Agricultural and Forest Meteorology 247 (2017) 356–364

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Research Paper

Repackaging precipitation into fewer, larger storms reduces ecosystem exchanges of CO_2 and H_2O in a semiarid steppe

W.J. Liu[a,1], L.F. Li[a,1], J.A. Biederman[b], Y.B. Hao[a,*], H. Zhang[a], X.M. Kang[c], X.Y. Cui[a], Y.F. Wang[a], M.W. Li[d], Z.H. Xu[e], K.L. Griffin[f], C.Y. Xu[g]

[a] College of Life Sciences, University of Chinese Academy of Sciences, Beijing, 10049, China
[b] Southwest Watershed Research Center, Agricultural Research Service, Tucson, AZ, 85719, USA
[c] Institute of Wetland Research, Chinese Academy of Forestry, Beijing, 10049, China
[d] Department of Foreign Languages, University of Chinese Academy of Sciences, Beijing, 10049, China
[e] Environmental Futures Centre and School of Environment, Griffith University, Brisbane, 4111, Australia
[f] Department of Earth and Environmental Sciences, Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY, 10964, USA
[g] School of Medical and Applied Sciences, Central Queensland University, Bundaberg, QLD 4670, Australia

ARTICLE INFO

Keywords:
Grassland
Net ecosystem CO_2 exchange
Gross primary productivity
Ecosystem respiration
Evapotranspiration
Water use efficiency
Precipitation frequency
Climate change

ABSTRACT

General circulation models predict that precipitation will become more extreme, i.e. rainfall events of larger size but reduced frequency. Studies in North American grasslands have shown that such repackaging of precipitation into fewer, larger events enhanced above ground net primary productivity (ANPP), likely due to deeper soil moisture infiltration favoring plant water use over evaporation. However, ANPP responses in other regions remain poorly understood, and responses of carbon and water exchanges with the atmosphere remain unknown. Here we manipulated rainfall in a steppe ecosystem of northern China over 4 years to investigate how temporal packaging of precipitation impacts ANPP, evapotranspiration (ET), net ecosystem CO_2 exchange (NEE) and the component fluxes gross primary productivity (GPP) and ecosystem respiration (RE). Experimental plots received precipitation equivalent to the 60-year growing-season average of 240 mm, variously packaged into 6, 10, 16, or 24 events representing extreme (P6) to historical average (P24) rainfall frequency. Extraordinarily extreme frequency (6 large events) reduced NEE, GPP, RE, ET and water use efficiency (WUE = |NEE|/ET). The average NEE, GPP and RE declined 35%, 45% and 48% respectively in the P6 treatment as compared to P16, which showed maximum ET and CO_2 exchange. After peaking in the 16-event treatment, GPP and WUE in P24 were not distinguishable from P6. These peaks suggest that P16 was optimal for photosynthesis, with sufficiently frequent rain to maintain unregulated plants and adequately deep soil moisture infiltration to favour transpiration, with associated carbon uptake, over evaporation. Path analysis indicated the lower CO_2 fluxes were influenced by reduced soil water content and leaf area index and higher soil temperature, with ET regulating the effects of these microclimatic drivers. ANPP showed a monotonic but non-significant decline with decreasing precipitation frequency, consistent with reduced CO_2 fluxes. We found an increase in ANPP of xerophyte plants partially compensated for the ANPP decline in the dominant eurytopic xerophyte plants. Our results suggest that extreme temporal repackaging of precipitation into few events with correspondingly long dry intervals may reduce the capacity of steppe ecosystems to assimilate atmospheric CO_2, although community diversity may moderate impacts.

1. Introduction

Mounting evidence suggests that frequency and intensity of extreme weather events will increase during expected global climate change (Jentsch et al., 2007; Smith et al., 2011). Atmospheric general circulation models predict that growing-season precipitation events will become larger in size but fewer in number in many regions (Weltzin et al., 2003; Smith 2011; Bloor and Bardgett, 2012; Hoover et al., 2014), but few studies have addressed the impacts of such temporal "repackaging" while holding seasonal totals constant. For semi-arid ecosystems, rainfall patterns are predicted to shift from frequent, small-size rain events with relatively short intervals to larger events with

* Corresponding author.
E-mail address: ybhao@ucas.ac.cn (Y.B. Hao).
[1] These authors contributed equally to this work.

http://dx.doi.org/10.1016/j.agrformet.2017.08.029
Received 23 February 2017; Received in revised form 19 August 2017; Accepted 21 August 2017
Available online 06 October 2017
0168-1923/ © 2017 Elsevier B.V. All rights reserved.

longer intervening dry intervals (Heisler-White et al., 2008; Cook et al., 2015). This repackaging of rainfall could significantly affect semi-arid ecosystems, in which water availability is the main limiting factor for evapotranspiration (ET), CO_2 exchanges with the atmosphere, and resulting plant productivity.

Semiarid grasslands cover ca. 9.1×10^6 km^2 and provide valuable goods and services including above-ground net primary production (ANPP) and storage of atmospheric CO_2, measured as net ecosystem exchange (NEE) (Bailey 1998; Knapp et al., 1998; Scott et al., 2010). Grassland productivity is limited by seasonal water availability and sensitive to climatic variation (Knapp and Smith 2001; Weltzin et al., 2003; Liu et al., 2012). Prior research suggests that grassland productivity is sensitive to the seasonal timing of rainfall, especially the duration of dry intervals between rainfall events (Fay et al., 2003; Heisler-White et al., 2008; Didiano et al., 2016). However, ecological theory suggests that species diversity enhances community resistance against environmental perturbations (diversity-stability hypothesis) (Hoover et al., 2014; Naeem and Li, 1997; Tilman et al., 2006). Therefore, we expect that at the community level, a mature ecosystem with more diversity will be less sensitive to altered precipitation frequency.

Previous studies have shown that altered precipitation frequency may have either positive (Heisler-White et al., 2008; Thomey et al., 2011) or negative (Kreyling et al., 2008) impacts on biological carbon cycling, suggesting multiple controls. Less frequent but larger precipitation events in grassland ecosystems may result in deeper water infiltration into the soil profile, increasing moisture storage and buffering against high water stress (precipitation < ET) (Knapp et al., 2008; Didiano et al., 2016). However, low-frequency precipitation results in transient resources available for plants and carbon cycling, and long dry intervals may down-regulate plant activity (e.g. leaf area, fine root volume) or cause mortality of plant parts or individuals (Vicente-Serrano et al., 2013). More frequent but smaller rainfall events are more likely to maintain a wet surface, promoting evaporation rather than moisture penetration into the root zone and subsequent transpiration. However, if rainfall amounts are sufficient to stimulate plant activity, then frequent events promote upregulation of biotic activity and positive effects on ecosystem carbon balance (Nielsen and Ball, 2015). Therefore, we expect that carbon cycle processes may be inhibited by either extremely low precipitation frequency with associated long dry periods or by high precipitation frequency with consistently small events that fail to wet the root zone.

Differential responses of GPP and ecosystem respiration (RE) may also regulate precipitation frequency impacts on net carbon uptake (i.e. NEE and ANPP). While RE is strongly coupled to GPP at hourly to annual time scales in semiarid ecosystems, GPP is generally more sensitive than RE to changes in water availability, resulting in a linkage between NEE and ET (Potts et al., 2006; Biederman et al., 2016). In semiarid ecosystems, rainfall after a prolonged dry period stimulates large RE pulses (i.e. the Birch Effect), while a sequence of events is often required to upregulate plants and stimulate GPP (Birch, 1958; Huxman et al., 2004). Therefore, we expect extreme low precipitation frequency to favour RE over GPP, reducing the magnitude of net carbon uptake (less-negative NEE).

