Limited Effects of Year-round Temperature Elevation on Temperate Grassland Species Grown in Infertile Soil

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Abstract— Using electric heating cables, the effect of temperature elevation by 3 ºC throughout the year on 19 grassland species was examined in an outdoor pot experiment in northern England. Overall, no significant treatment effect on growth was detected. Species' response to 3 ºC elevation was also unrelated to a temperature preference index reflecting the species' geographical distributions in the UK.

Despite efforts made to ensure that all plants were well watered, plants may have experienced unavoidable water stress, and although an attempt to correlate an index of drought tolerance with species' performance under warming was not statistically significant, species from permanently moist habitats showed a consistent negative response to heating, while in those from dry habitats the response was positive. Warming and possible associated drought also caused a reduction in root:shoot ratio in nearly every species.

Consistent with other work, we also found that higher temperatures advanced flowering in spring. Some species also failed to flower in the second year in the heated treatment, possibly owing to a failure of vernalisation.

In conclusion, the results of this experiment are consistent with the view that changes in precipitation may have larger effects on plant performance and distribution than changes in temperature, but that the latter may have large effects on phenology and flowering.

Keywords— Temperate grassland species, temperature, drought, growth, Ellenberg indicator, flowering.

I. INTRODUCTION

TEMPERATURE influences the physiology and productivity of species [9], [40], [16], [52] as well as their distribution [51], [37]. Thus all these variables will be affected by changes in climate.

Global climate is changing rapidly [29]; global mean surface air temperature may increase by up to 4.8 °C by the end of the 21st century in reaction to rising atmospheric concentrations of greenhouse gases. According to the UK Climate Impacts Programme, for example, it is predicted that the United Kingdom will experience an overall increase in temperature of between 0.5 °C and 3 °C by 2050 [50].

Plant communities may respond positively to warmer conditions in various ways including stimulation of primary productivity through altered rates of biochemical processes [30], extension of the growing season [34], [49] or enhanced access to nutrients [39]. However, climate warming may have adverse impacts on the productivity of plant communities as a result of an increase in temperature stress [51], water stress resulting from increased evapotranspiration [40], or through negative impacts on seedling establishment [42].

Changed distributions arising from climate change are often related to species-specific physiological thresholds of temperature and precipitation tolerance [52], but also to changing biotic interactions [8]. Furthermore, climate warming may induce changes in community structure; [21] found that in warmed plots aboveground biomass of forbs decreased, and that of shrubs increased, while aboveground biomass of grasses was unchanged.

Thus global climate change is expected to cause shifts in species ranges and possibly extinctions through effects on growing season length, biogeochemical and physiological processes and productivity, with possibly large consequences for the composition of plant communities [35], [40], [15].

Phenology, the temporal distribution of biological events throughout the year [4], is one of the traits most responsive to climate warming [44], [38]. Reference [3] found that phenological events such as leaf bud burst and flowering occurred earlier as a result of warming, and these simple processes are often used to track the effects of climate change on plant development. The shifts in phenological performance that result from an extended growing season may affect plant fitness [36] and contribute to changes in distribution and abundance of species [7], [49]. Both experimental warming and natural temperature gradient analysis suggest that initiation of leaf bud burst and flowering of 11 sub-alpine meadow species in Colorado, USA are determined mainly by temperature, whereas the onset of leaf senescence is triggered by photoperiod and/or genetic control [12]. However, in some studies it has been found that warming delays senescence [31], [43].

Elevation of temperature by 3°C during winter and spring has been carried out on calcareous grassland in the field at the Buxton Climate Change Impacts Laboratory, located within the grounds of the Health and Safety Laboratory (HSL), Buxton, Derbyshire, UK (53º 13' N, 1° 55' W) for well over a decade [19], [20]. However, large effects on community composition and productivity have not been observed. In the experiment reported here a range of grassland species from Buxton were subjected to 3°C increase in temperature throughout the year to study the effects of warming on plant development and above and below ground biomass

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production. It seems likely that the effect of year-round warming will differ from the winter/spring warming carried out in the field at Buxton. Temperature elevation all year round, in addition to potentially lengthening the growing season and advancing flowering date, may affect plant phenological patterns at a later stage. Constant warming may increase flowering duration, perhaps leading to increased incidence of pollination visits and subsequently to a higher frequency of pollination (and hence more seed production) especially if warmer conditions attract more insects.

