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Contrasting sensitivities of two dominant C_4 grasses to heat waves and drought

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Abstract Heat waves and droughts are predicted to increase in frequency and intensity with climate change. However, we lack a mechanistic understanding of the independent and interactive effects of severe heat and water stress for most ecosystems. In a mesic tallgrass prairie ecosystem, we used a factorial experimental approach to assess ecophysiological and productivity responses of two dominant C_4 grasses, *Andropogon gerardii* and *Sorghastrum nutans*, to a season-long drought and a mid-summer heat wave at four intensities. We hypothesized that drought would have greater impacts than heat waves, that combined effects would be greater than either factor alone, and that the dominant grasses would differ in their responses to heat and water heat stress. We detected significant reductions in photosynthesis, leaf water potential, and productivity with drought but few direct responses to the heat waves. Surprisingly, there was no additive effect of heat and water stress on any plant response. However, *S. nutans* was more sensitive than *A. gerardii* to drought. In this grassland, water stress will likely dominate photosynthetic and productivity responses caused by discrete drought and heat wave events, rather than direct or additive effects of heat stress, with differential sensitivity in these grasses altering future ecosystem structure and function.

Keywords Climate change · Climate extremes · Photosynthesis · Productivity · Mesic grassland

Introduction

Climate extremes, such as heat waves and drought, are projected to increase in frequency and intensity in the future, and thus there is a clear need to understand how they will impact ecosystems (Easterling et al. 2000; Meehl and Tebaldi 2004; IPCC 2013; Hansen et al. 2012). Despite being relatively short-term events, climate extremes have the potential to cause significant and long-term ecological change, and thus can have impacts disproportionate to their duration (Albertson and Weaver 1946; Tilman and Elhaddi 1992; Jentsch et al. 2007). Furthermore, heat waves and drought typically co-occur (Trenberth and Shea 2005; De Boeck et al. 2010a), so understanding their individual and interactive effects by observation alone is challenging. However, an experimental approach that manipulates both climate factors can improve our

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mechanistic understanding of the effects of such short-term events on ecological process.

Here, we present results from an experiment in which a growing season-long drought and mid-season heat waves at several magnitudes were imposed independently and in combination on an intact, mesic grassland ecosystem in the central US—the tallgrass prairie. Plant communities in these grasslands are characterized by strong dominance (Collins et al. 1998), with a few abundant C_4 grass species controlling ecosystem function, while many less abundant C_3 forbs account for the high diversity (Knapp et al. 1998). C_4 plants are considered more tolerant of heat and water stress than C_3 species, because they have higher water-use efficiencies and negligible effects of heat on photorespiration (Sage and Monson 1999). However, differential sensitivities to heat and water stress among the C_4 grasses may lead to divergent responses in these dominant species, particularly if the stress exceeds species-specific physiological thresholds (Gutschick and BassiriRad 2003).

We focused on the responses of two dominant C_4 grasses in tallgrass prairie, *Andropogon gerardii* Vitman and *Sorghastrum nutans* Nash, which together account for almost half of plant canopy cover, and the majority of total aboveground productivity in this ecosystem (Silletti and Knapp 2002; Smith and Knapp 2003). These grasses have been broadly viewed as functional equivalents, with a greater research effort focused on *A. gerardii* (Knapp et al. 1998; Silletti and Knapp 2002). While their overlapping geographic distributions suggest similar climatic requirements (Brown 1993), past studies suggest that these two grasses may respond differently to projected climate changes, with *A. gerardii* more sensitive to warming and *S. nutans* more sensitive to alterations in precipitation (Weaver and Fitzpatrick 1932; Brown 1993; Silletti and Knapp 2002; Swemmer et al. 2006; Nippert et al. 2009). However, due to the nature of these past studies, separating the effects of temperature from water stress, as well as identifying interactive effects of these drivers on the dominant species, has not been possible. Such differential sensitivities may lead to divergent responses to climate change and a reordering of species abundances with important consequences for ecosystem function.

To examine the individual and combined effects of short-term heat waves and drought on these dominant C_4 grasses, we experimentally imposed a mid-summer heat wave at four temperature levels (up to +7.7 °C above ambient) in plots receiving either ambient rainfall or a 66 % reduction in growing season rainfall to simulate a severe drought. The primary biotic response variables measured were leaf water status, net photosynthesis, and end of season aboveground productivity for each species. We hypothesized that the effects of drought would be greater than those of heat for both species, since water is the primary limiting factor in this ecosystem (Knapp et al. 1998). In addition, we hypothesized that the combined effects of heat waves and drought would be greater than that of either factor alone (i.e., additive effects, De Boeck et al. (2010b)), with the greatest negative effects on both physiology and productivity manifest with the highest temperature heat wave treatment under drought conditions. Finally, as suggested by previous research (Weaver and Fitzpatrick 1932; Brown 1993; Silletti and Knapp 2002; Swemmer et al. 2006; Nippert et al. 2009), we hypothesized that *A. gerardii* would be more sensitive to heat stress, whereas *S. nutans* would be more sensitive to water stress.

