

Simulated migration in a long-term climate change experiment: invasions impeded by dispersal limitation, not biotic resistance

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Summary

1. Successful poleward shifts of plant species ranges as a result of climate change will depend on interactions between migrating species and the communities they invade. Although poleward migration may be constrained by slow long-distance dispersal into suitable habitat, the invasion resistance of a plant community is expected to depend on the timeframe available for species- and genetic-level compositional shifts.

2. We tested whether range shifts of *Bromus erectus* and *Brachypodium pinnatum*, two dominant grasses of calcareous grasslands in the southern UK with different phenologies and competitive abilities, are limited by dispersal and whether local plant communities are able to adapt to changes in climate conditions and resist invasion from novel species. We added seeds of the two species to an infertile grassland in northern England, where both species are currently absent and where winter warming and summer drought have been simulated for short (1 year) and long (15 years) durations.

3. We predicted that seed addition would lead to higher establishment of the two species in grassland plots subjected to artificial winter warming than in plots with imposed summer drought, and we expected that invasion resistance of the extant grassland community would be higher in long-term than in short-term climate manipulations.

4. Warming induced earlier seedling emergence in both species and resulted in higher invader above-ground biomass at the end of the first growing season. Summer drought did not affect the invasion success of *Bromus* but it offset the beneficial effects of winter warming in *Brachypodium*. Invader performance was similar in communities with long- and short-term climate manipulations.

5. *Synthesis.* Climate induced poleward shifts will proceed even if slow long-distance dispersal of migrating species allows extant communities to adapt to a new climate regime. Asynchrony between the phenology of migrating species and seasonal resource use by invaded communities are likely to amplify migration success.

Key-words: *Brachypodium pinnatum*, *Bromus erectus*, invader phenology, invasion resistance, plant–climate interactions, resource availability, seed provenance, soil heterogeneity, summer drought, winter warming

Introduction

Interactions between migrating species and their recipient communities have been widely neglected in projections of plant species shifts as a result of climate change (Van der Putten, Macel & Visser 2010). There is increasing evidence that species interactions will lead to nonlinear or abrupt changes in species composition, which cannot be extrapolated from individual

species responses to environmental gradients (Walther 2010). Range shifts of plant species require the successful invasion of established plant communities by migrating species, which depends both on climatic barriers inhibiting or promoting individual species migration and the susceptibility of plant communities to invasion (Lonsdale 1999). Understanding the rate of dispersal and establishment of migrating species against the rate at which extant communities adapt to environmental change will be a key to predicting the fate of terrestrial systems in an era of rapid climate change. Most climate manipulation

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experiments in temperate grasslands suggest rapid responses of resident vegetation to experimental warming, including enhanced growth (Rustad *et al.* 2001) and compositional shifts (Harte & Shaw 1995; Grime *et al.* 2000), but increased invasions have been rarely reported (Sandvik *et al.* 2004). Although these studies could indicate (short-term) invasion resistance, they may also reflect the naturally low propagule pressure of potential immigrants because dispersal events from distant southern ecosystems are rare. Consequently, most climate manipulation experiments do not adequately reflect the reality of longer-term poleward migrations, especially if they are conducted in places, where climatic barriers currently inhibit the reproduction of potential invaders. Thus, quantifying the probability of establishment and survival of potential immigrants in relation to propagule availability is required to predict the long-term invasion resistance of ecosystems (Lonsdale 1999).

In response to changing climate conditions, a plant community may resist invasion by novel species if the availability of free resources remains low due to adaptation by local populations or communities. Individuals may persist through phenotypic plasticity if the changes are not severe (Berg & Ellers 2010), or populations could adapt through expansion of local genotypes better suited to the new climate regime (genetic restructuring; Reusch & Wood 2007). Adaptation may also occur at the community level via a shift in dominance among species. For example, high local substrate variation, such as soil depth heterogeneity, could allow the historical persistence and subsequent expansion of species more suited to a new climate regime; such has been recently shown with species in response to chronic drought along a soil depth gradient (Fridley *et al.* in press). Invasion resistance of a plant community may thus largely depend on the timeframe available for spatial and genetic restructuring in the local community, which in turn is restricted by the speed with which new species arrive, establish and spread.

Given successful dispersal, species migration depends on the ability of an invader to out-compete local species by using resources more efficiently or by exploiting unused resources at times when resource demand and growth rates of the resident vegetation are low (Davis, Grime & Thompson 2000; James *et al.* 2006). Consequently, invasion success is related to the biology of migrating species, particularly in the seasonal timing of growth and reproduction (Griffith & Watson 2006). In a changing climate, successful poleward migration may further depend on photoperiod and thermal control of phenology as well as tolerance of late frost events, which may vary between individuals from different latitudes (Savolainen, Pyhajarvi & Knurr 2007) but also between individuals grown under different environmental conditions (Vander Mijnsbrugge, Bischoff & Smith 2010). Thus, migration success may vary according to the seed source involved in the dispersal process.

