


## ARTICLE

# Woody-plant encroachment: Precipitation, herbivory, and grass-competition interact to affect shrub recruitment

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## Abstract

Woody-plant encroachment is a global phenomenon that has been affecting the southwestern United States since the late 1800s. Drought, overgrazing, herbivory, and competition between grasses and shrub seedlings have been hypothesized as the main drivers of shrub establishment. However, there is limited knowledge about the interactions among these drivers. Using a rainfall manipulation system and various herbivore exclosures, we tested hypotheses about how precipitation (PPT), competition between grasses and shrub seedlings, and predation affect the germination and first-year survival of mesquite (*Prosopis glandulosa*), a shrub that has encroached in Southern Great Plains and Chihuahuan Desert grasslands. We found that mesquite germination and survival (1) increased with increasing PPT, then saturated at about the mean growing season PPT level, (2) that competition between grasses and shrub seedlings had no effect on either germination or survival, and (3) that herbivory by small mammals decreased seedling establishment and survival, while ant granivory showed no effect. In addition to its direct positive effect on survival, PPT had an indirect negative effect via increasing small mammal activity. Current models predict a decrease in PPT in the southwestern United States with increased frequency of extreme events. The non-linear nature of PPT effects on Mesquite recruitment suggests asymmetric responses, wherein drought has a relatively greater negative effect than the positive effect of wet years. Indirect effects of PPT, through its effects on small mammal abundance, highlight the importance of accounting for interactions between biotic and abiotic drivers of shrub encroachment. This study provides quantitative basis for developing tools that can inform effective shrub management strategies in grasslands and savannas.

## KEYWORDS

ants, Chihuahuan desert, grass shrub-seedling competition, honey mesquite, *Prosopis glandulosa*, rainfall manipulation, seedling establishment, small mammal predation, woody-plant encroachment

## INTRODUCTION

Woody-plant encroachment is a global phenomenon (Devine et al., 2017; Gibbens et al., 2005; Miller & Rose, 1999; Tape et al., 2012) that has been affecting the southwestern United States since the late 1800s. European expansion into the West was accompanied by unregulated livestock grazing by settlers in the 19th century (Heady & Child, 1994). The basin that later became the Jornada Experimental Range near Las Cruces, New Mexico, decreased from 98% grassland in 1858 to 8% in 1998 (Bestelmeyer et al., 2018). This decline in grass cover coincided with the proliferation of woody plants, including honey mesquite (*Prosopis glandulosa*; henceforth referred to as “mesquite”). This native shrub, which was historically present in the Southern Great Plains and Southwestern United States but confined to local habitats (Johnston, 1963), increased from 4% cover in the Jornada Basin in 1858 to 59% cover in 1998 (Gibbens et al., 2005).

Precipitation (PPT) is one of the major drivers of ecosystem structure and functioning, especially in arid ecosystems (Noy-Meir, 1973; Sala et al., 1988). PPT influences shrub recruitment in grasslands directly through water availability and via feedbacks that reinforce shrub persistence (Schlesinger et al., 1990). The direct effects of PPT on shrubs are most important at the establishment stage (Harrington, 1991) because seedlings are more sensitive to drought than adult plants (Fay & Schultz, 2009; Matías et al., 2011; Mendoza et al., 2009). Several studies have highlighted the importance of water availability for seedling establishment in drylands (Padilla & Pugnaire, 2007). In addition, episodic germination resulting in cohorts of woody plant species establishment under unusually wet conditions have been documented in semiarid grasslands in Australia (Harrington, 1991) and North America (League & Veblen, 2006). However, such episodes of establishment may not be as important as has often been assumed (Watson et al., 1997a, 1997b) and biotic drivers may prevent realization of establishment potential under benign or highly favorable abiotic conditions (Rysavy et al., 2014).

Seed predation and seedling herbivory are two biotic factors that could constrain woody-plant encroachment. Native rodents and lagomorphs (henceforth “small mammals”) often destroy the seeds they consume (Ansley et al., 2017; Bahre & Shelton, 1993; Duval et al., 2005) and their defoliation of seedlings would further decrease recruitment (Weltzin et al., 1998). In addition, large-body-size seed-harvester ants from the genus *Pogonomyrmex* have shown foraging preference for seeds of three common shrubs in the Chihuahuan Desert, including Mesquite (Whitford, 1978). Fluctuations in ant and small mammal abundance are therefore likely to

interact with changes in PPT to determine the likelihood of the transitions from seedling to mature stages among shrubs invading grassland.

Interactions between grazing, fire, and drought have been regarded as one of the primary causes of woody-plant encroachment via its influence on competition between grasses and shrubs (Anadón et al., 2014; Archer et al., 1995; Briske, 2017; Van Aiken, 2000). Declines in grass cover and biomass accompanying grazing will promote shrub germination and establishment due to a relaxation of competition for limiting resources (Archer, 1994). Grazing-induced reductions in grass cover increases sunlight at the ground level triggering germination events while enhancing water and nutrient availability in shallow soil layers due to decreases in grass transpiration (Archer & Detling, 1986). These elevated resource availability conditions may favor recruitment of shrub seedlings.

The effects of water availability, seed/seedling predation, and grass competition on the establishment and survival of encroaching shrubs have been independently studied in the past. However, there is little knowledge about how these factors interact during the critical seedling establishment phase and their relative contribution to the overall success of encroaching species. Here, we aimed to understand the interactive effects of water availability, seed/seedling predation, and grass competition on germination and seedling survival of mesquite in a Chihuahuan Desert grassland. Three hypotheses guided our study: (1) water availability will increase germination and survival of mesquite. (2) Seed and seedling predation and grass competition decrease germination and survival of mesquite. And (3) water availability has direct and indirect effects on woody-plant encroachment through small mammal abundance and grass fitness.

To test our hypotheses, we conducted a field-based germination and seedling establishment experiment at the Jornada LTER (Long Term Ecological Research Network) site near Las Cruces, New Mexico, USA during two consecutive growing seasons. Our experiment consisted of a split-plot factorial design, where we compared three levels of PPT, two levels of grass competition, and four levels of herbivory.