Materials and methods

Study site and focal species

Research was conducted at the Konza Prairie Biological Station, a 3,487 ha native tallgrass prairie in NE Kansas, USA (39°05′N, 96°35′W). The site has a temperate mid-continental climate with cold, dry winters and warm, wet summers. This region is characterized by high interannual variability in precipitation and temperature, which can lead to a fourfold variability in aboveground net primary productivity (Knapp et al. 1998). Konza Prairie Biological Station is dominated by perennial C_4 grasses, in particular *A. gerardii* and *S. nutans*, which together account for most standing biomass and productivity (Smith and Knapp 2003) and regulate plant community diversity (Collins et al. 1998). Both species are long-lived clonal plants that primarily reproduce vegetatively via belowground buds on rhizomes (Benson and Hartnett 2006). As clones of each species grow, they sever their root and rhizome connections (Benson and Hartnett 2006) forming a dense matrix of tillers (individual stems) that are intermixed.

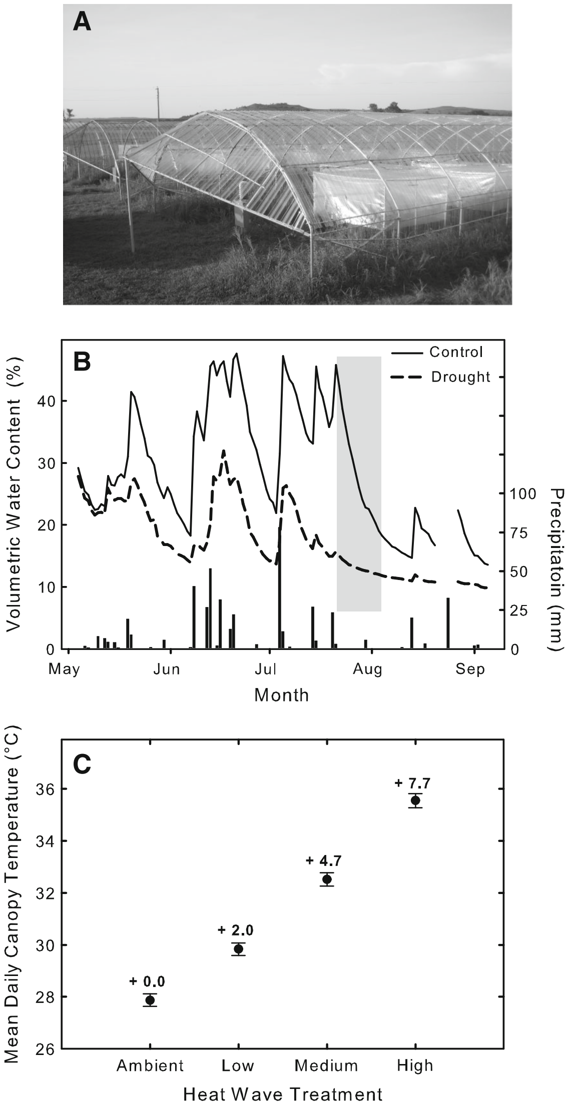

Fig. 1 Experimental infrastructure during the simulated heat wave (**a**) and the effects of drought and heat wave treatments on (**b**) volumetric water content (VWC, %) and (**c**) canopy temperature (CT, °C). **a** Shown in the foreground is one of the greenhouse structures modified to impose drought. The frame is partially covered with polycarbonate strips to reduce rainfall inputs by 66 % during the growing season. Nested within this structure are heat chambers with infrared lamps inside that imposed a two-week heat wave (21-July to 03-Aug-2010). **b** VWC is shown for the control and drought treatments (*left x*-axis) with a *box* highlighting the timing of the 2-week period that the heat wave treatments were applied. *Black bars* are ambient precipitation (*right x*-axis). *Note* missing data in late August was due to a power failure. **c** Mean daily canopy temperature (±1 SE) is shown for the four heat wave treatments

Experimental design

The Climate Extremes Experiment was established in 2010 on a site with deep (>1 m) silty clay loam soil adjacent to the long-term Rainfall Manipulation Plots experiment (Fay et al. 2000). The experimental treatments of the Climate Extremes Experiment consisted of a growing season-long drought (15-May to 30-Sep-2010) and a mid-season, two-week heat wave (21-Jul to 03-Aug-2010), at four temperature levels. The drought treatment was imposed using two modified 6 × 24 m cold frame greenhouse structures (Stuppy, Inc., Kansas City, MO, USA) constructed over native grassland plots (Fig. 1a). The roofs of these structures comprised 15.2 cm wide strips of Dynaglas Plus® clear corrugated polycarbonate plastic (PALRAM Industries LTD., Kutztown, PA, USA), which covered 75 % of the roof surface and excluded ~66 % of the ambient rainfall. For the control precipitation treatment, two additional greenhouse structures were covered with deer netting (TENAX Manufacturing Alabama, USA) which allowed all ambient rainfall to reach the plots but reduced photosynthetically active radiation by approximately 10 % (equivalent to the effects of the drought shelters, Fig. 1a). The control precipitation and drought treatments were randomly assigned to each shelter, and the shelters were oriented E-W and arrayed approximately 5 m from each other. Each shelter was hydrologically isolated by trenching to a depth of 1 m around the perimeter of each 6 × 24 m area; the trench was lined with 6 mil plastic and metal flashing to prevent subsurface and surface water flow.

