



# Contrasting responses of plant above and belowground biomass carbon pools to extreme drought in six grasslands spanning an aridity gradient

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Received: 4 January 2021 / Accepted: 2 December 2021 / Published online: 19 February 2022  
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## Abstract

**Background and aim** As global climate change intensifies, the frequency and duration of extreme droughts are predicted to increase, resulting in extended periods of reduced soil water availability across ecosystems. The allocation of carbon (C) to above- and below-ground plant biomass is a fundamental ecosystem property that varies spatially and temporally with water availability. Yet, how extreme

drought affects biomass C pools along an aridity gradient remains poorly understood.

**Methods** To elucidate the effects of extreme drought on above- and belowground carbon storage, we conducted a 3-year (2015–2017) precipitation manipulation experiment (66% reduction in growing season precipitation) to simulate a multi-year extreme drought across six grasslands spanning an aridity gradient from desert steppe, typical steppe, and meadow steppe in northern China.

**Results** Extreme drought significantly decreased aboveground biomass carbon (AGBC) and litter carbon (LC), but did not affect belowground biomass carbon (BGBC) across the six grasslands. As a result, grassland total carbon (TC) in plant biomass declined

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Responsible Editor: Xiao-Ping Xin.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s11104-021-05258-4>.

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overall by ~10%. Across the aridity gradient, drought-induced reductions in AGBC and LC increased with increasing aridity (i.e., reductions were greater in desert steppe than meadow steppe). In contrast, extreme drought increased BGBC in the drier grasslands (desert steppe and typical steppe), but decreased BGBC in the more mesic meadow steppe sites.

**Conclusion** We found that extreme drought elicited contrasting responses of plant above- and belowground carbon across an aridity gradient, and that regionally extreme drought will result in a loss of total plant carbon in grasslands dominated by aboveground plant carbon pools.

**Keywords** Biomass carbon · Climate change · Extreme drought · Grassland · Precipitation manipulation experiment

## Introduction

Grasslands are important terrestrial ecosystems covering more than 40% (59 million km<sup>2</sup>) of the earth's land surface (Hufkens et al. 2016) and they play a major role in the global carbon budget (Frank and Dugas 2001; Luo et al. 2020). Natural grasslands contribute more than 20% of total terrestrial biomass production and store one-third of all terrestrial carbon; thus, they have a considerable potential to influence global carbon reserves (Hoovers and Rogers 2016). In the future, extreme climatic events, such as extreme drought, will likely alter grassland biomass production and carbon storage (Smith 2011; Shi et al. 2014; Griffin-Nolan et al. 2019). We define extreme drought as a statistically rare, extended occurrence of low water availability that alters ecosystem structure and function beyond the range of typical or normal

variability in a particular site or region (Smith 2011). While short-term droughts frequently affect grasslands across the globe, especially those classified as arid and semi-arid (Schwinning et al. 2005; Heisler-White et al. 2008; Sherry et al. 2008; Slette et al. 2019), extreme, prolonged droughts have the potential to disproportionately influence global grassland carbon storage (Mcsherry and Ritchie 2013) through its effects on biomass production, carbon allocation, and respiration (Ciais et al. 2005; Reichstein et al. 2007; Mcsherry and Ritchie 2013; Frank et al. 2015; Zhou et al. 2016). Thus, knowledge on how extreme drought affects above- and belowground carbon pools is vital for predicting climate-biosphere feedbacks.

Several studies have investigated how extreme drought affects aboveground net primary production and carbon storage in grasslands (Ma et al. 2016b; Anadon-Rosell et al. 2017; Luo et al. 2020; Muraina et al. 2021). For example, extreme drought decreased plant aboveground carbon storage due to reduced water availability, increased evapotranspiration, reduced photosynthesis and decreased aboveground biomass production (Zhang et al. 2011; Craine et al. 2012; Xia et al. 2014). In contrast, drought may increase belowground carbon storage by promoting root growth and increased root/shoot ratios due to the development of drought resistance plant traits (Sanaullah et al. 2012; Burri et al. 2014; Li et al. 2021). However, Gilgen and Buchmann (2009) and Chen et al. (2020) reported that extreme drought decreased both above- and belowground carbon storage in a temperate grassland ecosystem. A recent study found that extreme drought reduced plant biomass and altered ecosystem carbon storage in grasslands globally (Hoover et al. 2018). These decreases in plant biomass carbon pools under drought could result from a reduction in leaf and stem biomass (Mcsherry and Ritchie 2013), which can lead to decreased turnover rates in root sucrose, a key compound for carbon translocation from leaf to root (Hasibeder et al. 2015).

Despite the well-documented response of aboveground carbon storage to extreme drought, the response of belowground carbon storage under contrasting aridity conditions is relatively unknown. For instance, increased belowground carbon storage during extreme drought results from positive root responses (Burri et al. 2014; Hasibeder et al. 2015), however, in some cold and semi-arid grasslands carbon allocation belowground is water rather

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than temperature limited. Thus, ecosystem carbon storage can be constrained by drought-induced severe soil water deficit (Niu et al. 2008; Wang et al. 2019b). In some other studies, no significant changes in belowground carbon were observed. In these cases, root biomass of some grasses increased while others decreased under drought, and this compensation held root biomass as well as root carbon constant (Bessler et al. 2009; Gilgen and Buchmann 2009). These complexities together with differences in climate, and vegetation, make it challenging to forecast the response of belowground carbon to extreme drought across an aridity gradient which may hinder accurate predictions of plant biomass carbon storage in grassland ecosystem.

The inconsistent results across multiple studies suggest that a comprehensive analysis of the response of plant above- and belowground carbon storage is needed to better understand the effect of extreme drought on grassland carbon dynamics. To better predict how extreme drought may affect carbon storage in grasslands, research needs to incorporate information across scales, while also accounting for the impacts of future changes in precipitation and temperature (Luo et al. 2004). While plants produce less aboveground carbon in arid environments due to lower precipitation (Cherwin and Knapp 2012; Burri et al. 2014), resource allocation serves as a key factor influencing aboveground production because aboveground biomass production and carbon allocation increase with increasing precipitation (McCulley et al. 2005; Liu et al. 2016). Belowground biomass responses to precipitation, on the other hand, are more variable. Precipitation can increase belowground biomass carbon in arid and semi-arid ecosystems, and decrease these responses in mesic ecosystems (Niu et al. 2008; Hasibeder et al. 2015; Wang et al. 2019a). We assessed the impact of extreme drought on plant ecosystem carbon storage in six grasslands along an aridity gradient. To do so, we conducted experiments using rainfall exclusion shelters to better understand the effects of extreme drought on plant above- and belowground carbon across six grassland sites in northern China. We hypothesized that: (1) grassland carbon storage would decrease under extreme drought due to lower above- and belowground carbon allocation, and (2) the response of plant above- and belowground carbon would depend

on grassland type and mean annual precipitation, decreasing from mesic to arid grassland.