## METHODS

### Study region and vegetation characteristics

The Jornada Experimental Range is an LTER site approximately 30 km north of Las Cruces, in southern New Mexico, USA (32°33′37.44″ N, 106°46′26.65″ W). The area

is a hot desert, with long-term mean annual precipitation (PPT) of 245 mm concentrated primarily during the summer (July–October) period (Wainwright, 2006). We carried out our experiment on the basin floor sand sheet geomorphic unit (Monger et al., 2006) where historic grasslands have undergone extensive encroachment by honey mesquite (*P. glandulosa*; Gibbens et al., 2005). Our experiments were conducted in an area still dominated by the  $C_4$  grass black grama (*Bouteloua eriopoda*).

## Experimental design and data collection

We conducted a manipulative experiment using a split-plot factorial design to assess the effects of three levels of PPT, two levels of grass–mesquite seedling competition, and four levels of seed/seedling predation. We used 10 replicates yielding a total of 30  $2.5 \times 5$  m plots. We planted five scarified seeds on each of the 240 nested replicates of the predation treatment. Germination was recorded weekly during the July–October growing season of 2016. The experiment was repeated (replicated in time with new seeds) in 2017.

We manipulated PPT using an automatic rainfall manipulation system (ARMS) (Gherardi & Sala, 2013). This system consists of a combination of rainout shelters (Yahdjian & Sala, 2002) that drain intercepted water into temporary storage tanks. When the water level in the tank reaches a designated level, it activates a float switch that turns on a solar-powered pump that transfers the water to irrigation plots. Our treatments consisted of 10 plots receiving 20% of ambient PPT, simulating extreme drought conditions; 10 plots receiving 180% of ambient PPT, representing extreme wet conditions; and 10 plots receiving ambient PPT. Treatments were imposed June–October 2016 and 2017. The ARMS design ensures that PPT frequency is the same in all treatments.

To test the effect of grass competition on mesquite seedlings, we split each plot within PPT manipulations where, in one half, we clipped the herbaceous vegetation to 5 cm every two weeks and left intact the remaining half. Plant material from the clipping was collected and disposed outside the plots to avert organic matter input to the soil (as would be the case in livestock grazing). Defoliation of grasses adversely influences their root biomass, elongation, and activity (Briske & Richards, 1995). Accordingly, competition in our study was not based on grasses being present/absent but rather on grasses being present, with either a reduction (induced by defoliation) or no reduction (e.g., undefoliated control) in their ability

to acquire/use resources as would occur in a grazed ecosystem.

To test seed/seedling predation, we installed a set of three different exclosures and one exclosure control where we added scarified mesquite seeds. Each exclosure allowed a certain class of predator to access seeds, whereas the exclosure control allowed access by all predators. One type of exclosure consisted of a PVC cylinder ( $D = 15$  cm  $\times$   $H = 10$  cm) coated with an insect-a-slip barrier (Fluon; AGC Inc.) to prevent ant access while allowing access by rodents and lagomorphs. Another type of exclosure consisted of a cylindrical hardware cloth cage ( $D = 15$  cm  $\times$   $H = 30$  cm;  $12.7 \times 12.7$  mm mesh) that prevented access by rodents and small mammals while allowing ant access. The third exclosure type consisted of a combination of the first two exclosures, wherein we placed the cylindrical cage inside the coated PVC cylinder to exclude ants and small mammals. Our exclosure “control” consisted of a metal rod inserted into the ground to mark where we planted seeds without exclosures, thus allowing any predator to access them. The predation treatments were replicated in the clipped and unclipped halves of each plot.

The response variables for this experiment were the germination of Mesquite seeds and the survival of its seedlings. Germination and survival were tracked by placing different-colored toothpicks on the north side of each germinating seed and following the subsequent survival of the seedling. This allowed us to differentiate among cohorts of seedlings. Here, we reported end-of-growing season survival pooled across cohorts.

We assessed small mammal abundance by counting dung pellets within two  $0.25\text{-m}^2$  quadrats randomly placed in each plot. Pellets in plots were then collected, transported to the lab, dried at  $60^\circ\text{C}$  for 48 h and weighed.

## Statistical analyses

We fit generalized mixed models of germination and survival as a function of PPT, competition, and predation treatments included as fixed effects using the function *glmer* from the package *lme4* (Bates et al., 2014) in R (R Core Team, 2018). We included plot identity nested within year as random effects in all models to account for the repeated-measures nature of our experiment where we sampled all plots in all years. We excluded interactions among treatments whenever non-significant to increase model stability. In all cases, we fit linear and nonlinear models and retained the model with the lowest AIC score. Poisson or logit link functions from the package *stats* were used according to the specific distribution of each response variable in order to comply with model

**TABLE 1** Summary of generalized mixed-effect model analysis for germination

Predictors	PPT, predation, and clipping effects on germination		
	Incidence rate ratios	CI	<i>p</i>
(Intercept)	0.17	0.06–0.48	<b>0.001</b>
PPT	1	0.99–1.00	<b>0.009</b>
log(PPT)	1.97	1.45–2.69	<b>&lt;0.001</b>
Ants	0.99	0.84–1.18	0.931
Small mammals	0.77	0.64–0.92	<b>0.004</b>
All predators	0.42	0.33–0.52	<b>&lt;0.001</b>
Clipping	1.02	0.89–1.17	0.772

Note: Total number of observations = 476. Marginal  $R^2$ /conditional  $R^2$  are 0.307/0.484, respectively. Random effects are as follows:  $\sigma^2 = 0.49$ ;  $\tau_{00 \text{ year: plot\_id}} = 0.17$ ;  $\tau_{00 \text{ plot\_id}} = 0$ ; ICC = 0.26;  $N_{\text{year}} = 2$ ;  $N_{\text{plot\_id}} = 30$ . Precipitation (PPT) and seed predation had significant effects on germination, whereas clipping did not. The table presents results of a nonlinear model selected over a linear model using AIC criterion. Boldface type highlights significant *p* values.

