Not all droughts are created equal: the impacts of interannual drought pattern and magnitude on grassland carbon cycling

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Abstract

Climate extremes, such as drought, may have immediate and potentially prolonged effects on carbon cycling. Grasslands store approximately one-third of all terrestrial carbon and may become carbon sources during droughts. However, the magnitude and duration of drought-induced disruptions to the carbon cycle, as well as the mechanisms responsible, remain poorly understood. Over the next century, global climate models predict an increase in two types of drought: chronic but subtle 'press-droughts', and shorter term but extreme 'pulse-droughts'. Much of our current understanding of the ecological impacts of drought comes from experimental rainfall manipulations. These studies have been highly valuable, but are often short term and rarely quantify carbon feedbacks. To address this knowledge gap, we used the Community Land Model 4.0 to examine the individual and interactive effects of pulse- and press-droughts on carbon cycling in a mesic grassland of the US Great Plains. A series of modeling experiments were imposed by varying drought magnitude (precipitation amount) and interannual pattern (press- vs. pulse-droughts) to examine the effects on carbon storage and cycling at annual to century timescales. We present three main findings. First, a single-year pulse-drought had immediate and prolonged effects on carbon storage due to differential sensitivities of ecosystem respiration and gross primary production. Second, short-term pulse-droughts caused greater carbon loss than chronic press-droughts when total precipitation reductions over a 20-year period were equivalent. Third, combining pulse- and press-droughts had intermediate effects on carbon loss compared to the independent drought types, except at high drought levels. Overall, these results suggest that interannual drought pattern may be as important for carbon dynamics as drought magnitude and that extreme droughts may have long-lasting carbon feedbacks in grassland ecosystems.

Keywords: carbon fluxes, climate change, climate extremes, drought, ecosystem respiration, grassland, gross primary production

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Introduction

Over the next century, global climate models project an increase in the frequency and severity of droughts due to higher temperatures and changes in precipitation (Dai, 2012; IPCC, 2013; Trenberth *et al.*, 2014; Cook *et al.*, 2015). While drought projections in specific regions are often uncertain, there are two general types of drought: 'pulse-droughts' and 'press-droughts', which differ in magnitude (i.e., the amount of precipitation reduction) and pattern (i.e., the interannual frequency). Pulse-droughts are short in duration, but extreme in magnitude (e.g., <5th percentile annual rainfall), and are expected to increase in frequency (IPCC, 2013). For example, the 2012 drought in the Central United States was the largest drought in 50 years and

resulted in major reductions in aboveground net primary production (ANPP) across the region (Cook *et al.*, 2014; Knapp *et al.*, 2015a). On the other hand, press-droughts are chronic but subtle reductions in water availability. Press-droughts can be driven by long-term reductions in precipitation (e.g., 10% decrease in mean annual precipitation), and/or warmer temperatures, which increase potential evapotranspiration and reduce soil moisture (Dai, 2012). When combined, press- and pulse-droughts may yield 'hot droughts' (Overpeck, 2013), which increase water deficits (Diffenbaugh *et al.*, 2015) and can elicit large and unexpected ecological responses (Hoover *et al.*, 2015). Indeed, observations of the 20th century show increased aridity associated with warming have intensified droughts globally (Dai, 2012; Trenberth *et al.*, 2014; Cook *et al.*, 2015).

In water-limited ecosystems such as grasslands, droughts can have major impacts on carbon cycles with

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potential feedbacks to climate change (Reichstein *et al.*, 2013; Frank *et al.*, 2015). Although grasslands have lower mean carbon storage on a per area basis than forests when averaged globally (including live and dead vegetation and soil), they are more geographically extensive so that the two biomes store similar amounts of carbon (White *et al.*, 2000). Grasslands in the US Great Plains often function as carbon sinks or are near equilibrium (Owensby *et al.*, 2006; Zhang *et al.*, 2011). However, it has been observed that these ecosystems can become carbon sources during drought (Zhang *et al.*, 2010, 2011). The source/sink dynamics of grassland ecosystems may be driven by the differential drought sensitivities of two key carbon fluxes: gross primary production (GPP) and ecosystem respiration (ER). A number of studies indicate that GPP is generally more sensitive to drought than ER (Ciais *et al.*, 2005; Zhang *et al.*, 2010; Shi *et al.*, 2014); droughts therefore tend to diminish carbon sinks and enhance carbon sources. Moreover, in addition to the immediate impacts during a particular event, there may be prolonged effects of drought on GPP and ER that last for many years, although this topic has received little attention.

Currently, we lack a comprehensive understanding of how press- and pulse-droughts impact carbon cycles at timescales greater than a decade. The majority of our knowledge on the ecological and biogeochemical effects of drought comes from experimental rainfall manipulations. Although highly informative, these field studies are often short in duration (<5 years), have a limited number of treatments (e.g., control, 50% and 75% reductions), and rarely examine gross and net carbon fluxes or long-term responses (Beier *et al.*, 2012). Land surface models with prognostic carbon cycles, when appropriately calibrated and tested, can potentially fill this knowledge gap, extending experimental results in both time and space (Smith *et al.*, 2014; Kayler *et al.*, 2015).

In this study, we used a land surface model to examine the effects of a wide range of press- and pulse-drought scenarios on carbon cycling in a mesic grassland ecosystem in the US Great Plains. The model was modified to represent site-level dynamics and validated against field observations. Drought was imposed by manipulating precipitation inputs to examine the direct effects of water limitation, thereby removing interactions with other environmental variables such as heat or humidity. Our drought scenarios were not intended to represent specific model projections; rather the goal was to examine a gradient of different drought patterns and magnitudes to identify key thresholds (Kayler *et al.*, 2015). We examined the effects of press- and pulse-droughts at annual to decadal timescales to test three hypotheses. First, we hypothesized that a sin-gle pulse-drought (equal to the 5th percentile of distribution of historic precipitation amounts) would have immediate and prolonged effects on carbon storage and cycling as compared to a control receiving average precipitation (equal to the 50th percentile). Second, we hypothesized that the effects of pulse-droughts would be greater than press-droughts of equivalent magnitude (i.e., equal total precipitation reductions over 20 years). Finally, we hypothesized that at an equal drought magnitude, the combined effects of press- and pulse-droughts would have greater effects on carbon storage than either drought type alone.

Materials and methods

Site description

We tailored the model to represent field conditions at the Konza Prairie Biological Station (KPBS), a tallgrass prairie ecosystem in northeastern KS, USA (39°05′N, 96°35′W). This mesic grassland is dominated by C_4 grasses that contribute up to 80% of ANPP, with forbs accounting for most of the remaining production (Knapp *et al.*, 1998). Climate in this region is characterized as temperate mid-continental, with warm summers and high interannual variability in precipitation (Knapp *et al.*, 1998). Precipitation is the most limiting factor in this ecosystem, and thus a strong predictor of ANPP (Briggs & Knapp, 1995; Knapp *et al.*, 2001).

