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Effect of the canopy of *Retama sphaerocarpa* on its understorey in a semiarid environment

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Summary

1. A dense understorey of annual and perennial herbs grow under the canopy of *Retama sphaerocarpa* shrubs in semiarid environments of south-east Spain, influencing plant productivity and diversity at a regional scale. We investigated the facilitation by the shrub on its understorey in field and laboratory experiments with Barley designed to explore the mechanisms of interaction between both vegetation layers and their spatial variation.
2. There was a gradient of spatial heterogeneity in soil chemical fertility under the shrub canopy, with organic matter and soil nitrogen contents higher at the centre than at the edge of the canopy. Dry mass production of Barley was also higher in soils from intermediate positions, and lower in soils from both the centre and edge of the canopy.
3. In the field, pots sown with Barley placed near the centre, at an intermediate position and at the edge of the canopy of *Retama* shrubs showed significant differences in productivity, suggesting a mulching effect of the canopy that also affects seedling establishment.
4. Micro-climatic measurements showed significant differences in total radiation reaching the soil, mean air and soil temperatures and maximum temperature among different positions in the understorey, increasing radially from the centre to the edge of the canopy.
5. These results and field observations suggest that the optimal association of climatic factors under the canopy would combine with a high soil fertility mediated by litter decomposition to increase biomass production mid-way between the centre and the edge of the canopy. Overstorey and understorey thus interact to increase nutrient retention locally, which benefits both the shrub and the herb layer.

Key-words: Arid environments, facilitation, litter, productivity, shrub canopy, species interactions
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Introduction

In arid and semiarid ecosystems, where variation in the spatial and temporal availability of water and nutrients is extreme, dominant woody plants cause changes in micro-climate and soil properties that lead to complex local interactions between vegetation and soil (Wilson & Agnew 1992). Floristic composition and productivity of annual plants in these regions are strongly affected by small-scale variation in resources (Gutiérrez & Whitford 1987; Gutiérrez *et al.* 1993; Pugnaire, Haase & Puigdefábregas 1996), particularly in the understorey of shrubs and trees, which concentrate flora and fauna under their canopies (see Allen 1991, West 1991 and Veetas 1992 for reviews). These so-called ‘fertile islands’ (García-Moya & McKell 1970; Garner & Steinberger 1989) are points of high biological activity scattered in a heterogeneous landscape in which facilitation is the dominant interaction.

Recent work has emphasized the role of facilitation in the dynamics of plant communities (Bertness & Callaway 1994), particularly in arid environments and deserts (McAuliffe 1988; Franco & Nobel 1989; Silvertown and Wilson 1994; Pugnaire, Haase & Puigdefábregas 1996), Arctic regions (Carlsson & Callaghan 1991; Chapin *et al.* 1994) and salt marshes (Bertness & Shumway 1993), suggesting that positive interactions among plants could be widespread (Callaway 1995).

Complex interactions between perennial and annual species are common in these vegetation systems where growth of annual plants may be facilitated by a higher soil fertility (García-Moya & McKell 1970; Hook, Burke & Lauenroth 1991; Gutiérrez *et al.* 1993), availability of water (Dawson 1993; Joffre & Rambal 1993) or microclimate amelioration (Valiente-Banuet & Ezcurra 1991) caused by perennial species. Light deprivation and mechanical and chemical effects of litter (Facelli & Pickett 1991b) can also reduce understorey growth.

One such system is formed by *Retama sphaerocarpa* (L.) Boiss., a leguminous shrub common in semiarid environments of south-east Spain. Feedback effects between *Retama* and its understorey suggest that both the shrub and the herb community may benefit from their interaction (Pugnaire, Haase & Puigdefábregas 1996). This interaction comprises several factors, from changes in soil fertility and micro-climate to effects on the soil seed bank and germination. We report in this paper several experiments in which we used Barley to test the interaction between the *Retama* canopy and its understorey, trying to quantify the extent to which *Retama* shrubs influence soil fertility, affect germination and plant growth, and alter the micro-climate beneath their canopy, making it more suitable for annual plant growth as well as the spatial variation of these effects.

