Response of ecosystem carbon exchange to warming and nitrogen addition during two hydrologically contrasting growing seasons in a temperate steppe

JIANYANG XIA*†, SHULI NIU* and SHIQIANG WAN*

*State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Xiangshan, Beijing 100093, China, †Graduate School of Chinese Academy of Sciences, Yuquanlu, Beijing 100049, China

Abstract

A large remaining source of uncertainty in global model predictions of future climate is how ecosystem carbon (C) cycle feedbacks to climate change. We conducted a field manipulative experiment of warming and nitrogen (N) addition in a temperate steppe in northern China during two contrasting hydrological growing seasons in 2006 [wet with total precipitation 11.2% above the long-term mean (348 mm)] and 2007 (dry with total precipitation 46.7% below the long-term mean). Irrespective of strong intra- and interannual variations in ecosystem C fluxes, responses of ecosystem C fluxes to warming and N addition did not change between the two growing seasons, suggesting independence of warming and N responses of net ecosystem C exchange (NEE) upon hydrological variations in the temperate steppe. Warming had no effect on NEE or its two components, gross ecosystem productivity (GEP) and ecosystem respiration (ER), whereas N addition stimulated GEP but did not affect ER, leading to positive responses of NEE. Similar responses of NEE between the two growing seasons were due to changes in both biotic and abiotic factors and their impacts on ER and GEP. In the wet growing season, NEE was positively correlated with soil moisture and forb biomass. Negative effects of warming-induced water depletion could be ameliorated by higher forb biomass in the warmed plots. N addition increased forb biomass but did not affect soil moisture, leading to positive effect on NEE. In the dry growing season, NEE showed positive dependence on grass biomass but negative dependence on forb biomass. No changes in NEE in response to warming could result from water limitation on both GEP and ER as well as little responses of either grass or forb biomass. N addition stimulated grass biomass but reduced forb biomass, leading to the increase in NEE. Our findings highlight the importance of changes in abiotic (soil moisture, N availability) and biotic (growth of different plant functional types) in mediating the responses of NEE to climatic warming and N enrichment in the semiarid temperate steppe in northern China.

Keywords: carbon, climatic warming, grassland, nitrogen, plant functional type, precipitation, respiration, soil moisture, temperature

Received 16 June 2008 and accepted 14 September 2008

Introduction

The unprecedented global warming and nitrogen (N) deposition (Galloway & Cowling, 2002; Gruber & Galloway, 2008) can profoundly impact terrestrial carbon (C) cycling and budgets, with consequent feedback to climatic change (Jones & Donnelly, 2004; Harpole

et al., 2007; Oberbauer *et al.*, 2007). Net ecosystem C exchange (NEE) represents the balance between gross ecosystem productivity (GEP) and ecosystem respiration (ER, Oberbauer *et al.*, 2007). Considering the different temperature sensitivities of photosynthesis and respiration (Woodwell *et al.*, 1983; Ryan, 1991), it is assumed that ecosystem C release will be stimulated more than C uptake under elevated temperature (Oechel *et al.*, 1993; Illeris *et al.*, 2004), resulting in decreased NEE under global warming. However, this

assumption has widely been debated because relative responses of ecosystem C uptake and release vary among different terrestrial ecosystems (Smith & Shugart, 1993; Corradi *et al.*, 2005; Oberbauer *et al.*, 2007). For example, ER has been reported to increase more than GEP under elevated temperature in a dry subarctic ecosystem (Illeris *et al.*, 2004) whereas, in a wet arctic ecosystem, GEP increases more than ER under warming (Oberbauer *et al.*, 2007). Irrespective of the commonly recognized positive relationship of ecosystem C fluxes with temperature, warming does not necessarily lead to increases in GEP or ER because other biotic and abiotic factors may play a predominant role in regulating plant growth and ecosystem C cycling and modulating their responses (Shaver *et al.*, 1998; Wan *et al.*, 2007). For example, water availability mediates the responses of C fluxes to climate change in arid and semiarid grassland in northern China (Niu *et al.*, 2008). Moreover, species interactions strongly influence grassland responses to climate change (Suttle *et al.*, 2007), especially the short-term climate effects on ecosystem C cycling (Kueppers & Harte, 2005).

Plant growth and net primary productivity in terrestrial biosphere have recently been revealed to increase under N enrichment at the global scale (Elser *et al.*, 2007; LeBauer & Treseder, 2008; Xia & Wan, 2008). However, changes in GEP and ER may not be equal or proportional under N addition, thus leading to changes in NEE that are not always in the same direction as the changes in GEP (Shaver *et al.*, 1998). Effects of N addition on NEE have been reported only in wet sedge tundra (Shaver *et al.*, 1998), boreal mire (Saarnio *et al.*, 2003), bog (Bubier *et al.*, 2007), and annual grassland (Harpole *et al.*, 2007) so far. More experimental evidence in natural terrestrial ecosystems is needed to seek for general patterns of the NEE responses to N addition/deposition across the globe. Moreover, temperature manipulation that simulates climate warming can stimulate net N mineralization and improve soil N availability in most terrestrial ecosystems (Rustad *et al.*, 2001; Melillo *et al.*, 2002). Global N enrichment and warming-stimulated soil N availability may synergistically affect ecosystem C exchange, ameliorate the progressive N limitation proposed under elevated atmospheric CO_2 concentration (Hungate *et al.*, 2003; Luo *et al.*, 2004; Reich *et al.*, 2006), and thus enhance C sequestration potential in terrestrial biosphere and slow down climate change.

The role of terrestrial ecosystem in regulating C exchange between the atmosphere and the biosphere has long been a subject of great debate (Bonal *et al.*, 2008). For example, early analyses (Buchmann & Schulze, 1999; Janssens *et al.*, 2001; Myneni *et al.*, 2001) have shown that temperate ecosystems are major C sinks whereas recent studies (Flanagan *et al.*, 2002; Aires *et al.*, 2008) claim that the role of these ecosystems in global C budget is still uncertain. In fact, the key of this issue now takes the climatic variations into consideration in analyses. These variations include interannual climate fluctuations, particularly the alternating dry/wet seasons (Flanagan *et al.*, 2002; Bonal *et al.*, 2008). Thus, an important research need is to understand how interannual variation in hydrological condition influences the warming and N effects on ecosystem C exchange. It is expected that changes in precipitation patterns associated with climate change have strong impacts on the structure and the function of temperate ecosystems (Weltzin *et al.*, 2003; Huxman *et al.*, 2004a; Suttle *et al.*, 2007). Climatic warming may negatively impact ecosystem C exchange via stimulating evapotranspiration, reducing soil moisture, and exacerbating water stress (Saleska *et al.*, 1999; Niu *et al.*, 2008). This condition will be aggravated when combined with decreased precipitation (Norby & Luo, 2004; Dermody *et al.*, 2007). It is also proposed that productivity of grassland ecosystems are co-limited by water and N availability (Kirchner, 1977; Hooper & Johnson, 1999), indicating the dependence of N effects on variations in hydrological condition. In fact, it has been reported that responses of grassland ecosystem to N addition will be strongly dependent on future precipitation patterns (Harpole *et al.*, 2007). Therefore, variation in hydrological condition is likely to influence the impacts of global climatic change on ecosystem C exchange, as is incorporated into some recent global climate–C cycle models (Cowling & Shin, 2006; Zhou *et al.*, 2008). However, this prediction still lacks mechanistic understanding of ecosystem C exchange in response to warming and N addition and their dependence on hydrological condition.

