}(\mathrm{MPa})$	1.88 (1.42, 2.33)	2.01 (1.50, 2.52)	0.37
Photosynthesis rates (µmol m ⁻² s ⁻¹)	30.44 (21.38, 39.49)	21.93 (10.58, 33.28)	0.108
Shrub density (plant/m²)	0.86 (-0.04, 1.77)	2.84 (0.86, 4.83)	0.015
Cum. soil resistance at 30cm (J)	1412 (1009, 1813)	628 (398, 859)	0.001
Soil resistance 0-5 cm (J)	50.81 (22.88, 79.75)	7.84 (1.57, 14.11)	0.008
Soil resistance 5-10 cm (J)	185.11 (123.23, 246.99)	45.01 (18.97, 71.04)	< 0.001
Soil resistance 10-15 cm (J)	294.26 (197.75, 390.77)	105.55 (63.00, 148.10)	< 0.001
Soil resistance 15-20 cm (J)	331.88 (223.42, 440.34)	125.92 (74.57, 177.27)	0.001
Soil resistance 20-25 cm (J)	279.53 (138.42, 420.63)	160.10 (108.29, 211.90)	0.103
Soil resistance 25-30 cm (J)	269.52 (68.31, 470.73)	183.69 (30.04, 331.34)	0.446
Electrical conductivity 0-25 cm (dS/m ²)	0.88 (0.58, 1.17)	0.70 (0.52, 0.88)	0.124
$\Psi_{\text{Soil}} 0 - 10 \text{ cm (MPa)}$	-89.94 (-119.89, -59.00)	-69.39 (-98.52, -40.25)	0.159
Ψ_{Soil} 10 – 25 cm (MPa)	-35.31 (-63.41, -7.00)	-35.13 (-56.71, -13.55)	0.987
Ψ _{Soil} 25 - 40 cm (MPa)	-6.23 (-12.31, -0.16)	-10.26 (-19.80, -0.72)	0.427
Ψ _{Soil} 40 - 60 cm (MPa)	-4.80 (-13.77, 4.16)	-5.52 (-10.45, -0.60)	0.846

Table 2.1. Site information for restoration treatment implementation. This includes API # (American Petroleum Institute well ID number), species, county, field office, latitude, longitude, elevation (feet), date of abandonment (DOA), time since abandonment (TSA, in years), geographical range (geo. range), transplant date, seed date, number of total greenhouse transplants (Transplant #), and number of total wildlings (Wildling #). SS1a and SS1b refer to three experimental blocks on the same site, planted at different times.

API#	4304730080	4303731863	4301931332	4303730617	4303731483	4303730163
Species	Sagebrush	Sagebrush	Blackbrush	Blackbrush	Blackbrush	Blackbrush
County	Uintah	San Juan	Grand	San Juan	San Juan	San Juan
Field Office	SITLA	SITLA	BLM Moab	BLM Moab	SITLA	SITLA
Latitude	40.329	38.244	38.522	38.427	37.737	37.311
Longitude	-109.757	-109.194	-109.846	-109.582	-110.274	-109.47
Elevation	5337	6703	5671	5357	4685	5352
DO A	10/6/2005	11/1/2007	8/11/1993	7/13/1981	6/4/1992	9/27/1974
TSA	15	12	26	38	27	45
Geo. range	NS1	SS1a, b	NB1	NB2	SB1	SB2
Transplant		3/19/2019,				
Date	3/14-15/2020	3/17/2020	11/14/2019	11/15/2019	3/18/2019	3/16-17/2019
Seed Date	3/15/2020	12/16/2019	12/13/2019	12/15/2019	12/14/2019	12/14/2019
Transplant #	192	511, 256	231	194	208	193
Wildling #	48	32, 16	48	48	48	48

Table 2.2. Average precipitation (ppt), minimum (min.), and maximum (max) temperatures for first summer after planting (March-September) in 2019 or 2020 (PRISM Climate Group).

