

Resistance and resilience of a grassland ecosystem to climate extremes

DAVID L. HOOVER,¹ ALAN K. KNAPP, AND MELINDA D. SMITH

Graduate Degree Program in Ecology and Department of Biology, 1878 Campus Delivery, Colorado State University,
Fort Collins, Colorado 80523 USA

Abstract. Climate change forecasts of more frequent climate extremes suggest that such events will become increasingly important drivers of future ecosystem dynamics and function. Because the rarity and unpredictability of naturally occurring climate extremes limits assessment of their ecological impacts, we experimentally imposed extreme drought and a mid-summer heat wave over two years in a central U.S. grassland. While the ecosystem was resistant to heat waves, it was not resistant to extreme drought, which reduced aboveground net primary productivity (ANPP) below the lowest level measured in this grassland in almost 30 years. This extreme reduction in ecosystem function was a consequence of reduced productivity of both C₄ grasses and C₃ forbs. However, the dominant forb was negatively impacted by the drought more than the dominant grass, and this led to a reordering of species abundances within the plant community. Although this change in community composition persisted post-drought, ANPP recovered completely the year after drought due to rapid demographic responses by the dominant grass, compensating for loss of the dominant forb. Overall, these results show that an extreme reduction in ecosystem function attributable to climate extremes (e.g., low resistance) does not preclude rapid ecosystem recovery. Given that dominance by a few species is characteristic of most ecosystems, knowledge of the traits of these species and their responses to climate extremes will be key for predicting future ecosystem dynamics and function.

Key words: aboveground productivity; climate extremes; community reordering; demographic compensation; dominant species; functional groups.

INTRODUCTION

Global change threatens ecosystems worldwide through chronic alterations in climate (temperature and precipitation) and resources (increasing atmospheric CO₂ and nitrogen deposition), as well as by increasing the frequency and intensity of climate extremes, such as drought, floods, and heat waves (Easterling et al. 2000, Smith et al. 2009, IPCC 2012). Despite prominent examples of the severe impacts of climate extremes (e.g., the central U.S. Dust Bowl of the 1930s, the 2003 European heat wave, and the 2012 U.S. drought [Weaver 1954, Ciais et al. 2005, Lal et al. 2012]), global change research has been dominated by the study of chronic environmental changes rather than discrete climate extremes (Jentsch et al. 2007, Smith 2011). Indeed, assessing the ecological consequences of climate extremes, as well as the mechanisms determining ecosystem response and recovery, remains a key challenge for ecologists today (Smith 2011).

Ecological responses to climate extremes are highly variable (Smith 2011), ranging from minimal ecosystem-

level impacts (Kreyling et al. 2008, Jentsch et al. 2011, Dreesen et al. 2012) to major effects on ecosystem structure and function with prolonged recovery (Weaver 1954, White et al. 2000, Haddad et al. 2002, Breshears et al. 2005, Ciais et al. 2005). Such variability in ecological resistance (capacity to withstand change) and resilience (capacity for recovery of function [Pimm 1984, Tilman and Downing 1994]) may be due to differences in ecosystem attributes, as well as a result of the magnitude, duration, and timing of the climate extreme. Thus, it is critical that both the driver (climate event) and the ecosystem response (ecological effects) are evaluated with respect to their extremity.

Smith (2011) defined an extreme climatic event (ECE) as “an episode or occurrence in which a statistically rare or unusual climatic period alters ecosystem structure and/or function well outside the bounds of what is considered typical or normal variability.” Determining if an ECE has occurred, therefore, requires both long-term climatic and ecological data, with the former available more often than the latter. In addition, Smith (2011) provided a mechanistic framework for assessing ecological responses to climate extremes. In brief, this framework depicts how impacts of climate extremes at the species level have the potential to have large impacts on ecosystem function, depending on the role and abundance of the species impacted. For example, a

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¹ E-mail: David.Hoover@Colostate.edu

period of climatic extremity that results in mortality or significant loss in fitness of dominant species (i.e., crossing of an ecological response threshold) may lead to community-level responses that include species re-ordering and compositional changes. Such alterations in community composition are predicted to have the greatest impact on ecosystem function, leading to an extreme ecological response (Smith 2011).

Much of our current understanding of the ecological effects of climate extremes is based on opportunistic studies of naturally occurring events (Weaver 1954, Breshears et al. 2005, Reichstein et al. 2007, Lal et al. 2012), with attendant difficulties in the attribution of specific climate drivers to ecosystem response and recovery (Déry and Wood 2005, De Boeck et al. 2010, Smith 2011). Experimental approaches are better suited to study climate extremes because climate drivers can be directly attributed to ecological responses (Reyer et al. 2013). Indeed, manipulative experiments explicitly linked to historical climatic records and interpreted in the context of long-term ecological data provide the best opportunity to advance our understanding of climate extremes (Smith 2011, Reyher et al. 2013). Finally, a range of biotic responses across several hierarchical levels must be measured during the event and the subsequent recovery period in order to identify the mechanisms governing ecosystem resistance and resilience and the potential for ECEs.

Here we directly test the ECE framework in a central U.S. grassland where we imposed extreme drought and a two-week heat wave in a fully factorial experiment over two years, and monitored subsequent recovery one year post-drought. In 2010 and 2011, we imposed a drought treatment by passively reducing growing season precipitation by 66% using rainout shelters, while control treatments received ambient rainfall plus supplemental irrigation to alleviate water stress. Nested within the drought and control treatments, we imposed a two-week heat wave mid-summer with four levels of infrared radiation inputs. Heat waves and drought typically co-occur in nature, thus our experimental design allowed us to examine the independent and interactive effects of extreme drought and heat on ecosystem structure and function during the two-year extreme period and for one-year post-drought.

