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Grassland invasions: effects of manipulations of climate and management

S.M. BUCKLAND*, K. THOMPSON, J.G. HODGSON and J.P. GRIME
Animal and Plant Sciences, The University of Sheffield, Western Bank, Sheffield S10 2TN, UK

Summary

1. Climate change, in combination with the impacts of land use, will give rise to new opportunities for grassland invasion. This paper reports on the repercussions of a field experiment.

2. Plant species, sown into experimental plots as part of a 6-year study investigating factors limiting the success of seedling invasions, were resurveyed in 1999, 3 years after terminating experimental manipulations of climate, soil fertility and disturbance.

3. The most dramatic observation was the protracted expansion in populations of *Brachypodium pinnatum*, despite being at the northern limit of its distribution in Britain. In contrast, all other sown species, including those of both southern and widespread distribution in Britain, had become extinct, declined or remained unchanged in abundance.

4. Patterns of establishment were strongly deterministic. Populations of the southern grass, *B. pinnatum*, were highest in areas of the experimental plots unamended by fertilizer and physical disturbance, but expansion was apparently promoted by cessation of management. Among invaders of widespread distribution, two were dependent upon fertilizer addition (*Arrhenatherum elatius* and *Dactylis glomerata*), one significantly increased its cover with a combination of fertilizer and disturbance (*Holcus lanatus*), and one benefited from disturbance (*Plantago lanceolata*).

5. Two southern perennials, *Origanum vulgare* and *Senecio erucifolius*, both remained present in 1999 in plots that were formerly heated and subject to drought (1991–96), whereas they had become extinct in control plots.

6. Although the most successful invader was a rhizomatous perennial grass, an alternative strategy for survival and expansion was revealed after the severe drought in 1995: gap recolonization by annuals with a persistent seed bank.

7. Most notably, this study revealed the hidden potential of a native species to establish beyond its current range of distribution and, contrary to many recognized weeds, the capacity to achieve dominance in the absence of eutrophication or disturbance. This highlights the potent effects of climate change when plant traits effective for establishment coincide with the removal of current barriers to dispersal.

Key-words: abandonment, *Brachypodium pinnatum*, climatic limits, land use.

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Introduction

An increased frequency of mild winters, droughts, storms and floods provides compelling evidence of global climate change. Within the UK, projections of future climate change have been provided by Hulme & Jenkins (1998). As a result, concerns are developing about the potential impacts on both agriculture (Hanson, Baker & Bourdon 1993; Chakraborty *et al.* 1998) and wildlife (Markham 1996; Coley 1998). In particular, where climate is known to govern the distribution of plants and animals (Pigott & Huntley 1981; Beerling 1993), climate change is likely to alter current limits of distribution. However, long before alarm developed over global impacts of climate change, human impacts on the spread of weedy and alien species were already apparent, as a result of activities such as travel, physical disturbance, agricultural intensification and land degradation or dereliction (Ratcliff 1984; Vitousek *et al.*

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*Present address and correspondence: Sarah Buckland, Macaulay Land Use Research Institute, Sourhope, Yetholm, Kelso, Roxburghshire TD5 8PZ, UK (fax 01573 420787; e-mail s.buckland@mluri.sari.ac.uk).

1997; Manchester & Bullock 2000). With declines in intensive agriculture or management, the consequences of dereliction will become more widespread (Muller 1996).

In order to investigate the impacts of future climate change on species' distributions, it is therefore pertinent to consider the interaction with major factors associated with land use, known already to affect the spread of weedy species. With these two broad concerns of climate change and land use in mind, a field experiment was started in 1990 at the Buxton Climate Change Impacts Laboratory in northern England. The specific purpose was to examine plant invasions into an upland pasture, subjected to various turf manipulations, situated at the northern limits of distribution for many species in Britain.