Site	Summer ppt (mm)	Temp (Min) C°	Temp (Max) C°
NB1	12.8	12.53	25.63
NB2	12.24	11.8	27.06
SB1	19.33	12.7	25.91
SB2	14.03	10.51	27.79
NS1	11.77	6.7	24.89
SS1a	25.88	7.11	22.13
SS1b	15.77	7.79	23.93

Table 2.3. Transplant survival results of generalized mixed effects model analysis using a binomial distribution to determine the effects of restoration treatments for northern and southern locations applied to a) sagebrush and b) blackbrush. Shown are transplant survival including estimate, standard error (SE), and p-values for sagebrush and blackbrush. Depression and debris were nested within blocks and block was considered a random factor. Negative estimates indicate a positive effect on survival.

Sagebrush	Treatment	Estimate	SE	P-value
North	Intercept	1.275	0.611	0.037
	Size Class	-0.247	0.143	0.085
	Block	-0.585	0.223	0.009
	Block (Depression)	0.207	0.145	0.155
	Block (Debris)	0.562	0.146	0.0001
South	Intercept	-3.128	0.934	0.0008
	Size Class	-0.398	0.081	< 0.0001
	Block	1.179	0.193	< 0.0001
	Block (Depression)	-0.151	0.038	< 0.0001
	Block (Debris)	-0.070	0.037	0.060

Blackbrush	Treatment	Estimate	SE	P-value
North	Intercept	5.165	1.136	<0.0001
	Size Class	-0.469	0.139	0.0008
	Block	-0.527	0.269	0.050
	Block (Depression)	-0.129	0.063	0.040
	Block (Debris)	-0.109	0.061	0.076
South	Intercept	-3.586	2.396	0.134
	Size Class	-0.405	0.142	0.004
	Block	0.830	0.262	0.002
	Block (Depression)	-0.098	0.037	0.007
	Block (Debris)	-0.072	0.036	0.046

values for blackbrush. Treatments included presence of a cage, depression, or debris. Depression and debris were nested within blocks and block was considered a random factor.

Treatment	Estimate	SE	P-value
Intercept	0.055	0.026	0.101
Block	-0.013	0.008	0.132
Block (Cage)	0.026	0.008	0.002
Block (Depression)	0.002	0.006	0.781
Block (Debris)	0.005	0.006	0.351
Cage*Block (Depression)	0.006	0.010	0.522
Cage*Block (Debris)	-0.020	0.010	0.042

Table 2.4. Seed emergence results of a linear mixed effects model analyses to determine the effects of treatments for a) northern and b) southern locations on seed emergence (based on proportion of total seeds planted) including estimate, standard error (SE), and p-

b)

Treatment	Estimate	SE	P-value
Intercept	0.0053	0.040	0.184
Block	-0.005	0.004	0.231
Block (Cage)	0.013	0.003	< 0.0001
Block (Depression)	-0.0004	0.002	0.827
Block (Debris)	0.0004	0.002	0.827
Cage*Block (Depression)	0.007	0.003	0.019
Cage*Block (Debris)	-0.015	0.00.	0.009

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Table 2.5. Seedling survivorship results of linear mixed effects model analyses to determine the effects of treatments for a) northern and b) southern locations on the proportion of seeds that survived from emergence including estimate, standard error (SE), and p-values for blackbrush. Treatments include presence of a cage, depression, or debris. Depression and debris were nested within blocks and block was considered a random factor.

