Water-use efficiency in response to climate change: from leaf to ecosystem in a temperate steppe

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Abstract

Water-use efficiency (WUE) has been recognized as an important characteristic of ecosystem productivity, which links carbon (C) and water cycling. However, little is known about how WUE responds to climate change at different scales. Here, we investigated WUE at leaf, canopy, and ecosystem levels under increased precipitation and warming from 2005 to 2008 in a temperate steppe in Northern China. We measured gross ecosystem productivity (GEP), net ecosystem CO_2 exchange (NEE), evapotranspiration (ET), evaporation (E), canopy transpiration (T_c), as well as leaf photosynthesis (P_{max}) and transpiration (T_l) of a dominant species to calculate canopy WUE ($WUE_c = GEP/T$), ecosystem WUE ($WUE_{gep} = GEP/ET$ or $WUE_{nee} = NEE/ET$) and leaf WUE ($WUE_l = P_{max}/T_l$). The results showed that increased precipitation stimulated WUE_c, WUE_{gep} and WUE_{nee} by 17.1%, 10.2% and 12.6%, respectively, but decreased WUE_l by 27.4%. Climate warming reduced canopy and ecosystem WUE over the 4 years but did not affect leaf level WUE. Across the 4 years and the measured plots, canopy and ecosystem WUE linearly increased, but leaf level WUE of the dominant species linearly decreased with increasing precipitation. The differential responses of canopy/ecosystem WUE and leaf WUE to climate change suggest that caution should be taken when upscaling WUE from leaf to larger scales. Our findings will also facilitate mechanistic understanding of the C–water relationships across different organism levels and in projecting the effects of climate warming and shifting precipitation regimes on productivity in arid and semiarid ecosystems.

Keywords: climate warming, evapotranspiration, grassland, gross ecosystem productivity, net ecosystem carbon exchange, photosynthesis, precipitation regimes, species composition, water-use efficiency

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Introduction

According to IPCC's prediction (2007), global average surface temperature will warm 1.8–4.0 °C and global precipitation regimes will change considerably by the end of the 21st century, which will greatly impact both ecosystem carbon (C) and water processes (Scanlon & Albertson, 2004; Niu *et al.*, 2008; Yu *et al.*, 2008). As a critical link between C and water cycles in terrestrial ecosystems, water-use efficiency (WUE), the ratio of CO_2 assimilation to water losses, has been identified as an effective integral trait for assessing ecosystem response to climate change (Baldocchi, 1994; Bacon, 2004; Hu *et al.*, 2008; Kuglitsch *et al.*, 2008; Beer *et al.*, 2009). WUE is also an important factor to simulate primary productivity in models (Roupsard *et al.*, 2009). Therefore, understanding ecosystem WUE and its key controlling processes in response to precipitation

change and warming are helpful to project climate change-terrestrial C feedbacks.

Ecosystem WUE is predicted to decrease under climate warming in a modeling study (Bell *et al.*, 2010), which is supported by an experimental study in Belgium grassland (De Boeck *et al.*, 2006). Previous studies on ecosystem WUE in response to precipitation change were mainly conducted by spatial or temporal gradient analysis. Across spatial precipitation gradients, ecosystem WUE or rain-use efficiency (RUE) has been reported to decrease (Huxman *et al.*, 2004b; Scanlon & Albertson, 2004; Bai *et al.*, 2008; Yu *et al.*, 2008) or not change (Lauenroth *et al.*, 2000) with increasing precipitation. Over a large typical grassland area (200–1200 mm), ecosystem RUE is low at both the dry end and the wet end of the annual precipitation spectrum, peaking around 475 mm (Paruelo *et al.*, 1999). For a given ecosystem, a number of studies have shown that ecosystem WUE decreases (Lauenroth *et al.*, 2000; Li *et al.*, 2008) or increases (Bai *et al.*, 2008) over time with increasing annual precipitation. This lack of consensus

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in previous studies stems in part from other controlling factors that may confound water effects across spatial or temporal scales. Compared with gradient studies, manipulative experiments can control water treatments without changing other environment factors, and thus discern direct effects of changing climate variables on ecosystem WUE. However, there have been few manipulative experiments studying the response of ecosystem WUE to changing precipitation and climate warming (Huxman et al., 2004a; De Boeck et al., 2006).

