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Photosynthetic response of two shrubs to rainfall pulses in desert regions of northwestern China

B. LIU*,+, W.Z. ZHAO*, and Z.J. WEN**

*Linze Inland River Basin Research Station, Key Laboratory of Inland River Ecohydrology, Cold and Arid Regions, Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China**
*School of Mathematics and Statistics, Lanzhou University, Lanzhou 730000, China***

Abstract

Pulses of rainfall are particularly pivotal in controlling plant physiological processes in ecosystems controlled by limited water, and the response of desert plants to rainfall is a key to understanding the responses of desert ecosystems to global climatic change. We used a portable photosynthesis system to measure the responses of the diurnal course of photosynthesis, light-response curves, and CO_2-response curves of two desert shrubs (*Nitraria sphaerocarpa* Maxim. and *Calligonum mongolicum* Turcz) to a rainfall pulse in a desert–oasis ecotone in northwestern China. The photosynthetic parameters, light- and CO_2-response curves differed significantly before and after the rainfall pulse. Their maximum net photosynthetic rate (P_N) values were 23.27 and 32.92 $\mu mol(CO_2)\ m^{-2}\ s^{-1}$ for *N. sphaerocarpa* and *C. mongolicum*, respectively, with corresponding maximum stomatal conductance (g_s) values of 0.47 and 0.39 $mol(H_2O)\ m^{-2}\ s^{-1}$. The P_N of *N. sphaerocarpa* after the rainfall was 1.65 to 1.75 times the value before rainfall, whereas those of *C. mongolicum* increased to approximately 2 times the prerainfall value, demonstrating the importance of the desert plants response by improving their assimilation rate to precipitation patterns under a future climate.

Additional key words: *Calligonum mongolicum*; *Nitraria sphaerocarpa*; photosynthetic parameters; rainfall pulse; response curves.

Introduction

In desert regions, rainfall events can be characterized as "pulses" that result from the infrequent, discrete, and largely unpredictable precipitation events (*e.g.*, Schwinning and Sala 2004). Pulses of rainfall are particularly pivotal in controlling plant physiological processes in ecosystems controlled by limited water (Ivans *et al.* 2006), and have been suggested to be an important driver of the arid ecosystem's vegetation structure and function (Noy-Meir 1973, Ehleringer *et al.* 1999). The infrequent, high-magnitude pulses are biologically relevant because they can trigger a cascade of ecosystem responses that affect plant nutrient-, water-, and carbon cycling (Schwinning and Sala 2004), and the impacts of these pulses depend on the number, timing, and intensity of storms (Schwinning and Sala 2004). Therefore, it is critical to evaluate the physiological responses of desert plant to rainfall pulses. Nevertheless, it is difficult to predict specific plant responses to rainfall pulses because of the strong effects of and interactions between rainfall, antecedent soil moisture, and the responses of different plant functional types, all of which vary among species, deserts, and seasons (Reynolds *et al.* 2004).

However, water availability is directly linked to rainfall, and rainfall patterns and soil water availability in desert ecosystems affect plant recruitment, photosynthesis and growth, competition, nutrient dynamics, and net ecosystem productivity (Stephenson 1990, Reynolds *et al.* 1999). Plants in ecosystems controlled by limited

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+Corresponding author; tel.: +86 931 4967139, e-mail: liubing@lzb.ac.cn

Abbreviations: A_{max} – assimilation at saturating CO_2; CCP – CO_2 compensation point; CE – carboxylation efficiency; C_i – intercellular CO_2 concentration; C_s – cell CO_2 concentration; CSP – CO_2 saturation point; CUE – CO_2-use efficiency; E – transpiration rate; g_s – stomatal conductance; LCP – light compensation point; LUE – light-use efficiency; LSP – light saturation point; PAR – photosynthetically active radiation; P_N – net photosynthetic rate; P_{Nmax} – light-saturated maximum assimilation; QE – quantum efficiency; R_{day} – photorespiration; R_{esp} – leaf respiration; RH – relative humidity; Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase; SMS – soil moisture storage; VPD – vapour pressure deficit; WUE – water-use efficiency; T – air temperature.

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water tend to adapt to drought by means of various physiological adjustments, such as changes in leaf water status (Arndt *et al.* 2000, Marron *et al*. 2002, Franks 2004) and in stomatal and nonstomatal limitation of photosynthesis (Cornic 2000, Flexas *et al*. 2004). Climate change will significantly affect desert plants since it will affect the rainfall quantity and frequency, which are major drivers of biological processes in arid ecosystems (Noy-Meir 1973). Desert ecosystems are predicted to exhibit some of the strongest responses to global climate change (Smith *et al.* 2000, Xu *et al*. 2007). Although changes in precipitation patterns under future climates will likely affect plant establishment, growth, and reproduction (Smith and Nowak 1990, Jackson *et al.* 2001), not all species will respond equally to changes in soil water content.

Photosynthesis responds to the initial stage of a rainfall pulse. The biochemical photosynthetic model of Farquhar *et al*. (1980) accounted well for responses to temperature stress, but did not account for the effect of changes in soil water on photosynthetic parameters (Harley and Baldocchi 1995). For this reason, subsequent researchers performed a series of observations on the response of photosynthesis to rainfall pulses and the resulting changes in soil moisture. For instance, Xu and Li (2006) and Xu *et al*. (2007) studied the water-use strategies of three central Asian desert shrubs and their responses to rain pulses. Ignace *et al*. (2007) found that the photosynthetic rate and stomatal conductance of *Heteropogon contortus* and *Eragrostis lehmanniana* bunchgrasses in the Sonoran Desert did not always increase after rainfall pulses, and found that the magnitude of the response was significantly correlated with the antecedent soil moisture and with the plant functional type. However, they did not study the relationship between photosynthetic response and soil moisture. Loik (2007) found that two widespread Great Basin Desert shrub species responded to a range of summer rainfall pulse magnitudes within about 2 days, and that stomatal conductance increased by about 0.3 mol m^{-2} s^{-1}; *Artemisia tridentata* generally responded more strongly than the co-dominant shrub species *Purshia tridentata*. Li *et al*. (2007) found that net photosynthetic rate, stomatal conductance, and transpiration rate of *Ulmus pumila* seedlings increased significantly in response to simulated precipitation increases from 0 to 20 mm in the Hunshandak Sandland of China, whereas net photosynthetic rate changed only slightly when precipitation exceeded 20 mm, indicating that precipitation greater than 20 mm had no significant effects on photosynthesis. When soil water content reached 10%, photosynthesis decreased as a result of stomatal limitations, but when soil water content exceeded 15%, these limitations largely disappeared, indicating that these elm seedlings might be able to tolerate moderate drought.

Although scientists have discussed the effects of drought on photosynthetic parameters in plants and the responses of photosynthesis to rainfall pulses, little work has been done on the responses of photosynthetic parameters to the surplus soil moisture that exists for a short time after a rainfall. Precipitation has clear regional patterns (Noy-Meir 1973, Schwinning and Sala 2004, Schwinning *et al*. 2004), and the photosynthetic responses of desert plants appear to vary widely both among and within species in different regions. For this reason, it is important to study the photosynthetic responses of desert plants to soil moisture, and particularly the response mechanisms, in order to understand the effects of soil moisture variations on photosynthetic parameters. Shrubs are the dominant plant species in many desert regions (Schwinning and Ehleringer 2001), and *N. sphaerocarpa* and *C. mongolicum* are typical dominant shrubs in the desert regions of China's Heihe River Basin. Under future climates, changes in the timing and magnitude of summer rainfall pulses will determine the extent to which these two species undergo changes in water status and photosynthetic carbon uptake, with implications for their fitness. To better understand these implications, we measured the changes in photosynthetic parameters and of light- and CO_2-response curves in these desert shrubs to reveal the response mechanisms of photosynthesis to rainfall pulses and changes in soil moisture.

