

Original article

Is the interaction between *Retama sphaerocarpa* and its understorey herbaceous vegetation always reciprocally positive? Competition–facilitation shift during *Retama* establishment

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Abstract

Retama sphaerocarpa is a Mediterranean shrub that when adult, facilitates the establishment of herbaceous plants under its canopy. We test the hypothesis that during the establishment of *R. sphaerocarpa* seedlings, the interaction with the herbaceous plants is negative. We carried out a greenhouse experiment in which seedlings of *R. sphaerocarpa* were grown under different conditions of competition with herbs, watering and date of emergence. Measurements of seedling mortality, biomass and growth were taken during the first growing season. We found a significant relationship between *R. sphaerocarpa* seedling mortality and competition in early spring, presumably due to higher water demand of herbaceous plants. Generally, presence of herbaceous species, lower availability of water and late emergence had negative effects on biomass and growth of *Retama* seedlings. Additional water compensated for the negative effects of competition, except on leaves and cladodes of *Retama* seedlings, suggesting that other resources, such as light, could be the subject of competition. In contrast, *Retama* seedlings exerted a positive influence on the herbaceous plants by increasing their survival and biomass, probably as a consequence of the high availability of nutrients provided by the *Rhizobia* nodules in the roots of *Retama* seedlings. We concluded that, at the regeneration stage of the shrub, the interaction between the herbaceous vegetation and the shrub is negative for the shrub and positive for the herbs. This suggests a shift from competition to facilitation with age of *Retama*, as reciprocal positive interactions have been described between herbaceous plants and adult individuals of the shrub.

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1. Introduction

Facilitation and competition are two main biotic processes in structuring plant communities (Callaway, 1995; Pugnaire and Luque, 2001; Dormann and Brooker, 2002). These two processes coexist in natural communities, and if the net outcome is negative we call it “competition”, whereas if the final balance is positive we speak about “facilitation” (Holmgren et al., 1997; Callaway and Pugnaire, 1999). In fact, several authors have experimentally demonstrated the existence of positive interactions between competing plants that were eclipsed by stronger negative interactions (Aguiar and Sala, 1994; Holzapfel and Mahall, 1999).

The interplay between facilitation and competition is a very dynamic process, and shifts between positive and negative interactions occur (Callaway, 1995; Bertness and Hacker, 1994; Callaway and Walker, 1997; Callaway and Pugnaire, 1999). Fluctuations in abiotic conditions may be one cause of change in the net balance between facilitation and competition (Bertness and Callaway, 1994). Life stage has been described as another cause of shifts between facilitation and competition (Callaway and Walker, 1997; Callaway and Pugnaire, 1999). Several authors have found that plants initially facilitated by nurse plants became strong competitors when older, and sometimes are responsible for the death of their benefactors (McAuliffe, 1984, 1986; Archer et al., 1988).

Retama sphaerocarpa is a leguminous shrub that dominates wide regions of central and southern Spain with semi-

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arid climate. It has a very deep rooting system (Haase et al., 1996a) and N-fixing capabilities due to the symbiosis with *Rhizobia* nodules in its roots. This enables it to colonise areas subjected to high environmental stress, in which it is usually the only woody species. Although *Retama* shrublands were traditionally favoured as a sylvopastoral system (Gómez-Sal et al., 1999), nowadays it is spreading due to its high capacity for colonising abandoned agricultural fields. Photosynthesis in adult individuals of *Retama* is mainly performed by their green stems, called cladodes, because their leaves are ephemeral. Pugnaire et al. (1996a,b) have described the facilitative effect of *Retama* on herbaceous plants growing in its understorey, constituting “islands of fertility” (Went, 1942; García-Moya and McKell, 1970; Garner and Steinberger, 1989). This facilitative effect is reciprocal, as the presence of herbaceous species improves the performance of adult *R. sphaerocarpa*, which led Pugnaire et al. (1996a) to describe this relationship as mutualism.

However, less attention has been paid to the competitive interactions between *R. sphaerocarpa* and its understorey herbaceous vegetation. Competition is more likely to occur during the regeneration stage of *Retama*, when seedlings of the species must compete with herbaceous plants (López-Pintor et al., 2000). Herbs in the understorey of *R. sphaerocarpa* are mainly annuals that germinate in autumn, coinciding with the period in which *Retama* seeds germinate (López-Pintor, 2001). Gómez and Hódar (1997) have found that the greatest densities of *Retama* seeds and seedlings occur under the canopy of adult plants of the same species, but most of these seedlings did not survive the first summer. Therefore, the understorey of *R. sphaerocarpa* is potentially a place of strong competition between its seedlings and herbaceous plants. Although *Retama* seeds are bigger than those of the herbaceous plants, giving *R. sphaerocarpa* seedlings an advantage in competition (Harper, 1977; Leishman and Westoby, 1994), the first weeks after emergence may well be a critical period. In fact, Haase et al. (1996b) have suggested that the cause of the high seedling mortality observed in natural conditions is competition with the herbs growing under adult plants.

