

SPECIAL FEATURE

ECOLOGICAL CONSEQUENCES OF CLIMATE EXTREMES

A climatically extreme year has large impacts on C₄ species in tallgrass prairie ecosystems but only minor effects on species richness and other plant functional groups

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Summary

1. The occurrence and intensity of climate extremes, such as extremely warm years, are expected to continue to increase with increasing tropospheric radiative forcing caused by anthropogenic greenhouse gas emissions.

2. Responses of terrestrial ecosystem processes and services – such as above-ground net primary productivity (ANPP) and maintenance of plant species diversity – to these extreme years for multiple years post-perturbation are poorly understood but can have significant feedback effects on net ecosystem CO₂ uptake and ecosystem carbon sequestration.

3. We exposed six 12 000-kg intact natural tallgrass prairie monoliths to an extremely warm year (+4 °C in 2003) in the second year of a 4-year study (2002–2005) using the EcoCELL whole-ecosystem controlled-environment, gas exchange facility. Six control monoliths were not warmed in the second year but were maintained under average field conditions. Natural diel and seasonal patterns in air temperature were maintained in both treatments throughout the study. Thus, with the exception of the second year in the ‘warmed’ treatment, we created 4 years of nearly identical climate in all EcoCELLs.

4. Interannual ANPP (10 cm clipping height) responses of the entire plant community to the extreme year were largely determined by responses of the dominant C₄ grasses. These included large decreases in ANPP in 2003 followed by complete recovery to levels observed in the control ecosystems in the year following warming. Species richness and productivity of the nitrogen-fixing plant functional group appeared to play a role in defining overall plant community ANPP, however, even though this richness and productivity could not explain the decrease in community ANPP observed in warmed ecosystems in the second year (2003) of the study or its recovery in the year after (2004). Surprisingly, very few of the 67 species present in plant communities during the 4-year study responded to the warm year at any time during or after the treatment.

5. *Synthesis.* Results from this study indicate that as extreme climate years become more prevalent, their immediate and lagged impacts on collective ecosystem processes, such as whole-community ANPP, may be very pronounced, but effects on component ecosystem processes may be limited to the dominant plant functional group (ANPP).

Key-words: above-ground net primary productivity – ANPP, anomalously warm year, EcoCELL whole-ecosystem controlled-environment gas exchange facility, grassland ecosystem,

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interannual climate variability, lagged responses, plant biodiversity, plant functional group, plant species diversity, plant–climate interactions

Introduction

During the last half century, climate extremes have become more frequent and their intensity has increased (Easterling *et al.* 2000). This trend is expected to continue as a result of growing tropospheric radiative forcing caused by ever-increasing anthropogenic greenhouse gas emissions (Intergovernmental Panel on Climate Change 2007). Quantitative research on the consequences of these more frequent and stronger climate extremes, such as anomalously warm years (e.g. Braswell *et al.* 1997; Arnone *et al.* 2008), on terrestrial ecosystem processes and services has been limited. These processes and services include: net primary productivity (NPP, Arnone *et al.* 2008; Sherry *et al.* 2008); net ecosystem productivity (NEP, or net ecosystem carbon dioxide (CO₂) uptake occurring during a year; Braswell *et al.* 1997; Schimel *et al.* 1997, 2001; Vukicevic, Braswell & Schimel 2001; Ciais *et al.* 2005; Doney & Schimel 2007; Arnone *et al.* 2008) and its component fluxes (Verburg *et al.* 2005; Arnone *et al.* 2008; Zhou *et al.* 2010); and plant community phenology (Sherry *et al.* 2007).

Global (Keeling, Chin & Whorf 1996; Myneni *et al.* 1997; Randerson *et al.* 1997; Cao & Woodward 1998; Vukicevic, Braswell & Schimel 2001) and site-specific (e.g. Law *et al.* 2002) data sets have demonstrated that climate and climatic variability influences the terrestrial biogeochemical processes that determine net ecosystem CO₂ exchange (NEE, the instantaneous rate of CO₂ flux whose annual sum equals NEP) at multiple time-scales. Terrestrial ecosystems control CO₂ fluxes to and from the atmosphere (e.g. Schimel 1995; Keeling, Chin & Whorf 1996; essentially equivalent to NEP) through photosynthesis and respiration, the balance between NPP and heterotrophic respiration (R_h). We conducted a 4-year study (Arnone *et al.* 2008) in the EcoCELL facility to quantify immediate and lagged impacts of a single climate variable, temperature, imposed as an extremely warm year (+4 °C), on ecosystem processes that modulate NEE. Results from this study (Arnone *et al.* 2008) showed that immediate (i.e. in the extremely warm year) reductions in annual NEP in ecosystems exposed to the temperature increase resulted primarily from large reductions in NPP – both above-ground (ANPP) and below-ground (BNPP). One-year lagged reductions in NEP were due to lagged decreases in R_h and 2-year lagged recovery of NEP (to pre-warm-year levels) resulting in part from decreases in NPP (and ANPP) and maintenance of slightly elevated levels of R_h . Thus, interannual changes in NPP and ANPP strongly modulated NEP, or the net ecosystem carbon (CO₂) sink.

The overarching question of the study presented here was unresolved, however: What role do various plant functional groups and species play in defining the responses in ANPP we observed (Arnone *et al.* 2008) to exposure to an extremely warm year? While observations from field studies clearly have demonstrated the large role that interannual variability in tem-

perature and precipitation (i.e. climate) can play in defining ANPP of grassland ecosystems (Briggs & Knapp 1995; Knapp & Smith 2001) and the productivity of individual functional groups and species (Sherry *et al.* 2008), these studies were unable to distinguish the relative roles of temperature and precipitation because large natural intra- and interannual variability in both factors confounded mechanistic inferences. Further, no data were available on the interannual effects of extremely warm years on grassland species biodiversity and whether the strong diversity – productivity relationships that have been established in manipulative ‘biodiversity experiments’ (e.g. Naeem *et al.* 1996; Tilman, Wedin & Knops 1996; Aarssen 1997; Hector *et al.* 1999; Niklaus *et al.* 2001) still hold across a narrower range of species-richness levels in large natural grassland community monoliths where the soil is undisturbed.

The main objectives of the research presented here were: (i) to determine the extent to which changes in plant community functional group and species abundances may explain the dramatic reduction in ANPP (and NPP) observed in intact tallgrass prairie (TGP) ecosystems during an experimentally imposed extremely warm year, and the equally dramatic recovery in ANPP that occurred in the following year when temperatures were returned to normal (i.e. average Oklahoma field temperature regime identical to conditions provided to the control ecosystems) (Arnone *et al.* 2008); (ii) to quantify the immediate and lagged effects of exposure of ecosystems to the extremely warm year on species diversity (richness) of entire plant communities and richness within the functional groups, and to evaluate the extent to which community ANPP is related to community and functional group species richness and (iii) to quantitatively explore the possible ecological mechanisms that modulate annual ANPP.

