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Effects of elevated temperature on photosynthesis in desert plant *Alhagi sparsifolia* S

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Abstract

Most plants growing in temperate desert zone exhibit brief temperature-induced inhibition of photosynthesis at midday in the summer. Heat stress has been suggested to restrain the photosynthesis of desert plants like *Alhagi sparsifolia* S. It is therefore possible that high midday temperatures damage photosynthetic tissues, leading to the observed inhibition of photosynthesis. In this study, we investigated the mechanisms underlying heat-induced inhibition of photosynthesis in *A. sparsifolia*, a dominant species found at the transition zone between oasis and sandy desert on the southern fringe of the Taklamakan desert. The chlorophyll (Chl) *a* fluorescence induction kinetics and CO_2 response curves were used to analyze the thermodynamic characters of both photosystem II (PSII) and Rubisco after leaves were exposed to heat stress. When the leaves were heated to temperatures below 43ºC, the initial fluorescence of the dark-adapted state (F_o), and the maximum photochemical efficiency of PSII (F_v/F_m), the number of active reaction centers per cross section (RCs) and the leaf vitality index (PI) increased or declined moderately. These responses were reversed, however, upon cooling. Moreover, the energy allocation in PSII remained stable. The gradual appearance of a K point in the fluorescence curve at 48ºC indicated that higher temperatures strongly impaired PSII and caused irreversible damage. As the leaf temperature increased, the activity of Rubisco first increased to a maximum at 34ºC and then decreased as the temperature rose higher. Under high-temperature stress, cell began to accumulate oxidative species, including ammoniacal nitrogen, hydrogen peroxide (H_2O_2), and superoxide ($O_2^{\cdot -}$), suggesting that disruption of photosynthesis may result from oxidative damage to photosynthetic proteins and thylakoid membranes. Under heat stress, the biosynthesis of nonenzyme radical scavenging carotenoids (Cars) increased. We suggest that although elevated temperature affects the heat-sensitive components comprising of PSII and Rubisco, under moderately high temperature the decrease in photosynthesis is mostly due to inactivation of dark reactions.

Additional key words: *Alhagi sparsifolia* S; elevated temperature; oxidative species; photosystem II; Rubisco activity.

Introduction

According to a recent report by the Intergovernmental Panel on Climate Change (IPCC), if the global temperature increases by 2–3ºC based on the global annual average temperature among 1980–1999, approximately 20 to 30 % of species would be very likely on the edge of extinction in the next hundred years, further resulting in negative effects on the structure and function of our ecosystems (IPCC 2007). Besides, ecosystems of both

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Abbreviations: ABS/CSm – the specific energy fluxes (per cross section) for absorption; Cars – carotenoids; Chl – chlorophyll; C_i – the intercellular CO_2 concentration; DI_o/CSm – the dissipated energy flux per cross section; ET_o/CSm – the electron transport flux per cross section; F_o – the minimal fluorescence of the dark adapted state; F_m – the maximal fluorescence of the dark adapted state; F_v/F_m – the maximum photochemical efficiency of PSII; H_2O_2 – hydrogen peroxide; HO· – hydroxyl radical; OEC – oxygen-evolving complexes; $O_2^{\cdot -}$ – superoxide; RA – Rubisco activase; RCs – the number of active reaction centers per cross section; R_p – the photorespiration rate; PI – leaf vitality index; PSII – photosystem II; ROS – reactive oxygen species; P_N – the rate of CO_2 assimilation. TR_o/CSm – the trapped energy fluxes per cross section.

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frigid and arid regions would likely be more easily impacted by global climate change compared to those of other regions. Additionally, the probability of occurrence of atrocious and extreme weather conditions at parts of these regions would increase. If the current trend of global warming continues, the type of climate is likely going to change from dry-hot to wet-hot in northwest regions of China, and the average annual temperature would present the tendency of rise (Shi and Shen 2003). When leaf temperature increases over the optimal temperature for plant growth, plant physiological metabolism inevitably leads to maladaptation, and the structure and function of photosynthetic proteins deteriorate, further resulting in decline of photosynthetic efficiency and lower net primary productivity.

It has been reported that leaves stressed by high temperatures have a lower rate of photosynthesis, and this was attributed to restriction of mesophyll but not stomatal photosynthetic capacity (Xu and Shen 1998, Zhou *et al.* 2010). Among photosynthetic components, PSII, which plays an important role in the electron transport chain, was found to be the most thermolabile component (Bukhov and Mohanty 1999). Physiological changes in PSII caused by high temperature may include the detachment of the light-harvesting complex, inactivity of reaction centers (RCs), and loss of oxygen-evolving complex (OEC) function, resulting in a decreased probability of electron transport. The influence of high temperature on photosynthetic components may also alter the energy distribution in PSII. For most plants at leaf temperatures above 35ºC, the initial decrease in photochemical efficiency is accompanied by a pronounced stimulation of nonphotochemical Chl *a* fluorescence quenching due to increased energy dissipation as heat (Lu and Zhang 2000, Kaňa *et al.* 2008). An increase in energy dissipation at high temperature reduces the energy available for photochemistry under stress conditions (Mathur *et al.* 2011). Additionally, the generation of reactive oxygen species (ROS) such as $O_2^{\cdot -}$ and H_2O_2 can increase resulting in intracellular accumulation and oxidative stress. It has been reported that $^1O_2$ and $HO^{\bullet}$ are formed during dark incubation of spinach thylakoids at elevated temperatures (Pospíšil *et al.* 2007). Increased ROS levels can induce oxidation of saturated fatty acids in the thylakoid membranes and decrease the saturation of fatty acids, leading to further damage of membrane fluidity. The light reaction stage of photosynthesis occurs in thylakoid membranes, and the fluidity of thylakoid membranes undoubtedly affects the stability of PSII proteins. Excessive accumulation of ROS can also directly denature photosynthetic proteins, thus suppressing photosynthesis.

