Contents lists available at ScienceDirect

Acta Oecologica

Original article

Ecophysiological responses of two dominant grasses to altered temperature and precipitation regimes

Jesse B. Nippert [a,*], Philip A. Fay [b], Jonathan D. Carlisle [c], Alan K. Knapp [d], Melinda D. Smith [e]

[a] Division of Biology, Kansas State University, Manhattan, KS 66506, USA
[b] USDA-ARS, Grassland Soil and Water Research Laboratory, Temple, TX, USA
[c] Department of Plants, Soils and Climate, Utah State University, Logan, UT, USA
[d] Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO, USA
[e] Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA

ARTICLE INFO

ABSTRACT

Ecosystem responses to climate change will largely be driven by responses of the dominant species. However, if co-dominant species have traits that lead them to differential responses, then predicting how ecosystem structure and function will be altered is more challenging. We assessed differences in response to climate change factors for the two dominant C_4 grass species in tallgrass prairie, Andropogon gerardii and Sorghastrum nutans, by measuring changes in a suite of plant ecophysiological traits in response to experimentally elevated air temperatures and increased precipitation variability over two growing seasons. Maximum photosynthetic rates, stomatal conductance, water-use efficiency, chlorophyll fluorescence, and leaf water potential varied with leaf and canopy temperature as well as with volumetric soil water content (0–15 cm). Both species had similar responses to imposed changes in temperature and water availability, but when differences occurred, responses by A. gerardii were more closely linked with changes in air temperature whereas S. nutans was more sensitive to changes in water availability. Moreover, S. nutans was more responsive overall than A. gerardii to climate alterations. These results indicate both grass species are responsive to forecast changes in temperature and precipitation, but their differential sensitivity to temperature and water availability suggest that future population and community structure may vary based on the magnitude and scope of an altered climate.

© 2009 Elsevier Masson SAS. All rights reserved.

1. Introduction

A defining characteristic of the climate in the midwestern North American Great Plains is variability (Borchert, 1950). Paleoclimate records indicate that this region has experienced considerable climatic variation at multiple intervals throughout the Holocene (Laird et al., 1996; Laird et al., 2003; Mayewski et al., 2004; Michels et al., 2007). Against this historical backdrop, human-influenced global warming is increasing the probability of rapid climate change, and increased variation and more frequent extreme events for key environmental drivers like precipitation and temperature (Easterling et al., 2000; Houghton et al., 2001; Alley et al., 2003, 2007). Air temperature for the Great Plains has been projected to increase by 4 °C by the year 2100 (range 2–8 °C; Christensen et al., 2007). In contrast, annual precipitation for this region is likely to remain similar to present amounts, but the size distribution of individual rainfall events and the seasonal distribution of rainfall are likely to change (Gordon et al., 1992; Easterling et al., 2000; Karl and Trenberth, 2003; Meehl et al., 2005; Christensen et al., 2007). As temperatures increase and precipitation becomes more variable, alterations in resource availability are likely to affect the physiological and community responses of the ecosystem (Knapp et al., 2002).

The extant climate and past changes in atmospheric CO_2 concentration, air temperature, and precipitation have been recognized as critical in determining the distribution, persistence, and production of grassland plant communities (Weltzin et al., 2003; Dukes et al., 2005). In the tallgrass prairie ecosystem, there is evidence that historic variability in precipitation and temperature has impacted both species composition and productivity (Wells, 1970; Lauenroth et al., 1999). Indeed, interannual environmental variability can result in a 4-fold range of annual aboveground productivity (200–800 g m^{-2}; Knapp et al., 1998). However, plant responses to current levels of climate variability may not adequately predict responses to future climate conditions (Nippert et al., 2006). Experimental manipulations of warming and

* Corresponding author. Tel.: +1 785 532-0114; fax: +1785 532 6653.
E-mail address: nippert@ksu.edu (J.B. Nippert).

precipitation variability have provided some insight into productivity and plant composition responses to climate change (Fay et al., 2002, 2003; Knapp et al., 2002; An et al., 2005) with responses driven primarily by the most abundant or dominant species.

A focus on responses of the dominant species has proven effective for understanding grassland community and ecosystem processes (McNaughton, 1985; Smith and Knapp, 2003; Silletti et al., 2004; Anderson et al., 2006), and the tallgrass prairie is an ideal system for this approach because the response of a few dominant C4 grasses (i.e., *Andropogon gerardii* Vitman (big bluestem) and *Sorghastrum nutans* (L.) Nash (Indian grass)), strongly influences this ecosystem's response to environmental change (Knapp et al., 1998). These species share many traits and frequently co-occur, but previous studies have suggested that they differ in responses to temperature and water availability (Silletti and Knapp, 2001, 2002; Swemmer et al., 2006). For example, in a retrospective study of long-term plant community composition data, cover of *A. gerardii* was found to be more responsive to variation in summer air temperature, whereas *S. nutans* responded more to changes in rainfall (Silletti and Knapp, 2001). In addition, *S. nutans* generally shows a greater ecophysiological and whole-plant response to alterations in resource availability (Silletti and Knapp, 2002; Silletti et al., 2004; Swemmer et al., 2006).

Our objective was to determine if leaf-level physiological responses to experimental increases in temperature and changes in precipitation regime, as forecast for the Midwest US, differed between these two species and if these responses were consistent with their long-term responses in cover and productivity (Knapp et al., 1998). We hypothesized: (1) ecophysiological responses in *S. nutans* would be more closely related to changes in water availability, while *A. gerardii* would respond more to changes in temperature; and (2) *S. nutans* would exhibit greater responsiveness to variation in key environmental drivers such as increased precipitation variability and warming.

2. Materials and methods

This study was performed on plants growing within a long-term climate change field experiment – the rainfall manipulation plots (RaMPs) – in native tallgrass prairie at the Konza Prairie biological station (KPBS). The timing and size of precipitation events in the RaMPs has been manipulated since 1998 (see Fay et al., 2000) and a warming treatment has been included since 2003.

2.1. Study system

The Konza Prairie biological station (KPBS) is a 3487 ha tallgrass prairie preserve located in northeastern Kansas, USA (39°05′N, 96°35′W). This location has a temperate mid-continental climate of cold, dry winters and warm, wet summers. The long-term mean annual precipitation is 835 mm, of which 75% occurs during the growing season (April–September) (Hayden, 1998). The long-term mean daily air temperature is 18 °C in May, peaks at 27 °C in July, and declines to 22 °C in September (Hayden, 1998). While a diverse array of plant species are found on site, the mean annual aboveground net primary productivity (ANPP: 420 g m^{-2}; Knapp et al., 1998) reflects the growth of the dominant C4 grasses, primarily *Andropogon gerardii* and *Sorghastrum nutans* (Smith and Knapp, 2003).

2.2. The RaMPs experiment

The RaMPs experiment consists of 12 fixed-location shelters (14 × 9 m) designed to experimentally manipulate precipitation (ambient and altered) and temperature (unwarmed and warmed).

