


## A seed–seedling conflict for *Atriplex polycarpa* shrubs competing with exotic grasses and their residual dry matter

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**Abstract.** Native saltbush, *Atriplex polycarpa*, shrub populations are widely diminished and fragmented in the southern San Joaquin Desert of California due to habitat conversion and invasion by exotic annual grasses of mostly Mediterranean origin. The role these grasses play in saltbush population demography is not well understood. We hypothesized that saltbush seedling recruitment and growth is limited by the competitive interactions with exotic grasses, preventing saltbush stands from maintaining their populations and expanding. We predicted that saltbush seedling recruitment would be reduced by (1) light and moisture competition with the grasses; and (2) the physical barrier of grass residual dry matter (RDM) formed during senescence. To test our predictions, we investigated saltbush seedling recruitment under field conditions across six saltbush populations. We examined how variations in edaphic structure and water availability by site may have affected saltbush seedling recruitment and longer-term population dynamics. In experimental plots where saltbush seeds were sowed, exotic grass RDM reduced saltbush seedling emergence compared to seeds sown in the absence of RDM; competition post-emergence was not significant. Saltbush seedlings transplanted into the field had lower mortality and less herbivory in invaded grassy habitats compared to seedlings planted in bare zones in between established, mature saltbush shrubs. Edaphic variation and water availability by site were likely key factors affecting the success of both grass invasion and saltbush recruitment. Our results suggest that there is a seed–seedling conflict: Sites favorable for saltbush seedling emergence (minimal grass cover among mature shrubs) are unfavorable for seedling survival due to high herbivory. Conversely, sites favorable for saltbush seedling survival (high grass coverage away from mature shrubs) are unfavorable for seedling emergence. The RDM produced by grasses represents an important stabilizing feedback favoring continued grass dominance.

**Key words:** *Atriplex polycarpa*; *Bromus*; Chenopodiaceae; competition; exotic annual grasses; recruitment; residual dry matter; San Joaquin Desert.

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### INTRODUCTION

One of the chief threats to desert ecosystems is invasion by exotic species (Brooks et al. 2016).

The San Joaquin Desert within the San Joaquin Valley in California, USA, has a Mediterranean-type rainfall pattern with cool moist winters and hot dry summers. The valley floor averages less

than 250 mm of rainfall annually that is highly variable and unpredictable and has sparse native vegetation that primarily consists of species found in the Mojave Desert (Polis 1991, Pavlik 2008, Belnap et al. 2016). Due to the massive transformation of this region for agriculture, it is the most imperiled desert in North America (Germano et al. 2011). More than 60% of the native desert habitat on the valley floor, including *Atriplex polycarpa* (Torr.) S. Watson (saltbush; Chenopodiaceae) shrublands, has been converted to agriculture. Much of the remaining native habitat is highly invaded by exotic annual grasses.

Drought-adapted plants have evolved mechanisms to cope with unpredictable and low water availability (Osmond et al. 1987, MacKinnon et al. 2014). Despite adaptive mechanisms, seed germination and seedling recruitment are especially vulnerable to desert constraints. Limited seedling recruitment, both emergence and survival, is a characteristic of long-lived plants, and recruitment is often a population bottleneck (Harper et al. 1955). A single mature saltbush shrub in the San Joaquin Desert of California may produce tens of thousands of seeds every year, but in most years relatively few of these seeds germinate and successfully establish seedlings. Once seedlings emerge (January–March), they survive at very low rates, especially when co-occurring with abundant exotic annual grasses (Ciblis et al. 1998, Dodd and Donovan 1999, Germano et al. 2001, Coleman and Pratt 2019, Phillips et al. 2019).

Arid and semi-arid regions in the western United States and California have been invaded by numerous exotic annual grass species such as *Bromus madritensis* L., *Bromus diandrus* Roth, and *Avena sativa* L., that suppress native plant recruitment for a variety of reasons. In some cases, the grasses grow in such dense stands that they out-compete natives and decrease species richness (Corbin and D'Antonio 2004, Yelenik and Levine 2011). Grass seedlings generally emerge sooner than native grass and shrub seedlings and produce a dense, shallow root system (Wainwright et al. 2012). The grasses commonly share the same rhizosphere as co-occurring natives, which can limit native recruitment through competition for resources, especially water (Schultz et al. 1955, Yelenik and Levine 2011).

The residual dry matter (RDM) formed from senesced shoots of the annual grasses is dense and fibrous and does not rapidly decompose after senescence in the arid climate (Chen et al. 2018). This differs from native forbs that typically produce less aboveground biomass and therefore less RDM, which is generally non-fibrous and fragments and decomposes more quickly—resulting in bare soil until the following growing season. Persistent and dense RDM modifies habitat by increasing shading of the soil surface and lowering light and temperature levels, thereby inhibiting seedling emergence and survival (Germano et al. 2001, Bartolome et al. 2007, Wolkovich et al. 2010, Coleman and Pratt 2019, Molinari and D'Antonio 2019). Light and temperature reduction from RDM may be especially detrimental for plants such as saltbush that exhibit the C<sub>4</sub>-photosynthetic pathway, which thrive in high light and temperature conditions, becoming competitively disadvantaged in shady habits compared to C<sub>3</sub> plants (Ehleringer and Pearcy 1983). This is further exacerbated by the Mediterranean climate where available moisture is very limited outside of the approximately 4–5-month winter wet season (Germano et al. 2011). Resource competition and habitat modification by RDM from exotic grasses were previously found to negatively affect seeding recruitment of *A. polycarpa* in the San Joaquin Desert by both suppressing emergence and reducing survival (Coleman and Pratt 2019). This study was conducted at only a single field site under semi-controlled conditions; therefore, more rigorous, controlled testing in native habitat is warranted.