**TABLE 2** Summary of generalized mixed effect model analysis for seedling survival

Predictors	PPT, predation, and clipping effects on survival		
	Odds ratios	CI	<i>p</i>
(Intercept)	0.01	0.00–0.18	<b>0.002</b>
PPT	1	0.99–1.00	0.229
log(PPT)	3.11	1.39–6.93	<b>0.006</b>
Ants	0.75	0.42–1.33	0.322
Rodents–lagomorphs	0.04	0.01–0.09	<b>&lt;0.001</b>
All predators	0.1	0.05–0.20	<b>&lt;0.001</b>
Clipping	1.21	0.74–1.97	0.451

Note: Total number of observations = 476. Marginal  $R^2$ /conditional  $R^2$  are 0.406/0.494, respectively. Random effects are as follows:  $\sigma^2 = 3.29$ ;  $\tau_{00 \text{ year: plot\_id}} = 0.57$ ;  $\tau_{00 \text{ plot\_id}} = 0$ ; ICC = 0.15;  $N_{\text{year}} = 2$ ;  $N_{\text{plot\_id}} = 30$ . PPT and seed predation had significant effects on survival, whereas clipping did not. The table presents results of a nonlinear model selected over a linear model using AIC criterion. Boldface type highlights significant *p* values.

assumptions. We included competition and predation treatments as dummy variables and calculated the difference of each treatment level with their respective baseline. To assess the effects of PPT on pellet density and mass, we fit a simple linear regression model across treatments. For clarity, we display the mean and standard error of raw response variables and lines representing

**TABLE 3** Overall model analyses indicating all nonsignificant interactions tested

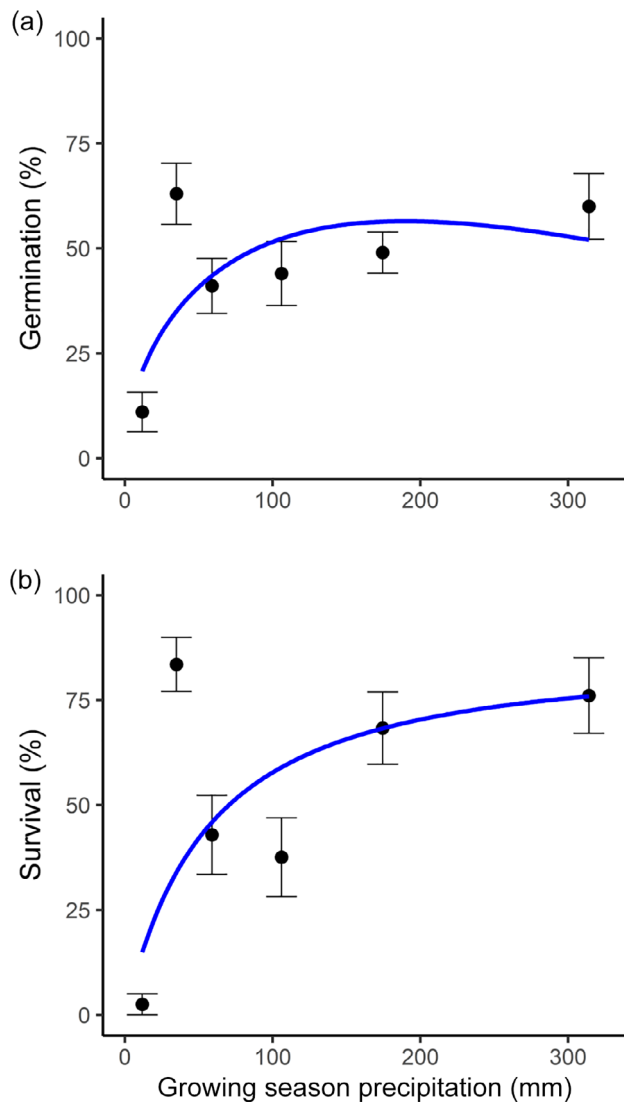
Predictors	PPT, predation, and grazing effects on germination		
	Incidence rate ratios	CI	<i>p</i>
(Intercept)	0.14	0.05–0.42	<b>&lt;0.001</b>
log(PPT_mm)	1.99	1.46–2.71	<b>&lt;0.001</b>
PPT_mm	1.00	0.99–1.00	0.071
Ants	1.12	0.75–1.67	0.583
Small mammals	1.03	0.68–1.55	0.906
All predators	0.48	0.29–0.81	<b>0.006</b>
Clipping	1.26	0.85–1.87	0.240
PPT_mm × ants	1.00	1.00–1.00	0.360
PPT_mm × small mammals	1.00	1.00–1.00	0.150
PPT_mm × all predators	1.00	1.00–1.00	0.276
PPT_mm × clipping	1.00	1.00–1.00	0.142
Ants × clipping	0.84	0.49–1.47	0.549
Small mammals × clipping	0.61	0.34–1.10	0.101
All predators × clipping	0.77	0.37–1.57	0.466
PPT_mm × ants × clipping	1.00	1.00–1.00	0.311
PPT_mm × small mammals × clipping	1.00	1.00–1.01	0.095
PPT_mm × all predators × clipping	1.00	1.00–1.01	0.131

Note: Total number of observations = 476. Marginal  $R^2$ /conditional  $R^2$  are 0.315/0.490, respectively. Random effects are as follows:  $\sigma^2 = 0.49$ ;  $\tau_{00 \text{ year: plot\_id}} = 0.17$ ;  $\tau_{00 \text{ plot\_id}} = 0.00$ ; ICC = 0.26;  $N_{\text{year}} = 2$ ;  $N_{\text{plot\_id}} = 30$ . PPT and predation are still significant simple effects and all interaction results are nonsignificant. Boldface type highlights significant *p* values.

back-transformed fitted values of the best model selected using AIC criterion (Bozdogan, 1987).

