Changes in plant interactions along a gradient of environmental stress

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A combination of competition and facilitation effects operating simultaneously among plant species appears to be the rule in nature, where these effects change along productivity gradients often in a non-proportional manner. We investigated changes in competition and facilitation between a leguminous shrub, *Retama sphaerocarpa*, and its associate understorey species along an environmental gradient in semi-arid southeast Spain. Our results show a change in the net balance of the interaction between the shrub and several of its associated species, from clearly positive in the water-stressed, infertile environment to neutral or even negative in the more fertile habitat. There was a weakening of facilitation along the fertility gradient as a consequence of improved abiotic conditions. Competition was the most intense for below-ground resources in the less fertile environment while total competition tended to increase towards the more productive end of the gradient. Changes in the balance of the interaction between and among different plant species along the gradient of stress were caused by a decline in facilitation rather than by a change in competition. As both competition intensity and facilitation change along gradients of resource availability, plant interactions are best viewed as dynamic relationships, the outcome of which depends on abiotic conditions.

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Complex combinations of competition and facilitation operating simultaneously among plant species seem to be widespread in nature (Walker and Chapin 1986, Aguiar and Sala 1994, Chapin et al. 1994, Callaway and Walker 1997, Holmgren et al. 1997, Holzapfel and Mahall 1999). Both competition intensity (Grime 1979, Tilman 1988) and facilitation (Bertness and Callaway 1994, Callaway 1999) change along gradients of resource availability, so that plant interactions are best viewed as dynamic relationships in which the outcome, in terms of productivity or fitness of the interacting species, depends on abiotic conditions. The effects of plant interactions are measured as some plant performance parameters, usually biomass differences between individuals with experimentally removed neighbours and control plants with intact neighbours. But plant size or biomass only renders the net balance of the interaction, i.e., the sum of all direct and indirect, positive and negative influences which may change in a non-proportional manner along productivity gradients (Callaway and Pugnaire 1999).

The dynamic nature of different positive and negative effects (Greenlee and Callaway 1996, Brooker and Callaghan 1998) is rarely considered. For example, while competition for light increases towards the more productive end in a gradient of environmental resource availability (Grime 1977, Chapin 1980, Grubb 1985, Tilman 1988, Keddy 1989), competition for below-ground resources may or may not change (Reynolds 1999). Experimental evidence supporting shifts in total competition intensity along productivity gradients seems to depend on whether above- and below-ground competition are negatively correlated, on changes in species composition or diversity (Peltzer et al. 1998), or

on the consistency of resource supply vs demand (Taylor and Aarsen 1990).

Positive interactions (i.e., facilitation) are expected to be more important in plant communities as abiotic stress or consumer pressure increases, because neighbours buffer one another from extremes of the abiotic environment and herbivory, while competitive interactions, in turn, dominate when physical stress and consumer pressure are both relatively low (Bertness and Callaway 1994).

Shifts in the net balance of an interaction (i.e., from competition to facilitation or vice versa) have been observed in several systems driven by factors such as life-history stage or physiology of interacting species (Callaway et al. 1991, Haase et al. 1996, Pugnaire et al. 1996a, Guo et al. 1998). Field experiments and substantive indirect evidence have also shown a strong relationship between the degree of abiotic stress and such changes (e.g., Bertness and Shumway 1993, Bertness and Hacker 1994, Greenlee and Callaway 1996). Other non-experimental studies also indicate that competitive effects are stronger in wet and cool years and facilitative in dry, hot years (Fuentes et al. 1984, De Jong and Klinkhamer 1988, McClaran and Bartolome 1989, Belsky 1994, Pugnaire and Lázaro 2000).

There are also examples where no evidence of change between competition and facilitation have been found under changing water stress conditions (Casper 1996), and a recent meta-analysis of published results did not find a conclusive trend in the relationship between competition/facilitation intensity and productivity in plants (Goldberg et al. 1999).

Most experiments documenting changes in the balance of plant interactions focus on stress due to low nutrient availability (Goldberg et al. 1999) but specific tests of changes along natural gradients caused by other, non-resource factors are less common (Callaway 1995).