Simulated global warming experiments on southern African succulent species by Musil *et al.* (2009) revealed that Rubisco activity decreased significantly when experimental temperature exceeded the maximum daytime temperature of 54ºC for 2 h. A reduction in linear electron flow appeared after 42ºC, however, suggesting that PSII may be more vulnerable than Rubisco to elevated temperatures. In contrast at moderately high temperature (10–15ºC above optimum for photosynthesis), the decline of leaf photosynthetic efficiency was chiefly due to the inactivity of Rubisco, while Chl *a* fluorescence signals from PSII were not affected by temperatures that caused significant inactivity of Rubisco (Crafts-Brandner and Salvucci 2000, Haldimann and Feller 2004, Sharkey 2005). Kubien and Sage (2008) found that if the amount of Rubisco decreased but the remaining Rubisco still had a high level of carboxylase activity, then total carboxylation efficiency did not decline at moderately high temperatures. In other words, at moderately high temperature, the decline of photosynthetic efficiency should be caused mainly by the reduced electron transport efficiency at the light reaction stage. Multiple components within PSII are affected by high-temperature-induced stress, so the parameters most indicative of changes in PSII function are still a matter of debate. Many studies have indicated that under various adverse circumstances, a Chl *a* fluorescence parameter like F_v/F_m cannot adequately reflect the physiological changes of PSII. Instead, the technology of Chl *a* fluorescence transient kinetics could provide more reliable information on dynamic changes in primary photochemistry and accurately reflect the extent of heterogeneity in the structure and function of photosynthetic components of PSII in response to changing environments. In addition, fluorescence induction curves have been found to be more sensitive than F_v/F_m for measuring the response of JIP–test parameters to stress, and so could provide a better indication of PSII function (Appenroth *et al.* 2001, van Heerden *et al.* 2004, Oukarroum *et al.* 2007). Adaptable regulation of different photosynthetic components in PSII under varying temperatures would inevitably change the fluorescence yield and alter the numerical values of inflections in fluorescence induction curves.

Plants regulate leaf temperature effectively by transpiration when they are exposed to high temperatures (Kana and Vass 2008). During the summer in arid region, both strong visible light and drought commonly cause decreases or even closure of the leaf stomatal aperture, resulting in decreased transpiration and the consequent increase in leaf temperature which can exceed 37ºC in a short time and trigger stomatal aperture opening. Subsequent transpiration reduces leaf temperature and maintains it between 35–40ºC in *A. sparsifolia*. Therefore, stress induced by high temperature has to be taken into consideration while studying the relation of leaf energy balance of desert species *A. sparsifolia* to both high air temperature and variable leaf temperature. In addition, at elevated temperatures, plants can produce nonenzyme antioxidant species such as vitamin E (Blokhina and Fagerstedt 2010) and ascorbic acid (Horemans *et al.* 2000, Lee *et al.* 2007) that rapidly scavenge ROS. For many photosynthetic processes their down-regulations usually occur above 40ºC (Kaňa *et al.* 2008). Desert plants exhibit short-time reductions in photosynthetic efficiency at peak summer temperatures. Moreover, desert plants cope with temperature extreme beyond the critical point for other species, indicating that these plants must have evolved unique adaptive mechanisms. We sought to determine how the photosynthetic apparatus of *A. sparsifolia* copes with the temperature extremes at the transition zone between the Cele oasis and sandy desert. We proposed the hypotheses that: (*1*) plants grown at different habitats develop different life forms, then for *A. sparsifolia* the responses of characteristic parameters deduced from Chl *a* fluorescence curve to heat stress should differ significantly from other species; (*2*) with increasing temperature, the defense mechanisms in PSII that are usually adopted by plants in the form of dissipation of excitation energies as heat with lower photochemical efficiency over 35ºC could likewise operate in *A. sparsifolia*; (*3*) for *A. sparsifolia* the activity of Rubisco can remain relatively high level under high temperature. In this research the Chl *a* fluorescence and CO_2 response curves were respectively used to analyze the characters of both PSII and Rubisco after leaves were treated with heat. Additionally, we also sought to determine the characters of both photosynthetic pigments and oxidative species accumulation during heat stress.

Materials and methods

Study site: The study area is located at transition zone between Cele oasis and sandy desert on the southern fringe of Taklamakan desert (35°17'55"–39°30'00"N, 80°03'24"–82°10'34"E). The region is classified as a typical continent desert (warm) high-temperature zone. Its summer is torrid and has little rainfall. The average annual temperature is 11.9ºC. The annual temperature reaches as high as 41.9ºC and as low as –23.9ºC. The total annual rainfall is 34.4 mm, but the total annual potential evaporation is approximately 2,595 mm. Total solar radiation is about 604.2 kJ cm^{-2} per year, with average annual daylight hours of 2,697 h. Strong dry and hot winds blow frequently in this region in summer.

Plants: The community of *A. sparsifolia*, which is characterized as a clonal and leguminous plant, distributes widely at the transition zone between Cele oasis and sandy desert, and is one of the important dominant species of the region. Samples of *A. sparsifolia* in the same sampling plot were collected randomly on sunny mornings at 10:30 h (Beijing Time) with low winds on Aug 8 and Aug 9, 2010. Well-growing shoots of the plant were selected randomly, and then washed lightly to remove leaf dust, cut and inserted into damp soil quickly, and covered with a plastic cover. Samples were immediately put into black plastic bags, which contained damp filter papers, and those black plastic bags were then put into a heat-resistant case before being transported to the laboratory. The black plastic bags with samples in them were immersed in water baths for 15 min at temperatures of 30, 38, 43, 48, 53, 58, and 63ºC. The temperature of the water bath changed to these temperatures after the sample was put in it. During the heating process the water bath was also covered to block out light. Twenty intact and mature leaves were used to measure leaf fluorescence and CO_2 response curves after each temperature treatment.

Fluorescence induction transient kinetics: Chl *a* fluorescence for samples exposed to elevated temperature was measured at room temperature (25ºC) using the plant efficiency analyzer (*Handy PEA*, *Hansatech*, King's Lynn, Norfolk, UK). Before the measurements the leaves were darkened adequately for 20 min. Excitation light of peak wave length 650 nm was focused on the surface of the leaf to provide a homogeneous spot about 4 mm in diameter. Light intensity was 3,600 µmol m^{-2} s^{-1} to generate fluorescence curves expanding from F_o to F_m for all the treatments (in this research $F_m = F_p$). The fluorescence curves were prepared using the PEA software. The calculation of fluorescence parameters like RCs and PI were calculated as previously described by Appenroth *et al.* (2001).

Measurements of diurnal changes for temperature, light intensity and F_v/F_m: The measurement of diurnal change in Chl *a* fluorescence was carried out on a sunny day with low winds on Aug 7, 2010. Ten intact and mature leaves turning toward the sun were marked before measurement. Chl *a* fluorescence was measured with adequately dark-adapted leaves (dark-adaptation for 20 min). The measurement was recorded every one hour from 08:00 to 20:00 h along with changes for air temperature and light intensity by a *WeatherHawk500* (*Campbell Scientific, Inc.*, Saltlake, USA).

