Journal of Arid Environments 187 (2021) 104432

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Shrubs facilitate perennial bunchgrass recruitment in drylands under experimental precipitation change

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ARTICLE INFO

Keywords:
Arid regions
Drought
Gradients
Population dynamics
Precipitation

ABSTRACT

Increasing extremes in climate related weather events pose a major threat to plant recruitment in drylands. Research has shown facilitation effects by shrubs to improve recruitment in arid regions, however it remains unclear if these effects vary between soil types, early life stages and in both severe precipitation and drought events. We test if shrubs facilitate abundance of both seedlings and juveniles between two soil types in artificial high precipitation, ambient and severe drought conditions. When the effect of shrubs was considered, seedling and juvenile responses were similar between sites. Shrubs increased seedling abundance by 40.9% in drought. In high precipitation, shrubs increased seedling abundance by 20% at one site and juvenile abundance 15% at both sites. These findings support the notion that shrubs can improve recruitment in both severe precipitation and drought years, but the strength of this effect varies with soil. Our results indicate that resource islands generated by shrubs in high precipitation years, may be an important factor driving population dynamics in arid systems as years oscillate between wet and dry.

1. Introduction

Understanding the impact of positive biotic interactions (i.e. facilitation effects) on early developmental stages in plants is crucial for predicting and managing the changes in plant population dynamics under global climate change. This may be particularly important in arid systems where precipitation regimes are changing (Stocker et al., 2013) (Fraaije et al., 2015; Pyke, 1990; Salihi and Norton, 1987) and recruitment is frequently limited by drought (Fraaije et al., 2015; Pyke, 1990; Salihi and Norton, 1987). Soil moisture and microclimate humidity are strong environmental filters during early life stages, often determining seed germination, establishment and survival (Fraaije et al., 2015; Valdez et al., 2019). Consequently, most plant mortality occurs from desiccation during the transition from seedling to juvenile (Pyke, 1990; Salihi and Norton, 1987; Valdez et al., 2019). Understanding if or how plant to plant facilitation effects can increase both seedling and juvenile survival is necessary for managing recruitment under changing precipitation regimes, because once plants reach the juvenile stage, survival probabilities greatly increase (Miriti, 2006; Pfister, 1998).

Research on facilitation of seedling and juvenile survival via the "nurse plant syndrome" (Franco and Nobel, 1989) has increased with recent examinations of biotic interactions along stress gradients. The stress gradient hypothesis (henceforth 'SGH') in its original form predicts facilitation among plants increases as abiotic stress increases (Bertness and Callaway, 1994). Shrub life forms have attracted particular attention in arid and semi-arid ecosystems as potential nurse plants, and evidence is growing for their efficacy in mediating stress for neighbors (Boyd and Davies, 2012; Fedriani et al., 2019; Gómez-Aparicio, 2009; Valiente-Banuet et al., 1991). As an example, a meta-analysis by Gómez-Aparicio (2009) investigating the utility of biotic interactions for restoration, found that earlier life stages of emergence and survival were most positively correlated with facilitative interactions, particularly in semi-arid environments. In sagebrush steppe of eastern Oregon, where the present study was conducted, research also shows support for positive nurse shrub effects of *Artemisia tridentata* (sagebrush) during early life stages (Chambers, 2001).found seedlings of *Pinus monophylla* to reach optimal survival near shrub canopies and attributed this to a modified microsite environment by sagebrush shrubs. Similarly, a post-fire restoration study conducted in this same region by (Boyd and Davies, 2010), found seedling density of perennial bunchgrasses to be 24-fold higher in microsites that contained a burned sagebrush canopy than burned interspace microsites.

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https://doi.org/10.1016/j.jaridenv.2020.104432
Received 15 April 2020; Received in revised form 21 December 2020; Accepted 29 December 2020
Available online 15 January 2021
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These studies did not however examine if facilitation effects remain when subjected to temporally driven precipitation stress. Given changing weather regimes and increasing severity in precipitation and drought events predicted for dryland systems, it is necessary to ask similar questions in the context of climate change to provide relevant information and contemporary solutions for natural resource managers. As noted by Tielbörger and Kadmon(Tielborger and Kadmon, 2000), environmental stress varies not only in space but also in time. It is thus reasonable to predict facilitation would increase with temporally imposed environmental stress, similar to how it has been shown to increase with spatially imposed environmental stress. However, gathering empirical support for temporal facilitation effects poses some logistical challenges given unpredictability in weather and the availability of data from long-term studies. Nonetheless innovative study designs involving artificial drought and precipitation manipulations, in recent years have provided growing evidence of temporally driven facilitation, similar to what has been found for spatial stress gradients (Dohn et al., 2013; Holthuijzen and Veblen, 2015; Tielborger and Kadmon, 2000; Zhang et al., 2018).