## Materials and methods

### Study sites and experimental design

This study was conducted as part of the Extreme Drought in Grasslands Experiment (EDGE, <http://edge.biology.colostate.edu/>) in six grasslands distributed along a broad aridity gradient (Supplementary Fig. S1). These six sites represented the major grassland types in Inner Mongolia, northern China (106°58'00"E-120°06'00"E, 41°25'00"N-49°21'00"N): desert steppe, typical steppe, and meadow steppe (Table 1). The desert steppe is located in the western region with dry-tolerant short grasses, such as *Stipa klemenzii* and *S. breviflora* while typical steppe ranges from the middle part of the region and is mainly composed of perennial xerophytic species, such as *S. grandis* and *Leymus chinensis*. Meadow steppe is situated in the sub-humid zone of the eastern part of the study area and is composed of herbaceous perennial mesophytic and xerophytic species, such as *L. chinensis*, *Styloscolex baicalensis* and *Filifolium sibiricum*. In addition, the meadow, typical and desert steppes are primarily underlain by chernozem, chestnut and brown calcic soil types, respectively. In 2014, we established identical precipitation manipulation experiments with two treatments (control and extreme drought) at each site. Plots were relatively homogeneous and the experiment involved a randomized complete block design with six replicates of each treatment at each site. To achieve an extreme drought at each site, we imposed a 66% reduction of ambient growing season (May to August) precipitation (growing season precipitation accounts for 60–75% of MAP in these ecosystems) by constructing rainout shelters that minimize microclimatic effects (Griffin-Nolan et al. 2019; Whitney et al. 2019; Carroll et al. 2021). Rainout shelters permit 90% of photosynthetically active radiation to pass through (Yahdjian and Sala 2002). To minimize potential greenhouse effects, roofs were constructed 2 m above the ground surface to allow air to circulate. Control plots did not have rainout shelters. Every plot was 6×6 m in size, with at least 2 m spacing from the closest plots and were hydrologically isolated

**Table 1** Site characteristics for six grasslands of Inner Mongolia along with their productivity

Site name (Site label)	Grassland type	Habitat type	MAT (°C)	Aridity index	MAP <sup>a</sup> (mm)	MAP <sup>b</sup> (mm)	Mean AGB (gm <sup>-2</sup> )		Mean BGB (gm <sup>-2</sup> )		Mean LB (gm <sup>-2</sup> )	
							Control	Drought	Control	Drought	Control	Drought
Urat (A)	Desert	Arid	5.6	0.51	175	137.5	41.18 ± 10.94	20.32 ± 4.62	175.81 ± 63.06	241.95 ± 86.13	20.80 ± 5.08	10.92 ± 3.30
Sheila Muren (B)	Desert	Arid	4.5	0.49	236	233.5	103.92 ± 23.59	36.30 ± 5.10	467.75 ± 85.23	547.80 ± 67.42	39.16 ± 5.74	16.05 ± 4.09
Xilinhot-Ley- mus (C)	Typical	Semi-arid	1.1	0.42	323	311.6	249.68 ± 20.56	134.68 ± 20.47	595.05 ± 107.27	772.40 ± 109.88	61.02 ± 11.47	40.41 ± 12.04
Xilinhot-Stipa (D)	Typical	Semi-arid	1.1	0.40	323	311.6	214.19 ± 28.27	113.91 ± 28.49	750.42 ± 125.12	832.25 ± 107.99	71.92 ± 13.95	55.79 ± 24.97
Erguna (E)	Meadow	Semi-arid	-3.6	0.25	354	307.8	243.54 ± 47.81	140.75 ± 25.96	985.88 ± 71.28	946.41 ± 167.09	46.32 ± 4.49	35.34 ± 3.78
Sher Tara (F)	Meadow	Semi-arid	-4.7	0.17	363	297.8	397.21 ± 66.85	366.06 ± 68.06	1217.42 ± 156.33	1075.70 ± 103.37	93.10 ± 10.37	65.38 ± 5.15

Mean (gm<sup>-2</sup> ± SD) aboveground biomass (AGB), belowground biomass (BGB) and Litter biomass (LB) were calculated using data from 2015 to 2017 in control and drought manipulated plots at each site. MAP<sup>a</sup> (mm) represents mean annual precipitation from 1972 to 2018, MAP<sup>b</sup> represents mean annual precipitation from 2015 to 2018 and MAT represents mean annual temperature from 1972 to 2018 derived from meteorological stations at each site

from the surrounding soil matrix by aluminum flashing buried 1 m deep to help prevent surface and sub-surface water flow. All plots included a 1 m external buffer zone to allow access to the plot and minimize the edge effects associated with the infrastructure.

### Biomass sampling and measurement

Aboveground live biomass, surface litter biomass, and belowground root biomass were harvested at the end of the growing season (i.e., August) in 2015, 2016 and 2017. Aboveground live biomass of all species was harvested by clipping to the ground level and surface litter biomass was collected from each experimental plot. For collection of belowground biomass, we used a soil core sampling method. Eight soil cores were taken at a depth of 40 cm at increments of 0–10, 10–20 and 20–40 cm in each experimental plot using a root auger (diameter 5 cm). The roots were washed of soil using a 0.5 mm mesh sieve. Live, litter, and belowground biomass were oven dried at 60 °C for 48 h and weighed separately. We calculated means and standard deviations of aboveground, belowground, and litter biomass within drought and control plots at each site (Table 1).

### Statistical analysis

We calculated carbon content (45% of plant dry matter weight, DM) of aboveground biomass (AGBC,  $\text{gm}^{-2}$ ), belowground biomass (BGBC,  $\text{gm}^{-2}$ ) and litter biomass (LC,  $\text{gm}^{-2}$ ) and expressed values as  $\text{g C m}^{-2} = \text{g DM m}^{-2} \times 0.45$  (Ni 2004; Piao et al. 2007; Fan et al. 2008; Ma et al. 2016a). Total carbon (TC) was the sum of AGBC, BGBC and LC. The response ratio was calculated by relative changes in above or belowground biomass carbon of drought versus control plots as follows: AGBC Response ratio =  $(\text{AGBC}_{\text{Treatment}} - \text{AGBC}_{\text{Control}}) / \text{AGBC}_{\text{Control}}$ , LC Response ratio =  $(\text{LC}_{\text{Treatment}} - \text{LC}_{\text{Control}}) / \text{LC}_{\text{Control}}$ , and BGBC Response ratio =  $(\text{BGBC}_{\text{Treatment}} - \text{BGBC}_{\text{Control}}) / \text{BGBC}_{\text{Control}}$  (Hsu et al. 2012; Zhang et al. 2017). The aridity index (AI) was derived from global aridity index and potential evapotranspiration climate database v2-CGIAR-CSI (cgisrcsi.community) using ArcGIS. To measure the effect of treatments and year on carbon pools at each site, we used one-way analysis of variance (ANOVA) for treatment and year separately. Further, repeated measure analysis of variance

(RMANOVA) was applied to identify the interaction of treatments and year (Supplementary Table S1). Tukey's HSD test was used to test for significant differences between treatments. We quantified total plant carbon (TC) as the sum of above, below and litter carbon over the 3 years of the experiment (2015–2017). Regression analysis was applied to assess the relationships between aridity index, mean annual precipitation, temperature and response ratio of total carbon pools. All statistical analyses were performed using R studio (ver. 3.6.2) and ggplot2 was used for creating figures.