Gas-exchange measurements: Net photosynthetic rate (P_N) was measured by the open gas-exchange system *Li-6400* (*LiCor*, Lincoln, NE, USA). The CO_2 concentration, temperature and relative humidity were about 400 µmol mol^{-1}, 25ºC, and 50% in the leaf chamber, respectively. The light intensity (1,700 µmol m^{-2} s^{-1}) approached the saturation light intensity. Because the size of measured leaves was too small to meet the settled size like 6 cm^2 in the leaf chamber, so a scanner was used to scan for the measured leaves, and the software of *Delta-T Scan* (*CB50EJ*, Cambridge, UK) read the surface area of measured leaves, then used to calculate the actual values of P_N. Four replicate measurements were performed at each temperature.

After heat treatments for 15 min, intact and mature leaves were adapted for 40 min under weak light intensity of 30 μmol m^{-2} s^{-1}, which was supplied by *6400-02B* LED light source equipped on *Li-6400* (*Li-Cor*, Lincoln, NE, USA). After the weak light adaptation, the program of A-C_i curve was selected along with setting a series of factors in leaf chamber to ensure accuracy of the test, such as the light intensity approaching saturation light intensity, temperature around 25ºC, the rate of gas flow for 500 μmol s^{-1} and the relative humidity of 50% in leaf chamber. The CO_2 concentration gradient was divided into eight levels: 0, 20, 50, 100, 150, 200, 300 and 400 μmol mol^{-1}. Four replicate measurements were done at each temperature. The same treatment for leaf area was mentioned above. The parameter of carboxylation efficiency was deduced from the initial slope of A-C_i curve which only contained the six foremost data points. The photorespiration rate (R_p) was the value when the C_i was defined as zero in A-C_i curve.

Oxidative species and photosynthetic pigments measurements: Intact and mature leaves after elevated temperature treatment were selected, brought into the liquid nitrogen storage, and used to measure their content of oxidative species and photosynthetic pigments. Measurements of ammoniacal nitrogen and $O_2^{\cdot -}$ were done according to Experimental Guide of Modern Plant Physiology (2004). Measurements of H_2O_2 were done according to methods described by Ferguson (1983). The pigments on a basis of fresh mass were extracted with 80% acetone, and determined using the extinction coefficients and equations described by Li (2000).

Statistical analysis: Descriptive statistics was used to calculate averages and standard deviations of the data from each set of replicates. Standard deviations were shown by error lines. The graphs were produced with *Origin 8.0* software (*OriginLab Inc.*, Hampton, USA). The Pearson correlations between photosynthetic pigments were analyzed by *SAS* software (*Institute Inc.*, Raleigh, USA). The fluorescence parameters are calculated according to the JIP test equations by a Biolyzer program developed at the Bioenergetic Laboratory University of Geneva, Switzerland, written by Ronald Maldonado.

Results

Diurnal changes of temperature, light intensity and F_v/F_m: Fluorescence parameter F_v/F_m was lowest at 14:00–16:00 h (Fig. 1*A*), when diurnal temperature and light intensity tended to peak (Fig. 1*B*). Compared to F_v/F_m at 12:00 h, F_v/F_m at 14:00 h decreased by 14.13%. By 18:00 h the F_v/F_m had recovery, almost to the 12:00 h level, indicating that if environmental conditions are favourable (suitable light intensity, temperature, and humidity), PSII activity of *A. sparsifolia* leaves can recover to the normal level in a very short time.

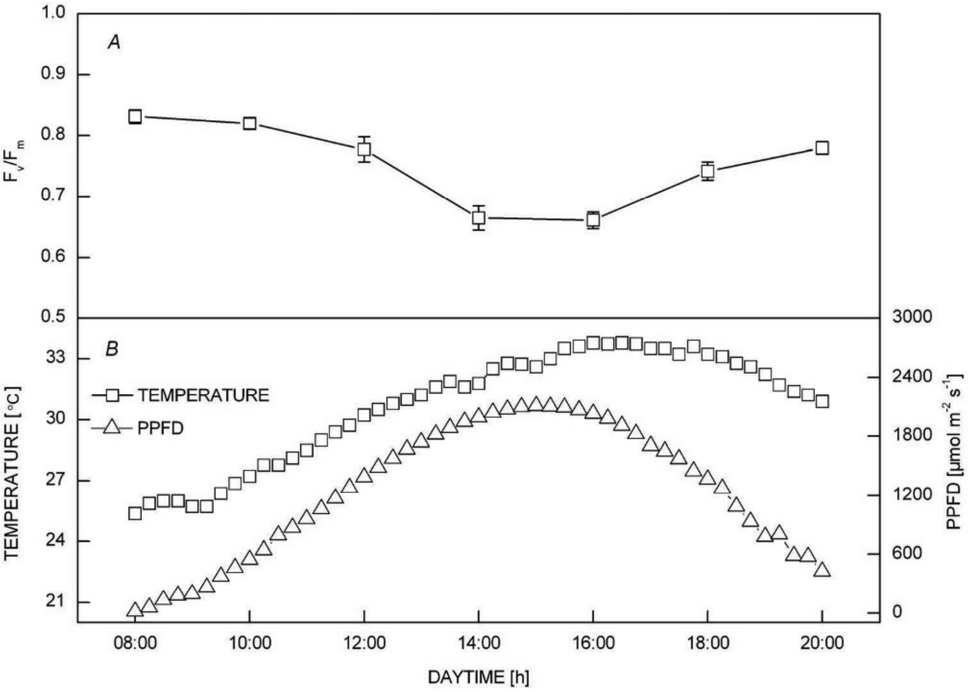

Fig. 1. Diurnal changes of fluorescence parameter like maximum photochemical efficiency of PSII (F_v/F_m) in *A. sparsifolia* leaves (n = 10, ± SD) (*A*) and fluctuations in diurnal temperature and photosynthetic photon flux density (PPFD) at 2 m above ground level (*B*).

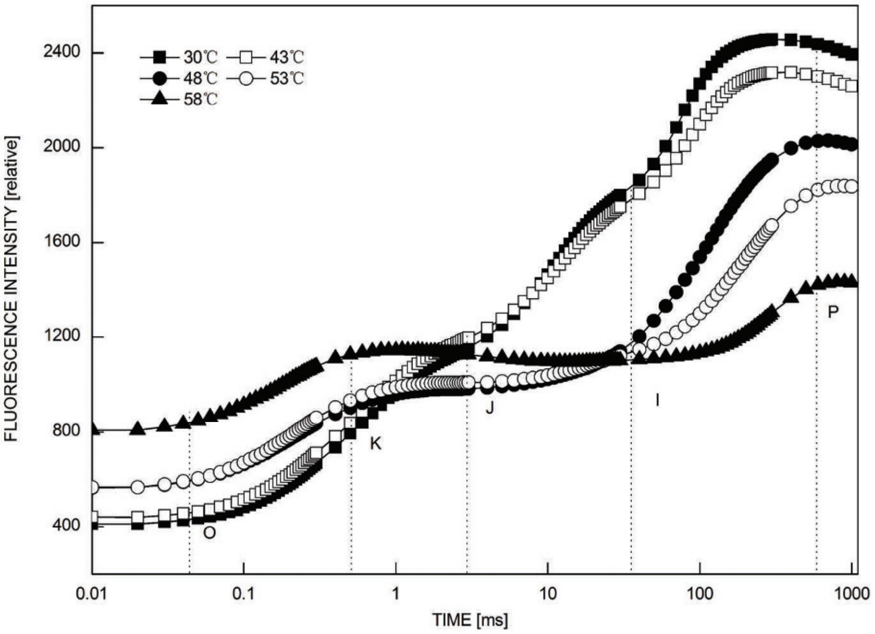

Fig. 2. Changes in Chl *a* fluorescence induction curves in *A. sparsifolia* leaves at elevated temperature for 15 min under 30, 43, 48, 53, and 58ºC ($n = 20$). The x-axis is presented in the log scale.

