Disentangling the effects of water and nutrients for studying the outcome of plant interactions in sand dune ecosystems

Yoann Le Bagousse-Pinguet, Estelle Forey, Blaise Touzard & Richard Michalet

Le Bagousse-Pinguet, Y. (corresponding author, y.b-pinguet@orange.fr): Limnological Institute, University of Konstanz, Mainaustrasse 252, 78464, Constance, Germany

Le Bagousse-Pinguet, Y. & **Touzard, B.** (b.touzard@ecologie.u-bordeaux1.fr): University of Bordeaux 1, UMR INRA 1202 BIOGECO, Avenue des Facultés, 33405, Talence Cedex, France

Forey, E. (estelle.forey@univ-rouen.fr): Ecology Lab, University of Rouen, EA 1293 ECODIV, FED SCALE, UFR Sciences et Techniques, 76821, Mont Saint Aignan Cedex, France

Michalet, R. (r.michalet@ecologie.u-bordeaux1.fr): University of Bordeaux 1, UMR 5805 EPOC, Avenue des Facultés, 33405, Talence cedex, France

Abstract

Questions: What is the relative role of water vs nutrients in driving changes in plant interactions in a dry and nutrient-poor dune system, where facilitation has been shown to highly contribute to the diversity and composition of plant communities?

Location: Atlantic coastal sand dune system, Aquitaine region, France.

Methods: We manipulated water (water addition) and nutrient (fertilizer addition) availabilities in a full-factorial experiment that lasted from September 2005 to September 2006. The responses of plants to neighbours were assessed through transplanting six target species within each experimental plot in the presence or absence (removal procedure) of the dominant shrub *Helichrysum stoechas*. We also measured changes in *H. stoechas* biomass among treatments.

Results: Watering mainly affected survival of the target species without neighbours and the direction of their responses to the shrub, whereas fertilization strongly increased the biomass of the shrub and intensity of the responses of the targets to the effects of the shrub. We did not observe any occurrence of biotic interactions (either positive or negative) for most of the target species in the unfertilized plots. In contrast, three of the six species exhibited significant facilitation in fertilized and un-watered plots, and significant competition in fertilized and watered plots.

Conclusions: Our results highlight the co-limitation of water and nutrients in coastal sand dunes. Nutrient availability mainly drove the neighbour effect of the shrub, whereas water availability affected the responses of the target species. Although further measurements of resource modifications by the shrub are needed to firmly conclude neighbour effects, our results provide new insights to the contrasting results in the literature on plant–plant interactions in unproductive communities. We propose that, depending on the system, changes in a given direct stress factor may either induce a collapse of interactions by decreasing neighbour performances and their effects, or a shift in the direction of interactions by affecting target species responses.

Introduction

Early theoretical models proposed that direct facilitation (as opposed to indirect facilitation *sensu* Levine 1999) should be more frequent in communities subjected to high physical disturbance or stress (Bertness & Callaway 1994; Callaway & Walker 1997; Holmgren et al. 1997; Brooker & Callaghan 1998). In contrast, competition is known to be the dominant interaction occurring in productive habitats (Grime 1973). Although most experimental studies have supported this latter prediction (Callaway et al. 2002; see reviews of Callaway 2007; Brooker et al. 2008), a number of studies have conversely found a shift from positive to negative interactions with increasing drought stress (Tielborger & Kadmon 2000; Maestre & Cortina 2004) or a collapse of positive interactions in extremely severe conditions (Kitzberger et al. 2000; de Bello et al. 2011). The meta-analysis of Maestre et al. (2005), showing that

facilitation does not overall increase significantly with increasing drought in water-stressed ecosystems, triggered an important debate on the robustness of the stress gradient hypothesis (SGH hereafter; Lortie & Callaway 2006; Maestre et al. 2006, 2009; Michalet 2006, 2007; Homgren & Scheffer 2010; Malkinson & Tielbörger 2010). Some authors have highlighted the importance of the strategy developed by both the benefactor and the beneficiary species (Liancourt et al. 2005a; Gomez-Aparicio et al. 2008; Maestre et al. 2009; Forey et al. 2010), the type of mechanism involved in the interaction (i.e. resource vs non-resource factors; Michalet 2007; Maestre et al. 2009; Saccone et al. 2009) or the feedback effects of neighbouring plants on local limiting factors (Gross et al. 2010; Soliveres et al. 2011). Although these contributions have certainly improved our knowledge of the different mechanisms of interactions operating in particular systems, there is still no overall consensus on the relative importance of facilitation for the diversity of plant communities in water-stressed ecosystems.

