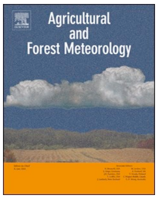
Agricultural and Forest Meteorology 291 (2020) 108039

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

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



Asymmetric effect of increased and decreased precipitation in different periods on soil and heterotrophic respiration in a semiarid grassland

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ARTICLE INFO

Keywords:
climate change
carbon cycling
precipitation magnitude and timing
plant growth
soil water content
temperate steppe

ABSTRACT

Climate models predict significant changes in precipitation magnitude and timing in semi-arid grasslands, where soil carbon release is particularly sensitive to changing precipitation.

Using data from a 4-year (2015-2018) field manipulation experiment, we explored effects of changed precipitation in different periods on soil respiration (SR) and heterotrophic respiration (HR) in a semi-arid grassland in northern China.

The results showed that: (1) Decreased precipitation both in the early (DEP), late (DLP), and entire growing season (DP) reduced SR, whereas DP and DLP rather than DEP reduced HR. The declines of SR in DLP and DP are larger than in DEP; (2) Increased precipitation in the early (IEP), late (ILP), and entire (IP) growing season promoted SR, but had little effect on HR. Enhancement of SR in IEP is larger than in ILP; (3) The change of SR and HR can be attributed to varied plant community cover which is related to soil water content; and (4) SR and HR are more sensitive to decreased than to increased precipitation, to DLP than DEP, and IEP than ILP.

The findings suggest an asymmetric response of soil carbon process to precipitation in different periods, highlighting that future study should not neglect the role of precipitation timing in regulating ecosystem carbon fluxes.

Introduction

Global change has intensified hydrological cycles, causing changes in both magnitude and timing of precipitation (Fay et al., 2008; Peng et al., 2013; IPCC, 2014). Ru et al. (2018) have shown that higher precipitation would shift from July and August to June and September in a semi-arid grassland in northern China. Volder et al. (2013) have reported that precipitation would shift from summer to spring in savannas of North America. Given that plants have different water requirements during different growth stages, increasing precipitation variability during different periods of the growing season may play an important role in regulating plant photosynthesis and respiration, and consequently influences carbon flux (Austin et al., 2004; Luo & Zhou, 2006; Chou et al., 2008; Gerten et al., 2008; Li et al., 2019).

Grassland soils contain enormous amounts of carbon relative to atmospheric pools (Budge et al., 2011). Small changes in CO_2 fluxes of grasslands have significant impacts on biosphere-atmosphere exchanges of CO_2 (Parton et al., 2012). Soil respiration (SR), which is the sum of the release of CO_2 produced by autotrophic (plant roots) and heterotrophic (microbes and soil fauna) respiration (HR), is tightly coupled with the amount and timing of precipitation in grassland ecosystems (Knapp et al., 2002; Chou et al., 2008; Niu et al., 2008; Ru et al., 2018). For example, small precipitation events tend to affect surface microbes with fast response times, whereas more intense precipitation often impacts plants more (Schwinning et al., 2004; Heisler-White et al., 2009). Activities of both microbes and plants will influence soil carbon dynamics by changing heterotrophic and autotrophic respiration processes (Ryan & Law, 2005; Kuzyakov, 2006; Inglima et al., 2009). Precipitation timing also can be important, given that it determines different stages of plant growth and thus the accumulation of respiratory substrates (Xu & Baldocchi, 2004; Sponseller, 2007; Parton et al., 2012). Studies have reported that precipitation in the

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Abbreviations: C, control; DEP, a 60% decrease in precipitation in the early growing season; DLP, a 60% decrease in precipitation in the late growing season; DP, a 60% decrease in precipitation in the entire growing season; IEP, a 60% increase in precipitation in the early growing season; ILP, a 60% increase in precipitation in the late growing season; IP, a 60% increase in precipitation in the entire growing season; MBC, soil microbial biomass carbon; MBN, soil microbial biomass nitrogen; BNPP, belowground net primary productivity; SOC, soil osrganic carbon; SEM, structural equation modeling; SWC, soil water content; DOC, dissolved organic carbon; C, carbon; N, nitrogen; ST, soil temperature; HR, heterotrophic respiration; SR, soil respiration

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https://doi.org/10.1016/j.agrformet.2020.108039
Received 29 September 2019; Received in revised form 5 May 2020; Accepted 17 May 2020

early growing season can alter SR (Chou et al., 2008; Ru et al., 2018) by affecting plant growth (Bates et al., 2006; Suttle et al., 2007; Fay et al., 2008; Stampfli & Zeiter, 2009; Evans et al., 2011; Chelli et al., 2016; Zhang et al., 2019a), root development (Svejcar et al., 2006), and microbial activity (Harper et al., 2005). Precipitation in the late growing season can influence SR by changing substrate supply for root and microbial activity (Harper et al., 2005; Moyano et al., 2008; Rachmilevitch et al., 2006; Bahn et al., 2009; Liu et al., 2016).

Asymmetry is a context used to examine the responses of ecosystem processes to precipitation changes. A 'double asymmetry' model had been proposed to forecast precipitation impacts on aboveground net primary productivity, i.e., positive asymmetry under conditions of nominal precipitation variability and negative asymmetry in extreme precipitation periods (Knapp et al., 2017). However, less is known about whether such asymmetry applies to other ecosystem processes, such as SR and HR. Studies have shown that responses of SR to precipitation change is nonlinear, with greater sensitivity to decreased precipitation (Suseela et al., 2012; Zhang et al., 2016; Miao et al., 2017; Zhang et al., 2019b). Zhou et al., 2008also demonstrated a threshold-like nonlinear pattern of HR in response to precipitation anomalies. Recently, a meta-analysis extended the double asymmetric model by providing evidence that asymmetric responses in microbial biomass to altered precipitation varies with climate humidity and soil texture (Zhou et al., 2018a).

