



# Interactions of *Acacia raddiana* with herbaceous vegetation change with intensity of abiotic stress

Fathia Abdallah<sup>a</sup>, Mohamed Chaieb<sup>b,\*</sup>

<sup>a</sup> Université de Sfax, Faculté des Sciences, Laboratoire de Biologie et d'Ecophysiologie des végétaux en milieu aride, Tunisia

<sup>b</sup> Université de Sfax, Faculté des Sciences, Laboratoire de Biologie et d'Ecophysiologie des végétaux en milieu aride 99/U.R/09-12, Département des Sciences de la Vie, Route de Sokra, Km 3.5, 3000 Gouvernorat de Sfax, Sfax, Tunisia

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## ABSTRACT

Theoretical models predict that the relative importance of facilitation and competition may vary inversely across gradients of abiotic stress. However, these predictions have not been thoroughly tested in the field, especially in arid and semi-arid environments. In this study, we evaluated how the net effect of *Acacia tortilis* subsp. *raddiana* (syn. *A. raddiana*) trees on the herbaceous species varies across a gradient of water stress in arid Tunisian ecosystems. Our results show that the influence of trees on the herbaceous stratum is beneficial. An *Acacia* tree improves the richness of herbaceous species around it by two to three times. The positive effect of *Acacia raddiana* on species composition is characterised in particular by a better development of some species of high pastoral value such as *Cenchrus ciliaris*, *Cynodon dactylon*, *Eragrostis papposa*, *Sisymbrium irio* and *Chenopodium album*. We fitted the relationship between seasonal rainfall and the relative neighbour effect index, which varied across this gradient, to a linear model. Our results show that herbaceous plant cover, plant biomass, plant density and diversity are higher under a tree canopy and this positive interaction still increase with higher abiotic stress conditions.

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## Introduction

Positive interactions between plant species are widespread in natural communities and have been acknowledged as a major driver of plant community dynamics and ecosystem processes (Bruno et al., 2003). Field studies have proven that facilitation and competition act simultaneously (Holzapfel and Mahall, 1999; Maestre et al., 2003), and theoretical models predict that their relative importance may vary across gradients of abiotic stress (Bertness and Callaway, 1994; Brooker and Callaghan, 1998). Substantial efforts to document this have been made in recent years by studies conducted in salt marshes (Bertness and Ewanchuk, 2002), alpine areas (Callaway et al., 2002), temperate grasslands (Greenlee and Callaway, 1996) and arid environments (Maestre et al., 2003). However, most of these studies were executed for only a relatively short period of time, and thus may not have been able to capture a wide range of abiotic conditions. Notably, some of them do not always support the theory that the magnitude of competition and facilitation varies inversely across gradients of abiotic stress (Penning et al., 2003).

Facilitative and competitive interactions are thought to be of great importance in arid and semi-arid areas. However, only a few studies have evaluated how changes in abiotic conditions modify the relative importance of facilitation and competition in these environments (Maestre et al., 2003; Maestre and Cortina, 2004; Pugnaire and Luque, 2001; Tielbörger and Kadmon, 2000). In this study, we evaluated how the net effect of *Acacia tortilis* (Forssk.) Hayne subsp. *raddiana* (Savi) Brenan (hereafter treated as species, *A. raddiana* Savi) on the herbaceous stratum varied across a gradient of abiotic stress in arid Mediterranean areas. Our working hypothesis is that the importance of facilitation relative to competition increases as abiotic stress increases.

## Materials and methods

### Study area

Our study was conducted at Bou Hedma National Park (South of Tunisia). This National Park (34°39'N and 9°48'E), is characterised by an arid Mediterranean bioclimate with a moderate winter (Le Houérou, 1959). The mean annual rainfall is about 180 mm. The annual mean temperature is about 17.2 °C while the minimal and maximal monthly temperature means were respectively 3.8 °C (December and January) and 36.2 °C (July and August).

The soil of the study area consists of quaternary sandy deposits. Vegetation cover is a pseudo-savanna with *A. raddiana* constitut-

\* Corresponding author. Tel.: +216 74 274 923; fax: +216 74 274 437.

E-mail address: [mohamed.chaieb@gnet.tn](mailto:mohamed.chaieb@gnet.tn) (M. Chaieb).

**Table 1**

Seasonal rainfall (mm) recorded at Bou Hedma National Park during the study years (2003/2004, 2004/2005 and 2005/2006).

Year	Season												Total (mm)
	Autumn			Winter			Spring			Summer			
	September	October	November	December	January	February	March	April	May	June	July	August	
2003/2004	63.5	22.4	20.5	57.8	3	0	36.5	7	6.7	1	0	0	218.4
2004/2005	8	0	21.5	30.1	0	4.5	5.3	0	0	0	0	0	69.44
2005/2006	61.5	2	6	103	70	48.9	0	9.5	0	0	4	1	305.9

ing the tree stratum. The *Acacia* trees are associated with perennial grass species (*Cenchrus ciliaris*, *Digitaria commutata*, *Stipagrostis ciliata*) and two species of the genus *Hammada* (*Hammada schmittiana*, *Hammada scoparia*) which belongs to Chenopodiaceae family. Appearance of annual plants is reported to be very responsive in the short-term to between year variability in annual precipitation.