The present study was carried out under field conditions in native saltbush habitat in a rangeland at the south end of the San Joaquin Desert, California (Appendix S1: Fig. S1). We sampled across sites representing a broad range of edaphic and hydrologic characteristics deemed important for saltbush population viability—hypothesizing that saltbush seedling recruitment is suppressed by the habitat-altering effects of exotic grasses. We predicted saltbush recruitment would be reduced by (1) structural modification of RDM during the dry season, and (2) competitive interactions with exotic grasses during the wet season. Furthermore, we predicted that distinct cohorts of shrubs would be identifiable by age due to past episodic recruitment during wet

years of abundant soil moisture availability and mortality events during consecutive drought years when grass populations were reduced. Alternatively, if saltbush was recruiting successfully annually, sites would have a continuous age structure. These predictions are consistent with the highly variable interannual rainfall patterns in the San Joaquin Desert (Germano et al. 2011) and observations that seedling emergence in the region is highly episodic (*personal observations of the authors*), perhaps coinciding with intermittent periods of drought when the grasses are diminished (Brome Crash Theory; Minnich 2008). Lastly, we predicted that microsite differences, particularly edaphic characteristics in our edaphically diverse study area (Bartow and Dibblee 1981, Spiegel et al. 2016), and water resource variation between the sites would affect saltbush recruitment success.

## METHODS

### Study area

The study was conducted in the Comanche Point region of Tejon Ranch at the southeast corner of the San Joaquin Desert, California (Table 1; Appendix S1: Fig. S1). This active rangeland has a broad range of abiotic factors that could affect saltbush recruitment, including topography (slope, aspect), soil (texture and depth), fire, hydrology, drought, and biotic factors (livestock grazing and native animal herbivory).

Comanche Point consists of low hills underlain by marine siltstone, sandstone, and conglomerate

formations (Dibblee and Minch 2008). The hills are extensively dissected by seasonal drainage channels and natural gullies (eroded badlands). Major seasonal creeks (arroyos) include Tejon Creek, Comanche Creek, and Little Sycamore Creek. Dominant soil series include Chanac, Pleito, and Badlands. The soil is relatively deep (100+ cm), and the dominant soil texture is sandy loam. Exotic annual grasses occur throughout the area, the most dominant of which are *B. madritensis*, *B. diandrus*, and *A. sativa*. We do not have data on nitrogen deposition, but the site is located at the southern terminus of the San Joaquin Desert and we estimate that it receives 7–11 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> (Bytnerowicz et al. 2016). Small, isolated, fast-moving grass fires are common in the region, with the last large fire encompassing the whole study area occurring in the summer of 2011.

The region has a Mediterranean-type climate with hot, dry summers and cool, moist winters (Germano et al. 2001, 2011, CDFW 2003). It is also classified as a desert in the context of the amount of annual rainfall (average rainfall = 178 mm/yr; Germano et al. 2011). In a typical year, rains begin in mid to late December and persist until late March or early April. The dry season typically spans from early May until November. Within the study area, we assessed saltbush recruitment at six sites differing in soil characteristics and landscape position (Table 2). We continually monitored air temperature and precipitation with a weather station (Davis Vantage Pro1, Davis Instruments, Hayward, California, USA; Appendix S1: Fig. S1) positioned central to the six sites.

### Naturally emerged seedling survival

Approximately two-month-old saltbush seedlings were tagged at the juvenile (beyond cotyledon) stage and monitored over time to determine survival (250 across five sites, Table 3). We measured survival once a month for 17 months (May 2016–October 2017) with a two-year re-measurement conducted in June 2019. The seedlings were tagged at their base within the plot used for demographic analysis described below, approximately two months after initial emergence in March 2016. The seedlings were chosen at random. All tagged seedlings co-occurred with exotic grasses, and grass cover was quantified (see Exotic Grass Cover).

Table 1. Site characteristics of six saltbush (*Atriplex polycarpa*) populations located in the Comanche Point region of Tejon Ranch in the San Joaquin Desert of California.

Site number	Latitude (°)	Longitude (°)	Elevation (m)	Slope/aspect
1	35.091943	-118.810477	225	20°/West facing
2	35.092488	-118.819262	233	Flat
3	35.135932	-118.832060	203	35°/West facing
4	35.136666	-118.828924	207	30°/West facing
5	35.131265	-118.813313	185	Flat
6	35.161564	-118.796194	191	45°/Southwest facing

Note: Geographic coordinates served as the central survey points for a demographic analysis of each site.

Table 2. Summary of sites where the various studies and experiments described herein were conducted across six saltbush (*Atriplex polycarpa*) populations.

Site number	1	2	3	4	5	6
Grass coverage	x	x	x	x	x	x
Soil composition	x	x	x	x	x	x
Tagged seedlings	x		x	x	x	x
Transplanted seedlings			x	x		
Demography	x	x	x	x	x	x
Seasonal water potentials	x	x	x	x	x	x

### Survival of transplanted seedlings in native saltbush shrubland compared to exotic grassland

The saltbush populations surrounding Comanche Point are isolated from other saltbush populations and abruptly give way to grassland habitat dominated by exotic annual grasses immediately adjacent to native shrubs. To test the competitive inhibition of grasses on saltbush survival and related to edaphic factors, we out-planted 9-month-old saltbush seedlings into both grassland (treatment) and saltbush shrubland (control). There were a limited number of available seedlings for transplantation; thus, a subset of two from the main six sites were chosen to achieve sufficient treatment replication (Table 2). The two sites were chosen based on their dense saltbush habitat with sparse inter-shrub grass coverage, while also having immediately adjacent grasslands entirely devoid of saltbush. Seedlings and native soil were collected from the sites on 29 January 2016. Seeds were opportunistically collected from multiple individuals from each site based on phenology

