Short-Term Canopy and Long-Term Effects Soil of a Native Shrub Under Arid Bioclimate: A Case Study From Tunisia

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Abstract

Interactions between plants (competition and facilitation) in terrestrial ecosystems include: (1) short-term effects primarily quantified with experimental removals; and (2) long-term effects primarily quantified with observational methods. This study, conducted in the National Park of Bou Hedma, examined (1) the relative contributions of short-term canopy and long-term soil effects 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.

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 beneath shrubs and shrub removed were due to short-term canopy effects, in particular on soil water content.

Our study provides the positive effect of savannas shrubs on the understorey vegetation biomass, species density and diversity in arid ecosystems. Additionally, grazing by large herbivores negatively influenced the dynamics of vegetation under an arid bioclimate.

Introduction

Interactions between plants plays a key role in defining community structure and dynamics, and 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 (Callaway and Walker 1997). Interactions are due to the habitat-modifying capacity of nurse plants, which can alter its environment both above ('canopy effect') and below-ground ('soil effect') (Gomez-Aparicio et al. 2005). Co-existing plants may interact and compete for light, nutrients, water, and space, but, at the same time, protect each other from stress such as herbivore impact, potential competitors or extreme environmental fluctuations, and/or provide additional resources through canopy leaching, microbial enhancement, decomposition, and mycorrhizal networks. Neighbours have short-term effects (STE) 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 (LTE) 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).

Most arid ecosystems have been grazed or are currently grazed by large introduced 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) provide better plant protections than biotic refuges (Milchunas and Noy-Meir 2002), notably because the outcome of plant–plant interactions is highly variable (Brooker et al. 2006).

Under the 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 C and assisting in nutrient cycling (Noumi et al. 2012; Noumi 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 may have 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 STE concern competition for the main resources (light, nutrient and water) and occur under a variety of climatic conditions depending on the resources and the species functional strategies (Maestre and Cortina 2004; Liancourt et al. 2009; Michalet et al. 2014).

The main aim of our study was: (1) to assess the relative contribution of short-term and long-term canopy vs. soil 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.

Materials And Methods

Study area and vegetation

The 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. 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 is a very open pseudo-savanna of *A. tortilis*, with several shrub species between trees (*Retama raetam, Lycium shawii*) and a sparse cover of grasses (*Cenchrus ciliaris*, *Digitaria commutata*). The vegetation of the Park is lightly grazed (stocking density of approximately 1 animal per 40 ha) by large introduced herbivores such as Saharan antilopes (*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).

Experimental design

The experiments were conducted from October 2017 to October 2019. In order to study plant interactions occurring during the recruitment of *A. tortilis*, we chose a pioneer shrub, *Lycium shawii*, as the nurse in this study. *L. shawii* is a species of thorny shrub adapted to desert environments, and can be found throughout the Arabian peninsula and in Africa. The thin leaved, rigid bush grows to 3 meters high, with many branches and alternating spines along the branches and on their tips that vary in size. 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 by large introduced herbivores of the Park plants often growing nearby include *Acacia tortilis* and *Prosopis cineraria*.

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 m x 50 m). Half of the plots was randomly chosen and fenced to exclude large herbivores using 2 m high fences (grazing treatment) with a mesh size of 50 × 50 mm. To assess biotic interactions with both the removal and observational methods, we created a patch treatment within each plot by selecting ten individuals of *Lycium* shrub and five naturally open areas. For five shrub plants the above-ground parts were cut at ground level. The basic design consisted of planting *A. tortilis* in three conditions of the patch treatment (Open, *Lycium* and *Lycium* removed).

Species sampling and environmental variables

During October 2018, 12 months after shrub removal, all plants growing in each plot 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 × 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):

RII = ($X$with neighbour – Xwithout neighbour)/

($X$with neighbour + Xwithout neighbour)

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.

Michalet et al. (2015) and Noumi et al. (2016) proposed two different indices for disentangling STE and LTE of neighbours in experiments associating both observational and removal procedures in the same community. STE (canopy effects in Michalet et al. 2015) were quantified using the removal method (with neighbours vs. removed-neighbours conditions) and LTE (soil effects in Michalet et al. 2015) comparing target responses in removed-neighbours vs. open conditions (Noumi et al. 2016).

