

# Dependence of carbon sequestration on the differential responses of ecosystem photosynthesis and respiration to rain pulses in a semiarid steppe

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## Abstract

Precipitation pulses play an important role in regulating ecosystem carbon exchange and balance of semiarid steppe ecosystems. It has been predicted that the frequency of extreme rain events will increase in the future, especially in the arid and semiarid regions. We hypothesize that large rain pulses favor carbon sequestration, while small ones cause more carbon release in the semiarid steppes. To understand the potential response in carbon sequestration capacity of semiarid steppes to the changes in rain pulse size, we conducted a manipulative experiment with five simulated rain pulse sizes (0, 5, 10, 25, and 75 mm) in Inner Mongolia steppe. Our results showed that both gross ecosystem productivity (GEP) and ecosystem respiration ( $R_e$ ) responded rapidly (within 24 h) to rain pulses and the initial response time was independent of pulse size. However, the time of peak GEP was 1–3 days later than that of  $R_e$ , which depended on pulse size. Larger pulses caused greater magnitude and longer duration of variations in GEP and  $R_e$ . Differences in the response time of microbes and plants to wetting events constrained the response pattern of heterotrophic ( $R_h$ ) and autotrophic ( $R_a$ ) components of  $R_e$  following a rain event.  $R_h$  contributed more to the increase of  $R_e$  in the early stage of rain pulse response, while  $R_a$  played a more important role later, and determined the duration of pulse response, especially for large rain events of >10 mm. The distinct responses of ecosystem photosynthesis and respiration to increasing pulse sizes led to a threshold in rain pulse size between 10 and 25 mm, above which post wetting responses favored carbon sequestration. The disproportionate increase of the primary productivity of higher plants, compared with those in the activities of microbial decomposers to larger pulse events suggests that the carbon sequestration capacity of Inner Mongolia steppes will be sensitive to changes in precipitation size distribution rather than just precipitation amount.

*Keywords:* autotrophic respiration, gross ecosystem productivity, heterotrophic respiration, rain pulse, semiarid steppe

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## Introduction

Grasslands are one of the world's most widespread vegetation types and comprise 32% of the earth's area of natural vegetation (Adams *et al.*, 1990). China has extensive grassland areas, which represent important renewable resources in the arid and semiarid regions located in the northern part of the country (Zhou *et al.*,

2002). Although rates of carbon fluxes are not the highest for grasslands, their large land mass argues towards an important role in global carbon storage and cycling (Franzluobber *et al.*, 2002). The amount of organic carbon stored in the arid and semiarid regions is almost twice the amount stored in temperate forest ecosystems, thus arid and semiarid ecosystems may play an important role in terrestrial carbon sequestration and feedbacks to climate change (Taylor & Lloyd, 1992; Shen *et al.*, 2008).

Grassland ecosystems in the arid and semiarid regions are very sensitive to climatic variation, and many funda-

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mental aspects of their structure and function are closely linked to spatial and temporal variation in precipitation (Knapp & Smith, 2001; Gao & Reynolds, 2003). A slight shift in seasonal precipitation patterns and/or the frequency of extreme rainfall events could have important consequence for grassland ecology and biogeochemistry. IPCC (2007) reported that both total rainfall amounts and the frequency of extreme rainfall events have increased. Further, this report predicts that future changes in extreme events may be greater than those expected for mean precipitation. Precipitation data in the arid and semiarid areas of northern China for the past 40 years show an obvious trend of increasing proportion of precipitation delivered by heavy rainfall events and decreasing proportion by light precipitation events (Liu *et al.*, 2005). Increases in rainfall variability could alter rapidly key carbon cycling processes and plant community composition of native grasslands, regardless of the amount of total precipitation (Knapp *et al.*, 2002; Harper *et al.*, 2005; Swemmer *et al.*, 2007). Rain pulses, which refer to infrequent, discrete and largely unpredictable precipitation events, are effective at activating important ecological processes at different levels of organization (Huxman *et al.*, 2004b). Roles of rain pulses in controlling ecosystem processes have been examined at a number of time scales, including the timing and size of small rainfall events within a season, and the interannual variability in precipitation (Austin *et al.*, 2004; Schwinning & Sala, 2004; Chou *et al.*, 2008; Fay *et al.*, 2008; Shen *et al.*, 2008).

Some previous studies examined the influences of rain pulses on soil respiration and found rapid and dramatic increase in soil CO<sub>2</sub> efflux after a pulse in a variety of arid or semiarid ecosystems (Liu *et al.*, 2002; Austin *et al.*, 2004; Smart & Peñuelas, 2005; Sponseller, 2007; Jenerette *et al.*, 2008). The carbon sequestration ability of an ecosystem is, nevertheless, determined by the balance of ecosystem carbon assimilation and respiration. Therefore, to assess the vulnerability of arid and semiarid ecosystems to climatic changes, particularly changes in the precipitation regime, it is critical to increase our understanding of how the key ecological processes (autotrophic respiration, heterotrophic respiration, and photosynthesis, etc.) respond to rainfall pulses. Generally, a rainfall pulse after a period of drought time results in a large, but short-lived, increase in respiration and CO<sub>2</sub> efflux immediately (Liu *et al.*, 2002; Lee *et al.*, 2004). The increase of carbon assimilation is, however, slower than that of respiration because responses of plant physiological processes need more time. Additionally, rooting depth of different plant functional types determines the portion of the soil profile from which plants absorb water, and further affects the recovery time of leaf water potential and

photosynthetic activity of plants to a rainfall after a prolonged drought (Schwinning *et al.*, 2003; Schwinning & Sala, 2004).

The effects of rain pulses on the magnitude of different ecosystem carbon flux components are also closely related with the size of rain pulses. Loik *et al.* (2004) reported that >47% of all of the precipitation events received in the arid and semiarid areas of the western USA were <5 mm. These small rain events can enhance the microbial respiration contribution to ecosystem carbon fluxes, but may not trigger autotrophic processes, because most microbes live near the soil surface, which can be wetted by small rainfall events (Austin *et al.*, 2004; Schwinning & Sala, 2004). Larger rain events can increase both photosynthetic and respiratory processes of ecosystems with different response time and magnitudes, which depends on plant functional type, soil type, and nutrient condition (Fay *et al.*, 2002; Huxman *et al.*, 2004a; Potts *et al.*, 2006a, b). Schwinning & Sala (2004) pointed out that a shift to larger pulse events is likely to increase disproportionately the primary productivity of higher plants, compared with the activities of microbial decomposition. The asynchronous and differentially sensitive biological responses to rainfall pulses may impact the capacity for carbon sequestration of arid and semiarid regions in a changing rainfall future. Field experiments to evaluate the time-course dynamics of carbon exchange components in response to the rain pulses with different sizes in arid and semiarid grasslands at the ecosystem level are urgently needed in a variety of ecosystems (Hunt *et al.*, 2004; Huxman *et al.*, 2004a; Jentsch *et al.*, 2007).

