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Carry over from previous year environmental conditions alters dominance hierarchy in a prairie plant community

Rebecca A. Sherry[1,]*, *John A. Arnone III*[2], *Dale W. Johnson*[3], *Dave S. Schimel*[4], *Paul S. Verburg*[2] *and Yiqi Luo*[1]

[1] *Department of Botany and Microbiology, 770 Van Vleet Oval, Room 136, University of Oklahoma, Norman, OK 73019-6131, USA*
[2] *Division of Earth and Ecosystem Sciences, Desert Research Institute, 2215 Raggio Parkway, Reno, NV 89512, USA*
[3] *Department of Natural Resources and Environmental Science, University of Nevada, Reno, NV 89557, USA*
[4] *National Center for Atmospheric Research, Boulder, CO 80305, USA*
*Correspondence address. Department of Botany and Microbiology, 770 Van Vleet Oval, Room 136, University of Oklahoma, Norman, OK 73019-6131, USA. Tel: +405-325-8578; Fax: +405-325-7619; E-mail: rsherry@ou.edu

Abstract

Aims

To determine if an experimentally applied anomalous weather year could have effects on species composition and community structure that would carry over into the following year.

Methods

We conducted a field experiment applying two levels of temperature (ambient and +4°C) and two levels of precipitation (ambient and doubled) and followed cover of plant species during the treatment year and one post-treatment year. Data analysis included ordination analysis, examination of species frequency distributions and comparison of cover of functional groups and individual species.

Important Findings

A drought during the summer and fall of the treatment year resulted in significant differences in community structure between the 2 years. C_3 and winter annual species were depressed in the spring of the second year following the dry autumn. Species richness and legume cover increased in the second, wetter, year. Treatments caused no overall differences in community structure but did alter the dominance hierarchy of species among treatments as well as years. Warming decreased relative cover of winter annuals and early spring-flowering species but increased other annuals. Warming and double precipitation together increased cover of C_4 perennial graminoids. In particular, the warming and precipitation treatments both increased the abundance of *Andropogon gerardii*, not individually altering the dominance hierarchy but together nearly doubling the relative cover of *A.gerardii*, making it the most abundant species in the combined treatment, while the cover of *Bromus arvensis*, the former dominant, decreased by 25%. The following year, *Andropogon* relative cover increased further in the former warmed plots, becoming dominant in both the formerly warmed and warmed plus double precipitation treatments. The year following treatments also saw an increase in relative cover of summer-blooming species in the formerly warmed plots and differences among the former treatments in species richness of functional groups. If the effects of one anomalous year on plant abundance can carry over into the following year, several warm years could have a significant impact on plant community structure.

Keywords: plant community structure • dominance hierarchy • warming • increased precipitation • lag effects

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INTRODUCTION

At least 63 plant species have shifted their range or changed in abundance in response to a 0.74°C increase in global annual temperature over the past century (IPCC 2007; Parmesan and Yohe 2003). In the next 100 years, the average annual temperature is expected to increase a further 1.8–4.0°C (IPCC 2007). Patterns of precipitation worldwide are expected to be more variable, with heavier rainfall events and longer average time between rain events (Easterling *et al.* 2000; Gordon *et al.*

1992; Groisman *et al.* 1999). These changes in rainfall distribution are expected to cause further modifications in plant distributions (IPCC 2007). Central Oklahoma is often predicted to receive a 20% increase in rainfall, as has been the trend for the past 50 years (Kunkel *et al.* 1999).

Researchers are only beginning to explore what these changes will mean for natural communities. Extreme climate years or episodic events, which are expected to become more frequent with future global climate change (Diffenbaugh *et al.* 2005; Mearns *et al.* 1984; Tebladi *et al.* 2006), can act as strong ecological filters determining which species persist at a site (Fuhlendorf *et al.* 2001; Kammer 2002; Parmesan *et al.* 2000). For example, arid ecosystems have strong reactions to El Niño years (Holmgren *et al.* 2006) and wet years in deserts are important for new recruitment of shrubs and other perennials; drought in both arid and moderate climates can cause local extinctions of certain species (Mirti *et al.* 2007; Parmesan *et al.* 2000). Such events can cause changes in species richness and community structure that may persist for years (Mirti *et al.* 2007; Tilman and El Haddi 1992).

It is already clear that the effects of climate change on communities will not be limited to plant species composition but will also affect higher trophic levels (Parmesan 2006) and ecosystem functions such as water cycling (Eldridge and Freudenberger 2005; Wang *et al.* 2007), productivity, decomposition of soil organic carbon, N mineralization and nutrient cycling (Chapin *et al.* 1995; Epstein *et al.* 1999; Fornara and Tilman 2008; Grime 1988; Hobbie 1992; Saleska *et al.* 2002; Wedin and Pastor 1993). Therefore, a predictive knowledge of how plant communities are likely to change is useful for predicting ecosystem productivity, carbon storage and flux, water retention and run-off and economic impacts of climate change.

The current correlation of vegetation with climate is used in general circulation models (GCMs) to predict future distributions of vegetation types using dynamic vegetation models (DVMs) (Crucifix *et al.* 2005). However, it is unlikely that all species in a community will shift together in the same direction (Pearson and Dawson 2003). Different methods and rates of dispersal will allow some species to adjust their range faster than others. The migration of some species may be completely blocked by urban or agricultural land (Higgins and Harte 2006). Concomitant changes in precipitation, temperature and neighboring species can create novel environments that may never before have been experienced by the members of a community (Williams and Jackson 2007) and that GCMs and DVMs cannot predict.

A first step in predicting future plant communities is to see how species respond in field experiments manipulating climate and other global change factors. Grasslands can vary greatly in their proportion of different functional groups, in the seasonality of their rainfall and in their total mean annual precipitation (MAP) and temperature (MAT). In tallgrass prairie, perennial C_4 grasses dominate and a short summer drought is common, while in the Mediterranean climate of California, annual C_3 grasses dominate during and after winter rains and very few species are active during the long, dry summer. With these vast differences in MAP, rainfall seasonality and community composition, differences in grassland response to climate change can be expected, necessitating the study of various types of grasslands.

