Competition and a short growing season lead to ecotypic differentiation at the two extremes of the ecological range

Pierre Liancourt* and Katja Tielbörger

Plant Ecology Department, Institute of Botany, University of Tübingen, Auf der Morgenstelle 3, 72076, Tübingen, Germany

Summary

1. Local adaptation is a major factor shaping a species' range. Studies on adaptation to local abiotic conditions are numerous, but adaptation to neighbour conditions has been almost neglected, and these two have rarely been separated experimentally. We hypothesized that adaptation to abiotic stress (e.g. fast development, drought resistance) dominates at the stressful end of the gradient, while adaptation to competition (e.g. large plant size) is more common at the benign end of the distribution range.

2. We conducted a reciprocal sowing experiment coupled with a removal experiment in the field for two winter annual grass species *Bromus fasciculatus* C. Presl. and *Brachypodium distachyon* (L.) Beauv. from Mediterranean and arid populations in Jordan. The two species were also grown under standard conditions for evaluating whether traits indicative of competitive ability and tolerance to stress are more common for either of the ecotypes.

3. Adaptation to abiotic stress could not be tested because our experiment was performed in a favourable year where water was not limiting in either of the sites.

Competition was intense in both sites for the two populations of each species but competitive exclusion was observed only in the Mediterranean site. Mediterranean populations produced consistently more biomass and exhibited later onset of flowering than arid populations, both in the field and under standard conditions.

4. Mediterranean populations also showed better competitive response ability however stress tolerance was no different to that of arid populations.

5. This study indicates that competition and length of the growing season are major selective constraints at the two extremes of the ecological range along aridity gradients. We suggest that drought stress increases in importance during dry years and studies on local adaptation along climatic gradients may help predict the effect of global change on future species' distributions.

Key-words: aridity gradient, biotic interactions, ecotype, local adaptation, phenology, stress

Introduction

Local adaptation, or within-species niche divergence leading to ecotypic differentiation, is one of the major mechanisms that shape species' ranges (Rehfeldt *et al.* 1999; Joshi *et al.* 2001; Wright *et al.* 2006). Indeed, experimental evidence for local adaptation to abiotic stress is numerous (e.g. Bazzaz 1973; Wu & Antonovics 1976; Higgins & Mack 1987; Aronson *et al.* 1992; Aronson *et al.* 1993; Volis *et al.* 1998; McKay *et al.* 2001; Ellis & Weis 2006; Sambatti & Rice 2007; Dechamps *et al.* 2008). Other studies have shown the potential role of competition as a selective force to induce

character divergence (Miller 1995; VanKleunen *et al.* 2005). However, the idea that ecotypes would be locally specialized to competitive environments is not so clear for several reasons. First, despite a recent research effort, few studies have addressed this question (McNeilly 1981; Martin & Harding 1981; Higgins & Mack 1987; Volis *et al.* 2002; Sambatti & Rice 2007; Rice & Knapp 2008). This is surprising because neighbours are the primary force determining the shape of the realized vs. the fundamental niche (Hutchinson 1957). Second, a few studies that confirmed this hypothesis usually used a replacement series design (McNeilly 1981; Martin & Harding 1981; Volis *et al.* 2002). This method is not the most suitable one to compare competitive ability between populations or between species since several points seriously undermine

*Correspondence author. E-mail: Pierre.liancourt@uni-tuebingen.de

its usefulness (Gibson *et al.* 1999; Jolliffe 2000; Freckleton & Watkinson 2000). For instance, replacement series designs generally produce results that may be size biased; they take intraspecific interactions as a reference point instead of no interactions; a fixed density for the experiment is usually chosen arbitrarily making the results difficult to generalize to natural density levels (Gibson *et al* 1999); it confuses the 'outcome of competition' (i.e. the winner) with the competitive ability *per se* without distinction between competitive effect, that is, ability to suppress fitness of other individuals, and competitive-response ability, that is, ability to avoid being suppressed (Goldberg & Landa 1991). Thirdly, among these few studies, two did not detect any differences in competitive ability between ecotypes from stressful and favourable environments (Higgins & Mack 1987; Sambatti & Rice 2007).

