



Chronic drought decreased organic carbon content in topsoil greater than intense drought across grasslands in Northern China

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ABSTRACT

Grasslands are expected to experience extreme climatic events such as extreme drought due to rising global temperatures. However, we still lack evidence of how extreme drought influence soil organic carbon (SOC) content in grassland ecosystems. We experimentally imposed extreme drought in two ways – chronic drought (66 % reduction in precipitation from May to August) and intense drought (100 % reduction in precipitation from June to July) to measure the effects of these two drought types on (SOC) content across six grassland sites that spanning desert steppe, typical steppe and meadow steppe in northern China. The experiment followed a randomized complete block design with six replicates of each treatment at each site. Our results showed that both chronic and intense drought decreased SOC content in the topsoil (0–10 cm) and the loss was higher in arid grasslands (desert steppe and typical steppe). Chronic drought decreased SOC content more than intense drought, with the effect again being strongest in arid grasslands. Furthermore, the response of SOC content to extreme drought was linked with the response of net primary productivity. Specifically, the response of SOC content was negatively correlated with drought sensitivity of above-ground net primary productivity (ANPP) but positively correlated with drought sensitivity of belowground NPP (BNPP). Overall, our results suggest that shifts in grassland SOC content with future drought will depend on the types of drought as well as the productivity responses and local climatic conditions such as precipitation, temperature, and aridity. The differential extreme drought impacts described here may facilitate predictions of climate change impacts on ecosystem carbon cycling.

1. Introduction

Global climate models predict an increase in the severity and

frequency of droughts due to higher temperatures and changes in precipitation by the end of the 21st century (Cook et al., 2015; Wang et al., 2018). Recent observations revealed that drought severity and

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frequency have already increased in the past two decades (Williams et al., 2020) and many grasslands ecosystems are experiencing drought stress globally (Wang and others, 2019c). ‘Drought’- described here as ‘meteorological drought’ which is defined as a period characterized by precipitation absence or marked rainfall deficiency (i.e. <50 %) in a particular site or region relative to normal (Slette et al., 2019)- can negatively affect plant growth and plant nutrient uptake (Chaves et al., 2003). On the other hand ‘extreme drought’ is also a ‘meteorological drought’ defined as a statistically rare, prolonged rainfall deficit in a region that alters ecosystem structure and function through increased vapor pressure deficit, increase plant soil respiration and severely reduced soil water content (Carroll et al., 2021; Knapp et al., 2020; Smith, 2011). Generally, there are two types of extreme drought: ‘chronic’ and ‘intense’, which differ in rainfall event size (i.e., the amount of precipitation reduction) and pattern (i.e., the intra-annual rainfall event frequency). Intense droughts (i.e., 100 % removal of precipitation in a period of time) are usually short in duration and are expected to increase in frequency (Luo et al., 2020). On the other hand, chronic droughts involve a reduction in precipitation event size over a longer duration in a particular site or region (Carroll et al., 2021).

Covering approximately 40 % of the Earth’s land surface, grasslands store nearly ~ 34 % of the terrestrial carbon with ~ 30 % of their carbon stored as soil carbon (Bai and Cotrufo, 2022; Wang et al., 2019c). In addition, grasslands cover 68 % of the total global agricultural area (Bossio et al., 2020) and stores almost 245 Pg SOC (Poeplau et al., 2019) thus playing a vital role in global terrestrial C cycle (Wang et al., 2019b). Extreme drought can alter ecosystem carbon cycling (Karlowsky et al., 2018) via changes to soil organic carbon (SOC) which is sensitive to many abiotic (soil moisture, respiration and temperature) (Jentsch et al., 2011) and biotic (plant and microbial activity) processes (Fuchslueger et al., 2014; Zhao et al., 2022). Chronic drought in arid and semi-arid grasslands caused losses of SOC content in top (0–10 cm) soil due to decrease productivity, disturbance of root physiology, modification of root structure and root-microbes interaction (Bogati and Walczak, 2022; Luo et al., 2020). Likewise, during the 2000–2004 chronic drought event of western North America, the strength of the grasslands carbon sink declined substantially, with reductions ranging between 30 and 298 Tg C yr⁻¹ (Schwalm et al., 2012) while variable response of SOC to extreme drought were also observed in more mesic grasslands (Hasibeder et al., 2015; Sippel et al., 2018). Impacts of chronic drought on SOC are often severe due to decreasing soil water availability (Bradford et al., 2020), large-scale vegetation die-off (Breshears et al., 2005), loss of soil microorganisms (Jiang et al., 2013), and reduced formation of soil organic matter (Schaeffer et al., 2017; Smith, 2011). However, some studies report semiarid and humid grassland ecosystems exhibit high resilience capacity (ability to recovery of function e.g., biomass productivity and microbial activities) after drought has subsided (Hoover et al., 2015). However, more arid grasslands may recover more slowly due to greater resource limitation compared to semiarid and mesic grasslands (Stuart-Haëntjens et al., 2018). Earlier studies also found that chronic drought changes microbial metabolic products which impact the chemistry of soil organic matter (Bradford et al., 2020; Malik and Bouskill, 2022), disrupting soil substrate availability and soil nutrient mobility leading to loss of grassland SOC content across different climatic regions from arid to mesic (Frank et al., 2015; Knapp and Smith, 2001). Similarly, manipulated intense drought reduced plant growth and poses significant stress to microbial communities (Malik and Bouskill, 2022) which lead to greater loss of SOC content in arid and semi-arid grasslands (Luo et al., 2020). In temperate and mesic grassland, plants may increase their investment on belowground growth to overcome extreme drought stress and may increase the diversity and activities of soil microbes which accelerate the input of organic C content to soil (Burri et al., 2014). Past manipulated drought experiments have explored the impact of both chronic and intense droughts on SOC content at a single site and climatic region, yet it is unlikely that ecosystem responses to altered rainfall patterns and drought can be extrapolated to other sites with multiple

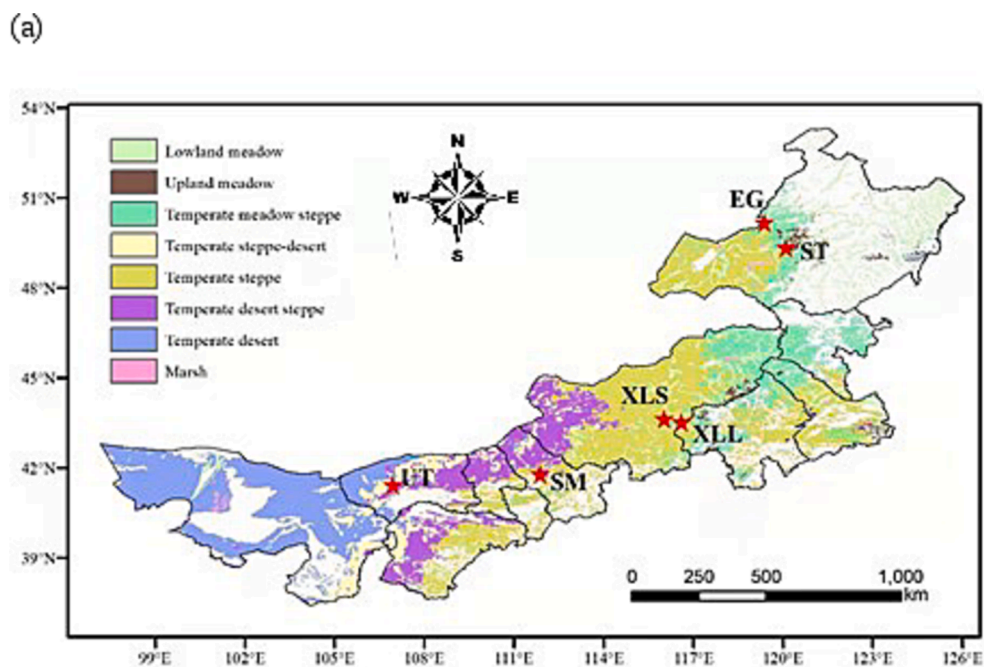
climatic zones (Hoover et al., 2015; Luo et al., 2020). To better predict the effect of extreme drought types on SOC content from arid to mesic grasslands, research needs to incorporate information from global and regional scales.

A recent study found that intense drought decreased aboveground primary productivity greater than chronic drought (Carroll et al., 2021), although, neither the chronic nor intense drought significantly affected belowground productivity and SOC content (Luo et al., 2020). It is expected that a loss of aboveground primary productivity following intense drought alters plant-driven carbon inputs to soil and enhances SOC decomposition (Knorr et al., 2005). Although increased root growth enhances SOC, a considerable proportion of SOC content increases under extreme drought which is likely driven by the suppression of the soil decomposer community (Crowther et al., 2019; Luo et al., 2020). To date, there are no clear evidence exists regarding the differential effect of intense and chronic drought on SOC content (Burri et al., 2014; Luo et al., 2020). In addition, sufficient information is also missing how chronic and intense drought influences the response of above-belowground productivity and SOC content across aridity. Therefore, we have conducted a 4-yr drought experiment to examine the effect of chronic vs. intense drought on SOC content in top (0–10 cm) soil across six grasslands that encompass desert steppe, typical steppe, and meadow steppe in northern China. We also examined how the response of grasslands net productivity influence SOC content under two drought types. Specifically, we hypothesized that (1) SOC content would decrease due to extreme drought with the effect being stronger at drier sites; (2) the response of SOC content would depend on drought type, with chronic drought having a larger impact than intense drought; and (3) the response of SOC content to extreme drought will be positively correlated with BNPP and negatively correlated with ANPP.

2. Material and methods

2.1. Study sites

This study was conducted as part of the Extreme Drought in Grasslands Experiment (EDGE) in six grasslands distributed along an aridity gradient. These six sites represent 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 (Fig. 1a). Northern China grasslands are experienced frequent land use change (e.g., grassland into cropland, grassland into farmland) particularly from 1949 to 1980. After 1980 s grasslands restoration, improvement and broad research are carrying out across Eurasian steppe in Inner Mongolia (Wu et al., 2015). The mean annual temperature (MAT) and mean annual precipitation (MAP) of study area ranged from 5.3 to -2.4 °C and 137.5 to 397.8 mm respectively in dry to wet sites during the experimental years which are derived from meteorological stations at each site (Table 1). The desert steppe is in the western region is dominated by drought-tolerant dominant short C₃ grasses, such as *Stipa klemenzii* and *Stipa breviflora* (Sui and Zhou, 2013). The typical steppe is in the middle part of the region and is mainly composed of perennial xerophytic grasses, such as *Stipa grandis* and *Leymus chinensis*. Finally, the meadow steppes are situated in the sub-humid zone of the eastern part of the study area and are dominated by the perennial rhizomatous grass, *L. chinensis*, as well as an abundance of perennial mesophytic and xerophytic species such as *Stipa baicalensis* and *Filifolium sibiricum* (Lei et al., 2015). May to August is considered as the growing seasons of the major three grassland types. Soils in this region are predominantly dark brown, humus rich-chestnut and chernozem soils according to the US system of soil taxonomy and world soil information system database popularly known as International Soil Reference and Information Centre (ISRIC, <http://www.isric.org>) (Batjes et al., 2017). Additionally, some areas include cinnamon soil, ash soil, meadow soil, sand and dark brown soil (Ma et al., 2008). The soils derived from loess and rich in calcium mainly were silty to sandy in texture, with >60 % sand and a strong acid



(b)