Beginning in April 2006, a field experiment was conducted to examine potential impacts of climate warming and N addition on NEE and its components (GEP, ER) in a semiarid temperate steppe in northern China. With the water and N limitation in this ecosystem, we hypothesize that (1) warming will negatively impact ecosystem C exchange because warming may aggravate water limitation by stimulating evaportranspiration (Niu *et al.*, 2008), (2) N addition will positively affect ecosystem C exchange considering the infertile soil in this study site (Yuan *et al.*, 2005). Based on the two hypotheses, interactions between warming and N addition in influencing ecosystem C exchange are expected. In addition, the observations in this study were from two hydrologically contrasting growing seasons (wet in 2006 and dry in 2007). Thus, we also test the impacts of hydrological variation on responses of ecosystem C exchange to warming and N addition.

Materials and methods

Study site

The research was conducted in Duolun County ($42°02'$N, $116°17'$E, 1324 m a.s.l), a semiarid area located in Inner Mongolia, China. Long-term (1953–2007) mean annual precipitation (MAP) is approximately 383 mm with 90% distributing from May to October. Mean annual temperature is $2.1\,°C$ with monthly mean temperature ranging from $18.9\,°C$ in July to $-17.5\,°C$ in January. The sandy soil of the study site is classified as chestnut according to the Chinese classification, or Haplic Calcisols according to the FAO classification. Mean bulk density is $1.31\,g\,cm^{-3}$ and pH is 7.7. The dominant plant species in this temperate steppe are *Stipa krylovii* Roshev., *Artemisia frigida* Willd., *Potentilla acaulis* L., *Cleistogenes squarrosa* (Trin.) Keng., *Allium bidentatum* Fisch. ex Prokh., and *Agropyron cristatum* (L.) Gaertn.

Experimental design

We used complete random block design with six treatments and replicated six times. Thirty-six $3\,m \times 4\,m$ plots were arranged in 6×6 matrix. The distance between any two adjacent plots was 3 m. One of the six plots in each row was randomly assigned to one of the six treatments, including control (C), day (6:00–18:00 hours) warming, night (18:00–6:00 hours) warming, diurnal (24 h) warming (W), N addition (N), and diurnal warming plus N addition (WN). The effects of day and night warming were not included in this study. In late August 2005, we compared ecosystem C fluxes, aboveground biomass, and root biomass in the plots that would be assigned to different treatments in 2006 and did not find any statistically significant difference (all $P > 0.05$). All the warmed plots were heated continuously by MSR-2420 infrared radiators (Kalglo Electronics Inc., Bethlehem, PA, USA) suspended 2.25 m above the ground. In each control or N addition plot, one 'dummy' heater with the same shape and size as the infrared heater was suspended 2.25 m high to simulate the shading effects of the infrared radiator. All the heaters under the warming treatments were set at a radiation output of approximately 1600 W. The warming treatment started on 23 April 2006. N additions were treated once a year with NH_4NO_3 ($10\,g\,N\,m^{-2}$) on July 19 in both years.

Soil temperature and moisture

Soil temperature at the depth of 10 cm was recorded automatically with a Datalogger (STM-01 Soil Temperature Measurement System; Henan Electronic Institute, Zhengzhou, China). Six measurements were taken with 10-min intervals and averages of the six measurements were stored as the hourly averages. Soil moisture (0–10 cm) was measured weekly using Diviner-2000 Portable Soil Moisture Probe (Sentek Pty Ltd., Balmain, NSW, Australia).

N availability

We assessed ammonium (NH_4^+) and nitrate (NO_3^-) concentrations in this study using buried cation and anion resin exchange capsules (Skogley & Dobermann, 1996). In both years, we deployed two capsules (PST-2; Unibest, Bozeman, MT, USA) in each plot on 15 May, 1 July, and 15 August, using PVC access tubes (WECSA Corp., Fort Collins, CO, USA). Individual capsules were placed at a depth of 10 cm below the soil surface with a tube at a $45°$ angle so as not to disturb the vertical soil column of both organic and mineral material. After 4 weeks, we retrieved the capsules, washed them with deionized water, stored them in zip-lock bags, and took them into the laboratory. In the lab, resin capsules were extracted with three sequential 20 mL solutions of $2\,M$ KCl on a shaker table for 60 min each. The combined 60 mL of extracts were analyzed for NH_4^+ and NO_3^- concentrations using a flow-injection Lachat automated colorimetry system (FIAstar 5000 Analyzer; Foss Tecator, Foss Ltd., Hillerød, Denmark). We estimated the inorganic N availability ($g\,m^{-2}$) from the sum of NH_4^+ and NO_3^- concentrations and the surface area of the resin capsules ($\approx 12.6\,cm^2$).

Ecosystem C fluxes measurements

Ecosystem C fluxes were measured with a transparent chamber ($0.5 \times 0.5 \times 0.5\,m^3$) attached to infrared gas analyzer (IRGA) (LI-6400; LiCor, Lincoln, NE, USA) placed and sealed on the plots. This static-chamber method has been successfully used to evaluate plot-level fluxes of CO_2 in this ecosystem (Niu *et al.*, 2008), and was validated in some previous studies (Steduto *et al.*, 2002; Huxman *et al.*, 2004b; Potts *et al.*, 2006; Bubier *et al.*, 2007; Risch & Frank, 2007). The polyethelene sheeting used for chamber construction allows >90% of photosynthetically active radiation to pass into the chamber. During the measurement, the chamber was sealed to the surface of an aluminum frame, which was inserted into the soil to a depth of about 3 cm at two opposite corners in each plot. Two small fans ran continuously to mix the air inside the chamber during measurement. Consecutive recordings of CO_2 concentrations were taken during a 90-s period after steady-state conditions were achieved within the chamber for 20 s. Increases in air temperatures within the chamber

during the measuring time period were less than $0.2\,^{\circ}C$. CO_2 concentrations were build up or draw down insufficiently (upper limit of range above and below ambient of about $10\,\mu mol\,mol^{-1}$) to significantly alter stomatal conductance, canopy photosynthesis, or soil respiration (Huxman *et al.*, 2004b). The details on these static-chamber flux calculations can be found in the soil-flux calculation procedure on Page 6-2 in the LI-6400 manual (LI-COR Inc., 2004). Following the measurements of NEE, the chamber was vented, replaced on each plot, and covered with an opaque cloth. The CO_2 exchange measurements were repeated, and the values obtained represented ER because light was eliminated (and hence photosynthesis). GEP was calculated as the difference between NEE and ER. Ecosystem C fluxes were measured twice a month on clear, sunny days between 9:00 and 12:00 hours from May to October in 2006 and 2007. The measured NEE once a day in this study was 112.6% of the observed daytime average based the diurnal pattern in the control plots (unpublished data).

Peak aboveground biomass and belowground net productivity

In May 2006, two permanent $1 \times 1\,m^2$ quadrats were established in each plot. Plant species composition was recorded in each quadrat at the end of August during the peak biomass in both years by visually estimating percent cover of each plant species. During the measurement, a $1 \times 1\,m^2$ frame with 100 equally distributed grids ($10 \times 10\,cm^2$) was put above the canopy in each quadrat. The percent cover of each species were recorded in all the grids and summed as the species cover in each quadrat. The number of plant species occurred was recorded as species richness in the quadrat.

We used a nondestructive method by developing regression equations between biomass and cover for each species to estimate peak aboveground biomass in this study. In order to include all the species occurred in our study, we set 80 calibration plots ($1 \times 1\,m^2$) near our experimental plots in both years. $10\,g\,N\,m^{-2}$ of NH_4NO_3 were added in half of the calibration plots ($n = 40$) at the same time we added N to the experimental plots. In late August, we measured the cover of each species in both N-addition and non-N-addition calibration plots. Then we clipped living aboveground biomass in the calibration plots and separated into different species. Living plant aboveground tissues were separated from dead tissues, oven-dried at $70\,^{\circ}C$ for 48 h, and weighed. We developed regression equations between biomass and cover for each species for both the non-N-added and N-added calibration plots. All species showed good correlations between biomass and cover in both 2006 and 2007. Finally, we estimated the biomass of each species in the C and W plots using the equations in the non-N-added calibration plots and biomass in the N and WN plots using the equations in the N-added calibration plots. Peak aboveground, grass, and forb biomass in each plot was the sum of biomass of all species, grass species, and forb species, respectively.

