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Characterizing Mojave Desert shrub ecotypes to establish seed transfer zones for military range restoration

Susanne Schwinning, Texas State University

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ECOTYPE ASSESSMENT FOR GUIDING ARID LAND RESTORATION IN THE DESERT SOUTHWEST OF THE U.S.

by

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LIST OF ABBREVIATIONS

Abbreviation	Description
AIC	Akaike information criterion
AIC_c	Akaike information criterion for small sample sizes
AMDU	*Ambrosia dumosa*
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
Δ	Carbon isotope discrimination
δD	Hydrogen stable isotope ratio
$\delta^{18}O$	Oxygen stable isotope ratio
FI	Fort Irwin garden
GLM	General linear model
h	Hour
JT	Joshua Tree garden
LATR	*Larrea tridentata*
m	Meter
mo	Month
PAR	Photosynthetically active radiation
PCA	Principle components analysis
PPT	Precipitation

φPSII	Photosystem II efficiency
SLA	Specific leaf area
T_{min}	Minimum average temperature
T_{max}	Maximum average temperature
UT	Utah garden
WUE	Water use efficiency

SUMMARY OF FINDINGS AND APPLICATION TO MILITARY INSTALLATIONS

The training grounds on Military installations are disturbed frequently by training activities or wildfire, diminishing over time their ability to provide realistic testing and training conditions. In desert environments, rates of vegetation recovery are especially slow and depend on rare occurrences of favorable years in which seed abundance is high and precipitation is reliable and above average for months to years. Ecological restoration seeks to short-cut natural recovery by transplanting greenhouse-raised seedlings and supporting early survivorship by watering. These restoration practices are costly, however, and implementation at a management scale would make sense only if there is a high probability of restoring a long-lived population that is well adapted to local environmental conditions. In this project we asked if and to what extent restoration success depends on genotype selection.

The US Armed Services has numerous military facilities in the Mojave Desert, the largest one of which is Fort Irwin National Training Center. Others include the Marine Corps Air Ground Combat Center (MCAGCC) Twentynine Palms, the Naval Air Weapons Station China Lake and Edwards Air Force Base. These installations are located across different climate regions within the Mojave Desert. Although dominant vegetation, composed chiefly of *Larrea tridentata* (creosotebush) and *Ambrosia dumosa* (burro-weed or white bursage), is ubiquitous throughout the dry valleys of the Mojave Desert, local populations may be composed of distinct genotypes that are adapted to the specific local temperature and precipitation patterns. In recognition of this, several federal and state agencies have sought to develop Seed Transfer Zones, or land

classifications within which seed can be collected and redistributed without risking maladaptation of restored populations.

The present study contributed to this larger goal by testing the viability of seed stock collected from populations across the climate range of the Mojave Desert in three climatically distinct common gardens. Specifically, our objectives were to a) establish a 3-year record of growth and survivorship after transplanting, b) determine which populations had the highest values of growth and survivorship in each garden and c) to develop generalizations that might guide restoration at military installations in the Mojave Desert.

To this end, we examined the growth and survivorship greenhouse-raised transplants, comprised of 38 populations representing 15 ecotypes across three common gardens located from the cooler, wetter northern border of the Mojave Desert to the hotter, drier southern border. The species comprised two co-dominant shubs of Mojave Desert valleys: *Larrea tridentata* and *Ambrosia dumosa*, as well as the early-successional sub-shrub *Sphaeralcea ambigua* (desert globemallow), which is an important additional food source to Mojave Desert fauna. The gardens were located at Fort Irvin (FI), near MCAGCC Twentynine Palms (JT) and near St George, Utah (UT) at the northern edge of the Mojave Desert.

Main findings

1. Growth and survivorship. Overall, transplant survivorship two-years post-transplanting was high, with the highest survivorships at FI (> 80% across species; Table 1). At FI, four populations of *L. tridentata*, five populations of *A. dumosa*, and eight

populations of *S. ambigua* achieved 100% survivorship, indicating exceptionally favorable odds for successful restoration at this location.