Interestingly, this debate is rather similar to the so-called Grime–Tilman competition debate. In both the Grime (1973) and Bertness & Callaway (1994) models, the importance of competition among plants drops with the decrease in productivity, whereas competition may still be intense in low-resource conditions according to both Tilman (1982) and Maestre et al. (2003, 2005). Some interesting advances were made during the Grime–Tilman debate in terms of our knowledge of variations in competition through disentangling direct factors along complex productivity gradients (Goldberg & Barton 1992; Goldberg & Novoplansky 1997; Liancourt et al. 2005b). Most of the experiments analysing changes in competition along natural productivity gradients rather support the Grime model, whereas most experiments using experimental gradients, conversely, support the Tilman model (Goldberg & Barton 1992). Among several explanations, these authors stressed several direct factors, such as water and nutrient change, along natural complex gradients (Gurevitch et al. 1992), whereas mostly nutrients have been manipulated along experimental gradients (Wilson & Tilman 1991). Similarly, most facilitation studies testing the SGH in water-stressed ecosystems have used natural productivity gradients, which are expected to be mainly driven by changes in water availability. Although nutrient availability is also very likely to vary along such gradients, to our knowledge, no studies have attempted to experimentally separate the effects of the two resources for understanding variations in positive interactions. To illustrate this statement, fertilization has already been shown to shift the effects of vegetation in response to water availability from negative to positive in water-limited grasslands and to impact the outcome of biotic interactions (Gross et al. 2009).

The main objective of our study is to experimentally disentangle the respective roles of nutrient and water stress in driving plant interactions, and in particular facilitation in unproductive communities. We chose the coastal sand dunes in the southwest of France (Aquitaine region), and in particular the stable grey dune community in the centre of Aquitaine, because this extremely unproductive community is primary limited by water and nutrient stresses (Forey et al. 2008, 2009). Furthermore, facilitation has been shown to be an important driver of community diversity and composition in this system (Forey et al. 2009, 2010). We watered and fertilized this community in a fully factorial design and transplanted six species likely to differ in stress tolerance ability due to their contrasting origin within the coastal dune system. Target species were transplanted either within or without the dominant shrub species, *Helichrysum stoechas* (L), using a removal procedure, and the biomass of the nurse shrub was measured in all environmental conditions in order to also indirectly assess variations in neighbour effects. Due to the lack of studies with similar goals, we do not have any *a priori* hypotheses on variations in the outcomes of interactions in this experiment with alleviation of water and/or nutrient stresses. Nonetheless, we might expect that water would rather affect the target species survival, whereas nutrient availability might impact plant growth (Goldberg & Novoplansky 1997; Goldberg et al. 2001; Liancourt et al. 2009). As we used mature individuals as the nurse shrubs, it is likely that they will be mainly impacted by nutrient availability for their growth and size, potentially affecting their effects on target species (Violle et al. 2009; Gross et al. 2010; Soliveres et al. 2011).

Methods

Study site

The experimental site was located in the central part of the Aquitaine Atlantic coastal dunes, 50 km west of Bordeaux (France), in the vicinity of Le Truc Vert (44° 43′ N, 01° 14′ W). The climate is temperate oceanic, mean annual precipitation is 875 mm with the rainiest period during winter. From the different types of coastal dune communities occurring at each site (Forey et al. 2008), we focused on the community that was least disturbed by sand deposition, located close to the forest and termed 'grey dunes'. Environmental stress (nutrient and water limitation) is very high in this community (Forey et al. 2008) because of the coarse sandy texture of the soils (Martinez & Psuti 2004). Species richness in the grey dunes in the centre of Aquitaine is approximately eight species per square meter, whereas it is 50% higher in the south of Aquitaine where nutrient and water stress are much lower (Forey et al. 2008).

Target species

Helichrysum stoechas (L), an evergreen chamaephyte, dominates the community and, in association with lichens, forms large grey patches on the soil surface. We chose *H. stoechas* as the potentially interacting species. This dominant perennial has been shown to strongly interact with beneficiary species and to structure plant communities (Forey et al. 2009, 2010).

To measure beneficiary species responses to the effects neighbouring *H. stoechas*, we selected six different target species with contrasting distributions and ecological requirements in the coastal sand dunes of Aquitaine: *Festuca vasconensis* (Markgr.-Dann) Auquier & Kerguelen, *Senecio inaequidens* (DC.), *Pancratium maritimum* (L.), *Cistus salvifolius* (L.), *Elymus farctus* (Viv.) Runemark ex Melderis and *Oenothera biennis* (L.). *E. farctus* is a ruderal/stress-intolerant species mostly found in the foredune communities, i.e. the most physically disturbed but least stressful conditions of this dune system. The five other species only occur in the stable grey dune communities. *F. vasconensis*, *P. maritimum* and *S. inaequidens* are only present in the wettest grey dunes of the region, located on the south Aquitaine coast, whereas *C. salvifolius* and *O. biennis* also occur in the most stressful grey dunes of the central and northern Aquitaine coast (Forey et al. 2008).

