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Plant strategies in extremely stressful environments: are the effects of nurse plants positive on all understory species?

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ABSTRACT

Facilitation by nurse plants likely increases from outside the canopy to the center of the canopy as stresses decrease towards the center of the canopy. These stress gradients may be important in controlling plant distributions, with stress-tolerant species specializing outside the canopy or at the canopy edge, and stress intolerant species specializing at the center of the canopy. We tested if interactions with nurse plants control the distribution of understory species, and if plants species specializing in the understory environment experience higher physiological stress when grown outside the canopy than species specializing in the open environments. We tested these predictions in field sites in the arid environment of Saudi Arabia. We measured the environmental conditions, understory species abundance, and functional and physiological traits of species found under nurse plant *Acacia gerrardii*. We found that *Acacia* trees have an overall facilitative impact on the understory species. Species found more commonly under nurse tree canopies experience significant physiological stress when growing outside canopies. In contrast, species found more commonly outside canopies do not experience significant physiological stress when growing either under canopies or outside canopies. Our results demonstrate that differences in species ability to tolerate environmental stresses are important in structuring herbaceous plant communities under nurse plants in these extremely stressful environments.

Introduction

Positive plant–plant interactions (i.e. facilitation) and the balance between facilitation and competition play a vital role in plant community structure and dynamics (Hacker and Bertness 1999; Gavini et al. 2019). Facilitation is predicted to be important in stressful environments (He et al. 2011), and should be an important factor maintain diversity and ecosystem function (Bruno et al. 2003; Brooker et al. 2008; Cavieres and Badano 2009), particularly in extremely harsh arid and semi-arid environments (Maestre et al. 2010; Butterfield and Briggs 2011; Mcintire and Fajardo 2014). Nurse plants can ameliorate environmental stress and provide an appropriate or more benign environment for neighboring typically smaller plants (see Callaway 2007). They can do this by enhancing nutrient availability in the soil (e.g. Vetaas 1992; Belsky 1994; Lu et al. 2018), moderating extreme temperatures (Pages et al. 2003) and ultraviolet radiation (Lenz and Facelli 2003), and reducing evaporation and increasing water availability (Breshears et al. 1998). Thus, nurse plants can control the diversity and composition of plant communities in arid environments (Valiente-Banuet and Verdú 2007; Al-Namazi 2019). Changing patterns of environmental stress under nurse plants can also affect the types of species under these canopies, and plant communities sort themselves on these gradients of environmental stress created by nurse plants (Al-Namazi et al. 2017).

The efficiency of nurse plant facilitation is typically examined by the amelioration in the rate of growth, survival, and reproduction of beneficiary species (Hastwell and Facelli 2003; Callaway 2007). Growth rates of herbaceous species growing under a canopy of a nurse plant tend to be greater than the growth rates of the same species growing in exposed areas (e.g. Raffaele and Veblen 1998; Rey and Alcántara 2000). Plant species under stress experienced outside nurse plant canopies can suffer a reduction in leaf area, chlorophyll content, and the maximal photochemical efficiency (see Balaguer et al. 2002). These physiological impacts, in turn, reduce the growth, fitness, and survival of the stress plants. Therefore, leaf functional and physiological traits such as leaf area, chlorophyll content or the photochemical efficiency can be appropriate measures of the stress experienced by plants (Huang and Gao 1999; Souza et al. 2004; Kalaji et al. 2011).

Facilitation is predicted be important when the stress experienced by individuals of a given species is high and species are near their extreme physiological tolerance limits. When stresses are low, other factors such as competition become important in determining the persistence of species in a community (Choler et al. 2001; Liancourt et al. 2005; Gross et al. 2010). As plant species vary in their abilities to tolerate stress, they may vary in their benefits accrued from nurse plants and their response to the presence of neighbor species (Greiner La Peyre et al. 2001; Lortie et al. 2004; Noumi 2020). Beneficiary species perhaps respond differently to the impact of nurse plant depending on the functional traits they express (He et al. 2012). Stress-tolerant species should be less responsive to the facilitative impact of neighbors than other non-stress-tolerant species. Thus, aspects of stress tolerance will be a major factor in controlling the

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distribution of species, and composition of communities under nurse plants, and in the surrounding habitat.

