*Applied Vegetation Science* ■■ (2012)

# The influence of trees on nutrients, water, light availability and understorey vegetation in an arid environment

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**Keywords**
Arid areas; *Acacia tortilis* subsp. *raddiana*; Grazing; Herb composition; Microclimate; Soil enrichment; Water stress; Water availability

**Nomenclature**
Greuter et al. (1989) and Chaieb & Boukhris (1998)

Received 24 September 2010
Accepted 10 March 2012
Co-ordinating Editor: Michael Huston

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## Abstract

**Questions:** Do *Acacia tortilis* trees facilitate herbaceous species development under arid conditions? Do tree–herb interactions change with water stress and grazing intensity?

**Location:** National Park in a Tunisian arid area (34°39′N, 9°48′E).

**Methods:** Soil water content, soil nutrient concentration, light intensity and microclimatic data were collected under the canopy and in open areas to evaluate the relative roles of *A. tortilis* (Forssk.) subsp. *raddiana* (Savi) trees in structuring vegetation composition and diversity patterns in a arid pseudo-savanna. Data were collected inside and outside Bou Hedma National Park, both during a dry and a wet year.

**Results:** In both unprotected and protected areas, the influence of the tree canopy on the herbaceous strata can be considered as positive, even though it is more significant inside the park. This positive interaction increased with higher abiotic stress conditions and decreased with grazing intensification. Soil nutrients (organic matter, total N, extractable P) and moisture availability was greater under tree canopies than in the open. Species composition of the herb layer also differed between *Acacia* trees and open areas. Some palatable species were found under trees, and were replaced by less desirable species in the open. Microclimate measurements showed significant differences in light intensity reaching the soil, mean air temperatures and relative humidity.

**Conclusions:** These results suggest that the optimal association of climate factors under the canopy would combine with a high soil fertility mediated by litter decomposition to increase plant cover under tree canopies.

## Introduction

Several studies have focused on the effects of savanna trees on functioning of the herb strata. Often different species grow under trees than in open areas (Belsky et al. 1993). By changing resource availability, trees can either increase or reduce plant productivity of the understorey (Belsky et al. 1993; Anderson et al. 2001). Because trees affect nutrients, light and water availability of the understorey vegetation simultaneously (Scholes & Archer 1997), it is difficult to determine changes in understorey species and productivity. Trees facilitate understorey plant growth through increased nutrient availability. Higher soil fertility under tree canopies has been reported for a wide range of savannas (Barnes et al. 2009; Callaway et al. 1991). However, it is still unknown how these "islands of fertility" around isolated trees develop. It has been proposed that trees act as nutrient pumps, taking up nutrients from deeper soil layers or from soil outside the canopy and depositing them under their canopy through litter fall or leaching (Scholes 1990). Other possibilities are that trees are an effective trap for atmospheric dust, or attract mammals that deposit their dung under tree canopies (Belsky 1994). The effects of trees on soil water content are, however, less clear.

There are some reports of increased soil moisture content under trees compared to open area (Koechlin et al. 1986). Several mechanisms could decrease transpiration of understorey plants or facilitate hydraulic lift (Ludwig et al. 2001). Hydraulic lift is the process of water movement from deep, relatively wet, to dry and shallow soil layers through the roots of plants that have access to both deep and shallow soil layers (Joffre & Rambal 1993; Caldwell et al. 1998). Other studies have shown reduced soil water availability under trees due to high tree water uptake (Amundson et al. 1995; Anderson et al. 2001). Shade can also have both positive and negative effects on below-ground plant production (Ludwig et al. 2001; Whitford 2002). Reduced light availability limits plant production but lowers temperatures in the shade, resulting in improved herb water status, and could potentially increase plant growth (Belsky 1994; Anderson et al. 2001).

In this work, our objective was to determine how individual *Acacia tortilis* (Forssk.) subsp. *raddiana* (Savi) trees affect the herb species composition and several attributes of the environment beneath the tree canopies, including soil water content, soil nutrient concentrations, soil surface proprieties and light availability. Also to investigate what factors can influence the tree–herb relations?

## Methods

### Study area

Our study was conducted at Bou Hedma National Park (Fig. 1). This park (34°39′N,9°48′E) is characterized by an arid Mediterranean climate with a moderate winter (Le Houérou 1959). The mean annual rainfall is about 180 mm (Table 1). The annual mean temperature is about 17.2 °C, while the minimum and maximum monthly temperature means are 3.8 °C (December and January) and 36.2 °C (July and August), respectively. The soils in the study area consist of Quaternary sandy deposits, with pseudo-savanna vegetation where *A. tortilis* subsp. *raddiana* constitutes the most important tree stratum. The herb stratum was dominated by perennial herb species (*Cenchrus ciliaris*, *Digitaria commutata* and *Stipagrostis ciliata*), two species of the genus *Hammada* (*H. schmittiana*, *H. scoparia*; Chenopodiaceae), as well as a number of annual species.

The study was conducted at the beginning of the 2004–2005 and 2005–2006 growing seasons. Two "sub-habitats" were distinguished (Fig. 2). The first was located under *A. tortilis* subsp. *raddiana* canopies (canopied sub-habitat) and the second in the open area, between the tree canopies (un-canopied sub-habitat = open area).

### Climate conditions during the investigation periods

The first year, characterized by low precipitation (which did not exceed 69.4 mm), was considered as a dry year. The second was a wet year, since annual precipitation reached 305.9 mm (Table 1). Rainfall during the autumn (September, October and November) is essential for annual species recruitment and the commencement of growth of perennial species (Floret & Pontanier 1978).

