



### Full Length Article

## Photosynthetic Acclimation of a Desert Species *Nitraria tangutorum* to Long Term Rain Addition in North-Western China

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### Abstract

Precipitation patterns might change because of global climate change in mid-latitude regions, while the study on how photosynthetic physiological characteristics acclimate and the response mechanisms to long term rain addition of desert plant in arid and semi-arid regions on the Northwest of China are still relatively scarce. In order to understand the acclimatization and explore the adaptive mechanism of typical desert plant *Nitraria tangutorum* Bobrov to rain addition, gas exchange parameters and photosynthetic physiology characteristics of *N. tangutorum* at the eastern edge of the Ulanbuh Desert on the Northwest of China under five rain addition treatments (increased 0%, 25%, 50%, 75% and 100% of local mean annual precipitation, respectively) were measured. The results show that photosynthetic capacity enhanced after rain addition. The impact extent of precipitation on photosynthesis was related to rain addition amount which was not less than 75% (110 mm) rain addition played significantly accelerated effects on photosynthesis and transpiration. The supplement watered plants carbon and water exchange were affected significantly which indicated that there was a process for *N. tangutorum* to adapt to the increased precipitation. The apparent quantum efficiency (AQY), light saturation point (LSP), initial carboxylation efficiency (CE) and CO<sub>2</sub> saturation point (CSP) increased, indicating an enhanced activity of carboxyl enzyme and increased the capacity of *N. tangutorum* to use light and carbon dioxide. Therefore, under global change scenario, *N. tangutorum* would improve the photosynthetic capacity and mediate the function of photosynthetic organization to adapt to new water conditions in the future. © 2019 Friends Science Publishers

**Key words:** *Nitraria tangutorum*; Simulated rain addition; Photosynthesis; Photosynthetic acclimation; Response mechanism

### Introduction

Global change models predicted that the precipitation patterns, especially precipitation amount and probability of extreme precipitation events in mid-latitude regions will change in the future (Gao *et al.*, 2001; Change, 2007). Changes of precipitation amounts can influence various physiological and ecological processes of plants including photosynthesis, nutrient dynamics, growth, and net ecosystem productivities (Brown *et al.*, 1997; Ehleringer *et al.*, 1999; Reynolds *et al.*, 1999; Weltzin and McPherson, 2000; Huxman *et al.*, 2004a; Xu and Li, 2006). Compared with other ecosystems, desert ecosystems where scarce water tends to show more sensitivity to variations in precipitation (Knapp, 2002; Weltzin *et al.*, 2003). In recent years, impacts of precipitation changes on plant growth and physiological activities in arid areas are focusing more attention (Danielle *et al.*, 2007; Zou *et al.*, 2010; Zhang *et al.*, 2013). As one of the most important photosynthetic parameters, net photosynthetic rate is an indicator of plants' carbon

assimilation abilities. Higher net photosynthetic rate suggests higher ability to synthesis and fix carbon from atmosphere (Xu and Li, 2006; Liu *et al.*, 2012). Nevertheless, desert species may show different adaptation mechanisms and response strategies to variation precipitation (Schwinning *et al.*, 2002; Schwinning and Ehleringer, 2003; Reynolds *et al.*, 2004; Zhao *et al.*, 2006; Zhang *et al.*, 2007). For example, Xu and Li (2006) and Xu *et al.* (2007) found that a non-preatophyte desert shrub species adjusts its morphology and stomatal conductance to acclimate variation in precipitation. Studies on the sensitivity of photosynthesis to summer precipitation pulses suggested that the shrub species in the southwestern Great Basin Desert, USA, coordinates water use capacity and photosynthetic carbon assimilation process to adapt to different patterns and magnitudes of summer rainfall pulses (Loik, 2007). Similarly, along a precipitation gradient in arid regions in China, the wetter the larger a leaf area was observed from a desert species *Nitraria tangutorum* (Li *et al.*, 2012). The abilities for species adapting to precipitation changes strongly affect their carbon

assimilation capacities, plant fitness, community compositions, and the whole ecosystem carbon balance, ultimately (Weltzin *et al.*, 2003; Huxman *et al.*, 2004b).

To predict responses of terrestrial ecosystems to global climate change, simulation methods including rain addition, prevention, ground warming, nitrogen addition have usually been used in agriculture, grassland, and forest ecosystems (Potts *et al.*, 2006; Danielle *et al.*, 2007; Loik, 2007; Xu *et al.*, 2007; Sarah *et al.*, 2009; QiuHong *et al.*, 2013). A plenty of studies have focused on the morphological or physiological responses of desert shrubs to variation in precipitation (Danielle *et al.*, 2007; Loik, 2007; Xu *et al.*, 2007). In present study site, significant effects of rain addition on photosynthetic characteristic (Danielle *et al.*, 2013), leaf shape (Li *et al.*, 2012), and soil respiration (Song *et al.*, 2012) *etc.* have been reported. However, these studies mainly based on short term observations, and how photosynthetic physiological characteristics of desert plant acclimate to long-term rain addition and the mechanisms are still unclear. Based on former results, it was predicted that, (1) a threshold of rain addition amount when the added rain amount start to affect the plant photosynthesis significantly should be exist because a small quantity of rain addition cannot compensate the water deficit caused by the dry environment; (2) plants should undergo a period to acclimate to the simulated precipitation since they have showed strong adaptability to the dry environments.

A five years manipulative experiment with five levels of precipitation additions (0%, +25%, +50%, +75%, +100% of local annual mean precipitation) were conducted during the whole growing season from 2008 to 2012 in a desert ecosystem dominated by a shrub species *N. tangutorum* in arid regions in the Northwest of China. *N. tangutorum* which is a typical desert plant plays an important ecological role in combating desertification due to its exceptional capabilities in forming phytogenic nebkha dunes which prevent or slow down the movement of sands. The main objectives of this research were to evaluate the response of photosynthesis and transpiration and explore the response mechanism of desert plant *N. tangutorum* to rain addition from the perspective of photosynthetic physiology. The following questions should be resolved: (1) how photosynthesis and transpiration of *N. tangutorum* varied in response to simulated rainfall addition; (2) whether there is a precipitation threshold that leading to significant physiological responses; (3) underlying mechanisms of photosynthetic responses to new water conditions.