#### Climatic conditions during the investigation periods

Measurements were done during three growing seasons 2003–2004, 2004–2005 and 2005–2006. The annual precipitation during the first and the third year was high reaching 218.4 mm and 305.9 mm, respectively. The precipitation of the second year was very low; it did not exceed 69.4 mm (Table 1). We used the amount of rainfall during the course of the study period as a proxy for the intensity of abiotic stress. There is a strong relationship between this variable and soil–water availability in arid and semi-arid areas, which in turn drives the performance of both *A. raddiana* and herbaceous strata.

#### Parameter of vegetation measurements

Studies were conducted during the three growing seasons in autumn (A), winter (W) and spring (S). Two “subhabitats” were distinguished in this study. The first subhabitat was located under *A. raddiana* canopies (canopied subhabitat) and the second in the open area, between the tree canopies (uncanopied subhabitat = open area).

Species composition, plant cover, plant biomass, plant density and diversity of the understory stratum were sampled to study the effect of *A. raddiana* on vegetation. In order to measure the floristic composition, total plant cover and individual species cover were assessed using the quadrat point method (Daget and Poissonet, 1971). A total of 72 transects were set up in the canopied subhabitat and 12 transects in the uncanopied subhabitat. Each transect was placed as a line of 7.5 m length. The mean crown diameter was deducted from the longest length of the vertically projected canopy surface. Observations were made every 5 cm, for a total of 150 points along each line to determine total plant cover (in %) and cover (in %) of each herbaceous species sampled. All these transects functioned as sites for repeated analyses with records of the herbaceous plants at the same place for nine seasons, so that temporal comparisons could be made.

To assess the plant biomass of aboveground parts of vegetation, we used the formula of Le Houérou (1987): plant biomass =  $c \cdot 43.1 \pm 3.6 \text{ kg ha}^{-1}$  ( $c$ : cover of perennial herbaceous vegetation in %).

Density of herbaceous species (individuals per square meter) was determined within 72 quadrats of 7.5 m<sup>2</sup> area at the canopied and 12 quadrats at the uncanopied subhabitat.

The importance and the distribution of species in the canopied and uncanopied subhabitats were studied by using the Shannon–Weaver index (Safi and Yarranton, 1973). This index is

defined by the following formula:

$$H' = - \sum P_i \log_2 P_i$$

$P_i$ : the relative frequency of the species:  $P_i = n_i/n$  where  $n_i$ : the mean cover of the species  $i$ , and  $n$  the total cover of all species (canopy projection to ground area).

To evaluate the change of the effect of *A. raddiana* on herbaceous strata under different water supply in different years, we calculated the Relative Neighbour Effect (RNE) index as follows:  $RNE = (S_U - S_C)/X$  where  $S_C$  and  $S_U$  are  $H'$ , plant cover, plant biomass or density on the canopied and uncanopied subhabitat, respectively, and  $X$  is either  $S_C$  (when  $S_C > S_U$ ) or  $S_U$  (where  $S_U > S_C$ ) (Markham and Chanway, 1996). To facilitate interpretation of the results, we have multiplied RNE values by  $-1$  (Callaway et al., 2002). RNE ranges from  $-1$  to  $1$  with positive values indicating facilitation and negative values indicating competition. We evaluated the relationship between RNE and seasonal rainfall using regression with Sigma Plot 2001 software (SPSS Inc., Chicago, IL, USA).

