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Contrasting Long-Term Survival of Two Outplanted Mojave Desert Perennials for Post-Fire Revegetation

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Post-fire recovery of arid shrublands is typically slow, and planting greenhouse-raised seedlings may be a means of jump-starting this process. Recovery can be further accelerated by understanding the factors controlling post-planting survival. In fall 2007 and 2009, we outplanted seedlings of two contrasting native evergreen shrubs—fast-growing Nevada jointfir and slow-growing blackbrush—across five burned sites in the Mojave Desert. To increase soil moisture and optimize seedling survival, we experimentally applied and evaluated soil amendments and supplemental watering. We also evaluated two herbicides that reduce competitive invasive annual grasses and two types of herbivore protection. Survival of jointfir outplanted in 2007 was 61% after 43 months, and site largely influenced survival, while herbicide containing imazapic applied more than one year after outplanting reduced survival. Reduced survival of jointfir outplanted in 2009 coincided with delayed seasonal precipitation that intensified foliar damage by small mammals. In contrast, blackbrush survival was 4% after 43 months, and was influenced by site, type of herbivore protection, and greenhouse during the 2007 outplanting, and soil amendment during 2009. Counter to expectations, we found that supplemental watering and soil amendments did not influence long-term survival of either blackbrush or jointfir. Shrub species with rapid growth rates and broad environmental tolerances, such as jointfir, make ideal candidates for outplanting, provided that seedlings are protected from herbivores. Re-introduction of species with slow growth rates and narrow environmental tolerances, such as blackbrush, requires careful consideration to optimize pre- and post-planting conditions.

Keywords *Coleogyne ramosissima*, *Ephedra nevadensis*, rehabilitation, restoration, transplant

Introduction

Restoring structure and function to native shrub communities is a primary goal of post-fire rehabilitation in the Mojave Desert where shrubs are not fire-adapted (Brown and Minnich, 1986; Webb et al., 2009). Desert fires incinerate shrubs and

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promote invasive annual plants, thereby modifying forage and thermal cover for sensitive wildlife (Esque et al., 2003; Vamstad and Rotenberry, 2010) and slowing recovery of species composition (Brown and Minnich, 1986). The invasion of Mediterranean grasses has fundamentally changed ecosystem processes in the Mojave Desert by altering the attributes of desert fires (Brown and Minnich, 1986). Fires in the Mojave Desert were once patchy and limited in extent, but the proliferation of invasive grasses now fuels extensive fires (Brooks and Matchett, 2006). Desert fires kill seeds in the topsoil and reduce the abundance of reproductive adults (Hassan and West, 1986; Esque et al., 2010b). Wind-blown transport of sediment in semiarid shrublands also increases 7- to 67-fold following fire (Whicker et al., 2002; Sankey et al., 2009), eliminating surface structures that capture seeds (Soulard et al., 2013), redistributing soil nutrients, and mechanically injuring growing plants (Zobeck and Fryrear, 1986). Restoring canopy cover reduces wind speed and soil erodibility, while entrapping eroded material (Floyd and Gill, 2011; Munson et al., 2011).

With natural recovery rates for arid lands estimated between decades and centuries (Webb and Wilshire, 1980; Webb et al., 2009), practices that accelerate re-vegetation are particularly desirable to land managers. Broadcast seeding is commonly used in arid lands (Grantz et al., 1998a; Glenn et al., 2001; DeFalco et al., 2012), but infrequent precipitation results in rare germination and establishment for many species (Beatley, 1974; Baskin and Baskin, 1998). Typically within a month of seeding, significant numbers of seeds can be redistributed by wind and surface flows or collected by granivores (DeFalco et al., 2012). Even with favorable germination conditions, emerging seedlings may not withstand subsequent lack of precipitation or competition from invasive annual grasses (Hardegree and Van Vactor 2004).

Outplanting, the transplantation of greenhouse-raised plants, bypasses the germination and establishment stages *in situ*, although success in the Mojave Desert has varied widely (Abella and Newton, 2009). Previous studies, however, have mainly involved compacted, overturned, farmed, or otherwise severely disturbed surface soils that are unlike soil conditions created by fires in desert shrublands (Brum et al., 1983; Grantz et al., 1998b; Glenn et al., 2001). To evaluate post-fire outplanting, we tracked seedling survival of the evergreen shrubs *Ephedra nevadensis* S. Watson (Nevada jointfir) and *Coleogyne ramosissima* Torr. (blackbrush) for 43 months after outplanting at recently burned sites in the northeastern Mojave Desert.