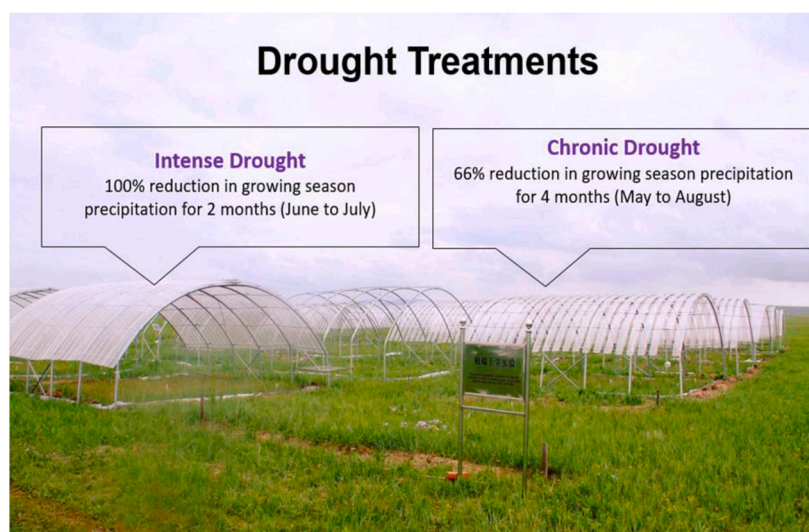


Fig. 1. Locations of the six grassland sites and model rainout shelters. The sites (UT = ‘Urat’, SM = ‘SheilaMuren’, XLL = ‘Xilinhoh-Laymus’, XLS = ‘Xilinhoh-Stipa’, EG = ‘Erguna’, and ST = ‘SherTara’) were ranked based on mean annual precipitation from low to high along a natural aridity gradient from the desert (arid) to Meadow (semi-arid) steppe in the grasslands of northern China (Muraina et al., 2021) (a). Two model rainout shelters are shown here: Intense and Chronic drought treatments (b). A layout of the experimental design (c). Detailed site information is provided in Table 1.

reaction ($\text{pH} > 7.0$) (Luo et al., 2020). Moreover, the typical steppe grasslands soil mainly characterized by loamy textured with sand content at $59.6 \pm 0.6\%$, silt at $23.8 \pm 0.4\%$, and clay at $16.7 \pm 0.4\%$ and freeze to a maximum depth of about 1910 mm during the winter. Average bulk density in our desert, typical and meadow steppe grassland sites were 1.52 ± 0.10 , 1.38 ± 0.12 , and $1.26 \pm 0.19 \text{ g cm}^{-3}$ respectively.

2.2. Experimental design

In April 2014, we established identical precipitation manipulation experiments with three treatments at each site: control (i.e., ambient precipitation), chronic drought, and intense drought (Fig. 1b). The experiment was a randomized complete block design with six replicates

of each treatment at each site. All plots were arranged in blocks, with each treatment randomly allotted within each block (Fig. 1c), to control for possible differences in environmental and soil gradients (Muraina et al., 2021). We imposed our treatments by constructing three types of rainout shelters: control plots (open-air shelters without roofs), chronic drought (open-air shelters with roofs omitting 66% of rainfall from May to August), and intense drought (open-air shelters with roofs omitting 100% of rainfall from June to July). Both chronic and intense drought-treatment plots were covered by a light scaffold that supported by transparent polyethylene sheet (Beijing Plastics Research Institute, Beijing, China). For chronic drought, the clear corrugated polyethylene sheet was arranged at such a density sufficient to passively reduce each rainfall event by $\sim 66\%$ during the growing season while intense treatment was achieved with a complete roof made from panels of clear

(c)

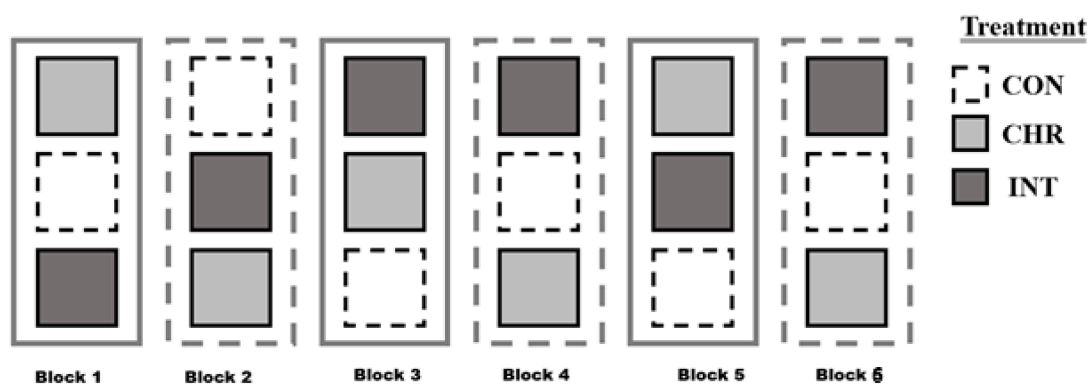


Fig. 1. (continued).

Table 1

Characteristics of six grassland sites in Northern China grasslands. MAP³ (mm) represents mean annual precipitation from 1972 to 2018 and MAP⁶ (mm) represents mean annual precipitation and MAT (°C) represents mean annual temperature during the experiment from 2015 to 2018 derived from meteorological stations at each site.

Site name	Urat	SheilaMuren	Xilinhot-Leymus	Xilinhot-Stipa	Erguna	Sher Tara
Latitude	41°25'00"N	41°47'00"N	43°33'6"N	43°32'25"N	50°10'46"N	49°21'00"N
Longitude	106°58'00"E	111°53'00"E	116°40'20"E	116°33'18"E	119°22'56"E	120°06'00"E
Terrain	Mountains, hills, high plains	Mountains, hills, high plains	Mainly Hilly	Mainly Hilly	Hills and high mesa	Hills and high mesa
Climate	Arid continental	Arid continental	Temperate semi-arid	Temperate semi-arid	Temperate continental monsoon	Temperate continental monsoon
Soil type	Light chestnut soil	Light chestnut soil	Dark chestnut soil	Dark chestnut soil	Chernozem	Chernozem
MAT (°C)	5.3	3.4	0.3	0.3	-2.0	-2.4
MAP ³ (mm)	175	236	323	323	354	363
MAP ⁶ (mm)	137.5	233.5	311.5	311.5	307.8	297.8
Aridity Index	0.166	0.253	0.395	0.420	0.490	0.514
Vegetation types	Desert steppe	Desert steppe	Typical steppe	Typical steppe	Meadow steppe	Meadow steppe

corrugated polyethylene sheeting and permit no rain for two months during growing season. The control precipitation treatments did not have rainout shelters in place, but have widely spaced (2 m) metal support structures. Rainout shelters permit 90 % of photosynthetically active radiation to pass through and minimize microclimatic effects (Yahdjian and Sala, 2002). To minimize potential greenhouse effects, we installed roofs 2 m above the ground surface. Every plot was 6 × 6 m in size which we established at each grassland in randomized locations, with at least 2 m spacing from the closest plot. We hydrologically isolated each plot from the surrounding soil matrix by trenching and burying 6 mil aluminum flashing 1 m deep to prevent surface and sub-surface water flow. Aboveground, 10 cm of aluminum flashing was partially buried around the perimeter of each plot to limit overland 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.

2.3. Sampling and measurement

We collected soil samples from a single 1 m × 1 m sub-plot in each replicate of 6 m × 6 m plot during the peak growing season in the end of August of each experimental year e.g., 2015, 2016, 2017, and 2018. Following the removal of litter, five soil cores were collected from each sub-plot using a soil corer (2.5 cm diameter) at (0–10 cm) soil depth (Luo et al., 2020). The soil samples collected in the same layer from each quadrant were mixed evenly to form a composite sample. Each sample was fumigated with 12 M HCl vapor for 12 h to removal of carbonates.

Generally, the carbonates are released as CO₂ by the HCL treatments in 6 to 8 h. Fumigating the soil with HCl may reduce or eliminate any organic C losses from the soil. After homogenization by hand a total 432 (18 plots × 6 sites × 4 years) soil samples were stored immediately in the refrigerator at 4°C. This storage temperature is recommended to slow down the soil microbial and other enzymatic activities. Later, all the soil samples were air dried in the laboratory and passed through a 2-mm sieve to remove coarse roots, stones and easily detectable plant litter prior to laboratory analysis. SOC content (g kg⁻¹) was determined using a PE 2400 Series II CHN Elemental Analyzer (Perkin-Elmer, Norwalk, CT, USA). We harvested all aboveground biomass at the end of the growing season (i.e., August) in each experimental year. Biomass was clipped at the ground level from a 1 m × 1 m sub-plot which was placed randomly in one of two sub-plots designated for destructive measurements (altering between years). Biomass was sorted to remove the previous year's growth. We estimated belowground net primary production (BNPP g m⁻²) using root ingrowth cores to measure fine root mass production. At the beginning of each growing season, two 2.5 cm diameter soil cores were sampled at 0–10 cm depth in each plot. A 20-cm cylindrical mesh basket filled with sieved, root-free soil was placed into each of the holes created by the soil cores. Any space between the ingrowth core and the intact soil was carefully filled with sieved soil. All ingrowth cores were removed at the end of the growing season, placed in plastic bags, and stored at 4 °C until processing. All soil was washed off the roots by first wet sieving the ingrowth core depth (0–10 cm) to remove excess soil and then submerging the remaining sample in a

shallow bowl of water and carefully picking out roots and removing any attached soil. Finally, all sorted aboveground and belowground biomass were immediately dried at 105 °C for 30 min to minimize respiration and decomposition and later were completely oven-dried at 60 °C for 48 h and weighed to estimate ANPP and BNPP in the laboratory (Table S2). The biomass was weighed twice with several hours' interval to ensure completed drying. Although SOC accumulation can still be substantial below 10 cm depths, our results do not reflect extreme drought effects on total soil carbon content but organic carbon only. However, this upper soil horizon (0–10 cm) represents the most biologically active component of soil and stores by far the greatest content of soil organic carbon (Crowther et al., 2019). In addition, most roots of *Stipa grandis* and *Leymus chinensis*, *Stipa klemenzii* and *Stipa breviflora* were distributed in the soil depth of 0–10 cm (Ao et al., 2009).

2.4. Statistical analysis

We performed all statistical tests using R Studio v.4.1.2 (R CoreTeam, 2021) and produced graphs using the *ggplot2*, *tibble*, *plyr* package (Wickham, 2016). We used some other packages of R studio *ggpubr* (Kassambara, 2017), *ggpmisc* (Aphalo, 2017), *gridextra* (Auguie and Antonov, 2017), *nlme* (Pinheiro et al., 2018) while plotting the graphs. We calculated the mean SOC content of control and treatment (e.g., chronic and intense drought) plots across individual years (e.g., 2015, 2016, 2017 and 2018) (Fig. 2) as well as mean SOC content of four years (Fig. 3) in six different study sites. Before statistical analysis, Shapiro–Wilk tests were used to test the normality and heteroscedasticity of all data. Due to the normal distribution of all data and homogeneity of variance, original data were used in our statistical analysis without log-transformation. The response ratio of SOC in each plot was calculated as the relative response ratio of SOC content in drought plots versus control