Abiotic stress and competition are unlikely to be equally important throughout the distribution range of the species. If we consider the distribution along an ecological gradient (e.g. productivity), stress is assumed to be more important for a species' performance at the harsh end whereas competition is more important at the favourable end of the gradient (Grime 1974; Welden & Slauson 1986; Brooker *et al.* 2005; Gaucherand *et al.* 2006). Since these two forces are likely to be involved in adaptive ecotypic differentiation, local adaptation may be found at the two extremes of the realized niche, selecting either for stress tolerant or competitive ecotypes (Petrů *et al.* 2006), and may thus shape the species' range along ecological gradients. In addition, both stress and a short growing season may overlap. Therefore, populations from harsh conditions may show a higher stress tolerance and traits related to specific adaptation to this environment. Conversely, populations from favourable environments may show a higher competitive response ability (adaptation to competitive environment) and traits related to this environment. To our knowledge, no study has attempted to explicitly test in the field for the respective role of these mechanisms on local adaptation and ecotypic differentiation at the two extremes of the ecological range.

Previous theoretical and empirical evidence suggests that there are several traits indicative of either competitive ability or stress tolerance. For example, plant size has been used by a myriad of studies as correlate for competitive ability (Grime 1974, See Westoby 1998 for review, Keddy *et al.* 2002). Therefore, plants from competitive environments should be, on the average, larger than plants from environments of large abiotic stress. Abiotic constraints are numerous, and we focus here mainly on drought stress and short growing season typical for deserts. Small body size is a general trait for herbaceous plant from arid/stressful environments (Aronson *et al.* 1992, 1993; Ellis & Weis 2006; Petrů *et al.* 2006; Sambatti & Rice 2007) that illustrates the classical trade-off between competitive ability and stress tolerance (Grime 1974). A short growing season, particularly when the onset of the season is unpredictable, selects for rapid development (Petrů *et al.* 2006; Frank, Sim & Weis 2007), so that the unpredictable and rare favourable conditions can be exploited in an optimal manner.

An ideal study system for testing differential selective regimes should include very steep environmental gradients and at the same time, species that can persist under a very large range of environmental conditions. Elevation gradients along the Dead Sea and the Lower Jordan River Valley are ideally suited to test our hypotheses. They range from *c.* 800 m elevation (the tops of the hills) to sea level or even below, in the Jordan Valley itself, within a very short distance (10–20 km), allowing many species to occur in many sites along the gradient. The upper elevations provide a Mediterranean climate with 500–600 mm annual rainfall, an 8-month growing season and relatively low between-year variability in rainfall. Lower elevations provide extremely arid conditions with 60–200 mm annual rainfall, high evapotranspiration, a short growing season (2–4 months) and extremely high variability and unpredictability in rainfall (Aronson *et al.* 1992; Petrů *et al.* 2006). Also, plant density and biomass per unit area decrease drastically from the Mediterranean end to the arid end and studies in the region suggest a decreasing importance and intensity of competition at the arid end (Holzapfel *et al.* 2006; Schiffers & Tielbörger 2006). Finally, Aronson *et al.* (1992, 1993) observed smaller body size and earlier flowering for arid populations compared to Mediterranean populations, indicating that ecotypic differentiation is likely in such environments and related to traits indicative of adaptation to abiotic vs. biotic stress.

We used a set of experiments with two annual plant species from an aridity gradient in Jordan to demonstrate shifts in importance of biotic vs. abiotic constraints for local adaptation. Importance of competition should increase towards the benign end and abiotic constraints (drought stress, short growing season) should be more important at the arid end. By combining cross-transplants in the field with neighbour removal, and by adding greenhouse experiments with plants grown in a standard environment, we tested the following hypotheses:

(1) When grown in a common environment, plants of arid origins demonstrate trait combinations indicative of adaptation to drought and short growing season, and Mediterranean plants exhibit traits indicative of competitive ability.

