Journal of Arid Environments 115 (2015) 44–52

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Restoring a desert ecosystem using soil salvage, revegetation, and irrigation

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ARTICLE INFO

Article history:
Received 25 February 2014
Received in revised form
13 December 2014
Accepted 8 January 2015
Available online

Keywords:
Fertile island
Outplanting
Recovery
Restoration
Topsoil

ABSTRACT

Effective restoration techniques are needed in many arid lands for reversing degradation and desertification. In the Mojave Desert of the American Southwest, we tested experimental techniques for enhancing survival of salvaged perennial plants and their establishment on severely disturbed sites. Rooting hormone, slurry, and soaking treatments were ineffective at enhancing plant survival of salvage. Survival of salvaged plants after one year of nursery care was 48% (1017 of 2105 plants). Of these survivors, 50% survived 27 mo after transplanting back to field restoration sites. On restoration sites, irrigation increased transplant survival by 50% (DRiWATER, a slow-release gel) and 79% (hand watering), compared to no irrigation (35% survival). Providing salvaged topsoil as a growth medium, without irrigation, doubled survival, nearly equivalent to irrigating plants. Survival varied by an order of magnitude across 23 species, and species amenable to salvage also generally survived transplanting to field sites ($r = 0.82$ between salvage and transplant survival). Selecting species amenable to restoration and identifying treatments effective at enhancing survival can reestablish native perennial plants, often considered a first step in restoring desert ecosystems.

1. Introduction

When desert ecosystems are severely disturbed, natural recovery may be slow or not provide functions for biodiversity conservation and ecosystem services (Allen, 1995; Bainbridge, 2007; Cortina et al., 2011). Active revegetation and restoration using effective, practical techniques can promote recovery and ecological functions (Aronson et al., 1993; Grantz et al., 1998; Burke, 2008). For example, revegetating desertified land in the Ulan Buh Desert reduced sand encroachment by 85% to Jilantai Salt Lake, among the most economically important salt sources in China (Gao et al., 2002). To achieve post-mining restoration in the Western Australia arid zone, soil treatments, combined with reintroducing plant propagules, created conditions suitable for plant establishment during times of high rainfall (Commander et al., 2013).

While these examples illustrate that revegetation is achievable, the same factors in deserts that limit natural recovery from disturbance complicate restoration (Allen, 1995; Burke, 2001; Brown and Al-Mazrooei, 2003). Intense granivory by invertebrates and mammals can remove large quantities of seed, and the amount remaining is subject to infrequent conditions suitable for germination (Suazo et al., 2013). An advantage of planting nursery-grown plants is that it bypasses necessity for field germination and seedling establishment (Bean et al., 2004). However, nursery-grown outplants face intense herbivory, often dry and nutrient-poor soil, and extreme climatic conditions (Commander et al., 2013). Selecting species most amenable to revegetation techniques and employing treatments to promote plant establishment can help increase restoration effectiveness (Abella and Newton, 2009). Protecting plants from herbivory (e.g., by enclosing plants in mesh cages), providing supplemental water, and promoting soil health are examples of treatments that can enhance plant survival (Bainbridge, 2007). Salvaging topsoil from areas to be disturbed for later re-application can promote soil health by retaining organic matter, soil microbes, and water-holding capacity, which may enhance plant establishment (Ghose, 2001). Reestablishing native perennial plants is often considered a first step in restoring desert ecosystems, because perennial plants form fertile islands. These fertile islands of nutrient-enriched soil and

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http://dx.doi.org/10.1016/j.jaridenv.2015.01.003

ameliorated microclimate regulate spatial patterning of biological activity and recruitment of annual plants (Padilla and Pugnaire, 2006; Cortina et al., 2011; Abella and Smith, 2013).

The objective of this study was to determine influences of species selection and experimental treatments on survival of salvaged perennial plants for restoration in a disturbed desert ecosystem. First, we anticipated that applying rooting hormone and soaking plants in water or water-retaining slurry upon salvage would increase species' ability to survive salvage (c.f. Fidelibus and Bainbridge, 1994). Second, we expected that transplant survival would be greater on field sites receiving salvaged topsoil compared to no topsoil (Burke, 2008). Third, we anticipated that DRiWATER (a slow-release irrigation gel) would increase survival similar to watering transplants by hand (Aref et al., 2006). Fourth, we expected ability to survive transplanting to vary among 23 species we evaluated (Bean et al., 2004). We conducted the experiment in a nationally designated protected area, where management goals include conserving biodiversity while allowing human recreation, also making esthetic restoration a priority.

2. Materials and methods

2.1. Study area and experimental sites

We conducted this experiment within the 563,513-ha Lake Mead National Recreation Area, managed by the National Park Service, in the eastern Mojave Desert of southwestern USA (Fig. 1). The Mojave is a hot desert receiving most of its precipitation in winter, with the remainder mainly monsoonal summer storms in July–August. A weather station near our experimental sites reported 1973–2012 averages of 16 cm/yr of precipitation (64% falling from November through April), 14 °C January daily high, and 41 °C July daily high (Valley of Fire State Park Weather Station, 610 m in elevation, Western Regional Climate Center, Reno, Nevada). Vegetation physiognomy is desert shrubland, with dominance by *Larrea tridentata*, *Ambrosia dumosa*, and *Atriplex hymenelytra*. Owing to numerous invertebrates, small mammals such as *Lepus californicus* (jackrabbit), and larger herbivores including *Ovis canadensis nelsoni* (bighorn sheep), granivory and herbivory is intense (Suazo et al.,