The temperate steppe is a common biome of semiarid regions on the Eurasian continent, providing essential ecosystem services. These ecosystems are experiencing changing precipitation regimes which may fundamentally affect their functioning (Piao et al., 2010). Here, we report on a 4-year (2015-2018) field manipulation experiment that increased and/or decreased precipitation of the early (April-June) and/or late (July-September) growing season in a temperate steppe in northern China to examine their impacts on SR and HR and the related ecological drivers. Specifically, we tested whether responses of SR and HR to changing precipitation are symmetrical, including if the (1) responses of SR and HR under increasing precipitation in the early/late growing season are the same as that under decreasing precipitation in the early/late growing season and (2) responses of SR and HR under changing precipitation in the early growing season are the same as that in the late growing season.

Materials and Methods

Site description

The study was conducted in a typical temperate steppe at the Duolun Restoration Ecology Station (42°02′N, 116°17′E, 1324 m a.s.l.) in Inner Mongolia, China. Mean annual precipitation over the previous 54 years (1961-2014) was ~ 383 mm with more than 90% of rainfall occurring in the growing season (from May to October). Mean annual temperature was 2.1 °C, with monthly mean temperatures of -17.5 °C in January and 18.9 °C in July. Soil is classified as chestnut, with an average bulk density of 1.31 g cm^{-3} and a pH of 7.7 (Song et al., 2016). Plant community is dominated by the perennial species Artemisia frigida Willd., Stipa krylovii Roshev., Potentilla acaulis L., Cleistogenes squarrosa (Trin.) Keng, Allium bidentatum Fisch.ex Prokh and Agropyron cristatum (L.) Gaertn (Yang et al., 2017).

Experimental design

We used a randomized block design with seven treatments: control (C), a 60% decrease in precipitation in the early growing season (from April to June, DEP), a 60% decrease in precipitation in the late growing season (from July to September, DLP), a 60% decrease in precipitation during the entire growing season (from April to September, DP), a 60% increase in precipitation in the early growing season (from April to June, IEP), a 60% increase in precipitation in the late growing season (from July to September, ILP), and a 60% increase in precipitation during the entire growing season (from April to September, IP). Each treatment had five replicates resulting in 35 plots total. The 35 permanent 4 × 4 m plots were established on April 15, 2015. From April 15th to June 30th of 2015, 2016, 2017, and 2018, control, DLP and ILP plots received ambient natural precipitation, whereas in DEP and DP plots precipitation was blocked using shelters, and IEP and IP plots received additional 60% precipitation with a handheld irrigation system. From June 30th to September 15th of 2015, 2016, 2017, and 2018, control, DEP, and IEP plots received ambient natural precipitation when DLP and DP plots had 60% precipitation blocked, and ILP and IP plots received additional 60% precipitation. On September 15th of each of the four years, all shelters were removed from plots. Slat paneled shelter used in the present study as in Yahdjian & Sala (2002) and Gherardi & Sala (2013), which tend to have minimal effects on temperature, light radiation, and wind speed. The highest end of the shelter was 1.2 m high and the lowest end 0.5 m. Shelters were 4 × 4 m with a 3.5 × 3.5 m area at the center that was used to measure and survey, the 0.5 m edge was considered a buffering zone to avoid edge effects. We separated the 3.5 × 3.5 m plot into two parts: one 2 × 1 m section at the center for vegetation monitoring, and the other section for species sampling and carbon flux measurement. There was a 1.5 m wide buffer zone between any two adjacent plots. The division of early (April-June) and late (July-September) growing seasons was determined based on the phenology of common species (Fig. S1). The decision to exclude 60% precipitation was made according to historical precipitation data over the past 54 years (1961-2014). The most severe drought in the early growing season occurred in 2007, during this drought precipitation was 59.6% lower than the average precipitation for the same period; the least precipitation in the late growing season occurred in 2009, when precipitation was 55.8% lower than the 54 years average for the same period; the most abundant precipitation in the early growing season occurred in 1979, when precipitation was 74% higher than the average for the same period; the most heavy precipitation in the late growing season occurred in 1983, when precipitation was 43.4% higher than the average for the same period.

Vegetation monitoring

Over the four years, community cover in one permanent 1 × 1 m quadrat of each plot was monitored. Monitoring was conducted annually in the early September when plant biomass reached its peak level (Yang et al., 2017). The cover of each species in each quadrat was estimated using a canopy interception technique based on 100 equally distributed grids (10 × 10 cm). The percent cover of each species was recorded in all the grids and summed as the community cover in each quadrat. Total canopy cover was calculated by summarizing the percent cover of all species in the quadrat.

Soil sampling and analysis

Two 20 cm soil cores were collected in each subplot with a 7 cm diameter soil auger in mid-September 2015-2018. The two soil cores were mixed and sieved with a 2 mm mesh to separate roots and gravel. Soil microbial biomass carbon (MBC) and nitrogen (MBN) were measured using the chloroform fumigation-extraction method (Liu et al., 2009). Fresh soil (15 g dry weight equivalent for soil microbial biomass) was fumigated with ethanol-free $CHCl_3$ for 24 h at 25°C. Additional aliquots of fresh soil were used as unfumigated controls. Both the fumigated and unfumigated samples were extracted after being shaken for 30 min in 60 mL of 0.5 M K_2SO_4. K_2SO_4 extracts were filtered through 0.45 mm filters and frozen at -20°C before analyzing for extractable carbon (C) and nitrogen (N) by a Total Organic C/N Analyzer (Elementar vario TOC, Elementar Co., Germany). MBC and MBN were calculated from differences between extractable C and N contents in the fumigated and the unfumigated samples using a conversion factor of 0.45 (Zhao et al., 2016; Gao et al., 2016). Soil dissolved organic carbon (DOC) was extracted from 10 g of fresh soil in 40 ml deionized water at 20 °C and shaken for one hour using an end-to-end shaker (Miao et al., 2019). Soil temperature (ST) and volumetric soil water content (SWC) at a depth of 10 cm was measured three times a month using a thermocouple probe (Li-8100-201) attached to a Li-8100 (LiCor Inc., Lincoln, Nebraska, USA) from mid- April to the end of October (Chi et al., 2013; Liang et al., 2013).

