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Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments

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Summary

1 Theoretical models have predicted that the relative importance of facilitation and competition will vary inversely across gradients of abiotic stress, with facilitation being the dominant interaction under high abiotic stress conditions. A critical reappraisal of current theoretical models is needed because experimental studies both support and refute their predictions.

2 A quantitative meta-analysis of field and common garden studies evaluating the effect of abiotic stress (low vs. high) on the net outcome of plant–plant interactions in arid and semi-arid environments was performed to evaluate the degree of empirical support for these models. We created four separate data sets corresponding to the categories of response variables commonly used to measure plant performance (survival, density, growth and fecundity).

3 The analyses showed that both the selection of the estimator of plant performance and the experimental approach followed have a strong influence on both the net outcome of plant–plant interactions and the effect of abiotic stress on such outcome. The effect of neighbours on the survival and growth of target plants was not significant at either stress level, but that on the density and fecundity of target plants was positive (facilitation) and negative (competition) at the low and high abiotic stress level, respectively. Density data showed that the net effect of neighbours was positive and negative at low and high abiotic stress levels, respectively, whereas other estimators suggested that the net effect of neighbours did not differ with stress level. None of our meta-analyses indicated that the magnitude of the net effect provided by neighbours, whether positive or negative, was higher under high abiotic stress conditions, and facilitation does not therefore appear to increase in importance with abiotic stress.

4 As the predictions of current theoretical models regarding the relationship between the net outcome of a plant–plant interaction and abiotic stress do not hold in arid and semi-arid environments, different models are needed. These should consider different sources of abiotic stress separately, and should be valid for performance measurements, such as survival, that integrate plant responses over time. The incorporation of these features into theoretical models will undoubtedly improve their predictive capabilities.

Key-words: abiotic stress, arid, competition, environmental gradients, facilitation, meta-analysis, plant–plant interactions, semi-arid

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Introduction

The role of intra- and inter-specific interactions between plant species as key drivers of plant community composition and dynamics has been acknowledged since the early days of ecology (Tansley 1917; Clements *et al.* 1929; Went 1942). For many years, negative interactions (i.e. competition) were believed to be the dominant biotic factor shaping plant communities (Keddy 1989), but the importance of positive interactions (facilitation) is now widely recognized (Callaway & Pugnaire 1999; Bruno *et al*. 2003). Despite an enormous body of empirical evidence, spatial and temporal variation of facilitative and competitive interactions in the field, and the way the balance between them is related to species traits and environmental conditions, remains unclear (Callaway *et al*. 2002; Callaway *et al.* 2003; Maestre & Cortina 2004a).

Many conceptual models have been developed with the aim of predicting how these interactions change along gradients of ecosystem productivity and resource availability (Grime 1973; Tilman 1988; Goldberg & Novoplansky 1997). The relationship between the outcome of a plant–plant interaction and the degree of abiotic stress has also been the subject of various theoretical models (Bertness & Callaway 1994; Callaway & Walker 1997; Brooker & Callaghan 1998). These models predict that the relative importance of facilitation and competition will vary inversely across gradients of abiotic stress, with facilitation being the dominant interaction under highly stressful conditions. Although a series of successful field-based validation experiments has suggested that these simple models may be applicable under different environments and sources of stress (e.g. Bertness & Hacker 1994; Greenlee & Callaway 1996; Pugnaire & Luque 2001; Bertness & Ewanchuk 2002; Callaway *et al*. 2002; Maestre *et al.* 2003), there is a growing number of empirical studies that do not support their predictions (Casper 1996; Kadmon & Tielbörger 1999; Tielbörger & Kadmon 2000; Pennings *et al*. 2003; Maestre & Cortina 2004a, 2004b). Such departures from theoretical predictions are not surprising, given that factors not accounted for in the models (such as local environmental conditions, the variability associated with species growth rate and life-history stages and the estimator of plant performance used) often impact on the net effect of a plant species on another, and on the interpretation of such effect (Goldberg 1996; Pugnaire *et al*. 1996; Barnes & Archer 1999; Hastwell & Facelli 2003).