Survivorship was lowest at JT and attributable to lower precipitation and higher temperatures. While the UT Garden received more than twice the precipitation than FI, survivorship was intermediate, most likely because of the lower winter temperatures, which frequently dip below 0 ºC in winter. However, relative growth rates, measured as the % increase in stem diameter over the second year, was highest in UT and only second-highest at FI, except in *S. ambigua*.

Survivorship among species followed trends of longevity, with the subshrub *S. ambigua* having the lowest values and *L. tridentata* having the highest values. However, *S. ambigua* was the only species to flower after transplanting, thus was successful in completing its life cycle.

Table 1. Overall survivorship (S) and relative growth rate of stem diameter (RGR), both expressed in percentages, of 33 months-old saplings of three species across three common gardens. MAP = mean annual precipitation, T_{avg} = average annual temperature.

	MAP	T_{avg}	*A. dumosa*		*L. tridentata*		*S. ambigua*	
	(mm)	(ºC)	S (%)	RGR(%)	S(%)	RGR(%)	S(%)	RGR(%)
UT	304	16.1	71	70	72	74	26	57
FI	143	17.2	86	15	87	22	99	14
JT	90	20.0	34	3	57	10	12	58

These results indicate that the restoration of Mojave Desert shrubs from greenhouse raised stock can be highly successful. Unsurprisingly, the major limitation for survivorship and growth of greenhouse-raised transplants is precipitation. However, even in some of the most inhospitable regions of the Mojave Desert, such as near Twentynine Palms (JT Garden), shrub cover can be restored.

2. Pitfalls in genotype selection and how to avoid them. While analyzing the growth and survivorship of *A. dumosa*, we discovered that larger transplants had generally greater chances of survival. This finding was not in itself surprising; it is frequently reported in restoration experiments and explained by the fact that resilience to several stresses (e.g., drought, herbivory, freezing) tends to increase with plant size. However, what was previously unappreciated was that growth rates under comparatively mild greenhouse conditions were also ecotype-dependent. This means that conclusions drawn from comparing the survivorship of genotypes after transplanting may be confounded by the growth response of seedlings to greenhouse condition (Figure 1).

The adaptative traits of plants fall on a universal ‘fast-slow’ spectrum, in which traits that permit fast growth under mild conditions limit stress tolerance and survival under harsh environmental conditions, while traits that convey high stress tolerance limit growth rates, even under favorable conditions (Reich 2014). Therefore, ignoring genotype effects on greenhouse performance can result in misguided genotype selection.

The remedy is a genotype selection process that uses transplant size (basal stem diameter) as a co-variate in the analysis of survivorship.