López-Pintor et al. (2000) found that seeds of *R. sphaerocarpa* germinated earlier under conditions simulating the microenvironment of its understorey as compared to simulated conditions of the microenvironment away from the understorey. This result was interpreted as a temporal mechanism to avoid competition with herbs, as early germination has been recognised widely as a mechanism to ensure establishment (Cook, 1979; Miller, 1987; Jones et al., 1997). Therefore, it seems that time of emergence of *Retama* seedlings is a factor that may influence the interaction with the herbaceous plants.

In this paper we experimentally investigated the interaction, under greenhouse conditions, between *R. sphaerocarpa* and its understorey herbaceous vegetation during the stage of establishment of the shrub. We tested the hypothesis that during the first growing season this interaction is negative.

We also analysed how different conditions of water availability and time of emergence of *R. sphaerocarpa* seedlings influence this interaction. Our second hypothesis was that water availability and date of emergence may modify competition intensity. We expected that a higher water availability and early emergence will diminish the negative effects of competition with the herbs. At the same time, we analysed not only the possible negative effects of herbs on *R. sphaerocarpa* seedlings but also the negative influence that *Retama* seedlings may exert on the herbaceous plants.

2. Material and methods

2.1. Plant material

During summer 1997, pods of *R. sphaerocarpa* were collected from 20 individuals of a mature shrubland located in Fresno del Torote (Central Spain, 40°35'N, 3°25'W), on alluvial soils of quaternary terraces with sandy-loam texture. The climate is dry Mediterranean with a mean annual temperature of 13.5 °C and 450 mm of annual mean precipitation with high interannual fluctuations.

Seeds of *R. sphaerocarpa* were manually extracted from the pods. Afterwards, all seeds were mixed and stored in dark conditions for 2 months, until the beginning of the experiment. As with many other leguminous shrubs of the Iberian Peninsula, *R. sphaerocarpa* seeds have physical dormancy due to their impermeable seed coat (Baskin and Baskin, 1989). Thus, seeds were scarified making a small incision at the opposite side to the embryo with a pair of pincers (Pérez-Fernández, 1996). Once this physical barrier is overcome, seeds germinate readily (Catalán Bachiller, 1991).

Samples of the soil seed bank were also taken from the understorey of adult *R. sphaerocarpa* individuals of the same population in the same period. We collected 200 cores of 10 × 10 and 6 cm depth, as the soil seed bank is mainly concentrated in the superficial layer (Ortega et al., 1997). The samples were collected at the end of the summer, prior to the arrival of autumn rains that provokes germination. The soil seed bank is highly diverse and mainly composed of winter annual species: graminoids, clovers and other forbs in which the *Cariophyllaceae* family is well represented. See López-Pintor (2001) for further details of the floristic composition of the soil seed bank.

2.2. Experimental design

All soil samples were mixed and homogenised and then subdivided into 160 subsamples that were placed onto a 25 cm deep layer of vermiculate separated by a fine layer of gauze, in 30 cm deep pots of 170 cm² area. In the centre of each pot, two scarified seeds of *R. sphaerocarpa* were sown to ensure the establishment of one of them (when the two seedlings emerged, the second was pulled out). Three factors were manipulated during the experiment: competition with

herbaceous species, date of emergence of *R. sphaerocarpa* seedlings and water availability. In pots subjected to no competition treatment, competition with herbaceous species was prevented by manual removal of the aerial and below-ground parts of all seedlings as soon as they emerged. Date of emergence of *R. sphaerocarpa* seedlings was controlled by manipulating the date in which seeds were sown. In half of the pots, *R. sphaerocarpa* seeds were sown at the beginning of the experiment, while in the other half seeds were sown 15 days later. Two different treatments of water availability, high and low, were applied by subjecting half of the pots to a double supply of water. This was to simulate two contrasting conditions of the highly variable precipitation regime in the area (Espigares and Peco, 1995). All pots were watered once a week, and also percent volumetric soil water content was measured weekly with a TDR probe 8 cm deep (IMKO, Micromodultechnik Co.). The average soil water content throughout the whole experiment in the pots subjected to high water availability was $23.16\% \pm 1.19$ S.E., and $10.41\% \pm 1.54$ S.E. in the pots subjected to low water availability. These values are representative of field conditions, as we have registered a mean value of 14.9% during spring and autumn, using the same instrument.

