

FUTURE DIRECTIONS No. 5

Refining the stress-gradient hypothesis for competition and facilitation in plant communities

Fernando T. Maestre^{1*}, Ragan M. Callaway², Fernando Valladares^{1,3} and Christopher J. Lortie⁴

¹Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Universidad Rey Juan Carlos, ESCET, C/ Tulipán s/n, 28933 Móstoles, Spain; ²Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA;

³Instituto de Recursos Naturales, Centro de Ciencias Medioambientales, CSIC, Serrano 115, 28006 Madrid, Spain; and

⁴Biology Department, York University, Toronto, ON M3J 1P3, Canada

Summary

1. The stress-gradient hypothesis (SGH) predicts that the frequency of facilitative and competitive interactions will vary inversely across abiotic stress gradients, with facilitation being more common in conditions of high abiotic stress relative to more benign abiotic conditions. With notable exceptions, most tests of the SGH have studied the interaction between a single pair or a few pairs of species, and thus have evaluated shifts in the magnitude and direction of pair-wise interactions along stress gradients, rather than shifts in the general frequency of interactions.

2. The SGH has been supported by numerous studies in many ecosystems, has provided a crucial foundation for studying the interplay between facilitation and competition in plant communities, and has a high heuristic value. However, recent empirical research indicates that factors like the variation among species and the nature of the stress gradient studied add complexity not considered in the SGH, creating an opportunity to extend the SGH's general conceptual framework.

3. We suggest that one approach for extending the SGH framework is to differentiate between the original idea of how 'common' interactions might be along stress gradients and the ubiquitous empirical approach of studying shifts in the strength of pair-wise interactions. Furthermore, by explicitly considering the life history of the interacting species (relative tolerance to stress vs. competitive ability) and the characteristics of the stress factor (resource vs. non-resource) we may be able to greatly refine specific predictions relevant to the SGH.

4. We propose that the general pattern predicted by the SGH would hold more frequently for some combinations of life histories and stress factor, particularly when the benefactor and beneficiary species are mostly competitive and stress-tolerant, respectively. However, we also predict that other combinations are likely to yield different results. For example, the effect of neighbours can be negative at both ends of the stress gradient when both interacting species have similar 'competitive' or 'stress-tolerant' life histories and the abiotic stress gradient is driven by a resource (e.g. water).

5. *Synthesis.* The extension of the SGH presented here provides specific and testable hypotheses to foster research and helps to reconcile potential discrepancies among previous studies. It represents an important step in incorporating the complexity and species-specificity of potential outcomes into models and theories addressing how plant–plant interactions change along stress gradients.

Key-words: abiotic stress, competition, environmental gradients, facilitation, plant–plant interactions, stress-gradient hypothesis

Introduction

The majority of facilitation research over the last two decades has been stimulated by the 'stress-gradient hypothesis' (SGH), a general conceptual model predicting that the relative frequency

of facilitation and competition will vary inversely across gradients of physical stress or ecosystem productivity (Bertness & Callaway 1994). The basic idea of the SGH is that facilitation 'should be particularly common in communities developing under high physical stress and in communities with high consumer pressure' and 'where the physical environment is relatively benign and consumer pressure is less severe, positive

*Correspondence author. E-mail: fernando.maestre@urjc.es

interactions should be rare; as a result competitive interactions should be the dominant structuring forces' (Bertness & Callaway 1994).

The SGH has been widely supported in the literature (see Callaway 2007), but some recent research has shown that results from studies within the same system may vary (e.g. Tielbörger & Kadmon 2000; Holzapfel *et al.* 2006), that facilitative effects may decrease or cease with extreme stress (Michalet *et al.* 2006), that their magnitude and direction may change through the ontogeny of the interacting species (Miriti 2006), and that transitions from competition to facilitation depend to a large degree on the characteristics of the species being tested (Choler *et al.* 2001), the nature of the stress gradient involved (Kawai & Tokeshi 2007), and the performance measure considered (Maestre *et al.* 2005). This variation within the general context of the SGH provides an opportunity to refine this key conceptual model to make it capable of predicting the complexity of potential outcomes when studying biotic interactions along stress gradients.

