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Chlorophyll *a* fluorescence of typical desert plant *Alhagi sparsifolia* Shap. at two light levels

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Abstract

Alhagi sparsifolia Shap. is exposed to a high-irradiance environment as the main vegetation found in the forelands of the Taklamakan Desert. We investigated chlorophyll *a* fluorescence emission of *A. sparsifolia* seedlings grown under ambient (HL) and shade (LL) conditions. Our results indicated that the fluorescence intensity in the leaves was significantly higher for LL-grown plants than that under HL. High values of the maximum quantum yield of PSII for primary photochemistry (φ_{Po}) and the quantum yield that an electron moves further than Q_A^- (φ_{Eo}) in the plants under LL conditions suggested that the electron flow from Q_A^- (primary quinone electron acceptors of PSII) to Q_B (secondary quinone acceptor of PSII) or Q_B^- was enhanced at LL compared to natural HL conditions. The efficiency/probability with which an electron from the intersystem electron carriers was transferred to reduce end electron acceptors at the PSI acceptor side and the quantum yield for the reduction of end electron acceptors at the PSI acceptor side were opposite to φ_{Po}, and φ_{Eo}. Thus, we concluded that the electron transport on the donor side of PSII was blocked under LL conditions, while acceptor side was inhibited at the HL conditions. The PSII activity of electron transport in the plants grown in shade was enhanced, while the energy transport from PSII to PSI was blocked compared to the plants grown at HL conditions. Furthermore, PSII activity under HL was seriously affected in midday, while the plants grown in shade enhanced their energy transport.

Additional key words: diurnal changes; electron transport chain; photosystem II activity; quantum yield; shade.

Introduction

As an energy source for carbon fixation, light regulates not only plant growth but also photosynthetic apparatus development in higher plants. Plants develop adaptive mechanisms in response to changes in light availability. Effects of different light conditions on chlorophyll (Chl) contents (Bailey *et al.* 2001), chloroplast ultrastructure, enzyme activities, and physiological and photochemical processes (Clijsters and Van Assche 1985, Ohnishi *et al.* 2005, Jiang *et al.* 2011) have been extensively investigated. In general, plant leaves under high-light conditions have a higher photosynthetic potential than those grown under low-light conditions, which is obvious from the amount of Rubisco and electron transfer carriers (Jiang *et al.* 2011). Moreover, plants grown under low-light (LL) conditions show considerably lower net photosynthesis than those grown under high-light (HL) conditions

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Abbreviations: ABS/RC – average absorbed photon flux per PSII reaction center; DI_o/RC – dissipated energy flux per PSII reaction center; ET_o/RC – electron transport flux from Q_A to Q_B; F_m – maximal fluorescence yield of the dark-adapted state; F_o – minimal fluorescence yield of the dark-adapted state; F_v – variable fluorescence; F_v/F_o – potential activity of PSII; HL – ambient, high-light irradiance; LL – shade, low-light irradiance, 50% of ambient light; PI_{abs} – performance index for energy conservation from photons absorbed by PSII antenna to the reduction of Q_B; RC – reaction center; TR_o/RC – maximum trapped excitation flux per PSII reaction center; W_k – the ratio of variable fluorescence at the K-step to the fluorescence difference F_j-F_o; φ_{Eo} – quantum yield of the electron transport flux from Q_A to Q_B; φ_{Po} – maximum quantum yield of primary PSII photochemistry; φ_{Ro} – the quantum yield for the reduction of end electron acceptors at the PSI acceptor side; ψ_{Eo} – the efficiency/probability that an electron moves further than Q_A^-; δ_{Ro} – efficiency with which an electron from Q_B is transferred to PSI acceptors.

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at the same saturating light intensity (Wang *et al.* 2006, Jiang *et al.* 2011).

Chl *a* fluorescence kinetics is one of the main methods for investigating PSII function and reactions under changing environmental and growth conditions (Strasser *et al.* 2004, Zhang *et al.* 2010, Kalaji *et al.* 2012, Lazár 2015). The Chl *a* fluorescence shows the characteristic OJIP kinetics when plotted on a logarithmic time scale (Lazár 2006). According to Strasser's theory of energy fluxes in biomembranes (Strasser 1978) and his new report (Strasser *et al.* 2010), the energy cascade starts from light absorption flux (ABS) by PSII antenna pigments, trapping flux (TR) [defined as the energy flux leading to the reduction of pheophytine (Pheo) and Q_A], electron transport flux (ET) (defined as the electron transport further than Q_A^-) could be demonstrated by Chl *a* fluorescence (Fig. 1). Hence, Chl *a* fluorescence can be used to analyze the efficiency of electron transfer from PSII to the acceptor side of PSI in the intersystem chain (Tsimilli-Michael and Strasser 2008, Strasser *et al.* 2010).

