

The importance of biotic interactions and local adaptation for plant response to environmental changes: field evidence along an elevational gradient

FABRICE GRASSEIN*†, SANDRA LAVOREL† and IRÈNE TILL-BOTTRAUD†

*Institute of Plant Sciences, University of Bern, Altenbergrain 21, Bern CH-3013, Switzerland, †Laboratoire d'Ecologie Alpine, CNRS UMR 5553, Université Joseph Fourier, BP53, 38041 Grenoble, Cedex 9, France

Abstract

Predicting the response of species to environmental changes is a great and on-going challenge for ecologists, and this requires a more in-depth understanding of the importance of biotic interactions and the population structuration in the landscape. Using a reciprocal transplantation experiment, we tested the response of five species to an elevational gradient. This was combined to a neighbour removal treatment to test the importance of local adaptation and biotic interactions. The trait studied was performance measured as survival and biomass. Species response varied along the elevational gradient, but with no consistent pattern. Performance of species was influenced by environmental conditions occurring locally at each site, as well as by positive or negative effects of the surrounding vegetation. Indeed, we observed a shift from competition for biomass to facilitation for survival as a response to the increase in environmental stress occurring in the different sites. Unlike previous studies pointing out an increase of stress along the elevation gradient, our results supported a stress gradient related to water availability, which was not strictly parallel to the elevational gradient. For three of our species, we observed a greater biomass production for the population coming from the site where the species was dominant (central population) compared to population sampled at the limit of the distribution (marginal population). Nevertheless, we did not observe any pattern of local adaptation that could indicate adaptation of populations to a particular habitat. Altogether, our results highlighted the great ability of plant species to cope with environmental changes, with no local adaptation and great variability in response to local conditions. Our study confirms the importance of taking into account biotic interactions and population structure occurring at local scale in the prediction of communities' responses to global environmental changes.

Keywords: biotic interactions, elevational gradient, environmental changes, grassland, local adaptation, reciprocal transplantation

Received 29 May 2013; revised version received 30 September 2013 and accepted 13 October 2013

Introduction

Attempts to forecast the impacts of climate change on diversity have generally used the bioclimatic envelope approach to predict species distribution and diversity under future climatic scenarios (Thuiller *et al.*, 2005; Randin *et al.*, 2009). Mountain ecosystems are likely to be very sensitive to climate change (Theurillat & Guisan, 2001; Beniston, 2003), and upward shifts of species can already be observed for trees and alpine species (Walther *et al.*, 2005; Kelly & Goulden, 2008). However, the validity or 'precision' of the bioclimatic approach based mainly on abiotic factors has been questioned by pointing out that many other parameters can determine plant distribution such as species dispersal abilities or biotic interactions (Anderson *et al.*, 2009; Boulangeat *et al.*, 2012).

To have a better understanding of the generality of response to climate change, one approach can be to compare several species or populations as replicates within an ecosystem (Parmesan *et al.*, 2005), and elevational gradients are an interesting case study with a hypothesized decrease of species performance with elevation due to lower temperatures (Körner, 2003). In a survey over a period of 30 years of tree abundance along an elevational gradient, Kelly & Goulden (2008) observed an increase in average elevation for dominant species most likely linked to climate warming (but see Schwilk & Keeley, 2012; Goulden & Kelly, 2012). This increase appeared synchronous between different species, but within species, populations at the trailing and leading edges differed in their response leading to a 'lean' upslope where species range remains constant but the central tendency shifts rather than the expected 'march' upslope where the entire species distribution and its range moves upslope (Peters & Lovejoy, 1992; Breshears *et al.*, 2008). Differences in the response of

Correspondence: Fabrice Grassein, tel. +41 31 631 49 92, fax +41 31 631 49 42, e-mail: fabricegrassein@aim.com
Sandra Lavorel and Irène Till-Bottraud Contributed equally.

populations at trailing and leading edges could be explained by the fact that the lower range limit is determined mostly by biotic interactions such as interspecific competition, while the upper range limit is set by abiotic factors such as temperature or length of growing season (MacArthur, 1972; Pulliam, 2000; Vittoz *et al.*, 2009).

Additionally to MacArthur (1972) view about the importance of competition at the lower range, biotic interactions may play an important role across the entire distribution of a species. The stress gradient hypothesis (SGH, Bertness & Callaway, 1994) predicts an increase in positive interactions (facilitation) with an increase in environmental stresses, such as those occurring at higher elevations in mountains ecosystems. This would favour the incoming of species from lower elevations (Bertness & Callaway, 1994; Choler *et al.*, 2001). Moreover, biotic interactions can modulate the response of species to climate change and are themselves likely to change in response to climate change (Klanderud & Totland, 2005; Thuiller *et al.*, 2008; Hillyer & Silman, 2010; Boulangeat *et al.*, 2012), yet they are still rarely considered in the study of plant response to environmental change.

Within species, individuals from different populations can differ significantly in their optimal environmental conditions for growth and survival. Individuals can thus exhibit large differences in fitness as well as in physiological adaptation to their local environment, and the ultimate output of this specialization of population is local adaptation (Waser & Price, 1985; Kawecki & Ebert, 2004). Local adaptation has been demonstrated in numerous studies using reciprocal transplant experiments along environmental gradients even over short distances or in the presence of gene flow between populations (Byars *et al.*, 2007; Gonzalo-Turpin & Hazard, 2009), although some reciprocal transplant experiments found no consistent evidence for local adaptation (Hereford & Winn, 2008; Byars *et al.*, 2009; Frei, 2013). This local adaptation could limit the ability of populations to respond to rapid environmental change in their own habitat, as well as to colonize new habitats, because of specialization to a limited range of favourable environmental conditions (Davis & Shaw, 2001; Chevin *et al.*, 2013).