We examined the distribution of species under nurse trees (*Acacia gerrardii* Benth.) and outside nurse tree canopies. We measured functional traits, and traits associated with stress tolerance in species growing under nurse tees and outside the nurse tree canopies. We tested the two predictions that are well established in the literature on plant facilitation: (1) the environment will be more favorable under nurse tree canopies than in the open areas. Communities under tree canopies will have higher density (i.e. more individuals) than communities outside canopies; (2) Individuals of a given species growing under a nurse tree canopy will have larger leaves, higher chlorophyll content, and be less physiologically stressed than individuals of the same species growing outside the canopy; in order to test a further novel prediction establishing how traits associated with stress tolerance are fundamental in understanding the distribution of species in stressful habitats structured by the presence of nurse plants: (3) Species will change in abundance from under the canopy to outside the canopy. Species more common outside the canopy will express traits conferring stress tolerance (e.g. lower leaf area, lower leaf chlorophyll, and less loss of chlorophyll function under stress) than those species more common under the canopy.

Materials and methods

Study site

The study was conducted in Sederah natural reserve in the National Wildlife Research Centre (NWRC), located on the arid Najd plains of western Saudi Arabia, about 45 km southern east of Taif Governorate in southwestern Saudi Arabia at the coordinates (21°14′ 55.6″ N, 40°43′44.8″E, see Figure 1). This reserve was declared as a nature reserved scientific center of 4 km² fenced since 1986 by NWRC. Then the area of the reserve was extended to comprise 19 km² adjacent to the NWRC and fenced since 1992. The fence around this reserve keeps domestic livestock out. We conducted the study in the spring from March to June 2013.

Climate data

Climate information data were available from weather station belonging to the wildlife research center in Sederah natural reserve. The annual precipitation in during the last twelve years ranges between 35 and 189 mm, with an annual average of 90 mm per year. The maximum air temperature is approximately 38°C in the summer and 23°C in the winter while the minimum air temperature is about 24°C in the summer and 8°C in the winter. The maximum soil temperature reaches up to 58°C in the summer. This region experienced a drought during the winter months (several months before the study). However, during the experiment period (March, April and May) the reserve received a small amount of rainfall (about 12.5, 21.1 and 11 mm respectively) – enough rainfall for plant growth during the spring season. Photosynthetically active radiation (PAR) was measured outside and under the canopies of *A. gerrardii* trees under full sun around high noon at the soil surface with AccuPAR LP-80 (Decagon Devices Inc., Pullman, WA, USA).
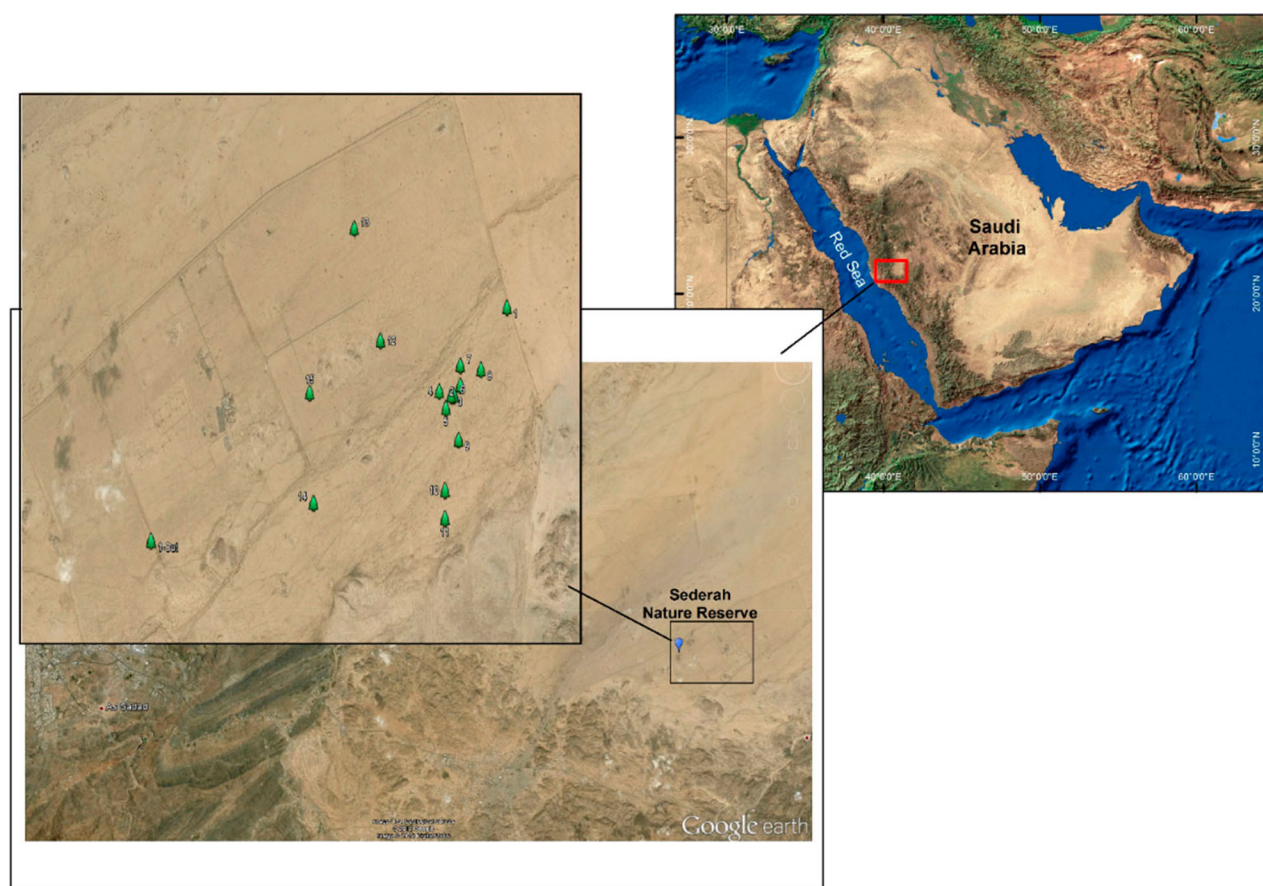