Alhagi sparsifolia Shap., a typical desert plant, has an important function in wind prevention and sand fixation at the transition of Cele oasis-desert ecotone in the southern Taklamakan desert. This plant grows in high-irradiance environments and is currently the main vegetation found in the forelands of the Taklamakan Desert. Furthermore, it can be found under canopies in inner oasis with many tree species. Previous studies found that the plant biomass accumulation was inhibited (Li *et al.* 2014). Hence, collectively the reduced photosynthetic efficacy, diurnal changes of Chl *a* fluorescence, and a clear mechanism of electron transport from PSII to PSI have not been

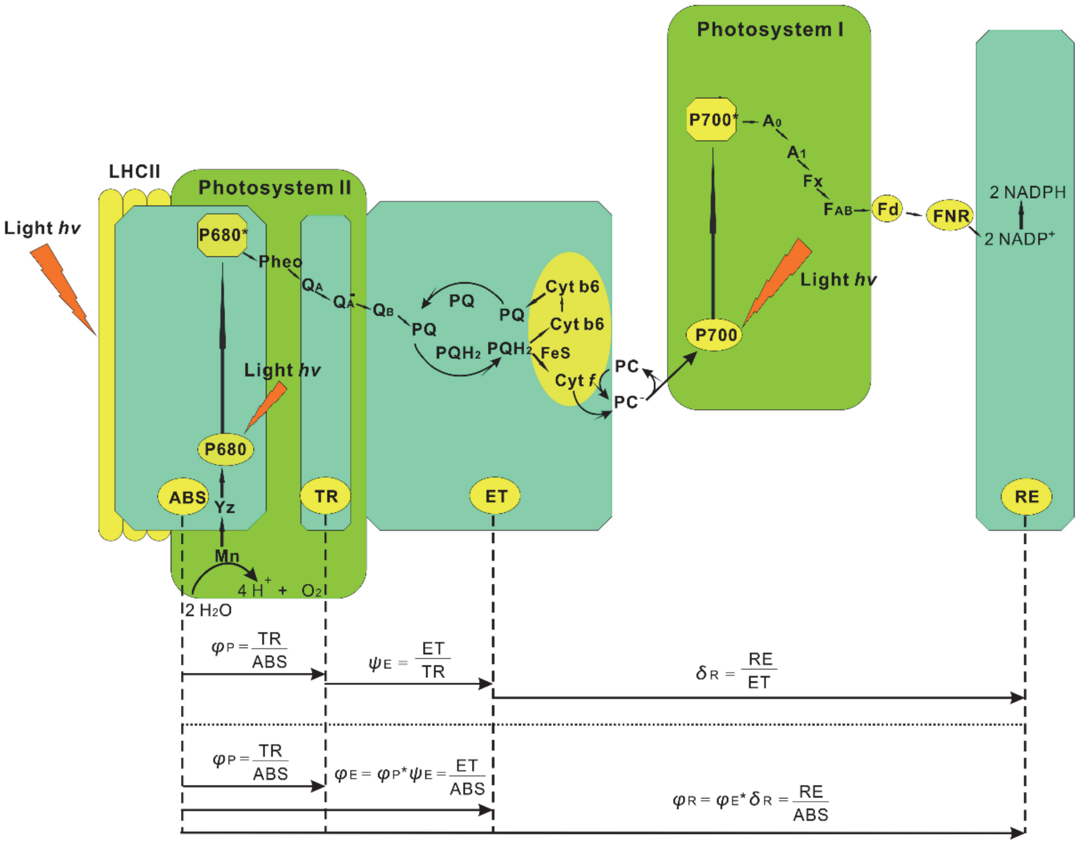

Fig. 1. Scheme of quantum yields and efficiencies, energy fluxes, and electron transport chain between PSII and PSI (based on Strasser *et al.* 2010). LHCII – Chl containing light-harvesting complex of PSII; Mn – manganese; Yz – tyrosine; P680 and P700 – the primary electron donors of PSII and I, respectively; Pheo – pheophytine; Q_A and Q_B – primary and secondary quinone electron acceptors of PS II, respectively; PQ – plastoquinone; PQH_2 – plastoquinol; Cyt b_6f – cytochrome b_6f complex, consisting of an Fe–S Rieske centre, cytochrome *f*, and cytochrome *b* low- and high-potential forms; PC – plastocyanin; A_0 and A_1 – spectroscopically identified primary and secondary electron acceptors in PSI; F_X, F_A, and F_B – iron sulfur center proteins; Fd – soluble ferredoxin; FNR – ferredoxin-$NADP^+$-reductase. $NADP^+$ – oxidized nicotinamide adenine dinucleotide phosphate; ABS – absorption flux; ET – electron transport flux; TR – trapped excitation flux; RE – electron transport flux until PSI acceptors; φ_{Eo} – quantum yield of the electron transport flux from Q_A to Q_B; φ_{Po} – maximum quantum yield of primary PSII photochemistry; φ_{Ro} – the quantum yield for the reduction of end electron acceptors at the PSI acceptor side; ψ_{Eo} – the efficiency/probability that an electron moves further than Q_A^-; δ_{Ro} – efficiency with which an electron from Q_B is transferred until PSI acceptors.

demonstrated in *A. sparsifolia* seedlings grown under low-light conditions.