The SGH initially proposed that positive interactions should be 'particularly common' or increase in 'frequency' under stressful conditions. But frequency does not necessarily translate to the 'intensity' of interactions and only qualitatively addresses the 'importance' of interactions (see Brooker *et al.* 2005). The focus of the latter is on the effect of neighbours on a particular species, either relative to the effect of the abiotic environment (importance) or not (intensity). Furthermore, most of the experimental studies aiming to test predictions from the SGH have studied the interaction between a single pair of species (e.g. Greenlee & Callaway 1996; Maestre & Cortina 2004), a few pairs of species (e.g. Donovan & Richards 2000), or one benefactor and a suite of beneficiaries (e.g. Callaway *et al.* 1991; Pugnaire & Luque 2001; Tewksbury & Lloyd 2001; but see Choler *et al.* 2001, Callaway *et al.* 2002 and Gómez-Aparicio *et al.* 2004). Thus, most experimental studies have actually evaluated how the magnitude and direction of pair-wise interactions change along stress gradients. A number of studies have substituted experimental manipulations for broad measurements of spatial associations, which include virtually all species in the community, and found clear patterns consistent with the SGH (e.g. Gutiérrez *et al.* 1993; Tewksbury & Lloyd 2001; Arroyo *et al.* 2003; Holzapfel *et al.* 2006). However, differentiating between the original idea of how 'common' interactions might be along stress gradients and shifts in the strength of pair-wise interactions is a good starting point to explore how we might make the conceptual framework of the SGH more explicit.

Subsequent modifications of the SGH since its formulation (Callaway & Walker 1997; Brooker & Callaghan 1998; Dormann & Brooker 2002) have proposed variation on its general theme, but retained the fundamental underlying conceptual principles. Recent syntheses and discussions on facilitation have also reviewed the strengths and limitations of the SGH (Maestre *et al.* 2005, 2006; Lortie & Callaway 2006; Callaway 2007), provided clear guidelines on the issues that should be tackled by future field studies to overcome them (Brooker *et al.* 2008), and proposed ideas for revising the

SGH in ways that might increase its conceptual usefulness (Cheng *et al.* 2006; Callaway 2007). However, none of these studies has significantly expanded the conceptual framework of the general SGH. With this essay we aim to do so by explicitly considering the effects of the type of stress gradient and the life-history characteristics of the interacting species when predicting the outcome of the interaction among two plant species along abiotic stress gradients. With this exercise, we provide a set of clear predictions that can be tested in the field and modelled.

The need to account for species and stress features when refining the SGH

'Stress' is not a precise concept, and therefore it is difficult to apply quantitatively to communities or ecosystems (Körner 2003; Lortie *et al.* 2004). However, it is a term that allows us to scale from reductionist, strictly quantifiable levels of analysis to broader concepts (Lortie *et al.* 2004). One of the most successful efforts to quantify stress as an ecological factor was made by Grime (1977). He argued that stressful environments are best defined as those in which producers are limited by the environment in their ability to convert energy to biomass, and it is under this focus on productivity that most community ecologists examine stress (Lortie *et al.* 2004; Brooker 2006; Callaway 2007). The SGH was in part derived from Grime's hypotheses about the relative importance of competition in plant communities (see Callaway 2007, p. 194), and therefore the concept of 'stress' when testing the SGH is the same as defined by Grime. There are other approaches to the role of stress and competition in structuring plant communities; that of Taylor *et al.* (1990) is different, but not incompatible, and our aim is not to reconcile them, but to start from an easy characterization of species according to their tolerance to stress.

Since stress measured at the 'plant's eye view' is relative to a particular species (Körner 2003), the outcome of biotic interactions along productivity-based stress gradients may vary depending on the stress tolerance and competitive ability of the interacting species (see Choler *et al.* 2001; Liancourt *et al.* 2005; Wang *et al.* 2008). The SGH, which makes a broad prediction for general patterns across species and systems, might be refined by incorporating species traits to explain why co-occurring species may not show the same response, either in magnitude or direction, to a common neighbour under the same environmental conditions (e.g. Callaway 1994; Choler *et al.* 2001; Maestre *et al.* 2001; Callaway *et al.* 2002).