In order to address WUE in response to climate change at large scale, attempts have been made to upscale WUE from leaves to canopies to the global levels (Tu et al., 2008). However, the controlling processes or factors on WUE may vary with the scale of analysis. Individual C and ecohydrological processes at different biological levels may differentially respond to climate change, leading to complex response patterns and changes in ecosystem C–water balance (Lindroth & Cienciala, 1996; Tu et al., 2008). In general, leaf or plant WUE, the ratio of plant photosynthesis to transpiration, usually decreases with an increase in rainfall because stomatal conductance limits transpirational water loss more than CO_2 assimilation (Farquhar & Sharkey, 1982). Canopy WUE, the ratio of gross ecosystem productivity (GEP) to canopy transpiration (T_c, Loomis & Connor, 1992; Yepez et al., 2007), may depend on the responses of both plant physiology and community structure. A plant community is composed of many coexisting species that may differ in both C uptake and water loss in a changing environment. Therefore, changes in WUE at the canopy level may not be simply the summed changes in leaf WUE of all the plant species in a community. Ecosystem WUE, the ratio of GEP to evapotranspiration (ET, Baldocchi, 1994; Ponton et al., 2006; Hu et al., 2008; Kuglitsch et al., 2008; Yu et al., 2008; Beer et al., 2009), or the ratio of net ecosystem CO_2 exchange (NEE) to ET (Huxman et al., 2004a; Scanlon & Albertson, 2004; Potts et al., 2006), is related to multiple components of ecosystem C and water processes. On one hand, ecosystem WUE involves water loss from both the canopy (T_c) and the soil surface (evaporation, E) that have different sensitivities to changes in temperature and water (Baldocchi, 1994; Hu et al., 2008; Jassal et al., 2009). On the other hand, ecosystem WUE based on NEE is associated with both C uptake (GEP) and release (ecosystem respiration, ER) processes that inherently differ in response to changing water availability (Oechel et al., 1998). Therefore, WUE in leaves, canopies and ecosystems involves different C and water process, and thus may respond differentially to climate change. Understanding the mechanisms underlying variation in WUE response at different scales is necessary to provide data for validating any upscaling method. Nevertheless, no

attempt has been made to compare WUE response to climate change at different organism scales.

The temperate steppe in Inner Mongolia represents an important part of the world largest grassland biome in the Eurasian continent, covering a total area of $41.1 \text{ hm} \times 10^5 \text{ hm}$ (Li et al., 2003) and storing 0.3–0.6 Pg soil organic C (Wang et al., 2000). This region is a typical arid or semiarid grassland that is predicted to be sensitive to climatic change (Christensen et al., 2004). Understanding ecosystem WUE in this area will help to predict primary productivity change in grassland under future climate change scenarios. This study was conducted to investigate the response of WUE to simulated climate change at different organism levels, as well as its underlying mechanisms based on a 4-year manipulative field experiment. According to climate history in the study site, air temperature has increased by 2.4 °C over the past 50 years (1953–2008). Summer precipitation is also projected to increase (Sun & Ding, 2010). In this study, we simulated climate warming with infrared radiator and increased summer precipitation (July and August) with a spray irrigation system. The study site has low mean annual precipitation (382.3 mm) but varies greatly among years. The four experimental years (2005–2008) cover the highest, lowest and average annual precipitations of the past 50 years, providing a unique chance for studying ecosystem responses to interannual precipitation fluctuations. Specifically, we address the following scientific questions: (1) How does WUE at different organism levels respond to changes in precipitation/water availability and warming? (2) How do the components of ET regulate C exchange and its responses to precipitation increase in this ecosystem?

Materials and methods

Experimental site

The experimental site was located in Duolun County (42°02′N, 116°17′E, 1324 m a.s.l.), Inner Mongolia of northern China. The grassland was dominated by Artemisia frigida Willd, Stipa krylovii Roshev., Potentilla acaulis L., Cleistogenes squarrosa (Trin.) Keng, Allium bidentatum Fisch. ex Prokh. and Agropyron cristatum (L.) Gaertn (Niu et al., 2008). The mean annual precipitation is 382.3 mm and the mean annual temperature is 2.1 °C averaged from 1952 to 2008. The soil is a Haplic Calcisols (FAO classification), with $62.75 \pm 0.04\%$ sand, $20.30 \pm 0.01\%$ silt and $16.95 \pm 0.01\%$ clay. Mean soil bulk density is 1.31 g cm^{-3}. The soil organic C concentration is 16.10 g kg^{-1} and pH is 6.84 (Liu et al., 2009).

Experimental design

The study was a part of the Duolun Global Change Multifactor Experiments (GCME). There were three pairs of 10 m × 15 m

plots; one plot in each pair was assigned as the increased precipitation treatment and the other as the control. In each $10 \, \text{m} \times 15 \, \text{m}$ plot, six sprinklers were evenly arranged into two rows with the distance between any two sprinklers being 5 m. Each sprinkler covered a circular area with a diameter of 3 m; therefore, the six sprinklers totally covered the $10 \, \text{m} \times 15 \, \text{m}$ plot. In July and August, 15 mm of water was added weekly to the increased precipitation plots. Therefore, a total of 120 mm precipitation (approximately 30% of mean annual precipitation in the study site) was supplied each year.

Within each $10 \, \text{m} \times 15 \, \text{m}$ plot, four $3 \, \text{m} \times 4 \, \text{m}$ subplots were treated as warmed and control subplots with two replicates. The subplots were randomly assigned to the temperature treatments. The warmed subplots have been heated continuously since April 28, 2005 using $1.65 \, \text{m} \times 0.15 \, \text{m}$ MSR-2420 infrared radiant heaters (Kalglo Electronics Inc., Bethlehem, PA, USA). The heaters were suspended 2.5 m above the ground. All the heaters in the warming treatments were set for a radiation input of approximately 1600 W. The efficiency for this type of infrared heater in this study is about 10%, or on the order of $13.3 \, \text{W} \, \text{m}^{-2}$ in this study, at an even annual wind speed of $4 \, \text{m} \, \text{s}^{-1}$ (Kimball, 2005). One 'dummy' heater with the same shape and size as the infrared radiator was suspended with the same height in the unwarmed control subplot to simulate the shading effects of the heater. Thus, there were four treatments (control, warming, increased precipitation and warming plus increased precipitation) with six replicates for each treatment.