With 7.2% of the total world grassland area, China's grasslands contribute 15.8% of carbon storage by the world grasslands (Ni, 2002). As the major components of China's grasslands, the typical steppe in Inner Mongolia is mainly located in the arid and semiarid areas of North China, which is highly sensitive to precipitation variation. Aboveground net primary productivity (ANPP) of the typical steppe was shown to be linearly related to annual precipitation (Bai *et al.*, 2004). They also found that the fluctuation of ANPP was closely related to interannual variations of precipitation and the intra-annual distribution of rainfall in this region.

In this study, a manipulative experiment with five levels of water treatments (0, 5, 10, 25, and 75 mm) was conducted in an Inner Mongolia typical steppe to simulate different rain pulse sizes. We hypothesized that (1) carbon sequestration of ecosystem depends on the differential responses of ecosystem photosynthesis and respiration to rain pulses, and (2) large rain pulses would favor carbon sequestration while small rain pulses would cause carbon release in the semiarid steppes.

## Materials and methods

### Site description

The experiment was conducted at a typical steppe in Duolun County, Inner Mongolia, China. According to the long-term climate data (1994–2004) from a meteorological station in Duolun County (about 30 km from our study site), mean monthly air temperatures range from  $-15.9^{\circ}\text{C}$  in January to  $19.9^{\circ}\text{C}$  in July and the annual mean temperature of  $3.3^{\circ}\text{C}$ . Mean annual precipitation is 399 mm, with the maximum monthly value occurring in July or August. The average growing season is about 150 days. The dominant soil type is chestnut soil (Chinese classification) or Calcic Luvisols according to the FAO classification. Soil bulk density was  $1.31 \pm 0.02 \text{ g cm}^{-3}$ . The composition of sand, silt, and clay was  $62.75 \pm 0.04\%$ ,  $20.30 \pm 0.01\%$ , and  $16.95 \pm 0.01\%$ , respectively. Soil organic carbon and total nitrogen contents were  $16.10 \pm 0.89$  and  $1.48 \pm 0.10 \text{ g kg}^{-1}$  (Liu *et al.*, 2009). The typical steppe was the primary native vegetation type of this semiarid region and dominated by *Stipa krylovii*, *Agropyron cristatum*, and *Artemisia frigida*. Our study site was located at the permanent study plot (>50 ha) which has been fenced to exclude grazing by Duolun Restoration Ecology Research Station since 2001.

### Experimental design and treatments

A random block design was used in the experiment, with four blocks (1 m space between blocks) as replicates. In each block, ten  $1 \text{ m} \times 1 \text{ m}$  plots were randomly arranged with 1 m spaces between plots. At the beginning of the growing season (about 2 months before the pulse treatment applied), the aboveground parts of five plots in each block were removed every week till the end of this experiment. In total, 40 plots were constructed, with 20 control plots (CK, with plants) and 20 clipped plots (CL, without aboveground parts of plants). Five water treatments were applied to the CK and CL plots within each block to simulate different rain pulse sizes (0, 5, 10, 25, and 75 mm), respectively ( $n = 4$  for each treatment). The experiment was conducted from June 19 to July 4, 2006 and water treatments were carried out in the morning and finished by noon on June 20, 2006. Water was pumped into a tank from a well near the plots and then applied into the plots using hand sprinklers to make sure the added water was evenly distributed at each plot. In order to reduce water runoff, only 5 kg water was applied into the plots each time and the amount of water was determined by a mass balance. Main meteorological factors during the experimental period were shown in Fig. 1. A plastic shelter was constructed to prevent natural rainfall from entering the experimental plots, and only used to cover the plots during the time of rainfall.

Clipping method was used to separate the autotrophic and heterotrophic parts of ecosystems respiration (Kuzyakov, 2006). It was assumed that the root growth in the clipped plots was largely suppressed by the continuous removal of aboveground biomass when we conducted the water treatments (about 2 months after clipping treatment). Thus, ecosystem respiration in CL plots would mainly come from the decomposition of soil organic carbon and litter, that is, microbial respiration or ecosystem heterotrophic respiration ( $R_h$ ). Then the ecosystem autotrophic respiration ( $R_a$ ) could be decided by the difference of  $R_e$  between control (CK, with plants) and CL plots. Obviously, this method may likely overestimate the contribution of heterotrophic part to ecosystem respiration, because the remained roots might still release some  $\text{CO}_2$  in CL plots. Among different partitioning methods reviewed by Hanson *et al.* (2000) and Kuzyakov (2006), our approach seems to be the most suitable for separating the different components of ecosystem respiration in a  $\text{C}_3$  species dominant grassland without destroying soil texture.

### Ecosystem $\text{CO}_2$ exchange measurements

Before the water treatment, a square metal base rim ( $50 \text{ cm} \times 50 \text{ cm}$  in area and 10 cm in height) was installed in each plot, with 3 cm left aboveground for the measurements of ecosystem  $\text{CO}_2$  exchange. Two PVC soil collars ( $80 \text{ cm} \times 80 \text{ cm}$  in area and 5 cm in height) were also installed in each plot (one inside the base, the other outside the base), usually 2 cm above ground, for the measurements of soil respiration. Ecosystem  $\text{CO}_2$  exchange, including net ecosystem exchange (NEE) and ecosystem respiration ( $R_e$ ), was measured by a cubic chamber ( $50 \text{ cm} \times 50 \text{ cm} \times 50 \text{ cm}$ ) attached to an infrared gas analyzer (LI-840, LI-COR Inc., Lincoln, NE, USA). Two small fans were fixed inside the top of the chamber to mix the air during measurement and one temperature probe was inserted inside the chamber to determine the air temperature. An air pump (6262-04, LI-COR Inc.) was used to connect the chamber and LI-840 and pumped air from chamber to LI-840 for measurement of  $\text{CO}_2$  concentration. A battery (12V, 20Ah) was used to supply power for the LI-840, air pump and the fans. Data were logged to a computer using the LI-840's data acquisition software. When measuring NEE, the transparent chamber was put on the metal base rim and sealed with four clamps. Generally, the  $\text{CO}_2$  concentrations inside the chamber were recorded every second for 2 min after the chamber was put on the base rim. Only the data of the last 100 s were used to calculate fluxes as NEE. After measuring NEE, the chamber was lifted and vented, then put on the base rim, covered by a lightproof cloth