Results from studies of the relationship between the outcome of plant–plant interactions and abiotic stress therefore suggest that the models proposed so far may not be generally applicable and that a critical reappraisal of their strengths and weaknesses, and the circumstances in which they are applicable, is needed. We therefore performed a quantitative meta-analysis of studies in arid and semi-arid environments. These biomes cover over 3.9 billion ha worldwide (Reynolds 2001), and both competition and facilitation are key drivers of their community composition, productivity, structure and dynamics (Fowler 1986; Callaway 1995; Whitford 2002). In addition, arid and semi-arid areas are among the most sensitive to the ongoing climatic change (Körner 2000), and increased understanding of the way that plant–plant interactions respond to abiotic stress would therefore aid prediction of the ecological consequences of such change.

Previous reviews have evaluated the importance and consequences of plant–plant interactions for community structure and composition (Connell 1983; Schoener 1983; Fowler 1986; Goldberg & Barton 1992), their degree of commonness between environments (Flores & Jurado 2003), the underlying mechanisms (Fowler 1986; Callaway 1995; Callaway & Pugnaire 1999) and their variation along productivity gradients (Goldberg & Novoplansky 1997; Goldberg *et al*. 1999) but none has considered the effects of stress on the outcome of plant–plant interactions in arid and semi-arid environments. Meta-analysis is a statistical tool that has been used to summarize field results in a wide variety of ecological topics, including competition and facilitation (Gurevitch *et al*. 1992; Goldberg *et al*. 1999; Gurevitch, Morrison & Hedges 2000) but, to our knowledge, only Gómez-Aparicio *et al*. (2004) have used this approach to investigate the effects of abiotic stress on such interactions, in an attempt to establish the generality of using facilitation by shrubs as a restoration tool in dry subhumid Mediterranean mountains.

SCOPE OF THE REVIEW AND DATA BASE BUILDING

We focused on studies conducted on arid and semi-arid environments, as defined by the index of aridity: P/PET, where P and PET are the mean annual precipitation and the mean annual potential evapotranspiration, respectively (FAO 1989). According to this criterion, arid and semi-arid areas have values of P/PET between 0.05 and 0.50. We define abiotic stress as any external condition, apart from the activities of other organisms, that reduces the growth, survival and/or fecundity of a plant (Grime 1979; Welden & Slauson 1986). We focus specifically on effects due to supply of one of three major resources: water, nutrients and light. Water and nutrients are usually scarce in arid and semi-arid ecosystems, and are often considered the most limiting resources for plants in these environments (Noy-Meir 1973; Whitford 2002). Light is rarely a limiting resource, but excess radiation is often a major source of stress for plants in these areas (Valladares 2003).

We selected for relevant studies published between January 1970 and December 2004, using print and online versions of the Science Citation Index and Biological Abstracts, searching for the terms ‘facilitation’, ‘positive interaction’, ‘competition’, ‘interference’, ‘mutualism’, ‘arid’, ‘semiarid’, ‘semi-arid’, ‘drought’, ‘abiotic gradient’, ‘environmental gradient’, ‘salinity’, ‘nutrient’, 'nitrogen', 'recruitment', 'survival', 'growth', 'fecundity', 'density' and 'abiotic stress'. In addition, a comprehensive search of suitable non-English (Spanish and French) articles and theses published during the same time period was conducted. These searches led to a large number of articles that were then examined, but only included in our quantitative synthesis if they met the following six *a priori* criteria.

1. The study was conducted under natural conditions in the field or in a common garden (glasshouse or growth chamber studies, as well as studies using cultivated plants, were not considered).

2. The study evaluated the effect of neighbours (either conspecific or not) on the performance of a target species or group of species (e.g. grasses, shrubs). In most cases, performance of the target species growing in the vicinity of a neighbour was compared with that of plants growing in open areas, naturally devoid of vascular plants. Alternatively, the performance of the target species growing in areas where neighbours were present at naturally occurring densities was compared with that in areas where neighbours were experimentally removed. Studies that simulated the presence of neighbours rather than using real plants (e.g. by adding branches or artificial shade) were not considered.

3. The study was simultaneously conducted at least in two sites differing in their degree of abiotic stress (spatial gradient), or at the same site in periods differing in their degree of abiotic stress (temporal gradient). Studies conducted over temporal gradients were included in the meta-analysis only if they were obtained from different individuals at each sampling date (to avoid lack of independence) and if the individuals being compared had the same age (to avoid age-dependent effects on plant performance). Studies that manipulated the degree of abiotic stress in a single site (e.g. by watering or by adding nutrients) were also included (and categorized as involving an experimental gradient).