Belowground net primary productivity (BNPP) measurement

BNPP was estimated using the root in-growth method. Two 50-cm deep cylindrical holes were excavated using a soil auger (7 cm in diameter) at two diagonal corners in each plot in mid-April. After removing roots and stones with 2-mm sieves, the holes were refilled with root-free soil from the same hole. The root in-growth samples were collected in October using a smaller soil auger (5 cm in diameter) at the center of the same holes (Kong et al., 2017; Ru et al., 2018). The samples were dried at 65°C for 48 hours and weighed to calculate BNPP.

SR and HR measurement

One PVC collar (11 cm in internal diameter and 5 cm in height) was inserted 3 cm into the soil of each subplot for SR measurement. SR was measured by a LI-8100 portable soil CO_2 flux system (Li-Cor Inc., Lincoln, NE, USA) between 9:00 AM and 12:00 AM (local time), April-October, with a frequency of three times a month from 2015 to 2018. In 2018, we supplemented HR data, and the methods of measurement were the same as that for SR, except the inserted depth of PVC collars (52 cm in height) into the soil (50 cm, Zhao et al., 2016; Smith et al., 2019). Although we tried to minimize the influence of dead root decay by postponing measurements 6 months after collar installation, there is still some bias with the mini-trenching method, i.e., overestimating root exclusion and underestimating heterotrophic activity due to the decline of root exudates and root litter input. Despite this, the method is still acceptable and one of the most used for partitioning SR components (Zhang et al., 2019a). Living plants inside the soil collars (if present) were removed by hand at least two days before measurements to eliminate aboveground plant respiration (Sagar et al., 2017).

Statistical analyses

Repeated-measures one-way ANOVAs were used to test effects of precipitation treatments (DEP, DLP, DP, IEP, ILP, and IP) and year on SR, SWC, ST, DOC, BNPP, MBC/MBN, and plant community cover from 2015 to 2018; precipitation treatment was viewed as a fixed factor, with the year as the repeated variable. Post hoc tests were used to test for significant differences in SWC, SR, and HR among precipitation treatments in each year of the experimental period. One-way ANOVAs were used to test effects of precipitation treatments on HR in 2018. Post hoc tests were used to test for a significant difference in the relative contribution of HR to SR among seven levels of the precipitation treatment and six months (April-October) of the growing season. Mean changes of SR across the 4 years, as well as HR in 2018 under DEP, DLP, DP, IEP, ILP, and IP were compared. Regression analysis was used to

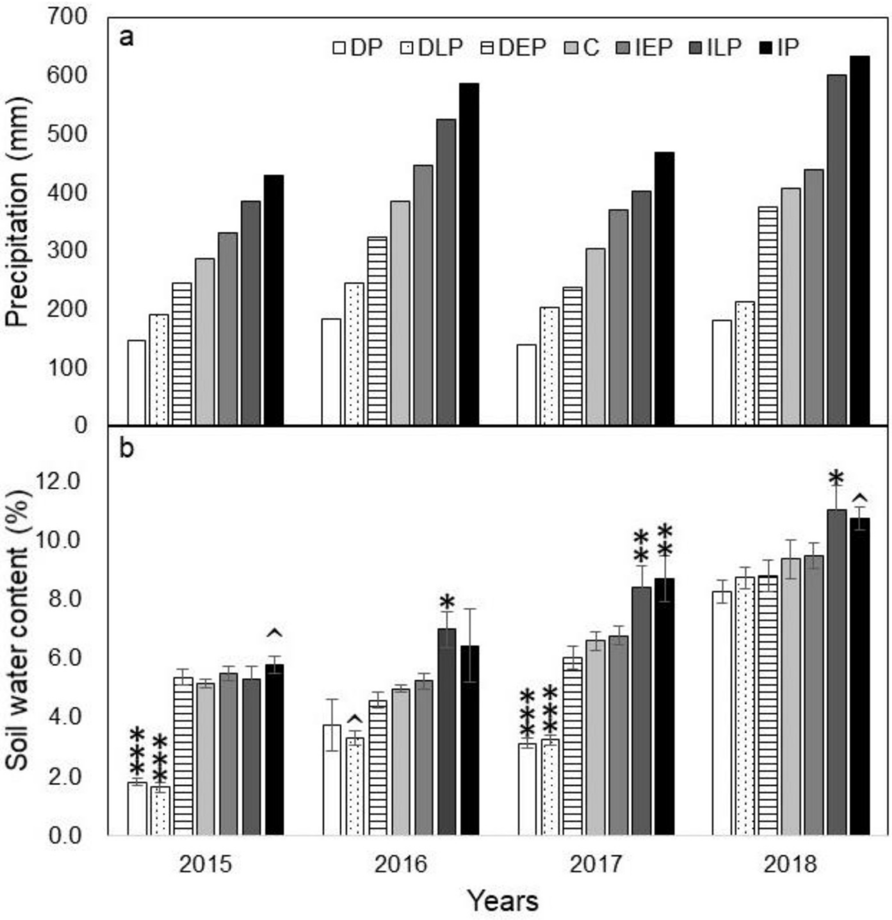

Figure 1. Precipitation and soil water content April-October in control (C), decreased precipitation in the early growing season (DEP, April-June), decreased precipitation in the late growing season (DLP, July-September), decreased precipitation in the entire growing season (DP, April- September), increased precipitation in the early growing season (IEP, April-June), increased precipitation in the late growing season (ILP, July-September), and increased precipitation in the entire growing season (IP, April-September) during the experimental periods (2015-2018). $P < 0.1$,$^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Table 1

Results of one-way ANOVAs on the effects of decreased/increased precipitation during the early growing season (DEP/IEP, April-June), decreased/increased precipitation during the late growing season (DLP/ILP, July-September), and decreased/increased precipitation during the entire growing season (DP/IP, April -September), on soil water content (SWC, % m^3 m^{-3}), soil temperature (ST,°C), dissolved organic carbon (DOC, mg kg^{-1}), microbial biomass carbon /microbial biomass nitrogen (MBC/MBN), belowground net primary productivity (BNPP), and community cover (%). Means are shown.