In this paper we examine whether a shift occurs in the interaction between a leguminous shrub, *Retama sphaerocarpa* (L.) Boiss., and its understorey vegetation along a gradient of environmental stress. *R. sphaerocarpa* shows a remarkable facilitative effect on its understorey in dry environments of southeast Spain, where many other shrubs, forbs, grasses and annual species grow under its canopy (Pugnaire et al. 1996a, b) forming patches of high diversity and productivity. However, this shrub is widely distributed across the Iberian Peninsula, occupying habitats of varying fertility. As hypothesized by Bertness and Callaway (1994), we expected that facilitation would be more important at the more stressful end of the gradient where belowground competition strength would also be more intense. We used field observations and manipulations to explore the relationships between relative intensity of plant interactions and environmental stress.

Experimental design

Field site

Our field site is located in the Rambla del Saltador, a valley near Tabernas, Almería, Spain (37°08′ N, 2°22′ W) with an ephemeral water course that only carries water after heavy rains. The valley is in the southern aspect of the Sierra de Los Filabres range and stretches from an elevation of near 600 m where the climate is semi-arid with a mean annual precipitation near 250 mm, to over 1800 m, with more mesic conditions. There is a dry season from June to September, when vapour pressure deficits reach over 4 kPa in the lower valley (Pugnaire and Haase 1996).

The valley, of about 20 km in length, is excavated on a mica-schist bedrock. Weathering and erosion have produced extensive alluvial fan systems and colluvial deposits at the base of the mountain slopes (Puigdefábregas et al. 1996).

The lower part of the valley, known as Rambla Honda, is mostly flat, and the bottom is filled with poorly sorted alluvial deposits – mainly sand – reaching up to 20 m in depth. The upper part of the valley is steeper, with rocky outcrops interspersed with rendzic leptosol soils. *Retama sphaerocarpa*, a leguminous shrub, covers the valley bottom of Rambla Honda with densities of ≈ 500 adult plants/ha and may also be found scattered on slopes of the upper valley, occasionally forming thickets. The largest shrubs may rarely be over 4 m in height, and most are between 1 and 3 m. Gaps between shrubs are almost bare of vegetation in the lower valley, but cover of winter annuals and other smaller shrub species increases with elevation. Many plant species grow in the understorey of *R. sphaerocarpa* shrubs, particularly in the lower valley, as a consequence of positive interactions between overstorey and understorey species (Pugnaire et al. 1996b).

Methods

We selected two locations within the valley, one in the Rambla Honda, at 630 m elevation and another one ca 10 km higher up in the valley at 1200 m elevation, with the same parent material and general orientation. Within each site, ten *R. sphaerocarpa* shrubs of average size were selected for sampling in spring 1998.

Samples of soil were collected underneath and outside the *R. sphaerocarpa* canopies from the upper 5 cm of soil and the < 2 mm fraction was retained for analysis. Because of the low clay content and the absence of gypsum and other salts, organic matter content was determined by combustion at 430°C. The fine particle fraction in the soil (clay + silt) was obtained by passing samples in which organic matter had been destroyed through a 0.05-mm sieve. Water content

at field capacity was determined at 333 kPa with a pressure membrane apparatus (Soil Moisture Equipment Corp., Santa Barbara, CA, USA). Bulk density was obtained by weighing a known volume of soil which had been dried at 110°C. Soil N content was determined by Kjeldahl analysis, NO_3^- by ion chromatography, and NH_4^+ by colorimetry.

Microclimatic conditions under shrubs at each site were recorded with two data loggers (CR10, Campbell Scientific, Logan, UT, USA) set for one week in late spring simultaneously in the upper and lower valley sites. Photosynthetically active radiation (PAR) was measured using a PAR sensor (Skye Ltd., Llandridod Wells, UK). Relative humidity was determined with a psychrometer (MTH-A1, ITC, Almería, Spain), and air temperature and soil temperature in the understorey and outside the canopy were measured with copper/constantan wire thermocouples. Readings were taken every 30 s and averaged every 5 min for all measurements.

General climate characteristics of the two sites were obtained from the nearest weather stations (Velefique and Tahal, 990 and 1006 m elevation, respectively, for rainfall and temperature of the upper valley site) and the Tabernas meteorological station (490 m elevation, 9 km to the south of our lower valley site), both provided by the Spanish Instituto Nacional de Meteorología.

