

Photosynthesis responses of endemic shrubs of Taklimakan Desert to adverse temperature, humidity and radiation

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Under the native habitat conditions, the seasonal gas exchange characteristics of two natural endemic plant species, *Calligonum taklimakanensis* B.R. Pan & G.M. Shen and *Tamarix taklamakanensis* M.T. Liu, which are located in the hinterland of the Taklimakan Desert, are measured and compared by Li-6400 photosynthesis system. The results indicate that temperature (°C), solar radiation (PAR), soil water content (SWC), and other environmental factors have obvious seasonal variations and the gas exchange characteristics of two plants have different changes in different growing seasons. For *C. taklimakanensis*, both in July and September, its daily changes of net photosynthetic rate tend to be obvious double peak curve, but in July its peak appeared earlier. Besides its maximum net photosynthetic rate (P_{max}), apparent quantum efficiency (Φ), range of effective photosynthetic radiation significantly less than that in September. Moreover, its water use efficiency (WUE) in July was also lower than that in September due to the higher transpiration rate (T_r). For *T. taklamakanensis*, although its daily change of net photosynthetic rate is a single peak curve in September, its peak time has not changed, and except that its WUE is higher in September like *C. taklimakanensis*, the maximum net photosynthetic rate (P_{max}), apparent quantum efficiency (Φ), light saturation point, and range of effective photosynthetic radiation has not changed or slightly declined. That is to say *C. taklimakanensis* select a season that habitat was better (like September) to progress relative effectively photosynthesis accumulation, in contrast, *T. taklamakanensis* still keep a relatively stable photosynthesis rate in different growth seasons. The difference of gas exchange characteristics of the two plants in different seasons shows that adaptation strategies of the two plants to extreme conditions in desert are different. Besides, both the higher photosynthetic accumulation rate and the higher water use efficiency in September also indicate that these two endemic desert shrubs possess the abilities and strategies to make the best of limited natural resources.

adversity, *Calligonum taklimakanensis*, *Tamarix taklamakanensis*, gas exchange characteristics, adverse environments, adaptive strategies, desert plant

As global climate changed and a series of environmental problems aggravated, such as high temperature, drought, land desertification, salinization, biodiversity loss, the plant ecophysiology characteristics under the adverse environment have become focused problems^[1–3].

In recent years, many scholars, from different views like anatomy, physiology, biochemistry and ecology,

Received September 2, 2007; accepted June 2, 2008

doi: 10.1007/s11434-008-6009-0

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Supported by Knowledge Innovating Project of the Chinese Academy of Sciences (CAS) (Grant No. KZCX3-SW-342-02), the Key Project of Ministry of Science and Technology of China (Grant No. 2004BA901A21-1), Key Programs for Science and Technology Development of Xinjiang (Grant No. 200633130), Major Program for Science and Technology of Xinjiang (Grant No. 200733144-2) and Knowledge Innovation Project of the Chinese Academy of Sciences (Grant No. KZCX3-SW-342-02)

investigated comprehensively physioecological response of plants to special environmental conditions: drought^[4-6], salinization^[7-9], high temperature^[10-12] and strong solar radiation^[13-15].

Because the plant photosynthesis is the most important chemical reaction on the earth, and is also one of the most sensitive reactions of plants to environmental conditions, and its characteristics can express growth status and habitats of plants objectively and accurately. Therefore, the response and adaptation of photosynthetic characteristics under adversity stress became a key and hotspot field in plant ecophysiology study. A large number of studies found that adaptation ways of plant photosynthetic characteristics to adversity stress were varied. Different plants under stress can use a great variety of means to deal effectively with the disadvantage effects of special circumstances on growth, for instance, through increasing the potential photosynthetic capacity, improving water use efficiency, accumulating and distributing of photosynthetic products effectively, self-adjusting transpiration rate and stomatal open extent, and choosing a favorable time to progress photosynthesis rapidly in order to take full advantage of limited resources^[16-22].

