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Photosynthetic response of desert plants to small rainfall events in the Junggar Basin, northwest China

Y. WU[*,**], X.J. ZHENG[*,+], and Y. LI[*]

State Key Lab of Oasis and Desert Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, Xinjiang, China[*]
University of Chinese Academy of Sciences, Beijing, China[**]

Abstract

Small rainfall events (≤ 5 mm) have short intervals, but account for a large proportion of the annual rainfall frequency in arid lands. To explore possible strategies used by desert plants to utilize the small rainfall events, we investigated the photosynthetic responses of 28 species to 1 mm and 6 mm of simulated rainfall in the Junggar Basin, northwest China. The species were grouped into four plant functional types: short-life-cycle herbs, long-life-cycle herbs, non-phreatophyte shrubs, and phreatophyte shrubs. The results showed that the net photosynthetic rate, stomatal conductance, and transpiration rate increased in most of the herbs, but they responded differently to the rainfall treatments. However, the water-use efficiency did not significantly differ after 1 and 6 mm rainfall treatments in most of the shrubs. The maximum water absorption by leaves and the percentage increase of a leaf water content (LWC) were higher in the herbs than those in the shrubs. Plants with dense trichomes had the highest LWC. The results suggested that the desert plants benefited from the micro-environment humidity provided by the small rainfall events.

Additional key words: leaf water uptake; photosynthetic rate; plant functional types; stomatal conductance; trichome; water-use efficiency.

Introduction

Rainfall, as the major water input for deserts (Noy-Meir 1973), is thought to have a considerable effect on plant survival and production (Briggs and Knapp 1995, Fay *et al*. 2003). Rainfall in arid regions is dominated by small events (lesser than 5 mm) rather than infrequent and highly unpredictable large rainfall events (Loik *et al*. 2004, Reynolds *et al*. 2004). In the Junggar Basin, northwest China, events up to 5 mm contribute by 81.4% of the total rainfall frequency, being 35.9% of the total annual mean precipitation. The average interval between small rainfall events is less than 10 days (Zheng *et al.* 2009, Wang 2009).

However, small rainfall events have been usually considered as "ineffective rainfall" because the water does not reach root zones (Nobel 1976, Weaver 1982, Dougherty *et al*. 1996). A large proportion of small rainfall is intercepted by plant canopies and generally evaporates within a day of a precipitation event (Loik *et al*. 2004, Owens *et al*. 2006). Absorption of water through leaves has been demonstrated in some studies (Boucher *et al.* 1995, Yates and Hutley 1995, Munné-Bosch and Alegre 1999, Munné-Bosch *et al.* 1999). In coastal redwood forests of California, western USA, prolonged and heavy fog events yielded clear examples of sap flow reversal, which suggested that there was direct leaf uptake of water by *Sequoia sempervirens* (Burgess and Dawson 2004). A similar phenomenon was observed in *Vellozia flavicans* in central Brazil (Oliveira *et al*. 2005). Approximately 80% of the dominant species in redwood forests followed this leaf uptake strategy (Limm *et al*. 2009). More evidence had been found in epiphytes and non-epiphytes in Xishuangbanna, southwest China, where plants absorbed fog water through their leaves (Zheng and Feng 2006).

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[+]Corresponding author; fax: +86 991 7885320, e-mail: zhengxj@ms.xjb.ac.cn
Abbreviations: *E* – transpiration rate; F_v/F_m – maximum photochemical efficiency of photosystem II; g_s – stomatal conductance; LWC – percentage increase of leaf water content; MWA – maximum water absorption by leaves; NR – natural rainfall (control); P_N – net photosynthetic rate; SR – simulated rainfall; SWC – soil water content; $T_{air} - T_{leaf}$ – the difference between air temperature and leaf temperature; WUE – water-use efficiency (= P_N/E).
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These results implied that leaf water uptake is a common strategy for acquiring water in some plants.

Trichomes on leaf surfaces improve the overall area available for water vapor condensation, which leads to increased water retention and duration on the leaf surface (Zhuang and Zhao 2010). Grammatikopoulos *et al*. (1994) demonstrated that water on hairy leaf surfaces quickly penetrated into mesophyll. Other possible mechanisms, such as the potential role of epidermal hydathodes (Martin and von Willert 2000), the cuticular pathway (Yates and Hutley 1995, Gouvra and Grammatikopoulos 2003), and fungal endophytes, have been also considered (Burgess and Dawson 2004). However, studies on intercepted water absorption have mainly focused on a small number of species (Munné-Bosch *et al*. 1999, Breshears *et al*. 2008, Tange *et al*. 2009, Limm and Dawson 2010).