Model description, setup, and environmental drivers

We used the Community Land Model version 4.0 (CLM) in Carbon-Nitrogen mode for this modeling experiment (Oleson *et al.*, 2010; Lawrence *et al.*, 2011). In this configuration, CLM is designed to capture the effects of climate, soil, hydrology, and nutrients on photosynthesis, respiration, and the emergent properties of plant growth and carbon stocks in the vegetation and soil. In the case of grasses, live carbon pools include leaf, fine root, and temporary carbohydrate storage. The model represents dead carbon as three litter and three soil organic matter pools comprising various stages of decomposition and recalcitrance, structured as a converging cascade. Photosynthesis in C_4 grasses, which we focused on, is modeled by a maximum carboxylation rate that becomes limited by light, leaf nitrogen, temperature, internal leaf CO_2, and soil water as a function of vertical root distributions. Heterotrophic respiration is a function of pool-specific carbon stocks and rate constants, soil temperature, and soil water. Nitrogen cycling is simulated through atmospheric and biological fixation, plant competition with microbial immobilization, and loss pathways including denitrification, volatilization, fire, and leaching (Oleson *et al.*, 2010).

We simulated the C_4 grass dominated ecosystem at the KPBS using 30-min inputs of diffuse and direct solar radiation, downwelling longwave radiation, temperature, precipitation, relative humidity, and wind obtained from the Clean Air Status and Trends Network, CASTNET (2003–2007;

www.epa.gov/castnet). Fire was turned off in the model. Soil properties were adjusted to match field observations including soil texture (38% clay, 21% sand, 41% silt; O'Lear & Blair, 1999), soil depth (90 cm), and root fraction (Knapp *et al.*, 2002). CLM was spun-up from bare ground conditions for 600 years using the accelerated decomposition scheme (Thornton & Rosenbloom, 2005) with repeating 2003–2007 climate inputs, after which the model was run under standard conditions for an additional 2000 years to ensure dynamic equilibrium. After spinup, we simulated conditions experienced by a rainfall manipulation experiment (as described in Hoover *et al.*, 2014) for model calibration. Two rainfall treatments were imposed during the growing seasons in 2010 (May 15–September 30) and 2011 (April 1–September 30). The control treatment received ambient rainfall plus supplemental irrigation (water added in 2011 due to natural drought) and the drought treatment received a 66% reduction in ambient precipitation. In the model, precipitation inputs occurred at the same daily pattern and amount as the field experiment, with water added at a rate of 12.7 mm h^{-1} (based on mean rate) starting at noon.

Our model calibration focused on comparisons with observed soil moisture and ANPP, and specifically how they differed between the control and drought treatments in each year of the experiment. These two variables were measured intensively in the field, are represented in CLM, and exert dominant controls on ecosystem carbon balance. Measured and modeled soil moisture corresponded to the top soil layers, 0–10 cm for the model and 0–15 cm for observations. Although these depths differ slightly, they both capture important surface dynamics and were compared in terms of seasonal pattern and the relative differences between control and drought treatments, not absolute values. ANPP corresponded to the total amount of aboveground biomass accumulated during the growing season. In the field, this was assessed by harvesting aboveground plant tissue in late August/early September (Hoover *et al.*, 2014), and in the model it corresponded to the total net aboveground production through August 31st. Several model functions were optimized during the calibration process. Leaf onset and offset dates were changed to match observed phenology from the field (forced onset on April 1st and offset on September 1st). For soil hydraulic conductivity, we reinstated the depth-dependent exponential decrease in saturated conductivity that was present in CLM version 3.0 (Oleson *et al.*, 2004), and multiplied the resulting values by 0.3 to optimize the calibration. Saturated conductivity is a highly uncertain parameter that can vary by orders of magnitude depending on the organic content of soil, and proved critical for accurate simulation of drought effects on soil moisture at the KPBS field site.

Precipitation treatments

Our model experiments included a large number of precipitation treatments that differed in interannual amounts, but not intra-annual pattern. When constructing climate inputs, we used the concept of an 'average year' to avoid idiosyncratic meteorological patterns associated with any particular year in the historical record. For the control scenario, monthly averages (daily event size, number of events per month, and time between events) were obtained from a 25-year precipitation record at KPBS (1984–2008; www.konza.ksu.edu, dataset AWOE12), with hourly precipitation intensity based on CASTNET data (2003–2007; www.epa.gov/castnet). Each month received the mean number of events (rounded to the nearest whole number), evenly spaced throughout the month, and based on the time between events in the observational record. For our experimental manipulations, we reduced precipitation by decreasing rainfall event size, a key feature of extreme dry years (Knapp *et al.*, 2015b).

In reality, precipitation conditions affect other meteorological variables; for example, humidity and downwelling longwave radiation are generally higher, whereas temperature (during daylight hours) and incoming shortwave radiation are lower during rain events. To account for this, we constructed average daily time series for nonprecipitation climate inputs for each month, derived from the Qian *et al.* (2006) reanalysis data set (1948–2004) and separated by dry and wet days. Wet days for a given month were defined as those when precipitation from the Qian *et al.* (2006) data set fell within 50% of the mean daily rain event size for each month from the 25 year record at KPBS (1984–2008; www.konza.ksu.edu, dataset AWOE12), and dry days as those with <0.01 mm day^{-1}. These climatologies were then associated with rain event days from our experimental time series so that wet and dry days received appropriate meteorological conditions. In all cases, we extracted reanalysis data from the grid cell (approximately 1.9°) containing the Konza field site.

Experiments

The primary objectives of our experiments were to (1) examine the impacts of drought magnitude and pattern on carbon cycling, specifically the key fluxes of GPP, ER, and resulting net ecosystem exchange (NEE), and (2) assess how these dynamics influence total grassland carbon storage at annual to century timescales. All experiments employed the same control; each year received an average amount and pattern of rainfall (844.8 mm yr^{-1}, described above). The various drought treatments were derived by reducing all precipitation events within a year by a given percentage. We conducted three experiments to address our hypotheses.

In the first experiment, we examined the immediate and prolonged effects of a single pulse-drought year on carbon fluxes. We imposed a drought that was equivalent to the 5th percentile of mean annual rainfall, or a 1 in 20 year event (533.1 mm), based on the historic distribution of rainfall at this location (described above). This drought year was followed by 2 years of average (control) rainfall. The extreme pulse-drought was compared to a control treatment that received average rainfall every year.

