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RELATIVE CONTRIBUTIONS OF SHORT-TERM CANOPY AND LONG-TERM SOIL EFFECTS OF A NATIVE SHRUB UNDER ARID BIOCLIMATE: A CASE STUDY FROM TUNISIA

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ABSTRACT

The objectives of the study, conducted in the National Park of Bou Hedma, were to examine: *(1)* the relative contributions of short-term canopy (STE) and long-term soil effects (LTE) of a shrub species in explaining differences in biomass, species diversity (richness) and species density of understory plants *(i)* between shrubs and open areas, *(ii)* between shrubs and removed shrubs; and *(2)* the role of grazing in driving changes in direction of short-term and long-term effects in shrub/understory species interactions.

We measured environmental conditions (soil nutrients and soil water) in plots that represented different neighborhood conditions (in open areas between shrubs, amongst intact shrubs and among removed shrubs), which were either fenced or exposed to grazing by large herbivores. We also studied understory species biomass, richness, density survival rate of a target species in plots represented different neighborhood conditions. Differences in species richness, density and biomass of understorey communities between shrub removed and open areas were mostly due to long-term soil effects whereas differences below shrubs and shrub removed were due to short-term effects in particular on soil water content.

Our study provides additional evidence that savannas shrubs have the potential to increase the diversity of arid systems at the landscape level. Additionally, grazing by large herbivores influenced negatively the dynamic of vegetation under arid bioclimate.

KEYWORDS: Plant-plant interactions, shrubs, arid areas, long-term soil effects, short-term canopy effects.

INTRODUCTION

Plant-plant interaction plays a key role in defining community structure and dynamics, regulating and determining the composition, functioning and productivity of plant communities and ecosystems (Brooker 2006, Craine and Dybzinski 2013). Interactions between neighbours in plant communities range from competitive, where interacting species limit each other's performance, to facilitative, where at least one of the interacting species benefits from the other (Callaway and Walker 1997). Most arid ecosystems have been grazed or are currently grazed by large herbivores, suggesting that any indirect plant interaction mediated by herbivores should have a strong and obvious impact on a large scale (Illius and O'Connor 1999). Therefore, although abiotic grazing refuges (e.g. boulders, dead branches) are considered to provide better protections for plants than biotic grazing refuges (Milchunas and Noy-Meir 2002), notably because the outcome of plant–plant interactions is highly variable (Brooker et al. 2006). The co-existing plants may interact and compete for light, nutrients, water, and space, but, at the same time, protect one another from stress such as the impacts of herbivores, potential competitors or extreme environmental fluctuations, and/or provide additional resources through canopy leaching, microbial enhancement, decomposition, and mycorrhizal networks. First, neighbours have short-term effects on other species, acting at a timescale from less than a day to a season, and mostly due to resource consumption (light, water, nutrient) or to the alteration of direct non-resource factors (microclimate, high irradiance, salinity, disturbances) by a living neighbour. Organisms are also known to have long-term effects on other species through ecosystem-engineer processes, acting on a scale of up to several hundreds of years, and including sediment trapping in marine (and dune) systems or soil weathering in terrestrial ecosystems (Michalet 2006, He and Bertness 2014).

Vegetation differences are also known to occur at a smaller scale, below shrubs or trees (Lopez-Pintor et al. 2006, Michalet et al. 2015). Small-scale below-shrubs vegetation differences are more likely due to short term effect than to long term effect. The main driver of below-shrub differences is generally the uptake of resource by the dominants, and in particular of light (Moro et al. 1997), nutrients and water (Cui and Caldwell 1997).

Under arid bioclimate of Tunisia, shrubs and trees have a strong capacity to modify soil properties with increasing soil organic matter, improving the soil structure, sequestering carbon and assisting in nutrient cycling (Noumi et al. 2012, 2015, Abdallah et al. 2016). In addition to the uptake of soil resources such as water and nutrients, shrubs may decrease the evaporative demand by shading (Maestre et al. 2003). In dry climates where high light has often negative effects on plant species, positive STE are mostly induced by canopy shading which decreases photoinhibition, vapour pressure deficit (VPD) and extreme temperatures (Gomez-Aparicio et al. 2005, Callaway 2007, Michalet 2007, Cuesta et al. 2010, Muhamed et al. 2013) and increases soil moisture through reduced evapotranspiration (Holmgren et al. 1997). Negative short-term effect concern competition for the main resources (light, nutrient and water) and are occurring in a variety of climate conditions depending on the resource and the species functional strategies (Maestre and Cortina 2004, Liancourt et al. 2009, Michalet et al. 2014).