## Materials and Methods

### Study Site Description

The trial was set up in a desert ecosystem, which is located between Hetao Plain and UlanBuh Desert in Dengkou County, Inner Mongolia Autonomous Region, China (106° 43' E, 40° 24' N), with an altitude of 1050 m. The area is

temperate continental arid climate, with an average annual temperature of 7.8°C. Annual average precipitation is 145 mm, mainly occurring between July and September, which accounts for about 60%~80% of annual precipitation. Average annual evaporation is about 2327 mm, annual hours of sunshine is approximately 3210 h. The dominant soil type is aeolian sandy soil and the gray-brown desert soil. The vegetation is dominated by a shrub species, *N. tangutorum*, occasionally associated with a few plants of *Artemisia desterorum* or *Psammochloa villosa*. The experiment was carried out in a patchy landscape with *N. tangutorum* interspersed with sand dunes. The mean height and size of the dune was  $1.24 \pm 0.14$  m and  $29.9 \pm 0.39$  m<sup>2</sup>, respectively. Plant cover was approximately 10%~30%. The natural precipitation at the study site was shown in Fig. 1.

### Precipitation Manipulation

A completely random design was used in this experiment, with 5 rain addition treatments and four replicates for each treatment (113 m<sup>2</sup> per plot, 20 plots in total). Five rain addition treatments were designed to simulate rain increase of 0% (CK), 25%, 50%, 75% and 100% of the average annual precipitation (145 mm) from 1978 to 2008 at the study site, respectively. During the growing season (May to September) of 2008, rain addition was applied twice every month, and the rain amounts added were 0, 3.6, 7.3, 10.9 and 14.5 mm each time for the five rain increase treatments. The rain addition was applied once a month since 2009, and the rain amounts added were 0, 7.3, 14.5, 21.8 and 29.0 mm once, respectively. A new rain simulator called full light spray irrigation system was used in the study site. Water which pumped into a tank from a well near the plots firstly was irrigated into the plots *via* the new simulation irrigation system. The more detailed information of using the rain simulator in sites was demonstrated (Song *et al.*, 2012). The rain addition was carried out only in the morning when air temperature was relatively low and the air was usually calm in order to reduce water loss. Experimental plots and distribution of nebkha dunes were shown in Fig. 2.

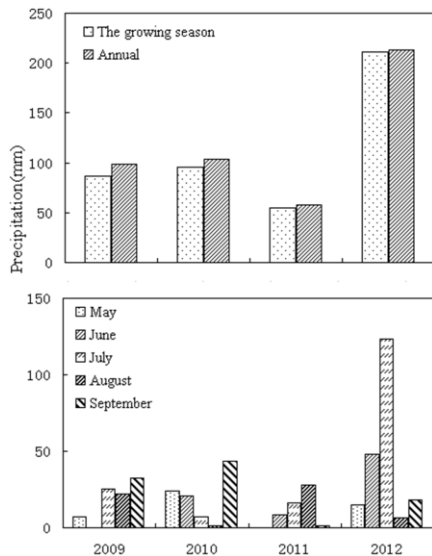
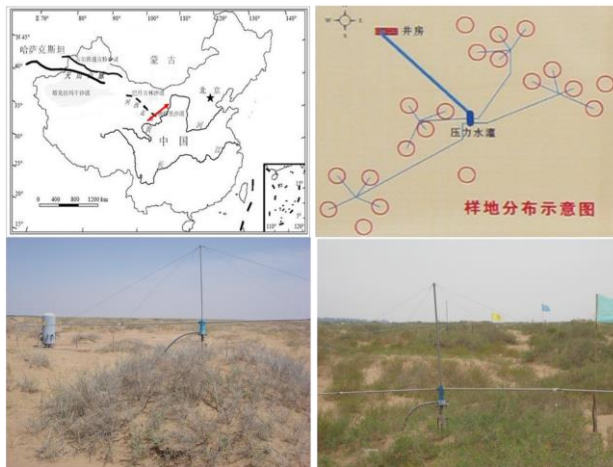
Field test data showed that the rain validity of the rain simulator was about 66%, and the rainfall distribution was high uniform as long as hydraulic pressure exceeded 1.4 KPa and wind speed lower than 2.5 m s<sup>-1</sup> which could be achieved easily in most cases in arid regions (unpublished). The specific dates of simulated rain addition are showed in Table 1.

### Gas Exchange Measurement

The experiments were carried out during the growing season (from June to September) 2009, 2010, and 2012. In the sample plots, mature and healthy leaves of each shrub species were selected, and leaf-level gas exchanges (net photosynthetic rate and transpiration rate) were measured using a portable photosynthesis system (LI-6400, Li-COR

**Table 1:** The time of simulated rainfall from 2008 to 2012

Year	Simulated rainfall time (month-date)				
2008	05-10, 25	06-10, 25	07-10, 25	08-10, 25	09-10, 25
2009	05-11	06-11	07-12	08-10	09-12
2010	05-13	06-13	07-13	08-13	09-13
2011	05-18	06-16	07-14	08-14	09-12
2012	05-16	06-16	07-16	08-16	09-16

**Fig. 1:** Precipitation distribution at the study site classified by year and month**Fig. 2:** Distribution of *N. tangutorum* population in experimental plots

*Inc.*, Lincoln, NE, USA) at 1 d before, and 1, 3, 5, 7, 9 and 11 d after rainfall between 8:00 and 10:00. Environmental factors such as photographic active radiation, air temperature, and relative humidity were recorded simultaneously. Air temperature and precipitation data were recorded by a standard meteorological station near the experiment plots.

## Leaf Photosynthetic Characteristics Measurement

Since the responses have great temporal, spatial, and functional group variations (Loik, 2007), the changes in photosynthetic parameters of light- and CO<sub>2</sub>-response curves in *N. tangutorum* shrubs were measured to better understand and explore the response mechanism of photosynthesis to different rain additions. The physiological parameters were measured between 8:00~12:00 to avoid plant physiological functions disorder induced by high light intensity and temperature. The measured leaves which were mature and healthy were exposed to at PPFD of 1600  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  to induced by 30 min before measurement.