Figure 1. A map showing the location of study site in Sederah Nature Reserve, south east of Taif city, in western Saudi Arabia, the location of the trees was also determined on the map.

Soil characteristics

Soil temperature under canopy and outside the canopy was measured by two Em50 Data Loggers (each one connected to 5 ECH₂O sensors). Five sensors were set for five days both under and outside the canopies of *Acacia* trees at 5 cm depth. Sensors take readings every 15 min, and then the average was calculated for each hour. For each selected individual tree, three compounded soil samples were collected from the upper 10 cm of the soil in each microhabitat: one compounded sample from underneath the canopy, one edge of the canopy and one from at least 2 m away from the edge of the canopy. All soil samples were air dried, homogenized and sieved to remove large particles. The proportion of sand, silt, and clay were determined using the hydrometer method (Bouyoucos 1962). Organic matter content was determined using the loss of mass by combustion with dichromate at 450°C (Rowell 1994). Soil water extracts (1:5 of soil: water) were prepared for the determination of electrical conductivity (EC) using a YSI conductivity (model 35), and pH using digital pH-meter (model 5995). Available nitrogen was estimated by the micro-Kjeldahl method (Bremner and Mulvaney 1982). Available phosphorus was estimated using Olsen's solution (sodium bicarbonate) as an extracting agent (Olsen et al. 1954). Sodium (Na), Potassium (K), and Calcium (Ca) were estimated by using flame photometry by following the prescribed laboratory methods (Jackson 1973). All other elemental concentrations (Mg, Na, Fe, and Mn) were measured by Perkin Elmer atomic absorption spectrophotometry after digestion with $HClO_4$, HNO_3 and H2SO₄ (Lindsay and Norvell 1978).

Plant measurements

Fifteen *A. gerrardii* trees were selected for this study. Canopy diameter ranged from 6 to 14 m, and the area under each tree was occupied by a herbaceous plant community. For each *A. gerrardii* tree canopy, two quadrates of 1 m² were selected under the canopy and two quadrats were selected outside the canopy (5–10 m from the edge of the canopy). Quadrats were selected on the North and South side of the tree stem to avoid the impact of shade extension in the morning and afternoon in the west and east directions respectively.

Mean abundance of all species (the number of individuals per species), Species density (the number of species occurring per (1 m²) unit area), and plant cover (the percentage of occupied area by a plant species in (1 m²) unit area) were recorded in all quadrats in each microhabitat (under and outside the canopy).