Water can also be a determining factor conditioning vegetation dynamic in arid and semiarid regions by Mahamane L. and Mahamane S. (2005). These are in agreement with the conclusions of other authors (Larcher 2000), in Mediterranean-type ecosystems, who showed that water availability was the most important factor determining seedling recruitment of understorey species. Several sets of observational and experimental data in semiarid areas showed that trees and shrubs facilitate the development of the herbaceous understorey through improvement in soil conditions and microclimate (Maestre et al. 2001).

Arid zones in Tunisia, which cover more than 70% of the total area (Floret and Pontanier 1982), are characterised by drought and high temperature and more or less general salinity. In this area, shrub species such as *Periploca angustifolia, Rhus tripartita, Acacia raddiana, Ceratonia siliqua, Lycium shawii,* etc. improve the stability of ecosystems where they are present, contribute to reduce the risks of desertification and are helpful in restoring degraded ecosystems (Maestre et al. 2001).

The main goal of our study was: *(1)* to assess the relative contribution of short-term and long-term effects in shrub/understory species interactions in an arid savanna ecosystem of central-south Tunisia; *(2)* to assess the role of grazing in driving changes in direction of short-term and long-term effects in shrub/understory species interactions.

MATERIAL AND METHODS

Study area and vegetation

Our study site is located in the Bou Hedma National Park (348°390 N, 9°480 E, southern Tunisia). The park covers an area of 5115 ha and is a UNESCO Word Heritage Site. Climate is Mediterranean lower arid in the nomenclature of Emberger (Le Houérou 1959). Mean annual rainfall is 180 mm with the lowest probability of rain during summer and winter seasons but with important inter-annual variations. Mean annual temperature is 17.3°C with a minimum of 4.0°C in January and a maximum of 36.3°C in August. The soil of the site is composed of quaternary sandy deposits of alluvial origin on a very flat slope. The vegetation is a savanna with *Acacia tortilis* subsp. *raddiana* as single tree species. The park is grazed by introduced wild herbivores (Noumi et al. 2015). The dominant vegetation type of the Park is a very open pseudo-savanna of *A. tortilis* with several shrub species between trees (*Retama. raetam*, *Hammada scoparia*, *Hammada schmittiana*, *Rhanterium suaveolens*, *Lycium shawii*, *Gymnocarpos decander*, *Ziziphus lotus*, *Rhus tripartita*) and a sparse cover of grasses (*Cenchrus ciliaris*, *Digitaria commutata*, *Cynodon dactylon*, *Schismus barbatus*, *Hordeum maritimum*, *Bromus madritensis*, *Stipa lagascae*) and legumes and forbs (*Diplotaxis harra*, *Diplotaxis simplex*, *Enarthrocarpus clavatus*, *Erodium triangulare*, *Echium humile*, *Reseda alba*, *Plantago albicans*, *Emex spinosus*, *Launea resedifolia*, *Launea angustifolia*, *Medicago minima*). The vegetation of the Park is slightly grazed (stocking density of approximately 1 animal per 40 ha) by large introduced herbivores such as Saharan antipodeans (*Addax nasomaculatus* and *Oryx leucoryx*), dorcas gazelle (*Gazella dorcas*), mhor gazelle (*Gazella dama mhor*), Barbary sheep (*Ammotragus lervia*) and some ostriches (*Struthio camelus*) (Le Houérou 2005).

Species selected

Lycium shawii is a species of thorny shrub adapted to desert environments, and can be found throughout the Arabian peninsula, and some places in Africa. The thin leaved, rigid bush grows up to 3 meters high, with a lot of branches and alternating spines that vary in size, and grow along the branches and on their tips. The leaves narrow towards their base. It produces small whitish-pink or purple flowers from September until April, and red pea-sized seedy berries that are edible. Plants often growing nearby include *Acacia tortilis* and *Prosopis cineraria*.