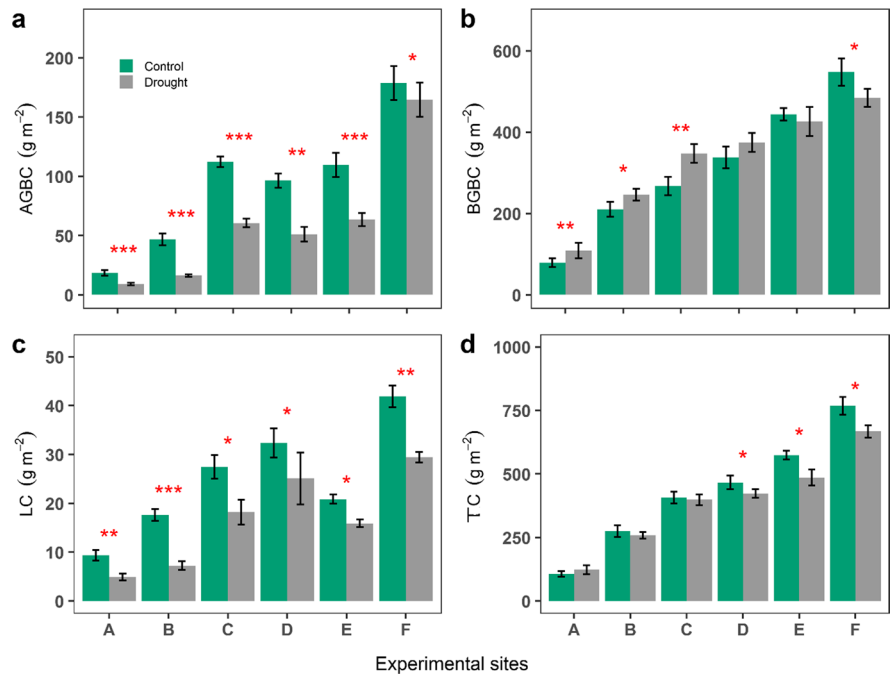
## Results

We observed the following effects of extreme drought: 1) aboveground biomass carbon (Fig. 1a) and litter carbon (Fig. 1c) decreased significantly across all sites (Table 2); 2) belowground biomass carbon (Fig. 1b) and total carbon (Fig. 1d) had mixed effects across the sites. Extreme drought reduced aboveground biomass carbon by 50% at the desert steppe (site A and B), more than 40% in the typical steppe (site C and D), and 5–39% in the meadow steppe (site E and F) (Fig. 2a). Belowground biomass carbon increased by 50% at the desert steppe sites and 21–48% at the typical steppe sites (Fig. 2b). The only site that experienced a decrease in belowground biomass carbon was the meadow steppe (2–6% decrease). Similar to aboveground biomass carbon, litter carbon also had a significant negative response to drought across all sites (Fig. 2c). Regarding total biomass carbon extreme drought had a positive effect in desert steppe, negative effect in meadow steppe, and mixed effects in the typical steppe sites (Fig. 2d).

When averaged across all sites, extreme drought significantly decreased aboveground biomass carbon by 35.0% ( $-32.8 \text{ gm}^{-2}$ ,  $P < 0.001$ ) (Fig. 3a), increased belowground biomass carbon by 5.4% ( $+16.8 \text{ gm}^{-2}$ ,  $P = 0.255$ ) (Fig. 3b) and decreased litter carbon by 28.1% ( $-6.9 \text{ gm}^{-2}$ ,  $P = 0.008$ ) (Fig. 3c). In addition, drought decreased total carbon by around 10% ( $-40.2 \text{ gm}^{-2}$ ;  $P = 0.041$ ) across the six grasslands (Fig. 3d).

To understand mechanisms driving these responses, we assessed the relationship between aboveground, belowground, litter and total carbon to an aridity index, temperature and precipitation.

**Fig. 1** Effects of extreme drought on (a) aboveground biomass carbon (AGBC), (b) belowground biomass carbon (BGBC), (c) litter carbon (LC) and (d) total biomass carbon (TC). Values represent mean carbon contents at each site (A–F) in three consecutive years (2015–2017). See Table 1 for site codes and descriptions. Error bars represent standard error of the mean. Asterisks for individual study sites indicates significant treatment differences at the 0.05(\*) and 0.01(\*\*) and 0.001(\*\*\*) level of probability. Site details are presented in Materials and Methods section



**Table 2** Results of the mean difference between control and drought plots in aboveground biomass carbon (AGBC), belowground biomass carbon (BGBC), and litter carbon (LC)

Grassland type	Site	Mean difference in $\text{g m}^{-2}$ (p value)		
		AGBC	BGBC	LC
Desert steppe	A	-9.38 (<0.001)	+36.83 (0.010)	-4.45 (0.011)
	B	-30.43 (<0.001)	+36.03 (0.019)	-10.40 (<0.001)
Typical steppe	C	-51.75 (<0.001)	+79.81 (0.011)	-9.28 (0.016)
	D	-45.12 (0.013)	+29.76 (0.303)	-7.26 (0.046)
Meadow steppe	E	-46.25 (<0.001)	-17.76 (0.649)	-5.94 (0.035)
	F	-14.10 (0.031)	-63.77 (0.050)	-12.47 (0.014)

We found that as aridity and mean annual temperature (MAT) increased, aboveground biomass carbon (AI:  $R^2=0.18$ ,  $P<0.001$ ; Fig. 4a, MAT:  $R^2=0.22$ ,  $P<0.001$ ; Fig. 6a) and litter carbon (AI:  $R^2=0.10$ ,  $P=0.021$ ; Fig. 4c, MAT:  $R^2=0.15$ ,  $P=0.007$ ; Fig. 6c) decreased, but belowground biomass carbon increased (AI:  $R^2=0.15$ ,  $P=0.003$ ; Fig. 4b, MAT:  $R^2=0.19$ ,  $P=0.0081$ ; Fig. 6b). Alternatively, increased precipitation increased aboveground biomass carbon ( $R^2=0.14$ ,  $P=0.013$ ; Fig. 5a) and litter carbon ( $R^2=0.17$ ,  $P=0.0049$ ; Fig. 5c) but decreased belowground biomass carbon ( $R^2=0.13$ ,  $P=0.014$ ; Fig. 5b). We found no significant relationship between total carbon and aridity ( $R^2=0.006$ ,  $P=0.71$ ; Fig. 4d), precipitation

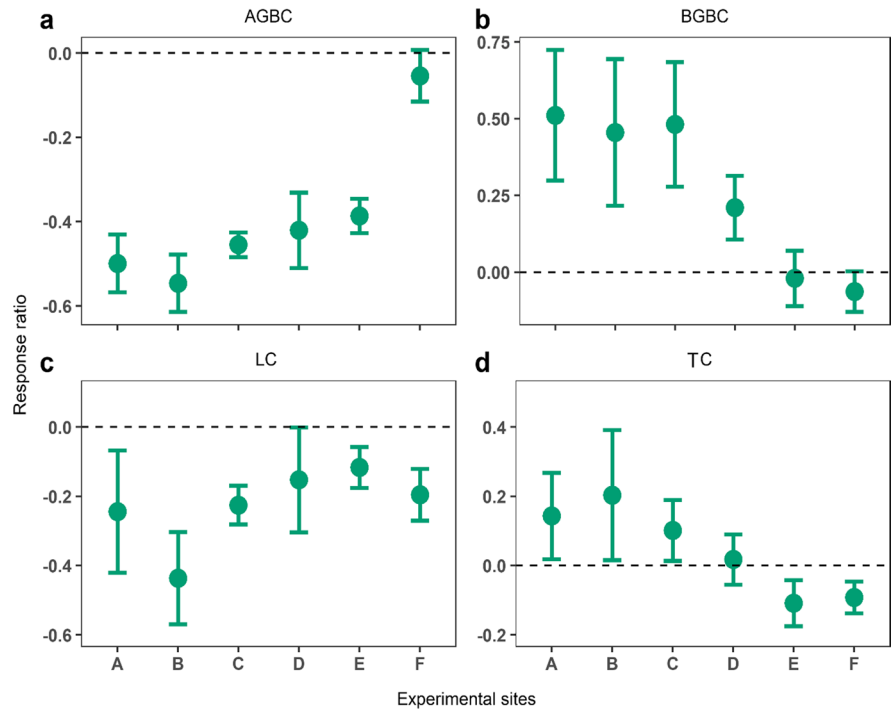
( $R^2=0.02$ ,  $P=0.18$ ; Fig. 5d) or temperature ( $R^2=0.0026$ ,  $P=0.82$ ; Fig. 6d).