### Soil water content

To determine soil moisture content, soil samples were taken around six trees along the main compass points, namely: north, south, east and west (Fig. 2). Four samples were collected in the open areas beyond the canopy of

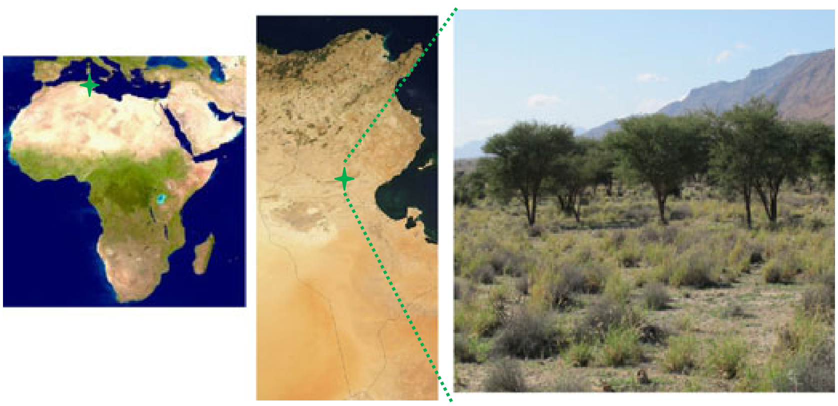

**Fig. 1.** Location of the study site: Bou Hedma National Park (South Tunisia).

**Table 1.** Monthly and annual rainfall (in mm) recorded at Bou Hedma National Park during the two experimental years.

| | S | O | N | D | J | F | M | A | M | J | J | A | Annual average | Rain days number/year |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2004/2005 | 8 | 0 | 21.5 | 30.1 | 0 | 4.5 | 5.3 | 0 | 0 | 0 | 0 | 0 | 69.4 | 15 |
| 2005/2006 | 61.5 | 2 | 6 | 103 | 70 | 48.9 | 0 | 9.5 | 0 | 0 | 4 | 1 | 305.9 | 22 |


Applied Vegetation Science
Doi: 10.1111/j.1654-109X.2012.01201.x 

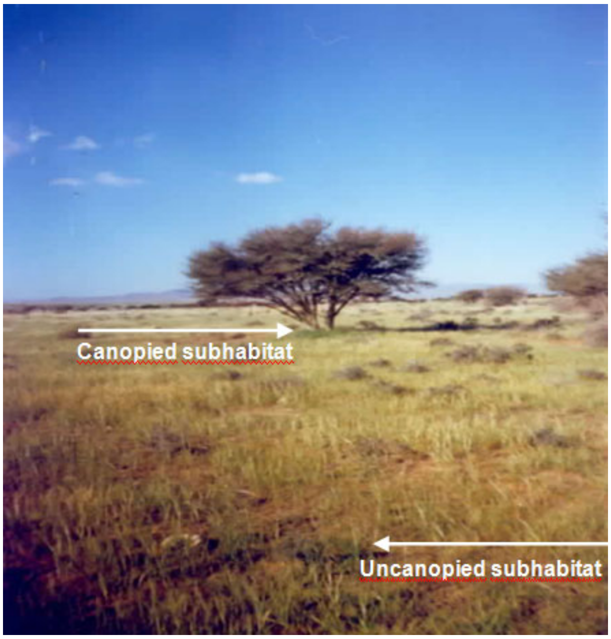


**Fig. 2.** Data collection from canopied and uncanopied subhabitat.

each tree. Soil samples were collected during the wet season, at a depth of 0–20 cm. Soil water content was determined gravimetrically by drying at 60 °C for 24 h.

### Soil nutrient concentration

Part of each soil sample collected was air-dried and passed through a 2-mm sieve and then analysed for total nitrogen (N) (Kjeldahl method; Jackson 1958), for organic matter (Wallkey & Black 1934) and phosphorus (calorimetric method; Murphy & Riley 1962).

### Vegetation sampling and soil surface proprieties

Six trees were sampled to study the effect of *A. tortilis* subsp. *raddiana* on floristic composition, total plant cover, individual species cover, diversity and soil surface properties using the point quadrat method (Daget & Poissonet 1971). In the protected area, a total of 24 transects were set up under the canopy, and 12 transects in the open (Fig. 2). In the unprotected area, a total of 12 transects were set up under the canopy, and six transects in the open. Each transect was 7.5-m long. Observations of floristic composition and soil surface proprieties were made every 5 cm, for a total of 150 points along each transect. As spatial heterogeneity is greater in canopied areas (compared to un-canopied areas) and in protected areas (compared to unprotected areas), we selected a number of transects of twice this size in both areas.

Density of perennial species per square meter was determined within 36 7.5-m$^2$ quadrats in the lightly grazed sites (24 and 12, respectively, at the canopied and un-canopied-sub-habitat) and 18 in the heavily grazed site (12 and six, respectively, at the canopied and un-canopied sub-habitat).

The importance and distribution of species in the canopied and un-canopied sub-habitats was studied using the Shannon–Weaver index (Safi & Yarranton 1973). This index has the following formula:

$$H' = -\sum \mathrm{P}_i \log_2 \mathrm{P}_i$$

where $\mathrm{P}_i$: relative frequency of the species: $\mathrm{P}_i = n_i/n$ where $n_i$: mean cover of species $i$, and $n$ is total cover of all species (canopy projection to ground area).

To evaluate changes of the effects of *Acacia* on the herb strata under different water supply in different years, we calculated the relative neighbour effect (RNE) as follows: RNE = (SU – SC)/$X$, where SC and SU are $H'$, plant cover, plant biomass or density on the canopied and un-canopied sub-habitat, respectively, and X is either SC (when SC > SU) or SU (where SU>SC) (Markham & Chanway 1996). To facilitate interpretation of the results, we multiplied RNE values by −1 (Whitford 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 SigmaPlot 2001 software (SPSS Inc., Chicago, IL, USA).

### Light intensity and microclimate data

Light intensity and microclimate assessments were undertaken in September at 2-h intervals, commencing at 08:00 h, with the last measurement taken at approximately 16:00 h. Measurements were taken under the canopies of six trees at the four cardinal points. Four measurements were taken under the canopies of trees for light and microclimate data five times per day. Four other measurements beyond the canopy of each tree were also taken to compare with measurements within the canopy. Relative humidity and air temperature were measured using Hobo® H8 Pro Series climate sensors (Onset Computer Corporation, Bourne, MA, USA). The Hobo sensors were placed 2 cm above the ground. The light intensity was measured using the Hobo® Optic USB Be Station.