Materials and methods

MONOLITH ECOSYSTEMS AND PLANT COMMUNITIES

We selected a TGP site at the Kessler Farm Field Laboratory at the University of Oklahoma (Washington, Oklahoma, USA, 35.05° W, 97.54° N) to extract monoliths for transport back to the Desert Research Institute (DRI) in Reno, Nevada, USA. We used TGP as a model terrestrial ecosystem for several reasons, including that (i) its ecology and biogeochemistry are well understood (Knapp *et al.* 1998); (ii) TGPs are among the most floristically diverse ecosystems in the world, and this high diversity occurs on a relatively small spatial scale that can be captured and accurately represented on plots of c. 3 m² (Collins *et al.* 1998); and (iii) grasslands represent more than 20% of the world’s terrestrial surface area and about 10% of global organic C stocks (Schimel 1995; Schlesinger 1997). We chose to excavate intact monoliths to minimize the confounding effects of soil disturbance on soil biogeochemical processes and ANPP.

Soils at the site belong to the Pulaski series, Typic Ustifluvents derived from alluvium, with a topsoil (0–15 cm depth) pH of 5.3 (Stevenson & Verburg 2006) and a subsoil (> 60 cm) pH of 8.4 (Soil

Conservation Service 1979). Nitrogen availability was low as evidenced by low soil solution N concentrations (no treatment effects, annual average for 4 years: $\text{NH}_4\text{-N}$, c. 0 mg N L^{-1} ; $\text{NO}_3\text{-N}$, 0.05 mg N L^{-1}) and low N leaching fluxes (average of $23 \pm 7 \text{ mg NH}_4\text{-N m}^{-2} \text{ year}^{-1}$ during the 4 years for control ecosystems, $24 \pm 2 \text{ mg NH}_4\text{-N m}^{-2} \text{ year}^{-1}$ for warmed ecosystems; average of $42 \pm 3 \text{ mg NO}_3\text{-N m}^{-2} \text{ year}^{-1}$ during the 4 years for control ecosystems, $32 \pm 3 \text{ mg NO}_3\text{-N m}^{-2} \text{ year}^{-1}$ for warmed ecosystems) (Verburg *et al.* 2009), as well as relatively low N mineralization rates (Wan *et al.* 2005). Soil organic C content in the 0–15 cm depth was $0.85 \pm 0.12\%$, while N content was $0.063 \pm 0.01\%$ with both C and N concentrations decreasing exponentially with depth. Total C stocks down to 90 cm depth equalled $6.87 \pm 0.67 \text{ kg C m}^{-2}$, and total N stocks equalled $0.53 \pm 0.05 \text{ kg N m}^{-2}$ ($n = 12$). Both C and N stocks were similar among monoliths assigned to the warmed versus control treatments. In general, these native TGP plant communities are considered to be N-limited (Blair *et al.* 1998). Earlier plant community inventories at this site indicated that the vegetation has been dominated by *Panicum virgatum* L., *Schizachyrium scoparium* (Michx.) Nash, *Andropogon gerardii* Vitman, *Sorghastrum nutans* (L.) Nash, *Ambrosia psilostachya* DC., *Amphiachyris dracunculoides* (DC.) Nutt, *Bromus japonicus* Thunb. and *Eragrostis* species.

The number of species observed in each monolith in the pretreatment year (2002) ranged from 11 to 25 with a similar mean number of species present in monoliths assigned to control and warmed treatments (controls: 17.7 ± 2.7 ; to-be-treated: 17.5 ± 4.0) and EcoCELL (controls: 26.5 ± 1.5 ; to-be-treated: 31.0 ± 0.1). During the 4 years of study, we recorded a total of 67 species of vascular plants with C_4 graminoids, viewed across all EcoCELLs, making up $77 \pm 6\%$ ($n = 4$ EcoCELLs) of the peak biomass in the pretreatment year.

Most plant species were dormant or nearly dormant at the time of excavation (late September to late October 2001). Above-ground vegetation was clipped before excavation to a height of 10 cm above the soil surface. Using a Ditchwitch® (The Charles Machine Works, Inc., Perry, OK, USA) equipped with a 3-m cutting bar attached to a tractor plus an 80-t trackhoe and 120-t crane, 12 intact monoliths, each of 5.36 m^3 were excavated to a depth of 1.8 m by inserting an epoxy-coated, bottomless, steel-reinforced, precast concrete box (inside dimension $2.44 \times 1.22 \times 1.80 \text{ m}$, LWD; outside dimension $2.7 \times 1.5 \times 1.85 \text{ m}$, LWD) snugly around each monolith island to form the container walls. Once the box was inserted to 1.85 m depth, it remained tethered to the crane cables while soil from around the pot was removed with the track hoe. The pit surrounding each box was then excavated to a depth of 2.4 m to improve access to the base perimeter of the box. A small tractor with a 1-m Ditchwitch® cutting bar was then lowered into the pit and used to cut horizontal openings through the soil underneath each monolith along the bottom edges of each box through which steel guides were welded that held the bottom steel plates. Four steel plates were inserted through the soil beneath each monolith – across its width – to form the bottom of the box. The steel plates were driven horizontally through the soil using one 4-t bulldozer to push each plate and one 4-t bulldozer on the opposite side of the box to hold it in position. The 10 cm distance between inserted plates permitted water to drain out of the monolith. Each plate was welded to the bottom perimeter of each box. Each containerized monolith was lifted onto a flatbed truck, wrapped in 45-cm-thick polystyrene foam insulation (Styrofoam®; The Dow Chemical Company, Midland, MI, USA) and transported to DRI.

Upon arrival, we removed insulation from each containerized monolith, lifted each monolith off the flatbed with a crane, and lowered each through the roof of the glasshouse that houses the four EcoCELLs. Each monolith was placed onto a $2.5 \times 1.5 \text{ m}$ stainless steel

drainage collection pan sitting inside an EcoCELL. We placed three monoliths in each of the four EcoCELLs.

EXPERIMENTAL DESIGN

The EcoCELLs are open-flow, mass-balance, whole-ecosystem gas-exchange systems (chambers) that use the principles employed in leaf-level, gas-exchange cuvettes but at a much larger scale (Griffin *et al.* 1996; Cheng *et al.* 2000; Verburg *et al.* 2005). Total volume of each EcoCELL is 184 m^3 of which 40 m^3 was occupied by three monoliths plus 45-cm-thick Styrofoam® insulation extending from the top edge of each container to the floor of the EcoCELL. Each monolith was placed on four load cells (truck scales; one on each bottom corner of the monolith containers), each with a capacity of 5000 kg and a combined precision of $\pm 1 \text{ kg}$. Environmental controls included air temperature inside each EcoCELL and the absolute amount of water vapour (humidity) flowing into each EcoCELL. The experiment was conducted under current ambient levels of CO_2 . Average annual absolute humidity was $9.0 \text{ mmol H}_2\text{O mol}^{-1}$ during the pretreatment year and $12.6 \text{ mmol H}_2\text{O mol}^{-1}$ during the treatment and post-treatment years in all four EcoCELLs. The EcoCELL chambers receive natural light, which is attenuated by 22% due to the glasshouse and EcoCELL roofs (Griffin *et al.* 1996). The EcoCELL facility was necessary for the Arnone *et al.* (2008) study, as well as for the study presented here, because of the need to control climate at time-scales of 5 min to create realistic diel and seasonal climate variability while replicating the same climate in four consecutive years (in the two control EcoCELLs and $+4 \text{ }^\circ\text{C}$ in the EcoCELLs warmed in the second year) while simultaneously and continuously measuring NEE.