## Discussion

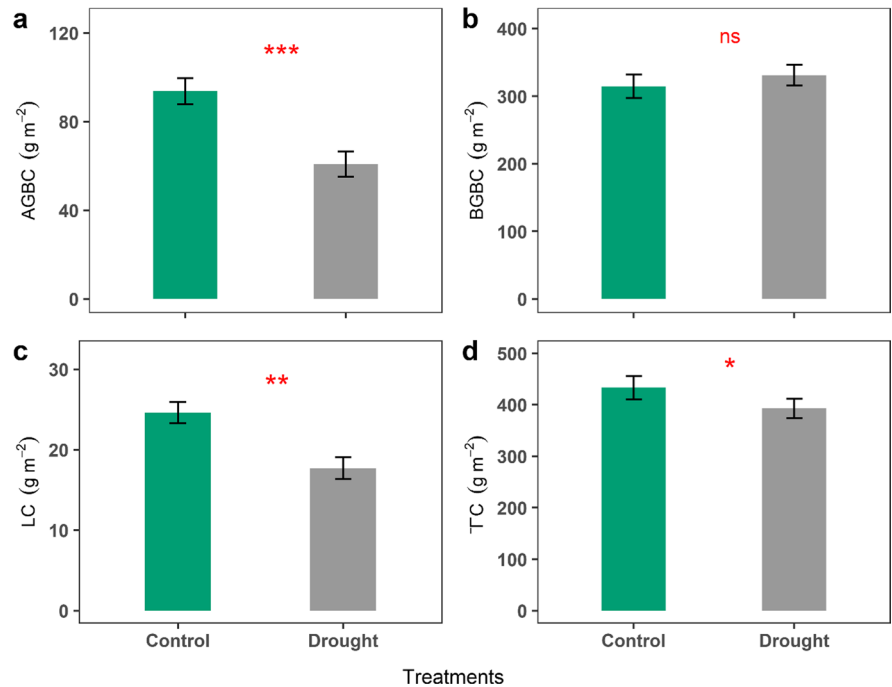
Effects of extreme drought on aboveground, belowground, and total biomass carbon

Understanding the effects of extreme drought on ecosystem carbon pools is vital to predicting global terrestrial carbon-climate feedback (Yue et al. 2017). While research demonstrates that grasslands serve as active carbon sinks, extreme drought and precipitation anomalies during the growing season (Novick

**Fig. 2** Response ratio of (a) aboveground biomass carbon (AGBC), (b) belowground biomass carbon (BGBC), (c) litter carbon (LC), and (d) total biomass carbon (TC) to extreme drought for sites A to F (See Table 1 for site codes and descriptions). Symbols indicate the mean value of the response ratio (treatment-control/control) for each site and vertical bars represent standard error of the mean



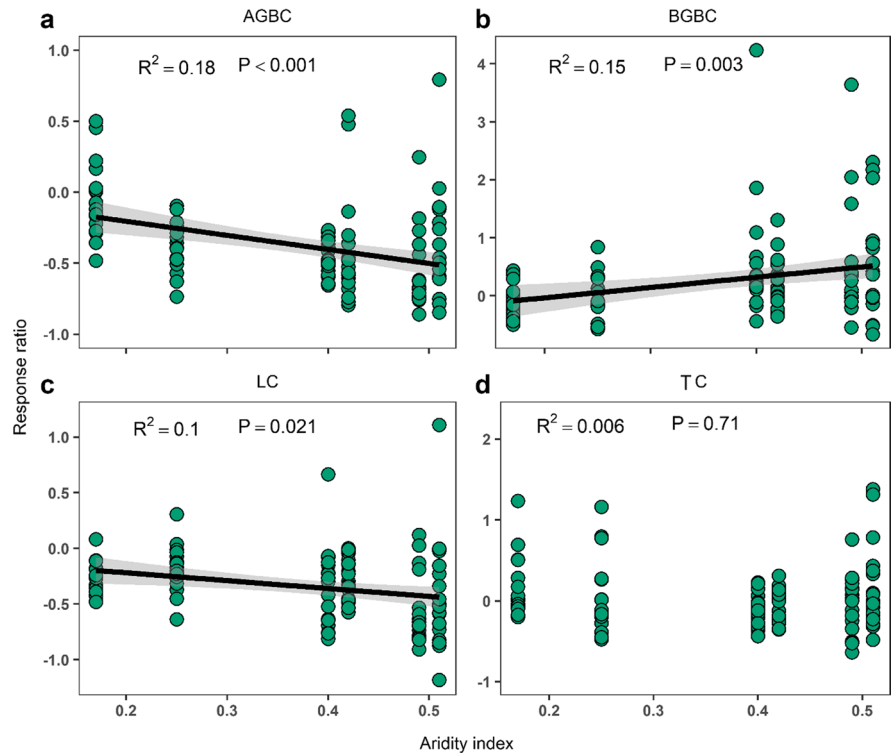
**Fig. 3** Effects of extreme drought and study site on (a) aboveground biomass carbon (AGBC), (b) belowground biomass carbon (BGBC), (c) litter carbon (LC) and (d) total biomass carbon (TC). Values are mean carbon content over the six sites in three consecutive years (2015–2017). Error bars represent standard error of the mean. Asterisks indicate significant treatment differences at the 0.05 (\*), 0.01(\*\*) and 0.001(\*\*\*) level of probability



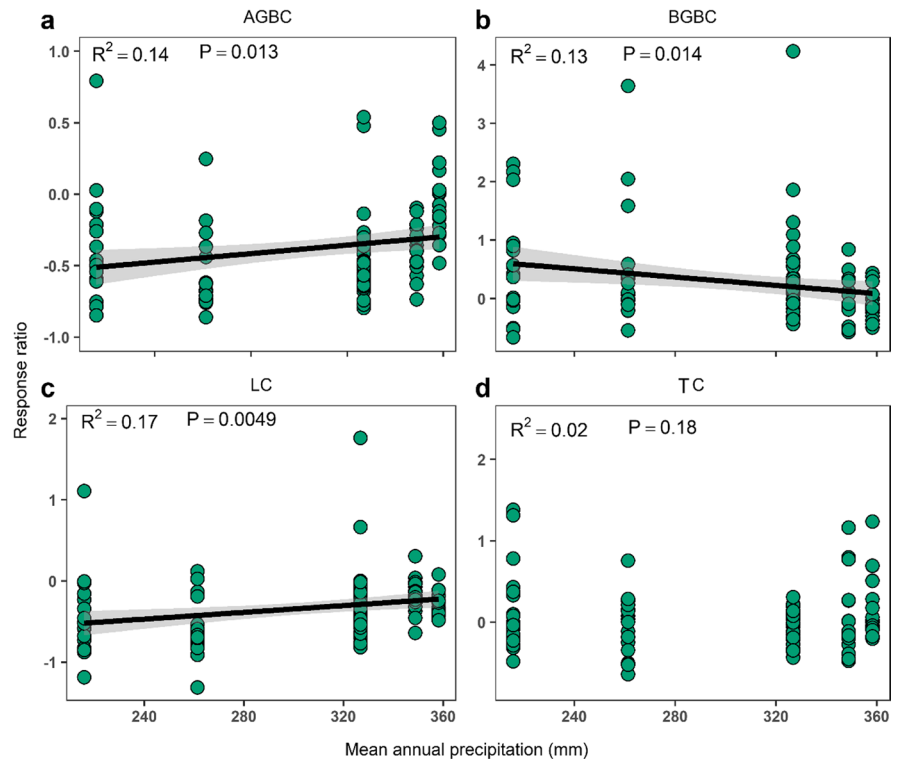
et al. 2004; Scott et al. 2009; Zhang et al. 2011) have the potential to shift these ecosystems from carbon sinks to carbon sources (Zhang et al. 2011). Our results show that extreme drought significantly

decreased aboveground plant carbon pools in all years across six sites spanning an aridity gradient (Supplementary Fig. S2). This decrease is attributed to the corresponding decrease of aboveground biomass in

**Fig. 4** Relationships between response ratio (treatment-control/control) of (a) aboveground biomass carbon (AGBC), (b) belowground biomass carbon (BGBC), (c) litter carbon (LC) and (d) total biomass carbon (TC) vs. aridity index. Points are from all six sites and gray lines indicate 95% confidence interval.