In the second experiment, we compared carbon dynamics for press- and pulse-droughts over 20-year timescales. Years with a pulse-drought always received the same magnitude drought within a given year (5th percentile), but varied in their interannual frequency over a 20-year period depending

on the scenario (e.g., 2in20 scenario has two drought events in 20 years; Table S1 and Fig. 1). Pulse-drought years were evenly distributed during the two decades, with nondrought years receiving control precipitation (Fig. 1). For a given scenario, the corresponding press-drought treatment received the same total rainfall over the 20-year period as did the pulse-drought treatment. However, instead of a mix of pulse-drought and control years, annual rainfall was reduced every year by a fixed amount (Fig. 1 and Table S1). Thus, in each scenario, the total amount of precipitation over the 20-
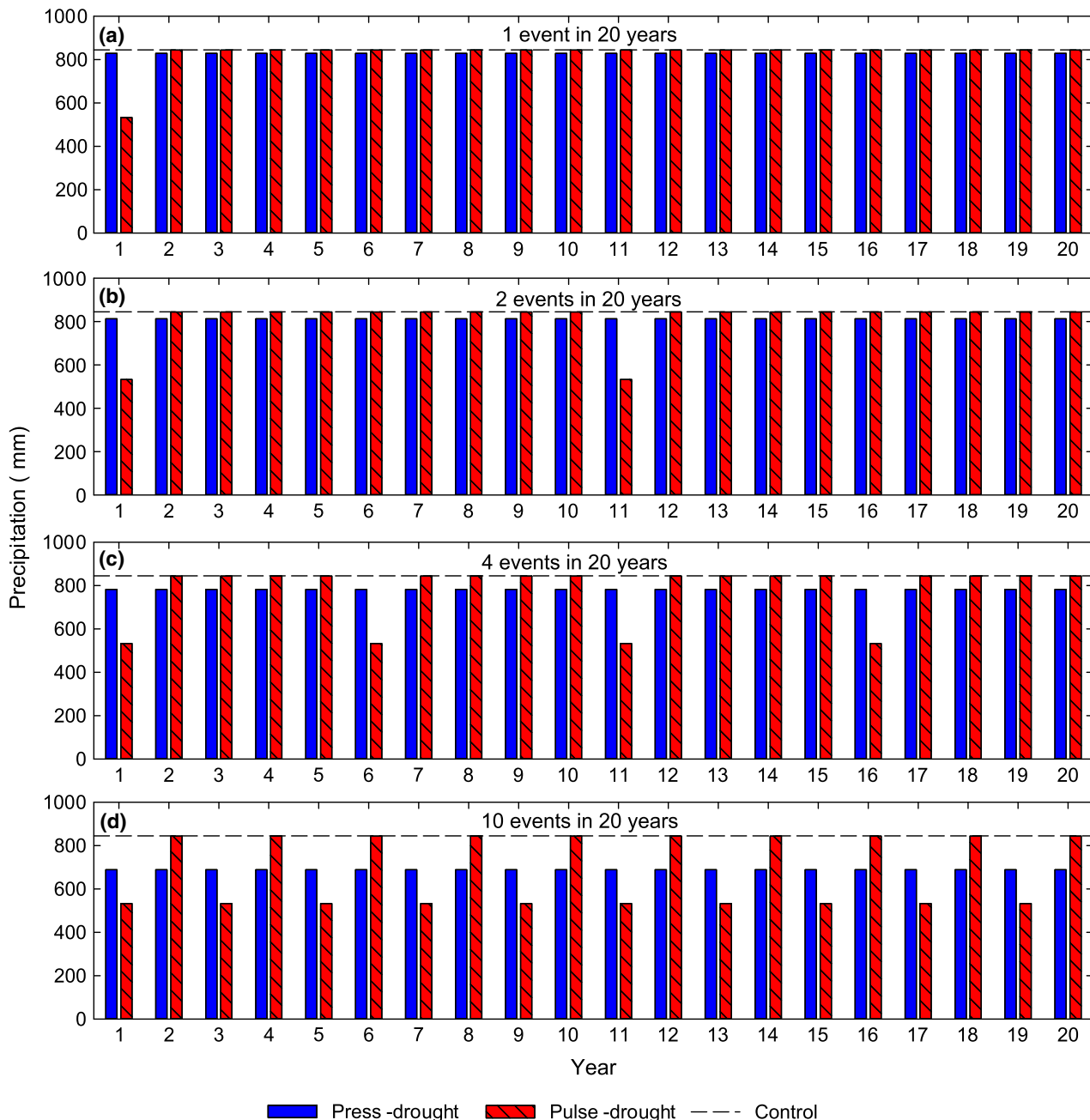
Fig. 1 Annual precipitation for control, press-drought, and pulse-drought treatments for several interannual drought patterns (a–d). The control treatment received the same precipitation amounts every year, equal to the long-term mean (844.8 mm yr^{-1}) and indicated by the dashed line. Pulse-drought treatments received an extreme drought (533.1 mm yr^{-1}, 5th percentile) during drought years and control precipitation for nondrought years. The frequency of pulse-drought years was increased for each scenario (a–d), as indicated at the top of each graph. For a given scenario, the press-drought received reduced rainfall every year, so that the total precipitation over the 20-year period and reduction from the control were equal to the pulse-drought. Pulse-drought years were a 36.9% reduction from control precipitation while press-drought reductions from control were as follows: (a) 1in20 = 1.8%; (b) 2in20 = 3.7%; (c) 4in20 = 7.4%; (d) 10in20 = 18.4%.

year period did not vary between the pulse and press treatments, only the interannual pattern and annual reduction percentage.

Finally, in the third experiment, we examined the interactive effects of press- and pulse-droughts using a subset of our scenarios: 2in20, 4in20, and 10in20. Climate models project that individual pulse-drought events will be exacerbated due to climate change because they will occur within a background of chronic press-drought. We therefore combined press- and pulse-droughts to create the interaction drought treatment. For example, the 2in20 interaction scenario combined the 1in20 press-drought with the 1in20 pulse-droughts treatments, so that every year had a press-drought by itself or in combination with a pulse-drought. As before, this ensured that all 2in20 scenarios received equal 20-year precipitation amounts, but differed in drought pattern. This also resulted in our interaction treatments receiving worse droughts in pulse years because we combined press- and pulse-droughts (Table S2; Fig. 2). However, during non-pulse-drought years, precipitation reductions in the interaction treatment were less than the press-drought treatment to make the total amount over 20 years equivalent with the other treatments.