The excursion of individual species beyond their present climatic boundaries is a recurring feature in simulations of the impact of future climates on vegetation cover (Woodward & Jones 1984; Huntley *et al.* 1995). Most of these simulations presuppose movement through seedling regeneration, a discontinuous process involving a series of steps (seed production, dispersal, establishment and persistence), each of which may be controlled critically by climate. Several investigations (Bell & Bliss 1979; Carter & Prince 1981; Pigott & Huntley 1981) have confirmed that the first two stages, seed production and dispersal, are sensitive to climate variations at the climatic limits of species' distributions. The focus of attention in the Buxton experiment was on the latter two stages, establishment and persistence. The experiment included a mixture of sown species. Some species had widespread distributions in Britain. Other species had distributions restricted to the warmer climes of southern Britain and which could potentially expand their northern boundaries in response to an amelioration in climatic conditions. In addition, species differed in ecology, life history and seedling characteristics in order to measure the capacity for invasion in a range of vegetation types and regenerative conditions.

It is widely recognized (Bazzaz 1986; Crawley 1987; Pysek & Prach 1993) that an understanding of plant invasions requires attention to both the invading species and the invaded vegetation. Davis, Grime & Thompson (2000) have proposed that invasibility depends on increased resource availability that may arise from a variety of causes, but often occurs only intermittently and results in invasion only if it coincides with availability of invading propagules. As a result, the experiment aimed to investigate the invasion of an ecologically contrasted range of species into native vegetation with and without various turf manipulations.

For 6 years (1990–96), the experiment involved manipulations of climate, comprising soil warming ± late spring night frosts, and drought, and management consisting of physical disturbance and fertilizer application. The main purpose of this study was to examine the longer term fate of the sown species, in particular examining their persistence in 1999, 9 years since introduction into the plots and 3 years after both climate and management treatments were terminated.

Methods

FIELD SITE

An account of both field site and methods appears in Buckland (1994). In addition, the field site is described in Burke & Grime (1996) and both site and methods in Akinola, Thompson & Buckland (1998), and thus a brief account only is given here. The field site is a north-west facing dale-side with a slope of *c.* 30°, and lies at 370 m a.s.l. (National Grid reference SK055706, 53°25′ latitude, 2°20′ longitude) near Buxton in Derbyshire, UK. The substratum is carboniferous limestone over which the soils are locally surface leached, resulting in a variable surface pH (3·9–7·5). Average annual rainfall is about 1200 mm and exhibits little seasonality. The infertile soils support a grassland community largely composed of slow-growing herbs and dwarf shrubs, often with calcifuges and calcicoles occurring in close proximity to each other.

EXPERIMENTAL MANIPULATION

Within 20, 2 × 2-m, plots, two opposed five-step gradients in soil fertility and physical disturbance were applied. This created 25 subplots, each with a unique combination of fertility and disturbance. A central area (1·5 × 1·5 m) within each plot comprised the experimental area to be monitored. To reduce the possibility of edge effects, the surrounding 250-mm border provided a buffer zone where the soil and vegetation received the same treatment as the subplot immediately adjacent to it. The plots were arranged in a 4 × 5 block.

The fertility gradient was created and maintained by applying NPK (20 : 10 : 10) granular agricultural grade fertilizer in October 1990 and April 1991 and at the same time each following year until the termination of the experiment in September 1996. The five-step gradient was created by adding fertilizer at rates of 0, 60, 120, 180 and 240 kg ha^{-1}. The five-step gradient in physical disturbance was first imposed in October 1990 and repeated each October until 1995. A specifically designed cutting tool (auger) was used to create circular gaps in the turf. The auger terminated in a circular plate with two cross-blades that cut the turf to a depth of 25 mm as it was twisted into the surface. Severed plant material and soil were removed from the blades at frequent intervals and as far as possible left in the subplots from which they were originated. Each gap exposed an area of *c.* 11 300 mm^2 and, by varying the number of gaps, a gradient in bare ground was established.

Seeds of 36 species were sown into the plots at the start of the experiment, of which seven grasses and nine forbs had widespread distributions and 20 species displayed some degree of southern restriction. Seeds of species of widespread distribution were collected

Table 1. List of sown species, their sowing rate and their percentage frequency in 500 subplots of 20 plots, in years 1991, 1996 and 1999