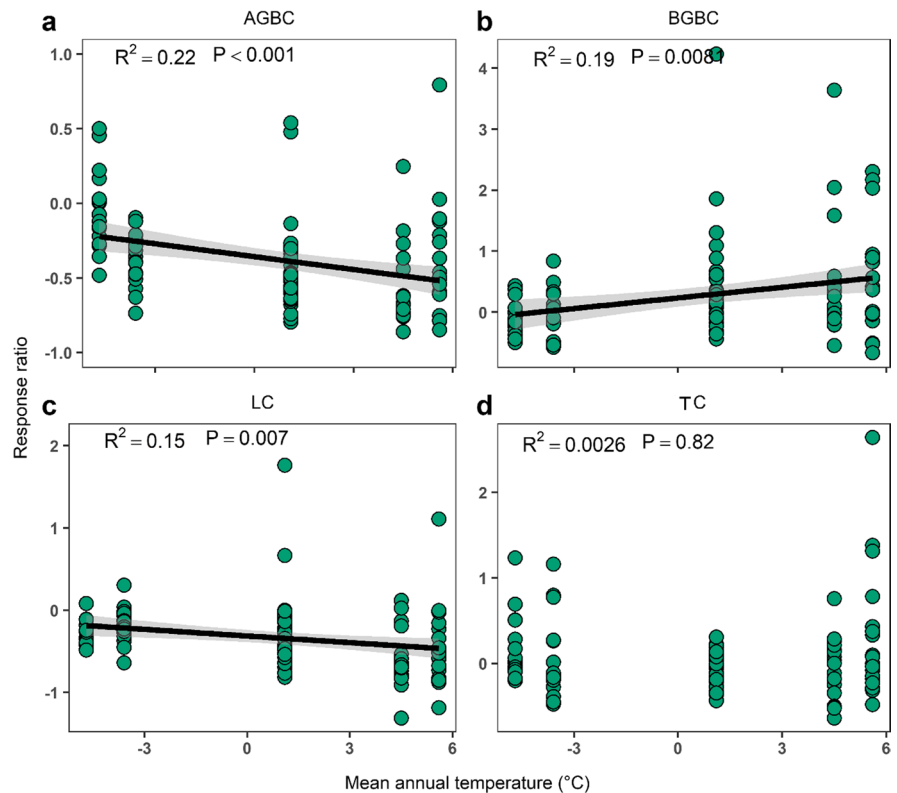


**Fig. 5** Relationships between response ratio (treatment-control/control) of (a) aboveground biomass carbon (AGBC), (b) belowground biomass carbon (BGBC), (c) litter carbon (LC) and (d) total biomass carbon (TC) vs. mean annual precipitation. Points are from all six sites and gray lines indicate 95% confidence interval.





**Fig. 6** Relationships between response ratio (treatment-control/control) of (a) aboveground biomass carbon (AGBC), (b) belowground biomass carbon (BGBC), (c) litter carbon (LC) and (d) total biomass carbon (TC) vs. mean annual temperature (°C). Points are from all six sites and gray lines indicate 95% confidence interval.



extreme drought plots (Kahmen et al. 2005; Smith et al. 2020). Previous research has reported that water availability plays a vital role in regulating plant C storage or release in terrestrial ecosystems. Extreme drought reduces water availability and creates water stress in plants leading to loss of aboveground plant carbon (Niu et al. 2008; Burri et al. 2014; Wang et al. 2018). Drought had no measurable impacts on ecosystem respiration; therefore, the reduction in total biomass carbon is likely caused by a decrease in above- and belowground productivity in these grasslands (Jentsch et al. 2011; Wang et al. 2015). Drought can impair physiological activities such that plants are unable to achieve optimum transpiration due to insufficient water and/or carbon supply, which will ultimately reduce biomass production and alter carbon allocation (van Heerwaarden et al. 2005; Wang et al. 2018). Although we found that belowground root biomass was sensitive to extreme drought in the semiarid sites due to lower root production (Badeck et al. 2005; Bowling et al. 2008; Carroll et al. 2021), our study and others (Srivastava et al. 2018) have found aboveground plant carbon pools (aboveground

and litter biomass) to be more sensitive to drought than belowground pools. In this case, drought causes an imbalance between water supply and demand, which results in the dehydration of plant leaves and damage to photosynthetic and metabolic systems leading to a decrease in aboveground biomass carbon (Wang et al. 2018; Liu et al. 2020).

To our knowledge, few studies have shown that extreme drought increased belowground biomass carbon (Sanaullah et al. 2012). We found that extreme drought increased belowground carbon from 0 to 40 cm depth in the drier sites (desert and typical steppe) but decreased belowground carbon at the more mesic meadow steppe sites. The decrease at the mesic sites could be due to a long history of higher precipitation. For example, a recent experiment in a mountainous meadow grassland with similar precipitation to our site suggested that extreme drought reduced belowground carbon allocation by 50% because shallow root systems (e.g., 0–10 cm) that evolved under higher precipitation regimes might not be adapted to drought (Hasibeder et al. 2015). Moreover, higher

precipitation promotes turnover of root sucrose that hinders metabolic activities of roots and the rate of root carbon allocation at 0–10 cm depth (Fuchsluger et al. 2014).

For the drier sites, the increase in belowground carbon could be attributed to dryland-adapted plants that allocate energy to get water during extreme drought through increased root growth between 20 and 40 cm depth (Milchunas and Lauenroth 2001; Saab et al. 1990; Tardieu and Davies 1992). In addition, in arid ecosystems, plant root growth to 30 cm could buffer against drought effects through hydraulic lift which in turn would increase root biomass production and root carbon storage (McCulley et al. 2005; Shi et al. 2014). In arid systems, plants can produce root biomass down to 50 cm depth under resource scarcity through increased root productivity and changes in species composition from shallow-rooted sedges (up to 25 cm) to deep rooted grasses (up to 50 cm) (Liu et al. 2018, 2020). Overall, we found that extreme drought increased belowground carbon storage at dry sites and decreased carbon storage at wet sites. This finding contradicts studies that found that extreme drought decreased root respiration, suppressed root growth due to impaired root cell integrity, and limited substrate supply which then caused decreased root carbon flux (Atkin et al. 2005). Moreover, in relatively wet ecosystems and greenhouse experiments, drought decreased canopy photosynthesis such that it restricted the supply of photosynthate to the roots across 0–20 and 20–30 cm depths (Huang and Fu 2000; Galvez et al. 2011). Thus, the complex response of belowground carbon in different grassland ecosystems indicates the necessity of further study the effects of extreme drought in deep soil (e.g., > 40 cm) across wide climatic gradients.

