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Facilitation of *Quercus ilex* in Mediterranean shrubland is explained by both direct and indirect interactions mediated by herbs

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Summary

1. Competitive and facilitative interactions shape plant communities. Whereas a number of studies have addressed competition and direct facilitation among plants in dry ecosystems, indirect facilitation has received little attention.

2. We investigated the relative importance of direct and indirect facilitation by the nurse plant *Retama sphaerocarpa* on late-successional *Quercus ilex* seedlings mediated by herb suppression in a Mediterranean shrubland in 2006 and 2007. We also studied whether facilitation outcome depended on the size of the facilitated seedlings.

3. A field experiment was carried out to test the effect of (i) position of *Q. ilex* seedling with respect to shrub canopy (under shrubs or in gaps), (ii) herb competition (presence or absence), and (iii) seedling size. 2006 was an average rainfall year while 2007 had a much more humid spring and a dryer summer than 2006.

4. In both years, nurse shrubs reduced seedling mortality whereas herbs increased it. In the average rainfall year, seedling mortality under shrubs was unaffected by herbs whereas in gaps it was significantly higher in presence of herbs. This showed that the nurse shrub indirectly facilitated the seedlings by reducing the competitive capacity of herbs. Conversely, facilitation was predominately direct during the humid spring and dry summer year since herbs hindered seedling survival similarly under the nurse shrub and in gaps. The nurse shrub directly facilitated the seedlings by reducing seedling photoinhibition and water stress.

5. Improvement of environmental conditions by *Retama* benefited smaller seedlings but not larger seedlings since the nurse shrub reduced mortality of smaller seedlings relative to that in gaps, but this effect was not observed for larger seedlings. This indicates that individuals within a seedling population may not have the same response to facilitation.

6. *Synthesis*. Both indirect and direct facilitation are important mechanisms for *Q. ilex* regeneration in *Retama* shrubland and their importance seems to vary with climatic conditions. Indirect facilitation by release of herb competition under nurse shrubs is important in years of dry springs when competition between nurse shrubs and herbs is high, whereas direct facilitation mediated by microclimate amelioration increases with summer aridity.

Key-words: chlorophyll fluorescence, herb competition, *Quercus ilex*, *Retama sphaerocarpa*, seedling size, water potential

Introduction

Biotic interactions are major drivers of the structure and dynamics of plant communities (Lortie *et al.* 2004). Competition has traditionally been considered as the major interaction

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that structures plant communities (Grime 1974). However, in the last decade, an increasing number of studies have also emphasized the importance of facilitative or positive interactions (Bertness & Callaway 1994; Callaway 1995; Brooker *et al.* 2008). Positive and negative interactions among organisms act simultaneously, and the net balance of these interactions determines the community organization and composition (Callaway & Walker 1997; Holmgren, Scheffer & Huston 1997; Brooker *et al.* 2008). The balance of plant–plant interactions is context-dependent, varying in response to abiotic stress, disturbance, life cycle stage, species identity and interactions with other neighbours (Callaway 2007).

Facilitation can be direct, i.e. one species increases the performance of a second species by ameliorating the abiotic environment (Callaway 1995; Pugnaire, Haase & Puigdefábregas 1996a; Pugnaire, Armas & Valladares 2004). Facilitation may also be indirect, i.e. a third species mediates interactions between the nurse species and the target species. Thus, some plants protect other plants from herbivores, attract pollinators, concentrate propagules of other species, or enhance mycorrhizae and soil microbial activity (Callaway 1995, 2007). The occurrence of a third plant species may also convert the competition between two species into indirect facilitation via suppression of a shared competitor (Miller 1994; Levine 1999; Callaway & Pennings 2000). Levine (1999) predicted that indirect facilitation mediated by a third competitor would mainly occur in a system in which the three species compete for different resources or use different mechanisms to acquire them. This argument is supported by previous studies (Siemann & Rogers 2003; Kunstler *et al.* 2006).

In contrast to direct facilitation and competition, indirect facilitation has received less attention. Most studies assessing indirect facilitation have focused on interactions between different trophic levels, such as those analysing defence against herbivory (Boulant *et al.* 2008; Gómez-Aparicio *et al.* 2008; Anthelme & Michalet 2009) or concentration of propagules of other species (Verdú & García-Fayos 2003; Aerts *et al.* 2006). Experimental field studies investigating indirect facilitation within the same trophic level are much less frequent (Brooker *et al.* 2008). Most studies of indirect facilitation among plants have been performed in productive or moderately productive environments; whereas some of them documented indirect facilitation (Levine 1999; Callaway & Pennings 2000; Siemann & Rogers 2003; Kunstler *et al.* 2006), others failed to detect this process (Pagès & Michalet 2003; Pagès *et al.* 2003). To our knowledge, no experimental field study to date has explored the importance of indirect facilitation in semi-arid or arid systems.