The objective of this study was to determine how repackaging of growing-season precipitation into a gradient of event sizes and frequencies affects plant productivity, CO_2 exchange, and ET in a steppe ecosystem. To meet this objective, we measured ANPP, CO_2 fluxes, ET and driving abiotic and biotic factors under variable precipitation frequency patterns. Specifically, we test the hypothesis that decreasing precipitation frequency, with longer dry intervals, will impact the ecosystem similarly to drought, decreasing gross and net CO_2 uptake as well as ANPP.

2. Materials and methods

2.1. Site description

This study was conducted at the Inner Mongolia Grassland Ecosystem Research Station in the Xilin River watershed of the Inner Mongolia Autonomous Region (43° 32′N, 116° 40′E, 1200 m a.s.l.). The study site has been fenced off since 1979 and is located on a smooth wide plain with low hills. The region is characterized by a temperate continental climate with mean annual temperature of −0.48° C and mean annual precipitation of 358 mm (Hao et al., 2010). Mean growing season precipitation is 318 mm, accounting for 89% of total annual precipitation, of which 75% (~240 mm) is considered ecologically effective precipitation (EP, recorded daily precipitation ≥ 3 mm during the growing season, Hao et al., 2012). Events smaller than ~3 mm are primarily evaporated and do not wet the soil profile sufficiently to stimulate plant responses. The xeric rhizomatous grass *Leymus chinensis* is the dominant species, but *Agropyroncristatum*, *Cleistogenessquarrosa* and *Carexduriuscula* are also common. Grass heights range from 50 to 60 cm and coverage can reach as high as 80%–90% during the growing season. Average ANPP for this site is 186 g m^{-2} (1980–2010; Hao et al., 2013). The soil is a dark chestnut Mollisol typical of steppe ecosystems with a depth of 100–150 cm and mean composition is 21% clay, 60% sand and 19% silt (Hao et al., 2008). The A horizon is 20–30 cm deep and there is no obvious $CaCO_3$ layer.

2.2. Collection and analysis of long-term data

Long-term daily precipitation data were obtained from the climate database of a local meteorological station (Xilin Gol League Meteorological Administration) for 1953–2010 (longest available historical data). Our analysis focused on effective precipitation during the growing season (May–September).

2.3. Rain-exclusion shelter design

The experimental plots were located in a relatively flat area of the station. We built sixteen 9 m^2 rain-exclusion shelters (3m × 3m), consisting of a steel frame supporting a clear 0.8 mm thick fibreglass reinforced polyester roof. These shelters were designed to exclude ambient rainfall in the experimental plots and had only minor shading effects (90% light transmission). The shelters had arched roofs (2.1 m and 1.8 m maximum and minimum heights, respectively) and covered a 2.0 m × 2.0 m plot centered under the shelter. The shelter sides and ends were kept open to maximise air movement and minimise temperature and relative humidity influences. The shelters were installed each 1st of May in each of the study years and covered the plots during the growing season. To evaluate microclimate effects, we compared the air temperature (HMP45C temperature probe, VAISALA, Woburn, MA, USA) and photosynthetically active radiation (PAR) (LI-190SB quantum sensor, LI-COR, Lincoln, NE, USA) measured under the shelters with those measured in an open space close to the plots and found no significant differences. The plots were surrounded by metal flashing extending approximately 0.4 m below and 0.1 m above the ground surface to isolate roots and prevent lateral water flux. We also established four ambient rainfall plots without shelters adjacent to the sheltered plots. Since ambient plots received naturally varying rainfall rather than the fixed amount applied to experimental plots, ambient plots were only considered as reference and were not included in the statistical analysis. All rain shelters were taken off at the end of the growing season to assure winter precipitation (predominantly snow) was not affected in our plots, since this study focused on the manipulation of growing season precipitation patterns.

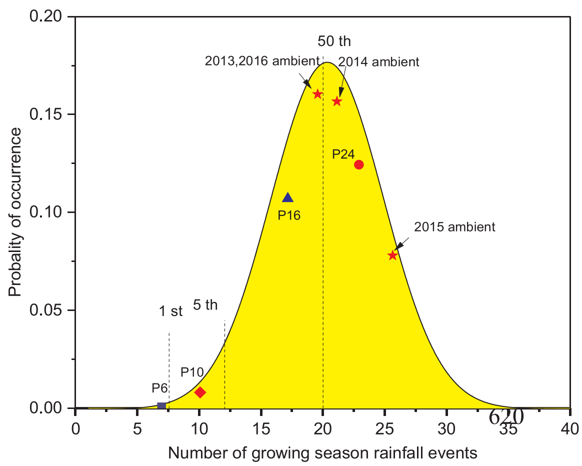

Fig. 1. Distribution of maximum single precipitation amount (solid line) and the increase precipitation frequency treatment resulted in 6-(P6: near the 1st percentile), 10- (P10: near the 5th percentile), 16- (P16), 24- event (near 50th percentile) based on an estimated probability function calculated from ~60 years of growing season rainfall events.

2.4. Experimental setup and protocol

The precipitation frequency treatments were carried out during the 2013–2016 growing seasons. The aim of this experiment was only to alter the frequency of rainfall events and dry interval duration, while maintaining constant growing-season precipitation of 240 mm, equivalent to the ~60-year mean. The experiment was a random block design containing four replicates of each of the four precipitation frequency treatments. Treatments ranged from ranged from the ~60-year mean of 24 precipitation events (P24) to medium (P16), extreme (P10, near the 5th percentile) to extraordinarily extreme (P6: near the 1st percentile) (Fig. 1). Event sizes were not constant: the amount of each rainfall event was determined based on the ~60-year mean seasonal distribution patterns. In the treatments, precipitation size was 10.0 mm (P24; range 3.8–21.8 mm), 15.0 mm (P16, range 6.0–26.5 mm), 24.0 mm (P10, range 11.6–41.5 mm) and 40.0 mm (P6, range 22.2–72.6 mm) during the experimental periods (Fig. 2). The precipitation intervals of the four treatments ranged from 5 days (P24) to 20 days (P6). The largest rain event for P6 (72.6 mm) was 2.2 times larger than the average annual maximum daily event over the historical ~60-year period. Rainfall events were simulated by a sprinkling can using local groundwater. Large events were applied over one to three days to ensure that the plots never received more than 24 mm, the historical daily maximum precipitation, within a single day (Huang et al. (2010). Soil water content (SWC) in the top 20 cm was measured weekly in the centre of each plot using time domain reflectrometry (Model TDR 300, Spectrum Technologies, Inc., USA).

2.5. Aboveground net primary productivity and leaf area index

We quantified ANPP at the end of the growing season in two 0.25 m^2 quadrats within each sheltered area. Each year, the location of the selected quadrats was different, in order to prevent resampling the same quadrat. After recording plant species, the above-ground vegetation was clipped at ground level and immediately returned to the laboratory. Plant materials were separated into live and standing dead material and weighed as a measure of the fresh weight of live and standing dead biomass. The plant materials were oven-dried at 65 °C to a constant weight, and the dry weights of the two components were recorded. Community composition and structure were assessed by counting the species within the ANPP quadrats at the time of sampling, and categorizing into four ecological functional groups (FGs): eurytopic xerophyte (Ex), xerophyte (Xe), meso-xerophyte (Mx) and xero-mesophyte (Xm), and measuring the percentage dry-weight of each species within the sampling quadrats. The leaf area index (LAI) was measured once every month using an LAI-2200C plant canopy analyser (Li-Cor, Lincoln, NE, USA).

