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Research article

Assimilative branches and leaves of the desert plant *Alhagi sparsifolia* Shap. possesses a different adaptation mechanism to shade☆

Li Lei [a,b,c], Li Xiang-yi [a,c,*], Xu Xin-wen [a], Lin Li-sha [a,c], Zeng Fan-jiang [a,c], Chen Feng-li [a,b]

[a] State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011 China
[b] University of Chinese Academy of Sciences, Beijing 100049, China
[c] Cele National Station of Observation & Research for Desert-Grassland Ecosystem in Xinjiang, Cele, 848300 Xinjiang China

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ABSTRACT

Leaves and assimilative branches are crucial to the life cycle of *Alhagi sparsifolia* Shap. (Fabaceae), which grows in high-irradiance environments and is the main vegetation in the forelands of the Taklamakan Desert. This plant has an important role in wind protection and sand fixation at the oasis–desert transition zone. The morphology, physiology, and photosynthesis of *A. sparsifolia* leaves growing under low-light conditions have been extensively investigated. However, whether the plant's assimilative branches adapt similarly to low light levels is unclear, as are its specific light adaptation mechanisms. In this report, we characterized the biomass allocation, morphology, and chlorophyll *a* fluorescence of leaves and assimilative branches of *A. sparsifolia*. The results indicated that low-light conditions limited the normal growth of *A. sparsifolia*. The fraction of biomass allocated to leaves increased, whereas that to assimilative branches decreased. In addition, leaf thickness and assimilative branch diameter decreased, resulting in higher specific leaf area, specific assimilative branch length, and area for higher light absorbing and higher efficiency of light-usage. The assimilative branches and leaves were responded oppositely under low-light conditions in that leaves had lower photosystem II activity and assimilative branches had higher light-use efficiency to maximize light energy absorption for growth of *A. sparsifolia*.

1. Introduction

As the energy source for carbon fixation by plants, light is one of the most important environmental factors regulating the development of the photosynthetic apparatus; light also regulates plant growth. The leaves of plants respond differently depending on light availability. Under high-light conditions, leaves have higher photosynthetic capacity per unit area and greater thickness than under low-light conditions (Murchie and Horton, 1997). Moreover, plant leaves grown under high-light conditions have more ribulose bisphosphate carboxylase/oxygenase and electron transfer carriers (Jiang et al., 2011). In contrast, plants grown under low-light conditions have much higher levels of light-harvesting complexes in photosystem II (PSII).

The photosynthetic properties of plants change in response to light conditions. The negative effects of low light on photosynthesis have long been established. In particular, a lack of light adversely impacts chlorophyll content (Bailey et al., 2001), chloroplast ultrastructure, enzyme activities, and physiological and photochemical processes (Bailey et al., 2001; Clijsters and Van-Assche, 1985; Ohnishi et al., 2005). The morphology of leaves in the shade is characterized by an increase in specific leaf area (SLA) and a decrease in thickness (Jiang et al., 2011; Wang et al., 2006).

Plant photosystems respond sensitively to environmental stresses (Briantais et al., 1996; Srivastava et al., 1997; Crafts-Brandner and Salvucci, 2002). Chlorophyll *a* fluorescence kinetics are valuable indicators of these responses (Chen et al., 2008; Zhang et al., 2010) and can be used to investigate PSII function and activity under different growth conditions Zhang et al., 2010; Hazem et al., 2012). Most studies of low-light conditions have focused on leaves, however most living plant branches have greenish

Abbreviations: Chl, chlorophyll; PAR, photosynthetic active radiation; PEA, plant efficiency analyzer; PSII, photosystem II; Q_A, primary quinine electron acceptors of PSII; Q_B, second quinine electron acceptors of PSII; RC, reaction center; SAA, specific assimilative branch area; SAL, specific assimilative branch length; SLA, specific leaf area.

* Corresponding author. Xinjiang Institute of Ecology and Geography, CAS, 40-3 South Beijing Rd., Urumqi, Xinjiang 830011, China. Tel.: +86 991 7885438; fax: +86 991 7885320.
E-mail address: lixy@ms.xjb.ac.cn (L. Xiang-yi).

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photosynthesizing tissues. To the best of our knowledge, little attention has been given to photosynthesis of the stem (Osmond et al., 1987; Nilsen and Sharifi, 1994; Berveiller et al., 2007; Yiotis et al., 2008) and to differences in developmental adaptations between leaves and assimilative branches under low-light conditions.

Alhagi sparsifolia Shap. (Fabaceae), considered a desert sun plant, grows in high-irradiance environments and is the dominant vegetation of the forelands of the Taklamakan Desert, Xinjiang Uyghur Autonomous Region, northwest China. The plant plays an important role in wind protection and sand fixation at the transition zone of oasis to desert. Leaves and assimilative branches are crucial to the life cycle of *A. sparsifolia*, especially in arid regions. The assimilative branches and leaves represent 15% and 18% of the above-ground biomass, respectively.