Within each structure, we established two rows of five 2 × 2 m plots (10 total) arranged diagonally from each other in a checkerboard arrangement, allowing for a 2 m buffer between plots. Plots were randomly assigned to one of four heat wave treatments (ambient, low, medium, and high), which were imposed mid-summer for 2 weeks. The timing of the simulated heat wave coincided with the period of greatest sensitivity to high temperature in this grassland (Craine et al. 2012). Heat wave treatments were imposed by placing transparent chambers that combined passive heating with infrared lamps (IR) over the plots (Fig. 1a). Chambers were 2 × 2 m wide and 1.5 m tall, with

1 m high clear polyethylene walls and covered with Dynaglas Plus® clear corrugated polycarbonate roofs. Ventilation was maintained by placing chambers 0.5 m above the ground surface with adjustable gaps between the roofs and walls. In order to achieve four distinct temperature levels, infrared lamps (HS/MRM 2420, 2,000W, Kalglo Electronics, Inc., Bethlehem, PA, USA) were placed within the heat chambers as follows: ambient = no lamp, low heat = one lamp at half power, medium heat = one lamp at full power, and high heat = two lamps at full power. Lamps were suspended 130 cm above the ground to ensure even coverage across the plot. Heated plots were warmed 24 h per day for the entire 2-week heat wave.

Environmental measurements

Soil moisture and canopy temperature were continuously monitored in each plot to evaluate the effectiveness of drought and heat wave treatments. Volumetric water content (VWC) was measured at a depth of 0–15 cm with 30 cm time-domain reflectometry (TDR) probes (Model CS616, Campbell Scientific, Inc., Logan, UT, USA) buried at a 45° angle in the center of each plot. Canopy temperature (CT) was measured with infrared thermometers (Model SI-111, Apogee Instruments, Inc., Logan, UT, USA) mounted in the SE corner of each plot at a height of 1.5 m. Data from all sensors were sampled every 30-s and averaged for 30-min periods (CR10X Datalogger, Campbell Scientific, Inc., Logan, UT, USA).

Plant ecophysiological measurements

Eight intensive sampling campaigns were conducted between 11:00 and 15:00 CDT throughout the growing season to measure leaf gas exchange (A_{net}) and mid-day leaf water potential (Ψ_{mid}) responses of *A. gerardii* and *S. nutans*. In each plot, a tiller (individual stem) of each species with leaves in the upper canopy was permanently tagged for repeated sampling of gas exchange throughout the experiment. Prior to each sampling campaign, an additional tiller, which was morphologically similar to the permanently tagged individual, was selected in each plot for destructive leaf water potential sampling. Thus, for A_{net} and Ψ_{mid}, we sampled a total of 20 individuals per species for each drought treatment and 5 individuals of each species for each drought by heat wave combination. For all individuals, the youngest fully expanded leaf was measured. Plot sampling order was randomized for each sampling campaign, and A_{net} was measured at 5-s intervals for 2–6 min with a LI-6400 system (LiCOR, Inc., Lincoln, NE, USA) equipped with an LED light source (light intensity was maintained at 2,000 μmol m^{-2} s^{-1}, CO_2 concentration at 400 μmol mol^{-1}, and relative humidity at ambient levels). A_{net} was then calculated for each leaf using an objective selection algorithm (Matlab 7.4, The MathWorks, Inc., Natick, MA, USA) to select a 1-min period of A_{net} when variability was minimal. Ψ_{mid} was measured on a single leaf per individual using a Scholander-type pressure chamber (PMS Instruments, Inc., Corvallis, OR, USA).

Aboveground productivity

Aboveground production of the dominant C_4 grasses was sampled at the end of the growing season (05-Sep-2010) by harvesting all aboveground plant material of each species in three 0.1 m^2 quadrats randomly located within each plot. Samples were oven dried at 60 °C for 48 h, and weighed to the nearest 0.1 g.

Statistical analyses

The experiment was a randomized block split-plot design with block nested within the drought treatment, heat wave treatments nested within drought treatment, with the block × heat wave treatment interaction as a random effect. We first ran a repeat measures mixed-model ANOVA with species, date, drought, and heat wave treatments in the model during the whole growing season and found significant main effect of species for both A_{net} and Ψ_{mid} (Table S1), with *S. nutans* having a higher mean A_{net} and lower Ψ_{mid} than *A. gerardii* (Table S2). In order to remove the confounding effects of baseline physiological differences between the species, we conducted ANOVAs separately for each species and compared their relative responses to the drought and heat wave treatments. We focused these analyses on three sampling periods: (1) the entire growing season, (2) the 2-week heat wave, and (3) the last day of the heat wave. The growing season and heat wave sample periods were analyzed using a repeated measures mixed-model ANOVA, while the last day of the heat wave and aboveground production was analyzed with a mixed-model

Table 1 Effects of the drought and heat wave treatments and sampling date on mean daily volumetric water content (VWC) and canopy temperature (CT) during the 2-week period in which the heat wave treatments were applied

