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ORIGINAL PAPER

Photosystem II activity of typical desert plant *Alhagi sparsifolia* Sharp.: response to exposure to natural light after being kept in shade

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Abstract
Key message ***Alhagi sparsifolia*** **Sharp. is commonly considered as a type of sun plant, but shade-grown plants cannot acclimate to the strong irradiance which is normal for plant in a short time when kept in low-light conditions for a while.**
Abstract *Alhagi sparsifolia* Sharp., commonly considered as a type of sun plant, is the main vegetation found in the forelands of Taklamakan desert; this plant has an important function in wind prevention and sand fixation at the transition zone. *A. sparsifolia* could adapt to shaded conditions after a period of exposure to low-light conditions. However, whether or not the sun plant *A. sparsifolia* can adapt to natural light intensity after initial exposure to shaded conditions remains unknown. The specific light adaptation mechanism of this species is yet to be identified. In this study, the characteristics of the photosystem II (PSII) of *A. sparsifolia* exposed to natural light after the initial treatment under shaded lighting conditions were examined. Our results indicated that the PSII activity of *A. sparsifolia* under the specified condition was low; the thickness of leaves was reduced and occurred as an adaptive response to capture high amounts of light and exhibit high intensity of light-use efficiency. Shade leaves differed in terms of chlorophyll. Furthermore, the excess excitation energy has been converted to thermal dissipation energy to maintain energy balance. Shade-grown plants cannot adapt to strong irradiance, which is normal in plants for a short period when they are initially maintained under low-light conditions. Therefore, *A. sparsifolia* should not be considered as a typical sun plant.

Keywords *Alhagi sparsifolia* S. · Chlorophyll *a* fluorescence transients · Exposure to natural light · Light adaptation · Sun plant

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Introduction

Light is one of the most important environmental factors that regulate the development of the photosynthetic system in higher plants; as the source of energy for carbon fixation, light exhibits a regulatory function in plant growth. Under different lighting conditions, leaves develop various characteristics (Boardman 1977; Anderson 1986). For example, leaves that developed under high-light intensity are thicker and smaller than those grown under the shade (Murchie and Horton 1997). Plants show a decrease in the quantum

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yield of photosystem II (PSII) during photosynthetic electron transport and photochemical quenching; by contrast, an increase in non-photochemical quenching occurs as consequences of PSII photoinhibition when a plant is grown under high-light intensity (Quiles and López 2004). Sun leaves exhibit a higher photosynthetic capacity and contain higher amounts of ribulose bisphosphate carboxylase/oxygenase and electron transfer carriers than shade leaves (Jiang et al. 2011). Moreover, sun leaves show strong tolerance to high-light intensity because of high carbon assimilation rates and enhanced ability to dissipate excess light energy, whereas shade leaves exhibit increased susceptibility to damage from high-light intensity (Demmig-Adams and Adams 1992; Osmond and Förster 2006).

The photosynthetic plasticity of plants varies in response to different light conditions. The adverse effect of light stress on photosynthesis has been described in detail. In particular, the specific negative effects of different light conditions on chlorophyll content (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 studied. Under shade light conditions, leaf morphology is characterized by an increase in specific leaf area (SLA) and thickness as well as a decrease in stomatal density (Wang et al. 2006; Jiang et al. 2011). Considering the shade leaf physiology, Lichtenthaler et al. (2007) and Dai et al. (2009) found that Chl content likely increases, whereas the ratio of Chl *a* to Chl *b*, along with photosynthetic rates, possibly decreases. As plants experience stress from the environment, photosystems are inhibited and damaged (Briantais et al. 1996; Srivastava et al. 1997; Crafts-Brandner and Salvucci 2002). To study the effects of different environmental stresses on photosynthesis, researchers use Chl *a* fluorescence kinetics as an informative tool. This tool can be used as a primary method to investigate PSII function and PSII reaction to changing environmental and growth conditions (Kalaji et al. 2012). Sensitive proteins are abundant in PSII, but the thermostability of PSII in the photosynthetic organ is weak (Havaux 1996; Baker 1991; Allakhverdiev et al. 2008); these previous studies were conducted in sustained light environments. In addition, previous studies investigated the response of leaves transferred from low-light intensity to high-light intensity (Lovelock et al. 1994; Pearcy 1994; Yamashita et al. 2000; Bungard et al. 2000; Montgomery and Chazdon 2002). However, these studies have focused on plants in rainforests; studies have been rarely conducted on typical desert plants grown under high irradiance conditions.

Some plants can be classified as sun plants or shade plants. For example, *Alhagi sparsifolia*, commonly regarded as a sun plant, is the main vegetation found in the forelands of Taklamakan desert and exhibits an important function in wind prevention and sand fixation at the transition zone. *A. sparsifolia* can also be found under canopy where many tree species are found in the inner oasis. *A. sparsifolia* can also survive under shaded conditions. However, *A. sparsifolia* is taller and contains fewer branches under low irradiance than under ambient conditions. *A. sparsifolia* are xerophytes with characteristically small and thick leaves. Studies have further confirmed that sun plants can adapt to shaded conditions after exposure to low-light conditions for a specific period (Eschrich et al. 1989; Atanasova et al. 2003). However, this plant grown under canopy is exposed to natural light as well as biotic and abiotic factors.

