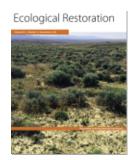


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Restoration of North American Salt Deserts: A Look at the Past and Suggestions for the Future ¹⁷

Jayne L. Jonas, M. Nikki Grant-Hoffman and Mark W. Paschke

ABSTRACT

North American salt deserts are typically characterized by slow-growing *Atriplex* shrubs and perennial grasses with biological soil crusts (BSC) important in shrub interspaces. Disturbance due to heavy livestock use, wildfire, and recreation and energy development has increased the need for restoration of salt deserts in the western United States. However, restoration often fails due to invasive annual species and poor native plant establishment. In addition to a literature review, we surveyed restored salt desert sites in National Conservation Areas and other public lands in western Colorado ranging in age (3–63 yr) and restoration methods to assess approaches that were more or less successful. We used non-parametric ordination techniques to compare plant communities to environmental and restoration explanatory variables. Restored communities tended to move toward reference condition over time, but soil type, seeding, and type of disturbance also influenced plant community recovery. Overgrazed sites passively restored by long-term livestock exclusion were most similar to reference sites, while sites affected by wildfire and soil-related disturbances were most different from reference with non-native invasive annual grass (primarily *Bromus tectorum*) and forbs being common. These undesirable species were also more abundant on seeded sites than non-seeded or references sites, although mixes with a higher proportion of native species tended to improve outcomes. Results suggest that disturbance type and management approaches can have a large impact on restoration success in Intermountain West salt deserts, though many questions require further research.

Keywords: Atriplex shrublands, Chenopod shrubs, cold desert, saltbush scrub, shadscale zone

♦ Restoration Recap **♦**

- Salt deserts in the Intermountain West of North America are harsh environments with little rainfall and saline soils in which unique shrub-dominated plant assemblages develop over long periods of time.
- Restoration of salt desert is often limited by aggressive non-native annual species and failure of seeded/ transplanted species to establish.
- Based on a literature review and survey of restored sites, pre-treatment of invasive annuals on-site prior to seeding/ transplanting, use of diverse mixes of native plant species and local ecotypes, and providing supplemental water to seedlings and excluding livestock during the establishment phase are likely to improve restoration success.
- Much remains to learn about North American salt desert ecosystems that could improve restoration success.

Inland salt deserts are found on most continents, but most extensively in the Intermountain West of North America and in southern Australia (Chapman 1960). In the western United States, they are the second largest ecosystem,

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Supplementary materials are freely available online at: http://uwpress.wisc.edu/journals/journals/er-supplementary.html

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occurring primarily in portions of the Great Basin and Colorado Plateau (Figure 1; Branson et al. 1967, West 1983, Blaisdell and Holmgren 1984, Garvin et al. 2004, EPA 2012). Because they have an arid climate and stressful soil conditions, attempts at restoration are prone to failure (Plummer 1966, Van Epps and McKell 1980, Ansley and Abernethy 1983, Blaisdell and Holmgren 1984).

We conducted a literature review focused primarily on North American salt deserts and a field survey of restored salt desert sites in western Colorado to examine approaches to restoration and post-restoration management most likely

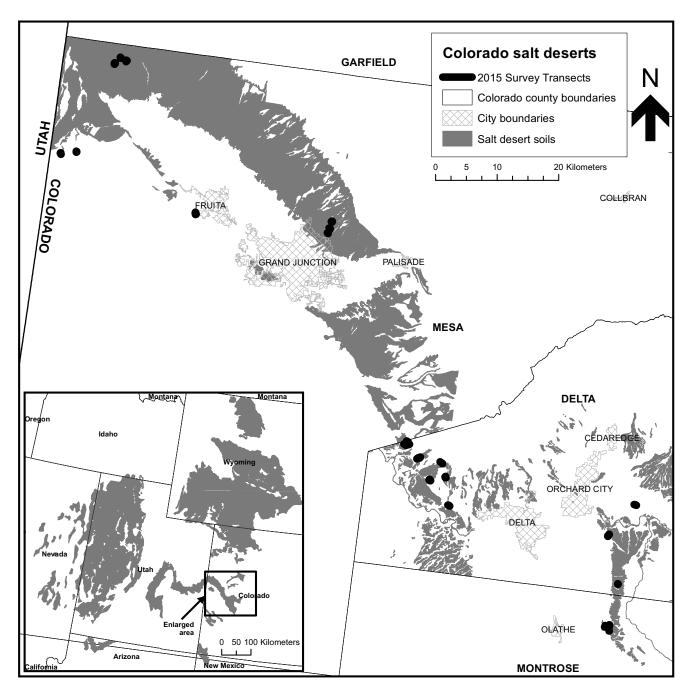


Figure 1. Map of survey sites (black dots) and salt desert-related range types (gray) in Mesa, Delta, and Montrose counties of Colorado, USA (SSURGO database, NRCS 2014). Inset: Extent of salt desert (gray) within the Central Basin and Range, Wyoming Basin, and Colorado Plateau based on US Environmental Protection Agency ecoregions (EPA 2012).

to improve long-term restoration success of degraded salt desert. We start with a brief review of salt desert ecology and then discuss the primary forms and consequences of disturbance in the context of a successional model. We then present results from our survey and discuss the relevance of those results to previous work on restoration in salt deserts. Finally, we provide recommendations for future study that may improve restoration success in these systems.

Ecology of Salt Deserts

Abiotic Characteristics

Salt deserts of the Intermountain West (Figure 1) occur in arid climates where annual precipitation ranges from 100 to 350 mm and can exhibit a high degree of interannual variability (Turner 1971, Wein and West 1971, Van Epps and McKell 1980, Blaisdell and Holmgren 1984). Winter snowfall is generally the most important source of moisture in salt desert systems, accounting for roughly 50% of annual precipitation (Blaisdell and Holmgren 1984, Whisenant and Wagstaff 1991). Summer storms can also be an important source of moisture in salt deserts (Lusby et al. 1963, Bleak et al. 1965, Turner 1971, Blaisdell and Holmgren 1984, NCDC 2015). However, summer storms tend to be localized and precipitation can be lost as runoff during high intensity storms (Lusby et al. 1963, Wein and West 1971, Blaisdell and Holmgren 1984). Temperature in salt deserts is highly seasonal with the frost-free period typically lasting from May or June until August or September (Supplementary Figure S1). However, with high daytime temperatures and low relative humidity leading to high evaporation rates (Lusby et al. 1963), periods conducive for plant growth in these systems can be much shorter than the frost-free period (Turner 1971, Blaisdell and Holmgren 1984).

Inland salt desert shrublands are often found on saline or alkaline soils of enclosed basins at the bottom of drainages (Chapman 1960) or on soils underlain by or derived from Mancos shale in the western US (Lusby et al. 1963, Blaisdell and Holmgren 1984). There can be high spatial and temporal variability in salinity-alkalinity of salt desert surface soils depending on many factors, including precipitation and evapotranspiration rates, parent material, vegetation, and management (Gates et al. 1956, Lusby et al. 1963, Naphan 1966, Roundy et al. 1983). Winter precipitation can increase salinity of surface soils by capillary rise of salts if the water table comes close enough to the surface, but spring precipitation can alleviate salinity by leaching or runoff of accumulated surface salts, especially in fine and medium textured soils (Roundy et al. 1983). As soil moisture declines through the late spring into summer due to plant uptake and increasing temperatures, there can be a concomitant increase in salinity-alkalinity of surface soils (Blaisdell and Holmgren 1984).