Experimental design

Our experiment lasted from September 2005 to September 2006 and included 28 experimental plots (5 × 5 m) randomly established within the grey dune community. All plots were located in flat areas, with a distance of at least 20 m between plots. The fertilization (with and without additional nutrients) and watering (with and without additional water) treatments were crossed fully factorially to produce four treatment combinations, i.e. control plots (no fertilization and no water: control), plots with fertilization (+F), plots with water (+W) and plots with fertilization and water (+F+W). Seven replicates for each of the four treatment combinations were randomly established in the 28 experimental plots.

In order to test the effects of fertilization, +F and +F+W treatment combinations were prepared by adding 60 g·m^{-2} (72 kg·N·ha^{-1}) of a slow-release granular NPK (12-12-17+ micro-elements) fertilizer, twice during the experiment: December 2005 and March 2006. In order to test the effect of watering, we added to the +W and +F+W treatment combinations 5 L·m^{-2} of water every 7 d between 08:00 and 10:00 h during the dry season (from March 2006 to September 2006), a level chosen to approximate a 50% increase of rainfall during the growing season.

We used both removal and transplantation procedures to assess the responses of our six target species to the effects of *H. stoechas* (neighbour presence). Thirty-six individuals of the nurse species *H. stoechas* were randomly selected in each of the 28 plots. Half of them were clipped to ground level. All above-ground biomass present within a radius of 20 cm around each removed nurse individual was eliminated from the plots, and we trenched all roots around the edge of the biomass removal areas.

Individuals of each of the six target species were collected in natural communities and directly transplanted in mid-September 2005. Before planting, shoots of all target species were standardized by cutting them back to a height of 5 cm. In each plot, three individuals of each target species were randomly transplanted beneath the 18 neighbouring *H. stoechas* and three individuals of each target species randomly in the 18 nurse removal areas. We assumed that during the experiment, interactions among target individuals were negligible due to their small biomass as compared to the dense *H. stoechas* neighbouring plants and due to the distance between target individuals (at least 20 cm).

In total, 1008 target individuals were planted [(4 treatment combinations × 7 replicates × 2 neighbouring combinations × 6 beneficiary species × 3 individuals of each beneficiary species].

Data collection

Target species performance (survival and biomass) without neighbours was used to assess individual responses to abiotic stress factors, i.e. fertilization and watering. Survival and biomass for all treatments was recorded after 1 yr, in late September 2006. Target plants were harvested and their biomass determined by drying at 70 °C for 72 h before weighing. Survival of target plants was calculated as a percentage of surviving individuals for each species per plot. We did not analyse growth data because survival was too low.

The response of the six target species to the effect of neighbours, i.e. the proportional change in survival due to the presence of *H. stoechas* neighbours, was quantified separately for each treatment combination (Control, +F, +W and +F+W) using the relative interaction index (RII; Armas et al. 2004):

$$\text{RII}_{\text{survival}} = \frac{\text{Survival}_{\text{with neighbours}} - \text{Survival}_{\text{without neighbours}}}{\text{Survival}_{\text{with neighbours}} + \text{Survival}_{\text{without neighbours}}}.$$
$$(1)$$

Relative interaction index values were calculated using the percentage survival per plot and per species with and without neighbours. Values of RII are symmetrical around 0; i.e. no difference from 0 indicates that the presence of

neighbours had no effect on target survival; negative values indicate competition, positive values indicate facilitation.

In order to indirectly assess the effects of neighbours on our target species, we also measured, in all treatment combinations, the above-ground biomass increment of *H. stoechas* (BI) during the experiment using the following formula:

$$BI = \text{final biomass} - \text{initial biomass} \qquad (2)$$

In each plot, we randomly chose five individuals of *H. stoechas*, both before and at the end of the experiment (December 2005 and September 2006, respectively). Samples were dried at 65 °C for 72 h and weighed. Individuals used were different from those used to quantify biotic interactions. In addition, the height (H) and two perpendicular measurements of the breadth (L and l) of all nurse individuals used to quantify biotic interactions were recorded before and at the end of the experiment to determine their volume increment (VI). The volume of each nurse individual was estimated using the following formula:

$$VI = H \times L \times l \qquad (3)$$

Data analysis

Survival without neighbours and RII were analysed using a three-way ANOVA model with fertilization, watering and species as fixed factors. Tukey's HSD tests were used to determine significant differences between treatment means when significant effects occurred. One-sample *t*-tests were also used to test significant deviations from zero for RII values. We also conducted two-way ANOVA to test the effects of fertilization, watering and their interactions on the BI and VI values of *H. stoechas*. Survival of target species and BI and VI values of *H. stoechas* were log-transformed before analyses. Residuals of all statistical models met parametric assumptions of normality and homogeneity. All analyses were done using JMP software 7.0 (SAS Institute, Cary, NC, US).