In this paper, we report the effects of an anomalous climate year on the plant community and species composition of a tallgrass prairie ecosystem. This work was part of a larger experiment designed to examine all aspects of ecosystem response to an extreme climate year and determine whether any affects carried over into the following year. Here we report the results of assessments of plant cover during and after 1 year of temperature and precipitation treatments. Increased temperature is likely to decrease soil moisture, which may give advantage to water efficient plants, such as C_4 species. However, Sage and Kubien (2003) predict that the timing of warming may be more important than the warming itself, with warmer winters favoring C_3 species. In the same vein, increased precipitation is thought to favor C_3 species by easing any moisture limitations. However, most previous climate manipulation experiments have found species-specific responses rather than uniform responses within a functional group (Walker *et al.* 2006; Williams *et al.* 2007; Zavaleta *et al.* 2003a). While we have found other ecosystem responses in our system after just 1 year of treatments (Arnone *et al.* 2008; Sherry *et al.* 2007, 2008; Zhou *et al.* 2006), changes in plant community structure may take longer, especially in systems dominated by perennials. In another nearby study with +2°C warming, a small increase in C_4 biomass was not noted until the second year of warming (Luo *et al.* 2009). On the other hand, a greater level of warming (+4°C) may elicit responses within 1 year.

Given the preceding considerations, we address the following questions: (i) Does 1 year of anomalous weather treatments cause changes in community structure and diversity? If so, do those changes have residual effects the following year? (ii) Do the anomalous weather treatments affect some functional groups more than others? If so, does that effect carry over into the following year? (iii) Are individual species affected by the anomalous weather year? If so, are those changes consistent within a functional group? And, do those changes persist into the following year? (iv) Finally, if changes are found, can they be attributed one environmental factor more than another?

MATERIALS AND METHODS

Study site

The experiment was conducted at the Kessler Farm Field Laboratory (KFFL) (34°58′54″N, 97°31′W) in McClain County, Oklahoma, ~25 miles southwest of the University of Oklahoma, Norman, on the Central Redbed Plains of Oklahoma (Tarr *et al.* 1980). The site is an old-field tallgrass prairie, abandoned from agriculture in 1974 and lightly grazed until 2002 when large herbivores were excluded. In summer, the site is dominated by the perennial C_4 grasses *Andropogon gerardii*, *Panicum virgatum* and *Schizachyrium scoparium*, and the C_3 forb *Ambrosia psilostachya*. In spring, the dominant plant is the C_3 winter annual grass *Bromus arvensis*. Plant nomenclature follows the United States Department of Agriculture (USDA) PLANTS Database (USDA NRCS 2008).

MAT at the site is 16.3°C, with monthly air temperature ranging from 3.3°C in January to 28.1°C in July. The MAP is 967 mm (averaged from 1948 to 1999, Oklahoma Climatological Survey). Precipitation is usually highest in May and June (240 mm), followed by September and October (192 mm), and lowest in January and February (82 mm) and July and August (125 mm). Total annual precipitation at the site for the years 2002, 2003 and 2004 was 854, 622 and 965 mm, respectively, 2003 being especially droughty during the summer and fall (Oklahoma Climatological Survey). The soil is a silt loam with 36% sand, 55% silt and 10% clay in the top 15 cm (Subedar and Luo, unpublished data). The proportion of clay increases with depth. The soils are part of the Nash–Lucien complex, typically having moderately high fertility, neutral pH (7.05), high available water capacity and a deep, moderately penetrable root zone (USDA 1979).

Experimental design

The experiment utilized a randomized block design with two levels of warming (ambient and +4°C) and two levels of precipitation (ambient and doubled). Twenty 3 × 2 m plots were placed 1.5 m apart in two rows 3 m apart. Warmed plots had two 165 cm by 15 cm radiant infrared heaters suspended above them at a height of 1.4 m (Kalglo electronics Inc., Bethlehem, PA). Previous experimentation determined that, at this height, two heaters, each with a radiation output of 100 watt/m^2, would warm the soil surface ~4°C (Wan *et al.* 2002). Rigorous testing has shown that the infrared radiation from the heater does not generate any visible light affecting photosynthesis (Kimball 2005). The remaining 10 plots each had two 'dummy' heaters, the same size and shape as the infrared heaters, constructed of metal flashing, suspended over the plots at the same height and position as in the warmed plots.

Five of the warmed plots and five of the unwarmed plots had attached 'water catchments', an angled sheet of corrugated plastic the same size as the plots. During a rainfall, these catchments directed precipitation onto the plots via three 12.5-mm diameter polyvinyl choride (PVC) pipes that distributed the water evenly over the plots. All plots were fitted with the PVC pipes whether or not they were attached to water catchments. With this design, extra precipitation was supplied to the doubled precipitation treatment plots only during natural rainfall. Heaters, dummy heaters, water catchments and PVC pipes were in place and functional for 1 year, from 20 February 2003 to 20 February 2004 (the treatment year). With this time frame, treatments began at the time of re-emergence of the earliest winter annuals and well before the emergence of other species; treatments ended long after all species had senesced. Data taken during the summer and fall of the pretreatment year, 2002, will be considered as reference measurements only.

In comparison to historical climate data, the effects of the warming treatment were extreme. The annual average daily air temperature in the warmed plots was increased to 22.0°C from 17.8°C in the control plots. Average August air temperature in the warmed plots (32.0°C) exceeded that of the warmest and driest August on record, 30.8°C in 1936 (Oklahoma Climatological Survey). Though 2003 saw only 64.7 cm of rain, it gave our double precipitation plots 129.5 cm of water, one-third above normal.

Each plot was divided into four equal quadrants. Scientific instruments were located in the northeast and southwest quadrants (Sherry *et al.* 2008). Species composition and cover was assessed in the northwest and southeast quadrants. For a direct assessment of biomass, half of the plot was clipped every summer after community structure data were taken, while the other half was clipped every fall after community structure evaluation. Air temperature at 15 cm above the soil surface and soil temperature at five depths below the surface were continuously monitored, along with soil moisture at five depths (for detailed description, see Sherry *et al.* 2008). Air temperature thermocouples were shielded from radiation by being placed between two pieces of curved PVC held ~1 cm apart at a 45° angle to the sun. Plant root simulator probes (Western Ag Innovations Inc., Saskatoon, Canada) monitored soil NH_4^+ and NO_3^- for a period of 1 month four times per year during this experiment (for details, see Sherry *et al.* 2008).