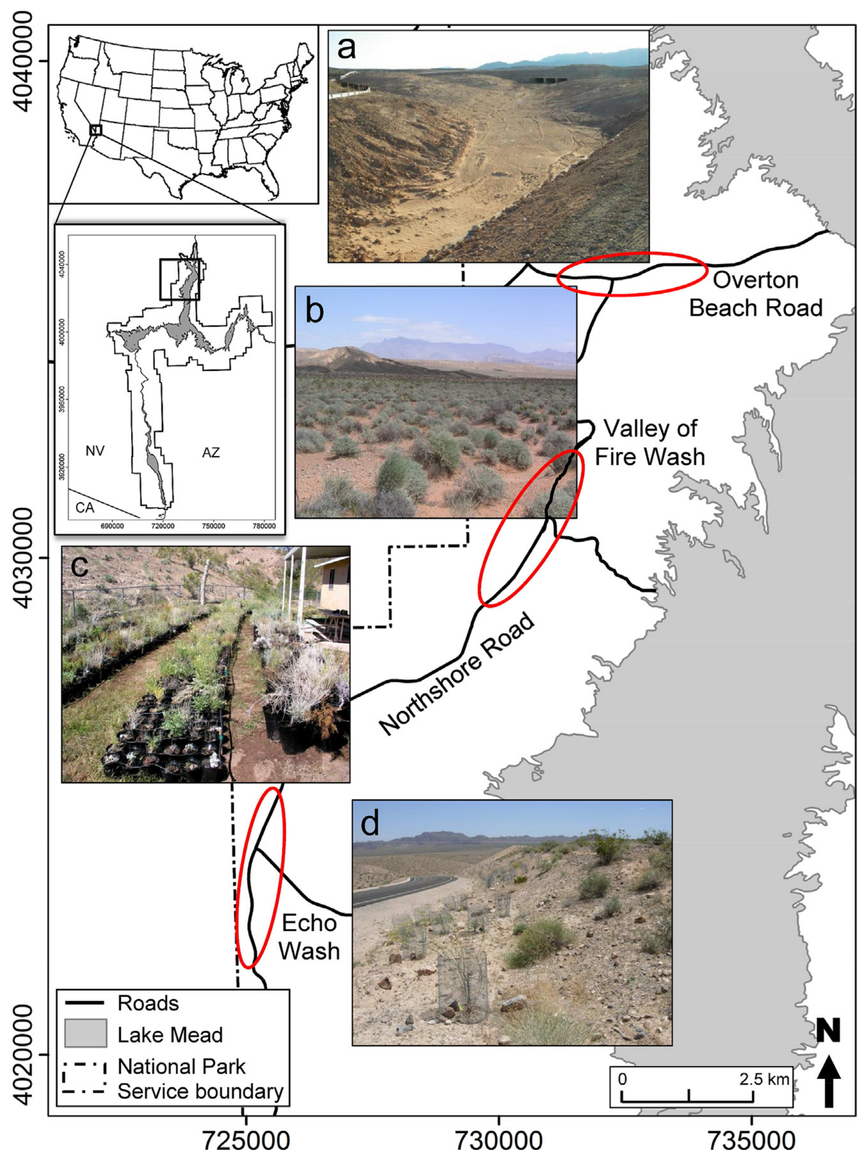

Fig. 1. Location of Lake Mead National Recreation Area in the Mojave Desert, USA, and study sites where we conducted a desert restoration experiment. Photos: a, severely disturbed site (after road removal) to be revegetated at Overton Beach; b, example of undisturbed desert at Valley of Fire Wash site; c, field nursery housing salvaged plants; and d, transplants back in the field at Echo Wash. Photo d by S.R. Abella; others by L.P. Chiquoine. Coordinates are UTM (m), North American Datum 1983.

2013). Livestock grazing is not authorized, but some trespass cattle and *Equus asinus* (feral domestic burro) inhabit the area.

Our three experimental sites were along Northshore Road in the northeastern part of the study area and occupied Gypsids and Calcids, suborders of Aridisols in U.S. soil taxonomy (Lato, 2006). Containing abundant gypsum or calcium carbonate, these soils have either gypsic or calcic horizons. As part of roadway maintenance and safety improvement, construction activities re-aligned Northshore Road to straighten and widen the road corridor. At each site beginning in 2008 using large machinery, the existing road pavement was torn up, topography re-contoured, and disturbed soil either smoothed or covered with topsoil salvaged from nearby areas to be destroyed by the new road (Fig. 1).

2.2. Plant salvage, treatments, and assessment

Table 1 shows the timeline of project activities and experimental treatments. Before construction activities, we salvaged perennial plants from the future new corridor of destruction using hand shovels to excavate as much of the root system as possible. We used bare-root salvage (i.e. minimal soil retained), which has an advantage of each plant being lighter in weight and easier to transport. We targeted plants to salvage that were larger than seedlings, but less than the 50th percentile of size, so that salvage operations and nursery processing could be done by hand. Twenty-three species of native perennials, including 2105 total individuals in rough proportion to species abundance within the area to be destroyed, were salvaged in fall 2008 (Table 2). Each plant was numbered uniquely to track it throughout the experiment.