2.6. Measurement of plot-level CO_2 fluxes

Prior to the initiation of the precipitation treatments, a square metal frame (50 cm × 50 cm in area and 10 cm in height) was installed to a depth of 7 cm in each plot. Ecosystem CO_2 fluxes, including NEE

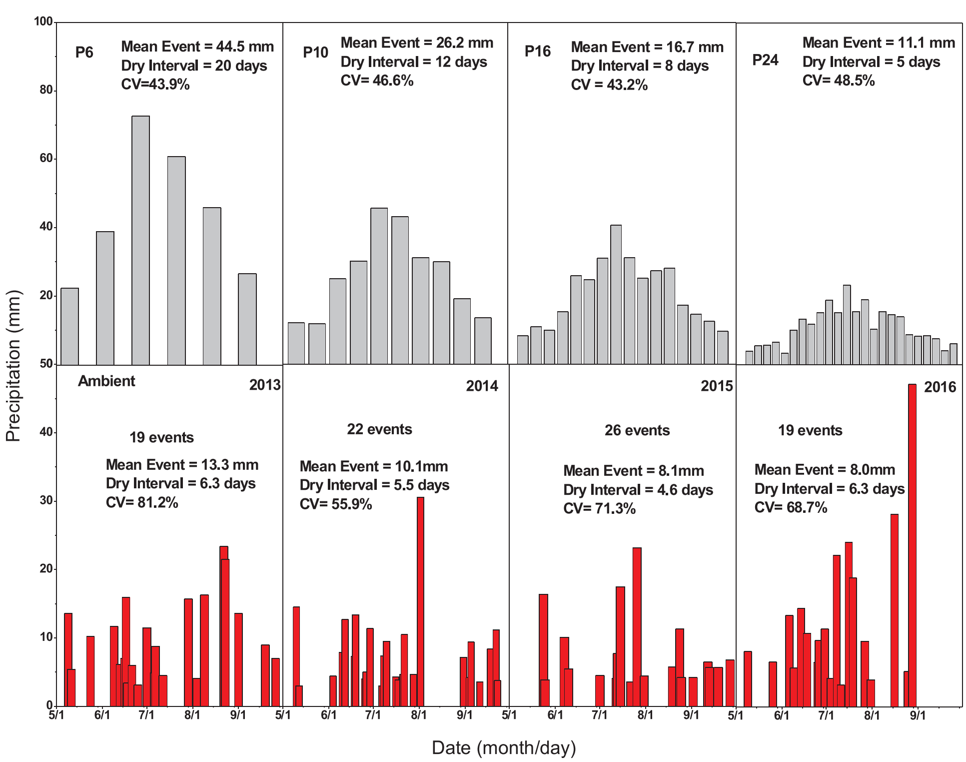

Fig. 2. Distribution of growing season rainfall events for the ambient (unsheltered) and experimental plots during the 2013–2016 growing seasons.

Table 1
Analysis of variance (ANOVA) for abiotic factors – soil water content (SWC), soil temperature (Ts) at soil depth of 20 cm and 10 cm, respectively and biotic factors- leaf area index (LAI) across all four years.

Factors	SWC			Ts			LAI		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Year	3	17.88	**< 0.0001**	3	43.91	**< 0.0001**	3	7.85	**< 0.0001**
Treat	3	15.64	**< 0.0001**	3	4.15	**0.006**	3	3.48	**0.02**
Year × Treat	9	3.38	**0.0005**	9	2.20	**0.02**	9	2.09	**0.03**
Sample date	23	25.25	**< 0.0001**	11	414.98	**< 0.0001**	4	14.76	**< 0.0001**
Treat × Date	69	3.20	**< 0.0001**	33	1.53	**0.03**	12	1.76	0.06
Year × Date	46	15.64	**< 0.0001**	28	57.69	**< 0.0001**	12	3.08	**0.001**
Treatment × Year × Date	138	3.64	**< 0.0001**	84	0.79	0.91	36	1.21	0.22

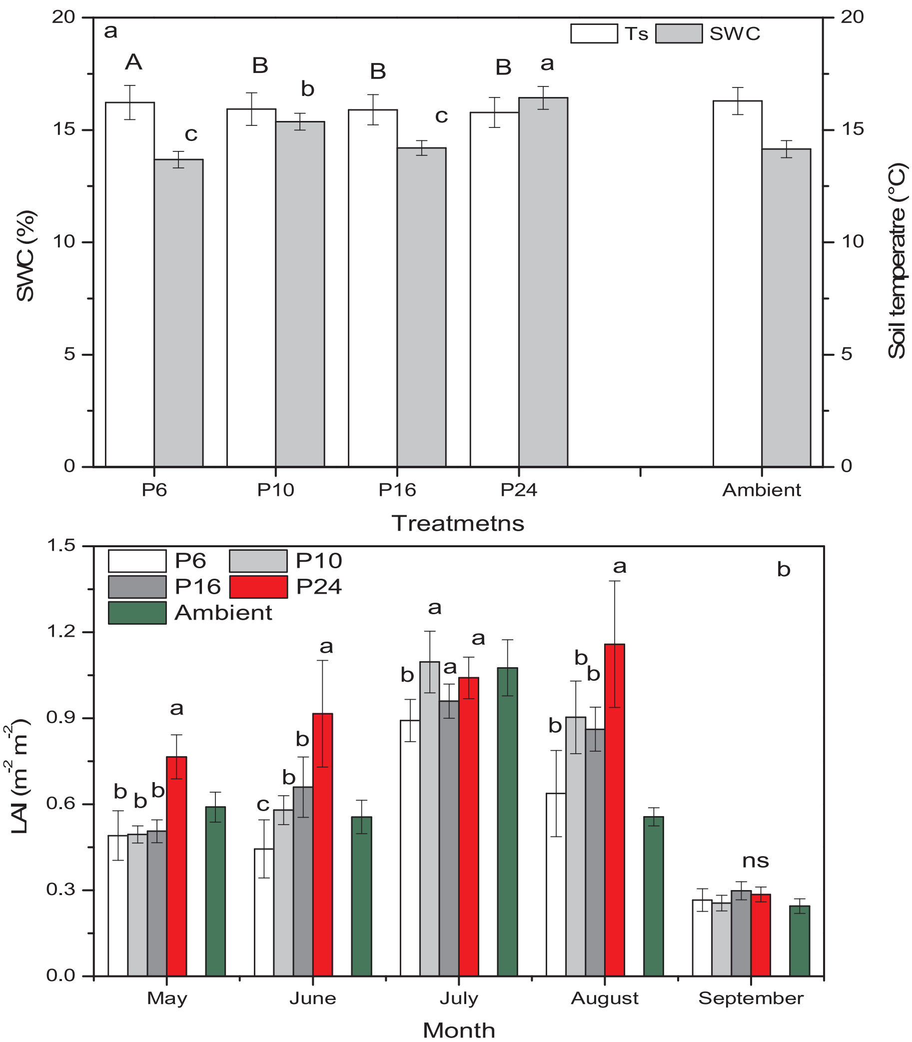

Fig. 3. (a) The volumetric soil water content (SWC), soil temperature (Ts) at 0.2 and 0.05 m soil depth, respectively, (b) and leaf area index (LAI) across the 2013–2016 study period. Error bars represent the standard error of the mean. Significant treatment differences are indicated by different letters (P ≤ 0.05) among treatments. The variation in SWC, Ts and LAI under ambient conditions was only used as a reference and not included in statistical analysis.