Direct facilitation is a recognized recruitment mechanism for plants in Mediterranean environments (Verdú & García-Fayos 2003; Gómez-Aparicio, Gómez & Zamora 2005a), but the importance of indirect facilitation remains to be assessed in this system. *Retama sphaerocarpa* (*Retama* henceforth) is one of the most studied Mediterranean nurse species. It promotes the development of a diverse herbaceous community due to changes in microclimate and soil fertility under its canopy (Pugnaire *et al.* 1996b; Pugnaire, Armas & Valladares 2004). Although herbs compete with the seedlings of woody species and impair woodland regeneration (Nambiar & Zed 1980; Rey Benayas *et al.* 2005), mid- and late-succession woody species such as *Quercus ilex* develop under *Retama* canopy (Tovar 2009). Several studies have demonstrated the direct facilitative effect of *Retama* on the plant community developed under its canopy, but no study has assessed its potential indirect facilitative effect (Pugnaire, Haase & Puigdefábregas 1996a; Pugnaire *et al.* 1996b; Rodríguez-Echeverría & Pérez-Fernández 2003; Pugnaire, Armas & Valladares 2004).

There is an increasing body of evidence that the response to facilitation and that the facilitating ability of nurse species are species specific (Gómez-Aparicio *et al.* 2004; Liancourt, Callaway & Michalet 2005; Padilla & Pugnaire 2009). However, to our knowledge, no study has tested whether the response to facilitation varies among individuals of the same species. Individuals of the same species may have distinct functional traits that may determine their performance. For example, *Q. ilex* seedlings produced by different mother trees exhibit significant size differences that influence their performance (Leiva & Fernández-Alés 1998). Seedling size can affect survival, with large seedlings having a greater chance of survival under stressful conditions than small seedlings (Cook 1980; Leishman & Westoby 1994).

In the present study, we addressed the following questions: (i) In addition to direct facilitation, is indirect facilitation mediated by herbs an important mechanism for *Q. ilex* regeneration in *Retama* shrubland? (ii) Does the response of *Q. ilex* seedlings to facilitation depend on seedling size? To answer these questions, we conducted a factorial field experiment in two consecutive years. We measured the performance of *Q. ilex* seedlings of contrasting size planted under *Retama* canopy and in gaps, as well as in the presence and absence of herbs.

Materials and methods

STUDY SITE AND SPECIES STUDIED

The study site is located in La Mancha, central Spain (38°38′ N, 3°28′ W), at an altitude of 714 m a.s.l. The climate is continental Mediterranean, with a mean annual precipitation of 370 mm and a mean annual temperature of 15.2 °C. Summers are very hot and dry and last for 3–5 months, while winters are cold with frequent frosts. The soil is a poorly developed inceptisol with relatively high clay and quartzite content. The experiment was performed on an abandoned flat wheat cropland that was planted with *R. sphaerocarpa, Pinus pinea* and *Q. ilex* in 2000. Each of these three species had the same density, and individuals were planted in rows separated 4 m and within each row the distance between plants was 3 m. Species were randomly distributed within each row. At the start of the experiment, *P. pinea* and *Q. ilex* trees were more than 2 and 1 m high, respectively, while *Retama* shrubs were *c.* 2 m high. The understorey vegetation was composed of an herbaceous community, which emerges in the autumn, flowers in spring and senesces during early summer. Annuals such as *Avena barbata*, *Bromus* spp., *Hordeum murinum*, *Lolium rigidum*, *Taeniatherum caput-medusae, Rapistrum rugosum* as well as several *Trifolium* species dominated this community.

The nurse species *R. sphaerocarpa* is a leguminous, broom-like deep-rooted shrub that is native to the Iberian Peninsula and north-west Africa, where it forms shrublands that have traditionally been managed for sheep grazing and hunting. In the last decades, this shrub has colonized large areas of abandoned cropland, and it has been used for subsidized plantation programs. The target benefactor species was *Q. ilex*, an evergreen late-successional oak tree native to the western Mediterranean Basin. It constitutes most of the community biomass in areas where it thrives. However, *Q. ilex* seedlings display low survival rates in forest plantations compared with other Mediterranean forest species (Baeza *et al.*, 1991).

EXPERIMENTAL DESIGN

A factorial field experiment was performed with three factors: (i) position with respect to the *Retama* canopy (under or outside), (ii) herb abundance (presence or absence) and (iii) *Q. ilex* seedling size. The experiment was conducted in 2006 and 2007. In 2006, the rainfall and mean temperature during the experimental period (February–September) were 255 mm and 19.2 °C, respectively, while in 2007 they were 352 mm and 17.7 °C, respectively. The mean historical rainfall (over a 70-year period) and temperature (over a 55-year period) during the same period were 256 mm and 17.5 °C, respectively. Thus, 2006 can be considered as an average rainfall year and 2007 as a humid year. Differences between years mainly occurred in spring (February to May), which was much more humid in 2007 than in 2006 (150 and 267 mm in 2006 and 2007, respectively). However, summer (June to September) was more humid in 2006 than in 2007 (105 and 85 mm in 2006 and 2007, respectively).

We randomly selected 30 *Retama* shrubs with an average canopy height and diameter of 2 and 2.3 m, respectively, and 30 gaps located 1.5–2 m outside of the shrub canopies, where the ground was not shaded during most of the day. Each *Retama* shrub was separated from its neighbour by at least 3–4 m. The distribution of the experimental *Retama* shrubs and gaps was not paired, i.e. a particular *Retama* shrub was not associated with a particular gap in the field. In each position (under shrub and gap), we distinguished two herb abundance levels (presence or absence). In the microsites with absence of herbs, herbaceous vegetation was removed with herbicide in an area of 0.55–0.6 m^2 (Oxyfluorfen 24%; Inteike, TradeCorp, Madrid, Spain) at the beginning of the experiment in both years. Finally, in each of these four microsites, *Q. ilex* seedlings were planted in 30 cm deep holes made with a mechanical auger, minimizing the disturbance of the herbaceous community at the microsites with herb presence. Planting was performed in February in both years. The experimental plot was fenced to exclude medium and large herbivores.

