Biogeosciences Discuss., 7, 5829–5858, 2010
www.biogeosciences-discuss.net/7/5829/2010/
doi:10.5194/bgd-7-5829-2010

Biogeosciences
Discussions

Impacts of increasing water and nitrogen availability on ecosystem CO_2 fluxes in a temperate steppe of Northern China

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Received: 29 May 2010 – Accepted: 13 July 2010 – Published: 3 August 2010

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

Changes in precipitation patterns and nitrogen (N) cycling across the globe are likely to affect ecosystem primary productivity and CO_2 exchanges, especially in the arid and semi-arid grasslands because of their co-limitation of water and N supply. To evaluate the effects of water and N availability on ecosystem CO_2 fluxes, we conducted a manipulative field experiment with water and N addition in a temperate steppe of Northern China. The growing-season CO_2 fluxes, including net ecosystem exchange (NEE), gross ecosystem photosynthesis (GEP) and ecosystem respiration (ER) were examined in 2006 and 2007 with remarkably different amount of precipitation. Net carbon uptakes were found in all of treatments over the growing season in both years. However, their magnitude had inter-annual variations which coincided with the seasonal changes of precipitation amount. During these two growing seasons, water and N addition significantly increased NEE, owing to higher stimulation of GEP than ER. Our results suggest that net primary productivity, especially dominant species' biomass, correlated closely with variations in GEP and ER. Soil moisture was the driving environmental factor controlling seasonal and inter-annual variability in GEP and ER subsequently inducing changes in NEE. Moreover, the strengths of both water and N addition effects were greatly depended on the initial water condition in this temperate typical steppe.

1 Introduction

Increasing total precipitation combined with occurrence of extreme rainfall events at the multitude regions has been predicted (IPCC, 2007). Due to anthropogenic activities, global nitrogen (N) cycling has also been significantly altered (Gruber and Galloway, 2008; Schlesinger, 2009). Changes in precipitation and N availability and with associated feedbacks from terrestrial ecosystems are expected to have profound effects on global carbon (C) cycling (Huxman et al., 2004; Harpole et al., 2007; LeBauer and Treseder, 2008). Arid ecosystems are inevitably more sensitive to those changes for their being co-limited by both water and N availability (Kirchner, 1977; Hooper and Johnson, 1999).

Net ecosystem carbon dioxide (CO_2) exchange (NEE), the index of ecosystem functioning relevant to CO_2 uptake depends on two contrasting processes, i.e. gross ecosystem photosynthesis (GEP) and ecosystem respiration (ER) (Valentini et al., 2000). Many studies have been conducted to delineate the responses of ecosystem CO_2 fluxes to precipitation, showing that both GEP (Flanagan et al., 2002; Ma et al., 2007) and ER (Yepez et al., 2007; Wan et al., 2007) increase with increasing precipitation. However, the magnitude of change in GEP may not be equal to that of ER or even proportional to each other under increasing precipitation (Huxman et al., 2004; Chen et al., 2009). As a result, the direction of changes in NEE is not always the same as that of GEP. For example, GEP has been reported, in one study, to increase more than that of ER by increasing precipitation in a stool grassland resulting in positive changes in NEE (Patrick et al., 2007), whereas in another study, the increase in GEP was offset by corresponding increase in ER, resulting in no net NEE changes in an agro-ecosystem (Verma et al., 2005). Additionally, antecedent moisture may also play an important role in modulating these responses (Potts et al., 2006), inducing non-linear responses of ecosystem to changes in water availability (Zhou et al., 2008). Risch and Frank (2007) observed that water additions increased ecosystem CO_2 fluxes at water-limiting sites but had no effects at sites with intermediate soil moisture availability.

Given the N limitation in terrestrial biosphere, plant growth and net primary productivity (NPP) might increase remarkably under N enrichment conditions across the globe (Xia and Wan, 2008). However, there is still no generalized conclusion on the changes in NEE, because not only plant but also soil C contributes to ecosystem C cycling. For instance, only a minor response of NEE to N addition was observed in a 3-yr N addition study in a Finnish peatland (Saarnio et al., 2003), whereas a significant positive effect of N addition on NEE was found in a temperate steppe (Xia et al., 2009). Limited researches on ecosystem-level CO_2 fluxes responses and apparently conflicting results on accumulation of soil C storage under N enriched conditions (Shaver et al., 1998; Mack et al., 2004; Bubier et al., 2007; Pregitzer et al., 2008) blurred our understanding about the general pattern of NEE responses to N enrichment across different ecosystems.

Additionally, changes in plant species composition and community structure may also strongly influence the responses of ecosystem CO_2 fluxes to N enrichment. For example, a recent study in Inner Mongolia steppe found that changes in the coverage of the dominant species could regulate the responses of ecosystem CO_2 fluxes under N addition (Niu et al., 2009). Moreover, increasing water availability can stimulate net N mineralization and improve soil N availability (Burke et al., 1997), resulting in a couple effect of increasing moisture and N availability on ecosystem CO_2 (Harpole et al., 2007; St Clair et al., 2009).

The temperate steppe in Northern China, one of the typical vegetation types in the Eurasian continent, located in arid and semiarid regions, is principally limited by water and N supply (Yuan et al., 2005; Niu et al., 2008). Therefore, it is supposed to be a kind of very sensitive ecosystem to the changes in both water and N availability. Recently, several studies have proven that CO_2 fluxes in this steppe were affected by either water or N availability (Niu et al., 2008; Xia et al., 2009; Chen et al., 2009). However, it is still very difficult to predict the responses of ecosystem-level CO_2 fluxes to future changes in precipitation and N availability, because of insufficient data available in this area (Niu et al., 2009). In this study, we carried out through a field manipulative experiment with water and N addition in a semiarid temperate steppe of Northern China to find possibly different changes of each component of ecosystem CO_2 fluxes (NEE, ER and GEP). Our objectives were (1) to study responses of C assimilation and respiration of this semiarid steppe ecosystem to water and N addition; and (2) to predict C sequestration ability with anthropogenic global change (especially precipitation and N enrichment) in such semiarid steppe. In addition, this study was conducted in two hydrologically contrasting years, which provided us an opportunity to evaluate the effects of precipitation on the responses of ecosystem CO_2 fluxes to water and N addition.