Low soil moisture as a result of extended drought leads to death of long-lived desert perennials (Bowers, 2005; Miriti et al., 2007); therefore, we implemented soil amendments and supplemental watering to increase moisture in the root zone during establishment. We investigated soil amendments of three types: natural organic mulch, a corn-based super absorbent polymer (Zeba), and a cellulose gum-based gel that releases water as it degrades (Rain Bird Irrigation Supplement). We predicted that soil amendments would prolong moisture availability near the roots (Bhardwaj et al., 2007), and watering would directly increase soil moisture, thereby increasing seedling survival over control plants. Furthermore, we hypothesized that influences of soil amendments and watering would be additive, such that plants receiving both would have greater survival compared with either alone.

Based on increased annual plant biomass following desert fires (Brooks, 1999; Esque et al., 2010a), we also applied herbicides to reduce the competitive impact of invasive annual grasses (DeFalco et al., 2007). We hypothesized that survival of seedlings outplanted into plots treated with herbicide would be greater than in control plots, and that a pre-emergent herbicide would have a more prolonged impact than a post-emergent.

Herbivores also cause significant outplanting failure, particularly in recently denuded areas where forage is limited (Abella and Newton, 2009); therefore, we compared two common types of protection – plastic cones and wire mesh cages. In addition to influencing herbivory, we hypothesized that cones and cages would alter seedling temperature, thereby impacting survival.

Methods

Study Area and Species

The study was conducted at five sites within Clark County, Nevada that burned once since wildfires were first documented during the 1980s (Figure 1). The Goodsprings (35°55′N, 115°26′W), Loop (36°09′N, 115°26′W), Fork (36°15′N, 114°13′W), and Tramp (36°18′N, 114°10′W) fires occurred in summer 2005, and the Scenic Fire (36°08′N, 115°28′W) occurred in summer 2006. All sites are blackbrush/mixed-shrublands but vary in elevation and precipitation (Figure 2). Most soils are aridisols within the suborders calcid or durid, whereas others are entisols within the suborder orthent (Soil Survey Staff, 1999). All soils are shallow with a lithic or paralithic contact, a duripan, or a calcic or petrocalcic horizon within 100 cm of the surface.

The study species can co-occur in North American desert shrublands and represent contrasting strategies for growth. Fast-growing Nevada jointfir (*Ephedra nevadensis* S. Watson) is a stem-photosynthesizing dioecious gymnosperm that readily re-sprouts after disturbance and is a widespread co-dominant at 300–1900 m elevation. Slow-growing blackbrush (*Coleogyne ramosissima* Torr.) is a nonclonal microphyllus shrub in the Rosaceae found at 700–2000 m elevation. Blackbrush can dominate undisturbed habitat, but does not readily recolonize after disturbances such as fire (Callison et al., 1985). Both species are wind-pollinated, mast-fruiting (i.e., individuals synchronously produce abundant seed 1–2 years per

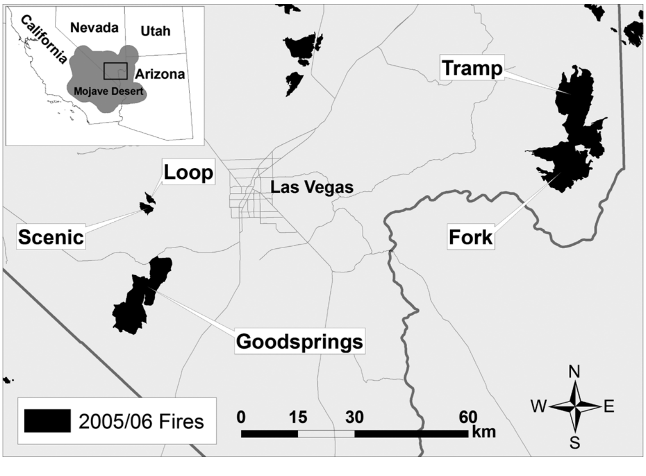

Figure 1. Location of four fires within the Southern Nevada Fire Complex (summer 2005) and the Scenic Fire (summer 2006) where we outplanted seedlings.