**Photosynthetic responses to photosynthetic photon fluence density (PPFD):** The photosynthetic light-response curves of the species were measured by a Li-6400 portable photosynthesis system. In-chamber photosynthetic photon flux density (PPFD) was controlled by 20 mm×30 mm leaf chamber with a light source (red +blue 6400-02B) at 2000, 1600, 1200, 1000, 800, 600, 400, 200, 150, 100, 80, 50, 20 and 0  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . The gas flow rate was set at 500  $\mu\text{mol}\cdot\text{s}^{-1}$ . Chamber temperature was controlled at 26°C. A CO<sub>2</sub>-injecting device was attached to the system to control reference CO<sub>2</sub> concentration at 380  $\mu\text{mol}\cdot\text{mol}^{-1}$ . The light response curves of net photosynthetic rate were measured. Advanced regression analysis of the non-linear curve showed that the relationship between net photosynthetic rate (Pn) and PPFD was best fitted by non-rectangle hyperbolic function:  $P_n = (\text{PAR} * \text{AQY} + P_{n\text{max}} - \text{SQRT}((\text{PAR} * \text{AQY} + P_{n\text{max}}) * (\text{PAR} * \text{AQY} + P_{n\text{max}}) - 4 * K * \text{AQY} * \text{PAR} * P_{n\text{max}})) / 2 * K - R_d$ , in which PAR is PPFD, Pn is net photosynthetic rate, Pnmax is net photosynthetic rate at light saturation point, AQY is apparent quantum efficiency of photosynthesis, Rd is dark respiration rate, K is the crank angle of fitting curve (Zou et al., 2010). The linear regression analysis was used to fit the initial portion of the light-response curve ( $\text{PAR} < 200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). The intersection of the regression line and the X-axis was the light compensation point (LCP), which was the radiation intensity where net photosynthetic rate was equal to zero. The X-axis value corresponding to the intersection of the regression line and  $y = P_{n\text{max}}$  was light saturation point (LSP) (Ye and Yu, 2008). Ultimately, the maximum net photosynthetic rate (Pnmax), apparent quantum yields (AQY), dark respiratory rates (Rd), light compensation points (LCP) and light saturation points (LSP) were calculated.

**Photosynthetic responses to intercellular CO<sub>2</sub> concentration (Ci):** The photosynthetic intercellular CO<sub>2</sub>-response curves of the species were measured by a Li-6400 portable photosynthesis system. A CO<sub>2</sub>-injecting device was attached to the system to control reference CO<sub>2</sub> concentrations at 400, 300, 200, 150, 120, 100, 80, 50, 400, 600, 800, 1000, 1200 and 1500  $\mu\text{mol}\cdot\text{mol}^{-1}$ . The gas flow rate was set at 500  $\mu\text{mol}\cdot\text{s}^{-1}$ . Chamber temperature was controlled at 26°C. In-chamber PPFD was controlled at

1600  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . The  $\text{CO}_2$  response curves of net photosynthetic rate were measured. Advanced regression analysis of the non-linear curve showed that the relationship between Pn and intercellular  $\text{CO}_2$  concentration ( $\text{Ci}$ ) was best fitted by exponential function:  $\text{Pn} = \text{Amax} (1 - e^{-\text{CE}\cdot\text{Ci}}) + \text{Rp}$ , in which  $\text{Ci}$  is intercellular  $\text{CO}_2$  concentration, Pn is net photosynthetic rate, Amax is assimilation rate at saturating  $\text{CO}_2$ , CE is the carboxylation efficiency, Rp is leaf light respiration rate (Walting *et al.*, 2000). The linear regression analysis was used to fit the initial portion of the A-Ci curve ( $\text{Ci} < 200 \mu\text{mol}\cdot\text{mol}^{-1}$ ). The intersection of the regression line and the X-axis was the  $\text{CO}_2$  compensation points (CCP), which was the  $\text{CO}_2$  concentration where net photosynthetic rate was equal to zero (Ye and Yu, 2008). Using the exponential function  $\text{CO}_2$  saturation points (CSP) was estimated when net photosynthetic rate reached to  $0.9 \cdot \text{Amax}$ . Ultimately, the parameters of maximum assimilation rate (Amax), carboxylation efficiency (CE), light respiratory rates (Rp),  $\text{CO}_2$  compensation points (CCP) and  $\text{CO}_2$  saturation points (CSP) were calculated.

### Statistical Analyses

After experiments, the selected leaves were scanned and the actual leaf area was calculated with Ipp 6.0 image analysis software. All the photosynthetic parameters were calculated based on the actual leaf area. All statistical tests were performed with SPSS (Ver.17.0) for Windows. One-way ANOVA was used to test for differences in leaf-level photosynthesis and transpiration rate, *etc.* among different precipitation treatments. When data were found significant differences, the least-significant-difference (LSD) multiple comparison tests was used to compare specific pairs of values. A simple regression method was used to analyze the relationship between net photosynthesis and total precipitation (TP). Throughout, means and standard errors were reported and  $P < 0.05$  was considered significant. Excel 2010 and Sigmaplot10.0 software were used to draw graphics.

## Results

### Net Photosynthetic Rate

The net photosynthetic rate (Pn) in watered plots did not change regularly after the precipitation in 2009 (Fig. 3). In June, 75% and 100% treatments showed significant greater Pn than CK on the fifth day after watering ( $P < 0.05$ ). In July, Pn in 50% and 75% treatments increased obviously, but only 75% treatment was greater than CK on the fifth day after watering ( $P < 0.05$ ). Additionally, there was a significant difference between 100% treatment and CK on the fifth day in August ( $P < 0.05$ ).

The Pn were enhanced in watered plots than in control plots in most days in 2010. 75% and 100% rain addition had a positive effect on Pn. As shown in Fig. 3, Pn in 75% and

100% treatments on the fifth day in June, as well as 75% treatment on the fifth day and 100% treatment on the third and fifth days in July, showed significantly increases compared with CK ( $P < 0.05$ ). In August, Pn in 75% treatment plots increased significantly on the seventh day (the field capacity could reach  $6.23 \pm 0.97\%$ ), while Pn in 100% treatment increased significantly on seventh, ninth, and eleventh days ( $P < 0.05$ ). Additionally, Pn were significantly higher than CK in 25, 50, 75 and 100% treatments on the third day after rain additions in September ( $P < 0.05$ ).

Pn increased obviously after rain addition, which were greater in watered plots than in control plots in most days in 2012. In June, 50%, 75% and 100% treatments on the fifth day and 75% and 100% treatments on the ninth day showed significant higher Pn compared with CK ( $P < 0.05$ ). Similarly, Pn was higher than CK in 50, 75 and 100% treatments on the first day and 100% treatment on the seventh day in July ( $P < 0.05$ ). In August, 100% rain addition increased Pn significantly on the first and fifth days ( $P < 0.05$ ). Finally, Pn was greater than CK in 75% treatment on the first and eleventh days after rain addition in September, consistently, 100% treatment on day 1/5/9/11 ( $P < 0.05$ ).