We created an extremely warm year using a constant $+4 \text{ }^\circ\text{C}$ temperature increase. This choice was based on analysis of mean annual air temperature measured at multiple locations in central Oklahoma where long-term records have been kept (1873–1999). Anomalously warm years were evident in the time course of annual mean air temperatures. In these clear cases, mean annual air temperature exceeded the long-term average (mean of the entire period of record) by $1\text{--}3.8 \text{ }^\circ\text{C}$. Comparison of annual temperature means with annual precipitation also showed that the two parameters were unrelated ($P > 0.80$, $r^2 < 0.15$), and thus indicated that imposing a single temperature treatment was realistic (i.e. warm years did not necessarily correlate with years with lower-than-average precipitation). We chose to simplify the way we imposed an extremely warm year since no overwhelmingly consistent intra-annual temperature pattern could be discerned from available historical data for the site, and because extremely warm years can occur by a combination of any number and duration of warmer-than-average events throughout the year.

Starting on 11 February 2002, temperatures inside the EcoCELLs were maintained at average Oklahoma-site air temperatures (based on 8-year [1993–2000], 5-min averages from a MESONET station [Brock *et al.* 1995] less than 1.6 km from the excavation site). Ambient air temperatures were adjusted weekly while maintaining diel patterns. We created an extremely warm year by heating the air passing through the air handlers and entering the two EcoCELLs that were maintained at a constant $+4 \text{ }^\circ\text{C}$ higher temperature in the second year of the 4-year study. Heat transfer through the sides of the monoliths was minimized by wrapping each monolith with a 45-cm Styrofoam® layer that allowed air temperature changes (diel to interannual) to affect the soil temperature primarily from the surface as occurs in all terrestrial ecosystems. Data from the field site indicated that the depth where soil temperature does not change significantly throughout the year averages between 1.4 and 1.5 m. This

depth corresponds to the mean annual air temperature (which at our site averaged 16 °C during the 1993–2000 period). Therefore, we installed a heat exchanger underneath the monoliths in each EcoCELL to maintain soil temperatures at 145 cm depth as close as possible to the 1993–2000 mean annual ambient air temperature (16 °C) measured at the excavation site to simulate realistic soil temperature profiles. Generally, temperatures at this depth were maintained within ± 0.3 °C of the set-point temperature for the duration of the study (with the exception of a few weekly deviations from set-points caused by occasional problems experienced with heat exchangers).

Precipitation was applied as nutrient-free, low-chlorine tap water using an overhead rain simulator with fixed intensity. The simulator was made of perforated polyethylene tubing with 2.4×1.2 m (L \times W) dimensions that delivered realistic raindrops and provided uniform coverage. We based frequency and amounts of precipitation on measurements from the MESONET site (same 8-year period used for temperature) with precipitation at each watering applied at the mean monthly total divided by the mean frequency for that month. The precipitation regime in the control and warmed EcoCELLs during the treatment year was the same as during the pretreatment year.

Plant communities were clipped to a height of 10 cm above the soil surface in the late summer of each year to: (i) simulate mowing, which is the main disturbance regime in this region that maintains TGP plant communities in their naturally highly diverse state (Knapp *et al.* 1998) and (ii) estimate annual ANPP_{>10 cm} (including standing dead tissues and litter). ANPP between 0 and 10 cm canopy height was subsampled annually at peak biomass by clipping two 30 \times 30 cm areas in each monolith to the soil surface. Averaged for the 4 years, the percentage of total ANPP occurring below 10 cm clipping height was $31 \pm 3\%$ with no differences observed between control and warmed communities. For most species in the TGP plant communities in the monoliths, the bulk (> 70%) of their ANPP occurred above the clipping height of 10 cm. For the few species with relatively short-statured growth habits, up to 50% of the ANPP could be represented below the 10 cm clipping height. In no year, however, did our ANPP sampling method of clipping at 10 cm height result in erroneously omitting a species from calculations of richness. The only effect of clipping height was that the true abundance (as measured by ANPP_{>10 cm}) of these few rarer species would have been slightly underrepresented (although interannual comparisons within species and evaluation of warming effects would have remained unaffected). Thus, ANPP_{>10 cm} data used in the present study (Fig. 1) as the basis

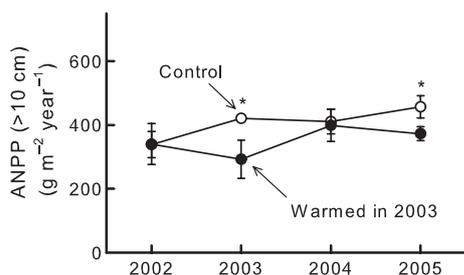


Fig. 1. Effects of a climatically extreme year (+ 4 °C in 2003) on mean (\pm SE) annual above-ground net primary productivity (ANPP_{>10 cm}) of intact tallgrass prairie ecosystems in the EcoCELLs (open circle, unwarmed controls; filled circle, warmed 4 °C in 2003; $n = 2$ EcoCELLs). Note that SE bars have been drawn for all means. In some cases, however, bars are shorter than the dimensions of the symbol. See Table 1 for summary statistics from repeated-measures ANOVA. Asterisks indicates a significant difference between treatments in 2003 ($P < 0.02$) and 2005 ($P < 0.07$) based on *post hoc* simple main effects (SME)-tests.

for all species and functional group abundance calculations averaged about 30% less than ANPP values reported in Arnone *et al.* (2008).

Calculations and statistical analyses

We calculated the abundance of the three major plant functional groups – graminoids, forbs and nitrogen-fixers – each year by summing the ANPP represented by all species in each group. In the same way, we subdivided the graminoids into C₃ and C₄ species. Finally, we calculated the abundance of each individual species in each functional group and plant community. The total ecosystem land area within each EcoCELL (*c.* 9 m², or three monoliths) was considered a plant community for purposes of statistical analyses. Species richness of entire plant communities and within each functional group was calculated as the total number of species present in each of these categories.

We used repeated-measures ANOVA ($n = 2$ EcoCELLs, e.g. von Ende 1993) to quantify the potential immediate and lagged effects of the extremely warm year on ANPP_{>10 cm} and species richness. Data were transformed (\log_{10}) prior to ANOVAs, when necessary, to comply with the requirements of homogeneity of variance for parametric ANOVAs (Zar 1984). When treatments only differed from each other in a single year (identified by examining interannual time course graphs of mean \pm SE values), repeated-measures ANOVA often did not show a significant treatment \times year interaction. In these cases, we used the simple main effects test in Stata (Stata Corp, College Station, TX, USA), using the Dunn's procedure, to assess whether treatments differed significantly from each other in specific years (Kirk 1982; Ender 2008).