(not all shrubs were in fruit) and were kept in clear aerated glass containers until propagation, while the native soil was kept dry in shallow 40 × 20 cm greenhouse flats. Seeds did not require moisture/temperature stratification or physical scarification prior to propagation. In April 2016, the seeds were sown 1 cm deep in the native soil in a greenhouse on campus at California State University, Bakersfield, and irrigated once a day for 10 min. Once germinated, seedlings were planted in individual 20 cm tree tubes and moved outdoors, watering once weekly for the next six months, after which watering was reduced and they were hardened off for two months. The seedlings were twice fertilized at one-quarter the manufacturer's recommended amount, once in July 2016 and once in November 2016 (Miracle-Gro All Purpose Plant Food, 100123; Scotts Miracle-Gro Company, Marysville, Ohio, USA). Seedlings were then out-planted at the two sites in early 2017 after adequate winter rainfall had occurred. At each site, seedlings were planted into both grassland (treatment) and saltbush shrubland (control) along a single randomly selected East/West oriented transect within each site ( $n = 38$  seedlings per transect). Seedlings were spaced 1 m apart and watered at the time of planting with 500 mL of water each. We measured the survival and height of each seedling once per month for eight consecutive months through the dry season (February–October 2017), with a single recent round of data collected in June 2019. We also noted the cause of mortality when damage was visible.

Table 3. Survival and mortality of naturally occurring *Atriplex polycarpa* seedlings tagged across six sites.

Site number	Number of seedlings tagged <sup>†</sup>	Number of survivors in 2017	Mortality (%) in 2017 <sup>‡</sup>	Number of survivors in 2019	Mortality (%) in 2019 <sup>‡</sup>	Grass coverage (%) in 2017 <sup>‡</sup>
1	67	15	78 <sup>A</sup>	3	96 <sup>B</sup>	60.4 (8.2) <sup>A</sup>
2	...	...	...	...	...	35.1 (4.6) <sup>B</sup>
3	63	29	54 <sup>B</sup>	2	97 <sup>B</sup>	18.4 (9.3) <sup>C</sup>
4	40	5	88 <sup>A</sup>	0	100 <sup>A</sup>	6.4 (1.9) <sup>D</sup>
5	40	25	40 <sup>B</sup>	17	58 <sup>C</sup>	71 (8.3) <sup>A</sup>
6	40	3	92 <sup>A</sup>	1	98 <sup>B</sup>	4.3 (0.76) <sup>D</sup>
Totals or mean	250	77	70	23	92	32.6

Notes: Two hundred fifty seedlings were tagged in May 2016 and monitored every month for survival until October 2017. Coverage of exotic grasses represents mean grass levels measured at each site on 20 February 2017 ( $n = 30$  measurements per site). Standard errors of the mean are shown in parentheses.

<sup>†</sup> Site 2 had no naturally occurring seedlings.

<sup>‡</sup> Values with different letters vary significantly between sites (Tukey's HSD,  $P < 0.05$ ).



### *Size class analysis to estimate demography and historic recruitment events*

Episodic seedling recruitment during high rainfall years and mature shrub mortality during severe drought years has been documented in California deserts (Casper 1996, Brown and Wu 2005, Miriti et al. 2007). Saltbush seedling recruitment is primarily episodic and associated with abundant soil moisture (*personal observation of the authors*). Similarly, mature shrub death is also episodic and linked primarily to drought (Sankary and Barbour 1972; *personal observation of the authors*). We observed an episodic seedling recruitment event in the winter and spring of 2016, which was at the end of a five-year drought phase (Minnich 2008). One reason why saltbush may recruit after successive years of intense drought could be that grasses are not as abundant, thus decreasing their competitive ability and the levels of remaining RDM. We predicted this might be an important factor for saltbush demographics. One way to determine if populations are expanding, stable, or contracting is to assess the age structure of a population. If a population contains a homogenous mix of ages, it indicates that recruitment is ongoing. If a population contains an even age of individuals or is composed of distinct even-aged cohorts, then it indicates that recruitment is episodic. We predicted that mature saltbush stands would contain distinctly aged cohorts due to past episodic recruitment events such as the one we observed in 2016.

A demographic analysis was conducted for each of the six sites to assess differences in age structure within and between sites. All measurements were taken between May and December 2016. The timeframe for measurements was due to the time-intensive approach for measuring each shrub. To account for changes to demographics with relatively fast-growing seedlings, we did not measure seedlings that germinated within the past growing season in the winter and spring of 2016. Saltbush produces anomalous secondary growth lacking clear growth rings, is multi-stemmed, and often experiences dieback of branches; therefore, there is no reliable way to non-destructively determine saltbush age in the field (Fahn and Zimmermann 1982). A common alternative approach is to use size as a proxy for age (Lefkovich 1965); therefore, we measured size (canopy volume) to qualitatively estimate

age. We assumed that smaller shrubs are younger and that larger shrubs are older.

Shrubs were selected for size measurements at each site by randomly staking a central survey point and measuring all shrubs within a 30-m radius of that point. We measured crown width (the shrub crown interval along the transect from the central point), cross width (the width perpendicular to crown width), and height of each shrub. We then used the crown width, cross width, and height to calculate the canopy volume in m<sup>3</sup> of each shrub with the following formula from Thorne et al. (2002):

$$\text{Canopy volume} = 2/3\pi \times \text{height} \times [(\text{crownwidth}/2) \times (\text{crosswidth}/2)].$$

### *Exotic grass cover*

We quantified grass abundance at each site on 20 February 2017 (climax of annual grass growth) by measuring the percentage of grass cover at random points at our six field sites ( $n = 30$  plots). Measurements occurred within the 30-m radius of the demographic analysis at each site and near to the naturally emerged and tagged seedlings. We used a 20 × 50 cm plot to collect percent coverage data (Daubenmire 1959). We determined percent coverage by analyzing the total percentage of ground covered by exotic grasses within each plot, then assigning each species the appropriate percentage to the nearest integer in increments of five.

### *Water availability*

Water availability may be a key factor affecting variation in saltbush population dynamics and grass invasion in the region (Spiegel et al. 2016). Saltbush tissue moisture was assessed by measuring branchlet water potential during the winter wet season and during the autumn end of dry season of 2017. Midday plant water potentials provide information on the moisture level the plants are accessing in the soil, how conductive the soil and plant is to water flow, and how high the transpiration rates are of the plants.

