

# Stability of tallgrass prairie during a 19-year increase in growing season precipitation

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## Summary

1. Precipitation is considered to be a key driver of ecosystem processes in mesic grasslands, and climate models predict changes in the amount and intensity of precipitation under future global change scenarios. Although most experimental rainfall studies decrease precipitation, seasonal rainfall is predicted to increase in the northern Great Plains under climate change.
2. We analysed changes in community composition and structure of upland and lowland native tallgrass prairie in central Kansas, USA, subjected to 19 years of irrigation designed to eliminate moisture stress throughout the growing season.
3. Irrigation had limited effects on species richness in both upland and lowland prairie. Total cover increased significantly and consistently with irrigation in drier uplands and in more mesic lowlands. Abundance of rhizomatous, tall, perennial species as well as C<sub>3</sub> forbs increased with irrigation.
4. The strongest response to irrigation came within the dominant functional type, C<sub>4</sub> perennial grasses. *Panicum virgatum* became the dominant species in irrigated lowlands, whereas *Andropogon gerardii* remained the dominant species in irrigated uplands and in control plots. Overall, irrigation had less effect on community composition and structure than other known drivers of grassland structure and function.
5. In comparison with other studies, our results demonstrate that water addition has less of an impact than fire, grazing or nitrogen addition on composition and dynamics in this mesic grassland. The strongest response to long-term irrigation occurred *within* the dominant functional type: tall, perennial, rhizomatous, C<sub>4</sub> grasses. Thus, functional redundancy will buffer this ecosystem from potential increases in rainfall due to climate change. Finally, our results highlight the limited utility of qualitative functional traits to predict how this mesic grassland will respond to climate change.

**Key-words:** *Andropogon gerardii*, functional traits, *Panicum virgatum*, precipitation experiment, species diversity, tallgrass prairie

## Introduction

Fire, grazing, topography and climatic variability are considered to be the major factors influencing plant community structure and dynamics in mesic grasslands worldwide (McNaughton 1985; Collins *et al.* 1998; Frank, McNaughton & Tracy 1998; Bond, Midgley & Woodward 2003). The temporal and spatial variability of these drivers generally alters the availability and spatial heterogeneity of limiting resources, such as soil moisture, nitrogen and light (Knapp 1984; Frank & Groffman 1998; Augustine & Frank 2001). In North American tallgrass prairie, for example, early sea-

son fire tends to increase production of C<sub>4</sub> grasses whereas grazing increases abundance of C<sub>3</sub> forbs, yet these responses vary with landscape position, fire frequency and interannual climate variability (Collins 2000; Fuhlendorf & Engle 2001; Collins & Calabrese 2012). Over time these biotic and abiotic drivers interact to affect composition, production and dynamics in mesic grasslands.

Climate, in particular mean annual rainfall, affects species composition, functional trait diversity and net primary production in grasslands regionally (Sala *et al.* 1988; Huxman *et al.* 2004; Sandel *et al.* 2010), whereas local factors such as grazing and fire impact grasslands within the constraints imposed by the available moisture (Olson, White & Sindelar 1985; Milchunas & Lauenroth 1993; Biondini, Patton &

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Nyren 1998). Grassland ecosystems are highly sensitive to changes in both rainfall amount and variability because their production is often water limited during at least part of the growing season (Sala *et al.* 1988; Esser 1992; Knapp, Briggs & Koelliker 2001). In some grassland regions, however, climate change scenarios predict an increase in mean annual precipitation (Meehl *et al.* 2006; Schoof, Pryor & Surprenant 2010). Thus, understanding how changes in precipitation will affect community structure and dynamics is essential for the development of predictive models of ecosystem responses to future scenarios of climate change.

Recently, Gerten *et al.* (2008) simulated ecosystem responses (including grasslands) to increased or decreased annual precipitation, as well as the impacts of short-term droughts during the growing season. They concluded that total annual precipitation is a more important driver of net primary production (NPP) than changes in the size and frequency of precipitation events within a growing season (Gerten *et al.* 2008). In contrast, experiments have demonstrated that within-season variability in rainfall alters NPP in both mesic and arid grasslands (Knapp *et al.* 2002; Heisler-White *et al.* 2009; Thomey *et al.* 2011). Many long-term rainfall manipulation experiments reduce rainfall or alter within season patterns of rain events without changing the total amount, yet climate change is likely to alter amounts and patterns of rainfall both within and among years. Therefore, Gerten *et al.* (2008) concluded that additional kinds of long-term rainfall experiments were needed to better link models to empirical observations.

Grasslands cover over 40% of the terrestrial land surface, and their response to changes in rainfall patterns will have significant consequences for global patterns of productivity and diversity under future climate scenarios (Knapp *et al.* 1993; Fay *et al.* 2003). Functional traits provide a mechanistic linkage between ecosystem structure and function that can be used to predict the ecological impacts of climate change (e.g. McGill *et al.* 2006; Suding *et al.* 2008; Okie & Brown 2009). Recently, Suding *et al.* (2008) proposed a 'response and effects' functional traits framework to better predict community and ecosystem responses to climate change. Functional traits result from historical selection pressures and have been directly related to abundance patterns in response to environmental drivers (Grime 2001; Lavorel & Garnier 2002; Suding, Goldberg & Hartman 2003). In herbaceous communities, key response traits include water use efficiency (e.g. C<sub>3</sub> vs. C<sub>4</sub>; forbs vs. grasses), clonality (caespitose vs. rhizomatous or stoloniferous) and plant height (Craine *et al.* 2001; Gough *et al.* 2012), traits that reflect selection pressures for capturing space, sunlight and the efficient use of limiting resources.