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 from May to October during 2005–2008.

Measuring components of ecosystem WUE

Ecosystem CO_2 and water fluxes were measured with a transparent chamber ($0.5 \, \text{m} \times 0.5 \, \text{m} \times 0.5 \, \text{m}$) attached to an infrared gas analyzer (IRGA; LI-6400, LiCor, Lincoln, NE, USA). One permanent square aluminum frame ($0.5 \, \text{m} \times 0.5 \, \text{m}$) was inserted into the soil in each subplot to a depth of approximately 3 cm in April 2005. During measurement, the chamber was placed on these frames. Measurements were taken twice a month during the growing season (May–October). Two small fans ran continuously to mix the air inside the chamber during the measurements. Nine consecutive recordings of CO_2 and water vapor concentrations 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 NEE and ET. The methods to measure ER and to calculate GEP were described in detail in the previous studies (Niu et al., 2008, 2009). Ecosystem WUE was calculated as GEP/ET (WUE_{gep}) or NEE/ET (WUE_{nee}).

Positive and negative NEE values represent net C uptake from and release by the ecosystem, respectively.

Soil E was measured by a LI-8100 portable soil CO_2 flux system (Li-Cor Inc.) at the same time as the soil respiration measurements. One PVC collar (11 cm in internal diameter and 5 cm in height) was permanently inserted 2–3 cm into the soil in each subplot. Soil respiration and E were measured twice a month at the same time as measurements of ecosystem gas exchange during growing seasons from 2005 to 2008. Measurements were taken by setting the LI-8100 chamber on the PVC collars for 1–2 min. Values of CO_2 and water vapor in the chamber were recorded once per second. The slopes of CO_2 and water vapor change over the measuring time were used to calculate soil respiration and E. The equation for calculating soil E was same as that for calculating soil respiration which can be found in the soil-flux calculation procedure in the LI-6400 manual (LI-COR Inc., 2003). Living plants inside the soil collars (if any) were removed by hand at least 1 day before the measurement to eliminate aboveground plant respiration and transpiration. T_c was calculated as the difference between ET and E. We calculated canopy WUE (WUE_c) as GEP/T_c.

Leaf level WUE

Photosynthetic rate (P_{max}) and transpiration rate (T_l) of a dominant species, *S. krylovii* Roshev., were measured by an open gas-exchange system (Li-6400; Li-Cor Inc.) with a $6 \, \text{cm}^2$ clamp-on leaf cuvette on clear days (August 31, 2005, September 5, 2007 and July 24, 2008). Leaf gas exchange was measured in the sunny morning between 09:00 to 11:00 hours (local time). During the measurement, leaves were illuminated at $1500 \, \mu\text{mol} \, \text{m}^{-2} \, \text{s}^{-1}$ using the LED light system. We did not control leaf temperature, water vapor or CO_2 concentrations. Leaf level WUE (WUE_l) was calculated as P_{max}/T_l.

Data analysis

We first calculated the monthly mean values of NEE, GEP, ER, E and ET, and then averaged the monthly values from May to October for a seasonal mean values for each year. A repeat measures analysis of variance (ANOVAs) with a split-plot design was used to analyze the main and interactive effects of warming, increased precipitation and year on ecosystem WUE and ecosystem C and water exchange. Between-subject effects were evaluated as block, warming, increased precipitation and their interactions and within-subject effects were year and its interactions with warming and increased precipitation. Leaf level gas exchange and WUE were analyzed using a four-way ANOVA for a split-plot design to determine the main and interactive effects of year, block, warming and increased precipitation. Linear regression analysis was used to evaluate the relationships between precipitation and ecosystem WUE and its components, or between soil moisture and leaf level WUE and its components. In order to compare with previous studies (Paruelo et al., 1999; Lauenroth et al., 2000; Bai et al., 2008; Li et al., 2008), we used annual precipitation for the relationship between precipitation and ecosystem WUE. All statistical analyses were performed using SAS V.8.1 (SAS Institute Inc., Cary, NC, USA).

Results

Microclimate

Annual precipitation varied from 198 mm in 2007 to 422.4 mm in 2006 with a mean of 322.9 mm during the 4 years (Table 1). Precipitation addition increased soil moisture by an average of 1.4v/v% over the 4 years across both the warmed and the control plots (Table 1). Experimental warming elevated soil temperature at 10 cm by 1.17 °C in the ambient precipitation subplots and by 0.74 °C in the increased precipitation subplots over the 4 years (Table 1).

Ecosystem and canopy WUE in response to climate change

Over the 4 years, precipitation addition stimulated WUE_c, WUE_{gep} and WUE_{nee} by 17.1%, 10.2% and 12.6%, respectively (all $P < 0.05$, Fig. 1). Experimental warming decreased WUE_c, WUE_{gep} and WUE_{nee} by 4.6% ($P = 0.17$), 5.9% ($P < 0.05$) and 7.7% ($P < 0.05$), respectively, over the 4 years (Fig. 1, Table 2). There were no interactive effects of experimental warming with year or precipitation addition on WUE_c, WUE_{gep} or WUE_{nee} ($P > 0.05$, Table 2). Across the 4 years and four treatments, WUE_c, WUE_{gep} and WUE_{nee} all linearly increased with increasing precipitation input (all $P < 0.01$, Fig. 2).