mantle and CO<sub>2</sub> fluxes were estimated again. Because most of the radiation would be prevented by the mantle, the increase rate of CO<sub>2</sub> concentration in the chamber was considered as ecosystem respiration ( $R_e$ ). We calculated the NEE and  $R_e$  according to the equation provided by Jasoni *et al.* (2005):

$$F_c = \frac{VP_{av}(1000 - W_{av})}{RS(T_{av} + 273)} \times \frac{dc}{dt},$$

where  $F_c$  is the CO<sub>2</sub> flux ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; for NEE, negative  $F_c$  values representing ecosystem carbon uptake; for  $R_e$ , positive  $F_c$  values representing ecosystem carbon release),  $V$  is the volume of chamber ( $\text{m}^3$ ),  $P_{av}$  is the average pressure (kPa) during the measurement period,  $W_{av}$  is the average water mole fraction ( $\text{mmol mol}^{-1}$ ) during measurement,  $R$  is the ideal gas constant ( $8.314 \text{ J mol}^{-1} \text{ K}^{-1}$ ),  $S$  is the surface area covered by chamber ( $\text{m}^2$ ),  $T_{av}$  is the average temperature ( $^{\circ}\text{C}$ ) during the measurement, and  $dc/dt$  is the slope of least squares linear regression of CO<sub>2</sub> concentration on time. Gross ecosystem productivity (GEP) was calculated by the sum of NEE and  $R_e$ :

$$\text{GEP} = -\text{NEE} + R_e.$$

Soil respiration ( $R_s$ ) was measured using a LI-6400 portable photosynthesis system attached with a LI-6400-09 soil CO<sub>2</sub> flux chamber (LI-COR Inc.).  $R_s$  determination started the day before the water treatments and everyday afterwards for a period of 14 days. NEE and  $R_e$  were measured on 1, 3, 5, 7, and 12 day (s) after the water treatment was applied. At the same time, soil temperature was also measured at the 10 cm depth with a thermocouple connected to the LI-6400 system. Volumetric water content (VWC) of the 0–12 cm soil layer in each plot was determined with a TDR-200 soil moisture probe (Spectrum Technologies Inc., Plainfield, IL, USA) immediately after the soil respiration measurements were made. Usually, the measurements of NEE,  $R_e$ , and  $R_s$  were conducted in the morning (8:30–11:00 hours) to enhance the comparability of data measuring in different days and avoid extremely high air temperature and humidity at noon.

#### Aboveground and belowground biomass measurement

One quadrat ( $0.5 \text{ m} \times 0.5 \text{ m}$  in size) was sampled from each plot to determine the aboveground biomass of plants. In each quadrat, the aboveground part of plants was collected and taken back to the lab. Fresh samples of each plant species were oven-dried at  $70^{\circ}\text{C}$  for about 48 h, and then weighed. After clipping the aboveground parts of plants, root samples of 0–20 cm were sampled with a soil core sampler (8 cm in diameter) and put into nylon bags. Samples were rinsed and passed through a

0.5 mm sieve in the lab, and root fragments on the sieves were collected. Root samples were oven-dried at  $70^{\circ}\text{C}$  for about 48 h, and then weighed to determine their biomass. We used root biomass of the 0–20 cm soil layer to represent the belowground biomass of different treatments since most roots of the dominant species were located in this layer.

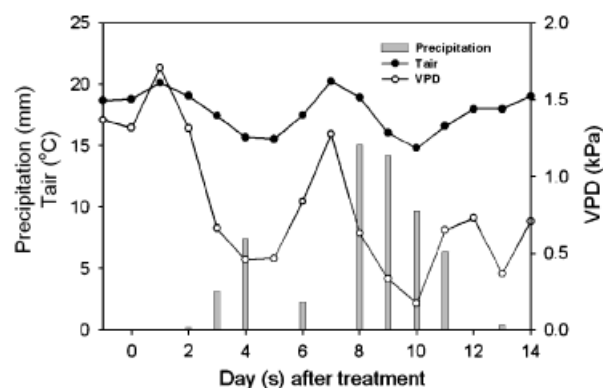
#### Statistical analysis

Statistical analyses were performed using SPSS 13.0. Differences in parameters such as aboveground biomass, belowground biomass, etc. among five water addition treatments were tested by analysis of variance (ANOVA) multiple comparisons (Duncan test). Quadratic equations were used to simulate the relationships between rain pulse size and ecosystem carbon fluxes. Linear, logarithmic and exponential regressions were made between ecosystem carbon fluxes and green aboveground biomass (GAB), soil moisture and soil temperature, respectively. The significances of regression coefficients were tested by ANOVA.

## Results

#### Variations of soil moisture, soil temperature, aboveground and belowground biomass

Soil moisture significantly increased after water addition treatments. The average soil water content of 75 and 25 mm treatments was significantly higher than that of the control (Table 1). No significant differences in soil temperature were observed among treatments during the experimental period (Table 1). There were no significant differences in the aboveground and below-

