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Effects of high temperature on the chlorophyll *a* fluorescence of *Alhagi sparsifolia* at the southern Taklamakan Desert

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Abstract Climate change is expected to result in an increase in the frequency and magnitude of extreme weather events. *Alhagi sparsifolia* is an important factor for wind prevention and sand fixation in the forelands of the Taklamakan Desert. The effects of high temperature on desert plants remain widely unknown. In this work, chlorophyll *a* fluorescence induction kinetics were investigated at different time stresses of 5, 20, 40, and 60 min at temperature gradients of 38–44 °C at 2 °C intervals. A pronounced K-step was found, and the values of the maximum quantum yield for primary photochemistry, the quantum yield of electron transport, the density of reaction centers and the performance index on absorption basis were lowest

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after 60 min at 44 °C, thus indicating that the oxygenevolving complex was damaged, the inactivated reaction centers increased, and the activity of the photosystem II (PSII) reaction center in leaves was seriously limited. Therefore, we suggest that under normal temperature (below 42 °C), the PSII of *A. sparsifolia* would be unaffected. When such temperature is maintained for 40 min, the activity of PSII would be limited, and when retained for 60 min, PSII may be severely damaged.

Keywords Alhagi sparsifolia · Chlorophyll

a fluorescence transient \cdot Extreme weather \cdot Heat stress \cdot Taklamakan Desert

Abbreviations

- ABS Absorbance
- Chl Chlorophyll
- CS Cross-section
- DI_o Dissipate
- OEC Oxygen-evolving complex
- PAR Photosynthetic active radiation
- PEA Plant efficiency analyser
- PI Performance index
- PSII Photosystem II
- RC Reaction center
- TR Energy trapping flux
- φ_{Do} Quantum yield of energy dissipation (at t = 0)
- φ_{Eo} Quantum yield of electron transport (at t = 0)
- Ψ_{o} Efficiency with which a trapped exciton can move an electron into the electron transport chain beyond Q_{A} (at t = 0)
- φ_{Po} Maximum quantum yield for primary photochemistry (at t = 0)
- W_k Ratio of variable fluorescence at K-step to the amplitude Fj Fo

Introduction

The frequency of extreme weather events is expected to increase because of the ongoing global climate change [IPCC (2007)]. The average global temperature is recorded to have increased by approximately 0.6 °C over the past 100 years and is projected to continue to rise rapidly, which can be ascribed to the ecological responses of both flora and fauna to climate change (Walther et al. 2002). The IPCC (2007) reported that climate warming would affect the structure and function of the ecological system, particularly those in cold and arid regions. Moreover, the rate of temperature increase in Xinjiang Uighur Autonomous Region has significantly exceeded the average temperature over the past 100 years (Shi and Shen 2003).

Climate change affects organism habitats through direct temperature warming and increased frequency of extreme weather events (Cardoso et al. 2008). For example, in Mondego, Portugal, the mean air temperature has increased by 0.15 °C per decade from 1931 to 2005, and a higher frequency of heat waves was observed over the last decade (Cardoso et al. 2008). The harsh weather can have devastating effects on the survival and breeding of both animals and plants (Romero et al. 2000; Cardoso et al. 2008; Piessens et al. 2009).

High temperature modifies the structure and damages the photosystem II (PSII). Temperatures higher than the optimal level for plant growth result in the deterioration of the structure and function of photosynthetic proteins, consequently leading to a decrease in photosynthetic efficiency (Briantais et al. 1996; Srivastava et al. 1997; Crafts-Brandner and Salvucci 2002; Sharkey 2005; Lu and Zhang 1999; Allakhverdiev et al. 2008; Kreslavski et al. 2009; Mohanty et al. 2012). PSII, with its oxygen-evolving complex (OEC), is one of the three major stress-sensitive sites in the photosynthetic machinery (Aro et al. 1993; Bukhov and Carpentier 2000; Nishiyama et al. 2005, 2006; Murata et al. 2007; Mohanty et al. 2007). Chlorophyll a fluorescence (OJIP) kinetics are an informative tool for studying the effects of different environmental stresses on photosynthesis and can thus be employed as the main method in the investigation of the function of PSII and its reactions to changes in the environment and growth conditions. PSII contains a number of sensitive proteins. In photosynthetic organs, the thermostability of PSII is weak (Čajánek et al. 1998; Tang et al. 2007). High temperature decreases the electron transport capacity in the acceptor side of PSII as well as the activity of the OEC.

Alhagi sparsifolia is the primary vegetation in the forelands of the Taklamakan Desert. This species is an important factor for wind prevention and sand fixation in the transition zone (Zeng et al. 2006). For many photosynthetic processes, down-regulation typically occurs

above 40 °C (Kaňa et al. 2008). However, the air temperature at midday goes beyond 42 °C during summer in this desert. Mild experimental climate warming has been reported to induce metabolic impairment and massive mortalities in succulent plants in South Africa (Musil et al. 2009).