We carried out an experiment in order to examine the characteristics of quantum flow from PSII to PSI in response to low-light conditions. The fast Chl *a* fluorescence kinetics of *A. sparsifolia* seedlings was analyzed. The objective of this study was to investigate (*1*) the diurnal Chl *a* fluorescence, measured with the same saturating light of the instrument by *Handy PEA*, and (*2*) the characteristics of the electron transport (ET) from PSII to PSI of plants grown under two levels of irradiance.

Materials and methods

Study site: The study was performed near the Cele Oasis, located at the southern fringe of the Taklamakan Desert at 1,365 m a.s.l. (84°43′30″–84°43′50″E, 37°01′01″–37°01′ 02″N). The Cele Oasis is located 90 km east of Hotan in Xinjiang Uighur Autonomous Region, NW China. The climate in the Taklamakan Desert is extremely arid because of its location in the Tarim Basin, which is surrounded by alpine mountain ranges of the Pamir in the west, the Tian Shan in the north, and the Kunlun in the south. The mean annual precipitation in the area is less than 40 mm, but evaporation can be as high as 2,600 mm per year, with a mean summer temperature of 26.1°C. Tributaries and ephemeral rivers, fed by melting snow in the mountains during the summer months, allowed the establishment of river oases along the desert margins. The Cele Oasis is surrounded by a 5 to 10 km belt of sparse vegetation dominated by woody phreatophytic species.

Plant treatments: *Alhagi sparsifolia*, the main vegetation found at the oasis–desert transition zone at the southern fringe of the Taklamakan Desert, was used in this study. Healthy seeds of *A. sparsifolia* were selected after 24 h of immersion in water. Eight seeds were used per plastic pot (diameter of 25 cm, height of 31 cm) filled with 20 kg of sandy soil on 15 April, 2012; the pots were kept in the field. The seeding depth was 1 cm. The soil in pots was mixed thoroughly with the soil taken from an oasis-desert transition zone under natural conditions of *A. sparsifolia*. Only two healthy and similar seedlings were retained per plot when the plants were established. Two light levels [ambient, HL, defined as the natural light condition, 100% of full sunlight, with a maximum photosynthetically active radiation of approx. 2,000 μmol(photon) m^{-2} s^{-1} and low-light intensity, LL, about 50% of full sunlight, using a piece of nylon net (5 m × 5 m × 1.2 m) with a maximum photosynthetically active radiation of approx. 1,100 μmol(photon) m^{-2} s^{-1}] were used when *A. sparsifolia* reached a stage of three expanded true leaves. The experimental design was set according to Li *et al.* (2014). Every three days, 500 ml of water was added per pot until June and then it was added every two days. Sixteen pots were prepared, each treatment was replicated five times, and the whole experiment was performed from April to August, 2012.

Measurements of Chl *a* fluorescence transients: Samples were dark-adapted for 20 min (Li *et al.* 2014), and the polyphasic Chl *a* fluorescence transients (OJIP) of 12 seedling plants was measured by a plant efficiency analyzer (*PEA, Hansatech Instruments Ltd.,* Norfolk, UK) on a sunny day from 8:00 to 20:00 h, at 2-h intervals. We obtained the parameters of Chl *a* fluorescence which could reflect the PSII activity of *A. sparsifolia* during the whole day. The Chl *a* fluorescence transient was induced by a saturating photon flux density at 3,500 μmol(photon) m^{-2} s^{-1} provided by an array of three light-emitting diodes (peak at 650 nm) in order to generate fluorescence curves expanding from F_o to F_m (F_t, fluorescence at time t after onset of actinic illumination; $F_o = F_{30\mu s}$, minimum fluorescence intensity; $F_j = F_{2ms}$, fluorescence intensity at the J-step; $F_i = F_{30ms}$, fluorescence intensity at the I-step; $F_p = F_m$, maximal fluorescence intensity at the peak P of OJIP) for all treatments. The PSII parameters derived from the OJIP transients were analyzed based on the method of Strasser *et al.* (2004, 2010).