Results

Target species responses to watering and fertilization in the absence of neighbours

In the absence of neighbours, the survival of targets was highly species-specific (Table 1), with three species (*O. biennis*, *S. inaequidens* and *C. salvifolius*) having lower survival than the other three species (Fig. 1). Watering significantly increased species' survival ($P \leq 0.001$; Table 1), but fertilization did not have any significant effect ($P > 0.05$). Furthermore, there was no significant

interaction among treatments, i.e. between watering, fertilization and species treatments.

Relative interaction index

In the control plots, RII for survival were not significantly different from zero, except for *E. farctus*, which had a positive RII value (one-sample *t*-test; Fig. 2). Watering overall decreased RII values, but this effect was species-dependent (watering × species interaction; Table 1). We observed a decrease in RII values with watering for *P. maritimum*, *S. inaequidens*, *E. farctus* and *C. salvifolius* (one-sample *t*-test; Fig. 2) There was also a significant fertilization × watering interaction on RII values (Table 1), with an overall tendency for RII values to increase in the fertilized un-watered plots and to decrease in the fertilized watered plots (Fig. 2).

Changes in *H. stoechas* size and biomass with watering and fertilization

Fertilization induced a 150% increase in biomass of *H. stoechas* (Fig. 3a), whereas unfertilized *H. stoechas* did not produce any significant biomass increment during the experiment (Fertilization effect on BI; $F_{15,12} = 20.92$, $P < 0.001$). In contrast, watering did not affect the biomass increment of *H. stoechas* ($F_{15,12} = 0.005$, $P = 0.947$) and there was no significant statistical interaction between watering and fertilization ($F_{15,12} = 0.41$, $P = 0.534$). The same trend was recorded for the volume increment of *H. stoechas* (Fig. 3b), although this fertilization effect was weaker and less significant than that found for the biomass increment ($F_{15,12} = 7.08$, $P = 0.019$).

Table 1. Results of the three-way ANOVA models for the effects of fertilization, watering, species and their interactions on survival without neighbours (left) and the relative interaction index (RII) for survival (right).

Source of variations	Survival_{without neighbours}			RII_{survival}		
	df	F	P	df	F	P
Fertilization	1	0.008	0.93	1	1.36	0.24
Watering	1	12.54	**<0.001***	1	6.63	**0.01**
Species	5	16.83	**<0.001***	5	1.63	0.16
Fertilization × Watering	1	0.90	0.34	1	4.16	**0.04***
Watering × Species	5	0.74	0.59	5	3.19	**0.009**
Fertilization × Species	5	0.58	0.26	5	0.37	0.86
Fertilization × Watering × Species	5	0.28	0.93	5	1.99	0.08
Error model	144			144		

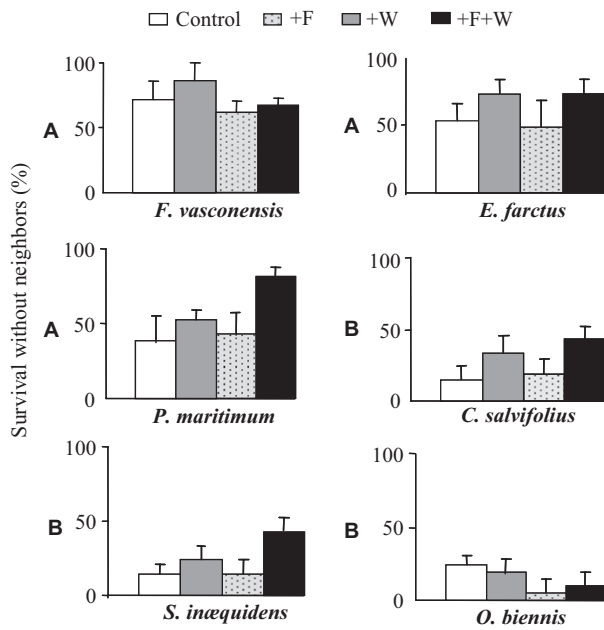Significant ($P < 0.05$) effects are indicated in bold. Asterisks help the readers see the significance of the results.

Fig. 1. Survival without neighbours (means ± SE) of the six target species (*Festuca vasconensis, Elymus farctus, Pancratium maritimum, Cistus salvifolius, Senecio inaequidens* and *Oenothera biennis*) in the four treatment combinations: control (white bars), +W (grey bars), +F (grey with dots) and +F+W (black bars; *n* = 7). Capital letters indicate significant means contrasts among species at *P* < 0.05 (post-ANOVA Tukey HSD test).

Fig. 2. Relative interaction index (RII) for survival (means ± SE) of the six target species (*Festuca vasconensis, Elymus farctus, Pancratium maritimum, Cistus salvifolius, Senecio inaequidens* and *Oenothera biennis*) in the four treatment combinations: control (white bars), +W (grey bars), +F (grey with dots) and +F+W (black bars; *n* = 7). Capital letters indicate significant means contrasts among species at *P* < 0.05 (post-ANOVA Tukey HSD test). Stars below bars indicate significant deviation from zero value (one-sample *t*-tests); ns: not significant, *P* < 0.05, **P* < 0.01.