Treatment	Estimate	SE	P-value
Intercept	0.131	0.064	0.043
Block	-0.031	0.021	0.145
Block (Cage)	0.087	0.026	0.001
Block (Depression)	0.003	0.018	0.845
Block (Debris)	0.021	0.018	0.229
Cage*Block (Depression)	0.028	0.031	0.361
Cage*Block (Debris)	-0.030	0.031	0.335

b)

Treatment	Estimate	SE	P-value
Intercept	-0.040	0.083	0.66
Block	0.004	0.009	0.649
Block (Cage)	0.022	0.006	0.0002
Block (Depression)	< 0.001	0.004	1.0
Block (Debris)	< 0.001	0.004	1.0
Cage*Block (Depression)	-0.014	0.006	0.030
Cage*Block (Debris)	-0.005	0.006	0.466

Table 2.6. Cost outcomes per propagule type, treatment (Dep = Depression, Deb = Debris), survival rates based on a target density of 10 plants per 10 m² area and extrapolated to 1-acre area for a) northern sagebrush, b) southern sagebrush, c) northern blackbrush, and d) southern blackbrush.

Propagule type	Treatment	Cost per propagule (\$)	Survival per propagule	Target density per 10m ²	Propagules required for target density	Propagule cost per target density (\$)	Treatment cost per 10m ² (S)	Transport cost (\$)	Total cost per 10m ² (\$)	Total cost per pad (\$)
Seedling	Cage	0.0003	0.000	10	NA	NA	10.00	NA	NA	NA
Seedling	Cage + Dep	0.0003	0.000	10	NA	NA	52.50	NA	NA	NA
Seedling	Cage + Deb	0.0003	0.000	10	NA	NA	31.25	NA	NA	NA
Seedling	Cage + Dep + Deb	0.0003	0.000	10	NA	NA	31.25	NA	NA	NA
Seedling	No cage	0.0003	0.000	10	NA	NA	10.00	NA	NA	NA
Seedling	Depression	0.0003	0.000	10	NA	NA	52.50	NA	NA	NA
Seedling	Debris	0.0003	0.000	10	NA	NA	31.25	NA	NA	NA
Seedling	Dep + Deb	0.0003	0.000	10	NA	NA	31.25	NA	NA	NA
Seedling*	No cage	0.0003	0.002	10	5000	1.53	10.00	0.00	11.53	461
Transplant	No treatment	3.400	0.286	10	34.97	118.88	0.00	3.50	122.38	4895
Transplant	Depression	3.400	0.161	10	62.11	211.18	170.00	6.21	387.39	15496
Transplant	Debris	3.400	0.095	10	105.26	357.89	80.00	10.53	448.42	17937
Transplant	Dep + Deb	3.400	0.077	10	129.87	441.56	250.00	12.99	704.55	28182
Wildling	No treatment	0.708	0.750	10	13.33	9.44	0.00	0.00	9.44	378

^{*} Refers to survival rate from previous study for seeding sagebrush with no treatment (Lysne and Pellant 2004).

Propagule type	Treatment	Cost per propagule (\$)	Survival per propagule	Target density per 10m ²	Propagules required for target density	Propagule cost per target density (\$)	Treatment cost per 10m ² (\$)	Transport cost (\$)	Total cost per 10m ² (\$)	Total cost per pad (\$)
Seedling	Cage	0.0003	0.000	10	NA	NA	10.00	NA	NA	NA
Seedling	Cage + Dep	0.0003	0.000	10	NA	NA	52.50	NA	NA	NA
Seedling	Cage + Deb	0.0003	0.000	10	NA	NA	31.25	NA	NA	NA
Seedling	Cage + Dep + Deb	0.0003	0.000	10	NA	NA	31.25	NA	NA	NA
Seedling	No cage	0.0003	0.000	10	NA	NA	10.00	NA	NA	NA
Seedling	Depression	0.0003	0.000	10	NA	NA	52.50	NA	NA	NA
Seedling	Debris	0.0003	0.000	10	NA	NA	31.25	NA	NA	NA
Seedling	Dep + Deb	0.0003	0.000	10	NA	NA	31.25	NA	NA	NA
Transplant	No treatment	3.400	0.051	10	196.08	666.67	0.00	19.61	686.27	27451
Transplant	Depression	3.400	0.074	10	135.14	459.46	170.00	13.51	642.97	25719
Transplant	Debris	3.400	0.059	10	169.49	576.27	80.00	16.95	673.22	26929
Transplant	Dep + Deb	3.400	0.089	10	112.36	382.02	250.00	11.24	643.26	25730
Wildling	No treatment	0.708	0.250	10	40.00	28.32	0.00	0.00	28.32	1133