Vegetation Characteristics

Plant composition, productivity, and cover is highly dependent on soil moisture regime, as well as soil type, soil salinity, herbivory (Lusby et al. 1963, Bleak et al. 1965, Roundy et al. 1983, West 1983, Blaisdell and Holmgren 1984), and management practices (Lusby et al. 1963, West and Caldwell 1983). Deep-rooting halotolerant shrub species, primarily *Atriplex* and other chenopod species, tend to dominate salt deserts with perennial grasses patchily distributed and biological soil crusts common in interspaces between plants (Table S1; Gates et al. 1956, Blaisdell and Holmgren 1984). Perennial forbs and native annuals are generally less common, though some, such as annual *Eriogonum* species, can be locally abundant when soil moisture is high (Gates et al. 1956, Bleak et al. 1965, Blaisdell and Holmgren 1984).

Over relatively small spatial scales, there can be high variability in plant composition with abrupt ecotones in some instances (Lusby et al. 1963, Goodman 1973). Although many different vegetation classifications have been used to describe assemblages within North American salt deserts, they are typically defined by the dominance of one or two species (Branson et al. 1967, Goodman 1973, Blaisdell and Holmgren 1984, CNHP 2005a,b). While specific drivers of plant composition are complex and poorly understood, species or ecotype tolerance to soil characteristics including soil salt content, stoichiometry of ions in soil solution, depth of salinity, flooding and soil aeration, depth to water table, and soil texture can be important (Gates et al. 1956, West and Ibrahim 1968, Goodman 1973, Roundy et al. 1983, West 1983, Blaisdell and Holmgren 1984). In addition, plant-soil feedbacks can exist in which plants alter soil properties inhibiting establishment of less halotolerant species (Ungar 1998). Some Atriplex species can vertically redistribute salts from deeper soils leading to a zone of increased surface salinity (Naphan 1966, Roundy et al. 1983, Ungar 1998, Meyer et al. 2001). Further, distribution of salts and nutrients can differ in soils beneath shrubs compared to shrub interspaces (Charley and West 1975, Meyer et al. 2001).

With plant cover typically $\leq 20\%$ (West 1983), biological soil crusts (BSCs) are particularly important in plant interspaces where they prevent or limit soil erosion, improve retention of water in the soil, limit establishment of exotic invasive plants, and serve as an important source of biologically-fixed nitrogen (Blaisdell and Holmgren 1984, Rosentreter and Eldridge 2004, Serpe et al. 2006, Deines et al. 2007, Skeen 2014).

Succession

Regeneration of mature salt desert potential natural vegetation following disturbance can take a century or more in North America (Figure 2; Goodman 1973, West 1979, Blaisdell and Holmgren 1984, Chambers and Norton 1993, LANDFIRE 2005). Drought and insect outbreaks were likely the most important natural drivers of state change in North American salt deserts, with multidecadal return intervals (LANDFIRE 2005, Bentz et al. 2008). Human uses, such as livestock grazing and development of transportation corridors and recreational facilities (e.g., trails and trailheads), can also lead to major alterations of salt desert systems. Moderate and stand-replacing fire is thought to carry through salt desert only rarely (West 1994) so is not discussed here as a typical part of natural (i.e., uninvaded) salt desert systems.

Drought

Drought-induced plant mortality is likely one of the main drivers of reversion to earlier seral states absent human impacts (Blaisdell and Holmgren 1984, LANDFIRE 2005). Although salt desert shrubs have morphological (e.g., deep taproots) and physiological (i.e., summer dormancy) adaptations that allow established plants to survive droughts,

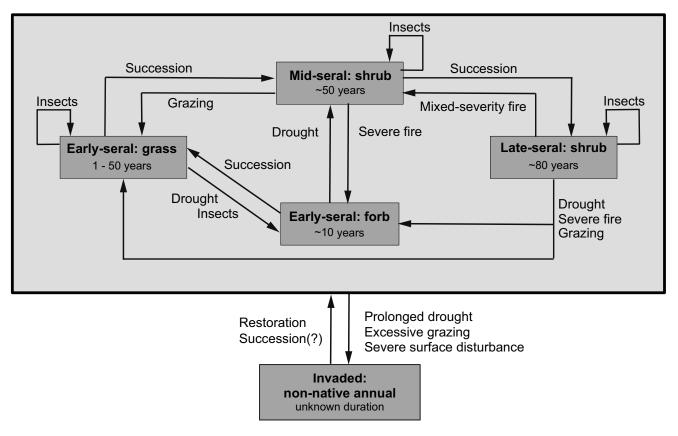


Figure 2. Successional relationships between seral states and disturbances for potential natural vegetation (in large gray box) in North American salt deserts as adapted and modified from LANDFIRE (2005). Impacts of human-linked disturbances on plant invasion are also indicated.

some species are more susceptible to drought than others (Ansley and Abernethy 1983, Blaisdell and Holmgren 1984, Chambers and Norton 1993, Alzerreca-Angelo et al. 1998, Smith and Hanlon 2010). Further, sensitivity to drought can vary for a given species depending on the plant assemblage in which it occurs. Chambers and Norton (1993) found *Krascheninnikovia lanata* (winterfat) had higher adult mortality during drought in grass-dominated stands than in shrub-dominated stands (Blaisdell and Holmgren 1984, Chambers and Norton 1993, Alzerreca-Angelo et al. 1998, Hoover et al. 2015). This may indicate that during drought grasses can outcompete shrubs for water moved by the shrub from deep to shallow soil (i.e., hydraulic lift) (Caldwell and Richards 1989, Bonham and Mack 1990).

Because of their deep-rooting morphology, impacts of drought on shrub reproduction (Blaisdell and Holmgren 1984, Schwinning et al. 2005), germination (Blaisdell and Holmgren 1984, Chambers and Norton 1993), and seedling establishment (Chambers and Norton 1993) are likely more important than effects on adult mortality in intact salt desert. Flowering and seed-set depends on precipitation in many drought-tolerant shrubs (e.g., *A. gardneri* [Gardner's saltbush], *K. lanata, Bassia americana* [green molly]) and grasses (e.g., *Pleuraphis jamesii* [galleta], *Sporobolus cryptandrous* [sand dropseed]) (Blaisdell and Holmgren 1984, Comstock and Ehleringer 1992, Chambers

and Norton 1993, Smith and Hanlon 2010). Roundy et al. (1983) suggest that seedling establishment is highest for seeds that germinate early, invest in high root growth rates, and physiologically adjust to saline conditions.

Livestock Grazing

Salt deserts have a limited ability to support livestock grazing due to low productivity (Parker 1966, Blaisdell and Holmgren 1984, Chambers and Norton 1993, Cibils et al. 1998, McArthur and Monsen 2004) and season of grazing has perhaps the largest impact on vegetation responses to grazing. Grazing during spring, when many shrub and cool-season grass species are initiating growth, can be detrimental to palatable native species and cause undesirable shifts in plant composition and production (Cook 1966, Knipe 1966, Chambers and Norton 1993, Kitchen and Hall 1996, Campbell et al. 2010). Winter grazing, when most species are dormant, can have no effect or even benefit some shrubs and grasses (Cook 1966, Holmgren and Hutchings 1972, Harper et al. 1990, Alzerreca-Angelo et al. 1998, Campbell et al. 2010). Biological soil crusts also seem better able to recover from and tolerate dormantseason grazing than growing-season use (Anderson et al. 1982). However, even under a winter-grazing regime, earlier than expected spring-like weather conditions that initiate plant activity can have negative consequences for salt desert vegetation as livestock will concentrate grazing on new plant growth (Knipe 1966). With earlier onset of spring conditions due to climate change (Schwartz et al. 2006), availability and utilization of spring growth is likely to increase under current winter grazing schedules.