The experiment took place inside a greenhouse, where the 160 pots were arranged in a $2 \times 2 \times 2$ completely randomised design (two competition treatments \times two date of emergence \times two watering treatments) with 20 initial replicates for each combination of treatments. Ten extra pots prepared in the same way were used as a control for the effect of *Retama* on herbaceous species, by not sowing *R. sphaerocarpa* seeds. Half the pots were subjected to each watering treatment. A plastic mesh forming 1 cm^2 grids was placed on the surface of all pots to facilitate the monitoring of emergence and survival of each seedling (Peco and Espigares, 1994; Espigares and Peco, 1995).

2.3. Data collection

The experiment lasted one growing season (7 months), from the autumn following *Retama* seeds and soil samples collection to the next summer. Mortality and growth variables (height and number of cladodes and leaves) of all *R. sphaerocarpa* seedlings were measured weekly.

Aerial and below-ground biomass measurements of *R. sphaerocarpa* seedlings were obtained by harvesting a third of the pots at three different times along the experiment: late winter (February), spring (April) and finally early summer (June). This procedure implied a gradual reduction in the number of replicates: from 20 at the first harvest to seven in the last one. The number of *Rhizobia* nodules in *Retama* seedling roots was counted under a stereoscope. Pots with late emerged *R. sphaerocarpa* seedlings were harvested 15 days later than the others, in order to compare *R. sphaerocarpa* seedlings of the same age. These three harvesting times will be referred to as T1, T2 and T3, respectively. Samples were sorted into above- and below-ground, and all

fractions were dried at 60°C for 3 days and then weighed. The number of herbaceous seedlings (dead and alive) in each pot was counted 1 month after the beginning of the experiment and also at T1, T2 and T3.

2.4. Data analysis

Relationships between final mortality of *R. sphaerocarpa* seedlings and the three treatments (competition, date of emergence and watering) were analysed through a log-linear analysis. Three-way ANOVAs were used to test treatment effects on biomass data of *Retama* seedlings in each of the three harvest times. Three-way repeated measurement ANOVAs were used to test differences between treatments on weekly data of growth variables measured in the period between T1 and T2 (see Section 3).

Final mortality rates of herbs were calculated by dividing the total number of dead seedlings by the total number of seedlings emerged in each pot. Aerial biomass of the herbaceous community was calculated at T1, T2 and T3, using the same procedure as with *Retama* seedlings. In the 10 control pots aerial biomass of the herbaceous community was measured only at the end of the experiment (T3). Two-way ANOVAs were performed to analyse the effect of competition with *R. sphaerocarpa* seedlings and water availability on mortality and biomass of herbaceous plants.

All statistical analyses were performed with the software package STATISTICA (Statsoft, Inc. 1993).

3. Results

3.1. Mortality of *Retama sphaerocarpa* seedlings

All *Retama* seed germinations occurred in the first 10 days after sowing, thus providing each pot with an established seedling. Log-linear analysis detected a significant relationship between final *R. sphaerocarpa* seedling mortality and competition treatment ($\chi^2 = 6.68$, $P < 0.01$). Seedlings subjected to competition with herbs experimented a higher mortality than those in the absence of competition (19.35% vs. 1.31%). No effect of date of emergence nor watering, neither interaction between treatments was found. Mortality of *Retama* seedlings occurred between days 68 and 133 from the beginning of the experiment (late winter to spring), coinciding with the period in which herbaceous species initiate their active growth (Fig. 1).

3.2. Biomass of *Retama sphaerocarpa* seedlings

Table 1 shows the results of the three-way ANOVAs performed on biomass data of *R. sphaerocarpa* seedlings at the three harvest times. Competition reduced significantly all fractions of *Retama* biomass except below-ground biomass at T1 (Fig. 2). Watering increased total and above-ground *Retama* seedling biomass only during the last period (T3).

