

Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe

Shuli Niu¹, Mingyu Wu^{1,2}, Yi Han^{1,2}, Jianyang Xia^{1,2}, Linghao Li¹ and Shiqiang Wan¹

¹Key Laboratory of Vegetation and Environmental Change, Institute of Botany, the Chinese Academy of Sciences, Beijing 100093, China; ²Graduate University of the Chinese Academy of Sciences, Yuquanlu, Beijing 100049, China

Summary

Author for correspondence:

Shiqiang Wan

Tel: +86 10 6283 6512

Fax: +86 10 6259 9059

Email: swan@ibcas.ac.cn

Received: 6 June 2007

Accepted: 28 July 2007

- Global warming and a changing precipitation regime could have a profound impact on ecosystem carbon fluxes, especially in arid and semiarid grasslands where water is limited. A field experiment manipulating temperature and precipitation has been conducted in a temperate steppe in northern China since 2005.
- A paired, nested experimental design was used, with increased precipitation as the primary factor and warming simulated by infrared radiators as the secondary factor.
- The results for the first 2 yr showed that gross ecosystem productivity (GEP) was higher than ecosystem respiration, leading to net C sink (measured by net ecosystem CO₂ exchange, NEE) over the growing season in the study site. The interannual variation of NEE resulted from the difference in mean annual precipitation. Experimental warming reduced GEP and NEE, whereas increased precipitation stimulated ecosystem C and water fluxes in both years. Increased precipitation also alleviated the negative effect of experimental warming on NEE.
- The results demonstrate that water availability plays a dominant role in regulating ecosystem C and water fluxes and their responses to climatic change in the temperate steppe of northern China.

Key words: carbon, evapotranspiration, global warming, grassland, precipitation.

New Phytologist (2008) **177**: 209–219

© The Authors (2007). Journal compilation © *New Phytologist* (2007)

doi: 10.1111/j.1469-8137.2007.02237.x

Introduction

Global warming resulting from rising atmospheric concentrations of CO₂ and other greenhouse gases has increased global mean temperature by 0.76°C since 1850, and will continue to increase it up to 1.8–4.0°C by the end of the 21st century (IPCC, 2007). It is expected that there will be concurrent shifts in global and regional precipitation regimes, with extreme rainfall events becoming more frequent (Dore, 2005; Groisman *et al.*, 2005). Given the limitation of temperature and soil water availability in plant growth and net primary productivity

(NPP), changes in the Earth's surface temperature and precipitation regime could profoundly impact terrestrial carbon cycling and sequestration, with consequent feedbacks to global climatic change.

Global warming has well been documented to stimulate both ecosystem C uptake and release across various terrestrial biomes (Rustad *et al.*, 2001; Melillo *et al.*, 2002; Shaw *et al.*, 2002; Peñuelas *et al.*, 2004; Welker *et al.*, 2004; Wan *et al.*, 2005). It is assumed that terrestrial ecosystems may act as a net C source under global warming scenarios because of the higher temperature sensitivity of ecosystem C release (auto- and

heterotrophic respiration) than C uptake (plant photosynthesis, plant growth and NPP) (Oechel *et al.*, 1993; Kirschbaum, 1995; Illeris *et al.*, 2004). However, this assumption has been widely debated, partly because of the ecosystem-specific responses and intra- and interannual variability of the responses (Smith & Shugart, 1993; Peñuelas *et al.*, 2004; Corradi *et al.*, 2005). In arid and semiarid regions, changes in precipitation may have an even greater effect on ecosystem C fluxes than the singular effect of rising CO₂ or temperature (Weltzin *et al.*, 2003; Potts *et al.*, 2006) because water availability dominates impacts on plant growth and net ecosystem productivity (Fang *et al.*, 2001; Knapp *et al.*, 2002; Weltzin *et al.*, 2003). Elevated temperature could stimulate evaporation and plant transpiration, leading to increased water loss from soil (Harte *et al.*, 1995; Wan *et al.*, 2002). Unless there is increased soil wetting, lower soil water availability associated with global warming will exacerbate water limitations in arid and semi-arid ecosystems, counteracting any potential direct positive temperature effects on plant growth and NPP.

Located in arid and semiarid regions, the temperate steppe in northern China represents one of the typical vegetation types in the Eurasian continent and is predicted to be sensitive to climatic change (Christensen *et al.*, 2004). Significant changes in both temperature and precipitation have been reported in this area (Gong *et al.*, 2004; IPCC, 2007). Model predications by Gao *et al.* (1997) and Piao *et al.* (2003) have shown that ecosystem productivity of the temperate steppe in northern China is sensitive to the driving forces of global change. However, direct experimental evidence on the response of ecosystem C cycling to climatic change in this area is still lacking.

A field experiment manipulating temperature and precipitation was conducted, beginning in April 2005, to examine the potential influence of climatic change on a semiarid temperate steppe in northern China. Given the water limitation in this area and the possible increase in evapotranspiration under global warming, we hypothesized that elevated temperature could negatively affect ecosystem C exchange, and that increasing precipitation/soil water availability could ameliorate the negative impacts of global warming. The specific objectives of this study were to evaluate how global warming influences ecosystem C and water fluxes and whether the impacts vary with intra- and interannual fluctuations of precipitation; and the extent to which increased precipitation stimulates net C exchange and ameliorates the negative impacts of global warming.

Materials and Methods

Study site

This study was carried out in Duolun county (N42°02', E116°17', 1324 m asl), a semiarid area located in Inner Mongolia, China. Mean annual temperature is 2.1°C with monthly mean temperatures of 18.9°C in July and -17.5°C

in January. Mean annual precipitation is 385.5 mm with 80% concentrated from June to September. Soil is chestnut soil (Chinese classification), Calcis-orthic Aridisol in the US Soil Taxonomy classification, with 62.75 ± 0.04% sand, 20.30 ± 0.01% silt and 16.95 ± 0.01% clay, respectively. Mean soil bulk density is 1.31 g cm⁻³ and pH is 6.84 ± 0.07. The temperate steppe is dominated by *Stipa krylovii*, *Artemisia frigida*, *Potentilla acaulis*, *Cleistogenes squarrosa*, *Allium bidentatum* and *Agropyron cristatum*, all perennial herbs. The temperate steppe at our experimental site has relatively low primary productivity (approx. 100–200 g m⁻² yr⁻¹), with leaf-area index ranging from 0 in early spring and late autumn to nearly 1 in the mid-growing season (Zhang, 2007).

Experimental design

The experiment used a paired, nested design with precipitation as the primary factor and warming as the secondary factor. There were three pairs of 10 × 15-m plots; one plot in each pair was assigned as the increased precipitation treatment and the other as the control. At each precipitation plot, six sprinklers were arranged evenly into two rows with a distance of 5 m between any two sprinklers. Each sprinkler covered a circular area with a diameter of 3 m, so the six sprinklers covered the 10 × 15-m plot. In July and August, 15 mm of water was added weekly to the increased precipitation plots. Therefore a total precipitation amount of 120 mm (approx. 30% of mean annual precipitation in the study site) was supplied each year (8 wk by 15 mm wk⁻¹).