How facilitation effects may vary depending on soil type is also an important factor to consider in light of severe weather events. This is because the microsite environment created by shrubs plays a key role in facilitation outcomes by influencing soil moisture through processes such as hydraulic redistribution and hydraulic lift (Cardon et al., 2013; Horton and Hart, 1998; McLaughlin et al., 2017; Richards and Caldwell, 1987; Scott et al., 2008). Shrubs also influence other microsite conditions by increasing soil organic matter, regulating soil temperatures and reducing solar radiation (Davies et al., 2007; Maestre et al., 2001; Moro et al., 1997). In sagebrush steppe of eastern Oregon where this study was conducted, soils are diverse and often form mosaics of many types in a small area (Lentz R & Simonsen G, 1986). Thus, because soil moisture can be a major limitation to recruitment (James et al., 2011) it is essential to test facilitation effects between soil types to gain insight into how facilitation effects might vary across larger regions given extremes in predicted precipitation regimes.

We use an approach framed by low, ambient and high precipitation levels that allows us to ask three primary questions. First, we ask whether sagebrush shrubs facilitate perennial bunchgrass recruitment, and if differences in facilitation effects are detectable given extremes in annual precipitation within the peak productivity months of April, May and June. We chose these months to study recruitment effects because the long, cold winters of the Northern Great Basin bring snow and low temperatures oftentimes into March delaying the onset of bunchgrass seedling emergence for most species into April. Second, we ask if facilitation effects by shrubs are more apparent for seedlings than for juveniles to understand if one life stage warrants more focus than the other from a management perspective. Third, we ask if facilitation effects vary by soil type. We ask this with the information given from a previous study examining the soils at both our study locations. These researchers identified Pernty soils with greater clay content and higher moisture holding capacity than Milcan soils (Lentz and Simonsen, 1986). Specifically, we test if facilitation effects are different between a site with a Milcan fine sandy loam soil (henceforth 'Milcan site') and a site with a Pernty very cobbly loam soil (henceforth 'Pernty site'). Given this framework, our hypotheses are as follows: 1. Shrubs facilitate recruitment processes in sagebrush steppe ecosystems and seasonally driven facilitation effects are most apparent in drought conditions and least apparent under heavy precipitation. 2. Within each site, seedlings and juveniles respond similarly to facilitation by shrubs under seasonally high drought and high precipitation events. 3. Facilitation of seedlings and juveniles is more apparent on sandier Milcan soils than on the Pernty soil with greater clay content.

2. Methods

2.1. Study locations

This study was conducted at two sites in the Northern Great Basin Experimental Range, 56 km west of Burns, OR, USA. The two sites were approximately 1.6 km apart (Milcan: 43.46 N, 119.69 W and Pernty: 43.46 N, 119.71 W). Elevation of both sites was about 1500 m with $<2^{\circ}$ slope with undulating topography. The climate consists of hot-dry summers and cool, semi-wet winters. Precipitation is highly variable and is received in a bimodal distribution with peaks in the winter and spring. The 30-year precipitation averages (1981–2010) in this region range from 240 to 270 mm, with the majority falling as rain or snow between October and May. There is a mosaic of 25 soil taxa comprising 29 complexes in this region of the Great Basin (Lentz and Simonsen, 1986). We chose two study sites each located on commonly found, but different, soil series. Soil at the "Milcan site" is classified as well drained Milcan fine sandy loam with a 0–2% slope and 5–15% clay content. Soil at the "Pernty site" is classified as Pernty very cobbly loam with 0–4% north slope and 25–35% clay content (Lentz and Simonson, 1986). Milcan soils maintain moderately high evapotranspiration rates, saturated hydraulic conductivity and excessive drainage (https://soilseries.sc.egov.usda.gov/osdlist.aspx, accessed: November 13th, 2019).

Vegetation in the study area is classified as sagebrush-bunchgrass steppe, with Big Sagebrush (*Artemisia tridentata* Nutt.) being the dominant shrub at both sites. Dominant perennial bunchgrass species at both sites were *Poa secunda* (J. Presl), *Achnatherum thurberianum* (Piper Barkworth), *Pseudoroegneria spicata* (Pursh. A. Love), *Koeleria macrantha* (Ledeb. Schult.), *Elymus elymoides* (Raf.) and *Festuca idahoensis* (Elmer). Both study sites were fully enclosed to prohibit cattle grazing (though neither site had been grazed in the previous 3 years) and were 100 m × 100 m in size.

2.2. Study design

To elucidate the effects of shrubs on recruitment given different precipitation levels, we used a randomized complete factorial design with sagebrush (with, without sagebrush) crossed with three water treatments (water added, ambient water, and water excluded). In the shrub removal plots, shrubs were cut at ground level in November 2012 and stems were painted with 5% Glyphosate Pro (Glyphosate, Monsanto, St. Louis, MO, USA) during March of 2013. Shrub removal was nearly 100% successful and the few shoots that occurred were clipped at ground level. To exclude water, drought canopies were applied to the plots. Canopies were made of clear acrylic material and placed no less than 80 cm above the ground to allow for shrub height and to intercept the most precipitation without altering other environmental factors (Yahdjian and Sala, 2002). The canopies intercepted precipitation for two growing seasons, simulating severe drought conditions. Canopies were applied to plots during the first week of March 2013 through June 2014 and measured 1.8 m × 1.8 m in size, overlapping the edge of the plot, to minimize edge effect.

