

Soil as a mediator in plant-plant interactions in a semi-arid community

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Abstract. Competition and facilitation may occur simultaneously in plant communities, and the prevalence of either process depends on abiotic conditions. Here we attempt a community-wide approach in the analysis of plant interactions, exploring whether in a semi-arid environment positive or negative interactions predominate and whether there are differences among co-occurring shrub species. Most shrubs in our plot exerted significant effects on their understorey communities, ranging from negative to positive. We found a clear case of interference and another case where the effect was neutral, but facilitation predominated and the biomass of annuals under most shrubs in our community was larger than in gaps. Effects on soil water and fertility were revealed as the primary source of facilitation; the build-up of soil organic matter changed soil physical properties and improved soil water relations. Facilitation by shrubs involved decoupling of soil temperature and moisture. Sheltering from direct radiation had an effect on productivity, but significant differences in understorey biomass did not parallel understorey light environment. A positive balance of the interaction among plants, essentially mediated by changes in soil properties, is the predominant outcome of plant interactions in this semi-arid community.

Keywords: Competition; Facilitation; Interference; Soil humidity; Water stress.

Nomenclature: Castroviejo et al. (1986-2001).

Abbreviations: A = photosynthetic rate; Fv/Fm = photochemical efficiency of photosystem II; gs = leaf conductance to water vapour; OM = organic matter; PAR = photosynthetic active radiation; Ψ_{PD} = Predawn water potential.

Introduction

Effects of abiotic factors on competition have been addressed for decades, but facilitation has more recently been revealed as a process as important as competition in many habitats (Callaway 1995). While plants may ameliorate physical stress, providing suitable habitats for the establishment of other species, competition for resources may reduce or override facilitation (Tielborger & Kadmon 2000; Pugnaire & Luque 2001). Bertness & Callaway (1994) predicted that the importance of facilitation increased with increasing environmental stress, and some reports show that the intensity of facilitation increases with stress (e.g. Pugnaire & Luque 2001; Tewksbury & Lloyd 2001; Cavieres et al. 2002). However, there are less data on how important facilitation is at the community level (Callaway et al. 2002) or how common it is in a given environment. Positive interactions among plants may be particularly common in dry environments, where shade, conservation of soil moisture and nutrient accretion seem to be the main facilitation mechanisms (Callaway & Pugnaire 1999). The environment under shrubs and trees often becomes a suitable habitat for plant growth (Muller 1953; Vetaas 1992; Haase et al. 1996), because the benefits of finding shelter may offset the detrimental effects of competition when abiotic factors are extreme. The final balance of the interaction between overstorey and understorey plants depends on how the different species modify their environment, which may include changes in nutrient dynamics (Hobbie 1992) and water availability (Breshears et al. 1998; Dunne & Parker 1999). These processes will ultimately determine whether positive or negative effects predominate under the canopy.

Evidence for facilitation in stressful environments is based on spatial patterns of plant cover or on neighbour removal experiments; however, relatively little is known about causal mechanisms of facilitation, and such a knowledge is a necessary next step for improving our understanding of vegetation processes. This work aims

to explore the mechanisms of biotic interactions in a semi-arid community. We test, in a natural experiment, how common facilitation was at the community level in a semi-arid environment and whether there were differences in facilitation among different co-occurring shrub species, while exploring the mechanisms involved in the productivity of understorey annual plant communities. We also test whether facilitation of herbaceous plants by woody species occurs through an attenuation of irradiance and improved nutrient and water availability. Finally we test whether shrub water status had any influence on its understorey community, as less stressed shrubs may enhance growth via increased litter production or improved water dynamics underneath them.

Methods

Field site and species

The field site was selected on an abandoned cropland where the community was apparently homogeneous. It was located at the Ramblilla de Genaro, a valley near Tabernas, Almería Province, Spain (37°01' N, 2°25' W, 350 m a.s.l.) in the northern foothills of the Sierra Alhamilla range, 20 km north of Almería city. The climate in this area is Mediterranean semi-arid with a mean annual precipitation of 242 mm and a pronounced dry season from June to September during which there is almost no rain in most years. Mean annual temperature in Tabernas (490 m altitude, 3 km to the east) is 17.9 °C with mean maxima of 10.7 °C in January and 34.7 °C in August. Other general characteristics of the site and climate have been described elsewhere (Pugnaire & Haase 1996; Pugnaire et al. 1996a, b). Cover of perennial species, determined by ten 50-m long transects, is low ($26.7 \pm 0.8\%$), and dominated by two long-lived tussock grass species, *Stipa tenacissima* and *Lygeum spartum* (with a total of 73% of plant cover). In marl communities shrubs are interspersed in the grassland; most common species are *Retama sphaerocarpa* ($6 \pm 2\%$ cover) and *Salsola oppositifolia* ($9.9 \pm 8\%$) as well as other salt-tolerant species because soil salinity is locally high (Peinado et al. 1992).

Five individuals of the six most frequent shrub species were randomly selected in a uniform flat area of about 1 ha. The species were *Arthrocnemum macrostachyum*, *Launaea arborescens*, *Lycium intricatum*, *Retama sphaerocarpa*, *Salsola oppositifolia* and *Thymus hyemalis*, all of which are typically found in semi-arid environments of SE Spain and some of which are also found near salt marshes (Peinado et al. 1992).

