



Limitations to the use of facilitation as a restoration tool in arid grazed savanna: a case study

Zouhaier Noumi, Mohamed Chaieb, Richard Michalet & Blaise Touzard

Keywords

Acacia tortilis; Drought; Facilitation; Herbivory; Importance of competition; Restoration; Savanna; Tunisia

Nomenclature

Greuter et al. (1984)

Received 16 December 2013

Accepted 23 November 2014

Co-ordinating Editor: Ralf Ohlemuller

Noumi, Z. (zouhaiern@yahoo.fr)¹,

Chaieb, M. (mohamed.chaieb@gnet.tn)¹,

Michalet, R.

(richard.michalet@u-bordeaux.fr)²,

Touzard, B. (corresponding author,

blaise.touzard@u-bordeaux.fr)³

¹Université Sfax, Faculté des Sciences, Département des Sciences de la Vie, Laboratoire de Biologie et d'Ecophysiologie des végétaux en milieu aride 99/U.R/09-12, Route de Sokra, Km 3.5, BP 802 3018, Gouvernorat de Sfax, Sfax, Tunisia;

²Université Bordeaux, UMR CNRS 5805 EPOC, Allée Geoffroy Saint-Hilaire, CS 50023 – 33615, Pessac Cedex, France;

³Université Bordeaux, UMR INRA 1202 BIOGECO, Allée Geoffroy Saint-Hilaire, CS 50023 – 33615, Pessac Cedex, France

Abstract

Question: There is increasing interest in using facilitation by nurse plants for restoring dry degraded ecosystems. However, most studies concern semi-arid areas, and the efficiency and importance of facilitation in arid grazed areas is still poorly understood. The goal of this study was to determine to what extent positive interactions among plants could be used as a restoration tool in an arid grazed region (southern Tunisia). In particular, we examined variations in plant interactions, along with water stress, grazing intensity and the type of nurse plant (grass vs chenopod shrub).

Location: *Acacia tortilis* open woodland community of the National Park of Bou-Hedma, Tunisia (33°30' N, 9°38' E).

Methods: Survival of transplants of *Acacia* was monitored during two growing seasons, with and without herbivores, in the presence/absence of a chenopod shrub and a perennial grass, and in three communities of contrasting water availability. We quantified the importance of biotic interactions and their variation across the community, grazing and neighbour type treatments.

Results: Competition was the only statistically significant interaction occurring between *Acacia* seedlings and both neighbours in all water and grazing conditions. The negative effect of neighbours was mostly for light and water. However, competition was important only at the start of the experiment during a relatively wet period, in the wettest community and in the absence of herbivores. Drought stress and disturbance were the most important drivers of target tree survival.

Conclusions: Facilitation cannot be used as a tool for ecological restoration in this arid system, mainly because the only available target tree species is too shade-intolerant and drought-tolerant to benefit from neighbours. In addition, the importance of plant–plant interactions vanished due to the overwhelming importance of stress and disturbance. Our study highlights the fact that nurse-based ecological restoration should not be an automatic process, but must be tailored to the species and environment in question.

Introduction

There is increasing interest in using direct facilitation as a tool in ecological restoration of semi-arid and arid ecosystems (Gómez-Aparicio et al. 2004; Gómez-Aparicio 2009). Nurse plants may improve soil fertility and decrease drought or temperature stress, allowing target tree and shrub seedlings to survive in these severe and often highly degraded environmental conditions (Callaway 1995; Maestre et al. 2009a). However, it has also been shown

that competition may be intense in water-stressed environments (Davis et al. 1998; Saccone et al. 2009), and there is still intense debate on how facilitation and competition vary along water stress gradients (Michalet 2006, 2007; Maestre et al. 2009b; Michalet et al. 2014).

Among others, Gómez-Aparicio et al. (2004) and Michalet (2007) stressed that differences among studies in species traits and strategies of both the nurse and the target species may explain discrepancies in the literature (Gómez-Aparicio 2009; Maestre et al. 2009b; Forey et al.

2010). Because of their high allocation to roots, grasses are more likely to compete for water with target species than shrubs or forbs (Davis et al. 1998; Gómez-Aparicio 2009). Legumes are excellent nurses because of their additional input of nitrogen (Pugnaire et al. 1996; Badano et al. 2009). Concerning the strategy of the target species, several authors have stressed that stress-intolerant species are better candidates for facilitation than stress-tolerant ones (Liancourt et al. 2005; Michalet et al. 2006; Saccone et al. 2009; Forey et al. 2010).

Michalet (2007) and Maestre et al. (2009b) argued that the limiting factors involved in the interactions might also drive the outcome of interactions, with competition prevailing in the case of resource factors (e.g. water availability) and facilitation in the case of non-resource factors, e.g. high light and high vapour pressure deficit (VPD). Most studies using facilitation as a tool for restoration have been conducted under moderate drought stress in semi-arid Spain (e.g. Gómez-Aparicio et al. 2004). Studies in arid and desert ecosystems are scarce (e.g. Jankju 2013). In very dry environmental conditions, facilitation may wane or even be replaced by competition, consistent with the theoretical predictions of Michalet et al. (2006) and Holmgren & Scheffer (2010), and the experiments of Tielbörger & Kadmon (2000), Badano et al. (2009) and Jankju (2013). Additionally, because in arid conditions the only potential species for ecological restoration are highly drought-tolerant but not shade-tolerant, we may expect weak direct positive or even negative effects of nurses (Holmgren & Scheffer 2010). Thus, we doubt that conclusions mainly made from experiments conducted in semi-arid areas can simply be applied to all water-stressed ecosystems. The use of facilitation as a tool for ecological restoration deserves to be assessed in arid and desert ecosystems.

Michalet (2006) also argued that the way plant interactions are measured in water-stressed conditions might explain the contrasting results in the literature. The observational method (comparison of the performance of the target with neighbours vs natural open areas) generally shows facilitation, whereas the removal method (comparison of the performance of the target with neighbours vs areas with neighbours removed) is more likely to show competition within the same system, as observed by Maestre et al. (2003) and Schöb et al. (2012), because of differences in soil conditions between natural open areas and vegetated patches (but see Sthultz et al. 2007).

