Extreme drought stress shifts net facilitation to neutral interactions between shrubs and sub-canopy plants in an arid desert

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Decision date: 23-Aug-2017

(Abstract)

The stress gradient hypothesis (SGH) predicts that the importance or intensity of competition and facilitation will change inversely along abiotic stress gradients. It was originally postulated that increasing environmental stress can induce a monotonic increase in facilitation. However, more recent models predicted that the relationship between severity and interaction exhibits a hump-shaped pattern, in which positive interactions prevail under moderate stress but decline at the extreme ends of stress gradients. In the present study, we conducted a field experiment along a temporal rainfall gradient for five consecutive years, in order to investigate interactions in a shrub-herbaceous plant community at the southern edge of the Badain Jaran Desert, and, more specifically, investigated the effects of *Calligonum mongolicum*, a dominant shrub species, on both abiotic environmental variables and the performance of sub-canopy plant species. We found that shrubs can improve sub-canopy water regimes, soil properties, plant biomass, density, cover, and richness and, more importantly, that the positive effect of shrubs on sub-canopy soil moisture during the summer diminishes as rainfall decreases, a pattern that partly explains the collapse of the positive interaction between shrubs and their understory plants. These results provide empirical evidence that the positive effect of shrubs on understory plant communities in extreme arid environments may decline and become neutral with increasing drought stress.

Introduction

Plant-plant interactions are currently one of most active research topics in ecology. Despite having been largely overlooked previously, the ecological significance of positive interactions among plants has been explored over the past two decades (Bertness and Callaway, 1994; Armas et al., 2012). In contrast to negative plant-plant interactions, which can reduce diversity and cause species extinctions (Hautier et al., 2009), positive interactions can ensure productivity and maintain diversity and community structure in stressful environments (Cavieres et al., 2007; Butterfield, 2009; Isabell et al., 2009). A large amount of evidence shows that both facilitation and competition can occur simultaneously and that their balance can vary dramatically in accordance with environmental conditions (Dickie et al., 2005; He et al., 2013). An increasing number of studies have attempted to integrate facilitation into empirical and theoretical research (Brooker et al., 2008; Callaway, 2002; Filazzola and Lortie, 2014) and ecological restorations (Gómez-Aparicio et al., 2004; but see Noumi et al., 2015). However, the effect of increasing environmental stress on the net outcome of plant-plant interactions remains a subject of debate (Michalet et al., 2006; Maestre et al., 2009; Holmgren and Scheffer, 2010; Kikvidze et al., 2011; Soliveres et al., 2015).

The stress gradient hypothesis (SGH), which is the most influential conceptual model, proposes that the frequency and importance of facilitation increases with increasing environmental severity (Bertness and Callaway, 1994) and that effects of stress amelioration on target plants can over-compensate the effects of their negative interactions (e.g., competition and inhibition) with increasing severity of physical conditions (Callaway, 2007). Even though the original prediction of the SGH has been supported by empirical studies and meta-analysis (Lortie and Callaway, 2006; He et al., 2013), it has also been actively debated (Maestre et al., 2005; Soliveres et al., 2014), and many recent studies have demonstrated that facilitation does not increase monotonically with increasing environmental severity but rather shows a unimodal pattern (Le Bagousse-Pinguet, 2014; Koyama and Tsuyuzaki, 2013). As a result, the SGH has been refined to indicate that positive interactions prevail under moderate environmental stress but are weakened, or even reversed under higher stress levels (Michalet et al., 2006; Malkinson and Tielborger, 2010; Holmgren and Scheffer, 2010; Liancourt et al., 2017; O'Brien et al., 2017). As suggested by a variety of ecologists (Armas et al., 2011; Butterfield, 2009; He et al., 2013; Michalet et al., 2014; Soliveres et al., 2015; Liancourt et al., 2017), the apparently opposing

views of the original and recent versions of the SGH may stem from inter-study differences in the nature of stress gradients (resource or non-resource stress), life-history of response species (stress tolerant or competitively inferior), scale of study focus (community or species level), component of stress factors (single or multiple stresses), or whether the observed gradient is complete. Even though a large number of studies from various ecosystems have explored the SGH, empirical tests of the hypothesis in extreme environments remains insufficient (but see de Bello et al., 2011; Armas et al., 2011; Castanho et al., 2015; Lopez et al., 2016; Liancourt et al., 2017).

