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INVASION NOTE

The effects of invasive grass on seedling recruitment of native *Atriplex polycarpa* (Torr.) S. Watson (Chenopodiaceae) shrubs in the San Joaquin Valley of California

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Abstract Invasive annual grasses are widespread across the arid Western United States, including native saltbush communities in the San Joaquin Valley of California. We hypothesized that the grasses limit saltbush seedling recruitment, leading to persistently invaded grasslands and thereby inhibiting saltbush succession. We predicted that this could happen due to (1), competition for water between grasses and saltbush seedlings and (2), a dense cover of senesced shoots known as residual dry matter (RDM). We conducted an experiment manipulating competition, RDM presence, and shade over a 2-year period. On a seasonal basis, we measured seedling density for the saltbush *Atriplex polycarpa*. Grass competition and RDM both reduced density, though RDM had a larger treatment effect. Final density was low in all treatments, but it was lowest in the treatment with both competition and RDM. We conclude that invasive grasses can negatively influence the recruitment of *A. polycarpa*, and that a primary mechanism through which this occurs is through inhibition by a dense cover of RDM. Removal of RDM is a promising technique to mitigate the negative impact on saltbush seedling recruitment.

Keywords *Atriplex polycarpa* · Competition · Invasive annual grasses · Recruitment · Residual dry matter

Introduction

Invasive species may affect the distribution and abundance of native species in their introduced ranges (MacDougall and Turkington 2005). One profound effect of invasive plants is to present a barrier to recruitment of native plants. Seedling recruitment is the key limiting step in the life cycle for many plants (Solbrig 1980), thus reduced recruitment can lead to declining populations, rarity, and eventual extirpation. At the community level, this has implications for succession and composition of mature plant communities. Invasive plants have been shown to negatively impact seedling recruitment (Tilman 1997; Seabloom et al. 2003). One community-type where this phenomenon appears to be important are the saltbush shrublands in the San Joaquin Valley of California. In these shrublands, invasive annual grasses are common among mature saltbushes and are abundant in areas adjacent to stands of shrubs. These invaded areas appear to be stable and the adjacent saltbush vegetation does not

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commonly colonize what appears to be suitable habitat. We hypothesized that dense stands of invasive annual grasses inhibit saltbush shrubland succession. We predicted that (1) resource competition from the grasses reduces soil moisture available to saltbush seeds and seedlings, thereby inhibiting recruitment and (2) the formation of dense residual dry matter (RDM) during the dry season shades the soil, limits available light, and lowers soil temperature, and thus also inhibits saltbush seedling recruitment. Dense RDM may be especially important for C_4-photosynthetic plants such as saltbushes that thrive in high light and temperature conditions. The precise mechanism by which recruitment is limited is important to examine in the context of understanding the impact of invasions generally; moreover, such information can be used to inform management and restoration efforts (Mikhiel et al. 1992; James et al. 2012).

Methods

We examined *Atriplex polycarpa* (Torr.) S. Watson seedling recruitment in response to invasive grass competition and RDM shade across a series of experimental plot treatments in a former cotton field that is now an ecological preserve (Environmental Studies Area or ESA) on campus at California State University, Bakersfield. The ESA is a former floodplain of the Kern River. The preserve has a homogenous sandy soil composition and is dominated by invasive grass and forb species including *Hordeum vulgare* L., *Bromus madritensis* L. ssp. *rubens* (L.) Hunshot, *Bromus diandrus* Roth, and *Erodium cicutarium* (L.) L'Hér., as well as a weedy native forb, *Amsinckia menziesii* (Lehm.) Nelson & J. F. Macbr, thus providing suitable conditions to test our hypothesis. Additionally, a small number (< 30) of *A. polycarpa* seedlings were planted on the site in 2007 and the mature shrubs since recruited abundant seedlings in areas not dominated by the grasses. Thus, the site provides suitable conditions for saltbush; moreover, naturally occurring stands of saltbush can be found < 1 km away in the same floodplain region.