Additionally, several studies have highlighted that in dry ecosystems the influence of disturbances (such as grazing or browsing) may be as important as that of drought stress for driving vegetation composition and diversity (Milchunas et al. 1988; Lavorel & Jauffret 2003; Noumi et al. 2010). Because in dry areas nurse plants may also

protect tree species against herbivores (Callaway 2007), the role of indirect facilitation as a tool for ecological restoration also deserves to be assessed in arid grazed areas. For example, Anthelme & Michalet (2009) found in the very dry conditions of the Ténéré Desert (Niger) that most of the beneficial effects of a nurse grass on the foundation tree *Acacia tortilis* subsp. *raddiana* were indirect through a mitigation of the impact of domestic grazers. In contrast, Riginos & Young (2007) found no indirect positive outcome for *Acacia* saplings in an East African savanna, and Aerts et al. (2007) showed that shrubs did not efficiently protect olive trees against browsing in a dry afro-montane forest. However, studies on indirect positive interactions remain scarce in dry ecosystems, likely because indirect facilitation was initially proposed to be an important process mainly in wet productive systems with a high level of herbivory (Bertness & Callaway 1994).

Most interaction studies have quantified the intensity of plant interactions but not their importance, although this latter index has been shown to be the most relevant for assessing the drivers of community composition and structure (Corcket et al. 2003; Brooker et al. 2005, 2013; Maa-louf et al. 2012). The importance of interactions has been defined as the change in performance of a target species due to neighbours as compared to the effect of other community drivers such as stress and disturbance (Brooker et al. 2005). However, most studies have focused on the importance of interactions as compared to the effect of stress alone. To our knowledge, there have been few previous attempts (Verwijmeren et al. 2013, 2014; Soliveres et al. 2014) to assess how grazing may alter the importance of interactions along an environmental stress gradient.

The main objective of this study was to experimentally assess the role of plant interactions for the ecological restoration of an arid grazed savanna in southern Tunisia. The only native tree species in these highly stressed conditions is *Acacia tortilis* subsp. *raddiana*. We manipulated plant interactions around planted seedlings of *Acacia* using both the removal and observational methods (*sensu* Maestre et al. 2005). Additionally, we used the two dominant neighbours with contrasting palatabilities as effect species: the grass *Cenchrus ciliaris* L. and the chenopod shrub *Hammada scoparia* (Pomel).

In order to quantify variation in the importance of interactions along a local stress gradient induced by topography, with and without grazing, the same design was applied in three different communities varying in stress levels and productivity, and we examined the interaction between stress and grazing using exclosures against large herbivores. We aim to answer the four following questions: (1) does the direction and importance of interactions vary with increasing stress; (2) does grazing affect the direction and importance of interactions; (3) does nurse identity

(grass vs chenopod shrub) affect the direction and importance of interactions; and (4) are results affected by the method used to quantify interactions (observational vs removal)?

Methods

Study site and communities

The experiment was conducted in the National Park of Bou-Hedma, central Tunisia (33°30' N, 9°38' E). The park, covering an area of approximately 5114 ha, was recognized as a UNESCO World Heritage Site in 1977. Following Emberger's classification (Emberger 1955), the climate is mediterranean arid inferior with temperate winters. The average annual rainfall is 151 ± 21 mm (1996–2008) but highly variable over the years, as in other arid mediterranean climates. Mean minimum temperature of the coldest month (Jan) is 3.9 °C and mean maximum temperature of the warmest month (Aug) is 36.2 °C.

According to Grouzis & Le Floch (2003), the dominant vegetation type in the park is a pseudo-savanna of *Acacia tortilis*, the only native forest tree of the northern edge of the Sahara Desert. Other dominant species are perennial grasses (*Cenchrus ciliaris* L., *Digitaria commutata* L.) and chenopod shrub species such as *Hammada scoparia* (Pomel) and *Hammada schmittiana* (Pomel). *Cenchrus* and *H. scoparia* were chosen as neighbouring species in our experiment because of both their status as dominant species and their contrasting palatabilities. *Cenchrus* is tolerant to grazing (Hodgkinson et al. 1989), whereas *H. scoparia* is an allelopathic species with very low palatability (Towhidi et al. 2011).

We selected three main communities (glacis, silty plain and sandy plain) occurring along a complex environmental stress gradient, driven by topography and soil depth (Noumi et al. 2010). The glacis, located at the bottom of a mountain range, is composed of Villafranchian calcareous crust and is covered with shallow loamy soils with a high stone content. Below the glacis on a very gentle slope, is the silty plain, with deeper and more fine-textured soils. The sandy plain is located at the bottom of this gentle slope, with deep sandy soils without stones. Biotic measurements of the three dominant species (height of *Acacia*, volume of *Hammada*, volume of *Cenchrus*) show that community biomass significantly decreases from the sandy plain to the glacis, with intermediate values for the silty plain (Appendix S1), highlighting that environmental stress increases from the sandy plain to the glacis with decreasing water availability in relation to soil depth, texture and stone content (Noumi et al. 2010).

Natural grazing by small herbivores (e.g. hares, *Lepus capensis*) and large herbivores such as Saharan antelopeans (*Addax nasomaculatus* and *Oryx leucoryx*), dorcas gazelle

(*Gazella dorcas*), mhor gazelle (*Gazella dama mhor*), Barbary sheep (*Ammotragus lervia*) and some ostriches (*Struthio camelus*) occurs inside the park throughout the year (Le Houérou 2005). The stocking density of large herbivores is ca. one animal per 40 ha inside the park. Other small mammals such as jerboas (*Jaculus jaculus*) can enter in the enclosures.

Experimental design

Our experiment was conducted from October 2006 to June 2008, which included a relatively wet period until June 2007 followed by a 1 yr-long very dry period (Appendix S2). We used a split-split-plot block design with four blocks and three treatments within blocks, community, grazing and patches. Each block represented a transect crossing the three communities (glacis, silty plain and sandy plain) and there was at least 250 m between each transect. In each block there were three main plots (one per community) always located in flat areas away from the shade of adult *Acacia* trees. Each main plot was subdivided into two equal subplots of 15×15 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 50×50 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 chenopod shrub *Hammada*, ten individuals of the grass *Cenchrus* and five naturally open areas. For half of the individuals of both the shrub and the grass, we removed the above-ground parts of the plants by cutting them at ground level. There was no re-growth of *Hammada* and only low re-growth of *Cenchrus* after rain events. Both were re-cut throughout the duration of the experiment.

