

Experimental warming amplified opposite impacts of drought vs. wet extremes on ecosystem carbon cycle in a tallgrass prairie

Chang Gyo Jung^{a,b,*}, Xia Xu^c, Shuli Niu^{d,e}, Junyi Liang^f, Xuecheng Chen^g, Zheng Shi^g, Lifen Jiang^{a,b}, Yiqi Luo^{a,b,h,*}

^a Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ, USA

^b Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ, USA

^c College of Biology and the Environment, Nanjing Forestry University, Nanjing, Jiangsu, China

^d Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China

^e Department of Resources and Environment, University of Chinese Academy of Sciences, Beijing, China

^f Environmental Science Division and Climate Change Science Institute, Oak Ridge National Laboratory, Oak Ridge, TN, USA

^g Department of Microbiology and Plant Biology, University of Oklahoma, Norman, OK, USA

^h Department of Earth System Science, Tsinghua University, Beijing, China

ARTICLE INFO

Keywords:

Climate warming

Drought

Ecosystem carbon cycle

Grasslands

Long-term experiment

Extreme precipitation

ABSTRACT

Climate warming is leading to greater precipitation variability, resulting in increased frequency and intensity of both drought and wet extremes. However, how these extreme events interact with climate warming and hay-harvest in grasslands to impact ecosystem functions has not yet been well explored. In this study, we took advantage of a long-term experiment to examine how climate warming and clipping (i.e., mimicking hay harvest) regulated impacts of naturally occurring drought and wet extremes on ecosystem CO₂ fluxes of a tallgrass prairie in the Great Plains, USA. Warming resulted in net ecosystem carbon release (i.e., positive net ecosystem CO₂ exchange, NEE) in the extreme drought year of 2011, but significantly enhanced net carbon uptake in the extremely wet year of 2015 in comparison with NEE in normal years. Warming-induced carbon release in the drought year was due to significantly enhanced ecosystem respiration (ER) from mid-summer to early-autumn, whereas warming-enhanced NEE in the wet year was due to an increase in aboveground net primary production (ANPP) compared to those in normal years. Drought diminished warming-induced increases in ANPP to about one sixth of that in the wet year in the unclipped plots. Interestingly, clipping offset the drought-mediated ecosystem carbon loss by increasing GPP and weakened the wet-enhanced ANPP. Overall, our results suggest that a future, warmer climate may exacerbate carbon losses in terrestrial ecosystems during drought extremes but stimulate the ecosystem carbon sink under wet extremes.

1. Introduction

Increasing frequency and intensity of either extreme drought or wet events during the 21st century have been projected by most global climate models according to the IPCC 5th assessment (IPCC, 2013). Moreover, studies from both observations and model simulations have shown that climate warming is a main catalyst for drought and wet extremes due to its impact on hydrological cycles (Dai, 2013; Mueller and Seneviratne, 2012; Pendergrass et al., 2017; Peng et al., 2014; Trenberth et al., 2014; Wetherald, 2010). Thus, studies on these climate extremes need to take warming effects into account (Dai, 2013; Trenberth et al., 2014). Climate warming, and extreme drought and wet events can have significant impacts on ecosystem carbon (C) cycles

(Ciais et al., 2005; Frank et al., 2015; Friedlingstein et al., 2006; Reichstein et al., 2007), potentially either strengthening or weakening ecosystem feedback to climate change (Luo, 2007). However, previous studies have mainly examined the effects of warming, drought, or extremely wet conditions separately (Doughty et al., 2015; Hoover et al., 2014b; Wilcox et al., 2015; Wu et al., 2013; Xu et al., 2016). So far, combined effects of warming and climatic extremes have only been explored with short-term mesocosm experiment (Roy et al., 2016) or field manipulations (Hoover et al., 2014a; Xu et al., 2013). Future climate warming is likely accompanied with drought and wet extremes; therefore, understanding how long-term warming alters ecosystem responses to naturally occurred drought or wet extremes in field experiments is vital for predicting and assessing consequences of future

* Corresponding authors at: Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ, USA.

E-mail addresses: cjung86@nau.edu (C.G. Jung), yiqi.luo@nau.edu (Y. Luo).

<https://doi.org/10.1016/j.agrformet.2019.107635>

Received 8 December 2018; Received in revised form 19 June 2019; Accepted 21 June 2019

Available online 26 June 2019

0168-1923/ © 2019 Elsevier B.V. All rights reserved.

climatic extremes.

Studies on ecosystem C cycles under drought have shown not only declines in gross primary production (GPP) due to suppressed photosynthesis (Chaves et al., 2009; Granier et al., 2007), but also decreases in ecosystem respiration (ER) (Doughty et al., 2015; Schwalm et al., 2012b). Since GPP has been shown to be a higher sensitivity to drought than ER (Schwalm et al., 2010; Shi et al., 2014), ecosystems are expected to lose C under drought extremes (Frank et al., 2015) and to decrease aboveground net primary production (ANPP) (Craine et al., 2012; Ma et al., 2012). It has also been found that drought caused higher net ecosystem C uptake in the woody savanna through reduced ER due to less decomposition during drought than environments without drought (Schwalm et al., 2012a). In contrast, increased precipitation stimulated more GPP than ER, leading to increases in ANPP (Isbell et al., 2015; Sherry et al., 2008; Thomey et al., 2011) and net ecosystem C uptake (Wu et al., 2011). While these studies on drought or wet extremes provide critical information about how climate extremes alter ecosystem C cycle, it is essential to understand interactive effects of climate extremes and climate warming on ecosystem processes.

Climate extremes (e.g., extreme drought and extreme wet events) and climate warming interact to either exacerbate or offset their individual effects (IPCC, 2013; Mueller and Seneviratne, 2012). For example, ANPP of a C₃ dominant grassland declined with increasing temperature and dryness over a long-term observation (Brookshire and Weaver, 2015). Short-term heat waves and extreme drought, in combination, significantly reduced ecosystem C uptake in a grassland ecosystem (Roy et al., 2016). Conversely, combined warming with reduced precipitation did not change ecosystem C balance and plant productivity of central U.S. grasslands (Hoover et al., 2014b; Xu et al., 2016). A combination of warming and increased precipitation consistently enhanced ANPP (Luo et al., 2008; Wu et al., 2011). Understanding diverse patterns of interactive effects of warming and climate extremes on ecosystems is essential to project ecosystem services in the future as they are most likely to occur simultaneously.

