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Plant community dynamics in a calcareous grassland under climate change manipulations

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Abstract

This study investigates the effects of field manipulations of local climate to determine the potential impact of climate change on plant community dynamics in a calcareous grassland. The experimental site is located in a grassland at the Wytham estate, Oxfordshire, UK. The one hectare study area is within a 10 ha abandoned arable field on Jurassic corallian limestone. Two climate change scenarios were used: warmer winters with increased summer rainfall and warmer winters with summer drought. Plant cover and species richness were significantly increased in plots receiving supplemented summer rainfall, while the amount of litter was significantly reduced. Litter formation was significantly increased by winter warming and drought. The responses of the plant community to the climate manipulations were related to the life-history attributes of the dominant species. Seedling recruitment was limited by microsite availability, which also varied in the different climate manipulations. The results are discussed in terms of successional dynamics. They suggest that warmer winters may delay succession, as gap formation in the sward will provide sites for colonisation of annuals, thereby enabling their persistence in the sward. Under wetter conditions during summer, perennial grasses tend to close the sward, thereby inhibiting the establishment of later successional species.

Introduction

General Circulation Models (GCMs) predict that global climate will change in the next century, as a result of anthropogenic increases in greenhouse gases (Houghton et al. 1996; Wigley & Raper 1992). According to the Climate Change Impact Review Group (CCIRG) (1991, 1996), it is predicted that the United Kingdom will experience an increase in anticyclonic activity, potentially leading to an increase of 20% in rainfall during summer (more thunderstorms). Additionally, the UK may experience a warming which will be most marked over winter (CCIRG 1991, 1996; Beerling & Woodward 1994; Houghton et al. 1996). However, long periods of drought are also expected between rain-bearing storms (Houghton et al. 1996).

Modifications in climate will affect ecosystem structure and function. Changes in soil moisture and temperature influence processes, such as litter decomposition, nutrient cycling, primary productivity, plant recruitment, survival, and the rate and direction of succession (Field et al. 1992; Couteaux et al. 1995). Warming will generally increase decomposition rates, soil nutrient availability and primary production (Hobbie 1996; Lukewille & Wright 1997; but see Hobbie & Chapin 1998). Experimental studies, simulating increasing temperatures in spring and autumn (Hillier et al. 1994; Spring et al. 1996), showed that the growing season was lengthened and that the biomass of species was increased. They also found that the abundance of individual species was reduced, such that when communities were compared, the total biomass remained constant regardless of the treatment. The higher primary productivity rates predicted in rich CO_2 environments, due to enhanced photosynthesis, are also strongly dependent on temperature, nutrient and water availability (Bazzaz 1990, Campbell et al. 1995, Baker et al. 1997).

Changes in community composition and structure occur when species show different patterns of response to changing resources, such that some species in a community are favoured under future environmental conditions (Harte & Shaw 1995). For example, experimental manipulations on C3 and C4 species under different temperatures, combined with elevated CO_2, showed important variations in net photosynthesis and relative growth rates between the different groups (Campbell et al. 1995). C3 species responded positively to these changes, while C4 species showed a decrease in growth, leading to a change in the proportion of the respective populations. In any given community, some species will do better than others under a changing climate and, as a result, competitive balances will shift, leading to changes in species dominance and composition (see Alward et al. 1999). Such modifications in ecosystem processes will lead to changes in plant and animal communities (e.g., Fajer et al. 1989; Ackerly & Bazzaz 1995; Masters et al. 1998).

In grassland communities, the success of species will also depend on life-history attributes, such as clonal reproduction, investment in seed production and the probability of seedling establishment (Graves & Reavey 1996). However, these differential responses will not only depend on the different competitive interactions among plant species (Bazzaz & Carlson 1984), but also on microsite availability for seedling recruitment and establishment (Harper 1977; Aguilera & Lauenroth 1995). The occurrence of suitable microsites for establishment of certain species will determine their presence and abundance within the community. In the long term, this may modify the successional trajectory of the community.

Here, we describe the effects of warmer winters, combined factorially with either wetter or drier summers, on the plant community dynamics in a calcareous grassland, and we examine, as far as we are able, the mechanisms that may be involved. We hypothesise that local climate change manipulations will exert differential effects on the establishment, growth and reproduction amongst species and growth forms, with potential consequences for changes in community structure.