Experimental design

In order to assess the relative importance of the canopy and soil effects of *L. shawii* on herbaceous understorey species, we randomly selected 8 experimental plots (50 x 50 m). We used a split-plot-block design with two treatments grazing and patches. Plots was subdivided into two equal subplots of 50 x 50 m, and one of the two was randomly chosen and fenced to exclude large herbivores using 2 m high fences (grazing treatment) with a mesh size of 50 x 50 mm. In order to assess biotic interactions with both the removal and observational methods, we created a patch treatment within each subplot by selecting ten individuals of the *Lycium* shrub and five naturally open areas. For half of the individuals of the shrub, we removed the above-ground parts of the plants by cutting them at ground level. In each patch treatment, we conducted a field experiment in which we transplanted *A. tortilis* in 3 conditions of *L. shawii* influence (Open, *Lycium* and *Lycium* removed). The experiments were conducted from October 2017 to October 2019.

Species sampling and environmental variables

During October 2018, 12 months after shrub removal, all plants growing in each quadrat were collected and identified to the species level. Plant material was dried at 70°C for 48 h and weighed. Aboveground biomass was recorded for each species in each quadrat and total aboveground biomass and species richness were calculated per quadrat (50 x 50 cm). Three soil variables were analyzed: oxidizable soil organic matter, which was determined by the Walkley-Black procedure (Nelson and Sommers 1982); extractable phosphate and total nitrogen, which were determined by Olsen’s bicarbonate extraction (Olsen and Sommers 1982) and Kjeldahl’s method, respectively. Soil moisture (volumetric soil water content) was measured at 30 cm depth with a time domain reflectometry probe (ThetaProbe ML2x; Delta T, Cambridge, UK) in all plots, with five replicates. Measurements were done 1, 7 and 14 days after a significant rain event (40 mm)

Plant−plant interaction indices

To investigate the effects of *L. shawii* on *A. tortilis* performance in the transplanted plots, we used the relative interaction index (RII) of Armas et al. (2004):

$$\mathrm{RII} = (X_{\text{with neighbour}} - X_{\text{without neighbour}}) / (X_{\text{with neighbour}} + X_{\text{without neighbour}}) \quad (1)$$

where: X corresponds to the performances *(survival)* of *A. tortilis* in the transplanted plots.

This index varies between −1 and 1. Negative values indicate a negative effect (competition), positive values a positive effect (facilitation), and 0 corresponds to no significant interaction.

Statistical analyses

The effects of our factors on survival of transplants, biomass, richness, density and environmental variables (soil water content and soil nutrient OM, TN and extractable P) were assessed with a two-way ANOVA model. All univariate analyses were done using JMP software 10.0 (SAS Institute, Cary, N.C.). Tukey's HSD tests were used to determine the significant differences between treatment means.

RESULTS AND DISCUSSION

There were significant effects of patch and grazing treatments on survival of *Acacia* transplants (Tab. 1), with lower survival in grazed areas during the experimental period (Fig. 1). Overall, grazing had a negative significant effect on survival of *Acacia* transplants. After one year of transplantation (October 2018), the survival rate of *Acacia* transplants twice better in ungrazed areas compared to grazed one (varied from 59% to 25% respectively).

Tab. 1: Results of the three-way ANOVA models for the effects of habitat, patches, method and their interactions on the survival rate at the two recording dates (October 2018 and 2019). Significant (P < 0.05) effects are indicated in bold characters.

		October 2018		October 2019	
Source of variation	df	F	P	F	P
Patches	2	12.22	**< 0.001**	5.57	**< 0.005**
Method	1	13.56	**< 0.001**	6.02	**< 0.005**
Grazing	1	14.44	**< 0.001**	4.31	**< 0.005**
Grazing x Patches	2	0.89	0.33	2.09	0.25
Patches x Method	1	1.77	0.87	5.19	0.59
Patches x Method	2	2.14	0.66	4.43	0.81
Grazing x Method	1	3.09	0.90	2.51	0.25
Grazing x Patches x Method	2	6.05	0.78	7.34	0.92

The patch effect had a significant effect on survival, with lower survival in *Lycium* patch, higher significant values in the open and with intermediate values in the *Lycium* removed (Tukey test in Fig. 1). After one year, survival rate varied from 48% in the *Lycium* patch, 55% in the *Lycium* removed and 75% in the open one.