For the ambient precipitation treatment (6 shelters), each rainfall event that occurred was collected and immediately reapplied (mid-Apr to mid-Oct). For the altered treatment (6 shelters), rainfall was collected and accumulated until the interval between precipitation events was increased by 50% and then applied. The altered precipitation pattern thus had: (1) longer inter-rainfall dry periods, (2) greater rainfall event sizes, and (3) fewer rainfall events compared to ambient patterns. The total amount of growing season rainfall is kept equal in both treatments. The warming treatments are nested within the precipitation treatments. Each shelter (ambient and altered treatments) includes four 2 × 2 m subplots. In two of the subplots, infrared heating lamps (Kalglo 240V HS-2420) raise the ambient air temperature year round by ~2 °C. Lamp height is repositioned periodically through the growing season to maintain the lamp 1.2 m above the plant canopy (1.2 m above the soil surface in winter) and provide 20–25 W m^{-2} of downward infrared radiation. The control (unwarmed) subplot dedicated to sampling contains a dummy lamp to control for physical shading by the lamps. The soil type in the RaMPs is an Irwin silty clay loam. The permanent wilting point for this soil in the A horizon (0–20 cm) is between 15–17%, while gravimetric water content at field capacity is approximately 31% (NRCS soil series descriptions: http://www.soils.usda.gov/). Further details on shelter design, construction, and experimental details have been previously reported and are also available online (Fay et al., 2000, 2002; http://www.konza.ksu.edu/ramps/).

2.3. Sampling protocol and variables measured

Plant measurements were conducted over two growing seasons with 4 intensive sampling days in 2005 (06/01, 07/17, 07/21, 08/15) and in 2006 (06/01, 06/07, 07/18 and 07/24). For each year, two dates in mid-July targeted a drought-recovery period; the first period (drought) was chosen when soil moisture was limiting and temperatures were >30 °C, and then the second period (recovery) occurred after rainfall was applied to both the altered and ambient treatment plots. Due to the nature of the altered precipitation treatments, this treatment received larger rainfall events than the ambient treatment to initiate the recovery period (50–78 mm vs. 37–38 mm in the ambient treatment).

For each sample period, two morphologically similar tillers (3–5 fully expanded leaves) were identified prior to sampling for each species within the unwarmed control subplot and a randomly selected warmed subplot. Physiological measurements were performed on the newest, yet mature leaves, at the widest portion of the grass blade. Because instantaneous physiological measurements can vary based on time of day, ambient and altered plots were paired and their measurement order was randomized for each sampling period. Sampling was conducted between 09:00–15:00 CST when solar radiation was typically above 70% of full sun levels.

We measured key physiological variables representing responses in photosynthesis, water stress, and water loss. These included the maximum photosynthetic rate at saturating light and ambient CO_2 (A_{sat}), dark-adapted chlorophyll fluorescence (F_v/F_m), stomatal conductance to water (g_s), instantaneous water-use efficiency (WUE: A_{sat}/E), and midday leaf water potential (ψ_{mid}). F_v/F_m was measured using a hand-held pulse amplitude modulated fluorometer (OS1-FL, Opti-sciences, Inc., Tyngsboro, MA, USA). Leaves were dark-adapted prior to measurement for 15–30 min immediately preceding diurnal gas exchange measurements. Leaf-level gas exchange was measured on one tiller per species using a LI-6400 gas exchange system with red/blue light source and CO_2-injector (LiCOR, Inc., Lincoln, NE, USA). Flow rate was kept constant at 400 μmol s^{-1}, light intensity inside the cuvette was 1500 μmol

m^{-2} s^{-1}, the CO_2 concentration was 370 μmol mol^{-1}. Relative humidity was maintained near ambient by adjusting the desiccant knob, as necessary. Temperature controls were used to maintain the block temperature near the ambient air temperature (measured and adjusted between each sample). We designated stability for our gas exchange measurements when the CV for photosynthesis and conductance rates was <1% over a 15-s interval. In general, stability occurred within 5–10 min per sample. One leaf per tiller from each species was measured for leaf water potential (ψ_{mid}) using a Scholander-type pressure bomb (PMS Instruments, Inc., Corvallis, OR, USA). F_v/F_m and ψ_{mid} values were averaged by species/subplot prior to statistical analysis. This measurement protocol was kept constant for all time periods for both years.

To verify that our fluorescence results reflected treatment responses rather than sampling protocol, we analyzed all F_v/F_m data for each sampling period for a 'time of day' effect. F_v/F_m was measured during the day in the same randomized order used for the gas exchange measurements, and increased daytime light stress and temperatures may decrease F_v/F_m values (Maxwell and Johnson, 2000). The diurnal sampling order did not significantly influence F_v/F_m for any of the dates we sampled (all sampling periods had $p > 0.10$).

To characterize the effects of the precipitation and temperature treatments on environmental conditions, we continuously measured canopy temperature and near-surface soil water content (0–15 cm). Canopy temperature was measured using an infrared thermometer sensor (Apogee) mounted 1.5 m aboveground in one unwarmed and one warmed subplot in four RaMPs. Volumetric soil water content (θ_{0-15}) was measured in the control and warmed subplots in each RaMP using 30-cm time-domain reflectometry (TDR) probes (Campbell Scientific) buried 0.50 m from the edge of each subplot at a 45° angle to sample 0–15 cm soil depth. These sensors were recorded in 30-min intervals using a Campbell CR10X data logger. Air temperature and relative humidity data was available from the nearby (0.3 km) Konza Prairie weather station.

2.4. Statistical analysis

The overall goal of this project was to assess sensitivity of A. gerardii and S. nutans to variation in soil moisture and temperature generated by the RaMPs treatments over time. To accomplish this goal, we used multiple linear regression (MLR) analysis in which measures of temperature (canopy and leaf) and θ_{0-15} were the predictor variables and each of the 5 measured physiological parameters were the response variables. For both years combined, separate MLR were conducted for each physiological variable using the step-wise selection procedure. We chose this approach rather than an ANOVA approach, in order to assess sensitivity (interpreted as the slope of the best-fit MLR) across a range of soil moisture and temperature conditions.