Herbaceous plant communities

Annual plant communities were sampled at the peak of biomass production in April, at four aspects (N, S, E, and W) under the canopy of each individual shrub and in ten gaps, using 10 cm × 10 cm quadrats. In the understorey, quadrats were positioned half-way between the shrub trunk and the projected edge of the canopy. The community of annual species in this environment was poorly developed and plant height generally did not exceed 10 cm. Within each quadrat we collected all the above-ground plant mass, sorted this material into individuals and species (except grasses, which were combined), and then dried it in a ventilated oven at 70 °C for 48 hr. Plant density was obtained from these data.

Estimation of solar radiation

Solar radiation was measured below the canopy of each shrub and in gaps with integrating paper sensors (IPS; Friend 1961; Barden 1987; Ackerly 1992; Wayne & Bazzaz 1993) constructed from small, 5 cm × 5 cm stacks of light-sensitive, heliographic paper (Oxalid KL, Kalle Repromedia España S.A., Spain) placed within a black cardboard envelope which had a circular aperture 1.5 cm in diameter to allow sunlight to reach the paper. IPSs were calibrated against two quantum sensors (Skye 400-700 nm, UK) connected to a Squirrel data logger (Grant, UK) under a range of sky conditions, and were able to accurately estimate integrated photosynthetically active radiation (PAR) of up to 500 mol.m⁻².

Four IPSs were placed at ground level under each of the five selected shrubs per species, midway between the centre and the outer limit of the canopy, at the N, S, W, and E aspects. Five additional IPSs were placed in gaps. Values of solar radiation reaching each microhabitat on a clear spring day (April 7, 1999) from 9:00 to 15:00 solar time were compared.

Soil properties

Soil samples were collected on the same dates from the upper 5 cm excluding litter and stones at the four cardinal aspects under the canopy of each shrub and in five gaps between them. Soil samples were placed in labelled paper bags and immediately transported to the laboratory for analysis. Two standard, commercially available plant substrata (washed river sand and peat) were included in the analyses for reference. Subsamples of each soil were passed through a 2 mm sieve and finely ground for nutrient analysis at the Unit of Analysis, Environmental Sciences Centre (CSIC, Madrid, Spain). Total phosphorus (P) and potassium (K) concentrations were determined by emission spectrometry in induc-

tively coupled plasma (Perkin Elmer ICP5500, USA) after samples were digested in a mixture of HNO_3 and HClO_4 in a warm sand bath at ambient pressure. Total nitrogen was determined by Kjeldahl analysis with $\text{SeSO}_4\text{-K}_2\text{SO}_4$ as catalyst in a Tecator 20 digestion system and a Kjelttec-auto 1030 analyser (Tecator, Sweden). Organic matter was determined by colorimetry. Because of the high gypsum content (Cantón et al. 2001), soils were weighed after 2 hr at 250 °C to eliminate the water imbibed in gypsum and thus to prevent overestimation of their organic matter content. Soil moisture at a depth of 10 cm was continuously monitored under the canopy of three to four shrubs per species in May and June 2000 using a SBIB-CHS sensor which simultaneously determines temperature, conductivity, and volumetric soil moisture. The sensor measures the soil complex permittivity (i.e., the dielectric constant) by separately determining the real and imaginary components of soil impedance (Topp et al. 1980, 2000). It is optimized to operate at 50 MHz, when the relaxation phenomena of the organic material is negligible and the weight of the electrical conductivity is low. SBIB sensors give fine measurements of soil moisture, continuously corrected for temperature. Each sensor was connected to a data logger (Onset Computers, Pocasset, MA, USA) and readings were taken every 1 min for periods of 4-5 days to monitor changes at the onset of the drought season.

Water status and physiology of shrubs

Leaf or cladode water vapour conductance of every shrub was measured in June 2000 in the early morning under full, saturating sunlight with a portable infrared gas analyser (model LCI, Analytical Development Company Ltd., Hoddesdon, UK). Pre-dawn water potentials were determined on terminal shoots using a pressure chamber (SKPM 1400, Skye Instruments Ltd., Llandrindod Wells, UK), and relative water content (RWC) was determined by weighing in the field about 1 g of freshly cut, 15-cm long shoot segments from each plant, which were then placed in a dark humid chamber at room temperature with their cut ends covered by saturated cotton wool until fully rehydrated; then they were weighed again and dried in a ventilated oven at 70 °C for at least 48 hours. Physiological conditions of shrubs were further assessed by measuring the photochemical efficiency of PSII (F_v/F_m) with a portable fluorimeter (PEA, Hansatech, Kings Lynn, UK). Leaves were dark-adapted for 30 minutes early in the morning on the same date as gas exchange measurements.

Statistical analysis

Differences between shrub species and gaps were determined by ANOVA (GLM procedure and Tukey's multiple comparison test of Systat 5.2.1; Systat Inc., Evanston, US). The four plots under every shrub sampled were pooled; biomass data were ln-transformed to meet normality criteria. A stepwise multiple regression model using the best-subset regression method, including non-redundant variables, was run to explore the relationships of main abiotic factors with understorey biomass. A hierarchical cluster analysis was performed to look for similarities among understorey communities using the mean number of individuals of the species found under the canopy of each shrub species (furthest neighbour method with Euclidean distances and standardized values; SPSS for Windows 11.0.0; SPSS Inc. 2001).