Another crucial issue not considered in the SGH is how different categories of stress may affect shifts between competition and facilitation. Abiotic stress may come from either non-resource-related conditions such as heat, cold, wind, salinity or soil structure, or resource-related conditions such as water, light and nutrients. Where stress is induced by precisely the same resource needed by both the 'facilitator' and the 'facilitated' species (hereafter denoted as benefactor and beneficiary, respectively), the general conceptual paradigm of the SGH may not hold (Callaway 2007). In water-limited

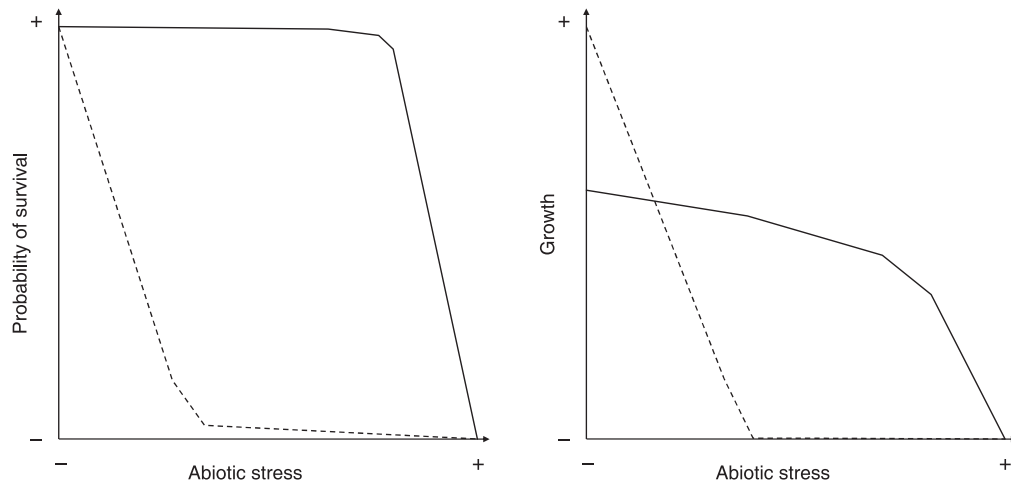


Fig. 1. Graphical representation of the probability of survival (left) and growth (right) along an abiotic stress gradient of a stress-tolerator (solid line) and a competitor (dashed line).

environments plants generally improve soil fertility and microclimate under their canopies (Cortina & Maestre 2005), but these changes do not always translate into increased water availability in their immediate vicinity (for examples see Sala *et al.* 1989; Valladares & Pearcy 2002; Bellot *et al.* 2004; Ludwig *et al.* 2004a). Therefore, when a limited resource is the only fundamental abiotic stress factor, facilitation can only occur when neighbours increase the availability of this resource (Maestre & Cortina 2004). There are at least three circumstances where one might expect this to occur. Firstly, a plant in arid systems with the capacity for hydraulic lifting can provide water to a neighbour, likely at a cost to itself, but to the advantage of the neighbour (Ludwig *et al.* 2004b). Secondly, shade from canopy shrubs and trees can retain soil moisture at the soil surface and facilitate neighbours with shallower roots (Maestre *et al.* 2003), although again probably to the detriment of the benefactor. Finally, shade can indirectly facilitate the water-relations of understorey neighbours by decreasing the vapour pressure difference between the leaf of the beneficiary and ambient air. This can occur without a substantial resource cost to the benefactor. However, if the below-ground spatial niches of interacting species overlap substantially, and the lack of a soil resource is the predominant driver of stress – situations potentially found in environments such as arid and semi-arid areas (e.g. Reynolds *et al.* 2000; Carrick 2003; Hipondoka *et al.* 2003; Ludwig *et al.* 2004b) – shifts in the balance of net interactions from competition to facilitation with increasing stress are less likely. However, we want to emphasize that it is difficult to be certain soil water stress is occurring without the concomitant effect of high temperature stress, and in this situation facilitation might be expected to commonly increase with stress. This differentiation between resource and non-resource stress factors may explain why studies conducted in alpine environments and salt marshes generally support predictions of the SGH (e.g. Callaway 1998; Bertness & Ewanchuk 2002; Callaway *et al.* 2002), while more studies in arid environments have not

(e.g. Tielbörger & Kadmon 2000; Maestre & Cortina 2004; Barchuk *et al.* 2005; but see Callaway 2007).