Although nitrogen is considered to be the primary limiting nutrient in most herbaceous communities (Vitousek & Howarth 1991; Elser *et al.* 2007; LeBauer & Treseder 2008), soil moisture also has a strong effect on NPP in these ecosystems (Briggs & Knapp 1995; Knapp, Briggs & Koelliker 2001; Muldavin *et al.* 2008). In general, nitrogen addition increases NPP and reduces species diversity in grasslands (Tilman 1987; Zavaleta *et al.* 2003; Stevens *et al.* 2004;

Suding *et al.* 2005; Harpole & Tilman 2007; Yahdjian, Gherardi & Sala 2011). One main mechanism for the reduction in diversity and changes in plant community structure is a decrease in light availability in the understorey that accompanies the increase in production by canopy species (Hautier, Niklaus & Hector 2009). Given that water addition also increases NPP in mesic grassland (Knapp, Briggs & Koelliker 2001), then, similar to nitrogen addition, diversity is predicted to decrease when water limitation is removed, yet this hypothesis lacks evidence from long-term field experiments.

The goal of this study was to investigate the response of species and functional trait composition to years of increased water availability in a native tallgrass prairie plant community. The long-term impact of annual water addition is poorly understood even though the climate change models predict an increase in growing season precipitation in parts of the mesic grassland region of central North America (Meehl *et al.* 2006; Schoof, Pryor & Surprenant 2010). Indeed, explicit consideration of the consequences of chronic resource alterations as a means of ecological change is considered to be a critical research need (National Research Council (NRC) 2001), for which theory is still being developed (Smith, Knapp & Collins 2009).

We examined the effects of 19 years of water addition throughout the growing season on changes in community composition and functional trait abundance in upland (drier) and lowland (wetter) areas of Konza Prairie, a native tallgrass prairie in northeastern Kansas, USA. Based on general theory of chronic resource addition (Smith, Knapp & Collins 2009), we predicted that increased moisture availability throughout the growing season would lead to non-linear and lagged changes in both species and functional trait abundances over time. In addition, we predicted that (i) species richness and diversity would decline with chronic water addition, (ii) abundance of C<sub>3</sub> forbs and woody species would increase whereas abundance of C<sub>4</sub> grasses would decrease with chronic water addition and (iii) significant responses would occur more frequently and earlier in drier uplands compared with lowland areas that have deeper soils and greater water holding capacity.

## Materials and methods

### STUDY SITE

This study was conducted at the Konza Prairie Biological Station (KPBS), a 3487 ha tallgrass prairie in the Flint Hills of northeastern Kansas, USA. The area experiences a typical mid-western continental climate with warm wet summers and cold dry winters. Mean annual air temperature is 12.8 °C (30-year average) with an average annual precipitation of 835 mm, *c.* 75% of which occurs during the growing season (Hayden 1998); however, inter-annual climate variation is high (Borchert 1950; Knapp 1984). More importantly, precipitation declines from June through September when air temperature and water stress are the greatest (Buis *et al.* 2009). Konza Prairie occurs on topographic gradients ranging from 320 to 444 m above sea level. The vegetation is dominated by perennial C<sub>4</sub> grasses, such as *Andropogon gerardii*, *A. scoparius*, *Panicum virgatum*, *Sorghastrum nutans*,

*Sporobolus asper* and *S. heterolepis* (nomenclature follows Great Plains Flora Association (1986)). Perennial forbs, including *Aster* spp., *Ambrosia psilostachya*, *Artemisia ludoviciana*, *Solidago* spp., *Kuhnia eupatorioides*, *Salvia azurea* and *Vernonia baldwinii*, are common throughout the vegetation. Much of the surrounding region is characterised by frequently burned, unplowed prairie grazed by domestic cattle. For a detailed description of the physical and biotic features of this tallgrass ecosystem, see Knapp *et al.* (1998b).

## EXPERIMENTAL DESIGN

To determine the effects of increased soil water availability on grassland community dynamics, a long-term irrigation experiment was initiated in an annually burned, ungrazed watershed at KPBS. Prior to the start of the experiment, the site was burned approximately once every 3 years. Details of the experimental design were described in Knapp, Briggs & Koelliker (2001). Briefly, in 1991, parallel irrigated and control transects were established along a topographic gradient (c. 7 m in elevation) running from upland to lowland prairie. In 1993 the initial transects were lengthened and another pair of irrigation and control transects was added. Each transect is 140 m long. The upland areas are characterised by well-drained, rocky soils, whereas the lowland areas have deeper, fine-textured soils with higher water holding capacity than upland soils. Recent analysis demonstrates that stratifying sites at KPBS based on topographic position effectively captures differences in environmental variation and species growth responses (Nippert *et al.* 2011).