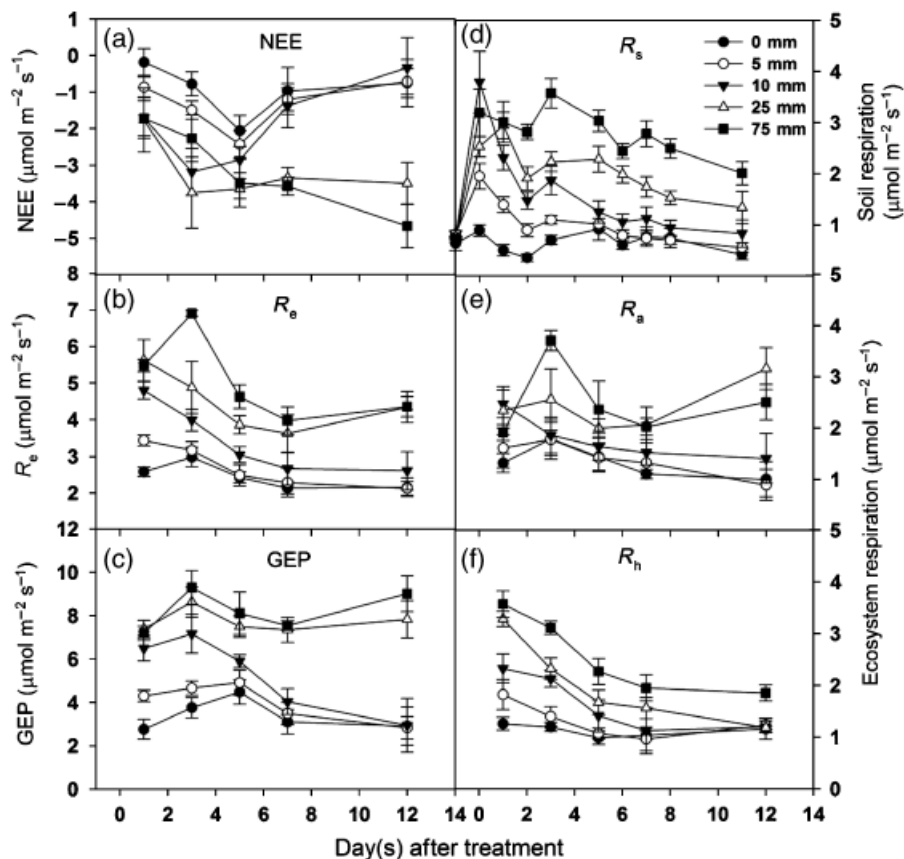


**Fig. 1** Daily precipitation and mean daily air temperature ( $T_{air}$ ) and vapor deficit (VPD) during the experimental period from 19 June to 8 July, 2006 in a typical steppe in Duolun, Inner Mongolia. Data were obtained from the automatic weather station near to the study site (about 500 m from our site).

**Table 1** Means of soil water content (VWC), soil temperature ( $T_s$ ), total aboveground biomass (TAB), green aboveground biomass (GAB) and belowground biomass (BB, 0–20 cm) under different rain pulse treatments

Pulse size (mm)	VWC (%)	$T_s$ ( $^{\circ}\text{C}$ )	TAB ( $\text{g DW m}^{-2}$ )	GAB ( $\text{g DW m}^{-2}$ )	BB ( $\text{g DW m}^{-2}$ )
0	$4.88 \pm 0.17^c$	$22.19 \pm 0.68^a$	$241.2 \pm 32.8^a$	$70.7 \pm 2.9^b$	$1458 \pm 163^a$
5	$5.72 \pm 0.20^c$	$21.98 \pm 0.72^a$	$226.7 \pm 23.4^a$	$87.3 \pm 4.5^{ab}$	$1640 \pm 136^a$
10	$6.53 \pm 0.50^c$	$21.82 \pm 0.73^a$	$271.0 \pm 45.5^a$	$97.9 \pm 14.2^{ab}$	$1552 \pm 190^a$
25	$9.36 \pm 1.27^b$	$21.15 \pm 0.70^a$	$253.2 \pm 20.4^a$	$104.2 \pm 5.8^a$	$1541 \pm 129^a$
75	$13.00 \pm 1.70^a$	$20.53 \pm 0.67^a$	$255.0 \pm 50.1^a$	$102.5 \pm 14.8^a$	$1443 \pm 79^a$

Data within columns are mean  $\pm$  SE. The significant differences in each parameter among different pulse sizes were determined by one-way ANOVA (Duncan's test). Different letters means significant difference at  $P < 0.05$ , and any same letters means nonsignificant difference at  $P > 0.05$ .



**Fig. 2** Changes in (a) net ecosystem exchange (NEE); (b) ecosystem respiration ( $R_e$ ); (c) gross ecosystem productivity (GEP); (d) soil respiration ( $R_s$ ); (e) autotrophic and (f) heterotrophic parts of  $R_e$  ( $R_a$  and  $R_h$ ) of plots with different rain pulse sizes treatments. Error bar was 1 SE.

ground biomass among different pulse treatments. However, significantly higher GAB was found in the 25 and 75 mm treatments than in the control (Table 1).

#### Variations of ecosystem carbon exchanges under different pulse size treatments

NEE increased significantly on the first day after the water addition (Fig. 2a). Compared with that of the control, the NEE values for the 5, 10, and 25 mm rain

pulse treatments reached the peak on the third day after the water addition. Then, NEE for the 5 and 10 mm rain pulse treatments decreased, and eventually approached the values not significantly different from that for the control on the seventh days after the water addition. However, NEE of the 25 mm treatment maintained a significantly higher value during the entire experimental period than that for the control (Fig. 2a). NEE for the 75 mm rain pulse treatment showed substantial increase by the end of measurement. Based on the whole mea-

**Table 2** Means of gross ecosystem productivity (GEP), net ecosystem CO<sub>2</sub> exchange (NEE), total ecosystem respiration ( $R_e$ ), heterotrophic  $R_e$  ( $R_h$ ), autotrophic  $R_e$  ( $R_a$ ) and the ratio of  $R_a$  to  $R_e$  ( $R_a/R_e$ ) under different rain pulse treatments

Pulse size (mm)	GEP ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	NEE ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$R_e$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$R_h$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$R_a$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$R_a/R_e$ (%)
0	3.40 ± 0.32 <sup>c</sup>	-0.95 ± 0.31 <sup>b</sup>	2.46 ± 0.16 <sup>c</sup>	1.13 ± 0.05 <sup>c</sup>	1.33 ± 0.14 <sup>b</sup>	52.6 ± 2.6 <sup>a</sup>
5	4.04 ± 0.39 <sup>bc</sup>	-1.34 ± 0.30 <sup>b</sup>	2.70 ± 0.26 <sup>c</sup>	1.30 ± 0.15 <sup>bc</sup>	1.40 ± 0.15 <sup>b</sup>	51.0 ± 3.6 <sup>a</sup>
10	5.31 ± 0.79 <sup>b</sup>	-1.89 ± 0.52 <sup>b</sup>	3.42 ± 0.42 <sup>bc</sup>	1.64 ± 0.25 <sup>bc</sup>	1.78 ± 0.19 <sup>b</sup>	52.2 ± 2.5 <sup>a</sup>
25	7.46 ± 0.41 <sup>a</sup>	-3.20 ± 0.37 <sup>a</sup>	4.46 ± 0.36 <sup>ab</sup>	2.00 ± 0.37 <sup>ab</sup>	2.42 ± 0.21 <sup>a</sup>	54.1 ± 5.2 <sup>a</sup>
75	8.23 ± 0.41 <sup>a</sup>	-3.14 ± 0.52 <sup>a</sup>	5.07 ± 0.52 <sup>a</sup>	2.55 ± 0.34 <sup>a</sup>	2.50 ± 0.32 <sup>a</sup>	49.2 ± 3.8 <sup>a</sup>