Four most common understory species: *Salvia aegyptiaca* L. (Lamiaceae), *Fagonia indica* Burm. F. (Zygopyllaceae), *Farsetia aegyptia* Turra (Brassicaceae) and *Lycium shawii* Roem. and Schult. (Solanaceae) were selected to examine physiological stress and functional traits across microhabitats (leaf area, chlorophyll content, and photochemical efficiency). Each of these species is a short-lived herbaceous perennial. Individuals of each species are found at both under the center of the canopy and outside the canopy, but these species are distributed differently under the nurse plant canopies. *Salvia aegyptiaca* and *Lycium shawii* are under canopy specialists (they are the dominant species under the canopy). *Fagonia indica* and *Farsetia aegeptia* are open area specialists, as they are found more frequently at the canopy edge and outside of canopy than other two species. The species used in the experiment were common throughout the region (in areas where sheep grazing is limited). Thus, the reserve is a core area for these species.

The photochemical efficiency or the maximum quantum yield of PSII (*Fv/Fm*) is a standard method of estimating stress in plants, and (unlike measures of stress such as water potential), is broadly comparable across species. The optimal value of *Fv/Fm* in many plant species often ranges between 0.79 and 0.84 (Kitajima and Butler 1975; Björkman and Demmig 1987; Maxwell and Johnson 2000; Rengifo et al. 2000). The photochemical efficiency of the four target species was measured in five leaves from each individual of five individuals of each species from each of the two microhabitats (under canopy and open areas) with Fluorescence monitoring system FMS2 (Hansatech Instruments Ltd, Pentney, King's Lynn, Norfolk, England) equipped with a leaf-clip holder. Photochemical efficiency was estimated using the following equation:

$$Fv/Fm = (Fm - Fo)/Fm$$

where *Fv* is the variable chlorophyll fluorescence (*Fm − Fo*), *Fo* is the minimal fluorescence level; *Fm* is the maximal fluorescence level. The measurements were taken in the field between 11:00 and 12:00 h. In addition, we measured the leaf area in a sample of five leaves from each individual of five individuals of each species from each of the two microhabitats (under canopy and open areas). The measurements of the leaf area were taken in the field with Portable Laser Leaf Area Meter (CI-202, CID Bio-Science, Inc., Camas, WA, USA). Total chlorophyll content in leaves was measured in a sample of five leaves from each individual of five individuals of each species from each of the two microhabitats. The measurements of chlorophyll content were taken in the field with CCM-200 PLUS chlorophyll meter (Opti-Sciences, Inc., Tyngsboro, MA, USA). Leaves were selected to minimize self-shading, but all leaves in the microhabitat under canopy were shaded by the nurse plant.

Data analysis

We tested the variation in the soil features among the microhabitats by comparing the means of variables among microhabitats using one-way analysis of variance (ANOVA). Data of plant abundance (plant cover and density), leaf area and chlorophyll content were also analyzed in an Analysis of Variance (ANOVA) with the microhabitats (under and outside of canopy) as the main effects and species as a random effect. Post hoc comparisons were conducted using a Tukey's hsd test to compare vegetation attributes among treatments.

The relationship between the facilitative effect of *A. gerrardii* and the understory herbaceous species was explored using a relative interaction index (RII, sensu Armas et al. 2004). RII was calculated based on differences in plant density with and without nurse plant (*A. gerrardii*) relative to the sum of both density values, according to the following formula:

$$RII = (D_{wn} - D_{nn})/(D_{wn} + D_{nn})$$

where D_{WN} and D_{NN} are plant density with or without a nurse tree, respectively. This index ranges from −1 to 1, with
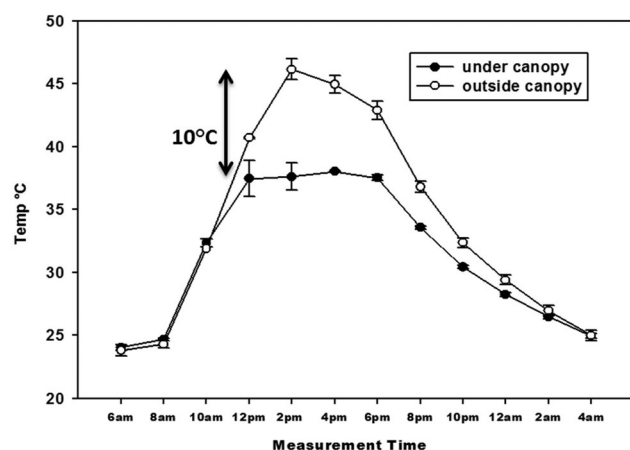
Figure 2. The mean of soil temperature (±SE) recorded by data loggers during day hours under the canopy (●) and outside the canopy (○).

positive values indicating facilitation and negative values competition.