Young *Acacia* individuals were used as target species. Seeds of *Acacia* were collected from adult trees growing inside the park. Seedlings were grown in a local nursery for 2 mo (from early Sept to late Oct 2006). Seeds were sown directly at the greenhouse and watered regularly before transplanting. A total of 600 seedlings of *Acacia* were transplanted in late October 2006 (5 replicates \times 5 patches \times 2 grazing conditions \times 3 communities \times 4 blocks).

Data collection

Survival of target individuals was recorded 8 and 19 mo after transplanting, in June 2007 after the first wet winter-spring period, and in June 2008 after the dry 1 yr-long period (Appendix S2). The experiment was stopped at that date, and *Acacia* seedlings were harvested because survival

was very low after this long dry period. Survival rate was calculated as a percentage of live individuals per treatment combination and per block.

The importance of biotic interactions for *Acacia* was calculated using the index of facilitation importance (C_{imp} ; Brooker et al. 2005; modified by Seifan et al. 2010):

$$C_{\text{imp}} = N_{\text{imp}} / (|N_{\text{imp}}| + |E_{\text{imp}}|) \quad (1)$$

where N_{imp} and E_{imp} are the neighbour and environmental contributions to target performance, respectively: $N_{\text{imp}} = P_{+\text{N}} - P_{-\text{N}}$ and $E_{\text{imp}} = P_{-\text{N}} - P_{\text{max} \pm \text{N}}$, where $P_{\text{max} \pm \text{N}}$ is the maximum value of target performance in all of the 24 subplots (4 blocks \times 3 communities \times 2 grazing conditions). This index scaled from -1 to 1 , with positive values indicating facilitation and negative values indicating competition. The importance index was only calculated on survival data.

Environmental measurements

In order to characterize the abiotic environment, we conducted soil water measurements and chemical analyses at different periods. All measurements were carried out only in the ungrazed subplots. Soil moisture (volumetric soil water content) was measured at a depth of 10 cm with a TDR probe (ThetaProbe ML2x; Delta T, Cambridge, UK) in the five patches of the three communities. Measurements were conducted three times in April 2007, three times after a 30-mm rain event (1, 7 and 15 d after the rain), with four replicates per treatment combination.

Five soil samples were collected in April 2007 at a depth of 5–10 cm in the three natural ungrazed patches (Open, *Hammada* and *Cenchrus*) of the three communities for granulometry and total C, N and P analyses (see Noumi et al. 2010).

Data analysis

Transplant survival (%) was analysed at the two recording dates, using two separate similar split-split-plot ANOVA models, with community as main plot effect, grazing as subplot effect and patches as sub-subplot effect. C_{imp} for survival was also analysed, at the two recording dates, using two separate similar split-split-plot ANOVA models with community as main plot effect, grazing as subplot effect and neighbour type (*Hammada* vs *Cenchrus*) and method (observational vs removal) as sub-subplot effects. Thus, in this second set of ANOVAs the patches treatment was replaced by the neighbour type and method treatments, both nested in the grazing treatment. Soil chemical characters (OM, N, C/N and P), soil particle sizes (<20 , 20–200, 200–2000 μm) and soil water content were analysed using a split-plot ANOVA model with

community as main plot effect and patches as subplot effect. Dependent variables were checked for normality and log- or arcsine root-transformed before ANOVAs, when necessary. *Post-hoc* Tukey tests were conducted after ANOVAs when necessary (for the patches and community treatments) and sample *t*-tests were conducted on C_{imp} values in order to detect significant differences from zero values. Computed *P*-values were corrected using the Holm method. All ANOVAs were carried out with JMP 8.0.2 (SAS Institute, Cary, NC, US).

Results

Survival of *Acacia*

In June 2007, after a relatively wet spring, there was a highly significant community effect with, overall, higher survival in the sandy plain, lower survival in the silty plain and intermediate survival in the glacia (Table 1, Fig. 1 and result of Tukey HSD: sandy plain a, glacia b, silty plain c). There was also a highly significant grazing effect with lower overall survival in the presence of herbivores than in ungrazed conditions (Table 1, Fig. 1). The patches effect was also highly significant (Table 1), and results of the Tukey test show that survival was highest in the open patches (a), lowest in the *Cenchrus* (c) and *Hammada* (c) patches and intermediate in both the removed *Cenchrus* (b) and removed *Hammada* (ab) patches, highlighting the general occurrence of competition for *Acacia* (Fig. 1). In addition, there was a weakly significant grazing \times patches interaction (Table 1). Without grazing, survival was higher in the three patches without neighbours (open, *Hammada* removed, *Cenchrus* removed) than below the canopy of both *Hammada* and *Cenchrus*, whereas with grazing, survival was higher in open areas than in the other four patches (*Cenchrus*, *Hammada*, *Cenchrus* removed *Hammada*

Table 1. Results of the split-split-plot ANOVA models for the effects of community, grazing, patches and their interactions on the survival (%) of *Acacia tortilis* target at the two recording dates (June 2007 and June 2008). Significant ($P < 0.05$) effects are indicated in bold.

