Drought timing influences the sensitivity of a semiarid grassland to drought

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ABSTRACT

Quantifying the sensitivity of ecosystems to droughts, particularly with different seasonal timing, could improve our predictions of ecosystem-climate feedbacks, but few experiments have explicitly addressed seasonal timing *per se* effects on ecosystem sensitivity to droughts. Here, we present a seasonal timing × drought manipulation experiment to examine sensitivity (relative change in response parameters to the relative change in precipitation) of key ecosystem processes (community biomass and ecosystem CO_2 fluxes) to pulse-drought with different seasonal timing (early, middle or late) on a temperate semiarid grassland. We found belowground and total biomass were positively sensitive (i.e. ecological processes promoted by droughts and vice versa) to early and middle droughts but negatively sensitive to late drought while aboveground biomass was insensitive to all droughts. Ecosystem CO_2 fluxes had the largest negative sensitivity to early drought and smallest negative sensitivity to middle drought, although gross ecosystem production showed larger negative response to droughts than ecosystem respiration, leading to reduction in net ecosystem production, regardless of seasonal timing. Our results highlight the crucial role of seasonal drought timing in regulating sensitivity of key carbon cycle processes to droughts and suggest that droughts at plant peak stage cause the least detrimental ecological consequences.

1. Introduction

Global climate models predict significant increases in the frequency and intensity of droughts as a result of ongoing global warming and an intensification of the hydrological cycle (Dai 2011; Sherwood & Fu 2014). At the global scale, droughts are considered the most widespread climate factor impacting the terrestrial carbon cycle (Reichstein et al. 2013; Frank et al. 2015). Occupying ca. 40% of the global terrestrial landscape (O'Mara 2012), grasslands store approximately one-third of global terrestrial carbon (Schuman et al. 2002; Poulter et al. 2014; Ahlström et al. 2015) and are particularly sensitive to climatic change (Christensen et al. 2004; Scott et al. 2015; Biederman et al. 2016), as most of them exist in dryland where growth-limiting precipitation is highly variable (Smith et al, 2019) and often becoming more erratic (e.g. Zhang et al., 2021). Notably, compared to chronic but subtle 'press-droughts', shorter term but extreme 'pulse-droughts' can cause greater carbon loss for an equivalent precipitation reduction (Hoover & Rogers 2016). As such, assessing how grasslands respond to pulse-drought is

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critically important for predicting climate-carbon cycle feedbacks. Nevertheless, we know little about whether and how the timing of drought events impacts key carbon cycling responses including biomass production and ecosystem CO_2 fluxes.

Droughts can occur throughout the year (Li et al., 2020a, Li et al., 2020b; Wang et al., 2020). Because plants at different phenological stages may have different resistance and resilience to drought, the response of ecosystems to droughts may vary with different seasonal drought timing. For example, droughts occurring in the early season have caused large reductions in current-year biomass due to limitation of peak biomass accumulation (D'Orangeville et al. 2018; Meng et al. 2019). In contrast, late season droughts have had little adverse impacts on current-year biomass but created large negative legacy effects on the following year biomass (Kannenberg et al. 2019). Besides, droughts effects on ecosystems may be context-dependence. Indeed, based on a global database of ring-width index, Huang et al. (2018) found that the average integrated legacy effects of droughts from dry season droughts was about nine times that from wet season droughts. Droughts happening in the hot summer were likely to cause larger water stress due to higher evapotranspiration than that in the relatively cool autumn (De Boeck et al. 2011). Additionally, leaf photosynthesis, ecosystem CO_2 fluxes, flowering and reproductive output responded differently to droughts in different times of the year (Dietrich & Smith 2016; Zeiter et al. 2016; Meng et al. 2019). Collectively, these findings highlight that the expected magnitude of drought impacts on terrestrial ecosystems likely depends on the seasonal timing. However, to date, how seasonal timing regulates effects of drought on belowground biomass is largely understudied.

Past studies have examined drought timing impacts, including field observations during naturally occurring droughts (Craine et al. 2012), experimental drought manipulations (De Boeck et al. 2011; Denton et al., 2016; Meng et al. 2019), and tree-ring research (D'Orangeville et al. 2018; Huang et al. 2018; Kannenberg et al. 2019). While often valuable, studies comparing droughted treatments against ambient control plots are subject to both the seasonal cycles of precipitation and interannual variability. For tree-ring research, droughts were usually identified in terms of climatic water deficit, which was calculated as the difference between precipitation and potential evaporation. In essence, this method hardly distinguished effects of drought timing and drought intensity. For experimental drought manipulations, a pulse-drought is normally defined as a precipitation-free period. Even though a constant length of the precipitation-free period is imposed in different times of year, the natural precipitation during the periods were not necessarily equal. In other words, various ecosystem responses to drought in different times of year may be attributable to not only timing but also intensity, limiting our understanding of drought timing effects *per se*.

Assessing ecosystem sensitivity to droughts with varied seasonal timing is an effective approach to address this knowledge gap. Ecological sensitivity may be defined as the unit change of output per unit change of input in either absolute terms (Wilcox et al. 2017) or relative terms (Zhang et al. 2017). In particular, the latter can maximize our ability to compare across response variables (e.g. among components of ecosystem CO_2 or biomass), multiple research approaches (e.g. manipulative experiment vs. model simulation) and different communities and ecosystems (e.g. tallgrass prairie vs. shortgrass prairie) (Smith et al. 2017).