Effect	VWC			CT		
	df	*F*	*p*	df	*F*	*p*
Drought	1, 2.03	214.3	**0.004**	1, 2	8.3	0.102
Heat	3, 23	3.6	**0.029**	3, 27.2	209.9	**<0.001**
Date	13, 311	675.7	**<0.001**	13, 238	941.8	**<0.001**
Drought × heat	3, 23	1.0	0.402	3, 27.2	1.0	0.396
Drought × date	13, 311	384.7	**<0.001**	13, 238	9.6	**<0.001**
Heat × date	39, 311	9.6	**<0.001**	39, 238	14.2	**<0.001**
Drought × heat × date	39, 311	6.3	**<0.001**	39, 238	1.4	0.069

Degrees of freedom (df) for numerator and denominator (estimated using Satterthwaite's method), *F* statistics and *p* values from mixed-model repeated measures ANOVAs are reported. Bold text indicates significance at $p \leq 0.05$

ANOVA. We also assessed differential sensitivity by examining the relationship between VWC and Ψ_{mid} (excluding measurements from within heated chambers) for each species by fitting nonlinear regression models through an iterative selection process (proc NLIN). All analyses were conducted in SAS (version 9.2, SAS Institute Inc., Cary, NC, USA) and significance was set a $p \leq 0.05$.

Results

Effects of drought and heat waves on environmental variables

The experimental infrastructure was successful in imposing a drought during the 2010 growing season and simulating a 2-week heat wave at four distinct temperatures (Fig. 1b, c). Between the start of the simulated drought (15-May-2010) and the end of season biomass harvest (05-Sep-2010), plots in the control shelters received 444.1 mm of rainfall, while drought plots received 148.0 mm, a 66 % reduction. Overall, this reduction in rainfall resulted in a 43 % reduction in VWC relative to control plots (control = 29.5 % ± 0.47, drought = 16.9 % ± 0.69, $p = 0.001$; Fig. 1b). During the 2-week heat wave, there was a strong interaction between date and the drought treatments (Table 1) due to more rapid and greater reductions in VWC with control precipitation (58 %) than with drought (23 %, Fig. 1b). The four heat wave treatments resulted in different mean daily CT's for the 2-week period in late July; ambient plots averaged 27.9 °C and the low, medium, and high treatments averaged 7, 17, and 28 % warmer than ambient plots, respectively (Fig. 1c). The maximum daily high CT recorded in the high treatment was 43.1 °C on 03-Aug-2010, the last day of the heat wave. In addition, we found a significant negative correlation between VWC and CT ($r = -0.78$, $p < 0.001$), across all treatments during this period.

Ecophysiological responses to the drought and heat wave treatments

We found little evidence for additive effects of heat and drought on the ecophysiological responses of the dominant grasses. There were significant effects of heat and drought on Ψ_{mid} (drought, heat, drought × date, heat × date) and drought on A_{net} (drought × date) for both species (Table 2). But, there were few interactions between the two treatments when assessed over the growing season or just during the heat wave, with the exception of A_{net} for *S. nutans* (drought × heat and drought × heat × date interactions; Table 2). We focused on the last day of the 2-week heat wave to assess the cumulative effects of the heat wave treatments and increase our ability to detect interactions between heat waves and drought. While there were significant interactions between the heat and drought treatments for both species, there were no combined effects of heat waves of any magnitude under drought conditions (Fig. 2a, b). Instead, the effects of the heat wave treatments were

Table 2 Effects of the drought and heat wave treatments on mid-day leaf water potential (ψ_{mid}) and net photosynthesis (A_{net}) of the dominant C_4 grasses (*Andropogon gerardii* and *Sorghastrum nutans*) over the growing season (including heat wave) and during the 2-week period in which the heat wave treatments were applied

Effect	*Andropogon gerardii*						*Sorghastrum nutans*					
	Ψ_{mid}			A_{net}			Ψ_{mid}			A_{net}		
	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Whole growing season												
Drought	1, 1.99	19.7	**0.048**	1, 1.91	3.8	0.195	1, 7.69	71.7	**<.001**	1, 1.97	6.4	0.130
Heat	3, 5.88	4.0	0.070	3, 75.5	2.0	0.116	3, 7.69	5.4	**0.027**	3, 5.42	4.0	0.077
Date	7, 141	97.6	**<.001**	7, 159	32.7	**<.001**	7, 140	97.6	**<.001**	7, 147	50.0	**<.001**
Drought × heat	3, 5.88	0.6	0.647	3, 75.5	0.6	0.602	3, 7.69	0.9	0.500	3, 5.42	5.7	**0.041**
Drought × date	7, 141	10.3	**<.001**	7, 159	3.2	**0.004**	7, 140	10.5	**<.001**	7, 147	6.3	**<.001**
Heat × date	21, 141	1.8	**0.023**	21, 159	0.6	0.894	21, 140	2.5	**0.001**	21, 150	1.3	0.219
Drought × heat × date	21, 141	1.3	0.170	21, 159	0.4	0.987	21, 140	0.9	0.552	21, 150	1.8	**0.022**
Heat wave only												
Drought	1, 1.99	33.7	**0.030**	1, 1.92	3.6	0.205	1, 6.98	92.3	**<.001**	1, 1.95	8.9	0.099
Heat	3, 5.87	6.0	**0.033**	3, 41.3	1.0	0.408	3, 6.98	14.4	**0.002**	3, 5.74	4.2	0.066
Date	2, 67.3	33.6	**<.001**	2, 68.1	24.8	**<.001**	2, 60.2	38.3	**<.001**	2, 65.2	38.0	**<.001**
Drought × heat	3, 5.87	1.2	0.395	3, 41.3	1.3	0.297	3, 6.98	1.6	0.281	3, 5.74	3.4	0.099
Drought × date	2, 67.3	0.9	0.426	2, 68.1	3.3	**0.043**	2, 60.2	1.0	0.368	2, 65.2	7.3	**0.001**
Heat × date	6, 67.3	1.8	0.109	6, 68.1	0.3	0.932	6, 60.2	0.8	0.559	6, 65.3	1.0	0.408
Drought × heat × date	6, 67.3	1.5	0.200	6, 68.1	1.0	0.433	6, 60.2	0.7	0.648	6, 65.3	3.2	**0.009**