2 Materials and methods

2.1 Site description

The experimental site for this study was located within a semiarid grassland in Duolun County (42°27′ N, 116°41′ E, 1350 m a.s.l.), Inner Mongolia, China. The dominant plant species of this site included *Stipa krylovii*, *Agropyron cristatum*, *Artemisia frigida*, *Potentilla acaulis* and *Cleistogenes squarrosa*. The mean monthly temperature in the study area is range from 19.9 °C in July to −15.9 °C in January with average annual temperature of 3.3 °C. The average annual precipitation from 1952 to 2007 is 382 mm, with 80% fell from June to September. The soils in the study site are classified as chestnut soils (Chinese classification) or Calcic-orthic Aridisol (US soil taxonomy classification system) (Yuan et al., 2005).

2.2 Experimental design and treatments

The experiment used a random block design with five replicate blocks, and each block consisted of four 2×2 m^2 plots, separated by 1-m walkways. Within each block, plots were assigned randomly to one of the following treatments: control (CK), water addition (W), N addition (N), addition of both water and N (NW). Water and N addition treatments were applied during the growing season (from June to September) of 2006 and 2007. In each W treatment plot, 15 mm water was added every two weeks during the whole growing season. The total amount, 120 mm, of added water equaled around 30% of the annual precipitation in this area. In each N treatment plot, 15 $g\,m^{-2}$ urea (equal to 6.96 $g\,N\,m^{-2}$) was added in dry form every month from June to September, and a total of 28 $g\,N\,m^{-2}\,yr^{-1}$ was added to each N treatment plot. The plots with combined addition of water and N treatment received the same amounts of water and N as in the single factor treatment.

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2.3 Measurements of ecosystem gas exchange

In May 2006, a square stainless steel frame (0.5×0.5 m^2 in area and 8 cm in height) was inserted into the soil to a depth of 5 cm in the center of each plot. The stainless steel frame provided a flat base between the soil surface and the CO_2 sampling chamber. During the growing season (June to September), the ecosystem CO_2 exchanges were measured on clear sunny days between 09:00 and 11:00 (local time) once every week in 2006 and twice every week in 2007. The ecosystem fluxes of CO_2 were determined with a transparent chamber (0.5×0.5×0.5 m^3) attached to an infrared gas analyzer (IRGA; LI-840, LI-COR Inc., Lincoln, NE, USA) and an air pump (LI-COR Inc.). During measurements the chamber was sealed to the base surface. Two small fans installed inside the chamber ran continuously to mix the air inside the chamber during measurements. Data were logged to a computer using the LI-840's data acquisition software. Consecutive recordings of CO_2 and H_2O concentration were taken at 1 s intervals during a 120 s period. CO_2 flux rates were determined from the time-courses of the concentrations to calculate net ecosystem exchange (NEE) according to the method of Chen et al. (2009). Following the measurements of NEE, the chamber was ventilated and reseated for immediate measurement of ecosystem respiration (ER). To measure ER, an opaque cloth was placed over the chamber and the CO_2 exchange measurement was repeated in the absence of sunlight. Gross ecosystem photosynthesis (GEP) was calculated as the difference between NEE and ER. Negative or positive NEE values represent net C uptake or release by the ecosystem, respectively. In order to examine responses of ecosystem water use efficiency (WUE) to treatments, we first used the time-courses of the H_2O concentration to calculate evapotraspiration (ET), and then calculated WUE as GEP divided by ET (WUE =GEP/ET).

The temperature and moisture of surface soil layer were concurrently determined while the ecosystem CO_2 fluxes were measured. The soil temperature at the depth of 10 cm was measured by a thermocouple probe (LI-COR 6400-09TC, LI-COR Inc.) and soil moisture content (0–10 cm) was measured with a TDR-200 soil moisture probe

(Spectrum Technologies Inc., Plainfield, IL, USA).

2.4 Measurements of aboveground and belowground net primary productivity

One strip ($1\times0.2\,\text{m}^2$) in each plot was sampled to determine the peak aboveground biomass on 21 August 2006 and 28 August 2007, respectively. Aboveground plants parts from current year were harvested and litter accumulated from past years were sorted out. Plant samples were oven-dried at 65 °C at least for 48 h, and then weighed to determine dry biomass. Total biomass of plant samples was used as an estimate of current-year aboveground net primary productivity (ANPP). For measurement of belowground net primary productivity (BNPP), a soil core (10 cm in diameter) in depth of 40 cm was sampled in each plot on 31 May 2006 and 29 May 2007, respectively, and separated into three samples according to their depths (0–10 cm, 10–20 cm and 20–40 cm). All visible roots were sorted out immediately from each soil sample and then those soil samples were put back to the hole at their original depths. On 24 August 2006 and 23 September 2007, the put-back soil cores (8 cm in diameter) were sampled again at three depths in each plot and all visible roots were collected. The root samples were washed and oven-dried at 65 °C for 48 h, then the roots was weighed and used to calculate BNPP (the growing-in method).

2.5 Measurements of soil organic C content

During the 2007 growing season, two soil cores (10 cm in depth and 3.8 cm in diameter) were collected and mixed completely from each plot every month from June to September. Roots and organic debris were removed by hand and then these samples were sieved through a 2 mm sieve. After being air-dried, samples were used to measure the organic C content using potassium dichromate-vitriol oxidation method (Lavian et al., 2001).