Therefore, it was clarified further that adaptation mechanisms of the plant physioecological, and particularly the changes mechanism of photosynthetic gas exchange characteristics under adverse habitat conditions will provide a theoretical basis for us to deal effectively with environmental deterioration and use reasonably plant resources, and especially to understand the physioecological adaptation mechanisms of the desert plants to extreme environmental conditions. It has important scientific guidance significance in studying processes of ecophysiological, safety of ecosystems and the restoration and reconstruction of damaged ecosystems of arid area ecosystems^[3].

The Taklimakan Desert is one of world-famous adverse environment regions^[23] and its natural conditions are extremely harsh, with high temperature, low humidity, high radiation, and more blown sand. Thus, only endemic plant species such as *Calligonum taklimakanensis* B. R. Pan & G. M. Shen, *Tamarix taklimakanensis* M.T. Liu and *Cynanchum kashgaricum* Liou f. are distributed in this area. During the long-term adaptation process, these plants all had biological characteristics of being photophil, resisting atmospheric drought,

and abiding high temperatures, wind erosion, sand buried and saline environment, and evolved the survival rules of adaptation deserts habitats, using fully and effectively all kinds of resources and maintaining the fastest growth and the least consumption. However, the number of the existing population of these plants was very small because their natural reproductions were very difficult under adverse habitat and limitation of resources conditions. Therefore these plants have been the rare species in China^[24]. Particularly, *T. taklimakanensis* has become gradually endangered species and been embodied by China Plant Red Data Book as the national third-level protected plants^[25], and *C. taklimakanensis* is even a new species discovered and named only in recent years^[26]. However, due to abominable of environmental conditions and short of deeply study, knowledge of them is still very scarce until now, and they were still only superficial or even in the exploring stage. In recent years, with global changed lasting and oil-gas resources of Tarim Basin exploited cosmically, the native habitats of these natural endemic plants were disturbed to different extents. In order to better protect and use these rare and endemic plants, it is necessary that their ecophysiology characteristic was studied deeply through modern experiment means.

The aim of this study is to understand photosynthetic physioecological characteristics of both *T. taklimakanensis* and *C. taklimakanensis*, the natural endemic shrub in the hinterland of desert, and furthermore explore and understand adaptation mechanism and strategy for these two endemic shrubs to the extreme environment of desert hinterland by measuring the response of their seasonal gas exchange characteristics to environmental factors such as temperature, radiation, soil moisture and air relative humidity, and then to provide the theoretical support for protecting effectively and using sustainably natural and rare species under adverse environments.

1 Study area

The natural conditions of Taklimakan Desert are extremely harsh with annual mean temperature of 12.4°C, extreme minimum temperature of -20.2°C, extreme maximum temperature of 45.6°C, $\geq 10^\circ\text{C}$ annual accumulated temperature of 4 621.8°C, frost-free period of 283 d, average annual precipitation amount of 11.1 mm,

annual average evaporation of 3 638.6 mm, annual average relative humidity of 29.4%, annual sunshine hours of 2 571.3 h, annual average wind speed of $2.5 \text{ m} \cdot \text{s}^{-1}$, and wind season is from April to August with average wind speed of $3.2 \text{ m} \cdot \text{s}^{-1}$, maximum instantaneous wind speed of $24 \text{ m} \cdot \text{s}^{-1}$ and frequently gale^[27]. Since surviving and reproducing of the natural vegetation are greatly limited by adverse environmental conditions, species and numbers of plants are very limited in this region. There are only natural vegetations of 12 species in 9 families in hinterland areas, which are not affected by rivers^[28].

The study area is in the hinterland of the Taklimakan Desert ($40^{\circ}02.823'N$, $84^{\circ}18.272'E$), and the sample spots are located in a lowland among dunes, and surrounded mostly by tall and flow complex dune with flowed aeolian sandy soil; average groundwater depth of 1.3 m, salinity of around 5.1 g/L, and the higher concentration salt ions: Cl^- , Na^+ , K^+ , SO_4^{2-} , HCO_3^- , Mg^{2+} . The major natural distribution plants are *T. taklamakanensis*, *C. taklimakanensis* and some associated perennial herbs, such as *Cynanchum kashgaricum* and *Hexinia polydichotoma*.