We used simple linear regression analysis (e.g. Zar 1984) to assess the role that individual functional groups, individual species and whole-community and within-functional-group species richness may play in defining ecosystem ANPP, and to determine how the extremely warm year may impact these relationships. Individual annual EcoCELL mean values were used as points in these analyses. Given the low experimental replication ($n = 2$ EcoCELLs) in this study, we define statistical significance at $P < 0.10$ (even though most statistically significant values were $P < 0.05$).

Results

Above-ground net primary productivity greater than 10 cm (ANPP_{>10 cm}) of entire plant communities in the pretreatment year (2002) was similar in all EcoCELLs and did not differ between communities assigned to the control and to-be-warmed treatments (Fig. 1). In the treatment year (2003), warming decreased ANPP_{>10 cm} by more than 30% relative to that measured in control ecosystems. Mean ANPP_{>10 cm} of warmed ecosystems recovered completely in the following year (2004) but dropped below ANPP_{>10 cm} measured in controls again in 2005 (see Table 1 for summary statistics covering the 4 years of the study).

These immediate (in 2003) and lagged (in 2005) interannual patterns in ANPP_{>10 cm} in response to the warm year were primarily defined by the responses of the graminoid functional group (particularly in 2003, not as strongly in 2005) (Fig. 2, Table 1). The mean contribution of graminoids to overall community ANPP in both treatments declined from 87% in warmed ecosystems and 80% in the controls in 2002 – 31% in warmed ecosystems and 50% in control ecosystems in 2003

Table 1. *F*-ratios and *P*-values of repeated-measures ANOVAs for data presented in Figs 1, 2, 3 and 5 for each dependent variable on independent variables treatment (control versus warmed in 2003); year and treatment × year

Data source (Figures)	Dependent variable	Independent variable						Transformation
		Treatment		Year		Treatment × year		
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	
1	ANPP: Community	7.99	0.4237	5.96	0.0313	4.22	0.0632	–
2a	ANPP: Graminoids	2.21	0.2753	9.55	0.0106	4.38	0.0588	log
2b	ANPP: Forbs	0.11	0.7695	65.13	0.0001	0.32	0.8083	log
2c	ANPP: N ₂ fixers	0.02	0.9092	1.23	0.3784	0.28	0.8368	log
3a	ANPP: C ₄ graminoid species	1.08	0.4075	7.59	0.0182	2.22	0.1867	log
3b	ANPP: C ₃ graminoid species	0.94	0.4350	5.53	0.0366	0.44	0.7336	log
5a	Number of species: Community	1.58	0.3361	20.47	0.0015	3.55	0.0874	log
5e	Change in species richness: Community	0.92	0.4391	12.03	0.0060	3.54	0.0880	–
5b	Number of species: Graminoids	0.40	0.5918	2.22	0.1862	0.96	0.4688	–
5f	Change in species richness: Graminoids	0.12	0.7585	2.15	0.1948	0.92	0.4851	–
5c	Number of species: Forbs	8.00	0.1056	10.71	0.0080	3.37	0.0957	–
5g	Change in species richness: Forbs	0.18	0.7144	10.71	0.0080	4.32	0.0604	–
5d	Number of species: N ₂ fixers	0.00	0.9858	10.47	0.0085	0.42	0.7456	log
5h	Change in species richness: N ₂ fixers	0.34	0.6176	6.14	0.0293	0.47	0.7136	–

Pre-ANOVA data transformation used to correct for non-homogeneity in variance noted in the last column. All analyses used $n = 2$ EcoCELLs and an annual time step. Significant *P*-values are shown in bold.

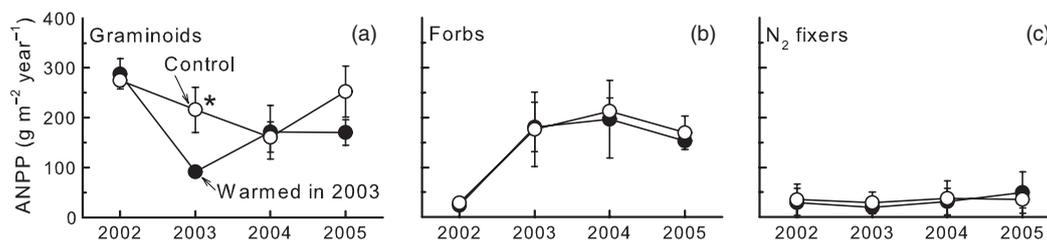


Fig. 2. Effects of a climatically extreme year (+4 °C in 2003) on mean (\pm SE) functional group annual above-ground net primary productivity greater than 10 cm ($\text{ANPP}_{>10\text{ cm}}$) of (a) graminoids, (b) forbs and (c) nitrogen fixers (open circle, unwarmed controls; filled circle, warmed in 2003; $n = 2$ EcoCELLs). Note that SE bars have been drawn for all means. In some cases, however, bars are shorter than the dimensions of the symbol. The asterisk shown in (a) indicates a $P < 0.02$ for the *post hoc* simple main effects (SME)-test in 2003. See Table 1 for ANOVA results.

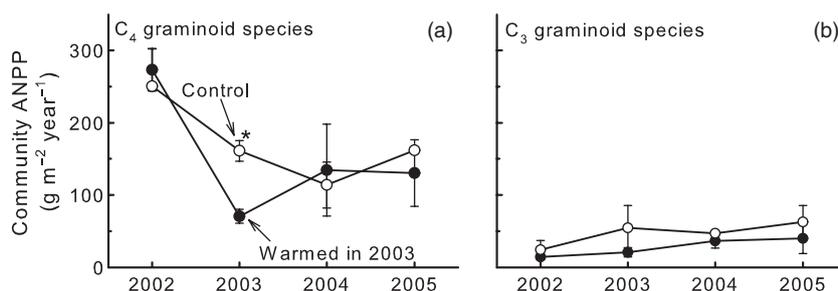


Fig. 3. Effects of a climatically extreme year (+4 °C in 2003) on mean (\pm SE) functional group annual aboveground net primary productivity greater than 10 cm ($\text{ANPP}_{>10\text{ cm}}$) of (a) C₄ and (b) C₃ graminoid species (open circle, unwarmed controls; filled circle, warmed 4 °C in 2003; $n = 2$ EcoCELLs). Note that SE bars have been drawn for all means. In some cases, however, bars are shorter than the dimensions of the symbol. The asterisk shown in (a) indicates a $P < 0.07$ for the *post hoc* simple main effects (SME)-test in 2003. See Table 1 for ANOVA results.