2.6 Statistical analysis

Growing season mean values in this study were averaged by the monthly mean values in 2006 and 2007, respectively. Three-way ANOVAs were used to analyze effects of year, water and N addition and their interactions on soil temperature and moisture, net primary productivity (ANPP and BNPP) and ecosystem CO_2 fluxes (NEE, ER and GEP). Two-way ANOVAs were applied to examine the main effects of water and N addition on measured variables each year, when the effect of year is significant ($P<0.05$). When main effects were found significant ($P<0.05$) while interactive effects insignificant, we only compared control (CK) and water addition (W) plots to test for effects of water addition and compared CK and N addition (N) plots to test effects of N addition. Regression analyses were used to examine the relationships of ecosystem CO_2 fluxes with soil temperature, soil moisture, net primary productivity (ANPP and BNPP) and rainfall in two growing seasons. All statistical analyses were performed with SAS programs (SAS Institute Inc., Cary, NC, USA).

3 Results

3.1 Abiotic and biotic factors

Annual precipitation in 2006 and 2007 was 374 mm and 198 mm, respectively (Fig. 1a). The amount of rainfall received during the growing season (June to September) was 103% and 49% of the long-term average in 2006 (308 mm) and 2007 (150 mm), respectively (Fig. 1b).

In the control plots, the average soil temperature of 2006 was significantly lower than that of 2007, while the average soil moisture was greater in 2006 than in 2007 (Tables 1 and 2). Water and N addition did not significantly affect soil temperature in both years (Tables 1 and 2). In both growing seasons, water addition had significant effects on soil moisture, as compared to the control plots, with a 26% ($P<0.001$) and 28% ($P<0.001$)

increase in 2006 and 2007, respectively. N addition did not show significant effects soil moisture, as compared to the control plots (Tables 1 and 3). There were no significantly interactive effects between water and N addition on soil temperature and moisture in both 2006 and 2007 (Table 3).

Both aboveground and belowground net primary productivity (ANPP and BNPP) were stimulated by water addition over the two growing season (42%, $P<0.001$; 36%, $P<0.1$), with a significant increase in ANPP (63%, $P<0.01$) in 2007 and BNPP (44%, $P<0.001$) in 2006 (Tables 1 and 3). N addition enhanced ANPP (49%, $P<0.001$) and BNPP (44%, $P<0.05$) over the two growing seasons, which could due primarily to the stimulation on ANPP (68%, $P<0.001$) and BNPP (67%, $P<0.05$) in 2006 as there were no significant effects in 2007. Besides, no interactive effects were found between water and N addition in both years (Table 3).

Soil organic carbon content (SOC) was significantly reduced by water addition (8%, $P<0.05$) but marginally stimulated by N addition (2%, $P<0.1$) in 2007 (Table 1). There were no significantly interactive effects between water and N addition on SOC ($P>0.1$, Table 1).

3.2 Seasonal and inter-annual variations of ecosystem CO_2 fluxes under water and N addition

Similar seasonal patterns of ecosystem CO_2 fluxes (NEE, ER and GEP) were found in both years in that all the maximum values of NEE, ER and GEP during the peak time of plant growth (July and August) (Fig. 2). The rates of ecosystem CO_2 fluxes were significantly lower in 2007 than those in 2006 (Tables 1 and 2, $P<0.001$), leading to lower growing season means (−1.27, 3.21 and 4.53 $\mu mol\, m^{-2}\, s^{-1}$) in 2007 than those (−3.95, 5.17, 9.07 $\mu mol\, m^{-2}\, s^{-1}$) in 2006 in the control plots (Table 1).

Both water and N addition significantly enhanced the rates of NEE (42%, $P<0.001$; 30%, $P<0.001$), ER (34%, $P<0.001$; 20%, $P<0.01$) and GEP (38%, $P<0.001$; 24%, $P<0.001$) over the two growing seasons (Table 1). Significantly interactive effects between year and treatment (W or N) showed that effects of water and N addition on ecosystem CO_2 fluxes had distinct year-to-year variations (Table 2). The stimulations of water addition on NEE, ER and GEP were significantly greater in 2007 (138%, $P<0.001$; 71%, $P<0.001$ and 90%, $P<0.001$) than those in 2006 (12%, $P<0.05$; 11%, $P<0.05$ and 11%, $P<0.01$) (Tables 1 and 3). However, N addition had a greater effects on NEE, ER and GEP in 2006 (30%, $P<0.001$; 29%, $P<0.001$ and 29%, $P<0.001$) than that in 2007 (31%, $P>0.05$; 4%, $P>0.05$ and 13%, $P<0.05$) (Tables 1 and 3).

3.3 Control factors of ecosystem CO_2 fluxes

Regression analyses, with NEE, ER and GEP as the dependent variables and ANPP, BNPP as the independent variables, respectively, showed that ANPP alone explained 65% and 71% variations of ER and GEP in 2006, respectively, while explained 82% and 80% when combined with BNPP (Fig. 3a,b,c). In 2007, 46% and 61% of the changes in ER and GEP could be explained by ANPP, respectively. No significant relationships existed between ER and BNPP or GEP and BNPP in 2007 (Fig. 3e,f).

Ecosystem CO_2 fluxes increased logarithmically with soil moisture in both years ($y=a\ln(x)+b$; Fig. 4). The slopes of equations (a values) can be considered as an index of sensitivity of CO_2 fluxes to soil moisture (θ_s), and GEP showed greater moisture sensitivity than that of ER in both years ($P<0.05$; Table 4). N addition significantly increased moisture sensitivity of GEP and ER in 2006, while showed little effects in 2007 (Table 4). Exponential relationships between ecosystem CO_2 fluxes and soil temperature were found in 2006 but not in 2007 (Fig. 5). In 2006, temperature sensitivity (Q_{10}) of ER was greater than that of GEP ($P=0.06$) in the control plots. Besides, N addition significantly increased Q_{10} of GEP and ER (23%, $P=0.001$ and 15%, $P=0.02$). No interactive effects among water and N addition were found (Table 4).