Data collection

From the summer of 2002 to the spring of 2005, community structure and species composition were assessed three times a year, in spring (late April) to include an assessment of the winter annual community, in summer at peak biomass (August) and in late fall (November) when C_4 species tend to dominate. The point-frame method was used to quantify cover of each species (Drew 1944). A 1 × 0.5 m frame with adjustable legs supporting a taut, double-string grid was placed over two quadrants in each plot. Cover (bare ground, litter or plant species) was recorded at each of the 50 points on the grid. Additionally, any plant species in the quadrant but not hit by the grid were recorded as one 'hit'. For each species, hits from the two subplots were averaged per plot.

Calculations

Raw absolute cover was calculated as the number of hits per species per plot divided by the total number of hits for that plot (including hits of litter and bare ground). Out of the three data collection times, the highest raw absolute cover value was selected for each species (and litter and bare ground categories) to be used in further analysis, ensuring we used the maximum cover value for each species. Maximum absolute cover was set = 1 for further analysis by dividing the raw maximum absolute cover value for each species (and litter and bare ground categories) by the total of the raw absolute maximum cover values for each plot. Relative cover was calculated by dividing the new absolute cover values for each species by the total absolute plant cover (leaving out the litter and bare ground categories). Eleven non-exclusive categories of functional groups based on flowering time (early spring, spring, summer and late summer), physiology (C3 photosynthesis, C4 photosynthesis and legume) and life history (winter annuals, other annuals, perennial forbs and perennial graminoids) were calculated as the sum of relative cover values for species in that group.

Species richness (S) was calculated as the total number of plant species per plot; the Shannon-Weiner index (H') as $H' = -\Sigma p_i \times \ln(p_i)$, where p_i is the relative cover of species i; Simpson's dominance index (D) as $D = \Sigma\, p_i^2$ and evenness (E) was calculated as $E = H'/\ln(S)$ (Krebs 1999). Species richness was also calculated for each of the 11 functional groups.

Statistical analysis

Absolute and relative cover values were arcsin square root transformed prior to analysis to achieve a normal distribution of residuals. Differences in overall community structure were visualized using the relative cover values in a nonmetric multidimensional scaling ordination (NMS, McCune and Grace 2002) using the software PC-Ord 5 (McCune and Mefford 2006) with the autopilot mode selected. To test for significance among groups discernable through the ordination, we performed a multi-response permutation procedure (MRPP) with pairwise comparisons between all years and among all treatments within years on the transformed relative cover measures, again with PC-Ord 5. Species must have occurred in at least three plots to be retained in the matrix for MRPP analysis. Sørenson relative distance measurements were used in computations to minimize the effects of outliers (McCune and Grace 2002).

To look for differences among treatments and years in diversity indices and functional groups, we used repeated measures analyses of variance (ANOVAs) separately on each index and functional group. Block, level of warming and precipitation level were main effects, and year was the repeated factor. Block was designated a random effect. (Due to non-sphericity (Mauchly's criterion $P < 0.0001$) and high co-linearity, a repeated measures multivariate analysis of variance (MANOVA) was prohibited (Sokal and Rohlf 1984).) Where significant effects were found, differences were further explored through post hoc analysis by consulting pairwise Tukey's tests.

To examine the species contributing to the observed changes in community structure, absolute rather than relative cover was used. Eighteen species that were either dominants or indicated by the NMS ordination to be important in distinguishing years or treatments (by contributing 45% or more of the variance to axes 1, 2 or 3) were further analyzed by graphing the change in maximum absolute cover over years for individual species. Differences among treatments and years in cover of these species were tested in individual repeated measures ANOVAs as described above.

Lastly, diversity indices and cover of physiological functional groups were analyzed by multiple linear regression to explore their relationships to environmental variables (soil temperature at 7.5 cm depth, soil moisture from 15 to 30 cm deep and available N) in three different time periods, spring (February–May), summer (June–September) and growing season (February–September).

The PROC MIXED procedure of SAS 9.1 (SAS Institute, Cary, NC) was used for ANOVA analysis. All statistical analyses, except for the ordination analyses, also used SAS 9.1.

RESULTS

Summer and fall 2002 data indicate that no significant differences in cover of species and functional groups existed among plots assigned to the different treatments in 2002 (Figs S1–S4). Nor were there differences in rank order of dominance. *Bromus arvensis* was the dominant species in that year, averaging 28.6 ± 3.4% of all plant cover, while *A.gerardii* cover averaged 8.7 ± 1.7%.

Treatment year

Relative to the temperature in control plots, the air temperature decreased by 0.4°C in the double precipitation plots, increased by 4.2°C in the warmed plots and by 4.8°C in the warming plus doubled precipitation treatment. Average soil moisture from 0 to 120 cm was 27.50 ± 0.18, 28.10 ± 0.19, 21.54 ± 0.20 and 25.28 ± 0.19% vol in control, double precipitation, warmed and warmed plus double precipitation treatments, respectively (Fig. 1). Differences in soil moisture among treatments were smallest during the spring before the onset of drought and greatest in the fall. Levels of available N did not differ among treatments in the spring of 2003 but were higher in double precipitation plots than in other treatments during the summer and winter of 2003 (Sherry *et al.* 2008). Levels of available N did not correlate with biomass but did have a weak positive relationship with temperature ($r^2 = 0.19$, $P = 0.06$).

MRPP analysis did neither detect differences in overall community structure among treatments in 2003 (Table 1) nor diversity indices differ significantly among treatments in 2003 (Table 2). However, there were significant differences among treatments for species richness within functional groups (Fig. 2; Table 2). Warming decreased the number of winter annual and early spring-flowering species by an average of two species compared to control plots (Fig. 2; Table 2) but increased summer-blooming species. Double precipitation decreased the number of perennial forb species by an average of two species compared to the control. A warming by precipitation interaction increased the number of (non-winter) annual species in warmed plots but not in the combined warming plus double precipitation treatment. A year by precipitation effect decreased the number of late summer-blooming

