



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* to rain addition, gas exchange parameters and photosynthetic physiology characteristics of *Nitraria 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 *Nitraria tangutorum* to adapt to the increased precipitation. The apparent quantum efficiency (AQY), light saturation point (LSP), initial carboxylation efficiency (CE) and CO₂ saturation point (CSP) increased, indicating an enhanced activity of carboxyl enzyme and increased the capacity of *Nitraria tangutorum* to use light and carbon dioxide. Therefore, under global change scenario, *Nitraria tangutorum* would improve the photosynthetic capacity and mediate the function of photosynthetic organization to adapt to new water conditions in the future.

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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-pretrophyte 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). 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 *Nitraria tangutorum* in arid regions in the Northwest of China. *Nitraria 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 *Nitraria tangutorum* to rain addition from the perspective of photosynthetic physiology. The following questions should be resolved: (1) how photosynthesis and transpiration of *Nitraria 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, *Nitraria tangutorum*, occasionally associated with a few plants of *Artemisia desterorum* or *Psammochoa villosa*. The experiment was carried out in a patchy landscape with *Nitraria tangutorum* interspersed with sand dunes. The mean height and size of the dune was 1.24 ± 0.14 m and 29.9 ± 0.39 m², 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 m² 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⁻¹ which could be achieved easily in most cases in arid regions (unpublished). The specific dates of simulated rain addition were 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 Inc., Lincoln, N.E., U.S.A.) at 1 d before, and 1, 3, 5, 7, 9 and 11 d after rainfall between 8:00 and 10:00.

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

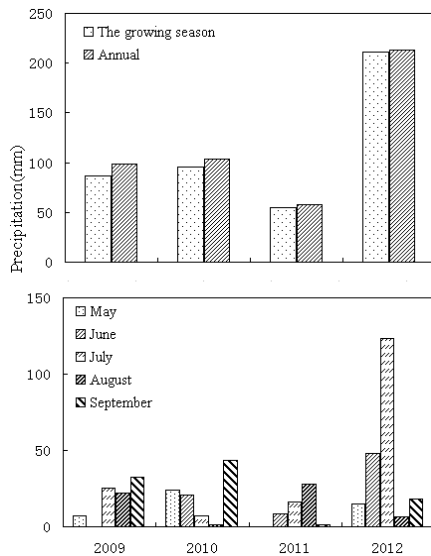


Fig. 1: Precipitation distribution at the study site classified by year and month

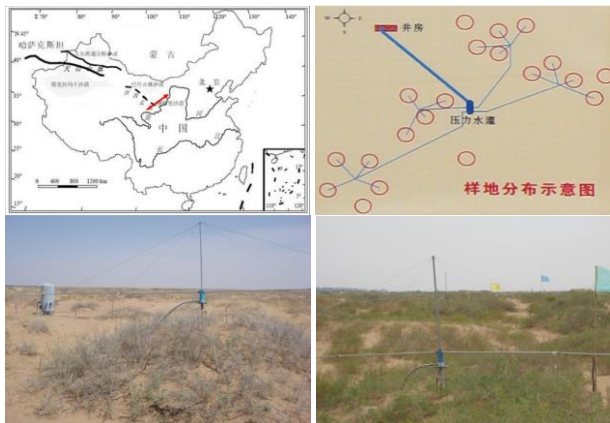


Fig. 2: Distribution of *Nitraria tangutorum* island in experimental plots

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 CO₂-response curves in *Nitraria 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 μmol·m⁻²·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 μmol·m⁻²·s⁻¹. The gas flow rate was set at 500 μmol·s⁻¹. Chamber temperature was controlled at 26° C. A CO₂-injecting device was attached to the system to control reference CO₂ concentration at 380 μmol·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: $P_n = \frac{PAR * AQY + P_{nmax} - \sqrt{(PAR * AQY + P_{nmax}) * (PAR * AQY + P_{nmax}) - 4 * K * AQY * PAR * P_{nmax}}}{2 * K - Rd}$, 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 respiratory 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 (PAR<200 μmol·m⁻²·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 = Pnmax 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 CO₂ concentration (Ci): The photosynthetic intercellular CO₂-response curves of the species were measured by a Li-6400 portable photosynthesis system. A CO₂-injecting device was attached to the system to control reference CO₂ concentrations at 400、300、200、150、120、100、80、50、400、600、800、1000、1200 and 1500 μmol·mol⁻¹. The gas flow rate was set at 500 μmol·s⁻¹. Chamber temperature was controlled at 1600 μmol·m⁻²·s⁻¹. The CO₂ response curves of net photosynthetic rate were measured. Advanced regression analysis of the non-linear curve showed that the relationship