Here, we aimed at studying whether and how drought timing *per se* would impact sensitivity of biomass and ecosystem CO_2 fluxes to drought. We asked: (a) Would different components of biomass or ecosystem CO_2 fluxes have similar sensitivities to the same drought? (b) Do drought effects on biomass and ecosystem CO_2 fluxes vary among drought events with different timing? To address these questions, an experimental pulse-drought was imposed in early-, middle-, or late-growing season for 3 years in a temperate semiarid grassland. Components of biomass (aboveground, belowground and total biomass) and ecosystem CO_2 fluxes were estimated and corresponding sensitivities

(relative change in output per unit of relative change in input) to droughts were quantified.

2. Materials and methods

2.1. Site description

We conducted this study in the Extreme Climate Events and Biodiversity-II (ECEB-II) experiment at the Inner Mongolia Grassland Ecosystem Research Station in the Xilin River Basin (43°32′ N, 116°40′ E, 1,200 m a.s.l), located in the Inner Mongolia Autonomous region, China. Mean annual temperature (1953–2017) is 2.5 °C and mean annual precipitation is 281 mm with 86% falling during the growing season from May to September. The experiment was established in a temperate semiarid steppe, dominated by *Leymus chinensis, Agropyron cristatum, Cleistogenes squarrosa,* and *Carexduriuscula,* which has not been grazed since 1979. Aboveground biomass progressively increased from May to August and reached peak at mid-August, then slightly decreased in September (Zhang et al., 2018). The soil at this experimental site is classified as Dark Chestnut in the Chinese soil classification Calcic Chernozem in World Reference Base for Soil Resources, with 60% sand, 21% clay and 19% silt (Hao et al. 2013).

2.2. Experiment design

In this study, a pulse-drought was considered a precipitation-free period. The longest rainfall interval between two successive precipitation events in the growing season from 1953 to 2010 (the longest weather record for this site) was 30 days. Thus, the extreme drought was defined as a rain-free period of 30 days (Li et al. 2020). In accordance with the observed timing of seedling establishment, growth and vegetation senescence, the growing season was divided into early (from early May to mid-June), middle (from late June to mid-August) and late (from late August to the end of September) periods. The treatments included: (1) ambient conditions for control (Ambient), (2) extreme drought imposed in the early-growing season (Early: 15 May-13 June), (3) extreme drought imposed in the mid-growing season (Middle: 20 July-18 August) and (4) extreme drought imposed in the later-growing season (Late: 20 August-18 September). Although the duration of each drought was 30 days, the natural ambient precipitation excluded during the periods was different. Thus, the three droughts in the same year correspond to different growing season precipitation reductions. Similarly, the same drought in different years corresponds to different growing season precipitation reductions. There were three replicates for each treatment and sixteen plots in total using a random block layout. The experiment is a part of the Extreme Climate Events and Biodiversity-II (ECEB-II) experiment that began in 2012.

Each plot (2.0 m × 2.0 m) was surrounded with a metal frame (40 cm deep in soil and 10 cm above ground) to prevent water exchange across plot boundaries. There is 2.0 m distance between blocks and 1.0 m distance between plots within each block. Droughts were achieved by rain shelters (3 m × 3 m), which consisted of a steel frame supporting a transparent polyester fiber board (permitting nearly 90% penetration of photosynthetically active radiation without limiting plant photosynthesis (Li et al., 2019)). The shelters were high enough (2.1 m and 1.8 m maximum and minimum heights, respectively) to maximize air movement and minimize temperature rise (Liu et al., 2017). The shelters were installed to cover the plots over the experimental drought periods to intercept all ambient rainfall into plots during the treatment periods and removed during the remainder of each growing season (Li et al., 2016).

2.3. Precipitation and soil water content measurements

Daily air temperature and precipitation data were obtained from a nearby (50 m approximately) temperature probe (HMP45C, VAISALA, Woburn, MA, USA) and a tipping bucket rain gauge (TE525MM,

Campbell Scientific Inc., Logan, UT, USA) at 2.2 and 1.5 m above ground, respectively. During the growing season, soil water content (SWC) in the 0–20 cm soil layer was measured in three randomly selected locations per plot during each measurement (every c. 5 d in 2015 and 2016 and every c. 10 d in 2014) by manually inserting a time domain reflectometry probe (TDR 300, Spectrum Technologies, Inc. CST, USA) into the soil, and their mean was used to represent the plot-level SWC for that day, similar to prior studies (Ru et al., 2018; Zhong et al., 2019). The probability of measuring the same location across subsequent measurements and potentially influencing measurement accuracy is small. We have good confidence in SWC measurement by this method because the variations in SWC across three locations per plot were small over the growing season (Fig. S2) and they matched SWC measured by a moisture sensor (CS616; Campbell Scientific Inc., Logan, UT, USA) which is located at 50-meter distance from the experiment platform (Fig. S3).

2.4. Community biomass measurements

Aboveground biomass (AGB) was estimated once a year by harvesting all aboveground plant materials in one 0.25 m^2 quadrat located within each 4 m^2 plot at the end of treatments (around 15th September). All live plant tissues (excluding dead tissues and litter) were oven dried at 65 °C for 48 h and weighed as AGB. We changed the locations of quadrats each year to prevent resampling of the same quadrat.