Water was supplied from a nearby ground water well and storage reservoir. As a result of topographic variability, 11 sprinklers were located in the upland transects and 10 in lowland prairie. At 10 m intervals along each of the irrigation transects, 1.0 m tall, high-impact, rotating sprinkler heads sprayed water in a 30 m diameter circle. The maximum application was 8 mm h<sup>-1</sup> in a 6 m wide strip centred on each irrigation transect. Irrigation was supplied periodically during the growing season such that soil moisture availability satisfied estimated potential evapotranspiration (PET) from May through September. Ambient soil moisture was measured continuously at an adjacent weather station (Konza Headquarters). Reference PET was estimated daily by a Penman combination equation (Lamm, Pacey & Manges 1987) with input from a nearby weather station and a precipitation gauge within 200 m of the transects. PET depends on temperature, ambient relative humidity, average wind speed and cloudiness, therefore supplemental irrigation depended on those factors as well as the amount of ambient rainfall received. Average annual precipitation for the 19 years of the study was 847 mm, which was very close to the long-term average for KPBS (835 mm). The amount of irrigation water added throughout each growing season varied from 469 mm in 1991 to 53 mm in 2008 (Fig. 1). The mean total of precipitation plus irrigation on the irrigated plots was 1108 mm per year, making average irrigation input 261 mm during the growing season each year.

Initially, soil moisture along each transect has monitored at 10–12 locations in upland and lowland, treatment and control transects at 1- to 2-week intervals at 15 cm depth with horizontally buried TDR probes and a hand-held meter (Knapp, Briggs & Koelliker 2001). Since 2006, soil moisture has been continuously monitored at 15 cm depth at three points along each of the treatment and control transects. Data showed that soil volume water content in ambient plots (<20%) can be half that of irrigated transects (>40%) during the growing season (Knapp, Briggs & Koelliker 2001; Fig. S1, Supporting information).

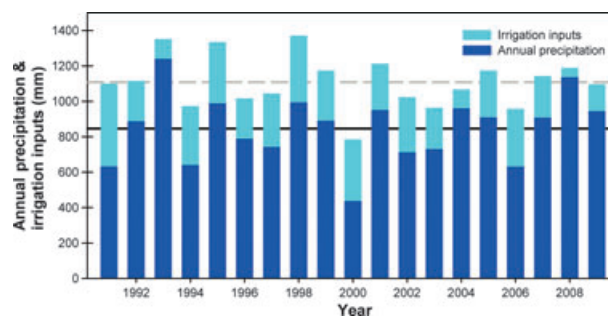


Fig. 1. Annual precipitation and irrigation additions from 1991 through 2009. Reference lines correspond to the mean annual precipitation (solid) and mean annual precipitation plus irrigation (dashed) inputs for all 19 years of study.

## SPECIES COMPOSITION

Plant community composition along the irrigation transect was measured in the zone of maximum water addition. Species composition was recorded in ten 10-m<sup>2</sup> permanently located circular plots adjacent to each riser along the irrigated transects and at 10 m intervals along the control transects. Cover of each species in each plot was visually estimated each year using a modified Daubenmire cover scale: 1 < 1% cover (e.g. present), 2 = 2–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–95% and 7 > 95% (see Collins & Smith 2006). Cover scale values for each species were converted to their mid-points for analyses.

## TRAIT DATA

A list of qualitative traits was compiled from literature searches and used to assign species to different functional groups (Cleland *et al.* 2008). Following Cleland *et al.* (2008) we categorised each species according to its life form (grass, forb and shrub), photosynthetic pathway (C<sub>3</sub> or C<sub>4</sub>), life history strategy (perennial or annual), reproductive strategy (rhizomatous, caespitose, obligate seeder), nitrogen fixation capabilities (N-fixer or non-N-fixer) and canopy position (upper, middle and lower).

## DATA ANALYSIS

As we were primarily interested in differences between irrigated and control plots, we considered the irrigation treatments in upland and lowland areas to be independent experiments. Thus, we compared species, community and trait responses in irrigated ( $n = 11$  quadrats) and control uplands ( $n = 11$ ), and conducted separate analyses of response variables in irrigated ( $n = 10$  quadrats) and control lowlands ( $n = 10$ ).

Total plant cover, species richness, Shannon's diversity and cover of each functional group were calculated for each plot. Statistical analyses of community structure, dominant species and functional trait abundance were conducted using linear mixed models procedures in SAS 9.1 (SAS Institute, Inc 2005) to determine the effect of chronic irrigation on response variables (e.g. mean species richness, mean total cover, mean abundance of C<sub>4</sub> grasses, etc.). We fit a repeated measures model to data from all 19 years with irrigation treatment (water addition and ambient rainfall) as a whole plot fixed effect and year as a repeated effect. Type III sums of squares were used to orthogonally compare the effect of irrigation over time. Mean values separations were performed using *post-hoc* *t*-tests of least

**Table 1.** Repeated measures analysis of variance for species richness, diversity (Shannon–Weiner index  $H'$ ) and total cover in irrigated and control upland and lowland tallgrass prairie

	Lowlands					Uplands				
	Effect	Num DF	Denom DF	F value	Pr > F	Effect	Num DF	Den DF	F value	Pr > F
Total cover	Trt	1	18	3.26	0.0876	Trt	1	20	30.2	< 0.0001
	Yr	18	304	14.84	< 0.0001	Yr	18	332	10.68	< 0.0001
	Trt × Yr	18	304	2.81	0.0001	Trt × Yr	18	332	4.29	< 0.0001
Species Richness	Trt	1	18	4.88	0.0404	Trt	1	20	1.71	0.2064
	Yr	18	304	7.55	< 0.0001	Yr	18	332	4.32	< 0.0001
	Trt × Yr	18	304	0.56	0.9253	Trt × Yr	18	332	1.47	0.0989
Diversity ( $H'$ )	Trt	1	18	0.76	0.3961	Trt	1	20	0.09	0.7712
	Yr	18	304	5.57	< 0.0001	Yr	18	332	13.61	< 0.0001
	Trt × Yr	18	304	0.78	0.7275	Trt × Yr	18	332	5.08	< 0.0001

Trt, treatment; DF, degrees of freedom; Yr, Year; Num, Numerator; Denom, Denominator; Pr, Probability.