### Data analysis

All data were subjected to one-way ANOVA using SPSS (SPSS for Windows, v.10.05) Values of probability below 0.05 ($P$ < 0.05) were regarded as statistically significant sub-habitats (canopied or un-canopied sub-habitat).The independent variables were sub-habitats, whereas total-plant cover, individual species cover, soil nutrients and soil surface proprieties were the dependent variables.


Doi: 10.1111/j.1654-109X.2012.01201.x  

**Table 2.** Soil properties and microclimate data in protected and unprotected areas under canopied and un-canopied sub-habitats.

| Sub-habitat | Protected area | | | Unprotected area | | |
|---|---|---|---|---|---|---|
| | Canopied sub-habitat | Un-canopied sub-habitat | *P* | Canopied sub-habitat | Uncanopied sub-habitat | *P* |
| Soil water content% | 2.11 ± 0.14 | 1.28 ± 0.14 | *** | 0.51 ± 0.10 | 0.36 ± 0.11 | NS |
| OM% | 0.90 ± 0.12 | 0.29 ± 0.05 | ** | 0.17 ± 0.05 | 0.07 ± 0.01 | NS |
| N% | 0.34 ± 0.02 | 0.26 ± 0.01 | ** | 0.13 ± 0.01 | 0.07 ± 0.03 | ** |
| P mg/kg | 48.02 ± 0.74 | 34.75 ± 3.96 | *** | 11.79 ± 2.23 | 3.58 ± 0.85 | ** |
| Light (mol $m^2$ $s^{-1}$PPFD) | 1.06 | 2.29 | *** | | | |
| Air temperature (°C) | 26.7 | 31.3 | *** | | | |
| Relative air humidity (%) | 41.1 | 25.6 | *** | | | |

NS, non significant; *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

## Results

### Soil water content and nutrient concentration

In the protected sub-habitat, soil water content was significantly higher under the tree canopy than in the open ($P < 0.01$, $F = 7.26$; Table 2), but no significant difference was recorded in the grazed area ($P > 0.05$, $F = 3.05$). Soil organic matter was more than three times higher under the canopy than in the open ($P < 0.01$, $F = 7.26$); however, in the unprotected area, a non-significant difference was recorded ($P > 0.05$, $F = 2.80$). In general, N concentration was significantly higher under trees than in open areas ($P < 0.01$, $F = 6.21$ and $P < 0.01$, $F = 3.91$, respectively, inside and outside the park). Extractable *P* was significantly higher under the canopy ($P < 0.001$, $F = 11.34$ and $P < 0.01$, $F = 18.35$, respectively, inside and outside the park).

### Soil surface properties and total plant cover

*Protected area*

Soil surface covered by litter was more than two to three times higher under the canopy than in the open ($P < 0.01$, $F = 10.41$ and $P < 0.001$, $F = 100.03$, respectively, during the dry and the wet year; Fig. 3). Stones represented the smallest fraction in the two are as, but were more abundant in the open area. Compared to the canopied sub-habitat, bare soil spreads over a vast area in the un-canopied sub-habitat in both the dry and the wet year ($P < 0.001$, $F = 14.89$ and $P < 0.001$, $F = 188.38$, respectively).

Vegetation covered approximately 9–60% of the soil surface under the tree canopy and 4–20% in the open (Fig. 3). Statistical analyses of total plant cover produced a significant difference between the canopied and un-canopied sub-habitats ($P < 0.001$, $F = 7.87$ and $P < 0.01$, $F = 11.32$, respectively, during the dry and the wet year).

*Unprotected area*

The main characteristic of the surface soil outside the park is the extension of sand following the degradation of vegetation cover. However, the sand was significantly more abundant in the un-canopied sub-habitat ($P < 0.01$, $F = 12.95$). In the dry year as well as the wet year, there was significantly more bare soil in the open area ($P < 0.001$, $F = 21.31$; $P < 0.01$, $F = 5.54$). No significant difference was recorded in litter distribution between the two sub-habitats, but it was more abundant under the tree canopy.

Plant cover varied from 4% to 13% in the canopied sub-habitats, and from 2% to 15% in the un-canopied sub-habitats. The main effect was a 'water availability' effect, where the highest values of plant cover were always observed during the wet year as compared to the dry year (Fig. 3). A positive effect of tree canopy ($P < 0.01$, $F = 7.76$)was just observed during the dry year, when vegetation was exclusively composed of perennial species.

### Herb density, composition and floral diversity

*Protected area*

When water resources were limited, the vegetation under the tree canopy as well as outside the tree canopy, was dominated by perennial species.This group included 77% to 85% of the recorded flora. Perennial species density (Fig. 4a) was significantly higher under the tree canopy ($P < 0.01$, $F = 4.81$ and $P < 0.01$, $F = 5.70$ during the dry and the wet year, respectively). However, some annual species, such as *Diplotaxis harra*, *Stipa capensis* and *Malva aegptiaca*, enjoyed a more favourable microclimate under the tree canopy for their development. During the wet year, vegetation in the open area was dominated by *S. capensis*, *Plantago ovata*, *Erodium laciniatum*, *Hammada schmittiana* and *H.scoparia*. Their cover varied from 0.5% to 11.83%. Other species, such as *Chrysanthemum coronarium*, *Diplotaxis simplex*, *Fagonia cretica*, *Diplotaxis harra*, *Medicago minima* and *Cutandia dichotoma*, were less represented; their covers did not exceed 0.3% (Table 3). Under the *A. tortilis* subsp. *raddiana* canopy, these species were replaced by a morediverse flora. *Cenchrus ciliaris*, *Cynodon dactylon*, *Eragrostis papposa*, *Stipagrostis ciliate*, *S. plumosa*, *Matthiola longipetala*,