In this study, we set a series of temperature and time gradients to investigate how PSII in *A. sparsifolia*, a species known to adapt to severe environments, tolerates different temperatures at different durations. This study aims (a) to confirm the changes in the PSII activity in the leaves of *A. sparsifolia* under different time stresses with elevated temperatures and (b) to predict the effects of extreme weather (high temperature) on plant growth. Findings of this study would be useful for estimating the general consequences of climate change on photosynthetic activity and plant productivity in the Taklamakan Desert.

Methods

Study site

This study was conducted on the extended observation plot of Xinjiang Cele National Field Scientific Observation and Research Station of Desertification and Grassland Ecosystem. This area is situated at the desert edge of the transition zone, near Qira (Cele) oasis, which is located at the southern fringe of Taklamakan Desert with coordinates 80°42'59" to 80°43'29"E and 37°01'00" to 37°01'30"N at an elevation of 1,360 m. We selected an isolated and enclosed study site to avoid disturbance factors. The flora in the area has been described by Thomas et al. (2000) and Li et al. (2002). The mean annual precipitation is less than 40 mm, whereas evaporation can be as high as 2,600 mm annually. The mean summer temperature is 26.1 °C, the maximum temperature is 42 °C, and the surface maximum temperature is 70.3 °C. Tributaries and ephemeral rivers, fed by snow melt from the mountains during the summer months, enabled the establishment of river oases along the desert margins.

Experiment material selection and treatment

The desert plant *A. sparsifolia* is the main floristic element of the oasis–desert transition zone in the southern fringe of the Taklamakan Desert. Samples of *A. sparsifolia* from the same plot were collected randomly on a sunny morning at 10:00 a.m. with low winds in the early August 2011. The average plant height was 43–62 cm and the crown diameter was 56–72 cm.

Well-growing shoots of the plant were randomly selected. Dust on the surfaces of the leaves was washed lightly

with distilled water. The branches were cut away, inserted into moist absorbent cotton, immediately placed in an incubator with 60 % relative humidity, and then taken back to the laboratory, enclosed in damp filter paper. The absorbent cotton was placed in a culture dish filled with distilled water and then transferred into a tissue culture incubator enclosed in damp filter paper. The viewport was covered with black plastic bags, and the entire experiment was carried out in darkness. The heat stress was timed at 5, 20, 40, and 60 min at temperature gradients of 38 to 44 ± 0.1 °C at 2 °C intervals to determine the effect of time stress on A. sparsifolia. Temperatures from 38 to 42 °C are considered real temperatures, whereas 44 °C is considered as extreme weather temperature. Eight intact mature leaves and assimilative branches were used to measure OJIP after each temperature treatment. Eight repetitions of each temperature gradient were measured.

Measurement of chlorophyll a fluorescence transient

The polyphasic OJIP transient was measured using a plant efficiency analyzer (Hansatech Instruments Limited, Norfolk, UK). The OJIP transient was induced by a saturation photon flux density at 3,500 µmol photons m⁻² s⁻¹ provided by an array of three light-emitting diodes (peak at 650 nm) to generate fluorescence curves expanding from minimal fluorescence (F_o) to maximal fluorescence (F_m) for all treatments (in this research, $F_m = F_p$). Data were initially sampled at 10 µs intervals for the first 300 µs to achieve an excellent time resolution of dark-adapted F_o as well as the initial rise kinetics. The time resolution of digitization was then switched to slower acquisition rates. The PSII parameters and OJIP transient were analyzed according to Strasser et al. (2000, 2004).

Statistical analysis

Descriptive statistics was used to calculate averages and standard deviations of the data from each set of replicates, and the results were expressed as mean \pm SE (standard error). Student's *t* test was used for statistical analysis of experimental data. The results were presented as standard error, and statistical significance was accepted when $P \leq 0.05$. The graphs were produced using Origin 8.0 (Origin Lab Inc., Hampton, USA) and Adobe Photoshop (Adobe Inc., San Jose, USA).

Results

Both the shape and the intensity of OJIP transients were altered based on timing heat stress and different temperature levels in *A. sparsifolia* in darkness (Fig. 1). OJIP transients were only slightly changed at 5 and 20 min (Fig. 1a, b), but decreased with increasing temperature at 40 min with no apparent K-step, and indicate that they have recovery of activity of PSII with 5, 20 and 40 min heat stress (Allakhverdiev et al. 2008; Kreslavski et al. 2009) (Fig. 1c). An evident K-step was found at 44 °C for 60 min (Fig. 1d). For the timing levels, the OJIP transients did not significantly change at 38, 40, and 42 °C (Fig. 1a–c). However, the OJIP transients were limited by increasing timing stress, with a pronounced K-step at 44 °C for 60 min (Fig. 1d).