Discussion

The main objective of our experiment was to assess if the alleviation of nutrient or/and water stresses differently affected plant interactions in a dry and nutrient-poor dune system. Our results indicated that both water and nutrients are co-limiting resources in our system. Watering affected (1) positively the survival of target species in the absence of neighbours, and (2) the direction of their responses (mainly from positive to negative responses) to the presence of the nurse shrub *H. stoechas* in fertilized conditions. In contrast, fertilization positively affected the biomass of the nurse shrub and drove the effects of the nurse shrub on the target species. Thus, our results suggest that variations in two types of stress affected different components of the biotic interactions.

Water availability: a driving factor of target species responses

In the absence of neighbours, watering significantly increased the survival of our target species, while fertilization had no effect (Fig. 1). Several authors have found that water stress primarily drives plant survival, whereas nutrient stress primarily affects plant growth
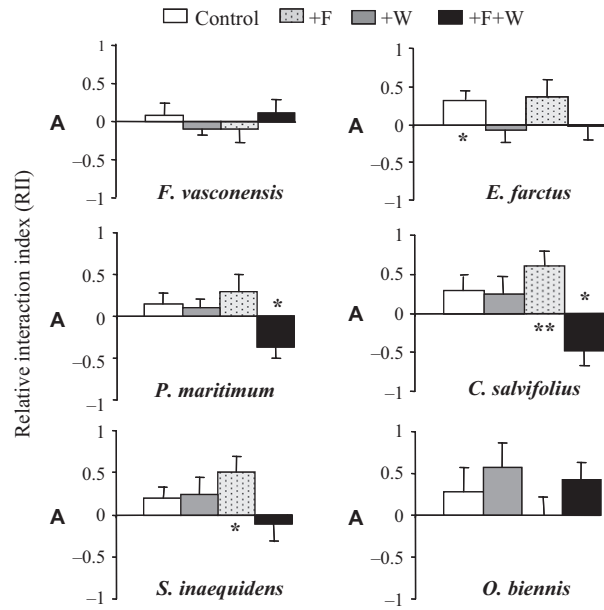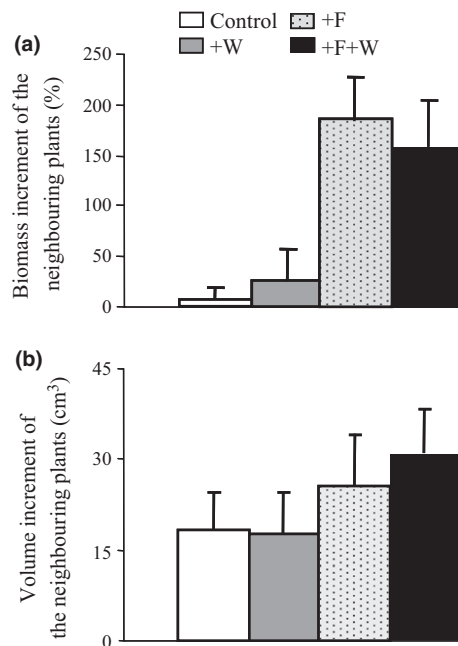

Fig. 3. Biomass (**a**) and volume (**b**) increments of the neighbouring plants in the four treatment combinations: control (white bar), +W (grey bar), +F (grey bar with dots) and +F+W (black bar).

(Goldberg & Novoplansky 1997; Goldberg et al. 2001; Liancourt et al. 2005b). Our results for survival are consistent with these studies, but we could not analyse growth data, due to very low target survival, to fully support the findings in the literature. Our results show that water was highly limiting in the dry grey dune community. Although our six transplanted target species certainly differ in their drought tolerance due to their contrasting climatic origins in the regional dune system (Forey et al. 2008), there was no interaction between the species and watering treatment. This suggests that, even for the most drought-tolerant species (i.e. the species naturally occurring at the site), water availability in the un-watered plots was below the optimal water requirement (Liancourt et al. 2005a) and/or that more replication was needed for differences among species to show up.

In the fertilized plots only, watering shifted overall target responses to neighbours from positive to negative (Fig. 2). Fertilization alone increased the biomass of the nurse shrubs, increasing their positive effect on water availability. In contrast, watering alleviated the stress for the target species, which likely experienced the competitive effect of the shrub for light. Thus, water availability, but not nutrient availability, drove the overall direction of the responses to neighbours. The increase in competition with decreasing water stress has been found in other papers where water or shade have been manipulated in dry ecosystems (Kadmon 1995; Corcket et al. 2003; Liancourt et al. 2005a), and supports Grime' (1974) theory predicting that competition should be important in low-stress conditions. The switch to facilitation in stressful conditions is also consistent with the SGH (Bertness & Callaway 1994). In contrast, our results contradict the findings of a number of studies conducted in water-stressed ecosystems, which found a shift from positive to negative interactions with increasing water stress in very dry conditions (Davis et al. 1998; Tielborger & Kadmon 2000; Maestre & Cortina 2004) or a collapse of positive interactions (Kitzberger et al. 2000).