Source of variation	df	June 2007		June 2008	
		F	P	F	P
Community	2	34.40	<0.001	23.81	<0.01
Error (Main Plot)	6				
Grazing	1	24.92	<0.001	3.18	0.11
Community \times Grazing	2	0.54	0.60	1.85	0.21
Error (Subplot)	9				
Patches	4	26.98	<0.001	2.63	<0.05
Grazing \times Patches	4	3.09	<0.05	1.35	0.26
Community \times Patches	8	2.25	<0.05	1.67	0.12
Community \times Grazing \times Patches	8	1.66	0.12	0.66	0.72
Error (Sub-Subplot)	72				

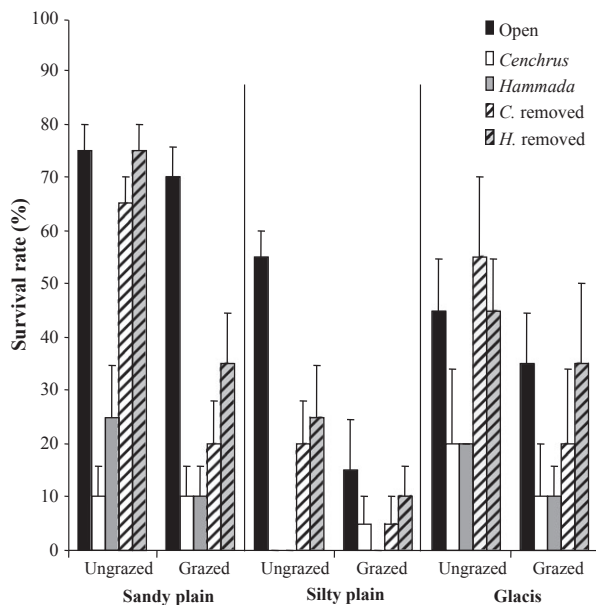


Fig. 1. Survival rate (means \pm SE) of the target species (*Acacia tortilis*) in the five patches (open, *Cenchrus*, *Hammada*, *Cenchrus* removed, *Hammada* removed) of the ungrazed and grazed plots of the three communities (sandy plain, silty plain and glacis) at the first recording date (June 2007).

removed; Fig. 1 and results of Tukey test not shown). Consequently, with grazing, whatever the community, the intensity of competition was much weaker with the removal method as compared to the observational method. Finally, there was a weakly significant community \times patch interaction because the patch effect was significant in both the sandy and silty plains but not in the glacis (Table 1, Fig. 1; results of Tukey test not shown). This latter result showed that the intensity of competition vanished in the glacis.

In June 2008, after a 1 yr-long dry period, survival strongly decreased in the three communities, but was higher on the sandy plain and the glacis than on the silty plain (Table 1, Appendix S3 and results of Tukey test: sandy plain a, glacis a, silty plain b).

The importance of interactions

The C_{imp} values were always negative, which again highlights that *Acacia* was always negatively affected by neighbours in our experiment (Fig. 2). In June 2007 there was a significant community effect because competition was overall almost twice as important in the sandy plain as in the two other communities (Table 2, Fig. 2). Grazing overall reduces the importance of competition (significant grazing effect; Table 2, Fig. 2). Moreover, there was a highly significant method effect because the importance of com-

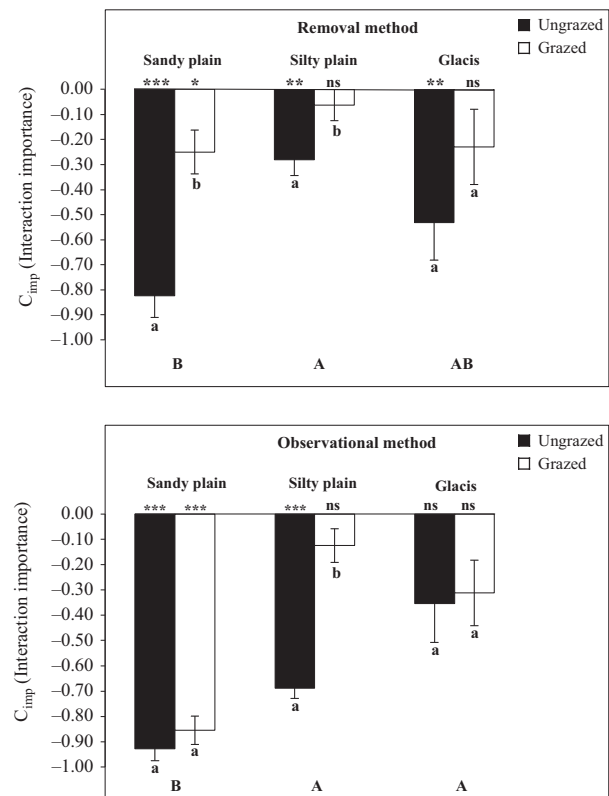


Fig. 2. Importance of competition (C_{imp}) for the target species (*Acacia tortilis*) in the two pooled nurses (*Cenchrus* and *Hammada*), measured with the removal and observational method (upper and lower panel, respectively) in the ungrazed and grazed plots of the three communities (sandy plain, silty plain and glacis) at the first recording date (June 2007). Capitals letters represent results of Tukey HSD tests for the community treatment ($P < 0.05$) and lowercase letters between bars are results of the grazing treatment within communities. Stars above bars represent results of the sample t -tests on C_{imp} values conducted to detect significant differences from zero ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$, ns: not significant). Computed P -values were corrected using the Holm method.

petition was overall higher with the observational method than with the removal method (Table 2, Fig. 2). However, there was a significant community \times method interaction, because this effect was only observed in the sandy plain and the silty plain, but not in the glacis. In the two former communities competition was less than half as important with the removal method as compared to the observational one. In contrast, competition had the same importance with both methods in the glacis (Table 2, Fig. 2). Finally, there was a significant community \times grazing \times method interaction, because the decrease in importance of competition with grazing was mostly observed in the sandy plain with the removal method, but in the silty plain with the observational method (Table 2, Fig. 2).

Table 2. Results of the split-split-plot ANOVA models for the effects of community, grazing, neighbour type, method and their interactions on the importance of competition (C_{imp}) at the two recording dates (June 2007 and June 2008). Significant ($P < 0.05$) effects are indicated in bold.

Source	df	June 2007		June 2008	
		F	P	F	P
Community	2	12.23	<0.01	5.94	<0.05
Error (Main Plot)	6				
Grazing	1	14.48	<0.01	2.57	0.14
Community \times Grazing	2	0.69	0.52	0.64	0.55
Error (Subplot)	9				
Neighbour Type	1	2.07	0.15	1.36	0.25
Method	1	12.73	<0.001	0.08	0.77
Community \times Neighbour Type	2	0.07	0.93	0.59	0.55
Grazing \times Neighbour Type	1	1.36	0.25	0.08	0.77
Community \times Method	2	5.52	<0.01	3.15	0.05
Grazing \times Method	1	1.88	0.17	3.07	0.08
Neighbour Type \times Method	1	0.16	0.68	0.00	1.00
Community \times Grazing \times Neighbour Type	2	0.16	0.85	0.08	0.92
Community \times Grazing \times Method	2	6.15	<0.01	1.79	0.18
Community \times Neighbour Type \times Method	2	0.46	0.63	0.25	0.77
Grazing \times Neighbour Type \times Method	1	1.20	0.28	0.08	0.77
Community \times Grazing \times Neighbour Type \times Method	2	0.81	0.45	0.08	0.92
Error (Sub-Subplot)	54				

At the end of the experiment, in June 2008, the importance of competition strongly decreased in all treatments (data not shown). There was only a weak significant community effect because the importance of competition was still important only in the sandy plain, although two times less important there than earlier during the experiment (Table 2).