The role of interspecific competition is rarely assessed in reciprocal transplant experiments in spite of strong evidence of its role on the performance of transplanted individuals (Rice & Knapp, 2008). In this study, we investigated the combined effects of biotic interactions and local adaptation on species performance in a context of environmental changes. We conducted a reciprocal transplant experiment along an elevational gradient for five co-occurring species dominating at different elevations in the French Alps. The elevational

gradient offers the experimental opportunity to test the consequences of climate change on plant communities (Byars *et al.*, 2007; Hillyer & Silman, 2010). We address the following main questions. (i) To what extent do environmental changes predicted along an elevational gradient affect the performance of plant species? (ii) How does surrounding vegetation affect plant performance in the original and the receiving environment? (iii) Does local adaptation exist within species and, if so, can it influence species' response to environmental change?

Materials and methods

Sites and species of the study

Reciprocal transplants were conducted between three sites, each species coming from two sites each, since no species was present at the three sites (see Fig. 1). The low site is located near Saint Pierre d'Allevard (*Le Planchamp*, Latitude: 45°22'15' N, Longitude: 06°01'25'E, elevation 650 m; hereafter Low) and is dominated by *Bromus erectus* Hudson with *Dactylis glomerata* L. as a co-occurring species. The intermediate site is located in the Romanche valley near the Lautaret Pass (*La Font des Vives*, Latitude: 45°02'02'N, Longitude: 06°22'51'E, elevation 2000 m; hereafter Intermediate) and is dominated by *Festuca paniculata* Schinz and Tell, with other coexisting species including

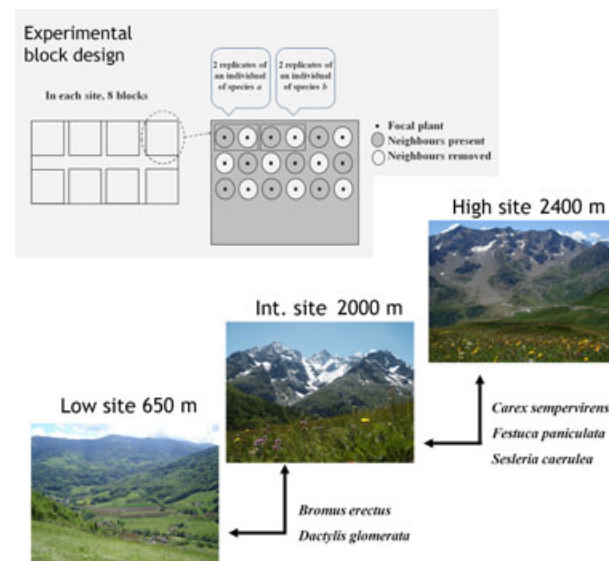


Fig. 1 Description of the reciprocal transplantation design. Two and three species were transplanted, respectively, between the Low and Intermediate (Int.) sites and between the Intermediate and High sites. In each site, blocks were used to take into account micro environmental heterogeneity. Two replicates of every sampled individual and species were present in each block, with a randomly chosen position for individuals within the block. To test the effect of neighbours, we manually removed the vegetation for half of the plants, and replicates of the same individuals with and without neighbours were cultivated close to each other to avoid micro environmental variability.

Bromus erectus, *Dactylis glomerata*, *Carex sempervirens* Vill and *Sesleria caerulea* Ard.. The high site is located along the road to the Galibier pass (Latitude: 45°03'09"N, Longitude: 06°24'11"E, elevation 2400 m; hereafter High) and is dominated by *Sesleria caerulea* with *Carex sempervirens* and *Festuca paniculata* as co-occurring species. Mean annual rainfall at the Low site, located in the external climatic part of the French Alps, is 1537 mm with homogenous distribution along the year and the mean monthly temperatures range from -4 °C in January to 24 °C in July. Mean annual rainfall at the Intermediate site is 960 mm with most of the precipitation during the winter, and the mean monthly temperatures range from -10 °C in January to 20 °C in July. Data are not available at the High site but can be estimated to be colder than Lautaret with more precipitations due to a higher elevation (Körner, 2003) since both sites are close enough to assume that they share similar climatic influences (transition between internal and external climatic zones of the French Alps). In spite of different climates, the three sites are close enough to share the same geology (Crystalline external massif of the Alps, Gidon, 1977) and share similar south orientation, as well as similar management with light grazing by horses, sheep and cows at the Low, Intermediate and High sites, respectively.

Ten individuals for each species and site were collected at least two metres apart in October 2005 in order to have a representative sample of the local genetic diversity. They were stored in an experimental garden in Grenoble during the winter. In April 2006, for planting at the Low site, 24 ramets (1 ramet = 1 tiller) of each individual were isolated, cut to 5 cm for the aerial parts and five centimetres for the roots and planted in plug trays (35 cells, 6 cm diameter). To further reduce the conditioning effect of the environment of origin, plants were cultivated for 1 week in a greenhouse in Grenoble with a soil mixture of ½ potting compost (Castorama®, Grenoble, France) and ½ perlite, and were watered every other day. After 1 week, ramets were transplanted in the field and were watered every day during 1 week to maximize survival. The same protocol was applied for the Intermediate site in June 2006 and the High site in July 2006, with a week of acclimatization at the Station Alpine Joseph Fourier (Lautaret pass, 2100 m) instead of Grenoble.