Table 2 showed the annual average Pn in 2009, 2010, and 2012. The annual average Pn in 50, 75 and 100% treatments were 7.1, 13.9 and 8.9% higher than control shrubs, respectively in 2009. Both 75% and 100% treatments had relatively high annual average Pn than shrubs in control plots in 2010 and 2012 ( $P < 0.05$ ). The annual average Pn in 75 and 100% treatments were 23.3 and 25.6% in 2010, 12.9 and 13.5% in 2012 higher than control shrubs, respectively.

### Transpiration Rate

After rain addition, transpiration rate (Tr) have no obvious changes in watered plots compared with control plots in 2009 (Fig. 4). In June, 75% and 100% treatments plots showed greater Tr than CK plots. But significant increases of Tr were observed only on the first and ninth days ( $P < 0.05$ ). Although 75% treatment displayed higher Tr than CK, there were no significant differences between them in July ( $P > 0.05$ ).

Increased obviously after precipitation, Tr were enhanced in watered plots than in control plots in most days in 2010. Tr in 75 and 100% treatments displayed significant increases compared with CK on the fifth day in June and July ( $P < 0.05$ ). In August, 75% water addition increased Tr significantly on the fifth day ( $P < 0.05$ ), while Tr under 75% water addition showed significant increase on the ninth day in September ( $P < 0.05$ ).

Tr increased obviously after rainfall, which were greater in watered plots than in control plots in most days in 2012. In June, compared with CK, Tr increased significantly in 50% treatment on the 5<sup>th</sup> day, 75% treatment on day 1/5/9,

**Table 2:** Differences in average annual Pn ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) among different rain addition treatments of *N. tangutorum* (mean  $\pm$  SE)

Year	CK	25%	50%	75%	100%
2009	11.85 $\pm$ 0.68a	11.69 $\pm$ 1.01a	11.94 $\pm$ 0.47a	13.50 $\pm$ 0.78a	12.81 $\pm$ 1.18a
2010	10.33 $\pm$ 0.35a	11.41 $\pm$ 0.38a	11.78 $\pm$ 0.40ab	12.74 $\pm$ 0.38b	12.98 $\pm$ 0.25b
2012	14.28 $\pm$ 0.17a	14.77 $\pm$ 0.34a	15.07 $\pm$ 0.44ab	16.12 $\pm$ 0.16b	16.21 $\pm$ 0.51b

Note: Different lowercase letters within the same row show significant difference at 0.05 level; Valued are expressed as average yearly gas exchange parameters from June to September in 2009, 2010, and 2012

**Table 3:** Differences in average annual Tr ( $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) among different rain addition treatments of *N. tangutorum* (mean  $\pm$  SE)

Year	CK	25%	50%	75%	100%
2009	5.18 $\pm$ 0.22a	5.05 $\pm$ 0.29a	5.20 $\pm$ 0.24a	6.01 $\pm$ 0.41a	5.77 $\pm$ 0.26a
2010	3.34 $\pm$ 0.31a	3.54 $\pm$ 0.23ab	3.84 $\pm$ 0.27ac	4.14 $\pm$ 0.34bc	4.45 $\pm$ 0.38c
2012	3.53 $\pm$ 0.27a	3.71 $\pm$ 0.14a	4.15 $\pm$ 0.31ab	4.43 $\pm$ 0.16b	4.83 $\pm$ 0.21b

Note: Different lowercase letters within the same row show significant difference at 0.05 level; Valued are expressed as average yearly gas exchange parameters from June to September in 2009, 2010, and 2012

100% treatment on day 1/3/9 ( $P < 0.05$ ). In July and August, Tr in 50%, 75% and 100% treatments were higher than CK on the first day ( $P < 0.05$ ). Finally, Tr in 75% treatment was significantly higher than CK on the third, fifth and ninth day after rain addition, and on the fifth and ninth day in 100% treatment in September ( $P < 0.05$ ).

Table 3 showed the annual average Tr in 2009, 2010, and 2012. Although the annual average Tr in 50, 75 and 100% treatments were 4.90, 15.96 and 11.42% higher than that of control shrubs, respectively in 2009, there were no significant differences among them ( $P > 0.05$ ). 75% and 100% treatments had relatively a high annual average Tr than the shrubs in control plots in 2010 and 2012 ( $P < 0.05$ ). Annual average Tr in 75 and 100% treatments were 23.88 and 33.17% higher than that of control shrubs in 2010, while the value were 25.55 and 36.97% in 2012, respectively.

### Leaf Photosynthetic Physiological Characteristics

The Pnmax increased gradually with the increase of precipitation (Table 4). The Pnmax under 25%, 50%, 75% and 100% treatments were 33.3, 36.9, 39.9 and 55.3% higher than control shrubs, respectively, in which the 75% and 100% treatments showed significant differences with CK ( $P < 0.05$ ). With the increase of precipitation, AQY increased gradually, and 75% treatment reached the maximum. AQY in 25%, 50%, 75% and 100% treatments were 17.24, 31.03, 37.93 and 24.14% higher than CK, respectively, in which the 50% and 75% treatments showed significant differences with CK ( $P < 0.05$ ). Although, LCP in four rain addition treatments were larger than CK, there were no significant differences between them ( $P > 0.05$ ). Similarly, rain additions had no significant effect on light saturation points (LSP) ( $P > 0.05$ ).

With the increasing of precipitation, CE increased gradually. Although, there were no significant differences

between 25, 50 and 75% treatments and CK ( $P > 0.05$ ), CE under 100% treatment was significantly higher than CK ( $P < 0.05$ ). The increment rate was 5.73%. CSP were greater in watered plots than in control plots. And 50, 75 and 100% treatments were approximately 30.31, 26.56, and 50.94% higher than CK, respectively ( $P < 0.05$ ). There were no significant treatment differences in CCP ( $P > 0.05$ ).