This study was conducted to investigate whether or not *A. sparsifolia* can adapt to natural light intensity after exposure to shaded conditions. We hypothesized that *A. sparsifolia* cannot acclimate in environments exposed to strong irradiance when this plant is grown under the shade and then subsequently exposed to natural light for a short time. The results of this study could provide information to understand the relationship between leaf development and varying light intensity.

Materials and methods

Study site

The study was carried out near Cele oasis, located on the southern fringe of the Taklamakan desert at 1,365 m above sea level (84°43′30″–84°43′50″E, 37°01′01″–37°01′02″N). Cele is located 90 km east of Hotan in Xinjiang Uyghur Autonomous Region, NW China. The climate in the Taklamakan desert is extremely arid due to its location in the Tarim basin, surrounded by the alpine mountain ranges of Pamir to the west, the Tian Shan to the north, and the Kunlun to the south. The mean annual precipitation in the area is <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 snow melt from 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

The desert plant *A. sparsifolia*, the main vegetation found at the oasis-–desert transition zone in the southern fringe of Taklamakan desert, was used in this study. *A. sparsifolia* samples in the same sampling plot were randomly selected

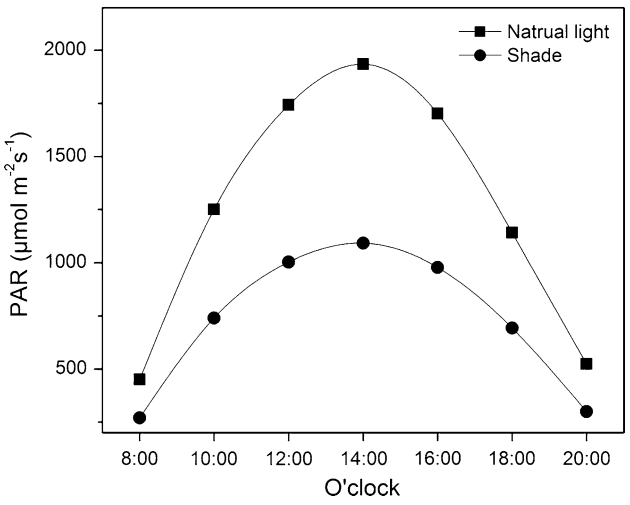

Fig. 1 Diurnal changes in the photosynthetic active radiation (*PAR*) in natural light and shade treatments (August)

and shaded with a piece of nylon net (5 × 5 × 1 m) on April 10, 2012. After 4 months, four of the eight nylon nets were taken down after which the PSII of the plants was characterized. *A. sparsifolia* was then exposed to natural light. On August 20 and 30, 2012, another set of PSII characterization was carried out. Each sample plot contained 6–8 plants, and the plant height was 60–80 cm.

Methods

Leaf thickness

Sixty healthy and fully mature leaves were selected in the middle of the second-order branching for the measurements; 30 leaves were randomly selected from each treatment to measure leaf thickness. Leaf thickness was measured using a vernier caliper with an accuracy of 0.01 mm. Five leaves

Table 1 The JIP-test formulate using data extracted from the fast Chl *a* fluorescence transient OJIP (Strasser et al. 2004, 2010)

Biophysical parameters derived from the fluorescence parameters	
Fluorescence parameters derived from the extracted	
$V_t = (F_t - F_o)/(F_m - F_o)$	Relative variable fluorescence at time t, V_K (300 μs), V_J (2 ms), V_I (2 ms)
$M_o = 4 \cdot (F_{300\mu s} - F_{50\mu s}) / (F_M - F_{50\mu s})$	Approximated initial slope (in ms^{-1}) of the fluorescence transient normalized on the maximal variable fluorescence F_V
Specific energy fluxes (per Q_A reducing PSII reaction center—RC)	
$ABS/RC = M_o \cdot (1/V_J) \cdot (1/\varphi_{Po})$	Absorption flux (of antenna Chls) per RC (also a measure of PSII apparent antenna size)
$TR_o/RC = M_o \cdot (1/V_J)$	Trapped energy flux (leading to Q_A reduction) per RC
$ET_o/RC = M_o \cdot (1/V_J) \cdot (1-V_J)$	Electron transport flux (further than Q_A^-) per RC
$DI_o/RC = (ABS/RC) - (TR_o/RC)$	Dissipate flux per RC
$RE/RC = M_o \cdot (1/V_J) \cdot (1-V_I)$	Electron flux reducing end electron acceptors at the PSI acceptor side per RC
Phenomenological fluxes or phenomenological activities	
$ABS/CS_o = F_o$	Absorption flux in cross section
$TR_o/CS_o = \varphi_{Po} \cdot (ABS/RC)$	Trapped energy flux in cross section
$ET_o/CS_o = \varphi_{Po} \cdot \psi_o \cdot (ABS/RC)$	Electron transport flux in cross section
$DI_o/CS_o = (ABS/CS_o) - (TR_o/CS_o)$	Dissipate flux in cross section
$RE/CS_o = \delta_{Ro} \cdot (ABS/CS_o) \cdot \varphi_{Eo}$	Electron flux reducing end electron acceptors at the PSI acceptor side in cross section
Density of reaction centers	
$RC/CS_o = \varphi_{Po} \cdot (V_J/M_o) \cdot (ABS/RC)$	Density of active reaction centers (Q_A reducing PSII reaction centers)
Quantum efficiencies or flux ratios	
$\varphi_{Po} = TR_o/ABS = F_v/F_m$	Maximum quantum yield for primary photochemistry
$\varphi_{Eo} = (F_v/F_m) \cdot \psi_o$	Quantum yield of electron transport
$\varphi_{Do} = (F_o/F_m)$	Quantum yield of energy dissipation
$\varphi_{Ro} = RE_o/ABS$	Quantum yield for reduction of end electron acceptors at the PSI acceptor side (RE)
$\delta_{Ro} = (1 - V_I)/(1 - V_J)$	Efficiency/probability with which an electron from the intersystem electron carriers is transferred to reduce end electron acceptors at the PSI acceptor side (RE)
Performance indexes	
$PI_{abs} = (RC/ABS) \cdot [\varphi_{Po}/(1 - \varphi_{Po})] \cdot [\psi_o/(1 - \psi_o)]$	Performance index (potential) for energy conservation from photons absorbed by PSII to the reduction of intersystem electron acceptors
$W_K = V_K - V_J$	The normalized relative variable fluorescence at the K step