Temperature manipulations employed at Buxton slightly exaggerate the scenarios currently predicted for the British Isles, and were designed to generate a perturbation large enough to affect ecosystem processes. Another objective of the manipulated temperature at Buxton was to examine the consequences of 'mild winters' which were significantly more frequent in Britain in the decade 1980-1990.

Large responses to temperature manipulations in the field experiment at Buxton may also have been constrained by the shallow, infertile soil at the site [19], [20]. Thus in the experiment reported here, we deliberately sought to examine the consequences of heating under conditions in which plant growth would be inevitably constrained by low soil volume and fertility, very much as it is at Buxton. We suspect rather different results would have been obtained if the effects of elevated temperature had been studied under fertile conditions. Thus although we hypothesise that warming will generally have positive effects on plant growth, we expect that the effects will be relatively small. We also test the hypotheses that species of southern distribution will benefit more from a rise in temperature than those of northern distribution, and that warming will result in alterations in flowering phenology (i.e. generally earlier flowering).

II.   MATERIAL AND METHODS

A. Plant Material and Experimental Design

Seeds of the studied species were originally collected from grassland populations in the Sheffield region and subsequently stored at -18°C. They were allowed to germinate during February 2005 after treatments to break dormancy in some species (e.g. chilling in *Linum catharticum*, *Carex flacca* and *Carex panicea*), had been carried out. Twelve of the study species are common in the calcareous grassland at Buxton, although not all are calcicoles; *Potentilla erecta*, for example, occupies patches of acidic surface-leached soil. For comparative purposes, we also included another seven species characteristic of more-fertile soils. For a list of the 19 species used see Fig. 1. Nomenclature follows [45]. Seedlings in modular trays of commercial peat-free compost were kept in cold frames for an establishment period of about 5 weeks starting from late February 2005. Later they were transferred into 4 litre plastic pots. Seedlings were selected as far as possible for uniformity of size and condition within each species. Plants were grown free from competition, with individuals kept in separate pots. The pots were partially filled with rendzina soil collected from the vicinity of the experimental site at Buxton. The amount of rendzina used gave a soil depth of 5 cm simulating a shallow soil profile. A

heating system involving attachment of a heating cable to the interior wall of the plant container above the level of the soil was installed to achieve a consistent warming of 3ºC above ambient (See supplementary material Fig. 1).

Plants replicated five times were arranged in a fully randomized design within five blocks, each containing 10 pots (5 heated and 5 control) {19 spp x 2 treatments x 5 replicates}. They were then placed on wooden benches inside an enclosure (poultry mesh) that was built to provide protection from birds and squirrels. The experiment was conducted between 5 April 2005 and 25 June 2006 at the University of Sheffield's Tapton Experimental Gardens.

Plants were treated once per week as necessary to prevent fungal infection (Cheshunt compound, containing 83% w/w ammonium carbonate and 15% w/w copper sulphate) and insect damage (Doff systemic insecticide containing 70g/litre dimethoate), while weeding was done manually throughout the experiment. In some cases insects and slugs which had been attracted to warm conditions in the treated pots were removed before causing damage. Nevertheless instances of herbivore attacks were observed and especially in the warmed pots, *Cirsium palustre* was targeted by slugs. Plants were watered with tap water at least three times a week. In an attempt to counter the drying effect of the heating cables, pots were watered more frequently (whenever plants showed signs of wilting) during the warm days of summer.

Time of flowering of species was monitored in the first year over the whole growing season. Individual plants were inspected on a regular basis to observe first flowering in both warmed and unwarmed pots. Although more species flowered in the second year, relatively few individual plants flowered, so it was not possible to make a comparison between plant species in terms of flowering time.

At the termination of the experiment, plants were harvested (both living and dead material) and root and shoot dry weights were measured after the tissue had been oven-dried at 80 °C for two days. An annual species that completed its life cycle at the end of the first growing season, *Linum catharticum*, was harvested in August 2005.