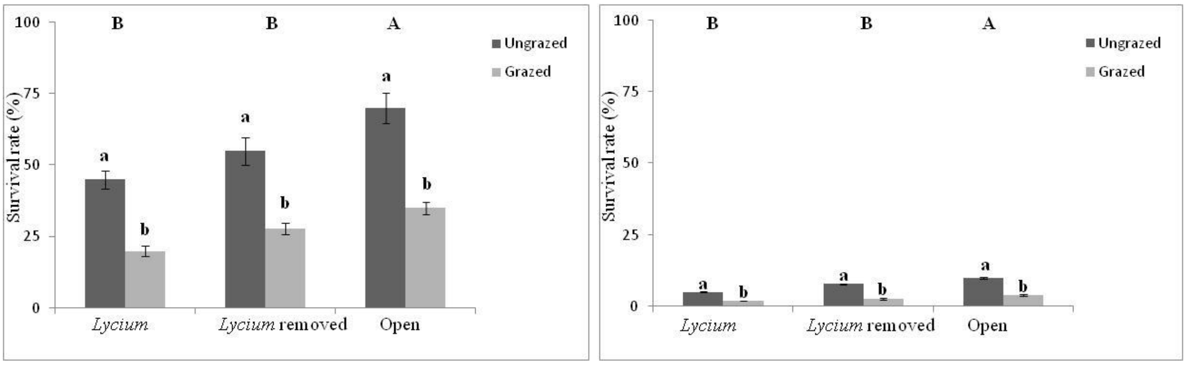


Fig. 1: Survival rate (means ± SE) of the target species restricted of three patches (Lycium, Lycium removed and open) in the ungrazed and grazed plots during three years of experiment (first measures during October 2018 and the second one during October 2019). Capitals letters represent results of Tukey HSD tests for the patch treatment (P < 0.05) and lowercase letters between bars are results of the grazing treatment.

In order to more clearly the effect of *Lycium* shrubs in survival we calculated the RII with two methods (observational vs. removal). The RII values were always negative, which again highlights that *Acacia* was always negatively affected by neighbours in our experiment (Tukey test in Fig. 2). Grazing overall reduces the intensity of competition. Moreover, there was a highly significant method effect wither higher intensity of competition with the observational method than with the removal method (Tukey test in Fig. 2).

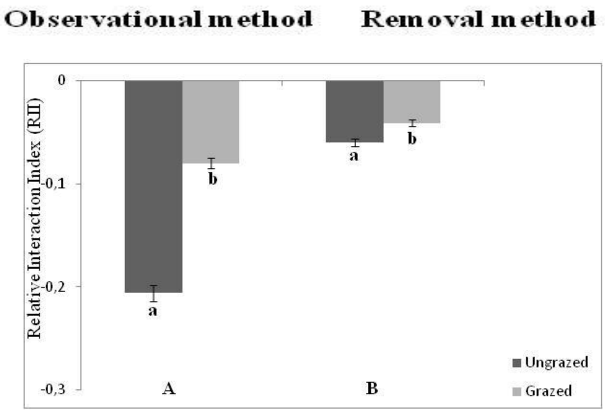


Fig. 2: Variations of the RII of the nurse – target species interaction along the grazing treatment using the two methods (observational versus removal) after the first measurements (October 2018).

In this study, we compare the relative LTE and STE effects of nurse plants on species diversity (richness), density and biomass. In ungrazed plots, statistical analyses of vegetation parameters showed a high significant effect of patch (Tukey test in Fig. 3). A similar trend was detected in grazed plots. Overall, our results showed less vegetation parameters in open patch as compared to *Lycium* and *Lycium* removed patches. Even if the effect of *Lycium* shrubs on species diversity and density was relatively low, our results showed a significant effect of shrubs on biomass. These differences can be attributed to differences in soil moisture and fertility.