Our objectives were to test whether an ECE was imposed by placing the drought and heat wave treatments and the ecosystem response observed within the long-term record and assess proposed mechanisms underpinning ecosystem response (resistance) and recovery (resilience) to extreme drought and heat, and thus explicitly link alterations in ecosystem function and plant community composition to the imposed extremes. We hypothesized that (1) ecosystem function (above-ground net primary production, ANPP) would be less resistant to drought and heat waves combined than either factor alone, with the independent effects of drought greater than heat; (2) the response of dominant

species would govern the extremity of the ecological responses, with the expectation that if the dominant species were negatively impacted then large ecosystem responses would be observed; and (3) recovery from an ECE would be prolonged if community composition and diversity were substantially altered by these climate extremes.

METHODS

Study site.—This study was conducted at the Konza Prairie Biological Station, a 3487-ha native tallgrass prairie in northeastern Kansas, USA (39°05' N, 96°35' W). The region is characterized as a temperate mid-continental climate, with average annual precipitation of 835 mm and mean July air temperature of 27°C (Knapp et al. 1998). In 2010, we established the Climate Extremes Experiment in an intact, native Kansas grassland, with deep (>1 m) silty clay loam soils, which was burned annually (as is typical for this region; see Fay et al. [2000] for more site details). This site is a good representative for the tallgrass prairie region because it is dominated by the two most abundant plant functional types (PFTs) of this ecosystem; a C₄ perennial, rhizomatous grass, *Andropogon gerardii*, which dominates much of the historic range of tallgrass prairie (Brown 1993) and a C₃ perennial, clonal forb, *Solidago canadensis*, which is the locally most abundant species (unlike the grasses, no single forb species dominates throughout this ecosystem).

Treatments.—During the 2010 and 2011 growing seasons (1 April–30 August), we imposed the drought and control (ambient precipitation) treatments using four passive rainout shelters (based on a design by Yahdjian and Sala [2002]) established over native grassland communities (Fig. 1a; also see Appendix A for plot layout). Across the central U.S. grassland region, the majority of annual precipitation occurs during the growing season and extended drought periods often occur during this time, and thus a reduction in rainfall during this period is highly relevant (Knapp et al. 1998). For the drought treatment, we reduced each growing season rainfall event by ~66% using two 6 × 24 m cold frame greenhouse structures (Stuppy, Kansas City, Missouri, USA) partially covered (75%; Fig. 1a) with strips of Dynaglas Plus clear polycarbonate plastic (PALRAM Industries, Kutztown, Pennsylvania, USA). For the control (ambient precipitation) treatment, two shelters were covered with deer netting (TENAX Manufacturing, Evergreen, Alabama, USA) to reduce photosynthetically active radiation by about 10% (equivalent to light reduction in drought shelters), but allow all ambient rainfall to pass through (Fig. 1a). Our goal was to have non-limiting soil moisture levels in control plots to contrast with low soil moisture in the drought plots, which necessitated adding supplemental water during extended dry periods to the control treatments. This was not required in 2010, but in 2011, control treatments received supplemental irriga-

tion (~12.7-mm event) when soil moisture dropped below a critical threshold for plant water stress (~20% volumetric water content of the top 15 cm). The soil within the 6 × 24 m footprint of each shelter was hydrologically isolated by trenching to a depth of 1 m, lining it with two layers of 6 mil (0.006 inches, 0.015 cm) plastic belowground, and placing metal flashing around the perimeter aboveground to prevent surface and subsurface water flow into the plots.

Nested within each rainout shelter, we established 10 2 × 2 m plots that were randomly assigned to one of four heat-wave treatments (ambient, low, medium, and high). Heat was added for two weeks in mid-summer (21 July to 3 August 2010, 13 July to 26 July 2011) using infrared heat lamps within passive warming chambers (Fig. 1a). The 2 × 2 m passive warming chambers were constructed of PVC frames, with 1 m high walls covered with 6-mil transparent polyethylene and clear corrugated polycarbonate roofs (Dynaglas Plus). These chambers were designed to minimize convective cooling. Ventilation was maintained by placing chambers 0.5 m above the ground surface with an adjustable gap between the roof and sidewalls to decrease or increase airflow if needed. Four heat input levels were imposed with 2000-W infrared heat lamps (HS/MRM 2420; Kalglo Electronics, Bethlehem, Pennsylvania, USA) as follows: control, no lamp; low heat, one lamp at one-half power (+250 W/m² output); medium heat, one lamp at full power (+500 W/m²); and high heat, two lamps at full power (+1000 W/m²).

In the recovery year (2012), no drought or heat wave treatments were imposed and all plots received ambient rainfall plus supplemental irrigation. All plots were watered weekly by hand if rainfall totals during that week were less than long-term averages (in which case the deficit was added). This allowed us to maintain precipitation inputs near the long-term monthly mean totals.

Abiotic data.—Daily precipitation data were obtained from a nearby (~250 m) U.S. Climate Reference Network station (KS Manhattan 6 SSW; data *available online*)² and combined with supplemental irrigation and excluded rainfall amounts to calculate precipitation treatment totals each year of the study (Appendix B: Table B1). Soil moisture and canopy temperature were continuously monitored in each plot to evaluate the effectiveness of drought and heat-wave treatments. Soil moisture was measured in the center of each plot at a depth of 0–15 cm with 30-cm time-domain reflectometry probes (Model CS616, Campbell Scientific, Logan, Utah, USA) inserted at a 45° angle. Canopy temperature was measured using infrared thermometers (Model SI-111, Apogee Instruments, Logan, Utah, USA) mounted in the southeast corner of each plot at a height of 1.5 m.