(2) There is local adaptation in populations from both environments, expressed as a home-site advantage in cross-transplants in the field.

(3) Adaptation to competition is more important at the benign end and adaptation to stress is more important at the arid end. Therefore, the home-site advantage will be more visible for Mediterranean plants when grown with neighbours (i.e. better competitive response ability), and for arid plants when grown without neighbours.

Material and methods

SITES AND TARGET SPECIES

Experiments were conducted during the 2006/2007 season at two sites in Wadi Shuayb (Fig. 1), a steep valley running from east to west, perpendicular to the Jordan River. It is located 20 km north-east

Fig. 1. View of Wadi Shuayb (left) and removal experiment in the semi-arid site (right) in March 2007. Photo credit: Pierre Liancourt.

of Amman, Jordan. The two sites were 10 km apart. The climate at the first site (850 m a.s.l.; 32°1′0·42″ N, 35°43′11·43″ E) is typically Mediterranean, while that of the second site (90 m a.s.l.; 31°56′24·94″ N, 35°39′43·27″ E) is semi-arid. Average annual precipitations were 417 and 195 mm for the Mediterranean and the semi-arid site respectively and were 475 and 249 mm the study year. The two sites differ also in length of the growing season. The first and last significant rains (< 10 mm) were registered the 29 October 2006/11 April 2007 and the 27 December/15 March 2007 for the Mediterranean and the semi-arid site respectively. The two sites have similar bedrock and aspect (i.e. limestone and north facing). The soil is Terra Rossa in the first site and desert lithosol in the second site. The floristic composition in the two sites is highly diverse (*c.* 250–300 species, personal observation). Vegetation in the Mediterranean site is composed of oak trees (*Quercus calliprinos*), shrubs (*Ononis natrix*, *Calicotome villosa*), and annual herbaceous vegetation including mainly tall grasses (*Hordeum spontaneum*, *Avena sterilis*) and legumes (*Vicia* sp., *Ononis* sp., *Trifolium* sp., *Medicago* sp.) as dominant species. Vegetation in the semi-arid site is composed of shrubs (*Phlomis* sp., *Astragalus spinosus*, *Teucrium polium*, *Retama raetam*), geophytes (*Anemone coronaria*, *Ranunculus asiaticus* very abundant, see Fig. 1) and a large variety of small annual grasses (e.g. *Crithopsis delileana*, *Bromus fasciculatus*, *B. lanceolatus*, *B. scoparius*, *Brachypodium distachyon*), forbs (*Plantago* sp., *Torilis* sp.), and legumes (*Trifolium* sp., *Ononis* sp., *Trigonella* sp., *Medicago* sp.). The average annual plant biomass per area was 300 ± 48 and 169 ± 29 g m^{-2} in the Mediterranean and the semi-arid sites, respectively, for the 2006/2007 season (the study season).

The two target species chosen for this study, *Bromus fasciculatus* C. Presl. and *Brachypodium distachyon* (L.) Beauv. (Poaceae), are both winter annual grass species (*Bromus* and *Brachypodium* hereafter). They are suitable focal species for our study since they

have a large distribution range from Mediterranean to desert environments and they are abundant and co-occur all along Wadi Shuayb. Ecotypic differences have been observed for these two species for nearby populations in Israel (Aronson *et al*. 1992, 1993).

EXPERIMENTS

Two experiments were set up to simultaneously test for differences in individual response to local environmental conditions and competitive response of *Bromus* and *Brachypodium* from Mediterranean and semi-arid populations (i.e. local adaptation).

Field experiment

The field experiment was performed for testing and separating biotic from abiotic effects in determining local adaptation. To this end, we performed a reciprocal sowing experiment coupled with a removal experiment of the two species from the two origins. The same full-factorial experimental design was established in the two sites of origin prior to the onset of the rainy season in October 2006 and consisted of 48 rectangular plots ($2 \times 1 \cdot 5$ m) per site, delimited within fenced areas (to exclude sheep and goats). The plots were randomly selected to be away from trees in the Mediterranean site and to contain herbaceous vegetation only (no shrubs). Above-ground vegetation of one half of the plots was removed by hand (mainly litter and seedlings of annuals, few perennials). These no-neighbour plots were kept free from vegetation by periodic careful removal of seedlings and re-sprouting perennials.