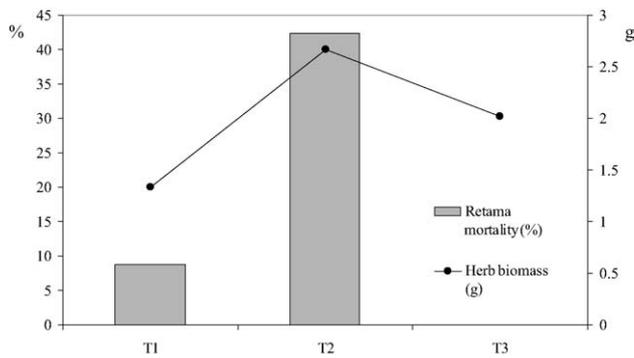


Fig. 1. Mean aerial herb biomass per pot and *R. sphaerocarpa* seedling mortality in the three harvest periods (T1, T2 and T3).

Early emergence of *Retama* seedlings increased their biomass, specially at T1 and T3. In general, above-ground biomass was about double than that of below (Fig. 2), so total biomass was driven by above-ground effects. A significant interaction of all three factors (watering, competition, and date of emergence) on total and below-ground biomass at T2 showed that the extra supply of water compensated for the negative effects of competition on the biomass of the late emerged seedlings (Fig. 2).

3.3. Growth of *Retama sphaerocarpa* seedlings

We analysed in detail the growth of *R. sphaerocarpa* seedlings during the period between T1 and T2 because it was the period in which seedling mortality occurred (Fig. 1). Besides, it was the time of maximum growth of herbaceous species, thus presumably maximum interference with seedling development.

A significant interaction between watering and time was found in the three growth variables of *Retama* seedlings (height ($F_{3,120} = 8.33$), number of cladodes ($F_{3,120} = 6.61$) and number of leaves ($F_{3,120} = 8.68$), $P < 0.001$). This interaction showed that the positive effects of watering became significant from day 112 onwards, coinciding with the arrival of spring that implied a higher temperature. There was also a significant interaction ($F_{3,120} = 4.34$, $P < 0.01$) be-

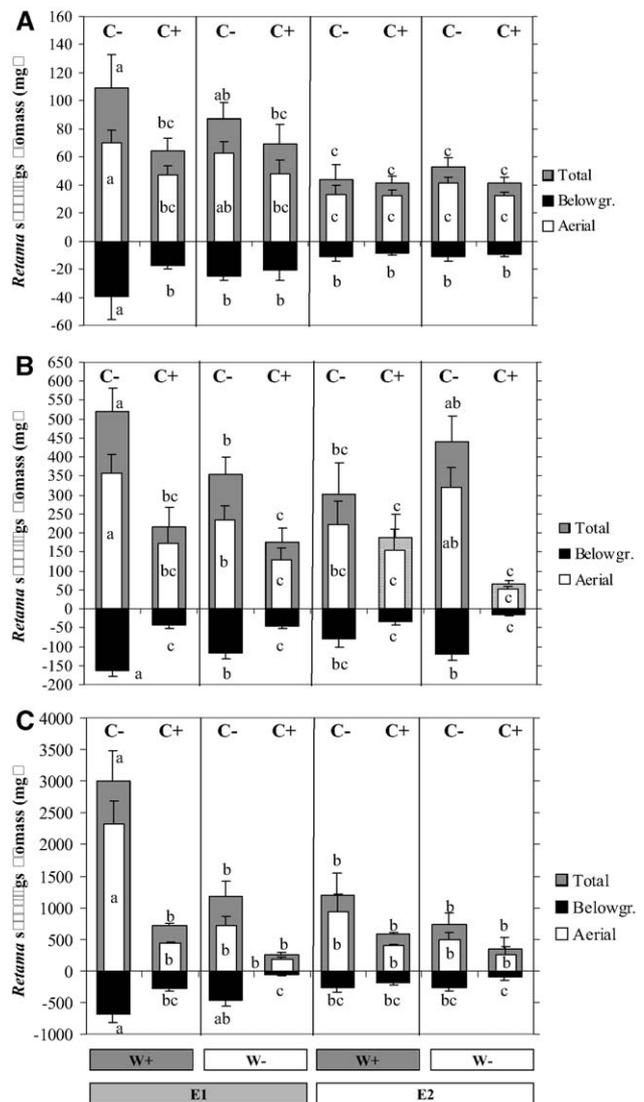


Fig. 2. Biomass of *R. sphaerocarpa* seedlings (mean \pm S.E.) at T1 (a), T2 (b) and T3 (c) in the different treatments (W-, low watering; W+, high watering; C+, herb competition; C-, no herb competition; E1, early emergence; E2, late emergence). Different letters indicate significant differences between treatments (LSD test, $P < 0.05$).