- STE; relative difference in target performance between shrub-control and shrub-removed plots.

- LTE; relative difference in target performance between shrub-removed and open plots.

2.5. 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

There were significant effects of patch and grazing treatments on survival of *Acacia* transplants (Table 1; Fig. 1). Grazing had a significant negative effect on survival of *Acacia* transplants. One year after transplantation, the survival rate of *Acacia* transplants in ungrazed areas was twice higher that in grazed areas (59% and 25%, respectively).

Table 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	0,9	2,51	0,25
Grazing x Patches xMethod	2	6,05	0,78	7,34	0,92

The patch treatment had a significant effect on survival. There was lower survival rate in *Lycium* patches, significantly higher survival rate in the open and intermediate survival rate where *Lycium* was removed (see Tukey test in Fig. 1). After one year, survival rate was 48% in the *Lycium* patch, 55% in the *Lycium* removed and 75% in the open patch.

In order to distinguish the effect of *Lycium* shrubs in the survival rate of *A. tortilis* we calculated the RII using two methods (observational vs. removal). The RII values were always negative, which again highlights that *Acacia* was always negatively affected by neighbours (see Tukey test in Fig. 2). Overall, grazing reduced 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 (see Tukey test in Fig. 2).

In this study, we compared the relative LTE and STE soil vs. canopy effects of nurse plants on species diversity (richness), density and biomass. In ungrazed plots, statistical analyses of vegetation parameters showed a highly significant effect of patch (see Tukey test in Fig. 3). A similar trend was detected in grazed plots. Overall, our results showed lower vegetation parameters in open patches 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.

The overall ANOVA of soil attributes showed significantly higher concentrations of all soil nutrients in the *Lycium* removed patch compared with open areas and the *Lycium* patch (see Tukey test in Fig. 4).There were strong differences in soil characteristics among grazing treatment (see 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.

One day after the rain, we did not observe any difference between different treatment (Fig. 5). Seven days after a fall of 40mm of rain, soil water was significantly higher in the *Lycium* patch, less in the *Lycium* removed patch, with lowest values in the open patch (see Tukey test in Fig. 5, $P < 0.05$). This tendency remained constant for 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.

Discussion

Our main objective was to assess firstly the relative contribution of short-term and long-term canopy vs. soil effects in shrub/understory species interactions in an arid savanna ecosystem of central-south Tunisia, and secondly the role of grazing in driving changes in direction of short-term and long-term effects in shrub/understory species interactions.

The LTE were stronger than STE for the *Lycium* shrub. The LTE on species density and richness were more strongly positive (facilitative) than STE. STE on biomass were strongly positive effect. Facilitation evidenced by the positive LTE was associated with habitats with higher soil organic matter and nutrient content, but the positive STE was associated with soil water content. The most important differences between open areas and shrubs were in soil moisture, but the removal treatment displayed 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 here. Contrasting results have been observed, but these 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). Several studies also reported higher negative STE with increasing drought stress in dry ecosystems (Davis et al. 1998; Tielbörger and Kadmon 2000; Maestre and Cortina 2004; Saccone et al. 2009), consistent with models predicting an increase in competition with decreasing resource availability (Tilman 1988; Taylor et al. 1990). Michalet (2007) argued that this occurs when soil water is the limiting resource for the involved species, whereas facilitation increases when STE of neighbours are due to a modification of a non-resource factor such as microclimate amelioration, as found by others (e.g. Gómez-Aparicio et al. 2005; Saccone et al. 2009; Cuesta et al. 2010; Muhamed et al. 2013; Michalet et al. 2014).

In contrast to parameters such as species density and diversity, the highest significant values of biomass were observed under *Lycium* shrub. The effects of Mediterranean shrubs on their understory herbaceous vegetation has received much attention and a variety of positive and negative effects have also been reported (Noumi 2015, 2020; Noumi et al. 2016). In line with some authors (Abdallah et al. 2008; Noumi et al. 2012; Abdallah et al. 2016), this study demonstrated that *Lycium* shrubs improve species biomass, which can be ascribed to the higher soil moisture under the *Lycium* shrub.