Data from both sensors were recorded every 30 minutes on a CR10X Datalogger (Campbell Scientific).

Biotic data.—ANPP was estimated at the end of each growing season (first week in September) by harvesting all aboveground plant material in three 0.1-m² quadrats located within each 4-m² plot. Harvesting at this time of year has been shown to capture peak biomass, and since the site was annually burned (i.e., no previous years' dead material), this provides a reliable estimate of ANPP (Knapp et al. 2007). For each year, the locations of quadrats were different to prevent resampling of the same quadrat. Samples were field sorted by growth form, oven dried at 60°C for 48 hours, and then weighed to the nearest 0.1 g. Community composition was assessed twice each year (early June, late August) in one permanent 1-m² subplot per 4-m² plot by visually estimating percentage aerial cover for each species separately. Maximum cover values of each species were used to determine relative cover of each species and to calculate species richness, Shannon's diversity (*H'*), and evenness. In 2012, individual stems (tillers) were censused within a 0.1-m² quadrat located within each plot to estimate stem density (stems/m²).

Long-term data.—Long-term (1900–2012) precipitation and air temperature data for Manhattan, Kansas (~10 km from the experimental site at the Konza Prairie Biological Station, KPBS) were obtained from the National Climate Data Center's Global Historical Climatology Network (data set USC00144972 *available online*).³ These data were used to calculate mean growing season precipitation and temperatures and to estimate their probability density functions (pdfs). Long-term (27-year) aboveground net primary production (ANPP) data from a site comparable to our study system (annually burned lowland) were obtained from the Konza Prairie Biological Station (data set PAB01 *available online*).⁴ These data were used to calculate mean annual ANPP and to estimate ANPP pdf.

Statistical analyses.—Precipitation totals and ANPP means for the control and drought treatments were compared to estimated pdfs of long-term growing season precipitation and ANPP for the site. Values were considered extreme if they exceeded the 5th percentiles of the pdfs. The experiment was a randomized block split-plot design, and we analyzed ANPP and community responses across all three years of the experiment (drought and recovery) using a repeated-measure mixed-model ANOVA with the heat wave treatments (random effect) nested within the drought treatments and year as a repeated effect (all mixed models analyses were conducted using SAS 9.3 [SAS Institute, Cary, North Carolina, USA]). For ANPP, significant interactions between treatments and years (*P* < 0.05) were further examined using the SAS lsmeans procedure to test pairwise comparisons. Community data was also