More recently, it has been suggested that leaf absorption of intercepted water may be important, not only during periods of dew or fog, but also during rainfall (Breshears *et al*. 2008, Munné-Bosch 2010). Water absorption by leaves enables plants to decouple leaf-level water and carbon relationship from soil water availability (Simonin *et al*. 2009). Relative water content, water potential, and leaf gas exchange have been shown to increase during fog (Zheng and Feng 2006), dew (Boucher *et al.* 1995, Munné-Bosch *et al*. 1999) and small rainfall events (Wang and Tang 2009). Therefore, small rainfall events could be important for improving plant water conditions. The objectives of this study were to investigate the photosynthesis of different plant functional types in response to small rainfall events, and clarify the role of leaf hairs in absorbance of water during small rainfall events.

Materials and methods

Study area and species: The research was carried out on the southeastern edge of the Junggar Basin (44°15′N–46°50′N, 84°50′E–91°20′E), near the Fukang Station of Desert Ecology, Chinese Academy of Sciences (44°17′N, 87°56′E, 475 m a. s. l.). The climate was a typical temperate, continental arid climate with a hot, dry summer and a cold winter. The annual mean temperature was 6.6°C, annual mean precipitation was about 160 mm, and the corresponding pan-evaporation was about 2,000 mm. The meteorological data were recorded by the *Campbell* automatic station (*Campbell Scientific*, Logan, UT, USA) located within the study area. The annual mean rainfalls was 168.4 mm, the annual rainfall frequency took up 77% of the annual precipitation frequency (data for the years 1998–2007). The rainfall and the average daily temperatures in 2012 are shown in Fig. 1. In the study region, the total rainfall from February to October 2012 was 94.6 mm. Most rainfall events were less than 5 mm, especially in the summer, and 68% of the rainfall frequency was less than 1 mm. The average daily temperature of the study period (day of year 124–257) was 24.4°C (Fig. 1). The soils were either a silty clay-loam, with a high salinity, or sandy. There are nine species growing in the silty clay-loam: *Karelinia caspia*, *Limonium gmelinii*, *Sophora alopecuroides*, *Salicornia europaea*, *Kalidium foliatum*, *Halostachys caspica*, *Halimodendron halodendron*, *Nitraria tangutorum*, and *Tamarix ramosissima*. Other species grow in the sandy soils. The groundwater table is nearly 5 m deep.

Based on herb phenology or shrub root patterns, 28 plant species were grouped into four functional types in this study (*see* the text table on the next page).

Experimental design: The field experiment lasted from May to September in 2012, which is the peak growth period for plants in this region. Nine (1 m × 1 m) plots

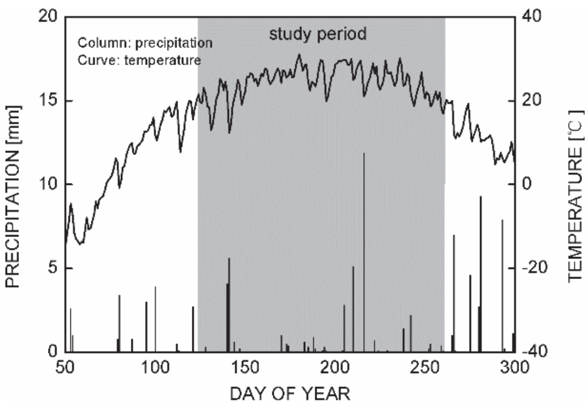

Fig. 1. Rainfall and average daily temperature at the Junggar Basin in 2012. The *shadow part* shows the study period (the first species was measured on day 124 of the year and the last species on day 257 of the year).

were used for each herb species and (2 m × 2 m) plots were used for each shrub species. Three plots acted as controls (*i.e.*, only natural rainfall, NR), three were subjected to 1 mm simulated rainfall (1SR) applied with a hand-held sprayer and the other three were subjected to 6 mm simulated rainfall (6SR) applied with a watering can. Water was added from 1.0–1.5 m above the plant canopy. All treatments were applied in the late afternoon of the day before measurements. To avoid interference by natural rainfall, the experiment was paused for at least 5 d after a natural rainfall event. Previous studies indicated that this was long enough to allow the top soil water content to return to normal levels (Liu *et al*. 2012, Ma *et al*. 2012). In this study, the largest natural rainfall event was 11.9 mm (Fig. 1) and the 5-d gap between the natural rainfall and the treatments was sufficient to avoid the buffer effect of xylem water (Bassiri Rad *et al*. 1999).