On site immediately after salvage, plants within species were randomly treated with either: 1) root-stimulating hormone (1H-Indole-3-butanoic acid; $C_{12}H_{13}NO_2$ [IBA]), at a concentration of 100 ppm in water, by dipping roots into the solution for a few seconds (Hortus USA Corp., New York, New York); 2) a 4 g/L slurry of Watersorb water crystals, a gel polymer designed to absorb and slowly release water to roots (Watersorb Corp., Fayetteville, Arkansas, USA); 3) IBA + slurry; 4) simply dipping roots in water; or 5) soaking roots in water overnight for 12–14 h before planting in pots the next morning. After treatment, we potted plants in 4-L (smaller plants) or 19-L (larger plants) plastic nursery pots filled with 1:3 organic mulch:sand. Plants were stored in a temporary field nursery (fenced, open at top) at Overton Beach and were given 3 cm of water each day through drip irrigation (Fig. 1c). The drip system operated 3× daily for 8 min each time.

We evaluated survival status (live/dead) in November 2009, after 12 mo of nursery residence since salvage. After plants were weaned off irrigation by watering them only twice daily in November and once daily in December 2009, we moved them to the field for planting in January 2010.

A total of 143 new plants, either seedlings or originating from root fragments, appeared in pots during nursery storage. As they appeared, we transplanted these new plants (which also were then tagged for tracking) into pots intermingled with the other pots and watered them in the same manner as other plants. We did not include the 143 new plants in statistical analyses of salvage survival and treatments, but we did subsequently include them in the field planting.

Table 1
Events and their timing during a desert restoration experiment in Lake Mead National Recreation Area, Mojave Desert.

Events	Timing	Description
Salvage + treatments	Oct 2008	Plants salvaged, treated with IBA, slurry, or water
Construction	Nov 2008–Dec 2009	Old road removed, site re-contoured
Salvage nursery care	Oct 2008–Jan 2010	Plants reside in pots with drip irrigation
Final salvage assessment	Nov 2009	Plant survival assessed after 12 mo of nursery care
Topsoil application	Dec 2009–Jan 2010	Stockpiled topsoil applied to old roadbed
Planting + treatments	Jan 2010	Salvaged plants installed in field; irrigation started
Field planting assessment	Mar 2010, 2011, 2012	Plant survival after 3, 15, and 27 mo in field

2.3. Field planting, treatments, and assessment

Topsoil was salvaged by heavy machinery scraping the upper 5–20 cm of soil. The salvaged soil was stored in piles (1.5–3 m high) on site. Salvaged topsoil was available in sufficient quantity to place in a layer up to 5 cm thick on about three-quarters of area within restoration sites in December 2009. In January 2010, we transplanted salvage survivors using hand shovels by digging holes appropriately sized, to accommodate either the 4-L or 19-L volume of pots in which plants had been kept. We filled the holes with water and then transferred in the potting soil and plant. We gave each plant 1 L of water and enclosed them in circular cages (1 m tall and open at the top), made of 0.5-cm mesh hardware cloth, with the bottom of cages buried 3 cm deep and affixed to the ground using rebar.

Plants were randomly assigned one of three irrigation treatments: DRiWATER (a slow-release irrigation gel), hand watering, or no watering beyond that given at the time of planting. We followed manufacturer recommendations for applying DRiWATER, by placing an 8-cm diameter plastic tube into the ground, angled toward plant roots and the top (covered with a plastic cap) near the soil surface. We then inserted a cylindrical DRiWATER gel into the buried tube (DRiWATER Inc, Santa Rosa, California, USA). We replaced gel packs monthly in summer (May through September) and every three months in cooler months (October through April). The amount of water delivered by DRiWATER is variable, dependent on how much water that roots extract (DRiWATER Inc, Santa Rosa, California, USA). The hand watering treatment delivered 0.5 L of water to each plant once a month. This delivered 10 cm of water for the year, representing a 63% augmentation of the long-term average rainfall of 16 cm/year.

We recorded plant survival at 3, 15, and 27 mo after transplanting, with the final assessment in March 2012. During the final assessment, we also counted live perennial plants in areas that had received or not received topsoil, but that had received no active revegetation (i.e. no salvaged perennial plants were planted). This would represent natural recruits.

2.4. Data analysis

Plant survival data were analyzed as two phases: salvage and field planting, and overall from salvage through planting. We conducted analyses of treatments using different subsets of the data set containing sufficient plants to analyze across species (or grouped by lifeform [cactus, grass, forb, shrub]). Because their survival was 100% or near and hence no variation among treatments, we did not analyze cactus species statistically. To perform statistical analyses, we used PROC GLIMMIX, with binomial error to accommodate the alive/dead response variable and incorporating a logit link function (SAS 9.1; SAS Institute, 2009).

To analyze plant survival of salvage after one year of nursery storage, four models were used. 1) We used a two-way factorial design to assess effects of water soaking (soaked overnight, no soaking) across lifeform (grass, forb, shrub) in a general linear

Table 2
Summary of species salvaged, planted in the field, and analyzed statistically among experimental factors during a desert restoration experiment in Lake Mead National Recreation Area, Mojave Desert. Survival is provided after 12 mo of nursery care for salvaged plants, and 27 mo after planting in the field for plants that survived salvage and nursery care. Total survival is based on the percentage of plants still alive in the field after 27 mo from the total initially salvaged.