The experimental design was a random block (8) design at each site (Fig. 1). At each site, the eight blocks were surrounded by electric fences (1 m height, 10 × 10 cm mesh, area covered: from 50 m² to 160 m²) to protect it from herbivores (wild ungulates and domestic stock). To test for the effect of the surrounding vegetation, vegetation was removed around half of the transplanted ramets. For this, we defined evenly spaced circular areas (20 cm in diameter) within each block. Aboveground vegetation was manually removed from half of these areas and was further cleared every 2 weeks during the growing season. Roots were cut (25 cm deep) around the edge of the neighbour removal areas. Areas were disposed following a grid in order to have an area with vegetation adjacent to areas without vegetation (see Fig. 1). One randomly selected individual ramet was transplanted into the centre of each area, with ramets with and without vegetation of a given individual disposed in adjacent areas. Position of species and individuals were randomly assigned within each block. This gave a total

of 10 (individuals) × 2 (populations of origin) × 2 (neighbour treatments) × 8 (replicates or blocks) = 320 transplants for each species (5) in each site (2 for each species) leading to 3200 plants for the whole experiment.

Measurement and analyses

At the vegetation peak of the second growing season (June 2007 for the Low site and July 2007 for the Intermediate and High sites), survival was scored and aerial biomass was collected.

Survival and biomass were analysed for each species separately using ANOVAS with generalized linear model (GLM) with site, population and treatment (neighbour removal) as main effects and their interactions. All effects were treated as fixed. Survival was analysed using a logistic transformation and final biomass was transformed (log or square root transformation) to verify the hypotheses of normality and homogeneity of variance. High mortality precluded the analysis of the effect of individual mother plants. Block effect and initial biomass of transplanted plants were not significant in the models, and were not included in further analyses. Because of significant site × treatment interactions in the global analyses (Table 1), the effect of neighbour removal on survival and biomass was further tested at each site using orthogonal contrasts.

Although we observed no significant interaction of population of origin with treatment or with site × treatment for biomass and survival of all species, ($P \times T$ and $S \times P \times T$ respectively, Table 1), population differentiation was investigated only for individuals without neighbours in order to observe the response of species only to the abiotic environment and to remove any potential confounding effect of the local community (which differed across sites). Local adaptation requires population differentiation (significant population effect) and a significant site × population interaction leading to the fact that the local population is the best in its native site (Kawecki & Ebert, 2004). For each species, population differences and site × population interaction for survival and biomass were tested for individuals cultivated without neighbours using orthogonal contrasts based on GLM ANOVAS testing effects for site, population and their interaction.

All statistical analyses were performed using the R software R 2.14.0 (R Core Team, 2012). We performed type II ANOVA using the 'Car' package (Fox & Weisberg, 2011). Orthogonal contrasts were investigated using the 'multcomp' package (Hothorn *et al.*, 2008). Means and SE for partial effects were estimated for factors plotted in the figures using the 'effects' package (Fox, 2003).

Results

Species response to environmental changes associated with elevation

Plants of *B. erectus* and *D. glomerata* (co-dominant species of the Low site) cultivated at the Intermediate site were smaller and survived less than at the Low site (Table 1;

Table 1 Analyses of variance (ANOVAs) testing the differences between sites, populations, treatments (neighbour removal) and their second and third order interactions for survival (a) and for biomass (b). Degrees of freedom (df), *F* ratio and *P*-values are indicated. Significant *P* values (threshold = 0.05) were indicated in bold

		<i>B. erectus</i>		<i>D. glomerata</i>		<i>C. sempervirens</i>		<i>F. paniculata</i>		<i>S. caerulea</i>	
	df	<i>F</i> ratio	<i>P</i> value	<i>F</i> ratio	<i>P</i> value	<i>F</i> ratio	<i>P</i> value	<i>F</i> ratio	<i>P</i> value	<i>F</i> ratio	<i>P</i> value
(a) Survival											
Site	1	53.544	<0.001	77.828	<0.001	5.673	0.018	54.329	<0.001	0.92405	0.924
Population	1	6.8525	0.009	5.361	0.021	14.401	<0.001	77.05	<0.001	4.064	0.044
S × P	1	1.221	0.269	2.652	0.103	3.84	0.05	0.457	0.4911	0.079	0.778
Treatment	1	1.212	0.271	11.133	<0.001	5.657	0.018	16.295	<0.001	61.634	<0.001
S × T	1	11.523	<0.001	21.719	<0.001	2.486	0.115	1.725	0.189	16.71	<0.001
P × T	1	0.035	0.851	2.314	0.128	0.439	0.507	1.477	0.224	0.716	0.397
S × P × T	1	1.152	0.283	0.47	0.493	1.908	0.167	0.017	0.9	0.232	0.63
(b) Biomass											
Site	1	35.3917	<.0001	28.9311	<.0001	3.3434	0.071	22.8895	<.0001	3.3153	0.071
Population	1	10.8273	0.001	3.7516	0.054	3.3702	0.07	15.8181	<.0001	4.3588	0.039
S × P	1	0.2721	0.6	0.6094	0.436	4.1257	0.045	5.2723	0.022	0.4881	0.486
Treatment	1	20.9815	<.0001	62.5245	<.0001	0.3714	0.544	0.0639	0.801	0.1029	0.749
S × T	1	7.6128	0.007	0.9486	0.331	0.0032	0.955	0.0861	0.769	0.6741	0.413
P × T	1	0.314	0.576	0.9924	0.32	0.0588	0.809	0.9811	0.323	0.4875	0.486
S × P × T	1	0.0415	0.839	1.5865	0.209	1.8132	0.182	0.0024	0.961	2.5946	0.109