comprised one group and used to measure the total thickness. The mean thickness was then obtained. Six groups were measured in each treatment. The mean leaf thickness for each sample of five leaves was calculated (Wilson et al. 1999). The experiments were performed with six replicates.

Specific leaf area (SLA)

Using the same samples measured for leaf thickness, we determined the leaf area with a Delta-T device (Cambridge, UK) area measurement system. The dry weight and measured leaf area of the samples were used to calculate specific leaf areas, in $cm^2\ g^{-1}$ (Wilson et al. 1999).

Proline, malondialdehyde (MDA), and chlorophyll (Chl)

Proline Approximately 0.2 g of fresh leaf tissue sample from each treatment was immersed in 5 ml of 30 ml l^{-1} sulfosalicylic acid in a test tube. The test tube was then placed in boiling water for 10 min. After cooling, the filtrate was extracted to obtain proline. Approximately 2 ml of filtrate sample was mixed with 2 ml of acid ninhydrin and 2 ml of glacial acetic acid in a test tube and then incubated in boiling water for 1 h. After cooling, 4 ml of toluene was added to the mixture. The test tube was dangled for 30 s and subsequently allowed to stand for a specific time. The top layer fluid was obtained and subjected to absorbance measurements at 520 nm using toluene as reference. Each treatment was investigated using five independent measurements

MDA Fresh plant leaves (0.5 g) from each treatment were ground with 5 ml of 5 % trichloroacetic acid (TCA). After the leaves were centrifuged at 3000 rpm for 10 min, 2 ml of the extract was mixed with 2 ml of 0.67 % thiobarbituric acid (TBA), heated at 95 °C for 30 min, quickly terminated at 0 °C, and centrifuged again. The absorbance of the supernatant was taken at 450, 532, and 600 nm. Each treatment was performed with five independent measurements

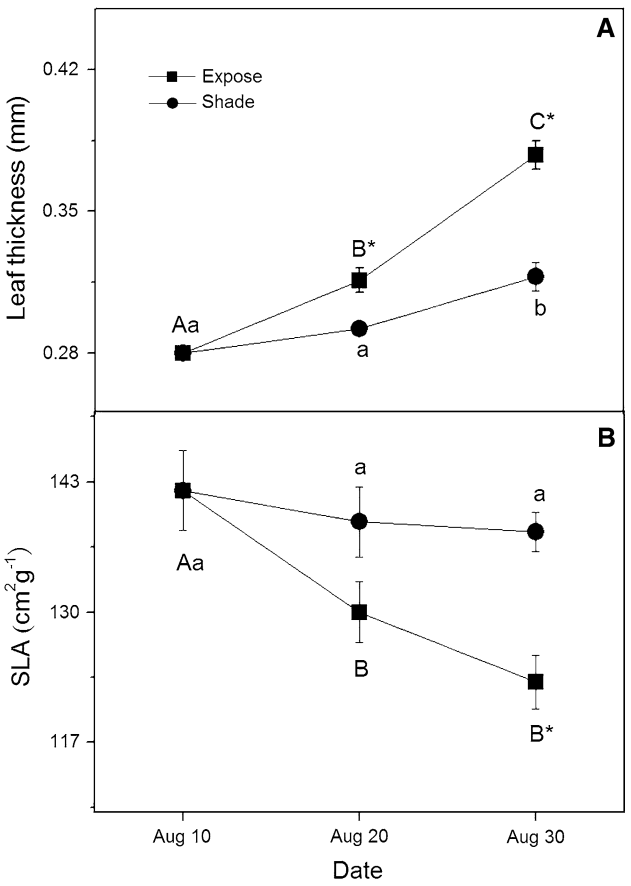

Fig. 2 Variables of leaf thickness (**a**) and SLA (**b**) in *A. sparsifolia* under shade and exposure to natural light conditions. *Different uppercase letters* indicate a significant difference in the exposed group at $p < 0.05$; *different lowercase letters* indicate a significant difference in the shade group at $p < 0.05$; asterisks indicate a significant difference between exposed and shade plants