A primary impact of the heating treatments was to elevate canopy temperatures. However, the infrared canopy temperature sensors were present in only a subset of the heated and control subplots. Canopy temperature was correlated to T_{leaf} with normally distributed residuals (Fig. 1, $r^2 = 0.77$; $y = 1.02x + 5.4$; $p < 0.0001$; RMSE = 2.7582; K–S normality statistic $p = 0.3283$). The 5.4 °C intercept in Fig. 1 most likely reflects methodological artifacts of temperature measurements using an IRGA versus infrared thermometer. During midday when evapotranspiration is highest, the canopy temperature sensor may slightly underestimate the true leaf temperature as vapor flux passes between the canopy and sensor. The relationship between canopy temperature and T_{leaf} holds across a large environmental gradient, but considerable variability in T_{leaf} exists at a given canopy temperature (Fig. 1). T_{leaf} was used as a predictor variable in the regression analyses. To
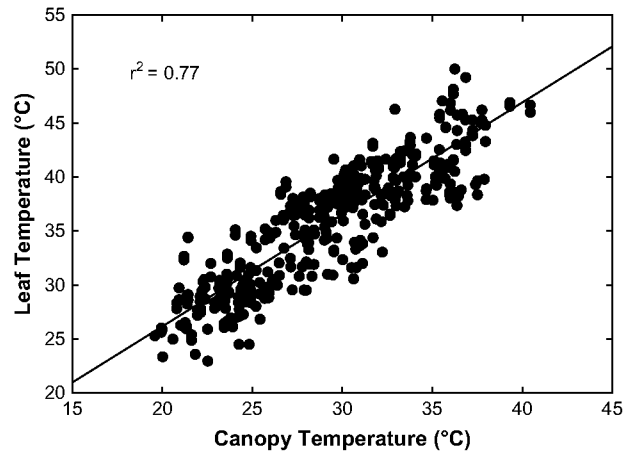

Fig. 1. Simple linear regression relating canopy temperature measured within a RaMPs shelter and leaf temperature measured inside an IRGA during gas exchange measurements ($y = 1.02x + 5.4$; total df = 386). Data are from both years and all treatment combinations (precipitation and temperature).

assess sensitivity of response of the two species to the targeted drought-recovery cycles in 2005 and 2006, we compared the differences between the drought and recovery periods using the slope of the response before and after watering for each species for each year separately. All analyses were performed using SAS statistical software (SAS v9.1, Cary, NC, USA).

3. Results

The precipitation and warming treatments altered the climate experienced by the plant communities in this experiment (Table 1; Figs. 2 and 3). Responses of surface soil water content (θ_{0-15}) and leaf temperature (T_{leaf}) to the treatments depended on the time periods compared (Table 1; Figs. 2 and 3). Both the precipitation and warming treatments significantly reduced θ_{0-15} compared to ambient precipitation patterns and unwarmed subplots, but not at all time periods (Fig. 2). In 2005, the precipitation treatment significantly lowered θ_{0-15} during the 06/01 and 07/21 periods (Table 1). In 2006, the precipitation and warming treatments significantly lowered θ_{0-15} during 06/07, and the precipitation treatment significantly lowered θ_{0-15} during 07/24 (Table 1). T_{leaf} was significantly increased by the warming treatment during the first sampling date in 2005, and the first two dates in 2006 (Table 1). Interactions of precipitation and warming treatments significantly increased T_{leaf} for the first two sample dates in 2005, but no interaction effects were present in 2006. There were no treatment-induced statistical differences in T_{leaf} or θ_{0-15} when analyzed by year in 2005 (Table 1), but the warming treatment and precipitation × warming significantly reduced θ_{0-15} in 2006 ($p < 0.05$; Table 1). Thus, these treatments did not result in a consistent temporal alteration of annual means, but rather the treatments extended and shifted the distribution of environmental variability in ways consistent with predictions of future climate for this location.

The altered precipitation and warming treatments resulted in a wide range in T_{leaf} (and canopy temperature) and θ_{0-15}, and we focused on comparing the sensitivity of key physiological responses of A. gerardii and S. nutans to this environmental variation. Our results indicate that T_{leaf} and θ_{0-15} explained a significant portion of the variation in the five key physiological parameters measured for both species (whole-model r^2 range: 0.24–0.55; Table 2). The total explained variance was similar between species, with the exception of A_{sat} responses in which higher r^2 values were present for

Table 1
Mixed-effects model ANOVA of treatment effects (fixed, altered precipitation and warming; random, RaMP) on the environmental variables volumetric water content of 0–15 cm soil (θ_{0-15}) and leaf temperature (T_{leaf}).

Date		θ_{0-15}			T_{leaf}		
		Precipitation	Warming	Precipitation × warming	Precipitation	Warming	Precipitation × warming
2005	F	0.20	0.13	1.63	0.09	0.04	0.01
	p	0.662	0.723	0.230	0.759	0.844	0.913
06/01	F	7.37	0.17	2.66	1.64	17.63	4.12
	p	**0.022**	0.683	0.112	0.209	**<0.001**	**0.050**
07/17	F	2.91	1.48	1.70	0.17	2.39	7.27
	p	0.119	0.232	0.201	0.680	0.131	**0.011**
07/21	F	34.97	2.56	1.36	0.05	1.70	0.57
	p	**0.0001**	0.119	0.252	0.823	0.201	0.455
08/15	F	3.74	0.37	0.35	0.30	0.43	2.14
	p	0.101	0.549	0.563	0.585	0.519	0.152
2006	F	0.05	20.59	5.22	0.00	0.19	0.00
	p	0.825	**0.001**	**0.046**	0.970	0.667	0.988
06/01	F	2.45	3.18	1.84	1.36	20.51	0.28
	p	0.169	0.088	0.189	0.252	**<0.001**	0.598
06/07	F	5.29	6.63	0.4	0.15	6.97	3.22
	p	**0.044**	**0.015**	0.531	0.6992	**0.012**	0.081
07/18	F	0.04	0.44	1.53	0.00	0.08	0.02
	p	0.855	0.510	0.225	0.9747	0.786	0.899
07/24	F	7.91	1.69	0.06	1.20	2.71	0.37
	p	**0.018**	0.202	0.803	0.282	0.109	0.550

F- and p-values are provided for both fixed effects and their interaction. Degrees of freedom for individual dates were (1,34) and by year (1,177). Significant responses ($p < 0.05$) are indicated in bold font.

S. nutans (Table 2). Additionally, the slope of the relationship between θ_{0-15} and A_{sat} was significantly higher for *S. nutans*, compared to *A. gerardii* (Table 2, final column). For both species, T_{leaf} had higher partial r^2 values for variation in WUE and F_v/F_m, whereas θ_{0-15} had higher r^2 for A_{sat} and ψ_{mid}. Responses of g_s to environmental variation differed by species. The best predictor for *A. gerardii* was T_{leaf} (partial $r^2 = 0.23$) while the best predictor of g_s for *S. nutans* was θ_{0-15} (partial $r^2 = 0.35$) (Table 2).