Components of ecosystem WUE in response to climate change

Precipitation addition significantly stimulated all the components of C and water cycling during the experi-

mental period (Table 2). Over the 4 years, NEE, GEP, ET, E and T_c were 32.6%, 31.5%, 19.5%, 19.1% and 19.5% higher under elevated than ambient precipitation, respectively (all $P < 0.05$, Table 2, Fig. 3). Year significantly interacted with precipitation addition to impact ecosystem C and water processes (Table 2). For example, precipitation addition stimulated GEP and ET by 70.4% and 37.5% in dry 2007, and by 24.8% and 12.6% in normal 2008, respectively (Fig. 3). Experimental warming significantly reduced NEE by 9.6% and E by 3.7% (all $P < 0.05$), but did not affect GEP, ET, T_c and E/ET over the 4 years (Table 2, Fig. 3). Neither year nor precipitation addition interacted with warming to affect any component of ecosystem C and water cycling.

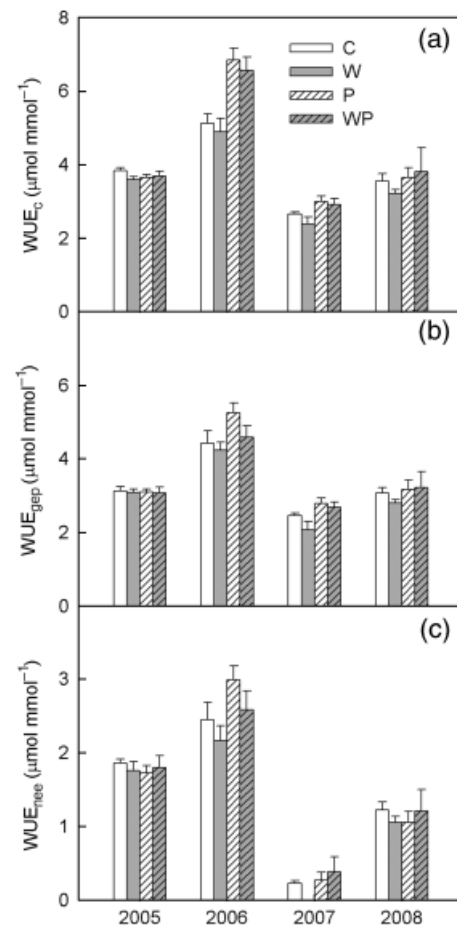GEP, NEE and E linearly increased with the amount of precipitation input across the 4 years and four

Fig. 1 Canopy (WUE_c, a) and ecosystem water-use efficiency (WUE_{gep}, b, and WUE_{nee}, c) in response to increased precipitation and climate warming from 2005 to 2008. The values in the figure represent the seasonal mean values (means ± 1 SE) across the growing season in each year. C, control; W, warming; P, increased precipitation; WP, both warming and increased precipitation.

Table 1 Measured annual precipitation (PPT), soil temperature (ST) and soil moisture (SM) during growing season under four treatments (Tr)

Tr	2005	2006	2007	2008
PPT	322.8	422.4	198	348.4
ST				
C	16.73 ± 0.18^b	15.30 ± 0.22^{bc}	17.33 ± 0.25^b	15.78 ± 0.20^b
W	18.23 ± 0.27^a	16.28 ± 0.20^a	18.46 ± 0.27^a	16.85 ± 0.23^a
P	16.54 ± 0.19^b	14.72 ± 0.21^c	17.10 ± 0.24^b	15.95 ± 0.32^b
WP	17.68 ± 0.22^a	15.39 ± 0.22^b	17.77 ± 0.37^{ab}	16.43 ± 0.29^{ab}
SM				
C	9.74 ± 0.34^{ab}	11.29 ± 0.26^b	9.56 ± 0.18^c	10.12 ± 0.33^b
W	8.55 ± 0.66^b	10.94 ± 0.46^b	9.22 ± 0.44^c	9.52 ± 0.32^b
P	11.24 ± 0.74^a	13.33 ± 0.34^a	11.75 ± 0.23^a	11.99 ± 0.27^a
WP	9.10 ± 0.59^b	11.42 ± 0.29^b	10.55 ± 0.34^b	11.10 ± 0.40^a

Different letters (a, b, c, d) among the four treatments indicate statistical differences at $P < 0.05$ in each year.
C, control; W, warming; P, increased precipitation; WP, warming plus increased precipitation.

Table 2 Results (i.e., P-values) of split-plot design with repeated measures ANOVAs on the effects of block (B), increased precipitation (P), warming (W), year (Y), and their interactions on seasonal means of net CO_2 exchange (NEE), gross ecosystem productivity (GEP), evapotranspiration (ET), evaporation (E), transpiration (T_c), the ratio of E/ET, canopy water-use efficiency (WUE_c), as well as ecosystem water-use efficiency based on GEP (WUE_{gep}) and NEE (WUE_{nee})