(negative value means ecosystem takes up CO_2 from the atmosphere) and RE were measured by placing a transparent chamber (0.5 m × 0.5 m × 0.5 m) attached to an infra-red gas analyser (LI-840A, LI-COR Inc., Lincoln, NE, USA) over the metal frame. The chamber was equipped with a temperature sensor and two small fans to mix the air, ensuring even CO_2 sampling. A pump (6262-04, LI-COR Inc.) circulated air from the chamber into an infra-red gas analyser, and the CO_2 concentration was recorded every second for 2 min after the chamber was put on the frame. The data for the first and last 10 s were deleted, and NEE was calculated. After measuring NEE, the chamber was lifted and vented, placed back on the frame, and covered by a lightproof cloth to estimate RE (NEE in the dark). Soil temperature (Ts) was concurrently monitored at the 10 cm depth of soil with a thermometer (TL-883, Tonglixing technology Co., Ltd., China). All flux measurements were completed during the morning (9:00–1:30) on sunny days. Previous studies in this ecosystem suggest this measurement schedule would ensure the comparability of data throughout the growing season and avoid high afternoon temperatures, which can depress photosynthesis and/or rapidly change the chamber pressure (Chen et al., 2009). GPP was calculated by the difference between RE and NEE.

2.7. Data calculation and analysis

To integrally assess the effect of varied precipitation frequency on carbon fluxes and ET during the whole growing season, an evaluating

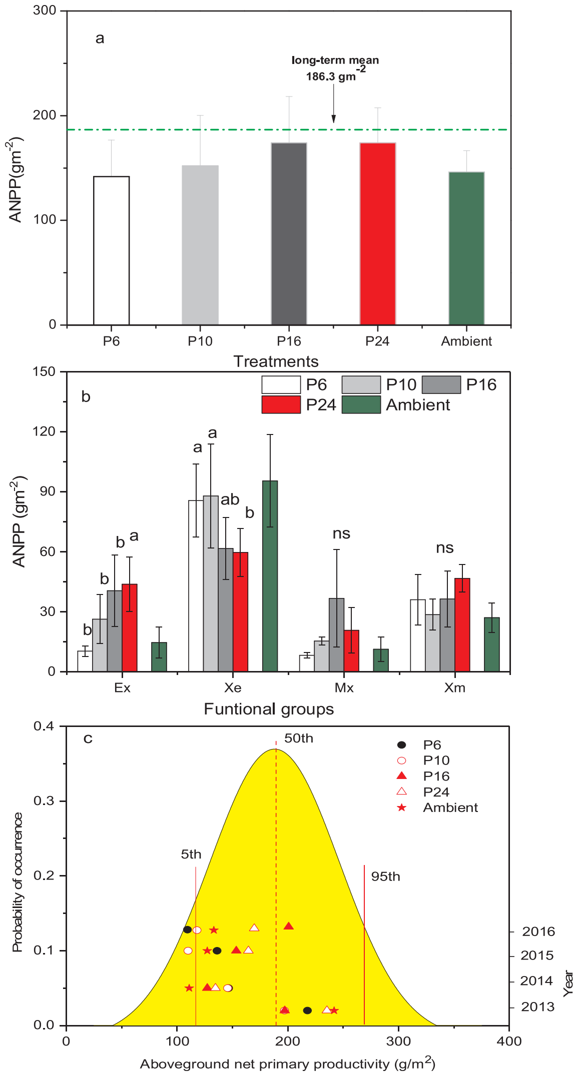

Fig. 4. Response of total aboveground net primary productivity (ANPP; g m^{-2}) to ambient and experimental precipitation frequency treatments in 2013–2016 growing seasons. (a) Total average ANPP for four studied years. (b) Average ANPP by functional group for eurytopic xerophyte (Ex), xerophyte (Xe), meso-xerophyte (Mx) and xero-mesophyte (Xm) groups during 2013 − 2016 growing seasons. (c) After four years of growing season precipitation frequency treatments, most of ANPP fell into the 5th-95th percentile based on an estimated probability function for 31 years of ANPP measurements for the study site. Data presented were means ± 1SE and the different letters indicate significant differences ($P \le 0.05$) among treatments. ns = statistically non-significant. ANPP under ambient conditions was only used as a reference and not included in statistical analysis.

index was developed.

$$Index_{pf} = M_r \times {}^{1}\!/_{\Delta T} \quad (1)$$

M_r is the amount of rainfall each irrigated into the treatment plots during an entire growing season. ΔT is the interval of two precipitation events, which was fixed for each treatment (Fig. 2). We also calculated the water use efficiency (WUE) as the ratio of the absolute value of NEE to ET (Potts et al., 2006; Tian et al., 2016).

We used analysis of variance (ANOVA) to test the effects of precipitation treatment and experiment year on plot microclimate, LAI, ANPP, ET, and CO_2 fluxes using a repeat measures analysis of the general linear model in SAS 9.2 (SAS Institute, Cary, NC, USA). First, the interaction between frequency manipulation effects with time as random factor was assessed. If the interaction was not significant, the model was simplified to test only for frequency manipulation effects by leaving out the interaction effect and using time as a random effect. The level of significance assumed for all statistical tests was $P < 0.05$. Before conducting an ANOVA, the normality of error terms was evaluated using the Kolmogorov-Smirnov test, and data were square root transformed if errors were not normally distributed. Homoscedasticity was evaluated using the *Levene* test for equality of variances. When treatment effects were significant, Duncan's Multiple Range Test was used to compare mean values among the treatments. We performed path analysis to test the effects of varied precipitation frequency on ANPP through functional groups, and the effects of the factors (SWC, LAI and Ts) on NEE by using the standardization of multiple linear regression models that are included with the *CORR* and *REG* package in the SAS statistical software (Grace 2006). Specially, the adequacy of the model was tested using chi-square (χ^2) tests, standardized root mean-square residual (SRMR) index, root-mean-square error of approximation (RMSE) index and goodness-of-fit index (CFI) (Grace et al., 2010). The RMSE estimates the amount of approximation error per degree of freedom in the model, while SRMR is considered as a badness-of-fit measure in which higher values mean poor fit. CFI close to one indicate a good model fit. The mentioned-above statistical analyses were conducted in SAS 9.2 (SAS institute, Cary, NC, USA).

Difference in species composition among treatments was tested using a pairwise distance matrix of *Bray-Curtis* dissimilarity, based on the total annual abundance of each species summed across the four replicates. Ordination of the distance matrix using a non-metric multidimensional scaling (NMS) followed by analysis of similarity (ANOSIM) for each year was used to assess community-level divergence between treatments and control (Primer v6; Primer-E, Plymouth, UK).

3. Results

3.1. Growing season precipitation

During the growing season, effective natural precipitation was 253 mm, 254 mm, 202 mm and 152 mm during 2013–2016, respectively in the ambient condition, and there were 19–26 rain events per growing season (Fig. 2). These effective precipitation totals and frequencies were close to the ~60-year mean excepting 2016, which was drier.

3.2. Variations in soil water status, soil temperature and leaf area index

Across treatments with decreasing precipitation frequency, average

Table 2
Effects of precipitation frequency treatment on ANPP for the whole community and four functional groups during 2013–2016 growing seasons.

Factors	ANPP-Community			Ex		Xe		Mx		Xm	
	df	F	P	F	P	F	P	F	P	F	P
Year	3	5.94	**0.002**	9.40	< **0.0001**	2.29	0.09	3.79	**0.02**	1.40	0.25
Treatment	3	0.97	0.41	8.71	**0.0001**	0.72	0.54	0.88	0.46	1.24	0.31
Treatment × Year	9	0.63	0.77	1.82	0.09	0.65	0.75	1.86	0.08	0.57	0.81

Ex: eurytopic xerophyte, Xe: xerophyte, Mx: meso-xerophyte and Xm: xero-mesophyte.
The *df* for Ex, Xe, Mx and Xm was same with ANPP.

Table 3
Analysis of variance (ANOVA) for gross primary productivity (GPP), net ecosystem CO_2 exchange (NEE), ecosystem respiration (RE), evapotranspiration (ET) and water use efficiency (WUE) across all four years of the experiment.

