

Do positive interactions increase with abiotic stress? A test from a semi-arid steppe

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Theoretical models predict that the relative importance of facilitation and competition may vary inversely across gradients of abiotic stress. However, these predictions have not been thoroughly tested in the field, especially in semi-arid environments. In this study, we evaluated how the net effect of the tussock grass *Stipa tenacissima* on the shrub *Pistacia lentiscus* varied across a gradient of abiotic stress in semi-arid Mediterranean steppes. We fitted the relationship between accumulated rainfall and the relative neighbour index (our measures of abiotic stress and of the net effect of *S. tenacissima* on *P. lentiscus*, respectively), which varied across this gradient, to a quadratic model. Competitive interactions dominated at both extremes of the gradient. Our results do not support established theory. Instead, they suggest that a shift from facilitation to competition under high abiotic stress conditions is likely to occur when the levels of the most limiting resource are so low that the benefits provided by the facilitator cannot overcome its own resource uptake.

Keywords: facilitation; competition; *Stipa tenacissima*; environmental gradient; *Pistacia lentiscus*; abiotic stress

1. INTRODUCTION

Positive interactions between plant species are widespread in natural communities and have been acknowledged as a major driver of plant community dynamics and ecosystem processes (Bruno *et al.* 2003). Recent field studies have proven that facilitation and competition act simultaneously (Holzapfel & Mahall 1999; Maestre *et al.* 2003a), and theoretical models predict that their relative importance may vary inversely across gradients of abiotic stress (Bertness & Callaway 1994; Brooker & Callaghan 1998). A substantial effort has been made in recent years to validate these models, with support provided by field experiments conducted in salt marshes (Bertness & Ewanchuck 2002), alpine areas (Callaway *et al.* 2002), temperate grasslands (Greenlee & Callaway 1996) and arid environments (Maestre *et al.* 2003a). However, most of these studies were typically performed at only one or two locations, and thus may not have been able to capture a wide range of abiotic conditions. Exceptions are recent

studies conducted at sites spanning large geographical areas (Bertness & Ewanchuck 2002; Callaway *et al.* 2002; Pennings *et al.* 2003). Notably, some of them do not always support the theory that the magnitude of competition and facilitation varies inversely across gradients of abiotic stress (Pennings *et al.* 2003).

Facilitative and competitive interactions are thought to be of great importance in arid and semi-arid areas (Whitford 2002). However, only a few studies have evaluated how changes in abiotic conditions modify the relative importance of facilitation and competition in these environments (Tielbörger & Kadmon 2000; Pugnaire & Luque 2001; Maestre *et al.* 2003a). Furthermore, none of these studies was conducted at multiple sites across a gradient of abiotic stress. In this study, we evaluated how the net effect of the tussock grass *Stipa tenacissima* L. on the shrub *Pistacia lentiscus* L. varied across a gradient of abiotic stress in semi-arid Mediterranean steppes. Recent studies have shown that *S. tenacissima* facilitates the establishment of *P. lentiscus*, and that the net effect of this interaction results from unequal positive and negative effects (Maestre *et al.* 2001, 2003a). Our working hypothesis is that the importance of facilitation relative to competition increases as abiotic stress increases.

2. MATERIAL AND METHODS

Our study was conducted at 10 experimental sites located in the province of Alicante (southeast Spain). Site selection aimed to capture a significant range of the typical variability in average rainfall found in semi-arid *S. tenacissima* steppes, and to reduce between-site variability associated with vegetation type, slope aspect and soil type. The climate was Mediterranean semi-arid, with annual rainfall values ranging from 220 to 388 mm, and annual temperatures in the range of 16–18 °C (averages for the 1960–1990 period). All sites were located in open steppes dominated by *S. tenacissima*, and shared slope aspect (south-facing) and soil type (Lithic Calciorthid; Soil Survey Staff 1990).