		Percentage frequency		
Species	Sowing rate (m^{-2})	1991	1996	1999
Widespread species				
Agrostis stolonifera	550	4	1	2
Arabidopsis thaliana	550	23	23	0
Arabis hirsuta	50	3	6	0
Arrhenatherum elatius	200	4	27	28
Chamanerion angustifolium	300	2	0	0
Chenopodium album	300	10	3	0
Dactylis glomerata	350	17	53	39
Galium aparine	150	13	8	1
Holcus lanatus	150	58	83	77
Lolium perenne	400	9	3	0
Plantago lanceolata	350	90	88	76
Poa annua	950	24	2	0
Trifolium repens	350	21	3	0
Urtica dioica	300	6	0	0
Southern species				
Ballota nigra	400	0	0	0
Brachypodium pinnatum	200	12	28	57
Bryonia dioica	50	0	0	0
Campanula glomerata	300	24	4	0
Centaurea scabiosa	100	9	1	0
Chaerophyllum temulentum	200	4	2	0
Conyza canadensis	450	7	0	0
Daucus carota	100	28	2	0
Filipendula vulgaris	300	2	2	2
Foeniculum vulgare	50	1	0	0
Hypericum maculatum	250	*p*	12	13
Hypericum perforatum	550	*p*	15	9
Lactuca serriola	550	24	1	0
Malva sylvestris	50	3	1	0
Melilotus altissima	100	2	0	0
Origanum vulgare	300	30	4	4
Saxifraga tridactylites	1100	0	0	0
Senecio erucifolius	650	17	1	2
Smyrnium olusatrum	100	16	0	0
Solanum nigrum	300	5	0	0

Deschampsia cespitosa, although a sown species, was omitted from the list owing to its presence in the native vegetation.
'*p*' refers to the sown *Hypericum* spp. being present in 1991 but could not be distinguished from the native *Hypericum* spp.

from populations established within a 50-km radius of Sheffield, whereas a number of visits further south were necessary to make collections of species restricted to southern Britain. Seed-sowing rate was adjusted to seed size, although in a small number of cases sowing rate was reduced because of a shortage of seeds. A small number of additional species, plus a few of the original species, was also sown in 1994. Total sowing rates of species are listed in Table 1.

At the whole-plot level there were four climate treatments, each with five replicates. These were: (i) control; (ii) mild winter, simulated by soil-warming cables operating between 1 November and 31 May over the period 1991–96; (iii) mild winter followed by an artificial night air frost in early June (Thorpe, MacGillivray & Priestman 1993); and (iv) artificial summer drought, applied by automatic rain shelters that excluded rainfall in July and August. All treatments (climate, fertilizer addition and disturbance) were discontinued in 1996.

The responses of the vegetation to the experimental treatments were monitored by an annual survey of all 20 plots between 1991 and 1996 and subsequently in 1999. An estimate of vertically projected cover was made using a scale from 0 to 5 (1, < 5% cover; 2, 6–25%; 3, 26–50%; 4, 51–75%; 5, 76–100%) in each of 25 subplots of a 1·5 × 1·5-m quadrat. Nomenclature follows Stace (1991).

As there were no detectable long-term effects of the frost treatment (Buckland 1994), the effects of the mild winter were determined using the mean of all 10 replicates subjected to winter warming. In cases where there were no effects at the whole-plot level (climate treatment), the effects of the subplot treatments (levels of soil fertility and physical disturbance) were examined by pooling data from the climate treatments. The effects of treatment were tested by one-way ANOVA, transforming data if necessary to equalize variances.

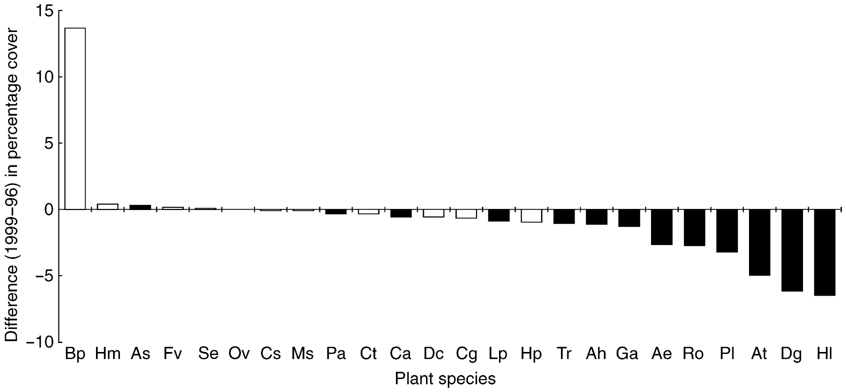

Fig. 1. The change in cover per plot of sown species in 1999 that were present in 1996. Species names are represented by their initials but names in full can be found in Table 1. Black bars indicate widespread species and white bars southern species.