Factors	GPP			NEE		RE		ET		WUE	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Year	3	28.79	**< 0.0001**	46.40	**0.0001**	1.01	0.39	6.24	**0.0004**	23.78	**< 0.0001**
Treat	3	21.49	**< 0.0001**	10.40	**< 0.0001**	14.16	**< 0.0001**	18.32	**< 0.0001**	**3.55**	**0.01**
Year × Treat	9	1.32	0.22	0.64	0.75	3.76	**0.0002**	2.73	**0.004**	0.90	0.53
Sample date	11	122.82	**< 0.0001**	28.80	**< 0.0001**	118.27	**< 0.0001**	72.79	**< 0.0001**	**11.38**	**< 0.0001**
Treat × Date	33	1.13	0.29	0.86	0.68	1.39	0.79	2.46	**< 0.0001**	2.51	**< 0.0001**
Year × Date	28	19.50	< 0.0001	13.78	< 0.0001	27.25	**< 0.0001**	20.29	**< 0.0001**	11.44	**< 0.0001**
Treatment × Year × Date	84	2.06	**< 0.0001**	1.55	**0.004**	1.82	**0.0001**	2.34	**< 0.0001**	1.93	**< 0.001**

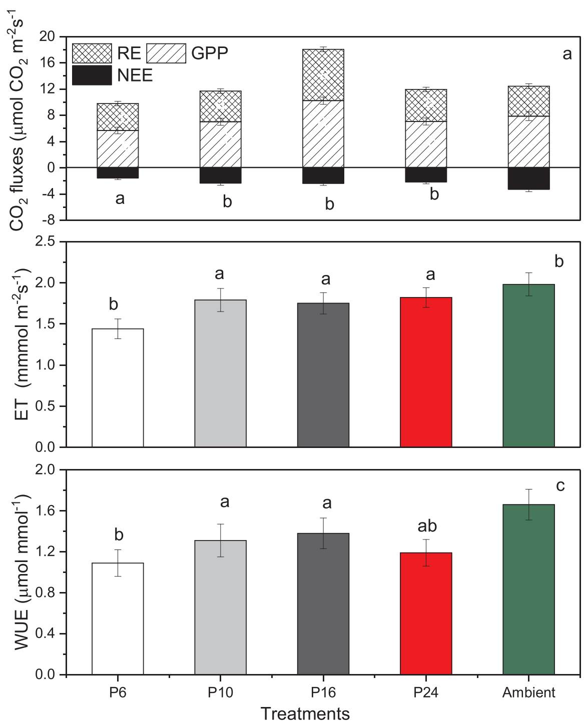

Fig. 5. (a) Overall response of CO_2 fluxes (gross primary productivity (GPP), ecosystem respiration (RE) and net ecosystem exchange (NEE)) of experimental plots, (b) Evapotranspiration (ET) and (c) water use efficiency (WUE) to varied precipitation frequency. Data presented were means ± 1SE.Significant treatment differences are indicated by different letters (P ≤ 0.05) among treatments. The variation in CO_2 fluxes, ET and WUE under the ambient conditions (olive data bar) was only used as a reference and not included in statistical analysis.

SWC declined and soil temperature (Ts) increased (F = 15.64, P < 0.0001 and F = 4.15, P = 0.006. Table 1 and Fig. 3a). Mean SWC for P6 was significantly lower than that of the P10 and P24 (Fig. 3a). In the experimental plots, the maximum soil moisture (29.6%) was recorded in P24 (Fig. S1). At most sampling dates, the SWC in P24 was higher than that in P6 (Fig. S1). In contrast, Ts exhibited a maximum in the six-event treatment, suggesting an inverse relationship between moisture and temperature. Similar to SWC, average LAI increased with precipitation frequency (Fig. 3b). LAI was significantly greater for P24 than for P6 during all months but September.

3.3. Response of aboveground ANPP to extreme precipitation frequency

AT the community level, the extreme precipitation treatments P6 and P10 had lower mean ANPP than P16 and P24 (Fig. 4a), although no significant trends were identified (F = 0.97, P = 0.41). However, there were interannual differences among the four growing seasons (F = 5.94, P = 0.002, Table 2, Fig. S2). At the functional group level, ANPP did decline significantly with reduced precipitation frequency in the Ex group, while the opposite pattern was observed in the Xe group (Fig. 4b). Most ANPP values fell into the 5th–95th percentiles of the 30-year ANPP statistical distribution for the study site (Fig. 4c). The community composition across precipitation treatments did not show any substantial changes (Fig. S3).

3.4. Response of CO_2 and water fluxes to extreme precipitation

Extremely low precipitation frequency generally reduced ET and CO_2 exchanges NEE, GPP and RE, as well as WUE (Table 3, Fig. 5, Fig. S4). NEE, RE, and ET all had the lowest magnitudes in the extraordinarily extreme treatment (P6). GPP and WUE also had the lowest magnitudes in P6, but after reaching maximal values in the intermediate treatments (P10, P16), GPP and WUE declined in P24. NEE ranged from −1.57 to −2.4 μmol CO_2 $m^{-2}s^{-1}$ and was reduced by 27–35% in the P6 treatment as compared with the higher-frequency treatments (P16 and P24) (Fig. 5a). RE ranged from 4.11 to 7.83 μmol CO_2 $m^{-2}s^{-1}$ and was reduced by up to 48% in the P6 treatment. GPP ranged from 5.68 to 10.23 μmol CO_2 $m^{-2}s^{-1}$ and was reduced by up to 45% in the P6 treatment. ET ranged from 1.44 to 1.82 mmol CO_2 $m^{-2}s^{-1}$ and was reduced by up to 21% in the P6 treatment (Fig. 5b).

3.5. Relationships among CO_2, water fluxes and precipitation frequency

The precipitation frequency index ($index_{pf}$) explained significant variability in ET and CO_2 exchanges across all treatments (Fig. 6). Larger $index_{pf}$, indicative of greater precipitation frequency and shorter dry intervals, was associated with greater magnitudes of net and gross CO_2 uptake (NEE and GPP) as well as greater respiration (RE) and ET. Magnitudes of the net and gross CO_2 exchanges showed similar positive relationships with ET (Fig. 7) as with $index_{pf}$, suggesting that greater precipitation frequency is associated with enhanced water availability to drive biotic carbon cycle processes. In both cases (Fig. 6, Fig. 7) GPP was more sensitive than RE (steeper slope) to water availability, consistent with the increasing magnitudes of NEE and ANPP.

3.6. Abiotic and biotic factors control over the response of ANPP and CO_2 fluxes

Path analysis showed that greater precipitation frequency, represented by $index_{pf}$, had a positive effect on community-level ANPP (Fig. 8a, standardised coefficient = 0.24, Z = 1.90, P = 0.05). At the functional group level, increasing precipitation frequency increased the mean productivity of the dominant functional group, Ex (Fig. 8a; standardised coefficient = 0.14, Z = 0.53, P = 0.59), associated with a positive effect on community-level ANPP (standardised coefficient = 0.45, Z = 3.9, P < 0.001). On the other hand, greater precipitation frequency had a negative effect on functional group Xe. These suggested that with reduced precipitation frequency, the ANPP reduction in Ex was partially compensated by the ANPP increase in Xe.