We have studied the capacity of *Bromus erectus* and *Brachypodium pinnatum*, two contrasting dominants of calcareous grassland in southern England, to move northward and invade species-rich grassland outside their current distribution range under different climate change scenarios. Although the two

grasses co-occur in their native range, drought-tolerant *Bromus* is often associated with shallow outcrops, while the more competitive *Brachypodium* colonizes deeper soils (Grime, Hodgson & Hunt 2007). The two species also have different phenologies: *Bromus* is able to grow late in the season and during winter, whereas leaf production in *Brachypodium* is restricted to spring and summer (Kahlert, Ryser & Edwards 2005). To test whether range shifts of these species are limited by dispersal or by climate and, concomitantly, whether local communities have the capacity to adapt to a new climate regime and resist invasion from novel species, we added seeds of the two grasses to an unproductive grassland at Buxton, northern England, UK, where extant plant communities of 3 × 3 m have been subjected to different combinations of winter warming and summer drought over both long (15 years) and short (1 year) durations and which have proved to be resistant to these climate manipulations in terms of species composition (Grime *et al.* 2000, 2008). We predicted that community invasibility would be higher in climate manipulation treatments where the productivity of the resident vegetation was reduced by climate forcing and in short-term climate manipulation, where little if any adaptation of the extant plant community to climate forcing was expected. With seed addition, we expected *Bromus* to be the more successful invader under scenarios of summer drought (higher drought tolerance) and winter warming (due to its growth phenology) and *Brachypodium* to perform better than *Bromus* under higher competition from the extant plant community, especially in deeper soils. Moreover, we expected seedlings from more northern seed provenances to perform better as a result of higher frost tolerance and more similar photoperiod.

Materials and methods

The Buxton Climate Change Impacts (BCCI) study was established in 1993 to determine whether predicted climate conditions prevailing in c. 2100 would significantly impact calcareous grasslands of northern England. Annual climate manipulation has included winter warming (3°C above ambient from November to April imposed by heating cables installed on the soil surface) and summer drought (interception of all rainfall throughout July and August by automated transparent shelters) in semi-natural grassland on a dale side at the Health and Safety Laboratory, Harpur Hill, Derbyshire, UK. The experimental design includes factorial combinations of the *long-term winter warming* (W_L) and *long-term summer drought treatments* (D_L), which are applied to 3 × 3 m grassland plots arranged in a fully randomized block design replicated five times. In fall 2007, an additional treatment simulating the combined effects of winter warming and summer drought was set up in one spare plot of each block (*short-term warming and drought treatment*; WD_S). These plots received the same treatment as the controls until 2007. Vegetation is cut in October each year to a height of c. 50 mm and the clippings removed to simulate sheep grazing. Climate manipulations and their influence on the extant plant community are described in more detail in Grime *et al.* (2008) and Fridley *et al.* (in press).

Bromus erectus Huds. and *Brachypodium pinnatum* (L.) Beauv. are of general southern distribution in Britain and reach their northernmost range limit in the lowlands of north-east England, but are currently not able to colonize higher altitudinal grasslands in the

Pennines, where the BCCI study is located (Preston, Pearman & Dines 2003). *Bromus* disperses primarily by seeds, whereas *Brachypodium* relies almost exclusively on vegetative regeneration and has generally poor seed set (Grime, Hodgson & Hunt 2007). For each species, seeds were collected in August 2008 from three unproductive grasslands located along a latitudinal gradient in the lowlands east of the Pennines. The southernmost provenances were collected in the vicinity of Warsop Vale (*Bromus*) and North Anston (*Brachypodium*), intermediate provenances at Maltby common, and the northernmost provenances near Cadeby, Conisbrough (Fig. 1). Coordinates of seed collection sites, average seed mass and germination percentages under laboratory conditions are given in Table S1 in Supporting Information.