Impacts of drought and warming on ecosystems may vary with land management (Canadell and Schulze, 2014). Hay harvesting, a common land management practice in grasslands, might substantially counteract impacts of climate change on ecosystem functions and structure (Cernusca et al., 2008; Luo et al., 2009; Schmitt et al., 2010; Shi et al., 2016). Clipping treatments, which simulate hay harvesting, resulted in a shift in plant communities due to changes in light availability and germination timing (Collins et al., 1998; Ruprecht and Szabó, 2012). Shifting species composition, in turn, can lead to alteration in ecosystem responses to global change (Chen et al., 2017). Although many studies examined precipitation effects on plant production so as to maximize hay harvests in grasslands (Jungers et al., 2015; Parton et al., 2012), how the land management affects ecosystem C cycle under both climate extremes and climate warming remains poorly understood.

The objective of this study is to assess how ecosystem CO₂ fluxes, such as net ecosystem CO₂ exchange (NEE), GPP, ER, and ANPP, were altered by either drought or wet extremes under experimental warming and clipping. We took advantage of a long-term warming and clipping experiment that started in 1999 in a prairie grassland in Oklahoma, USA, which has naturally fluctuating precipitations. This region in the Great Plains has experienced intensified interannual precipitation variability (Basara and Christian, 2018; Weaver et al., 2016). We examined how climate warming and clipping regulated impacts of naturally occurring drought and wet extremes on ecosystem C processes (i.e., GPP, ER, NEE, and ANPP) measured over seven years (2009–2015). We compared ANPP, GPP, ER, and NEE in the extremely dry and extremely wet years vs. those years with normal precipitation under the treatments of warming and clipping. During that period, 2011 was an extremely dry year while 2015 was an extremely wet year according to long-term precipitation record. By doing so, we assessed how warming and clipping mediated impacts of drought and wet extremes on ecosystem C processes.

2. Materials and methods

2.1. Study site and experimental design

The experiment site was located in the Kessler Atmospheric and Ecological Field station (KAEFS) in McClain County, central Oklahoma in the Great Plains of the United States (34°58′31.8″N, 97°31′19.6″W). This site had been remained uncultivated and ungrazed for 40 years before the experiment began in 1999. This grassland was dominated by the C₄ grasses (*Schizachyrium scoparium* and *Sorghastrum nutans*) and the C₃ forbs (*Ambrosia psilostachya*, *Solidago nemoralis* and *Solidago rigida*). We used a nested design with warming as the main factor and clipping as a secondary factor. The experiment consisted of six replicates, i.e., six pairs of plots and each pair has two square plots with a length of 2 m, making a total of 12 plots. Within each pair, one plot has been warmed continuously since November 21, 1999, while another plot has remained under ambient temperature as control. Infrared heaters (165 cm x 15 cm; Kalglo Electronics, Bethlehem, PA, USA) were capable of a radiation output of 100 W m⁻². These heaters were suspended 1.5 m above the ground in each warmed plot. On average, air temperature was increases by 1.1 °C, and daily mean soil temperature increases by 2.0 °C and 2.6 °C in unclipped and clipped subplots, respectively (Luo et al., 2001; Wan et al., 2002). In the unwarmed plot, to mimic the shading effect of the heater, a ‘dummy’ heater has suspended at the same height. For each pair of plots, the distance between the center of the warmed and control plots was approximately 5 m to avoid heating the control plot. The distance between two pairs varied from 20 to 60 m. Each plot was further divided into four subplots of 1 m × 1 m. Plants in two diagonal subplots were clipped at a height of 10 cm above the ground once a year to mimic hay harvesting while the other two subplots were kept unclipped. Therefore, the experiment had four treatments: unclipped and control (ambient) temperature (UC), unclipped and warming (UW), clipped and control temperature (CC), and clipped and warming (CW). After clipping, the clipped biomass was brought back to the laboratory for estimates of ANPP.

2.2. Precipitation, air and soil temperature, and soil moisture measurements

The precipitation data from 1896 to 1993 and from 1994 to 2015 were retrieved from Oklahoma climatology survey (Purcell, Blanchard and Norman stations) and Oklahoma Mesonet (Washington station), respectively (Brock et al., 1995; McPherson et al., 2007). Data in year of 1903, 1906, 1907, 1908, 1910, 1911, 1914, 1919, and 1947 were missed. The data from 1896 to 1993 came from observations at three stations (Purcell, Blanchard and Norman stations). Washington station is 200 m away from our experimental site, which is the closest meteorological station for climatic data. The other stations were also within short distance to the experimental site. Purcell and Blanchard stations are in the same county of the field station, having distances of 13 and 21 km, respectively. Norman station is in Cleveland County and 24 km away from the field station. When data were available from more than one station at a given time, we averaged the data across those meteorological stations. Given the relative short distances between all the stations to our study site, we assumed that there is no significant difference among the data sets.

Air temperature was measured by thermocouples at the height of 25 cm above the ground in the center of control and warming plots, respectively. Soil temperature at a 2.5 cm depth was measured by thermocouples in the center of one unclipped subplot and one clipped subplot. Detailed information for air and soil temperature measurements was described previously (Luo et al., 2009; Xu et al., 2012). Soil volumetric water content (VWC) was measured manually at depth of 12 cm using Time Domain Reflectometry (TDR) equipment (Soil Moisture Equipment Corp., CA, USA). Three measurements were made in each subplot. The frequency of soil VWC measurements was from two to four weeks.

2.3. Identifying the dry and wet events

In our study, extreme precipitation years were defined based on percentile thresholds (i.e., below 10th or above 90th percentile for extreme drought or extremely wet years, respectively). Based on those percentile thresholds, we divided the whole study period (2009–2015) into three categories: the dry year (2011), normal years (2009–2010 and 2012–2014) and wet year (2015). The Standardized Precipitation Evapotranspiration Index (SPEI), which involves both precipitation and evapotranspiration (Beguería et al., 2014; Vicente-Serrano et al., 2010), was used to support percentile thresholds for precipitation, i.e., extreme drought (< -2) and extremely wet (> 2) (Fig. S3). SPEI at a 3-month time interval was calculated for monitoring drought through ‘SPEI’ package in R (Beguería et al., 2017).