The SGH refined

Focusing on a species or a chosen suite of species, a simple way to illustrate how differences in life history and physiology among co-existing species can influence the outcome of their interaction might be to classify them as either ‘competitive’ or ‘stress-tolerant’ (following the CSR classification of Grime 1977, 2001). While many species have been found to primarily follow these broad strategies in different habitats (e.g. Grime *et al.* 1997; Pierce *et al.* 2007; Wellstein *et al.* 2007; Zelnik & Čarni 2008), most of them usually share attributes of different strategies. For the sake of simplicity, we consider that when a competitive and a stress-tolerant species interact, the former has greater competitive ability, while that the latter species has greater tolerance to stress, irrespective of where they are placed along the CSR continuum (Fig. 1). Stress is taken here according to Brooker and Callaghan (1998) as a combination of both stress and disturbance. Stress includes all phenomena limiting photosynthesis either directly (e.g. extreme temperatures) or indirectly (e.g. low water availability), and disturbance includes all phenomena leading to biomass loss (e.g. herbivory). Levels of environmental severity vary not only over space but also over time, and this variation can be random, episodic, cyclic or exhibit a monodirectional trend, as discussed by Brooker and Callaghan (1998). To simplify our predictions and make them tractable, we do not consider time as a gradient for stress since we are aimed at the net plant–plant interaction occurring over an ecologically relevant unit of time: the growth season. By integrating these two broad functional categories with variation in the nature of the stress factor (i.e. resource and non-resource stress factor) and by distinguishing among the types of responses expected of beneficiary species, we can begin to establish categorical differences in how species are predicted to respond along stress gradients (Table 1).

Table 1. The predicted relationship between abiotic stress and the outcome of a given plant–plant interaction. Stress gradients can be promoted by resource and non-resource limitations. The traits of the interacting species are also incorporated, and generally include two broad categories of species (C = ‘competitive’ or S = ‘stress-tolerant’). + = net facilitation, – = net competition, 0 = neutral interaction. Differences in the magnitude of facilitative interactions within a given interaction and stress level are noted by the number of + symbols employed

Abiotic stress promoted by	Stress level	C benefactor		S benefactor	
		C beneficiary	S beneficiary	C beneficiary	S beneficiary
Resource (e.g. water)	Low	–	–	0	–
	Medium	+	+	+	+
	High	–	++	–	–
Non-resource (e.g. temperature)	Low	–	–	–	–
	Medium	++	+	+	0
	High	+	++	++	+

RESPONSES WHEN ABIOTIC STRESS IS RESOURCE DRIVEN

When both the benefactor and beneficiary species are ‘competitive’ (per Grime 1977), facilitation may become dominant at moderate stress levels, when a resource like water becomes more abundant in the vicinity of a benefactor species through mechanisms such as reduced evapotranspiration and improved water retention capacity of the soil (Raffaele & Veblen 1998; Maestre *et al.* 2003). Although the evidence for this is limited, competition may become important under high stress levels because amelioration of microclimate and soil conditions cannot make up for the water consumption of the benefactor (Kitzberger *et al.* 2000; Maestre & Cortina 2004). The low competitive ability of the stress-tolerant species makes its effects on the competitor to be null or slightly positive under low stress levels.

When the benefactor is competitive, the growth of the beneficiary may be inhibited as we move along the abiotic stress gradient because of the shortage of the limiting resource. However, since a stress-tolerant plant should be able to survive until resource levels are very low (e.g. Vilagrosa *et al.* 2003), facilitative interactions should be expected to be prevalent until these levels are reached. Thus, when both interacting species are stress tolerant, facilitation can be expected to be the dominant net outcome at moderate stress levels, but competition may occur at both low and high stress levels, as found in the field by Maestre & Cortina (2004; see Callaway 2007, pp. 216–217), who studied the interaction between the stress-tolerant species *Stipa tenacissima* and *Pistacia lentiscus* along a rainfall gradient. Similar patterns were also found with rhizomatous perennial plants along a nutrient gradient by Rebele (2000).

When the beneficiary and benefactor species are stress tolerant and competitive, respectively, competition should be intense at low abiotic stress because of the increased resource uptake rates of the benefactor compared to the beneficiary species (Grime 2001). The magnitude of this net outcome may be reduced concomitantly with the increase of abiotic stress, and facilitation should become apparent at intermediate stress levels. As the competitor will die at stress levels at which the

stress-tolerant species will still be alive (e.g. Sánchez-Gómez *et al.* 2006), the beneficiary is likely to continue benefiting from the effects of the benefactor on microclimate and from its legacy on soil properties (Facelli & Brock 2000), and thus the magnitude of net facilitation will increase at high stress levels.