Environmental measurements

One day after the rainfall event, in April 2007, the soil water content was lower in the glacia than in the two other communities (community effect; $P < 0.001$), but there were no significant differences among patches (data not shown). Seven days after the rainfall event, this community effect was less significant ($P < 0.05$), but there was a significant patches effect, with higher soil water content values in the open than in the four other patch conditions (*Cenchrus*, *Hammada*, *Cenchrus* removed and *Hammada* removed) of the three communities (data not shown). Finally, 15 d after the rainfall event, differences among communities were no longer significant ($P = 0.34$), whereas differences among patches increased. Whatever the communities, the soils of the open patches were still the wettest, but the soils of the two with-neighbours plots became the driest (and in particular *Cenchrus*), with intermediate values for soils of the two removed patches (see Tukey tests in Appendix S4).

There were strong differences in soil characteristics among communities (Appendix S5). Soil mineral particle

size was much smaller in the silty plain than in the other two communities. However, the dominance of coarse mineral particles in the glacia was likely due to the abundance of calcareous sands, whereas in the sandy plain it was mostly siliceous sands from alluvial deposits (Z. Noumi, pers. obs.). As a consequence, organic matter content (and total N and P as well) was much higher in the soils of the silty plain than in those of the other two communities. Although soil particle size was the same for the sandy plain and the glacia, total organic matter was lowest in the sandy plain, likely because organic matter decomposition was the lowest in the glacia (highest C/N ratios; Appendix S5) due to high drought stress.

Differences in soil characteristics among patches were weaker than those among communities. The only obvious trend was a lower organic matter and total N content in the open patches than in the *Cenchrus* and *Hammada* patches (App. S5), although differences were not significant in any community.

Discussion

Our main objective was to assess the direction and importance of plant interactions during ecological restoration of an arid grazed savanna, and in particular to analyse their variation with stress, grazing, the type of nurse and the method used to quantify interactions. The most important result was observed for the direction of interactions, which was either negative or null but never positive in all experimental conditions. However, the importance of competi-

tion was strongly affected by our treatments. Competition was the highest in the wettest topographic position (sandy plain) and disappeared over time in all communities with increasing drought stress. Competition was also lower in the presence of herbivores than without grazing and when measured with the removal method than with the observational method. Thus, competition was only important in the most benign environmental conditions, i.e. at the beginning and wettest part of our experiment and in the ungrazed wettest community. Finally, the identity of the nurse species did not affect the importance of interactions.

The direction of interactions

Our study was conducted in a highly water-stressed system in which competition is the only observed plant interaction. Whatever the community, the nurse species, the grazing level and the method used, we never found any positive interaction in our arid system for the target species *Acacia*. This result does not support the stress-gradient hypothesis (SGH), which predicts that facilitation should be more frequent in conditions of high stress and disturbance and competition in the converse environmental conditions (Bertness & Callaway 1994; He et al. 2013; Muhamed et al. 2013). In contrast, it is consistent with the results of a number of experiments that found an increase in competition in very dry conditions (Davis et al. 1998; Saccone et al. 2009; Forey et al. 2010).

Pennings et al. (2003) also found dominant competitive interactions in the most stressful salt marshes of North America (south of their range), whereas previous studies conducted in less stressed climatic conditions (further north) showed an overall increase in facilitation with increasing salt stress. These authors concluded that this inconsistency was due to the functional strategies of the target species used in the experiments. They argued that northern marsh floras are dominated by salt-sensitive species that are likely to be facilitated by neighbours, whereas southern marsh floras are dominated by salt-tolerant species that are unlikely to benefit from neighbour amelioration. Liancourt et al. (2005) have also shown, in European calcareous grasslands, that drought-intolerant target species are better candidates for facilitation than drought-tolerant ones, because the former are more sensitive to the positive effects of shade (for water availability, air humidity, temperature, photoinhibition), whereas the latter are more sensitive to the negative effect of shade for the light resource (see also Gómez-Aparicio et al. 2004). Although our design, which only included one target species, did not allow us to really test this hypothesis in our system, *Acacia*, the only tree species growing in these arid conditions, is known to be highly drought-tolerant (Munzbergova & Ward 2002; Abdallah et al. 2008; Noumi et al. 2010) but

not shade-tolerant (Osunkoya et al. 2005). Thus, in opposition to the SGH but following the arguments of Pennings et al. (2003) and the model of Holmgren & Scheffer (2010), the most arid conditions are certainly not the most favourable for using facilitation as a tool in ecological restoration, because the only available target tree species are too stress-tolerant to benefit from neighbours.

Another likely explanation for the absence of facilitation found in our system is the functional strategies of the two nurse species, the grass *Cenchrus* and the chenopod shrub *Hammada*. The strong competitive effect of *Poaceae* and *Chenopodiaceae* is well documented (Davis et al. 1998; Forsyth et al. 2001), and our soil moisture measurements showed that water was less available below the canopy of both nurse species than in the open and the grass- and chenopod-removed patches. Furthermore, our soil analyses showed that both nurse species had very weak or no positive effects on soil chemical and physical features. Further experiments should assess if facilitation can be observed in our system using leguminous shrubs, known to be much better nurses than grasses or chenopod shrubs (Pugnaire et al. 1996, 2004; Cuesta et al. 2010).