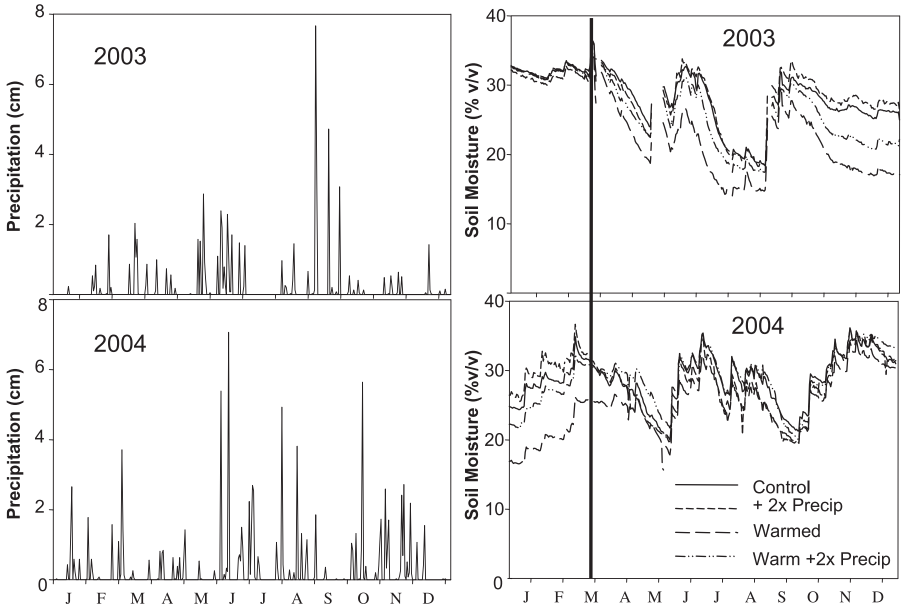

Figure 1: precipitation (left) and soil moisture at 15–30 cm soil depth (right) for the treatment year 2003 (top) and the post-treatment year 2004 (bottom). The solid dark line on the soil moisture plots indicates 20 February, the date that treatments were begun in 2003 and ended in 2004.

Table 1: summary MRPP statistics for comparisons of overall plant community structure in 2003 and 2004

Comparison	*T*	*P*	*A*
2003 vs 2004	−4.26	0.002	0.026
2004: Control vs 2× precipitation	1.07	0.86	−0.04
2004: Control vs warmed	0.30	0.58	−0.011
2004: Control vs warm + 2× precipitation	0.23	0.51	−0.016
2004: 2× Precipitation vs warmed	0.54	0.67	−0.024
2004: 2× Precipitation vs warm + 2× precipitation	0.44	0.59	−0.033
2004: Warmed vs warm + 2× precipitation	0.55	0.67	−0.023

T is the test statistic. *A* is the chance-corrected within-group agreement or effect size. *A* = 1 would indicate that all items within groups were identical (McCune and Grace 2002).

species, C_4 species and perennial graminoid species by an average of two species compared to controls (Fig. 2; Table 2).

Changes in relative cover of plant functional groups broadly reflected the same pattern (Fig. 3; Table 3). Winter annuals and early spring-flowering species had on average 21.6 and 21.85% less cover, respectively, in warmed and warmed plus double precipitation plots than in control and double precipitation plots. Other annual species increased in cover by 20.4% in warmed treatments compared to control and double precipitation. A warming by double precipitation interaction resulted in 22.3% greater cover of perennial graminoids in warmed plus double precipitation plots than in controls (Fig. 3; Table 3).

Frequency distributions of species in 2003 (Fig. 4) showed that both the warming and the double precipitation treatments increased the relative cover of *Andropogon* compared to *Bromus* (18 and 20%, respectively) and interacted additively in the combined warming plus double precipitation treatment, such that *Andropogon* increased 50% in relative cover from the control, replacing *Bromus* as the dominant species for that treatment. The absolute cover of 5 of the 18 individually analyzed species varied significantly among treatments in 2003 (Fig. 5; Table S1; Figs S1 and S2).

Total plant cover had a significant negative correlation with temperature (r^2 = 0.48, $P < 0.05$). Summer temperature had a significant negative correlation with cover of C_3 species and a weak positive correlation with C_4 cover (Fig. 6), due to a significant inverse relationship between C_3 and C_4 cover ($r^2 = 0.85$, $P < 0.05$). Legume abundance correlated negatively with average soil moisture (Fig. 6). Average available N did not correlate with cover, temperature or soil moisture (not shown).

Post-treatment year

After treatments ended in the spring of 2004, temperature in warmed plots immediately returned to control levels (Sherry *et al.* 2008). Levels of soil moisture in the warmed plus doubled precipitation plots quickly caught up with those in the control and double precipitation plots, but average soil moisture in the formerly warmed plots did not reach the level of the control plots until 4 months later (Fig. 1, Sherry *et al.* 2008). Temperature and soil moisture had a significant negative relationship only during the spring of 2004 (February–May, $r^2 = 0.22$, $P > 0.05$). Available N had no correlations with biomass, temperature or soil moisture in 2004.

MRPP did not detect differences in overall community structure among the former treatment plots (Table 1). Again,

Table 2: *f* statistics from repeated measures ANOVAs on overall diversity indices and on species richness of functional groups

Source	Year	Warming	2× Precipitation	Year× warming	Year × precipitation	Warming × precipitation	Year × warm × precipitation
Shannon diversity	1.35	0.02	0.13	0.05	0.68	0.21	0.01
Evenness	0.43	0.01	0.11	0.03	0.40	0.32	0.01
Simpson dominance	1.28	0.01	0.46	0.29	0.32	0.71	0.02
Species richness	**5.34***	0.00	0.15	0.01	1.39	0.07	0.00
Early spring species richness	**13.7*****	**15.9*****	0.08	1.30	0.08	0.33	1.30
Spring species richness	**10.9****	2.45	0.27	1.48	0.27	2.45	2.45
Summer species richness	0.05	**9.2****	1.69	3.81	0.42	1.69	1.91
Late summer species richness	1.91	0.31	0.31	2.75	**7.64****	0.08	0.08
C3 species richness	**14.78*****	1.26	0.41	2.57	0.23	1.64	0.64
Legume species richness	0.04	0.91	2.95	0.04	0.33	0.33	0.33
C4 species richness	1.54	0.86	0.00	3.46	**7.78****	0.00	0.86
Winter annual species richness	**16.5*****	**18.9*****	0.34	2.10	0.34	0.76	0.76
Other annual species richness	2.02	2.02	0.42	0.42	0.42	**6.02***	0.82
Perennial forbs species richness	0.31	0.60	**4.45***	0.01	0.60	0.11	0.01
Perennial graminoid species richness	1.30	0.79	0.14	0.752	**4.65***	0.40	1.30

Degrees of freedom = 28 in all cases. Statistically significant results are in bold.
$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

