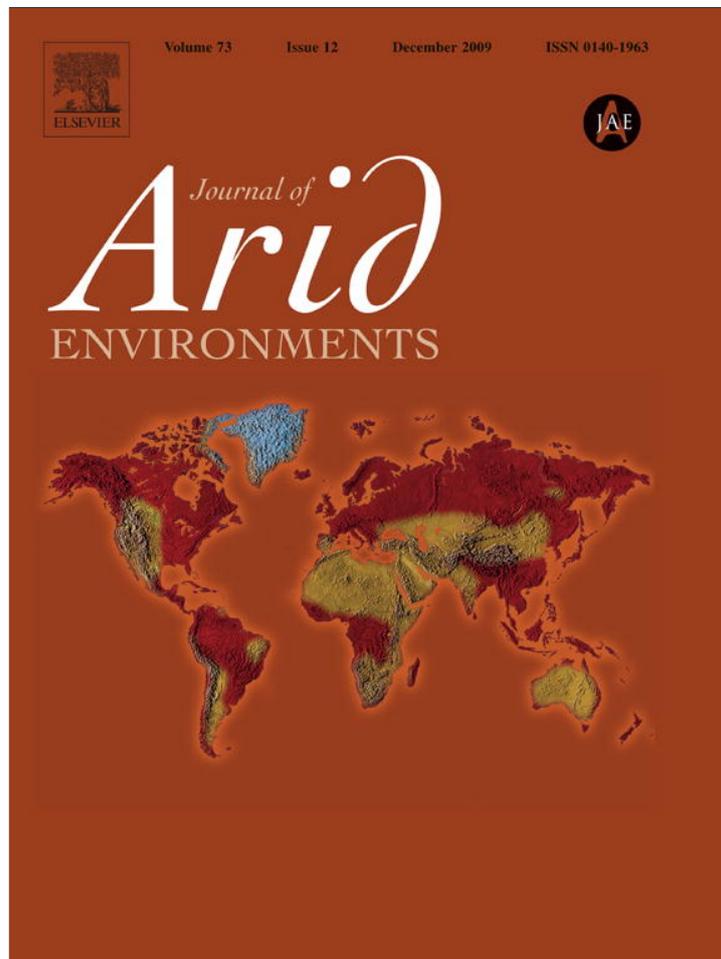


Provided for non-commercial research and education use.  
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

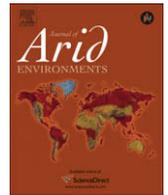
In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

## Journal of Arid Environments

journal homepage: [www.elsevier.com/locate/jaridenv](http://www.elsevier.com/locate/jaridenv)

## Abiotic conditions, neighbour interactions, and the distribution of *Stipa tenacissima* in a semiarid mountain range

C. Armas\*, Z. Kikvidze<sup>1</sup>, F.I. Pugnaire

Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, General Segura 1, E-04001 Almería, Spain

## ARTICLE INFO

## Article history:

Received 6 January 2009

Received in revised form

9 April 2009

Accepted 10 June 2009

Available online 8 July 2009

## Keywords:

Aboveground interactions

Aridity gradient

Belowground interactions

Productivity gradient

Shrub-grass steppes

Species distribution

## ABSTRACT

Abiotic conditions and interactions among plants are important factors determining plant geographical distributions. With the aim of analyzing the distribution of a perennial grass species in a semiarid mountain range, we experimentally tested above- and belowground effects of shrubs on the grass along a gradient of aridity. We measured growth, physiology and reproductive output of *Stipa tenacissima* tussocks surrounded by intact or manipulated neighbour shrubs. Performance of *Stipa* improved under mesic conditions, but the net effect of shrubs on *Stipa* did not change along the gradient. Belowground, we did not find significant effects, suggesting belowground resource partitioning between tussocks and shrubs. Aboveground net effects of shrubs on *Stipa* were generally positive and independent from abiotic conditions. The improved performance of *Stipa* at the mesic end of gradient suggests that its absolute physiological optimum lies out of its realized range. Overall, the arid end of the geographical distribution of *Stipa* in this mountain range may be determined by environmental severity. The coincidence of the upper limit of *Stipa* with the lower tree limit suggests that the more mesic end of *Stipa* distribution may depend on other factors; most likely competition with trees, which, unlike shrubs, could be excluding *Stipa tenacissima* from forests.

© 2009 Elsevier Ltd. All rights reserved.

### 1. Introduction

Two key factors determine species distribution in a given habitat, abiotic conditions and species interactions. Interactions among plants may either be positive (facilitation), which extend the species geographical range (Michalet et al., 2006); negative (competition and interference), which exclude species from suitable habitats and thus reduce their range; or neutral, having no effect on distribution (Callaway, 2007). But while abiotic conditions are routinely addressed to explain distribution patterns, interactions have received much less attention (Bruno et al., 2003; Lortie et al., 2004; Lortie and Callaway, 2009). Competitive exclusion restricts species range by reducing their realised niche, particularly in productive communities (Grime, 2001). On the contrary, positive interactions help to expand the range of a species in harsh environments (Bruno et al., 2003; Hacker and Gaines, 1997) particularly

when environmental severity is not too strong (Michalet et al., 2006). However, although there is data on how positive and negative interactions affect processes at the community level, assessments of the importance of plant interactions for the distribution of a particular species are scarce (Callaway, 2007).