An index of belowground net productivity was estimated by using root ingrowth method. In early May of 2006 and 2007, we excavated two 50 cm deep cylindrical holes using a soil auger (8 cm in diameter) in each plot. The soils were refilled to the same hole after removing roots via 2 mm sieves. We collected root ingrowth samples in late October by using a smaller soil auger (6 cm in diameter) at the center of the original root ingrowth holes. The dry mass of root was determined by oven-drying at $70\,^{\circ}C$ to constant weight.

Plant canopy development

We monitored plant canopy development in 2007 by using a standard of canopy greenness, the Normalized Difference Vegetation Index (NDVI), which was frequently used for satellite studies (e.g. Myneni *et al.*, 1997). To monitor NDVI, we measured spectral reflectance under cloud-free conditions by using the ASD FieldSpec® Handheld spectrometer (Analytical Spectral Devices, Boulder, CO, USA). Reflectance measurements were made throughout the growing season at15-day intervals between 11:00 to 13:00 hours. Each sample was the mean of four spectra obtained with a fiber optic collector (25° field of view) at a height of 50 cm. NDVI was calculated as (reflectance at $775\,nm$ − reflectance at $675\,nm$)/(reflectance at $775\,nm$ + reflectance at $675\,nm$).

Data analysis

Seasonal mean values used in this study were calculated from the monthly mean values, which were first averaged from all measurements in the same month. We included values both before and after N addition to evaluate the N effect, because N addition was considered to have no effect on ecosystem C exchange at the beginning of growing season when the precipitation was infrequent and low and the soil was dry in this study. Three-way ANOVA was used to examine the effects of, warming, N addition, and their possible interactions on ecosystem C fluxes. If there is significant interannual variability (year effect $P < 0.05$), Repeated Measures ANOVA (RMANOVA) were used to examine warming and N addition effects on soil moisture and ecosystem C fluxes over the growing seasons in 2006 and 2007, respectively. Between-subject effects were evaluated as warming or N addition treatment and within-subject effects were time-of-season. Regression

with correction for autocorrelation and stepwise multiple linear analyses were used to examine the relationships of ecosystem C fluxes with soil temperature, soil moisture, soil N availability, species richness, peak grass biomass, peak forb biomass, and belowground net primary productivity measured. All statistical analyses were conducted with SAS software (SAS Institute Inc., Cary, NC, USA).

Results

Soil microclimate

Seasonal dynamics of both precipitation and air temperature produced one-peak patterns, which were higher in summer and lower in spring and autumn (Fig. 1). In comparison with the long-term (1953–2007) MAP (383 mm), total precipitation in 2006 (408 mm) was 6.5% higher. However, total precipitation in 2007 (209.3 mm) was the lowest in the past 55 years, with total precipitation 44.4% lower than the long-term MAP. Similarly, total precipitation over the entire growing season (May to October) in 2006 (387 mm) was 11.2% above the long-term mean (348 mm), whereas the growing season of 2007 (194 mm) was the driest during the past 55 years, with total precipitation 44.3% below the long-term mean. In contrast to precipitation, no difference in mean annual ($P = 0.383$) or seasonal ($P = 0.458$) air temperature was detected between 2006 and 2007 (Fig. 1).

Soil temperature at the 10 cm depth was higher in 2007 than 2006 ($P < 0.001$, three-way ANOVA). Warming significantly increased ($P < 0.001$) soil temperature whereas N addition showed no effect ($P = 0.948$). There was no interaction between warming and N addition in affecting soil temperature ($P = 0.361$). From 1 August 2006 to 31 October 2007 with continuous temperature records, mean soil temperature was 1.79 °C higher in the warmed plot than the control plot (Fig. 2a). The
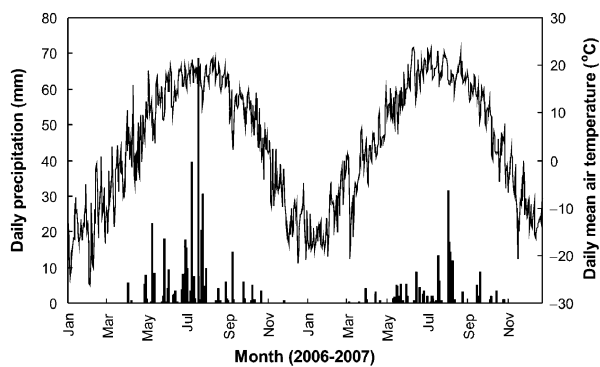

Fig. 1 Daily precipitation (bars) and daily mean air temperature (line) in 2006 and 2007. Data are from the eddy tower adjacent (approximately 200 m) to the experimental plots.

interannual fluctuations in precipitation between the two growing seasons caused higher soil moisture in 2006 than 2007 ($P < 0.001$, three-way ANOVA). Warming significantly reduced volumetric soil moisture at the depth of 0–10 cm by 5.0% ($P = 0.001$) whereas neither N addition ($P = 0.859$) nor its interaction ($P = 0.859$) with warming ($P = 0.180$) affected soil moisture. When analyzed separately by year using RMANOVA, soil moisture decreased significantly under warming in both 2006 ($P = 0.025$) and 2007 ($P = 0.018$), but no effects of N addition or its interaction with warming were observed (Table 1; Fig. 2b).

Interannual variability in plant growth and ecosystem C fluxes

Peak aboveground biomass in the dry year (48.4 g m^{-2}) was significantly lower than that in the wet year (108.4 g m^{-2}; $P < 0.001$). When divided aboveground biomass into different plant functional types, all grass biomass, forb biomass and grass : forb ratio were lower in 2007 than those in 2006 (all $P < 0.001$).

There were substantial interannual variations in NEE ($P < 0.001$), GEP ($P < 0.001$), and ER ($P = 0.039$). In the control plots, seasonal mean NEE (0.87 μmol m^{-2} s^{-1}), GEP (2.82 μmol m^{-2} s^{-1}), and ER (-1.95 μmol m^{-2} s^{-1}) in 2007 were 60.3%, 34.7%, and 10.5% lower than those in 2006 (2.19, 4.31, -2.17 μmol m^{-2} s^{-1}), respectively.

Effects of warming and N addition on ecosystem C fluxes

N addition significantly increased NEE ($P = 0.002$) whereas no effects of warming ($P = 0.620$) or its interaction with N addition ($P = 0.660$) were detected. When analyzed separately by year using RMANOVA, N addition significantly enhanced NEE in both years ($P = 0.006$ and 0.049, Table 2) and the enhancement in 2006 (22.7%) was similar with that in 2007 (22.5%; Fig. 3a and b). In addition, N-induced stimulation of seasonal mean NEE was lower in the warmed plots (20.0% in 2006 and 18.3% in 2007) than that in the unwarmed plots (25.3% and 26.8% in 2006 and 2007, respectively; Fig. 3a and b). Sampling date significantly interacted with N addition to impact NEE in both 2006 and 2007 (Table 2). There were little differences in NEE between the control and the N-addition plots before the date of N addition (19 July) in either 2006 ($P = 0.318$) or 2007 ($P = 0.377$). However, N addition significantly increased NEE after N was added (Fig. 3) in both 2006 ($P = 0.001$) and 2007 ($P = 0.035$).