RESPONSES WHEN ABIOTIC STRESS IS NON-RESOURCE BASED

Facilitation should be particularly evident at intermediate stress levels when the interacting species are competitive. This can be the situation in arctic and alpine ecosystems where amelioration of harsh environmental conditions by the benefactor, frequently driven by architecture-mediated protection from winds and low temperatures (e.g. Carlsson & Callaghan 1991; Baumeister & Callaway 2006), offsets resource competition with it. As competitors sustain high rates of resource uptake under stress (Grime 2001), the magnitude of facilitation will be sharply reduced at high stress levels, when the maximum tolerance of the beneficiary species growing without neighbours is reached, but net facilitative interactions should still be observed.

The outcome of the interaction probably follows the general pattern predicted by the SGH, that is, increases in facilitation with increases in abiotic stress, when the beneficiary and benefactor species are competitive and stress tolerant, respectively. However, as the benefactor has lower competitive ability than the beneficiary, its positive effects should increase until a plateau is reached, which is defined by the stress levels at which plants growing without neighbours die. It is interesting to note that similar responses to these predictions have been suggested by Callaway *et al.* (2002), who conducted a world-wide assessment of the effects of elevation on the outcome of plant–plant interactions in alpine environments, and by Badano *et al.* (2007), who evaluated the effect of stress-tolerant native cushion plants on the growth of the potentially more competitive (and exotic) *Taraxacum officinale* and *Cerastium arvense* at different altitudes in the Chilean Andes.

When both species are stress tolerant, they are likely to compete for resources all along the abiotic stress gradient.

However, facilitation should be mostly evident at high levels of abiotic stress, where amelioration of harsh environmental conditions by the benefactor offsets resource competition with it. Therefore, as we move along the stress gradient the net outcome of the interaction will shift from competition to facilitation, being mostly neutral at moderate stress levels. Similar responses have been reported by studies conducted in coastal areas, where burial by sand is one of the main factors limiting plant growth (Franks 2003; Franks & Peterson 2003). When the beneficiary and benefactor species are stress tolerant and competitive, respectively, the outcome of the interaction is likely to range from strongly negative to strongly positive along the stress gradient. Competition should be intense when abiotic stress is low because of the increased resource uptake rates of the benefactor relative to the beneficiary species. As the benefactor is likely to die at stress levels at which the beneficiary species will survive, the beneficiary should continue benefiting from the amelioration of stress promoted by the benefactor well-beyond its death and until the architecture-mediated protection provided by the latter is maintained.

Concluding remarks

The general pattern predicted by the SGH has been widely demonstrated (Callaway 2007), but for a number of reasons the 'commonness' (*sensu* Bertness and Callaway 1994) or importance (*sensu* Brooker *et al.* 2005) of facilitative interactions may diminish in some exceptionally stressful conditions (Michalet *et al.* 2006; Callaway 2007). We cannot think of a reason why the intensity (*sensu* Brooker *et al.* 2005) of facilitation should diminish at any level of stress, but if stress is high enough, even intense facilitation may not suffice to allow a stress-intolerant plant to survive or grow, and thus the importance of facilitation (*sensu* Brooker *et al.* 2005) may diminish. Therefore, to best test the refinements proposed in this article for the SGH, empirical studies should incorporate the fullest possible extent of a stress gradient where the beneficiary species is present, and include species with different competitive-stress tolerance capacities. If responses relate to the type of stress (i.e. resource vs. non-resource), then future studies should explicitly define the stressors and design the experiment accordingly. This would also afford future synthetic efforts the capacity to contrast the relative importance of different types of stress gradients.

The predictions introduced in this article focus on pair-wise interactions, but to be expressed in the terms of the original formulation of the SGH, they must ultimately be extended to communities through spatial pattern analyses and patterns of association (e.g. Dullinger *et al.* 2007; Valiente-Banuet & Verdú 2008; Maestre *et al.* 2008). By including an assessment of the relative frequencies of species with particular competitive abilities and stress tolerances within a community, these predictions can be refined to specifically predict how certain species respond to stress, or at the very minimum whether we might expect net negative or net positive interactions within a group of species at a certain point along stress gradients.

Detailed understanding of the mechanistic cause of stress may increase predictive precision even further. However, plants interact in groups, thus even detailed knowledge on the ecology of species in pair-wise interactions may be confounded by the intrinsically diffuse nature of interactions in natural communities (Wilson & Keddy 1986) and indirect interactions with third species (Miller 1994; Callaway & Pennings 2000; Callaway & Howard 2006).