We measured midday branchlet water potentials ( $\Psi_w$ ) from outer canopy (sun-exposed) and south-facing sides of the same three mature saltbush shrubs per site in the winter wet season (21 February 2017) and at the peak of the autumn dry season (4 October 2017). On both sampling dates, the weather was sunny. Three shrubs were

randomly selected per site. We clipped three branchlets from each shrub (subsamples), bagged them, and placed them in a cooler with ice packs ( $n = 3$  samples and 3 subsamples per site per season). We then transported the samples back to a laboratory at CSU Bakersfield, and water potentials were measured with a pressure chamber within 3 h of harvest (Model 2000 Pressure Chamber Instrument; PMS Instruments, Corvallis, Oregon, USA).

Concurrent with branchlet water potential measurements in February and October 2017, we collected soil samples from various depths (surface, 10, 20, 50, and 100 cm) at each site and measured for soil water potential with a dew point potentiometer (WP4C; Meter Group, Pullman, Washington, USA) to assess soil moisture differences at different soil depths. One sample was taken from each sampling depth at each site.

#### *Edaphic characteristics*

We randomly collected three 10-cm soil cores at each site, within the demographic and percent percentage grass cover measurement areas. The three core samples from each site were then homogenized prior to analysis. Each sample was analyzed (Utah State University Analytical Laboratories, Logan, Utah, USA), using standard analytical techniques and procedures (Underwood and Guo 2013), for texture and a range of chemical properties (characteristics, i.e., pH, salinity, plant-available macronutrients including N, P, K, S, and the percent organic matter).

#### *Grass competition and RDM effects on seedling emergence*

We tested the effects of exotic grasses on saltbush emergence by manipulating competition and RDM across an in situ field experiment with treatments similar to those used in Coleman and Pratt (2019). This experiment was not conducted at the six sites as they were all actively grazed by cattle. We instead conducted the experiment at a site where cattle were excluded (Appendix S1: Fig. S1). The enclosure was located <1 km from the six main sites and in the same region. At the time of our experiment, the fenced enclosure was dominated by a dense cover of RDM, mostly *B. diandrus* and *B. madritensis*.

We randomly established sixty 20 × 50 cm plots to assess seed germination. We raked away

the previous year's RDM and weeded by hand where necessary. Seeds of saltbush were then sown in the plots (100 seeds per plot) and spread with a rake. Exotic grass competition and RDM were manipulated with the following treatments: (1) RDM (grass thatch) was either directly added to a specified amount onto the soil surface, or not added ( $\pm$ RDM); and (2) plots were either weeded or not to test competition ( $\pm$ weeded). We randomly assigned each plot to one of four treatments ( $n = 15$  plots/treatment): (1) +RDM/-Weeded, (2) -RDM/-Weeded, (3) +RDM/+Weeded, (4) -RDM/+Weeded.

We standardized the amount of RDM added to +RDM plots by adding RDM until the light level (400–700 nm) at the soil surface underneath the RDM was approximately 300  $\mu\text{mol}$ s of quanta·m<sup>-2</sup>·s<sup>-1</sup> measured on a clear sunny day at midday (ambient PPFD ~2000  $\mu\text{mol}$ s quanta·m<sup>-2</sup>·s<sup>-1</sup>; Li 250A, Li-Cor Corporation, Lincoln, Nebraska, USA). This light level corresponded to the amount of shade produced from a moderately dense layer of RDM with a dry mass of about 0.015 kg/m<sup>2</sup>, which was comparable to the RDM of moderately grass-invaded old-field areas throughout the San Joaquin Desert (Bartolome et al. 2007). The RDM added to the plots was collected in situ. When weeding, we avoided disturbing saltbush seeds and seedlings in the plots by frequently visiting the site when the annual grasses and forbs were just germinating (January–March) so they could be removed when small. We weeded plots as necessary at the same time as plot measurements were made.

To determine the effects of the treatments, we measured saltbush density (individuals/plot) from 20 February 2017 (immediately following emergence) to 26 April 2017. We used a 20 × 50 cm plot that was color-coded to aid assignment to different coverage classes (Daubenmire 1959). Measurements were made approximately every other week after initial emergence in the winter and spring of 2017 to capture the rapid emergence and mortality that occurred during that time (February–April).

#### *Statistical analyses*

Statistical analyses were conducted using JMP 13 (SAS Institute, Cary, North Carolina, USA), Minitab 18 (Minitab Inc., State College, Pennsylvania, USA), and (R Foundation for Statistical

Computing, v 3.6.2;  $\alpha = 0.05$ ). All data were checked for normality and constant variance and were log transformed, as necessary. In some cases, transformations failed, and non-parametric models were used. We conducted non-parametric analyses using the methods described in Barnard et al. (2007).

To assess variation in survival by site between tagged saltbush seedlings, we used a general linear model with binomial distribution (dead vs. alive) with Tukey's HSD to test post hoc differences by site. We individually tested survival data from 4 October 2017 and June 2019. We assessed the total number of surviving seedling transplants as of 4 October 2017 by site ( $n = 2$ , sites 3 and 4) and by treatment (grassland vs. saltbush) with heterogeneity chi-square tests with the Yate's correction (Barnard et al. 2007). Expected values of 19 ( $n = 38/2$ ) were used in accord with the null hypothesis that survival would not differ by treatment and would be 50%. A second null hypothesis was that survival would not vary by site. We chose 50% as a null hypothesis for mortality because 50% base mortality of seedlings from a previous study (Coleman and Pratt 2019). This was reasonable to account for both higher survival and higher mortality to the null relative to both the treatment (grassland transplants) and the control (saltbush shrubland transplants).