Water is the primary limiting resource in arid and semi-arid environments, where predictions of the SGH are less consistent, especially at the extreme ends of aridity gradients (Maestre et al., 2005; Lortie and Callaway, 2006; Armas et al., 2011; Butterfield et al., 2016). In dryland systems, the modulation of water availability by benefactor plants determines the dynamic patterns of plant-plant interactions (Michalet et al., 2014; Butterfield et al., 2016; O'Brien et al., 2017). For example, neighbour plants facilitate the performance of target species by modulating available soil moisture and, subsequently, affecting community composition (Butterfield et al., 2016). By decreasing evaporation and improving moisture retention by canopy shading and organic matter accumulation, respectively (Kidon and Gutschick, 2013; Pugnaire et al., 1996), benefactor plants can indirectly increase the water content of shallow soil. The spatial distribution of available moisture in shallow soil can also be directly influenced by the hydraulic lift of woody and herbaceous plants (Kizito et al., 2012; Bruelheide et al., 2010). However, target plants can be inhibited when soil moisture is negatively influenced by indirect effects, like canopy interception, or direct effects, like water competition. For instance, under severe water deficits, the negative interactions are more likely to prevail, owing to the intensified competition for scarce available water amongst plants (Tielbörger and Kadmon, 2000; Maestre and Cortina, 2004). As reported by Butterfield et al. (2016), such direct and indirect effects of benefactor plants on available soil moisture can change along rainfall gradients, thereby causing temporal and spatial variation in the outcomes of plant-plant interactions in dryland systems (also see Zhang et al., 2016; Liancourt et al., 2017; O'Brien et al., 2017). Therefore, clarifying the possible responses of facilitative effects, based on variations in external abiotic factors, may help elucidate changes in the pattern of plant interactions in extreme environments (Butterfield, 2009; Michalet et al., 2014).

Rainfall is a major driver of biological processes in arid ecosystems (Noy-Meir, 1973). In desert regions, rainfall events exhibit temporal variability and are highly discontinuous and unpredictable (Noy-Meir, 1973; Schwinning and Sala, 2004), which can trigger a cascade of responses that affect plant growth, reproduction, and net ecosystem productivity (Reynolds et al., 1999). It has also been predicted that rainfall will fluctuate more dramatically with increasing global climate change, in terms of increased contrast between arid and wet regions and between arid and wet seasons (IPCC, 2013). This will undoubtedly generate complex variation in plant-plant interactions, owing to changes in facilitative effects, beneficiary responses, or even both (Michalet et al., 2014). Therefore, understanding the relationships between rainfall fluctuation and species interactions in arid regions will provide information that can be used to predict the responses of vegetation to future rainfall changes (Soliveres et al., 2013). Many previous studies that have investigated the effects of water regimes on plant-plant interactions have often selected different locations along drought gradients (Armas et al., 2011; Granda et al., 2102; Kidron and Gutschick, 2013; Ziffer-Berger et al., 2014) or used varying water levels in controlled environments (Maalouf et al., 2012; Gao et al., 2014; Grant et al., 2014; Rysavy et al., 2014; Castanho et al., 2015). However, few reports have addressed the balance between competition and facilitation along drought gradients from the same community for multiple growing seasons (but see Abdallah and Chaieb, 2012; Tielborger and Kadmon, 2000; Metz and Tielbörger, 2016; O'Brien et al., 2017).

In the present study, we investigated potential variation in the effects of shrubs on understory vegetation along temporal rainfall gradient in an arid community in the Hexi desert region. We chose to study *Calligonum mongolicum*, a common shrub plant in the region, since it plays an important role in improving species diversity and maintaining community stability in our study site, due to their positive effects on microhabitat and understory vegetation (Zhang and Zhao, 2015; Zhang et al., 2016). Different patterns of rainfall among years can create a drought-stress gradient for studying possible variations in the effects of shrubs on understory plants. Herein, we examine the response of vegetation patches and plant communities to rainfall fluctuation among years and to understand the effects of drought stress on the interactions between herbaceous plants and sup-canopy shrubs. Based on the well-documented SGH theory and previous studies of plant-plant interactions in dryland systems (Li et al., 2010; Zhang and Zhao, 2015; Kidron and Gutschick, 2013; Michalet et al., 2015; Butterfield et al., 2016), it can be expected that *C. mongolicum* shrubs will positively affect the understory plant

community by increasing available soil moisture and that the extent of these positive effects on water availability and plant-plant interaction outcomes will change along the temporal rainfall gradient. On this basis, we predict that the positive effect on microhabitat soil moisture and plant-plant interactions will collapse or even shift to negative effects under severe water deficit, in accordance with recent refinements to the SGH. To better understand the mechanisms underlying shrub-herbaceous plants interactions, the soil properties and light conditions of different microhabitats were also measured.