Materials and methods

Study area: Our experiment was conducted in a desert–oasis ecotone in the middle of China's Heihe River Basin, between 39°22'N and 39°23'N and between 100°07' E and 100°08'E. The environment is dominated by a continental arid temperate climate at an elevation of approximately 1,350 m a.s.l., with a dry, hot summer and a cold winter. The annual rainfall averages 116.8 mm, of which 65% falls between July and September, with low rainfall intensity, and only 3% falls during the winter (December, January, and February). The annual temperature averages 7.6°C, and ranges between –27.3°C in January and 39.1°C in July. The growing season is from May to October, and the frost-free period is about 165 days. The wind direction is mainly from the northwest, and the wind speed averages 3.2 m s^{-1}, with frequent gales (wind speed $\geq$ 21 m s^{-1}). The groundwater table generally ranges from 2 to 5 m in depth. The typical zonal soil is characterized as a desert soil, with a coarse texture (grains between 0.05 and 0.25 mm in diameter account for 80 to 90% of the total). The plant cover is low, ranging from 5 to 7%. The organic matter content ranges from 0.12 to 0.83%, and the soluble salt content is less than 0.1% of the total ionic content (Zhao and Liu 2010). The vegetation found on fixed and semifixed dunes is composed mostly of desert shrubs, dominated by *Haloxylon ammodendron*, *C. mongolicum*, *Tamarix* *ramosissima*, and *N. sphaerocarpa*, with an average height of 3 m. Of these species, *N. sphaerocarpa* and *C. mongolicum* account for approximately 75% of the total number of shrubs in the study area. The interdune lowlands are dominated by annual herbaceous species such as *Bassia dasyphylla*, *Halogeton arachnoideus*, *Suaeda glauca*, and *Agriophyllum squarrosum*, which have shallower roots than the trees.

Photosynthetic measurements: The experiments were carried out during the summer growing season. We chose the samples of *N. sphaerocarpa* and *C. mongolicum* that ranged between 2.2 and 2.5 m in height, with canopies that were largely intact and free of obvious signs of damage. In the sample plot (100 m × 100 m), we selected the youngest mature and healthy assimilative organs of each shrub species, and measured the diurnal course of photosynthesis using a portable photosynthesis system (*LI-6400, Li-COR Inc*., Lincoln, NE, USA) at 1 d before a 21.6-mm rainfall pulse and 1, 3, 5, 7, and 15 d after the rainfall. Each set of diurnal measurements was carried out at 1-hour intervals from 07:00 to 19:00 h, with measurements of ten shrubs per species. We measured the following photosynthetic parameters: net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), the intercellular CO_2 concentration (C_i), and photosynthetically active radiation (PAR). Simultaneously, we calculated the light-use efficiency (LUE) = P_N/PAR, physiological water-use efficiency (WUE) = P_N/E, and CO_2-use efficiency (CUE) = P_N/C_i. In addition, we calculated the light- and CO_2-response curves from 10:00 to 16:00 h 1 d before the rainfall, 3 and 7 d after the rainfall, using light intensities and CO_2 concentrations of 0, 50 , 100, 200, 300, 600, 1,000; 1,500; and 2,000 µmol m^{-2} s^{-1} (light) and µmol(CO_2) mol^{-1}(CO_2). Simultaneously, we measured meteorological data using a automatic weather station (*Onset Computer Corporation*, Pocasset, MA, USA) (Fig. 1).

Meteorological measurements: Meteorological data were measured at the study site using an *HG1000* automatic weather station (*Onset Computer Corporation*, Pocasset, MA, USA). Rainfall was measured with a tipping-bucket rain gauge (model *TE525*, metric; *Texas Electronics*, Dallas, TX, USA). Volumetric soil moisture was measured using the *EnviroSMART*™ Soil Water Content Profile Probes (*Campbell Scientific Inc*., Logan, UT, USA) from the weather station installed at eight depths below the soil surface (10, 20, 30, 40, 50, 60, 80, and 100 cm). Soil water content was calculated as the mean value of these readings for the top 100 cm of the soil. The meteorological data were measured at a frequency of 10 Hz and recorded every 5 min using a *CR1000* datalogger (*Campbell Scientific Inc*., Logan, UT, USA), then stored as the 30-min mean data, whereas rainfall data were stored as the 10-min mean data. Soil water content was measured every 2 d by means of oven-drying to validate the soil moisture data provided by the automatic weather station during the study period.

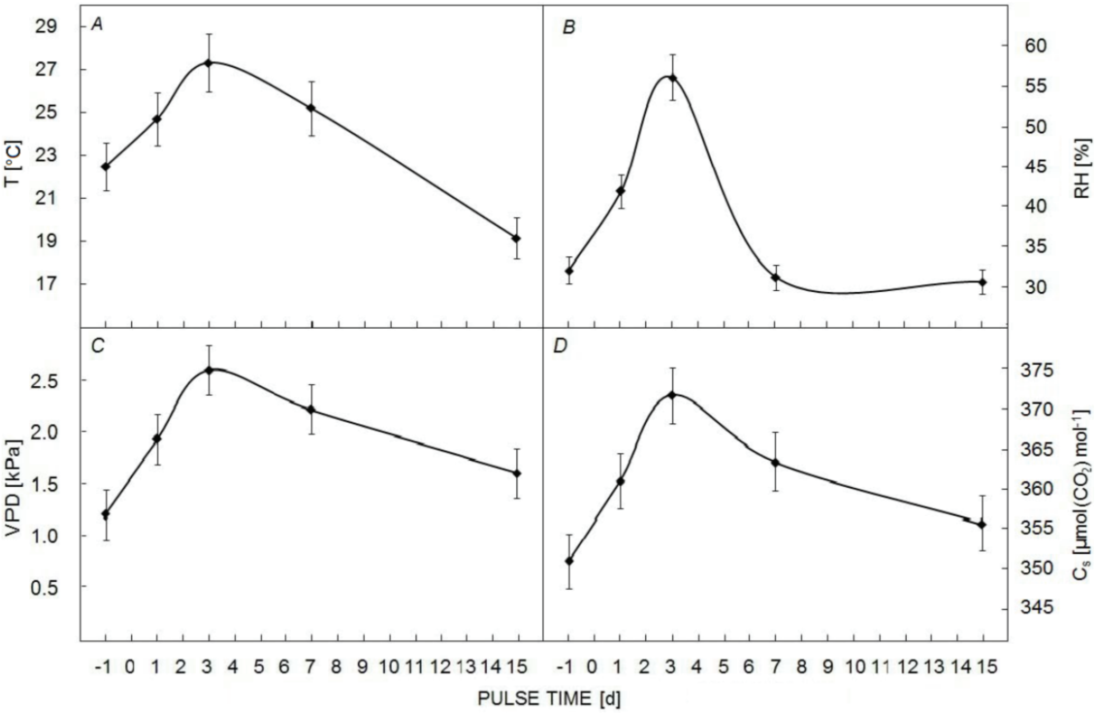

Fig. 1. The changes of (*A*) air temperature (T), (*B*) relative humidity (RH), (*C*) vapour pressure deficit (VPD), and (*D*) cell CO_2 concentration (C_s) during the rainfall pulse.

