



Do shrubs improve reproductive chances of neighbors across soil types in drought?

Elizabeth K. Swanson¹ · Roger L. Sheley² · Jeremy J. James³

Received: 5 December 2018 / Accepted: 11 November 2019 / Published online: 25 November 2019
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

Plant reproduction is highly sensitive to stress from severe weather. While facilitation has been shown to buffer negative impacts along stress gradients, less is known about facilitating plant reproduction in drought periods. Because intensity and frequency of drought are predicted to increase, plant reproductive facilitation has important implications for a species ability to adapt to changes in climate. Our primary study objective is to test if nurse shrubs act as reproductive micro-refugia across soil types, by improving reproductive potential of perennial bunchgrass neighbors subjected to severe drought. To investigate this objective, we designed a fully factored study testing direct interaction between shrub and bunchgrasses in eastern Oregon sagebrush steppe, at two sites with different soil types. The study consisted of six simple effect treatments combining three moisture regimes (moist, ambient, and drought) with two shrub conditions (shrub intact or shrub removed). Our results indicate when facilitation of reproductive potential occurs, it occurs strongly and particularly in drought, consistent with the stress gradient hypothesis (SGH), where several species produced at least 54% more inflorescences in the presence of shrub neighbors. In addition, we found facilitation to be consistent with the SGH at the species level likely reflecting differences in plant strategy and perception of strain, but to follow alternative SGH models more closely at the site level where facilitation declined on the drier soil. Ultimately, our findings highlight the importance of facilitation in improving plant reproductive potential in drought, and support the role of nurse shrubs as micro-refugia in a changing climate.

Keywords Phenology · Sagebrush steppe · Facilitation · Range maintenance · Climate refugia

Introduction

Drought is a defining feature of arid ecosystems across the globe, but changes in drought patterns due to climate change likely will have negative effects on plant reproduction with

consequences expressed at the population level (Hedhly et al. 2009; Halpern et al. 2010). For example, as greater extremes of dry vs. wet conditions (Medvigy and Beaulieu 2012), or shifts from winter to spring and summer precipitation (Christensen et al. 2004) are becoming more frequent (IPCC 2013; Mann et al. 2017), evidence suggests that these shifts may stress some species beyond their physiological thresholds (Jump and Peñuelas 2005; Loarie et al. 2009; Anderson 2016). Sexual reproduction is essential for evolutionary adaptation to stress and thus species that cannot alter reproductive physiology in response to environmental stress are at greater risk of extinction or extirpation (Jump and Peñuelas 2005; Aitken et al. 2008; Anderson 2016). Because reproductive traits are sensitive to changes in climate (Hedhly et al. 2009; Smith 2011; De Storme and Geelen 2014; García-Cervigón et al. 2016; Gray and Brady 2016), we explore if concepts from the stress gradient hypothesis (SGH) can be applied to reproductive facilitation along a simulated precipitation gradient that includes drought and if the outcomes are generalizable across soil types.

Communicated by Christiane Roscher.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00442-019-04559-x>) contains supplementary material, which is available to authorized users.

✉ Elizabeth K. Swanson
Elizabeth.kay.swanson@gmail.com

¹ Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA

² United States Department of Agriculture-Agricultural Research Service, Burns, OR 97720, USA

³ Division of Agriculture and Natural Resources, Sierra Foothills Research and Extension Center, University of California, Browns Valley, CA 95918, USA

The SGH in its original form predicts that positive interactions increase with increasing environmental severity (Bertness and Callaway 1994). While there is significant empirical evidence supporting this linear model (Armas et al. 2011; Kawai and Tokeshi 2007; Callaway et al. 2002; also see He et al. 2013 and references therein), other studies have found that facilitation follows a humpback (unimodal) model transitioning into competition as beneficiaries mature to reproductive age (Gasque and Garca-Fayos 2004; Miriti 2006; Niinemets 2010; Paterno et al. 2016), conditions become too stressful (Maestre and Cortina 2004; Michalet et al. 2006, 2014) or alternatively, facilitation collapses and interactions become neutral (Koyama et al. 2013; Michalet et al. 2014; Kjær et al. 2018; Zhang et al. 2018).

Considering the mechanisms that drive the patterns found in these models, those that increase soil moisture availability or prevent loss appear most pertinent to facilitation in abiotic stress. Accordingly, evidence has shown hydrologic microsite generation through processes such as hydraulic redistribution (Richards and Caldwell 1987; Horton and Hart 1998; Scott et al. 2008; McLaughlin et al. 2017) to increase soil moisture availability particularly in arid conditions (Michalet et al. 2006; Butterfield et al. 2016) and contribute to positive interactions between shrubs and neighboring plants. Broader community metrics such as species diversity can also influence microsite stress amelioration. For example, Wright et al. (2014) found that microclimates beneath plant canopies were cooler, had greater surface soil moisture, and were less prone to vapor pressure deficits in high diversity communities compared to low diversity communities. These mechanisms are particularly important at the seedling establishment stage, where individuals are vulnerable to desiccation in arid environments (but see Montgomery et al. 2010 for an alternative). However, mechanisms that prevent desiccation are possibly less important during the reproductive phase as adult plants compete more readily for soil moisture at greater depths (Adair et al. 2011) and mechanisms such as aforementioned hydraulic redistribution become more applicable. Thus, interaction outcomes driven by these mechanisms can vary depending on stress tolerance of a particular species (Liancourt et al. 2005) and if the stress originates below or aboveground (Montgomery et al. 2010). The interaction may then be attributed to individual physiological performance (Malkinson and Tielbörger 2010; Montgomery et al. 2010), perception of stress (Liancourt et al. 2017), or life stage (Miriti 2006; Schiffers and Tielbörger 2006).

Interaction outcomes can also vary as a result of how a study is conducted, which variables are used, and how those variables are defined. For example, in a study conducted in sagebrush steppe by Holthuijzen and Veblen (2015), the researchers found no evidence of reproductive facilitation between similar nurse shrub and perennial bunchgrass

species along a precipitation gradient. One of their key measurement variables was defined as ‘reproductive potential’; however, their definition of this variable differed significantly from the ‘reproductive potential’ used in the present study. In the present study, we define ‘reproductive potential’ as a quantitative measure, where we do not infer facilitation unless a significant quantitative difference in the presence of shrub neighbors is detected vs. when the neighbor is removed. In the Holthuijzen and Veblen study (2015), the researchers define reproductive potential categorically as: ‘yes’ to facilitation if inflorescences were present on an individual or ‘no’ if inflorescences were not present. In contrast to the Holthuijzen and Veblen study (2015), other research has shown nurse shrubs to facilitate reproductive traits. For instance, in a study of facilitation conducted in the Mediterranean mountains of southern Spain, researchers evaluated a full suite of reproductive traits among the response variables (see Garca-Cervigon et al. 2016). Here, the authors evaluated facilitation by *Juniperus sabina* (L.) on the perennial forb *Helleborus foetidus* (L.). They found that the number of viable carpels per flower and seed set was facilitated by the nurse plant in a site with higher abiotic stress, compared to a lower stress, more mesic site. Other studies examining facilitation of alternative reproductive traits such as frutescence (Soliveres et al. 2010) or pollination rates (Gasque and Garca-Fayos 2004) have found a neutral effect. Because of the variation in outcomes, more studies on reproductive facilitation are necessary to identify reliable patterns across a range of environments, gradients, and variables.