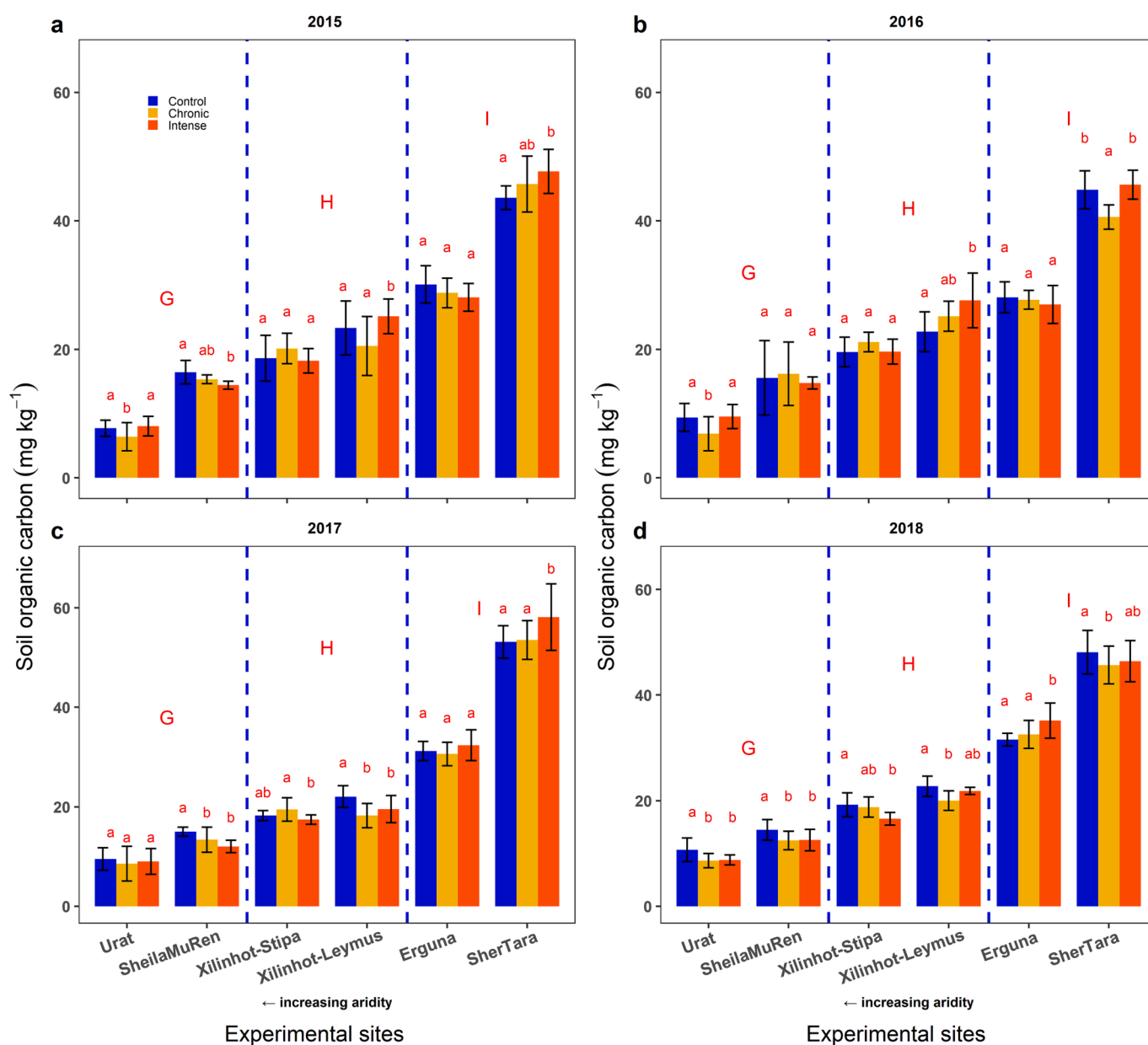


Fig. 2. Effects of chronic and intense droughts on soil organic C content for the six grasslands sites along the aridity gradient for individual years: 2015 (a), 2016 (b), 2017 (c), and 2018 (d). Error bars represent mean ± standard deviation (SD). Lowercase letters above the bars indicate differences among the three treatments at each site. Capital letters above the bars indicate differences among grasslands with different aridity (Urat and SheilaMuren are 'Arid' sites, Xilinhot-Leymus and Xilinhot-Stipa are 'Semi-arid' sites, Erguna and SherTara are 'Mesic' sites). Please see Table 1 for detailed site description.

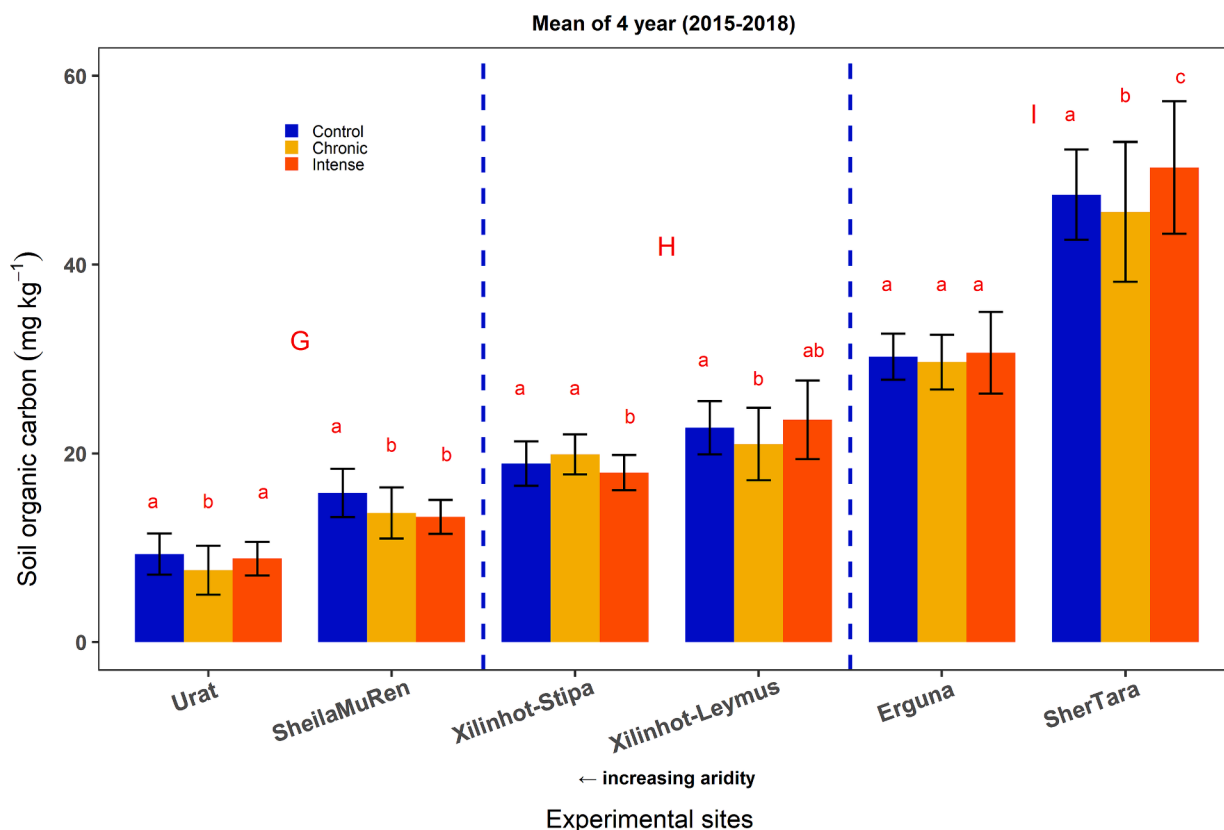


Fig. 3. Effects of chronic and intense droughts on soil organic carbon (SOC) content for the six grassland sites along the aridity gradient averaged across experimental years (2015–2018). Error bars represent mean \pm standard deviation (SD). Lowercase letters above the bars indicate differences among the three treatments at each site. Capital letters above the bars indicate differences among grasslands with different aridities (Urut and SheilaMuren are ‘Arid’ sites, Xilinhot-Leymus and Xilinhot-Stipa are ‘Semi-arid’ sites, Erguna and SherTara are ‘Mesic’ sites). Please see Table 1 for detailed site description.

plots: $SOC_{\text{response ratio}} = (SOC_{\text{Treatment}} - SOC_{\text{Control}}) / SOC_{\text{Control}}$ (Hsu et al., 2012; Zhang et al., 2017). This was estimated separately for each drought type (i.e., chronic vs. intense). We calculated response ratios for both ANPP and BNPP independently. This allowed us to test for potential relationships between the drought sensitivity of SOC content and that of primary productivity at each site (Crowther et al., 2019). To measure the effect of treatments and year on SOC content at each site, we used one-way analysis of variance (ANOVA) for treatment and year separately. Further, two-way ANOVA was applied to identify the interaction of treatments and year (Table 2). Repeated-measures analysis of variance (RMANOVA) was used for testing the effects of treatments, years, sites, and their interaction on SOC content where, site, treatment, and year were included as fixed effects, and the block was included as a random effect (Table 3). These factors i.e., year, treatment, sites and their interaction analysis independently allowed us to focus on responses to the two types of droughts on SOC content within each site. We used Tukey’s HSD test to test for significant differences between treatments. To assess the relationships across sites and to avoid potential pseudo-replication (Griffin-Nolan et al., 2019), we used generalized linear mixed-effects models fit by residuals maximum likelihood (REML) approach using the ‘lme’ function from the ‘nlme’ library (Pinheiro et al., 2018) where SOC is the ‘dependent variable’ and response ratio of ANPP or BNPP is the ‘independent variable’ in the models. Both marginal and conditional R^2 values for generalized mixed-effects models were calculated using the `r.squaredGLMM` function of the `MuMIn` package (Bartón, 2016) developed by Nakagawa and Schielzeth, 2013 to show the relationship between the drought-induced response ratio of SOC content with the response ratio of net primary productivity while accounting for site differences. In each general linear mixed effect models, rainout shelter (blocks) was considered as a ‘fixed factor’ and

Table 2

Results of two-way ANOVAs testing the effects of treatment and year on soil organic carbon (SOC) content in six grasslands across 2015–2018. Degrees of freedom (df), F-test values, and P-values are given. Significant P values ($P < 0.05$) are shown in bold.

Sites (Actual name)	Variable	SOC		
		df	F	P
A (Urut)	Treatment	2	4.24	0.018
	Year	1	8.31	0.005
	Treatment \times Year	2	5.10	0.031
B (SheilaMuren)	Treatment	2	0.47	0.622
	Year	1	4.45	0.038
	Treatment \times Year	2	0.735	0.482
C (XilinhotStipa)	Treatment	2	5.17	0.008
	Year	1	3.62	0.041
	Treatment \times Year	2	3.14	0.032
D (XilinhotL)	Treatment	2	3.38	0.039
	Year	1	7.01	0.010
	Treatment \times Year	2	2.53	0.022
E (Erguna)	Treatment	2	0.389	0.679
	Year	1	22.20	<0.001
	Treatment \times Year	2	5.83	0.035
F (SherTara)	Treatment	2	1.29	0.280
	Year	1	5.15	0.026
	Treatment \times Year	2	0.304	0.738

Table 3

Results of repeated-measures ANOVAs testing the effects of treatment, site and year on the soil organic carbon (SOC) content in six grasslands across 2015–2018. Degrees of freedom (df), F-test values, and *P*-values are given. Significant *P* values (*P* < 0.05) are shown in bold.

	df	SOC	
		F	<i>P</i>
Treatments	2	3.27	0.024
Sites	5	1332.76	<0.001
Years	1	2.37	0.012
Treatments × Years	2	0.52	0.095
Treatments × Sites	10	1.99	0.050
Years × Sites	5	8.08	<0.001
Treatments × Years × Sites	17	3.72	<0.001

sites as a ‘random factor’. Further regression analysis was applied to assess the proportional changes (response ratio) of SOC content in response to climatic variables of each site: mean annual precipitation (MAP), mean annual temperature (MAT) and aridity index (AI). Aridity index was calculated as the ratio of MAP to potential evapotranspiration (PET), with values closer to 0—denoting greater aridity) (Li et al., 2017). We calculated PET using a method given by (Hargreaves and Samani, 1985):

$$PET = 0.0023 \times R_a \times (T_{\max} - T_{\min})0.5 \times (T + 17.8)$$

Where R_a is the extraterrestrial solar radiation (MJ/m²/day), T_{\max} and T_{\min} are the maximum and minimum temperatures (°C), respectively; and T is the mean air temperature (°C).