Results

Model calibration

After a relatively small number of model adjustments (described above), CLM was able to capture the important drought-carbon dynamics at the KPBS field site. This included drought-related reductions in soil moisture (Fig. S1) and ANPP (Fig. S2) during the 2010 and 2011 growing seasons. Soil moisture was reduced significantly in 2010 (difference of 11.7% daily volumetric
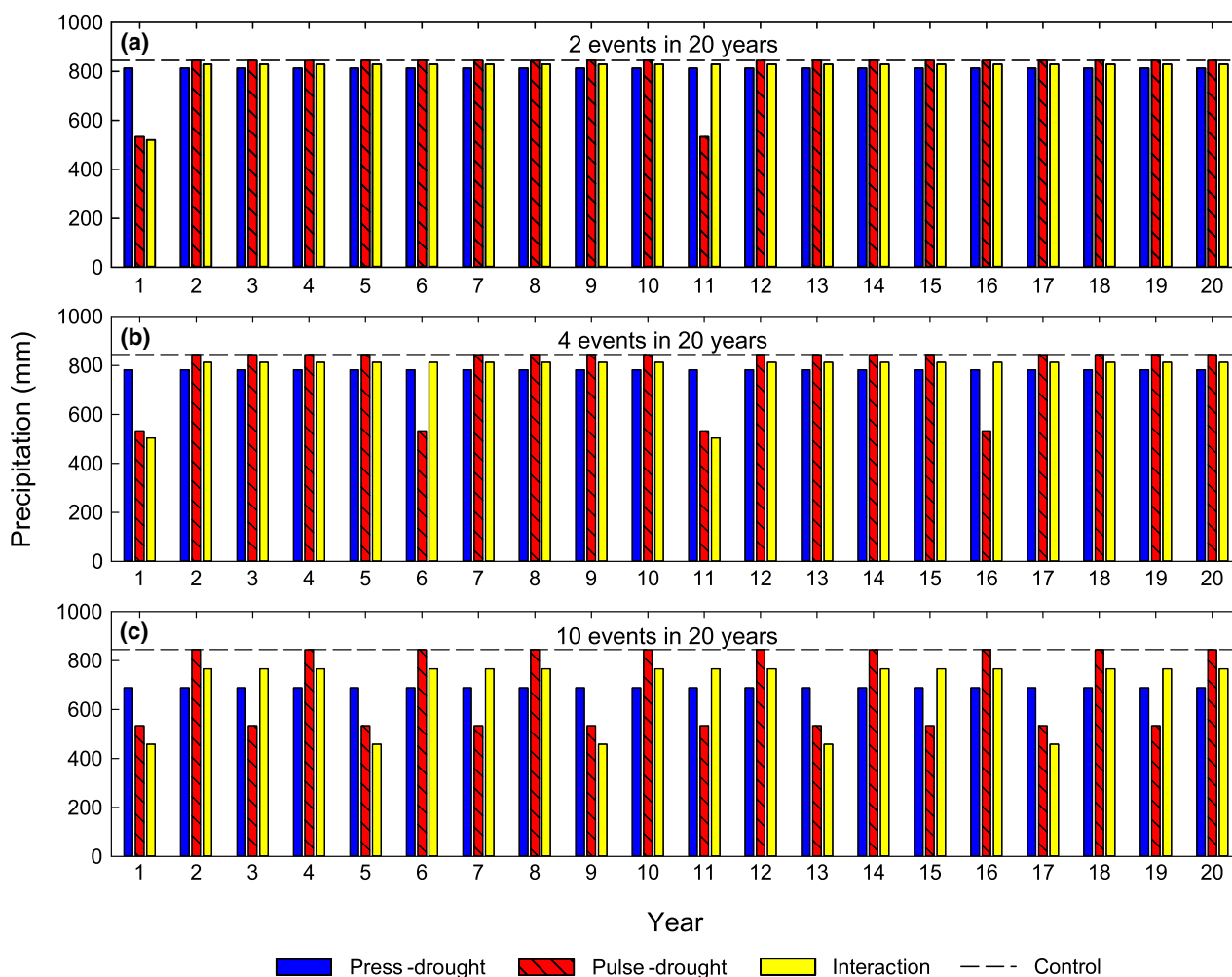

Fig. 2 Annual precipitation for control, press-drought, pulse-drought, and interaction drought (press + pulse) treatments at several interannual drought patterns (a–c). The control, press-drought, and pulse-drought treatments are the same as Fig. 1. The interaction drought treatment combined both press- and pulse-drought treatments, but maintained the same total precipitation over the 20-year period as the press- and pulse-droughts within a given scenario. When comparing the interaction drought with equivalent press- and pulse-drought treatments, there were fewer but slightly more intense pulse-drought years, and press-droughts were slightly weaker.

water content between June 1st and August 31st in the observations, and 6.6% in the model) and 2011 (difference of 14.1% in the observations and 13.5% in the model). Equally important for longer-term dynamics, the model simulated a lagged effect; that is, soil moisture was not completely replenished during the dormant season, which did not include any rainfall manipulations (see soil moisture differences in the beginning of the 2011 growing season in Fig. S1). These reductions in soil moisture decreased annual ANPP in the model by similar amounts compared to observations. ANPP reductions in 2011 (44% in the observations and 40% in the model) were substantially greater than 2010 (14% in the observations and 19% in the model) because of (1) carryover in soil moisture depletion from 2010, (2) reduced grass biomass at the start of the growing season, and (3) a natural drought in 2011 that compounded experimental conditions (Hoover *et al.*, 2014).

Single pulse-drought event

A single extreme pulse-drought had immediate and prolonged effects on carbon cycling and storage (Fig. 3). Uptake (negative NEE) was reduced during the drought year (year one), which was more pronounced later in the growing season due to cumulative water stress (July and August). The reduction in NEE was driven by differential drought sensitivities of ER and GPP, with GPP having greater relative reductions. For example, in August of the drought year, GPP was reduced by 35% from the control while ER was reduced by only 8%. The net effect of this differential sensitivity was to decrease total carbon storage by approximately 50 g C m^{-2} by the end of the year. During the recovery year, GPP was slightly higher than control levels (+1.9% or +13.4 g C m^{-2} yr^{-1}), while ER remained lower (−3.2% or −22.5 g C m^{-2} yr^{-1}). Thus, the ecosystem transitioned from a net carbon source to a net carbon sink in the year following drought.

Press- vs. pulse-droughts

Over a 20-year period, the single pulse-drought year had a greater negative impact on ecosystem carbon than did a press-drought of equal magnitude (Fig. 4). As previously discussed, the pulse-drought had notable effects during the event. While the system became a sink in the following years, it was not enough to return total carbon stocks to predrought levels within two decades. As seen in Fig. 4a, GPP was higher than the control in years 2 and 3, and mean annual carbon stocks actually exceeded control levels in year 4 before dropping again. This 'overshoot' phenomenon has been previously documented in controlled experiments (e.g.,

Etherington, 1967), but seldom shown in models. In CLM, the overshoot was mainly a result of internal plant dynamics (photosynthesis vs. maintenance respiration) and higher plant-available nitrogen levels in years 2 and 3. Conversely, the corresponding press-drought (i.e., 1in20, or 1.8% reduction in precipitation for all 20 years) had very little effect on carbon stocks.