In the present study, we focus on eastern Oregon sagebrush steppe as our model system and use the interaction between sagebrush shrubs (benefactor) and six perennial bunchgrasses (beneficiaries) to test hypotheses framed by the SGH and its alternatives. In sagebrush steppe systems, evidence suggests that perennial bunchgrass populations are susceptible to extinction if frequent recruitment does not occur given the relatively short lifespans and short-lived seed banks of most species (Svejcar et al. 2014). If nurse shrubs increase the opportunity for seed production and seedling recruitment by facilitating reproductive potential through drought periods, then incorporating biotic interactions into management decisions has important implications for reducing extinction or extirpation risk. Though perennial bunchgrasses reproduce both sexually via flowers and asexually via tillering, we focus on sexual reproduction as this has been shown to be more important than clonal reproduction for population fitness in arid bunchgrass systems (Liston et al. 2003). Sexual reproduction also provides more opportunity for adaptation (Hedhly et al. 2009). Therefore, assessment of the capacity for sagebrush to serve as micro-refugia for perennial bunchgrasses in this system should focus on indicators of change in reproductive potential. Reproductive potential

is here defined as the potential for a species to successfully reproduce and is determined by inflorescence production. Inflorescences are the structural vehicles determining success of sexual reproduction (Kirchoff and Claßen-Bockhoff 2013). The more inflorescences an individual produces, the greater potential that individual has to reproduce. In addition, arguments by Freckleton et al. (2009) and Malkinson and Tielbörger (2010) describe the need for response variables more closely linked to demographic features of population growth or fitness to more reliably predict the importance of facilitation in pairwise studies like this one.

Although inflorescences are not a perfect measure of fecundity, they are a good indicator of facilitation. This is true particularly in environments such as sagebrush steppe, where the higher drought tolerance of species at the end of precipitation gradients decreases the probability those species will be facilitated (Liancourt et al. 2005; Michalet et al. 2006; Noumi et al. 2016) and can limit the potential for a meaningful response in less sensitive traits (Smith 2011; Gray and Brady 2016). In addition to physiological sensitivity, inflorescences are a significant morphological feature driving plant population dynamics, because they provide the architectural function necessary for floral display, display dynamics, and display geometry while also serving as the transport pathway that provides nutrients for flowers and fruit throughout growth (Harder and Prusinkiewicz 2013). These factors optimize the chance for pollination and dispersal (Kirchoff and Claßen-Bockhoff 2013). Given the importance and sensitivity of reproductive features such as inflorescences, assessing if sagebrush shrubs can buffer negative effects on their production in drought conditions will provide us a better understanding of the vulnerability of plant populations to climate change in arid systems.

Our main study objective is aimed at understanding if neighboring sagebrush shrubs can facilitate the reproductive potential of perennial bunchgrasses in years of drought. We framed our hypotheses on the assumption that water stress is the primary driver of facilitation in semi-arid sagebrush steppe. Because perennial bunchgrasses are adapted to arid conditions, we hypothesize that sagebrush will have no effect on perennial bunchgrasses in ambient precipitation (i.e., interactions will be neutral), but will be negative (indicating competition) in the high precipitation treatment, where water is abundant. Most importantly, we hypothesize that reproductive potential of perennial bunchgrasses will be facilitated by neighboring sagebrush shrubs in drought conditions and this pattern will be consistent across soil types. If this is true, we may be able to use nurse plantings to ameliorate the negative effects of drought on reproduction of key grass species in areas of restoration interest as reviewed by Padilla and Pugnaire (2006) and shown empirically to be effective for seedling establishment (Gómez-Aparicio 2004).

Methods

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: Latitude 43°46' N, Longitude-119°692' W, and Pernty: Latitude 43°46' N, Longitude 119°710' W). Elevation of both sites was about 1500 m with <2° slope with undulating topography. Climate consists of hot, dry summers and cool, semi-wet winters. Precipitation is highly variable and is generally 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 (PRISM 2016). 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 complexes. Soil at the “Milcan site” is classified as well drained Milcan fine sandy loam with a 0–2% slope. Soil at the “Pernty site” is classified as Pernty very cobbly loam with 0–4% north slope (Lentz and Simonsen 1986). Pernty soils are moister with 25–35% clay content, while Milcan soils contain 5–15% clay content and have higher evapotranspiration rates (soilseries.sc.egov.usda.gov). Milcan soils are also excessively drained and have higher saturated hydraulic conductivity than Pernty soil (soilseries.sc.egov.usda.gov). Vegetation is classified as sagebrush-bunchgrass steppe, with Big Sagebrush (*Artemisia tridentata* [Nutt]) being the dominant shrub at both sites. Perennial bunchgrass species examined in this study 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 × 100 m in size.

Data collection

We first used a systemized random sampling technique along seven transects within a 100 × 100 m macropot to obtain a sample pool of 140 plots with a size of 1.5 × 1.5 m. From this sample, we could then identify plots that contained an adult sagebrush individual and the greatest abundance of perennial grasses, where we required at least one individual of each species to occur. 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 randomly assigned one of the six treatments.

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. Rain exclusion canopies were applied to plots during the first week of March 2013 through June 2014 (see Online Resource 1 for a picture of the canopies). Rain exclusion covers were 1.8×1.8 m overlapping the edge of the plot, to minimize edge effect. Covers 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 drought conditions.

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 (Online Resource 3). 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 5 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 that 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 hand held moisture probe (OMEGA HSM50).

To conduct plot sampling, plots were divided into four sampling quadrants according to each cardinal direction (North, South, East and West) to mitigate effects of shade, or other directionally dependent environmental variables. For each of our species of interest, a single individual, nearest the center of each quadrant, was sampled. Up to a maximum of four individuals of each species were thus sampled in each plot. When a species was not present in a quadrant, it was counted as zero and removed prior to analysis. Our response variable of measure was the mean number of reproductive culms for each species. Because *P. secunda* is the earliest to flower of the perennial grasses, data were collected on this species at peak flowering, which was during the last week of May 2014. Data on the remaining grasses were collected over the last 2 weeks of June and first week of July 2014, when flowering for all species had peaked.

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 reproductive culms using a generalized linear mixed effect model (GLMM) with a negative binomial distribution to account for overdispersion of discrete counts (Zuur et al. 2009). GLMMs were fitted with the `glmer` function in package ‘lme4’ (Bates et al. 2014) in R 3.4.3. To elucidate the effects of shrubs on reproductive potential of neighboring community members under stress, we used a 2 (with, without sagebrush) \times 3 (moisture regimes) randomized complete factorial design consisting of six total treatments combined as “simple effects”, a statistical technique used to simplify models and prevent redundancy when additional analyses are required to test hypotheses beyond the primary model. Simple effect treatments were as follows: shrub intact with ambient conditions which we considered the control (shrub intact), shrub intact and water added (shrub intact + water), shrub intact with a drought canopy (shrub intact + drought), shrub removed and no water manipulation (shrub removed), shrub removed and water added (shrub removed + water), and shrub removed with a drought canopy (shrub removed + drought). For our within-site analyses, these treatments were paired to simulate a precipitation gradient as follows: shrub removed + water vs. shrub intact + water = moist; shrub removed vs. shrub intact = ambient; shrub removed + drought canopy vs. shrub intact + drought canopy = drought.