Results

Herbaceous plant community

Above-ground biomass of herbs that developed in spring showed significant differences between gaps and the understorey of the six shrub species (Fig. 1). While *Thymus hyemalis* had an inhibitory effect on understorey plant growth, biomass under *Lycium intricatum* did not

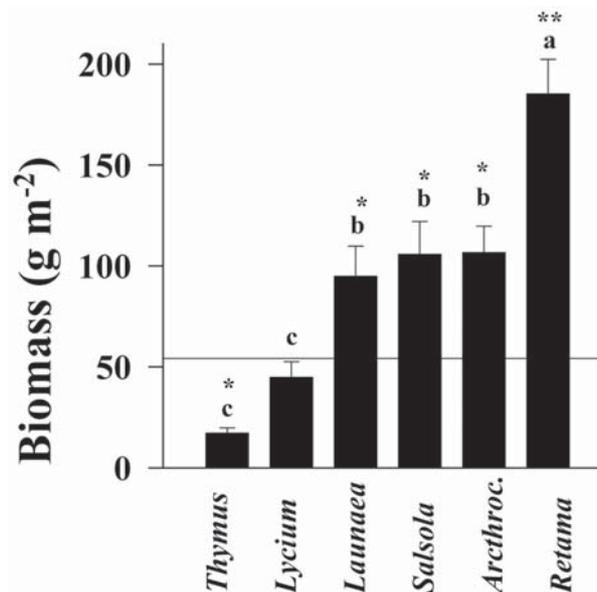


Fig. 1. Above-ground biomass of herbs that developed in spring in gaps (horizontal line) and under the canopy of six shrub species near Tabernas, Almería (Spain). Significant deviations from gap values shown by * ($P < 0.05$) and ** ($P < 0.01$). Data are means \pm 1 SE ($n = 5$). Bars with the same letter are not significantly different ($P > 0.05$; ANOVA, Tukey's multiple comparison test).

Table 1. Species and plant density (individuals m⁻²) in the understory of six shrub species and in gaps in a semiarid environment near Tabernas, Almería, Spain (values are mean ± 1 SE; n = 5).

	Shrub species						Gaps
	<i>Arctrocnemum</i>	<i>Launaea</i>	<i>Lycium</i>	<i>Retama</i>	<i>Salsola</i>	<i>Thymus</i>	
<i>Anagallis arvensis</i>	0 ± 0	0 ± 0	0 ± 0	5 ± 5	0 ± 0	0 ± 0	0 ± 0
Apiaceae	0 ± 0	0 ± 0	5 ± 5	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Arenaria leptoclados</i>	0 ± 0	0 ± 0	25 ± 16	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Asphodelus tenuifolius</i>	5 ± 5	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Asteraceae	0 ± 0	0 ± 0	10 ± 10	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Asterolinon linum-stellatum</i>	140 ± 34	35 ± 23	0 ± 0	25 ± 25	5 ± 5	395 ± 112	195 ± 76
<i>Calendula tripterocarpa</i>	15 ± 10	5 ± 5	20 ± 9	65 ± 26	15 ± 15	5 ± 5	10 ± 12
<i>Carrichtera annua</i>	105 ± 27	90 ± 39	125 ± 45	140 ± 66	60 ± 19	5 ± 5	10 ± 8
<i>Clypeola jonthlaspi</i>	100 ± 66	0 ± 0	0 ± 0	10 ± 10	0 ± 0	0 ± 0	0 ± 0
<i>Diplotaxis ilorcitana</i>	215 ± 90	50 ± 22	15 ± 10	15 ± 10	35 ± 22	0 ± 0	15 ± 10
<i>Erodium cicutarium</i>	50 ± 21	20 ± 12	15 ± 10	10 ± 6	30 ± 9	15 ± 10	20 ± 4
<i>Euphorbia falcata</i>	20 ± 15	10 ± 6	5 ± 5	15 ± 10	25 ± 14	5 ± 5	10 ± 8
<i>Euphorbia helioscopia</i>	20 ± 12	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	5 ± 4
<i>Gynandrisis sisyrrinchium</i>	15 ± 10	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	5 ± 4
<i>Helianthemum ledifolium</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	60 ± 34	20 ± 12
Lamiaceae	0 ± 0	5 ± 5	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Leontodon hispidulus</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	5 ± 5	0 ± 0	0 ± 0
<i>Linaria oliganta</i>	90 ± 39	55 ± 29	15 ± 10	105 ± 52	15 ± 10	35 ± 15	55 ± 18
<i>Linum strictum</i>	60 ± 37	55 ± 33	5 ± 5	10 ± 6	15 ± 15	140 ± 86	75 ± 25
<i>Logfia clementei</i>	5 ± 5	0 ± 0	0 ± 0	0 ± 0	0 ± 0	5 ± 5	0 ± 0
<i>Logfia minima</i>	0 ± 0	0 ± 0	0 ± 0	35 ± 22	90 ± 90	5 ± 5	5 ± 12
<i>Medicago minima</i>	0 ± 0	50 ± 34	25 ± 16	15 ± 15	0 ± 0	65 ± 40	65 ± 33
<i>Medicago truncatula</i>	0 ± 0	0 ± 0	0 ± 0	70 ± 27	70 ± 20	50 ± 44	40 ± 17
<i>Mesembrianthemum</i>	0 ± 0	0 ± 0	15 ± 10	0 ± 0	5 ± 5	0 ± 0	0 ± 0
<i>Paronichia argentea</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	5 ± 5	0 ± 0
<i>Plantago ovata</i>	0 ± 0	0 ± 0	10 ± 10	0 ± 0	0 ± 0	20 ± 20	35 ± 14
Poaceae	910 ± 234	425 ± 97	380 ± 95	670 ± 107	655 ± 222	1360 ± 261	645 ± 174
<i>Reichardia tingitana</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	5 ± 5	0 ± 0	10 ± 5
<i>Silene tridentata</i>	0 ± 0	0 ± 0	10 ± 10	20 ± 15	15 ± 15	55 ± 33	75 ± 46
<i>Silene littorea</i>	45 ± 20	55 ± 12	130 ± 37	65 ± 53	70 ± 37	330 ± 201	65 ± 31
<i>Sonchus tenerrimus</i>	120 ± 45	60 ± 31	40 ± 34	65 ± 22	150 ± 33	0 ± 0	0 ± 0
<i>Spergularia rubra</i>	0 ± 0	0 ± 0	10 ± 10	0 ± 0	0 ± 0	5 ± 5	0 ± 0
<i>Thymus baeticus</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	15 ± 10	0 ± 0
<i>Trigonella polyceratia</i>	10 ± 10	0 ± 0	0 ± 0	25 ± 25	10 ± 6	15 ± 15	25 ± 14
Unknown	10 ± 10	5 ± 5	5 ± 5	30 ± 30	5 ± 5	60 ± 19	20 ± 12