Refinements of the SGH presented here are by no means definitive, but we hope they will foster further empirical and theoretical work in this field. This article also provides a conceptual framework within which to develop new mathematical models for the role of facilitative interactions along environmental gradients, and which is needed to accurately understand the processes that organise plant communities (Brooker *et al.* 2008).

Acknowledgements

We thank David Gibson and four anonymous referees for comments and improvements on earlier versions of this manuscript. FTM was supported by a Ramón y Cajal contract from the Spanish Ministerio de Ciencia e Innovación (MCINN), co-funded by the European Social Fund, by the Fundación BBVA grant INTERCAMBIO (BIOCON06/105), by the British Ecological Society (Studentship 231/1975), and by the Comunidad de Madrid grant REMEDINAL (S-0505/AMB/0335). FV was supported by the MCINN grant ECOCLIM (CGL2007 66066 c04-02 BOS). RMC was supported by the NSF, DoD, and USDA of the United States, The Andrew W. Mellon Foundation, the Rocky Mountain Research Station, and the Sponsored Research Office of The University of Montana. CL was supported by a NSERC Discovery Grant, Canada.

References

- Arroyo, M.T.K., Cavieres, L.A., Peñaloza, A. & Arroyo-Kalin, M.A. (2003) Positive associations between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecology*, **169**, 12–129.
- Badano, E.I., Villarreal, E., Bustamante, R.O., Marquet, P.A. & Cavieres, L.A. (2007) Ecosystem engineering facilitates invasions by exotic plants in high-Andean ecosystems. *Journal of Ecology*, **95**, 682–688.
- Barchuk, A.H., Valiente-Banuet, A. & Díaz, M.P. (2005) Effect of shrubs and seasonal variability of rainfall on the establishment of *Aspidosperma quebracho-blanco* in two edaphically contrasting environments. *Austral Ecology*, **30**, 695–705.
- Baumeister, D. & Callaway, R.M. (2006) Facilitative effects of *Pinus flexilis* during succession: a hierarchy of mechanisms benefits other plant species. *Ecology*, **87**, 1816–1830.
- Bellot, J., Maestre, F.T., Chirino, E., Hernández, N. & Ortiz de Urbina, J. (2004) Afforestation with *Pinus halepensis* reduces native shrub performance in a Mediterranean semiarid area. *Acta Oecologica*, **25**, 7–15.
- Bertness, M. & Callaway, R.M. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 191–193.
- Bertness, M. & Ewanchuk, P.J. (2002) Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia*, **132**, 392–401.
- Brooker, R.W. (2006) Plant–plant interactions and environmental change. *New Phytologist*, **171**, 271–289.
- 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., 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., Kunstler, G. *et al.* (2008) Facilitation in plant communities: the past, the present and the future. *Journal of Ecology*, **96**, 18–34.
- Callaway, R.M. (1994) Facilitative and interfering effects of *Arthrocnemum subterminale* on winter annuals. *Ecology*, **75**, 681–686.