The experimental design accounted for the effect of shrub in ambient conditions and effect of water alone was not of interest in this study. Because *P. spicata* was exclusive to the Pernty site and *K. macrantha* was exclusive to the Milcan site we conducted separate within-site and across-site analyses for better model fit. For analysis within sites, the fixed effect variables were species ($n = 6$), and treatment ($n = 6$), while plot ($n = 42$) served as the random effect in the model. For across-site analysis, the ‘site’ variable ($n = 2$) became a fixed effect in the model, species ($n = 4$), and treatment ($n = 6$) remained fixed and plot ($n = 84$) remained as a random effect. Our response variable for all analyses was the mean number of inflorescences for each individual, with discrete counts summed to the plot level (our experimental unit) and extracted as estimated marginal means for each species in each treatment. First, we evaluated main and interaction effects within and across sites using a Type II Walds Chi-square (χ^2) test ($\alpha = 0.05$). Afterward, we performed pairwise comparisons to test for differences in inflorescence production between treatments and sites for each species (i.e., the response ratio), using the response ratios and Wald’s z test as our indicator for or against facilitation ($\alpha = 0.05$). Response ratios were back-transformed from the log scale and range from one to infinity and one to zero.

Significant Walds z with response ratios above 1 indicates facilitation; response ratios near one indicate neutral interactions; response ratios approaching zero indicate competition. Pairwise tests were conducted using the estimated marginal means with a ‘Tukey’ adjustment from the ‘emmeans’ package (Lenth 2019) in R 3.4.3.

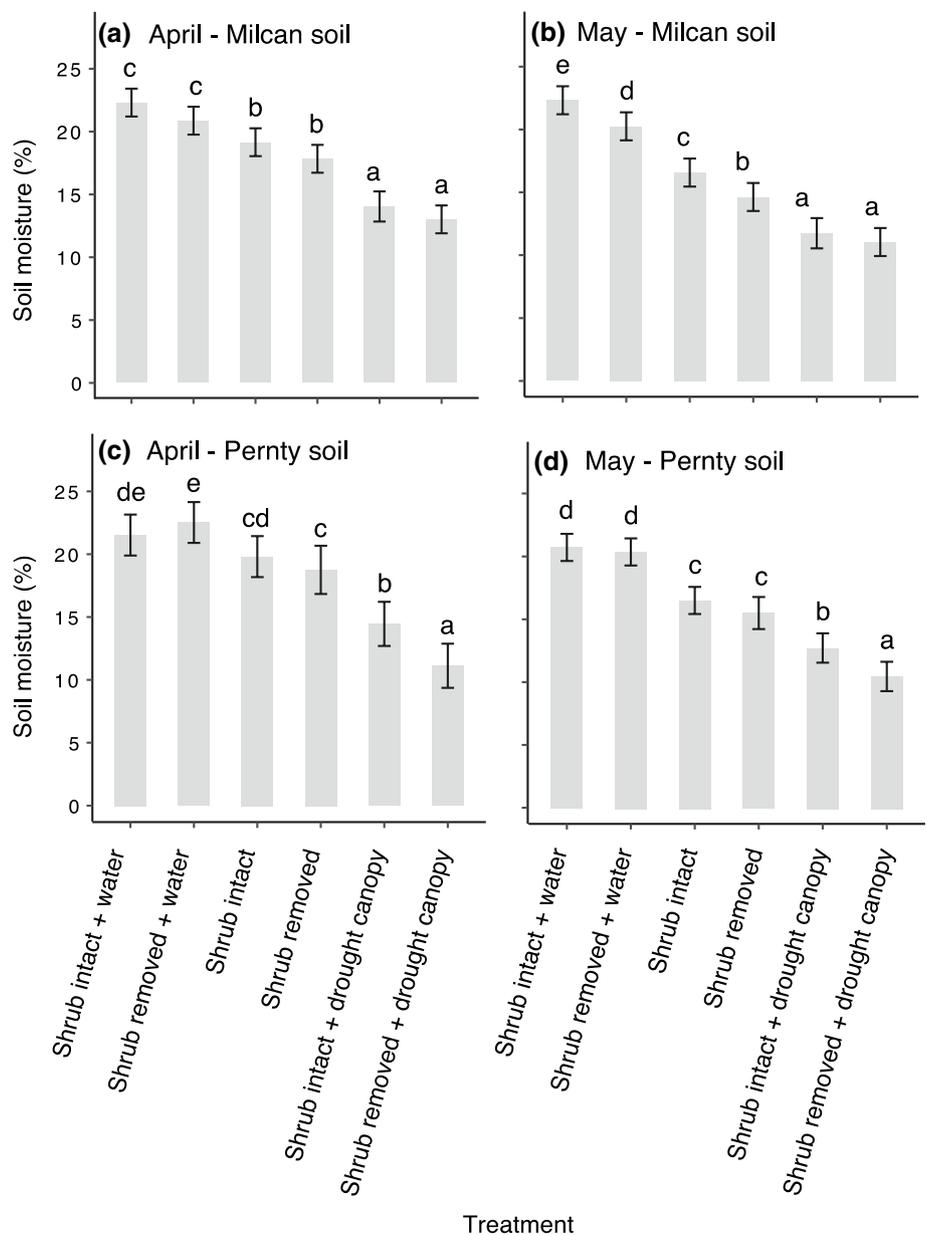
Results

Environmental conditions

Mean monthly temperature for April and May in 2014 were typical of the region (5.3 °C and 10.4 °C, respectively)

and nearly the same as the 30-year mean temperature for April and May (5.3 °C and 9.5 °C, respectively; see Online Resource 2). Ambient precipitation in April of 2014 was 20.75 mm and consistent with the 30-year mean normal precipitation for April (23 mm; see Online Resource 3) for the region. In May of 2014, ambient precipitation was very low at 12 mm, which is less than half of the 30 year normal for that month (27.25 mm; see Online Resource 3). 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 22.26% lower than the water treatment with or without a shrub present (Fig. 1b, d). This pattern was the same in April. Soil moisture in the shrub intact + water treatment was 14.21% greater than the soil moisture in the

Fig. 1 Mean soil moisture (CI) among treatments for April and May at **a, b** Milcan and **c, d** Pernty sites. Different letters indicate significant differences in soil moisture from Tukey tests



shrub intact with ambient water treatment at the Pernty site (Fig. 1a) and 17.4% greater in the shrub intact with ambient water at the Milcan site (Fig. 1c). 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 22% lower soil moisture than when the shrub was left intact at the Pernty site (Fig. 1c, d). This was not the case at the Milcan site, where no significant difference was detected when the shrub was removed vs. when it was intact in drought treatments (Fig. 1a, b).

Facilitation within sites

Analysis revealed species varied significantly in their response across treatments (Table 1). Within sites, there was more variation in species response to treatments at the Milcan site than at the Pernty site (Table 1). Drought conditions incited the strongest facilitated response among species. Facilitation of reproductive potential in drought was most prevalent at the Pernty site, where three out of five species were facilitated in drought conditions compared with one out of five species at the Milcan site (Fig. 2). In drought conditions *E. elymoides* was facilitated at both sites (Fig. 2). Inflorescence production for this species was 81% higher (Fig. 3; Table 2) in the shrub intact + drought canopy treatment than in the shrub removed + drought canopy treatment at the Pernty site (Fig. 3; Table 2). Similarly, mean inflorescence for *E. elymoides* was about 78% higher in the shrub intact + drought canopy treatment than the shrub removed + drought canopy treatment at the Milcan site (Fig. 3; Table 2). *A. thurberianum* was also a strongly facilitated species in drought, where mean inflorescence was about 88% higher in the presence of sagebrush than without at the Pernty site (Fig. 3; Table 2). In contrast, in drought

conditions at the Milcan site, there was no evidence of facilitation for this species by its sagebrush neighbor. Finally, we found evidence of facilitation in drought conditions for *P. spicata* (Fig. 2) occurring exclusively at the Pernty site, with an estimated mean inflorescence that was 77% greater in the presence of sagebrush than without (Fig. 3; Table 2).