In each of the 25 grassland plots, two quadrats of 25 × 25 cm were established for each species, one of shallow soil depth (< 12 cm) and the other deep (≥ 12 cm) wherever possible. In three randomly selected corners of each quadrat, 50 seeds of one species and provenance (30 in the case of *Bromus* from Cadeby) were sown into subplots of 10 × 10 cm after the vegetation was cut in November 2008, resulting in a total of 150 subplots for each species. Quadrats were covered with wire cages until 2009 to prevent seed predation by mice. Seedling emergence and survival were surveyed in April, June and October 2009, and May 2010. At each census, newly emerged seedlings were marked with a coloured ring so that cohorts of seedlings with different emergence dates could be distinguished throughout the experiment. In the WD_S treatment, the first census took place in June 2009; thus seedlings could not be classified into winter and spring cohort in this treatment. In October 2009, a random subset of seven seedlings of the winter cohort (i.e. seedlings germinated between November 2008 and April 2009) and seven seedlings of the spring cohort (germinated between April and June 2009) were harvested in the long-term treatments (where fewer seedlings were available, subsets contained 0–6 seedlings). A random subset of 14 seedlings was harvested in the WD_S treatment. As a surrogate of the above-ground competitive effect of neighbours, annual productivity of the resident vegetation was measured by harvesting all living and dead plant material in the 10 × 10 cm subplots to a height of 3 cm above ground before the vegetation was cut in October 2009. Above-ground biomass of individual seedlings and surrounding vegetation was measured after drying the plant material to constant weight. Soil depth of each subplot was defined as the median of five measurements taken at the four corners and the centre of the 10 × 10 cm quadrat. The effectiveness of the summer drought treatment was verified by measuring volumetric water content (VWC) of the top soil (0–5 cm) on 17 August 2009, i.e.

towards the end of the drought treatment, using a Decagon (Pullman, WA, USA) ECH2O EC-5 moisture sensor. Quadrats with > 25% VWC were excluded from data analyses due to our suspicion of water seepage from adjacent plots (see Fridley *et al.* in press).

To analyse the distribution of resident vegetation biomass along the soil depth gradient, generalized additive models (GAMs) were fitted separately to above-ground biomass values of all subplots in the same climate treatment using the *R mgcv* library (version 1.6–2). Success of *Bromus* and *Brachypodium* was measured in terms of seedling emergence rate (proportion of seeds emerged between November 2008 and October 2009), average above-ground seedling biomass and total above-ground seedling biomass per subplot. The latter was corrected for the number of seeds sown and was calculated as $B_{\text{Total}} = (N_{\text{W}} \times B_{\text{W}} + N_{\text{S}} \times B_{\text{S}}) / S \times 50$, where N_{W} and N_{S} are the number of living winter and spring seedlings in October 2009, B_{W} and B_{S} represent the average biomass of the harvested winter and spring seedlings, and S equals the number of sown seeds (usually 50). Effects of climate treatments, soil depth and resident vegetation biomass on success measures were analysed separately for *Bromus* and *Brachypodium* using the univariate GLM procedure of SPSS Statistics (Release 17.0.0, SPSS Inc., 2008, Chicago, IL, USA). The layout of the experiment was a split-plot design with five blocks (whole-plots) and six subplots within each of the five treatment combinations of a block (split-plots). The factors included in the ANCOVA and ANOVA were block, climate treatment (whole-plot factor) and seed provenance (split-plot factor). As randomization of the whole-plot factor is not complete in a split-plot design, the factor climate treatment was tested against the whole-plot error, seed provenance and its interactions against the residuals (Sahai & Ageel 2000). Soil depth and surrounding vegetation biomass were included as covariates in the analyses. As effect sizes of the covariates were small and effects often restricted to one climate treatment, ANOVA results (with *post hoc* pairwise Tukey's HSD tests) are shown for the main factors alongside ANCOVA results for the covariates. In cases where data did not meet assumptions of normality or homogeneity of variances, logarithmic, square root or arcsine (mortality) transformation improved data structure satisfactorily.

Results

After 15 years of climate manipulation, above-ground biomass production of the resident vegetation was not affected by W_L (GAM, $P > 0.7$; Fig. 2), but decreased in response to D_L and WD_L, especially in deep subplots (GAM, $P < 0.01$). Above-ground biomass production was positively related to soil depth in controls and communities subjected to W_L (GAM, $P < 0.01$ and $P < 0.05$ respectively) but was independent of soil depth in D_L and WD_L communities (GAM, $P > 0.3$). In the WD_S treatment, above-ground biomass production was negatively affected in deep but not in shallow subplots (GAM, $P < 0.05$).

Seedling emergence rate between November 2008 and October 2009 of *B. erectus* was higher in W_L and WD_L than in D_L communities but did not differ from controls (Fig. 3a and Table 1). Similar results occurred in *B. pinnatum* seeds, but in contrast to *Bromus*, seedling emergence did not increase in response to WD_L (Fig. 3b). In both species, seedling emergence rates did not differ between seed provenances and were not affected by the amount of surrounding vegetation. In W_L and D_L communities, seedling emergence of *Bromus* slightly decreased with increasing soil depth (Table 1; see Fig. S2),

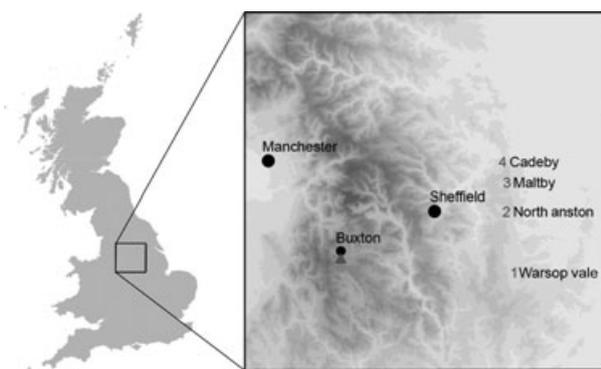


Fig. 1. Location of the experimental site (triangle) in the Pennines near Buxton, Derbyshire, UK and the seed collection sites in the lowlands east of the Pennines (1–4). Coordinates are given in Table S1.