Field site and species

The field site is in the Rambla Honda, a valley with ephemeral surface drainage on the southern slope of the Sierra de los Filabres range, *c.* 40 km north of Almería, south-east Spain (37° 08′N, 2° 22′W, 630 m altitude). The regional climate is semiarid; the available 5-year record (1990–1994) gives a mean annual temperature of 15·7 °C and a mean annual rainfall of 259 mm (R. Lázaro, unpublished data). There is a pronounced dry season from May to September, with practically no rainfall in this period. Longer-term (1965–1991) climatic records for Tabernas (490-m elevation; 17·9 °C, 218 mm), 10 km to the south of the field site, indicate high inter-annual variation in the rainfall pattern and total amounts of rainfall (Lázaro & Rey 1991).

The valley bottom is filled with thick and poorly sorted alluvial deposits on a mica-schist bedrock (Puigdefábregas *et al.* 1996) and is covered by open shrubland dominated by *R. sphaerocarpa*. Soils are characterized by a very low water holding capacity, a pH ranging from slightly acidic (6·5) to moderately alkaline (8), low electrical conductivity and low cation exchange capacity (Puigdefábregas *et al.* 1996).

Retama sphaerocarpa is a practically leafless shrub with evergreen photosynthetic stems which occurs in the Mediterranean part of northern Africa and in the Iberian Peninsula. The shrub has a deep root system which is functional at depths of > 20 m (Haase *et al.* 1996) and provides access to deep water sources.

Materials and methods

SOIL COLLECTION AND ANALYSIS

In early October 1993, six mature *Retama* shrubs of approximately 2-m height and 5 m^2 of projected canopy area were selected in the valley bottom of the Rambla Honda. Samples of surface soil to 5-cm depth were collected concentrically under each shrub. The sampling locations were: (1) around the centre of the canopy near the basal insertion of the branches (centre canopy soil, CS); (2) half-way between the centre and the edge of the canopy (intermediate canopy soil, IS); (3) just at the edge of the canopy (outer canopy soil, OS). All samples were passed through a 2-mm sieve to remove stones and litter. Six samples from each position were bulked and used as substrate for the experiments. A subsample from each shrub and position was air-dried and used for soil analysis. Soil texture was determined using discontinuous sedimentation granulometry (Porta 1986) resulting in five particle size classes: coarse sand (2000–500 μm), fine sand (500–50 μm), coarse silt (50–20 μm), fine silt (20–2 μm) and clay (< 2 μm). Total N was determined using a micro-Kjeldahl digestion method (López & López 1985). pH was measured in a suspension of soil in distilled water (1 : 2·5) using a CRISON 2002 pH meter. Electrical conductivity was determined with a CRISON 525 conductivimeter. Organic matter was determined by mass loss after combustion at 430 °C.

Samples of litter were collected from 25 cm × 25 cm quadrats placed near the centre, half-way between the centre and the edge, and just at the edge under the canopy of 10 *Retama* shrubs. The samples were cleaned, air dried and weighed. A subsample was oven-dried at 80 °C and weighed. All samples were separated into five fractions: (1) recent *Retama* cladodes (mostly shed in August 1993); (2) old *Retama* cladodes (mostly shed in the summer of 1992); (3) litter of annual and perennial understorey plants (dating from 1993); (4) wood; (5) fine material consisting mainly of old disintegrated *Retama* cladodes.