Material and methods

Study area

The study area was located at the Linze Inland River Basin Research Station, Chinese Academy of Sciences (CAS), which is one of Chinese Ecosystem Research Network Stations located at the southern edge of the Badain Jaran Desert (between 39°22′ and 39°23′ N and between 100°07′ and 100°08′ E at 1380 m above sea level). The average annual rainfall in the study area was 116.8 mm, with about 60% of the total precipitation received during the summer, whereas the annual potential evaporation was about 2390 mm. The mean daily temperature was about 7.6 °C, with the lowest temperature (-27.3 °C) occurring in January, and the highest temperature (39.1 °C) occurring in July. Due to multiple stresses, such as low precipitation, high evaporation, and violent wind, the vegetation cover of the study area ranged from only 5 to 7%. There was no grazing in the study area.

Study species

Calligonum mongolicum (Turcz.), which belongs to the Polygonaceae, is a common perennial shrub species in the study area. The species is widely distributed on flat desert sand dunes that occur at the periphery of oases and is important for the formation of vegetation communities in the region. Common annual species in the region include *Bassia dasyphylla*, *Salsola collina*, *Chloris virgata*, *Agriophyllum squarrosum*, *Halogeton arachnoideus*, and *Corispermum lehmannianum*, the growth periods of which generally range from June to September.

Understory plant measurements

In early July 2013-2016, twenty-five similar-sized *C. mongolicum* shrubs were randomly selected from within a permanent sample plot (100 m × 200 m) and marked accordingly. *C. mongolicum* was the dominant species in the sample plot, and all the sub-canopy species (target species) were annuals. In September of each year, a single 1 m × 1 m quadrat was established under the canopy of each selected shrub, and an open-area quadrat was placed in shrub interspaces, extending from 5 m to 8 m for each selected shrub. Then the above-ground biomass, individual density, total cover, and species richness of the understory vegetation were measured within each of the quadrats. In late September of 2012, we randomly selected 19 shrubs from the permanent sample plot and measured the individual density, total cover, and species richness of understory plants within quadrats (1 m × 1 m) that were established both underneath the shrubs and within shrub interspaces. The total cover of understory species was estimated using the Braun-Blanquet scale (Westhoff and Van der Maarel, 1978), and aboveground biomass of the understory species was measured using an electronic balance, after oven-drying at 80 °C for 48 h. Due to rodent and pest damage, the samples of six and four of the shrubs selected in 2013 and 2015 were eliminated before analysis.

Environmental measurements

To investigate the effects of several key abiotic environmental variables, we randomly selected 10 similar-sized *C. mongolicum* shrubs from the permanent sample plot. To measure soil organic matter (SOM) and bulk density (BD), we collected two or three soil cores (5 cm diameter, 10-15 cm in depth) from both underneath the shrubs and within open areas in August 2013-2015. The soil samples collected from each area were mixed, stored in plastic bags, air-dried, passed through a 2-mm sieve, and then analysed using the dichromate oxidation method (Kalembasa and Jenkinson, 1973). To measure potential evaporation rate (PER), we inserted glass tubes (1.6 cm × 15 cm) into the ground, with the rim of the tubes at 3 cm above the soil surface, between July and August of 2013 and 2014. The tubes were filled with deionized water up to 3 cm below the rim, i.e., to the level of the soil surface, and decreases in water level were measured after one week. There was no precipitation during the measurement period. To measure photosynthetically active radiation (PAR), we used a Field Scout Light Meter (Spectrum, Technologies, Inc., USA) in August 2013-2015. The probe was placed at a north-south direction at 5 cm above the soil surface in both under-shrub and open-area locations, and the values were recorded on clear days from 10:00 to 12:00 and from 14:00 to 16:00. To measure soil

water content (SWC), we collected soil cores (5 cm diameter, 5-15 cm in depth) from different locations in each month from July to early September. To eliminate the influence of uneven rainfall pulses on SWC, we selected the sampling date when there had been no precipitation for the previous 5 d (the interval between any two sampling dates was larger than 20 d). The SWC was determined gravimetrically by oven-drying for 48 h at 110 °C.