Statistics: Descriptive statistics was used to calculate the average and standard deviation of the data for each set of replicates, and the results were expressed as mean or mean ± SD. The *Student*'s *t*-test was used for statistical analysis of experimental data. All the analyses were carried out with *SPSS 16.0* (*SPSS Inc.,* Chicago, IL, USA).The graphs were made using *Origin 8.0* (*OriginLab Inc.,* Hampton, USA) and *Adobe Photoshop* (*Adobe Inc.,* San Jose, USA).

Results

The shape and fluorescence intensity of the OJIP transients changed in response to the different light conditions for *A. sparsifolia* seedlings. The Chl *a* fluorescence intensity in the leaves was significantly higher under LL than that under HL growth conditions. Under both light conditions, the fluorescence intensity decreased from 8:00 to 14:00 h and recovered from 14:00 to 20:00 h (Figs. 2, 3).

The expression F_v/F_o derived from PSII indicates the rate constant ratio of k_P/k_N ($F_v/F_o = k_P/k_N$; k_P, photochemical de-excitation; k_N, nonphotochemical de-excitation rate constant) (Strasser *et al.* 2000). Under both light conditions, F_v/F_o decreased at midday and then recovered. The values of F_v/F_o in the plants grown under the LL conditions were significantly higher than those under ambient HL conditions (Fig. 4). Under HL, the values of the specific light energy flux absorbed by PSII antenna per reaction centre (ABS/RC), maximal trapping flux per RC (TR_o/RC), electron transport flux (further than Q_A^-) per RC (ET_o/RC), and the flux of dissipated excitation energy per RC (DI_o/RC) in midday (14:00 h) were the highest of the whole day. However, specific energy fluxes (ABS/RC, TR_o/RC, ET_o/RC, DI_o/RC) showed significantly diverging trends (Fig. 5).

The efficiency of trapping, electron transport, and the reduction of the end acceptors of the photosynthetic electron transport chain are shown in Figs. 6 and 7. The maximum quantum yield for PSII photochemistry (φ_{Po} = TR/ABS) and the efficiency/probability that an electron moves further than Q_A^- (ψ_{Eo} = ET/TR) of the LL-grown plants were higher. The efficiency/probability, with which an electron from the intersystem electron carriers is transferred to reduce end electron acceptors at the PSI acceptor side (δ_{Ro} = RE/ET), was lower under the LL conditions than that under ambient HL (Fig. 6). Similarly, φ_{Po}, electron transport (φ_{Eo} = ET/ABS), and reduction of end electron acceptors (φ_{Ro} = RE/ABS) showed the same general trends. Moreover, the electron transport flux (ET) and reduction of end electron acceptors (RE) per reaction center (RC) also was consistent with the above changes (Fig. 7).

The leaf performance index on the absorption basis (PI_{abs}) can indicate energy conservation from photons absorbed by PSII to the reduction in intersystem electron acceptors, which is a very sensitive parameter of environmental stress (Wang *et al.* 2012). The values of PI_{abs} were also higher under the LL conditions than under

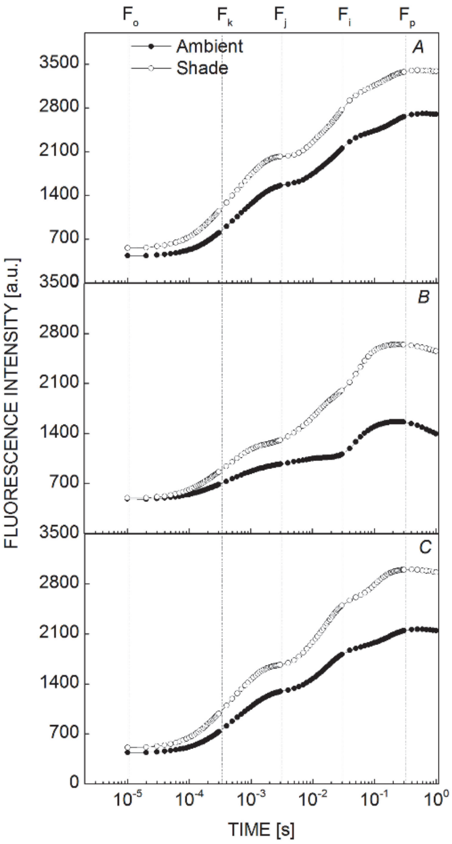

Fig. 2. OJIP transients in the leaves of *Alhagi sparsifolia* seedlings under ambient and shade conditions. *A*: OJIP transient at 8:00 h; *B*: OJIP transient at 14:00 h (midday); *C*: OJIP transient at 20:00 h. $F_o = F_{30\mu s}$; $F_k = F_{300\mu s}$; $F_j = F_{2ms}$; $F_i = F_{30ms}$; $F_p = F_{300ms}$.