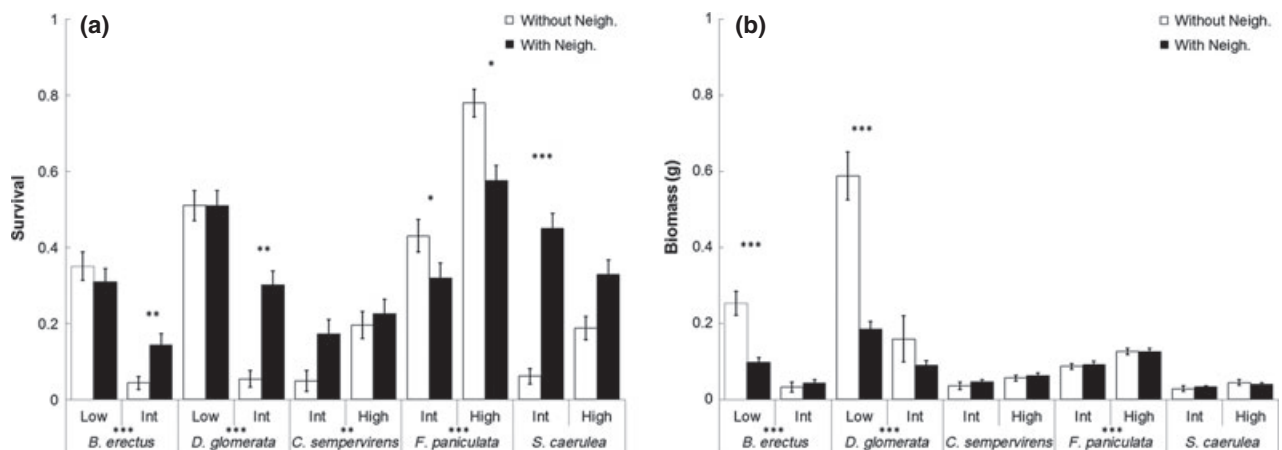


Fig. 2 Effects of neighbours on survival (a) and biomass (b) for each species cultivated in two of the three sites (Low and Intermediate, or Intermediate and High), without (white bars) and with neighbours (black bars). Means and SE were calculated with all the individuals of both populations for each species, and were estimated using partial effect in a GLM model (see Table 1). Stars along the *x* axis indicate significant differences between the two sites for a given species, and stars above the bars indicate significant differences in individuals cultivated with and without neighbours for each combination of species and site (* <0.05 , ** <0.01 , *** <0.001)

Fig. 2). Conversely, plants of *F. paniculata* (dominant at the Intermediate site) cultivated at the High site were bigger and plants of *C. sempervirens* (more abundant at the High site) and *F. paniculata* survived better at the High site than at the Intermediate site. For *S. caerulea* (dominant at the High site), we observed no difference between sites for biomass and survival (Table 1). The lack of differences for survival was the result of contrasted effects of the presence of surrounding vegetation in the two sites (Fig. 2a, Table 1a).

Effect of neighbours

The presence of neighbours affected both survival and biomass, but results were highly variable between sites and species (Fig. 2). The presence of neighbours had no effect on survival at the Low site, increased survival (indicating a facilitation effect of neighbours) at the Intermediate site for *B. erectus*, *D. glomerata*, *S. caerulea* and only marginally for *C. sempervirens* ($P = 0.072$), and decreased survival (indicating a competition effect of neighbours) of

F. paniculata at the Intermediate and High sites (Fig. 2a). The presence of neighbours decreased biomass (competition) for both species at the Low site and had no significant effect on biomass at the other sites (Fig. 2b).

Population differentiation

In our experiment, site \times population interaction was only significant for the survival and the biomass of *C. sempervirens* (Fig. 3). We observed a significant population differentiation for survival for *C. sempervirens* at the Intermediate site and for *F. paniculata* at both sites (Fig. 3a), with the highest survival for the population coming from Intermediate site for both species. We observed a significant population differentiation for biomass at the Low site for *D. glomerata* and at the High site for *C. sempervirens* and *F. paniculata* (Fig. 3b). For all three species, the population with the lower biomass was coming from the site where species was more abundant: the Low, Intermediate and High sites, respectively, for *D. glomerata*, *F. paniculata* and *C. sempervirens*. No significant pattern of local adaptation (greater performance for populations in their site of origin) for survival or biomass was observed for any species (Fig. 3).

Discussion

The reciprocal transplantations in our experiment allowed us to show the variability in species' performance

along our gradient in term of biomass and survival, two important factors of plant fitness (Violle *et al.*, 2007). Additionally, we demonstrated that biotic interactions can influence plant performance but their direction (competition or facilitation) depends on local environmental conditions. Finally, we found no evidence of local adaptation.