Litter biomass serves as an important carbon pool that links above- and belowground carbon storage. Our results showed that extreme drought caused litter biomass carbon to decrease across all sites and all years (Supplementary Fig. S2), likely due to reduced litter production because aboveground biomass is reduced. In addition, increased temperatures and reduced precipitation that occur during drought can reduce litter decomposition rates and litter carbon accumulation (Bloor and Bardgett 2012; Liu et al. 2020).

## Differential response of biomass carbon to extreme drought and precipitation

While we found negative responses of aboveground and litter carbon to experimental drought across all sites, the level of the responses varied among sites. Arid grassland sites responded more negatively than mesic sites. Interestingly, we found the opposite results for belowground biomass carbon. We observed a mixed response of ecosystem carbon to extreme drought with positive responses in arid grassland sites and negative responses in mesic grassland sites. Few studies have reported that aboveground carbon showed the least negative response in water limited drier ecosystem under extreme drought due to low soil moisture and low soil fertility (Li et al. 2021). The lack of a positive response of belowground carbon to extreme drought in wet sites may result from higher root turnover and decreased root-shoot ratio (Austin and Sala 2002; Bai et al. 2008). Overall, our results suggest that extreme drought at drier sites increases belowground carbon while having the opposite effect at wet sites.

We observed that aboveground, belowground, and litter carbon pools were significantly regulated by increasing aridity, temperature and precipitation. Higher temperature had a similar influence as aridity on aboveground, belowground and litter carbon pools. One reason may be that higher temperatures increased plant respiration during drought leading to a decline in aboveground C (Raich et al. 2006). However, higher temperatures under drought have been found to promote belowground carbon allocation via increased root production and root carbon residues (Raich et al. 2006; Liu et al. 2020). In contrast, the opposite trends in carbon storage were observed with precipitation. In addition, lack of a relationship between total carbon with aridity, temperature or precipitation may be attributed to pooling above- and belowground components with opposite responses in our analysis. Aboveground carbon pools can have a positive relationship with precipitation (Hossain and Beierkuhnlein 2018); however, other studies have demonstrated that aboveground plant carbon storage increases in drier ecosystems and decreases in mesic ecosystems (Lauenroth et al. 2000; Epstein et al. 2002). Similarly, McCulley et al. (2005) reported that aboveground biomass carbon increased while belowground biomass carbon showed a non-significant relationship

with increasing precipitation. In our study, the positive linear response of aboveground carbon and litter carbon implies that higher precipitation mitigates the negative effects of aboveground carbon loss. Our results, are consistent with those from previous studies, suggesting that precipitation limitation constrains aboveground plant biomass production (Knapp et al. 2004; Guo et al. 2019). We also found a negative relationship between belowground biomass carbon and precipitation, consistent with other studies (Galvez et al. 2011; Hasibeder et al. 2015).

## Conclusions

Earth system models predict that climate will become more variable and droughts more extreme in the future. Thus, it is crucial to study the effects of extreme drought on carbon storage in grasslands—the world’s largest terrestrial ecosystem. Our findings add to this understanding by revealing the effects of extreme drought on carbon storage at six grassland sites spanning an aridity gradient. First, we found that extreme drought reduced plant biomass carbon by ~10%, which was driven by decreases in aboveground biomass carbon and litter carbon. Second, arid grasslands (desert steppe and typical steppe) were more sensitive to loss of plant aboveground carbon while belowground carbon loss was higher in mesic Meadow steppe. We also found that increased precipitation promoted aboveground carbon and litter carbon, decreased belowground biomass carbon, and had no effect on total carbon indicating that aboveground biomass carbon but not belowground was strongly mediated by precipitation.

**Acknowledgements** This work was generated using data from the China EDGE Network, supported by the National Key R&D Program of China (2017YFA0604802, 2019YFE0117000) and National Natural Science Foundation of China (31971533, 41320104002). Support was provided to MDS, AKK and SLC by the Konza Prairie Long-term Ecological Research Program, the Drought-Net Research Coordination Network funded by the US National Science Foundation (DEB-1354732) and by the Macrosystems Biology/Emerging Frontiers Programs (EF-1137342, EF-1137378, EF-1137363).

## Declarations

**Conflict of interest** No conflict of interest was reported by the authors.

## References

- Anadon-Rosell A, Hasibeder R, Palacio S et al (2017) Short-term carbon allocation dynamics in subalpine dwarf shrubs and their responses to experimental summer drought. *Environ Exp Bot* 141:92–102. <https://doi.org/10.1016/j.envexpbot.2017.07.006>
- Atkin O, Bruhn D, Hurry V, Tjoelker M (2005) Evans Review No. 2 - The hot and the cold : Unravelling the variable response of plant respiration to temperature. *Evans Review No. 2 The hot and the cold : unravelling the variable response of plant respiration to temperature.* <https://doi.org/10.1071/FP03176>
- Austin AT, Sala OE (2002) Carbon and nitrogen dynamics across a natural precipitation gradient in Patagonia, Argentina. *J Veg Sci* 13:351–360. <https://doi.org/10.1111/j.1654-1103.2002.tb02059.x>
- Badeck FW, Tcherkez G, Nogués S et al (2005) Post-photosynthetic fractionation of stable carbon isotopes between plant organs - a widespread phenomenon. *Rapid Commun Mass Spectrom* 19:1381–1391. <https://doi.org/10.1002/rcm.1912>
- Bai Y, Ianguo JWU, Ing QIX et al (2008) Primary Productio and rain use efficiency across a precipitation gradient on the Mongolia Plateau. *Ecology* 89:2140–2153. <https://doi.org/10.1890/07-0992.1>
- Bessler H, Temperton VM, Roscher C et al (2009) Above-ground overyielding in grassland mixtures is associated with reduced biomass partitioning to belowground organs. *Ecology* 90:1520–1530. <https://doi.org/10.1890/08-0867.1>
- Bloor JMG, Bardgett RD (2012) Stability of above-ground and below-ground processes to extreme drought in model grassland ecosystems: interactions with plant species diversity and soil nitrogen availability. *Perspect Plant Ecol Evol Syst* 14:193–204. <https://doi.org/10.1016/j.ppees.2011.12.001>
- Bowling DR, Pataki DE, Randerson JT (2008) Carbon isotopes in terrestrial ecosystem pools and CO<sub>2</sub> fluxes. *New Phytol* 178:24–40. <https://doi.org/10.1111/j.1469-8137.2007.02342.x>
- Burri S, Sturm P, Prechsl UE et al (2014) The impact of extreme summer drought on the short-term carbon coupling of photosynthesis to soil CO<sub>2</sub> efflux in a temperate grassland. *Biogeosciences* 11:961–975. <https://doi.org/10.5194/bg-11-961-2014>
- Carroll CJW, Slette IJ, Griffin-Nolan RJ et al (2021) Is a drought a drought in grasslands? Productivity responses to different types of drought. *Oecologia*. <https://doi.org/10.1007/s00442-020-04793-8>
- Chen N, Zhang Y, Zu J et al (2020) Agricultural and Forest meteorology the compensation effects of post-drought regrowth on earlier drought loss across the tibetan plateau grasslands. *Agric For Meteorol* 281:107822. <https://doi.org/10.1016/j.agrformet.2019.107822>
- Cherwin K, Knapp A (2012) Unexpected patterns of sensitivity to drought in three semi-arid grasslands. *Oecologia* 169:845–852. <https://doi.org/10.1007/s00442-011-2235-2>
- Ciais P, Reichstein M, Viovy N et al (2005) Europe-wide reduction in primary productivity caused by the heat