3. Results

Overall extreme drought significantly decreased SOC content among grasslands with the effect being more pronounced in more arid sites (across aridity i.e., mesic-Erguna, SherTara vs semi-arid-Xilinhoh-Laymus, Xilinhoh-Stipa vs arid-Urat, SheilaMuren: *P* < 0.05). In Urat site chronic drought significantly decreased SOC content (mean: 5.39 mg kg⁻¹ ± sd: 2.19 mg kg⁻¹) in 2015 (Fig. 2a), (mean: 6.86 mg kg⁻¹ ± sd: 2.65 mg kg⁻¹) in 2016 (Fig. 2b) and both chronic (mean: 8.66 mg kg⁻¹ ± sd: 1.36 mg kg⁻¹) and intense (mean: 8.77 mg kg⁻¹ ± sd: 0.95 mg kg⁻¹) drought in 2018 respectively compared to control (Fig. 2d). In SheilaMuren site intense drought significantly decreased SOC content (mean: 13.42 mg kg⁻¹ ± sd: 0.62 mg kg⁻¹) in 2015 (Fig. 2a) and both chronic (mean: 12.40 mg kg⁻¹ ± sd: 2.53 mg kg⁻¹), (mean: 11.47 mg kg⁻¹ ± sd: 1.76 mg kg⁻¹) (Fig. 2c) and intense drought (mean: 12.02 mg kg⁻¹ ± sd: 1.24 mg kg⁻¹), (mean: 11.54 mg kg⁻¹ ± sd: 2.02 mg kg⁻¹) (Fig. 2d) in 2017 and 2018 respectively compared to control. Xilinhoh stipa sites experienced to decreased SOC content only under intense drought (mean: 16.54 mg kg⁻¹ ± sd: 1.20 mg kg⁻¹) in 2018 (Fig. 2d). Both chronic (mean: 18.24 mg kg⁻¹ ± sd: 2.43 mg kg⁻¹) and intense (mean: 19.25 mg kg⁻¹ ± sd: 2.72 mg kg⁻¹) drought decreased SOC content in Xilinhoh Leymus sites in 2017 (Fig. 2c) and only chronic drought (mean: 20.01 mg kg⁻¹ ± sd: 1.84 mg kg⁻¹) in 2018 (Fig. 2d), however intense drought increase SOC content in Xilinhoh Leymus sites in 2015 (Fig. 2a) and 2016 (Fig. 2b) respectively compared to control. Similarly, intense drought increased SOC content at Erguna sites in 2018 (mean: 35.14 mg kg⁻¹ ± sd: 3.33 mg kg⁻¹) (Fig. 2d) and at SherTara site in 2015 (mean: 47.69 mg kg⁻¹ ± sd: 3.44 mg kg⁻¹) (Fig. 2a) and (mean: 58.12 mg kg⁻¹ ± sd: 6.70 mg kg⁻¹) (Fig. 2c) in 2017 respectively compared to control.

When averaged across years we found that chronic drought decreased SOC content from 2015 to 2018 in site Urat (4.20 mg kg⁻¹; *P* = 0.026; mean ± sd: 7.63 ± 2.58 mg kg⁻¹), SheilaMuren (3.92 mg kg⁻¹; *P* = 0.039; mean ± sd: 13.70 ± 2.70 mg kg⁻¹), Xilinhoh-Leymus (2.72 mg kg⁻¹; *P* = 0.023; mean ± sd: 21 ± 3.82 mg kg⁻¹) and SherTara (2.83 mg kg⁻¹; *P* = 0.005; mean ± sd: 45.60 ± 7.40 mg kg⁻¹) compared to

control. On the other hand, intense drought decreased SOC content in SheilaMuren (3.72 mg kg⁻¹; *P* = 0.039; mean ± sd: 13.28 ± 1.79 mg kg⁻¹) and Xilinhoh-Stipa (2.27 mg kg⁻¹; *P* = 0.039; mean ± sd: 17.97 ± 1.85 mg kg⁻¹). The mesic site (SherTara) was the only site where SOC content increased during the intense drought (4.18 mg kg⁻¹; *P* = 0.018; mean ± sd: 50.30 ± 7.01 mg kg⁻¹) compared to control (Fig. 3). We observed no effect of chronic drought at Xilinhoh-Stipa (mean ± sd: 19.90 ± 2.11 mg kg⁻¹; *P* = 0.121) and Erguna (mean ± sd: 29.67 ± 2.89 mg kg⁻¹; *P* = 0.077), and no effect of intense drought at Urat (mean ± sd: 8.85 ± 1.79 mg kg⁻¹; *P* = 0.204), Xilinhoh-Leymus (mean ± sd: 23.54 ± 4.15 mg kg⁻¹; *P* = 0.318) and Erguna (mean ± sd: 30.64 ± 4.31 mg kg⁻¹; *P* = 0.474) sites respectively (Fig. 3). The response of SOC content to drought depended on site-level drought extremity and the responses varied by treatment (chronic or intense drought) (Fig. 4b) and sites (arid, semi-arid, or mesic) (Fig. 4a). Chronic drought reduced SOC content by 9–13.8 % at the high aridity sites (Urat: *P* = 0.007), 11.4 % at the semi-arid sites (Xilinhoh-Laymus: *P* = 0.010), and 4.4–8.6 % at mesic sites (SherTara: *P* = 0.031) (Fig. 4a). Intense drought had an inconsistent effect on SOC content across sites. Specifically, it decreased SOC content by 3.2–9.4 % in arid sites (SheilaMuren *P* = 0.022) and 8.3 % in semi-arid site (Xilinhoh-Stipa *P* = 0.043). However, it increased SOC content by 0.2–7.70 % in the mesic grassland site (SherTara: *P* = 0.037) (Fig. 4a). When averaged all sites and years, extreme drought typically lead to decreased SOC content by 1.8–7.5 % compared to control and the effect being higher for chronic drought (*P* = 0.008) (Fig. 4b).

To understand how SOC content is influenced by NPP, we investigated the response ratio of SOC content in response to ANPP and BNPP. The response of SOC content across sites was correlated with the response in aboveground net primary productivity (ANPP) and belowground net primary productivity (BNPP). Specifically, we showed evidence that the response of SOC content to chronic drought is negatively related in response of ANPP (*R*² marginal = 0.17, *R*² conditional = 0.32, *P* < 0.001), but there was no relationship between the two for the intense drought (*R*² marginal = 0.015, *R*² conditional = 0.18, *P* = 0.21) (Fig. 5a-b). Our results also showed that the response ratio of SOC content in response to intense drought is positively related to response of BNPP (*R*² marginal = 0.39, *R*² conditional = 0.45, *P* < 0.001) but not for chronic drought (*R*² marginal = 0.038, *R*² conditional = 0.051, *P* = 0.062) (Fig. 5c-d). To test whether the SOC content under both chronic and intense droughts were driven by climatic variables e.g., MAP, MAT and AI, we examined linear regression model, between response ratio of SOC content with climatic variables. Our results showed that the response ratio for SOC content significantly and positively correlated with MAP which indicates that SOC content increase with MAP under both chronic (*R*² = 0.53, *P* = 0.01) and intense drought (*R*² = 0.45, *P* = 0.021) (Fig. 6a-b). In contrast, we found a significant negative relationship between response ratio SOC content with mean annual temperature (MAT) and aridity index (AI) under chronic (MAT: *R*² = 0.63, *P* = 0.009; AI: *R*² = 0.68, *P* = 0.039) and intense drought (MAT: *R*² = 0.39, *P* = 0.018; AI: *R*² = 0.36, *P* = 0.032) (Fig. 6c-f) which exhibited that SOC content decreased with increases MAT and AI.

4. Discussion

To understand how two types of extreme drought (chronic vs. intense) influence grassland SOC content across an aridity gradient, we experimentally imposed extreme drought across six grassland sites ranging from desert to meadow steppe in northern China. Our results generally support our first hypothesis that drought negatively influenced SOC content in top soil (0–10 cm) and the response was site as well as time-dependent where arid and semi-arid grasslands experienced greater loss and intense drought increased SOC content in the most mesic grassland site (Table 3, Fig. 2). Generally, extreme droughts lead to decreased carbon allocation in plants biomass (Ingrisch et al., 2018; Naudts et al., 2011) and reduced carbon transfer to the roots and the rhizosphere (Fuchslueger et al., 2014; Hasibeder et al., 2015) causing

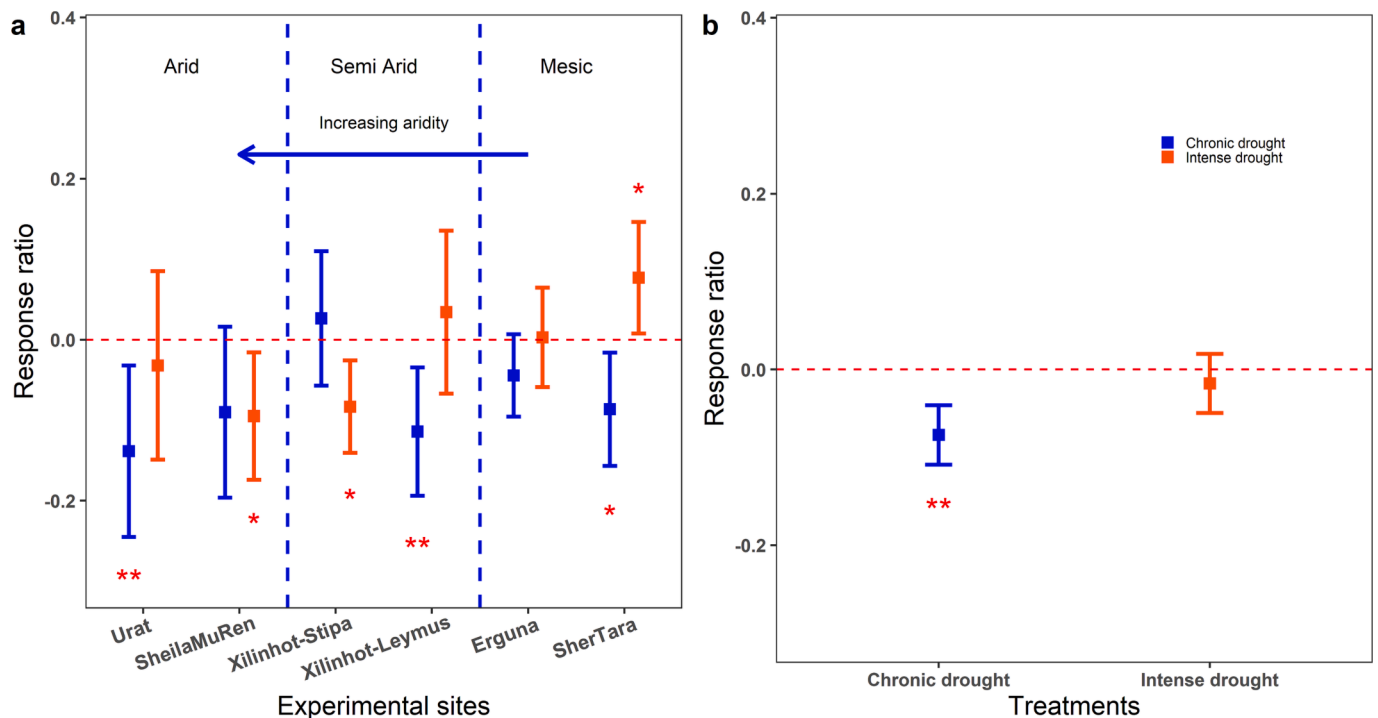


Fig. 4. Response ratios of soil organic carbon (SOC) content to chronic and intense droughts. Results for each grassland site (a) and for all combined sites (b) are shown. Two different colors (red and blue) square symbols indicate the mean value of the response ratio of soil organic C for each treatment in a site and vertical bars represent 95% confidence intervals. Negative and positive values indicate decline and increase in SOC compared to the control (the horizontal red dashed line). The SOC response ratio was calculated as $(SOC_{\text{Treatment}} - SOC_{\text{Control}}) / SOC_{\text{Control}}$. Asterisks over the error bars represent significant treatment effects at the 0.05 (*) and 0.01 (**) levels of probability. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