- Callaway, R.M. (1998) Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. *Oikos*, **82**, 561–573.
- Callaway, R.M. (2007) *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht, The Netherlands.
- Callaway, R.M. & Howard, T.G. (2006) Competitive networks, indirect interactions, and allelopathy: a microbial viewpoint on plant communities. *Progress in Botany*, **69**, 317–335.
- Callaway, R.M. & Pennings, S.C. (2000) Facilitation may buffer competitive effects: indirect and diffuse interactions among salt marsh plants. *American Naturalist*, **156**, 416–424.
- Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958–1965.
- Callaway, R.M., Nadkarni, N.M. & Mahall, B.E. (1991) Facilitating and interfering effects of *Quercus douglasii* in central California. *Ecology*, **72**, 1484–1499.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R. et al. (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.
- Carlsson, B.A. & Callaghan, T.V. (1991) Positive plant interactions in tundra vegetation and the importance of shelter. *Journal of Ecology*, **79**, 973–983.
- Carrick, P.J. (2003) Competitive and facilitative relationships among three shrub species, and the role of browsing intensity and rooting depth in the Succulent Karoo, South Africa. *Journal of Vegetation Science*, **14**, 761–772.
- Cheng, D.L., Wang, G.X., Chen, B.M. & Wei, X.P. (2006) Positive interactions: crucial organizers in a plant community. *Journal of Integrative Plant Biology*, **48**, 128–136.
- Choler, P., Michalet, R. & Callaway, R.M. (2001) Facilitation and competition on gradients in alpine plant communities. *Ecology*, **82**, 3295–3308.
- Cortina, J. & Maestre, F.T. (2005) Plant effects on soils in drylands: implications on community dynamics and ecosystem restoration. *Tree Species Effects on Soils: Implications for Global Change* (eds D. Binkley & O. Menyailo), pp. 85–118. NATO Science Series, Springer Verlag, Berlin.
- 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.
- Dormann, C.F. & Brooker, R.W. (2002) Facilitation and competition in the high Arctic: the importance of the experimental approach. *Acta Oecologica*, **23**, 297–301.
- Dullinger, S., Kleinbauer, I., Pauli, H., Gottfried, M., Brooker, R., Nagy, L. et al. (2007) Weak and variable relationships between environmental severity and small-scale co-occurrence in alpine plant communities. *Journal of Ecology*, **95**, 1284–1295.
- Franks, S.J. (2003) Competitive and facilitative interactions within and between two species of coastal dune perennials. *Canadian Journal of Botany*, **81**, 330–337.
- Facelli, J.M. & Brock, D.J. (2000) Patch dynamics in arid lands: localized effects of *Acacia papyrocarpa* on soils and vegetation of open woodlands of south Australia. *Ecography*, **23**, 479–491.
- Franks, S.J. & Peterson, C.J. (2002) Burial disturbance leads to facilitation among coastal dune plants. *Plant Ecology*, **168**, 13–21.
- Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J. & Baraza, E. (2004) Applying plant positive interactions to reforestation in Mediterranean mountains: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications*, **14**, 1128–1138.
- Greenlee, J.T. & Callaway, R.M. (1996) Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in western Montana. *American Naturalist*, **148**, 386–396.
- Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, **111**, 1169–1194.
- Grime, J.P. (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd edn. Wiley, Chichester.
- Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H. et al. (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos*, **79**, 259–281.
- Gutiérrez, J.R., Meserve, P.L., Contreras, L.C., Vasquez, H. & Jaksic, F.M. (1993) Spatial distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porlieria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile. *Oecologia*, **95**, 347–352.
- Hipondoka, M.H.T., Aranibar, J.N., Chirara, C., Lihavha, M. & Macko, S.A. (2003) Vertical distribution of grass and tree roots in arid ecosystems of Southern Africa: niche differentiation or competition? *Journal of Arid Environments*, **54**, 319–325.
- Holzapfel, C., Tielbörger, K., Pavag, H.A., Nigel, J. & Sternbeug, H. (2006) Annual plant–shrub interactions along an aridity gradient. *Basic and Applied Ecology*, **7**, 268–279.
- Kawai, T. & Tokeshi, M. (2007) Testing the facilitation-competition paradigm under the stress-gradient hypothesis: decoupling multiple stress factors. *Proceedings of the Royal Society B*, **274**, 2503–2508.
- Kitzberger, T., Steinaker, D.F. & Veblen, T.T. (2000) Establishment of *Austrocedrus chilensis* in Patagonian forest-steppe ecotones: facilitation and climatic variability. *Ecology*, **81**, 1914–1924.
- Körner, C. (2003) Limitation and stress – always or never? *Journal of Vegetation Science*, **14**, 141–143.
- Liancourt, P., Callaway, R.M. & Michalet, R. (2005) Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology*, **86**, 1611–1618.
- Lortie, C.J. & Callaway, R.M. (2006) Re-analysis of meta-analysis: support for the stress-gradient hypothesis. *Journal of Ecology*, **94**, 7–16.
- Lortie, C.J., Brooker, R.W., Kikvidze, Z. & Callaway, R.M. (2004) The value of stress and limitation in an imperfect world: a reply to Körner. *Journal of Vegetation Science*, **15**, 577–580.
- Ludwig, F., De Kroon, H., Berendse, F. & Prins, H.H.T. (2004a) The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology*, **170**, 93–105.
- Ludwig, F., Dawson, T.E., Prins, H.H.T., Berendse, F. & De Kroon, H. (2004b) Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. *Ecology Letters*, **7**, 623–631.
- Maestre, F.T. & Cortina, J. (2004) Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceedings of the Royal Society of London*, **B271**(Suppl.), S331–S333.
- Maestre, F.T., Bautista, S., Cortina, J. & Bellot, J. (2001) Potential for using facilitation by grasses to establish shrubs on a semiarid degraded steppe. *Ecological Applications*, **11**, 1641–1655.
- 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., Valladares, F. & Reynolds, J.F. (2006) The stress-gradient hypothesis does not fit all relationships between plant-plant interactions and abiotic stress: further insights from arid environments. *Journal of Ecology*, **94**, 17–22.
- Maestre, F.T., Escobar, C., Martínez, I. & Escudero, A. (2008) Are soil lichen communities structured by biotic interactions? A null model analysis. *Journal of Vegetation Science*, **19**, 261–266.
- 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. (1994) Direct and indirect species interactions in an early old-field plant community. *American Naturalist*, **143**, 1007–1025.
- Miriti, M.N. (2006) Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology*, **94**, 973–979.
- Pierce, S., Luzzaro, A., Caccianiga, M., Ceriani, R.M. & Cerabolini, B. (2007) Disturbance is the principal α -scale filter determining niche differentiation, coexistence and biodiversity in an alpine community. *Journal of Ecology*, **95**, 698–706.
- Pugnaire, F.I. & Luque, M.T. (2001) Changes in plant interactions along a gradient of environmental stress. *Oikos*, **93**, 42–49.
- Raffaële, E. & Veblen, T.T. (1998) Facilitation by nurse shrubs of resprouting behavior in a post-fire shrubland in northern Patagonia, Argentina. *Journal of Vegetation Science*, **9**, 693–698.
- Rebele, F. (2000) Competition and coexistence of rhizomatous perennial plants along a nutrient gradient. *Plant Ecology*, **147**, 77–94.
- Reynolds, J.F., Kemp, P.R. & Tenhunen, J.D. (2000) Effects of long-term rainfall variability on evapotranspiration and soil water distribution in the Chihuahuan Desert: a modeling analysis. *Plant Ecology*, **150**, 145–159.
- 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-Gómez, D., Valladares, F. & Zavala, M.A. (2006) Performance of seedlings of Mediterranean woody species under experimental gradients of irradiance and water availability: trade-offs and evidence for niche differentiation. *New Phytologist*, **170**, 795–806.
- Taylor, D.R., Aarssen, L.W. & Loehle, C. (1990) On the relationship between r/K selection and environmental carrying capacity: a new habitat template for plant life history strategies. *Oikos*, **58**, 239–250.
- Tewksbury, J. & Lloyd, J.D. (2001) Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia*, **127**, 425–434.