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. Overall, our study showed the negative impact of large herbivores on different studied vegetation parameters. The impact of grazing on the net outcome of the interaction between plant species depends on the intensity of grazing. For example, some studies (e.g. Smit et al. 2007; Vandenberghe et al. 2009) showed that the net outcome of interactions between the coexisting species shifted from a neutral to positive interaction (i.e. facilitation), then the positive interaction declined and disappeared with an increasing intensity of grazing. 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 (Xie and Wittig 2004).

Conclusions

Our results confirmed the positive effect of *L. sha*wii on the understorey vegetation biomass, species density and diversity in arid ecosystems. Shrubs have been used and studied as nurse plants in degraded rangeland in Kenya, in Mediterranean open woodlands, in the semi-arid subtropical Andes, in Californian woodlands (Callaway, 1992) and in the Sonoran Desert (Carrillo-Garcia et al. 1999). The separation of nurse-shrub species LTE from their STE demonstrates that positive LTE (i.e. facilitation) are due to increased soil nutrients in the shrub patches and the positive STE are due to increase in soil water content.

Declarations

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Conflict of interest

The authors declare that there are no conflicts of interest.

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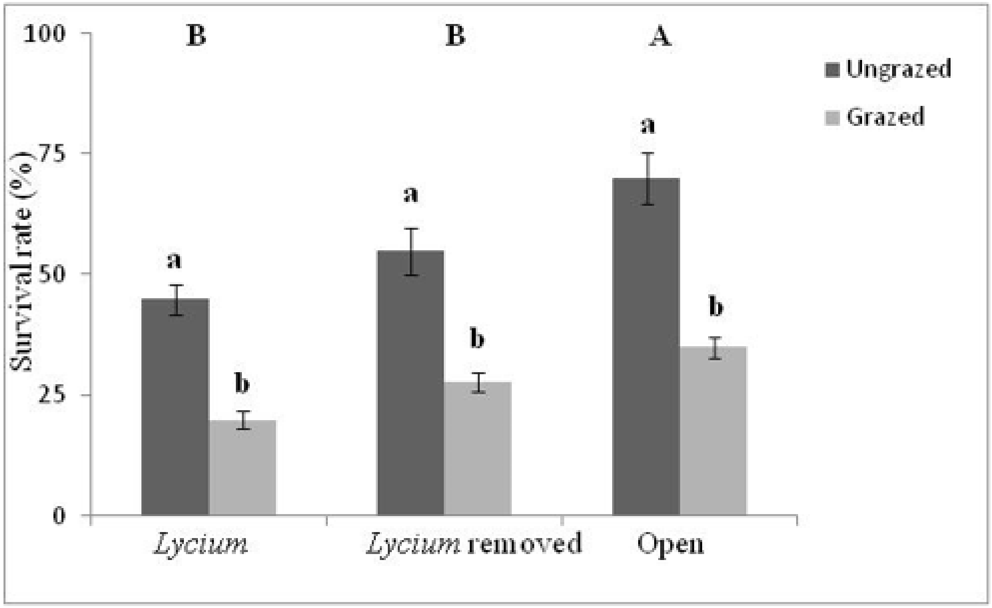
Figures