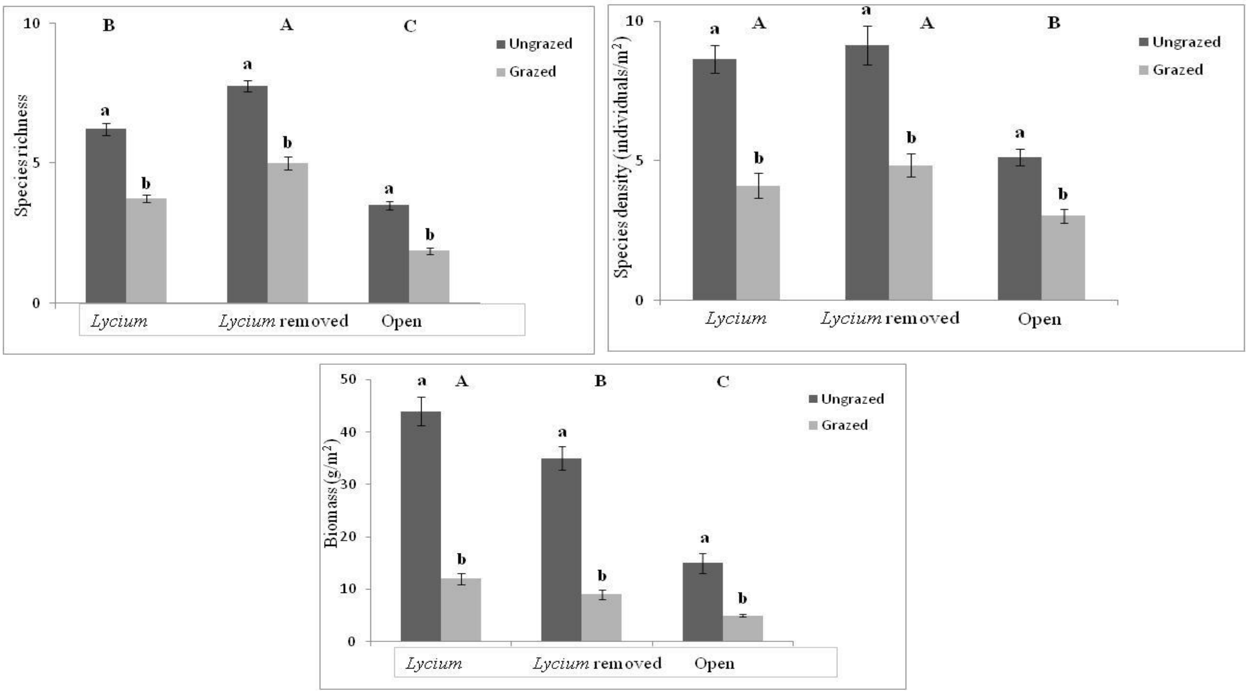
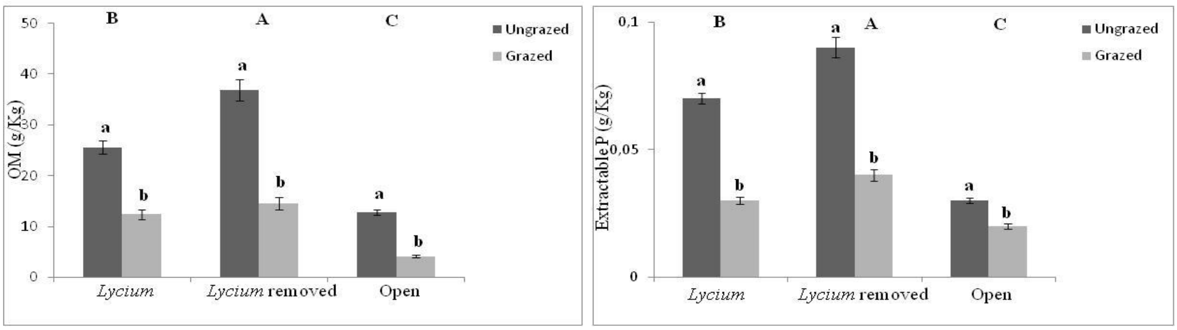


Fig. 3: Species density, richness and biomass restricted of three patches (Lycium, Lycium removed and open) in the ungrazed and grazed plots. Capitals letters represent results of Tukey HSD tests for the patch treatment (P < 0.05) and lowercase letters between bars are results of the grazing treatment.

The overall ANOVA of soil attributes showed significantly higher concentrations of all the nutrients in soils under *Lycium* removed patch compared with the open areas and the *Lycium* patch (Tukey test in Fig. 4). There were strong differences in soil characteristics among grazing treatment (Tukey test in Fig. 3). The soil organic matter content (OM), the soil nitrogen content (N) and the extractable phosphorus (P) was significantly higher in the ungrazed soils compared to grazed one.