Species	Salvage		Field			Inclusion in treatment effects[b]					
	Survival	Plants	Survival	Plants	Survival	Salvage		Field planting			
	% (95% CI[a])	(no.)	% (95% CI)	(no.)	(Tot. %)	W	IBA/slurry	Topsoil/I	IT × S	IT × L	I × S
Cactus											
Ferocactus cylindraceus	100 (100–100)	5	100 (100–100)	5	100						
Opuntia acanthocarpa	86 (57–100)	7	67 (33–100)	6	57						
Opuntia basilaris	100 (100–100)	103	93 (88–97)	103	92						Yes
Sclerocactus johnsonii	100 (100–100)	8	100 (100–100)	8	100						
Grass											
Pleuraphis rigida	41 (31–53)	75	14 (3–28)	29	5						Yes
Forb											
Astragalus preussii	33 (23–43)	91	3 (0–9)	33	1	Yes	Yes		Yes	Yes	Yes
Baileya multiradiata	38 (31–46)	160	30 (21–39)	104	19		Yes	Yes	Yes	Yes	Yes
Enceliopsis argophylla	24 (15–35)	74	17 (0–39)	18	4		Yes			Yes	Yes
Eriogonum inflatum	28 (22–33)	280	27 (18–36)	89	9	Yes	Yes	Yes	Yes	Yes	Yes
Gutierrezia sarothrae	50 (13–88)	8	25 (0–75)	4	13	Yes					
Sphaeralcea ambigua	61 (53–68)	136	50 (40–60)	105	38	Yes	Yes	Yes	Yes	Yes	Yes
Stephanomeria pauciflora	42 (32–51)	98	47 (35–60)	55	27	Yes	Yes	Yes	Yes	Yes	Yes
Suaeda moquinii	26 (17–35)	98	50 (31–69)	26	13	Yes	Yes			Yes	Yes
Shrub											
Acacia greggii	19 (0–38)	16	0 (0–0)	3	0	Yes					
Ambrosia dumosa	68 (64–72)	475	60 (55–65)	360	45	Yes	Yes	Yes	Yes	Yes	Yes
Atriplex confertifolia	84 (72–97)	32	54 (36–71)	28	47	Yes		Yes	Yes	Yes	Yes
Atriplex hymenelytra	59 (41–74)	27	47 (24–71)	17	30	Yes		Yes		Yes	Yes
Encelia virginensis	67 (44–89)	18	36 (14–57)	14	28					Yes	
Ephedra torreyana	15 (10–20)	147	36 (18–55)	22	28	Yes	Yes			Yes	Yes
Hymenoclea salsola	72 (55–90)	29	19 (5–38)	21	14		Yes			Yes	Yes
Isocoma acradenia	52 (32–72)	25	38 (13–63)	16	24	Yes	Yes			Yes	
Larrea tridentata	48 (41–55)	154	53 (43–64)	73	25	Yes	Yes	Yes	Yes	Yes	Yes
Psorothamnus fremontii	40 (21–51)	39	14 (0–36)	14	5	Yes	Yes			Yes	

[a] Confidence interval.
[b] W, water; I, irrigation; IT, irrigation type (DRiWATER or hand watering); S, species; L, lifeform.

model (GLM), with effects of water soaking within lifeforms compared by *a priori* contrasts. 2) For plants not soaked overnight, we modeled survival as a two-way GLM to test effects of IBA rooting hormone (applied or not) and species. 3) We further analyzed plants not soaked overnight and treated with slurry or not as a three-way GLM including IBA, slurry, and species as fixed effects and all interactions (tested over error variance). Given no interactions existed and species was the only significant term, we compared survival across species using Tukey-adjusted contrasts. 4) Lastly, we used the same model as for (3), except that we tested effect of lifeform by grouping species as forb or shrub (there were insufficient grass individuals to include).

For those plants that survived salvage and were transplanted back to restoration sites, we also used four models to analyze survival at 27 mo after transplanting. 1) We analyzed influences of topsoil salvage (yes, no) and irrigation (yes, no) across lifeform (forb, shrub) and all interactions using a GLM with binomial error. 2) We compared irrigation type (DRiWATER, hand watering, or none) across species using a two-way factorial GLM with Tukey-adjusted contrasts. 3) We then used the same model as for (2), but with species grouped to lifeform, to assess effects of irrigation type across lifeform. 4) Lastly, we grouped irrigation treatments into irrigation/no irrigation and modeled treatment across species using a two-factor GLM. We then performed *a priori* contrasts of irrigation treatment within species.

We calculated an overall ‘budget’ for survival of each species based on tracking individual plants throughout the experiment. This budget included original number of individuals salvaged; those lost through mortality during nursery storage; gained via recruitment in nursery storage; and of the balance of salvaged plants available, the number of individuals surviving at 3, 15, and 27 mo after planting back in the field.

Table 3
Statistical results for influences of lifeform, species, and experimental treatments on survival of salvaged plants during a desert restoration experiment in Lake Mead National Recreation Area, Mojave Desert. *P*-values in bold note <0.05; italics <0.10.