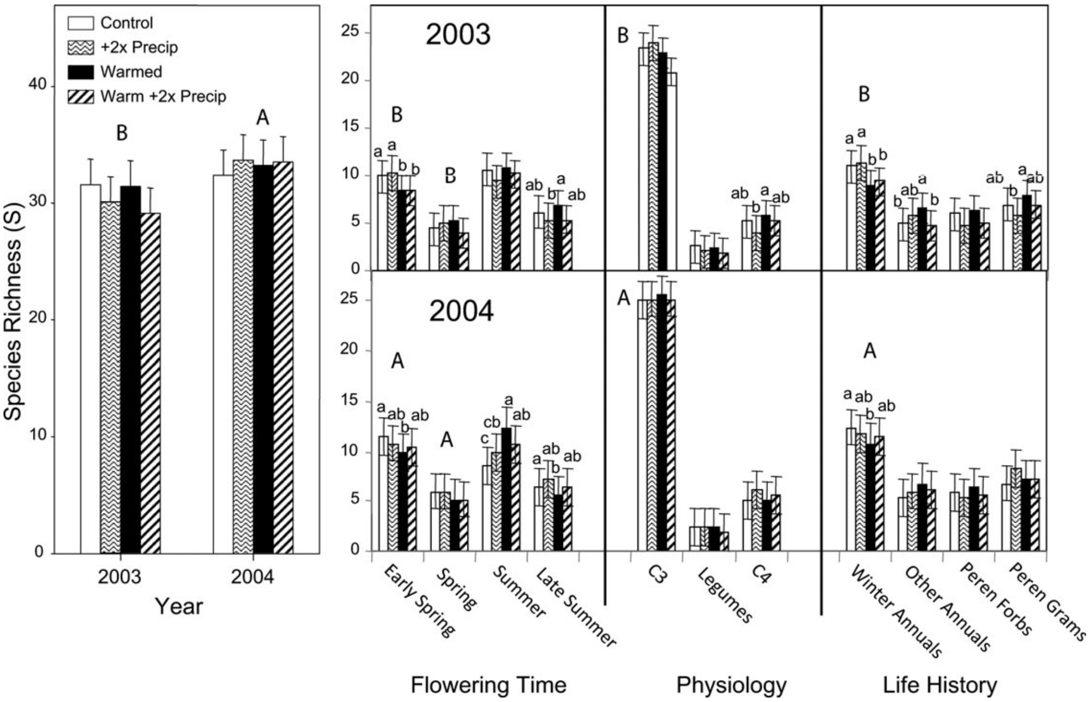

Figure 2: overall species richness (*S*) in 2003 and 2004 (left) and species richness of each functional group (right). Different uppercase letters indicate significant differences between years ($P < 0.05$). Different lower case letters indicate significant differences among treatments within a functional group within a single year ($P < 0.05$). Other diversity indices did not vary significantly among treatments or years.

overall measures of diversity did not differ among treatments, but species richness within functional groups did (Fig. 2; Table 2). The formerly warmed plots had an average of two fewer species of winter annual and early spring-blooming species and two more summer-blooming and other annual species than control plots. Summer-blooming species were the only functional group to differ significantly in cover among treatments in 2004, increasing an average of 28% in the former warmed treatments compared to control and former double precipitation plots (Table 3; Fig. 3).

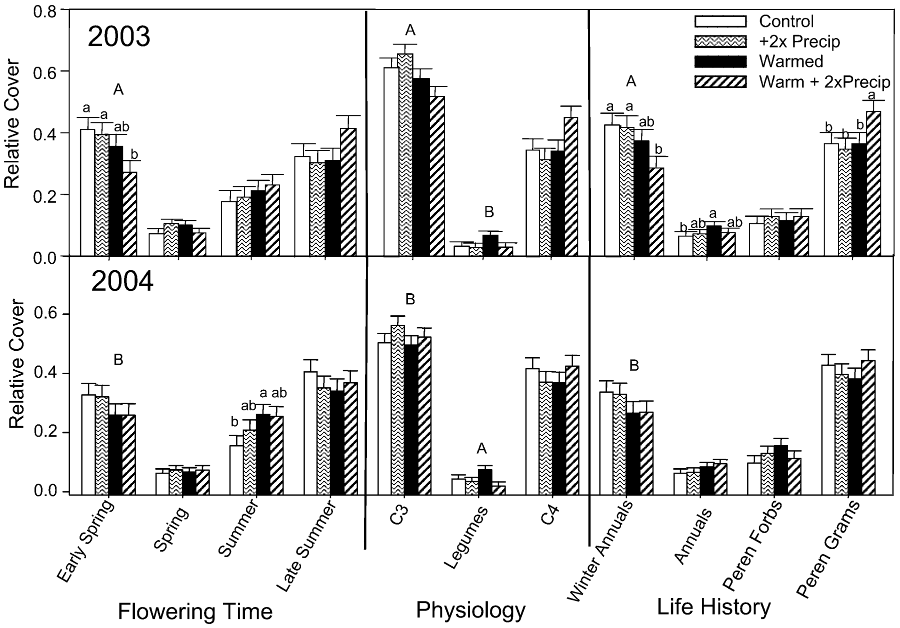

Figure 3: relative cover of functional groups by year and treatments. Different uppercase letters indicate significant differences between years ($P < 0.05$). Different lower case letters indicate significant differences among treatments within functional groups and years ($P < 0.05$). (Peren = perennial, grams = graminoids.)

Table 3: ***f*** **values from repeated measures ANOVAs on relative cover of functional groups (Fig. 2)**

	Flowering time				Physiology			Life history			
	Early spring	Spring	Summer	Late summer	C_3	Legumes	C_4	Winter annuals	Other annuals	Perennial forbs	Perennial graminoids
Year	5.37	1.14	1.13	2.03	**6.54***	**4.53***	3.00	**6.95***	0.88	0.93	2.43
Warming	**11.2****	0.00	**4.96***	0.19	0.32	0.00	0.84	**11.4****	**6.95***	0.57	1.72
2× Precipitation	0.22	0.02	0.56	1.82	0.00	0.30	0.11	0.29	0.09	0.13	1.68
Year × warm	1.38	0.55	0.57	0.20	0.00	1.26	0.40	1.19	0.04	0.03	1.49
Year × precipitation	1.17	0.27	0.03	1.05	0.01	0.00	0.03	1.04	0.41	0.18	0.37
Warm × precipitation	0.54	3.03	0.37	3.81	2.26	2.05	1.66	0.65	0.80	1.14	**5.27***
Year × warm × precipitation	0.72	1.88	0.65	0.20	0.09	0.00	0.05	1.00	0.92	0.70	0.10

Degrees of freedom = 28 in all cases.
$*P \leqslant 0.05$, $**P \leqslant 0.01$.