Data analysis: We analyzed the light- and CO_2-response curves using the Photosyn Assistant 1.1 software (http://www.scientific.force9.co.uk/photosyn.htm). The response of net photosynthetic rate (P_N) to light level (Q) can be modeled using a non-rectangular hyperbola in the Farquhar model (Prioul and Chartier 1977). We also calculated the following parameters from these curves: apparent quantum efficiency (QE), the light compensation point (LCP), the light saturation point (LSP), the light-saturated maximum assimilation (P_{Nmax}), and the photorespiration (day respiration) rate (R_{day}).

All of these parameters can be determined by fitting data to the model, which is expressed as the following equation (Prioul and Chartier 1977):

$$P_N = \frac{\mathrm{QE\,Q} + P_{Nmax} - \sqrt{(\mathrm{QE\,Q} + P_{Nmax})^2 - 4\,\mathrm{QE\,Q}\;K\;P_{Nmax}}}{2K} \tag{1}$$

where K is the progressive rate of curvature between the linear gradient and the maximum value (0,1).

The response of assimilation is modeled as a function of leaf C_i. This fits a model curve described by a rectangular hyperbola (Olsson and Leverenz 1994):

$$P_N = (\mathrm{CE} \times C_i \times A_{max})/(\mathrm{CE} \times C_i + A_{max}) - R_{esp} \tag{2}$$

where CE is the carboxylation efficiency, A_{max} is assimilation at saturating CO_2 and is respiratory processes (dark and light), and R_{esp} is leaf respiration.

We tested for significant changes in the photosynthetic parameters in response to the rainfall pulse period by means of repeated-measures *ANOVA* using version *13.0* of the *SPSS* software (*SPSS Inc*., Chicago, IL, USA). Where we found significant differences, we used the least-significant-difference (LSD) test to compare specific pairs of values.

Results

Response of photosynthetic parameters to rainfall pulse: The photosynthetic parameters of *N. sphaerocarpa* and *C. mongolicum* responded significantly to the rainfall pulse ($P<0.001$; Table 1), but the two species did not differ significantly, indicating that the response resulted from the rainfall pulse rather than differences between the species. The maximum value of most photosynthetic parameters appeared on the seventh day after rainfall, except for PAR and *E*. P_N and g_s of *N. sphaerocarpa* decreased immediately after the rainfall and then recovered, and the response resembled an S-curve, whereas P_N and g_s of *C. mongolicum* increased immediately after the rainfall and then followed a bimodal curve (Fig. 2*A,B*). Their maximum P_N values were 23.27 and 32.92 μmol(CO_2) m^{-2} s^{-1} for *N. sphaerocarpa* and *C. mongolicum*, respectively, with corresponding maximum g_s values of 0.47 and 0.39 mol(H_2O) m^{-2} s^{-1}. The response curve for *E* of *N. sphaerocarpa* also resembled

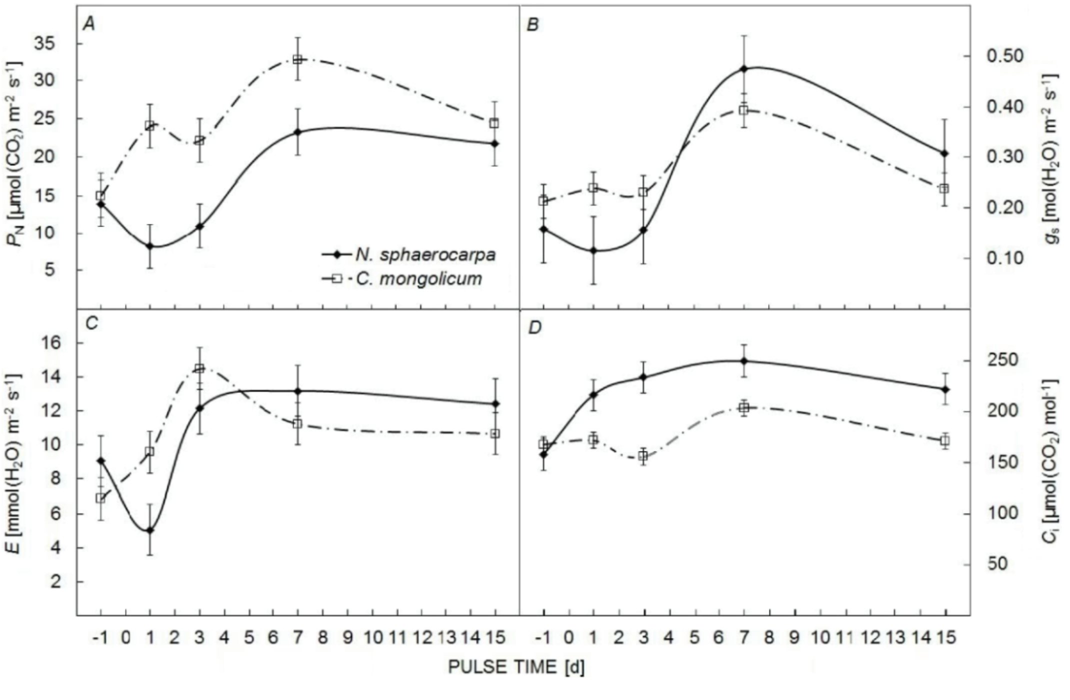

Fig. 2. The responses of (*A*) net photosynthetic rate (P_N), (*B*) stomatal conductance (g_s), (*C*) transpiration rate (*E*), and (*D*) intercellular CO_2 concentration (C_i) were simultaneously measured when we measured the photosynthetic parameter using a portable photosynthesis system.

Table 1. *ANOVA* results (*F* values) for the response of the photosynthetic parameters to the rainfall pulse. Significance levels: *** – P<0.001; ** – P<0.01; * – P<0.05. C_i – intercellular CO_2 concentration; CUE – CO_2-use efficiency; df – degrees of freedom; E – transpiration rate; g_s – stomatal conductance; LUE – light-use efficiency; PAR – photosynthetically active radiation; P_N – net photosynthetic rate; SMS – soil moisture storage; WUE – water-use efficiency.