Predominance of competition is expected under mesic abiotic conditions and vice versa, importance of facilitation increases in harsh conditions (Bertness and Callaway, 1994; Brooker and Callaghan, 1998). Additionally, indirect facilitation among species is expected to be more frequent under mesic compared to harsh conditions (Bertness and Callaway, 1994; Callaway, 2007; Brooker et al., 2008). Teasing apart above- and belowground interactions may help to reveal how the balance between competitive and facilitative interactions varies with environmental severity and along productivity gradients. However, often current theory only take into account competitive interactions (but see Brooker et al., 2005). One of such models was proposed by Newman (1973) and developed by Tilman (1988) and other authors (see reviews in Brooker et al., 2005; Cahill, 2002; Miller et al., 2005). They suggested the existence of a trade-off in the ability of plants to compete for soil resources and light, with the total strength of competition being invariant along productivity gradients due to a shift from below- to aboveground competition with increased resource

\* Corresponding author. Tel.: +34 950 281 045; fax: +34 950 277 100.

E-mail addresses: [cris@eeza.csic.es](mailto:cris@eeza.csic.es) (C. Armas), [zaal@k.u-tokyo.ac.jp](mailto:zaal@k.u-tokyo.ac.jp) (Z. Kikvidze), [fip@eeza.csic.es](mailto:fip@eeza.csic.es) (F.I. Pugnaire).<sup>1</sup> Present address: The University of Tokyo, 562 Environmental Bldg., 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8567, Japan.

availability and plant productivity. Many experimental tests supported this view, but few were performed under natural arid conditions (but see Pugnaire and Luque, 2001).

Here we test the importance of both the abiotic environment and above- and belowground interactions with shrubs for a perennial tussock grass, *Stipa tenacissima* L. (hereafter *Stipa*), a key element of arid communities in the western Mediterranean region (Puigdefábregas and Mendizabal, 1998). *Stipa* is well adapted to deal with aridity (Balaguer et al., 2002; Pugnaire et al., 1996; Ramírez et al., 2007; Valladares and Pugnaire, 1999), and morphological and functional traits help *Stipa* to spread and become dominant in areas within the range of 200–400 mm of annual precipitation (Maestre et al., 2007; Sánchez, 1995). *Stipa* co-occurs with small shrubs, sharing dominance like in most semiarid steppe formations worldwide (Aguar and Sala, 1999; Le Houérou, 1986). It has been hypothesised that competition is weak between these two growth forms due to resource partitioning, but some studies found strong competition (e.g., Jurena and Archer, 2003; Le Roux et al., 1995), others failed to detect significant competition (e.g., Briones et al., 1998; Sala et al., 1989), and another group showed both positive and negative effects (Armas and Pugnaire, 2005; Maestre et al., 2003). Overall, there are many studies on shrub–tussock interactions focused on belowground competition whilst aboveground effects have been largely overlooked.

We experimentally tested above- and belowground effects of neighbouring shrubs on *Stipa* tussocks and the performance of *Stipa* plants in an environmental and plant productivity gradient within a typical habitat of *Stipa*, the Sierra Alhamilla range (SE Spain), where the species is found in elevations ranging 300–900 m. The lower limit is hot and dry while higher up conditions are considerably more mesic (Fig. 1). We expected that the distribution range of *Stipa* in this mountain system would be limited by abiotic conditions and plant interactions, and specifically, we tested: (1) that belowground competition would be more intense at the arid and less productive limit of gradient while aboveground competition would be more intense at the more mesic and productive end of the gradient; and (2) positive effects of shrub canopies on *Stipa* might occur, and they would be more intense at the harsher end of the abiotic gradient (i.e., lower limit of plant productivity). We manipulated above- and belowground interactions of neighbouring shrubs on *Stipa* tussocks. One year later we compared their performance to control individuals. We could not tease apart belowground facilitative effects of shrubs, if any, as they would have been related to improvements in soil nutrient and organic matter contents (Callaway, 2007; Armas and Pugnaire, 2005) and thus would have a similar effects on soil under control and manipulated plants.

The overall objectives of this study were to clarify the importance of shrub effects on *Stipa* under different aridity levels and, then, provide some hypotheses that link the abiotic and biotic environments of *Stipa* to its geographical range in this semiarid mountain system.

## 2. Materials and methods

### 2.1. Study site and species

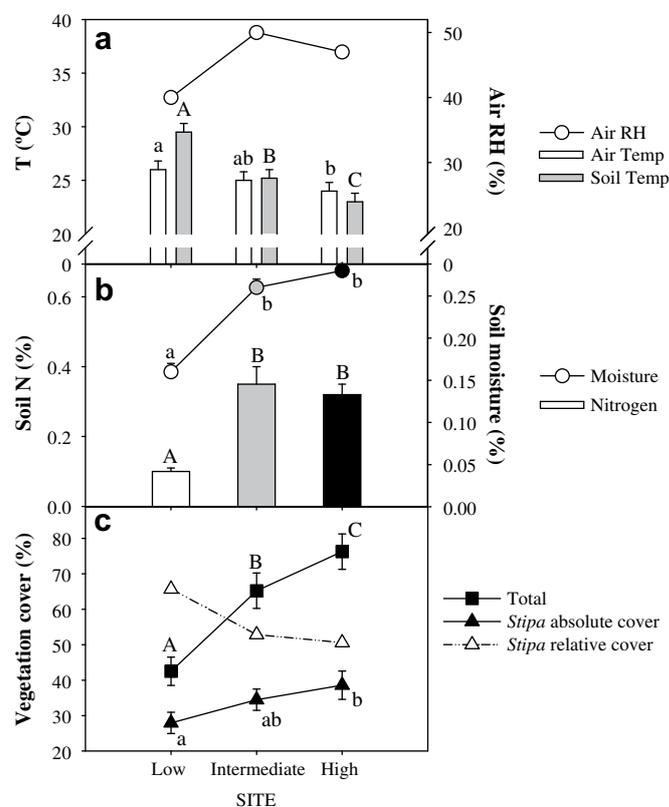
In April 2004 we selected three field sites at different elevations (350, 540 and 790 m a.s.l.) on the northern foothills of the Sierra Alhamilla range, Almería Province, SE Spain (37°01'N, 2°23' W). The experimental sites were selected facing west with somewhat similar slopes (15–25°). The climate is semiarid with a mean annual precipitation of 230 mm at the bottom and 347 mm at the top (Armas, 2004), with a pronounced dry season from June to September during which there is no rain in most years. Differences