To further assess sensitivity in physiological responses between the two C4 grasses, we focused on two mid-season drought-recovery periods in July, 2005 and 2006. The drought- recovery period was characterized by low water availability and high air temperatures

typical of mid-July for the first sample date, and then alleviation from drought with the application of rainfall to both the ambient and altered treatments for the second sample date. During both years, the rainfall applications significantly increased soil moisture content for the second sampling period (Table 3). However, the two drought-recovery periods differed in that the maximum ambient air temperatures increased between sampling periods in 2005, but decreased in 2006 (Table 3). VPD (air to leaf vapor pressure deficit) increased following the rainfall application in both years, driven largely by decreases in RH (from 60 to 50% in 2005, 50 to 30% in 2006; Table 3). In 2005, A_{sat}, g_s and WUE declined for both species in the recovery period despite the increase in soil water content and ψ_{mid}.
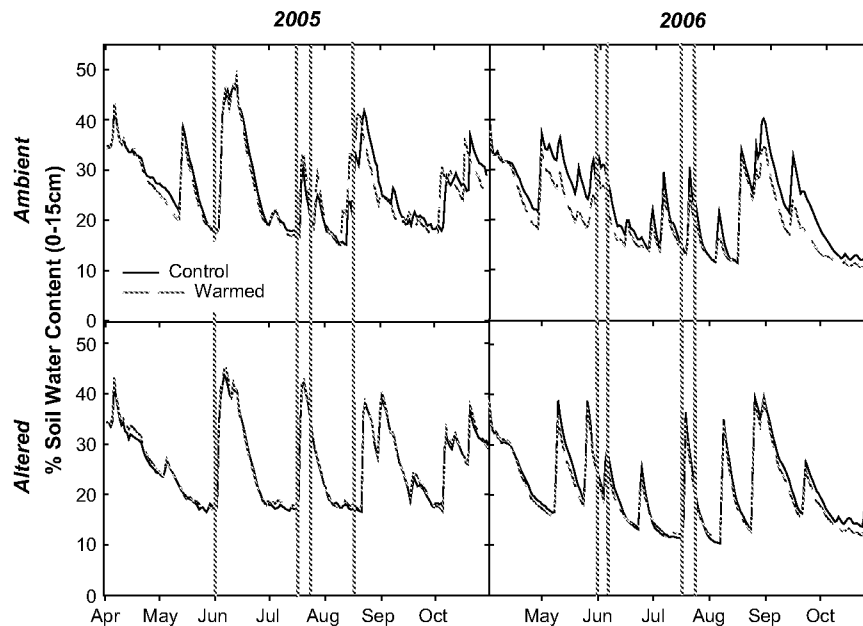

Fig. 2. Treatment effects of altered precipitation pattern and increased air temperature on soil water content from 0–15 cm. Data are 24-h means for the growing seasons of 2005 and 2006. The top row shows the response to ambient precipitation patterns, and the bottom row shows the response to altered precipitation pattern (see Section 2). Line color denotes temperature treatments (black, ambient air temperature; red, warmed). Vertical grey lines indicate dates of physiological sampling.
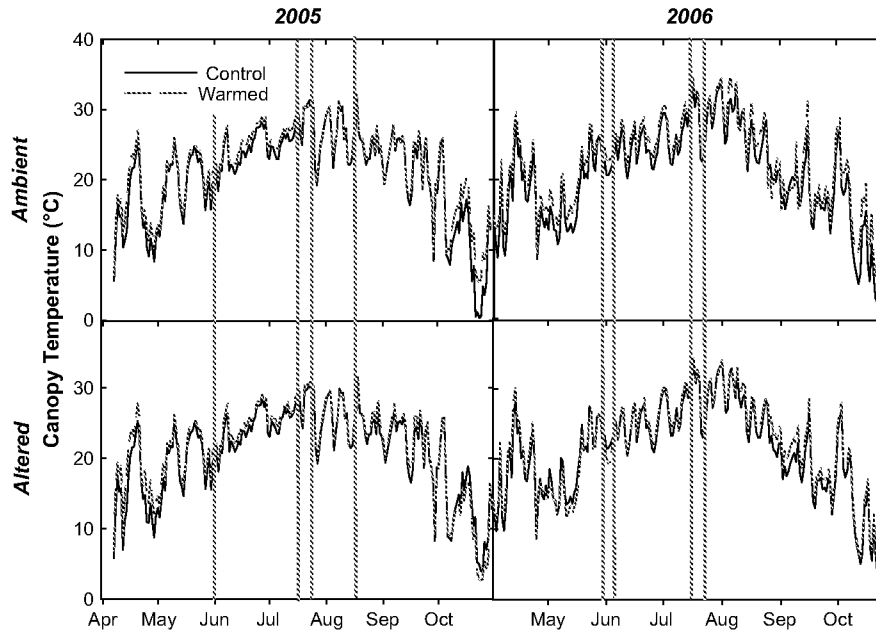
Fig. 3. Treatment effects of altered precipitation pattern and increased air temperature on canopy temperature (°C). Data are 24-h means for the growing seasons of 2005 and 2006. The top row shows the response to ambient precipitation patterns, and the bottom row shows the response to altered precipitation pattern (see Section 2). Line color denotes temperature treatments (black, ambient air temperatures; red, warmed). Vertical grey lines indicate dates of physiological sampling.

However, A_{sat} and g_m declined significantly more in *A. gerardii* when compared to *S. nutans* (Fig. 4A,B). In 2006, A_{sat}, g_s, and WUE increased in the recovery period similarly in both species (Fig. 4A–C) following the rainfall application. Here, ψ_{mid} responded significantly more for *S. nutans* in 2006 following water additions, increasing to a higher mean value than *A. gerardii* (Fig. 4E). F_v/F_m did not vary significantly in response to the increase in water availability by species or between years (Fig. 4D).

Changes in instantaneous WUE were compared by species and year to simultaneous measurements of VPD (Fig. 5). WUE was calculated as a change in the ratio of A_{sat} to E measured on individual leaves, while VPD was calculated using the mean air temperature and relative humidity data from the nearby (0.3 km) Konza Prairie weather station, at the corresponding time periods as gas exchange measurements. Results over both summers and species show a significant negative correlation between VPD and WUE (Fig. 5).

4. Discussion

Previously, community-level comparisons between the two co-dominants *A. gerardii* and *S. nutans* suggested that there was

differential sensitivity to interannual variability in water and temperature in native tallgrass prairie (Silletti and Knapp, 2001, 2002). However, when the physiological responses of *A. gerardii* were related to more subtle intra-annual changes in soil water resulting from the RaMPs treatment protocol, few responses were found (Fay et al., 2002). Our research focused on differences between *A. gerardii* and *S. nutans* within the RaMPs but during years with greater water and temperature stress. In general, these physiological results conducted during drought support previous community-level comparisons of differential sensitivity to water and temperature stress between these co-dominant species (Silletti and Knapp, 2001, 2002; Swemmer et al., 2006).

Previous studies of these two species provide a broad base for describing their ecophysiological traits. *A. gerardii* and *S. nutans* are both NADP-ME subtype C_4 grasses. Grasses with this C_4 subtype are characterized by little net O_2 production or consumption in bundle sheath cells and low rates of CO_2 leakage out of the bundle sheath (Raven, 1977; Chen et al., 1994). As NADP-ME C_4 grasses, plant photosynthetic biochemistry varies little among these two species. However, differences in the maximum rates of gas exchange and varying stomatal characteristics do occur (Knapp, 1993). Maximum

Table 2
MLR model (stepwise) results for physiological responses of *A. gerardii* and *S. nutans* to leaf temperature (T_{leaf}) and soil water content (θ_{0-15}).