This study was conducted to characterize the development of leaves and assimilative branches of *A. sparsifolia* and determine whether the assimilative branches adapt to low-light conditions in the same way that leaves do. The specific light adaptation mechanism of the plant was also investigated. Biomass allocation, morphology, and chlorophyll *a* fluorescence were assessed in *A. sparsifolia* plants grown in the shade. This study will assess the adaptation strategy of the assimilative branches under low-light environment and determine the specific light adaptation mechanisms of *A. sparsifolia* grown in arid regions. The results will further our understanding of the development of leaves and assimilative branches in desert plants.

2. Results

The ratio of the number of leaves to that of assimilative branches of *A. sparsifolia* increased with decreasing light intensity (Fig. 1), and dry mass fractions of leaves and branches increased as the amount of photosynthetically active radiation declined. In contrast, dry mass fraction of assimilative branches and stem leaves decreased. Dry mass per leaf and per assimilative branch also decreased. Similarly, leaf thickness and assimilative branch diameter also decreased, whereas the area per leaf, area per assimilative branch, and assimilative branch length increased, causing SLA, SAL, and SAA to increase (Fig. 2). The leafing intensity based on twigs and stems increased. In contrast, the assimilative branching intensity decreased with decreasing light intensity (Fig. 3).

The shape and intensity of OJIP transients were altered by decreased light intensity on the leaves and assimilative branches of *A. sparsifolia*. The OJIP transient intensity in the leaves and assimilative branches increased with decreasing light intensity. The chlorophyll *a* fluorescence intensity in the assimilative branches changed significantly, whereas it only changed slightly in the leaves (Fig. 4).

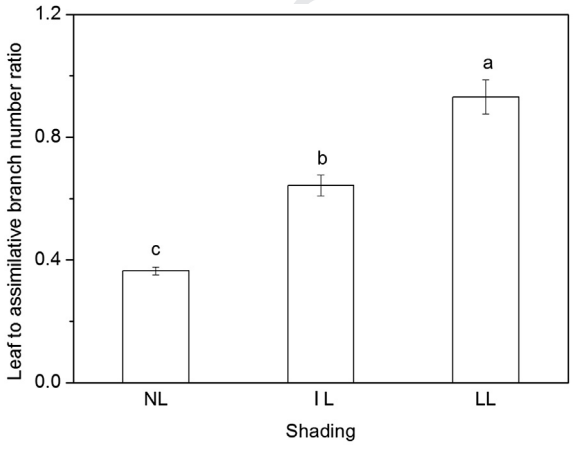

Fig. 1. Leaf-to-assimilative branch number ratio of *A. sparsifolia* under different light conditions. NL, normal light; IL, intermediate light; LL, low light.

The changes in quantum efficiencies are shown in Fig. 5. The value of the maximum quantum yield for primary photochemistry (φ_{Po} = TR_o/ABS) and the quantum yield of electron transport (φ_{Eo} = ET_o/ABS) of the leaves decreased with decreasing light intensity. An opposite trend was observed in assimilative branches. Low-light conditions decreased the reaction center density (RC/CS_o) of the leaves and increased it in the assimilative branches. However, 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) increased in leaves and decreased in assimilative branches (Fig. 5).

The difference of two traces of relative variable fluorescence, $V(t)$, between F_j and F_o shows the K-band with a maximum $V_K = (F_K - F_o)/(F_J - F_o)$ (where F_K is the fluorescence intensity measured at 300 μs). V_{IK} increased in leaves with decreasing light intensity, whereas that of the assimilative branches showed no significant changes with irradiance gradients. In contrast, the performance index on the absorption basis (PI_{abs}) in the leaves decreased, whereas that in the assimilative branches significantly increased under low light (Fig. 5).

3. Discussion

We evaluated the effects of three different light conditions on the biomass allocation, physiology, and photochemistry parameters of *A. sparsifolia*. These factors have not yet been well characterized in desert plants with assimilative branches or leaves. Our results showed that biomass allocation and PSII properties of leaves and assimilative branches changed significantly under different light conditions.

3.1. Characteristics of morphology under low-light conditions

Under low-light conditions, plants distribute more biomass into leaves (Wang et al., 2006; Walters et al., 1993). Previous studies have demonstrated that leaves with higher SLA have higher light-use efficiency than those with lower SLA (Poorter et al., 1998; VanderWerf et al., 1998). In the present study, the fraction of leaf mass increased with decreasing light intensity, whereas that of assimilative branches per unit mass decreased. Moreover, leaf thickness and assimilative branch diameter were reduced, causing higher SLA, SAL, and SAA. Given that *A. sparsifolia* is a desert plant that grows under high-light conditions, low light levels would not be optimal for its efficient photosynthesis. Thus, under low-light conditions, the leaves and assimilative branches became thinner, resulting in higher SLA, SAL, and SAA to improve light-use efficiency. The carbon (biomass) allocation was shifted to leaves, which use light more efficiently, rather than to assimilative branches. The plant uses this strategy to optimize photosynthesis under these conditions.