between Pn and intercellular CO₂ concentration (C_i) was best fitted by exponential function: $Pn = A_{max} (1 - e^{-CE \cdot C_i}) + R_p$, in which C_i is intercellular CO₂ concentration, Pn is net photosynthetic rate, A_{max} is assimilation rate at saturating CO₂, CE is the carboxylation efficiency, R_p is leaf light respiration rate (Walting *et al.*, 2000). The linear regression analysis was used to fit the initial portion of the A-C_i curve (C_i < 200 μmol·mol⁻¹). The intersection of the regression line and the X-axis was the CO₂ compensation points (CCP), which was the CO₂ concentration where net photosynthetic rate was equal to zero (Ye and Yu, 2008). Using the exponential function CO₂ saturation points (CSP) was estimated when net photosynthetic rate reached to 0.9 * A_{max}. Ultimately, the parameters of maximum assimilation rate (A_{max}), carboxylation efficiency (CE), light respiratory rates (R_p), CO₂ compensation points (CCP) and CO₂ 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. 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 fifth day, 75% treatment on day 1/5/9, 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 2: Differences in average annual Pn ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) among different rain addition treatments of *Nitraria 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 *Nitraria 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

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 significantly 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%, 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

Physiological Responses and Adaptation of *Nitraria tangutorum* to Precipitation

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). 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 affect the physiological activities of *Nitraria tangutorum*. In addition, the higher transpiration rate of *Nitraria 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 significant 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 hypothesis. Therefore, linear-regression analysis was used to evaluate the relationships between net photosynthetic rate,

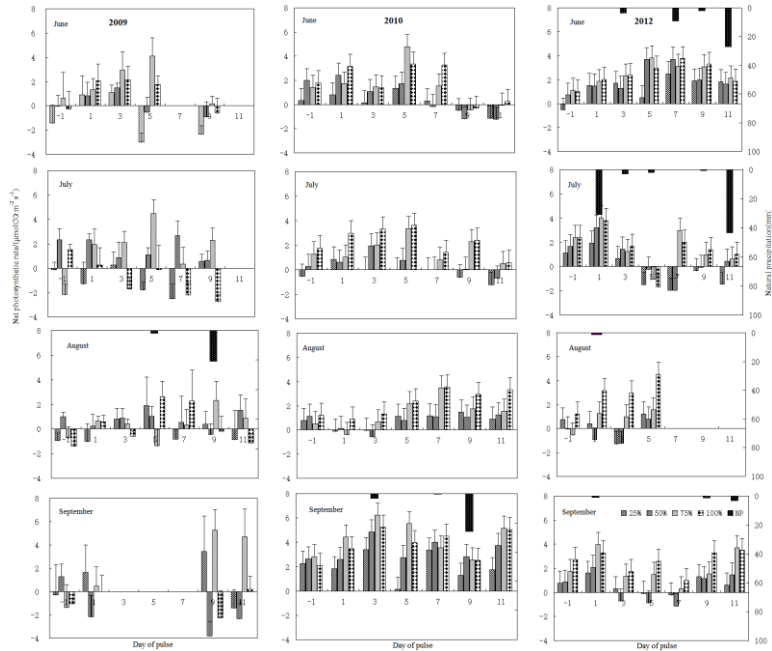


Fig. 3: Responses of net photosynthetic rate to rain addition treatments (mean ± SE)
 Note: Values are expressed as a difference of supplemental summer watered to control plots. Differences are presented for 1 day prior and up to 11 days after supplemental watering. Filled black rectangle represented natural precipitation