	NEE	GEP	ET	E	T_c	E/ET	WUE_c	WUE_{gep}	WUE_{nee}
B	0.117	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.072	0.454	**0.013**	**<0.001**
P	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.078	**<0.001**	**0.004**	**0.004**
W	**0.042**	0.057	0.371	**0.046**	0.478	0.123	0.173	**0.049**	**0.031**
B × P	0.800	0.845	0.794	0.815	0.797	0.652	0.579	0.709	0.528
B × W	0.372	0.719	0.904	**0.011**	0.820	0.126	0.227	0.259	**0.026**
P × W	0.703	0.837	0.861	0.211	0.784	0.190	0.320	0.811	0.063
Y	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Y × B	**0.019**	**<0.001**	0.507	**<0.001**	0.269	0.053	**0.012**	**<0.001**	**<0.001**
Y × P	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.558	**<0.001**	**0.040**	**0.006**
Y × W	0.457	0.562	0.072	0.144	0.105	0.328	0.943	0.303	0.136
Y × B × P	**0.005**	**0.001**	**0.037**	**0.004**	**0.033**	0.945	0.135	**0.001**	**0.001**
Y × B × W	0.768	0.829	0.715	0.555	0.694	0.170	0.721	0.519	0.210
Y × P × W	0.644	0.654	0.243	0.587	0.188	0.796	0.870	0.231	0.355

The bold numerals highlight the significance at $P < 0.05$.
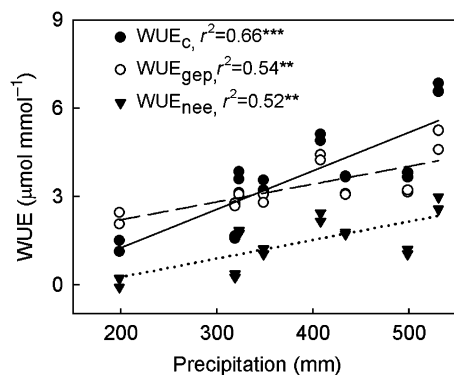

Fig. 2 Relationships between annual precipitation input and canopy (WUE_c) or ecosystem water-use efficiency (WUE_{gep} and WUE_{nee}) across the 4 years and four treatments. ** and *** represent significant relationship at $P < 0.01$ and 0.001, respectively.

treatments (all $P < 0.01$, Fig. 4a) whereas T_c and ET had no significant correlations with precipitant input (Fig. 4b). In addition, GEP showed positive dependence upon ET and T_c in the unwarmed control and warmed plots (Fig. 5a, c), but not in the precipitation addition or warming plus precipitation addition plots (Fig. 5b, d).

Leaf level WUE in response to climate change

Precipitation addition stimulated the maximum photosynthetic rate (P_{max}) and transpiration rate (T_1) of the dominant species *S. krylovii* by 23.9% and 61.5%, respectively, over the 3 years (Table 3, Fig. 6a and b).

Increase in T_1 was much higher than P_{max}, leading to 27.4% reduction of WUE_1 under the increased precipitation treatment (Fig. 6c). Experimental warming significantly decreased P_{max} by 10.2%, but did not impact T_1 and WUE_1 (Table 3, Fig. 6a). Both P_{max} and T_1 of *S. krylovii* showed positive dependence upon soil moisture across the 3 years and four treatments (Fig. 7a). In contrast, WUE_1 was negatively correlated with soil moisture (Fig. 7b).

Discussion

Ecosystem WUE in response to climate change

Although ecosystem WUE can be expressed in different ways (GEP/ET or NEE/ET), WUE_{gep} is used most often in previous studies (Law *et al.*, 2002; Ponton *et al.*, 2006; Kuglitsch *et al.*, 2008; Yu *et al.*, 2008). The overall mean WUE_{gep} (6–10.8 g CO_2 kg^{-1} H_2O) during the growing season in the Inner Mongolia steppe observed in this study is larger than that in North American tallgrass prairies (0.5–6 g CO_2 kg^{-1} H_2O, Law *et al.*, 2002) and in Chinese alpine and temperate grasslands (1.1–5.1 g CO_2 kg^{-1} H_2O, Hu *et al.*, 2008). Low temperature (-2 °C) in alpine grassland may limit plant growth, and high precipitation (>900 mm) in tallgrass prairies usually causes ineffective water use (Huxman *et al.*, 2004b).