Species response to environmental change

The main effect of environmental changes on plant species in mountain ecosystems is believed to be on their elevational distribution, with uncertainties about the rate of colonization of higher sites with newly favourable conditions or the persistence in sites with modified environmental conditions, i.e. potentially less optimal abiotic conditions and/or more biotic interactions with new arriving species (Beniston, 2003; Breshears *et al.*, 2008). Some studies demonstrated that an upslope shift of species distribution already occurred (Walther *et al.*, 2005; Kelly & Goulden, 2008) but studies about the ability of species to respond to a large range of environmental conditions occurring across their elevational distribution remain rare.

Studying the performance of species along an elevational gradient is associated with the 'null' hypothesis of a decrease in performance with elevation as a result of lower temperature and a shorter growing season (Körner, 2003). Our results did not fully support this

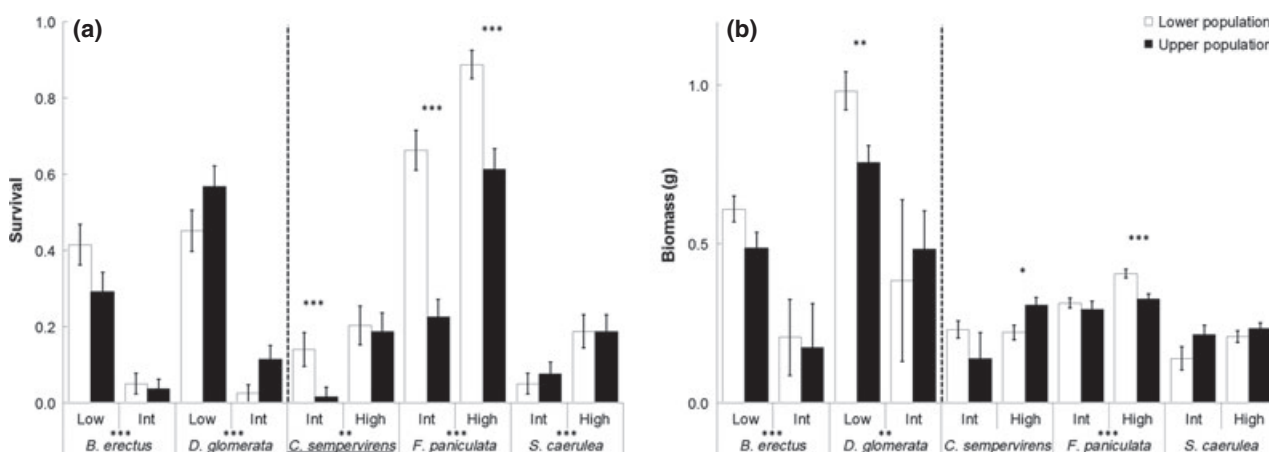


Fig. 3 Population differentiation for survival (a) and biomass (b) for each species in two of the three sites (Low and Intermediate, or Intermediate and High). Means and SE were calculated with all the individuals of both populations for each species cultivated without neighbours in order to test local adaptation to abiotic conditions, and were estimated using partial effect in a GLM model (see Table 1). Stars along the x axis indicate significant differences between the two sites for a given species, and stars above the bars indicate significant differences between populations of a species cultivated in a given site (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Underlined species indicated a significant site \times populations interaction ($p < 0.05$). To facilitate the understanding of the figure, the two pairs of transplantations were separated by a vertical dashed line and the lower and upper populations have the same label for each pair of transplantation sites (Low populations of *B. erectus* and *D. glomerata* and Intermediate populations of the three other species are represented as white bars, and Intermediate populations of *B. erectus* and *D. glomerata* and High populations of the three other species are represented as black bars, respectively; see Fig. 1).

hypothesis because performance indeed decreased with elevation for the two species planted in the lower pair of sites (*B. erectus* and *D. glomerata*), but we observed different responses to elevation for the three species planted in the upper pair of sites. Moreover, the response of species to similar environmental changes appeared idiosyncratic since we observed contrasted responses for species sampled from the same initial locations (*C. sempervirens*, *F. paniculata* and *S. caerulea*). This could be explained by different responses of species to environmental changes occurring at local scale, both for biotic and abiotic environmental conditions related to their environmental requirements or to different species strategy to cope with competition or with stress for example (Grime 1977, Liancourt *et al.*, 2005).

While climatic parameters such as temperature varying along elevational gradients can explain the global distribution of species (Körner, 2003; Thuiller *et al.*, 2005), other environmental factors, such as neighbours identity, soil fauna, soil parameters, are likely to change at a more local scale, altering community functioning and limiting range expansion as well as performance of species (Kardol *et al.*, 2010). As a matter of fact, even if general patterns can be formulated at the global scale for species' response to global environmental change, predictions about species performance at a more local scale require taking into account processes at the community level where local environmental conditions can vary drastically over short distances (De Bello *et al.*, 2013).

Biotic interactions

Following the stress gradient hypothesis (Bertness & Callaway, 1994), biotic interactions are predicted to vary with environmental stress that can occur along an elevational gradient, with an increase in the relative importance of facilitation at higher elevations (Choler *et al.*, 2001; Callaway *et al.* 2002, le Roux & McGeogh, 2008).