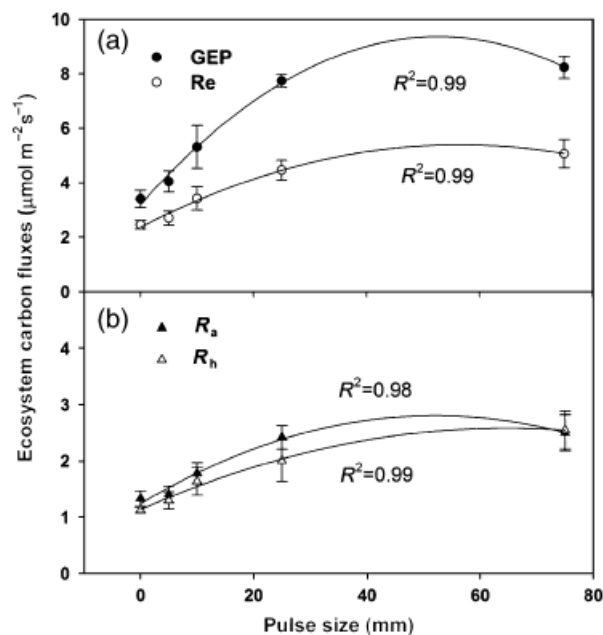
Data within columns are mean ± SE. The significant differences in each parameter among different pulse sizes were determined by one-way ANOVA (Duncan test). Different letters means significant difference at  $P < 0.05$ , and any same letters means nonsignificant difference at  $P > 0.05$ .

surement period, the average NEE for the 25 and 75 mm rain pulse treatments was significantly higher than those for the other treatments, and no significant differences in the average NEE existed among the 0, 5, and 10 mm rain pulse treatments (Table 2).

Soil ( $R_s$ ) and ecosystem ( $R_e$ ) respiration varied with rain pulse treatments in similar ways (Fig. 2b and d). Water addition stimulated  $R_e$  and  $R_s$  in all water addition treatments. The responses of  $R_e$  and  $R_s$  to rain pulses were quicker than those of NEE. The  $R_e$  and  $R_s$  for the 5, 10, and 25 mm rain pulse treatments reached the highest values on the first day after the water addition, and those for the 75 mm rain pulse treatment on the third day after the treatment. The  $R_e$  values for the 5 and 10 mm water additions returned to the level of the control on the third and seventh day after the treatment, respectively. However, the  $R_e$  values for the 25 and 75 mm rain pulse treatments were significantly higher than that for the control during the entire measurement period. The average  $R_e$  values for the 25 and 75 mm rain pulse treatments were significantly higher than those for the 0 and 5 mm rain pulse treatments, but there were no significant differences in the average  $R_e$  values among the 0, 5 and 10 mm rain pulse treatments (Table 2).

GEP for the 5 and 10 mm rain pulse treatments showed similar patterns to those of  $R_e$ , while the variations in GEP for the 25 and 75 mm rain pulse treatments were similar to those of NEE (Fig. 2c). The average GEP values for the 10, 25, and 75 mm rain pulse treatments were significantly higher than those for the 0 and 5 mm rain pulse treatments (Table 2). The relationships between pulse size and GEP or  $R_e$  could be fitted by quadratic curves (Fig. 3a). With the increase of rain pulse size, the response of GEP to pulse size became more sensitive than that of  $R_e$ .

The autotrophic and heterotrophic component of  $R_e$  showed different responses to water addition (Fig. 2f). Heterotrophic respiration ( $R_h$ ) in all rain pulse treatments increased on the first day after the water addi-



**Fig. 3** Responses of different components of ecosystem CO<sub>2</sub> fluxes to rain pulse sizes: (a) gross ecosystem productivity (GEP) and ecosystem respiration ( $R_e$ ), the regressive equations for GEP and  $R_e$  were  $y = -0.0022x^2 + 0.2341x + 3.1981$  and  $y = -0.0009x^2 + 0.1072x + 2.366$ , respectively; (b) autotrophic ( $R_a$ ) and heterotrophic ( $R_h$ ) ecosystem respiration, the regressive equations for  $R_a$  and  $R_h$  were  $y = -0.0006x^2 + 0.0603x + 1.2388$  and  $y = -0.0003x^2 + 0.0447x + 1.1344$ , respectively.

tion, and then decreased rapidly (Fig. 2f). The responses of autotrophic respiration ( $R_a$ ) were slower than those of  $R_h$ , especially for the 25 and 75 mm rain pulse treatments (Fig. 2e). The  $R_a$  for the 25 and 75 mm rain pulse treatments reached the highest values on the third day after the water addition and kept significantly higher rate than that of control treatment until the end of experiment. The mean  $R_a$  and  $R_h$  values for the 25 and 75 mm rain pulse treatments were significantly higher than those for the 0, 5, and 10 mm rain pulse

treatments. The relative contribution of  $R_a$  to total  $R_e$ , ranging from 49.2% to 54.1%, did not show significant differences among five different pulse treatments (Table 2). Significant quadratic relationships existed between  $R_a$  or  $R_h$  and pulse size (Fig. 3b).

#### *Relationships of ecosystem carbon exchanges and soil moisture, soil temperature, and GAB*

The rates of NEE,  $R_e$ , and GEP increased significantly with increasing soil moisture, and the relationships between ecosystem carbon fluxes (NEE,  $R_e$ , and GEP) could be described well by logarithmic equations (Fig. 4). Significant positive relationships were also found between soil moisture and the autotrophic or heterotrophic parts of  $R_e$ , respectively. The response of  $R_h$  to soil moisture was more sensitive than that of  $R_a$ , which was indicated by the greater slope of the regression equation.

Distinctly different relationships between  $R_e$  and soil temperature were observed under high vs. low soil water availability (Fig. 5). Under high soil water condition ( $VWC \geq 15\%$ ),  $R_e$  showed significantly positive relationship with soil temperature, while  $R_e$  decreased with increasing soil temperature under low water availability ( $VWC < 15\%$ ). The rate of NEE decreased significantly with increasing soil temperature under both high and low soil water conditions (Fig. 5b). GEP also showed significantly negative relationship with soil