We compared a range of factors across all our field sites. Variation in canopy volume (as a proxy for demographic composition) was analyzed with Kruskal–Wallis tests. We used Mann–Whitney tests for differences in survival of naturally emerged seedlings. Histograms were fit with the default smoothing function in R software package ggplot2 to visualize the patterns in the distributions. To assess differences in the level of grass invasion between the six sites, we used a one-way ANOVA and Tukey's HSD post hoc. Branchlet water potentials were compared by season and site with a two-way ANOVA and a Tukey's HSD post hoc test. An interaction term between site and season was included in the model. Both site and season were fixed factors.

For the experiment examining the role of grass RDM and competition on saltbush seedling emergence, the maximum density of saltbush (count of individuals germinated/plot) was analyzed with a Kruskal–Wallis test. Maximum density represented

the number of saltbush seedlings that germinated of the 100 seeds added to each plot, as a measure of apparent seed emergence. It is possible that this value would not represent emergence if some individuals died before the point of maximum density; however, this is unlikely as our plots were largely free from disturbance and when a seedling died it stayed in place and was easily observed. Moreover, mortality of seedlings did not begin until after the winter wet season and after the maximum densities were recoded. Thus, maximum density provided a reliable estimate of seedling emergence. We used contrasts to test for differences between individual factor levels (i.e., +RDM vs. –RDM and +weeded vs. –weeded). Variation between sites by canopy volume, branchlet and soil water potentials, seedling emergence, and edaphic characteristics was summarized with a principal components analysis (PCA) model. Two principal components were determined to be most informative from a SCREE plot. For the PCA, all the site loadings were divided by 8 so that they scaled in a similar range to the coefficients for the various factors to facilitate plotting on the same figure.

## RESULTS

### *Naturally emerged seedling survival*

Survival of naturally emerged seedlings to the juvenile growth stage varied among the six sites. Of 250 tagged seedlings in May 2016, 173 (70%) had perished by October 2017. As of June 2019, 227 (92%) of the individuals had perished (Table 3). Survival varied by site in 2017 ( $F_{1,4} = 12.75$ ,  $P < 0.001$ ), with greater survival at Sites 3 and 5, and lower survival at Sites 1, 4, and 6 (Table 3). Site differences by 2019 were observed ( $F_{1,4} = 30.62$ ,  $P < 0.001$ ), with the greatest survival at Site 5, lower survival at Sites 1, 3, and 6, and no survival at Site 4 (Table 3). The mean height of the surviving individuals surveyed in June 2019 was approximately 40 cm and these individuals appeared to be well established.

### *Survival of transplanted seedlings in native saltbush shrubland vs. exotic grassland*

Eight months after out-planting, survival of saltbush seedlings transplanted into grassy habitat was twice as high compared to seedlings transplanted into established saltbush habitat ( $\chi^2 = 10.98$ ,  $df = 1$ ,  $P < 0.001$ ). The number of

surviving individuals was higher at Site 3 compared to Site 4 ( $\chi^2 = 48.191$ ,  $df = 1$ ,  $P < 0.001$ , Fig. 1A). Seedling mortality among the seedlings planted among shrubs appeared to be due to herbivory from kangaroo rats (*Dipodomys heermanni*), jackrabbits (*Lepus californicus*), and cottontail rabbits (*Sylvilagus audubonii*) between March and May 2017, as each seedling was repeatedly clipped at the base until mortality occurred. In contrast, herbivory-induced mortality was not observed for seedlings growing in the grassy habitat, and mortality in this treatment was caused by other unknown factors (e.g., drought stress) in the summer of 2017 (Fig. 1B). In June 2019, 47% of saltbush individuals transplanted into grassy habitat died (Fig. 1), whereas 100% of saltbush individuals transplanted amongst established saltbush shrubs had died.

**Exotic grass cover**

The level of exotic grass cover in the winter wet season (February 2017) varied significantly by site ( $F_{1,5} = 80.36$ ,  $P = 0.004$ ; Table 3). Sites 1 and 5 had a higher grass cover compared to the other sites (Table 3).

**Size class analysis to estimate demography and historic recruitment events**

Distinct size-structured cohorts were present both within and across sites. The six sites had a wide range of saltbush size distributions suggesting that sites differed in their population demographics, which was likely controlled by a range of site-specific factors ( $H = 73.18$ ,  $df = 5$ ,  $P < 0.001$ ; Fig. 2, Table 4). There were only a few old shrubs ( $>1\text{ m}^3$ ) at sites 3 and 4, suggesting that these sites were more recently established or that mortality of shrubs prevented them from attaining old age. Sites 3 and 4 had more shrubs per unit area. Sites 1, 2, 5, and 6 had many mature shrubs along with a range of smaller ones, suggesting ongoing recruitment combined with lower levels of mortality. Notably, size structure at all sites was at least bimodal (two more size cohorts), which may represent two (or more) past recruitment events.

**Water availability**

The study region is highly seasonal, with a hot dry summer and interannually variable precipitation occurring in the winter (Appendix S1:

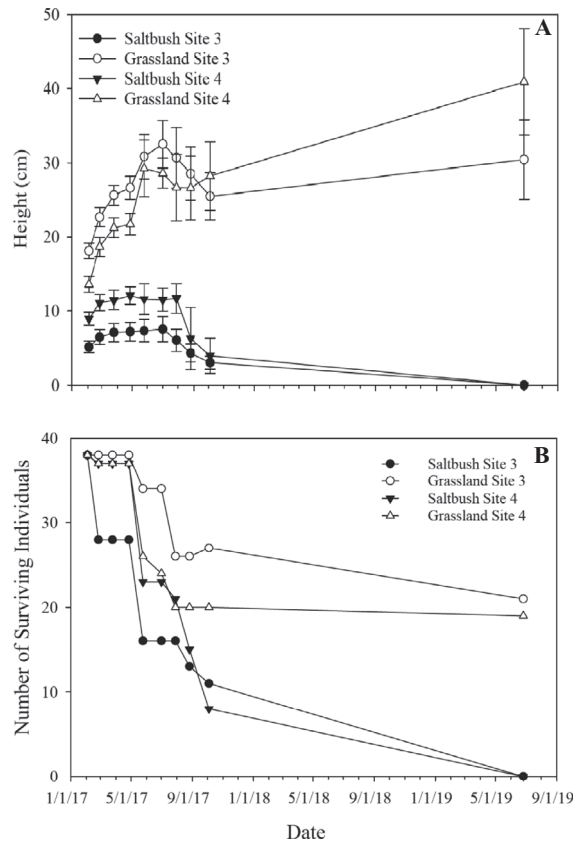


Fig. 1. (A) Mean heights and (B) the number of surviving transplanted saltbush (*Atriplex polycarpa*) seedlings between February 2017 and June 2019 located in the Comanche Point region of Tejon Ranch in the San Joaquin Desert of California. At each site, half of the seedlings ( $n = 38$ ) were planted in native saltbush habitat, while the other half were planted in adjacent exotic annual grassland. Seedlings were planted in late January 2017. Symbols means and error bars in panel A show standard errors of the mean.