Our results supported the SGH with the increase in elevation between the Low and Intermediate sites. Indeed for *B. erectus* and *D. glomerata*, we observed competition for biomass at the Low site while facilitation for survival occurred at the Intermediate site. Although this pattern is concordant with an elevational SGH, the lack of similar observations between the Intermediate and High sites suggest that biotic interactions were related to a factor confounded with elevation. On the one hand, facilitation occurred only at the Intermediate site, and only for three of five species. Both mean precipitations and punctual measurements of soil humidity (F. Grassein, personal observations) indicated that the Intermediate site was more stressful than the two other sites for water availability, and thus the

greater importance of facilitation at the Intermediate site may be a consequence of a greater water stress independently of the position of the site along the elevational gradient. Although not monitored in details in our study, water availability has been highlighted as an important driver of biotic interactions that can even counteract classical prediction along elevational gradient in dry mountains (Cavieres *et al.*, 2006; Schöb *et al.*, 2013). Our results illustrate the importance to consider the multiple stress gradients occurring along an elevational gradient, especially when opposing gradients such as aridity and temperature are combined in dry mountains environments (le Roux & McGeogh, 2008; Michalet *et al.*, 2013). On the other hand, we observed competition only for biomass and facilitation only for survival, which also supports SGH for water availability. Indeed, previous studies have reported facilitation for survival in link with water availability at Lautaret (our Intermediate site; Gross *et al.*, 2009), and greater water availability has been demonstrated to increase the competition for biomass in grasslands similar to our Low site (Corcket *et al.*, 2005; Liancourt *et al.*, 2005). Our results thus support the importance of considering biotic interactions at a local scale to understand the performance of species in new habitats (Araújo & Luoto, 2007; Boulangeat *et al.*, 2012).

By comparing different species, we also observed that despite being exposed to similar neighbours' identity the output of biotic interactions vary among species from competition to facilitation for survival in the Intermediate site. Different responses could result from different degrees of deviation from the physiological optimum (strain; Welden & Slauson, 1986; Gross *et al.*, 2010) explaining different degrees of sensitivity of species to the stress gradient (Liancourt *et al.*, 2005). Additionally, the shifting point from facilitation to competition can also vary depending on the relative position of the population or site compared to the distribution of the whole species. Such changes have been reported in a study in similar sites with facilitation or competition for species in sites at higher or lower elevations, respectively, than their mean distribution (Choler *et al.*, 2001). Although we observed no difference between populations for biotic interactions that could support this hypothesis, facilitation for survival for *B. erectus* and *D. glomerata* and competition for *F. paniculata* at the Intermediate site seems to support the view that facilitation is more frequent in the upper part than in the lower part of the distribution.

Local adaptation

As a consequence of large differences in climatic conditions across our sites, population differentiation and

local adaptation were expected along our elevational gradient (Byars *et al.*, 2007; Gonzalo-Turpin & Hazard, 2009). However, our results showed no local adaptation whatever the species. Although we observed some differences between population, they were not consistent with a pattern of local adaptation since they occur in only one site (Low and Intermediate sites, respectively, for *D. glomerata* and *C. sempervirens*), or were not consistent with the criterion of a greater performance of local vs. foreign populations (Kawecki & Ebert, 2004) (greater survival for the Intermediate population of *F. paniculata* in both sites). Local adaptation has been described over narrow ranges of environments (Byars *et al.*, 2007) and even in the presence of gene flow along an elevational gradient (Gonzalo-Turpin & Hazard, 2009). Some hypotheses can be proposed to explain the absence of local adaptation in our study. First, contrary to other studies manipulating 'single' factors such as soil type (Sambatti & Rice, 2006) or flooding (Lenssen *et al.*, 2004), elevational gradients involve changes in multiple environmental factors (temperature, soil moisture, light, precipitation..., Körner, 2003) and the variability for multiple environmental factors rather than for a single one may reduce the probability of local adaptation to a given factor (in particular if there is a negative correlation between the responses to the two factors). Secondly, we observed some population differences indicating that populations differed genetically when grown in a common garden. However, we previously highlighted that phenotypic plasticity can occur in addition to population differentiation for two of our species (*D. glomerata* and *F. paniculata*, Grassein *et al.*, 2010). Phenotypic plasticity allowing individuals to adjust to different conditions is one of several mechanisms which can hamper evolutionary change towards local adaptation (Kawecki & Ebert, 2004; Chevin *et al.*, 2013; Pratt & Mooney, 2013), making thus the lack of local adaptation more an alternative hypothesis rather than an exception to the local adaptation 'law'. Finally, using a meta-analysis of 32 plants species, Leimu & Fischer (2008) showed that local adaptation was less common than generally assumed. This study also pointed out a greater probability to detect local adaptation for greater population size and a relatively low effect of other parameters such as plant life history of geographic scale. Although we focused only on grass species, we thus assumed that our conclusion about the generality of a lack of local adaptation was unlikely related to the fact that we used only perennial grasses or the use of small populations since all our species were sampled in sites with high abundance and have a large geographical range.

By estimating both survival and biomass of two transplanted populations coming from different points

along the distribution range of each species, our results pointed out that the population with the greatest survival can differ from the population with the greatest biomass as illustrated with *D. glomerata*. Additionally, population differentiation was not consistent between species sampled and transplanted at the same sites as for *C. sempervirens* and *F. paniculata*. Rather than a selection for different optimal environmental conditions for different species, those differences could be better explained by the fact that populations sampled in a site for different species correspond to different position along the range for each species. For example, the biomass produced at high elevations for *C. sempervirens* and *F. paniculata* was greater for the 'central' populations although the provenance differed between the two species (the central populations were coming from the High and Intermediate sites, respectively). Moreover, the survival of the peripheral population of *D. glomerata*, which is also a leading edge population, was higher than that of the central population at the leading edge site. Already well-studied in biogeographical and evolutionary studies (Sagarin & Gaines, 2002; Eckert *et al.*, 2008), the different responses of central vs. peripheral populations across the species' geographical range become an important component of species' response to environmental changes (Safriel *et al.*, 1994; Davis & Shaw, 2001). As illustrated by our results, the understanding of the response of species to environmental change can be improved by taking into account their population structuration in the landscape (Anderson *et al.*, 2009), given the fact that trailing and leading edge populations can show different responses in different areas of the species distribution (Hampe & Petit, 2005; Breshears *et al.*, 2008).