2.4. Ecosystem CO₂ flux measurements

To measure ecosystem CO₂ fluxes, including NEE and ER, two square aluminum frames (0.5 × 0.5 m) in each plot were permanently installed into the soil at 3 cm depth, one in the clipped subplot and another in the unclipped subplot. The frame had flat base of 3 cm wide to fully seal the gap between soil and the chamber. NEE and ER are measured by LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA) attached with a static chamber (0.5 × 0.5 × 0.6 m), which is covered with a thick cloth to create dark conditions for determinations of respiration rates. The measurements were made at 2- to 4-week intervals from 2009 to 2015 and measurement time was between 9:30 am and 12:00 pm under clear sky conditions to keep similar solar radiations. Some months were persistently cloudy at the measurement time so that measurement data in some months were not available, e.g., May and August in the wet year. Negative and positive values of NEE indicate carbon sink and source, respectively. GPP was derived by difference between NEE and ER. Details on the chamber design and measuring procedures were described in a previous study at the same experimental site (Niu et al., 2013). For overall assessments of interactive effects between precipitation extremes and warming, monthly values of carbon fluxes (i.e., GPP, ER and NEE) were averaged for each type of precipitation regime years (i.e., dry, normal, and wet years). Seasonality curves were generated with monthly measurements with smoothing (‘geom_smooth’, span = 0.6) (Wickham, 2009).

As for ANPP measurements, plant biomass was clipped, as described above for simulating hay harvesting, and dried at 65 °C for 72 h. ANPP in unclipped plots was indirectly estimated by the pin-contact method (Frank and McNaughton, 1990). Detailed procedure for ANPP estimations in unclipped plots can be found in a previous study in the same experiment (Sherry et al., 2008).

2.5. Statistical analysis

All statistical analyses were conducted with R version 3.3.0 (RCoreTeam, 2016). The effects of warming, clipping, and precipitation extremes on NEE, ER, GPP, and ANPP were assessed using linear mixed-effect models conducted in the ‘lme4’ package (Bates et al., 2014). In the linear mixed model, warming, clipping and precipitation extremes (extreme hereafter as one factor of treatment in this study), as well as their interaction, were considered as the fixed effect while the plots ($n = 6$ for replicates) were set as the random effect nested within measurement time. To overcome statistical limitations resulting from unbalanced measurement times, we used nonparametric bootstrapping method to generate observations for normal years, which resamples the observations within plots 1 to 6 for each treatment (UC, UW, CC and CW). By applying a bootstrapping sampling procedure, we first obtained 10,000 times of monthly values in normal years and then we calculated monthly means for further statistical analysis. As for the ANPP, we resampled ANPP for each treatment within each plot from the five years of measurements in normal years.

Table 1

Results from linear mixed effect model to examine responses of carbon fluxes (Net Ecosystem CO₂ Exchange, NEE; Gross Primary Production, GPP; Ecosystem Respiration, ER; and Above-ground Net Primary Production, ANPP) to warming, clipping, precipitation extremes (i.e., Extreme), and their interactive effects. Bolds indicate significance at the level of $p < 0.05$.

Dependent Variable	Effect	df	F-value	p-value
NEE	Warming	1	2.87	0.09
	Clipping	1	25.81	< 0.01
	Extreme	2	5.67	< 0.01
	Warming:Clipping	1	0.24	0.62
	Warming:Extreme	2	1.31	0.27
	Clipping:Extreme	2	0.48	0.62
	Warming:Clipping:Extreme	2	0.22	0.81
GPP	Warming	1	0.23	0.63
	Clipping	1	29.39	< 0.01
	Extreme	2	1.26	0.28
	Warming:Clipping	1	0.02	0.90
	Warming:Extreme	2	0.04	0.96
	Clipping:Extreme	2	1.07	0.34
	Warming:Clipping:Extreme	2	0.09	0.91
ER	Warming	1	4.07	< 0.01
	Clipping	1	8.26	< 0.01
	Extreme	2	4.02	< 0.01
	Warming:Clipping	1	0.42	0.51
	Warming:Extreme	2	0.84	0.43
	Clipping:Extreme	2	3.07	< 0.01
	Warming:Clipping:Extreme	2	0.03	0.97
ANPP	Warming	1	90.92	< 0.01
	Clipping	1	3.01	0.09
	Extreme	2	56.20	< 0.01
	Warming:Clipping	1	0.00	0.97
	Warming:Extreme	2	13.46	< 0.01
	Clipping:Extreme	2	2.45	0.10
	Warming:Clipping:Extreme	2	1.56	0.22

To examine interactive effects of warming, clipping, and extreme events on ecosystem CO₂ fluxes, we used the linear model as \sim Warming × Clipping × Extreme + (1|Plot) in the R package, lme4 (Bates et al., 2014). Warming, clipping and extreme were treated as fixed effects and plots as random effects. ANOVA was used to examine the effects of precipitation extremes on CO₂ fluxes for warming and clipping treatments as well as warming-induced changes in CO₂ fluxes among different precipitation extremes. When there was a significant interaction, ‘lsmeans’ package was used to perform post hoc comparisons with the false discovery rate (FDR) to correct inflated Type 1 error (Benjamini and Hochberg, 1995; Benjamini and Yekutieli, 2001; Lenth, 2016). Degree of freedom (df) in pairwise comparisons was estimated using the Satterthwaite approximation (Satterthwaite, 1946). We used means and pooled standard deviation (SD) to weighted standard error (SE) due to unequal numbers of measurements among the three precipitation extremes. Details of the statistical models used are shown in Tables 1, S1–S4.

3. Results

3.1. Extremely dry and wet years

The mean annual precipitation at this experimental site is 877 mm over the past 120 years, and has a wide range from 487 mm to 1605 mm, including extremely dry and wet years as defined by 10th (at 611 mm) and 90th (at 1154 mm) percentile thresholds, respectively (Fig. S1), and precipitation anomalies (Fig. S2). During the study period from 2009 to 2015, annual precipitation ranged from 549 mm in 2011 to 1605 mm in 2015, with mean annual precipitation of 909 mm (Fig. 1). According to the definition of extreme years based on the percentile thresholds, 2011 and 2015 were identified as extremely dry and wet years, respectively. The rest of the years were considered normal years (841 mm on average, inset, Fig. 1). In the 3-month scale of

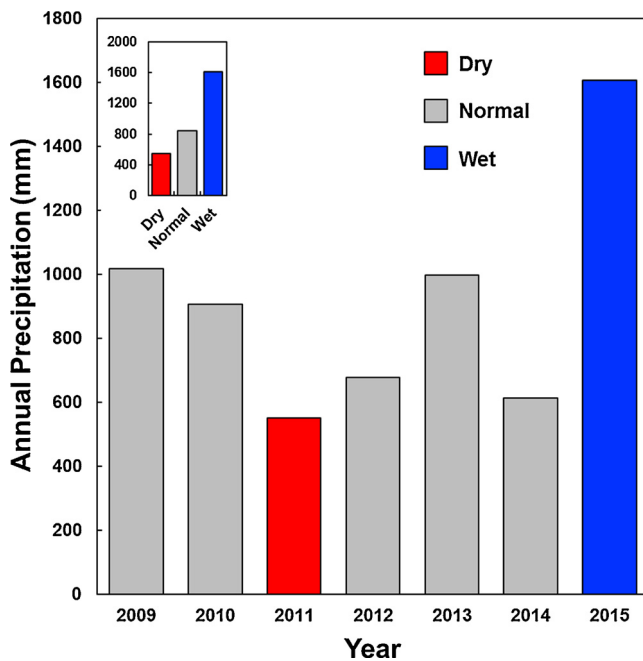


Fig. 1. Annual precipitation of the study period (2009–2015). Red, grey, and blue colors indicate dry, normal, and wet years, respectively. Inset figure indicates annual precipitation in dry, normal and wet years, respectively. The annual precipitation in normal years is the average of five years of precipitation. The data are retrieved from Oklahoma Mesonet Washington Station (200 m away from the study site). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