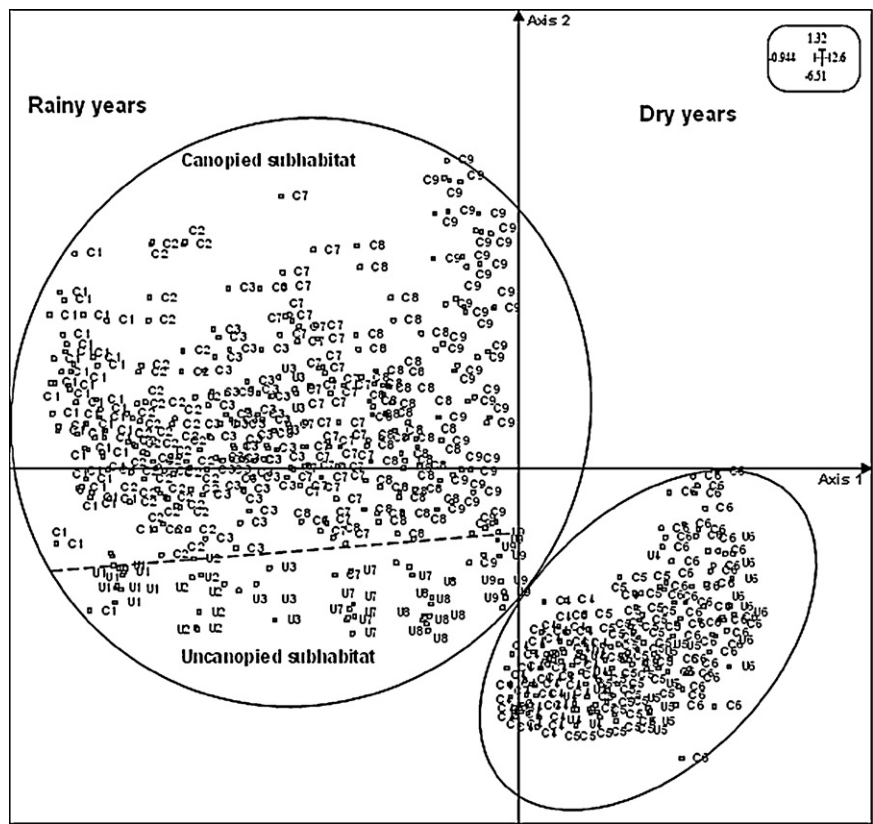
#### Microclimatic data

Representative microclimatic measurements below the *Acacia* canopies were carried out during the first week of September 2006 and 2007. This period is at the end of summer and prior to the autumn and winter rains. This means that the trees had endured a long hot summer period without any rainfall and that the density of the tree canopy is not affected dramatically by any new dense foliage growth. The microclimate effects under the tree were thus measured when the tree canopy was least effective. Air temperatures as well as relative humidity were measured at the canopied and uncanopied subhabitats using Hobo® H8 Pro Series climatic sensors (Onset Computer Corporation, Bourne, MA, USA).

#### Data analysis

Subhabitat composition was analysed using multivariate analysis of species frequency data. Correspondence analysis (CA) (Greenacre, 1984) was used to examine variation in plant species composition among transects and to investigate possible gradients in species composition. CA is recommendable for such an analysis since it can be viewed as a canonical correlation analysis between the indicator variables of transects and those of species. As such, and as indicated in its name, it expresses optimally the correspondence between transects and species. CA was applied to the transect species matrix, with species frequency (in %) data for the  $n = 78$  species in the  $t = 756$  transect plots. All analyses were performed using ADE4 software (Biometry and Evolutionary Biology Lab., Univ. Lyon).

All data were subjected to two-way ANOVA by using SPSS (11.5). Values of probability lower than 0.05 were considered as statistically significant. “Subhabitat” (canopied or uncanopied subhabitat) and “Seasons” (rainy season or dry season) are the independent variables whereas  $H'$ , plant cover, plant biomass and density are the dependant variables.



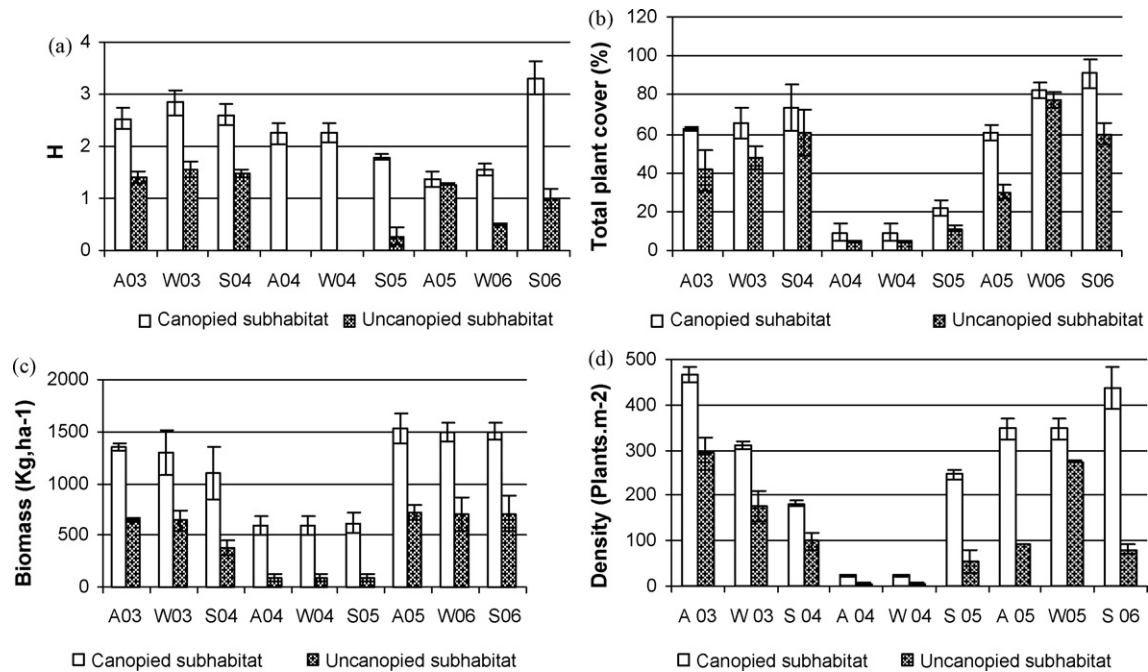
**Fig. 1.** Factorial map of the 756 transect plots for the correspondence analysis (CA) ordination (codes: C=canopied subhabitats; U=uncanopied subhabitats; 1–9=seasons in their chronological order: 1–3=A, W, S 2003–2004; 4–6=A, W, S 2004–2005; 7–9=A, W, S 2005–2006).