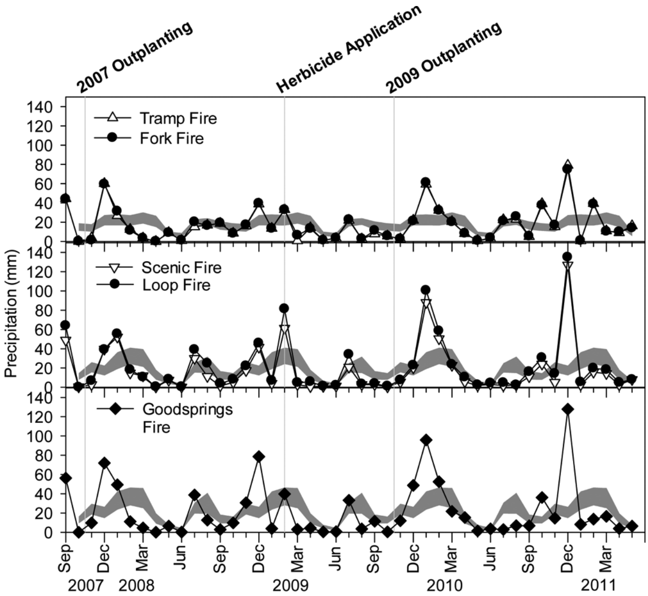

Figure 2. Monthly precipitation for lower-elevation Tramp (1030–1210 m a.s.l.) and Fork (1045–1275 m) sites (upper panel), mid-elevation Scenic (1180–1215 m), and Loop (1190–1305 m) sites (middle panel), and higher-elevation Goodsprings (1280–1465 m) site (lower panel) in Clark County, Nevada. The 95% confidence interval around the 1945–2005 monthly averages (dark gray shading) were derived from the Fork, Scenic, and Goodsprings sites, respectively. Monthly precipitation was derived from the PRISM Climate Mapping Program, Oregon State University (http://www.prismclimate.org).

decade), and have large seeds that are dispersed or consumed by heteromyid rodents (Meyer and Pendleton, 2005; Hollander and Vander Wall, 2009).

Experimental Design

We outplanted 3,101 blackbrush and 510 jointfir seedlings across fifteen 14 × 14–m plots at each of the Loop, Goodsprings, Tramp, and Fork fires in October/November 2007 ($N = 60$ plots). Plots were situated in groups of three where soil, slope, and burn severity were similar within groups and randomly assigned a herbicide treatment of Roundup (Monsanto Company, St. Louis, MO), Journey (BASF Corporation, Research Triangle Park, NC), or no herbicide.

Seedlings were propagated at two local greenhouses. Blackbrush were cultivated for 4 months or 1 year, and jointfir for 9 months at one greenhouse; and blackbrush were cultivated for 1 year at the other. Approximately equal numbers of seedlings representing the greenhouses, ages, and species were stratified among the sixty plots. Within each plot, seedlings were spaced evenly (1 plant per 2–4 m^2) and then randomly assigned one of eight soil moisture amendment × watering treatment combinations (Table 1). The soil amendments were (1) Rain Bird Irrigation Supplement (Rain Bird IS, DriWater, Inc., Santa Rosa, CA), (2) Zeba (Absorbent Technologies, Inc., Beaverton, OR), (3) weed-free garden mulch, or (4) no amendment. Watering treatments were water reservoir or no supplemental water.

Table 1. Number of outplanted seedlings assigned to each treatment by species in 2007 and 2009

2007 Outplanting

Soil amendment*	Nevada jointfir		Blackbrush	
	Watered	Not watered	Watered	Not watered
Rain Bird IS	64	65	380	398
Zeba	65	64	389	395
Mulch	60	67	385	391
Control	66	64	375	402

2009 Outplanting

Soil Amendment*	Nevada jointfir	Blackbrush
Rain Bird IS	213	350
Mulch	214	353
2 × Mulch	212	353
Control	223	351

Note: The treatments were stratified over 15 plots at each of 4 sites in 2007 (60 plots), and over 20 plots at a single site in 2009.

*Soil Amendments: Rain Bird IS, Rain Bird Irrigation Supplement (manufactured by DriWater, Inc., Santa Rosa, CA); Zeba (Absorbent Technologies, Inc., Beaverton, OR); Mulch, 1 L weed-free garden mulch; 2 × Mulch, 2 L weed-free garden mulch; Control, no amendment.

Two years later, we outplanted 1,407 blackbrush and 862 jointfir into twenty 14 × 14–m plots at the Scenic Fire. Seedlings were grown at a single greenhouse and stratified among four soil amendment treatments (organic mulch, 2 × organic mulch, Rain Bird IS, or none; Table 1).