B. Installation and Operation of Heating System

Heating cables (Thermoforce Ltd, Cockermouth, UK) were fastened around the inner surface of the pots (using resistance wire) to increase the temperature within the pot to 3°C above ambient. The temperature of heated pots was controlled with respect to ambient by means of temperature probes, suspended just above the soil surface in both the heated and control pots, linked to a computer that interrogated both ambient and heated pots to assess the level of temperature elevation. If the elevation exceeded the set temperature, power to the heating cables was switched off via a control relay. The method employed to raise the air temperature around the plants growing in the pots would not be expected to cause major alterations to micro-climate variables such as rainfall and wind speed. The vacant volume of the pots (soil was shallow and occupied only the first 5 cm depth) confined the warm air and prevented it from escaping. The control system ensured that a consistent 3°C rise in temperature was maintained throughout the experimental

period. Temperature measurements made at random using thermometers showed that warming on average was kept consistently ~ 3°C higher than control. Ambient climate of the experimental location (Tapton experimental gardens-Sheffield) is characterised by mild winters and cool summers, with an average annual air temperature of 9.5°C, and mean monthly temperature between 4°C (Jan) and 16°C (July). Annual precipitation averages 813 mm.

C. Data analysis

Analysis of variance (ANOVA) was used to examine the effect of the warming treatment and the effect of species on the total biomass of the studied species. ANOVA was also performed to detect possible interactions between species and treatment type on the shoot dry weight and root to shoot ratio of the test species. To meet the test requirements, data were log-transformed (natural log) where appropriate. In addition, correlation analysis was carried out to assess the relationship between an index of response to heating and species temperature preferences and Ellenberg moisture indicator values.

The index of response to heating was calculated as the difference between biomass in heated and control treatments as proportion of the control. Species' temperature preferences, based on their geographical distributions in the UK, were quantified as TJuly [25]: the mean summer temperature value of the 10-km squares where a plant species occurs in Britain, Ireland and the Channel Islands (See supplementary material Fig. 2). To calculate this value, [25] used climatic data of the UK Climate Impact Programme and daily weather measurements from other meteorological stations, averaged over a 30-year period [3].

Two-sample t-test was used to compare differences in flowering time between species. Statistical analyses were conducted using Minitab software version 14. Despite the numerous t-tests performed on responses of different species to the treatment, we did not use a Bonferroni correction, since its conservative approach runs the risk of failure to detect significant effects, but we do interpret uncorrected test results with caution.

III. RESULTS

Species showed a mixture of negative and positive responses, and most effects were small (Fig. 1). The warming treatment (3 °C elevation above ambient) did not have a significant effect on the total biomass of the test species (ANOVA, F= 0.62, 1,142 df, P= 0.432); the mean total dry mass of untreated plants was 2.08 g, (SEM=± 0.35) and the warmed treatment was 1.69 g (SEM=± 0.29). (back-transformed natural log means in both cases). No interaction between treatment type (control versus warming) and species was detected (ANOVA, F= 1.14, 18,142 df, P= 0.318). However, species of fertile soils had a significantly greater total dry mass than species of infertile soils (ANOVA, F=6.34, 1,176 df, P= 0.013). At the individual level, biomass production of both warmed and control pots in all species were similar; none of the differences was statistically significant even with a p value unadjusted for multiple tests.
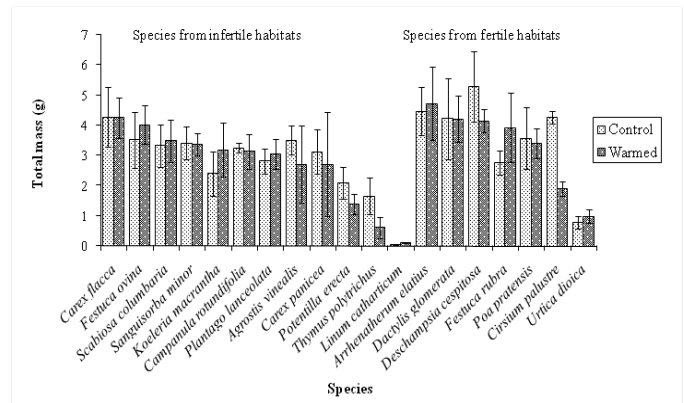

Fig. 1. The total biomass production (g) of the studied species in response to a 3°C year-round increase above ambient.