**Results**

*Floristic composition*

The 756 transect plots contained a total of 78 species representing 62 genera and 23 families. Asteraceae, Poaceae, Fabaceae,

Chenopodiaceae, Brassicaceae represented 63% of the species pool, with 15, 11, 9, 7 and 8 species, respectively (Table 2). The first two axes of the correspondence ordination (Fig. 1) – which together explain 12.5% of the variance in species space – were retained for interpretation. Overall, the CA ordination showed two important contrasts, type of community (*Acacia* tree effect) and the year of



**Fig. 2.** Flora diversity (a), total plant cover (b), plant biomass (c) and density on the canopied and uncanopied subhabitats during nine different seasons.

**Table 2**

List of genera and species of the herbaceous stratum in Bou Hedma National Park.

Family	Species
Caryophyllaceae	<i>Paronychia arabica</i> (L.) DC
Chenopodiaceae	<i>Atriplex halimus</i> L. <i>Bassia indica</i> (Wight) A. J. Scott <i>Hammada schmittiana</i> (Pomel) Botsch. <i>Hammada scoparia</i> (Pomel) Iljin <i>Salsola vermiculata</i> Aggr. <i>Salsola villosa</i> Schuttes <i>Chenopodium album</i> L.
Brassicaceae	<i>Diplotaxis simplex</i> (Viv.) Spreng. <i>Diplotaxis harra</i> (Forssk) Boiss. <i>Moricandia suffruticosa</i> (Desf.) Coss. et Dur. <i>Eruca vesicaria</i> (L.) Cav. <i>Enarthrocapus clavatus</i> Godron <i>Lobularia lybica</i> (Viv.) C.F.W. Meissn <i>Matthiola longipetala</i> (Vent.) DC <i>Brassica tournefortii</i> Gouan <i>Sisymbrium irio</i> L.
Euphorbiaceae	<i>Euphorbia retusa</i> Forssk. <i>Euphorbia cornuta</i> Forssk
Geraniaceae	<i>Erodium glaucophyllum</i> L'Héritier <i>Erodium laciniatum</i> Desf.
Poaceae	<i>Stipagrostis ciliata</i> (Desf.) De V <i>Stipagrostis plumosa</i> (L.) Munro ex. T. Anderson <i>Stipagrostis pungens</i> (Desf.) de Winter <i>Cenchrus ciliaris</i> L. <i>Cutandia dichotoma</i> (Forssk.) Trab. <i>Cynodon dactylon</i> (L.) Pers <i>Eragrostis papposa</i> (Roem. & Schult.) Steud. <i>Schismus barbatus</i> (L.) Thell. <i>Stipa capensis</i> Thunb. <i>Digitaria nodosa</i> Parl.
Fabaceae	<i>Argyrolobium uniflorum</i> (Dc) Jaub. Et Spach. <i>Lotus creticus</i> L. <i>Medicago minima</i> (L.) L. <i>Medicago truncatula</i> Gaertn. <i>Astragalus corrugatus</i> Bertol. <i>Astragalus armatus</i> Willd. <i>Retama raetam</i> (Forssk.) Webb <i>Acacia tortilis</i> (Forssk.) <i>Hippocrepis areolata</i> Desv.
Liliaceae	<i>Asphodelus tenuifolius</i> Cav. <i>Scilla villosa</i> Desf.
Malvaceae	<i>Malva aegyptiaca</i> L.
Plantaginaceae	<i>Plantago albicans</i> L. <i>Plantago amplexicaulis</i> Cv. <i>Plantago ovata</i> Forssk.
Resedaceae	<i>Reseda lutea</i> L. <i>Reseda alba</i> L.
Neuradaceae	<i>Neurada procumbens</i> (L.)
Solanaceae	<i>Lycium chawii</i> Roem. & Schult.
Zygophyllaceae	<i>Fagonia cretica</i> L. <i>Peganum harmala</i> L.
Asteraceae	<i>Artemisia herba alba</i> Asso. <i>Artemisia campestris</i> L. <i>Onopordum espiniae</i> (Desf.) Pomel <i>Rhanterium suaveolens</i> Desf. <i>Chrysanthemum coronarium</i> L. <i>Senecio gallicus</i> L. <i>Anacyclus clavatus</i> (Desf.) Pers. <i>Anacyclus cyrtolepidoides</i> Pomel <i>Atractylis carduus</i> (Forssk.) C. Chr. <i>Launaea resedifolia</i> (L.) Kuntze <i>Launaea angustifolia</i> (L.) Kuntze <i>Cynara cardunculus</i> L. <i>Centaurea contracta</i> Viv. <i>Centaurea dimorpha</i> Viv.