Similar to NEE, GEP was significantly increased by N addition ($P < 0.001$) but not by warming or its interaction with N addition ($P = 0.763$; Table 1). When analyzed separately by year using RMANOVA, N addition significantly enhanced GEP in both years (Table 2), but
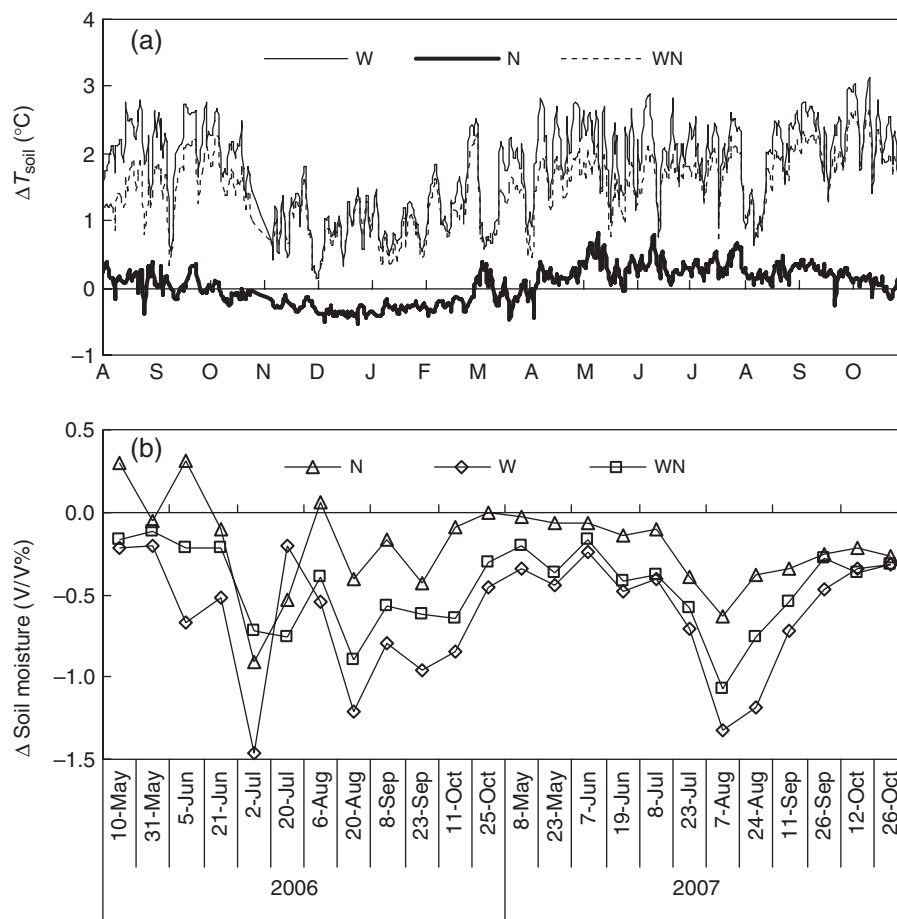
Fig. 2 Treatment-induced changes in daily soil temperature from 1 August 2006 to 31 October 2007 at the depth of 10 cm (a) and volumetric soil moisture (v/v %) in the two growing seasons at the depth of 0–10 cm (b). W: warming, N: N (nitrogen) addition, WN: warming plus N addition.

Table 1 Results (*P*-values) of three-way ANOVA on the effects of warming (W), N (nitrogen) addition (N), year (Y), and their interactions on net ecosystem CO_2 exchange (NEE), gross ecosystem productivity (GEP), ecosystem respiration (ER)

	NEE	GEP	ER
N	0.002	0.002	0.121
W	0.620	0.447	0.523
N × W	0.660	0.763	0.311
Y	<0.001	<0.001	0.039
Y × N	0.183	0.261	0.844
Y × W	0.647	0.593	0.775
Y × N × W	0.893	0.842	0.664

Table 2 Results (*P*-values) of repeat-measurement ANOVA on the effects of warming (W), N (nitrogen) addition (N), sampling date (D), and their interactions on net ecosystem CO_2 exchange (NEE), gross ecosystem productivity (GEP), ecosystem respiration (ER)

	2006			2007		
	NEE	GEP	ER	NEE	GEP	ER
N	0.006	0.007	0.152	0.049	0.028	0.249
W	0.541	0.448	0.540	0.977	0.822	0.685
N × W	0.709	0.854	0.406	0.650	0.918	0.450
D	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
D × N	<0.001	<0.001	0.097	0.096	0.259	0.361
D × W	0.461	0.650	0.566	0.137	0.351	0.423
D × N × W	0.691	0.266	0.685	0.947	0.616	0.548

the increases in GEP were lower in the dry year of 2007 (11.4%) than in the wet year of 2006 (16.0%; Fig. 3c and d). Unlike NEE, the increases in GEP by N addition were slightly lower in the unwarmed plots (13.6% and 10.6% in 2006 and 2007, respectively) than those in the

warmed plots (18.4% and 12.1% in 2006 and 2007, respectively; Fig. 3c and d). N addition significantly interacted with sampling date to affect GEP in 2006 (*P* < 0.001, Table 2). GEP did not differ between the
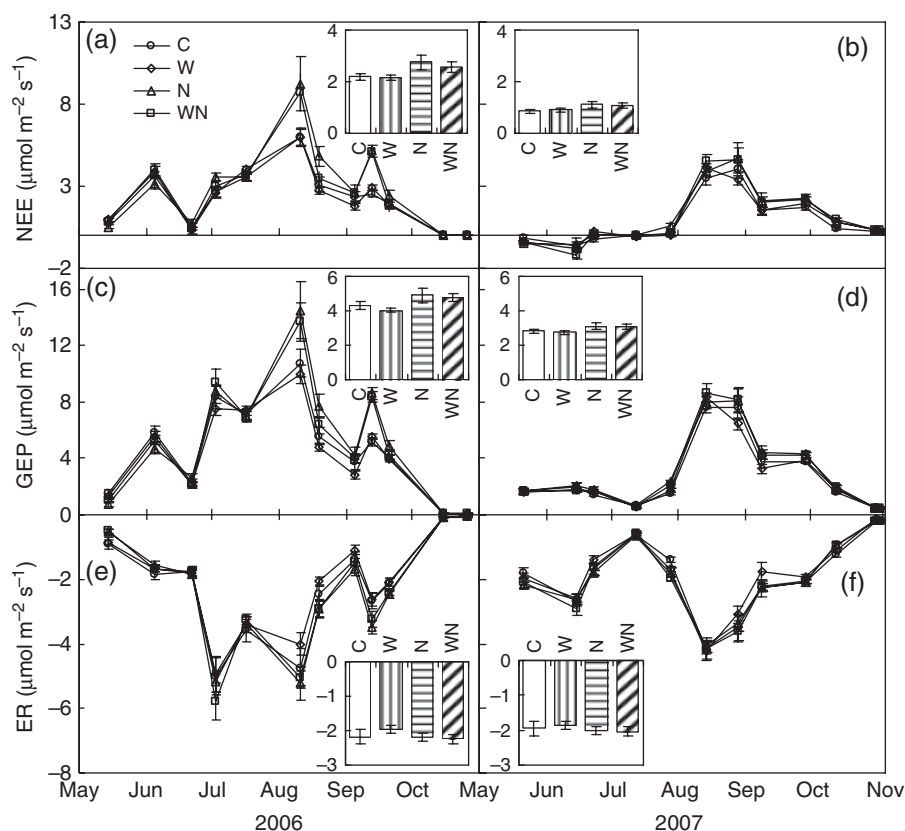
Fig. 3 Seasonal dynamics and means (insets means $\pm$ 1 SE) of net ecosystem CO_2 exchange (NEE) (a, b), gross ecosystem productivity (GEP) (c, d), and ecosystem respiration (ER) (e, f) in 2006 (left panels) and 2007 (right panels). C: control, W: warming, N: N (nitrogen) addition, WN: warming plus N addition.

control and the N addition plots before N addition (19 July) in either 2006 ($P = 0.886$) or 2007 ($P = 0.255$). However, GEP was significantly stimulated in the short-term by N addition in both 2006 ($P < 0.001$) and 2007 ($P = 0.037$, Fig. 3).