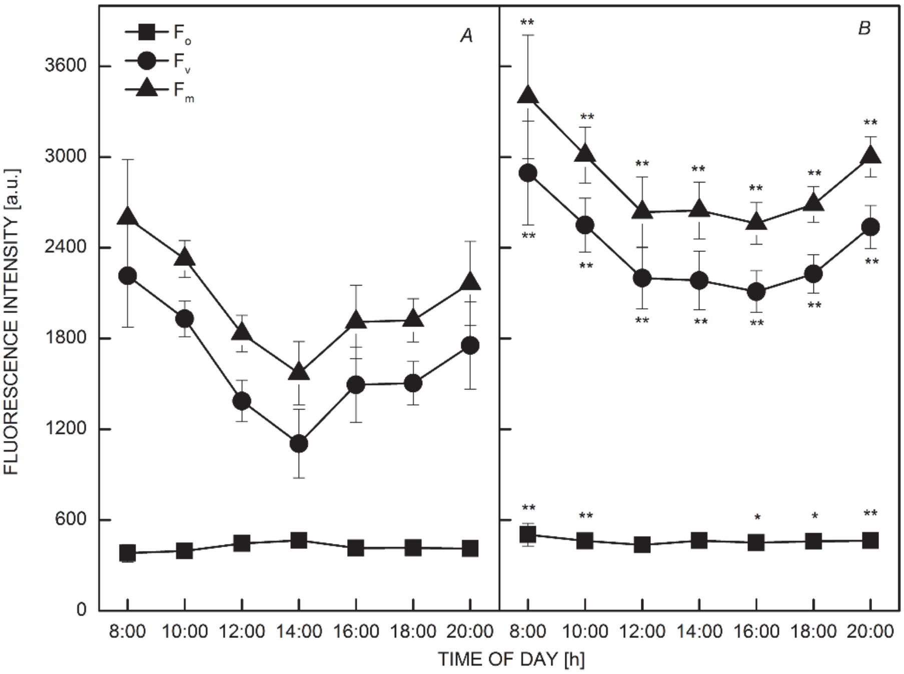

Fig. 3. Fluorescence intensity of F_o, F_v, F_m in the leaves of *Alhagi sparsifolia* seedlings under ambient and shade conditions (mean ± SD). F_o – minimal fluorescence (approximately 20 µs); F_v – variable fluorescence at time t; $F_m = F_p$, maximal recorded fluorescence intensity at the peak P of OJIP. *A*: ambient conditions, *B*: shade conditions.

ambient HL conditions, except at 8:00 and 10:00 (Fig. 8*A*). The ratio of variable fluorescence at the K-step to the fluorescence difference $F_j - F_o$ with $W_k = (F_k - F_o)/(F_j - F_o)$ of the plants grown under LL was higher than that of the plants grown under ambient HL (Fig. 8*B*).

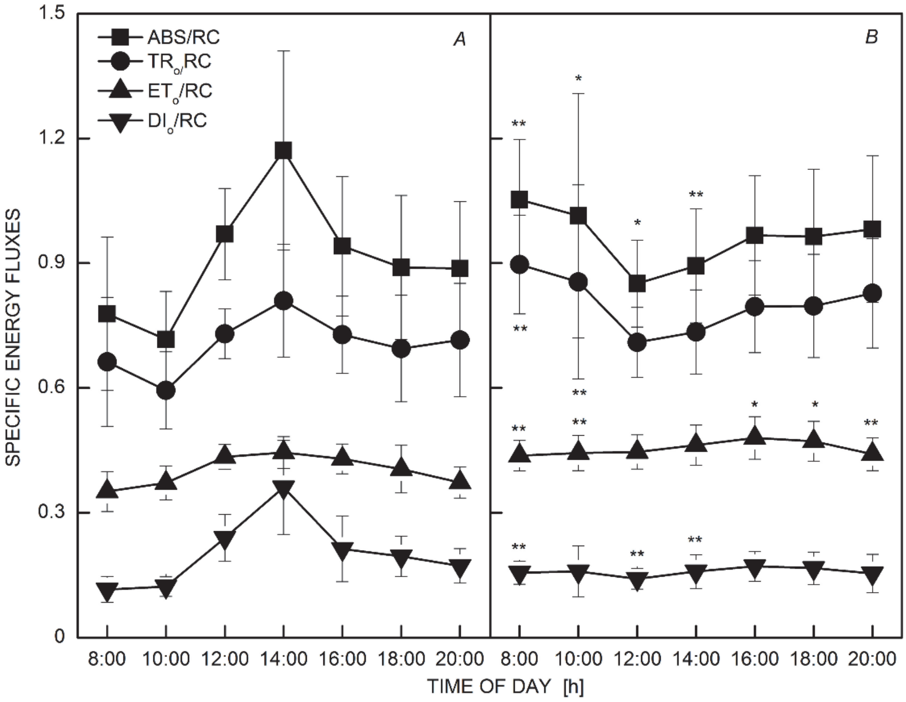

Fig. 5. Specific energy fluxes (per Q_A reducing PSII reaction centre – RC) under ambient ad shade irradiance (mean ± SD). ABS/RC – absorption flux per RC; TR_o/RC – maximal trapping flux per RC; ET_o/RC – electron transport flux per RC; DI_o/RC – flux of dissipated excitation energy per RC. *A*: ambient conditions, *B*: shade conditions.