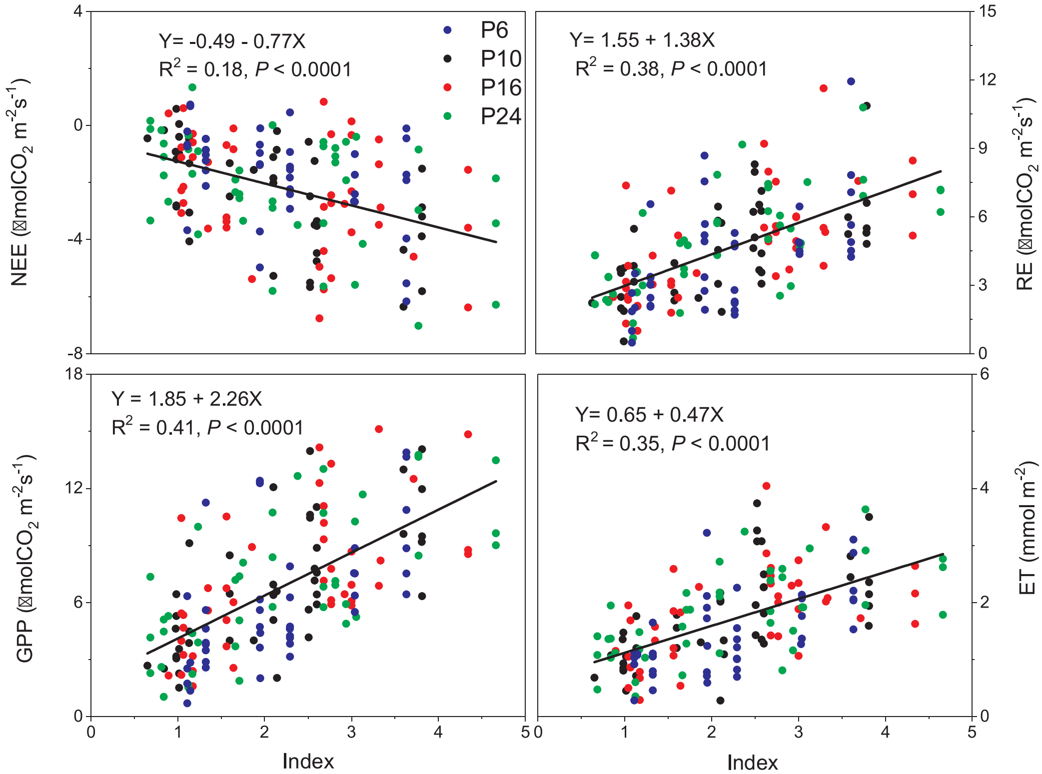

Fig. 6. Relationship between evaluating index of varied precipitation frequency and net ecosystem exchange (NEE), ecosystem respiration (RE) gross primary productivity (GPP), and evapotranspiration (ET).

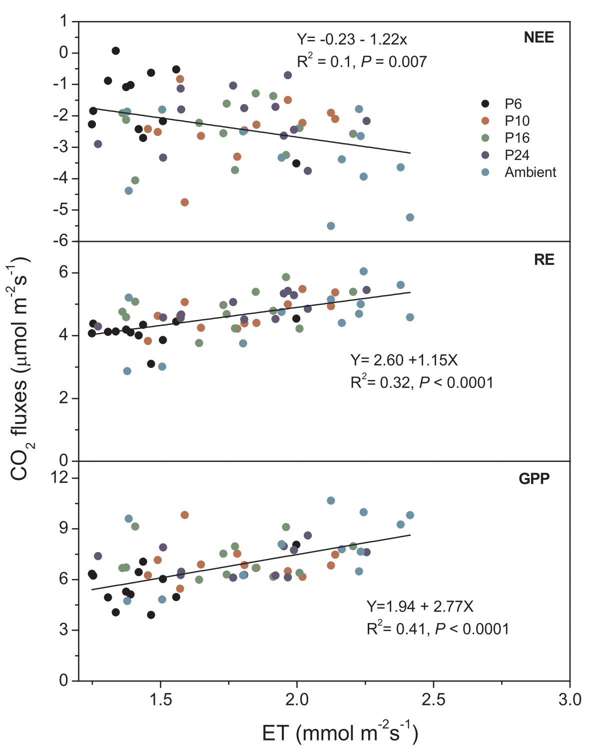

Fig. 7. Relationship between mean evapotranspiration (ET) and ecosystem CO_2 fluxes, net ecosystem exchange (NEE), ecosystem respiration (Re) and gross primary productivity (GPP) across four study years.

Path analysis suggested that the direct effects of the abiotic factors SWC and Ts on NEE were positive (less net uptake), with path coefficients of 0.2 − 0.3. However, the direct effects of the biotic factor LAI were stronger and negative (associated with greater net uptake) with path coefficient of −0.49. SWC and Ts were both positively related to ET, which was in turn associated with greater net uptake (path coefficient: −0.55) (Fig. 8b).

4. Discussion

In this study, we manipulated both the size and number of growing season rainfall events while maintaining a constant seasonal rainfall amount. Our results showed that moderate temporal repackaging of precipitation into fewer, larger storms had minimal or even positive effects, but extreme frequency reductions reduced ecosystem productivity and fluxes of CO_2 and water, supporting our main hypothesis. However, the results suggested several nuances that merit discussion and future exploration including compensatory responses of diverse plant functional groups and the possibility that high-frequency, small rainfall events also curtail ecosystem fluxes and productivity. Below we discuss potential mechanisms for the responses observed here and evaluate their impacts on our understanding of how temporal repackaging of rainfall may affect ecosystem services in semiarid grasslands.

Here, multiple lines of evidence suggest that extreme reductions in precipitation frequency curtail ecosystem carbon cycling, reducing both gross and net CO_2 uptake. ANOVA analysis showed significant treatment effects for NEE, GPP and RE (Table 3), and mean NEE was lowest for the extraordinarily extreme precipitation treatment (P6, Fig. 5a). Path analysis showed negative impacts on ANPP, consistent with the gas flux data, although the monotonic declining pattern in mean ANPP (Fig. 4) was non-significant. Because these results generally differ from prior studies showing the opposite response (Heisler-White et al., 2008; Thomey et al., 2011), it is useful to examine our results for evidence of specific mechanisms of response to precipitation frequency.

Positive relationships between C fluxes and water availability, as suggested by $index_{pf}$ (Fig. 6) or ET (Fig. 7), demonstrate how reduced precipitation frequency suppressed C fluxes through lowering water availability. GPP was more sensitive than RE to changes in water availability (i.e. steeper slopes, Fig. 6, Fig. 7), explaining patterns of reduced net productivity (Fig. 4, Fig. 5), consistent with ecosystem-scale results in drylands (Biederman et al., 2016). Consistent