Methods

Study site and experimental design

The experiment was performed in a lowland calcareous grassland at the Wytham estate, Oxfordshire, UK. The study was conducted on a 1 ha site, situated in the centre of a 10 ha ex-arable field on Jurassic coralian limestone with shallow soil. (Further details of the site and of the Wytham Estate are given in Masters et al. 1998 and Gibson 1986, respectively). The site was surrounded by a 2 m high fence to exclude deer and sheep, which are the main vertebrate grazers. The site is characterised by wet and mild winters with a mean minimum and maximum temperatures of 3.3 °C and 9.8 °C, respectively. The mean annual rainfall is 685 mm, falling mainly in winter and spring. Summer is dry and warm with a mean minimum and maximum temperatures of 11.2 °C and 22.8 °C, respectively. During the period covered by this study, winter and summer temperatures were close to the long-term mean values. In winter and summer the mean minimum and maximum temperature were of 3.8 °C and 10.2 °C, and 11.9 °C and 23.1 °C, respectively. The mean annual rainfall during the period of this study was 598 mm. The site is part of the UK Environmental Change Network (ECN), and detailed meteorological data from Radcliffe meteorological station (Oxford), near the experimental site, is available in the Internet web at: http://www.geog.ox.ac.uk.

A randomised block design, with five replicates, was used to simulate the effects of warmer winters with either wetter or drier summers. Hence, there were six treatments per block: (1) Control (C, ambient climatic conditions); (2) Winter warming (WW); (3) Supplemented summer rainfall (SR); (4) Winter warming and supplemented summer rainfall (WW × SR); (5) Summer drought (SD), and (6) Winter warming and summer drought (WW × SD). These manipulations were applied to 3 × 3 m plots, separated by 2 m walkways. The general aims and rationale of the experiment are given in Cummins et al. (1995) and Masters et al. (1998).

Winter warming was achieved through 1 kW heating cables, which were laid on the soil surface (after Hillier et al. 1994). Warmed plots were maintained at 3 °C above ambient temperature, from November 1 to April 30 of the following year. Supplemented summer rainfall involved the weekly application of deionised water (20% above the 10-year weekly average) from June 1 to September 30. Summer drought was achieved by imposing a complete drought throughout July and August, by the use of mobile rain shelters (scaled up from the design of Buckland 1994), which slide over the plot when rain is detected by a sensor. The treatments commenced during 1994 and are ongoing.

Within each ‘climate’ treatment plot, four 25 cm × 25 cm permanent quadrats were delimited in February 1995. The four 25 cm × 25 cm quadrats were regularly positioned along one side of the plot in order to overcome any potential heterogeneity, and were 30 cm from the edge of the plot to minimise edge effects.

The plant community at the beginning of the study in 1993, comprised 79 plant species. In terms of frequency of encounter these were, 63% perennial grasses, 22% perennial forbs, 3% annual forbs, 2% woody species and 2% mosses.

Nomenclature follows Stace (1991).

Sampling

Vegetation was recorded at four-week intervals, from March 1995 to February 1996. The total number of seedlings and adult individuals of forb species, within each 25 cm × 25 cm quadrat, were recorded. Forb species reproducing vegetatively within a 15 cm radius of a ‘parent’ plant were considered to comprise a single individual. Perennial grass presence was recorded as percentage cover, as it was not possible to distinguish individuals. Plant litter, stone and bare ground were estimated by direct observation, and recorded as percentage cover.

Statistical analysis

Analysis of Variance (ANOVA) was used with three levels of summer watering (C, ambient rainfall; SR, supplemented rainfall plots; SD, droughted plots) and two levels of winter warming (+WW, warmed plots; −WW, unwarmed plots) (after Masters et al. 1998). To determine treatment effects on species density and cover on individual sampling dates, ANOVAs were performed, and the Tukey test used to determine pairwise differences among treatments. Repeated Measures ANOVA (with levels as above) was used to determine whether the treatments were having a long-term impact (repeated measures main effect) or whether effects were transient (repeated measures treatment × date interaction). Analyses were performed using STATISTICA, version 4.5 (StatSoft, Inc. 1993). Species cover data were arcsine-square transformed, while count data for individual species were square-root transformed prior to analysis (Sokal & Rohlf 1995).