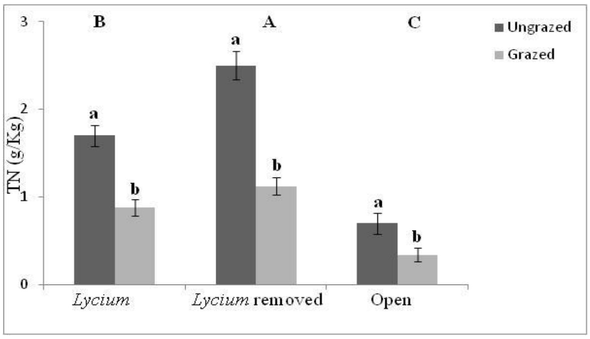


Fig. 4: Soil parameters (Organic Matter, Extractable Phosphorus and Total Nitrogen) restricted of three patches (Lycium, Lycium removed and open) in the ungrazed and grazed plots. Capitals letters represent results of Tukey HSD tests for the patch treatment (P < 0.05) and lowercase letters between bars are results of the grazing treatment.

One day after the rain, we did not observe any difference between grazing treatment and the three patches (*Lycium*, *Lycium* removed and open) (Fig. 5). Seven days after a fall of 40 mm of rain, there was significantly more soil water in the *Lycium*, less in the *Lycium* removed and the open patch had the lowest values (see Tukey test in Fig. 5, *P* < 0.05). This tendency remained constant 10 days in grazed and ungrazed plots. Finally, 15 days after the rainfall event, neither patch nor grazing had any effect on soil moisture values.

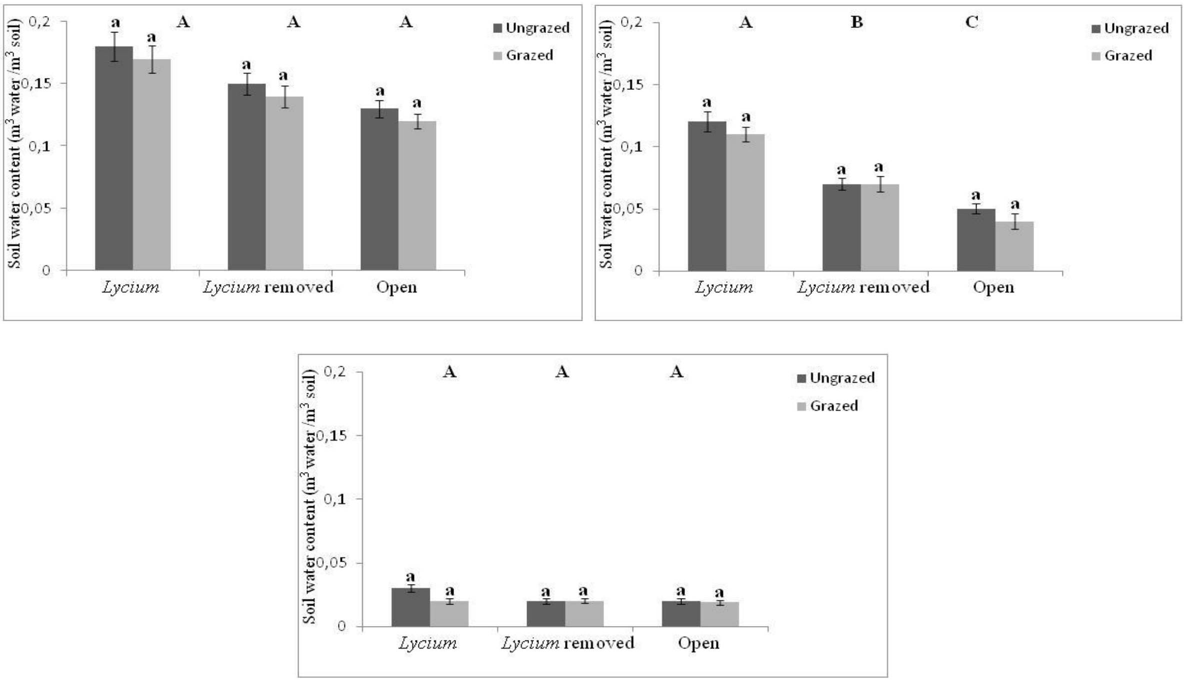


Fig. 5: Temporal change of soil water content restricted of three patches (Lycium, Lycium removed and open) in the ungrazed and grazed plots. Samplings were carried out 1, 7 and 15 days after a rain of 40 mm. Capitals letters represent results of Tukey HSD tests for the patch treatment (P < 0.05) and lowercase letters between bars are results of the grazing treatment.