² <https://www.ncdc.noaa.gov/crn/observations.htm>

³ www.ncdc.noaa.gov/oa/climate/ghcn-daily/index.php

⁴ <http://www.konza.ksu.edu/knz/pages/data/knzdata.aspx>

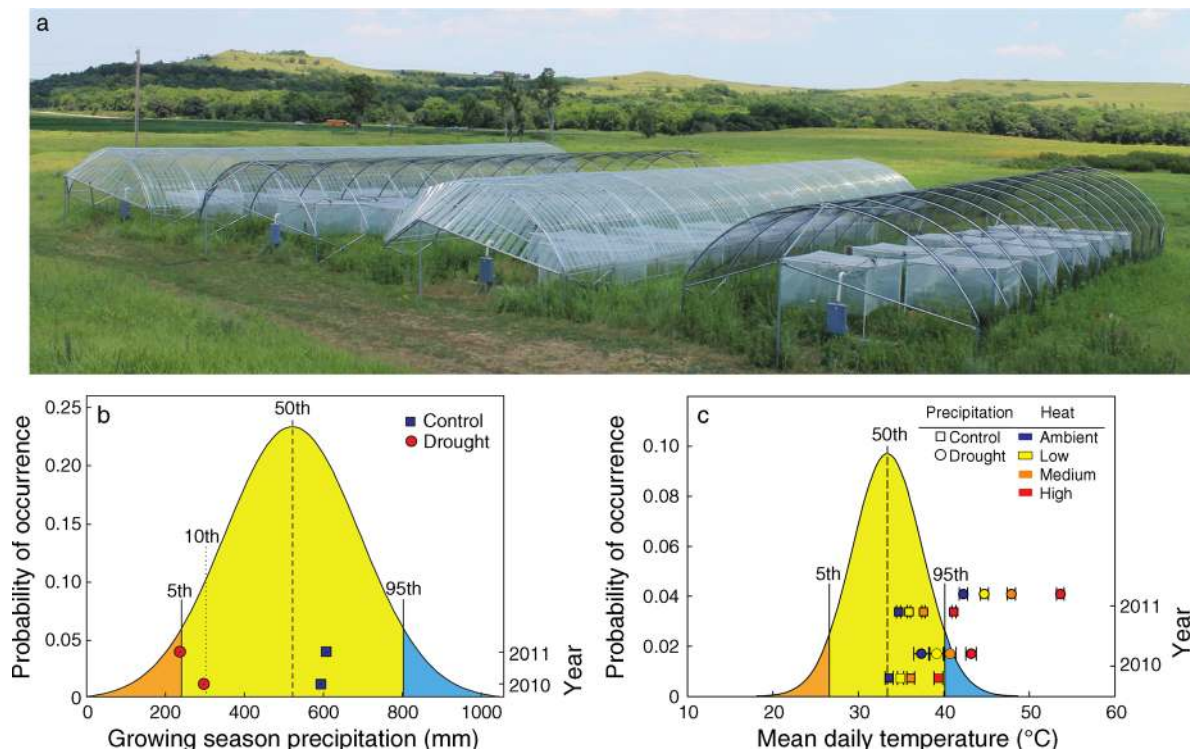


FIG. 1. The Climate Extremes Experiment established in 2010 in a central U.S. grassland. (a) During the 2010 and 2011 growing seasons, four large shelters were used to impose two treatments: drought (partial roofs on shelters reduced ambient rainfall by 66%) or ambient (control) rainfall inputs (no roofs on shelters). Nested within the rainfall shelters, heat wave treatments were imposed using passive heat chambers combined with infrared lamps during two-weeks mid-summer. (b) The drought treatment resulted in severe drought in 2010 (exceeding the 10th percentile, dotted line) and extreme drought in 2011 (exceeding 5th percentile, solid line) based on an estimated probability function calculated from 112 years of growing season precipitation for the study site. In contrast, growing-season precipitation was slightly above average in both years (50th percentile, dashed line) for the control treatments. (c) Maximum daily canopy temperatures (mean \pm SE) resulting from the four heat treatments during the two-week heat wave in under control in drought conditions compared to 112 years of maximum daily air temperature. Canopy temperatures ranged from near average (50th percentile, dashed line) to extreme (well beyond the 95th percentile, solid line).

analyzed using nonmetric multidimensional scaling (NMDS) followed by analysis of similarity (ANOSIM) using relative abundance data for each year to assess community-level divergence between treatments (divergence criteria was determined at $P < 0.05$; Primer v6; Primer-E, Plymouth, UK). To assess how much each individual species contributed to the treatment divergence in each year, we calculated similarity percentages using SIMPER analysis based on a Euclidian distance matrix for each year separately. In addition, 2012 stem densities were analyzed with a mixed-model ANOVA with the heat wave treatments nested within the drought treatments.

RESULTS

Historical context of precipitation and heat treatments.—Within the context of a 112-year climate record for this location, the magnitude of the precipitation and temperature treatments ranged from near average to extreme during the first two years of the experiment (Fig. 1b, c). Growing season precipitation inputs were

reduced in 2010 and 2011 below the 10th and 5th percentiles of historic amounts, respectively (Fig. 1b). These amounts contrasted sharply with the slightly above average rainfall inputs to control plots during these years (Fig. 1b; Appendix B: Table B1). The cumulative two-year period of growing season precipitation input to the drought plots was 533.4 mm, or 28.0 mm less than the driest consecutive two-year period (1933–1934) during the historic 1930s Dust Bowl drought. The drought treatment reduced mean growing season soil moisture by 43% and 56% in 2010 and 2011, respectively (Appendix B: Fig. B1). The two-week heat wave imposed a gradient in maximum canopy temperatures that ranged from average (near the 50th percentile) to extreme (well beyond the 95th percentile) based on long-term means of air temperature (Fig. 1c). Although control and drought plots received the same thermal inputs within a given treatment and across both years, canopy temperatures were much higher in drought than the control plots (Fig. 1c) due to

TABLE 1. Analysis of variance (ANOVA) for three components of aboveground net primary productivity (ANPP) across all three years of the experiment.

Effect	Total			Grasses			Forbs		
	df	F	P	df	F	P	df	F	P
Drought	1, 2.0	15.6	0.060	1, 2.0	0.1	0.828	1, 1.9	24.0	0.043
Heat	3, 5.7	0.9	0.511	3, 5.7	0.2	0.924	3, 29.8	0.3	0.816
Drought × Heat	3, 5.7	1.0	0.475	3, 5.7	0.1	0.960	3, 29.8	0.3	0.851
Year	2, 60.0	74.0	<0.001	2, 57.8	88.3	<0.001	2, 60.5	15.7	<0.001
Drought × Year	2, 60.0	33.1	<0.001	2, 57.8	38.6	<0.001	2, 60.5	11.0	<0.001
Heat × Year	6, 60.0	0.4	0.883	6, 57.8	0.3	0.949	2, 60.5	0.6	0.727
Drought × Heat × Year	6, 60.0	2.2	0.055	6, 57.8	2.0	0.080	2, 60.5	0.9	0.489

interactions between the precipitation and heat treatments.

ANPP and plant community responses.—Despite the extremity of the heat waves imposed, the drought treatment dominated all ecological responses. Across all ANPP and plant community metrics, there were no significant effects of the heat treatments or interactions with the drought treatment during either the drought or recovery periods (Tables 1 and 2). There was a marginally significant three-way interaction between drought, heat and year ($P = 0.055$), however this was a disorderly interaction, with no apparent trends in heat effects over time or with respect to the drought treatment. On the other hand, there were clear effects of drought, with significant drought × year interactions for ANPP (total, grass, and forbs) and community metrics (evenness and H' ; Tables 1 and 2). Because there were no significant direct or interactive effects of even the highest heat wave treatment on ANPP or plant community composition, we focus hereafter on plant community and ecosystem responses to the drought treatment.

Total ANPP was reduced by 20% in the first year of drought and by ~60% during the second year (Fig. 2a). The large reduction in total ANPP during the second year was driven by reductions in ANPP for both grass (–45%) and forb (–76%) plant functional types (Fig. 2a). To assess whether the total ANPP response to drought was statistically extreme, we compared our results with long-term (27-year) ANPP data. After two consecutive years of drought, total ANPP was well below the 5th percentile of the statistical distribution of

ANPP for the study site (Fig. 2b). Further, when placed in the context of the long-term functional relationship between growing season precipitation and ANPP, both the growing season precipitation and ecological response were statistically extreme in 2011 (i.e., both below 5th percentile, Fig. 2c).