2 Materials and methods

2.1 Plots and sample strains

Plots were chosen in inter-dune plains where the number of vegetation was relatively more centralized than other places in the hinterland of the desert. In April 2006, observation well was dug in advance in the plot. Then, 2 826 m² large observational plot was designated, with the well as the centre and 30 m as a radius, in which 5 *T. taklamakanensis* and 5 *C. taklimakanensis* were selected randomly, which have relatively healthy and similar growth, and made a mark.

2.2 Soil moisture and underground water

Within two meters around observation well, three points were chosen randomly to drill soil sample stratified which start from the surface and take 20 cm as a layer, until contact with groundwater, and is final total nine layers. The soil samples were weighed immediately after bringing back to get wet weight, and then dried at 105°C until constant weight by oven, and weighed dry weight after cooling. Then weight percentage of water content of soil samples of each layer was calculated.

Groundwater level was recorded every time, and the water samples of observation well were collected and brought back to laboratory for analyzing water quality, such as, salinity, mineralization, hardness and content of water-soluble salt ion.

2.3 Plant gas exchange parameters

The seasons in Taklimakan Desert is changing very significantly. Considering plant growth cycle and the climate change, summer (July) and autumn (September) were chosen to measure plant gas exchange parameters because there are less wind-blown sand as well as obvious difference in temperature, humidity and intensity of radiation in these two seasons. Mature leaves or assimilation twigs were chosen on the top of new branches from every sample individual chose which exposed to the sun, and then their gas exchange characteristics was measured by using Li-6400 photosynthesis system (LI-COR, Lincoln, USA), in clear and calm weather.

(i) Daily change. The observations in vivo was carried out every two hours in the period from 08:00 to 20:00 in a fine day both in mid July and late September 2006, using standard chamber ($2 \text{ cm} \times 6 \text{ cm}$) which both upper and lower are transparent, for measuring and recording physiological index of gas exchange: net photosynthetic rate (P_n), transpiration rate (T_r), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), and at the same time, recording the micro-meteorological parameters: photosynthetically available radiation (PAR), air temperature, leaf temperature, air relative humidity, ambient CO_2 concentration (C_a) and so on. Both *T. taklamakanensis* and *C. taklimakanensis* have 5 replications respectively in every observation.

(ii) Light response curve. Light response curve was measured using 6400-02B LED Light Source chamber ($2 \text{ cm} \times 3 \text{ cm}$). Measurement temperature was set up a constant of 30°C according to environment climate characteristics of high temperature and high radiation of the hinterland of the desert. CO_2 concentrations was taken the ambient concentration and ensured its changes range was not more than one day normal fluctuations. Light intensity decreased gradually at 11 grads from $2000 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ to $0 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and the maximum, minimum time waiting for the balance and the maximum allowable deviation scope was set up. Afterwards, data were read and record by automatic observation procedures of the instrument. Every kind of plant

measured repeated 3 times.

The relevant parameters of light response curve were calculated by non-rectangular hyperbolic model^[29] and derivation calculus to quadratic equation fitted between P_n and PAR^[30]:

$$P_n = \frac{\phi \text{PAR} + P_{\max} - \sqrt{\{(\phi \text{PAR} + P_{\max})^2 - 4K \times \phi \times \text{PAR} P_{\max}\}}}{2k} - R_{\text{day}}$$

where P_n is net photosynthetic rate; Φ is the apparent quantum efficiency; P_{\max} is the maximum photosynthetic rate; K is convexity; R_{day} is dark respiration coefficient; PAR is photosynthetically available radiation.

Namely, the maximum net photosynthetic rate (P_{\max}), the apparent quantum efficiency (Φ), convexity (K) and other model parameters were calculated first by model stepwise regression analysis, and then beeline equation of net photosynthetic rate when photosynthetically available radiation (PAR) was below $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was derived, and its intersection with the X-axis is the light compensation point, and then derivation calculus to the quadratic equation fitted P_n and PAR is light saturation point^[30].