Predictor	Response	A. gerardii			S. nutans			Slope p-value
		r^2	SE	Slope	r^2	SE	Slope	
T_{leaf}	A_{sat}	0.01	0.08	−0.12	0.04	0.08	−0.26	0.28
	g_s	0.23	0.52	−0.93	0.04	0.49	−1.58	0.40
	WUE	0.46	0.02	−0.19	0.43	0.02	−0.22	0.39
	ψ_{mid}	0.07	0.09	0.36	0.07	0.01	0.38	0.81
	F_v/F_m	0.40	$4.61e^{-4}$	$4.61e^{-3}$	0.35	$5.85e^{-4}$	$5.25e^{-3}$	0.55
θ_{0-15}	A_{sat}	0.23	6.85	45.90	0.34	7.20	62.39	0.04
	g_s	0.10	45.70	301.89	0.35	42.94	381.88	0.08
	WUE	0.09	1.44	8.26	0.10	1.79	10.53	0.33
	ψ_{mid}	0.25	7.95	65.32	0.25	8.12	68.02	0.95
	F_v/F_m	0.04	0.04	0.14	0.06	0.05	0.22	0.78

Each row shows the fit statistics (partial r^2, standard error, and parameter slope) for predictor variables (leaf temperature (T_{leaf}), and volumetric water content (θ_{0-15})). The p-values in the final column indicate differences by species in the slope of predictor and response variables compared. Analyses include data combined across both years.

Table 3
Mean environmental conditions during the drought – recovery sampling periods (09:00–15:00 CST) for 2005 and 2006.

	07/17/05	07/21/05	07/18/06	07/24/06
θ_{0-15}	0.14 (0.01)	0.33 (0.01)	0.12 (0.01)	0.19 (0.01)
T_{air}	37.6 (0.5)	39.7 (0.6)	42.6 (0.4)	39.3 (0.3)
VPD	1772.3 (167.2)	2717.9 (109.4)	2246.1 (76.4)	3293.5 (79.5)

Values are whole-site means plus standard error in parentheses. Volumetric soil water content (θ_{0-15}) is expressed as a percent, air temperature (T_{air}) in °C, and leaf to air vapor pressure deficit (VPD) in pascals.

gas exchange rates for both species are similar, but vary based on sampling location, time of year, and by study. In general, the range of values reported across studies is similar (maximum A_{sat} mean range 25–35 μmol m^{-2} s^{-1} and maximum g_s mean range 250–350 mmol m^{-2} s^{-1}) (Heckathorn and DeLucia, 1991; Knapp, 1993; Silletti and Knapp, 2001; Swemmer et al., 2006). S. nutans has a higher stomatal density than A. gerardii (mean 324 vs. 168 mm^{-2}), but smaller guard cells (mean 24 vs. 38 μm length) (Knapp, 1993). The optimum soil temperature for growth in A. gerardii is 25 °C (DeLucia et al., 1992) and the optimum air temperature ranges between 30–34 °C (Knapp, 1985). Both species are highly drought tolerant and maintain gas exchange over a wide range of environmental conditions. During a year with above-average precipitation, the mean ψ_{mid} for A. gerardii was −1.5 MPa, and the mean ψ_{mid} was −2.5 MPa in a dry year (Knapp et al., 1993). However, the minimum water potential at which positive net photosynthesis still occurs is −6.5 MPa for A. gerardii and −5.5 MPa for S. nutans (Heckathorn and DeLucia, 1991, 1994). Cumulatively, these results show broad similarity by species, but that over a range of environmental conditions, A. gerardii exhibits ecophysiological responses characteristic of a higher drought tolerance while S. nutans may have a higher tolerance to changes in air temperature. If these species have varying sensitivity to water and temperature, these effects are most likely to be seen during mid-summer when air temperatures remain high but water availability fluctuates with episodic precipitation events and alterations in soil water content.

Despite the high level of variability in this system (McAllister et al., 1998; Nippert et al., 2007), multiple linear regression (MLR) analyses revealed significant relationships between T_{leaf} and θ_{0-15} and key plant ecophysiological response variables (Table 2). The relative importance of T_{leaf} or θ_{0-15} as a predictor of the response variables we measured was largely similar for both C$_4$ grass species. However, the variance explained by T_{leaf} and θ_{0-15} differed between species for g_s. For example, more variance in g_s was explained by T_{leaf} in A gerardii, but by θ_{0-15} in S. nutans. In addition, the physiological responsiveness to changes in temperature and soil moisture (as indicated by slopes of the relationships) was consistently higher (though not always significantly) for S. nutans than A. gerardii (final column, Table 2).

The results of the mid-season drought – recovery periods when environmental conditions changed over short periods of time provides a unique context for the relationships noted in the MLR analysis (Table 2). θ_{0-15} increased during the 'recovery' period for both years following rainfall applications, VPD increased concurrently, and T_{air} varied between drought and recovery for 2005 and 2006 (Table 3). In 2005, gas exchange variables (A_{sat}, g_s, WUE) were lower in the 'recovery' period despite increases in θ_{0-15} (Fig. 4A–C). The most likely explanation for this response is the increase in ambient T_{air} and VPD between the drought and recovery sampling periods (Table 3). While rates for both species declined, A_{sat} and g_s in A. gerardii decreased more than in S. nutans between drought – recovery in 2005, suggesting a greater impact of the higher T_{air} on A. gerardii during this period (Fig. 4A,B). This response is consistent with our MLR results showing a stronger correlation between g_s

and temperature for A. gerardii (Table 2). The environmental conditions in 2006 were similar to 2005, except that T_{air} decreased between consecutive sampling periods (Table 3). Both species had higher rates of A_{sat} and g_s following rainfall applications, although in this case, the rate of change was higher for S. nutans (Fig. 4A,B). Increased VPD during the recovery period in 2006 did not result in lower WUE for either species (Fig. 4C). WUE nearly doubled for S. nutans, likely from increased g_s and increased water availability. Collectively, the results over both years suggest a greater negative effect of high T_{air} on A. gerardii, because alleviation of water stress in the recovery period resulted in minimal corresponding increases in A_{sat}, g_s, and WUE. The positive response of S. nutans to increased θ_{0-15} only occurred when T_{air} also decreased in 2006. For example, A_{sat}, g_s, WUE and ψ_{mid} increased in S. nutans when θ_{0-15} increased and T_{air} decreased in the recovery of 2006 (Fig. 4). The varying species responses during the two drought-recovery cycles provide additional support for both hypotheses. The physiological variables we measured do not show alleviation from stress for A. gerardii following water additions because T_{air} remained high. The response of S. nutans during the 'recovery' period in 2006 exhibits the greater responsiveness of this species to improved soil water content compared to A. gerardii.