Changes in quantum efficiencies are depicted in Fig. 2. The maximum quantum yield for primary photochemistry (φ_{Po}) and the quantum yield of electron transport (φ_{Eo}) were significantly decreased by increasing the temperature for 60 min in darkness (Fig. 2a, c). Treatments with increasing temperature resulted in an increase in the probability that a trapped exciton moves an electron into the electron transport chain beyond Q_A (ψ_o) as well as a quantum yield of energy dissipation (φ_{Do}), except for a decrease 60 min from 38 to 42 °C (Fig. 2b, d).

Figure 3 shows the reaction center parameters of the leaves of *A. sparsifolia* under different time treatments. Treatment resulted in a decrease in the density of reaction centers (RC/CS_o), but an increase in absorption flux per reaction center (ABS/RC), trapping flux per reaction center (TR_o/RC), and dissipated energy flux per reaction center (DI_o/RC).

The ratio of variable fluorescence at the K-step to the amplitude Fj - Fo (W_k) increased by 123.1 % with increasing temperature from 38 to 44 °C at 60 min (Fig. 4).

The fluorescence parameters (Fj - Fo)/(Fp - Fo) of the leaves of *A. sparsifolia* under different time treatments of 5, 20, 40, and 60 min did not exhibit a uniform change (Fig. 5). At 20 and 40 min, (Fj - Fo)/(Fp - Fo)decreased with the increasing temperature, whereas at 60 min, (Fj - Fo)/(Fp - Fo) increased at 38–42 °C and decreased significantly at 44 °C.

With increasing temperature, the performance index on absorption basis (PI_{ABS}) decreased by 482.2 % at 44 °C compared to that at 38 °C for 60 min (Fig. 6).

Discussion

Threats of global warming and climate change have resulted in heat stress and drought, two major stresses for plants. Most previous investigations on high-temperature stress have focused on the regulation of PSII in a single leaf (Briantais et al. 1996; Čajánek et al. 1998; Crafts-Brandner and Salvucci 2002; Musil et al. 2009). The fluorescence transient test, reflecting energy fluxes, and transportation of Fig. 1 OJIP transient of the leaves of A. sparsifolia (38, 40, 42, and 44 °C, in the dark) under different time treatments of 5 (a), 20 (b), 40 (c), and 60 min (d). Data are mean \pm SE of eight independent measurements

Fig. 2 Quantum efficiencies of the leaves of A. sparsifolia (38, 40, 42, and 44 °C, in the dark) under different time treatments of 5, 20, 40, and 60 min. φ_{Po} (a) denotes the maximum quantum yield for primary photochemistry (at t = 0), ψ_0 (**b**) is the efficiency at which a trapped exciton can move an electron into the electron transport chain beyond Q_A (at t = 0; $\varphi_{\rm Eo}$ (c) denotes the quantum yield of electron transport (at t = 0); and φ_{Do} (d) is the quantum yield of energy dissipation (at t = 0). The same letters indicate no significant difference between same stress time and different temperature levels, whereas different letters indicate a significant difference (P < 0.05). Data are mean \pm SE of eight independent measurements



electron in PSII can be used as indicators of plant damage (Strasser et al. 2000, 2004).

The rise in chlorophyll fluorescence induction reveals a characteristic O-J-I-P polyphasic transient at room temperature (Strasser et al. 2000, 2004). Fluorescence transient rises from the origin point O to the fluorescence peak P

faster when the reoxidation of Q_A^- is inhibited by any stress, thus resulting in a characteristic O-K-J-I-P polyphasic transient when plotted on a logarithmic scale.

In our study, a marked K-step was found at 44 °C for 60 min in darkness (Fig. 1). Phase K results from an inhibition of the electron donor to the secondary electron donor of PSII,

Fig. 3 Reaction center parameters of the leaves of A. sparsifolia (38, 40, 42, and 44 °C, in the dark) under different time treatments of 5, 20, 40, and 60 min RC/CS_o (a) denotes the density of reaction centers; ABS/RC (b) stands for the absorption flux per reaction center; TR_o/RC (c) is the trapping flux per reaction center; and DI_o/RC (d) is the dissipated energy flux per reaction center. The same letters indicate no significant difference between same stress time and different temperature levels, whereas different letters indicate a significant difference (P < 0.05). Data are mean \pm SE of eight independent measurements

1.0

0.8

0.6

0.4

0

Wk



Fig. 4 Ratio of variable fluorescence at the K-step to the amplitude $Fj - Fo(W_k)$ of the leaves of *A. sparsifolia* (38, 40, 42, and 44 °C, in the dark) under different time treatments of 5, 20, 40, and 60 min. The *same letters* indicate no significant difference between same stress time and different temperature levels, whereas *different letters* indicate a significant difference (P < 0.05). Data are mean \pm SE of eight independent measurements

which can be attributed to a damaged OEC. Thus, phase K can be used as a specific indicator of OEC damage. The results reveal that the donor side of PSII might be damaged (Allakhverdiev et al. 2008; Kreslavski et al. 2009).