Within each 10 × 15-m plot, four 3 × 4-m subplots were treated as the warmed and control subplots with two replicates. The subplots were randomly assigned to the temperature treatments. The warmed subplots have been heated continuously since 28 April 2005 using 165 × 15-cm MSR-2420 infrared radiators (Kalglo Electronics, Bethlehem, PA, USA) suspended 2.5 m above the ground. The effects of infrared radiators on soil temperature were spatially uniform within the warmed plots (Wan *et al.*, 2002). In the unwarmed control subplot, one 'dummy' heater with the same shape and size as the infrared radiator was suspended 2.5 m high to simulate the shading effects of the heater. Thus there were six replicates for each treatment (control, warming, increased precipitation, warming plus increased precipitation).

Measuring variables

Soil temperature and moisture Soil temperature at the depth of 10 cm was recorded with a CR1000 datalogger (Campbell Scientific, Logan, UT, USA) at 1-h intervals from 4 June 2005. Soil moisture content (0–10 cm) was measured using a portable soil moisture device (Diviner 2000, Sentek Pty Ltd, Balmain, Australia). Volumetric soil water content and ecosystem gas exchange were both measured once or twice a month over the growing season of 2005 and 2006.

Measurements of ecosystem gas exchange In April 2005, two square aluminium frames (0.5×0.5 m) were inserted into the soil to a depth of approx. 3 cm at two opposite corners in each subplot. The distance between the frames and the subplot edge was 0.3 m. Care was taken to minimize soil disturbance during installation. The aluminum frames provided a flat base between the soil surface and the CO_2 sampling chamber.

Ecosystem gas exchange (CO_2 and water fluxes) was measured with a transparent chamber ($0.5 \times 0.5 \times 0.5$ m) attached to an infrared gas analyser (IRGA; LI-6400, Li-Cor, Lincoln, NE, USA) on one of the two frames in each subplot. During measurements the chamber was sealed with the base surface. Two small fans ran continuously to mix the air inside the chamber during measurements. Nine consecutive recordings of CO_2 and water vapour concentration were taken on each base at 10-s intervals during a 90-s period. CO_2 and H_2O flux rates were determined from the time-courses of the concentrations to calculate net ecosystem exchange (NEE) and evapotranspiration (ET). The method was similar to that reported by Steduto *et al.* (2002). Following the measurements of NEE, the chamber was vented, replaced on the base, and covered with an opaque cloth. After the CO_2 concentration in the chamber was steadily increased (usually 0.5 min after the chamber was covered), the CO_2 exchange measurements were repeated. Because the second set of measurements eliminated light (and hence photosynthesis), the values obtained represented ecosystem respiration (ER). Gross ecosystem productivity (GEP) was then calculated as the difference between NEE and ER. Ecosystem water-use efficiency (WUE) was calculated as NEE/ET . Positive and negative NEE values represent net C uptake by, and release from, the ecosystem, respectively.

Seasonal gas exchange was usually measured once or twice a month at the middle of the two precipitation treatment events. Diurnal patterns of gas exchange were measured at a 3-h interval on 29 July 2005 and 13 July 2006.

Leaf gas-exchange measurement An open gas-exchange system (LI-6400; Li-Cor) with a 6-cm² clamp-on leaf cuvette was used to measure the leaf photosynthesis and transpiration

rate of the dominant plant, *A. cristatum*. At each subplot, one expanded leaf of one individual in *A. cristatum* was selected for measurement on 31 August 2005. Leaf gas exchange was measured between 09:00 and 11:00 h (local time) in the morning. Leaves were illuminated at $1500 \text{ mol m}^{-2} \text{ s}^{-1}$ using the LED light system. The maximum photosynthetic rate (P_{max}), transpiration rate (E), stomatal conductance (g_s), and vapour pressure deficit (VPD) were recorded.

Statistical analyses Repeated-measures ANOVA was used to examine warming and precipitation effects on soil microclimate, ecosystem C and water fluxes over the growing season in 2005 and 2006. Between-subject effects were evaluated as warming or precipitation treatment; within-subject effects were time-of-season. One-way ANOVA was used to examine the statistical difference in seasonal averages for measuring variables among the four treatments. All statistical analyses were conducted with SPSS software (SPSS 11.0 for WINDOWS).

Results

Microclimate changes induced by warming and precipitation treatments

In comparison with the long-term averages (1953–2005) of mean annual temperature (MAT, 2.1°C), both 2005 (2.6°C) and 2006 (2.8°C) had higher MAT. However, 2005 had lower annual precipitation (322.8 mm) whereas 2006 had higher annual precipitation (407.7 mm) than the long-term mean annual precipitation (MAP, 385.5 mm; Fig. 1).

Experimental warming manipulated with infrared radiators significantly elevated soil temperature ($P < 0.05$). Across the whole experimental period, mean soil temperature at 10 cm depth was 1.39 and 1.02°C higher under warming than the control in the natural and increased precipitation plots, respectively. Volumetric soil moisture at 0–10 cm depth fluctuated greatly over the growing season (Fig. 2a,b). Warming decreased seasonal mean volumetric soil moisture by 1.72 (v/v%) in 2005 and 1.34 (v/v%) in 2006 (all $P < 0.05$) across the increased and natural precipitation plots. Increased precipitation significantly elevated seasonal mean soil moisture

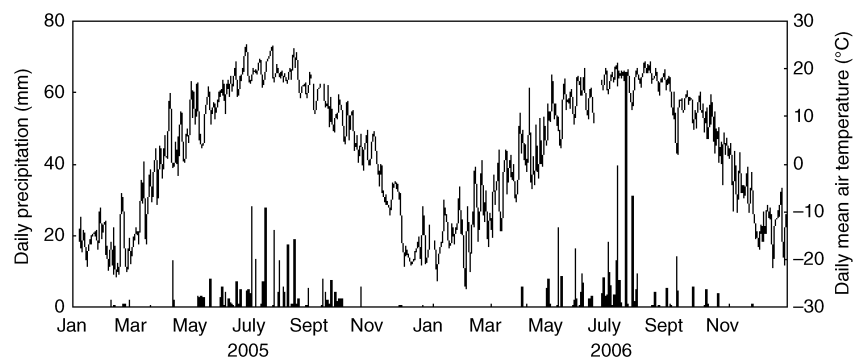


Fig. 1 Daily precipitation (bars) and daily mean air temperature (line) in 2005 and 2006. Data for 2005 are from the Meteorological Station of Duolun County, Inner Mongolia, 26 km from the study site. Data in 2006 are from the eddy tower adjacent (approx. 100 m) to the experimental plots.