F_v/F_m did not vary significantly by species before or after the imposed drought-recovery cycle for either year (Fig. 4D). Previously, measurements of F_v/F_m in these C$_4$ grass species have been relatively insensitive to short-term changes in summer water availability or peak summer temperatures (Nippert et al., 2007). Similarly, Resco et al. (2008) reported minimal changes in F_v/F_m before and after precipitation pulses in a semi-arid ecosystem except following long periods of drought and considerable loss of photosynthetic activity. These authors suggest A_{sat} is likely a better physiological indicator of short-term plant stress responses to changing water availability (Resco et al., 2008).

Changes in instantaneous leaf WUE were negatively related to changes in VPD for all sampling dates during both years (Fig. 5). During periods with high VPD, WUE was the lowest. This relationship was similar by species for both years (but see lower r^2 for S. nutans in 2005).

In theory, WUE should be inherently related to changes in VPD, since WUE is an expression relating changes in A_{sat}/E, and the derivation of E reflects changes in g_s and VPD. The relationships contrasted in Fig. 5 represent independent data because WUE was derived from gas exchange measurements performed on leaves inside an IRGA, while VPD was estimated concurrently using independent environmental data collected at the plot-scale. These results confirm theoretical expectations that leaf E would increase with increases in VPD without concurrent changes in g_s (and thus changes in A_{sat}). If the carboxylation efficiency (V_{cmax}) varied significantly between species, then sensitivity to VPD alone would not explain interspecific differences in WUE. We have previously reported a similar V_{cmax} for A. gerardii and S. nutans across a range of growing conditions at this site (Nippert et al., 2007). Thus, varying sensitivity to VPD is the most likely driver of changes in WUE for both species during 2005 and 2006.

In general, responses of A. gerardii and S. nutans to changes in water availability and temperature were similar over the entire study period (Table 2), but responses differed following a drought-recovery cycle (Fig. 4). Our results are consistent with how known demographic and biomass allocation strategies vary between the two species. For example, S. nutans can reproduce vegetatively throughout the season via new tiller production (McKendrick et al., 1975), and has greater allocation to rhizomes than A. gerardii (Swemmer et al., 2006). In contrast, A. gerardii reproduces vegetatively only at the beginning of the growing season when soil moisture is highest and temperatures are moderate, and has been
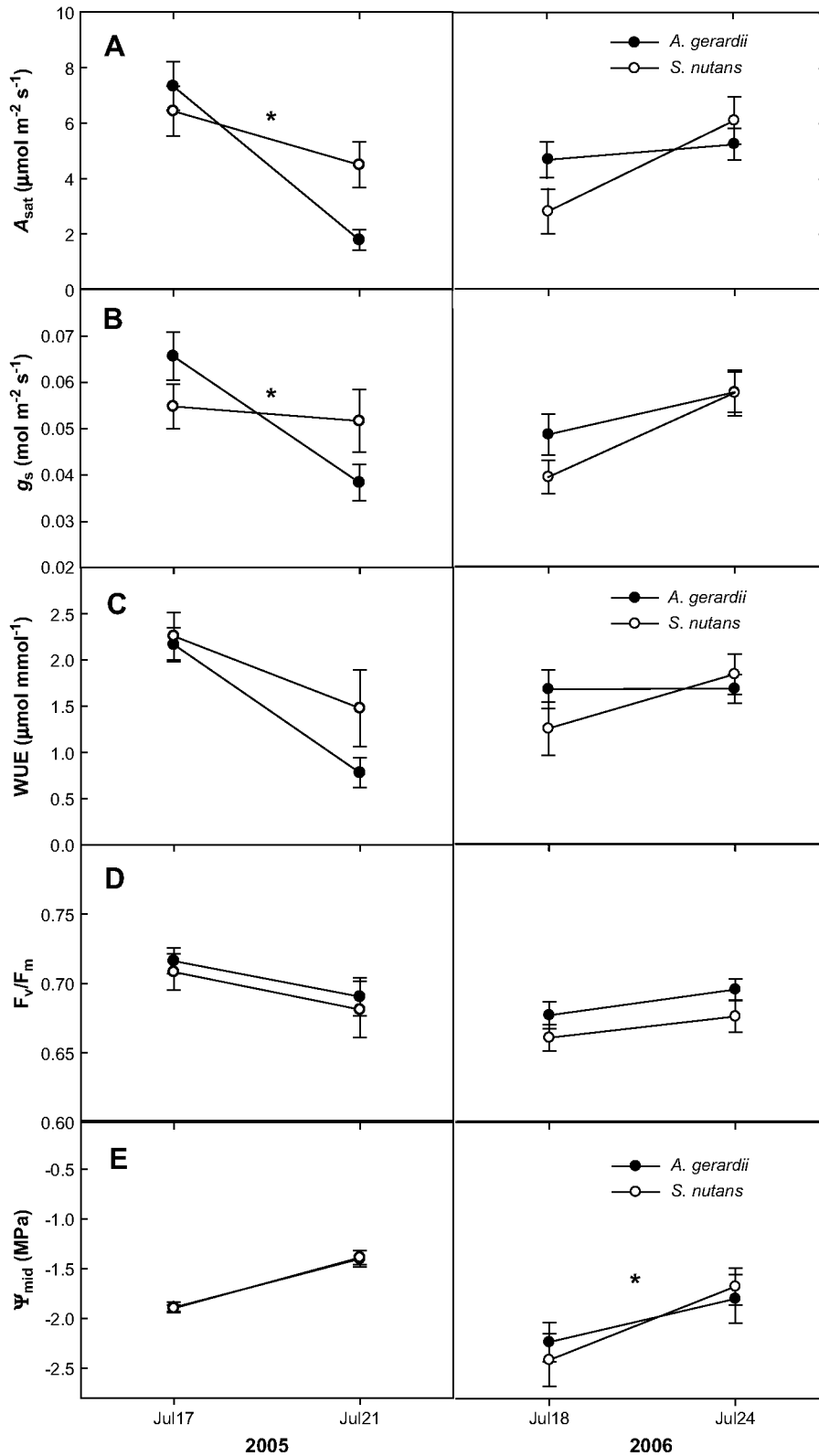
Fig. 4. Physiological responses for both species during drought-recovery periods in July 2005 and 2006. Water was applied to all plots (ambient and altered) between drought-recovery during each year. Each point is the overall mean response (± 1 SE) by sample date and species. Asterisks indicate a statistically significant difference ($p < 0.05$) between species during the drought and recovery periods.

shown to have greater root production and reduced flowering during drought (Swemmer et al., 2006). This similarity between the physiological and morphological/reproductive responses by species, suggests a consistent whole-plant response to resource limitation, especially during periods of extreme stress (e.g., drought).