2.4 Measurement of leaf area

Although leaves or twigs of *T. taklamakanensis* and *C. taklimakanensis* are irregularly shaped assimilation organ, their stomata is evenly distributed on the surface, and so put them evenly in leaf chamber when measured to avoid each other overlaying and in order diffuse light can be full of the whole leaf chamber, and all leaf surface exposed in the leaf chamber can accept equal light-shine, thus, total surface area of all folioles or assimilation twigs can be seen as photosynthetic effective area^[19]. After photosynthetic effective area and physiological parameters measured, fixed observation leaves or assimilation twigs were cut down and scanned, their actual leaf surface areas were calculated by area analysis software Delta-T Scan (Cambridge, UK). Finally, actual physiological parameters were calculated in accordance with the actual photosynthetic effective area.

All data were handled by the Microsoft office Excel

and then analyzed statistically by SPSS13.0 for windows.

3 Results

3.1 Environmental factors in different growing seasons

In different seasons, the observation results of the groundwater level and water quality showed that: the level and quality of water overall were changed insignificantly, except the total alkalinity increased slightly, the remaining indicators were descend a little in September compared with that in July (Table 1); and the soil moisture changed obviously in nine soil layers from surface to 160 cm, as shown in Figure 1, and from 20 cm below the surface, in September, soil moisture of these soil layers were higher than that in July, and its differences reached a extreme significant level ($t = -4.91$, $P = 0.001$).

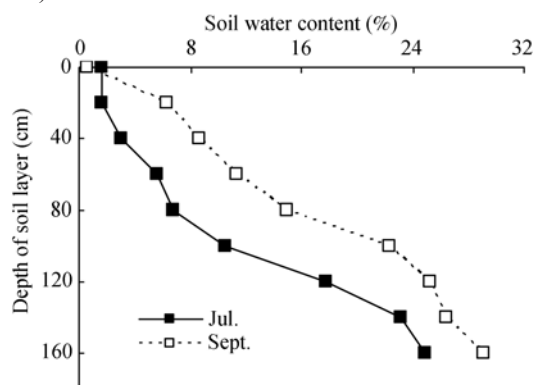


Figure 1 Change of plots soil moisture in different growing seasons.

During the same period, meteorological observations of microhabitat showed: in July and September, the maximum values of environmental factors, such as temperature, relative humidity and radiation are 46.6°C , 38.8°C , 5.81%, 6.31%, $1985 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and $1813 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ respectively, and the mean values are also reached $38.^\circ\text{C}$, 31.1°C , 12.3%, 14.1%, $1289 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and $1053 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the observation period from 8:00 to 20:00 (Figure 2). So both in summer

Table 1 Change of plots groundwater level and water quality in different growing seasons

	Groundwater level (m)	Total alkalinity (mmol/L)	Total hardness (mmol/L)	Mineralization (g/L)	Salinity (g/L)	Major salt ion content (g/L)				
						Cl^-	$\text{Na}^+ + \text{K}^+$	SO_4^{2-}	HCO_3^-	Mg^{2+}
July	1.28	3.24	18.99	5.19	5.05	1.956	1.463	1.164	0.198	0.178
September	1.31	3.64	17.94	5.08	4.90	1.881	1.425	1.117	0.222	0.170

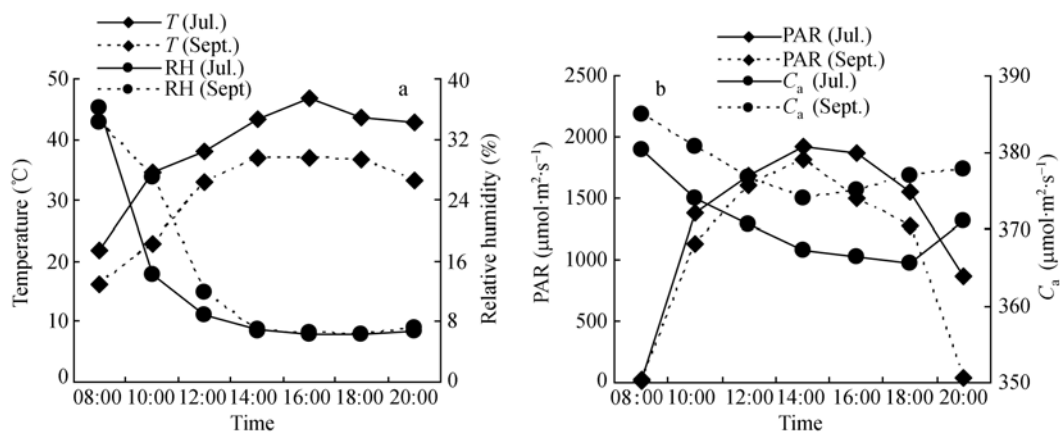


Figure 2 Changes of plot environmental factors in different growing seasons.