Ecosystem CO_2 fluxes exhibited quadratic relationships with the growing season precipitation (Fig. 6). NEE, ER and GEP increased with precipitation before rainfall reached 460, 390 and 410 mm, respectively, and then declined with increasing precipitation in the non-N addition plots (Fig. 6b). However, NEE, ER and GEP in the N addition plots were peaked at 530, 420 and 450 mm rainfall amount, respectively

(Fig. 6c).

4 Discussion

4.1 Effects of water addition on ecosystem CO_2 fluxes

Water addition significantly increased NEE in both years, owing to greater stimulation on GEP than on ER. Similar results were also found by previous studies in the same area (Niu et al., 2008; Chen et al., 2009) and other temperate ecosystems (Patrick et al., 2007; Risch and Frank, 2010). Given the importance of plant growth in photosynthetic and respiratory processes, more aboveground biomass means more leaf area for photosynthesis (Zhang et al., 2007), while greater plant biomass also means greater plant maintenance and growth respiration (Flanagan et al., 2005), and more substrate supply for microbial respiration (Li et al., 2008a). In this study, both ANPP (24%, 44%) and BNPP (63%, 20%) were increased by water addition in both years. Therefore, our results suggest that water addition can increase GEP and ER through stimulation on plant growth in this semiarid steppe ecosystem, consistent with the results from other grasslands (Harpole et al., 2007).

Magnitudes of water-induced effects on ecosystem CO_2 fluxes in 2007 were obviously greater than those of 2006, although the same amount of water was added in both years. It has been proposed that antecedent water condition may mediate the influences of increasing precipitation on plant photosynthesis and respiration (Reynold et al., 2004; Potts et al., 2006; Cable et al., 2008). For example, Potts et al. (2006) reported that a 50% reduction in previous-year monsoon-season drought treatment enhanced ecosystem C accumulation, comparing to a 50% increase treatment, which was attributable to greater reductions in ER compensate for decreases in NEE. However, in our ecosystem, a drier natural water condition in 2007 than in 2006 resulted in a greater stimulation on GEP and ER under water addition in 2007. This response could be due to enhanced microbial activity (Yan et al., 2010) and physical displacement of CO_2 from soil pore spaces following water infiltration into dry soil, which have been observed to occur upon rewetting of dry soil (Kieft et al., 1987; Yang, 1998). Additionally, greater stimulation on WUE (Table 1) by water addition might contribute to larger increase in GEP and ER in 2007 than that in 2006, which has been also reported in the previous studies (Baldocchi, 1997; Krishnan et al., 2006). Li et al. (2008a) suggested that it may be due to a large increase in soil moisture after a substantial rain event could not efficiently used for taking up C but evaporated quickly to the atmosphere in this steppe, while a large increase in soil moisture following a drier condition might be opposite. Thus, a drier natural water condition in 2007 than in 2006 resulted in a greater response of NEE to water addition in 2007, indicating that water availability especially antecedent moisture, is critically important in regulating responses of GEP and ER, and correspondingly NEE also.

4.2 Effects of N addition on ecosystem CO_2 fluxes

With a tight link between greater net primary productivity to increased photosynthesis (Pregitzer et al., 2008) and respiration (Xu and Wan, 2008) as well under N fertilization, N addition can stimulate ER and GEP through enhancing plant growth (Johnson et al., 2000; Sullivan et al., 2008). In this study, N addition stimulated NEE in both years because of greater increase in GEP than in ER. Substantial increases in ANPP (68%) and BNPP (67%) resulted in stimulations to GEP and ER under N addition in relatively wet 2006. However, N addition had no significant effects on ANPP and BNPP in dry 2007, but still showed positive effects on NEE and GEP. Harte et al. (1995) implied that community structure could strongly influence grassland responses to climatic change, especially responses of ecosystem C cycling. A recent study in a similar steppe by Xia et al. (2009) also emphasized the importance of functional groups in regulating the responses of ecosystem CO_2 fluxes to N addition. After separating ANPP into grasses and forbs biomass, we found that both GEP (r^2=0.26, $P<0.05$ and r^2=0.30, $P<0.05$) and ER (r^2=0.21, $P<0.05$ and r^2=0.29, $P<0.05$) are positively correlated with grasses biomass, in 2006 and 2007, while not with forbs biomass, even forbs biomass was substantially increased under N addition in 2006 (+30%, $P<0.05$). Therefore, the positive responses of NEE could account for the increasing grasses biomass under N addition in both years. Our observations indicate that plant growth, especially those of functional groups is important in modulating the responses of ecosystem CO_2 fluxes to N addition.

Moreover, N addition significantly increased chlorophyll concentration of dominant plant species in our experiment (data not shown), which might be another reason for increase in NEE with no variations in ANPP and BNPP in 2007. Hunter and Visser (1989) and Keller et al. (2001) have reported that increasing chlorophyll concentration can lead to higher photosynthetic performance under N addition indicating positive relationships between photosynthesis and leaf chlorophyll content. Our observation of leaf-level gas-exchanges in 2007 also showed that the maximum photosynthetic rate of the dominant species, *Stipa krylovii*, was significantly increased by N addition, which was in agreement with results of two other studies in the same area (Wan et al., 2009; Niu et al., 2009). These results suggest that enhancement of leaf-level photosynthesis under N addition may increase ecosystem-level C assimilation rate (Cheng et al., 2009), even without significant changes in the vegetation biomass and increase in soil C storage (Table 1).