## RESULTS

Precipitation had a significant effect on Mesquite seed germination (Tables 1 and 3) and seedling survival (Tables 2 and 3), with each initially increasing linearly with increasing PPT then subsequently decreasing the rate of increase as PPT kept increasing beyond mean growing season PPT (~100 mm/yr, Figure 1a,b). Germination ranged from ~9% in the extreme drought treatment to ~50% during years approximating the mean growing season PPT. Mesquite seedling survival ranged from ~3% in the extreme drought conditions to 65% during years receiving the mean growing season PPT. These

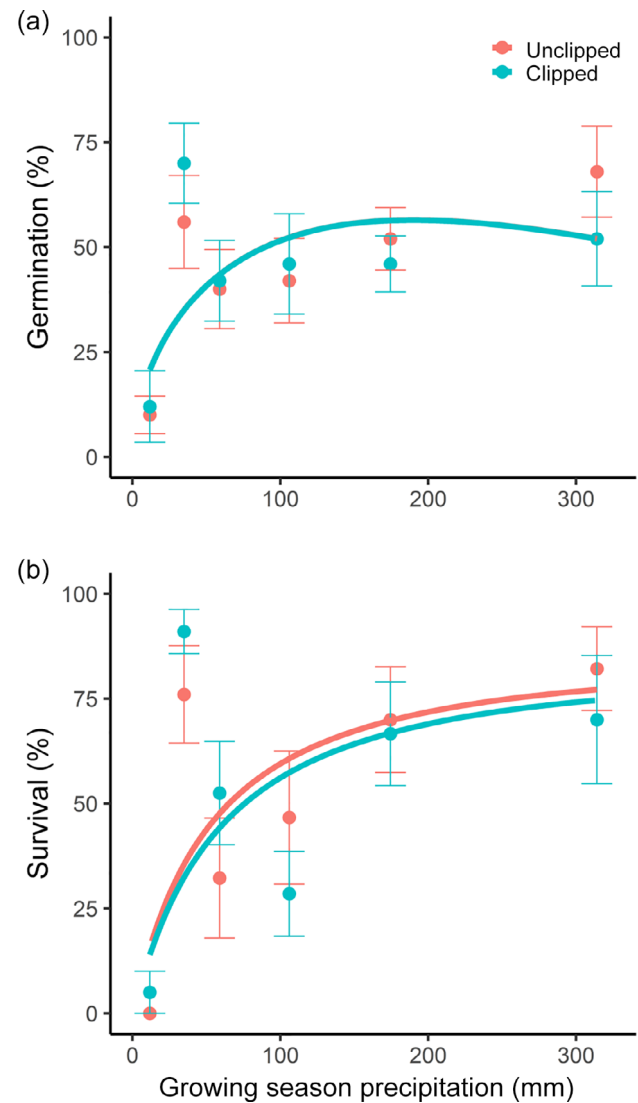


**FIGURE 1** Effect of growing season precipitation (PPT) on mesquite seed germination and first-year seedling survival. (a) Germination increased with PPT at a rate that decreased with increasing PPT. (b) Survival also increased with PPT in a similar fashion. Points indicate mean and bars indicate  $\pm$ SE for each year of the experiment. Lines indicate back-transformed fitted values of best model selected through AIC criterion

results revealed asymmetric responses of mesquite germination and survival to drought and extremely wet years.

Grass competition effects on the early stages of mesquite recruitment were negligible. We found no statistically significant differences between the clipped and unclipped/control treatments for either germination or survival in any of the PPT regimes (Figure 2; Tables 1 and 2).

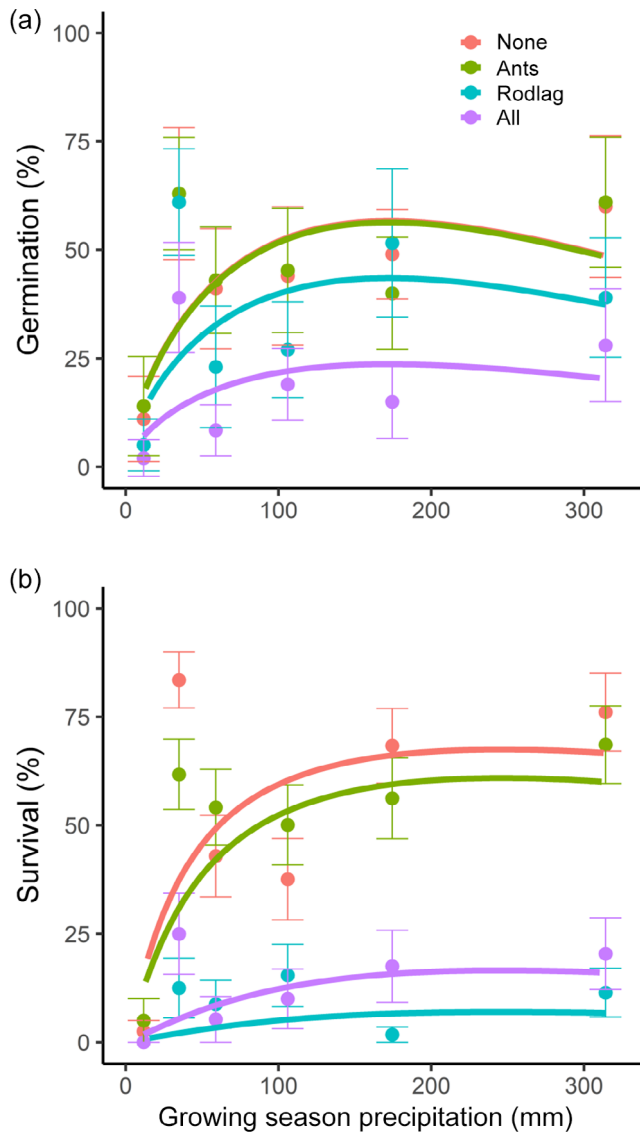
There were large differences among seed/seedling predation treatments on seed germination (Figure 3a and Table 1) and seedling survival (Figure 3b and Table 2).