All soil characteristics underneath and outside the shrub canopies were compared by t-tests.

Facilitation assessment

To estimate the extent of facilitation at the two extremes of this gradient, dry mass of individual plants belonging to five different species growing under *R. sphaerocarpa* canopies and in gaps between shrubs were determined in the upper valley site, and four species in the lower valley site. Ten plants were collected per species and site, including annuals, forbs, and small shrubs at both sites. Above-ground biomass of average individual plants was collected, dried at 70°C for 48 h and weighed. To quantify specific leaf area (area of leaf per unit dry mass), the area of four mature leaves of each plant was measured with an area meter (Mk2, Delta-T, Cambridge, UK), dried at 70°C for 24 h and weighed.

Competition experiment

To specifically test for changes in the net interaction intensity along the gradient, we used seedlings of *Artemisia barrelieri*, a shrub species naturally occurring at both locations, as a test phytometer. Seeds were germinated in the lab and seedlings grew in a greenhouse for about 1 month. In April, when they were about 3 cm tall, seedlings were planted in our two field sites and in two habitats, gap and understorey, with a factorial design and ten replicates. Seedlings were planted in pairs, one plant of each was included in a 7-cm-long, 5-cm-wide PVC tube to exclude root competition. Planted seedlings were watered to help establishment and harvested in June, when water shortage was exerting a strong effect because of the low spring rainfall.

The interaction effects were assessed by the log response ratio (Hedges et al. 1999), using total biomass and root biomass as the response units. This index ($lnRR = ln[B_{removal}/B_{control}]$, where B here is biomass) has been used heavily in the animal literature to quantify interaction strength, as well as in recent plant literature (Goldberg et al. 1999), and its statistical properties have been also explored (Hedges et al. 1999).

We expected that resource availability and productivity, in addition to climatic conditions, would affect competition intensity at both extremes of the gradient. At the low elevation site standing biomass both in the understorey of *R. spaherocarpa* shrubs and in gaps were lower than at the high elevation site, presumably because of less soil resources; biomass in the understorey was also much larger than in gaps at the low elevation site (Pugnaire et al. 1996a) but differences in biomass between the understorey and gaps were less evident at the high elevation site. In addition, climate was expected to be moderate at the high elevation site and more extreme at the low elevation site.

We assume that root interactions among understorey plants are always competitive and that the effects of the *R. sphaerocarpa* canopy are facilitative at both elevation sites.

Data were analysed with a three-way MANOVA using elevation, habitat and competition treatment as fixed factors; significance in differences among means were tested by LSD post hoc comparisons with the Statistica 4.5 software package (StatSoft 1993).

Results

As expected, the two sites along the Rambla del Saltador valley showed very different properties regarding climate and soil. Long-term data (Fig. 1) show the upper valley as more mesic than the lower valley, receiving more rainfall (330 vs 240 mm annual average) with a slightly lower mean temperature (15.9 vs 16.7°C); consequently, the evaporative demand is lower and water shortage less limiting for plant growth than in the lower valley site. Climatic characteristics were also more mesic in the upper valley site during the spring days we measured. Both average air and soil temperatures were lower in the high elevation site, with outstanding differences in the maximum temperature
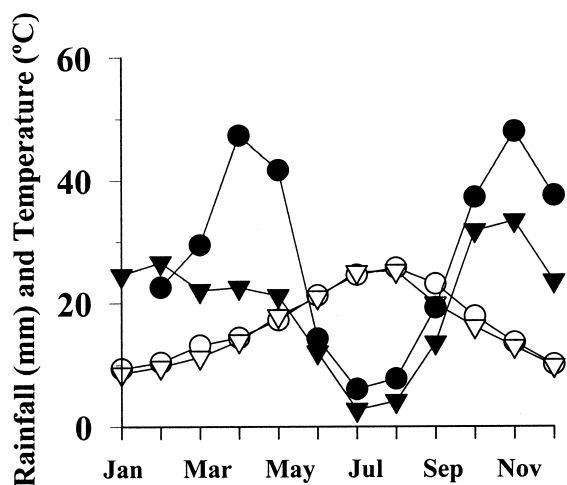
Fig. 1. Seasonal patterns of rainfall (solid symbols) and temperature (open symbols) in the lower (circle) and upper (triangle) valley sites within the Rambla del Saltador valley. Data were taken from the Tahal and Velefique (upper valley) and Tabernas (lower valley) weather stations, the closest available to our field sites.