We planted seedlings that largely varied in size in both years. In 2006, to promote seedling size differences, we varied (i) the seeding date in the nursery, which affected emergence time and, therefore, the length of the growing period (14 months vs. 11 months), and (ii) we used different nitrogen fertilization rates. In 2007, we did not apply any cultivation treatment and randomly selected the plants from a standard nursery crop that had a high variation in seedling size. In 2006, the 10th and 90th percentiles of plant height were 9 and 22 cm, respectively, while in 2007 they were 12 and 28 cm, respectively. The seedlings were cultivated following standard nursery cultivation methods (Villar-Salvador *et al.* 2004). The acorns used to grow seedlings were of the same provenance in both years.

MICROCLIMATE, SOIL AND HERB COMMUNITY CHARACTERISTICS

To analyse the effect of the nurse shrub on the environmental conditions under its canopy and on the characteristics of the herb community, we measured several abiotic and biotic variables under the *Retama* canopy and in the gaps. Incident photosynthetic photon flux density at seedlings' mid-height was measured using a quantum photo/radiometer (HD 9021; Delta OHM, Casselle Di Selvazzano, Italy) for all of the planted seedlings. Measurements were carried out in May of both years on clear days between 12:00 and 14:00 hours solar time. Seedling leaf temperature and the relative humidity and the temperature in the air were measured in spring of 2006 under the canopy of nine shrubs and in nine gaps. The latter were measured in both presence and absence of herbs with a thermo-hygrometer (HI 9065; HANNA Instruments, Eibar, Spain). The seedling leaf temperature was only measured in the microsites with herbs using a thermocouple inserted under a dry average-sized oak leaf, which was held horizontally during the measurements.

Soil samples excluding litter and stones were collected 5–10 cm deep under the canopy of nine shrubs and in nine gaps for nutrient analyses. After air-drying, the samples were sieved through a 2-mm sieve and finely ground. The organic matter was analysed using the method proposed by Walkley & Black (1934). Total N concentration was determined by Kjeldahl analysis with $SeSO_4$-K_2SO_4 as the catalyst, while the K concentration was measured with an Optic PLASMA ICP (Perkin-Elmer, model 4300 DV; Waltham, MA, USA), according to MAPA (1986). Soil pH was determined for a 1:2.5 mass-to-volume soil and water suspension. Soil temperature at a 5-cm depth was recorded with a digital thermometer in May 2006 in both presence and absence of herbs under nine *Retama* shrubs and in nine gaps. Finally, soil water content in a 0–30 cm soil profile was measured in all planted seedlings in late spring (25 May 2006 and 30 May 2007) and in mid-summer (18 July 2006 and 15 July 2007) using Time Domain Reflectometry (TDR; Tektronix, Beauverton, CO, USA) according to Cassel, Kachanoski & Topp (1994). Two 35 cm long stainless-steel rods were inserted 1 month after planting at a 5–10 cm distance from plants.

In late May of both years, when flowering of the herbaceous community was ending, we visually recorded the percentage of herb cover around each *Q. ilex* seedling, as well as the specific composition and abundance of herbs under nine nurse shrubs and in nine gaps using a 50 × 50 cm quadrat. Herb species were classified as graminoids and non-graminoids. In early June, when the herbaceous community started to wither, the above-ground herb biomass contained in a 50 × 50 cm quadrat was measured under nine *Retama* shrubs and in nine gaps after drying at 50 °C for 2 days. The *Retama* shrubs and gaps used to measure the relative air humidity and the air, leaf and soil temperature were randomly selected among all shrubs under which *Q. ilex* seedlings were planted, whereas the *Retama* shrubs and gaps used to determine the soil nutrient concentration and herb mass were randomly selected among shrubs and gaps where no seedlings were planted.

QUERCUS ILEX SEEDLING PERFORMANCE

The mortality of *Q. ilex* seedlings was recorded at the end of spring (last week of May) and at the end of the summer (last week of September) in both years. We measured the spring (February to June), summer (June to September) and all first growing season (February to September) seedling mortality. Seedling growth was measured as the stem volume increase and calculated as the difference between the seedling stem volume at the end of the summer and at the planting date. Stem volume was calculated from the height and diameter of the stem, assuming a cone-shaped stem. The diameter was measured immediately above the cotyledon insertion points. We measured the maximum photochemical efficiency of photosystem II (F_v/F_m) and the leaf water potential (ψ) in mid summer of both years (7 July 2006 and 2 July 2007) in 3–8 seedlings per treatment to assess the physiological performance of oak seedlings. The F_v/F_m ratio is a good indicator of plant photoinhibition caused by stress factors such as drought, high radiation and frost (Maxwell & Johnson 2000), whereas ψ is a measure of the water status of plants (Flexas *et al.* 2004). F_v/F_m was measured with a portable fluorometer (Hansatech Instruments, Norfolk, England) at predawn and midday (between 12:00 and 14:00 hours solar time) after 30 min of dark adaptation. Leaf water potential was determined at midday using a pressure chamber; it was measured at midday because the value then usually reflects the maximum water stress experienced by the plant within a day. We only measured ψ once a day to prevent distorting the water and carbon economy of seedlings.