The values of Fv/Fm lower than 0.79 indicate that plant is under stress (Kitajima and Butler 1975; Rengifo et al. 2000). Differences between the mean values of Fv/Fm for the target species among the two microhabitats were tested around the hypothesized mean (0.79) using a t-test for each of the four target species. Unless otherwise noted, statistical methods were implemented by using the statistical software package SPSS version16.0 (SPSS Inc, Chicago, USA).

Results

Mean soil temperature was 47°C outside the canopy compared to 37°C under the canopy during the hours around mid-day (Figure 2). Photosynthetically active radiation (PAR) was 1913 ± 30 μmol/m^2/s outside the canopy compared with 211 ± 14 μmol/m^2/s under the canopy (Light transmission just outside the canopy was approximately 1700 μmol/m^2/s (88%) of light in open area). The soil under canopy was richer in organic matter (OM) and mineral nutrient such as nitrogen (N), potassium (K), magnesium (Mg) and calcium (Ca) than that of outside canopy or open areas (Table 1).

Plant cover and density of understory species growing under the canopies of *Acacia* trees was significantly higher compared with that of species growing in the exposed area outside the canopy. The mean of plant species density under canopy (1.04 ± 0.12 individuals/m^2) was significantly greater than species density in the open area (0.55 ± 0.08 individuals/m^2) (d.f. = 1, $F = 11.50$, $P = 0.001$). Similarly, the mean plant cover under canopy ($2.60 \pm 0.60\%$) was significantly greater than the mean plant cover in open areas ($0.33 \pm 0.06\%$) (d.f. = 1, $F = 13.90$, $P < 0.0001$). Most understory species experienced facilitation (positive RII index) with the nurse trees, but, some species experienced negative interactions with the nurse trees (negative RII index) (Figure 3).

We found significant differences between individuals of the canopy specialist species (*L. shawii* and *S. aegyptiaca*) and the outer canopy specialist (*F. aegyptia* and *F. indica*) between the two microhabitats. The canopy specialists had bigger leaves with more chlorophyll under the canopy but had significant declines in the open. Open area specialists had smaller leaves with less chlorophyll but did not suffer

Table 1. The mean (±SE) for soil features through the two microhabitats: under canopy (Canopy) and outside the canopy (Open). The F and P values report the significance of the differences between soil features in Canopy and Open microhabitats.

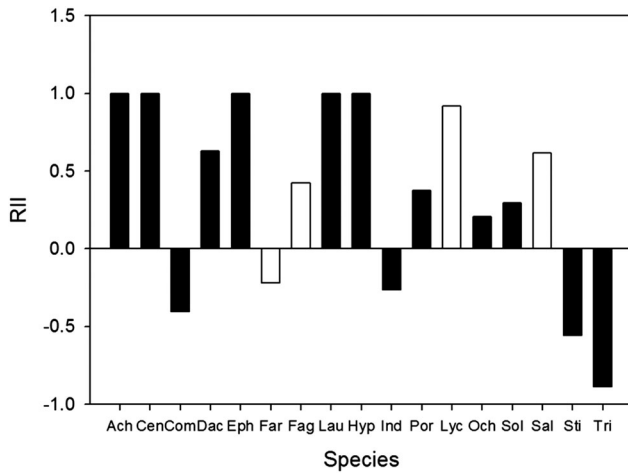|	N	P	OM	Fe	Mn	pH	COND	Cl	SO	Ca	Mg	Na	K
Canopy	1086 ± 160	513 ± 49	0.833 ± 0.24	8807 ± 504	135 ± 7.20	7.72 ± 0.13	283 ± 35	0.64 ± 0.16	1.25 ± 0.36	1.62 ± 0.25	0.46 ± 0.17	0.38 ± 0.09	0.37 ± 0.04
Open	918 ± 135	533 ± 41.50	0.44 ± 0.07	9454 ± 680	126 ± 3.70	8.35 ± 0.11	79 ± 20	0.25 ± 0.03	0.18 ± 0.09	0.39 ± 0.12	0.09 ± 0.02	0.16 ± 0.03	0.15 ± 0.03
F	0.63	0.09	2.39	0.60	1.07	12.68	11.99	5.21	7.47	17.62	4.33	5.14	20.31
P	0.44	0.77	0.14	0.45	0.31	0.002	0.003	0.03	0.01	<0.0001	0.05	0.03	<0.0001

Figure 3. The relative interaction index between *A. gerrardii* and the understory herbaceous species *Achyranthes aspera* (Ach.), *Cenchrus ciliaris* (Cen), *Indigofera spinosa* (Ind.), *Commicarpus grandifloras* (Com), *Dactyloctenium scindicum* (Dac), *Ephedra foliate* (Eph), *Fagonia indica* (Fag), *Farsetia aegyptia* (Far), *Hyparrhenia hirta* (Hyp), *Launaea mucronata* (Lau), *Lycium shawii* (Lyc), *Portulaca oleracea* (Por), *Ochradenus baccatus* (Och), *Salsola imbricata* (Sals), *Salvia aegyptiaca* (Sal), *Stipagrostis* sp. (Sti), *Tribulus terrestris* (Tri). The white bars represent the four target species.