DETERMINATION OF SOIL CHEMICAL FERTILITY

Ten 2-kg aliquots of each composite soil sample (CS, IS and OS) were placed into polyethylene pots with an upper diameter of 15·3 cm and sown with 50 seeds of spring Barley *var.* KIM and used to test for differences in soil fertility. The experiments were carried out at the Estación Experimental de Zonas Áridas, Almería (18·2 °C mean annual temperature and 227 mm of annual rainfall), starting on 29 October 1993. Pots containing Barley seeds were kept outdoors covered with a transparent plastic sheet at 2·5-m height to exclude rainfall. Soil in the pots was maintained nearly at field capacity during the experiment by regular applications of deionized water, and the pots were periodically rearranged at random to avoid positional effects. Barley seedlings were harvested 47 days after

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sowing, when maximum growth had been achieved and the first signs of senescence were observed in some leaves. The total number of germinated seeds and average height of plants were registered for each pot. Shoots and roots were collected separately. Roots were carefully cleaned of attached soil particles. Both roots and shoots were oven-dried at 70 °C for 48 h and weighed. A random subsample of five shoots was used to calculate mean dry weight per shoot. For each pot, the leaf area of a random subsample of five leaves was measured with an area measurement system (Mk 2, Delta-T Devices, Burwell, UK). The subsamples were then oven-dried and weighed, and the data used to calculate specific leaf area (SLA). Total N was analysed in both shoots and roots with a Kjeldahl autoanalyser (Kjeltec Auto model 1030 Analyser, Tecator, UK).

EFFECT OF LITTER ON PRODUCTIVITY

The effect of litter on germination and productivity was assessed in pots filled with bulked soil taken from the intermediate position under the canopy (IS) sown with 50 seeds of Barley. Two different amounts of litter, consisting of recently shed *Retama* cladodes, were added to each set of pots (L_1: 1000 g m^{-2} and L_2 : 2000 g m^{-2}) and compared with the control (L_o, no litter added). These amounts corresponded approximately to the average litter pool found in the intermediate and the centre of *Retama* canopies, respectively. The experimental set-up, measured parameters and analytical procedures for pots with barley were as described above. Barley seedlings in the litter treatments were counted only after they emerged through the litter layer.

EFFECT OF THE CANOPY

The effect of the different positions under the *Retama* canopy on productivity was assessed on one set of pots containing bulked surface soil taken from the intermediate position under the canopy (IS) sown with spring Barley *var.* KIM (15 seeds pot $^{-1}$) on 18 March 1994 and placed at three positions relative to the canopy (centre, intermediate and outer) below 10 mature *Retama* shrubs located in a fenced area at the bottom of the Rambla Honda. Pots were watered with deionized water at weekly intervals, harvested on 27 May 1994 and analysed as described above.

STATISTICAL ANALYSIS

One-way ANOVA was used to test the effect of soil type, amount of litter and position under the canopy on plant variables. Differences in soil properties, dry mass of litter fractions, radiation and temperature data were also tested by ANOVA. Data were normalized when needed by log, square-root or arcsine transformations prior to the statistical analysis. When significant differences were found, means were separated using *a posteriori* Scheffé test (Sachs 1982). To overcome pseudoreplication in the first experiment, the level of significance in the *a posteriori* test was kept at $P < 0{\cdot}001$. All statistical analysis were performed with the SPSS statistical package.

Table 1. Characteristics of soil from three positions in the understorey of *Retama sphaerocarpa* shrubs. Data are mean ± 1 SE; $n = 6$. Values in a row followed by the same letter are not statistically different (Scheffé test, $P < 0{\cdot}01$). Significance of ANOVA given by *** $P < 0{\cdot}001$, ** $P < 0{\cdot}01$, *$P < 0{\cdot}05$; NS, not significant.