in precipitation along the elevation range as well as differences in bedrock cause a pronounced gradient of plant communities along the slope; shrubs (typically *Anthyllis cytisoides*, *Cistus clusii* and *Rosmarinus officinalis*) become gradually more common with increasing elevation, although *Stipa* dominates the community until 900 m (Cabello, 1997). Above this elevation there are forests of the evergreen oak, *Quercus ilex*, which naturally occurs here and plantations of *Pinus halepensis*. *Stipa* is absent from these forests (Cabello, 1997; Ruiz de la Torre, 1990).

At each location we sampled communities using ten 50 m-long transects randomly distributed. Care was taken to set transects far enough to avoid sampling the same individuals. We identified species found along transects and measured the length of intercepted segments. From these data we obtained vegetation cover and *Stipa*'s absolute and relative cover. Total vegetation cover was considered as an indirect measurement of plant productivity at each site.

### 2.2. Experimental manipulations

In May 2004 we selected 32 *Stipa* tussocks of 0.8–1 m<sup>2</sup> basal cover and 70–90 cm tall in each site. Target tussocks were surrounded by neighbour shrubs, mainly *Cistus clusii* Dunal and *Rosmarinus officinalis* L. We applied a factorial design of neighbour exclusion following recommendations of McPhee and Aarssen (2001). We used two levels of belowground (decreased [–B] and control [+B]) and two of aboveground (decreased [–A] and control [+A]) interactions with eight replicates each. In one treatment



**Fig. 1.** Characteristics of the three sites along the elevation gradient; mean daily air and soil temperatures and air relative humidity (A); soil nitrogen content and moisture (B) during 1 week in summer and; absolute and relative plant cover (C) along the elevation gradient (mean  $\pm$  SE,  $n = 3, 8$  and  $10$ , for climatic characteristics and soil humidity, for soil nitrogen and for plant cover, respectively). Error bars indicated when larger than symbol. Bars or symbols with different letters denote significant differences ( $P < 0.05$ ) among sites for each variable measured.

( $-A + B$ ), neighbour plants around eight tussocks were bended down and tied with a wire to the soil, therefore reducing above-ground interactions between *Stipa* and neighbours but maintaining root interactions. In another treatment ( $+A - B$ ) we made 10 cm deep trenches around another eight tussocks to disconnect the root systems of *Stipa* and neighbour plants while aboveground parts were left intact. Trenches were carved just below *Stipa* plant projected canopy cover. Next we combined both treatments to another set of eight tussocks ( $-A - B$ ), therefore decreasing simultaneously below- and aboveground interactions between tussocks and shrubs. Finally, we selected eight tussocks as control, with unaltered interactions between *Stipa* and neighbours ( $+A + B$ ).

The root system of *Stipa tenacissima* is shallow, and most of the roots grow in the first 10–20 cm of the soil profile – although there could be a small proportion of roots growing below 50 cm from soil surface (Sánchez, 1995; Puigdefábregas et al., 1999). Most of the roots are concentrated just underneath *Stipa*'s canopy (Puigdefábregas et al., 1999). As trenches were carved just below each *Stipa* plant projected canopy cover, there was a small probability of damaging *Stipa* roots, while, at the same time, these trenches isolate most of the root system of *Stipa* plants from their neighbours.

The aim of these manipulations was to study above- and belowground effects of shrubs – irrespective of the species – on *Stipa*. Thus, we did not control for species-specific interactions of each shrub species on *Stipa*. We assumed that the effect of annuals on *Stipa* was negligible compared to shrub effects. This tussock species is quite big compared to annual plants, which usually form ephemeral communities with a lifespan of 2–3 months per year (personal observation).

We could not base our experiments on completely random locations of target plants along the entire transect; therefore our design did not fully control pseudoreplication (sensu Hurlbert, 1984). However, we took care to select plants at random within large areas ( $\sim 70 \times 70$  m). The largest and smallest distance between tussocks was 30 and 1 m, respectively. This design may be characterized as “stratified random” and could at least partially reduce pseudoreplication.

### 2.3. Microclimate and soil properties

We documented differences in abiotic conditions at each elevation. However, we did not measure microclimatic effects of shrubs because some are well known (Armas and Pugnaire, 2005) and because they would be detected through growth responses in *Stipa* tillers.

In June 2004 and 2005 we measured volumetric humidity of soil in open spaces 20 cm below the surface and air relative humidity and temperature 10 cm above the soil. Measurements ( $n = 3$ ) were recorded every 5 min for consecutive 5 days in different seasons with ECH<sub>2</sub>O (Decagon Services, WA, USA) and microclimatic sensors (Onset Computers, Pocasset, MA, USA) connected to data loggers.