4.3 Potential carbon sequestration with increasing precipitation in the future

IPCC (2007) predicted that precipitation would increase in the future, especially in arid and semiarid ecosystems. Precipitation is a dominant driving force for ecosystem CO_2 fluxes in semiarid ecosystems (Flanagan et al., 2002; Aires et al., 2008; Niu et al., 2008), but it is still not clear that how carbon assimilation and respiration will respond to possible increase of precipitation in the future (Zhou et al., 2008; Shen et al., 2009). Our results showed that the differential responses of GEP and ER to increasing precipitation resulted in significant enhancements of NEE when the growing season precipitation was above precipitation amount of 2007 (150 mm), which was the lowest record of precipitation amount from 1952 to 2007 (Fig. 6a and Table 1). This result indicates that it has been favorable for net ecosystem C sequestration in most growing seasons of nearly 50 yr, also confirmed by other studies in this region (Hao et al., 2008; Niu et al., 2009). However, including precipitation amount, changes in the seasonal distribution of precipitation, size and frequency of rain events may also greatly impact ecosystem CO_2 fluxes, inducing fluctuation of ecosystems between net C sinks and sources (Emmerich and Verdugo, 2007). Therefore, Inner Mongolia steppe might shift back and forth between carbon source and sink during past 50 yr, although the precipitation amount in most of these years were advantageous for carbon sequestration (Zhang et al., 2009). Such situation may also occur in other ecosystems as reported in previous studies. For example, Kwon et al. (2008) found that a dry spring in 2004 caused a net C source, while a wet spring and similar summer condition caused a net C sink in 2005 in a sagebrush-steppe ecosystem. Besides, a greater sensitivity to increasing precipitation and a higher precipitation threshold under N addition suggests that N favor C uptake under increasing precipitation in this region (Table 4 and Fig. 6c). Thus, our results indicate that the temperate steppe should be a potential C sink in the growing seasons in the last 50 yr, and an enhancement of a CO_2 uptake should be expected for future because of the predicting increasing precipitation and N enrichment in this region.

5 Conclusions

Stronger stimulations of water and N additions to GEP than to ER induced significant increases in net CO_2 assimilation (NEE), but with large inter-annual variations in the magnitudes of these enhancements. The decreasing magnitude of water-induced effects on NEE with increasing precipitation demonstrated that responses of CO_2 fluxes relevant processes to water addition depended significantly on natural water condition. The increasing effects of N addition on GEP and ER with increasing precipitation clearly demonstrated that the predominant role of water availability and the secondary role of nitrogen in regulating ecosystem CO_2 fluxes, especially in dry year in this temperate steppe, Northern China. Regression results of ecosystem CO_2 fluxes with growing season rainfall indicate that the contribution of this temperate steppe to C uptake will be largely magnified in the future with possible increases in precipitation and N enrichment.

Acknowledgements. We thank Wenli Zhang, Haixia Miao and Ping Zhang for their helps on setting up the field facilities and field measurements. This study was supported by the National Basic Research Program of China (973 program) (2010CB833501), the National Natural Science Foundation of China (30800141), and the Innovative Research Group Project of National Natural Science Foundation of China (30821062).

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Table 1. Growing season means of soil moisture (θ_v, %) and temperature (T_{soil}, °C), net primary productivity (ANPP and BNPP, $\mathrm{g\,m^{-2}}$), ecosystem CO_2 fluxes (NEE, ER and GEP, $\mathrm{\mu mol\,m^{-2}\,s^{-1}}$), ecosystem water use efficiency (WUE, $\mathrm{\mu mol\,CO_2\,mmol^{-1}\,H_2O}$) and soil organic C content (SOC, $\mathrm{g\,kg^{-1}}$) under different treatments in 2006 and 2007. Values represent the Means±SE (n=5). CK: control plots; W: water addition; N: N addition; NW: addition of both water and N. ND indicates no determined.

		θ_v	T_{soil}	ANPP	BNPP	NEE	ER	GEP	WUE	SOC
2006	CK	10.46±0.12	19.0±0.4	157.6±15.8	457.3±35.9	−3.95±0.18	5.17±0.23	9.07±0.33	5.60±0.22	ND
	W	13.18±0.17	18.6±0.4	195.6±16.5	658.3±46.0	−4.40±0.13	5.76±0.28	10.09±0.30	7.13±0.83	ND
	N	10.46±0.25	18.7±0.4	264.1±17.6	734.8±44.4	−5.14±0.18	6.68±0.21	11.69±0.16	7.63±0.41	ND
	NW	12.92±0.18	18.1±0.4	327.3±33.0	727.6±120.0	−5.59±0.26	7.03±0.19	12.49±0.18	8.36±0.29	ND
2007	CK	8.31±0.09	22.1±0.4	128.2±11.8	342.8±54.6	−1.27±0.10	3.21±0.16	4.53±0.15	3.32±0.25	17.2±0.5
	W	10.67±0.14	21.6±0.3	209.3±18.2	412.8±26.7	−3.02±0.22	5.47±0.27	8.62±0.29	4.88±0.44	15.9±0.3
	N	8.91±0.24	22.0±0.4	162.5±15.5	343.2±21.0	−1.66±0.17	3.34±0.22	5.11±0.27	3.63±0.38	17.6±0.3
	NW	11.24±0.20	21.1±0.4	267.0±30.6	431.8±35.2	−3.26±0.06	5.67±0.34	9.09±0.32	5.17±0.33	16.9±0.6

Table 2. Results (P-values) of three-way ANOVA on the effects of year, water addition (W), N addition (N) and their interactions on soil temperature (T_{soil}, °C), soil moisture (θ_v, %), net primary productivity (ANPP and BNPP, $\mathrm{g\,m^{-2}}$) and ecosystem CO_2 fluxes (NEE, ER and GEP; $\mathrm{\mu mol\,m^{-2}\,s^{-1}}$).

