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RESEARCH NOTE

Developing methods of assisted natural regeneration for restoring foundational desert plants

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ABSTRACT

Assisted natural regeneration (ANR) is a restoration and management technique for enhancing the natural recruitment of desired species. To test ANR strategies in an arid environment, we applied irrigation and shelters to natural seedlings of the ecologically foundational shrub *Larrea tridentata* to enhance revegetation of a disturbed site in the Mojave Desert, USA. Irrigation did not improve seedling survival and growth. Shelters reduced 2-year survival by 31% but tripled height growth of surviving seedlings. Utility of shelter for ANR thus hinged on uncertain tradeoffs among seedling survival, height growth, and implementation costs. Mixed results suggest that further evaluating other combinations of treatments and with different species is required to understand ANR's potential for restoration in arid lands.

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Reestablishing native plants is frequently fundamental to improving soil health and successful ecological restoration on disturbed sites in drylands (Qi et al. 2015). Seeding and outplanting nursery-grown seedlings are two main techniques for restoring native plants, but these techniques can be expensive and contingent on uncertain germination and seedling survival (Pérez et al. 2019). Seeding and outplanting further assume that propagule limitation is a main impediment to restoration and that introducing propagules will facilitate plant establishment. Assisted natural regeneration (ANR) is an alternative aimed at encouraging site conditions favorable for natural regeneration through actions such as alleviating limitations on viable seed production, germination, and seedling survival (McCreary et al. 2011). This approach has the potential advantages of favoring local genetics, avoiding resource-intensive preparation and transport of plant material, and lowering costs. However, an uncertainty in applying ANR is whether restoration can utilize natural regeneration and which methods produce successful ANR.

Much of the existing ANR research and application has occurred in forests with tree seedlings, with less focus in drylands. Applying ANR in drylands would seem to have both challenges and opportunities. Regeneration of desert perennials is episodic, contingent on extreme and variable desert climates and often extreme herbivory (Housman et al. 2003). This suggests the potential of ANR to exploit rare recruitment events if

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factors limiting recruitment could be alleviated. If ANR can be effective, it could aid a fundamental component of dryland restoration of reestablishing fertile islands. Fertile islands are shaded, nutrient-enriched soils below many perennial plants, and provide nurse plant effects for stimulating further plant recruitment (Varela et al. 2017).

To develop ANR techniques for drylands, we used the Mojave Desert and its dominant shrub, *Larrea tridentata* (hereafter *Larrea*), as a model system. *Larrea* is a foundational species across much of the desert because it forms fertile islands, provides nurse-plant effects, and offers cover for wildlife (de Soyza et al. 1997). *Larrea* produces periodic large seed crops, does not form persistent soil seed banks, and has infrequent seedling establishment (Boyd and Brum 1983). The species is slow to recover naturally after severe disturbance and has exhibited minimal amenability to restoration seeding (Abella et al. 2012). These characteristics seem to make *Larrea* an ideal candidate for ANR, but whether ANR can be viable is unclear. The objective of this study was to test the hypothesis that the ANR treatments of irrigation and protection increase the survival and growth of natural *Larrea* seedlings.

We conducted the experiment in the eastern Mojave Desert, USA. This desert has hot summer temperatures, moderately cold winters, and a primarily winter-spring rainfall pattern delivering most annual precipitation. The 0.25-ha experimental site was in the Dead Mountains Wilderness, administered by the U.S. Bureau of Land Management. The site (35°02′09″N, −114°41′35″W), 286 m in elevation, is in southern California, 30 km northwest of the city of Needles. The site contained compacted soil, disturbed by a dirt road and adjoining parking area and campground. The road was used as access for the recreational parking area and campground before all were decommissioned in 2015. Plant cover on the disturbed surface was minimal compared to the 10–15% cover of mostly *Larrea* in surrounding less-disturbed shrublands. Climate, measured at Needles (elevation 277 m), had the following 1942 through 2018 averages: 6/18 °C daily minimum/maximum temperature for January, 29/43 °C for July, and 11.3 cm/year of precipitation (Western Regional Climate Center, Reno, Nevada, USA). Precipitation per year between 1942 and 2018 ranged from 2 to 28 cm.

In February 2017 on the 0.25-ha disturbed surface, we located 72 *Larrea* seedlings, 1–2 years old and 4–40 cm tall. The seedlings were $\geq$2 m from each other, growing in the open, and served as replicates.