4. The study contained enough information to assign the data presented to two categories of abiotic stress (low and high). Many studies used precipitation data as a proxy for abiotic stress and data obtained under the highest and lowest precipitation levels, respectively, were assigned to low and high stress categories. Although plant performance in arid and semi-arid environments is a response to soil water availability, rather than to precipitation *per se* (Reynolds *et al*. 2004), the two variables are usually strongly related (Breshears *et al*. 1997; Haase *et al*. 1999; Maestre *et al*. 2001; Bellot *et al*. 2004). Thus, we consider that precipitation is a valid surrogate of abiotic stress. Where contrasting water availability was due to topography (e.g. north- vs. south-facing slopes), data from areas with the highest and lowest water availability levels were assigned to low and high stress categories, respectively. Under contrasting nutrient conditions, we assigned to the low and high stress categories the data obtained under the highest and lowest nutrient availability levels, respectively, except in saline habitats. In these habitats, the degree of abiotic stress increases as the concentration of micronutrients associated with salinity (e.g. sodium, chloride and boron) increases and low and high stress categories were therefore represented by data obtained under the lowest and highest salinity levels, respectively. Although conditions associated with low radiation may be detrimental under certain circumstances in arid and semi-arid environments (Forseth *et al.* 2001; Valladares & Pearcy 2002), we assume that the beneficial effects of shade (improved water availability and reduced photoinhibition) are dominant and therefore assigned data obtained under the lowest and highest radiation levels, respectively, to the low and high stress categories.

5. The same plant–plant or plant–group of plants interaction was evaluated in both the low and high abiotic stress levels.

6. The results of the study were quantitative and usable. When suitable studies lacked information such as number of replicates, reliability (standard deviation or standard error) or climatic data, the authors were contacted and asked for their original data.

Separate meta-analyses were conducted for studies reporting different plant performance estimators (Gurevitch *et al.* 2000). Four separate data sets were created corresponding to the four most common categories of response variables: survival, density (measured as number of individuals or cover of a given species per unit area), growth (measured as biomass, height, diameter or number of leaves) and fecundity (measured as number of flowers/inflorescences, number of fruits/seeds or weight of flowers/fruits/seeds). Some articles reported results for more than one responding species (or size/age within a single species) or for more than one experiment. In these cases, each species, size/age class and experiment was included separately in the meta-analysis. If an article reported results from a single experiment for more than one response variable (e.g. survival and fecundity), the results were included in different meta-analyses. If an article reported results over the course of the experiment, only the results obtained at the end of the experiment were used. Thus, in all cases a single experiment was represented only once in a given meta-analysis for a given responding species. When the data were reported in a graphical form, the graphs were scanned with the Deskscan II cx v 2.0 (Hewlett-Packard, USA) software. The data from these graphs were extracted with the software TechDig v1.1b (Jones 1998).

STATISTICAL ANALYSES

Survival data were summarized in 2 × 2 contingency tables according to the scheme of Hyatt *et al.* (2003). An odds ratio metric was obtained for each study, calculated as the ratio of the odds of survival in the presence of neighbours (neighbour treatment) to the odds of survival in their absence (control) (Rosenberg *et al.*

2000). In some studies all the individuals of the target species died or survived and 1 was therefore added to the number of individuals in each category for each study (Hyatt *et al*. 2003) to avoid values that would require division by 0. The meta-analysis was conducted with the natural logarithm of the odds ratio, so that values higher and lower than 0 indicate that the odds of surviving were higher or lower in the presence of a neighbour, respectively.

In the case of continuous data for which the mean and the standard deviation or standard error were available (growth, density and fecundity) we used the Hedges' *d* (Gurevitch & Hedges 2001), a metric that has been commonly used in previous meta-analyses (e.g. Gurevitch *et al*. 1992; Rustad *et al*. 2001; Gómez-Aparicio *et al*. 2004), and whose statistical properties are well known (Gurevitch & Hedges 2001). It estimates the effect of neighbours by calculating a standardized measure of the differences in plant performance between the neighbour and control treatments. Positive and negative values of the Hedges' *d* indicate improved performance of the target species in the presence or absence of a neighbour, respectively.