Table 2 (Continued)

Family	Species
Apiaceae	<i>Deverra tortuosa</i> (Desf.) DC.
Polygonaceae	<i>Rumex roseus</i> L. <i>Emex spinosus</i> (L.) Campd.
Aizoaceae	<i>Aizoon canariense</i> L. <i>Mesembryanthemum crystallinum</i> L.
Labiatae	<i>Salvia aegyptiaca</i> L.
Boraginaceae	<i>Echium pycnanthum</i> Desf.
Plumbaginaceae	<i>Limonium pruinosum</i> (L.) Chaz.
Cistaceae	<i>Helianthemum kahiricum</i> Del. <i>Helianthemum sessiliflorum</i> (Desf.) Pers
Primulaceae	<i>Anagallis arvensis</i> L.

sampling (rainy or dry years). Axis 1 is interpreted as representing a disturbance gradient since it separates transect data from the dry year (which were located on the positive values of this axis) from transect data from the 2 rainy years (on the negative values). For all seasons from the rainy years axis 2 opposes the canopied subhabitats (on the positive values of axis 2) and the uncanopied subhabitats (on the negative values of this axis). An additional analysis of species frequencies led us to divide the species into two species assemblages. The first group was composed of species favoured by the presence of *Acacia* trees such as *Cenchrus ciliaris*, *Cynodon dactylon*, *Eragrostis papposa*, *Sisymbrium irio*, *Chenopodium album*, *Atriplex halimus* and *Salsola brevifolia*. The second group was composed of species indifferent to the effect of the tree canopy cover. Frequencies of these species were identical in the canopied and uncanopied subhabitats and variable from one season to another. This group included more than 60% of the recorded flora. The most frequent species observed in this group were: *Paronychia arabica*, *Stipa capensis*, *Plantago ovata*, *Erodium triangulare* and *Hammada schmittiana*.

#### Flora diversity

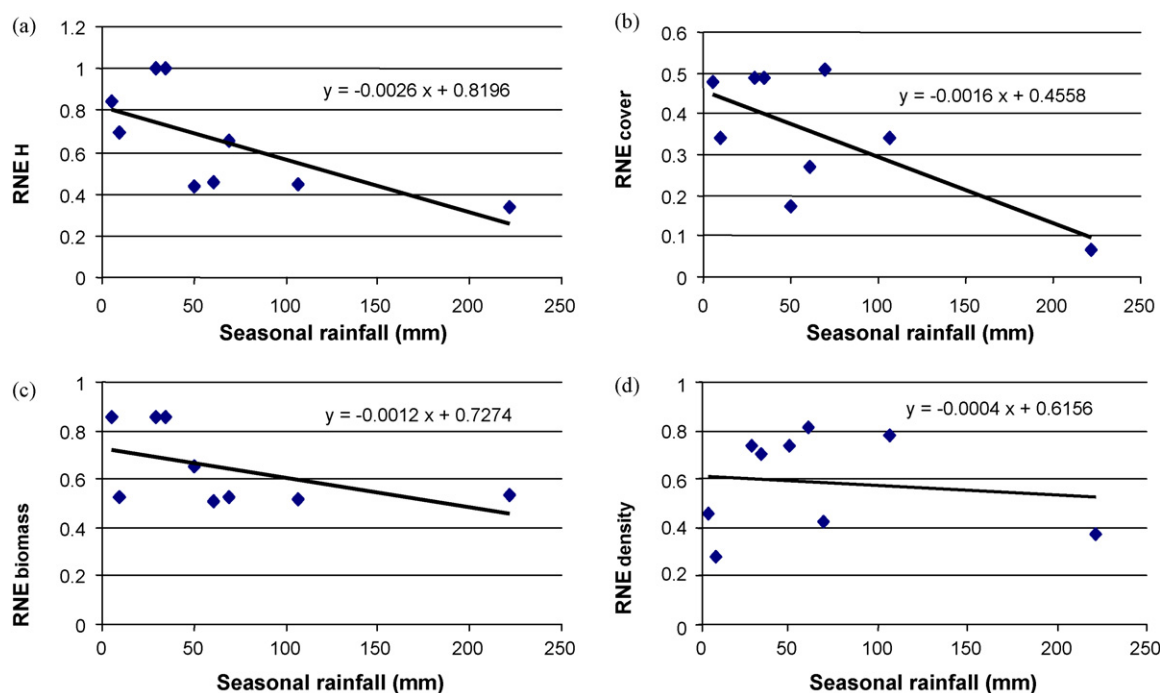
During the rainy seasons (Fig. 2a), ANOVA showed significant differences in flora diversity between canopied subhabitats and uncanopied subhabitats ( $F = 39.56$ ,  $p < 0.001$ ). This pattern is confirmed during the dry seasons with a positive effect of the *Acacia* tree on this parameter of diversity ( $F = 21.43$ ,  $p < 0.01$ ). There was no interaction between “Seasons” and “Subhabitat” on  $H'$  ( $F = 0.60$ ,  $p > 0.05$ ). The effect of *Acacia* on this variable was the same in the course of time.