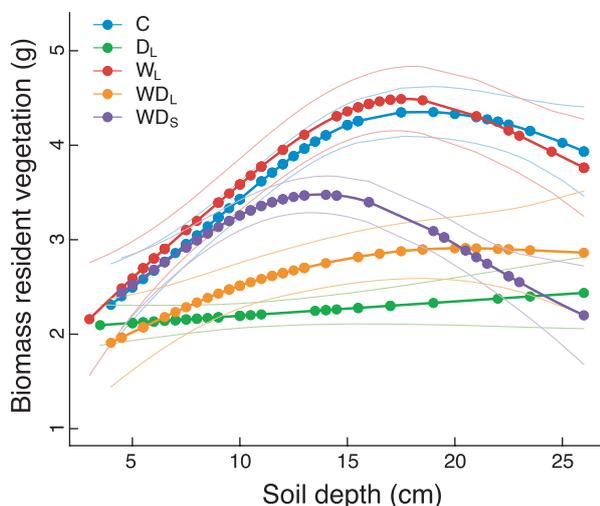


Fig. 2. Above-ground biomass production of the resident vegetation in subplots of 10 × 10 cm arranged along the soil depth gradient in controls (C) and the long-term climate treatments summer drought (D_L), winter warming (W_L), combined winter warming and summer drought (W_{D_L}) and short-term winter warming and summer drought (W_{D_S}). Curves are fitted as generalized additive models (GAMs) ± SE; dots represent the distribution of the subplots along the soil depth gradient. Data used to fit the GAMs are shown in Fig. S1.

although this could also have resulted from very early seedling mortality. Overall, effects of climate manipulations on seedling emergence rates were rather small, but winter warming induced earlier emergence in both species. Between November 2008 and April 2009, seedlings emerged from 62.7% (± 0.03 SE) of the *Bromus* seeds but only from 12.9% (± 0.02) of the *Brachypodium* seeds sown in the controls. In the same period, seedlings emerged from 86.3% (± 0.02) of the *Bromus* seeds and 68.5% (± 0.03) of the *Brachypodium* seeds in communities subjected to W_L (W_{D_L} 86.6 \pm 0.02 and 62.7 \pm 0.03 respectively). This shift in the timing of seedling emergence as a result of winter warming led to considerable differences in seedling biomass at the end of the first growing season: in both species and all treatments, seedlings that emerged between November and April (winter cohort) had *c.* 1.5 times more above-ground biomass than seedlings that emerged between May and June (spring cohort; split-split plot ANOVA of two cohorts in 117 and 113 subplots, respectively; *Bromus*: $F_{1,199} = 157.6$, $P < 0.001$; *Brachypodium*: $F_{1,179} = 174.5$, $P < 0.001$; Fig. 4a,b). Within the two cohorts, no effect of climate manipulations on seedling biomass was found in *Brachypodium* (Fig. 4b and Table 2; no data available for W_{D_S}). By contrast, winter seedlings of *Bromus* had roughly 20% higher above-ground biomass in the W_L and W_{D_L} treatments than in controls and D_L communities (Fig. 4a). The combined effect of higher above-ground biomass of winter seedlings in warmed plots and higher number of winter seedlings in the same treatments resulted in a 52%, 70% and 38% increase of total *Bromus* biomass in W_L , W_{D_L} and W_{D_S} treatments compared with controls (Fig. 3a and Table 1). By contrast, total seedling biomass of *Brachypodium* was only affected by the W_L treatment,

where it was increased by 59% compared with controls (Fig. 3b).

Seed provenance and surrounding vegetation biomass did not affect above-ground biomass of *Bromus* seedlings or total *Bromus* biomass per subplot. However, total *Bromus* biomass decreased with increasing soil depth in the W_L treatment (Table 1; see Fig. S3). *Brachypodium* seedlings were not affected by soil depth and surrounding vegetation biomass (Tables 1 and 2), but winter and spring cohorts from Warsaw seeds, the southernmost provenance, had 29% and 35% higher above-ground biomass than seedlings from Cadeby seeds, the northernmost provenance (Table 2; Tukey's HSD, $P < 0.001$). This resulted in 37% higher total seedling biomass in subplots sown with Warsaw seeds than those sown with Cadeby seeds (Table 1; Tukey's HSD, $P < 0.001$). The difference in above-ground biomass between the two provenances cannot be attributed to seed mass, which was of comparable size (Tukey's HSD, $P = 0.397$; see Table S1).