In all cases, the Q statistic (Hedges & Olkin 1985) was used to evaluate if the size of the effect of neighbours differed with abiotic stress. Q is basically a weighted sum of squares following a χ^2 distribution, and describes the variation in effect size between groups. In addition, the total heterogeneity of each meta-analysis, Q_H, was also calculated as described in Rosenberg *et al.* (2000). Q_H is tested against a χ^2 distribution with $n - 1$ degrees of freedom. A significant value of this statistic indicates that the variance among effect sizes is greater than expected by sampling error (Rosenberg *et al.* 2000), and suggests that other variables should be evaluated. When a significant Q_H was found in a meta-analysis, we split the data set into observational and experimental studies for further evaluation of the data as described above. Publication bias, i.e. the greater possibility of publishing significant results, was tested by using weighted histograms and funnel plots (Gurevitch *et al.* 2001). A weighted histogram (where weight is the inverse of the variance of the effect size in each study) whose distribution is depressed around 0, suggests that there is such a bias. Spearman's rank correlation tests examining the relationship between the standardized effect size and the sample size across studies were also conducted (Begg & Mazumdar 1994): significance indicates that larger effect sizes in either direction are more likely to be published than smaller effect sizes.

All the meta-analyses were conducted with the program MetaWin version 2.1.4 (Rosenberg *et al.* 2000). In all cases a random-effects model was used to estimate mean effects sizes (Gurevitch & Hedges 2001) because the fixed-effects model assumption that all observed variation is due to sampling error is very difficult to meet when using a broad range of studies. The confidence intervals of effect sizes were estimated using bootstraping procedures (Rosenberg *et al.* 2000).

Results

SURVIVAL

A total of 26 studies met the selection criteria, yielding 110 suitable cases that were included in the meta-analysis (55 for each level of abiotic stress, see Appendix S1 in Supplementary Material). Only six of these studies evaluated an abiotic stress gradient promoted by resources other than water. The presence of neighbours had no significant effects on the survival of the target species, irrespective of the level of abiotic stress (Fig. 1a), and the size of the effect did not differ between levels of abiotic stress ($Q_B = 1.37$, d.f. = 1, $P = 0.267$). The test of the overall heterogeneity was not significant ($Q_H = 96.28$, d.f. = 109, $P = 0.803$), suggesting that the model explained the variance found in the data. An examination of the weighted histogram (Appendix S2) and of the funnel plot (not shown) suggested that there was no bias in reporting results from these studies. This result was further reinforced by a non-significant rank correlation test ($R_s = -0.02$, $P = 0.875$).

DENSITY

Eight studies, all conducted along water-stress gradients, provided a total of 100 cases for the meta-analysis (50 for each level of abiotic stress, Appendix S3). The presence of neighbours significantly affected the density of the focal species at both stress levels, but in opposite directions (Fig. 1b). At the low stress level, higher densities of the target species were found when they were growing in the vicinity of a neighbour, whereas at the high stress level, higher densities were found in the absence of neighbours. These differences were significant ($Q_B = 21.6$, d.f. = 1, $P < 0.001$). An examination of the weighted histogram (Appendix S2) and of the funnel plot (not shown) again suggested that there was no bias in reporting results, confirmed by a non-significant rank correlation test ($R_s = 0.035$, $P = 0.730$). As the test of the overall heterogeneity was significant ($Q_H = 157.37$, d.f. = 99, $P < 0.001$), we divided the density data set into experimental and observational studies for further analyses (Fig. 2a). When observational studies were analysed, the results were similar to those obtained from the whole data set ($Q_B = 29.40$, d.f. = 1, $P = 0.010$; $Q_H = 142.75$, d.f. = 83, $P < 0.001$), but for experimental data the effect of neighbours was not significant at either stress level and there were no significant differences in effect size between levels ($Q_B = 0.07$, d.f. = 1, $P = 0.786$; $Q_H = 16.3$, d.f. = 17, $P = 0.362$).