Doi: 10.1111/j.1654-109X.2012.01201.x 

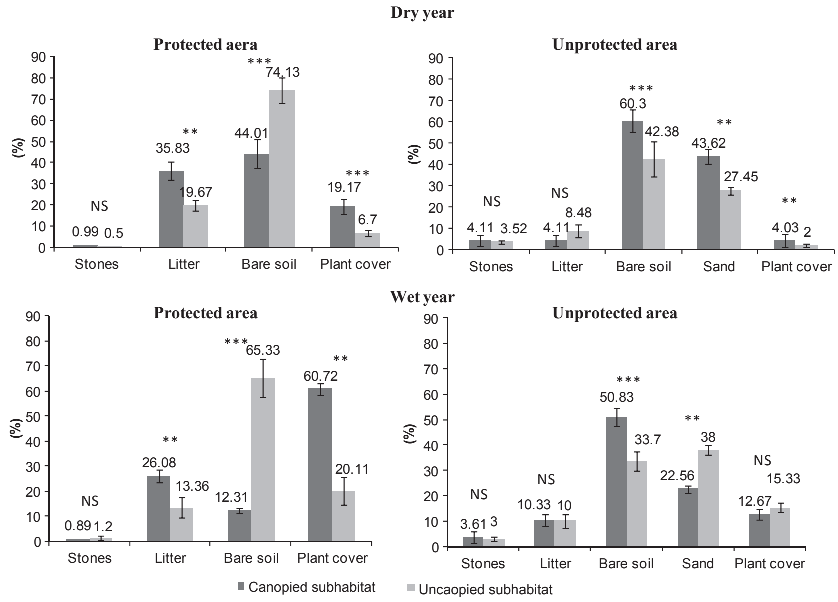


**Fig. 3.** State of the soil surface sampled for 2 years (wet year and dry year) in protected and unprotected areas under canopied and un-canopied sub-habitats.

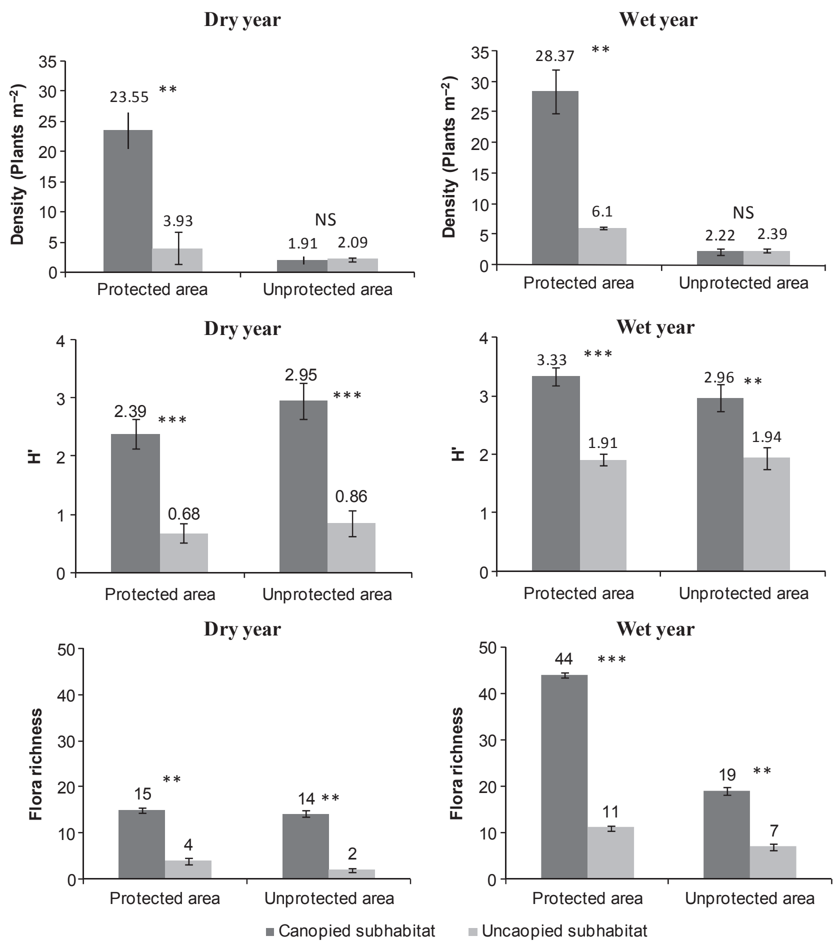


**Fig. 4.** Perennial density (**a**), species diversity (**b**) and richness sampled for 2 years (wet year and dry year) in protected and unprotected areas under canopied and un-canopied sub-habitats.

**Table 3.** Variations in herb species cover (%) recorded for 2 years (wet year and dry year) in protected areas under canopied and un-canopied sub-habitats.