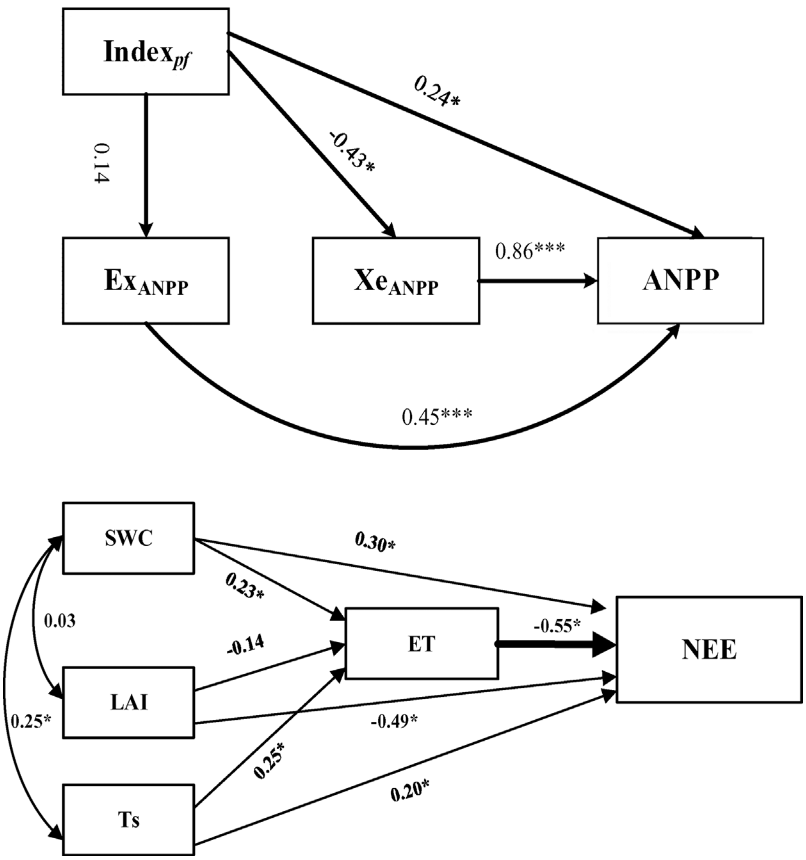

Fig. 8. Path diagrams illustrating (a) the effects of varied precipitation frequency on ANPP through functional groups: eurytopic xerophyte (Ex) and xerophyte (Xe). The diagram includes the direct effect of 4-year interannual precipitation frequency index on 4-year mean ecosystem productivity. Indirect effects of frequency index on total ANPP through Ex and Xe (χ^2 = 0.5, *df* = 1, *P* = 0.47, RMSE < 0.001, CFI = 1.000, SRMR = 0.004), (b) the directive effects of the abiotic factors- soil water content (SWC) at a depth of 0.20 cm, soil temperature (Ts) at a depth of 5 cm, and biotic factors-leaf area index (LAI) on net ecosystem CO_2 exchange (NEE) through 4-year studies. The indirect effects of abiotic and biotic factors through evapotranspiration (ET) on ecosystem CO_2 fluxes. The model fits supported NEE data (χ^2 = 0.1, *df* = 1, *P* = 0.68, RMSE < 0.001, CFI = 1.000, SRMR = 0.002). Significance codes mean: * $P < 0.10$, ** $P < 0.05$ and *** $P < 0.001$.

relationships between C fluxes and ET across a range of water availability (Fig. 7) suggests that the main mechanism of precipitation frequency impacts on ANPP (Fig. 4) and CO_2 exchanges (Fig. 5) was altered water availability, rather than an altered plant capacity to use available water. Path analysis likewise shows that ET amplified the interacting effect of biotic and abiotic factors on ecosystem CO_2 fluxes (Fig. 8b). Because ET represents primarily the consumption of soil available water, these results suggest the importance of soil moisture in regulating the response of ecosystem CO_2 fluxes to altered precipitation frequency.

Temporal repackaging of precipitation between many/small events and few/large events affects both the dry period intervals as well as depths of soil moisture infiltration into the root zone. Frequent rainfall positively affects biotic communities by reducing stresses associated with wetting-drying cycles (Huxman et al., 2004; Hao et al., 2012). Conversely, low precipitation frequency increases the number of days when soil is dry, lowering temporally averaged SWC (Table 1), with negative consequences for ANPP and NEE (Fig. 5, Fig. 8b), consistent with prior ANPP results (Schwinning and Sala, 2004). This is likely because longer dry intervals lead to plant down-regulation, as expressed by reduced LAI (Table 1, Fig. 3b, Fig. 8b), which tends to increase bare soil evaporation and thereby lower ecosystem-scale water use efficiency (Huang et al., 2010; Scott and Biederman, 2017). Additionally, infrequent rainfall pulses onto ecosystems with down-regulated plants tend to stimulate respiration pulses without necessarily stimulating photosynthesis (Birch, 1958; Huxman et al., 2004). The resulting imbalance (RE > GPP) is consistent with the reduced NEE found here in P6 (Fig. 5).

At the other extreme, frequent small rainfall events may only wet the soil surface without infiltrating the full root zone and stimulating productivity as much as larger rain events (Lee et al., 2004; Fay et al., 2008; Chen et al., 2009). A frequently wet shallow surface layer also promotes soil evaporation, lowering WUE (Scott and Biederman, 2017). The present study applied progressive reductions from historically average precipitation frequency (P24). While several response variables declined monotonically (NEE, RE, ANPP), both GPP and WUE were maximum at P16 and lower at both P6 and P24, suggesting a possible shift in controls. Our LAI results strongly suggest that long dry interval duration led to plant down-regulation at P6 (Table 1, Fig. 3; Fig. 8). We suggest that in the P24 treatment, frequent shallow wetting may have limited plant water availability, reducing GPP and WUE relative to the P16 treatment. However, our experiment did not explore higher-frequency extremes (Fig. 1).

Our results suggest that ecosystem diversity moderated the negative response of productivity and fluxes to extreme precipitation frequency, consistent with prior results in a greenhouse experiment (Schneider et al., 2014). Above-ground productivity of the functional group Ex appeared to decline with reduced precipitation frequency while productivity of the Xe group increased in P6 (Fig. 4), consistent with previous finding that higher SWC favoured Ex growth, while Xe was more tolerant to droughts (Wang et al., 2001). Collectively, the buffering of declines in ANPP may be attributed to a "compensatory effect" where reducing the variability of productivity in one functional group increases growth in another (Bai et al., 2004; Wang et al., 2011; Hao et al., 2013). Compensatory effects like this can be a critical mechanism by which biodiversity can buffer climate variability and maintain ecosystem stability in this steppe ecosystem.

Because altered precipitation frequency has been less well-studied than precipitation amount, we highlight several lessons from this study which may guide future research. First, we recommend further exploration of more extreme high-frequency, small event treatments (i.e. to the right side of the distribution in Fig. 1) to further examine the potential shift in controls between dry period duration and soil moisture infiltration depth. Second, we recommend improved measurements of the mechanisms by which dry period interval and infiltration depth impact productivity and fluxes. These include continuous SWC monitoring at multiple depths and metrics to quantify up/down-regulation (in addition to LAI), such as root zone imagery. Our ongoing research further aims to partition above- and below-ground responses with separate measurement of soil respiration and RE. Finally, the opposite responses of plant functional groups could be explored in monoculture plot experiments, to test whether compensatory responses observed (Fig. 4) are competitive or inherent in each functional group.

5. Conclusion

The present study has important implications for understanding and predicting the effects of precipitation events becoming larger with longer intervening dry intervals as has been recently reported (Smith 2011; Hoover et al., 2014). Our results illustrate the importance of extreme precipitation frequency, not just rainfall amount, on the assimilation of atmospheric CO_2. We found that while holding the seasonal rainfall total constant at the historical mean, reduction of rainfall frequency from 24 to 16 events had negligible or slightly positive impacts on CO_2 and water fluxes as well as ANPP. More extreme reduction to 6 events, however, produced significant reduction in gas fluxes and a declining pattern in ANPP. Functional group diversity moderated these community-level impacts. Collectively these results imply that Chinese steppe ecosystems may be resilient to small changes in climatic rainfall frequency, while extreme reductions may threaten both primary productivity and storage of atmospheric CO_2.

Acknowledgements

Financial support was provided by The National Key Research and Development Program of China (Grant No. 2016YFC0501801), The Chinese Academy of Sciences (Grant No. KJRH2015-010), the National Youth Science Foundation of China (Grant No. 31300417), and Special Funds for Science and Education Fusion of University of Chinese Academy of Sciences. We acknowledge the effort and thoughtful comments of three anonymous reviewers, which helped distil diverse results into a clear, cohesive contribution.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2017.08.029.

References

Bai, Y., Han, X., Wu, J., Chen, Z., Li, L., 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature 431, 181–184.

Bailey, R.G., 1998. Ecoregions: the Ecosystem Geography of the Oceans and Continents. Springer, New York.

Biederman, J.A., Scott, R.L., Goulden, M.L., Vargas, R., 2016. Terrestrial carbon balance in a drier world: the effects of water availability in southwestern North America. Global Change Biol. 22, 1867–1879.