The index of response to heating is plotted against species temperature preferences (TJuly) in Fig. 2a, but there appears to be no direct relationship between the two variables. Although species appear to differ in their temperature requirements (or at least in their geographical distributions), this was not reflected in any difference in their response to heating.

Although the experiment was designed to study the impact of warming, it was suspected that plants might have experienced periods of unintended water stress. Despite efforts made to ensure that all plants were well watered, it was inevitable sometimes for plants to experience occasional drying conditions owing to relatively long experimental duration, high temperatures in summer (especially in the warming treatment) and shallowness of soil profile (restricting potential field capacity).

If there was an effect of drought, we expect that the ability of plant species to respond to and benefit from warming would be reduced by the influence of unavoidable drought intervals. In particular plant species associated with wetland habitats should be more vulnerable to water stress than those of drier habitats.

As an index of drought tolerance, we used Ellenberg F values (See supplementary material Table 1). Ellenberg indicator values are a tool to express the ecological behaviour of plant species. In respect to F values, plant species that usually only occur on sites with low moisture supply are given low F indicator values. Plants that require high moisture supply are allocated high indicator values of up to 12.

Although not statistically significant, the negative correlation between the index of response to heating and Ellenberg F values strongly suggests an underlying negative relationship (Fig. 2b). Species from permanently moist habitats (F value of 7 or 8) showed a consistent negative response to heating, while in those of dry habitats (F value of 2 or 3) the response was positive.
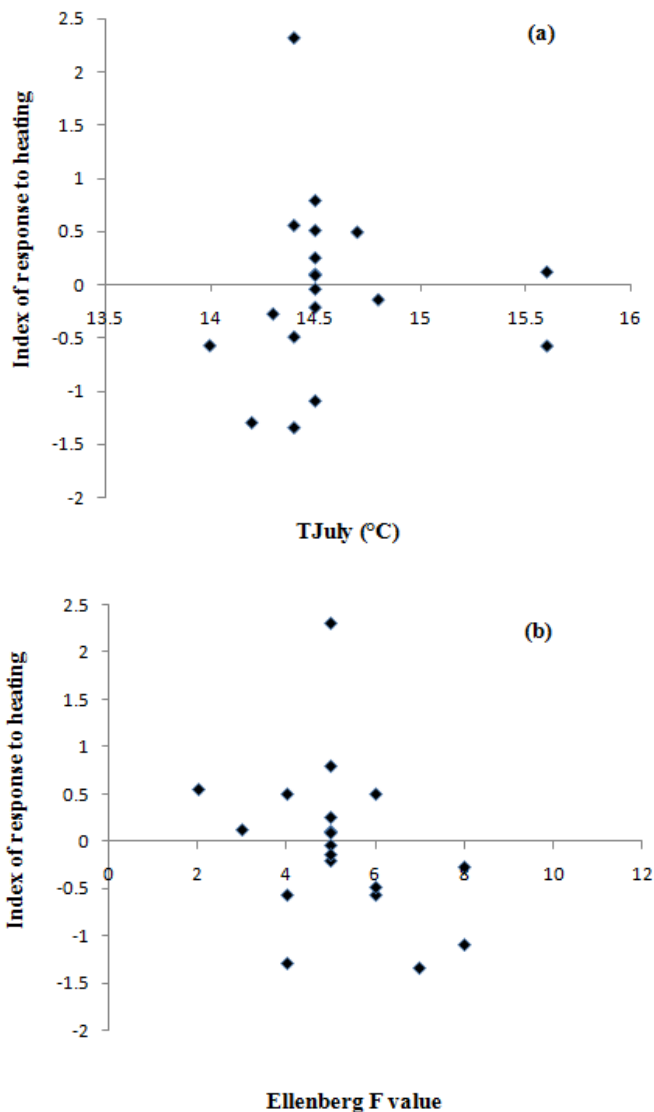
Fig. 2. Relationships between species performance under year-round warming, and environmental indicators and plant traits. For explanation see text.

Fig. 3. Root:shoot ratio of species grown under year-round warming of 3°C above ambient.