The high precipitation treatment was simulated through the addition of double the 30 year monthly average precipitation for April and May, resulting in 46 mm and 55 mm of rainfall respectively (Figs. 2–). This required a water application rate of 40 L per week for April 2014 and 48 L per week in May 2014 to each plot with uniform coverage delivered at a rate to prevent pooling. We chose this amount of moisture as it occurs on average once every five years in this system, where any amount greater would have been anomalous, and an amount less than this would be too close to the normal to create a testable gradient. To ensure our treatments were having an effect on moisture availability, soil moisture content of all plots was measured once in April and once in May 48 h after water application at a depth of approximately 10 cm using a handheld moisture probe (OMEGA HSM50).

Seed from six dominant bunchgrass species was purchased in the fall

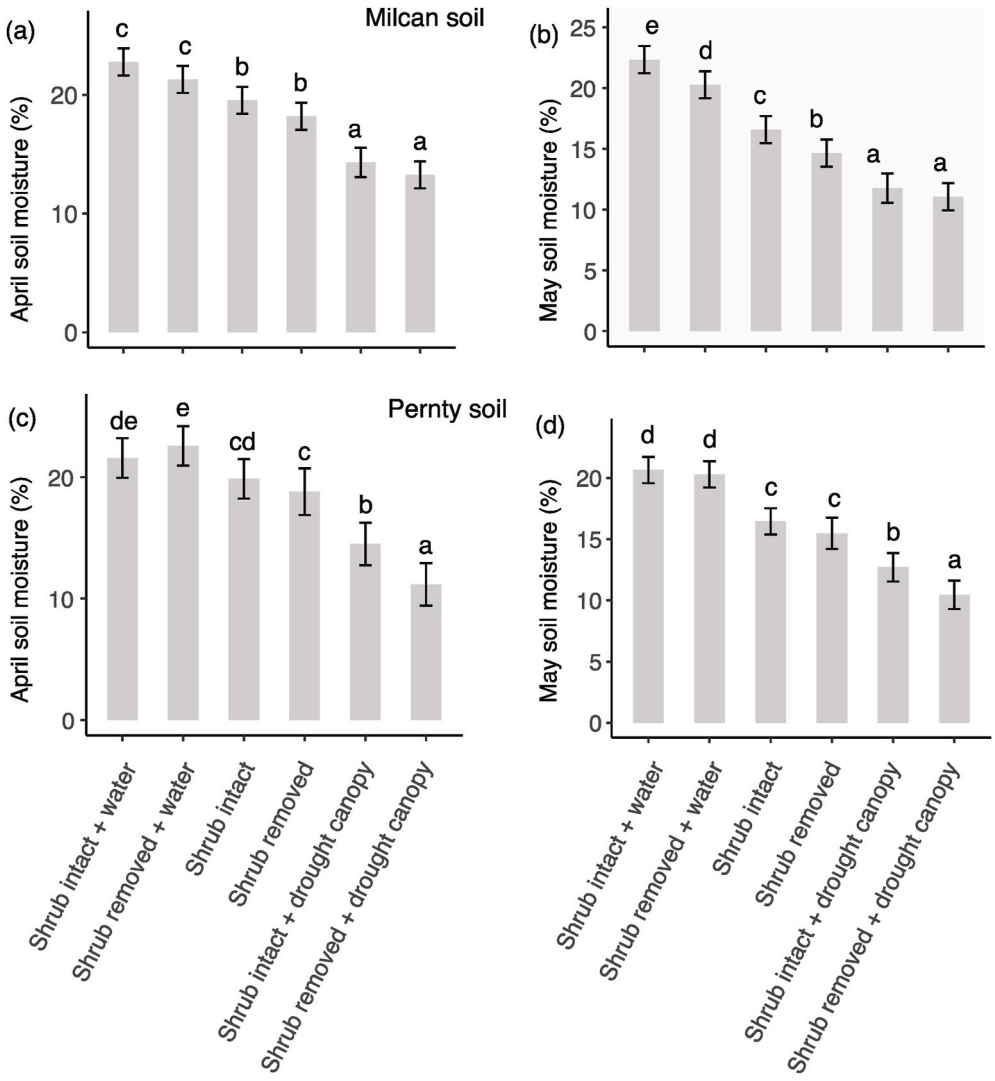

Fig. 1. Mean soil moisture (%) among treatments for April and May at the Milcan fine sandy loam (1a, 1 b) and Pernty very cobbly loam (1c, 1 d) sites. Different letters indicate significant differences in soil moisture from Tukey tests. Error bars given from confidence intervals ($\alpha = 0.05$).