None of N addition, warming, or their interactions affected ER (Table 1). When analyzed separately by year using RMANOVA, the effects of warming, N addition, and their interactions were not statistically significant for ER (Table 2) in either year. No interaction was found between sampling date and N addition to affect ER in either 2006 or 2007 (Table 2).

Treatment effects on control factors over ecosystem C fluxes

When analyzed separately by year using RMANOVA, soil N availability increased by 10.2% and 17.8% under N addition in 2006 ($P = 0.039$) and 2007 ($P < 0.001$), respectively. Warming did not affect soil N availability in 2006 ($P = 0.468$), but showed a marginally positive effect in 2007 (8.2%, $P = 0.061$). N addition stimulated peak aboveground biomass only in 2006 (19.2%, $P < 0.001$;

Table 3 Results (P-values) of two-way ANOVA on the effects of warming (W), N (nitrogen) addition (N), and their interactions on peak aboveground biomass (AGB), peak grass biomass (GB), peak forb biomass (FB), and peak grass : forb biomass ratio (GB : FB)

	AGB	GB	FB	GB : FB
2006				
N	< 0.001	0.611	< 0.001	0.159
W	0.255	0.078	0.784	0.031
N × W	0.066	0.329	0.094	0.662
2007				
N	0.208	0.054	0.038	0.040
W	0.376	0.719	0.355	0.469
N × W	0.192	0.222	0.783	0.499

Table 3), with no effect of warming was detected in either 2006 or 2007 (Table 3). When separating aboveground biomass into different plant functional types, differential responses between grass and forb were observed to warming and N addition. Warming marginally reduced grass biomass in 2006 (17.0%, $P = 0.078$;
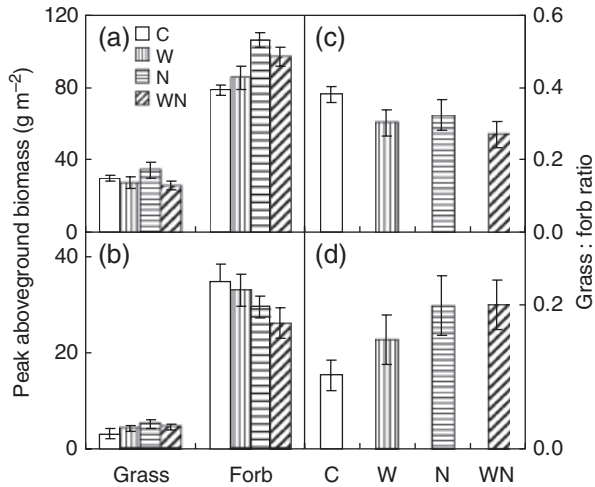
Fig. 4 Effect of warming and nitrogen (N) addition on peak aboveground biomass (a, b) of grass and forb and the grass : forb ratio (c, d) in 2006 (a, c) and 2007(b, d), respectively. See Fig. 3 for abbreviations.

Fig. 5 Temporal dependence of net ecosystem carbon (C) exchange (NEE; filled cycles and solid line), gross ecosystem productivity (GEP; open cycles and dotted line), and ecosystem respiration (ER; open triangles and dashed lines) on soil moisture (a) and soil temperature (b) across the two growing seasons.

Table 3, Fig. 4a) whereas it did not affect it in 2007 (Table 3, Fig. 4b). No effect of warming on forb biomass was observed in either 2006 or 2007 (Table 3, Fig. 4a and b). N addition marginally increased grass biomass by 35.8% ($P = 0.054$) in 2007, but had no effect in 2006 (Table 3, Fig. 4a). Forb biomass was stimulated by 24.0% ($P < 0.001$) in 2006 but was reduced by 17.7% ($P = 0.038$) under N addition in 2007 (Table 3, Fig. 4b). The differential responses between grass and forb also induced changes in grass : forb ratio under the warming and N addition treatments. For example, grass : forb ratio was decreased by warming in 2006 ($P = 0.031$; Table 3, Fig. 4c), but was increased by N addition in 2007 ($P = 0.040$; Table 3, Fig. 4d).

Impacts of biotic and abiotic factors on ecosystem C fluxes

The seasonal dynamics of NEE, GEP, and ER produced a one-peak pattern in both 2006 and 2007 (Fig. 3). Across the two growing seasons, NEE ($R^2 = 0.54$, $P = 0.008$), GEP ($R^2 = 0.63$, $P < 0.001$), and ER ($R^2 = 0.59$, $P < 0.001$; Fig. 5a) all increased linearly with increasing soil moisture, with steeper slope of the regression in GEP than in ER ($P < 0.05$; Fig. 5a). ER increased exponentially with soil temperature ($R^2 = 0.20$, $P = 0.037$; Fig. 5b) whereas no relationship was found between soil temperature and NEE or GEP. In 2006, seasonal variation in NEE showed no relationship with either soil temperature or moisture. However, the combination of soil moisture and soil temperature explained 70% and 87% of the seasonal variation in GEP and ER ($ER = ae^{bT}M + c$), respectively. In 2007, NEE and GEP, but not ER, increased linearly with NDVI ($R^2 = 0.68$, $P = 0.006$;
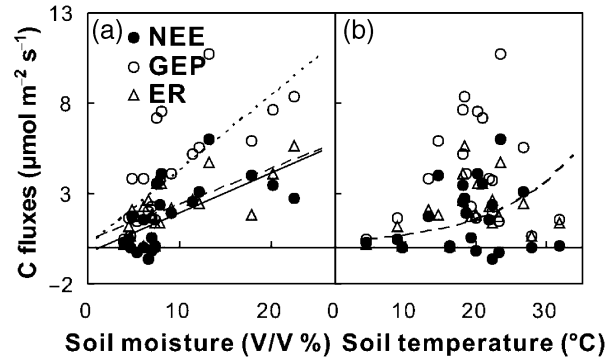
$R^2 = 0.55$, $P = 0.023$). NDVI and soil moisture together accounted for 92% and 91% of the seasonal variation in NEE and GEP, respectively. Ninety-three percent of seasonal variation in ER could be accounted for by the combination of soil moisture and soil temperature. The above results suggest all the concurrent seasonal variations in soil moisture, soil temperature, and plant growth contributed to the temporal variability in ecosystem C fluxes.

Across the 24 plots, seasonal mean NEE showed positively linear dependence upon mean soil moisture ($P = 0.006$; Fig. 6b), peak forb biomass ($P = 0.010$; Fig. 6d) in 2006, and peak grass biomass in 2007 ($P = 0.017$; Fig. 6c). On the contrary, negative correlations between mean NEE and mean soil temperature ($P = 0.008$; Fig. 6a) and peak forb biomass ($P = 0.031$; Fig. 6d) were found across the 24 plots in 2007. Stepwise multiple regression analyses demonstrated that 41.8% of the spatial variation in NEE could be explained by the combination of peak forb biomass (partial $R^2 = 0.22$, $P = 0.022$) and soil moisture (partial $R^2 = 0.20$, $P = 0.014$) in 2006. In 2007, soil temperature alone contributed to 30.1% ($P = 0.005$) of the spatial variation in NEE.