Figure 5. The mean (±SE) of the maximum quantum yield of PSII (*Fv/Fm*) of the four target species *Fagonia indica*, *Farsetia aegyptia*, *Lycium shawii* and *Salvia aegyptiaca* in the under canopy microhabitat (filled bars) and open microhabitat (open bars). *, **, and *** indicate mean yields significantly different from the hypothesized mean of 0.79 with $p < 0.05$, $p < 0.01$, and $p < 0.0001$, respectively. Non-significant differences between mean and hypothesized yields are reported by n.s.

a reduction in these traits in the more stressful open areas (Figure 4). Furthermore, although all species had high photochemical efficiency under the canopy, there was a significant difference in the photochemical efficiency of the canopy specialist species among the two microhabitats. The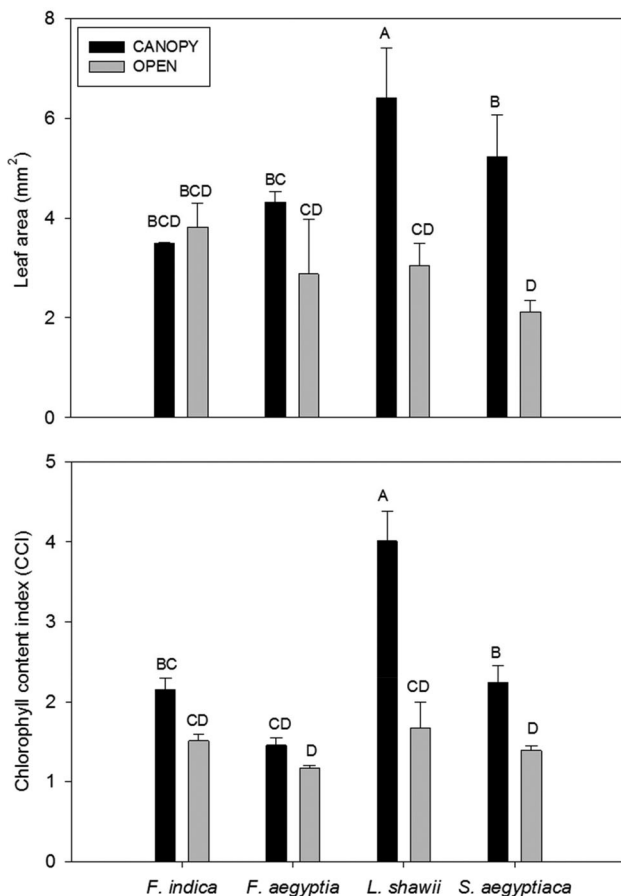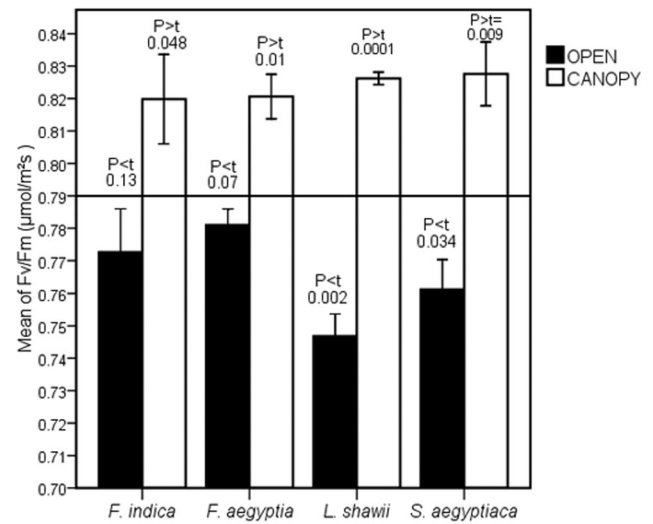 photochemical efficiency of individuals of canopy specialist species that growing in the stressful open microhabitat was significantly lower compared with individuals of the same species but growing in the less stressful canopy microhabitat (Figure 5). In contrast, in the open area specialist species, there were no significant differences from 0.79 between individuals growing in the center of the canopy and outside the canopy. Moreover, the photochemical efficiency of individuals of these species that growing in the stressful microhabitat is very close to the optimal value of the photochemical efficiency (0.79). Overall, all species had higher efficiency under the canopy than in the open. Canopy specialists were significantly stressed in the open while open specialists were not significantly stressed.