of 2013 from BFI Native Seeds (Moses Lake, WA) and ecotypes were selected based on environmental similarity of collection site to local site conditions. Species were as follows: *Poa secunda* (J. Presl.), *Achnatherum thurberianum* (Piper. Barkworth), *Pseudoroegneria spicata* (Pursh. A. Love), *Koeleria macrantha* (Ledeb. Schult.), *Elymus elymoides* (Raf.) and *Festuca idahoensis* (Elmer). Seed was inspected for viability at the USDA-ARS National Forage Seed Production Research Lab in Corvallis, Oregon and pre-mixed in equal proportions on a per weight basis to ensure 100% pure-live seeds were added to each plot. Seed was proportioned to facilitate broadcasting by hand during the first of November 2013 at a density of 3000 seeds per plot (500 live seeds of each species equating to approximately 250 seeds per m^{-2}).

2.3. Data collection

We first used a systematic random sampling technique along seven transects within a 100 m × 100 m macroplot to obtain a sample pool of 140 plots. From this sample, we could then identify plots that contained an adult sagebrush individual. Out of the 140 potential plots, 66 plots met our criteria in the Milcan site and 83 met our criteria in the Pernty site. These plots were assigned a number (1–66 and 1–83 respectively). From this secondary pool we used a random number generator to select n = 42 plots at each site. Plots were 1.5 × 1.5 m in size and randomly assigned one of the six treatments.

Plots were divided into 4 sampling quadrants according to each cardinal direction (North, South, East and West) to mitigate effects of shade, or other directionally dependent environmental variables. Our measured response variables were the mean number of seedlings and the mean number of juveniles within each treatment. A 1 m^2 sampling square was placed at the center of each cardinal quadrant, and newly emerged seedlings were marked biweekly from April 2014 through the first week of June 2014. Seedlings were marked at each sampling session to ensure they were counted once. Juvenile data was collected the first week of June 2014. Individuals were considered seedlings with the presence of a coleoptile, cotyledon, or one fully developed leaf (James et al., 2011). Because the juvenile stage can last for several years in some perennial bunchgrasses, we considered individuals to be juveniles if more than one leaf was present up to a total of 10 and no indication of reproductive culms. Seedling and juvenile counts were summed to the plot level with n = 7 replicates per treatment.

2.4. Data analysis

Differences in soil moisture among treatments were tested using ANOVA and Tukey HSD ($\alpha = 0.05$). We analyzed the effect of treatment on seedling and juvenile abundance using a generalized linear model