| Family | Species | Dry year | | | Wet year | | |
|---|---|---|---|---|---|---|---|
| | | Canopied Sub-habitat | Un-canopied Sub-habitat | *P* | Canopied Sub-habitat | Uncanopied Sub-habitat | *P* |
| Caryophyllaceae | *Paronychia arabica (L.)* DC. | – | – | | 6 ± 1.57 | 0 | ** |
| Chenopodiaceae | *Bassia indica* (Wight) A. J. Scott | – | – | | 0.03 ± 0.01 | 0 | NS |
| | *Hammada scoparia* (Pomel) Iljin | 0.98 ± 0.3 | 2.94 ± 1.23 | * | 1.5 ± 0.29 | 3.5 ± 0.99 | ** |
| | *Hammada schmittiana* (Pomel) Botsch. | 1 ± 0.31 | 0.76 ± 0.48 | NS | 1 ± 0.26 | 0.83 ± 0.72 | NS |
| | *Chenopodium album* L. | – | – | | 6.1 ± 1.7 | 0 | * |
| Cruciferae | *Alyssum parviflorum* | – | – | | 0.04 ± 0.03 | 0 | NS |
| | *Diplotaxis simplex* (Viv.) Spreng. | – | – | | 3.4 ± 0.81 | 0.06 ± 0.05 | ** |
| | *Diplotaxis harra (*Forssk) Boiss. | 0.01 ± 0.01 | 0 | NS | 0.6 ± 0.16 | 0.17 ± 0.14 | NS |
| | *Moricandia suffruticosa* (Desf.) Coss. et Dur. | 0.32 ± 0.13 | 0 | NS | 0.24 ± 0.16 | 0 | NS |
| | *Eruca visicaria* (L.) Cav. | – | – | | 0.06 ± 0.04 | 0 | NS |
| | *Enarthrocapus clavatus* Godron | 0 | – | | 0.62 ± 0.21 | 0 | * |
| | *Matthiola longipetala* (Vent.) DC. | 0 | 0 | | 0.08 ± 0.05 | 0 | NS |
| | *Alyssum parviflorum* Hochst. | 0 | 0 | | 0.06 ± 0.05 | 0 | NS |
| | *Sisymbrium irio* L. | 0 | 0 | | 0.26 ± 0.12 | 0 | NS |
| Euphorbiaceae | *Euphorbia retusa* Forssk. | 0 | 0 | | 0.01 ± 0.01 | 0 | NS |
| Geraniaceae | *Erodium glaucophyllum* L'héritier | 0 | 0 | | 0.40 ± 0.15 | 0 | NS |
| | *Erodium laciniatum* Desf. | 0 | 0 | | 0.52 ± 0.013 | 0.50 ± 0.37 | NS |
| Poaceae | *Stipagrostis ciliata* (Desf.) De V | 0.09 ± 0.05 | 0 | NS | 0.09 ± 0.05 | 0 | NS |
| | *Stipagrostis plumosa* (L.) Munro ex. T. An | 0 | 0 | | 0.01 ± 0.01 | 0 | NS |
| | *Cenchrus ciliaris* L. | 1.12 ± 0.36 | 0.17 ± 0.10 | * | 0.92 ± 0.05 | 0 | ** |
| | *Cutandia dichotoma* (Forssk.) Trab. | 0 | 0 | | 1.67 ± 0.59 | 0.28 ± 0.24 | * |
| | *Cynodon dactylon* (L.) Pers | 0 | 0 | | 8.811.68 | 0 | *** |
| | *Eragrostis papposa* (Roem. & Schult.) Steu | 0.80 ± 0.19 | 0 | NS | 2.92 ± 1.15 | 0 | * |
| | *Stipa capensis* Thunb. | 2.07 ± 0.96 | 0.75 ± 0.54 | NS | 30 ± 2.58 | 11.83 ± 3.82 | *** |
| | *Digitaria nodosa* Parl. | 0 | 0 | | 0.16 ± 0.09 | 0 | NS |
| Fabaceae | *Medicago minima* (L.) L. | 0 | 0 | | 0 | 0.220.19 | ** |
| | *Astragalus corrugatus* Bertol | 0 | 0 | | 0.03 ± 0.02 | 0 | NS |
| Liliaceae | *Asphodelus tenuifolius* Ca | 0 | 0 | | 0.58 ± 0.19 | 0 | NS |
| | *Asparagus stipularis* Forssk. | 0.02 ± 0.01 | 0 | NS | 0.02 ± 0.01 | 0 | NS |
| Malvaceae | *Malva aegptiaca* L. | 0.03 ± 0.03 | 0 | NS | 3.40 ± 1.33 | 0 | NS |
| Plantaginaceae | *Plantago ovata* Forssk. | 0 | 0 | | 14.6 ± 72.18 | 3.38 ± 2.68 | ** |
| | *Plantago amplexicaulis* Cav. | 0 | 0 | | 0.06 ± 0.03 | 0 | NS |
| Neuradaceae | *Neurada procumbens* (L.) | 0 | 0 | | 0.32 ± 0.13 | 0 | NS |
| Solanaceae | *Lycium chawii* Roem. & Schult. | 1.02 ± 0.35 | 0 | NS | 1.05 ± 0.33 | 0 | * |
| Zygophyllaceae | *Fagonia cretica* L. | 0 | 0 | | 0.89 ± 0.24 | 0 | * |
| | *Peganum harmala* L. | 0 | 0 | | 0.06 ± 0.04 | 0 | NS |
| Asteraceae | *Artemisia herba alba* Asso. | 0.35 ± 0.2 | 0 | NS | 0.15 ± 0.1 | 0 | NS |
| | *Artemisia campestris* L. | 0.04 ± 0.0 | 0 | NS | 0.050.03 | 0 | NS |
| | *Rhanterium suaveolens* Desf. | 0.20 ± 0.1 | 0 | NS | 0.18 ± 0.06 | 0 | NS |
| | *Chrysanthemum coronarium* L. | 0 | 0 | | 0 | 0.06 ± 0.05 | * |
| | *Anacyclus cyrtolepidoides* Pomel | 0 | 0 | | 0.02 ± 0.02 | 0 | NS |
| | *Deverra tortuosa* (Desf.) DC. | 0.21 ± 0.0 | 0 | NS | 0.56 ± 0.16 | 0.160.14 | NS |
| Polygonaceae | *Rumex roseus* L. | 0 | 0 | | 0.1 ± 0.06 | 0 | NS |
| Aizoaceae | *Aizoon canariense* L. | 0 | 0 | | 0.19 NS 0.12 | 0 | NS |
| Labiatae | *Salvia aegyptiaca* L. | 0 | 0 | | 0.17 ± 0.09 | 0 | NS |
| Boraginaceae | *Echium pycnantum* Desf. | 0 | 0 | | 0.36 ± 0.15 | 0 | NS |

NS, non significant; **P* < 0.05, ***P* < 0.01, ****P* < 0.001.


Applied Vegetation Science
Doi: 10.1111/j.1654-109X.2012.01201.x © 2012 International Association for Vegetation Science

*Digitaria nodosa*, *Salvia aegyptiaca*, *Moricandia suffruticosa*, *Enarthrocarpus clavatus*, *Artemisia herba alba*, *Rhanterium suaveolens*, *Cutandia dichotoma* and *Helianthemum sessiliflorum*were among the palatable species recorded under the tree canopy. During the studied period, floral diversity was higher under the tree canopy than in the open. In fact, *H'* was 2.4–3.34 in the first sub-habitat, but did not exceed 1.91 in the second (Fig. 4b) Flora; richness was four times more important under the tree canopy during the dry than the wet year. In total, 44 species were recorded in the canopied sub-habitat and 11 species in the un-canopied sub-habitats (Fig. 4c).