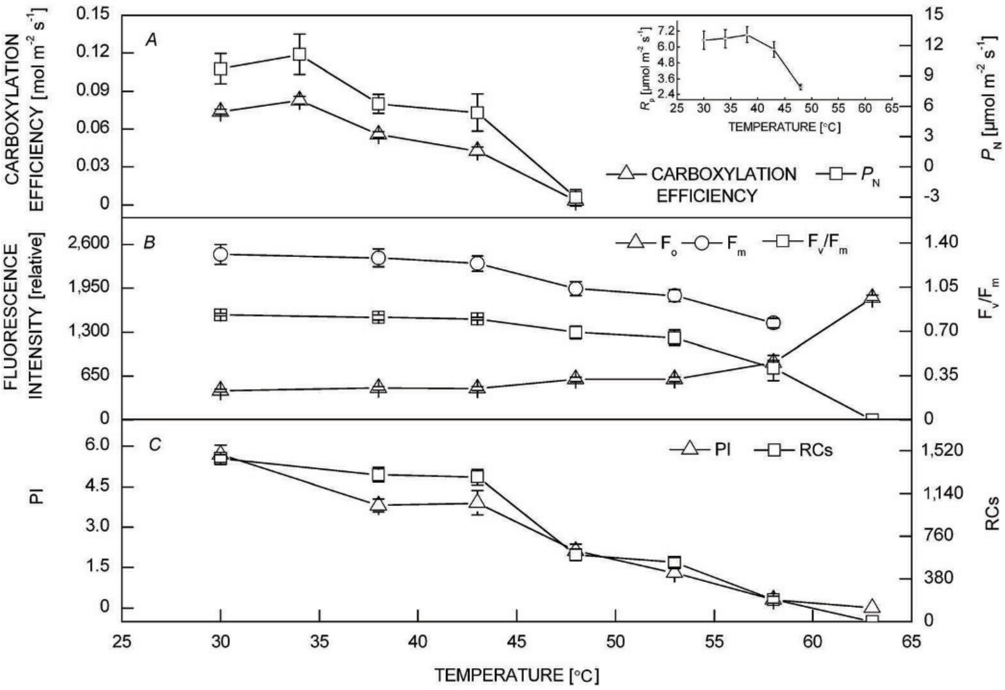

Fig. 3. The panel (*A*) presents the effects of elevated temperature on photosynthetic CO_2 assimilation, photorespiration rate (R_p) and carboxylation efficiency of *A. sparsifolia* leaves. Parameters of linear fitting based on the initial stage of A-C_i curves which only contains the six foremost data points ($n = 4$, ± SD). Changes of parameters like the initial fluorescence of the dark adapted state (F_o), the maximum fluorescence of the dark adapted state (F_m), the maximum photochemical efficiency of PSII (F_v/F_m) (*B*), the performance index (PI) and the amount of active PSII reaction centers per cross section (RCs) (*C*) under elevated temperature in *A. sparsifolia* leaves ($n = 20$, ± SD).

Fluorescence induction transient curves: The initial fluorescence "O" (F_o) arises when excitation light is focused on Chl molecules, which was related to the process that exciton energy generates in pigment antennae and subsequent electrons produced by open RCs. So, the intensity of F_o depended on the initial density of exciton in PSII pigment antennae, the structure of the pigment antennae and the state of excitation energy transfer from pigment antennae to the RCs (Krause and Weis 1984, Yamada *et al*. 1996), activities of RCs (Yamane *et al*. 1997), and/or residual dark reduction of Q_A (Bukhov and Carpentier 2000). The appearance of the

J step results from net photochemical reduction of Q_A^- (Strasser and Strasser 1995, Strasser *et al.* 2004). The intermediate I step and P step are due to slow reducing plastoquinone (PQ) pools, as well to different redox states of the RCs (Lazár 2009, Strasser and Strasser 1995, Haldimann and Strasser 1999). The value of I decreased obviously over 43ºC, reversely, J increased. The total complementary area (from time 0 to t_{Fmax}) decreased with elevated temperature, and this decrease was significant after 43ºC (Fig. 2). It was proposed that the process responsible for eliciting the K-step (300–400 μs) is a natural phenomenon in oxygenic plants, but is usually "hidden" in the O-J rise (Strasser *et al.* 2004). With increased heat stress over 43ºC, the typical O-J-I-P transient was gradually transformed into an O-K-J-I-P transient.

Changes of F_o, F_m, and F_v/F_m under elevated temperature: As leaf temperature increased, F_m and F_v/F_m decreased, while F_o reversed (Fig. 3*B*). We did not observe significant changes in F_m, F_v/F_m, or F_o when leaf temperature was under 43ºC. The F_m decreased by 5.5%, F_v/F_m decreased by 3.6%, and F_o increased by 6.5% relative to initial values at 30ºC. The value of F_v/F_m was slightly affected by moderately high temperatures in accordance with Yin *et al.* (2010). Above 43ºC all three parameters changed significantly. At 48ºC F_m decreased by 20.7%, F_v/F_m decreased by 16.8%, and F_o increased by 38.2%. The decrease in F_v/F_m from heat stress at 48ºC 16.8% almost paralleled the diurnal decrease of 14.13% at 14:00 h. The decline slope of F_v/F_m between 30ºC and 43ºC was –0.012.

Effects of PI, RCs, and energy allocation in PSII: With increasing temperature, both PI and RCs decreased slightly at temperature below 43ºC. The decline slope of PI between 30ºC and 43ºC was –0.138. Above 43ºC, the changes were significant (Fig. 3*C*). Compared to the value at 30°C, PI decreased by 62.61% at 48ºC, which slightly lower than the decrease observed between diurnal 14:00 h and 12:00 h *in situ* (data not shown).