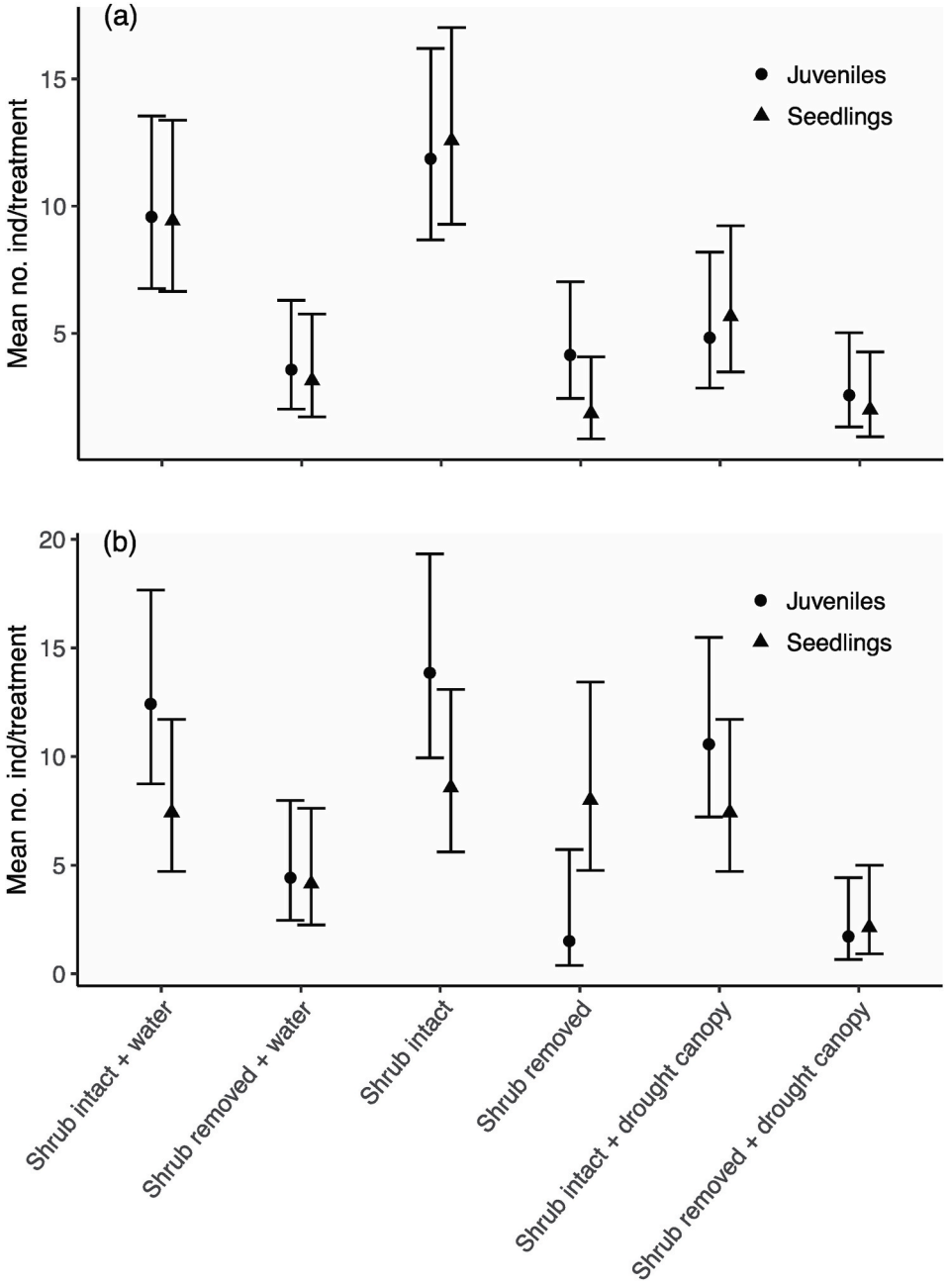

Fig. 2. Difference in predicted mean number of individuals between seedlings and juveniles for each treatment at the Milcan (panel a) and Pernty site (panel b) in each treatment ($\alpha = 0.05$). Error bars are given from confidence intervals.

(GLM) with a quasi-poisson distribution to account for over dispersion of discrete counts (Zuur et al., 2009). GLMs were fitted with the glm function in R 3.4.3.. Treatment factors of 'shrub' and 'water manipulation' were grouped as simple effects and combined as a main 'treatment' effect in the analysis. For analysis within sites the fixed effect variables were species (n = 6), and treatment (n = 6). For between-site analysis the 'site' variable (n = 2) and treatment variable became fixed effects in the model. Our response variables for all analyses were the mean number of seedlings and the mean number of juveniles, with discrete counts summed to the plot level (our experimental unit) and extracted as estimated marginal means for each treatment. First, we evaluated main and interaction effects within and across sites with analysis of variance Type II or III F tests ($\alpha = 0.05$). We chose Type III tests for models that showed evidence for an interaction effect. Afterward, we performed pairwise comparisons to test for differences in means between treatments and sites for each variable, using this as our indicator for or against facilitation ($\alpha = 0.05$). Pairwise tests were conducted using predicted marginal means with a 'Tukey' adjustment from the 'lsmeans' package (Lenth, 2017) in R 3.4.3. We used the differences in predicted marginal means of our treatment contrasts (i.e. the response ratio) and Wald's z test as our indicator for facilitation. Response ratios were back-transformed from the log scale and rage from one to infinity and one to zero. Significant Wald's z with response ratios above 1 indicate facilitation; Significant Wald's z response ratios near one indicate competition. Our paired contrasts of interest were as follows: 'shrub intact vs. shrub removed (ambient conditions)', 'shrub intact + drought canopy vs. shrub removed + drought canopy (drought conditions)', and 'shrub intact + water vs. shrub removed + water (moist conditions)'. We consider evidence for facilitation when the response ratios between the shrub intact vs. shrub removed (plus one of the three water regimes)

contrasts are positively large and of significance and consider neutral interaction when the response ratios between shrub intact vs. shrub removed (plus one of the three water regimes) are small enough to be insignificant.

3. Results

3.1. Environmental conditions

Mean monthly temperature for April and May in 2014 were typical of the region and approximate the 30-year mean temperatures for those months (Fig. S1). Ambient precipitation in April of 2014 was consistent with the 30-year normal precipitation levels (Fig. S2) for the region. In April, soil moisture in the shrub intact + water treatment was 14.2% greater than the soil moisture in the shrub intact + ambient conditions at the Pernty site and 17.4% greater in the shrub intact + ambient conditions at the Milcan site (Fig. 1 a, c). In May of 2014 ambient precipitation was very low and recorded at less than half of the 30-year normal for that month. This low precipitation was reflected in the mean soil moisture for May at both sites where we found the ambient shrub intact treatment to be at least 22.2 lower than the water treatment with or without a shrub present (Fig. 1 b, d). Soil moistures were lowest in the treatments with drought canopies across both sites in April and May. Additionally, shrub removal in combination with the drought canopy resulted in about 22% lower soil moisture than when the shrub was left intact at the Pernty site in both April and May (Fig. 1 c, d). This was not the case at the Milcan site where no significant difference was detected for either month when the shrub was removed versus when it was intact in drought treatments (Fig. 1 a, b).