	T_{soil}	θ_v	ANPP	BNPP	NEE	ER	GEP
Year	<0.001	<0.001	0.002	<0.001	<0.001	<0.001	<0.001
W	0.036	<0.001	<0.001	0.094	<0.001	<0.001	<0.001
N	0.208	0.123	<0.001	0.023	<0.001	<0.001	<0.001
W×N	0.525	0.840	0.711	0.133	0.657	0.806	0.750
Year×W	0.722	0.129	0.339	0.402	<0.001	<0.001	<0.001
Year×N	0.839	0.001	0.007	0.034	<0.001	0.001	0.001
Year×W×N	0.937	0.916	0.639	0.229	0.871	0.659	0.781

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Table 3. Results (*P*-values) of two-way ANOVA on the effects of water addition (W), N addition (N) and their interactions on soil moisture (θ_v, %), temperature (T_{soil}, °C), net primary productivity (ANPP and BNPP, g m^{-2}) and ecosystem CO_2 fluxes (NEE, ER and GEP; $\mu\text{mol m}^{-2}\,\text{s}^{-1}$) in 2006 and 2007.

		θ_v	T_{soil}	ANPP	BNPP	NEE	ER	GEP
2006	W	<0.001	0.227	0.035	0.187	0.032	0.060	0.002
	N	0.200	0.322	<0.001	0.025	<0.001	<0.001	<0.001
	W×N	0.839	0.704	0.572	0.158	0.980	0.613	0.661
2007	W	<0.001	0.081	0.001	0.239	<0.001	<0.001	<0.001
	N	0.001	0.441	0.126	0.821	0.054	0.528	0.067
	W×N	0.942	0.606	0.942	0.665	0.631	0.895	0.847

Table 4. Sensitivity of ER and GEP to soil temperature (Q_{10}) and moisture (θ_s) under different treatments in 2006 and 2007. Values represent the mean±SE. CK: control plots; N: N addition; W: water addition; NW: addition of both water and N. Different letter means significant difference among treatments at $P<0.05$.

		Q_{10}		θ_s	
		2006 (n=11)	2007 (n=17)	2006 (n=11)	2007 (n=17)
ER	CK	1.86 ± 0.10^{a}	0.96 (ns)	3.28 ± 0.44^{c}	1.77 ± 0.10^{a}
	W	1.87 ± 0.04^{a}	0.75 (ns)	3.60 ± 0.28^{bc}	1.83 ± 0.17^{a}
	N	2.13 ± 0.16^{a}	0.65 (ns)	4.44 ± 0.28^{ab}	1.79 ± 0.26^{a}
	NW	2.11 ± 0.05^{a}	1.11 (ns)	4.85 ± 0.04^{a}	1.90 ± 0.18^{a}
GEP	CK	1.65 ± 0.08^{c}	0.73 (ns)	5.81 ± 0.61^{b}	3.21 ± 0.46^{a}
	W	1.69 ± 0.07^{bc}	0.88 (ns)	6.03 ± 0.29^{b}	3.24 ± 0.27^{a}
	N	2.04 ± 0.11^{a}	1.03 (ns)	6.66 ± 0.27^{b}	3.48 ± 0.29^{a}
	NW	1.90 ± 0.10^{ab}	0.82 (ns)	7.78 ± 0.14^{a}	3.10 ± 0.17^{a}

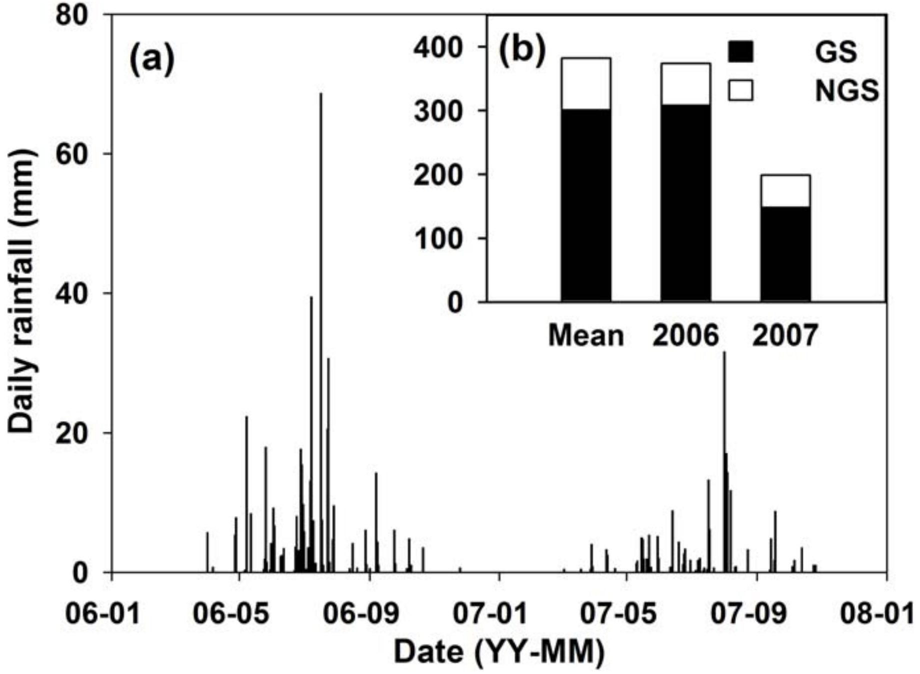

Fig. 1. Daily precipitation in 2006 and 2007 **(a)**. Inset figure **(b)** shows long-term mean (1952–2007), 2006, and 2007 total growing season rainfall (June–September, GS, close bar) and total non-growing season rainfall (NGS, open bar).