This effect was obvious for three of the six target species, which were facilitated in the un-watered, fertilized plots (*C. salvifolius* and *S. ineaquidens*) and/or suppressed by competition in the watered and fertilized plots (*C. salvifolius* and *P. maritimum*). Although the species × watering × fertilization was only marginally significant, the three other species did not show a shift from positive to negative interactions with decreasing water stress in the fertilized plots. Many authors have shown that species responses to interactions are dependent on both their stress tolerance and competitive abilities, and the position of the experimented community within their realized niches (Welden & Slauson 1986; Choler et al. 2001; Liancourt et al. 2005a; Michalet et al. 2006; Michalet 2007;

Forey et al. 2010; Saccone et al. 2010; Le Bagousse-Pinguet et al. 2012a). Thus, within a given community, only species that deviated from their optimal conditions are likely to experience facilitation, while stress-tolerant species may suffer from competition (Gross et al. 2010). Our results on survival without neighbours showed that our six target species deviated from their optimal conditions in the community and that watering reduced this deviation. Results on responses to neighbours showed that the effect of *H. stoechas* also decreased this deviation, particularly in three of these species. It is very likely that facilitation was related to decreasing water stress in the microhabitat of the canopy of the shrub. This suggests that those three species were more sensitive to water stress, although this was not shown in our results for target survival without neighbours.

Nutrient availability: a likely driving factor of neighbour effects

Interestingly, the switch from facilitation to competition with watering was only observed in the fertilized plots, whereas almost no significant interactions occurred in the unfertilized plots. Fertilization also strongly increased the biomass and canopy volume of *H. stoechas*, whereas watering had no effect on this shrub. Together, these results provide strong arguments that nutrient availability, but not water availability, is likely the driving factor of the neighbour effects.

Neighbour effects have rarely been specifically assessed in interaction studies, which have mostly focused on species responses to neighbours, although some authors have stressed the need to separate the two components in competition studies (Gaudet & Keddy 1988; Goldberg 1990, 1996; Suding et al. 2003, 2008; Liancourt et al. 2009; Violle et al. 2009). Such attempts are even more rare in facilitation studies (Gross et al. 2009). We acknowledge that in our experiment, neighbour effects were only indirectly measured, because straightforward assessments of such effects would include measurements of resource modification by the neighbours (Goldberg 1990; Crain 2005; Violle et al. 2009; Gross et al. 2010). However, because our results on survival without neighbours demonstrated that nutrient addition had no effects on the target species but only on the neighbour species, we suggest that changes in target species responses to neighbours with fertilization were primarily due to changes in neighbour effects.

Insights into the SGH debate

Forey et al. (2010) showed, along a coast to inland sand deposition gradient, that physical disturbance induced by burial under sand was the direct factor driving neighbour

effects but that the direction of interactions was rather species-dependent. No plant interaction occurred in the most disturbed community, whereas in the least disturbed community there were facilitative responses in drought-intolerant species and competitive responses in drought-tolerant species. Together, their and our results show that, depending on the constraints of a system, changes in a given direct factor may either induce a decrease in neighbour biomass, and thus benefactor effects on target species, or a switch in the direction of interactions by affecting the stress experienced by the target species (Gross et al. 2010). Thus, if the complex environmental gradient under study is mainly driven by changes in an 'effect factor' (e.g. nutrients in our study, or disturbance), the likely outcome of plant interactions at the most severe end of the gradient will be a collapse of interactions (Michalet et al. 2006). Similar drops in plant interactions due to a decrease in nurse effects have also been recently shown along grazing disturbance gradients in terrestrial (Barraza et al. 2006; Brooker et al. 2006), marine (Bullieri et al. 2011) and freshwater (Le Bagousse-Pinguet et al. 2012b) ecosystems. In contrast, in another complex gradient mainly driven by a 'response factor' (e.g. water in our study), the most predictable outcome will be a shift in the direction of interactions along the gradient. In this latter scenario several studies suggest that either competition or facilitation may occur at the severe end of the gradient, depending on whether the stress factor is a resource or a non-resource factor, respectively (Michalet 2007; Maestre et al. 2009; Saccone et al. 2009). The direction of plant interactions may also be dependent on the deviation experienced by the target species in the studied community (Liancourt et al. 2005a; Gross et al. 2010; Le Bagousse-Pinguet et al. 2012a). Thus, by showing that different direct factors can either affect the beneficiary responses or the benefactor responses, our results highlight that disentangling direct factors within complex environmental and productivity gradients is a promising research avenue for understanding the role of both competition and facilitation in severe and low-productive environmental conditions.

Acknowledgements

References

Armas, C., Ramón, O. & Pugnaire, F.I. 2004. Measuring plant interactions: a new comparative index. *Ecology* 85: 2682–2686.