and fall, the desert hinterland have shown a significantly climate characteristics of high-temperature, low humidity and high radiation, and the habitat in July is harsher than in September. Test of significance of difference showed that, in different seasons, except for the change of air relative humidity was not significant ($t = -1.106$, $P = 0.311$), radiation intensity reached a significant level ($t = 2.674$, $P = 0.037$), and the seasonal differences of temperature even reached an extremely significant level ($t = 8.451$, $P < 0.001$), moreover, the ambient CO₂ concentrations also have extremely significant level ($t = -10.2$, $P < 0.001$).

3.2 Gas exchange characteristics in different growing seasons

The daily changes process of gas exchange indicated that in different months *C. taklimakanensis* had higher net photosynthetic rate than *T. taklamakanensis*, and had obviously phenomenon of photosynthesis midday depression that is the net photosynthetic rate dropped significantly around 14:00, and showed a double-peak curve change, but the appeared time of the first of peak in different seasons is different, such as in July is 10:00, while in September was moved late to 12:00; and *T. taklamakanensis* compared with *C. taklimakanensis* only in July put up slightly double-peaks curve change and the peak before the lunch break presented around 12:00, but in September from 10:00 to 18:00 *T. taklamakanensis* always maintained a relatively stable net photosynthetic rate (Figure 3a).

Stomatal conductances of two shrubs in different seasons were both largest between 10:00 to 12:00. However, unlike net photosynthetic rate of *T. takla-*

makansensis which was lower than that of *C. taklimakanensis*, the stomatal conductance of *T. taklamakanensis* was significantly greater than *C. taklimakanensis* both in summer and fall (Figure 3b).

Figure 3c showed that transpiration rate of the two plants in July was significantly higher than that in September, and their peak also appeared in July (16:00) posterior to in September (14:00), and transpiration rate of *T. taklamakanensis* in all periods of the daily course was almost higher than that of *C. taklimakanensis*, especially in July. The differences of intercellular CO₂ concentration of daily change process of the two plants were also very obviously, corresponded to the smallest of the open extent of the two plants stomatal in the early morning and evening (Figure 3b), intercellular CO₂ concentration of their were the highest in that time, and in the rest periods of a day, the changes of intercellular CO₂ concentration were relatively smooth, but in the period from 10:00 am to 18:00 pm, the intercellular CO₂ concentration of *T. taklamakanensis* was far higher than that of *C. taklimakanensis* (Figure 3d).

3.3 Photosynthesis ability in different growing seasons

Light response curve of the two plants was calculated and analyzed by non-rectangular hyperbola model and the results showed that the potential photosynthesis capacities of them were different in July and September. The maximum net photosynthetic rate (P_{max}) and apparent quantum efficiency (Φ) of *T. taklamakanensis* had not big seasonal variety, and these in September were only slightly higher than that in July; but these of *C. taklimakanensis* increased very substantially from July to September like the maximum net photosynthetic rate