We also collected eight  $\sim 200$  cm<sup>3</sup> soil samples from the upper 10 cm of soil in bare ground in each field site. Each sample was thoroughly homogenized and air-dried in the laboratory, and total soil nitrogen (N) was determined by Kjeldahl analysis in a semi-automatic analyser (Velp Cientifica s.r.l., Italia).

### 2.4. Growth and reproductive output

In June 2005 we sampled the first mature, fully developed leaf of three tillers from each tussock ( $n = 8$  plants per treatment within each site). We determined leaf length and dry mass. For each leaf, we selected a 10-cm segment in the central part and measured its width. Dry mass of samples was then determined and the specific leaf area (SLA) obtained from both measurements. Dry mass was

determined after drying leaf material at 70 °C for 72 h. We also determined the dry mass of whole tillers.

We also randomly selected 10 tillers from each target tussock and recorded the number of double (split) tillers, as well as recorded the number of spikes of eight tussocks randomly selected inside a 10 × 10 m subplot in each site to estimate reproductive performance of *Stipa*. Data were then corrected for *Stipa*'s relative cover in each site.

### 2.5. Physiological responses

Physiological measurements were conducted to test how control plants (i.e., surrounded by intact shrub neighbours) responded to abiotic conditions along the elevation gradient. During three sunny days in June 2005 we selected mature, fully developed green leaves facing east from different tillers of control tussocks ( $n = 9$  per site). We measured pre-dawn relative water content (RWC), early morning photochemical efficiency of photosystem II ( $F_v/F_m$ ) and leaf water vapour conductance ( $g_s$ ) and photosynthetic rate ( $A$ ). RWC was calculated following Barrs and Weatherley (1962).  $F_v/F_m$  was measured with a portable fluorimeter (PEA, Hansatech, Kings Lynn, UK) in leaves that were previously dark-adapted for 30 min.  $A$  and  $g_s$  were measured under ambient CO<sub>2</sub> concentrations on sunlit leaves facing east during the early morning hours (7:00–8:30 solar time) – i.e., at the time of maximum photosynthetic rates (Armas and Pugnaire, 2005) – using a portable infrared gas analyzer (LCi; Analytical Development Company Ltd., Hoddesdon, UK). Measurements were expressed on a projected leaf area basis using Cregg's (1992) correction for cylindrical leaves.

We also collected the first mature leaf from a randomly selected tiller from six plants in each site. They were oven-dried and then ground with a mill (Fritsch Pulveriseke, Germany) and analyzed for total N, C, and  $\delta^{13}C$  using a Roboprep-CN elemental analyser and mass spectrometer (Europa Scientific, Crewe, UK).  $\delta^{13}C$  was calculated following Ehleringer and Osmond (1989).

### 2.6. Data analyses

Differences in plant cover between the three field sites were tested using one-way ANOVA of mean values of cover per transect and at a significance level of 0.05. Differences in plant performance among treatments and field sites were tested using a nested ANOVA in order to avoid any pseudoreplication side effect. Preliminary analyses showed that the results for nested and full factorial ANOVA were similar. Significance level was set to 0.05. Treatment levels were: (1) aboveground interactions (two levels: intact and reduced); and (2) belowground interactions (two levels: intact and reduced) nested within three sites: low, intermediate and high sites along the elevation gradient. The four tested variables were: (1) leaf length; (2) leaf dry mass; (3) tiller dry mass; and (4) SLA. Differences in plant physiological responses between the three field sites were tested using one-way ANOVA. Homogeneity of variances was checked using Levene's test. Post-hoc differences were explored with Scheffé's test. Leaf and tiller mass were log-transformed to normalize their distribution. Data are presented as mean value  $\pm 1$  SE throughout. Data were analysed with the SPSS 17.0 software (SPSS Inc., Chicago, IL, USA).

## 3. Results

### 3.1. Abiotic conditions

Soil and air temperatures decreased significantly, and humidity increased at intermediate and high elevation sites compared to the

low site, evidencing a change in abiotic conditions along the elevation gradient (Fig. 1). Soil nitrogen content was also higher at high elevations, which together with increased soil moisture enhanced plant productivity. All these changes suggest a gradient in resources for plant production, and as a consequence, total plant cover increased gradually from low to high sites (Fig. 1). *Stipa* remained the most common species at all sites, never comprising less than half of the total plant cover. However, and although the absolute *Stipa* cover increased, its relative cover decreased with elevation. Cover changes were accompanied with changes in leaf and tiller growth; at the high elevation site *Stipa* produced lighter leaves and tillers, but leaf length remained unchanged. This resulted in higher SLA than at the intermediate and lower sites (Table 1). Nitrogen content in leaves was highest at mid elevation, probably reflecting soil N content (compare Table 1 with Fig. 1). Reproductive output of *Stipa* increased also with elevation (Table 1) producing significantly more spikes per surface area at the top than at the bottom sites.

Physiological responses also differed along the elevation gradient, with the sharpest changes occurring at the highest site (Table 1). Over there, plants showed significantly higher values of  $g_s$  and  $A$  than on the other sites and RWC was also higher than on the lowest site.  $F_v/F_m$  was similar at all sites without any sign of photosystem damage. Mean value of  $\delta^{13}C$  for *Stipa* plants was  $-23.86 \pm 0.26\text{‰}$ , typical for a  $C_3$  species (Ehrlinger and Osmond, 1989), and coincides with other data for *Stipa* (Maestre and Cortina, 2006).  $\delta^{13}C$  values tended to decrease with elevation ( $P = 0.167$ , Table 1), which may point to *Stipa* lower water use efficiency at higher elevations in response to improved water balance (see also Ramírez et al., 2008).