Degrees of freedom (df) for numerator and denominator (estimated using Satterthwaite's method), *F* statistics and *p* values from mixed-model repeated measures ANOVAs are reported. Bold text indicates significance at $p \leq 0.05$

only significant under control precipitation (Fig. 2a, b). In the control rainfall treatment, A_{net} for *A. gerardii* decreased as the average heat wave temperature increased (Fig. 2a). In contrast, *S. nutans* was unaffected by the low and medium heat wave treatments, but A_{net} was decreased by $\sim$80 % from ambient levels for the high heat wave treatment (Fig. 2b). Consistent with these responses, there was a negative effect of the heat wave treatments on VWC for the control precipitation, but not the drought treatment (Fig. 2c).

There were direct effects of the heat wave and drought treatments on the dominant grasses, but these direct effects differed between Ψ_{mid} and A_{net}. In general, Ψ_{mid} was affected by both heat and drought, while A_{net} was only sensitive to drought. The drought and heat wave treatments resulted in similar responses in Ψ_{mid} for both *A. gerardii* and *S. nutans* with significant drought × date and heat × date interactions (Table 2). For both species, the effects of drought on Ψ_{mid} were not evident until mid-July, and treatment differences emerged earlier in Ψ_{mid} than A_{net} (Fig. 3). Once significant treatment differences were manifest, they persisted for the reminder of the sampling periods in both species (Fig. 3). These dominant grasses also responded similarly to VWC, at VWC greater than 20 %, Ψ_{mid} did not vary in response to changes in VWC in either species, but below this threshold Ψ_{mid} decreased sharply in both grasses with reduced VWC (Fig. 4). There were significant heat wave × date interactions for both species (Table 2, growing season). The greatest decrease in Ψ_{mid} occurred with the high heat treatment and the differences among the heat wave treatments persisting nine days after the heat wave ended (Fig. 5). In contrast, A_{net} for both species was only sensitive to drought as evident by drought × date interactions (Table 2).

While both species were sensitive to heat and water stress, there was evidence for differential sensitivity to drought but not heat. A_{net} differed between the two species in specific ways during the drought. First, drought-induced reductions in A_{net} occurred earlier in *S. nutans* (29-Jul-2010) than *A. gerardii* (03-Aug-

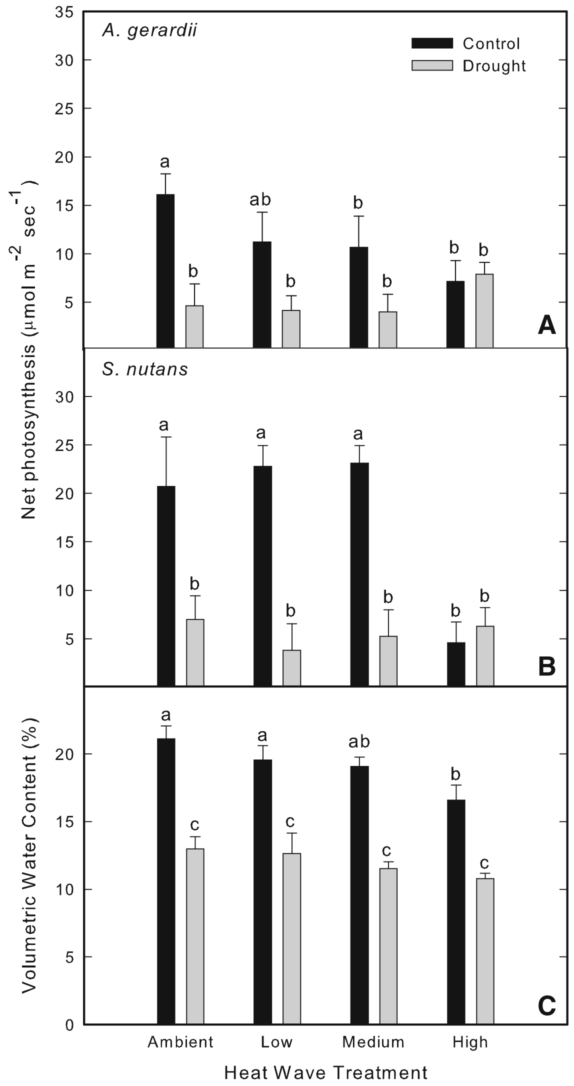

Fig. 2 Interactive effects of drought and the heat wave treatments on net photosynthesis (A_{net}) of *A. gerardii* (**a**) and *S. nutans* (**b**), as well as mean volumetric water content (**c**) measured on the last day of the simulated heat wave, 03-Aug-2010. *Error bars* indicate one standard error and *different letters* denote significant differences among heat and drought treatment combinations within each of the three independent analyses ($p \leq 0.05$)