The prolonged effects of drought on carbon storage became a bigger factor on the divergence between press- and pulse-droughts when the 1in20 event was repeated every 20 years (Fig. 5a). Over the century, the 1in20 press-drought had almost no effect on total carbon, while the negative carbon anomaly continued to increase in the pulse-drought treatment. At slightly higher drought frequencies (2in20 or 4in20 events), the press-drought continued to have a negligible impact on carbon stocks and the divergence between press- and pulse-drought treatments increased (Fig. 5b, c). However, at a 10in20 drought frequency, that is, an extreme drought every other year, the press treatment also lost a substantial amount of carbon and nearly converged with the pulse treatment, suggesting a threshold frequency (Fig. 5d).

To investigate this further, we ran every possible annual frequency scenario over a 20-year period. It was clear that increasing the magnitude of the press-drought or the frequency of the pulse-drought increased carbon loss (Fig. 6). However, within each drought scenario (equivalent 20-year precipitation reduction for press- and pulse-droughts), pulse-droughts always had greater carbon loss than did press-droughts. Differences were largest in intermediate droughts (approximately 3in20 through 8in20 scenarios). An important threshold existed in these experiments at an approximate 9% reduction in mean annual rainfall (78 mm yr^{-1}) for the press-drought treatment (equal to a 5in20 pulse-drought). Up until this threshold, the press-drought scenarios had little-to-no effect on net carbon storage; yet after this threshold was crossed, the press-drought scenarios quickly lost carbon. After the near-convergence at 10in20, the two treatments again diverged somewhat. This was driven by the presence of multi-year extreme droughts, which had compounding impacts on carbon fluxes and highlight the nonlinear impacts of consecutive droughts in this system. By definition, the two drought types converged exactly by the 20in20 scenario.

Interaction between press- and pulse-drought

The interaction between pulse and press-drought treatment had an intermediate effect on carbon at low frequencies (2in20 and 4in20 scenarios). However, at high frequencies (10in20 scenario), the interaction had a greater effect on carbon loss than either press- or
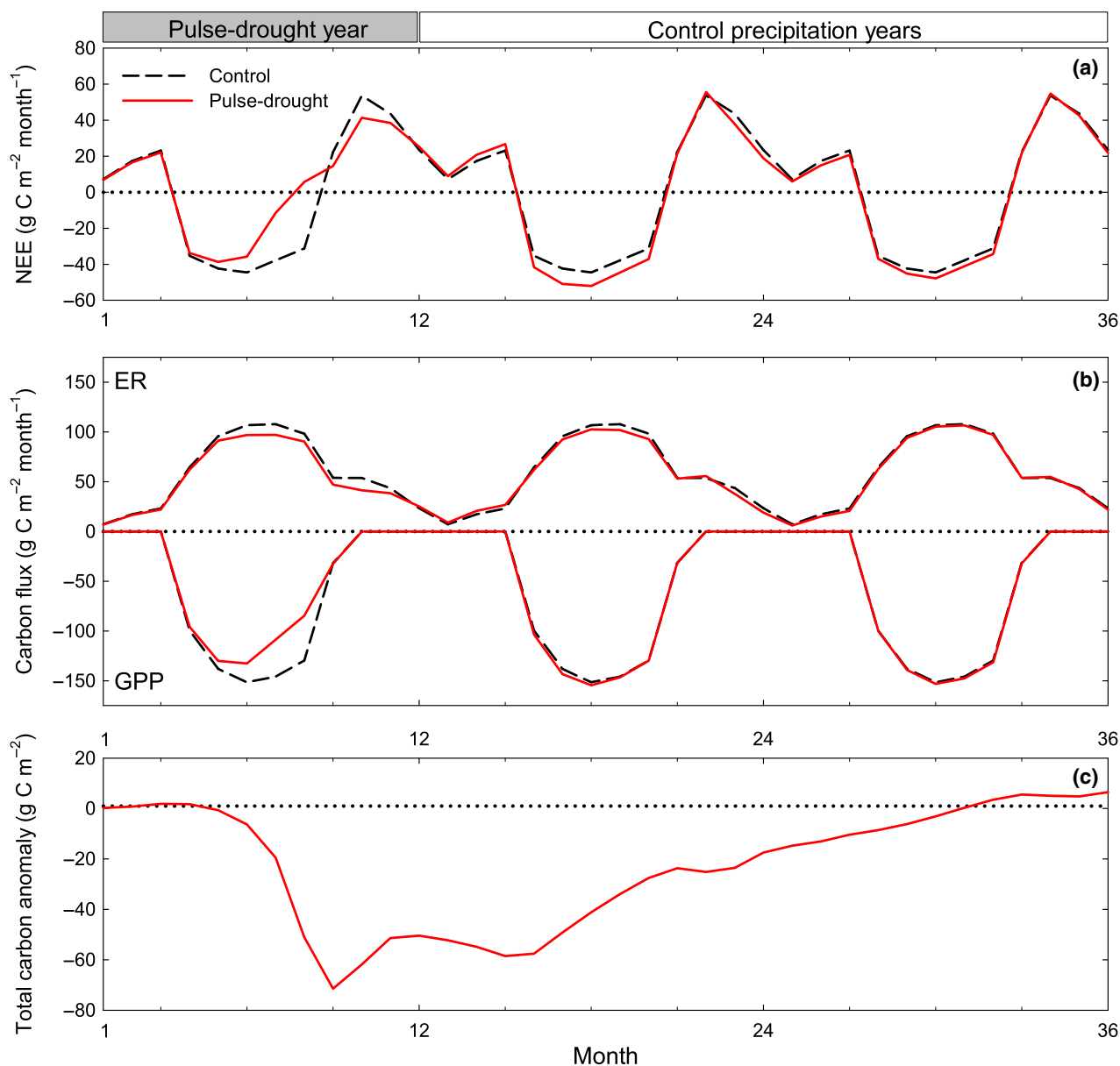
Fig. 3 Immediate and prolonged effects of an extreme pulse-drought on carbon fluxes. The control treatment received average rainfall every year (844.8 mm yr^{-1}), while the pulse-drought treatment received a 1 event in 20-year drought (1in20; equivalent to 5th percentile for annual precipitation) during year one and control precipitation for the two subsequent years (see bars above figure). (a) Net ecosystem exchange (NEE, positive represents a flux to the atmosphere); (b) Ecosystem respiration (ER) and gross primary production (GPP); (c) Total carbon anomaly (pulse – control). The dotted line at zero is for reference.

pulse-drought alone (Fig. 7). At these drought levels, the slightly increased extreme drought intensity from the interaction scenario pushed the system more so than the pulse treatment, despite the extreme drought years being half as frequent (Fig. 2).