Propagule type	Treatment	Cost per propagule (\$)	Survival per propagule	Target density per 10m ²	Propagules required for target density	Propagule cost per target density (\$)	Treatment cost per 10m ² (\$)	Transport cost (\$)	Total cost per 10m ² (\$)	Total cost per pad (\$)
Seedling	Cage	0.133	0.014	10	720.00	95.63	10.00	0.00	105.63	4225
Seedling	Cage + Dep	0.133	0.026	10	378.95	50.33	52.50	0.00	102.83	4113
Seedling	Cage + Deb	0.133	0.006	10	1600.00	212.50	31.25	0.00	243.75	9750
Seedling	Cage + Dep + Deb	0.133	0.008	10	1309.09	173.86	73.75	0.00	247.61	9905
Seedling	No cage	0.133	0.000	10	NA	NA	10.00	0.00	NA	NA
Seedling	Depression	0.133	0.000	10	NA	NA	52.50	0.00	NA	NA
Seedling	Debris	0.133	0.006	10	1800.00	239.06	31.25	0.00	270.31	10813
Seedling	Dep + Deb	0.133	0.008	10	1200.00	159.38	73.75	0.00	233.13	9325
Transplant	No treatment	3.400	0.045	10	222.22	755.56	0.00	22.22	777.78	31111
Transplant	Depression	3.400	0.047	10	212.77	723.40	170.00	21.28	914.68	36587
Transplant	Debris	3.400	0.052	10	192.31	653.85	80.00	19.23	753.08	30123
Transplant	Dep + Deb	3.400	0.078	10	128.21	435.90	250.00	12.82	698.72	27948
Wildling	No treatment	0.708	0.000	10	NA	NA	0.00	0.00	NA	NA

Propagule type	Treatment	Cost per propagul e (\$)	Survival per propagule	Target density per 10m ²	Propagules required for target density	Propagule cost per target density (\$)	Treatment cost per 10m ² (\$)	Transport cost (\$)	Total cost per 10m ² (\$)	Total cost per pad (\$)
Seedling	Cage	0.133	0.007	10	1440	191.25	10.00	0.00	201.25	8050
Seedling Seedling	Cage + Dep Cage + Deb	0.133 0.133	0.005 0.003	10 10	2057.14 2880	273.21 382.50	52.50 31.25	$0.00 \\ 0.00$	325.71 413.75	1302 16550
Seedling	Cage + Dep + Deb	0.133	0.000	10	NA	NA	73.75	0.00	NA	NA
Seedling	No cage	0.133	0.000	10	NA	NA	10.00	NA	NA	NA
Seedling	Depression	0.133	0.000	10	NA	NA	52.50	NA	NA	NA
Seedling	Debris	0.133	0.000	10	NA	NA	31.25	NA	NA	NA
Seedling	Dep + Deb	0.133	0.000	10	NA	NA	73.75	NA	NA	NA
Transplant	No treatment	3.400	0.030	10	333.33	1133.33	0.00	33.33	1166.67	4667
Transplant	Depression	3.400	0.037	10	270.27	918.92	170.00	27.03	1115.95	4464
Transplant	Debris	3.400	0.027	10	370.37	1259.26	80.00	37.04	1376.30	5505
Transplant	Dep + Deb	3.400	0.062	10	161.29	548.39	250.00	16.13	814.52	3258
Wildling	No treatment	0.708	0.020	10	500	354.00	250.00	50.00	654.00	2616