**FIGURE 2** Effect of grass competition on mesquite seed germination and first-year seedling survival across growing season precipitation (PPT) treatments. Grass competition was reduced by clipping grasses; plots with unclipped grasses served as controls. Competition from dominant grass species did not show significant effects on either (a) seed germination or (b) seedling survival. Points (unclipped, red; clipped, blue) indicate mean and bars indicate  $\pm$ SE for each year of the experiment. Lines (unclipped, red; clipped, blue) indicate back-transformed fitted values of best model selected through AIC criterion

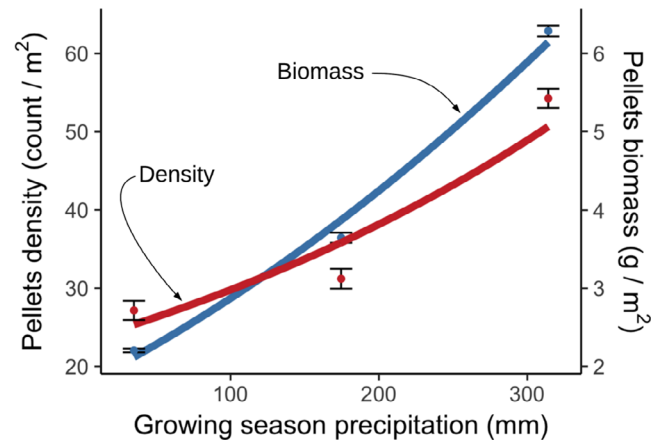
When all predators were excluded from accessing Mesquite seeds and seedlings, mean ( $\pm$  SE) seed germination peaked at  $44.7\% \pm 3.1\%$  and seedling survival reached a maximum of  $51.9\% \pm 4.1\%$ . Allowing all predators access to seeds and seedlings had a significant impact on Mesquite establishment yielding the lowest rates of germination and survival. Small mammals reduced both seed germination and seedling survival. The presence/absence of ants did not statistically influence either seed germination or seedling survival.





**FIGURE 3** Effect of predation on mesquite seed germination and first-year seedling survival. (a) Germination was significantly affected by all-predator and small-mammal treatments. Ants did not have a significant effect. (b) Survival responded similarly with significant effects of all predators and small mammal treatments and no effect of the ant treatment. Points indicate mean and bars indicate  $\pm$ SE. Lines indicate back-transformed fitted values of best model selected through AIC criterion. For both points and lines, red denotes no predator access (none), green denotes ants only treatment, blue denotes small mammals (rodlag), and purple denotes all predator access

The mean density and biomass of small mammal pellets increased with PPT (Figure 4). Mean ( $\pm$ SE) pellet biomass increased from  $2.1 \pm 0.04$  g/m<sup>2</sup> in the 35-mm treatment to  $6.2 \pm 0.04$  g/m<sup>2</sup> in the PPT treatment, and pellet abundance increased from  $25.4 \pm 1.2$  pellets/m<sup>2</sup> to  $50.5 \pm 1.2$  pellets/m<sup>2</sup>. These results indicate that small mammal visitation to plots, and hence their potential



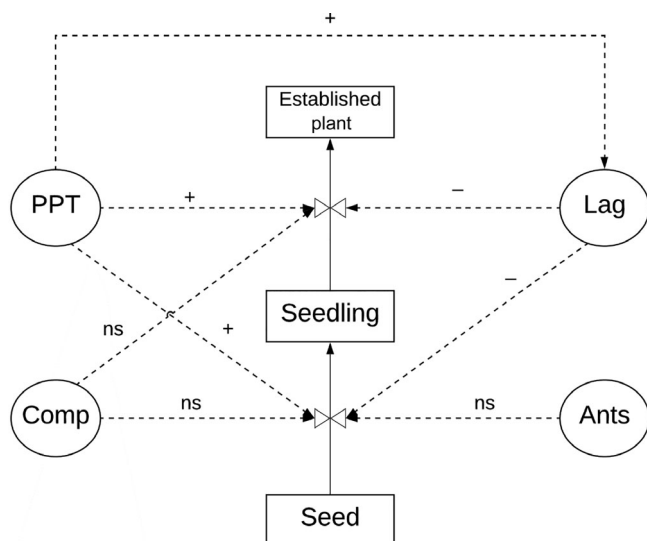
**FIGURE 4** Pellet density and biomass as a function of growing season precipitation (PPT). Density of pellets from small mammals (red;  $t = 2.273$ ,  $p < 0.05$ ) and pellet biomass (blue;  $t = 3.166$ ,  $p < 0.05$ ) increased with PPT. Pellets  $\text{Biomass} = \exp(1.32 + 0.004 \times \text{PPT})^2$ ; pellets  $\text{Density} = \exp(3.15 + 0.002 \times \text{PPT})$

impact on seeds and seedlings through predation, increased with increasing PPT.

## DISCUSSION AND CONCLUSION

Our results showed that PPT and predation interact to determine the establishment of woody plants in the Chihuahuan Desert (Figure 5). As expected, increases in growing season PPT improved seed germination and seedling survival. Both recruitment parameters exhibited positive logarithmic curves, that approximated a plateau at  $\sim 100$  mm of growing-season PPT. Interestingly, this corresponds to the long-term average for the growing season and highlights an asymmetry in the response to dry and wet years. Our data suggest that historically, Mesquite recruitment would not have been restricted to years of above-average PPT but rather, could have occurred in years of “typical” and even below-average growing season PPT. Going forward, under projections of an increase in the frequency of extreme PPT conditions (Demaria et al., 2019), our data suggest extremely dry years will reduce mesquite establishment, but extremely wet years will not produce a proportional compensatory increase. The net potential effect of increased PPT variability might therefore result in a reduction of mesquite establishment.

Seed and seedling predation modulated PPT effects on mesquite germination and survival at this Chihuahuan Desert site. The presence of small mammals negatively affected both parameters, whereas ant presence was inconsequential. This could be explained by the fact that mesquite seeds possess a hard seed coat and are relatively larger and heavier than other available seeds such as those



**FIGURE 5** System diagram depicting how the flow of seeds into seedling and established plants are affected by precipitation (PPT), competition between grasses and shrub seedlings (Comp) and predation by small mammals (Lag) and ants (Ants). Our field experiments indicate that seed germination is positively affected by PPT (+), negatively affected by the presence of small mammals (–), and unaffected by grass competition and the presence of ants (ns). Seedling survival is positively affected by PPT and negatively affected by the presence of small mammals

of perennial grasses and forbs. The hard seed coat would be a barrier to accessing the nutrients in the seed endosperm and carrying large mesquite seeds could require an energetic cost higher than that associated with the transport of smaller seeds (French et al., 1976).