Strasser and Strasser (1995) developed the analytical formulation of the energy flow of the photosynthetic apparatus, according to models of the architecture of the photosynthetic unit and the models of energetic communication among the pigment assemblies, based on the theory of energy fluxes in biomembranes. The energy pipeline leaf model clearly revealed the efficiency of energy flow from antennae to the electron transport chain components through the RCs of PSII (Fig. 4): a small part of the energy absorbed (ABS) by light-harvesting Chl dissipates in the form of thermal energy (DI_o) and fluorescence, and most of ABS are trapped by RCs (TR_o) in which excitation energies are converted to redox energies to reduce Q_A, and Q_A^- can be oxidized, generating electron transport (ET_o) for CO_2 fixation or other process. With increased temperature ABS changed very little until the heat stress hit 58ºC, and TR_o and ET_o slightly decreased between 30ºC and 43ºC while DI_o reversed to increase.

Inhibition of photosynthetic CO_2 assimilation and carboxylation efficiency: With increasing leaf temperature, carboxylation efficiency first increased, peaking at 34ºC, and then decreased with the lowest point of 0.003 μmol m^{-2} s^{-1} at 48ºC, and the similar trend was showed by P_N (Fig. 3*A*). The findings of both P_N and carboxylation efficiency under elevated temperature were in line with previous studies (Sage 2002, Salvucci and Crafts-Brandner 2004, Kaňa *et al.* 2008). As temperature increased, R_p first increased to the peak at 38ºC, and then decreased at higher temperature. These changes in carboxylation efficiency together with negative values of photosynthesis rate observed at 48ºC indicated that heat stress inhibits the carboxylation phase of the Calvin cycle.

Oxidative species and photosynthetic pigments: As leaf temperature increased, ROS began to accumulate intracellularly (Fig. 5). Similar experiments reported that the appearance of free radicals was observed in the dark in thylakoid membrane exposed to high temperature at 47ºC (Pospíšil *et al.* 2007) and 75ºC (Hideg and Vass 1993). It has been proposed that the generation of oxidative species is due to heat-induced changes at the PSII donor site (Pospíšil *et al.* 2007). During the

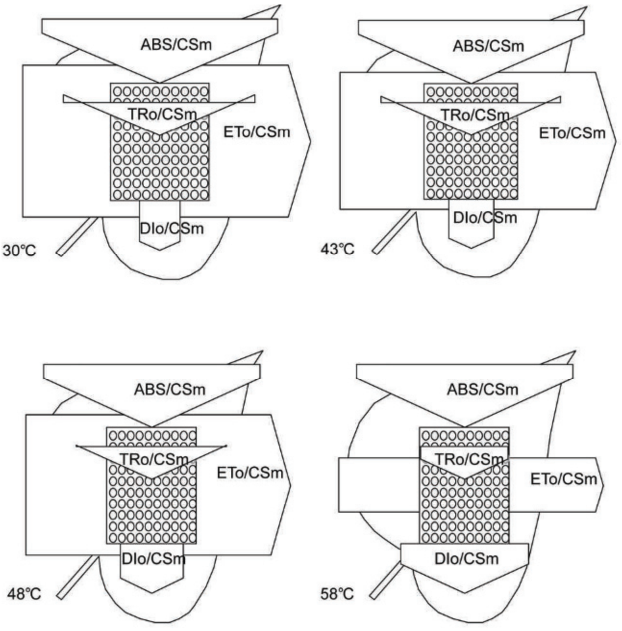

Fig. 4. Energy pipeline leaf model of *A. sparsifolia* leaves at elevated temperatures. ABS/CSm – the specific energy fluxes per cross section (for absorption); TR_o/CSm – the trapped energy fluxes per cross section; ET_o/CSm – the electron transport flux per cross section; DI_o/CSm – the dissipated energy flux per cross section.

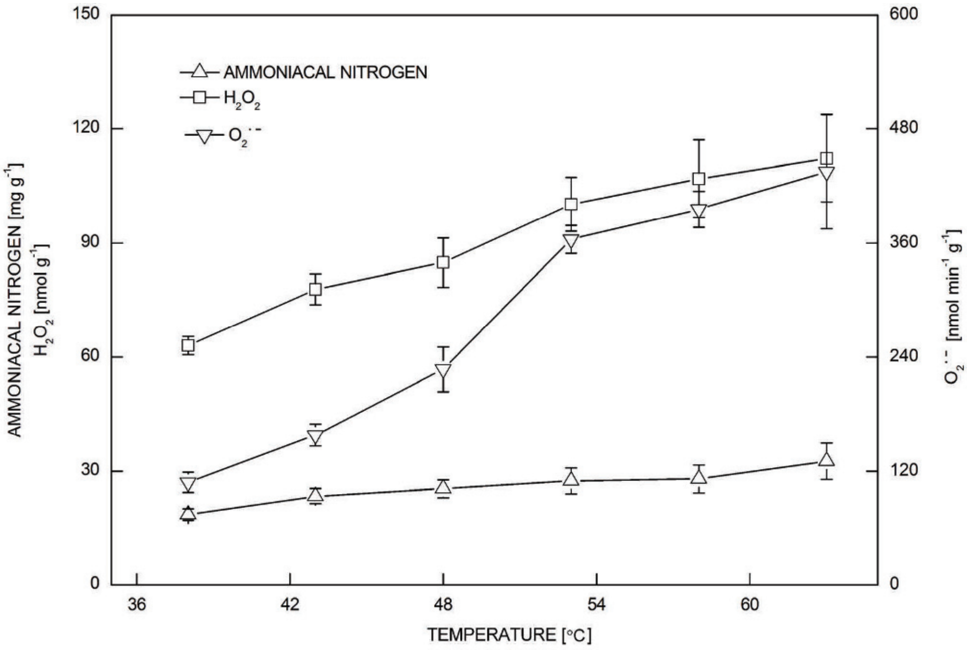

Fig. 5. Changes of ammoniacal nitrogen, hydrogen peroxide (H_2O_2), and superoxide ($O_2^{\cdot -}$) concentrations in response to elevated temperature (*n* = 3, ± SD).