*P* values < 0.00096 were considered significant based on Bonferroni corrections for multiple comparisons (in bold).

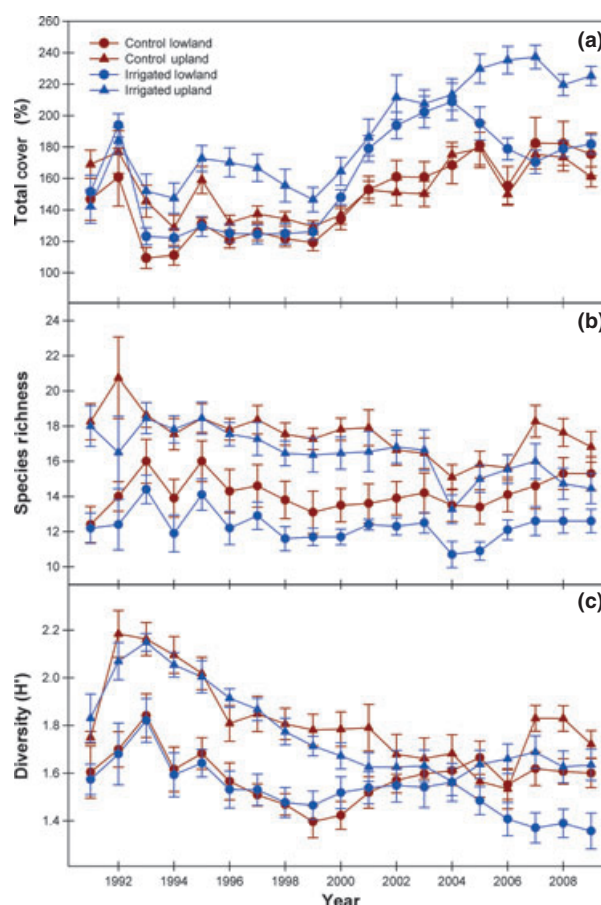
squares mean values produced by the MIXED procedure. Significance was determined by adjusting the *P*-values using Bonferroni correction for a false discovery rate of 0.05.

## Results

Total cover increased through time in all treatments (Table 1, Fig. 2a). In uplands, total cover was initially higher in control compared with irrigated plots, but this trend rapidly reversed. Irrigated plots had significantly greater cover than control plots in the uplands for the last 14 years of treatment leading to a significant year by treatment interaction. In lowlands, cover was similar initially. Irrigated plots had significantly greater cover from 2001 through 2004 leading to a significant treatment by year interaction; however, total cover in the irrigated plots then decreased to pretreatment levels from 2005 through 2009.

Irrigation had limited impacts on species richness or diversity. Overall species richness declined significantly over time in uplands and varied from year-to-year in lowlands (Table 1, Fig. 2b). In lowlands, control plots had consistently greater species richness than irrigated plots, and this trend was mostly true in uplands, as well, but treatment effects were not significant, nor were there treatment by year interactions in either upland or lowland areas (Fig. 2b). Shannon's diversity also declined sharply over time in both irrigated and control plots (Table 1, Fig. 2c). Diversity in uplands was generally lower in irrigated plots, but only significantly so in 1991 and 2008 (significant treatment by year interaction).

In both uplands and lowlands, the dominant vegetation type was always a  $C_4$ , non-nitrogen fixing, upper canopy, perennial grass. In lowlands there was a significant year effect for the abundance of all functional traits except annuals and woody plants (Table 2). In addition, there was a significant year by treatment interaction for forbs,  $C_3$  species, perennials and rhizomatous species. In most cases, these differences reflected increased abundance of these functional types on irrigated transects relative to controls (Fig. 3). We found a significant year effect in uplands, as well, for all functional types except annuals (Fig. 3). There were also many more sig-



**Fig. 2.** Annual average ( $\pm 1$  SE) (a) total cover, (b) plant species richness and (c) diversity (Shannon–Weiner index,  $H'$ ) for the upland control, upland irrigated, lowland control and lowland irrigated transects.

nificant year by treatment interactions (forbs,  $C_3$  species, non-N fixers, perennials and rhizomatous species) in uplands indicating a stronger response to irrigation in the drier upland soils (Table 2). As in the lowlands, these interrelated functional traits generally had higher abundances on irrigated compared with control transects (Fig. 3).