and remained between 30 and 55% for the next 2 years. The response of the graminoid functional group was clearly related to the specific response of the C₄ graminoids (Fig. 3a, Table 1) since no significant change in the $\text{ANPP}_{>10\text{ cm}}$ of C₃ graminoids was observed during the years in either control or

warmed-in-2003 ecosystems (Fig. 3b, Table 1). The extremely warm year also had no effect on forb or N₂ fixer $\text{ANPP}_{>10\text{ cm}}$, but abundance (expressed as $\text{ANPP}_{>10\text{ cm}}$) of forbs increased dramatically in both treatments (from an average of $26 \pm 3 \text{ g m}^{-2} \text{ year}^{-1}$ to $178 \pm 2 \text{ g m}^{-2} \text{ year}^{-1}$) from 2002 to

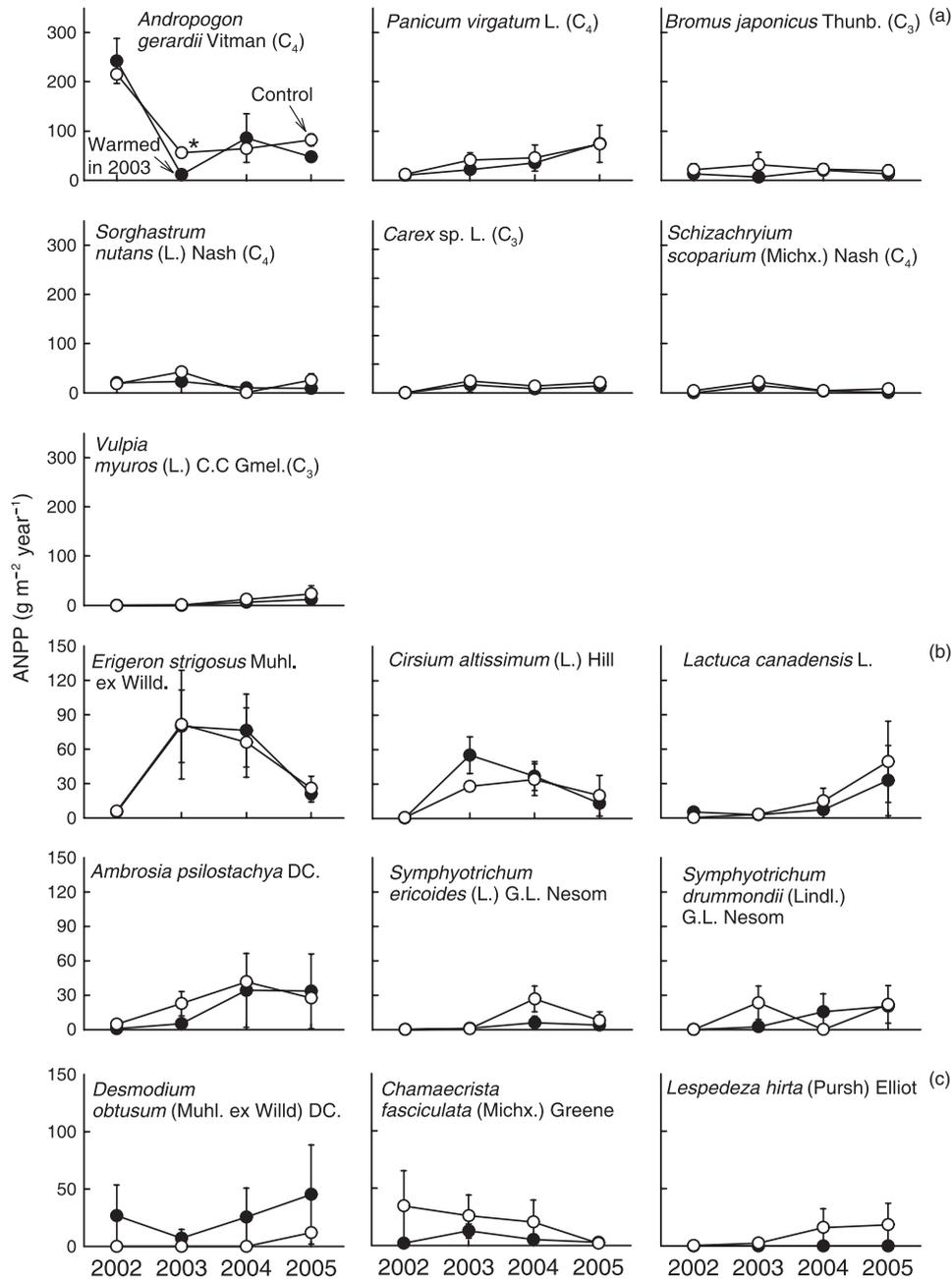


Fig. 4. Effects of a climatically extreme year (+4 °C in 2003) on mean (\pm SE) functional group annual aboveground net primary productivity greater than 10 cm ($\text{ANPP}_{>10\text{ cm}}$) of (a) the most dominant graminoid species, (b) the most dominant forb species present and (c) the most dominant nitrogen-fixing species present in plant communities during the 4-year study. Note that SE bars have been drawn for all means. In some cases, however, bars are shorter than the dimensions of the symbol. The asterisk shown in (a) indicates a $P < 0.02$ for *post hoc* simple main effects (SME)-test. See Table S2 for ANOVA results.

2003, and remained at that higher level in the two post-treatment years. N_2 fixers contributed relatively little to overall $\text{ANPP}_{>10\text{ cm}}$ of plant communities (6–13% during the 4 years).

Only a relatively small number of species contributed to $\text{ANPP}_{>10\text{ cm}}$ and interannual changes in $\text{ANPP}_{>10\text{ cm}}$ of functional groups and plant communities (Fig. 4, Table S1 in Supporting Information). Of the 17 graminoid species observed during the course of the 4 years, only seven species were major contributors (greater than 4% $\text{ANPP}_{>10\text{ cm}}$) in

any year (Fig. 4a, Table S1). Of these, four were C_4 species (*A. gerardii*, *Panicum virgatum*, *S. nutans* and *S. scoparium*), and three were C_3 species (*B. japonicus*, *Carex* sp. and *Vulpia myuros* (L.) C.C. Gmel.). Only *A. gerardii* responded significantly to warming and helped to explain the interannual patterns observed in the C_4 graminoids (Fig. 3a), graminoids in general (Fig. 2a) and $\text{ANPP}_{>10\text{ cm}}$ (Fig. 1, Table S2). Similarly, only six of the 44 forb species observed during the course of the experiment were notable contributors to community ANPP (greater than 4% ANPP) in any year (Fig. 4b,

Tables S1 and S2). Of these six species (*Erigeron strigosus* Muhl. ex Willd., *Cirsium altissimum* (L.) Hill, *Lactuca canadensis* L., *A. psilostachya* DC., *Symphyotrichum ericoides* (L.) G.L. Nesom and *Symphyotrichum drummondii* (Lindl.) G.L. Nesom), none responded significantly to the treatment (Table S2). ANPP greater than 10 cm (ANPP_{>10 cm}) of six other minor forb species, however, responded positively or negatively to the extremely warm year, either in the treatment year or in the years following (i.e. significant treatment × year interactions; Tables S1 and S2: *Achillea millefolium* L., *Rudbeckia hirta* L., *Solanum carolinense* L., *Symphyotrichum* sp., *Triodanis perfoliata* (L.) Nieuwl. and *Spiranthes vernalis* Engelm. & A. Gray). Likewise, of the six nitrogen-fixing species observed during the 4 years of the experiment (Tables S1 and S2), only two were major contributors to community ANPP_{>10 cm} and neither of them (*Desmodium obtusum* (Muhl. ex Willd.) DC. and *Chamaecrista fasciculata* (Michx.) Greene) responded significantly to the extremely warm year (Fig. 4c, Table S2).