3.2. Facilitating recruitment in drought, ambient and high precipitation years (Hypothesis 1)

In partial support of our first hypothesis, we found evidence for facilitation of bunchgrass recruitment. However, the response varied with precipitation manipulation (Table 1). In contrast to the second part of our hypothesis, facilitation effects were not consistently more apparent under drought and least apparent under moist conditions for both seedlings and juveniles (Table 2). The stronger facilitation effect during drought conditions occurred only for seedlings at the Pernty site.

When subjected to drought conditions, shrubs significantly increased seedling abundance by 40.9% ($z = 3.005$; $P = 0.0318$) while there was no significant effect on seedling abundance in either the high precipitation or ambient treatments (Table 2).

In contrast, at the Milcan site, facilitation was most apparent for seedlings under ambient treatment conditions (Table 2) where predicted marginal mean abundance was 57.9% greater in the presence of shrubs than in the removal plots ($z = 4.100$; $P = 0.0006$). Facilitation was also apparent in the water addition treatments where predicted marginal mean abundance for seedlings was 20.0% greater in the presence of shrubs than in removal plots (Table 2; $z = 2.843$; $P = 0.05$).

Table 1
Type II and III ANOVA table of main and interaction effects ($\alpha = 0.05$; Milcan: $N = 237$ seedlings, $N = 251$ juveniles; Pernty: $N = 213$ seedlings, $N = 352$ juveniles). Table includes density degrees of freedom (df), life stages, and analyses within and across sites. Bold numbers are significant.

Main and Interaction Effects		df	*F*	*P*
within sites	Milcan seed	5	9.247	**0.000011**
	Milcan juvenile	5	8.6222	**0.000012**
	Pernty seed	5	5.2647	**0.001098**
	Pernty juvenile	5	7.04	**0.000130**
	Milcan stage x treatment	5	0.6747	0.64400
	Pernty stage x treatment	5	2.6053	**0.03261**
between sites	(seed) site x treatment	5	0.9022	0.4849
	(juvenile) site x treatment	5	1.2896	0.2787

Table 2
Response ratio for paired treatment contrasts of seedling and juvenile abundance within each site. Response ratios are the difference in predicted marginal means between treatment pairs and are based on a generalized linear model from a quasi-poisson distribution. Shrub removed vs. intact treatment pairs were under artificial seasonal precipitation: moist (water addition), ambient (no water manipulation) and drought (drought canopy). Response ratios are back-transformed from the log scale. Evidence of facilitation is based on z-ratios for the difference in predicted marginal means at $\alpha = 0.05$ (i.e. $P > 0.05$ = ns; $P < 0.05$ = *; $P < 0.01$ = **; $P < 0.001$ = ***). Response ratios range from one to infinity and one to zero. Significant Wald's z with response ratios above 1 indicate facilitation; Significant Wald's z response ratios near one indicate competition.

	Pernty		Milcan	
Treatment	**Seedling *RR***	**Juvenile *RR***	**Seedling *RR***	**Juvenile *RR***
Moist	**2.08** (ns)	**2.48** (*)	**3.00** (*)	**2.68** (*)
Ambient	4.76 (ns)	1.73 (ns)	**6.76** (***)	**2.86** (**)
Drought	**5.09** (*)	**4.11** (**)	2.83 (ns)	1.87 (ns)

For juveniles, there was strong evidence for facilitation effects during drought simulation at the Pernty site, where predicted marginal mean abundance was 31.1% greater in the presence of shrubs than without (Table 2; $z = 3.445$; $P = 0.0075$). This was not the case in the Milcan site, where we found no evidence that shrubs facilitated juveniles under drought conditions. To our surprise, facilitation was apparent at both sites in the artificial precipitation treatments, where there were significantly more juvenile perennial bunchgrasses in the presence of the shrub than without (Table 2). At the Pernty site predicted marginal mean abundance of juveniles was 14.8% greater in the presence of shrubs than without (Table 2; $z = 2.914$; $P = 0.04$). Similarly, at the Milcan site, predicted marginal mean abundance of juveniles was 16.8% greater in the presence of shrubs than without (Table 2: $z = 3.187$; $P = 0.018$).

3.3. Facilitation through life stages (Hypothesis 2)

In support of our second hypothesis, we found evidence seedlings and juveniles had similar responses to shrubs across treatments at both sites (Fig. 2 a,b). We found only one instance where seedling and juvenile response to shrubs varied. This occurred at the Pernty site in the high precipitation treatments where shrubs positively influenced juveniles and an effect on seedling was not apparent (Fig 2 b; $z = 2.914$; $P = 0.04$).

3.4. Facilitation between soil types (Hypothesis 3)

Contrary to our hypothesis, perennial grass recruitment did not vary among sites with different soil types (Table 1). Although abundances of both seedlings and juveniles varied, we found no statistical difference in seedling abundance between soil types in any of the treatments (Fig. 3a; all $P > 0.05$). For example, seedling abundance was lowest in shrub removal plots under artificial drought conditions at the Pernty site and ambient conditions at the Milcan site, with respective predicted marginal means of 1.57 individuals (SE = 0.7780) and 1.85 individuals (SE = 0.8085). Abundance was greatest for seedlings in the presence of shrubs, with a predicted marginal mean of 8.57 individuals at the Pernty site (SE = 1.8171), and a predicted marginal mean of 12.57 individuals (SE = 2.1035) at the Milcan site.