Discussion

Leaf functional traits and traits associated with stress tolerance play a key role in the assembly of communities and the distribution of species under nurse plant canopies, and in adjacent open area habitats (Schöb et al. 2012). We demonstrate that canopy specialist species had big leaves with high chlorophyll content but poor photochemical efficiency under stress. In contrast, open specialist species had small leaves with lower chlorophyll but did not suffer a significant loss in efficiency under stress. Leaf area and chlorophyll content of the species growing under canopy were larger than that of individuals of the same species but growing in the exposed open areas. These traits are associated with plant strategies of growth and resource acquisition under nurse plant canopies. Functional traits such as leaf area and chlorophyll content have been found to be involved in a vital trade-off between a rapid production of biomass and an efficient conservation of nutrients and resources (Poorter and Garnier 1999; Garnier et al. 2001; Balaguer et al. 2002). The reduction in leaf area and chlorophyll content could be due to the stress on the individuals growing in the exposed open area microhabitat, or as part of an adaptive stress tolerance strategy. Although our results demonstrate the changes between the

Figure 4. The mean (±SE) of leaf area and chlorophyll content of the target species: *Fagonia indica*, *Farsetia aegyptia*, *Lycium shawii* and *Salvia aegyptiaca* in the under canopy microhabitat (filled bars) and open microhabitat (open bars).

functional traits of species through environmental variation among small microhabitats, they are also consistent with the findings of other studies that have been conducted on a large scale environmental gradients (Balaguer et al. 2002; Yang et al. 2009). Though the impact of these changes in functional traits on species distributions at small scales is poorly understood.

The photochemical efficiency in the individuals of target species growing outside the canopies of *A. gerrardii* was significantly lower than that of understory species that growing under the canopies of *A. gerrardii* trees. This indicates that the individuals in the canopy microhabitat grow near their physiological optimum while individuals in the outside were more stressed. However, the response of leaf function and photosynthetic efficiency for plants was variable across species under the canopy and outside the canopy among the four species in term of the amount of chlorophyll, the leaf area, and the photochemical efficiency. The leaf area and leaf content of chlorophyll in the individuals of canopy specialist species (*S. aegyptiaca* and *L. shawii*) growing in the least stressful microhabitat under canopy differ greatly from the individuals that growing in the extremely stressful microhabitat outside the canopy. In contrast, there is no significant variation in the leaf area and the chlorophyll content between the individuals of edge specialist species (*F. aegyptia* and *F. indica*) through the two microhabitats. Moreover, the measurements of photochemical efficiency indicate that the individuals of canopy specialist species growing in the stressful microhabitat outside the canopy suffer from the stress more than the individuals of edge specialist species in the same microhabitat.

Our results demonstrate that the stress gradients established by the nurse plants have a significant effect of structuring the herbaceous plant communities. *A. gerrardii* trees create a benign microhabitat that has microclimate remarkably different from the external climate in many aspects. In addition to the significant effects of ameliorating environmental stress, *Acacia* (Including *A. gerrardii*) species are from the most nitrogen fixers that contribute to increasing the fertility of the soil as it is well known from several experimental studies (see Radwanski and Wickens 1967; Pandey et al. 2000). The soil features in the under canopy microhabitat were very rich in nutrients elements, similar to nutrient increases found in other studies (e.g. Vetaas 1992; Belsky 1994; Lu et al. 2018). The improvements in the canopy microhabitat increased the number of individuals and abundance of plant species under canopy compared with that of species growing in the open areas. These results are consistent with the results of other studies examining the effects of nurse plant facilitation in arid environments (Belsky 1994; Ludwig et al. 2003; Abdallah and Chaieb 2010; Abdallah et al. 2012). The improvements of the microhabitat by *A. gerrardii* trees also reflect on the functional traits of the individuals of species growing underneath their canopies, as the functional traits (e.g. leaf area, chlorophyll content, and photochemical efficiency) of the individuals of target species in this microhabitat were at the optimum performance and indicate that these plants were less stressed compared with the individuals in the open microhabitat. However, the functional traits of the open area specialist species suggest these species experience more stress in the stressful microhabitat in the open area than that under canopy, but they were less stressed than the canopy specialist species.