Seasonal mean GEP was linearly and positively correlated with mean soil moisture in both 2006 ($P = 0.003$) and 2007 (Fig. 6f), peak grass biomass in 2007 ($P = 0.031$; Fig. 6g), and peak forb biomass in 2006 ($P = 0.016$; Fig. 6h), whereas negatively with mean soil temperature in 2006 ($P < 0.001$; Fig. 6e). Stepwise multiple regression analyses showed that peak forb biomass (partial $R^2 = 0.43$, $P = 0.014$) and soil temperature (partial $R^2 = 0.23$, $P = 0.017$) together accounted for 66.5% of the spatial variation in GEP in 2006. In 2007, soil moisture alone was responsible for 20.5% ($P = 0.026$) of the spatial variation in GEP.
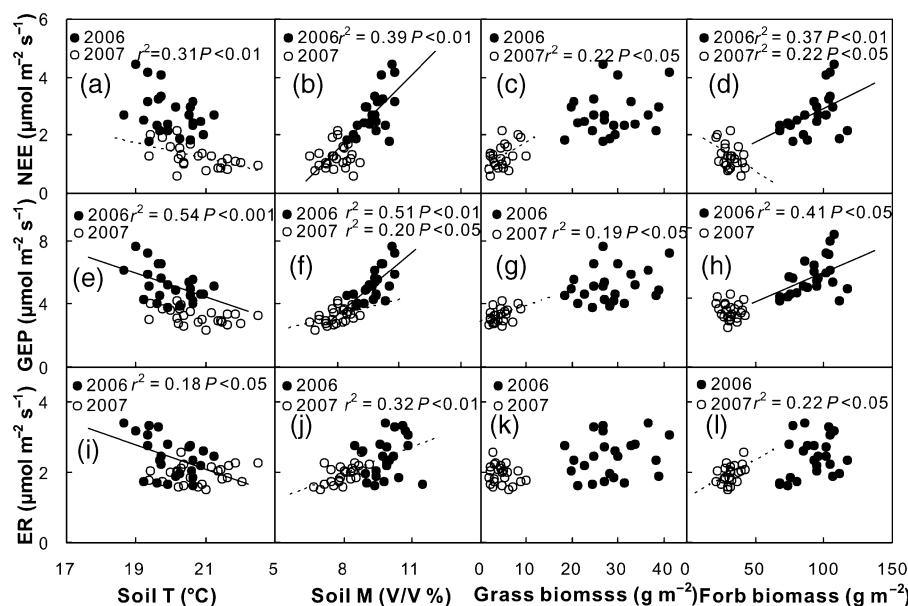
Fig. 6 Spatial dependence of seasonal mean net ecosystem C (carbon) exchange (NEE), gross ecosystem productivity (GEP), and ecosystem respiration (ER) on soil temperature (a, e, i), soil moisture (b, f, j), peak grass biomass (c, g, k), and peak forb biomass (d, h, l), respectively, across the 24 plots in 2006 (filled cycles and solid lines) and 2007 (open cycles and dotted lines).

Across the 24 plots, seasonal mean ER in 2007 showed positively linear correlation with mean soil moisture ($P = 0.004$; Fig. 6j) and peak forb biomass ($P = 0.033$; Fig. 6l). On the contrary, a negative correlation between mean ER and mean soil temperature ($P < 0.001$; Fig. 6i) was observed in 2006. Stepwise multiple regression analyses demonstrated that soil temperature explained 17.6% ($P = 0.041$) of the variation in ER in 2006. In 2007, 92.3% of the spatial variability in ER could be attributable to the combination of soil N availability (partial $R^2 = 0.57$, $P = 0.005$) and soil moisture (partial $R^2 = 0.36$, $P = 0.002$). These results suggest that both biotic (grass and forb biomass) and abiotic (soil moisture, soil temperature, and soil N availability) factors played important roles in regulating spatial variations in ecosystem C fluxes in the temperate steppe.

Discussion

NEE and its components in the temperate steppe

In the temperate steppe in northern China, greater ecosystem C uptake (GEP) than release (ER) leads to a net C sink (positive NEE) in both years. This is similar with that reported in an annual grassland (Harpole et al., 2007), some arctic ecosystems (Bubier et al., 2007; Oberbauer et al., 2007), and a former study in this area (Niu et al., 2008).

The interannual variations in NEE and its two components are positively related to those in precipitation,

demonstrating that precipitation determines the annual C exchange. Our results are in agreement with those in a previous study in the same study area (Niu et al., 2008) and those in other temperate grassland ecosystems (Suyker & Verma, 2001; Flanagan et al., 2002; Aires et al., 2008). The positive linear correlations between ecosystem C fluxes and soil moisture at the temporal (Fig. 5a) and spatial (Fig. 6b, f, and j) scales support the above findings. However, the interannual variability is different between the two components of NEE. Consistent with that in boreal and temperate forests (Barr et al., 2002), GEP fluctuates more strongly (34.7% lower in 2007 than 2006) than ER (10.5% lower in 2007 than 2006) in the temperate steppe, indicating that GEP is more sensitive to interannual climatic variation than ER in this study area. The different magnitudes of the interannual variability in GEP and ER could have been ascribed to their different water sensitivities, which is reflected by their different slopes when plotted against soil moisture (Fig. 5a). The greater dependence of GEP than ER on soil moisture across the two growing seasons supports the previous findings that GEP is more sensitive to soil water availability than ER in the semiarid temperate steppe.

Warming effects

It has been proposed that warming effects on ecosystem C exchange will likely be modulated by soil water regimes (Welker et al., 2004; Niu et al., 2008). For

example, Welker *et al.* (2004) have reported that the responses of C exchange to warming are different among dry, mesic, and wet tundra, indicating the dependence of warming effect on hydrological conditions. However, in our ecosystem, the warming effects on ecosystem C exchange (NEE) do not differ between the two hydrologically contrasting growing seasons. In the growing season with extra precipitation (2006), the insensitivity of NEE to elevated temperature could have been attributed to the counteractive effects of warming-induced changes in different control factors. Irrespective of no changes in peak aboveground biomass, warming-induced reductions in the growth of grass species (Table 3, Fig. 4a) and stimulation of forb biomass (8.6%) in 2006 lead to an increase in the proportion of forb biomass (lower grass : forb ratio) in the community. The warming-induced changes in species composition are consistent with a previous study in an annual grassland (Zavaleta *et al.*, 2003), in which warming increases forb production and abundance but does not affect grass. The positive responses of forb biomass (Fig. 6d and h) could have ameliorated the negative impacts of lower soil water availability (Fig. 6b and f) on NEE and GEP under warming condition. Given no effects of warming on plant growth and community composition in the dry season (2007), the insensitivity of NEE to warming could have been accounted for by the concurrent water limitation of GEP and ER in this growing season (Fig. 6f and j). In addition, consistent with some previous studies (Rustad *et al.*, 2001; Mellilo *et al.*, 2002), we have observed warming-induced increase in soil N availability, especially in the dry period. The positive effect of enhanced N availability could have also ameliorated the negative impacts of warming-induced water depletion.

Insignificant changes in GEP and ER have resulted in a consequently little NEE response under warming in the 2 years (Table 1; Fig. 4). A previous study has also observed insignificant changes in C exchange components under experimental warming in 2006 in the same area (Niu *et al.*, 2008). Our results are inconsistent with those in a recent study in tundra (Oberbauer *et al.*, 2007), in which both GEP and ER respond positively to climate warming. This highlights the ecosystem-specific responses of ecosystem C exchange to climate change depending on initial conditions (Shaver *et al.*, 1998, 2000). In addition, our results in the wet growing season support the proposition that warming-induced species shifts can mediate warming impacts on ecosystem C exchange (Campell & Smith, 2000; Harte *et al.*, 2006). Our findings have important implications for global climate–C cycle models, in that shifts in species composition should be taken into consideration to project the C-cycle responses to future climate change (Dufresne *et al.*, 2002; Fung *et al.*, 2005).