Outplanting Procedure

We dug a 30 × 30 × 30–cm hole for each seedling and mixed 30 g Zeba granules, 1 L weed-free garden mulch, or 2 L weed-free garden mulch into the native soil. We installed Rain Bird IS according to the manufacturer's directions and replaced gel packs 7 and 16 months after the 2007 outplanting. During planting, we also mixed 2 L water into the native soil profile for all treatments, including controls. For the watering treatment, we installed a 0.5 L closed-top plastic reservoir with a 30-cm wick buried below rooting depth (adapted from Bainbridge, 2007). Reservoirs were refilled monthly from December 2007 until October 2008.

After planting, each seedling was provided an additional 2 L of water, tagged with a unique number, and protected from herbivores with a 17 cm diameter × 46 cm tall plastic cone (Tree Sentry, Summit Environmental Group, Toledo, OH). In early 2008, we observed warmer daytime air temperatures inside the cones than outside. To assess the influence of this temperature increase on the seedlings, we replaced cones on half the number of plants in the 2007 outplanting with closed-top 6-mm mesh cages. We also placed HOBO Pro Series Temp/Ext Temp (H08–031–08) or

StowAway Temperature (STEB16) loggers (Onset Computer Corporation, Pocasset, MA) in 26 cones and 12 cages to record interior and exterior temperatures from February to November 2008. Similarly, we established temperature loggers on cones at the Scenic Fire from February 2010 to January 2011. In mid-October 2009 we removed protection from seedlings outplanted in 2007.

Herbicide Application

Backpack sprayers were used to apply herbicides to pre-assigned plots in February 2009 with a 2-m buffer (18 × 18–m treated area). Based on manufacturers' recommendations, Roundup (active ingredient glyphosate) was applied as a 1% solution without surfactant, and Journey (active ingredients imazapic and glyphosate) as a 2% solution with 0.25% methylated seed oil surfactant (C. Deuser 2009, Lake Mead NRA, pers. comm.). Emerging red brome plants (*Bromus madritensis* ssp. *rubens*) were targeted while avoiding outplanted seedlings. Due to the variable brome density in each plot, application of Roundup varied from 1.95×10^{-4} to 7.80×10^{-3} kg glyphosate acid equivalent ha^{-1} and Journey varied from 9.85×10^{-5} to 3.94×10^{-3} kg imazapic ha^{-1} and 1.97×10^{-4} to 7.87×10^{-3} kg glyphosate acid equivalent ha^{-1}. Seedlings were protected from herbicide by their protective cones or plastic bags temporarily placed over cages.

Seedling Survival

We assessed seedlings outplanted in 2007 monthly from January–November 2008, and annually thereafter. We assessed 2009 seedlings shortly after outplanting (mid-November 2009), in early spring (February 2010), and in late summer (August 2010). Seedlings were rated as alive (green tissue), dormant (loss of green coloration, stems flexible), or dead (no green tissue, stems brittle). Mammalian herbivore damage was noted as severed twigs or stems with tooth marks.

Statistical Analyses

We used an information-theoretic approach to determine plausible explanations for seedling survival (Burnham and Anderson, 2002). Use of Akaike's Information Criterion corrected for small sample size (AICc) is favored over methods such as stepwise, backward, or forward selection because candidate models are developed based on the biology and ecology of the system (Burnham and Anderson, 2002). We developed potential explanations for survival into separate accelerated failure time models (Wei, 1992) based on two guidelines: 1) we expected that variables influencing survival would differ between species and outplanting date; therefore, we analyzed jointfir and blackbrush and 2007 and 2009 plants separately, and 2) prior to model development, we selected the most appropriate distribution type (e.g., Weibull) for the failure model by comparing log-likelihood values of intercept-only models. We developed models by combining variables of seedling age and restoration prescription (e.g., soil amendment, watering, herbicide) for each species at each date (Table 1). Multicollinearity did not occur among variables based on Pearson's $|r| < 0.75$ and variation inflation factors <10 (Neter et al., 1996).

We computed a log-likelihood for each survival model using the LIFEREG procedure in SAS (SAS, Cary, NC), and then calculated AICc (Burnham and Anderson, 2002). We compared the difference in each AICc from the model with the lowest AICc to obtain ΔAICc: ΔAICc <2 suggests substantial support for the model; ΔAICc between 4 and 7, considerably less support; and so on (Burnham and Anderson, 2002). The importance of each variable (a value ranging from 0 to 1 for least to most important) was derived by summing the Akaike weights (w_is) across all candidate models where the variable occurred (Burnham and Anderson, 2002).