### 3.2. Neighbour net effects on *Stipa*

Manipulations of aboveground neighbour interaction had several net effects on *Stipa* growth, while belowground manipulations did not (Table 1 and Fig. 2). Overall, there was a lack of any significant statistical interaction among sites and neighbour above- and belowground manipulations (Table 1), thus, evidencing that shrub effects on *Stipa* growth were similar on all sites.

Plants experiencing reduced aboveground interaction of neighbour canopies produced lighter leaves, smaller tillers and shorter leaves, which resulted in higher SLA than those surrounded by intact neighbour canopies (i.e., control plants, Fig. 2). At the

same time, *Stipa* plants with reduced neighbour canopies produced three times more split tillers than control plants ( $10.8 \pm 1.9$  vs.  $32.9 \pm 3.6\%$ ;  $F_{1,54} = 66.41$ ,  $P < 0.05$ ), but the number of split tillers did not change with elevation ( $F_{2,54} = 0.21$ ,  $P > 0.81$ ).

## 4. Discussion

Environmental conditions, which determine plant productivity in this semiarid mountain range, varied within the habitat where *Stipa* is the dominant species. Performance of *Stipa* changed with abiotic conditions and was reflected in increased reproductive output and carbon exchange rates, and in better water relations at higher elevations. We did not find significant belowground effects of shrubs on *Stipa*, while aboveground effects of shrubs on *Stipa* were generally positive all over the abiotic gradient. Overall, our results support the hypothesis suggesting essential belowground resource partitioning between semiarid tussocks and shrubs (Briones et al., 1998; Gebauer et al., 2002; Sala et al., 1989) and provide clues related to the biogeographical distribution of *Stipa tenacissima* in this mountain range.

A central paradigm of functional plant ecology states that differences in plant function are essential components of species fitness, accounting for their relative dominance in different habitats (Lambers et al., 1998). Abiotic conditions limit plant growth and restrict species colonization to habitats with suitable conditions. Several morphological and physiological mechanisms enable *Stipa* to withstand strong aridity and perform well under very harsh circumstances, as indicated by the physiological status and growth patterns found in our study and nearby areas (Balaguer et al., 2002; Pugnaire et al., 1996; Ramírez et al., 2007; Valladares and Pugnaire, 1999). Nevertheless, this species is able to take advantage of a decrease in habitat aridity: *Stipa*'s cover per unit area, SLA, carbon exchange rates, water status and spike production were all increased near the moister end of the gradient. These results show that *Stipa* performed better at higher elevations where abiotic conditions became less severe.

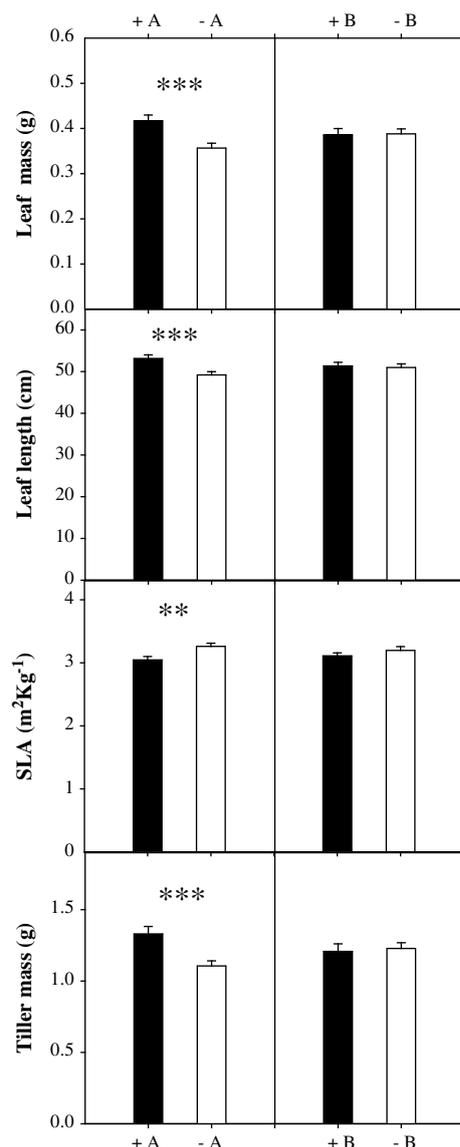
Although *Stipa* cover increased with elevation, it decreased relative to shrubs, probably because these woody species respond to better environmental conditions more strongly than *Stipa*. Yet, aboveground manipulations showed that neighbouring shrubs had positive effects on *Stipa* tiller production. However, contrary to the stress gradient hypothesis (Bertness and Callaway, 1994; Brooker and Callaghan, 1998), which predicts that neighbour effects should

**Table 1**

Performance of *Stipa* plants on an elevation gradient in SE Spain (mean  $\pm$  SE,  $n = 32$ , 9 and 6, for leaf and tiller characteristics, for physiology or reproductive output and, for nutrient content or  $\delta^{13}C$ , respectively).