The most likely future environmental change for this region is reduced water availability, as both higher air temperatures and
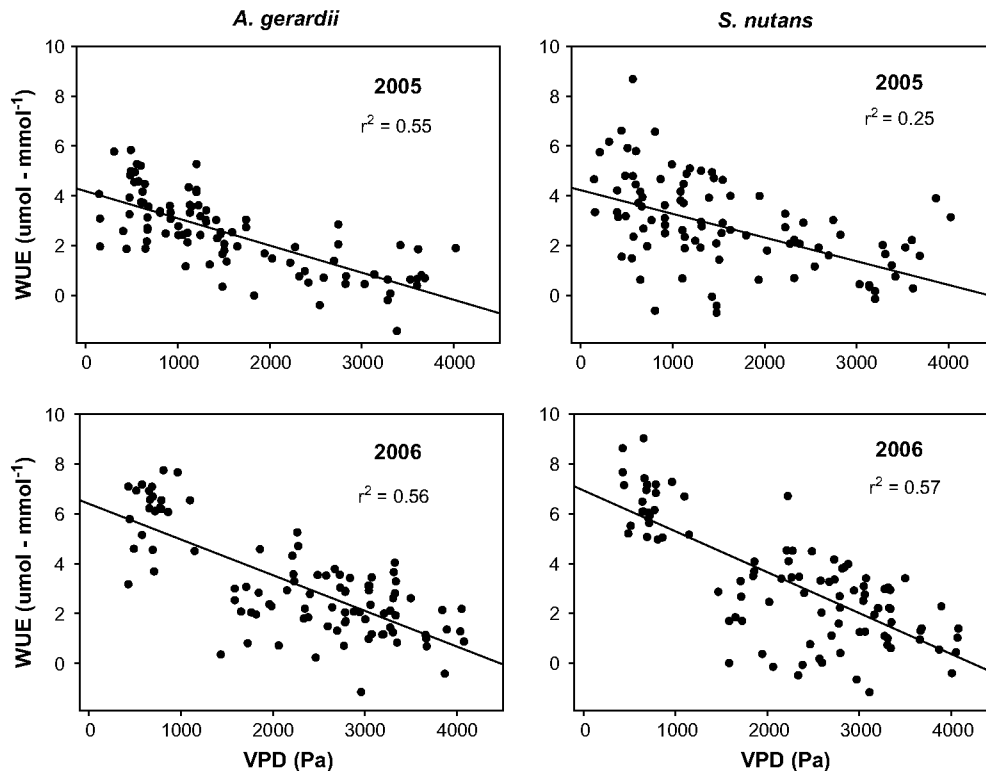
Fig. 5. Changes in instantaneous water-use efficiency (WUE) as a function of the vapor pressure deficit (VPD) for both species and years. WUE was calculated as A_{sat}/E using gas exchange data, while VPD was calculated using the mean air temperature and relative humidity data from the nearby (0.3 km) Konza Prairie weather station.

more extreme rainfall regimes reduce soil water content. If this change is manifest, our results suggest *S. nutans* may be the most adversely affected, because *A. gerardii* is more stable (and less sensitive) to changes in water availability. Changes in the abundance of either species, particularly *A. gerardii*, have been shown to impact plant diversity and aboveground productivity in the tallgrass prairie (Collins et al., 1998; Knapp et al., 2002; Smith and Knapp, 2003). Thus, if changes in the ecophysiological traits we measured (e.g., reduced photosynthetic rates) translate to changes in growth, abundance, or survivorship for either C_4 grass species, then future changes in precipitation patterns and air temperatures may alter the relative role of each species in the overall dynamics of the tallgrass prairie ecosystem.

5. Conclusions

The altered temperature and precipitation treatments reduced soil water availability and increased leaf temperature during portions of the growing season, consistent with predictions of future climate for the study region. Leaf-level responses to these environmental changes indicate that: (1) both species responded similarly for most of the ecophysiological variables we measured; (2) when differences occurred, T_{leaf} was a better predictor of ecophysiological variability for *A. gerardii*, while θ_{0-15} was a better predictor of variation for *S. nutans*; and (3) *S. nutans* was more responsive to alterations in water and temperature stress than *A. gerardii* under the same conditions.

Acknowledgements

References

Alley, R.B., Marotzke, J., Nordhaus, W.D., Overpeck, J.T., Peteet, D.M., Pielke, R.A., Pierrehumbert, R.T., Rhines, P.B., Stocker, T.F., Talley, L.D., Wallace, J.M., 2003. Abrupt climate change. Science 299, 2005–2010.

Alley, R.B., et al., 2007. Climate Change 2007: The Physical Science Basis, Summary for Policy Makers. Geneva, Switzerland, IPCC Secretariat. Working Group 1 Fourth Assessment Report of the Intergovernmental Panel on Climate Change (2-2-2007).

An, Y.A., Wan, S.Q., Zhou, X.H., Subedar, A.A., Wallace, L.L., Luo, Y.Q., 2005. Plant nitrogen concentration, use efficiency, and contents in a tallgrass prairie ecosystem under experimental warming. Global Change Biol. 11, 1733–1744.

Anderson, T.M., Dong, Y., McNaughton, S.J., 2006. Nutrient acquisition and physiological responses of dominant serengeti grasses to variation in soil texture and grazing. J. Ecol 94, 1164–1175.

Borchert, J.R., 1950. The climate of the central North American grassland. Ann. Assoc. Am. Geog 40, 1–39.

Chen, D.X., Coughenour, M.B., Knapp, A.K., Owensby, C.E., 1994. Mathematical simulation of C_4 grass photosynthesis in ambient and elevated CO_2. Ecol. Mod 73, 63–80.

Christensen, J.H., et al., 2007. Regional climate projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group 1 to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M., Steinauer, E.M., 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280, 745–747.

DeLucia, E.H., Heckathorn, S.A., Day, T.A., 1992. Effects of soil-temperature on growth, biomass allocation and resource acquisition of *Andropogon gerardii* Vitman. New Phytol 120, 543–549.

Dukes, J.S., Chiariello, N.R., Cleland, E.E., Moore, L.A., Shaw, M.R., Thayer, S., Tobeck, T., Mooney, H.A., Field, C.B., 2005. Responses of grassland production to single and multiple global environmental changes. PloS Biol. 3, 1829–1837.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Mearns, L.O., 2000. Climate extremes: observations, modeling, and impacts. Science 289, 2068–2074.

Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M., Collins, S.L., 2000. Altering rainfall timing and quantity in a mesic grassland ecosystem: design and performance of rainfall manipulation shelters. Ecosystems 3, 308–319.

Fay, P.A., Carlisle, J.D., Danner, B.T., Lett, M.S., McCarron, J.K., Stewart, C., Knapp, A.K., Blair, J.M., Collins, S.L., 2002. Altered rainfall patterns, gas exchange, and growth in grasses and forbs. Int. J. Plant Sci. 163, 549–557.

Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M., Collins, S.L., 2003. Productivity responses to altered rainfall patterns in a C_4-dominated grassland. Oecologia 137, 245–251.

Gordon, H.B., Whetton, P.H., Pittock, A.B., Fowler, A.M., Haylock, M.R., 1992. Simulated changes in daily rainfall intensity due to the enhanced greenhouse-effect – implications for extreme rainfall events. Clim. Dynam 8, 83–102.