Similarly, we found little variation in juvenile abundance between soil types (Table 1). As with seedlings, abundance was greatest for juveniles in the presence of shrubs with a predicted marginal mean of 13.85 individuals at the Pernty site (SE = 2.1968), and a predicted marginal mean of 11.85 individuals (SE = 1.7176) at the Milcan site (Fig. 3b). Abundance was lowest for juveniles without shrubs in drought conditions at both the Pernty and Milcan site with the same predicted marginal mean of 2.57 individuals (Fig. 3b; SE = 0.9463 and SE =

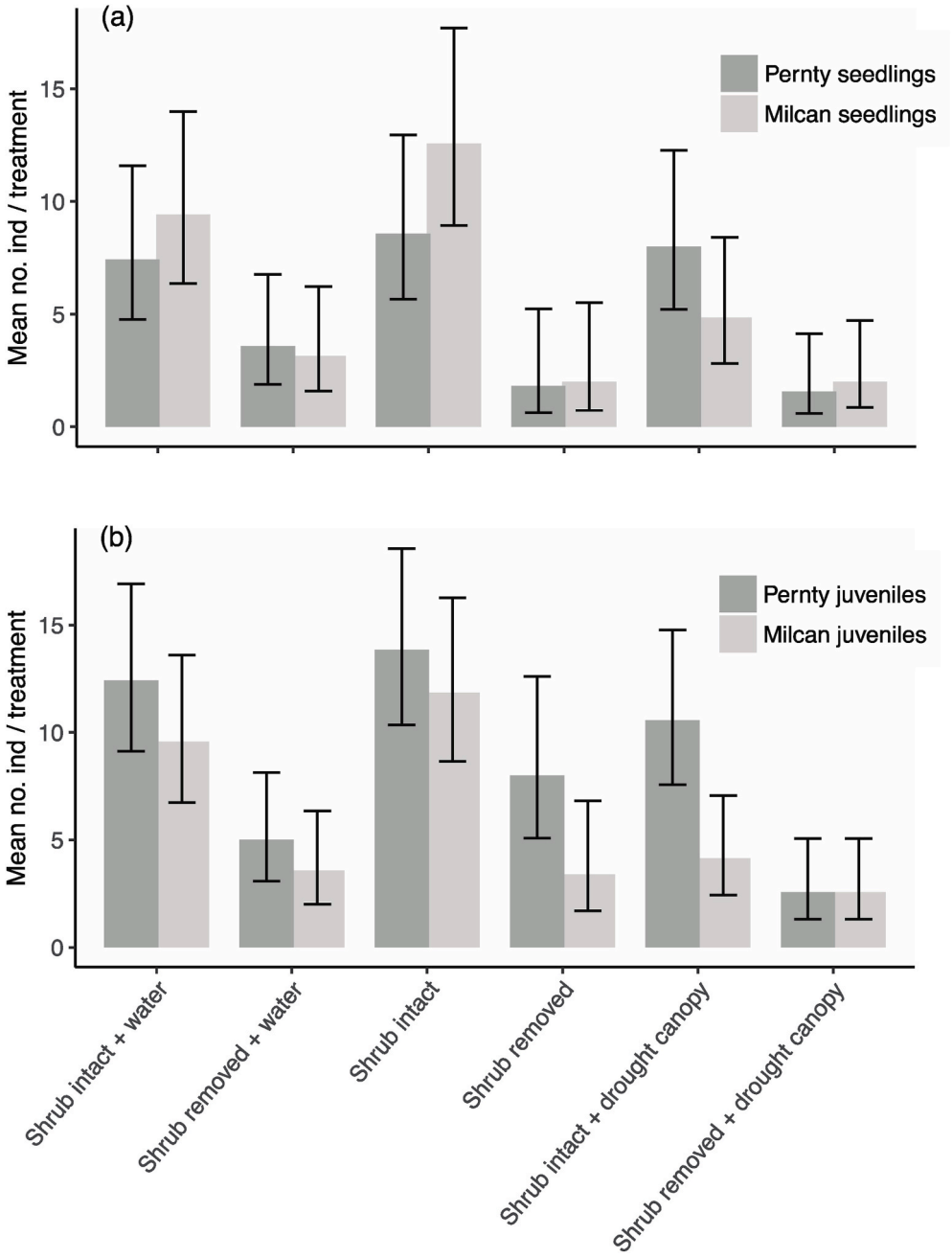

Fig. 3. Predicted marginal mean number of individuals for seedlings and juveniles in each treatment at the Pernty and Milcan sites given from a generalized linear model. Comparisons show the similarity in predicted mean abundance within treatments across sites for seedlings (panel a) and juveniles (panel b) ($\alpha = 0.05$). Error bars represent confidence intervals.