	Low	Intermediate	High	S	A (S)	B (S)	A $\times$ B (S)
				$F_{2,84}$	$F_{3,84}$	$F_{3,84}$	$F_{3,84}$
Leaf dry mass (g)	$0.40 \pm 0.02^{ab}$	$0.41 \pm 0.02^a$	$0.36 \pm 0.01^b$	3.31*	4.96**	1.47 <sup>ns</sup>	0.36 <sup>ns</sup>
Leaf length (cm)	$51.29 \pm 1.13^a$	$52.37 \pm 0.99^a$	$49.88 \pm 1.06^a$	1.59 <sup>ns</sup>	4.84**	2.06 <sup>ns</sup>	0.54 <sup>ns</sup>
SLA ( $m^2 kg^{-1}$ )	$3.03 \pm 0.07^a$	$3.17 \pm 0.07^{ab}$	$3.26 \pm 0.06^b$	3.48*	3.32*	1.58 <sup>ns</sup>	0.62 <sup>ns</sup>
Tiller dry mass (g)	$1.29 \pm 0.07^a$	$1.27 \pm 0.05^{ab}$	$1.10 \pm 0.04^b$	3.59*	4.56**	0.40 <sup>ns</sup>	0.09 <sup>ns</sup>
				$F_{2,27}$			
# spikes per percent cover	$18.2 \pm 4.0^a$	$29.4 \pm 6.0^{ab}$	$38.3 \pm 3.6^b$	4.66*			
$g_s$ ( $mol m^{-2} s^{-1}$ )	$0.11 \pm 0.01^a$	$0.12 \pm 0.01^a$	$0.26 \pm 0.02^b$	15.40***			
$A$ ( $\mu mol m^{-2} s^{-1}$ )	$9.99 \pm 0.76^a$	$11.54 \pm 0.42^a$	$16.22 \pm 1.16^b$	4.63*			
RWC (%)	$85.52 \pm 0.56^a$	$87.53 \pm 0.42^{ab}$	$88.92 \pm 0.87^b$	6.99**			
$F_v/F_m$	$0.798 \pm 0.003^a$	$0.779 \pm 0.005^b$	$0.792 \pm 0.006^{ab}$	3.79*			
Leaf nitrogen content (%)	$0.62 \pm 0.01^a$	$0.78 \pm 0.03^a$	$0.63 \pm 0.01^a$	1.60 <sup>ns</sup>			
$\delta^{13}C$ (‰)	$-23.92 \pm 0.30^a$	$-23.47 \pm 0.24^a$	$-24.20 \pm 0.25^a$	0.98 <sup>ns</sup>			

Different letters in a row show significant differences between sites at  $P < 0.05$ . Last four columns show  $F$  values from the nested ANOVA model for leaf and tiller characteristics and the one-way ANOVA for physiology or reproductive output, as well as the significance (\*, \*\*, \*\*\*, at  $P < 0.05$ , 0.01, 0.001, respectively; ns = non-significant). Legend for the different factors: S = site; A = aboveground interaction; B = belowground interaction.



**Fig. 2.** Neighbour effects on leaf and tiller dry mass, leaf length and specific leaf area (SLA) of *Stipa* plants growing with: intact (control; +A) or reduced (–A) aboveground interaction of neighbour canopies and, with; intact (control; +B) or reduced (–B) belowground interaction of neighbour roots (mean  $\pm$  SE,  $n = 48$  for each bar). Asterisks above bars indicate significant differences between aboveground treatments (\*\* and \*\*\* for  $P < 0.01$  and  $P < 0.001$ , respectively). Belowground interactions did not have any significant effect on *Stipa*.

change along environmental abiotic gradients, the effect of shrubs on *Stipa* did not change with elevation (see Donovan and Richards, 2000; and review of Brooker et al., 2008). We did not find either a shift from root to shoot competition with increased resource availability and plant productivity (Tilman, 1988). Shifts in interaction sign and intensity along environmental gradients have been shown experimentally in many systems (Cahill, 2002; Goldberg et al., 1999; Kikvidze et al., 2005; Maestre et al., 2005; Pugnaire and Luque, 2001). Conversely, we found that tiller productivity decreased in response to reduced aboveground interactions, but uniformly at all three elevation sites. Interestingly, reduced aboveground interactions led to a three-fold increase in split tillers, also independently from elevation. This effect was probably caused by altered light quality – we suspect that our manipulations could shift red/far-red ratios and activate the phytochrome system in *Stipa* (see, e.g., Tomlinson and O'Connor, 2004).

We found little belowground effects of shrubs on *Stipa*. True neutralism due to root segregation may be the most parsimonious interpretation of these results (but see Alados et al., 2006; Armas and Pugnaire, 2005) as differences in root architecture between shrubs and *Stipa* would contribute to resource partitioning (Sánchez, 1995). Furthermore, *Stipa* tussocks capture water from open runoff areas, and larger bare zones in drier climates provide more runoff water to the tussocks (Cerdà, 1997; Puigdefábregas et al., 1999). This is important at the low end of the elevation gradient, the more arid site. Higher up, however, aridity decreases as well as the dependence of *Stipa* on runoff sources. Shrubs may occupy exactly the open spaces at higher elevations and, although they reduce the runoff area, they did not significantly affect the water balance of *Stipa*.

Overall, our results suggest that the physiological optimum of *Stipa* does not coincide with its geographical range in this mountain, because *Stipa* performs better at the more mesic site, the upper end of our gradient. At the same time, co-occurring shrubs do not appear to exert restrictive effects on mature *Stipa* tussocks in these conditions; on the contrary, we detected positive aboveground effects of shrubs on *Stipa* even at the high elevation site. Then, the sharp end of *Stipa*'s range in our system could be due to the presence of trees. In this mountain range, the lower end of the forests coincides with the upper end of the distribution of *Stipa*. Competition for light may be the probable main process excluding *Stipa* from these forests (García-Fayos and Gasque, 2006; Gasque and García-Fayos, 2004). As a matter of fact, *Stipa* spreads readily into cleared evergreen oak forests (Ponce, 1989).