The importance of interactions and their variation along treatments

Competition was the strongest in our study when stress and disturbance were lowest and strongly decreased with the increase of either stress or/and disturbance. This decrease in the importance of competition along our spatial stress gradient is in agreement with Grime's model (1974) and consistent with the results of previous studies using an importance index (Corcket et al. 2003; Brooker et al. 2005). Furthermore, competition intensity was also similarly affected by our treatments, as shown by the occurrence of significant interactions between the patches and either community or grazing treatments in the ANOVA on survival. Our results are consistent with those of Maalouf et al. (2012), who found similar patterns of variation in the intensity and importance of interactions along stress and disturbance gradients in dry calcareous grasslands. Maalouf et al. (2012) concluded that both metrics of interactions are more likely to be positively related in stressful environments than in benign conditions (see also Pugnaire & Luque 2001). However, the lowest *Acacia* survival was not observed in the driest community (glacis) but in the silty plain, which suggests that another stress factor might exist in the silty plain. The silty plain is characterized by the presence of a glazed soil crust, likely limiting soil porosity and water infiltration rate (Hoogmoed & Strosnijder 1984), which could affect seedling survival of *A. tortilis* (Floret & Pontanier 1982). This glazed crust is absent from the glacis because of the presence of numer-

ous calcareous gravels, and from the sandy plain because of its sandy soil structure.

The importance of competition strongly decreased through time to reach very low levels at the end of the experiment. This decrease in the importance of competition may also be due to the increasing importance of drought stress, as suggested by the very low amount of rainfall received during the summer period and even during the second winter–spring period (Appendix S2), as compared to the relatively wet first winter–spring period. Other studies have shown similar decreases in the importance or intensity of competition along temporal stress gradients (Greenlee & Callaway 1996; Forey et al. 2010). However, because we did not use different cohorts of *Acacia* seedlings to test for the effect of different climatic conditions, our design does not allow us to separate the effect of time from the effect of climatic conditions to really obtain conclusions on that point.

Although consistent with several theoretical models (e.g. Grime 1974; Tilman 1982; Taylor et al. 1990) and some competition intensity experiments (Sammul et al. 2006), our study is the first to show a decrease in the importance of competition (as measured with the importance index) due to grazing disturbance. However, inconsistent with Bertness & Callaway's (1994) model and with a number of other studies (see e.g. Anthelme & Michalet 2009), we did not observe any indirect facilitation in the presence of herbivores. This suggests that the two nurse species had no protective effects or that these effects were too low to outweigh the negative effects of competition for light and water. Indeed, none of these neighbouring species are spiny. Additionally, the grass *Cenchrus ciliaris* is known to be highly grazed (Hodgkinson et al. 1989), and thus only *Hammada* was expected to protect *Acacia* against herbivores because of its low palatability (Towhidi et al. 2011). Surprisingly, in the similarly very dry Aïr-Tenere Desert (Niger), Anthelme & Michalet (2009) found that the bunch grass *Panicum turgidum* indirectly facilitates *A. tortilis* (protection against herbivores). However, the circum-saharian species *Acacia* is known to form genetically different populations around the Sahara, which may influence interactions with herbivores and neighbouring plants (Whitham et al. 2003; Michalet et al. 2011).

The importance of competition was also slightly but significantly lower when measured with the removal method compared with the observational one. This result is inconsistent with the model of Michalet (2006), who argued that competition should be lower with the observational method than with the removal one because of long-term positive soil effects included in the former but not in the latter. These long-term positive soil effects of nurses have been documented in many water-stressed ecosystems

commonly subjected to soil erosion on slopes (Maestre et al. 2009a). In contrast, in our system with a very gentle slope, we showed, conversely, that the soils of the *Cenchrus*- and *Hammada*-removed patches were drier than the soils of the open patches. The lower soil moisture of the removed patches as compared to the open patches may be due to higher water infiltration into deep soil layers in the former than in the latter because of root colonization and rodent burrowing (Z. Noumi pers. obs.). We also cannot exclude that the lower survival of *Acacia* found in the two removed plots than in the open might be related to a legacy effect on soil fertility of our removal treatment; decomposition of the remaining dead roots might have modified seedling root–shoot allocation, increasing their drought and grazing sensitivity.

With the observational method, we found an interaction between the drought and grazing treatment, where the importance of competition strongly decreased from the sandy plain to the silty plain only with grazing. This result is consistent with the modelling study of Kefi et al. (2013). This interaction was not found with the removal method because the importance of competition was already very low in both the without grazing treatment in the silty plain and with grazing only in the sandy plain.

Facilitation as a tool in ecological restoration of arid grazed ecosystems?

The main objective of this study was to assess the role of plant interactions in arid grazed ecosystems and, in particular, the potential of facilitation as a restoration tool in this system. In contrast to results from restoration studies conducted in semi-arid ecosystems, the direction of interactions was always negative for the target species *Acacia*. This result was very likely due to the high drought tolerance of the target species and the high competitive effects of both the grass and the chenopod shrub used as a nurse species. In opposition to the predictions made with the SGH, this arid ecosystem was not a suitable system for using facilitation as a restoration tool, since the only available tree species is poorly adapted to grow in proximity to neighbouring plants. We also showed that plant interactions were important only in the least stressed and grazed conditions, which are very rare in arid ecosystems where water availability is generally very low, both spatially and temporally, and grazing disturbance is frequent. In conclusion, our results question the suitability of facilitation as a relevant tool for ecological restoration in arid grazed ecosystems, in contrast to results from semi-arid areas. Thus, our study stresses that ecological restoration should not be an automatic process but must be tailored to the species and environment in question.

Acknowledgements

We are grateful to Lazher Hemdi, manager of the National Park of Bou-Hedma for his very important support throughout this study. We thank Sabrina Sérac for her review of English on all versions of the manuscript, Robin W. Brooker for helpful discussions during the reviewing process and Estelle Forey for help in the field during transplantations.