To a remarkable extent, survival of the 3908 *Bromus* and 3757 *Brachypodium* seedlings that emerged between November 2008 and October 2009 was high during the first growing season. In *Brachypodium*, only 1.3 (± 0.2) % of the seedlings died between April and October 2009, independent of climate treatment (ANOVA of 140 subplots: $F_{4,16} = 1.105$, $P = 0.386$). First-year summer mortality of *Bromus* seedlings was slightly lower in W_{D_S} plots (0.9 \pm 0.4%) than in controls (4.6 \pm 0.9%) and W_{D_L} communities (3.8 \pm 0.8%; ANOVA of 144 subplots: $F_{4,16} = 3.821$, $P = 0.022$; Tukey's HSD, $P = 0.002$ and $P = 0.030$ respectively). During the following winter and spring (October 2009–May 2010), mortality was still independent of climate treatment in *Brachypodium* (ANOVA of 130 subplots: $F_{4,16} = 0.838$, $P = 0.523$) but it increased to 7.9 (± 0.2) % (Fig. 3b). In *Bromus*, winter and spring mortality remained below 5% in controls, D_L , W_{D_L} and W_{D_S} treatments, but reached 15.6 (± 0.3) % in the W_L plots (ANOVA of 137 subplots: $F_{4,16} = 8.825$, $P = 0.001$; Tukey's HSD, $P = 0.002$; Fig. 3a).

Discussion

DISPERSAL LIMITATION VERSUS CLIMATIC BARRIERS

Our results suggest that the low current seed rain of potential invaders is an important contributor to the observed lack of new species immigration following climate forcing in temperate grasslands (Harte & Shaw 1995; Rustad *et al.* 2001; Grime *et al.* 2008). Sowing the grassland of the BCCI study with seeds of *B. erectus* and *B. pinnatum*, two potential dominants of calcareous grassland in northern England in a warmer and drier climate, resulted in the establishment of the majority of sown seeds, with > 80% of the seedlings surviving past 1 year. Successful establishment and seedling growth in all climate treatments, including the controls (Fig. 3), indicate that migration of *Bromus* and *Brachypodium* is not currently limited by climatic barriers to the growth of established plants but rather to barriers that are inhibiting initial dispersal into grassland of higher latitude and elevation. For instance, dispersal may be