Abiotic conditions seem thus to be more important towards the harsher abiotic end of the gradient, where the selective force of habitat conditions is proportionally more important. Conversely, competition with other species in the more productive end should prevail over abiotic conditions, which may be proportionally less important (e.g., Grime, 2001).

#### 4.1. Concluding remarks

*Stipa* is a good example of an aridity-tolerant species which responded positively to reduced aridity, indicating that its physiological optimum lies out of its geographical range. Consequently, the arid end of the geographical distribution of *Stipa* may be determined by environmental severity, whilst at the more mesic end of its distribution in this semiarid mountain range it depends on other factors; most likely competitive exclusion.

#### Acknowledgements

This work was supported by Spanish Ministry of Education and Science grants CGL2004-00090 and CGL2007-63781. C. A. is supported by a CSIC-I3P grant. We thank M.J. Jorquera for lab assistance and A. Delgado for isotope analyses.

#### References

- Aguilar, M.R., Sala, O.E., 1999. Patch structure, dynamics and implications for functioning of arid ecosystems. *Trends in Ecology and Evolution* 14, 273–277.
- Alados, C.L., Gotor, P., Ballester, P., Navas, D., Escos, J.M., Navarro, T., Cabezero, B., 2006. Association between competition and facilitation processes and vegetation spatial patterns in alpha steppes. *Biological Journal of the Linnean Society* 87, 103–113.
- Armas, C., 2004. Balance de la interacción entre plantas superiores en ambientes semiáridos: mecanismos y procesos. Universidad Autónoma de Madrid, Madrid.
- Armas, C., Pugnaire, F.I., 2005. Plant interactions govern population dynamics in a semi-arid plant community. *Journal of Ecology* 93, 978–989.
- Balaguer, L., Pugnaire, F.I., Martínez-Ferri, E., Armas, C., Valladares, F., Manrique, E., 2002. Ecophysiological significance of chlorophyll loss and reduced photochemical efficiency under extreme aridity in *Stipa tenacissima* L. *Plant and Soil* 240, 343–352.