We used root length and specific root length to estimate belowground biomass (BGB) at the end of the growing season (late September) in 2014 to 2016 (Li et al. 2019; Li et al. 2020). Briefly, first, one transparent minirhizotron tube (45° angle from the ground surface, 70 mm external diameter, 100 cm length and 20 cm remaining above ground) was installed in the soil of each plot in May 2012. Then, a root scanner system (CI-600 Root Growth Monitoring System, CID Inc., Vancouver, WA, USA) was inserted into the transparent minirhizotron tube to scan images (grayscale with 400 dpi) at three vertical depths of 0–14 cm, 14–28 cm and 28–42 cm. Next, the program RootAnalysis (Analysis Ome Co. Ltd, Beijing, China) was used to analyze root length in each image. The sum of the root lengths at the three depths in each tube was the plot-level root length. Last, BGB was estimated according to Equation (1) (Fischer et al. 2007).

$$\text{BGB}\left(g m^{-2}\right) = \frac{L \times D}{SRL \times AOI \times DOF} \tag{1}$$

where L was the measured root length; D was the vertical depth sampled (m), SRL was specific root length (estimated at 36 m g^{-1} in this site (Cheng et al. 2016)); AOI was the measurement area of an image (m^2); and DOF was depth of field of each image (0.0025 m in this study). This method has been validated with traditional soil-coring methods at this site (Li et al. 2019). Total biomass (TB) was calculated as the sum of AGB and BGB.

2.5. CO$_2$ flux measurements

One square stainless steel frame (50 cm × 50 cm, 10 cm high) was inserted 7 cm into the soil in each plot in May 2012. We used an infrared gas analyser (LI-840A, LI-COR Inc., Lincoln, NE, USA) and a transparent chamber (50 cm × 50 cm × 50 cm with a placket on one side), connected with one air pump (6262–04, LI-COR Inc. Lincoln, NE, USA) and two plastic tubes to measure ecosystem CO$_2$ fluxes. The chamber was placed on the frame without and with a lightproof cloth cover to respectively measure net ecosystem exchange (NEE) and ecosystem respiration (ER) between 9:00 and 11:30 on sunny days. Thus, photosynthetically active radiation is sufficient, and the air/soil temperature are relatively stable during the measurements. The difference in ecosystem CO$_2$ fluxes across four treatments were mainly determined by treatment-induced changes in soil water availability and thereby biological processes (e.g. plant photosynthesis and respiration). Every measurement continued for 90 s, and the data (CO$_2$ and H$_2$O concentration, etc.) were recorded per second. Only the middle 70 s of the records were used to calculate CO$_2$ fluxes (the time-gradient of CO$_2$ concentration changes). The chamber was lifted and vented between two consecutive measurements to replace the air in the chamber. CO$_2$ fluxes were measured at approximately 10-day intervals throughout the whole growing season (Fig. 4). For detailed information about the measurement and calculation, see Chen et al. (2009). Gross ecosystem production (GEP) was calculated as the difference between NEE and ER. Net ecosystem production (NEP) was the net ecosystem CO$_2$ uptake (i.e. NEP = -NEE = GEP - ER).

2.6. Statistical analyses

For manipulative precipitation drought experiments, droughts intensity was normally indicated by the amount of decreased precipitation given that precipitation was the only changed environmental variable while temperature may not be directly affected in plot-scale experiments. Therefore, when calculating sensitivity of ecological attributes to precipitation drought in this plot-scale experiment, only precipitation amount was involved in the equation. Sensitivity was calculated according to equation (2), which represents relative change in output per unit of relative change in input and has been widely used in previous studies (Smith et al. 2017; Zhang et al. 2017). This metric allowed us to eliminate effects caused by different amounts of precipitation during drought periods and directly compare the timing effects *per se.*

$$\text{Sensitivity} = \frac{(\overline{Y}_d - \overline{Y}_c)/\overline{Y}_c}{(GSP_c - GSP_d)/GSP_c} \tag{2}$$

where $\overline{Y}_d$ and $\overline{Y}_c$ are the variables' means across replicates of drought and control groups, respectively, and GSP$_d$ and GSP$_c$ are the precipitation amounts in drought and control groups during the growing season, respectively. There was one sensitivity value for each variable each drought treatment each year. Negative sensitivity represents suppression of ecological response by droughts while positive sensitivity represents promotion of ecological response by droughts. A sensitivity of + 1/-1 indicates that a relative reduction in precipitation (e.g. −10%) induces the same relative increase/decrease in response parameters (e.g. + 10%/-10%). The absolute sensitivity value is not of primary importance. Instead, this study focuses on sensitivity differences in various components of biomass and in ecosystem CO$_2$ fluxes with respect to the seasonal timing of drought.

Because water loss through evaporation affects ecological drought intensity, we also calculated the sensitivity to precipitation deficit (precipitation minus potential evaporation) (Text S1). Overall, the sensitivities to precipitation amount showed a similar pattern with the sensitivities to precipitation deficit although the magnitude of these two sensitivities differed (Table 2 vs. Table S1, Fig. 3 vs. Fig. S5). To facilitate comparison with past studies (Smith et al. 2017; Wilcox et al. 2017; Zhang et al. 2017), we mainly focused on the sensitivity to precipitation amount.