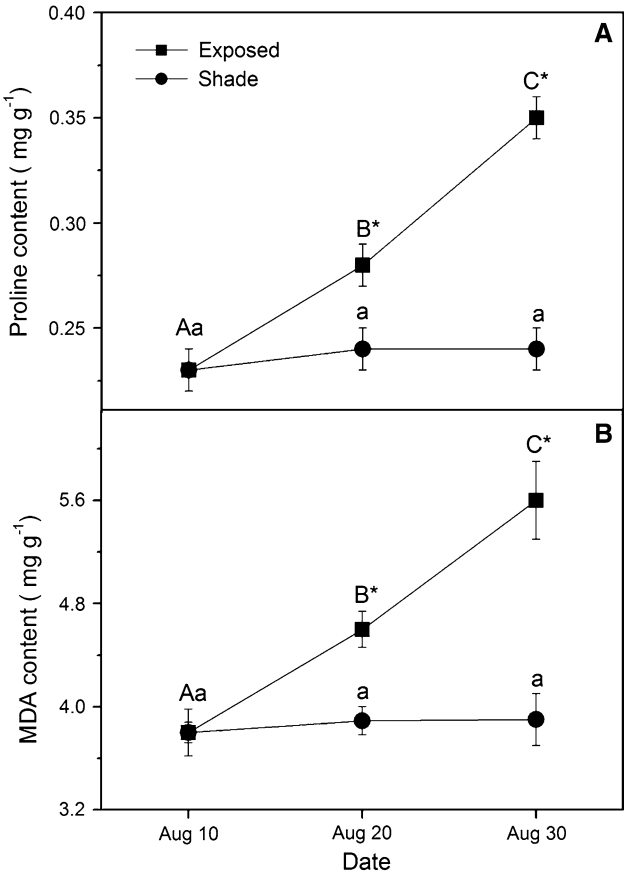

Fig. 3 Changes in proline (**a**) and MDA (**b**) contents of *A. sparsifolia* upon exposure to natural light after the initial shade treatments. *Different uppercase letters* indicate a significant difference in the exposed group at $p < 0.05$; *different lowercase letters* indicate a significant difference in the shade group at $p < 0.05$; asterisks indicate a significant difference between exposed and shade plants

Chlorophyll Pigments, based on the fresh mass, were extracted with 80 % acetone and determined using the extinction coefficients and equations described by Lichtenthaler (1987). Each treatment was performed with five independent measurements

Measurements of chlorophyll *a* fluorescence transient

Ten healthy and mature leaves were selected randomly in the middle of the second-order branching to examine PSII. The polyphasic Chl *a* fluorescence transient (OJIP) was measured using a fluorometer (PEA, Hansatech) at 12:00, with the noon maximum irradiance of ~1,100 μmol m^{-2} s^{-1} (Fig. 1). Chl *a* fluorescence transient was induced by a saturating PFD at 3,500 μmol photons m^{-2} s^{-1} provided by an array of three light-emitting diodes (peak = 650 nm) to generate the fluorescence curves expanding from dark-adapted minimum fluorescence (F_o) to F_m for all of the treatments (in this study, $F_m = F_p$). Data were initially sampled at an interval of 10 μs for the first 300 μs. This condition provided excellent time resolution of F_o and the initial rise kinetics. The time resolution of digitization was then switched to slower acquisition rates than the initial values. The PSII parameters and OJIP transient (Table 1) were analyzed according to Strasser et al. (2000, 2004, 2010).

Data presentation

Descriptive statistics was used to calculate the average and standard deviation of the data for each set of replicates. The results were expressed as mean or mean ± standard error. Parts of measurements were subjected to independent sample *t* test and ANOVA to determine the significant differences ($p < 0.05$). The graphs were produced using Origin 8.0 (OriginLab Inc., Hampton, USA) and Adobe Photoshop (Adobe Inc., San Jose, USA).

Results

Leaf thickness decreased upon exposure to natural light, thereby changing the SLA (Fig. 2). Proline and MDA

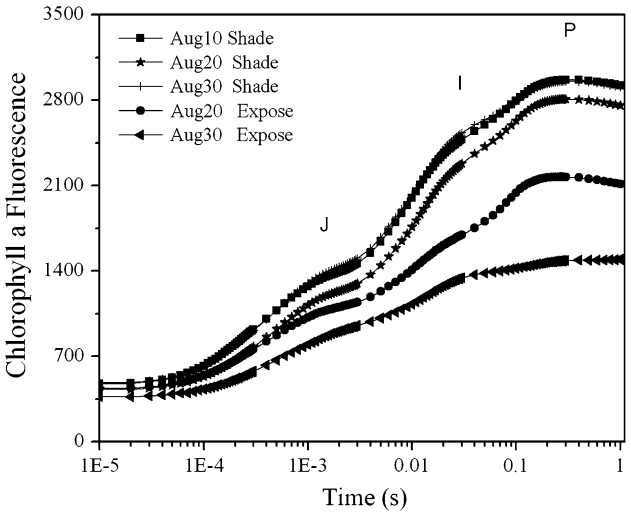

Fig. 5 Chlorophyll *a* fluorescence transients of *A. sparsifolia* upon exposure to natural light after the initial shade treatments