We established ninety 20 × 50 cm plots on 5 December 2015, prior to the onset of winter rains. We randomized plot placement and orientation within the study area, which was approximately 100 × 100 m of flat area in the ESA with uniform environmental conditions and dominated by invasive annual grasses. A minimum of one meter was maintained between each plot to avoid interactions with adjacent plots. We completely cleared each plot of plants by raking away the RDM of the previous year and by hand weeding where necessary. The plots were marked with pin flags to ensure that the same area was surveyed over the course of the study. We sowed 100 seeds of *A. polycarpa* per plot and haphazardly spread them with a rake. We manipulated invasive grass competition and RDM with the following treatments: (1) RDM was either directly added to a specified amount within the range of natural conditions (see below) or completely removed (± RDM); (2) invasive grass presence was manipulated to test competition (+weeded/ −weeded); and (3) shade cloth was placed over plots to mimic the shade generated by RDM (+Shade Cloth). We randomly assigned each plot to one of six treatments (n = 15 plots/treatment): (1) +RDM/ −Weeded, (2) −RDM/ −Weeded, (3) +RDM/ +Weeded, (4) −RDM/ +Weeded, (5) +Shade Cloth/ −Weeded, and (6) +Shade Cloth/ +Weeded.

The RDM treatment was standardized based on two considerations. First, we standardized the amount of RDM on each +RDM plot until the light level at the soil surface underneath the RDM was approximately 300 μmol of quanta m^{-2} s^{-1} measured on a clear sunny day at solar noon (ambient light level at solar noon ~ 2000 μmol quanta m^{-2} s^{-1}; Li 250A, Li-Cor Corporation, Lincoln, Nebraska, USA). Another factor was that we chose RDM to be at a level that is commonly found in natural areas. The amount of RDM we chose was approximately 0.015 kg dry mass/m^2. The amount of RDM found in dry annual grasslands in the region ranges from about zero to 0.06 kg dry mass/m^2 (Bartolome et al. 2002), thus the amount we applied to our plots was at the lower end of the range. The RDM that was added to the plots came from on site and consisted primarily of shoots of *H. vulgare* and *B. diandrus*.

To manipulate competition, grasses were weeded from some plots (+weeded treatment). When weeding, care was taken to avoid disturbing *A. polycarpa* seeds and seedlings in the plots. This was accomplished by daily visits to the site when the grasses and forbs were just germinating (January–March 2016) so they could be removed when very small. We weeded plots concurrently with the repeated plot measurements.

For the shade cloth treatments, we fastened commercial shade cloth (model # 72015, Easy Gardener Inc., Waco, Texas, USA) to rebar at a height of 0.5 m over the plots. The edge of the cloth in each plot was fastened with a 10 cm gap over the soil to allow for air flow, while also preventing side light. We standardized the degree of light inhibition at the soil surface in the shade cloth plots (i.e., one layer of shade cloth was enough) to correspond with the light inhibition level of the +RDM plots (300 μmol quanta m^{-2} s^{-1}). This treatment was specifically designed to recreate only the shade cast by the RDM because the C_4 saltbushes require high light and thrive at high temperatures, thus they are sensitive to shade.

Lastly, we monitored moisture and temperature conditions at the study site. We installed soil moisture and temperature probes at a 10-cm depth (n = 3 per treatment) (Decagon 5TM, ECTM, and EC20 soil probes; Decagon Devices, Pullman, Washington, USA). Probes were placed underneath the plots and inserted horizontally from a hole dug outside of the plot to minimize disturbance. A depth of 10 cm was chosen because this is a depth at which we predicted *A. polycarpa* seedlings and invasive grasses would share soil space and compete for resources. Data from the soil probes were mostly collected concurrently with the other measurements between 11:00 AM and noon. Different sensors may read different ranges of values between some maximum and minimum value. Because of this, and because we only needed to assess relative differences in soil moisture, we converted each sensor value to a relative one (percentage of maximum recorded for the season). The site was completely homogenous and flat; thus, each sensor would have experienced a similar absolute maximum value (saturated) over the course of the rainy season. We monitored the amount of rainfall at the site with a manual rain gauge (Stratus Precision Rain Gauge, All Weather, San Diego, California). We also continuously measured air temperature every 2 h throughout the experiment with two air temperature data loggers suspended at 0.5 m above the ground (Pendant HOBO temperature data logger; Onset, Cape Cod, Massachusetts, USA). One temperature logger was left in the open and suspended inside a ventilated and white reflective shield to monitor air temperature, while a second logger was suspended inside a shade cloth treatment to monitor air temperature in the shade.