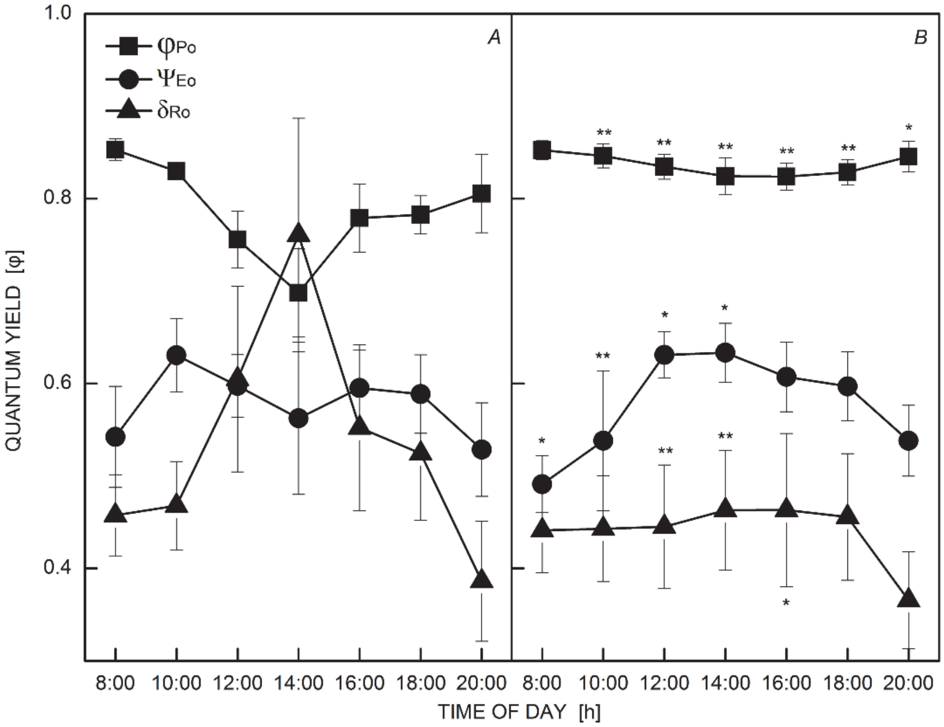

Fig. 6. Quantum yield of trapping, electron transport, and reduction of the end acceptors in electron transport (mean ± SD). φ_P – maximum quantum yield for primary photochemistry; ψ_E – efficiency/probability that an electron moves further than Q_A^-; δ_R – efficiency/probability with which an electron from the intersystem electron carriers is transferred to reduce end electron acceptors at the PSI acceptor side. *A*: ambient conditions, *B*: shade conditions.