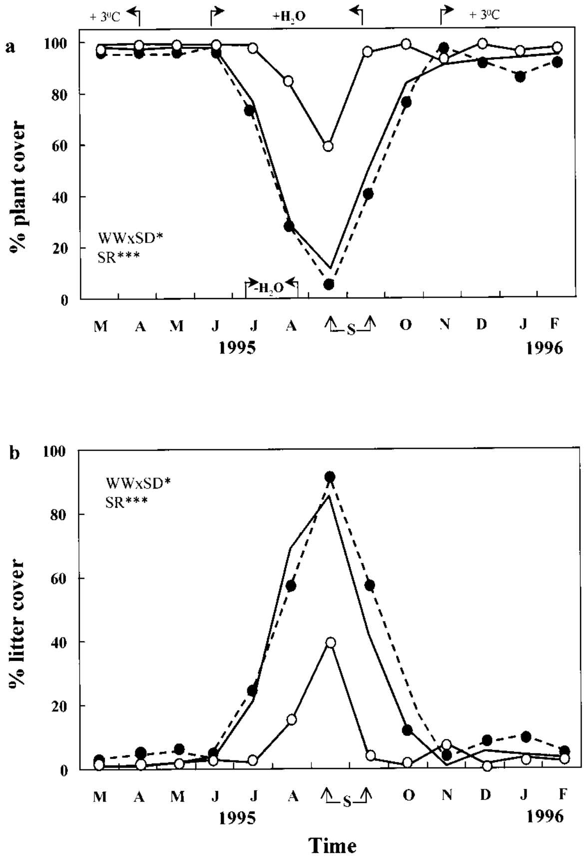

Figure 1. Changes as a result of climate manipulations in (a) plant cover, (b) litter cover. Control (—), supplemented summer rainfall (SR) (–○–) winter warming and summer drought (- -●- -). Difference from control: $* \; p < 0.05$, $^{***} \; p < 0.001$. September recording on 1 and 30. Arrows indicate start (↱) and end (↰) of climate treatment.

Results

During the period covered by this study (March 1995 until February 1996), a total of 69 plant species was recorded from the experiment on 12 sample dates. The most common species were perennial grasses, such as *Holcus lanatus*, *Arrhenatherum elatius* and *Agrostis stolonifera*, perennial forbs, such us *Clinopodium vulgare*, *Glechoma hederacea* and *Pastinaca sativa*, and annuals forbs, such as *Ranunculus parviflorus*, *Geranium dissectum* and *Crepis capillaris*.

Table 1. Results of Repeated Measures ANOVA for plant cover, litter cover and species richness as affected by the climate manipulation treatments. Winter warming (WW); supplemented summer rainfall (SR); summer drought (SD); winter warming and supplemented summer rainfall (WW×SR); and winter warming and summer drought (WW×SD).

Climate treatments	Plant cover			Litter cover			Species richness		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
WW	1,4	2.71	0.120	1,4	0.91	0.354	1,4	11.5	0.003
SR	2,8	93.3	<0.001	2,8	109.1	<0.001	2,8	34.3	<0.001
SD	2,8	0.02	0.911	2,8	0.35	0.563	2,8	2.91	0.099
WW×SR	2,20	0.05	0.835	2,20	0.82	0.378	2,20	0.89	0.425
WW×SD	2,20	5.13	0.035	2,20	5.88	0.041	2,20	1.78	0.242
WW×TIME	12,278	0.91	0.533	12,278	0.61	0.767	12,278	3.34	0.008
SR×TIME	24,278	35.4	<0.001	24,278	26.5	<0.001	24,278	12.4	<0.001
SD×TIME	24,278	1.54	0.115	24,278	1.86	0.071	24,278	1.90	0.068
WW×SR ×TIME	24,278	0.51	0.905	24,278	0.26	0.976	24,278	2.72	0.023
WW×SD ×TIME	24,278	8.31	0.001	24,278	2.45	0.017	24,278	1.49	0.121