To test our hypothesis, we performed a plantation experiment where 1-year-old *P. lentiscus* seedlings were planted at two microsites: 'Tussock' and 'Open'. The Tussock microsite was located upslope from and adjacent to isolated *S. tenacissima* tussocks of medium size (1–1.5 m in width); the Open microsite was located in the inter-tussock areas devoid of vascular vegetation (see Maestre *et al.* 2001 for details). Before planting, we randomly selected 18 planting points per microsite and site. *Pistacia lentiscus* seedlings were grown in the open air at the University of Alicante (located 2–60 km away from the experimental sites) for 11 months in 150 ml plastic containers with a mixture of peat and coconut fibre (50% : 50%) containing slow-release fertilizer (Osmocote plus; Scotts, Columbus, OH, USA). We used local provenance seeds provided by the regional forest services (Banc de Llavors, Generalitat Valenciana). Seedlings of homogeneous size were introduced in manually dug planting holes (25 cm × 25 cm × 25 cm) in late winter 2003 (17–20 February). After planting, we found no differences in seedling diameter between microsites (one-way ANOVA, $p > 0.08$ at all sites). The experiment was conducted under natural conditions without any watering or weeding. During the course of the experiment some seedlings were excavated by rabbits (*Oryctolagus cuniculus*), leaving a minimum of 13 and a maximum of 18 seedlings per microsite.

We used seedling survival after the first summer in the field (as measured on 25 September 2003) to evaluate seedling response to microsite. We took the measurements this early because this period is critical for the establishment of *P. lentiscus* seedlings under semi-arid conditions (Maestre *et al.* 2003b). We used the amount of rainfall during the course of the experiment as our estimate of abiotic stress. There is a strong relationship between this variable and soil-water availability in semi-arid steppes (Puigdefàbregas & Sánchez 1996), which in turn drives the performance of both *S. tenacissima* and *P. lentiscus* (Haase *et al.* 1999; Flexas *et al.* 2001). We collected rainfall at some point during the 24–48 h after each rainfall event from on-site rainfall gauges. To evaluate the effect of *S. tenacissima* on *P. lentiscus*, we calculated the Relative Neighbour Effect (RNE) index as follows: $RNE = (S_T - S_O)/X$, where S_O and S_T are seedling survival on the Open and Tussock microsites, respectively, and X is either S_O (when $S_O > S_T$) or S_T (when $S_T > S_O$). To facilitate interpretation of the results, we multiplied RNE values by -1

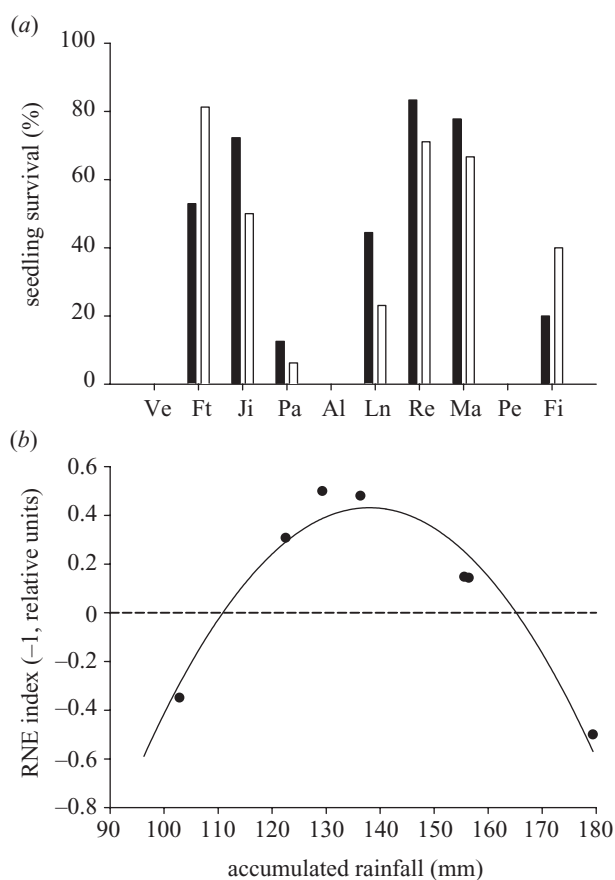


Figure 1. (a) Survival of *Pistacia lentiscus* seedlings on the Tussock (filled bars) and Open (open bars) microsites after the first summer in the field, and (b) relationship between accumulated rainfall and the values of the relative neighbour index (RNE) obtained at the experimental sites. In (a), survival values are based on 13–18 seedlings per microsite and site. The codes on the x-axis of this graph are the abbreviations of the name of the experimental sites, which are sorted by accumulated rainfall in ascending order. In (b), positive and negative values of the RNE indicate facilitation and competition, respectively; $R^2 = 0.95$ and $p = 0.002$.