lower SOC content in top (0–10 cm) soil (Barthel et al., 2011; Burri et al., 2014). Although the supply of carbon from belowground roots to soil via root death and turnover are strongly dependent on soil microorganisms (Bardgett et al., 2005), extreme drought can suppress microbial mineralization and root exudation which in turn reduces SOC (Canarini and Dijkstra, 2015; Fuchslueger et al., 2014). Several studies have illustrated that extreme summer short term drought alters the allocation of fresh assimilates to roots thereby increasing root and microbial respiration in mountainous meadow grasslands—a primary cause of SOC loss (Bahn et al., 2009; Hasibeder et al., 2015). Similar and slightly opposite results was observed from a recent extreme drought experiment (growing season precipitation reduction for 2 years) which suggested that extreme drought significantly reduced SOC content in a moderately arid grassland but increased in a low aridity grassland (Luo et al., 2020). Importantly we observed the difference in SOC content across treatments was lower during the first year of our experiment and this difference was maintained and greater over the four years across six sites. Thus, treatment, time, and site also significantly influenced SOC content (Table 3). We also observed a mixed effect (mostly negative) of extreme drought on SOC content across the different grassland except most mesic sites (Fig. 3). Mesic sites with tall grasses generally have the greatest soil moisture availability and higher productivity which positively influences SOC content (5.1 mg kg^{-1}) directly through physical and chemical protection of soil organic matter and indirectly through soil available moisture and controls plant productivity under drought (Anacker et al., 2021; Collins and Calabrese, 2012; Luo et al., 2020). In addition, our mesic grassland sites are characterized by chernozem soil with a high percentage of humus (5–15%), available calcium ions bound to soil particles, and rich organic matter which protects, stabilizes and increase (4.18 mg kg^{-1}) SOC content in a well-aggregated soil structure (Guillaume et al., 2022; Percival et al., 2000; Rasmussen et al., 2018). Previous extreme drought experiments with very similar site characteristics to our sites suggested that extreme drought decrease 2.4 mg

kg^{-1} SOC content in top soil (e.g., 0–10 cm) (Karlowsky et al., 2018; Luo et al., 2020). This is probably because drying of soil during extreme drought has major impacts on the activity of rhizosphere microorganisms especially in arid and semi-arid grassland which limit the soil substrate mobility and slow down the soil microbial metabolism that alter organic C release in soil (Karlowsky et al., 2018; Nunan et al., 2017). While we did not measure the drought induced change in microbial metabolism, considering site similarities we may assume similar mechanisms as well as suggest for future study. In addition, we hope our study will prompt numerous calls for regionally to globally distributed grassland experiments to better predict why grasslands SOC in some climatic gradients (mostly arid sites grasslands) are more sensitive to climate extreme than semi-arid and mesic.

Our results further demonstrated that drought type (i.e., chronic vs. intense) differentially influenced SOC content depending on site characteristics (Table 2). Similar to our second hypothesis we found, chronic drought reduced SOC content more than the intense drought. Although intense drought decreased SOC content in arid and semi-arid grasslands, it increased in the most mesic grassland site (Fig. 4). This is probably because intense drought restricted organic C accumulation into soils by drought sensitive plant roots in arid and semi-arid grasslands (Luo et al., 2015). Our results showed that both chronic and intense drought significantly influences grassland productivity although the response may vary depending on grassland type. For example, chronic drought had a more negative effect on ANPP than intense drought in four North American desert grasslands abundant with *Bouteloua eriopoda*, *Bouteloua gracilis* and mixed-grass prairie dominated by *Pascopyron smithii* and *B. gracilis* (Griffin-Nolan et al., 2019) although intense drought had a larger impact on BNPP for the most mesic of these sites (Carroll et al., 2021). While one might expect that reduced BNPP in mesic grasslands has a negative effect on SOC content (Carroll et al., 2021; Hasibeder et al., 2015), our results do not support this prediction and we found that intense drought increase SOC content in most mesic grassland sites. In

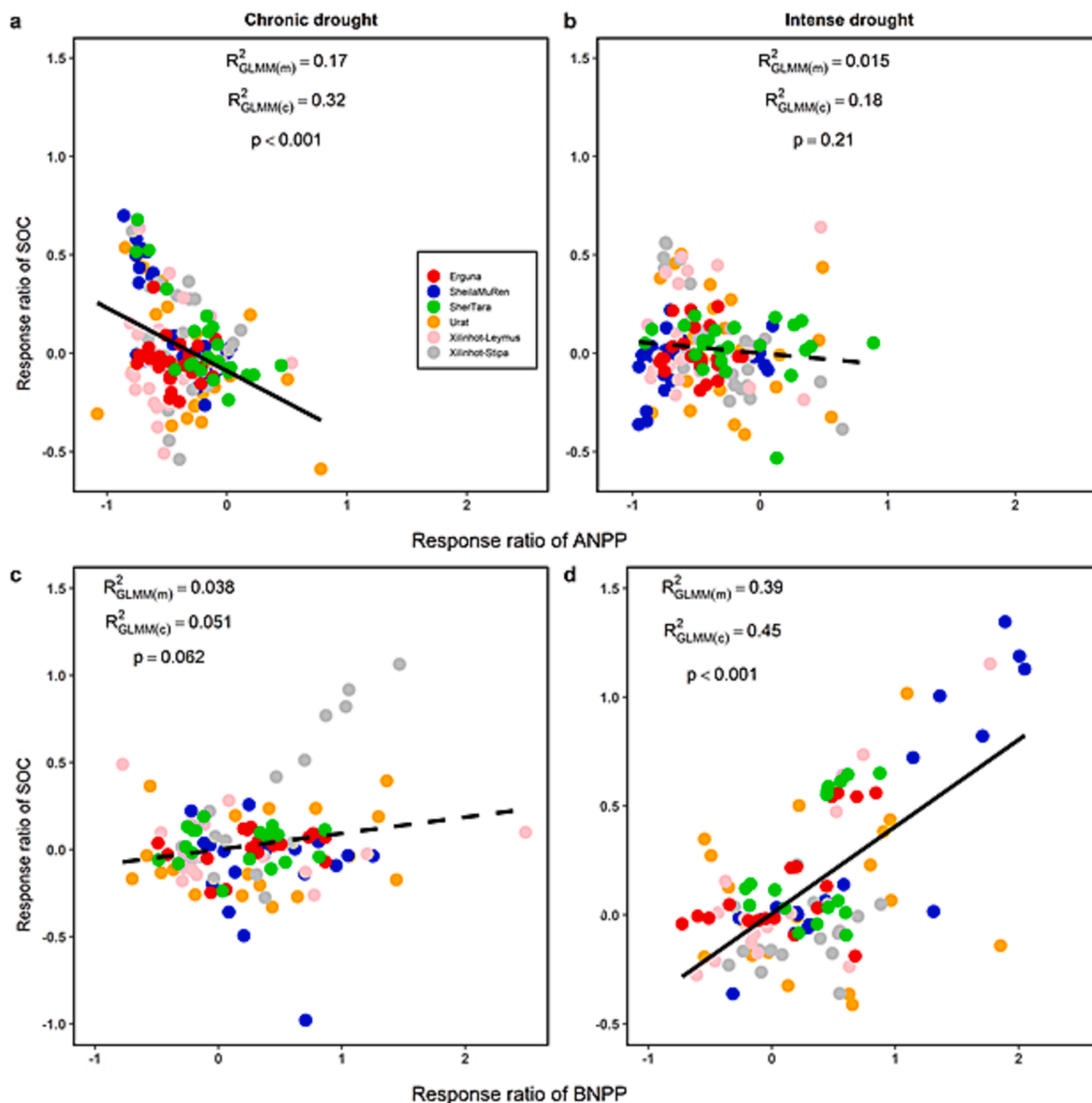


Fig. 5. Relationships among response ratio of SOC vs response ratio of ANPP and BNPP across six grasslands sites. The SOC, ANPP and BNPP response ratio was calculated as $(SOC_{Treatment} - SOC_{Control}) / SOC_{Control}$, $(ANPP_{Treatment} - ANPP_{Control}) / ANPP_{Control}$ and $(BNPP_{Treatment} - BNPP_{Control}) / BNPP_{Control}$ respectively in a given year. The plotted regression lines were derived from general linear mixed effect models (GLMM) where rainout shelter (blocks) as a fixed effect and sites as a random effect. Both the marginal (m) R^2 and conditional (c) R^2 values for the GLMM are shown inside the figures. Each color represents a site.

contrast with previous findings, Liu et al., 2020 found that extreme water stress (e.g., 40 % of soil field capacity for one month-September) increased fine root turnover and decreased root longevity leading to an increase in SOC content. Another 2-year extreme drought study in the same climatic region of China found that neither chronic (66 % precipitation reduction in May - August) nor intense drought (100 % precipitation reduction in June - July) drought significantly decreased SOC content up to top 10 cm, however, the mesic grassland sites showed increased SOC for intense drought (Luo et al., 2020) which is similar to our findings. It is unknown what mechanisms drives the intense droughts having a greater effect on SOC content than chronic drought in that study. While we did not measure the mechanism behind this but based on past results we can assume that drought type influences arid and semi-arid grassland SOC dynamics differently (Hoover et al., 2015). These specific results suggest that types of extreme drought along with

site characteristics are key for understanding drought impacts on SOC content. Our results will have direct implications for future extreme drought model simulations to determine soil carbon dynamics on global grasslands with identical protocol to fight against climate extreme.

We third hypothesis is that the response of SOC content to extreme drought would be associated with simultaneous changes in plant productivity (both ANPP and BNPP). We found that chronic drought decreased both ANPP and SOC content and this effect increased with increasing aridity (i.e., SOC reductions were greater in arid compared to mesic grasslands) (Fig. 5a). This is because decreases in ANPP at drier sites (Table S2) affect soil processes by lowering soil moisture availability and soil solute mobility, while increasing soil carbon decomposition and respiration (Ren et al., 2017a,b; Schrama and Bardgett, 2016). Despite plants in semi-arid grasslands being adapted to short-term drought, ANPP declined progressively under prolonged chronic

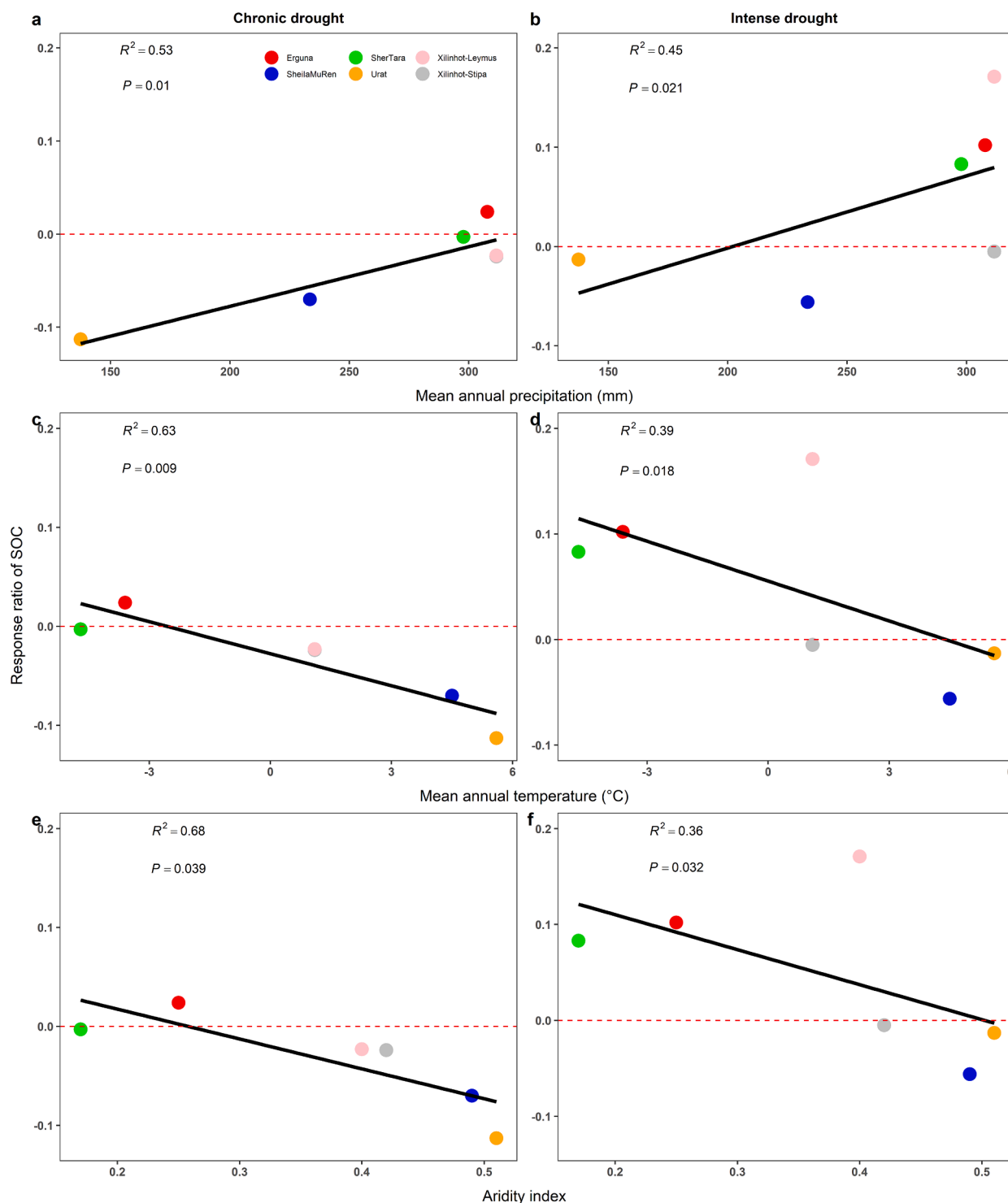


Fig. 6. Relationships between response ratio ($\text{SOC}_{\text{Treatment}} - \text{SOC}_{\text{Control}} / \text{SOC}_{\text{Control}}$) of SOC vs. MAP (Mean Annual precipitation) (a, b), MAT (Mean annual temperature) (c, d) and AI (Aridity index) (e, f) under chronic and intense drought. Six different color represents individual sites and straight lines indicate the linear regression model. The Red dashed line indicates response ratio (RR) = 0 or no effect. The gray area represents the 95 % confidence band. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