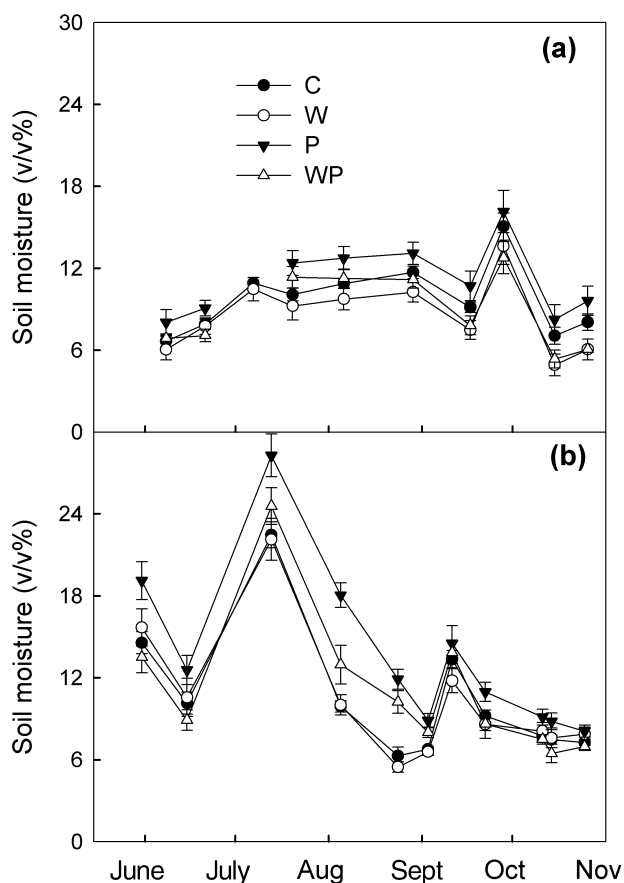


Fig. 2 Effects of experimental warming and increased precipitation on volumetric soil water content at 0–10 cm depth in (a) 2005; (b) 2006. C, control; W, warming; P, increased precipitation; WP, warming plus increased precipitation.

by 1.37 and 3.18 (v/v%) in 2005 and 2006 in the unwarmed subplots ($P < 0.05$; Fig. 2a,b), respectively, but insignificantly increased soil moisture by 0.30–0.65 (v/v%) in the warmed subplots in both years ($P > 0.05$).

Interannual differences in C and water fluxes caused by precipitation

The temporal dynamics of NEE, ER, GEP and ET followed the seasonal patterns of air temperature in both years, which were higher in summer and lower in spring and autumn (Fig. 3). In addition, there were substantial interannual variations in ecosystem CO_2 and water fluxes ($P < 0.001$). In the unwarmed control subplots under natural precipitation, seasonal mean NEE ($3.71 \mu\text{mol m}^{-2} \text{s}^{-1}$), GEP ($5.99 \mu\text{mol m}^{-2} \text{s}^{-1}$) and ET ($1.93 \text{ mmol m}^{-2} \text{s}^{-1}$) in 2005 were 25.3, 14.5 and 36.3% greater than in 2006 ($2.77 \mu\text{mol m}^{-2} \text{s}^{-1}$, $5.12 \mu\text{mol m}^{-2} \text{s}^{-1}$, $1.23 \text{ mmol m}^{-2} \text{s}^{-1}$), respectively. By contrast, ER ($-2.28 \mu\text{mol m}^{-2} \text{s}^{-1}$) and WUE ($1.86 \mu\text{mol CO}_2 \text{ mmol}^{-1} \text{H}_2\text{O}$) in 2005 were 3.1 and 31.7% lower than in 2006 ($-2.35 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $2.45 \mu\text{mol CO}_2 \text{ mmol}^{-1} \text{H}_2\text{O}$), respectively.

Monthly mean NEE in the growing season changed greatly between the two years. The difference in monthly mean NEE between years coincided with the difference in monthly mean soil moisture, but was contrary to the difference in monthly mean soil temperature (Fig. 4), suggesting controls of soil water content over the interannual variability of NEE.

Negative warming effects on C and water fluxes varied with year and water availability

The main effect of warming was statistically significant on NEE and GEP in 2005 (Table 1). Under natural precipitation, NEE and GEP were, on average, 12.3 and 11.1% lower ($P < 0.05$), respectively, in the warmed than in the control subplots over the 2005 growing season (Fig. 3a,e). Warming-induced reductions in the seasonal mean NEE and GEP in 2005 were 4.9 and 3.6%, respectively, in the increased precipitation plots. Experimental warming slightly, but insignificantly, decreased ET (5.7%) and WUE (5.4%) in 2005. In 2006, marginal reductions (3.7–11.4%) in all measured variables were observed under the warming treatment.

Table 1 Results (F values) of repeated-measurement ANOVA on the effects of warming (W), increased precipitation (P), measuring date (D), and their interactions on net ecosystem CO_2 exchange (NEE), gross ecosystem productivity (GEP), ecosystem respiration (ER), ecosystem evapotranspiration (ET) and ecosystem water-use efficiency (WUE)

	2005					2006				
	NEE	ER	GEP	ET	WUE	NEE	ER	GEP	ET	WUE
D	193***	187***	320***	178***	18***	73***	96***	149***	26***	78***
$D \times P$	1.57	2.16*	1.69^	2.92**	1.25	13***	5.98***	18***	2.84**	2.34*
$D \times W$	0.89	0.57	1.45	0.52	0.25	2.36*	1.19	2.55*	1.95^	1.62
$D \times P \times W$	2.15*	0.71	2.41*	0.20	0.44	1.44	0.78	1.71^	1.97^	2.62*
P	2.25	4.18^	8.86**	7.30*	0.08	42***	12**	36***	4.03^	5.22*
W	9.99**	1.34	20***	1.94	0.00	1.78	0.10	0.80	2.95	2.60
$P \times W$	1.59	0.02	2.30	0.01	1.21	0.01	0.97	0.02	2.27	0.03