GROWTH

A total of 26 studies met the selection criteria, yielding a total of 102 suitable cases (Appendix S4). Nine of these studies evaluated an abiotic stress gradient promoted by resources other than water. The effect of

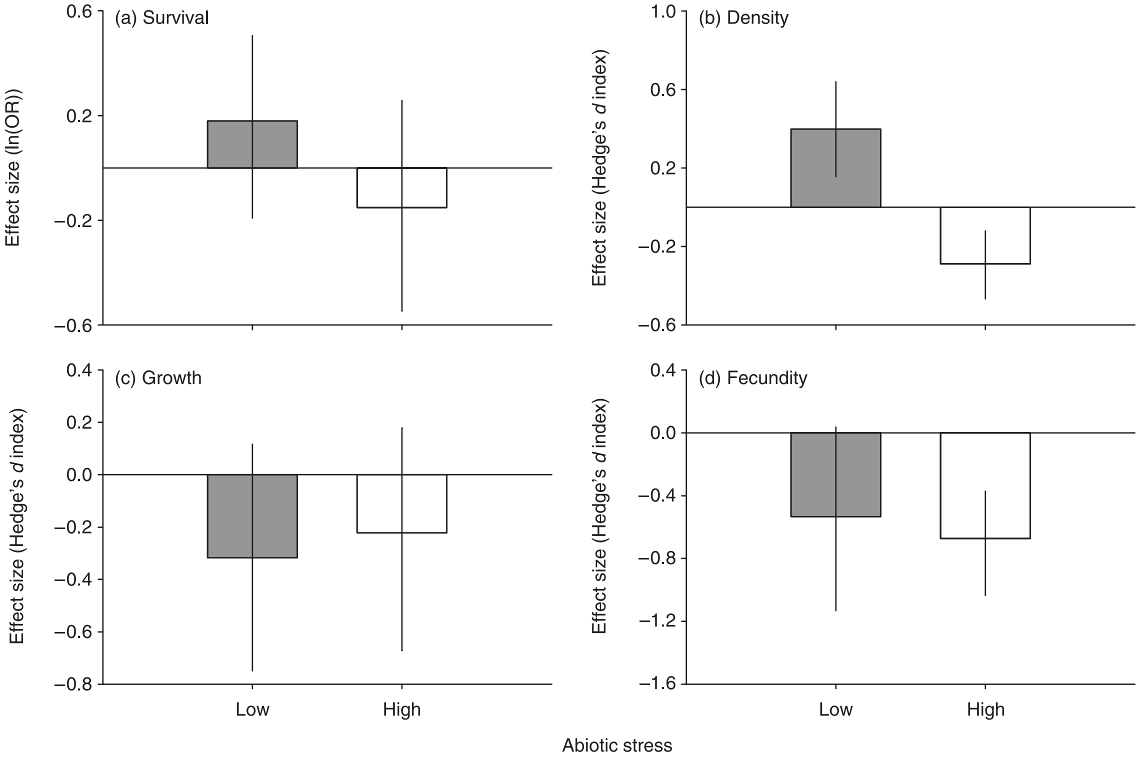

Fig. 1 Results of the random-effects model for survival (A), density (B), growth (C) and fecundity (D) data in the presence of neighbours under low (dark grey) and high (white) levels of abiotic stress. Values reported are the mean effect size and the bootstraped confidence interval (9999 randomizations). Significant effects of neighbours are indicated by confidence intervals that do not overlap zero.