Exposure to the extremely warm year did, however, slightly affect community and functional group species richness (Fig. 5, Table 1). Overall numbers of species present in plant communities in both treatments ranged between 25 and 35, with forbs dominating with 15–25 species per EcoCELL, fol-

lowed by graminoids with 8–12 species per EcoCELL, and nitrogen-fixers with 2–5 species per EcoCELL during the 4 years of the study (Table S1). Warming caused a temporary decrease in species richness of communities in the year after warming (2004) (Fig. 5e, Table 1) that resulted from a temporary decrease in forb species richness (Fig. 5g, average of 3.5 species fewer; Table 1). The number of graminoid species per EcoCELL remained relatively stable in both treatments (Fig. 5b) while the number of nitrogen-fixing species in both treatments increased significantly (from two to four species, Fig. 5d) through time (Table 1).

Annual community ANPP generally appeared to be unrelated to community and functional group species richness (Fig. 6a–c) with one significant exception: nitrogen-fixing species richness, although low compared with graminoids and forb species, was strongly and positively related to annual community ANPP_{>10 cm} (Fig. 6d) both when viewed across treatments and within treatments (Table S3). A similar relationship was observed between community ANPP_{>10 cm} and ANPP_{>10 cm} of nitrogen-fixers (Fig. 7d). Not surprisingly, increased numbers of nitrogen-fixing species were reflected in increased ANPP_{>10 cm} of this functional group (Fig. 7c). Forb ANPP_{>10 cm} also increased with increasing nitrogen-fixing species richness when viewed across control and

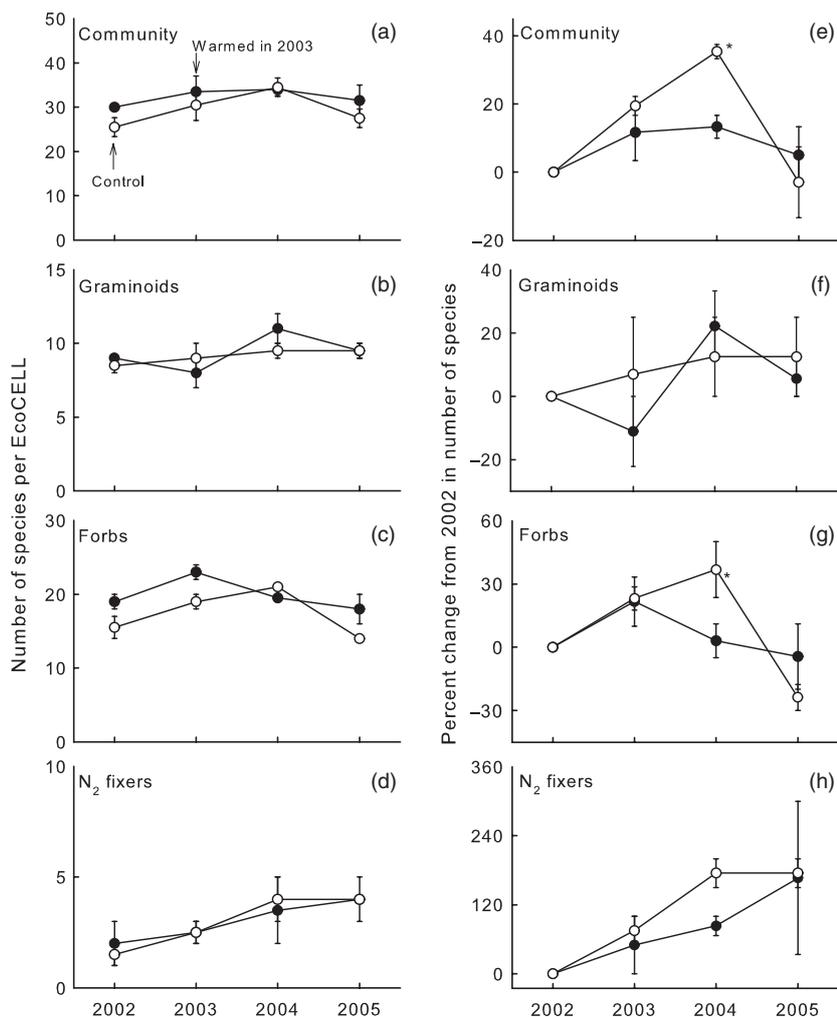


Fig. 5. Effects of a climatically extreme year (+4 °C in 2003) on mean (\pm SE) species richness in the (a) entire plant community, (b) graminoid functional group, (c) forb functional group and (d) nitrogen-fixer functional group during the 4-year study. Figure panels (e) through (h) show the percentage change in species richness relative to richness observed in 2002 (mean \pm SE). Note that SE bars have been drawn for all means. In some cases, however, bars are shorter than the dimensions of the symbol. The asterisk shown in panels (e) and (g) indicates a $P < 0.04$ for *post hoc* simple main effects (SME) tests. Also note that the apparent difference between treatment means in 2004 in panel (h) is not statistically significant ($P > 0.35$) based on *post hoc* SME test. See Table 1 for ANOVA results.

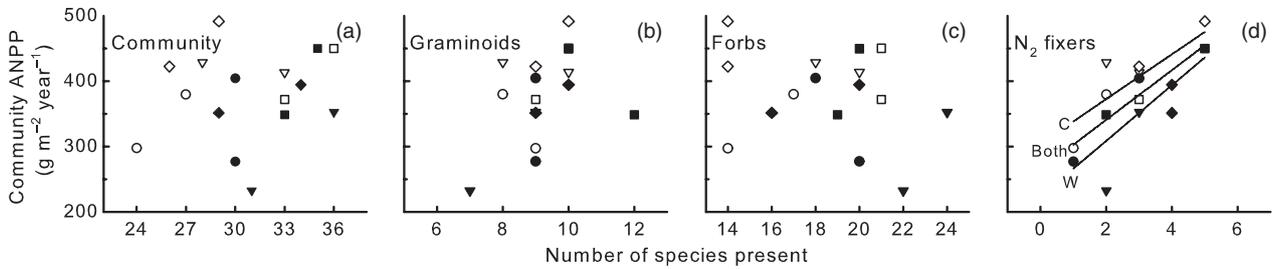


Fig. 6. Simple linear regressions of annual community aboveground net primary productivity greater than 10 cm ($\text{ANPP}_{>10 \text{ cm}}$) on (a) community species richness, (b) graminoid species richness, (c) forb species richness and (d) nitrogen-fixing species richness. Each point represents an annual aboveground net primary productivity greater than 10 cm ($\text{ANPP}_{>10 \text{ cm}}$) value and corresponding species richness value measured in an EcoCELL in a year. Circles represent values for 2002, triangles value for 2003, squares value for 2004 and diamonds value for 2005; open symbols, unwarmed controls; filled symbols, warmed 4 °C in 2003. See Table S3 for F , P and r^2 values for linear regression analyses for both treatments ('B') combined; the control treatment alone ('C'); and the warmed-in-2003 treatment alone ('W'). Regression lines are depicted only for analyses with slopes that are significant.

warmed-in-2003 ecosystems (Fig. 7b). However, graminoid $\text{ANPP}_{>10 \text{ cm}}$ appeared to be unrelated to nitrogen-fixing species richness (Fig. 7a).