### Discussion

The abilities of organisms to acquire carbon and utilize water depend on the availability of soil water content (Huxman *et al.*, 2004b). Responses of different plants to identical precipitation event or the same species to different precipitation events are different (Schwinning *et al.*, 2002; Schwinning and Ehleringer, 2003; Schwinning *et al.*, 2004; Loik, 2007; Xu *et al.*, 2007; Mabapa *et al.*, 2018). For example, the increase of summer precipitation did not significantly increase the carbon fixation for typical shrubs in northern Mojave Deserts (Snyder *et al.*, 2004). Studies on rainfall variability and carbon cycling in a mesic grassland ecosystem showed that increased rainfall variability leads to decreased carbon assimilation (Knapp, 2002). Nevertheless, in a study in Big Bend National Park, an increase in summer precipitation results in increasing carbon uptake and assimilation (Patrick *et al.*, 2007). In present study, net photosynthetic and transpiration rates were increased in almost plots after rain addition. The fact that desert plants exhibit a positive response to rain addition was according to Patrick *et al.* (2007) and Loik *et al.* (2004). The consistency of photosynthetic rate and transpiration rate was mainly due to the increase of water content in soil surface by increasing rainfall, which affects the physiological activities of *N. tangutorum*. In addition, the higher transpiration rate of *N. tangutorum* could provide sufficient raw materials for photosynthesis to ensure higher photosynthetic capacity when there was more water (He *et al.*, 2013). However, among the four rain addition treatments (25%, 50%, 75% and 100%), only 75% and 100% treatments showed great effect on annual average net photosynthetic and transpiration rates. These results implied that rainfall magnitudes especially for large amounts (75% and 100% treatments) played key roles in regulating photosynthetic responses to precipitation in desert system and is consistent with our first hypothesis. These results could be attributed to the more soil moisture in plots with 75% and 100% rain addition treatments. Because only rain fall amounts up to a certain threshold would supplement soil water content effectively and cause physiological and ecological responses of relatively deeply rooted desert shrubs (Golluscio *et al.*, 1998; Loik *et al.*, 2004; Cheng *et al.*, 2006; Emmerich and Verdugo, 2008).

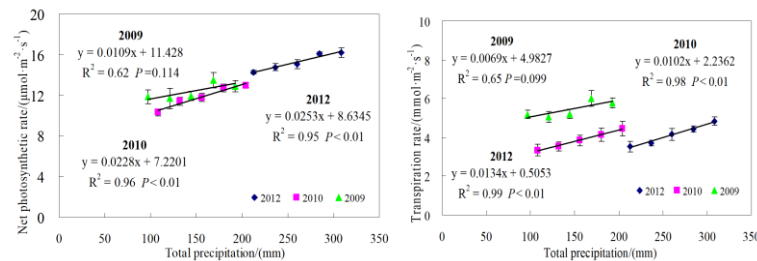
In the initial stages of the experiment, variations of plant photosynthetic parameters were not significant among treatments. But after three years experiment, rain additions showed significantly affected on plant photosynthesis and transpiration activities which is consistent with second



**Table 4:** Effects of rain addition on Pn-PAR and A-Ci curve characteristic parameters of *N. tangutorum* (mean  $\pm$  SE)

	CK	25%	50%	75%	100%
Pnmax/ $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	13.41 $\pm$ 1.67a	17.88 $\pm$ 2.75ab	18.22 $\pm$ 1.40ab	18.76 $\pm$ 1.54b	20.83 $\pm$ 0.61b
AQY/ $\mu\text{mol}\cdot\text{mol}^{-1}$	0.029 $\pm$ 0.0017a	0.034 $\pm$ 0.0030a	0.038 $\pm$ 0.0008b	0.040 $\pm$ 0.0027b	0.036 $\pm$ 0.0024ab
CE/ $\mu\text{mol}\cdot\text{mol}^{-1}$	0.127 $\pm$ 0.016a	0.122 $\pm$ 0.004a	0.125 $\pm$ 0.008a	0.124 $\pm$ 0.010a	0.135 $\pm$ 0.001b
LCP/ $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	20.63 $\pm$ 4.26a	27.92 $\pm$ 4.96a	23.39 $\pm$ 5.95a	18.33 $\pm$ 5.12a	21.69 $\pm$ 5.48a
LSP/ $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	481.85 $\pm$ 43.03a	552.28 $\pm$ 46.95a	510.67 $\pm$ 34.28a	496.10 $\pm$ 59.10a	607.36 $\pm$ 26.20a
CCP/ $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	45.14 $\pm$ 4.09a	49.16 $\pm$ 1.50a	49.45 $\pm$ 4.88a	47.95 $\pm$ 7.40a	41.44 $\pm$ 2.79a
CSP/ $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	320.94 $\pm$ 45.80a	373.38 $\pm$ 39.00ab	417.33 $\pm$ 19.00b	405.43 $\pm$ 29.54b	483.01 $\pm$ 57.606b

Note: Different lowercase letters within the same row show significant differences at 0.05 level

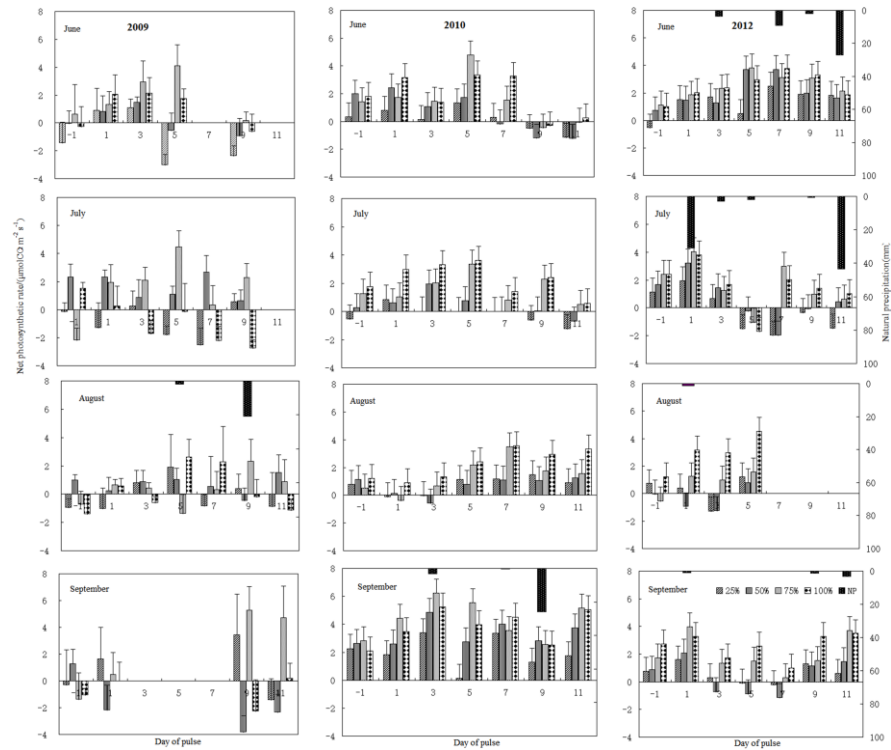
**Fig. 5:** Relationship between Pn, Tr of *N. tangutorum* and total annual precipitation (TAP) in 2009 (filled triangles), 2010 (filled squares) and 2012 (filled diamonds)