In 2004, 4 of the 18 individually analyzed species varied significantly among treatments in absolute cover (Table S1; Figs S1 and S2). Of these, one species acted in accordance with its functional group and two species showed differences among treatments where functional groups had not. *Bromus* barely remained dominant in the control and double precipitation plots, but *Andropogon* surpassed *Bromus* in the formerly warmed plots and remained dominant in the former warmed plus double precipitation plots (Fig. 4), having 25 and 37% greater cover, respectively, than *Bromus*. However, these two dominant species did not differ significantly in absolute cover among former treatment plots (Fig. 5).

C_3 and C_4 cover were again tightly negatively correlated ($r^2 = 0.52$, $P < 0.05$), but C_3 and C_4 cover had no correlation with temperature in 2004. C_4 cover did show a significant positive correlation with summer soil moisture, while C_3 cover had a weak negative relationship (Fig. 6). Legume cover correlated with higher temperatures and lower soil moisture (Fig. 6).

Comparisons between years

Temperature had a significantly negative correlation with soil moisture in 2003, but no relation in 2004. Average soil temperature and soil moisture in control plots differed little between 2003 and 2004 growing seasons (20.3 ± 1.9°C, 25.3 ± 0.66, 19.4 ± 0.12°C and 24.6 ± 0.13%, respectively). However, spring soil moisture was 10.6% higher than the year's average in spring 2003, prior to drought, and 5.8% lower than the year's average in spring 2004, before full recovery from drought (Fig. 1).

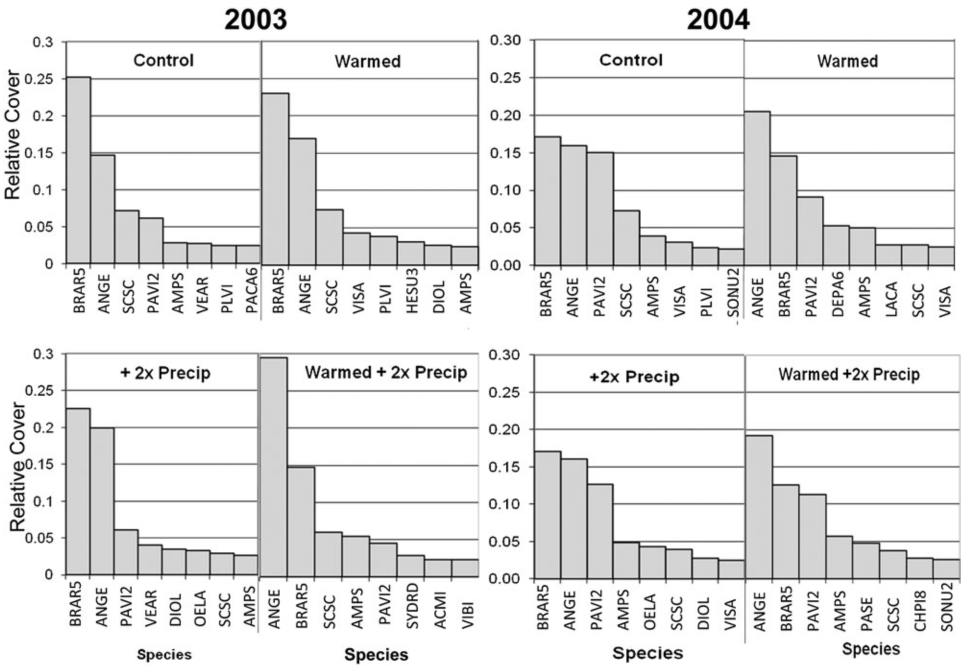

Figure 4: rank order of species abundances (relative cover) for the eight most abundant species in each treatment in 2003 and 2004. Abbreviations follow the USDA PLANTS Database (Table S1; USDA NRCS 2008): ACMI = *Achillea millefolium*, AMPS = *Ambrosia psilostachyia*, ANGE = *Andropogon gerardii*, BRAR5 = *Bromus arvensis*, CHPI8 = *Chrysopsis pilosa*, DEPA6 = *Desmodium paniculatum*, DIOL = *Dichanthelium oligosanthes*, HESU3 = *Heterotheca subaxillaris*, LACA = *Lactuca canadensis*, OELA = *Oenothera laciniata*, PACA6 = *Panicum capillare*, PASE = *Paspalum setaceum*, PAVI2 = *Panicum virgatum*, PLVI = *Plantago virginica*, SCSC = *Schizachyrium scoparium*, SONU2 = *Sorghastrum nutans*, SYDRD = *Symphyotrichum drummondii*, VEAR = *Veronica arvensis*, VISA = *Vicia sativa*, VIBI = *Viola bicolor*.

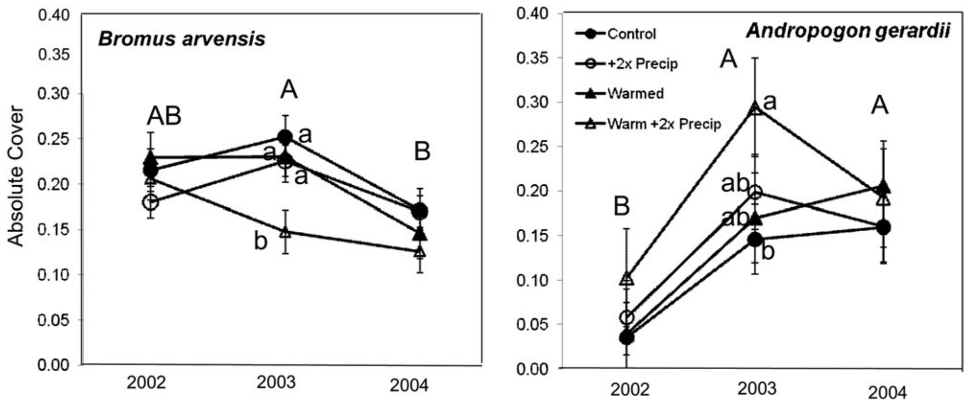

Figure 5: absolute cover of the two dominant species in the pretreatment (2002), treatment (2003) and post-treatment (2004) years. (Spring data were not available for 2002, so cover of *Bromus* may be underestimated for that spring.) Identical uppercase letters indicate no significant differences between years ($P < 0.05$). Different lower case letters indicate differences among treatments within years ($P < 0.05$ for *Bromus*, $P = 0.08$ for *Andropogon*).