Measurements were made approximately every other week after initial germination in the winter and spring of 2016 to capture the rapid germination that occurred during that time (February–April). Thereafter, measurements were done at least once a month depending on how rapidly seedling mortality was occurring. During the summer months, most annual species had senesced so weeding and measurements were less frequent at that time.

There were key aspects of the plant responses to the treatments that we examined to test our hypotheses. The first response of interest was the maximum seedling density. This represents the number of *A. polycarpa* seedlings that germinated of the 100 seeds added to each plot, as a measure of apparent seed germination. It is possible that this value would not represent germination if some individuals died before the point of maximum density; however, our sites 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 after the maximum densities were recoded. Thus, maximum density provides a reliable estimate of seedling germination. The second response was the final seedling density at the end of the experiment (January 2017), which gave a measurement of overall germination minus mortality after 1 year.

The experiment was designed as a multi-factorial treatment appropriate for analysis with a multi-factor ANOVA including repeated measures. For all the response variables, the data were not normal, and could not be transformed to meet the assumptions of parametric statistics. Thus, we used a 2-way nonparametric ANOVA method described in Barnard et al. (2007). Independent variables in models included two treatment factors: RDM presence and competition, which both had two levels (+RDM and −RDM; +Weeded and −Weeded) and included an interaction term. The shade treatment was meant to mimic the shading effect of +RDM, thus it was analyzed in a model that included shade type (+Shade and +RDM) and competition (+Weeded and −Weeded) and an interaction term.

We separately analyzed variation in soil moisture and soil temperature (at 10 cm depth) by treatment and by season (winter 2016 to winter 2017). This was done to relate treatment and seasonal variation in soil conditions to the predicted effects on *A. polycarpa* germination (Winter 2016), mortality (Spring to Fall 2016) and survival (Winter 2017) of seedlings. To avoid pseudoreplication, we analyzed the mean from each sensor for each season (Spring March–May, Summer June–August, Fall September–November, Winter December–February).

Results

Atriplex polycarpa seedling density was strongly affected by the treatments. Maximum density was highest in plots where RDM was absent and seedlings of other species were removed by weeding during January through March 2016 (Fig. 1a). Maximum density was significantly lower in plots where RDM was added and other species were not removed. Adding RDM while weeding or adding shade cloth with or without weeding resulted in intermediate maximum densities. Final density of seedlings of *A. polycarpa* was 80–100% lower than maximum density in all treatments (Fig. 1a). The most extreme effect was in plots that were not weeded if RDM was added (final density was zero). Final density was significantly above zero ($P < 0.05$) in weeded treatments and in plots that were not weeded if RDM and was absent.

All saltbush seeds germinated between February and March 2016. Both competition and RDM reduced the maximum density of seedlings in plots, though RDM had a larger treatment effect (competition: $H = 4.41$, df = 1, $P = 0.03$; RDM: $H = 26.5$, df = 1, $P < 0.01$; Fig. 1a). There was no interaction between competition and RDM ($H = 0.06$, df = 1, $P = 0.80$). The shade cloth covered plots did not reduce maximum density to the degree of +RDM plots, suggesting that RDM affected germination in ways other than simply casting shade ($H = 23.2$, df = 1, $P < 0.01$).

Soil and air temperatures could affect important plant responses such as germination. Soil temperature at 10 cm depth did not vary by treatment ($H = 1.79$, df = 5, $P < 0.87$), though it did predictably vary by season ($H = 163.7$, df = 4, $P < 0.01$), being higher in the hot summer and lower in the winter and in between these two extremes at other times (Fig. 1b).

Competition for resources, particularly for water in this arid environment, was expected to be important for controlling seedling responses. Soil moisture varied by treatment ($H = 51.4$, df = 5, $P < 0.01$). The presence of RDM did not affect soil moisture compared to the absence of RDM ($H = 0.08$ df = 1, $P = 0.77$), whereas the +RDM treatment had reduced soil moisture than the +shade cloth plots ($H = 41.5$, df = 1, $P < 0.01$). Weeded and unweeded plots did not differ in soil moisture ($H = 0.91$, df = 1, $P = 0.34$; Fig. 1c). RDM and competition did not interact to affect soil moisture ($H = 0.73$, df = 1, $P = 0.25$).