differ from biomass in gaps (Fig. 1). All other shrub species had significantly more biomass of annuals in their understory than there was in gaps. The positive effect of shrubs was not equal in all cases, though, as the biomass below *Retama sphaerocarpa* was almost twice the biomass under the other species (Fig. 1).

A total of 35 annual and perennial species was found in gaps and in the understory of our shrubs (Table 1), but this number included all the grasses combined in one group, as species could not be identified. There were no significant differences among aspects in the number of

understorey species. The total number of species found in gaps and under the canopy of the different shrubs, and the average number of species per sample, were not significantly different among shrubs (Table 2). However, 40% of the species excluding Poaceae were found only under shrubs (Table 1). A cluster analysis of species density under each shrub and in gaps showed that the community under *Thymus* was similar to the community in gaps (Fig. 2) and that the communities most differentiated from gaps were those under *Retama* and *Salsola*. All other communities lie between these two extremes.

	N_{cum}	N_{samp}	N_{ind}	Mass
<i>Arctrocnemum macrostachyum</i>	18	10 ± 0.5 ^a	1600 ± 332 ^{ab}	3.2 ± 0.6 ^b
<i>Launaea arborescens</i>	14	8.0 ± 1.0 ^a	803 ± 133 ^c	5.3 ± 0.4 ^b
<i>Lycium intricatum</i>	19	8.0 ± 0.5 ^a	797 ± 58 ^c	3.0 ± 0.7 ^b
<i>Retama sphaerocarpa</i>	19	9.2 ± 0.7 ^a	1174 ± 122 ^b	7.0 ± 0.8 ^a
<i>Salsola oppositifolia</i>	19	8.8 ± 0.6 ^a	1114 ± 85 ^b	4.4 ± 0.6 ^b
<i>Thymus hyemalis</i>	21	10.0 ± 1.3 ^a	1851 ± 344 ^a	0.4 ± 0.1 ^c
Gaps	21	10.8 ± 0.7 ^a	1356 ± 114 ^b	2.0 ± 0.3 ^c

Table 2. Cumulative number of species in the understory; (N_{cum}); mean number of species per sample (N_{samp}); number of individuals per m² (N_{ind}); mean individual plant mass (Mass, mg.m⁻²) found in the understory of six shrub species and in gaps in the field. Values are mean ± 1 SE, n = 5. Values in a column followed by the same letter are not significantly different ($P > 0.05$; ANOVA; Tukey's multiple comparison test).

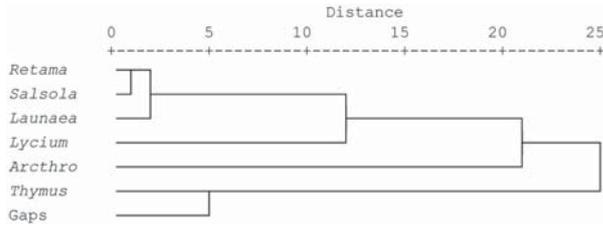


Fig. 2. Hierarchical cluster analysis of community composition (average number of individuals of each species) under each shrub species and in gaps, using the furthest neighbour method with Euclidean distance and standardized values.

Irradiance in the understorey

In the middle of the day the available PAR under the canopy of different shrub species was 30-50% of that in gaps (Fig. 3). PAR transmission through the canopy varied significantly among the different species, with *Salsola oppositifolia* and *Lycium intricatum* casting the darkest shade. Architectural features of the canopy and specific foliage traits (i.e., leaf size, internode length, leaf angle and orientation, leaf area index) seemed to be more important determinants of PAR transmission than canopy height or volume, as shown by the lack of relationship between canopy size and ground level PAR (data not shown). This fact explained why the PAR available under sub-shrubs (e.g. *Thymus*, 0.3-0.6 m height) was very similar to that under relatively tall shrubs (e.g. *Retama*, 1.3-2.2 m height). Within a species, however, increasing canopy height and volume significantly decreased the integrated PAR available under the canopy (data not shown).