Plant group	Description	Species
Short-life-cycle herbs	Herbs where the aboveground part survives until July	*Amberboa turanica* (Compositae) *Cancrinia discoidea* (Compositae) *Corispermum lehmannianum* (Chenopodiaceae) *Erysimum cheiranthoides* (Brassicaceae) *Erodium oxyrrhynchum* (Geraniaceae) *Euphorbia turczaninowii* (Euphorbiaceae) *Nonea caspica* (Boraginaceae) *Nepeta micrantha* (Labiatae)
Long-life-cycle herbs	Herbs where the aboveground part survives until mid-September	*Agriophyllum squarrosum* (Chenopodiaceae) *Bassia dasyphylla* (Chenopodiaceae) *Ceratocarpus arenarius* (Chenopodiaceae) *Karelinia caspia* (Compositae) *Limonium gmelinii* (Plumbaginaceae) *Peganum harmala* (Zygophyllaceae) *Sophora alopecuroides* (Leguminosae) *Salicornia europaea* (Chenopodiaceae) *Tribulus terrester* (Zygophyllaceae)
Non-phreatophyte shrubs	Shrubs with shallow root systems that mainly use rainfall or shallow soil water (Xu and Li 2006)	*Ceratoides latens* (Chenopodiaceae) *Calligonum leucocladum* (Polygonaceae) *Haloxylon ammodendron* (Chenopodiaceae) *Haloxylon persicum* (Chenopodiaceae) *Kalidium foliatum* (Chenopodiaceae) *Reaumuria songarica* (Tamaricaceae)
Phreatophyte shrubs	Shrubs with deep root systems that use deep soil water or groundwater (Xu and Li 2006)	*Alhagi sparsifolia* (Leguminosae) *Halostachys caspica* (Chenopodiaceae) *Halimodendron halodendron* (Leguminosae) *Nitraria tangutorum* (Zygophyllaceae) *Tamarix ramosissima* (Tamaricaceae)

Top soil water content (SWC): To assess the effects of the water treatments on soil water, the SWC (%) was measured at 10-cm depth with a *Delta-T Device* moisture meter (type *WET-2*, *Delta-T Devices Ltd*., Burwell, Cambridge, UK) (four times and with four separate directions within each plot) before the gas exchange measurements. Then the average SWC in each individual plot and the mean SWC for each treatment were calculated.

Chlorophyll (Chl) fluorescence and gas exchange measurement: Chl fluorescence was measured on fully expanded leaves in the early morning (07:00–07:30 h, local time, before the sun rose), using a portable plant efficiency analyzer (*Pocket PEA*, *Hansatech*, King's Lynn, UK). The light intensity was 2,500 μmol(photon) m^{-2} s^{-1}. F_v/F_m (maximum photochemical efficiency of photosystem II) was recorded immediately after dark adaptation for 20 min. For each species, nine replicates from three individual plants were chosen to calculate the average F_v/F_m for each treatment. The F_v/F_m value in the range of 0.79–0.84 is the approximate optimal value for many plant species. Plants show lower values when they are under stress (Kitajima and Butler 1975, Maxwell and Johnson 2000).

Gas exchange measurements were also taken during the same day (08:30–11:30 h, local time) by a *Li-6400* portable photosynthesis system (*Li-Cor*, Lincoln, NE, USA) containing an *Arabidopsis* chamber. PPFD was recorded by the quantum sensor on the *Li-6400*. During the measurement periods, the PPFD values were between 1,000 and 1,500 μmol m^{-2} s^{-1}. Leaf areas were calculated from photographs obtained from the leaf scans taken using *CI-400 CIAS* software (*Computer Imaging Analysis Software*, *CID Co*., Logan, UT, USA). The net photosynthetic rate (P_N) [μmol(CO_2) m^{-2} s^{-1}], stomatal conductance (g_s; in [mol m^{-2} s^{-1}]), and transpiration rate (E) in [mmol(H_2O) m^{-2} s^{-1})], T_{air} and T_{leaf} were recorded, and the water-use efficiency (WUE) was calculated in [μmol(CO_2) $mmol^{-1}$(H_2O)] and the difference between air temperature and leaf temperature ($T_{air} - T_{leaf}$) was calculated. For each treatment, five leaves from five representative plants were measured.

Relative effectiveness calculation: Generally, 6SR has been considered as effective rainfall (>5 mm, Sala and Lauenroth 1982), thus, we compared the effects of 1SR to that of 6SR. To estimate how effective the 1 mm rainfall event was, we defined the "relative effectiveness" of each parameter under 1 mm rainfall. The ratio was calculated as follows (taking g_s as an example):

$$g_s \text{ relative effectiveness} = \frac{g_s(1\,\text{mm}) - g_s(\text{control})}{g_s(6\,\text{mm}) - g_s(\text{control})}$$

P_N-relative effectiveness, E-relative effectiveness, and WUE-relative effectiveness were calculated in the same way. We standardized the deviation for each parameter to values between 0 and 1 regardless of whether a parameter increased or decreased after 1SR. This avoided the offset between positive and negative values within the same functional type. Thus, the relative effectiveness reflected the average magnitude of change. The relative effectiveness of each species was calculated, and then we obtained the mean relative effectiveness values for each plant functional type.

Leaf water uptake capacity: To assess the leaf water uptake capacity of the different species, the MWA and the LWC of excised leaves or twigs were calculated. Leaves or twigs were sampled from the control plants after the gas exchange measurements. The surface of each cut petiole was quickly sealed with thermosetting adhesive to prevent evaporation and then they were immediately placed in an ice box and taken back to the laboratory as soon as possible.