3.2. Activity of PSII under low-light conditions

The rise in chlorophyll *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 fraction of Qa^- of the primary quinine acceptor of PSII (Q_A^-) is affected by stress (Strasser et al., 2000; Strasser et al., 2004). In the present study, the relative intensity of the OJIP transient intensities of leaves and assimilative branches increased in the K-band zone (300 μs) with decreasing light intensity. Here, no

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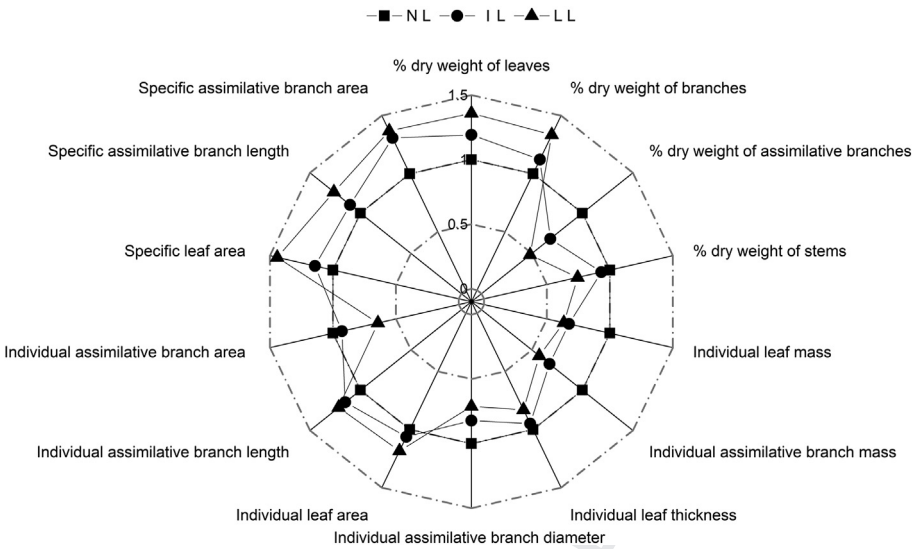

Fig. 2. Radar plot presentation of a constellation of morphological variable of *A. sparsifolia* under different light conditions. NL, normal light; IL, intermediate light; LL, low light.

pronounced "K" step was found (Fig. 4). The chlorophyll *a* fluorescence intensity changed significantly in the assimilative branches but only slightly in the leaves. The results revealed that the activity of donor side of PSII of the assimilative branches under low-light condition was higher than that under normal light condition.

According to the equations of the JIP test, we estimated the maximum quantum yield for primary photochemistry ($\varphi_{Po} = F_v/F_m = TR_o/ABS$), the quantum yield of electron transport ($\varphi_{Eo} = ET_o/ABS$), and the quantum yield of energy dissipation ($\varphi_{Do} = DI_o/ABS$) (Fig. 5). The φ_{Po}, δ_{Ro} (RE/ET), and φ_{Eo} values of the leaves decreased as the light intensity decreased, indicating that the light-dependent reactions were inhibited and that the electron flow from Q_A^- to the secondary quinone acceptor of PSII (Q_B) or Q_B^- was blocked with decreasing light intensity. In contrast, the φ_{Po} and φ_{Eo} values were higher in the assimilative branches under lower irradiance conditions, suggesting that electron flow in the assimilative branches was more efficient with increasing light intensity.

Excess excitation energy is dissipated as heat to maintain a balance between energy absorption and use, which protects cells (Hagemeyer et al., 1999; Perales-Vela et al., 2007). Generally, with increasing stress, the value of RC/CS_o is reduced. This decrease in the number of Q_A reducing reaction centers increased the apparent average antenna size (ABS/RC) and, therefore, also TR_o/RC and DI_o/RC (Ali et al., 2006). In the present study, the RC/CS_o in the leaf cross section of *A. sparsifolia* decreased, whereas ABS/RC, TR_o/RC,