Soil properties

The organic matter content of soil in gaps and under the canopy of the six shrub species ranged between 2.5 and 6%, being highest under *Retama sphaerocarpa* (Table 3). Mean values of organic matter under each shrub strongly correlated with soil nitrogen ($r = 0.893$; $P < 0.01$) and phosphorus ($r = 0.792$; $P < 0.05$) as well as with biomass of annuals ($r = 0.877$; $P < 0.01$). Soil nutrient content paralleled organic matter content, with N- and P-concentrations the highest under *Retama* and K under *Salsola oppositifolia* (Table 3). Gap soils and soils under *Thymus hyemalis* showed the lowest N, P, and K values. Soil N and P concentrations were correlated with the biomass of understorey plants ($r = 0.786$ and $r = 0.84$, respectively; $P < 0.05$).

Soil moisture at 10 cm depth under different canopies and in gaps varied significantly. In most cases there was a well-defined daily pattern of moisture change (Fig. 4) cycling at exactly 24 hr; the amplitude of such

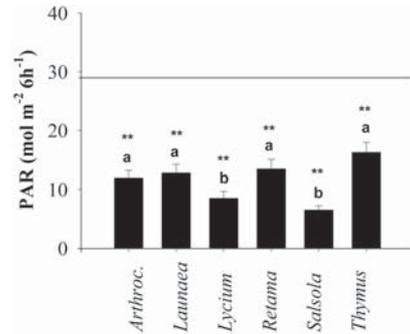


Fig. 3. Integrated PAR over 6 hr (9-15 solar time) of a spring day (7 April 1999) in gaps (horizontal line) and under the canopy of six shrub species. Significant deviations from gap values shown by * ($P < 0.05$) and ** ($P < 0.01$). Values are mean \pm 1 SE ($n = 5$). Bars with the same letter are not significantly different ($P > 0.05$; ANOVA, Tukey's multiple comparison test).

changes, obtained by Fourier analysis, was different for the different species. The largest amplitude was found under *Thymus hyemalis* (daily change $> 2.5\%$) and the lowest under *Retama* (daily change $< 0.1\%$). On average, soil moisture differed significantly among shrubs, being highest under *Retama* ($3.36 \pm 0.01\%$) and lowest in gaps ($1.04 \pm 0.01\%$) and under *Lycium intricatum* ($2.3 \pm 0.01\%$) and *Thymus hyemalis* ($2.8 \pm 0.01\%$). Soil moisture was inversely correlated to radiation reaching the soil ($r = -0.886$; $P < 0.01$) and positively correlated with the number of species of annuals ($r = 0.78$; $P < 0.05$). Soil temperature varied slightly under different shrubs (Fig. 4), being highest in gaps (34.7 ± 0.07 °C) and lowest under *Salsola oppositifolia* (30.8 ± 0.05 °C). Soil temperature and moisture were positively correlated in gaps and under some but not all shrubs. Those where soil temperature and moisture did not correlate had the highest facilitative effect on the biomass of annuals.

Including gaps and all the shrubs, the mean number of understorey species was positively correlated to soil humidity ($r = 0.78$; $P < 0.05$) and negatively to irradiance ($r = -0.88$; $P < 0.01$). Individual plant mass was, overall, significantly correlated with the shrub's relative water content ($r = 0.972$; $P < 0.01$) and with soil organic matter ($r = 0.74$; $P < 0.05$).

A stepwise multiple regression using the best-subset model building showed that soil OM, ground-level radiation, and soil moisture significantly explained the biomass found in the understorey of shrubs:

$$\text{Biomass} = 0.44 * \text{OM} + 0.36 * \text{Soil moisture} + 0.04 * \text{PAR} - 2.5; R^2 = 0.998; P = 0.002.$$

The contribution of each mentioned variable was significant (none of the P -values were > 0.006), and all the standardized regression coefficients were positive.

Table 3. Physical and chemical soil properties under the canopy of six shrub species near Tabernas (Almería, Spain). Organic matter (OM) and concentrations of nitrogen (N), phosphorus (P) and potassium (K). Values are mean \pm 1 SE, $n = 5$. Values in a column followed by the same letter are not significantly different ($P > 0.05$; Tukey's multiple comparison test).

Species	OM(%)	N(%)	P (ppm)	K(ppm)
<i>Arthrocnemum macrostachyum</i>	3.60 \pm 0.03 ^a	0.208 \pm 0.030 ^d	133 \pm 3 ^{de}	283 \pm 12 ^d
<i>Launaea arborescens</i>	2.74 \pm 0.14 ^a	0.171 \pm 0.001 ^{cd}	87 \pm 7 ^b	203 \pm 9 ^{bc}
<i>Lycium intricatum</i>	3.15 \pm 0.04 ^a	0.253 \pm 0.021 ^e	100 \pm 6 ^{bc}	383 \pm 13 ^e
<i>Retama sphaerocarpa</i>	6.03 \pm 0.09 ^b	0.422 \pm 0.007 ^f	155 \pm 9 ^e	233 \pm 3 ^{cd}
<i>Salsola oppositifolia</i>	3.30 \pm 0.11 ^a	0.163 \pm 0.010 ^c	118 \pm 4 ^{cd}	483 \pm 26 ^f
<i>Thymus hyemalis</i>	2.53 \pm 0.08 ^a	0.088 \pm 0.005 ^b	58 \pm 3 ^a	150 \pm 6 ^b
Gaps	2.79 \pm 0.98 ^a	0.040 \pm 0.006 ^a	40 \pm 1 ^a	77 \pm 2 ^a