Field-collected seeds of the two target species, *Bromus* and *Brachypodium*, from populations originating from the two experimental sites (Mediterranean and semi-arid) were used for the reciprocal

sowing experiment. The seeds were collected at random from a large number of individuals (> 50) per species within many different patches in May 2006 at the two sites (> 500 seeds per species and per site). There were six replicates (plots) per combination of treatments (population × species × competition) in the experiment in each site. Only seeds from one population of one species were used per plot. Within each plot, six small plastic rings (*c.* 5 cm in diameter) were placed on the ground in two rows with an interval of approximately 50 cm between rings, and between each ring and the edge of the plot. Three seeds were put in the middle of each plastic ring to optimize the chance of having one individual germinating. The rings were then covered with organza and fixed to the ground with small nails. This was done to prevent seed movement due to run-off after precipitation, as well as to facilitate location of the target individuals. If more than one seed germinated per ring, the additional seedlings were removed. The organza was removed after germination. We assumed that our experimental design precludes any competition between the six target individuals within a plot. The use of organza and plastic rings has proven to be successful in previous studies and we know that they have a negligible effect on the germination microclimate (C. Ariza, personal communication). In summary, the experimental design included two populations × two species × two competition levels × six replicates (i.e. 48 plots) in both the Mediterranean and semi-arid site.

Greenhouse experiment

The greenhouse experiment was set up for measuring differences between populations in traits correlated with adaptation to competitive vs. arid conditions. For this purpose, the performance of the two populations of each species was investigated in standard conditions in a greenhouse located 20 km north of the Mediterranean site at approximately the same elevation. Seeds from the two populations of each species were collected in spring 2006 and germinated in late December 2006 and individuals (one per pot) were grown in 1-L pots in the greenhouse until late April 2007. The substrate used was a 4 : 1 mixture of red Mediterranean soil and sand. Pots were fully watered every second day during this period. Eight replicates per population per species were used for this experiment.

MEASUREMENTS AND DATA ANALYSES

Field experiment

Mortality, number of inflorescences and above-ground biomass of target individuals from the field experiment were recorded in late April 2007. Plants were harvested before anthesis to avoid genetic pollution of the communities due to the reciprocal sowing experiment. Above-ground biomass of transplants was measured by clipping living shoots at ground level and drying them at 70 °C for 48 h before weighing. Parallel studies have indicated that above-ground biomass is a very good predictor of fecundity (Eberhart 2006). Mortality (i.e. failure to survive to seed production) was calculated as a percentage per plot and values of biomass and number of inflorescences were averaged per plot before analysis to avoid pseudoreplication, since the plots are the genuine replicates in our experiment (Hulbert 1984).

Data were analysed with four-way ANOVAs in which site, population, species and competition treatment were fixed factors. A significant interaction between population and site, or population, site and other factors, showing higher performance for a population in its home site, were interpreted as indicators of local adaptation. A significant population × neighbour interaction was interpreted as a difference in competitive response between populations. Proportion of plants

flowering was square root-transformed, biomass data were log-transformed and mortality data were arcsine square root-transformed prior to analysis to reduce heteroscedasticity (Sokal & Rohlf 1995).

Greenhouse experiment

For evaluating the pace of development, the number of individuals flowering was registered at mid-term (mid-March 2007) and at the end of the experiment (late-April 2007). Individuals were harvested at the end of the experiment and above-ground biomass of transplants was calculated by clipping living shoots at ground level and drying them at 70 °C for 48 h before weighing. The exact time to flowering was not measured in the greenhouse experiment. However, since all the individuals produced inflorescences by the end of the experiment, the number of individuals that produced inflorescences at the mid-term measurement could be used as a proxy for the speed of development.