- and drought in 2003. *Nature* 437:529–533. <https://doi.org/10.1038/nature03972>
- Craine JM, Nippert JB, Elmore AJ et al (2012) Timing of climate variability and grassland productivity. *Proc Natl Acad Sci U S A* 109:3401–3405. <https://doi.org/10.1073/pnas.1118438109>
- Epstein H, Burke I, Lauenroth W (2002) Regional patterns of decomposition and primary production rates in the production rates in the U.S. Great plain. *Ecology* 83:320–327. <https://doi.org/10.2307/2680016>
- Fan J, Zhong H, Harris W et al (2008) Carbon storage in the grasslands of China based on field measurements of above- and below-ground biomass. *Clim Chang* 86:375–396. <https://doi.org/10.1007/s10584-007-9316-6>
- Frank AB, Dugas WA (2001) Carbon dioxide fluxes over a northern, semiarid, mixed-grass prairie. *Agric For Meteorol* 108:317–326
- Frank D, Reichstein M, Bahn M et al (2015) Effects of climate extremes on the terrestrial carbon cycle: concepts, processes and potential future impacts. *Glob Chang Biol* 21:2861–2880. <https://doi.org/10.1111/gcb.12916>
- Fuchslueger L, Bahn M, Fritz K et al (2014) Experimental drought reduces the transfer of recently fixed plant carbon to soil microbes and alters the bacterial community composition in a mountain meadow. *New Phytol* 201:916–927. <https://doi.org/10.1111/nph.12569>
- Galvez DA, Landhäusser SM, Tyree MT (2011) Root carbon reserve dynamics in aspen seedlings: does simulated drought induce reserve limitation? Root carbon reserve dynamics in aspen seedlings: does simulated drought induce reserve limitation? *Tree Physiol* 31:250–257. <https://doi.org/10.1093/treephys/tp1012>
- Gilgen AK, Buchmann N (2009) Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation. *Biogeosciences* 6:2525–2539. <https://doi.org/10.5194/bg-6-2525-2009>
- Griffin-Nolan RJ, Blumenthal DM, Collins SL et al (2019) Shifts in plant functional composition following long-term drought in grasslands. *J Ecol* 107:2133–2148. <https://doi.org/10.1111/1365-2745.13252>
- Guo S, Xu Y, He C et al (2019) Differential responses of soil quality in revegetation types to precipitation gradients on the Loess Plateau. *Agric For Meteorol* 276–277:107622. <https://doi.org/10.1016/j.agrformet.2019.107622>
- Hasibeder R, Fuchslueger L, Richter A, Bahn M (2015) Summer drought alters carbon allocation to roots and root respiration in mountain grassland. *New Phytol* 205:1117–1127. <https://doi.org/10.1111/nph.13146>
- Heisler-White JL, Knapp AK, Kelly EF (2008) Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. *Oecologia* 158:129–140. <https://doi.org/10.1007/s00442-008-1116-9>
- Hoover DL, Wilcox KR, Young KE (2018) Experimental droughts with rainout shelters: a methodological review experimental droughts with rainout shelters: a methodological review. *Ecosphere* 9:1–14. <https://doi.org/10.1002/ecs2.2088>
- Hoovers DA, Rogers BM (2016) Not all droughts are created equal: the impacts of interannual drought pattern and magnitude on grassland carbon cycling. *Glob Chang Biol* 22:1809–1820. <https://doi.org/10.1111/gcb.13161>
- Hossain ML, Beierkuhnlein C (2018) Enhanced aboveground biomass by increased precipitation in a central European grassland. *Ecol Process* 7:1–13. <https://doi.org/10.1186/s13717-018-0149-1>
- Hsu J, Powel J, Adler P (2012) Sensitivity of mean annual primary production to precipitation. *Glob Chang Biol* 18:2246–2255. <https://doi.org/10.1111/j.1365-2486.2012.02687.x>
- Huang B, Fu J (2000) Photosynthesis, respiration, and carbon allocation of two cool-season perennial grasses in response to surface soil drying. *Plant Soil* 227:17–26. <https://doi.org/10.1023/A:1026512212113>
- Hufkens K, Keenan TF, Flanagan LB et al (2016) Productivity of north American grasslands is increased under future climate scenarios despite rising aridity. *Nat Clim* 6:710–714. <https://doi.org/10.1038/NCLIMATE2942>
- Jentsch A, Kreyling J, Elmer M et al (2011) Climate extremes initiate ecosystem-regulating functions while maintaining productivity. *J Ecol* 99:689–702. <https://doi.org/10.1111/j.1365-2745.2011.01817.x>
- Kahmen A, Perner J, Bunchmann N (2005) Diversity-dependent productivity in semi-natural grasslands following climate perturbations. *Funct Ecol* 19:594–601. <https://doi.org/10.1111/j.1365>
- Knapp A, Huxman TE, Smith MD et al (2004) Convergence across biomes to a common rain-use efficiency convergence across biomes to a common rain-use efficiency. *Nature* 429:651–654. <https://doi.org/10.1038/nature02561>
- Lauenroth WK, Burke IC, Paruelo JM (2000) Patterns of production and precipitation-use efficiency of winter wheat and native grasslands in the central Great Plains of the United States. *Ecosystems* 3:344–351. <https://doi.org/10.1007/s100210000031>
- Li X, Zuo X, Yue P et al (2021) Drought of early time in growing season decreases community aboveground biomass, but increases belowground biomass in a desert steppe. *BMC Ecol Evol* 21:1–13. <https://doi.org/10.1186/s12862-021-01842-5>
- Liu S, Zhang F, Du Y et al (2016) Ecosystem carbon storage in alpine grassland on the Qinghai plateau. *PLoS One* 11:1–14. <https://doi.org/10.1371/journal.pone.0160420>
- Liu H, Mi Z, Lin L et al (2018) Shifting plant species composition in response to climate change stabilizes grassland primary production. *Proc Natl Acad Sci U S A* 115:4051–4056. <https://doi.org/10.1073/pnas.1700299114>
- Liu H, Lin L, Wang H et al (2020) Simulating warmer and drier climate increases root production but decreases root decomposition in an alpine grassland on the Tibetan plateau. *Plant Soil*. <https://doi.org/10.1007/s11104-020-04551-y>
- Luo Y, Su B, Currie WS et al (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience* 54:731–739. [https://doi.org/10.1641/0006-3568\(2004\)054\[0731:PNLOER\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0731:PNLOER]2.0.CO;2)
- Luo W, Zuo X, Griffin-Nolan RJ et al (2020) Chronic and intense droughts differentially influence grassland carbon-nutrient dynamics along a natural aridity gradient. *Plant Soil*. <https://doi.org/10.1007/s11104-020-04571-8>