Leaves or twigs were divided into five groups (five repetitions for each species, 5–10 leaves per group) and the fresh mass (M_f, g) was weighed immediately. The leaf or twig area (S, cm^2) was determined by *CI-400 CIAS* software. Then the leaves or twigs were submerged in distilled water and the cut petioles were kept above the water surface. The leaves or twigs were towel-dried and were weighed to obtain the water-saturated mass (M_s). The dry mass (M_d) was recorded after the leaves or twigs had been dried at 65°C for 48 h. MWA and LWC were calculated as:

$$\text{MWA} = 1{,}000\ (M_s - M_f)/S$$

$$\text{LWC} = (M_s - M_f)/(M_f - M_d) \times 100\%$$

Data analysis: *Minitab 16* statistics software was used to analyze the data. Descriptive statistics were used to calculate the means and standard errors for each replicate, one-way analysis of variance (*ANOVA*) was used to test the significant differences between treatments (significance level was $P<0.05$), and *Fisher*'s multiple comparison test was used to compare differences between the variable means for the different treatments.

Results

Soil water content: SWCs in the control (NR), 1SR and 6SR plots were 1.35 ± 0.35%, 1.36 ± 0.36%, and 7.75 ± 0.57%, respectively (mean ± SE, $n = 17$, $F = 70.1$, $P<0.001$). The SWC did not increase after the 1SR application. However, SWC increased significantly after the 6SR application.

F_v/F_m and $T_{air} - T_{leaf}$: F_v/F_m for all species stayed within the optimal range (0.78–0.84, Table 1) in all treatments. significantly changed for 6 of 17 herbs and 10 of 11 shrubs after both rainfall applications (Table 1).

Photosynthetic responses to the rainfall treatments: The P_N-relative effectiveness for all functional types was more than 25% (Fig. 2*A*). Notably, after 1SR, P_N significantly increased in *E. cheiranthoides* among the short-life-cycle herbs, and in *C. latens* and *H. persicum* among the non-phreatophyte shrubs (Fig. 3*AC*). In contrast, *S. europaea* among the long-life-cycle herbs and *N. tangutorum* from the phreatophyte shrubs showed unexpected decreases in P_N (Fig. 3*B*,*D*).

After the 1SR treatment, the g_s-relative effectiveness varied significantly among the four functional types ($F = 3.84$, $P = 0.025$), and reached 71.8% for non-phreatophyte shrubs (Fig. 2*B*). The g_s of the long-life-cycle herbs responded to 1SR positively. In particular, the g_s-relative effectiveness of *C. arenarius* increased by 78% (Fig. 3*F*). However, g_s of *S. alopecuroides* decreased after the rainfall applications (0.65 ± 0.06 mol m^{-2} s^{-1} for control, 0.47 ± 0.04 mol m^{-2} s^{-1} for 1SR, 0.29 ± 0.02 mol m^{-2} s^{-1} for 6SR, Fig. 3*F*). In the non-phreatophyte shrubs, g_s for *H. persicum* increased significantly after the 1SR applications (0.07 ± 0.01 mol m^{-2} s^{-1} for control NR, 0.13 ± 0.01 mol m^{-2} s^{-1} for 1SR Fig. 3*G*).

The E-relative effectiveness was greater than 30% for all functional types (Fig. 2*C*). Two exceptions were *N. caspica* among the short-life-cycle herbs (34.9 ± 3.35 for control NR, 31.1 ± 1.39 for 1SR, and 19.5 ± 0.10 mmol(H_2O) m^{-2} s^{-1} for 6SR, Fig. 3*I*) and *S. alopecuroides* in the long life-cycle herbs [12.8 ± 0.75 for control NR, 10.6 ± 0.61 for 1SR, and 7.54 ± 0.35 mmol(H_2O) m^{-2} s^{-1} for 6SR, Fig. 3*J*]. Their E values decreased after the rainfall treatments. For other species, the E values were either stable or increased after the rainfall applications (Fig. 3*I–L*).

WUE-relative effectiveness was greater than 50% for all functional types, while the phreatophyte shrubs reached 76.5% (Fig. 2*D*). The WUE of most shrubs were more sensitive to the rainfall applications than the herbs (Fig. 3*M–P*). For example, WUE for *C. lehmannianum* in the short-life-cycle herbs, *H. persicum* in the nonphreatophyte shrubs, and *H. caspica* and *T. ramosissima* in the phreatophyte shrubs significantly decreased after 1SR (Fig. 3*M*,*O*,*P*).

Table 1. F_v/F_m and ($T_{air} - T_{leaf}$) for 28 species. The values (mean ± SE; for F_v/F_m, $n = 3$; for $T_{air} - T_{leaf}$, $n = 5$) with *different letters* indicating a significant difference among treatments ($P<0.05$). The data were collected in 2012.