#### Total plant cover and plant biomass

Seasonal rainfall during the course of the study period varied between 3.16 mm and 73.96 mm (Table 1). Herbaceous plant cover varied from 9% to 91% in the canopied subhabitats, and from 5% to 77% in the uncanopied subhabitats (Fig. 2b). A higher herbaceous plant cover in the canopied subhabitat versus the uncanopied subhabitat was found at all nine observed seasons. The difference was significant between the two subhabitats during the raining seasons ( $F = 10.09$ ,  $p < 0.05$ ) and highly significant during the dry seasons ( $F = 40.32$ ,  $p < 0.01$ ), with plant cover in the canopied subhabitat being two times higher than in the uncanopied subhabitat.

Statistical analyses of plant biomass produced a highly significant difference between the two subhabitats both for the rainy and dry seasons, respectively ( $F = 34.12$ ,  $p < 0.001$  and  $F = 27.94$ ,  $p < 0.001$ ). The highest biomass was recorded under *A. raddiana* canopies. There, plant biomass varied from 590 to 1530 kg ha<sup>-1</sup>; data ranged from 86 to 720 kg ha<sup>-1</sup> in the uncanopied subhabitats (Fig. 2c).





**Fig. 3.** Relationship between seasonal rainfall and the relative neighbour index:  $RNE_H$  (a),  $RNE_{cover}$  (b),  $RNE_{biomass}$  (c) and  $RNE_{density}$  (d) obtained during nine different seasons.

There was no interaction between “Seasons” and “Subhabitat” on plant cover ( $F=0.05$ ,  $p>0.05$ ) and plant biomass ( $F=0.79$ ,  $p>0.05$ ). The effect of *Acacia* on these two parameters was the same during the nine seasons of experiments.

#### Plant density

Herbaceous plant density varied from 24 Plants  $m^{-2}$  to 465 Plants  $m^{-2}$  in the canopied subhabitats, and from 6 Plants  $m^{-2}$  to 293 Plants  $m^{-2}$  in the uncanopied subhabitats (Fig. 2d). Higher plant density on the canopied subhabitat versus uncanopied subhabitat was found in all nine seasons of the observation period.

Plant density was significantly affected by *A. raddiana* canopy and seasonal rainfall. Under the *Acacia* canopies herbaceous plant density was mostly above 300 Plants  $m^{-2}$  during the rainy seasons and on average approx. 1/3 lower outside the tree canopies. The difference was high during the dry seasons ( $F=53.88$ ,  $p<0.01$ ) with species density in the canopied subhabitat being four times higher than in the uncanopied subhabitat. There was no interaction between “Seasons” and “Subhabitat” on plant density ( $F=15.7$ ,  $p>0.05$ ). The effect of *Acacia* on this parameter was

constant in statistical terms during the nine seasons of experiments.

#### Relative Neighbour Effect: RNE

RNE based on the different vegetation parameters could be related to the seasonal amounts of rainfall, with lower RNE values under higher precipitation (not obvious in case of plant density): Fig. 3. This means that facilitation is more pronounced under more severe abiotic stress (low seasonal rainfall).

#### Microclimatic conditions

A difference of 3 °C was found between the air temperatures in the canopied and uncanopied subhabitat, with the highest values outside the tree canopy (Table 3). In September, the mean air temperatures varied from 19.7 °C to 29.9 °C in the canopied area and from 19.8 °C to 35.1 °C in the open area. The highest average value of air humidity recorded in the canopied subhabitat was 73%. The average air humidity recorded in the uncanopied subhabitat was 70%. This means that due to the somewhat lower temperature air

**Table 3**  
Microclimatic data occurring under *Acacia raddiana* canopies and in open areas.

Typical air temperature and humidity in September	8:00 h	10:00 h	12:00 h	14:00 h	16:00 h
<i>Air temperature (°C)</i>					
Average outside canopy	19.8	26.2	31.3	35.1	32.7
Average below canopy	19.7	25.5	26.5	29.9	29.8
Difference between outside and below canopy (°C)	0.1	0.7	4.8	5.2	2.9
Difference between outside and below canopy (%)	0.5	2.7	18.1	17.4	9.7
<i>Relative humidity (%)</i>					
Average outside canopy	70.4	46.0	31.9	22.1	23.1
Average below canopy	73.4	54.5	44.4	31.0	29.1
Difference between outside and below canopy (% r.h.)	3.0	8.5	12.5	8.9	6.0
Difference between outside and below canopy (%)	4.1	15.6	28.2	28.7	20.6
<i>Tree data</i>					
Height	1.5 m-main branching starts				
Spread	N-S=7.5 m, E-W=7; 49% branching and leaf cover				
Girth	United or multi-stemmed				

humidity is little higher within the influence area of the trees. The diurnal extremes are even more pronounced: the greatest difference in air humidity below tree canopy as compared to outside its reach occurring at noon was in the order of 12%.