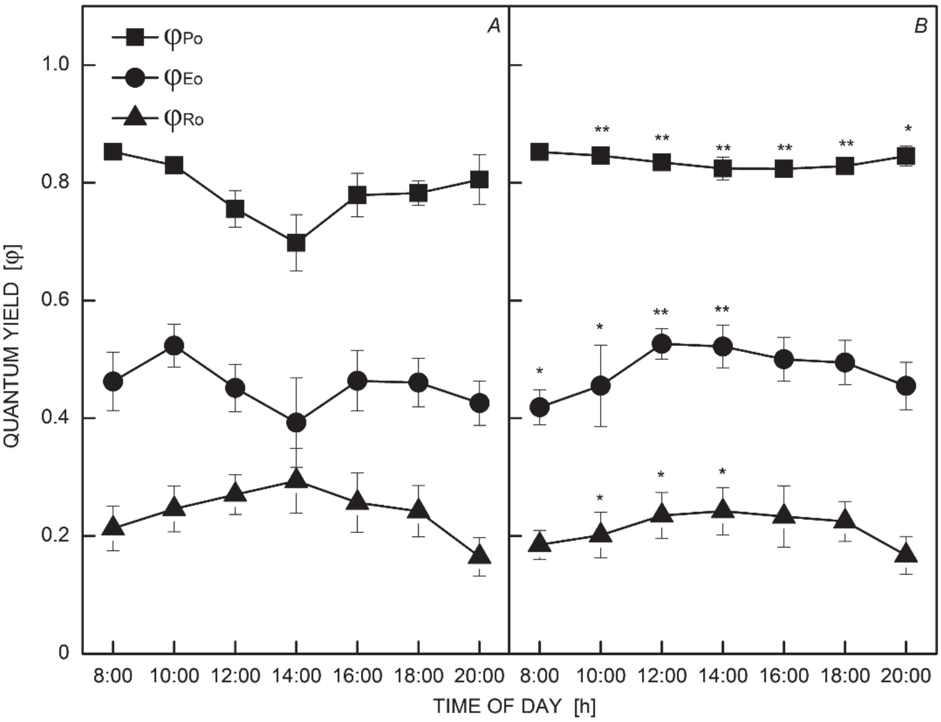

Fig. 7. Quantum yields of trapping, electron transport, and reduction of end acceptors in electron transport (mean ± SD). φ_P – maximum quantum yield for primary photochemistry; φ_E – quantum yield for electron transport; φ_R – quantum yield for reduction in end electron acceptors at the PSI acceptor side. *A*: ambient conditions, *B*: shade conditions.

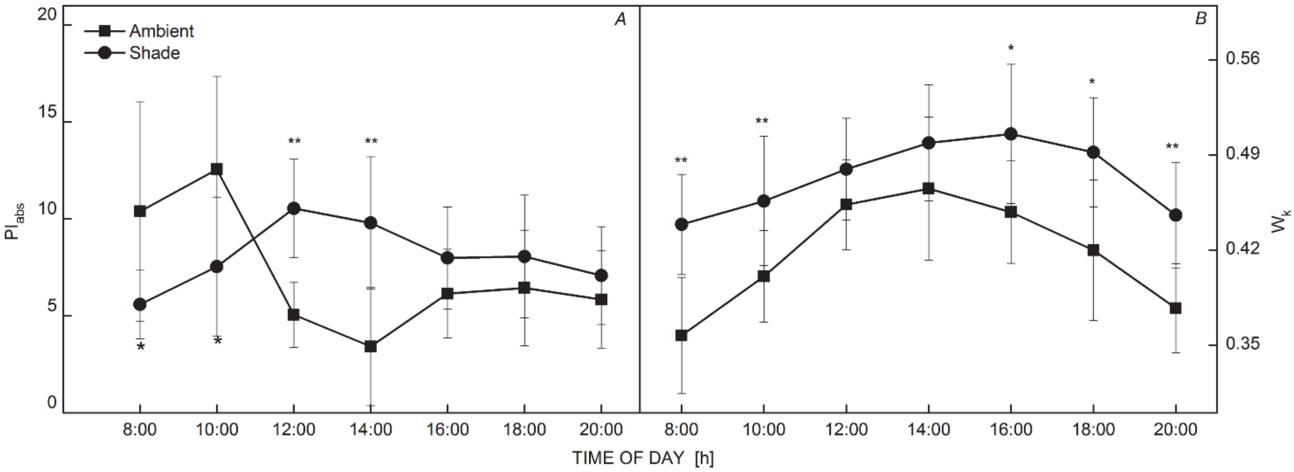

Fig. 8. Performance index on the absorption basis (PI_{abs}; *A*) and the ratio of variable fluorescence at the K-step to the amplitude $F_j – F_o$ (W_k; *B*) of the leaves of *Alhagi sparsifolia* Shap. under ambient and shade conditions (mean ± SD).

Discussion

Under environmental stresses, the concentration of the reduced primary quinone acceptor of PSII (Q_A^-) changes, causing the Chl fluorescence intensity changes (Strasser *et al.* 2000, Strasser *et al.* 2004); it represents the successive reduction of the electron acceptor pools of PSII (Govindjee 1995). The OJIP transient curves showed the absorbed energy from the light, and if the electron transfer from reaction center to quinone pool (Q_A and Q_B) is inhibited, the fluorescence intensity is dramatically reduced (Mehta *et al.* 2010). In the present study, the fluorescence intensity in midday was the lowest one and it was significantly higher under LL than that under ambient HL (Fig. 2), as well as the fluorescence intensity at F_o (minimal fluorescence, when all RCs are open, $F_o \approx F_{20\mu s}$), F_v (variable fluorescence, $F_v = F_m – F_o$), and F_m (maximal fluorescence, when all RCs are closed, $F_m = F_p$) also agree with this intensity (Fig. 3). These results could elaborate the reasons of electron flow blockage at the acceptor site of PSII and decreased the pool size of Q_A^- under ambient condition compared to shade conditions (Strasser and Srivastava 1995, Lazár 1999, Lu and Vonshak 2002). The present study also showed that both under ambient HL and shade

LL conditions the potential activity of PSII decreased in midday; it was higher under LL than under ambient HL (Fig. 4). Together, these results indicated that the acceptor side of PSII and the pool size of Q_A^- was inhibited at the HL conditions compared to those of LL, and PSII activities of both HL and LL conditions were limited in midday.