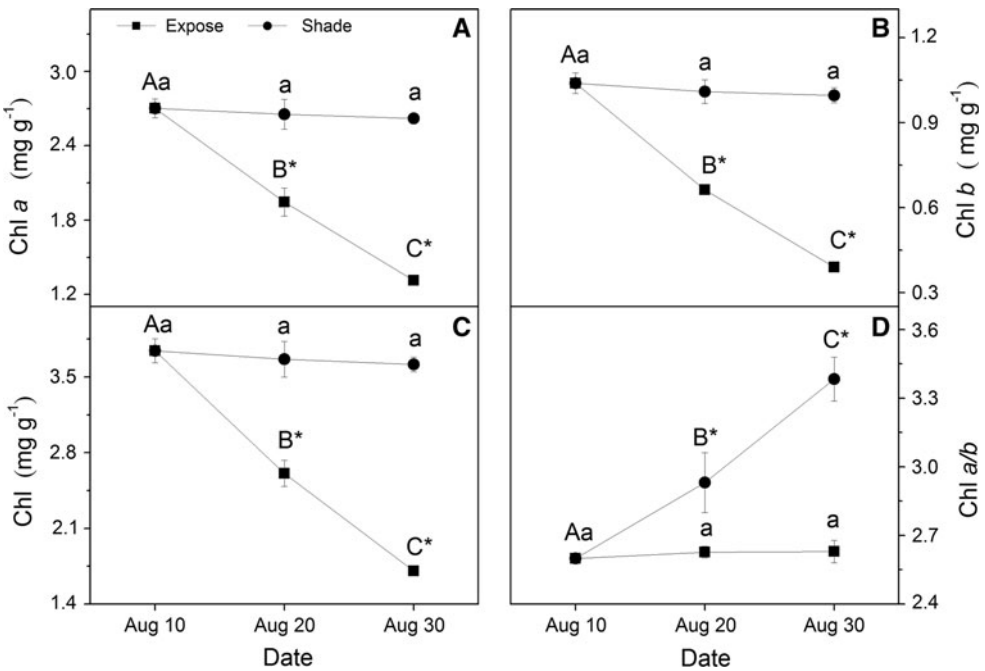

Fig. 4 Changes in Chl *a* (**a**), Chl *b* (**b**), Chl (**c**), and Chl *a*/*b* ratio (**d**) of *A. sparsifolia* upon exposure to natural light after the initial shade treatments. *Different uppercase letters* indicate a significant difference in the exposed group at $p < 0.05$; *different lowercase letters* indicate a significant difference in the shade group at $p < 0.05$; asterisks indicate a significant difference between exposed and shade plants

levels increased as treatments were increased (Fig. 3); Chl content decreased and the ratio of Chl *a* to *b* increased under high-light intensity (Fig. 4). The growth rate under continued shaded lighting condition did not change significantly.

The shape and intensity of Chl *a* fluorescence transients decreased after the leaves were exposed to natural light, but no apparent "*K*" step at ~300 μs was found. Moreover, growth continued under shaded lighting conditions without significant changes (Fig. 5).

The maximum quantum yield for primary photochemistry ($\varphi_{Po} = F_v/F_m$), quantum yield of electron transport (φ_{Eo}), and a trapped exciton that moved an electron into the electron transport chain beyond Q_A (ψ_o) of the shade-grown plants decreased under natural light. In Fig. 6, high-light intensity decreased the density of reaction centers (RC/CS_o), performance index (PI_{abs} and PI_{tot}), and the ratio of variable fluorescence at *K* step at an amplitude of $F_j - F_o$ (W_K); by comparison, high-light intensity increased the 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 absorption flux in the cross section (ABS/CS_o), trapped energy flux in the cross section (TR_o/CS_o), electron transport flux in the cross section (ET_o/CS_o), and dissipate flux in the cross section (DI_o/CS_o) decreased after the leaves were exposed to natural light. The growth rates under continued shaded lighting conditions did not change significantly.

The PSII parameters of plants exposed to natural light were highly changed compared with those exposed to natural light. These results indicated that the shade-grown plants could not acclimate in environments exposed to strong irradiance, which is normal in plants for a short time when these plants are maintained under low-light conditions (Fig. 7).

Discussion

The effects of different light conditions on the leaf morphology, pigment content, physiology, and photosynthesis of plant leaves were extensively studied. To the best of our knowledge, studies have been rarely conducted regarding the effect of natural light exposure of plants after they are maintained in shaded environments. In this study, *A. sparsifolia* plants were initially maintained under shaded conditions. Afterward, the plants were exposed to natural light. We observed that the PSII of *A. sparsifolia* leaves changed significantly.