**Table 2.** Repeated measures analysis of variance for photosynthetic pathway (C3, C4), growth form (grass, forb, shrub), nitrogen fixing ability (N-fixer, non-N-fixer), life history (annual, perennial), canopy position (upper, middle, lower) and clonality (caespitose, rhizomatous, obligate seeder) in irrigated and control upland and lowland tallgrass prairie

	Lowlands					Uplands				
	Effect	Num DF	Denom DF	F value	Pr > F	Effect	Num DF	Denom DF	F value	Pr > F
C3	Trt	1	18	0.46	0.5082	Trt	1	20	19.86	<b>0.0002</b>
	Yr	18	304	6.76	< <b>0.0001</b>	Yr	18	332	5.42	< <b>0.0001</b>
	Trt × Yr	18	304	2.84	<b>0.0001</b>	Trt × Yr	18	332	3.64	< <b>0.0001</b>
C4	Trt	1	18	2.43	0.1367	Trt	1	20	6.43	0.0197
	Yr	18	304	14.37	< <b>0.0001</b>	Yr	18	332	9.26	< <b>0.0001</b>
	Trt × Yr	18	304	1.42	0.1209	Trt × Yr	18	332	1.85	0.0189
Grass	Trt	1	18	2.48	0.1327	Trt	1	20	5.41	0.0306
	Yr	18	304	14.07	< <b>0.0001</b>	Yr	18	332	9.63	< <b>0.0001</b>
	Trt × Yr	18	304	1.45	0.1053	Trt × Yr	18	332	2.05	<b>0.0074</b>
Forb	Trt	1	18	0.47	0.5024	Trt	1	20	8.49	0.0086
	Yr	18	304	6.92	< <b>0.0001</b>	Yr	18	332	5.48	< <b>0.0001</b>
	Trt × Yr	18	304	2.88	<b>0.0001</b>	Trt × Yr	18	332	2.89	< <b>0.0001</b>
Shrub	Trt	1	18	2.77	0.1131	Trt	1	20	11.25	0.0032
	Yr	18	304	1.51	0.0838	Yr	18	332	4.95	< <b>0.0001</b>
	Trt × Yr	18	304	0.91	0.5626	Trt × Yr	18	332	1.53	0.0764
Non-N-fixer	Trt	1	18	2.92	0.1047	Trt	1	20	19.7	<b>0.0003</b>
	Yr	18	304	13.77	< <b>0.0001</b>	Yr	18	332	9.82	< <b>0.0001</b>
	Trt × Yr	18	304	2.14	0.0050	Trt × Yr	18	332	3.97	< <b>0.0001</b>
N-fixer	Trt	1	18	0.36	0.5559	Trt	1	20	8.79	0.0076
	Yr	18	304	6.38	< <b>0.0001</b>	Yr	18	332	6.23	< <b>0.0001</b>
	Trt × Yr	18	304	0.98	0.4823	Trt × Yr	18	332	1.3	0.1846
Annual	Trt	1	18	1.25	0.2787	Trt	1	20	0.15	0.7057
	Yr	18	304	1.28	0.2020	Yr	18	332	1.97	0.0109
	Trt × Yr	18	304	1.94	0.0129	Trt × Yr	18	332	2.19	0.0036
Perennial	Trt	1	18	0.62	0.4403	Trt	1	20	30.18	< <b>0.0001</b>
	Yr	18	304	13.46	< <b>0.0001</b>	Yr	18	332	10.93	< <b>0.0001</b>
	Trt × Yr	18	304	2.43	0.0011	Trt × Yr	18	332	4.38	< <b>0.0001</b>
Upper canopy	Trt	1	18	11.01	0.0038	Trt	1	20	8.88	0.0074
	Yr	18	304	12.06	< <b>0.0001</b>	Yr	18	332	8.96	< <b>0.0001</b>
	Trt × Yr	18	304	1.94	0.0131	Trt × Yr	18	332	2.15	0.0045
Mid canopy	Trt	1	18	0.23	0.6386	Trt	1	20	3.04	0.0967
	Yr	18	304	4.78	< <b>0.0001</b>	Yr	18	332	5.17	< <b>0.0001</b>
	Trt × Yr	18	304	2.08	0.0067	Trt × Yr	18	332	2.37	0.0015
Lower canopy	Trt	1	18	1.81	0.1949	Trt	1	20	1.9	0.1833
	Yr	18	304	3.33	< <b>0.0001</b>	Yr	18	332	7.57	< <b>0.0001</b>
	Trt × Yr	18	304	2.06	0.0072	Trt × Yr	18	332	2.31	0.0020
Caespitose	Trt	1	18	11.28	0.0035	Trt	1	20	1.11	0.3045
	Yr	18	304	12.41	< <b>0.0001</b>	Yr	18	332	5.09	< <b>0.0001</b>
	Trt × Yr	18	304	1.8	0.0243	Trt × Yr	18	332	1.26	0.2145
Rhizomatous	Trt	1	18	6.35	0.0214	Trt	1	20	9.89	0.0051
	Yr	18	304	9.52	< <b>0.0001</b>	Yr	18	332	6.19	< <b>0.0001</b>
	Trt × Yr	18	304	3.24	< <b>0.0001</b>	Trt × Yr	18	332	6.21	< <b>0.0001</b>
Obligate seeder	Trt	1	18	3.25	0.0881	Trt	1	20	10.4	0.0042
	Yr	18	304	3.79	< <b>0.0001</b>	Yr	18	332	5.28	< <b>0.0001</b>
	Trt × Yr	18	304	1.65	0.0479	Trt × Yr	18	332	3.08	< <b>0.0001</b>

Trt, treatment; DF, degrees of freedom; Yr, Year; Num, Numerator; Denom, Denominator; Pr, Probability.

P values < 0.00096 were considered significant based on Bonferroni corrections for multiple comparisons (in bold).