N addition effects

Although a great deal of research has been conducted on the responses of plant communities to N addition and has considered the implications for ecosystem C balance (Williams & Silcock, 1997; Berendse *et al.*, 2001; Heijmans *et al.*, 2001), there is little research effort on the changes in NEE response to N addition. Saarnio *et al.* (2003) have found only minor response of NEE to N addition in a 3-year N addition study in Finnish peatland. Harpole *et al.* (2007) have reported that N addition tends to reverse the positive effect on NEE due to water addition. However, N addition has been observed to increase NEE in the two hydrologically contrasting growing seasons because of the larger stimulation in GEP than in ER in our ecosystem, which is consistent to the hypothesis of Bubier *et al.* (2007). Our observations suggest an overall enhancement of ecosystem C sequestration under N addition in the temperate steppe.

By stimulating GEP but not changing ER, N addition exerts consistent positive effects on NEE in the two hydrologically contrasting growing seasons. However, N addition has differential impacts on the growth of two major plant functional types in the two growing seasons. In the wet growing season (2006), N addition increases peak aboveground biomass (primarily forb biomass) with no effect on grass biomass (Table 3). The increase in forb biomass could have led to the stimulation of GEP (Fig. 6h) under N addition in 2006. However, given no relationship between ER and plant growth, the positive N effects on NEE in 2006 could have been contributed to the N-induced stimulation of forb biomass. In contrast to the wet growing season, reductions in forb biomass and increases in grass biomass in the dry growing season in 2007 have caused no changes in peak aboveground biomass in this year (Table 3). Higher GEP associated with grass biomass (Fig. 6g) and lower ER related to forb biomass (Fig. 6l) could have accounted for the positive responses of NEE to N addition in 2007 (Fig. 6c and d). Moreover, less stimulation of seasonal mean NEE induced by N addition in the warmed than unwarmed plots (Fig. 3a and b) suggests antagonistic effects of the two treatments. The suppression of N responses of NEE under warming could also have been attributed to the reduced soil water availability. Our observations highlight the importance of differential plant growth of distinctive functional groups across years in modulating the responses of ecosystem C exchange to N addition.

Impacts of drought events

It is expected that drought can reduce gross primary productivity as well as NEE in terrestrial ecosystems (Ciais *et al.*, 2005; Granier *et al.*, 2007) and act as the main

source of interannual variation in terrestrial C sequestration (Pereira *et al.*, 2007). In this study, lower seasonal mean C fluxes in 2007 than those in 2006 and greater C release than uptake (negative NEE; Fig. 3b) until late July in 2007 indicate critical roles of soil water availability in regulating ecosystem C exchange in the semiarid temperate steppe in northern China. Moreover, larger reductions in GEP (34.7%) than ER (10.5%) in 2007 compared with the respective C flux in 2006 suggest drought may restrain ecosystem C uptake more than C release. The findings are consistent with those of model simulations (Zeng *et al.*, 2005) and observational studies (Ciais *et al.*, 2005; Breshears *et al.*, 2005) that drought induces substantial terrestrial ecosystem C loss.

Although it is anticipated that global warming will make drought events more frequent (Cook *et al.*, 2004; Manabe *et al.*, 2004), warming may have insignificant impacts on ecosystem C exchange in our system. Similar positive responses of ecosystem exchange to N addition between the wet (22.7%) and dry (22.5%) growing seasons imply independence of the N effect on ecosystem C fluxes upon hydrological conditions in this temperate steppe. This is inconsistent with a recent assumption (Harpole *et al.*, 2007) that grassland ecosystem response to N addition will be strongly dependent on precipitation patterns. Thus, irrespective of the dependence of interannual variability in ecosystem C fluxes on precipitation, drought may not alter the impacts of warming and N addition on ecosystem C exchange in the semiarid temperate grassland in northern China.

Conclusions

In contrast to the common expectation of stimulation of ecosystem C release under elevated temperature, we found insignificant responses to warming of ecosystem C exchange and its components in the temperate steppe in northern China, which could have been attributable to the offset of the positively direct effects by the negatively indirect effects via aggravating water limitation (Wan *et al.*, 2007; Niu *et al.*, 2008). N addition stimulated ecosystem C exchange (NEE) primarily by increasing C assimilation process (GEP), which emphasizes the limitation of soil N availability on ecosystem C exchange in this semiarid grassland. Moreover, this study was conducted during two hydrologically contrasting growing seasons (wet in 2006 and dry in 2007) and, thereby, offered a unique opportunity to understand how drought event affects ecosystem C fluxes and their responses to warming and N addition in the temperate steppe. Although warming and N effects on plant productivity and species composition were dependent on precipitation regimes, drought event did not alter the relative responses of ecosystem C

exchange to warming and N addition. These findings will improve our understanding of C sequestration response to the simultaneous climate change drivers in arid and semiarid grassland ecosystems.

References

Aires LMI, Pio CA, Pereira JS (2008) Carbon dioxide exchange above a Mediterranean C_3/C_4 grassland during two climatologically contrasting years. *Global Change Biology*, **14**, 539–555.

Barr AG, Griffis TJ, Black TA *et al.* (2002) Comparing the carbon budgets of boreal and temperate deciduous forest stands. *Canadian Journal of Forest Research*, **32**, 813–822.

Berendse F, van Breemen N, Rydin H *et al.* (2001) Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in Sphagnum bogs. *Global Change Biology*, **7**, 591–598.

Bonal D, Bosc A, Ponton S *et al.* (2008) Impact of severe dry season on net ecosystem exchange in the Neotropical rainforest of French Guiana. *Global Change Biology*, **14**, 1917–1933.

Breshears DD, Cobb NS, Rich PM *et al.* (2005) Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of USA*, **102**, 15144–15148.

Bubier JL, Moore TR, Bledzki LA (2007) Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog. *Global Change Biology*, **13**, 1168–1186.

Buchmann N, Schulze E-D (1999) Net CO_2 and H_2O fluxes of terrestrial ecosystems. *Global Biogeochemical Cycles*, **13**, 751–760.

Campell BD, Smith SDM (2000) A synthesis of recent global change research on pasture and rangeland production: reduced uncertainties and their management implications. *Agriculture, Ecosystems and Environment*, **82**, 39–55.

Ciais Ph, Reichstein M, Viovy N *et al.* (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, **437**, 529–533.

Cook ER, Woodhouse CA, Eakin CM, Meko DM, Stahle DW (2004) Long-term aridity changes in the Western United States. *Science*, **306**, 1015–1018.

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.

Cowling SA, Shin Y (2006) Simulated ecosystem threshold responses to co-varying temperature, precipitation and atmospheric CO_2 within a region of Amazonia. *Global Ecology and Biogeography*, **15**, 553–566.

Dermody O, Weltzin JF, Engel EC, Allen P, Norby RJ (2007) How do elevated [CO₂], warming, and reduced precipitation interact to affect soil moisture and LAI in an old field ecosystem? *Plant Soil*, **301**, 255–266.

Dufresne JL, Friedlingstein P, Berthelot M *et al.* (2002) On the magnitude of positive feedback between future climate change and the carbon cycle. *Geophysical Research Letters*, **29**, 1405, doi: 10.1029/2001GL013777.

Elser JJ, Bracken MES, Cleland EE *et al.* (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, **10**, 1135–1142.

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.

Fung IY, Doney SC, Lindsay K, John J (2005) Evolution of carbon sinks in a changing climate. *Proceedings of the National Academy of Sciences of USA*, **102**, 11201–11206.