Using field evidence for several species, we demonstrated the great variability of species in response to transplantation in different environments. Specifically, we demonstrated that survival and biomass are two distinct aspects of species performance, and that they can vary independently between species and populations depending on their sensitivity to environmental change (Jump & Peñuelas, 2005; Klanderud & Totland, 2005; Chevin *et al.*, 2013). Even though we did not observe local adaptation that could limit the response of species, our results demonstrated that the response to environmental changes can differ between populations of a given species sampled at the core or at the edges of species distribution (Davis & Shaw, 2001; Hampe & Petit, 2005; Anderson *et al.*, 2009). Finally, positive or negative influence of biotic interactions was mainly related to specific site conditions rather than to elevational effects alone, and was also varying between species supporting the hypotheses that response to biotic interactions can vary between species relatively to the deviance from

their optimal niche (notion of strain, Welden & Slauson, 1986). These results support the need to incorporate among-populations variation and biotic interactions into prediction models of the species distribution in response to global environmental change (Araújo & Luoto, 2007; Thuiller *et al.*, 2008; Boulangeat *et al.*, 2012).

Acknowledgements

Fabrice Grassein was funded by a PhD scholarship from the Cluster Environment of Région Rhône-Alpes. This work was conducted as a part of the project ANR-05-BDIV-009-01 QDIV. It contributes to CNRS GDR 2574 Traits and was conducted as part of CNRS Zone Atelier Alpes. We thank Joelle Benoit, Brice Giffard, Cilia Grebenstein, Gaelle Liroux and Marie Pascale Colace for field assistance during the experiment, and the Station Alpine Joseph Fourier for the logistic facilities at the Lautaret Pass and at the University of Grenoble.

References

- Anderson BJ, Akçakaya HR, Araújo MB, Fordham DA, Martinez-Meyer E, Thuiller W, Brook BW (2009) Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1415–1420.
- Araújo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, **16**, 743–753.
- Beniston M (2003) Climatic change in mountain regions: a review of possible impacts. *Climatic Change*, **59**, 5–31.
- Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193.
- Boulangeat I, Gravel D, Thuiller W (2012) Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters*, **15**, 584–593.
- Breshears DD, Huxman TE, Adams HD, Zou CB, Davison JE (2008) Vegetation synchronously leans upslope as climate warms. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11591–11592.
- Byars SG, Papst W, Hoffmann AA (2007) Local adaptation and cogeographical selection in the alpine plant, *Poa hiemata*, along a narrow altitudinal gradient. *Evolution*, **61**, 2925–2941.
- Byars SG, Parsons Y, Hoffmann AA (2009) Effect of altitude on the genetic structure of an Alpine grass, *Poa hiemata*. *Annals of Botany*, **103**, 885–899.
- Callaway RM, Brooker RW, Choler P, *et al.* (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.
- Cavieses LA, Badano EI, Sierra-Almeida A, Gómez-González S, Molina-Montenegro MA (2006) Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytologist*, **169**, 59–69.
- Chevin L-M, Collins S, Lefèvre F (2013) Phenotypic plasticity and evolutionary demographic responses to climate change: taking theory out to the field. *Functional Ecology*, **27**, 967–979.
- Choler P, Michalet R, Callaway RM (2001) Facilitation and competition on gradients in alpine plant communities. *Ecology*, **82**, 3295–3308.
- Corcket E, Liancourt P, Callaway R, Michalet R (2005) The relative importance of competition for two dominant grass species as affected by environmental manipulations in the field. *Ecoscience*, **10**, 186–194.
- Davis MB, Shaw RG (2001) Range shifts and adaptive responses to quaternary climate change. *Science*, **292**, 673–679.
- De Bello F, Lavorel S, Laverigne S, Albert CH, Boulangeat I, Mazel F, Thuiller W (2013) Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. *Ecography*, **36**, 393–402.
- Eckert CG, Samis KE, Loughheed SC (2008) Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. *Molecular Ecology*, **17**, 1170–1188.
- Fox J (2003) Effect Displays in R for Generalised Linear Models. *Journal of Statistical Software*, **8**, 1–27.
- Fox J, Weisberg S (2011) *An R Companion to Applied Regression*, 2nd edn. Sage, Thousand Oaks, CA.
- Frei ER (2013) *Adaptation and Plasticity of Plant Populations in the Swiss Alps in the Context of Climate Change*. Unpublished PhD thesis. ETH Zurich, Zurich.
- Gidon M (1977) - Carte géologique simplifiée des Alpes occidentales, du Léman à Digne, au 1/250.000. ed. Didier & Richard et BRGM, Paris.
- Gonzalo-Turpin H, Hazard L (2009) Local adaptation occurs along altitudinal gradient despite the existence of gene flow in the alpine plant species *Festuca eskia*. *Journal of Ecology*, **97**, 742–751.
- Goulden ML, Kelly AE (2012) Reply to: Schwilke & Keeley (2012), A plant distribution shift: temperature, drought or past disturbance? Available at: <http://www.plosone.org/article/comments/info%3Adoi%2F10.1371%2Fjournal.pone.0031173> (accessed 4 November 2013).
- Grassein F, Till-Bottraud I, Lavorel S (2010) Plant resource-use strategies: the importance of phenotypic plasticity in response to a productivity gradient for two subalpine species. *Annals of Botany*, **106**, 637–645.
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169–1194.
- Gross N, Kunstler G, Liancourt P, De Bello F, Suding KN, 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 KN, 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**, 9–19.
- Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.
- Hereford J, Winn AA (2008) Limits to local adaptation in six populations of the annual plant *Diodia teres*. *New Phytologist*, **178**, 888–896.
- Hillyer R, Silman MR (2010) Changes in species interactions across a 2.5 km elevation gradient: effects on plant migration in response to climate change. *Global Change Biology*, **16**, 3205–3214.
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**, 346–363.
- Jump AS, Peñuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, **8**, 1010–1020.
- Kardol P, Campy CE, Souza L, Norby RJ, Weltzin JF, Classen AT (2010) Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem. *Global Change Biology*, **16**, 2676–2687.
- Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. *Ecology Letters*, **7**, 1225–1241.
- Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11823–11826.
- Klanderud K, Totland Ø (2005) The relative importance of neighbours and abiotic environmental conditions for population dynamic parameters of two alpine plant species. *Journal of Ecology*, **93**, 493–501.
- Körner C (2003) *Alpine Plant Life: Functional Plant Ecology Of High Mountain Ecosystems*. Springer, Heidelberg.
- Leimu R, Fischer M (2008) A Meta-Analysis of Local Adaptation in Plants. *PLoS ONE*, **3**, e4010.
- Lenssen JPM, Van Kleunen M, Fischer M, De Kroon H (2004) Local adaptation of the clonal plant *Ranunculus reptans* to flooding along a small-scale gradient. *Journal of Ecology*, **92**, 696–706.
- Liancourt P, Corcket E, Michalet R (2005) Stress tolerance abilities and competitive responses in a watering and fertilization field experiment. *Journal of Vegetation Science*, **16**, 713–722.
- MacArthur RH (1972) *Geographical Ecology: Patterns in the Distribution of Species*. Princeton University Press, New Jersey.
- Michalet R, Schöb C, Lortie CJ, Brooker RW, Callaway RM (2013) Partitioning net interactions among plants along altitudinal gradients to study community responses to climate change. *Functional Ecology*, doi: 10.1111/1365-2435.12136 (in press).
- Parmesan C, Gaines S, Gonzalez L, Kaufman DM, Kingsolver J, Townsend Peterson A, Sagarin R (2005) Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos*, **108**, 58–75.
- Peters RL, Lovejoy TE (1992) *Global Warming and Biological Diversity*. Yale University Press, New Haven.
- Pratt JD, Mooney KA (2013) Clinal adaptation and adaptive plasticity in *Artemisia californica*: Implications for the response of a foundation species to predicted climate change. *Global Change Biology*, **19**, 2454–2466.