Significance: ^, $P < 0.10$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

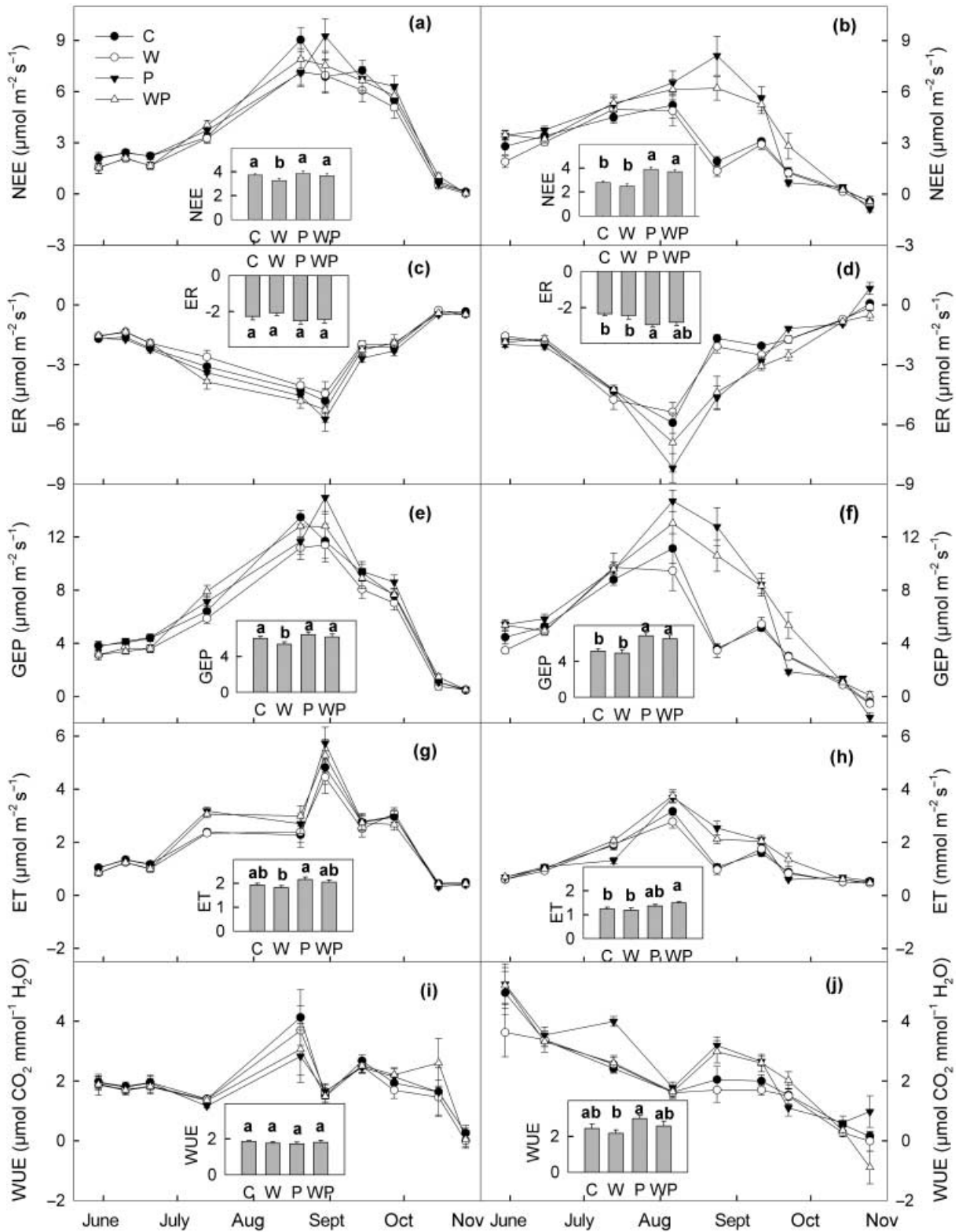


Fig. 3 Seasonal dynamics and means (mean \pm 1 SE) of (a,b) net ecosystem CO₂ exchange (NEE); (c,d) ecosystem respiration (ER); (e,f) gross ecosystem productivity (GEP); (g,h) ecosystem evapotranspiration (ET); (i,j) ecosystem water-use efficiency (WUE) in 2005 (left) and 2006 (right). Different letters in insets indicate significant difference ($P < 0.05$) in seasonal averages among treatments. C, control; W, warming; P, increased precipitation; WP, warming plus increased precipitation.

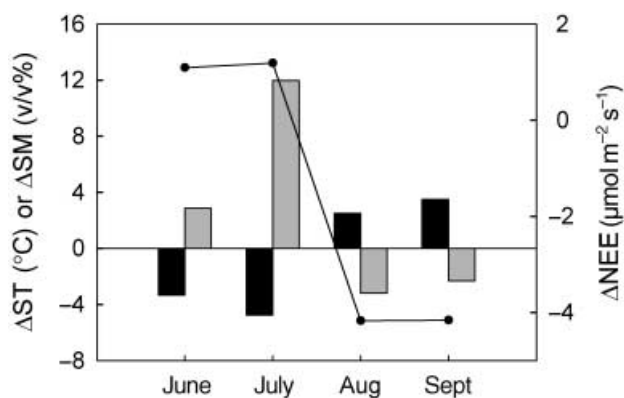


Fig. 4 Differences in monthly mean soil temperature (ST, black bars), soil moisture (SM, grey bars) and net ecosystem CO₂ exchange (NEE, line) between 2005 and 2006. Each bar represents the monthly mean value in 2006 minus that in 2005.

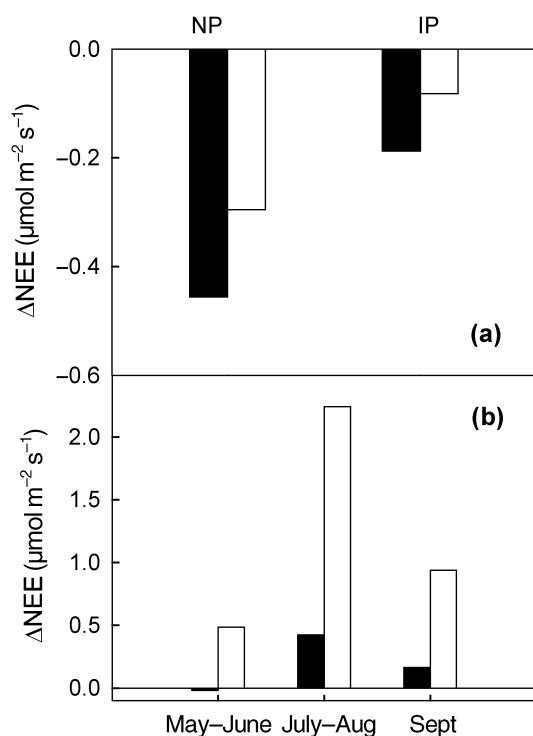


Fig. 5 (a) Warming-induced changes in seasonal mean net ecosystem CO₂ exchange (NEE) in natural (NP) and increased precipitation (IP) plots in 2005 (closed bars) and 2006 (open bars). (b) Precipitation-induced changes in NEE in early, mid- and late growing season in 2005 (closed bars) and 2006 (open bars).

The warming-induced decrease in NEE was larger in the drier year of 2005 than in the wetter 2006 (Fig. 5a) under both natural and increased precipitation treatments. In both years, the magnitude of NEE reductions under warming was lower in the increased than in the natural precipitation plots (Fig. 5a).

Positive effects of increased precipitation on C and water fluxes

Increased precipitation significantly stimulated GEP and ET in 2005, and enhanced NEE, ER, GEP and WUE in 2006 (all $P < 0.05$; Table 1). There were also interannual variabilities in the responses of ecosystem C and water parameters to increased precipitation. Stimulations of seasonal mean NEE (40.4%), ER (25.9%), and GEP (33.8%) in 2006 were all greater than those in 2005 (3.9, 10.8, and 6.6; Fig. 3). No interactive effects of warming and precipitation treatments on NEE, ER, GEP, ET and WUE were detected in either year (Table 1).

Precipitation-induced changes in NEE were greater in the mid-growing season (July and August) than in the early (May and June) and late (September) growing season in both 2005 and 2006 (Fig. 5b). Furthermore, precipitation-induced changes in seasonal mean NEE were larger in 2006 than in 2005 (Fig. 5b).

Temperature response of C and water fluxes

Diurnal dynamics of NEE and GEP in the control plots exhibited quadratic relationships with air temperature (T_{air}) in both years ($P < 0.001$; Fig. 6c–f). Both NEE and GEP increased with air temperature before T_{air} reached 28°C, and thereafter declined with further increase in T_{air} (Fig. 6c–f). NEE, ER and ET were all exponentially correlated with air temperature across the growing season ($P < 0.001$).