The effects of population origin, species, and their interaction on the number of individuals flowering at mid-term measurement were analysed using a χ^2-likelihood ratio with logistic regression models. Final biomass was analysed with two-way ANOVAs in which species and origin were fixed factors. To compare biomass production for the two populations of the two species in the greenhouse and in the field without neighbours, we performed a three-way ANOVA with site (Mediterranean, semi-arid and greenhouse), species and population as fixed factors. Biomass data were log-transformed before analyses.

All analyses were carried out with JMP 5·0·1 (SAS Institute 2002).

Results

FIELD EXPERIMENT

Mortality was primarily registered in the Mediterranean site. Generally, higher mortality was registered for *Bromus* than for *Brachypodium*. For both species, the presence of neighbours significantly increased mortality in the Mediterranean site and semi-arid populations were more affected by neighbours than Mediterranean populations, indicating differences in competitive response between the two populations (Table 1, Fig. 2a).

Biomass production was significantly higher for *Brachydodium* than for *Bromus*. Overall, we recorded a significant effect of neighbours; competitive effects of neighbours led to a dramatic decrease in growth of the two species at both sites (Table 1, Fig. 2b). Individuals from both species of Mediterranean populations always produced more biomass than those from semi-arid populations, irrespective of the presence of neighbouring vegetation and both species produced more biomass in the semi-arid site (Table 1, Fig. 2b). However, the non-significant neighbour × population interaction indicated that the two populations did not differ in competitive response measured on biomass (Table 1). The non-significant neighbour × site interaction indicated that competition intensity measured on biomass was equally intense at the two sites (Table 1).