As in other dryland systems, grazer preferences and plant responses to grazing can cause shifts in composition of salt desert plant communities (Stewart et al. 1940, Lusby et al. 1963, Turner 1971, Norton 1978, Bjerregaard et al. 1984, Blaisdell and Holmgren 1984, Whisenant and Wagstaff 1991). For example, both *K. lanata* and *A. gardneri* are palatable to livestock and can be removed under heavy grazing (Holmgren and Hutchings 1972, West 1979, Ansley and Abernethy 1983, Harper et al. 1990, Smith and Hanlon 2010, Goodrich and Zobell 2011), while *A. confertifolia* (shadscale) is unpalatable and increases as it is released from competition with more palatable species (Holmgren and Hutchings 1972, Chambers and Norton 1993, Alzerreca-Angelo et al. 1998).

Insect Outbreaks

State-changing insect outbreaks in salt desert are estimated to have occurred at roughly the same frequency as drought (~60-70 years) (LANDFIRE 2005). Scientific studies directly examining historical frequency of insect outbreaks or assessing the impact of insects on vegetation in salt deserts were not found, but several studies discuss insects as a likely or possible influence on salt desert plant community dynamics (Sharp and Barr 1960, Turner 1971, Holmgren and Hutchings 1972, Grant-Hoffman et al. 2015). For example, Turner (1971) suggested that the combination of drought and herbivory by small mammals and insects limited establishment of shrub and grass species at a site in western Colorado, while Holmgren and Hutchings (1972) noted that insect outbreaks were likely responsible for detectable shifts in plant dominance in Utah salt desert. Hutchings (1952) described widespread mortality of A. confertifolia due to snout moth (Pyralidae) larvae that was followed by *Halogeton glomeratus* (saltlover) invasion in Idaho (in Blaisdell and Holmgren 1984). Floral and seed predation may also be important in salt deserts (Haws et al. 1983, Moore and Stevens 1983). Moore and Stevens (1983) found seed production of A. canescens (four-wing saltbush) could be driven to near zero when colonized by the case-bearing moth *Coleophora atriplicivora*.

Human Development

Activities associated with human use and development (e.g., energy and transportation corridors, military operations, surface mining, recreation and off-road vehicle use) can transport invasive species (Gelbard and Belnap 2003) and cause severe disturbance to soil (Blaisdell and Holmgren 1984). Such disruption of the soil surface damages BSCs, which tend to be very sensitive to soil disturbance and, like the plant community, can take a century or more

to fully recover (Belnap 1993). Degradation of soil crusts in combination with alteration of native plant communities increases susceptibility to erosion (Lusby et al. 1963, Newhall et al. 2004, Rosentreter and Eldridge 2004) and colonization by invasive plants (Serpe et al. 2006, Deines et al. 2007).

Invasive Species

Some non-native species are able to exploit unique characteristics of salt deserts to quickly invade following disturbance (Harper et al. 1996, Meyer et al. 2001, Duda et al. 2003, Goodrich and Zobell 2011). Invasive annuals are able to germinate, grow, and establish due to high soil moisture availability in spring (Blaisdell and Holmgren 1984, Bradford and Lauenroth 2006). This ability to exploit early spring moisture contributes to increased propagule pressure and competitive superiority of these invasive species (Hirsch-Schantz et al. 2014). While slow regeneration of native shrubs and biological soil crusts facilitate establishment of invasive annual plants following disturbance (Blaisdell and Holmgren 1984, Young and Longland 1996, Bradford and Lauenroth 2006).

Invasive species can limit growth and reproduction of native salt desert species (Freeman and Emlen 1995, Harper et al. 1996). Once established, invasive species can initiate positive feedbacks for soil microbial dynamics, nitrogen cycling, and wildfire regime, that are uncharacteristic of the system and can limit shrub regeneration (Duda et al. 2003, Garvin et al. 2004, Newhall et al. 2004, Pendleton et al. 2004, Haubensak et al. 2009, Hirsch-Schantz et al. 2014). In greenhouse studies, Harper et al. (1996) and Garvin et al. (2004) found higher K. lanata survival in fumigated, fungicide-treated or autoclaved soils from H. glomeratusinvaded sites than in untreated soils from those same sites. Additionally, compression and destruction of BSCs can cause a temporary increase in available nitrogen and other nutrients bound in BSC biomass that can be quickly exploited by invasive species (Pendleton et al. 2004) like H. glomeratus which has poor forage value and is toxic to sheep (Goodrich and Zobell 2011).

Another invasive, *Bromus tectorum* (cheatgrass), can create a significant bed of fine fuel leading to frequent fire in a system that is not fire-adapted (Newhall et al. 2004, LANDFIRE 2005). Moderate-severity to stand-replacing fires were estimated to have occurred rarely (West 1994, LANDFIRE 2005), but Newhall et al. (2004) report that the recent average fire return interval in *B. tectorum*-invaded salt desert sites is once every 7 years. Although most commonly attributed to disturbance, natural processes leading to shrub mortality have also been associated with plant invasion (Garvin et al. 2004, Bradford and Lauenroth 2006). Garvin et al. (2004) hypothesized that several years of above average precipitation in the early 1980's led to high mortality of chenopod shrubs, especially *A. confertifolia* and *K. lanata*, by increasing their susceptibility to

pathogenic fungi; following this loss of shrubs, the annual invasive weeds B. tectorum and H. glomeratus established (Garvin et al. 2004).

Assessment of Western Colorado **Salt Desert Restoration Projects**

Objectives

Since the early 1950's, the Bureau of Land Management (BLM) has attempted to reestablish western Colorado salt desert communities following wildfire, overgrazing, and soil disturbance (e.g., trailhead or pipeline construction) with limited success. We surveyed salt deserts along a disturbance gradient in National Conservation Areas and other public lands of western Colorado to: 1) assess restoration strategies likely to be more or less successful in establishing native communities; and 2) identify avenues for future research that seem most likely to improve restoration effectiveness (Figure 1) to serve as a case study for improving success of future restorations in similar Intermoutain West salt deserts.