Data analysis

Linear mixed-effects model (LMM) that was fitted using maximum likelihood estimation was used to measure the effects of growing-season rainfall on abiotic factors modulated by shrubs. To analyse the effect on SWC, the rainfall of each growing season and habitat type (quadrats beneath shrubs or in open areas) and months (when soil moisture was investigated) were included as fixed terms, with paired shrubs as random terms. The mixed-effect model took the form: SWC ~ habitat × rainfall × month, random = ~ 1 | paired shrubs. To analysis the effect on other abiotic factors, rainfall and habitat were included as fixed terms, with paired shrubs as random terms. The mixed-effect model took the form: response variable ~ habitat × rainfall, random = ~ 1 | paired shrubs, with SOM, PER, PAR, and BD as response variables.

Generalized linear mixed-effect model (GLMM) was used to measure the effects of growing-season rainfall and soil moisture on sub-canopy plant communities. To analyse the effect of rainfall on the understory plants modulated by shrubs, rainfall and habitat were included as fixed terms, with paired shrubs as random terms. The mixed-effect model took the form: response variable ~ habitat × rainfall, random = ~ 1 | paired shrubs. To analyse the effect of soil moisture on the understory plants, SWC was treated as fixed term, with model form as: response variable ~ SWC, random = ~ 1 | year / paired shrubs / month. In both analyses, biomass, density, cover, and richness were included as response variables. Biomass was fitted using Gaussian distribution, density and richness were fitted using Poisson distribution, and cover was fitted using Binomial distribution.

Relative interaction intensity (RII) was used to assess the effect of shrubs on understory vegetation (Armas et al. 2004) and was calculated based on the biomass, density, cover, and richness of understory vegetation, as follows: RII = (value $_{under\ shrub}$ - value $_{bare\ soil}$) / (value $_{under\ shrub}$ - value $_{bare\ soil}$). The RII indices were used to directly compare the performances of understory plants among different

sampling periods or locations, with positive values indicating facilitation, negative values indicating competition, and zero values indicating no significant interaction. One-way ANOVA was performed to assess variation in the strength and direction of interactions between shrubs and understory plants among years.

All analyses and graphics are performed in the R environment (version 3.3.2, R Development Core Team). The LMM was performed using the 'lme' function from the nlme package, and the GLMM was performed using 'glmer' and 'lmer' functions from the lme4 package (Galecki and Burzykowski, 2013). These fitted models were examined using graphical and numerical summaries, in order to assess whether both the within-group and random errors met the assumptions of normality and homogeneous residuals (Pinheiro and Bates, 2000). Where necessary, the 'varIdent' variance function structure was used as a weights argument in the 'lme' function, in order to allow different residuals for each level of factors and to fit the heteroscedactic model (Pinheiro and Bates, 2000; Gałecki and Burzykowski, 2013). The 'glht' function of the multcomp package was used to perform Tukey's post hoc analysis at the 0.05 level.

Results

Summer rainfall varied among years (Fig. 1) and declined from 96.6 mm in 2013 to 83.4 mm in 2012, 65.6 mm in 2014, 39.2 mm in 2015, and 49.4 mm in 2016. The main difference occurred in the months of July and August, which coincide with critical stages in the growth of herbaceous plants in our study area.

The areas under shrubs generally had greater soil moisture than the open spaces between shrubs (Fig. 2, Table 1), especially in 2013 and 2014 and earlier in the growing season (Fig. 2). The results of the mixed model ANOVA indicated that shrub presence significantly affected soil moisture in 2013 (habitat: $F_{1, 95} = 13.209$, $P < 0.001$) and 2014 (habitat: $F_{1, 95} = 9.057$, $P = 0.003$) and that the effect varied among the different sampling periods (habitat × month: $F_{2, 95} = 4.619$, $P = 0.012$). However, soil moisture did not vary among different habitats in 2015 (habitat: $F_{1, 95} = 0.239$, $P = 0.626$) or 2016 (habitat: $F_{1, 95} = 0.972$, $P = 0.327$), nor were there interactive effects between habitat type and sampling month in 2015 (habitat × month: $F_{2, 95} = 0.339$, $P = 0.714$) or 2016 (habitat: $F_{1, 95} = 0.612$, P

= 0.545). Compared with soil from the open areas, soil from the under-shrub sites had more organic matter and lower bulk density (Table 1, 2), and both the potential evaporation rate and photosynthetically active radiation decreased from the shrub interspaces (i.e., open areas) to the under-shrub sites (Table 1, 2).