Although the majority of interactions remained neutral in ambient conditions, we found evidence for facilitation of *F. idahoensis*. Facilitation of this species occurred exclusively at the Milcan site (Fig. 2), where inflorescence production was about 76% higher in the presence of sagebrush than when sagebrush was removed (Fig. 3; Table 2).

Finally, contrary to our hypothesis, we found no support for competitive interactions in moist conditions (Fig. 2).

Species response across sites

In partial disagreement to our hypothesis, analysis revealed that species varied significantly in their response across sites (Table 1). Overall, the species responses varied the least across sites in ambient conditions with a shrub neighbor (Fig. 4). The species with the largest response ratio across sites was *E. elymoides*, occurring in treatments, where the shrub neighbor was removed (Fig. 4). For *E. elymoides*, the greatest effect of shrubs across sites occurred in moist conditions when the shrub was removed ($z=3.366$, $p=0.0008$), followed by ambient conditions also when the shrub neighbor was removed ($z=2.369$, $p=0.0178$), where inflorescent production was much greater in the Milcan site than the Pernty site. Another strongly affected species was *A. thurberianum* with a large difference in inflorescence across sites (Fig. 4). When exposed to drought conditions without a shrub neighbor, mean inflorescence of *A. thurberianum* was significantly greater at the Milcan site than at the Pernty site (Fig. 4; $z=3.438$, $p=0.0006$). Though the ratio in response between sites was much smaller, the species, whose response varied most frequently was *F. idahoensis*, with significant differences between sites found in three out of the six treatment groups (Fig. 4). This is also the only species, where inflorescence production was less at the Milcan site than the Pernty site when the shrub was removed (both *E. elymoides* and *A. thurberianum* had greater inflorescences in the Milcan site than the Pernty site in treatment without a shrub neighbor, indicating a possibly stronger effect of shrub neighbors at the Pernty site for these species). The most significant difference across sites for *F. idahoensis* occurred in drought conditions with the shrub neighbor intact ($z=-2.505$, $p=0.0123$), followed by moist conditions without the shrub neighbor ($z=-2.294$, $p=0.0218$), and finally, ambient conditions also without the shrub neighbor ($z=-1.910$, $p=0.0562$). No significant difference in response to treatment groups was found across sites for *P. secunda* (Fig. 4). For clarity, *P. spicata* occurred exclusively

Table 1 ANOVA type II Chi-square results for the main and interaction effects of species, treatment and site on reproductive potential of perennial bunchgrasses

Effects	<i>n</i>	χ^2	<i>df</i>	<i>p</i>
Species	6	106.55	5	<0.001
Treatment	6	94.00	5	<0.001
Site	2	0.0137	1	0.9069
Species × treatment	–	53.335	25	<0.001
Species × site	–	26.443	3	<0.001
Treatment × site	–	8.2841	5	0.1412
Species × treatment × site	–	22.694	15	0.0908
Milcan species × treatment	–	50.977	25	<0.001
Pernty species × treatment	–	20.599	20	0.4211

For interactions that include the variable ‘Site’, analysis across sites was conducted only for species that were found in both locations ($n=4$)

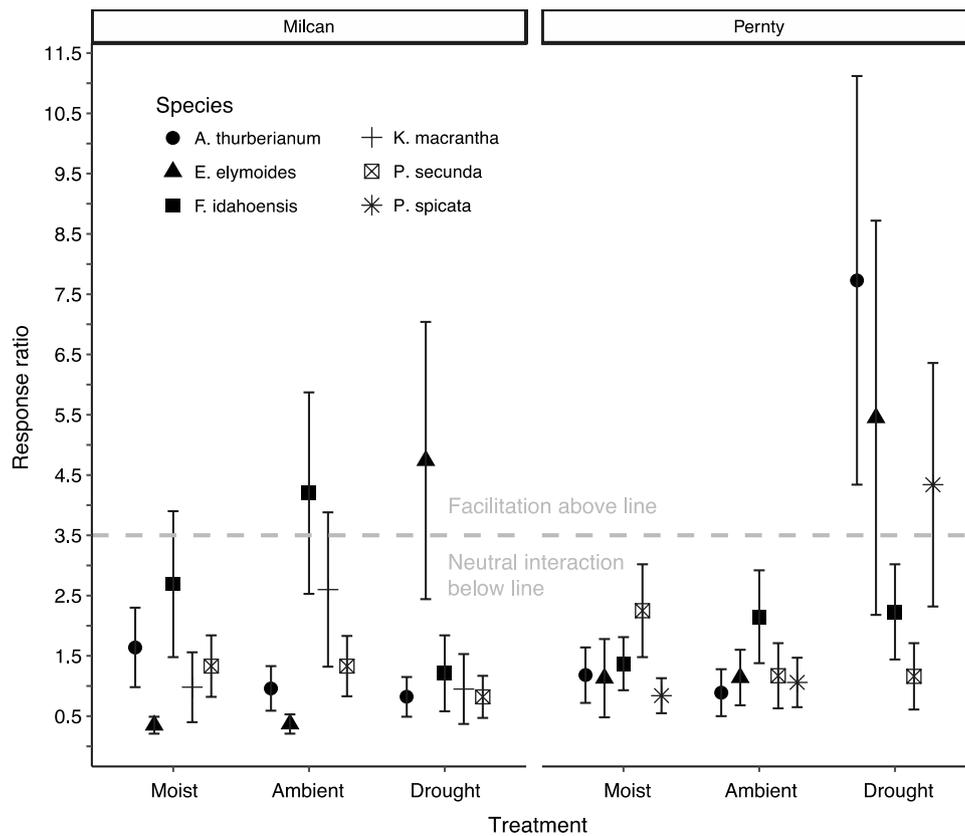


Fig. 2 Response ratios (SE) to each treatment combination for all species at the Milcan and Pernty sites. Treatment combinations include moist (water addition), ambient (no water manipulation) and drought (canopy to exclude precipitation). Response ratios near one indicate neutral interactions; below one indicates a positive response to shrub removal (competition) and above one indicates a negative response to shrub removal (facilitation). Inference line (dashed) is

given using Wald’s *z* test as our indicator for facilitation at $\alpha=0.05$, with positively significant response ratios indicative of facilitation above the line and non-significant response ratios indicating neutral interactions below the line. There were no statistically significant responses below one, and therefore, we infer no evidence of competition. Ratios are given from a negative binomial generalized mixed model and back-transformed from the log scale

at the Pernty site and was removed from across site analysis. Similarly, *K. macrantha* occurred exclusively at the Milcan site and was also removed from analysis across sites.