Long-term irrigation resulted in shifts in the abundances of two dominant grasses, but surprisingly, the strongest differences occurred in lowland plots where soil moisture is generally higher during the growing season than in uplands. Significant year effects occurred for *Panicum virgatum* and *Andropogon gerardii* in lowlands and uplands (Table 3). However, the only significant year by treatment interactions for dominant grasses was for *P. virgatum* in lowlands

(Table 3, Fig. 4a). Specifically, cover of *P. virgatum* was about 50% lower in irrigated compared with control plots at the start of the experiment in 1991. By 2009, cover of *P. virgatum* on irrigated lowlands had increased by over 60% (Fig. 4) replacing *A. gerardii* as the dominant species. In each of the three other treatments, *A. gerardii* was the dominant species at the start and remained the most abundant species throughout the experiment (Fig. 4a,b).

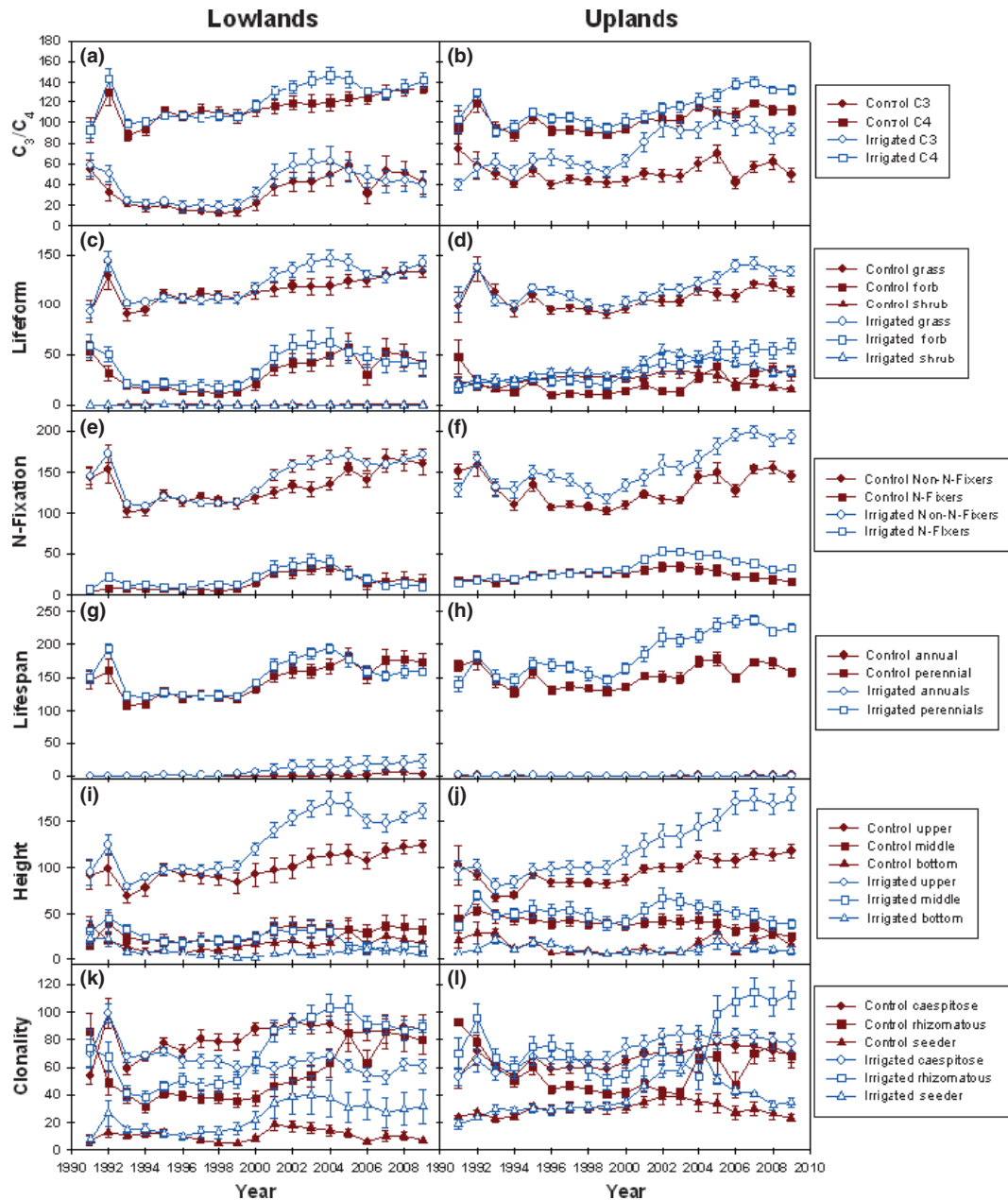


Fig. 3. Annual average ( $\pm 1$  SE) trait abundances for the upland control, upland irrigated, lowland control and lowland irrigated transects. (a, b) Photosynthetic pathways (c, d) growth form (e, f) nitrogen fixing ability (g, h) life history (i, j) canopy position and (k, l) clonality.

**Discussion**

We predicted that species diversity and abundance of C<sub>4</sub> grasses would decline, and abundance of C<sub>3</sub> forbs would increase with long-term water addition. Also, we predicted that irrigation would lead to a larger number of significant responses in drier uplands compared with lowlands. Although the latter prediction was correct, grass and forb abundances and species diversity changed relatively little in response to water addition even though total cover and net primary production (Knapp, Briggs & Koelliker 2001) increased. Despite complete removal of water limitation during the growing season for 19 years, tall, perennial, C<sub>4</sub> grasses

continued to dominate this system, and the changes in species diversity and community structure that occurred often varied from year to year (significant year effects, but relatively few consistent treatment effects over time; Tables 1 and 2).