Results

PERSISTENCE OF THE SOWN SPECIES

Table 1 displays the frequency of sown species in the subplots of all 20 plots at the start (1991) and at the end (1996) of the 6-year manipulative experiment and for the more recent survey in 1999. Despite the presence of seedlings of all but three southern-sown species in 1991, the data revealed that there was a marked failure of species to persist, especially short-lived and southern species. Between 1991 and 1996, seven species became extinct and a further 15 showed a decreased frequency. By 1999, only four species of widespread distribution (*Arrhenatherum elatius*, *Dactylis glomerata*, *Holcus lanatus* and *Plantago lanceolata*) and one species of southern distribution (*Brachypodium pinnatum*) were present at frequencies of greater than 20%. Moreover, after cessation of the fertility and disturbance treatments in 1996, no further increase in the populations of the widespread perennial grasses was detected. In contrast, there was a dramatic increase in *B. pinnatum.* By 1999, *B. pinnatum* was the most abundant of the sown grasses in terms of mean percentage cover per plot (22·2 ± 2·3%), just overtaking *H. lanatus* (20·2 ± 1·3%). The outstanding performance of *B. pinnatum* is illustrated in Fig. 1, which displays the change in cover from 1996 to 1999 of the sown species. Whereas the dominant widespread species lost cover, *B. pinnatum* continued to expand at an accelerating rate.

Two other southern species, although present at very low populations, were noteworthy in that their persistence was promoted by the climate treatments. Figure 2 displays the trends in abundance of *Origanum vulgare* and *Senecio erucifolius* in each of the climate treatments. The populations declined to extinction in the control plots but appeared sustainable in the plots formerly heated and subject to drought (1991–96).

EFFECTS OF FERTILITY AND DISTURBANCE

There were no significant effects of climate treatment on the abundant species and therefore within-plot treatments were examined regardless of the whole-plot treatment. Cover was summed in the four subplots of each extreme corner and analysed by one-way ANOVA to determine the significance of the different combinations of fertility and disturbance treatments, on patterns of species persistence. From Table 2 it can be seen that each species was restricted to a distinctive part of the

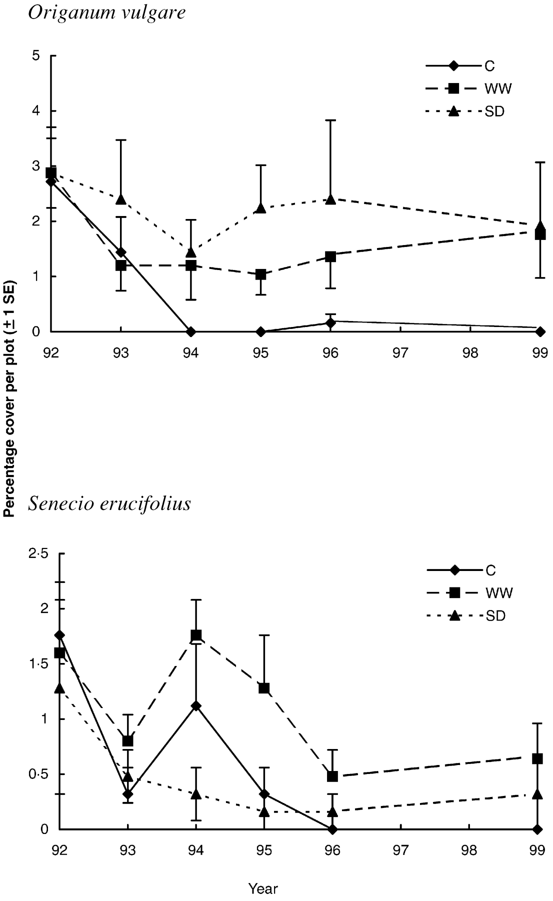

Fig. 2. The mean cover for two southern perennials, *Origanum vulgare* and *Senecio erucifolius*, in each of the climate treatments during the 6-year manipulative experiment (1991–6) and subsequently in 1999 after 3 years of natural climate. Legend key identifies the climate treatments: C, control; WW, winter warming; SD, summer drought

Table 2. The results of one-way ANOVA to determine the effects of the fertility and disturbance treatments on the patterns of invasion of the most successful sown species