## Discussion

Under *Acacia raddiana* canopies in an arid-Mediterranean pseudosavanna of northern Africa floristic diversity, plant cover, plant biomass and density of perennial herbs were always higher than those values recorded in uncanopied subhabitats. These differences increased when yearly precipitation was low. Obviously the *Acacia* trees play a facilitative role on the understory vegetation. This effect remained constant during nine contrasting seasons of sampling over a wet-dry-wet 3 years period. The facilitative effect of the trees is therefore not connected to the climate and must be explained by other mechanisms. *Acacia raddiana* damps microclimatic extremes below its canopy. Comparable results were reported by Callaway et al. (1991) with alpine plants and Belsky et al. (1989) in a semi-arid savanna, who recorded a reduction of temperature extremes of air and soil under the plant canopies. This again led to a decrease of the air evaporative demand (Amundson et al., 1995) and an increase of soil moisture. These authors report that under tree canopy the soil is more fertile than that of the open areas. This is certainly the case also in the vegetation studied here: *Acacia* has a high potential of nitrogen fixation, improving soil fertility also for co-occurring non-leguminous plants (Abdallah et al., 2008; Joffre and Rambal, 1988). This will result from root (and nodule) biomass turnover and litter decomposition from dead leaves (Amiotti et al., 2000; Vinton and Burke, 1995). As a result, patches of higher fertility are created (Hagos and Smit, 2005; Kotzen, 2003). Far from the *A. raddiana* canopy, constraints are always intense (more water and nutrient stresses) and competition for these resources is more pronounced (Begon et al., 1990). As already shown in Senegal for this genus by Akpo and Grouzis (2004), our study showed that *Acacia* functions as an ecosystem key factor that promotes flora diversity, plant cover, plant biomass and density in its herbaceous understory vegetation by improving the abiotic environment.

Additionally and in agreement with predictions of established models of plant–plant interactions (Bertness and Callaway, 1994; Bertness and Ewanchuk, 2002; Brooker et al., 2005; Liancourt et al., 2005; Pugnaire and Luque, 2001), our results show that facilitation interactions between *A. raddiana* and herbaceous species are more pronounced under increased abiotic – drought – stress. These results agree with those put forward by Gómez-Aparacio et al. (2004) conducted in the Sierra Nevada of Spain, who showed that facilitation increases with aridity, both spatially and temporally. Contrasting findings were obtained in North American salt marshes by Penning et al. (2003) and by Tielbörger and Kadmon (2000) in the Negev desert. Maestre et al. (2005) showed that facilitation does not increase with stress in arid environment. In arid ecosystems of south-east Spain, Maestre et al. (2003) have shown that water saving under reduced evaporation due to shading by the nurse plant *Stipa tenacissima* was outweighed by its own water uptake, leading to direct resource competition with the subordinated shrub *Pistacia lentiscus*. However, water availability and performance of *Pistacia lentiscus* were lowest in open areas between the tussocks. This means that, irrespective of competitive demands for soil water of *Stipa tenacissima* its facilitation effect was positive and it increased with aridity. Therefore, the effect was complex, driven probably by differences in physical soil properties and water infiltration rate. Certainly, small-scale changes in ecosystem attributes such as plant cover, slope or soil properties can substantially affect runoff dynamics and soil water availability (Gómez-Plaza et al., 2001) and modify the dynamics of plant interactions in arid environments (Schenk et al., 2003).

Our findings do not match results of some previous studies reporting a decrease in the magnitude of the facilitative effects with abiotic stress (Bellot et al., 2004; Maestre and Cortina, 2004). These discrepancies could be due to differences in the degree of the prevailing abiotic stress, to differences in the magnitude of individual rainfall events, and to the duration of the dry period which may substantially affect competitive interactions in arid environments (Goldberg and Novoplansky, 1997). Aguiar and Sala (1999) emphasize that the method used to quantify biotic interactions may strongly affect the outcome of experiments in arid environments. High levels of natural or anthropogenically induced disturbances may produce strong variation in soil depth-related occurrence of dominant species. This may explain the contrasting results about facilitation under abiotic stresses observed in the recent literature.

## Conclusions

Our results demonstrate that positive effects of *A. raddiana* upon the herb layer vegetation are important in arid Tunisian systems. The trees facilitate establishment and development of herbaceous species. This positive effect of *A. raddiana* on species diversity, plant cover, plant biomass and density of the herbaceous stratum still increases with seasonal water stresses. The weak inter-seasonal variation of the different measured and calculated vegetation parameters of the understory herb layer, compared to a higher sensitivity of vegetation located in the uncanopied sub-habitat, indicates that *A. raddiana* plays an important role buffering environmental variations (Parker and Muller, 1982).