Discussion

The goal of this study was to examine the effects of interannual drought pattern and magnitude on carbon

cycling in a mesic grassland at timescales longer than those possible to investigate with experimental manipulations in the field. We used CLM to simulate a range of press- and pulse-drought scenarios as well as their interactions and examine the impacts on GPP, ER, NEE, and total carbon storage. This investigation revealed three main findings. First, 1 year of extreme pulse-drought had both immediate and prolonged effects on carbon storage and cycling, which was driven largely by differential responses of ER and GPP. Secondly,
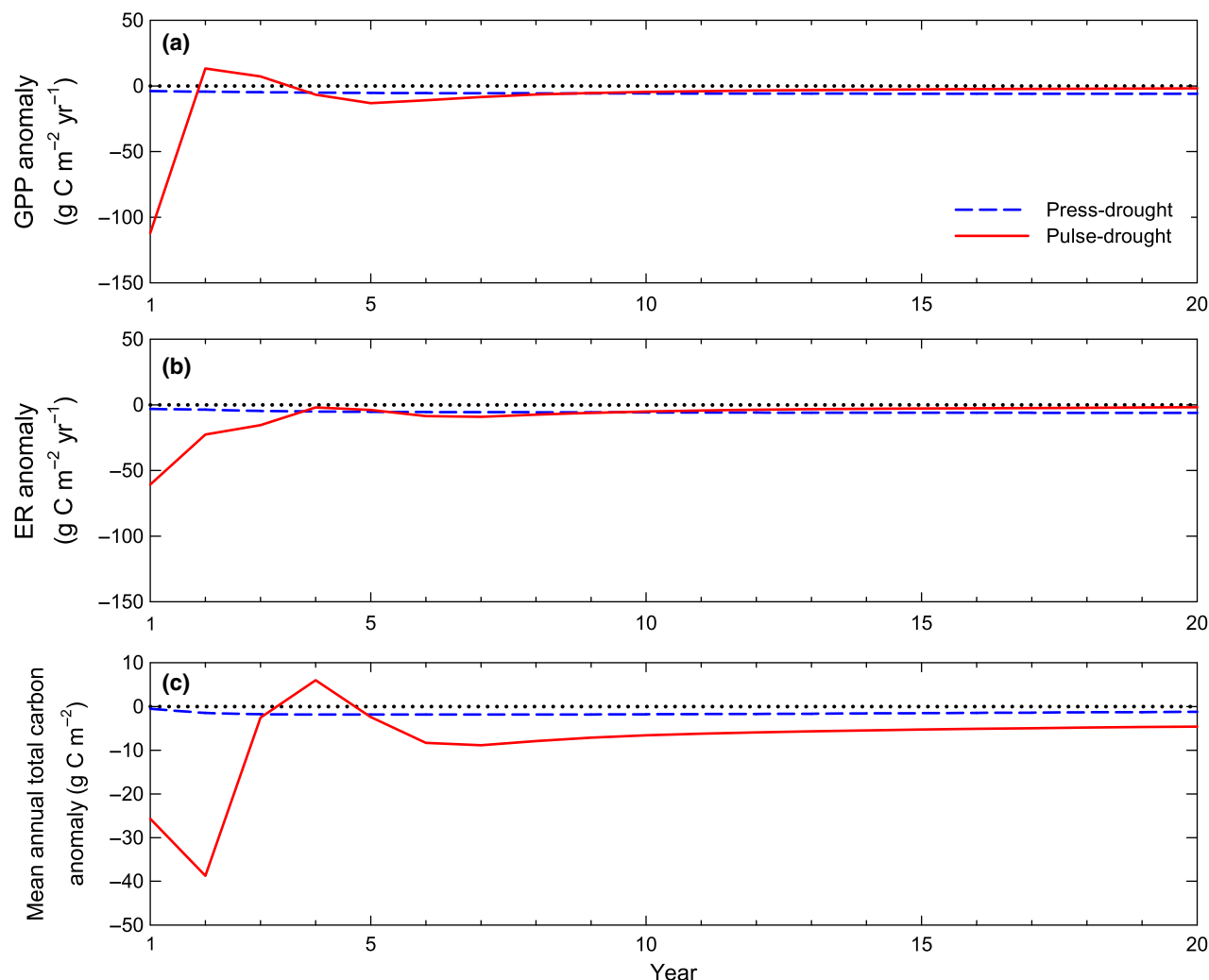
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Fig. 4 Carbon anomalies for press- and pulse-droughts over two decades. Pulse-drought for a 1 event in 20 years (1in20; equivalent to 5th percentile for annual precipitation) was imposed in year one and the 19 years following received control precipitation. The press-drought received the same total rainfall reduction as the pulse-drought treatment during this period, but it was imposed by reducing every year's total precipitation by 1.8%. (a) Annual gross primary production (GPP) anomaly; (b) annual ecosystem respiration (ER) anomaly; (c) mean annual total carbon anomaly. Anomalies for the press- and pulse-drought treatments are relative to the control (precipitation treatment – control). Dotted line at zero is for reference.

pulse-droughts had a considerably greater negative effect on carbon storage than press-droughts. Finally, the interaction between drought types was not important until relatively high drought levels, wherein it pushed the system above and beyond individual effects of press- and pulse-droughts.

Effects of a single pulse-drought year

During the 1-year extreme pulse-drought, there was a net loss of carbon from this simulated grassland ecosystem due to the differential sensitivities of GPP and ER. As the drought progressed into the growing season,