NMS ordination of species relative cover and MRPP analysis of groups detected significant differences in overall community structure between years (Table 1; Fig. S5). Together three axes accounted for 85.5% of the variation between years. Axis 1 alone accounted for 52.9% of the variation and was negatively correlated with cover of the perennials *A.gerardii* (r^2 = 0.81) and *Solanum carolinense* (r^2 = 0.56), both more abundant during 2003. Axis 1 was also positively correlated with presence of the summer annual *Heterotheca pilosa* (r^2 = 0.69), more abundant in 2004. Axis 2 accounted for 13.6% of the variation and was negatively correlated with cover of *B.arvensis* (r^2 = 0.69) and *Ulmus rubra* seedlings (r^2 = 0.51), which were more abundant in the spring of 2003 (prior to drought).

Winter annuals, early spring- and spring-blooming species, and C_3 species significantly increased in species richness from 2003 to 2004 (Table 2; Fig. 2). Doubled precipitation interacted significantly with year in four functional groups, lowering species richness in double precipitation plots for late

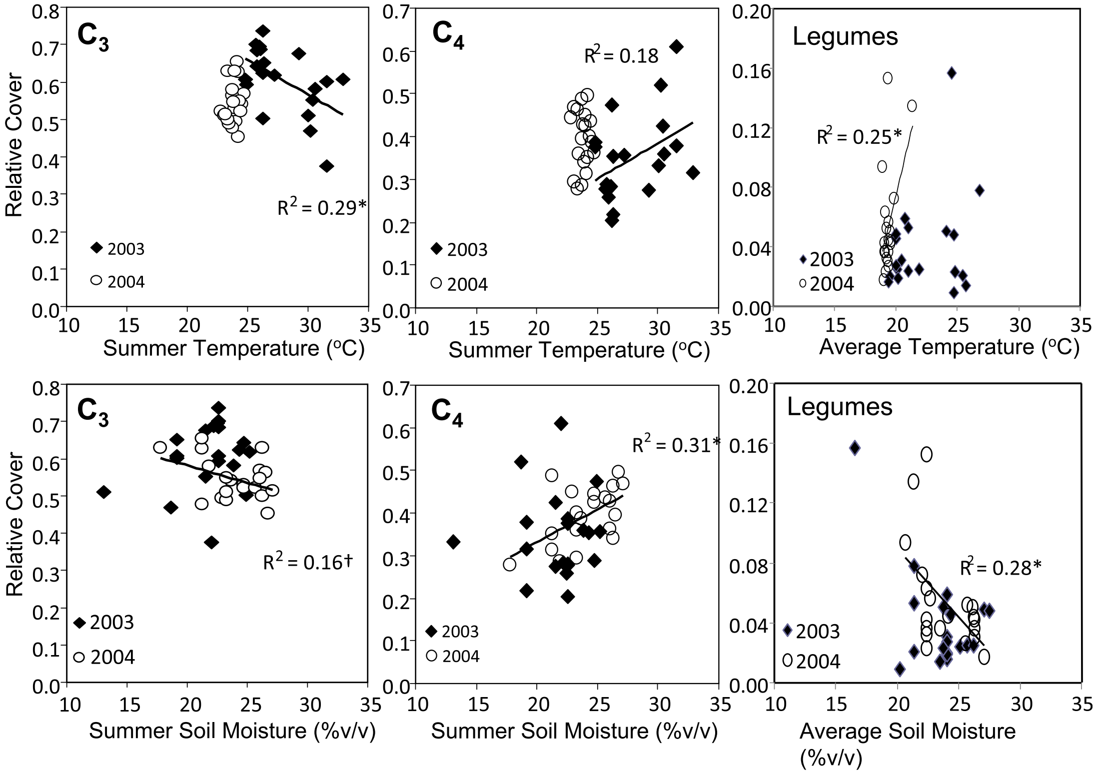

Figure 6: linear correlation of relative cover of C_3, C_4 and legume cover with soil temperature at 7.5 cm depth (top) and soil moisture at 15–30 cm depth (bottom). $^*P \leqslant 0.05$, $^†P \leqslant 0.08$.

summer-blooming species, C_4 species and perennial graminoids compared to controls in 2003 but increasing (non-winter) annual species. None of the main factors interacted with year in affecting cover of functional groups. Cover of C_3 and winter annual species decreased 10.2 and 17.3%, respectively, from 2003 to 2004, while leguminous species increased 25.5% (Fig. 3).

Of the 18 species examined individually, five showed significant differences in absolute cover between years (Figs S1 and S2). *Bromus* was the dominant species in 2003, averaging 25% of the plant cover, but fell to second in 2004, averaging 15% of the relative cover (Fig. 4). *Panicum virgatum*, another C_4 perennial grass, increased in relative abundance in 2004 to the extent that it could be called a third dominant (Fig. 4).

C_3 and legume cover correlated negatively with C_4 cover in both years ($r^2 = 0.49$, $P < 0.05$). Temperature was positively related to C_4 cover in 2003 but negatively during 2004, while the opposite pattern was seen for cover of C_3 species. Soil moisture did not correlate with C_3 or C_4 cover in 2003 but was negatively related to C_3 cover and positively related to C_4 cover in 2004. Legume cover had a positive relationship to temperature and a significantly negative relationship with soil moisture in both years (Fig. 4).

DISCUSSION

Seasonal patterns of soil moisture differed between the 2 years and interacted with treatments, making interpretation of results complex. Drought in the summer and fall of 2003 caused a soil moisture deficit that carried over into the spring of 2004. Despite lower soil moisture in warmed plots than controls in spring 2003, warmed plots had greater biomass during that spring (Sherry *et al.* 2008). C_3 and annual species declined later in 2003 when drought gave perennial and C_4 species an advantage. Soil moisture was low in spring 2004, giving later blooming species an advantage during that year. The changing pattern of cover in the two dominant species reflects the soil moisture conditions. The C_4 species, *Andropogon*, increased during the dry year of 2003, and the C_3 winter annual, *Bromus*, decreased in the dry spring of 2004, accounting for the changes in the dominance hierarchy (Figs 4 and 5). This change in dominance hierarchy occurred despite low *Andropogon* coverage in warmed plots before treatments were applied (2002, Fig. S4) and a decrease in the absolute cover of *Andropogon* in the post-treatment year (2004, Fig. 5). Temperature was negatively correlated with C_3 cover and positively correlated with C_4 cover in 2003, while in 2004, these groups showed correlations with soil moisture. Therefore, warming-related exacerbation of low moisture in spring 2004 is the likely one major cause of differences among former treatment plots in the post-treatment year of 2004.