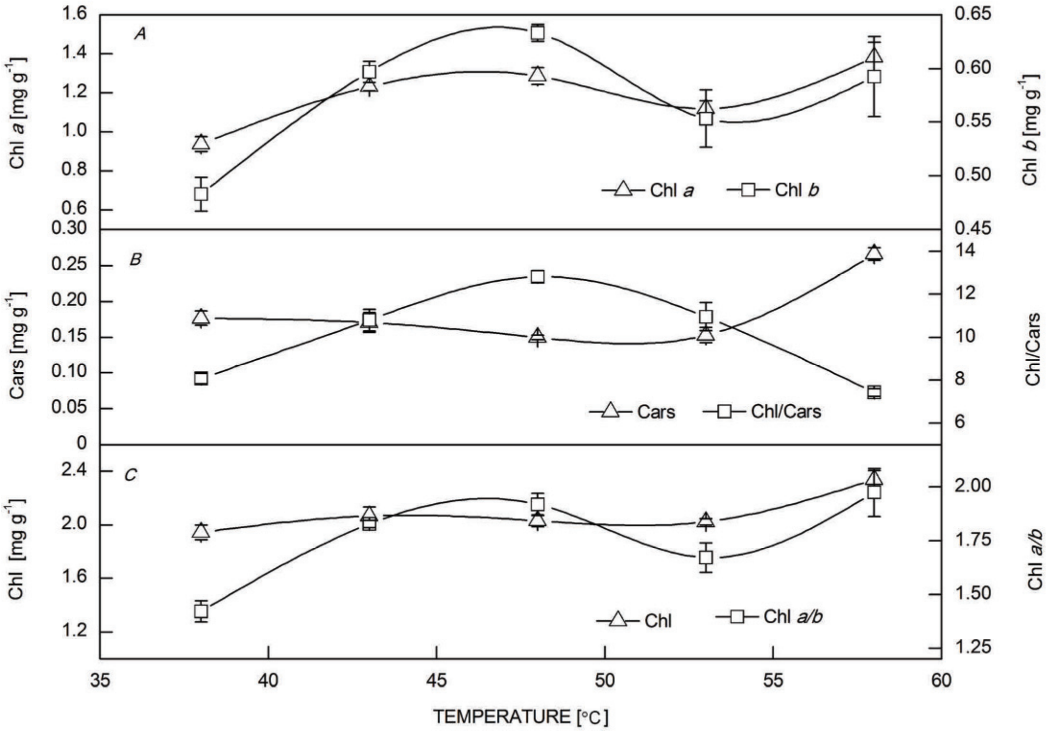

Fig. 6. Effects of elevated temperature on contents of photosynthetic pigments expressed on a basis of fresh mass. Chl – chlorophyll; Cars – carotenoids. (*n* = 3, ± SD).

temperature elevation to 53ºC levels of photosynthetic pigments like Chl *a*, Chl *b*, Chl, as well as Chl *a/b* appeared as an "S"curve– it first increased then decreased and increased finally, except that the trends of both Cars and Chl/Cars were different from that of the previous four pigments. The content of Cars had a clear upward trend over 53ºC, and Chl/Cars presented a curve like inverted "U" – it first increased then decreased (Fig. 6). If Cars content did not change after heat stress, the patterns of Cars and Chl/Cars with elevated temperature should also

Table 1. Pearson correlation coefficients of photosynthetic pigments expressed on a basis of fresh mass under elevated temperature. Chl – chlorophyll; Cars – carotenoids; * – significant correlation of two parameters at 0.05 statistical level; ** – significant correlation of two parameters at 0.01 statistical level.

Pigments	Chl *a*	Chl *b*	Chl *a/b*	Chl	Cars	Chl/Cars
Chl *a*	1.000					
Chl *b*	0.927**	1.000				
	<0.01					
Chl *a/b*	0.746**	0.508*	1.000			
	<0.01	0.031				
Chl	0.992**	0.957**	0.659**	1.000		
	<0.01	<0.01	<0.01			
Cars	0.419	0.019	0.808**	0.321	1.000	
	0.083	0.939	<0.01	0.193		
Chl/Cars	0.265	0.507*	–0.329	0.364	–0.759**	1.000
	0.287	0.031	0.182	0.137	<0.01	

present as an "S"curve like the other four pigments. Furthermore, the Pearson correlation coefficient analysis showed that there was a strong correlation between changes in Chl *a*, Chl *b*, Chl, and Chl *a/b* ($P<0.01$) but the correlation among Cars, Chl/Cars and the other four pigments was poor (Table 1), further implying that the content of Cars was influenced by heat stress.

Discussion

Effects of elevated temperature on PSII: The process of initial fluorescence is characterized as a purely physical phenomenon. It is magnified by the separation of light-harvesting Chl protein complexes of PSII from the PSII core complexes, resulting in decline of excitation energy transfer from the pigment antennae to RCs although a part of this phenomenon could possibly reflect accumulation of the reduced form of Q_A^-. Under heat stress, F_o can be used as an indicator for irreversible damage in PSII, associated with light-harvesting complex dissociation, blocking of electron transport on the reductant side of PSII (Costa *et al.* 2002) and functional disconnection of P_{680} from the inner antenna of PSII (Bartošková *et al.* 1999). As the temperature increased from 30ºC to 43ºC, a slight increase in F_o showed that at moderately high temperature the donor side of PSII almost function expeditiously to ensure electron flow for photochemical reaction. The expression F_v/F_m is an excellent indication of the quantum yield of primary photochemistry of PSII. Under the temperature ranged from 30ºC to 43ºC, a slight decline in F_v/F_m indicated that moderately high temperature does not impair the photochemical yield of PSII, and the stabilization of primary charge separation in RCs and its rate maintain relatively high level. Similar conclusion was reported by Lípová *et al.* (2010) that the observed F_v/F_m distinctly decrease after 40ºC and its value of 0.4 at about 58ºC is likely due to a part of PSII centers remaining active which do not enter into the gel and remain in the form of aggregations on the top of the gel. F_m reflects the processes in case of closed reaction centers including excition transfer in antennae, trapped efficiency of excitation by RCs. A theoretical study confirmed that the initial redox state of cytochrome b_{559} (cyt b_{559}) strongly affects F_m level (Lazár *et al.* 2005). With elevated temperature F_m firstly decreased slightly, showing that some components of electron transfer chain are not influenced and relatively high efficiency of electron transfer to cyt b_{559} can maintain high electron flux for further chemical reactions. Moreover, the decreased PSII function can be reflected in a slower total complementary area especially above 43ºC which reflects the heterogeneity of electrons from Q_A^- transferred into the electron transport chain. Additionally, decrease in the intensity of P has been proposed to be related to partial heat inactivation of the OEC (Pospíšil and Dau 2000, Mathur *et al.* 2011). In this research, the obvious decrease in P after 43ºC again indicates that the heat-damaged donor side including the OEC has limited capacity for donating electrons. At temperatures over 43ºC, significant decreases in these physiological parameters were observed, which suggest that high temperature produces damage on PSII including the donor side, reaction centers and main electron acceptors. The similar magnitude in the F_v/F_m decline that occurred at 48ºC with the diurnal decrease at 14:00 h *in situ* indicates that PSII is proposed to endure extremely high temperature stress and under relatively high temperature has capacity to partly recover its inhibited function, especially primary charge separation. Yamamoto *et al.* (2008) reviewed that partial recovery of the heat-damaged PSII was mainly due to the faster turnover of D1 protein that plays crucial role in carrying redox complex for charge separation and subsequent electron transport reaction.