The number of inflorescences produced was significantly higher for *Brachypodium* than for *Bromus* without neighbour only, as indicated by the significant species × neighbour interaction. *Brachypodium* produced more inflorescence in the semi-arid than in the Mediterranean site (significant
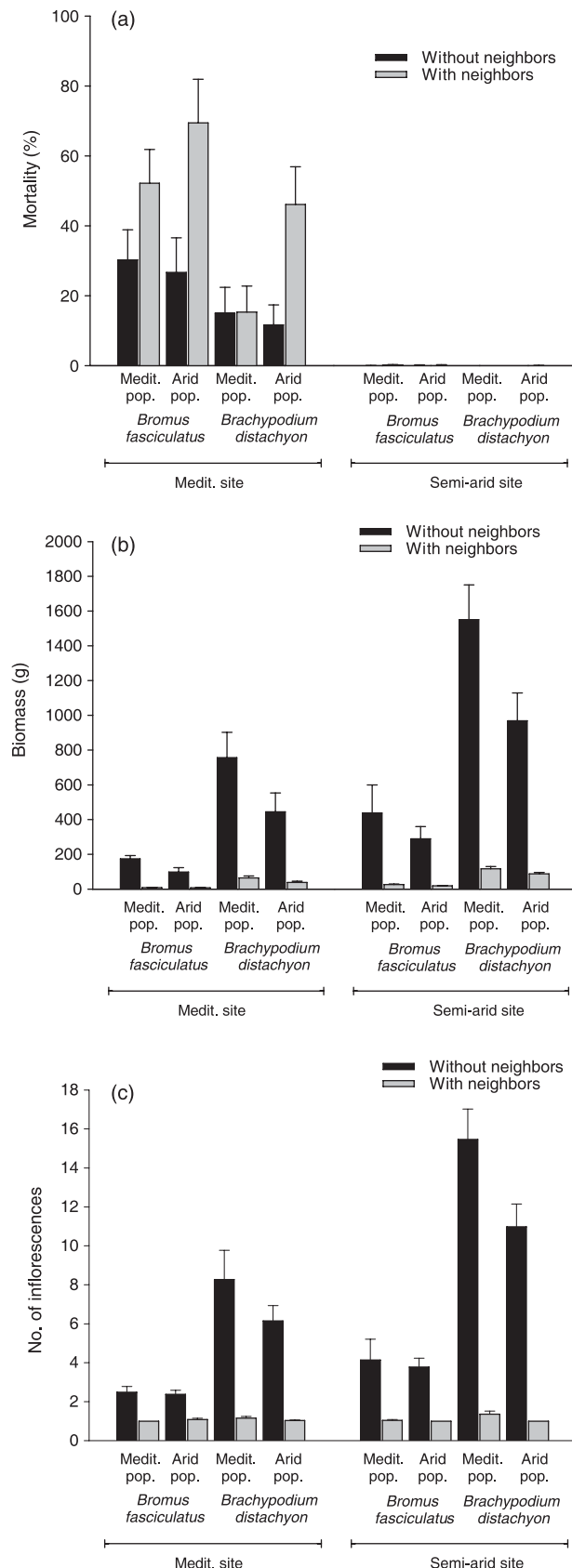
Fig. 2. Effects of neighbours on (a) mortality, (b) biomass and (c) number of inflorescences of *B. fasciculatus* and *B. distachyon* from Mediterranean and semi-arid populations in the Mediterranean and the semi-arid site. (Data are mean and SE, *n* = 6 replicates).
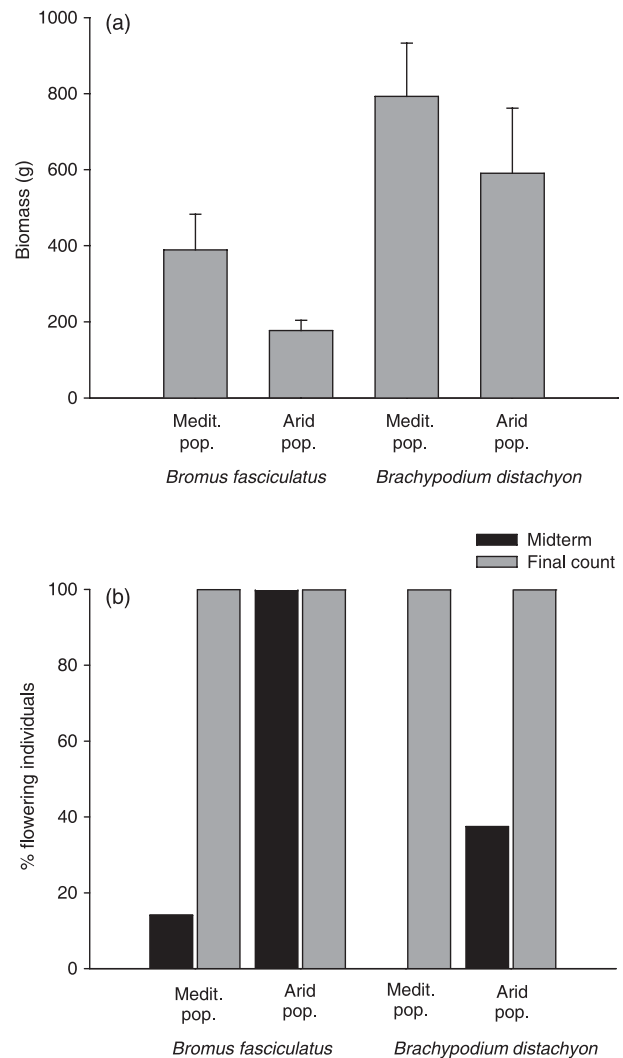

Fig. 3. (a) Percentage of flowering individuals for the mid-term (mid-March) and final (late-April) counts and (b) biomass of *B. fasciculatus* and *B. distachyon* from Mediterranean and semi-arid populations grown in standard conditions (greenhouse) (*n* = 8 replicates).

site × species interaction, Table 1, Fig. 2c). Overall, we found that Mediterranean populations produced more inflorescences than semi-arid populations. Competition also strongly affected the number of inflorescences but the significant site × neighbour interaction indicated that this effect was stronger in the semi-arid than in the Mediterranean site. However, unlike for mortality this was mainly due to the differences observed without neighbours.