reached: up to 5.5°C in air temperature and 11.8°C in soil temperature. Soil temperature under *R. sphaerocarpa* canopies was very similar in both sites, though, suggesting the importance of micro-climate amelioration for understorey plant growth, particularly in the lower valley. Air relative humidity was similar at both elevations.

Soils at the two elevation sites showed very different values in all measured parameters. Upper valley soils had higher amount of organic matter, higher N concentration, higher proportion of fine soil particles and higher water holding capacity as well as lower bulk density than lower valley soils (Table 1). Differences between gap and understorey soils were significant in both localities, but the positive effect of the canopy was more important in the lower valley, where soil organic matter and nitrogen concentrations, and the proportion of fine soil particles were of a considerably lower magnitude in gaps (Table 1). The effect of the canopy on the physical properties of the soil rendered a higher water holding capacity and better soil structure which permits a higher soil aeration.

As a consequence of lower soil fertility and more stressful environmental conditions, the positive effect exerted by the *R. sphaerocarpa* canopy was relatively more important in the lower valley site than in the upper valley site. In the lower valley site, differences in the biomass of understorey plants vs plants in the open were much greater than at the higher site (Table 2). Differences in relative mass between understorey and gap plants were significant in the lower valley (Table 2), but not in the upper valley, a trend paralleled by specific leaf area (SLA), which was higher in plants growing underneath than outside *R. sphaerocarpa* canopies in the lower valley but similar in the higher valley (data not shown). The only species present at both sites, *Eryngium campestris*, clearly corresponded with the pattern of between site and habitat differences (Table 2). Plants growing in gaps in the lower valley site were smaller than individuals growing in the upper valley site, but amelioration by *R. sphaerocarpa* increased size 2.7 times in the lower valley vs 1.2 times in the upper valley (Table 2).

Competition experiment

Total plant mass of *A. barrelieri* seedlings were larger under canopies than in gaps (Fig. 2) and the root exclosures significantly increased plant mass in the understorey but not in gaps. Root exclosures increased root size and significantly decreased the root-to-shoot ratio (R/S) in both habitats (Fig. 2). Total plant mass and shoot mass of *A. barrelieri* seedlings were larger at the upper valley site than at the lower valley site (Fig. 3). Understorey plants in the lower valley with reduced root competition were larger than plants subjected to competition, and had larger roots and, hence, higher R/S ratio (Fig. 3). On the contrary, understorey plants in the upper valley had lower R/S values than gap plants and did not differ in total mass (Fig. 3). In the lower valley, seedlings were larger growing under the canopy than in gaps, and had larger aboveground mass and lower R/S ratio. The root exclosure treatment increased the R/S ratio in gap plants (Fig. 3). There were no significant statistical interactions among factors.

Table 1. Properties of soil in gaps and under *Retama sphaerocarpa* canopies at the upper and lower parts of the Rambla del Saltador valley. Values are means ± 1 s.e. ($n = 10$). For differences between locations (t-test), * $P < 0.05$, ** $P < 0.01$, ns: not significant.

	Upper valley		Lower valley		
	Gaps		Understorey	Gaps		Understorey
Organic matter (%)	3.4 ± 0.5	**	6.7 ± 0.7	1.4 ± 0.0	**	3.9 ± 0.7
N concentration (g mg^{-1})	1.6 ± 0.0	*	3.0 ± 0.0	0.9 ± 0.2	*	2.4 ± 0.5
Clay + silt (%)	19.2 ± 1.0	ns	22.5 ± 1.7	9.6 ± 0.1	**	15.6 ± 0.2
Volumetric water content at field capacity (%)	20.2 ± 1.0	**	27.9 ± 1.6	14.7 ± 0.7	**	17.5 ± 0.5
Bulk density (g cm^{-3})	1.4 ± 0.1	***	1.1 ± 0.1	1.8 ± 0.1	*	1.5 ± 0.0

Table 2. Mass of plants growing in gaps and under *Retama sphaerocarpa* canopies at the upper and lower parts of the Rambla del Saltador valley, and expressed as a function of the maximum mass. Values are means ± 1 s.e. ($n = 10$). For differences between locations and sites (t-test), ** $P < 0.01$, and *** $P < 0.001$, ns: not significant.