SPEI, the dry and wet years corresponded to approximately -2 and 2, respectively (Fig. S3). For example, the severity of drought in 2011 kept increasing until June under the warming condition. July of 2015 showed a very wet condition (Fig. S3). Precipitations in 2012 and 2014 were close to 10th percentile as presumably marginal drought years, but the SPEI indices did not exceed -2 although SPEI in some months in those years was below -1, which was moderately dry. In addition, the warming treatment generally caused more drought, and the severity of drought was especially high in 2011 (inset, Fig. S3).

3.2. Warming and clipping effects on ecosystem CO₂ fluxes in the dry, normal, and wet years

Neither the dry nor the wet year had any significant effect on NEE, GPP, and ER, compared to normal years, except for warming without clipping (i.e., the UW treatment) (Fig. 2). GPP was not significantly different across years under any treatments (Fig. 2e–h). Drought significantly stimulated ER under UW, but slightly decreased ER during the wet year, resulting in a significant ecosystem C source in the dry year but C sink in the wet year (Table 1, S1 and S2; Fig. 2b, j). ANPP was significantly lower in the dry year compared to normal years in unwarmed plots, with or without clipping (UC and CC, Fig. 2m, o). ANPP under UW and CW was significantly lower in the dry year and higher in the wet year than that in normal years ($p < 0.05$, Table 1, S1 and S2; Fig. 2n, p).

Drought significantly increased warming effects on NEE (Fig. 3a). Specifically, there was no significant difference of warming effects on GPP between climate extremes (the dry and wet years) and normal years, but warming effects on ER were significantly increased due to drought (Fig. 3b, c). This led to a reduced ecosystem C sink ($p < 0.05$, Table 1 and Fig. 3a). Warming-induced increment in ANPP was significantly higher in the wet year than in normal years in unclipped plots ($p < 0.01$, Table S3 and S4; Fig. 3d).

Over a season, the warming treatment (i.e., UW) stimulated ER from

the middle of June to the end of September in the dry year in comparison with that under UC (red vs. yellow lines in Fig. 4c). This was the primary time period when the warming treatment exerted strong effects on ecosystem gas exchanges, leading to net ecosystem C source in the dry year (shaded areas in Fig. 4a–c). On the other hand, the significantly higher ecosystem C sink under warming in the wet year than normal years (Fig. 2b, f, j) was mainly due to more stimulated GPP in spring of the wet year than normal years (Fig. 4g, h).

Clipping alleviated the drought-mediated net ecosystem C loss (i.e., positive NEE) via significantly enhanced GPP under CW in comparison with that under UW ($p < 0.01$, Table 1 and Fig. 2). Warming in the dry year resulted in net ecosystem C loss in the unclipped plots but maintained C sink in the clipped plots (Tables S1 and S2; Fig. 2a–d). Overall, clipping stimulated GPP in the spring across all years and the warming treatment (Fig. 4b, e, h). On the other hand, clipping minimized the warming effects, albeit statistically not significantly, on NEE, GPP, and ANPP, but not ER in the wet year (Fig. 3, Table 1).

4. Discussion

In this study, we examined how warming and clipping modified the impacts of naturally occurring drought and wet extremes on the grassland ecosystem C cycle. Our study provides insights into long-term grassland responses to future drought and wet extremes under warming and hay harvesting conditions. Our results indicate that future warming likely exacerbates C loss through significantly enhanced ER during drought. However, it stimulates ecosystem productivity and C sequestration during wet extremes. Hay harvesting likely dampens drought or wet impacts on ecosystem C processes.

4.1. Warming causes ecosystem C loss during extreme drought

Previous studies have reported that drought alone or drought under warming caused an ecosystem C loss due to more reduction in GPP than ER (Roy et al., 2016; Schwalm et al., 2012a; Shi et al., 2014). However, our results indicate that the warming treatment caused an ecosystem C loss during the drought year but the control treatment without warming sequestered C in the same year. The warming-induced C loss under drought was due to significantly enhanced ER rather than decreased GPP. The infrared heating system caused not only increases in surface temperature but also decreases in soil moisture in this experiment (Figs. S3–S6) (De Boeck et al., 2016, 2017; Wan et al., 2002), which might further exacerbate the naturally occurring drought in 2011. Despite a potential exacerbation by drought, we observed increases in ER, which mainly occurred between mid-summer and early-autumn (Fig. 4). However, during that period, soil moisture contents among the four treatments were very similar (Fig. S7). Thus, the increased ER under warming during the dry year unlikely resulted from artefact of the heating system.

The season for peak biomass growth is typically from mid-summer to early-autumn in the region where our study site is located (Xu et al., 2016). This season often coincides with droughts and high temperatures. In the dry year of 2011, experimental warming slightly stimulated plant growth in spring and enhanced ANPP. Naturally occurring drought, however, drove soil water contents to the permanently wilting point (Fig. S7) and as a consequence, similarly low levels of GPP under all the four treatments from mid-summer to early-autumn were exhibited (Fig. 4b). That is probably the mechanism underlying a minor warming effect on GPP in our experiment in the dry year. However, the soil moisture was around 10%, which is at about the permanently wilting point for plant growth. This moisture level may still be enough to support respiratory C release, e.g., maintenance respiration during drought (Atkin and Macherel, 2009; Flexas et al., 2005), which is higher under warming than the control.