In arid and semiarid ecosystems, water is the most important limiting factor for primary productivity (Knapp & Smith, 2001; Huxman *et al.*, 2004b; Bai *et al.*, 2008; Niu *et al.*, 2008). Water addition stimulated GEP and NEE more than ET, leading to increases in WUE_{gep}
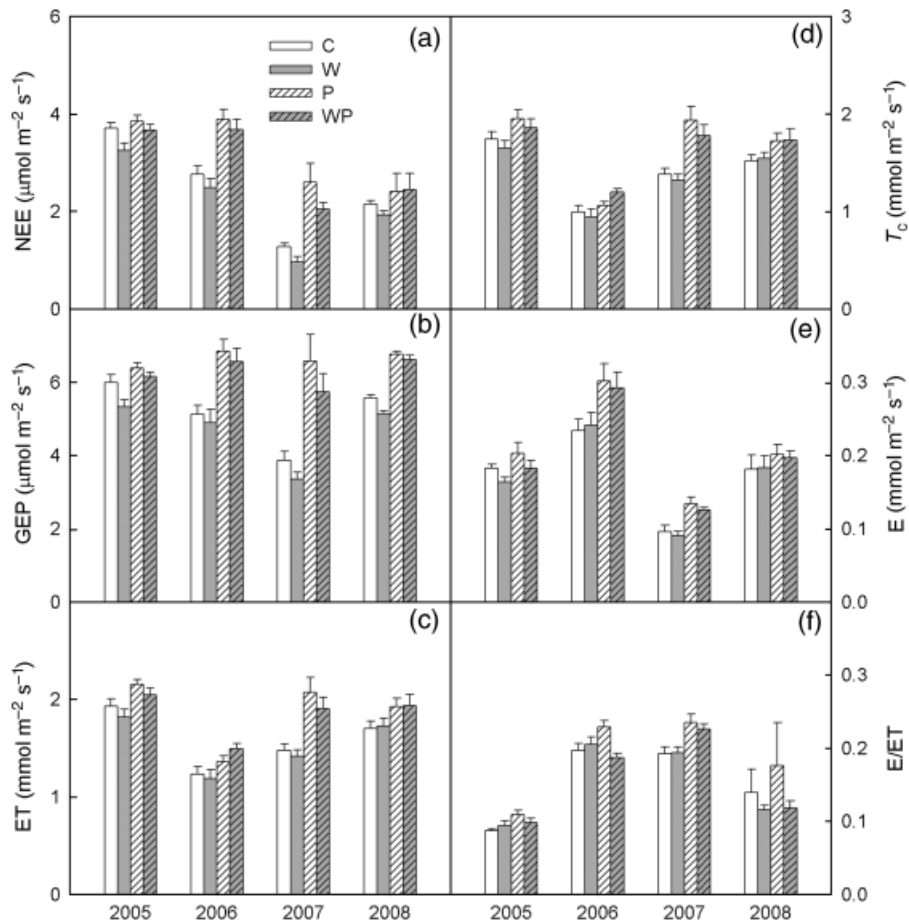
Fig. 3 Net ecosystem CO_2 exchange (NEE, a), gross ecosystem productivity (GEP, b), evapotranspiration (ET, c), transpiration (T_c, d), evaporation (E, e), and the ratio of E/ET (f) in response to increased precipitation and warming (seasonal means ± 1 SE). See Fig. 1 for abbreviations.

and WUE_{nee} under elevated precipitation (Fig. 1). Precipitation could explain 64% of the changes in GEP and 54% of changes in WUE_{gep} in this study (Figs 2 and 4). The positive dependence of WUE_{gep} and WUE_{nee} on precipitation is largely due to the positive correlation of GEP and NEE but no correlation of ET with precipitation (Fig. 4). Our results indicate that the response of WUE_{gep} and WUE_{nee} to precipitations is primarily controlled by C rather than water processes. Although there are few studies on grassland ecosystem response of WUE to precipitation, positive correlations between RUE and precipitation over time have been reported in temperate grassland in China (Bai *et al.*, 2008). In a temperate grassland gradient with annual precipitation ranging from 200 to 1200 mm, RUE first increased and then decreased with increasing precipitation, peaking around 475 mm (Paruelo *et al.*, 1999). Our results are congruent with this pattern up to 470 mm in precipitation. At our study site, water loss through runoff is low given the soil contains more than 60% sand (Bai *et al.*,

2008). Therefore, WUE_{gep} in our study can represent RUE in response to environmental factors.

There was a clear trend for less WUE_{gep} and WUE_{nee} in the heated plots (Fig. 1), which was predominantly reflected by a sharp decrease in NEE or GEP, but no significant differences in ET between the ambient and elevated temperature treatments (Table 1, Fig. 3). Reductions in ecosystem WUE under a warmer climate have also been reported in previous studies (Allen *et al.*, 2003; de Boeck *et al.*, 2006). Lower GEP rates are largely due to stomatal regulation (Niu *et al.*, 2008) which could be a water-saving adaptive mechanism to drier conditions induced by warming.

WUE at different scales respond differently to climate change

WUE has been widely studied at the leaf level through chamber and C isotopic measurements, and at the regional scales through modeling (Farquhar *et al.*,

1989; Ehleringer & Field, 1992). In this study, we examined ecosystem WUE and their responses to precipitation and temperature change. This approach provides
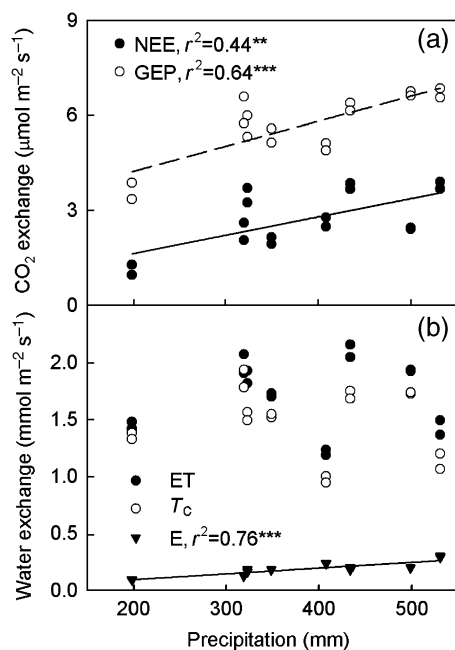

Fig. 4 Relationships between annual precipitation input and ecosystem carbon (GEP and NEE) or water exchange (E, T_c, and ET). ** and *** represent the relationship was significant at $P < 0.01$ and 0.001, respectively.

an improved estimate of ecosystem WUE because both above- and belowground processes are included inherently.