Survey Methods

A total of 90 transects across 19 salt desert sites in Mesa, Delta, and Montrose counties, Colorado, representing a range of topoedaphic characteristics and restoration approaches, were examined in June 2015 (Figure 1). Canopy and ground cover were sampled using the point-intercept technique (Elzinga et al. 1998) every 2 meters along 50-m line transects. Cover along each transect was classified into the following categories: bare ground, litter, BSC, native forb, native grass, native shrub, non-native invasive annual forbs (hereafter, undesirable forbs), non-native invasive annual grass (hereafter, undesirable grass; i.e., *B. tectorum*), and non-native forage grass (i.e., Agropyron cristatum [crested wheatgrass]). We also recorded physical attributes of each transect (i.e., slope, aspect, topographic position, elevation). Sixteen sites were subject to some form of restoration and 3 sites were considered untreated reference sites (Table 1). Agency records were consulted to classify sites into 5 disturbance categories: long-term grazed reference (hereafter, reference), heavy livestock use (e.g., sheep bedding areas, over-grazing), grazing exclusion, wildfire, or soil disturbance (e.g., trailhead, pipeline or road construction). Although details were not available, reference sites have likely been grazed by domestic livestock since at least the 1890s at stocking rates typical of the region over time. For seeded sites, we noted seeding methods (i.e., broadcast or drill-seeded), seed mix composition (Supplementary Table S2), and seeding rates when provided in records. Year of restoration ranged from 1952 to 2012. For each site that had been subject to restoration, we calculated the number of years since restoration as well as annual

precipitation (mm) and maximum temperature (°C) in the year of restoration (t) and the year following restoration (t + 1) from weather stations at Fruita (1902–2012), Grand Junction (6 ESE 1962–2015 and Walker Field 1900–2015), Olathe (2007-2015), and Montrose (1905-1982) (NCDC 2015). For each site, only data from the closest weather station(s) with coverage for the relevant years were used to calculate weather variables. Soil type of each transect was determined based on range site classification using the Soil Survey Geographic Dataset (SSURGO, NRCS 2014). If SSURGO did not identify the range site for a transect, it was assigned the same soil type as the nearest transect of similar topographic position.

Two sets of analyses were conducted using relative cover data; one using all transects and one using only transects from seeded sites. The environmental matrix for analysis of all transects included time since treatment, disturbance category, range site, and seeding (Table 1), as well as elevation, slope, topographic position, and aspect. Analysis of seeded transects also included characteristics of the seed mix (seed mix richness, proportion of native species in seed mix, herbicide application, mulch application, and seeding method) and weather in the growing season of (t) and first growing season after (t + 1) treatment in the environmental matrix. Seeding rates were not available for enough sites to include in our analyses. Non-metric multidimensional scaling (NMS) ordination analyses were conducted using Bray-Curtis distance and 9999 runs of the data; correlation between continuous variables and ordination scores was conducted using the environmental fit function in R (packages vegdist and vegan, R v 3.3.2). Separate permutation MANOVAs (perMANOVAs) were used to assess impacts of disturbance, soil type, grazing, and seeding on plant communities as represented by NMS axes scores (Euclidean distances, 9999 permutations, packages vegan and RVAideMemoire, R v 3.3.2). Dunn-Sidak adjusted alpha (α') was used for post hoc pairwise comparisons of significant perMANOVAs to maintain an overall $\alpha = 0.10$.

Results

All Transects. There were significant main effects of disturbance, seeding, and soil type on restored communities across all transects surveyed (Supplementary Table S3). We did not detect an effect of elevation or slope, but there was a strong signal of increasing native shrubs and BSCs in communities over time (Figure 3A-B, Supplementary Table S4). Long-term grazed reference transects did not differ significantly from transects in grazing exclosures, but did differ from all other disturbance types (heavy livestock use, soil disturbance, wildfire) (Figure 3A). Grazing exclosures were most aligned with BSCs, while undesirable forbs and grasses were closely associated with soil disturbances and wildfire, respectively (Figure 3A). In assessing the impact of seeding, we found undesirable grasses and litter were

Table 1. Classification used for permutation MANOVAs on ordination axes scores for transects in restored salt desert sites surveyed during June 2015 in Mesa, Delta, and Montrose counties, Colorado, USA. Excl = exclosure, SD = saltdesert, SemiD = semidesert, Reference = long-term grazed reference.

Site name	SSURGO Range site	Disturbance	Seeded	Age (years)	Transects sampled
Badger Wash Excl	Silty SD	Grazing exclusion	No	62	6
Devil's Canyon	Sandy SD	Grazing exclusion	No	17	4
Peach Valley Excl	Salt flats	Grazing exclusion	No	50	1
	Silty SD	Grazing exclusion	No	50	7
Relic Excl	Clayey SD	Grazing exclusion	No	53	4
Alkali Excl	Salt flats	Heavy livestock use	No	63	3
Indian Wash	Clayey SD	Heavy livestock use	Yes	49	12
Ute	SD breaks	Heavy livestock use	Yes	3	3
Alkali	Silty SD	Reference	_	_	3
Badger Wash	Silty SD	Reference	_	_	7
Dominguez	Stony SD	Reference	_	_	8
Buried pipeline	Stony SD	Soil disturbance	Yes	17	3
Highway 50 site 1	Stony SD	Soil disturbance	Yes	15	2
Highway 50 site 2	Salt flats	Soil disturbance	Yes	11	2
	Stony SD	Soil disturbance	Yes	11	2
Highway 92 site 1	Silty SD	Soil disturbance	Yes	6	2
	Stony SD	Soil disturbance	Yes	6	2
NCA Lower trailhead	Loamy SD	Soil disturbance	Yes	3	3
NCA Upper trailhead	Stony SD	Soil disturbance	Yes	3	3
Wave Eagle trailhead	Salt flats	Soil disturbance	Yes	3	1
2 Road site 1	Sandy SD	Wildfire	Yes	20	4
2 Road site 2	SemiD loam	Wildfire	No	20	4
Peeples	Stony SD	Wildfire	No	21	4

associated with seeded areas, which had communities differing significantly from unseeded and reference areas (Figure 3B). We also detected significant differences in restored plant communities among soil types; however, transects were unevenly distributed among soil types (Table 1) so this result should be interpreted with caution.

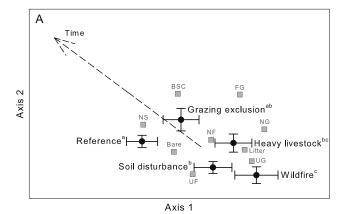
Seeded transects. Among seeded and reference transects, communities differed in terms of disturbance (Supplementary Table S3). Unlike analysis of all transects, forage grasses increased over time among seeded sites (Figure 3C, Supplementary Table S4). This result is driven by the two oldest restoration projects (Indian Wash 49 years old, 2 Road Fire 20 years old) both of which used the non-native grass A. cristatum as one of only two species seeded. The legacy of seeding forage grasses rather than native species also manifests in the native:non-native species factor of our analysis being significant and moving communities in approximately the opposite direction of the Time factor in ordination space (Figure 3C, Supplementary Table S4). Increasing seed mix richness was significant and associated with an increase in the signature of native shrubs and a decrease in the signature of undesirable grasses (Figure 3C, Supplementary Table S4). Mulch was used on eight and herbicide applied to four of the more recent restorations, however we were not able to analyze either mulch or herbicide impacts on our survey sites due to statistical non-convergence.

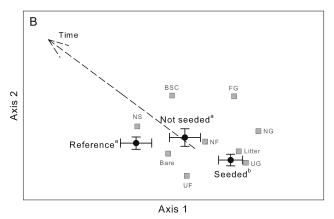
Discussion

Passive Restoration

Long-term overuse as livestock range is one cause of severe degradation of North American salt deserts, including shifts in plant community composition and destruction of biological soil crusts (Stewart et al. 1940, Lusby et al. 1963, Cook 1966, Turner 1971, Jones and Longland 1999). Recovery from overgrazing can be a long-term process (Lusby 1970, Blaisdell and Holmgren 1984, Harper et al. 1990, Whisenant and Wagstaff 1991) likely due to the slow successional trajectory of these systems (Figure 2). At Badger Wash, an experiment was initiated in 1953 to examine impacts of grazing on salt desert by establishing paired grazed and ungrazed watersheds (Lusby et al. 1963). Hydrology quickly responded to removal of livestock with increased water-absorbing capacity of the soil and decreased runoff and sediment yield on ungrazed compared to grazed watersheds (Lusby et al. 1963, Knipe 1966, Lusby 1970, 1979). There were few effects of grazing on bulk density and bulk density was not correlated with infiltration, runoff, or erosion at the site (Lusby et al. 1963) indicating that grazing likely impacted hydrologic dynamics through changes in the structure and composition of vegetation and BSCs (Lusby et al. 1963, Bowker 2007).