It is often assumed that structure and function of mesic grassland ecosystems are governed by the interactions between fire frequency, grazing, nitrogen availability and inter-annual precipitation variability, the impacts of which are moderated by landscape position (Collins & Calabrese 2012). Indeed, there is strong evidence demonstrating that fire and grazing significantly impact grassland structure and function in North America (Collins *et al.* 1998; Fuhlendorf & Engle 2004; Collins & Smith 2006), and elsewhere (Milchunas

**Table 3.** Repeated measures analysis of variance of mean percent cover of *Andropogon gerardii* and *Panicum virgatum* in irrigated and control lowland and upland transects

Effect	Num DF	Denom DF	F value	Pr > F
<b>Lowlands</b>				
<i>Andropogon gerardii</i>				
Trt	1	18	0.13	0.7241
Yr	18	304	14.19	<b>&lt; 0.0001</b>
Trt × Yr	18	304	1.0	0.4552
<i>Panicum virgatum</i>				
Trt	1	18	18.16	<b>0.0005</b>
Yr	18	304	11.28	<b>&lt; 0.0001</b>
Trt × Yr	18	304	5.46	<b>&lt; 0.0001</b>
<b>Uplands</b>				
<i>Andropogon gerardii</i>				
Trt	1	20	1.48	0.2343
Yr	18	332	8.36	<b>&lt; 0.0001</b>
Trt × Yr	18	332	1.86	0.0181
<i>Panicum virgatum</i>				
Trt	1	20	0.39	0.5397
Yr	18	332	3.25	<b>&lt; 0.0001</b>
Trt × Yr	18	332	0.63	0.8749

Trt, treatment; DF, degrees of freedom; Yr, Year; Num, Numerator; Denom, Denominator; Pr, Probability.

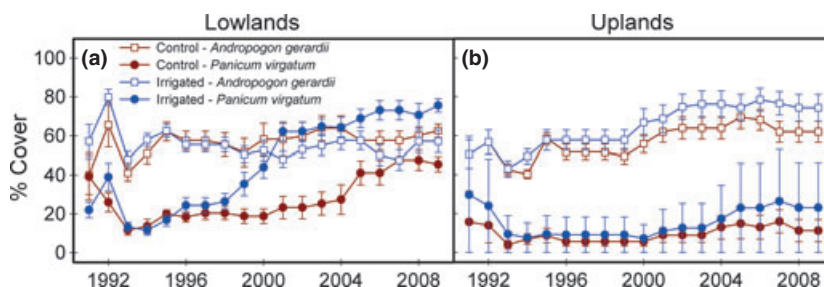
P values < 0.00096 were considered significant based on Bonferroni corrections for multiple comparisons (in bold).

& Lauenroth 1993; Buis *et al.* 2009; Burns, Collins & Smith 2009). In addition, inter-annual climate variability, particularly precipitation, is widely known to affect grassland net primary production both regionally, and within a site over time (Sala *et al.* 1988; Huxman *et al.* 2004; Muldavin *et al.* 2008). However, our long-term irrigation experiment demonstrated that plant community composition and dynamics are only weakly governed by precipitation alone. Moreover, when changes in species composition were attributed to irrigation (e.g. the increase in *P. virgatum*), these shifts occurred primarily *within* the same plant functional type (tall, clonal, perennial C<sub>4</sub> grasses) that also dominated control plots, leading to a functionally stable plant community under long-term water addition. Indeed, this ecosystem is dominated by clonal species, and the dominant C<sub>4</sub> grasses are all rhizomatous perennials, which increased both with and without water addition (Figs 3 and 4). This response by tall, rhizomatous perennials

to water addition is consistent with responses by species with these traits to nitrogen addition (Gough *et al.* 2012).

This limited overall response to irrigation is surprising given the documented importance of soil moisture in grassland ecosystems (Knapp *et al.* 2008; Heisler-White *et al.* 2009). Addition of other limiting resources, particularly nitrogen and potentially phosphorus, has been shown to increase NPP and dramatically alter community composition and structure in mesic grasslands (Gough *et al.* 2000; Suding *et al.* 2005; LeBauer & Treseder 2008). Our results suggest that the effects of resource limitation on grassland structure and function differ between moisture and nutrients, and may cast doubt on the existence of a single general mechanism by which resource addition decreases species diversity (see also Dickson & Foster 2011). In the current experiment, long-term water addition during the growing season led to a significant increase in above-ground production (Knapp, Briggs & Koelliker 2001). However, species richness was on average only 16% lower in irrigated plots relative to the control in lowland areas, whereas annual nitrogen addition in this same grassland led to a 50% decline in richness (Collins *et al.* 1998). Thus, increased production in response to resource addition, *per se*, does not necessarily lead to a general decline in species richness, likely because nitrogen availability imposes stronger limitations on NPP than does water availability in mesic grassland.

In general, the response of species richness and diversity to short-term irrigation in grasslands is highly variable. In some cases diversity increased with an increase in soil moisture (Zavaleta *et al.* 2003; Harpole, Potts & Suding 2007), some found no significant effect (Goldberg & Miller 1990; Harpole, Potts & Suding 2007), whereas others showed rapid negative effects of irrigation on grassland diversity (Suttle, Thomsen & Power 2007; Czóbel *et al.* 2008). In our study, long-term increases in soil moisture had limited effects on species richness and diversity, and richness declined in both treatment and control plots over time. The overall decline in species richness across treatments can likely be attributed to annual burning at this site. Annual burning has been shown to increase grass abundance and reduce forb richness in this tallgrass prairie (Collins 1987; Collins & Smith 2006; Veen *et al.* 2008), thus fire frequency may override the effects of annual water amendments in this native grassland.