If the warming treatment led to drought, one might expect that root: shoot ratios would increase in response to climate warming and drier soils [6]. On the contrary, although in no individual species was the change significant, it appears that the combined effects of high temperature and possible associated drought reduced root development, causing a reduction in R: S ratios in nearly every species (Fig. 3). However, this reduction was not consistent across species, and therefore there was a significant species effect (ANOVA, F= 6.67, 18,142 df, P<0.001). Overall, however, warming caused a significant reduction in R:S ratio (ANOVA, F= 17.71, 1,142 df, P<0.001). The interaction between the effects of species and treatment was marginally non-significant (ANOVA, F=1.58, 18,142 df, P=0.07).
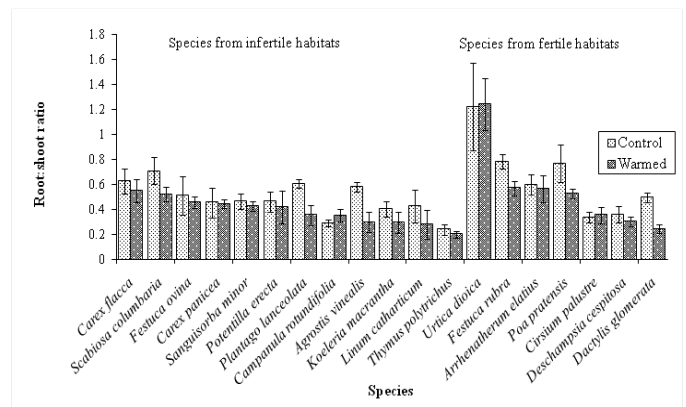
In the first year seven species flowered while in the second 12 did so. Species that flowered in the first year varied in their flowering phenology in response to warming (Fig. 4). Elevation of temperature by 3°C resulted in only a slight change in flowering time in most species; however, the effect on two species (*Linum catharticum* and *Potentilla erecta*) was more substantial, leading these plants to commence flowering significantly earlier. In the second year, it appears that the warming treatment had little effect on the number of replicates that flowered in most species (data not shown), but there was a clear negative impact on two species (*Arrhenatherum elatius* and *Festuca rubra*); in the warmed pots all replicates of these species failed to flower while in the control 4 out of 5 plants flowered.
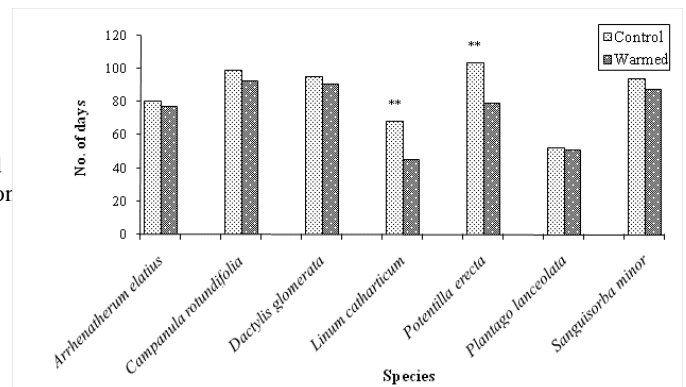

Fig. 4. Flowering time variation of species subjected to a 3°C temperature elevation, expressed as days to first flowering from 5/04/2005. (2-sample t-test, (** = p<0.01)

IV. DISCUSSION

This study investigated how flowering time and biomass production above and below ground are affected by warming. Exposing the studied species to a warmer climate had little effect on biomass production. The minimal effects of warming on many plant species in this trial, where plants were grown in pots, is consistent with that observed in the long-term field

experiment at Buxton [19], [20], and with the results of some other studies (e.g. [26]), especially in the longer term [54]. Why was growth not promoted by year-round warming? One possibility is that growth is strongly limited by low volume and fertility of the soil available. Another possible contributory factor is that lower soil moisture levels in warmed pots might have triggered a decrease in stomatal conductance [48] causing transpirational losses to be minimised. Decreased stomatal conductance contributes to lower photosynthetic rates which consequently results in curtailment of biomass production.

Apart from possible effects of drought, direct negative effects of increased temperatures have also been observed in other studies. Reference [17] investigated the effects of ambient air temperature +3°C on the physiology of grassland species in Belgium; plants in the elevated air temperature chambers suffered more from midday stress on warm summer days than those in ambient chambers. Chlorophyll fluorescence measurements indicated an increased intensity of midday stress as a result of heating, causing down-regulation of photosystem 2 [17]. Chlorophyll fluorescence gives information about the extent to which PSII is using the energy absorbed by chlorophyll and the extent to which it is being damaged by excess light and heat.