Mixed-effects models were employed to test the drought and year effects on AGB, BGB, and TB while plots were included as a random effect using package nlme in R. Duncan's test was used to assess the differences among four treatments in these variables each year and in ecosystem CO$_2$ fluxes in each measurement.

Additionally, we used student's *t*-test to assess whether the sensitivities of each variable significantly differed from zero. Duncan's test was also used to assess the differences in sensitivity of each component of CO$_2$ fluxes (NEE, ER, and GEP) and biomass (AGB, BGB and TB) among the three drought treatments, respectively. Treatment effects were considered to be statistically significant at $P \leq 0.05$ and marginally significant at $P \leq 0.10$ given the small sample size (n = 3). All statistical analyses were performed with R v.3.4.4.

3. Results

3.1. Rainfall, air temperature, and soil water content

The growing season (1 May-30 September) precipitation (GSP) was 256 mm, 243 mm and 186 mm in 2014, 2015 and 2016, respectively. GSP in the early, middle and later drought treatments was reduced by 13.2%, 14.6% and 19.0% in 2014, 13.6%, 21.6% and 15.5% in 2015, and 22.4%, 22.3% and 24.6% in 2016, respectively (Fig. S1). Mean Air temperature across the growing season was 15.1, 14.9 and 15.9 °C. Air temperature during the middle drought was obviously higher than that during early and later droughts (Fig. S2). There were no significant differences in soil water content between treatments prior to the treatment implementation. Soil water content continually decreased in drought plots during each treatment period and rapidly recovered when rewetting again after drought (Fig. 1). Soil water content had significant negative sensitivity to all three droughts, but differences in sensitivities were not significant (Fig. S6).

3.2. Community biomass

The effects of three precipitation droughts on absolute values of each component of biomass (BGB, AGB and TB) were not significant (Fig. 2 and Table 1). Nevertheless, overall, the sensitivities of biomasses to droughts (relative change in biomass per unit of relative change in precipitation) were significant or marginally significantly higher than zero at (Table 2). Thereinto, AGB was not sensitive to early and late droughts but had a marginally significantly positive sensitivity to the middle drought (Table 2; Fig. 3a). There were no significant differences in AGB sensitivity between different drought timings (Fig. 3a). In contrast, BGB and TB had significant or marginally significant sensitivities to all three droughts (Table 2), but the direction and magnitude

of the sensitivities depended on drought timing. BGB and TB showed negative sensitivities to the middle and early droughts but positive sensitivities to the late drought (Fig. 3a).

3.3. Ecosystem CO_2 fluxes

The magnitude of ER NEP, and GEP significantly decreased during the drought periods regardless of timing. Thus, both ecosystem carbon absorption and emission were suppressed by drought (Fig. 4). After the middle drought, the suppressed ecosystem CO_2 fluxes rapidly recovered to ambient control levels and, in some cases, even higher than that in ambient control (such as ER in 2014, Fig. 3g). Nevertheless, the negative effects of the early drought on CO_2 fluxes continued for relatively longer times after the treatment was finished. ER and GEP recovery after the late drought treatment were incomplete due to lack of adequate time at the end of each growing season (Fig. 4).

All CO_2 fluxes had significant negative sensitivity to drought (Fig. 3b and Table 2). However, GEP was more sensitive to any drought than was ER. Generally, sensitivities of CO_2 fluxes were highest in the early drought treatment but lowest in the middle drought treatment (Fig. 3b).