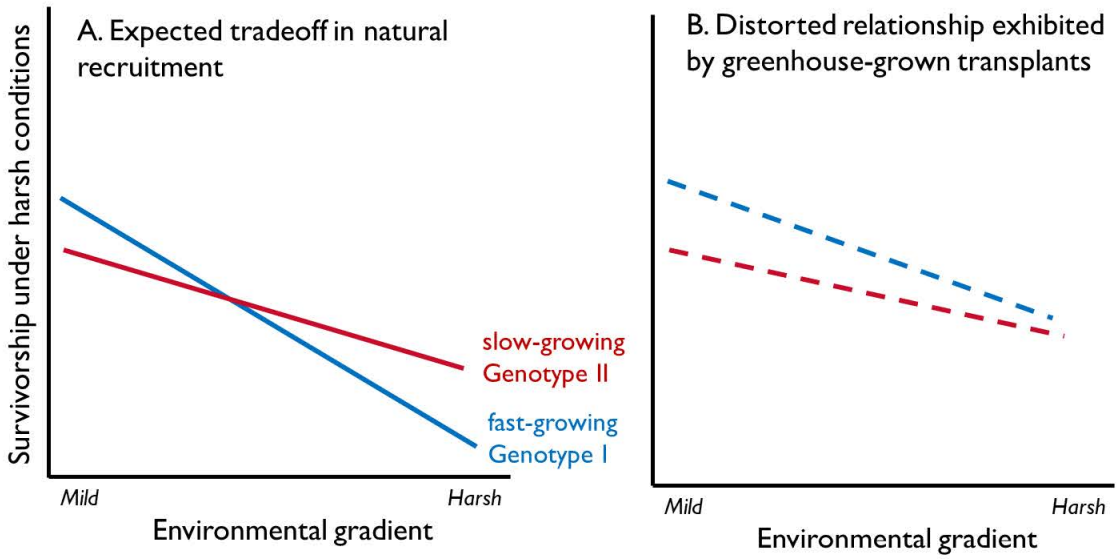

Figure 1. The growth-survivorship tradeoff and how it would be distorted by growing plants in the greenhouse before outplanting: A. Under natural conditions, fast-growing genotypes attain greater size under mild conditions, which favors survivorship, and slow-growing plants survive better under harsh conditions. B: In the greenhouse, fast-growing plants attain larger size than slow-growing plants, which positively influences survivorship after transplanting across environmental gradients.

3. Ecotypes adapted to a drier environment have higher survivorship anywhere. We examined the effect of garden, ecotype and their interaction on 2-year survivorship, correcting for the effect of initial transplant size by using transplant size as a covariate in the analysis. Significant garden x ecotype interactions would indicate that different ecotypes are uniquely well adapted for different climate regions. If fact, we found no such interactions.

In *A. dumosa*, both garden and ecotype had strong effects on survivorship (Table 2). Ecotypes from regions with lower average precipitation in October tended to have higher survivorship. Those ecotypes also had lower specific leaf area (SLA), following general expectations for drought tolerance (Reich 2014). This correlation between traits and climate of origin was only observed in the two drier gardens, FI and JT. SLA in UT was twice as high as in PI and JT, suggesting considerable phenotypic plasticity in SLA.

Thus, if SLA were used a trait indicator for drought tolerance in *A. dumosa*, it should be used only to compare individuals in the same common garden and in a climate regime the is typical for the species' core habitat.

By contrast, *L. tridentata* had no significant ecotypic variation in survivorship (Table 2). There were some correlations between climate of origin and certain photosynthetic traits. For example, ecotypes from regions with higher average precipitation in February had higher SLA and lower rates of gas exchange in summer. We conclude that while this species may have physiological and morphological trait variation between ecotypes, their effects on survivorship may be negligible.

Table 2. Effects on survivorship from March 2014 to March 2017.

	Ambrosia dumosa			*Larrea tridentata*		
	Wald χ^2	df	*p*-value	Wald χ^2	df	*p*-value
Garden	270.76	2	< 0.001	29.37	2	< 0.001
Ecotype	59.75	18	< 0.001	3.57	12	0.990
Garden × Ecotype	28.059	35	0.791	10.282	19	0.946
Initial Size	17.17	1	< 0.001	1.50	1	0.221

Our analysis is limited by the relatively short duration of the study, compared to the long lifespan of the two shrub species, decades in the case of *A. dumosa*, and many centuries in the case of *L. tridentata*. For example, we did not assess reproductive fitness components, such as age of first reproduction and seed production. Arguably, from the viewpoint of restoring disturbed military training grounds back to 'natural' conditions, the survivorship of transplanted shrubs is the primary objective. In this respect, *L. tridentata* had outstanding qualities for restoration across climate gradients and no apparent sensitivity to where seeds were sourced. By contrast, seed sourcing had a

significant effect on the survivorship of *A. dumosa*; transplants raised from seeds collected in drier regions had higher survivorship across the three gardens. Given that military training grounds will always have high disturbance levels, choosing the most stress-tolerant genotypes may serve the military's mission to maintain realistic testing and training conditions best.