Leaf-level gas exchange

Warming and increased precipitation had marginal effects on leaf-level gas exchange ($P > 0.05$). Climatic warming increased VPD by 10.4 and 3.8% in the natural and increased precipitation plots, respectively (Fig. 7d). The maximum leaf photosynthetic rate (P_{max}), transpiration rate (E) and stomatal conductance (g_s) of the dominant species *A. cristatum* were 5.6, 16.0 and 7.9% lower in the warmed than in the control subplots, respectively (Fig. 7a–c). By contrast, increased precipitation stimulated P_{max} , E and g_s of *A. cristatum* by 5.9, 20.7 and 20.1%, respectively (Fig. 7a–c).

Discussion

Intra- and interannual changes in C and water fluxes

The seasonal dynamics of C fluxes observed in this study were indicative of the vegetation development that reflects temperature changes. Carbon uptake began increasing as air temperature rose and leaf-area index was enhanced. During midsummer, when the rates of vegetation growth were greatest, NEE, GEP, and ER rates reached the maximum. Later in the growing season, GEP and ER tended to decrease

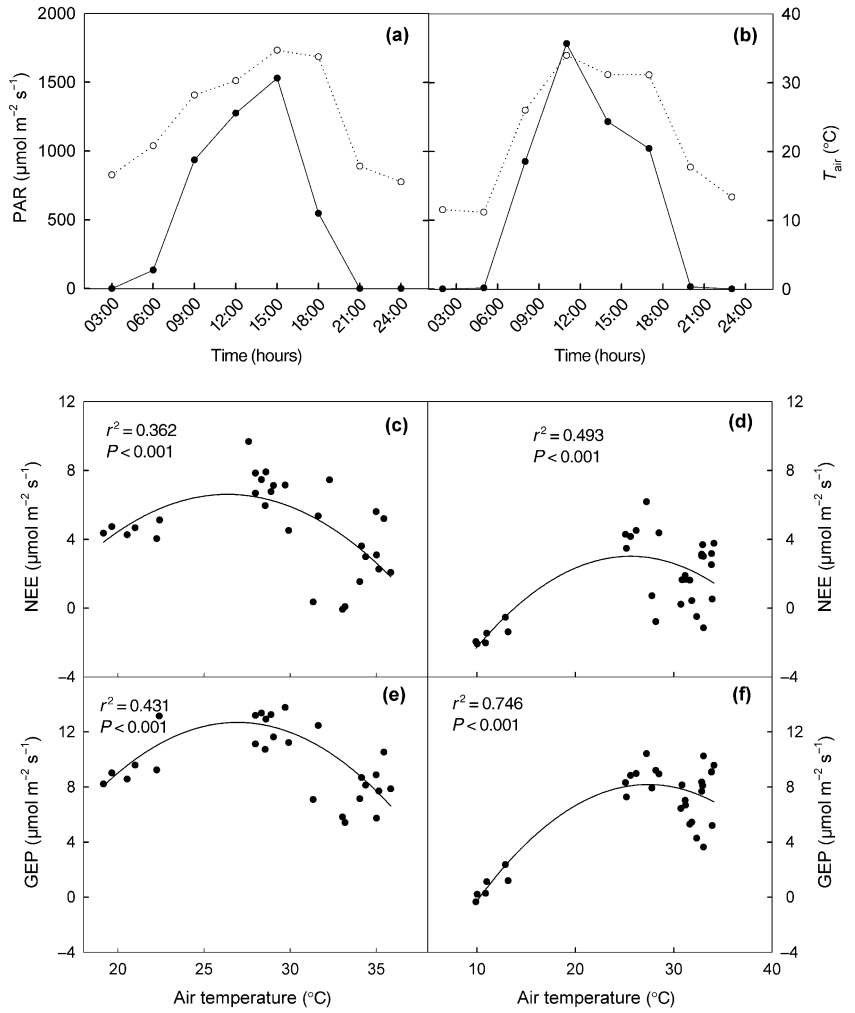


Fig. 6 Diurnal patterns of (a,b) photosynthetic active radiation (PAR, solid line) and air temperature (T_{air} , dotted line), and the relationships of (c,d) net ecosystem CO_2 exchange (NEE) and (e,f) gross ecosystem productivity (GEP) with air temperature measured under the ambient temperature treatment on 29 July 2005 (left) and 13 July 2006 (right).

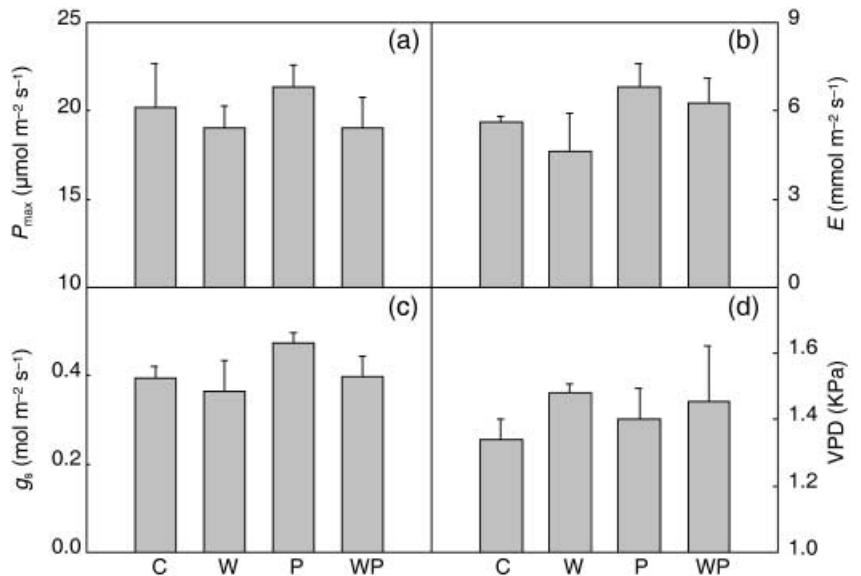


Fig. 7 Effects of warming and increased precipitation on (a) saturated photosynthetic rate (P_{max}); (b) transpiration rate (E); (c) stomatal conductance (g_s); (d) vapour pressure deficit (VPD) measured on 31 August 2005. C, control; W, warming; P, increased precipitation; WP, warming plus increased precipitation.

as plant senescence occurred and air temperature declined (cf. Figs 1, 3). Similarly to the C fluxes, plant transpiration and soil evaporation also increased with air and soil temperature in spring and early summer, leading to an increase in ET (Fig. 3g,h). Senescence of plant tissue and decline in soil temperature in the late autumn would lead to a decrease in ET. Our findings on the seasonal dynamics of C and water fluxes in the temperate steppe of northern China are comparable with those reported in other temperate grasslands (Suyker & Verma, 2001; Flanagan *et al.*, 2002; Li *et al.*, 2005). Moreover, our NEE values in the temperate steppe of northern China are within the range of those reported for other grassland ecosystems (Flanagan *et al.*, 2002; Hunt *et al.*, 2002; Li *et al.*, 2005).