2010). Secondly, there was a larger relative decrease in A_{net} for *S. nutans* in the drought plots before vs. after the heat wave (94 % in *S. nutans*, 81 % in *A. gerardii*; Fig. 3). Finally, the difference in A_{net} between the control precipitation and drought treatment immediately after the heat wave was greater in *S. nutans* (85 % reduction) than in *A. gerardii* (64 % reduction, Fig. 3).

Effects of the drought and heat wave treatments on aboveground production

Drought significantly reduced end-of-season aboveground production in *S. nutans* by 37 %, but had no effect on production in *A. gerardii* (Fig. 6; Table 3). Surprisingly, the heat wave treatments did not reduce aboveground production for either species despite clear visual signs of heat-induced foliar senescence, and thus there were no significant interactions or additive effects of heat and drought for either species (Table 3).

Discussion

Forecasts of more frequent and severe drought and heat waves portend ecological responses from individual to ecosystem scales (Smith 2011), particularly if the magnitude or combination of climate stressors pushes species beyond response thresholds (Gutschick and BassiriRad 2003). Given that the attributes of dominant species strongly influence most ecosystem processes (Whittaker 1965; Grime 1998; Ellison et al. 2005), we focused on the ecophysiological and aboveground productivity responses of two dominant C_4 grasses in central US grasslands as a key to predicting ecosystem responses to drought, heat waves of different magnitudes and their interactions. While previous research suggested that these species respond differentially to heat and water stress (Silletti and Knapp 2002; Swemmer et al. 2006; Nippert et al. 2009), our experimental design permitted us to directly test this purported differential sensitivity. Moreover, because we imposed heat waves of different magnitudes, we could further determine if there are species-specific response thresholds. Overall, we found (1) that both species were affected more by direct effects of drought than heat waves, (2) there were no additive effects of heat waves and drought, and (3) evidence for differential sensitivity to drought between the dominant C_4 grasses, with *S. nutans* more sensitive than *A. gerardii*.

The levels of drought and heat waves imposed in this experiment were severe, but not outside the range of recent climate of this site (1984–2008, Konza Prairie LTER data set AWE012). Over this 25-year period, mean annual precipitation was 840.3 ± 38.9 mm, and the driest year (1988) received 481.5 mm. These

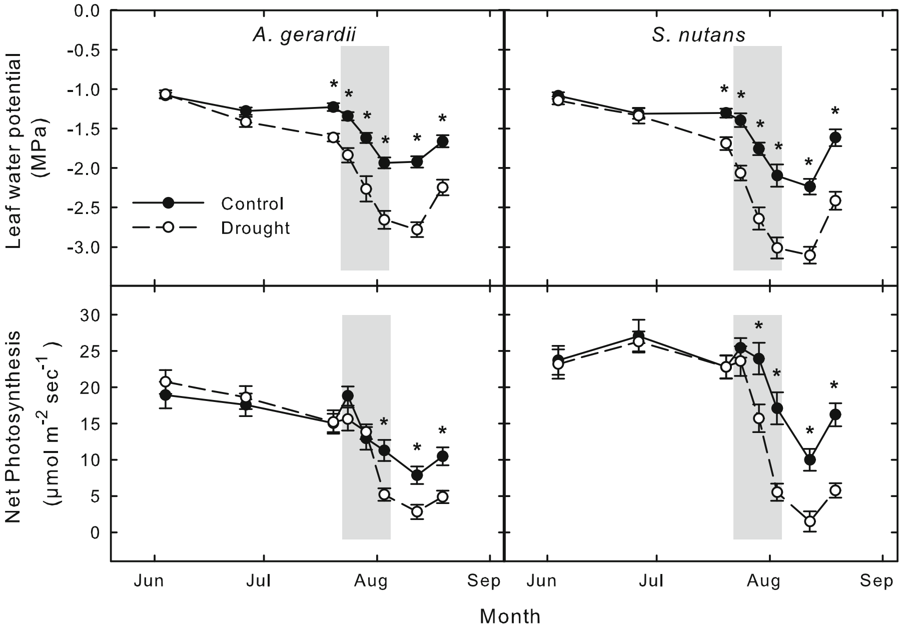

Fig. 3 Responses of mid-day leaf water potential (Ψ_{mid}) and net photosynthesis (A_{net}) for *A. gerardii* and *S. nutans* to the drought treatment over the growing season. The *gray box* highlights the 2-week period that the heat wave treatments were applied. *Error bars* indicate one standard error and *asterisks* denote a significant difference ($p \leq 0.05$) between the control and drought treatments for a given date