Barraza, E., Zamora, R. & Hodar, J.A. 2006. Conditional outcomes in plant–herbivore interactions: neighbours matter. *Oikos* 113: 148–156.

Bertness, M.D. & Callaway, R.M. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9: 191–193.

Brooker, R.W. & Callaghan, T.V. 1998. The balance between positive and negative plant interactions and relationship to environmental gradients: a model. *Oikos* 81: 196–201.

Brooker, R.W., Scott, D., Palmer, S.C.F. & Swaine, E. 2006. Transient facilitative effects of heather on Scots pine along a grazing disturbance gradient in Scottish moorland. *Journal of Ecology* 94: 637–645.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.J., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielborger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, F., Kikvidze, Z., Olofson, J., Pugnaire, F.I., Saccone, P., Schiffer, K., Seifan, M., Tourzard, B. & Michalet, R. 2008. Facilitation in plant communities: the past, the present and the future. *Journal of Ecology* 96: 18–24.

Bullieri, F., Cristaudo, C., Alestra, T. & Benedetti-Cecchi, L. 2011. Crossing gradients of consumer pressure and physical stress on shallow rocky reefs: a test of the stress gradient hypothesis. *Journal of Ecology* 99: 335–344.

Callaway, R.M. 2007. *Positive interactions and interdependence in plant communities*. Springer, Dortrecht, NL.

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., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Ascheboug, E.T., Armas, C., Kikodze, D. & Cook, B.J. 2002. Interdependence among alpine plants increases with stress: a global model. *Nature* 417: 844–848.

Choler, P., Michalet, R. & Callaway, R.M. 2001. Competition and facilitation on gradients in alpine communities. *Ecology* 82: 3295–3308.

Corcket, E., Callaway, R.M. & Michalet, R. 2003. Insect herbivory and grass competition in a calcareous grassland: results from a plant removal experiment. *Acta Oecologica* 24: 139–146.

Crain, J.M. 2005. Reconciling plant strategy theories of Grime and Tilman. *Journal of Ecology* 93: 1041–1052.

Davis, M.A., Wrage, K.J. & Reich, P.B. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *Journal of Ecology* 86: 652–661.

de Bello, F., Doležal, J., Dvorský, M., Chlumská, Z., Řeháková, K., Klimešová, J. & Klimeš, L. 2011. Cushions of *Thylacospermum caespitosum* (*Caryophyllaceae*) do not facilitate other plants under extreme altitude and dry conditions in the north-west Himalayas. *Annals of Botany* 108: 567–573.

Forey, E., Chapelet, B., Vitasse, Y., Tilquin, M., Touzard, B. & Michalet, R. 2008. The relative importance of disturbance and environmental stress at local and regional scales in French coastal sand dunes. *Journal of Vegetation Science* 19: 493–502.

Forey, E., Lortie, C.J. & Michalet, R. 2009. Spatial patterns of association at local and regional scales in coastal sand dune communities. *Journal of Vegetation Science* 20: 916–925.

Forey, E., Touzard, B. & Michalet, R. 2010. Does disturbance drive the collapse of biotic interactions at the severe end of a diversity–biomass gradient? *Plant Ecology* 206: 287–295.

Gaudet, C.L. & Keddy, P.A. 1988. A comparative approach to predicting competitive ability from plant traits. *Nature* 334: 242–243.

Goldberg, D.E. 1990. Components of resource competition in plant communities. Grace, J.B., Tilman, D. (eds.) *Perspectives on plant competition*, pp. 357–364. Academic Press, San Diego, CA, US.

Goldberg, D.E. 1996. Competitive ability in plants: consistency, contingency and correlated traits. *Philosophical Transactions of the Royal Society of London, Series B* 351: 1377–1385.

Goldberg, D.E. & Barton, A.M. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *The American Naturalist* 139: 771–801.

Goldberg, D.E. & Novoplansky, A. 1997. On the relative importance of competition in unproductive environments. *Journal of Ecology* 85: 409–418.

Goldberg, D.E., Turkington, R., Olsvig-Whittaker, L. & Dyer, A.R. 2001. Density dependence in an annual plant community: variation among life history stages. *Ecological Monographs* 71: 423–446.

Gomez-Aparicio, L., Zamora, R., Castro, J. & Hodar, J.A. 2008. Facilitation of tree saplings by nurse plants: microhabitat amelioration or protection against herbivores? *Journal of Vegetation Science* 19: 161–172.

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344–347.

Grime, J.P. 1974. Vegetation classification by reference to strategies. *Nature* 250: 26–31.

Gross, N., Kunstler, G., Liancourt, P., de Bello, F., Suding, K.N. & Lavorel, S. 2009. Linking individual response to biotic interactions with community structure: a trait-based framework. *Functional Ecology* 23: 1167–1178.