water became more limiting and resulted in a larger reduction in GPP than ER, causing a drop in NEE. Such differential drought sensitivities of GPP and ER have been observed in previous studies (Schwalm *et al.*, 2010; Shi *et al.*, 2014). Water limitation on aboveground production is well documented in grasslands of the central United States (Sala *et al.*, 1988; Knapp *et al.*, 2001), so the large response of GPP to drought is not surprising. On the other hand, there are several environmental factors other than water availability that have large influences on soil respiration rates, such as temperature, quantity and quality of carbon substrates, and nutrients (Luo & Zhou, 2006). Therefore, the
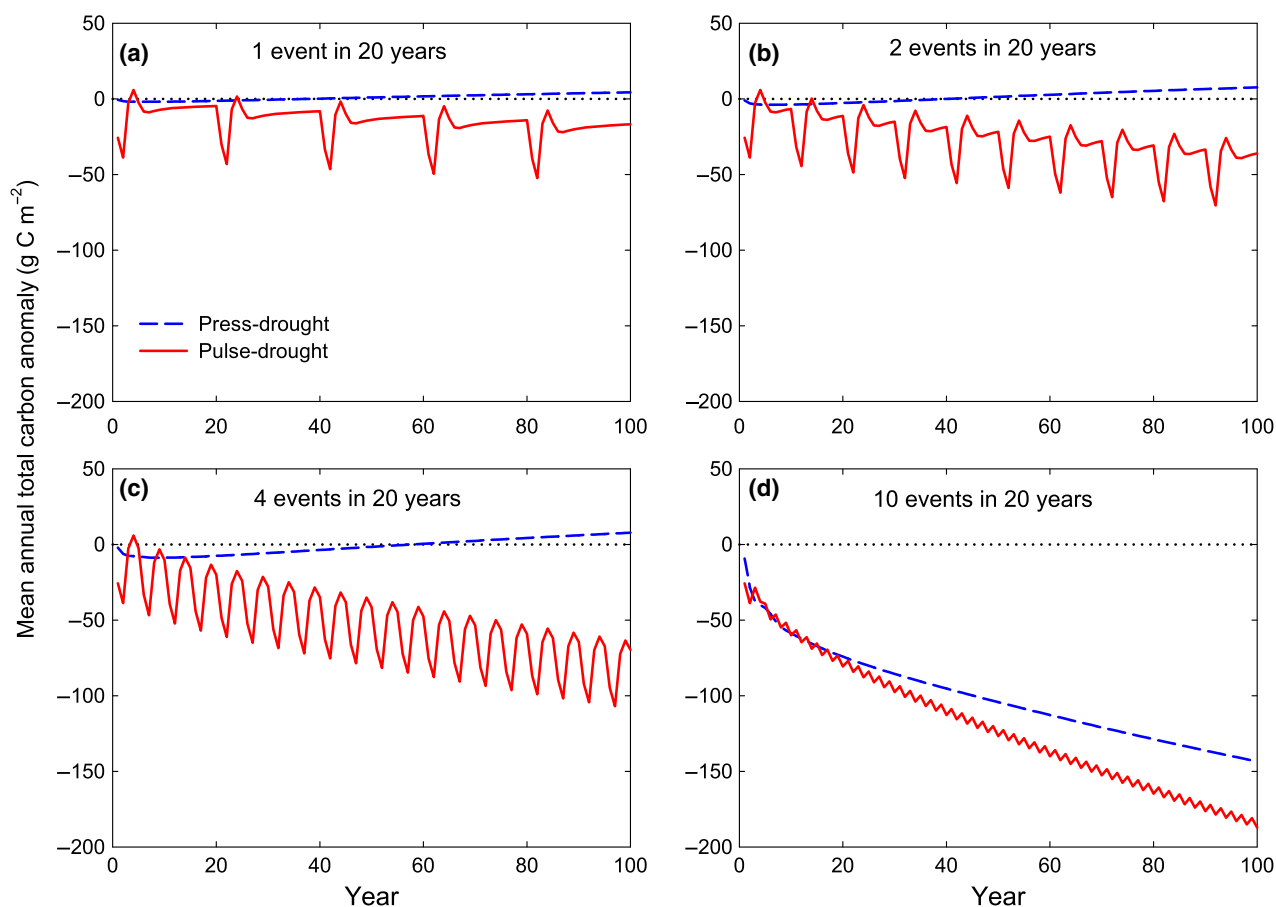
Fig. 5 Total carbon anomalies for press- and pulse-droughts under four interannual drought scenarios for 100 years (a–d). Anomalies for the press- and pulse-drought treatments are relative to the control (precipitation treatment – control). The dotted line at zero is for reference.

magnitude of the differential sensitivities of GPP and ER to drought will govern how much carbon is lost to the atmosphere during drought.

The legacy of the pulse-drought year on carbon fluxes and storage was apparent in the years immediately following drought as the ecosystem transitioned from a net carbon source to a net carbon sink. In the first year postdrought, GPP was slightly higher than control levels because soil moisture largely recovered and there was an excess of plant-available nitrogen from reduced uptake during the drought year, which stimulated production. At the same time, ER remained lower; although heterotrophic respiration was increased from drought-induced litterfall ($+9.3$ g C m^{-2}), maintenance and hence overall autotrophic respiration was substantially lower (-31.8 g C m^{-2}) because of reduced plant matter. These dynamics mirror the general observation that productivity is relatively independent of vegetation carbon content while respiration increases with carbon stocks (Luo *et al.*, 2015).

Interannual drought pattern and carbon cycling

One of the fundamental questions we investigated was, *for a given magnitude, are all droughts created equal?* To examine this, we created precipitation scenarios that differed in drought pattern but not total precipitation over 20-year periods and repeated those scenarios for a century. In all cases, pulse-droughts caused greater carbon losses than press-droughts of equivalent magnitude, with the greatest differences evident at intermediate drought frequencies. This suggests that, alone, chronic but subtle reductions in water availability due to increased temperatures or minor reductions in rainfall may have little impacts on carbon cycling in this system, provided the effects of the press-drought do not exceed a certain threshold in drought magnitude. In this study, an approximate 9% reduction in precipitation represented a critical threshold whereby further reductions resulted in pronounced carbon losses. This threshold effect likely applies to other
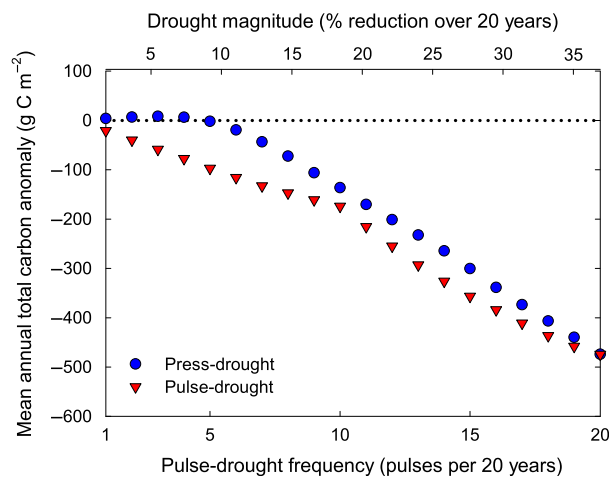
Fig. 6 Mean annual total carbon anomalies during years 80–100 for press- and pulse-drought treatments across 20 different interannual pulse-drought scenarios (bottom *x*-axis). For a given drought scenario, both press- and pulse-droughts received equal reductions in precipitation over 20 years (relative to the control) as indicated by the top *x*-axis. Anomalies for the press- and pulse-drought treatments are relative to the control (precipitation treatment – control). The dotted line at zero is for reference.
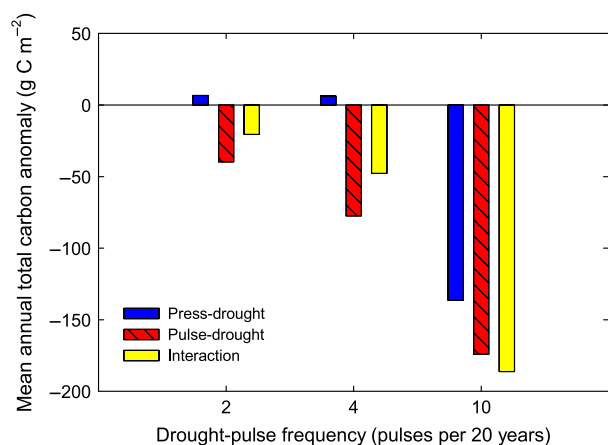