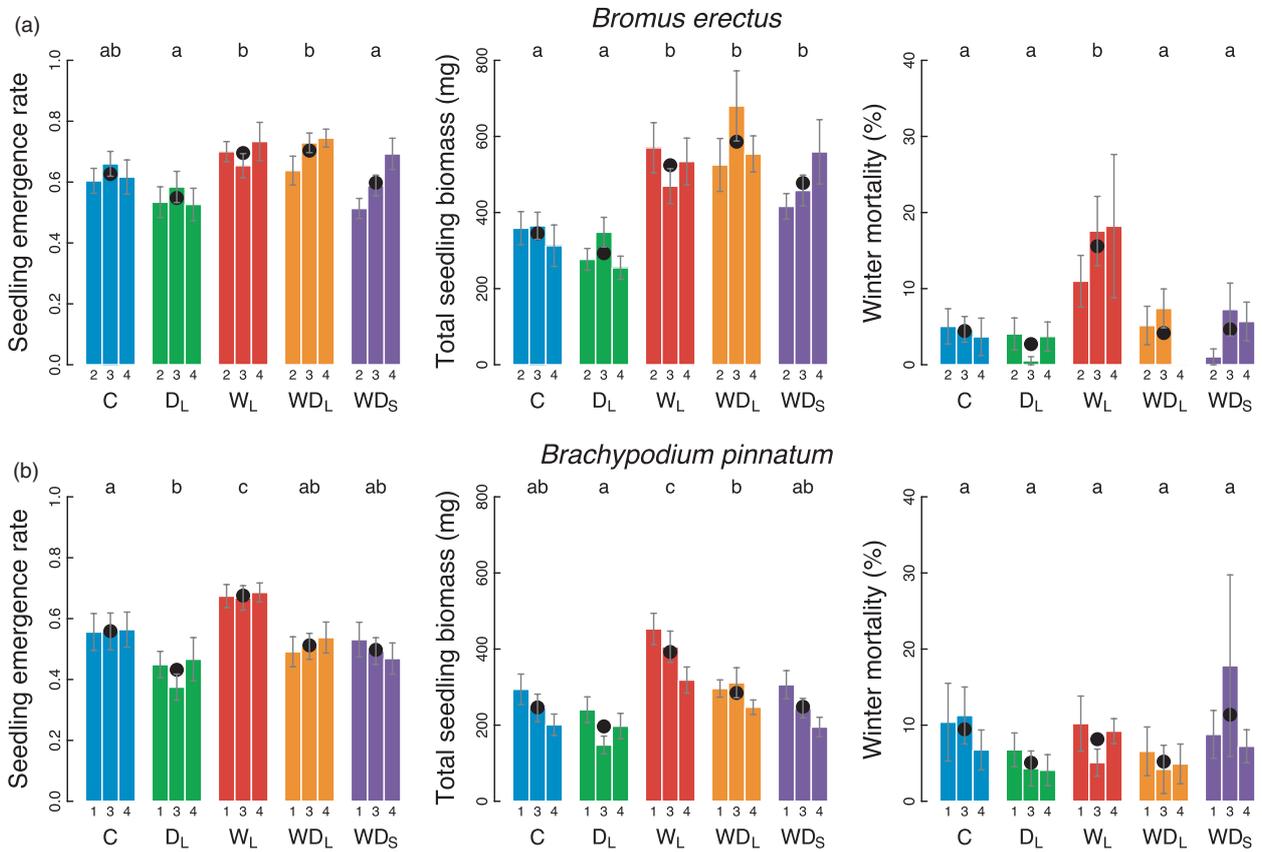


Fig. 3. Seedling emergence rate in 2009, total seedling biomass 100 cm⁻² in October 2009 and mortality between October 2009 and May 2010 of (a) *Bromus erectus* and (b) *Brachypodium pinnatum* in the controls (C) and the long-term climate treatments summer drought (D_L), winter warming (W_L), combined winter warming and summer drought (WD_L) and the short-term winter warming and summer drought treatment (WD_S). Bars represent means (±SE) of individual seed provenances, which are arranged from southernmost (1) to northernmost (4) provenance (details see Fig. 1); black circles show means across all provenances. Identical letters above two circles indicate no statistical differences between overall means (ANOVA followed by Tukey’s HSD tests).

Table 1. Split-plot ANCOVA and ANOVA results for the effects of climate treatment (whole-plot factor), seed provenance (split-plot factor), soil depth and biomass of the resident vegetation (covariates) on seedling emergence rate and total above-ground seedling biomass 100 cm⁻² (mg) of *Bromus erectus* and *Brachypodium pinnatum* seedlings. Climate treatments include control, long-term summer drought, winter warming, combined winter warming and summer drought, and short-term winter warming and summer drought. Bold font indicates *P*-values < 0.05

Source of variation	<i>Bromus erectus</i>						<i>Brachypodium pinnatum</i>					
	Seedling emergence rate			Total seedling biomass (mg) *			Seedling emergence rate			Total seedling biomass (mg)		
	<i>F</i>	d.f.	<i>P</i> -value	<i>F</i>	d.f.	<i>P</i> -value	<i>F</i>	d.f.	<i>P</i> -value	<i>F</i>	d.f.	<i>P</i> -value
ANCOVA												
Soil depth	4.774	1,107	0.031	4.823	1,107	0.030	0.148	1,103	0.702	2.355	1,103	0.128
Vegetation biomass	0.000	1,107	0.987	0.098	1,107	0.755	0.046	1,103	0.831	0.736	1,103	0.393
ANOVA												
Climate treatment	6.570	4,16	0.002	11.088	4,16	<0.001	4.584	4,16	0.011	9.500	4,16	<0.001
Block	1.701	4,16	0.197	1.349	4,16	0.294	1.575	4,16	0.228	1.606	4,16	0.220
Whole-plot error	–	16	–	–	16	–	–	16	–	–	16	–
Provenance	2.813	2,109	0.064	1.002	2,109	0.371	0.282	2,105	0.755	9.530	2,105	<0.001
Climate × provenance	1.247	8,109	0.279	1.380	8,109	0.213	0.343	8,105	0.947	0.918	8,105	0.505
Residuals	–	109	–	–	109	–	–	105	–	–	105	–

*Log transformed.