The changes in SLA and leaf thickness in this study are consistent with those presented in previously reported data. Studies have also shown that SLA is possibly an indicator of plant adaptation to high- or low-resource habitats (Poorter and Pothman 1992; Walters et al. 1993; Wilson et al. 1999). In the present study, SLA indicated the expected return on previously captured resources, showing

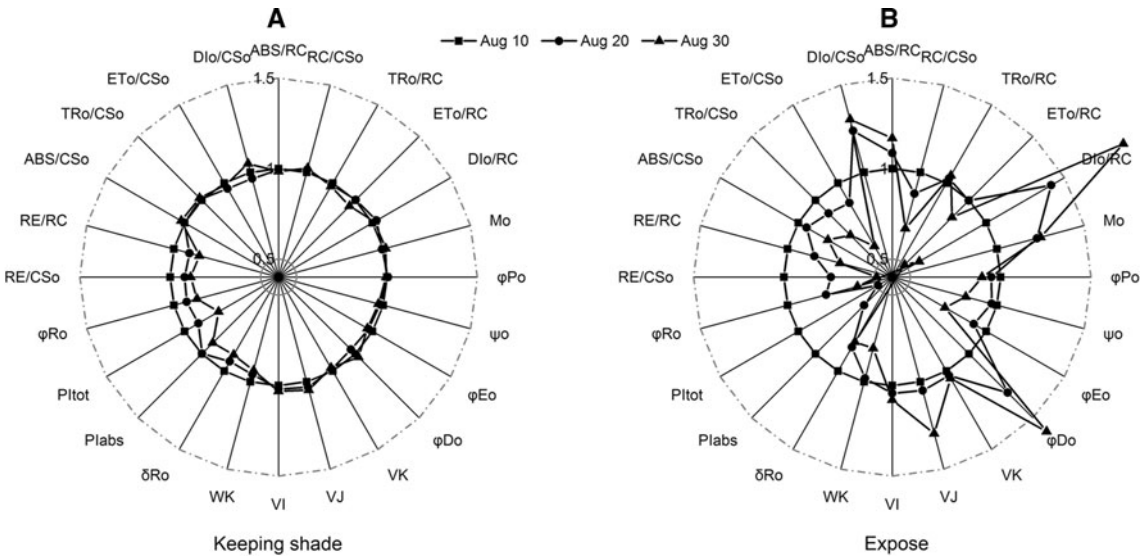

Fig. 6 Radar plot presentation of several parameters of chlorophyll *a* fluorescence upon exposure to natural light after the initial shade treatments. *ABS* absorbance, *CS* cross section, DI_o dissipate, *ET* electron transport, M_o approximated initial slope of the fluorescence transient normalized on the maximal variable fluorescence F_v, *PI* performance index, *RE* reduce end electron acceptors at the PSI acceptor side, *RC* reaction center, *TR* energy trapping flux, φ_{Do} quantum yield of energy dissipation (at $t = 0$), φ_{Eo} probability that an absorbed photon will move an electron into the electron transport chain beyond Q_A, ψ_o efficiency at which a trapped exciton can move an electron into the electron transport chain beyond Q_A, φ_{Po} maximum quantum yield of primary photochemistry; V_K, V_J, and V_I relative variable fluorescence at time *K* (300 μs), *J* (2 ms), and *I* (30 ms) steps, respectively, δ_{Ro} efficiency at which an electron from the intersystem electron carriers is transferred to reduce the final electron acceptors at the PSI acceptor side

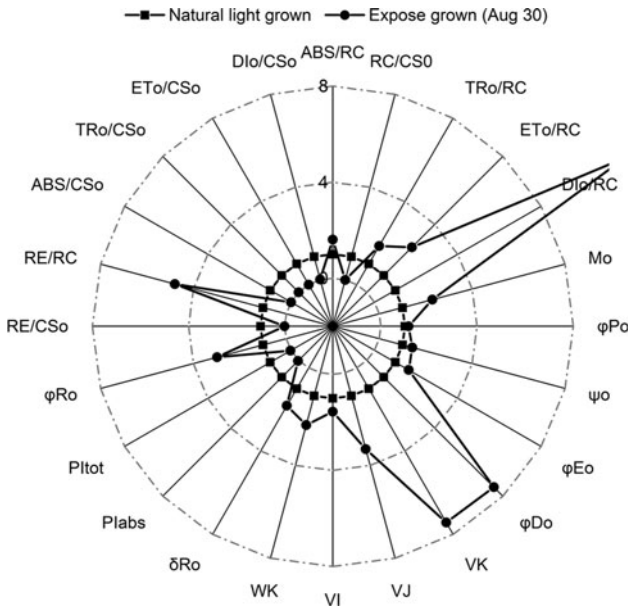

Fig. 7 Radar plot presentation of the compared parameters of plants grown under natural light after the initial shade treatments (Aug 30). *ABS* absorbance, *CS* cross section, *DI* dissipate, *ET* electron transport, M_o approximated initial slope of the fluorescence transient normalized on the maximal variable fluorescence F_v, *PI* performance index, *RE* reduce end electron acceptors at the PSI acceptor side, *RC* reaction center, *TR* energy trapping flux, φ_{Do} quantum yield of energy dissipation ($t = 0$), φ_{Eo} probability that an absorbed photon can move an electron into the electron transport chain beyond Q_A, ψ_o efficiency at which a trapped exciton can move an electron into the electron transport chain beyond Q_A, φ_{Po} maximum quantum yield for primary photochemistry, V_K, V_J, and V_I relative variable fluorescence at time *K* (300 μs), *J* (2 ms), and *I* (30 ms) steps, respectively; δ_{Ro} efficiency at which an electron from the intersystem electron carriers is transferred to reduce the final electron acceptors at the PSI acceptor side