Perennials, including *Achnatherum hymenoides* (indian ricegrass) and *Elymus elymoides* (bottlebrush squirreltail),





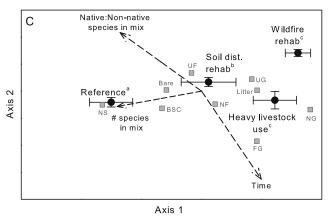


Figure 3. Average (± 1 SE) nonmetric multidimensional scaling (NMS) axes scores (black dots) based on A) disturbance type and B) seeding for all transects surveyed in western Colorado salt deserts. Panel C) results based on disturbance type for seeded and reference transects only; analysis included additional variables related to seeding methods. Gray triangles indicate cover groups: BSC = biological soil crust, bare = bareground, NS = native shrub, NF = native forb, NG = native grass, UF = undesirable forb, UG = undesirable grass, FG = nonnative (forage) grass. Dotted lines indicate significant correlations between continuous explanatory variables and NMS ordination scores. Factors followed by the same letter do not differ significantly at $\alpha = 0.10$.

tended to be more frequent in ungrazed watersheds within 10 years of livestock exclusion at Badger Wash (Turner 1971). In addition, Eriogonum microthecum (slender buckwheat), a native annual forb, was only present in ungrazed watersheds (Turner 1971). Turner (1971) also found survival and recruitment of palatable shrubs (A. gardneri and Chrysothamnus greenei [Greene's rabbitbrush]) were higher on ungrazed watersheds, while the unpalatable shrub A. confertifolia increased in grazed watersheds. Although our 2015 survey, (which included Badger Wash) found native shrubs to be more associated with reference sites than grazing exclosures, we did not identify shrubs to species. Therefore, our result may have been driven by dominance of unpalatable species in long-term grazed areas that served as our reference sites. Long-term grazing exclusion was associated with increased cover of BSCs in our survey. This is similar to Anderson et al. (1982) who reported recovery of BSCs occurred by ~15 years after livestock exclusion in Utah salt deserts.

Active Restoration

Where native plants and soil crusts have been compromised, passive restoration through a change in management may not be feasible because of the length of time required for natural recovery and the ability of invasive species to quickly gain site dominance (Blaisdell and Holmgren 1984, Kitchen and Hall 1996, Newhall et al. 2004). Active restoration of these long-lived native plant communities, however, is exceedingly difficult (Bleak et al. 1965, Plummer 1966, Van Epps and McKell 1980, Jordan 1983, Blaisdell and Holmgren 1984, Monsen 1994, Grant-Hoffman et al. 2015). In our survey, undesirable grasses and forbs tended to be characteristic of the most disturbed sites, especially those affected by wildfire or soil disturbance. This illustrates the challenge of achieving restoration success in North American salt deserts and highlights the need to understand the ecology of these systems in designing restorations.

Potential limitations to successful restoration include poor seed germination, mismatches between plant ecotypes and site conditions, low soil moisture during critical growth periods, competition with non-native species, seedling mortality due to frost, improper seeding techniques, loss of seed to granivores, herbivory, soil compaction, pathogens, and lack of mycorrhizal fungi (Van Epps and McKell 1980). Although the goal of western US rangeland revegetation programs through the 1980's was often to increase livestock forage production, typically with the use of vigorous non-native perennial grasses (e.g., Ag. cristatum) (Hull 1963, Plummer 1966, Roundy 1999), Roundy (1999) points out several "lessons" that can be applied to ecologically-focused restoration efforts that are echoed by Hirsch and Monaco (2011), these include considering vegetation and soil conditions when choosing native plant species and ecotypes, selecting appropriate seedbed preparation techniques and sowing methods, understanding current climate, and identifying post-restoration management strategies so they are matched to the ecology of the site. Post-restoration monitoring often spans only the first several years after restoration; however, both our literature review and survey results indicate a slow trajectory of plant community development in salt deserts. As shown in our survey, restored communities tend to shift toward reference over much longer periods of time than typically allowed to determine project success.

Types of Propagules. A variety of propagule types (e.g., wild seedlings, bare-root or container stock, seed) have been used for salt desert revegetation. Among transplants, container-grown stock generally fare better than bare-root stock (Van Epps and McKell 1980, Aldon 1983). Van Epps and McKell (1980) found container-grown shrub transplants had roughly 80% survival after more than five years, while bare-root stock had just over 45% survival. Although average cover of survivors was similar between container and bare-root plants, container-grown transplants were less affected by competition with annual exotic species (Van Epps and McKell 1980) likely due to the developed root systems of containerized plants. Success of bare-root stock varies between species, with A. canescens, Artemisia tridentata (big sagebrush), Ar. nova (black sagebrush), and Sarcobatus vermiculatus (greasewood) performing better than A. confertifolia, K. lanata, A. cuneata (Castle Valley clover), and Ericameria nauseosa (rubber rabbitbrush) (Van Epps and McKell 1980).

There has been limited success of seeding in salt desert restoration (Van Epps and McKell 1980, Aldon 1983, Ansley and Abernethy 1983). While transplants of local A. canescens ecotypes had approximately 67% survival after 5 years and had also established progeny (Aldon 1983), direct seeding in a year with adequate spring precipitation was associated with only 9% survival of emerged seedlings after five years (Aldon 1983). Jessop and Anderson (2007) reported no survival of seeded species and few significant effects of post-fire seeding on exotic B. tectorum after three years, although invasive annual forb cover was significantly lower in seeded compared to unseeded plots. In our survey, seeded communities were associated with undesirable grasses, differing from both reference and unseeded areas where native species were more prevalent in the communities. Seeded sites tended to be those that experienced more intense forms of disturbance, either completely removing native plant communities (e.g., pipeline and trailhead construction) or likely causing higher rates of native plant mortality (e.g., wildfire). We found that seeding after soil disturbance was more successful (i.e., closer to reference) than seeding after wildfire, but undesirable species were still an issue. These results illustrate the challenge of establishing native salt desert communities from seed following disturbance. Nevertheless, the greatly reduced cost of seeding relative to using transplants makes seeding an attractive approach to revegetation.

Seeds of most salt desert shrub species can be locally collected late fall through winter (Shaw and Monsen 1983). However, native salt desert shrubs and grasses can have low seed viability (Bleak et al. 1965, Shaw and Monsen 1983, McArthur and Monsen 2004). And, although viable seeds of salt desert species can germinate quickly under ideal conditions (Aldon 1983, Blaisdell and Holmgren 1984), they often have specific germination requirements that can further limit establishment from seed without pre-treatment (Ansley and Abernethy 1983, Roundy et al. 1983, Winkel et al. 1995, Garvin et al. 1996, Meyer and Carlson 2007, Qu et al. 2008, Smith and Hanlon 2010). Factors affecting germination of halophytic species include photoperiod, temperature, soil water availability, and soil salinity (Roundy et al. 1983, Ungar 1983, Qu et al. 2008) and requirements can vary among ecotypes (Ansley and Abernethy 1983, Meyer et al. 1998, Meyer and Carlson 2007). Although high salinity can prevent germination in halophytes, it does not necessarily induce dormancy or kill seeds, rather exposure to saline conditions may help break dormancy (i.e., osmotic priming) (Ungar 1983, Katembe et al. 1998, Qu et al. 2008).