4. Discussion

4.1. Effects of droughts on community biomass

Different biomass components showed various sensitivities to droughts; belowground biomass, which was the dominant influence on total biomass, had marked responses (Fig. 3) while aboveground biomass was generally insensitive to droughts. In a meta-analysis study, Wilcox et al. (2017) reported that there were no significant differences between the positive sensitivity of aboveground and below biomass to precipitation decreases. Here, the greater belowground biomass
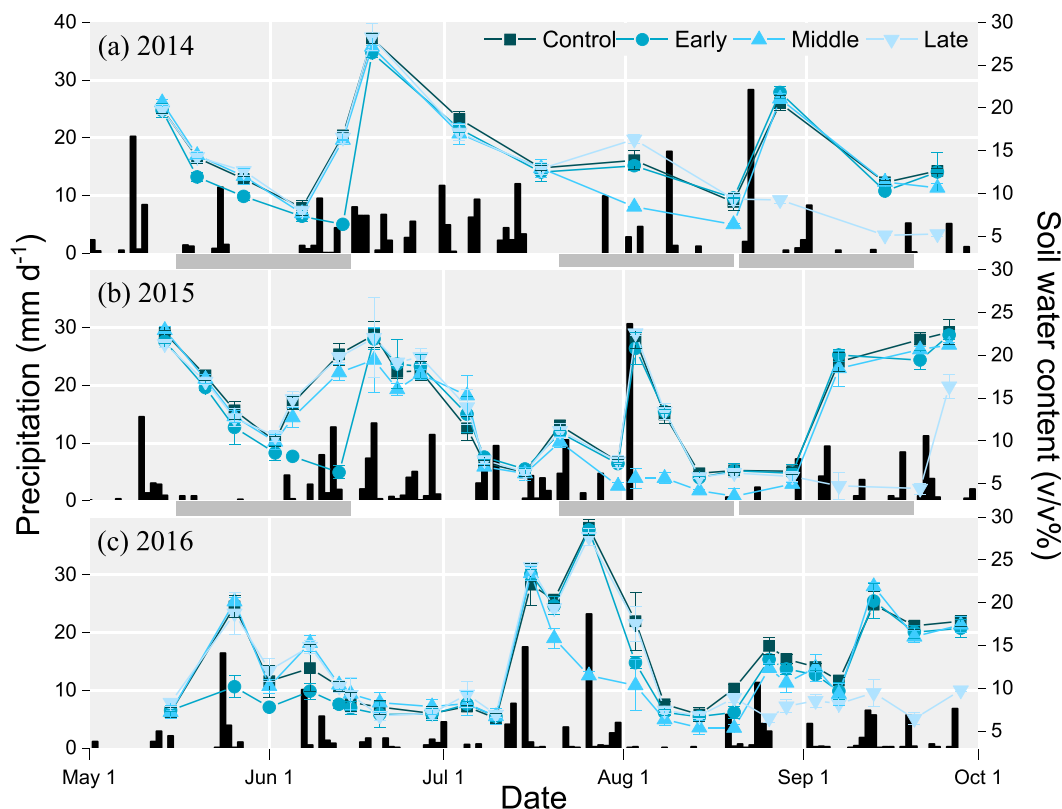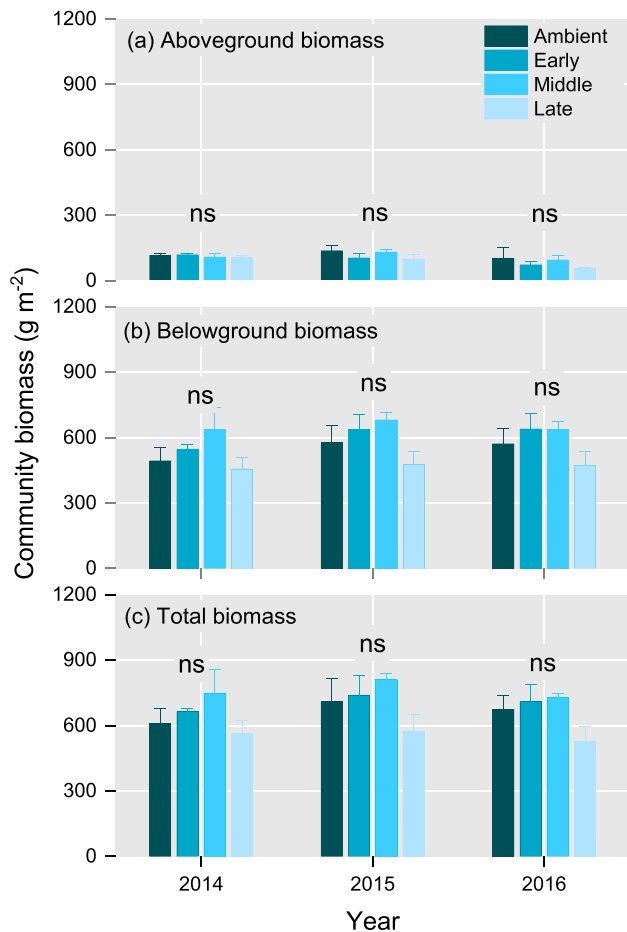

Fig. 1. Natural precipitation (black column) and soil water content (line) in four treatments during growing season from 2014 to 2016. Ambient, Early, Middle and Late represent ambient control, and drought imposed in early-, mid- and late-growing season, respectively. Three grey shaded strips indicate three drought periods in order. Error bars indicate 1 SE.

Fig. 2. Response of biomass to three precipitation droughts from 2014 to 2016. Empty column, solid column in upper part, solid column in lower part of graph indicate total biomass and aboveground biomass and belowground biomass, respectively. Ambient, Early, Middle and Late represent ambient control, and drought imposed in early-, mid- and late growing season, respectively. ns represents no significant differences in responses at α = 0.05. Error bars indicate 1 SE.

Table 1

Results from mixed-effects model analyses about the effects of precipitation drought imposed in early-, mid-, and late-growing season on aboveground, belowground and total biomass (AGB, BGB, and TB).

Fixed effect	df		AGB		BGB		TB	
	num	den	*F*	*P*	*F*	*P*	*F*	*P*
Early	1	8	0.26	0.62	0.52	0.49	0.32	0.59
Middle	1	8	0.25	0.63	0.31	0.10	0.42	0.10
Late	1	8	3.07	0.12	0.81	0.39	1.37	0.27
Year	2	16	3.53	**0.05**	3.95	**0.04**	2.32	0.13
Early × year	2	16	0.32	0.73	0.88	0.43	0.26	0.77
Middle × year	3	16	0.14	0.87	0.57	0.59	0.20	0.82
Late × year	3	16	0.41	0.67	0.70	0.51	1.05	0.37

Early, Middle and Late represent drought imposed in early, middle and late growing season, respectively.

P values in bold are statistically significant to an alpha value of 0.05.

den df, denominator degrees of freedom; num df, numerator degrees of freedom

sensitivity to reduced precipitation than aboveground biomass sensitivity seems to conflict with this claim. Unexpectedly, the large ranges of belowground biomass sensitivity from positive (early and middle drought) to negative (late drought) values in this study suggested that early and middle droughts enhanced belowground biomass while late drought reduced belowground biomass. However, droughts did not

Table 2

Results from *t*-test of sensitivity of ecosystem CO_2 fluxes and biomass to precipitation drought imposed in early-, mid- and late-growing season, respectively.