### *Unprotected area*

In this area, there was a significant difference for *Stipa capensis*, *Astragalus corrugatus*and *Rhanterium suaveolens*, with the highest cover in the un-canopied sub-habitat. *Paronychia arabica*, *Cynodon dactylon*, *Lycium chawii* and *Cleome amblyocarpa* were more widespread in the canopied sub-habitat (Table 4). Perennial species density was significantly affected by grazing intensity (Fig. 4a). Density was fairly constant in the unprotected site, but there was no significant difference between the two sub-habitats in the two studied years ($P > 0.05$, $F = 0.04$, $P > 0.05$, $F = 0.21$, respectively, during the dry and wet year). During both the dry and wet year, floral diversity was higher under the tree canopy than in the open. In fact, *H'* was about 2.95 in the first sub-habitat, but varied between 0.86 and 1.94 in the second (Fig. 4b). Floral richness was four times more important under the tree canopy during the dry than in the wet year. In total, 23 species were recorded in the canopied sub-habitat and seven species were recorded in the un-canopied sub-habitat (Fig. 4c).

## Effect of water stress on tree–herb interactions

In both the protected and unprotected area, the RNE value calculated for different parameters of the vegetation increased with the drought, signifying that the positive effect (or facilitation) of trees increased with increasing water stress (Fig. 5a). On the other hand, this parameter decreased with intense grazing in both the dry and wet year (Fig. 5b).

## Light intensity

The data recorded under the canopies of *A. tortilis* subsp. *raddiana* trees shows that there is a significant difference in light intensity (measured as PPFD) between the areas

**Table 4.** Variations in herb species cover (%) recorded for 2 years (wet year and dry year) in unprotected areas under canopied and un-canopied sub-habitats.

| Family | Species | Dry year | | | Wet year | | |
|---|---|---|---|---|---|---|---|
| | | Canopied Sub-habitat | Un-canopied Sub-habitat | *P* | Canopied Sub-habitat | Un-canopied Sub-habitat | *P* |
| Caryophyllaceae | *Paronychia arabica* (L.) DC. | 0.17 ± 0.10 | 0 | NS | 1.11 ± 0.57 | 0.33 ± 0.21 | NS |
| Chenopodiaceae | *Hammada scoparia* (Pomel) Iljin | 0.28 ± 0.11 | 1.33 ± 0.94 | NS | 0.33 ± 0.21 | 1.84 ± 1.06 | NS |
| Cruciferae | *Enarthrocapus clavatus* Godron | – | – | – | 0.11 ± 0.07 | 0 | NS |
| Poaceae | *Stipagrostis pungens* | 0.94 ± 0.67 | 0 | NS | 1.56 ± 0.91 | 0 | NS |
| | *Cenchrus ciliaris* L. | – | – | – | 0.33 ± 0.11 | 0 | NS |
| | *Cynodon dactylon* (L.) Pers | 0.28 ± 0.17 | 0 | NS | 0.44 ± 0.31 | 0 | NS |
| | *Stipa capensis* Thunb. | 0.39 ± 0.10 | 0 | NS | 0.55 ± 0.29 | 0.67 ± 0.33 | * |
| | *Schismus barbatus* | – | – | – | 0.22 ± 0.10 | 0 | NS |
| Fabaceae | *Medicago minima* (L.) L. | 0.06 ± 0.03 | – | NS | – | – | – |
| | *Lotus creticus* (L.) | 0.78 ± 0.58 | 0 | NS | 0.06 ± 0.04 | 0 | NS |
| | *Argyrolobium uniflorum* | – | – | – | 0.06 ± 0.02 | 0 | NS |
| | *Retama retam* (Forssk.)Webb | – | – | – | 0.28 ± 0.12 | 0 | NS |
| Asteraceae | *Astragalus armatus* | 1.44 ± 0.81 | 0 | NS | 1.11 ± 1 | 1.67 ± 0.62 | NS |
| | *Astragalus corrugatus Bertol.* | – | – | – | 0.06 ± 0.02 | 1 ± 0.81 | * |
| Liliaceae | *Asphodelus tenuifolius* Ca | 0.28 ± 0.13 | 0 | NS | – | – | – |
| Plantaginaceae | *Plantago albicans* | 0.44 ± 0.24 | 0 | NS | 0.11 ± 0.09 | 0 | NS |
| Neuradaceae | *Neurada procumbens* (L.) | 0.83 ± 0.42 | 0 | NS | – | – | * |
| Solanaceae | *Lycium chawii* Roem. & Schult. | 0.78 ± 0.43 | 0 | NS | 2.28 ± 1.27 | 0 | NS |
| | *Rhanterium suaveolens* Desf. | 1.11 ± 0.55 | 5.17 ± 1.67 | * | 4.83 ± 1.54 | 10 ± 2.01 | * |
| Capparaceae | *Cleome amblyocarpa* (Barratte & Murb) | 0.33 ± 0.1 | 0 | NS | 5.72 ± 1.95 | 1.67 ± 1 | NS |
| Boraginaceae | *Echium pycnantum* Desf. | – | – | – | 0.11 ± 0.05 | 0 | NS |
| Geraniaceae | *Erodium laciniatum* (Cav.) Willd. | – | – | – | 0.22 ± 0.083 | 0 | NS |