- Barrs, H.D., Weatherley, P.E., 1962. A reexamination of the relative turgidity technique for estimating water deficits in leaves. *Australian Journal of Biological Sciences* 15, 413–428.
- Bertness, M.D., Callaway, R.M., 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9, 191–193.
- Briones, O., Montaña, C., Ezcurra, E., 1998. Competition intensity as a function of resource availability in a semiarid ecosystem. *Oecologia* 116, 365–372.
- Brooker, R.W., Callaghan, T.V., 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* 81, 196–207.
- Brooker, R.W., Kikvidze, Z., Pugnaire, F.I., Callaway, R.M., Choler, P., Lortie, C.J., Michalet, R., 2005. The importance of importance. *Oikos* 109, 63–70.
- Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.J., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F.I., Quiroz, C.L., Saccone, P., Schiffrers, K., Seifan, M., Touzard, B., Michalet, R., 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96, 18–34.
- Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18, 119–125.
- Cabello, J., 1997. Factores ambientales, estructura y diversidad en comunidades de matorral de ambiente mediterráneo semiárido (Tabernas-Sierra Alhamilla-Níjar, SE Ibérico). Universidad de Almería, Almería.
- Cahill, J.F., 2002. Interactions between root and shoot competition vary among species. *Oikos* 99, 101–112.
- Callaway, R.M., 2007. Positive Interactions and Interdependence in Plant Communities. Springer, Dordrecht.
- Cerdà, A., 1997. The effect of patchy distribution of *Stipa tenacissima* L. on runoff and erosion. *Journal of Arid Environments* 36, 37–51.
- Cregg, B.M., 1992. Leaf area estimation of mature foliage of *Juniperus*. *Forest Science* 38, 61–67.
- Donovan, L.A., Richards, J.H., 2000. Juvenile shrubs show differences in stress tolerance, but no competition or facilitation, along a stress gradient. *Journal of Ecology* 88, 1–16.
- Ehleringer, J.R., Osmond, C.B., 1989. Stable isotopes. In: Pearcy, R.W., Ehleringer, J.R., Mooney, H.A., Rundel, P.W. (Eds.), *Plant Physiological Ecology. Field Methods and Instrumentation*. Chapman & Hall, London, UK, pp. 281–300.
- García-Fayos, P., Gasque, M., 2006. Seed vs. microsite limitation for seedling emergence in the perennial grass *Stipa tenacissima* L. (Poaceae). *Acta Oecologica* 30, 276–282.
- Gasque, M., García-Fayos, P., 2004. Interaction between *Stipa tenacissima* and *Pinus halepensis*: consequences for reforestation and the dynamics of grass steppes in semi-arid Mediterranean areas. *Forest Ecology and Management* 189, 251–261.
- Gebauer, R.E., Schwinning, S., Ehleringer, J.R., 2002. Interspecific competition and resource pulse utilization in a cold desert community. *Ecology* 83, 2602–2616.
- Goldberg, D.E., Rajaniemi, T., Gurevitch, J., Stewart-Oaten, A., 1999. Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology* 80, 1118–1131.
- Grime, J.P., 2001. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. Wiley & Sons, Chichester, UK.
- Hacker, S., Gaines, S.D., 1997. Some implications of direct positive interactions for community species diversity. *Ecology* 78, 1990–2003.
- Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54, 187–211.
- Jurena, P.N., Archer, S., 2003. Woody plant establishment and spatial heterogeneity in grasslands. *Ecology* 84, 907–919.
- Kikvidze, Z., Pugnaire, F.I., Brooker, R.W., Choler, P., Lortie, C.J., Michalet, R., Callaway, R.M., 2005. Linking patterns and processes in alpine plant communities: a global study. *Ecology* 86, 1395–1400.
- Lambers, H., Chapin, F.S., Pons, T.L., 1998. *Plant Physiological Ecology*. Springer-Verlag, New York, USA.
- Le Houérou, H.N., 1986. The desert and arid zones of Northern Africa. In: Evinari, M., Noy-Meir, I., Goodall, D.W. (Eds.), *The Ecosystems of the World. Hot Deserts and Arid Shrublands*, Elsevier Science, pp. 104–147.
- Le Roux, X., Bariac, T., Mariotti, A., 1995. Spatial partitioning of the soil water resource between grass and shrub components in a West African humid savanna. *Oecologia* 104, 147–155.
- Lortie, C.J., Brooker, R.W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F.I., Callaway, R.M., 2004. Rethinking plant community theory. *Oikos* 107, 433–438.
- Lortie, C.J., Callaway, R.M., 2009. David and Goliath. Comparative use of facilitation and competition studies in the plant ecology literature. *Web Ecology* 9, 54–57.
- Maestre, F.T., Cortina, J., 2006. Ecosystem structure and soil-surface conditions drive the variability in the foliar  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of *Stipa tenacissima* in semiarid Mediterranean steppes. *Ecological Research* 21, 44–53.
- Maestre, F.T., Bautista, S., Cortina, J., 2003. Positive, negative and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. *Ecology* 84, 3186–3197.
- Maestre, F.T., Valladares, F., Reynolds, J.F., 2005. Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology* 93, 748–757.
- Maestre, F.T., Ramírez, D.A., Cortina, J., 2007. *Ecología del esparto (Stipa tenacissima L.) y los espartales de la Península Ibérica. Ecosistemas*, 2007/2002.
- McPhee, C.S., Aarssen, L.W., 2001. The separation of above- and below-ground competition in plants – a review and critique of methodology. *Plant Ecology* 152, 119–136.
- Michalet, R., Brooker, R.W., Cavieres, L.A., Kikvidze, Z., Lortie, C.J., Pugnaire, F.I., Valiente-Banuet, A., Callaway, R.M., 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters* 9, 767–773.
- Miller, T.E., Burns, J.H., Munguia, P., Walters, E.L., Kneitel, J.M., Richards, P.M., Mouquet, N., Buckley, H.L., 2005. A critical review of twenty years' use of the resource-ratio theory. *American Naturalist* 165, 439–448.
- Newman, E.I., 1973. Competition and diversity in herbaceous vegetation. *Nature* 244, 310.
- Ponce, G., 1989. La degradación de la vegetación en el corredor de Almansa. *Investigaciones Geográficas* 7, 205–218.
- Pugnaire, F.I., Luque, M.T., 2001. Changes in plant interactions along a gradient of environmental stress. *Oikos* 93, 42–49.
- Pugnaire, F.I., Haase, P., Incoll, L.D., Clark, S.C., 1996. Response of the tussock grass *Stipa tenacissima* to watering in a semi-arid environment. *Functional Ecology* 10, 265–274.
- Puigdefábregas, J., Mendizabal, T., 1998. Perspectives on desertification: western Mediterranean. *Journal of Arid Environments* 39, 210–224.
- Puigdefábregas, J., Solé, A., Gutiérrez, L., del Barrio, G., Boer, M., 1999. Scales and processes of water and sediment redistribution in drylands: results from the Rambla Honda field site in Southeast Spain. *Earth-Science Reviews* 48, 39–70.
- Ramírez, D.A., Bellot, J., Domingo, F., Blasco, A., 2007. Can water responses in *Stipa tenacissima* L. during the summer season be promoted by non-rainfall water gains in soil? *Plant and Soil* 291, 67–79.
- Ramírez, D.A., Valladares, F., Domingo, F., Bellot, J., 2008. Seasonal water-use efficiency and chlorophyll fluorescence response in alpha grass (*Stipa tenacissima* L.) is affected by tussock size. *Photosynthetica* 46, 222–231.
- Ruiz de la Torre, J., 1990. Mapa Forestal de España. Almería. Hoja 6–11: Mapa Forestal de España. ICONA. Ministerio de Agricultura y Pesca, Madrid.
- Sala, O.E., Golluscio, R.A., Lauenroth, W.K., Soriano, A., 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* 81, 501–505.
- Sánchez, G., 1995. *Arquitectura y dinámica de las matas de esparto (Stipa tenacissima, L.), efectos en el medio e interacciones con la erosión*. Tesis Doctoral thesis, Universidad Autónoma de Madrid. Facultad de Ciencias. Departamento Interuniversitario de Ecología.
- Tilman, D., 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, New Jersey.
- Tomlinson, K.W., O'Connor, T.G., 2004. Control of tiller recruitment in bunchgrasses: uniting physiology and ecology. *Functional Ecology* 18, 489–496.
- Valladares, F., Pugnaire, F.I., 1999. Tradeoffs between irradiance capture and avoidance in semi-arid environments assessed with a crown architecture model. *Annals of Botany* 83, 459–469.