During the critical germination/initial establishment phase of the shrub life cycle, grasses may have positive, neutral, or negative effects on their recruitment (Aguiar & Sala, 1999; Soriano et al., 1994). For example, grasses may facilitate shrub recruitment by serving as refugia for seeds and shelter seedlings against the desiccating conditions of hot deserts, therefore promoting shrub recruitment on protected areas relative to that on grazed areas (Browning & Archer, 2011). However, we observed no grass facilitation with respect to either germination or first-year establishment of mesquite. Alternatively, grasses may compete with shrub seedlings and defoliation of grasses could therefore promote mesquite recruitment. However, mesquite germination and first-year survival were comparable on clipped and unclipped plots in our field experiments. This is consistent with field experiments in the southern Great Plains, which have also shown that grass defoliation and grazing history have little impact on mesquite recruitment (Brown & Archer, 1989, 1999; Jurena & Archer, 2003). The dominant grass on our study site, black grama, has 90% of its roots concentrated in the upper 20 cm of the

soil profile, whereas 2.5 cm tall mesquite plants have tap-roots reaching depths of 85 cm (Gibbens & Lenz, 2001). Accordingly, resource partitioning with grasses may occur very early in the mesquite life cycle (Brown & Archer, 1990). If grass effects on early mesquite recruitment are generally neutral, then its proliferation in Chihuahuan Desert grasslands may be determined primarily by PPT interacting with changes in small mammal abundance.

The density and biomass of small mammal pellets increased with PPT suggesting linkages among PPT, plant biomass, and small-mammal activity. In our study, the observed increases in pellet density and mass with PPT reflects preferential visitation by small mammals to plots receiving more moisture and exhibiting higher productivity (Reichmann et al., 2013). Over broader spatial scales, increases in PPT would also translate into increases in small mammal abundance (Schooley et al., 2018) and ostensibly further increase seed and seedling predation. Our results support the notion that PPT may therefore have both direct positive effects and indirect negative effects on mesquite recruitment (Figure 5). From a woody-plant encroachment perspective, understanding these interactive effects of PPT on shrub recruitment is crucial because direct and indirect effects affect establishment outcomes in opposite ways. The positive direct effects of PPT on germination and establishment could be offset by the indirect negative effects associated with increases in small mammal abundance and the accompanying increases in seed and seedling predation (Figure 5).

Current models predict a decrease in PPT in the southwestern United States with an increased frequency of extreme events by the end of the century (IPCC, 2013). As discussed earlier, the nonlinear relationship between mesquite establishment and PPT suggests that increases in mesquite recruitment during wet years will not fully compensate for the reductions in its recruitment experienced during drought years from a purely PPT perspective. Since both drought and wet conditions are projected to increase in frequency, one might project that the future climate will be less favorable for mesquite establishment. However, if drought also reduces small mammal abundance there may be a net increase in mesquite recruitment. Our study highlights the importance of accounting for biotic and abiotic interactions when explaining past and projecting future patterns of woody-plant encroachment in grasslands.

Our results also reject the episodic recruitment hypothesis for mesquite in the Chihuahuan Desert. Woody-plant recruitment in arid and semiarid environments is often presumed to be “episodic,” but there is debate as to whether shrub encroachment is a consequence of infrequent, large recruitment pulses or low-level but relatively

continuous recruitment (Bowers et al., 2004; Brown & Archer, 1999; Lewis et al., 2011; Meyer & Pendleton, 2005; Staver et al., 2007; Watson et al., 1997a). Models suggest both continuous and episodic recruitment may be required to maintain populations or explain encroachment success (Chesson et al., 2004; Watson et al., 1997a). Our field experiments align with those of Brown and Archer (1999) and show (1) extremely wet years will not necessarily trigger episodes of massive mesquite germination and establishment and (2) mesquite recruitment can be expected in years of average and even below-average PPT. However, our results also suggest that increases in PPT variability may gradually erode Mesquite populations because the reductions in recruitment experienced during extremely dry years will not be fully offset by enhanced recruitment during extremely wet years—unless compensated for by PPT-induced declines in small mammal populations.

Our experiment was aimed at quantifying drivers and their interactions during the early phases of woody-plant encroachment. How mesquite recruitment responds to PPT variability and predation pressure moving into the future may help to inform where, and under what conditions, management interventions would be most cost effective. In the southern Great Plains and the Chihuahuan Desert, brush management treatments such as prescribed fire, herbicide, applications and mechanical treatments (Hamilton et al., 2004) are often employed by land managers to reduce the cover of mesquite shrubs for maintaining a grassland state or restoring a shrub-encroached site back to its historical condition. These restoration endeavors can be costly and often involves extensive planning for implementation on both private and public lands. Information on mesquite recruitment probabilities under various PPT regimes and small mammal abundances can aid such planning. Our results thus provide a quantitative basis for developing a “shrub encroachment” early warning system to identify when and where shrub encroachment is most likely to occur in a grassland. Armed with such a tool, land managers could plan, develop, and strategically deploy management actions more effectively.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Weber-Grullon et al., 2021) are available from the EDI Data Portal at: <https://doi.org/10.6073/pasta/6965a303e898f19ffd0c15eacca1135b>.