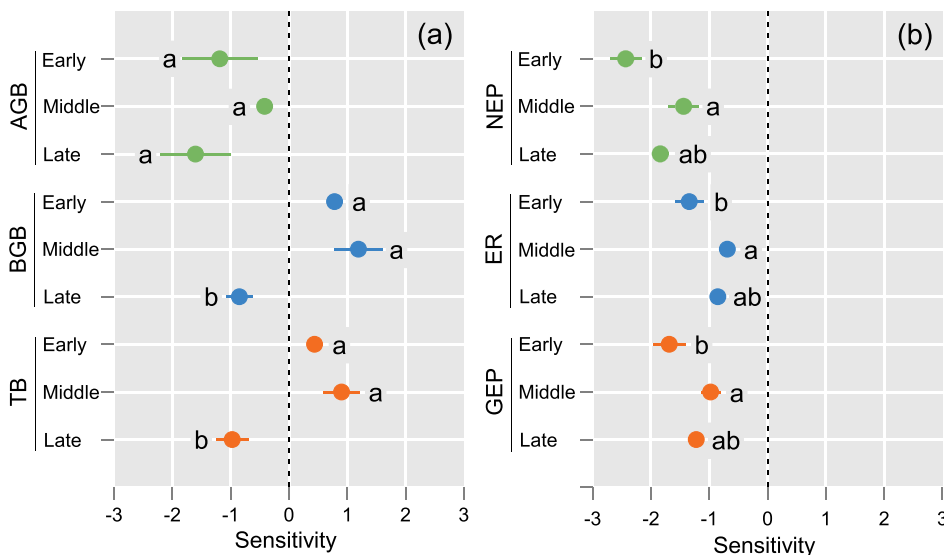|	df	Early		Middle		Late	
		t	*P*	t	*P*	t	*P*
NEP	2	8.90	**0.01**	5.53	**0.03**	15.38	**<0.01**
ER	2	5.43	**0.03**	5.82	**0.03**	9.54	**0.01**
GEP	2	6.01	**0.03**	5.78	**0.03**	14.25	**<0.01**
AGB	2	1.83	0.21	4.06	0.06	2.64	0.11
BGB	2	−27.92	**<0.01**	−2.92	0.10	3.67	0.07
TB	2	−3.64	0.07	−2.84	0.10	3.44	0.07

Early, Middle and Late represent drought imposed in early-, mid- and late growing season, respectively.

NEP: net ecosystem production, ER: ecosystem respiration, GEP: gross ecosystem production, AGB: aboveground biomass, BGB: belowground biomass, and TB: total biomass.

P values in bold are statistically significant at an alpha value of 0.05.

show significant effects on absolute values of biomass, highlighting that directly assessing drought timing impacts without eliminating differences in reduced precipitation amount may confound the effects of drought intensity and drought timing. To date, a general pattern of belowground biomass responses to drought is still lacking (Luo et al. 2017). Kahmen et al. (2005) suggested that belowground biomass responses to drought depend on plant diversity while aboveground biomass was independent of plant diversity. Past studies examining drought effects usually did not consider drought timing. In some manipulative experiments, materials and methods clearly reveal drought treatments applied at different times, but the impacts of seasonal timing were not addressed. For example, for a multiple-year drought experiment in a pasture at Früebüel, the drought period varied in different years (from August 3 to September 27 in 2007 but from June 26 to August 13 in 2008) (Hartmann and Niklaus, 2012). Our results provided an example that discrepant impacts of drought on biomass across studies may have resulted from different drought timing.

In this study, early and middle drought increased belowground biomass but caused no dramatic changes in aboveground biomass, thus *increasing* total biomass and root-shoot ratios. Similar results were found in another drought experiment (Dreesen et al. 2012). Our results differ from a semiarid grassland study where spring and summer droughts reduced aboveground biomass but did not affect belowground biomass (Meng et al. 2019), and from a mesic grassland study where late spring drought, early summer drought and late summer drought had no effects on belowground net primary productivity but the latter two droughts reduced aboveground net primary productivity (Denton et al., 2016). In fact, most previous studies have found that drought increased belowground biomass, usually at the cost of decreasing above ground biomass and consequently reducing total biomass (Carter et al. 1997; Kahmen et al. 2005). Carbon isotope labelling experiments have shown that drought caused translocation of a relatively larger portion of newly assimilated carbon to root rather than shoot (Huang & Fu 2000; San-aullah et al. 2012; Burri et al. 2014; Karlowsky et al. 2018). Furthermore, increased nutrient availability resulting from rewetting after drought ("Birch effect", (Birch 1958, 1964; Evans & Burke 2013)) had potential to stimulate or even overcompensate plant growth (Dreesen et al. 2012), particularly in high plant diversity systems (Isbell et al. 2015; Kreyling et al. 2017; Wagg et al. 2017). In our study, the plant root biomass could have decreased during the early or middle drought but recovered after drought. Consequently, the plant community could have maintained or even further strengthened the root system, particularly in July when the plant community had peak canopy and maximum growing rates for acquiring water and nutrition under the ongoing drought regime (growing season precipitation was 287 mm, 256 mm, 243 mm and 186 mm from 2013 to 2016). In turn, the stronger root system would have contributed to the stability of the plant community in response to droughts. Besides, compensation effects between grass and