The effects of Mediterranean shrubs on their understory herbaceous vegetation have often received much attention and a variety of positive and negative effects have also been reported

(Noumi 2015, 2020, Noumi et al. 2016). Still, little is known about the relative contributions of short-term canopy and long-term effects soil of shrubs especially under arid bioclimate. The main focus of this study was to determine whether *Lycium* shrubs modified the species richness, biomass, density and the availability of certain resources (nutrients, water); the role of grazing in driving changes in direction of short-term and long-term effects in shrub/understory species interactions.

The results of this study showed that LTE were stronger than STE for the *Lycium* shrub. LTE on species density and richness were strongly positive (facilitative) than STE. STE were strongly positive effect on biomass. Facilitation evidenced by the positive LTE was associated with habitats with greater soil organic matter and nutrient content, but the positive STE was associated to soil water content. Our environmental measurements clearly demonstrated that the most important differences between open areas and shrubs were for soil moisture, but removal treatment showed the highest values of soil nutrient content (total N and P, organic matter). Most plant–plant interaction studies conducted in dry ecosystems have stressed the importance of differences in soils between open and vegetated patches for explaining patterns in species biomass, richness and composition among patches (Walker et al. 2001, Maestre et al. 2003, Pugnaire et al. 2004, Miriti 2007, Weedon and Facelli 2008, Michalet et al. 2015). However, few have separated LTE from STE, to assess their relative contribution to understory performances, as done in our study. Among these few contrasting results have been observed, and mainly depend on climatic conditions. In arid southern Australia Weedon and Facelli (2008) found that positive LTE of a chenopod shrub were overwhelmed by negative STE. In contrast, Anthelme and Michalet (2009) found only positive LTE but no STE in the Tenere Desert (Niger).

In contrast to the others parameters such as species density and diversity, the highest significant values of biomass were observed under *Lycium* shrub. In accordance with some authors (Abdallah et al. 2008, Noumi et al. 2012, Noumi 2015, Abdallah et al. 2016), the main results of this study showed that *Lycium* shrubs improve the biomass of species. The recorded increase can be allotted to the higher soil moisture under the *Lycium* shrub. Thus, competitions for water alone explain the dominance of negative of *Lycium* shrub on survival of *Acacia* transplants. Another likely explanation for the absence of facilitation found in our system is the functional strategies of the nurse species.

The negative impact of large herbivores on the performance of *Acacia* seedlings was obvious, during the experiment as survival rate was twice as high in the fenced area as in the grazed area. *Acacia* is an endangered keystone species in this region (Noumi et al. 2012) and grazing should consequently influence the whole structure and dynamics of the ecosystem. Overall, our study showed the negative impact of large herbivores on different studied vegetation parameters. In contrast to suggestions that herbivory has a limited effect on vegetation dynamics in dry areas (Cipriotti and Aguiar 2005), our results support the view of Illius and O’Connor (1999) that even in arid systems with a highly variable climate, plant communities can be seriously affected by herbivores. The increase of soil organic matter and nutrient content which accompanies grazing exclusion, can be a result of an increase in the amount of plant litter on the one hand and a decrease in soil compaction on the other hand (Xie and Wittig 2004). This result in favourable living conditions for those organisms vital for the incorporation of the humus into the soil (Liu et al. 1997).

CONCLUSIONS

The results of this study confirmed the positive effect of shrubs on the understorey vegetation composition in arid ecosystems. The net effect of shrubs on their own environment, whether it is positive or negative, is strongly dependent on the nature of the woody cover. The separation of LTE of nurse-shrub species from their STE demonstrate in our system that positive LTE (i.e. facilitation) are due to increased soil nutrient in the shrub patches and the positive STE are due to increase in soil water content.

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