While we detected no overall effects of extreme drought on plant species richness, there were significant effects of drought over time for evenness and H' (Table 2). In addition, community composition was altered substantially in the second year of the drought (Appendix C: Fig. C1). Community divergence between control and drought treatments was driven by shifts in dominant species abundances (Fig. 3a and b; Appendix C). Large reductions in the abundance of *S. canadensis* during the second year of the drought was the primary reason for this divergence (Appendix C: Table C2).

Recovery from drought.—After the two-year drought, all plots received growing season rainfall inputs similar to the long-term average, permitting us to assess the initial extent of ecosystem recovery and quantify drought legacy effects. We observed complete recovery in ecosystem function (total ANPP, Fig. 3c) just one year post-drought. Although forb ANPP continued to be dramatically reduced (by 80%) post-drought due to reduced stem densities and abundance of the formerly dominant *S. canadensis* (Fig. 3a, b, c), there was a concurrent 46% increase in grass ANPP (Fig. 3c). This compensation by the grasses was accompanied by a 60% increase in tiller density (Fig. 3d) and an increase in relative abundance of *A. gerardii* (Fig. 3a and b insets).

TABLE 2. ANOVA for three common metrics of community structure across all three years of the experiment.

Effect	Richness			Evenness			H'		
	df	F	P	df	F	P	df	F	P
Drought	1, 33.6	1.4	0.250	1, 2.0	0.1	0.797	1, 2.0	0.0	0.892
Heat	3, 33.6	0.7	0.548	3, 33.1	2.7	0.063	3, 30.5	0.5	0.671
Drought × Heat	3, 33.6	1.7	0.187	3, 33.1	1.6	0.214	3, 30.5	1.5	0.233
Year	2, 63.2	5.9	0.004	2, 63.7	3.8	0.029	2, 62.5	1.8	0.177
Drought × Year	2, 63.2	1.5	0.235	2, 63.7	12.0	<.0001	2, 62.5	4.8	0.012
Heat × Year	6, 63.2	0.9	0.500	6, 63.7	0.7	0.622	6, 62.5	1.7	0.147
Drought × Heat × Year	6, 63.2	1.4	0.229	6, 63.7	0.6	0.744	6, 62.5	0.9	0.528

Note: H' is Shannon's diversity index.