Table 1

Anova results of the effect of treatments (C, competition; W, watering and E, emergence) on the biomass of *R. sphaerocarpa* seedlings in the three harvest times (T1, T2 and T3). (TB, total biomass; AB, above-ground biomass; BB, below-ground biomass). Sample size (N) and degrees of freedom (d.f.) of each analysis are indicated

		C		W	P	E	P	C \times W \times E	
		F	P					F	P
T1, N = 45, d.f. = 1, 37	TB	5.03	0.031	0.05	n.s.	18.68	0.000	1.02	n.s.
	AB	5.66	0.023	0.01	n.s.	19.38	0.000	0.81	n.s.
	BB	2.39	n.s.	0.24	n.s.	9.98	0.003	0.75	n.s.
T2, N = 40, d.f. = 1, 32	TB	26.99	0.000	1.06	n.s.	2.04	n.s.	4.22	0.048
	AB	18.34	0.000	1.29	n.s.	0.97	n.s.	3.55	n.s.
	BB	51.18	0.000	0.27	n.s.	6.54	0.015	5.03	0.032
T3, N = 38, d.f. = 1, 30	TB	14.57	0.001	7.33	0.011	4.26	0.048	1.07	n.s.
	AB	13.77	0.001	8.36	0.007	3.49	n.s.	1.53	n.s.
	BB	11.67	0.002	2.91	n.s.	4.95	0.034	0.08	n.s.

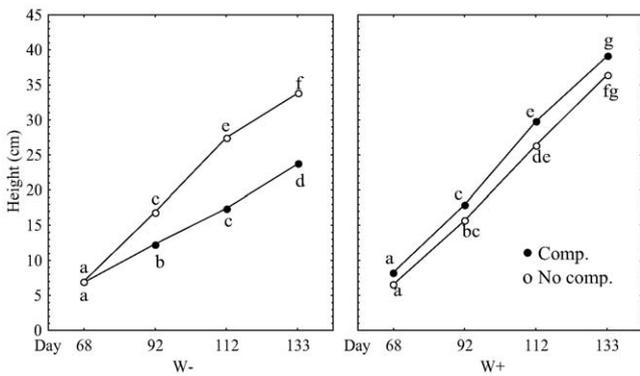


Fig. 3. Interaction between watering, competition and time on height of *R. sphaerocarpa* seedlings. W–, low watering; W+, high watering. X axis represents days from the beginning of the experiment. Different letters indicate significant differences (LSD test, $P < 0.05$).

Table 2

Number of cladodes, leaves and *Rhizobia* nodules in roots of *R. sphaerocarpa* seedlings (mean \pm S.E.) in the different combinations of treatments at T2 (W–, low watering; W+, high watering; C+, herb competition; C–, no herb competition; E1, early emergence; E2, late emergence)

Treatment	Number of cladodes	Number of leaves	Number of <i>Rhizobia</i> nodules
W–, C+, E1	0.083 \pm 0.053	14.083 \pm 1.658	8.25 \pm 2.269
E2	0.208 \pm 0.136	9.542 \pm 1.564	1.00 \pm 2.269
W–, C–, E1	1.375 \pm 0.340	23.958 \pm 2.531	0.33 \pm 1.853
E2	0.583 \pm 0.239	14.000 \pm 2.663	5.57 \pm 1.715
W+, C+, E1	0.458 \pm 0.245	17.750 \pm 1.167	7.50 \pm 2.269
E2	0.375 \pm 0.107	13.792 \pm 1.139	4.67 \pm 2.620
W+, C–, E1	3.250 \pm 0.885	32.583 \pm 4.404	7.17 \pm 1.853
E2	1.125 \pm 0.576	16.167 \pm 5.280	6.83 \pm 1.853

tween the effects of watering, competition and time in the height of *Retama* seedlings: in conditions of low water availability, *Retama* seedlings growing in competition with herbs were smaller than those growing alone, and the intensity of this effect increased with time (Fig. 3). However, with a high water supply, no differences in the height of seedlings subjected to different competition treatments were found (Fig. 3).

Competition also reduced the number of cladodes ($F_{1,40} = 19.64$, $P = 0.0001$) and leaves ($F_{1,40} = 14.50$, $P = 0.0005$) of *R. sphaerocarpa* seedlings, but without the compensating effects of watering in these cases (Table 2). Late emergence of *R. sphaerocarpa* seedlings reduced the number of cladodes and leaves ($F_{1,40} = 5.99$ and 17.72 , $P < 0.01$, respectively) (Table 2).