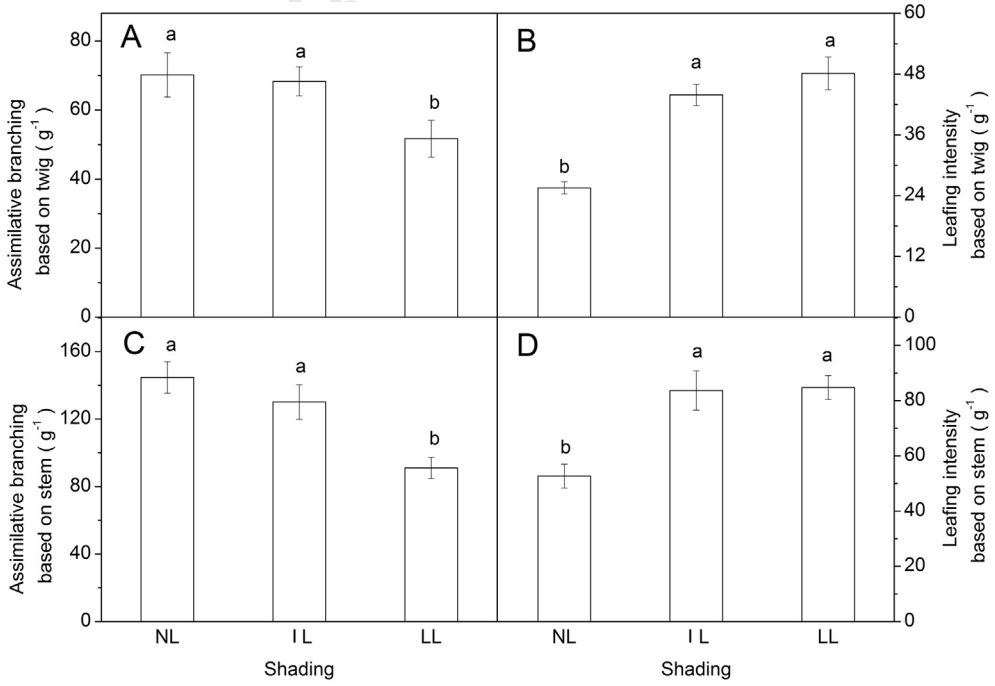

Fig. 3. Assimilative branching based on twigs (A), leafing intensity based on twigs (B), assimilative branching based on stems (C), and leafing intensity based on stems (D) under different light conditions. NL, normal light; IL, intermediate light; LL, low light.

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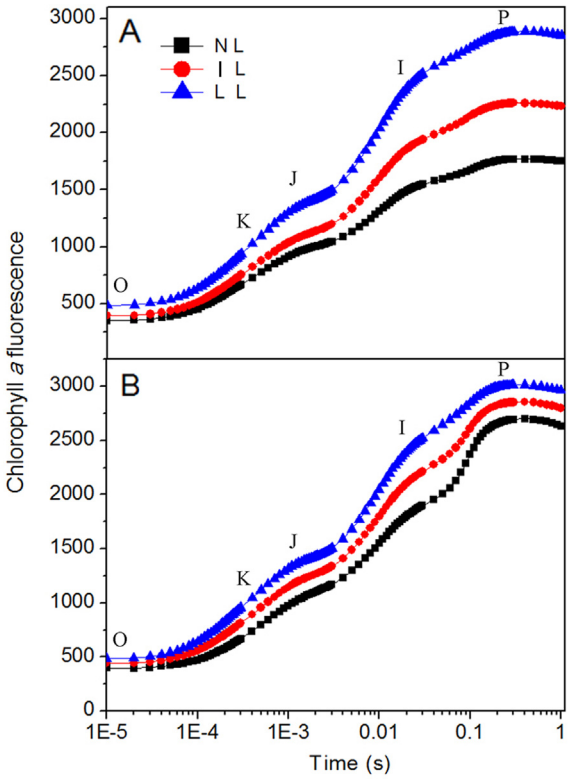

Fig. 4. OJIP transient of the leaves and assimilative branches of *A. sparsifolia* under different light conditions (averaged). $n = 10$. (A) assimilative branch, (B) leaf. NL, normal light; IL, intermediate light; LL, low light.

and DI_o/RC increased, with increasing light levels. Opposite trends were observed in the assimilative branches (Fig. 6). The leaf and assimilative branch model, refers to the excited cross section of leaf and assimilative branch, and then deals with the phenomenological energy fluxes per CS_o (Fig. 6). The absorption flux in cross section (ABS/CS_o) and trapped energy flux in cross section (TR_o/CS_o) of leaves as well as assimilative branches increased with decreasing light intensity. There was no change in the electron transport flux in cross section (ET_o/CS_o) and dissipate flux in cross section (DI_o/CS_o) of the leaves, while the values of these two parameters in assimilative branches increased with lower light intensity (Fig. 6). These changes in PSII suggested that the leaves dissipate more excess excitation energy to protect the cells under low irradiance via non-photochemical pathways, while assimilative branches trap more energy for higher light-use efficiency. Similar results were reported previously (Chen et al., 2008; Zhang et al., 2010; Ali et al., 2006; Wang et al., 2012).

The increase in relative variable fluorescence, V_{OJ}, at about 300 μs, V W_K of the leaves was higher under low-light than under high-light conditions. However the K-band of the assimilative branches decreased (Fig. 5), which indicated that low-light conditions limited the acceptor side of the electron transport chain in the leaves. However, the assimilative branches had a more efficient electron transport chain. The above values changed PSII parameters of leaves grown under low-irradiance, drastically decreased the overall photosynthesis performance index (PI_{abs}, PI_{totle}), and the value of assimilative branch increased in LL condition. This sensitive index reflects the effects of environmental stresses on leaves and assimilative branches (Wang et al., 2012).