Effect	DF	*F*	*P*
a) Lifeform and water			
Lifeform	2, 22	0.4	0.648
Water	1, 22	2.6	0.120
Lifeform × water	2, 22	2.5	0.104
b) Species and IBA (no water, no slurry)			
Species	4, 333	3.5	**0.008**
IBA	1, 333	0.0	0.983
Species × IBA	4, 333	2.3	*0.058*
c) Species, IBA, and slurry (no water)			
Species	5, 1138	26.6	**<0.001**
IBA	1, 1138	0.4	0.533
Species × IBA	5, 1138	0.5	0.752
Slurry	1, 1138	1.5	0.226
Species × slurry	5, 1138	0.7	0.649
IBA × slurry	1, 1138	2.4	0.121
Species × IBA × slurry	5, 1138	0.9	0.495
d) Lifeform, IBA, and slurry (no water)			
Lifeform	1, 20	28.1	**<0.001**
IBA	1, 20	0.7	0.424
Lifeform × IBA	1, 20	0.3	0.594
Slurry	1, 20	1.3	0.273
Lifeform × slurry	1, 20	0.7	0.407
IBA × slurry	1, 20	5.8	**0.026**
Lifeform × IBA × slurry	1, 20	0.6	0.454

3. Results

3.1. Weather conditions

Weather during the experiment was generally typical of the Mojave Desert climate. The four-year period of the experiment received 96% of average long-term precipitation, and temperature also was near average (Online Appendix 1). Generally, the period of plant salvage, construction, topsoil salvage, and plant nursery storage had below-average precipitation, whereas the 30-month period encompassing field planting received 119% of average precipitation. Two of three fall/winter/spring hydrological years during this 30-month period had above-average precipitation, and one summer was above and the other near average.

3.2. Salvage treatments

Water, IBA rooting hormone, and slurry applied to plants at the time of salvage did not increase survival in the nursery (Table 3, Fig. 2). In fact, some treatments reduced survival, such as soaking the shrubs in water. Across treatments, survival varied significantly among species. *A. dumosa*, *Sphaeralcea ambigua*, and *L. tridentata* displayed among the greatest ability to survive salvage, and *Ephedra torreyana* and *Eriogonum inflatum* the least (Fig. 2c).

3.3. Field treatments

Survival of salvaged plants and seedlings transplanted back to field restoration sites varied statistically among species, lifeform, and irrigation treatment (Table 4). While topsoil salvage exhibited $p = 0.11$, its effects were ecologically noteworthy. Overall, transplants on salvaged topsoil exhibited 56% survival, compared to 25% without topsoil. Salvaging topsoil increased survival by at least a third across lifeform and irrigation treatments and in some cases by up to 5× (Fig. 3a). Moreover, topsoil salvage alone (with no irrigation of plants) resulted in survival nearly equivalent to irrigating plants.

Table 4
Statistical results for influences of lifeform, species, and experimental treatments on survival of transplants in the field during a desert restoration experiment in Lake Mead National Recreation Area, Mojave Desert. *P*-values in bold note <0.05; italics <0.10.

Effect	DF	*F*	*P*
a) Lifeform, topsoil, and irrigation			
Lifeform	1, 10	1.5	0.255
Topsoil	1, 11	3.0	0.109
Irrigation	1, 9	7.0	**0.027**
Lifeform × topsoil	1, 10	0.6	0.471
Lifeform × irrigation	1, 6	1.8	0.223
Topsoil × irrigation	1, 9	0.6	0.475
Lifeform × topsoil × irrigation	1, 6	0.6	0.485
b) Species and irrigation type			
Species	3, 6	8.5	**0.014**
Irrigation type	2, 4	7.0	**0.049**
Species × irrigation type	6, 12	1.7	0.200
c) Lifeform and irrigation type			
Lifeform	1, 2	24.3	**0.039**
Irrigation type	2, 4	14.7	**0.014**
Lifeform × irrigation type	2, 4	0.2	0.814
d) Species and irrigation			
Species	6, 12	7.4	**0.002**
Irrigation	1, 2	12.2	*0.073*
Species × irrigation	6, 12	0.6	0.730

Type of irrigation affected survival differently among species (Fig. 3b). DRiWATER and hand watering resulted in similar survival for *A. dumosa* and significantly higher than no irrigation. In contrast, hand watering produced higher survival than both DRiWATER and no water for *S. ambigua*. Compared to no irrigation, the two irrigation types similarly enhanced survival by 65% overall