The biomass and density of the herbaceous plants was augmented by shrub presence, but was also significantly related to rainfall during the growing season (Fig. 3, Table 3). The biomass, density, cover, and richness of the understory vegetation were higher beneath shrubs than in interspaces, during years when the growing-season rainfall was greater, whereas less difference was found, during years when the growing-season rainfall was lower (Fig. 3). Furthermore, the magnitude of positive interactions between the shrubs and their understory plants was related to rainfall among years; the net interactions shifted from significantly facilitative to neutral with decreasing levels of growing-season rainfall (Fig. 4). In analysis of SWC on sub-canopy plants, the positive slopes of fixed term in fitted models indicated that sub-canopy biomass (1.92 ± 0.260; $F_{1,44} = 54.324$, $P < 0.001$), density (0.13 ± 0.026; $F_{1,44} = 25.425$, $P < 0.001$), cover (0.80 ± 0.055; $F_{1,44} = 545.8$, $P < 0.001$), and richness (0.24 ± 0.063; $F_{1,44} = 14.206$, $P = 0.001$) generally show positive relationship with soil moisture.

Discussion

Our results indicated that the positive effect of shrubs on the available moisture of topsoil gradually disappears along a temporal rainfall gradient, which is consistent with studies of other dryland systems (Butterfield et al., 2016). Indeed, higher soil water availability was found in shrub patches under moderate drought stress than in bare soil, and this positive effect diminished and eventually disappeared under extreme water deficit. Similarly, the net interaction between shrubs and their understory plants also switched from positive to neutral along the drought gradient during the growing season. This variation in plant-plant interaction at the extreme end of a drought gradient does not support the monotonic increase in the severity-interaction that is predicted by the early version of the SGH (Bertness and Callaway, 1994; Callaway, 2007; He et al., 2013) but is in accordance with recent refinements to the SGH (Michalet et al., 2006; Maestre et al., 2009; Holmgren and Scheffer, 2010). These results also reinforce the idea that the balance of plant-plant interactions is primarily mediated by

plant effects on environmental stresses and resource availability in microhabitats, both which are ultimately controlled by external limiting factors (Butterfield, 2009).

During the growing season, the effect of shrubs on available moisture in shallow soils showed a positive relationship with rainfall. Soil moisture was higher beneath shrubs than in open areas during wet years, which, however, exhibited no differences among habitats in dry year (Fig. 2). This is in accordance with the findings of a simulation study of dryland systems in the western United States (Butterfield et al., 2106), which demonstrated that rainfall is almost always positively correlated with simulated positive effects of plants on soil moisture, and of Schöb et al. (2013), who reported a similar relationship between plant effect on soil moisture and rainfall along an elevation gradient in the Sierra Nevada Mountains. Butterfield et al. (2016) proposed that this correlation could result from differences in the evaporation rates of canopy and interspace microsites that determine the retention of rainfall pulses. This is supported by the significant difference that we observed between the potential evaporation rate of soil beneath shrubs and in open areas. As noted by Kidon and Gutschick (2013), reducing potential evaporation could be one of the major causes of the higher moisture contents of shrub patches, when compared to shrub interspaces. Furthermore, soil moisture retention can be directly increased by improving physical conditions, since the accumulation of soil organic matter under shrubs results in higher soil moisture (Armas and Pugnaire, 2005). The collapse of facilitative effects on soil moisture in the present study suggests that positive plant-plant interactions that result from soil moisture improvement are likely to diminish or shift to neutral or even negative at the extreme end of drought gradient, which supports the prediction of recent refined SGH and is consistent with field experiments (Michalet et al., 2015; Noumi et al., 2016).