Evapotranspiration in the mid-growing season (July and August), when plant growth is more active, accounted for 50.4 and 54.1% of total evapotranspiration in the growing season (May–October) of 2005 and 2006, respectively. In another experimental site adjacent to this study site, we found that daytime evapotranspiration (07:00–18:00 h) accounted for 90% of the daily total evapotranspiration (S. W. and co-workers, unpublished data). The results suggest that plant transpiration accounts for the majority of ecosystem evapotranspiration in the temperate steppe. A similar result has also been reported in semiarid grassland in North America (Yepez *et al.*, 2005).

In the temperate steppe in northern China, we observed greater ecosystem C uptake (GEP) than C release (ER) and a consequent C sink (positive NEE) in 2005 and 2006. In addition, there were marked interannual variabilities in all three C-flux parameters (Fig. 3), which could be attributed to differences in annual precipitation. Substantial year-to-year variabilities in NEE have also been reported in various ecosystems (Flanagan *et al.*, 2002; Scott *et al.*, 2004; Zhao *et al.*, 2006). Moreover, the differences in monthly mean NEE between the two years coincided with the differences in monthly mean soil moisture, but were contrary to the differences in monthly mean soil temperature (Fig. 4). Specifically, monthly mean soil temperatures in June and July were 3.32–4.75°C higher in 2005 than 2006 (Fig. 4). A higher monthly NEE is expected in June and July 2005, based on the exponential correlations between NEE and temperature. However, soil moisture was 2.87–11.98 (v/v%) lower in June and July in 2005 than in 2006, because of the lower precipitation during these two months in 2005 (Fig. 1). The significant lower soil moisture in these two months may have constrained plant growth and ecosystem productivity, as NEE was 35.9–47.1% lower in June and July in 2005 than in 2006. In contrast, soil temperature in August and September was 2.50–3.48°C lower, while soil moisture was 2.32–3.19 (v/v%) higher in 2005 than 2006, leading to 53.9–65.4% greater NEE in August and September in 2005 than in 2006. These observations indicate that water availability plays a predominant role in regulating interannual variability of ecosystem C and water exchange in the temperate steppe.

Warming effects on ecosystem C and water fluxes

Elevated temperature can increase ecosystem C uptake and release in natural ecosystems (Billings *et al.*, 1982; Christensen *et al.*, 1998; Welker *et al.*, 2004; Wan *et al.*, 2005; Zhou *et al.*, 2007) directly by stimulating plant activities, and indirectly by promoting soil nitrogen mineralization (Melillo *et al.*, 2002; Weintraub & Schimel, 2003; Wan *et al.*, 2005). A meta-analysis across various terrestrial ecosystems revealed that experimental warming stimulated soil respiration by 20% and enhanced plant productivity by 19% (Rustad *et al.*, 2001). However, climatic warming does not necessarily lead to increased C uptake and/or release in terrestrial ecosystems, given the highly variable initial conditions and indirect effects of warming (Shaver *et al.*, 2000; Wan *et al.*, 2005, 2007). Ecosystem C processes could also be constrained by warming as a consequence of inhibition of microbial and root respiration as well as suppression of plant physiological activity by warming-induced atmospheric and soil water deficits (Fig. 1; Saleska *et al.*, 1999; Wan *et al.*, 2002, 2007).

In the temperate steppe in northern China, experimental warming reduced GEP more than ER (Table 1), leading to a decrease in NEE (Fig. 3a,b). The negative warming effect on NEE could be largely attributable to the lower soil moisture (Fig. 2) and consequently lower leaf stomatal conductance and photosynthesis under elevated temperature (Fig. 7a,c). The negative warming impact on NEE was aggravated by low soil water availability. For example, greater reductions in NEE under experimental warming (Fig. 5a) were observed in the drier year 2005 (with 322.8 mm annual precipitation) than in the wetter year 2006 (407.7 mm annual precipitation); and in the natural precipitation plots than in the increased precipitation plots. Unlike GEP and NEE, we found that ER was reduced only slightly by experimental warming in the temperate steppe ($P > 0.05$; Table 1). Given the widely observed exponential correlations of auto- and heterotrophic respiration with temperature (Zhou *et al.*, 2007), elevated temperature could have directly stimulated root and microbial respiration. However, warming-induced reductions in soil water availability could suppress root and microbial activities and respiration and offset the direct positive temperature effect, leading to insignificant changes in ecosystem respiration. These findings support our previous hypothesis that water availability mediates the responses of ecosystem C exchange to climatic warming in the semiarid temperate steppe.

The quadratic responses of NEE and GEP to air temperature in the diurnal course (Fig. 6c–f) may also account for the negative response of CO₂ exchange to experimental warming. When calculated with the diurnal temperature response of CO₂ exchange, the optimal temperature for NEE and GEP was approx. 28°C (Fig. 6). Irrespective of the higher PAR at midday (Fig. 6a,b), higher temperature and VPD could reduce leaf stomatal conductance (Moriani *et al.*, 2002; Li *et al.*, 2005; Barron-Gafford *et al.*, 2007), leading to lower canopy

photosynthesis. Experimental warming increased VPD and aggravated stomatal resistance (Fig. 7c,d), thus further limiting C assimilation.

Effects of increased precipitation on ecosystem C, water fluxes and water-use efficiency

Our study focused on the active growing season to investigate the effect of water supply on ecosystem C flux. The differences in NEE were hardly detectable between the natural and increased precipitation plots before the precipitation treatment (May and June 2005) (Fig. 5b). As expected, increased precipitation in summer stimulated C and water fluxes in our study site from July 2005. Moreover, in the early (May–June) growing season of 2006 and the late (September) growing seasons of 2005 and 2006, in which the precipitation treatment was not applied, NEE was still higher in the increased than natural precipitation plots (Fig. 5b), suggesting carry-over effects of precipitation on NEE via altering abiotic and biotic factors. Consistent with our observations, the stimulation of ecosystem C and water fluxes by increased precipitation has also been reported in other grassland ecosystems (Sala *et al.*, 1988; Meyers, 2001; Flanagan *et al.*, 2002; Huxman *et al.*, 2004; Harper *et al.*, 2005; Hastings *et al.*, 2005; Patrick *et al.*, 2007).

There were temporal variations of the enhancement of ecosystem C fluxes in response to increased precipitation depending on ambient soil water conditions. The magnitude of precipitation-induced increase in NEE was greater in the mid- than early and late growing season (Fig. 5b). In addition, greater increases in NEE were observed in the wetter year 2006 than the drier 2005 (Fig. 5b). These results are in line with long-term measurements of CO₂ fluxes in the Chihuahuan Desert, where rainfall increments in a low-rainfall season have less impact on ecosystem CO₂ flux than an increment of the same amount of rainfall in a high-rainfall season (Mielnick *et al.*, 2005).