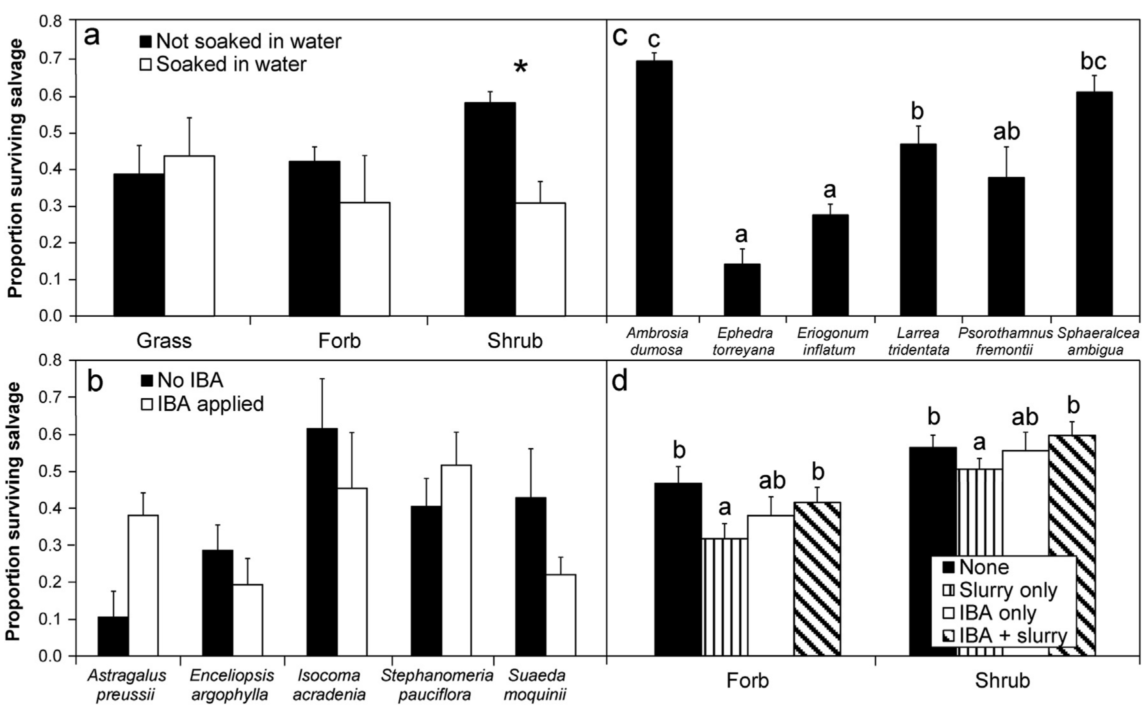

Fig. 2. Influences of lifeform, species, and treatments on survival of salvaged plants after 12 mo of nursery care during a desert restoration experiment in Lake Mead National Recreation Area, Mojave Desert. Values are means and error bars are 1 SEM. (a) Influences of lifeform and soaking plants in water overnight after salvage. The asterisk notes difference ($p < 0.05$) between treatments within a lifeform. (b) Influences of species and application of IBA, a rooting hormone. (c) Survival across species that received both IBA and slurry but no water. Species without shared letters differ at $p < 0.05$. (d) Effects of slurry and IBA on plant survival. Means within lifeforms without shared letters differ at $p < 0.05$.

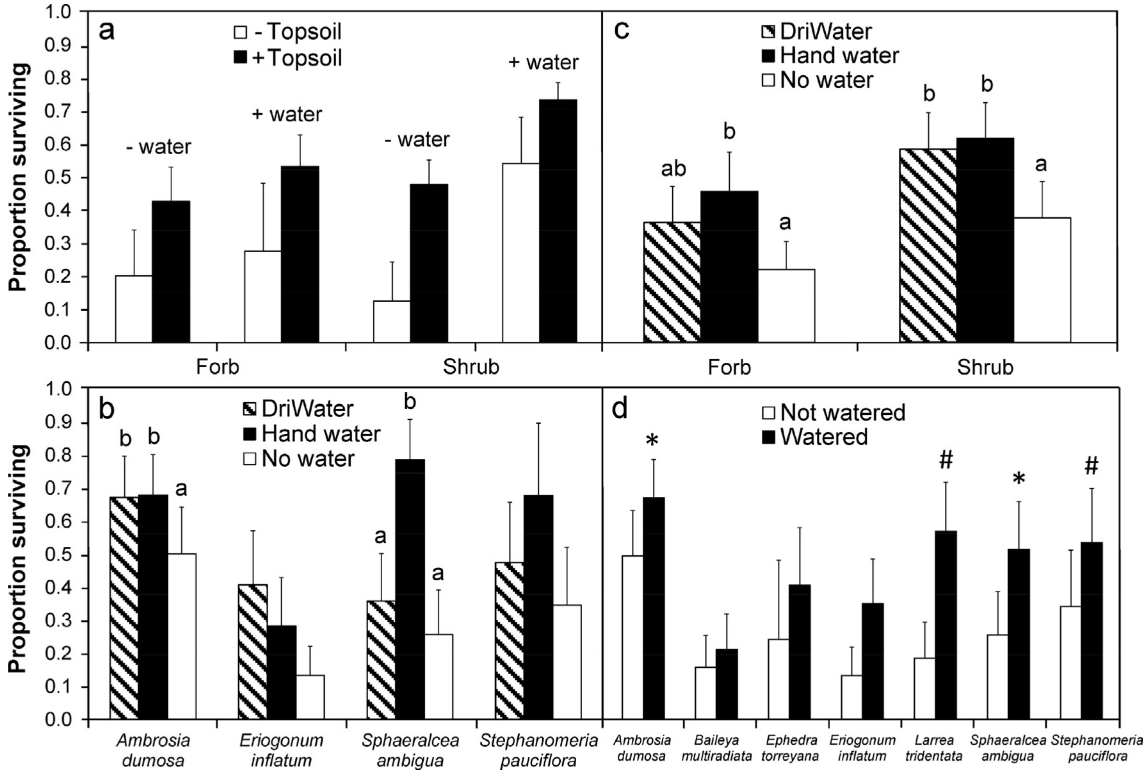

Fig. 3. Influences of lifeform, species, topsoil salvage, and irrigation on plant survival 27 mo after planting in the field during a desert restoration experiment in Lake Mead National Recreation Area, Mojave Desert. Values are means and error bars are 1 SEM. (a) Effects of topsoil and irrigation across plant lifeforms. (b) Effects of irrigation type within plant species (treatments without shared letters within species differ at $p < 0.05$). (c) Effects of irrigation type within plant lifeform (treatments without shared letters within lifeforms differ at $p < 0.05$). (d) Influences of irrigation/no irrigation within species, where symbols note differences between treatments within a species (*$p < 0.05$; #$p < 0.10$).

across lifeforms (58% survival with irrigation, 35% without; Fig. 3c). In comparing overall irrigation/no irrigation among species within lifeforms, irrigation increased survival, but statistical significance and magnitude of the increase varied among species (Fig. 3d). Species benefitting most from irrigation and showing significant increases were *L. tridentata*, *S. ambigua*, *Stephanomeria pauciflora*, and *A. dumosa*.