0.7998, respectively).

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4. Discussion

4.1. Environmental stress from severe weather events may induce temporally driven nutritional and ameliorative facilitation effects

In this study, our strongest evidence for facilitation surprisingly occurred under moist conditions, where water was not a limiting factor. At the Milcan site where we assume stress to be greater, given the characteristics attributed to soil types with lower clay content, both seedling and juvenile abundance were greater in the high precipitation treatments (Fig. 2a). At the Pernty site, with higher clay content, juvenile abundance was greater in the high precipitation treatments (Fig. 2b). Research on shrub nutrient islands provides a possible rationale for this finding. For example, in our model sagebrush steppe system,

research has shown that nutrients are concentrated under shrubs (Boyd and Davies, 2010; Davies et al., 2007; Doescher et al., 1984) and several studies have found that nutrient islands created by nurse plants in other arid systems improve neighbor outcomes, including seedling establishment (Allegrezza et al., 2016; Maestre et al., 2001; Ward et al., 2018). It is possible the facilitation of juveniles under high precipitation, is the result of this age class simply having enough root structures to take advantage of nutritional facilitation in high moisture conditions.

Although our results indicate that the magnitude of facilitation effects may vary by site, in contrast, these effects are very similar between seedling and juvenile life stages (Table 1). This indicates that drought, though important, may only be one condition limiting recruitment with practical consequences for successful restoration in drylands (Corbin and D'Antonio, 2004; James et al., 2011). Other abiotic and biotic processes related to soil should be equally considered. This is exemplified in the current study, where the abiotic condition of precipitation interacts with the biotic effect of a shrubs unique ameliorative capacity, which may vary given specific soil characteristics.

On the sandier Milcan soils, facilitation was less apparent for both seedlings and juveniles (Table 2). Here, facilitation collapsed under drought conditions, possibly due to stress thresholds being met when conditions became severely arid (Kjær et al., 2018; Soliveres et al., 2015) but remained important for seedling and juvenile establishment in ambient and high precipitation conditions. On Pernty cobbly loam soils, shrubs supported seedling abundance only under drought but were insignificant (albeit positive) in ambient and high precipitation conditions, perhaps because these conditions did not elicit the type of stress amelioration that seedlings necessitate.

4.2. Conclusions and implications

The most important finding of this study is that shrubs can enhance recruitment in years of high precipitation between soil types, but also enhance recruitment in drought years depending on severity and soil type. These findings suggest that in order to improve restoration, it may be beneficial to understand how positive biotic interactions propel source/sink dynamics across time and space, as weather drives oscillations between wet and dry growing seasons. This knowledge would improve predictability of the impacts of climate change on restoration outcomes for plant populations in semi-arid systems.

Though we found no evidence of competition in this study, it is important to note that competitive interactions are apparent in several studies under arid conditions where water is limited (Maestre and Cortina, 2004; Michalet, 2007; Tielborger and Kadmon, 2000). Where facilitation collapsed under drought conditions on the Milcan soils, response ratios were still positive, albeit insignificant (see Table 2). One limitation of our study is that it only considers seedling and juvenile abundance at one point in time and it is unclear if interactions become competitive later in the season as soils dry out. It has been noted by several authors that in order to generate a cohesive facilitation theory, studies should incorporate a full range of the gradient of interest in time, space or intensity (Kawai and Tokeshi, 2007; Maestre et al., 2009). We would suggest for future studies that examine temporally driven facilitation effects, to measure soil moisture and abundance across the entire growing season to allow for broader inference.

In conclusion, facilitation by nurse shrubs improved recruitment in this study by increasing abundance of seedlings and juveniles. In addition, seedlings and juveniles were similar in their response to shrubs, varying only when water resources were abundant on the higher clay Pernty soils. This supports the notion proposed by (Liancourt et al., 2017), that differences in level of strain experienced by individuals determine the outcome of positive interactions between nurses and beneficiaries. From a theoretical point, facilitation may simply alleviate the strain on an individual organism's physiological range of tolerance. Importantly, the magnitude of strain experienced by an individual may be driven by micro-site conditions, and broader factors related to soil-water interactions.

CRediT authorship contribution statement

Elizabeth K. Swanson: Writing - original draft, conceived and designed the study, collected and analyzed the data. **Roger L. Sheley:** Writing - original draft, conceived and designed the study. **Jeremy J. James:** conceived and designed the study, made editorial contributions.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank B. Bingham and C. Swanson for assistance with drought canopies and A. Muldoon for statistical support. We also thank the United States Department of Agriculture, Agricultural Research Service seed lab in Corvallis, Oregon for the use of their facilities. This research was funded through the United States Department of Agriculture, Agricultural Research Service,Area-wide Project for Ecologically Based Invasive Plant Management of Annual Grasses in the Great Basin Ecosystem. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2020.104432.

Statement of human and animal rights

This article does not contain any studies with human participants or animals performed by any of the authors.

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