Water status and physiology of shrubs

Predawn water potentials (Ψ_{pd}) showed significant differences among the six shrub species (Table 4). The relative water content followed a similar pattern, with *Retama sphaerocarpa* and *Launaea arborescens* showing the highest values and *Arthrocnemum macrostachyum* the lowest (Table 4). The most stressed shrubs, based on the level of photochemical efficiency of photosystem II (Fv/Fm) were *Lycium intricatum* and *Thymus hyemalis*, while *Retama sphaerocarpa* and *Launaea arborescens* showed the best physiological conditions (Table 4). Overall, physiological variables were unrelated to total biomass or species richness under the canopy, showing that the shrub physiological status did not directly influence understory growth. Physiological variables were also unrelated to the measured soil humidity.

Discussion

Most shrubs in our field site had significant effects on their understory communities compared to gaps, ranging from negative to positive. We found a clear case of interference (by *Thymus hyemalis*) and a species where the effect was neutral (*Lycium intricatum*), but facilitation predominated, and most of the screened

shrubs had under the canopy a biomass of herbs larger than in gaps. Not all the species had the same effect, however, as the outstanding positive effect of *Retama sphaerocarpa* clearly separated it from the other shrub species (Fig. 1). Shrubs also increased the realized niche of 14 species that did not establish in gaps (Table 1).

Shrubs could be graded by their effects on soil fertility. At one end of the gradient was *Retama sphaerocarpa*, with the highest soil levels of OM and nutrients; at the other end was *Thymus hyemalis* with opposite traits. Other shrub species were placed in between. The canopy may have created a favourable environment for micro-

Table 4. Pre-dawn water potentials (Ψ_{pd}), relative water content (RWC), and photochemical efficiency of photosystem II (Fv/Fm) of six shrub species growing near Tabernas (Almería, Spain) in June 2000. Values are mean \pm 1 SE, $n = 3 - 5$. Values in a column followed by the same letter are not significantly different ($P > 0.05$; Tukey's test).

Species	Ψ_{pd} (Mpa)	RWC	Fv/Fm
<i>A. macrostachyum</i>	-5.2 \pm 0.03 ^a	0.52 \pm 0.05 ^c	0.72 \pm .02 ^{ab}
<i>L. arborescens</i>	-0.2 \pm 0.0 ^d	0.75 \pm 0.11 ^{ab}	0.80 \pm 0.01 ^a
<i>L. intricatum</i>	-4.1 \pm 0.9 ^{ab}	0.59 \pm 0.01 ^c	0.64 \pm 0.04 ^b
<i>R. sphaerocarpa</i>	-1.7 \pm 0.2 ^c	0.80 \pm 0.02 ^a	0.78 \pm 0.05 ^a
<i>S. oppositifolia</i>	-4.7 \pm 0.9 ^{ab}	0.64 \pm 0.02 ^b	0.69 \pm 0.03 ^b
<i>T. hyemalis</i>	-3.0 \pm 0.8 ^b	0.37 \pm 0.02 ^d	0.67 \pm 0.02 ^b

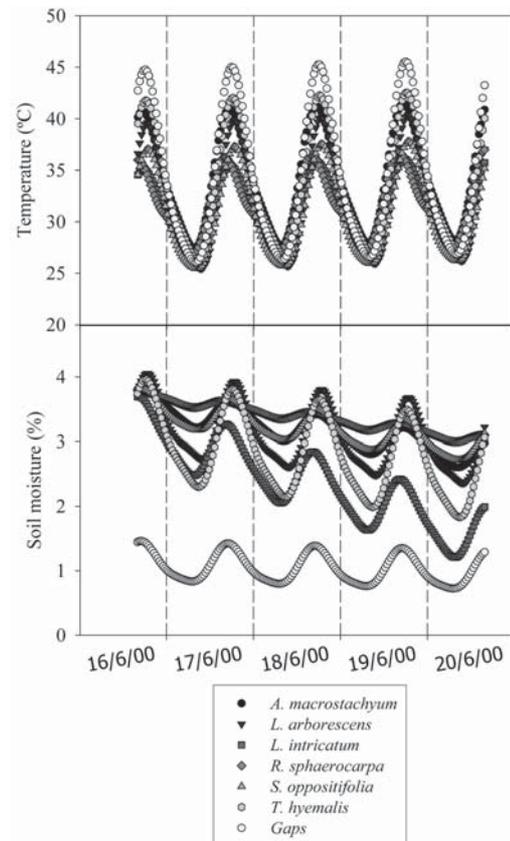


Fig. 4. Temperature (top) and volumetric soil moisture (bottom) at a depth of 10 cm under the canopy of six shrub species and in gaps in late spring 1999.

organisms under most shrubs, with effects on nutrient dynamics. Under the canopy of shrubs in arid environments the amount of bacteria and fungi is larger than outside (Aguilera et al. 1999) and mineralization rates are higher (Moro et al. 1997). On the other hand, species such as *Thymus* are known by their anti-microbial effects affecting both fungi and bacteria development (Salmeron et al. 1995; Dorman & Deans 2000), implying that decomposition is halted and nutrients are relatively less available under *Thymus* canopies. Large numbers of individuals indicated that germination was not inhibited in our case, but interference effects resulted in a significant reduction of plant biomass under *Thymus*.