NS non significant, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

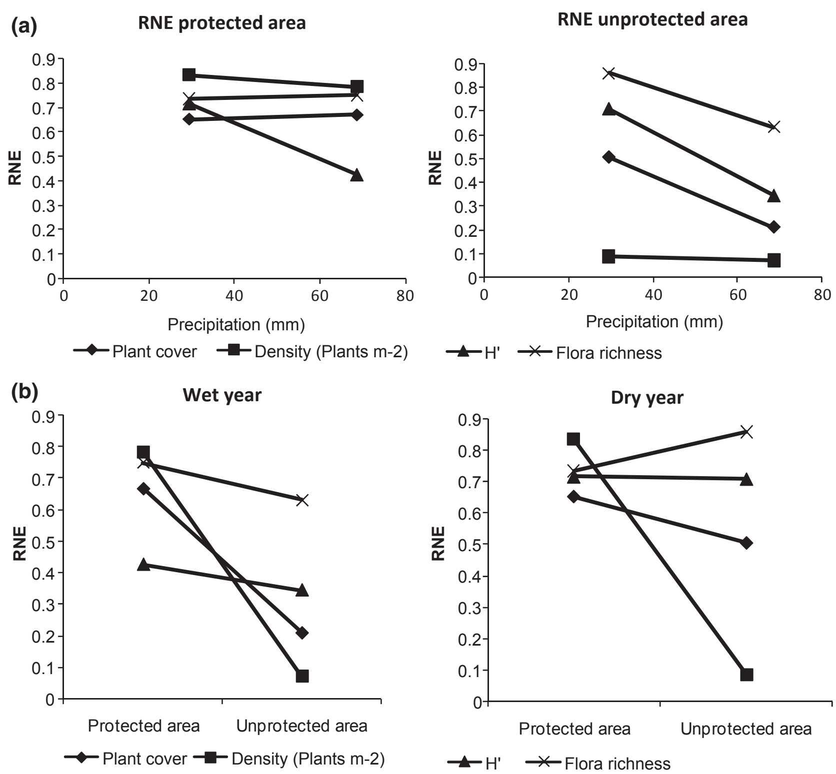


**Fig. 5.** Neighbour effect (RNE) index recorded for 2 years (wet year and dry year) in protected and unprotected areas under canopied and un-canopied sub-habitats.

under and beyond the canopy of a tree, the latter being in full sunlight (Table 2). The daily average PPFD in the un-canopied sub-habitat was 1.45 $mol{\cdot}m^{-2}{\cdot}s^{-1}$. In canopied sub-habitat the daily average PPFD was 0.71 $mol{\cdot}m^{-2}{\cdot}s^{-1}$. Therefore, differences in light intensity between the open area and under the tree canopy were 0.74 $mol{\cdot}m^{-2}{\cdot}s^{-1}$ PPFD, between 08:00 and 16:00 h. This means that the tree canopy intercepts, on average, 48.97% of the light. The maximum difference occurred at midday, with a 53.65% reduction in light level under trees.

### Microclimate data

The average air temperatures recorded between 08:00 and 16:00 h was 26.56 °C under the tree canopy and 29.1 °C in the open area (Table 2). This means that there is an average difference of 2.54 °C between air temperatures under trees compared to open areas; the largest difference (5.3 °C) between the two areas occurred at 14:00 h. The highest air humidity under and the tree canopy was 43.2% but only 33.6% in the open. Hence, there is an average 9.6% difference between the two sub-habitats; moreover, the largest difference (15.5%) occurred at midday (Table 2).

## Discussion

### Soil fertility

Organic matter, N and other soil chemical variables are often higher under trees than in the open in semi-arid and arid areas. In the protected and unprotected area, our study showed that various soil fertility indices (N, P) were significantly higher under the canopy of *A. tortilis* subsp. *raddiana* than in the open. These results are in agreement with those obtained earlier (Callaway et al. 1991; Anderson et al. 2001; Barnes et al. 2009), showing that understorey soil characteristics are strongly influenced by the overstorey plant cover. *A. tortilis* subsp. *raddiana* is classified among trees with a high $N_2$-fixing potential (Gueye & Ndoye 2003). Nitrogen fixation through microbial symbioses under leguminous trees is a possible source of N enrichment (Palm 1995).

On other hand, droppings from birds can also be a source of nutrients under trees, and bird droppings covered the ground under the *A. tortilis* subsp. *raddiana* canopy. Birds were active in all study trees and built an average of ten nests in each *Acacia* (Abdallah et al. 2008). If such activity persists over the lifetime of a tree, these dropping willconstitute an important input of nutrients. Some


Doi: 10.1111/j.1654-109X.2012.01201.x 

mammals also spend time under trees and provide nutrients in their dung. Although they are a minor source of nutrient enrichment (Belsky 1994) inside the park, since they are few in number, they could present an important nutrient source outside the park boundary.

In the protected area, our results suggest that litter covers much of the soil surface under the tree canopy. Nutrient enrichment of soils under tree canopies could be due, in part, to nutrient inputs from litter (Walter et al. 1993). In dry grasslands, litter may help to conserve soil moisture and thus increase plant yield and diversity. Indeed, several studies have demonstrated that litter accumulation and decomposition is a primary mechanism for sustainable soil fertility (Chapin 1991; Koukoura et al. 2003). Facelli & Brock (2000) found that above- and below-ground litter decomposition and mineralization produces a regular gradient in nutrient availability from canopied to open areas. We can therefore assume that the dramatic decline in litter outside the park (Carrera et al. 2008) plays an important role in decreases in organic matter and consequently soil nutrients and moisture. On the other hand, N concentrations of *A.tortilis* leaves are substantially higher than those in other $N_2$-fixing woody species, such as *A. aneura*, *A. niloticaa*nd *A. indica* (Deans et al. 2003), and their decomposition can increase the soil concentration of this element.

### Microclimate conditions

Trees and shrubs have an obvious effect on the microclimate under their canopies (Valiente-Banuet & Ezcurra 1991; Vetaas 1992). Among abiotic characteristics, a reduction of light availability has been emphasized as a main facilitation mechanism for understorey species in Mediterranean-type ecosystems (Maestre et al. 2001; Gómez-Aparicio et al. 2005). Our micrometeorological data show that *A. tortilis* subsp. *raddiana* canopies produced significant changes in light intensity, air temperature and humidity in the understorey. These results agree with those of Callaway et al. (1991), who found that tree shading can decrease air and soil temperatures, consequently this has an important bearing on plant evapotranspiration and hence on plant water status (Amundson et al. 1993). In fact, the positive effect of shade is related to the higher water availability as a result of decreased evaporation and increased water use efficiency due to lower plant transpiration (Ludwig et al. 2001; Whitford 2002). Hence, canopies ameliorate the microclimate inside and/or near canopies, improving the suitability of these sub-habitats for seedling establishment (Callaway 1995). However, we noted that reducing the effect of shade on soil moisture in the unprotected area could be attributed to the nature of the edaphic substrate, which contains more sand with a lower water retention capacity. The formation of sand in this area isrelated to degradation because of the reduced plant cover, especially the disappearance of perennial species whose root systems promote soil fixation.