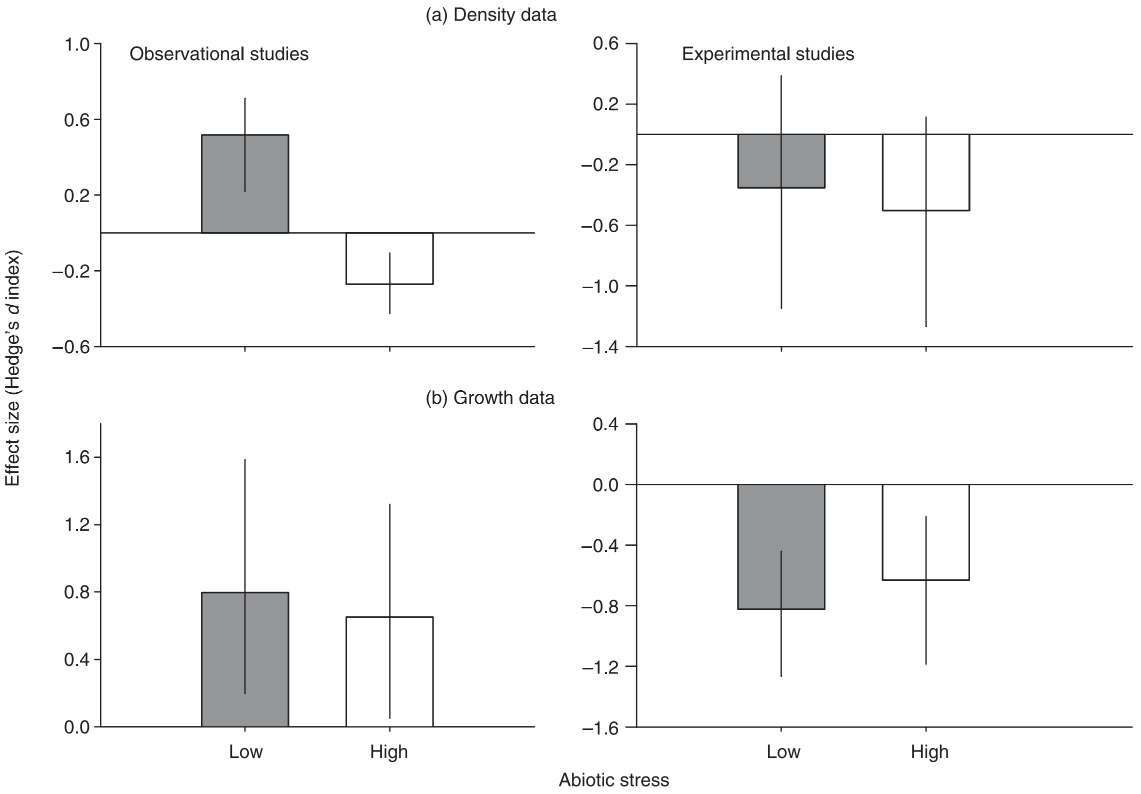

Fig. 2 Results of the random-effects model conducted separately with those data sets with significant heterogeneity (density and growth), showing the effect of neighbours under low (dark grey) and high (white) levels of abiotic stress. Values reported are the mean effect size and the bootstraped confidence interval (9999 randomizations). Significant effects of neighbours are indicated by confidence intervals that do not overlap zero.

neighbours on the growth of the target species was not significant at either stress level (Fig. 1c) and did not differ between stress levels ($Q_B = 0.16$, d.f. = 1, $P = 0.767$). An examination of the weighed histogram (Appendix S2) and of the funnel plot (not shown) suggested that there was no reporting bias and the rank correlation test was not significant ($R_s = -0.09$, $P = 0.367$). The test of the overall heterogeneity was, however, significant ($Q_H = 182.39$, d.f. = 101, $P < 0.001$), and, as observed with density data, the effect size response depended on the experimental approach followed (Fig. 2b). Observational evidence indicated that the target species had higher growth in the presence of neighbours at both stress levels, but experimental data suggested that the effect of neighbours was always negative. The magnitude of the effect size did not differ between the two levels of abiotic stress (observational: $Q_B = 0.19$, d.f. = 1, $P = 0.774$; $Q_H = 76.23$, d.f. = 29, $P < 0.001$; experimental: $Q_B = 0.40$, d.f. = 1, $P = 0.547$; $Q_H = 87.41$, d.f. = 71, $P = 0.098$).

FECUNDITY

A total of 11 studies were analysed (22 cases for each level of abiotic stress, Appendix S5). Only two of these studies evaluated an abiotic stress gradient promoted by resources other than water. Target plants had lower fecundity when growing in the presence of neighbours at high, but not at low, abiotic stress (Fig. 1d). However, the size of the effect did not differ between stress levels ($Q_B = 0.91$, d.f. = 1, $P = 0.712$) and the test of the overall heterogeneity was not significant ($Q_H = 50.88$, d.f. = 43, $P = 0.191$). An examination of the weighted histogram (Appendix S2) and of the funnel plot (not shown), and a non-significant rank correlation test ($R_s = -0.14$, $P = 0.368$), suggested that there was no reporting bias.

Discussion

Our quantitative synthesis of available field and common garden studies indicates that the selection of the estimator of performance has a strong influence on the interpretation of the net outcome of plant–plant interactions in arid and semi-arid environments. For example, although the lack of an effect of neighbours on survival and growth of target plants at either stress level suggests an overall neutral effect, fecundity was negatively affected by neighbours at the high stress level. The interpretation of the effects of abiotic stress on the outcome of interactions also depended on the estimator of performance, with density data suggesting that the net effect of neighbours was positive (facilitation) at low and negative (competition) at high abiotic stress, whereas other estimators suggested that the net effect of neighbours did not differ with stress level.