	Position			
	Centre	Intermediate	Outer	*P*
pH	7·3 ± 0·1[a]	7·1 ± 0·1[a]	7·1 ± 0·0[a]	NS
EC (µS/cm)	651 ± 198[a]	622 ± 64[a]	435 ± 23[a]	NS
Coarse sand (%)	31·6 ± 2·4[a]	40·3 ± 5·0[a]	35·6 ± 6·3[a]	NS
Fine sand (%)	56·9 ± 2·3[a]	47·5 ± 4·6[a]	51·9 ± 6·0[a]	NS
Coarse silt (%)	2·9 ± 0·4[a]	3·1 ± 0·7[a]	4·4 ± 0·7[a]	NS
Fine silt (%)	5·1 ± 0·6[a]	5·9 ± 0·6[a]	6·9 ± 0·9[a]	NS
Clay (%)	3·4 ± 0·3[a]	3·1 ± 0·1[a]	2·6 ± 0·1[a]	NS
Organic matter (%)	3·9 ± 0·3[a]	3·6 ± 0·4[a]	2·1 ± 0·2[b]	**
Total N (mg g^{-1})	1·7 ± 0·2[a]	1·8 ± 0·2[a]	0·9 ± 0·1[b]	**

Results

SOIL CHARACTERISTICS AND PRODUCTIVITY

The surface soils from the three microsites (CS, IS and OS) were coarse-textured and had a pH approximately neutral and low electrical conductivity. Most soil physical properties did not differ significantly among microsites under the canopy (Table 1). As expected, soil organic matter and total N were significantly higher in soils from the inner understorey positions than from the edge, but no significant differences in physical nor chemical properties were found between the two inner microsites.

The three soil types differed significantly in dry mass production of Barley as well as in N concentration and N uptake (Table 2). Thus soil from the intermediate position (IS) produced larger, taller plants and more total dry mass than CS soils ($P < 0{\cdot}05$) while much lower values were obtained in OS soils. Concentration of N in leaves and roots and total uptake of N by Barley plants followed the same pattern. Differences among the three soil positions in leaf area per unit leaf mass (SLA) and root/shoot ratio were not significant. Barley seeds had significantly lower germination rate (73%) in soil from the edge of the canopy (OS) than in the two inner positions (92% in IS and 94% in CS).

THE EFFECT OF LITTER

In the field, biomass of litter as well as its different fractions decreased radially from the centre of the canopy to the edge (Table 3). Because of the large variation between individual samples, the means of some fractions of the central and intermediate positions were not significantly different, however. Total litter amounted to 1·7 kg m^{-2} (dry mass) in the centre, and decreased to 69% in the intermediate position and to 20% at the edge of the canopy. Litter of herbaceous species accounted 5·0 ± 0·7% of total litter in the centre and increased to 6·1 ± 1·0% in the intermediate and 8·7 ± 2·0% at the edge of the canopy. This fraction of litter decomposes more easily than *Retama* cladodes and may help to increase the turnover rate of organic matter by facilitating decomposition.

In the pot experiment, the addition of litter had a significant and negative effect on both dry mass production and N concentration and uptake of Barley seedlings (Table 4), but the quantity of litter added did not have significant effects. The dry mass of individual Barley plants and the number of germinations per pot were slighty lower in pots covered by litter than in controls, but differences were not significant. Nevertheless, a slightly smaller plant size along with a lower germination rate accounted for the significant decrease in total biomass in both litter treatments (Table 4). Structural attributes of Barley such as SLA and root/shoot ratio were not affected by the treatment (data not shown), while Barley seedlings in the L_2 pots were on average taller than those in L_o and L_1.

Table 2. Germination rate, dry mass production, morphological traits, N uptake and N concentration of Barley plants grown in soil from three different positions in the understorey of *Retama sphaerocarpa* shrubs. Data are means ±1 SE; *n* = 10. Values in a row followed by the same letter are not statistically different (Scheffé test, $P < 0{\cdot}001$). Significance of ANOVA given by *** $P < 0{\cdot}001$; NS, not significant.