Discussion

Facilitation within sites is species-specific

Our work highlights the role facilitation plays in maintaining reproductive potential for perennial bunchgrasses in seasonal drought. In our case, positive interactions increased in drought. However, we found this effect to be non-linear and both site and species-specific. A possible explanation for this departure from the original SGH model is a closer alignment with the species-specific responses of the ‘strain’ gradient hypothesis presented by Liancourt and colleagues (2017; also see ‘individual stress model’ in Soliveres et al. 2015), where plants perceive stress and are most receptive

to facilitation when exposed to less optimal conditions based on a plants specific physiological performance (Choler et al. 2001; Liancourt et al. 2005). In our case, the receptivity of species to facilitation was most apparent on Pernty soil, where three of five species responded positively to shrub presence in drought conditions. Furthermore, the decrease in facilitation on the site with the drier Milcan soils, where two out of five species were facilitated could have resulted from the physiological strain experienced by species being pushed beyond an optimum threshold that is explained more closely by the unimodal model of facilitation (sensu Michalet et al. 2006). In this way, moderate-to-severe stress elicits facilitation, but extremely severe stress causes a ‘collapse’ in positive interaction (Michalet et al. 2014). An important distinction in the current study from the model described by Michalet and colleagues is their model was originally built on an aridity gradient, where interaction was inferred via species richness and measures of abundance, whereas our findings result from a simulated precipitation gradient using

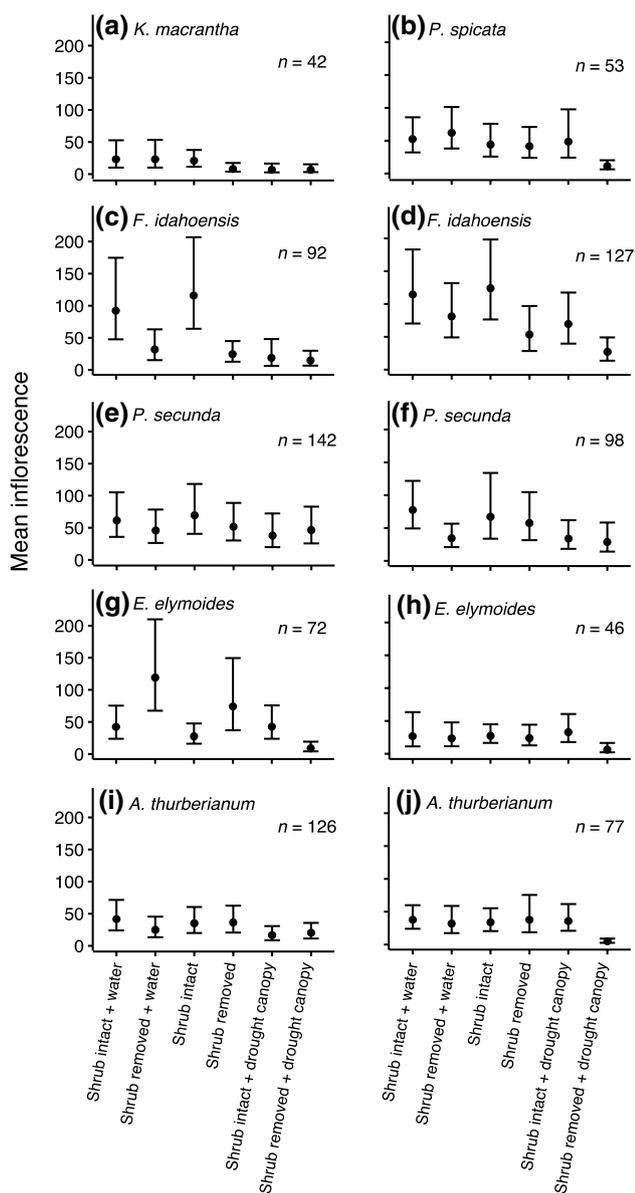


Fig. 3 Estimated mean number of inflorescences (CI, $\alpha=0.05$) for dominant perennial bunchgrass species in treatments at the Milcan (top) and Pernty (bottom) sites. **a** *K. macrantha* occurred exclusively at the Milcan site and **b** *P. spicata* occurred exclusively at the Pernty site. The other species, **c, d** *F. idahoensis*, **e, f** *P. secunda*, **g, h** *E. elymoides*, **i, j** and *A. thurberianum* occurred at both sites. Means were generated from a generalized mixed effect model fit to a negative binomial distribution and are given on the response scale

a variable more closely linked to demography as suggested by Malkinson and Tielbörger (2010). Species specificity clearly plays an important role in determining facilitation outcomes as studies using multiple species analyses have suggested (Liancourt et al. 2005; Paterno et al. 2016; Liczner et al. 2017). Species-specific changes in performance across stress gradients, where nurse shrub amelioration is limited by a physiological threshold of the beneficiary, was

conceptualized by Soliveres et al. (2015) and derived largely from an earlier study by Liancourt et al. (2005) in mesoxeric grasslands of eastern France. These researchers found facilitation to be a factor of both the variable of measure and species-specific tolerance to water stress, where species with a lower stress tolerance were facilitated, whereas higher stress tolerant species were not facilitated. In addition, when the water stress was removed that species became competitive. These findings highlight the idea that resource limited response in species is a trade-off of competitive ability (Grime 1979) and tolerance to, or perception of, stress (Liancourt et al. 2005; also see Maestre et al. 2009; Liancourt et al. 2017). In addition, this trade-off will vary depending on the trait being measured. The capacity for a species to be facilitated as reflected in reproductive traits may be a function of the resources needed by that species being matched by the resources provided by the benefactor as previously discussed. However, we would also like to suggest that some species utilize the resources provided by nurses more efficiently than other species not because they are more stressed (for example, *E. elymoides* is known to have a high tolerance to drought; see Khasanova et al. 2013), but rather because certain species may opportunistically utilize facilitation to regulate population growth rates in times of stress. Of the species in our study that were facilitated, *E. elymoides* was the most ‘social’, being facilitated by sagebrush across both sites. Interestingly, Shelle and James (2014) found intraspecific facilitation by *E. elymoides* to increase as the plants mature. It is possible tradeoffs in facilitation and competition for a particular trait do occur, and as resource use changes across an individual’s lifespan, this ontogenetic shift acts as potential driver of intraspecific facilitation Miriti (2006). Using this logic it is perceivable that for certain species, earlier life-stage traits may drive intraspecific competition for limited resources but traits expressed at reproductive age (e.g., inflorescence) elicit intraspecific facilitation in semi-arid environments (but see Loayza et al. (2017) for an alternative case in extreme aridity). Our study supports the notion that obligate facilitation, where some species have a greater propensity to be facilitated, because they have higher physiological stress tolerances, is possible, and may depend on species identity and life-stage. Interestingly, *A. thurberianum* was one of the most strongly facilitated species, but is also typically considered highly tolerant to drought due to its tightly rolled leaves, which limit transpiration (Schlatterer and Hironaka 1972). Daily shifts in leaf water potential can be a mechanism of facilitation (Wright et al. 2015) driving microsite amelioration around shrubs through increased humidity and cooling of air and soil (Holmgren 2000; Quero et al. 2006) further limiting transpiration. These mechanisms are a possibly why *A. thurberianum* is considered highly tolerant to drought, and supports the empirical studies that evidenced