	Upper valley			Lower valley		
	Gap		Understorey	Gap		Understorey
Andryala ragusina	–		–	1.4 ± 0.1	**	2.6 ± 0.2
Avena sterilis	0.4 ± 0.1	ns	0.3 ± 0.1	–		–
Eryngium campestris	7.0 ± 0.8	ns	8.8 ± 0.9	1.5 ± 0.2	***	4.1 ± 0.3
Lavandula stoechas	4.4 ± 0.1	ns	5.8 ± 0.5	–		–
Marrubium vulgare	–		–	67 ± 23	***	243 ± 60
Pallenis sp.	4.6 ± 0.8	ns	6.9 ± 0.9	–		–
Stipa capensis	–		–	0.2 ± 0.0	***	1.1 ± 0.1
Thymus baeticus	17.3 ± 2.0	ns	17.9 ± 2.0	–		–
Relative mass Gap/Understorey	83.7 ± 6.3	ns	95.4 ± 4.5	34.6 ± 7.3	***	100

The log response ratio (lnRR) varied among localities and habitats. In the upper valley site root competition was highest in the understorey. In contrast, in the lower valley, root competition was smaller in the understorey than in gaps (Fig. 4a). Below-ground competition intensity followed a different pattern; the maximum value was obtained in gaps of the lower valley site, but competition intensity was also relevant in all other sites (Fig. 4b).

Plant interaction intensity differed in both sites. The shrub effect (lnRR of gap and understorey plants) decreased with elevation (Fig. 5) suggesting that the balance of the interaction approached the point where facilitation equals competition (i.e., a decrease in the facilitation effect). The slope was different depending on whether the index was based on "facilitation" data showing the effect exerted by the shrub canopy on its understorey (data from Table 1) or the root "competition" data obtained from the *Artemisia* experiment (Fig. 3).

Facilitation of *R. sphaerocarpa* on its understorey vegetation in the lower Rambla del Saltador valley is well documented (Pugnaire et al. 1996a). In this environment only strong stress-tolerant species live outside the canopy of the dominant shrub, *R. sphaerocarpa*, because of the dry climate and local soil characteristics. The positive effect of the shrub canopy on its understorey vegetation is based on physical amelioration of micro-environmental conditions, organic matter and nutrient accruement in the soil (Moro et al. 1997a) and improved water relations. As a consequence of strong gradients under the canopy, many annual and perennial species establish in the understorey of *R. spaherocarpa* in an ordered fashion (Moro et al. 1997b) and time-dependent feedback processes intensify within-patch resource accumulation (Wilson and Agnew 1992). This way, shrub canopies contribute outstandingly to local and regional species richness and community stability (Pugnaire and Lázaro 2000).

Discussion

The balance of the interaction between several plant species and *R. sphaerocarpa* shrubs changed along a natural gradient of environmental stress. The balance changed from positive for plants growing in the understorey of shrubs in the lower valley site to neutral or negative for understorey plants in the upper valley site. The weakening of facilitation along the fertility gradient appeared to be a consequence of improved abiotic conditions, as predicted by current theory (Bertness and Callaway 1994, Brooker and Callaghan 1998).