These results are due, at least in part, to the fact that requirements for survival or growth are likely to differ from those for fecundity (Biere 1995; Escos *et al.* 2000). Furthermore, measures like density, cover or biomass of naturally occurring plants in arid and semi-arid environments are affected by factors, such as the density of dispersers and predators (Rey & Alcántara 2000; Traveset, Riera & Mas 2001), that are beyond the binary interaction between two neighbouring plant species. Thus, there is no reason to expect different aspects of plant performance to respond in a similar way regarding facilitation and competition (Goldberg *et al.* 1999, 2001; Hastwell & Facelli 2003). The theoretical models formulated so far do not explicitly mention that their predictions may hold only for a given estimator of performance (Bertness & Callaway 1994; Callaway & Walker 1997; Brooker & Callaghan 1998), but our finding that the effect of abiotic stress on the outcome of a plant–plant interaction varies with the estimator used provides a clear warning that it is dangerous to generalize. We agree with Hastwell & Facelli (2003) that the effects of facilitation on growth should be considered separately from its effects on survival, and suggest that different models should be developed for different plant performance measures.

More detailed analysis of the data sets showing significant heterogeneity showed that the approach (experimental or observational) substantially affected the interpretation of the effects of neighbours on the performance of a given target species. Such contrasting results have also been found previously in the high Arctic (Dormann & Brooker 2002). Our conclusions cannot be considered as definitive, due to the low number of studies and/or cases available, but the consideration of the experimental approaches when studying plant–plant interactions clearly deserves more attention.

Despite the differences found between the different estimators of performance and approaches employed, all our meta-analyses agree that the magnitude of the net effect of neighbours, whether positive or negative, is not higher under more stressful conditions. Thus, our results do not support the theoretical predictions that the 'importance' (Callaway & Walker 1997) or 'intensity' (Brooker & Callaghan 1998) of facilitation increases with the increase in abiotic stress. These models implicitly assume that environmental harshness is ameliorated when growing in the vicinity of neighbours, as plants buffer one another from extremes of the abiotic environment (Callaway & Walker 1997). This is clearly evident in stressful environments not primarily limited by water, such as in the tundra and in salt marshes, where the presence of neighbours alleviates most of the abiotic stress by improving soil conditions and microclimate in their surroundings (Carlsson & Callaghan 1991; Callaway 1994). However, in arid and semi-arid environments, the availability of water determines the concentration of nutrients in easily utilisable forms, and thus largely controls nutrient mineralization (Austin *et al.* 2004). Thus, it is not surprising that significant responses to increases in nutrient availability tend to occur only under appropriate levels of water availability (Gutiérrez & Whitford 1987; Brooks 2003; Peek & Forseth 2003). In arid and semi-arid environments, plants generally improve soil conditions and microclimate in their surroundings (Reynolds *et al.* 1999; Whitford 2002), but do not necessarily increase the availability of water; indeed, they may even decrease it (Knoop & Walker 1985; Sala *et al.* 1989; Forseth *et al.* 2001; Bellot *et al.* 2004). Thus, if water is the predominant stress factor, plants growing in the vicinity of neighbours may not experience an overall reduction of abiotic stress. Neighbours may increase water availability if shading reduces evaporation (Maestre *et al.* 2003), and by improving soil properties like texture and soil organic matter (Puigdefábregas *et al.* 1999), or may reduce it through direct water uptake and rainfall interception (Valladares & Pearcy 2002; Maestre *et al.* 2003; Bellot *et al.* 2004). The relative importance of competition in harsh environments has been a controversial topic (Grime 1973; Newman 1973; Fowler 1986; Goldberg & Novoplansky 1997), but there is growing experimental evidence that competition for water is intense in arid and semi-arid environments (e.g. Fonteyn & Mahall 1981; Burger & Louda 1995; Flores-Martínez *et al.* 1998). Furthermore, it has been experimentally demonstrated that competition for water may occur even when the net outcome of a plant–plant interaction is facilitation (Maestre *et al.* 2003).