Source of variation	SWC (%)	ST (°C)	DOC (mg kg^{-1})	MBC/MBN	BNPP (g m^{-2} yr^{-1})	Community cover (%)
DEP	6.2	14.7	38.5	6.5	183	75.9
DLP	4.2***	14.6	44.0*	9.2***	153	45.0***
DP	4.2***	15.2***	46.6***	6.9	116*	30.2***
IEP	6.7	14.3	36.5	6.3*	172	85.7**
ILP	7.9***	14.4	36.0	5.9	182	86.8**
IP	7.9***	14.6	37.1	7.0	151	95.08***

*P< 0.05, **P< 0.01, ***P< 0.001.

test effects of precipitation manipulation on SR, HR, and the contribution of HR on SR. Linear regression analyses were used to relate factors that have been suggested to influence SR and HR, including SWC, ST, DOC, MBC/MBN, BNPP, and plant community cover. Moreover, we also related changes of soil organic carbon (SOC) to changes of SR to examine the effect of soil carbon content on SR. Based on linear regression results, we employed structural equation modeling (SEM) according to known effects and potential relationships among drivers of SR and HR. SEM analyses were performed using AMOS 18.0 (Amos Development Co., Greene, Maine, USA). Other analyses were conducted using SPSS 16.0 (SPSS, Inc., Chicago, Illinois, USA).

Results

Change in precipitation and SWC

There were strong interannual fluctuations in growing-season precipitation. April-October precipitation was 3.8, 19.1, and 29.4% higher in 2015 (372.3 mm), 2016 (427.2 mm), and 2018 (464.1 mm), respectively, but 4.2% lower in 2017 (343.4 mm), than the long-term (1955-2014) mean precipitation from April to October (358.7 mm; Fig. 1a). Mean precipitation of the growing season during 2015-2018 under DEP, DLP, and DP were 33.7, 96.1, and 129.8 mm, lower by 68.7,

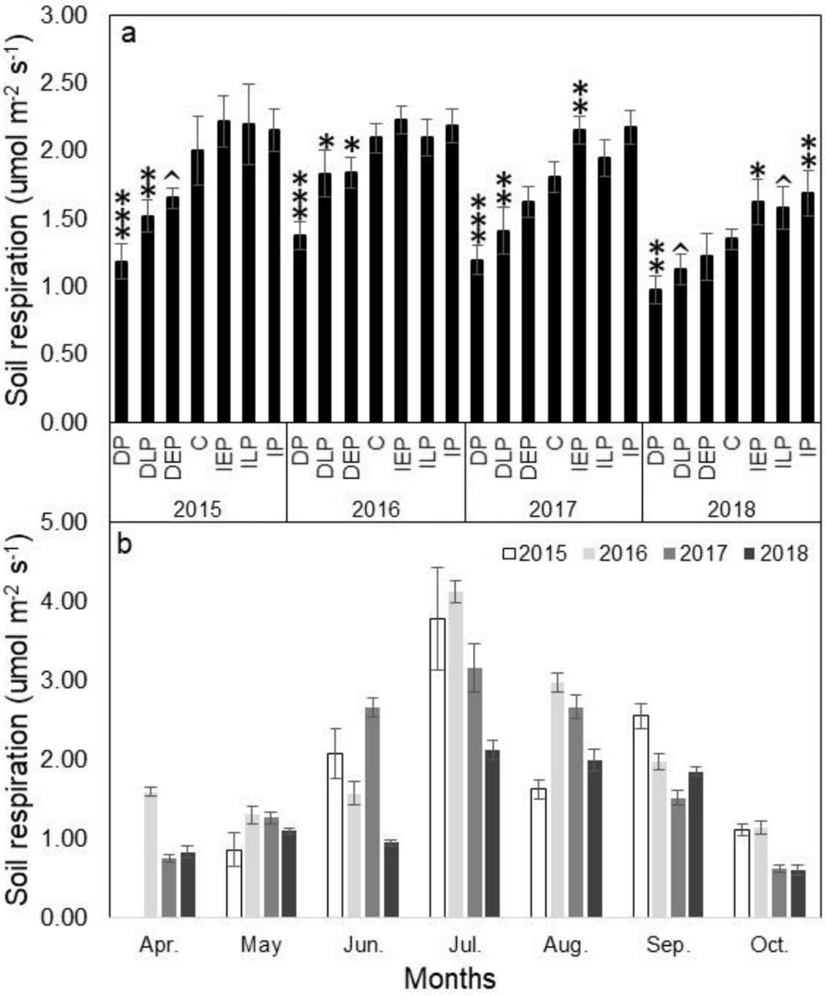

Figure 2. Annual and seasonal dynamics of soil respiration in C, DEP, DLP, DP, IEP, ILP, and IP from 2015 to 2018. See Fig. 1 for abbreviations. P<0.1,*P<0.05, **P<0.01, ***P<0.001.

59.0, and 60.0%, respectively, than the mean precipitation in the early, late, and entire growing season across the past 60 years (1955-2014; Fig. 1a). Mean precipitation of the growing season 2015-2018 under IEP, ILP, and IP were 135.0, 384.4, and 519.4 mm, higher by 68.7, 59.0, and 60.0%, respectively, than the mean precipitation in the early, late, and entire growing season over the past 60 years (1955-2014; Fig. 1a).

Change in precipitation timing significantly affected SWC ($F_{140,6} = 38.6$, $p < 0.001$). Both DLP ($p < 0.001$) and DP ($p < 0.001$) reduced SWC by an average of 2.3% from 2015 to 2018 (Fig. 1b, Table 1). In contrast, both ILP ($p < 0.001$) and IP ($p < 0.001$) increased SWC by an average of 1.4% across the four years, whereas neither DEP nor IEP influenced SWC (Fig. 1b, Table 1).