hypothesis. Therefore, linear-regression analysis was used to evaluate the relationships between net photosynthetic rate, transpiration rate and total precipitation (natural and simulated precipitation) in 2009, 2010 and 2012, respectively. Results showed that there were good linear relationships between them (Fig. 5). The relationships in 2009 were not significant ( $P > 0.05$ ), and precipitation explain only 62% and 65% variation of net photosynthetic rate and transpiration rate, respectively. One years later, the relationships became significant ( $P < 0.01$ ), and precipitation explained more than 95% variations of net photosynthetic and transpiration rates in 2010 and 2012, respectively (Fig. 5). The standpoint that precipitation inputs explain much more of the variation in ecosystem processes is consistent with Huxman *et al.* (2004a). These results could be attributed to the early years of the experiment that *N. tangutorum* shrubs have grown in drought and high temperature environments for a long time, and have formed special physical and morphological characteristics (Snyder *et al.*, 2004; Xu and Li, 2006). After three years rain addition, the number of feeder roots in the up soil which could support more photosynthetic assimilating organs for photosynthesis increased significantly and *N. tangutorum* have adapted to new water conditions gradually (Xu *et al.*, 2007).

Desert plants have formed particular physical and morphological characteristics gradually to adapt specific conditions in the long-term evolution processes, and revealed kinds of mechanisms and strategies to deal with changes in rainfall patterns (Golluscio *et al.*, 1998; Schwinning *et al.*, 2002; Schwinning and Ehleringer, 2003; Reynolds *et al.*, 2004; Weng and Lai, 2005; Zhao *et al.*, 2006; Zhang *et al.*, 2007). Therefore, it is critical to develop an improved understanding about respond mechanisms of

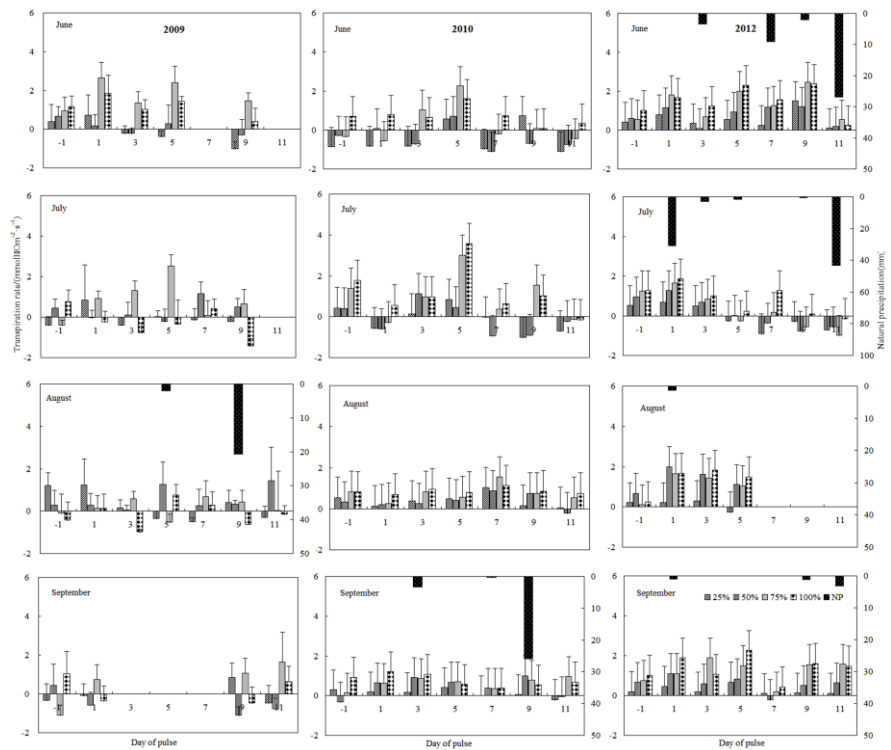
plant physiological process to variable precipitation in arid ecosystem. Observations about the responses of photosynthesis to light intensity and carbon dioxide concentration could help us understand the underlying physiological adaptations mechanisms to precipitation for plants, which are beneficial to reveal the variation behavior of photosynthesis with water conditions (Wang *et al.*, 2007).

Pnmax represents the maximum photosynthetic capacity at an optimum condition (Hiroyuki *et al.*, 2008). A positive response of carbon assimilation rate of *N. tangutorum* in 75 and 100% treatments indicated that the adaptive ability and potential photosynthetic ability were enhanced when rain addition amounts over 75% of the annual mean precipitation in this study. The AQY represents the net photosynthetic rate at low light levels. Rain addition caused the increases of AQY, suggesting stronger photosynthetic activities of leaf mesophyll cells, much more pigment protein complexes that absorb and convert optical energy, and enhanced abilities to absorb, transform and use optical energy at low light levels (Richardson and Berlyn, 2002; Liu *et al.*, 2012). LCP corresponds to the PAR when net photosynthesis rate is equal to 0, and LSP corresponds to the PAR when net photosynthesis rate reaches maximum. The two parameters together reflect the plants' demand for light (Ye and Yu, 2008; Gao *et al.*, 2009). LSP increased after precipitation, suggested a shift for light utilization amplitude of *N. tangutorum* to high light intensity and an increase in the optical energy use and conversion efficiency, which will help improve the efficiency of photosynthesis, and finally facilitate the accumulation of assimilation products. CSP stands for the ability of species to use high carbon dioxide concentration. CE reflects the amounts and activities of RuBP carboxylase enzyme (Farquhar *et al.*, 1980; Ye, 2010). CE and CSP of *N. tangutorum* increased



**Fig. 3:** Responses of net photosynthetic rate to rain addition treatments (mean  $\pm$  SE)

Note: Values are expressed as a difference of supplemental summer watered to control plots. Differences are presented for 1 day prior and up to 11 days after supplemental watering. Filled black rectangle represented natural precipitation



**Fig. 4:** Responses of transpiration rate to rain addition treatments of *Nitraria tangutorum*

Note: Values are expressed as a difference of supplemental summer watered to control plots. Differences are presented for 1 day prior and up to 11 days after supplemental watering. Filled black rectangle represented natural precipitation

after rain addition (Table 4) suggesting that rain addition increased and enhanced the activities of photosynthetic carbon cycle enzyme and utilization amplitude of high carbon dioxide concentration for desert plant, eventually promoted carbon assimilation rate (Farquhar *et al.*, 1980; Walting *et al.*, 2000; Ye, 2010).