drought (Meng et al., 2021). SOC content can also be constrained by drought-induced suppression of plants physiological activities (e.g., increased respiration, disturb the availability of microbiota to the plant roots and decrease in enzymes activity) resulting in a loss of SOC as well as other soil nutrient (e.g., N and P) in arid grasslands (Bogati and Walczak, 2022; Li et al., 2017; Sardans and Peñuelas, 2012). However, we did not observe a significant relationship between ANPP and SOC

sensitivity to intense drought (Fig. 5b). It is likely that intense drought decreased the aboveground productivity of dominant species (e.g., *S. grandis*, *L. chinensis*, *S. baicalensis*) in arid sites and influenced the aboveground carbon available to transfer to belowground structures or fixed in plant root exudates and rhizosphere where it is urgently needed rather than release into the soil (Xu and Zhou, 2005) which could result in no significant interaction between ANPP and SOC relationship.

However, further studies are needed to identify the mechanism behind the lack of an ANPP-SOC relationship under intense drought. The response of SOC to extreme drought was also influenced by BNPP sensitivity –increase belowground net primary productivity led to enhance SOC content. Because root allocation is critical for plant survival during droughts (Harrison and LaForgia, 2019), it is important to understand how extreme drought influences belowground productivity and associated changes to SOC content. Our results suggest that the effects of extreme drought on the belowground productivity-SOC relationship also depended on drought types and sites. Specifically, intense drought increased SOC with increasing BNPP, except in arid grassland sites (Fig. 5d). Intense drought leads to dramatic reductions in photosynthesis and a shift in the allocation of plant biomass belowground which stimulates belowground microbial processing (microbial biomass, necromass, growth and turnover of soil microbes) – all factors that contribute to increased SOC content (Burri et al., 2014; Liu et al., 2017). Remus and Augustin (2016) and Hoover et al. (2015) each reported strong relationships between root growth, rhizodeposition (a mechanism of carbon release to soil through plant root), and root-derived C input when herbaceous annual or perennial grass species experienced extreme drought (35 % reduction of precipitation in year round) during the growing season. In addition, extreme drought (e.g., intense summer drought for 8 weeks) influenced rhizodeposition which increased the activity of soil microbial populations, therefore adding easily accessible C source to the soil (from the rhizodeposits) (Hasibeder et al., 2015; Lynch, 2002; Preece and Peñuelas, 2016), and increasing SOC content (Pausch and Kuzyakov, 2018; Sanaullah et al., 2012). Nevertheless, we did not observe a significant relationship between BNPP and SOC sensitivity to chronic drought (Fig. 5c). Although chronic drought has positive (Jaman et al., 2022), stable or no effect (Kreyling et al., 2008) on belowground biomass carbon in arid, semi-arid and temperate grassland, no significant effect on SOC content was also observed due to chronic drought in our study. While the intense drought often does not show widespread grass mortality, chronic drought may push them beyond mortality thresholds both in aboveground biomass and belowground roots with a substantial impact to the soil microbial function and SOC content (Lei et al., 2020). Moreover, long term precipitation absence in chronic drought causes reduce perennial grass cover in arid and semi-arid ecosystem (<40 %) which leaves these ecosystems susceptible to soil erosion, surface soil textures and soil parent material (Hoover et al., 2015). Similar to our findings, Luo et al., 2020, reported that chronic drought had no effect on SOC in high and medium aridity grassland. Our result further suggests that BNPP and SOC responses are not linked with chronic drought, however response of BNPP and SOC was influenced by intense drought (Fig. 5d). Primary productivity (ANPP and BNPP) was significantly correlated to the wet and dry climatic characteristics. The highest primary productivity was in the wet climatic zone dominated by perennial mesophytic and xerophytic species, such as *Stipa baicalensis*, *Filifolium sibiricum*, and the lowest primary productivity were during the drier sites dominated by short grasses, such as *S. klemenzii* and *S. breviflora* were recorded in Inner Mongolia grassland (Chen et al., 2012). Lei et al. (2015) also reported that total loss of NPP among meadow steppe, typical steppe and desert steppe decreased by 4067.35, 1403.94 and 1363.43 g C/m⁻² over nearly 50 years, respectively. These results closely related to the species diversity, richness and composition in the different types of grasslands and the environmental adaptability of these different species (Tilman et al., 1997). The plant diversity of grassland provides a buffer against environmental fluctuations because different species respond differently to these fluctuations, leading to functional compensations among species.

We also observed that SOC was significantly regulated by climatic factors such as aridity, temperature, and precipitation. Higher temperatures had a similar influence as aridity on SOC (Fig. 6c-f). Earlier research reported that increased temperature can have a positive effect on SOC due to the transfer of new fresh C substrates to soil from different SOC pools e.g., plant litter, root, and microbial residues (Luo et al., 2017;

Wang et al., 2019a); however, increased temperature often has a negative effect due to accelerated decomposition (Liu et al., 2016; Nie et al., 2019). There is a general expectation that increasing temperature (but not limited with water) leads to increases in net primary productivity which provides the input to SOC (Kirschbaum, 1995). Previous experiments have demonstrated that increasing temperature can promote SOC mineralization via an effect on microbial metabolic activities (Yu et al., 2022). Moreover, increased temperature increases root biomass and enhances root microbial interactions with drought resistance species and may be attributable to the ready availability of C substrates to soil (Dheri and Nazir, 2021). In contrast, increased temperature enhance the rates of enzymatic reactions, extracellular enzyme activity and soil respiration which together substantially increase SOC loss (Wang et al., 2020). SOC was found to be higher in cooler and wetter ecosystem compared to hotter and drier ecosystem as decomposition is more sensitive to higher temperature (Torn et al., 2009). Increasing precipitation can stimulate productivity, which contributes to more litter and root inputs into soil, accelerating SOC accumulation in water-restricted arid regions (Beer et al., 2010; Wynn et al., 2006). However, SOC has a positive relationship with precipitation in both dry and wet environments (Hossain and Beierkuhnlein, 2018). Although climatic parameters (e.g., temperature and precipitation) may influence SOC depending on dry vs wet sites, overall, we found temperature and aridity had a negative effect on SOC content under both chronic and intense droughts while precipitation may mitigate the negative effects of SOC loss (Fig. 6a-f).

5. Conclusions

Effects of extreme drought on SOC content of grasslands vary depending on drought type (chronic vs. intense) as well as site characteristics. Our empirical approach revealed that extreme drought lead to decreased grassland organic carbon content in topsoil (0–10 cm), with greater losses observed in more arid grasslands under chronic drought conditions. While intense drought actually increased SOC content in the most mesic grasslands, it led to losses in other more arid grasslands. Importantly, our study also shows that SOC content responded variably to drought depending on the response of primary productivity (e.g., ANPP and BNPP) and climate (e.g., MAT, MAP and AI) which indicates that productivity (both ANPP and BNPP) and climate together regulate SOC content potential of grasslands during drought. Although our 4 years' extreme drought experiment provide a valuable understanding of how extreme drought-impacted SOC content, we suggest a long-term extreme drought experiment (more than a decades) to detect the effects of extreme drought on SOC content. In addition, given these findings, the authorities and policy makers responsibility for protection, restoration and grassland management should prioritize in these geographic regions which are highly sensitive to extreme drought and low drought resistance.

CRedit authorship contribution statement

Md. Shahariar Jaman: Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Qiang Yu:** Conceptualization, Methodology, Project administration, Writing – review & editing. **Chong Xu:** Data curation, Visualization. **Mahbuba Jamil:** Writing – review & editing. **Yuguang Ke:** Writing – review & editing. **Tian Yang:** Writing – review & editing. **Alan K. Knapp:** Writing – review & editing. **Kate Wilkins:** Conceptualization, Methodology, Writing – review & editing. **Scott L. Collins:** Writing – review & editing. **Robert J. Griffin-Nolan:** Conceptualization, Methodology, Validation, Writing – review & editing. **Yiqi Luo:** Writing – review & editing. **Wentao Luo:** Data curation, Writing – review & editing. **Honghui Wu:** Methodology, Supervision, Writing – review & editing.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2024.116832>.