Soil organic matter also influences soil physical properties related to soil moisture (Jenny 1980; Chancellor 1994; Duchaufour 1995). For instance, daily variations in soil temperature and moisture were smallest under *Retama*, and largest in gaps and under *Thymus hyemalis*. Apparently, the accretion of organic matter decoupled soil humidity and temperature under these shrubs. Organic matter increases the water-holding capacity by keeping small soil aggregates together, while large soil aggregates are related to high bulk densities and low water retention capacities (Boix-Fayos et al. 2001). These two contrasting sets of traits are present in soils from our six shrubs, with end points in *Retama* and *Thymus*, suggesting that the relationship between soil temperature and humidity depends on soil structure. The amount of organic matter affects soil thermal conductivity and heat capacity. At a given moisture content, increasing the percentage of soil organic matter decreases thermal conductivity. Likewise, at a given moisture level, thermal conductivity and heat capacity increase with bulk density; holding constant bulk density, both properties increase with soil moisture (Abu-Hamdeh 2001). Thus, understory soils enriched in OM are buffered against high temperatures, avoiding extremes that may be harmful to both micro-organisms and plants.

Differences in soil moisture under the different shrub species (Fig. 4) may be a consequence of the balance between evaporation, transpiration, and water supply (Joffre & Rambal 1993) and of the rooting depth of plants. Thus, shrubs with a well-developed herbaceous community in the understory may show moisture values lower than shrubs hosting fewer herbs underneath because of higher transpiration rates (Domingo et al. 2000).

The improvement of soil fertility by shrubs, and particularly the accretion of OM, is apparently the primary source of facilitation in our environment. Although sheltering from direct sunlight did have an effect on understory growth, the biomass under the canopy of the different shrub species did not correlate with the incident radiation reaching the soil. This does not agree well with the interpretation of experimental manipulations in

other arid ecosystems, where shade is probably the most important facilitation factor (Nobel 1984; Belsky et al. 1993; Georgiadis 1989; Callaway et al. 1991; Valiente-Banuet & Ezcurra 1991; Moro et al. 1997; Holmgren 2000).

Physiological measurements revealed no overall effect of shrub water status on understory growth.

Concluding remarks

There were significant transient (climatic) and permanent (soil-related) micro-environmental differences under the canopy of the different shrub species that changed the herbaceous community. The influence of the shrubs on the herbs underneath varied from negative (*Thymus*) to very positive (*Retama*) and was mostly caused by changes in the physical and chemical characteristics of the soil. The most important factor seemed to be organic matter accretion, which had an effect on soil water relations. Overall, our data are consistent with the idea that facilitation prevails over competition in extreme environments but for particular species, the net balance of the interaction with other species will depend on a number of direct and indirect species-specific effects related to water conservation and supply.

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References

- Abu-Hamdeh, N.H. 2001. Measurement of thermal conductivity of sandy loam and clay loam soils using single and dual probes. *J. Agric. Eng. Res.* 79: 179-185.
- Ackerly, D.D. 1992. Light, leaf age, and leaf nitrogen concentration in a tropical vine. *Oecologia* 89: 596-600.
- Aguilera, L.E., Rodríguez, J.L. & Meserve, P.L. 1999. Variation in soil micro-organisms and nutrients underneath and outside the canopy of *Adesmia bedwellii* (Papilionaceae) shrubs in arid coastal Chile following drought and above average rainfall. *J. Arid Environ.* 42: 61-70.
- Barden, L.S. 1987. Invasion of *Microstegium vimineum* (Poaceae) an exotic, annual, shade tolerant C4 grass into North Carolina floodplain. *Am. Midl. Nat.* 118: 40-45.
- Belsky, A.J., Mwangi, S. M., Amundson, R.G., Duxbury, J.M. & Ali, A.R. 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-