DATA ANALYSIS

Differences among microsites in 2006 with regard to air relative humidity and leaf temperature were analysed with two-way ANOVA, where the main factors were position (under *Retama* canopy vs. gaps) and herb abundance (absence vs. presence of herbs). The differences between the nurse shrub locations and the gaps, both in presence of herbs, in soil nutrient concentration, soil pH and leaf temperature in 2006 were analysed with Student's *t*-test. Differences in irradiance among treatments were analysed with ANOVA where the main factors were year (2006 vs. 2007), position and herb abundance. Soil water content was analysed with repeated-measures ANOVA where between-effects were year and position and the within-effect was season (spring vs. summer). Total herbaceous mass was analysed with ANOVA, where the main factors were year and position. Differences in the floristic composition of the herbaceous community were analysed with semi-parametric MANOVA, where dependent variables were the cover of every herb species. Graminoid and non-graminoid covers were analysed with ANOVA in which the main factors were year, position and herb guild (graminoid vs. non-graminoid).

Seedling mortality was analysed using a generalized linear model with a binomial distribution and a logit link function that included a herb competition surrogate (see below) and seedling stem volume at the planting date as co-variables. Seedling stem volume was highly correlated with total plant mass ($r = 0.92$, $P < 0.001$), which was determined in 30 plants randomly harvested from the same lot of plants used for the field experiment in 2006 after removing the growing media and oven drying for 48 h. Growth and F_v/F_m in both years were analysed using ANCOVA. The factors in these analyses were year and position; as in the previous analysis, the surrogate of herb competition and seedling stem volume at the planting date were co-variables. We used a herb competition co-variable instead of a qualitative factor (absence vs. presence of herbs) in these analyses because the herb community under *Retama* canopies and in gaps had a different floristic composition and above-ground biomass (Table 1), which can lead to a distinct competition capacity of herbs at each position. The herb competition co-variable values were calculated for each planted seedling in the spring (late May) and summer (mid-July) using the first factor scores obtained from a Principal Component Analysis on herb cover, soil volumetric water content and photon flux density around the seedlings. The values of soil water content and irradiance were relative values from field measurements taken under each *Retama* canopy and in each gap; they were calculated as the relative reduction in soil humidity and irradiance in the microsite with herbs with respect to the adjacent microsite without herbs. This removes the effect of the nurse shrub. As the ψ of many of the plants exceeded the measurement limit of the pressure chamber (6.8 MPa) in both years, data were grouped into ψ classes, and the effect of year, position, herb competition and initial seedling volume was analysed by an ordinal multinomial lineal model with a generalized logit link.

Data were checked for normality and homogeneity of variance, and were transformed, when necessary, to correct deviations from these assumptions. All statistical analyses were performed with the STATISTICA 6.0. package (StatSoft, Inc., Tulsa, OK, USA), except the semi-parametric MANOVA, which was performed with R.2.8 (R Development Core Team 2008).

Table 1. Microclimate features, soil properties, herb biomass and the cover of graminoid and non-graminoid herbs in the four studied microsites. Microclimatic and soil variables were measured in 2006. Values are mean ± SE. Means with different superscript letters are significantly different at $P < 0.05$ after a Tukey *post hoc* test. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. †Statistical data are reported in the text

	Microsites				*F*		
	Under Retama		Gap				
Variables	Without herbs	With herbs	Without herbs	With herbs	Position (*P*)	Herb Competition (HC)	*P* × CH
Irradiance (%)	38 ± 1.2^{c}	28 ± 0.9^{d}	100 ± 0.0^{a}	46 ± 1.5^{b}	430^{***}	225^{***}	19.9^{***}
Air relative humidity (%)	10.1 ± 0.8	9.8 ± 0.7	10.0 ± 1.0	9.8 ± 0.8	0.04	0.08	0.007
Air temperature (°C)	36.2 ± 0.5	36.0 ± 0.5	36.1 ± 0.5	37.4 ± 0.5	1.4	1.25	0.02
Soil temperature (°C)	30.4 ± 1.1^{b}	28.2 ± 0.5^{b}	41.4 ± 0.6^{a}	39.5 ± 1.0^{a}	179.7^{***}	5.82^{**}	0.01
Leaf temperature (°C)		43.1 ± 2.6^{b}		49.6 ± 1.4^{a}		$t = 6.82^{***}$	
Soil organic matter (%)		1.1 ± 0.07		1.1 ± 0.05		$t = -0.40$	
Soil N (mg kg^{-1})		0.8 ± 0.05		0.8 ± 0.1		$t = -0.98$	
Soil K (mg kg^{-1})		193 ± 41.2		186 ± 46.5		$t = -0.32$	
Soil pH		5.7 ± 0.2		5.8 ± 0.5		$t = 0.49$	
Herb mass in 2006 (g)		42 ± 3^{b}		67 ± 4^{a}		†	
Herb mass in 2007 (g)		67 ± 7		81 ± 6		†	
Graminoid cover in 2006 (%)		31 ± 5		27 ± 5		†	
Non-graminoid cover in 2006 (%)		4 ± 2.0^{b}		49 ± 7^{a}		†	
Graminoid cover in 2007 (%)		19 ± 6		20 ± 4		†	
Non-graminoid cover in 2007 (%)		19 ± 4.9		26 ± 6		†	

Results

MICROCLIMATE, SOIL AND HERB COMMUNITY CHARACTERISTICS

Herbs and the *Retama* canopy reduced irradiance similarly in both years (statistical results not shown). The *Retama* canopy reduced irradiance by 33%. The reduction of irradiance by herbs was greater in gaps than under the *Retama* canopy (Position × Herb competition interaction, Table 1). The *Retama* canopy with herbs was the microsite with the lowest irradiance.