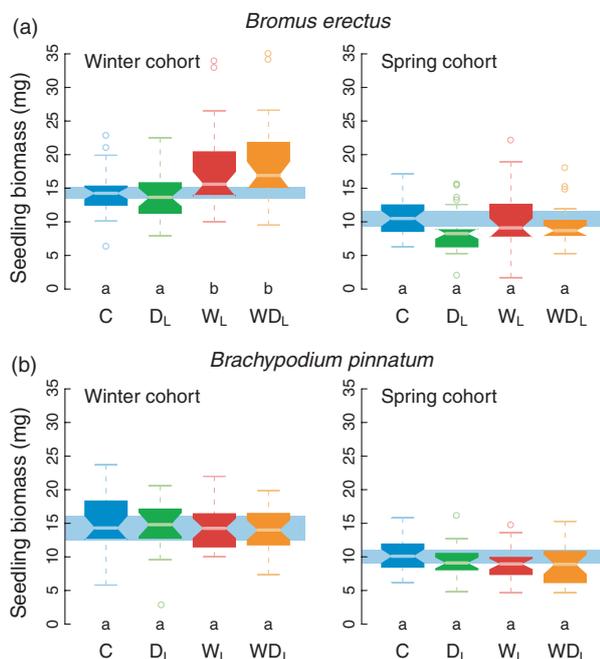


Fig. 4. Above-ground biomass of (a) *Bromus erectus* and (b) *Brachypodium pinnatum* seedlings germinated during winter (November 2008–April 2009) and spring (May 2009–June 2009) respectively, in controls (C) and the long-term climate treatments summer drought (DL), winter warming (WL) and combined winter warming and summer drought (WDL; no data available for the short-term warming and drought treatment). Horizontal blue bars indicate 95% confidence interval for the median of the control. Identical letters below two boxes indicate no statistical differences between means (ANOVA followed by Tukey's HSD tests).

limited by low seed production at the northern range limit due to photoperiod or shorter growing seasons, which result in migration being dependent on rare long-distance dispersal. Self-incompatibility may further reduce the migration rate of a species if dispersal events are rare (Küster *et al.* 2010). If reproductive barriers at the northern range limit are overcome as a result of climate warming, as seems likely for many species (Normand *et al.* 2009), the absence of new species immigration in the BCCI grassland will ultimately be a short-term phenomenon.

COMMUNITY INVASIBILITY

We found no differences in total invader biomass and mortality between plant communities experiencing climate forcing for long (15 years) and short (1 year) durations (Fig. 3, centre and right). Spatial shifts of extant species along the soil depth gradient (Fridley *et al.* in press) and potential genetic restructuring after 15 years of climate manipulations are likely to be insufficient to prevent species invasions in the longer term. Consequently, rates of poleward migrations for calcareous grassland species will largely depend on the speed at which individual species are able to disperse under climate change.

Invasion success of *Bromus* and *Brachypodium* was not related to the productivity of the extant plant community, either at the level of climate manipulations (3×3 m plots) or at the subplot level. At the level of climate manipulations, resident vegetation biomass was most severely affected by summer drought (Fig. 2), but invaders were most successful in communities with winter warming (Fig. 3, centre). We had expected

Table 2. Split-plot ANCOVA and ANOVA results for the effects of winter warming and summer drought (whole-plot factors), seed provenance (split-plot factor), soil depth and resident vegetation biomass (covariates) on above-ground biomass (mg) of *Bromus erectus* and *Brachypodium pinnatum* seedlings germinated during winter (November 2008–April 2009) and spring (May 2009–June 2009) respectively. Only long-term climate treatments are included because data on seedling cohorts are not available. Bold font indicates P -values < 0.05

Source of variation	<i>Bromus erectus</i>						<i>Brachypodium pinnatum</i>					
	Winter seedlings*			Spring seedlings†			Winter seedlings			Spring seedlings		
	<i>F</i>	d.f.	<i>P</i> -value	<i>F</i>	d.f.	<i>P</i> -value	<i>F</i>	d.f.	<i>P</i> -value	<i>F</i>	d.f.	<i>P</i> -value
ANCOVA												
Soil depth	1.579	1,87	0.212	0.443	1,84	0.508	0.314	1,68	0.577	3.288	1,83	0.073
Vegetation biomass	0.133	1,87	0.716	0.539	1,84	0.465	2.523	1,68	0.117	3.085	1,83	0.083
ANOVA												
Warming	8.944	1,12	0.011	0.121	1,12	0.734	0.843	1,12	0.375	4.064	1,12	0.065
Drought	0.008	1,12	0.932	3.081	1,12	0.104	0.893	1,12	0.362	1.076	1,12	0.319
Warming \times drought	0.419	1,12	0.530	1.279	1,12	0.280	0.303	1,12	0.591	0.936	1,12	0.351
Block	2.191	4,12	0.131	0.495	4,12	0.740	1.771	4,12	0.195	0.890	4,12	0.498
Whole-plot error	–	12	–	–	12	–	–	12	–	–	12	–
Provenance	1.739	2,89	0.182	0.538	2,86	0.586	9.003	2,70	<0.001	15.232	2,85	<0.001
Warming \times provenance	0.039	2,89	0.962	1.373	2,86	0.259	0.456	2,70	0.635	0.926	2,85	0.400
Drought \times provenance	0.737	2,89	0.482	0.183	2,86	0.833	2.424	2,70	0.096	0.915	2,85	0.405
Warming \times drought \times provenance	0.777	2,89	0.463	1.260	2,86	0.289	1.320	2,70	0.274	0.616	2,85	0.543
Residuals	–	89	–	–	86	–	–	70	–	–	85	–

*Log transformed.