Birch, H.F., 1958. The effect of soil drying on humus decomposition and nitrogen availability. Plant Soil 10, 9–31.

Bloor, J.M.G., Bardgett, R.D., 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. Perspectives in Plant Ecology. Evol. Syst. 14, 193–204.

Chen, S., Lin, G., Huang, J., Jenerette, G.D., 2009. Dependence of carbon sequestration on the differential responses of ecosystem photosynthesis and respiration to rain pulses in a semiarid steppe. Global Change Biol. 15, 2450–2461.

Cook, B.L., Ault, T.R., Smerdon, J.E., 2015. Unprecedented 21 st century drought risk in the american southwest and central plains. Sci. Adv. 1, e1400082. http://dx.doi.org/10.1126/sciadv.14000821.

Didiano, T.J., Johnson, M.T.J., Duval, T.P., 2016. Disentagling the effects of precipitation amount and frequency on the performance of 14 grassland species. PLoS One 11. http://dx.doi.org/10.1371/journal.pone.0162310.

Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M., Collins, S.L., 2003. Productivity responses to altered rainfall patterns in a C_4-dominated grassland. Oecologia 137, 245–251.

Fay, P.A., Kaufman, D., Nippert, J.B., Carlisle, J.D., Harper, C.W., 2008. Changes in grassland ecosystem function due to extreme rainfall events implications for responses to climate change. Global Change Biol. 14, 1600–1608.

Grace, J.B., Andersons, T.M., Olffs, H., Scheiners, S.M., 2010. On the specification of structural equation models for ecological systems. Ecol. Monogr. 80, 67–87.

Grace, J.B., 2006. Stucutual Equantion Modeling and Naturan Systems. Cambridge Universtiy press, New York, pp. 378.

Hao, Y., Wang, Y., Mei, X., Huang, X., Cui, X., Zhou, X., Niu, H., 2008. CO_2, H_2O and energy exchange of an Inner Mongolia steppe ecosystem during a dry and wet year. Acta Oecol. 33, 133–143.

Hao, Y., Wang, Y., Mei, X., Cui, X., 2010. The response of ecosystem CO_2 exchange to small precipitation pulses over a temperate steppe. Plant Ecol. 209, 335–347.

Hao, Y.B., Kang, X.M., Cui, X.Y., Ding, K., Wang, Y.F., Zhou, X.Q., 2012. Verification of a threshold concept of ecologically effective precipitation pulse: from plant individuals to ecosystem. Ecol. Inf. 12, 23–30.

Hao, Y., Kang, X., Wu, X., Cui, X., Liu, W., Zhang, H., Li, Y., Wang, Y., Xu, Z., Zhao, H., 2013. Is frequency or amount of precipitation more important in controlling CO_2 fluxes in the 30-year-old fenced and the moderately grazed temperate steppe? Agric. Ecosyst. Environ. 171, 63–71.

Heisler-White, J.L., Knapp, A.K., Kelly, E.F., 2008. Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. Oecologia 158, 129–140.

Hoover, D.L., Knapp, A.K., Simith, M.D., 2014. Resistance and resilience of a grassland ecosystem to climate extremes. Ecology 95, 2646–2656.

Huang, X., Hao, Y., Wang, Y., Wang, Y., Cui, X., Mo, X., Zhou, X., 2010. Partitioning of evapotranspiration and its relation to carbon dioxide fluxes in Inner Mongolia steppe. J. Arid Environ. 74, 1616–1623.

Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. Oecologia 141, 254–268.

Jentsch, A., Kreyling, J., Beierkuhnlein, C., 2007. A new generation of climate-change experiments: events: not trends. Front. Ecol. Environ. 5, 365–374.

Knapp, A.K., Smith, M.D., 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science 291, 481–484.

Knapp, A.K., Briggs, J.M., Hartnett, D.C., Collins, S.L., 1998. Grassland Dynamics:long-term Ecological Research in Tallgrass Prairie. Oxford University Press, New York, NY, USA.

Knapp, A.K., Beier, C., Briske, D.D., Classen, A.T., Luo, Y., Reichstein, M., 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. Bioscience 58, 811–821.

Kreyling, J., Wenigmann, M., Beierkuhnlein, C., Jentsch, A., 2008. Effects of extreme weather events on plant productivity and tissue die-Back are modified by community composition. Ecosystems 11, 752–763.

Lee, X., Wu, H.J., Sigler, J., Siccama, T., 2004. Rapid and transient response of soil respiration to rain. Global Change Biol. 10, 1017–1026.

Liu, Y.S., Pan, Q.M., Zheng, S.X., Bai, Y.F., Han, X.G., 2012. Intra-seasonal precipitation amount and pattern differentially affect primary production of two dominant species of Inner Mongolia grassland. Acta Oecol. Int. J. Ecol. 44, 2–10.

Naeem, S., Li, S., 1997. Biodiversity enhances ecosystem reliability. Nature 390, 507–509.

Nielsen, U.N., Ball, B.A., 2015. Impacts of altered precipitation regimes on soil communities and biogeochemistry in arid and semi-arid ecosystems. Global Change Biol. 21 4107–1421.

Potts, D.L., Huxman, T.E., Cable, J.M., English, N.B., 2006. Antecedent moisture and seasonal precipitation influence the response of canopy-scale carbon and water exchange to rainfall pulses in a semi-arid grassland. New Phytol. 170, 849–860.

Schneider, A.C., Lee, T.D., Kreiser, M.A., Nelson, G.T., 2014. Comparative and interactive effects of reduced precipitation frequency and volume on the growth and function of two perennial grassland species. Int. J. Plant Sci. 175, 702–712.

Schwinning, S., Sala, O.E., 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141, 211–220.

Scott, R.L., Biederman, J.A., 2017. Partitioning evapotranspiration using long-term carbon dioxide and water vapor fluxes: new approach to ET partitioning. Geophys. Res. Lett. 44, 6833–6840.

Scott, R.L., Hamerlynck, E.P., Jenerette, G.D., Moran, M.S., Barron-Gafford, G.A., 2010. Carbon dioxide exchange in a semidesert grassland through drought-induced vegetation change. J. Geophys. Res. Biogeosci. 115, G03026. http://dx.doi.org/10.1029/2010JG001348.

Smith, M.D., 2011. An ecological perspective on extreme climatic events: a syntheticdefinition and framework to guide future research. J. Ecol. 99, 656–663.

Thomey, M.L., Collins, S.L., Vargas, R., 2011. Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland. Global Change Biol. 17, 1505–1515.

Tian, D., Niu, S.L., Pan, Q.M., 2016. Nonlinear responses of ecosystem carbon fluxes and water-use efficiency to nitrogen addition in Inner Mongolia grassland. Funct. Ecol. 30, 490–499.

Tilman, D., Wedin, D., Knops, J., 2006. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379, 718–720.

Vicente-Serrano, S.M., Gouveia, C., Camarero, J.J., Begueria, S., 2013. Response of vegetation to drought time-scales across global land biomes. PNAS 110, 52–57.

Wang, R.Z., Earle, A.R., Zu, Y.G., Nie, S.Q., 2001. Demography of reproductive and biomass allocation of grassland and dune *Leymus Chinensis* on the Songnen Plain: north-eastern China. J. Arid Environ. 49, 289–299.

Wang, Y.F., Cui, X.Y., Hao, Y.B., Mei, X.R., Yu, G.R., Huang, X.Z., Kang, X.M., Zhou, X.Q., 2011. The fluxes of CO_2 from grazed and fenced temperate steppe during two drought years on the Inner Mongolia Plateau. China. Sci. Total Environ. 410, 182–190.

Weltzin, J.F., Loik, M.E., Schwinning, S., 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. Bioscience 53, 941–952.