Species	F_v/F_m control	1 mm	6 mm	$T_{air}–T_{leaf}$ [ºC] control	1 mm	6 mm
A. turanica	0.858 ± 0.002	0.852 ± 0.001	0.855 ± 0.003	0.48 ± 0.11	0.55 ± 0.19	1.09 ± 0.27
C. discoidea	0.839 ± 0.003[a]	0.828 ± 0.005[ab]	0.821 ± 0.004[b]	1.24 ± 0.09[ab]	1.57 ± 0.18[a]	0.99 ± 0.03[b]
C. lehmannianum	0.825 ± 0.006	0.807 ± 0.013	0.810 ± 0.004	0.74 ± 0.10	0.65 ± 0.07	0.68 ± 0.11
E. cheiranthoides	0.809 ± 0.007	0.794 ± 0.012	0.803 ± 0.010	0.81 ± 0.08	0.78 ± 0.08	0.73 ± 0.09
E. oxyrrhynchum	0.845 ± 0.003	0.844 ± 0.003	0.848 ± 0.004	0.93 ± 0.09[b]	1.16 ± 0.05[a]	1.21 ± 0.04[a]
E. turczaninowii	0.854 ± 0.002[a]	0.844 ± 0.003[b]	0.842 ± 0.002[b]	1.44 ± 0.03	1.09 ± 0.20	1.14 ± 0.10
N. caspica	0.808 ± 0.004[a]	0.808 ± 0.004[a]	0.789 ± 0.013[b]	1.01 ± 0.14	0.98 ± 0.10	0.88 ± 0.04
N. micrantha	0.774 ± 0.013[ab]	0.763 ± 0.010[b]	0.794 ± 0.004[a]	1.01 ± 0.22	0.79 ± 0.07	1.05 ± 0.05
A. squarrosum	0.803 ± 0.007	0.791 ± 0.005	0.800 ± 0.009	0.47 ± 0.08	0.51 ± 0.08	0.62 ± 0.11
B. dasyphylla	0.814 ± 0.005	0.812 ± 0.008	0.819 ± 0.005	1.41 ± 0.16[a]	1.42 ± 0.13[a]	0.85 ± 0.06[b]
C. arenarius	0.823 ± 0.005[a]	0.781 ± 0.015[b]	0.795 ± 0.004[ab]	0.89 ± 0.04	0.96 ± 0.11	1.04 ± 0.03
K. caspia	0.839 ± 0.006	0.834 ± 0.004	0.836 ± 0.003	1.08 ± 0.05[a]	0.68 ± 0.07[b]	0.92 ± 0.09[ab]
L. gmelinii	0.822 ± 0.004	0.828 ± 0.004	0.830 ± 0.005	0.99 ± 0.17	1.06 ± 0.11	1.05 ± 0.04
P. harmala	0.835 ± 0.005[b]	0.852 ± 0.002[a]	0.847 ± 0.004[a]	0.50 ± 0.07	0.76 ± 0.13	0.79 ± 0.06
S. alopecuroides	0.864 ± 0.001	0.858 ± 0.004	0.850 ± 0.007	0.56 ± 0.02[b]	0.63 ± 0.05[b]	0.77 ± 0.02[a]
S. europaea	0.817 ± 0.002	0.809 ± 0.004	0.810 ± 0.006	0.38 ± 0.05[b]	0.53 ± 0.02[a]	0.59 ± 0.03[a]
T. terrester	0.813 ± 0.001[ab]	0.808 ± 0.003[b]	0.814 ± 0.001[a]	0.73 ± 0.03	0.67 ± 0.09	0.78 ± 0.21
C. latens	0.840 ± 0.002	0.836 ± 0.006	0.844 ± 0.005	0.99 ± 0.02[a]	0.89 ± 0.03[b]	0.75 ± 0.01[c]
C. leucocladum	0.801 ± 0.003	0.812 ± 0.007	0.804 ± 0.005	0.57 ± 0.06[b]	0.62 ± 0.03[ab]	0.72 ± 0.02[a]
H. ammodendron	0.784 ± 0.004	0.792 ± 0.003	0.784 ± 0.009	0.11 ± 0.05[a]	–0.12 ± 0.09[b]	–0.11 ± 0.05[b]
H. persicum	0.789 ± 0.005[b]	0.797 ± 0.002[b]	0.816 ± 0.003[a]	–0.13 ± 0.08[a]	–0.36 ± 0.04[a]	–0.74 ± 0.11[b]
K. foliatum	0.842 ± 0.001[a]	0.833 ± 0.003[b]	0.823 ± 0.004[c]	0.29 ± 0.03[b]	0.29 ± 0.02[b]	0.39 ± 0.03[a]
R. songarica	0.836 ± 0.006[b]	0.849 ± 0.004[a]	0.849 ± 0.002[ab]	0.57 ± 0.05[b]	0.68 ± 0.03[ab]	0.80 ± 0.05[a]
A. sparsifolia	0.845 ± 0.008	0.831 ± 0.004	0.844 ± 0.007	0.65 ± 0.09	0.70 ± 0.01	0.68 ± 0.04
H. caspica	0.837 ± 0.004	0.832 ± 0.004	0.836 ± 0.008	0.17 ± 0.10[b]	0.22 ± 0.06[b]	0.52 ± 0.10[a]
H. halodendron	0.840 ± 0.005	0.847 ± 0.005	0.833 ± 0.007	0.85 ± 0.07[ab]	0.91 ± 0.05[a]	0.63 ± 0.07[b]
N. tangutorum	0.836 ± 0.009	0.849 ± 0.005	0.841 ± 0.005	0.31 ± 0.01[b]	0.44 ± 0.01[ab]	0.49 ± 0.08[a]
T. ramosissima	0.857 ± 0.003	0.854 ± 0.002	0.854 ± 0.001	0.19 ± 0.03[c]	0.30 ± 0.01[b]	0.46 ± 0.03[a]