Competition and RDM both affected the final density of seedlings after 1 year (competition: $H = 5.20$, df = 1, $P = 0.02$; RDM: $H = 5.20$, df = 1, $P = 0.02$). Moreover, there was no interaction between the two treatments ($H = 2.41$, df = 1, $P = 0.12$). Competition in the context of shade (both RDM and shade cloth) reduced the final density of seedlings ($H = 7.77$, df = 1, $P < 0.01$). Final density was lower in the RDM treatment compared to shade cloth treatment ($H = 4.07$, df = 1, $P = 0.04$; Fig. 1a).

Discussion

Invasive annual grasses diminish *A. polycarpa* recruitment. The grasses chiefly limited recruitment by the presence of their senesced shoots (RDM). The effect of RDM seemed to be chiefly due to limiting seedling germination as maximum seedling densities in +RDM plots were the lowest. Factors that limit germination greatly reduce successful recruitment of seedlings because most of the seedlings suffer mortality in this arid, seasonal, and disturbed environment. This result supports our hypothesis that the presence of invasive grasses likely limits saltbush recruitment in areas where there are remnant stands of saltbush; moreover, our study specifically pinpoints the presence of invasive grass RDM as a key factor limiting saltbush recruitment and their ability to expand their populations into otherwise suitable habitat.

The effect of RDM on saltbush density was partially due to shading of the soil. Maximum density was greater in our shade cloth treatment compared to the +RDM treatment, which indicates that RDM has effects beyond just shade. The shade cloth treatment reduced light levels at the soil surface that may have reduced seedling density. Saltbush seeds are both light and temperature sensitive and have a narrow optimum (9–15 °C) for germination (Sankary and Barbour 1972; Mikhiel et al. 1992). After geminating, we predicted the shade effect would be important because