Factor	df	SMS [mm]	P_N [μmol(CO_2) m^{-2} s^{-1}]	g_s [mol(H_2O) m^{-2} s^{-1}]	E [mmol(H_2O) m^{-2} s^{-1}]	C_i [μmol(CO_2) mol^{-1}]	PAR [μmol m^{-2} s^{-1}]	WUE [mmol mol^{-1}]	LUE	CUE [mol m^{-2} s^{-1}]
Time after pulse	1,2	29.48^{***}	22.48^{***}	11.25^{***}	6.06^{***}	6.95^{***}	5.39^{***}	5.43^{***}	5.93^{***}	15.56^{***}
Species	4,8	5.55	2.90	0.02	1.08	2.73	1.63	0.50	0.14	0.04
Time after pulse × Species	4,8	0.52	9.19^{***}	18.13^{***}	5.25^{***}	7.18^{***}	4.91^{***}	1.60	1.21	3.01*

Table 2. Differences in photosynthetic parameters of the light- and CO_2-response curves before and after the rainfall pulse. Values represent means (n = 10) ± SD; values in a column followed by *different letters* differ significantly (LSD, P<0.05). A_{max} – assimilation at saturating CO_2; CCP – CO_2 compensation point; CE – carboxylation efficiency; CSP – CO_2 saturation point; LCP – light compensation point; LSP – light saturation point; P_{Nmax} – light-saturated maximum assimilation; QE – quantum efficiency; R_{day} – photorespiration; R_{esp} – leaf respiration.

Parameters	Before rainfall *N. sphaerocarpa*	*C. mongolicum*	After rainfall *N. sphaerocarpa*	*C. mongolicum*	Response magnitude *N. sphaerocarpa*	*C. mongolicum*
LCP [μmol m^{-2} s^{-1}]	-30.90 ± 0.82^{d}	-1.52 ± 0.53^{ab}	-38.10 ± 1.0^{e}	-2.10 ± 0.20^{b}	-7.2 ± 0.43^{c}	-0.58 ± 0.23^{a}
LSP [μmol m^{-2} s^{-1}]	$1,018 \pm 8.40^{d}$	$1,069 \pm 10.66^{c}$	$1,117 \pm 6.45^{b}$	$1,368 \pm 12.36^{a}$	99 ± 6.45^{e}	299 ± 9.67^{f}
P_{Nmax} [μmol(CO_2) m^{-2} s^{-1}]	14.9 ± 0.90^{b}	13.7 ± 0.70^{b}	26.1 ± 1.00^{a}	27.4 ± 1.30^{a}	11.2 ± 1.23^{b}	13.7 ± 1.65^{c}
QE [mol mol^{-1}]	0.0128 ± 0.0023^{b}	0.0100 ± 0.0010^{b}	0.0226 ± 0.0018^{a}	0.0200 ± 0.0012^{a}	0.0098 ± 0.0018^{b}	0.0100 ± 0.0020^{b}
R_{day} [μmol m^{-2} s^{-1}]	0.500 ± 0.100^{b}	0.019 ± 0.002^{d}	0.860 ± 0.040^{a}	0.042 ± 0.005^{d}	0.360 ± 0.050^{c}	0.023 ± 0.004^{d}
CCP [μmol(CO_2) mol^{-1}]	0.732 ± 0.22^{a}	-30.4 ± 2.62^{c}	0.902 ± 0.23^{a}	-40.2 ± 3.92^{d}	0.17 ± 0.03^{a}	-9.8 ± 1.96^{b}
CSP [μmol(CO_2) mol^{-1}]	627 ± 20.07^{c}	921 ± 27.75^{b}	675 ± 34.23^{c}	$1,022 \pm 65.83^{a}$	48 ± 10.26^{d}	101 ± 17.08^{d}
CE [mol m^{-2} s^{-1}]	0.0361 ± 0.012^{bc}	0.0246 ± 0.005^{c}	0.0596 ± 0.006^{a}	0.0491 ± 0.007^{ab}	0.0235 ± 0.005^{c}	0.0245 ± 0.007^{c}
A_{max} [μmol m^{-2} s^{-1}]	20.74 ± 2.04^{c}	22.62 ± 3.60^{c}	34.22 ± 4.10^{b}	45.19 ± 5.20^{a}	13.48 ± 2.64^{d}	22.57 ± 2.50^{c}
R_{esp} [μmol m^{-2} s^{-1}]	0.0074 ± 0.041^{a}	-0.1589 ± 0.015^{b}	0.0119 ± 0.002^{a}	-0.3041 ± 0.076^{c}	0.0045 ± 0.001^{a}	-0.1452 ± 0.067^{b}

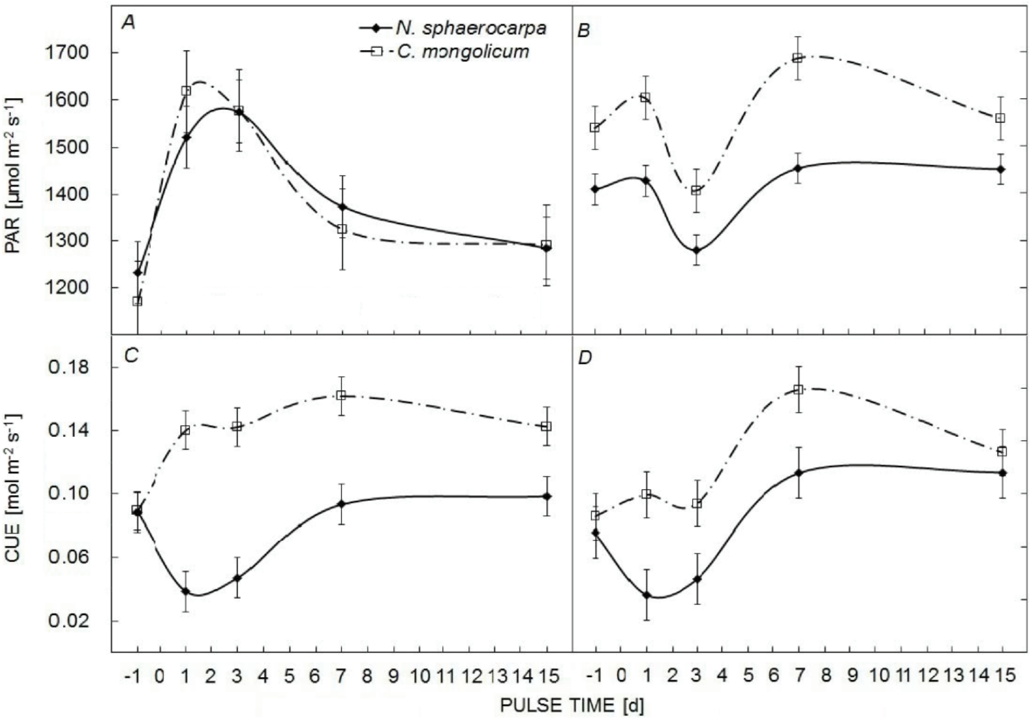

Fig. 3. The responses of (*A*) photosynthetically active radiation (PAR), (*B*) water-use efficiency (WUE), (*C*) CO_2-use efficiency (CUE), and (*D*) light-use efficiency (LUE) to the rainfall pulse.