Our results showed that the response of WUE_l to climate change was dramatically different from the response of canopy and ecosystem WUE. Increases in precipitation stimulated WUE_c, WUE_{gep} and WUE_{nee} (Fig. 1) but reduced WUE_l of the dominant plant (Fig. 6). In this study, E accounted for a small proportion (9–24%) of ET during the growing season (Fig. 3f), which is much lower than the modeled value in grassland ecosystems in northern China (36–61% averaged across May–September, Hu *et al.*, 2009). The response of ET to increased precipitation was largely dominated by the response of T_c. Our results suggest that T_c contributes more to the response of ecosystem WUE to precipitation and temperature change in the temperate steppe while E does little, a comparison which is hardly addressed in previous studies. Since E/ET did not significantly change under increased precipitation (Table 1, Fig. 3), WUE_{gep} changed similarly to WUE_c in response to increased precipitation (Fig. 1). The increases in ER did not offset the increases in GEP, leading to similar responses of WUE_{gep} and WUE_{nee} to increased precipitation (Fig. 1). However, at the plant level, the increase in transpiration was more than that in photosynthesis (Fig. 6), leading to decreased WUE_l under elevated precipitation. WUE_l
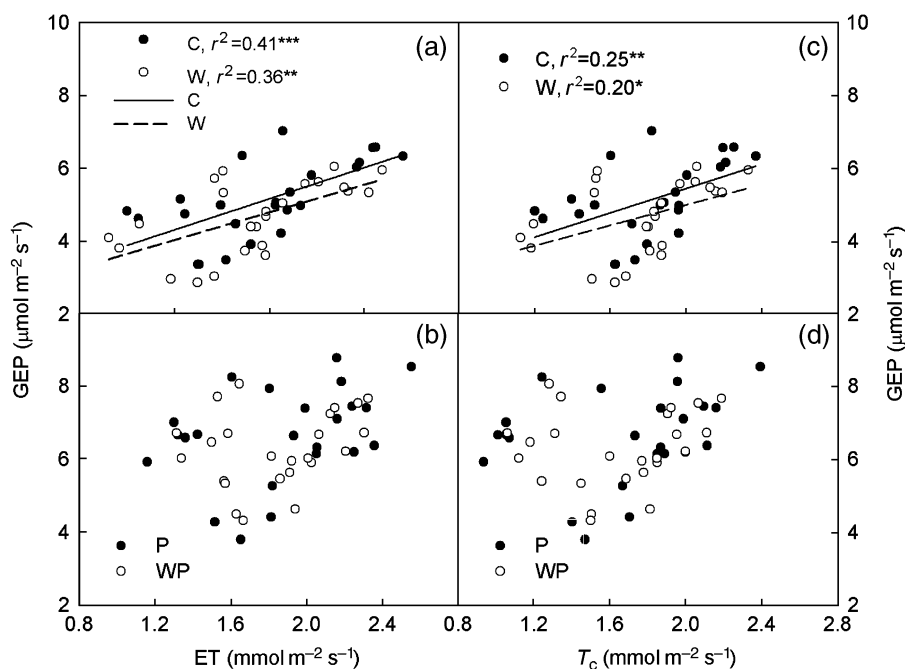

Fig. 5 Relationships between gross ecosystem productivity (GEP) and evapotranspiration (ET, a and b) or canopy transpiration (T_c, c and d) in the ambient (a, c) or increased (b, d) precipitation plots. *, ** and *** represent the relationship was significant at $P < 0.05$, 0.01 and 0.001, respectively.

Table 3 Results (i.e., *P*-values) of split-plot factorial ANOVAs on the effects of block (B), increased precipitation (P), warming (W), year (Y), and their interactions on leaf maximum photosynthetic rate (P_{max}), transpiration rate (T_1), water-use efficiency (WUE_l) and soil moisture (SM)

	P_{max}	T_1	WUE	SM
B	0.232	0.375	0.343	0.010
P	<0.001	<0.001	0.001	<0.001
W	0.021	0.618	0.730	0.005
B × P	0.054	0.085	0.009	0.373
B × W	<0.001	0.017	0.025	0.078
P × W	0.800	0.310	0.473	0.532
Y × B × P	0.126	0.743	0.699	0.918
Y	0.133	0.258	0.299	0.067
Y × B	0.584	0.689	0.768	0.450
Y × P	0.079	0.240	0.139	0.521
Y × W	0.265	0.874	0.955	0.980
Y × P × W	0.287	0.185	0.196	0.960
Y × B × W	0.021	0.618	0.730	0.005

primarily reflects stomatal regulation of leaf photosynthesis and transpiration and their response to climate change. At the ecosystem scale, interactions among stomatal conductance, aerodynamic conductance, entrainment of dry air in the planetary boundary layer and changes in leaf temperature can offset each other so that ET changes in different ways with T_1 (Baldocchi *et al.*, 2001).