GREENHOUSE EXPERIMENT

As observed in the field experiment at both sites, in standard conditions biomass production was significantly higher for *Brachypodium* than for *Bromus*, and for Mediterranean populations compared to semi-arid populations (species $F_{1,29} = 10.06$, $P = 0.004$, population $F_{1,29} = 5.43$, $P = 0.027$). The comparison between the biomass production in the greenhouse and the field sites without neighbour showed the

Table 1. Results of four-way ANOVAs testing the effects of species, neighbours, site and population of origin (all fixed factors) on biomass, number of inflorescences and mortality. Bold indicates significant *P* values ($P < 0.05$)

Source of variation	Biomass			Number of inflorescences			Mortality		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
Species	1	229·95	**< 0·001**	1	107·08	**< 0·001**	1	21·08	**< 0·001**
Neighbour	1	631·25	**< 0·001**	1	413·35	**< 0·001**	1	14·19	**< 0·001**
Population	1	16·45	**< 0·001**	1	4·13	**0·046**	1	2·80	0·099
Site	1	77·65	**< 0·001**	1	25·70	**< 0·001**	1	59·48	**< 0·001**
Species × Neighbour	1	1·44	0·234	1	93·33	**< 0·001**	1	1·42	0·238
Species × Population	1	0·27	0·603	1	3·53	0·064	1	0·12	0·731
Neighbour × Population	1	1·16	0·284		3·01	0·087	1	1·86	0·176
Site × Species	1	0·80	0·373	1	5·11	**0·027**	1	1·10	0·297
Site × Population	1	0·42	0·520	1	1·00	0·321	1	0·72	0·398
Site × Neighbour	1	0·16	0·692	1	23·91	**< 0·001**	1	6·13	**0·016**
Population × Species × Neighbour	1	0·24	0·623	1	2·08	0·153	1	0·95	0·332
Population × Species × Site	1	0·02	0·879	1	0·59	0·444	1	0·31	0·582
Population × Neighbour × Site	1	0·18	0·671	1	0·00	0·998	1	4·76	**0·032**
Species × Neighbour × Site	1	0·51	0·479	1	3·77	0·056	1	0·26	0·609
Population × Species × Neighbour × Site	1	0·81	0·370	1	0·04	0·842	1	0·21	0·650
Error	76			76			78		

same information (species $F_{1,69} = 69.66$, $P < 0.001$, population $F_{1,69} = 14.14$, $P < 0.001$). Biomass production was similar in the greenhouse and the Mediterranean site, and both were lower than semi-arid site (site $F_{2,69} = 10.56$, $P < 0.001$). The non-significant interaction between site, population and species indicated that the differences observed between species and population in the greenhouse were similar to those observed in the field (site × species $F_{2,69} = 2.01$, $P = 0.142$; site × population $F_{2,69} = 0.21$, $P = 0.810$; site × species × population $F_{2,69} = 0.12$, $P = 0.885$, Table 1, Figs 2a and 3a).

Our results showed that semi-arid populations flowered earlier than Mediterranean populations, that is, more individuals were flowering at the mid-term measurement (population, $\chi^2 = 17.31$, d.f. = 1, $P < 0.001$, Fig. 3b). We also found that *Bromus* produced inflorescences more rapidly than *Brachypodium* (species, $\chi^2 = 7.03$, d.f. = 1, $P = 0.008$).

Discussion

Populations of both *Bromus* and *Brachypodium* from the two extremes of the aridity gradient showed local adaptation to their home environment. We were able to separate biotic and abiotic constraints for local adaptation and our results indicate the larger importance of competition for populations at the Mediterranean site. These findings were supported by our observation of ecotypic differentiation in morphological and phenological traits.