In addition to affecting the soil moisture of drylands, shrubs can also affect other abiotic factors in their understory microhabitats (Ludwig et al., 2004; Kidron, 2011; Wang et al., 2011). Our results indicated that evaporation, irradiance, soil organic matter, and bulk density are all modulated beneath *C. mongolicum* shrubs. They have facilitative effects in underproductive ecosystems, generally benefiting their neighbours, and contributing to positive plant-plant interactions. For example, shrubs can improve soil properties in the understory, due to their capture of wind-dispersed particles and increases in arthropod activity, litter deposition, and nitrogen fixation (Davies et al., 2007; Travers and Eldridge, 2012). However, some of the abiotic factors modulated by shrubs can also affect understory plants

negatively. For example, heavy shading by canopies has been reported to limit the photosynthetic activity of understory species (Hautier et al., 2009), thereby impairing their establishment, growth, and reproduction (Schramm and Ehrenfeld, 2010). Such negative effects are more likely to occur under deep shade, though, and shift to facilitation at intermediate light levels (Holmgren et al., 2012). These effects on abiotic factors are not mutually exclusive but, rather, contribute to the overall impact of shrubs on target plants and, subsequently, contribute to the plant-plant interactions of shrub patches at a fine spatial scale (Segoli et al., 2012; Zhang et al., 2016; O' Brien et al., 2017). In the present study, the effects of *C. mongolicum* on evaporation, irradiance, and soil properties were not affected by variation in rainfall, which suggests that these effects do not directly modulate the temporal variation in plant interactions. It is possible, however, that they influence the relationship between soil moisture and rainfall and, consequently, affect plant interactions indirectly. For instance, moderate shade, low evaporation, and improved soil properties can increase the retention of rainfall pulses beneath shrubs, thereby instigating a positive relationship between soil moisture and rainfall under extreme drought conditions.

The results of the present study indicated that the positive net effect of *C. mongolicum* shrubs on their understory plants shift from positive to neutral with decreasing rainfall during the growing seasons of years at the extreme end of drought stress. Such temporal variation in plant-plant interactions under extreme drought stress does not support the original SGH and, instead, is more consistent with the recent refined SGH. Both field studies in water-limited environments and meta-analyses at species and community levels have also demonstrated that the intensity and/or importance of positive effects diminish under extreme drought stress, or shift to neutral or even negative effects (Tielbörger and Kadmon, 2000; Maestre and Cortina, 2004; Soliveres et al., 2014; Castanho et al., 2015; Liancourt et al., 2017; O' Brien et al., 2017; but see Lopez et al., 2016). Contrary to the SGH, the results of these studies are highly inconsistent, since many other factors (e.g., life-history strategy and ontogenetic process) can interact with the external water conditions that, consequently, modulate the outcome of plant-plant interactions (Michalet, 2007; Butterfield et al., 2010; Castanho et al., 2105).

As recently suggested by He and Bertness (2014), the results of departure from the SGH will be improperly interpreted, if weak stress gradients and stresses outside of species' niche are examined, temporally dependent effects are involved, or multiple stresses interact with facilitative effects.

However, the present study does not appear to be affected by these problems. For example, we randomly selected mature shrubs each year, instead of using permanent shrubs across all years, which avoid the influence of temporal effect on plant-plant interactions. Meanwhile, a natural rainfall gradient among years was examined, which ensure that our analyses work on a valid stress gradient. Additionally, other possible limiting factors, such as nutrients and light, can be excluded because no differences were observed in the effects of shrubs on these abiotic factors along the rainfall gradient. Yet, it should be noticed that our study does not involve an intact stress gradient (e.g. low, medium, high and extreme levels, as suggested by He and Bertness 2014), but only considered the situation at its extreme end. Thus, we cannot currently conclude from our result that the relationship (i.e., curve) between stress severity and facilitation is humped-back shape along the entire rainfall gradient. Nevertheless, we can confidently refute the notion of a monotonic severity-interaction relationship at the extreme end of the drought gradient as predicted by the early SGH.