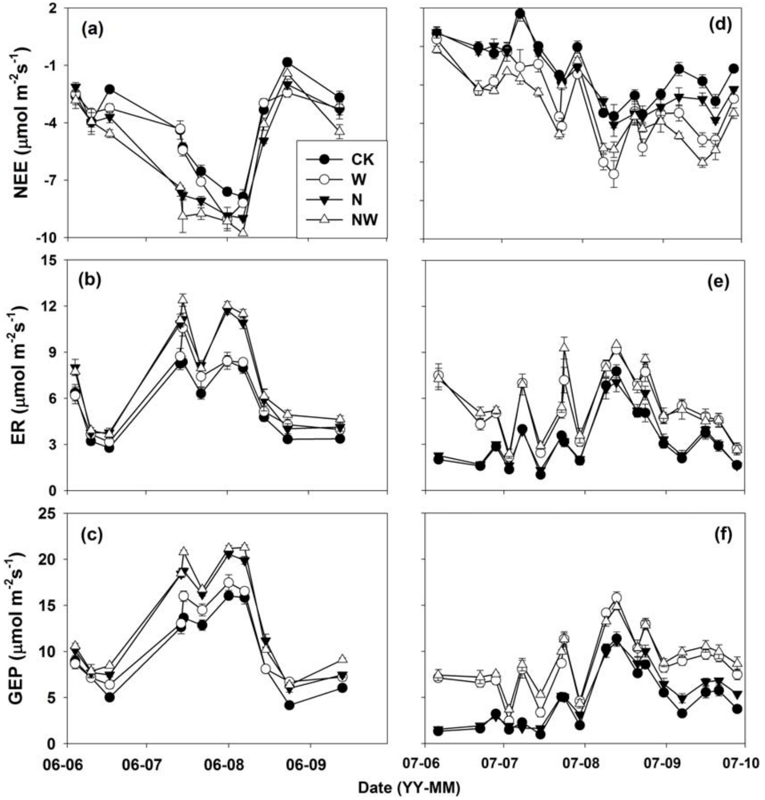

Fig. 2. Seasonal variations in net ecosystem CO_2 exchange (NEE), ecosystem respiration (ER) and gross ecosystem photosynthesis (GEP) in 2006 (left panels) and 2007 (right panels). CK: control plots (solid circle); W: water addition (open circle); N: N addition (solid triangle); NW: addition of both water and N (open triangle).

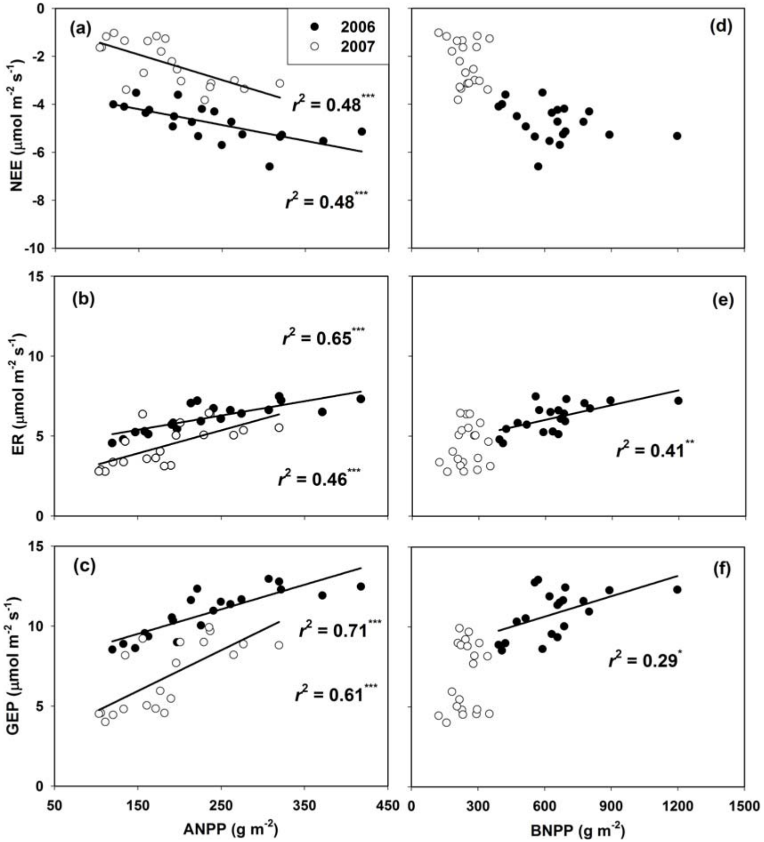

Fig. 3. Linear correlations of growing season mean net ecosystem CO_2 exchange (NEE; **a**,**d**), ecosystem respiration (ER; **b**,**e**) and gross ecosystem photosynthesis (GEP; **c**,**f**) with aboveground and belowground net primary productivity (ANPP and BNPP) across different plots in 2006 (solid circle) and 2007 (open circle) with the correlation coefficient and its significance.