The experimental design was a 2 $\times$ 2 factorial consisting of two levels each (present or absent) of irrigation or protection. We randomly assigned one of the four treatment combinations to each of the 72 seedlings, until there were 18 seedlings per treatment. We implemented treatments in February 2017. Irrigation was slow-release gel applied per manufacturer recommendations (DRiWATER Inc., Santa Rosa, California, USA). The application consisted of placing the gel in a cylindrical plastic tube (8 cm in diameter), burying the tube in the ground angled toward the root zone, and covering the tube's top with a plastic cap (Figure 1). We replenished gels in April, June, and August 2017 to provide a year of supplemental moisture. According to the manufacturer, the amount of moisture delivered by the gels is variable, contingent on how much plant roots extract. The protection treatment consisted of installing a green, 10 cm diameter $\times$ 60 cm tall, double-walled, plastic tree shelter around seedlings (Tubex, South Wales,

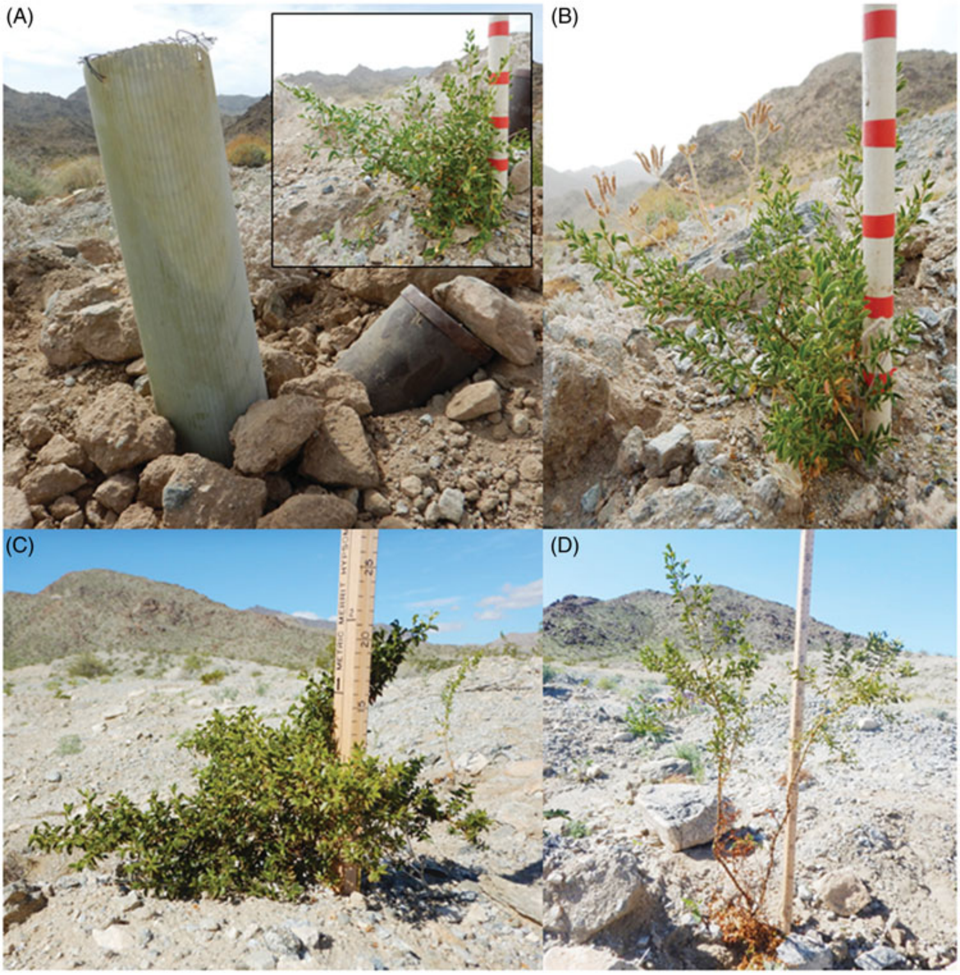

Figure 1. Examples of natural *Larra tridentata* recruits and treatments applied to them in an assisted natural regeneration experiment in the Mojave Desert, California, USA. (A) Factorial combination of protection via a tree shelter and irrigation via slow-release gel in the brown tube applied to the *Larrea* individual shown in the inset photo. (B,D) The same individual 21 cm tall in April 2017 (B) that grew to be 58 cm tall in March 2019 (D) that had received a shelter (briefly removed in the photo for taking plant measurements) and had 20% brown foliage concentrated on the lower part of the plant. (C) 22-cm tall *Larrea* in March 2019 that had received no treatment and had been 12 cm tall in April 2017. Photos by L. Chiquoine, M. Balogh, A. Rader, and S. Porter.