	Percentage cover in each contrasted corner of the plot				
Species	IU	ID	FU	FD	*P*
Arrhenatherum elatius	0·8a	0·5a	16·8b	7·5b	0·0001
Dactylis glomerata	1·8a	2·5a	19·3b	20·8b	0·0001
Holcus lanatus	9·0a	16·8ab	20·5bc	30·3c	0·001
Plantago lanceolata	18·3a	29·8b	13·8a	24·3ab	0·01
Brachypodium pinnatum	48·0c	31·8b	6·2a	4·5a	0·0001

Mean percentage cover for each corner of the plot matrix [infertile-undisturbed (IU), infertile-disturbed (ID), fertile-undisturbed (FU), fertile-disturbed (FD)] was calculated from the cover of the four most extreme subplots of each corner of a plot (pooling climate treatments). Treatments with the same letter were not significantly different by Tukey's multiple range test. *P* is the probability of significance.

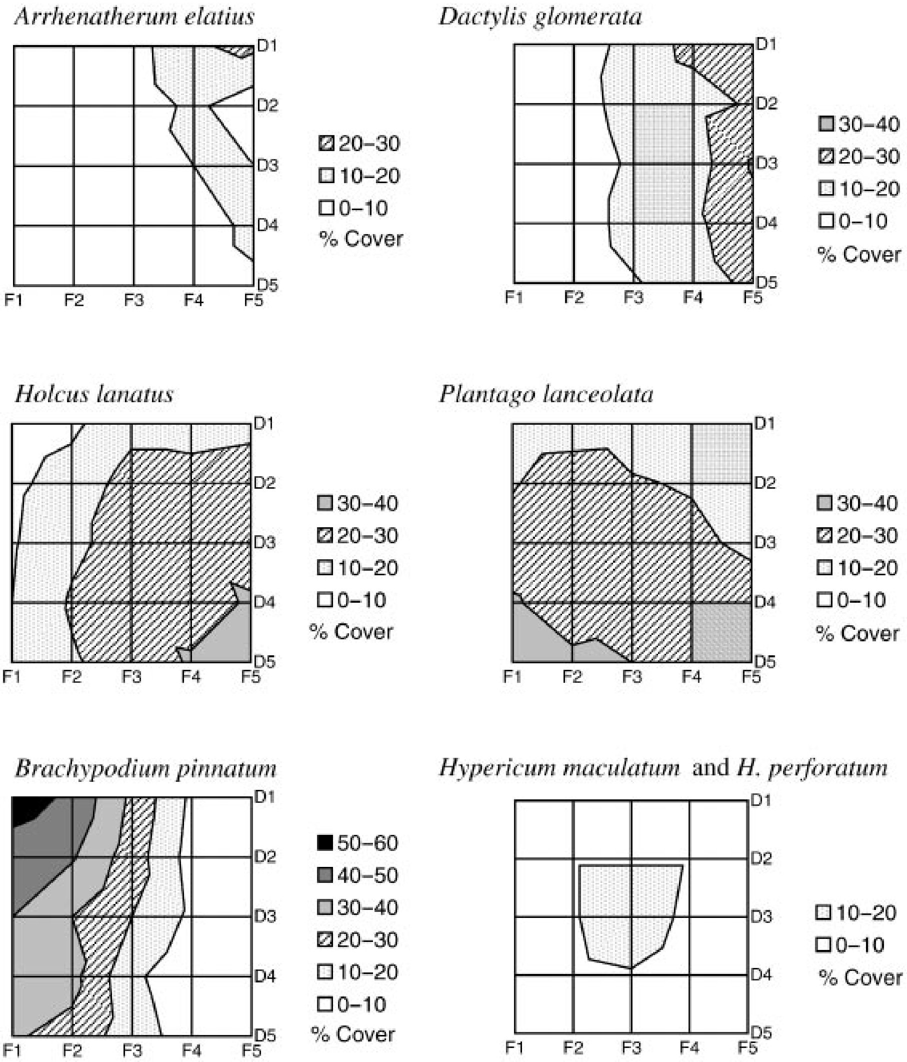

Fig. 3. The percentage cover in 1999 of the most successful of the sown species mapped onto the plot matrix comprising two five-step gradients in soil fertility (F1–F5) and physical disturbance (D1–D5).