Discussion

Interannual patterns in $\text{ANPP}_{>10 \text{ cm}}$ (Fig. 1, ' $\text{ANPP}_{>10 \text{ cm}}$ ') mirrored those calculated based on a clipping height of 0 cm ($\text{ANPP}_{>0 \text{ cm}}$; Arnone *et al.* 2008) for the same ecosystems used in the present study; so did the environmental explanations for these patterns and responses (described in the introduction of this article). In a parallel field study at the site in Oklahoma where monoliths were excavated (Sherry *et al.* 2008), year-long warming (using infrared heaters) also caused

a marked reduction in autumn-harvest $\text{ANPP}_{>10 \text{ cm}}$ followed by recovery in the year after warming when heaters were turned off. As in the EcoCELL study (present study and Arnone *et al.* 2008), interannual patterns in the field also were attributed to warming-induced drying and relief from drying in the year following warming. In the present study, while it was not surprising that the response of the dominant species (C_4 grasses – Fig. 3a, and especially *A. gerardii*, Fig. 4a) in these plant communities largely defined the $\text{ANPP}_{>10 \text{ cm}}$ responses of plant communities to extreme warming in 2003 (e.g. Smith & Knapp 2003), it was surprising that the inhibitory effects seen in 2003 mainly were due to reductions of C_4 graminoid $\text{ANPP}_{>10 \text{ cm}}$ (Fig. 2), and not to decreases in C_3 graminoid or C_3 forb $\text{ANPP}_{>10 \text{ cm}}$. This result was unexpected

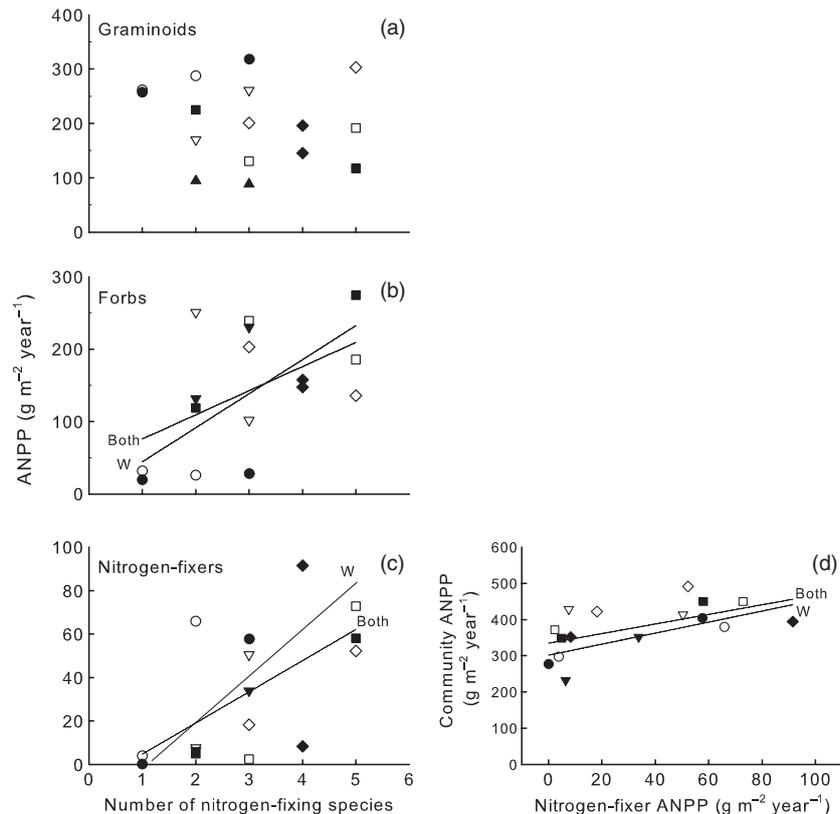


Fig. 7. Simple linear regressions of (a) annual aboveground net primary productivity greater than 10 cm ($\text{ANPP}_{>10 \text{ cm}}$) of graminoid species, (b) annual $\text{ANPP}_{>10 \text{ cm}}$ forb species and (c) annual $\text{ANPP}_{>10 \text{ cm}}$ nitrogen-fixing species each on annual nitrogen-fixing species richness and (d) annual community $\text{ANPP}_{>10 \text{ cm}}$ on total annual $\text{ANPP}_{>10 \text{ cm}}$ of nitrogen-fixing species. See legend to Fig. 6 for further details. See Table S3 for F , P and r^2 values for linear regression analyses.

because C_4 grasses are putatively well-adapted to heat and drought conditions (Christie & Delting 1982; Seastedt *et al.* 1994; Tieszen *et al.* 1997).

Based on the analysis of multi-year weekly time course data recorded from these TGP ecosystems (Arnone *et al.* 2008), the extreme year-long heat wave that we imposed was likely severe enough to cause reductions in leaf stomatal conductance and photosynthesis due to high vapour pressure deficits (VPDs) even in C_4 grasses (as seen in Arnone *et al.* 2008) that were present in all ecosystems (Arnone *et al.* 2008; see also Bunce 1982 and Oren *et al.* 1999). We also speculate, based on data presented in Arnone *et al.* (2008), that high-VPD-induced soil surface evaporation may have led to the observed large reductions in topsoil water availability that may have preferentially inhibited growth of the dominant C_4 grasses, which predominantly use water from the topsoil (Nippert, Knapp & Briggs 2006). Also, earlier appearance of forb species in the spring (J. Larsen, pers. comm.; also observed in field plots in the parallel interannual 'warming' study in Oklahoma: Sherry *et al.* 2007, 2008) relative to graminoid species, particularly in the warmed treatment in 2003, could help explain the greater suppression of graminoids in warmed ecosystems in that year. Recovery of community ANPP_{>10 cm} and C_4 graminoid productivity in the first year (2004) after the extremely warm year (2003), relative to the performance of unwarmed control ecosystems, appears to be due to relief from temperature-induced drying effects experienced in 2003. The interannual variability in community ANPP_{>10 cm} observed across both treatments fell within the range observed in field plots during many years (Briggs & Knapp 1995). Also, the reductions in ANPP_{>10 cm} that we observed in the warmed ecosystems in 2003 were similar in magnitude to reductions (below annual mean ANPP values) observed in TGP ecosystems in the field in years with below-average precipitation (Knapp & Smith 2001; Wan *et al.* 2005).