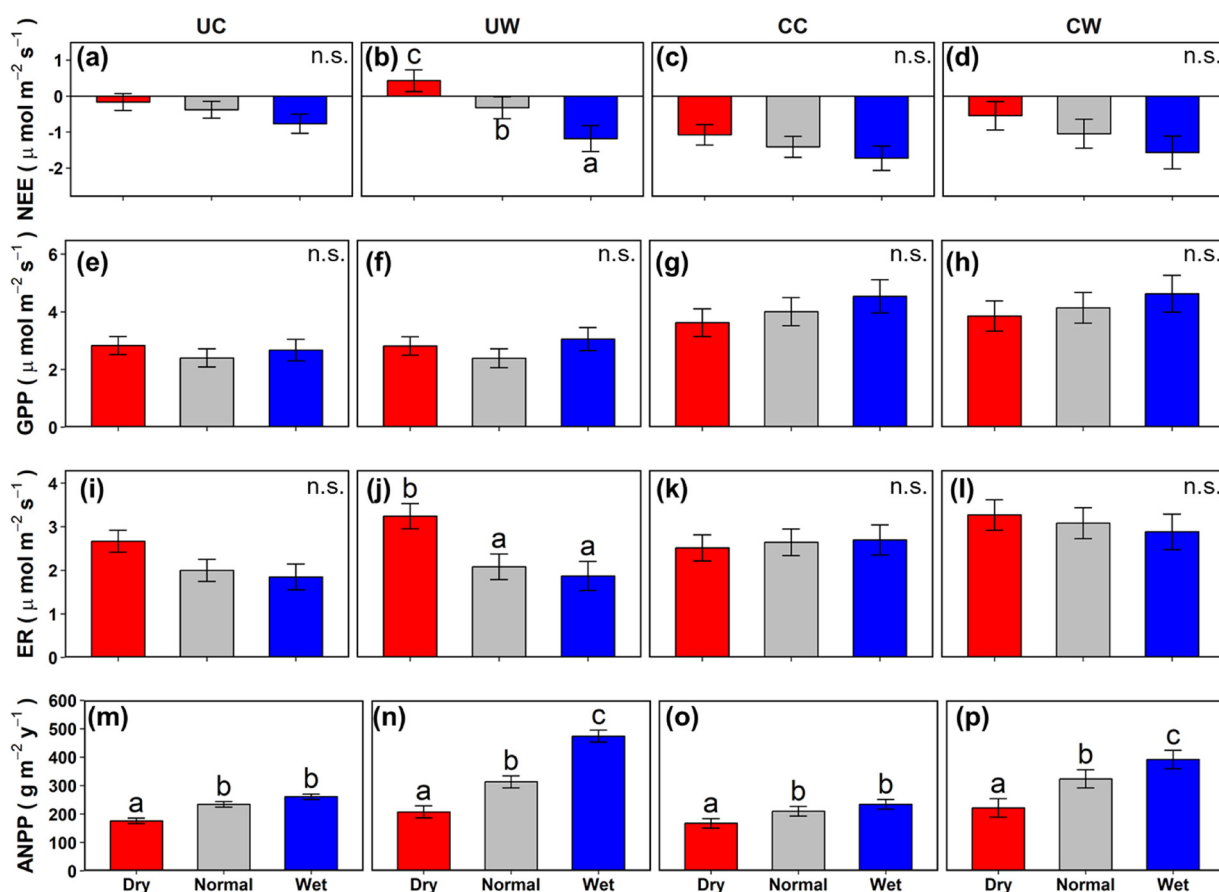


Fig. 2. Carbon fluxes and plant growth in dry, normal, and wet years at four treatments (i.e., unclipped and ambient, UC; unclipped and warming, UW; clipped and ambient, CC; clipped and warming, CW). Panels a – d for Net Ecosystem CO₂ Exchange (NEE), panels e–h for Gross Primary Production (GPP), panels i–l for Ecosystem Respiration (ER), and panels m – p for Above-ground Net Primary Production (ANPP). Different letters over bars indicate statistical significance among the three types of precipitation years (FDR, $p < 0.05$). Red, grey, and blue colors indicate dry, normal, and wet years, respectively. Detailed statistic results are in Tables S1 and S2. Error bars indicate standard error. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2. Warming enhances ecosystem production and C sink during the wet extreme

The experimental warming in our study greatly amplified wet effects on plant growth and ecosystem C exchanges, in comparison with those without warming. In the unclipped control plots without warming (i.e., UC), additional precipitation in the wet year of 2015 slightly but insignificantly stimulated ANPP (Fig. 2m). Our results at ambient temperature is consistent with previously published results (Wu et al., 2011). The increase in ANPP in the wet year of 2015, relative to those in normal years, was much higher under warming (Fig. 2n) than ambient conditions (Figs. 2m and 3 d). The strong stimulation of ANPP by warming in the wet year resulted from occurrence of additional precipitation during the fast-growing period for plants from May to July (Fig. S3).

Previous studies have shown that increasing precipitation stimulates net ecosystem C sink but magnitudes of stimulation are dependent on biome types. For example, water addition treatments significantly enhanced a net ecosystem C sink in the tallgrass prairie but no stimulation in the mixed grass prairie was observed (Wilcox et al., 2015; Xu et al., 2016). Our study also showed slightly larger, albeit not significantly, NEE in the wet year than normal years under ambient temperature (Fig. 2a). Furthermore, the warming treatment significantly enhanced C sink in the wet year in comparison with that in normal years (Fig. 2b). This is in line with a previous study, i.e., the positive effects on ecosystem C sink is intensified under the warming treatment and increased precipitation together (Wu et al., 2011). This is due to slightly increased

GPP and decreased ER in the wet year relative to those in normal years. Furthermore, C₄-dominated grasslands in higher rainfall regions such as the tallgrass prairie showed less limitation to growth than drier and intermediate precipitation regions (Cleland et al., 2013; Niu et al., 2013; Wilcox et al., 2015), partly because plants in these ecosystems can utilize water from winter and early spring (Vermeire et al., 2008).

4.3. Clipping diminishes impacts of drought and wet extremes on ecosystem C processes

Our study showed that clipping contributed to stronger net ecosystem C uptake but had smaller warming-mediated increases in C sink and ANPP than that under the unclipping treatment (Fig. 2). Previous studies suggested that clipping stimulates an ecosystem C sink (Zhang et al., 2015) via compensation mechanisms to the defoliation (Boege, 2005; Oesterheld and McNaughton, 1991; Wang et al., 2017). The clipping effect on ANPP was not significant in this study. In comparison, the clipping treatment generally reduced ANPP across the previous studies (Knapp et al., 2012; Shi et al., 2016). Clipping is also found previously to counteract with warming-mediated increases in ANPP, especially in the region where it has relatively high mean annual precipitation (Klein et al., 2007). This is consistent with our study, which shows that clipping reduced warming effects on NEE and ANPP in the wet year (Figs. 2b, d and 3 a).