that leaves with high SLA are productive (Poorter and Van der Werf 1998; Van der Werf et al. 1998). This variation in SLA is a result of a change in leaf thickness. Similar to other shade plant species, *A. sparsifolia* contains leaves with less thickness and high SLA (Wilson et al. 1999). High-SLA leaves function effectively in resource-rich environments, whereas low-SLA leaves function effectively in resource-poor environments (Wilson et al. 1999). In our study, natural light-exposed leaves were compared with shade-grown leaves. The results showed that leaf thickness was higher and SLA was lower in the exposed leaves than in the shade leaves (Fig. 2). The intensity of natural light probably inhibited the photosynthesis of *A. sparsifolia* because this plant originally grows under low lighting conditions but has been exposed to natural light. *A. sparsifolia* prefers less leaf thickness, inducing an increase in SLA to obtain high productive efficiency. This mechanism is used by the plant as adaptive responses to changes in light intensity. However, further investigation should be conducted to elucidate the detailed mechanisms of such adaptive responses.

The accumulation of proline and MDA has an important function in counteracting environmental stress (Zhao et al. 2003). Proline is distributed in the cytoplasm, adjusting organic substance concentrations in plants and maintaining the balance between the protoplast and the external environment. Thus, proline can stabilize the cell protein structure, thereby preventing the degeneration and inactivation of enzymes in plants (Santa-Cruz et al. 1999). MDA is the main product obtained when reactive oxygen species initiate lipid peroxidation in plant leaves (Gosset et al. 1994; Xu et al. 2010). In this study, plant leaves exposed to natural light exhibited higher concentrations of proline and MDA (Fig. 3) than those grown under shaded conditions. This result suggested that the antioxidant system of *A. sparsifolia* leaves was limited upon exposure to natural light. Hence, lipid peroxidation was increased and stress was induced by natural light.

Growth under high-light conditions compared with growth under low-light conditions commonly results in lower Chl *a* to *b* ratio and lower electron transport rate, but the change in Chl content varies depending on species (Feng et al. 2004; Baig et al. 2005; Bjorkman 1981); such variation occurs because sun leaves contain less LHCP2 and more reaction centers on a total Chl basis than shade leaves with more grana thylakoid antenna (Lichtenthaler et al. 2000, Laisk et al. 2005). In our experiment, Chl content was significantly lower and Chl *a* to *b* ratio was higher in natural light than in the shade (Fig. 4). This condition helps decrease light absorption. Furthermore, this result may indicate that shade leaves are transformed to sun leaves after exposure to natural light because of the change in light intensity, causing Chl change.

An increase in Chl *a* fluorescence reveals the characteristics of the OJIP polyphasic transient at room temperature when plotted on a logarithmic time scale. Chlorophyll fluorescence intensity changes when the concentration of the primary quinine acceptor of PSII (Q_A^-) changes under stress (Strasser et al. 2000, 2004). In the present study, the relative intensity of the OJIP transient intensities of leaves decreased in the *K* band zone (300 μs) when exposed to natural light. No pronounced "*K*" step was found (Fig. 5). Chl *a* fluorescence intensity of the exposed leaves to natural light changed significantly, whereas this parameter in the shade leaves slightly changed. These results revealed that natural light limits the donor side of the electron transport chain.

Fluorescence transient test, showing energy fluxes and electron transport in PSII, can be used to determine damage indicators (Strasser et al. 2000, 2004). For the maximum quantum yield of primary photochemistry ($F_v/F_m = \varphi_{Po}$), the efficiencies of ψ_o, φ_{Eo} and δ_{Ro} decreased under natural