It is unclear why the forb and nitrogen-fixing functional groups (Fig. 2) plus most of the individual species from all functional groups (Fig. 4a–c, Tables S1 and S2) did not respond significantly to the extremely warm year. These results – and those for the C_4 grasses (Figs 2a, 3a and 4a) – do, however, point to resilience of TGP species to persist under strong natural interannual climate variability and physical disturbance (Knapp *et al.* 1998) and also under year-long extremely warm temperatures imposed in our study. While ANPP_{>10 cm} of six relatively minor forb species within the community (of the 44 total forb species observed) responded to the warm year (either in that year or in subsequent years) with either increasing or decreasing productivity (*Achillea*, *Rudbeckia*, *Solanum*, *Symphyotrichum* sp., *Triodanis*, *Spiranthes*), it is not clear why these interannual temperature-induced shifts occurred in the way that they did (Tables S1 and S2). The varied interannual responses of this small group of species do demonstrate, however, that persistent temperature extremes may cause some species to become greater or lesser members of TGP communities.

Likewise, the relatively minor effects of exposure to the extremely warm year on community and functional group plant species diversity (Fig. 5) were not completely unex-

pected. TGP in the field are exposed to naturally high interannual climate variability (e.g. Knapp *et al.* 1998), and yet long-term plant species composition of these natural ecosystems remains relatively constant (L. Wallace, pers. comm.; Knapp *et al.* 1998). The relatively high species richness of the forb functional group (Table S2), relative to the richness of the other two groups, seems to have increased the odds that the temporary lagged warming-induced declines in overall plant community species richness (Fig. 5a,e) that occurred in the year following warming were due to reductions in forb species' numbers (Fig. 5g).

The absence of any apparent positive (or negative) relationships between plant community ANPP_{>10 cm} and community species richness (Fig. 6), or community ANPP_{>10 cm} and species richness of either the graminoid or forb functional groups, was unexpected given the frequent and strong positive relationships reported from 'biodiversity' experiments (e.g. Naeem *et al.* 1996; Tilman, Wedin & Knops 1996; Aarssen 1997; Loreau 2000; Niklaus *et al.* 2001). One possible reason for the apparent divergence of our results from those of other studies may be that most 'biodiversity' experiments utilize designed and constructed planted communities established in physically disturbed topsoils with a wide range of plant species diversity levels. Alternatively, our experiment utilized natural plant communities that have been growing in undisturbed soils (aside from grazing that stopped 20 years before the monoliths were excavated), but without a large difference in monolith-to-monolith variation in plant species diversity (richness). Regardless of these divergences, results from our study suggest, at the very least, a much weaker productivity – diversity relationship that has been reported in other studies (but not all: e.g. Symstad & Tilman 2001) where plant species diversity has been manipulated. The almost doubled levels of plant species richness present in our study (relative to richness levels used in even the highest diversity treatments in studies where diversity was manipulated) may also indicate that the diversity–productivity relationship becomes weaker at very high levels of plant community species diversity.

An exception to the otherwise absent relationship between ANPP_{>10 cm} and plant species richness in our study was the strong positive relationships observed between community ANPP_{>10 cm} and species richness (and productivity, Fig. 7d) of the nitrogen-fixing functional group (Fig. 6d). The most obvious explanation for these strong relationships is that increases in the number, and ANPP_{>10 cm}, of nitrogen-fixing species led to increases in inputs of symbiotically fixed nitrogen to ecosystems primarily via the decomposition of litter (probably mostly roots, since shoots were clipped and removed each year) of nitrogen-fixing species that then increased soil N availability and the productivity of co-occurring, non-nitrogen-fixing forb species (Fig. 7b). The apparent lack of a relationship between ANPP_{>10 cm} of the dominant graminoid functional group and number of nitrogen fixers present in a plant community (Fig. 7a) was somewhat surprising. One possible explanation for this may be the occurrence of associative nitrogen fixation in graminoid rhizospheres

(e.g. Dobbelaere, Vanderleyden & Okon 2003) that could have decoupled some graminoid species from dependency on symbiotically fixed nitrogen. Data published earlier from this EcoCELL experiment (Verburg *et al.* 2009) showed a link between soil N availability (as measured by net N taken up into annual biomass production) and annual ANPP, BNPP and NPP and their responses to the extremely warm year (Arnone *et al.* 2008). While all nitrogen-fixing species in our plant communities had root nodules, we did not quantify inputs of symbiotically fixed N to ecosystems. Many studies in grasslands, although, have reported similar positive effects of legume species on soil N availability and ANPP (e.g. Turner *et al.* 1997; Spehn *et al.* 2000; An *et al.* 2005; Niklaus, Wardle & Tate 2006; Oelmann *et al.* 2007), mostly as a result of indirect nitrogen transfer via degradation of above- and BNPP plant tissue or nodules (Vallis, Henzell & Evans 1977; Haystead & Marriott 1979; Dubach & Russelle 1994; Laidlaw, Christie & Lee 1996; Høgh-Jensen & Schjoerring 2000; Weigelt, Bol & Bardgett 2004; Temperton *et al.* 2007). These observations, along with data from our study, suggest that even at low levels of nitrogen-fixer richness and ANPP_{>10 cm}, the presence of nitrogen-fixing species in a plant community with relatively low bioavailable nitrogen is an important determinant of overall ANPP and NPP. These findings also point out that functional properties of particular species in plant communities often can affect ANPP more than richness *per se* (see also Hooper & Vitousek 1997).

Taken together, the results of our study show that (i) inter-annual patterns in ANPP_{>10 cm}, and responses to the climatically extreme year, were defined best by the collective responses of C₄ grasses rather than by responses of individual species of any functional group; (ii) overall and functional group species richness is at most only temporarily reduced by exposure to a very warm year and (iii) plant community diversity (species richness) was not a major factor influencing annual community ANPP or responses to the extremely warm year, but increasing species richness within the nitrogen-fixing plant functional group increased overall community ANPP. Thus, while exposure of species-rich TGP to climatically extreme (warm) years may prolong the suppression of net annual uptake of CO₂ beyond the extreme year (Arnone *et al.* 2008), it may not dramatically impact plant community structure or composition.

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Supporting Information

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

Table S1. Annual above-ground net primary productivity by functional group and species for the 4 years of the experiment.

Table S2. *F*-ratios and *P*-values for repeated measure ANOVAS of the dependent variable ANPP_{>10 cm} for each species on the independent variables: treatment (+4 °C warming in 2003); year; and treatment × year (*n* = 2).

Table S3. *F*-ratios, *P*-values, and *r*²-values for simple linear regression analyses of the dependent and independent variables listed in each figure ('Data source') for data sets covering all 4 years of the study (2002–2005) that include both (B) treatments – 16 individual data points, only the control (C) treatment – 8 data points, or only the warmed (W) treatment – 8 data points.

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