Higher GEP and ET under increased precipitation in the temperate steppe (Fig. 3e–h) could have resulted from a higher photosynthesis rate (Fig. 7a), transpiration rate (Fig. 7b) and canopy leaf-area index (data not shown). Enhanced plant photosynthesis and above-ground activity resulted in stimulation of below-ground C input, root and microbial activities and respiration (unpublished data), contributing to greater whole-ecosystem respiration. Nevertheless, the precipitation-induced increase in GEP was greater than that observed in ER, leading to an enhanced C sink in the temperate steppe (Fig. 3a,b).

Ecosystem C and water fluxes are usually coupled because of stomatal control over both CO₂ and water exchange between plants and the atmosphere. However, under the increased precipitation treatment in our study, ecosystem WUE increased by 22.2 and 19.2% in the control and warmed subplots, respectively, in 2006 (Fig. 3j), suggesting differential responses of ecosystem C and water exchanges to the increased precipitation. In the semiarid temperate steppe, increased precipitation may stimulate C exchange more than

it does on evapotranspiration, thus improving WUE at the ecosystem level. Our results are inconsistent with previous studies in which higher plant WUE under drier conditions was reported (Ehleringer & Cooper, 1988; Rytter, 2005). Our observations clearly demonstrate the predominant role of water availability in regulating ecosystem C processes in the temperate steppe of northern China.

Conclusions

A better understanding of the environmental controls over ecosystem C and water fluxes is essential to predict the responses of terrestrial C and water cycling in natural ecosystems to atmospheric and climatic change. Contrary to the common expectations of stimulated ecosystem C fluxes under warming, we found reductions in all the measured C fluxes in the temperate steppe in northern China. The decreased ecosystem C fluxes could be attributed to offsetting of the direct and positive effects of elevated temperature by the indirect and negative effects via exacerbating water stress. These results suggest the uniqueness of the temperate steppe in the semiarid region of northern China. This grassland ecosystem is more xeric and water-stressed than many other ecosystems. Precipitation, rather than temperature, dominates the interannual variability of ecosystem C fluxes. Increased precipitation not only enhanced ecosystem C fluxes, but also ameliorated the negative impacts of climatic warming on ecosystem C fluxes. Our observations indicate the critical role of precipitation/water availability in regulating ecosystem C cycling and its response to climatic change in water-limited ecosystems.

Acknowledgements

We thank three anonymous reviewers for their thoughtful comments, which helped in improving an earlier version of the manuscript. This study is conducted as part of a comprehensive research project (Global Change Multi-factor Experiment-Duolun) sponsored by Institute of Botany, the Chinese Academy of Sciences. Authors thank Shihuan Song, Wenming Bai and Xin Li for help in setting up the field facilities, Yanfang Zhang, Zhixiong Li and Wenjing Cheng for help in field measurements, and Shiping Chen for providing meteorological data. This study was supported financially by the National Natural Science Foundation of China (30521002, 90511006, 30590382) and the Chinese Academy of Sciences (Hundred Talents Program and KSCX2-SW-127).

References

- Barron-Gafford GA, Grieve KA, Murthy R. 2007. Leaf- and stand-level responses of forested mesocosm to independent manipulations of temperature and vapor pressure deficit. *New Phytologist* 174: 614–625.

- Billings WD, Luken JO, Mortensen DA, Peterson KM. 1982. Arctic tundra: a source or sink for atmospheric carbon dioxide in a changing environment? *Oecologia* 53: 7–11.
- Christensen TR, Jonasson S, Michelsen A, Callaghan TV, Havström M. 1998. Environmental controls on soil respiration in the Eurasian and Greenlandic Arctic. *Journal of Geophysical Research* 103: 29015–29021.
- Christensen L, Coughenour MB, Ellis JE, Chen ZZ. 2004. Vulnerability of the Asian typical steppe to grazing and climatic change. *Climatic Change* 63: 351–368.
- Corradi C, Kolle O, Walter K, Zimov SA, Schulze ED. 2005. Carbon dioxide and methane exchange of a north-east Siberian tussock tundra. *Global Change Biology* 11: 1910–1925.
- Dore MHL. 2005. Climatic change and changes in global precipitation patterns: what do we know? *Environment International* 31: 1167–1181.
- Ehleringer JR, Cooper TA. 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* 76: 562–566.
- Fang JY, Piao SL, Tang ZY, Peng CH, Ji W. 2001. Interannual variability in net primary production and precipitation. *Science* 293: 1723a.
- Flanagan LB, Wever LA, Carlson PJ. 2002. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. *Global Change Biology* 8: 599–615.
- Gao Q, Yu M, Zhang XS, Guan F. 1997. Dynamic modeling of northeast China transect responses to global change – a regional vegetation model driven by remote sensing information. *Acta Botanica Sinica* 39: 800–810.
- Gong DY, Shi PJ, Wang JA. 2004. Daily precipitation changes in the semi-arid region over northern China. *Journal of Arid Environments* 59: 771–784.
- Groisman PY, Knight RW, Easterling DR, Karl TR, Hegerl GC, Razuvayev VN. 2005. Trends in intense precipitation in the climate record. *Journal of Climate* 18: 1326–1350.
- Harper CW, Blair JM, Fay PA, Knapp K, Carlisle JD. 2005. Increased rainfall variability and reduced rainfall amount decreases soil CO₂ flux in a grassland ecosystem. *Global Change Biology* 11: 322–334.
- Harte J, Torn MS, Chang FR, Feifarek B, Kinzig AP, Shaw R, Shen K. 1995. Climate warming and soil microclimate: results from a meadow-warming experiment. *Ecological Applications* 5: 132–150.
- Hastings SJ, Oechel WC, Muhlia-Melo A. 2005. Diurnal, seasonal and annual variation in the net ecosystem CO₂ exchange of a desert shrub community (Sarcocaulis) in Baja California, Mexico. *Global Change Biology* 11: 927–939.
- Hunt JE, Kelliher FM, McSeveny TM, Byers JN. 2002. Evaporation and carbon dioxide exchange between the atmosphere and a tussock grassland during a summer drought. *Agricultural and Forest Meteorology* 111: 65–82.
- Huxman TE, Cable JM, Ignace DD, Eilts JA, English NB, Weltzin J, Williams DG. 2004. Response of net ecosystem gas exchange to a simulated precipitation pulse in a semiarid grassland: the role of native versus non-native grasses and soil texture. *Oecologia* 141: 295–305.
- Illeris L, Christensen TR, Mastepanov M. 2004. Moisture effects on temperature sensitivity of CO₂ exchange in a subarctic heath ecosystem. *Biogeochemistry* 70: 317–330.
- IPCC. 2007. *IPCC WGI Fourth Assessment Report. Climatic change 2007: the physical science basis*. Geneva: Intergovernmental Panel on Climate Change.
- Kirschbaum MUF. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic storage. *Soil Biology and Biochemistry* 27: 753–760.
- Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD, Carlisle JD, Harper CW, Danner BT, Lett MS, McCarron JK. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298: 2202–2205.
- Li SG, Asanuma J, Eugster W, Kotani A, Liu JJ, Urano T, Oikawa T, Davaa G, Oyunbaatar D, Sugita M. 2005. Net ecosystem carbon dioxide exchange over grazed steppe in central Mongolia. *Global Change Biology* 11: 1941–1955.
- Melillo JM, Steudler PA, Aber JD, Newkirk K, Lux H, Bowles FP, Catedral C, Magill A, Ahrens T, Morisseau S. 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* 298: 2173–2175.
- Meyers TP. 2001. A comparison of summertime water and CO₂ fluxes over rangeland for well watered and drought conditions. *Agricultural and Forest Meteorology* 106: 205–214.
- Mielnick P, Dugas WA, Mitchell K, Havstad K. 2005. Long term measurements of CO₂ flux and evapotranspiration in a Chihuahuan desert grassland. *Journal of Arid Environments* 60: 423–436.
- Moriana A, Villalobos FJ, Fereres E. 2002. Stomatal and photosynthetic responses of olive (*Olea europaea* L.) leaves to water deficits. *Plant, Cell & Environment* 25: 395–404.
- Oechel WC, Hastings SJ, Vourltis G, Jenkins ML, Riechers G, Grulke N. 1993. Recent change of arctic tundra ecosystems from a carbon sink to a source. *Nature* 361: 520–523.
- Patrick L, Cable J, Potts D *et al.* 2007. Effects of an increase in summer precipitation on leaf, soil, and ecosystem fluxes of CO₂ and H₂O in a sotol grassland in Big Bend National Park, Texas. *Oecologia* 151: 704–718.
- Peñuelas J, Gordon C, Llorens L, Nielsen TR, Tietema A, Beier C, Bruna P, Emmett BA, Estiarte M, Gorissen A. 2004. Non-intrusive field experiments show different plant responses to warming and drought among sites, seasons and species in a North–South European gradient. *Ecosystems* 7: 598–612.
- Piao SL, Fang JY, Chen AP. 2003. Seasonal dynamics of terrestrial net primary production in response to climatic changes in China. *Acta Botanica Sinica* 45: 269–275.
- Potts DL, Huxman TE, Enquist BJ, Weltzin JF, Williams DG. 2006. Resilience and resistance of ecosystem functional response to a precipitation pulse in a semi-arid grassland. *Journal of Ecology* 94: 23–30.
- Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen JHC, Gurevitch J, GCTE-NEWS. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126: 543–562.
- Rytter RM. 2005. Water use efficiency, carbon isotope discrimination and biomass production of two sugar beet varieties under well-watered and dry conditions. *Journal of Agronomy and Crop Science* 191: 426–438.
- Sala OE, Parton WJ, Joyce LA, Lauenroth WK. 1988. Primary production of the central grassland region of the United States. *Ecology* 69: 40–45.
- Saleska SR, Harte J, Torn MS. 1999. The effect of experimental ecosystem warming on CO₂ fluxes in a montane meadow. *Global Change Biology* 5: 125–141.
- Scott RL, Edwards EA, Shuttleworth WJ, Huxman TE, Watts C, Goodrich DC. 2004. Interannual and seasonal variation in fluxes of water and carbon dioxide from a riparian woodland ecosystem. *Agricultural and Forest Meteorology* 122: 65–84.
- Shaver GR, Canadell J, Chapin FS, III *et al.* 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. *Bioscience* 50: 871–882.
- Shaw MR, Zavaleta ES, Chiariello NR, Cleland EE, Mooney HA, Field CB. 2002. Grassland responses to global environmental changes suppressed by elevated CO₂. *Science* 298: 1987–1990.
- Smith TM, Shugart HH. 1993. The potential response of global terrestrial carbon storage to a climatic change. *Water, Air and Soil Pollution* 70: 629–642.
- Steduto P, Çetinközü Ö, Albrizio R, Kanber R. 2002. Automated closed-system canopy-chamber for continuous field-crop monitoring of CO₂ and H₂O fluxes. *Agricultural and Forest Meteorology* 111: 171–186.
- Suyker AE, Verma SB. 2001. Year-round observations of the net ecosystem exchange of carbon dioxide in a native tallgrass prairie. *Global Change Biology* 7: 279–289.
- Wan SQ, Luo Y, Wallace LL. 2002. Changes in microclimate induced by experimental warming and clipping in tallgrass prairie. *Global Change Biology* 8: 754–768.