Table 2 Contrasts between treatments at the Milcan and Pernty sites

Site	Species	Treatment	Response ratio \pm SE	95% CI (lower, upper)	<i>z</i>
Milcan	<i>E. elymoides</i>	Moist	0.35 \pm 0.14 ^{ns}	(0.11–1.15)	–2.502
		Ambient	0.37 \pm 0.16 ^{ns}	(0.10–1.34)	–2.186
		Drought	4.74 \pm 2.30 ^{**}	(1.18–18.99)	3.194
	<i>F. idahoensis</i>	Moist	2.69 \pm 1.21 ^{ns}	(0.74–9.78)	2.185
		Ambient	4.20 \pm 1.67 ^{**}	(1.34–13.10)	3.599
		Drought	1.21 \pm 0.63 ^{ns}	(0.27–5.34)	0.373
	<i>K. macrantha</i>	Moist	0.98 \pm 0.58 ^{ns}	(0.17–5.42)	–0.024
		Ambient	2.60 \pm 1.28 ^{ns}	(0.63–10.66)	1.934
		Drought	0.95 \pm 0.58 ^{ns}	(0.16–5.43)	–0.079
	<i>P. secunda</i>	Moist	1.33 \pm 0.51 ^{ns}	(0.45–3.98)	0.764
		Ambient	1.33 \pm 0.50 ^{ns}	(0.44–3.95)	0.751
		Drought	0.82 \pm 0.35 ^{ns}	(0.23–2.85)	–0.444
	<i>A. thurberianum</i>	Moist	1.64 \pm 0.66 ^{ns}	(0.52–5.18)	1.231
		Ambient	0.96 \pm 0.37 ^{ns}	(0.32–2.91)	–0.080
		Drought	0.82 \pm 0.33 ^{ns}	(0.25–2.65)	–0.469
	<i>P. spicata</i>	Moist	0.844 \pm 0.29 ^{ns}	(0.30–2.31)	–0.478
		Ambient	1.06 \pm 0.41 ^{ns}	(0.35–3.25)	0.168
		Drought	4.34 \pm 2.02 [*]	(1.15–16.35)	3.157
<i>E. elymoides</i>	Moist	1.13 \pm 0.65 ^{ns}	(0.21–5.87)	0.220	
	Ambient	1.144 \pm 0.46 ^{ns}	(0.35–3.65)	0.329	
	Drought	5.45 \pm 3.27 ^{**}	(0.98–30.21)	2.826	
Pernty	<i>F. idahoensis</i>	Moist	1.37 \pm 0.44 ^{ns}	(0.54–3.46)	0.976
		Ambient	2.15 \pm 0.77 ^{ns}	(0.77–5.97)	2.151
		Drought	2.23 \pm 0.79 ^{ns}	(0.81–6.17)	2.262
	<i>P. secunda</i>	Moist	2.25 \pm 0.77 ^{ns}	(0.84–6.00)	2.367
		Ambient	1.17 \pm 0.54 ^{ns}	(0.30–4.44)	0.336
		Drought	1.16 \pm 0.55 ^{ns}	(0.29–4.56)	0.325
	<i>A. thurberianum</i>	Moist	1.18 \pm 0.46 ^{ns}	(0.38–3.62)	0.440
		Ambient	0.89 \pm 0.39 ^{ns}	(0.25–3.14)	–0.246
		Drought	7.73 \pm 3.39 ^{***}	(2.21–27.05)	4.659

Response ratios are the difference in estimated marginal means between treatment pairs and are based on a generalized mixed effect model from a negative binomial distribution. Shrub removed vs. intact treatment pairs were under seasonal precipitation gradient: moist (water addition), ambient (no water manipulation) and drought (drought canopy). Walds (*z*) reports a ratio test of probability for the difference in means

* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, ns = not significant

species-specific responses depend on the resources needed by that species being matched by the resources provided by the nurse plant (see Montgomery et al. 2010 and Paterno et al. 2016 for example). Sagebrush shrubs extract soil moisture at deeper levels than perennial bunchgrasses (Inouye 2006) and have been shown to increase surface soil moisture (Richards and Caldwell 1987) and nitrogen uptake into inflorescences through hydraulic lift (Cardon et al. 2013). Water that percolates deeper takes longer to deplete and is more readily available for uptake by plants (Chesson et al. 2004). In this case, percolation and hydraulic lift could have been a factor influencing greater facilitation at the Pernty site for *P. spicata*, a relatively deep rooting species, which had over four times more inflorescence in the presence of its sagebrush neighbor than when it was removed.

Shrubs buffer environmental differences across sites

One of the most striking findings in this study is that there was very little variation in response of species across sites in the treatments with the shrub neighbor but significant variation across sites when sagebrush was removed (Fig. 4). We propose a possible cause for this result is that shrubs buffer environmental differences across population locales. This finding has important implications, because it supports the notion that shrubs expand the range of a species distribution (Jones and Gilbert 2016) and the potential for shrubs to serve as reproductive climate refugia. When sagebrush was removed, inflorescent production was much greater at the Milcan site than when shrubs were removed at the Pernty site for *A. thurberianum* and *E. elymoides*. The differential

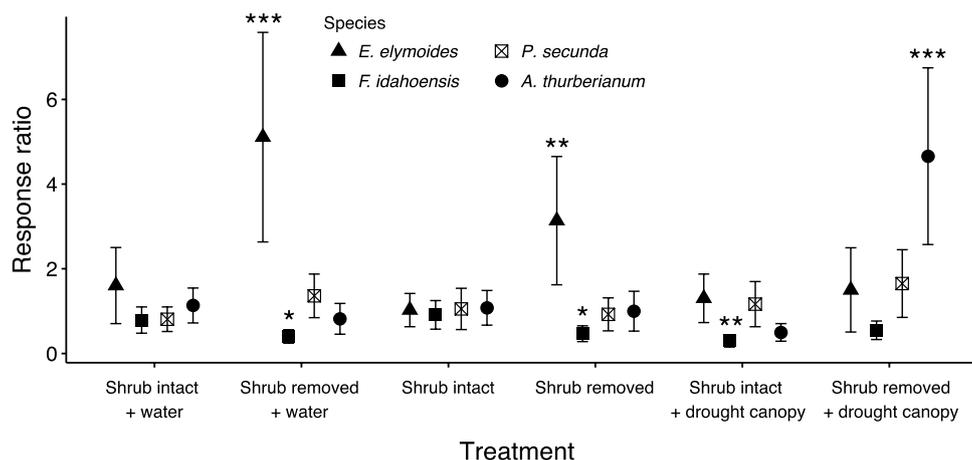


Fig. 4 Difference in response of species to each treatment across sites given by response ratios (CI, $\alpha=0.05$). Ratios result from a negative binomial generalized mixed model and back transformed from the log scale. Response ratios range from one to zero and one to infinity. Response ratios near one indicate no difference between sites; ratios below one indicate lower inflorescent production at the Milcan site

than the Pernty site; ratios above 1 indicate greater inflorescent production at the Milcan site than the Pernty site. There were $n=7$ replicates of each treatment in each site except for shrub intact + drought canopy at the Pernty site, where one drought canopy was damaged and $n=6$. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

response to shrub removal for these species is possibly due to species-specific stress thresholds being crossed at the higher stress Milcan site before they were reached at the moderate stress Pernty site. This indicates shrubs may be more effective facilitators at the Pernty site with moderate stress levels, supporting the unimodal alternative of the SGH (Michalet et al. 2014). In contrast, *F. idahoensis* responded in the opposite direction, where inflorescent production was much less at the Milcan site when the shrub was removed than at the Pernty site when the shrub was removed under ambient and moist conditions (Fig. 4). We posit this may again be due to differential species stress tolerance and differences in perception of strain (Liancourt et al. 2017) in determining facilitation outcomes. Because *F. idahoensis* was facilitated in ambient conditions at the Milcan site, it is possible ambient conditions were the optimum level of strain for this species to be receptive to facilitation. In this study, we demonstrated how facilitation supports reproductive potential across multiple species and soil types in times of severe seasonal drought. Although this study resulted in several important findings there were several limitations that should be noted. Though we found no significant evidence for competitive effects on reproductive potential among perennial bunchgrasses in this study, it is possible competition and facilitation may not operate along the same pathways for all variables (Montgomery et al. 2010). A more comprehensive survey of soil moisture would have provided us greater detail and possibly more direct causation as to differences in soil contributing to our results. Uncertainties remain regarding site environmental differences and the interaction between soil and water. In addition, although we included all

of the perennial bunchgrass species present at each site, we are uncertain if indirect effects of species or the soil microbial community caused some species to be facilitated at the expense of others. Despite these limitations, we have shown that shrubs may have the potential to serve as reproductive climate refugia across population locales. Ultimately, species that show strong propensity to be facilitated, like *E. elymoides* may be more competitive under emerging precipitation patterns, promising better chances for maintaining population growth in a changing climate.