Based on our experience at a nearby long-term 2°C climate-warming experiment, the increase in C_4 cover was not unexpected. However, in that experiment the increase in C_4 cover was not seen until the third year of warming (Luo *et al.* 2009).

C_4 species at drier short- and mixed-grass prairie sites have shown the opposite response to that seen at this tallgrass site, declining with warming or drought (Alward *et al.* 1999; Lauenroth and Dodd 1978). The C_4 photosynthetic pathway is primarily an adaptation to high light and high temperatures, and although it does confer an increase in water use efficiency, other traits can provide even greater drought tolerance for arid habitats (Knapp and Medina 1999; Pearcy and Ehleringer 1984). C_4 species typically show a greater response to temperature than C_3 species, while C_3 species usually show a greater response to water (Kemp and Williams 1980; Lauenroth and Dodd 1978; Paruelo and Lauenroth 1996; Wilson 2007). Responses of C_4 grasses to a changed precipitation regime may depend on the existing level of soil moisture, i.e. whether the site is typically dry or mesic (Knapp 1984; White *et al.* 2000).

This study did not find functional group responses to the doubled precipitation treatment in terms of cover, likely due to the minimal rainfall in the summer of 2003 when double precipitation plots received little more water than other plots. The average soil moisture of double precipitation plots was increased only 2% (absolute volumetric water content) above that of control plots over the entire treatment period. The timing of rainfall matters, both for overall biomass production and for which plant species benefit (Epstein *et al.* 1999; Morecroft *et al.* 2004; Paruelo and Lauenroth 1996; Skinner *et al.* 2002). However, the double precipitation treatment did affect biomass (Sherry *et al.* 2008) and species richness of functional groups.

The response of a particular species may not be a direct effect of the treatments. Species may display indirect responses due to changes in the abundance of competitor species or mineralization rates (Klein *et al.* 2004). If competition is involved, the response of a species to warming or precipitation may differ dramatically at another site with different neighbors. Differential responses of species and functional groups to changes in climatic variables may also depend on their phenology. Often, as in our system with a relatively mild winter, C_3 species are most active in the winter and spring, while C_4 species are most active during summer (Sage and Monson 1999; Skinner *et al.* 2002). Additionally, the winter annuals and several other C_3 species emerge earlier in the spring than C_4 species (Sherry *et al.* 2007). This phenological complementarity means that changes in the timing or seasonality of rainfall may affect one group and not the other or may affect vastly different life cycle stages in the two groups (Gulmon *et al.* 1983; Skinner *et al.* 2002). This experiment was not designed to determine whether responses were due to changing competitive conditions or to better fit of physiological tolerances or to a combination of the two. However, summer-blooming perennials being released from competition with spring-blooming species in the dry spring of 2004 is one possible mechanism explaining our results. Earlier emergence and growth of C_3 species in the spring may give them an advantage in competition for light and space in normal or high-rainfall years (Dunnett and Grime 1999) and their early growth may shade the later emerging C_4 species, reducing their potential photosynthesis and growth.

Changes in species abundance have frequently been observed in warming experiments and in long-term observations of climate warming (i.e. Chapin and Shaver 1985; Dunnett *et al.* 1998; Harte and Shaw 1995; Herben *et al.* 1995; Silvertown *et al.* 1994; Walker *et al.* 2006; Willis *et al.* 1995). Typically, such changes are species specific and cannot be generalized to functional groups. Among manipulative climate change experiments in grassland, most have taken place where the climate, functional group composition of the community and/or functional group of the dominant species are vastly different from the North American tallgrass prairie (i.e. California annual grasslands (Zavaleta *et al.* 2003a) or synthetic eastern North American old-field communities (Engel *et al.* 2009)). The ecosystem of the TasFACE climate change experiment in Tasmania is closest to our system, having both C_3 and C_4 grasses (Williams *et al.* 2007). In that experiment, warming increased C_4 biomass and decreased C_3 biomass overall, but some individual species had significant responses that were the opposite to the rest of their functional group. In our study, responses of low abundance species may not have been statistically detectable and therefore our experiment does truly test all species within a functional group.

Some species might respond differently if treatments were applied for a longer period of time than in this study. For example, in a separate experiment also at the KFFL, continuous 2°C warming since 1999 did not increase C_4 plant abundance during the first or second year but has done so ever since (Luo *et al.* 2009). In the 1-year step warming experiment considered here, we had expected that if responses were seen, the high proportion of perennials at this site would cause a carry over effect into the post-treatment year. However, the only lag effect observed in functional groups was in summer-blooming species; the effect disappeared when considering annuals versus perennials.

Changes in cover can be due to changes in the number of plants or to changes in the size of plants. Our data did not distinguish between the two. In perennial grasslands, changes in diversity and community structure often depend on the dynamics of the annual species, consistent with the 'core–satellite' description of Hanski (1982). The dominant grasses wax and wane, and other species opportunistically use the space in between the matrix of dominants (Hartnett and Fay 1998; Hobbs *et al.* 2007; Zavaleta *et al.* 2003a, 2003b).

Though inter-annual climate variability may have helped maintain plant diversity in the past by creating temporal heterogeneity, climate change is expected to be directional. Not only will average annual temperature increase but also anomalous weather years will be more frequent (Tebaldi *et al.* 2006). In such a situation, experimental warming studies and long-term correlations observed between climate and plant abundance should help predict future plant community structure at the level of species composition rather than simply vegetation type. In the case of central Oklahoma tallgrass prairie, this means an increase in the wind-pollinated, C_4 perennial grasses and a decrease in annuals, especially winter annuals, which are often weedy, like the exotic *B.arvensis.*

CONCLUSION

Warming treatments had similar effects to a dry year, although only year varied significantly in ordination analyses. Both warming and dry conditions decreased the relative cover of winter annual species, including the dominant, *B.arvensis*. The wetter year also increased legume cover and total species richness. The anomalous weather treatments did change the dominance hierarchy, an effect which carried over into the year following treatments. An increase in both cover and richness of summer-blooming species in formerly warmed plots was also seen in the year following treatments. If the effects of one anomalous year on functional group abundance and the dominance hierarchy can carry over into the following year, several warm years could have a significant impact on plant community structure.

SUPPLEMENTARY MATERIAL

Supplementary Material is available at *Journal of Plant Ecology* online.

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