plot matrix and that this restriction was statistically significant. This is illustrated graphically when the cover is mapped onto the plot matrix, as in Fig. 3. *Arrhenatherum elatius* was largely confined to the extreme fertile-undisturbed corner, *D. glomerata* to the fertile end, and *H. lanatus* and *P. lanceolata* were widely dispersed but the former was highest in the fertile-disturbed corner and the latter in the infertile-disturbed corner. *Brachypodium pinnatum* displayed a steep increase in cover towards the infertile-undisturbed corner, and the two *Hypericum* spp. occupied the centre region of the plot.

Discussion

SPECIES INVASION

Differences in species invasion and persistence were demonstrated in relation to the within-plot management treatments, but in the case of the climate treatments effects were not generally detected, either as a main effect at the whole-plot level or as an interaction with a subplot treatment (Buckland 1994). The absence of climatic constraints for the species of widespread distribution was most marked in the rapid establishment of *H. lanatus* and *P. lanceolata*, which both achieved high frequencies in 1991 (Table 1). Not surprisingly, for two relatively fast-growing and weedy species, their patterns of invasion, together with two other successful perennials of widespread distribution (*A. elatius* and *D. glomerata*), were controlled significantly by the gradients in soil fertility and physical disturbance (Table 2 and Fig. 3). The 1999 survey provided further evidence for the outcome of competition to be strongly deterministic, illustrated by the restricted patterns of species' distributions. Seed was sown evenly over each plot, so that the opportunity was provided from the start for species to invade all sectors of the standardized heterogeneity in turf conditions, created in each plot. Following the end of the management experiment in 1996, the widespread species appeared unable to continue to expand, potentially increasing the opportunity for other, less competitive or less gap-dependent, species.

BRACHYPODIUM PINNATUM

A spectacular increase in cover was observed in the slow-growing southern invader, *B. pinnatum*. This strongly rhizomatous species established in all plots and, regardless of climate treatments, spread vigorously throughout the unfertilized areas. During the 6-year experiment it appears that incursion into the heavily fertilized parts of the plot was restricted either by the presence of the faster-growing perennials, such as, *A. elatius*, *D. glomerata* and *H. lanatus*, or by the treatments themselves. Results from the 1999 survey suggest that, with the lack of fertilizer addition and disturbance, their potential to competitively exclude *B. pinnatum* has subsided. For example, in the area of the plots comprising the highest three levels of fertility, in 13 of the 20 plots for *A. elatius* and in 15 of the 20 plots for *D. glomerata*, percentage cover diminished between 1996 and 1999 (mean losses –4·9 ± 1·2% and –10·3 ± 1·2%, respectively). In contrast, for the same region, the cover of *B. pinnatum* increased in 18 of the 20 plots (mean increase +9·7 ± 1·2%). Consequently, it would appear that *B. pinnatum* has increased its cover in areas previously occupied by the faster-growing grasses in addition to increases in the infertile areas of the plots.

The capacity for aggressive expansion of *B. pinnatum* is of concern to Dutch ecologists, who have recognized that, without management, this species is gaining dominance in many Dutch grasslands (Bobbink & Willems 1991, 1993). Similarly, in Britain, Hurst & John (1999) observed detrimental effects of *B. pinnatum* on species diversity of ancient chalk grasslands. In limestone grasslands in the Netherlands and in northern England, soils are phosphorus-limited (Grime & Curtis 1976; Bobbink 1991). It may be that *B. pinnatum* is adapted to low-phosphorus soils, not only in relation to its low relative growth rate (Ryser & Lambers 1995) but as a result of high rates of mycorrhizal infection. Further tests are required to establish the importance of root–soil interactions for the success of *B. pinnatum* in grasslands with different nutrient limitations.

However, the replacement of the fast-growing grasses by *B. pinnatum* may not only be attributable to its low relative growth rate, permitting survival on infertile soils, but also due to its low palatability to generalist herbivores (Grime *et al.* 1996). It is likely that *B. pinnatum* benefited from its resistance to both molluscs and small mammals, both common at the Buxton site.