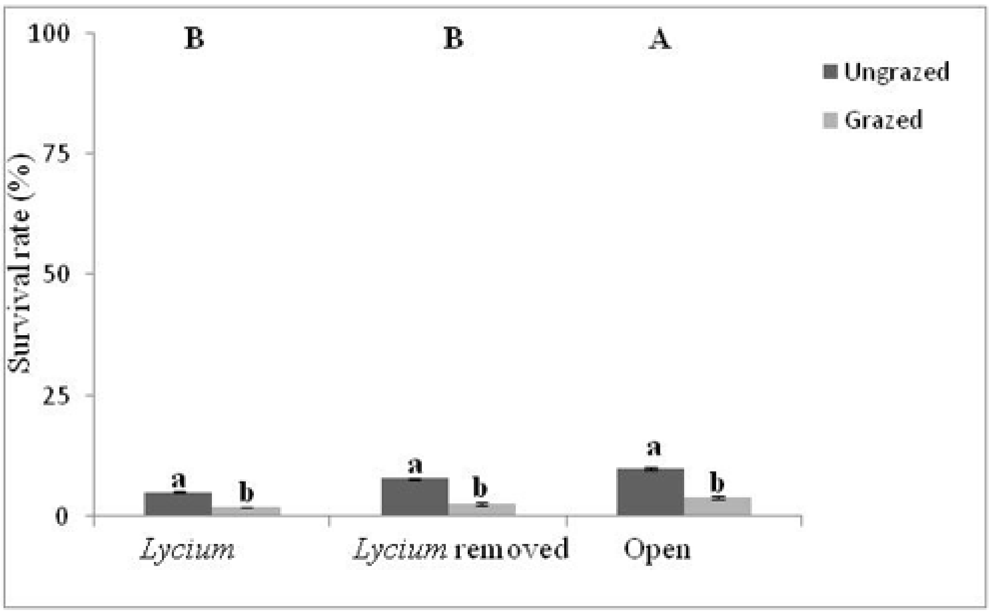


Fig. 1.

Figure 1

Survival rate (means ± SE) of the target species in the three patches (Lycium, Lycium removed and open) of the ungrazed and grazed plots. Capitals letters represent results of Tukey's HSD tests for the patch treatment (P < 0.05) and lowercase letters between bars are results of the grazing treatment

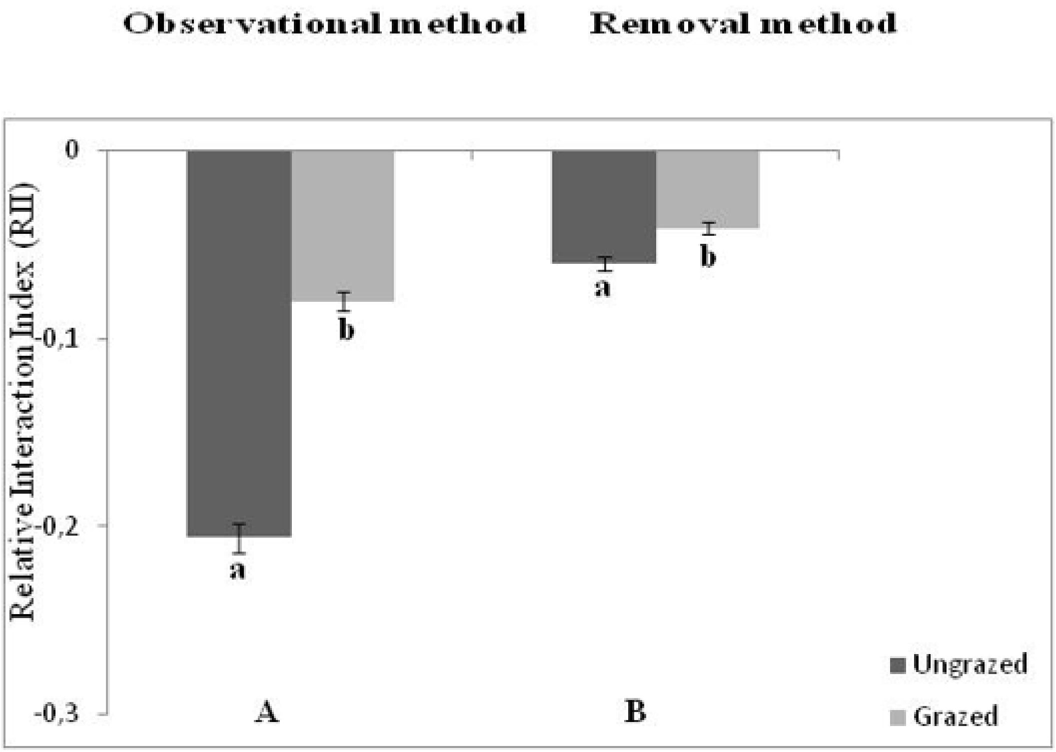


Figure 2

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)