Gross, N., Liancourt, P., Choler, P., Suding, K.N. & Lavorel, S. 2010. Strain and vegetation effects on local limiting resources explain the outcomes of biotic interactions. *Perspectives in Plant Ecology, Evolution and Systematics* 12: 9–49.

Gurevitch, J., Morrow, L.L., Wallace, A. & Walsh, J.S. 1992. A meta-analysis of competition in field experiments. *The American Naturalist* 140: 539–572.

Holmgren, M., Scheffer, M. & Huston, M.A. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78: 1966–1975.

Homgren, M. & Scheffer, M. 2010. Strong facilitation in mild environments: the stress gradient hypothesis revisited. *Journal of Ecology* 98: 1269–1275.

Kadmon, R. 1995. Plant competition along soil moisture gradients: a field experiment with the desert annual *Stipa capensis*. *Journal of Ecology* 83: 253–262.

Kitzberger, T., Steinaker, D.F. & Veblen, T.T. 2000. Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology* 81: 1914–1924.

Le Bagousse-Pinguet, Y., Liancourt, P., Gross, N. & Straile, D. 2012a. Indirect facilitation promotes macrophyte survival and growth in freshwater ecosystems threatened by eutrophication. *Journal of Ecology* 100: 530–538.

Le Bagousse-Pinguet, Y., Gross, E.M. & Straile, D. 2012b. Release from competition and protection determine the outcome of plant interactions along a grazing gradient. *Oikos* 121: 95–101.

Levine, J.M. 1999. Indirect facilitation: evidence and predictions from a riparian community. *Ecology* 80: 1762–1769.

Liancourt, P., Callaway, R.M. & Michalet, R. 2005a. Stress-tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology* 86: 1611–1618.

Liancourt, P., Corcket, E. & Michalet, R. 2005b. Stress-tolerance abilities and competitive responses in a watering and fertilization field experiment. *Journal of Vegetation Science* 16: 713–722.

Liancourt, P., Viard-Cretat, F. & Michalet, R. 2009. Contrasting community responses to fertilization and the role of competitive ability of dominant species. *Journal of Vegetation Science* 20: 138–147.

Lortie, C.J. & Callaway, R.M. 2006. Re-analysis of meta-analysis: support for the stress gradient hypothesis. *Journal of Ecology* 94: 7–16.

Maestre, F.T. & Cortina, J. 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceeding of the Royal Society of London, Series B* 271: 331–333.

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., Callaway, R.M., Valladares, F. & Lortie, C.J. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97: 199–205.

Malkinson, D. & Tielbörger, K. 2010. What does the stress-gradient hypothesis predict? Resolving the discrepancies. *Oikos* 119: 1546–1552.

Martinez, M.L. & Psuti, N.P. 2004. *Coastal dunes: ecology and conservation*. Springer, Berlin, DE.

Michalet, R. 2006. Is facilitation in arid environments the result of direct complex interactions? Commentary. *New Phytologist* 169: 3–6.

Michalet, R. 2007. Highlighting the multiple drivers of change in interactions along stress gradients. *New Phytologist* 173: 3–6.

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.

Saccone, P., Delzon, S., Pages, J.P., Brun, J.J. & Michalet, R. 2009. The role of biotic interactions in altering tree seedling responses to an extreme climatic event. *Journal of Vegetation Science* 20: 403–414.

Saccone, P., Pages, J.P., Girel, J., Brun, J.J. & Michalet, R. 2010. *Acer negundo* invasion along a successional gradient: early direct facilitation by native pioneers and late indirect facilitation by conspecifics. *New Phytologist* 187: 831–842.

Soliveres, S., Eldridge, D.J., Maestre, F.T., Bowker, M.A., Tighe, M. & Escudero, A. 2011. Microhabitat and reduced competition among understorey plants as drivers of facilitation across environmental gradients: towards a unifying framework. *Perspectives in Plant Ecology, Evolution and Systematics* 13: 247–258.

Suding, K.N., Goldberg, D.E. & Hartman, K.M. 2003. Relationship among species traits: separating levels of response and identifying linkages to abundance. *Ecology* 84: 1–16.

Suding, K., Lavorel, S., Chapin, F., Cornelissen, J., Díaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T. & Navas, M.-L. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* 14: 1125–1140.

Tielborger, K. & Kadmon, R. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* 81: 1544–1553.

Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ, US.

Violle, C., Garnier, E., Lecoeur, J., Roumet, C., Podeur, C., Blanchard, A. & Navas, M.L. 2009. Competition, traits and resource depletion in plant communities. *Oecologia* 160: 747–755.

Welden, C.W. & Slauson, W.L. 1986. The intensity of competition versus its importance – an overlooked distinction and some implications. *Quarterly Review of Biology* 61: 23–44.

Wilson, S.D. & Tilman, D. 1991. Components of plant competition along an experimental gradient of nitrogen availability. *Ecology* 72: 1050–1065.