The extended amplitude of light and carbon dioxide utilization implied that leaves could capture more light and CO<sub>2</sub> during the day, and the abilities of physiological metabolism for *N. tangutorum* leaves enhanced, which would be beneficial to photosynthetic products accumulation (Farquhar *et al.*, 1980). Species usually show unique strategies in responding to alternative precipitation patterns. Typical desert plants *N. tangutorum* improve its photosynthetic capacity to adapt new water conditions by mediating its carboxylase activity and photosynthetic organization functions. The increased capability of photosynthetic is the result of comprehensive optimizing leaf physiological activity and photosynthetic property (Reynolds *et al.*, 2004).

Understanding the underlying mechanisms of typical desert plant photosynthetic responses to rain addition is critical to predict the adaptability of desert ecosystem by future rainfall changes (Danielle *et al.*, 2007). Plants may increase fixed carbon abilities to response to precipitation through increasing leaf-level CO<sub>2</sub> exchange rate or expanding leaf areas, or both (Huxman *et al.*, 2004a). Data showed that sufficient rain addition improved the photosynthesis production capacity of *N. tangutorum*. Therefore, we deduce that the whole ecosystem carbon assimilation will be improved in the future global climate change (Patrick *et al.*, 2007). Our research provides a foundation for predicting and modeling the role that desert plants played in northwest arid regions in the future climate change especially for precipitation pattern changes.

## Conclusion

As precipitation increased, net photosynthetic rate and transpiration rates increased for *N. tangutorum*. Not less than 75% (110 mm) rain addition play a significantly accelerated effects on photosynthesis and transpiration. There was a process for *N. tangutorum* to adapt to the increased precipitation. Rainfall affected physiological characteristics significantly on leaf scale of *N. tangutorum*. Increasing precipitation enhanced photosynthetic and carboxylase activity of leaf mesophyll cells, that would increase the ability of using and transforming optical energy as well as carbon dioxide, ultimately, improve the accumulation of photosynthetic products.

## Acknowledgements

The first author acknowledges the financial grant from Introduction of Talented Personnel Research Fund of Guizhou University (GDRJHZ (2015) 08), Science and

Technology Project of Guizhou Province (QKHJC[2019] 1106), and Construction Program of Biology First-class Discipline in Guizhou (GNYL[2017] 009).

## References

- Brown, J.H., T.J. Valone and C.G. Curtin, 1997. Reorganization of an arid ecosystem in response to recent climate change. *Proc. Natl. Acad. Sci. USA*, 94: 9729–9733
- Change, I.C., 2007. *The physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, pp: 5–17. Manning, M., Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (Eds.). Cambridge University Press, Cambridge, UK; New York, USA
- Cheng, X.L., S.Q. An, B. Li, J. Chen, G. Lin and Y. Liu, 2006. Summer rain pulse size and rainwater uptake by three dominant desert plants in a desertified grassland ecosystem in northwestern China. *Plant Ecol.*, 184: 1–12
- Danielle, D.I., T.E. Huxman, J.F. Weltzin and D.G. Williams, 2007. Leaf gas exchange and water status responses of a native and non-native grass to precipitation across contrasting soil surfaces in the Sonoran Desert. *Oecologia*, 152: 401–413
- Ehleringer, J.R., S. Schwinning and R. Gebauer, 1999. Water-use in arid land ecosystems. In: *Physiological Plant Ecology*, pp: 347–365. Press, M.C., J.D. Scholes and M.G. Barker (Eds.). Blackwell Science, Edinburgh, UK
- Emmerich, W.E. and C.L. Verdugo, 2008. Precipitation thresholds for CO<sub>2</sub> uptake in grass and shrub plant communities on Walnut Gulch Experimental Watershed. *Water Resour. Res.*, 44: 5–16
- Farquhar, G.D., S.V. Caemmerer and J.A. Berry, 1980. A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C3 species. *Planta*, 149: 78–90
- Gao, S., P. Su, Q. Yan, S. Ding and L. Zhang, 2009. Leaf anatomical structure and photosynthetic physiological characteristics of C4 desert species *Salsola collina* and *S. arbuscula*. *Chin. J. Plant Ecol.*, 33: 347–354
- Gao, X.J., Z.C. Zhao and Y.H. Ding, 2001. Climate change due to greenhouse effects in China as simulated by a regional climate model. *Adv. Atmos. Sci.*, 18: 1224–1230
- Golluscio, R.A., O.E. Sala and W.K. Lauenroth, 1998. Differential use of large summer rainfall events by shrubs and grasses: A manipulative experiment in the Patagonian steppe. *Oecologia*, 115: 17–25
- He, J., B. Wu, Y.L. Cao and B. Yao, 2013. Light responses of *Nitraria tangutorum* to rain addition treatments. *For. Res.*, 26: 58–64
- Hiroiyuki, M., N. Hibiki, U. Masaki, T. Ohtsuka, H. Koizumi and T. Nakatsubo, 2008. Photosynthetic characteristics and biomass distribution of the dominant vascular plant species in a high Arctic tundra ecosystem, Ny-Alesund, Svalbard: implications for their role in ecosystem carbon gain. *J. Plant Res.*, 121: 137–145
- Huxman, T.E., M.C. Jessica, D.I. Danielle, J.A. Eilts, N.B. English and W.D.G. Williams, 2004a. Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: the role of native versus non-native grasses and soil texture. *Oecologia*, 141: 295–305
- Huxman, T.E., K.A. Snyder, D. Tissue, A.J. Leffler, K. Ogle and W.T. Pockman, 2004b. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, 141: 254–268
- Knapp, A.K., 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science*, 298: 2202–2205
- Li, Y.H., Q. Lu, B. Wu, Y.J. Zhu, D.J. Liu and J.X. Zhang, 2012. A review of leaf morphology plasticity linked to plant response and adaptation characteristics in arid ecosystems. *Chin. J. Plant Ecol.*, 36: 88–98
- Liu, B., W.Z. Zhao and Z.J. Wen, 2012. Photosynthetic response of two shrubs to rainfall pulses in desert regions of northwestern China. *Photosynthetica*, 50: 109–119
- Loik, M.E., 2007. Sensitivity of water relations and photosynthesis to summer precipitation pulses for *Artemisia tridentata* and *Purshia tridentata*. *Plant Ecol.*, 191: 95–108