Acknowledgements We thank B. Bingham and C. Swanson for assistance with drought canopies, A. Muldoon for statistical support and L. Ziegenhagen for help with plant identification. We also thank E. Denton, L. Pyle and several anonymous reviewers for comments that greatly improved this manuscript. 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.

Author contribution statement ES, RS, and JJ conceived and designed the study. ES collected and analyzed the data. ES and RS wrote the manuscript. JJ made editorial contributions.

Compliance with ethical standards

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

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

References

- Adair CE, Reich PB, Trost JJ, Hobbie SE (2011) Elevated CO₂ stimulates grassland soil respiration by increasing carbon inputs rather than by enhancing soil moisture. *Glob Chang Biol* 17:3546–3563
- Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol Appl* 1:95–111. <https://doi.org/10.1111/j.1752-4571.2007.00013.x>
- Anderson JT (2016) Plant fitness in a rapidly changing world. *New Phytol* 210:81–87. <https://doi.org/10.1111/nph.13693>
- Armas C, Rodríguez-Echeverría S, Pugnaire FI (2011) A field test of the stress-gradient hypothesis along an aridity gradient. *J Veg Sci* 22:818–827
- Bates D, Maechler M, Bolker B, Walker S (2014) lme4: linear mixed-effects models using Eigen and S4. R package version 1.1–7. <http://CRAN.R-project.org/package=lme4>. Accessed 1 Sept 2015
- Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends Ecol Evol* 9:191–193. [https://doi.org/10.1016/0169-5347\(94\)90088-4](https://doi.org/10.1016/0169-5347(94)90088-4)
- Butterfield BJ, Bradford JB, Armas C, Prieto I, Pugnaire FI (2016) Does the stress-gradient hypothesis hold water? Disentangling spatial and temporal variation in plant effects on soil moisture in dryland systems. *Funct Ecol* 30:10–19. <https://doi.org/10.1111/1365-2435.12592>
- Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET, Armas C, Kikodze D, Cook BJ (2002) Positive interactions among alpine plants increase with stress. *Nature* 417:844–848. <https://doi.org/10.1038/nature00812>
- Cardon ZG, Stark JM, Herron PM, Rasmussen JA (2013) Sagebrush carrying out hydraulic lift enhances surface soil nitrogen cycling and nitrogen uptake into inflorescences. *Proc Natl Acad Sci USA* 110:18988–18993. <https://doi.org/10.1073/pnas.1311314110>
- Chesson P, Gebauer RLE, Schwinning S, Huntly N, Wiegand K, Ernest MSK, Sher A, Novoplansky A, Weltzin JF (2004) Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141:236–253. <https://doi.org/10.1007/s00442-004-1551-1>
- Choler P, Michalet R, Callaway RM (2001) Facilitation and competition on gradients in alpine plant communities. *Ecology* 82:3295–3308. [https://doi.org/10.1890/0012-9658\(2001\)082%5b3295:FACOGI%5d2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082%5b3295:FACOGI%5d2.0.CO;2)
- Christensen NS, Wood AW, Voisin N, Lettenmaier DP, Palmer RN (2004) The effects of climate change on the hydrology and water resources of the Colorado River basin. *Clim Change* 62:337–363. <https://doi.org/10.1023/B:CLIM.0000013684.13621.1f>
- De Storme N, Geelen D (2014) The impact of environmental stress on male reproductive development in plants: biological processes and molecular mechanisms. *Plant Cell Environ* 37:1–18. <https://doi.org/10.1111/pce.12142>
- Freckleton RP et al (2009) Measuring the importance of competition in plant communities. *J Ecol* 97:379–384
- García-Cervigón AI, Iriondo JM, Linares JC, Olano JM (2016) Disentangling facilitation along the life cycle: impacts of plant-plant interactions at vegetative and reproductive stages in a Mediterranean forb. *Front Plant Sci* 7:129. <https://doi.org/10.3389/fpls.2016.00129>
- Gasque M, García-Fayos P (2004) Interaction between *Stipa tenacissima* and *Pinus halepensis*: consequences for reforestation and the dynamics of grass steppes in semi-arid Mediterranean areas. *For Ecol Manage* 189:251–261. <https://doi.org/10.1016/j.foreco.2003.08.014>
- Gómez-Aparicio L (2009) The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *J Ecol* 97(6):1202–1214
- Gray SB, Brady SM (2016) Plant developmental responses to climate change. *Dev Biol* 419:64–77. <https://doi.org/10.1016/j.ydbio.2016.07.023>
- Grime JP (1979) Plant strategies, vegetation processes and ecosystem properties. Wiley, Chichester
- Halpern SL, Adler LS, Wink M (2010) Leaf herbivory and drought stress affect floral attractive and defensive traits in *Nicotiana quadrivalvis*. *Oecologia* 163:961–971. <https://doi.org/10.1007/s00442-010-1651-z>
- Harder LD, Prusinkiewicz P (2013) The interplay between inflorescence development and function as the crucible of architectural diversity. *Ann Bot* 112:1477–1493. <https://doi.org/10.1093/aob/mcs252>
- He Q, Bertness MD, Altieri AH (2013) Global shifts towards positive species interactions with increasing environmental stress. *Ecol Lett* 16:695–706. <https://doi.org/10.1111/ele.12080>
- Hedhly A, Hormaza JJ, Herrero M (2009) Global warming and sexual plant reproduction. *Trends Plant Sci* 14:30–36. <https://doi.org/10.1016/j.tplants.2008.11.001>
- Holmgren M (2000) Combined effects of shade and drought on tulip poplar seedlings: trade-off in tolerance or facilitation? *Oikos* 90:67–78. <https://doi.org/10.1034/j.1600-0706.2000.900107.x>
- Holthuijzen MF, Veblen KE (2015) Grass-shrub associations over a precipitation gradient and their implications for restoration in the great basin, USA. *PLoS One* 10:e0143170. <https://doi.org/10.1371/journal.pone.0143170>
- Horton JL, Hart SC (1998) Hydraulic lift: a potentially important ecosystem process. *Trends Ecol Evol* 13:232–235. [https://doi.org/10.1016/S0169-5347\(98\)01328-7](https://doi.org/10.1016/S0169-5347(98)01328-7)
- Inouye RS (2006) Effects of shrub removal and nitrogen addition on soil moisture in sagebrush steppe. *J Arid Environ* 65:604–618. <https://doi.org/10.1016/j.jaridenv.2005.10.005>
- IPCC (2013) Climate change 2013: the physical science basis. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, New York, NY, 1535 pp
- Jones NT, Gilbert B (2016) Biotic forcing: the push-pull of plant ranges. *Plant Ecol* 217:1331–1344. <https://doi.org/10.1007/s11258-016-0603-z>
- Jump AS, Peñuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol Lett* 8:1010–1020. <https://doi.org/10.1111/j.1461-0248.2005.00796.x>
- Khasanova A, James JJ, Drenovsky RE (2013) Impacts of drought on plant water relations and nitrogen nutrition in dryland perennial grasses. *Plant Soil* 372:541. <https://doi.org/10.1007/s11104-013-747-4>
- Kawai T, Tokeshi M (2007) Testing the facilitation-competition paradigm under the stress-gradient hypothesis: decoupling multiple stress factors. *Proc Biol Sci* 274:2503–2508. <https://doi.org/10.1098/rspb.2007.0871>
- Kirchoff BK, Claßen-Bockhoff R (2013) Inflorescences: concepts, function, development and evolution. *Ann Bot* 112:1471–1476
- Kjær U, Olsen SL, Klanderud K (2018) Shift from facilitative to neutral interactions by the cushion plant *Silene acaulis* along a primary succession gradient. *J Veg Sci* 29:42–51. <https://doi.org/10.1111/jvs.12584>
- Koyama A, Tsuyuzaki S, Foster B (2013) Facilitation by tussock-forming species on seedling establishment collapses in an extreme drought year in a post-mined peatland. *J Veg Sci* 24(3):473–483
- Lenth RV (2019) emmeans: estimated marginal means, aka least-squares means. R package version 1.3.3