Michalet et al. (2014) recently clarified two alternative models (collapse of facilitation and switch from facilitation to competition) to the SGH in water-limited environments, based on the changes of plant effect under extreme stress and the responses of target species to environmental limitation. In the first alternative model, the collapse of positive interactions under extreme environments is primarily driven by the relationship between the plant effect on limiting factors and external environmental factors. In contrast, in the second alternative model, the switch from facilitation to competition is mainly driven by the response of target plants to abiotic stress. Here, we assume that the departure from the SGH observed in the present study is primarily the result of changes in plant effect caused by external rainfall input, as the mechanism of the first alternative model to SGH. On the one hand, the low evaporation rate (Kidon and Gutschick, 2013), high water infiltration efficiency (Sarr et al., 2001; Pan et al., 2014), and improved physical conditions (Boix-Fayos et al., 2001) of the top soil in shrub patches may contribute to the higher moisture retention of the soil beneath shrubs than in soil from shrub interspaces. In contrast, rainwater rapidly evaporates from bare soil during the heat of summer, which makes it difficult for herbaceous plants in shrub interspaces to benefit from rainfall pulses. Therefore, in wet years, this positive effect on soil moisture is likely to be great, thereby generating the observed facilitative plant interactions, whereas, in dry years, the effect of shrubs on soil moisture diminishes, thereby resulting in the collapse of positive interactions (also see Butterfield et al., 2010; Butterfield et al., 2016; O, Brien, 2017). On the other hand, the second alternative (switch from

facilitation to competition) has been supported by many studies in water-limited ecosystems (Michalet, 2007; Maestre et al., 2009). Competition is important in drylands when water-demanding neighbours interact with herbaceous species (Maestre and Cortina, 2004; Armas and Pugnaire, 2005). However, competition for soil moisture is probably weak in our study area, owing to strong segregation between the roots of *C. mongolicum* shrubs and their understory plants. Observations indicated that, for mature *C. mongolicum*, the distribution of absorbing roots is relatively deep, generally surpassing 1 m. Using the oxygen isotopic tracing method, we found that mature *C. mongolicum* shrubs in our study area mainly utilize deep soil water (below 1.5 m in depth) and even groundwater, in agreement with the shrubs' vertical root distribution (unpublished data, H. Zhou and W. Z. Zhao).

Conclusion

The present study documents the collapse of a positive plant-plant interaction at the extreme end of a stress gradient, which is in support of recent refinements to the SGH. Previous studies have suggested that the weak negative relationship between interaction outcomes and drought stress in highly water-limited environments primarily results from increasing competition for water along drought gradients (Michalet, 2007; Maestre et al., 2009). However, competition for water may not play major roles in plant-plant interactions under extreme drought conditions, when species are not negatively interacting for soil water, such as root segregation in our study. We assume that the changing outcomes of interactions result from the relationship of shrub effect on soil moisture and external rainfall input among years. When drought stress becomes extreme, facilitative effects on soil moisture wane, owing to scarce rainfall input, which probably results in a shift from net facilitation to neutral interactions between shrubs and their sub-canopy plants. The results of the present study suggest that clarifying the effect of plants on soil moisture along drought gradients is important for elucidating the relationship between plant-plant interactions and drought stress in water-limited ecosystems. This may facilitate the development of more precise models of plant-plant interactions under extreme water deficit and help improve the prediction of plant-plant interactions modulated by soil moisture, in regard to climate change in drylands.

Acknowledgments

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Table Legends

Table 1 Results of linear mixed-effect models ANOVA for the effect of shrubs on the soil water content (SWC), potential evaporation rate (PER; $mm \cdot d^{-1}$) , soil organic matter (SOM; $g \cdot kg^{-1}$), photosynthetically active radiation (PAR; $mol \cdot m^{-2} \cdot s^{-1}$) and Bulk density (BD; $g \cdot cm^{-3}$) of the understory plants.

Variables	Fixed terms	*F*	*P*
SWC	habitat	12.510	**0.001**
	month	39.323	**<0.001**
	rainfall	23.921	**<0.001**
	habitat × month	5.044	**0.007**
	habitat × rainfall	9.769	**0.002**
	month × rainfall	4.253	**0.015**
	habitat × month × rainfall	1.589	0.205
PER ($mm \cdot d^{-1}$)	habitat	21.383	**0.001**
	rainfall	1.831	0.184
	habitat× rainfall	1.065	0.310
SOM ($g \cdot kg^{-1}$)	habitat	68.457	**<0.001**
	rainfall	3.510	0.070
	habitat× rainfall	0.393	0.535
PAR ($mol \cdot m^{-2} \cdot s^{-1}$)	habitat	547.942	**<0.001**
	rainfall	4.573	**0.038**
	habitat× rainfall	2.401	0.128
BD ($g \cdot cm^{-3}$)	habitat	125.00	**<0.001**
	rainfall	0.110	0.745
	habitat× rainfall	0.109	0.739

P values at <0.05 level are in bold.

Table 2 Variation of potential evaporation rate (PER) , soil organic matter (SOM), photosynthetically active radiation (PAR) and Bulk density (BD) in different habitats.