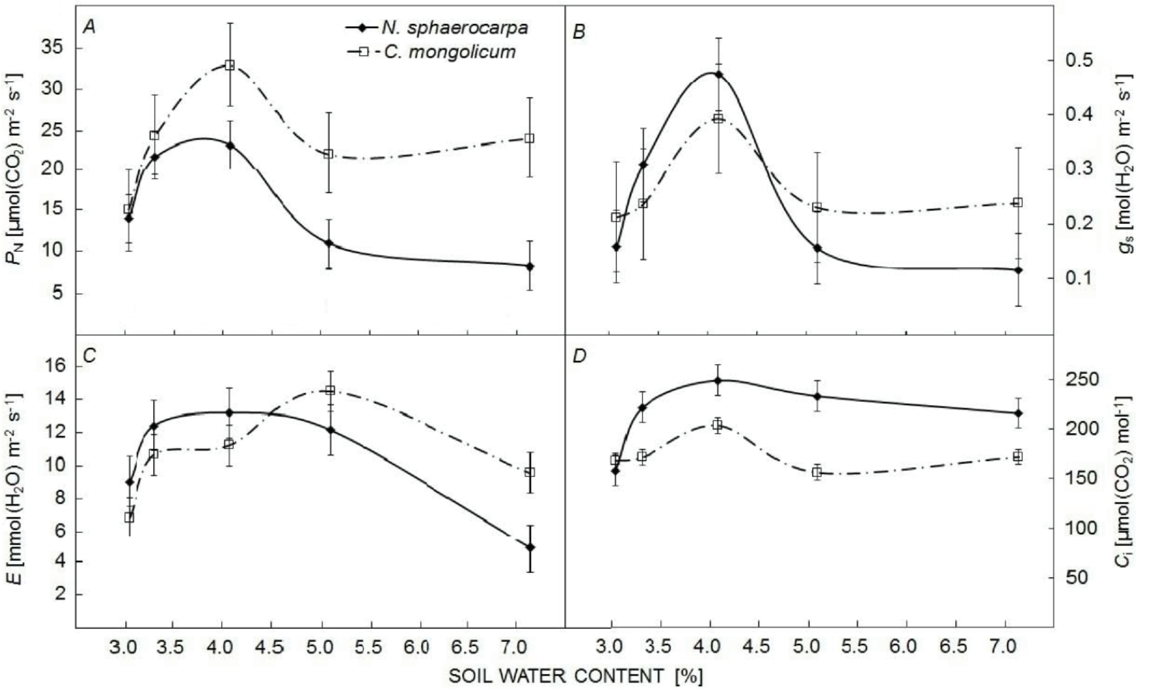

Fig. 4. The responses of (*A*) net photosynthetic rate (P_N), (*B*) stomatal conductance (g_s), (*C*) transpiration rate (*E*), and (*D*) intercellular CO_2 concentration (C_i) to the pulse of soil moisture.

an *S*-curve, with the maximum *E* [13.19 mmol(H_2O) m^{-2} s^{-1}] occurring on the seventh day after rainfall, whereas the curve for *C. mongolicum* more closely resembled a parabola, with the maximum [14.49 mmol(H_2O) m^{-2} s^{-1}] occurring on the third day after the rainfall (Fig. 2*C*). However, the changes in C_i for *N. sphaerocarpa* resembled a parabola, whereas those of *C. mongolicum* resembled the *S*-curve, and the two species did not differ significantly, with maximum values of 249.00 and 203.22 μmol(CO_2) mol^{-1}, respectively.

The response of LUE to the rainfall pulse was significant ($P<0.001$; Table 1), but did not differ significantly between the species, nor was there a significant interaction effect. PAR increased immediately after the rainfall, and the differences were significant ($P<0.001$; Table 1). The response curve for PAR resembled a parabola. The maximum PAR for *N. sphaerocarpa* appeared on the third day after the rainfall, but for *C. mongolicum*, it occurred on the first day, with values of 1,575.11 and 1,617.00 μmol m^{-2} s^{-1}, respectively (Fig. 3*A*). The WUE of both shrubs followed a bimodal curve (Fig. 3*B*), but CUE followed different patterns; for *N. sphaerocarpa*, it followed the *S*-curve whereas for *C. mongolicum*, it followed a bimodal curve, with maximum values of 0.16 and 0.025 mol m^{-2} s^{-1}, respectively (Fig. 3*C*). LUE followed a parabola for *N. sphaerocarpa* and the bimodal curve for *C. mongolicum*, with maximum values of 0.018 and 0.025, respectively (Fig. 3*D*).

Responses of photosynthetic parameters to soil moisture: The responses of the photosynthetic parameters to changes in soil moisture were significant for both species after the rainfall pulse ($P<0.001$; Table 1). The response curves as a function of soil moisture were generally parabolic (Fig. 4). The maximum of most photosynthetic parameters appeared when soil water content reached 4.08% after the rainfall (Fig. 4), except for *E* (Fig. 4*C*). The response of P_N to soil moisture was lower for *N. sphaerocarpa* than for *C. mongolicum*, with mean values of 15.64 and 23.70 μmol(CO_2) m^{-2} s^{-1}, respectively (Fig. 4*A*). The curves for g_s differed from those for P_N. The g_s values of *N. sphaerocarpa* were larger than those of *C. mongolicum* at soil water contents less than 4.5%, and *vice versa* at soil water contents greater than 4.5%. The average values were similar after the rainfall pulse, with values of 0.24 and 0.26 mol(H_2O) m^{-2} s^{-1}, respectively (Fig. 4*B*). The *E* value of *N. sphaerocarpa* reached its highest value at a soil water content of 4.08%, *vs.* 5.09% for *C. mongolicum* (Fig. 4*C*). However, the pattern of the C_i response to soil moisture did not differ significantly between the two species, although the response for *N. sphaerocarpa* was larger than that for *C. mongolicum* (Fig. 4*D*).

The relationship between PAR and soil moisture resembled a parabola, and PAR averaged 1,397.82 and 1,396.16 μmol m^{-2} s^{-1} for *C. mongolicum* and *N. sphaerocarpa*, respectively (Fig. 5*A*). The responses of WUE and CUE to soil moisture were stronger for *C. mongolicum* than for *N. sphaerocarpa* (Fig. 5*B,C*), and LUE of both species responded significantly but similarly to soil moisture (Fig. 5*D*).

Changes in the light- and CO_2-response curves in response to the rainfall pulse: The photosynthetic capacity of both shrubs was significantly affected by the rainfall pulse and the resulting changes in soil moisture ($P<0.001$; Table 2), and the light- and CO_2-response curves differed significantly before and after the rainfall.