3.4. Plant survival 'budget'

There were 2105 original plants salvaged; 1017 (48%) of these survived salvage, and 143 plants were gained via recruitment into pots during nursery storage (Table 2). Seven plants were damaged or lost during the process of transplanting, resulting in 1153 plants to place in the field. Of these, 571 (50%) were still alive after 27 months. Thus, plants alive at restoration sites at the end of the experiment constituted 27% of those originally salvaged plus seedlings recruited in the nursery (571 of 2105 plants). Surviving the first 3 and 15 months in the field was critical, because mortality rate thereafter declined. Survival was 92% at 3 months, 61% at 15 months, and 50% at 27 months.

Regarding species, four cacti species overall survived salvage best (99%; 122 of 123 plants) and also best survived field planting (93%; 113 of 122 plants). Two of eight forb species exhibited >25% total survival (salvage through field planting) and 6 of 10 shrub species exhibited >25% total survival. The best-performing species included the forbs *S. ambigua* and *S. pauciflora*, and the shrubs *Atriplex confertifolia*, *A. dumosa*, *A. hymenelytra*, *L. tridentata*, and *Encelia virginensis*.

Salvage survival was related to field-planting survival (Fig. 4). With few exceptions, such as *Hymenoclea salsola*'s high salvage but low field survival, species that best survived salvage also did well in field planting.

Out of an original planting density of 459/ha, with 50% survival the density of live perennial plants was 228/ha in areas receiving salvaged plants at the end of the experiment (March 2012). In contrast, there were no natural recruits (including seedlings) in areas with or without topsoil but that had not received salvaged perennials (Fig. 5). Any non-planted seedlings occurring in previous years died before the final assessment, which occurred following a dry winter and spring (Online Appendix 1).

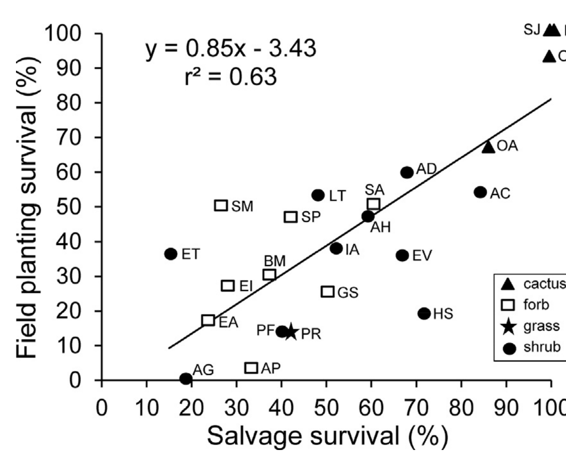

Fig. 4. Relationship between survival of salvage and transplanting back to the field at 27 mo. Species are abbreviated as first letter of genus and species (e.g., AG = *Acacia greggii*; Table 1).

Fig. 5. Views of a desert restoration experiment in Lake Mead National Recreation Area, Mojave Desert, USA. Top left: undisturbed desert in the foreground looking toward ongoing road construction in the background where revegetation occurred after construction was completed. Top right: typical lack of vegetation at the end of the experiment in disturbed areas that had not received revegetation treatments. Bottom left: foreground is the end of the revegetation area (showing *Baileya multiradiata* with DRiWATER) with disturbed roadside in the background not receiving revegetation treatments and containing no perennial plants. Bottom right: typical planting arrangement of salvaged plants along the disturbed and revegetated roadside. All photos by S.R. Abella, except top left by L.P. Chiquoine.

4. Discussion

4.1. Topsoil

Plant survival was qualitatively improved for all species when planted on restored topsoil versus on disturbed subsoil, and benefits of topsoil salvage nearly equaled those of irrigating plants. Several factors regarding topsoil salvage might have promoted plant survival while also providing other ecosystem benefits. Studies of upper soil layers in undisturbed desert suggest that plants placed in topsoil benefited from greater soil nutrients, soil water-holding capacity, and soil biota including mycorrhizae (Allen, 1995). While organic matter, nutrients, soil biota, and seeds can be lost during the soil salvage process (e.g., via 'dilution' if topsoil is mixed with subsoil) and ensuing storage, we stored soil less than a year. This was less than a threshold of 6 years for nearly complete loss of biotic components from stored topsoil in India arid land (Ghose, 2001). Although not easy when using large machinery, salvage operations that precisely collect only upper soil layers avoid diluting topsoil with subsoil (Scoles-Sciulla and DeFalco, 2009). Because soil total N can be twice as concentrated in the upper 8 cm of soil compared to deeper layers (Nishita and Haug, 1973), precisely salvaging upper layers is critical to maximize retention of nutrients and mycorrhizae while minimizing costs and space needed for storage. To further increase efficiency, future work could test salvaging only 'fertile island' soil below perennial shrubs, because this soil can contain orders of magnitude greater concentrations of nutrients and soil biota than interspace soil between shrubs (Padilla and Pugnaire, 2006).

4.2. Irrigation

DRiWATER and hand watering resulted in similar overall increases in plant survival over no irrigation, but there were some species-specific responses to irrigation type. Major differences in water delivery between the two types include that hand watering provides a periodic pulse (compared to DRiWATER available more slowly and consistently), is applied to the soil surface (DRiWATER is inserted 10–15 cm below the surface), and is delivered around plants (DRiWATER can spread around plants but was originally given on just one side). It is unclear if these differences in location and periodicity of water delivery somehow interacted with root traits or physiology to make *S. ambigua* unresponsive to DRiWATER, as compared to equivalent amenability to irrigation types in *A. dumosa*.