## References

- Abdallah, F., Noumi, Z., Touzard, B., Ouled Belgacem, A., Neffati, 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.
- Aguiar, M.R., Sala, O.E., 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends Ecol. Evol.* 14, 273–277.
- Akpo, L.E., Grouzis, M., 2004. Interactions arbre/herbe en bioclimat semi-aride: influence de la pâture. *Sécheresse* 15, 253–261.
- Amiotti, N.M., Zolba, P., Sánchez, L.F., Peinemann, N., 2000. The impact of single trees on properties of loess-derived grassland soils in Argentina. *Ecology* 1, 3283–3290.
- Amundson, R.G., Ali, A.R., Belsky, A.J., 1995. Stomatal responsiveness to changing light intensity increases rain use efficiency of below-tree-crown vegetation in tropical savannas. *J. Arid Environ.* 29, 139–153.
- Begon, M., Harper, J.L., Townsend, C.R., 1990. *Ecology: individuals, populations and communities*. Blackwell Scientific Publications, Cambridge.
- Bellot, J., Maestre, F.T., Chirino, E., Hernandez, E., Ortiz de Urbina, J., 2004. Afforestation with *Pinus halepensis* reduces native shrub performance in Mediterranean semiarid area. *Acta Oecol.* 25, 7–15.
- Belsky, A.J., Amundson, R.G., Duxbury, J.M., Riha, S.J., Ali, A.R., Mwonga, S.M., 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna. *J. Appl. Ecol.* 26, 1005–1024.
- Bertness, M., Callaway, R.M., 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9, 191–193.
- Bertness, M., Ewanchuk, P.J., 2002. Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia* 132, 392–401.
- Brooker, R., 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., Callaghan, T.V., 1998. The balance between positive and negative plant interaction and its relationship to environmental gradients: a model. *Oikos* 81, 196–207.
- Bruno, J.F., Stachowicz, J.J., Bertness, M., 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18, 119–125.
- Callaway, R.M., et al., 2002. Positive interactions among alpine plants increase with stress. *Nature* 417, 844–888.
- Callaway, R.M., Nadkarni, N.M., Mahall, R.E., 1991. Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology* 72 (4), 1484–1499.
- Daget, P., Poissonet, J., 1971. An ecological analysis method of prairies. Criteria's of application. *Annales Agronomiques* 22, 5–41.
- Goldberg, D., Novoplansky, A., 1997. On the relative importance of competition in unproductive environments. *J. Ecol.* 85, 409–418.
- Gómez-Aparacio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., Baraza, E., 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecol. Appl.* 14, 1128–1138.

- Gómez-Plaza, A., Martínez-Mena, M., Albaladejo, J., Castillo, V.M., 2001. Factors regulating spatial distribution of soil water content in small semiarid catchments. *J. Hydrol.* 253, 211–226.
- Greenacre, M.J., 1984. Theory and applications of Correspondence analysis. Academic Press, London.
- Greenlee, J.T., Callaway, R.M., 1996. Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in western Montana. *Am. Nat.* 148, 386–396.
- Hagos, M.G., Smit, G.N., 2005. Soil enrichment by *Acacia mellifera* subsp. *detinens* on nutrient poor soil in a semi-arid Southern Africa savanna. *J. Arid Environ.* 61, 47–59.
- Holzapfel, C., Mahall, B.E., 1999. Bidirectional facilitation and interference between shrubs and annuals in the Mojave desert. *Ecology* 80, 1747–1761.
- Joffre, R., Rambal, S., 1988. Soil water improvement by trees in the rangelands of southern Spain. *Acta Oecol.* 9, 405–422.
- Kotzen, B., 2003. An investigation of shade under six different tree species of the Negev desert towards their potential use for enhancing micro-climatic conditions in landscape architectural development. *J. Arid Environ.* 55, 231–274.
- Le Houérou, H.N., 1987. Aspects météorologiques de la croissance et du développement végétal dans les déserts et les zones menacées de désertification. PNUE, Nairobi et OMM, Genève.
- Le Houérou, H., 1959. Ecological and floristic researches on the vegetation of the southern Tunisia. *Mémoire Inst. Rech. Sah., Alger*, 1er Vol. Les milieux naturels, la végétation.
- Liancourt, P., Callaway, R.M., Michalet, R., 2005. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology* 86, 1611–1618.
- Markham, J.H., Chanway, C.P., 1996. Measuring plant neighbor effects. *Funct. Ecol.* 10, 548–549.
- Maestre, F.T., Cortina, J., 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proc. R. Soc. Lond. B (Suppl.)* 271, 331–333.
- Maestre, F.T., Bautista, S., Cortina, J., 2003. Positive, negative, and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. *Ecology* 84, 3186–3197.
- Maestre, F.T., Valladares, F., Reynolds, J.F., 2005. Is the change of plant-plant interaction with abiotic stress predictable? A meta-analysis of field results in arid environments. *J. Ecol.* 93, 748–757.
- Parker, V., Muller, C.H., 1982. Vegetation and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in California annual grassland. *Am. Midl. Nat.* 107, 69–81.
- Penning, 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.
- Safi, M.I., Yarranton, G.A., 1973. Diversity, floristic richness and species evenness during a secondary (post-fire) succession. *Ecology* 54 (4), 897–902.
- Schenk, H.J., Holzapfel, C.G., Mahall, B.E., 2003. Spatial ecology of a small desert shrub on adjacent geological substrates. *Ecology* 91, 383–395.
- Tielbörger, K., Kadmon, R., 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* 81, 1544–1583.
- Vinton, M.A., Burke, I.C., 1995. Interactions between individual plant species and soil nutrient status in short grass steppe. *Ecology* 76, 1116–1133.