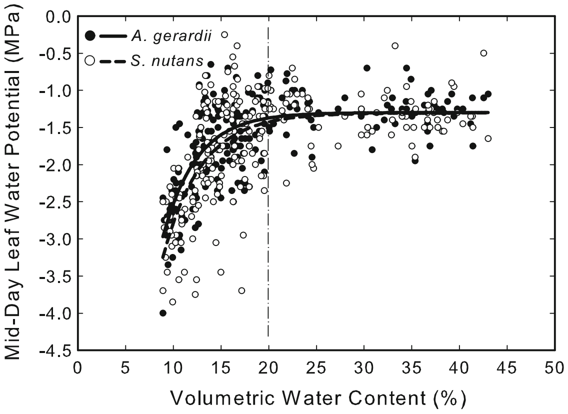

Fig. 4 Volumetric water content (VWC) versus mid-day leaf water potential (Ψ_{mid}) for *A. gerardii* and *S. nutans* for all measurements during the growing season (excluding measurements from within heated chambers). Regression lines for each species based on parameter estimates from PROC NLIN ($F = 186.6$, $p < 0.001$). *Dashed line* at 20 % VWC, below which Ψ_{mid} declines rapidly with decreasing VWC

values were similar to our two precipitation treatments (control = 836.9, drought = 476.6 mm). The simulated heat wave occurred for two weeks in late July, when mean daily temperatures over the 25-year period were 26.4 ± 0.4 °C, and the warmest year (1999) was 29.7 ± 0.6 °C. Mean daily canopy temperature in this study (Fig. 1c), overlapped and exceeded this range in temperature (ambient = 27.2 ± 0.4 °C and high = 36.6 ± 0.3 °C), and the maximum daily canopy temperature (high = 43.1 °C) is virtually identical to the 25-year record high air temperature measured at this site (43.2 °C, 1983). Despite the severity of the imposed heat and water stress, the effects of the drought treatments exceeded those of the heat wave treatments for both species. Significant direct effects of drought on physiology (Ψ_{mid} and A_{net}, both species) and productivity (ANPP, *S. nutans* only) were evident, while there were only minor physiological responses to the two-week heat wave treatments (Ψ_{mid}, both species). These results suggest that under the range of drought and heat wave treatments imposed in this experiment, the impacts of water stress on the dominant C_4 grasses were greater than heat stress.

Contrary to our hypothesis, the two-week heat wave had no additive effects when combined with drought, regardless of the intensity of the heat wave treatments. When we examined the effects of the heat wave and drought treatments on the last day of the 2-week heat

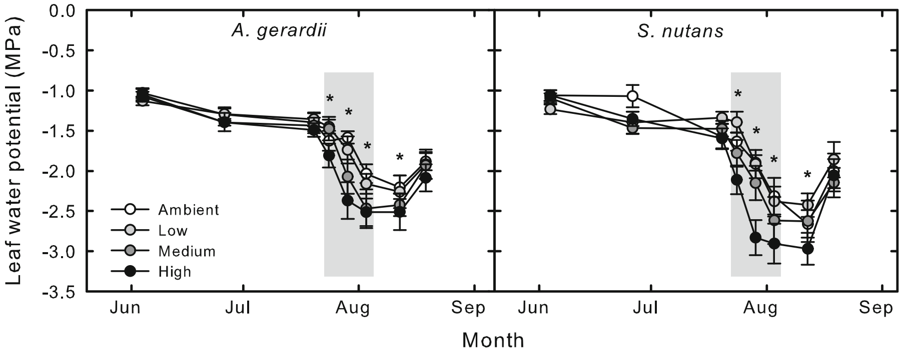

Fig. 5 Effects of the heat wave treatments on mid-day leaf water potential (Ψ_{mid}) for *A. gerardii* and *S. nutans*. The *gray box* highlights the 2-week period that the heat wave treatments were applied. *Error bars* indicate one standard error and *asterisks* denote a significant difference ($p \leq 0.05$) between the heat wave treatments for a given date

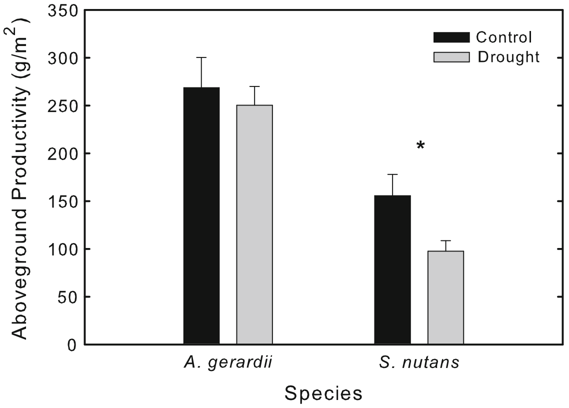

Fig. 6 Drought effects on aboveground production for *A. gerardii* and *S. nutans*. *Error bars* indicate one standard error and *asterisks* denote a significant difference ($p \leq 0.05$) between the control and drought treatments for a given species

Table 3 Effects of the drought and heat wave treatments on aboveground productivity for each species separately