We argue that, in arid and semi-arid environments, the direct influence of abiotic stress promoted by nutrients and light will be subordinate to that of water, especially as aridity increases. In strongly water-limited environments we should expect facilitation to occur only when neighbours increase availability beyond their own water uptake requirements, allowing increased benefits in terms of improved soil fertility and microclimate to increase plant performance compared with areas without neighbours. We suggest that a threshold level in water availability will define, for a given plant–plant interaction and soil fertility status, the transition from competitive to facilitative interaction. A direct test of this hypothesis cannot be made with the experimental results available so far, but it is indirectly supported by several studies. Callaway *et al.* (1991) found extensive variation in herbaceous biomass under individual trees in oak savannas (ranging from much higher to lower than in adjacent open grassland). All trees increased nutrient levels considerably over those found in grassland, and reduced radiation to a similar extent, but facilitation was dependent on the root architecture of individual trees. Increased tree fine-root biomass in the upper soil horizons had a strong negative effect on understorey biomass, suggesting that competition for available water was critical in determining the net outcome of the interaction between trees and understorey grasses. In a series of experimental plantings conducted in the same area during consecutive years, Maestre *et al.* (2003, 2004) studied the interaction between adult *Pinus halepensis* and seedlings of the shrub *Pistacia lentiscus* in semi-arid forests in south-east Spain. Although soil nutrient levels increased and radiation was reduced under the canopy of *Pinus*, the net effect of the interaction between *Pinus* and *Pistacia* was negative in below-average rainfall years and positive in above-average years, suggesting that microsite benefits provided by *Pinus* were only apparent when water availability was high enough to overcome competitive effects. Similarly, Maestre & Cortina (2004a) evaluated the interaction between adult individuals of the tussock grass *Stipa tenacissima* and *Pistacia* seedlings in 10 steppes located along a rainfall gradient (their measure of abiotic stress). They found a transition from a net competitive to a net facilitative effect of *Stipa* as they moved from more to less stressful conditions, again suggesting that water availability was driving the transition.

We argue that making realistic predictions of the outcome of a plant–plant interaction along gradients of abiotic stress in arid and semi-arid environments will depend on both the limiting resource and the measures of plant performance being considered. As conceptual models with more than two predictors are not easily handled and tested, we suggest that different models should be developed for different sources of abiotic stress. We also suggest that, to be widely applicable in arid and semi-arid environments, these models should be valid for performance measurements, such as survival, that integrate plant responses through pulses of resources (rainfall events) and interpulse periods (see Goldberg & Novoplansky 1997 for a complete discussion of the importance of these pulses in the context of plant–plant interactions). The incorporation of these features into theoretical models will undoubtedly improve their predictive capabilities.

The characteristics of the data sets employed impose certain limitations on our quantitative synthesis. Even though we had an acceptable number of examples for some measurements of plant performance (survival, density and growth), in no case were we able to use more than 26 different studies. Furthermore, we found clear indications of heterogeneity in the data bases developed for two of our performance measures (density and heterogeneity), which were not removed after splitting the data into observational and experimental studies. Thus, the results of our meta-analyses should be interpreted with care. More studies are clearly needed and these should focus on the dynamics of facilitation and competition, both in space and time, across multiple levels of abiotic stress, in order to test for the presence of thresholds and non-linear relationships, and should include multiple measures of plant performance. As noted in previous reviews (Goldberg *et al.* 1999; Gurevitch, Curtis & Jones 2001), the lack of information regarding number of replicates, climatic characteristics of the study sites and standard deviations or errors precludes the inclusion of valuable articles in quantitative reviews.

The relationship between abiotic stress and the net outcome of a plant–plant interaction is inherently complex, and surprises are likely to arise even in well-studied systems where the underlying mechanisms are known (e.g. Maestre *et al.* 2003; Maestre & Cortina 2004a). Progress in our understanding of this relationship is crucial to enable prediction of the impacts of ongoing climate changes on plant communities (Bertness & Ewanchuck 2002), as abiotic stress, such as water limitation, is expected to increase in many ecosystems, particularly in arid and semi-arid areas (Houghton *et al*. 2001).

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC1017/JEC1017sm.htm

Appendix S1 List of studies included in the meta-analysis of survival data.

Appendix S2 Relative frequency of effect size values weighed by 1/variance for survival, density, growth and fecundity data.

Appendix S3 List of studies included in the meta-analysis of density data.

Appendix S4 List of studies included in the meta-analysis of growth data.

Appendix S5 List of studies included in the meta-analysis of fecundity data.

Appendix S6 References included in Appendices S1–S6 and not cited in the main text.

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