Successful colonization of *B. pinnatum* at Buxton, at the northern edge of its range in Britain, suggests that lack of dispersal is currently preventing its northward extension. On first inspection, the causes of distributional limits of *B. pinnatum* appear to be similar to those restricting the northward extensions of populations of *Cirsium acaule*; the two species occur in similar habitats and their geographical distributions coincide. Work by Pigott (1968) demonstrated that *C. acaule* was restricted at its northern outposts by limitations on seed production and dispersal. When these barriers are overcome, however, *C. acaule* appears to be fully capable of local persistence and consolidation by rhizome expansion. This conclusion is supported by the observation that isolated populations of some antiquity of both species are known to occur in north Derbyshire (Clapham 1969). There is no doubt that extensive rhizome expansion has been responsible for the spread of *B. pinnatum* at Buxton. However, the potential for further spread of *B. pinnatum* by seed dispersal cannot be discounted. Seed production by *B. pinnatum* at Buxton was examined in 1999 and 2000 and it was found to be producing large numbers of viable seed. Consequently, further research is required to examine whether the failure of existing north Derbyshire populations of *B. pinnatum* to spread is due to climate or self-incompatibility. Work by Schlapfer & Fischer (1998) on natural populations of *B. pinnatum* suggest a very low ratio of sexual vs. vegetative recruitment, notwithstanding their detection of high clonal diversity.

CLIMATIC LIMITS

In contrast to *B. pinnatum*, the relatively poor persistence of the other southern species suggests that the operation of a climatic sieve is largely responsible for the present geographical distribution of these species in Britain. This conclusion is supported by the additional evidence (Table 1) that both initial establishment in

1991 and persistence in 1996 was markedly inferior in the four perennial species with the most southern of geographical distributions (Perring & Walters 1976) (*Bryonia dioica*, *Foeniculum vulgare*, *Melilotus altissima* and *Smyrnium olusatrum*) and superior in the most northern of the southern species, *B. pinnatum* and *Hypericum perforatum*. The results therefore corroborate previous autecological studies that have identified the role of species-specific physiological constraints on certain stages of the life cycle in preventing populations crossing climatic boundaries (Pigott 1968; Davison 1977; Crawford & Palin 1981; Pigott & Huntley 1981; Beerling 1993). In climate change experiments Wookey *et al.* (1993), found that climate amelioration was required at the high-arctic site but not at the more benign sub-arctic site, before plants were observed to respond to supplementary mineral nutrients. Also working in the arctic on soil-warming experiments, Starr, Oberauer & Pop (2000) noted that plants with determinate growth were at a competitive disadvantage relative to those plants that could respond to a lengthened growing season.

Identification of the physiological constraints limiting the vigour of a species at its climatic boundary does not, by itself, provide the basis for predictions of the species' biogeographical response to any future relaxations of the climatic constraints. Data presented in this paper strongly suggest that other species' traits will play a crucial role in determining the speed and continuity of response to global climate change. In particular, our results suggest differences in behaviour between annuals and perennials. By 1996, there was no record of surviving southern annuals. Several factors might explain this phenomenon, including failure to produce and ripen seeds under adverse climatic conditions. It might also be the case that the frequency of disturbance or small plot size failed to provide adequate microsites to permit re-establishment of dispersed seed. However, a more generic cause of failure in these plants may be related to the absence of mechanisms by which adverse years can be survived in a vegetative state. The resulting dependence of many annuals upon seedling regeneration is likely to make populations close to their climatic boundaries extremely precarious and to generate movements in their geographical distributions that are tightly coupled to climate fluctuations (Carter & Prince 1981; Ratcliff 1984; Thompson, Hodgson & Rich 1995).

A very different pattern of response to global warming may be anticipated for perennials. As demonstrated by the classic study of *Cirsium acaule* (Pigott 1968), species with long life histories are in a strong position to pioneer extension of their boundaries. Unlike most annuals and monocarpic perennials, there is a potential in such species for outlier populations to function as 'toe-holds' from which further advances can occur in years that are unusually favourable for seed production, dispersal and establishment. Small populations of the two perennial southern forbs, *O. vulgare* and *S. erucifolius*, remained in plots in which the climate had been modified, even though the modifications had ceased 3 years previously. The mild winter and drought treatments may have provided a necessary 'window' of opportunity for seedling establishment sufficient to create a viable population.