The three-way ANOVA performed with the number of *Rhizobia* nodules in the roots of *Retama* seedlings at T2 showed a significant interaction between date of emergence and competition ($F_{1,32} = 6.32$, $P = 0.01$). When competing with herbs, early emerged seedlings had more nodules than late emerged ones (Table 2). No influence of any of the treatments was observed on the number of nodules at T3.

3.4. Influence of *Retama sphaerocarpa* seedlings on biomass and mortality of herbaceous plants

Mortality rates of herbaceous plants at the end of the experiment were higher in control pots ($F_{2,75} = 6.24$, $P = 0.003$) (Fig. 4). Also, at T3 (the only moment in which aerial herb biomass in control pots could be tested), control pots had less herbaceous biomass than those with *Retama* seedlings ($F_{2,15} = 36.90$, $P < 0.0001$), having the pots with early emerged *Retama* the maximum biomass (Fig. 5). In contrast, at T2 we found more herbaceous biomass in the pots with late emerged *Retama* seedlings compared with those of early emergence ($F_{1,11} = 5.47$, $P < 0.04$) (Fig. 5). However, the significant interaction between watering and presence of *Retama* seedlings at T3 ($F_{2,15} = 7.45$, $P < 0.01$) showed that the effect of emergence depended on watering: the existence of more herbaceous biomass in the pots with late emerged *Retama* seedlings compared to control pots only occurred in conditions of a high water supply, and when water was

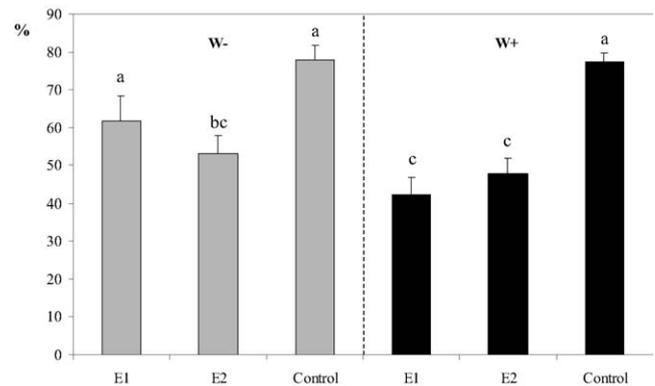


Fig. 4. Herbaceous seedling mortality rates (mean \pm S.E.) in the different treatments (control, no *R. sphaerocarpa* seedlings; E1, early emergence of *R. sphaerocarpa* seedlings; E2, late emergence of *R. sphaerocarpa* seedlings; W–, low watering; W+, high watering). Different letters indicate significant differences (LSD test, $P < 0.05$).

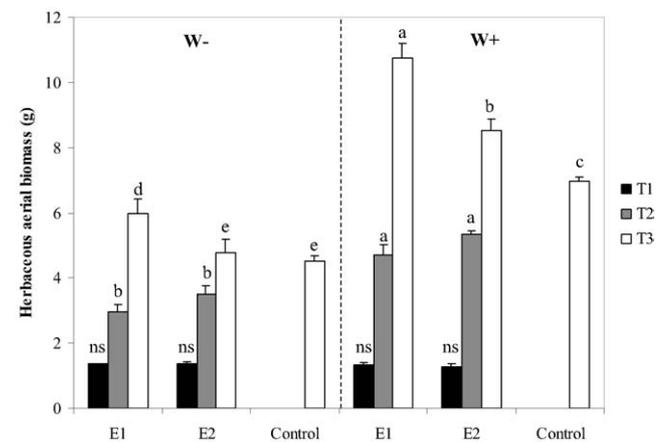


Fig. 5. Aerial biomass of the herbaceous plants (mean \pm S.E.) at T1, T2 and T3 in the different treatments (W–, low watering; W+, high watering; E1, early emergence of *Retama* seedlings; E2, late emergence of *Retama* seedlings; control, not *R. sphaerocarpa* seedlings). Different letters indicate significant differences between treatments (LSD test, $P < 0.05$).