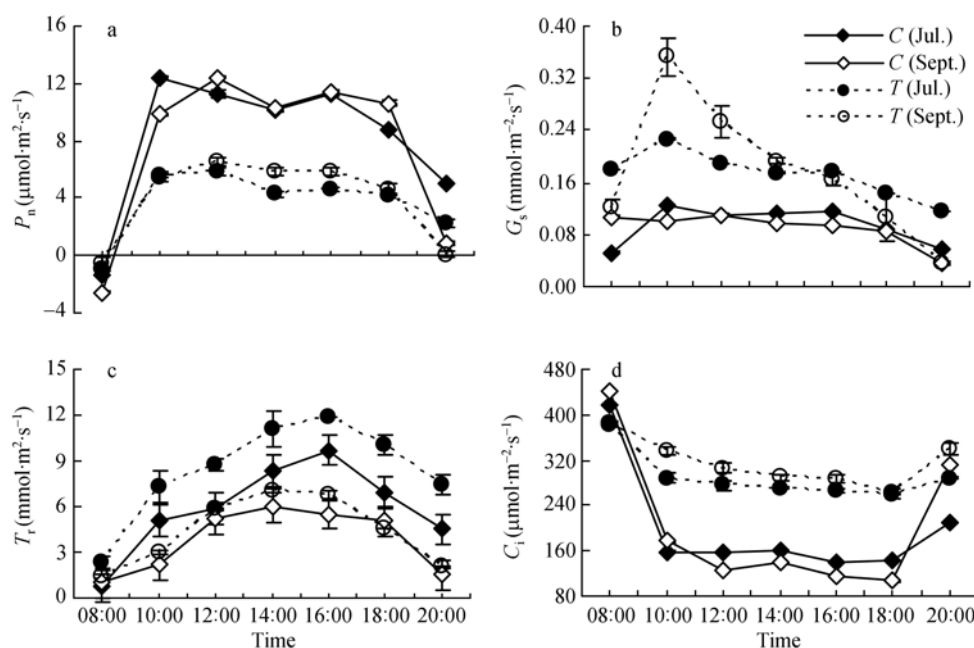


Figure 3 Changes of the photosynthesis parameters of two plants in different growing seasons.

(PAR) increased from $10.78 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ to $17.53 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and the apparent quantum efficiency (Φ) increased from 0.013 to 0.023 (Table 2). It was indicated that in September the capacity of photosynthesis of *C. taklimakanensis* is substantial increased, but that of *T. taklamakanensis* is unchanged essentially.

Table 2 Changes of maximum net photosynthetic rate (P_{max}), convexity (K), the apparent quantum efficiency (Φ) and dark transpiration coefficient (R_{ady}) and light saturation point (LSP) and light compensation point (LCP) of two plants in different growing seasons

Species	<i>T. taklamakanensis</i>		<i>C. taklimakanensis</i>	
	Jul.	Sept.	Jul.	Sept.
P_{max} ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	10.17	10.45	10.78	17.53
K	0.52	0.81	0.94	0.68
Φ ($\text{mol} \cdot \text{mol}^{-1}$)	0.016	0.018	0.013	0.023
R_{ady} ($\text{mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	1.83	1.58	1.69	1.68
LCP ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	124.6	89.7	120.9	77.5
LSP ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	1761.8	1348.4	1410.6	1796.1

Though ANOVA, *C. taklimakanensis*' determination coefficient of light curve and the model both in July and September are 0.998 ($R^2 = 0.998$), but *T. taklamakanensis*' in July is 0.998 ($R^2 = 0.998$) and that in September is 0.996 ($R^2 = 0.996$).

The similar trend has also appeared in light saturation point (LSP) and light compensation point (LCP) of the two plants. *C. taklimakanensis*' light compensation point fell from $120.9 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in July to $77.5 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in September, and its light saturation point rose from $1410.6 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in July to 1796.1

$\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in September, and its increase of light saturation point reached $385.5 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ from July to September. However, during the same period, *T. taklamakanensis*' light saturation point decreased by $413.4 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. That light use ability of two plants showed significant differences, and in September its light compensation points were more obvious decline and its capacity of using low light has increased.