- Wan S, Hui D, Wallace LL, Luo Y. 2005. Direct and indirect warming effects on ecosystem carbon processes in a tallgrass prairie. *Global Biogeochemical Cycles* 19: GB2014. doi: 10.1029/2004GB002315.
- Wan S, Norby RJ, Ledford J, Weltzin JF. 2007. Responses of soil respiration to elevated CO₂, air warming, and changing soil water availability in a model old-field grassland. *Global Change Biology* 13: 2411–2424.
- Weintraub MN, Schimel JP. 2003. Interactions between carbon and nitrogen mineralization and soil organic matter chemistry in Arctic tundra soils. *Ecosystems* 6: 129–143.
- Welker JM, Fahnestock JT, Henry GR, O'Dea KW, Chimners RA. 2004. CO₂ exchange in three Canadian High Arctic ecosystems: response to long-term experimental warming. *Global Change Biology* 10: 1981–1995.
- Weltzin JF, Loik ME, Schwinning S *et al.* 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience* 53: 941–952.
- Yepez EA, Huxman TE, Ignace DD, English NB, Weltzin JF, Castellanos AE, Williams DG. 2005. Dynamics of transpiration and evaporation following a moisture pulse in semiarid grassland: a chamber-based isotope method for partitioning flux components. *Agricultural and Forest Meteorology* 132: 359–376.
- Zhang WL. 2007. Carbon fluxes of typical steppe and cropland ecosystems in the agri-pasture transition region of Inner Mongolia, China. PhD thesis. Beijing: Institute of Botany, the Chinese Academy of Sciences.
- Zhao L, Li YN, Xu SX, Zhou HK, Gu S, Yu GR, Zhao XQ. 2006. Diurnal, seasonal and annual variation in net ecosystem CO₂ exchange of an alpine shrubland on Qinghai–Tibetan plateau. *Global Change Biology* 12: 1940–1953.
- Zhou XH, Wan SQ, Luo YQ. 2007. Source components and interannual variability of soil CO₂ efflux under experimental warming and clipping in a grassland ecosystem. *Global Change Biology* 13: 761–775.



About New Phytologist

- *New Phytologist* is owned by a non-profit-making **charitable trust** dedicated to the promotion of plant science, facilitating projects from symposia to open access for our Tansley reviews. Complete information is available at www.newphytologist.org.
- Regular papers, Letters, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as-ready' via *OnlineEarly* – our average submission to decision time is just 28 days. Online-only colour is **free**, and essential print colour costs will be met if necessary. We also provide 25 offprints as well as a PDF for each article.
- For online summaries and ToC alerts, go to the website and click on 'Journal online'. You can take out a **personal subscription** to the journal for a fraction of the institutional price. Rates start at £135 in Europe/\$251 in the USA & Canada for the online edition (click on 'Subscribe' at the website).
- If you have any questions, do get in touch with Central Office (newphytol@lancaster.ac.uk; tel +44 1524 594691) or, for a local contact in North America, the US Office (newphytol@ornl.gov; tel +1 865 576 5261).