References

- Anacker, B.L., Seastedt, T.R., Halward, T.M., Lezberg, A.L., 2021. Soil carbon and plant richness relationships differ among grassland types, disturbance history and plant functional groups. *Oecologia* 196, 1153–1166. <https://doi.org/10.1007/s00442-021-04992-x>.
- Ao, M., Miura, R., Tominaga, T., 2009. Root and rhizome systems of perennial grasses grown in inner Mongolian grassland, China. *Grassl. Sci.* 55, 187–192. <https://doi.org/10.1111/j.1744-697X.2009.00158.x>.
- Aphalo, P.J., 2017. ggpmisc: Miscellaneous extensions to 'ggplot2' of R package.
- Auguie, B., Antonov, A., 2017. Miscellaneous Functions for "Grid" Graphics.
- Bahn, M., Schmitt, M., Siegwolf, R., Richter, A., Brüggemann, N., 2009. Does photosynthesis affect grassland soil-respired CO₂ and its carbon isotope composition on a diurnal timescale? *New Phytol.* 182, 451–460. <https://doi.org/10.1111/j.1469-8137.2008.02755.x>.
- Bai, Y., Cotrufo, M.F., 2022. Grassland soil carbon sequestration: Current understanding, challenges, and solutions. *Science* 377. <https://doi.org/10.1126/science.abo2380>.
- Bardgett, R.D., Bowman, W.D., Kaufmann, R., Schmidt, S.K., 2005. A temporal approach to linking aboveground and belowground ecology. *Trends Ecol. Evol.* 20, 634–641. <https://doi.org/10.1016/j.tree.2005.08.005>.
- Barthel, M., Hammerle, A., Sturm, P., Baur, T., Gentsch, L., Knohl, A., 2011. The diel imprint of leaf metabolism on the ¹³C signal of soil respiration under control and drought conditions. *New Phytol.* 192, 925–938. <https://doi.org/10.1111/j.1469-8137.2011.03848.x>.
- Bartón, K., 2016. MuMIn: Multi-Model Inference. Available from <https://cran.r-project.org/web/packages/MuMIn/index.html>.
- Batjes, N.H., Ribeiro, E., Van Oostrum, A., Leenaars, J., Hengl, T., Mendes De Jesus, J., 2017. WoSIS: Providing standardised soil profile data for the world. *Earth Syst. Sci. Data* 9, 1–14. <https://doi.org/10.5194/essd-9-1-2017>.
- Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C., Arain, M.A., Baldocchi, D., Bonan, G.B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luyssaert, S., Margolis, H., Oleson, K.W., Rouspard, O., Veenendaal, E., Viovy, N., Williams, C., Woodward, F.I., Papale, D., 2010. Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. *Science* 329, 834–838. <https://doi.org/10.1126/science.1184984>.
- Bogati, K., Walczak, M., 2022. The impact of drought stress on soil microbial community, enzyme activities and plants. *Agronomy* 12, 1–26. <https://doi.org/10.3390/agronomy12010189>.
- Bossio, D.A., Cook-Patton, S.C., Ellis, P.W., Fargione, J., Sanderman, J., Smith, P., Wood, S., Zomer, R.J., von Unger, M., Emmer, I.M., Griscom, B.W., 2020. The role of soil carbon in natural climate solutions. *Nat. Sustain.* 3, 391–398. <https://doi.org/10.1038/s41893-020-0491-z>.
- Bradford, J.B., Schlaepfer, D.R., Lauenroth, W.K., Palmquist, K.A., 2020. Robust ecological drought projections for drylands in the 21st century. *Glob. Chang. Biol.* 26, 3906–3919. <https://doi.org/10.1111/gcb.15075>.
- Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. *Proc. Natl. Acad. Sci.* 102, 15144–15148. <https://doi.org/10.1073/pnas.0505734102>.
- Burri, S., Sturm, P., Prechsl, U.E., Knohl, A., Buchmann, N., 2014. The impact of extreme summer drought on the short-term carbon coupling of photosynthesis to soil CO₂ efflux in a temperate grassland. *Biogeosciences* 11, 961–975. <https://doi.org/10.5194/bg-11-961-2014>.
- Canarini, A., Dijkstra, F.A., 2015. Dry-rewetting cycles regulate wheat carbon rhizodeposition, stabilization and nitrogen cycling. *Soil Biol. Biochem.* 81, 195–203. <https://doi.org/10.1016/j.soilbio.2014.11.014>.
- Carroll, C.J.W., Slette, I.J., Griffin-Nolan, R.J., Baur, L.E., Hoffman, A.M., Denton, E.M., Gray, J.E., Post, A.K., Johnston, M.K., Yu, Q., Collins, S.L., Luo, Y., Smith, M.D., Knapp, A.K., 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>.
- Chaves, M.M., Maroco, J.P., Pereira, J.S., 2003. Understanding plant responses to drought - From genes to the whole plant. *Funct. Plant Biol.* 30, 239–264. <https://doi.org/10.1071/FP02076>.
- Chen, Y., Li, Y., Zhao, X., Shang, W., Han, J., Awada, T., 2012. Effects of grazing exclusion on soil properties and on ecosystem carbon and nitrogen storage in a sandy rangeland of Inner Mongolia, Northern China. *Environ. Manage.* 50, 622–632. <https://doi.org/10.1007/s00267-012-9919-1>.
- Collins, S.L., Calabrese, L.B., 2012. Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *J. Veg. Sci.* 23, 563–575. <https://doi.org/10.1111/j.1654-1103.2011.01369.x>.
- Cook, B.I., Ault, T.R., Smerdon, J.E., 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Sci. Adv.* 1, 1–7. <https://doi.org/10.1126/sciadv.1400082>.
- Crowther, T.W., Riggs, C., Lind, E.M., Borer, E.T., Seabloom, E.W., Hobbie, S.E., Wubs, J., Adler, P.B., Firn, J., Gherardi, L., Hagenah, N., Hofmockel, K.S., Knops, J.M.H., McCulley, R.L., MacDougall, A.S., Peri, P.L., Prober, S.M., Stevens, C.J., Routh, D., 2019. Sensitivity of global soil carbon stocks to combined nutrient enrichment. *Ecol. Lett.* 22, 936–945. <https://doi.org/10.1111/ele.13258>.
- Dheri, G.S., Nazir, G., 2021. A review on carbon pools and sequestration as influenced by long-term management practices in a rice–wheat cropping system. *Carbon Manag.* 12, 559–580. <https://doi.org/10.1080/17583004.2021.1976674>.
- Frank, D., Reichstein, M., Bahn, M., Thonicke, K., Frank, D., Mahecha, M.D., Smith, P., van der Velde, M., Vicca, S., Babst, F., Beer, C., Buchmann, N., Canadell, J.G., Ciais, P., Cramer, W., Ibrom, A., Miglietta, F., Poulter, B., Rammig, A., Seneviratne, S.I., Walz, A., Wattenbach, M., Zavala, M.A., Zscheischler, J., 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>.
- Fuchsluger, L., Bahn, M., Fritz, K., Hasibeder, R., Richter, A., 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>.
- Griffin-Nolan, R.J., Blumenthal, D.M., Collins, S.L., Farkas, T.E., Hoffman, A.M., Mueller, K.E., Ocheltree, T.W., Smith, M.D., Whitley, K.D., Knapp, A.K., 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>.
- Guillaume, T., Makowski, D., Libohova, Z., Bragazza, L., Sallaku, F., Sinaj, S., 2022. Soil organic carbon saturation in cropland-grassland systems: Storage potential and soil quality. *Geoderma* 406, 115529. <https://doi.org/10.1016/j.geoderma.2021.115529>.
- Hargreaves, G.H., Samani, Z.A., 1985. Reference crop evapotranspiration from temperature. *Appl. Eng. Agric.* 1, 96–99. <https://doi.org/10.13031/2013.26773>.
- Harrison, S., LaForgia, M., 2019. Seedling traits predict drought-induced mortality linked to diversity loss. *Proc. Natl. Acad. Sci.* 116, 5576–5581. <https://doi.org/10.1073/pnas.1818543116>.
- Hasibeder, R., Fuchsluger, 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>.
- Hoover, D.L., Duniway, M.C., Belnap, J., 2015. Pulse-drought atop press-drought: unexpected plant responses and implications for dryland ecosystems. *Oecologia* 179, 1211–1221. <https://doi.org/10.1007/s00442-015-3414-3>.
- Hossain, M.L., 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>.
- Ingrisch, J., Karlovsky, S., Anadon-Rosell, A., Hasibeder, R., König, A., Augusti, A., Gleixner, G., Bahn, M., 2018. Land use alters the drought responses of productivity and CO₂ fluxes in mountain grassland. *Ecosystems* 21, 689–703. <https://doi.org/10.1007/s10021-017-0178-0>.
- Jaman, M.S., Wu, H., Yu, Q., Tan, Q., Zhang, Y., Dam, Q.K., Muraina, T.O., Xu, C., Jing, M., Jia, X., Wang, J., He, N., Luo, W., Knapp, A., Wilkins, K., Collins, S.L., Luo, Y., 2022. Contrasting responses of plant above and belowground biomass carbon pools to extreme drought in six grasslands spanning an aridity gradient. *Plant Soil*. <https://doi.org/10.1007/s11104-021-05258-4>.
- Jentsch, A., Kreyling, J., Elmer, M., Gellesch, E., Glaser, B., Grant, K., Hein, R., Lara, M., Mirzae, H., Nadler, S.E., Nagy, L., Otieno, D., Pritsch, K., Rascher, U., Schädler, M., Schloter, M., Singh, B.K., Stadler, J., Walter, J., Wellstein, C., Wöllecke, J., Beierkuhnlein, C., 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>.
- Jiang, X., Rauscher, S.A., Ringler, T.D., Lawrence, D.M., Park Williams, A., Allen, C.D., Steiner, A.L., Michael Cai, D., Mcdowell, N.G., 2013. Projected future changes in vegetation in western North America in the twenty-first century. *J. Clim.* 26, 3671–3687. <https://doi.org/10.1175/JCLI-D-12-00430.1>.
- Karlovsky, S., Augusti, A., Ingrisch, J., Akanda, M.K.U., Bahn, M., Gleixner, G., 2018. Drought-induced accumulation of root exudates supports post-drought recovery of microbes in mountain grassland. *Front. Plant Sci.* 871, 1–16. <https://doi.org/10.3389/fpls.2018.01593>.
- Kassambara, A., 2017. Package 'ggpubr': A "ggplot2". Based Publication Ready Plots.