Effects of climate manipulations on the plant community

The various climate manipulation treatments have a significant effect on a range of attributes of the plant community. In illustrating the results, only treatments showing significant differences are discussed and displayed graphically. There were significant differences in plant and litter cover with time (Table 1, Figure 1a). Plant cover was significantly increased in plots with supplemented summer rainfall ($F_{2,8} = 93.3$, $p < 0.001$), while significantly reduced under a combination of winter warming and summer drought ($F_{2,20} = 5.13$, $p < 0.05$). Changes in plant cover were related to the time of year these treatments were applied (SR and WW×SD), with significant interactions being observed between treatment and date ($F_{24,278} = 35.4$, $p < 0.001$ and $F_{24,278} = 3.31$, $p < 0.001$, respectively). Litter cover showed almost a mirror image to that of plant cover (Figure 1b). Supplemented summer rainfall treatments significantly reduced the amount of litter ($F_{2,8} = 109.1$, $p < 0.001$), while the combination of winter warming and summer drought treatments significantly increased it ($F_{2,20} = 5.88$, $p < 0.05$). Significant interactions were also found between time and SR and WW×SD ($F_{24,278} = 26.5.4$, $p < 0.001$ and $F_{24,278} = 2.45$, $p < 0.05$, respectively).

Species richness was significantly affected by the climate manipulations (Table 1, Figure 2). Winter warmed plots showed a significant reduction in number of species over time ($F_{1,4} = 11.49$, $p < 0.01$). An average reduction of approximately 10% was noted between April to July. Nevertheless, in plots under supplemented summer rainfall, a significantly higher number of species was observed ($F_{2,20} = 34.35$, $p < 0.001$). The number of species was almost doubled, compared to controls, when supplemented rainfall was applied (from June until September). Further, plots under this treatment remained 10% higher in species richness until the end of the study period. Individual ANOVAs for each sampling date, indicated significant differences in species numbers in the watered plots from August 1995, which persisted throughout the sampling period (Figure 2).

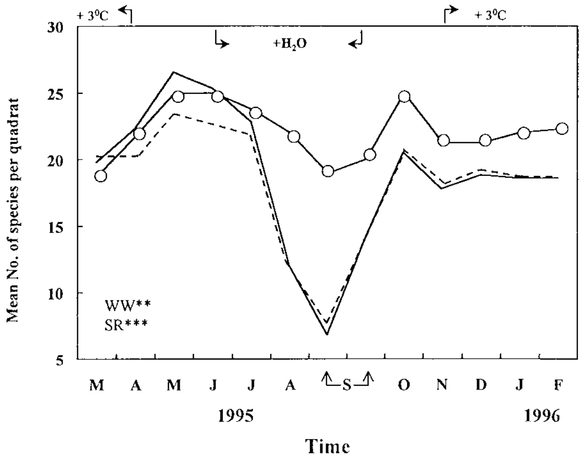

Figure 2. The effects of climate manipulation on species richness. Control (—), winter warming (WW) (- - -), supplemented summer rainfall (SR) (–○–). Difference from control: * $p < 0.05$, *** $p < 0.001$. September recording on 1 and 30. Arrows indicate start (↱) and end (↰) of climate treatment.