References

- Abdallah, F., Nouni, Z., Touzard, B., Ouled Belgacem, A., Nefati, M. & Chaieb, M. 2008. The influence of *Acacia tortilis* (Forssk.) subsp. *raddiana* (Savi) and livestock grazing on grass species composition, yield and soil nutrients in arid environments of South Tunisia. *Flora* 203: 116–125.
- Aerts, R., Negussie, A., Maes, W., November, E., Hermy, M. & Muys, B. 2007. Restoration of dry afro-montane forest using pioneer shrubs as nurse-plants for *Olea europaea* ssp. *cuspidata*. *Restoration Ecology* 15: 129–138.
- Anthelme, F. & Michalet, R. 2009. Grass-to-tree facilitation in an arid grazed environment (Aïr Mountains, Sahara). *Basic and Applied Ecology* 10: 437–446.
- Badano, E.I., Perez, D. & Vergara, C.H. 2009. Love of nurse plants is not enough for restoring oak forests in a seasonally dry tropical environment. *Restoration Ecology* 17: 571–576.
- Bertness, M.D. & Callaway, R.M. 1994. Positive associations in communities. *Trends in Ecology & Evolution* 9: 191–193.
- Brooker, R.W., Kikvidze, Z., Pugnaire, F.I., Callaway, R.M., Choler, P., Lortie, C.J. & Michalet, R. 2005. The importance of importance. *Oikos* 109: 63–70.
- Brooker, R.W., Kikvidze, Z., Kunstler, G., Liancourt, P. & Seifan, M. 2013. The concept and measurement of importance: a comment on Rees et al. 2012. *Journal of Ecology* 101: 1369–1378.
- Callaway, R.M. 1995. Positive interactions among plants. *Botanical Review* 61: 306–349.
- Callaway, R.M. 2007. *Positive interactions and interdependence in plant communities*. Springer, Dordrecht, NL.
- Corcket, E., Liancourt, P., Callaway, R.M. & Michalet, R. 2003. The relative importance of competition for two dominant grass species as affected by environmental manipulations in the field. *Ecoscience* 10: 186–194.
- Cuesta, B., Salvador, P.V., Puértolas, J., Rey Benayas, J.M. & Michalet, R. 2010. Facilitation of *Quercus ilex* in Mediterranean shrubland is explained by both direct and indirect interactions mediated by herbs. *Journal of Ecology* 98: 687–696.
- Davis, M.A., Wrage, K.J. & Reich, P.B. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *Journal of Ecology* 86: 652–661.
- Emberger, L. 1955. Une classification biogéographique des climats. Montpellier, Faculté des Sciences, Service botanique. *Revue des travaux de Laboratoire de Botanique et de Zoologie* 7: 3–43.
- Floret, C. & Pontanier, R. 1982. L'aridité en Tunisie présaharienne. Climat, sol, végétation et aménagement, Paris. *Travaux et documents de l'ORSTOM* no150, p. 544.
- Forey, E., Touzard, B. & Michalet, R. 2010. Does disturbance drive the collapse of biotic interactions at the severe end of a diversity–biomass gradient? *Plant Ecology* 206: 287–295.
- Forseth, I.N., Wait, D.A. & Casper, B.B. 2001. Shading by shrubs in a desert system reduces the physiological and demographic performance of an associated herbaceous perennial. *Journal of Ecology* 89: 670–680.
- Gómez-Aparicio, L. 2009. The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *Journal of Ecology* 97: 1202–1214.
- Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J. & Baraza, E. 2004. Applying plant positive interactions to reforestation of Mediterranean mountains: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* 14: 1128–1138.
- Greenlee, J.T. & Callaway, R.M. 1996. Abiotic stress and the importance of interference and facilitation in montane bunchgrass communities in western Montana. *The American Naturalist* 148: 386–396.
- Greuter, W., Burdet, H.M. & Long, G. 1984. *Med-checklist: a critical inventory of vascular plants of the circum-Mediterranean countries*. Conservatoire et Jardin botanique, Ville de Genève, Geneva, CH.
- Grime, J.P. 1974. Vegetation classification by reference to strategies. *Nature* 250: 26–31.
- Grouzis, M. & Le Floch, E. 2003. *Un arbre au désert - Acacia raddiana*. Editions IRD, Montpellier, FR.
- He, Q., Bertness, M.D. & Altieri, A.H. 2013. Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters* 16: 695–706.
- Hodgkinson, K.C., Ludlow, M.M., Mott, J.J. & Baruch, Z. 1989. Comparative responses of the savanna grasses *Cenchrus ciliaris* and *Themeda triandra* to defoliation. *Oecologia* 79: 45–52.
- Holmgren, M. & Scheffer, M. 2010. Strong facilitation in mild environments: the stress gradient hypothesis revisited. *Journal of Ecology* 98: 1269–1275.
- Hoogmoed, W.B. & Stroosnijder, L. 1984. Crust formation on sandy soils in the Sahel I. Rainfall and infiltration. *Soil and Tillage Research* 4: 5–23.
- Jankju, M. 2013. Role of nurse shrubs in restoration of an arid rangeland: effects of microclimate on grass establishment. *Journal of Arid Environments* 89: 103–109.
- Kefi, S., Rietkerk, M., Alados, C.L., Pueyo, Y., Papanastasis, V.P., ElAich, A. & de Ruiter, P.C. 2013. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* 449: 213–215.
- Lavorel, S. & Jauffret, S. 2003. Are plant functional types relevant to describe degradation in arid, southern Tunisian steppes? *Journal of Vegetation Science* 14: 399–408.