- Pulliam HR (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.
- R Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available at: <http://www.R-project.org/> (accessed 15 October 2013).
- Randin CF, Engler R, Normand S *et al.* (2009) Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology*, **15**, 1557–1569.
- Rice KJ, Knapp EE (2008) Effects of Competition and Life History Stage on the Expression of Local Adaptation in Two Native Bunchgrasses. *Restoration Ecology*, **16**, 12–23.
- le Roux PC, McGeogh MA (2008) Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic change*, **86**, 309–329.
- Safriel U, Volis S, Kark S (1994) Core and peripheral populations and global climate change. *Israel Journal of Plant Sciences*, **42**, 331–345.
- Sagarin RD, Gaines SD (2002) The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters*, **5**, 137–147.
- Sambatti JBM, Rice KJ (2006) Local adaptation, patterns of selection, and gene flow in the Californian serpentine sunflower (*Helianthus exilis*). *Evolution; International Journal of Organic Evolution*, **60**, 696–710.
- Schöb C, Armas C, Guler M, Prieto I, Pugnaire FI (2013) Variability in functional traits mediates plant interactions along stress gradients. *Journal of Ecology*, **101**, 753–762.
- Schwilk DW, Keeley JE (2012) A plant distribution shift: temperature, drought or past disturbance? *PLoS ONE*, **7**, e31173.
- Theurillat J-P, Guisan A (2001) Potential Impact of Climate Change on Vegetation in the European Alps: a Review. *Climatic Change*, **50**, 77–109.
- Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 8245–8250.
- Thuiller W, Albert C, Araújo MB *et al.* (2008) Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 137–152.
- Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional!. *Oikos*, **116**, 882–892.
- Vittoz P, Randin C, Dutoit A, Bonnet F, Hegg O (2009) Low impact of climate change on subalpine grasslands in the Swiss Northern Alps. *Global Change Biology*, **15**, 209–220.
- Walther G-R, Beißner S, Burga CA (2005) Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, **16**, 541–548.
- Waser NM, Price MV (1985) Reciprocal Transplant Experiments with *Delphinium nelsonii* (Ranunculaceae): evidence for Local Adaptation. *American Journal of Botany*, **72**, 1726–1732.
- Welden CW, Slauson WL (1986) The intensity of competition versus its importance: an overlooked distinction and some implications. *The Quarterly Review of Biology*, **61**, 23–44.