If energy is not dissipated safely, excessive light energy leads to accumulation od toxic species and damages of the photosynthetic apparatus when leaves are exposed to more light than they can utilize for photosynthesis (Quiles and López 2004). Excess excitation energy is converted into thermal energy which is dissipated as heat in order to maintain the energy balance between absorption and utilization (Hagemeyer 2004, Perales-Vela *et al.* 2007). ABS/RC, *i.e.* the effective antenna size of active reaction centers, is influenced by a ratio of active/inactive RCs (Mehta *et al.* 2010). In general, the increasing stress resulted in enhanced ABS/RC, TR_o/RC, and DI_o/RC (Ali *et al.* 2006). This result implies that electron transfer in leaves was blocked and the acceptor side of PSII was damaged under ambient HL conditions.

According to the equations of the JIP test, we estimated the maximum quantum yield for primary photochemistry ($\varphi_{Po} = F_v/F_m = TR/ABS$), the efficiency/probability that an electron moves further than Q_A^- (ψ_{Eo}), and the quantum yield of electron transport ($\varphi_{Eo} = ET/ABS$). The values of φ_{Po}, ψ_{Eo}, and φ_{Eo} in the seedling plants were higher under LL than under ambient HL (Figs. 6, 7). This result indicated that the light-dependent reaction and electron flow from the Q_A^- to the secondary quinone acceptor of PSII (Q_B) or Q_B^- were enhanced under LL more than that under ambient HL conditions (Chen *et al.* 2008, Strasser *et al.* 2010). It showed that the quantum efficiencies in PSII electron transfer chain of the plants grown under LL were enhanced compared to those of under ambient HL.

The efficiency/probability with which an electron from the intersystem electron carriers is transferred to reduce end electron acceptors at the PSI acceptor side (δ_{Ro}) and the quantum yield for the reduction of the end electron acceptors at the PSI acceptor side (φ_{Ro}) are divergent with φ_{Po}, ψ_{Eo}, and φ_{Eo}. The δ_{Ro} and φ_{Ro} values of the plants grown under LL were lower than those of the plants grown under ambient HL conditions (Figs. 6, 7). Our results indicated that lower quantum efficiencies of transfer from PSII to PSI were found in the shaded plants compare to those grown under ambient HL conditions, and the acceptor side of PSI was inhibited. These results may suggest that more energy was transferred to PSII, however, fewer energy was accepted by PSI under LL. Thus, as a consequence of lower photosynthetic capacity, the plants accumulated lower biomass under the shade (Wang *et al.* 2006, Li *et al.* 2014). However, more data on PSI activity in *A. sparsifolia* grown at ambient and shade conditions should be measured.

The performance index on the absorption basis (PI_{abs}) is sensitive to stresses and thus distinctively reflects the effect of environmental stresses on plants (Kalaji *et al.* 2012, Wang *et al.* 2012). The PI_{abs} in the seedlings of *A. sparsifolia* grown under LL were higher than those grown under ambient HL conditions (Fig. 8*A*). This result indicated that the PSII activity of the plants grown under shade was enhanced compared to that of the plants grown under ambient conditions (Kalaji *et al.* 2012, Wang *et al.* 2012). W_k of the plants grown at shade was higher than those grown under ambient condition which indicated that the donor side of PSII under shade conditions was seriously inhibited compared to ambient conditions (Chen *et al.* 2008).

High irradiance with high temperature in midday lead to the daily variation of the net photosynthetic rate in leaves that generated a bimodal curve in which the occurance of "midday depression" phenomenon was obvious (Ma *et al.* 2014). It was consistent with our results of Chl *a* fluorescence. We showed that part of RCs of the HL-grown plants experienced reversible inactivation, then quantum efficiency was reduced in midday. In contrast, the activity of RCs and quantum efficiencies of the LL-grown plants increased in midday. These results suggested that the plants grown under HL increased their thermal dissipation in order to protect the photosynthetic apparatus. However, LL conditions relieved the environmental stress in the plants and enhanced their energy transport in midday.

In conclusion, we showed that the donor side of PSII under shade was inhibited, while the acceptor side of PSII was inhibited under the ambient conditions. The PSII activity under the ambient conditions was seriously affected, while the plants grown under shade relieved the environmental stress and enhanced their energy transport in midday. The PSII activity of the plants grown in shade was enhanced, while the energy transport from PSII to PSI was blocked compared to that of the plants grown under ambient conditions. Thus, the plants exhibited the lower photosynthetic capacity and it resulted in the lower biomass under the shade conditions. However, more data on PSI of *A. sparsifolia* grown at ambient and shade conditions are needed.

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