Figures

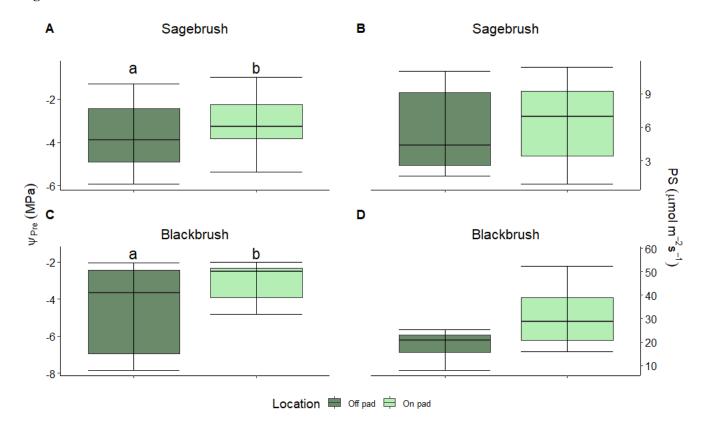


Figure 1.1. Boxplots summarizing the range of measured values ± 1 standard error for both predawn water potentials (Ψ_{Pre} ; A, C) and photosynthetic rates (PS; B, D) on and off pad for sagebrush (A, B) and blackbrush (B, D). Letters represent significant differences on and off pad for site averages (p < 0.05).

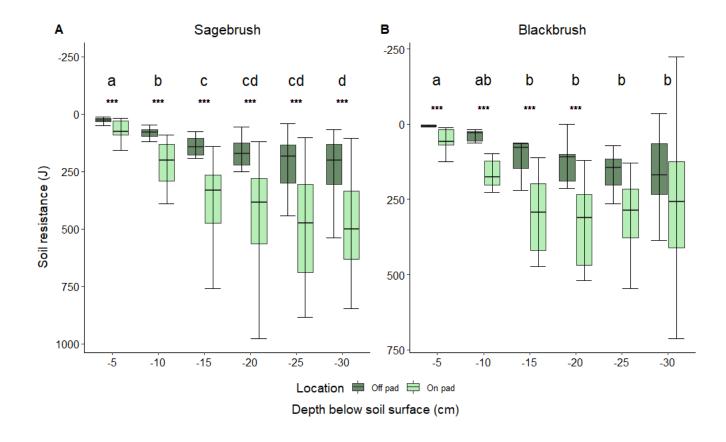


Figure 1.2. Boxplots summarizing the range of measured values with ± 1 standard error for soil compaction resistance for each 5 cm increment below the surface on and off pad for A) sagebrush and B) blackbrush. Letters represent significant differences between each 5 cm depth below soil surface (p < 0.05). Stars represent significant differences between on and off pad estimated SR values for that depth (p < 0.05).

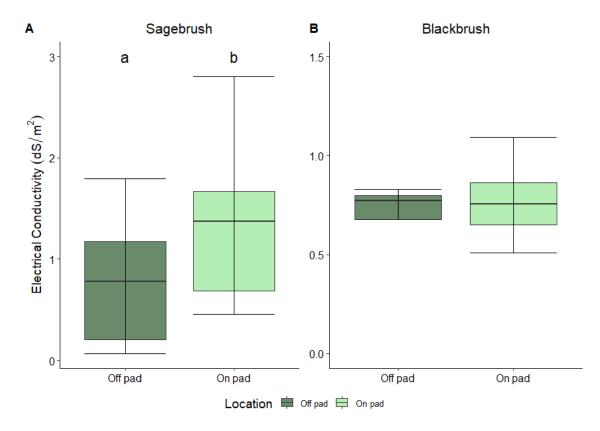


Figure 1.3. Boxplots summarizing the range of measured values with ± 1 standard error for electrical conductivity on and off pad for A) sagebrush and B) blackbrush communities. Letters represent significant differences on and off pad for site averages (p < 0.05).