In conclusion, low-light conditions limited the normal growth of *A. sparsifolia*. The leaves displayed lower PSII activity under low-light conditions, as has been reported in other studies. However, the assimilative branches had more efficient electron transfer and higher reaction center density in cross section, causing higher light-use efficiency. During the growth of *A. sparsifolia* under low light, more biomass was distributed into twigs. Moreover, the dry mass of leaves (as a fraction of total dry mass) increased, whereas that of the assimilative branches decreased under low irradiance. The area and productive efficiency of the assimilative branches were lower than in leaves. Thus, low light levels were beneficial to leaves, which absorbed more light for photosynthesis per unit area. In addition, the assimilative branches developed higher PSII activity to obtain maximum light energy for plant growth.

4. Materials and methods

4.1. Study site

The study was performed near the Cele Oasis at the southern fringe of the Taklamakan Desert at 1365 m a.s.l. (37°01′01″–37°01′02″

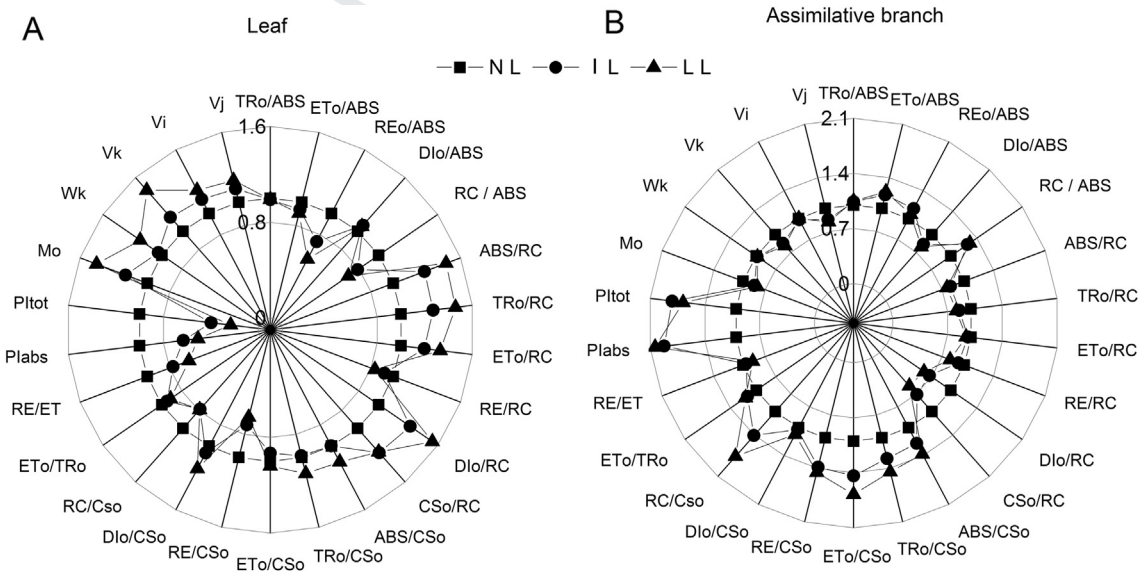

Fig. 5. Radar plot presentation of a constellation of parameters of chlorophyll a fluorescence with different light conditions. NL, normal light; IL, intermediate light; LL, low light.

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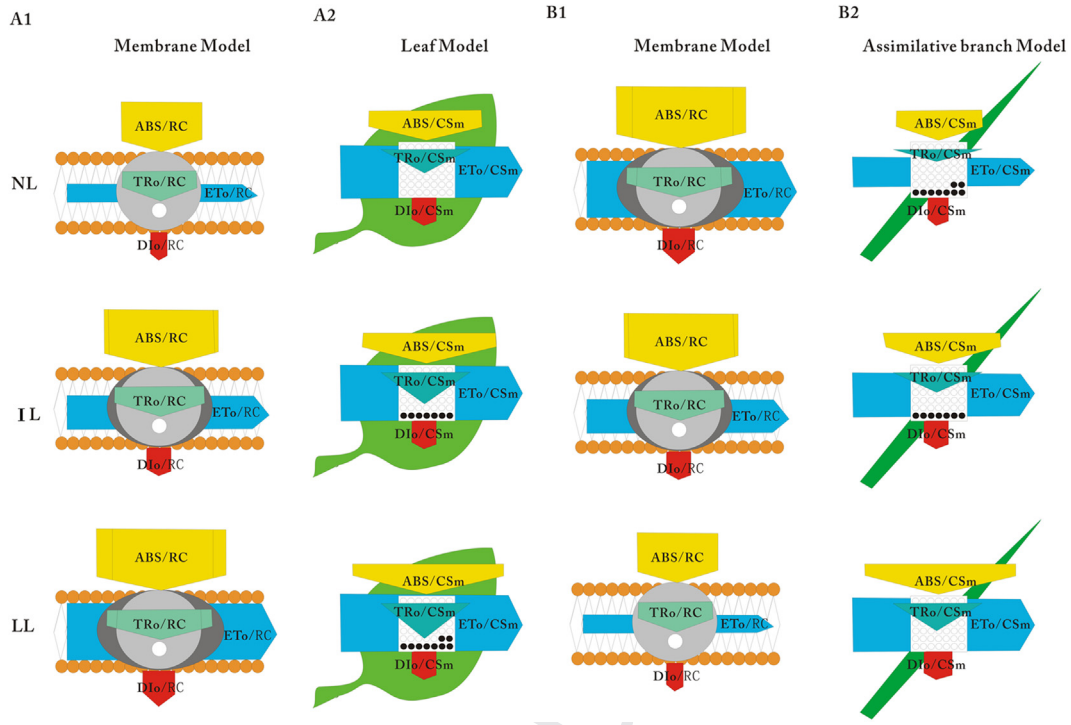