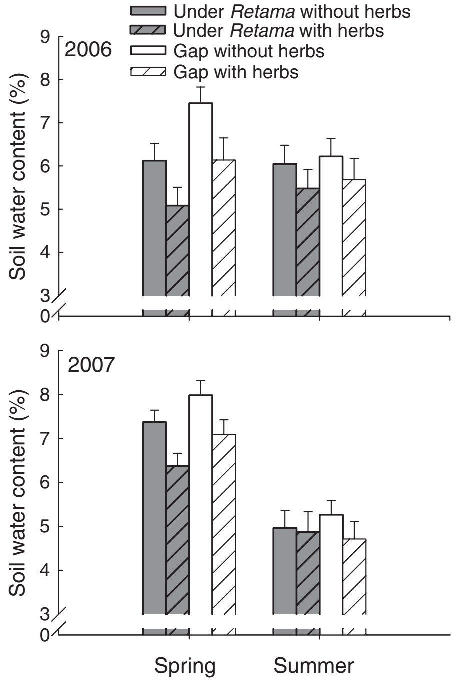

Fig. 1. Soil water content at the four microsites in 2006 (above) and 2007 (below). Data represent mean values ± SE.

Leaf and soil temperature were significantly lower under the *Retama* canopy than in gaps. Neither soil chemical properties nor relative humidity or temperature of the air significantly differed among the four microsites (Table 1).

Soil water content in spring was 14% higher in 2007 than in 2006, while in summer it was 16% lower in 2007 than in 2006 (Year × Season interaction; $F_{1,302} = 45.63$, $P < 0.001$) (Fig. 1). Soil water content was lower under the *Retama* canopy than in gaps, but this difference was only observed in spring and not in summer (Position × Season interaction; $F_{1,302} = 5.87$, $P = 0.016$). Herbs reduced soil water content both under the *Retama* canopy and in gaps, although this reduction was statistically significant in spring but not in summer (Herb competition × Season interaction; $F_{1,302} = 8.61$, $P = 0.004$). Soil water content under the *Retama* canopy with herbs in spring was 20% lower in 2006 than in 2007.

Herb mass was lower in 2006 than in 2007 ($F_{1,57} = 12.22$, $P = 0.01$) and under *Retama* canopy than in gaps ($F_{1,57} = 11.78$, $P = 0.02$) (Table 1). However, the relative reduction of herb mass under *Retama* compared to gaps was higher in 2006 than in 2007 (38% vs. 18%, respectively). The composition of the herbaceous community under the *Retama* canopy differed from the composition detected in gaps in 2006 but not in 2007 (Year × Position interaction; $F_{1,\ 35} = 4.54$, $P < 0.001$). In 2006, the non-graminoid cover was significantly lower under the *Retama* canopy than in gaps, whereas the graminoid cover did not differ significantly between positions. By contrast, the cover of both groups of herbs were similar under the *Retama* canopy and in gaps in 2007 (Year × Position × Herb guild interaction; $F_{1,\ 64} = 9.02$, $P = 0.004$).

QUERCUS ILEX SEEDLING PERFORMANCE

Seedling mortality of the introduced plants at the end of the experiment was 83.3% in 2006 and 76.9% in 2007, but these differences were not statistically significant (Table 2).

Table 2. Results of the ANCOVA models used to test the effects of year, position, herb competition and seedling size on *Quercus ilex* seedling mortality. The Year × Position, Year × Herb competition × Position, and Year × Position × Herb competition × Seedling size interactions were not analysed in spring because there was no mortality under *Retama* canopy in May 2007

Year/	Spring		Summer		Cumulative (spring + summer)	
Factor	χ^2	P	χ^2	P	χ^2	P
Year (Y)	57.8	< 0.001	0.13	0.71	2.02	0.15
Herb competition (HC)	26.5	< 0.001	3.62	0.057	6.95	0.008
Seedling size (SS)	1.72	0.19	0.005	0.94	0.03	0.86
Position (P)	9.60	0.002	11.35	< 0.001	14.6	< 0.001
Y × HC	0.51	0.47	1.35	0.24	0.309	0.58
Y × SS	0.27	0.60	0.003	0.96	0.005	0.95
Y × P			1.03	0.31	0.62	0.43
HC × SS	0.34	0.58	0.0004	0.98	0.016	0.90
HC × P	0.40	0.53	4.04	0.044	4.82	0.028
SS × P	0.09	0.77	3.79	0.051	3.85	0.049
Y × HC × SS	0.59	0.44	0.87	0.35	1.16	0.28
Y × HC × P			3.6	0.057	3.96	0.047
Y × SS × P			0.56	0.45	0.52	0.47
HC × SS × P	0.19	0.66	0.002	0.96	0.0003	0.99
Y × HC × SS × P			2.9	0.087	2.45	0.12