Fig. S2). Water resources were variable by site and season. Midday branchlet water potential varied predictably by season, being less negative in the winter wet season and more negative during the autumn dry season ( $F_{1,1} = 2096.63$ ,  $P < 0.001$ ). Saltbush water potentials also varied by site ( $F_{1,5} = 58.10$ ,  $P < 0.001$ ; Appendix S1: Fig. S3), and there was an interaction between season and site ( $F_{1,5} = 63.65$ ,  $P < 0.001$ ; Table 5), indicating that shrubs at the different sites responded differently to the changing seasons.



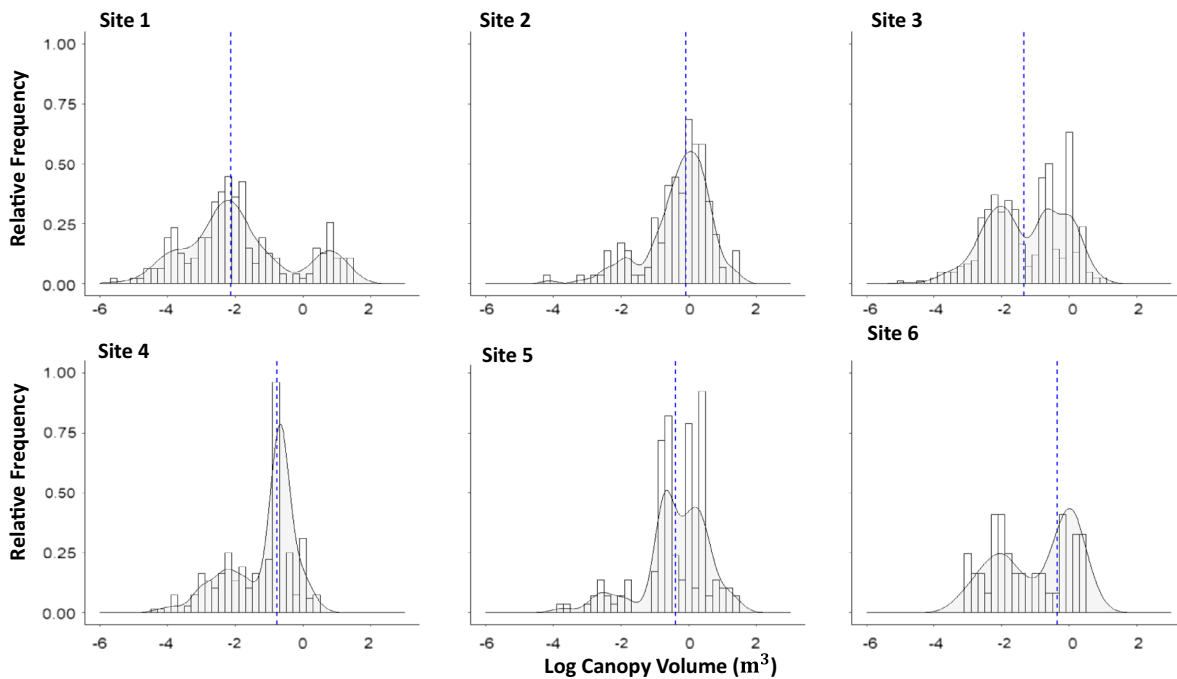


Fig. 2. Demographic composition of six saltbush (*Atriplex polycarpa*) sites between May and December 2016. At each site, canopy volume ( $\text{m}^3$ ) was measured as a proxy for age as an estimate for demographic composition. We assumed large individuals were mature and small individuals were young. Histograms show the log canopy volume plotted against relative frequency to compare sites more clearly. Each peak represents a potential recruitment event, and the blue dashed line represents the median. Distributions were fit using a smoothing function.

Soil moisture was limited during the dry season at all sites and soil depths (soil water potentials  $< -4$  MPa; Appendix S1: Fig. S4). All sites had higher water potential in winter months than in the autumn indicating more available moisture at this time. All sites had the same water potential, except for Site 4 that did not reach as high a value of water potential suggesting less moisture at this site. This was likely driven by the fine texture (sandy clay loam) and 14 $\times$  higher salinity of the soil at this site (Appendix S1: Table S1). Some of these factors were highly variable, yet we did not see any associations between these factors and the various response variables that we measured.

#### Grass competition and RDM effects on seedling emergence

Exotic grass RDM affected saltbush seedling emergence in our plots, whereas competition with the grasses had no noticeable effect. Peak saltbush emergence varied among the treatments

( $H = 17.85$ ,  $df = 3$ ,  $P = 0.005$ ; Fig. 3). The presence of RDM reduced the emergence of seedlings when RDM was absent ( $H = 16.98$ ,  $df = 1$ ,  $P < 0.001$ ). Competition for resources from the exotic grasses did not affect emergence ( $H = 0.39$ ,  $P = 0.533$ ). Seedling mortality was 100% for all treatments by April 2017.