Hayden, B.P., 1998. Regional climate and the distribution of tallgrass prairie. In: Knapp, A.K., Briggs, J.M., Hartnett, D.C., Collins, S.L. (Eds.), Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie. Oxford University Press, New York, pp. 19–34.

Heckathorn, S.A., DeLucia, E.H., 1991. Effect of leaf rolling on gas-exchange and leaf temperature of Andropogon gerardii and Spartina pectinata. Bot. Gaz 152, 263–268.

Heckathorn, S.A., DeLucia, E.H., 1994. Drought-induced nitrogen retranslocation in perennial C_4 grasses of tallgrass prairie. Ecology 75, 1877–1886.

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A. (Eds.), 2001. Climate Change 2001: The Scientific Basis. Contributions of Working Groups I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Karl, T.R., Trenberth, K.E., 2003. Modern global climate change. Science 302, 1719–1723.

Knapp, A.K., 1985. Effect of fire and drought on the ecophysiology of Andropogon gerardii and Panicum virgatum in a tallgrass prairie. Ecology 66, 1309–1320.

Knapp, A.K., 1993. Gas-exchange dynamics in C_3 and C_4 Grasses – consequences of differences in stomatal conductance. Ecology 74, 113–123.

Knapp, A.K., Briggs, J.M., Blair, J.M., Turner, C.L., 1998. Patterns and controls of aboveground net primary productivity in tallgrass prairie. In: Knapp, A.K., Briggs, J.M., Hartnett, D.C., Collins, S.L. (Eds.), Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie. Oxford University Press, New York, pp. 193–221.

Knapp, A.K., Fahnestock, J.T., Hamburg, S.P., Statland, L.B., Seastedt, T.R., Schimel, D.S., 1993. Landscape patterns in soil plant water relations and primary production in tallgrass prairie. Ecology 74, 549–560.

Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S., McCarron, J.K., 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298, 2202–2205.

Laird, K.R., Cumming, B.F., Wunsam, S., Rusak, J.A., Oglesby, R.J., Fritz, S.C., Leavitt, P.R., 2003. Lake sediments record large-scale shifts in moisture regimes across the northern prairies of North America during the past two millennia. Proc. Natl. Acad. Sci. USA 100, 2483–2488.

Laird, K.R., Fritz, S.C., Maasch, K.A., Cumming, B.F., 1996. Greater drought intensity and frequency before AD 1200 in the Northern Great Plains, USA. Nature 384, 552–554.

Lauenroth, W.K., Burke, I.C., Gutmann, M.P., 1999. The structure and function of ecosystems in the central North American grassland region. Great Plains Res 9, 223–259.

Maxwell, K., Johnson, G.N., 2000. Chlorophyll fluorescence – a practical guide. J. Exp. Bot 51, 659–668.

Mayewski, P.A., Rohling, E.E., Stager, J.C., Karlen, W., Maasch, K.A., Meeker, L.D., Meyerson, E.A., Gasse, F., van Kreveld, S., Holmgren, K., Lee-Thorp, J., Rosqvist, G., Rack, F., Staubwasser, M., Schneider, R.R., Steig, E.J., 2004. Holocene climate variability. Quat. Res. 62, 243–255.

McAllister, C.A., Knapp, A.K., Maragni, L.A., 1998. Is leaf-level photosynthesis related to plant success in a highly productive grassland? Oecologia 117, 40–46.

McKendrick, J.D., Owensby, C.E., Hyde, R.M., 1975. Big bluestem and indiangrass vegetation reproduction and annual reserve carbohydrate and nitrogen cycles. Agro-Ecosystems 2, 75–93.

McNaughton, S.J., 1985. Ecology of a grazing ecosystem: the Serengeti. Ecol. Mon 55, 259–294.

Meehl, G.A., Arblaster, J.M., Tebaldi, C., 2005. Understanding future patterns of increased precipitation intensity in climate model simulations. Geophys. Res. Lett. 32, L18719.

Michels, A., Laird, K.R., Wilson, S.E., Thomson, D., Leavitt, P.R., Oglesby, R.J., Cumming, B.F., 2007. Multidecadal to millennial-scale shifts in drought conditions on the Canadian prairies over the past six millennia: implications for future drought assessment. Global Change Biol. 13, 1295–1307.

Nippert, J.B., Fay, P.A., Knapp, A.K., 2007. Photosynthetic traits in C_3 and C_4 grassland species in mesocosm and field environments. Environ. Exp. Bot 60, 412–420.

Nippert, J.B., Knapp, A.K., Briggs, J.M., 2006. Intra-annual rainfall variability and grassland productivity: can the past predict the future? Plant Ecol 184, 65–74.

Raven, J.A., 1977. Ribulose bisphosphate carboxylase activity in terrestrial plants: significance of O_2 and CO_2 diffusion. Curr. Adv. Plant Sci. 9, 579–590.

Resco, V., Ignace, D.D., Sun, W., Huxman, T.E., Weltzin, J.F., Williams, D.G., 2008. Chlorophyll fluorescence, predawn water potential and photosynthesis in precipitation pulse-driven ecosystems – implications for ecological studies. Funct. Ecol 22, 479–483.

Silletti, A.M., Knapp, A.K., 2001. Responses of the co-dominant grassland species Andropogon gerardii and Sorghastrum nutans to long-term manipulations of nitrogen and water. Am. Mid. Nat 145, 159–167.

Silletti, A.M., Knapp, A.K., 2002. Long-term responses of the grassland co-dominants Andropogon gerardii and Sorghastrum nutans to changes in climate and management. Plant Ecol 163, 15–22.

Silletti, A.M., Knapp, A.K., Blair, J.M., 2004. Competition and coexistence in grassland codominants: responses to neighbour removal and resource availability. Can. J. Bot 82, 450–460.

Smith, M.D., Knapp, A.K., 2003. Dominant species maintain ecosystem function with non-random species loss. Ecol. Lett. 6, 509–517.

Swemmer, A.M., Knapp, A.K., Smith, M.D., 2006. Growth responses of two dominant C_4 grass species to altered water availability. Int. J. Plant. Sci. 167, 1001–1010.

Wells, P.V., 1970. Historical factors controlling vegetation patterns and floristic distributions in the central Great Plains region of North America. In: Dort, W., Jones, J.K. (Eds.), Pleistocene and Recent Environments of the Central Great Plains. University of Kansas Press, Lawrence, KS, pp. 211–221.

Weltzin, J.F., Loik, M.E., Schwinning, S., Williams, D.G., Fay, P.A., Haddad, B.M., Harte, J., Huxman, T.E., Knapp, A.K., Lin, G.H., Pockman, W.K., Shaw, M.R., Small, E.E., Smith, M.D., Smith, S.D., Tissue, D.T., Zak, J.C., 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. Bioscience 53, 941–952.