- rainfall savannas. *J. Appl. Ecol.* 30: 143-155.
- Bertness, M.D. & Callaway, R. M. 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9: 191-193.
- Boix-Fayos, C., Calvo-Cases, A., Imeson, A.C. & Soriano-Soto, M.D. 2001. Influence of soil properties on the aggregation of some Mediterranean soils and the use of aggregate size and stability as land degradation indicators. *Catena* 44: 47-67.
- Breshears, D.D., Nyhan, J.V., Heil, C.E. & Wilcox, B.P. 1998. Effects of woody plants on microclimate in a semiarid woodland: Soil temperature and evaporation in canopy and intercanopy patches. *Int. J. Plant Sci.* 159: 1010-1017.
- Callaway, R.M. 1995. Positive interactions among plants. *Bot. Rev.* 61: 306-349.
- Callaway, R.M. & Pugnaire, F.I. 1999. Facilitation in plant communities. In: Pugnaire, F.I. & Valladares F. (eds.) *Handbook of functional plant ecology*, pp. 623-648. Marcel Dekker, New York, NY, US.
- Callaway, R.M., Nadkarni, N.M. & Mahall, B.E. 1991. Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology* 72: 1484-1499.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R. Paolini, L., Pugnaire, F.I., Cook, B.J., Aschehoug, E.T., Armas, C. & Newingham, B. 2002. Positive interactions among alpine plants increase with stress: a global experiment. *Nature* 417: 844-848.
- Castroviejo, S. (coord.) 1986-2001. *Flora Iberica*. CSIC, Madrid, ES.
- Cantón, Y., Solé, A., Queralt, I. & Pini, R. 2001. Weathering of a gypsum-calcareous mudstone under semi-arid environment in SE Spain: laboratory and field-based experimental approaches. *Catena* 44: 111-132.
- Cavieres, L., Arroyo, M.T.K., Molina-Montenegro, M. & Torres, C. 2002. Nurse effects of *Bolax gummifera* (Apiaceae) in the alpine vegetation of the Chilean Patagonian Andes. *J. Veg. Sci.* 13: 547-554.
- Chancellor, W.J. 1994. *Advances in soil dynamics*. American Society of Agricultural Engineers, St Joseph, MI, US.
- Domingo, F., Villagaría, L., Brenner, A.J. & Puigdefábregas, J. 2000. Measuring and modelling the radiation balance of a heterogeneous shrubland. *Plant Cell Environ.* 23: 27-38.
- Dorman, H.J.D. & Deans, S.G. 2000. Antimicrobial agents from plants: antibacterial activity of plant volatile oils. *J. Appl. Microbiol.* 88: 308-316.
- Duchaufour, P. 1995. *Pédologie: sol, végétation, environnement*. 4th ed. Masson, Paris, FR.
- Dunne, J.A., & Parker, V.T. 1999. Species-mediated soil moisture availability and patchy establishment of *Pseudotsuga menziesii* in chaparral. *Oecologia* 119: 36-45.
- Friend, D.T.C. 1961. A simple method of measuring integrated light values in the field. *Ecology* 42: 577-580.
- Georgiadis, N.J. 1989. Microhabitat variation in an African savanna: effects of woody cover and herbivores in Kenya. *J. Trop. Ecol.* 5: 93-108.
- Haase, P., Pugnaire, F.I., Clark, S.C. & Incoll, L.D. 1996. Spatial pattern in a two-tiered semi-arid shrubland in southeastern Spain. *J. Veg. Sci.* 7: 527-534.
- Hillel, D. 1980. *Fundamentals of soil physics*. Academic Press, New York, NY, US.
- Hobbie, S. 1992. Effects of plant species on nutrient cycling. *Trends Ecol. Evol.* 7: 336-339.
- Holmgren, H. 2000. Combined effects of shade and drought on tulip poplar seedlings: trade-off in tolerance or facilitation? *Oikos* 90: 67-78.
- Jenny, H. 1980. *The soil resource: origin and behavior*. Springer, Berlin, DE.
- Joffre, R. & Rambal, S. 1993. How tree cover influences the water balance of Mediterranean rangelands. *Ecology* 74: 570-582.
- Moro, M.J., Pugnaire, F.I., Haase, P. & Puigdefábregas, J. 1997. Mechanisms of interaction between *Retama sphaerocarpa* and its understory layer in a semi-arid environment. *Ecography* 20: 175-184.
- Muller, C.H. 1953. The association of desert annuals with shrubs. *Am. J. Bot.* 4: 53-60.
- Nobel, P.S. 1984. Extreme temperatures and thermal tolerances for seedlings of desert succulents. *Oecologia* 62: 310-317.
- Peinado, M., Alcaraz, F. & Martínez-Parras, J.M. 1992. *Vegetation of Southeastern Spain*. J. Cramer, Berlin, DE.
- Pugnaire, F.I. & Haase, P. 1996. Comparative physiology and leaf growth of two perennial tussock grass species in a semi-arid environment. *Ann. Bot.* 77: 81-86.
- Pugnaire, F.I. & Luque, M.T. 2001. Changes in plant interactions along a gradient of environmental stress. *Oikos* 93: 42-49.
- Pugnaire, F.I., Haase, P. & Puigdefábregas, J. 1996a. Facilitation between higher plant species in a semiarid environment. *Ecology* 77: 1420-1426.
- Pugnaire, F.I., Haase, P., Puigdefábregas, J., Cueto, M., Incoll, L.D. & Clark, S.C. 1996b. Facilitation and succession under the canopy of the leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. *Oikos* 76: 455-464.
- Salmeron, J., Jordano, R. & Pozo, R. 1995. Antimycotic and antiaflatoxic activity of oregano (*Origanum vulgare* L.) and thyme (*Thymus vulgaris* L.). *J. Food Prot.* 53: 697-700.
- Tewksbury, J. J., & Lloyd, J. D. 2001. Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia* 127: 425-434.
- Valiente-Banuet, A. & Ezcurra, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacan Valley, Mexico. *J. Ecol.* 79: 961-971.
- Vetaas, O.R. 1992. Micro-site effects of trees and shrubs in dry savannas. *J. Veg. Sci.* 3: 337-344.
- Wayne, P.M. & Bazzaz, F.A. 1993. Birch seedling responses to daily time courses of light in experimental forest gaps and shadehouses. *Ecology* 74: 1500-1515.

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