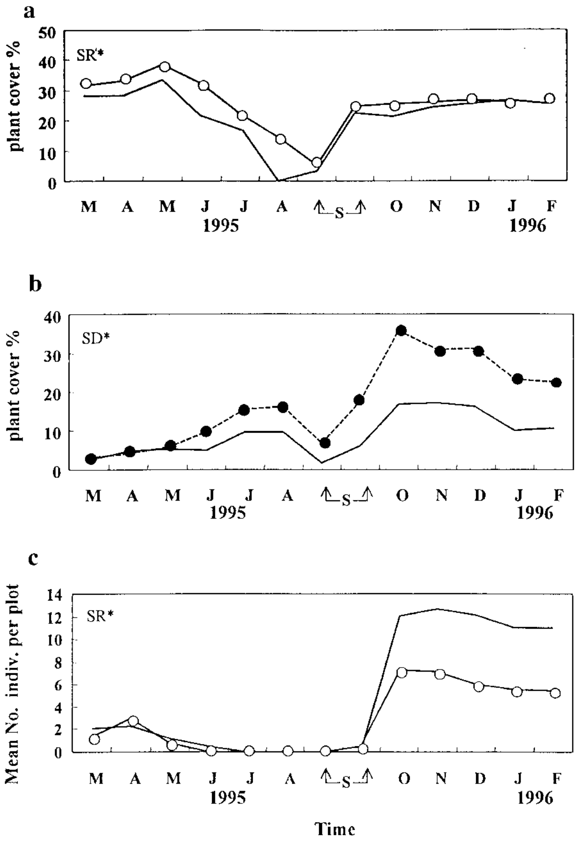

Figure 3. The effects of climate treatments on (a) plant cover of *Holcus lanatus*, and (b) *Pastinaca sativa*, (c) number of individuals of *Ranunculus parviflorus*. Control (—), winter warming (WW) (- - -), supplemented summer rainfall (SR) (–○–), summer drought (–●–). Difference from control: * $p < 0.05$. September recording on 1 and 30.

Effects of climate manipulations on individual species

Three dominant plant species, with different life-history strategies, were selected for detailed study.

Holcus lanatus, a perennial grass, was significantly enhanced in cover in plots subjected to supplemented summer rainfall ($F_{2,20} = 7.71$, $p < 0.05$, Figure 3a), while the cover of *Pastinaca sativa*, a monocarpic perennial forb, increased in plots under summer drought conditions, a trend which increased with time ($F_{2,20} = 5.85$, $p < 0.05$, Figure 3b). *Ranunculus parviflorus*, a winter annual forb, was significantly reduced in plots where supplemented summer rainfall was applied ($F_{2,20} = 5.65$, $p < 0.05$, Figure 3c). This species was recorded as individuals, as its cover was low.

In order to categorise species as to their response to the climate manipulations, a treatment response classification was created by considering the number of sample times a species was significantly more or less abundant. Species were grouped according to their response to winter warming (WW), supplemented summer rainfall (SR), summer drought (SD) and their respective combinations (WW×SR and WW×SD). Two groups of species were recognised for each treatment, in addition to those showing no significant response:

Winter warming treatment:

Abundance significantly ($p < 0.05$) increased (WW+) or decreased (WW−).

Summer rainfall treatment:

Abundance significantly ($p < 0.05$) increased (SR+) or decreased (SR−).

Summer drought treatment:

Abundance significantly ($p < 0.05$) increased (SD+) or decreased (SD−).

Table 2 demonstrates that three of the common perennial grasses, *Agrostis stolonifera*, *Arrhenatherum elatius* and *Holcus lanatus*, responded positively to supplemented summer rainfall and displayed increased cover. Similar responses were observed in the perennial forbs, *Glechoma hederacea* and *Knautia arvensis*, where higher numbers of individuals were also recorded. The annual forbs, *Geranium dissectum* and *Ranunculus parviflorus*, showed the opposite response with the lowest number of individuals being found in this treatment. *Clinopodium vulgare*, a perennial forb, was more common in warmed plots, while *Pastinaca sativa* was more abundant in plots where summer drought conditions were imposed. No species showed specific trends when climate treatments were combined (WW×SR and WW×SD).

Effects of climate manipulations on seedling recruitment

The relationships between forb seedling densities, plant cover, bare ground and litter cover were investigated for the different climate treatments and compared to controls. Two sampling dates (end September 1995 and February 1996) were contrasted, as they reflect different phenological stages of the plant community and were within the periods of specific treatment applications (Figure 4). In September 1995, there were significant differences in plant and litter cover between the watered plots and controls ($F_{2,8} = 46.1$, $p < 0.001$ and $F_{2,8} = 36.7$, $p < 0.001$ respectively). In watered plots, plant cover was significantly increased, while litter cover was significantly reduced. In plots

Table 2. Classification of species by significant responses to the climate manipulations over time. Abundance significantly increased (+) ($p < 0.05$) or decreased (−) by winter warming (WW), supplemented summer rainfall (SR) or summer drought (SD).

Treatment	WW+	WW−	SR+	SR−	SD+	SD−
Species	*Clinopodium vulgare#*		*Agrostis stolonifera** *Arrhenatherum elatius** *Glechoma hederacea#* *Holcus lanatus** *Knautia arvensis#*	*Geranium dissectum#* *Ranunculus parviflorus#*	*Pastinaca sativa**	

= mean number of individuals; * = relative plant cover.