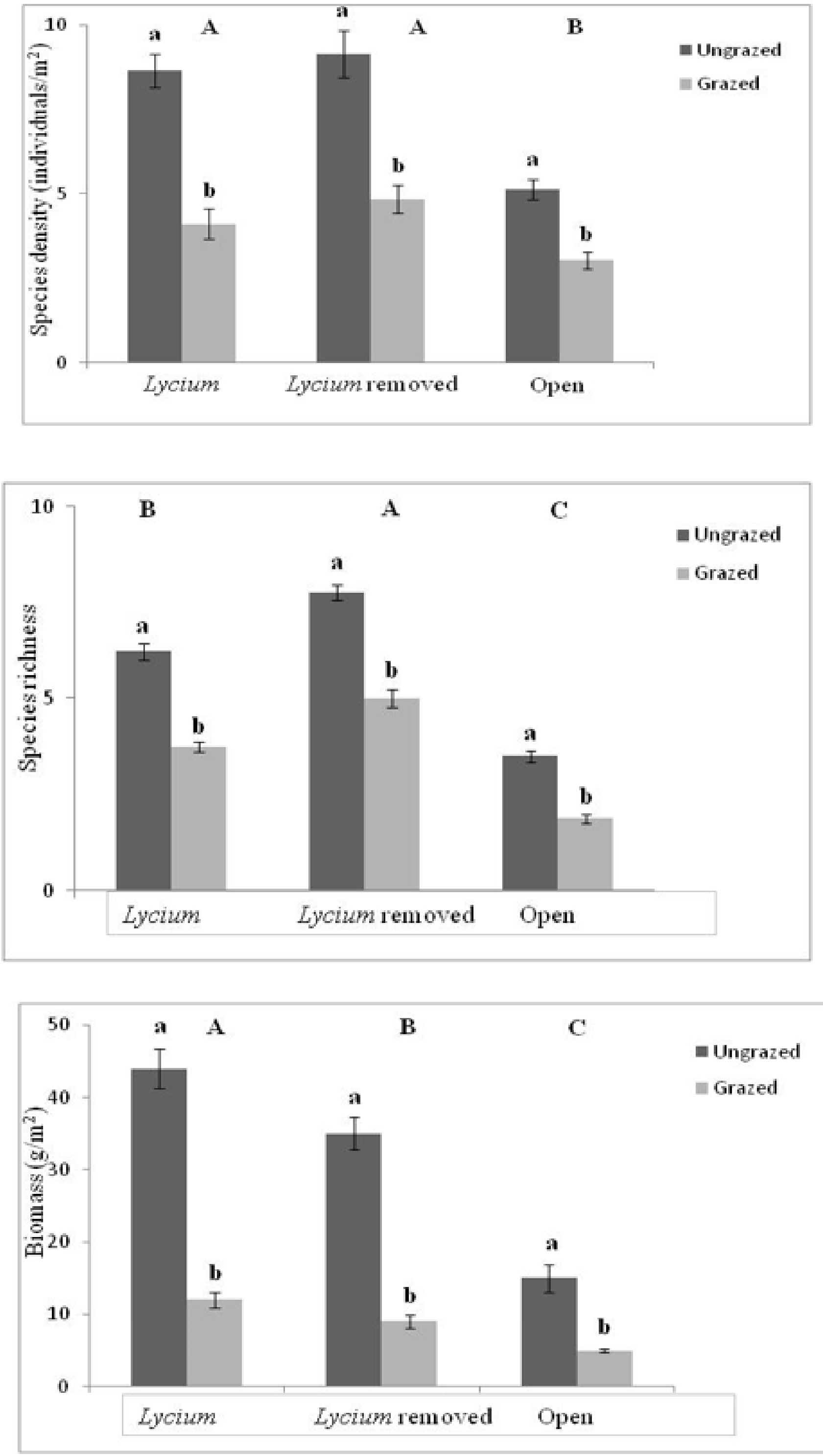


Figure 3

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

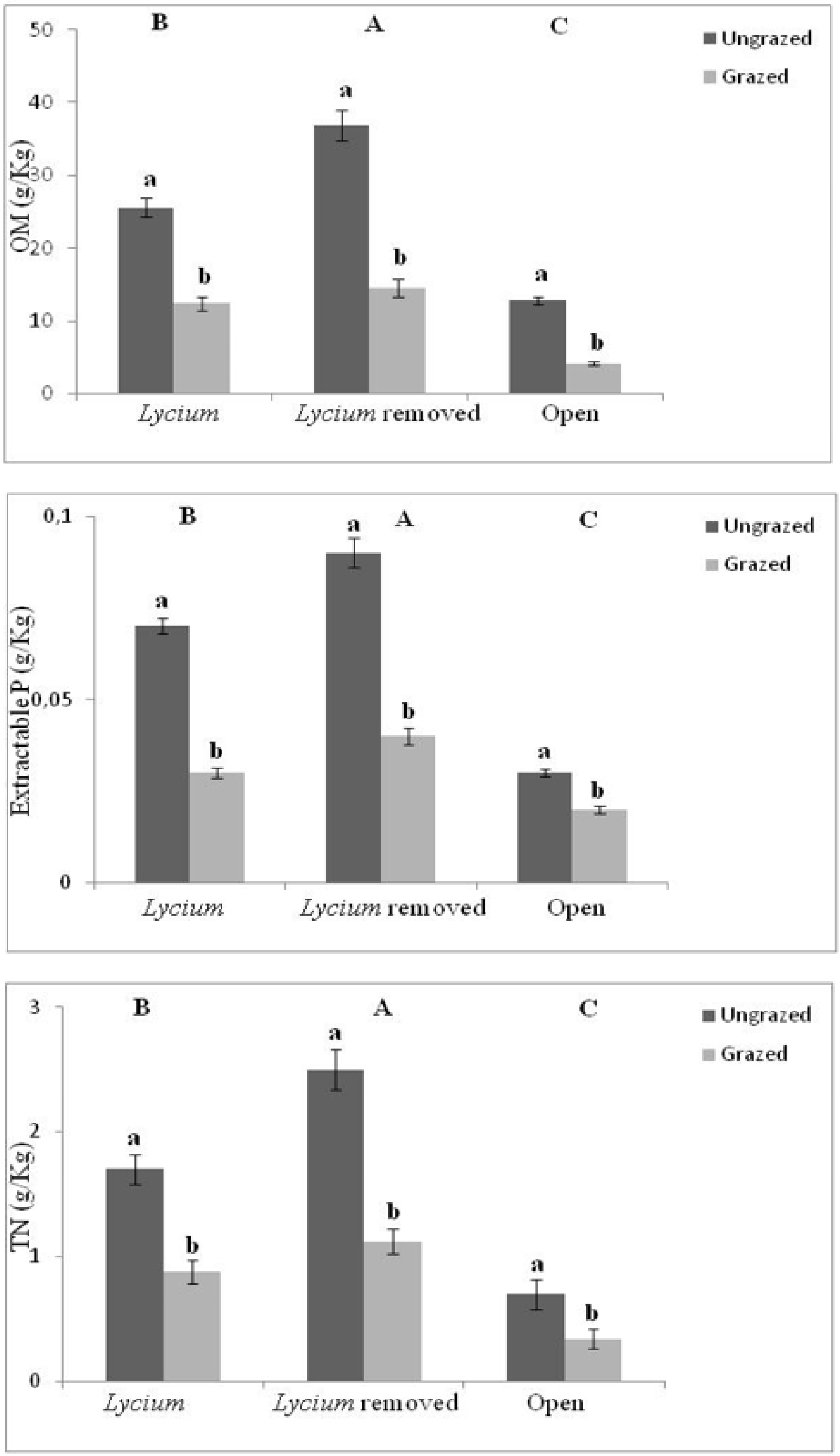


Figure 4