	Soil type			
	Centre	Intermediate	Outer	*P*
Germination rate (%)	93·8 ± 1·6[a]	92·2 ± 1·4[a]	73·2 ± 3·6[b]	***
Dry mass production (g / pot)	7·1 ± 0·1[a]	8·56 ± 0·17[b]	3·06 ± 0·12[c]	***
Individual dry mass (g)	0·11 ± 0·01[a]	0·14 ± 0·01[a]	0·04 ± 0·00[b]	***
Height (cm)	29·2 ± 0·6[a]	30·7 ± 0·4[a]	23·8 ± 0·8[b]	***
SLA (cm^{2}g^{-1})	471 ± 13[a]	441 ± 6[a]	431 ± 9[a]	NS
Root / shoot	0·67 ± 0·02[a]	0·79 ± 0·02[a]	1·10 ± 0·03[a]	NS
N uptake (mg pot^{-1})	126 ± 2[a]	174 ± 4[b]	47 ± 2[c]	***
N concentration (mg g^{-1})				
shoots	18·3 ± 0·4[ab]	20·6 ± 0·4[a]	16·6 ± 0·3[b]	***
roots	17·1 ± 0·4[a]	19·9 ± 0·2[b]	13·9 ± 0·4[c]	***

Table 3. Dry mass (g) of litter fractions collected from 25 × 25 cm plots in three positions under *Retama* shrubs (mean ± 1 SE, *n* =10). Statistics as in Table 1

	Position			
	Centre	Intermediate	Outer	*P*
Recent cladodes	30·8 ± 2·8[a]	28·3 ± 3·0[a]	11·8 ± 1·2[b]	***
Old cladodes	45·9 ± 5·0[a]	31·1 ± 4·8[a]	6·9 ± 1·3[b]	***
Annual / perennial	4·7 ± 0·4[a]	3·9 ± 0·3[a]	1·7 ± 0·4[b]	***
Wood	3·8 ± 1·4[a]	0·1 ± 0·1[b]	0·3 ± 0·1[c]	**
Fine material	18·7 ± 2·3[a]	8·2 ± 2·1[b]	0·0 ± 0·0[c]	***
Total	104·0 ± 7·9[a]	71·8 ± 7·5[b]	20·7 ± 1·7[c]	***
kg m^{-2}	1·66	1·14	0·33	

Table 4. Germination rate, dry mass production, morphological traits, and N concentration and uptake of Barley plants grown in pots with three levels of *Retama* litter: control (L_0), L_1 (1000 g m^{-2}) and L_2 (2000 g m^{-2}). Values are means ± 1 SE; *n* = 10. Statistics as in Table 1

	Litter			
	L_0	L_1	L_2	*P*
Germination rate (%)	92 ± 1[a]	89 ± 5[a]	76 ± 9[a]	NS
Height (cm)	30·7 ± 0·4[a]	31·3 ± 0·4[a]	33·0 ± 0·6[b]	**
Total dry mass (g pot^{-1})	8·6 ± 0·2[a]	6·10 ± 0·38[b]	5·65 ± 0·64[b]	**
Individual dry mass (g)	0·14 ± 0·01[a]	0·11 ± 0·01[a]	0·12 ± 0·01[a]	NS
N uptake (mg pot^{-1})	174 ± 3[a]	106 ± 7[b]	101 ± 11[b]	***
N content (mg g^{-1})				
shoots	20·6 ± 0·4[a]	17·7 ± 0·5[b]	19·0 ± 0·8[ab]	*
roots	29·9 ± 0·2[a]	17·1 ± 0·4[ab]	16·7 ± 1·0[b]	*

MICRO-CLIMATE AND LIGHT QUALITY UNDER *RETAMA* CANOPIES

In the field, a mean photosynthetic photon flux density (PPFD) of 709 μmol m^{-2} s^{-1} was measured at the edge of the canopy during daylight hours, and significantly decreased towards the centre of the canopy (Table 5). Integration throughout the day gave a total of 37·0 mol m^{-2} at the edge of the canopy, of which only 75% reached the soil surface at intermediate positions and 60% at the centre (Table 5). The quantum sensor placed at the edge of the canopy received almost unobstructed sunlight until 12·00 h, just before the daily maximum occurred, and was temporarily or partly shaded during the remainder of the day. The shading effect of the canopy commenced about 1 h earlier in the mid-canopy position and was more pronounced during the afternoon. The central position had already been partly shaded since just before 09·00 h.