For blackbrush, all main effects models that included herbicide treatment performed worse than the intercept only model (ΔAICc >5); therefore, herbicide treatment was eliminated from the set of candidate models, and all plants alive at the time of cage replacement were included in the analysis (2,513 plants). Many treatment combinations had 100% survival of blackbrush when cages were replaced, so we used the LIFETEST procedure in SAS to perform nonparametric comparisons of survival for blackbrush prior to that time.

Results

Jointfir

Prior to herbicide application, no model explained post-planting survival of jointfir seedlings better than the intercept-only model (Table 2; w_is = 0.6494). Following herbicide application, overall survival for jointfir outplanted in 2007 was 61% after 43 months, and site and herbicide were the most influential factors (Table 2; w_is = 0.9997 and 0.7655, respectively, summed over all candidate models). Jointfir survival was lowest at the Loop site (Figure 3a) and lower in plots treated with Journey than those treated with Roundup or no herbicide (Figure 3b). Supplemental watering, soil amendment, and protection type were not well-supported as explanations for survival by the set of most plausible models. Similarly, survival was strongly influenced by plot (Table 2; summed w_is = 1.0000; Figure 3c) for jointfir outplanted in 2009.

Blackbrush

Prior to cage replacement, site and age significantly influenced blackbrush survival (Site: log-rank test $\chi^2(\mathrm{df}=3, N=3101) = 80.52$, $p < 0.001$; Age blocked by site: log-rank test $\chi^2(\mathrm{df}=1, N=3101) = 152.67$, $p < 0.001$). The influence of site over these first 4.5 months was mixed: Loop had lower survival over the first 2 months, but survival at Fork decreased over the third and fourth month post-planting compared with the other sites (Figure 4a). Year-old seedlings had higher 4.5-month survival (85%) compared with 4-month-old seedlings (64%; Figure 4b).

Subsequent to cage replacement, overall survival of blackbrush outplanted in 2007 was 4% after 43 months, and protection, site, and greenhouse all influenced survival (Table 2; w_is = 1.0000, 1.0000, and 0.8974, respectively). Maximum daily air temperature was elevated inside cones by approximately 4.4°C (Figure 5a, inset). Consequently, seedlings with cones initially had higher survival during winter months, but after 24 months, survival was higher for seedlings in mesh cages (Figure 5a). The influence of site was mixed: Fork and Tramp had lower survival over the first year, while Loop and Goodsprings had decreased survival over the second year (Figure 5b). Greenhouse also influenced survival, with plants from one greenhouse having consistently higher survival after outplanting (Figure 5c).

Table 2. Analysis of seedling survival for Nevada jointfir and blackbrush outplanted into post-fire experimental plots in southern Nevada in 2007 and 2009

Model*	k	AICc	ΔAICc	w_i
Jointfir, 2007 outplanting prior to herbicide application[a]				
Intercept only	2	425.6	0.0	0.6494
Site	6	428.6	2.9	0.1491
Water	4	428.7	3.1	0.1362
Site, Water	8	431.6	5.9	0.0332
SA	6	432.4	6.8	0.0214
Jointfir, 2007 outplanting after herbicide application[b]				
Site, Herbicide	9	498.2	0.0	0.5543
Site	6	500.5	2.3	0.1727
Site, Herbicide, SA	13	501.3	3.2	0.1138
Site, Herbicide, Water	11	502.1	4.0	0.0767
Site, SA	10	503.9	5.7	0.0322
Site, Water	8	504.5	6.3	0.0234
Jointfir, 2009 outplanting				
Plot	19	−1700.0	0.0	0.7682
Plot, SA	23	−1697.6	2.4	0.2318
Blackbrush, 2007 outplanting after cage replacement[c]				
Site, Protect, GH	11	3793.1	0.0	0.7726
Site, Protect, GH, Water	13	3797.1	4.0	0.1048
Site, Protect, Age	11	3797.6	4.5	0.0828
Blackbrush, 2009 outplanting				
SA	7	1472.8	0.0	0.9355
SA, Plot	27	1479.1	6.3	0.0397

Note: Models are ranked by ΔAICc. Only those models with some level of support (ΔAICc <7) are presented here. Akaike weights (w_i) are included for comparing the relative importance of the environmental and treatment attributes.