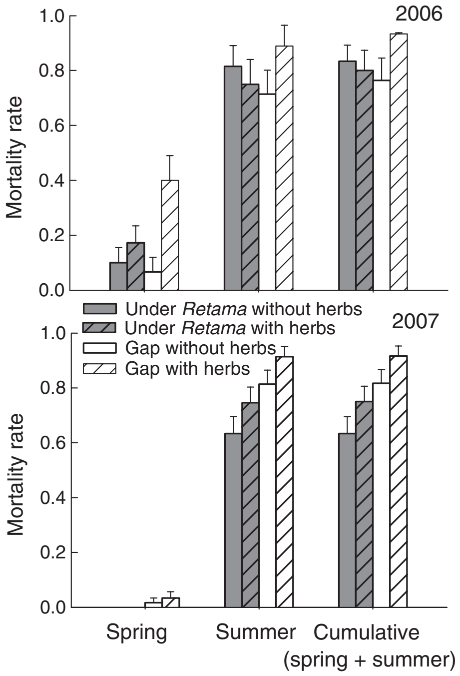

Fig. 2. Mortality rate of *Quercus ilex* seedlings at the four microsites during spring, summer and the whole first growing season in 2006 (above) and 2007 (below). Data represent mean ± SE.

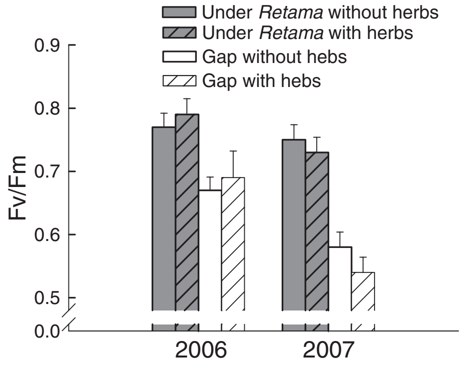

Fig. 4. Photochemical efficiency (F_v/F_m) of photo-system II of *Quercus ilex* seedlings planted at the four microsites in 2006 and 2007. Data represent the average between morning and midday data. Values are mean ± SE.

Significant mortality occurred in the spring of 2006, but not in the spring of 2007 (Fig. 2). Seedling mortality was lower under the *Retama* canopy than in the gaps and in the absence of herbs than in their presence in both years (Table 2 and Fig. 2). However, the negative effect of the herbaceous community differed between years. Herbs increased seedling mortality in gaps but not under *Retama* canopy in 2006, and this effect was already apparent in spring. In contrast, herbs similarly increased seedling mortality at both positions in 2007, and it occurred later, in summer (Year × Herb competition × Position interaction, Table 2). Plant size negatively affected *Q. ilex* seedling mortality (Fig. 3); however, this effect was only observed in gaps but not under the *Retama* canopy (Position × Seedling size interaction in Table 2). No factor influenced seedling growth (data not shown).

F_v/F_m was higher under the *Retama* canopy than in gaps in both years ($F_{1,76} = 5.03$, $P = 0.027$; Fig. 4) and higher in 2006 than in 2007 ($F_{1,76} = 5.28$, $P = 0.024$). F_v/F_m tended to be lower at midday than at predawn, although this was only observed in 2007 but not in 2006 (Measurement time × Year interaction, $F_{1,76} = 3.79$ $P = 0.052$). Neither herb competition ($F_{1,76} = 0.02$, $P = 0.89$) nor seedling size affected F_v/F_m ($F_{1,76} = 0.10$, $P = 0.75$).

Leaf water potential was higher in 2006 than in 2007 ($\chi^2 = 28.6$, $P < 0.001$). The frequency of *Q. ilex* seedlings with higher (less negative) ψ was greater under the *Retama*

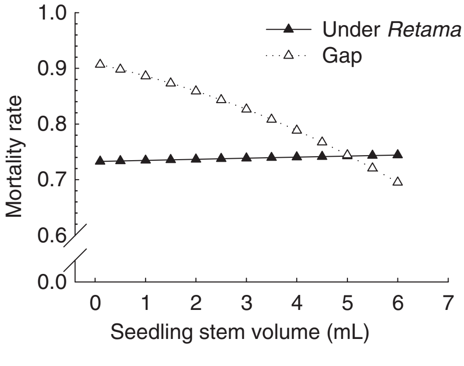

Fig. 3. Mortality probability of *Quercus ilex* seedling as a function of seedling size under the *Retama* canopy and in gaps across the 2 years. Lines are the fitted logistic regressions. The α and β parameters of the logistic regression were 2.2773 and −0.227, respectively, for the gap and 1.0087 and 0.01018, respectively, under *Retama*.

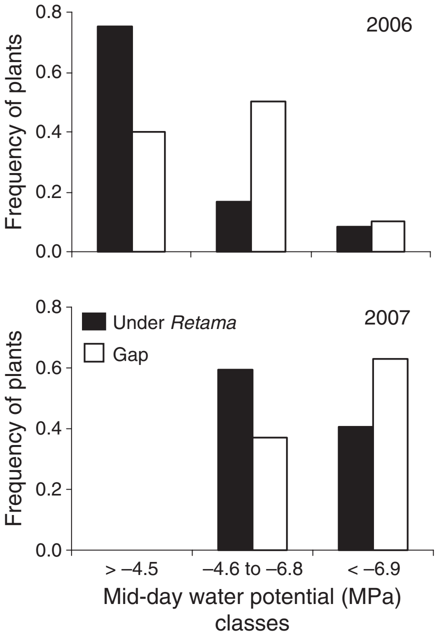

Fig. 5. Frequency of *Quercus ilex* seedlings according to midday leaf water potential classes under the *Retama* canopy and in gaps in 2006 (top) and in 2007 (below). The number of sampled plants under the *Retama* canopy and in gaps in 2006 was 12 and 10, respectively, whereas 24 plants per position were sampled in 2007.

canopy than in gaps. This difference was more apparent in 2006 than in 2007 (Year × Position interaction, $\chi^2 = 6.20$, $P = 0.045$; Fig. 5). Neither herb competition ($\chi^2 = 0.13$, $P = 0.94$) nor plant size ($\chi^2 = 5.00$, $P = 0.08$) had any effect on ψ.