Mean soil surface temperature (33·7 °C) measured at the edge of the canopy during daylight hours decreased by 2·9 °C towards the intermediate location, and by 4·7 °C towards the centre of the canopy (Table 5). Differences in both daily means and daylight means of temperature were significant between the three positions. Maximum temperature under the canopy was 7 °C lower than at the edge (54·6 °C), where slightly lower minimum temperatures were measured at night.

A mean red/far red ratio of 1·01 ± 0·02 was measured at the surface of 10 pots placed at the edge of the canopy. The two inner positions had significantly ($P < 0{\cdot}001$) smaller ratios, decreasing to 0·85 ± 0·01 and 0·76 ± 0·02 towards the intermediate and centre positions, respectively.

EFFECT OF THE CANOPY ON GERMINATION AND PRODUCTIVITY

Total dry mass production, dry mass of individual plants, number of seedlings and N-uptake values decreased from the centre to the edge of the canopy (Table 6). SLA did not differ among positions but root/shoot ratio was significantly higher in pots placed at the edge of the canopy.

Discussion

VARIATION IN SOIL CHARACTERISTICS AND FERTILITY

Soil chemical analyses and plant productivity showed a gradient in fertility from the inner parts of the canopy to the openings, being organic matter and total N highest in the two inner microsites than in samples from the edge. Organic matter, N and other soil chemical variables are often higher under tree and shrub canopies than in gaps in semiarid and arid zones such as African savannahs (Bernhard-Reversat 1982), Chilean matorral (Gutiérrez *et al.* 1993) and North American grasslands and deserts (García-Moya & McKell 1970; Charley & West 1975; Barth & Klemmedson 1978; Virginia & Jarell 1983; Hook *et al.* 1991; Halvorson *et al*. 1994), showing that understorey soil characteristics are strongly influenced by the overstorey plants.

Table 5. Photosynthetic photon flux density (PPFD) and temperature in three different positions under *Retama* shrubs (SE aspect). Statistics as in Table 1

	Position			
	Centre	Intermediate	Outer	*P*
PPFD (μmol m^{-2}s^{-1})				
Daylight mean	426^{a}	533^{b}	709^{c}	***
Maximum	1662	1735	2194	
Daily total†	22·2	27·8	37·0	
Temperature (°C)				
Daily mean	23·8^{a}	25·1^{b}	26·7^{c}	***
Daylight mean	28·9^{a}	30·7^{b}	33·6^{c}	***
Maximum‡	47·4^{ab}	47·2^{a}	54·6^{b}	*
Minimum‡	12·6^{a}	12·7^{a}	12·1^{a}	NS

† In mol m^{-2}.
‡ Mean of four sensors.

Table 6. Dry mass production, morphological variables and N uptake of Barley plants grown in pots filled with the same soil (from an intermediate position) and placed in the three positions under the *Retama* canopy. Values are means ± 1 SE, $n = 10$. Statistics as in Table 1

	Position			
	Centre	Intermediate	Outer	*P*
Total dry mass (g pot^{-1})	6·6 ± 0·6^{a}	4·4 ± 0·4^{b}	2·7 ± 0·3^{c}	***
Individual dry mass (mg)	147 ± 18^{a}	89 ± 19^{a}	26 ± 4^{c}	***
SLA (cm^{2} g^{-1})	262 ± 17^{a}	240 ± 14^{a}	275 ± 18^{a}	NS
Root / shoot	1·0 ± 0·1^{a}	1·9 ± 0·3^{a}	3·8 ± 0·7^{b}	***
N uptake (mg pot^{-1})	100 ± 9^{a}	57 ± 4^{b}	40 ± 5^{c}	***