With our results supporting those of Aref et al. (2006), who found enhanced shrub growth with DRiWATER in Saudi Arabia but also species-specific responses, refining understanding of soil moisture dynamics and interactions with species is warranted. Species do not equally use DRiWATER, and further work is needed to identify optimal amounts required to minimize costs (Newton, 2001; Aref et al., 2006). Some species do not even require a full gel pack while others use frequent replacement packs. Additional research also is needed to identify whether variations in DRiWATER application (e.g., burial depth or angle of the tubes relative to root mass) could facilitate use of DRiWATER by species such as *S. ambigua*.

4.3. Species traits, lifeform, and survival

There was an order of magnitude range among species in their ability to survive salvage and field planting. If relationships between species traits and suitability to revegetation exist, a model forecasting amenability of candidate species before restoration projects begin could help target efforts toward species with greatest chance of success. Our results, combined with published literature, suggested mixed evidence regarding overall relationships of species traits with survival, but they revealed considerations for further research.

Lifeform, life span, rooting habit, mycorrhizal association, and resiliency to disturbance are some of the numerous traits that could influence amenability to revegetation (Smith et al., 1997). Among lifeforms, cacti performed best, forbs were not generally among the best species excepting the suffrutescent *S. ambigua*, and shrubs were variable but overall performed better than forbs. It appeared that species of smaller stature – including the forbs *Astragalus preussii*, *Baileya multiradiata*, and *E. inflatum* and the perennial grass *Pleuraphis rigida* – had lower survival generally than larger species. This may partly correlate with life span because these small-statured species are also shortest lived, but *S. ambigua* and *S. pauciflora* are considered relatively short-lived and performed well. Rooting habits are not known for all species in our study and they also can vary among soil types, but relationships of survival with rooting also appear mixed. For example, two of our similarly top-performing species differ in their rooting habits: *A. dumosa* has a shallower, more compact root system than *L. tridentata*'s broader and deeper system (Schwinning and Hooten, 2009). Mycorrhizal associations also could influence survival, and one of our weakest-performing species, *B. multiradiata*, exhibited highest density of mycorrhizal hyphae and arbuscles among 19 Mojave Desert species in a previous study (Titus et al., 2002).

The strong correlation ($r = 0.82$) across species between salvage survival and subsequent transplant survival at field sites decreased, but persisted ($r = 0.49$), even with exclusion of cacti (Fig. 4). Owing to this correlation, species traits might similarly influence amenability to both salvage and planting. Particular attention is needed to evaluate methods to enhance survival of small-statured forbs, which generally performed poorly in both the salvage and field survival phases. On the other hand, these may be species for which developing seeding or soil seed bank treatments is more effective than salvage and transplanting.

Interestingly, recent analyses of how perennial plant lifeforms (ranging from short-lived forbs to long-lived shrubs) respond to disturbance suggest that response to disturbance and amenability to active revegetation could be inversely related, at least for some species. In general, short-lived forbs and grasses increase after disturbance in the Mojave Desert, while cacti and long-lived shrubs decrease (Abella, 2010; Shryock et al., 2014). We found essentially the opposite pattern for salvage and transplant survival: cactus and some long-lived shrubs (such as *L. tridentata*) performed best, while short-lived forbs and grasses generally performed poorest. An exception was the short-lived forb *S. ambigua*, which increases after disturbance and performed reasonably well in our revegetation experiment (Fig. 4). A potential overall relationship across desert perennial plant lifeforms, where lifeforms most reduced by disturbance are most amenable to revegetation, warrants further evaluation.

4.4. Functional benefits

To improve arid land restoration technology, a next step in this research could be evaluating progression of ecological functions on restoration sites. For example, dynamics of fertile island formation are not well understood in either undisturbed or restored desert ecosystems. Some processes like leaf litter deposition, trapping of seed, and microclimate amelioration might begin immediately around restored perennial plants. Other processes like accumulation of soil nutrient pools and 'cultivation' of annual plant communities could begin later (Padilla and Pugnaire, 2006). Flowering and seed production of surviving transplants also warrants attention, because in addition to expanding plant populations, this can quickly provide food resources for other desert biota (Abella et al., 2012). Federally endangered *Gopherus agassizii* (desert tortoise), for example, can rely on green foliage of native perennial plants, including *S. ambigua*, which was one of our most readily established species, for food and water during dry years with few annual plants (Martin and Van Devender, 2002). Reestablishing perennial plants, often considered a first step in desert restoration, is feasible through careful species selection and use of effective treatments.

Acknowledgments

This study was funded by the Federal Highway Administration through a cooperative agreement between the National Park Service (Lake Mead National Recreation Area [LMNRA]) and the University of Nevada Las Vegas (to S.R. Abella), with time donation from Natural Resource Conservation LLC to prepare the manuscript. We thank Cayenne Engel, Donovan Craig, Alex Suazo, Joslyn Curtis, Pam Sinanian, Sylvia Tran, Carrie Norman, Janis Lee, Dara Scherpenisse, Eric Cotto, Toshi Yoshida, Ryan Howell, Tiffany Pereira, and LMNRA collaborators for help with fieldwork and plant care; Sharon Altman for creating figures and reviewing the manuscript; and two anonymous reviewers for helpful comments on the manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2015.01.003.

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