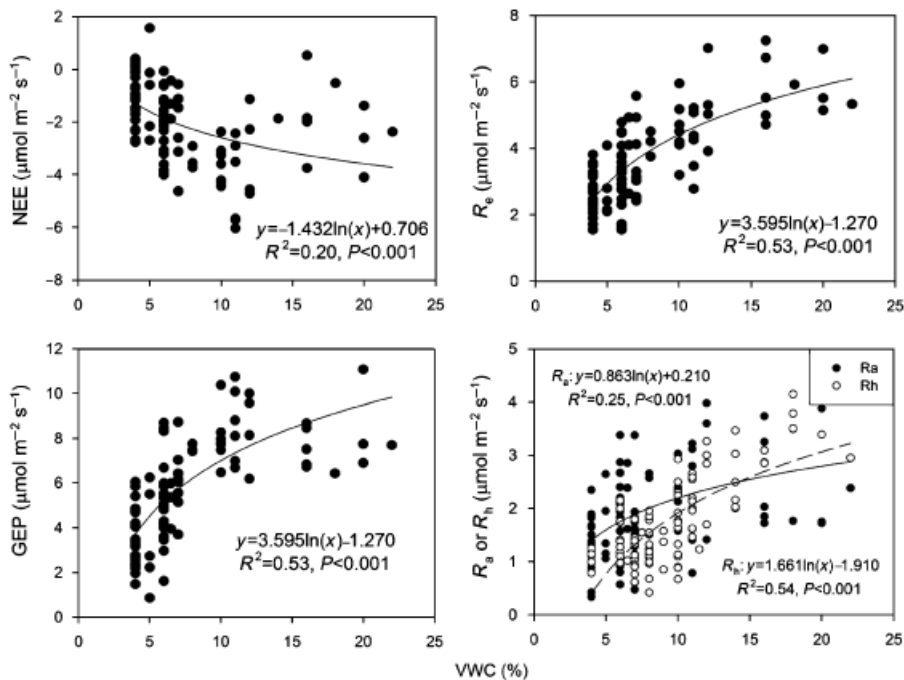
temperature under the low soil water condition but no significant relationship under the high soil water condition (Fig. 5c).

There were significant linear relationships between GAB and NEE, GEP, or  $R_e$ , respectively (Fig. 6a–c). The autotrophic part of  $R_e$  also showed an obvious increase with increasing GAB, while the heterotrophic part of  $R_e$  did not have significant relationship with GAB (Fig. 6d). No significant relationship existed between the ecosystem carbon exchanges and the belowground biomass or total aboveground biomass ( $P > 0.05$ ).

## Discussion

### *Responses of ecosystem photosynthesis and respiration to rain pulses*

The two major components of ecosystem carbon exchange, GEP and ecosystem respiration ( $R_e$ ) showed contrasting responses to simulated rainfall events of different sizes in a semiarid steppe ecosystem (Fig. 2). Our results provided experimental supports for a general model of ecosystem carbon exchange following rain pulses by Huxman *et al.* (2004b). In this model, general responses of an ecosystem to rain pulses can be organized into four components: response time, magnitude of response, timing of peak response, and duration of response. In addition, our results added to this concep-



**Fig. 4** Relationships between VWC and (a) net ecosystem exchange (NEE); (b) ecosystem respiration ( $R_e$ ); (c) gross ecosystem productivity (GEP); (d) heterotrophic ( $R_h$ ) and autotrophic ( $R_a$ ) ecosystem respiration.

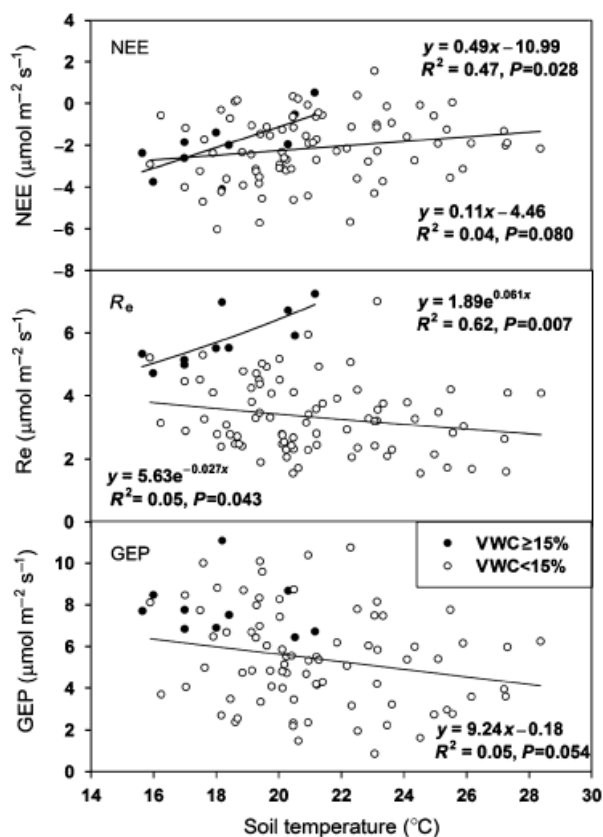


Fig. 5 Relationships between  $T_s$  and (a) net ecosystem exchange (NEE); (b) ecosystem respiration ( $R_e$ ); (c) gross ecosystem productivity (GEP), heterotrophic ( $R_h$ ), and autotrophic ( $R_a$ ) ecosystem respiration under two different soil moisture conditions.

tual framework by documenting: (1) autotrophic responses may be faster than previously suggested, with increases in photosynthesis observed within 24 h; (2) the timing of responses may be independent of pulse size while response magnitude, time to peak response, and response duration were sensitive to the pulse size (Fig. 7).

Several previous studies suggested that soil microbes responded to changes in soil water potential within hours, while grasses responded to soil moisture change in the order of hours to days (Huxman *et al.*, 2004b; Ogle & Reynolds, 2004; Schwinning & Sala, 2004). The GEP and  $R_e$  were not measured on the day when the water treatments were applied, but the soil respiration data showed the rate of soil  $\text{CO}_2$  efflux increased significantly (by two to four times) within several hours after the water treatments (Fig. 2d). Because a substantial component of  $R_e$  is  $R_s$ , we expect that  $R_e$  similarly responded within hours after the rain pulse. On the first day following the rain pulses, significant increases in GEP and  $R_e$  were observed, which indicates that both GEP and  $R_e$  were influenced by water additions within

24 h. The response time of GEP and  $R_e$  was independent of pulse size from 5 to 75 mm. Schwinning & Sala (2004) proposed that many small rain events (<5 mm or even 2 mm) were insufficient in magnitude to elicit a plant response but could cause a rapid increase in activity of soil organisms. The relatively quick response of GEP in our study could be attributed to the shallow rooting depth of grasses. Schwinning *et al.* (2003) reported that a deep-rooted shrub did not show significant physiological responses to summer rainfall events of up to 20 mm, but a  $\text{C}_4$  grass increased its photosynthetic activity within hours of a 5 mm rain event. Cheng *et al.* (2006) also showed that a perennial grass (*Stipa bungeana*) in an arid grassland of Inner Mongolia depended more on light rains (<10 mm), while a semishrub (*Artemisia ordosica*) was more dependent on heavy rains (>20 mm). Therefore, the faster photosynthetic response time to rain pulses and no relation of the response time to pulse size was due to the fact that the dominant species in our study site are grasses.