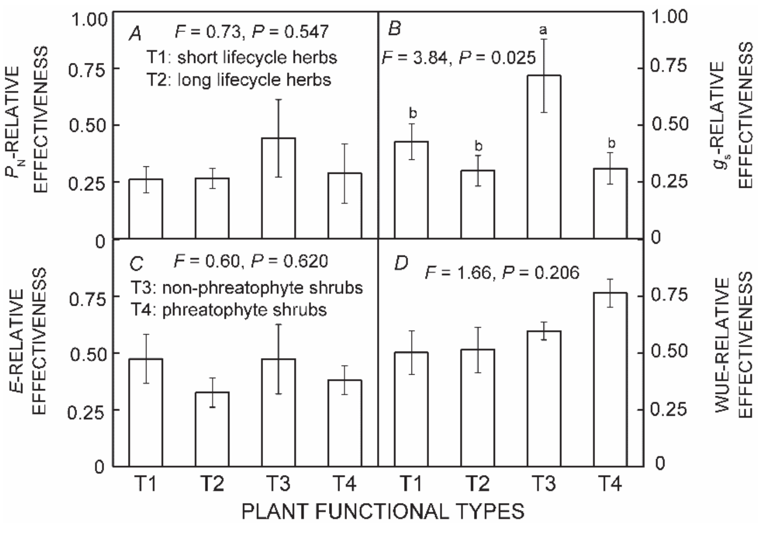

Fig. 2. Relative effectiveness of (*A*) net photosynthetic rate (P_N), (*B*) stomatal conductance (g_s), (*C*) transpiration rate (*E*), and (*D*) water-use efficiency (WUE) for four plant functional types. *Different letters* indicate significant differences among the four plant functional types for g_s-relative effectiveness ($P<0.05$). Short-life-cycle herbs (T1), long-life-cycle herbs (T2), non-phreatophyte shrubs (T3), and phreatophyte shrubs (T4) = 8, 9, 6, and 5 plant species, respectively. The relative effectiveness was defined as the effect after a 1 mm rainfall event compared to that after a 6 mm rainfall event. The data were collected in 2012.