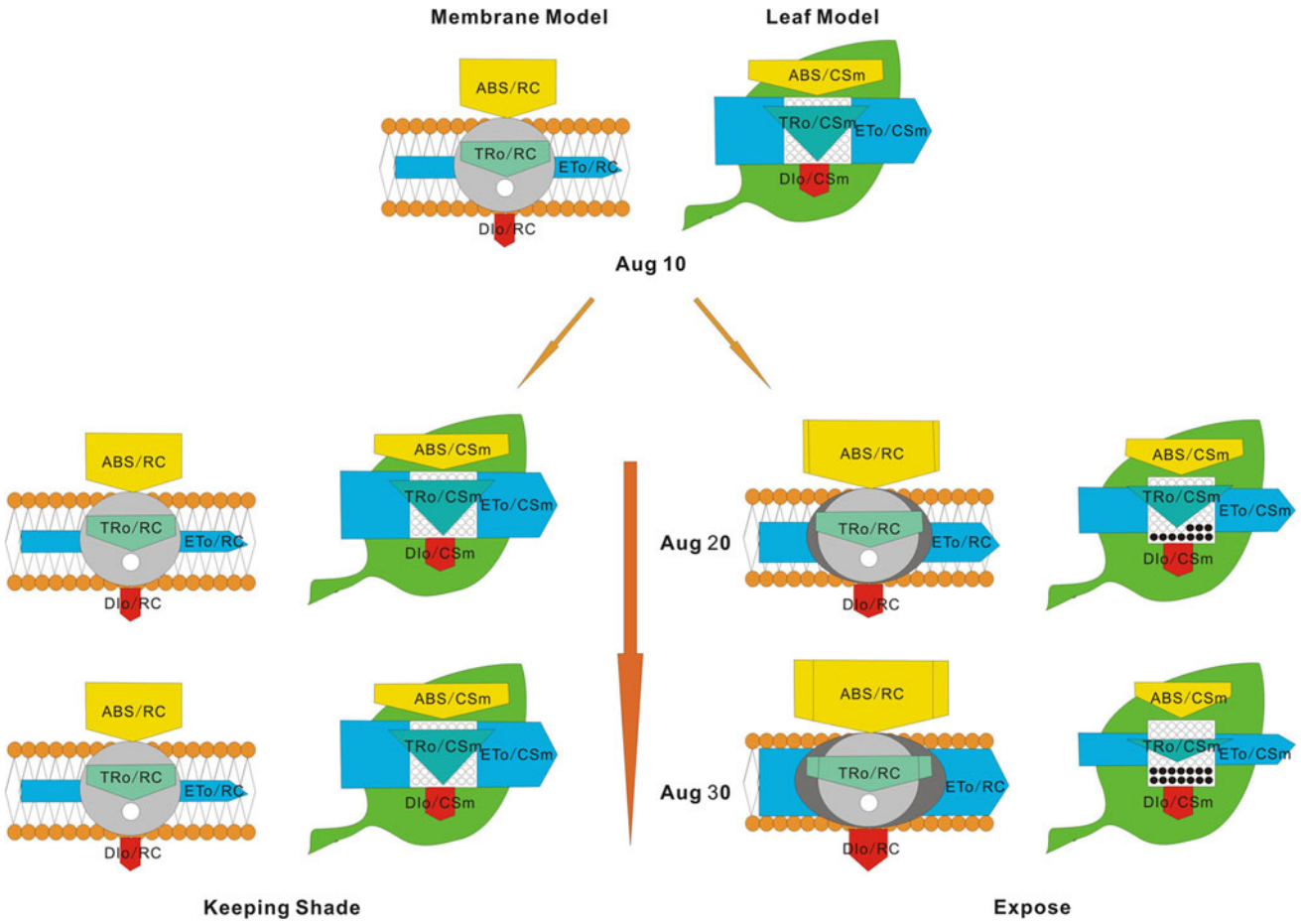

Fig. 8 Pipeline model of specific fluxes (membrane model) or phenomenological fluxes (leaf) of *A. sparsifolia* upon exposure to natural light after the initial shade treatments. *Filled circles* inactivation reaction centers; *unfilled circles* activity reaction centers. *ABS/RC* absorption flux per RC, TR_o/RC trapped energy flux per RC ($t = 0$), ET_o/RC electron transport flux per RC ($t = 0$), DI_o/RC dissipated energy flux per RC ($t = 0$), *ABS/CSm* absorption flux per excited cross section, TR_o/CSm trapped energy flux per excited cross section, ET_o/CSm electron transport flux per excited cross section, DI_o/CSm dissipated energy flux per excited cross section

light (Fig. 6). This result agrees with that of Rintamaki and colleagues (1994), indicating that the light-dependent reaction is inhibited and the electron flow from Q_A^- to secondary quinone acceptor of PSII (Q_B) or Q_B^- is blocked; the function of PSII is also inhibited. Ali and colleagues (2006) reported that the oxygen-evolving complex (OEC) is inhibited by Cr, thereby decreasing the number of active PSII reaction centers and PSII electron transport. As stress is increased, RC/CS_o is inhibited and the number is reduced, resulting in a subsequent increase in ABS/RC, TR_o/RC, and DI_o/RC (Ali et al. 2006). In the present study, leaves harvested more light energy, consistent with the responses of RC/CS_o after exposure to natural light (Fig. 6). We also observed the energy fluxes phenomenon of the membrane and leaf model per CS_o shown in Figs. 6 and 8. These results suggested that excess excitation energy has been converted to thermal dissipation to maintain energy balance between absorption and utilization; this mechanism can also protect plants from potential photooxidative damage (Zhang et al. 2010).

The ratio of variable fluorescence at K step to the amplitude $F_j - F_o$ for ~300 μs, W_K, and K band decreased under natural light when compared with shaded lighting conditions. Moreover, no apparent "K" step was found in the whole experiment (Figs. 5, 6). This result indicated that low-light conditions limited the acceptor side of the electron transport chain in the leaves. PI_{abs} and PI_{tot} correspond to the overall function of PSII more sensitively than other JIP-test parameters. Exposure to natural light inhibited the overall function of PSII.

In conclusion, the subsequent exposure of plants to natural light after they were grown under shaded conditions resulted in low PSII activity of the sun plant *A. sparsifolia*. After 20 days of exposure to natural irradiance, *A. sparsifolia* plants, which were initially grown in shaded environments, were unable to cope with high-light intensities.

Shade-grown plants could not adapt to strong irradiance, which is normal in plants for a short period when these plants are initially maintained under low-light conditions. Therefore, *A. sparsifolia* should not be considered as a typical sun plant.

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