3.4 Water use efficiency in different growing seasons

Water use efficiency (WUE) in different growing seasons was also changed. The daily average and maximum water use efficiency of *C. taklimakanensis* is far higher than that of *T. taklamakanensis* (Table 3) that showed accumulation capacity of photosynthetic carbon assimilation of *C. taklimakanensis* was significantly stronger than that of *T. taklamakanensis* under the same habitat. In terms of the same species, compared with July, in September the average water use efficiency of *C. taklimakanensis* and *T. taklamakanensis* increased 46.7% and 91.8% respectively, and the daily maximum water use efficiency increased 86.9% and 132.1% re-

Table 3 Compared WUE of two plants in different growing seasons

Species	Ave. WUE		Max. WUE	
	($\mu\text{mol CO}_2 \cdot \text{mmol}^{-1} \text{H}_2\text{O}$)		($\mu\text{mol CO}_2 \cdot \text{mmol}^{-1} \text{H}_2\text{O}$)	
	Jul.	Sept.	Jul.	Sept.
<i>T. taklamakanensis</i>	0.49	0.94	0.78	1.81
<i>C. taklimakanensis</i>	1.52	2.23	2.44	4.56

spectively. The results also showed that two plants in September have both accelerated to some extent the effectively photosynthetic accumulation with the seasonal changes of environmental conditions.

4 Conclusions and discussions

As endemic shrubs in the Taklimakan Desert, both *T. taklamakanensis* and *C. taklimakanensis* have high adaptation ability to the adverse environment of the desert^[28]. Particularly, in July, the harshest environmental conditions, both of them can maintain effectively normal growth. However, through studying their gas exchange characteristics found that the strategies of adapting extreme environmental conditions of two species are different.

4.1 Response of gas exchange to adverse environment

C_4 plants are usually considered to be distributed mostly in high-temperature and arid region, because it can adapt to that environment better^[31]. However, in this study, *C. taklimakanensis* as a typical C_4 desert plant^[32], but its responses to the changes of the desert adverse environmental conditions are more sensitive than *T. taklamakanensis*, a C_3 plant. *C. taklimakanensis* chose the way of maintaining only necessary growth that is reducing the growth speed and processing photosynthesis midday depression to withstand the adverse environments, especially, the stress of high temperature, low humidity and strong radiation at noon, in July, the environmental conditions are more harsher. During photosynthesis lunch break, *C. taklimakanensis*' stomatal limit value (L_s) reduced, but its intercellular CO_2 concentration (C_i) increased and therefore it could be considered that lunch break caused by the non-stomatal limiting factors according to the method of Berry and Downton^[33,34]. That is to say, adverse environmental conditions have affected the photosynthetic activity of the leaf cells, and thereby debased the plant's capacity of photosynthetic carbon assimilation, therefore *C. taklimakanensis*' maximum of net photosynthetic rate and the apparent quantum efficiency were significantly lower than the other results of *Calligonum* in Su's and Deng's studies^[32,35].

As to the transpiration rate, although *Calligonum* is generally considered as desert plant which is provided with the characteristic of high photosynthesis and low

transpiration^[35], in this study, *C. taklimakanensis* always has a high transpiration rate, which, to a certain extent, restricts the accumulation of photosynthesis product of *C. taklimakanensis*, but it may be also a necessary strategy formed through long-term adaptation to withstand initiatively adverse environmental. Gong's study have also suggested that all of desert plant have not low transpiration characteristic, especially, *Calligonum* just has a high transpiration rate under high temperature and low humidity environment conditions^[6].

As a C_3 photosynthesis plant, *T. taklamakanensis*' net photosynthetic rate is significantly lower than *C. taklimakanensis*', but *T. taklamakanensis*' degree of sensitivity to the environment is far smaller than *C. taklimakanensis*'. Not only its daily process of the net photosynthetic rate shows only weakly double-peak curve, but also its apparent quantum use efficiency had maintained a relatively high level in July. These showed that *T. taklamakanensis* still have a strong ability to assimilate CO_2 under extreme environments in July, but its accumulation of photosynthesis efficiency is very low and its daily average water use efficiency is only $0.49 \mu mol CO_2 \cdot mmol^{-1} H_2O$ (Table 3), which is because *T. taklamakanensis* chose the way of high transpiration rate to resist actively high temperature and low humidity climate of desert (Figure 3).

During photosynthesis lunch break, its stomatal limit value (L_s) increased, but its intercellular CO_2 concentration (C_i) decreased, which showed that photosynthetic activity of leaf cells of *T. taklamakanensis* have been not affected by the environmental factors at noon. *T. taklamakanensis* is only by adjusting open and close of the stomatal and transpiring plentifully to resist the impact of high temperature and low humidity, therefore *T. taklamakanensis* has more stronger tolerance ability to extreme environments of the hinterland of desert, which is also one of the important reasons that *T. taklamakanensis* can become the most widely distributed natural plants in the Taklimakan Desert^[28].