*Plot and treatment attributes: Site, planting location of Fork, Goodsprings, Loop, or Tramp; Plot, which plot the seedling was planted in; Water, with or without water reservoir; SA, soil amendment comparison among none, mulch, 2 × mulch (2009 only), Zeba (2007 only), and Rain Bird IS treatments; Herbicide, comparison among none, Roundup, and Journey treatments; Protect, comparison between plastic cone or wire cage; GH (blackbrush only), greenhouse where plants were grown before outplanting; Age (blackbrush only), comparison between 4-month- or 12-month-old plants.

[a] Analysis of jointfir survival prior to herbicide application (15 months) included all 510 jointfir plants.

[b] Analysis of jointfir survival after herbicide application included those jointfir plants alive at the time of herbicide application (442 plants).

[c] All main effects models that included herbicide treatment performed worse than the intercept only model (ΔAICc >5); therefore, all plants alive at the time of cage replacement were included in the analysis (2,513 plants).

Supplemental watering, soil amendment, and seedling age did not significantly contribute to our understanding of variation in survival among the set of most plausible models. In contrast, the strongest predictor of survival for blackbrush outplanted in

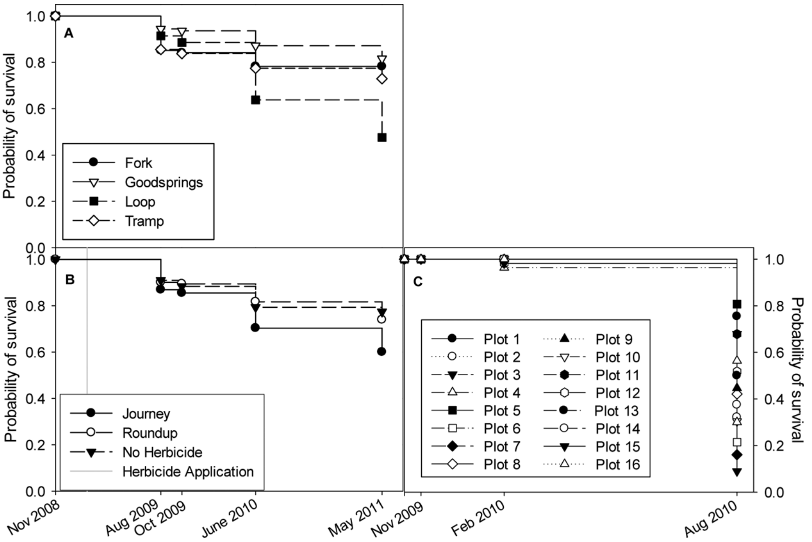

Figure 3. Survival functions for the best explanatory variables (highest weights in model with lowest AICc value) for Nevada jointfir seedlings outplanted in 2007 ($N = 442$): (a) site and (b) herbicide treatment. Survival functions for the best explanatory variable for jointfir seedlings outplanted in 2009 ($N = 862$), plot (c).

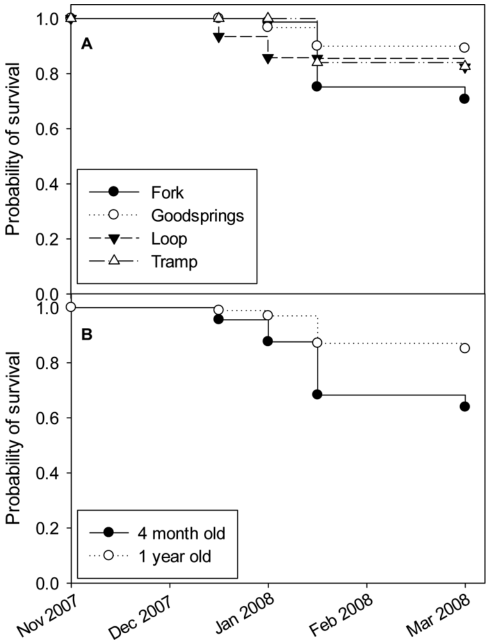

Figure 4. Survival functions for blackbrush seedlings outplanted in 2007 prior to cage replacement ($N = 3{,}101$): (a) site and (b) age of plant.