Fig. 3. Sensitivity of biomass (left panel) and ecosystem CO_2 fluxes (right panel) to three precipitation droughts across three years. Early, Middle and Late represent drought imposed in early-, mid- and late growing season, respectively. Sensitivity is calculated as the relative amount of productivity decrease divided by the relative amount of precipitation decrease. Negative sensitivity represents suppression of ecological response by droughts while positive sensitivity represents promotion of ecological response by droughts. NEP: net ecosystem production, ER: ecosystem respiration, GEP: gross ecosystem production, AGB: aboveground biomass, BGB: belowground biomass, and TB: total biomass. Different letters represent significantly different sensitivity across three droughts for each variable at $\alpha = 0.05$. Error bars indicate 1 SE.

non-grass functional groups buffered effects of droughts on aboveground biomass (Li et al., 2020a, Li et al., 2020b).

The decreases in belowground and total biomass in the late drought treatment might be because the plants in these plots had already suffered from soil water deficiency (soil water content was lower than the wilting point of 0.12 m^3 m^{-3}) for some time before the start of treatment (Fig. 1). Low ambient precipitation before the treatment, combined with subsequent artificial drought, might have exceeded the tolerance threshold of the plant community. This highlighted the important role of antecedent effects (i.e. soil water state in this study) in ecosystem responses to climate extremes (Potts et al. 2006; Wu et al. 2011; Li et al. 2016). Another possible reason for the reduction in belowground and total biomass of the late drought treatment was that the limited photosynthetic capacity in the 10 days following the drought was unable to produce adequate carbohydrates to rebuild the root system at the end of the growing season. Collectively, antecedent effects of soil moisture and recovery after drought could have co-determined the sensitivity of belowground biomass to droughts.

4.2. Effects of droughts on ecosystem CO_2 fluxes

In this study, both gross and net ecosystem CO_2 uptake (GEP and NEP) and emission (ER) were suppressed by drought regardless of seasonal timing (Fig. 3). This was most likely due to stomatal closure and leaf abscission in order to prevent transpiration, as well as inhibition of soil microbial activity under water stress (Li et al. 2020). Additionally, gross ecosystem production was more sensitive than ecosystem respiration to the three drought treatments, resulting in decreases in net carbon sink (Fig. 4a), which is consistent with previous general findings (Chen et al. 2009; Wu et al. 2011; Yu et al. 2013; Li et al. 2016; Biederman et al. 2016).

However, the sensitivity of specific CO_2 fluxes to drought depended on the drought timing in our experiment. Variations in the precipitation effects on carbon exchange with drought timing have also been observed in many previous studies but with high context-dependence (Chou et al. 2008; Hao et al. 2010; Jongen et al. 2011). For example, both community photosynthesis and ecosystem respiration were more negatively affected by drought in summer than in spring or autumn in an experimental herbaceous community (De Boeck et al. 2011). In contrast, similar to our study, reduction in carbon exchange induced by drought was larger at the beginning than at the end of the growing season in a poplar plantation, (Zhou et al. 2013), although there are many differences in characteristics between forests and grasslands. The variability

of drought effects with seasonal timing was mainly attributed to two factors, magnitude and duration of droughts. When drought occurred at the stage of canopy development, normally in spring or early growing season, the adverse ecological effects caused by drought might continue throughout the rest of the growing season (Zhou et al. 2013). On the other hand, if drought happened in times with high air temperature, more likely in summer or middle growing season, higher evapotranspiration could cause greater water stress by such drought compared to one in a relatively cool period with equal precipitation decline. Thus, drought in a hot season could cause higher plant mortality than in a cool season, triggering more profound impacts (De Boeck et al. 2011). It also suggested that quantifying precipitation drought alone may not fully reflect impacts on ecosystem water status. Instead, indexes taking into account both moisture input (precipitation amount) and output (e.g. potential evapotranspiration), such as precipitation deficits (precipitation amount minus potential evapotranspiration), should also be considered.

In this study, the sensitivity of CO_2 fluxes was higher to early drought and lower to middle drought (Fig. 3). The large magnitude of early drought sensitivity is associated with large drought legacy effects on ecosystem CO_2 fluxes. In other words, the negative effects of the early drought on CO_2 fluxes continued for relatively longer times after the treatment was finished (Fig. 4). A typical example is the large reductions in all three ecosystem CO_2 fluxes at the ninth day (day of year is 174) after the early treatment finished in 2015 (Fig. 4c, h, and k). This could be because early drought damaged leaf and thereby canopy development (Zhou et al. 2013). The small middle drought sensitivity was related to great resilience. Ecosystem CO_2 fluxes rapidly recovered as soon as the middle drought finished. We unexpectedly observed that ecosystem respiration in middle drought after the treatment was higher than that of ambient control in 2014 (Fig. 4g). The great resilience of ecosystem CO_2 fluxes to middle drought might be due to large positive responses of belowground biomass. Strong root systems promoted uptake of water and nutrients, contributing to the restoration of drought-induced leaf damage and subsequent leaf physiological processes.