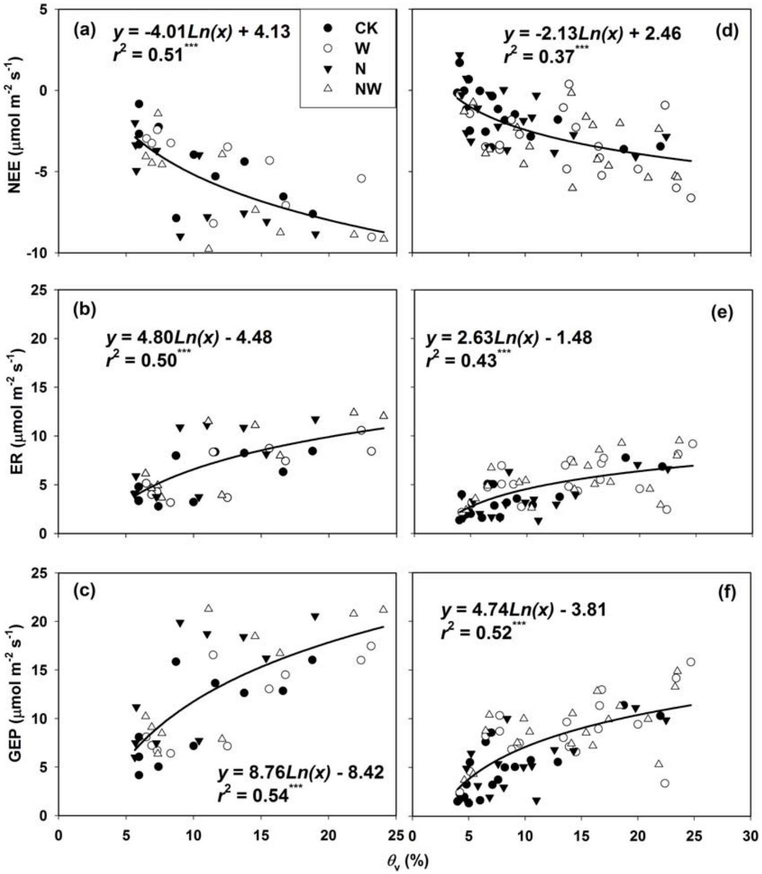

Fig. 4. Temporal dependence of net ecosystem CO_2 exchange (NEE), ecosystem respiration (ER) and gross ecosystem photosynthesis (GEP) to soil moisture (θ_v, %) across different plots in 2006 (left panels) and 2007 (right panels). See Fig. 2 for the abbreviations of treatments.

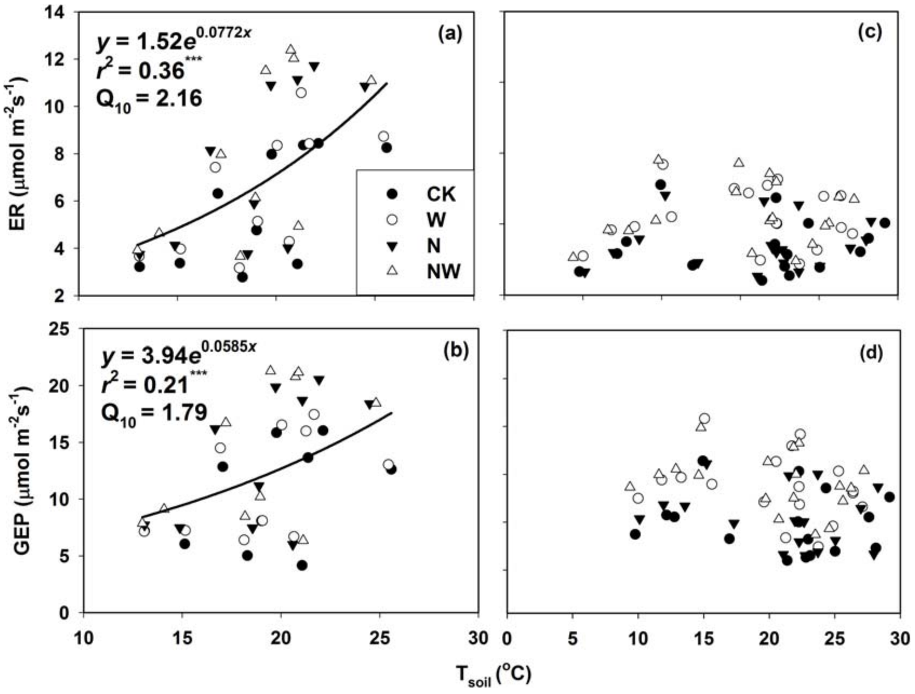

Fig. 5. Temporal dependence of net ecosystem CO_2 exchange (NEE), ecosystem respiration (ER) and gross ecosystem photosynthesis (GEP) to soil temperature (T_{soil}, °C) across different plots in 2006 (left panels) and 2007 (right panels). See Fig. 2 for the abbreviations of treatments.

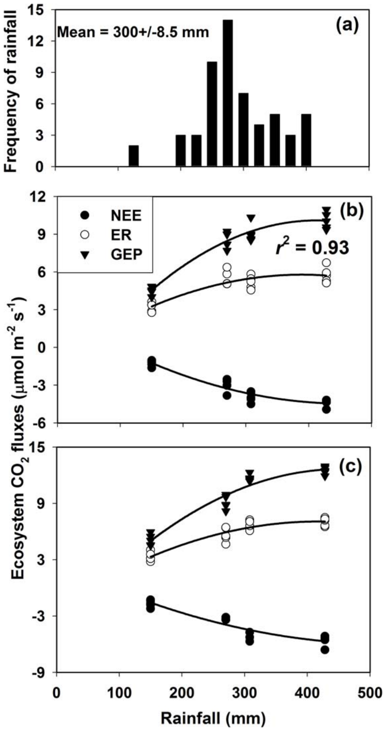

Fig. 6. Frequency of rainfall in growing season from 1952 to 2007 **(a)**. Responses of net ecosystem CO_2 exchange (NEE, solid line with solid circle) ecosystem respiration (ER, dashed line with open circle), and gross ecosystem photosynthesis (GEP, dotted line with solid triangle) to rainfall in CK plots **(b)**, the regressive equations for NEE, ER and GEP were $y=3.407\text{E}-005x^2-0.031x+2.682$, $y=-4.438\text{E}-005x^2+0.035x-0.927$ and $y=-8.086\text{E}-005x^2+0.067x-3.612$, respectively; and in N supplemented plots **(c)**, the regressive equations for NEE, ER and GEP were $y=3.039\text{E}-005x^2-0.032x+2.607$, $y=-5.239\text{E}-005x^2+0.044x-2.090$ and $y=-8.404\text{E}-005x^2+0.076x-4.494$, respectively.

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