#### Variation across sites

Relationships between the numerous response variables that we measured were summarized with a PCA analysis (Fig. 4). The first component (PC1) explained 45% of the variation. Sites 2 and 4 loaded most strongly with PC1 with Site 1 to a lesser degree. The positive end of this PC reflects lower summer moisture availability and large plants with a diverse range of canopy sizes, which tracked closely with Site 2. The negative end of PC1 reflects high seedling emergence, density, mature shrub density, and soil salinity, which tracked closely with Site 4. Sites 3 and 4 loaded strongly with the second component

Table 4. Shrub characteristics of six *Atriplex polycarpa* sites.

Site number	Number of shrubs measured	Density (individuals/m <sup>2</sup> )	Min canopy volume (m <sup>3</sup> )	Median canopy volume (m <sup>3</sup> )	Max canopy volume (m <sup>3</sup> )	Interquartile range of canopy volume (m <sup>3</sup> )
1	235	0.083	$2.1 \times 10^{-4}$	0.014	26	0.076
2	145	0.051	$8 \times 10^{-5}$	0.814	27.3	1.986
3	418	0.148	0.005	0.045	12.4	0.4127
4	337	0.119	$4.7 \times 10^{-5}$	0.175	3.16	0.2471
5	144	0.051	0.0008	0.407	28.4	2.223
6	160	0.057	0.001	0.441	3.13	1.0505
Mean	230	0.081	0.001	0.315	17	1.00

Note: All shrubs were measured within a 30-m radius at each site.

Table 5. Results of a two-way ANOVA of saltbush (*Atriplex polycarpa*) midday branchlet water potentials between six sites ( $n = 9$  per site) and two seasons.

Source of variation	df	SS	MS	F	P
Site	5	60.20	12.040	58.10	0.000
Season	1	434.52	434.524	2096.63	0.000
Site $\times$ season	5	65.96	13.191	63.65	0.000
Error	96	19.90	0.207		
Total	107	580.58			

Note: Measurements were taken on clear, sunny days in the winter (February 21; wet season) and autumn (October 4; end of dry season) of 2017. df, degrees of freedom; MS, Mean Square Within Groups; SS, Sum of Squares.

(PC2), which explained 24% of the variation. The positive end of PC2 reflects low winter water availability, elevated N and P, and soil salinity, which tracks closely with Site 4. The negative end of PC2 reflects high grass coverage and seedling emergence, which best describes Site 1. All sites fall in their own unique regions of the loading plot indicating that each site has its own unique set of defining factors.

## DISCUSSION

### *Exotic grasses and seedling recruitment: A seed/seedling conflict in saltbush populations*

We predicted that exotic grass competition and RDM would be key factors affecting saltbush recruitment (Coleman and Pratt 2019, Phillips et al. 2019). We found that RDM significantly diminished saltbush emergence, whereas competition with exotic annual grasses did not. This suggests that habitat modification by exotic grass RDM may be the primary factor limiting saltbush populations and is supported by a recent

experiment (Coleman and Pratt 2019). The effect of the RDM is likely due to the decreased soil light and temperature levels under thick layers of RDM, which may be especially detrimental to the C<sub>4</sub>-photosynthetic pathway of *Atriplex* species (Ehleringer and Pearcy 1983). The presence of dense RDM is likely a significant impediment to saltbush recruitment and represents a stabilizing feedback that favors persistent grass dominance in arid communities (Park and Jenerette 2019).

The lack of a competitive effect between annual grasses and saltbush seedlings may be due to largely spatially separated use of soil resources between their two different root system growth forms. Grass roots are fibrous and shallowly rooted, whereas saltbushes produce woody taproots that penetrate far deeper into the soil profile, even at the seedling stage (Chen et al. 2018, Phillips et al. 2019). The spatial separation of the root systems of annual grasses and saltbushes in the soil profile suggests that they largely avoid below-ground competition (Cleland et al. 2016). The role of exotic species in affecting seedling recruitment has been documented in numerous other studies (Schultz et al. 1955, Hamilton et al. 1999, Corbin and D'Antonio 2004, Liu and Stiling 2006). Seedlings are a sensitive stage in the life cycle of many plants, especially long-lived woody shrubs like saltbushes. Saltbushes emerge during the wet season, which is during the winter months when days are at their shortest. The combination of short daylengths and shading from RDM may be too much for the C<sub>4</sub>-photosynthetic saltbushes to overcome because of their low quantum efficiency compared to C<sub>3</sub> species (Ehleringer and Pearcy 1983).

Transplanted saltbush seedlings survived differently in grassland vs. saltbush-dominated

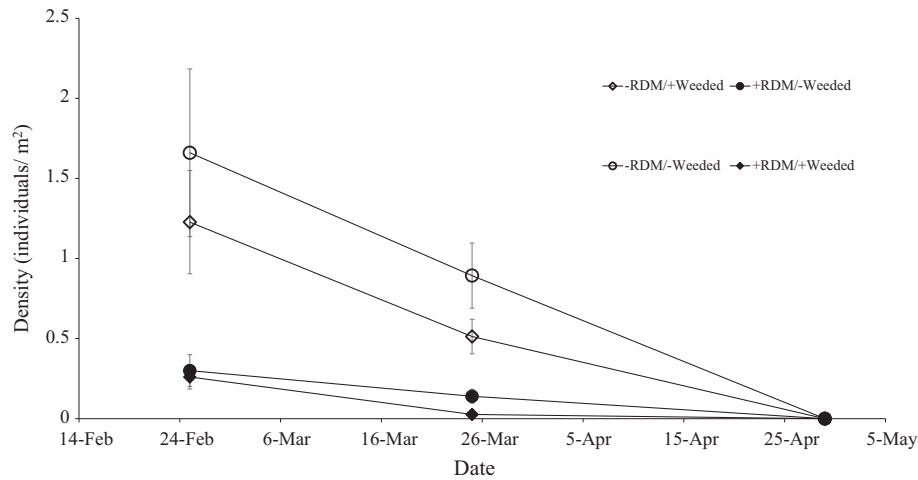


Fig. 3. Seed sowing experiment showing mean density of saltbush (*Atriplex polycarpa*) seedlings by treatment between February and April 2017. Plots were variably weeded or unweeded of exotic annual grasses and treated or untreated with a standard amount of residual dry matter (RDM) to assess the grass-related effects on saltbush emergence and rate of mortality. Symbols means and errors bars are 95% confidence intervals.