- Lentz R, Simonsen G (1986) A detailed soils inventory and associated vegetation of Squaw Butte Range Experiment Station (Special report 760). Oregon State University, Corvallis
- Liancourt P, Callaway RM, Michalet R (2005) Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology* 86:1611–1618. <https://doi.org/10.1890/04-1398>
- Liancourt P, Le Bagousse-Pinguet Y, Rixen C, Dolezal J (2017) SGH: stress or strain gradient hypothesis? Insights from an elevation gradient on the roof of the world. *Ann Bot* 120:29–38
- Liczner AR, Sotomayor DA, Filazzola A, Lortie CJ (2017) Germination response of desert annuals to shrub facilitation is species specific but not ecotypic. *J Plant Ecol* 10:364–374. <https://doi.org/10.1093/jpe/rtw030>
- Liston A, Wilson BL, Robinson WA, Doescher PS, Harris NR, Svejcar T (2003) The relative importance of sexual reproduction versus clonal spread in an aridland bunchgrass. *Oecologia* 137:216–225. <https://doi.org/10.1007/s00442-003-1332-2>
- Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. *Nature* 462:1052–1055. <https://doi.org/10.1038/nature08649>
- Loayza AP, Herrera-Madariaga MA, Carvajal DE et al (2017) Con-specific plants are better “nurses” than rocks: consistent results revealing intraspecific facilitation as a process that promotes establishment in a hyper-arid environment. *AoB Plants* 9:plx056
- Maestre FT, Cortina J (2004) Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proc Biol Sci* 271(Suppl 5):S331–S333. <https://doi.org/10.1098/rsbl.2004.0181>
- Maestre FT, Callaway RM, Valladares F, Lortie CJ (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J Ecol* 97:199–205
- Malkinson D, Tielbörger K (2010) What does the stress-gradient hypothesis predict? Resolving the discrepancies. *Oikos* 119:1546–1552. <https://doi.org/10.1111/j.1600-0706.2010.18375.x>
- Mann ME, Rahmstorf S, Kornhuber K, Steinman BA, Miller SK, Coumou D (2017) Influence of anthropogenic climate change on planetary wave resonance and extreme weather events. *Sci Rep* 7:45242. <https://doi.org/10.1038/srep45242>
- McLaughlin BC, Ackerly DD, Klos PZ, Natali J, Dawson TE, Thompson SE (2017) Hydrologic refugia, plants, and climate change. *Glob Chang Biol* 23:2941–2961. <https://doi.org/10.1111/gcb.13629>
- Medvigy D, Beaulieu C (2012) Trends in daily solar radiation and precipitation coefficients of variation since 1984. *J Clim* 25:1330–1339. <https://doi.org/10.1175/2011JCLI4115.1>
- Michalet R, Brooker RW, Cavieres LA, Kikvidze Z, Lortie CJ, Pugnaire, Valiente-Banuet A, Callaway RM (2006) Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecol Lett* 9(7):767–773
- Michalet R, Le Bagousse-Pinguet Y, Maalouf J-P, Lortie CJ (2014) Two alternatives to the stress-gradient hypothesis at the edge of life: the collapse of facilitation and the switch from facilitation to competition. *J Veg Sci* 25:609–613. <https://doi.org/10.1111/jvs.12123>
- Miriti MN (2006) Ontogenetic shift from facilitation to competition in a desert shrub. *J Ecol* 94:973–979
- Montgomery RA, Reich PB, Palik BJ (2010) Untangling positive and negative biotic interactions: views from above and below ground in a forest ecosystem. *Ecology* 91:3641–3655
- Niinemets Ü (2010) Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *For Ecol Manag* 260:1623–1639
- Noumi Z, Chaieb M, Le Bagousse-Pinguet Y, Michalet R (2016) The relative contribution of short-term versus long-term effects in shrub-understory species interactions under arid conditions. *Oecologia* 180:529–542
- Padilla FM, Pugnaire FI (2006) The role of nurse plants in the restoration of degraded environments. *Front Ecol Environ* 4:196–202
- Paterno GB, Siqueira Filho JA, Ganade G (2016) Species-specific facilitation, ontogenetic shifts and consequences for plant community succession. *J Veg Sci* 27:606–615. <https://doi.org/10.1111/jvs.12382>
- Quero JL, Villar R, Marañón T, Zamora R (2006) Interactions of drought and shade effects on seedlings of four *Quercus* species: physiological and structural leaf responses. *New Phytol* 170:819–833. <https://doi.org/10.1111/j.1469-8137.2006.01713.x>
- Richards JH, Caldwell MM (1987) Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73:486–489. <https://doi.org/10.1007/BF00379405>
- Schiffers K, Tielbörger K (2006) Ontogenetic shifts in interactions among annual plants. *J Ecol* 94:336–341
- Schlatterer EF, Hironaka M (1972) Some factors influencing tolerance to moisture stress of three range grasses. *J Range Manage* 25:364–367
- Scott RL, Cable WL, Hultine KR (2008) The ecohydrologic significance of hydraulic redistribution in a semiarid savanna: hydraulic redistribution in a semiarid savanna. *Water Resour Res* 44:13. <https://doi.org/10.1029/2007WR006149>
- Sheley RL, James JJ (2014) Simultaneous intraspecific facilitation and interspecific competition between native and annual grasses. *J Arid Environ* 104:80–87. <https://doi.org/10.1016/j.jaridenv.2014.01.019>
- Smith MD (2011) An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *J Ecol* 99:656–663
- Soliveres S, DeSoto L, Maestre FT, Olano JM (2010) Spatio-temporal heterogeneity in abiotic factors modulate multiple ontogenetic shifts between competition and facilitation. *Perspect Plant Ecol Evol Syst* 12:227–234
- Soliveres S, Smit C, Maestre FT (2015) Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities. *Biol Rev Camb Philos Soc* 90:297–313. <https://doi.org/10.1111/brv.12110>
- Svejcar T, James J, Hardegree S, Sheley R (2014) Incorporating plant mortality and recruitment into rangeland management and assessment. *Rangeland Ecol Manag* 67(6):603–613
- Wright A, Schnitzer SA, Reich PB (2014) Living close to your neighbors: the importance of both competition and facilitation in plant communities. *Ecology* 95:2213–2223
- Wright A, Schnitzer SA, Reich PB (2015) Daily environmental conditions determine the competition-facilitation balance for plant water status. *J Ecol* 103(3):648–656. <https://doi.org/10.1111/1365-2745.12397>
- Yahdjian L, Sala OE (2002) A rainout shelter design for intercepting different amounts of rainfall. *Oecologia* 133:95–101. <https://doi.org/10.1007/s00442-002-1024-3>
- Zhang G, Zhao W, Zhou H, Yang Q, Wang X (2018) Extreme drought stress shifts net facilitation to neutral interactions between shrubs and sub-canopy plants in an arid desert. *Oikos* 127:381–391. <https://doi.org/10.1111/oik.04630>
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R, 1st edn. Springer-Verlag, New York. <https://doi.org/10.1007/978-0-387-87458-6>