Fig. 6. Pipeline model for specific fluxes (membrane model) or phenomenological fluxes (leaf and assimilative branch) after *A. sparsifolia* grown under different light conditions. The response of each of the parameters can be seen as relative branch width of each arrow compared to the control sample (NL). NL, normal light; IL, intermediate light; LL, low light; A1, membrane model of leaf; A2, leaf model; B1, membrane model of assimilative branch; B2, assimilative branch model ≙, inactivation reaction centers; ○, activity reaction centers.

N, 84°43′30″–84°43′50″ E). The Cele Oasis is located 90 km east of Hotan in Xinjiang Uighur Autonomous Region, China. The climate in the Taklamakan Desert is extremely arid because of its location in the Tarim Basin, which is surrounded by the mountain ranges of Pamir to the west, Tian Shan to the north, and Kunlun to the south. The mean annual precipitation in the area is less than 40 mm, but evaporation can be as high as 2600 mm per year, with a mean summer temperature of 26.1 °C. Tributaries and ephemeral rivers, fed by snow melt in the mountains during the summer months, form river oases along the desert margins. The Cele Oasis is surrounded by a 5–10 km belt of sparse vegetation dominated by woody phreatophytic species.

4.2. Plant treatments

Alhagi sparsifolia, which is the dominant vegetation of the oasis–desert transition zone at the southern fringe of the Taklamakan Desert, was used in this study. Samples of *A. sparsifolia* growing naturally in the area were randomly selected. Three light intensities — normal light (NL), intermediate light (IL), and low light (LL) — were created with nylon net (5 × 5 × 1 m). On April 10, 2012, when the plants had three expanded true leaves, the nylon net was placed over them. The maximum irradiance was approximately 1100 μmol m^{-2} s^{-1} at noon (Fig. 7). Each sample plot contained about six to eight plants. Characterization of biomass allocation, morphology, and PSII was conducted on August 15, 2012, when the plants were about 60 cm tall.

4.3. Leaf and assimilative branch traits

Leaf lamina thickness between the veins was measured using a Verdict analog thickness gauge mounted on a steel sheet, which was in contact with the leaves on the glass slide. We measured the thickness of five healthy, mature leaves to an accuracy of 0.01 mm, and each measurement was repeated eight times. The mean leaf thickness for each sample of the five leaves was calculated (Wilson et al., 1999).

The diameter at the middle of assimilative branches was measured using a Vernier caliper with an accuracy of 0.01 mm. For each treatment, we measured 20 independent assimilative branches.

Per individual leaf area, assimilative branch area, and assimilative branch length were measured using the area measurement system (Delta-T Devices, Cambridge, UK). The dry weight, measured leaf area, assimilative branch length, and area of the samples were used to calculate SLA (cm^2 g^{-1}), SAL (mm g^{-1}), and SAA ($cm^2 \cdot mg^{-1}$).

Leafing/assimilative branching intensity was calculated as the number of leaves/the number of assimilative branches borne on a stem/twig divided by the twig dry mass (Yang et al., 2008).

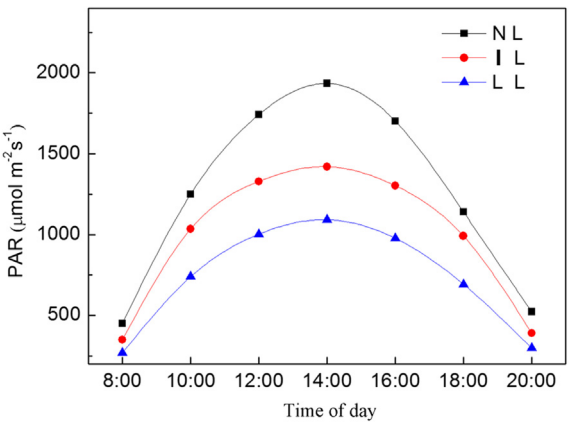

Fig. 7. Diurnal changes in photosynthetic active radiation (PAR, averaged) under different light conditions (August). It was measured in sunny day which are representative day. NL, normal light; IL, intermediate light; LL, low light.

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4.4. Plant biomass accumulation

Alhagi sparsifolia plants with good above-ground growth were randomly selected. Dust on the surfaces was gently removed with distilled water. The plants were taken back to the laboratory, and then the leaves, assimilative branches, twigs, and stems were separated using scissors. The number of sections was recorded, the area was scanned for measurement, and the samples were dried in an oven at 80 °C for 48 h to measure the dry biomass accumulation of each section.