Habitats	PER $(mm \cdot d^{-1})$	SOM $(g \cdot kg^{-1})$	PAR $(mol \cdot m^{-2} \cdot s^{-1})$	BD $(g \cdot cm^{-3})$
under shrub	3.58 ± 1.460 [a]	2.46 ± 0.566 [b]	562.94 ± 327.171 [a]	1.53 ± 0.0473 [a]
bare soil	5.42 ± 1.492 [b]	1.61 ± 0.428 [a]	1690.02 ± 121.481 [b]	1.68 ± 0.0873 [b]

Letters show Tukey's post hoc analysis between different habitats with mixed-models ANOVA; means with the same letter are not significantly different at $P < 0.05$ level. Data are means ± SD.

Table 3 Results of linear mixed-effect models ANOVA for the effect of shrubs on the biomass (g · m^{-2}), density (m^{-2}), cover (%), and richness of the understory plants.

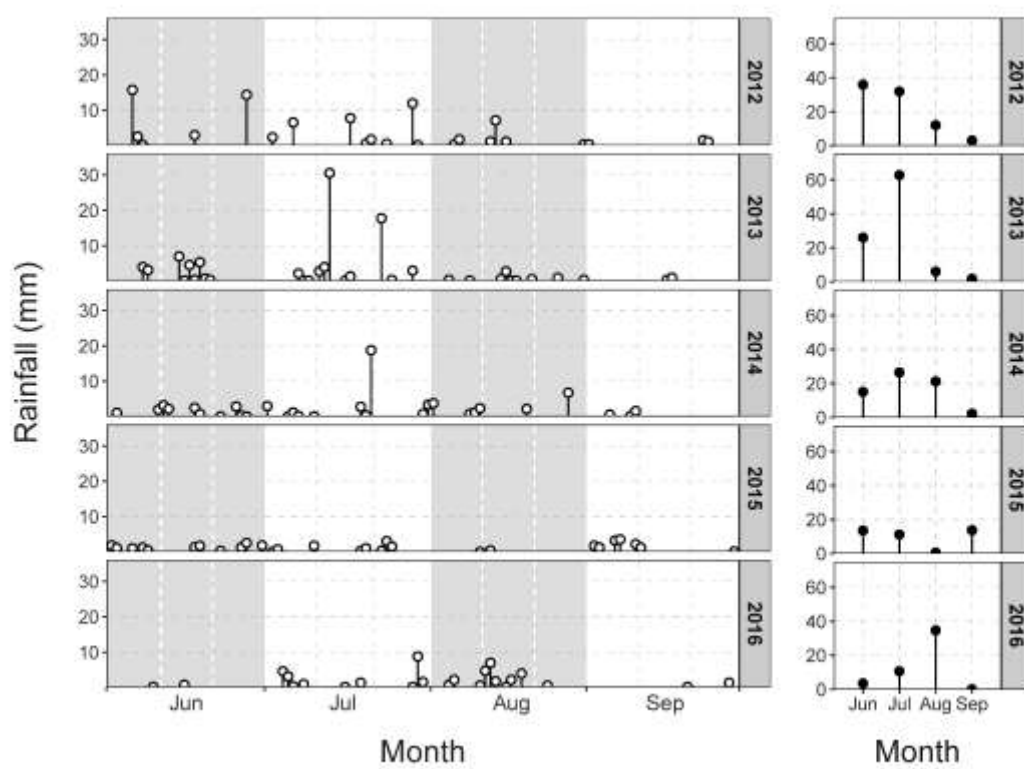| Variables	Fixed terms	*F*	*P*
Biomass (g · m^{-2})	habitat	243.970	**<0.001**
	rainfall	82.635	**<0.001**
	habitat × rainfall	103.714	**<0.001**
Density (m^{-2})	habitat	63.570	**<0.001**
	rainfall	37.185	**<0.001**
	habitat × rainfall	8.367	**0.003**
Cover (%)	habitat	43.941	**<0.001**
	rainfall	86.635	**<0.001**
	habitat × rainfall	5.585	**0.017**
Richness	habitat	22.342	**<0.001**
	rainfall	86.923	**<0.001**
	habitat × rainfall	7.810	**0.006**

P values at <0.05 level are in bold.

Figure Legends

Figure 1

Figure 2

Figure 3

Figure 4