The characteristics of species play important role in the distribution of these species among the different microhabitats around the nurse plant, as the canopy specialist species are stressed and less likely to survive as they have less ability to tolerate the extreme stresses of the open areas, so their distributions are limited to the center of the canopy. Although we found these results among small microhabitats, they are consistent with studies on large environmental gradients (e.g. Liancourt et al. 2005). Intriguingly, competition may be important in structuring communities in the canopy center habitats. Open area specialist species may be inferior competitors, so they may get competitively displaced from the center of the canopy but are capable of persisting in the stressful microhabitats (Al-Namazi et al. 2017). Species vary in their responses to the impact of nurse plant with most species experiencing strong positive effects of the nurse plants, but some experience negative effects (Figure 4). The results of our study demonstrate the importance of abiotic stresses in controlling species distributions under the canopy and in the adjacent open area habitats. The high density of individuals, and higher plant cover under the canopy could set the stage for a gradient of increasing competitive interactions with increasing habitat productivity (Sammul et al. 2000) from the open areas to the center of the canopy. We explore this hypothesis in a related study (Al-Namazi et al. 2017).

Our results suggest that the understory species growing under the nurse trees vary in their responses to the facilitative impact of a nurse plant. Although, nurse trees such as *Acacia* trees are important facilitators to the understory herbaceous species, their impact was not consistent across species. Some species gain benefits from facilitation by nurse plant while other species do not. The capacity to tolerate the high stresses of the environments outside the canopy determines the distribution of species in these stressful environments (Huang and Gao 1999; Souza et al. 2004) while the high stresses outside the canopy limit the distribution of the stress intolerant species to under the canopy. Stress-tolerant species have a high ability to grow under the relative stressful microhabitat so they are not affected by the facilitative impact from nurse plant, so they are more common in the microhabitat away from the center of canopy (e.g. close to or in the open area), while non-stress-tolerant species cannot persist in the stressful environment and they prefer to benefit from the facilitative impact of nurse, so they are more dominant under the center of the canopy.

We demonstrate that facilitation plays a key role in the distribution of plant community in the arid environments. Facilitation is not just as a force in ameliorating abiotic stress, but also as a selective force important in the assembly of communities, and the evolution of plant strategies in extremely stressful environments (Butterfield and Briggs 2011; Schöb et al. 2012). Further, interactions between species can change on short environmental gradients (Zhang and Wang 2016). Facilitation controls the distribution of understory species, as these species distribute in the microhabitats around nurse plant depending on the intensity of facilitation in the microhabitat and the characteristics of understory species and their stress-tolerance ability.

In conclusion, nurse trees ameliorate the features of the arid environment in Saudi Arabia by reducing radiation, buffering the temperature, and increasing the soil fertility which improves the features of the arid environment, and creates a benign microhabitat for some understory species

growing under their canopy. The benign microhabitat at the canopy center results in greater plant species abundance, and shifts in the functional traits of understory species. However, the plant species vary in their responses to nurse plants. Therefore, facilitation is likely an important selective force that plays an important role in the evolution of plant strategies in arid environments, and in the assembly of plant communities of understory species in the different microhabitats around the nurse plant. Stress-tolerant species and non-stress-tolerant species are functionally different. Non-stress tolerant species require nurse plants to perform well. These species are stressed in the absence of nurse plant, so they gain more from facilitation and they are dominant at the center of canopy microhabitat. The stress-tolerant species do not need nurse plant to live in the stressful environments, and they grow and survive stresses and do well at the more stressful habitats outside the canopy. Abiotic stress controls the distribution of understory species, particularly in the stressful microhabitat. Our results suggest the small-scale stress gradients established by these nurse trees establish conditions where stress controls species distributions outside the canopies, but other factors such as competition controls species distributions in the low stress habitats near the center of nurse tree canopies.

Acknowledgements

Disclosure statement

Notes on contributors

Ali Al-Namazi is an assistant professor at King Abdulaziz City for Science and Technology (KACST) with research interest in plant ecology particularly plant–plant interactions.

Stephen Bonser is an associate professor at UNSW Sydney, Australia. He leads a research group in plant evolutionary ecology, and his research interests focus on the evolution of ecological strategies

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