Reference [10] found that both above-ground and below-ground biomass production of grassland species was reduced (by 29% and 25% respectively) due to warming of 3°C in sun-lit climate-controlled chambers in Belgium, as negative impacts of increased heat and drought stress in summer prevailed. Reference [11] found that year-round warming using overhead heaters in the Rocky Mountains of Colorado resulted in a significantly lower biomass in four of nine perennial species. Continuous, multi-year exposure to projected future climate conditions reduced above-ground biomass in a French grassland [5].

It has been suggested that plants exposed to drought often enlarge their root systems, increasing water uptake [6] and leading to higher R:S ratio, but in this trial no such increase was found, and indeed the warming treatment seems to have had the opposite effect. However, higher temperatures could have counteracted any drought-driven R:S increase. Reference [14] reported that warming without soil drying had a negative effect on root biomass in temperate grasslands through increased root death.

Although plants were watered frequently, and efforts were made to prevent drought stress, there was a strong suggestion that these efforts were not completely successful. Conditions such as shallow soil depth, relatively long growth duration and combined effects of 3°C and high natural ambient temperatures (the summer of 2006 was unusually warm in the UK) would deplete soil moisture. This study suggests that unless precipitation increases, the productivity of many temperate grasslands could decline under climate warming. However, if productivity is limited most by low temperature or low nutrient concentrations (rather than by water), such as in polar and alpine regions, warming may be beneficial through alleviation of these constraints either directly through higher temperature or indirectly via increased nutrient mineralization rates [39], [2]. Results from a warming experiment in the Rocky Mountains of Colorado showed that two primary microclimate effects of warming are a decrease in soil moisture and an increase in nitrogen mineralization [22].

Plant growth and flowering, particularly in the second year, might have been reduced due to restricted nutrient availability. Initial biomass accumulation in the first growing season may have accelerated the decrease of soil nutrient reserves from already infertile soils. In such circumstances, that is nutrient-poor soils exploited by species characterised by low turnover rates of living plant tissue and litter with low decomposition rates, an increase in soil temperature may not lead to increased mineralization. Nutrient availability will depend on the balance between the positive effect of warming on mineralization and the negative effect of reduced soil moisture. It is possible that in the warming treatment increased mineralisation and decreased soil moisture have contrasting effects on plants such that the net effect is small.

Reference [43] distinguished two patterns of phenology in tundra species: a) periodic species characterised by a deterministic growing period controlled by genetic constraints and b) aperiodic species that continue to function until environmental conditions become unfavourable. If the species examined here fall into the former category, then warming may simply have shifted the growing season, without any net effect on productivity. For example, reference [46] examined the impact of lengthening growing season (by removal of snow in spring) and soil warming on *Polygonum bistorta*. Plants responded to the treatments by becoming active earlier and senescing earlier, resulting in a growth period of similar duration to that of the control. They found that the treatments had no effect on leaf size or leaf number and suggested that the response of this species to lengthened growth season was limited by genetically determined internal constraints.

Thus it appears that the shallow soil used in this experiment, coupled with increased evaporative water loss at higher temperature, potentially resulting in drier soils, may strongly limit soil and plant processes (nutrient mineralisation and biomass production respectively) so that potential temperature-driven increases in process rates were not achieved [33], [40].

In contrast to the rather equivocal effects of the heating treatment on growth and biomass allocation, the results of this experiment support other work on the effect on increased spring temperature on flowering. For example, [1] reported that a rise in average minimum temperatures of 1.2°C contributed to earlier spring flowering in 89 of 100 species investigated in the Washington, DC area in the USA, while [27] found a powerful impact of 2 °C warming on flowering times in a species-rich temperate grassland in Tasmania, although there was also a strong interaction with the timing of rainfall.

The failure of some species to flower in the second year in the heated treatment may be related to a failure of vernalisation. Exposure to low temperature can induce flowering in many temperate species. Thus, continuous warming may have prevented initiation of flowering in some species. Most temperate perennial grasses are known to have a winter chilling requirement for maximum flowering to occur [23], and some of the plants may not have received adequate chilling to enable full flowering in the second season of this experiment.