Ecosystem responses to environmental change are usually driven by the responses of dominant species. However, if other coexisting species have differential responses, deducing response of ecosystem function from plants will be more challenging (Yu *et al.*, 2005). Even though *S. krylovii* is one of the dominant species in the temperate grassland at the study site (Yuan *et al.*, 2005; Zhan *et al.*, 2007), other coexisting species may have differential sensitivity and responses to changing water availability and could possibly counteract the reduced WUE_l of *S. krylovii* (Niu *et al.*, 2009). Moreover, self-shading within a canopy will change the energy budget and potentially reduce transpirational losses at canopy level. Another possible reason for the positive response of WUE_{gep} to precipitation addition is the increased belowground productivity (Bai *et al.*, 2010). Higher root productivity may have larger root surface area, which can facilitate greater water uptake and hence improve ecosystem WUE. Our observations suggest that any attempt to upscale WUE from leaf to ecosystem to the global scale (Tu *et al.*, 2008) should be cautious and take into consideration of the diverse response of WUE at different organism levels.
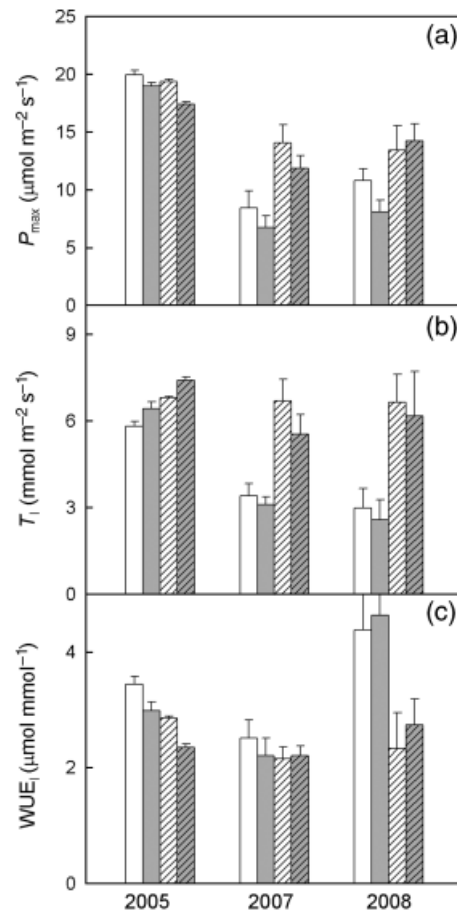

Fig. 6 Responses of the maximum photosynthetic rate (P_{max}, a), transpiration rate (T_1, b) and water-use efficiency (WUE_l, c) (means ± 1 SE) in the dominant species *Stipa krylovii* to increased precipitation and warming in 2005, 2007 and 2008. See Fig. 1 for abbreviations.

Implications for climate change

Our findings have important implications for understanding climate change effects on primary productivity and C sequestration in arid and semiarid ecosystems. With the projected increase in precipitation in the Inner Mongolia steppe (Ni & Zhang, 2000), we expect that GEP will consequently increase because of increased water availability and the efficiency of water use at the canopy and ecosystem levels. However, elevated temperature will decrease GEP. As a consequence, changes in ecosystem primary productivity under climate change will depend on the relative impact of concurrent changes in precipitation and temperature. Our results indicate that WUE plays an important role in regulating ecosystem C uptake and sequestration in response to climate change in arid and semiarid ecosystems. This study, to our knowledge, is
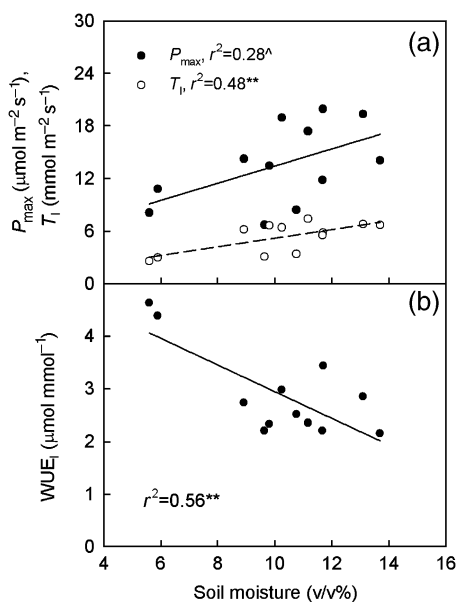
Fig. 7 Relationships between soil moisture and the maximum photosynthetic rate (P_{max}), transpiration rate (T_l, a) and water-use efficiency (WUE_l, b) of *Stipa krylovii*. ^ and ** represent significant relationship at $P < 0.1$ and 0.01, respectively.

the first to compare WUE in response to warming and elevated precipitation at different levels of organization in grassland ecosystems, which is crucial to understanding the coupled relationship between C and water cycling. Ecological modeling for projections of climate-ecosystem C feedbacks should consider WUE changes under climate scenarios to improve model accuracy.

Conclusion

Using a manipulative field experiment, this study has divided up specific components of ecohydrological and C cycle processes and performed an evaluation of how each specific component responds to climate warming and increased precipitation. Our results showed that ecosystem WUE in response to climate change was dominated by the response of GEP rather than ET. The different responses of canopy/ecosystem WUE and plant WUE to precipitation addition and warming indicate that the response of canopy and ecosystem WUE to climate change cannot be simply upscaled from plant WUE. Our results provide direct field evidence that climate change actually influences different ecohydrological components, thus changing C-water balance at different organism levels. These findings will facilitate improvement of process-based terrestrial ecosystem models and our understanding of GEP response to climate change.

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