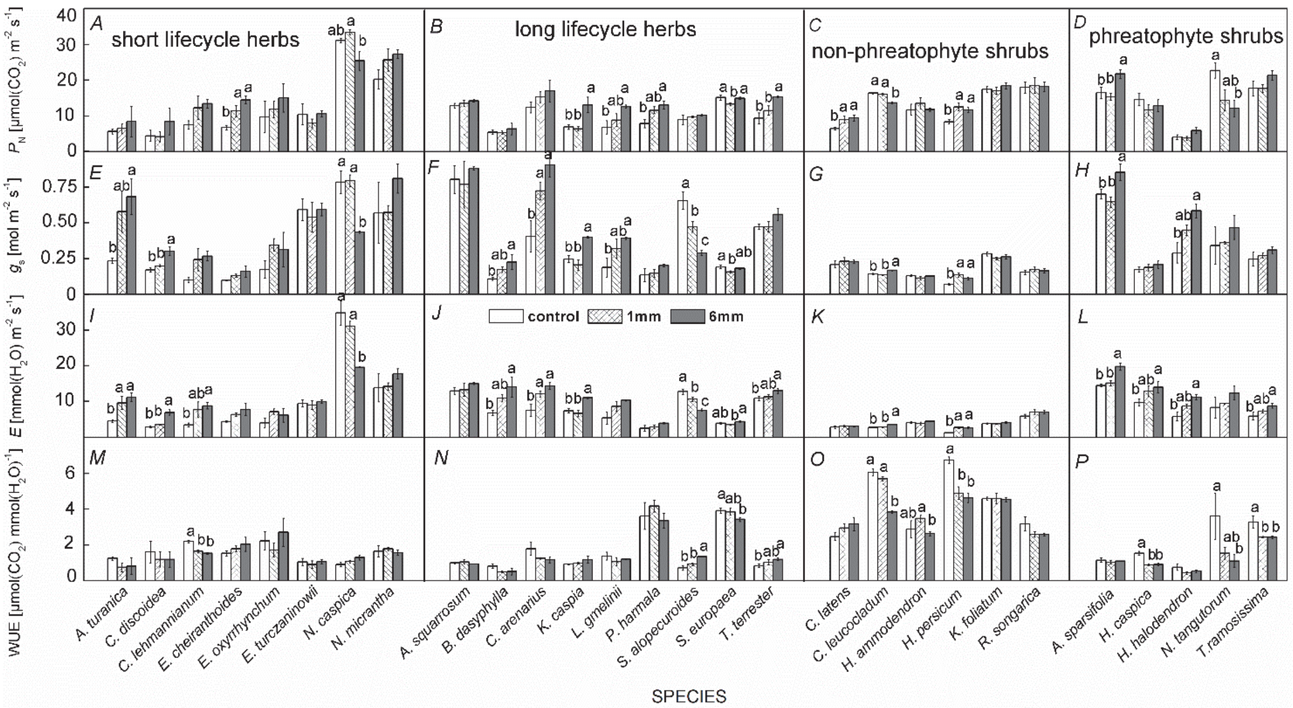

Fig. 3. Net photosynthetic rate (P_N) (*A–D*), stomatal conductance (g_s) (*E–H*), transpiration rate (*E*) (*I–L*), and water-use efficiency (WUE) (*M–P*) of 28 species after 1 mm and 6 mm rainfall events at the southeastern edge of the Junggar Basin, northwest China, 2012. *Different letters* attached to columns indicate significant differences among treatments (P<0.05). Error bars represent standard errors of the mean, n = 5.

Leaf water uptake capacities: Leaves from the four plant functional types showed different leaf water uptake capacities. MWA and LWC showed similar gradual decline trends for the four functional types, with the maximum value occurring in the short-life-cycle herbs and the minimum value in the phreatophyte shrubs (Fig. 4). The short-life-cycle herb, *C. discoidea*, which is covered with dense trichomes, had the highest MWA (30.6 mg cm^{-2}) and LWC (81.6%). *H. halodendron* and *H. caspica* (phreatophyte shrubs) have smooth leaves and the lowest MWA (1.55 mg cm^{-2}) and LWC (3.27%). Compared to the plants with no trichomes, plants with sparse and dense trichomes showed a notable increasing trend in LWC (Fig. 5*B*). These results suggested that more water was absorbed by hairy leaves than non-hairy leaves.

Regression analysis: P_N was significantly related to g_s in control NR and 1SR treatments [NR: y = 37.35 x + 0.82 (R^2 = 0.927), 1SR: y = 40.35 x – 3.75 (R^2 = 0.553), and 6SR: y = 10.65 x + 10.13 (R^2 = 0.016), Fig. 6*A*]. For long-life-cycle herbs, the relationships between P_N and g_s were weak [NR: y = 6.65 x + 7.34 (R^2 = 0.144), 1SR mm: y = 4.66 x + 8.05 ($R^2 \approx 0$), and 6SR: y = 5.27 x + 10.73 (R^2 = 0.114), Fig. 6*B*]. No linear relationship was found for non-phreatophyte and phreatophyte shrubs (Fig. 6*C*,*D*).

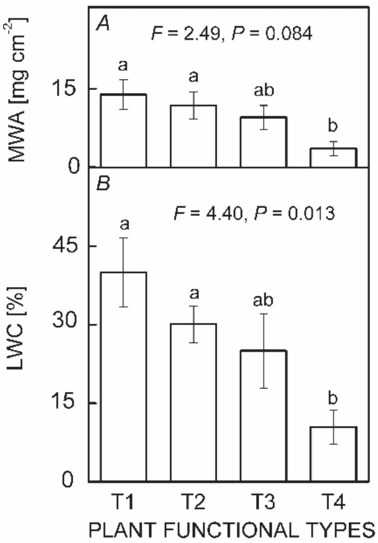

Fig. 4. Maximum water absorption (MWA) (*A*) and leaf water content (LWC) (*B*) of the four plant functional types (mean ± SE). *Different letters* attached to columns indicate significant differences among the different plant functional types (P<0.05). Error bars represent standard errors of the mean, n = 8, 9, 6, and 5 for short-life-cycle herbs (T1), long-life-cycle herbs (T2), non-phreatophyte shrubs (T3), and phreatophyte shrubs (T4), respectively. The data were collected in 2012.

Discussion

The results of the correlation analysis suggested that P_N was more dependent on g_s under water deficit conditions. The non-phreatophyte shrubs had significantly higher g_s-relative effectiveness values (71.8%) than the other three functional types (less than 50%). This was mainly because of the small change in g_s even after 6SR rainfall. The roots of non-phreatophyte shrubs are located between the herb roots and the phreatophyte shrub roots (Xu and Li 2009). Therefore they face a fierce competition from herbs for shallow water and are far away from the groundwater. Thus non-phreatophyte shrubs suffer the greatest water deficits in this ecosystem. In order to reduce water loss from transpiration, the non-phreatophyte shrubs had uniformly lower g_s values and significantly higher WUE than the other functional types. Although WUE-relative effectiveness for all functional types was greater than 50%, it was 76.5% higher in the phreatophyte shrubs. In many phreatophyte shrub species, the 1SR application reduced WUE to a level that was similar to that after 6SR. The results implied that even a 1SR event was meaningful to phreatophyte shrubs.