†Square root transformed.

that the negative effect of summer drought on resident vegetation biomass would decrease competition and hence increase site availability for invading species. At the level of invasion subplots (10 × 10 cm), no signs of competitive interaction between the extant vegetation and invader performance were found in *Brachypodium* and only marginal effects of soil depth were detected in *Bromus* (Table 1). This suggests that if effects of competition are to be observed, they must become apparent at a later stage of seedling establishment.

INVADER GROWTH PHENOLOGY AND RESOURCE AVAILABILITY

Reduced productivity of the resident vegetation may increase nutrient availability to potential invaders after drought periods. Measurements of plant N supply in an ancillary study has shown no differences in plant N supply between climate manipulations before and during the drought event and a doubling of N supply in the D_L communities immediately after the drought in September (Fridley *et al.* in press). However, by the end of November, an increase in N supply of the same magnitude was also measured in the other climate treatments. High levels of N probably continued during winter as a result of reduced nutrient acquisition by resident species after the main growing season. *Bromus* can grow late in the season or even during winter (Kahlert, Ryser & Edwards 2005). Consequently, its high invasion success in treatments with winter warming (Fig. 3a, centre) and the fact that winter seedlings had higher biomass in warmed compared with non-warmed plots (Fig. 4a, left) corroborate the hypothesis that invasion success is tied to the ability of a species to exploit nutrients at times when they are abundant (Davis, Grime & Thompson 2000). In *Brachypodium*, winter seedlings had also higher above-ground biomass than spring seedlings, but in contrast to *Bromus*, seedling biomass within cohorts did not differ between climate manipulations (Fig. 4b). This indicates that winter warming extended the growing season for this species but seedlings were not able to make use of high N availability during winter because leaf growth ceases in autumn. These results suggest that the synchrony of invader phenology with seasonal resource availability, which in turn is determined by the phenology of the resident vegetation, is conducive to invasion and may allow even a weak competitor, in this case *Bromus*, to invade intact vegetation.

INVADER IDENTITY AND SEED PROVENANCE

As expected, the two southern species were not negatively affected by summer drought and both *Bromus* and *Brachypodium* seedlings performed similarly in controls and the D_L communities (Fig. 3, centre). Nevertheless, a difference in drought tolerance was observed between the two species in the winter warming treatments. *Brachypodium* benefited from winter warming only in the absence of summer drought, whereas *Bromus* increased total seedling biomass irrespective of summer drought. The latter possibly enhanced the frost resistance of *Bromus* seedlings, an effect that is indicated by low seedling

mortality in WD_L and WD_S compared with W_L treatments (Fig. 3a, right). The connection between drought and frost resistance could simply be a consequence of morphology as individuals in the communities subjected to drought had shorter leaves than those in communities that did not experience drought, but physiological mechanisms have also been put forward to explain the positive relationship between nutrient-stress tolerance and frost tolerance in temperate grassland species (MacGillivray *et al.* 1995). Despite rising temperatures, frost is likely to remain as a regular disturbance in Central Europe and the UK as a result of the predicted increase in temperature variability (Schär *et al.* 2004). Frost tolerance may thus be indispensable for the poleward expansion of plant ranges, especially in species that sustain growth during winter. We expected that possible differences in frost tolerance between seed provenances of lower and higher latitudes would affect winter mortality. This was not the case (Fig. 3, right), but seed provenance affected total above-ground biomass of *Brachypodium* seedlings (Fig. 3b, centre), which indicates lower relative growth rates of northern provenances and may in turn be an adaptation to growing season length and late frost events (Griffith & Watson 2006; Savolainen, Pyhajarvi & Knurr 2007).

Conclusions

Our results support the present understanding that increased winter temperatures and longer growing seasons will facilitate poleward migration of plant species (Kreyling 2010). In this respect, our field study is broadly consistent with climate-envelope modelling studies in which climate is the principal driver of species range shifts (Morin, Viner & Chuine 2008). In contrast, the effect of drought as a promoter of community invasibility is less clear and may largely depend on the identity of the migrating species and its interaction with the invaded plant community. Our study should be a critical reminder that evaluating the susceptibility of ecosystems to climate changes that occur on time-scales of decades to centuries must include long-term immigration considerations in addition to climate manipulation. In any given year, long-distance dispersal events are rare for most species (Nathan *et al.* 2008) and yet nearly all of the existing north-temperate and boreal flora migrated hundreds of kilometre to warm and cold refugia repeatedly during the Pleistocene (Comes & Kadereit 2003). This wider biogeographic context that includes not just more southern species but also those introduced from other continents, should be a key consideration in the next generation of experimental climate impact studies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Data used to fit the GAMs shown in Fig. 2.

Figure S2. Relationship between seedling emergence rate of *Bromus erectus* and soil depth.

Figure S3. Relationship between total seedling biomass of *Bromus erectus* and soil depth.

Table S1. Provenance details and characteristics of the seed material used in the invasion experiment.

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