From the JIP test, the maximum quantum yield for primary photochemistry ($\varphi_{Po} = Fv/Fm$), the quantum yield of electron transport (φ_{Eo}), the motion of a trapped exciton into the electron transport chain beyond Q_A (ψ_o), and the quantum yield of energy dissipation (φ_{Do}) could be estimated (Fig. 2). The φ_{Po} and φ_{Eo} values are slightly

Fig. 5 Fluorescence parameters (Fj - Fo)/(Fp - Fo) of the leaves of *A. sparsifolia* (38, 40, 42, and 44 °C, in the dark) under different time treatments of 5, 20, 40, and 60 min. The *same letters* indicate no significant difference between same stress time and different temperature levels, whereas *different letters* indicate a significant difference (P < 0.05). Data are mean \pm SE of eight independent measurements

changed from 5 to 40 min and are seriously affected by the temperature treatment at 60 min, which indicates that the increase of ψ_{o} at 5–40 min is attributed to the enhanced electron flow from $Q_{\rm A}^{-}$ to $Q_{\rm B}$ or $Q_{\rm B}^{-}$, which facilitates normal photosynthesis. The activity of PSII RC in leaves was also damaged seriously by high temperature in darkness. The results are shown in Fig. 1.

Excess excitation energy was converted into thermal dissipation, thus maintaining the energy balance between absorption and utilization to protect the cell growth under



Fig. 6 Performance index on absorption basis PI_{ABS} of the leaves of *A. sparsifolia* (38, 40, 42, and 44 °C, in the dark) under different time treatments of 5, 20, 40, and 60 min. The *same letters* indicate no significant difference between same stress time and different temperature levels, whereas *different letters* indicate a significant difference (P < 0.05). Data are mean \pm SE of eight independent measurements

various environment stresses (Hagemeyer 1999; Perales-Vela et al. 2007). In general, with the increasing stress, RC/ CS_o is inhibited and the number of RC/CS_o is reduced. Consequently, the decrease in the number of RC/CS_o resulted in increased ABS/RC, TR_o/RC, and DI_o/RC (Ali et al. 2006). In our study, among the reaction center parameters of the leaves of *A. sparsifolia*, RC/CS_o decreased, whereas ABS/RC, TR_o/RC and DI_o/RC increased in darkness. This finding implies that energy was dissipated to maintain the energy balance to certain extent. Otherwise, a blockage in electron transfer on the acceptor side of PSII would occur (Zhang et al. 2010; Chen et al. 2008).

 $W_{\rm K}$ was increased at 44 °C compared with other temperature gradients, and a pronounced K-step was found at 44 °C for 60 min in darkness (Figs. 1, 4). This result indicates that the high temperature (44 °C) has limited the acceptor side of the electron transport chain. The ratio of (Fj - Fo) to (Fp - Fo) declined at 44 °C at 60 min compared to that at 5–40 min. The K-step was found at 44 °C in 60 min (Figs. 1d, 5), indicating that the fraction of inactivated reaction centers that cannot transport electrons from $Q_{\rm A}$ to $Q_{\rm B}$ increased (Dai et al. 2004). The results are shown in Fig. 3a. The above changes resulted in a drastic decrease in the overall photosynthesis performance index (PI_{ABS}), which is a parameter that is sensitive to environment stress (Wang et al. 2012).

In conclusion, normal temperature (below 42 °C) would not affect the PSII of *A. sparsifolia* in darkness with respect to the different time gradient stresses in this area. An elevation in air temperature to 44 °C under extreme weather in ambient environment would limit the activity of PSII when retained for 40 min and would result in severe damage when retained for 60 min. Such conditions may result in the photoinhibition and metabolic impairment of *A. sparsifolia* at the southern Taklamakan Desert before its adaption to 44 °C which is transient elevation in air temperature under extreme weather conditions.

Author contribution Lei Li is responsible for conception and design, analysis and interpretation, data collection and critical revision of the article. Xin-wen Xu, Lisha Lin, Fan-jiang Zeng performed research and analyzed data. Xiang-yi Li obtained funding and took the overall responsibility.

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