5. Conclusion

Drought timing regulated drought effects on ecosystem carbon cycling. The larger gross ecosystem production sensitivity to droughts than ecosystem respiration regardless of seasonal timing demonstrated that drought could cause adverse impacts on the carbon exchange. Importantly, ecosystem CO_2 fluxes were more sensitive to early drought
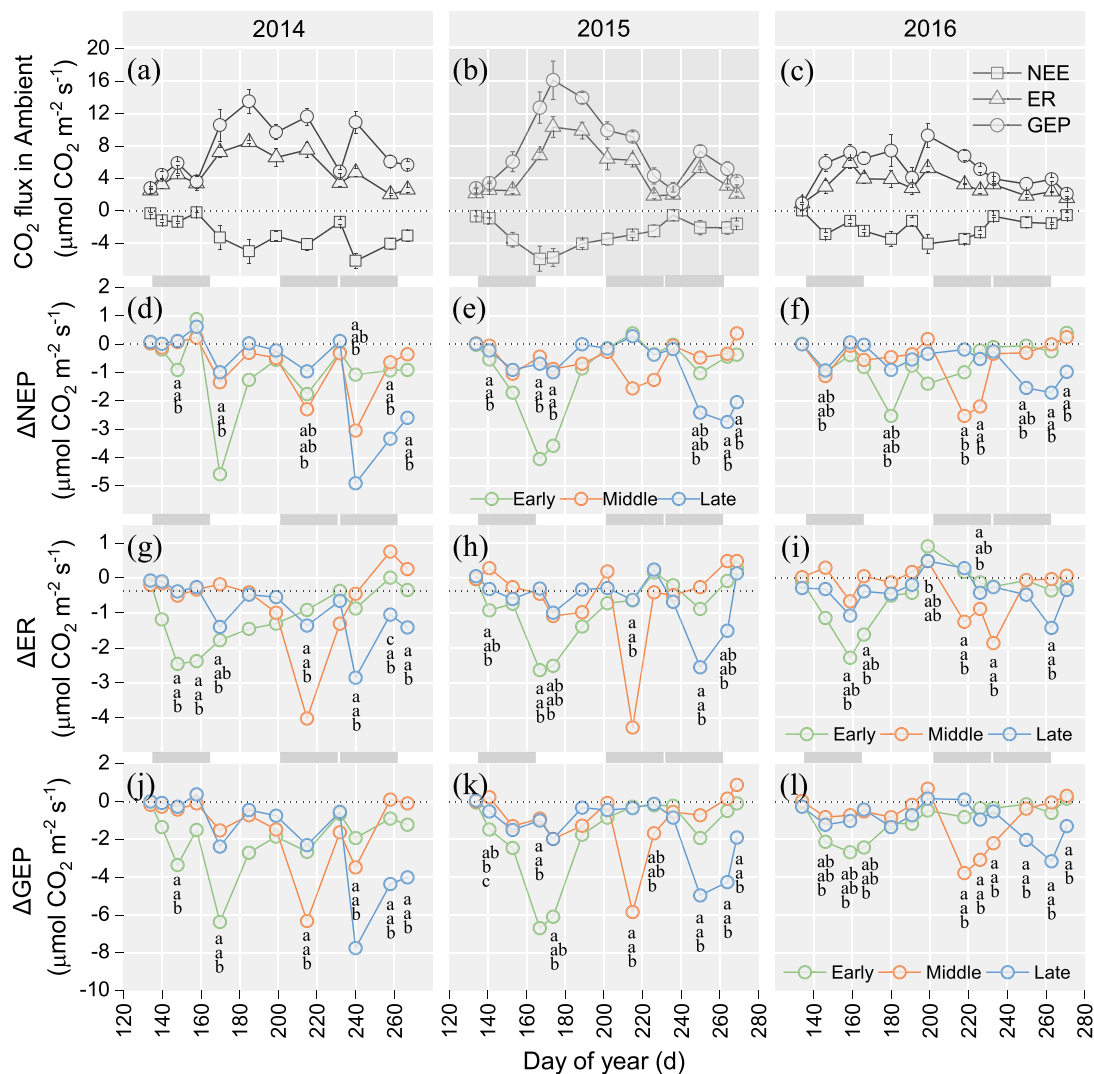
Fig. 4. Temporal dynamics of CO_2 fluxes in ambient control (a, b, c) and treatment effect (Δ) on CO_2 fluxes from 2014 to 2016. Δ is calculated as mean of treatment minus that in ambient control. NEP: net ecosystem production, ER: ecosystem respiration, and GEP: gross ecosystem production. Early, Middle and Late represent drought imposed in early-, mid- and late growing season, respectively. Duncan's test, based on raw data (i.e. three values (replicates) for each treatment each measurement), was used to assess the differences among four treatments Different letters represent different sensitivity at α = 0.05 (values of ambient defaulted as a). Only significant difference among treatments was showed. Error bars in a-c indicate 1 SE. Because the variability of Δ value made no sense, the error bars for each delta value were not presented. Three grey shaded strips between indicate three drought periods in order. Error bars indicate 1 SE.

than middle and late droughts, suggesting that reduction in the carbon uptake could be most severe if drought occurred in the early-growing season. In addition, belowground biomass was a major contributor to total biomass in this grassland. The sensitivity of belowground and total biomass even varied from positive (either early or middle drought) to negative (late drought). Our study indicated that when assessing ecosystem sensitivity to climate change, especially extreme events, it is necessary to take into account the events' timing in addition to its magnitude. Incorporating seasonal timing effects of drought in C cycling models can improve simulation of carbon dynamics.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2022.115714.

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