- Tielbörger, K. & Kadmon, R. (2000) Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology*, **81**, 1544–53.
- Valiente-Vanuet, A. & Verdú, M. (2008) Temporal shifts from facilitation to competition occur between closely related taxa. *Journal of Ecology*, **96**, 489–494.
- Valladares, F. & Pearcy, R.W. (2002) Drought can be more critical in the shade than in the sun: a field study of carbon gain and photoinhibition in a Californian shrub during a dry El Niño year. *Plant Cell and environment*, **25**, 749–759.
- Vilagrosa, A., Bellot, J., Vallejo, V.R. & Gil-Pelegrín, E. (2003) Cavitation, stomatal conductance, and leaf dieback in seedlings of two co-occurring Mediterranean shrubs during an intense drought. *Journal of Experimental Botany*, **54**, 2015–2024.
- Wang, Y.S., Chu, C.J., Maestre, F.T. & Wang, G. (2008) On the relevance of facilitation in alpine meadow communities: an experimental assessment with multiple species differing in their ecological optimum. *Acta Oecologica*, **33**, 108–113.
- Wellstein, C., Otte, A. & Waldhardt, R. (2007) Seed bank diversity in mesic grasslands in relation to vegetation type, management and site conditions. *Journal of Vegetation Science*, **18**, 153–162.
- Wilson, S.D. & Keddy, P.A. (1986) Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. *American Naturalist*, **127**, 862–869.
- Zelnik, I. & Čarni, A. (2008) Distribution of plant communities, ecological strategy types and diversity along a moisture gradient. *Community Ecology*, **9**, 1–9.

Received: 22 September 2008; accepted: 10 December 2008

Handling Editor: David Gibson