It was proposed that the frame of K-step appearance was considered as resulting from a deviation from the usually established balance between the several electron transport reactions responsible for the fluorescence rise (Strasser 1997). The appearance of the K step may be a specific response to elevated temperature stress, which may be caused by inhibition of the OEC (Srivastava *et al.* 1997, Pospíšil and Dau 2000), inhibition of electron transport from pheophytin to Q_A (Guissé *et al.* 1995), inhibition of electron transport from Q_A^- to the secondary quinone acceptor (Q_B) (Goltsev *et al.* 1994) and may reflect changes in the structure of the architecture of antenna of PSII (Srivastava *et al.* 1997). Appearance of K step at 48ºC which more or less corresponded with significant declines of F_m and F_v/F_m after 43ºC further demonstrated that high temperature from 43ºC to 48ºC impaired the PSII activity and induced the irreversible damage.

With increased temperature, the absorbed energy did not decrease markedly, and below 43ºC the energy flux for trapping slightly changed, but the amount of active RCs decreased above 30ºC, indicating that under heat stress the RCs are reversibly inhibited, and the transiently inactive RCs act as energy traps which absorb light energy but do not transfer the captured light energy to the electron transport chain. The partly inactive RCs lead to a slight decline in both rate of primary charge separation and subsequent efficiency of electron transport. Once stress factors are removed, the inactive RCs could recover to the active level, which can be confirmed again by the diurnal changes of RCs that presented the similarly diurnal tendency with F_v/F_m (data not shown). The changes of TR_o were similar to ET_o, while DI_o showed an increase, indicating that high temperature causes the amounts of active RCs to decrease, but the efficiency of remaining active RCs increases, so that excessive excitation energy can be dissipated better. When leaf temperatures were below 43ºC, the pattern of energy allocation in PSII is still stable. The photosynthetic PI combines three independent functional steps of photosynthesis, the density of RCs in the Chl bed, excitation energy trapping and conversion to electron transport, into a single multiparametric expression (Strasser *et al.* 2004). In this research, the decline of PI under 43ºC was mainly due to the decline in RCs density and partly to the slight decrease in the efficiencies of excitation energy trapping and conversion. Under 43ºC the slope of the PI decline was significantly larger than that of F_v/F_m, which could show that in case of heat stress the fluorescence parameter PI performs more sensitivity than F_v/F_m, and PI may more accurately reflect the effect of heat stress on PSII.

If temperatures rose above 43ºC, a severe heat injury in PSII would occur. The crucial temperature for irreversible PSII damage in *A. sparsifolia,* which ranged at 43–48ºC, is relatively high compared to nondesert plants such as barley (Kaňa *et al.* 2008), pea (Srivastava and Strasser 1996), and wheat (Lu and Zhang 2000). This indicates that the photosynthetic apparatus of plants adapted to arid regions are better able to adapt to high temperatures. Adaptation to high temperature typically causes a shift of the temperature optimum of the photosynthetic apparatus to higher temperatures. Although the plant *A. sparsifolia* has been acclimated to the severe drought and high-temperature environments of the desert in both leaf morphogenesis and water-use physiology, and has evolved a sophisticated adaptive mechanism, we found that PSII exposed to heat stress is still a relatively fragile component of the electron transport chain, as confirmed by the diurnal changes of F_v/F_m (Fig. 1*A*).

Effects of elevated temperature on Rubisco activity: Zhang *et al.* (2010) used gas exchange and Chl *a* fluorescence technology to assess changes in carboxylation efficiency and photochemical efficiency in *Lonicera japonica* leaves under elevated ozone. They reported that the decrease of both carboxylation efficiency and photochemical efficiency indicated the Calvin cycle impaired and electron transport damaged, respectively. Stasik and Jones (2007) also used the method of A-C_i curve to analyze the Rubisco activity in wheat at moderately high temperature. Additionally, Somersalo and Krause (1989) reported that fully dark condition was helpful for repairing the damaged components of PSII, moreover, weak light intensity, approximately 10–30 μmol m^{-2} s^{-1}, was found to help recover damaged PSII components. Indeed, treatment with weak light intensity for 40 min following moderate heat stress could minimize the disturbance of PSII activity and restore the carboxylation efficiency of *A. sparsifolia* leaves, and should better reflect whether changes of photosynthetic efficiency were related to the changes of Calvin cycle process (*e.g.* changes of Rubisco activity).

The relation degree between P_N and carboxylation efficiency was larger than that of P_N and R_p, which showed that moderately high temperature reduces the rate of photosynthesis more than can be explained by stimulated photorespiration although R_p increases may result in hunger injure at high temperature. The similar conclusion was reached by Sharkey (2005) and Kaňa *et al.* (2008). Heat stress led to a decline in protein activity and the extent of damage to proteins increased with increased temperature. When the intensity of excitation light was close to the light saturation point and enzymes like Rubisco were fully active, the initial slope of A-C_i curve indicated the carboxylation efficiency, which depends on the amount of active Rubisco (Lambers *et al.* 1998). Robinson and Portis (1988) reported that changes in carboxylation state of Rubisco were mediated by the activity of Rubisco and were related to the ATP status of the chloroplast. Therefore, under both saturated light and adequate ATP, the initial slope of the A-C_i curve should reflect the active state of Rubisco. From 30ºC to 43ºC, the value of F_v/F_m did not decrease significantly, and high activity of PSII could still provide sufficient excitation electrons to generate adequate ATP and NADPH for the phosphorylation cycle. This would induce the regeneration of RuBP at moderately high temperature, but the carboxylation efficiency decreased. This suggests that at moderately high temperature the activity of Rubisco was depressed. Such heat sensitivity of Rubisco was reported previously and was attributed to the heat sensitivity of Rubisco activase (RA) (Salvucci and Crafts-Brandner 2004) and, an imbalance between the rates of Rubisco inactivation and reactivation by activase (Crafts-Brandner and Salvucci 2000). Von Caemmerer *et al.* (1994) reported that leaves of antisense tobacco contained only 34% as much Rubisco as those of wild-type species, but other photosynthetic components (*e.g.* RuBP regeneration) were not significantly affected, and the rate of CO_2 assimilation by the antisense plants was significantly lower over a wide range of CO_2 partial pressures. Furthermore, we found that the progressive decrease in Rubisco activation that accompanied increasing leaf temperatures closely correlated with the extent of photosynthetic inhibition. These results suggest that the activity of Rubisco plays an important role in maintaining the rate of CO_2 assimilation under heat stress. Therefore, under moderately high temperature stress, the decline of Rubisco activity is also the primary constraint on photosynthesis. Under heat stress, Rubisco activity can be used as an index to assess the thermal stability of plants.