4.5. Measurements of chlorophyll a fluorescence transients

The polyphasic chlorophyll *a* fluorescence (OJIP) transients (Strasser and Govindjee, 1992) were measured using a plant efficiency analyzer (Hansatech Instruments Limited, Norfolk, UK) at 10:00 on sunny days. All the measurements were carried out *in situ* below the nylon net (LL and IL) without damaging the plant. Chlorophyll *a* fluorescence was induced by a saturated photon flux density at 3500 μmol photons m^{-2} s^{-1} provided by an array of three light-emitting diodes (peak 650 nm) to generate fluorescence curves expanding from F_o to F_m for all treatments (in this study, $F_m = F_p$). Initially, the data were sampled at 10 μs intervals for the first 300 μs. This condition provided an excellent time resolution of the dark-adapted minimum fluorescence (F_o) and initial rise kinetics. The time resolution of digitization was then switched to slower acquisition rates. The PSII parameters derived from the OJIP transient were analyzed based on the study of Strasser et al. (Table 1) Strasser et al., 2000; Strasser et al., 2004; Strasser et al., 2010).

Table 1
The JIP-test formulate using data extracted from the fast Chlorophyll *a* fluorescence transient O-J-I-P (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 centre − 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 centres	
$RC/CS_o = \varphi_{Po}\cdot(V_J/M_o)\cdot(ABS/RC)$	Density of active reaction centers (QA-reducing PSII reaction centers)
Quantum efficiencies or flux ratios	
$\varphi_{Po} = TR_o/ABS = F_v/F_m$	Maximum quantum yield for primary photochemistry
$\varphi_{Eo} = (F_v/F_m)\cdot\psi_0$	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
$PI_{tot} = PI_{abs}\cdot\delta_{Ro}/(1 - \delta_{Ro})$	Performance index (total)
$W_K = V_K - V_J$	The normalized relative variable fluorescence at the *K* step

4.6. Statistical analysis

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 ± standard error (SE). Student's *t*-test was used for the statistical analysis of experimental data. Statistical significance was accepted when $P \leq 0.05$. The graphs were produced using Origin 8.0 (OriginLab Inc., Hampton, USA) and Adobe Photoshop (Adobe Inc., San Jose, USA).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.plaphy.2013.11.009

References

Ali, N.A., Dewez, D., Didur, O., Popovic, R., 2006. Inhibition of photosystem II photochemistry by Cr is caused by the alteration of both D_1 protein and oxygen evolving complex. Photosynth Res. 89, 81–87.
Bailey, S., Walters, R.G., Jansson, S., Horton, P., 2001. Acclimation of Arabidopsis thaliana to the light environment: the existence of separate low light and high light responses. Planta 213, 794–801.
Berveiller, D., Kierzkowski, D., Damesin, C., 2007. Interspecific variability of stem photosynthesis among tree species. Tree Physiol. 27, 53–61.
Briantais, J.-M., Dacosta, J., Goulas, Y., Ducruet, J.-M., Moya, I., 1996. Heat stress induces in leaves an increase of the minimum level of chlorophyll fluorescence, Fo: a time-resolved analysis. Photosynth. Res. 48, 189–196.
Chen, S., Yin, C., Dai, X., Qiang, S., Xu, X., 2008. Action of tenuazonic acid, a natural phytotoxin, on photosystem II of spinach. Environ. Exp. Bot. 62, 279–289.
Clijsters, H., Van-Assche, F., 1985. Inhibition of photosynthesis by heavy metals. Photosynth. Res. 7, 31–40.
Crafts-Brandner, S.J., Salvucci, M.E., 2002. Sensitivity of photosynthesis in a C_4 plant, maize, to heat stress. Plant Physiol. 129, 1773–1780.
Hagemeyer, J., 1999. Ecophysiology of plant growth under heavy metal stress. In: Prasad, J., Hagemeyer, J. (Eds.), Heavy Metal Stress in Plants. Springer, Berlin, pp. 157–181.
Hazem, M.K., Robert, C., Suleyman, I.A., Karolina, B., 2012. Fluorescence parameters as early indicators of light stress in barley. J. Photochem. Photobiol. B 112, 1–6.
Jiang, C.D., Wang, X., Gao, H.Y., Shi, L., Chow, W.S., 2011. Systemic regulation of leaf anatomical structure, photosynthetic performance, and high-light tolerance in sorghum. Plant Physiol. 155, 1416–1424.
Murchie, E.H., Horton, P., 1997. Acclimation of photosynthesis to irradiance and spectral quality in British plant species: chlorophyll content, photosynthetic capacity and habitat preference. Plant Cell. Environ. 20, 438–448.
Nilsen, E.T., Sharifi, M.R., 1994. Seasonal acclimation of stem photosynthesis in woody legume species from the Mojave and Sonoran deserts of California. Plant Physiol. 105, 1385–1391.