U.K.). Shelters were buried into the soil and anchored upright using rocks and staples affixing the shelter to the ground.

Three times within a 2-year period after treatment installation, we assessed seedling status (live or dead, distinguished by green foliage being present or absent) and height in April 2017 (spring, two months after treatment installation), November 2017 (autumn, nine months), and in March 2019 (spring, 2 years after installation). We also categorized (in 5% increments) the portion of total foliage that was brown after we noted in November 2017 that some sheltered seedlings had brown foliage.

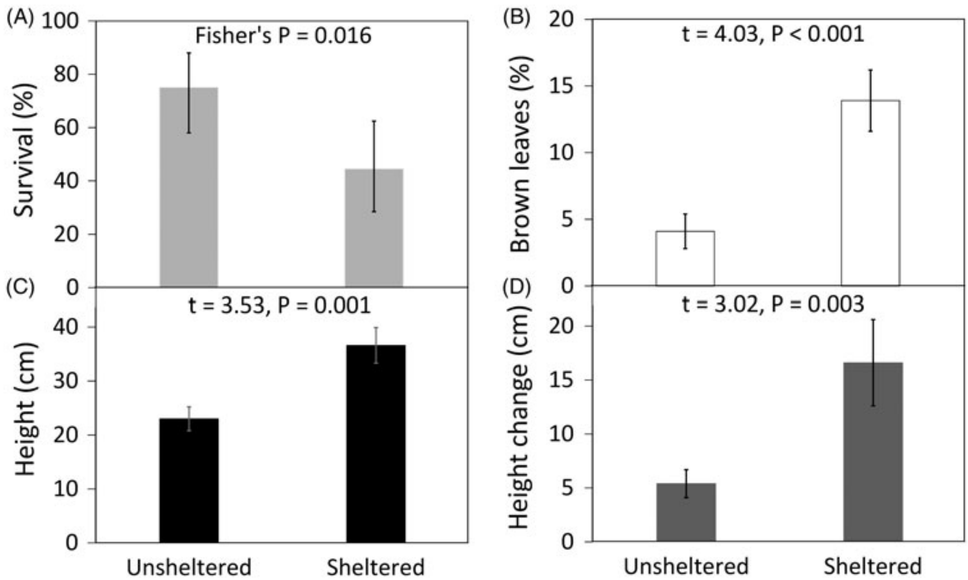

Figure 2. Characteristics of *Larrea tridentata* regeneration in March 2019 after 2 years of protection in shelters as an assisted natural regeneration treatment in the Mojave Desert, California, USA. (A) Plant survival with 95% asymmetrical confidence intervals and Fisher's exact test comparing the proportion alive between treatments. (B) Mean percentage of brown leaves, (C) plant height, and (D) change in plant height (March 2019 minus April 2017), with ±1 SEM error bars, and t tests comparing means between treatments. Irrigation had minimal influence, so the tests represent a reduced model containing protection as a main effect.

Overall plant survival was high and similar among treatments in the first year (86% survival in April 2017 and 82% survival in November 2017) but had lowered and diverged among treatments by March 2019, so we performed statistical analyses on the cumulative March 2019 data 2 years after treatment installation. We used Fisher's exact test to compare the proportion of live/dead seedlings among treatments after 2 years (PROC FREQ, SAS 9.4). To compare mean seedling height in March 2019, the change in height between April 2017 and March 2019, and the mean percentage of brown foliage in March 2019, we used a factorial, two-factor analysis of variance (PROC GLM, SAS 9.4). Irrigation and its interaction with protection were not significant in any model, so we ran final reduced models including only protection as a main effect for Fisher's exact test for survival and t tests for means.