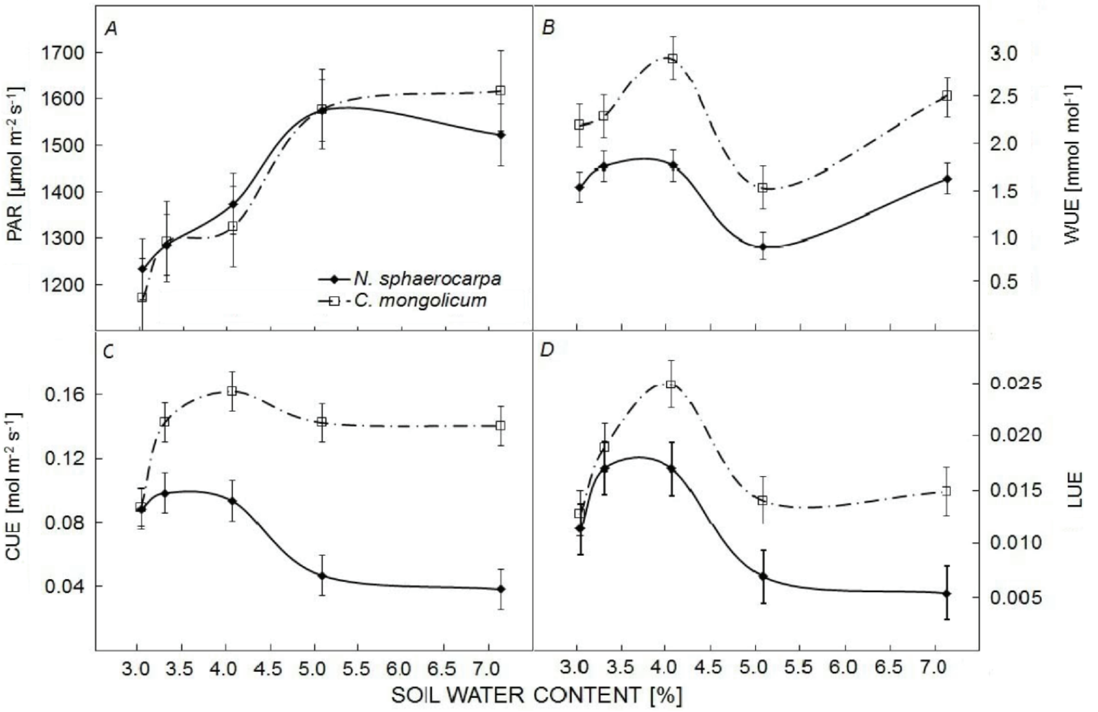

Fig. 5. The responses of (*A*) photosynthetically active radiation (PAR), (*B*) water-use efficiency (WUE), (*C*) CO_2-use efficiency (CUE), and (*D*) light-use efficiency (LUE) to the pulse of soil moisture.

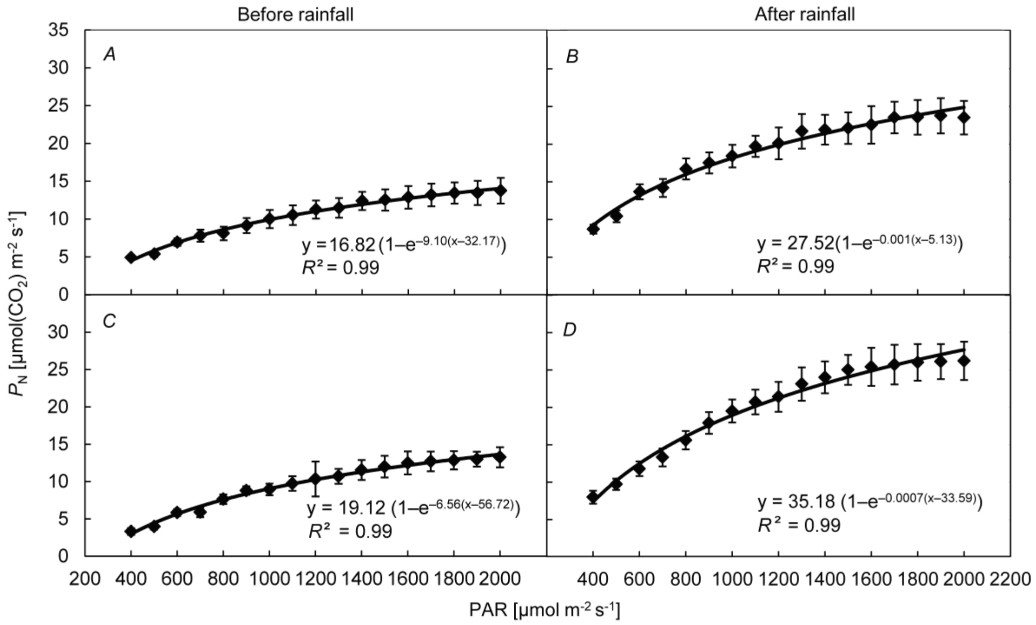

Fig. 6. The responses of the photosynthetic light-response curves to the rainfall pulse. P_N – net photosynthetic rate; PAR – photosynthetically active radiation.

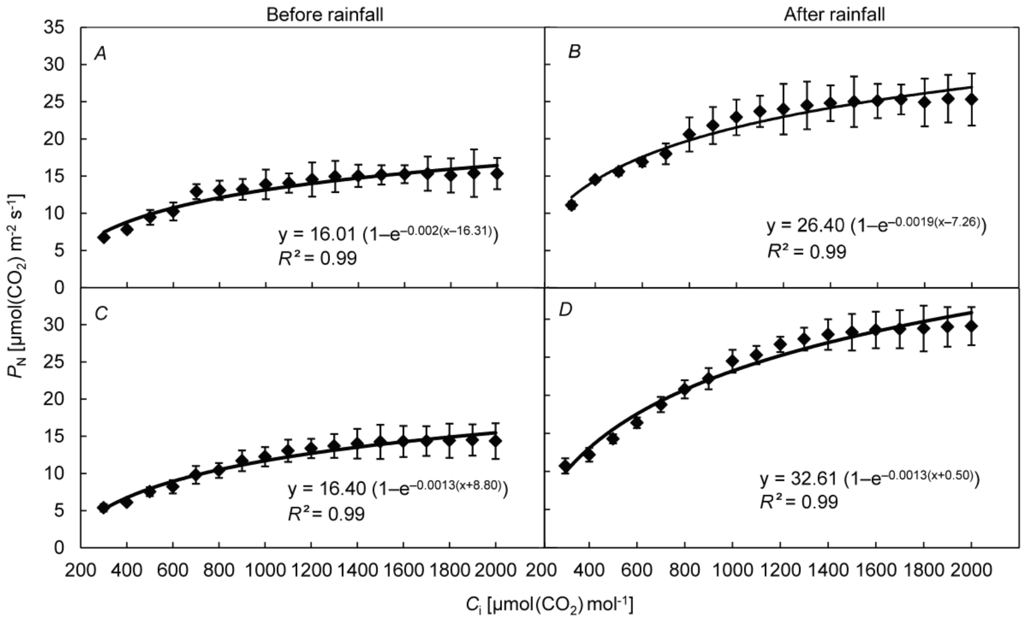

Fig. 7. The responses of the photosynthetic CO_2-response curves to the rainfall pulse. P_N – net photosynthetic rate; C_i – intercellular CO_2 concentration.

The response curves fitted the MnMolecular function well ($R^2 = 0.99$; Figs. 6, 7). The P_N values of *N. sphaerocarpa* after the rainfall were 1.65 to 1.75 times the value before rainfall, whereas those of *C. mongolicum* increased to approximately 2 times the prerainfall value (Table 2). However, the P_N of both shrubs did not decrease at high light intensity (2,000 µmol m^{-2} s^{-1}; Fig. 6) or high CO_2 concentration [2,000 µmol(CO_2) mol^{-1}; Fig. 7], which indicates that neither shrub experienced inhibition by high light or CO_2 levels. The values of all the parameters of the light-response curves for the two shrubs were significantly different before and after the rainfall, except for LCP and R_{day} of *C. mongolicum* ($P<0.05$; Table 2). The magnitude of the response of P_{Nmax} and QE were smaller for *N. sphaerocarpa* than for *C. mongolicum* (Table 2), which means that the photosynthetic capacity and light-use efficiency were higher, and their responses to improved soil moisture were stronger, for *C. mongolicum* than for *N. sphaerocarpa*.