In conclusion, we found little or no effect of year-round warming of 3 °C on plant growth, possibly because growth was constrained by low soil fertility and, at least intermittently, also by drought. Consistent with an effect of drought, there was a suggestion that plants of moist soils were particularly disadvantaged by warming. There was no evidence that species of southern distribution benefited more from warming than those of northern distribution, but warming did result in earlier flowering in some species.

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SUPPLEMENTARY MATERIAL

Fig. 1. Heating cables used in the experiment to elevate temperature by 3 ^{o}C above ambient within the pot. (MATERIAL AND METHODS: PLANT MATERIAL AND EXPERIMENTAL DESIGN)
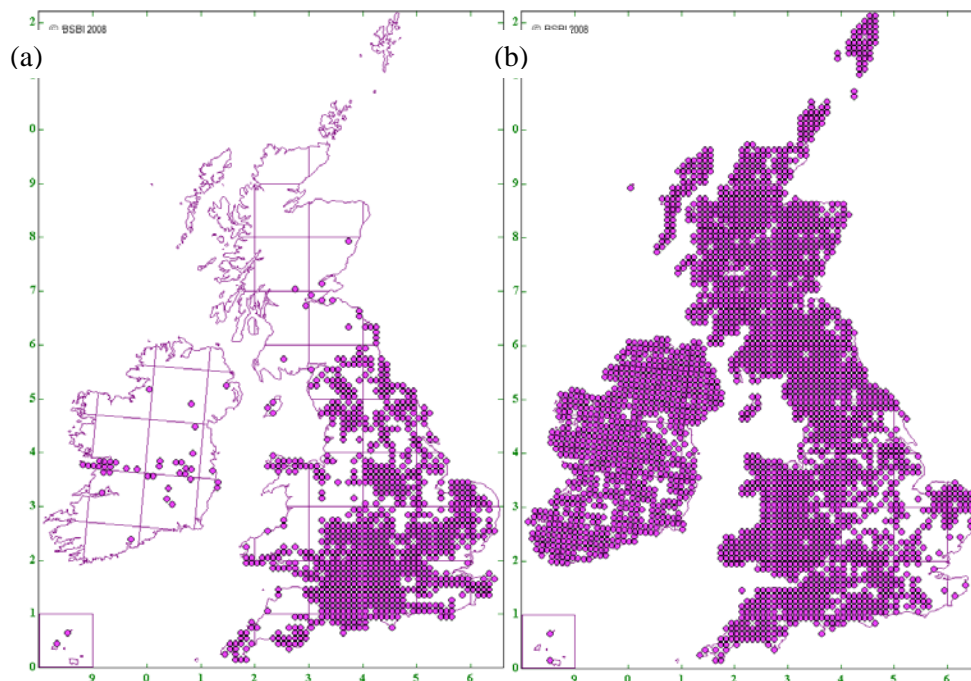
Fig. 2. Distribution maps for (a) *Sanguisorba minor* and (b) *Carex panicea* in Britain and Ireland, representing species with high and low mean July temperatures respectively. Each symbol represents a 10x10 km square in which the species is present. (from the BSBI maps scheme database; census of 1987-1999).

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TABLE 1.
TJULY AND ELLENBERG F (MOISTURE) VALUES OF THE STUDIED SPECIES

Species	TJuly	Ellenberg value (moisture)
Arrhenatherum elatius	14.5	5
Agrostis vinealis	14	6
Cirsium palustre	14.5	8
Carex flacca	14.5	5
Carex panicea	14.3	8
Campanula rotundifolia	14.4	2
Deschampsia cespitosa	14.4	6
Dactylis glomerata	14.5	5
Festuca ovina	14.5	5
Festuca rubra	14.5	5
Koeleria macrantha	14.7	4
Linum catharticum	14.4	5
Potentilla erecta	14.4	7
Plantago lanceolata	14.5	5
Poa pratensis	14.8	5
Scabiosa columbaria	15.6	3
Sanguisorba minor	15.6	4
Thymus polytrichus	14.2	4
Urtica dioica	14.5	6

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