Only about half as many sheltered as unsheltered *Larrea* seedlings survived after 2 years, a significant difference (Figure 2). However, surviving sheltered seedlings grew three times faster and were three times taller than surviving unsheltered seedlings. Sheltered seedlings proportionally had three times the brown foliage as unsheltered seedlings. Irrigation was not significant for any measure. Two-year survival of irrigated seedlings was 67% compared to 53% for non-irrigated seedlings. Between April 2017 and March 2019, irrigated seedlings increased in height by 8.4 cm (standard error of the mean [SEM] = 2.4) compared to 11.0 cm (SEM = 2.1) for non-irrigated seedlings. Across treatments, the 29 seedlings that were dead in March 2019 had been initially smaller (13.5 cm tall on average in April 2017) than the 43 alive in March 2019 (18.5 cm tall on average in April 2017).

The data suggested that the two treatments tested for assisting the establishment of natural *Larrea* recruits had either minimal influence (slow-release irrigation) or reduced survival while tripling height growth of surviving seedlings (protection via shelters). Effectiveness of protection thus hinged on whether: (1) the added height growth of surviving seedlings compensated for reduced total survival and potentially altered plant morphology, and (2) the ecological benefits were worth the labor and cost of the treatment.

Protection increased plant height and altered morphology, but effects of these changes are unclear. *Larrea* can begin flowering by age 3–4 years (Abella et al. 2012). It is uncertain if the taller seedlings would have reproductive advantages (e.g., higher rates of pollination or seed production) over shorter seedlings, because the taller, sheltered seedlings had proportionately less green foliage. Additionally, while we did not destructively sample survivors to evaluate if shelters altered root:shoot ratios, shelter studies in other regions suggest these alterations are possible (Oliet et al. 2019). Reproductive allocation in *Larrea* can hinge on the biomass of green foliage and shoot development, which in turn can be affected by herbivory (Newingham et al. 2012). It is possible that a benefit of taller plants is that they are elevated above heights accessible to some small mammal herbivores, reducing susceptibility to herbivory. However, desert small mammals can remove entire shoots and branches of *Larrea* directly from the ground (Newingham et al. 2012). Shelters made plant morphology more conical. Shapes of mature *Larrea*, as conical or hemispherical, provide different habitat structure and ecological functions (de Soyza et al. 1997). However, Bainbridge (2007) noted that greenhouse-grown *Larrea* outplanted in shelters returned to apparently natural architectures after shelters were removed.

The uncertain ecological benefits of shelters relative to the costs of implementation suggest that net benefits for ecological restoration were marginal at best. The shelter type that we used cost $3/shelter. The labor required to transport a shelter on foot 1.5 km to the restoration site in a wilderness setting, install and check on a shelter, and remove a shelter at the end of the experiment required 15 min/plant.

Results could have differed given different sets of contingency factors. The experiment spanned two dry years, with 57% (2017) and 66% (2018) of average (11.3 cm/year) precipitation, although January and February 2019 leading up to the March 2019 sampling were wet with an average of 271% of normal precipitation. We expected that irrigation and protection would especially aid seedlings during the dry 2017 spring and summer, but this expectation was not realized as most mortality occurred during this period including for treated seedlings. This result contrasts with previous experiments where supplemental summer irrigation enhanced *Larrea* growth (Newingham et al. 2012) and where irrigation (either watering by hand or slow-release gel) tripled survival of outplants (Abella et al. 2015). Shelters can increase humidity around plants through condensation on shelter interiors, but effects of reduced wind and gas exchange interacting with higher temperatures can have complex, poorly understood effects on species-specific water balances inside shelters (Oliet et al. 2019). These influences can vary with the color and design of shelters (e.g., with ventilation holes). Lethal temperatures inside shelters from a greenhouse-like effect, too little sunlight, or inadequate gas exchange could have killed foliage inside shelters (Scoles-Sciulla et al. 2015). Another potential contingency factor is seedling size, as the full range of available sizes of seedlings were included in the experiment. It is possible that focusing effective ANR treatments on the youngest, smallest, most vulnerable seedlings could maximize ANR benefits.

Shelters and irrigation have improved survival of greenhouse-grown *Larrea* seedlings outplanted at some restoration sites, including the same shelter and irrigation types used here (Abella et al. 2012). This raises a general question: are the treatments important to health of planted seedlings the same as for ANR? Our experiment implies this may not be the case.

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