(Callaway *et al.* 2002). We evaluated the relationship between RNE and accumulated rainfall using regression with SIGMAPLOT 2001 software (SPSS Inc., Chicago, IL, USA). Three out of the 10 experimental sites had no live seedlings at the time of measurement and thus we removed them from the regression analysis.

3. RESULTS

Our site selection covered a wide range of abiotic stress; accumulated rainfall during the course of the experiment varied between 96 mm and 179 mm. After the first summer in the field, seedling survival ranged between 0% and 83% (figure 1a). Higher survival on the Tussock versus Open microsites was found at five of the experimental sites. Three sites had no live seedlings, and at two sites there was higher survival on the Open microsite. Accumulated rainfall showed a significant quadratic relationship with the RNE values (figure 1b). According to this relationship, competitive interactions were prevalent at the extremes of the abiotic gradient evaluated.

4. DISCUSSION

Contrary to the predictions of established models of plant–plant interactions (Bertness & Callaway 1994; Brooker & Callaghan 1998), our results show that competitive interactions between *S. tenacissima* and *P. lentiscus* dominate at both extremes of a gradient of abiotic stress. Similar findings, but over a broader geographical scale, were obtained in North American salt marshes by Pennings *et al.* (2003) and, on a temporal scale at one site in the Negev Desert, by Tielbörger & Kadmon (2000). Pennings *et al.* (2003) suggest that large-scale shifts in plant community composition and structure may modify the response of plant–plant interactions to climate owing to the intervention of evolutionary processes. Such processes are unlikely to explain our results given the experimental nature of our work and the geographical scale that we studied. Small-scale changes in ecosystem attributes such as plant cover, slope or soil textural properties can substantially affect runoff dynamics and soil-water availability (Gómez-Plaza *et al.* 2001), and modify the dynamics of plant interactions in semi-arid environments (Schenk *et al.* 2003). Differences in soil texture between microsites show very little inter-site variation in our study area (Maestre *et al.* 2001), but both total plant cover and slope values showed some degree of inter-site variation (range of 17%–47% and 11°–28°, respectively). However, the main mechanism by which *S. tenacissima* facilitates *P. lentiscus* seedlings is the improvement of soil moisture and microclimate by the shading provided by its canopy, rather than by direct water inputs coming from runoff and the improvement of soil fertility (Maestre *et al.* 2003a). Thus, we believe that the differences in slope, soil properties and vegetation structure between our study sites did not modify the effect of abiotic stress on the interaction that we are investigating.

Implicit in theoretical models of plant–plant interactions is the assumption that environmental harshness is ameliorated by the facilitator species. If this does not occur, competitive interactions are likely to dominate even under high abiotic stress conditions (Tielbörger & Kadmon 2000). Thus, a shift from facilitation to competition under high abiotic stress conditions may occur when the levels of the most limiting resource are so low that the benefits provided by the facilitator cannot overcome its own resource uptake. This could explain our results, since the competition for water between *S. tenacissima* and *P. lentiscus* is intense (Maestre *et al.* 2003a). It is interesting to note that our findings do not match those of previous studies reporting an increase in the magnitude of the facilitative effects of *S. tenacissima* with abiotic stress (García-Fayos & Gasque 2002; Maestre *et al.* 2003a). These discrepancies could be due to differences in the degree of abiotic stress registered, and to differences in the magnitude of the individual rainfall events and the duration of the dry period, which may substantially affect competitive interactions in semi-arid environments (Goldberg & Novoplansky 1997). Nevertheless, we cannot exclude the possibility that other sources of environmental stress (e.g. temperature) could form gradients that are not perfectly aligned with rainfall, and thus affect the interpretation of our results.

Understanding how facilitation and competition respond to abiotic conditions is crucial to predicting

accurately the impacts of ongoing climatic changes on plant communities (Bertness & Ewanchuk 2002). Our results highlight the difficulties of this task even in well-studied systems where the mechanisms underlying positive and negative interactions are known. Future studies focusing on the dynamics of facilitation and competition across multiple sites and years, and on the relative importance of the mechanisms governing these interactions, will undoubtedly improve our ability to predict these impacts.

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