- Loik, M.E., D.D. Breshears, W.K. Lauenroth and J. Belnap, 2004. A multi-scale perspective of water pulses in dry-land ecosystems: climatology and eco-hydrology of the western USA. *Oecologia*, 141: 269–281
- Mabapa, P.M., K.K. Ayisi and I.K. Mariga, 2018. Comparison of gas exchange in *Moringa oleifera* and other drought tolerant tree species for climate change mitigation under semi-arid condition of Northern South Africa. *Intl. J. Agric. Biol.*, 20: 2669–2676
- Patrick, L., J. Cable, D. Potts and D.I. Danielle, 2007. Effects of an increase in summer precipitation on leaf, soil, and ecosystem fluxes of CO<sub>2</sub> and H<sub>2</sub>O in a sotol grassland in Big Bend National Park, Texas. *Oecologia*, 151: 704–718
- Potts, D.L., T.E. Huxman, R.L. Scott, D.G. Williams and D.C. Goodric, 2006. The sensitivity of ecosystem carbon exchange to seasonal precipitation and woody plant encroachment. *Oecologia*, 150: 453–463
- QiuHong, F., C. Mauro, C. Ruimei, L. Shirong and S. Zuomin, 2013. Leaf functional trait responses of *Quercus aquifolioides* to high elevations. *Intl. J. Agric. Biol.*, 15: 69–75
- Reynolds, J.F., R.K. Paul, K. Ogle and R.J. Fernández, 2004. Modifying the ‘pulse-reserve’ paradigm for deserts of North America: Precipitation pulses, soil water, and plant responses. *Oecologia*, 141: 194–210
- Reynolds, J.F., R.A. Virginia, P.R. Kemp and S.D.C. Tremmel, 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecol. Monogr.*, 69: 69–106
- Richardson, A.D. and G.P. Berlyn, 2002. Spectral reflectance and photosynthetic properties of *Betula papyrifera* (Betulaceae) leaves along an elevational gradient on Mt. Mansfield, Vermont, U.S.A. *Amer. J. Bot.*, 89: 88–94
- Sarah, B., L.H. Jana, P. Elise, D.G. Williams and J. Newcomb, 2009. Elevated carbon dioxide alters impacts of precipitation pulses on ecosystem photosynthesis and respiration in a semi-arid grassland. *Oecologia*, 162: 791–802
- Schwinning, S. and S.J.R. Ehleringer, 2003. Dominant cold desert plants do not partition warm season precipitation by event size. *Oecologia*, 136: 252–260
- Schwinning, S., O.E. Sala, M.E. Loik and J.R. Ehleringer, 2004. Thresholds, memory, and seasonality: Understanding pulse dynamics in arid/semiarid ecosystems. *Oecologia*, 141: 191–193
- Schwinning, S., K. Davis and R.J.R. Ehleringer, 2002. Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. *Oecologia*, 130: 345–355
- Song, W.M., S.P. Chen, B. Wu, Y. Zhu, Y. Zhou and Y. Li, 2012. Vegetation cover and rain timing co-regulate the responses of soil CO<sub>2</sub> efflux to rain increase in an arid desert ecosystem. *Soil Biol. Biochem.*, 49: 114–123
- Snyder, K.A., L.A. Donovan, J.J. James and R.L.T.H. Richards, 2004. Extensive summer water pulses do not necessarily lead to canopy growth of Great Basin and northern Mojave Desert shrubs. *Oecologia*, 141: 325–334
- Walting, J.R., M.C. Press and W.P. Quick, 2000. Elevated CO<sub>2</sub> induces biochemical and ultrastructural changes in leaves of the C<sub>4</sub> cereal sorghum. *Plant Physiol.*, 123: 1143–1152
- Wang, H., F. Wang, G. Wang and K. Majourhat, 2007. The responses of photosynthetic capacity, chlorophyll fluorescence and chlorophyll content of nectarine (*Prunus persica* var. *Nectarina* Maxim) to greenhouse and field grown conditions. *Sci. Hort.*, 112: 66–72
- Weltzin, J.F. and G.R. McPherson, 2000. Implications of precipitation redistribution for shifts in temperature savanna ecotones. *Ecology*, 81: 1902–1913
- Weltzin, J.F., M.E. Loik, S. Schwinning, D.G. Williams, P.A. Fay, B.M. Haddad, J. Harte, T.E. Huxman, A.K. Knapp, G. Lin and W.T. Pockman, 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience*, 53: 941–952
- Weng, J.H. and M.F. Lai, 2005. Estimating heat tolerance among plant species by two chlorophyll fluorescence parameters. *Photosynthetica*, 43: 439–444
- Xu, H. and Y. Li, 2006. Water-use strategy of three central Asian desert shrubs and their responses to rain pulse events. *Plant Soil*, 285: 5–17
- Xu, H., Y. Li, G.Q. Xu and T. Zou, 2007. Ecophysiological response and morphological adjustment of two Central Asian desert shrubs towards variation in summer precipitation. *Plant Cell Environ.*, 30: 399–409
- Ye, Z.P. and Q. Yu, 2008. Comparison of new and several classical models of photosynthesis in response to irradiance. *Chin. J. Plant Ecol.*, 32: 1356–1361
- Zhang, J.X., B. Wu, Y.J. Zhu, Y. Li, Q. Lu and B. Yao, 2013. Responses of *Nitraria tangutorum* to water and photosynthetic physiology in rain enrichment scenario. *Acta Ecol. Sin.*, 33: 172–177
- Zhang, S.B., Z.K. Zhou and H. Hu, 2007. Gas exchange and resource utilization in two alpine oaks at different altitudes in Hengduan Mountains. *Can. J. For. Res.*, 37: 1184–1193
- Zhao, Z.G., G.Z. Du, X.H. Zhou and M.T. Wand, 2006. Variations with altitude in reproductive traits and resource allocation of three Tibetan species of Ranunculaceae. *Aust. J. Bot.*, 54: 691–700
- Zou, T., Y. Li, H. Xu and G.Q. Xu, 2010. Responses to precipitation treatment for *Haloxylon ammodendron* growing on contrasting textured soils. *Ecol. Res.*, 25: 185–194

[Received 21 Dec 2018; Accepted 18 Jun 2019; Published (online); 10 Nov 2019]