Seedlings may be particularly sensitive to environmental conditions (Roundy et al. 1983, Qu et al. 2008) and stress caused by salinity, low soil moisture, and competition (Bleak et al. 1965, Roundy et al. 1983). For example, Ansley and Abernethy (1983) found *A. gardneri* field emergence was low, from ~5% without watering to no more than 17% with watering, despite high germination rates in the lab. Little seems to be known about specific conditions needed to support seedling establishment in salt deserts, but use of a variety of salt desert-adapted species and ecotypes may be valuable.

Plant Taxa. Increasing the number of native species in seed mixes may be key to improving restoration outcomes. Restoration seed mixes used on our survey sites included 2-6 species, which is below the 8-10 species recommended for salt desert by Blaisdell and Holmgren (1984). Nevertheless, prominence of undesirable species decreased as the number of species in the seed mix increased in our survey. Similar trends have also been shown in other semi-arid systems where seed mixes with more native species led to improved restoration outcomes (Barr et al. 2016). Although we were not able to include seeding rates in our analyses, restorations for which records were available used seed mixes dominated by grasses (79-93% by weight) and did not include forbs (Supplementary Table S2). Though not widely used, early-seral native species (e.g., forbs) can establish relatively quickly providing soil stabilization and competition to invasive annuals (Bleak et al. 1965, Smith and Hanlon 2010). Bleak et al. (1965) found that seeded native annual forbs grew, flowered, and contributed viable seed to the seedbank even though they did not persist in the plant community. Diverse seed mixes, including a variety of early- and late-seral species, with species and ecotypes matched to site conditions are likely to have the best long-term performance in salt deserts (Bleak et al. 1965, McArthur and Monsen 2004, Smith and Hanlon 2010). Studies explicitly examining seed mix richness or composition for restoration of salt deserts were not found; additional work is needed to assess potential benefits of including more species, particularly native early-seral species and perennial forbs, and decreasing the amount of grass seed in salt desert restoration seed mixes.

In addition to using diverse seed mixes, properly matching species with site conditions is also crucial when identifying taxa for seed mixes. This may be particularly important in salt deserts because distinct assemblages can form over relatively small spatial scales and can be linked to differing physiological capacities to withstand salinity/alkalinity (Gates et al. 1956, Goodman 1973, Bjerregaard et al. 1984, Hodgkinson 1987). For example, Gates et al. (1956) found that Ar. tridentata and K. lanata had the lowest tolerance to exchangeable sodium concentrations, while three other common salt desert species, A. confertifolia, Sa. vermiculatus, and A. nuttallii (Nuttall's saltbush), were able to grow on soils over a much wider range of exchangeable sodium concentrations. Although many salt-tolerant species are able to grow under neutral conditions, they are likely most competitive against nonhalophytes on saline, sodic, and/or alkaline soils (Hodgkinson 1987, Ungar 1998). Native species successfully used in North American salt desert restoration, as well as seeding recommendations or environmental tolerances of species identified in our literature review are summarized in Supplementary Table S5. When identifying species for restoration seed mixes, considering such environmental and competitive relationships may increase the likelihood of successful establishment.

Ecotypic variation within species can also lead to differences in planting success (Bleak et al. 1965, Plummer 1983, Shaw and Monsen 1983). McArthur and Monsen (2004) suggest that some salt desert species fare best when propagules used for restoration come from the restoration site itself. It may be especially important to use local ecotypes for species with wide geographic distributions and ecological tolerances across their range, such as *A. canescens* and *K. lanata* (Plummer 1983, Stevens and Monsen 2004). On sites with relatively intact communities, collecting seed prior to planned disturbances may improve restoration outcomes.

One of the primary goals of early salt desert revegetation was increasing forage to support livestock production (Hull 1963, Blaisdell and Holmgren 1984). To this end, nonnative forage grasses, especially *Psathyrostachys junceus* (Russian wildrye), *Ag. desertorum* (desert wheatgrass) and *Ag. cristatum*, were often seeded (Hull 1963, Bleak et al. 1965, Plummer 1966). Although they may limit invasion

by aggressive non-native annuals (Smith et al. 2016), early vigorous establishment of these non-native grasses can prevent or delay establishment of native species (Bleak et al. 1965, Newhall et al. 2004). At our survey sites, *Ag. cristatum* remained an important part of communities in which it was seeded after 20 or more years, similar to the findings of Grant-Hoffman et al. (2012).

Seeding Methods and Site Manipulation. Disturbance severity and soil characteristics impact which planting methods or other site manipulations are most appropriate for restoration of salt desert vegetation. No studies were found that explicitly compared methods in salt desert and reports of effectiveness of individual methods were inconsistent. Recommendations for interseeding, for example, differ and are context-dependent. Blaisdell and Holmgren (1984) indicate that interseeding into existing stands of salt desert shrub vegetation has had limited success. Bleak et al. (1965) reported establishment of both native and nonnative forage species (including grasses, forbs, and shrubs) improved if seeds were planted near established shrubs and during years with adequate early growing-season moisture. Stevens and Monsen (2004) recommend use of a rangeland drill to interseed perennial grasses into established B. tectorum stands, which can increase consistency in planting depths.

Planting depth impacts emergence and should be appropriate for each species and site. To encourage emergence, Plummer (1966) recommended planting small seeds no more than 0.64 cm (0.24 in.) and large seeds no more than 1.27 cm (0.5 in.) deep in salt desert. However, Bleak et al. (1965) found greater germination success when seeds were planted deeper in salt desert than recommended for the same species in sagebrush habitats as seeds were more protected from surface soil moisture stress, wind erosion, and high levels of solar radiation. Ultimately, ideal depth will vary by species according to seed size with larger seeds tolerating deeper sowing.

Mulch has also been shown to improve seedling establishment and may reduce surface stressors. Establishment of grass, forb, and shrub species (both native and nonnative) tends to be improved when planted in ways that conserve soil moisture, including application of gravel or brush mulch (Bleak et al. 1965, Winkel et al. 1995). Winkel et al. (1995) found that a 2-cm gravel mulch layer led to the highest emergence (40-85%) and survival (94-100%) of P. jamesii seedlings after 20 days compared to surface seeding, 1-cm seeding depth, and 4-cm gravel mulch treatments under two of three watering regimes (water at seeding, water every five days) in a greenhouse experiment. Gravel and brush mulches may be particularly useful in extremely water-limited environments, such as salt deserts, because they limit the amount of moisture wicked away from seeds or developing root systems compared to organic mulches (Bainbridge 2007). Other methods for increasing water infiltration and abating erosion, particularly on slopes, include contour furrows, gully plugs, ripping, and pitting. Because shale underlying salt desert is not permeable and there is low plant cover and high potential evaporation, these techniques are generally not considered effective in salt deserts (Wein and West 1973, West 1983, Blaisdell and Holmgren 1984). Wein and West (1973) reported positive feedbacks between soils, surface water flow and vegetation associated with gully plugs and contour furrows that can increase soil salinity in these structures over time. Although many native chenopod shrubs may not be negatively affected, these soil conditions may benefit the establishment of exotic *H. glomeratus* (Wein and West 1973). In addition, these structures can also quickly be degraded by erosion and sediment fill (West 1983).