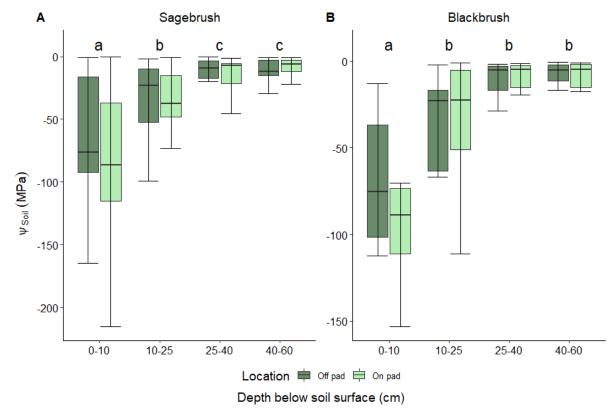


Figure 1.4. Boxplots summarizing the range of measured values with \pm 1 standard error for soil water potentials (Ψ_{Soil}) at each soil depth below surface on and off pad for A) sagebrush and B) blackbrush. Letters represent significant differences between each depth (p < 0.05).

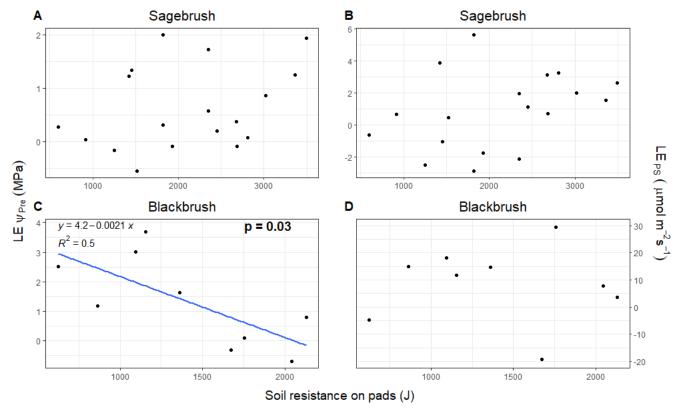


Figure 1.5. Effects of on-pad soil mechanical resistance on the magnitude of location effects (LE). Location effects are expressed as the differences in on-pad and off-pad values of the differences in predawn water potentials (Ψ_{Pre} ; A, C) and photosynthesis rates (PS; B,D) for both sagebrush and blackbrush. Positive slopes indicate higher values on pad. *P*-values <0.05 indicate significant regressions.

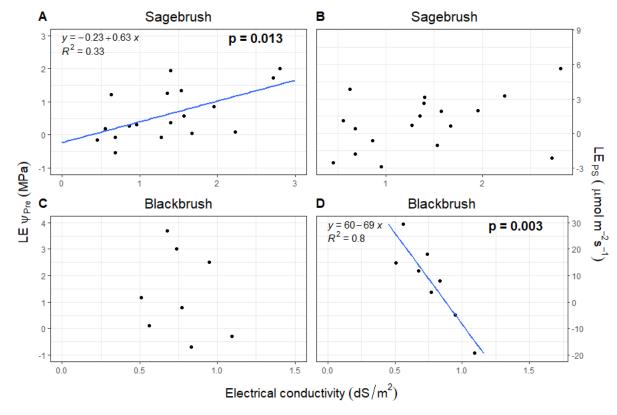


Figure 1.6. Effects of on-pad soil electrical conductivity on the magnitude of location effects (LE). Location effects are expressed as the difference in on-pad and off-pad values of the difference in predawn water potentials (Ψ_{Pre} ; A, C) and photosynthetic rates (PS; B, D) for both sagebrush and blackbrush. Positive slopes indicate higher values on pad. *P*-values <0.05 indicate significant regressions.