Except for the response time, all other variables of the response model including the magnitude of response, the timing of peak response, and the response duration depended on rain pulse size (Fig. 7). Generally, larger pulses resulted in a greater magnitude and longer duration of GEP and  $R_e$ . While significant increases of GEP and  $R_e$  were observed within 1 day following experimental rainfall, the timing of peak GEP was 1–3 days later than that for  $R_e$ , and the length of this lag time depended on pulse size. Similar time lags were also reported by Ogle & Reynolds (2004), which was attributed to physiological acclimation and the growth of new roots and leaves. Additionally, the response magnitude and duration of GEP to different pulse sizes may depend on the plant functional properties of the dominant species, especially the ability to use summer rainwater. In a separate study on a similar steppe, we showed that most dominant grasses could shift their water sources from surface soil water to deep soil layer water during dry season, while shrubs always relied on the soil water in the deeper layers (Zhao *et al.*, 2009). The shift in the water use enhances the utilization of both small and larger rains by grasses, which not only strengthens the adaptation of grass species to soil water availability, but also benefits the maintenance of leaf photosynthesis and ecosystem productivity under future precipitation scenarios.

The differential responses of ecosystem photosynthesis and respiration to increasing rain pulse size resulted in a significant enhancement of ecosystem net carbon assimilation with the 25 and 75 mm rain pulse treatments (Fig. 3 and Table 2). However, the rain pulse <10 mm did not show significant change in the carbon sequestration because of the similar responses of GEP



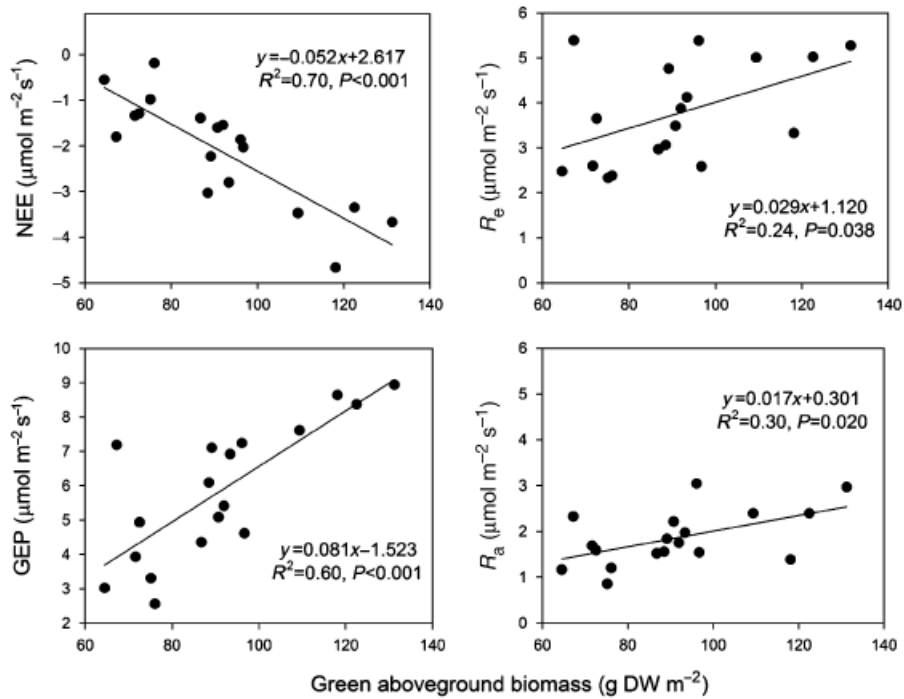


Fig. 6 Relationships between green aboveground biomass and (a) net ecosystem exchange (NEE); (b) ecosystem respiration ( $R_e$ ); (c) gross ecosystem productivity (GEP); (d) heterotrophic ( $R_h$ ), and autotrophic ( $R_a$ ) ecosystem respiration.

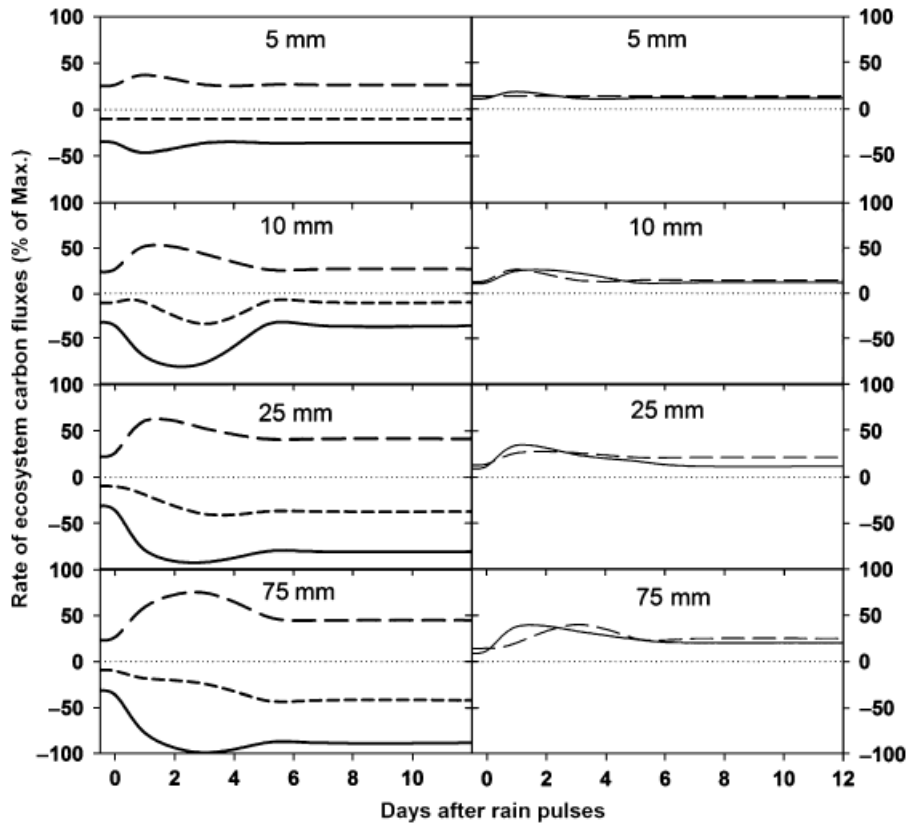


Fig. 7 Response models of net ecosystem exchange (NEE, bold short-dashed line), ecosystem respiration ( $R_e$ , bold long-dashed line), gross ecosystem productivity (GEP, bold solid line), heterotrophic ( $R_h$ , thin solid line), and autotrophic ( $R_a$ , thin long-dashed line) ecosystem respiration to rain pulses.

and  $R_e$  to the rain pulse events. These results indicated that a threshold pulse size should exist between 10 and 25 mm, that is, a rain event larger than this threshold is necessary to initiate carbon sequestration in this semi-arid steppe.