- Le Houérou, H.N. 2005. Problèmes écologiques de développement de l'élevage en Région sèche. *Science et changement planétaires. Sécheresse* 16: 89–96.
- Liancourt, P., Callaway, R.M. & Michalet, R. 2005. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology* 86: 1611–1618.
- Maalouf, J.P., Le Bagousse-Pinguet, Y., Marchand, L., Touzard, B. & Michalet, R. 2012. The interplay of stress and mowing disturbance for the intensity and importance of plant interactions in dry calcareous grasslands. *Annals of Botany* 110: 821–828.
- Maestre, F.T., Bautista, S. & Cortina, J. 2003. Positive, negative, and net effects in grass–shrub interactions in Mediterranean semiarid grasslands. *Ecology* 84: 3186–3187.
- Maestre, F.T., Valladares, F. & Reynolds, J.F. 2005. Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology* 93: 748–757.
- Maestre, F.T., Bowker, M.A., Puche, M.D., Hinojosa, M.B., Martinez, I., García-Palacios, P., Castillo, A.P., Soliveres, S., Luzuriaga, A.L. (...) & Escudero, A. 2009a. Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecology Letters* 12: 930–941.
- Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. 2009b. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97: 199–205.
- Michalet, R. 2006. Is facilitation in arid environments the result of direct or complex interactions? *New Phytologist* 169: 3–6.
- Michalet, R. 2007. Highlighting the multiple drivers of change in interactions along stress gradients? *New Phytologist* 173: 3–6.
- Michalet, R., Brooker, R.W., Cavieres, L.A., Kikvidze, Z., Lortie, C.J., Pugnaire, F.I., Valiente-Banuet, A. & Callaway, R.M. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters* 9: 767–773.
- Michalet, R., Xiao, S., Touzard, B., Smith, D.S., Cavieres, L.A., Callaway, R.M. & Whitham, T.G. 2011. Phenotypic variation in nurse traits and community feedbacks define an alpine community. *Ecology Letters* 14: 433–443.
- Michalet, R., Le Bagousse-Pinguet, Y., Maalouf, J.P. & Lortie, C.J. 2014. Two alternatives to the stress-gradient hypothesis at the edge of life: the collapse of facilitation and the switch from facilitation to competition. *Journal of Vegetation Science* 25: 609–613.
- Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. 1988. A generalized-model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist* 132: 87–106.
- Muhammed, H., Le Bagousse-Pinguet, Y., Touzard, B. & Michalet, R. 2013. The role of biotic interactions for the early establishment of oak seedlings in coastal dune forest communities? *Forest Ecology and Management* 297: 67–74.
- Munzbergova, Z. & Ward, D. 2002. *Acacia* trees as keystone species in Negev desert ecosystems. *Journal of Vegetation Science* 13: 227–236.
- Noumi, Z., Touzard, B., Michalet, R. & Chaieb, M. 2010. The effects of browsing on the structure of *Acacia tortilis* (Forssk) Hayne ssp. *raddiana* (Savi) Brenan along a gradient of water availability in arid zones of Tunisia. *Journal of Arid Environments* 74: 625–631.
- Osunkoya, O.O., Othaman, F.E. & Kahar, R.S. 2005. Growth and competition between seedlings of an invasive plantation tree, *Acacia mangium* and those of a native Borneo heathforest species, *Melastoma beccarianum*. *Ecological Research* 20: 205–214.
- Pennings, S.C., Seling, E.R., Houser, L.T. & Bertness, M.D. 2003. Geographic variation in positive and negative interactions among salt marsh plants. *Ecology* 84: 1527–1538.
- Pugnaire, F.I. & Luque, M.T. 2001. Changes in plant interactions along a gradient of environmental stress. *Oikos* 93: 42–49.
- Pugnaire, F.I., Haase, P. & Pugdefábregas, J. 1996. Facilitation between higher plant species in a semiarid environment. *Ecology* 77: 1420–1426.
- Pugnaire, F.I., Armas, C. & Valladares, F. 2004. Soil a mediator in plant–plant interactions in a semi-arid community. *Journal of Vegetation Science* 15: 85–92.
- Riginos, C. & Young, T.P. 2007. Positive and negative effects of grass, cattle, and wild herbivores on *Acacia* saplings in an East African savanna. *Oecologia* 153: 985–995.
- Saccone, P., Delzon, S., Pages, J.P., Brun, J.J. & Michalet, R. 2009. The role of biotic interactions in altering tree seedling responses to an extreme climatic event. *Journal of Vegetation Science* 20: 403–414.
- Sammul, M., Oksanen, L. & Magi, M. 2006. Regional effects on competition–productivity relationship: a set of field experiments in two distant regions. *Oikos* 112: 138–148.
- Schöb, C., Kammer, P.M. & Kikvidze, Z. 2012. Combining observational and experimental methods in plant–plant interaction research. *Plant Ecology & Diversity* 5: 27–36.
- Seifan, M., Seifan, T., Ariza, C. & Tilbörger, K. 2010. Facilitating an importance index. *Journal of Ecology* 58: 356–361.
- Soliveres, S., Smit, C. & Maestre, F.T. 2014. Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities. *Biological Reviews* 90: 297–313.
- Stultz, C.M., Gehring, C.A. & Whitham, T.G. 2007. Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semi-arid woodland. *New Phytologist* 173: 135–145.
- Taylor, D.R., Aarssen, L.W. & Loehle, C. 1990. On the relationship between r/k selection and environmental carrying capacity: a new habitat templet for plant life-history strategies. *Oikos* 58: 239–250.
- Tilbörger, K. & Kadmon, R. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* 81: 1544–1553.

- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ, US.
- Towhidi, A., Saberifar, T. & Dirandeh, E. 2011. Nutritive value of some herbage for dromedary camels in the central arid zone of Iran. *Tropical Animal Health and Production* 43: 617–622.
- Verwijmeren, M., Rietkerk, M., Wassen, M.J. & Smit, C. 2013. Interspecific facilitation and critical transitions in arid ecosystems. *Oikos* 122: 341–347.
- Verwijmeren, M., Rietkerk, M., Bautista, S., Mayor, A., Wassen, M.J. & Smit, C. 2014. Drought and grazing combined: contrasting shifts in plant interactions at species pair and community level. *Journal of Arid Environments* 111: 53–60.
- Whitham, T.G., Young, W.P., Martinsen, G.D., Gehring, C.A., Schweitzer, J.A., Shuster, S.M., Wimp, G.M., Fischer, D.G., Bailey, J.K.(...) & Kuske, C.R. 2003. Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology* 84: 559–573.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Size of the three dominant species (height of *Acacia tortilis*, volume of *Hammada scoparia* and volume of *Cenchrus ciliaris*) in the three communities.

Appendix S2. Mean monthly rainfall recorded at the Bou-Hedma National Park climate station during the course of the experiment.

Appendix S3. Survival rate of the target species (*Acacia tortilis*) in the five patches (open, *Cenchrus*, *Hammada*, *Cenchrus* removed, *Hammada* removed) of the ungrazed and grazed plots of the three communities at the second recording date (June 2008).

Appendix S4. Soil water content in the five patches (open, *Cenchrus*, *Hammada*, *Cenchrus* removed and *Hammada* removed) of the three communities.

Appendix S5. Soil parameters of the three natural patches (open, *Cenchrus*, *Hammada*) in the three communities.