Soil respiration

There was strong intra- and interannual variability in SR (Fig. 2a, b). SR was usually greater in July and lower in April-May and September-October (Fig. 2b). When analyzed across the 4 years using seasonal mean SR, DEP, DLP, and DP reduced SR by 0.23, 0.34, and 0.63, respectively (absolute change, Fig. 2a). In contrast, IEP, ILP, and IP stimulated SR by 0.24, 0.14, and 0. 24 from 2015 to 2018, respectively (absolute change, Fig. 2a). Results of the main effects in each year showed that DP and DLP significantly reduced soil respiration from 2015 to 2018, whereas DEP decreased the SR in 2015 ($P < 0.1$) and 2016 ($P < 0.05$) by 17.4 and 12.4% (Fig. 2a), respectively. IEP significantly increased the SR in 2017 ($P < 0.01$) and 2018 ($P < 0.05$) by 19.2 and 20%, respectively, and IP significantly increased the SR in 2018 by 25% (Fig. 2a). In contrast, ILP has no significant effect on SR from 2015 to 2018 (Fig. 2a). SR was more sensitive to IEP than to ILP ($P < 0.05$) (Fig. S2). In contrast, SR was reduced more in DLP ($P < 0.05$) and DP ($P < 0.001$) than in DEP, and the negative response of SR to decreased precipitation was larger than the positive response of SR to increased precipitation ($P < 0.01$) (Fig. S2).

Heterotrophic respiration

Consistent with SR, HR was usually higher in July and lower in April-May and September-October in 2018 (Fig. 3b). However, HR in the late growing season was generally higher than in the early growing season except in October (Fig. 3b).

DLP and DP significantly reduced HR by an average of 0.21 and 0.20 in 2018 (absolute change), respectively, whereas DEP had no significant effect (Fig. 3a). In contrast, IEP, ILP, and IP had no significant effect on HR (Fig. 3a). HR was more sensitive to decreased precipitation than to increased precipitation, and the response magnitude of HR to DLP was larger than to DEP (Fig. S3).

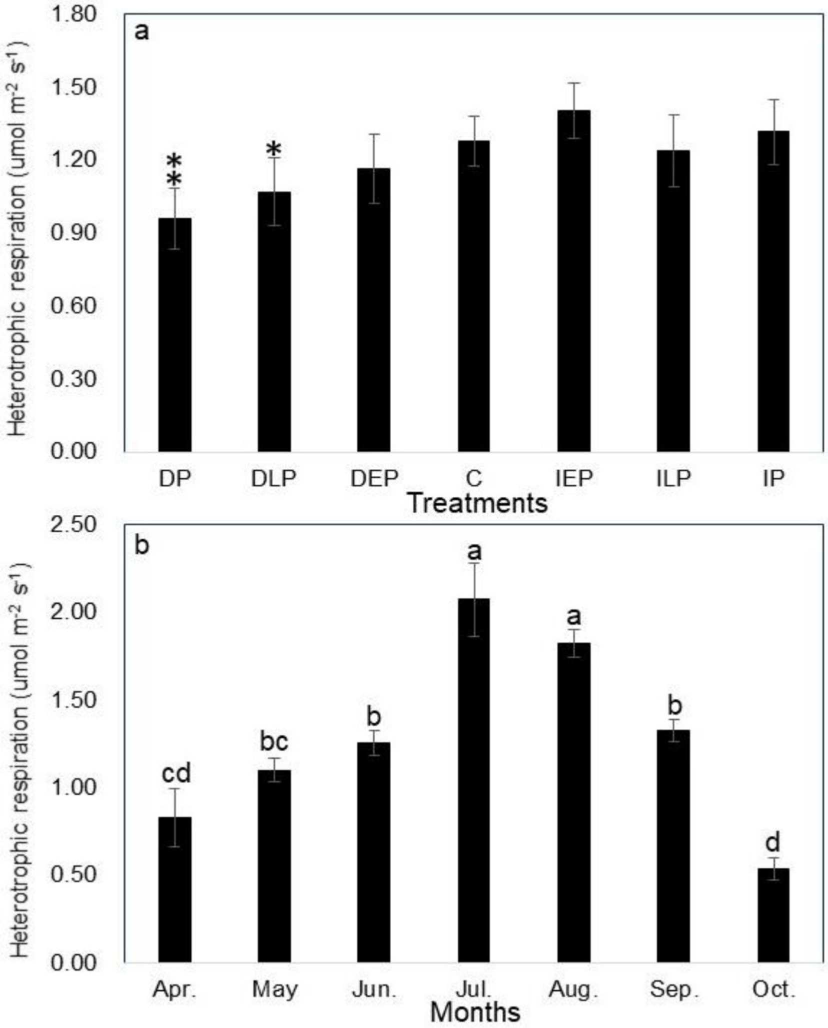

Figure 3. Seasonal dynamics of heterotrophic respiration in C, DEP, DLP, DP, IEP, ILP, and IP in 2018. See Fig. 1 for abbreviations. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