There was an important decrease in the facilitative intensity with elevation because of the amelioration of climatic conditions and the increase in resource availability. The shrub did not have the same effect at both elevations, because understorey conditions improved proportionally more in the lower site by the effect of the shrub, compared to gap conditions.
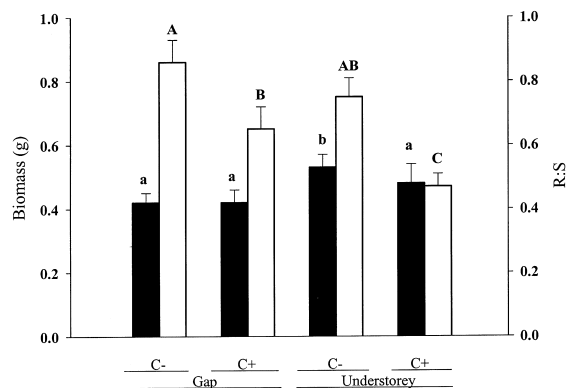

Fig. 2. Total mass (solid bars) and root allocation patterns (open bars) of *Artemisia barrelieri* plants grown in gaps and in the understorey of *Retama sphaerocarpa* shrubs, with (C+) and without (C−) root competition from neighbours. Values are mean + 1 s.e. Bars in each category with the same letter are not significantly different ($P < 0.05$; MANOVA, LSD post hoc comparison tests).
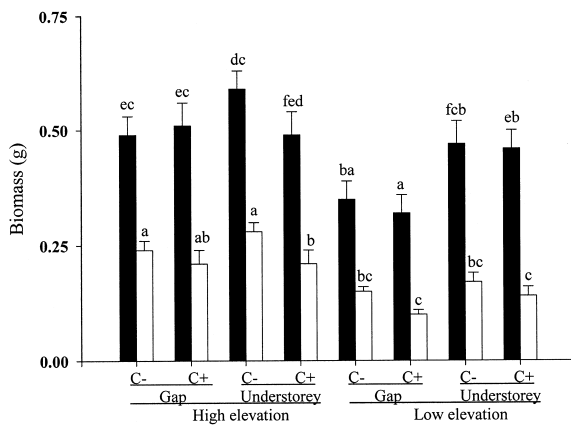
Fig. 3. Total mass (solid bars) and root mass (open bars) of *Artemisia barrelieri* plants grown in the lower and upper Rambla del Saltador valley sites, in gaps and in the understorey of *Retama sphaerocarpa* shrubs, with (C +) and without (C −) root competition from neighbours. Values are mean + 1 s.e. Bars in each category with the same letter are not significantly different ($P < 0.05$; MANOVA, LSD post hoc comparison tests).

Competition intensity, as assessed in the *A. barrelieri* experiment using relative indexes showed a complex pattern. Based on total biomass ratios, competition was maximum in the most fertile environment (Fig. 4a), i.e., the understorey of the upper valley site, where total biomass of *A. barrelieri* plants was also maximal. This result supports Grime's (1979) view that competition increases with resource availability. However, underground biomass ratios suggest that competition intensity was greater where stress was highest, i.e., in gaps of the lower valley site (Fig. 4b) though competition for below-ground resources proved important in all four habitats. Our data show that a shift occurred in the intensity of competition, increasing for below-ground resources as environmental stress increased, in the line of reasoning of Tilman (1988, 1994, 1997, Wilson and Tilman 1991) and others (see Reynolds 1999 and references therein). Below-ground competition was correlated with decreased root growth, and our results suggest that any index of competition intensity should include below-ground biomass.

By measuring competition and facilitation by different ways we were able to separate both components of the interaction. Both positive and negative effects of plant interactions changed along the gradient of habitat fertility because of changes in abiotic conditions, and the outcome of the interaction seems to be more a consequence of a decline in facilitation than a change in competition (Fig. 5).

Environmental conditions higher up in the valley are more mesic than in the lower valley and the climate is no longer arid (Fig. 1). Along with higher rainfall, more regularly scattered throughout a longer period of time, the lower evaporative demand in the higher valley site

means a larger amount of water available to the plant. Soils with higher soil organic matter in the upper valley are able to retain more water than sandy soils of the lower valley site, thus having a higher fertility which explains why plants living in the understorey and in gaps did not differ in size (Table 2).