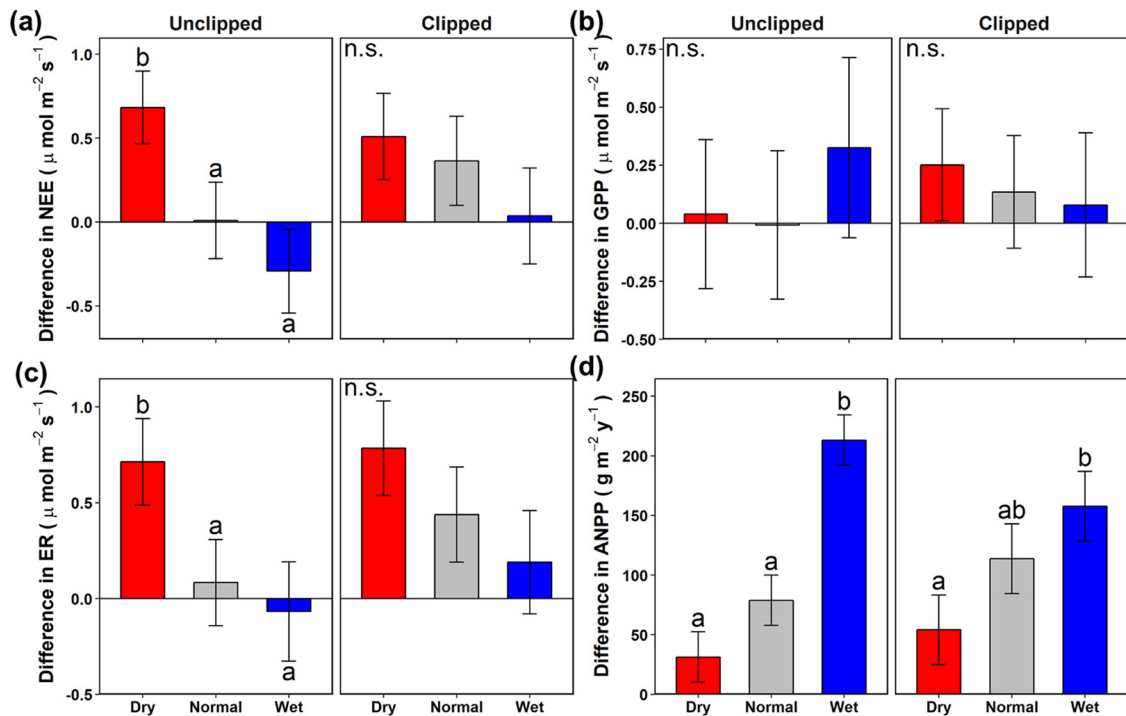


Fig. 3. Warming effects on carbon fluxes (differences in warming-ambient) without or with clipping under dry, normal, and wet years. (a) Net Ecosystem CO₂ Exchange (NEE), (b) Gross Primary Production (GPP), (c) Ecosystem Respiration (ER) and (d) Above-ground Net Primary Production (ANPP). Different letters over bars indicate statistical significance among precipitation years (FDR, $p < 0.05$). Red, grey, and blue colors indicate dry, normal, and wet years, respectively. Error bars indicate standard error. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

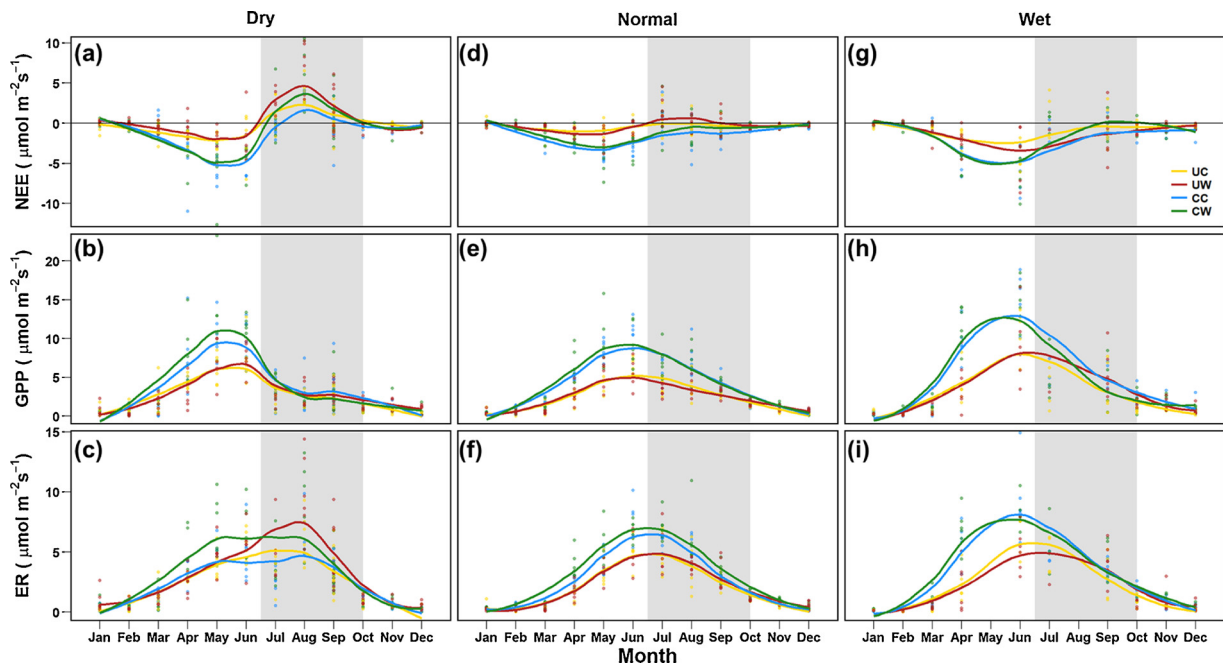


Fig. 4. Seasonal dynamics of carbon fluxes of the ecosystem across the three extremes. Lines with different colors represent manipulated treatments for Net Ecosystem CO₂ Exchange (NEE) (a, d, g), Gross Primary Production (GPP) (b, e, h), and Ecosystem Respiration (ER) (c, f, i). Shaded area indicates the season from middle of June to end of September. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Conclusions

Our results demonstrate that future climate warming may exacerbate the ecosystem C loss under extreme drought conditions but amplify the ecosystem C sink under wet extremes. The warming-mediated exacerbation of the ecosystem C loss results from stimulated ER from summer to early-autumn in the drought year of 2011. The warming

treatment significantly stimulates NEE and ANPP due primarily to strong stimulation of plant growth during the spring of a wet year. Clipping, however, plays a role not only in alleviating drought-caused ecosystem C loss through enhanced GPP in a dry year but also reducing the warming effect on the C sink and ANPP in a wet year.

Authors' contributions

Y.L. designed the experiments. C.J., X.X., S.N., J.L., X.C., Z.S., and L.J. collected the data. C.J., L.J., and Y.L. performed data analyses. All authors collaboratively discussed the results and wrote the manuscript.