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## REFERENCES

- Aguiar, M., and O. Sala. 1999. “Patch Structure, Dynamics and Implications for the Functioning of Arid Ecosystems.” *Trends in Ecology and Evolution* 14: 273–7.
- Anadón, J. D., O. E. Sala, and F. T. Maestre. 2014. “Climate Change Will Increase Savannas at the Expense of Forests and Treeless Vegetation in Tropical and Subtropical Americas.” *Journal of Ecology* 102: 1363–73.
- Ansley, R. J., W. E. Pinchak, and M. K. Owens. 2017. “Mesquite Pod Removal by Cattle, Feral Hogs and Native Herbivores.” *Rangeland Ecology & Management* 70: 469–76.
- Archer, S., ed. 1994. *Woody Plant Encroachment into Southwestern Grasslands and Savannas: Rates, Patterns and Proximate Causes*. Denver, CO: Society for Range Management.
- Archer, S., and J. K. Detling. 1986. “Evaluation of Potential Herbivore Mediation of Plant Water Status in a North American Mixed-Grass Prairie.” *Oikos* 47: 287–91.
- Archer, S. R., D. S. Schimel, and E. A. Holland. 1995. “Mechanisms of Shrubland Expansion: Land Use, Climate or CO<sub>2</sub>?” *Climatic Change* 29: 91–9.
- Bahre, C. J., and M. L. Shelton. 1993. “Historic Vegetation Change, Mesquite Increases, and Climate in Southeastern Arizona.” *Journal of Biogeography* 20: 489–504.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. Fitting Linear Mixed-Effects Models Using lme4. *arXiv preprint arXiv:1406.5823*.
- Bestelmeyer, B. T., D. P. C. Peters, S. R. Archer, D. M. Browning, G. S. Okin, R. L. Schooley, and N. P. Webb. 2018. “The Grassland-Shrubland Regime Shift in the Southwestern United States: Misconceptions and Their Implications for Management.” *Bioscience* 68: 678–90.
- Bowers, J. E., R. M. Turner, and T. L. Burgess. 2004. “Temporal and Spatial Patterns in Emergence and Early Survival of Perennial Plants in the Sonoran Desert.” *Plant Ecology* 172: 107.
- Bozdogan, H. 1987. “Model Selection and Akaike’s Information Criterion (AIC): The General Theory and its Analytical Extensions.” *Psychometrika* 52: 345–70.
- Briske, D. D. 2017. “Rangeland Systems: Foundation for a Conceptual Framework.” In *Rangeland Systems: Processes, Management and Challenges*, edited by D.D. Briske, 1–21. Cham: Springer International Publishing.
- Briske, D. D., and J. H. Richards. 1995. “Plant Responses to Defoliation: A Physiological, Morphological and Demographic Evaluation.” In *Wildland Plants: Physiological Ecology and Developmental Morphology*, edited by D. J. Bedunah and R. E. Sosebee, 635–710. Denver, CO: Society for Range Management.



- Brown, J., and S. Archer. 1989. "Woody Plant Invasion of Grasslands: Establishment of Honey Mesquite (*Prosopis Glandulosa* Var. *Glandulosa*) on Sites Differing in Herbaceous Biomass and Grazing ...." *Oecologia* 80: 19–26.
- Brown, J. R., and S. Archer. 1990. "Water Relations of a Perennial Grass and Seedlings vs Adult Woody Plants in a Subtropical Savanna, Texas." *Oikos* 57: 366–74.
- Brown, J. R., and S. Archer. 1999. "Shrub Invasion of Grassland: Recruitment Is Continuous and Not Regulated by Herbaceous Biomass or Density." *Ecology* 80: 2385.
- Browning, D., and S. Archer. 2011. "Protection from Livestock Fails to Deter Shrub Proliferation in a Desert Landscape with a History of Heavy Grazing." *Ecological Applications* 21: 1649–22.
- Chesson, P., R. L. Gebauer, S. Schwinning, N. Huntly, K. Wiegand, M. S. Ernest, A. Sher, A. Novoplansky, and J. F. Weltzin. 2004. "Resource Pulses, Species Interactions, and Diversity Maintenance in Arid and Semi-Arid Environments." *Oecologia* 141: 236–53.
- Demaria, E. M., P. Hazenberg, R. L. Scott, M. B. Meles, M. Nichols, and D. Goodrich. 2019. "Intensification of the North American Monsoon Rainfall as Observed from a Long-Term High-Density Gauge Network." *Geophysical Research Letters* 46: 6839–47.
- Devine, A. P., R. A. McDonald, T. Quaife, and I. M. D. Maclean. 2017. "Determinants of Woody Encroachment and Cover in African Savannas." *Oecologia* 183: 939–51.
- Duval, B. D., E. Jackson, and W. G. Whitford. 2005. "Mesquite (*Prosopis Glandulosa*) Germination and Survival in Black-Grama (*Bouteloua Eriopoda*) Grassland: Relations between Microsite and Heteromyid Rodent (*Dipodomys* spp.) Impact." *Journal of Arid Environments* 62: 541–54.
- Fay, P. A., and M. J. Schultze. 2009. "Germination, Survival, and Growth of Grass and Forb Seedlings: Effects of Soil Moisture Variability." *Acta Oecologica* 35: 679–84.
- French, N., W. Grant, W. Grodzinski, and D. Swift. 1976. "Small Mammal Energetics in Grassland Ecosystems." *Ecological Monographs* 46: 201–20.
- Gherardi, L. A., and O. E. Sala. 2013. "Automated Rainfall Manipulation System: A Reliable and Inexpensive Tool for Ecologists." *Ecosphere* 4: art18.
- Gibbens, R. P., and J. M. Lenz. 2001. "Root Systems of some Chihuahuan Desert Plants." *Journal of Arid Environments* 49: 221.
- Gibbens, R. P., R. P. McNeely, K. M. Havstad, R. F. Beck, and B. Nolen. 2005. "Vegetation Change in the Jornada Basin from 1858 to 1998." *Journal of Arid Environments* 61: 651–68.
- Hamilton, W. T., A. McGinty, D. N. Ueckert, C. W. Hanselka, and M. R. Lee. 2004. *Brush Management: Past, Present, Future*. College Station, TX: Texas A&M University Press.
- Harrington, G. N. 1991. "Effects of Soil Moisture on Shrub Seedling Survival in Semi-Arid Grassland." *Ecology* 72: 1138–49.
- Heady, H., and R. Child. 1994. *Rangeland Ecology and Management*. San Francisco, CA: Westview Press.
- IPCC. 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.
- Johnston, M. C. 1963. "Past and Present Grasslands of Southern Texas and Northeastern Mexico." *Ecology* 44: 456–66.
- Jurena, P. N., and S. R. Archer. 2003. "Woody Plant Establishment and Spatial Heterogeneity in Grasslands." *Ecology* 84: 907–19.
- League, K., and T. Veblen. 2006. "Climatic Variability and Episodic Pinus Ponderosa Establishment along the Forest-Grassland Ecotones of Colorado." *Forest Ecology and Management* 228: 98–107.
- Lewis, S. L., P. M. Brando, O. L. Phillips, G. M. F. van der Heijden, and D. Nepstad. 2011. "The 2010 Amazon Drought." *Science* 331: 554–4.
- Matias, L., R. Zamora, and J. Castro. 2011. "Repercussions of Simulated Climate Change on the Diversity of Woody-Recruit Bank in a Mediterranean-Type Ecosystem." *Ecosystems* 14: 672–82.
- Mendoza, I., R. Zamora, and J. Castro. 2009. "A Seeding Experiment for Testing Tree-Community Recruitment under Variable Environments: Implications for Forest Regeneration and Conservation in Mediterranean Habitats." *Biological Conservation* 142: 1491–9.
- Meyer, S. E., and B. K. Pendleton. 2005. "Factors Affecting Seed Germination and Seedling Establishment of a Long-Lived Desert Shrub (*Coleogyne ramosissima*: Rosaceae)." *Plant Ecology* 178: 171–87.
- Miller, R., and J. Rose. 1999. "Fire History and Western Juniper Encroachment into Sagebrush Steppe." *Journal of Range Management* 59: 80–8.
- Monger, H. C., G. H. Mack, B. A. Nolen, and L. H. Gile. 2006. "Regional Setting of the Jornada LTER." In *Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin Long-Term Ecological Research Site*, edited by K.M. Havstad, L.F. Huenneke, and W.H. Schlesinger, 15–43. Oxford: Oxford University Press.
- Noy-Meir, I. 1973. "Desert Ecosystems: Environment and Producers." *Annual Review of Ecology and Systematics* 4: 25–52.
- Padilla, F. M., and F. I. Pugnaire. 2007. "Rooting Depth and Soil Moisture Control Mediterranean Woody Seedling Survival during Drought." *Functional Ecology* 21: 489–95.
- R Core Team. 2018. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Reichmann, L. G., O. E. Sala, and D. P. C. Peters. 2013. "Precipitation Legacies in Desert-Grassland Primary Production Occur through Previous-Year Tiller Density." *Ecology* 94: 435–43.
- Rysavy, A., M. Seifan, M. Sternberg, and K. Tielbörger. 2014. "Shrub Seedling Survival under Climate Change – Comparing Natural and Experimental Rainfall Gradients." *Journal of Arid Environments* 111: 14–21.
- Sala, O. E., W. J. Parton, W. K. Lauenroth, and L. A. Joyce. 1988. "Primary Production of the Central Grassland Region of the United States." *Ecology* 69: 40–5.
- Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. "Biological Feedbacks in Global Desertification." *Science* 247: 1043–8.
- Schooley, R. L., B. T. Bestelmeyer, and A. Campanella. 2018. "Shrub Encroachment, Productivity Pulses, and Core-Transient Dynamics of Chihuahuan Desert Rodents." *Ecosphere* 9: e02330.