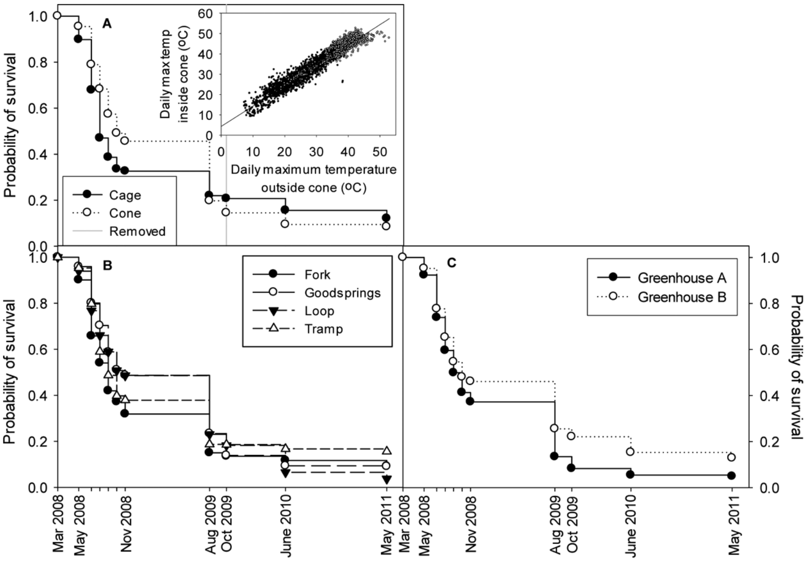

Figure 5. Survival functions for the best explanatory variables for blackbrush seedlings outplanted in 2007 after cage replacement ($N = 2{,}513$): (a) type of seedling protection, (b) site, and (c) greenhouse where plant was propagated. Inset within Figure A is a graph of daily maximum temperature inside the protective plastic cones (T_{cone}) versus daily maximum temperature outside the cones ($T_{cone} = 1.0 \times T_{out} + 4.4°C$; $r^2 = 0.934$).

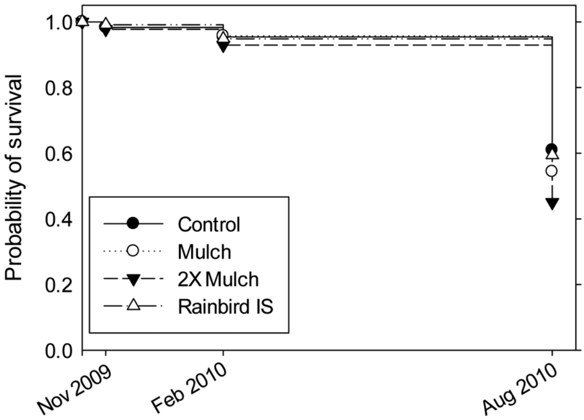

Figure 6. Survival functions for the best explanatory variable for blackbrush seedlings outplanted in 2009 ($N = 1{,}407$), soil amendment.

2009 was soil amendment (Table 2; summed $w_i s = 0.9576$), and seedlings with $2 \times$ mulch had lower survival than all other treatments (Figure 6).

Discussion and Conclusions

Counter to previous observations of short-term watering benefits on Mojave Desert species establishment (Abella et al., 2012), we found that supplemental watering and soil amendments did not influence 3.5 year survival of either blackbrush or jointfir. In a similar outplanting study on the Colorado Plateau, an initial increase in survival with supplemental watering disappeared over 4.5 years (Minnick and Alward, 2012). This equilibrated survival implies that abiotic factors override the ephemeral benefits of soil treatments in arid lands over time. The lack of effectiveness may be explained by the relatively small volume of soil under the influence of moisture treatments compared to the adjacent volume of untreated soil drawing away soil moisture. Indeed, the localized increase in soil moisture from hand watering was more ephemeral and smaller in magnitude than from a 2 mm rainfall event (data not shown). Although we attempted to increase survival in, 2009 by doubling the amount of mulch, the elevated organic content likely caused localized hydrophobic soils near plant roots, rendering the light spring rains typical of the Mojave Desert ineffectual at increasing soil moisture.

Seedling survival differed appreciably between the two species we outplanted, likely a result of the inherently higher growth rate of jointfir, which allowed plants to quickly exploit resources when soil moisture was high. Overall, survival of outplanted jointfir after one year was comparable to another study in the Mojave Desert (Edwards et al., 2000), but there are no similar published studies for blackbrush. Jointfir is dioecious and blackbrush is self-incompatible (Pendleton and Pendleton, 1998). Therefore, to become a reproductively-viable population, seedlings outplanted within denuded areas must survive to reproductive maturity and achieve a minimum density for successful wind pollination. Although plants were immature, low survival resulted in 53% of plots with one or zero live blackbrush after 43 months. In contrast, two or more jointfir seedlings (i.e., $\geq$102 plants ha^{-1}) survived past 43 months in 88% of plots, even though we outplanted jointfir at lower initial densities (408–816 plants ha^{-1}) than blackbrush (2,449–3,265 plants ha^{-1}). The density of plants necessary for pollination is not known for either species, but jointfir, unlike blackbrush, does not rely solely on sexual reproduction.