When seeding in invaded sites, protecting seeds and/ or transplants from competition by decreasing invasive annual species propagule pools with herbicide and/or mechanical manipulation (e.g., disking, harrowing, etc.) prior to seeding may be key to successful establishment (Monsen 1994, Ungar 1998, Stevens and Monsen 2004, Sheley et al. 2007). Monsen (1994) outlines an approach to B. tectorum control that includes either spring tilling (or prescribed burning) before seed set followed by either fall tilling or herbicide treatment prior to late fall or early winter seeding of native species. This combination of treatments is aimed at reducing B. tectorum seed production and recruitment to benefit establishment and survival of native species (Monsen 1994). Comparing preemergence herbicides, rimsulfuron decreased emergence of B. tectorum while imazapic did not in both salt desert and sagebrush soils (Hirsch et al. 2012). However, it is also important to recognize that unique physical and chemical characteristics of salt desert soils may alter efficacy of some herbicides (Morris et al. 2009, Hirsch et al. 2012). For example, Hirsch et al. (2012) found that both imazapic and rimsulfuron increased seedling mortality of three grass species (B. tectorum, Ag. cristatum, E. elymoides) in sagebrush soils, but neither herbicide affected seedling mortality in salt desert soils.

Weather Conditions and Planting Season. Natural recruitment in salt desert plant communities tends to be episodic and related to precipitation (Bleak et al. 1965, Aldon 1972, West 1979, Aldon 1983, Blaisdell and Holmgren 1984). For example, germination of many salt desert species relies on adequate soil moisture and/or release from salinity stress, both of which are largely determined by weather patterns (Blaisdell and Holmgren 1984, Katembe et al. 1998, Meyer and Carlson 2007, Qu et al. 2008). Water limitation is also important for determining plant survival in salt deserts (Goodman 1973, Van Epps and McKell 1980) with seedlings being particularly susceptible to drought-induced mortality (Bleak et al. 1965, Jordan 1983). Although our survey failed to detect a relationship between precipitation or temperature and plant communities in seeded restoration sites, we retrieved weather data from stations up to 25 km from survey sites and only for the year of seeding and the first-year post-seeding, so it is possible that we did not have adequate spatial or temporal resolution to detect trends.

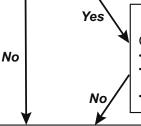
Recent advancements in predicting periodic climate oscillations, such as El Niño Southern Oscillation (ENSO), provide hope that restoration efforts in arid environments can be planned at times when precipitation and temperatures are more likely to allow restoration success (Holmgren 2009, Sitters et al. 2012). In the Great Basin of the western US, where most salt desert vegetation occurs, periods of above average precipitation have been associated with the rather predictable ENSO cycles (Ropelewski and Halpert 1987) associated with the negative phase of the Southern Oscillation Index (Stenseth et al. 2003). Further refinement of ENSO forecasting in the Great Basin (Smith et al. 2015) could provide managers of salt desert vegetation a valuable tool for planning revegetation efforts.

Van Epps and McKell (1980) evaluated the use of commercial antidesiccants (WiltPruf, Wilt-Pruf Products, Essex, CT and Weathershield XX, NCH Corporation, Irving, TX) as a way of alleviating water limitation in salt desert revegetation, but found no impact on plant survival. They also found little effect of providing supplemental water during the initial month after fall transplanting for nine species of salt desert shrubs, though the extra water did promote establishment of exotic annual species (Van Epps and McKell 1980). However, Aldon (1983) found that drip irrigation provided for a longer time (i.e., from the time of planting in the late summer-early fall until the first hard frost) increased survival of *A. canescens* seedlings. In other deserts of the Intermountain West, establishment of shrubs has been facilitated by deep watering of shrub transplants to encourage formation of deep roots to support transplant survival through subsequent dry periods (Bainbridge 2007). By placing a pipe with small holes facing the seedling to a depth of 30-35 cm, deep watering can efficiently deliver water to shrub roots below the zone where annual invasive species are most competitive for soil moisture (Bainbridge 2007).

Planting during times of highest soil moisture availability, such as just prior to spring snowmelt, during summer monsoons or just before winter snowfall, can encourage seed germination and seedling growth, as well as limit the need for supplemental watering (Plummer 1966, Aldon 1983, Skeen 2014). Although information about seasonal timing of seeding was not available for enough of our survey sites to include in our analyses, late fall or early winter seeding has traditionally been recommended because it limits fall germination, assists in breaking seed dormancy, allows seeds and germinants to benefit from spring snowmelt, and minimizes losses to seed predators (Bleak et al. 1965, Plummer 1966, Shaw and Monsen 1983, Blaisdell and Holmgren 1984, Stevens and Monsen 2004). Seeding too early in the fall increases the likelihood

1. Evaluate site to be restored

- · Soil surface relatively intact?
- Established vegetation present?



2a. Passive restoration

Consider a long-term change in managment

- · Rest from livestock use
- · Restrict livestock to early dormant-season grazing at low stocking rates
- · Limit activites that disturb or fragment the soil surface

2b. Active restoration

Site preparation

- If site invaded by non-native annuals, treat in spring with herbicide (before set seed) and in fall with herbicide or mechanically (before seeding natives)
- If considering herbicide, test small area to assess efficacy

Propagule type(s)

- Transplants with developed root systems perform best; seed may be more cost effective upfront
- Seeding plus strategic use of shrub transplants may improve establishment

Species richness

 Aim to plant 8+ species; success likely to improve with number of species planted

Species composition

- · Native species should be emphasized
- Include species from many functional groups (e.g., native annuals and perennials; shrubs, forbs, and grasses)

Propagule supply

- · Collect from site prior to disturbance, if possible
- · Match varieties/ecotypes to physical, chemical, and biological conditions of site

Seeding method

- · Little is known; studies inconsistent
- If soils are relatively intact, minimize surface disturbance

Planting season

- Spring planting timed to period of highest soil moisture likely best for transplants
- Early winter seeding generally best for many species, though some species may benefit from spring seeding
- Try to identify germination and establishment requirements of seeded species

Planting depth

- Increase planting depth according to seed size; plant large seeds deeper than small seeds.
- Planting depth may need to be deeper in salt deserts than recommended for other systems, but more work is needed.

Seed bed cover/ Erosion abatement

- Brush mulch or a thin layer of gravel mulch may be best
- · Avoid absorbant mulches that can wick moisture from soil

Water supply

- · Consider dormant season seeding just prior to an expected El Niño summer (i.e., when SOI expected to be negative) to maximize likelihood of precipitation
- · Provide drip irrigation or deep-watering strategically until plants established; costly and more study needed
- · Antidessicants and soil manipulations (e.g., gully plugs, contour furrows, pitting) found not to be effective.

3. Post-restoration management

Livestock

- Protect site from grazing until plant are vigorous enough to withstand dormant season use (at least 3+ years)
- Stock at light to moderate rates, limit use to the dormant season, and ensure grazing ceases prior to initiation of spring plant growth.