Trichomes played a very important role in sustaining water conditions in the desert plants. The leaves of most herbs (12 of 17) had either sparse or dense trichomes. In general, a sandy soil retains a lower water content compared to a silty clay-loam soil. Correspondingly, eight of the nine species that live in the silty clay-loam soil had non-trichome leaves (*K. caspia* had sparse trichomes). The high trichome density helped plants to avoid excessive water loss under water stress conditions (Fu *et al.* 2013). Therefore, *E* of many species increased after rainfall treatments. Even 1 mm of rainfall could provide a relatively wet micro-environment for surrounding photosynthetic cells; there would be also a change in the water vapor pressure of the air inside and outside the leaf (Asbjornsen *et al.* 2011). The ($T_{air} - T_{leaf}$) in 16 of the

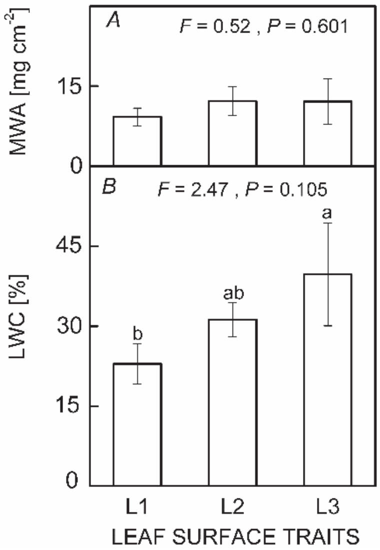

Fig. 5. Maximum water absorption (MWA) (*A*) and leaf water content (LWC) (*B*) for the different leaf surface traits (mean ± SE). *Different letters* attached to columns indicate significant differences among different leaf surface traits (*P*<0.05). Error bars represent standard errors of the mean, *n* = 16, 6, and 6 for no trichomes (L1), sparse trichomes (L2), and dense trichomes (L3), respectively. The data were collected in 2012.

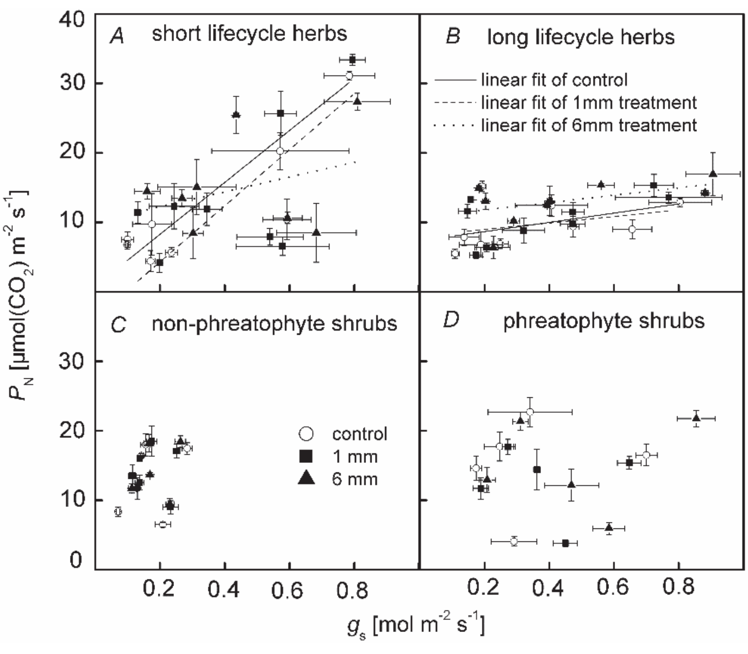

Fig. 6. Relationship between net photosynthetic rate (P_N) and stomatal conductance (g_s) for each functional type. Error bars represent standard errors of the mean, *n* = 5. The data were collected in 2012.

28 species were significantly changed by the rainfall application improving plant water retention and water absorption. The results also showed that the plants without trichomes could benefit from small rainfall events.

In addition, the F_v/F_m for all species stayed within the optimal range (around 0.8), and this implied that the plants could utilize small rainfall events even if they were not under severe water stress.

Conclusion: The 1 mm rainfall events had a limited, but positive influence on desert plants. For most herbs, P_N, g_s, and E were stable or increased after 1 mm rainfall. The WUE values were generally less affected. For shrubs, the P_N responses varied among species, but the g_s and E values were unchanged or increased. The WUE values were either constant or significantly reduced to levels that were similar to those after 6 mm rainfall. Most herbs with trichomes took up water through their leaves during small rainfall events. Meanwhile, the non-hairy shrubs could benefit from the micro-environment humidity provided by small rainfall events. Thus, small rainfall events could affect leaf-level gas exchange and it may have water balance implications at the individual plant or functional type levels.

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