Ohnishi, N., Allakhverdiev, S.I., Takahashi, S., Higashi, S., Watanabe, M., Nishiyama, Y., Murata, N., 2005. Two-Step mechanism of photodamage to photosystem II: step 1 occurs at the oxygen-evolving complex and step 2 occurs at the photochemical reaction center. Biochemistry-us 44, 8494–8499.

Osmond, C.B., Smith, S.D., Gui-Ying, B., Sharkey, T.D., 1987. Stem photosynthesis in a desert ephemeral, *Eriogonum inflatum*. Characterization of the leaf and stem CO_2 fixation and H_2O vapor exchange under controlled conditions. Oecologia 72, 542–549.

Perales-Vela, H.V., Gonzalez-Moreno, S., Montes-Horcasitas, C., Canizares-Villanueva, R.O., 2007. Growth, photosynthetic and respiratory responses to sub-lethal copper concentrations in *Scenedesmus incrassatulus* (Chlorophyceae). Chemosphere 67, 2274–2281.

Poorter, H., Van der Werf, A., 1998. Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. In: Lambers, H., Poorter, H., Van Vuuren, M.M.I. (Eds.), Inherent Variation in Plant Growth, Physiological Mechanisms and Ecological Consequences, pp. 309–336. Leiden, the Netherlands.

Srivastava, A., Guissé, B., Greppin, H., Strasser, R.J., 1997. Regulation of antenna structure and electron transport in Photosystem II of *Pisum sativum* under elevated temperature probed by the fast polyphasic chlorophyll a fluorescence transient: OKJIP. BBA-Biomembranes 1320, 95–106.

Strasser, R.J., Srivastava, A., Tsimilli-Michael, M., 2000. The fluorescence transient as a tool to characterize and screen photosynthetic samples. In: Yunus, M., Pathre, U., Mohanty, P. (Eds.), Probing Photosynthesis: Mechanisms, Regulation and Adaptation, pp. 445–483. London, UK.

Strasser, R.J., Srivastava, A., Tsimilli-Michael, M., 2004. Analysis of the chlorophyll a fluorescence transient. In: Papageorgiou, G., Govindjee (Eds.), Advances in Photosynthesis and Respiration. Chlorophyll Fluorescence a Signature of Photosynthesis. Kluwer, the Netherlands, pp. 321–362.

Strasser, R.J., Tsimilli-Michael, M., Qiang, S., Goltsev, V., 2010. Simultaneous *in vivo* recording of prompt and delayed fluorescence and 820-nm reflection changes during drying and after rehydration of the resurrection plant *Haberlea rhodopensis*. BBA – Bioenergetics 1797, 1313–1326.

Strasser, R.J., Govindjee, 1992. On the O-J-I-P fluorescence transient in leaves and D1 mutants of *Chlamydomonas reinhardtii*. In: . In: Murata, N. (Ed.), Research in Photosynthesis, second ed., vol. 2. Kluwer Academic, Dordrecht, pp. 529–532.

Van der Werf, A., Geerts, R.H.E.M., Jacobs, F.H.H., Korevaar, H., Oomes, M.J.M., De Visser, W., 1998. The importance of relative growth rate and associated traits for competition between species during vegetation succession. In: Lambers, H., Poorter, H., Van Vuuren, M.M.I. (Eds.), Inherent Variation in Plant Growth, Physiological Mechanisms and Ecological Consequences, pp. 489–502. Leiden, The Netherlands.

Walters, M.B., Kruger, E.L., Reich, P.B., 1993. Growth, biomass distribution and CO_2 exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. Oecologia 94, 7–16.

Wang, G.G., Bauerle, W.L., Mudder, B.T., 2006. Effects of light acclimation on the photosynthesis, growth, and biomass allocation in American chestnut (*Castanea dentata*) seedlings. Forest Ecol. Manag. 226, 173–180.

Wang, S.Z., Zhang, D.Y., Pan, X.L., 2012. Effects of arsenic on growth and photosystem II (PSII) activity of Microcystis aeruginosa. Ecotox. Environ. Safe 84, 104–111.

Wilson, P.J., Thompson, K., Hodgson, J.G., 1999. Specific leaf area and leaf dry matter contents as alternative predictors of plant strategies. New Phytol. 143, 155–162.

Yang., D.M., Li, G.Y., Sun, S.C., 2008. The generality of leaf size versus number trade-off in temperate woody species. Ann Bot 102, 623–629.

Yiotis, C., Psaras, G.K., Manetas, Y., 2008. Seasonal photosynthetic changes in the green-stemmed Mediterranean shrub Calicotome villosa: a comparison with leaves. Photosynthetica 46, 262–267.

Zhang, D.Y., Pan, X.L., Mu, G.J., Wang, J.L., 2010. Toxic effects of antimony on photosystem II of Synechocystis sp. as probed by in vivo chlorophyll fluorescence. J. Appl. Phycol. 22, 479–488.

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