Discussion

Pulses of rainfall can trigger a cascade of ecosystem responses that affect plant nutrient, water, and carbon cycling (Ivans *et al.* 2006), these responses ultimately affect the balance of ecosystem respiration and photosynthate accumulation in low-rainfall ecosystems (Huxman *et al.* 2004). In the present study, the photosynthetic parameters of the two desert shrubs responded significantly to rainfall pulse, but the maximum value of most photosynthetic parameters appeared on the seventh day after rainfall, which indicated that the response of the shrubs to the rainfall pulse exhibited a time-lag and compensated for the removal of the drought stress. Because water stress has a characteristic hysteresis effect (Boyer 1970), the compensation effect exhibited a time-lag in the recovery process after the rainfall event. The antecedent soil moisture and the change in soil moisture after the rainfall were both important for explaining the responses of the desert plants to the rainfall pulse (Ogle and Reynolds 2004, Reynolds *et al.* 2004). However, the magnitude of the response of the photosynthetic parameters is determined by the drought duration and the water availability (Yan *et al.* 2000, Schwinning *et al.* 2002). And, the P_N values of the two desert shrubs increased with increasing soil moisture, then decreased when soil water content exceeded *ca.* 4.08%, because the surplus soil moisture interferes with gas exchange. Although the two species generally showed similar patterns of response to changes in soil moisture, *N. sphaerocarpa* and *C. mongolicum* differ in their responses with different values of soil moisture when their photosynthetic parameters reach their maximum level.

Desert plants engage both long-term adaptations and short-term modulations to maintain their water balance by depressing metabolic activity, thereby shielding themselves from the adverse effects of insufficient soil moisture (Eagleson 1982). The desert shrubs *N. sphaerocarpa* and *C. mongolicum* are typical super-xerophytic shrubs, with deep root systems, and both can usually continue to photosynthesize at low levels of soil moisture. Water absorption is directly affected by plant and soil water status, and this may explain why plant responses to rainfall pulses are temporally and spatially heterogeneous (Meiresonne *et al.* 2003, Zeppel *et al.* 2004). Photosynthetic organs can respond quickly to environmental changes through changes in stomatal conductance (Farquhaar and Sharkey 1982, Dai *et al.* 2000). After the rainfall pulse, g_s for *N. sphaerocarpa* approached that for *C. mongolicum*, whereas P_N of the latter remained higher, and this difference agrees with the WUE of multifunctionalization reported by Gebauer and Ehleringer (2002), Ivans *et al.* (2003). Rainfall can also increase the rate of enzyme response in the Calvin cycle (Woodrow *et al.* 1984), thereby increasing P_{Nmax} of *N. sphaerocarpa* and *C. mongolicum*. Simultaneously, the rainfall pulse will enhance the activation of proteins in photosystem II in the chloroplasts (Siefermann-Harms 1992), this will accelerate the rate of electron transport in photosystem I (Okada *et al.* 1976), thereby decreasing CCP and increasing CSP of *N. sphaerocarpa* and *C. mongolicum*. However, the LCP of *N. sphaerocarpa* was lower than that of *C. mongolicum* both before and after the rainfall, whereas the R_{day} was larger. This means that *N. sphaerocarpa* can adapt well to a low-light environment and maintain its metabolism by consuming the photosynthate that accumulates during favourable periods to alleviate the environmental stress caused by drought and high temperatures.

Desert plants can adapt to environments controlled by limited water by increasing their WUE and closing stomata during periods of drought stress (Flexas and Medrano 2002, Silva *et al.* 2004). These changes affect electron transport and photophosphorylation in the photosynthetic system, and the reaction mechanisms responsible for CO_2 assimilation (Kaiser 1987). *C. mongolicum* had a lower CCP, higher CSP, and higher P_{Nmax}, and a larger response magnitude, than *N. sphaerocarpa*, suggesting that *C. mongolicum* can adapt well to changes in CO_2 concentration after a rainfall pulse. CE increased significantly after the rainfall, and the CE values for *N. sphaerocarpa* were higher than those for *C. mongolicum* both before and after the rainfall ($P<0.05$; Table 2). This means that the ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity and carboxylase activity of *N. sphaerocarpa* were higher, and that rainfall can relieve the photophosphorylation and Rubisco activity, resulting in decreased P_N. In addition, the magnitude of the response to rainfall of all parameters in the light- and CO_2-response curves for *N. sphaerocarpa* was smaller than those for *C. mongolicum*. This suggested that *C. mongolicum* had a strong compensation effect and strong response to the rainfall pulse.

The photosynthetic rates of *C. mongolicum* and *N. sphaerocarpa* were increased significantly in response to rainfall pulses when soil moisture increased by 15% in desert regions of China (Figs. 4, 5). Changes in precipitation patterns under a future climate are predicted to result in a 15% increase in annual rainfall in arid regions (Arritt *et al.* 2000). Under a future climate, the timing and magnitude of rainfall pulses will determine the extent to which these desert shrubs will undergo changes in their photosynthetic carbon uptake (*i.e.*, Easterling *et al.* 2000, Loik 2007). Our results suggest that both shrubs can take advantage of rainfall pulses by improving their assimilation rate, though details of their response mechanisms differ, and may therefore benefit from the predicted climate change that will occur in arid regions.

References

Arndt, S.K., Clifford, S.C., Popp, M, Wanek, W.: Contrasting adaptations to drought stress in field-grown *Ziziphus mauritiana* and *Prunus persica* trees: water relations, osmotic adjustment and carbon isotope composition. – Aust. J. Plant. Physiol. **27**: 985-996, 2000.

Arritt, R.W., Goering, D.C., Anderson, C.J.: The North American monsoon system in the Hadley Centre coupled ocean-atmosphere GCM. – Geophys. Res. Lett. **27**: 565-568, 2000.

Boyer, J.S.: Leaf enlargement and metabolic rates in corn, soybean and sunflower at various leaf water potentials. – Plant. Physiol. **46**: 233-235,1970.

Cornic, G.: Drought stress inhibits photosynthesis by decreasing stomatal aperture – not by affecting ATP synthesis. – Trends Plant. Sci. **5**: 187-188, 2000.

Dai, X.B., Zhai, H.Q., Zhang, H.S.: [Effect of soil drought stress on photosynthetic rate and carbonic anhydrase activity of rice leaf.] – Acta. Phytophysiol. Sin. **26**: 133-136, 2000. [In Chin., English summ.]

Eagleson, P.S.: Ecological optimality in water limited natural soil-vegetation systems. – Water Sci. Res. **18**: 325-354, 1982.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Mearns, L.O.: Climate extremes: observations, modeling, and impacts. – Science **289**: 2068-2074, 2000.

Ehleringer, J.R., Schwinning, S., Gebauer, R.L.E.: Water use in arid land ecosystems. – In: Press, M.C. (ed.): Advances in Plant Physiological Ecology. Pp. 347-365. Blackwell Sci., Oxford 1999.

Farquhar, G.D., von Caemmerer, S., Berry, J.A.: A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. – Planta **149**: 78-90, 1980.

Farquhar, G.D., Sharkey, T.D.: Stomatal conductance and photosynthesis. – Annu. Rev. Plant. Physiol. **33**: 317-345, 1982.

Flexas, J., Bota, J., Loreto, F., Cornic, G., Sharkey, T.D.: Diffusive and metabolic limitations to photosynthesis under drought and salinity in C_3 plants. – Plant Biology **3**: 269-279, 2004.