In our study, soil under *Retama* shrubs in the bottom of Rambla Honda showed no significant differences in texture or chemical variables between the centre (CS) and the intermediate (IS) soil positions, though dry mass production of Barley in IS was higher than in CS. Barley plants were larger, had higher concentration of N in shoots and roots and hence, had greater N uptake. The improved growth of Barley in IS soils can only be attributed to differences in potential mineralization rate, which is higher in IS (Moro *et al.* 1997), suggesting a more favourable microhabitat for soil micro-organisms at intermediate positions under the canopy than at the centre of the shrub. In addition, the amount of decomposed organic matter per kg of soil was also higher in IS soils (Moro *et al.* 1997). Though differences in microbial activity between understorey soils and gaps in arid and semiarid areas are the norm (Hook *et al.* 1991; Gallardo & Schlesinger 1992), differences in microbial activity at different microsites below the shrub canopies have not been described. Less favourable conditions for microbial activity in the middle of the canopy may result from higher concentration of toxic substances leached from the litter layer, which is thicker in the centre, or from the canopy. *Retama* cladodes contain a high concentration of alkaloids (Martín-Cordero, Gil & Ayuso 1993) which make them unpalatable to livestock and which may also influence soil microbial activity.

THE ROLE OF LITTER

The effect of litter on population and community dynamics has received less attention than the historical view of litter as a mediator of energy flow (Bergelson 1991), and its influence on the structure and dynamics of annual communities has been shown in recent studies (Bergelson 1990; Facelli & Pickett 1991a,b; Tilman & Wedin 1991; Eriksson 1995). Litter of *Retama* promotes changes in the community structure, reducing the germination and establishment of all major species (Moro *et al.* 1997) with a decrease in biomass production with increasing litter cover as a direct consequence. Our results suggest that litter mainly influences germination and seedling establishment, because survival after emergence through the litter layer did not differ significantly from the control. Litter most likely influences germination and establishment of annual plants through light deprivation and changes in light spectral quality along with mechanical obstruction and leaching of phytotoxic compounds (Bergelson 1991; Facelli & Pickett 1991b; Tilman & Wedin 1991).

EFFECTS OF THE CANOPY

Trees and shrubs have an obvious effect on the microclimate under their canopies (Valiente-Banuet & Ezcurra 1991; Vetaas 1992). Our micro-meteorological data show that *Retama* canopies produced significant changes in PPFD, spectral light quality, and soil temperature in the understorey. Because of the very sparse canopy of *Retama* shrubs, light levels in the shade of the canopy are not normally limiting to plant growth in the understorey. On the other hand, shading significantly reduced soil (and surface air) temperatures, which has an important bearing on evapotranspiration and hence on plant water status. Amelioration of the micro-climate below the shrubs had a profound positive effect on growth of barley seedlings. Even comparatively minor micro-climatic gradients at very small spatial scales had significant effects on understorey plants growing beneath the *Retama* canopy, as indicated by the substantial decrease in plant productivity from the centre to the intermediate canopy positions. The canopy also produces spatial variation in soil moisture by rainfall interception (Pressland 1973; Mauchamp & Janeau 1993; M. J. Moro, unpublished data) and hydraulic lift of water from deep-seated sources (Caldwell & Richards 1989; Caldwell 1990; Dawson 1993).

However, the herbaceous cover could benefit the shrub by protecting the soil from high temperatures and irradiation, by storing nutrients and providing easily decomposing litter (Pugnaire, Haase & Puigdefábregas 1996).

In conclusion, in semiarid ecosystems tall perennial plants provide local patches in which the combined effects of canopy, herbs and litter cover produce complex interactions resulting in ameliorated micro-environments and nutrient enrichment that favour growth of both the shrub and its understorey. These systems are important nuclei of biological diversity and biomass productivity, and contribute significantly to spatial variation, productivity and biodiversity on regional scales.

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