Effects of heat stress on oxidative species and photosynthetic pigments: When ambient environment deviates from the normal condition enough to impact the cell function, the dynamic balance between the production of oxidative species and the production of protective species is destroyed, leading to the significant accumulation of oxidative species. Once oxidative species form in excess, they damage cellular macromolecules. It is well documented that there is a close relationship between the accumulation of oxidative species and the decline of function of photosynthetic components (op den Camp *et al*. 2003). As the leaf temperature increased, the concentration of oxidative species continually increased, which could disorder the functional regulation of photosynthetic membranes, further decreasing the photosynthetic activity of PSII. High temperature could cause accumulation of harmful metabolic products such as ammoniacal nitrogen in cells that are generated from the decomposition of proteins. Elevated concentrations of NH^+_4 have harmful effects on the formation of transmembrane proton gradient ($\Delta\psi$) (Bloom 1997). In turn, changes in $\Delta\psi$ could affect the rate constant (k_{et}) of electron transport reactions (Lazár 2009). Hence, the accumulation of ammoniacal nitrogen would result in the decrease of $\Delta\psi$, which would in turn reduce the values of k_{et} and affect the the efficiency of photochemistry.

Triantaphylidès and Havaux (2009) reported that in the nonenzymatic and enzymatic detoxification mechanisms, Cars were the most efficient compounds for quenching pro-oxidants. To reduce the excessive excitation energy absorbed by the Chl antennae, Cars play a role in thermal dissipation and quenche the excess absorbed energy to protect the photosynthetic membranes against oxidative damage. When high-temperature stress occurred, the amounts of total Cars increased significantly compared to Chl and other photosynthetic pigments. A similar finding was reported by Veres *et al.* (2006) who showed that in high-temperature environment, the content of total Cars increased markedly in psammophytes during the summer compared with Chl. Havaux *et al.* (1996) reported that the dark-adapted leaves employed a sophisticated, rapid biosynthetic mechanism to produce extra xanthophylls under heat stress. The increase in Cars content we observed may be due to the biosynthesis of xanthophyll meant to preserve the physical structure of thylakoid membranes. This phenomenon is in accordance with the conclusion of Snider *et al.* (2010) who reported that maintaining a sufficient antioxidant species pool prior to heat stress was an innate mechanism for coping with rapid leaf temperature increases.

We observed that as the distance from the oasis increased into the desert, the amounts of *A. sparsifolia* became gradually less until very little remained at the desertification region about 10 km away from the Cele oasis. According to Lichtenthaler (1998), the major natural stress factors that could reduce the plants' vitality and cause damage to plants are high irradiance, heat, low temperature, sudden and late frost, water shortage, long rainy periods, natural mineral deficiency (*e.g.* nitrogen shortage) and viral, fungal, and bacterial pathogens. In arid regions, abiotic factors like high irradiance, heat, water shortage, salt stress, as well as sand burial could be the main stress factors. Bruelheide *et al.* (2010) indicated that the terrain of Cele region appears to have higher altitude in the south and lower altitude in the north, additionally the ground water level slowly increases from 17.15 m at the Cele County to 3.5 m at the light desertification region. In addition, the biennial plants of *A. sparsifolia* with strong, deep roots, on average, have approximate 6-m length and 17 ramets, so that the root could reach the ground water. Li *et al.* (2002) showed that water deficit caused by drought stress had no effects on the transpiration of *A. sparsifolia* and it maintained the positive turgor during the summer. Therefore, water shortage is unlikely to be the reason that caused the amounts of *A. sparsifolia* to decline. *A. sparsifolia* seedlings exposed to higher salinity (150–250 mmol l^{-1}, conductivity: 6.33–9.52 mS cm^{-1}) were able to maintain growth without nanyo signs of salinity toxicity or damage, and were moderately salt-tolerant (Zeng *et al.* 2008). Zhu and Yang (2007) reported that the conductivity values of surface and ground waters in Cele River, Hetian Oasis and the interior of the desert were 1.18, 1.88, and 6.73 mS cm^{-1}, respectively. Therefore, salt stress is unlikely to be the reason behind the decreased population of *A. sparsifolia* away from the oasis. In accordance with our observed data, the strongest photosynthetic photon flux density (PPFD) was 2,013 μmol m^{-2} s^{-1}, and the light-saturated point was about 1,982 μmol m^{-2} s^{-1}. Thus, we concluded that slight high-light intensity and the consequent low rate of photosynthesis is unlikley to have caused a decrease in their number in the light desertification area. Deng *et al.* (2002) reported that in June the diurnal course of photosynthesis of *A. sparsifolia* was bimodal, the lowest phase appearing at 13:00 h, the leaf temperature above air temperature from 14:00 to 16:00 h, and the highest air temperature was about 38ºC but the PPFD was much lower than the light saturated point. Based on these facts, we could reach a reasonable conclusion that although *A. sparsifolia* has developed a strong stress-resistance mechanism (*e.g.* under moderately high temperature the stability of PSII activity) to adapt to the extremely atrocious environment of the desert, the occurrence of high temperature on hot summer noon must have caused the decline of cell vitality, especially through damage on photosynthetic proteins (*e.g.* inactivity of Rubisco). It is worth noting that in arid deserts, sand burial can also influence the physical and biotic microenvironment of the plants. Heavy sand burial can impair the growth of the plants and decrease their survival (Lu *et al.* 2006). In the desert, the temperature of ground surface can exceed 70ºC at noon, so considering our finding, it is plausible that high-temperature stress may be the main factor that limits the growth and spread of *A. sparsifolia*. It has been showed that temperature of plants can increase after irradiation by about 6–8ºC in dependence on actinic light in a case when transpiration is stopped (Kaňa and Vass 2008). Our research showed that in August the g_s was bimodal, the lowest phase appearing at around 14:00 h (data not shown), showing that *A. sparsifolia* did not use evaporative cooling to regulate leaf temperature effectively. When high light or other stress is superimposed on heat stress, the inhibition of PSII may take place more easily. It has been reported that the primary targets of thermal damage in plants are oxygen-evolving complex (Yamashita and Butler 1968) and the associated photosynthetic electron transport chain, carbon fixation by Rubisco. Further research about the mixed effects of heat and light or drought stress on OEC activity and other photosynthetic components of desert plants may be worthy.

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