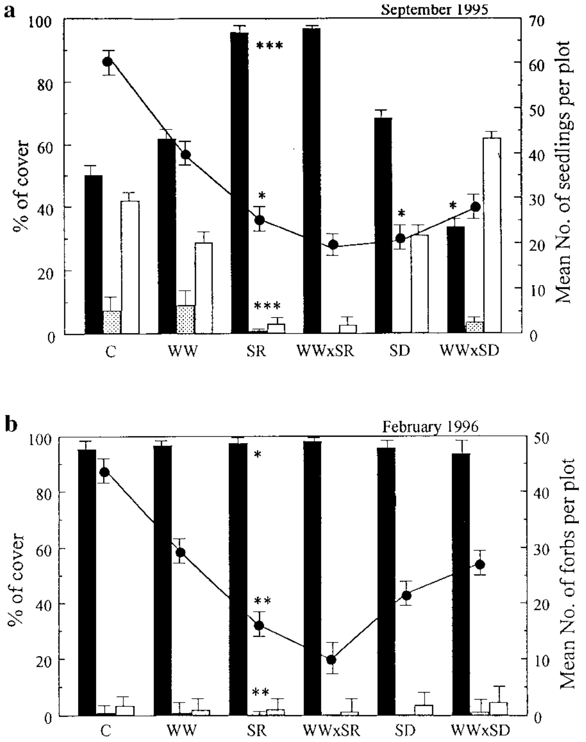

Figure 4. Relationships between forb seedling densities, plant cover, bare ground and litter cover within each climate treatment at different seasons (a) autumn, September 1995, (b) winter, February 1996. Number of seedlings (–●–), plant cover (■), bare ground (X), litter (□). Difference from control: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, error bars: ± s.e.m.

with the combination of winter warming and summer drought treatments, plant cover values were significantly lower when compared to controls ($F_{2,20} = 5.38$, $p < 0.05$). Annual seedling recruitment was significantly lower in plots with supplemented summer rainfall and summer drought ($F_{2,8} = 5.40$, $p < 0.05$ and $F_{2,8} = 4.52$, $p < 0.05$ respectively) (Figure 4a).

In February 1996, a recovery of the plant community was observed as higher plant cover values were noted in all treatments, with a corresponding decrease in bare ground and litter. However, differences remained significant between watered plots and controls ($F_{2,8} = 6.79$, $p < 0.05$) (Figure 4b). The amount of bare ground was significantly lower in plots with supplemented summer rainfall ($F_{2,8} = 9.51$, $p < 0.01$). The number of forbs was again significantly lower in watered plots than controls ($F_{2,8} = 11.1$, $p < 0.01$).

Discussion

The climate manipulations had a major impact on the dynamics of the calcareous grassland. In the Wytham community, where water availability is a limiting factor, additional water had a significant positive effect on plant cover and species richness. Such an increase in cover of perennial species agrees with other experimental studies, where the addition of a limiting resource produced an increase in biomass (e.g., Tilman 1982; Tilman & Wedin 1991). The addition of water both reduced seedling mortality and prolonged the life span of adult plants. Consequently, more species were observed in these plots. These results are somewhat unexpected. One would predict that the better performance of the highly competitive perennial grasses under supplemented summer rainfall would cause some of the less competitive forbs to be affected, or at least microsites for their germination to be reduced. The results obtained in this study probably reflect the early successional nature of the grassland, where the sward is still open, at least at certain times of the year. Winter warmed plots displayed no significant difference in plant cover when compared to the controls. However, lower plant cover values, noted at the end of the warmed period, indicated an early spring drought induced by the warming. Indeed, measurements carried out in the field indicated lower soil moisture in the warmed plots (Jamieson et al. 1998).

These results are in agreement with other studies that showed that grass cover in heated plots, was reduced as a consequence of lower soil moisture at the end of the growing season (Harte & Shaw 1995). However, enhanced summer drought caused no significant difference in total vegetation cover compared to controls. This unexpected result can be explained by looking at the composition of the community, since under summer drought the growth of the monocarpic perennial forb, *Pastinaca sativa*, was increased while that of perennial grasses was reduced. The significant reduction in plant cover observed in the combined winter warming and summer drought treatment is probably a reflection of the increasing water stress within the plant community.