Effect	*Andropogon gerardii*			*Sorghastrum nutans*		
	df	*F*	*p*	df	*F*	*p*
Drought	1, 1.9	0.1	0.747	1, 32	**4.9**	**0.034**
Heat	1, 30.5	0.1	0.989	1, 32	0.3	0.840
Drought × heat	1, 30.5	0.4	0.753	1, 32	0.8	0.516

Degrees of freedom (df) for numerator and denominator (estimated using Satterthwaite's method), *F* statistics and *p* values from mixed-model repeated measures ANOVAs are reported. Bold text indicates significance at $p \leq 0.05$

wave period, significant interactions were detected for A_{net} in both species, however, these interactions were opposite to our expectations; the heat wave effects were only observed in the control rainfall treatment (Fig. 2a, b). A_{net} did not differ with the heat wave treatments when combined with drought for either species nor did we observe an additive effect on aboveground productivity. This lack of response was surprising, given that in a similar study, De Boeck et al. (2010b) reported additive effects of drought and heat waves. Instead, it appears in this ecosystem, that the high degree of water stress imposed by the drought treatment negated any additional effects of the heat wave treatments.

What remains unclear is whether the heat wave effects on A_{net} in the control treatment were direct or if they occurred indirectly through water stress as noted in several experimental and observational studies (Milbau et al. 2005; Marchand et al. 2006; Reichstein et al. 2007; De Boeck et al. 2010b; Arnone et al. 2011). The direct effects of heat could have led to thermal damage to the photosynthetic machinery. If there had been significant thermal damage to the photosynthetic capacity of these grasses, we would have expected differences in A_{net} among the heat wave treatments to persist after the treatments ended, as well as a negative response in end of season productivity; neither of these occurred. Also, thermal damage may have been avoided since the maximum temperature imposed in this experiment was within the measured range of thermal tolerance for *A. gerardii* (Knapp 1985). However, we cannot rule out the potential direct effects increasing temperature on metabolic processes, such as respiration, which could decrease A_{net} if respiration and assimilation had different responses to temperature (positive for respiration, neutral or negative for assimilation). Additionally, there are several lines of evidence to suggest that the heat wave treatments indirectly affected A_{net} via water stress. First, there were significant differences in VWC among the heat wave treatments with control precipitation; these differences became more pronounced as the heat wave progressed. This would be expected during a naturally occurring heat wave, which typically co-occur with low precipitation (Trenberth and Shea 2005; De Boeck et al. 2010a), which when combined with high evapotranspiration rates due to heat, decreases VWC. For these grasses, we saw evidence for water stress emerging once VWC drops below ~20 %, where Ψ_{mid} declines rapidly (Fig. 4). By the last day of the heat wave, several of the heat treatments in the control had dropped below this VWC (Fig. 2c), and we observed direct effects of heat on Ψ_{mid} for both species throughout the heat wave, suggesting that heat may have reduced plant water status indirectly through enhanced vapor pressure deficits, decreased VWC or both. Overall, these results show that under the control precipitation, the heat wave treatments imposed both heat and water stress, and thus we could not separate the interactive effects of heat and attribute the decline in photosynthesis to a single driver. In order to separate the direct and indirect effects of heat, water would have to be added to keep soil moisture above limiting levels (for example, greater than 20 % VWC in this ecosystem).

While there was no evidence for differential sensitivity to heat between the two dominant grasses, we did observe different responses to drought. Greater sensitivity to drought in *S. nutans* relative to *A. gerardii* is consistent with past studies (Weaver and Fitzpatrick 1932; Brown 1993; Silletti and Knapp 2002; Swemmer et al. 2006; Nippert et al. 2009). However, none of these studies imposed drought at this magnitude under controlled experimental conditions. *S. nutans* responded earlier to the drought and with greater absolute and relative decreases in A_{net} than *A. gerardii*. Consistent with this response was a significant decrease in aboveground productivity for *S. nutans*, while *A. gerardii* did not respond to drought. These divergent responses occurred despite similar responses in Ψ_{mid}. This suggests greater resistance to drought in *A. gerardii* than *S. nutans* and that a drought of greater magnitude may be required before a loss of productivity occurs in *A. gerardii*. Indeed, earlier experiments found significant reductions in aboveground productivity in response to drought for *A. gerardii*, but at almost twice as negative relative to Ψ_{mid} measured in this study (Knapp 1984). The reduction in aboveground productivity in *S. nutans* but not *A. gerardii* could have important implications for plant community structure by increasing the competitive advantage of *A. gerardii* in this grassland.

Conclusions

Understanding the responses of dominant species to climate extremes is essential to predicting future grassland dynamics and is particularly important if these species differ in their sensitivities to the climate drivers. In this study, we examined the individual and combined effects of heat waves and drought on two dominant C_4 grasses in a tallgrass prairie ecosystem. There were two main conclusions from this research. First, drought effects dominated the photosynthetic and productivity responses of these grass species, rather than direct or additive effects of heat waves. Second, differential sensitivity to drought between the two dominant C_4 grasses was apparent, with greater reductions in photosynthesis and productivity for *S. nutans* than *A. gerardii*. In a future with more frequent heat wave and drought, water stress will likely dominate photosynthetic and productivity responses in these grasses, rather than direct or additive effects of heat stress, with differential sensitivity likely affecting both ecosystem structure and function.

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