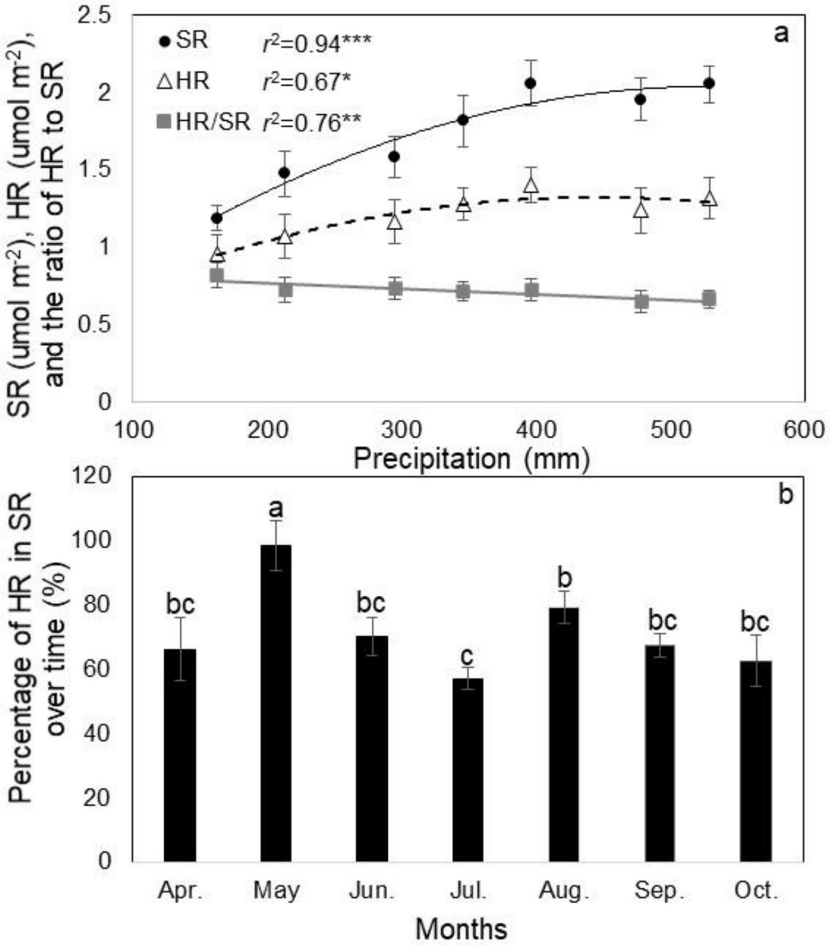

Figure 4. The relative contributions of heterotrophic respiration (HR) to soil respiration (SR) in 2018. See Fig. 1 for abbreviations.

Contributions of HR to SR

Relative contributions of HR to SR changed among months ($F_{34,6} = 4.3$, $p < 0.01$), with the highest occurring in May and the lowest in July (Fig. 4b). Both SR and HR showed a nonlinear increase along precipitation gradients. The relative contribution of HR to SR decreased linearly with increasing precipitation (Fig. 4a).

Factors influencing SR and HR

Regressions analysis showed that SR was positively correlated to BNPP ($p < 0.01$, $r^2 = 0.07$) and plant community cover ($p < 0.001$, $r^2 = 0.50$), and negatively correlated to ST ($p < 0.001$, $r^2 = 0.19$) and DOC ($p < 0.001$, $r^2 = 0.16$). There was a quadratic relationship between SR and SWC ($p < 0.001$, $r^2 = 0.10$). MBC/MBN showed no relationship (Fig. 5).

HR was positively correlated to BNPP ($p < 0.05$, $r^2 = 0.15$) and community cover ($p < 0.001$, $r^2 = 0.52$), and negatively correlated to DOC ($p < 0.01$, $r^2 = 0.22$) and MBC/MBN ($p < 0.05$, $r^2 = 0.13$; Fig. 5g). There was a quadratic relationship between HR and SWC ($p < 0.01$, $r^2 = 0.47$). ST showed no relationship (Fig. 5).

The SEM model explained 77 and 42% of the change in SR ($\chi^2 = 7.911$, $P = 0.543$, $df = 9$) and HR ($\chi^2 = 14.011$, $P = 0.300$, $df = 12$) under different precipitation levels, respectively (Fig. 6). This model revealed that precipitation manipulation changed SR and HR through influencing SWC and DOC, and consequent effects on plant community cover (Fig. 6).

Discussion

Changes in both the amount and timing of precipitation are important aspects of climate change. This can alter the dynamics of water availability and biological processes in soils, with significant ecosystem-level consequences. Our study shows that both the amount and timing of precipitation are important in regulating SR and HR in this semi-arid grassland, highlighting the importance of photosynthetic substrate supply in regulating soil carbon processes. Moreover, the nonlinear relationships of SR and HR with soil water content indicate that in addition to soil water availability, there are other factors regulating soil carbon dynamics.

Effect of changing precipitation in different periods on SR

A change in precipitation amount and a shift in timing may influence soil CO_2 efflux (Harper et al., 2005; Chou et al., 2008; Kwon et al., 2008; Zhang et al., 2019a). Chou et al. (2008) showed that early- and late-season rain events significantly increased SR for 2-4 weeks after wetting, whereas augmentation of wet-season rainfall had no significant effect. Our study shows that decreased precipitation suppresses and increased precipitation stimulates SR in this semi-arid grassland where water is expected to play an important role in controlling SR. The finding is consistent with Song et al. (2012) that soil CO_2 efflux was increased by precipitation addition in the early growing season (May-July) but is not consistent with their result that increased precipitation in the late growing season (September) did not influence soil carbon processes. The factors that determine dynamic patterns of soil CO_2