Overall, we found intense competition in these 'ruderal' communities (*sensu* Grime 1974) dominated by annual species but we confirmed our assumption of the predominant role of negative biotic interactions at the favourable end of the gradient of water availability (see also Kadmon 1995; Schiffers & Tielbörger 2006). Most interestingly, competition was intense enough to lead to competitive exclusion at the Mediterranean site only. Therefore competition should have a

strong selective effect primarily on Mediterranean populations. It may also influence the long-term population dynamics of annual species in semi-arid environments (Chesson *et al.* 2004), since biomass and the number of inflorescences were dramatically decreased with neighbours. This could be an important mechanism involved in competitive exclusion. A closer look at the results indicates that the main fitness parameter affected by competition was mortality, while competition effects on the second important parameter (fecundity) did differ between populations. This indicates that competitive exclusion of competitively inferior ecotypes is driven mainly by effects on mortality. Therefore, selection should operate on maximizing survival under competitive conditions.

The most salient evidence for a home-site advantage was that Mediterranean populations were less affected by competitive exclusion than semi-arid populations (Fig. 2) at the Mediterranean site. Competition is a strong selective force driving character divergence (Miller 1995; VanKleunen, Fischer & Schmid 2005) and our study provides evidence that competition selected for individuals with greater competitive response ability in the productive Mediterranean environment.

We furthermore hypothesized that the two populations would differ in their tolerance to drought stress, which would be expressed as higher fitness of semi-arid populations at their (dry) home site, especially without neighbours. However, we did not observe differences in drought tolerance and, accordingly, there was no home-site advantage for the semi-arid populations. However, it must be noted that the study period was exceptionally wet and we did not experimentally manipulate rainfall. For example, own data of biomass production indicates that abiotic stress was very low during the study season (*c.* 156% of the annual average biomass production). It is therefore not surprising that we observed evidence for

competition in both environments, since competition in dry environments takes place during pulses of water (Goldberg & Novoplansky 1997; Chesson *et al.* 2004), but weaker evidence for adaptation to stress. However, Aronson *et al.* (1992, 1993) conducted a drought-induced greenhouse experiment on *Bromus* and *Brachypodium* from Israeli desert and Mediterranean populations, and their results suggest that desert populations are more stress-tolerant than Mediterranean populations. We therefore suggest that there is ecotypic differentiation in drought tolerance in our species, but that these are more likely to be observed during dry years.

Consistent with our hypothesis and with previous findings (Aronson *et al.* 1992; Petrů *et al.* 2006), early flowering and small-sized ecotypes occurred in the relatively unpredictable and xeric environment of the semi-arid site whereas late flowering and larger-sized ecotypes occurred in the Mediterranean environment. Small size and early flowering time are likely to confer a fitness advantage in the semi-arid site where the vegetative season is short, and where water availability is low and limits biomass accumulation (Petrů *et al.* 2006). Indeed, early flowering under a short vegetation season has been demonstrated to be adaptive for the annual plant *Brassica rapa* (Frank *et al.* 2007). It may furthermore be adaptive to be small in this environment as a result of faster reproduction. Vice-versa, large size may confer a fitness advantage under a favourable climate where competition is more important (Grime 1974; Brooker *et al.* 2005; Gaucherand *et al.* 2006). If the above traits are adaptive, natural selection (i.e. stress and length of the vegetative season, and competition) on these traits was likely to be very strong and similar for both grass species. It is therefore interesting to find such strong differences in life history within a life form usually regarded as classically r-selected (i.e. annuals) and treated as homogeneous. This suggests a nested pattern for r–K selection (*sensu* McArthur & Wilson 1967) between life forms, between species within life form and also between populations within species.

We used a reciprocal transplant/sowing experiment as a classical way to test local adaptation (Joshi *et al.* 2001; Becker *et al.* 2006; Ellis & Weis 2006; Sambatti & Rice 2007). We found that the length of the vegetative season (selecting for early flowering time) in xeric habitats and competition (selecting for a larger size and greater competitive response ability) in productive habitats are likely to be the main constraints for within-species niche divergence between semi-arid and Mediterranean populations. Our study provides evidence of the crucial role of these two forces on local adaptation to determine species' ranges along climatic gradients (Rehfeldt *et al.* 1999; Joshi *et al.* 2001; Wright *et al.* 2006). Therefore, studies on local adaptation along climatic gradients may help in providing more accurate predictions on the effect of global change on future species' distributions (Fig. 1).

Acknowledgments

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