Markedly decreased jointfir survival at the Loop site coincided with removal of herbivore protection in fall 2009, at which time the number of damaged plants tripled, compared with less than doubling at the other 2007 outplanting sites (data not shown). Even with protective cones, jointfir outplanted in 2009 were also vulnerable to herbivores (17% of plants damaged), and severed branches and stems had 1–2 mm-wide tooth marks, consistent with small mammal herbivory (DeFalco et al., 2010). Herbivory may have been less important initially because above-average precipitation in fall, 2007 stimulated growth of perennials and winter annuals, thus providing abundant forage. The increased small mammal population that resulted (Beatley, 1969) ultimately damaged our outplanted jointfir seedlings when 2008–2009 fall/winter rainfall arrived late, and winter annual production was predictably low (Beatley, 1974). Although we did not monitor small mammals during our experiment, precipitation-mediated pulses in animal populations are coincident with increased herbivory in the Mojave Desert (Beatley, 1969). Vulnerability to herbivores in post-fire environments has also been documented for young Joshua trees (*Yucca brevifolia*) during extended drought (DeFalco et al., 2010; T. Esque, unpublished data). Conversely, we noted minimal herbivore damage to blackbrush, even after protection was removed, likely due to tannins that deter herbivory (Provenza and Malechek, 1983).

In contrast to times of low rainfall, declining survival during periods of high precipitation may be attributed to abundant invasive annual grasses (Beatley, 1974; Hunter, 1991). Their rapid resource uptake competitively impedes desert perennials (DeFalco et al., 2003, 2007) by placing species with slower uptake rates at a disadvantage (Gebauer and Ehleringer, 2000). Herbicides containing imazapic, such as Journey, reduce invasive annual plant biomass in the Mojave Desert by 50–80% (L. DeFalco, unpublished data) and diminish post-emergent growth of downy brome (*Bromus tectorum*) in the Great Basin (Hirsch et al., 2012). However, fast-growing jointfir was susceptible to imazapic following outplanting, as reported for other shrubs and perennial grasses (Shinn and Thill, 2004; Sbatella et al., 2011).

Plastic cones elevated maximum daily air temperatures around the seedlings by more than 4°C, initially enhancing, but ultimately reducing blackbrush survival as temperatures warmed in spring. In contrast, survival of jointfir was no different for plants protected with cages or cones, suggesting broad environmental tolerances consistent with its widespread elevational distribution (Stevenson, 1993). Distribution of blackbrush, on the other hand, is considered limited by the narrow environmental conditions necessary for recruitment (Meyer and Pendleton, 2005). In addition to conditions after outplanting, survival of blackbrush was strongly influenced by greenhouse, and the improved short-term survival of older plants further suggests the importance of propagation conditions. Although this study did not directly compare practices for propagating seedlings, their impact on post-outplant survival warrants further study.

Establishment of predisturbance plant species is one step toward restoring structure and function of disturbed arid shrublands. Following fire, rodent-dispersed species such as blackbrush and jointfir lend themselves to an outplanting approach for re-establishment because their seeds may be entirely redistributed or consumed when broadcast into denuded areas (Meyer and Pendleton, 2005; DeFalco et al., 2012). The mast-fruiting behavior of blackbrush and jointfir, in particular, means that seeds are available only once or twice per decade to naturally recolonize from nearby sources and to collect for reseeding disturbances. Our study suggests that shrub species with rapid growth and broad environmental tolerances require minimal treatment beyond effective herbivore protection for revegetating post-fire environments. Comparable species that also mature swiftly or reproduce vegetatively are most likely to create self-sustaining source populations within large burned areas. Reintroducing slow-growing species with narrow environmental tolerances and low overall survival, however, requires careful consideration to optimize pre- and post-planting conditions, such as outplanting older or larger seedlings, increasing outplanting densities, and weighing the costs and benefits of herbivore protection.

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Supplemental Material

Supplemental data for this article can be accessed on the publisher's website.

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