Discussion

Retama sphaerocapa facilitated *Q. ilex* seedlings, which is consistent with greater recruitment of *Q. ilex* under *Retama* canopy than in the gaps observed in other *Retama* shrublands (Tovar 2009). This study provides further evidence for the role of facilitation in the secondary succession of Mediterranean ecosystems (Maestre *et al.* 2001; Gómez-Aparicio *et al.* 2004). However, the mechanism underlying facilitation in this system is complex since it differed between years and depended on seedling size.

TEMPORAL VARIATION IN THE RELATIVE IMPORTANCE OF DIRECT AND INDIRECT FACILITATION

In both years, *Retama* facilitated *Q. ilex* seedling survival, whereas herbs reduced it, demonstrating that herbs competed with oak seedlings. However, the effects of *Retama* and herbaceous vegetation on seedling survival differed between years. Herb competition started earlier in the growing season in the average rainfall year than in the humid year as indicated by early higher spring mortality that occurred in the former relative to the latter year. This can be explained by the dryer spring of the average rainfall year in comparison to the humid year.

Our results suggest that there is a link between the prevailing facilitation mechanism and climate conditions. Facilitation was predominantly indirect in the average rainfall year, when spring was drier than in the humid year. By contrast, facilitation was direct in the humid year, when summer was drier than in the average rainfall year. This assertion is supported by the following results. First, herbs increased *Q. ilex* mortality in gaps but not under the *Retama* canopy in the average rainfall year (Fig. 2). The lower herb mass found under *Retama* canopy as compared to the gaps, specially in the average rainfall year, suggests that the nurse shrub reduced the competitive capacity of the herbs, and hence indirectly improved seedling survival, as previously reported in other studies (Li & Wilson 1998; Siemann & Rogers 2003; Kunstler *et al.* 2006). Additionally, species composition of the herbaceous community differed between years. In the average rainfall year, graminoids predominated over non-graminoids under the nurse shrub, whereas both herb guilds had similar abundance in gaps. By contrast, in the humid year, graminoid and non-graminoid cover were similar both under the *Retama* canopy and in the gaps. Differences in species composition may affect the competitive capacity of the community (Gordon *et al.* 1989), and graminoids tend to prevail under drought conditions (Goldberg *et al.* 2001). Secondly, seedling mortality in the absence of herbs did not differ between gaps and under the nurse shrub in the average rainfall year, but it did during the humid year. This demonstrates lack of direct facilitation in the former case, but the existence of direct facilitation in the latter case. In the average rainfall year, resource competition between the nurse shrub and *Q. ilex* seedlings may have overwhelmed the direct positive effects of *Retama* canopy on *Q. ilex* seedlings (Ludwig *et al.* 2004; Maestre & Cortina 2004). Thirdly, the reduction in oak seedling survival caused by herbs was similar under the shrub and in the gaps in the humid year, suggesting a lack of indirect facilitation. Consistently, relative differences in herb mass or in the composition of the herbaceous community were smaller or non-existent between positions in the humid year respective to the average rainfall year.

Thus, in response to our first question, indirect facilitation may also be an important mechanism for *Q. ilex* regeneration in Mediterranean shrublands that are mostly known for direct facilitation (Pugnaire *et al.* 1996b; Gómez-Aparicio *et al.* 2004; Pugnaire, Armas & Valladares 2004). In addition, the mechanism underlying facilitation may vary with climatic conditions. Indirect facilitation can be important in years of dry springs where competition for water between nurse shrubs and herbs is high, resulting in benefits for *Q. ilex* seedling establishment, whereas direct facilitation mediated by microclimate amelioration seems to increase with summer aridity. Therefore, not only summer drought but also spring climatic conditions may determine facilitation interactions. This hypothesis should be experimentally tested in the future.

UNDERLYING MECHANISMS OF DIRECT AND INDIRECT FACILITATION

Variations in soil nutrient and water content do not explain the direct facilitation observed in our system. Soil fertility did not differ between positions, probably because our nurse shrubs were too young to have induced changes in soil properties (Pugnaire *et al.* 1996b). Soil water content was lower or similar under the *Retama* canopy in comparison with the gaps, as documented in other dry environments (Tielbörger & Kadmon 2000; Valladares & Pearcy 2002). Irradiance reduction seemed to be the main driving force for direct facilitation of *Q. ilex* seedlings. The lower irradiation measured under the shrub canopy explains the lower leaf temperature found in this microsite, which probably reduced *Q. ilex* transpiration under *Retama* (Smith & Geller 1980). Consequently, *Q. ilex* seedlings were less water stressed and photoinhibited under the nurse shrub than in the gaps, which could explain their higher survival rate under the shrubs (Hikosaka, Kato & Hirose 2004; Baquedano & Castillo 2006). The higher ψ and F_v/F_m values found under *Retama* relative to gaps support this argument. Therefore, the physiological results of this study provide a mechanistic explanation for the role that moderate shade plays in direct facilitation in dry environments such as Mediterranean ecosystems (Maestre *et al.* 2001; Gómez-Aparicio *et al.* 2005b). Seedlings were less water stressed and photoinhibited (Figs 4 and 5) in the average rainfall year than in the humid year. The higher summer rainfall and soil water content in the former year can explain this difference.