Small mammal and insect herbivory/granivory

- · Assess granivore use of the site; consider use of sacrifice or diversionary seed to distract granivores
- Assess small herbivore use of the site; consider protecting areas of relatively high seeded species establishment (e.g., exclusion cages).

Figure 4. Decision tree and recommendations to assist with restoration planning for salt desert sites in the Intermountain West of North America based on a literature review and western Colorado field survey. Refer to the text for further discussion of each point. SOI = Southern Oscillation Index.

of early germination leading to winter mortality. Seeds planted in the spring may not be able to break dormancy and seedlings will require high soil moisture longer into the summer in order to successfully establish (Bleak et al. 1965, Plummer 1966). However, different species may need to be seeded at different times to maximize establishment from seed because species and ecotypes have evolved different strategies for dealing with seasonal patterns of water availability (Bleak et al. 1965, Aldon 1972, Van Epps and McKell 1980, Aldon 1983), for example requirements for breaking seed dormancy and for germination (Supplementary Table S5). Even with optimal seasonal timing of seeding it may take several years before some species are able to germinate (Garvin et al. 1996).

Microbial Inoculation. Soil microbial communities can influence growth and competitive abilities of salt desert species and may be key to facilitating recovery of disturbed salt desert systems (Belnap 1993, Duda et al. 2003, Pendleton et al. 2007). Duda et al. (2003) suggest that despite potential competitive superiority of K. lanata, changes in soil microbial communities associated with H. glomeratus invasion inhibit growth of K. lanata and support development of *H. glomeratus* monocultures. In another study, mycorrhizal inoculation of A. canescens during propagation from seed led to increased biomass, height, and cover two years after transplanting into alkaline and/ or saline native soils or spent oil shale (Call and McKell 1984). However, not all plant species respond to mycorrhizal fungi and BSCs similarly as impacts vary among salt desert species from beneficial to detrimental (Pendleton et al. 2007). Given the potential importance of soil microbes for supporting salt desert restoration, this is an area in great need of additional research.

Post-Restoration Management. In addition to drought, plant survival can be influenced by herbivory during the first years of establishment (Bleak et al. 1965, Van Epps and McKell 1980). Mortality generally stabilizes 3 or 4 years after planting so establishment should be evaluated after this period and before livestock are reintroduced (Van Epps and McKell 1980). In the absence of livestock, invasive species can be suppressed by native perennials (Lusby et al. 1963, Turner 1971, Holmgren and Hutchings 1972, Whisenant and Wagstaff 1991, Jones and Longland 1999). Once livestock are reintroduced, they should be stocked at light to moderate rates and limited to late fall and early winter grazing when negative effects on native plants are least likely (Cook 1966, Harper et al. 1990, Whisenant and Wagstaff 1991, Chambers and Norton 1993, Newhall et al. 2004).

Although small mammals and insects are more challenging to manage, evidence suggests they can substantially impact salt desert plant communities through herbivory and granivory (Bleak et al. 1965, Currie and Goodwin 1966, Plummer 1966, Van Epps and McKell 1980, Blaisdell and Holmgren 1984, Ostoja 2008). Van Epps and McKell

(1980) attributed 50% of field mortality among containergrown seedlings to small mammal herbivory. Effects on A. canescens plants has been shown to vary among ecotypes, ranging from negligible feeding to complete crown removal (Van Epps and McKell 1980, Aldon 1983, Young et al. 1983, Longland and Bateman 1998); differences in defensive chemicals among ecotypes may contribute to differences in the level of damage by insects and small mammals (Sanderson et al. 1987).

Awareness of small mammal and insect populations in and near restoration sites, understanding how they might affect restoration plantings, and considering strategies for dealing with them (Ostoja 2008), may help improve salt desert restoration success. Although information for salt deserts is lacking, work from Intermountain West sagebrush steppe habitats may be useful. For example, broadcast seeding was more prone to seed loss by harvester ants that primarily forage at the surface, while rodents could locate and retrieve buried seeds in a sagebrush steppe study (Ostoja 2008). To manage granivory in restoration of sagebrush steppe, Ostoja (2008) and Longland and Ostoja (2013) suggest reducing edge:interior of restoration sites, creating buffers in which "sacrifice seed" is planted at higher density than restoration seed, winter application of "diversionary seed" to increase probability of native species germinating from seed caches, and deterring small mammals by use of owl perches. Additionally, harvester ants seemed to discriminate against seed infected with mycorrhizal fungi, so restoration seed coated with mycorrhizae may be more likely to be rejected by harvester ants (Ostoja 2008). Although small mammals and insects can negatively impact salt desert shrub communities, they also provide valuable services including prey for predatory animals, improving soil structure by burrowing, burrows serving as habitat for other animals, and accumulation of seed caches that can germinate (Blaisdell and Holmgren 1984). A better understanding of how small mammals and insects impact restoration success in salt deserts is needed.

Recommendations and Research Needs

Based on the results of our survey of salt desert restoration sites in western Colorado, as well as an extensive literature review of both natural ecological processes and restoration approaches for salt deserts in the Intermountain West, we recommend some approaches that may help improve restoration success (Figure 4) and identify research priorities to further support our ability to successfully restore these systems. Many of these recommendations may also be applicable to similar water-limited systems.

 Given difficulty of active restoration in Intermountain West salt desert ecosystems, the possibility of passive restoration combined with improved management should be considered.

- Where passive restoration is not preferred or possible, transplants or diverse seed mixes utilizing local ecotypes (as much as possible) should be considered.
- When economically feasible, the use of shrub transplants can increase restoration success. Concentrating plantings in small islands can reduce costs and allow for eventual spread of shrub seedlings to surrounding areas.
- Adequate moisture is essential for plant establishment. Revegetation efforts can be planned to occur during years when regional precipitation is predicted to be above average (e.g., positive phase ENSO) or when supplemental water can be secured for the site.
- To promote robust root development of establishing native shrubs, supplemental water should be supplied using deep pipe irrigation (Bainbridge 2007). In other desert systems, this method has improved survival and growth of plants after irrigation has ceased.
- Where restoration is to occur in sites invaded by non-native annuals, the site should be pre-treated to remove or reduce competition to native seeds or transplants. The most appropriate methods for achieving this will depend on the type of existing vegetation, site characteristics and weather conditions at the time of treatment but may include disturbance caused by mechanical planting equipment, tillage, herbicide application, and/or prescribed burning.
- Livestock grazing should be carefully managed in areas undergoing restoration. Although others have recommended excluding livestock for the first three years after revegetation, newly establishing plants may need protection from livestock longer depending on climatic conditions. After three years, sites should be evaluated on a year-by-year basis to determine if plants are vigorous enough to withstand grazing. When palatable species production can support livestock, grazing should be confined to the dormant-season (i.e., late fall–winter).
- There has been limited documentation of science-based restoration approaches and outcomes in North American salt desert plant communities. Whenever possible, land managers conducting restoration should strive to include replicated treatment applications with sufficient control areas for valid comparisons in order to document success and failure of various approaches. Areas for future research that are not well-understood in salt deserts, but potentially important for native plant establishment and survival in restorations, include:
 - Overcoming seed dormancy for native shrubs,
 - Role of seed mix diversity and seeding rates in revegetation success,
 - Use of different types of mulches for improving germination and seedling establishment,

- Role of soil microbes (biological soil crusts, mycorrhizae), and
- Impacts of granivory and herbivory by small mammals and insects.

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