Acknowledgments

We thank many laboratory members for their help with field works. This work was financially supported by the National Science Foundation Grant DEB-1655499 and US Department of Energy, Terrestrial Ecosystem Sciences Grant DE-SC0006982 and the sub-contracts 4000158404 and 4000161830 from Oak Ridge National Laboratory (ORNL) to the Northern Arizona University. ORNL's work was supported by the US Department of Energy (DOE), Office of Science, Office of Biological and Environmental Research. ORNL is managed by UT-Battelle, LLC, for the U.S. Department of Energy under contract DE-AC05-00OR22725.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agrformet.2019.107635>.

References

- Atkin, O.K., Macherel, D., 2009. The crucial role of plant mitochondria in orchestrating drought tolerance. *Ann. Bot.* 103 (4), 581–597.
- Basara, J.B., Christian, J.I., 2018. Seasonal and interannual variability of land-atmosphere coupling across the Southern Great Plains of North America using the North American regional reanalysis. *Int. J. Climatol.* 38 (2), 964–978.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2014. Fitting Linear Mixed-Effects Models Using lme4. *arXiv preprint arXiv:1406.5823*.
- Beguieria, S., Vicente-Serrano, S.M., Beguieria, M.S., 2017. Package 'SPEI'.
- Beguieria, S., Vicente-Serrano, S.M., Reig, F., Latorre, B., 2014. Standardized precipitation evapotranspiration index (SPEI) revisited: parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. *Int. J. Climatol.* 34 (10), 3001–3023.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B (Methodol.)* 289–300.
- Benjamini, Y., Yekutieli, D., 2001. The control of the false discovery rate in multiple testing under dependency. *Ann. Stat.* 1165–1188.
- Boege, K., 2005. Influence of plant ontogeny on compensation to leaf damage. *Am. J. Bot.* 92 (10), 1632–1640.
- Brock, F.V., et al., 1995. The Oklahoma Mesonet: a technical overview. *J. Atmos. Oceanic Technol.* 12 (1), 5–19.
- Brookshire, E., Weaver, T., 2015. Long-term decline in grassland productivity driven by increasing dryness. *Nat. Commun.* 6, 7148.
- Canadell, J.G., Schulze, E.D., 2014. Global potential of biospheric carbon management for climate mitigation. *Nat. Commun.* 5.
- Cernusca, A., Bahn, M., Berninger, F., Tappeiner, U., Wohlfahrt, G., 2008. Effects of land-use changes on sources, sinks and fluxes of carbon in European mountain grasslands. *Ecosystems* 11 (8), 1335–1337.
- Chaves, M.M., Flexas, J., Pinheiro, C., 2009. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Ann. Bot.* 103 (4), 551–560.
- Chen, J., et al., 2017. Warming effects on ecosystem carbon fluxes are modulated by plant functional types. *Ecosystems* 20 (3), 515–526.
- Ciais, P., et al., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437 (7058), 529–533.
- Cleland, E.E., et al., 2013. Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. *Ecology* 94 (8), 1687–1696.
- Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M., Steinauer, E.M., 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280 (5364), 745–747.
- Craine, J.M., et al., 2012. Timing of climate variability and grassland productivity. *Proc. Natl. Acad. Sci.* 109 (9), 3401–3405.
- Dai, A., 2013. Increasing drought under global warming in observations and models. *Nat. Clim. Change* 3 (1), 52–58.
- De Boeck, H.J., Bassin, S., Verlinden, M., Zeiter, M., Hiltbrunner, E., 2016. Simulated heat waves affected alpine grassland only in combination with drought. *New Phytol.* 209 (2), 531–541.
- De Boeck, H.J., Kockelbergh, F., Nijs, I., 2017. More realistic warming by including plant feedbacks: a new field-tested control method for infrared heating. *Agric. For. Meteorol.* 237, 355–361.
- Doughty, C.E., et al., 2015. Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature* 519 (7541), 78–82.
- Flexas, J., Galmes, J., Ribas-Carbo, M., Medrano, H., 2005. The Effects of Water Stress on Plant Respiration, Plant Respiration. Springer, pp. 85–94.
- Frank, D., et al., 2015. Effects of climate extremes on the terrestrial carbon cycle: concepts, processes and potential future impacts. *Glob. Change Biol.* 21 (8), 2861–2880.
- Frank, D.A., McNaughton, S.J., 1990. Aboveground biomass estimation with the canopy intercept method: a plant growth form caveat. *Oikos* 57–60.
- Friedlingstein, P., et al., 2006. Climate-carbon cycle feedback analysis: results from the C4MIP model intercomparison. *J. Clim.* 19 (14), 3337–3353.
- Granier, A., et al., 2007. Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agric. For. Meteorol.* 143 (1), 123–145.
- Hoover, D., Knapp, A., Smith, M., 2014a. Contrasting sensitivities of two dominant C4 grasses to heat waves and drought. *Plant Ecol.* 215 (7), 721–731.
- Hoover, D.L., Knapp, A.K., Smith, M.D., 2014b. Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology* 95 (9), 2646–2656.
- IPCC, 2013. Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change 1535 pp.
- Isbell, F., et al., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* 526 (7574), 574.
- Jungers, J.M., Sheaffer, C.C., Fargione, J., Lehman, C., 2015. Short-term harvesting of biomass from conservation grasslands maintains plant diversity. *Gcb Bioenergy* 7 (5), 1050–1061.
- Klein, J.A., Harte, J., Zhao, X.-Q., 2007. Experimental warming, not grazing, decreases rangeland quality on the Tibetan Plateau. *Ecol. Appl.* 17 (2), 541–557.
- Knapp, A., et al., 2012. A test of two mechanisms proposed to optimize grassland aboveground primary productivity in response to grazing. *J. Plant Ecol.* 5 (4), 357–365.
- Lenth, R.V., 2016. Least-squares means: the R Package lsmeans. *J. Stat. Softw.* 69, 1–33.
- Luo, Y., 2007. Terrestrial carbon-cycle feedback to climate warming. *Annu. Rev. Ecol. Evol. Syst.* 683–712.
- Luo, Y., et al., 2008. Modeled interactive effects of precipitation, temperature, and [CO₂] on ecosystem carbon and water dynamics in different climatic zones. *Glob. Change Biol.* 14 (9), 1986–1999.
- Luo, Y., Sherry, R., Zhou, X., Wan, S., 2009. Terrestrial carbon-cycle feedback to climate warming: experimental evidence on plant regulation and impacts of biofuel feedstock harvest. *Gcb Bioenergy* 1 (1), 62–74.
- Luo, Y., Wan, S., Hui, D., Wallace, L.L., 2001. Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* 413 (6856), 622–625.
- Ma, Z., et al., 2012. Regional drought-induced reduction in the biomass carbon sink of Canada's boreal forests. *Proc. Natl. Acad. Sci.* 109 (7), 2423–2427.
- McPherson, R.A., et al., 2007. Statewide monitoring of the mesoscale environment: a technical update on the Oklahoma Mesonet. *J. Atmos. Oceanic Technol.* 24 (3), 301–321.
- Mueller, B., Seneviratne, S.I., 2012. Hot days induced by precipitation deficits at the global scale. *Proc. Natl. Acad. Sci.* 109 (31), 12398–12403.
- Niu, S., Sherry, R.A., Zhou, X., Luo, Y., 2013. Ecosystem carbon fluxes in response to warming and clipping in a Tallgrass Prairie. *Ecosystems* 16 (6), 948–961.
- Oosterheld, M., McNaughton, S., 1991. Effect of stress and time for recovery on the amount of compensatory growth after grazing. *Oecologia* 85 (3), 305–313.
- Parton, W., et al., 2012. Impact of precipitation dynamics on net ecosystem productivity. *Glob. Change Biol.* 18 (3), 915–927.
- Pendergrass, A.G., Knutti, R., Lehner, F., Deser, C., Sanderson, B.M., 2017. Precipitation variability increases in a warmer climate. *Sci. Rep.* 7 (1), 17966.
- Peng, S.-S., et al., 2014. Afforestation in China cools local land surface temperature. *Proc. Natl. Acad. Sci.* 111 (8), 2915–2919.
- RCoreTeam, 2016. R: A Language and Environment for Statistical Computing. (R Foundation for Statistical Computing).
- Reichstein, M., et al., 2007. Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: a joint flux tower, remote sensing and modelling analysis. *Glob. Change Biol.* 13 (3), 634–651.
- Roy, J., et al., 2016. Elevated CO₂ maintains grassland net carbon uptake under a future heat and drought extreme. *Proc. Natl. Acad. Sci.* 113 (22), 6224–6229.
- Ruprecht, E., Szabó, A., 2012. Grass litter is a natural seed trap in long-term undisturbed grassland. *J. Veg. Sci.* 23 (3), 495–504.
- Satterthwaite, F.E., 1946. An approximate distribution of estimates of variance components. *Biom. Bull.* 2 (6), 110–114.
- Schmitt, M., Bahn, M., Wohlfahrt, G., Tappeiner, U., Cernusca, A., 2010. Land use affects the net ecosystem CO₂ exchange and its components in mountain grasslands. *Biogeosciences (Online)* 7 (8), 2297.
- Schwalm, C., et al., 2012a. Reduction in carbon uptake during turn of the century drought in western North America. *Nat. Geosci.* 5 (8), 551–556.
- Schwalm, C.R., et al., 2010. Assimilation exceeds respiration sensitivity to drought: a FLUXNET synthesis. *Glob. Change Biol.* 16 (2), 657–670.
- Schwalm, C.R., et al., 2012b. Reduction in carbon uptake during turn of the century drought in western North America. *Nat. Geosci.* 5 (8), 551–556.
- Sherry, R.A., et al., 2008. Lagged effects of experimental warming and doubled precipitation on annual and seasonal aboveground biomass production in a tallgrass prairie. *Glob. Change Biol.* 14 (12), 2923–2936.
- Shi, Z., et al., 2014. Differential Effects of Extreme Drought on Production and Respiration: Synthesis and Modeling Analysis.
- Shi, Z., et al., 2016. Dual mechanisms regulate ecosystem stability under decade-long warming and hay harvest. *Nat. Commun.* 7.
- Thomey, M.L., et al., 2011. Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland. *Glob. Change Biol.* 17 (4), 1505–1515.
- Trenberth, K.E., et al., 2014. Global warming and changes in drought. *Nat. Clim. Change*