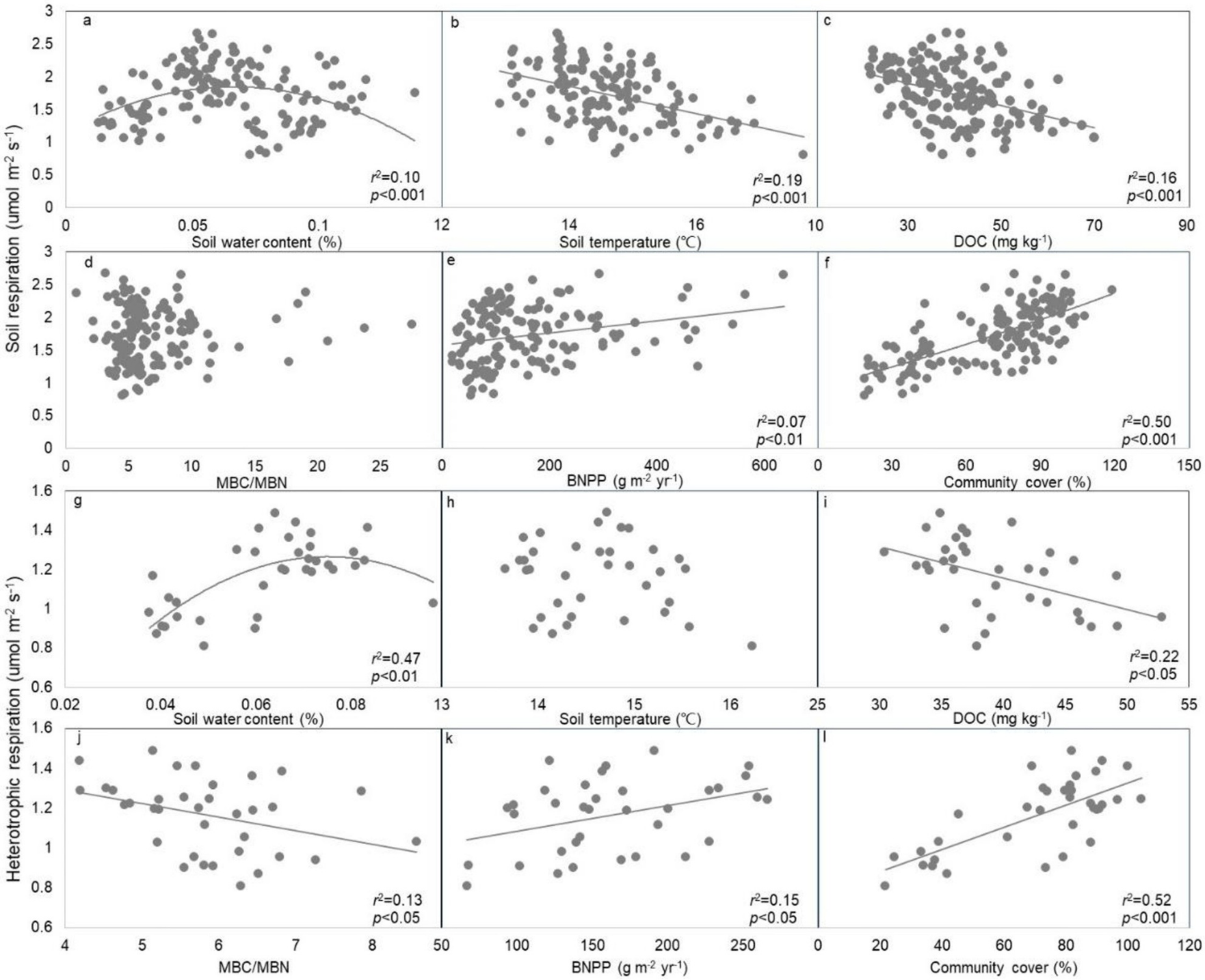

Figure 5. Relationships of soil respiration from 2015 to 2018, and heterotrophic respiration in 2018, with soil water content (SWC, % m^3 m^{-3}), soil temperature (ST,°C), dissolved organic carbon (DOC, mg kg^{-1}), microbial biomass carbon /microbial biomass nitrogen (MBC/MBN), belowground net primary productivity (BNPP), and community cover (%). The points in panels a-f represent annual means from 2015 to 2018, and the points in panels g-l represent means in 2018.

efflux can be attributed to plant community cover. We found precipitation manipulation changed soil water content, leading to a change of plant community cover that is related to canopy photosynthesis, soil organic matter accumulation (Fig. S4), and root exudation (Hartley et al., 2007; Flanagan et al., 2013), and consequently affects SR.

Effect of changing precipitation in different periods on HR

Decreasing precipitation generally reduces HR (Suseela et al., 2012). Consistent with the study, our result shows that DLP reduces HR by decreasing plant community cover. Decreased community cover suppresses canopy photosynthesis. Microbes, that are more dependent on photosynthate and soil substrate availability, are reduced by decreased precipitation (Yan et al., 2011; Flanagan et al., 2013), leading to the decline of HR. Moreover, increasing soil water stress under DLP suppresses HR by decreasing the activity of extracellular enzymes that degrade polymeric organic matter in soils (Suseela et al., 2012). DLP may also limit HR by slowing the diffusion of labile substrates, and thus decrease the rates of microbial uptake of soluble substrates (Stark & Firestone, 1995; Yan et al., 2011). However, HR remains constant under DEP conditions because of little change of SWC and plant community cover in DEP.

Our findings demonstrate that increased precipitation in the early, late, or entire growing season has no significant effect on HR, indicating that HR is insensitive to increased precipitation in this system. The finding is consistent with that microbial biomass is more sensitive to extreme decreases in precipitation than to extreme increases (≥60%). Several potential mechanisms may explain insensitivity of HR to increased precipitation. First, substrate availability constrains an increase in HR. Second, increased precipitation may lead to oxygen limitation (Zhou et al., 2018a), which inhibits microbial growth. Third, low overall soil microbial biomass in this semi-arid grassland may limit responses of HR to precipitation increases (Shamir & Steinberger, 2007; Chen et al., 2015).