Harbouring a community of plants in the understorey has a positive effect for *R. sphaerocarpa* itself (Pugnaire et al. 1996b). A dense understorey of annual and perennial species helps to decompose *R. sphaerocarpa* litter (Moro et al. 1997b), efficiently traps wind-blown dust and litter, and lowers understorey soil temperatures while preventing nutrients from leaching (Pugnaire et al. 1996b). All these processes contribute to a local increase of resources from which the shrub also benefits. Some of these processes are shown by our data: in both the upper and lower sites understorey soils were more fertile than gap soils (Table 1) and in
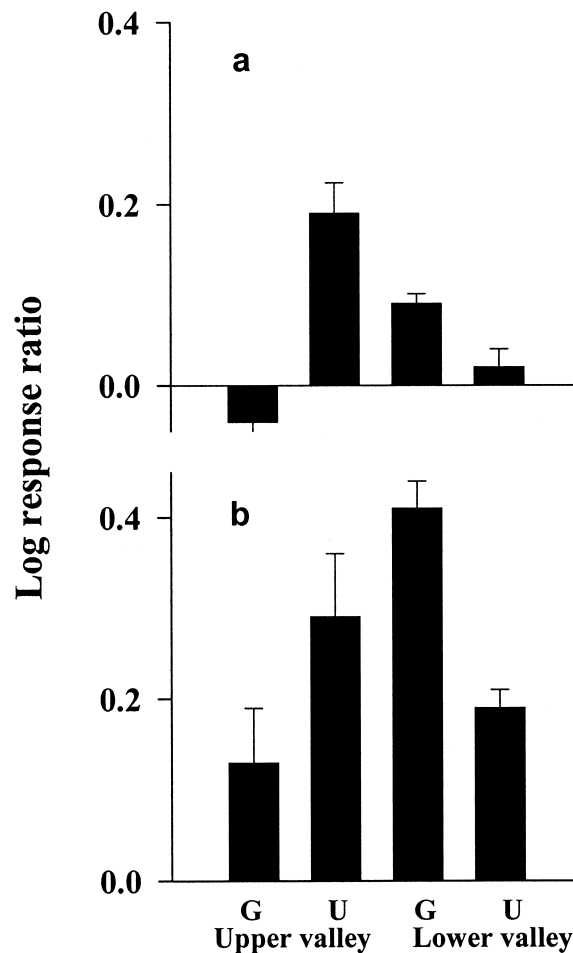

Fig. 4. Intensity of the interaction measured as log response ratio (lnRR) considering total (a) and below-ground (b) mass of *Artemisia barrelieri* seedlings grown in gaps (G) and in the understorey (U) of *R. sphaerocarpa* shrubs at two elevations in the Rambla del Saltador valley. Positive values indicate competition.
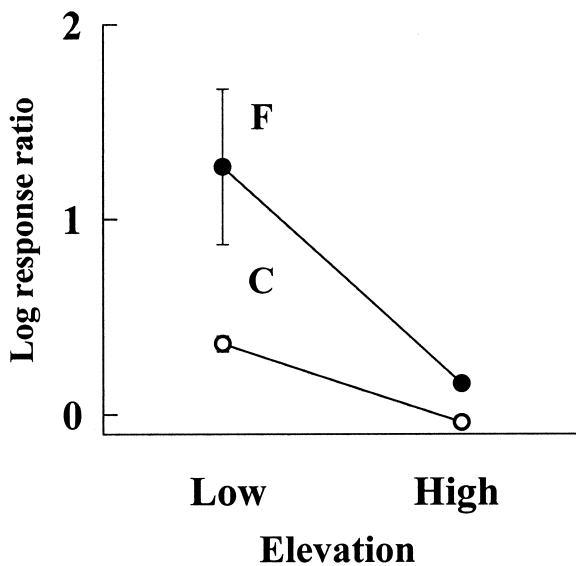
Fig. 5. Changes in plant interaction intensity along the gradient of environmental stress. F is the log response ratio (lnRR) calculated between understorey and gap biomass of plants (from Table 2). C is an assessment of the competition effect measured as the lnRR using *Artemisia barrelieri* plants grown without root exclosures in gaps and under the canopy of *R. sphaerocarpa* shrubs (from Fig. 3).

the lower valley site plants growing in the understorey were larger than plants growing outside.

In summary, changes in the balance of the interaction between and among different plant species along a gradient of environmental stress were caused by a decline in facilitation rather than by a change in competition. Facilitation proved to be more important in more stressful environments, while aboveground competition strength decreased with increasing stress but there was a simultaneous increase in below-ground competition.

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