- 4 (1), 17–22.
- Vermeire, L.T., Heitschmidt, R.K., Haferkamp, M.R., 2008. Vegetation response to seven grazing treatments in the Northern Great Plains. *Agric. Ecosyst. Environ.* 125 (1–4), 111–119.
- Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *J. Clim.* 23 (7), 1696–1718.
- Wan, S., Luo, Y., Wallace, L., 2002. Changes in microclimate induced by experimental warming and clipping in tallgrass prairie. *Glob. Change Biol.* 8 (8), 754–768.
- Wang, M., Bezemer, T.M., van der Putten, W.H., Brinkman, E.P., Biere, A., 2017. Plant responses to variable timing of aboveground clipping and belowground herbivory depend on plant age. *J. Plant Ecol.* 11 (October (5)), 696–708.
- Weaver, S.J., Baxter, S., Harnos, K., 2016. Regional changes in the interannual variability of US warm season precipitation. *J. Clim.* 29 (14), 5157–5173.
- Wetherald, R.T., 2010. Changes of time mean state and variability of hydrology in response to a doubling and quadrupling of CO₂. *Clim. Change* 102 (3–4), 651–670.
- Wickham, H., 2009. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.
- Wilcox, K.R., Fischer, J.C., Muscha, J.M., Petersen, M.K., Knapp, A.K., 2015. Contrasting above- and belowground sensitivity of three Great Plains grasslands to altered rainfall regimes. *Glob. Change Biol.* 21 (1), 335–344.
- Wu, P., Christidis, N., Stott, P., 2013. Anthropogenic impact on Earth's hydrological cycle. *Nat. Clim. Change* 3 (9), 807–810.
- Wu, Z., Dijkstra, P., Koch, G.W., Peñuelas, J., Hungate, B.A., 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Glob. Change Biol.* 17 (2), 927–942.
- Xu, X., et al., 2012. Interannual variability in responses of belowground NPP and NPP partitioning to long-term warming and clipping in a tallgrass prairie. *Glob. Change Biol. Bioenergy* 18, 1648–1656.
- Xu, X., Sherry, R.A., Niu, S., Li, D., Luo, Y., 2013. Net primary productivity and rain-use efficiency as affected by warming, altered precipitation, and clipping in a mixed-grass prairie. *Glob. Change Biol.* 19 (9), 2753–2764.
- Xu, X., et al., 2016. Unchanged carbon balance driven by equivalent responses of production and respiration to climate change in a mixed-grass prairie. *Glob. Change Biol.* 22, 1857–1866.
- Zhang, T., et al., 2015. Light-intensity grazing improves alpine meadow productivity and adaptation to climate change on the Tibetan Plateau. *Sci. Rep.* 5, 15949.