**Fig. 4.** Annual average ( $\pm 1$  SE) percent cover of *Andropogon gerardii* and *Panicum virgatum* in (a) lowland and (b) upland irrigated and control transects.

Dominance by *P. virgatum* has been linked to declines in species richness in restored grassland (Baer *et al.* 2003, 2004). In our study *P. virgatum*, a species known to respond positively to increased soil moisture (Knapp 1984), became the dominant species in the lowlands starting in 2001, and shortly after, significant differences in diversity and richness emerged between irrigation and control plots. Furthermore, above average rainfall in five of the last 6 years of this study led to an increase in *P. virgatum* in lowland control plots as well. Thus, increased annual precipitation, which is predicted in this region as a consequence of climate change, could increase the abundance *P. virgatum* relative to other C<sub>4</sub> grasses, such as *A. gerardii*, which may result in a decline in species diversity when coupled with other factors, such as nitrogen deposition (Collins *et al.* 1998; Baer *et al.* 2003, 2004).

Annual burning could potentially constrain the type of fast compositional changes we might expect to see under a wetter climate regime. Although North American tallgrass prairie evolved with fire (Axelrod 1985), other manipulations (N addition) have produced rapid shifts in species composition and abundance in frequently burned prairie (Vinton *et al.* 1993; Hartnett, Hickman & Walter 1996). In addition, production in annually burned sites is more water limited than unburned sites (Knapp *et al.* 1998a); therefore, we would expect annually burned grasslands to be more sensitive to water additions than sites burned less frequently. Other grasslands have shown rapid shifts in composition and structure in response to water additions (Grime *et al.* 2000; Suttle, Thomson & Power 2007; Czóbel *et al.* 2008). This ecosystem has been shown to respond rapidly to a variety of manipulations including grazing, nutrient additions, drought and altered burning regimes (Owensby, Hyde & Anderson 1970; Gibson, Seastedt & Briggs 1993; Tilman & Downing 1994; Steinauer & Collins 1995; Spasojevic *et al.* 2010). Thus, tallgrass prairie has the potential to respond rapidly even with annual burning to many changes in resource availability and disturbance regimes, yet remains relatively stable in response to increased precipitation.

The hierarchical response framework (HRF, Smith, Knapp & Collins 2009) predicts that chronic resource addition results in non-linear dynamics including community reordering – a change in the relative abundance of species within a community – and that some communities are more resistant to change than others. Our results provide strong empirical support for the HRF. After years of water addition, species reordering occurred after a 10-year lag period and *P. virgatum* now dominates the lowland community once dominated by *A. gerardii*. In contrast, irrigated uplands remained dominated by *A. gerardii* to date despite some increase in the abundance of *P. virgatum* over time. Our analyses showed that most functional trait responses were unaffected by irrigation, but the most dramatic change to occur was *within* the dominant functional type in this ecosystem – perennial, rhizomatous C<sub>4</sub> grasses, all of which have high water use and nutrient use efficiencies (Tilman & Wedin 1991). Thus, although water, light and nutrients together co-limit NPP in mesic grasslands (Knapp *et al.* 1998a), our

results suggest that other factors (fire, grazing and nitrogen addition) have greater effects on grassland community composition and structure than does growing season precipitation.

Our results have important implications for modelling community and ecosystem responses to climate change. Gerten *et al.* (2008) argued that total seasonal rainfall had a greater effect on NPP than within-season variability. They also highlighted the need for additional long-term rainfall manipulation experiments to better understand ecosystem responses to future climate change, and to provide more realistic parameters for modelling the impact of climate change on ecosystems. Our long-term experiment directly addressed those challenges by increasing availability and reducing inter-annual variability of a key resource, soil moisture. We found that 19 years of water addition during the growing season had less effect on community structure than other key drivers in this grassland: fire, grazing and nitrogen availability. In doing so, our results highlighted the degree of redundancy that exists within a single, dominant functional type (perennial, clonal, tall C<sub>4</sub> grasses), which may mask the utility of ‘soft’ functional traits to predict community responses to climate change (Suding *et al.* 2008), while buffering the functional response of this grassland ecosystem to chronic resource alteration.

## Acknowledgements

We thank Alan Knapp for comments on an earlier version of the manuscript, Christian Gunning for help with R programming and Meghan Avolio for the repeated measures ANOVAs. This work resulted from a Distributed Graduate Seminar (Ushering in a New Era of Functional Ecology: Dynamics in a Changing Environment), conducted through the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (EF-0553768), the University of California, Santa Barbara, and the State of California. Support for data set (WAT-012) was provided by NSF to Kansas State University for the Konza Prairie Long-term Ecological Research program. The authors have no financial or other conflicts of interest related to the data found in this manuscript.

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Received 19 December 2011; accepted 20 March 2012

Handling Editor: Scott Wilson

## Supporting information

Additional Supporting information may be found in the online version of this article.

**Fig. S1.** Mean ( $\pm 1$  SE) soil moisture during the growing season in irrigated and control transects from 2006 through 2009.

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