- Kirschbaum, M.U.F., 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biol. Biochem.* 27, 753–760. [https://doi.org/10.1016/0038-0717\(94\)00242-S](https://doi.org/10.1016/0038-0717(94)00242-S).
- Knapp, A.K., Chen, A., Griffin-Nolan, R.J., Baur, L.E., Carroll, C.J.W., Gray, J.E., Hoffman, A.M., Li, X., Post, A.K., Slette, I.J., Collins, S.L., Luo, Y., Smith, M.D., 2020. Resolving the dust bowl paradox of grassland responses to extreme drought. *Proc. Natl. Acad. Sci.* 117, 22249–22255. <https://doi.org/10.1073/pnas.1922030117>.
- Knapp, A.K., Smith, M.D., 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291, 481–484. <https://doi.org/10.1126/science.291.5503.481>.
- Knorr, W., Prentice, I.C., House, J.I., Holland, E.A., 2005. Long-term sensitivity of soil carbon turnover to warming. *Nature* 433, 298–301. <https://doi.org/10.1038/nature03226>.
- Kreyling, J., Beierkuhnlein, C., Elmer, M., Pritsch, K., Radovski, M., Schloter, M., Wöllecke, J., Jentsch, A., 2008. Soil biotic processes remain remarkably stable after 100-year extreme weather events in experimental grassland and heath. *Plant Soil* 308, 175–188. <https://doi.org/10.1007/s11104-008-9617-1>.
- Lei, T., Wu, J., Li, X., Geng, G., Shao, C., Zhou, H., Wang, Q., Liu, L., 2015. A new framework for evaluating the impacts of drought on net primary productivity of grassland. *Sci. Total Environ.* 536, 161–172. <https://doi.org/10.1016/j.scitotenv.2015.06.138>.
- Lei, T., Feng, J., Zheng, C., Li, S., Wang, Y., Wu, Z., Lu, J., Kan, G., Shao, C., Jia, J., Cheng, H., 2020. Review of drought impacts on carbon cycling in grassland ecosystems. *Front. Earth Sci.* 14, 462–478. <https://doi.org/10.1007/s11707-019-0778-4>.
- Li, Y., Feng, A., Liu, W., Ma, X., Dong, G., 2017. Variation of aridity index and the role of climate variables in the Southwest China. *Water* 9, 1–14. <https://doi.org/10.3390/w9100743>.
- Liu, J.F., Arend, M., Yang, W.J., Schaub, M., Ni, Y.Y., Gessler, A., Jiang, Z.P., Rigling, A., Li, M.H., 2017. Effects of drought on leaf carbon source and growth of European beech are modulated by soil type. *Sci. Rep.* 7, 1–9. <https://doi.org/10.1038/srep42462>.
- Liu, H., Lin, L., Wang, H., Zhang, Z., Shangguan, Z., Feng, X., He, J.S., 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>.
- Liu, L., Wang, X., Lajeunesse, M.J., Miao, G., Piao, S., Wan, S., Wu, Y., Wang, Z., Yang, S., Li, P., Deng, M., 2016. A cross-biome synthesis of soil respiration and its determinants under simulated precipitation changes. *Glob. Chang. Biol.* 22, 1394–1405. <https://doi.org/10.1111/gcb.13156>.
- Luo, W., Elser, J.J., Lü, X.T., Wang, Z., Bai, E., Yan, C., Wang, C., Li, M., Zimmermann, N. E., Han, X., Xu, Z., Li, H., Wu, Y., Jiang, Y., 2015. Global Biogeochemical Cycles under changing climatic conditions. *Global Biogeochem. Cycles* 29, 1298–1308. <https://doi.org/10.1002/2015GB005089>. Received.
- Luo, Z., Feng, W., Luo, Y., Baldock, J., Wang, E., 2017. Soil organic carbon dynamics jointly controlled by climate, carbon inputs, soil properties and soil carbon fractions. *Glob. Chang. Biol.* 23, 4430–4439. <https://doi.org/10.1111/gcb.13767>.
- Luo, W., Zuo, X., Griffin-Nolan, R.J., Xu, C., Sardans, J., Yu, Q., Wang, Z., Han, X., Peñuelas, J., 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>.
- Lynch, J.M., 2002. Resilience of the rhizosphere to anthropogenic disturbance. *Biodegradation* 13, 21–27. <https://doi.org/10.1023/A:1016333714505>.
- Ma, W.H., Yang, Y.H., He, J.S., Zeng, H., Fang, J.Y., 2008. Above- and belowground biomass in relation to environmental factors in temperate grasslands, Inner Mongolia. *Sci. China Ser. C Life Sci.* 51, 263–270. <https://doi.org/10.1007/s11427-008-0029-5>.
- Malik, A.A., Bouskill, N.J., 2022. Drought impacts on microbial trait distribution and feedback to soil carbon cycling. *Funct. Ecol.* 36, 1442–1456. <https://doi.org/10.1111/1365-2435.14010>.
- Meng, B., Li, J., Maurer, G.E., Zhong, S., Yao, Y., Yang, X., Collins, S.L., Sun, W., 2021. Nitrogen addition amplifies the nonlinear drought response of grassland productivity to extended growing-season droughts. *Ecology* 102, 1–10. <https://doi.org/10.1002/ecy.3483>.
- Muraina, T.O., Xu, C., Yu, Q., Yang, Y., Jing, M., Jia, X., Jaman, M.S., Dam, Q., Knapp, A. K., Collins, S.L., Luo, Y., Luo, W., Zuo, X., Xin, X., Han, X., Smith, M.D., 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>.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>.
- Naudts, K., Van den Berge, J., Janssens, I.A., Nijs, I., Ceulemans, R., 2011. Does an extreme drought event alter the response of grassland communities to a changing climate? *Environ. Exp. Bot.* 70, 151–157. <https://doi.org/10.1016/j.envexpbot.2010.08.013>.
- Nie, X., Peng, Y., Li, F., Yang, L., Xiong, F., Li, C., Zhou, G., 2019. Distribution and controlling factors of soil organic carbon storage in the northeast Tibetan shrublands. *J. Soils Sediments* 19, 322–331. <https://doi.org/10.1007/s11368-018-2037-9>.
- Nunan, N., Leloup, J., Ruamps, L.S., Pouteau, V., Chenu, C., 2017. Effects of habitat constraints on soil microbial community function. *Sci. Rep.* 7, 1–10. <https://doi.org/10.1038/s41598-017-04485-z>.
- Pausch, J., Kuzakov, Y., 2018. Carbon input by roots into the soil: quantification of rhizodeposition from root to ecosystem scale. *Glob. Chang. Biol.* 24, 1–12. <https://doi.org/10.1111/gcb.13850>.
- Percival, H.J., Parfitt, R.L., Scott, N.A., 2000. Factors controlling soil carbon levels in New Zealand grasslands is clay content important? *Soil Sci. Soc. Am. J.* 64, 1623–1630. <https://doi.org/10.2136/sssaj2000.6451623x>.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R.C., 2018. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-137, 108–153.
- Poeplau, C., Germer, K., Schwarz, K.U., 2019. Seasonal dynamics and depth distribution of belowground biomass carbon and nitrogen of extensive grassland and a *Miscanthus* plantation. *Plant Soil* 440, 119–133. <https://doi.org/10.1007/s11104-019-04074-1>.
- Preece, C., Peñuelas, J., 2016. Rhizodeposition under drought and consequences for soil communities and ecosystem resilience. *Plant Soil* 409, 1–17. <https://doi.org/10.1007/s11104-016-3090-z>.
- R CoreTeam, 2021. R: A Language and Environment for Statistical Computing.
- Rasmussen, C., Heckman, K., Wieder, W.R., Keiluweit, M., Lawrence, C.R., Berhe, A.A., Blankinship, J.C., Crow, S.E., Druhan, J.L., Hicks Pries, C.E., Marin-Spiotta, E., Plante, A.F., Schädel, C., Schimel, J.P., Sierra, C.A., Thompson, A., Wagai, R., 2018. Beyond clay: towards an improved set of variables for predicting soil organic matter content. *Biogeochemistry* 137, 297–306. <https://doi.org/10.1007/s10533-018-0424-3>.
- Remus, R., Augustin, J., 2016. Dynamic linking of 14C partitioning with shoot growth allows a precise determination of plant-derived C input to soil. *Plant Soil* 408, 493–513. <https://doi.org/10.1007/s11104-016-3006-y>.
- Ren, C., Chen, J., Lu, X., Doughty, R., Zhao, F., Zhong, Z., Han, X., Yang, G., Feng, Y., Ren, G., 2017a. Responses of soil total microbial biomass and community compositions to rainfall reductions. *Soil Biol. Biochem.* 116, 4–10. <https://doi.org/10.1016/j.soilbio.2017.09.028>.
- Ren, C., Zhao, F., Shi, Z., Chen, J., Han, X., Yang, G., Feng, Y., Ren, G., 2017b. Differential responses of soil microbial biomass and carbon-degrading enzyme activities to altered precipitation. *Soil Biol. Biochem.* 115, 1–10. <https://doi.org/10.1016/j.soilbio.2017.08.002>.
- Sanaullah, M., Chabbi, A., Rumpel, C., Kuzyakov, Y., 2012. Carbon allocation in grassland communities under drought stress followed by 14C pulse labeling. *Soil Biol. Biochem.* 55, 132–139. <https://doi.org/10.1016/j.soilbio.2012.06.004>.
- Sardans, J., Peñuelas, J., 2012. The role of plants in the effects of global change on nutrient availability and stoichiometry in the plant-soil system. *Plant Physiol.* 160, 1741–1761. <https://doi.org/10.1104/pp.112.208785>.
- Schaeffer, S.M., Homyak, P.M., Boot, C.M., Roux-Michollet, D., Schimel, J.P., 2017. Soil carbon and nitrogen dynamics throughout the summer drought in a California annual grassland. *Soil Biol. Biochem.* 115, 54–62. <https://doi.org/10.1016/j.soilbio.2017.08.009>.
- Schrama, M., Bardgett, R.D., 2016. Grassland invasibility varies with drought effects on soil functioning. *J. Ecol.* 104, 1250–1258. <https://doi.org/10.1111/1365-2745.12606>.
- Schwalm, C.R., Williams, C.A., Schaefer, K., Baldocchi, D., Black, T.A., Goldstein, A.H., Law, B.E., Oechel, W.C., Paw, U., Scott, R.L., 2012. Reduction in carbon uptake during dry of the century drought in western North America. *Nat. Geosci.* 5, 551–556. <https://doi.org/10.1038/ngeo1529>.
- Sippel, S., Reichstein, M., Ma, X., Mahecha, M.D., Lange, H., Flach, M., Frank, D., 2018. Drought, heat, and the carbon cycle: A review. *Curr. Clim. Chang. Reports* 4, 266–286. <https://doi.org/10.1007/s40641-018-0103-4>.
- Slette, I.J., Post, A.K., Awad, M., Even, T., Punzalan, A., Williams, S., Smith, M.D., Knapp, A.K., 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, M.D., 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>.
- Stuart-Haëntjens, E., De Boeck, H.J., Lemoine, N.P., Mänd, P., Kröel-Dulay, G., Schmidt, I.K., Jentsch, A., Stampfli, A., Anderegg, W.R.L., Bahn, M., Kreyling, J., Wohlgemuth, T., Lloret, F., Classen, A.T., Gough, C.M., Smith, M.D., 2018. Mean annual precipitation predicts primary production resistance and resilience to extreme drought. *Sci. Total Environ.* 636, 360–366. <https://doi.org/10.1016/j.scitotenv.2018.04.290>.
- Sui, X., Zhou, G., 2013. Carbon dynamics of temperate grassland ecosystems in China from 1951 to 2007: an analysis with a process-based biogeochemistry model. *Environ. Earth Sci.* 68, 521–533. <https://doi.org/10.1007/s12665-012-1756-2>.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277, 1300–1302. <https://doi.org/10.1126/science.277.5330.1300>.
- Torn, M.S., Swanston, C.W., Castanha, C., Trumbore, S.E., 2009. Storage and turnover of organic matter in soil. In: *Biophysico-Chemical Processes Involving Natural Nonliving Organic Matter in Environmental Systems*. John Wiley & Sons, Ltd, pp. 219–272. <https://doi.org/https://doi.org/10.1002/9780470494950.ch6>.
- Wang, N., Quesada, B., Xia, L., Butterbach-Bahl, K., Goodale, C.L., Kiese, R., 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>.
- Wang, J.Y., Ren, C.J., Feng, X.X., Zhang, L., Doughty, R., Zhao, F.Z., 2020. Temperature sensitivity of soil carbon decomposition due to shifts in soil extracellular enzymes after afforestation. *Geoderma* 374, 114426. <https://doi.org/10.1016/j.geoderma.2020.114426>.
- Wang, L., Wang, P., Sheng, M., Tian, J., 2018. Ecological stoichiometry and environmental influencing factors of soil nutrients in the karst rocky desertification ecosystem, Southwest China. *Glob. Ecol. Conserv.* 16, e00449.
- Wang, M., Yang, W., Wu, N., Wu, Y., Lafleur, P., Lu, T., 2019a. Patterns and drivers of soil carbon stock in southern China's grasslands. *Agric. For. Meteorol.* 276–277. <https://doi.org/10.1016/j.agrformet.2019.107634>.

- Wang, Q., Yang, Y., Liu, Y., Tong, L., Zhang, Q.P., Li, J., 2019c. Assessing the impacts of drought on grassland net primary production at the global scale. *Sci. Rep.* 9, 1–8. <https://doi.org/10.1038/s41598-019-50584-4>.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.
- Williams, A.P., Cook, E.R., Smerdon, J.E., Cook, B.I., Abatzoglou, J.T., Bolles, K., Baek, S. H., Badger, A.M., Livneh, B., 2020. Large contribution from anthropogenic warming to an emerging North American megadrought. *Science* 370, 314–318. <https://doi.org/10.1126/SCIENCE.ABF3676>.
- Wu, J., Zhang, Q., Li, A., Liang, C., 2015. Historical landscape dynamics of Inner Mongolia: patterns, drivers, and impacts. *Landsc. Ecol.* 30, 1579–1598. <https://doi.org/10.1007/s10980-015-0209-1>.
- Wynn, J.G., Bird, M.I., Vellen, L., Grand-Clement, E., Carter, J., Berry, S.L., 2006. Continental-scale measurement of the soil organic carbon pool with climatic, edaphic, and biotic controls. *Global Biogeochem. Cycles* 20. <https://doi.org/10.1029/2005GB002576>.
- Xu, Z.-Z., Zhou, G.S., 2005. Effects of water stress and high nocturnal temperature on photosynthesis and nitrogen level of a perennial grass *Leymus chinensis*. *Plant Soil* 269, 131–139. <https://doi.org/10.1007/s11104-004-0397-y>.
- Yahdjian, L., Sala, O.E., 2002. A rainout shelter design for intercepting different amounts of rainfall. *Oecologia* 133, 95–101. <https://doi.org/10.1007/s00442-002-1024-3>.
- Yu, H., Sui, Y., Chen, Y., Bao, T., Jiao, X., 2022. Soil organic carbon mineralization and its temperature sensitivity under different substrate levels in the Mollisols of Northeast China. *Life*. <https://doi.org/10.3390/life12050712>.
- Zhang, B., Tan, X., Wang, S., Chen, M., Chen, S., Ren, T., Xia, J., Bai, Y., Huang, J., Han, X., 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>.
- Zhao, D., Zhu, Y., Wu, S., Lu, Q., 2022. Simulated response of soil organic carbon density to climate change in the Northern Tibet permafrost region. *Geoderma* 405, 115455. <https://doi.org/10.1016/j.geoderma.2021.115455>.