Galloway JN, Cowling EB (2002) Reactive nitrogen and the world: 200 years of change. *AMBIO*, **31**, 64–71.

Granier A, Reichstein M, Breda N *et al.* (2007) Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology*, **143**, 123–145.

Gruber N, Galloway JN (2008) An Earth-system perspective of the global nitrogen cycle. *Nature*, **451**, 293–298.

Harpole WS, Potts DL, Suding KN (2007) Ecosystem responses to water and nitrogen amendment in a California grassland. *Global Change Biology*, **13**, 2341–2348.

Harte J, Saleska S, Shih T (2006) Shifts in plant dominance control carbon-cycle responses to experimental warming and widespread drought. *Environmental Research Letters*, **1**: 1, 014001, doi: 10.1088/1748-9326.

Heijmans MPD, Berendse F, Arp WJ, Masselink AK, Kless H, de Visser W, Van Breemen N (2001) Effects of elevated carbon dioxide and increased nitrogen deposition on bog vegetation in the Netherlands. *Journal of Ecology*, **89**, 268–279.

Hooper DU, Johnson L (1999) Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. *Biogeochemistry*, **46**, 247–293.

Hungate BA, Dukes JS, Shaw MR, Luo Y, Field CB (2003) Nitrogen and climate change. *Science*, **302**, 1512–1513.

Huxman TE, Cable JM, Ignace DD, Eilts JA, English NB, Weltzin J, Williams DG (2004b) 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.

Huxman TE, Smith MD, Fay PA *et al.* (2004a) Convergence across biomes to a common rain-use efciency. *Nature*, **429**, 651–654.

Illeris L, Christensen TR, Mastepanov M (2004) Moisture effects on temperature sensitivity of CO₂ exchange in a subarctic heath ecosystem. *Biogeochemistry*, **70**, 317–330.

Janssens IA, Lankreijer H, Matteucci G *et al.* (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology*, **7**, 269–278.

Jones MB, Donnelly A (2004) Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO₂. *New Phytologist*, **164**, 423–439.

Kirchner TB (1977) The effects of resource enrichment on the diversity of plants and arthropods in a shortgrass prairie. *Ecology*, **58**, 1334–1344.

Kueppers LM, Harte J (2005) Subalpine forest carbon cycling: short- and long-term influence of climate and species. *Ecological Applications*, **15**, 1984–1999.

LeBauer DS, Treseder KK (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, **89**, 371–379.

Luo YQ, Su B, Currie WS *et al.* (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience*, **54**, 731–739.

Manabe S, Wetherald RT, Milly PCD, Delworth TL, Stouffer RJ (2004) Century-scale change in water availability: CO₂-quadrupling experiment. *Climatic Change*, **64**, 59–76.

Melillo JM, Steudler PA, Aber JD *et al.* (2002) Soil warming and carbon-cycle feedbacks to the climate system. *Science*, **298**, 2173–2176.

Myneni RB, Dong J, Tucker CJ *et al.* (2001) A large carbon sink in the woody biomass of Northern forests. *Proceedings of the National Academy of Sciences of USA*, **98**, 14784–14789.

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386**, 698–702.

Niu S, Wu M, Han Y, Xia J, Li L, Wan S (2008) Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe. *New Phytologist*, **177**, 209–219.

Norby RJ, Luo YQ (2004) Evaluating ecosystem responses to rising atmospheric CO₂ and global warming in a multi-factor world. *New Phytologist*, **162**, 281–293.

Oberbauer SF, Tweedie CE, Welker JM *et al.* (2007) Tundra CO₂ fluxes in response to experimental warming across latitudinal and moisture gradients. *Ecological Monographs*, **77**, 221–238.

Oechel WC, Hastings SJ, Vourlrtis 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.

Pereira JS, Mateus JA, Aires LM *et al.* (2007) Net ecosystem carbon exchange in three contrasting Mediterranean ecosystems – the effect of drought. *Biogeosciences*, **4**, 791–802.

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.

Reich PB, Hobbie SE, Ellsworth TLDS *et al.* (2006) Nitrogen limitation constrains sustainability of ecosystem response to CO₂. *Nature*, **440**, 922–925.

Risch AC, Frank DA (2007) Effects of increased soil water availability on grassland ecosystem carbon dioxide fluxes. *Biogeochemistry*, **86**, 91–103.

Rustad LE, Campbell JL, Marion GM *et al.* (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.

Ryan MG (1991) Effects of climate change on plant respiration. *Ecological Applications*, **1**, 157–167.

Saarnio S, Jarvio S, Saarinen T, Vasander H, Silvola J (2003) Minor changes in vegetation and carbon gas balance in a boreal mire under raised CO_2 or NH_4NO_3 supply. *Ecosystems*, **6**, 46–60.

Saleska SR, Harte J, Torn MS (1999) The effect of experimental ecosystem warming on CO_2 uxes in a montane meadow. *Global Change Biology*, **5**, 125–141.

Shaver GR, Canadell J, Chapin III FS *et al.* (2000) Global warming and terrestrial ecosystems: a conceptual framework for analysis. *Bioscience*, **10**, 871–882.

Shaver GR, Johnson LC, Cades DH *et al.* (1998) Biomass and CO_2 flux wet sedge tundras: responses to nutrients, temperature, and light. *Ecological Monographs*, **68**, 75–97.

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, Çetinkökü Ö, Albrizio R, Kanber R (2002) Automated closed-system canopy-chamber for continuous eld-crop monitoring of CO_2 and H_2O uxes. *Agricultural and Forest Meteorology*, **111**, 171–186.

Skogley EO, Dobermann A (1996) Synthetic ion-exchange resins: soil and environmental studies. *Journal of Environmental Quality*, **25**, 13–24.

Suttle KB, Thomsen MA, Power ME (2007) Species interactions reverse grassland responses to changing climate. *Science*, **315**, 640–642.

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 S, Norby RJ, Ledford J, Weltzin JF (2007) Responses of soil respiration to elevated CO_2, air warming, and changing soil water availability in a model old-field grassland. *Global Change Biology*, **13**, 2411–2424.

Welker JM, Fahnestock JT, Henry GHR, O'Dea KW, Chimner RA (2004) CO_2 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.

Williams BL, Silcock DJ (1997) Nutrient and microbial changes in the peat profile beneath Sphagnum magellanicum in response to additions of ammonium nitrate. *Journal of Applied Ecology*, **34**, 961–970.

Woodwell GM, Hobbie JE, Houghton RA, Melillo JM, Moore B, Peterson BJ, Shaver GR (1983) Global deforestation: contribution to atmospheric carbon dioxide. *Science*, **222**, 1081–1086.

Xia J, Wan S (2008) Global response patterns of terrestrial plant species to nitrogen addition. *New Phytologist*, **179**, 428–439.

Yuan ZY, Li LH, Han XG, Huang JH, Jiang GM, Wan SQ (2005) Soil characteristics and nitrogen resorption in *Stipa krylovii* native to northern China. *Plant and Soil*, **273**, 257–268.

Zavaleta ES, Shaw MR, Chiariello NR, Thomas BD, Cleland EE, Field CB, Mooney HA (2003) Grassland response to three years of elevated temperature, CO_2, precipitation, and N deposition. *Ecological Monographs*, **73**, 585–604.

Zeng N, Qian H, Rodenbeck C, Heimann M (2005) Impact of 1998–2002 midlatitude drought and warming on terrestrial ecosystem and the global carbon cycle. *Geophysical Research Letters*, **32**, L22709, doi: 10.1029/2005GL024607.

Zhou X, Weng E, Luo Y (2008) Modeling patterns of nonlinearity in ecosystem responses to temperature, CO_2, and precipitation changes. *Ecological Applications*, **18**, 453–466.