Flexas, J., Medrano, H.: Drought-inhibition of photosynthesis in C_3 plants: stomatal and non-stomatal limitation revisited. – Ann. Bot. **89**: 183-189, 2002.

Franks, P.J.: Stomatal control and hydraulic conductance, with special reference to tall trees. – Tree Physiol. **24**: 865-878, 2004.

Gebauer, R.L.E., Ehleringer, J.R.: Water and nitrogen uptake patterns following moisture pulses in a cold desert community. – Ecology **81**: 1415-1424, 2000.

Harley, P.C., Baldocchi, D.D.: Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. I. Leaf model parameterization. – Plant Cell Environ. **18**: 1146-1156, 1995.

Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Ogle, K., Pockman, W.T., Sandquist, D.R., Potts, D.L., Schwinning, S.: Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. – Oecologia **141**: 254-268, 2004.

Ignace, D.D., Huxman, T.E., Weltzin, J.F., Williams, D.G.; 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, 2007.

Ivans, C.Y., Leffler, A.J., Spaulding, U., Stark, J.M., Ryel, R.J., Caldwell, M.M.: Root responses and nitrogen acquisition by *Artemisia tridentata* and *Agropyron desertorum* following small summer rainfall events. – Oecologia **134**: 317-324, 2003.

Ivans, S., Hipps, L., Leffler, A.J., Ivans, C.Y.: Response of water vapor and CO_2 fluxes in semiarid lands to seasonal and intermittent precipitation pulses. – J. Hydrometeorol. **7**: 995-1010, 2006.

Jackson, R.B., Carpenter, S.R., Dahm, C.N., McNight, D.M., Naiman, R.J., Postel, S.L., Running, S.W.: Water in a changing world. – J. Appl. Ecol. **11**:1027-1045, 2001.

Kaiser, W.M.: Effect of water deficits on photosynthetic capacity. – Physiol. Plant. **71**: 142-149, 1987.

Li, Y.G., Jiang, G.M., Liu, M.Z., Niu, M.Z., Gao, L.M., Cao, X.C.: Photosynthetic response to precipitation/rainfall in predominant tree (*Ulmus pumila*) seedlings in Hunshandak Sandland, China. – Photosynthetica **45**: 133-138, 2007.

Loik, M.E.: Sensitivity of water relations and photosynthesis to summer precipitation pulses for *Artemisia tridentata* and *Purshia tridentata*. – Plant Ecol. **191**: 95-108, 2007.

Marron, N., Delay, D., Petit, J.M., Deyer, E., Kahlem, G., Delmotte, F.M., Brignolas, F.: Physiological traits of two *Populus* × *euramericana* clones, Luisa Avanzo and Dorskamp, during a water stress and re-watering cycle. – Tree. Physiol. **22**: 849-858, 2002.

Meiresonne, L., Sampson, D.A., Kowalski, A.S., Janssens, I.A., Nadezhdina, N., Cermak, J., Van Slycken, J., Ceulemans, R.: Water flux estimates from a Belgian Scots pine stand: a comparison of different approaches. – J. Hydrol. **270**: 230-252, 2003.

Noy-Meir, I.: Desert ecosystems: environment and producers. – Annu. Rev. Ecol. Syst. **4**: 25-52, 1973.

Ogle, K., Reynolds, J.F.: Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. – Oecologia **141**: 282-294, 2004.

Okada, M., Kitajima, M., Butler, W.L.: Inhibition of photosystem I and photosystem II in chloroplasts by UV radiation. – Plant. Cell. Physiol. **17**: 35-43, 1976.

Olsson, T., Leverenz, J.W.: Non-uniform stomata closure and the apparent convexity of the photosynthetic photon flux density response curve. – Plant Cell Physiol. **17**: 701-710, 1994.

Prioul, J.F., Chartier, P.: Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO_2 fixation: A critical analysis of the methods used. – Ann. Bot. **41**: 789-800, 1977.

Reynolds, J.F., Kemp, P.R., Ogle, K., Fernandez, R.J.: Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. – Oecologia **141**: 194-210, 2004.

Reynolds, J.F., Virginia, R.A., Kemp, P.R., De Soyza, A.G., Tremmel, D.C.: Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. – Ecol. Monogr. **69**: 69-106, 1999.

Schwinning, S., Davis, K., Richardson, L., Ehleringer, J.R.: Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. – Oecologia **130**: 345-355, 2002.

Schwinning, S., Ehleringer, J.R.: Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. – J. Ecol. **89**: 464-480, 2001.

Schwinning, S., Sala, O.E.: Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. – Oecologia **141**: 211-220, 2004.

Schwinning, S., Sala, O.E., Loik ,M.E., Ehleringer, J.R.: Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. – Oecologia **141**: 191-193, 2004.

Siefermann-Harms, D.: The yellowing of spruce in polluted atmospheres. – Photosynthetica **27**: 323-341,1992.

Silva, F.C.E., Shvaleva, A., Maroco, J.P., Almeida, M.H., Chaves, M.M., Pereira, J.S.: Responses to water stress in two *Eucalyptus globulus* clones differing in drought tolerance. – Tree Physiol. **24**: 1165-1172, 2004.

Smith, S.D., Huxman, T.E., Zitzer, S.F., Charlet, T.N., Housman, D.C., Coleman, J.S., Fenstermaker, L.K., Seemann, J.R., Nowak, R.S.: Elevated CO_2 increases productivity and invasive species success in an arid ecosystem. – Nature **408**: 79-82, 2000.

Smith, S.D., Nowak, R.S.: Ecophysiology of plants in the Intermountain lowlands. – In: Osmond, C.B., Pitelka, L.F., Hidy, G.F. (ed.): Plant Biology of the Basin and Range. Pp. 179-241. Springer-Verlag, New York 1990.

Stephenson, N.L.: Climatic control of vegetation distribution: The role of the water balance. – Amer. Natur. **135**: 649-670, 1990.

Woodrow, I.E., Murphy, D.J., Latako, E.: Regulation of stromal sedoheptulose 1,7 - bisphosphatase activity by pH and Mg^{2+} concentration. – J. Biol. Chem. **259**: 3791-3795, 1984.

Xu, H., Li, Y.: Water-use strategy of three central Asian desert shrubs and their responses to rain pulse events. – Plant. Soil. **285**: 5-17, 2006.

Xu, H., Li, Y., Xu, G.Q., Zou, T.: Ecophysiological response and morphological adjustment of two Central Asian desert shrubs towards variation in summer precipitation. – Plant. Cell. Environ. **30**: 399-409, 2007.

Yan, S., Wan, C., Sosebee, R.E., Wester, D.B., Fish, E.B., Zartman, R.E.: Responses of photosynthesis and water relations to rainfall in the desert shrub creosote bush (*Larrea tridentata*) as influenced by municipal biosolids. – J. Arid. Environ. **46**: 397-412, 2000.

Zeppel, M.J.B., Murray, B.R., Barton, C., Eamus, D.: Seasonal responses of xylem sap velocity to VPD and solar radiation during drought in a stand of native trees in temperate Australia. – Funct. Plant Biol. **31**: 461-470, 2004.

Zhao, W.Z., Liu, B.: The response of sap flow in shrubs to rainfall pulses in the desert region of China. – Agron. Forest Meteorol. **150**: 1297-1306, 2010.