Fig. 7 Mean annual total carbon anomalies during years 80–100 for press-drought, pulse-drought, and interaction drought (press + pulse) treatments under three drought scenarios. For each drought scenario, all three drought treatment received the same total rainfall over a 20-year period, and only differed in interannual drought pattern. Anomalies for the drought treatments are relative to the control (precipitation treatment – control).

systems as stomata generally exhibit a threshold closure response to water availability (Schulze, 1986; Bond & Kavanagh, 1999). However, the value at which this threshold occurs will differ considerably depending on climate and vegetation characteristics. Identifying these nonlinear ecological responses and thresholds

to climate drivers is essential to forecast ecological responses to a changing climate (Kardol *et al.*, 2012; Kreyling *et al.*, 2014; Kayler *et al.*, 2015).

In the future, pulse-droughts will likely occur within a background of press-droughts (IPCC, 2013; Overpeck, 2013), with unexpected ecological consequences (Hoover *et al.*, 2015), and thus it is important to examine the interactive effects of these two drought types. We simulated this interaction by combining press- and pulse-drought treatments and comparing them to the two drought types alone of equivalent magnitude. We predicted that the interactive effects of the two drought types would result in greater carbon loss than either drought type alone, but this was not always the case. At lower drought frequencies, the interaction drought treatment had intermediate effects on total carbon. This was likely due to the strength of pulse-drought relative to press-drought; by removing pulse-drought years and replacing them with press-drought (of a magnitude below the critical thresholds), GPP was impacted less, and less carbon was lost from the system. However, under the 10in20 scenario, the press + pulse-drought treatment had greater carbon loss than either press or pulse-drought alone because the magnitude of the press treatment was great enough to limit carbon uptake. This emphasizes the point that after ecosystem-specific thresholds are crossed, the ecological impacts of pulse-droughts may be significantly and nonlinearly exacerbated within a background of more subtle press-droughts.

Implications and future work

Reports of projected precipitation changes largely focus on the annual amount and intra-annual patterns (IPCC, 2013; Melillo *et al.*, 2014). Over the past decade, there have been many rainfall manipulation experiments in grasslands across the globe that have imposed such predicted changes in precipitation and examined the impacts on key carbon cycling processes. These studies have found that productivity and soil respiration are impacted by reductions in rainfall amounts (Gilgen & Buchmann, 2009; Otieno *et al.*, 2010; Cherwin & Knapp, 2012; Byrne *et al.*, 2013; Evans & Burke, 2013) and intra-annual rainfall pattern (Knapp *et al.*, 2002; Heisler-White *et al.*, 2009; Wilcox *et al.*, 2015). However, with such an emphasis on precipitation amount and intra-annual pattern, we currently lack an understanding of the effects of interannual precipitation variability on key carbon cycling process in grasslands (Gherardi & Sala, 2015).

The results from this study suggest that interannual drought pattern may be more important than amount for grassland carbon cycling and storage. We found

that the tallgrass prairie ecosystem lost substantially more carbon when a given drought level was imposed as individual extreme drought years compared to chronic but smaller reductions in rainfall. This finding likely applies to other systems with intermediate-to-high precipitation in which relatively small reductions in rainfall do not notably increase time spent in a water-limited state (Farrior *et al.*, 2015). At the xeric end of the spectrum, however, press-droughts may be more influential in leading to chronic water stress. We therefore suggest there is an urgent need to (1) analyze climate data and conduct experiments with a strong focus on interannual drought pattern, (2) assess the resistance and resilience of grassland composition and function to different interannual drought patterns, (3) extend these findings and hypotheses to other systems with varying precipitation regimes, including drylands and forests, and (4) quantify carbon feedbacks using integrated observation-modeling approaches. Future modeling work would benefit from including competition between species or grass functional types (e.g., C_3 vs. C_4), and analyzing responses within the context of downscaled climate projections.

Since 1830, 97% of the tallgrass prairie ecosystem of the US Great Plains has been modified, primarily by conversion to agriculture (the current tallgrass prairie ecosystem covers 21 548 km^2; White *et al.*, 2000). However, the carbon loss from just a single extreme pulse-drought year in this study (50 g C m^{-2}), when scaled across this remnant ecosystem, is equal to the annual emissions of approximately 840 000 US passenger cars (~3.95×10^6 metric tons CO_2E; EPA, 2015a), and slightly greater than all the residential CO_2 emissions for the State of Kansas in 2012 (EPA, 2015b). The other two grasslands ecosystems of the Great Plains occupy much greater areas today than the remnants of the tallgrass prairie (the mixed grass prairie covers 225 803 km^2 and the shortgrass prairie covers 62 115 km^2; White *et al.*, 2000). Given that regional droughts are common in North America (Cook *et al.*, 2014), it is important to assess that the effects of drought pattern on carbon cycling for the other two grassland ecosystems, as well as the other major land cover for this region: agriculture. Because of their quick responses and large stocks of belowground carbon, temperate grassland ecosystems may prove influential for the future terrestrial carbon balance.

Summary

Climate extremes, such as drought, may impact regional and global carbon cycles both during and after the event; however, the sign and magnitude of carbon feedbacks to the atmosphere remain poorly understood (Reichstein *et al.*, 2013). Grasslands, such as the Great Plains of the United States currently store a large amount of carbon belowground and are likely to experience more intense and frequent droughts in the future (IPCC, 2013; Cook *et al.*, 2015). In this study, we found that carbon storage and cycling in a simulated grassland was fairly resistant to chronic but subtle press-drought, while extreme pulse-droughts led to much greater carbon loss to the atmosphere. A key mechanism driving this pattern was the differential sensitivities of GPP and ER. These results suggest that climate change may turn this vast carbon store into a carbon source.

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Supporting Information

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

Table S1. Precipitation amounts and patterns for press- and pulse-drought treatments.
Table S2. Precipitation amounts and patterns for press-drought, pulse-drought and interaction drought treatment.
Figure S1. Observed vs. modeled soil moisture for model calibration.
Figure S2. Observed vs. modeled aboveground net primary productivity for model calibration.