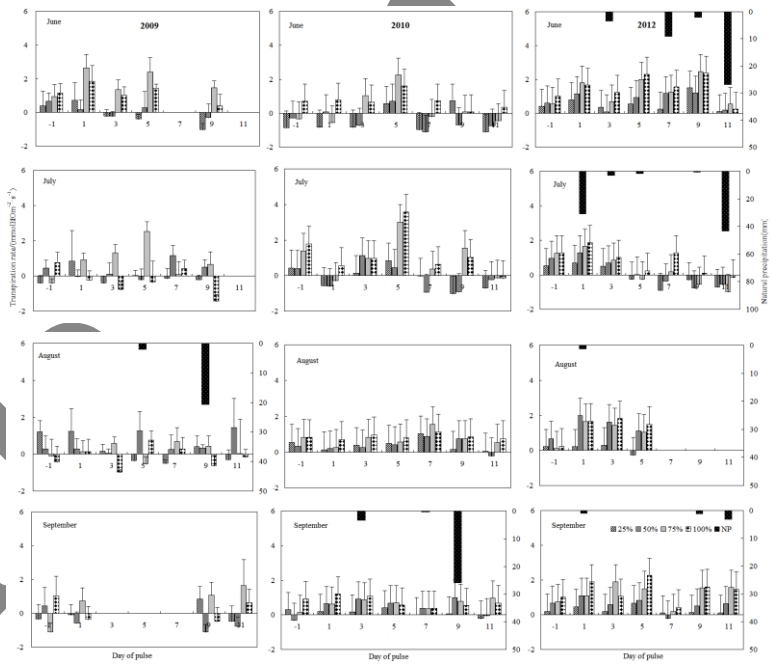


Fig. 4: Responses of transpiration rate to rain addition treatments of *Nitraria tangutorum*
 Note: Values are expressed as a difference of supplemental summer watered to control plots. Differences are presented for 1 day prior and up to 11 days after supplemental watering. Filled black rectangle represented natural precipitation

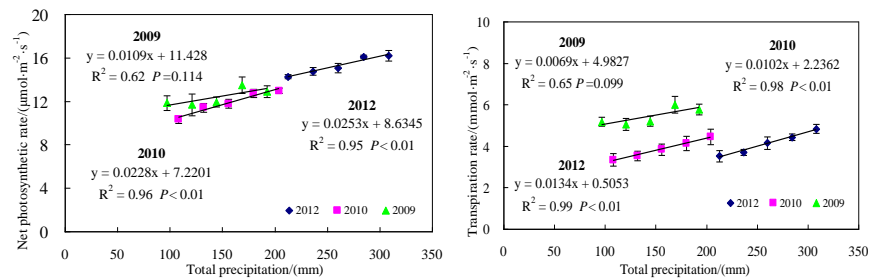
transpiration rate and total precipitation (natural and simulated precipitation) in 2009, 2010 and 2012, respectively. Results showed that there were good linear relationships between them (Fig. 5). The relationships in 2009 were not

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

Table 4: Effects of rain addition on Pn-PAR and A-Ci curve characteristic parameters of *Nitraria 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/ $\text{mol}\cdot\text{mol}^{-1}$	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/ $\text{mol}\cdot\text{mol}^{-1}$	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 *Nitraria tangutorum* and total annual precipitation (TAP) in 2009 (filled triangles), 2010 (filled squares) and 2012 (filled diamonds)

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 *Nitraria 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 *Nitraria tangutorum* have adapted to new water conditions gradually (Xu *et al.*, 2007).

Underlying Physiological Adaptations Mechanisms to Precipitation

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). An positive response of carbon assimilation rate of *Nitraria 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 *Nitraria 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 *Nitraria tangutorum* increased 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 CO₂ during the day, and the abilities of physiological metabolism for *Nitraria 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 *Nitraria tangutorum* improve its photosynthetic capacity to adapt new water conditions by mediating its carboxylase activity and photosynthetic organization functions. The increased capability of photosynthesis 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 respond to precipitation through increasing leaf-level CO₂ exchange rate or expanding leaf areas, or both (Huxman et al., 2004a). Data showed that sufficient rain addition improved the photosynthesis production capacity of *Nitraria 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 *Nitraria tangutorum*. Not less than 75% (110 mm) rain addition play a significantly accelerated effects on photosynthesis and transpiration. There was a process for *Nitraria tangutorum* to adapt to the increased precipitation. Rainfall affected physiological characteristics significantly on leaf scale of *Nitraria 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.

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