Levine (1999) predicted that indirect facilitation is more likely when different pairs of competitors compete for different resources or have different mechanisms to acquire them. The three competitors of our particular system are likely to compete for the same resource, i.e. soil water. We suggest that nurse shrubs and herbs competed mainly for soil water because the soil water content under *Retama* shrubs in spring was lower than in gaps in both years. However, *Retama* only suppressed herb competitive capacity in the average rainfall year, probably because soil water content under the *Retama* canopy with herbs in spring was 20% lower than the soil water content in the spring of the humid year. The reduction in soil water content imposed by *Retama* under its canopy did not hinder *Q. ilex* performance probably because it is more drought tolerant than herbs (Levitt 1980; Larcher 1995).

Many studies have shown that shading by adults is the main factor responsible for reducing the competition of herbs with tree seedlings (Li & Wilson 1998; Pagès *et al.* 2003; Siemann & Rogers 2003; Kunstler *et al.* 2006). In our study, shade *per se* was unlikely to be a major mechanism of herb suppression because shrub shade was similar in both years, but shade could have exacerbated the water stress caused by low soil water content in the spring of the average rainfall year (Valladares & Pearcy 2002). In contrast to our results, some previous studies have found greater herb biomass under *Retama* shrubs than in gaps (Pugnaire *et al.* 1996b; Rodríguez-Echeverría & Pérez-Fernández 2003). This can be attributed to the extremely dry climate of some regions, where facilitative interactions can overcome the competitive interactions, and to the fact that these studies were performed on grazed woodlands, where herbivores may reduce herb biomass to a greater extent in open spaces than under shrubs (Osem, Perevolotsky & Kigel 2007).

Herbs and *Q. ilex* seedlings also competed for water because herbs reduced water availability for the seedlings in spring (Fig. 1) as observed in previous studies (Rey Benayas *et al.* 2005; van der Waal *et al.* 2009). This can be due to herb canopy interception of rainfall or to direct exploitation by roots. Competition for water has been shown to be a major interaction between herb species and tree seedlings in water-stressed systems (Knoop & Walker 1985; Ludwig *et al.* 2004; van der Waal *et al.* 2009), while competition for nutrients is more commonly involved in mesic systems (Pagès & Michalet 2003). Nevertheless, herbs and *Q. ilex* seedlings might also compete for soil nutrients, and diminution of herb competition by nurse shrub might have increased nutrient availability to the *Q. ilex* seedlings (Pagès *et al.* 2003).

RESPONSE TO FACILITATION DEPENDED ON *Q. ILEX* SEEDLING SIZE

The response to facilitation has been demonstrated to vary among species (Gómez-Aparicio *et al.* 2004; Liancourt, Callaway & Michalet 2005; Padilla & Pugnaire 2009). Our study goes a step further and indicates that not all individuals within a species have the same response to facilitation. Thus, amelioration of abiotic and biotic conditions by *Retama* benefited smaller seedlings but not larger seedlings since *Retama* reduced mortality of smaller seedlings relative to gaps but not of larger seedlings. Large seedlings frequently have lower mortality than small seedlings under higher stressful conditions (Cook 1980; Leishman & Westoby 1994; Villar-Salvador *et al.* 2008), such as those found in gaps. This can be explained on the basis that large seedlings probably contain more nutrient and storage compounds (Cook 1980; Leishman & Westoby 1994; Villar-Salvador *et al.* 2008) and have higher rates of photosynthesis (Cuesta, unpubl. data) than smaller seedlings. Differences in seedling size within a population can be attributed to genetic differences among individuals as demonstrated for *Q. ilex* (Leiva & Fernández-Alés 1998), but also to emergence time or seed size (Jurado & Westoby 1992; Green & Juniper 2004; De Luis, Verdú & Raventós 2008). We suggest that if *Q. ilex* seedling size has a genetic basis and determines mortality probability, nurse shrubs may contribute to maintain genetic diversity of *Q. ilex* populations.

Conclusions

Both indirect and direct facilitation are important processes of oak regeneration in *Retama* shrublands. The pioneer shrub *R. sphaerocapa* facilitated *Q. ilex* seedlings both by suppressing herb competition (indirect facilitation) and/or by ameliorating microclimatic conditions under its canopy (direct facilitation). Prevalence of indirect and direct facilitation differed between years of distinct climatic conditions. Indirect facilitation seems to be important in years of dry springs, whereas direct facilitation may increase with summer aridity. Since large areas of the Iberian Peninsula have been planted with or colonized by pioneer shrubs, and seedling stage is the most critical phase in Mediterranean woodland regeneration, nurse shrubs could enhance shrubland conversion into forests and play an important role in both passive (i.e. secondary succession) and active restoration of Mediterranean woodlands (Padilla & Pugnaire 2006; Rey Benayas, Bullock & Newton 2008). Furthermore, future studies should assess the incidence of indirect interactions among plants in other Mediterranean shrublands, in which direct positive interactions are known to drive community structure.

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