Contribution of HR to SR along precipitation gradients

Previous studies reported that microbes concentrated in surface soil are very sensitive to increased precipitation (Collins et al., 2008; Chen et al., 2009; Moyano et al., 2013; Zhang et al., 2019a). However, our study shows that contribution of HR on SR is reduced along precipitation gradients. One possible reason for the difference may be small precipitation events stimulate HR, but heavy precipitation (≥60%) stimulates plant growth more than microbial activities, promoting root respiration (Subke et al., 2011; Yan et al., 2011). This result

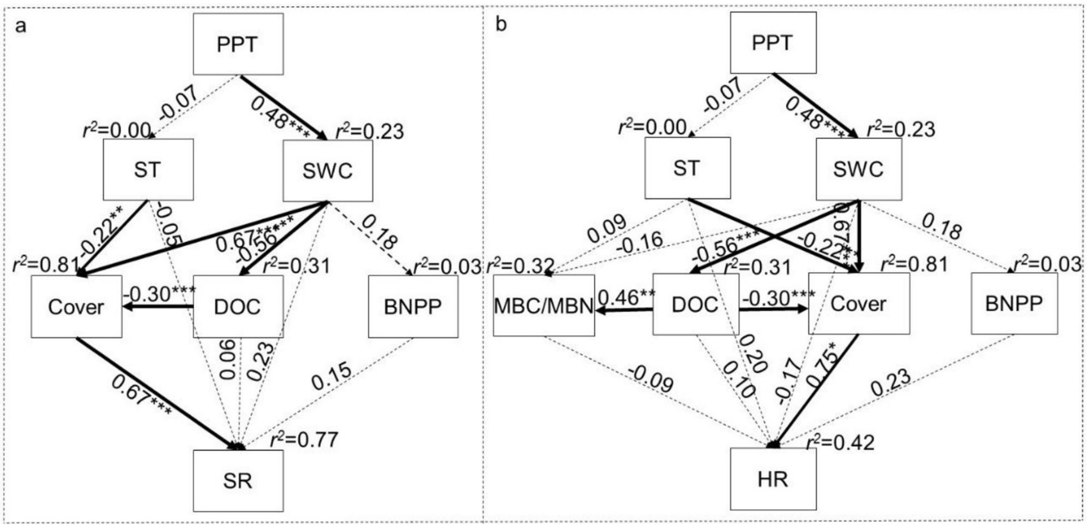

Figure 6. Results of structural equation modeling showing causal relationships among precipitation treatments (PPT) soil water content (SWC, % m^3 m^{-3}), soil temperature (ST,°C), dissolved organic carbon (DOC, mg kg^{-1}), microbial biomass carbon /microbial biomass nitrogen (MBC/MBN), belowground net primary productivity (BNPP), and community cover (%) to soil respiration (SR) and heterotrophic respiration (HR). Solid arrows indicate significant relationships. Dotted arrows indicate non-significant relationships. R^2 values represent the proportion of variance explained for each variable. The numbers above the arrows indicate path coefficients. $^*P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

indicates that increased precipitation in large magnitude will favor input of C into the soil, enhance soil C sequestration, and increase SOC stability.

Asymmetric effect of increased and decreased precipitation in different periods on SR and HR

Our study shows asymmetric responses of soil C processes to both direction and timing of precipitation changes. The results demonstrated a greater sensitivity of SR and HR to decreased precipitation, which is in accordance with several previous studies (Zhou et al., 2008; Suseela et al., 2012; Miao et al., 2017; Zhang et al., 2019a), and also parallels negative asymmetry hypothesis of Knapp et al. (2017). Several mechanisms may explain the observed changes. First, plants and their decomposers that are long-term inhabitants of arid ecosystems tend to be insensitive to increased precipitation due to their inherent life-history traits (Huxman et al., 2004; La Pierre et al., 2016). Second, SR and HR are limited by water in dry conditions but are more likely to be limited by temperatures and/or nutrients in wetter conditions (Evans & Young, 1989; Huxman et al., 2014; Zhou et al., 2018b). Third, increased infiltration in sandy soil in this study resulted in less water use by plants, and may lead to the nonlinear response of SR and HR to increased precipitation (Bai et al., 2008; Zhou et al., 2018a). This result suggests that changes in SR and HR become decoupled from that of soil moisture with increasing water availability (Gill et al., 2002; Porporato et al., 2004; Burkett et al., 2005; Liu et al., 2016).

Moreover, our observations showed a larger decline of both SR and HR in DLP than in DEP, which primarily can be attributed to drought magnitude. A severe drought in the late growing season may cause SR and HR to decline substantially. Moreover, the synchronization of drought and high temperature in the late growing season, both peaking during the period of high plant growth (Bai et al., 2008), will exacerbate effects of drought on SR and HR due to increased cost for growth, maintenance, and nutrient absorption (Craine et al., 1999; Flanagan & Johnson, 2005; Bahn et al., 2009; Xia et al., 2009; Yan et al., 2011). Our study also demonstrated that IEP stimulated SR more than ILP, although the precipitation amount is larger in ILP than in IEP. IEP serves to advance plant phenology and increase soil CO_2 flux. In contrast, ILP may extend peak plant growth, leading to large substrate consumption without new substrate input, and thus limit root and root-associated respiration (Knapp et al., 1998). Moreover, decreasing temperatures in the late growing season are also detrimental to root growth and that may impact SR.

Conclusions

Previous studies have suggested that ecosystem responses to precipitation changes can be nonlinear. However, it is not clear whether the responses of ecosystem to changes in extreme precipitation timing are still non-linear. Our study shows that annual and seasonal patterns in SR and HR are sensitive to changing precipitation in different periods, and the soil carbon dynamic exhibits threshold responses to shifts in extreme precipitation timing. Identifying these nonlinearities and thresholds could be conducive to refine the general double asymmetric model and reduce uncertainties associated with climate change decision-making. This study contributes to a growing body of evidence that more precise predictions of the role of semi-arid grasslands in terrestrial C balance should include the study of how extreme precipitation timing during the growing season regulates soil carbon processes.

Author Contributions

ZY proposed the scientific hypotheses and supervised the project. YW and GF collected data, ZY, GL, and RX performed data analyses, ZY wrote the draft of the manuscript, and GL and HS contributed substantially to revisions.

Declaration of Competing Interest

We declare that this manuscript has not been published or accepted for publication, and is not under consideration for publication, in another journal or book. Its submission for publication has been approved by all relevant institutions. All persons entitled to authorship have been so named. The authors declare no competing financial interests.

Acknowledgments

We thank Tong Zhang, Jiajia Zhang, Xiaoxin Qiao for assistance both in the field and lab. This project was financially supported by National Natural Science Foundation of China (31570429). The authors declare no competing financial interests.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2020.108039.

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