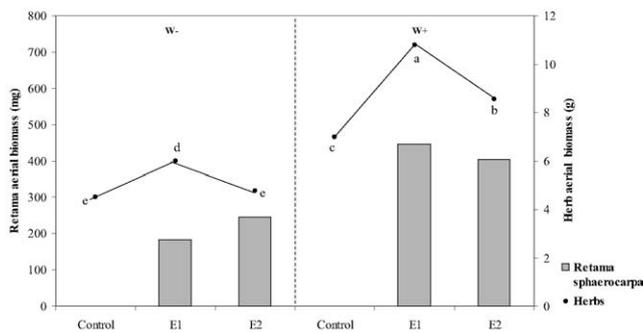


Fig. 6. Interaction between watering and presence of *Retama* seedlings on the aerial herbaceous plants biomass at T3. *R. sphaerocarpa* seedling aerial biomass is also indicated in bars. W-, low watering treatment; W+, high watering treatment; control, no *R. sphaerocarpa* seedlings; E1, early emergence of *Retama* seedlings; E2, late emergence of *Retama* seedlings. Different letters indicate significant differences between treatments (LSD test, $P < 0.05$).

limiting there was no difference in the herbaceous biomass between both treatments (Fig. 6).

Watering improved the status of herbs by decreasing its final mortality rates ($F_{1,75} = 4.57$, $P = 0.03$) (Fig. 4) and increasing its biomass at T2 and T3 ($F_{1,11} = 51.72$, $P < 0.0001$ and $F_{1,15} = 187.64$, $P < 0.0001$, respectively) (Fig. 5). It is possible that these benefits were influenced by the minor number of herbaceous seedlings per pot found in watering pots ($F_{1,75} = 15.74$, $P < 0.001$) (mean \pm S.E.: 462.65 ± 18.4 in the low watering treatment and 370.04 ± 9.1 with a high water supply).

4. Discussion

Monitoring of mortality and growth of *R. sphaerocarpa* seedlings growing with herbaceous plants during the first growing season has revealed the existence of competition between the seedlings of this shrub and the herbaceous cover that is facilitated in the understory of adult individuals. Herbaceous plants become competitive against *Retama* seedlings by limiting the survival and growth of the shrub. This confirms our hypothesis of a negative interaction during the stage of establishment of the shrub. Although *Retama* seedlings experienced a negative (competitive) impact from neighbouring herbaceous plants, the seedlings did not produce a competitive impact on the herbaceous plants, and in fact produced a facilitative effect at the end of the establishment phase, increasing survival and biomass of herbaceous plants.

4.1. Effects of herbs on *Retama sphaerocarpa* seedlings

The negative effect that herbaceous plants exerted on the establishment of *R. sphaerocarpa* increased seedling mortality. Many authors found that competition with herbaceous species provokes seedling mortality in woody plants (Archer, 1989; Harrington, 1991; Kolb and Robberecht, 1996; Davis et al., 1999). In our experiment, seedling mortality occurred

at the beginning of spring, coinciding with the maximum growth of herbaceous vegetation (Fig. 1). This agrees with the results of Williams and Hobbs (1989), who observed that spring was the critical period for the establishment of the shrub *Baccharis pilularis* in annual grasslands of California, as annuals depleted soil water in the superficial layers of the soil.

In general terms, competition with herbs, low availability of water, and late emergence are disadvantages for the growth of *Retama* seedlings. Although no significant relationship between date of emergence and seedling mortality was found, seedlings that emerged later were smaller and had less biomass and fewer leaves and cladodes. Thus, the hypothesis that early emergence may avoid competition with herbs (López-Pintor et al., 2000) seems to be also confirmed. Competition-driven seedling mortality becomes a strong force in early establishment of *R. sphaerocarpa* although in our experiment its effects may have been underestimated by the not randomly distribution in time of the mortality and the survivorship of the bigger individuals (working against the competition effect).

We have observed that water compensated for the negative effects of competition on biomass at T2 but not at the end of the experiment (T3), when the extra water input did not increase the biomass of *Retama* seedlings competing with herbs (Fig. 2). At the same time, the height of *Retama* seedlings growing with herbs increased with watering (Fig. 3) but not the number of leaves and cladodes. Various authors have described how the effect of herbaceous plants on woody species seedlings mostly consists in a reduction of water availability (Knoop and Walker, 1985; Zutter et al., 1986; Gordon et al., 1989). Also, Davis et al. (1998,1999) minimised the effects of competition with herbs on oak seedlings by increasing water inputs. Our results correspond with Huston and De Angelis's (1994) theory, which states that increasing supply of resources decreases intensity of competition. The fact that extra water supply reduced in some cases competition effects indicates the existence of competition for water, but the experiment also showed evidence of competition for another resource that water did not compensate for. It is likely that this resource is light, as heights of *Retama* seedlings and herbaceous plants were very similar and, in some cases, herbs almost completely covered *Retama* seedlings. Also, late emerged seedlings had always less below-ground biomass than those emerged earlier (Fig. 2). This agrees with Tilman's (1982) resource competition model that explains the inverse correlation between light intensity and soil resources, provoking tradeoffs in the allocation of aerial and below-ground biomass in plants. Late emerged seedlings could be subject to more light stress than early emerged ones due to the greater growth of herbs, and this could have influenced in the decrease of the biomass of roots in favour of aerial parts. The fact that extra water increased aerial but not below-ground biomass at T3 (Fig. 2c), points in that direction. Besides, Valladares and Pugnaire (1999) concluded that *R. sphaerocarpa* is particu-