- Ma A, He N, Yu G et al (2016a) Carbon storage in Chinese grassland ecosystems: influence of different integrative methods. *Sci Rep* 6:1–10. <https://doi.org/10.1038/srep21378>
- Ma X, Huete A, Cleverly J et al (2016b) Drought rapidly diminishes the large net CO<sub>2</sub> uptake in 2011 over semi-arid Australia. *Sci Rep* 6:1–9. <https://doi.org/10.1038/srep37747>
- McCulley RL, Burke IC, Nelson JA et al (2005) Regional patterns in carbon cycling across the Great Plains of North America. *Ecosystems* 8:106–121. <https://doi.org/10.1007/s10021-004-0117-8>
- Mcsherry ME, Ritchie ME (2013) Effects of grazing on grassland soil carbon: a global review. *Glob Chang Biol* 19:1347–1357. <https://doi.org/10.1111/gcb.12144>
- Milchunas DG, Lauenroth WK (2001) Belowground primary production by carbon isotope decay and long-term root biomass dynamics. *Ecosystems* 4:139–150. <https://doi.org/10.1007/s100210000064>
- Muraina TO, Xu C, Yu Q et al (2021) Species asynchrony stabilises productivity under extreme drought across northern China grasslands. *J Ecol* 109:1665–1675. <https://doi.org/10.1111/1365-2745.13587>
- Ni J (2004) Forage yield-based carbon storage in grasslands of China. *Clim Chang* 67:237–246. <https://doi.org/10.1007/s10584-004-0070-8>
- Niu S, Wu M, Han Y et al (2008) Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe. *New Phytol* 177:209–219. <https://doi.org/10.1111/j.1469-8137.2007.02237.x>
- Novick KA, Stoy PC, Katul GG et al (2004) Carbon dioxide and water vapor exchange in a warm temperate grassland. *Oecologia* 138:259–274. <https://doi.org/10.1007/s00442-003-1388-z>
- Piao S, Fang J, Zhou L et al (2007) Changes in biomass carbon stocks in China's grasslands between 1982 and 1999. *Glob Biogeochem Cycles* 21:1–10. <https://doi.org/10.1029/2005GB002634>
- Raich JW, Russell AE, Kitayama K et al (2006) Temperature influences carbon accumulation in moist tropical forests. *Ecology* 87:76–87. <https://doi.org/10.1890/05-0023>
- Reichstein M, Ciais P, Papale D 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 Chang Biol* 13:634–651. <https://doi.org/10.1111/j.1365-2486.2006.01224.x>
- Saab IN, Sharp RE, Pritchard J, Voetberg GS (1990) Increased endogenous abscisic acid maintains primary root growth and inhibits shoot growth of maize seedlings at low water potentials. *Plant Physiol* 93:1329–1336. <https://doi.org/10.1104/pp.93.4.1329>
- Sanauallah M, Chabbi A, Rumpel C, Kuzyakov Y (2012) Carbon allocation in grassland communities under drought stress followed by <sup>14</sup>C pulse labeling. *Soil Biol Biochem* 55:132–139. <https://doi.org/10.1016/j.soilbio.2012.06.004>
- Schwinning S, Starr BI, Ehleringer JR (2005) Summer and winter drought in a cold desert ecosystem (Colorado plateau) part II: effects on plant carbon assimilation and growth. *J Arid Environ* 61:61–78. <https://doi.org/10.1016/j.jaridenv.2004.07.013>
- Scott RL, Jenerette GD, Potts DL, Huxman TE (2009) Effects of seasonal drought on net carbon dioxide exchange from a woody-plant-encroached semiarid grassland. *J Geophys Res Biogeosci* 114:1–13. <https://doi.org/10.1029/2008JG000900>
- Sherry RA, Weng E, Arnone JA et al (2008) Lagged effects of experimental warming and doubled precipitation on annual and seasonal aboveground biomass production in a tallgrass prairie. *Glob Chang Biol* 14:2923–2936. <https://doi.org/10.1111/j.1365-2486.2008.01703.x>
- Shi Z, Thomey ML, Mowl W et al (2014) Differential effects of extreme drought on production and respiration: synthesis and modeling analysis. *Biogeosciences* 11:621–633. <https://doi.org/10.5194/bg-11-621-2014>
- Slette IJ, Post AK, Awad M et al (2019) How ecologists define drought, and why we should do better. *Glob Chang Biol* 25:3193–3200. <https://doi.org/10.1111/gcb.14747>
- Smith MD (2011) The ecological role of climate extremes: current understanding and future prospects. *J Ecol* 99:651–655. <https://doi.org/10.1111/j.1365-2745.2011.01833.x>
- Smith MD, Koerner SE, Knapp AK et al (2020) Mass ratio effects underlie ecosystem responses to environmental change. *J Ecol* 108:855–864. <https://doi.org/10.1111/1365-2745.13330>
- Srivastava K, Jentsch A, Kreyling J et al (2018) Short-term carbon dynamics in a temperate grassland and heathland ecosystem exposed to 104 days of drought followed by irrigation. *Isot Environ Health Stud* 54:41–62. <https://doi.org/10.1080/10256016.2017.1371714>
- Tardieu F, Davies WJ (1992) Stomatal response to abscisic acid is a function of current plant water status. *Plant Physiol* 98:540–545. <https://doi.org/10.1104/pp.98.2.540>
- van Heerwaarden LM, Toet S, van Logtestijn RSP, Aerts R (2005) Internal nitrogen dynamics in the Graminoid *Molinia caerulea* under higher N supply and elevated CO<sub>2</sub> concentrations. *Plant Soil* 277:255–264. <https://doi.org/10.1007/s11104-005-7140-1>
- Wang Y, Jiang Q, Yang Z et al (2015) Effects of water and nitrogen addition on ecosystem carbon exchange in a meadow steppe. 1–16. <https://doi.org/10.1371/journal.pone.0127695>
- Wang Y, Meng B, Zhong S et al (2018) Aboveground biomass and root/shoot ratio regulated drought susceptibility of ecosystem carbon exchange in a meadow steppe. *Plant Soil* 432:259–272. <https://doi.org/10.1007/s11104-018-3790-7>
- Wang M, Yang W, Wu N et al (2019a) Patterns and drivers of soil carbon stock in southern China's grasslands. *Agric For Meteorol* 276–277. <https://doi.org/10.1016/j.agrfor.2019.107634>
- Wang N, Quesada B, Xia L et al (2019b) Effects of climate warming on carbon fluxes in grasslands— a global meta-analysis. *Glob Chang Biol* 25:1839–1851. <https://doi.org/10.1111/gcb.14603>
- Whitney KD, Mudge J, Natvig DO et al (2019) Experimental drought reduces genetic diversity in the grassland foundation species *Bouteloua eriopoda*. *Oecologia* 189:1107–1120. <https://doi.org/10.1007/s00442-019-04371-7>
- Xia J, Liu S, Liang S et al (2014) Spatio-temporal patterns and climate variables controlling of biomass carbon stock of

- global grassland ecosystems from 1982 to 2006. *Remote Sens* 6:1783–1802. <https://doi.org/10.3390/rs6031783>
- Yahdjian L, Sala OE (2002) A rainout shelter design for intercepting different amounts of rainfall. *Oecologia* 133:95–101. <https://doi.org/10.1007/s00442-002-1024-3>
- Yue K, Fornara D, Yang W et al (2017) Influence of multiple global change drivers on terrestrial carbon storage : additive effects are common. *Ecol Lett* 20:663–672. <https://doi.org/10.1111/ele.12767>
- Zhang L, Wylie BK, Ji L et al (2011) Upscaling carbon fluxes over the Great Plains grasslands: sinks and sources. *J Geophys Res Biogeosci* 116. <https://doi.org/10.1029/2010JG001504>
- Zhang B, Tan X, Wang S et al (2017) Asymmetric sensitivity of ecosystem carbon and water processes in response to precipitation change in a semi-arid steppe. *Funct Ecol* 31:1301–1311. <https://doi.org/10.1111/1365-2435.12836>
- Zhou X, Zhou L, Nie Y et al (2016) Similar responses of soil carbon storage to drought and irrigation in terrestrial ecosystems but with contrasting mechanisms: a meta-analysis. *Agric Ecosyst Environ* 228:70–81. <https://doi.org/10.1016/j.agee.2016.04.030>

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