EXTREME EVENTS

The main conclusion from the experiment confirms the vulnerability of shorter-lived species relative to perennials, at their limits of distribution. As a result of vegetative reserves accumulated in good years, perennials are able to persist through poor years. However, other results obtained from this investigation suggest that it would be unwise to rely upon a simple dichotomy between short- and long-lived species. Other factors have to be considered in developing models of the northward expansion of plant ranges in global change scenarios.

Evidence of a potential to persist in a short-lived species was obtained for *Arabidopsis thaliana*. The resurgence of this species following the 1995 drought (Fig. 4) illustrated the extent to which possession of a persistent seed bank can maintain an inconspicuous toe-hold even in an obligate ephemeral. It is noteworthy that a recent history of experimental droughts was associated with a magnified response by *A. thaliana* to the 1995 drought. It could be surmised that the repeated disturbance from successive droughts created

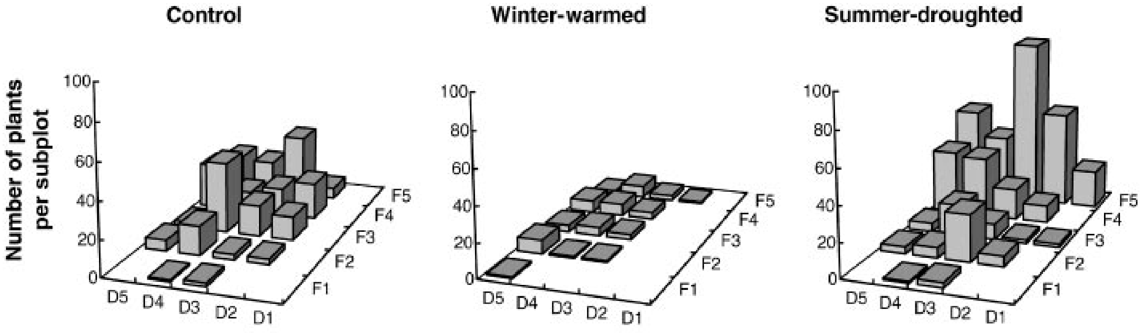

Fig. 4. Total number of *Arabidopsis thaliana* plants in each of the subplots summed from five replicates per climate treatment counted on 7 June 1996.

and sustained bare ground in the plots; this permitted invasion by *A. thaliana* and resulted in the accumulation of a seed bank from which new recruits could recolonize in response to episodic extreme events. In contrast, the seed bank was smaller in heated plots (Akinola, Thompson & Buckland 1998), where annuals may have failed to establish in gaps owing to the early growth of resident perennials. Overall, our results support the hypothesis (Davis, Grime & Thompson 2000) that successful invasion appears to depend less upon the traits of the invader but more upon the spatial and temporal coincidence of resource and seed availability.

IMPLICATIONS FOR GRASSLAND MANAGEMENT

Large grasses were the most successful of the sown species in this experiment (Table 1 and Fig. 3). Generally, however, in this phosphorus-deficient system, the continued success of most species (e.g. *Dactylis glomerata*, *Arrhenatherum elatius*, *Holcus lanatus*) was strongly dependent on continued fertilizer application; once this ceased, they went into a relatively steep decline. Our results are consistent with the idea that, for many European grasslands, reducing soil fertility should be the primary objective of conservation (Marrs 1993; Janssens *et al.* 1998).

Brachypodium pinnatum, however, behaved quite differently, continuing to expand rapidly after cessation of fertilizer input. *Brachypodium* is a problem in limestone grasslands throughout northern and central Europe, particularly where management is reduced or withdrawn (Bobbink & Willems 1987; Stampfli & Zeiter 1999). Where *Brachypodium* becomes dominant, species richness is reduced, with very slow-growing dicots that are so typical of short limestone grassland being particularly badly affected (Hurst & John 1999). Our results confirm the ability of *Brachypodium* to dominate limestone grasslands, particularly under conditions of low disturbance and low fertility (Fig. 3). The twin failures of dispersal (from outside the region) and seed production (within the region) are strongly implicated as the main causes of the inability of *Brachypodium* to present a current threat to limestone grasslands in northern England. However, climate change may already be altering this picture substantially. If seed production is currently limited by climate, a changing climate may permit *Brachypodium* to spread rapidly from the isolated clones already present in north Derbyshire.

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