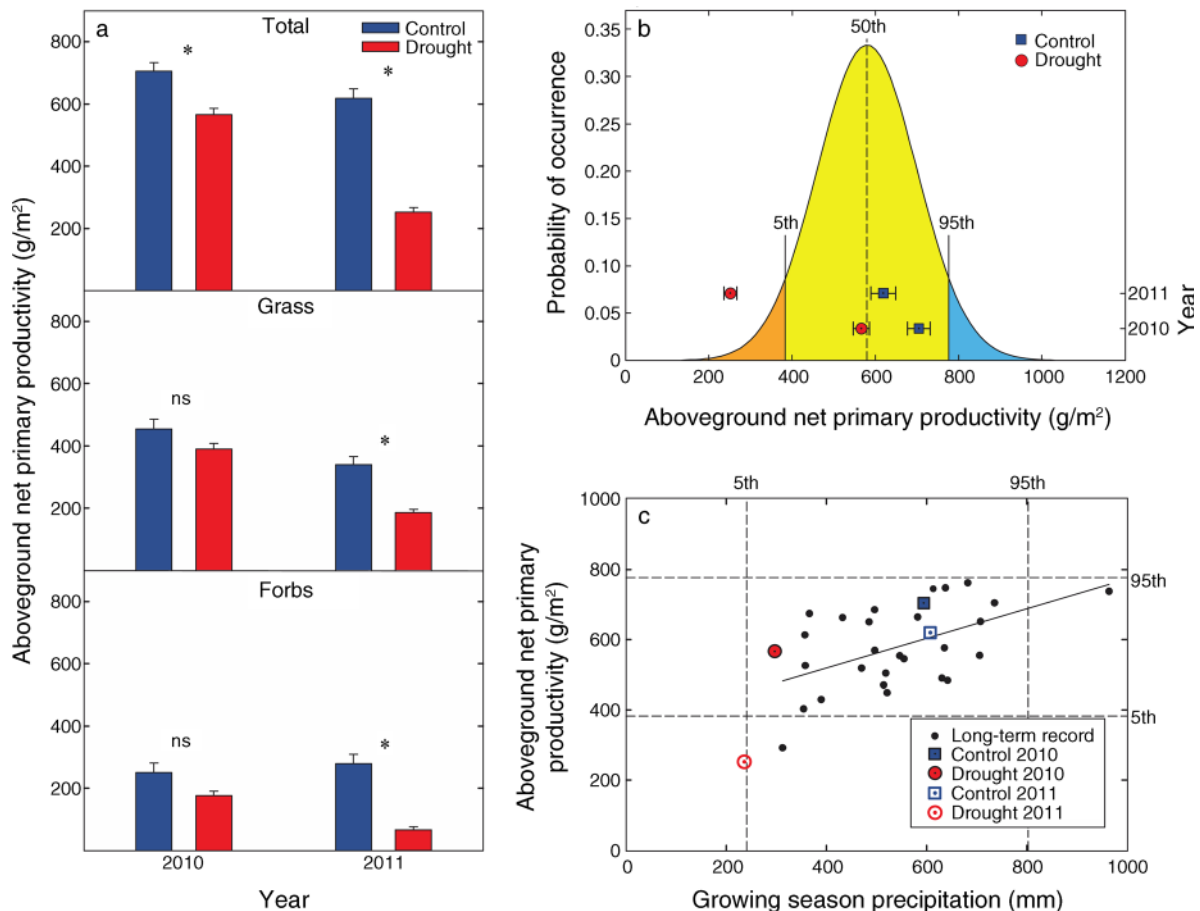


FIG. 2. Response of aboveground net primary productivity (ANPP) to one (2010) and two years (2011) of experimentally imposed growing season drought in a central U.S. grassland. (a) Total, grass, and forb ANPP during drought years. Bars are means \pm SE. Asterisks denote significant treatment differences ($P < 0.05$) for each year (ns stands for nonsignificant differences). (b) After two years of growing season drought, reductions in total ANPP exceeded the 5th percentile based on an estimated probability function for 27 years of ANPP measurements for the study site. (c) Relationship between growing season precipitation and ANPP ($r^2 = 0.27$, $P = 0.005$) over a 27-year period at the study site (long-term data sets from Figs. 1a and 2b). Total ANPP for control and drought treatments in both years are overlaid on this relationship. Based on this relationship, the second year of drought was considered an extreme climatic event, i.e., both precipitation and ANPP were statistically extreme (dashed lines show 5th and 95th percentiles for each variable).

DISCUSSION

In this study, we exposed a native tallgrass prairie ecosystem to extreme drought and a two-week heat wave for two years, and then evaluated short-term recovery. Our objectives were to determine if an ECE occurred in response to the treatments based on long-term climate and productivity records for the site, and then to assess mechanisms underpinning ecosystem resistance and resilience. We imposed drought and heat treatments that were statistically extreme, based on over a century of climate records for this location. Drought effects dominated community and ecosystem responses, with no effect of the heat treatments on ANPP or the plant community, nor any interactive effects with drought, despite the magnitude of the heat treatments and the resultant high canopy temperatures. The ecosystem

response to the imposed drought was extreme during 2011, with total ANPP reduced well below the 5th percentile of the historical distribution of ANPP values for this site. Thus, our experimental approach allowed us to explicitly attribute an extreme ecological response to an imposed climate extreme, meeting the definition of an ECE (Smith 2011). However, despite this extreme response, we observed complete recovery in ecosystem function (total ANPP) one-year post drought due to a rapid demographic response by the dominant *C₄* grass, *A. gerardii*, compensating for the loss of the dominant *C₃* forb, *S. canadensis*. Collectively, these results suggest that this ecosystem differs in its resistance to two types of extremes—showing little response to mid-summer heat waves but an extreme response to a two-year season-long drought. Yet, despite low resistance to drought, this ecosystem exhibited high resilience, with

the dominant species governing the resistance and resilience of this ecosystem.

Resistance.—While both the drought and heat wave treatments were statistically extreme from a climatological perspective, only drought significantly impacted ANPP and plant community composition. Thus, contrary to our expectations there were no interactive or additive effects of heat and drought on ANPP and the plant community, despite evidence for these interactive effects from other studies (De Boeck et al. 2011). As previously mentioned, little to no ecological responses to a climate extreme may be due to the ecosystem's resistance to the magnitude, duration or timing of the climate driver. Given that canopy temperatures exceeded the 95th percentile for past air temperatures in both precipitation treatments, the resistance to the simulated heat waves was not likely a result of too low of magnitude of IR input. In addition, while the timing of the heat wave coincided with the purported greatest sensitivity to heat for this ecosystem (Craine et al. 2012), it was also near the time of peak production (Knapp et al. 2001), which could have minimized the impact on plant mortality or end of season total ANPP. Thus, it is possible that if the heat wave occurred over a longer period of time, or if the heat wave had occurred earlier in the growing season, we may have observed a greater response to the heat treatments.

We used the ECE framework to assess potential mechanisms by which an extreme climate driver may elicit an extreme ecological response, and we hypothesized that dominant species would govern the extremity of the ecological responses. While total ANPP was reduced in both years of drought relative to the control, there was a three-fold difference in total ANPP reductions between the first and second year of the drought. This difference in the impact of drought on ANPP occurred with only a modest difference in precipitation between years (60.8 mm; Appendix B: Table B1). During the first year of the drought much of the reduction in ANPP was driven by equivalent reductions in both grass and forb production (Fig. 2a), and thus the primary mechanism of response was physiological (reduced growth). Indeed, no shift in community structure (species richness, evenness, or H') or composition was detected in the first year of the drought (Table 1b; Appendix C: Fig. C1). Extremity in ecological responses is predicted to occur when systems cross extreme response thresholds, in which the tolerance of one or more species in a community is exceeded (Smith 2011, Kardol et al. 2012). This would lead to a significant decrease in abundance of a species due to reduced growth, reproduction and/or mortality of individuals, and a subsequent shift in plant community composition (via species reordering). Depending on which species are impacted, effects on ecosystem function could be small if only rare species are affected or large if dominant species are affected (Smith and Knapp 2003, Hillebrand et al. 2008). In the second year of the drought, the extreme reduction

in ANPP was driven by significant reductions in grass and forb biomass, however the dominant forb *S. canadensis* exhibited greater sensitivity than the dominant grass *A. gerardii* to the drought. This resulted in a significant shift in species composition and reordering of species abundances (*A. gerardii* increased in dominance but *S. canadensis* became much less abundant, Fig. 3a and b). It appears that an increase in drought intensity in 2011 and/or the cumulative effects of two consecutive years of drought may have exceeded an extreme response threshold for the dominant C_3 forb. Previous work in this ecosystem has shown that forbs rely on deep soil moisture to avoid water stress during dry periods, while grasses rely mostly on shallow soil moisture, tolerating the dry periods (Nippert and Knapp 2007). It is possible that the cumulative effects of two years of drought and the extremity of drought in 2011, depleted these deeper soil moisture layers, leading to increased mortality of the dominant C_3 forb. Thus a drought avoidance strategy failed for the forb in the second year of the drought, while a drought tolerance strategy allowed persistence of the dominant grass.