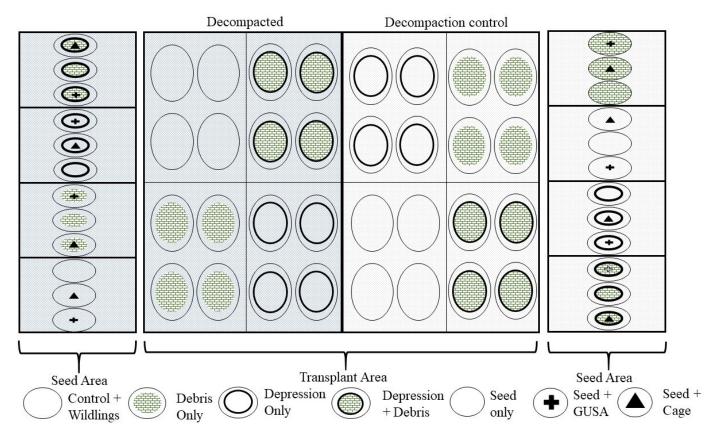


Figure 2.1. Study block layout including transplanting and seeding areas. The two outer seed strips are split into the four treatment types (control, debris only, depression only, debris and depression). Within each of those plots, the circles represent where seeds were planted, either hand-raked (sagebrush) or in caches (blackbrush). The transplant block is within the seed strips, split in half for decompaction and subdivided for the four treatment types (same as above). The circles represent clusters of transplants.

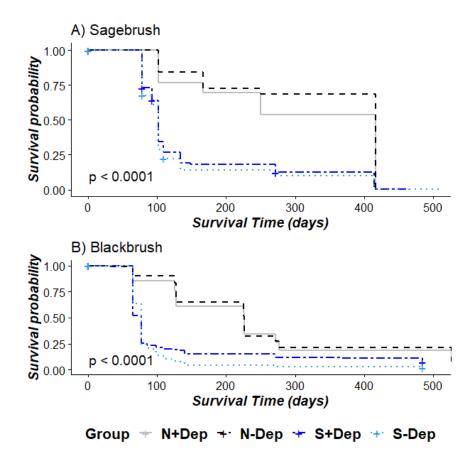


Figure 2.2. Kaplan Meier survivorship curves show the probability of individuals surviving over time for each location (N = north, S = south) and treatment (Dep = depression) for A) sagebrush and B) blackbrush. *P-values* represent differences across treatments and locations.

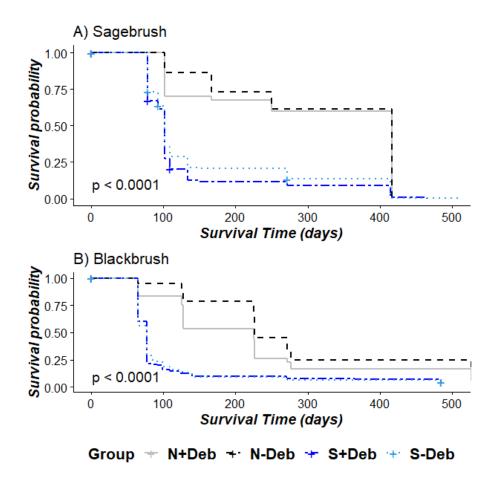


Figure 2.3. Kaplan Meier survivorship curves show the probability of individuals surviving over time for each location (N = north, S = south) and treatment (Deb = debris) for A) sagebrush and B) blackbrush. *P-values* represent differences across treatments and locations.

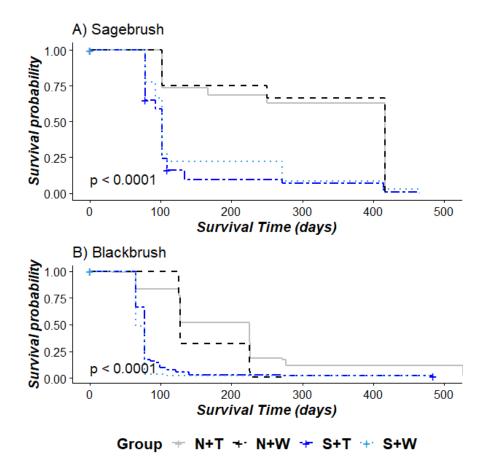


Figure 2.4. Kaplan Meier survivorship curves show the probability of individuals surviving over time for each location (N = North, S = South) and seedling propagule (T = transplant, W = wildling) for A) sagebrush and B) blackbrush. *P-values* represent differences across treatments and locations.

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