- Soriano, A., O. E. Sala, and S. B. Perelman. 1994. "Patch Structure and Dynamics in a Patagonian Arid Steppe." *Vegetatio* 111: 127–35.
- Staver, A. C., W. J. Bond, and E. C. February. 2007. "Continuous v. Episodic Recruitment in Acacia Karroo in Hluhluwe-Imfolozi Park: Implications for Understanding Savanna Structure and Dynamics." *South African Journal of Botany* 73: 314.
- Tape, K. D., M. Hallinger, J. M. Welker, and R. W. Ruess. 2012. "Landscape Heterogeneity of Shrub Expansion in Arctic Alaska." *Ecosystems* 15: 711–24.
- van Auken, O. W. 2000. "Shrub Invasions of North American Semi-arid Grasslands." *Annual Review of Ecology and Systematics* 31: 197–215.
- Wainwright, J. 2006. "Climate and Climatological Variations in the Jornada Basin." In *Structure and Function of the Chihuahuan Desert Ecosystem*, edited by K. Havstad, L. Huenneke, and W. Schlesinger, 44–80. Oxford: Oxford University Press.
- Watson, I. W., M. Westoby, and A. M. Holm. 1997a. "Continuous and Episodic Components of Demographic Change in Arid Zone Shrubs: Models of Two Eremophila Species from Western Australia Compared with Published Data on Other Species." *Journal of Ecology* 85: 833–46.
- Watson, I. W., M. Westoby, and A. M. Holm. 1997b. "Demography of Two Shrub Species from an Arid Grazed Ecosystem in Western Australia 1983–93." *Journal of Ecology* 85: 815–32.
- Weber-Grullon, L., L. Gherardi, W. Rutherford, S. Archer, and O. Sala. 2021. Drought and Herbivory Effects on Woody Plant Seedling Establishment and Grass Competition in the Jornada Basin, 2016–2018 ver 1. Environmental Data Initiative. <https://doi.org/10.6073/pasta/6965a303e898f19ffd0c15eacca1135b>
- Weltzin, J. F., S. R. Archer, and R. K. Heitschmidt. 1998. "Defoliation and Woody Plant (Shape Prosopis Glandulosa) Seedling Regeneration: Potential vs Realized Herbivory Tolerance." *Plant Ecology* 138: 127–35.
- Whitford, W. G. 1978. "Foraging in Seed-Harvester Ants *Proconomyrmex* spp." *Ecology* 59: 185–9.
- Yahdjian, L., and O. E. Sala. 2002. "A Rainout Shelter Design for Intercepting Different Amounts of Rainfall." *Oecologia* 133: 95–101.

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