In this study, we observed strong resistance to extreme heat waves but not extreme drought. As seen in previous experiments, climate extremes do not always elicit extreme ecological responses (Kreyling et al. 2008, Jentsch et al. 2011, Dreesen et al. 2012). For example, in this same mesic grassland, Knapp et al. (2002) imposed an experimental rainfall regime that was extreme from the perspective of the number and size of rainfall events (but not total rainfall amount), and reported significant but not extreme ecological responses. While we observed no effects of the two-week heat wave on ANPP, other studies suggest that this ecosystem may be sensitive to prolonged warming; tallgrass prairie monoliths exposed to an anomalously warm year ($+4^{\circ}\text{C}$) had 30% reductions in ANPP (Arnold et al. 2008, 2011). However, the authors attributed this decline in production to warming-induced soil drying and thus water availability was likely the growth-limiting factor. Therefore this grassland ecosystem appears to be more sensitive to the direct effects of water stress than heat stress. The low resistance to extreme drought we observed is comparable to some but not all drought studies in grasslands. For example, such rapid losses in ecosystem function with drought have been observed in another mesic tallgrass prairie (a 50-year drought caused a $>45\%$ reduction in ANPP after one year [Tilman and Downing 1994]), while a semiarid grassland was observed having greater resistance to drought (4–7 years of 50% precipitation removal were required before significant reductions in ANPP were measured [Evans et al. 2011]). Such contrasting sensitivities between semiarid and mesic grasslands may be a consequence of climate history and the plant traits of the species that have become dominant in these ecosystems under such regimes.

Resilience.—Contrary to our hypothesis, the altered community composition that occurred in the second year of drought did not preclude rapid recovery in ecosystem

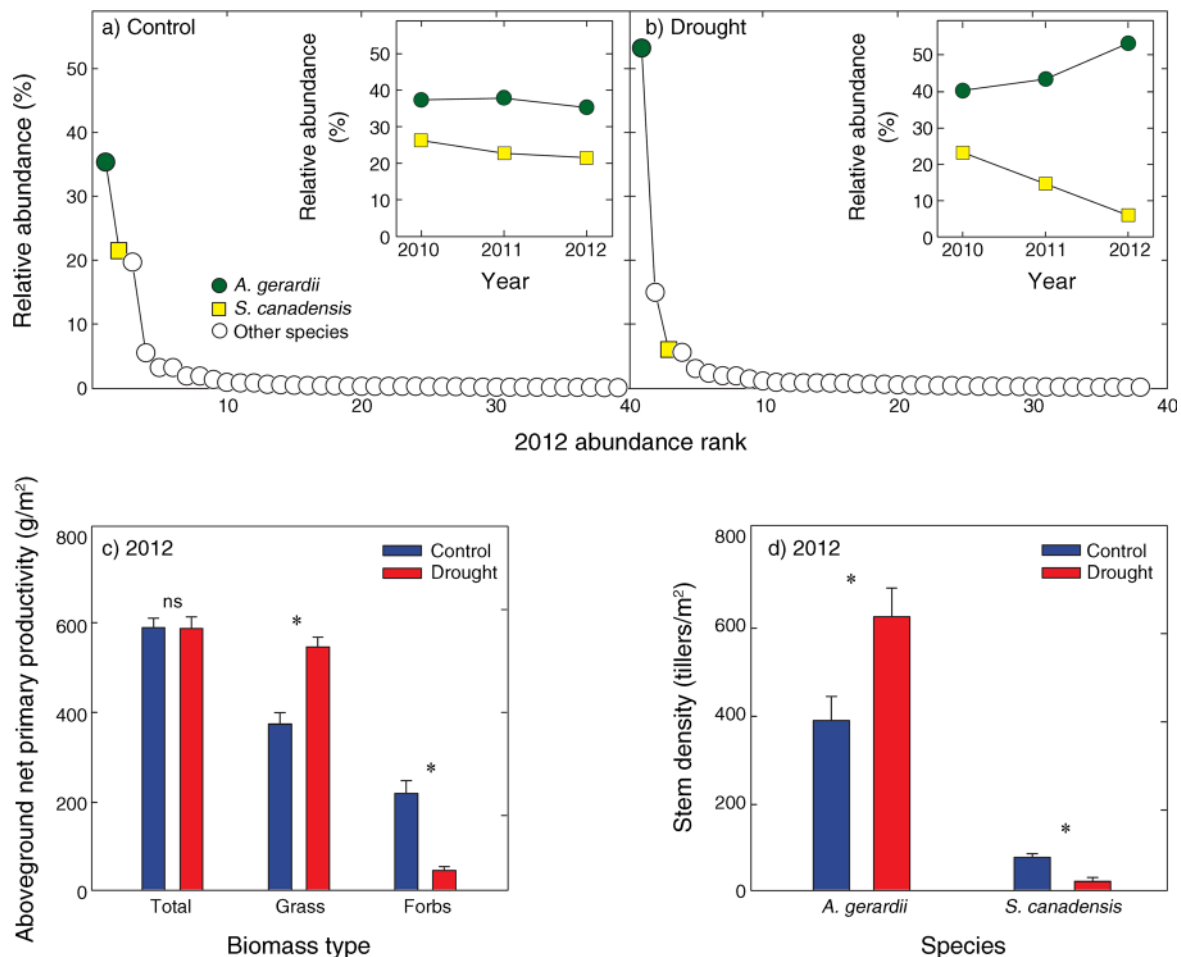


FIG. 3. Recovery from extreme drought in 2012; both control and previously droughted plots received ambient rainfall plus supplemental irrigation to achieve long-term mean precipitation inputs in 2012. Rank abundance curve of all species in (a) control and (b) previously droughted plots one year post-drought (2012). Insets show relative abundance of the dominant C₄ grass (*Andropogon gerardii*) and dominant C₃ forb (*Solidago canadensis*) for control and drought treatments during the two-year drought (2010–2011), and the subsequent recovery year (2012). (c) Response of total, grass, and forb aboveground net primary productivity (ANPP) during the 2012 recovery year. (d) Stem densities of *A. gerardii* and *S. canadensis* during the 2012 recovery year. For panels b and c, bars are means + SE, and asterisks denote significant differences between precipitation treatments ($P \leq 0.05$) for each biomass type or species (ns stands for nonsignificant differences).