### Total plant cover and understorey species composition

In agreement with Vetaas (1992), Belsky et al. (1993) and Jeddi & Chaieb (2010), the main results of this study show that, inside the National Park of Bou Hedma, total plant cover and perennial density were higher under the tree canopy. The improvement recorded can be related to higher soil fertility, higher water availability and a more favourable microclimate under the *A. tortilis* subsp. *raddiana* canopy. Nutrients such as nitrate, phosphorus, anions and cations and various trace elements are essential to the nutrition of all plants (Bell 1982). In the Tunisian arid zone, characterized by soils with low levels of these elements, the increase in concentration of such nutrients can act as a determinant of the composition, structure and productivity of vegetation. Additionally, the woody species may protect herbaceous plants from herbivory, particularly when they have spines (Milchunas & Noy-Meir 2002). In windswept arid zones, trees provide a better protection for species growing under their canopy, which probably explains the increase in total plant cover observed under tree canopy compared to the open area.

In the long term, shade created by the tree canopy might be an important factor in determining the occurrence of herbaceous species under trees. When *Acacia* trees start to establish, among the major environmental change for understorey herb species is the provision of shade, and this light reduction probably leads to the disappearance of the open area species, which are then replaced by other species (Ludwig et al. 2004). In our study site, the positive effect of *A. tortilis* subsp. *raddiana* was related to the appearance in canopied area of grass species known for their high palatability, such as *Cynodon dactylon*, *Cutandia dichotoma*, *Cenchrus ciliaris* and *Eragrostis papposa*. These results confirm observations from Botswana (Veenendaal 1991) and Nigeria (Sanford et al. 1982), which show a linear relation between woody cover and graminaceous species. Our results are in agreement with those obtained in Australia (Christie 1975; Ludwig et al. 2004), indicating that *Cenchrus ciliaris*, a perennial grass, grows better under woody cover. The abundance of some nitrogen-rich species (*Chenopodium album* and *Sysimbrium irio*) can be assigned to their ability to use the high amount of available soil nutrients under tree canopies.

The effect of the presence of *Acacia* trees changed with the type of land management (protected areas vs unprotected areas). As already demonstrated (Vandenberghea et al. 2008; Brooker et al. 2006; Smith et al. 2007), our study also showed that the facilitative effect of *Acacia* trees decreases with increasing grazing intensity. In fact, compared to protected areas, the positive effect of the *A. tortilis* canopy on its understorey vegetation was less (especially during the dry year) in unprotected areas but tended to disappear during the wet year. Moreover, both water limitation and a long history of human-induced disturbances have led to low vegetation cover and large areas of sand and bare soil in Tunisia. These results confirm those in other areas (Belsky et al. 1993), showing differences between tree cover and grassland zones. Indeed, under arid and Saharan climates, which are characterized by high summer temperature, the shade from trees constitutes a shelter for animals. The pasture plant species under trees are generally selectively grazed, and these palatable species have become threatened. Intense grazing of rangelands often results in highly competitive palatable species being replaced by less palatable species, which are often considered less desirable or even worthless (Callaway & Tyler 1999), such as *Astragalus armatus* and *Cleome amblyocarpa*. Similar results have been reported in West & Smith (1997) and Aronson & Le Floc'h (1995), who also recorded rarefaction of valuable pastoral species in grazed areas.

### Effect of water stress and grazing intensification on tree–herb interactions

Trees and shrubs are considered as key organisms in Mediterranean ecosystems, since they promote succession by facilitation. The idea that the role of facilitative interactions increases as environmental conditions becomes more stressful has become a ruling paradigmin ecology (Tewksbury & Lloyd 2001; Holmgren & Scheffer 2010). The shade from canopies of long-lived *Acacia* trees can have a strong effect on the structure of arid Tunisian ecosystems, leading tolarge increases in plant cover, species richness and density. This effect was higher during the dry year, when water stress in open areas was more extreme. Under these conditions, the plant cover, species richness and density of both perennials and annuals in the open were consistently lower than in the canopied sub-habitat, suggesting that *Acacia* canopies may act as an environmental buffer. This buffering appears to lead to differences in the importance of facilitation as a function of ambient levels of water stress. Under higher abiotic stress, the vegetation under *Acacia* canopies contributes more to site-level diversity than under low abiotic stress. Thus, as predicted by Bertness & Callaway (1994) and more recently by Hacker & Gaines (1997), the positive influence of *Acacia* canopies plays a larger role in maintaining plant cover, density, species richness and diversity as abiotic stress increases. Contrasting findings of Penning et al. (2003) and Maestre et al. (2005) suggest that facilitation does not increase with stress in arid environments. Similarly, Holmgren & Scheffer (2010) suggest that positive interactions may be more important than generally thought under moderately stressful rather than under extreme conditions.

## Conclusion

Our results confirmed the positive effect of *A. tortilis* subsp. *raddiana* on the understorey vegetation cover density, diversity and composition in arid ecosystems. This positive effect can mainly be ascribed to grass species such as *Cynodon dactylon*, *Cenchrus ciriaris*, *Cutandia dichotoma* and *Eragrostis papposa*, which showed a strong preference for the canopied sub-habitat. This broad tree canopy causes a significant reduction in light intensity, air temperature and humidity that increases soil moisture content and facilitates the establishment of more resistant vegetation under the unfavourable climate conditions that characterize these environments. As *A. tortilis* subsp. *raddiana* is a leguminous species, it is not surprising that it had a strong positive effect on soil nutrient enrichment,which represents another factor that encourages growth of a herb strata. However, it seems that grazing and abiotic stress gradients are two factors influencing the tree–herb interaction. The relative importance of facilitation increases with increasing abiotic stress and decreases with grazing.

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