Water and temperature were often considered as two major abiotic factors influencing the ecosystem carbon exchange processes in grasslands (Xu *et al.*, 2004; Davidson & Janssens, 2006). In this study,  $R_e$  showed significant correlation with soil temperature only under relatively high soil moisture condition ( $VWC > 15\%$ ), which suggested that the soil water availability was the most important limiting factor for ecosystem carbon exchanges in semiarid steppe during the growing season. The higher sensitive response of GEP to soil moisture than that of  $R_e$  might be a major reason for the greater responses of ecosystem carbon gain than that of carbon release with the increasing pulse size (Fig. 4). Similar findings have also been shown for other grasslands (Potts *et al.*, 2006b). Therefore, based on our short-time experiment, the increasing frequency of larger rain events in the future is likely to disproportionately increase the primary productivity of higher plants, compared with the activities of microbial decomposers, which may increase the carbon sequestration capacity of Inner Mongolia arid and semiarid steppes. However, long-term trend of carbon sequestration in the arid and semiarid ecosystems may also relate to the changes in community composition which results likely from climate change. Thus, cautions must be taken when applying our results to predict future carbon sequestration of this region.

#### *Responses of ecosystem autotrophic and heterotrophic respiration to rain pulses*

$R_e$  consists of plant (leaves and root)-mediated  $R_a$  and belowground microbial-mediated  $R_h$  (Bond-Lamberty *et al.*, 2004). The difference in the response time of microbes and plants to wetting events constrains the response patterns of  $R_a$  and  $R_h$  following a rain event. Rapid increases in soil  $CO_2$  efflux following wetting events have been observed in a variety of ecosystems (Liu *et al.*, 2002; Fierer & Schimel, 2003; Smart & Peñuelas, 2005; Sponseller, 2007). In this study, we also found rapid  $CO_2$  releases from soil within several hours after the simulated rain pulses (Fig. 2d). The response duration of ecosystem respiration to small pulse (5 mm) was shorter than that of soil respiration. A 5 mm pulse stimulated a significant but short time (only last 1 day) increase in  $R_h$  without influencing the rate of  $R_a$ . Austin *et al.* (2004) reported that shallowly located soil microbial communities could be highly responsive to even smaller rainfall events (down to 2 mm). While, larger

events ( $\geq 5$  mm) were required to infiltrate to a depth where it becomes plant-available and could trigger assimilation processes, and simultaneously increased respiration rate of roots and aboveground vegetation (Reynolds *et al.*, 2004). Our study showed that the rain pulse larger than 5 mm stimulated the  $R_a$  in the semi-arid steppe, but only the pulse larger than 10 mm could maintain relative long response duration of  $R_a$  and eventually enhance significantly the rate of  $R_a$  in comparison with that of the control. The significant linear relationship between the GAB and  $R_a$  indicated that more green leaves and/or possible new root growth of plants were important mechanism for higher  $R_a$  rate following a large pulse (Schwinning & Sala, 2004).

The  $R_a$  and  $R_h$  values increased as a nonlinear function of rain pulse size, reaching an asymptote at about 50 and 75 mm, respectively (Fig. 3b). Sponseller (2007) reported a similar response pattern of soil respiration to precipitation amount and the soil carbon releases reached the peak value at the 50 mm water addition treatment in a desert ecosystem. An explanation for this response pattern of  $R_h$  is that substrate limitation following pulse restricts the magnitude and duration of microbial respiration (Sponseller, 2007; Jenerette *et al.*, 2008). A recent study in a Duolun steppe showed that the addition of soil carbon inputs could significantly enhance the rate of soil respiration, which indicated that microbial activity was limited by soil nutrient supply in this temperate steppe (Xiao *et al.*, 2007). Similar to the disproportional responses of photosynthesis and respiration, there also was 1–2 days delay between the arrival time of peak  $R_a$  and  $R_h$ . Therefore,  $R_h$  contributed more to the increase of  $R_e$  in the early stage of rain pulse response, while the autotrophic component played more important roles during the later stage and would determine the duration of pulse response, especially for large rain events of larger than 10 mm. Generally, heterotrophic respiration contributes 30–50% of total soil respiration for most terrestrial systems (Raich & Schlesinger, 1992; Bond-Lamberty *et al.*, 2004). Lower contributions ( $< 20\%$ ) from heterotrophic respiration are more common in grassland ecosystems (Hanson *et al.*, 2000). However, Wan & Luo (2003) reported that rhizosphere respiration could account for up to 48% of total soil respiration during the growing season in a tall grass prairie. Based on the measurements of 16 days, the contribution of autotrophic respiration to total ecosystem respiration was 51.8% during whole pulse response and did not show significant differences with increasing pulse size (Table 2). That is, the rate of  $R_a$  and  $R_h$  scaled with the size of rain pulse but the proportional contribution of each to  $R_e$  was consistent and independent of the rain pulse size.

## Conclusions

Arid and semiarid steppe ecosystems are highly sensitive to the variability of rain pulse size. Both ecosystem photosynthesis (GEP) and respiration ( $R_e$ ) responded rapidly to rain pulse and the response time of them was independent of pulse size between 5 and 75 mm. However, the time to reach peak GEP was 1–3 days later than that of  $R_e$ . The relatively quick response of GEP in this study might result from the shallow rooting depth of grasses. Larger rain pulses could cause greater magnitude and longer duration of elevated ecosystem processes following rewetting. Similarly, the heterotrophic respiration contributed more to the increase of  $R_e$  on the early stage of rain pulse response, while the autotrophic component played more important role during the later stage, which determined the duration of pulse response, especially for large rain events of more than 10 mm. The distinct responses of ecosystem photosynthesis and respiration to increasing pulse size resulted in a threshold which should be between 10 and 25 mm. A rain event larger than this threshold would be favorable for improving carbon sequestration capacity of semiarid steppe of Inner Mongolia.

The increasing frequency of larger rain events in this area is likely to disproportionately increase the primary productivity of higher plants, compared with the activities of microbial decomposers. This might increase the capacity for carbon sequestration of arid and semiarid steppes in Inner Mongolia. The strengthening of rain pulse would prolong the interval dry period between pulses, and the changes in the wet–dry cycles also affect the responses of carbon fluxes of ecosystems. To predict the changes of steppe ecosystems under future precipitation scenarios, further studies are needed to investigate long term responses of carbon exchange processes to variations in rainfall pattern and how pulse driven ecosystem–atmospheric CO<sub>2</sub> exchanges may be affected by changes in soil and plant carbon pools as well as community composition.

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