function. Instead, the large reduction in the production of *S. canadensis* was completely compensated by increases in *A. gerardii* in just one year following drought (Fig. 3). Loss of dominant species can have prolonged and significant ecosystem effects (Smith and Knapp 2003, Breshears et al. 2005, Sasaki and Lauenroth 2011), however the changes in community composition we observed are consistent with two proposed biotic mechanisms enhancing functional resilience: shifts in the abundance of dominant species and demographic (recruitment) compensation (Hillebrand et al. 2008, Lloret and Escudero 2012). Compensation by *A. gerardii* further increased the divergence in community structure between drought and control plots the year following drought (Appendix C), and this compensation was likely driven rapid demographic recruitment of tillers post-drought (Fig. 3d). In this grassland, greater than 99% of

aboveground shoots are vegetatively produced from belowground buds (Benson and Hartnett 2006), and therefore bud bank demography is an important mechanism behind responses of this grass to environmental stress and disturbance. *A. gerardii* has a large dormant bud bank, consisting of multiple years of cohorts (Ott and Hartnett 2012), and therefore has the capability to respond rapidly post-drought. This post-drought recruitment response of *A. gerardii* was also observed during the years immediately following the historic 1930s Dust Bowl (Weaver 1954). Given this is a region with a history of severe short-term droughts (Woodhouse and Overpeck 1998, Burnette and Stahle 2012), such a demographic response may be key to the dominance of *A. gerardii* and the high resilience of this ecosystem.

The immediate recovery observed in this study exceeded previous reports of resilience in tallgrass

prairie (Tilman and Downing 1994, Haddad et al. 2002, Sherry et al. 2008) and indicates that there were no legacy effects that impacted ANPP (Sala et al. 2012). For example, Haddad et al. (2002) observed prolonged effects (nine years) of a single drought event on production, while we observed full recovery in ANPP in just one year. Our results also contrasts with legacy effects of drought observed by others (Yahdjian and Sala 2006, Sala et al. 2012, Reichmann et al. 2013), whereby drought-induced structural changes in the vegetation reduced production in the subsequent year. Although we observed changes in community structure due to two years of extreme drought, no legacy effects on ANPP occurred because of the demographic response of *A. gerardii*. Without such a compensation mechanism, reductions in ecosystem function may have persisted post-drought. The magnitude of the drought we imposed was comparable to the 1930s Dust Bowl, however the length was shorter (two vs. eight years), which may have also been key to the rapid recovery in function. The long duration of the Dust Bowl resulted in much more dramatic community changes than observed in our study; mesic species were lost and replaced by xeric species, leading to a prolonged, 20-year recovery in community structure (Weaver 1968). Therefore, while this ecosystem was resilient to the short-term drought imposed in this experiment, drought of extended duration would more likely reduce resilience in ecosystem function.

Summary.—We draw three broad insights from our research. First, extremity in a climate driver does not necessarily mean extremity in an ecological response. In our experiment, we observed an ECE associated with drought, while extreme heat had no effect on ecosystem function. Factors such as the intensity, duration and the timing of the extreme event will ultimately determine resistance. Central U.S. grasslands have a long history of both short-term and decadal-scale droughts (Woodhouse and Overpeck 1998, Burnette and Stahle 2012), yet functional resistance was lost after only two years of extreme drought. This emphasizes the need to quantify the timing of loss of function with climate extremes. To date, this has been difficult due to the rarity of naturally occurring extremes and because they must often be studied retrospectively (after loss of function is evident) with limited temporal resolution. Second, low resistance of ecosystem function to climate extremes does not preclude high resilience. Despite the extreme reduction in ANPP after two years of imposed drought, full recovery of this important ecosystem function required only one growing season post-drought. This raises the intriguing possibility that resilience in function, rather than resistance, might be expected for ecosystems with a history of climate extremes. Finally, the presence of a dominant species capable of rapidly recruiting new individuals and restoring function after an extreme climatic event underpinned high ecosystem resilience in this grassland. This compensatory response was primarily

driven by the growth of a single dominant C_4 grass, *A. gerardii*, which is an important species for the resilience in this ecosystem (Weaver 1954, Sherry and Arnone 2012). Given that most ecosystems are dominated by a few species (Whittaker 1965), knowledge of the traits that influence dominant species responses to and recovery from climate extremes will be key for predicting ecosystem dynamics and function in a future with more extreme events.

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SUPPLEMENTAL MATERIAL

Appendix A

The Climate Extremes Experiment (CEE) ([Ecological Archives E095-230-A1](#)).

Appendix B

The amount of growing season precipitation inputs and mean soil water content for the drought and control treatments ([Ecological Archives E095-230-A2](#)).

Appendix C

Shift in community composition with drought (2010–2011) and during the one-year recovery period (2012) ([Ecological Archives E095-230-A3](#)).