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

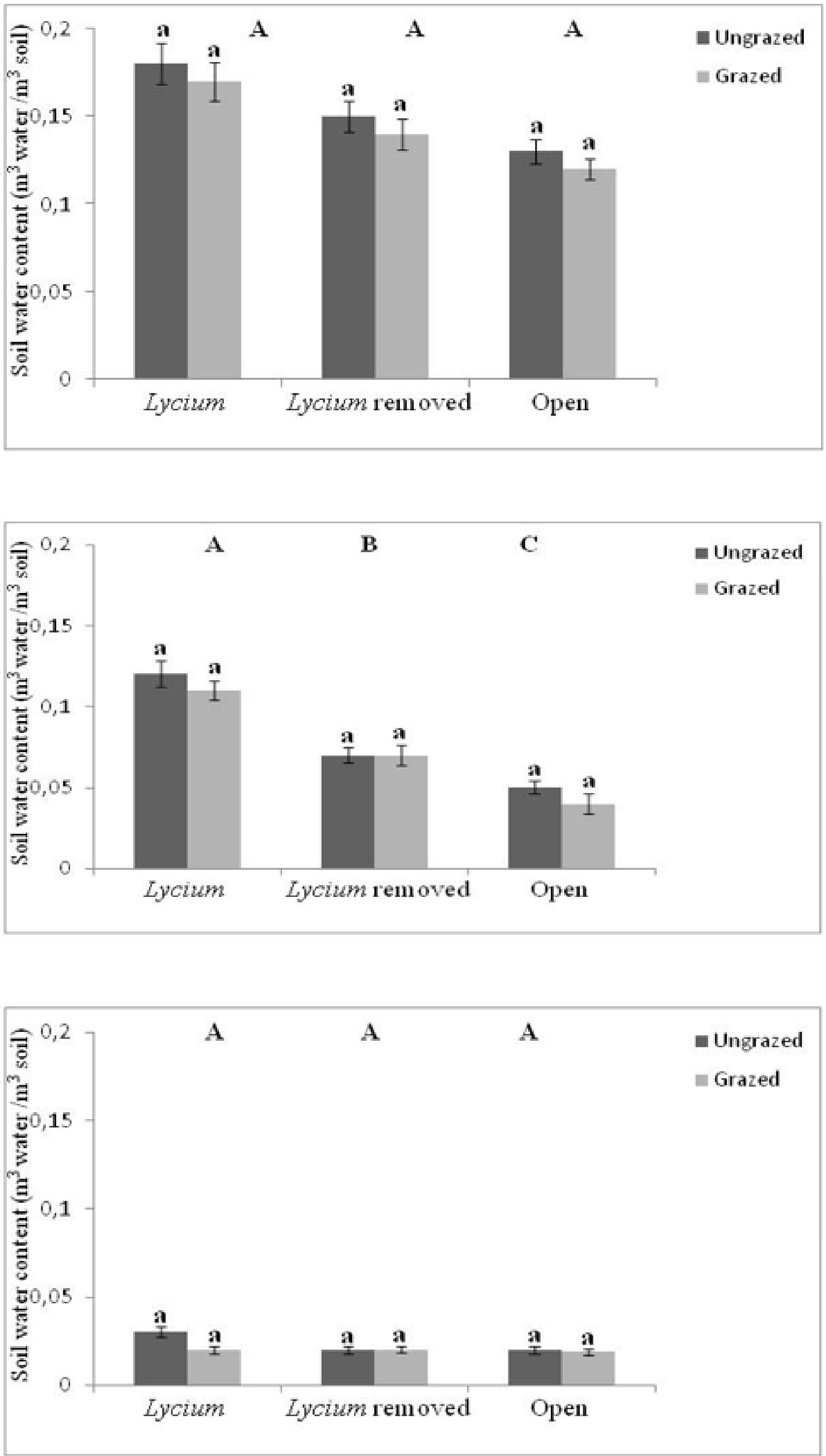


Figure 5

Temporal change of soil water content in the three patches (Lycium, Lycium removed and open) of 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's HSD tests for the patch treatment ($P < 0.05$) and lowercase letters between bars are results of the grazing treatment