larly sensitive to a reduction in photosynthesis compared to other woody Mediterranean species. The fact that we did not observe compensation in the production of photosynthetic structures (aerial biomass and the number of leaves and cladodes) with additional water tends to reinforce this hypothesis.

4.2. Effects of *Retama sphaerocarpa* seedlings on herbs

Retama seedlings, however, exerted a positive influence on herbaceous plants, highlighted by the decrease of their mortality rates (Fig. 4). In addition, less aerial biomass of herbaceous plants was found in the pots without *Retama* seedlings (Fig. 5). The effect of date of emergence of *Retama* seedlings on the herbaceous biomass changed from T2 to T3. At T2 the early emergence of *Retama* seedlings affected the herbaceous plants negatively by reducing their aerial biomass, while at T3 pots with early emerged *Retama* seedlings had more herbaceous biomass than those with late emerged ones (Fig. 5). The fact that herbaceous plants benefited from those individuals of *Retama* with a maximum growth (watered and early emerged ones) revealed the facilitation exerted by *R. sphaerocarpa* (Fig. 6). Our results indicate that *R. sphaerocarpa* can exert a facilitative effect on the herbaceous plants of its understorey very early, at the end of the first growing season of establishment of the shrub (T3). The higher number of *Rhizobia* nodules found in the roots of early emerged *Retama* seedlings growing in competition with herbs (Table 2) could be the mechanism responsible for this facilitation, by providing the herbs with a higher availability of nutrients.

Several studies have revealed the existence of nutrient limitation for the growth of herbaceous plants competing with seedlings of woody plants. For example, Davis et al. (1999) described the positive effect of an extra input of soil nitrogen for herbaceous plants competing with oak seedlings. Some evidence of the limitation of nutrients can be drawn from our experiment. At T3, differences in herbaceous biomass between control and late emerged *Retama* seedling pots appeared only when water was not limiting (Fig. 6). We can consider that these differences are the consequence of a higher nutrient (nitrogen) supply due to the presence of *Retama* seedlings with *Rhizobia* nodules in their roots. As water was probably the main limiting factor, differences in biomass due to the different nutrient supply only appeared when water was not limiting. Swank and Oechel (1991) also postulated the synergistic effects of water and nutrient limitation, since nutrients are absorbed by roots from solution, thus making water supply in the soil strongly influence nutrient availability.

In conclusion, we have demonstrated the existence of a negative interaction between *R. sphaerocarpa* and its understorey herbaceous vegetation during the regeneration stage of the shrub. Pugnaire et al. (1996a) described the mutualistic relationship between the herbs and *R. sphaerocarpa* when the latter is an adult shrub: while the shrub provided the herbs

with a beneficiary microenvironment, the herbs provided the shrub with labile organic material. Our experiment has revealed that the positive effect of *R. sphaerocarpa* on herbs is manifested from the stage of shrub establishment, but we have shown that, at this stage, the herbaceous plants not only do not facilitate but also compete with *Retama* seedlings, limiting its survival and growth. Thus, the sign of the relationship is different at different life stages, specifically at the regeneration stage of *R. sphaerocarpa*. Callaway and Walker (1997) described life stage as one possible cause of shifts between facilitation and competition in plant communities, referring to cases in which plants initially facilitated by nurse plants usually become strong competitors when they grow (McAuliffe, 1984, 1986; Archer et al., 1988; Flores-Martínez et al., 1998; Barnes and Archer, 1999). Our results suggest that this study is another example of shift in the sign of an interaction with time. It seems likely that the positive effect of the herbs on the growth of *R. sphaerocarpa* described in the literature (Pugnaire et al., 1996a) will appear later, after the first growing season, when it is established and the herbaceous plants (mainly annuals) die and decomposition increases the availability of nutrients in the soil. Longer lasting experiments are needed to explore shifts between competition and facilitation over different life stages, to fully understand the dynamics of the interaction between *R. sphaerocarpa* and its understorey herbaceous community.

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