The significant reduction in species richness due to winter warming may be related to higher plant and seedling mortality. This was indeed noted at the beginning of spring 1995. Similar results were obtained in another artificial soil warming experiment, where heating negatively affected species richness, mainly due to a reduction in soil water content (Farnsworth et al. 1995). In watered quadrats, survival was enhanced and the plots thereby supported higher species richness.

Litter cover was also significantly affected by the climate manipulations. The reduction in the amount of litter in the watered plots was related to the persistence of the above-ground living biomass. The opposite trend was observed in warmed and droughted plots, where the turnover of plant tissues was higher than in controls. Such differences in plant litter production could have important consequences on soil organic-matter accumulation, litter decomposition and mineralisation rates, with the concomitant effects on carbon cycling (Couteaux et al. 1995; Hirschel et al. 1997).

The responses of the plant community to the climate manipulations generally varied according to life-history traits, while some were species-specific. Commonly, changes were related to morphological traits of the dominant species (e.g., Grime 1979; Noble & Slatyer 1980). Traits, such as the possession of deep tap roots may have allowed *P. sativa* to tolerate drought conditions, by enabling plants to exploit water and nutrient resources from deeper soil layers (Tutin 1980). Other studies have show that tap-rooted species are able to exploit the warmer conditions in their artificial communities by producing a more branched root-stock (Spring et al. 1996). In other species, bud position, dense adventitious roots, trailing stolons and rhizomatous structures enabled perennial grasses and some perennial forbs, such as *Glechoma hederacea*, to exploit the increased availability of water under supplemented summer rainfall.

Life-history traits not only impinge on the performance of individual species, but also competitive interactions between species (Grace 1990). Increased perennial grass growth reduced gaps in the sward, thus preventing the establishment of species recruiting from seed (see also Ross & Harper 1972; Gross & Werner 1982). Thus, in watered plots, seedling establishment of annual species was limited by microsite availability. The higher number of species observed in these plots was not a result of establishment of new species, but of prolonged life span of perennial species that did not desiccate during summer. However, a reduction in species richness under supplemented water is predicted in the longer term, because of the eventual closing of the sward by the highly competitive perennial grasses. Where drought conditions were imposed, the decrease in seedling recruitment was likely to be related to the joint effects of reduced performance of annual species (lower fitness) and the presence of a dense litter cover, reducing microsite availability as noted in other studies (Facelli & Pickett 1991; Bosy & Reader 1995).

The variability in the response of individual species to changing resources under the climate manipulations enables predictions in relation to successional trajectories under a changing climate. A warmer climate, with no change in precipitation, will result in a decrease in soil moisture during the growing season (Mitchell et al. 1990; Campbell et al. 1997). Gaps in the perennial grass sward will provide sites for colonisation and establishment of annual species, while competitive interactions between annual forbs and perennial grasses will probably be more intense. These in turn could obstruct the colonisation of later successional species and delay succession. Under wetter conditions, we have demonstrated an increase in dominance of perennial grasses, leading to a closed sward structure, with fewer gaps for the establishment of forb species, and thereby a reduction in species richness, diversity and persistence of grassland. In this way, progression to a late successional community may be slowed, as tree and shrub establishment would be retarded (Connell & Slatyer 1977; Pickett et al. 1987). Under drought conditions, we would expect the opposite effect, as open gaps in the grassland sward structure would enable the colonisation of later successional species that may accelerate the succession. Similar results are predicted in some rangelands where woody plants replace grasses due to higher water use efficiency (Polley et al. 1996). However, competition in the open gaps between annual forbs and later successional species, such as phanerophyte seedlings, delay their establishment as observed in some Mediterranean environments (Sternberg 1994). Our results and predictions are in agreement with other climate change studies (Hobbie et al. 1993; Chapin et al. 1995) that have suggested that realistic predictions of the future distribution of vegetation with respect to climate must give emphasis to the indirect effects of climate on resource supply.

Long-term studies, such as those which are ongoing on the site, should provide further useful tools to test predictions of the responses of grassland plant communities to global environmental change.

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