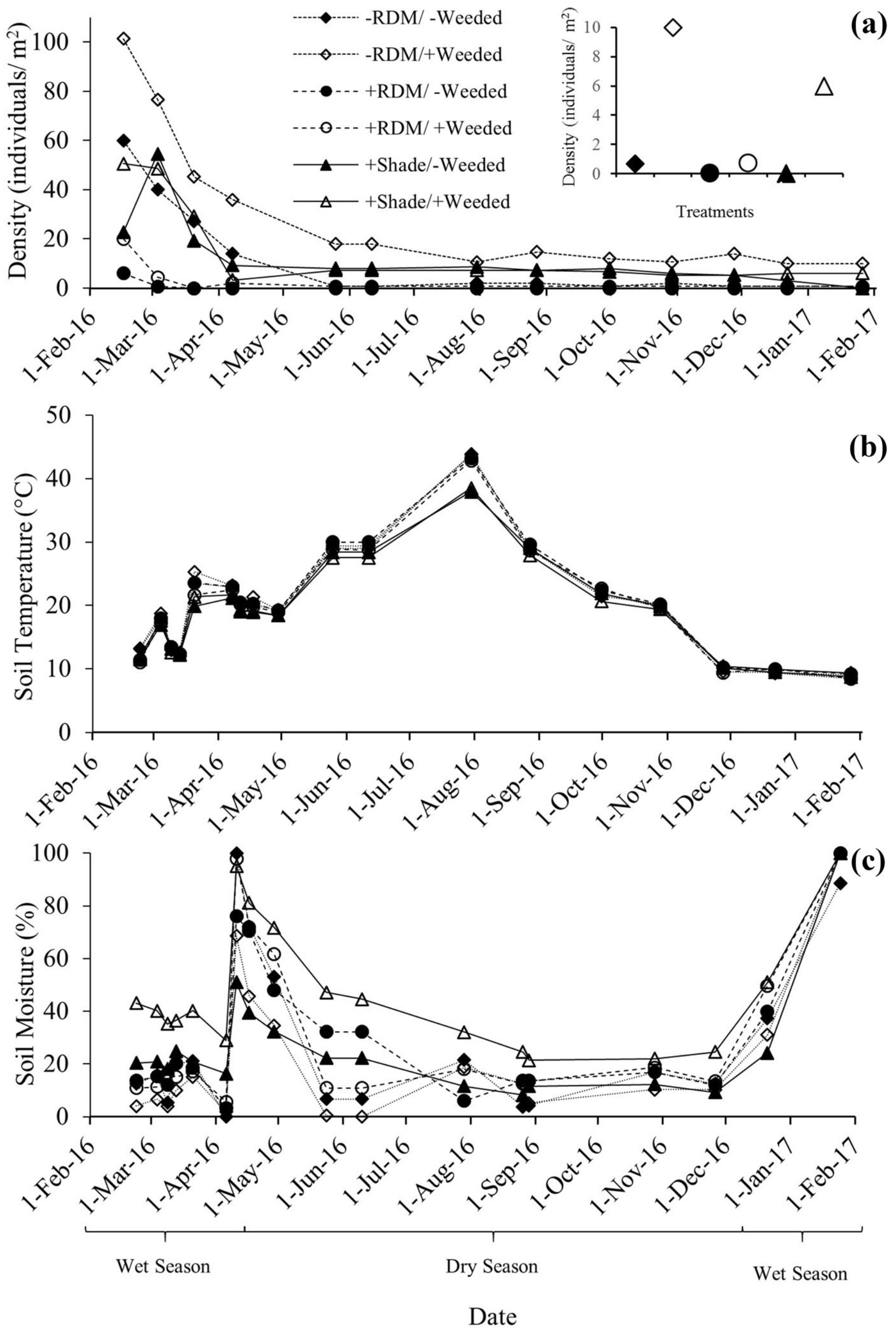

Fig. 1 Mean density of *Atriplex polycarpa* seedlings (panel **a**, n = 15 per treatment), mean soil temperature (panel **b**, n = 3 per treatment) at a depth of 10 cm, and mean soil moisture (panel **c**, n = 3 per treatment, expressed as a percentage of maximum) at a depth of 10 cm. All measurements were taken between January 2016 and January 2017 at the Environmental Studies Area on campus at California State University, Bakersfield. Error bars are excluded for clarity. The inset in panel **a** shows the final densities in January 2017, consistent with the main figure. *RDM* residual dry matter and +weeded refers to removal of competitors and −weeded refers to plots where competitors were not removed

A. polycarpa is a C_4-photosynthetic species, thus it has higher photosynthetic light requirements (lower quantum efficiency) than a typical C_3 photosynthetic plant (Ehleringer and Pearcy 1983). No seedlings survived in the shade cloth treatment with competition, consistent with our prediction that C_4 saltbushes do not tolerate shade and competition from C_3 competitors. The combination of competition and shade is common in the understory of invasive grassland RDM in the early growing season when grasses and other annuals are germinating.

Resource competition during the growing season also influences saltbush seed germination, but not to the same degree as RDM. Water was not clearly a limiting factor in resource competition. Soil moisture must not have been measured at the depth where the seedlings were rooted, because moisture was recorded as zero over a period of about 2 weeks in the treatment where the seedlings did best. It is possible that the saltbush seedlings rapidly extend a taproot below the rooting zone of the grasses and avoid competition for water. Instead, the shade cast by grass shoots may be the more important factor affecting saltbush seedlings.

All plots had high mortality regardless of treatment, but some of our plots (−RDM and +weeded) had some survival. This is important because natural stands of saltbush occur in arid environments and typically form low density stands with bare patches between the mature shrubs. The small number of survivors we observed are at a density that, if they all survive to maturity, will form a dense mature stand. The density of mature naturally occurring saltbush shrublands in the arid region we sampled are 0.081 shrubs/m^2 (Coleman, unpubl. data), whereas the seedlings in our plots corresponded to 3 shrubs/m^2. Saltbushes can produce large seed crops of viable seeds (pers. obs., Sankary and Barbour 1972). Of the seeds that germinate, many suffer mortality leading to a bottleneck in the demography of this species (Solbrig 1980). Nevertheless, if only a small number of these seedlings survive, leading to successful recruitment, the populations of these saltbushes may expand if recruitment levels are enough to surpass the level of adult mortality.

Invasive plants have been shown to hinder native seedling recruitment in many regions and by different mechanisms (Tilman 1997; Seabloom et al. 2003; MacDougall and Turkington 2005; Chen et al. 2018). Identifying the precise mechanism is an important research goal because it aids management strategies aimed at promoting native plant restoration. Our results predict that an environment that is low in invasive grass RDM should be best for recruitment. This is an important consideration from a land management perspective, and controlling for RDM during the dry season, instead of controlling for competition during the wet season (as is often done), would be a more effective method for increasing saltbush recruitment levels.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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