4.2 Adaptation of potential photosynthetic capacity to the adverse environments

In addition, responses of two plants to the adverse environment also express in changes of their potential photosynthetic capacity. Studies about photosynthetic capacity of many desert plants showed that July and August are generally the peak period of plant growth, but

due to the impact of stresses of drought and other adverse environmental factors, plant photosynthesis rate of this period will be lower than that of the time in mature phase, the end of September^[35–37]. Two plants in this study also showed a similar phenomenon. But the environmental conditions of the hinterland of the Taklimakan Desert is much harsher than that of other areas, so it is completely possible that the accumulation of plant photosynthesis was impacted and inhibited by more environmental factors. Because compared with July, the environmental conditions in September became better apparently (Figure 2), the potential photosynthetic capacity of *C. taklimakanensis* has raised in large extents (Figure 3, Table 2), which is same as *Haloxylon ammodendron*, another C₄ desert plants, their peak period of photosynthesis will shift backward when they undergo the stress of environmental conditions^[36]. It is indicated that *C. taklimakanensis* like most desert plants is provided with a characteristic that to evaded a harsh environment and made full use of limited resources to accumulate substance.

Compared with *C. taklimakanensis*, *T. taklamakanensis*' photosynthesis rate did impact relatively smaller by environmental factors in July, so in September, the environmental conditions are better, its transpiration rate decreased a little, and except its water use efficiency increased markedly, the others like the maximum net photosynthetic rate, the apparent quantum use efficiency and photosynthetic effective radiation range were not increased and even slight declined. It was showed that *T. taklamakanensis* has maintained a relatively stable photosynthetic capacity at least within the growing season from July to September, and its growth did not affect significantly by the alteration of environmental conditions, and it is also reflected from another point of view *T. taklamakanensis* have very strong adaptation ability to adverse environmental.

4.3 Response of water use efficiency to adverse environments

Many studies concluded that desert plants have higher water use efficiency, particularly, when water is scarce, for ensuring water use effectively and withstanding

drought stress^[1,4,38]. But in fact, desert plants often took on very high transpiration rate to reduce leaf temperature in order to prevent its leaves from burning by high temperature^[20,39]. Liu^[40] believed that only succulent xerophytes will maintain low transpiration rate and the transpiration rate of some less-succulent xerophytes was even more than that of mesophyte, and xerophyte only in the drought period maintained a low transpiration to save water. Water use efficiency of both *C. taklimakanensis* and *T. taklamakanensis* in this study, was lower than that of the relevant research results of other desert area plants^[35,36,41], because in the entire growing season the two species had always maintained a high transpiration and need a lot of water to withstand the high temperatures hurt its leaves. The difference between *C. taklimakanensis* and *T. taklamakanensis* lie in that although capacity of tolerance extreme environment of *T. taklamakanensis* was more greater than that of *C. taklimakanensis*, due to the different ways of photosynthetic carbon assimilation and the differences of plant own transpiration characteristic, water use efficiency of *C. taklimakanensis* has always been higher than that of *T. taklamakanensis*, but when environmental conditions were improved the elevated extent of water use efficiency of *T. taklamakanensis* was greater than *C. taklimakanensis*. It is fully showed that environmental factors have a marked impact not only on the ability of plant photosynthesis, but also on the ability of water consumption and water use of plants. And such a great effect, from another perspective, also reflected under the current growth environment that although the soil moisture have a significant difference between summer and fall, it do not affect the need of water consumption of plant transpiration, especially in summer, plants instead can always maintain more higher transpiration level. That is said that in the natural vegetation distribution area, groundwater and soil moisture are fully able to meet the need of water consumption of plants growth and there is no water scarceness or drought stress that is also the most important reasons why the natural vegetation still can survive and multiply under such harsh environmental conditions in the hinterland of the Taklimakan Desert.

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