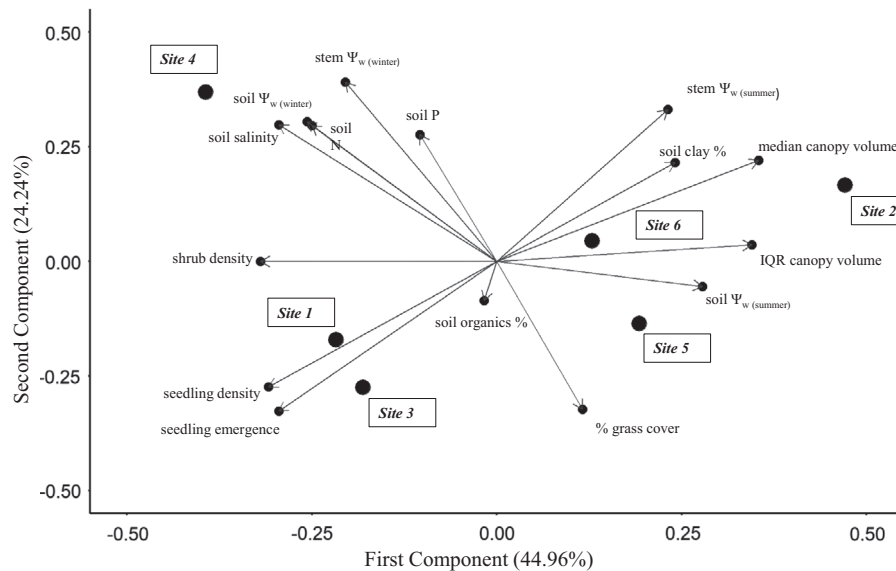


Fig. 4. Principal components analysis matrix assessing variation between six saltbush (*Atriplex polycarpa*) sites. The model used a SCREE plot to select two principal components. Abbreviations are IQR, interquartile range;  $\Psi_w$ , water potential (values shown are absolute and not negative); seedling emergence, number of seedlings which germinated and were tagged for survival in January 2017; seedling density, number of seedlings counted within the demographic analysis at each site.

habitats. We predicted that seedlings transplanted into relatively bare zones among mature saltbush shrubs would have greater survival than those planted in grass-dominated

areas. This was not the case. Higher saltbush mortality occurred in the shrublands, which appeared to be primarily due to herbivory by small mammals using the mature saltbushes as

cover from predators. Seedling predation as a limiting factor of recruitment is a well-known phenomenon (Bartholomew 1970, Maron and Simms 1997, Cushman et al. 2011, Busch et al. 2012). Small desert mammals are also known to prefer native plant taxa in some habitats, thus providing a competitive advantage to exotics (Callaway et al. 1999, Pearson et al. 2011).

Our results indicate that low RDM levels between established shrubs create an environment favorable for seedling emergence, but unfavorable for seedling survival, whereas grassy areas are unfavorable for seedling emergence, but favorable for seedling survival. Overall, saltbush suffers from a lack of favorable site conditions for recruitment to occur. Such seed–seedling conflicts have been previously described (Lamont et al. 1993, Schupp 1995).

#### *Variation across sites*

The presence of a diversity of sizes of mature shrubs at some Sites (1, 5, and 6) suggests episodic recruitment and that factors causing mortality of established shrubs were such that plants were able to attain a mature age. Other Sites (2, 3, and 4) had a less diverse size range suggesting that recruitment may be less common. The factors controlling demography in long-lived plants that produce secondary anomalous growth, and therefore a lack of discrete annual growth rings, are difficult to ascertain. Since saltbush stands are not expanding throughout the San Joaquin Desert; then mortality must be equal to or greater than recruitment. The balance between annual grasses and saltbush has largely reached some level of equilibrium. It is likely that before exotic annual grasses invaded, saltbushes occupied a much greater extent of the landscape. Annual grasses and mature saltbush shrubs do not directly compete—but annual grasses and saltbush seedlings do. Every loss of ground by saltbush (mature shrub mortality) has likely largely resulted in gains of ground by exotic grasses.

Mature shrub water status, seedling survival, demography, and edaphic characteristics all varied by site. The PCA summary showed that grass cover and seedling emergence were associated with greater winter soil moisture and lower soil salinity. This makes sense as these winter germinating annual plants would need adequate soil moisture to germinate and establish as seedlings.

Another pattern was that denser stands of shrubs were associated with drier winter soil moisture conditions. This could mean that dense stands of shrubs are using more water or that hydrology differs, such as canopy interception losses or soil infiltration rates, that is not allowing rainfall to penetrate the soil. It could also mean that the soil is simply better drained due to coarser soil texture, sandier soil. Dense RDM significantly affects these processes as well (Bartolome et al. 2007).

#### *Synthesis*

Exotic grass RDM is the primary biotic factor impeding saltbush from recruiting. There appears to be a seed–seedling conflict wherein saltbush seedlings emerge more successfully in the absence of RDM, but then have higher rates of mortality due to increased exposure to native herbivorous mammals. This leads to a stabilizing feedback that promotes grass persistence and prevents saltbush population growth. Somewhere in the balance of these two adverse conditions (RDM suppression vs. herbivory suppression), there is positive recruitment. These findings have implications for management and restoration of saltbush communities in the San Joaquin Desert. A simple management tactic of clearing away RDM and seeding with saltbush seeds could be effective if combined with exclosures designed to reduce herbivory. Another solution could be to conduct intense intermittent livestock grazing as a management tool for high RDM, followed by seeding with saltbush. If herbivory is controlled, transplanting out-grown saltbush seedlings may be a more effective method of restoration compared to the generally used method of direct seed casting.

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